Denisia	**31**	1-529	13. 7. 2012

Monograph of the Dileptids (Protista, Ciliophora, Rhynchostomatia)

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A b s t r a c t : Dileptids are holotrichously ciliated, rapacious ciliates with a conspicuous proboscis carrying a complex ciliary pattern. Most species have a wide or global distribution, occurring in limnetic, marine, and terrestrial environments as well as in benthic and planktonic habitats. Light- and electronmicroscopical investigations suggested the dileptids as strongly derived crown Litostomatea (Gymnostomatea pro parte, Haptoria p.p., Trichostomatia p.p.) because of their complex morphology and ontogenesis. However, recent molecular studies show the opposite: the dileptids form a distinct clade at the base of the litostomateans, supporting the subclass Rhynchostomatia established by JANKOWSKI (1980). The last common ancestor of dileptids and other litostomateans (Haptoria, Trichostomatia) was possibly a rather complex ciliate with a paroral membrane (~ circumoral kinety) and many adoral membranelles (~ preoral kineties).

The genus *Dileptus* was established by DUJARDIN (1841). Although afterwards some interesting studies on dileptid biology and diversity were performed, progress was slow during the next ninety years. In 1931, KAHL revised the dileptids recognizing three genera (*Dileptus*, *Paradileptus*, *Trachelius*) and 25 nominal species, including eight new ones. After KAHL's classic study, more protozoologists became interested in the biology and taxonomy of the dileptids, which culminated in the monograph of DRAGESCO (1963). He revised the genus *Dileptus* and recognized about 50 species, showing that dileptid diversity doubled between 1931 and 1963. In the following decades, the number of genera and species increased slowly but steadily. In our monograph, we recognize 12 genera and 181 nominal species, of which 66 are possibly reliable dileptid taxa; however, only 46 species and subspecies are so well described that their identity is not threatened. We establish two new genera (*Apotrachelius* and *Microdileptus*) and 18 new species and subspecies including those recently described by VĎAČNÝ & FOISSNER (2008a, b): *Apodileptus edaphicus*, *A. visscheri rhabdoplites*, *Apotrachelius multinucleatus*, *Dileptus sphagnicola*, *Dimacrocaryon amphileptoides paucivacuolatum*, *D. arenicola*, *D. brasiliense*, *Microdileptus microstoma*, *M. semiarmatus*, *Pseudomonilicaryon brachyproboscis*, *P. fraterculum*, *P. gracile antevacuolatum*, *P. gracile oviplites*, *P. marinum minimum*, *Rimaleptus brasiliensis*, *R. canadensis*, *R. longitrichus*, and *R. tirjakovae*. Further, we redescribe and/or provide additional figures for ten species: *Apodileptus visscheri visscheri*, *Dileptus anatinus*, *D. costaricanus*, *Monomacrocaryon polyvacuolatum*, *M. terrenum*, *Pelagodileptus trachelioides*, *Pseudomonilicaryon falciforme*, *P. thononense*, *Rimaleptus armatus*, and *R. binucleatus*. The synonymy rate is 27.5% but increases to 60.5% when taxa with "unclear identity" are included.

The monograph commences with a detailed general section, showing the dileptid morphology, ultrastructure, resting cysts, ontogenesis, conjugation, ecology, and phylogeny. Further, we provide protocols for the methods used in studying the dileptid organization (live observation, silver nitrate impregnation, protargol impregnation, scanning electron microscopy) and a detailed terminology. In the main section of the monograph, we provide, if available, the following data for each species: author, date, and journal page of the original description; a list of synonyms; nomenclatural matters; a morphological treatise including the original description, redescriptions, and all figures published; morphometric data; details on ontogenesis and resting cysts; a comparison with related species; and a detailed compilation of ecological and faunistic data. The monograph ends with a carefully prepared reference section and an index to the scientific names mentioned in the text.

K e y w o r d s : 18S rRNA gene, benthos, biodiversity, conjugation, distribution, ecology, Haptoria, limnetic, marine and terrestrial habitats, Litostomatea, plankton, new genera, new species, nomenclature, ontogenesis, synonymy rate.

Contents

Introduction

Biodiversity studies came into fashion since various international activities emphasized their importance for human well-being (World Conservation Monitoring Centre 1992). However, a central goal of these activities, viz., the study and description of individual species, is still a matter of a few specialists because financial resources for alpha-taxonomy are usually very limited and the modern universities often neglect this discipline. This is a global trend known as taxonomic impediment and is especially pronounced in protists (Cotterill et al. 2008, Cotterill & Foissner 2009). Nonetheless, there is an increased willingness of ranked scientific journals to publish this kind of research, the present monograph being a good example. Likewise, financial support can be obtained from regional and government agencies. With the "Monograph of the Dileptids", we continue our attempt to revise larger groups of ciliates so comprehensively that users need not go back to the original literature, which is often very old and thus difficult to obtain (Foissner 1993; Berger 1999, 2006, 2008; Aescht 2001; Foissner & Xu 2007).

Dileptids are holotrichously ciliated litostomatean ciliates with a conspicuous proboscis (Kahl 1931, Dragesco 1963, Lynn 2008). Most species have a wide or global distribution and prefer terrestrial habitats, while limnetic and, especially, marine species are rare. However, we possibly know only the most common species because dileptids are predators rarely attaining high abundances. Thus, they are easily overlooked or the material is too sparse for detailed investigation.

Dileptus has been seen probably already by Leeuwenhoek (Dobell 1932). But the formal recognition occurred much later by Dujardin (1841) because Mueller (1786) and Ehrenberg (1838) mixed it with *Vibrio* and *Amphileptus*. Dujardin (1841) founded *Dileptus* with three nominal species without fixing any as the type; this was done by Fromentel (1875), using *D. folium*. Unfortunately, this species turned out to be a junior synonym of *Litonotus cygnus* (Wrześniowski 1870, Kahl 1931). This and other nomenclatural problems will be discussed in our monograph.

Although some interesting studies were performed after *Dileptus* had been established, little progress occurred in the next ninety years, when Kahl (1931) revised the genus, recognizing 25 nominal species including eight new ones. After Kahl's classic study, more protozoologists became interested in the dileptids, which culminated in the monograph of Dragesco (1963), who reviewed the biology and taxonomy of *Dileptus* and recognized about 50 species, showing that their diversity doubled between 1931 and 1963. With the onset of silver impregnation, several species were redescribed and some were discovered, mainly by Foissner (1984, 1989), Wirnsberger et al. (1984), Song et al. (1988), Song (1994b), Song & Wilbert (1989), and Foissner et al. (1995, 1999, 2002). In the present monograph, we recognized 12 genera and 66 species, of which 18 were new to science including the five new species described by Vďačný & Foissner (2008a, b), indicating that dileptid diversity is far from being exhausted. Only 46 out of the 66 species can be considered so well-described that their identity is not threatened. The synonymy rates match those of ciliates in general (Aescht 2001, Foissner et al. 2008a), i.e., is 27.5% for dileptid species but increases to 60.5% when taxa with "unclear identity" are included.

Light- and electronmicroscopic taxonomists considered dileptids as highly derived crown litostomateans because of their complex morphology and ontogenesis (Puytorac et al. 1993, Grain 1994, Xu & Foissner 2005, Vďačný & Foissner 2009). However, this is not supported by the recent molecular investigations, which show the dileptid clade at the base of the litostomateans (Vďačný et al. 2011). Further, their genetic distinctness is so pronounced that subclass rank appears appropriate, supporting the Rhynchostomatia proposed by Jankowski (1980). The last common ancestor of the dileptids and other litostomateans (Haptoria and Trichostomatia) was possibly a rather complex ciliate with a paroral membrane and many adoral membranelles (Vďačný et al. 2010).

Dileptus served as model organism for cell biologist in investigations of the influence of physical and chemical factors on morphogenesis and regeneration. Most of these studies were performed by Golińska (1965–1996). More recently, Vďačný & Foissner (2008a, 2009) provided detailed data on ontogenesis and conjugation. Feeding was studied by Visscher (1923) and Dragesco (1962). Modern investigations on the ecology of dileptids are lacking, except for a few studies by Butkay (2004) and Sonntag et al. (2007). Foissner et al. (1995, 1999) reviewed those species which are used as quality indicators in limnetic habitats.

In our monograph, we provide a detailed general section on the dileptids and critically review the taxonomy, ecology, and faunistics of all dileptids described. Further, we provide tables on genera associated with dileptids and nominal species; protocols for studying dileptids; and introduce a precise terminology.

A General Section

1 Morphology and Principal Terms

In this section, we explain the principal morphology and terminology. The latter is based on Foissner & Xu (2007) and done briefly because all specific terms are illustrated in Figures 1–17. For general protistological and specific ciliate terminology, we refer to the excellent compilations of Corliss (1979), Margulis et al. (1993), Puytorac (1994), and Lynn (2008).

1.1 Size and Shape, Morphometry (Figs 1, 2; Tables 1, 2)

The dileptids range from about 100 × 15 µm to 1,500 × 150 µm in vivo. The volume of one of the largest species, *Monomacrocaryon gigas*, is about 1000 times larger than that of one of the smallest species, *Rimaleptus alpinus*. This is a small range, as in the spathidiids (Foissner & Xu 2007), when compared to the colpodids (200,000; Foissner 1993). We have used four categories of size (as reflected in body length; arbitrarily if unrealistically set up with non-overlapping ranges) as follows: small (100–300 µm), medium (300–500 µm), large (500–1,000 µm), and very large (> 1,000 µm). Likewise, we have established four categories of proboscis length (Fig. 1).

The dileptid body typically consists of a proboscis, a trunk, and a tail (Fig. 1). These variables produce a huge variety of shapes classified in Figure 1. However, most shapes fall into three categories: narrowly dileptid (length:width ratio 3:1–6:1), very narrowly dileptid (l:w 6:1–9:1), and cylindroidally dileptid (l:w 9:1–12:1). Most species are slightly flattened laterally, especially the proboscis. Many of the terrestrial species are small and/or slender, as is typical for soil organisms in general (Foissner 1987a). However, those living in mosses and leaf litter may be rather large, for instance, *Rimaleptus conspicuus*. The shape is stabilized by bundles of cortical microtubules (Grain & Golińska 1969), but the cortex remains flexible and the shape may thus strongly deform in over- or under-nourished cells. True polymorphism is absent, thus we prefer "vegetative cells" rather than "trophonts" or "theronts". A few specimens show pronounced contractility, viz., *Rimaleptus lacazei*, *Monomacrocaryon tenue*, and *Pseudomonilicaryon dimorphum*. Unfortunately, the base of the contractility (myonemes?) is not known.

Invariably, the oral opening is at the base of the proboscis, which is part of the oral apparatus and has a complex ciliature and ontogenesis. Both the proboscis and the oral opening show a variety of features important for species identification. They will be discussed in the section on "oral apparatus".

Detailed morphometrics are available from about 48 populations belonging to 37 species, mainly due to the studies of the Foissner group and the present monograph (Table 1). Morphometric data provide important information about the stability of features and their significance for species recognition. Most useful are characteristics with variation coefficients between 5–10% because they are sufficiently, but

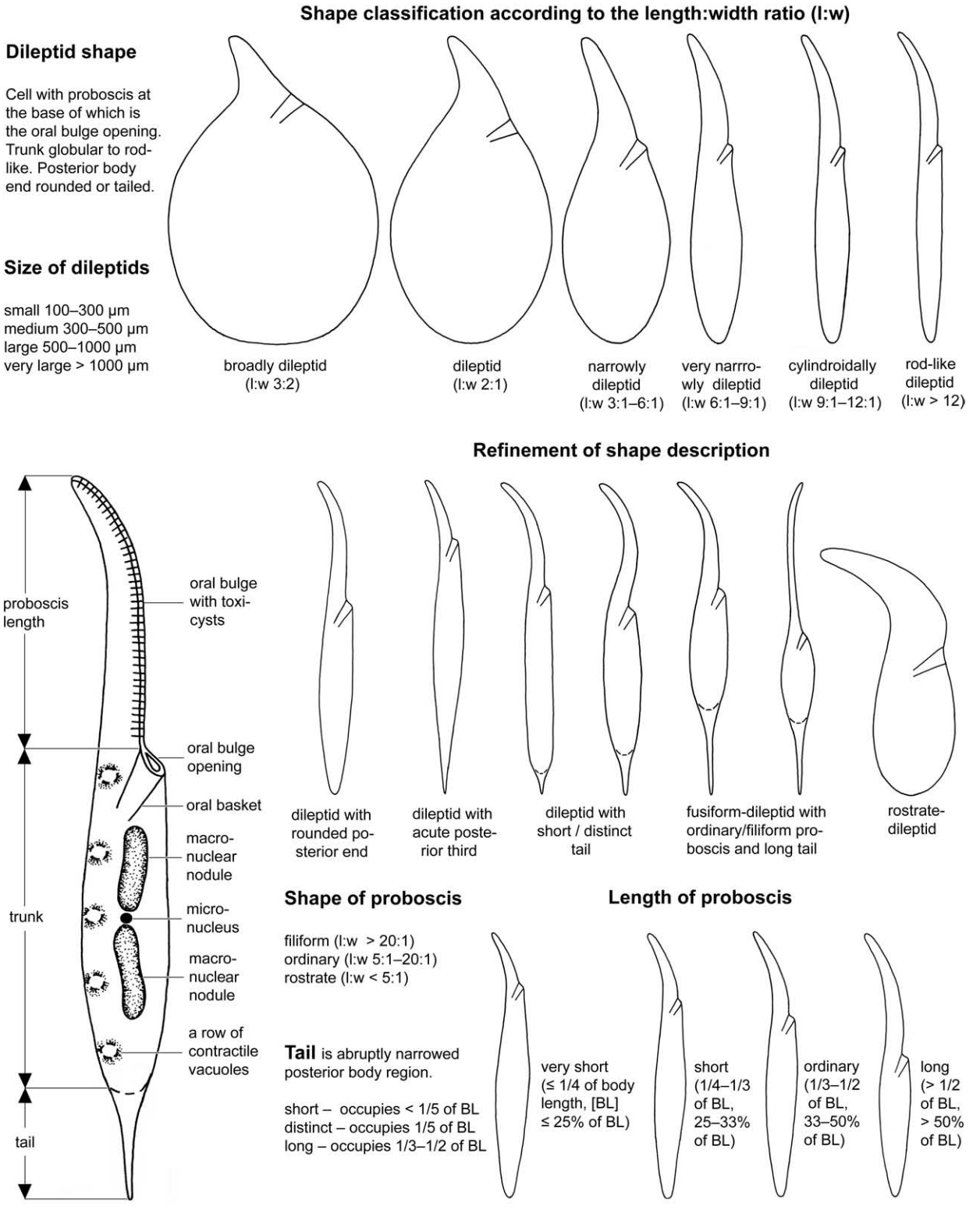


Fig. 1: Classification (terminology) of body size and body shape in dileptid ciliates.

not too highly, variable. An example is the number of ciliary rows (Tables 1, 2) which, additionally, is positively correlated with body width (Fig. 2), usually having a higher variability (~ 15%). Generally, the mean coefficients of variation are slightly higher in dileptids than in other groups of ciliates but are far from being "highly variable" (Table 2). The impression of high variability often focuses on a single or a few features, in dileptids on the length of the proboscis and tail (Fig. 1), both being rather fragile easily becoming distorted or lost when cells are studied in vivo under even mild coverslip pressure.

Experimental studies showed that the number of ciliary rows depends not only on genetic mechanisms but also on nutrition. The number of kineties and the interkinetal distances are upward regulated in overfed cells, while downward regulation is still unknown (DRZEWIŃSKA & GOLIŃSKA 1987).

Table 1: Summary of morphometric investigations on dileptid ciliates.

Family	No. of species	No. of populations	Total no. of individuals	Mean coefficient of variation (%) [values in brackets indicate minimum and maximum]				
				Body, length	Body, width	Body, length: width ratio	Proboscis, % of body length	Ciliary rows, number
Tracheliidae	2	2	25	15.0 (11.5–18.5)	15.0 (11.8–18.1)	14.1 (13.5–14.6)	18.8 (17.2–20.5)	16.2 (11.5–21.0)
Dimacrocaryonidae	19	28	418	15.2 (6.3–25.6)	16.1 (7.3–26.2)	19.3 (8.0–33.7)	13.7 (4.8–35.4)	10.1 (6.3–24.0)
Dileptidae	16	18	312	16.0 (7.4–30.2)	15.9 (3.6–28.3)	18.8 (12.7–28.9)	13.4 (7.6–28.1)	8.7 (4.6–15.4)
∑	37	48	755					
∑/n				15.5	16.0	18.9	13.8	9.8

Table 2: Comparison of average coefficients of variation in dileptids (I, this monograph), haptorids in general (II, FOISSNER 1984), colpodids (III, FOISSNER 1993), and hypotrichs (IV, FOISSNER 1982).

Characteristics	I	II	III	IV
Body, length	16	14	11	11
Body, width	16	15	13	14
Length:width, ratio	19	?	?	?
Proboscis, length	13	?	?	?
Ciliary rows, number[a]	8.7	7.4	7.4	7

[a] Adoral membranelles in IV (hypotrichs).

1.2 Nuclear Apparatus (Figs 3b–e, 4)

The nuclear apparatus is in the trunk and usually conspicuous. In the dileptids, there are four basic patterns and some subtypes, all shown in Figures 3b–e and 4. The molecular investigations and the Hennigian argumentation schemes indicate that the mononucleate or binucleate pattern is plesiomorphic, while the moniliform and the multinucleate patterns are derived (Figs 31, 32, 34, 35). Some patterns probably evolved convergently several times.

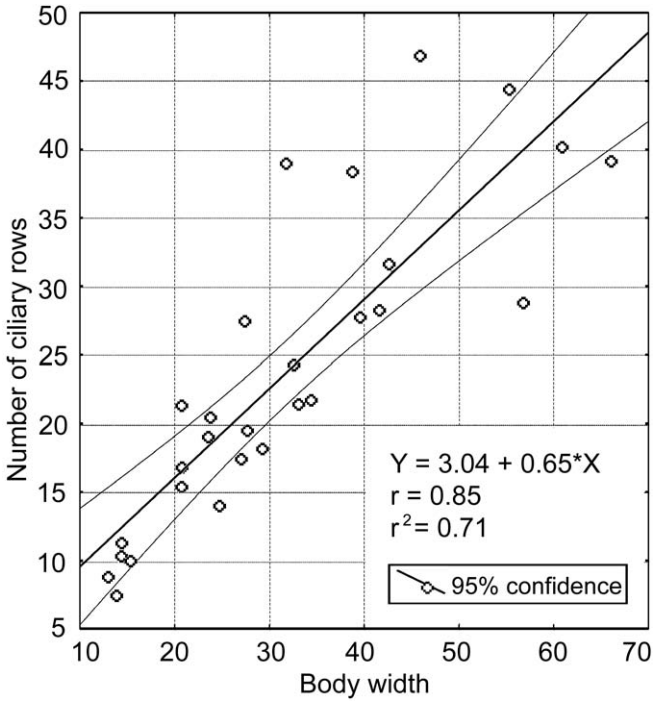


Fig. 2: Scatterplot showing a positive correlation between body width and number of ciliary rows in dileptid ciliates.

The nuclear apparatus, especially the macronuclear pattern, is one of the most important features for genus and species recognition. Five out of the 12 genera recognized are based on this pattern: *Monomacrocaryon* (single macronucleus), *Rimaleptus* (two macronuclear nodules), *Dileptus* (multinucleate), *Apodileptus* (the macronuclear nodules fuse into a globular mass during ontogenesis), and *Pseudomonilicaryon* (macronucleus moniliform).

The nuclear patterns are as stable or as variable as those of other ciliates and are sometimes obscured by post-divisional, post-conjugational, or ontogenetic processes (Foissner & Xu 2007, Vďačný & Foissner 2008a, 2009). **When in doubt, look at very early dividers which invariably show the "real" nuclear pattern.** So far, chromatin extrusion has not been described.

The macronucleus contains globular, oblong, or irregular masses about 1–5 µm in size. Usually, they are recognizable in vivo and impregnate deeply with protargol. There is some indication that these inclusions represent nucleoli: (i) the central mass of the macronucleus of *Colpoda steinii* and *Dileptus* sp. deeply impregnates with protargol and represents a compound nucleolus, according to cytochemical and electronmicroscopical investigations (Raikov 1982, Foissner 1993); (ii) chromatin bodies are usually smaller than 1 µm and numerous, while nucleoli are often larger than 1 µm and comparatively rare (Raikov 1982). These features apply to the macronuclear structures impregnating with various protargol methods and recognizable with transmission electron microscopy (Fig. 3c). Thus, we designate these structures as "nucleoli", being aware that this needs confirmation by cytochemical investigations. See Vinnikova (1974b) and Bohatier et al. (1978) for electronmicroscopical descriptions of the macronucleus of *Dileptus margaritifer* and Kink (1973) for an investigation of the nuclear apparatus of *Apodileptus visscheri*.

The ploidy of most macronuclei of *D. margaritifer* is about 12n. Some macronuclei may, however, reach a ploidy degree of 30–60n. The total ploidy level of all macronuclei of a specimen can amount to 2000–5000n (Vinnikova 1977).

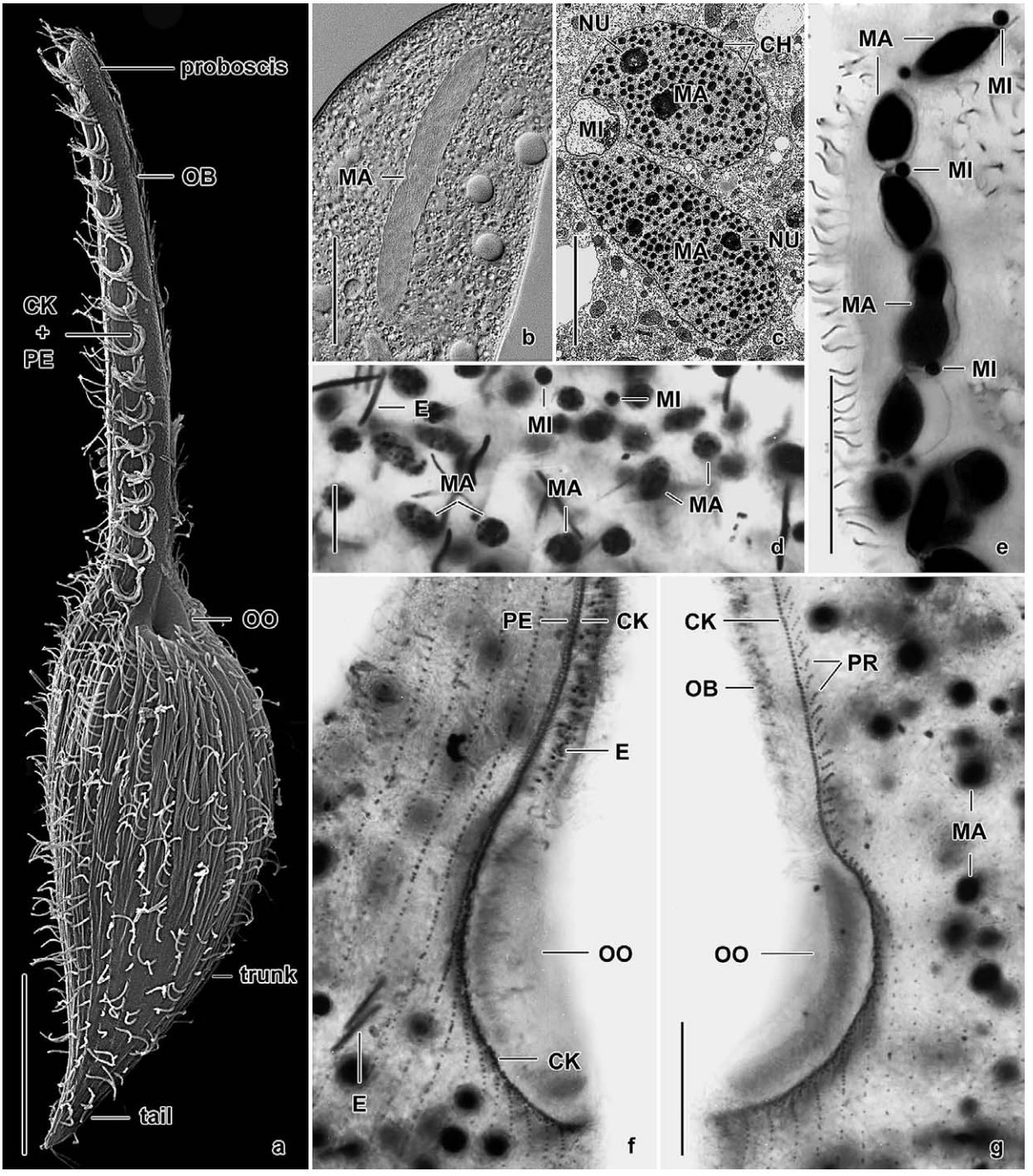


Fig. 3: Main features of dileptids in vivo (b), after protargol impregnation (d–g), in the scanning (a) and transmission (c) electron microscope. **a** – overview showing general body organization; **b–e** – there are four basic nuclear patterns in dileptids: a cylindroidal macronucleus with a single micronucleus (b); two macronuclear nodules with a single micronucleus in between (c); many macronuclear nodules and micronuclei scattered throughout cytoplasm (d); a moniliform macronuclear strand with several micronuclei (e); **f, g** – ciliary pattern of right and left side of proboscis. CH – chromatin bodies, CK – circumoral kinety, E – extrusomes, MA – macronucleus (nodules), MI – micronucleus, NU – nucleoli, OB – oral bulge, OO – oral bulge opening, PE – perioral kinety, PR – preoral kineties. Scale bars: 5 µm (c, d), 20 µm (e–g), and 30 µm (a, b).

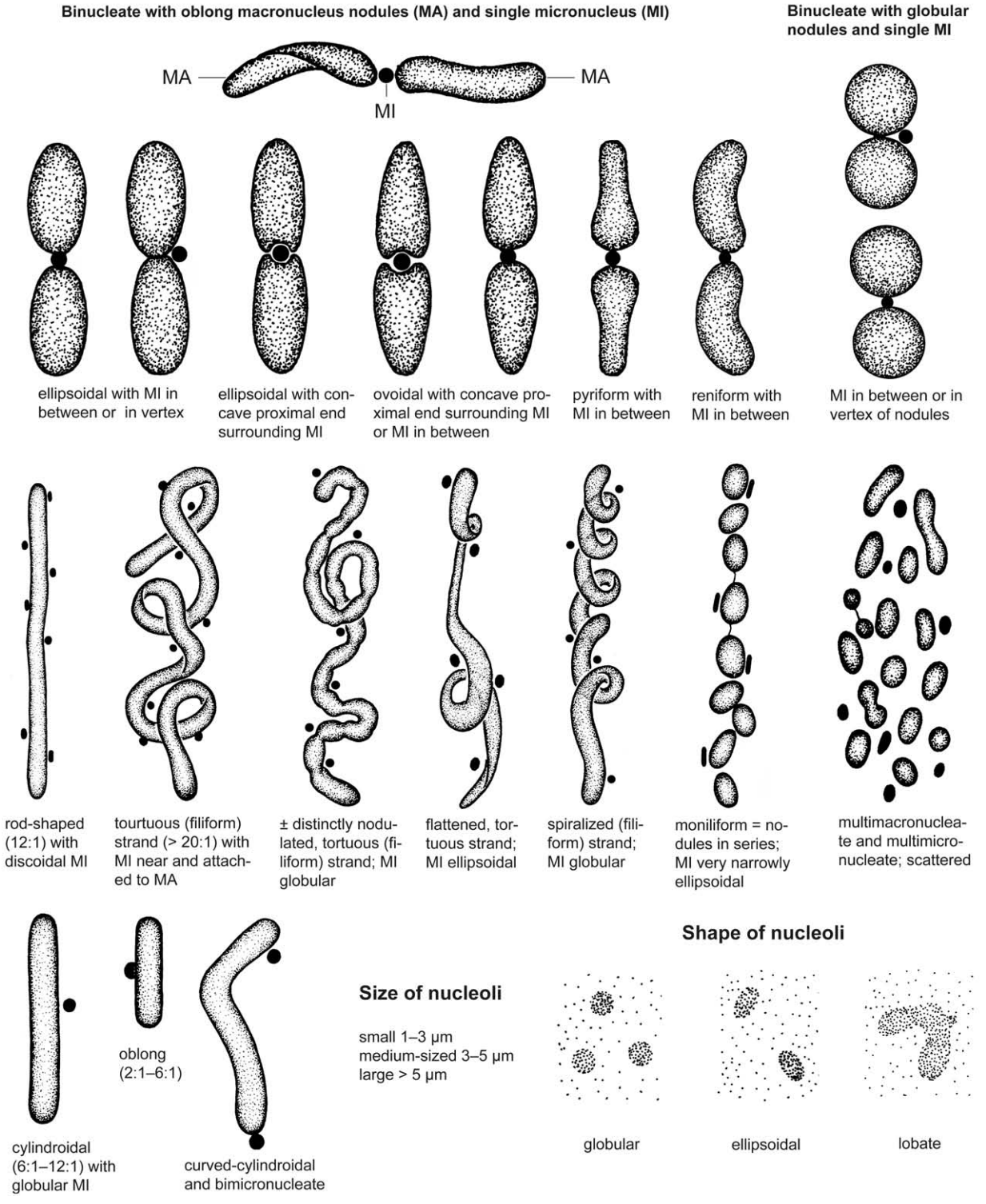


Fig. 4: Nuclear types in dileptid and spathidiid ciliates (modified from FOISSNER & XU 2007). Micronuclear shape is considered as a species character and as a subtype of nuclear classification. The micronuclei shown, represent the shapes known, i.e., do not refer to a certain macronuclear type; this applies also to the shape and size of the nucleoli. MA – macronucleus (nodule), MI – micronucleus.

1.3 Contractile Vacuoles and Cytopyge (Fig. 5)

Most dileptids have at least two contractile vacuoles in the dorsal side of the trunk; monovacuolate species have been described but are highly questionable. The number of contractile vacuoles is related to body size: small species have two to four, large ones may have > 50 and not only in the dorsal side of the trunk but also in its ventral side and the full length of the proboscis, for instance, *Pseudomonilicaryon fraterculum* and *P. japonicum*. Basically, six contractile vacuole patterns can be distinguished and are important for species recognition (Fig. 5).

The fluid collected by the contractile vacuoles is expelled via one to three intrakinetal excretory pores per vacuole. Rarely, the excretory pores are outside the kineties or scattered throughout the cell's periphery, for instance, in *Trachelius ovum*. In small species with two contractile vacuoles and two dorsal brush rows, the excretory pores are usually associated with brush row 2, for instance, in *Rimaleptus armatus* and *Microdileptus breviproboscis*. In the large species, the contractile vacuoles are not in line but in a more or less broad stripe, for instance, in *Pseudomonilicaryon anser*.

Details on the contractile vacuoles of *Dileptus margaritifer* have been reported by Ferber & Hausmann (1985). They found: the total number of vacuoles was greater in longer specimens; there are no collection canals or vesicles; the average diastolic diameter is 4 µm (range 2–5 µm); the average frequency of contractions was 25 s; the vacuoles towards the front and back ends of the cell contract less frequently than those towards the cell centre; there is no correlation between vacuolar output and volume of the intervacuolar cytoplasm or the intervacuolar cell surface area; there is an apparent gradient in the functional activity of the contractile vacuoles, with a maximum encountered immediately behind the cytopharynx.

Usually, there is a "defecation vacuole" subterminally. It contains indigestible food remnants which are released via the cytopyge in posterior body end. Details on the dileptid cytopyge are not known. Silver preparations do not show special structures in the posterior pole area.

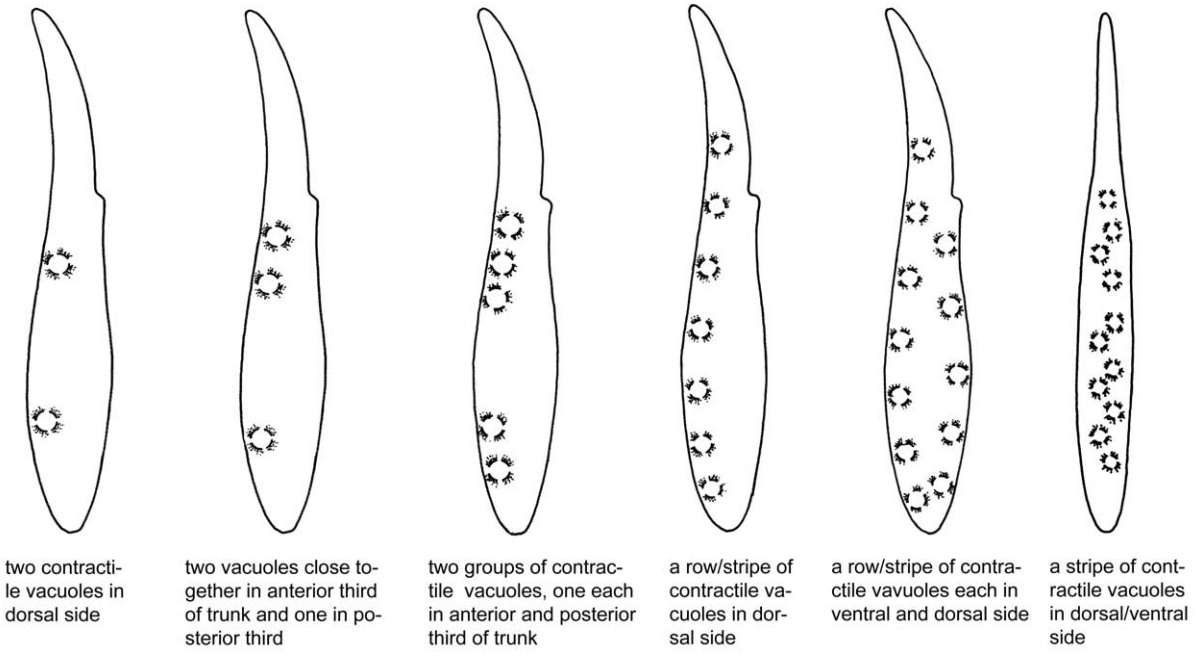


Fig. 5: Contractile vacuole patterns in dileptid ciliates.

1.4 Extrusomes (Figs 6, 7c, 9b–f, 17a–d)

Shape, size, and arrangement of the extrusomes are highly diverse and are thus a main diagnostic feature of the individual species (Fig. 6). Accordingly, the extrusomes must be carefully studied in vivo because they often become distorted in protargol preparations or do not impregnate at all. Indeed, the extrusome features are so important that species cannot be recognized without this information.

All dileptids are predators. Thus, they have toxicysts of ordinary fine structure (Grain & Golińska 1969; Fig. 7c). Most of the well-investigated species have two shape and/or size types of toxicysts, here named "type I" (for the more conspicuous ones) and "type II" (usually inconspicuous rods less than 5 µm long). Further, all dileptids have mucocysts, appearing as "cortical granules" in the light microscope (Figs 133b, c). See Hausmann (1978) and Rosati & Modeo (2002) for excellent general reviews on extrusomes, and Dragesco et al. (1965) for a study on the structure and origin of the toxicysts and mucocysts in *Dileptus*. Extrusome production occurs throughout the life cycle. When the proboscis is excised, the extrusomes move from the cytoplasm into the regenarating proboscis (Doroszewski & Golińska 1967).

We have summarized extrusome shape and terminology in Figure 6. The toxicysts are studded in the oral bulge and scattered in the cytoplasm; very rarely, they may be attached also to the somatic cortex, viz., in *Rimaleptus nistroviensis*. For determining the shape, size and arrangement of the toxicysts only fully developed (mature) organelles may be used, that is, those which are anchored to the oral bulge or somatic cortex (Fig. 6); cytoplasmic toxicysts are frequently not fully developed. This is evident, inter alia, from their impregnation capacity: anchored toxicysts usually do not impregnate with protargol, while various cytoplasmic developmental stages often impregnate deeply.

Shape and arrangement of the mucocysts are much less diverse than in toxicysts, at least in the light microscope (Fig. 6). They are globular, broadly ellipsoidal, or ellipsoidal and ≤ 2 µm long. In the light microscope, the mucocysts appear granular ("cortical granules") and are arranged in rows following the slightly oblique course of the postciliary microtubular ribbons (Williams et al. 1981, Foissner et al. 2002; Figs 94f, 133b). When densely arranged, the mucocysts form an opaque sheet in the cortex, obscuring more or less completely the ciliary pattern, depending on their affinity to protargol. In the light microscope, usually only one type of cortical granules is recognizable, for instance, in *Dileptus sphagnicola* (Fig. 86d) and *Pseudomonilicaryon japonicum* (Fig. 133b), while two types can be distinguished in the transmission electron microscope: one type is globular and deeply stained, while the other is oblong and of typical mucocyst structure (Dragesco et al. 1965, Grain & Golińska 1969, Kink 1973; Figs 9b–f). The refractivity of the cortical granules depends on species, indicating differences in their composition, e.g., the highly refractive granules lining the oral sac of *Dimacrocaryon* (Figs 17a, b). The mucocysts are not easily released. Methyl green-pyronin, which causes mucocyst extrusion in many ciliates (Foissner 1991), is usually ineffective. By chance, we were successful in obtaining some good SEM micrographs from released mucocysts in *Apotrachelius multinucleatus* (Figs 47s, u, v) and *Pelagodileptus trachelioides* (Fig. 141f). They look like typical mucocysts (Hausmann 1978). Possibly, the voluminous coat in some protargol-impregnated species is caused by mucocysts, e.g., in *Microdileptus breviproboscis* (Fig. 9i).

1.5 Cytoplasm and Colour (Figs 7, 17)

All dileptids are colourless. However, when packed with highly refractive food and/or lipid droplets, they appear dark or black under low bright-field magnification, for instance, *Dileptus anatinus* (Figs 89a, b) and *D. margaritifer* (Figs 94a–e). Some species are green due to ingested or symbiotic algae (zoochlorellae), for instance, *D. viridis*.

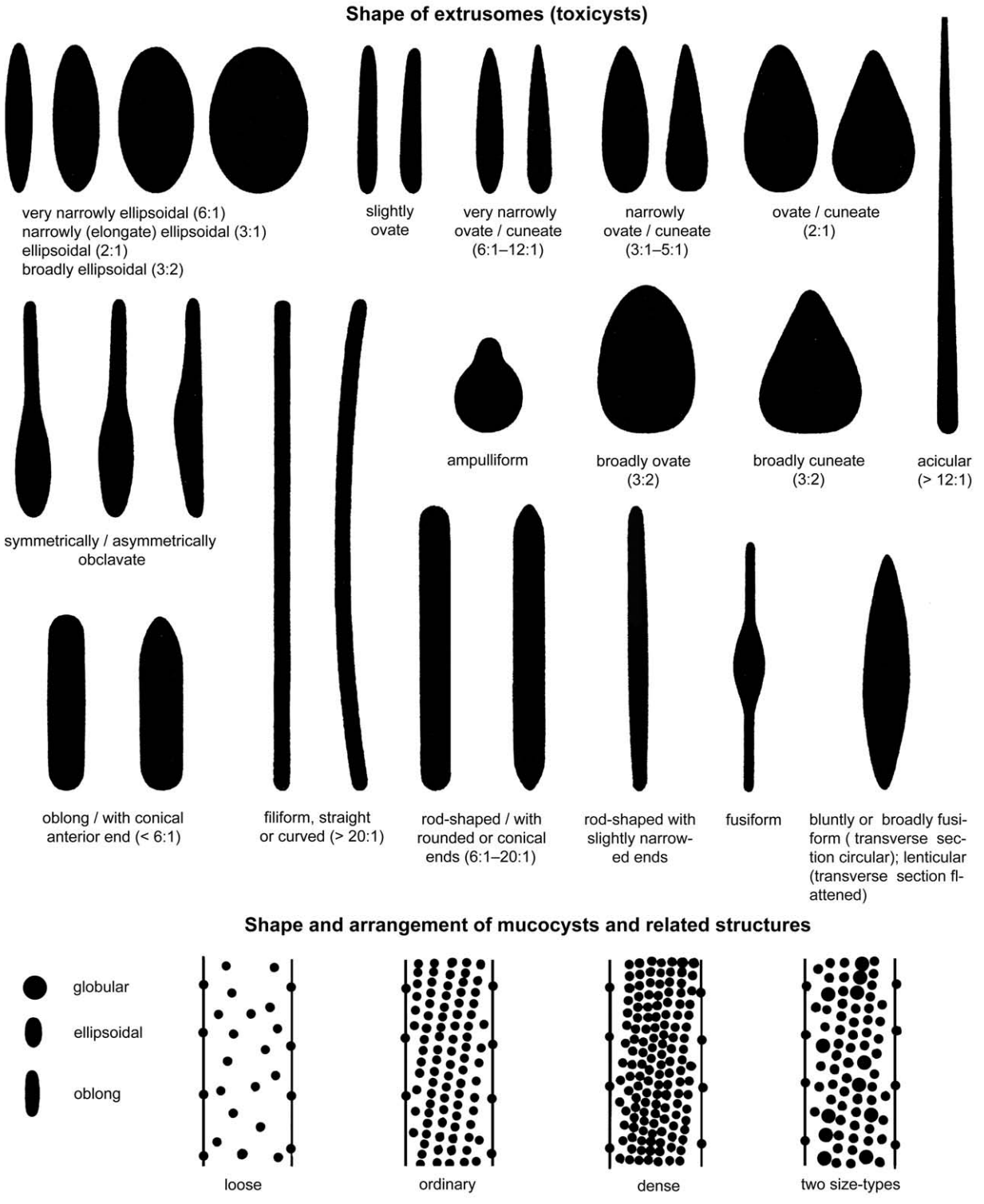
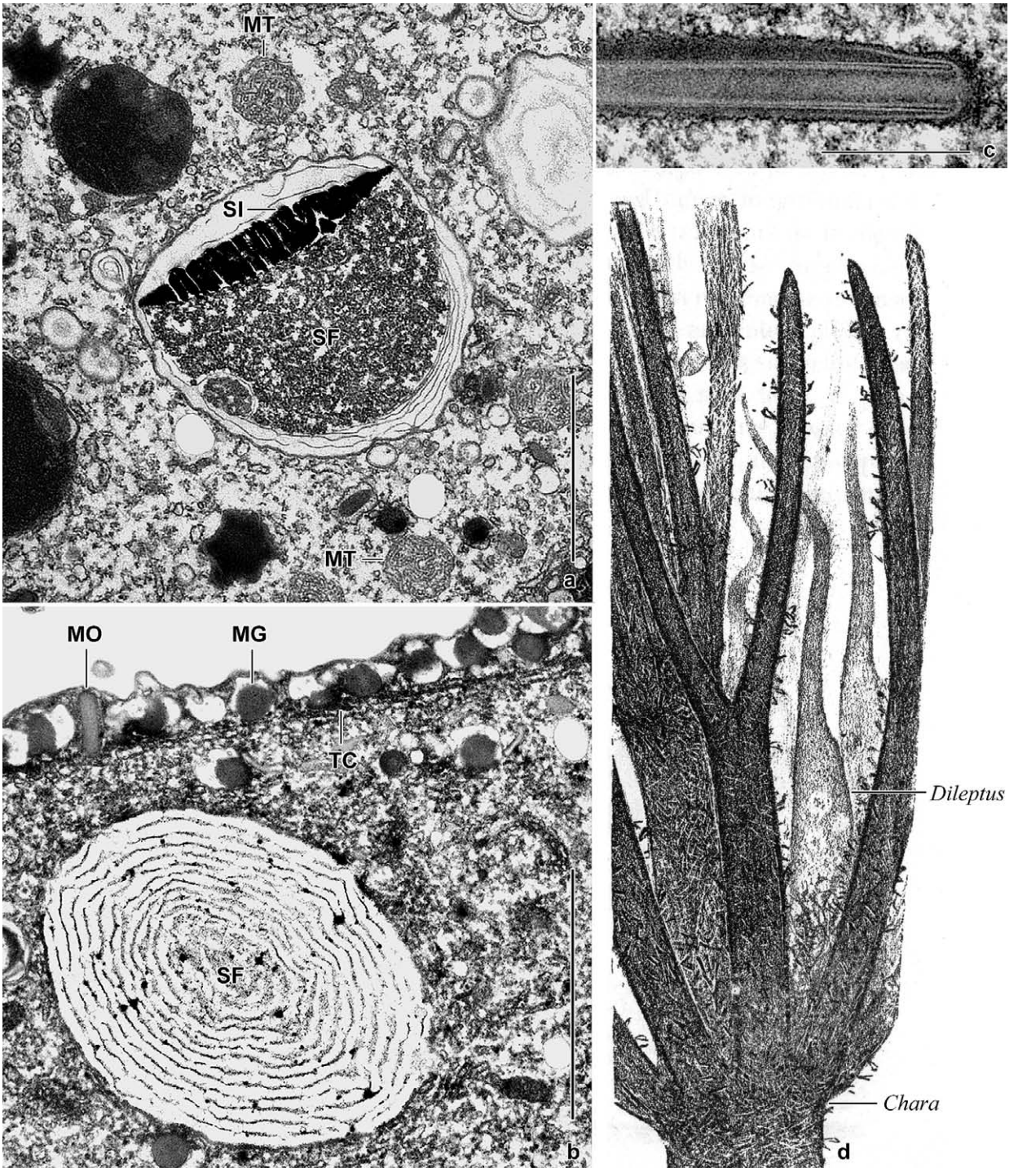


Fig. 6: Shape of extrusomes (toxicysts) in dileptid and spathidiid ciliates. Length about 3–20 µm, often 5–10 µm for toxicysts, while 1.2–2 µm for mucocysts (modified from FOISSNER & XU 2007).



Figs 7a–c: *Dimacrocaryon amphileptoides amphileptoides*, TEM-micrographs of the cytoplasm (originals). **a, b** – this species feeds, inter alia, on silicoflagellates recognizable by the glass scales (SI). When digestion is advanced, conspicuous myelin figures become recognizable (b). Note oblong and globular mucocysts in the cortex; **c** – distal portion of a toxicyst. **Fig. 7d:** Several *Dileptus* specimens aggregated in the leaf rosetts of *Chara* (from Fauré-Fremiet 1910). MG – globular mucocyst, MO – oblong mucocyst, MT – mitochondria, SF – ingested silicoflagellate, SI – siliceous scales. TC – tela corticalis. Scale bars: 2 μm (a, b) and 1 μm (c).

In contrast to many other ciliates, e.g., the hypotrichs and colpodids, the dileptids lack cytoplasmic crystals although HAUSMANN (1982) depicts a crystal in *D. margaritifer*; those found in the defecation vacuoles are most likely from the prey. The young food vacuoles are usually large because the prey is often ingested as a whole; however, such vacuoles soon dissociate into several smaller ones with granular contents, for instance, in *Microdileptus breviproboscis* (Figs 80l–n). Mitochondria and other general cytoplasmic organelles are as in other ciliates (Figs 7, 17).

1.6 Movement

Dileptids show three kinds of movement associated with their habit and great body flexibility: gliding and creeping, semisessile, and swimming. Most common is gliding and creeping slowly to rapidly on and among mud and soil particles. However, when approaching the free water, they swim by left spiralling rotation about the main body axis (SERAVIN 1970), whereby the proboscis performs complex probing actions, for instance, in *Pseudomonilicaryon fraterculum* (Figs 115v–y). Only few species have a semisessile habit: the highly contractile *P. dimorphum* can attach to water plants with the contracted tail, forming pseudopodium-like processes; *P. anser* and *P. fraterculum* can attach to various substrates by thigmotactic cilia; and *Dileptus jonesi* forms a mucous thread attaching the cell to various substrates. A nice case of attachment has been reported by FAURÉ-FREMIET (1910), who observed that *Dileptus* aggregated in the leaf rosetts of *Chara* (Fig. 7d). Finally, the two euplanktonic species, *Pelagodileptus trachelioides* and *Paradileptus elephantinus*, swim constantly in the water column, vigorously probing with the proboscis. For details on movement, see the individual species descriptions and the study by DOROSZEWSKI (1961).

1.7 Somatic Ciliature and Ultrastructure

1.7.1 Fine Structure of Kinetids (Figs 9a, b, d)

The dileptids belong to the litostomatean ciliates whose somatic basal bodies have the following fibrillar associates (LYNN 2008; Figs 9a, b, d): a kinetodesmal fibre, a postciliary microtubule ribbon right of the kinety, and two transverse microtubule ribbons left of the kinety. The dileptids follow this pattern but have two modifications (DUMONT 1961, GRAIN & GOLIŃSKA 1969, KINK 1973, GOLIŃSKA 1996). First, the postciliary microtubule ribbons are especially long and extend slightly obliquely posteriorly, filling the interkinetal space. They are recognizable in good protargol preparations (Fig. 77i) and in the scanning electron microscope, where the microtubule bundles produce minute cortical ridges (Figs 119g, m). Second, dileptids have well developed "root fibres", i.e., microtubule bundles that originate from the proximal end of the basal bodies and extend through the tela corticalis into the endoplasm.

1.7.2 Fine Structure of Cilia (Figs 9g–i)

The cilia of all dileptids as yet impregnated with protargol show a unique property not described in any other group of ciliates: the proximal half impregnates faintly, as usual, while the distal half impregnates deeply and then appears slightly thickened (Fig. 9i). Thus, we investigated the cilia of *Dimacrocaryon amphileptoides amphileptoides* with the transmission electron microscope. The result was negative, i.e., the cilia look the same as those of other ciliates (Figs 9g, h). This matches the scanning electron microscopical investigations in more than 10 species (this monograph): they show only ordinary cilia. Thus, the problem remains unsolved.

1.7.3 Ciliary Patterns (Figs 8a–h, 10)

Dileptids are strongly asymmetric. Thus, both a ventral and a dorsal side as well a right and a left side can be distinguished. However, the boundaries are indistinct because all ciliary rows are alike. We suggest to designate as somatic kinety 1 that row which bears the perioral kinety anteriorly (Fig. 8a).

Two basic ciliary patterns occur in the somatic ciliature of the dileptids: the tracheliid and the dileptid

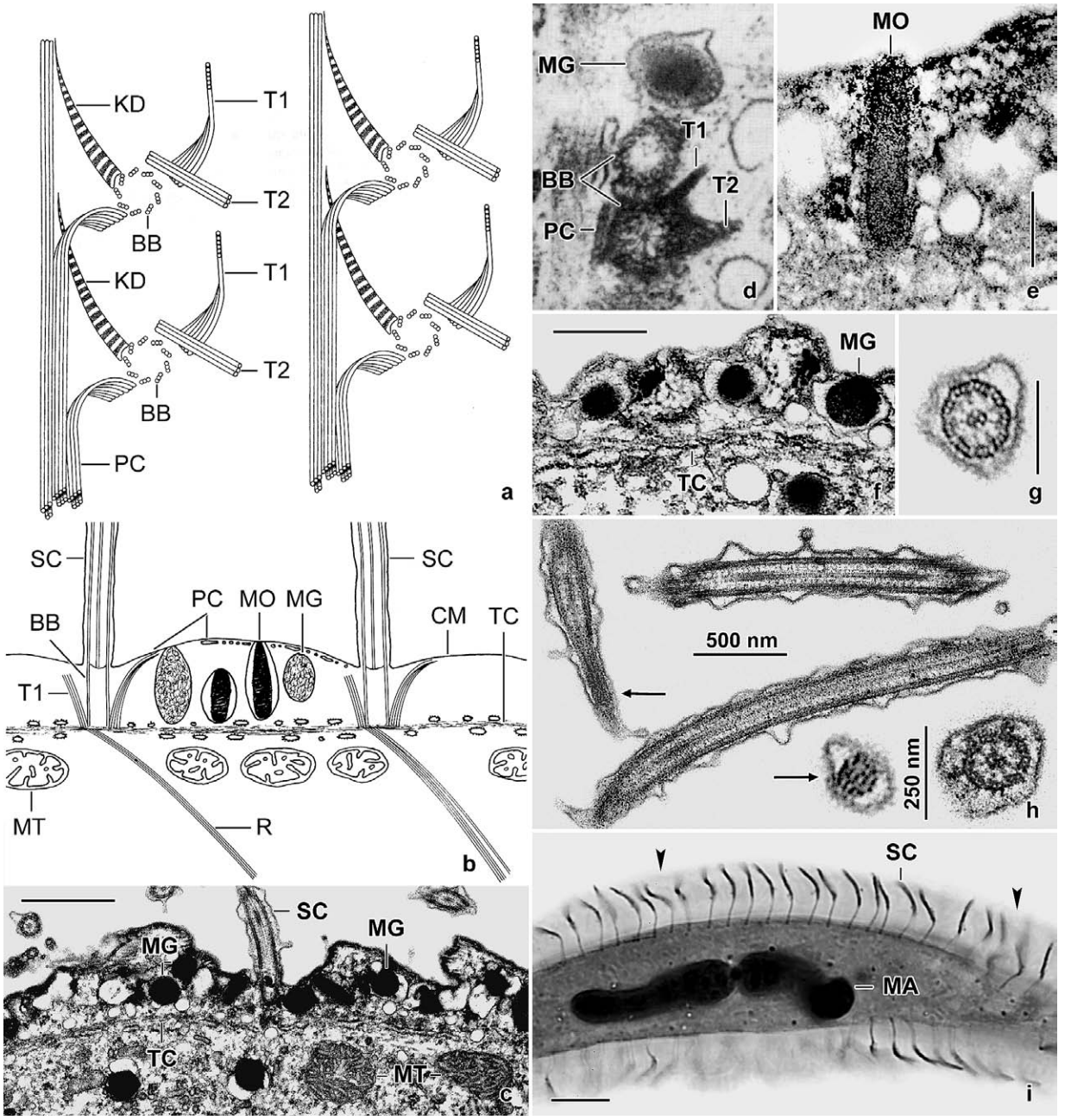


Fig. 9: Fine structure of the somatic cortex (a–c, e–i) and of an oral dikinetid (d). **a** – schematic surface view showing the cortical fibre system of litostomatean ciliates (from Lynn 2008). The somatic kinetids are single basal bodies with a convergent postciliary microtubule ribbon, a short kinetodesmal fibre, and two transverse microtubule ribbons; **b, c** – transverse section of the cortex of *Apodileptus visscheri* (b, from Kink 1973) and *Dimacrocaryon amphileptoides* (c, original); **d** – fibrillar associates of an oral dikinetid (from Grain & Golińska 1969); **e, f** – the cortex of *D. amphileptoides* contains oblong (e) and globular (f) mucocysts; **g–i** – *D. amphileptoides amphileptoides* (g, h) and *Microdileptus breviproboscis* (i) in the transmission electron microscope (g, h) and in the light microscope after protargol impregnation (i). The distal half of the cilia is intensely impregnated in all dileptids (i). However, no specific structure can be seen in the TEM (g, h), where the cilia appear ordinary the whole length. Arrows mark distal end of cilia. Arrowheads denote a yellowish-impregnated substance covering the whole body of *M. breviproboscis*. BB – basal bodies, CM – cell membrane, KD – kinetodesmal fibre, MA – macronucleus, MG – globular mucocysts, MO – oblong mucocysts, MT – mitochondria, PC – postciliary microtubule ribbons, R – root fibres, SC – somatic cilia, TC – tela corticalis, T1, 2 – primary and secondary transverse microtubule ribbons. Scale bars: 250 nm (g, h), 500 nm (e, f, h), 1 µm (c), and 10 µm (i).

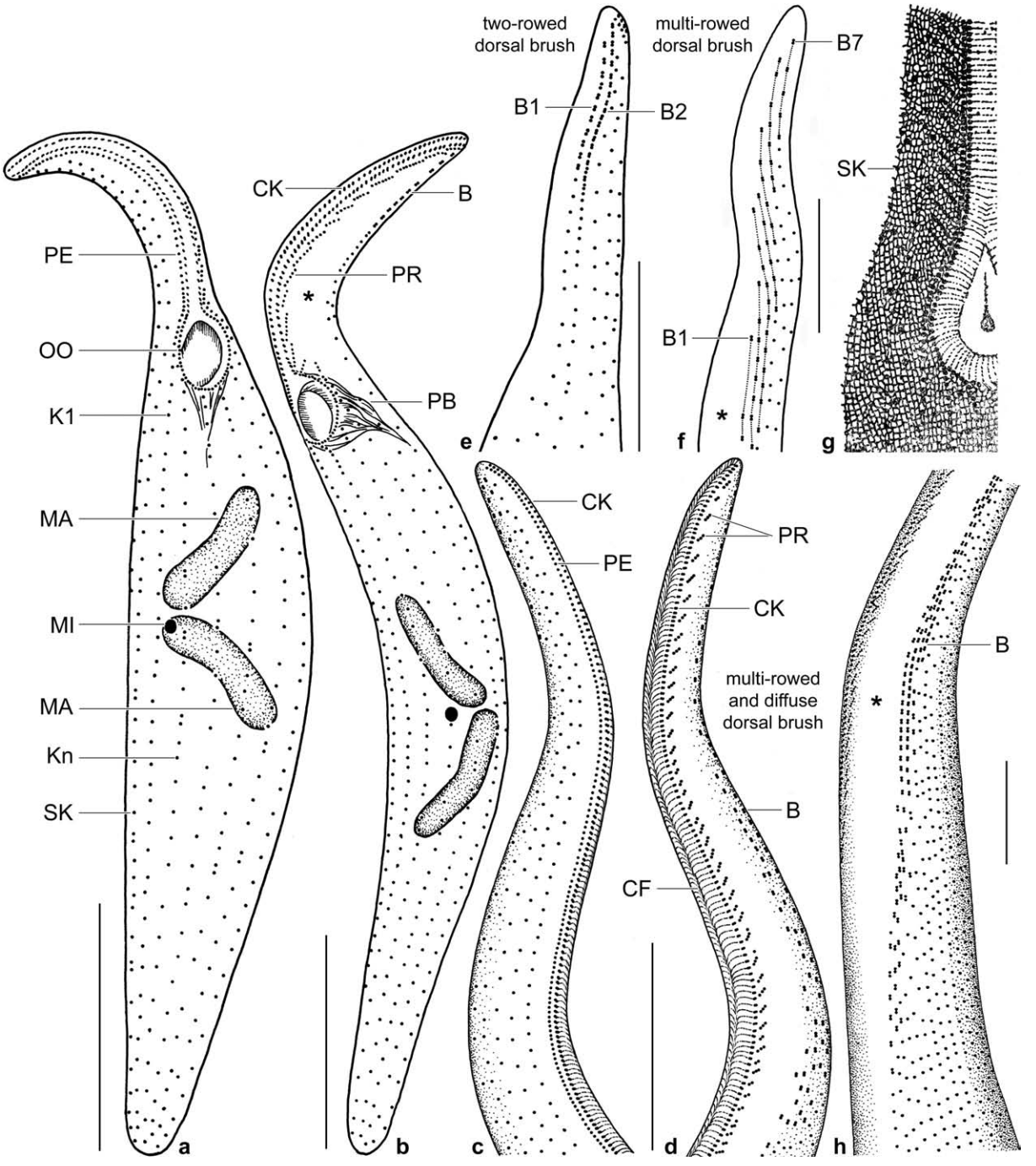


Fig. 8: Somatic ciliary and silverline pattern in dileptid ciliates. From Foissner 1979 (g; *Dileptus margaritifer*), 1989 (c, d; *Monomacrocaryon polyvacuolatum*); Vďačný & Foissner 2009 (f; *M. terrenum*); Foissner et al. 1995 (h; *Dileptus margaritifer*); and originals (a, b, e; *Rimaleptus canadensis*). **a–d** – the somatic ciliary rows extend meridionally, following the curvature of the body. The number of ciliary rows decreases on the left side of the proboscis, leaving more or less wide unciliated stripes (asterisks); **e, f, h** – the dorsal and left side ciliary rows have dikinetids and bristles in the anterior portion, forming various patterns important for species identification; **g** – the silverlines usually form a very narrowly meshed pattern. B(1–7) – dorsal brush (rows), CF – central fibre, CK – circumoral kinety, K1 – kinety 1, Kn – last kinety, MA – macronuclear nodules, MI – micronucleus, OO – oral bulge opening, PB – pharyngeal basket, PE – perioral kinety, PR – preoral kineties, SK – somatic kinety. Scale bars: 20 µm (e, f, h) and 30 µm (a–d).

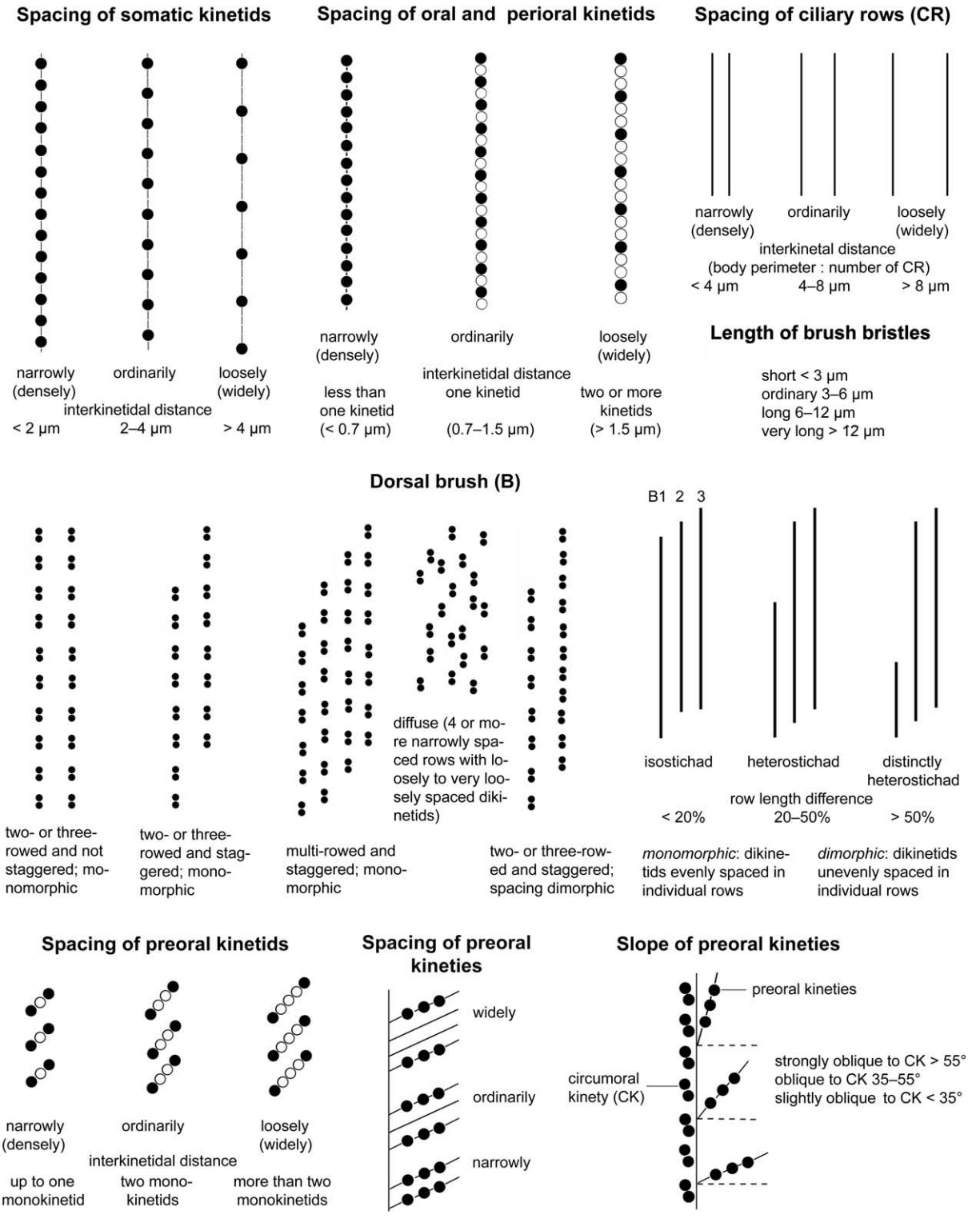


Fig. 10: Terminology of the somatic and oral ciliature in dileptid ciliates. B – dorsal brush, CK – circumoral kinety, CR – ciliary rows.

pattern, differing only in the presence vs. absence of a ventrolateral "fossa", a concavity with specialized ciliature. The fossa, whose function is not known, occurs only in *Trachelius* and *Apotrachelius* (Figs 44w, x, 46j, 47d, f, t).

The dileptids have a simple, holotrichous (~ complete) ciliature composed of, basically, two types of cilia: ordinary ones and dorsal bristles. The ordinary cilia form rows (kineties) composed of serially arranged monokinetids (= single, ciliated basal bodies). Usually, the rows are equidistant and extend meridionally from the circumoral kinety to the posterior body end, where they are more or less shortened, depending on the presence vs. absence of a tail (Figs 8a, b). See Figure 10 for the description of spacing of ciliary rows.

The cilia within the rows are densely, ordinarily, or loosely spaced (Fig. 10). Usually, they are more densely spaced orally than postorally. Frequently, the kineties contain some dikinetid-like kinetids, especially in the middle third. The posterior basal body of these pairs is ciliated, while the anterior is bare. Likely, the anterior kinetids are a reservoir for growing and/or dividing cells.

This basic pattern is modified not only by the dorsal brush, which will be described in the next section, but also by the proboscis that produces a staggered pattern on the right side and a blank stripe on the left. The right side pattern is caused by the gradual reduction of the width of the proboscis and the length of the ciliary rows from proximal to distal, where the rows abut on the unshortened perioral kinety. Depending on species, the staggered pattern is pronounced when the ciliary rows become gradually shorter along the whole length of the proboscis (Fig. 8a) or inconspicuous when shortening occurs only in the distal region of the proboscis (Fig. 8c). The blank stripe on the left side of the proboscis is caused by length reduction of some or all left side ciliary rows, which then commence (or end) at level of the oral bulge opening (Figs 8b, d, h). Depending on the number of shortened ciliary rows and the width of the proboscis, the blank stripe is narrow or wide. So, a variety of patterns is produced, especially in the genus *Pseudomonilicaryon* (Figs 107, 108). The taxonomic significance of these patterns is not known but we would be not surprised if molecular studies suggest that some characterize new genera or subgenera.

1.7.4 Dorsal Brush (Figs 10–12)

The anterior region of some dorsal and/or left lateral ciliary rows is modified to the so-called "dorsal brush" or, simply, "brush", first impregnated by Gelei (1934). The area consists of specialized, narrowly to widely spaced mono- and dikinetids with bristle-like cilia usually distinctly shorter than ordinary somatic cilia. The function of the brush is not known.

At first glance, the dorsal brush looks rather similar in all dileptids, except for the number of rows. However, the investigations of Foissner et al. (2002), Vďačný & Foissner (2008b), and the present monograph show a considerable diversity, not only in the number of brush rows but also in other features, such as the spacing and shape of the bristles. Unfortunately, the dorsal brush is difficult to investigate because the bristles are usually small and narrowly spaced. Thus, a combination of live observation, protargol impregnation, and scanning electron microscopy is ideal. In vivo, one must take care to have viable specimens because the bristles are fragile and thus change shape easily.

A variety of brush features is used to characterize and distinguish species. Most are shown in Figures 10–12, and thus will be mentioned only briefly. The dorsal brush can be short (longest row ≤ 15% of body length in protargol preparations), ordinary (15–35%), or long (≥ 35% of body length). The individual brush rows may be of similar length (isostichad) or of different length (heterostichad), or of very different length (distinctly heterostichad). Usually, the dorsal brush is isomorphic, that is, composed of bristles throughout; rarely, it is heteromorphic, that is, mixed with ordinary cilia (Fig. 11). Furthermore, the brush rows may be staggered and the dikinetids narrowly, ordinarily, or widely spaced. Six main types of brush

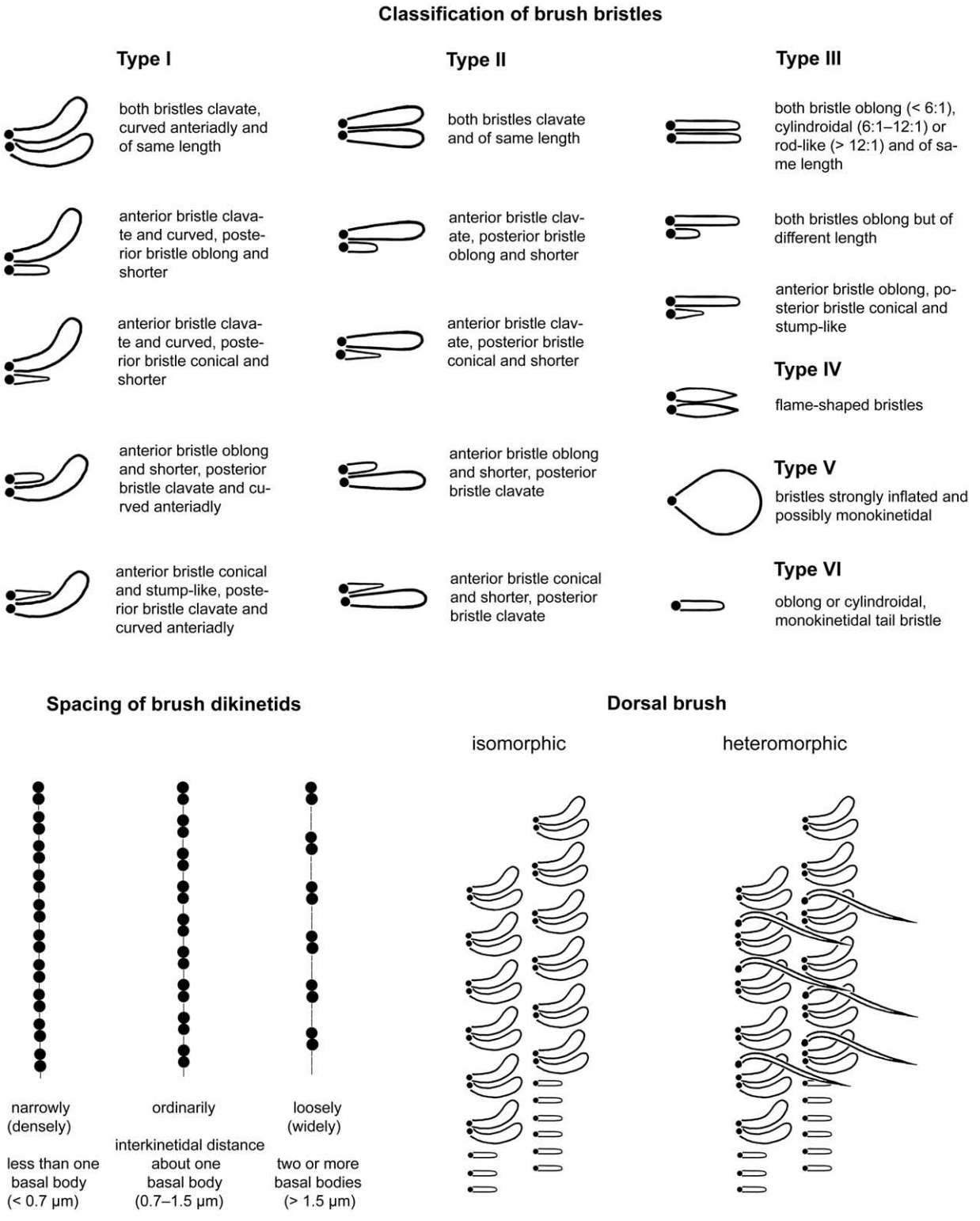


Fig. 11: Classification of dorsal brush bristles, spacing of brush dikinetids, and types of dorsal brush in dileptid ciliates.

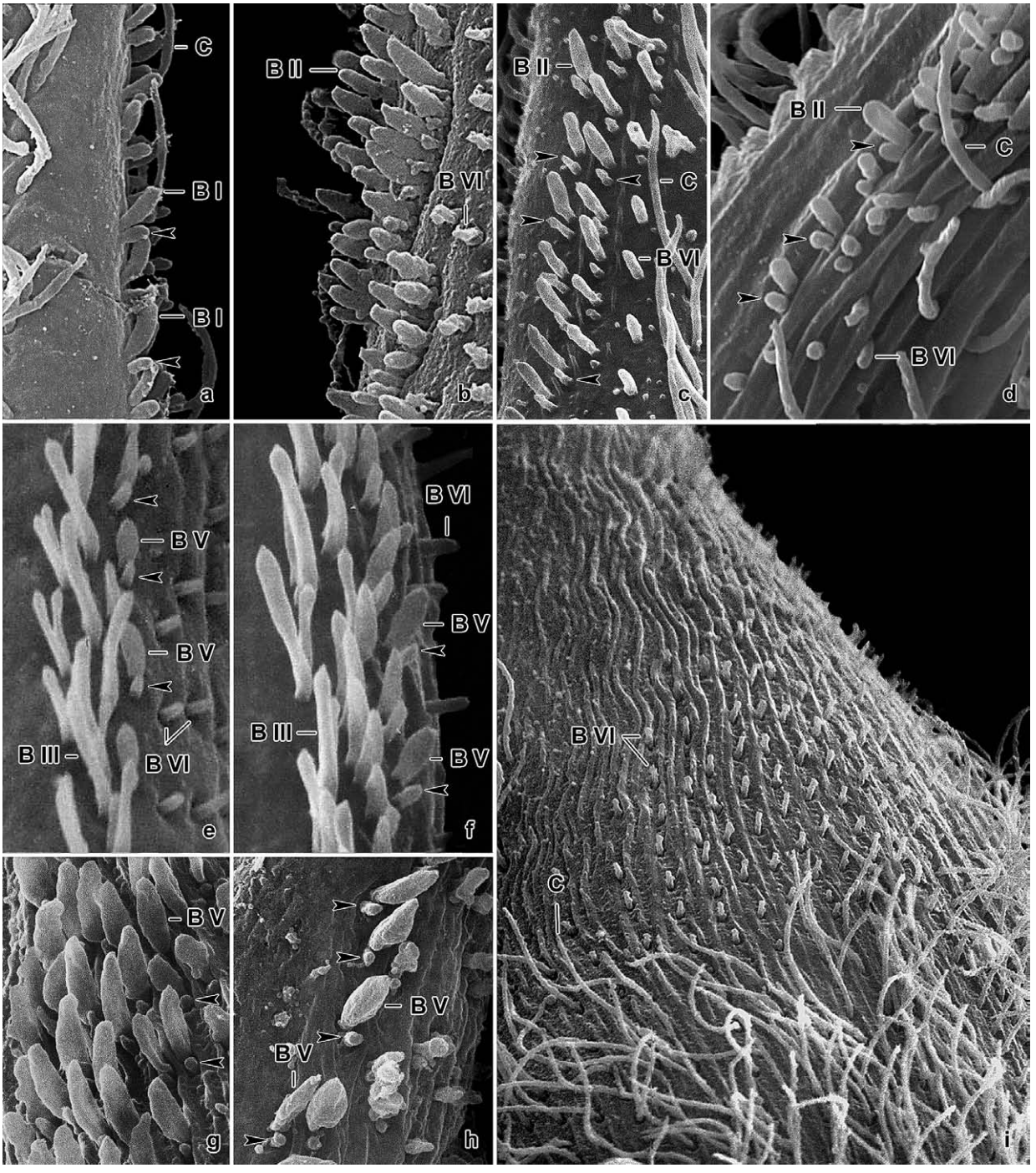


Fig. 12: Dorsal brush bristles of dileptids in the SEM. Arrowheads mark stump-like bristles. **a, d** – *Monomacrocaryon terrenum* has type I bristles: the anterior bristle is clavate and about 1.5 µm long, while the posterior one is stump-like and 0.8 µm long; **b** – *Pseudomonilicaryon fraterculum* has tongue-shaped bristles both being about 2 µm long; **c** – *Apodileptus visscheri* has type II bristles in the middle portion of the brush: the anterior bristle is clavate and about 1.5 µm long, while the posterior one is stump-like and 0.5 µm long; **e, f, h** – *Pseudomonilicaryon angustistoma* has three types of bristles: type III bristles are rod-shaped and of similar length or the anterior bristle is shorter (1.3–1.5 µm) than the posterior one (2.5–3.8 µm); the anterior bristle of type V is strongly inflated and 1.3 µm long, while the posterior bristle is conical and about 0.5 µm long; type VI tail bristles are monokinetidal and 0.5 µm long; **g, i** – an undescribed *Dileptus* from Botswana has type V and VI bristles, the latter forming monokinetidal tails. C – ordinary cilia, B I–VI – types of brush bristles.

bristles can be distinguished, ranging from stumps to strongly inflated bristles (Figs 11, 12). The individual brush rows usually commence with dikinetids at anterior dorsal body end; rarely, they have an "anterior tail" of ordinary cilia or bristles, e.g., in *Dileptus sphagnicola* (Figs 86t, u). At the posterior end of each brush row, there is usually a "posterior tail", i.e., a more or less long portion with short (≤ 3 µm) bristles (Figs 12c, i). At the proximal end of the brush, the rows continue as ordinary somatic kineties and extend to the posterior end of the cell. Only some of these features are presently used for species recognition because their taxonomic value is poorly known. However, the data available indicate a considerable value, and thus the brush description should be as detailed as possible.

See section on ontogenesis, for the origin and development of the dorsal brush during cell division.

1.8 Silverline Pattern (Figs 8g, 115k–n, 117f–l)

As in all haptorids, the dileptids basically have a very narrowly meshed silverline pattern with polygonal meshes 0.5–2 µm in size (Fig. 8g). However, the dileptids are possibly unique in that the silverline pattern is irregularly meshed also in the brush area (Figs 115n, 117f), where it usually assumes a platyophryid pattern, that is, consists of comparatively ordered and large meshes divided by a median silverline extending between two brush rows each (Foissner 1984, Foissner & Xu 2007). Thus, we were surprised to discover a dileptid with another pattern, i.e., *Pseudomonilicaryon fraterculum*, which has a platyophryid silverline pattern in the right side of the proboscis (Figs 115k, l, 117g, j, l). We do not know the significance of this observation because very few dileptids have been investigated for their silverline pattern. However, we know that *Apodileptus visscheri* does not have a platyophryid pattern, indicating that it is a feature of large species or of a special group of species.

1.9 Oral Apparatus

1.9.1 Light Microscopic Structure and Terminology (Figs 13–15)

We summarized the oral structures that are important for light microscopical species identification in Figures 13–15. These are: the shape and size of the oral bulge opening, the shape of the oral basket, the arrangement of the extrusomes, and details of the ciliary patterns. We distinguish two regions in the oral bulge: the proboscis oral bulge (that portion which is on the proboscis) and the oral bulge opening, which is at the proximal end of the proboscis oral bulge and opens the oral basket when prey is engulfed (Fig. 15). See Figure 13 for shape and length classification of the proboscis.

1.9.2 General and Fine Structure (Figs 14–16, 17a, b)

The location and structure of the dileptid oral apparatus differ significantly from those of other haptorid ciliates in that the oral bulge is bipartite (see above) and the ciliary pattern shows three (vs. one) kinds of kineties: the circumoral kinety, the perioral kinety(ies), and the preoral kineties (Fig. 14). For literature, see figure explanations.

The oral bulge is a more or less distinct, convex zone without cilia on the ventral side of the proboscis; usually, it is more distinct around the oral bulge opening (Fig. 15). The bulge is not only horizontally bipartite (see above) but also vertically due to the so-called central fibre, which divides the bulge in a broad right branch and a narrow left branch. In most but not all species, only the right branch contains extrusomes (Figs 16b–e). The surface of the bulge is more or less striated by the transverse microtubule ribbons originating from the non-ciliated basal bodies of the circumoral kinety; they form, by overlapping of their proximal region, the bulge's central fibre (Figs 15b, 16b–d).

The oral (pharyngeal) basket is at the proximal end of the proboscis oral bulge. Although the basket is comparatively small, dileptids can engulf large prey either by disintegrating it outside the cell (see next

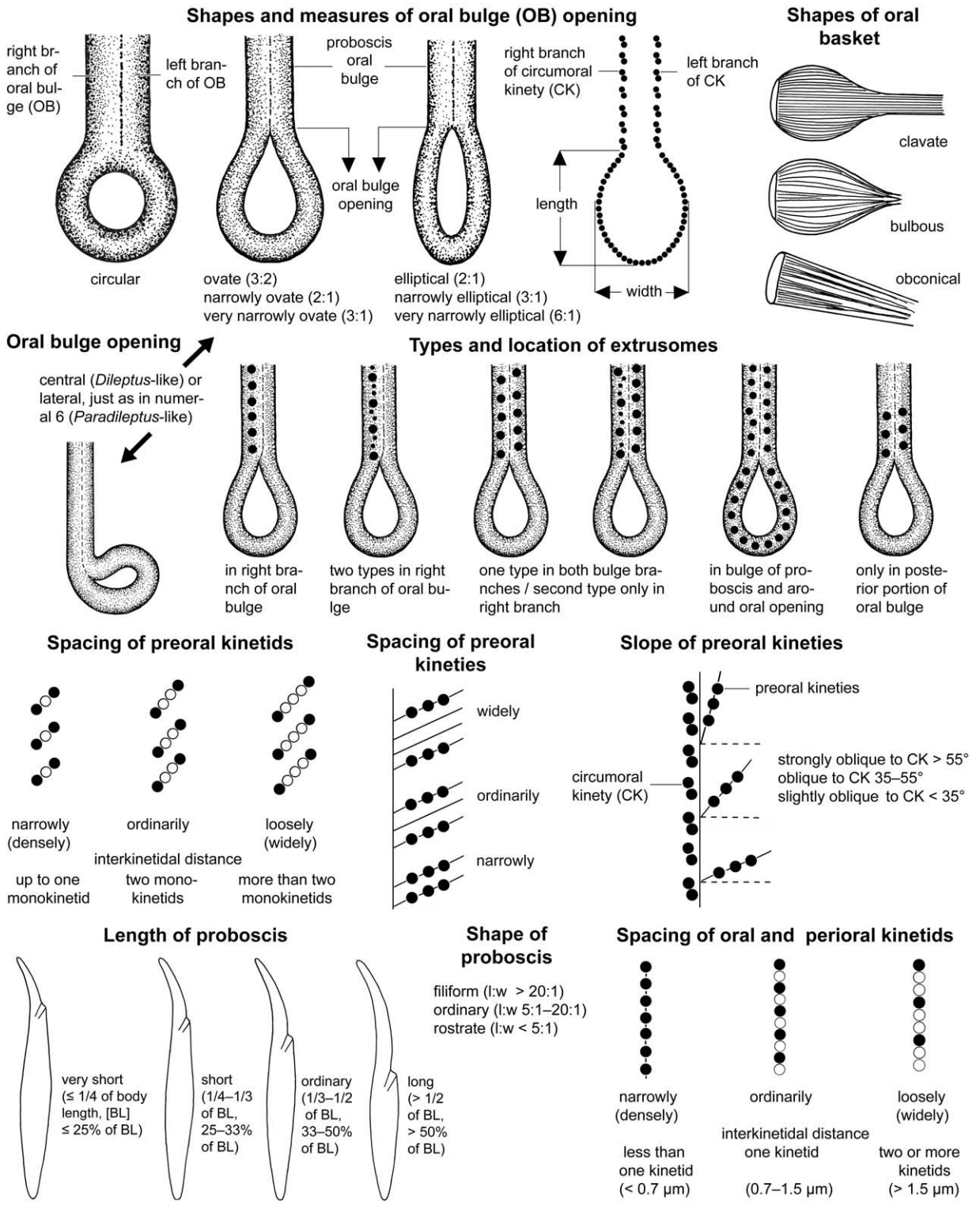


Fig. 13: Terminology of oral structures and classification of proboscis.

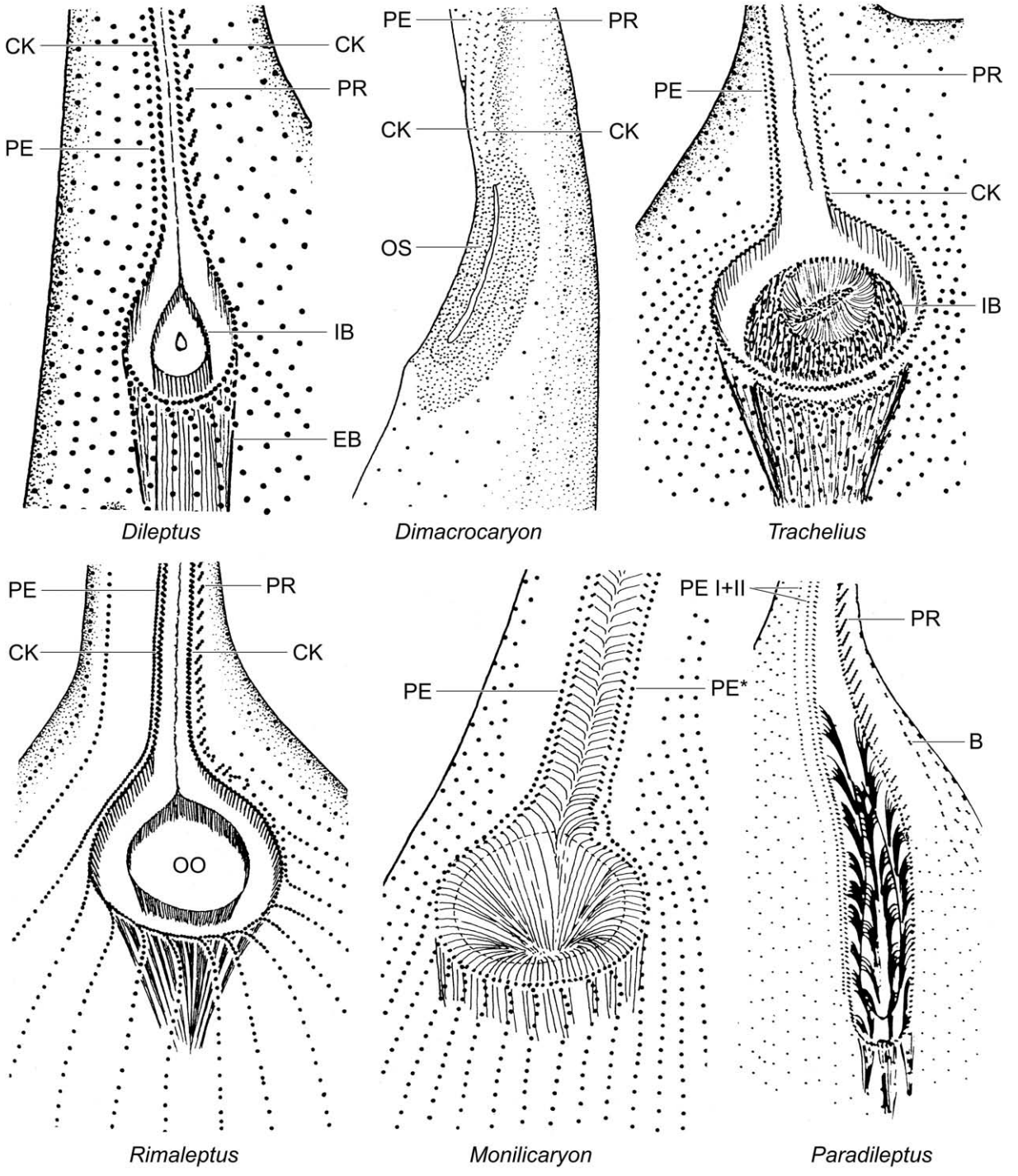


Fig. 14: Oral ciliary patterns in dileptid ciliates after protargol impregnation. From FOISSNER (1984, 1995, 1997a) and PACKROFF & WILBERT (1991). In most dileptid genera, the right branch of the circumoral kinety is accompanied by a single perioral kinety and the left branch by many slightly to strongly oblique preoral kineties, which became linearly arranged in *Monilicaryon*, producing a perioral-like kinety. There are two perioral kineties side by side in *Paradileptus*. B – dorsal brush, CK – circumoral kinety, EB – external basket, IB – internal basket, OO – oral bulge opening, OS – oral sac, PE (I+II) – perioral kinety (1 and 2), PE* – perioral-like kinety, PR – preoral kineties.

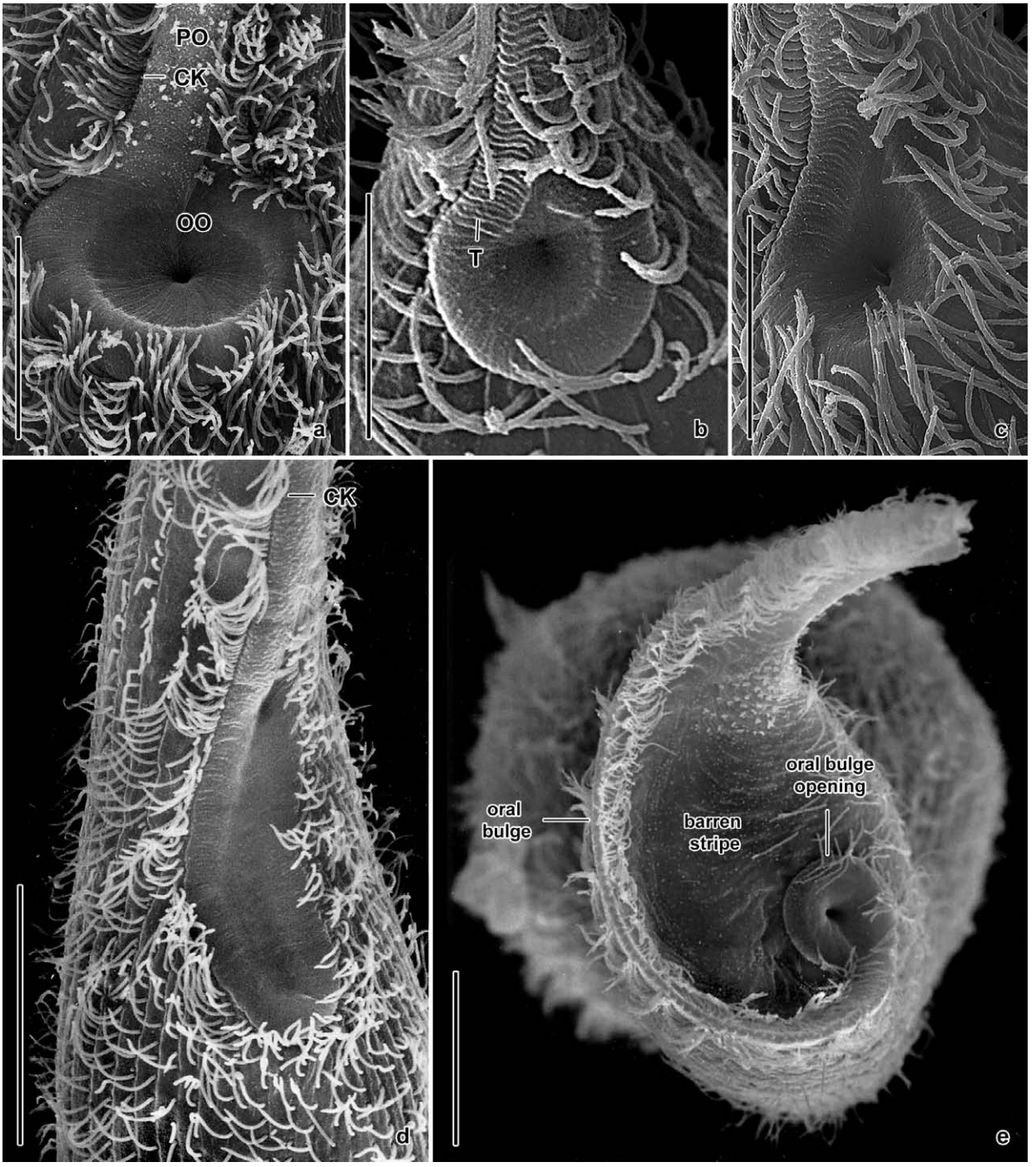


Fig. 15: Shape of oral bulge opening in various dileptid ciliates in the SEM. From FOISSNER et al. 1999 (e), FOISSNER et al. 2002 (d), and originals (a–c). **a** – an undescribed *Dileptus* from Botswana has a perfectly circular oral opening; **b, c** – *Monomacrocaryon terrenum* has a circular oral opening (b) which, however, appears ovate when viewed obliquely (c). The oral bulge is transversely striated by fibre bundles, very likely transverse microtubule ribbons; **d** – *Pseudomonilicaryon angustistoma* has a narrowly elliptical oral opening; **e** – in *Paradileptus elephantinus*, the left half of the base of the proboscis is broadened dish-like, taking along the oral bulge and the bulge opening which is thus located laterally and inverted, just as in numeral 6. CK – circumoral kinety, OO – oral bulge opening, PO – proboscis oral bulge, T – transverse microtubule bundles. Scale bars: 10 µm (a–c) and 20 µm (d, e).

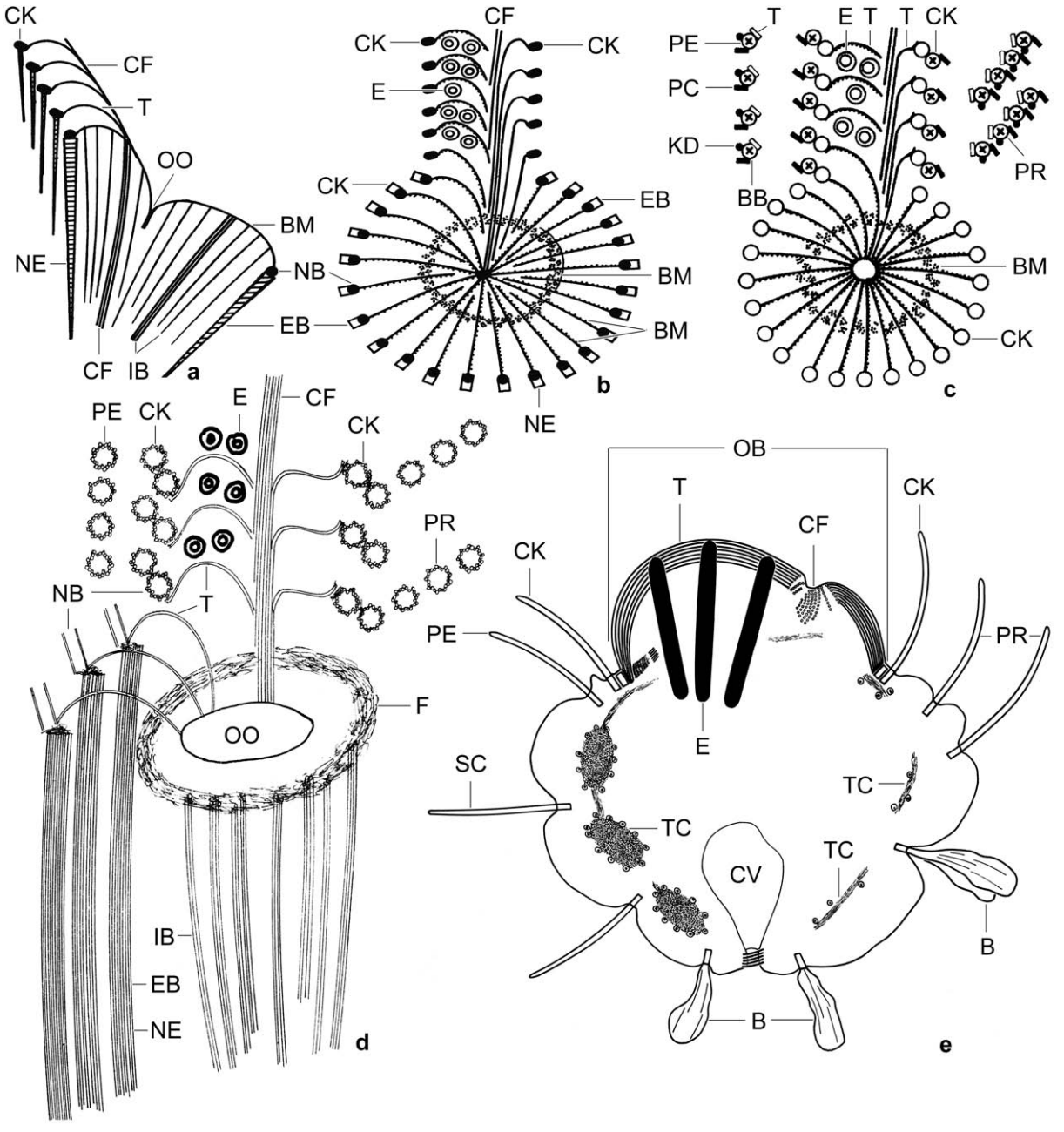


Fig. 16: Schemes of the oral apparatus of *Dileptus margaritifer* (a–c, e) and *Apodileptus visscheri* (d), based on TEM investigations. **a** – portion of the oral bulge, showing the origin of the internal and external oral basket (from Golińska 1996). The internal basket is made of transverse microtubule bundles, while the external basket is composed of nematodesmata originating from the non-ciliated basal bodies around the oral bulge opening; **b, c** – frontal views of proboscis and pharyngeal basket (b, from Golińska 1966; c, from Golińska 1995). The circumoral kinety is composed of dikinetids in the proboscis, while of monokinetids bearing nematodesmata around the oral bulge opening. Empty circles symbolize nonciliated basal bodies; **d** – slightly oblique view of oral ciliary pattern and pharyngeal basket (from Kink 1973); **e** – transverse section of proboscis (from Grain & Golińska 1969). The right branch of the oral bulge contains toxicysts and is much broader than the left branch. B – dorsal brush, BB – basal bodies, BM – bulge microtubules, CF – central fibre, CK – circumoral kinety, CV – contractile vacuoles, E – extrusomes (toxicysts), EB – external oral basket, F – fibrous material, IB – internal oral basket, KD – kinetodesmal fibre, NB – nonciliated basal bodies, NE – nematodesmata, OB – oral bulge, OO – oral bulge opening, PC – postciliary microtubule ribbon, PE – perioral kinety, PR – preoral kineties, SC – somatic cilia, T – transverse microtubule ribbon, TC – tela corticalis.

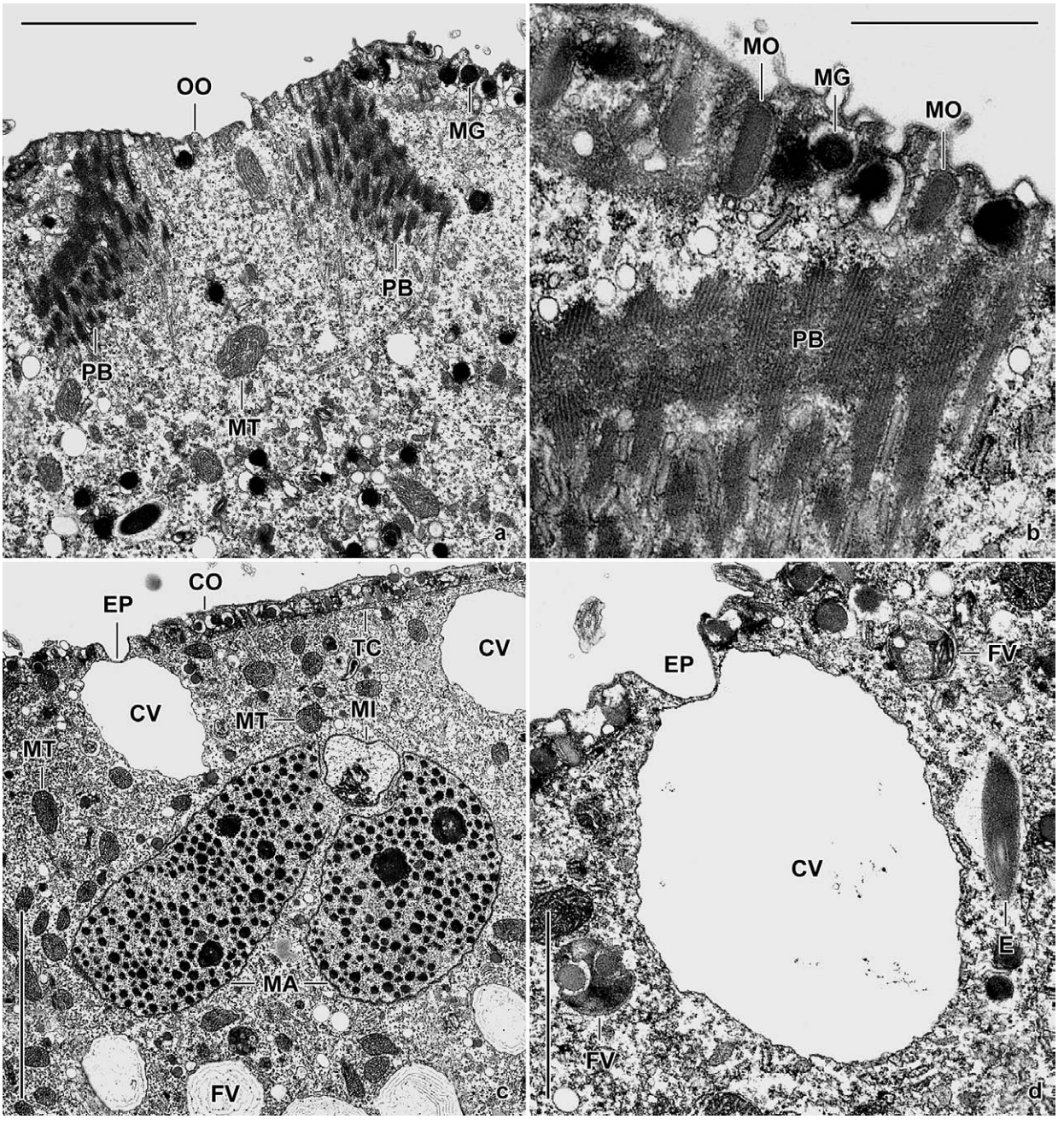


Fig. 17: *Dimacrocaryon amphileptoides amphileptoides*, Norwegian population in the TEM. **a, b** – in the light microscope, a pharyngeal basket is not recognizable either in vivo or after protargol impregnation, where the oral opening is lined by rather deeply impregnating granules. However, a pharyngeal funnel composed of many nematodesma bundles and containing oblong and globular granules, likely mucocysts, is recognizable in the electron microscope. It is not known why the oral basket rods do not impregnate in *Dimacrocaryon*; **c, d** – in the centre of the trunk, there are two oblong macronuclear nodules with a single micronucleus in between. The micronucleus is bright, while the two macronuclear nodules contain many globular inclusions, of which the large ones are possibly nucleoli (c). The contractile vacuoles have an ordinary fine structure (d). The cytoplasm is studded with mitochondria, toxicysts, and minute food vacuoles containing silicoflagellates. CO – cortex, CV – contractile vacuoles, E – extrusome (toxicyst), EP – excretory pore, FV – food vacuoles, MA – macronuclear nodules, MG – globular mucocysts, MI – micronucleus, MO – oblong mucocysts, MT – mitochondria, OO – oral opening, PB – nematodesmata of pharyngeal basket, TC – tela corticalis. Scale bars: 1 µm (b), 2 µm (d), 3 µm (a), and 5 µm (c).

chapter) or by opening the oral bulge/basket widely. Typical examples are *Dimacrocaryon amphileptoides* (Fig. 57c), *Microdileptus breviproboscis* (Figs 79j–l, 80l, m), and the planktonic dileptids (Figs 137i, 140i). The oral basket is a rather complex structure produced by three elements (Figs 14, 16a–d, 17a, b): the external basket is formed by thick microtubule bundles (nematodesmata) originating from the nonciliated basal bodies around the oral opening; the internal basket is produced by small bundles of bulge microtubules held together by a fibrous ring distally; and the oral opening s. str. is lined by the proximal portion of the transverse microtubule ribbons, originating from the nonciliated basal bodies around the oral opening.

The circumoral kinety extends along the base of the oral bulge and is composed of narrowly to very narrowly spaced, paired basal bodies (dikinetids), forming a single keyhole-shaped ciliary row (Figs 14–16). However, this plesiomorphic state is present only in the Tracheliida, while the Dileptida show an apomorphic condition, where the ciliated basal body of the pairs is reduced around the oral bulge opening. The dikinetids are obliquely arranged, and only the more anteriorly located basal body of a pair is ciliated, producing – together with the perioral kinety – a dense ciliation ("mane"), showing nice metachronal ciliary waves (Fig. 72f). The circumoral kinety is interrupted at the distal end of the proboscis, where the right branch curves left almost touching the straight left branch. Proximally, the circumoral kinety is confluent with the nonciliated basal bodies surrounding the base of the oral bulge opening. The posterior (or left) basal bodies of the dikinetids are bare but associated with transverse microtubule bundles, forming the proboscis' central fibre and lining the oral opening s. str. Furthermore, the nonciliated basal bodies are associated with nematodesmata producing the external oral basket (Figs 16a–d).

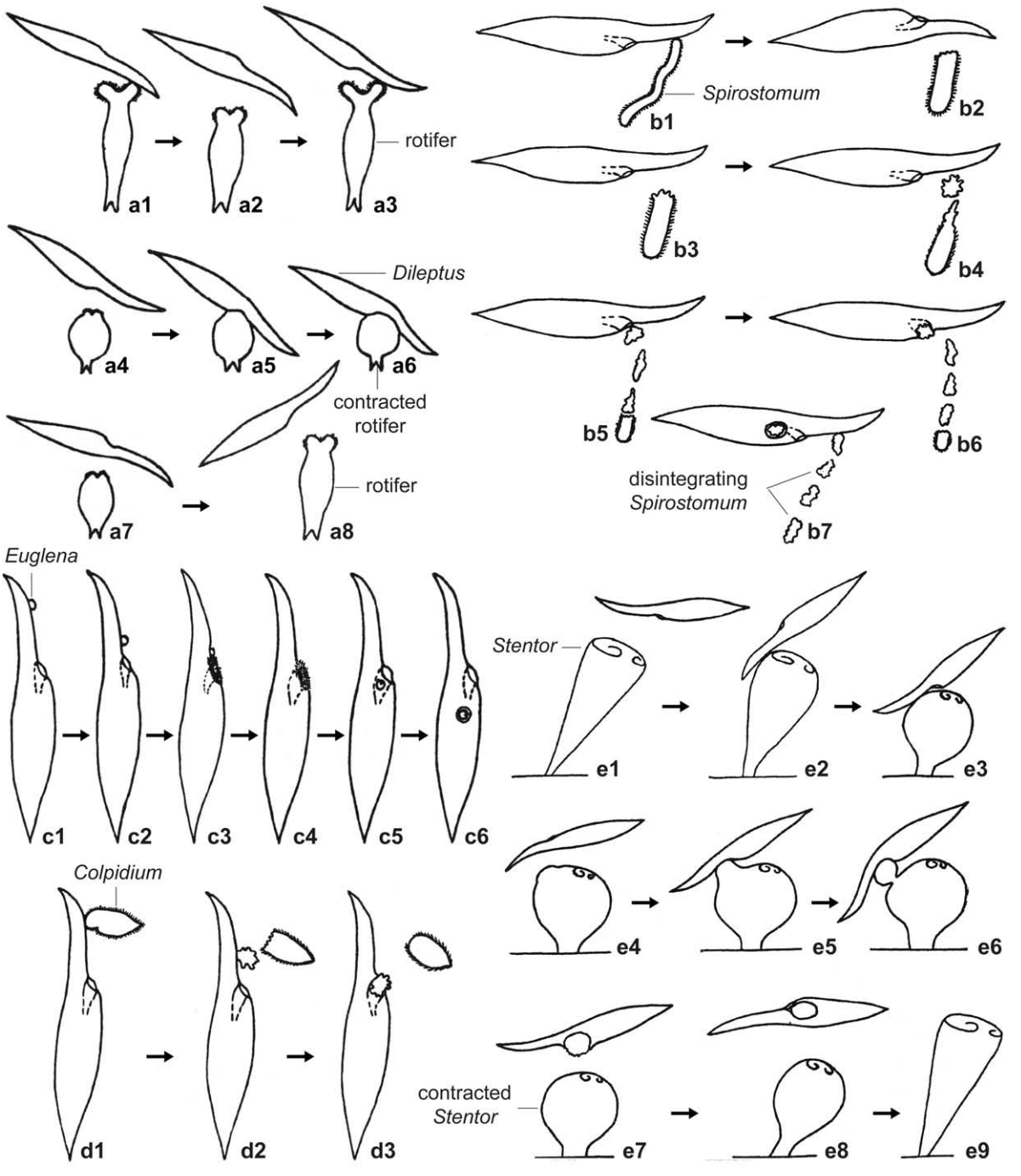
The perioral kinety extends right of the right branch of the circumoral kinety, i.e., along the proboscis proximal to which it continues as an ordinary somatic kinety (Fig. 14). It is composed of ordinarily to very narrowly spaced monokinetids with few special fine structural characteristics (Figs 16b–d). Thus, the perioral kinety is a somatic kinety with a condensed anterior portion. Usually, there is one perioral kinety, two occur only in the euplanktonic genera *Pelagodileptus* and *Paradileptus* (Fig. 14).

The preoral kineties extend obliquely along the left branch of the circumoral kinety and contribute to species recognition (Figs 13, 14). Usually, each kinety consists of only two to four kinetids with a fine structure similar to that of the somatic kinetids, except for the fibrillar associates, which are rotated counterclockwise by about 120° (Figs 16c, d). The preoral kineties are ciliated and thus contribute to the dense ciliature of the proboscis.

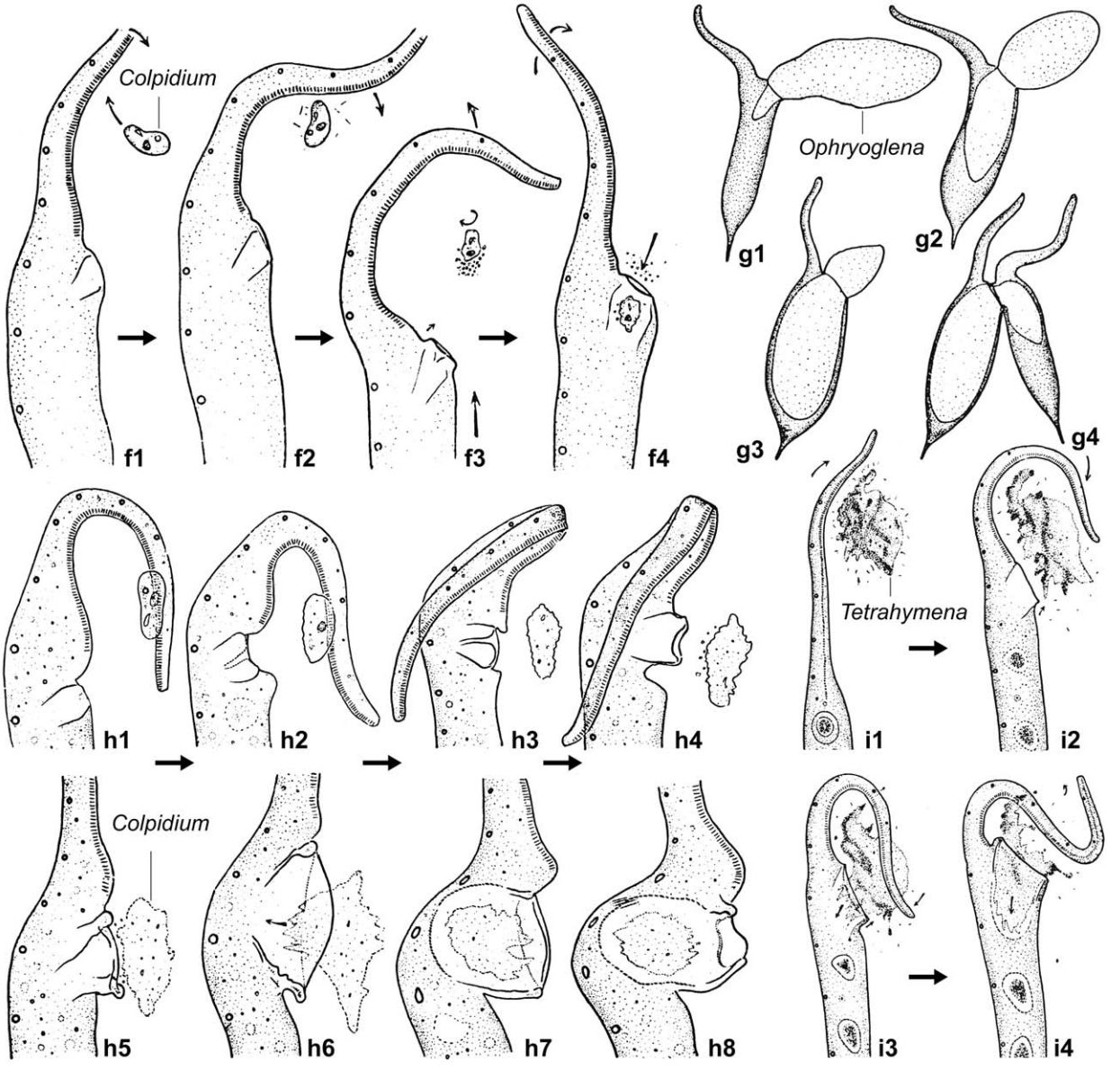
1.9.3 Food and Feeding (Figs 18a–i)

Dileptids are predators and have a similar food spectrum as other rapacious ciliates (Lynn 2008). Specifically, they feed on amoebas, flagellates, ciliates, and even on microscopic metazoans, such as rotifers, planarians, and larvae of copepods. Bacteria, diatoms (e.g., *Nitzschia palea, N. sigmoidea, Synedra ulna*, *Cymbella* sp., *Rhoicosphenia curvata*) and other algae found in food vacuoles are possibly remnants from prey, although heterotrophic (*Chilomonas*) and autotrophic (*Euglena*) flagellates are engulfed in laboratory experiments (Visscher 1923). The menu of the individual species is often much shorter than listed above, and some are likely specialists. For instance, *Dimacrocaryon amphileptoides* and *D. brasiliense* prefer testate amoebas (e.g., *Euglypha* sp., *Schoenbornia viscicula, Trinema lineare*), *Microdileptus microstoma* and *M. breviproboscis* favour naked amoebas, *Trachelius ovum* feeds mostly on peritrichs, and *Pseudomonilicaryon japonicum* prefers rotifers.

Visscher (1923) and Dragesco (1962) reviewed the literature and performed very interesting experiments on feeding in *Dileptus margaritifer* (Fig. 18). Both agree that the toxicysts play a major role in prey capture and lysis which mostly occurs outside the cell, i.e., the prey is ingested in fluid form. However,



Figs 18a–e: *Dileptus margaritifer*, diagrammatic sketches illustrating the process of feeding (from VISSCHER 1923). For further explanation, see text. **a1–8** – effect of toxicysts of *Dileptus* on rotifers, **b1–7** – when *Dileptus* comes in contact with *Spirostomum* (b1), the latter contracts vigorously and remains momentarily motionless (b2). Cytolysis begins at area of contact (b3) and as *Spirostomum* reacts negatively, swimming rapidly away, the cytolytic process continues (b4–6). Meanwhile, *Dileptus* has engulfed one or more masses of the disintegrating *Spirostomum* (b5–7); **c1–6** – successive stages in process of ingesting *Euglena*; **d1–3** – effect of toxicysts of *Dileptus* on *Colpidium*; **e1–9** – effect of toxicysts of *Dileptus* on *Stentor*.



Figs 18f–i: *Dileptus margaritifer*, feeding processes (from DRAGESCO 1962). **f1–4** – when *Colpidium* contacts the proboscis, toxicysts are released and immobilize the prey (1, 2). The proboscis continues moving, while the prey rapidly disintegrates and the oral opening widens (3) to engulf the *Colpidium* debris (4); **g1–4** – after partial immobilization of the prey, *Dileptus* commences ingestion (1). When three quarters of the prey were inside the predator (2, 3), a second *Dileptus* attacked the protruding prey portion (4); **h1–8** – detailed analysis of feeding of *D. margaritifer* on *Colpidium campylum*. The proboscis touches and kills the prey with the toxicysts (1). Then, prey lyses and widening of the predator's oral basket commences (2). Now, the proboscis moves away from the prey and the widened proboscis oral bulge moves forward, eventually touching the lysed prey (3–5). When engulfing the lysed prey, the oral basket opens trumpet-like (6). Then, the basket begins to close, forming the food vacuole (7, 8). These processes require the following times (seconds): opening of the oral basket (3), prey ingestion (2), closing of the oral basket (1.5). Further, a starved *Dileptus* can ingest 70 *Colpidium* within 2h. **i1–4** – when *Tetrahymena patula* touches the proboscis, it becomes cytolyzed immediately (1). Then, the proboscis encages the lysed prey (2) and transports it to the widely open oral basket (3), where it is vigorously engulfed (4).

Microdileptus breviproboscis (Figs 79j–l) and sometimes also *Dileptus margaritifer* (Figs 18g1–g4) engulf large prey whole. It is not known what determines whether prey is or is not lysed before ingestion.

Visscher (1923) concludes: (i) *D. margaritifer* normally feeds on living organisms, but under certain conditions it ingests inanimate particles; (ii) it discriminates between living organisms and inanimate substances, ingesting the former in large amounts, while the latter are only sparingly ingested; (iii) *Dileptus* selects from among different kinds of organisms, eating some with great readiness, while others are rarely ingested; (iv) it captures its prey by means of toxicysts which either paralyze the prey, e.g., *Euglena*, or bring about cytolysis of all or part of the protoplasm of the prey, e.g., *Colpidium* and *Stentor*; (v) the toxicysts are probably of a liquid nature, highly toxic, with specific cytolytic properties; (vi) the toxicysts of *Dileptus* are used for the purpose of capturing food; (vii) selection of food in *Dileptus* depends on two factors: (*a*) the physiological state of the organism itself, which appears to determine whether a substance shall be ingested in large or small amounts, and (*b*) the chemical properties of its toxicysts, which determine in large measure whether any living organism can or can not be successfully captured; (viii) specialized structures as, for example, the trichocysts of *Paramecium* and the pellicle of *Euplotes*, serve as protection against the attacks of *Dileptus*.

Dragesco (1962) basically confirms the results of Visscher (1923) and adds the following: (i) *Dileptus* shows very low food specialization but there can be two or three physiological races within a spesies, for instance, in *D. margaritifer*; (ii) the prey, which is killed by the extruded toxicysts, is ingested rapidly using two mechanisms: opening of the mouth and strong aspiration, both mechanisms are, however, insufficiently known; (iii) the movement of the proboscis is independent from ingestion, and the cell can kill ciliate prey without absorbing it. On the other hand, it can ingest prey without killing it before (*D. margatitifer* can kill a zooid of *Carchesium* but half of the prey is taken by another predator).

Further details were added by Miller (1968), who recognized that feeding of *D. margaritifer* begins shortly before dawn and continues until bright day light, terminating sharply between 8:30 and 9:00 a.m. Moreover, he could clarify proboscis truncation as a reaction to extensive feeding.

Estève (1982) showed cannibalism of trypsin-treated conspecifics. Further, Estève (1984) proved that phagocytosis is calcium-dependent and probably regulated by calmodulin and glucose and/or mannose residues. Ultrastructural changes included a local differentiation of the glycocalyx, an interaction between cilia of prey and predator membrane and some fibrillar links between cytostomal vesicles and microtubules of transverse fibres. The pharyngeal cytoplasm, which forms the membrane of the food vacuoles, is very prominent (Fauré-Fremiet 1961). See Verni & Gualtieri (1997) for a general review on feeding.

Prey ciliates evolved two defence strategies against dileptid predators: chemical defence by toxic granules, e.g., the pigment granules of *Stentor coeruleus* (Terazima et al. 1999, Miyake et al. 2001), and mechanical defence, in that the prey releases trichocysts propelling it away from *Dileptus* (Knoll et al. 1991, 1993), while backward swimming is of minor importance (Harumoto 1994). When potential prey, e.g., *Colpidium kleini*, is added to cultures of *Dileptus margaritifer*, it does not show any morphological changes (Fyda & Wiąckowski 1998). However, this must not be generalized. *Euplotes*, e.g., transforms into the "winged state" when *Dileptus margaritifer* is present (Görtz et al. 1999, Kuhlmann et al. 1999).

1.10 Regeneration

Ewald Schild (1921), an Austrian amateur microscopist, was possibly the first who performed regeneration experiments on *Dileptus*. He showed that pieces of *D. margaritifer* degenerated when they did not contain nuclear material; this was confirmed by Golińska & Grain (1969). Later, more detailed experiments showed that *Dileptus* is an interesting model for regeneration experiments. We will not go into details because some excellent reviews are available (Sokoloff 1924, Grain & Bohatier 1977, Frankel 1989),

and the data are of minor importance for taxonomic purposes. However, it is important to know of the great regeneration capacity of dileptids because regenerating specimens occur rather frequently in nature, especially, when the fragile proboscis whose regeneration needs about 5 h (Golińska & Kink 1976) has been lost. And certainly the cell shape changes greatly in regenerating fragments and post-divisional specimens (Figs 20l–g, 21a–m, 113a–r).

2 Life Cycle

The dileptids have an ordinary life cycle (Fig. 19). The excysted cells feed and become vegetative cells that divide and eventually encyst when environmental conditions become adverse. The sexual life cycle is known only in two dileptids, viz., *Dileptus margaritifer* (Visscher 1927, Vinnikova 1974a) and *Rimaleptus tirjakovae* (Vďačný & Foissner 2008a). The data show that there is one or several preconjugational divisions, causing conjugants to be smaller than vegetative cells. Exconjugants feed and divide obtaining vegetative size after some days.

2.1 Ontogenesis

Data on binary fission of dileptids have been reported for *Apodileptus visscheri*, *Dileptus anatinus*, *D. jonesi*, *D. margaritifer*, *Pseudomonilicaryon anser* (Jones 1951; Golińska 1972, 1995; Bohatier & Kink 1977), and *Trachelius ovum* (Hamburger 1903, Penard 1922) as well as for three *Paradileptus* species: *P. conicus*, *P. elephantinus*, and *P. ovalis* (Huber-Pestalozzi 1945, Fryd-Versavel et al. 1975). However, most of these studies are very incomplete, providing only a single stage and/or a few schematic figures or micrographs. The exceptions are the detailed investigations of Golińska (1972, 1995), who studied mainly the formation of the opisthe's infraciliature, using transmission electron microscopy and protargol impregnation. However, Golińska did not provide detailed line drawings of the process. These were given only recently by Vďačný & Foissner (2009), who studied concomitantly development of cell shape, nuclear apparatus, and ciliary pattern of *Monomacrocaryon terrenum*, using protargol impregnation. The results of this study are reported here in the original wording. Golińska & Jerka-Dziadosz (1973) showed that division of *D. margaritifer* needs a certain volume of endoplasm, i.e., a certain size of the cell. See Golińska (1979, 1982, 1983, 1984, 1986, 1988), Jerka-Dziadosz & Golińska (1977), and Frankel (1989) for the regulation of the ciliary pattern.

Division mode. Fission is homothetogenic, i.e., the posterior end of the proter is in contact with the anterior end of the opisthe. Division occurs in freely motile (non-encysted) condition. Stomatogenesis is holotelokinetal, that is, all somatic kineties proliferate circumoral kinetids. The parental oral apparatus and dorsal brush are not reorganized.

Body changes and development of proboscis. Very early dividers are longer than morphostatic specimens by an average of about 30 µm, while body width and the ratio of body and proboscis length hardly change (~ 31% vs. 34%; Table 3). Thus, early dividers are the largest and most slender cells because they are longer (322 µm vs. 278 µm), but not significantly wider than morphostatic specimens (50 µm vs. 48 µm; Fig. 20l). In contrast to spathidiids, there are neither a slight indentation in the prospective fission area or division blebs. In mid-dividers, when the macronucleus condenses, the body shortens and broadens from 322 × 50 µm to 303 × 56 µm, i.e., these cells are the smallest and stoutest dividers (Figs 20m, n). At this stage, a minute bare protuberance, the precursor of the oral bulge, develops along the prospective anterior end of the opisthe, dividing the cell into a conical posterior daughter shorter by about one fifth than the broad proter (Figs 20g, h, m, n). In late mid-dividers, a remarkable process commences, i.e., the proboscis bud develops as a small convexity in the opisthe's brush area underneath the developing division furrow

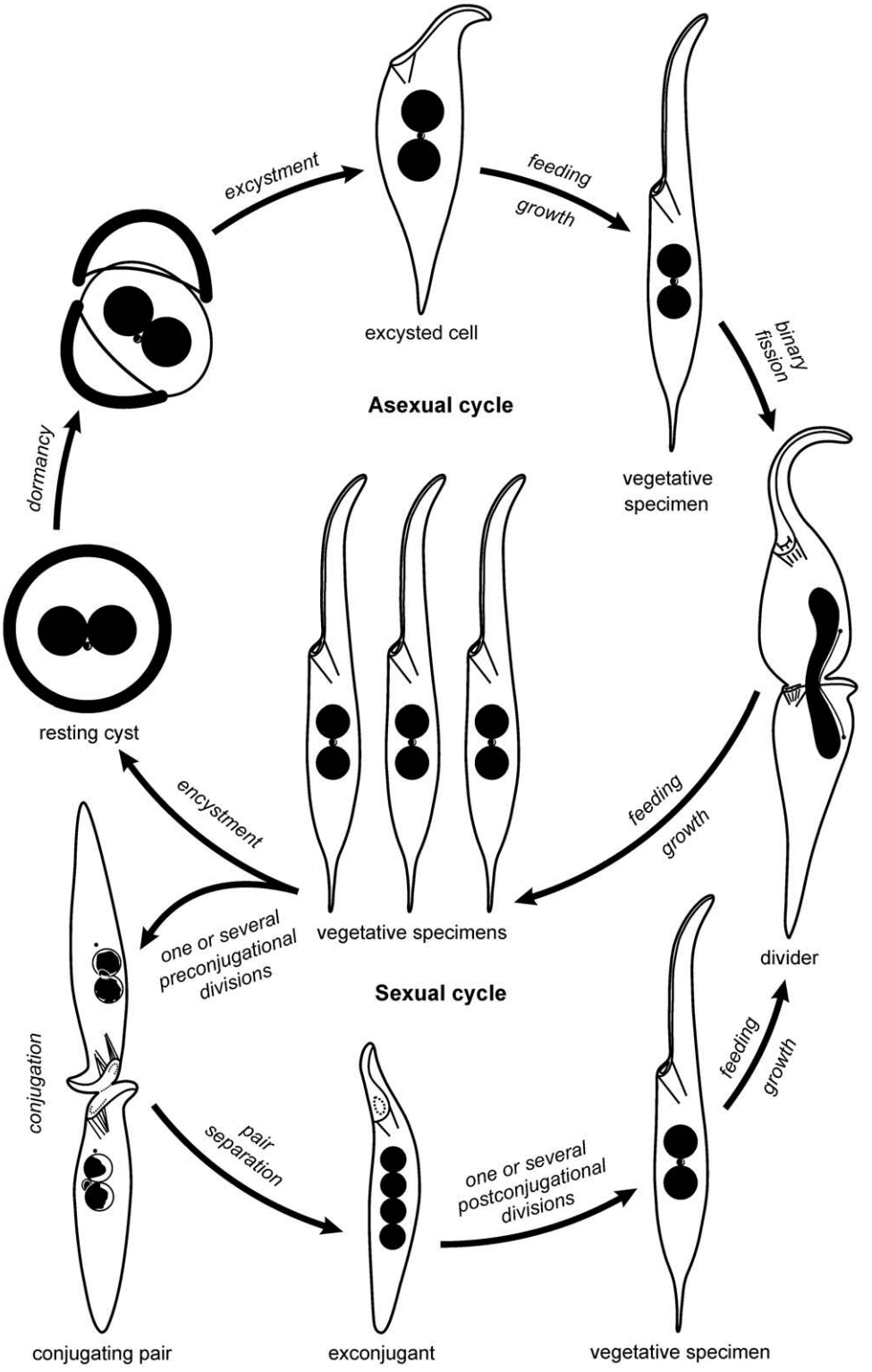


Fig. 19: Asexual and sexual life cycle of dileptids. Based on VISSCHER (1927), JONES (1951), VINNIKOVA (1974a) and, especially, VĎAČNÝ & FOISSNER (2008a, 2009).

Table 3: Morphometric data on morphostatic cells, dividers, and post-dividers of *Monomacrocaryon terrenum* (from Vďačný & Foissner 2009). Data based on mounted, protargol-impregnated (Foissner's method with Stieve fixation), and randomly selected specimens from a semi-pure culture. Measurements in µm. CV – coefficient of variation in %, M – median, Max – maximum, Mean – arithmetic mean, Min – minimum, n – number of specimens investigated, SD – standard deviation, SE – standard error of mean. **Continued on page 529**.

Characteristics	Stage[a]	Mean	M	SD	SE	CV	Min	Max	n
Body, length	Morphostatic	278.4	283.0	23.1	5.0	8.3	227.0	315.0	21
	Very early divider	310.9	306.0	30.6	6.7	9.8	265.0	372.0	21
	Early divider	322.1	323.0	32.3	7.0	10.0	252.0	369.0	21
	Mid-divider	303.5	303.0	25.6	5.6	8.4	246.0	350.0	21
	Late divider	308.3	313.0	32.5	13.3	10.6	249.0	340.0	6
	Very late divider	310.3	314.0	–	–	–	268.0	345.0	4
	Proter post-divider	207.6	211.0	21.0	4.6	10.1	153.0	240.0	21
	Opisthe post-divider	169.7	172.0	25.4	5.5	15.0	137.0	223.0	21
Body, width	Morphostatic	47.8	49.0	5.8	1.3	12.2	35.0	56.0	21
	Very early divider	49.7	49.0	4.5	1.0	9.1	44.0	60.0	21
	Early divider	50.1	51.0	4.0	0.9	8.0	43.0	63.0	22
	Mid-divider	55.8	56.0	5.7	1.3	10.3	43.0	70.0	21
	Late divider	52.7	54.0	3.3	1.3	6.2	49.0	56.0	6
	Very late divider	59.4	61.0	–	–	–	48.0	69.0	4
	Proter post-divider	48.3	49.0	5.7	1.3	11.9	40.0	63.0	21
	Opisthe post-divider	43.5	43.0	4.4	0.9	10.0	36.0	53.0	21
Body length:width, ratio	Morphostatic	5.9	5.7	0.6	0.1	11.0	4.7	7.3	21
	Very early divider	6.3	6.5	0.8	0.2	13.2	4.7	7.5	21
	Early divider	6.4	6.5	0.8	0.2	13.0	4.6	7.8	21
	Mid-divider	5.5	5.4	0.8	0.2	14.7	4.2	7.2	21
	Late divider	5.9	6.2	0.8	0.3	13.0	4.5	6.5	6
	Very late divider	5.3	5.3	–	–	–	4.3	6.3	4
	Proter post-divider	4.4	4.4	0.7	0.1	15.5	3.2	5.5	21
	Opisthe post-divider	4.0	4.1	0.8	0.2	19.5	2.7	5.7	21
Anterior body end to oral opening, distance	Morphostatic	94.0	94.0	12.3	2.7	13.1	78.0	113.0	21
	Very early divider	97.1	102.0	12.6	2.8	13.0	70.0	114.0	21
	Early divider	101.7	102.0	11.5	2.5	11.3	72.0	125.0	21
	Mid-divider	92.3	93.0	13.1	2.9	14.2	59.0	117.0	21
	Late divider	81.4	80.0	10.7	4.4	13.1	70.0	100.0	6
	Very late divider	88.8	89.0	–	–	–	74.0	103.0	4
	Proter post-divider	95.4	98.0	13.1	2.9	13.7	62.0	113.0	21
	Opisthe post-divider	50.7	51.0	10.2	2.2	20.1	30.0	67.0	21
Proboscis, % of body length	Morphostatic	33.7	33.0	2.9	0.6	8.6	29.0	38.3	21
	Very early divider	31.2	31.5	2.4	0.5	7.8	26.4	35.0	21
	Early divider	31.7	31.4	2.8	0.6	8.7	27.8	36.1	21
	Mid-divider	30.3	30.1	2.8	0.6	9.3	21.0	33.9	21
	Late divider	26.7	26.8	4.4	1.8	16.4	20.6	32.5	6
	Very late divider	28.6	29.2	–	–	–	25.6	30.3	4
	Proter post-divider	46.0	45.8	4.6	1.0	10.0	35.7	54.6	21
	Opisthe post-divider	30.0	29.5	5.4	1.2	18.1	17.2	41.6	21
Proter, length	Very early divider	177.8	176.0	19.4	4.2	10.9	144.0	220.0	21
	Early divider	180.5	180.0	19.3	4.2	10.7	142.0	215.0	21
	Mid-divider	169.5	168.0	17.6	3.8	10.4	145.0	205.0	21
	Late divider	166.5	172.0	17.9	7.3	10.7	142.0	191.0	6
	Very late divider	174.5	176.0	–	–	–	149.0	198.0	4
Proter, width	Very early divider	49.5	49.0	4.7	1.0	9.4	42.0	60.0	21
	Early divider	50.1	51.0	4.0	0.9	8.0	43.0	63.0	22
	Mid-divider	55.8	56.0	5.7	1.3	10.3	43.0	70.0	21
	Late divider	52.7	55.0	3.3	1.3	6.2	49.0	56.0	6
	Very late divider	59.4	61.0	–	–	–	48.0	69.0	4
Proter length:width, ratio	Very early divider	3.6	3.7	0.5	0.1	13.7	2.7	4.4	21
	Early divider	3.6	3.6	0.5	0.1	13.4	2.7	4.6	21
	Mid-divider	3.1	2.9	0.5	0.1	15.6	2.2	4.2	21
	Late divider	3.2	3.3	0.4	0.2	13.8	2.6	3.6	6
	Very late divider	3.0	3.0	–	–	–	2.3	3.6	4

[a] Very early dividers are characterized by the proliferation of basal bodies in the dorsal kineties slightly posterior to mid-body, while early dividers have developed oral kinetofragments. Mid-dividers have a continuous circumoral kinety and the macronucleus commences condensation. Late dividers have a dumbbell-shaped macronucleus, while it is divided into two pieces connected by a fibrous strand in very late dividers.

(Fig. 20o, arrow). In late dividers, the bud becomes more distinct due to the body's constriction which occurs in a dorsoventral gradient (Figs 20p, q). Slightly before separation, the daughter cells are connected with the broadly rounded posterior end of the proter and the developing oral opening of the opisthe (Figs 20i–k, q). Very early post-divisional opisthes have a characteristic triangular shape because the parental acute posterior body third is maintained and the proboscis extends along the anterior body end hardly projecting dorsally, resembling the oral bulge of "polar" haptorids (Fig. 21j). Late opisthe post-dividers have a considerably shorter proboscis (50 μm vs. 94 μm) and a shorter (170 μm vs. 280 μm) and stouter body (4.0:1 vs. 5.9:1) than morphostatic cells. Thus, post-divisional development is associated with intense growth and stretching of the proboscis, first providing the body with a spatulate (Fig. 21a) and then with a dileptid appearance (Figs 21k–m). In contrast, post-divisional proters are rather similar to morphostatic specimens because no changes occur in the parental oral apparatus, the somatic ciliature, and the dorsal brush. However, they are easily distinguished from morphostatic cells by the broadly rounded posterior end (vs. acute posterior third; Figs 21f–i). Further, they differ from morphostatic cells by the shorter (~ 208 μm vs. 280 μm) and stouter body (4.4:1 vs. 5.9:1) as well as by the proportion of body and proboscis length (46% vs. 34%), while the length of the proboscis (95 μm vs. 94 μm) is quite similar (Table 3). Thus, the proter post-divisional development is associated mainly with intense growth and patterning of the trunk.

Stomatogenesis. Stomatogenesis of dileptids includes three main processes: the production of the circumoral and perioral kinety as well as of the preoral kineties. The anarchic fields, which will become circumoral kinetofragments, are generated in all somatic kineties during the first round of basal body proliferation, while the perioral and preoral kinetofragments are formed during the second round which occurs only in the right lateral and dorsal kineties, respectively (Fig. 23c).

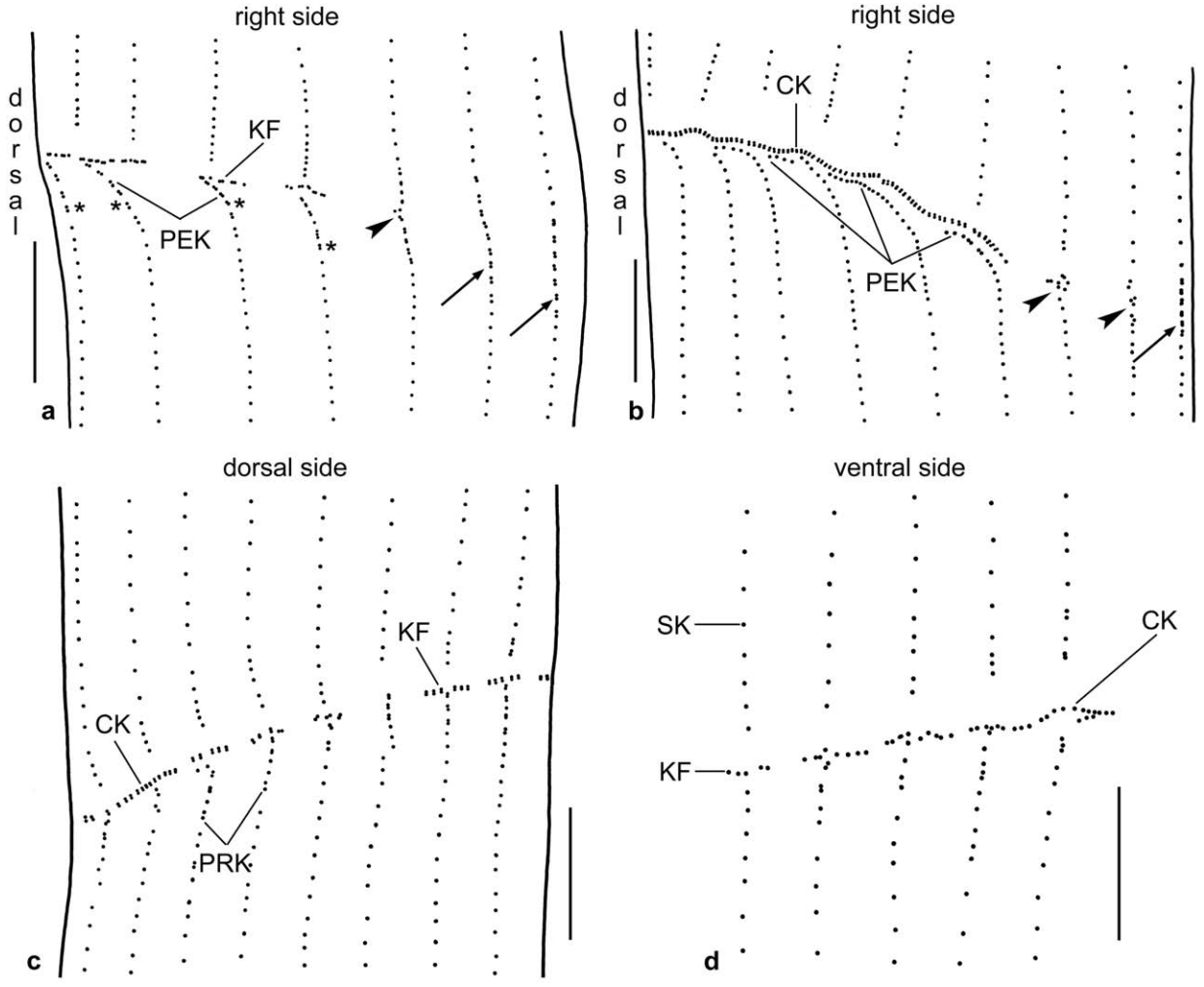
Development of circumoral kinety and oral basket. Division commences with the production of basal bodies in the dorsal kineties slightly posterior to mid-body, making the proter longer than the opisthe by a ratio of 1.3:1 (Table 3). Later on, proliferation of basal bodies commences in the ventral kineties slightly posterior to the level of the dorsal region, resulting in a slightly oblique division furrow (Figs 20a, b). The newly produced basal bodies form minute anarchic fields following a dorso-ventral gradient (Figs 20a, b, arrowheads); then they arrange transversely to the main body axis (Figs 20a, c), forming short circumoral kinetofragments which grow and unite with the fragments from the other kineties to generate the circumoral kinety (Figs 20a–c). Interestingly, the circumoral kinetofragments originating from the right and left as well as the dorsal kineties are composed of dikinetids (Figs 20a–c), while those produced by the ventral kineties consist of monokinetids (Fig. 20d). This peculiarity leads to the composite character of the circumoral kinety: oral dikinetids in the proboscis, while oralized somatic monokinetids around the oral opening.

The new oral opening and oral basket become distinct in late dividers. The nematodesmata of the external basket originate exclusively from the basal bodies of the monokinetidal part of the circumoral kinety, while the rods of the internal basket, which is possibly formed by transverse microtubule arrays originating from the oralized somatic monokinetids, seem to be embedded in the cytoplasm surrounding the developing oral opening (Figs 20i–k).

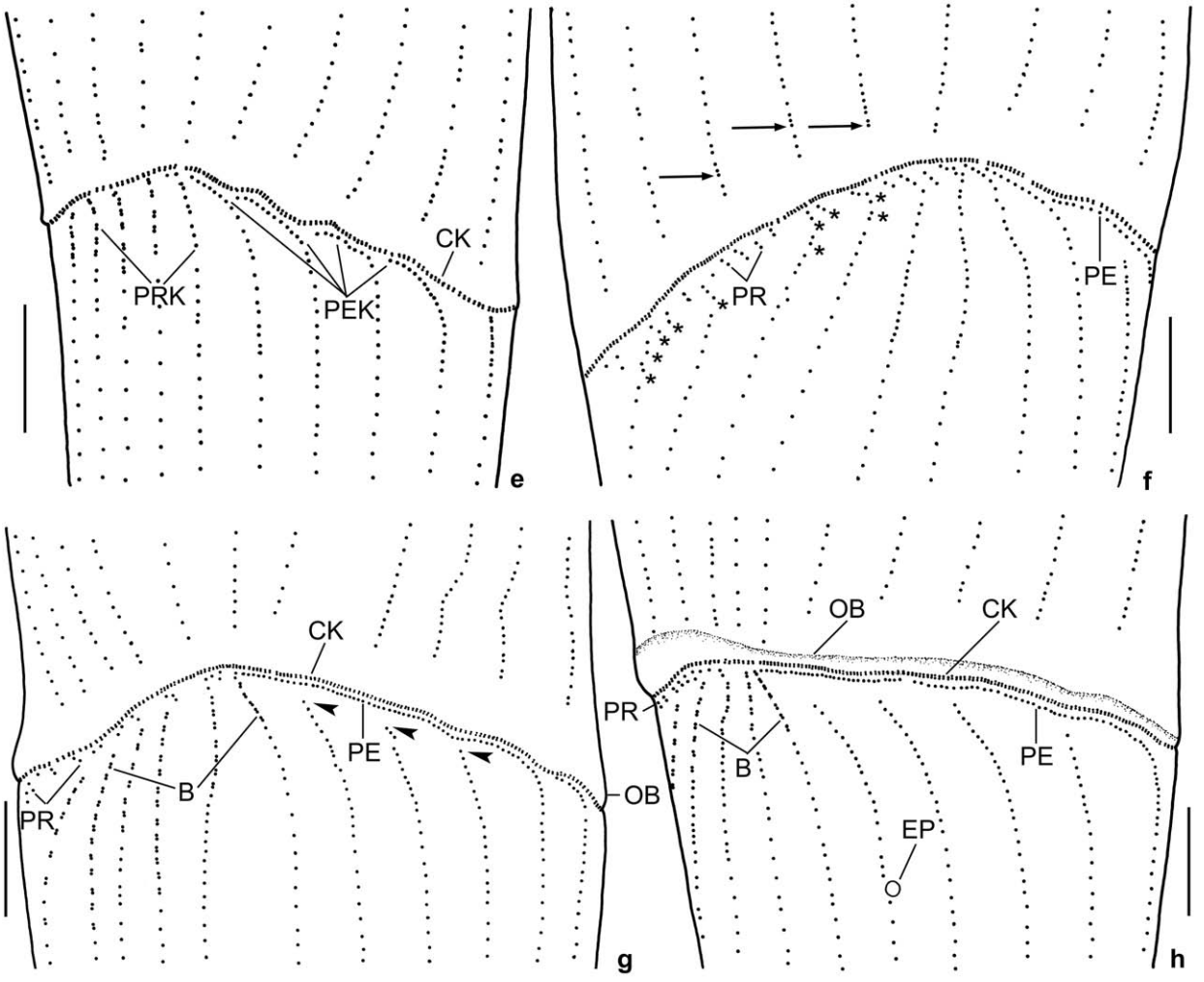
Development of perioral kinety. On the right side, the anterior portion of about seven opisthe ciliary rows elongates by a second round of basal body proliferation (Fig. 20a, asterisks) and curves dorsally along the growing circumoral kinetofragments (Figs 20b, e). Later on, the curved portions detach from the ciliary rows – except for the ventralmost ciliary row which is thus continuous with the perioral kinety in morphostatic specimens – and fuse to a continuous perioral kinety with narrowly spaced basal bodies (Figs 20g, h, j). This process begins in mid-dividers (specimens with condensed macronucleus) and is

completed in very late dividers or post-divisionally, as evident from small irregularities and/or ciliary rows still connected to the new perioral kinety (Fig. 21a, arrowheads). In post-dividers, the perioral kinety elongates concomitantly with proboscis growth by intrakinetal proliferation of basal bodies.

Development of preoral kineties. During the second round of basal body proliferation, rather long preoral kinetofragments are produced in the anterior portion of about six dorsal kineties (Fig. 20e). In mid-dividers, the individual kinetofragments split into about four minute portions, each consisting of two to three kinetids, which migrate rightwards to form the preoral kineties (Fig. 20f, asterisks). Taking the averages of split short rows (4) and the ciliary rows producing fragments (6), there are about 24 preoral kineties, which is half the number found in morphostatic cells (Table 3). Thus, half of the preoral kineties



Figs 20a-d: *Monomacrocaryon terrenum*, ciliary pattern of early dividers after protargol impregnation (from Vďačný & Foissner 2009). **a, b** – right side views, showing intrakinetal proliferation of basal bodies in the lateral kineties (arrows), following a dorso-ventral gradient. The new oral dikinetids form minute anarchic fields (arrowheads) which develop to kinetofragments producing the circumoral kinety. A second round of basal body production in the anterior region of the opisthe's right side kineties generates the monokinetidal perioral kinetofragments. During this process, dikinetid-like kinetids are recognizable (asterisks) which, however, are just divided basal bodies. The productive portion, where basal bodies become very narrowly spaced, curves dorsally (b) and separates from the ciliary rows to form the perioral kinety (see Figs 20e and 20g); **c, d** – the oral kinetofragments are dikinetidal on the dorsal side, while monokinetidal on the ventral side; they are arranged transversely to the opisthe's ciliary rows, forming a T-shaped pattern. CK – circumoral kinety, KF – circumoral kinetofragments, PEK – perioral kinetofragments, PRK – preoral kinetofragments, SK – somatic kinety. Scale bars: 10 μm.



Figs 20e-h: *Monomacrocaryon terrenum*, ciliary pattern of mid-dividers after protargol impregnation (from Vďačný & Foissner 2009). **e** – dorsal view of an early mid-divider, showing production of preoral kinetofragments in five dorsal ciliary rows. Like the perioral kinetofragments, they are generated by a second round of basal body production. During this process, dikinetid-like kinetids become recognizable caused, however, by just divided basal bodies (monokinetids); **f** – mid-divider patterning preoral kineties: the individual preoral kinetofragments split into about four preoral kineties that migrate rightwards along the circumoral kinety (asterisks). Arrows mark intrakinetal proliferation of somatic kinetids, producing typical triads; **g** – a third round of basal body proliferation occurs on the dorsal side after the production of the preoral kineties and produces the multi-rowed dorsal brush. Arrowheads mark sites where the curved anterior portion of the opisthe's right side ciliary rows detached and fused to the new perioral kinety (cp. Fig. 20e); **h** – late mid-divider with developing oral bulge. The preoral kineties are arranged almost perpendicularly to the new circumoral kinety. B – dorsal brush, CK – circumoral kinety, EP – excretory pore of a contractile vacuole, OB – oral bulge, PE – perioral kinety, PEK – perioral kinetofragments, PR – preoral kineties, PRK – preoral kinetofragments. Scale bars: 10 μm.

are generated post-divisionally during growth of the proboscis, possibly by proliferation of the existing preoral kineties or by migrating kinetids from the anterior end of those somatic kineties which terminate at the base of the proboscis (Fig. 21e).

Development of somatic ciliature and dorsal brush. The mature ciliary pattern of dileptids develops post-divisionally and includes three specific processes in middle-sized and large species: (1) the formation of a suture along the right branch of the circumoral kinety; (2) the formation of a barren stripe along the left branch of the circumoral kinety; and (3) the formation of a staggered dorsal brush. The two first

peculiarities may be inconspicuous or even absent in small species with less than 10 ciliary rows (see *Pseudomonilicaryon brachyproboscis*).

The formation of the right side suture occurs in that only the more dorsally located kineties extend to the tip of the proboscis, while the more ventrally extending kineties are gradually shortened (Figs 21a, b asterisks). The barren stripe along the left branch of the circumoral kinety originates in a similar way, i.e., some kineties left of the oral opening do not elongate (Fig. 23a).

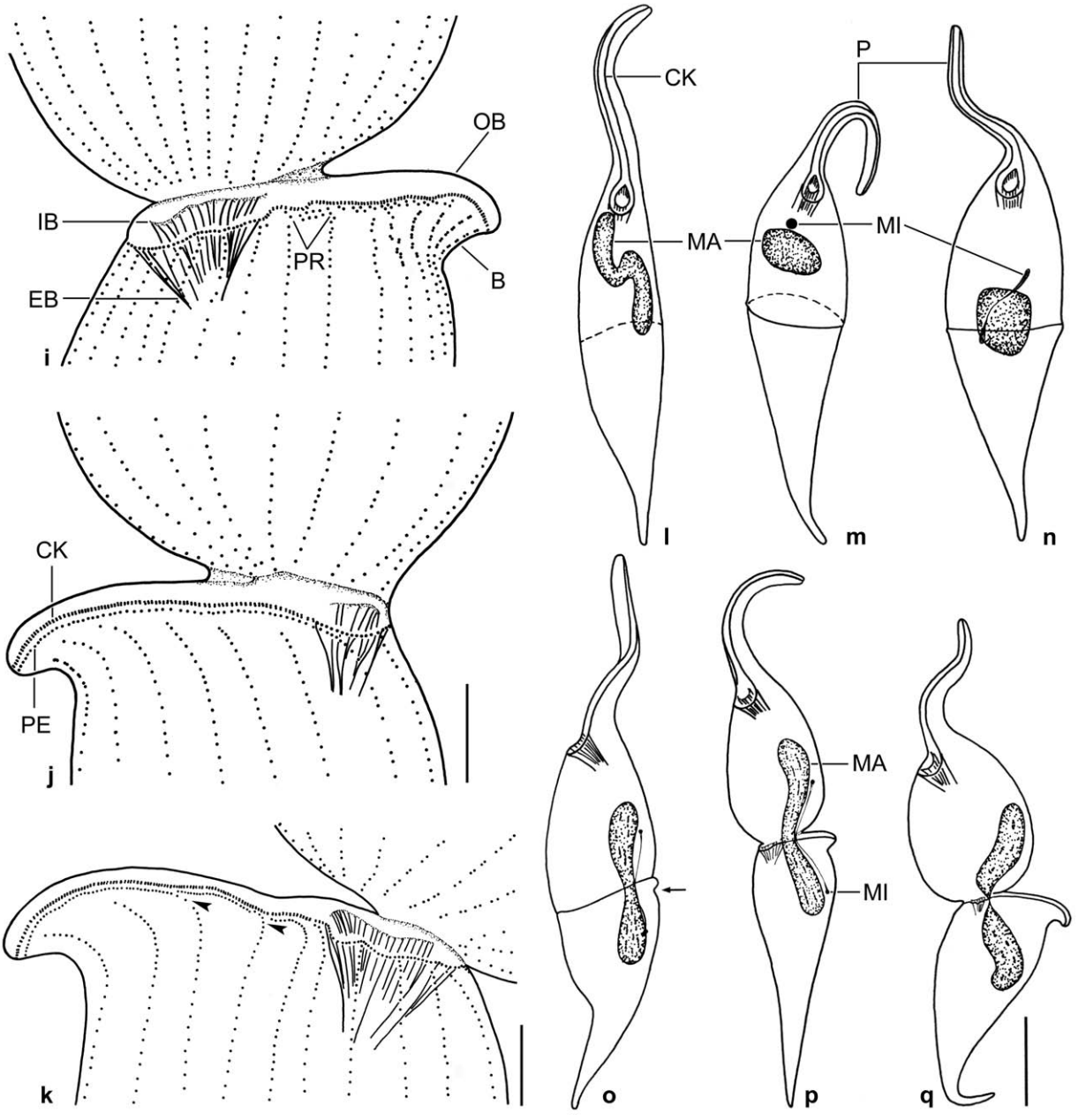
The formation of the dorsal brush and the staggered arrangement of the brush rows is a complex process. In late mid-dividers, a third round of basal body proliferation produces the dikinetidal dorsal brush. This is an intense process which occurs in the six or seven dorsal ciliary rows that have produced the preoral kineties (Figs 20g, h). Initially, all brush rows abut to the newly formed preoral kineties and thus do not have a staggered pattern (Fig. 20h). In this stage, the opisthe's dorsal brush occupies a rather large, convex area because the interkinetal distance between the brush rows is only slightly smaller than that between ordinary ciliary rows (Figs 20g, h). In late dividers and post-dividers, the elongation of the proboscis causes a decrease of the interkinetal distances (Fig. 20i) and the staggered pattern of the brush rows in that the rows gradually elongate from ventral to dorsal (Figs 21c–e). A distinct increase of the number of brush dikinetids occurs only in late post-dividers, where basal bodies with short bristles and non-ciliated dikinetids appear in the posterior region of the brush (Figs 21c, d). Now, the entire dorsal surface of the proboscis is covered with brush kinetids and the number of dikinetids increases from an average of 34 (n = 4) in early post-dividers to 56 in morphostatic cells (Table 3).

Nuclear division. In very early dividers, the macronucleus is still highly similar to that of morphostatic cells, i.e., it is cylindroidal, more or less curved, and 84 µm long on average (Table 3). Later on, the macronucleus elongates to an average length of 100 µm and becomes S- or U-shaped (Fig. 20l). In mid-dividers, the macronucleus condenses to a globular, homogenously impregnated mass about 50 µm across (Figs 20m, n). When the proboscis bud appears, the macronucleus begins to divide, becoming dumbbell-shaped (Fig. 20o). Then, the dividing macronucleus extends to a long rod constricting in the fission area (Fig. 20p). When cell fission is finishing, the macronucleus is divided into two oblong pieces connected with their pointed ends (Fig. 20q). After cell fission, the macronucleus elongates and migrates to mid-body (Figs 21f–m).

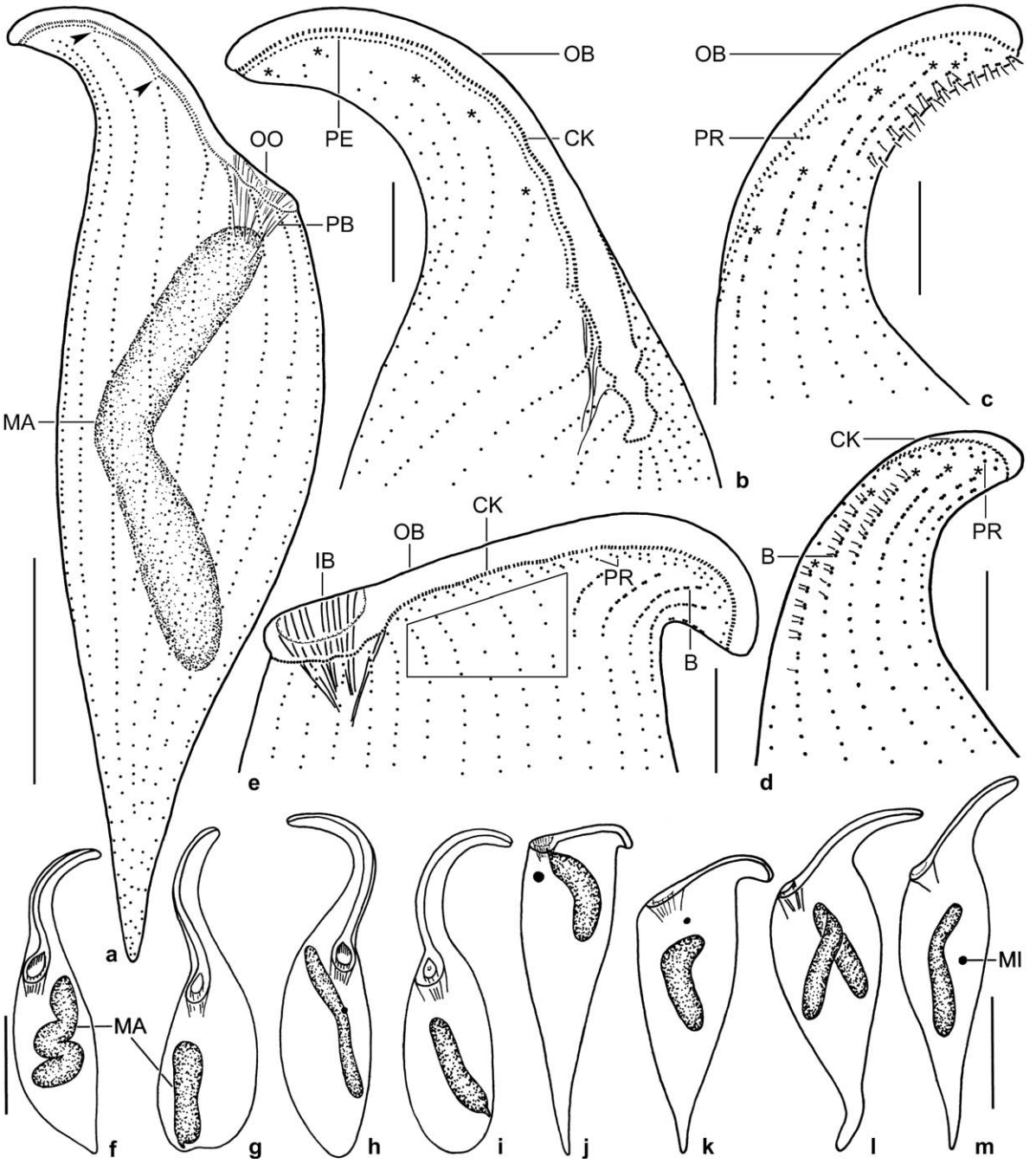
During the first stages of ontogenesis, the micronucleus increases in size from an average of 3.6 µm to 6.3 µm (Table 3). When the macronucleus is condensed to a globular mass, the micronucleus begins to divide becoming dumbbell-shaped, with the narrowly cuneate halves connected by a fibre bundle (Fig. 20n). Later on, the bundle conspicuously elongates and the daughter's micronuclei become globular and homogenously impregnated (Fig. 20o). In very late dividers, the micronuclei achieve the species-specific size (4 µm across), but are still connected by a long fibre (Fig. 20p). During post-divisional cell growth, the micronucleus moves to mid-macronucleus (Figs 21h, j, k, m).

In *Dileptus margaritifer*, the macronuclear nodules divide individually, showing longitudinally oriented microtubules that penetrate the nucleolus, which disintegrates into long strains. The macronuclear membrane remains intact (Vinnikova 1974c).

Dileptid division mode. The ontogenesis of *Monomacrocaryon terrenum* basically agrees with data from other dileptids, all displaying the following events: (i) cell division occurs in active (non-encysted) condition; (ii) the macronucleus is homomeric; (iii) stomatogenesis is holotelokinetal (all ciliary rows produce kinetofragments) and the parental oral apparatus does not reorganize; (iv) small anarchic fields are formed on the top of the broken ciliary rows and develop into circumoral kinetofragments growing and uniting to the circumoral kinety; (v) the perioral kinety is formed by the alignment of the densely ciliated anterior region of the right side ciliary rows; (vi) the preoral kineties are produced by splitting of the

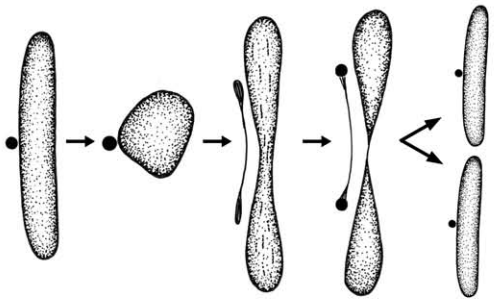


Figs 20i-q: *Monomacrocaryon terrenum*, ciliary pattern of very late dividers (i-k) and body as well as nuclear changes in an early divider (l), mid-dividers (m, n), and late dividers (o-q) after protargol impregnation (from Vďačný & Foissner 2009). **i, j** – left and right side view of a late divider, showing the only slightly projecting proboscis and the developing oral basket as well as oral opening. The nematodesmata of the external basket originate exclusively from the basal bodies of the monokinetidal part of the circumoral kinety, while the rods of the internal basket seem to be embedded in the cytoplasm surrounding the developing oral opening; **k** – right side view of a very late divider. The proboscis becomes more distinct due to the body's constriction, which occurs in a dorsoventral gradient. Arrowheads mark sites where the densely ciliated anterior portion of the opisthe's right side ciliary rows curves dorsally and will detach to contribute to the perioral kinety; **l** – ventral view of an early divider, showing the elongating macronucleus which becomes S-shaped; **m, n** – ventral views of mid-dividers with condensed macronucleus and dividing micronucleus; **o-q** – lateral views of late and very late dividers, showing division of macronucleus and micronucleus. Arrow denotes proboscis bud; B – dorsal brush, CK – circumoral kinety, IB – internal basket, EB – external basket, MA – macronucleus, MI – micronucleus, OB – oral bulge, P – proboscis, PE – perioral kinety, PR – preoral kineties. Scale bars: 10 μm (i-k) and 50 μm (l-q).



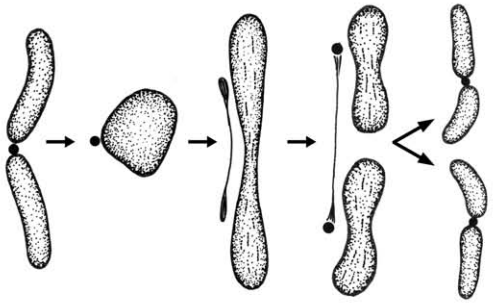
Figs 21a-m: *Monomacrocaryon terrenum*, post-dividers after protargol impregnation (from Vďačný & Foissner 2009). **a** – right side view of ciliary pattern and nuclear apparatus of an opisthe post-divider. Arrowheads denote small irregularities in the new perioral kinety; **b** – ventrolateral view of a specimen with spathidiid circumoral kinety. Asterisks mark gradually shortened right side somatic kineties; **c, d** – dorsolateral views of proboscis, showing staggered dorsal brush rows (asterisks); **e** – left side view of anterior body portion of a very early opisthe post-divider. The region, where new preoral kineties are possibly produced post-divisionally, is framed by an irregular quadrilateral; **f-m** – genesis of body shape and nuclear apparatus in proter (f-i) and opisthe (j-m) post-dividers. Drawn to scale. B – dorsal brush, CK – circumoral kinety, IB – internal basket, MA – macronucleus, MI – micronucleus, OB – oral bulge, OO – oral opening, PB – pharyngeal basket, PE – perioral kinety, PR – preoral kineties. Scale bars: 10 µm (b-e), 30 µm (a), and 50 µm (f-m).

***Monomacrocaryon* mode**



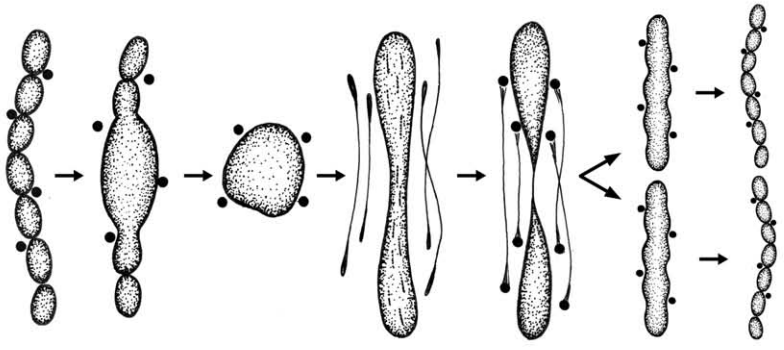
In mid-dividers, the macronucleus condenses to a globular mass that divides once, becoming a rod constricted in the mid. When cell division is finishing, the macronucleus is divided into two pieces.

***Monomacrocaryon* mode - binucleate dileptids**



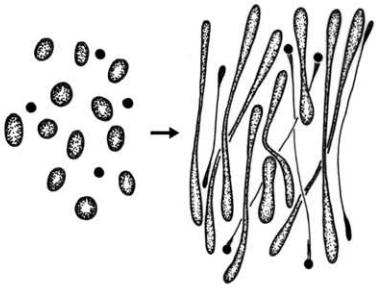
The two macronuclear nodules fuse to a globular mass that divides twice, generating two nodules each in proter and in in opisthe.

***Monomacrocaryon* mode - dileptids with moniliform macronucleus**



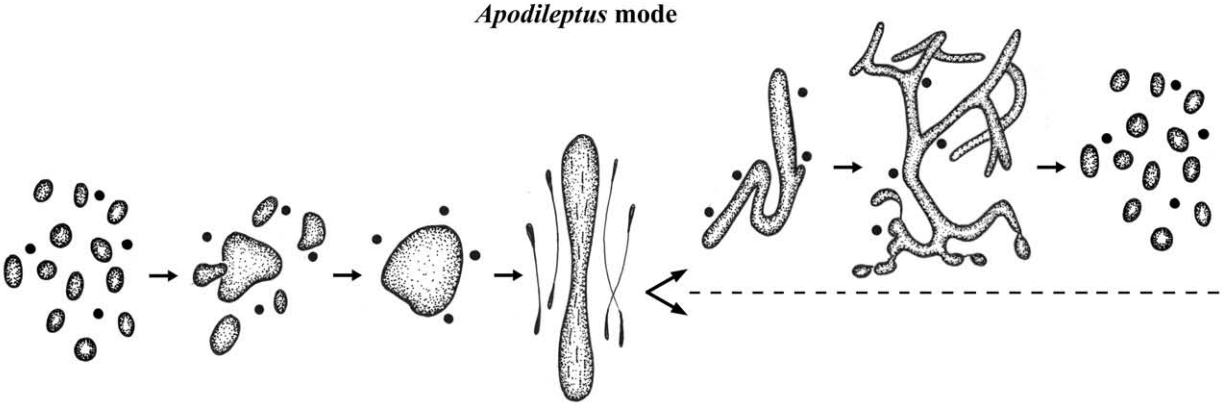
In early dividers, the nodules begin to fuse, usually in mid-portion of the macronuclear chain. In mid-dividers, all nodules have fused to a globular mass that becomes dumbell-shaped. Later, the macronucleus divides into two pieces. In post-dividers, the pieces elongate and become nodulated as typical for the individual species.

***Dileptus* mode**



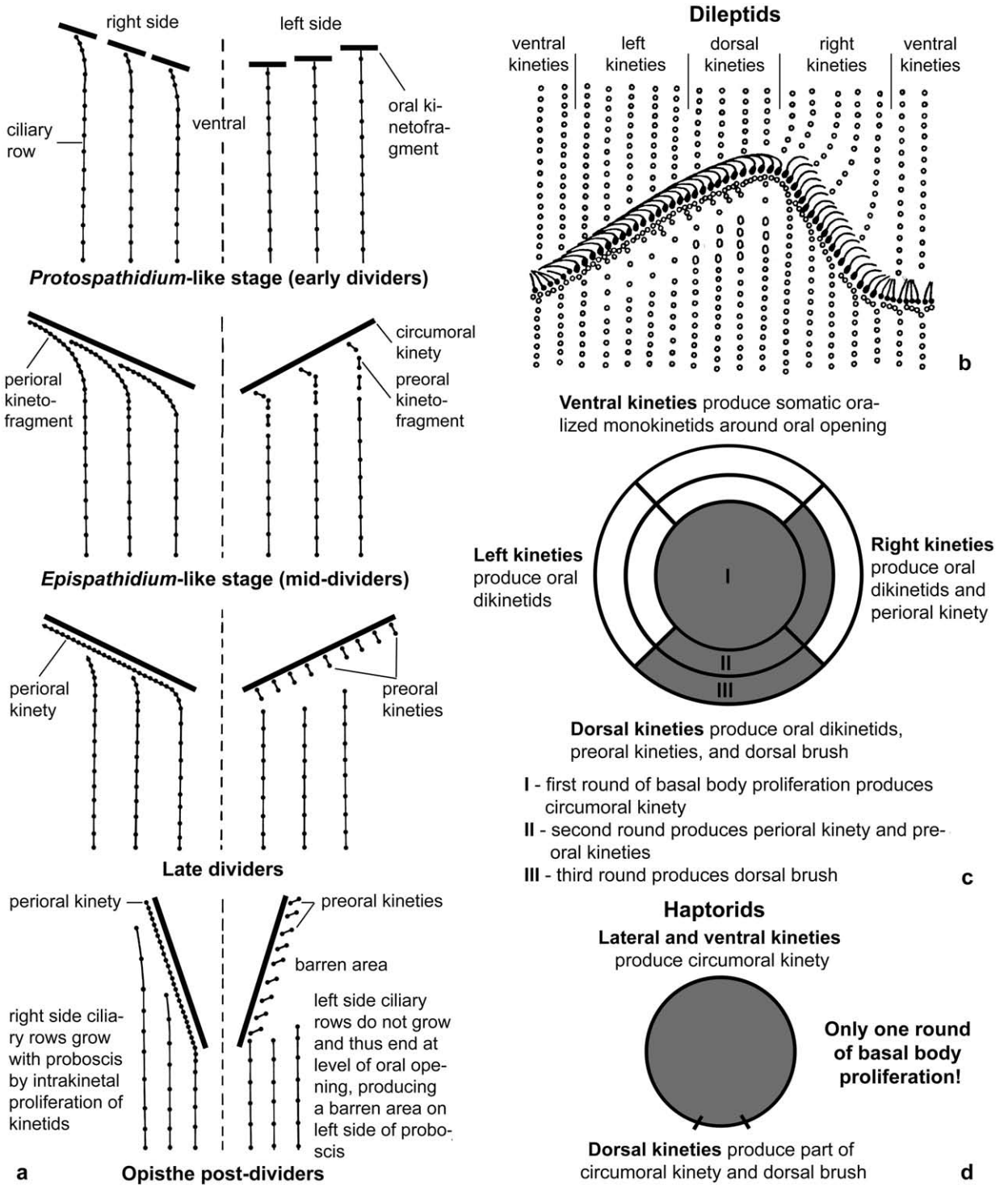
In the multinucleate genus *Dileptus*, each nodule divides individually.

***Apodileptus* mode**



In mid-dividers, the scattered macronuclear nodules fuse to a globular mass dividing into two pieces. In post-dividers, each piece becomes a short strand which develops to a three-dimensional reticulum that eventually fragments into many nodules.

Fig. 22: Division modes of macronucleus in dileptids.



Figs 23a–d: Ontogenesis of ciliary pattern in dileptids (a–c) and haptorids (d). From Golińska 1995 (b) and Vďačný & Foissner 2009 (a, c, d). **a** – schematic presentation of the formation of the dileptid ciliary pattern from a *Protospathidium*-like stage in early dividers via an *Epispathidium*-like stage in mid-dividers; **b–d** – defining ventral, lateral, and dorsal ciliary rows according to their ontogenetic activities in dileptids (b, c) and haptorids (d) in general. There are three rounds of basal body proliferation in dileptids, while only one round in haptorids. The active regions are shaded gray.

anterior region of the dorsal ciliary rows into several minute portions which migrate rightwards along the circumoral kinety; (vii) the dorsal brush develops very late, i.e., after the production of the preoral kineties in late mid-dividers; and (viii) the proboscis basically matures post-divisionally.

Some variation occurs in the dileptid division, just as in spathidiids (Foissner & Xu 2007). Main deviations comprise: (i) the presence/absence of a transient indentation in the prospective fission area (present in *Pseudomonilicaryon brachyproboscis*, absent in *Monomacrocaryon terrenum*); (ii) the presence/absence of macronucleus condensation in mid-dividers (the nodules fuse to a mass in *P. brachyproboscis*, while they divide individually, for instance, in *Dileptus jonesi*); and (iii) size and shape changes of the micronucleus during early division (the micronucleus shows a two-fold size increase but no shape changes in *M. terrenum*, while it becomes globular due to width increase in *P. brachyproboscis*). For further details on modes of nuclear division in dileptids, see Fig. 22.

Comparative ontogenesis. Ontogenesis of dileptids is much more complex than in other litostomateans, displaying many peculiarities and reaching a complexity comparable to that found in "higher" ciliates. A most interesting feature is the three rounds of basal body proliferation, while the majority of ciliates displays usually only one round (Figs 23c, d; Foissner 1996a). In dileptids, the circumoral kinetofragments are formed via small anlagen fields (Golińska 1995, Vďačný & Foissner 2009), a widespread mode among ciliates but as yet not found in other litostomateans (Foissner 1996a). Further, the circumoral kinetofragments of dileptids are transversely arranged from the beginning of their formation, while they are longitudinally oriented when formed and then rotate clockwise to become horizontally arranged in spathidiids (Foissner & Xu 2007). Interestingly, a similar process occurs during the formation of the perioral kinety. A further peculiarity of *Dileptus* ontogenesis is the complex genesis of the circumoral kinety: the ventral kinetofragments are composed of oralized somatic monokinetids, while the kinetofragments originating from lateral and dorsal kineties are composed of oral dikinetids (Golińska 1995, Vďačný & Foissner 2009). On the other hand, the circumoral kinetofragments of ordinary haptorids are exclusively dikinetidal (Foissner 1996a), except for the Enchelyina which lack oral dikinetids at all (Foissner & Foissner 1988a). Unlike all haptorids investigated so far (Berger et al. 1983, Foissner 1996a, Foissner & Xu 2007), dileptids develop the dorsal brush as the last ciliary structure, that is, in late mid-dividers.

At first glance, the complex ontogenesis of dileptids appears to be caused by the proboscis. However, two observations suggest that this is only part of the truth, viz., the unique formation of the circumoral kinetofragments and the late genesis of the dorsal brush. Both peculiarities are obviously independent of spatial constraints and the presence/absence of a proboscis.

2.2 Sexual cycle

2.2.1 Serotypes

Recent molecular studies suggest a rapid diversification of mating systems in ciliates (Phadke & Zufall 2009). There are three mating types in *Dileptus margaritifer*. Each type secrets its own gamons into the cultural medium (Afon'kin & Yudin 1986). Detailed investigations showed a non-Mendelian inheritance, suggesting that serotypes are under epigenetic control (Yudin & Uspenskaya 2000, 2002).

Afon'kin (1991) made an interesting study on cell-cell recognition in *Dileptus*. Thus, we cite the summary literally: "The number of homo- and heterotypic pairs marked with Chinese ink was registered during conjugation of complementary clones of *D. margaritifer*. For each mating type both homo- and heterotypic pairs were studied. At the early stage of the process, i.e., two hours after the mixing of the clones, all three types of pairs (two homotypic and one heterotypic) were present in the mixture, their ratio being approximately 1:2:1. Five to six hours after beginning the experiment heterotypic pairs predominated

in the mixtures. The homotypic pairs were formed in great number in mixtures of clones where one of the mating types was represented by only a few cells, but they disintegrated later. It is suggested that the formation of pairs is due to the expression of mating-type nonspecific adhesive molecules on the cell surface. The complementary cells in pairs are assumed to continue to stimulate the expression of the adhesines with their mating pheromones. The fact that heterotypic pairs appear to be more stable than homotypic ones is ascribed to this hypothesis. The stimulation of expression of the hypothetical mating-type nonspecific adhesines with heterotypic mating pheromones may be regarded as a mechanism that prevents inbreeding in ciliates."

2.2.2 Conjugation

HERTWIG (1904) and VISSCHER (1927) provided pioneer data on the conjugation of *Dileptus margaritifer* (misidentified as *D. gigas*). Later, VINNIKOVA (1974a, 1976) and GOLIŃSKA & AFON'KIN (1993) studied

Table 4: Comparison of main conjugation events in dileptids (from VĎAČNÝ & FOISSNER 2008a).

Characteristics	***Rimaleptus tirjakovae*** **(VĎAČNÝ & FOISSNER 2008a)**	***Dileptus margaritifer*** **(VINNIKOVA 1974a)**	***Dileptus margaritifer*** **(VISSCHER 1927)**
Early conjugants, length	distinctly shorter than vegetative cells (105 µm vs. 210 µm)	slightly shorter than vegetative cells (130 µm vs. 160 µm)[a]	distinctly shorter than vegetative cells (175 µm vs. 400 µm)
Early conjugants, number of ciliary rows	less than vegetative cells (13 vs. 21)	not known	not known
Conjugational division	probably no	may occur	no
Type of conjugation	heteropolar and temporary	heteropolar and temporary	heteropolar and temporary
Union mode	dorsal-to-ventral	dorsal-to-ventral	dorsal-to-ventral
Body becomes shorter and stouter, and proboscis shortens immensely	yes	yes	yes
Ciliary changes	distinct	distinct[b]	not known
Micronuclei undergoing maturation divisions, number	1	almost all	only one of the many
Maturation divisions, number	3	3	3
Differences between pronuclei	slightly different in size	different in size and shape	no differences
Synkaryon divisions, number	2	1–4 (2)[c]	3 (4)[d]
Macronuclear anlagen, number	2	1–11 (4)[c]	4 (4)[d]
New micronuclei, number	1	1–4 (1)[c]	4
Degenerating synkaryon derivatives, number	1	0	0
Pair separation	after formation of macronuclear anlagen	after formation of macronuclear anlagen[e]	after formation of synkaryon

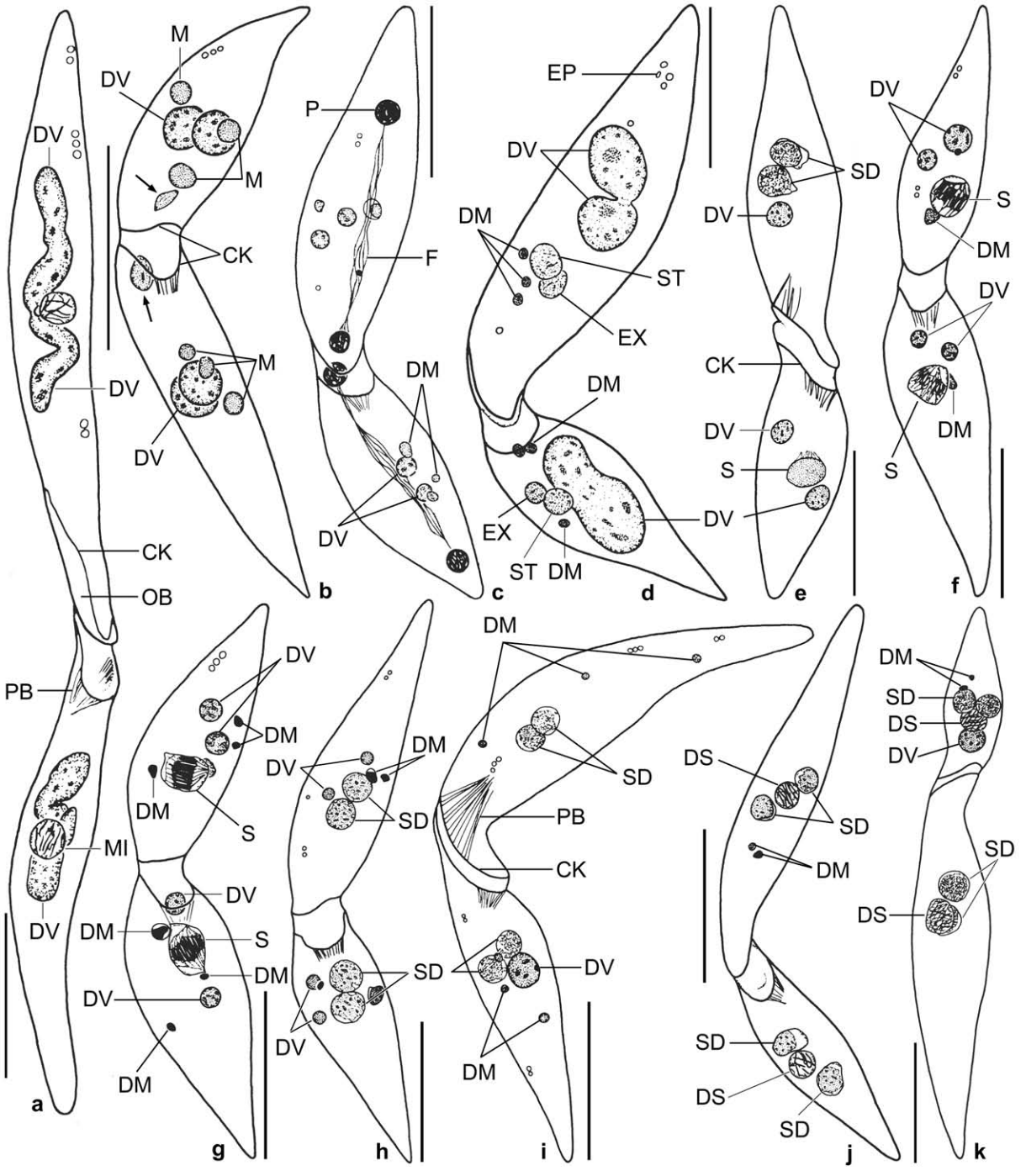
[a] Length of the cells measured without the proboscis.

[b] This is sustained by observations of GOLIŃSKA & AFON'KIN (1993).

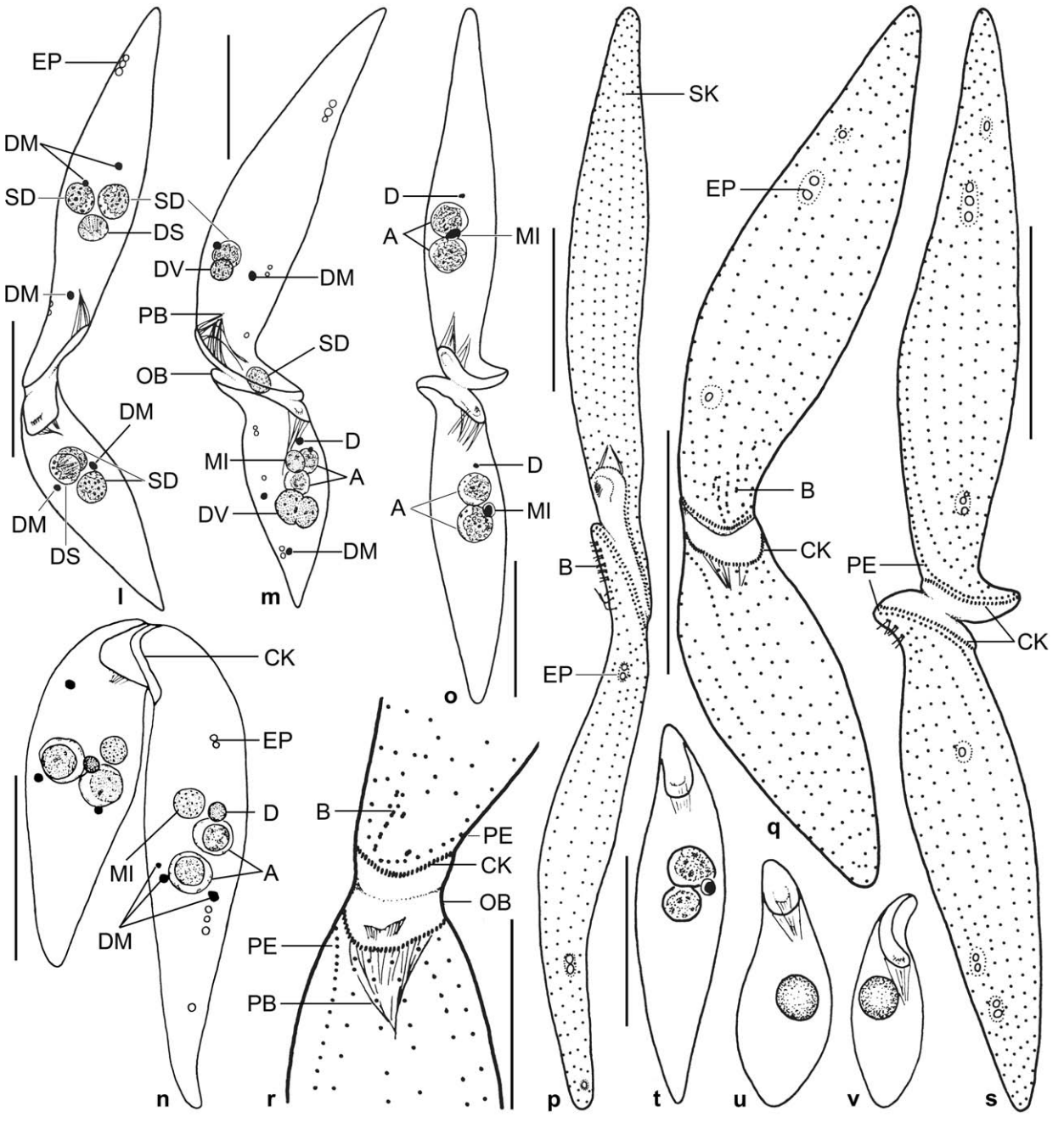
[c] Numbers in brackets indicate the most commonly found number.

[d] Numbers in brackets are according to HERTWIG (1904).

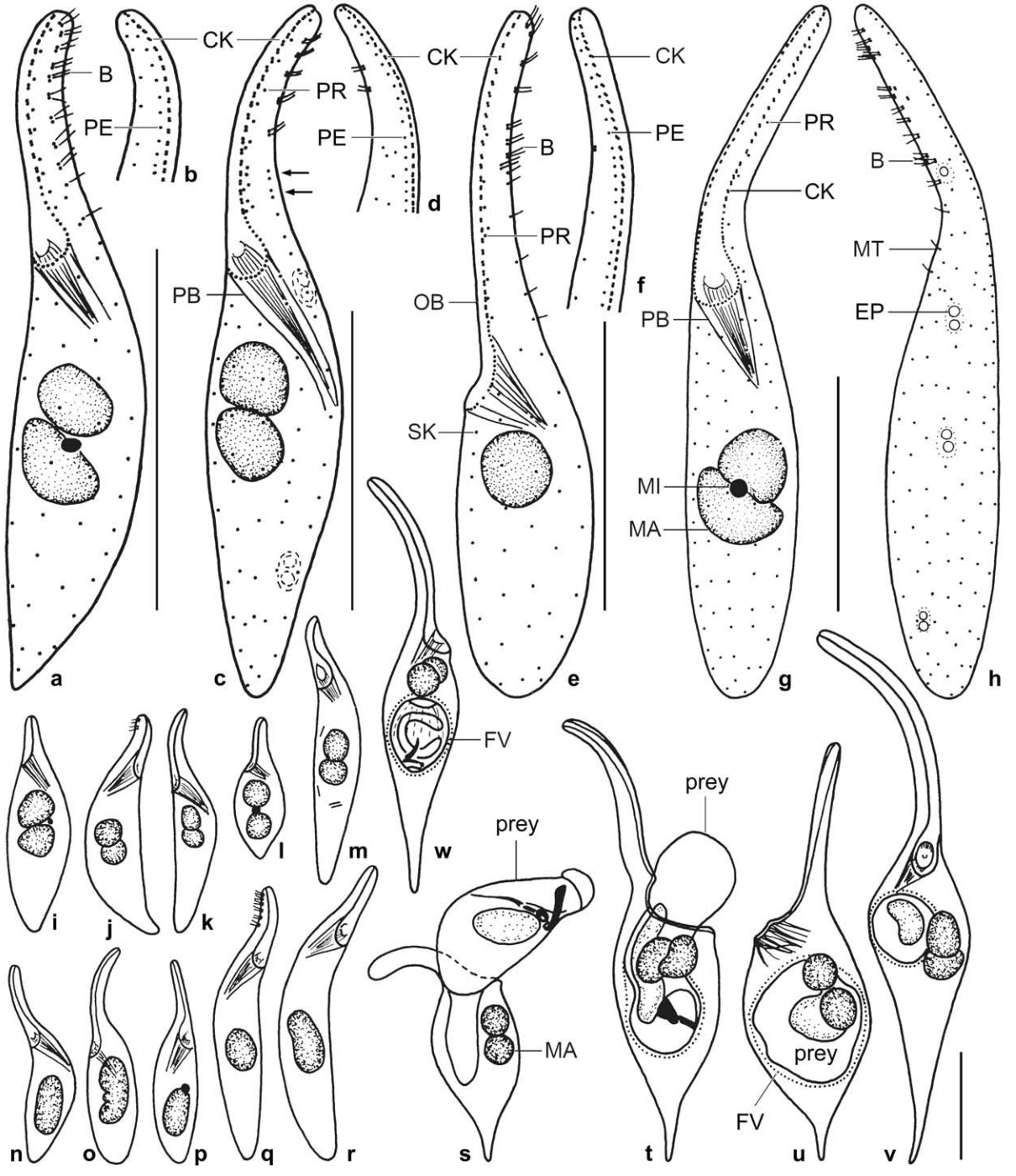
[e] Conjugants separate usually about 24 h after the onset of conjugation.



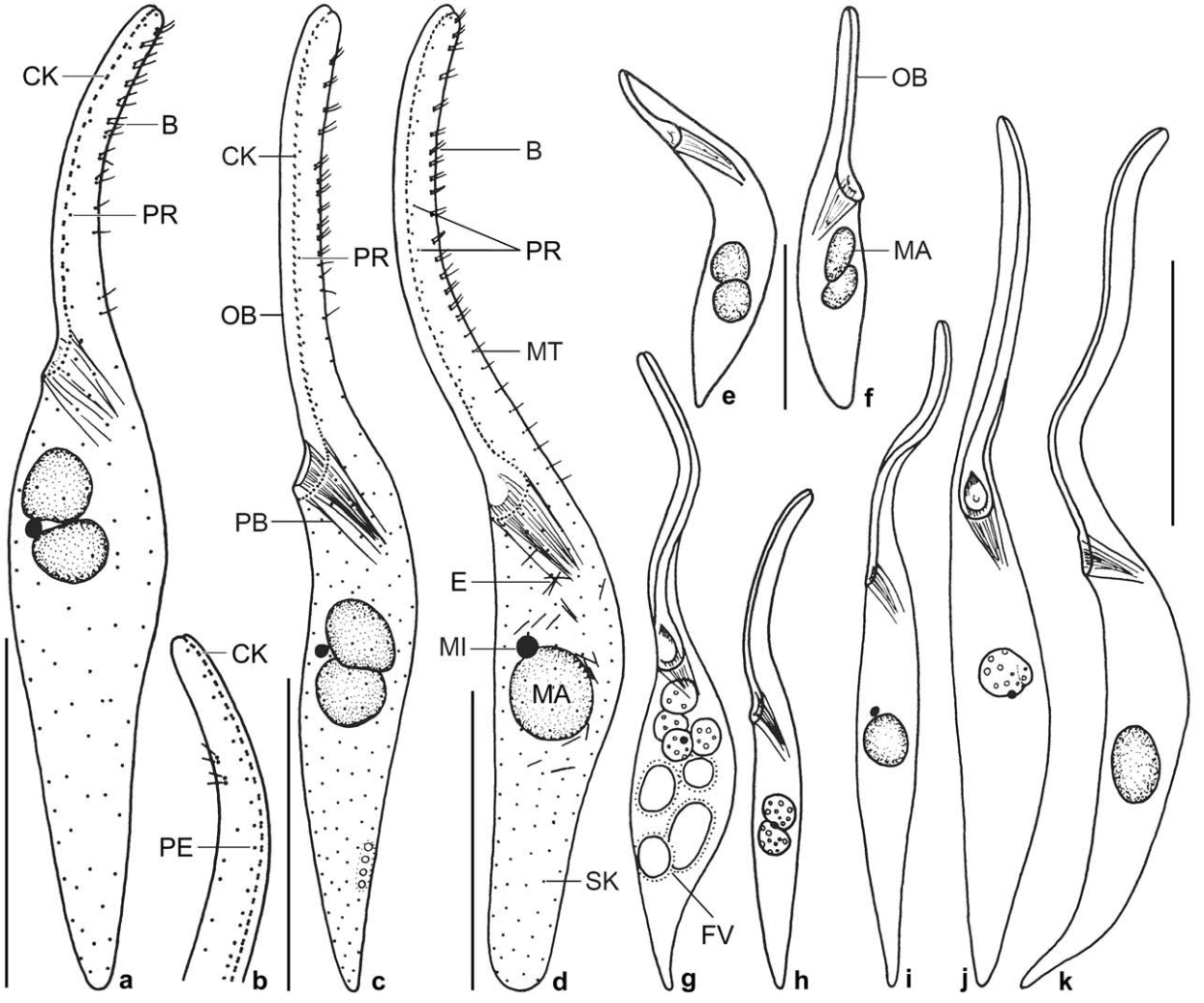
Figs 24a-k: *Rimaleptus tirjakovae*, protargol-impregnated conjugants (from VĎAČNÝ & FOISSNER 2008a). **a** – very early stage; **b** – prophase of third maturation division (arrows); **c** – telophase of third maturation division; **d** – conjugants after exchange of pronuclei; **e** – synkaryon in the shorter partner and derivatives of the first synkaryon division in the longer partner; **f, g** – metaphase of first synkaryon division; **h, i** – the two derivatives of the first synkaryon division; **j, k** – prophase of second synkaryon division. CK – circumoral kinety, DM – degenerating maturation derivatives, DS – dividing synkaryon derivatives, DV – degenerating vegetative macronucleus, EP – excretory pores, EX – exchanged pronucleus, F – fibres of division spindle, M – maturation derivatives, OB – oral bulge, P – pronucleus, PB – pharyngeal basket, S – synkaryon, SD – synkaryon derivatives, ST – stationary pronucleus. Scale bars: 30 μm.



Figs 24l-v: *Rimaleptus tirjakovae*, protargol-impregnated conjugants (l-s) and exconjugants (t-v). From Vďačný & Foissner (2008a). **l** – prophase of second synkaryon division. The individual synkaryon derivatives are about 7 µm across and are covered by a distinct membrane slightly separated from the nucleoplasm, which contains many faintly impregnated granules; **m** – derivatives of the first synkaryon division in the longer partner and derivatives of the second synkaryon division in the shorter partner; **n** – derivatives of second synkaryon division; **o** – very late stage. Two synkaryon derivatives become macronuclear anlagen, one differentiates into the micronucleus, and the last degenerates; **p**-**s** – ciliary pattern of the specimens shown in (a, c, f, o), i.e., of a very early conjugant (p), mid-conjugants (q, r), and a very late conjugant (s); **t-v** – very early exconjugants, as shown by the small and stout body. Drawn to scale. A – macronuclear anlagen, B – dorsal brush, CK – circumoral kinety, D – degenerating synkaryon derivatives, DM – degenerating maturation derivatives, DS – dividing synkaryon derivatives, DV – degenerating vegetative macronucleus, EP – excretory pores of a contractile vacuole, MI – micronucleus, OB – oral bulge, PB – pharyngeal basket, PE – perioral kinety, SD – synkaryon derivatives, SK – somatic kinety. Scale bars: 30 µm.



Figs 25a-w: *Rimaleptus tirjakovae*, protargol-impregnated exconjugants (from VĎAČNÝ & FOISSNER 2008a). **a, c, e** – ciliary pattern of left side and nuclear apparatus of early exconjugants. Arrows mark non-ciliated brush kinetids; **b, d, f** – right side ciliary pattern of the proboscis of the specimens shown in (a, c, e); **g, h** – ciliary pattern of ventral and dorsal side and nuclear apparatus of an exconjugant; **i-r** – early exconjugants with short proboscis. The macronuclear anlagen may fuse, forming a globular or ellipsoidal mass; **s-v** – exconjugants engulfing *Metopus hasei*; **w –** exconjugant having engulfed a peritrich ciliate. B – dorsal brush, CK – circumoral kinety, EP – excretory pores, FV – food vacuole, MA – macronucleus, MI – micronucleus, MT – monokinetidal tail of dorsal brush, OB – oral bulge, PB – pharyngeal basket, PE – perioral kinety, PR – preoral kinety, SK – somatic kinety. Scale bars: 30 μm (i-w); drawn to scale.



Figs 26a-k: *Rimaleptus tirjakovae*, protargol-impregnated exconjugants (from VĎAČNÝ & FOISSNER 2008a). **a, c** – ciliary pattern of left side and nuclear apparatus of late exconjugants. The preoral kinetids form a very lose kinety resembling the right side perioral kinety; **b** – right side ciliary pattern of the proboscis of the specimen shown in (a); **d** – ventrolateral ciliary pattern and nuclear apparatus of a late exconjugant. The definite body shape has been regained but body size is still only half of that in vegetative cells; **e, f** – early exconjugants. Drawn to scale; **g-k** – exconjugant nuclear reconstruction. Macronuclear anlagen may fuse to an ellipsoidal mass or undergo further division yielding four macronuclear anlagen. Drawn to scale. B – dorsal brush, CK – circumoral kinety, E – extrusomes, FV – food vacuoles, MA – macronucleus, MI – micronucleus, MT – monokinetidal tail of dorsal brush, OB – oral bulge, PB – pharyngeal basket, PE – perioral kinety, PR – preoral kineties, SK – somatic kinety. Scale bars: 30 μm (a-f) and 50 μm (g-k).

preparatory changes and nuclear divisions during conjugation of *D. margaritifer* and *Pseudomonilicaryon anser*, using protargol impregnation and TEM. Only very recently, VĎAČNÝ & FOISSNER (2008a) studied cell size and shape, nuclear changes, and the ciliary pattern during and after conjugation of *Rimaleptus tirjakovae*. Their data basically agree with previous ones, especially, in that conjugation is temporary and heteropolar, and partners unite bulge-to-bulge. However, differences occur in the number of micronuclei undergoing maturation, in the number of synkaryon divisions, in the number of macronuclear anlagen, in the number of degenerating synkaryon derivatives, and in pair separation with respect to nuclear development (Table 4). Despite the curious body organization, dileptid conjugation is consistent with some previous observations on didiniid, acaryophryid, and spathidiid haptorians (PRANDTL 1906, SERRANO et al. 1990,

Xu & Foissner 2004). However, dileptids display massive changes in body shape and ciliary pattern, causing early and late conjugants to resemble *Spathidium*, while mid-conjugants resemble *Enchelyodon* or *Protospathidium* (Visscher 1927, Vďačný & Foissner 2008a).

For details on conjugation of *Dileptus margaritifer*, see that species. Conjugation and postconjugational reorganization of *Rimaleptus tirjakovae* are reported here in full length.

Pair formation (Figs 24a, p). Only one pair was in a very early stage of pair formation, showing that the partners are much smaller than vegetative cells (~ 105 × 13 μm vs. 210 × 20 μm). Further, all conjugating specimens possess distinctly fewer ciliary rows (13 vs. 21), suggesting more than one preconjugational division. Whether conjugation is isogamic or anisogamic is difficult to state due to the few pairs available. Obviously, it is isogamic with respect to shape and morphology, while probably anisogamic with respect to size because the average length ratio of the partners is 1.4:1 in the 15 pairs measured.

Pair formation is heteropolar, namely, the partners unite with the ventral side in such a way that the tip of one proboscis is placed on the base of the other (Figs 24a, p). The right side of the unit area of one partner faces the right side of the unit area of the other partner: thus the perioral kineties and the right branch of the circumoral kinety are visible when the specimens are observed in the same focal plane (Figs 24p, s). The union mode is ventral-to-dorsal in terms of the dorsal brush because the brush of only one partner is visible when the pair is observed in the same focal plane (Figs 24q, r). The conjugants may form rod-like or strongly arched pairs; no correlation between pair shape and progress through conjugation was found.

The onset of conjugation is associated with distinct body changes (Fig. 24a): (i) the proboscis shortens by about 87% causing the cells first to become spatulate and then more or less fusiform; (ii) both the internal and external oral baskets disintegrate and become smaller; and (iii) the number of contractile vacuoles decreases. Conspicuous ciliary changes occur in connection with body diminution (Fig. 24p): (i) the number of preoral kineties as well as perioral and dorsal brush kinetids distinctly decreases; (ii) the anterior portion of the right side somatic kineties begins to curve dorsally; and (iii) the interkinetal distances increase. Thus, early conjugants achieve a spathidiid appearance in body shape and ciliary pattern.

In very early conjugants, the vegetative macronuclear nodules lose their globular shape and commence to fuse and to stretch. Furthermore, the micronucleus swells and shows fibrous structures, possibly chromosomes (Fig. 24a). The food vacuoles disappear, making cells more transparent.

Maturation divisions and pronuclei (Figs 24b–d, q, 27). When the maturation divisions commence, further body diminution occurs (i.e., from about 105 × 13 μm to about 60 × 17 μm) and conspicuous changes in the length:width ratio occur, both as compared with the vegetative cells (about 3.6:1 vs. 10.6:1) and the partners (2.9:1 in the shorter vs. 4.2:1 in the longer). The proboscis is reduced to a rounded triangular lip (Fig. 24q): (i) the circumoral kinety, which is restricted to the ventral side in the vegetative cells, extends now also along the dorsal side, and the oral dikinetids possibly assume a more vertical orientation; (ii) there is a further decrease in the number of perioral kinetids; and (iii) the preoral kineties may even be entirely resorbed. Eventually, the shape of maturating specimens becomes *Enchelyodon*- or *Protospathidium*-like (i.e., resembles "polar" haptorids without proboscis; Figs 24b, c, q).

There are three maturation divisions. During the first division, the micronucleus swells from a diameter of about 2.7 μm to 7–8 μm (Fig. 24a). The second division yields four globular maturation derivatives that impregnate homogenously and slowly degenerate, except for one which enters the third maturation division (Fig. 24b, arrows). The degenerating maturation derivatives impregnate more heavily than the disintegrating macronucleus (Fig. 24d). The remaining maturation derivative moves into the anterior body end and assumes a highly characteristic, fusiform shape during the prophase (Fig. 24b, arrows). Then, the derivative begins to divide producing a conspicuous spindle (Fig. 24c), which is resorbed before the

synkaryon develops (Fig. 24d). One pronucleus becomes stationary, whilst the other migrates into the partner to form the synkaryon (Figs 24d, e, 27).

Synkaryon formation and synkaryon divisions (Figs 24e–n, r, 27). No further changes occur in body shape and ciliary pattern during synkaryon formation and the first synkaryon division (Fig. 24r). After the first synkaryon division, the oral area commences to elongate to a spathidiid oral bulge (Figs 24i, j, l, m). This is associated with conspicuous changes in the ciliary pattern (Fig. 24s): (i) the circumoral kinety arranges around the ventral portion of the emerging proboscis; (ii) the number of perioral kinetids increases at the base of the proboscis; and (iii) the anterior portion of the right side somatic kineties starts to curve dorsally, highly resembling a spathidiid ciliary pattern. Thus, the enchelyodonid pattern, characteristic for the maturating specimens, becomes spatulate.

A synkaryon each is formed in the partners by fusion of the migratory pronucleus with the stationary one (Fig. 24e). The first synkaryon division follows pronuclear fusion and is characterized by an inflation of the synkaryon and the appearance of at least 10 chromosomes attached to fibrous structures during the metaphase (Figs 24f, g). The first synkaryon division generates two globular, abutting synkaryon derivatives (Figs 24h, i), which stepwise divide mitotically (Figs 24j–l), producing four synkaryon derivatives in each partner (Fig. 24n). The individual synkaryon derivatives are about 7 μm across and are covered by a distinct membrane slightly separated from the nucleoplasm, which contains many faintly impregnated granules. Finally, two synkaryon derivatives become macronuclear anlagen: one differentiates into the micronucleus; and the last degenerates (Figs 24m, n). The degenerating vegetative macronucleus and the maturation derivatives are still recognizable in some late conjugants (Figs 24k, m, 27).

Pair separation (Figs 24o, s). Slightly before separation, the partners form a rod-like structure connected with the basal portion of the proboscides (Fig. 24o). Conjugants separate in the spathidiid stage after the second synkaryon division, when the nuclear apparatus consists of two macronuclear anlagen and one micronucleus in the vertex formed by these abutting anlagen. The resorption of the vegetative macronucleus and maturation derivatives is now complete because they are absent from very late conjugants and early exconjugants (Fig. 24o).

Exconjugant reorganization. In the absence of detailed data from cultures, we could not distinguish with certainty between exconjugants and preconjugants. However, we could distinguish by morphometric analysis (Table 5) early and mid-exconjugants and/or preconjugants from vegetative specimens by their much smaller size (88 × 15 μm vs. 212 × 20 μm), the stouter body (~ 6:1 vs. 10.5:1), and by the distinctly shorter proboscis (28 μm vs. 86 μm). Further, there were only 15 conjugation pairs among over 500 small and very small supposed exconjugants, suggesting that we missed the peak of conjugation and thus also preconjugation division(s).

The morphometric data show (Table 5) that postconjugational reorganization is associated with intense proboscis and body growth (Figs 25a–h, 26a–k), as indicated by the body length:width ratio (6:1 in exconjugants vs. ~ 4:1 in conjugating specimens). The reconstruction of the oral basket begins in late conjugants (Figs 24i, l, m, o) and is completed soon after pair separation (Figs 24u, v, 25a, c, e, g). Thus, the basket is relatively larger in the small exconjugants than in the large vegetative cells (Figs 25c, n–r). The number of groups of excretory pores increases and they soon appear in the growing proboscis (compare Fig. 25c with Fig. 25h). Many developing extrusomes, which impregnate heavily with protargol, are scattered in the cytoplasm (Figs 25m, 26d) and possibly migrate into the proboscis where they lose impregnability (see description of species). Subsequently, the exconjugants feed on medium-sized ciliates to gather nutrients for further growth and reorganization (Figs 25s–w). The definitive body shape is eventually regained in late exconjugants (Figs 26c, d, h–k), while reaching the vegetative body size needs one or several postconjugational divisions.

Table 5: Morphometric data on vegetative (V) and exconjugant (E) specimens of *Rimaleptus tirjakovae* (from VĎAČNÝ & FOISSNER 2008a). Data based on mounted, protargol-impregnated (Foissner's method), and randomly selected specimens from a non-flooded Petri dish culture. Measurements in µm. CV – coefficient of variation in %; M – median; Max – maximum; Mean – arithmetic mean; Min – minimum; n – number of specimens investigated; SD – standard deviation; SE – standard error of mean.

Characteristics	Stage	Mean	M	SD	SE	CV	Min	Max	n
Body, length	V	212.3	218.0	40.8	8.9	19.2	148.0	281.0	21
	E	87.8	78.0	31.8	5.0	36.2	40.0	153.0	41
Body, width	V	20.4	20.0	4.2	0.9	20.8	15.0	31.0	21
	E	15.0	15.0	2.8	0.4	18.5	10.0	22.0	41
Body length:width, ratio	V	10.6	9.9	2.2	0.5	20.7	7.5	15.0	21
	E	5.9	5.5	2.1	0.3	35.1	2.7	10.6	41
Anterior body end to oral bulge opening, length	V	86.4	86.0	17.3	3.8	20.0	51.0	115.0	21
	E	28.1	20.0	18.8	2.9	66.9	2.0	66.0	41
Proboscis, % of body length	V	40.8	41.1	4.6	1.0	11.2	34.5	56.1	21
	E	29.4	30.5	11.8	1.8	40.0	2.8	50.8	41
Oral bulge opening, length	V	12.3	12.0	1.8	0.4	14.6	10.0	16.0	21
	E	6.8	7.0	1.6	0.2	23.1	4.0	10.0	41
Oral bulge opening, width	V	9.7	9.0	2.4	0.8	25.2	7.0	14.0	10
	E	5.6	6.0	1.3	0.3	23.4	3.0	7.0	15
Oral basket, maximum length	V	23.4	23.0	3.8	0.8	16.3	18.0	32.0	21
	E	15.5	16.0	4.1	0.7	26.8	6.0	23.0	40
Anterior body end to macronucleus, distance	V	119.8	116.0	25.2	5.5	21.0	70.0	159.0	21
Nuclear figure, length	V	19.2	20.0	3.6	0.8	18.8	14.0	31.0	21
	E	15.6	16.0	2.8	0.4	18.2	10.0	22.0	41
Anterior macronuclear nodule, length	V	11.9	12.0	2.3	0.5	19.7	9.0	16.0	21
Anterior macronuclear nodule, width	V	11.9	12.0	1.9	0.4	15.9	8.0	15.0	21
Posterior macronuclear nodule, length	V	11.5	10.0	2.1	0.5	18.5	9.0	16.0	21
Posterior macronuclear nodule, width	V	11.5	12.0	1.7	0.4	15.2	8.0	15.0	21
Macronuclear nodules, number	V	2.0	2.0	0.0	0.0	0.0	2.0	2.0	21
	E	2.0	2.0	0.4	0.1	19.7	1.0	3.0	41
Micronucleus, largest diameter	V	2.7	2.5	–	–	–	2.5	3.0	16
Micronucleus, number	V	1.0	1.0	0.0	0.0	0.0	1.0	1.0	16
Ciliary rows, number	V	21.3	21.0	2.5	0.5	11.8	19.0	29.0	21
	E	13.8	14.0	2.4	0.4	17.3	9.0	19.0	41
Cilia in mid-body in 10 µm, number	V	4.7	5.0	0.6	0.1	12.4	4.0	6.0	21
Anterior body end to last dorsal brush dikinetid, distance	V	49.3	50.0	10.5	2.3	21.3	35.0	72.0	21
	E	16.1	14.0	12.1	1.9	75.4	0.0	43.0	41
Dorsal brush dikinetids, total number	V	39.5	40.0	8.6	1.9	21.8	22.0	59.0	21
	E	11.9	8.0	10.0	1.6	83.5	0.0	32.0	41
Dikinetidal portion of dorsal brush, % of body length	V	23.4	23.9	3.2	0.7	13.5	18.1	27.8	21
Groups of excretory pores, number	V	6.3	6.0	1.2	0.4	18.4	5.0	8.0	10

Table 6: Comparison of macronuclear pattern in vegetative and exconjugant specimens of *Rimaleptus tirjakovae* (from VĎAČNÝ & FOISSNER 2008a).

State	Macronuclear pattern (proportion, %)					Number of specimens analyzed
	Two globular nodules	Two ellipsoidal nodules	Four globular nodules	One globular nodule	One ellipsoidal nodule	
Vegetative cells	98.8	–	–	0.4	0.8	866
Early exconjugants[a]	83.3	6.5	1.3	2.8	6.1	582
Late exconjugants[b]	89.6	–	2.6	2.6	5.2	77

[a] Exconjugants with few food vacuoles.

[b] Exconjugants with several fresh food vacuoles.

Ciliary pattern. The general appearance and ciliary pattern of very early exconjugants resembles that of *Spathidium* sensu lato due to the short, only slightly projecting proboscis. The very early exconjugants have widely spaced somatic kinetids (Figs 25a, c, e, 26a), which proliferate throughout the kineties causing late exconjugants to be ordinarily ciliated (Figs 26c, d). The number of ciliary rows remains unchanged in conjugants and exconjugants (on average 13 and 14, respectively; Table 5), showing that the vegetative number (on average 21) is regained during or after postconjugational division(s).

In very early exconjugants, the dorsal brush is rather inconspicuous and composed of only a few dikinetids (Figs 25a, c, e, h). However, non-ciliated basal bodies or dikinetids do appear near the posterior end of the parental remnants of the dorsal brush (Fig. 25c, arrows). They originate from either restructured somatic kinetosomes or, more likely, de novo because almost the entire dorsal surface of the proboscis is covered with paired and single brush bristles in late exconjugants (Figs 26c, d); however, their number is still much lower than in vegetative cells.

The perioral kinety is preserved during conjugation but in a rather reduced state (Fig. 24s). During growth of the proboscis, the perioral kinety elongates by intrakinetal proliferation of basal bodies until it attains the vegetative appearance (Figs 25b, d, f, 26b). The oblique preoral kineties, which are usually composed of two basal bodies, are entirely resorbed during conjugation (Figs 24q, r). Soon after pair separation some monokinetids appear close to the left side oral dikinetids, forming a very loose kinety resembling the right side perioral kinety (Figs 25a, c, e, g, 26a). Later, the number of preoral basal bodies increases concomitantly with proboscis elongation (Fig. 26c), but the vegetative pattern is obtained only in late exconjugants (Fig. 26d).

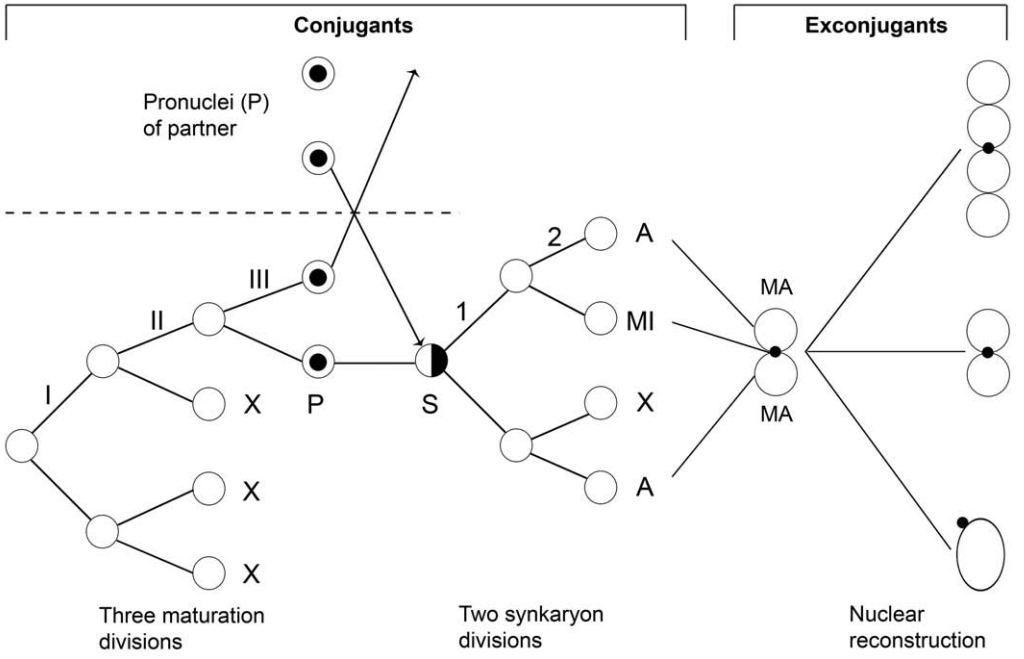


Fig. 27: Scheme of the nuclear processes during and after conjugation of *Rimaleptus tirjakovae* (from Vďačný & Foissner 2008a). There are three maturation divisions and two synkaryon divisions, which produce four synkaryon derivatives, of which two become macronuclear anlagen, one becomes the micronucleus, and one degenerates. The majority of exconjugants (83%) have the vegetative macronuclear pattern (Table 6): two globular macronuclear nodules; rarely do the macronuclear nodules fuse to a globular or ellipsoidal mass or undergo a further division producing four globular nodules. I, II, III – maturation divisions, 1, 2 – synkaryon divisions, A – macronuclear anlagen, MA – macronucleus, MI – micronucleus, P – pronuclei, S – synkaryon. In the conjugants and exconjugants, circles are nuclear derivatives of divisions. Crosses mark degenerating nuclei.

Nuclear apparatus. Among 582 early exconjugants, about 83% have the vegetative macronuclear pattern (i.e., two globular nodules; Figs 24t, 25a, c, i–m, 26e), 6.5% possess two ellipsoidal nodules (Fig. 26f), 6% have one ellipsoidal nodule (Figs 25n–p, r), 3% have one globular nodule (Figs 24u, v, 25e, q), and only 1.5% have four nodules (Table 6). Thus, the macronuclear anlagen may fuse to a globular or ellipsoidal mass or may occasionally undergo further division as is shown by exconjugants with four globular nodules (Figs 26g, 27). The micronucleus is slightly larger in very early exconjugants than in late ones, and is surrounded by a membrane, which is visible only soon after the separation of the conjugants, i.e., in specimens with very short proboscis (Figs 24o, t). See KARADZHAN (1985) for changes in the DNA content of the macronuclear anlagen; possibly, there occurs diminution of the genetic material.

2.3 Encystment, Resting Cysts and Excystment

Comparatively little information is available on the dormant period of the dileptid life cycle. Generally, food depletion/addition is a main stimulus for encystment/excystment (CORLISS & ESSER 1974, FOISSNER & XU 2007). This is supported by our observations since all resting cysts we studied during the preparation of the monograph were obtained by maintaining isolated specimens without food in depression slides with a small quantity of Eau de Volvic or centrifuged soil percolate. On the other hand, JONES (1951) noted that gradual accumulation of *Dileptus*' excretion products induced encystment in crowded cultures. When he changed the medium constantly over a period of five days, the crowding per se did not result in encystment. This indicates that the changing medium prevented the accumulation of excretion products and hence encystment.

Encystment. This process was studied in only a few species, viz., in *Trachelius ovum* by FABRE-DOMERGUE (1891), *Dileptus* sp. by PROWAZEK (1904), *D. jonesi* (misidentified as *D. anser*) by JONES (1951), and *Apodileptus visscheri* by KINK (1973, 1978). However, JONES (1951) doubted several of PROWAZEK's observations. Firstly, PROWAZEK (1904) postulated that the cell takes up water during early stages of encystment, causing the cytoplasm to become turbid. Actually, water is passed out of the cell, since the encysting specimen has a much smaller volume than the precystic individual. Secondly, PROWAZEK (1904) mentioned a plug by which the cyst is attached to the substrate (Fig. 28c). This is very unlikely in JONES' opinion, but the presence of a plug is supported by our recent observations on *Pseudomonilicaryon fraterculum*. Thirdly, PROWAZEK (1904) noted a slight cyst wall depression that he considered to be derived from the cytostome. This is unlikely in JONES' and our opinion.

The most detailed study is that of KINK (1978) on *Apodileptus visscheri*, using transmission electron microscopy. She recognized four stages. During stage 1, when the cells are slightly thickened and the proboscis is shortened, the oral and somatic cilia are displaced into the cell's cytoplasm, while the unciliated basal bodies of the circumoral kinety remain. The tela corticalis is disrupted at many places. During stage 2, when the cells are rounded up and the proboscis is distinctly shortened, the resorption of the ciliature proceeds and the cilia disintegrate in the cytoplasm without forming autophagous vacuoles. The oral basket begins dedifferentiation, while the unciliated oral basal bodies appear unchanged. During stage 3, when the body becomes globular and the proboscis disappears, the dedifferentiation of the oral basket proceeds and masses of microfibrillar material appear in the pharyngeal region. During stage 4, when the cells begin to form the cyst wall, ciliary decomposition is almost finished and the microfibrillar aggregations described in stage 3 disappear. The nonciliated oral basal bodies are likely resorbed in situ during stages 3 and 4.

All other reliable observations on encystment of dileptids can be summarized as follows: (i) cells entering encystment show weak motility, slowly rotating on the spot; (ii) during the initial stages, the body diminishes by about one half and becomes a more or less perfect sphere; (iii) the proboscis is put on the

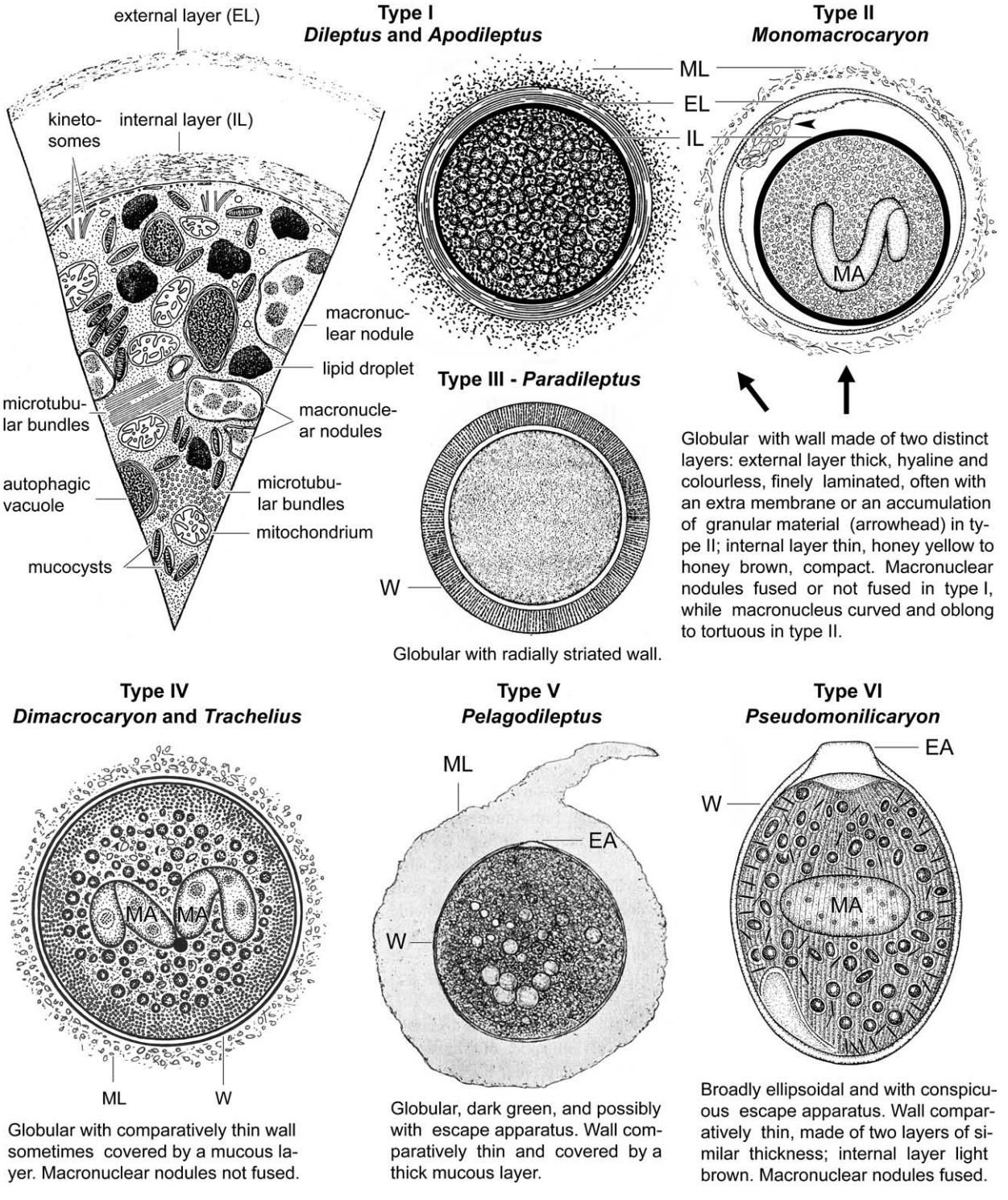
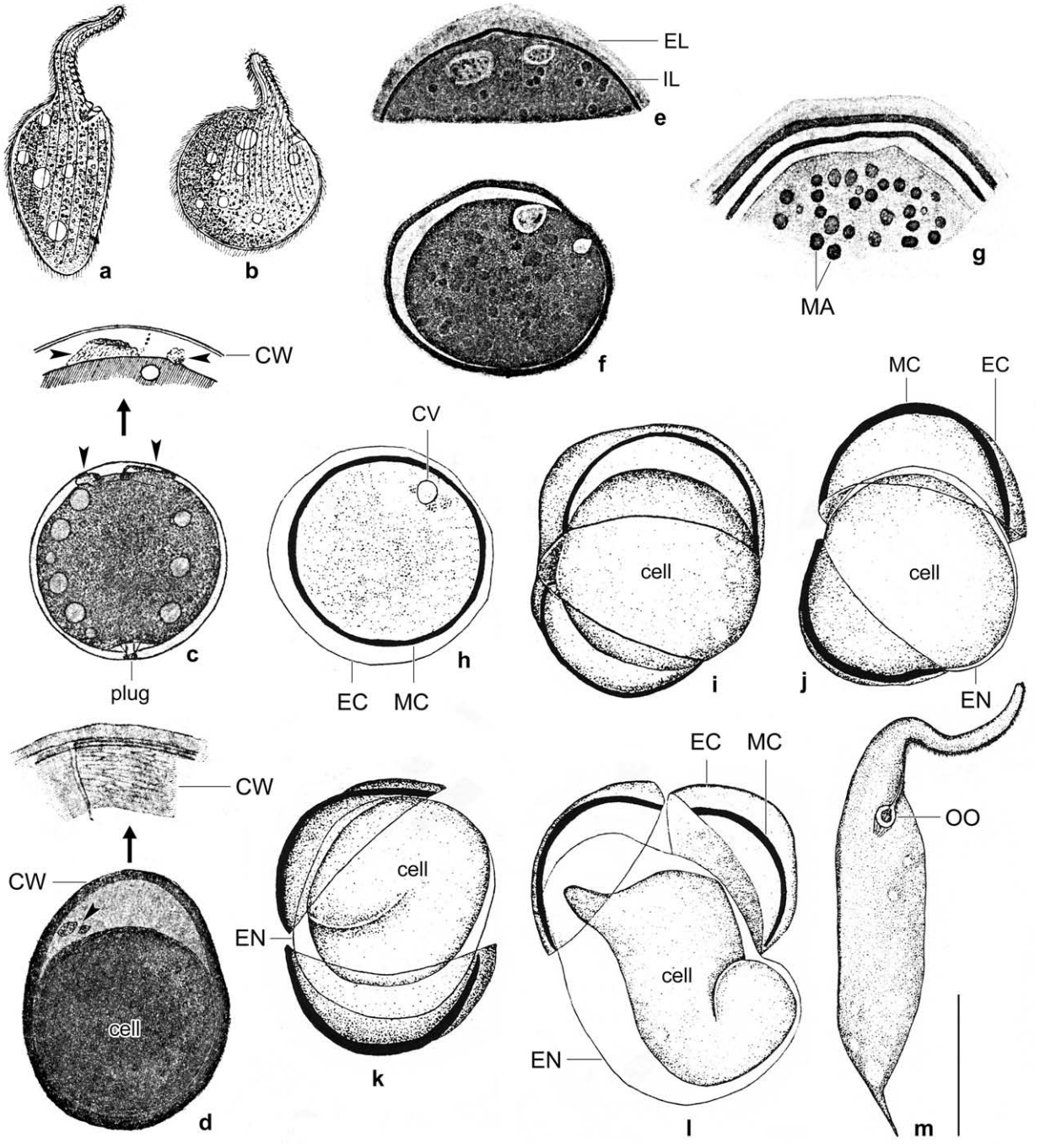


Fig. 29: Fine structure and types of resting cysts in dileptid ciliates. Type I (*Apodileptus visscheri* and *Dileptus margaritifer*) from KINK (1973) and FOISSNER et al. (1995), type III (*Paradileptus conicus*) from WENRICH (1929), type V (*Pelagodileptus trachelioides*) from HUBER & NIPKOW (1927); types II (*Monomacrocaryon terrenum*), IV (*Dimacrocaryon amphileptoides amphileptoides*), and VI (*Pseudomonilicaryon fraterculum*) are originals. For sizes, see description of individual species. IL – internal cyst layer, EA – escape apparatus, EL – external cyst layer, MA – macronucleus (nodule), ML – mucous layer, W – cyst wall.



Figs 28a–m: Encystment (a–g) and excystment (h–m) processes of *Dileptus* sp. from life (a–g; from PROWAZEK 1904) and of *D. jonesi* in Schaudinn-Carmalum-Lyon's Blue preparations (h–m; from JONES 1951). **a, b** – specimens prior to encystment, showing body diminution and shortening of proboscis; **c–g** – successive stages of differentiation of cyst and cyst wall. Arrowheads in (c, d) denote material extruded between cell and cyst wall; **h** – early excystment stage showing a single contractile vacuole; **i** – frontal view of opened cyst; **j** – lateral view of opened cyst; **k** – lateral view of differentiating cell within endocyst; **l** – late excystment stage showing greatly enlarged endocyst and well differentiated cell; **m** – cell five minutes after emergence from cyst. CV – contractile vacuole, CW – cyst wall, EC – ectocyst, EL – external cyst layer, EN – endocyst, IL – internal cyst layer, MA – macronuclear nodules, MC – mesocyst, OO – oral bulge opening. Scale bar 50 µm (h–m). Size not given for (a–g).

ventral or dorsal side of the body and gradually shortens until being entirely resorbed into the body (Fig. 28b); (iv) the contractile and food vacuoles disappear, causing the cytoplasm to become homogenous and hyaline; (v) the ciliature is gradually resorbed, but without any topographical regularity, and is completely lost after formation of the cyst wall; (vi) the nematodesmata of the oral basket form a single "relaxed" bundle that is attached to the surface of the cell; (vii) according to PROWAZEK (1904), some of the many macronuclear nodules degenerate and are resorbed, others are extruded between cell and cyst wall, and the remaining nodules fuse into two or three masses (Figs 28c, e–g). According to JONES (1951) and KINK (1973), the macronuclear nodules decrease in size, become irregularly shaped and tightly spaced but do not fuse; (viii) there is no micronuclear reorganization, but the chromatin of the micronuclei becomes more condensed; (ix) the ectocyst (external cyst layer sensu PROWAZEK 1904 and KINK 1973) is formed by laying down extremely thin, colourless layers until a thickness of 2 to 7 µm is attained (Figs 28c, d); (x) a 2 µm thick pigmented mesocyst (internal cyst layer sensu PROWAZEK 1904 and KINK 1973) is formed next (Figs 28e–g); and (xi) the formation of an endocyst was not observed because it could not be seen in the resting cyst due to the colour and thickness of the mesocyst (JONES 1951).

Resting cysts. Only few data are available on the morphological diversity of the dileptid resting cysts: FABRE-DOMERGUE (1891) studied cysts of *Trachelius ovum*, WENRICH (1929) and HUBER-PESTALOZZI (1945) of *Paradileptus elephantinus*, ZACHARIAS (1894) and HUBER & NIPKOW (1927) of *Pelagodileptus trachelioides*, KINK (1973) of *Apodileptus visscheri*, and FOISSNER et al. (1995) of *Dileptus margaritifer*. Thus, during the preparation of this monograph, we investigated the cyst of several further species. This showed a comparatively high diversity, ranging from simple globes to cysts with a conspicuous escape apparatus. As yet, we could distinguish six types (Fig. 29).

The ultrastructure of the resting cyst of *Apodileptus visscheri* was studied by KINK (1973) in the TEM. Her observations are very detailed and are thus cited here in full length: "The resting cysts of *Dileptus visscheri* possess two envelopes: the external one (ectocyst), which originates earlier during encystment, and an internal one (endocyst), which is formed later between the cell membrane and the external cyst wall.

The external cyst wall of *D. visscheri* is built up from a fibrous material, loosely packed in concentric strands. The inner cyst wall is also made from concentrically arranged fibrillar strands, but they are tightly packed. The width of the wall is unequal on the circumference of the same cyst. During aging of the cyst, the cytoplasm of the encysted ciliate gradually condenses and moves out from the inner envelope. Within the space an amorphic material appears.

The cytoplasm is covered by the cell membrane, which is regularly folded. Under the cell membrane, similarly as in trophonts, there are a layer of very small vesicles and microtubular fibrils, which probably represent kinetosomal postciliary fibers.

In the superficial zone of the cytoplasm, occasionally some kinetosomes can be observed. They are rare and irregularly arranged, what is in striking contrast to the trophic cell where they are precisely arranged in kineties. The kinetosomes in the cysts are localized in different distances from the cell membrane, and they probably do not contact the membrane. The kinetosomes are accompanied by microtubular fibres which originate from the proximal end of the kinetosomes and extend towards the cell membrane. The course of the fibrils indicates that they correspond to the transverse and postciliary fibers in trophonts. The root fiber was not observed; most probably, it disappears during encystment. It was impossible to resolve whether the kinetodesma persists in the cyst or not. No fibrils with a periodic structure were found.

From the fact that the kinetosomes bear transverse and postciliary fibers, it can be deduced that they are remnants of the somatic ciliature or of the feeding cilia from the proboscis of the trophic cell. All kinetosomes found in cysts are devoid of cilia. In cross sections no images of cilia were observed

either in the cytoplasm or within the space between the cell membrane and the cyst wall. This suggests disappearance of the ciliature. Another possibility exists, namely that the cilia are resorbed before the cyst walls are produced.

In the resting cysts of *D. visscheri* the microfibrillar layer, which forms the boundary between endo- and ectoplasm in the trophic cells, completely disappears. In young cysts, strands of fibrillar material of different size can be occasionally observed. The character of these fibrillar strands suggests that they are remnants of the microfibrillar layer. They are arranged in different distances from the membrane. In old cysts, no fibrillar strands were found.

The disappearance of the microfibrillar layer is accompanied by structural mixing of the ecto- and endoplasmic components. The mucocysts, which represent typical ectoplasmic organelles in trophonts, are scattered throughout the cytoplasm. They can be observed under the cyst surface, where they are frequent in young cysts, as well as inside the cytoplasm, which in turn is typical for older cysts. Only one kind of mucocysts was found in the encysted ciliates. All mucocysts were filled with electron-dense material. Occasionally, a stripping of the mucocyst contents was seen.

The arrangement of the mitochondria also shows the mixing of ecto- and endoplasmic components. These organelles are characteristic for the endoplasm of trophic *Dileptus*. In the cysts, the mitochondria were found close to the cell membrane as well as inside the cytoplasm. Whether there are structural changes in the mitochondria of the encysted individuals could be not clarified.

In young and old cysts there are bundles of microtubular fibers arranged randomly in the cytoplasm. They probably correspond to the fibrillar bundles observed under the light microscope. The bundles seen in the electron microscope are of different diameter and contain about 2000 microtubules each. The observations suggest the possibility of splitting of large bundles into several small bundles. The microtubules in each bundle show similar, parallel arrangement. The packets of microtubular material are situated directly in the cytoplasm, and no autophagic vacuoles were observed around them. Any interconnection between the microtubules was not seen; likewise, no contact between the bundles and the kinetosomes was observed.

The length of the bundles, the number of microtubules and their arrangement suggest that they represent the remnants of the cytopharyngeal basket of the oral apparatus of the trophic cell. If so, then this supports the conclusion that the kinetosomes of the oral ciliature are completely resorbed.

The material filling the macro- and micronuclei in encysted forms of *D. visscheri* is morphologically different from the contents of the trophic nuclei. In the macronuclei of the cysts large agglomerations of granular material of different osmophility occur. The chromatin of the micronuclei is more condensed in comparison with the trophic form. The nuclei are covered by a double membrane.

In young cysts of *D. visscheri* very often vesicles filled with electron-dense material are seen. These vesicles represent autophagic vacuoles. They contain mucocysts, toxicysts and other membranous structures. The vacuoles are dispersed randomly through the cytoplasm. In older cysts, the autophagic vacuoles contain material of low density.

In the light microscopic study, we observed contractile vacuoles in the cyst. In the ultrastructural studies of young cysts vesicles were found. They show some resemblance to the contractile vacuoles of the trophic cells. The vacuole in the cyst is surrounded by a single membrane, the cytoplasm surrounding the vacuole is reach in flattened vesicles, which would correspond to the spongiplasm accompanying the contractile vacuoles in trophonts. The site of the contact between the vacuole and the cell membrane (excretory pore) was not found.

The cytoplasm of the encysted cells shows a considerable condensation of cellular structures. The density of the cytoplasm is greater in older cysts than in younger ones. It contains numerous, membrane-free

ribosomes and irregular agglomerations of electron-dense material, probably lipids. In old cysts, there are more such agglomerations than in young cysts, and they are closer to the surface. The cytoplasm does not contain toxicysts, which are so characteristic for the endoplasm and oral region of trophonts. On sections through young cysts, toxicysts are present, but only in the autophagic vacuoles."

Excystment. The excystment process in *Dileptus jonesi* (misidentified as *D. anser*) was studied by JONES (1951). The events after excystation in *Apodileptus visscheri* were examined by KINK (1976).

JONES' observations read as follows: "Cysts usually remained in the excysting medium for 4.5 hours before the first signs of activation were observed. Contractile vacuole activity and a very slow cyclosis constituted the first signs of excystment. Figures 12 and 17 (reproduced here as Fig. 28h) show a cyst in the early stages of excystment. The thick, colorless ectocyst can be seen closely investing the pigmented mesocyst. This, in turn, appears to be in contact with the animal, although an endocyst is present. However the endocyst cannot be seen in the resting cyst or in the early stages of excystment. A large contractile vacuole can be seen in both figures. Contractile vacuole activity continues; the animal swells, rupturing the outer cyst membranes, and the swollen animal tightly invested by the thin endocyst can be seen through the fissure. Figures 14 and 18 (reproduced here as Fig. 28i) show the ruptured cyst, with the animal protruding slightly through the opening toward the observer. Two large contractile vacuoles are visible. Elevation of the endocyst occurs at this time. Figures 13 and 19 (reproduced here as Fig. 28j) show slightly elevated endocysts. The mesocyst is shown in optical section in these figures, and appears more heavily pigmented than is actually the case. Contractile vacuole activity increases gradually and differentiation begins at this stage. Cilia appear and the animal begins to spin slowly within the endocyst. The endocyst now increases in diameter, and the animal increases its speed of rotation (Figs. 15 and 20; reproduced here as Fig. 28k). The animal in Fig. 15 appears as a blur due to the rapidity of its rotation. This photograph clearly demonstrates the three cyst membranes. Figure 20 (reproduced here as Fig. 28k) shows in side view an animal which has elongated sufficiently to double on itself. This figure, which shows the endocyst well, was drawn 5 hours and 20 minutes after the cyst had been placed in the excystment medium. Five minutes later, the animal had the appearance shown in Figs. 16 and 21 (reproduced here as Fig. 28l). The proboscis has begun to differentiate and the endocyst has become greatly enlarged, spreading the 2 cyst halves widely apart. Here again the three cyst membranes are clearly shown. At this stage of excystment, the animal pushes against the endocyst, first with its proboscis, then with the pointed caudal end, in an effort to be free of the endocyst. Finally the endocyst ruptures and the animal escapes. It requires from 5.5 to 6 hours for the completion of excystment."

JONES (1951) then continues with the description of the excysted cells: "The newly excysted animal is easily differentiated from the mature trophic animal. There are three conspicuous features by which the newly excysted *D. anser* may be recognized. The shape of the proboscis is perhaps the most obvious in that it is shortened and bears a blunted tip (Fig. 22; reproduced here as Fig. 28m). The cytoplasm of the entire organism is tan and hyaline-like in appearance. These two characters strongly reflect the appearance of the early precystic animal. A third, less obvious difference is the arrangement of the contractile vacuoles. At this early stage they are arranged more or less irregularly along the body. Later, they become aligned along the dorsal margin, extending from the base of the proboscis to the posterior end. Figure 22 (reproduced here as Fig. 28m) shows an animal 5 minutes after its emergence from the cyst".

KINK (1976) studied processes after excystation using in vivo observation and TEM. She noted that cells grow intensively after excystation to reach the trophic size. The growth includes both the somatic part of the body as well as the oral parts that consist of the oral bulge opening and the proboscis. From the time of excystation and during growth of the cell, the oral apparatus is able to capture and ingest prey. Growth of an oral apparatus while functioning has not previously been reported in ciliates. The proliferation of new

oral kinetosomes in the growing oral apparatus occurs only around the oral bulge opening. An extensive proliferation of somatic ciliature occurs in the anterior portion of the kineties abutting on the oral opening. Thus, there is a growth zone around the oral opening, supplying new kinetosomes for the growing oral opening, the elongating proboscis, and the growth of the rest of the body. The oral kinetosomes are formed randomly in large numbers, appearing similar to an anarchic field, while the somatic kinetosomes arise singly from dikinetid-like kinetids.

3 Ecology, Occurrence and Geographic Distribution

Little is known about these subjects for most species reviewed in this monograph. Modern investigations on the ecology of dileptids are lacking, except for a few studies by, for instance, Butkay (2004) and Sonntag et al. (2007). Their results are mentioned in the species description of *Pelagodileptus trachelioides*. *Dileptus margaritifer* has been used as a model organism in various ecological (e.g., Holyoak & Sachdev 1998, Petchey 2000) and pharmacological (e.g., Samovar & Orlovskaja 1979, Orlovskaja 1982) studies. According to Philpott's (1930) observations, the venome of *Crotalus* has no effect on *Monomacrocaryon gigas*. Another kind of experiments was performed by Metzner (1933), who cut off the proboscis of *Dileptus margaritifer* either with the oral bulge opening or without. Interestingly, stomous and astomous proboscides have the same feeding reactions as normal (= complete) *Dileptus* specimens. Hull (1961) showed that *D. margaritifer* is attacked by the suctorian *Podophrya collini* which survived for 20 days on this *Dileptus* diet.

Generation time and respiration are known only for a few species. Specifically, *Monomacrocaryon gigas* has 0.3 to 1.4 divisions within 24 h according to Rudin (1937). The generation time of *Dileptus margaritifer* is about 17 h at an uptake rate of 10–13 *Tetrahymena* cells/h (Khlebovich 1976), while about 11 h at 20 °C according to Petrova et al. (1976). As concerns *Paradileptus* sp., Mueller (1989) gives a generation time of about 210 h at 8.5 °C. Klekowski (1981) calculated for *Pseudomonilicaryon anser* an oxygen consumption of 3000 pl O_2/ind./h at 23 °C, while Chorik & Shubernetsky (1978) mentioned 2400 pl O_2/ind./h at 23 °C.

Several dileptids are used as indicators of water quality: *Dileptus margaritifer*, *Monilicaryon monilatum*, *Paradileptus elephantinus*, *Pelagodileptus trachelioides*, and *Trachelius ovum*. A detailed description of the morphology and ecology of these species was given in the "ciliate atlas" (Foissner et al. 1995, 1999). Derkach et al. (1995) studied the effects of heavy metal cations on the adenylate cyclase activity and culture growth of *Dileptus margaritifer*. They showed that various heavy metals inhibit the activity of the adenylate cyclase in the following order: Hg^{2+}, Cd^{2+}, Zn^{2+}, Pb^{2+}, and Cu^{2+}.

Dileptids occur throughout the year in a wide range of biotopes. Out of 66 recognized dileptid species and subspecies, 26 taxa have been recorded in terrestrial or semi-terrestrial habitats, 21 taxa in freshwater biotopes, and 12 taxa in both terrestrial and limnetic environments (Table 7). Terrestrial species live in soil, mosses, bark of trees, and in leaf and needle litter. Most freshwater species are bottom-dwellers, gliding in and on organic mud, stones, macrophytes, between algae, and in the air-water interface (for a review, see Foissner et al. 1995). Some freshwater species, e.g., *D. margaritifer*, *Monomacrocaryon gigas*, *Pseudomonilicaryon anser* and *Trachelius ovum*, can be occasionally found in the plankton of stagnant and running waters, while *Paradileptus elephantinus* and *Pelagodileptus trachelioides* live exclusively in the pelagial of lakes and ponds (Foissner et al. 1999). Only seven dileptids have been found in brackish water, the sea and/or in saline soils: *Apotrachelius multinucleatus*, *Dileptus estuarinus*, *Pseudomonilicaryon marinum marinum*, *P. marinum minimum*, *P. massutti*, *Rimaleptus lacazei*, and *R. tirjakovae*. No species is symbiotic or parasitic on or in other organisms. However, *Dileptus margaritifer* may act as a vector for various viruses (Teras 1986, Teras & Kesa 1990).

Table 7: Habitat, biogeographic distribution, and description quality of dileptids. The list contains 66 taxa, of which 12 are new species or subspecies. Habitats: L – limnetic (in benthos or periphyton), M – marine, P – plankton, SS – saline soils, T – terrestrial (soil, mosses, litter). Biogeographic regions: H – Holarctis (North America, Greenland, Eurasia with Iceland, Canary Islands, Korea, Japan, and north Africa), P – Palaeotropis (Africa south of Sahara desert, Madagascar, India), A – Australis (mainly Australia), N – Neotropis (Central and South America), Ar – Archinotis (Antarctica and islands in the southern oceans). Description quality: + poor; ++ incomplete, i.e., either live aspect or ciliary pattern insufficiently described; +++ excellent, i.e., original description and/or redescription includes morphometry and appropriate figures from live and silver-prepared specimens.

Species/subspecies	Habitat[a]	Biogeographic distribution					Description quality
		H	P	A	N	Ar	
Apodileptus edaphicus nov. spec.	T	+	–	–	–	–	+++
Apodileptus visscheri rhabdoplites nov. sspec.	L	+	–	–	–	–	+++
Apodileptus visscheri visscheri (Dragesco, 1963) nov. comb., nov. stat.	L, T	+	+	+	–	–	+++
Apotrachelius multinucleatus nov. spec.	M	+	–	–	–	–	+++
Dileptus anatinus Golińska, 1971	L	+	–	–	–	–	++
Dileptus beersi Jones, 1956	L, T	+	–	–	+	–	+++
Dileptus costaricanus Foissner, 1995	T	+	+	–	+	–	+++
Dileptus dubius Vuxanovici, 1959	L	+	–	–	–	–	+
Dileptus estuarinus Dragesco, 1960	M	+	–	–	–	–	+
Dileptus jonesi Dragesco, 1963	L	+	–	–	–	–	++
Dileptus margaritifer (Ehrenberg, 1833) Dujardin, 1841	L, T	+	+	–	–	–	+++
Dileptus multinucleatus Vuxanovici, 1959	L	+	–	–	–	–	+
Dileptus sphagnicola nov. spec.	L	+	–	–	–	–	+++
Dileptus viridis (Ehrenberg, 1833) Foissner, 1987	L	+	–	–	–	–	+
Dimacrocaryon amphileptoides amphileptoides (Kahl, 1931) Jankowski, 1967[b]	L (?), T	+	+	+	+	+	+++
Dimacrocaryon amphileptoides paucivacuolatum nov. sspec.	T	+	–	–	–	–	+++
Dimacrocaryon arenicola nov. spec.	T	–	–	–	+	–	+++
Dimacrocaryon brasiliense nov. spec.	T	–	–	–	+	–	+++
Microdileptus breviproboscis (Foissner, 1981) nov. comb.	T	+	–	–	+	–	+++
Microdileptus microstoma (Vďačný & Foissner, 2008) nov. comb.	T	+	+	–	–	–	+++
Microdileptus semiarmatus (Vďačný & Foissner, 2008) nov. comb.	T	+	–	–	–	–	+++
Monilicaryon monilatum (Stokes, 1886) Jankowski, 1967	L	+	+	–	–	–	+++
Monomacrocaryon gigas (Claparède & Lachmann, 1859) Vďačný et al., 2011	L	+	–	–	–	–	+
Monomacrocaryon polyvacuolatum (Foissner, 1989) Vďačný et al., 2011	L, T	+	+	–	+	–	+++
Monomacrocaryon tenue (Penard, 1922) Vďačný et al., 2011	T	+	–	–	–	–	+
Monomacrocaryon terrenum (Foissner, 1981) Vďačný et al., 2011	T	+	+	–	+	–	+++
Paradileptus elephantinus (Švec, 1897) Kahl, 1931	P	+	+	+	–	–	++
Pelagodileptus trachelioides (Zacharias, 1984) Foissner et al., 1999	P	+	–	–	–	–	++
Pseudomonilicaryon aculeatum (Dragesco, 1960) nov. comb.	L	+	–	–	–	–	+
Pseudomonilicaryon anguillula (Kahl, 1931) nov. comb.	L(?), T	+	–	–	–	–	+++
Pseudomonilicaryon angustistoma Foissner et al., 2002	T	–	+	–	–	–	++
Pseudomonilicaryon anser (Mueller, 1773) nov. comb.	L, T(?)	+	+	–	–	–	++
Pseudomonilicaryon brachyproboscis Vďačný & Foissner, 2008	T	+	–	–	–	–	+++
Pseudomonilicaryon dimorphum (Wang, 1940) nov. comb.	L	+	–	–	–	–	+
Pseudomonilicaryon edaphoni (Song, 1994) nov. comb.	T	+	–	–	–	–	++

Species/subspecies	Habitat[a]	Biogeographic distribution					Description quality
		H	P	A	N	Ar	
Pseudomonilicaryon falciforme (KAHL, 1931) nov. comb.	T	+	–	–	–	–	+++
Pseudomonilicaryon fraterculum nov. spec.	T	+	–	–	–	–	+++
Pseudomonilicaryon gracile antevacuolatum nov. sspec.	T	+	+	–	–	–	++
Pseudomonilicaryon gracile gracile (KAHL, 1931) FOISSNER, 1997 nov. stat.	T	+	+	–	–	–	+
Pseudomonilicaryon gracile oviplites nov. sspec.	T	–	–	–	+	–	+++
Pseudomonilicaryon gracile singulare (VUXANOVICI, 1962) nov. comb., nov. stat.	L	+	–	–	–	–	+
Pseudomonilicaryon japonicum FOISSNER et al., 2002	T	+	–	–	+(?)	–	+++
Pseudomonilicaryon kahli (ŠRÁMEK-HUŠEK, 1957) nov. comb.	L, T	+	+	–	–	–	++
Pseudomonilicaryon marinum marinum (KAHL, 1933) nov. comb., nov. stat.	M	+	–	–	–	–	+
Pseudomonilicaryon marinum minimum nov. sspec.	M	+	–	–	–	–	+
Pseudomonilicaryon massutti (KAHL, 1933) FOISSNER et al., 2002	M, SS	+	+	–	–	–	+++
Pseudomonilicaryon thononense (DRAGESCO, 1963) nov. comb.	L, T	+	–	–	+	–	+++
Rimaleptus alpinus (KAHL, 1931) nov. comb.	T	+	+	+	+	+	+++
Rimaleptus armatus (FOISSNER & SCHADE in FOISSNER, 2000) nov. comb.	T	+	+	–	–	–	+++
Rimaleptus binucleatus (KAHL, 1931) FOISSNER, 1984	L(?), T	+	+	+	–	–	+++
Rimaleptus bivacuolatus (da CUNHA, 1913) nov. comb.	L	–	–	–	+	–	+
Rimaleptus brasiliensis nov. spec.	T	–	–	–	+	–	+++
Rimaleptus canadensis nov. spec.	T	+	–	–	–	–	+++
Rimaleptus conspicuus (KAHL, 1931) nov. comb.	L, T	+	–	+	–	–	+++
Rimaleptus gabonensis (DRAGESCO & DRAGESCO-KERNÉIS, 1986) nov. comb.	L	–	+	–	–	–	+
Rimaleptus lacazei (GOURRET & ROESSER, 1886) nov. comb.	M	+	–	–	–	–	+
Rimaleptus longitrichus (VĎAČNÝ & FOISSNER, 2008) nov. comb.	T	+	–	–	–	–	+++
Rimaleptus marouensis (DRAGESCO, 1963) nov. comb.	L	–	+	–	–	–	+
Rimaleptus mucronatus (PENARD, 1922) VĎAČNÝ et al., 2011	L, T	+	+	+	+	–	+++
Rimaleptus nistroviensis (CHORIK, 1967) nov. comb.	L	+	–	–	–	–	+
Rimaleptus orientalis (SONG et al., 1988) nov. comb.	T	+	–	–	–	–	+++
Rimaleptus ovalis (VUXANOVICI, 1959) nov. comb.	L	+	–	–	–	–	+
Rimaleptus robustus (VUXANOVICI, 1959) nov. comb.	L	+	–	–	–	–	+
Rimaleptus similis (FOISSNER, 1995) nov. comb.	T	–	–	+	+	–	+++
Rimaleptus tirjakovae (VĎAČNÝ & FOISSNER, 2008) nov. comb.	SS	+	–	–	–	–	+++
Trachelius ovum (EHRENBERG, 1831) EHRENBERG, 1838	L, P	+	+	–	–	–	++

[a] Only substantiated records.
[b] Some data might refer to the subspecies *Dimacrocaryon amphileptoides paucivacuolata* because it was rarely separated before.

The terrestrial dileptids share several distinct features that are probably adaptations to the soil environment (VĎAČNÝ & FOISSNER 2008b): (i) Body shape is usually very slender or even vermiform, and average body length is smaller by about 300 µm than in freshwater species (FOISSNER 1987a). Both peculiarities might be related to the restricted space available in the soil pores, i.e., the narrowness of the habitat. (ii) Reduction of the proboscis to one quarter or less of body length, for instance, in *Pseudomonilicaryon brachyproboscis*, *Rimaleptus armatus*, and three *Microdileptus* species. This peculiarity is possibly related to the fragility of

the proboscis and the space available for prey digestion. The physical load is likely higher in soil than in free water, e.g., by passive and active transport of soil particles with sharp edges and/or heavy weight. The proboscis is for prey recognition and prey capture. In the small terrestrial dileptids it might be advantageous to increase the space for digestion by shortening of the proboscis because prey cannot escape so easily in the narrow soil pores. However, a short proboscis likely decreases prey recognition; possibly this is compensated by the long dorsal bristles (see next item). Interestingly, a very short proboscis occurs also in *Monilicaryon monilatum*, typically found in the benthic mud of limnetic habitats (Foissner 1997a). (iii) The dorsal bristles are usually longer in soil than in limnetic dileptids (up to 15 µm vs. about 5 µm), e.g., in *Rimaleptus alpinus* and *R. longitrichus*. If a sensory function of the brush bristles is assumed, long bristles may be of advantage in recognizing the prey in a habitat where it is more difficult to notice signals, for instance, prey movement in a water film. The long bristles might compensate for the disadvantage of the short proboscis (see above). (iv) Pronounced flexibility of the body which fosters movement in a wrinkled and narrow habitat, i.e., in soil pores. However, distinct body flexibility is not confined to terrestrial species but occurs in all dileptids. This might explain the high diversity of dileptids in terrestrial habitats.

As in most ciliates, little is known on the geographic distribution of dileptids. Many have been discovered or found in the Holarctis, while only very few species (e.g., *Dimacrocaryon amphileptoides*, *Rimaleptus alpinus* and *R. mucronatus*) have been recorded from all biogeographic regions. However, the actual distribution of most species is not known because few reliable records are available. This and some other basic data are shown in Table 7.

4 Phylogeny and Evolution

Dileptids are part of the class Litostomatea, a highly diverse taxon comprising hundreds of species ranging from aerobic, free-living predators to anaerobic endocommensals. This was traditionally reflected by classifying the Litostomatea into the subclasses Haptoria and Trichostomatia. Dileptids were assigned to the Haptoria because their overall morphology and way of life are similar to many other members of this subclass, especially, to spathidiids (Corliss 1979, Foissner & Foissner 1988a, Lynn 2008). Moreover, dileptids were considered as crown haptorians, possibly originating from a spathidiid ancestor by development of a proboscis with a complex ciliature (Xu & Foissner 2005). This assumption was also corroborated by the formation of various spathidiid body shapes and ciliary patterns during ontogenesis and conjugation of dileptids (Vďačný & Foissner 2008a, 2009). However, the phylogenetic position of the dileptids within the Haptoria became controversial when their first 18S rRNA gene sequence was published because it classified them basal to all other haptorians (Strüder-Kypke et al. 2006, Gao et al. 2008, Vďačný et al. 2010). Our recent analyses based on eight new dileptid 18S rRNA gene sequences showed that dileptids cluster outside the haptorian clade, forming a monophylum, the subclass Rhynchostomatia, which is sister to the subclass Haptoria including the Trichostomatia (Vďačný et al. 2011a, b).

In chapter 4.1, the ground pattern of the Litostomatea is described. This is important for understanding the deep litostomatean evolution and reconstruction of the dileptid morphological evolution, which is treated in chapter 4.2. In the last two chapters, the molecular phylogeny of the dileptids is compared with the morphological results.

4.1 Ground Pattern and Deep Evolution of the Litostomatea

The ground pattern of a monophyletic taxon is a combination of apomorphies and younger plesiomorphies present in the stem species (last common ancestor) from which the monophylum evolved (Ax 1995). Based on morphology and ontogeny of litostomateans and armophoreans (i.e., the sister group of the Litostomatea),

Vďačný et al. (2010) hypothesized that the last common ancestor of the Litostomatea possessed the following more recent plesiomorphies: (i) an oblong body with ventrally located oral apparatus; (ii) plate-like arranged postciliary microtubules to the right of and between the ciliary rows; and (iii) a telokinetal stomatogenesis commencing in the dorsal or dorsolateral kineties and with migrating oral kinetofragments. Further, Vďačný et al. (2010, 2011a) argued that the last common ancestor of the Litostomatea evolved the following apomorphies: (i) monokinetidal somatic kineties anteriorly differentiated into a three-rowed dikinetidal dorsal brush; (ii) a complex oral ciliary pattern comprising a dikinetidal circumoral kinety and several preoral kineties; (iii) toxicysts fostering a predatory way of life; (iv) a cytopharynx of the rhabdos type; and (v) a heteropolar conjugation mode (Fig. 30). Thus, the ground oral ciliary pattern of the ancient Litostomatea was morphologically more complex than that of extant haptorians and trichostomatians, which lost the preoral kineties and sometimes also the circumoral kinety, e.g., the free-living Enchelyidae and the endocommensal Trichostomatia. According to our analyses, dileptids are morphologically nearest to the last common progenitor of the Litostomatea, as they are the only litostomateans that maintained the ancestral oral apparatus (ventrally located oral opening, presence of many preoral kineties).

Molecular phylogenies consistently show a deep bifurcation of the Litostomatea (Vďačný et al. 2011a, b). The first lineage is named Rhynchostomatia and comprises tracheliids and dileptids s.str., both characterized by a ventrally located oral opening at the base of a proboscis that carries a complex oral ciliature. The second lineage includes the free-living haptorians and the endocommensal trichostomatians, both characterized by body polarization and simplification of the oral ciliature. The polar position of the oral opening is not correlated with the length and shape of the oral bulge, thus representing a strong apomorphy of the Haptoria and Trichostomatia (Fig. 30). However, according to the molecular phylogenies, the position of the oral opening was modified in some of the more derived trichostomatians. Specifically, the opening sunk into an anterior oral cavity in *Balantidium*, and was displaced posteriorly in the isotrichids (e.g., *Dasytricha* and *Isotricha*).

4.2 Morphological Evolution of Dileptids

Morphological evolution of dileptids has been recently studied in detail by Vďačný et al. (2011b). The results of their study are reported here in full length.

4.2.1 Characters and Character States

The cladistic analyses are based on five groups of diagnostic and phylogenetically informative characters in dileptids: the morphology of the oral apparatus (characters 1–7), pattern and division mode of the nuclear apparatus (characters 8–10), contractile vacuole pattern (character 11), patterns of the somatic ciliature (characters 12–14), and habitat (character 15). The genus *Spathidium* is chosen as the outgroup because it is morphologically nearest to dileptids and belongs to the subclass Haptoria, which is a sister group of the Rhynchostomatia (Vďačný et al. 2010, 2011a, b). The characters and character states are summarized in Table 8, and their distribution is given in Table 9.

Character 1: **Structure of circumoral kinety.** The outgroup has a circumoral kinety composed exclusively of dikinetids. This state is maintained in only a single dileptid genus, *Trachelius*. All other dileptids display a unique, highly derived state, i.e., a hybrid circumoral kinety composed of dikinetids in the proboscis and oral monokinetids associated with nematodesmata around the oral bulge opening (e.g., Golińska 1991, 1995). Interestingly, nematodesmata-bearing monokinetids (so-called “oralized somatic monokinetids”) also occur in the acropisthiids and enchelyine haptorians (Foissner & Foissner 1985, 1988a), where they are not part of a circumoral kinety, but are localized in the anterior portion of the somatic ciliary rows and bear nematodesmata forming the external oral basket.

The ancestral oral opening of the stemline of the Haptoria and Trichostomatia was apical and in the centre of the oral bulge. When both bulge and oral opening extend posteriorly (e.g., *Arcuospathidium* and *Apobryophyllum*), the ancestral opening (arrowheads) remains unchanged, still being the first site where food enters the cell. In contrast, the ancestral oral bulge of the Rhynchostomatia is keyhole-shaped and can open only in the widened posterior part, which is far subapically.

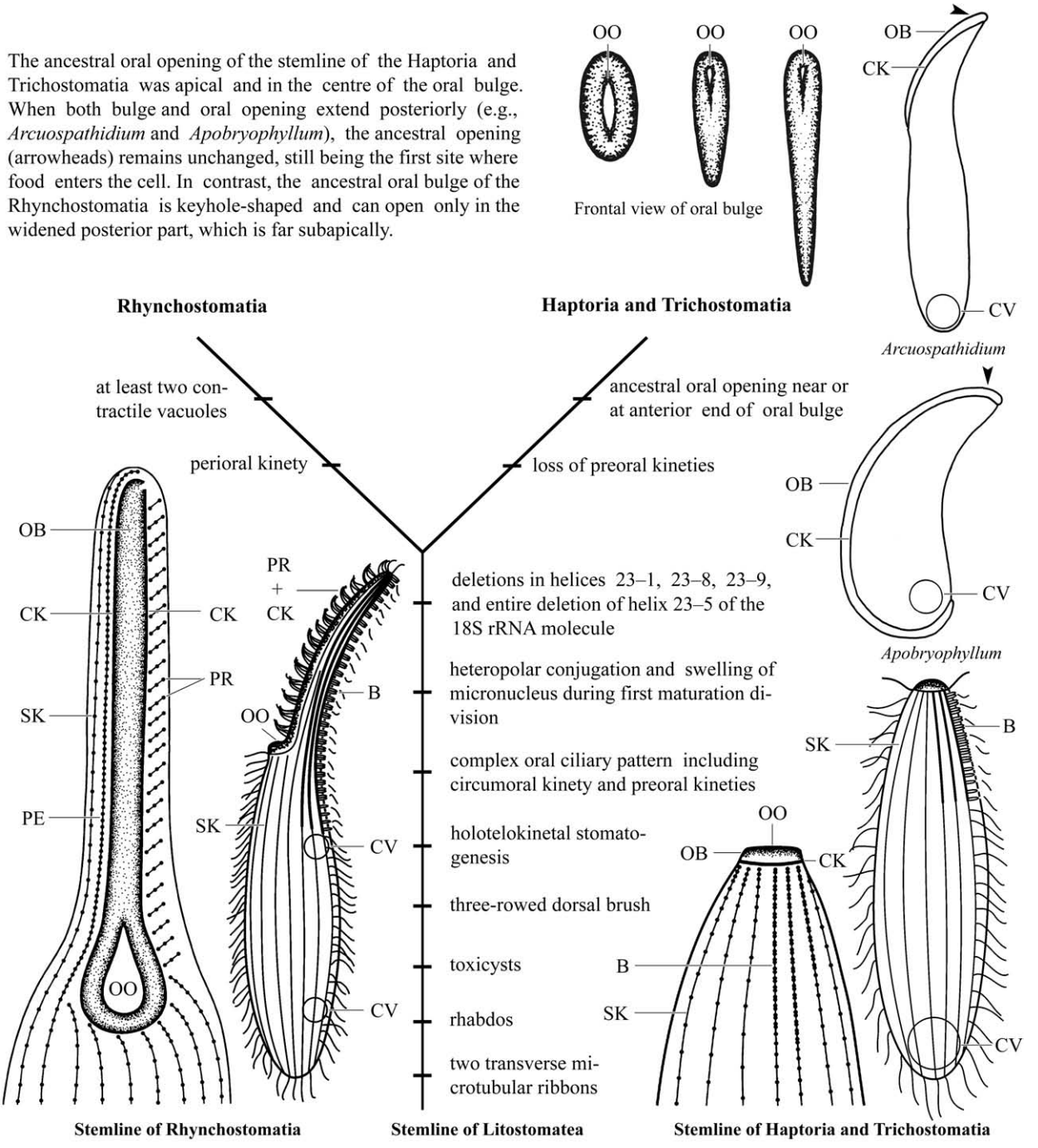


Fig. 30: An evolutionary scenario for the morphological evolution of two main litostomatean lineages (from Vďačný et al. 2011a). Only apomorphies are shown. The first lineage is named Rhynchostomatia and comprises tracheliids and dileptids s.str., both characterized by a ventrally located oral opening at the base of a proboscis that carries a complex oral ciliature. The second lineage includes the free-living Haptoria and the endocommensal Trichostomatia, both characterized by body polarization and simplification of the oral ciliature. As explained in this figure, the polar position of the oral opening is not correlated with the length and shape of the oral bulge, thus representing a strong apomorphy of the haptorians and trichostomatians. However, the position of the oral opening was modified in some trichostomatians, viz., in the balantidiids and isotrichids. B – dorsal brush, CK – circumoral kinety, CV – contractile vacuoles, OB – oral bulge, OO – oral opening, PE – perioral kinety, PR – preoral kineties, SK – somatic kineties.

Character 2: **Preoral kineties.** The left branch of the circumoral kinety is associated with many short, oblique preoral kineties in all dileptid genera, *Monilicaryon* being an exception, displaying instead a single perioral-like kinety (Foissner 1997). However, this kinety very likely originates from a linear arrangement of many short preoral kineties. We base this assumption on the pattern of several "typical" dileptids in which the preoral kineties are so strongly oblique that they almost form a single, perioral-like kinety.

Character 3: **Perioral kinety.** In almost all dileptid genera, the right branch of the circumoral kinety is accompanied by a single, densely ciliated perioral kinety. Two perioral kineties side by side, in addition to the circumoral kinety, represent a derived state occurring only in a specialized group of planktonic dileptids, viz., *Paradileptus* and *Pelagodileptus* (Foissner et al. 1999), where many densely spaced cilia might increase the efficiency of food acquisition.

Character 4: **Localization of oral bulge opening.** The oral bulge opening is on the ventral surface at the base of the proboscis in most dileptids. Only in *Paradileptus* is the opening on the left side and rotated by approximately 180° (Wenrich 1929). Obviously, this is a derived state.

Character 5: **Shape of oral bulge opening.** Three variants can be distinguished. Roundish openings occur in many haptorians and most dileptids, suggestive of a plesiomorphic state. In the genus *Paradileptus*, the roundish oral bulge opening became inverted, i.e., the posterior end of the opening faces the anterior end of the cell (see above). When the roundish opening is stretched, a more or less elliptical pattern is formed as found in the genera *Pelagodileptus* and *Dimacrocaryon*, but also in *Pseudomonilicaryon angustistoma* (Foissner 1984; Foissner et al. 1999, 2002). The occurrence of elliptical to very narrowly elliptical oral openings in several, possibly fairly distantly related genera indicates that this feature evolved convergently several times.

Character 6: **Oral basket.** Nine out of the ten dileptid genera have a distinct oral basket composed of long rods (nematodesmata) like in many other haptorians. However, in *Dimacrocaryon*, the basket rods are so fine that they are recognizable only with TEM. Additionally, the oral basket is lined with highly refractive granules, thus appearing in vivo as a conspicuous oral sac. This state is considered an apomorphy.

Character 7: **Shape of internal oral basket.** The oral apparatus is composed, inter alia, of an internal and external basket. The nematodesmata of the external basket originate from the basal bodies around the oral bulge opening and form a conical structure. The internal basket is formed by laminar transverse microtubule arrays embedded in fibrillar material (Grain & Golińska 1969). Three shape variants of the internal oral basket evolved: obconical, club-like, and bulbous. The obconical internal basket is common in haptorians and most dileptids, indicating it as the ancestral state. *Trachelius* has a strongly developed, long, club-shaped internal basket, while that of most *Rimaleptus* species is short and bulbous.

Characters 8 and 9: **Nuclear pattern.** Jankowski (1967) first recognized the number and arrangement of the macronuclear nodules as a very stable feature of high cladistic significance in dileptids. The molecular data from several heterotrichs, such as *Blepharisma* and *Stentor*, suggest the monomacronucleate state as ancestral (Schmidt et al. 2007, Thamm et al. 2010). This is sustained during the ontogenesis where a monomacronucleate pattern occurs transiently even in species with two or several macronuclear nodules (Penard 1922, Golińska 1965, Vďačný & Foissner 2009). When Haeckel's ontogenetic principle is applied, the *Monomacrocaryon* pattern should be considered to be the plesiomorphic state. Further, the *Monomacrocaryon* pattern is quite common in haptorids in general and in the outgroup in particular.

Four macronuclear patterns can be distinguished, each considered to define a distinct genus. The number and pattern of the micronuclei is correlated with the macronucleus, and thus will not be used in the cladistic analysis.

Monomacrocaryon pattern (Fig. 12b): The macronucleus is a more or less long rod, sometimes slightly to

markedly constricted in the middle. This pattern occurs only in *Trachelius* and *Monomacrocaryon*.

Dimacrocaryon pattern (Fig. 12c): Two oblong nodules with a single micronucleus in between occur in two dileptid genera, viz., *Dimacrocaryon* and *Rimaleptus*. Rarely, *Monomacrocaryon* has a rather pronounced constriction in the mid-portion of the macronucleus with a single micronucleus close to it, showing how the binucleate state may have evolved.

Monilicaryon pattern (Fig. 12e): At least four serially arranged nodules form a moniliform or distinctly nodulated strand. This pattern has been found in four possibly closely related genera, viz., *Monilicaryon*, *Pseudomonilicaryon*, *Pelagodileptus*, and *Paradileptus*. A moniliform macronucleus very likely evolved from the *Dimacrocaryon* pattern by doubling the nodule number. Thus, in the first step a chain of four nodules was generated, still present in some species (e.g., *Pseudomonilicaryon edaphoni*, *P. aculeatum*) and highly characteristic for early exconjugants (Visscher 1927, Vinnikova 1974a, Vďačný & Foissner 2008a). Later, further divisions added more nodules.

Dileptus pattern (Fig. 12d): Usually more than 50 small, oblong nodules scattered in the trunk. This pattern is typical for two genera, viz., *Dileptus* and *Apodileptus*. The *Dileptus* pattern very likely evolved from the *Monilicaryon* pattern by fragmentation of the moniliform macronuclear strand. This hypothesis is supported by the conjugation data. In ex-conjugants of *Dileptus margaritifer*, four macronuclear anlagen transiently form a *Monilicaryon* pattern. Later, the anlagen divide amitotically generating hundreds of scattered nodules (Visscher 1927).

Character 10: **Division mode of macronucleus (Fig. 22).** Three division modes occur, the first mode being most widespread in ciliates and thus considered as plesiomorphic (Raikov 1996).

Monomacrocaryon mode: In mid-dividers, the macronucleus condenses to a globular mass that becomes a long rod that divides into two oblong pieces (Vďačný & Foissner 2009). Two modifications of this mode evolved: (i) in the binucleate dileptids, the condensed mass divides twice generating two nodules each in the proter and opisthe, while (ii) in dileptids with moniliform macronucleus, the mass divides once into two oblong pieces which elongate and become nodulated (Golińska 1965).

Apodileptus mode: In mid-dividers, the scattered macronuclear nodules fuse to a globular mass that divides into two pieces. In post-dividers, each piece becomes a short strand and later a three-dimensional reticulum that fragments into many nodules, as in multinucleate spathidiids and fuscheriids (Foissner et al. 2002, Gabilondo & Foissner 2009).

Dileptus mode: In the multinucleate genus *Dileptus*, each nodule divides individually (Hayes 1938, Jones 1951, Golińska 1971). This is a rare mode occasionally found also in multinucleate hypotrichs, specifically, in the genus *Pseudokeronopsis*, where this character is considered apomorphic and defines the subfamily Pseudokeronopsinae (Berger 2006).

Character 11: **Contractile vacuole pattern.** Most haptorids and spathidiids possess a single, terminal contractile vacuole, while all described dileptids have at least two, one each in the anterior and posterior half of the trunk. However, there is a second dorsal vacuole in some spathidiids, e.g., *Arcuospathidium bulli* (Foissner 2000) and *Spathidium faurefremieti* (Foissner 2003), suggesting a bi- or multivacuolate ancestor of dileptids. We suppose that the first derived state is a dorsal row (stripe) of vacuoles and the second derived state is a stripe of vacuoles each in the dorsal and ventral side of the cell. The cladogram shows that various contractile vacuole patterns evolved convergently in dileptids, and thus the feature is of significance mainly at species level.

Character 12: **Right side fossa.** This concavity, surrounded and lined by narrowly spaced kineties, is present only in *Trachelius* (Ehrenberg 1838, Foissner 1997).

Character 13: **Dorsal brush pattern.** In the outgroup and in *Trachelius*, the brush rows start at the

same level anteriorly, while all other dileptids have a stagered brush with the rows gradually shortened anteriorly from left to right. The stagered pattern is not caused by simple spatial constraints since there is sufficient space available for full-length brush rows in both the large species and in the small ones with a two-rowed brush. Thus, the stagered brush is considered as an apomorphy.

Character 14: **Number of dorsal brush rows.** In many haptorids and most spathidiids, the dorsal brush is composed of three rows, a pattern found in only one dileptid genus, viz., *Trachelius* (Song & Wilbert 1989, Foissner 1997). All other dileptids have one, two or many rows. In the two-rowed species, such as *Dimacrocaryon amphileptoides*, a third row may be present in some specimens (Foissner 1984), possibly a vestige of the ancestral state. In accordance with Foissner et al. (2002), we consider a lower or higher number than three brush rows as apomorphic.

Character 15: **Habitat.** Several dileptid genera show a distinct habitat preference. For instance, *Trachelius* occurs mainly in the periphyton, where it feeds predominantly on peritrichs, while *Pelagodileptus* and *Paradileptus* are restricted to the pelagial (Foissner et al. 1999); *Monilicaryon* inhabits benthic mud (Foissner 1997, Foissner et al. 1995), while *Dimacrocaryon* and *Rimaleptus* prefer terrestrial biotopes (Foissner 1998). Periphyton-inhabiting protists have a number of features (e.g., pronounced flexibility of the body) pre-adapting them for the exploitation of soil (Schönborn 1966). Schönborn's model also shows that a variety of freshwater niches may be colonized from the periphyton, which is thus supposed to be the ancestral habitat, from which dileptids spread into the benthic, pelagic and soil environments.

Characters and genera not considered: The following features were not included in the cladistic approach because they are known only in a small portion of the species or are merely relevant to intrageneric evolution: the presence/absence of a tail, the somatic ciliary pattern of the right and left side of the proboscis, ontogenetic peculiarities (e.g., presence/absence of a transient indentation in the prospective fission area), the fate of the parental degenerating macronucleus during conjugation (e.g., nodules fusing into a mass that degenerates or the nodules degenerating individually), the fate of the macronucleus during encystment (e.g., fusing or not fusing), and resting cyst characteristics (e.g., cyst wall structure and presence/absence of escape apparatus).

Two genera, *Teuthophrys* and *Branchioecetes*, traditionally assigned to the dileptids, were excluded. *Teuthophrys* belongs to the spathidiids (Foissner et al. 1999, Strüder-Kypke et al. 2006), and *Branchioecetes* is still very poorly known (Kahl 1931) and invalid because no type species was fixed (Article 13.3 of the ICZN 1999).

4.2.2 Hennigian Argumentation and Morphological Trees

Vďačný et al. (2011b) elucidated the morphological evolution of dileptids using both Hennig's traditional (i.e., manual) method (Fig. 31) and computer-assisted statistical methods, including Bayesian inference (BI) and maximum parsimony (MP) algorithm (Fig. 32). As expected, the cladograms generated by each approach are similar because they are based on the same characters. The Hennigian argumentation tree provides better resolution among the multinucleate family Dileptidae. The family Dimacrocaryonidae is paraphyletic in cladograms generated by both approaches since we have been unable to identify a morphological synapomorphy for *Monomacrocaryon* and the *Dimacrocaryon-Rimaleptus* lineage.

Dileptids share the following synapomorphies: (i) a proboscis with a complex oral ciliature and (ii) at least two dorsal contractile vacuoles. Based on the Hennigian argumentation, we propose that their last common ancestor inherited the following plesiomorphies from the last common progenitor of the class Litostomatea: (i) a dikinetidal circumoral kinety; (ii) an oblong, unsegmented macronucleus; and (iii) a three-rowed, not staggered dorsal brush. The proboscis of the ancestor was most likely immobile and

Table 8: Characters, character states, and coding used for the cladogram shown in Figure 31 (from VĎAČNÝ et al. 2011b). For distribution of character states in the taxa, see Table 9.

No.	Characters	Plesiomorphic	Apomorphic
1	Structure of circumoral kinety	dikinetidal (coded 0)	hybrid (coded 1)
2	Preoral kineties	oblique (coded 0)	aligned to a perioral-like kinety (coded 1)
3	Number of perioral kineties	1 (coded 0)	2 (coded 1)
4	Localization of oral bulge opening	ventral (coded 0)	ventrolateral and inverted (coded 1) apical (coded 2)
5	Shape of oral bulge opening	roundish (coded 0)	narrowly elliptical (coded 1)
6	Oral basket lined with granules	no (coded 0)	yes (coded 1)
7	Shape of internal oral basket	obconical (coded 0)	club-shaped (coded 1) bulbous (coded 2)
8	Number of macronuclear nodules	1 (coded 0)	2 (coded 1) ≥ 4 (coded 2)
9	Macronuclear pattern	mononucleate (coded 0)	binucleate (coded 1) moniliform (coded 2) multinucleate, scattered (coded 3)
10	Division mode of macronucleus	ordinary mode (coded 0)	*Apodileptus* mode (coded 1) *Dileptus* mode (coded 2)
11	Contractile vacuole pattern	one terminal vacuole (coded 0)	dorsal stripe (coded 1) many scattered vacuoles (coded 2)
12	Lateral fossa	absent (coded 0)	present (coded 1)
13	Dorsal brush pattern	not staggered (coded 0)	staggered (coded 1)
14	Number of dorsal brush rows	3 (coded 0)	1 (coded 1) 2 (coded 2) ≥ 4 (coded 3)
15	Habitat	periphyton (coded 0)	benthos (coded 1) soil (coded 2) pelagial (coded 3)

Table 9: Distribution of characters and their coding in the taxa for the computer programs MrBayes and PAUP* (from VĎAČNÝ et al. 2011b). For characters and character states, see Table 8. Explanations: ? = not known, – = not applicable.

Taxa	Characters				
	1–7	8–10	11	12–14	15
Trachelius	0000001	000	2	10000	0
Monomacrocaryon	1000000	000	2	01010	2
Dimacrocaryon	100011?	110	1	01100	2
Rimaleptus	1000002	110	1	01100	2
Monilicaryon	1100000	220	1	01011	1
Pseudomonilicaryon	1000000	220	1	01010	2
Paradileptus	1011000	220	2	01010	3
Pelagodileptus	1010100	220	2	01010	3
Apodileptus	1000000	231	1	01010	1
Dileptus	1000000	232	2	01010	1
Spathidium (outgroup)	0–2000	000	0	00000	2

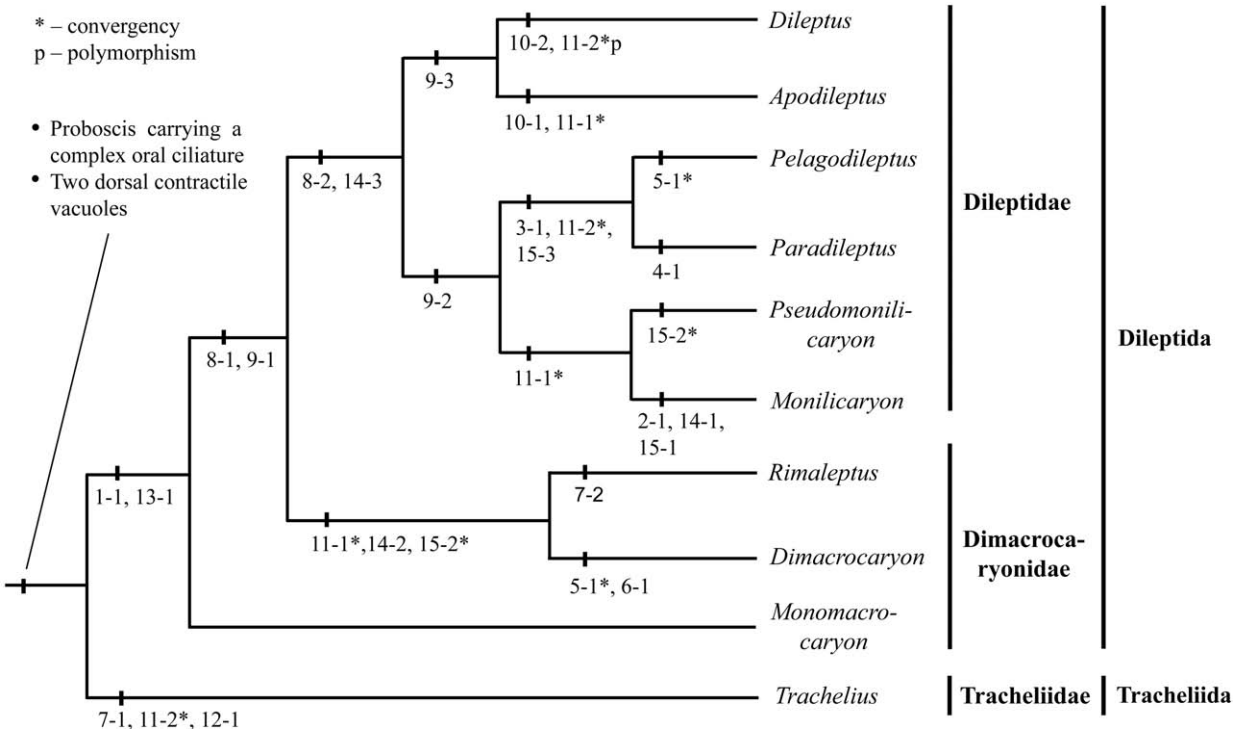


Fig. 31: Cladogram of ten dileptid genera generated by traditional Hennigian argumentation (from Vďačný et al. 2011b). For character coding, see Table 8 and section on character states. Only apomorphies are shown.

short, i.e., resembling that of *Trachelius*. This is also consistent with the maturation processes of the proboscis (Vďačný & Foissner 2009).

The cladogram is based on 15 characters dividing dileptids into two major lineages: (i) the monotypic order Tracheliida containing the family Tracheliidae and (ii) the order Dileptida uniting the families Dimacrocaryonidae and Dileptidae. This deep split into two orders is moderately to poorly supported with a posterior probability (PP) of 0.62 and MP bootstrap values of 75% (Fig. 32).

Order Tracheliida. This order is defined by three apomorphies: (i) a club-shaped internal oral basket; (ii) a lateral fossa with specialized ciliature; and (iii) many scattered contractile vacuoles. The latter feature evolved at least two times convergently, viz., in the *Pelagodileptus-Paradileptus* clade and in some species of the genus *Dileptus*. Tracheliids display several old plesiomorphies inherited from the last common ancestor of the class Litostomatea: (i) a dikinetidal circumoral kinety; (ii) a three-rowed, not staggered dorsal brush; and (iii) a short, immobile proboscis. Thus, this order differs from the order Dileptida by several important morphological traits, i.e., by the unique fossa, the structure of the circumoral kinety (dikinetidal vs. hybrid), and the dorsal brush pattern (not staggered vs. staggered).

Order Dileptida. This order unites nine genera, sharing the following strong synapomorphies: (i) a hybrid circumoral kinety; (ii) a staggered dorsal brush and, possibly in connection, (iii) a stripe without cilia on the left side of the proboscis. In both the Hennigian argumentation scheme and the morphological trees generated from statistical methods, there are three lineages within this order (Figs 31, 32): (i) *Monomacrocaryon* with an unsegmented macronucleus; (ii) *Dimacrocaryon* and *Rimaleptus* with two macronuclear nodules; and (iii) a large clade comprising six genera having many macronuclear nodules. The first two lineages are united into the family Dimacrocaryonidae, while the third clade represents the

family Dileptidae. A sister relationship of the *Dimacrocaryon-Rimaleptus* clade and the family Dileptidae is indicated by the segmented macronucleus consisting of at least two nodules. Further, this relationship is supported by a posterior probability of 0.86 and 66% MP bootstraps. However, in the absence of a recognized morphological synapomorphy for the genus *Monomacrocaryon* and the *Dimacrocaryon-Rimaleptus* clade, we cannot exclude the possibility that the relationship between the *Dimacrocaryon-Rimaleptus* clade and the family Dileptidae is an artefact.

Family Dimacrocaryonidae. This family is paraphyletic in both the Hennigian argumentation scheme and the computer-generated cladograms (see above). The classification of *Monomacrocaryon* within the family Dimacrocaryonidae is based on the similarity of the nuclear pattern. The two macronuclear nodules of *Dimacrocaryon* and most *Rimaleptus* species are usually so close together that they appear as a single, oblong structure resembling the macronucleus of *Monomacrocaryon*. Further, only these three genera have a single micronucleus which is, however, very likely a plesiomorphic feature.

The genera *Dimacrocaryon* and *Rimaleptus* likely descend from a common ancestor inhabiting terrestrial habitats (Figs 31, 32). This is also the most parsimonious explanation for the pronounced similarities in the nuclear apparatus (two macronuclear nodules with a single micronucleus in between) and the oral as well as the somatic ciliature (dileptid oral ciliary pattern and a two-rowed dorsal brush). However, the oral apparatus of the genus *Dimacrocaryon* deviates not only from that of *Rimaleptus* but also from that of all other dileptids, in having (i) an oral basket lined with highly refractive granules; (ii) a hardly protruding oral bulge; and (iii) a narrowly elliptical oral bulge opening. The latter feature probably evolved convergently as explained in the description of the characters. The cladograms suggest that the peculiarities of the oral apparatus of *Dimacrocaryon* arose relatively recently. The single apomorphy of *Rimaleptus* is the short, bulbous internal oral basket.

Family Dileptidae. The monophyly of the family Dileptidae is supported by two apomorphies: (i) more than three dorsal brush rows and (ii) four or more macronuclear nodules. Further, it is moderately supported by Bayesian interference (0.93 PP) and by 71% MP bootstraps (Fig. 32). However, the internal relationships of the family Dileptidae are rather poorly resolved in the computer-generated trees. Therefore, we refer here mainly to the cladogram created by traditional Hennigian argumentation, where we recognized two separate branches: the *Monilicaryon* and the *Dileptus* branch (Fig. 31).

The *Monilicaryon* branch unites four genera, exhibiting a moniliform macronuclear strand of at least four nodules. They form two clades which differ mainly in the oral ciliary pattern: *Pseudomonilicaryon* and *Monilicaryon* maintained the plesiomorphic state, while *Paradileptus* and *Pelagodileptus* each evolved an additional perioral kinety. The monilicaryonid and paradileptid pattern can be derived from that of *Pseudomonilicaryon* (Fig. 33). The single apomorphy of the first clade is the dorsal stripe of contractile vacuoles that very likely evolved convergently, for instance, in the Dimacrocaryonidae. The important cladistic characteristics of the mud-inhabiting *Monilicaryon* are: (i) a perioral-like kinety left of the oral bulge formed by linearly arranged preoral kineties and (ii) a dorsal brush composed of several kineties which appear as a single, fragmented row. In the computer-generated trees, *Monilicaryon* is sister to the *Dileptus* branch. However, this node is only very poorly supported (0.50 PP). The genus *Pseudomonilicaryon* lacks a distinct apomorphy, with the possible exception of a preference for soil environment. The *Paradileptus-Pelagodileptus* clade is strongly supported by three apomorphies: (i) right branch of the circumoral kinety accompanied by two perioral kineties side by side, (ii) many scattered contractile vacuoles, and (iii) a planktonic way of life. Further, this clade is strongly supported by all statistical analyses (0.95 PP, 90% MP). *Pelagodileptus* evolved a very narrowly elliptical oral bulge opening, while *Paradileptus* broadened the left half of the proboscis base to a dish-like platform taking along the oral bulge and the bulge opening which became inverted and laterally located (Fig. 33).

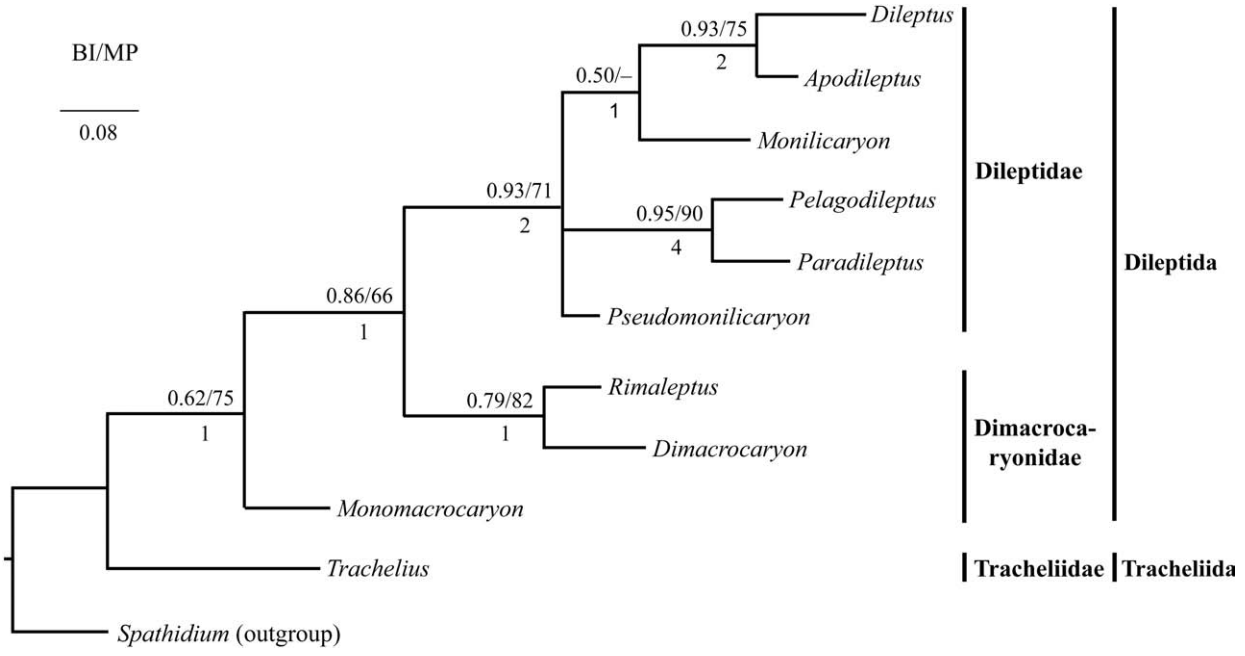


Fig. 32: Phylogenetic tree of ten dileptid genera inferred from 15 characters using the genus *Spathidium* as outgroup (from Vďačný et al. 2011b). Bayesian inference and maximum parsimony were used to construct the tree, both resulting in the same topology. Nodal supports are indicated by posterior probabilities for the Bayesian inference (BI) and bootstrap values for the maximum-parsimony (MP) analysis shown above and by Bremer indexes shown below each node. For character coding and distribution of characters among taxa, see Tables 8 and 9. The scale bar indicates the fraction of substitutions per site.

The apomorphy of the *Dileptus* branch is the nuclear pattern, i.e., many macronuclear nodules and several micronuclei scattered throughout the cytoplasm. The monophyly of this clade is strongly to moderately supported by Bayesian inference (0.93 PP) and by 75% MP bootstraps (Fig. 32). This clade comprises two genera: *Dileptus* and *Apodileptus*, which are distinguishable only during binary fission. In *Dileptus* each macronuclear nodule divides individually, while the multinucleate condition of *Apodileptus* results from the fragmentation of an extensive reticulum into multiple nodules after division (Fig. 22). The latter mode evolved convergently in several distantly related haptorians, for instance, in *Spathidium turgitorum* (Foissner et al. 2002) and *Fuscheria uluruensis* (Gabilondo & Foissner 2009).

4.3 Molecular Evolution of Dileptids

The 18S rRNA gene of the dileptids is only about 1640 nucleotides long, significantly shorter than that of other ciliates, because of deletions in the helices 23–1, 23–8, 23–9, and the deletion of the entire helix 23–5 (Vďačný et al. 2011b). This is also typical for all other litostomatean sequences (Leipe et al. 1994; Wright & Lynn 1997a, 1997b; Wright et al. 1997; Strüder-Kypke et al. 2006; Vďačný et al. 2011a). The level of intraspecies sequence variation is relatively low with an average of 0.23%. The most dissimilar is *Trachelius ovum*, showing an average pairwise difference of 4.5% to all other dileptids. The average pairwise difference among representatives from the order Dileptida is 2.1%.

Dileptids s.str. and tracheliids consistently form a clade, the subclass Rhynchostomatia, which is sister to the subclass Haptoria including the Trichostomatia. This deep split within the Litostomatea is fully sustained by four different methods (Fig. 34). In all analyses, *T. ovum* is sister to dileptids s.str. This node is fully supported by Bayesian inference and strongly supported by 98% ML, 97% MP and 99% NJ bootstrap values (Fig. 34), justifying, together with three strong morphological apomorphies, the

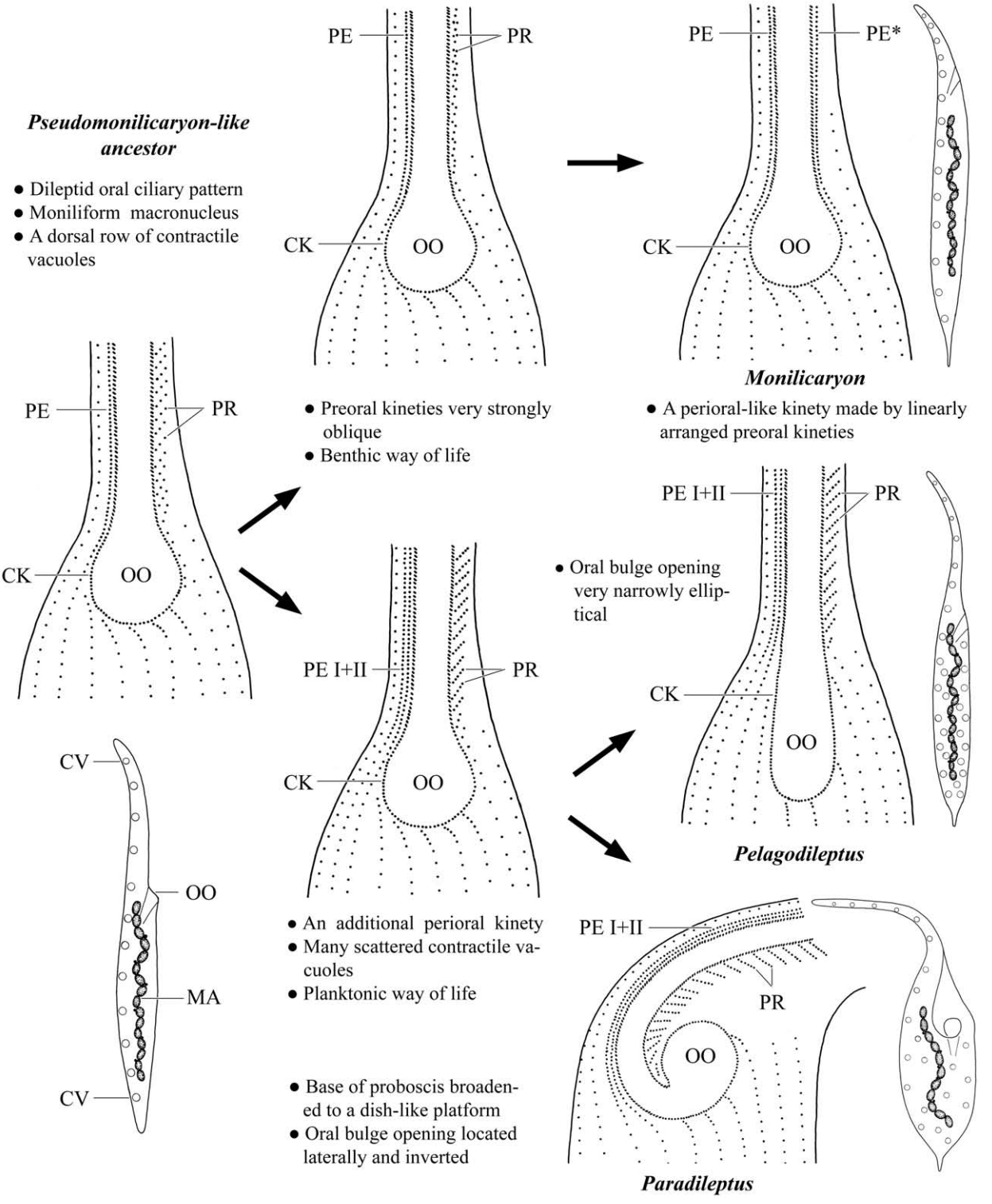


Fig. 33: Supposed evolution of the oral ciliary patterns and body shapes from a *Pseudomonilicaryon*-like ancestor (from Vďačný et al. 2011b). CK – circumoral kinety, CV – contractile vacuoles, MA –moniliform macronuclear strand, OO – oral bulge opening, PE (I+II) – perioral kinety (1 and 2), PE* – perioral-like kinety, PR – preoral kineties.

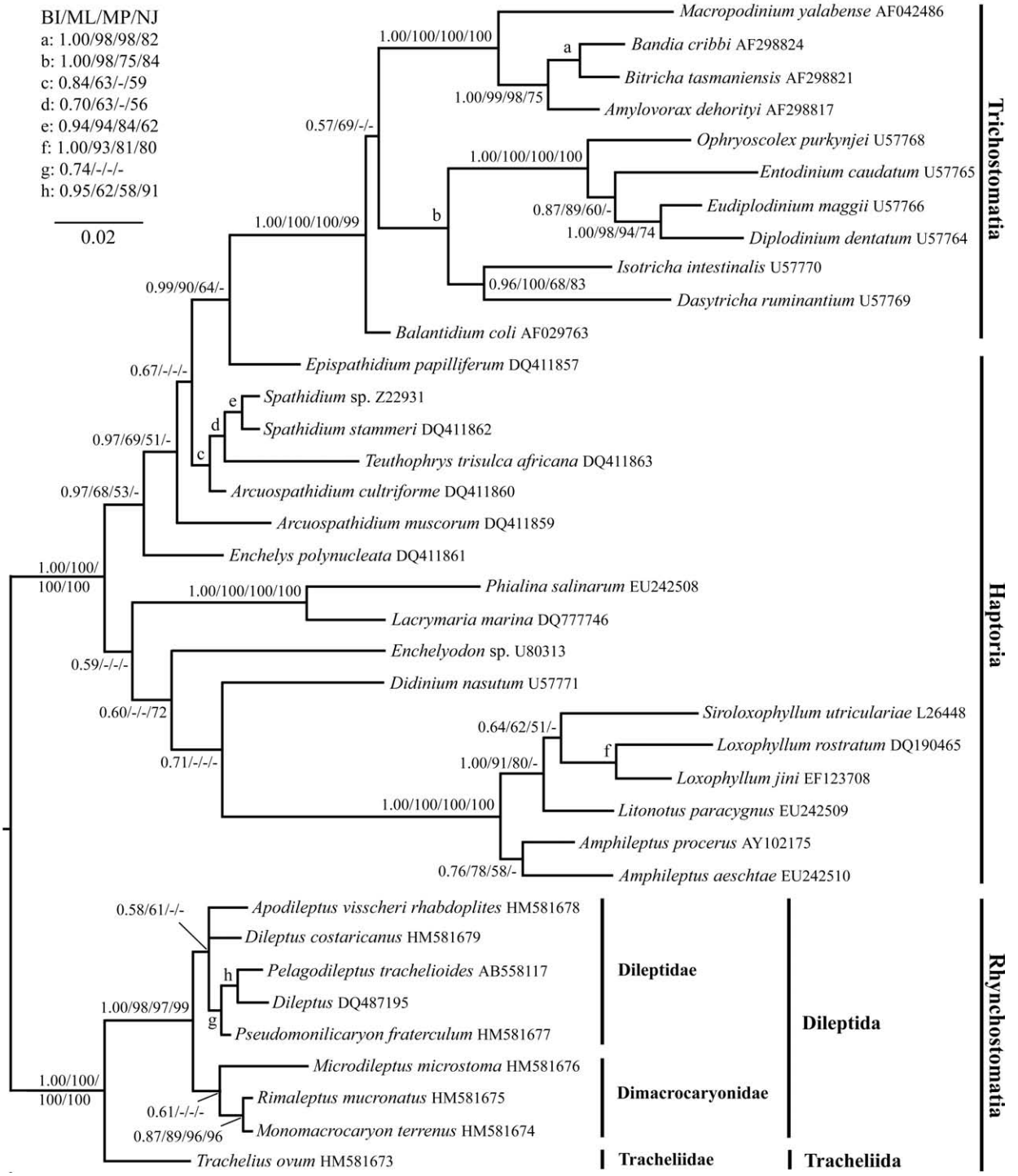


Fig. 34: Small subunit rRNA gene phylogeny based on 1442 nucleotide characters of 37 litostomatean taxa (from VĎAČNÝ et al. 2011b). The three was constructed using Bayesian inference, maximum likelihood, maximum parsimony, and neighbour-joining with the GTR + I + Γ substitution model. Posterior probabilities (PP) for the Bayesian inference and bootstrap values for the maximum-likelihood (ML), maximum-parsimony (MP), and neighbour-joining (NJ) analyses are shown at nodes (a dash indicates values below 0.50 or 50%, respectively). The scale bar indicates two substitutions per one hundred nucleotide positions.

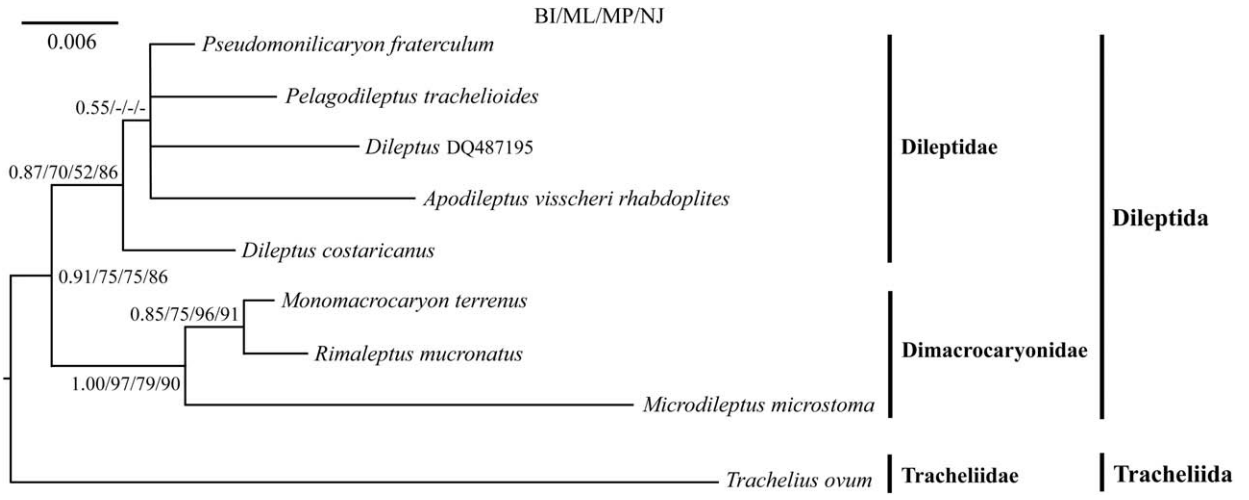


Fig. 35: Small subunit rRNA gene phylogeny based on 1635 nucleotide characters of nine dileptid taxa (from VĎAČNÝ et al. 2011b). Bayesian inference, maximum likelihood, maximum parsimony, and neighbour-joining were used to construct the tree, all resulting in a very similar topology. Posterior probabilities (PP) for the Bayesian inference and bootstrap values for the maximum-likelihood (ML), maximum-parsimony (MP), and neighbour-joining (NJ) analyses are shown at nodes (a dash indicates values below 0.50 or 50%, respectively). The scale bar indicates six substitutions per one thousand nucleotide positions.

establishment of the order, Tracheliida. Such high ranking is also suggested by various morphological peculiarities described in the morphological section. All other dileptids form a monophylum, the order Dileptida (Figs 6, 7). The analyses consistently depict two clusters within this order, viz., the family Dimacrocaryonidae (1.00 PP, 97% ML, 79% MP, and 90% NJ) with one or two macronuclear nodules and a single micronucleus, and the family Dileptidae (0.87 PP, 70% ML, 52% MP, and 86% NJ) with at least four macronuclear nodules and many micronuclei (Fig. 35). The internal relationships of the family Dileptidae are very poorly resolved in all analyses, as there is a basal polytomy that is suggestive of a radiation event (Figs 34, 35).

4.4 Comparison of Morphological and Molecular Phylogenies

The morphological trees are basically congruent with those based on the 18S rRNA gene sequences, especially in that the genus *Trachelius* is sister to the dileptids s.str., and the order Dileptida as well as the multinucleate family Dileptidae are monophyletic. The family Dimacrocaryonidae is monophyletic in the molecular trees, while paraphyletic in the morphological analyses. This discrepancy is caused by the lack of morphological synapomorphies for the genus *Monomacrocaryon* and the *Dimacrocaryon-Rimaleptus* clade. Accordingly, the basal position of *Monomacrocaryon* within the order Dileptida in the morphological trees is very likely artificial. The molecular data indicate that the unsegmented macronucleus of *M. terrenum* evolved from a binucleate state by fusion of the macronuclear nodules and not vice versa as suggested by morphological phylogenies. Further, dimacrocaryonid dileptids consistently cluster outside the *Dileptus/ Pseudomonilicaryon/Pelagodileptus* clade in morphological cladograms and molecular trees.

Table 10: Classification of dileptids (bold face) according to CHEISSIN & POLJANSKY (1963).

Class Holotricha
- **1. Order Gymnostomatida**
- 2. Order Trichostomatida
- 3. Order Hymenostomatida
- 4. Order Astomatida
- 5. Order Apostomatida
- 6. Order Thigmotrichida

Table 11: Classification of dileptids (bold face) according to JANKOWSKI (1975).

Subclass Fragmophora
1. Order Prostomatida (Paramastigina, Inferotrichina, Prionostomatina, Trachelocercina, Rhynchophorina, Cyclotrichina, Didesmina)
2. Order Orthostomatida
3. Order Plagiopylida
4. Order Pleurostomatida (Amphileptina, Loxodina, Scaphotrichina, Thysanophorina)
5. **Order Rhynchostomatida**
6. Order Rimostomatida
7. Order Colpodida
8. Order Isotrichida
9. Order Paraisotrichida

Table 12: Classification of dileptids (bold face) according to CORLISS (1979).

Class Kinetofragminophora de PUYTORAC et al., 1974
- Subclass Gymnostomata BÜTSCHLI, 1889
  1. Order Primociliatida CORLISS, 1974
  2. Order Karyorelictida CORLISS, 1974
  3. Order Prostomatida SCHEWIAKOFF, 1896
     1. Suborder Archistomatina de PUYTORAC et al., 1974
     2. Suborder Prostomatina SCHEWIAKOFF, 1896
     3. Suborder Prorodontina CORLISS, 1974
  4. **Order Haptorida CORLISS, 1974**
  5. Order Pleurostomatida SCHEWIAKOFF, 1896

Table 13: Classification of dileptids (bold face) according to LIPSCOMB & RIORDAN (1990).

Class Litostomatea SMALL and LYNN, 1981
- Subclass Haptoria CORLISS, 1974
  1. Order Haptorida CORLISS, 1974
     1. Suborder Helicoprorodontina FOISSNER & FOISSNER, 1988
     2. Suborder Vestibulifera
     3. Suborder Acropisthinna FOISSNER & FOISSNER, 1988
     4. Suborder Enchelyina FOISSNER & FOISSNER, 1988
     5. **Suborder Dileptina JANKOWSKI, 1978**
  2. Order Pleurostomatida SCHEWIAKOFF, 1896
     1. Suborder Lacrymariidae nov. subord.
     2. Suborder Didiniina JANKOWSKI, 1978
     3. Suborder Pleurostomatina nov. subord.

Table 14: Classification of dileptids (bold face) according to FOISSNER & FOISSNER (1988a).

Class Litostomatea SMALL & LYNN, 1981
- 1. Subclass Haptoria CORLISS, 1974
  1. Order Haptorida CORLISS, 1974
     1. Suborder Enchelyina nov. subord.
     2. Suborder Acropisthiina nov. subord.
     3. **Suborder Dileptina JANKOWSKI, 1978**
  2. Order Spathidiida nov. ord.
     1. Suborder Spathidiina JANKOWSKI, 1980
     2. Suborder Belonophryina JANKOWSKI, 1980
     3. Suborder Didiniina JANKOWSKI, 1978
  3. Order Pleurostomatida SCHEWIAKOFF, 1896
     1. Suborder Amphileptina JANKOWSKI, 1967
     2. Suborder Litonotina nov. subord.
  4. Order Pseudoholophryida nov. ord.
     1. Suborder Pseudoholophryina nov. subord.
     2. Suborder Helicoprorodontina nov. subord.
  5. Order Archistomatida PUYTORAC et al., 1974
  6. Order Cyclotrichida JANKOWSKI, 1980
- 2. Subclass Trichostomatia BÜTSCHLI, 1889

Table 15: Classification of dileptids (bold face) according to PUYTORAC (1994).

Subphylum Filicorticata de PUYTORAC et al., 1993
- Class Litostomatea SMALL and LYNN, 1981
  1. Order Haptorida CORLISS, 1974
     1. Suborder Acropisthiina FOISSNER & FOISSNER, 1988
     2. Suborder Belonophryina JANKOWSKI, 1980
     3. Suborder Archistomatina de PUYTORAC et al., 1974
  2. Order Spathidiida FOISSNER & FOISSNER, 1988
     1. Suborder Spathidiina JANKOWSKI, 1980
     2. Suborder Didiniina JANKOWSKI, 1980
     3. Suborder Lacrymariina LIPSCOMB & RIORDAN, 1980
     4. Suborder Trachelophyllina GRAIN in de PUYTORAC et al., 1993
     5. **Suborder Dileptina JANKOWSKI, 1978**
     6. Suborder Enchelyina FOISSNER & FOISSNER, 1988
  3. Order Helicoprorodontida GRAIN in de PUYTORAC et al., 1993
  4. Order Pleurostomatida SCHEWIAKOFF, 1896
  5. Order Mesodiniida GRAIN in de PUYTORAC et al., 1993

Table 16: Classification of dileptids (bold face) according to LYNN & SMALL (2002) and LYNN (2008).

Class Litostomatea SMALL & LYNN, 1981
- 1. Subclass Haptoria CORLISS, 1974
  1. **Order Haptorida CORLISS, 1974**
  2. Order Pleurostomatida SCHEWIAKOFF, 1896
  3. Order Cyclotrichiida JANKOWSKI, 1980 incertae sedis
- 2. Subclass Trichostomatia BÜTSCHLI, 1889

Table 17: Classification of dileptids (bold face) according to JANKOWSKI (2007).

Class Litostomatea
1. Order Haptorida CORLISS, 1974
   1. Suborder Acropisthiina FOISSNER & FOISSNER, 1988
   2. Suborder Belonophryina JANKOWSKI, 1980
   3. Suborder Archistomatina PUYTORAC et al., 1974
2. Order Spathidiida FOISSNER & FOISSNER, 1988
   1. Suborder Spathidiina JANKOWSKI, 1980
   2. Suborder Didiniina JANKOWSKI, 1978
   3. Suborder Lacrymariina LIPSCOMB & RIORDAN, 1980
   4. Suborder Trachelophyllina subordo n.
   5. Suborder Dileptina JANKOWSKI, 1978
   6. Suborder Enchelyina FOISSNER & FOISSNER, 1988
3. Order Helicoprorodontida ordo n.

Table 18: Classification of dileptids (bold face) used in this monograph.

Class Litostomatea SMALL & LYNN, 1981
1. Subclass Rhynchostomatia JANKOWSKI, 1980
   1. Order Tracheliida VĎAČNÝ et al., 2011
   2. Order Dileptida JANKOWSKI, 1978
2. Subclass Haptoria CORLISS, 1974
   1. Order Haptorida CORLISS, 1974
   2. Order Lacrymariida LIPSCOMB & RIORDAN, 1990
   3. Order Didiniida JANKOWSKI, 1978
   4. Order Pleurostomatida SCHEWIAKOFF, 1896
   5. Order Spathidiida FOISSNER & FOISSNER, 1988
   6. Order Pseudoholophryida FOISSNER & FOISSNER, 1988
3. Subclass Trichostomatia BÜTSCHLI, 1889

5 Classification

The major classification schemes for the dileptids are shown in Tables 10–18. We did not change the original presentations, e.g., incorrect datings and spellings of names etc.

In the past, dileptids were classified as a subgroup of the order Gymnostomatida due to the holotrichous ciliature (BÜTSCHLI 1889, KAHL 1931, CHEISSIN & POLIANSKI 1963; Table 10). CORLISS (1974, 1979) placed the dileptids in his order Haptorida, which he established for rapacious ciliates having a dorsal brush and toxicysts (Table 12). Based on the conspicuous proboscis, JANKOWSKI (1975) classified dileptids in a distinct order, Rhynchostomatida (Table 11), which he later raised to subclass rank (JANKOWSKI 1980). However, this was not accepted by SMALL & LYNN (1981, 1985), who followed CORLISS (1979). Further, they added important characters on the fine structure of the somatic and oral kinetids, creating the class Litostomatea. Within the Litostomatea, they recognized the subclasses Haptoria and Trichostomatia, classifying the dileptids in the order Haptorida (Table 16). Using morphological and ultrastructural data, FOISSNER & FOISSNER (1988a) detailed the haptorian system and classified dileptids in the suborder Dileptina due to the comparatively complex oral ciliary pattern (Table 14). This classification was accepted by LIPSCOMB & RIORDAN (1990, 1992), using 46 ultrastructural and light microscopical characters in their cladistic analysis (Table 13). PUYTORAC (1994) and JANKOWSKI (2007), also using light and electronmicroscopic data, recognized the suborder Dileptina, but placed it into the order Spathidiida (Tables 15 and 16). The recent molecular data basically support the Rhynchostomatia concept, in which dileptids are sister to all other litostomateans, i.e., the haptorians and trichostomatians (Table 17).

6 Synonymy rate

The synonymy rate is important for calculating the number of valid taxa, locally and globally (for review, see FOISSNER et al. 2008a). The synonymy rate (SR) was calculated as proportion of synonyms (S) to all reliable dipletids (RD) including their synonyms (S): SR = S/(RD + S). We took into consideration only those objective and subjective nomenclatural synonyms, where the data were sufficient to be sure that it is a dileptid; subspecies were treated as species (Tables 19 and 20).

In the dileptids, the generic synonymy rate is 20%, which matches the rate for the total ciliate genera (AESCHT 2001). However, if taxa with “unclear identity”are included, the rate increases to 45.5% (Table 19). In ciliate species, the synonymy rate is around 20% (FOISSNER et al. 2008a). This matches the 27.5% found in dileptids. However, when the taxa with “unclear identity” are added, the rate inceases to 60.5% (Table 20), mainly due to the poorly described taxa of FROMENTEL (1874–1876) and DUMAS (1929, 1930, 1937).

Table 19: List of genera associated with dileptid ciliates. We recognize 12 dileptid genera and two to three synonyms (*Harmodirus*, *Ophryocerca*, *Phragelliorhynchus*). All others are not dileptids but may belong to reliable genera, e.g., *Amphileptus*, or their identity is unclear.

Genus	Type species (basionym)	Present status/remarks
Amphileptus EHRENBERG, 1830	*Amphileptus cygnus* EHRENBERG, 1830	reliable non-dileptid genus
Apodileptus VĎAČNÝ et al., 2011	*Dileptus visscheri* DRAGESCO, 1963	reliable dileptid genus
Apotrachelius nov. gen.	*Apotrachelius multinucleatus* nov. spec.	reliable dileptid genus
Cephalorhynchus DIESING, 1865	*Trachelius laticeps* EHRENBERG, 1840	identity unclear
Ctenoctophrys WEILL, 1946	*Ctenoctophrys chattoni* WEILL, 1946	identity unclear
Dileptus DUJARDIN, 1841	*Amphileptus margaritifer* EHRENBERG, 1833	reliable dileptid genus
Dimacrocaryon JANKOWSKI, 1967	*Dileptus amphileptoides* KAHL, 1931	reliable dileptid genus
Harmodirus PERTY, 1852	*Ophryocerca ovum* EHRENBERG, 1831	objective synonym of *Trachelius*
Liosiphon EHRENBERG, 1853	*Liosiphon strampfii* EHRENBERG, 1853	subjective synonym of *Nassula* in CORLISS (1961); supposed synonym of *Dileptus* in JANKOWSKI (2007); identity unclear in our opinion
Microdileptus nov. gen.	*Dileptus microstoma* VĎAČNÝ & FOISSNER, 2008	reliable dileptid genus
Micruncus DELPHY, 1938	*Micruncus complanatus* DELPHY, 1938	identity unclear
Monilicaryon JANKOWSKI, 1967	*Amphileptus monilatus* STOKES, 1886	reliable dileptid genus
Monomacrocaryon VĎAČNÝ et al., 2011	*Dileptus terrenus* FOISSNER, 1981	reliable dileptid genus
Ophryocerca EHRENBERG, 1831	*Ophryocerca ovum* EHRENBERG, 1831	subjective synonym of *Trachelius*
Paradileptus WENRICH, 1929	*Amphileptus flagellatus* ROUSSELET, 1890	reliable dileptid genus
Pelagodileptus FOISSNER et al., 1999	*Dileptus trachelioides* ZACHARIAS, 1984	reliable dileptid genus
Phragelliorhynchus HERRICK, 1884	*Phragelliorhynchus nasutus* HERRICK, 1884	synonym of *Dileptus* in KAHL (1931) and JANKOWSKI (2007); identity unclear in our opinion
Pseudodileptus	–	see footnote
Pseudomonilicaryon FOISSNER, 1997	*Dileptus gracilis* KAHL, 1931	reliable dileptid genus
Rimaleptus FOISSNER, 1984	*Dileptus binucleatus* KAHL, 1931	reliable dileptid genus
Trachelius SCHRANK, 1803	*Ophryocerca ovum* EHRENBERG, 1831	reliable dileptid genus
Trichoda MUELLER, 1773	*Trichoda acarus* MUELLER, 1773	nomen oblitum in BERGER (1999)
Vibrio MUELLER, 1773	–	outdated

[1] Considered as a nomen nudum in AESCHT (2001). JANKOWSKI (personal communication) informed us that he saw the name *Pseudodileptus* in a journal, which he could not remember, where it was used for *Amphileptus trachelioides* ZACHARIAS. Very likely, the genus *Paradileptus* was meant.

Table 20: List of species associated with dileptids and their current names and states. Altogether, there are 181 nominal species, of which 66 are recognized as reliable dileptids, 25 are considered as synonyms of reliable dileptids, 90 belong to other non-dileptid genera (14) and/or their identity is unclear (76).

Taxon (basionym)	Current name/combination	Present state
Amphileptus cygnus CLAPARÈDE & LACHMANN, 1859	*Pseudomonilicaryon anser* (MUELLER, 1773) nov. comb.	synonym
Amphileptus flagellatus ROUSSLETT, 1890	*Paradileptus elephantinus* (ŠVEC, 1897) KAHL, 1931	synonym
Amphileptus gigas CLAPARÈDE & LACHMANN, 1859	*Monomacrocaryon gigas* (CLAPARÈDE & LACHMANN, 1859) VĎAČNÝ et al., 2011	reliable dileptid
Amphileptus irregularis MASKELL, 1887	*Dileptus margaritifer* (EHRENBERG, 1833) DUJARDIN, 1841	synonym
Amphileptus lacazei GOURRET & ROESER, 1886	*Rimaleptus lacazei* (GOURRET & ROESER, 1886) nov. comb.	reliable dileptid
Amphileptus longicollis EHRENBERG, 1831	*Pseudomonilicaryon anser* (MUELLER, 1773) nov. comb.	synonym
Amphileptus margaritifer EHRENBERG, 1833	*Dileptus margaritifer* (EHRENBERG, 1833) DUJARDIN, 1841	reliable dileptid
Amphileptus massiliensis GOURRET & ROESER, 1886	–	identity unclear
Amphileptus monilatus STOKES, 1886	*Monilicaryon monilatum* (STOKES, 1886) JANKOWSKI, 1967	reliable dileptid
Amphileptus moniliger EHRENBERG, 1835	*Paradileptus elephantinus* (Švec, 1897) KAHL, 1931	synonym
Amphileptus rotundus MASKELL, 1887	*Trachelius ovum* (EHRENBERG, 1831) EHRENBERG, 1833	synonym
Amphileptus tracheloides MASKELL, 1887	–	identity unclear
Amphileptus viridis EHRENBERG, 1833	*Dileptus viridis* (EHRENBERG, 1833) FOISSNER, 1987	reliable dileptid
Apodileptus edaphicus nov. spec.	*Apodileptus edaphicus* nov. spec.	reliable dileptid
Apodileptus visscheri rhabdoplites nov. sspec.	*Apodileptus visscheri rhabdoplites* nov. sspec.	reliable dileptid
Apotrachelius multinucleatus nov. spec.	*Apotrachelius multinucleatus* nov. spec.	reliable dileptid
Dileptus aculeatus DRAGESCO, 1960	*Pseudomonilicaryon aculeatum* (DRAGESCO, 1960) nov. comb.	reliable dileptid
Dileptus acutus DUMAS, 1929	–	identity unclear
Dileptus aduncus DUMAS, 1929	–	identity unclear
Dileptus alpinus KAHL, 1931	*Rimaleptus alpinus* (KAHL, 1931) nov. comb.	reliable dileptid
Dileptus americanus KAHL, 1931	*Rimaleptus binucleatus* (KAHL, 1931) FOISSNER, 1984	synonym
Dileptus amphileptoides KAHL, 1931	*Dimacrocaryon amphileptoides amphileptoides* (KAHL, 1931) JANKOWSKI, 1967	reliable dileptid
Dileptus anas FROMENTEL, 1876	–	identity unclear
Dileptus anatinus GOLIŃSKA, 1971	*Dileptus anatinus* GOLIŃSKA, 1971	reliable dileptid
Dileptus anguillula KAHL, 1931	*Pseudomonilicaryon anguillula* (KAHL, 1931) nov. comb.	reliable dileptid
Dileptus arcuatus DUMAS, 1929	–	identity unclear
Dileptus armatus FOISSNER & SCHADE in FOISSNER, 2002	*Rimaleptus armatus* (FOISSNER & SCHADE in FOISSNER, 2000) nov. comb.	reliable dileptid
Dileptus beersi JONES, 1956	*Dileptus beersi* JONES, 1956	reliable dileptid
Dileptus biacuta DUMAS, 1937	–	identity unclear
Dileptus bicaudatus DUMAS, 1929	–	identity unclear
Dileptus bicornis DUMAS, 1929	–	identity unclear
Dileptus bicristatus DUMAS, 1929	–	identity unclear
Dileptus binucleatus KAHL, 1931	*Rimaleptus binucleatus* (KAHL, 1931) FOISSNER, 1984	reliable dileptid
Dileptus bivacuolatus da CUNHA, 1913	*Rimaleptus bivacuolatus* (da CUNHA, 1913) nov. comb.	reliable dileptid
Dileptus branchiatus DUMAS, 1929	–	identity unclear

Taxon (basionym)	Current name/combination	Present state
Dileptus breviproboscis FOISSNER, 1981	*Microdileptus breviproboscis* (FOISSNER, 1981) nov. comb.	reliable dileptid
Dileptus calceolus FROMENTEL, 1876	–	identity unclear
Dileptus caudatus FROMENTEL, 1876	–	identity unclear
Dileptus cavicaudus DUMAS, 1929	–	identity unclear
Dileptus cilunculus DUMAS, 1930	–	identity unclear
Dileptus cinereus DUMAS, 1929	–	identity unclear
Dileptus clavipes DUMAS, 1929	–	identity unclear
Dileptus conspicuus KAHL, 1931	*Rimaleptus conspicuus* (KAHL, 1931) nov. comb.	reliable dileptid
Dileptus conspicuus var. *telobivacuolatus* GELLÉRT, 1955	*Rimaleptus conspicuus* (KAHL, 1931) nov. comb.	synonym
Dileptus corniculatus DUMAS, 1929	–	identity unclear
Dileptus corniger FROMENTEL, 1876	–	identity unclear
Dileptus costaricanus FOISSNER, 1995	*Dileptus costaricanus* FOISSNER, 1995	reliable dileptid
Dileptus costatus DUMAS, 1929	–	identity unclear
Dileptus crinitus FROMENTEL, 1876	–	identity unclear
Dileptus crispatus DUMAS, 1930	–	identity unclear
Dileptus cristatus DUMAS, 1937	–	identity unclear
Dileptus cuspidatus DUMAS, 1929	–	identity unclear
Dileptus cylindricus FROMENTEL, 1876	–	identity unclear
Dileptus cylindroïdes DUMAS, 1929	–	identity unclear
Dileptus decorus DUMAS, 1929	–	identity unclear
Dileptus diaphanus DUMAS, 1929	–	identity unclear
Dileptus difforme DUMAS, 1929	–	identity unclear
Dileptus dimorphus WANG, 1940	*Pseudomonilicaryon dimorphum* (WANG, 1940) nov. comb.	reliable dileptid
Dileptus dubius VUXANOVICI, 1959	*Dileptus dubius* VUXANOVICI, 1959	reliable dileptid
Dileptus ectromeloïdes DUMAS, 1937	–	identity unclear
Dileptus edaphoni SONG, 1994	*Pseudomonilicaryon edaphoni* (SONG, 1994) nov. comb.	reliable dileptid
Dileptus elephantinus ŠVEC, 1897	*Paradileptus elephantinus* (ŠVEC, 1897) KAHL, 1931	reliable dileptid
Dileptus estuarinus DRAGESCO, 1960	*Dileptus estuarinus* DRAGESCO, 1960	reliable dileptid
Dileptus exiguus DUMAS, 1930	–	identity unclear
Dileptus falciformis DUMAS, 1930	–	identity unclear
Dileptus falciformis KAHL, 1931	*Pseudomonilicaryon falciforme* (KAHL, 1931) nov. comb.	reliable dileptid
Dileptus fasciola FROMENTEL, 1876	*Litonotus fasciola* (EHRENBERG, 1838) WRZEŚNIOWSKI, 1870	*Litonotus*
Dileptus fastigiatus DUMAS, 1929	–	identity unclear
Dileptus folium DUJARDIN, 1841	*Litonotus cygnus* (MUELLER, 1773) FOISSNER et al., 1995	*Litonotus*
Dileptus gabonensis DRAGESCO, 1963	*Rimaleptus gabonensis* (DRAGESCO & DRAGESCO-KERNÉIS, 1986) nov. comb.	reliable dileptid
Dileptus gallina FROMENTEL, 1876	–	identity unclear
Dileptus gibbosus DUMAS, 1929	–	identity unclear

continued

Taxon (basionym)	Current name/combination	Present state
Dileptus gigas grojecensis WRZEŚNIOWSKI, 1870	*Pseudomonilicaryon anser* (MUELLER, 1773) nov. comb.	synonym
Dileptus gigas varsaviensis WRZEŚNIOWSKI, 1870	*Dileptus margaritifer* (EHRENBERG, 1833) DUJARDIN, 1841	synonym
Dileptus gonophyllus DUMAS, 1929	–	identity unclear
Dileptus gracilis KAHL, 1931	*Pseudomonilicaryon gracile gracile* (KAHL, 1931) FOISSNER, 1997 nov. stat.	reliable dileptid
Dileptus grandis DRAGESCO, 1963	*Pseudomonilicaryon massutii* (KAHL, 1933) FOISSNER et al., 2002	synonym
Dileptus granulosus DUJARDIN, 1841	*Dileptus margaritifer* (EHRENBERG, 1833) DUJARDIN, 1841	synonym
Dileptus gulosus DUMAS, 1930	–	identity unclear
Dileptus helicoïdes DUMAS, 1929	–	identity unclear
Dileptus hians DUMAS, 1930	–	identity unclear
Dileptus jonesi DRAGESCO, 1963	*Dileptus jonesi* DRAGESCO, 1963	reliable dileptid
Dileptus kahli ŠRÁMEK-HUŠEK, 1957	*Pseudomonilicaryon kahli* (ŠRÁMEK-HUŠEK, 1957) nov. comb.	reliable dileptid
Dileptus lacrimula FROMENTEL, 1876	–	identity unclear
Dileptus lacrymarioïdes DUMAS, 1929	–	identity unclear
Dileptus limbatus DUMAS, 1929	–	identity unclear
Dileptus lineatus DUMAS, 1930	–	identity unclear
Dileptus longitrichus VĎAČNÝ & FOISSNER, 2008	*Rimaleptus longitrichus* (VĎAČNÝ & FOISSNER, 2008) nov. comb.	reliable dileptid
Dileptus marginellus DUMAS, 1929	–	identity unclear
Dileptus marinus KAHL, 1933	*Pseudomonilicaryon marinum marinum* (KAHL, 1933) nov. comb., nov. stat.	reliable dileptid
Dileptus marinus var. *minimus* JONES, 1974	*Pseudomonilicaryon marinum minimum* nov. sspec.	reliable dileptid
Dileptus marouensis DRAGESCO, 1963	*Rimaleptus marouensis* (DRAGESCO, 1963) nov. comb.	reliable dileptid
Dileptus massutii KAHL, 1933	*Pseudomonilicaryon massutii* (KAHL, 1933) FOISSNER et al., 2002	reliable dileptid
Dileptus meleagris FROMENTEL, 1876	*Loxophyllum meleagris* (MUELLER, 1773) DUJARDIN, 1841	*Loxophyllum*
Dileptus microstoma VĎAČNÝ & FOISSNER, 2008	*Microdileptus microstoma* (VĎAČNÝ & FOISSNER, 2008) nov. comb.	reliable dileptid
Dileptus minimus DUMAS, 1930	–	identity unclear
Dileptus mucronatus PENARD, 1922	*Rimaleptus mucronatus* (PENARD, 1922) VĎAČNÝ et al., 2011	reliable dileptid
Dileptus multinucleatus VUXANOVICI, 1959	*Dileptus multinucleatus* VUXANOVICI, 1959	reliable dileptid
Dileptus musculus FROMENTEL, 1876	–	identity unclear
Dileptus nistroviensis CHORIK, 1967	*Rimaleptus nistroviensis* (CHORIK, 1967) nov. comb.	reliable dileptid
Dileptus orbicularis DUMAS, 1929	–	identity unclear
Dileptus orientalis SONG et al., 1988	*Rimaleptus orientalis* (SONG et al., 1988) nov. comb.	reliable dileptid
Dileptus ovalis VUXANOVICI, 1959	*Rimaleptus ovalis* (VUXANOVICI, 1959) nov. comb.	reliable dileptid
Dileptus paradoxus DUMAS, 1937	–	identity unclear
Dileptus piscis FROMENTEL, 1876	–	identity unclear
Dileptus pistillaris DUMAS, 1930	–	identity unclear
Dileptus polyvacuolatus FOISSNER, 1989	*Monomacrocaryon polyvacuolatum* (FOISSNER, 1989) VĎAČNÝ et al., 2011	reliable dileptid
Dileptus proboscideus LEPŞI, 1957	–	identity unclear
Dileptus reclinis DUMAS, 1929	–	identity unclear

continued

Taxon (basionym)	Current name/combination	Present state
Dileptus resplendens DUMAS, 1929	–	identity unclear
Dileptus robustus VUXANOVICI, 1959	*Rimaleptus robustus* (VUXANOVICI, 1959) nov. comb.	reliable dileptid
Dileptus saaleri SCHWARZ, 1962	*Pelagodileptus trachelioides* (ZACHARIAS, 1894) FOISSNER et al., 1999	synonym
Dileptus semiarmatus VĎAČNÝ & FOISSNER, 2008	*Microdileptus semiarmatus* (VĎAČNÝ & FOISSNER, 2008) nov. comb.	reliable dileptid
Dileptus similis FOISSNER, 1995	*Rimaleptus similis* (FOISSNER, 1995) nov. comb.	reliable dileptid
Dileptus singularis VUXANOVICI, 1962	*Pseudomonilicaryon gracile singulare* (VUXANOVICI, 1962) nov. comb., nov. stat.	reliable dileptid
Dileptus sinuosus DUMAS, 1929	–	identity unclear
Dileptus spiralis GELEI, 1954	–	identity unclear
Dileptus sphagnicola nov. spec.	*Dileptus sphagnicola* nov. spec.	reliable dileptid
Dileptus striatus FROMENTEL, 1876	–	identity unclear
Dileptus subcylindroïdes DUMAS, 1930	–	identity unclear
Dileptus submarginatus DUMAS, 1929	–	identity unclear
Dileptus tenuis PENARD, 1922	*Monomacrocaryon tenue* (PENARD, 1922) VĎAČNÝ et al., 2011	reliable dileptid
Dileptus terrenus FOISSNER, 1981	*Monomacrocaryon terrenum* (FOISSNER, 1981) VĎAČNÝ et al., 2011	reliable dileptid
Dileptus tirjakovae VĎAČNÝ & FOISSNER, 2008	*Rileptus tirjakovae* (VĎAČNÝ & FOISSNER, 2008) nov. comb.	reliable dileptid
Dileptus thononensis DRAGESCO, 1960	*Pseudomonilicaryon thononense* (DRAGESCO, 1960) nov. comb.	reliable dileptid
Dileptus torquescens DUMAS, 1929	–	identity unclear
Dileptus trachelioides ZACHARIAS, 1894	*Pelagodileptus trachelioides* (ZACHARIAS, 1894) FOISSNER et al., 1999	reliable dileptid
Dileptus truncatus DUMAS, 1929	homonym	identity unclear
Dileptus truncatus FROMENTEL, 1876	–	identity unclear
Dileptus uvula FROMENTEL, 1876	–	identity unclear
Dileptus visscheri DRAGESCO, 1963	*Apodileptus visscheri visscheri* (DRAGESCO, 1963) nov. comb.	reliable dileptid
Dileptus vitreus DUMAS, 1929	–	identity unclear
Dimacrocaryon amphileptoides paucivacuolatum nov. sspec.	*Dimacrocaryon amphileptoides paucivacuolatum* nov. sspec.	reliable dileptid
Dimacrocaryon arenicola nov. spec.	*Dimacrocaryon arenicola* nov. spec.	reliable dileptid
Dimacrocaryon brasiliense nov. spec.	*Dimacrocaryon brasiliense* nov. spec.	reliable dileptid
Micruncus complanatus Delphy, 1938	–	identity unclear
Ophryocerca ovum EHRENBERG, 1831	*Trachelius ovum* (EHRENBERG, 1831) EHRENBERG, 1833	reliable dileptid
Paradileptus caducus KAHL, 1935	*Pelagodileptus trachelioides* (ZACHARIAS, 1894) FOISSNER et al., 1999	synonym
Paradileptus canellai DRAGESCO, 1966	*Pelagodileptus trachelioides* (ZACHARIAS, 1894) FOISSNER et al., 1999	synonym
Paradileptus conicus WENRICH, 1929	*Paradileptus elephantinus* (ŠVEC, 1897) KAHL, 1931	synonym
Paradileptus estensis CANELLA, 1951	*Paradileptus elephantinus* (ŠVEC, 1897) KAHL, 1931	synonym
Paradileptus minutus DRAGESCO, 1972	*Paradileptus elephantinus* (ŠVEC, 1897) KAHL, 1931	synonym
Paradileptus ovalis HUBER-PESTALOZZI, 1945	*Paradileptus elephantinus* (ŠVEC, 1897) KAHL, 1931	synonym
Paradileptus robustus WENRICH, 1929	*Paradileptus elephantinus* (ŠVEC, 1897) KAHL, 1931	synonym
Phragelliorhynchus nasutus HERRICK, 1884	–	identity unclear
Pseudomonilicaryon angustistoma FOISSNER et al., 2002	*Pseudomonilicaryon angustistoma* FOISSNER et al., 2002	reliable dileptid

continued

Taxon (basionym)	Current name/combination	Present state
Pseudomonilicaryon brachyproboscis VĎAČNÝ & FOISSNER, 2008	*Pseudomonilicaryon brachyproboscis* VĎAČNÝ & FOISSNER, 2008	reliable dileptid
Pseudomonilicaryon gracile antevacuolatum nov. subsp.	*Pseudomonilicaryon gracile antevacuolatum* nov. subsp.	reliable dileptid
Pseudomonilicaryon gracile oviplites nov. sspec.	*Pseudomonilicaryon gracile oviplites* nov. sspec.	reliable dileptid
Pseudomonilicaryon japonicum FOISSNER et al., 2002	*Pseudomonilicaryon japonicum* FOISSNER et al., 2002	reliable dileptid
Pseudomonilicaryon fraterculum nov. spec.	*Pseudomonilicaryon fraterculum* nov. spec.	reliable dileptid
Rimaleptus canadensis nov. spec.	*Rimaleptus canadensis* nov. spec.	reliable dileptid
Rimaleptus brasiliensis nov. spec.	*Rimaleptus brasiliensis* nov. spec.	reliable dileptid
Tentaculifera mexicana SOKOLOFF, 1931	*Paradileptus elephantinus* (ŠVEC, 1897) KAHL, 1931	synonym
Trachelius ambiguus EHRENBERG, 1831	*Spirostomum ambiguum* (MUELLER, 1876) EHRENBERG, 1835	*Spirostomum*
Trachelius anas EHRENBERG, 1831	–	identity unclear
Trachelius anaticula EHRENBERG, 1833	–	identity unclear
Trachelius anhinga SCHRANK, 1803	*Lacrymaria olor* (MUELLER, 1876) BORY DE SAINT-VINCENT, 1824	*Lacrymaria*
Trachelius apiculatus PERTY, 1852	*Trachelophyllum apiculatum* (PERTY, 1852) CLAPARÈDE & LACHMANN, 1859	*Trachelophyllum*
Trachelius cicer SCHRANK, 1803	*Trachelius ovum* (EHRENBERG, 1831) EHRENBERG, 1833	synonym
Trachelius colymbus SCHRANK, 1803	–	identity unclear
Trachelius cygnus SCHRANK, 1803	*Litonotus cygnus* (MUELLER, 1773) FOISSNER et al., 1995	*Litonotus*
Trachelius dendrophilus EHRENBERG, 1853	–	identity unclear
Trachelius falx SCHRANK, 1803	–	identity unclear
Trachelius globulifer EHRENBERG, 1838	*Heteronema globuliferum* (EHRENBERG, 1838) STEIN, 1878	*Heteronema* (flagellate)
Trachelius lamella EHRENBERG, 1838	*Litonotus lamella* (MUELLER, 1773) FOISSNER et al., 1995	*Litonotus*
Trachelius laticeps EHRENBERG, 1840	–	identity unclear
Trachelius leidyi FOULKE, 1884	*Trachelius ovum* (EHRENBERG, 1831) EHRENBERG, 1833	synonym
Trachelius meleagris EHRENBERG, 1838	–	identity unclear
Trachelius noduliferus PERTY, 1852	–	identity unclear
Trachelius planaria SCHRANK, 1803	*Litonotus fasciola* (MUELLER, 1773) WRZEŚNIOWSKI, 1870	*Litonotus*
Trachelius proteus OKEN, 1815	*Lacrymaria olor* (MUELLER, 1876) BORY DE SAINT-VINCENT, 1824	*Lacrymaria*
Trachelius pusillus PERTY, 1852	*Trachelophyllum pusillum* (PERTY, 1952) CLAPARÈDE & LACHMANN, 1858	*Trachelophyllum*
Trachelius strictus DUJARDIN, 1841	–	identity unclear
Trachelius stylatus SCHRANK, 1803	–	identity unclear
Trachelius subtilis PENARD, 1922	*Trachelius ovum* (EHRENBERG, 1831) EHRENBERG, 1833	synonym
Trachelius teres DUJARDIN, 1841	–	identity unclear
Trachelius trichophorus EHRENBERG, 1838	*Peranema trichophorum* (EHRENBERG, 1838) STEIN, 1878	*Peranema* (flagellate)
Trachelius utriculus SCHRANK, 1803	*Litonotus fasciola* (MUELLER, 1773) WRZEŚNIOWSKI, 1870	*Litonotus*
Trachelius vorax EHRENBERG, 1833	*Trachelius ovum* (EHRENBERG, 1831) EHRENBERG, 1833	synonym
Vibrio anser MUELLER, 1773	*Pseudomonilicaryon anser* (MUELLER, 1773) nov. comb.	reliable dileptid

continued

7 List of Genera and Nominal Species Associated with Dileptids

8 Summary of New Taxa and Nomenclatural Acts

Within the framework of the revision, five papers (Vďačný & Foissner 2008a, 2008b, 2009; Vďačný et al. 2011a, 2011b) have been published. In these publications and within the present monograph, the following nomenclatural acts have been undertaken.

New higher taxa

Dimacrocaryonidae Vďačný et al., 2011 (type genus: *Dimacrocaryon* Jankowski, 1967); p. 143

Tracheliida Vďačný et al., 2011 (type family: Tracheliidae Ehrenberg, 1838); p. 110

Reactivated higher taxa

Rhynchostomatia Jankowski, 1980 (type order: Dileptida Jankowski, 1978); p. 109

New genera

Apodileptus Vďačný et al., 2011 (type species: *Dileptus visscheri* Dragesco, 1963); p. 323

Apotrachelius nov. gen. (type species: *A. multinucleatus* nov. sp.); p. 135

Microdileptus nov. gen. (type species: *Dileptus microstoma* Vďačný & Foissner, 2008); p. 242

Monomacrocaryon Vďačný et al., 2011 (type species: *Dileptus terrenus* Foissner, 1981); p. 143

New species

Apodileptus edaphicus nov. sp.; p. 339

Apotrachelius multinucleatus nov. sp.; p. 135

Dileptus sphagnicola nov. sp.; p. 269

Dimacrocaryon arenicola nov. sp.; p. 167

Dimacrocaryon brasiliense nov. sp.; p. 162

Microdileptus microstoma (Vďačný & Foissner, 2008) nov. comb.; p. 252

Microdileptus semiarmatus (Vďačný & Foissner, 2008) nov. comb.; p. 257

Pseudomonilicaryon brachyproboscis Vďačný & Foissner, 2008; p. 408

Pseudomonilicaryon fraterculum nov. sp.; p. 371

Rimaleptus canadensis nov. sp.; p. 196

Rimaleptus brasiliensis nov. sp.; p. 214

Rimaleptus longitrichus (Vďačný & Foissner, 2008) nov. comb.; p. 232

Rimaleptus tirjakovae (Vďačný & Foissner, 2008) nov. comb.; p. 228

New subspecies

Apodileptus visscheri rhabdoplites nov. ssp.; p. 334

Dimacrocaryon amphileptoides paucivacuolatum nov. ssp.; p. 178

Pseudomonilicaryon gracile antevacuolatum nov. ssp.; p. 397
Pseudomonilicaryon gracile oviplites nov. ssp.; p. 399
Pseudomonilicaryon marinum minimum nov. ssp.; p. 359

New combinations

Amphileptus gigas Claparède & Lachmann, 1859 transferred to *Monomacrocaryon*; p. 154
Amphileptus lacazei Gourret & Roeser, 1886 transferred to *Rimaleptus*; p. 185
Dileptus aculeatus Dragesco, 1960 transferred to *Pseudomonilicaryon*; p. 387
Dileptus alpinus Kahl, 1931 transferred to *Rimaleptus*; p. 191
Dileptus anguillula Kahl, 1931 transferred to *Pseudomonilicaryon*; p. 414
Dileptus armatus Foissner & Schade in Foissner, 2000 transferred to *Rimaleptus*; p. 200
Dileptus bivacuolatus da Cunha, 1913 transferred to *Rimaleptus*; p. 195
Dileptus breviproboscis Foissner, 1981 transferred to *Microdileptus*; p. 243
Dileptus conspicuus Kahl, 1931 transferred to *Rimaleptus*; p. 187
Dileptus dimorphus Wang, 1940 transferred to *Pseudomonilicaryon*; p. 384
Dileptus edaphoni Song, 1994 transferred to *Pseudomonilicaryon*; p. 387
Dileptus falciformis Kahl, 1931 transferred to *Pseudomonilicaryon*; p. 388
Dileptus gabonensis Dragesco & Dragesco-Kernéis, 1986 transferred to *Rimaleptus*; p. 186
Dileptus kahli Šrámek-Hušek, 1957 transferred to *Pseudomonilicaryon*; p. 433
Dileptus longitrichus Vďačný & Foissner, 2008 transferred to *Rimaleptus*; p. 232
Dileptus marinus Kahl, 1933 transferred to *Pseudomonilicaryon*; p. 357
Dileptus marouensis Dragesco, 1963 transferred to *Rimaleptus*; p. 184
Dileptus microstoma Vďačný & Foissner, 2008 transferred to *Microdileptus*; p. 252
Dileptus nistroviensis Chorik, 1967 transferred to *Rimaleptus*; p. 181
Dileptus orientalis Song et al., 1988 transferred to *Rimaleptus*; p. 240
Dileptus ovalis Vuxanovici, 1959 transferred to *Rimaleptus*; p. 181
Dileptus polyvacuolatus Foissner, 1989 transferred to *Monomacrocaryon*; p. 157
Dileptus robustus Vuxanovici, 1959 transferred to *Rimaleptus*; p. 183
Dileptus semiarmatus Vďačný & Foissner, 2008 transferred to *Microdileptus*; p. 257
Dileptus similis Foissner, 1995 transferred to *Rimaleptus*; p. 236
Dileptus singularis Vuxanovici, 1962 transferred to *Pseudomonilicaryon*; p. 396
Dileptus tenuis Penard, 1922 transferred to *Monomacrocaryon*; p. 144
Dileptus terrenus Foissner, 1981 transferred to *Monomacrocaryon*; p. 145
Dileptus tirjakovae Vďačný & Foissner, 2008 transferred to *Rimaleptus*; p. 228
Dileptus thononensis Dragesco, 1960 transferred to *Pseudomonilicaryon*; p. 404
Dileptus visscheri Dragesco, 1963 transferred to *Apodileptus*; p. 324
Vibrio anser Mueller, 1773 transferred to *Pseudomonilicaryon*; p. 359

Neotypifications

Apodileptus visscheri (Dragesco, 1963) Vďačný, Orsi, Bourland, Shimano, Epstein & Foissner, 2011 neotypified here with a Salzburg population, now considered of subspecific rank; p. 324

Dimacrocaryon amphileptoides (Kahl, 1931) Jankowski, 1967 neotypified with a Salzburg population by Foissner (1984), now considered of subspecific rank; p. 169

Monilicaryon monilatum (Stokes, 1886) Jankowski, 1967 neotypified with a Bavarian population by Foissner (1997a); p. 344

Pseudomonilicaryon anser (Mueller, 1773) nov. comb. neotypified with an Austrian population by Wirnsberger et al. (1984); p. 361

Pseudomonilicaryon gracile (Kahl, 1931) Foissner, 1997 neotypified with a Bavarian population by Foissner (1989), now considered as *P. gracile antevacuolatum*; p. 396

Pseudomonilicaryon massutii (Kahl, 1933) Foissner, Agatha & Berger, 2002 neotypified with a Namibian population by the latter authors; p. 353

Rimaleptus alpinus (Kahl, 1931) nov. comb. neotypified with a Bavarian population by Foissner (1989); p. 191

Rimaleptus conspicuus (Kahl, 1931) nov. comb. neotypified with an Icelandic population by Foissner (1989); p. 187

Rimaleptus mucronatus (Penard, 1922) Vďačný, Orsi, Bourland, Shimano, Epstein & Foissner, 2011 neotypified with an Austrian population by Foissner (1984); p. 247

Trachelius ovum (Ehrenberg, 1831) Ehrenberg, 1833 neotypified with a Bavarian population by Foissner (1997a); p. 117

Nomina correcta

Monilicaryon monilatum for *M. monilatus* (see Aescht 2001), p. 344

Monomacrocaryon terrenum for *M. terrenus*, p. 152

Pseudomonilicaryon gracile for *P. gracilis* (see Aescht 2008), p. 392

Nomina nuda

Rhynchostomatida Jankowski, 1975; p. 109

Dileptidae Jankowski, 1978 (validated by Jankowski in 1980); p. 262

Dileptus Dujardin, 1840 (validated by Dujardin in 1841); p. 265

Dileptus difforme Dumas, 1929; p. 474

Dileptus granulosus Dujardin, 1841; p. 292

New homonyms

Dileptus falciformis Dumas, 1930 is homonymous with *Dileptus falciformis* Kahl, 1931 [According to Article 23.9.5 of the ICZN (1999) a replacment name is not needed because Kahl's species has been combined with *Pseudomonilicaryon*]; p. 388

Recognized and new synonyms (including supposed synonyms)

Amphileptus cygnus Claparède & Lachmann, 1859 is synonymous with *Pseudomonilicaryon anser*

(MUELLER, 1773) nov. comb.

Amphileptus flagellatus ROUSSELETT, 1890 is supposedly synonymous with *Paradileptus elephantinus* (Švec, 1897) KAHL, 1931

Amphileptus irregularis MASKELL, 1887 is synonymous with *Dileptus margaritifer* (EHRENBERG, 1833) DUJARDIN, 1841

Amphileptus longicollis EHRENBERG, 1831 is synonymous with *Pseudomonilicaryon anser* (MUELLER, 1773) nov. comb.

Amphileptus moniliger EHRENBERG, 1835 is synonymous with *Paradileptus elephantinus* (ŠVEC, 1897) KAHL, 1931

Amphileptus rotundus MASKELL, 1887 is synonymous with *Trachelius ovum* (EHRENBERG, 1831) EHRENBERG, 1833

Dileptus americanus KAHL, 1931 is synonymous with *Rimaleptus binucleatus* (KAHL, 1931) nov. comb.

Dileptus conspicuus var. *telobivacuolatus* GELLÉRT, 1955 is synonymous with *Rimaleptus conspicuus* (KAHL, 1931) nov. comb.

Dileptus gigas grojecensis WRZEŚNIOWSKI, 1870 is synonymous with *Pseudomonilicaryon anser* (MUELLER, 1773) nov. comb.

Dileptus gigas varsaviensis WRZEŚNIOWSKI, 1870 is synonymous with *Dileptus margaritifer* (EHRENBERG, 1833) DUJARDIN, 1841

Dileptus grandis DRAGESCO, 1963 is synonymous with *Pseudomonilicaryon massutii* (KAHL, 1933) FOISSNER et al., 2002

Dileptus granulosus DUJARDIN, 1841 is synonymous with *Dileptus margaritifer* (EHRENBERG, 1833) DUJARDIN, 1841

Dileptus saaleri SCHWARZ, 1962 is synonymous with *Pelagodileptus trachelioides* (ZACHARIAS, 1894) FOISSNER et al., 1999

Harmodirus PERTY, 1852 is objectively synonymous with *Trachelius* SCHRANK, 1803

Ophryocerca EHRENBERG, 1831 is objectively synonymous with *Trachelius* SCHRANK, 1803

Paradileptus caducus KAHL, 1935 is synonymous with *Pelagodileptus trachelioides* (ZACHARIAS, 1894) FOISSNER et al., 1999

Paradileptus canellai DRAGESCO, 1966 is synonymous with *Pelagodileptus trachelioides* (ZACHARIAS, 1894) FOISSNER et al., 1999

Paradileptus conicus WENRICH, 1929 is synonymous with *Paradileptus elephantinus* (ŠVEC, 1897) KAHL, 1931

Paradileptus estensis CANELLA, 1951 is synonymous with *Paradileptus elephantinus* (ŠVEC, 1897) KAHL, 1931

Paradileptus minutus DRAGESCO, 1972 is synonymous with *Paradileptus elephantinus* (ŠVEC, 1897) KAHL, 1931

Paradileptus ovalis HUBER-PESTALOZZI, 1945 is synonymous with *Paradileptus elephantinus* (ŠVEC, 1897) KAHL, 1931

Paradileptus robustus WENRICH, 1929 is synononymous with *Paradileptus elephantinus* (ŠVEC, 1897) KAHL, 1931

Phragelliorhynchus HERRICK, 1884 is supposedly synonymous with *Dileptus* DUJARDIN, 1841

Tentaculifera mexicana Sokoloff, 1931 is synonymous with *Paradileptus elephantinus* (Švec, 1897) Kahl, 1931

Trachelius cicer Schrank, 1803 is synonymous with *Trachelius ovum* (Ehrenberg, 1831) Ehrenberg, 1833

Trachelius leidyi Foulke, 1884 is synonymous with *Trachelius ovum* (Ehrenberg, 1831) Ehrenberg, 1833

Trachelius subtilis Penard, 1922 is synonymous with *Trachelius ovum* (Ehrenberg, 1831) Ehrenberg, 1833

Trachelius vorax Ehrenberg, 1833 is synonymous with *Trachelius ovum* (Ehrenberg, 1831) Ehrenberg, 1833

9 Collecting, Culturing, Observing and Staining of Dileptid Ciliates

9.1 Collecting

The methods for collecting and culturing dileptid ciliates are treated only briefly as detailed descriptions are provided either in the introductions to the families or in the species descriptions. Furthermore, the general procedures as described, e.g., by the Committee on Cultures (1958) and Lee & Soldo (1992) apply also to the dileptids. The beginner may also consult the valuable booklet by Finlay et al. (1988).

9.1.1 Limnetic and Marine Samples

Most described dileptids are from limnetic or limnetic-terrestrial habitats, such as ditches and puddles with fallen leaves. Some have been discovered in "standing samples" with rotting materials, such as algal masses and water plants. Few species each have been reported from activated sludge (Madoni 1981), the lake plankton (Foissner et al. 1999), streams and rivers (Dudich 1967, Detcheva 1983b, Foissner 1997a), and marine sites (Kahl 1930, 1933). In all these habitats, dileptids and other ciliates are sampled with conventional methods, that is, plankton nets (mesh-wide ≤ 20 µm), by scraping the Aufwuchs, investigating mud and algal masses, and mats of cyanobacteria.

Our own experiences with limnetic and marine samples are frustrating. Although we saw several species, most were rare and did not grow in cultures. They never became as abundant as in soil samples. An almost unexplored habitat are bog ponds and puddles, where we found at least two new species.

9.1.2 Moss and Soil Samples

Since Kahl (1930) and Wenzel (1953), terrestrial mosses are known to be a rich source for dileptids. Later, this knowledge was extended to soil (Foissner 1984, 1998; Foissner et al. 2002, 2005). This is confirmed by the present monograph, where over 15 new species are described from soil collected worldwide. Recent experience suggests floodplain soils as a centre of dileptid diversity, possibly "collecting" some or most of the limnetic species. The best way for growing these species is the non-flooded Petri dish method described by Foissner (1987a). In 2002, Foissner, Agatha & Berger updated the description, which is here quoted in full.

9.1.2.1 Sampling and Sample Processing

The material collected included mineral top soil (0–5 cm, rarely up to 10 cm depth) with fine plant roots, the humic layer, and the deciduous and/or grass litter from the soil surface. In soil with few organic materials and in sandy habitats, litter was sieved off the sand with an ordinary kitchen sieve, so that the final sample consisted of about 80% litter and 20% sand and gravel. Usually, 10 small subsamples were collected with a shovel from an area of about

100 m² and mixed to a composite sample. Bark samples were usually taken from one to three trees. The bark was collected with a knife, selecting for regions grown with mosses or lichens and/or containing some soil.

Generally, a "good" sample consists of 50% litter, humus and roots and 50% mineral soil. The litter and humus are very important because they release many nutrients when the sample is rewetted, stimulating growth of bacteria, fungi, flagellates, and amoebae, that is, the main food of ciliates. The nutrient increase obviously decouples microbiostasis, as explained in Foissner (1987a, 1997c).

All samples were air-dried for at least one month and then sealed in plastic bags. Such samples can be stored for years without any significant loss of species, provided they are from arid or temperate environments (Foissner 1997b, Foissner et al. 2002).

9.1.2.2 The Non-flooded Petri Dish Method

a) Put the material in a Petri dish and loosely spread it over its bottom in at least a 1 cm, better 2 to 3 cm thick layer. As concerns the present samples, usually sufficient material was available to fill a 2 cm high Petri dish 13 cm across or, rarely, a 3 cm high dish 18 cm in diameter. Basically, a large Petri dish (18 cm) is preferable because it provides more material for preparations.

b) Slightly over-saturate but do not flood the sample with distilled water. Water should be added to the sample until 5–20 ml will drain off when the Petri dish is tilted (45°) and the soil gently pressed with a finger. Complete saturation takes up to 12 hours, so check cultures after this time. Never flood the sample, that is, make an Aufguss ("infusion") because then only a few common species will develop. Further, the material should have been dry for at least one month.

c) Cover Petri dish and pinch a clip between bottom and lid for air exchange. Generally, care must be taken that samples do not putrefy. This happens easily with saline material, soil containing animal excrements, and samples with very easily decomposable litter. If so, change the water in the sample and do not cover it for some days so that plenty of air is available; further, slightly under-saturate sample with water. Heavily saline soil (≥ 20‰) should be "washed", if no ciliates develop: over-saturate the sample with water, as described above. After three days, remove the percolate and saturate again with water. Repeat this two to four times, until ciliates develop.

d) A distinct succession occurs in the rewetted samples. Thus, they must be inspected on days 2, 6/7, 13/14, 21/22, and 30. Later inspections usually add only few species, likely because microbiostasis (ciliatostasis; see Foissner 1987a) increases and metazoan (rotifers, nematods) and protozoan (mainly heliozoans!) predators often become abundant. For inspection, the Petri dish is tilted some seconds and a rather large drop (~ 0.3 ml) of the drained water ("soil percolate") taken with a pipette and inspected for species; several such drops must be investigated from different sites of the Petri dish, until the last drop adds but few species.

9.1.2.3 Collecting Material for Preparations

If a "difficult" species is noted, which happens in more than 70% of the samples, material for preparations must be collected. To obtain many specimens, the Petri dish is gently tilted (45°–60°) several times for a minute or so and the percolating water collected with a Pasteur pipette from several sites of the dish. If only little water (< 10 ml) drains off and/or the species of interest is very rare, the sample should be sprinkled with 10–15 ml distilled water. This will cause an osmotic shock, detaching or rinsing many specimens from the soil particles and capillaries within about 10 min. Then, the procedure described above is repeated, that is, the Petri dish is tilted several times and the percolating soil water added to the first collection. Finally, the soil sample is again saturated with clean table or tap water and stored for the next investigation. Certainly, these procedures strongly change the milieu, and thus a rather different ciliate community may develop after a week or two, possibly containing further "difficult" species. If so, the whole procedure is repeated, and so on.

Much care must be taken to keep the percolate clean of large (> 2 µm) soil particles, which would disturb the investigation of the preparations, while particles smaller than 2 µm hardly disturb, if not too numerous. To get clean material, note the following:

a) Usually, the percolating soil water which contains the organisms will be clean because the soil particles soon become stabilized by microbial activities, mainly by fungal hyphae and bacterial mucus. Thus, extreme care must be taken not to destroy the soil structure developed in the non-flooded Petri dish culture. Accordingly, the Petri dish must be handled gently and, if necessary, distilled water sprinkled softly on the surface. To increase percolation, mild finger pressure on the soil may be applied. Depending on the material sampled, the percolate has a light brown to orange colour (from lignins, humus colloids, etc.), which does not disturb the preparations (but see below).

b) The percolate is now gently shaken and large soil particles allowed to settle for about one minute. Then, the supernatant, which is now ready for preparations, is collected with a Pasteur pipette. Be careful not to lose bottom-dwellers. Occasionally, it may be helpful to sieve the percolate through a plankton net with 50–100 µm mesh-size or to concentrate it by mild centrifugation (max. 2000r/min for a few seconds), especially for preparations with expensive chemicals (osmium tetroxide in Chatton-Lwoff silver nitrate impregnation).

9.1.3 Cultivation

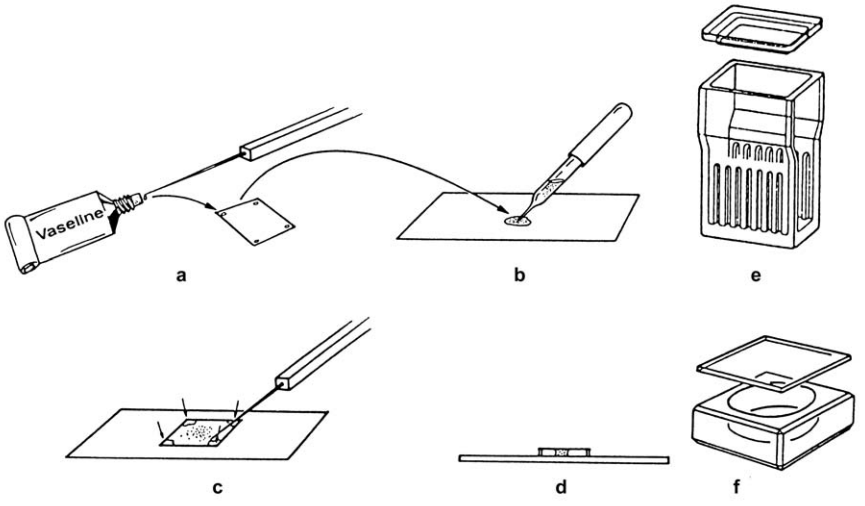
All dileptids are predators feeding on other protists and small metazoans; cannibalism is not known. Thus, co-cultivation of prey is required. Culture methods have been described for some dileptids by, e.g., Visscher (1923), Doroszewski & Golińska (1967), Kink (1973), and in the present monograph (see *Dileptus sphagnicola* and *Pseudomonilicaryon fraterculum*). Basically, the media used are simple, viz., yolk suspension and extracts of lettuce, hay, soil or beef providing growth of both, the dileptids and the prey, usually *Colpidium* (now *Dexiostoma*) *campylum* and *Tetrahymena pyriformis*. Details will be provided in the individual species descriptions.

Our experiences with pure cultures of dileptids and many other haptorids are frustrating: most clones either die or grow poorly dying after one or two weeks. However, fairly good results are occasionally obtained with **semi-pure cultures** set up with some ml of unfiltered soil percolate from the non-flooded Petri dish culture and table water enriched with one to three crushed wheat grains to support growth of bacterivorous ciliates, which then serve as a food for the dileptids contained. This simple method provided well-growing cultures of, for instance, *Apodileptus visscheri* and *Pseudomonilicaryon fraterculum*. Further, masses of dileptids occasionally develop in the non-flooded Petri dish cultures, showing division, conjugation, and encystment.

9.2 Observing Living Ciliates

Many physical and chemical methods have been described for retarding the movement of ciliates in order to observe structural details (see Foissner 1991 for literature). Chemical immobilization (e.g., nickel sulphate) or physical slowing down by increasing the viscosity of the medium (e.g., methyl cellulose) are, in our experience, usually unsuitable. These procedures often change the shape of the cell or cause premortal alterations of various cell structures. The following simple method is therefore preferable: place about 0.5 ml of the raw sample on a slide and pick out (collect) some specimens with a micropipette under a compound microscope equipped with a low magnification (e.g., objective 4:1, eyepiece 10×). If specimens are large enough, they can be collected from a Petri dish under a dissecting microscope. Working with micropipettes, the diameter of which must be adjusted to the size of the specimens, requires some training. The collected specimens are now in a very small drop of fluid. Apply small dabs of vaseline (Petroleum jelly) to each of the four corners of a coverslip (or on the slide; it is useful to apply the jelly by an ordinary syringe with a thick needle). Place this coverslip on the droplet containing the ciliates. Press on the vaselined corners with a mounted needle until ciliates become slightly squeezed between slide and coverslip (Figs 36a–d). As the pressure is increasing, the ciliates gradually become less mobile and more transparent. Hence, first the location of the main cell organelles (e.g., nuclear and oral apparatus, contractile vacuole) and then the details (e.g., extrusomes, micronucleus) can easily be observed under low (×100–400) and high (×1000, oil immersion objective) magnifications.

The shape of the cells is of course altered by this procedure. Therefore, specimens taken directly from the sample with a large-bore (opening ~ 1 mm) pipette must first be investigated under low magnification (×100–400). Some species are too fragile to withstand handling with the micropipette and coverslip trapping without deterioration. Investigation with low magnification also requires some experience but it guarantees that undamaged cells are recorded. Video-microscopy is very useful at this point of



Figs 36a-d. Preparation of a slide for observing living ciliates. **Fig. 36e.** Staining jar for 8 and 16 (back to back) slides, respectively. **Fig. 36f.** Watch-glass for cleaning ciliates for scanning electron microscopy. All from FOISSNER (1991).

investigation, especially for registrating body shape and swimming behaviour.

A compound microscope equipped with differential interference contrast is best for observing living ciliates. If not available, use bright-field or phase-contrast; the latter is only useful for very flat species.

9.3 Staining Procedures

Although there are numerous methods for staining ciliates, most of the older procedures (e.g., hematoxylin; see KIRBY 1950 for an excellent compilation of protocols) have been outdated by silver impregnation techniques and electron microscopy. Various silver stains are available, but all need some experience and are usually individually modified. However, familiarity with at least protargol impregnation and scanning electron microscopy (SEM) is an absolute prerequisite for studying dileptid ciliates. These are thus described in great detail in order also to give even beginners a fair chance to obtain usable slides.

Apart from silver impregnation, various other staining techniques are useful for taxonomic work with ciliates, especially the Feulgen nuclear reaction and supravital staining with methyl green-pyronin in order to reveal, respectively, the nuclear apparatus and the mucocysts.

Simple, viz., molecular formulae are given for the chemicals used, since usually only these are found in the catalogues of the suppliers (e.g., Merck). In a laboratory manual it is thus convincing to use this style too, instead of the more correct constitutional or structural formulae.

Supravital staining with methyl green-pyronin. This simple method is an excellent technique for revealing the mucocysts of most ciliates (those of tetrahymenids and rather many haptorids, however, usually do not stain). Mucocysts are stained deeply and very selectively blue or red, and can be observed in various stages of swelling because the cells are not killed instantly. The nuclear apparatus is also stained.

P r o c e d u r e

1. Pick out the desired ciliates with a micropipette and place the small drop of fluid in the centre of a slide.
2. Add an equally sized drop of methyl green-pyronin and mix the two drops gently by swiveling the slide.

R e m a r k s : If ciliates were already mounted under the coverslip, add a drop of dye at one edge of the coverslip and pass it through the preparation with a piece of filter paper placed at the other end of the coverslip.

3. Place a coverslip with vaselined corners on the preparation and squeeze specimens slightly.

   R e m a r k s : Observe immediately. Cells die in the stain within some minutes. Mucocysts stain very quickly and many can be observed at various stages of swelling. To reveal the nuclear apparatus, cells should be fairly strongly squashed (= flattened). The preparation is temporary. After 5–10 minutes the cytoplasm often becomes heavily stained and obscures other details.

R e a g e n t s

1 g methyl green-pyronin (Chroma-company, Küferstrasse 2, P.O. Box 1110, D–73257 Köngen, Germany)

add 100 ml distilled water and filter

R e m a r k s : This solution is very stable and can be used for years.

Protargol impregnation (protocol A in Foissner 1991 and recent experience). Protargol stains are indispensable for descriptive research on ciliates. Many protargol methods have been described, and none is perfect. Here, the variation which produces good results for dileptids in our laboratory is communicated. This procedure works well with most ciliate and flagellate species (some, however, only rarely impregnate well, e.g., *Loxodes*, *Paramecium*) but requires at least 20 specimens. Contrary to the silver carbonate method, a single specimen cannot usually be handled successfully. Depending on the procedure used, protargol can reveal many cortical and internal structures, such as basal bodies, cilia, various fibrillar systems, and the nuclear apparatus. The silverlines, however, never impregnate. The shape of the cells is usually well preserved in permanent slides, which is an advantage for the investigation but makes photographic documentation difficult. However, micrographs as clear as those taken from wet silver carbonate impregnations can be obtained if the cells are scraped off, selected with a micropipette, put on a new slide, pressed down with the coverslip, and photographed prior fixing with sodium thiosulphate. A centrifuge may be used for step 2; staining jars (Fig. 36e) are necessary for steps 6–16. **The procedure is complicated and subject to many factors. Thus, be well organized and study the "Remarks" carefully.**

The method described is basically the same as in Foissner (1991), with a small but important change: instead of using distilled water, tap water is used in most steps. This avoids swelling and detachment of the albumen, a main problem in the 1991 protocol. Further, a second developer, which produces more contrast, is introduced.

P r o c e d u r e

1. Fix organisms in Bouin's or Stieve's fluid or in alcohol (50–100% depending on species and material), alcohol-formalin, or in other fixatives for 10–30 minutes.

   R e m a r k s : To use the appropriate fixative is of paramount significance. Surprisingly, simple alcohol frequently provides excellent impregnations, although shrinkage may be rather pronounced. Alcohol-formalin and Champy's and Da Fano's fixatives are sometimes also useful. The fixation time has little influence on the quality of the preparation within the limits given. Ratio fixative: sample fluid should be at least 1:1. Pour ciliates into fixative, using a wide-necked dish to bring the organisms in contact with the fixative as fast as possible. Most fixatives may be supplemented with some drops of 2% osmium tetroxide for better fixation of fragile ciliates, e.g., the hypotrich *Urosoma*, which, however, fixes perfectly with alcohol. This increases the stability of the cells but usually reduces their impregnability.

2. Concentrate by centrifugation and wash organisms 3–4 times in tap water.

   R e m a r k s : There are now two choices: either continue with step 3 or transfer the material through 30–50–70–70% alcohol (ethanol) where it remains stable for years. Transfer preserved material back through the graded alcohol series into tap water prior to continuing with the next step. Impregnability of preserved material may be slightly different.

3. Clean 8 slides (or less if material is very scarce) per sample. The slides must be grease-free (clean with alcohol and flame).

   R e m a r k s : Insufficiently cleaned slides may cause the albumen to detach. Mark slides on back if several samples are prepared together. We use staining jars with 8 sections so that we can work with 16 slides simultaneously by putting them back to back (Fig. 36e).

4. Put a small drop each of albumen-glycerol and concentrated organisms in the centre of a slide. Mix drops with a mounted needle and spread over the middle third.

   R e m a r k s : Use about equally sized drops of albumen-glycerol and suspended (in tap water) organisms to facilitate spreading. The size of the drops should be adjusted so that the middle third of the slide is covered after spreading. Now remove sand grains, etc. The thickness of the albumen layer should be equal to that

of the organisms. Some thicker and thinner slides should, however, also be prepared because the thickness of the albumen layer may influence the quality of the preparation. Cells may dry out and/or shrink if the albumen layer is too thin; if it is too thick it may detach or the cells cannot be studied with the oil immersion objective.

5. Allow slides to dry for at least 2 hours or overnight at room temperature.

   R e m a r k s : Slides may be allowed to dry for up to 48 hours; longer times decrease quality. Oven-dried (2 hours at 60 °C) slides are usually also of poorer quality.

6. Place slides in a staining jar (Fig. 36e) filled with 95% alcohol (ethanol) for 20–30 minutes. Place a staining jar with protargol solution into an oven (60 °C).

   R e m a r k s : Slides should not be transferred through an alcohol series into concentrated alcohol as this causes the albumen layer to detach! Decrease hardening time to 15–20 minutes if the albumen is rather old and/or not very sticky.

7. Rehydrate slides through 70% alcohol and two tap water steps for 5 minutes each.

8. Place slides in 0.2% potassium permanganate solution. Remove first slide (or pair of slides) after 30 seconds and the others at 15 second intervals. Collect slides in a staining jar filled with tap water.

   R e m a r k s : Bleaching is by permanganate and oxalic acid (step 9). The procedure described above is necessary because each species has its optimum bleaching time. The sequence in which slides are treated should be recorded as the immersion time in oxalic acid must be proportional to that in the permanganate solution. The albumen layer containing the organisms should swell slightly in the permanganate solution and the surface should become uneven. If it remains smooth, the albumen is too sticky and this could decrease the quality of the impregnation. If the albumen swells strongly, it is possibly too weak (old) and liable to detach. Use fresh $KMnO_4$ solution for each series.

9. Quickly transfer slides to 2.5% oxalic acid. Remove first slides (or pair of slides) after 60, 90, 120 and 160 seconds, the others at 20 second intervals. Collect slides in a staining jar filled with tap water.

   R e m a r k s : Same as for step 8! Albumen layer becomes smooth in oxalic acid. Hard tap water should be mixed with distilled water 1:1.

10. Wash slides two times in tap water and one time in distilled water for 3 minutes each.

11. Place slides in the warm (60 °C) protargol solution and impregnate for 10–15 minutes at 60 °C.

    R e m a r k s : Protargol solution can be used only once. Organize 6 staining jars for developing the slides: distilled water – tap water – tap water – fixative (sodium thiosulphate) – tap water – 70% alcohol – 100% alcohol (ethanol).

12. Remove staining jar with the slides from the oven and take one slide from the mid of the series for adjusting the developer. Dip the slide into distilled water for 1–2 seconds and then transfer it into the acetone developer. As soon as the albumen turns yellowish, remove the slide, dip it into the first two tap water steps for about 2 seconds each, and control the impregnation with the compound microscope. If the cells appear impregnated, then submerge the slides in the fixative (sodium thiosulphate) for 5 minutes. If the cells appear not or too faintly impregnated, then take a second slide from the staining jar and do the same procedure with the ordinary developer. If necessary, adjust the developer (see reagents), and continue to develop the rest of the slides.

    R e m a r k s : We now use two different developers: the ordinary one and that proposed by Dieckmann (1995), which is preferable but, for unknown reasons, does not work for all materials and fixatives. For instance, it sometimes does not work with material that was not stored in 70% alcohol for a few days. In spite of this problem, the Dieckmann developer should be tried first because it stains the cytoplasm weaker than the ordinary developer, enhancing the contrast of the preparation. The impregnation intensity is sufficient if the ciliary pattern is just recognizable. The permanent slide will be too dark if the ciliary pattern is distinct at this stage of the procedure! The intensity of the impregnation can be controlled by the concentration of the developer and the time of development: 5–10 seconds usually suffice for the diluted ordinary developer, while 20 seconds to 5 minutes, usually about 1 minute, are sufficient for the acetone developer! Some species (e.g., most microthoracids) must be treated with undiluted developer. Development time increases with bleaching time. The thinner the albumen layer, the faster the development.

13. Fix slides in sodium thiosulphate for 5 min. Then wash in tap water three times for about 3 minutes each.

    R e m a r k s : Both, sufficient fixation and thorough wash out of the fixative are of paramount importance for the stability of the preparation.

14. Transfer slides to 70% – 100% – 100% alcohol for 3–5 minutes each.
15. Clear by two 10 minute transfers through xylene.
16. Mount in synthetic neutral medium.

R e m a r k s : Do not dry slides between steps 15 and 16. The preparation is stable, provided step 13 is done correctly. The mounting medium should be rather viscous to avoid air-bubbles being formed when the solvent evaporates during drying.

R e a g e n t s

a) Bouin's fluid (prepare immediately before use; components can be stored)

15 parts saturated, aqueous picric acid ($C_6H_3N_3O_7$; preparation: add an excess of picric crystals to, e.g., 1 litre of distilled water; shake solution several times within a week; some undissolved crystals should remain; filter before use)

5 parts formalin (HCHO; commercial concentration, about 37%)

1 part glacial acetic acid (= concentrated acetic acid; $C_2H_4O_2$)

b) Stieve's fluid (slightly modified; prepare immediately before use; components can be stored)

38 ml saturated, aqueous mercuric chloride (dissolve 60 g $HgCl_2$ in 1 litre of boiling distilled water)

10 ml formalin (HCHO; commercial concentration, about 37%)

3 ml glacial acetic acid (= concentrated acetic acid; $C_2H_4O_2$)

c) Alcohol-formalin (prepare immediately before use; components can be stored)

50 ml 70% alcohol (ethanol)

5 ml formalin (HCHO; commercial concentration, about 37%)

R e m a r k s : The two components can be used in a wide variation of concentrations, even vice versa. Further, they can be used individually in various concentrations. The often excellent results obtained with pure alcohol fixation are partially caused by the poor preservation of the cytoplasm, that then impregnates only faintly, enhancing the contrast of the cortical structures.

d) Albumen-glycerol (2–6 month stability at 3 °C)

15 ml egg albumen

15 ml concentrated (98–100%) glycerol ($C_3H_8O_3$)

R e m a r k s : Pre-treatment of the egg albumen and preparation of the albumen-glycerol: Separate the white carefully from the yolk and embryo of three eggs (free range eggs are preferable to those from battery chickens, whose egg white is less stable and sticky). Shake the white by hand (do not use a mixer!) for a minute in a narrow-mouthed 250 ml Erlenmeyer flask until a stiff white foam is formed. Allow the flask to stand for 30–60 seconds. Then pour the viscous rest of the egg white in a second Erlenmeyer flask and shake again until a stiff foam is formed. Repeat until most of the egg white is either stiff or becomes watery; usually 4–6 Erlenmeyer flasks of foam are obtained. Leave all flasks undisturbed for about 10 minutes and discard the watery albumen from the last flask. During this time a glycerol-like fluid percolates from the foam. This fluid is collected and used. Add an equal volume of concentrated glycerol and a small thymol crystal ($C_{10}H_{14}O$) for preservation of the mixture. Mix by shaking gently and pour mixture into a small flask. Leave undisturbed for two weeks in the refrigerator. A whitish slime settles at the bottom of the flask. Decant the clear portion, discard slime and thymol crystal. Store it at about 3 °C. A "good" albumen-glycerol drags a short thread when touched with a needle. The albumen is too thin (not sticky enough) or too old if this thread is not formed. Fresh albumen which is too thin may be concentrated by leaving it open for some weeks so that water can evaporate. If the albumen is too sticky, which may cause only one side of the organisms to impregnate well, it is diluted with distilled water or old, less sticky albumen to the appropriate consistency. The preparation of the albumen-glycerol must be undertaken with great care because much depends on its quality. Unfortunately, all commercial products which we have tried detach during impregnation.

e) 0.2% potassium permanganate solution (stable for about 1 day)

0.2 g potassium permanganate ($KMnO_4$) are dissolved in 100 ml distilled water

f) 2.5% oxalic acid solution (stable for about 1 day)

2.5 g oxalic acid ($C_2H_2O_4 \cdot 2H_2O$) are dissolved in 100 ml distilled water

g) 0.4–0.8% protargol solution (stable for about 1 week when not heated)

100 ml distilled water

add 0.4–0.8 g protargol

R e m a r k s : Use light-brown "protargol for microscopy" presently hardly available but some companies showed interest to produce it again. Some dark-brown, cheaper products do not work! Sprinkle powder on the surface of the water of a wide-mouthed bottle and allow to dissolve without stirring. Concentration of the protargol depends on its "strength", that is, on the silver contents.

h) Ordinary developer (mix in sequence indicated; sodium sulphite must be dissolved before hydroquinone is added)

95 ml distilled water

5 g sodium sulphite (Na_2SO_3)

1 g hydroquinone ($C_6H_6O_2$)

R e m a r k s : This recipe yields the stock solution which is stable for some weeks and should be used undiluted for certain ciliates (step 12). Usually, however, it must be diluted with tap water in a ratio of 1:20 to 1:50 to avoid too rapid development and one-sided impregnation of the organisms. Freshly prepared developer is usually inadequate (the albumen turns greenish instead of brownish). The developer should thus be aged artificially by adding some sodium carbonate (Na_2CO_3) or by adding 1 ml old, slightly brownish stock solution to 99 ml fresh developer. Alternatively, air-aged solutions can be used, that is, a developer that has been kept uncovered for some days in a wide-mouthed bottle. It first turns yellowish, then light brown (most effective) and later dark brown and viscous (at this stage the developer has lost most of its activity but is still suitable for artificial ageing of fresh developer (see above). Take great care with the developer as its quality contributes highly to that of the slides. If the developer has lost its activity (which is not always indicated by a brown colour!), the silver is not or only insufficiently reduced and the organisms stain too faintly. A fresh developer should therefore be prepared for each "impregnation week" and some old developer kept.

Acetone developer (stable for about two weeks; add components in the series given and solve each before adding the next)

80 ml distilled water

1.4 g boric acid (H_3BO_3)

0.3 g hydroquinone ($C_6H_6O_2$)

2 g sodium sulphite (Na_2SO_3)

15 ml acetone

R e m a r k s : This is the low-speed developer used by Dieckmann (1995), who obtained the recipe by Fryd-Versavel (pers. comm.). Pour the developer into a staining jar and immerse slides, one by one, controlling impregnation intensity when the albumen becomes light brown or light green. See step 12 for details.

i) Fixative for impregnation (stable for several years)

50 g sodium thiosulphate ($Na_2S_2O_3 \cdot 5H_2O$) are dissolved in 1000 ml distilled water

Silver nitrate impregnation (Foissner 1991 and recent experience). This method can provide excellent results but has several problems: (i) the gelatin, in which the specimens are embedded, is too weak, i.e., does not become solid sufficiently, and the preparations are lost or full of clouds; (ii) the gelatin becomes cloudy and/or gets small fissures above the individual cells, even if "good" gelatin is used; (iii) the impregnation is too faint, especially on the "back side", that is, the side oriented to the microscope slide; and (iv) the impregnation bleaches more or less strongly within a few days or months.

Problem (i) can be solved by using "Gelatin, from Bovine Bone", Wako company, Japan. Problem (ii) occurs when the preparation becomes too warm, i.e., when the gelatin commences melting. Thus, keep the preparation < 10 °C throughout the procedure. Problem (iii) is partially caused by the inability of the UV-light to penetrate sufficiently the gelatin and the cells. Thus, silver reduction must be done from above and below (see step 12) and chemical development should follow UV reduction. The fourth problem we solved only recently (see steps 13–15). It makes the protocol rather complex but is worth to be done because stable preparations can be obtained. Several slides should be prepared simultaneously from the same material. If only few specimens are available, these must be handled with micropipettes during steps 1–7 (difficult task!); for ample material a centrifuge may be used. Until dehydration (step 16), keep all solutions cold (< 10 °C) as warming causes clouds or even detaches the gelatin from the slide. The Da

Fano solution is of paramount significance because it decides about the strength of the impregnation. If too much is used, precipitations may develop; if too less, the impregnation may become too faint. The method is not simple and requires experience. Since some steps must be done quickly, it is necessary to be well organized.

P r o c e d u r e

1. If possible, concentrate ciliates by gentle centrifugation (the fixative is expensive) or collect individual ciliates and drop them into the fixative.
2. Put ciliates into Champy's fluid and fix for 1–30 minutes.

   R e m a r k s : The ratio of material to fixative should be at least 1:1, better 1:2. The fixation time apparently does not influence the results greatly. We usually fix for about 10 minutes. Fixation should be carried out in a fume hood since osmic vapours are highly toxic.
3. Remove fixative by centrifugation or micropipette and postfix in Da Fano's fluid for at least 5 minutes. Continue this replacement until the solution is the colour of Da Fano's fluid (2–3 times are usually enough).

   R e m a r k s : Material can be stored in Da Fano's fluid for years.
4. Place a very clean, grease-free slide on a hot-plate (35–60 °C).

   R e m a r k s : The slides must be grease-free (clean with alcohol and flame); even commercially pre-cleaned slides should be cleaned with a alcohol-moist cloth.
5. Place a small piece (about 2–4 mm in diameter) of gelatin in centre of the warmed slide and allow to melt.

   R e m a r k s : Gelatin should have been stored in the refrigerator for at least one week before use. Fresh gelatin may cause cloudy silver deposits.
6. Quickly add an equal-sized or smaller drop of concentrated specimens to the molten gelatin and remove slide from hot-plate.

   R e m a r k s : Use as few Da Fano's fluid as possible. Mix organisms thoroughly into the gelatin using a mounted needle.
7. Quickly spread the drop on the slide or remove excess fluid under the dissecting microscope with a warmed micropipette until ciliates remain just nicely embedded in a thin gelatin layer.

   R e m a r k s : Steps 6 and 7 must be done quickly to avoid hardening and/or desiccation of the gelatin; if gelatin solidifies during the procedure return the slide to the hot-plate for a few seconds. Excess fluid can be removed only if ciliates are large. For small (< 100 µm) species and generally it is more convenient to spread the drop over the slide until the gelatin layer has the appropriate thickness. If the drop does not spread well, the slide is not grease-free. The gelatin layer must be thin to allow the silver nitrate and UV-light to pass through. Material should be well concentrated. If too much Da Fano's fluid has been used or remains, precipitations develop or the gelatin detaches.
8. Immediately transfer slide to a cold, moist chamber (e.g., a covered Petri dish with damp filter paper covering its bottom). Leave for about 5 minutes until gelatin has hardened.

   R e m a r k s : Gelatin must be hardened (check with the tip of a mounted needle under dissecting microscope if in doubt) but must not desiccate and/or freeze. Desiccated or frozen slides are of poor quality. Harden gelatin in refrigerator or by placing the moist chamber on ice.
9. Flush slide in cold distilled water for 3–10 seconds.

   R e m a r k s : This step is essential and determines the quality and intensity of the impregnation. If the gelatin is washed too long, the impregnation may become too faint; if it is insufficiently washed coarse silver precipitations cover the gelatin. It is recommended that at least 4 slides, washed 3, 5, 7 and 10 seconds, respectively, are prepared.
10. Immediately transfer slide to cold silver nitrate solution for 30–60 minutes.

    R e m a r k s : Keep silver nitrate solution cold, as warming melts and detaches the gelatin from the slide. 30 minutes impregnation suffices for large ciliates (e.g., *Paramecium*). Immersion of more than 60 minutes intensifies impregnation only slightly and may cause darkening of cytoplasmic inclusions. The gelatin layer becomes slightly milky in the silver nitrate solution. A distinct milky coat indicates that too much Da Fano's fluid has been used and/or remained (step 7).
11. Flush slide with cold distilled water for a minute.
12. Immediately submerge slide in an ~ 2 cm high layer of cold distilled water. Irradiate slides for 30 minutes each from above and below to obtain fully impregnated cells, using ultraviolet sources (< 254 nm) placed 5–15 cm

above and below the slides until gelatin turns golden brown.

R e m a r k s : Tilt dish gently back and forth and change water after 2–3 minutes of irradiation to avoid silver precipitations. Take care that water remains cold (<10 °C).

13. After UV-irradiation, put slides for 15 minutes in cold ordinary protargol developer diluted 1:1 with distilled water.
14. Wash slides in cold distilled water for 3 minutes.
15. Immerse slides in the cold silver fixer (sodium thiosulphate) used for protargol impregnation for 5 minutes.
16. Wash slides five times in cold distilled water for about 10 hours; keep the preparation cool in the refrigerator.

    R e m a r k s : Washing out the chemicals from the developer and fixer is of paramount significance for stabilizing the preparation.
17. Transfer slides to chilled 30% and then 70% alcohol (ethanol) for 10 minutes each.
18. Complete dehydration by two transfers at least 10 minutes long through 100% alcohol (ethanol) at room temperature.

    R e m a r k s : The gelatin hardens, the alcohol needs not be chilled. Dehydrate thoroughly to avoid milky “water spots” in the mounted slides.
19. Clear by 2 transfers of at least 10 minutes through xylene.

    R e m a r k s : A prolonged stay in xylene (e.g., 2 days) sometimes produces extremely clear preparations.
20. Mount in synthetic neutral mounting medium.

    R e m a r k s : Do not dry slides between steps 19 and 20! The mounting medium should be rather viscous to avoid air-bubbles being formed when the solvent evaporates during drying. If air-bubbles develop in the mounted and hardened slide, re-immerse in xylene for some days until the coverslip drops off. Remount using a more viscous medium and remove materials protruding from the gelatin. Usually, some air-bubbles are found immediately after mounting; these can be pushed to the edge of the coverslip with a finger or mounted needle. The preparation is stable. However, the drop margin may bleach more or less. The infraciliature should stand out dark brown or black against the light brown-coloured gelatin and the unstained cytoplasm. Silver deposits on the gelatin surface indicate that too much Da Fano’s fluid remained (steps 7–9).

R e a g e n t s

a) Champy’s fixative (prepare shortly before use; 9 ml of the fluid usually suffice for 1–2 fixations; use fume hood)

   7 parts (3.5 ml) 1% aqueous chromic acid (CrO_3)

   7 parts (3.5 ml) 3% aqueous potassium dichromate ($K_2Cr_2O_7$)

   4 parts (2.0 ml) 2% aqueous osmium tetroxide (OsO_4)

b) Da Fano’s fluid (stable for several years; large amounts can thus be prepared)

   900 ml distilled water (or sea-water, without additional NaCl, for marine ciliates)

   10 g cobalt nitrate ($Co(NO_3)_2 \cdot 6H_2O$)

   100ml formalin (HCHO; commercial concentration, about 37%)

   10 g sodium chloride (NaCl)

c) Gelatin (may be used as long as not colonized by bacteria or fungi; the molten gelatin must be clear and yellowish in colour; use a good product!)

   10 g powered gelatin

   0.1 g sodium chloride (NaCl)

   100 ml distilled water

   R e m a r k s : Mix these components and melt gelatin in a water bath, stirring frequently. Pour mixture into small, sterile cups and store them in the refrigerator. Filled cups can be used for years.

d) Silver nitrate solution (may be used for several preparations, i.e., for about 40 slides if these are made on the same day; used solutions older than 1 day may cause problems)

   3 g silver nitrate ($AgNO_3$)

   add 100 ml distilled water

The following materials must be prepared on the day preceding the preparation:

a) Salinated gelatin
b) Osmium tetroxide (takes about 10 hours to dissolve)
c) Chill a moist chamber, i.e., a large Petri dish (step 12); the reduction dish; the silver nitrate solution; distilled water; the chemical developer and fixer; and alcohol (30%, 70%) in appropriate amounts.

Preparation for Scanning Electron Microscopy (SEM). Ciliate species cannot usually be identified solely by scanning electron microscopy because only a limited number of characters is revealed. However, SEM is useful for the beginner by allowing a three-dimensional view of the specimen and for the specialist in documenting details which are difficult to reveal with other methods. Only the method used by ourselves is described here; it changed considerably since FOISSNER (1991). See textbooks for general SEM-techniques.

Procedure

1. Pour ciliates into Parducz' fixative and leave for about 30 minutes.

   Remarks: Concentrate and clean material as thoroughly as possible (see step 2). Ratio of sample:fixative should be at least 1:1, better 1:2. Add some drops of 5 n HCl if fixative becomes milky when the material is added. Fixation must be done in a wide-mouthed bottle so that the organisms come in contact with the fixative immediately. Then put the fixed sample in a narrow glass tube (diameter ~ 2 cm), where the organisms can settle. Parducz' fluid preserves most ciliates very well. However, the cirri of the hypotrich ciliates usually disintegrate into their component cilia. Hypotrichs should thus be fixed either in concentrated sublimate (dissolve 60 g $HgCl_2$ in 1 litre hot distilled water and allow to cool) or in a mixture composed of 4 parts concentrated sublimate and 1 part 2% osmium tetroxide. A much better fixative for hypotrichs is that used by Barry WICKLOW (pers. comm.): mix equal amounts of 2% aqueous osmium tetroxide and 3% glutaraldehyde and fix cells for 15–30 min. Wash in distilled water and proceed as described below (steps 2–7). Unfortunately, such material cannot be stored because crystals are formed. Thus, critical point drying must follow immediately. The fixative preserves also many other ciliates well, although the metachronal ciliary waves are frequently not as distinct as with Parducz' fluid.

2. Wash and clean the material (ciliates or other protists) in tap water.

   Remarks: Washing must be done in a watch-glass (Fig. 36f) and with a micropipette to remove bacteria and organic debris. This cleaning of the material is essential but rather difficult and laborious, especially with small species (< 100 µm) and field material; thus cultures and/or pre-cleaned material (see below) should be used. The cleaning is performed as follows: Ciliates settle at the bottom of the fixation tube after 30 minutes (step 1). Remove as much supernatant as possible with a pipette (use a centrifuge only if the specimens did not settle well). Then transfer the material to a watch-glass and allow to settle for about 5 minutes (use fume hood). Quickly remove most of the fixative with a micropipette under the dissecting microscope. Now wash the ciliates with tap water by several passages through a large-bore (diameter about 1 mm) pipette. Bacteria and debris adhering to the ciliates are hereby mechanically removed. Again allow to settle, but control sedimentation with the dissecting microscope; remove supernatant containing bacteria and debris with a micropipette as soon as ciliates have settled. This procedure must be repeated until the material is clean. Use fractionated sedimentation if the sample contains several species differing in size and/or mass.

   Field material: Larger species (> 100 µm) are picked out with a micropipette and collected in a small bottle. Then pour the fixative over the cells. Several hundred specimens must be collected because loss of material may be considerable during the following steps. Small species can be prepared by this method only if abundant material is available. Some accumulation can often be achieved by the following simple method: leave a freshly collected sample containing ample mud to stand for some hours at room temperature. Due to oxygen depletion the ciliates usually move to the surface where they can be skimmed off with a teaspoon.

3. Transfer the cleaned ciliates with a small drop of tap water into the preparation chamber (Fig. 37).

   Remarks: Place a small amount of commercial cotton wool on the bottom plankton net of the chamber. Then put a drop of specimens into the cotton and load the preparation with washer 1. The net must be dry to avoid spreading of the drop to the chamber margin and the washer. Place the top plankton net carefully on the drop, that is, on washer 1, using forceps. Weight top net with washer 2, close chamber with lid and immediately transfer into 30% ethanol. The plankton net must have a mesh-size < 12 µm and can be used many times. It should fit exactly into the chamber, which is best achieved using an appropriate punch. Alternatively, metal grids with 10–20 µm mesh size, as used by soil scientists, can be applied. They are stable for years.

The cleaned material can be stored in ~ 1% osmium tetroxide for years. However, when the fixative contained aldehyds (formalin, glutaraldehyde), the osmium should be changed two or three times within the first month, otherwise it becomes black from remnants of the fixative.

4. Dehydrate chamber with ciliates in an ethanol series (30–50–70–90–100–100%) for 5 minutes each.
5. Dry chamber with ciliates in a critical-point drying apparatus.

   R e m a r k s : We use CO_2 and change the alcohol at least 10 times. Amylacetate, as used previously (Foissner 1991), proved to be superfluous.
6. Use a mouth protection fabric and put a glass shield between the dissecting microscope and the sample to avoid any rewetting of the dried organisms by your breath! Open chamber and place ciliates on a SEM-stub.

   R e m a r k s : The dried ciliates usually form small lumps in the cotton wool. The cotton and the net are carefully transferred with forceps to the SEM-stub, where the organisms are separated from the cotton and the net by knocking on the forceps. If there are small lumps of organisms, they can be dispersed under the dissecting microscope with a mounted eyelash. The ciliates spread easily if cleaning and drying were sufficient.

   P r e p a r a t i o n o f t h e S E M - s t u b : We use commercial aluminium SEM-stubs with 25 mm in diameter. To fix the organisms and to get a black, homogenous background the stub is covered with a graphit-tab available from several providers, e.g., the Gröpl Company, Frauenhofnerstrasse 40, A-3430 Tulln, Austria (order no. G 3347 or G 3348, i.e., tabs with a diameter of 12 or 25 mm). Note that small species (< 30 µm) tend to sink into the graphit. For these, the graphit-tabs are pre-sputtered 3 times with gold.
7. Sputter with gold. This is a very critical step! Use low (4 mA) sputter energy. Sputter about 10 times for 30 seconds each, with breaks of about 5 minutes to avoid heating. Cilia become curled and denaturated if sputter energy is too high and/or the sample is slightly rewetted by your breath or perspiration!

R e a g e n t s

Parducz' fixative (prepare immediately before use)

4 ml aqueous 2 % osmium tetroxide (OsO_4)

1 ml saturated, aqueous mercuric chloride ($HgCl_2$; preparation see protargol protocol)

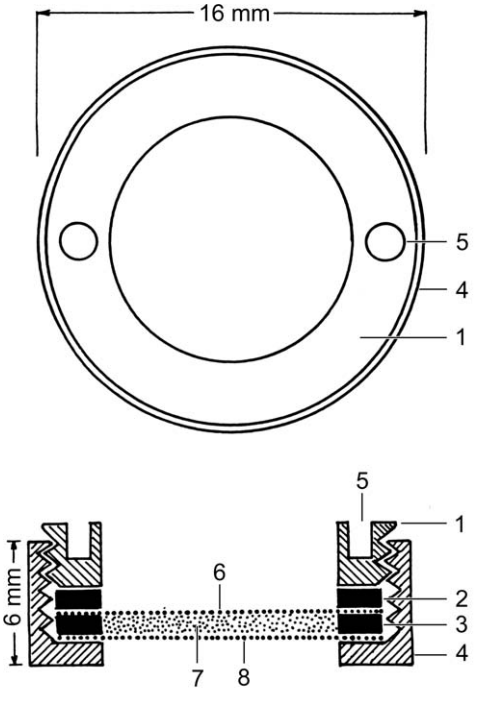


Fig. 37. Brass chamber for critical point-drying of protists (from Foissner 1991). 1 – threaded chamber lid; 2 – washer 2; 3 – washer 1; 4 – threaded chamber jacket; 5 – holes for forceps tips, used to screw lid into jacket; 6 – top net; 7 – sample; 8 – bottom net.

B Systematic Section

1 How to Use the Monograph?

A few technical explanations are necessary for the proper use of the monograph.

(i) The original descriptions are either cited literally or are adapted to the style used in this monograph. In the latter case, great care was taken to add or remove nothing. Further, we included computer scans of all illustrations, even those of poor quality, so that the species is shown as originally published.

(ii) We quantified several features in three or more steps, for instance, the distance of the ciliary rows (Fig. 10): very narrowly to narrowly spaced (≤ 4 μm), ordinarily spaced (4–8 μm), widely to very widely spaced (≥ 8 μm). Usually, we left "ordinary" when the kinety distance was within the range given.

(iii) Usually, authors and dates are omitted from the names of the species in the Remarks section because this information is found in the individual species descriptions.

(iv) For the species/subspecies concept used, see Foissner & Xu (2007).

(v) Orders, families, genera, and species are arranged according to their appearance in the taxonomic keys.

(vi) With few exceptions, pre-Ehrenberg (1838) taxa or synonyms are not included in the synonymy lists.

2 A User-Friendly Flow Chart Key to 66 Dileptid Species

The key contains the 66 dileptids considered identifiable in this monograph. It is easy to use because all characters asked are shown and can be recognized in live specimens, using bright field or interference contrast microscopy. Reliable identification of dileptids requires detailed observation of body size and shape (e.g., length:width ratio, shape and proportion of proboscis to body length, shape of posterior body end), the nuclear and contractile vacuole apparatus as well as the extrusome shape and pattern. Body shape and the arrangement of the contractile vacuoles can be easily observed at low magnification (about ×100–400), while macronucleus and extrusomes must be studied at high magnification (oil immersion objective). Keep in mind that the shape of the cells is altered under coverslip pressure. Further, the euplanktonic dileptids (*Paradileptus elephantinus* and *Pelagodileptus trachelioides*) become rapidly morbid and globular when transferred onto the slide. Therefore, fresh specimens must be taken from the sample with a large-bore (opening ~ 1 mm) pipette and first investigated under low magnification.

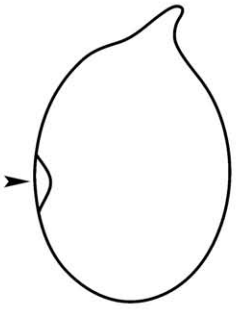
All identifications should be checked against the detailed descriptions in the systematic section, especially, against the chapters "taxonomy" and "remarks". These contain important notes on distinguishing the species from its nearest relatives and/or other similar-looking taxa. Further, in these chapters the most important and outstanding features of the species are emphasized and discussed. Only if all important traits match, the identification can be considered as reliable. If you are insecure at a certain couplet follow both leads, or be aware of having discovered a not yet described species or genus.

On the ten key plates, we provide/show the following data/features for each species: body shape and size range; nuclear apparatus (shaded black); arrangement of contractile vacuoles (depicted as clear circles); and extrusomes (if data available). If a certain species has two types of extrusomes, both are shown and usually placed left of the proboscis. The larger and/or more conspicuous type is referred to as type I.

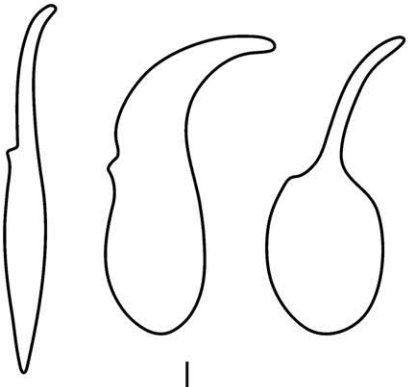
Illustrated key I

Body shape

Ovoidal with fossa on right side (arrowhead)
Proboscis immobile or only slightly mobile



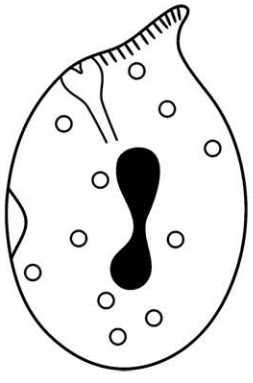
Oblong, rarely rostrate or ovoidal without fossa
Proboscis agile



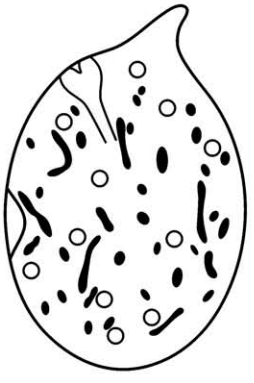
Macronucles
Extrusomes
Habitat

Dumbbell-shaped
Rod-shaped
Limnetic

Many scattered nodules
Extrusomes absent
Marine



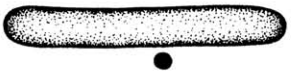
Trachelius ovum
125–615 µm



Apotrachelius multinucleatus
250–300 µm

Macronuclear pattern

A single oblong to rod-shaped piece — See illustrated key II (*Monomacrocaryon*)



Two nodules — See illustrated key III (*Dimacrocaryon*, *Rimaleptus*, *Microdileptus*)

Moniliform strand — See illustrated key VIII (*Monilicaryon*, *Pseudomonilicaryon*, *Paradileptus*, *Pelagodileptus*)

Many scattered nodules — See illustrated key VI (*Dileptus*, *Apodileptus*)

Illustrated key II – *Monomacrocaryon*

Body length and contractility

- ≤ 110 µm long and contractile up to 50% of body length

M. tenue
60–110 µm

- > 180 µm and not or only slightly contractile

Contractile vacuole pattern

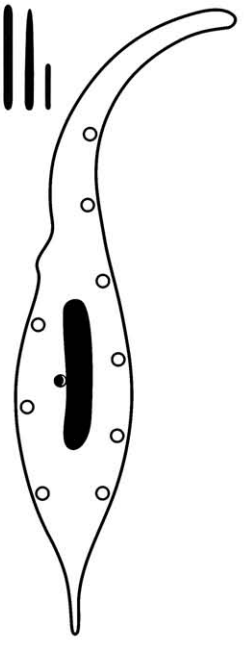
- Only a dorsal stripe of vacuoles

M. terrenus
180–560 µm

- A dorsal and ventral stripe of vacuoles

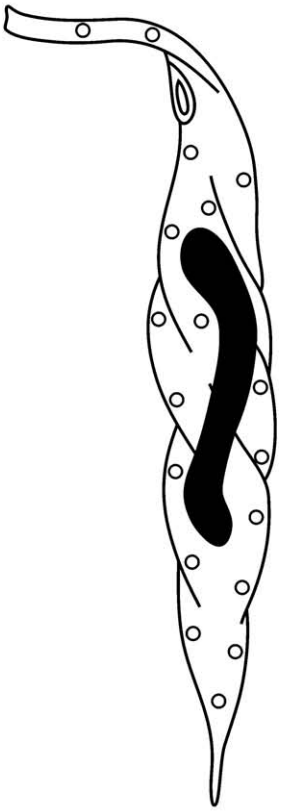
Body shape and length

- Body not twisted and up to 500 µm long



M. polyvacuolatum
200–500 µm

- Body twisted and ≥ 1000 µm long



M. gigas
1000–1600 µm

Illustrated key III – *Dimacrocaryon*, *Rimaleptus*, *Microdileptus*

Oral opening lined by refractive granules deeply impregnating with protargol

No — Yes

Colour

Grass green due to zoochlorellae

Colourless
See illustrated key IV

Body shape

Narrowly dileptid with tail or acute posterior third

Broadly dileptid with rounded posterior end

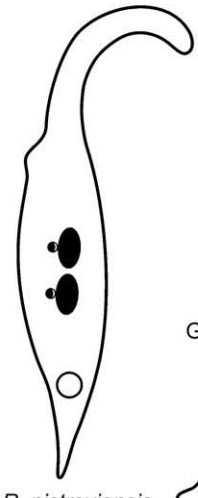
Contractile vacuole pattern

A single subterminal vacuole

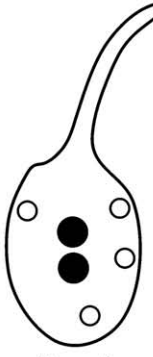
A dorsal row of vacuoles

Macronuclear nodules

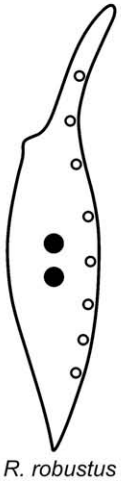
Globular — Pyriform



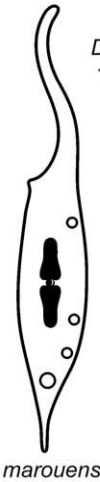
R. nistroviensis
170–190 µm



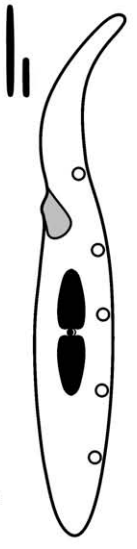
R. ovalis
160 µm



R. robustus
300 µm



R. marouensis
300 µm



D. brasiliense
125–250 µm

Oral opening

Ovate — Narrowly elliptical

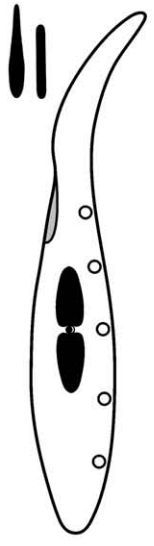
Refractive granules

Refractive granules

Extrusomes

Oblong plus very narrowly ovate

Only oblong

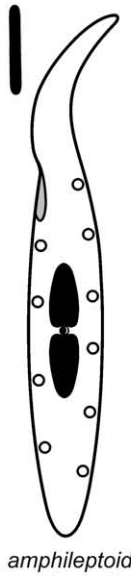


D. arenicola
120–240 µm

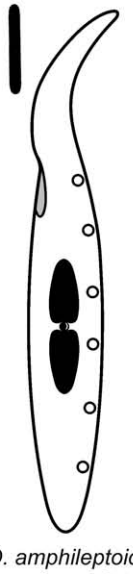
Contractile vacuole pattern Number of ciliary rows

A dorsal and ventral stripe of vacuoles
19 ciliary rows

Only a dorsal stripe
27 ciliary rows



D. amphileptoides amphileptoides
170–400 µm



D. amphileptoides paucivacuolatum
165–290 µm

Illustrated key IV – *Rimaleptus*, *Microdileptus*

Body contractile

No — Yes

Posterior body end

Rounded, acute or with short tail — With long tail (arrowheads)

Contractile vacuole pattern

Two dorsal vacuoles — A dorsal row/stripe of vacuoles
See illustrated key V

Body shape

Rostrate — Narrowly dileptid

R. conspicuus
125–200 µm

Body length

Usually about 120 µm (rarely up to 160 µm) — 130–400 µm

R. gabonensis
300 µm

R. lacazei
up to 500 µm

Nuclear apparatus

A single micronucleus (arrowhead) between macronuclear nodules — Two micronuclei (arrowheads) attached laterally to macronuclear nodules

Type I extrusomes

Bluntly oblong with minute anterior dome — Narrowly ovate — Rod-shaped

Extrusomes also around oral opening

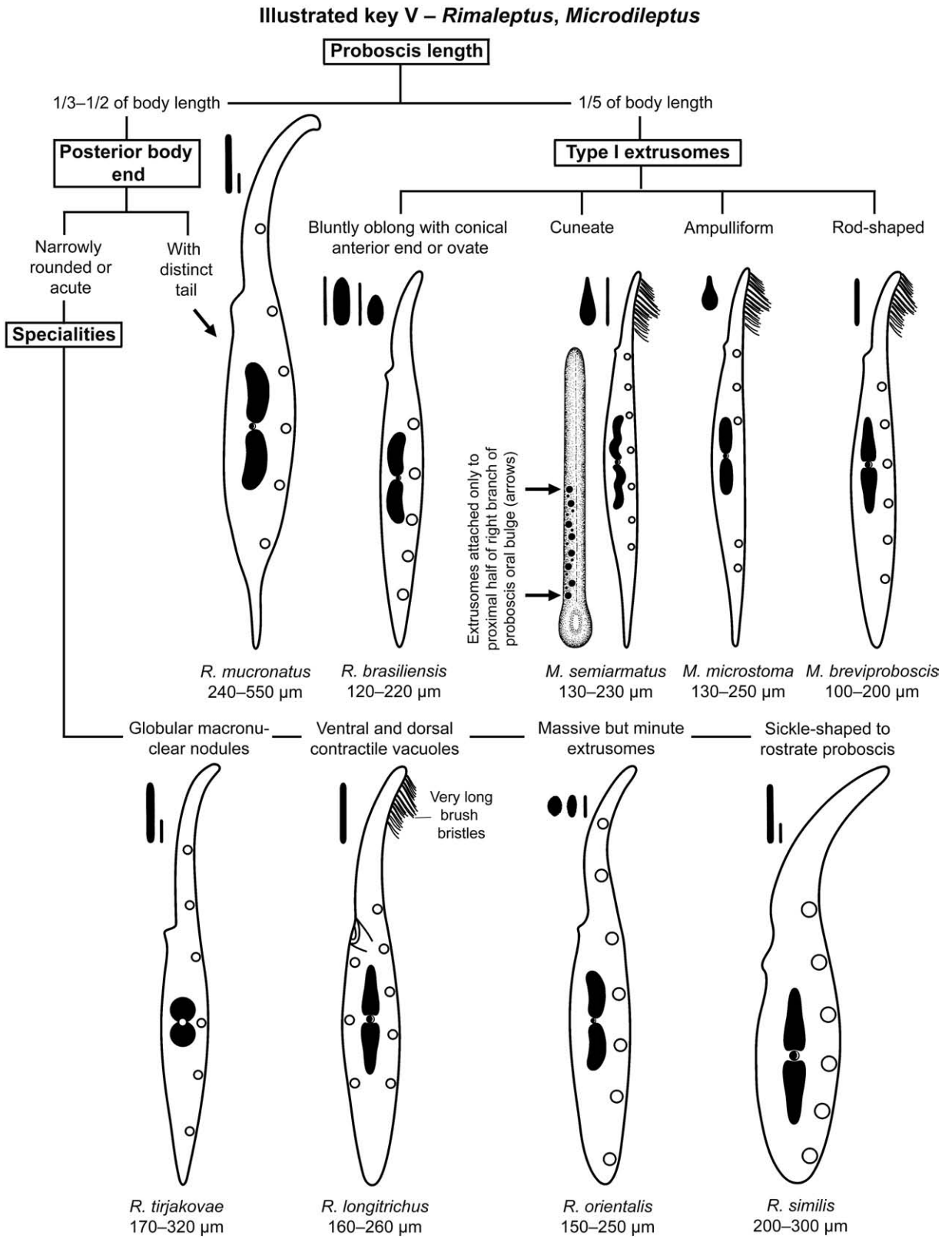
R. alpinus
60–160 µm

R. bivacuolatus
100–150 µm

R. canadensis
130–230 µm

R. armatus
140–250 µm

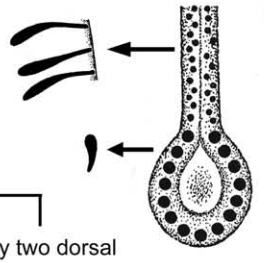
R. binucleatus
170–400 µm



Illustrated key VI – *Dileptus*, *Apodileptus*

Colour

- Grass green due to zoochlorellae → **Proboscis length**
  - 1/4 of body length → *D. viridis* 220–270 µm
  - 1/2 of body length → *D. dubius* 115 µm
- Colourless → **Contractile vacuole pattern**
  - Only dorsal vacuoles → **Special features**
    - Yes
      - Short proboscis, Marine → *D. estuarinus* 800–1100 µm
      - Rod-shaped body → *A. edaphicus* 350–600 µm
      - Producing a mucous thread → *D. jonesi* 250–600 µm (mucous thread)
      - Only two dorsal vacuoles → *D. multinucleatus* 185 µm
    - No — See illustrated key VII
  - Dorsal and ventral vacuoles → **Extrusomes around oral opening**
    - Yes

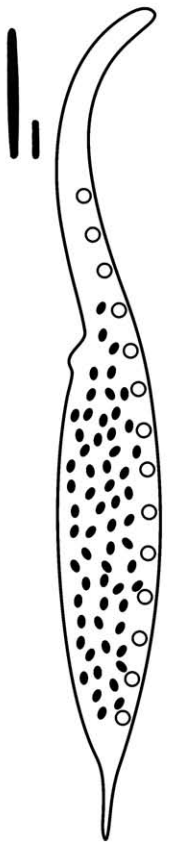


    - No → **Type I extrusomes**
      - Acicular 20 µm long → *D. costaricanus* 200–340 µm
      - Rod-shaped 10 µm long → *D. sphagnicola* 350–650 µm
      - → *D. anatinus* 800–1200 µm

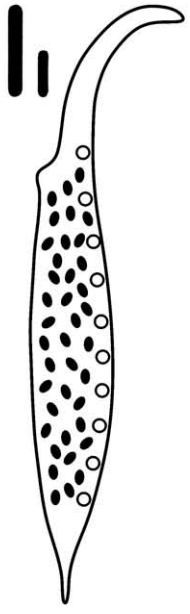
Illustrated key VII – *Dileptus*, *Apodileptus*

Type I extrusomes

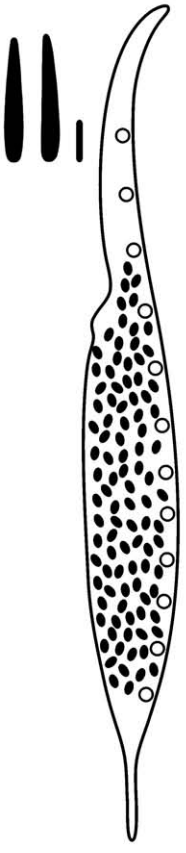
- Rod-shaped
  - **Number of macronuclear nodules**
    Number of ciliary rows
    - Over 200 nodules, 50 ciliary rows
    - 55 nodules, 22 ciliary rows
- Narrowly ovate
  - **Number of macronuclear nodules**
    Number of ciliary rows
    - Over 200 nodules, 50 ciliary rows
    - 90 nodules, 25 ciliary rows



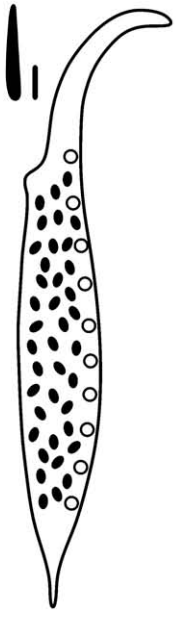
D. margaritifer
200–600 µm,
rarely up to 1000 µm



A. visscheri rhabdoplites
180–300 µm

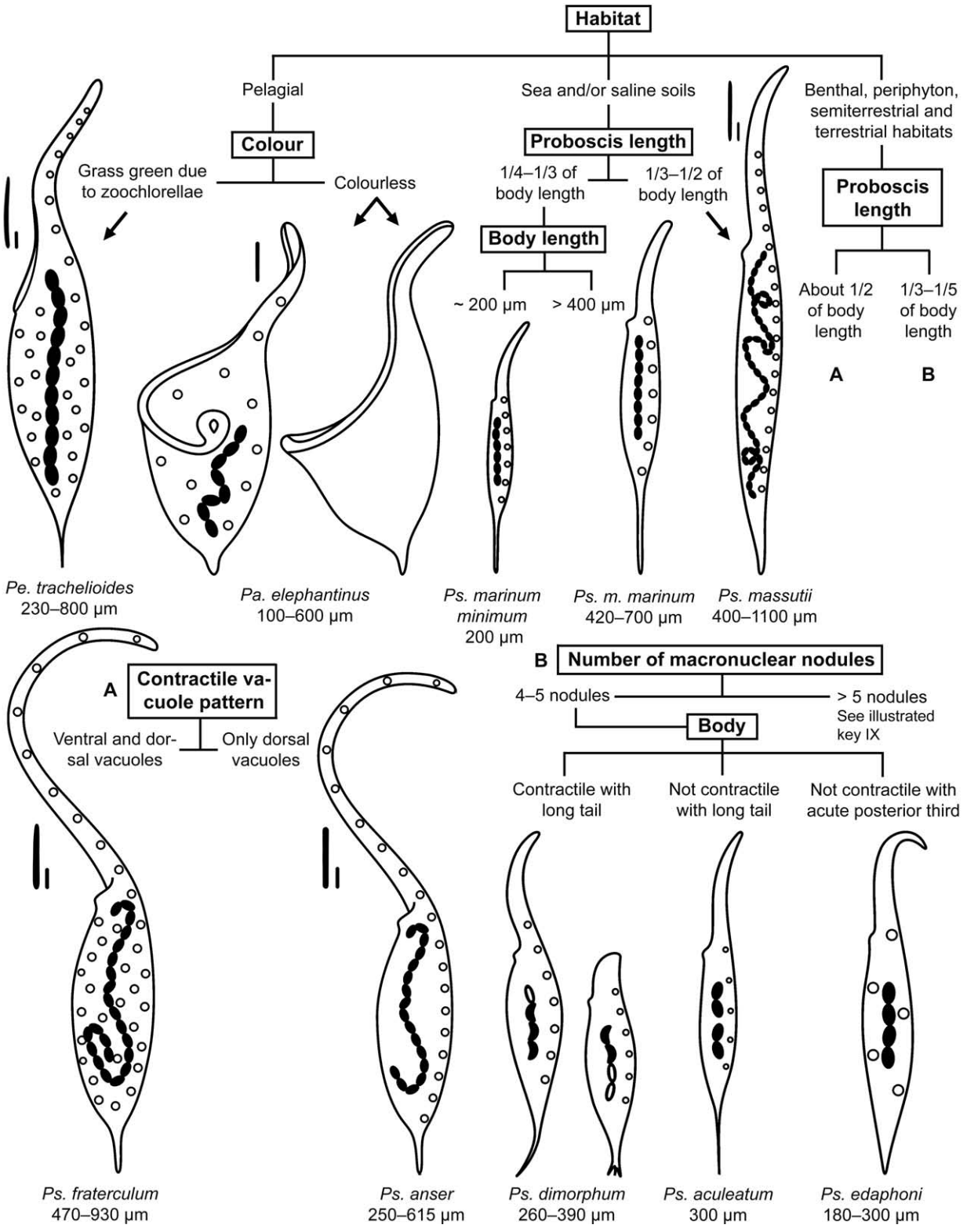


D. beersi
340–900 µm

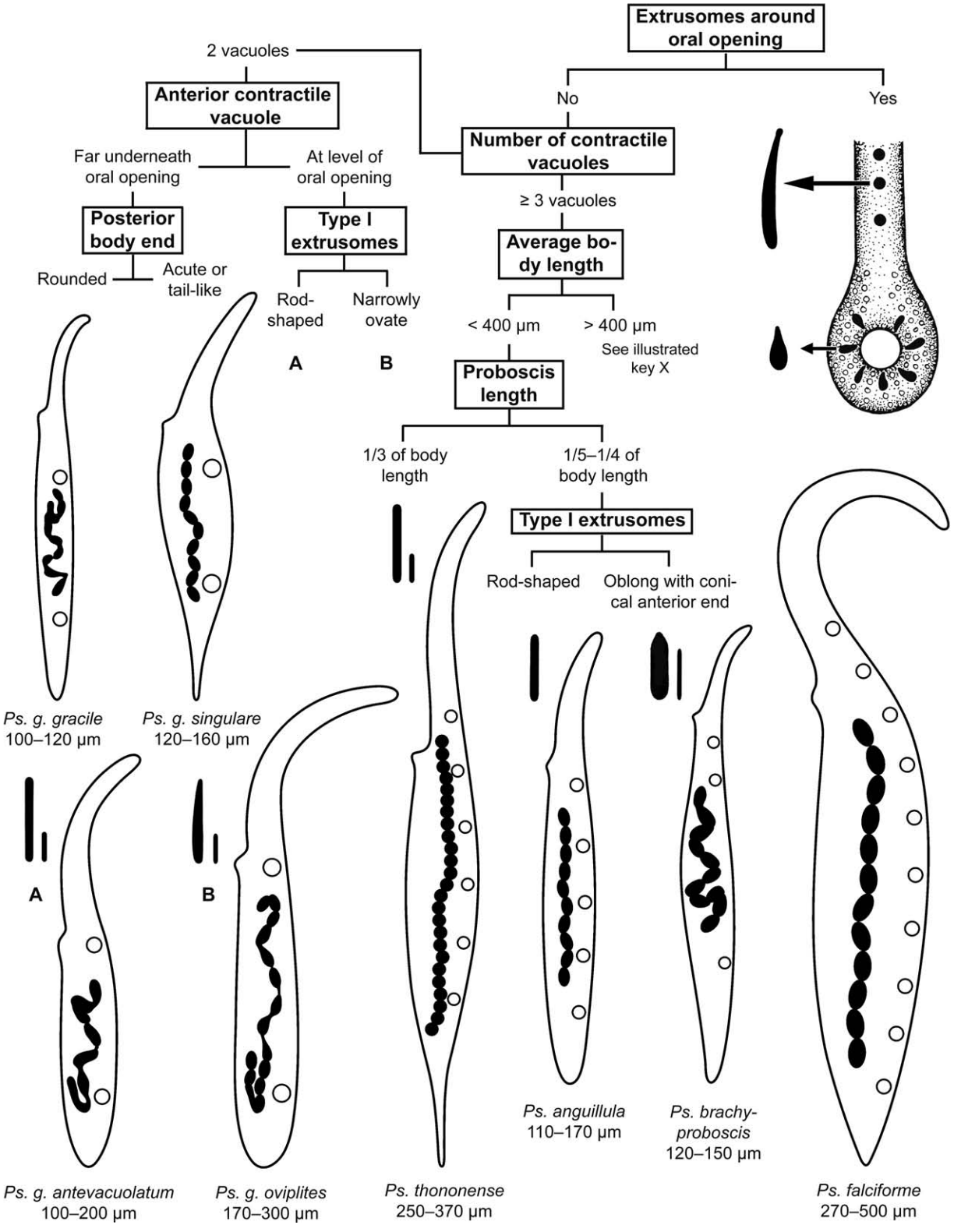


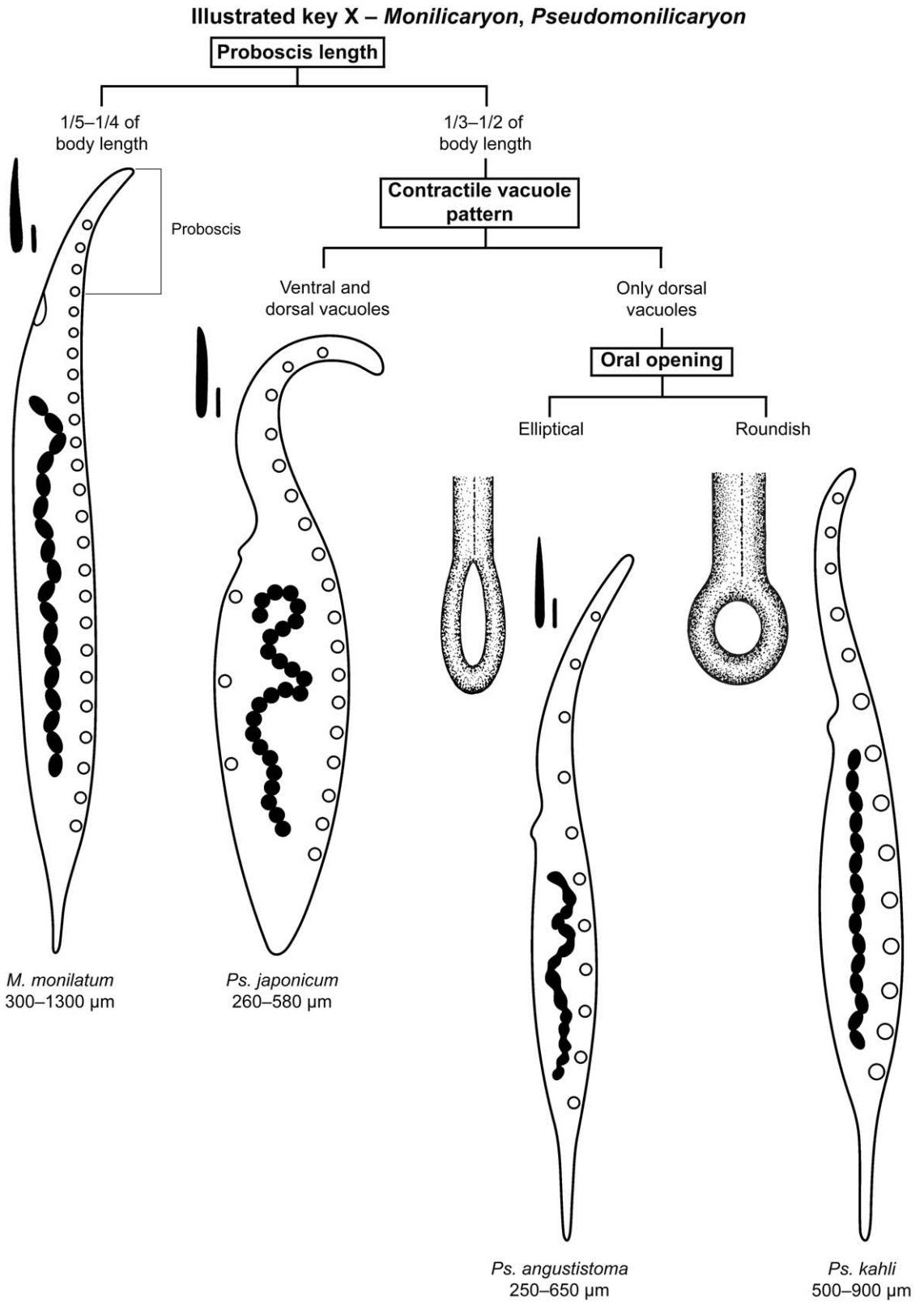
A. visscheri visscheri
180–430 µm

Illustrated key VIII – *Monilicaryon*, *Pseudomonilicaryon*, *Paradileptus*, *Pelagodileptus*



Illustrated key IX – *Monilicaryon*, *Pseudomonilicaryon*





Subclass Rhynchostomatia Jankowski, 1980

1975 Rhynchostomatida (Dileptida) Jankowski, Konspekt novoj sistemy Ciliophora: 26 (a nomen nudum due to lack of description or definition)

1980 Rhynchostomata subcl. nov. Jankowski, Trudy zool. Inst., Leningr. **94**: 105 (very brief characterization)

2011 Rhynchostomatia Jankowski, 1980 – Vďačný, Orsi, Bourland, Shimano, Epstein & Foissner, Eur. J. Protistol. **47**: 309 (improved diagnosis)

Diagnosis: Free-living Litostomatea with body partitioned into proboscis and trunk with or without tail. At least two dorsal contractile vacuoles. Oral bulge opening ventral at base of proboscis. Oral ciliary pattern complex, i.e., right branch of circumoral kinety accompanied by at least one perioral kinety, left branch by many minute, oblique preoral kineties, forming a single perioral-like kinety in some species.

Type order (by subsequent designation): Dileptida Jankowski, 1978.

Etymology: Not given in original description. Derived from the Greek nouns *rhynchos* (proboscis) and *stoma* (mouth), obviously referring to the oral bulge opening at the base of the proboscis.

Remarks: The Rhynchostomatida were introduced with ordinal rank by Jankowski (1975) but without any definition, and are thus unavailable (Article 13.1 of the ICZN 1999). Although Jankowski (1980) established the subclass Rhynchostomata validly five years later, he dropped it in Jankowski (2007). Vďačný et al. (2011b) resurrected and redefined the Rhynchostomata changing its suffix to *-ia*, as usual for ciliate subclasses (Lynn 2008).

Based on both morphological and molecular data, Vďačný et al. (2011b) recognized two orders within the Rhynchostomatia: Tracheliida and Dileptida. Tracheliids are easily distinguished in vivo from dileptids by body shape (broadly ovoidal vs. narrow to rod-like) and the presence (vs. absence) of a lateral fossa. Further, the proboscis of the tracheliids is immobile and short, and thus less conspicuous than that of the dileptids (Fig. 38).

Key to Orders

1 Body ovoidal and with fossa on right side. Proboscis immobile or only slightly mobile, its dorsal side distinctly shorter than the ventral one ..... Tracheliida (p. 110)

– Body oblong or rostrate, without fossa. Proboscis agile, its ventral and dorsal side of similar length .....Dileptida (p. 142)

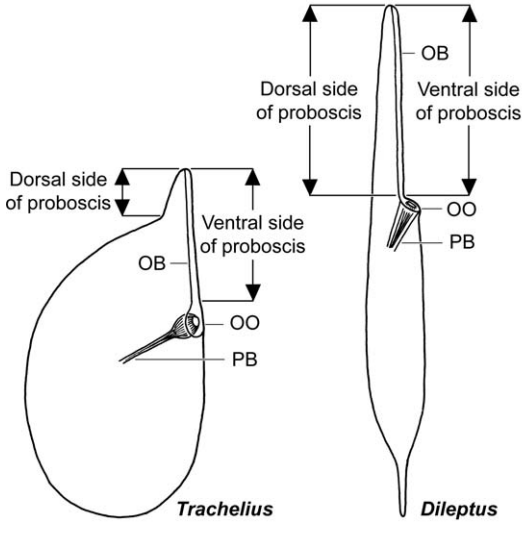


Fig. 38: Comparison of proboscis in tracheliids and typical dileptids. The proboscis of the tracheliids is short because its dorsal side is much shorter than the ventral one. OB – oral bulge, OO – oral bulge opening, PB – pharyngeal basket.

Order Tracheliida Vďačnýet al., 2011

2011 Tracheliida ord. n. Vďačný, Orsi, Bourland, Shimano, Epstein & Foissner, Eur. J. Protistol. **47**: 310

Diagnosis: Body broadly dileptid. Proboscis immobile or only slightly mobile, its dorsal side distinctly shorter than the ventral one. A distinct groove (fossa) on right side containing and surrounded by condensed somatic ciliature. Dorsal brush not staggered and three- to four-rowed. Circumoral kinety dikinetidal throughout. Internal oral basket clavate.

Type family (by original designation): Tracheliidae Ehrenberg, 1838.

Etymology: Composite of the stem of the generic name *Trachelius* and the order suffix *-ida*.

Remarks: The order Tracheliida comprises a single family with two monotypic genera: *Trachelius* and *Apotrachelius* nov. gen. They share two unique features, viz., a lateral fossa and a strongly developed, clavate internal oral basket composed of innumerable fine fibres. Further, their proboscis appears shorter when compared with that of typical dileptids because its dorsal side is much shorter than the ventral one (Fig. 38). Tracheliids display several traits that have not been found in other dileptids but are common in most haptorians: (i) the circumoral kinety is dikinetidal throughout (vs. monokinetidal around oral bulge opening) and (ii) the dorsal brush is not staggered (vs. staggered). These features are very likely plesiomorphies inherited from the last common ancestor of the Litostomatea, supporting the basal position of the tracheliids within the subclass Rhynchostomatia as shown in the cladistic and molecular phylogenetic analyses (for details, see General section and Vďačný et al. 2011b).

Family Tracheliidae Ehrenberg, 1830

1830 Trachelina Ehrenberg, Abh. dt. Akad. Wiss. Berl. year **1832**: 42 [included as a sectio in the family Allotreta]

1831 Trachelina – Ehrenberg, Abh. dt. Akad. Wiss. Berl. year **1831**: 106 [included as a family in the "Abtheilung" Allotreta]

1831 Ophryocercina Ehrenberg, Abh. dt. Akad. Wiss. Berl. year **1831**: 112 (junior synonym)

1831 Trachelinorum – Hemprich & Ehrenberg, Symbolae physicae Animalia Evertebrata: 31 [including only *Trachelius lamella* N.? *Kolpoda lamella* named *Colpoda platyura*]

1838 Trachelina – Ehrenberg, Infusionsthierchen: 319 (taxonomic revision)

1852 Tracheliina E. – Perty, Zur Kenntnis kleinster Lebensformen: 150 (brief review)

1859 Trachelina – Stein, Organismus der Infusionsthiere I: 20 (brief review)

1867 Trachelina St. – Stein, Organismus der Infusionsthiere II: 169 (brief review)

1881 Tracheliidæ, Ehr. – Kent, Manual infusoria II: 522 (brief review)

1889 Trachelina (Ehrbg) Stein 1860 – Bütschli, Protozoa: 1690 (brief review)

1895 Trachelina – Blochmann, Mikroskopische Thierwelt: 92 (brief review)

1896 Trachelina (Ehrbg.) Stein – Schewiakoff, Zap. imp. Akad. Nauk **4**: 215 (taxonomic revision)

1901 Trachelina Ehrbg. St. – Roux, Mém. Inst. natn. génev. **19**: 40 (brief review)

1931 Tracheliidae Ehrenberg, 1838 – Kahl, Tierwelt Dtl. **21**: 203 (taxonomic revision; incorrectly dated)

1936 Tracheliidæ Ehrenberg, 1840 – Bhatia, Fauna of British India: 115 (brief review; incorrectly dated)

1953 Tracheliidae Kent – Reichenow, Protozoenkunde: 1102 (brief review)

1979 Tracheliidae Ehrenberg, 1838 – Corliss, Ciliated protozoa: 216 (characterization, classification; incorrectly dated)

2002 Tracheliidae Ehrenberg, 1838 – Lynn & Small, Phylum Ciliophora: 482 (guide to ciliates; incorrectly dated)

2007 Tracheliidae Ehr., 1838 – Jankowski, Protista II: 572 (handbook; incorrectly dated)

2008 Tracheliidae Ehrenberg, 1838 – Lynn, Ciliated protozoa: 370 (characterization, classification; incorrectly dated)

Diagnosis: With characteristics of order (above).

Type genus (by subsequent designation): *Trachelius* Schrank, 1803.

Remarks: Within the family Tracheliidae, we recognize two monotypic genera: *Trachelius* and *Apotrachelius* nov. gen. They are similar in body shape and size as well as in the contractile vacuole pattern, but differ by the macronucleus (dumbbell-shaped vs. scattered nodules), the presence/absence of oral bulge extrusomes, and the shape of the oral bulge opening (dileptid vs. paradileptid).

Key to Genera and Species

1 Macronucleus unsegmented but often strongly constricted in mid and thus appearing as composed of two nodules in vivo. With oral bulge extrusomes. Freshwater ..... *Trachelius ovum* (p. 114)

– Macronucleus in many scattered nodules. Without oral bulge extrusomes. Saltwater ..... *Apotrachelius multinucleatus* (p. 135)

Trachelius Schrank, 1803

1803 *Trachelius* Schrank, Fauna Boica: 20

1831 *Ophryocerca* Ehrenberg, Abh. dt. Akad. Wiss. Berl. year **1831**: 112 (objective synonym)

1838 *Trachelius* – Ehrenberg, Infusionsthierchen: 320 (taxonomic revision)

1852 *Harmodirus* – Perty, Zur Kenntnis kleinster Lebensformen: 151 (objective synonym)

1859 *Trachelius* – Claparède & Lachmann, Mém. Inst. natn. génev. **6**: 345 (taxonomic revision)

1865 *Trachelius* – Diesing, Sber. Akad. Wiss. Wien **52**: 507 (taxonomic revision)

1865 *Cephalorhynchus* Diesing, Sber. Akad. Wiss. Wien **52**: 507 [established for an unfigured species of Ehrenberg, viz., *Trachelius* (?) *laticeps*. In the absence of any figure, both *Cephalorhynchus* and *T. laticeps* should be considered as indeterminable; see also Aescht (2001)]

1875 *Trachelius* – Fromentel, Études Microzoaires: 182 (taxonomic revision)

1881 *Trachelius*, Ehrenberg – Kent, Manual infusoria II: 522 (brief review)

1889 *Trachelius* (Schrank 1803) emend. Clap. und L. – Bütschli, Protozoa: 1692 (brief review)

1895 *Trachelius* (Schrank) Clap. u. L. – Blochmann, Mikroskopische Thierwelt: 93 (brief review)

1896 *Trachelius* Schrank – Schewiakoff, Zap. imp. Akad. Nauk **4**: 216 (taxonomic revision)

1901 *Trachelius* Schrank – Roux, Mém. Inst. natn. génev. **19**: 41 (brief review)

1911 *Trachelius* (Schrank 1803) emend. Cl. u. L. 1858 – Hamburger & Buddenbrock, Nord. Plankt. **7**: 33 (brief review)

1931 *Trachelius* Schrank, 1803 – Kahl, Tierwelt Dtl. **21**: 210 (taxonomic revision)

1936 *Trachelius*, Schrank, 1803, emend. Claparède & Lachmann, 1858–61 – Bhatia, Fauna of British India: 117 (brief review)

1979 *Trachelius* Schrank, 1803 – Corliss, Ciliated protozoa: 216 (characterization, classification)

1997 *Trachelius* Schrank, 1803 – Foissner, Limnologica **27**: 202 (improved diagnosis)

2001 *Trachelius* Schrank 1803 – Aescht, Denisia **1**: 164 (catalogue of generic names of ciliates)

2007 *Trachelius* Schrank, 1803 – Jankowski, Protista II: 574 (brief generic review)

2008 *Trachelius* Schrank, 1803 – Lynn, Ciliated protozoa: 371 (list of genera)

non *Trachelius*, Schrank – Dujardin, 1841, Zoophytes: 398 (only flagellates and non-dileptid ciliates included)

non *Trachelius* Schrank – Perty, 1852, Zur Kenntnis kleinster Lebensformen: 150 (only flagellates and non-dileptid ciliates included)

Nomenclature and taxonomy: Schrank (1803) established the genus *Trachelius* with eight poorly described nominal species (Table 21); he did not fix a type species. Claparède & Lachmann (1859) redefined *Trachelius* and confined it to a single species, *T. ovum*; Fromentel (1875) followed. However, *T. ovum* is not eligible to be fixed as the type species because it was not originally included in the genus *Trachelius* (Article 67.2 of the ICZN 1999). At present, only *T. cicer*, which is a senior synonym of *T. ovum* but a nomen oblitum (see below), may be declared as type species. According to Article 67.1.2 of the ICZN (1999), the name of a type species remains unchanged even when it is a junior synonym or homonym, or a suppressed name. Thus, we fix *T. cicer* as the type species of the genus *Trachelius*. We shall bid the International Commission on Zoological Nomenclature to use its plenary power to fix *T. ovum* as the type species of *Trachelius*.

Trachelius has two objective synonyms, *Ophryocerca* and *Harmodirus*, which Ehrenberg (1831) and Perty (1852) founded on the same species, *Trachelius ovum*. Apstein (1915) proposed the genus as nomen conservandum.

There is only one other genus similar to *Trachelius*, viz., *Apotrachelius* nov. gen., which differs by the many scattered macronuclear nodules (vs. mononucleate), the absence (vs. presence) of oral bulge extrusomes, and the paradileptid (vs. dileptid) oral bulge opening. From all other dileptid genera, *Trachelius* is easily distinguished in vivo by body shape (ovoid vs. oblong or rostrate) and the presence (vs. absence) of a lateral fossa.

Improved diagnosis: Small- to medium-sized Tracheliidae with broad body. Macronucleus dumbbell-shaped. With oral bulge extrusomes. Oral bulge opening dileptid.

Type species (by subsequent designation): *Trachelius cicer* Schrank, 1803. However, *Ophryocerca ovum* Ehrenberg, 1831 will be proposed to be fixed as the type species of *Trachelius* under the plenary power of the International Commission on Zoological Nomenclature.

Etymology: Not given in original description. Derived from the Greek noun *trachelos* (throat). Masculine gender.

Remarks: Altogether 29 species were originally described or combined with *Trachelius* (Table 21). However, we recognize only one, *T. ovum*, which has eight synonyms. Fourteen *Trachelius* species were transferred to other genera and twelve remained indeterminate. Recently, Lin et al. (2004) neotypified *Amphileptus gutta* Cohn, 1866, which was combined with *Trachelius* by Hamburger & Buddenbrock (1911), as *Orthodonella gutta* (Cohn, 1866) Kahl, 1931.

Table 21: List of species combined with the genus *Trachelius* and their current affiliation.

Original name	Authorship/ Combining author	Supposed valid name	Notes
Amphileptus guta	COHN, 1866	*Orthodonella gutta* (COHN, 1866) KAHL, 1931	neotypified by LIN et al. (2004); see Figs 43l-n
Amphileptus gutta	KALMUS, 1929	?	see Figs 43p-t
Amphileptus tracheloides	MASKELL, 1887	?	*Ophryoglena*? (see Fig. 43x)
Trachelina gutta	GHOSH, 1921	?	*Ophryoglena*?
Trachelius (Amphileptus) tracheloides (MASKELL, 1887)	KAHL, 1931	?	*Ophryoglena*?
Trachelius ambiguus	EHRENBERG, 1831	*Spirostomum ambiguum* (MUELLER, 1786) EHRENBERG, 1835	synonym
Trachelius anas	EHRENBERG, 1831	?	pleurostome haptorid?
Trachelius anaticula n. sp.	EHRENBERG, 1833	?	likely *Amphileptus piger*
Trachelius anhinga	SCHRANK, 1803	*Lacrymaria olor* (MUELLER, 1876) BORY DE SAINT-VINCENT, 1824	synonym
Trachelius apiculatus	PERTY, 1852	*Trachelophyllum apiculatum* (PERTY, 1852) CLAPARÈDE & LACHMANN, 1859	synonym
Trachelius cicer	SCHRANK, 1803	*Trachelius ovum* (EHRENBERG, 1831) EHRENBERG, 1833	nomen oblitum
Trachelius colymbus	SCHRANK, 1803	?	pleurostome haptorid?
Trachelius cygnus	SCHRANK, 1803	*Litonotus cygnus* (MUELLER, 1773) FOISSNER et al., 1995	synonym
Trachelius dendrophilus	EHRENBERG, 1853	?	flagellate
Trachelius falx	SCHRANK, 1803	?	pleurostome haptorid?
Trachelius? *globulifer*	EHRENBERG, 1838	*Heteronema globuliferum* (EHRENBERG, 1838) STEIN, 1878	flagellate
Trachelius gutta COHN	HAMBURGER & BUDDENBROCK, 1911	*Orthodonella gutta* (COHN, 1866) KAHL, 1931	see Fig. 43m
Trachelius gutta	KAHL, 1931	?	see Fig. 43u
Trachelius gutta	BIERNACKA, 1963	?	see Fig. 43v
Trachelius gutta (COHN)	BHATIA, 1936	?	*Ophryoglena*? (see Fig. 43o)
Trachelius lamella	EHRENBERG, 1838	*Litonotus lamella* (MUELLER, 1773) FOISSNER et al., 1995	synonym
Trachelius (?) *laticeps*	EHRENBERG, 1840	?	flagellate
Trachelius leidyi	FOULKE, 1884	*Trachelius ovum* (EHRENBERG, 1831) EHRENBERG, 1833	synonym
Trachelius meleagris	EHRENBERG, 1838	?	pleurostome haptorid?
Trachelius noduliferus	PERTY, 1852	?	trachelophyllid haptorid?

Original name	Authorship/ Combining author	Supposed valid name	Notes
Trachelius ovum	EHRENBERG, 1831	*Trachelius ovum* (EHRENBERG, 1831) EHRENBERG, 1833	nomen protectum (see this study)
Trachelius planaria	SCHRANK, 1803	*Litonotus fasciola* (MUELLER, 1773) WRZEŚNIOWSKI, 1870	synonym
Trachelius proteus	OKEN, 1815	*Lacrymaria olor* (MUELLER, 1786) BORY DE SAINT-VINCENT, 1824	synonym
Trachelius pusillus	PERTY, 1852	*Trachelophyllum pusillum* (PERTY, 1952) CLAPARÈDE & LACHMANN, 1858	synonym
Trachelius strictus	DUJARDIN, 1841	?	ciliate fragment?
Trachelius stylatus	SCHRANK, 1803	?	pleurostome haptorid?
Trachelius subtilis sp. n.	PENARD, 1922	*Trachelius ovum* (EHRENBERG, 1831) EHRENBERG, 1833	new synonym
Trachelius teres	DUJARDIN, 1841	?	*Cyclidium*?
Trachelius tracheloides MASKELL, 1887	JONES, 1974	*Apotrachelius multinucleatus* nov. spec.?	new synonym?
Trachelius? *trichophorus*	EHRENBERG, 1838	*Peranema trichophorum* (EHRENBERG, 1838) STEIN, 1878	flagellate
Trachelius utriculus	SCHRANK, 1803	*Litonotus fasciola* (MUELLER, 1773) WRZEŚNIOWSKI, 1870	synonym
Trachelius vorax n. sp.	EHRENBERG, 1833	*Trachelius ovum* (EHRENBERG, 1831) EHRENBERG, 1833	synonym

Trachelius ovum (EHRENBERG, 1831) EHRENBERG, 1833 (Figs 39a–m, 40a–o, 41a–s, 42a–y, 43a–x, 44a–y, 45a–v; Tables 22, 23)

1803 *Trachelius cicer* SCHRANK, Fauna Boica: 60 (nomen oblitum, without figure)

1831 *Ophryocerca ovum* EHRENBERG, Abh. dt. Akad. Wiss. Berl. year **1831**: 112 (objective synonym; nomen protectum, see nomenclature; without figure)

1833 *Trachelius ovum* – EHRENBERG, Abh. dt. Akad. Wiss. Berl. year **1833**: 277 (combining author, without figure)

1833 *Trachelius vorax* N. sp. EHRENBERG, Abh. dt. Akad. Wiss. Berl. year **1833**: 275 (synonymy proposed by SCHEWIAKOFF 1896, FOISSNER & FOISSNER 1988b, and FOISSNER et al. 1995; without figure)

1838 *Trachelius ovum* – EHRENBERG, Infusionsthierchen: 323 (first taxonomic reviser)

1838 *Trachelius vorax* – EHRENBERG, Infusionsthierchen: 321 (taxonomic revision)

1841 *Amphileptus ovum* – DUJARDIN, Zoophytes: 487 (combining author, objective synonym)

1841 *Amphileptus vorax* – DUJARDIN, Zoophytes: 486 (= *Trachelius vorax* sensu EHRENBERG 1833)

1852 *Harmodirus ovum* – PERTY, Zur Kenntnis kleinster Lebensformen: 151 (objective synonym)

1859 *Trachelius ovum* EHR. – CLAPARÈDE & LACHMANN, Mém. Inst. natn. génev. **6**: 345 (taxonomic revision)

1859 *Amphileptus vorax* – CLAPARÈDE & LACHMANN, Mém. Inst. natn. génev. **6**: 351 (= *Trachelius vorax* sensu EHRENBERG 1833)

1881 *Trachelius ovum*, EHR. – KENT, Manual infusoria II: 522 (taxonomic revision)

1881 *Amphileptus vorax*, EHR. sp. – KENT, Manual infusoria II: 525 (= *Trachelius vorax* sensu EHRENBERG 1833)

1884 *Trachelius leidyi* – FOULKE, Proc. Acad. nat. Sci. Philad. year **1884**: 52 (synonymy proposed by SCHEWIAKOFF 1896 and FOISSNER et al. 1995, without figure)

1887 *Amphileptus rotundus*, sp. nov. – MASKELL, Trans. Proc. N. Z. Inst. **20**: 9 (synonymy proposed by FOISSNER et al. 1995)

1888 *Trachelius ovum*, EHR. – STOKES, J. Trenton nat. Hist. Soc. **1**: 167 (without figure)

1891 *Trachelius ovum* – FABRE-DOMERGUE, J. Anat. Paris **27**: 74 (still valuable morphological study)

1895 *Trachelius ovum* EHRBG. – BLOCHMANN, Mikroskopische Thierwelt: 93 (brief description of a German population)

1896 *Trachelius ovum* EHRBG. – SCHEWIAKOFF, Zap. imp. Akad. Nauk **4**: 218 (second taxonomic reviser)

1901 *Trachelius ovum* EHRBG. – ROUX, Mém. Inst. natn. génev. **19**: 41 (brief description of a Swiss population)

1903 *Trachelius ovum* – HAMBURGER, Arch. Protistenk. **2**: 445 (still valuable morphological study)

1911 *Trachelius ovum* EHRBG. – HAMBURGER & BUDDENBROCK, Nord. Plankt. **7**: 33 (brief description of a Finnish population)

1914 *Trachelius ovum* EHR. – SMITH, Kans. Univ. Sci. Bull. **9**: 155 (description of a Kansas population)

1922 *Trachelius ovum* EHRENB. 1838 – PENARD, Études Infusoires: 80 (brief description of a Swiss population)

1922 *Trachelius subtilis* sp. n. PENARD, Études Infusoires: 83 (proposed synonym)

1925 *Trachelius ovum* EHRBG. – WETZEL, Arch. Protistenk. **51**: 223 (morphological study)

1930 *Trachelius ovum* EHRBG. – KLEIN, Arch. Protistenk. **69**: 245 (silverline pattern)

1930 *Trachelius ovum* EHRBG. – SCHNEIDER, Arch. Protistenk. **72**: 498 (extrusomes)

1931 *Trachelius ovum* EHRENBERG, 1831 – KAHL, Tierwelt Dtl. **21**: 210 (third taxonomic reviser)

1931 *Trachelius subtilis* PENARD, 1922 – KAHL, Tierwelt Dtl. **21**: 211 (taxonomic revision)

1933 *Trachelius subtilis* PENARD 1922 – WANG & NIE, Contr. biol. Lab. Sci. Soc. China **10**: 29 (description of a Chinese population)

1950 *Trachelius ovum*, nov. var. – VÖRÖSVÁRY, Annls biol. Univ. szeged. **1**: 361 (description of a winter variety; possibly a misidentification)

1957 *Trachelius* cf. *ovum* EHR. ? – LEPȘI, Trav. Mus. Hist. nat., "Gr. Antipa" **1**: 88 (brief description of a Roumanian population)

1957 *Trachelius* sp. – LEPȘI, Buletin şti. Acad. Repub. pop rom. **9**: 232 (dwarf form)

1959 *Trachelius ovum* EHR. – BIERNACKA, Polskie Archwm Hydrobiol. **5**: 54 (ecology)

1960 *Trachelius ovum* EHR. – BOVEE, J. Protozool. **7**: 356 (ecology)

1960 *Trachelius ovum* EHRB. – CASPERS & SCHULZ, Int. Revue ges. Hydrobiol. **45**: 545 (ecology)

1960 *Trachelius ovum* EHRENBERG – DRAGESCO, Trav. Stn biol. Roscoff (N. S.) **12**: 185 (ecology)

1960 *Trachelius ovum* EHR. – GROOT & GRAFF, Publtiës hydrobiol. Vereen. **5**: 77 (ecology)

1961 *Trachelius ovum* EHRB. – BUCK, Jh. Ver. vaterl. Naturk. Württ. **116**: 201 (ecology)

1961 *Trachelius ovum* EHR. – PATRICK, Proc. Acad. nat. Sci. Philad. **113**: 243 (ecology)

1961 *Trachelius ovum* EHRBG. – WEBB, J. Anim. Ecol. **30**: 141 (ecology)

1962 *Trachelius ovum* EHRB. – KALTENBACH, Wass. Abwass. Wien **1962**: 14 (ecology)

1964 *Trachelius ovum* – CASPERS & SCHULZ, Arch. Hydrobiol. **60**: 64 (ecology)

1965 *Trachelius ovum* EHRB. – EHLERS, Abh. Landesmus. Naturk. Münster **27**: 17 (ecology)

1966 *Trachelius ovum* EHRENBERG – CAIRNS & YONGUE, Notul. Nat. **No. 383**: 8 (ecology)

1968 *Trachelius ovum* Ehrenberg, 1841 – Chorik, Svobodnoživuŝie infuzorii vodoemov Moldavii: 71 (brief description of a Moldavian population; misdated)

1969 *Trachelius ovum* Ehrenberg – Wilbert, Arch. Hydrobiol. **35** (Suppl.): 458 (ecology)

1970 *Trachelius ovum* Ehrb. – Nusch, Arch. Hydrobiol. **37** (Suppl.): 300 (ecology)

1971 *Trachelius ovum* Ehrenberg – Buck, Münchn. Beitr. Abwass.- Fisch.- Flussbiol. **19**: 39 (ecology)

1972 *Trachelius ovum* Ehrenberg – Bick, Ciliated protozoa: 54 (ciliate key)

1972 *Trachelius ovum* Ehrenberg – Dragesco, Annls Fac. Sci. Univ. féd. Cameroun **11**: 75 (ecology)

1972 *Trachelius ovum* – Noll, Arch. Hydrobiol. **70**: 360 (ecology)

1973 *Trachelius ovum* Ehr. – Bick & Bertram, Forsch.-Ber. Landes NRhein-Westf. No. **2266**: 14 (ecology)

1973 *Trachelius ovum* Ehrenberg – Cairns & Yongue, Revta Biol., Lisb. **9**: 30 (ecology)

1975 *Trachelius ovum* Ehrbg. – Czapik, Acta hydrobiol., Kraków **17**: 26 (ecology)

1975 *Trachelius ovum* – Nusch, Verh. Ges. Ökologie year **1975**: 42 (food acquisition)

1976 *Trachelius ovum* – Lüpkes, Int. J. Speleol. **8**: 131 (first record in a cave)

1977 *Trachelius ovum* Ehrb. – Bereczky, Opusc. zool., Bpest **14**: 63 (ecology)

1979 *Trachelius ovum* Ehrenberg – Hollowday, Microscopy **33**: 535 (food acquisition)

1979 *Trachelius ovum* Ehrb., 1831– Mamaeva, Infuzorii bassejna Volgi: 33 (ecology)

1979 *Trachelius ovum* Ehrb. – Mücke, Arb. Inst. landw. Zool. Bienenkd. **5**: 242 (ecology)

1979 *Trachelius ovum* Ehrenberg – Stössel, Schweiz. Z. Hydrol. **41**: 122 (ecology)

1981 *Trachelius ovum* Ehrb. – Riedel-Lorjé, Arch. Hydrobiol. **61** (Suppl.): 163 (ecology)

1982 *Trachelius ovum* Ehrenberg 1831 – Bernerth, Cour. Forsch.-Inst. Senckenberg **57**: 195 (ecology)

1982 *Trachelius ovum* Ehrenberg – Jutrczenki, Decheniana **135**: 109 (ecology)

1983 *Trachelius ovum* Ehr. – Bereczky, Oertel & Nosek, Arch. Hydrobiol. **68** (Suppl.): 52 (ecology)

1984 *Trachelius ovum* Ehrenberg, 1831 – Albrecht, Decheniana **137**: 151 (ecology)

1984 *Trachelius ovum* Ehrb. – Alekperov, Hydrobiol. J. **20**: 18 (ecology)

1986 *Trachelius ovum* (Ehrenberg, 1831) – Dragesco & Dragesco-Kernéis, Faune tropicale **26**: 167 (brief review and figures from an African population)

1986 Trachelius ovum Ehrbg – Hul, Acta hydrobiol., Kraków **28**: 153 (ecology)

1987 *Trachelius ovum* Ehrenberg – Bauer, Arch. Hydrobiol. **77** (Suppl.): 17 (ecology)

1987 Trachelius ovum Ehrbg – Hul, Acta hydrobiol., Kraków **29**: 207 (ecology)

1987 *Trachelius ovum* Ehrenberg, 1831 – Lokot', Èkologiâ resničnyh prostejših: 35 (ecology)

1988 *Trachelius ovum* (Ehrenberg, 1831) – Foissner, Hydrobiologia **166**: 44 (saprobic classification)

1989 *Trachelius ovum* Ehrenberg, 1831 – Song & Wilbert, Lauterbornia **3**: 43 (detailed morphological study)

1990 *Trachelius ovum* – Niederlehner & Cairns, Water, Air, Soil Pollution **52**: 192 (ecology)

1991 *Trachelius ovum* Ehrenberg, 1831 – Packroff & Wilbert, Arch. Protistenk. **140**: 124 (ecology)

1994 *Trachelius ovum* Ehrenberg, 1831 – Szentiványi & Tirjaková, Acta zool. Univ. Comenianae **38**: 94 (ecology)

1995 *Trachelius ovum* (Ehrenberg, 1831) Ehrenberg, 1838 – Foissner, Berger, Blatterer & Kohmann, Informationsberichte des Bayer. Landesamtes für Wasserwirtschaft **1/95**: 208 (taxonomic and ecological revision)

1997 *Trachelius ovum* (Ehrenberg, 1831) Ehrenberg, 1838 – Foissner, Limnologica **27**: 202 (neotypification, authoritative redescription)

1998 *Trachelius ovum* (Ehrenberg, 1831) – Tirjaková, Folia faunistica Slovaca **3**: 16 (ecology)

2002 *Trachelius ovum* (Ehrenberg, 1831) – Baláži & Matis, Biologia, Bratisl. **57**: 156 (ecology)

2003 *Trachelius ovum* (Ehrenberg, 1831) – Tirjaková, Acta zool. Univ. Comenianae **45**: 38 (ecology)

2011 *Trachelius ovum* (Ehrenberg, 1831) Ehrenberg, 1833 – Vďačný, Orsi, Bourland, Shimano, Epstein & Foissner, Eur. J. Protistol. **47**: 297 (18S rRNA gene sequence of a Salzburg population)

non *Trachelius ovum* Ehrbg. – Levander, 1901, Acta Soc. Fauna Flora fenn. **20 (5)**: 11 (marine, without figure, possibly *Apotrachelius multinucleatus*)

non *Trachelius ovum* Ehrbg. – Levander, 1901, Acta Soc. Fauna Flora fenn. **20 (6)**: 7 (marine, without figure, possibly *Apotrachelius multinucleatus*)

non *Trachelius ovum* Ehrenberg – Ruggiu, 1965, Boll. Zool. **32**: 326 (marine, without figure, possibly *A. multinucleatus*)

non *Trachelius ovum* Ehrenberg, 1838 – Lopez-Ochoterena, Madrazo-Garibay, Calderon-Aragon & Coronado-Gutierrez, 1976, Revta Soc. mex. Hist. nat. **37**: 209 (marine, macronucleus ellipsoidal, one terminal contractile vacuole; possibly a distinct species)

non *Trachelius ovum* Ehrenberg, 1838 ? – Aladro-Lubel, Martínez-Murillo & Mayén Estrada, 1990, Manual de ciliados psamofilos marinos y salobres de Mexico: 54 (marine, macronucleus ellipsoidal, one terminal contractile vacuole; possibly a distinct species)

non *Trachelius ovum* – Santagelo & Lucchesi, 1992, Hydrobiologia **230**: 84 (marine, without figure, possibly *A. multinucleatus*)

non *Trachelius ovum* – Wilbert, 1995, Acta Protozool. **34**: 281 (salt lake with up to 32‰, without figure, possibly *A. multinucleatus*)

Nomenclature and taxonomy: *Trachelius ovum* (Ehrenberg, 1831) Ehrenberg, 1833 was originally described as *T. cicer* by Schrank (1803). However, *T. cicer* does not take precedence over the younger name, *T. ovum*, because both conditions of Article 23.9.1 of the ICZN (1999) are met: (i) *T. cicer* Schrank, 1803 has been not used after 1899 and (ii) the junior synonym, *T. ovum* (Ehrenberg, 1831) Ehrenberg, 1833, has been used in at least 25 works, published by at least ten authors in the immediately preceding fifty years, encompassing a span of not less than ten years (see list of synonyms). Thus, *T. cicer* becomes a nomen oblitum and *T. ovum* a nomen protectum.

According to Schewiakoff (1896), *Trachelius ovum* has seven synonyms (for details, see synonymy list above): *Amphileptus rotundus*, *Amphileptus ovum*, *Harmodirus ovum*, *Ophryocerca ovum*, *Trachelius cicer, Trachelius leidyi*, and *Trachelius vorax* (= *Amphileptus vorax*). This was accepted by Kahl (1931) and Foissner et al. (1995). We add the binucleate *Trachelius subtilis* Penard, 1922 because there is strong indication that Penard (1922) misinterpreted the nuclear pattern, as the macronucleus of *T. ovum* is often strongly mid-constricted, thus appearing as two abutting nodules in vivo.

There is only one other ciliate similar to *T. ovum*, viz., *Apotrachelius multinucleatus* described below, which differs by the many macronuclear nodules (vs. one nodule), the absence (vs. presence) of oral extrusomes, and the saltwater (vs. freshwater) habitat.

Improved diagnosis (neotype population): Size about 350 × 175 µm in vivo. Shape broadly dileptid with broadly rounded posterior end, proboscis oral bulge about 1/3 of body length. Macronucleus dumbbell-shaped, several globular micronuclei. Many scattered contractile vacuoles with 1 pore each. Extrusomes attached to proboscis oral bulge, almost rod-shaped, about 4 µm long. On average 100 ciliary rows, 3 anteriorly differentiated into a distinctly heterostichad dorsal brush, monokinetidal tail of row 3 extends to

third fourth of body. Oral bulge opening about 20 µm across. Preoral kineties oblique, ordinarily spaced, each usually composed of 3 narrowly spaced cilia. Freshwater.

Type locality: Ehrenberg (1831) discovered *Trachelius ovum* in a pond from the Zoological Garden of Berlin, Germany, E13°19' N52°30'. The neotype is from the Eger stream, Fichtelgebirge, Bavaria, Germany, E14°8' N50°32' (Foissner 1997a). According to Article 76.3 of the ICZN (1999), the place of origin of the neotype becomes the type locality of the nominal species-group taxon, despite any previously published statement of the type locality.

Type material: Foissner (1997a) deposited four neotype slides (inv. nos 1998/69–72) with protargol-impregnated German specimens in the Biology Centre of the Museum of Upper Austria, Linz (LI). Relevant specimens are marked by black ink circles on the coverslip.

Gene sequence: The 18S rRNA gene sequence of a Salzburg population has been deposited in GenBank (HM581673). The sequence is 1636 nucleotides long and has a GC content of 42.3%. It is a consensus sequence based on 21 clones.

Etymology: Not given in original description. The specific epithet *ovum* (egg) obviously refers to body shape.

Description: All known and some new data are put together because the morphological conspecificity is beyond reasonable doubt for most populations mentioned in the list of synonyms. The review emphasizes the old, detailed studies of Fabre-Domergue (1891) and Hamburger (1903) as well as the recent studies of Song & Wilbert (1989) and Foissner (1997a); the last study is considered an authoritative redescription because detailed data and neotype slides were provided.

Size in vivo similar in most populations, usually about 250–400 × 75–350 µm. Length 360 µm (Ehrenberg 1831); 390 µm (Dujardin 1841); 145–435 µm (Perty 1852); 450 µm (Kent 1881); 127 µm (Maskell 1887); up to 400 µm (Bütschli 1889, Blochmann 1895); usually 300–370 µm, rarely up to 600 µm (Fabre-Domergue 1891); 300–600 µm (Schewiakoff 1896, Roux 1901); 390 µm (Hamburger & Buddenbrock 1911); 295 µm (Smith 1914); 250–400 µm (Penard 1922); 615 µm (Scheffelt 1922); 200–400 µm (Kahl 1931, Bick 1972); 300–480 µm (Wang & Nie 1933); 190–240 µm (Lepşi 1957b); 340 µm (Chorik 1968); 380 µm (Hollowday 1979); 150–200 µm (Kusano 1985). Kahl (1931) and Biernacka (1959) observed dwarf forms 60–70 µm and 85 µm long, respectively.

Body very flexible but not contractile. Shape broadly to narrowly dileptid, that is, length:width ratio on average 1.9:1 (1.2–3.7:1), according to the figures available in the literature and our own data based on in vivo micrographs, protargol preparations, and SEM micrographs (Table 22). Proboscis inconspicuous, conical with anterior portion usually curved dorsally, only slightly motile; length of proboscis oral bulge highly variable, viz., 20% to 57% of body length, on average about 36% (Table 22). Trunk almost globular, rarely oblong, left side convex, right side sometimes conspicuously flattened, especially in under-nourished cells (Figs 39a–m, 40a–d, g, 41a–c, 42t, x, v, 43a, b1, b2, c1, d, e1, f, h, i, 44a–d, f, i, k, q, r, u, w, 45a–g, n–p). Rather sensitive to coverslip pressure, that is, cells round up and throw off the proboscis, sometimes concomitantly ejecting food vacuoles and cytoplasm to reduce the volume and swim away (Ehrenberg 1838, Hamburger 1903).

On right side, in mid-portion of trunk, a unique organelle called groove or fossa. Fossa elliptical, about 25–35 × 10–15 µm in size after protargol impregnation; contains and is surrounded by condensed somatic ciliature, some ciliary rows end at fossa margin, while others extend to its bottom and proceed posteriorly (Figs 43b3, 44g, i, w, x, 45k). Function of fossa not known. Balbiani (1888) considered it as a mouth, which was refuted by Fabre-Domergue (1891); Hamburger (1903) and Penard (1922) observed that *Trachelius* attaches to the stalk of peritrich prey, using the fossa as a sucker; Kahl (1931) speculated that

the fossa regulates the cell volume and considered the fossa ciliature as thigmotactic.

Nuclear apparatus usually in centre of trunk, may be displaced by large food items. Macronucleus highly variable in shape: dumbbell-like (Figs 40e, 43h, 44f, i, u, 45f–h), cylindroidal-curved (Figs 41a, c, 42c, 43a, b1, b2, e1, f), ellipsoidal (Figs 39g, j, 43w, 44d), or reniform (Figs 44a, b). Smith (1914), Penard (1922), Kahl (1931), Wang & Nie (1933), Nusch (1974), and Song & Wilbert (1989) likely misinterpreted the dumbbell-like macronucleus as two abutting nodules (Figs 40d, 42t, x, 43c1, c2, d, 44e, k, q). Size of macronucleus given only by Foissner (1997a), that is, 75 × 20 µm (Table 22). Nucleoli evenly distributed, small and globular (Figs 40e, 41i, 45h). Micronuclei close or attached to macronucleus, about 3.5 µm across, often difficult to distinguish from similarly sized and stained cytoplasmic inclusions, number thus difficult to determine: one according to Penard (1922), Bick (1972), Hollowday (1979), and Song & Wilbert (1989), while nine according to Bütschli (1889), five to thirteen according to Hamburger (1903), and two to five according to Foissner (1997a).

Contractile vacuole pattern identical in most populations (for exceptions, see "non *T. ovum*" in the synonymy list), i.e., many vacuoles scattered underneath cell surface of trunk and proboscis' proximal half (Figs 39g, i, j, l, m, 40a–d, g–i, 41a, b, 42t, x, 43b1, c1, d, e1, f, h, w, 44a, b, d, f, k, 45a, c, d). Vacuoles connected with an extensive system of branching and anastomosing canals (Figs 40l, o) described in detail by Fabre-Domergue (1891). Invariably one intrakinetal pore per vacuole according to Hamburger (1903; Figs 41n, o), Kahl (1931; Fig. 43e2), Song & Wilbert (1989; Figs 44n, o, s), and Foissner (1997a; Figs 44w, y), while three pores one after the other according to Bütschli (1876), indicating that his population might be a distinct taxon.

Extrusomes in vivo rod-shaped, forming several rows in proboscis oral bulge (Figs 43e3, e4, 44h). Kahl (1931), additionally, figured a ring of extrusomes (cortical granules?) in the oral bulge opening (Fig. 43e3), but did not mention this in the description. After protargol impregnation about 3 µm long and rod-shaped, when exploded of typical toxicyst structure (Fig. 44l). Should be studied in further populations and in more detail.

Cortex flexible, about 2 µm thick, slightly furrowed by ciliary rows in SEM micrographs (Figs 41p, 43c2, e2, 45s). Several rows of rather loosely spaced cortical granules between each two kineties (Fig. 44m); individual granules resemble oral bulge extrusomes in protargol preparations but are shorter; exploded granules form a filamentous cover, showing their mucocyst nature (Fig. 43g). Mitochondria underneath cortex, globular to ellipsoidal (Fig. 41p). Silverline pattern narrowly meshed, meshes polygonal and about 0.5 µm in size, not yet studied in detail (Figs 43q, 44j, p). Cytoplasm colourless, usually strongly vacuolated; large vacuoles surrounded by cytoplasmic strands forming a rough network; packed with 1–4 µm-sized granules, rod-like bacteria, and two to several large food vacuoles usually containing peritrich ciliates; sometimes an accumulation of small lipid droplets or defecation vacuoles in posterior pole area (Figs 41d–f, h, m, q, s, 42t, u3, v, x, 44r, u, 45a–e). Reliable observations on movement lacking.

Cilia about 8 µm long in vivo, shrunken to 4–5.5 µm in SEM; in protargol preparations as typical for dileptids, i.e., with thick, strongly impregnated distal half; narrowly to ordinarily spaced. Ciliary rows narrowly and equidistantly spaced, meridionally arranged, gradually shortened right and left of oral bulge; number studied only in German populations: 86–109 according to Song & Wilbert (1989) and 90–120 according to Foissner (1997a). Right side ciliary rows abut on perioral kinety at obtuse angles (~ 140°; Figs 44t, w), not almost rectangularly as figured by Dragesco & Dragesco-Kernéis (Fig. 44i). First row right of circumoral kinety extends as perioral kinety with narrowly spaced cilia to tip of proboscis (Figs 44i, o, s, t, v, w, 45m). Left side ciliary rows abut on preoral kineties at almost right to obtuse angles (Fig. 44i, o, s, v). Anterior end of ventral ciliary rows more densely ciliated and slightly curved rightwards abutting on circumoral kinety (Figs 44i, o, s, v, w). Dorsal brush exactly on dorsal side of proboscis, composed of

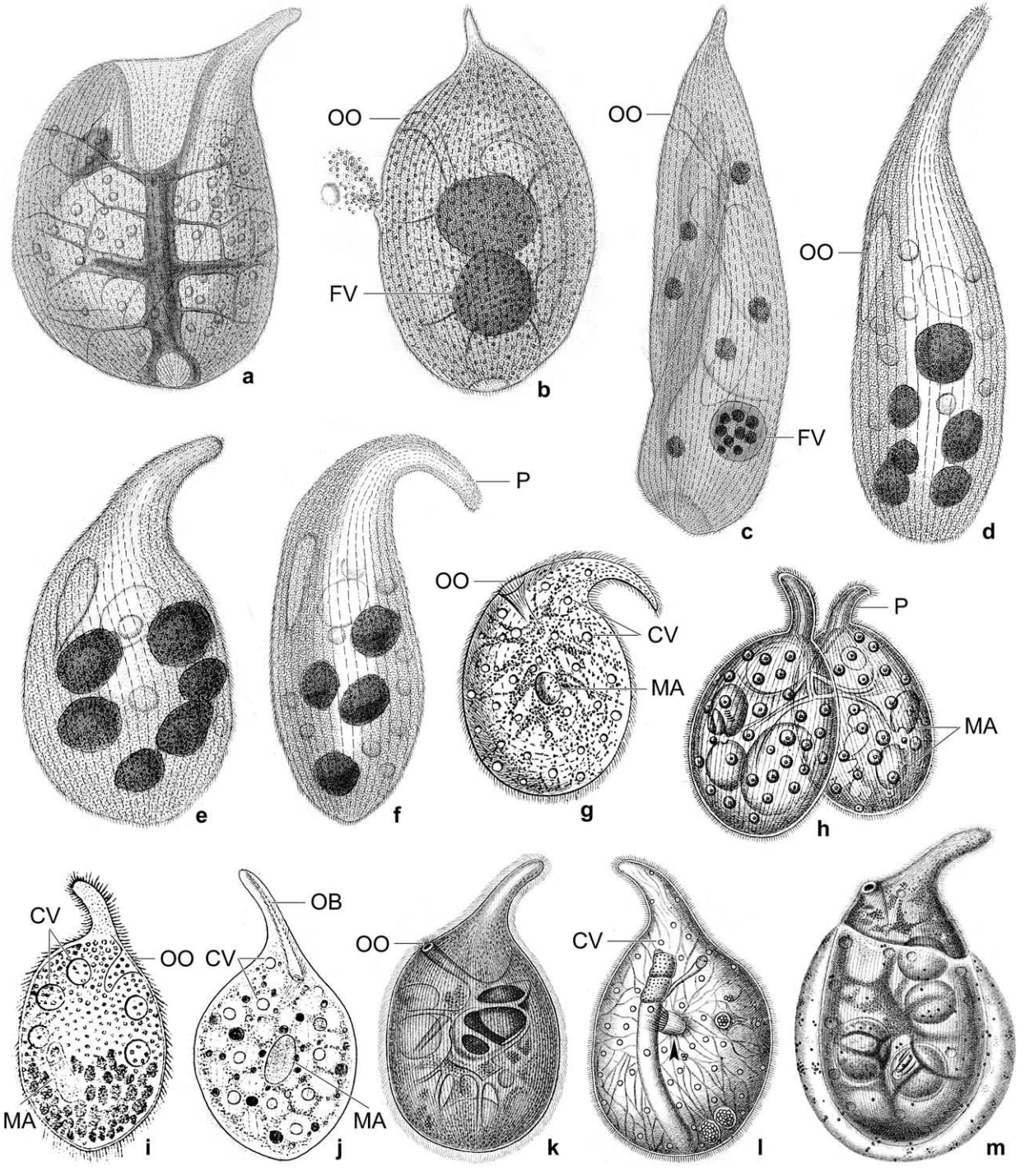
three to four rows commencing apically (row 4, if present, inconspicuous, composed of alternating mono- and dikinetids); distinctly heterostichad because middle row shorter by about 45% than longest row 3 (Fig. 44y), isostichad according to Song & Wilbert (Fig. 44n); heteromorphic especially in posterior third, that is, contains dikinetids with a bristle and an ordinary cilium and/or monokinetids with ordinary cilia; some kineties abut on left side of brush, forming an inconspicuous suture (Fig. 44y, arrowheads); proboscis brush bristles very soft and closely spaced, thus appearing as a single, rather conspicuous structure (Kahl 1931). Brush dikinetids associated with type III bristles gradually shortening from about 3.5 µm anteriorly to 2 µm posteriorly in SEM (Fig. 45r). According to Kahl (1931), all brush rows continue with a bristle tail reaching rear body end (Fig. 43e1), while our SEM data, based on two populations, show that only row 3 has a tail of 1.7 µm long, monokinetidal bristles extending to third fourth of body (Figs 45p, s).

Oral bulge opening usually at end of anterior body third, does not project; dileptid, i.e., circular both in vivo and in preparations, about 10 µm across in SEM (Figs 40n, 41c, 42a, s, 43e3, 44i, o, v, 45i, n, q). Oral bulge and bulge opening indistinct in SEM micrographs because rather flat and more or less covered by the oral ciliature (Figs 45n, q). Pharyngeal basket embedded in viscous cytoplasm in vivo, obliquely directed to cell centre; internal basket clavate and composed of innumerable fibres, conspicuous in vivo and protargol preparations; external basket comparatively inconspicuous, impregnates only in distal portion (Figs 40m, 42a, b, 42u2, 43c4, 44s, u–w, 45j, m). Circumoral kinety composed of narrowly spaced dikinetids throughout, those in proboscis associated with fibres extending posteriorly to form a loose funnel (Figs 44i, o, s, v–w, 45i, j). About 50 oblique to slightly oblique, ordinarily spaced preoral kineties, as estimated from figures, each composed of two to four, usually three narrowly spaced cilia (Figs 44i, o, s, v, 45j).

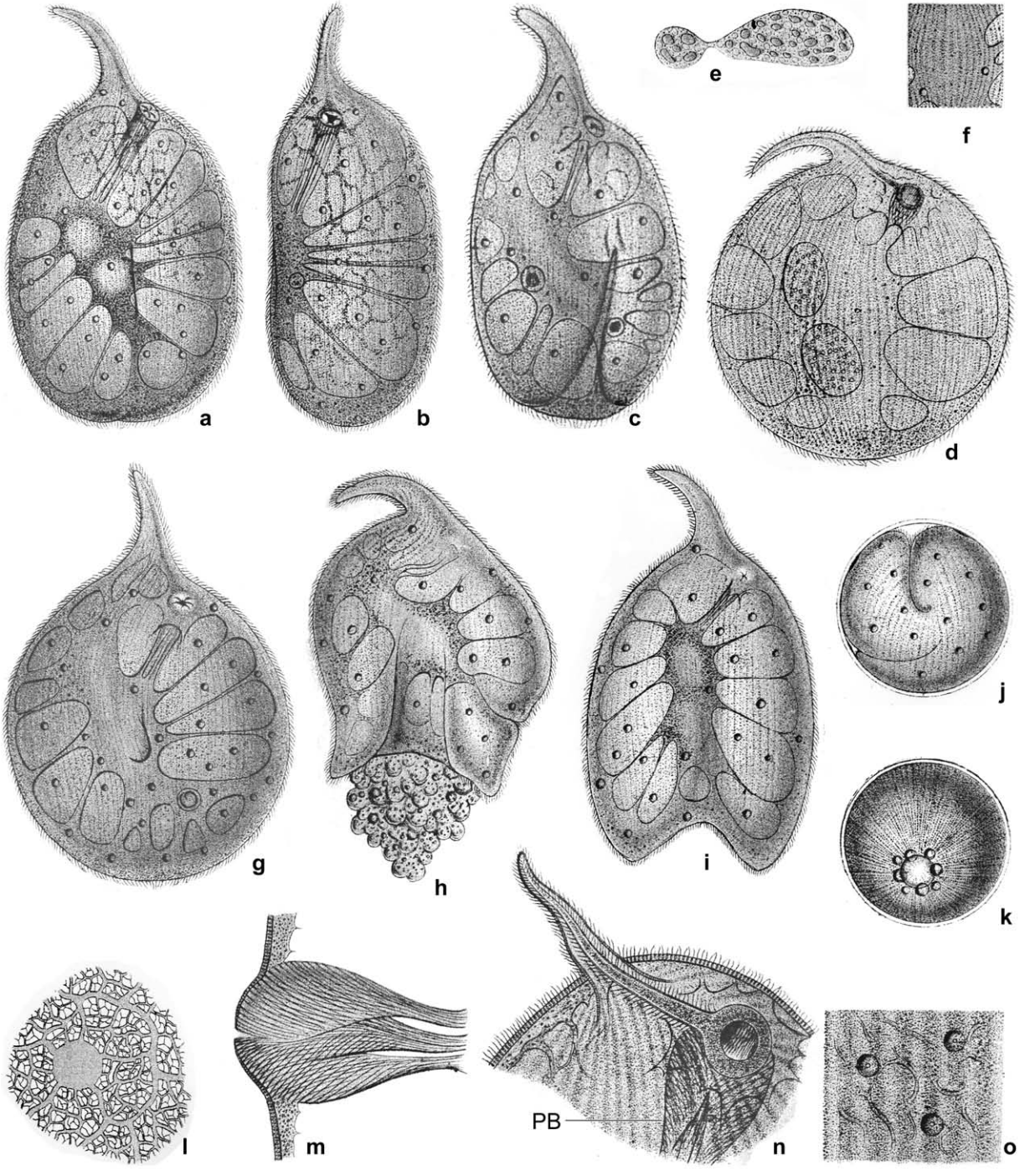
Encystment and resting cyst (Figs 40j, k): Fabre-Domergue (1891) observed encystment and early resting cysts. His data can be summarized as follows: (i) during the initial stages, the proboscis is put on the ventral side of the body; (ii) the body diminishes by about one half and becomes a more or less perfect sphere; (iii) the cytoplasm loses the strongly vacuolated appearance and becomes homogenous; (iv) the contractile vacuoles disappear except for one terminal vacuole surrounded by several small vacuoles; (iv) the resting cysts are about 150 µm across and have a smooth, about 5 µm thick wall.

Notes on division (Figs 41i, 42d, i–m): Body and nuclear division were studied by Hamburger (1903). Basically, the processes are similar to those of other dileptids, but have been not yet studied with modern methods: (i) cell division occurs in active (non-encysted) condition (but see Nusch 1975 below); (ii) the parental oral apparatus remains unchanged; (iii) slightly before separation, the daughter cells are connected with the posterior end of the proter and the developing oral bulge opening of the opisthe; (iv) the proboscis appears in mid-dividers as a small convexity in the opisthe's dorsal area and matures post-divisionally; and (v) the macronucleus is homomeric and becomes rod-like in mid-dividers. Two peculiarities occur: (i) the division furrow sections the fossa into two equal parts (Figs 42i, j) and (ii) slightly before separation, the opisthe rotates about the dorsoventral axis, causing the proter's and opisthe's main body axis to form a right angle (Fig. 42l).

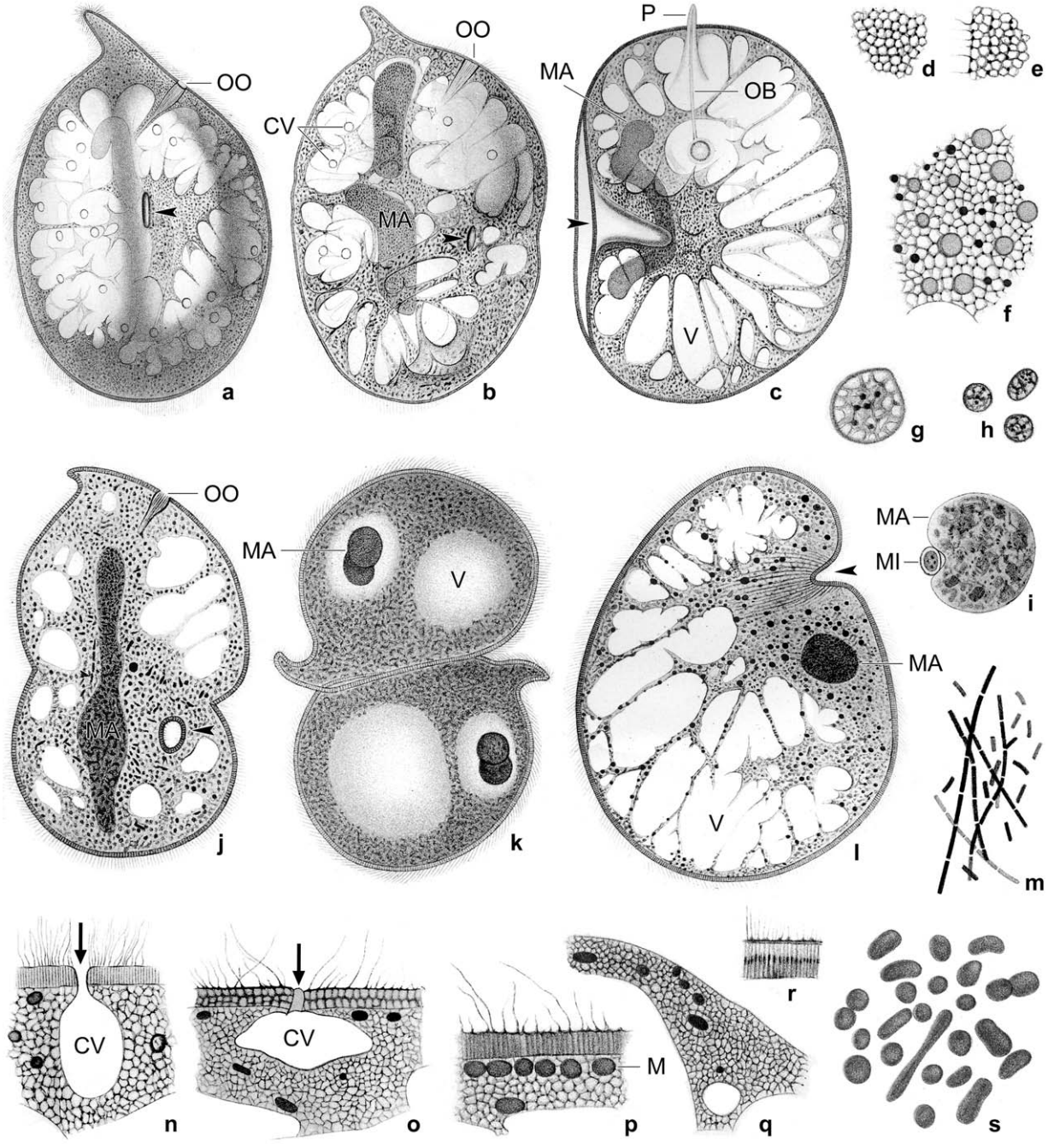
Notes on conjugation (Figs 39h, 41k): Conjugation occurs very rarely in *Trachelius ovum*, as only two records are available, showing, however, different conjugation modes: homopolar according to Bütschli (1889), while heteropolar according to Hamburger (1903). The latter mode is more likely because it has been observed also in other dileptids. Hamburger (1903) provided the following data: (i) partners unite bulge-to-bulge; (ii) in each partner, there is a small vacuole enclosing two globular macronuclear nodules and a large empty vacuole; (iii) oral bulge opening, oral basket and lateral fossa not recognizable during conjugation (Fig. 41k).



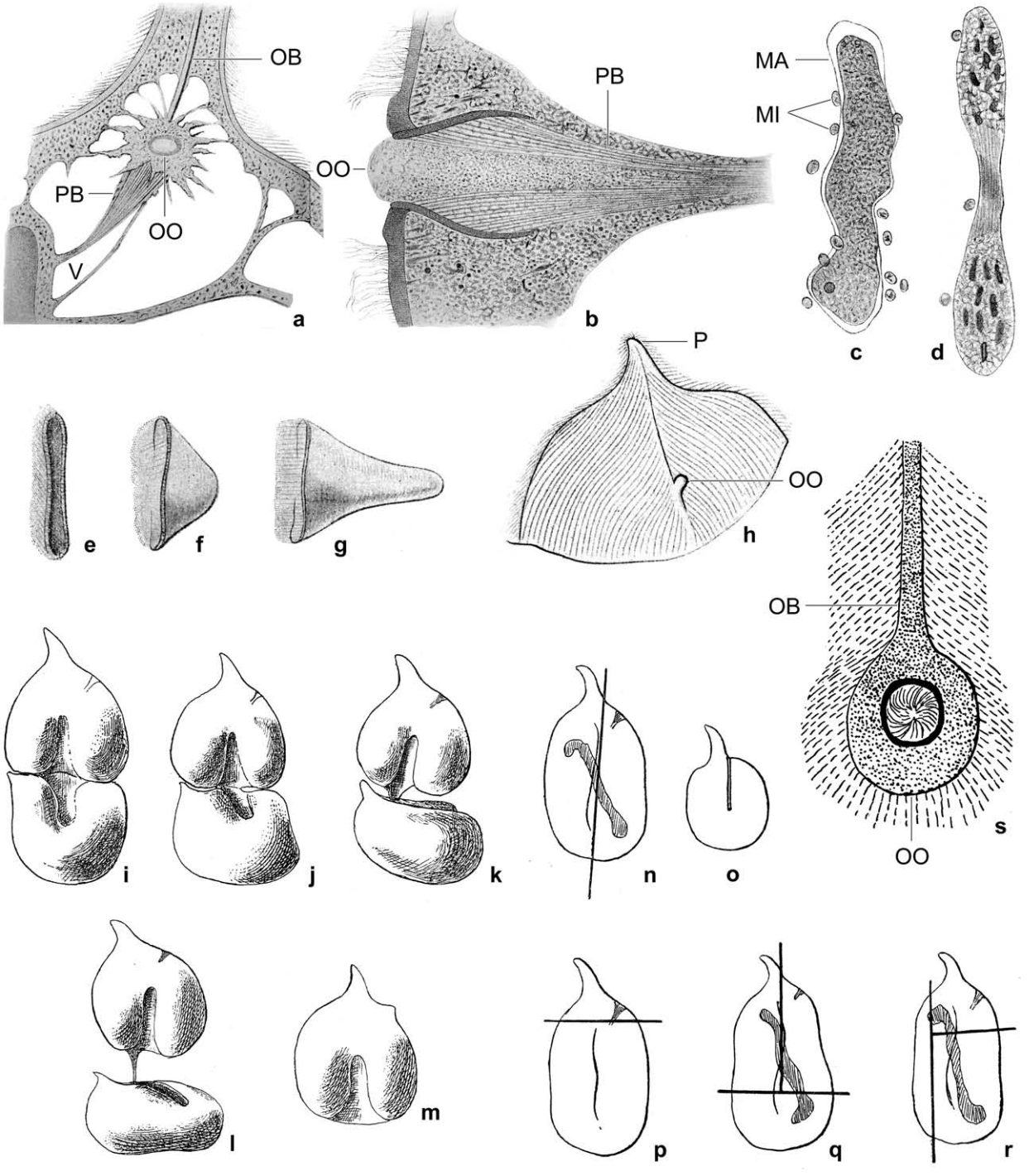
Figs 39a–m: *Trachelius ovum* and its supposed synonyms from life. **a–c** – specimens from type population, length about 360 µm (from EHRENBERG 1838); **d–f** – *Trachelius vorax*, length about 220 µm (from EHRENBERG 1838); **g** – English specimen, length 450 µm (from KENT 1881); **h, l, m** – conjugating specimens, a vegetative cell, and an excysting specimen, length not given (from BÜTSCHLI 1889); **i** – *Amphileptus rotundus*, length 127 µm (from MASKELL 1887); **j** –Swiss specimen, length 320 µm (from ROUX 1901); **k** – German specimen, length 400 µm (from BLOCHMANN 1895). CV – contractile vacuoles, FV – food vacuoles, MA – macronucleus, OB – oral bulge, OO – oral bulge opening, P – proboscis.



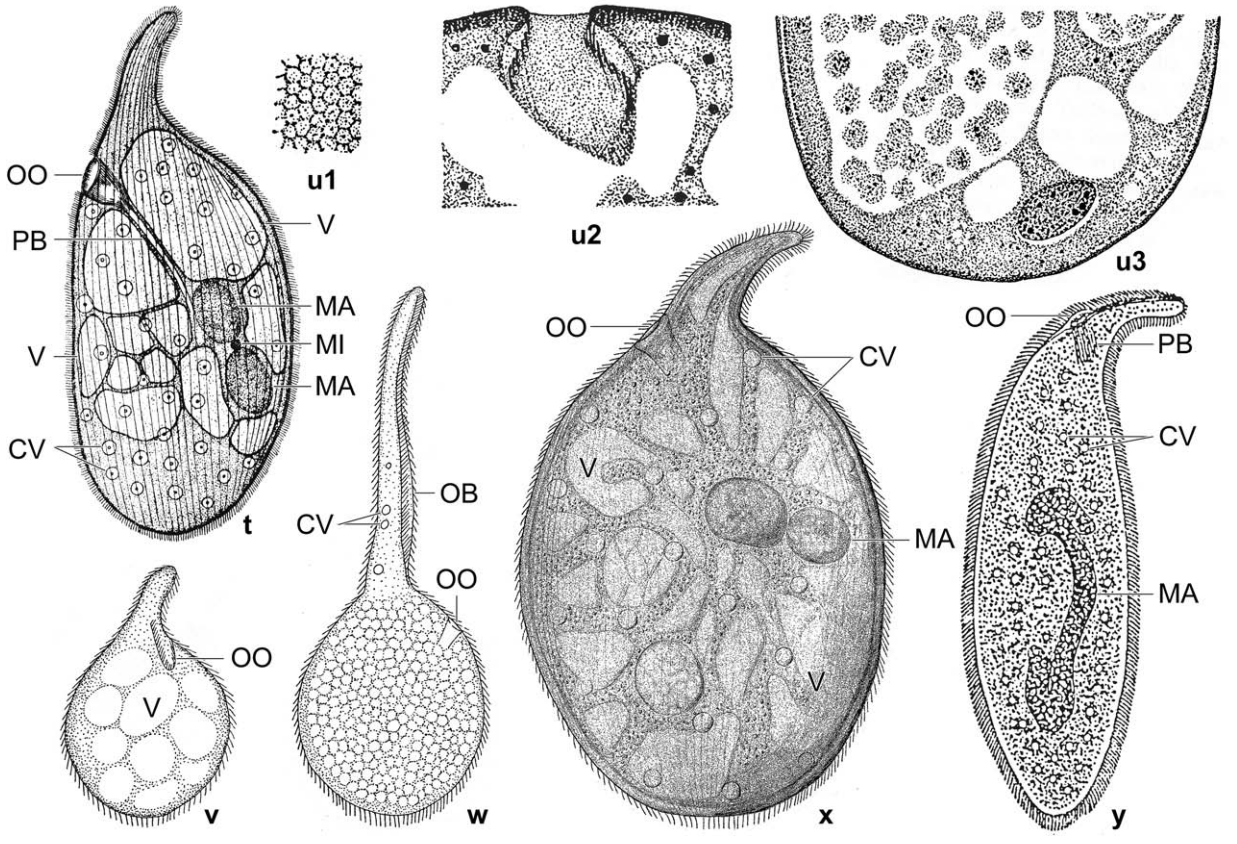
Figs 40a–o: *Trachelius ovum* from life (from FABRE-DOMERGUE 1891). **a–d, g** – ventrolateral and ventral overviews showing, inter alia, the variability of body shape, length 375 µm, 380 µm, 275 µm, 335 µm, and 365 µm; **e** – the macronucleus is dumbbell-shaped and contains many oblong nucleoli; **f** – frontal view of fossa; **h** – a wounded specimen; **i** – right side view of an early proter post-divider, length 360 µm; **j, k** – encystment and early resting cyst, diameter 150 µm; **l** – a contractile vacuole with collecting canals; **m** – lateral view of oral basket; **n** – detail of oral apparatus, showing the massive pharyngeal basket, the short proboscis, and the *Dileptus*-like oral bulge opening; **o** – surface view showing three contractile vacuoles and their connections. PB – pharyngeal basket.



Figs 41a–s: *Trachelius ovum* fixed with osmium vapours and after various stains (from HAMBURGER 1903). Sizes not provided. **a, c** – right side and ventral view showing general body organization, i.e., the broadly dileptid body with a short proboscis, the fossa (arrowheads), and the vacuolated cytoplasm; **b, j** – right side views of an early and a mid-divider. The fossa is situated underneath mid-body (arrowheads); **d, e** – surface view showing the alveolar pattern; **f, h, s** – endoplasmic granules (likely mitochondria) after eosin (f, h) and Dahlia (s) stain; **g** – fine structure of micronucleus; **i** – a histological section through the macronucleus and one of many micronuclei; **k** – conjugating specimens; **l** – a histological section through an opisthe at fossa level (arrowhead); **m** – rod-shaped bacteria are scattered throughout the cytoplasm; **n, o** – histological sections of contractile vacuoles with opened and closed excretory pore (arrows); **p, r** – histological sections of cortex and underlying mitochondria; **q** – endoplasmic strand with several granules. CV – contractile vacuoles, M – mitochondria, MA – macronucleus, MI – micronucleus, OB – oral bulge, OO – oral bulge opening, P – proboscis, V – vacuoles.



Figs 42a–s: *Trachelius ovum* from life (i–r) and after various stains (a–h, s). From HAMBURGER (1903). Sizes not provided. **a** – ventral view of oral region, showing the roundish oral bulge opening and the clavate oral basket; **b** – lateral view of oral basket; **c** – the nuclear apparatus consists of an oblong macronucleus and many adjacent micronuclei; **d** – nuclear apparatus of a divider; **e–g** – frontal, ventrolateral, and lateral view of fossa; **h, s** – ciliary pattern in oral region; **i–m** – late division stages (i–l) and a proter post-divider (m); **n–r** – regeneration experiments (for explanation, see text). MA – macronucleus, MI – micronuclei, OB – oral bulge, OO – oral bulge opening, P – proboscis, PB – pharyngeal basket, V – vacuole.



Figs 42t–y: *Trachelius ovum* (u, v, x, y) and its supposed synonyms (t, w) from life (t, v–x) and in acid fuchsin (u1–u3) and opal blue (y) stains. From Smith 1914 (x), Wetzel 1925 (u1–u3), Wang & Nie 1933 (t), Vörösváry 1950 (y), and Lundin & West 1963 (v, w). **t** – *Trachelius subtilis*, length 190 µm; **u1–3** – *Trachelius ovum*, surface view showing the alveolar pattern (u1) and histological sections through the oral basket (u2) and body (u3); **v** – *Trachelius ovum*, Michigan specimen, length not given; **w** – *Trachelius* sp., length not given; **x** – *Trachelius ovum*, Kansas specimen, length 295 µm; **y** – *Trachelius ovum*, Hungarian specimen, length 315 µm. CV – contractile vacuoles, MA – macronucleus, MI – micronucleus, OB – oral bulge, OO – oral bulge opening, PB – pharyngeal basket, V – vacuoles.

Notes on regeneration (Figs 42n–r): Hamburger (1903) made four experiments on regeneration of *T. ovum*. (i) After longitudinal section (Fig. 42n), the ventral part of the cell remained straight and rotated slowly about the main axis, while the dorsal part of the cell rotated very quickly about the section centre enclosing the wound (Fig. 42o); both parts of the cell regenerated in about twelve hours. (ii) After transverse section (Fig. 42p), the anterior part of the cell, very likely without macronucleus, died in one day, while the posterior part containing the macronucleus regenerated in about five hours. (iii) When the cell was sectioned into three parts each having at least a small portion of the macronucleus (Fig. 42q), all pieces survived and regenerated. (iv) When cells were sectioned as shown in Fig. 42r, the pieces containing part of the macronucleus regenerated, while those without macronucleus died in a few hours.

Occurrence and ecology (mainly from Foissner et al. 1995): *Trachelius ovum* occurs worldwide in the periphyton, benthos, and plankton of mesosaprobic running and stagnant waters with peak abundances during the cold half of the year (Zimmer 1898, Kalmus 1928, Nusch 1970, Bick & Kunze 1971, Heuss 1976, Albrecht 1984; Fig. 45v). The upper temperature limit is 25 °C according to Bick & Bertram (1973) and 28 °C according to Bernerth (1982; Fig. 45t). *Trachelius ovum* usually feeds on colonial peritrichs, especially *Carchesium polypinum* (Nusch 1970, Bernerth 1982). Nusch (1975) observed one *Trachelius*

Table 22: Morphometric data on *Trachelius ovum* (TO; from FOISSNER 1997a) and *Apotrachelius multinucleatus* nov. sp. (AM). Data based on mounted, protargol-impregnated (*T. ovum* with Foissner's technique, *A. multinucleatus* with Wilbert's method), and randomly selected environmental specimens. Measurements in µm. CV – coefficient of variation in %, M – median, Max – maximum, Mean – arithmetic mean, Min – minimum, n – number of specimens investigated, SD – standard deviation, SE – standard error of mean.

Characteristics	Species	Mean	M	SD	SE	CV	Min	Max	n
Body, length	TO	188.3	200.0	34.9	10.1	18.5	115.0	230.0	12
	AM	398.0	404.0	45.9	12.7	11.5	304.0	480.0	13
Body, width	TO	112.7	112.5	13.3	3.8	11.8	85.0	130.0	12
	AM	261.7	248.0	47.5	13.2	18.1	208.0	348.0	13
Body length:width, ratio	TO[a]	1.7	1.7	0.2	0.1	14.6	1.1	2.0	12
	AM	1.5	1.6	0.2	0.1	13.5	1.2	1.8	13
Anterior body end to oral bulge opening, distance	TO	73.5	79.0	17.5	5.1	23.8	40.0	100.0	12
	AM	104.0	110.0	20.9	5.8	20.1	59.0	140.0	13
Proboscis, % of body length	TO[a]	39.3	39.5	8.1	2.3	20.5	25.8	57.4	12
	AM	26.1	25.8	4.5	1.2	17.2	19.4	32.8	13
Oral bulge opening, length	AM	34.7	35.0	4.0	1.2	11.6	27.0	39.0	12
Oral bulge opening, width	AM	33.4	35.0	6.0	2.1	18.1	21.0	39.0	8
Internal oral basket, length	AM	51.2	51.0	6.7	2.2	13.1	43.0	62.0	9
Anterior body end to first macronuclear nodule, distance	AM	85.1	90.0	34.4	9.5	40.5	33.0	156.0	13
Macronucleus (nuclear figure), length	TO[a]	76.5	75.0	12.4	3.6	16.2	50.0	95.0	12
Macronuclear nodule, length	AM	25.1	18.0	20.5	5.7	81.9	5.0	62.0	13
Macronucleus, width	TO[a]	20.9	20.0	2.6	0.7	12.3	18.0	25.0	12
Macronuclear nodule, width	AM	6.4	6.0	1.8	0.5	27.5	4.0	10.0	13
Macronuclear nodules, number	TO[a]	1.0	1.0	0.0	0.0	0.0	1.0	1.0	12
	AM	108.2	102.0	27.9	7.7	25.8	75.0	182.0	13
Micronuclei, largest diameter	TO	3.4	3.0	–	–	–	3.0	4.0	12
	AM	2.8	3.0	–	–	–	2.5	3.0	11
Micronuclei, number	TO	4.0	4.5	1.2	0.4	31.2	2.0	5.0	10
	AM	5.5	6.0	1.0	0.5	18.2	4.0	6.0	4
Ciliary rows in mid-body, number	TO	101.7	100.0	11.7	4.8	11.5	90.0	120.0	6
	AM	209.1	185.0	43.8	13.2	21.0	160.0	295.0	11
Cilia in mid-body in 10 µm, number	AM	4.2	4.0	0.6	0.2	14.2	3.0	5.0	13
Dorsal brush rows, number	TO	3.2	3.0	–	–	–	3.0	4.0	12
	AM	4.0	4.0	0.0	0.0	0.0	4.0	4.0	3
Anterior body end to last dikinetid of brush row 3, distance	TO[a]	54.2	50.0	8.5	2.4	15.7	45.0	70.0	12

[a] Calculated from original data.

ovum engulfing ten *Carchesium*-zooids one after the other, prior to rounding off and forming a digestive or division cyst. Further peritrichs serving as food: *Astylozoon fallax*, *Epistylis hentscheli*, and *Vorticella campanula* (Hammann 1952, Stössel 1979, Riedel-Lorjé 1981, Reck 1987, Schneider 1988, Canter et al. 1992). Small algae, flagellates, various ciliates, and large (up to 500 µm) rotifers, such as *Asplanchna priodonta*, were also ingested (Kaltenbach 1962; Bick 1972a, 1972b; Czapik 1975; Hollowday 1979). Schönborn (1982) observed that the *Trachelius ovum*-population of a middle-sized river consumed 246 000 mg/m^2 of nutrients per year, i.e., had a daily uptake of 240 flagellates and *Vorticella* cells with a total volume of 16 × 10^6 µm^3. P:N-ratio of excretion products about 1:5 (Bownik-Dylinska 1981). Albrecht (1984) classified *Trachelius ovum* as an oligo- to meso-stenohaline species on basis of literature data and his investigations of oversalted (up to 0.4%) rivers in Germany. This is supported by recent records from the Baltic Sea (Telesh et al. 2008). Schönborn (1982) calculated the following production data for a population from the alpha-mesosaprobic Saale River in Germany: generation time 120–336 h, average abundance 2 ind./cm^2, productivity 142 ind./cm^2/a, P/B = 71. Biomass of 10^6 specimens: 1572 mg (Nesterenko & Kovalchuk 1991), 851 mg (Schönborn 1982), about 3000 mg when an average size of 300 × 200 µm is assumed (Foissner et al. 1995). Prefered average O_2-concentrations of 6–8 mg/l (Fig. 45u) and a pH range of 5.3–8.4 (Niederlehner & Cairns 1990). Stössel (1979) found *T. ovum* in Swiss rivers at 4–24 °C and preferentially at 2.6–3.6 mg/l DOC (total range 0.4–7.2 mg/l); Bernerth (1982) found a range of 6–18.4 mg/l DOC. Further abiotic parameters, see Table 23.

Records from running waters: in mud of a cave brook in Germany (Griepenburg 1933, see also Gittleson & Hoover 1969); in summer plankton of the Rhine River, Germany (Noll 1972); in plankton of the Elbe River, in mud from the sewage-water area in the surroundings of the town of Hamburg, and in the periphyton and benthos of the mesosaprobic Hamburg harbour, and in the Isebekkanal in Hamburg, Germany (Roy 1938; Caspers & Schulz 1960, 1964; Tent 1981; Bartsch & Hartwig 1984; Krieg 2000); numerous in the stygorhitral (10 cm) of the Fulda River, Germany (Lüpkes 1976); in the periphyton of an oligo- to beta-mesosaprobic brook close to the town of Bonn, Germany (Jutrczenki 1982); in the periphyton of alpha-mesosaprobic and alphameso- to polysaprobic running waters in Germany and the former Yugoslavia (Primc 1981, 1984; Bauer 1987); sometimes numerous in beta- to alpha-mesosaprobic brooks and rivers in Upper Austria and Bavaria, Germany (AOÖLR 1992, 1993a, 1994; Foissner & Moog 1992; Foissner et al. 1992a, b, 1995); in the periphyton and sediment of a clean foothill stream in Germany (Packroff & Zwick 1996); beta-mesosaprobic rivers in the former Czechoslovakia (Šrámek-Hušek 1956a, 1957; Szentiványi & Tirjaková 1994; Tirjaková 1998, 2003; Baláži & Matis 2002); in summer up to 60 ind./l in the free water and in the periphyton of the mesosaprobic Danube River in Hungary (Bereczky 1975, 1977a; Bereczky et al. 1983); Danube River (Enăceanu & Brezeanu 1970); in several freshwaters of Bulgaria (Detcheva 1992); in alphameso- to polysaprobic parts of Polish rivers (Czapik 1982; Hul 1986, 1987); in autumn in the River Lielupe, Latvia (Liepa 1973); in the plankton of the Pripyat River, Ukraine (Nebrat 1992); in Ukrainian brooks and rivers (Kravchenko 1969, Kovalchuk 1997a); rare and with low abundance in the shallow water zone of the Volga River during spring (Mamaeva 1979c); occassionally abundant in a polluted river in Delhi, India (Kaur & Mehra 2001); in a soft-water river in east of the USA (Patrick 1961); in July in the benthos of a slightly to moderately polluted (3.5–10.3 mg/l BSB_5) American river (Cairns & Yongue 1973); in the fine-grained sand of an African river (Dragesco 1972b, Dragesco & Dragesco-Kernéis 1986).

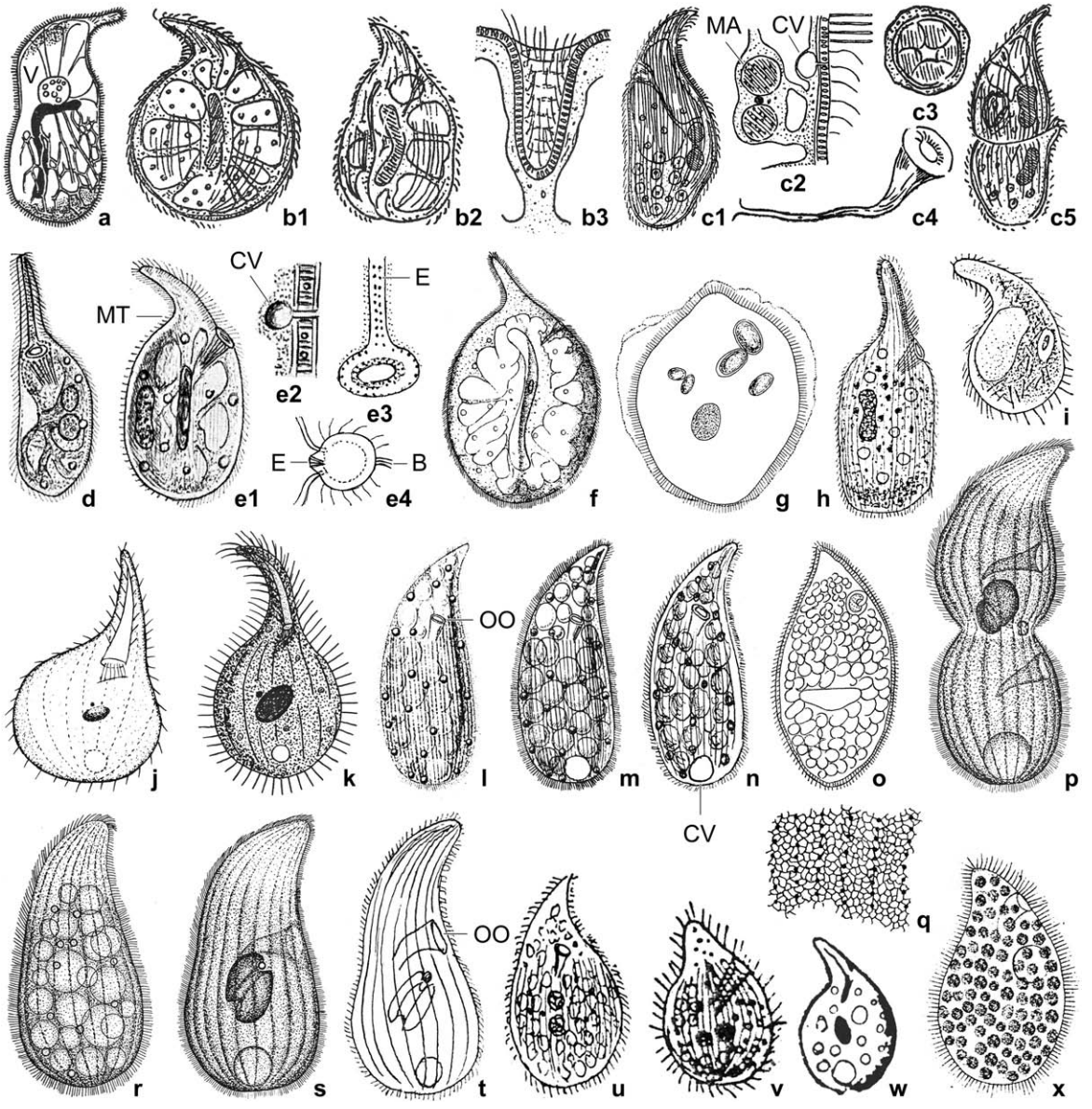
Records from slowly running and stagnant waters: worldwide in the benthos and pelagial of backwaters, lakes, ponds, and city waters (e.g., Dobrovliansky 1914, André 1915, Riggenbach 1922, Baldensperger 1927, Gajewskaja 1933, Liebmann 1938, Vornatscher 1938, Canella 1954, Bovee 1960, Vuxanovici 1960, Buck 1961, Ehlers 1965, Ruggiu 1965, Mücke 1979, Hotano & Watanabe 1981, Alekperov 1984,

Table 23: Autecological data on *Trachelius ovum*. Column 1 from Bick & Kunze (1971; summary of data from literature, supplemented with data sets from Bereczky 1975 [one analysis of the mesosaprobic Danube River in Hungary] and from Heuss 1976 [33 analyses at low individual numbers from lowland brooks of Germany]); column 2 from Bernerth (1982; 36 analyses from the cooling system of a conventional power plant fed by the mesosaprobic lower part of the Main River); column 3 from Mihailowitsch (1989; two to three analyses from a salt-polluted river in Germany); columns 4 and 5 from Reck (1987; many analyses from a eutrophic lake in Germany; column 4 = total range, column 5 = > 600 ind./l); column 6 from Foissner et al. (1995; six analyses from various Austrian rivers with saprobity indices between 2.1–3.1; many specimens occurred at SI = 2.3, otherwise rare).

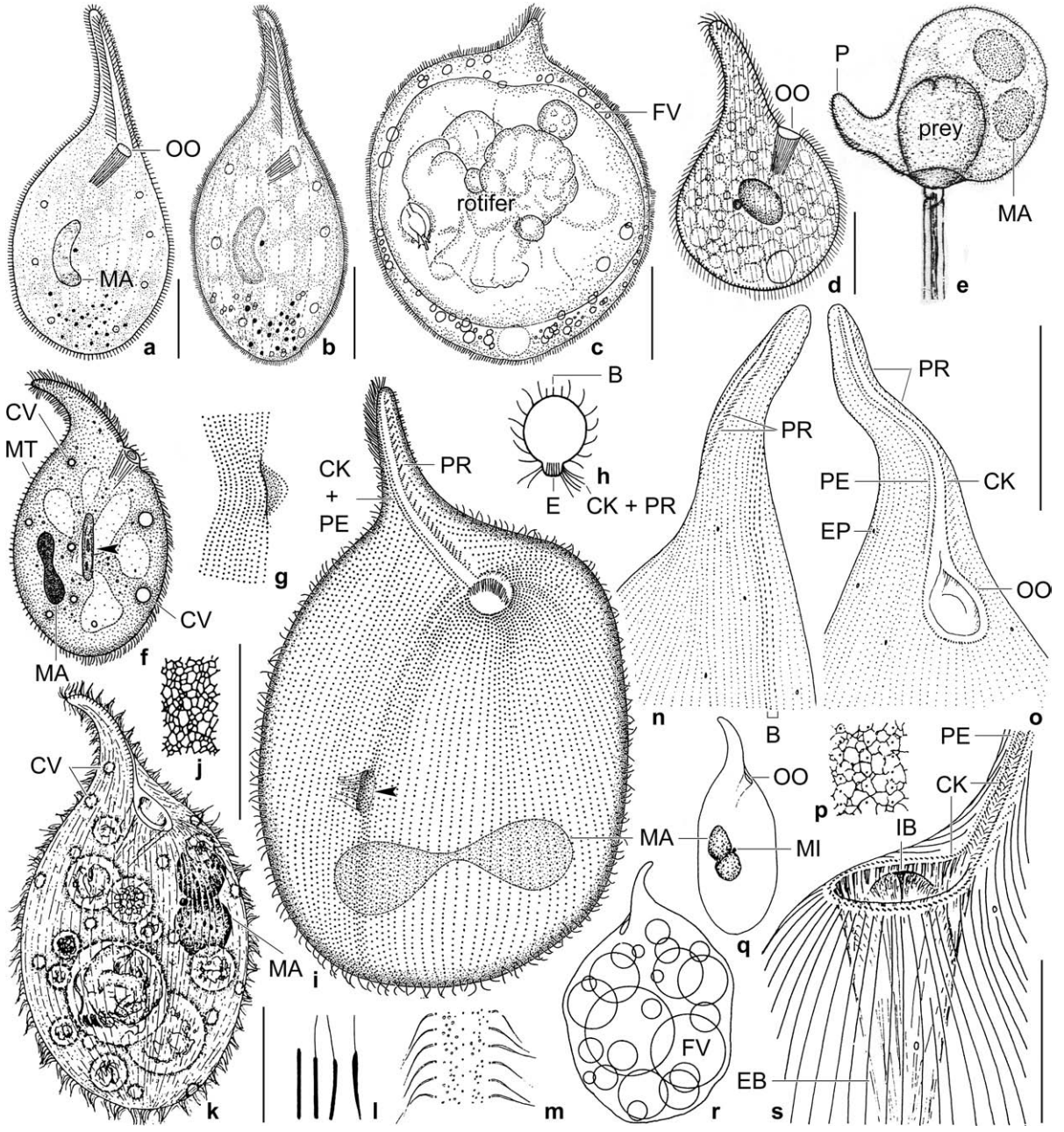
Parameters	References					
	1	2	3	4	5	6
Temperature (°C)	3–23	4.5–28	6–20.5	4.4–22	17	4–12
Conductivity (µS/cm)	459–726	340–820	631–919	–	–	93–467
pH	7.7	6.6–8.0	7.8–7.9	7.3–9.4	9.2–9.4	7.2–8.2
O_2 (mg/l)	3.2–12.9	1.3–11.0	8.0	0.7–15.9	11.7–15.0	6.1–12.9
O_2 (saturation %)	31–112	–	–	6–163	120–154	60–105
BSB_5 (mg/l)	2.4–12.0	–	–	–	–	0.9–>6.1
$KMnO_4$ (mg/l)	15–50	–	–	–	–	6–58
H_2S (mg/l)	0.0–0.9	–	–	–	–	–
CO_2 (free, mg/l)	5.2–15.0	–	13.5–89.0	–	–	–
NH_4^+-N (mg/l)	0.42	–	0.00–0.43	0.03–0.16	0.04–0.05	<0.01–0.12
NO_3^--N (mg/l)	0.63	–	2.50–3.00	–	–	0.56–1.40
NO_2^--N (mg/l)	0.05	–	0.04–0.08	–	–	0.00–0.02

Schönborn 1985, Chardez 1987, Packroff & Wilbert 1991); in forest puddles, peatbogs, and calcareous bogs (e.g., Levander 1900, Schmidt 1916, Scheffelt 1922, Schneider 1930, Groot & Graaf 1960, Cairns & Yongue 1966, Grolière 1977); in activated sludge (Biernacka 1959, Banina 1983, Kutikowa 1984) and in a cooling plant in Moldavia (Chorik & Vikol 1973); rare in a rotating biological contactor north of Madrid, Spain (Martín-Cereceda et al. 2001).

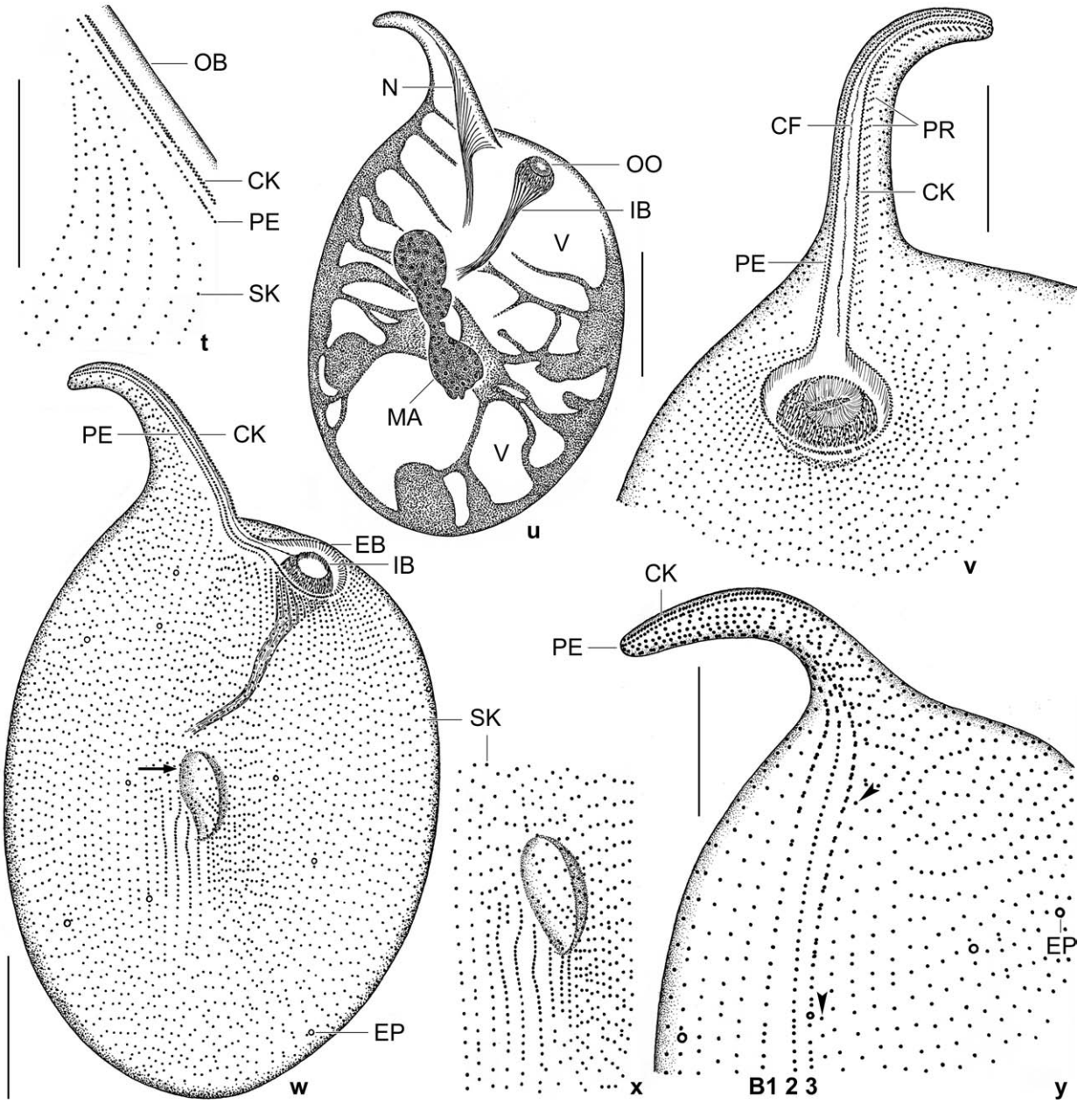
There are many further records. We did not include all of them but selected for biogeographic regions and interesting habitats: in the aerobic sediment of a eutrophic lake (Priest Pot) in England (Webb 1961, Finlay & Maberly 2000); bog pond in France (Grolière & Njiné 1973); Llobregat River in Barcelona, Spain (Gracia et al. 1989); in freshwaters of Italy (Dini et al. 1995); in a large lake (Großer Plöner See) in northern Germany (Zacharias 1894a); in a seeping puddle and in water-irrigated meadow puddles (Dingfelder 1962); rare in the periphyton of the Poppelsdorfer Pond in the town of Bonn, Germany (Wilbert 1969, Song & Wilbert 1989); numerous in the periphyton of oligosaprobic, oligo- to beta-mesosaprobic, and alpha-mesosaprobic backwaters in Germany (Nusch 1970); in summer up to 2220 ind./l in the epi- and metalimnion (0–7 m) of a eutrophic lake (Plußsee) in Germany (Reck 1987); Eifel maar lakes in Germany (Packroff 1992); many sites, including *Sphagnum* ponds, in Switzerland (André 1912, Mermod 1914); in hypertrophic pond at Salzburg University, Austria (Blatterer 1989, Vďačný et al. 2011b); in polluted wells of Prague, Czech Republic (Vejdovský 1882; Šrámek-Hušek 1952); Turiec river basin in the West Carpathians, Slovakia (Tirjaková & Degma 1996); in dystrophic lakes in Poland (Czapik & Fyda 1995); town of Budapest, Hungary (Krepuska 1917); Kalános stream in Hungary (Vörösváry 1950; likely a misidentification because of macronucleus and location of oral basket as shown in Fig. 42y); in the periphyton of lakes and reservoirs in Azerbaijan (Alekperov 1988, 1989, 1990; Aliev 1988); in the



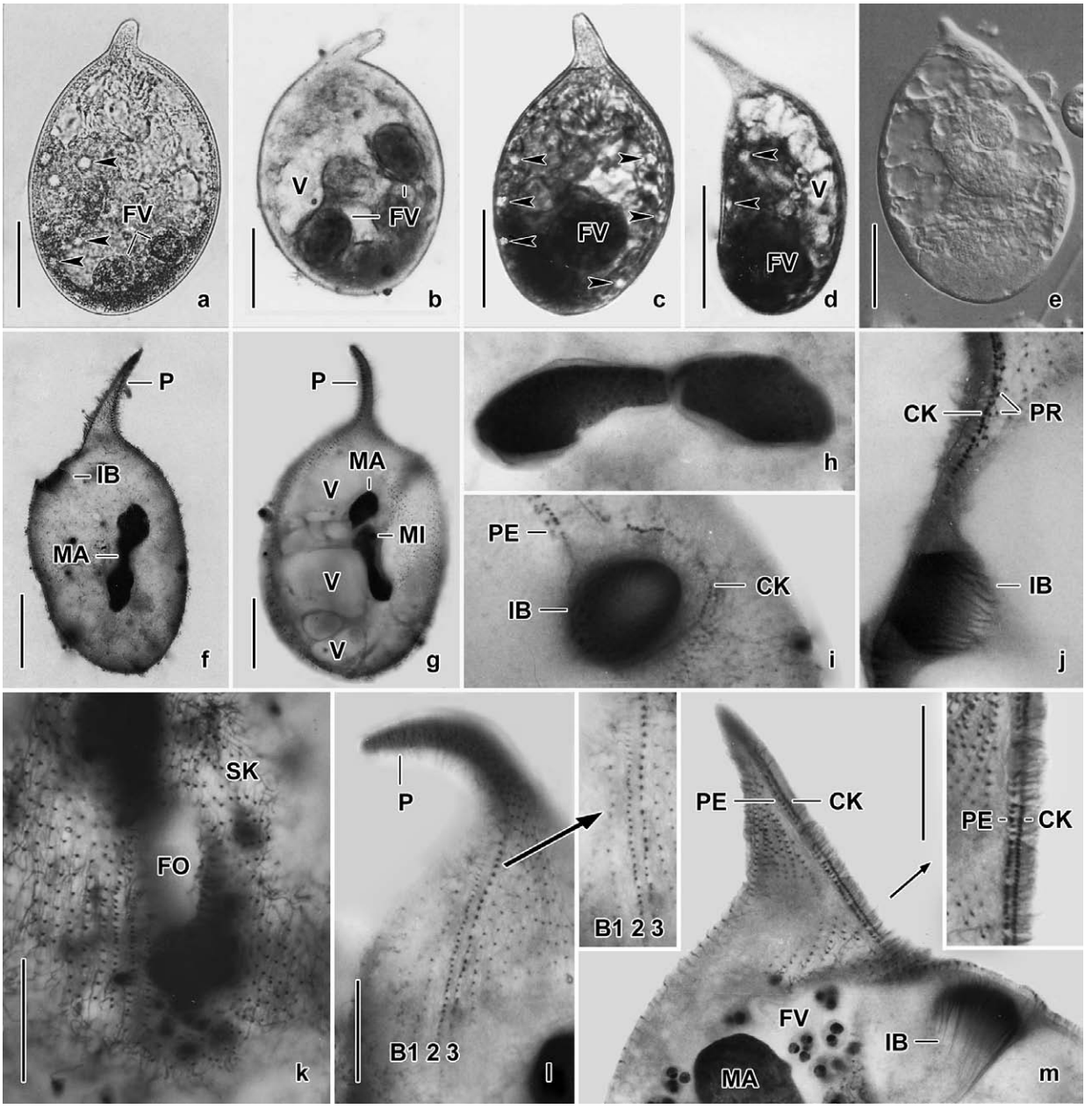
Figs 43a–x: *Trachelius ovum* (a, b, e–k, q, w), *T. subtilis* (c, d), *T. gutta* (l–p, r–v), and *Amphileptus tracheloides* (x) from life (a–f, h–p, r–x), in an opal blue stain (g), and after silver nitrate impregnation (q). Synonymy, see Table 21. **a** (from Scheffelt 1922) – German specimen, length 615 µm; **b1–3** (from Penard 1922) – a broad and a slender specimen (b1, 2), and optical section of fossa (b3); **c1–5** (from Penard 1922) – *Trachelius subtilis*, left side view of a representative specimen, length 250 µm (c1); optical section (c2); frontal view of oral bulge opening (c3); oral basket (c4); and a late divider (c5); **d** (from Kahl 1931) – ventral view of *T. subtilis*, length 280 µm; **e1–4** (from Kahl 1931) – right side view of a representative specimen, length 300 µm (e1); optical section showing cortical granules and a contractile vacuole (e2); frontal view of oral bulge and arrangement of extrusomes (e3); and optical section of proboscis (e4); **f** (from Hamburger & Buddenbrock 1911) – Finnish specimen, length 390 µm; **g** (from Schneider 1930) – squeezed specimen with extruded mucocysts (cortical granules) covering cell, length 180 µm; **h** (from Buck 1961) – German specimen, length not given; **i** (from Lepşi 1957b) – Roumanian specimen, length 190–240 µm; **j, k** (from Aladro-Lubel et al. 1990 and Lopez-Ochoterena 1976) – Mexican specimens, length about 125 µm; **l** (from Cohn 1866) – *Amphileptus gutta*, length 120 µm; **m** (from Hamburger & Buddenbrock 1911) – *Trachelius gutta*, redrawn from Cohn (1866); **n** (from Kahl 1931) – *Amphileptus gutta*, redrawn from Cohn (1866); **o** (from Bhatia 1936) – *Trachelius gutta*, length 214 µm; **p, r, s** (from Kalmus 1929) – *Amphileptus gutta*, lateral view of a late divider and two morphostatic specimens, length not given; **q** (from Klein 1930) – silverline pattern; **t** (from Kahl 1931) – *Amphileptus gutta*, very likely redrawn from Kalmus (1929); **u** (from Kahl 1931) – *Trachelius gutta*, length 100 µm; **v** (from Biernacka 1963) – *Trachelius gutta*, length 60 µm; **w** (from Biernacka 1959) – Polish dwarf specimen, length 85 µm; **x** (from Maskell 1887) – *Amphileptus tracheloides*, length 200 µm. B – dorsal brush, CV – contractile vacuoles, E – extrusomes, MA – macronucleus, MT – monokinetidal tail of dorsal brush.



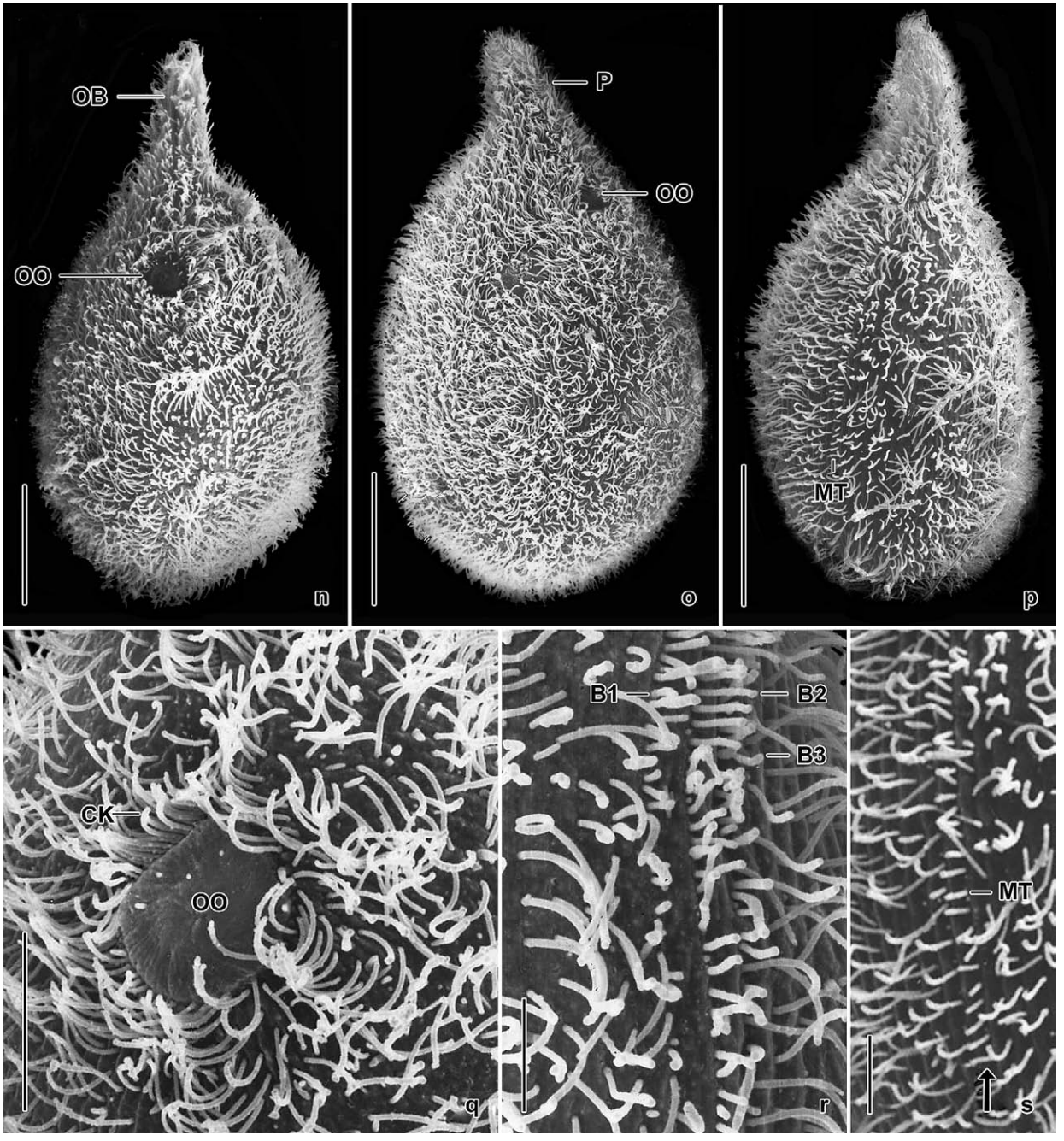
Figs 44a–s: *Trachelius ovum* from life (a–f, h, k, m, q, r) and after protargol (g, i, l, n–p, s) and KLEIN silver nitrate (j) impregnation. From BICK 1972 (a), HOLLOWDAY 1979 (b, c), CHORIK 1968 (d), NUSCH 1974 (e), DRAGESCO & DRAGESCO-KERNÉIS 1986 (f–i), and SONG & WILBERT 1989 (j–s). **a** – semi-schematic view; **b, c** – a slender and a stout specimen digesting a rotifer; **d** – Moldavian specimen; **e** – a specimen engulfing a peritrich ciliate; **f** – a representative specimen, redrawn from KAHL (1931). Arrowhead denotes fossa; **g** – ciliary pattern around and in fossa; **h** – optical section of proboscis; **i** – ventrolateral view of ciliary pattern and nuclear apparatus. Arrowhead denotes fossa; **j, p** – silverline pattern after silver nitrate and protargol impregnation; **k** – a representative German specimen; **l** – extrusomes; **m** – cortical granulation; **n, o** – dorsolateral and ventrolateral view of proboscis' ciliary pattern; **q, r** – a slender and a stout German specimen; **s** – semi-schematic view of oral ciliary pattern. B – dorsal brush, CK – circumoral kinety, CV – contractile vacuoles, E – extrusomes, EB – external oral basket, EP – excretory pore of a contractile vacuole, FV – food vacuoles, IB – internal oral basket, MA – macronucleus, MI – micronucleus, MT – monokinetidal tails of brush rows, OO – oral bulge opening, P – proboscis, PE – perioral kinety, PR – preoral kineties. Scale bars: 50 μm (s) and 100 μm (a–d, i, k, n, o).



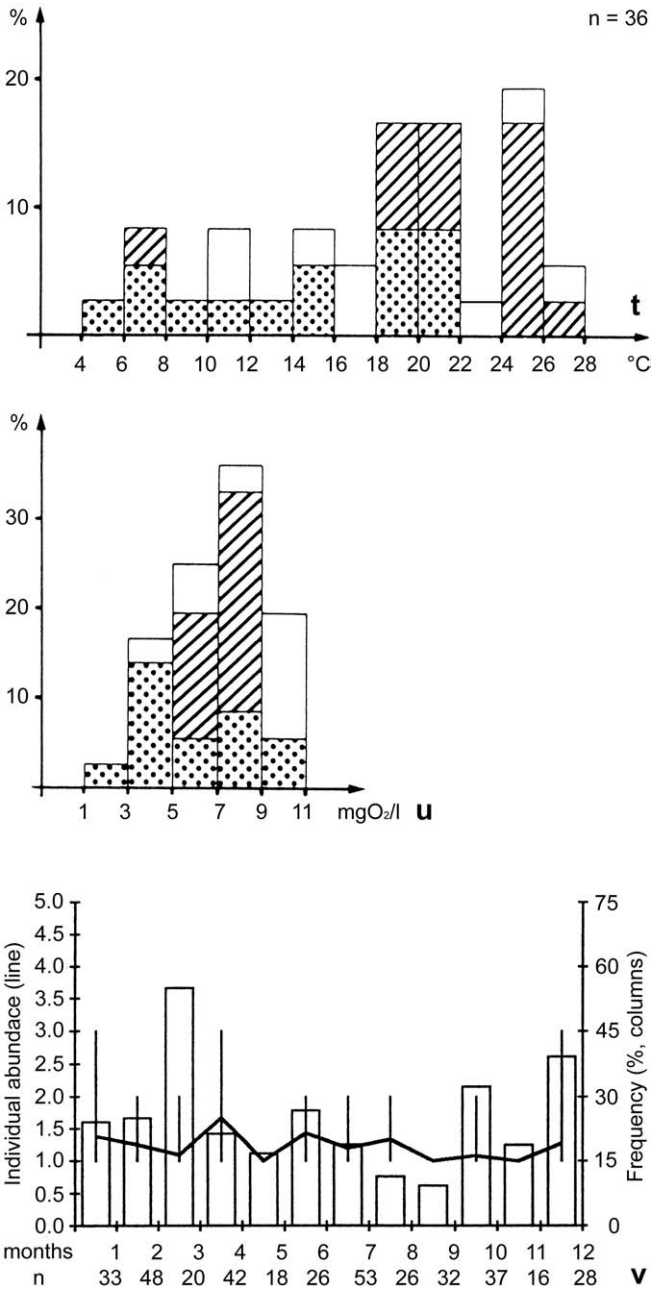
Figs 44t–y: *Trachelius ovum*, German neotype specimens after protargol impregnation (from Foissner et al. 1995 and Foissner 1997a). **t** – ciliary pattern of proboscis' right side; **u** – general body organization, showing the strongly vacuolated cytoplasm, the dumbbell-shaped macronucleus, the clavate internal oral basket, and the nematodesmata originating from the oral dikinetids of the proboscis; **v** – ventral view of proboscis' ciliary pattern; **w** – right side view of ciliary pattern with fossa marked by an arrow. There are many scattered contractile vacuoles with a single pore each. The internal oral basket is obliquely directed to the cell centre, clavate, and composed of innumerable fibres, while the external basket is inconspicuous and impregnated only in the distal portion; **x** – ciliary pattern around and in the fossa of the specimen shown in (w); **y** – dorsal view of proboscis' ciliary pattern. The dorsal brush is three-rowed and distinctly heterostichad because the middle row is shorter by about 45% than the longest row 3. Arrowheads denote somatic kineties abutting on left side of brush. B1–3 – dorsal brush rows, CF – central fibre, CK – circumoral kinety, EB – external oral basket, EP – excretory pore of a contractile vacuole, F – fibres, FV – food vacuoles, IB – internal oral basket, MA – macronucleus, MI – micronucleus, OB – oral bulge, OO – oral bulge opening, PE – perioral kinety, PR – preoral kineties, SK – somatic kineties, V – vacuolated cytoplasm. Scale bars: 20 μm (t, v, y) and 50 μm (u, w).



Figs 45a–m: *Trachelius ovum*, German neotype specimens from life (a–e) and after protargol impregnation (f–m). From FOISSNER et al. (1995) and FOISSNER (1997a). **a–c, e** – slightly squeezed specimens, showing many scattered contractile vacuoles (arrowheads) and some large food vacuoles. The proboscis appears short because its dorsal side is distinctly shorter than the ventral one; **d** – a swimming specimen, showing the distinctly flattened right side, the strongly vacuolated cytoplasm, and some scattered contractile vacuoles (arrowheads); **f, g** – general organization; **h** – the mid of the macronucleus is often so strongly constricted that it appears to be composed of two nodules; **i** – oral infraciliature, showing the circumoral kinety composed of dikinetids throughout and the internal oral basket consisting of innumerable fibres; **j** – proboscis' left side ciliary pattern and oral basket; **k** – fossa and surrounding cilia; **l** – dorsal view of proboscis' ciliary pattern, showing the three-rowed, distinctly heterostichad dorsal brush; **m** – ciliary pattern of proboscis' right side. The right branch of the circumoral kinety is accompanied by a perioral kinety composed of narrowly spaced basal bodies extending to the tip of the proboscis, while the somatic ciliary rows are gradually shortened along the oral bulge. B1–3 – dorsal brush rows, CK – circumoral kinety, FO – fossa, FV – food vacuoles, IB – internal oral basket, MA – macronucleus, P – proboscis, PE – perioral kinety, PR – preoral kineties, SK – somatic kineties, V – vacuoles. Scale bars: 20 μm (l, m), 30 μm (k), 50 μm (f, g), and 100 μm (a–e).



Figs 45n–s: *Trachelius ovum*, German neotype specimens in the scanning electron microscope (from FOISSNER et al. 1995 and FOISSNER 1997a). **n–p, s** – ventral, ventrolateral, and dorsal overview, showing the broadly dileptid body and the comparatively small oral bulge opening (n). The proboscis appears short because its dorsal side (o) is distinctly shorter than the ventral one (n, o). Only brush row 3 has a monokinetidal tail extending to third fourth of body (p, s); **q** – oral ciliature and roundish oral bulge opening. The proboscis bulge is indistinct because it is flat, comparatively narrow, and more or less covered by the oral cilia; **r, s** – the dorsal brush consists of three distinctly heterostichad rows, of which only row 3 continues posteriorly with 1.7 µm long, monokinetidal tail bristles (s, arrow). The brush dikinetids are associated with type III bristles gradually shortening from about 3.5 µm anteriorly to 2 µm posteriorly. B1–3 – dorsal brush rows, CK – circumoral kinety, MT – monokinetidal bristle tail of brush row 3, OB – oral bulge, OO – oral bulge opening, P – proboscis. Scale bars: 5 µm (r, s), 10 µm (q), and 30 µm (n–p).



Figs 45t–v: Ecograms of *Trachelius ovum*. From BERNERTH 1982 (t, u) and FOISSNER et al. 1995 (v). **t, u** – % distribution of records in the temperature and O_2 spectrum in the cooling water system of a conventional, large power plant fed by the beta- to alpha-mesosaprobic Main River in Germany. Designation of sampling sites: dots = inlet of power plant, bands = outlet of power plant, white = other sites in the power plant; **v** – frequency (%) and average estimated individual abundance (bars = minimum, maximum according to the Zelinka and Marvan scale: 1, 2, 3, 5, 7, 9) in the beta- to alpha-mesosaprobic Rivers Amper and Vils in Bavaria during the years 1987–1991. The average abundance (line) was calculated from the estimated abundance per record. n – number of samples per month.

plankton of water reservoirs of the former USSR (NEBRAT 1980); in the periphyton of the Glubokoje Lake, Kossino, Russia (DUPLAKOFF 1933); in the Volga river basin, Russia (ZHUKOV et al. 1998); in summer (15–20 °C) up to 16 ind./l in the plankton of four lakes in the Baikal area, Russia (LOKOT' 1987); Lake Baikal (OBOLKINA 1995); in freshwaters of Thailand (CHARUBHUN & CHARUBHUN 2000); Lake Ho Hu, Nanking, China (WANG & NIE 1933); pond in the surroundings of the town of Qingdao, China (SONG & CHEN 1999); Pond Mizutori-no-numa, Japan (KUSANO 1985); common in Lake Cromwell, Quebec, Canada (PUYTORAC et al. 1972); in freshwater bodies, USA (Edmonson 1906, LACKEY 1938); rare in a small creek of Kansas, USA (SMITH 1914); pond on shore of Lake Erie, Ohio, USA (STEHLE 1923); in a water body of the Upper

Peninsula of Michigan, USA (Lundin & West 1963); sewage plant in Mexico (Aladro-Lubel et al. 2006); freshwater bodies in the Pantanal of Mato Grosso, Brazil (Lopes Hardoim & Heckman 1996); pool in the surroundings of the town of Sydney, Australia (Schewiakoff 1893).

Records from brackish or sea waters are possibly misidentifications (Boutchinsky 1895, Levander 1901, Verschaffelt 1930, Ruggiu 1965, López-Ochoterena et al. 1976, Aladro-Lubel et al. 1990, Santagelo & Lucchesi 1992, Wilbert 1995). Most of them could have been *Apotrachelius multinucleatus*, while the populations of López-Ochoterena et al. (1976) and Aladro-Lubel et al. (1990), which have an ellipsoidal macronucleus and only one contractile vacuole in posterior body end, could be a distinct species.

Saprobic classification: Sládeček et al. (1981), Wegl (1983), and Foissner (1988a) classified *Trachelius ovum* as a beta-mesosaprobic ciliate with the following valencies: o = 1, b = 7, a = 2, I = 3, SI = 2.1. Friedrich (1990): beta- to alpha-mesosaprobic; b = 5, b–a = 10, a = 5, I = 8, SI = 2.5. Buck (1971): most frequent at a saprobity index of 2.54 ± 0.29. Stössel (1979) questioned the indicative value of *T. ovum* because it is strongly associated with peritrich ciliates, the preferred food. Literature research showed, indeed, a very broad range of occurrence with preference of mesosaprobic areas. Therefore, Foissner et al. (1995) allocated the valencies as follows: alpha- to beta-mesosaprobic; o = 1, b = 4, a = 4, p = 1, I = 1, SI = 2.5. Usually indicates an abundance of peritrich ciliates.

Apotrachelius Vďačný, Al-Rasheid & Foissner nov. gen.

Diagnosis: Small- to medium-sized Tracheliidae with broad body. Many scattered macronuclear nodules. Oral bulge extrusomes lacking. Oral bulge opening paradileptid.

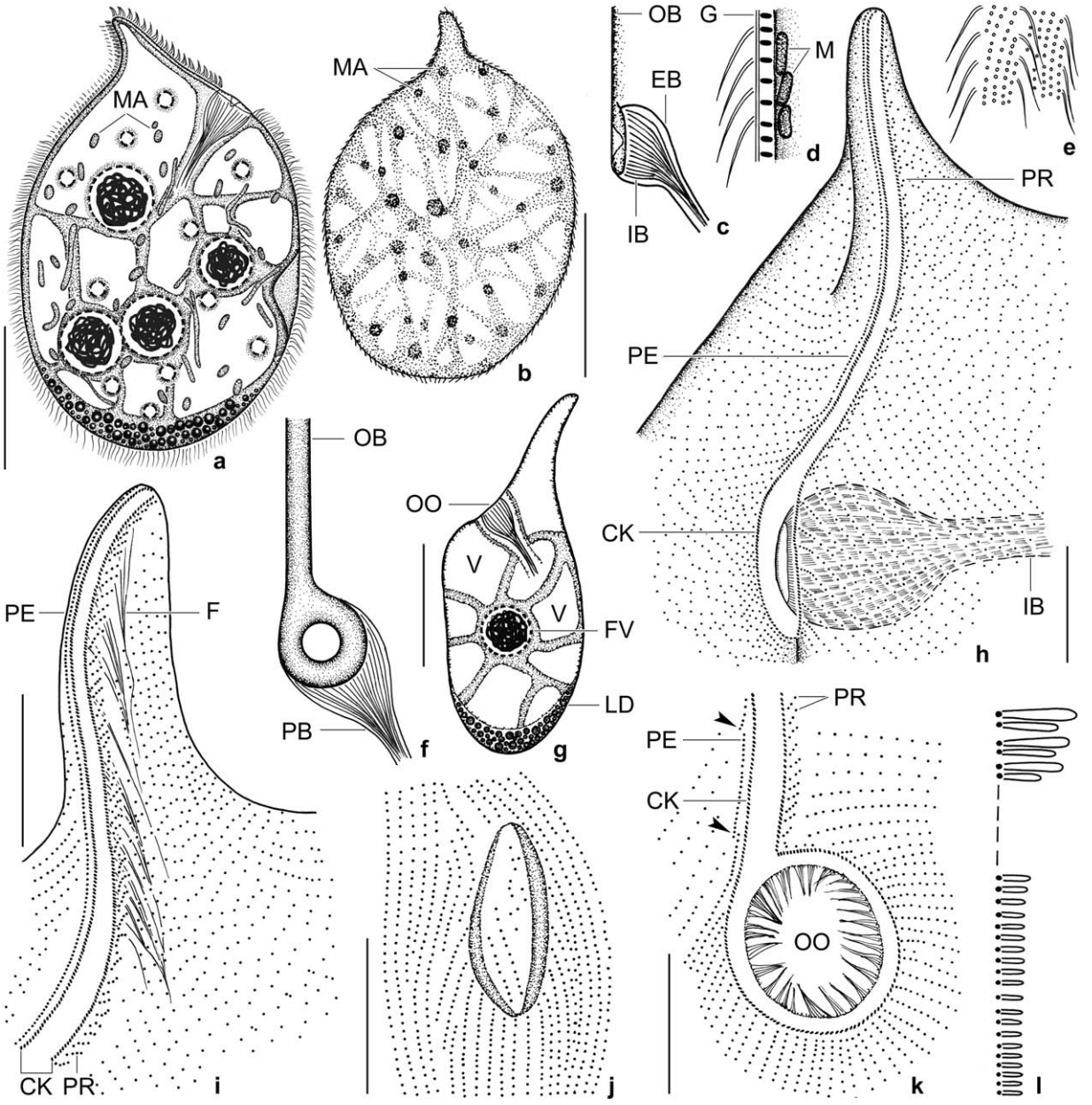
Type species: *Apotrachelius multinucleatus* nov. sp.

Etymology: Composite of the Greek prefix *apo* (derived from) and the generic name *Trachelius*, referring to the *Trachelius*-like general organization. Masculine gender.

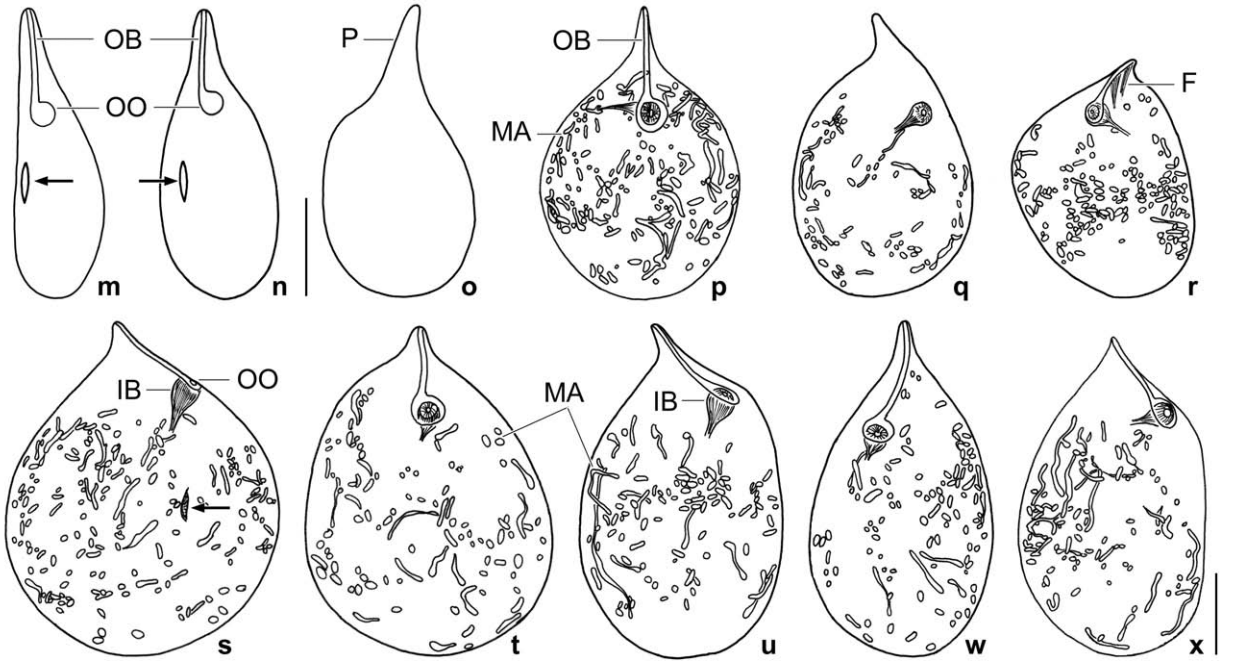
Remarks: *Apotrachelius* is related to *Trachelius* as evident from the following combination of features: (i) broadly dileptid body with a lateral fossa; (ii) ciliary rows gradually shortened right and left of oral bulge, and thus not producing a blank stripe; (iii) dorsal brush not staggered; (iv) circumoral kinety dikinetidal throughout; and (v) internal oral basket clavate. However, *Apotrachelius* differs not only from *Trachelius* but from all other dileptids in having lost the oral extrusomes, a main character of free-living litostomateans (Corliss 1979, Lynn 2008). This negative feature has been found and used, inter alia, as a generic character in two fuscheriid genera, viz., *Coriplites* and *Apocoriplites* (Foissner 1988b, Oertel et al. 2008), and as a species character in several spathidiids, for instance, *Arcuospathidium cooperi*, *A. vermiforme*, and *Apertospathula inermis* (Foissner & Xu 2007). A further curious feature of *Apotrachelius* is the laterally located oral bulge opening, a trait characteristic for only one other dileptid genus, *Paradileptus*. However, *Paradileptus* has two perioral kineties, staggered dorsal brush rows, a broad blank stripe left of the oral bulge, and lacks a fossa. This indicates that the laterally located oral bulge opening of *Apotrachelius* evolved convergently. Thus, the lack of extrusomes and the *Paradileptus*-like oral bulge opening justify generic separation of *Apotrachelius multinucleatus* and *Trachelius ovum*. Additionally, *Apotrachelius multinucleatus* does not have a single macronucleus, as *Trachelius*, but many scattered nodules, showing that this feature also evolved two times.

Apotrachelius multinucleatus Vďačný, Al-Rasheid & Foissner nov. sp. (Figs 46a–x, 47a–v; Table 22)

1974 *Trachelius tracheloides* Maskell, 1887 – Jones, Univ. South Alabama Monogr. **1**: 25 (misidentification)



Figs 46a–l: *Apotrachelius multinucleatus* nov. sp., Arabian specimens (a, c–l; originals) and a North American *multinucleatus*-like specimen (b; from JONES 1974) from life (a–g, l) and after protargol impregnation (h–k). **a, g** – right side view of a representative specimen and left side view of a slender specimen, length 300 µm; **b** – *Trachelius tracheloides*, length 200 µm, is possibly a misidentified *A. multinucleatus*; **c, f** – lateral and frontal view of oral bulge and oral basket. The oral bulge opening is *Paradileptus*-like, that is, the proximal portion of the oral bulge curves leftwards taking along the bulge opening. The internal oral basket is clavate and composed of innumerable fibres about 50 µm long; **d, e** – optical section and surface view, showing cortical granulation; **h, i, k** – ciliary pattern in oral area. The circumoral kinety is dikinetidal throughout and its left branch is associated with many oblique preoral kineties, while the right branch is accompanied by a perioral kinety. Arrowheads (k) mark breaks in the perioral kinety; **j** – ciliary pattern around and inside of fossa, showing that some somatic kineties end at fossa margin, while others extend to its bottom and proceed posteriorly; **l** – fine structure of brush row 3. CK – circumoral kinety, EB – external basket, F – fibres, FV – food vacuole, G – cortical granules, IB – internal basket, LD – lipid droplets, M – mitochondria, MA – macronuclear nodules, OB – oral bulge, OO – oral bulge opening, PB – pharyngeal basket, PE – perioral kinety, PR – preoral kineties, V – vacuoles. Scale bars: 20 µm (i–k), 30 µm (h), and 100 µm (a, b, g).



Figs 46m–x: *Apotrachelius multinucleatus* nov. sp. from life (m–o) and after protargol impregnation (p–x, Wilbert's method). **m, n** – ventral overviews showing the *Paradileptus*-like oral bulge opening and the localization of the fossa (arrows); **o** – shape variant; **p–x** – variability of body size and nuclear apparatus. Drawn to scale. Arrow in (s) denotes the fossa. F – fibres, IB – internal basket, MA – macronuclear nodules, OB – oral bulge, OO – oral bulge opening, P – proboscis. Scale bars 100 μm.

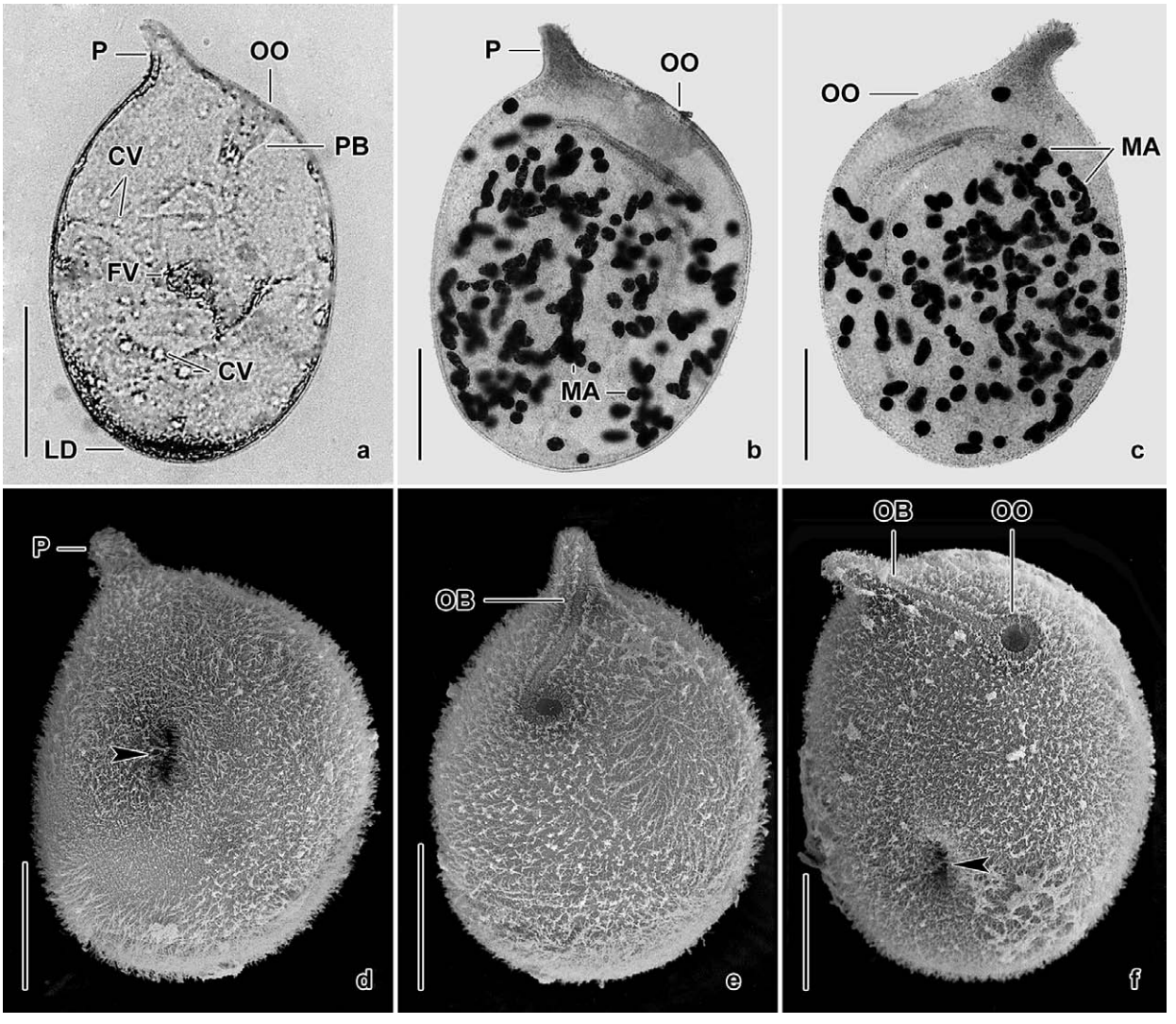
Diagnosis: Size about 300 × 150 μm in vivo. Shape broadly dileptid with broadly rounded posterior end, proboscis oral bulge about 1/4 of body length. Many scattered macronuclear nodules and several globular micronuclei. Many scattered contractile vacuoles with 1 pore each. On average 209 ciliary rows, 4 anteriorly differentiated into a distinctly heterostichad dorsal brush with monokinetidal tails extending posteriorly. Oral bulge opening about 20 μm across. Preoral kineties oblique to strongly oblique, ordinarily to widely spaced, each usually composed of 3 narrowly spaced cilia. In marine coastal waters.

Type locality: Brackish coastal pond at Safwa village, Saudi Arabian Gulf coast, E50°06' N26°39'.

Type material: One holotype slide (inv. no. 195) and six paratype slides (inv. nos 196-201) with protargol-impregnated specimens have been deposited in the Biology Centre of the Museum of Upper Austria, Linz (LI). Relevant specimens are marked by black ink circles on the coverslip.

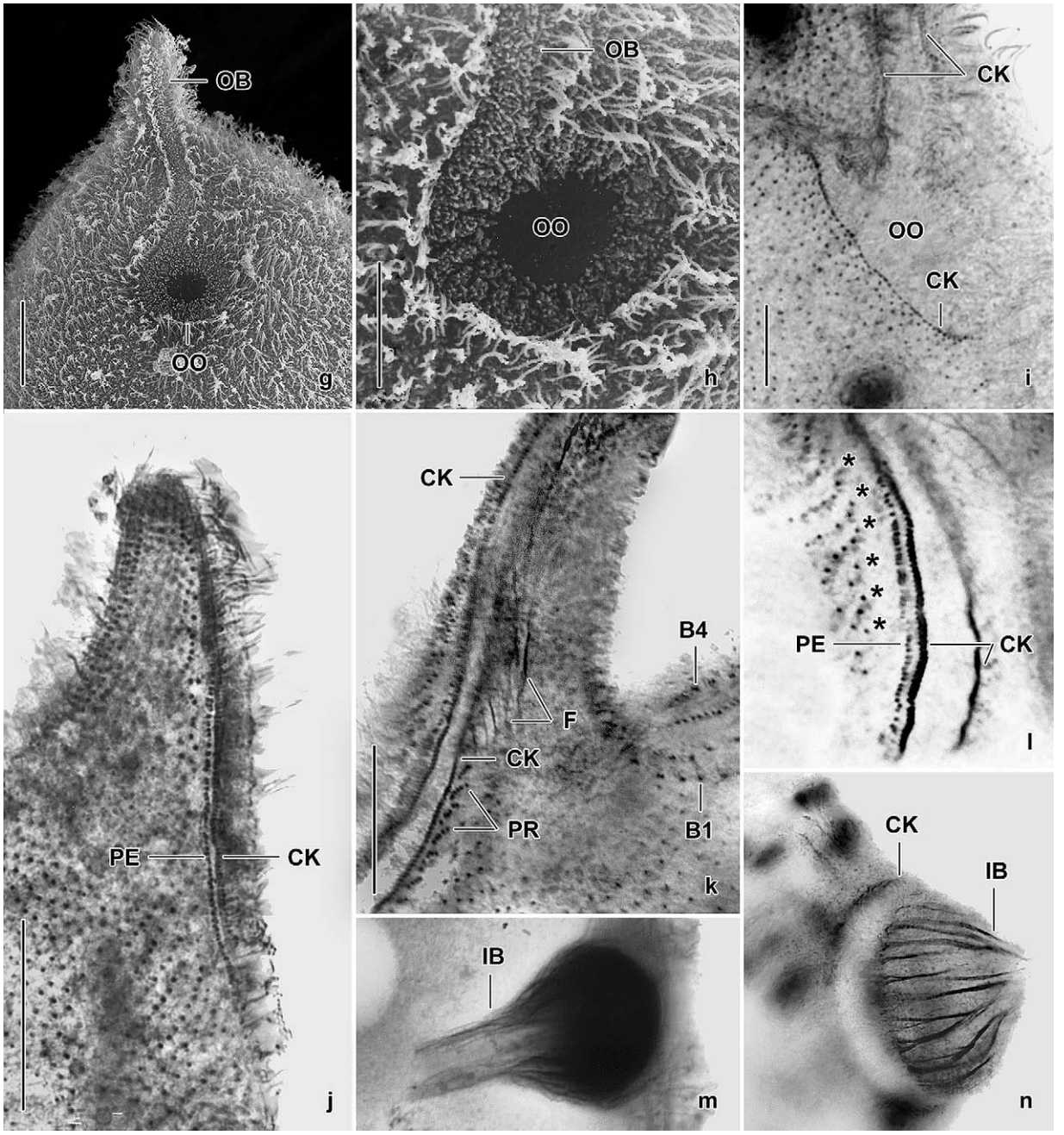
Etymology: Composite of the Latin numeral *multi* and the noun *nucleus*, referring to the many macronuclear nodules, a main feature of the species.

Description of Saudi Arabian population: Size about 250–300 × 150 μm in vivo, while about 400 × 250 μm in the protargol preparations due to a strong inflation with Wilbert's method (Table 22); very flexible but not contractile. Shape dileptid to broadly dileptid both in vivo and in preparations, that is, length:width ratio 3:2–2.5:1; body flattened about 2:1. Proboscis occupies one fifth to one third of body length, usually one fourth; conical with anterior portion slightly curved dorsally. Trunk usually ovoidal to globular, rarely oblong, left side convex, right flattened and with conspicuous, about 25 μm long fossa in protargol preparations (Figs 46a, g, m–x, 47a–f, q, r, t). Nuclear apparatus in trunk and proximal proboscis half. About 75–180 scattered macronuclear nodules; individual nodules highly variable, that is, globular to strand-like and 5–62 × 4–10 μm in size, sometimes connected by fine bridges and thus very likely

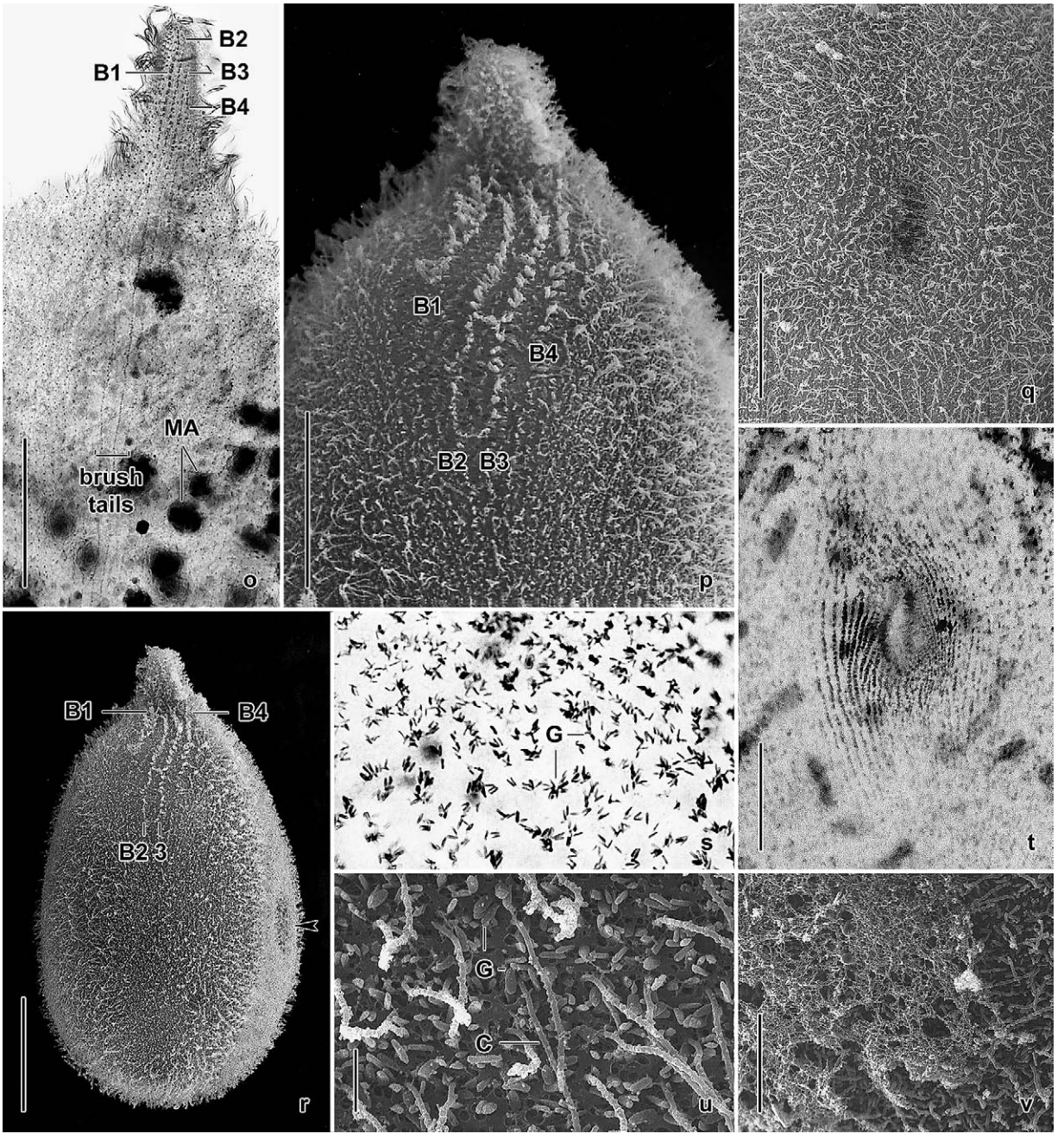


Figs 47a–f: *Apotrachelius multinucleatus* nov. sp. from life (a), after protargol impregnation (b, c, Wilbert's method), and in the scanning electron microscope (d–f). **a** – right side view of a representative specimen, length 300 µm. Note the overall similarity with *Trachelius ovum*; the strongly vacuolated cytoplasm; the inconspicuous, conical proboscis; the scattered contractile vacuoles; and the accumulation of lipid droplets in posterior pole area; **b, c** – lateral views showing the many scattered macronuclear nodules; **d–f** – right side (d), ventral (e), and ventrolateral (f) views, showing the broadly dileptid body with the inconspicuous proboscis. Note that the oral bulge opening is *Paradileptus*-like, i.e., the oral bulge forms a 6-like pattern (e). Arrowheads denote the fossa. CV – contractile vacuoles, FV – food vacuole, LD – lipid droplets, MA – macronuclear nodules, OB – oral bulge, OO – oral bulge opening, P – proboscis, PB – pharyngeal basket. Scale bars: 50 µm (d–f) and 100 µm (a–c).

originating from a three-dimensional reticulum, as in *Apodileptus*; several small, globular nucleoli in each nodule. Micronuclei 2.5–3 µm across, scattered between macronuclear nodules, exact number difficult to determine because hardly distinguishable from similar-sized and impregnated cytoplasmic inclusions (Figs 46a, p–x, 47b, c; Table 22). Many scattered contractile vacuoles, each with a single, intrakinetal excretory pore about 2 µm across (Figs 46a, 47a). No oral extrusomes detectable in the light microscope. Cortex in vivo flexible, about 2 µm thick and distinctly separated from cytoplasm; often studded with minute holes due to just extruded cortical granules in SEM-prepared specimens (Figs 46d, 47u). Cortical



Figs 47g–n: *Apotrachelius multinucleatus* nov. sp. in the scanning electron microscope (g, h) and after protargol impregnation (i–n). **g, h** – oral body portion. The oral bulge opening is paradileptid, that is, it is formed like the numeral 6. The dense granulation of the oral bulge is caused by partially extruded mucocysts; **i** – oral ciliary pattern, showing that the circumoral kinety is composed of dikinetids both in the proboscis and around the oral bulge opening; **j, l** – right side view of oral ciliary pattern. The first row right of the circumoral kinety extends as a perioral kinety to the tip of the proboscis. Asterisks mark gradually shortened ciliary rows along the proboscis oral bulge; **k** – ventrolateral view of oral ciliary pattern. The circumoral kinety of the proboscis is associated with fibres, very likely nematodesmata, extending posteriorly to form a loose funnel; **m, n** – the internal oral basket, which is about 50 µm long, is clavate and composed of innumerable fibres. B1, 4 – brush rows 1 and 4, CK – circumoral kinety, F – fibres, IB – internal basket, OB – oral bulge, OO – oral bulge opening, PE – perioral kinety, PR – preoral kineties. Scale bars: 10 µm (h, i), 20 µm (g, k), and 30 µm (j).



Figs 47o–v: *Apotrachelius multinucleatus* nov. sp. after protargol impregnation (o, s, t) and in the scanning electron microscope (p–r, u, v). **o, p** – dorsal views of proboscis' ciliary pattern; (p) is a detail of the anterior body portion of the specimen shown in (r). The dorsal brush is composed of four heterostichad rows, which continue posteriorly with a monokinetidal tail. Brush dikinetids are associated with slightly inflated bristles gradually shortening from about 3.8 μm anteriorly to 1.8 μm posteriorly; **q, t** – ciliary and cortical granule pattern around the fossa. Some somatic kineties terminate at the fossa margin, while others extend to its bottom and proceed posteriorly; **r** – dorsal overview showing the broadly dileptid body with a distinct fossa (arrowhead) and the short proboscis carrying a four-rowed, distinctly heterostichad dorsal brush; **s** – cortical granules impregnate deeply with protargol often making difficult observations of the ciliary pattern. The granules are oblong and about 1 × 0.2 μm in size; **u** – in SEM-prepared specimens, the cortex is often studded with minute holes due to the extruded cortical granules; **v** – the exploded cortical granules form a spongious cover. B1–4 – dorsal brush rows, C – cilia, G – cortical granules, MA – macronuclear nodules. Scale bars: 2 μm (u), 10 μm (v), 30 μm (o–q, t), and 50 μm (r).

granules narrowly spaced in somatic and oral bulge cortex, about 1.5 × 0.2 µm in vivo (0.9–1.2 µm long in SEM); do not stain with methyl green-pyronin, but usually impregnate deeply with protargol making observation of ciliary pattern difficult; when exploded form a spongious cover (Figs 46d, e, 47s, u, v). Mitochondria underneath cortex, ellipsoidal and about 4 × 2 µm in size (Fig. 46d). Cytoplasm colourless and hyaline because strongly vacuolated, except for posterior body portion appearing brown-black at low magnification due to an accumulation of lipid droplets 1–5 µm across (Figs 46a, g, 47a). Feeds on small, yellow-green cryptomonads, which are collected in food vacuoles up to 60 × 40 µm in size and usually localized in centre of trunk. Swims moderately fast.

Cilia about 8 µm long in vivo, narrowly spaced; in protargol preparations as typical for dileptids, i.e., with thick, strongly impregnated distal half; arranged in an average of 209 longitudinal, narrowly spaced rows gradually shortening right and left of oral bulge (Figs 46h, i, k, 47d–f, j, l; Table 22). First row right of circumoral kinety extends as perioral kinety with narrowly to ordinarily spaced cilia to tip of proboscis, frequently with some irregularities, e.g., short breaks and/or connected to somatic ciliary rows in posterior portion (Figs 46h, i, k, arrowheads; 47j, l). Ciliature condensed and curved towards fossa, i.e., some somatic kineties end at fossa margin, while others extend to its bottom and proceed posteriorly (Figs 46j, 47q, t). Dorsal brush exactly on dorsal side of proboscis, composed of four heterostichad rows commencing apically and continuing posteriorly with monokinetidal tails composed of 1–2 µm long, very narrowly spaced type VI bristles (Figs 46l, 47o, p, r). Brush dikinetids associated with type II bristles gradually shortening from about 5 µm (3.8 µm in SEM) anteriorly to 2 µm (1.8 µm in SEM) posteriorly; posterior bristles of dikinetids shortened by about one fourth, their length decreases to 2 µm posteriorly.

Oral bulge opening at end of anterior body fourth, does not project from body proper; *Paradileptus*-like, that is, proximal portion curved leftwards, just as in numeral 6; about 20 µm across in vivo, while 35 µm across after protargol impregnation due to strong body inflation (Figs 46a, f, k, m, n, 47e, f–h; Table 22). Pharyngeal basket embedded in viscous cytoplasm in vivo, obliquely directed to cell centre; internal basket clavate and composed of innumerable fibres about 50 µm long in protargol preparations; external basket comparatively inconspicuous and impregnated only in distal portion (Figs 46c, f–h, k, 47m, n; Table 22). Circumoral kinety composed of narrowly spaced dikinetids throughout, those of proboscis associated with fibres extending posteriorly to form a loose funnel; right branch curves around anterior end of proboscis, left branch ends subapically almost touching curved right end (Figs 46h, i, k, r, 47i, k, l). About 35 oblique to strongly oblique, ordinarily to widely spaced preoral kineties associated with left branch of circumoral kinety, some kineties convex and more or less distinctly connected with left side ciliary rows; individual preoral kineties composed of two to six, usually of three narrowly spaced cilia (Figs 46h, i, k, 47k).

Notes on North American population: Jones (1974) misidentified an Alabaman population as "*Trachelius tracheloides* Maskell, 1887" which is, however, a misidentified *Ophryoglena*, as already recognized by Kahl (1931). Certainly, Jones' specimens (Fig. 46b) highly resemble *Apotrachelius multinucleatus* in body shape and size (200 µm and 250–300 µm), the nuclear apparatus and, especially, the saline habitat. However, the contractile vacuole pattern is different: Jones' specimens have only one terminal vacuole, while *A. multinucleatus* has many scattered vacuoles. Nevertheless, Jones (1974) did not figure the terminal vacuole and possibly overlooked the small scattered vacuoles due to the strongly vacuolated cytoplasm. If this is the case, conspecificity of the Alabaman and Saudi Arabian populations is very likely.

Occurrence and ecology: *Apotrachelius multinucleatus* was discovered in a large (about 200 × 200 m, max. depth 4 m), brackish (~ 12–28‰) pool at Safwa village in the Al Qatif oasis, about 15 km north of Dammam (Saudi Arabia) and about 2 km inshore from the Saudi Arabian Gulf coast. The pool, which was surrounded by salt-tolerant tall reeds (*Phragmites communis*) and black mangrove (*Avicennia marina*), was connected with the Gulf via the water table. *Apotrachelius multinucleatus* was collected at the margin of the

pool, where the muddy, sandy sediment is strongly rooted by the plants mentioned above. During the hot season, when the water table decreases, the sediment becomes microaerobic or anaerobic. The contractile vacuoles indicate that *A. multinucleatus* can live at very low salinities, possibly even in freshwater. Very likely, *A. multinucleatus* occurs also at the South Korean sea coast (Dr. Kwon, pers. comm.). Further, Al-Rasheid (1997, 1999) reported *Trachelius ovum* from the saline (18‰) Al-Hassa oasis. Possibly, this was *A. multinucleatus*, although Al-Rasheid (1997) mentioned "macronucleus in two parts".

Remarks: *Apotrachelius multinucleatus* is easily recognizable in vivo due to the broadly dileptid body, the small proboscis, the many macronuclear nodules, the scattered contractile vacuoles, and the lack of oral extrusomes. This is fortunate because it is difficult to fix and to impregnate with protargol, making morphometry and observations on the ciliary pattern difficult. There is only one species similar to *A. multinucleatus*, viz., *Trachelius ovum*. However, *A. multinucleatus* is easily distinguished from *T. ovum* by the many small macronuclear nodules (vs. one large nodule) and the absence (vs. presence) of oral extrusomes, a feature checked very carefully with optimum technical equipment in several specimens. *Apotrachelius multinucleatus* is also different from *Trachelius gutta*, originally a poorly described species from saline habitats (for figures, see *Trachelius ovum*) now well redescibed and neotypified as *Orthodonella gutta* by Lin et al. (2004). They differ in body size (300 µm vs. 120 µm), the number of ciliary rows (209 vs. 50), and the contractile vacuole pattern (many scattered vacuoles vs. one or few terminal vacuoles).

Order Dileptida Jankowski, 1978

1975 Rhynchostomatida (Dileptida) Jankowski, Konspekt novoj sistemy Ciliophora: 26 (a nomen nudum due to lack of description or definition)

1978 Dileptida ordo n. Jankowski, Morfologiâ, sistematika i èvolûciâ životnyh: 89 (very brief characterization)

1980 Dileptida Jankowski, 1978 – Jankowski, Trudy zool. Inst., Leningr. **94**: 120 (conspectus of ciliate system)

1988 Dileptina Jankowski, 1978 – Foissner & Foissner, Arch. Protistenk. **135**: 228 (brief review, lowering rank to suborder)

1990 Dileptina Jankowski, 1978 – Lipscomb & Riordan, J. Protozool. **37**: 298 (cladistic analysis of litostomateans)

1994 Dileptina Jankowski, 1978 – Puytorac, Ciliophora: 12 (system of litostomateans)

2007 Dileptina Jank., 1978 – Jankowski, Protista II: 570 (handbook)

2011 Dileptida Jankowski, 1978 – Vďačný, Orsi, Bourland, Shimano, Epstein & Foissner, Eur. J. Protistol. **47**: 310 (improved diagnosis)

Diagnosis: Body broadly to rod-like dileptid, rarely rostrate. Proboscis agile, its ventral and dorsal side of similar length. Dorsal brush staggered and two- or multi-rowed. Circumoral kinety hybrid, i.e., oral dikinetids in proboscis and monokinetids around oral bulge opening. Internal oral basket bulbous or obconical.

Type family (by subsequent designation): Dileptidae Jankowski, 1980.

Etymology: Composite of the stem of the generic name *Dileptus* and the order suffix *-ida*.

Remarks: In 1975, Jankowski classified dileptids at ordinal rank as "Rhynchostomatida (Dileptida)" in his conspectus of the system of Ciliophora. However, this name is unavailable because (i) unpublished (appeared in an abstract) under Article 9.9 and (ii) without description and definition under Article 13.1 of the ICZN (1999). Three years later, Jankowski (1978) established validly the order Dileptida and diagnosed it briefly as follows: "holotrichous ciliates with agile proboscis and posteriorly located oral opening". Based on a very detailed cladistic study, Vďačný et al. (2011b) redefined the order, using especially details

of the somatic and oral ciliature. The monophyly of this order was fully supported by molecular data and by two strong morphological synapomorphies: a hybrid circumoral kinety and a staggered dorsal brush (Vďačný et al. 2011b). The order Dileptida comprises two families: the Dimacrocaryonidae with one or two macronuclear nodules, and the Dileptidae with at least four macronuclear nodules.

Key to Families

1 Macronucleus unsegmented or in two nodules ..... Dimacrocaryonidae (p. 143)
– Macronucleus in at least four moniliform or scattered nodules ..... Dileptidae (p. 262)

Family Dimacrocaryonidae Vďačný et al., 2011

2011 Dimacrocaryonidae fam. n. Vďačný, Orsi, Bourland, Shimano, Epstein & Foissner, Eur. J. Protistol. **47**: 310

Diagnosis: Dileptida with macronucleus in one or two nodules. Dorsal brush two-rowed, rarely multi-rowed. Oral apparatus dileptid.

Type genus (by original designation): *Dimacrocaryon* Jankowski, 1967.

Remarks: The Dimacrocaryonidae unites four genera whose macronucleus is unsegmented (*Monomacrocaryon*) or in two nodules (*Dimacrocaryon*, *Rimaleptus*, *Microdileptus*). This family is monophyletic in molecular phylogenies, but it is paraphyletic in both the Hennigian argumentation scheme and the computer-assisted cladograms (Vďačný et al. 2011b). This discrepancy is caused by the lack of morphological synapomorphies for the genus *Monomacrocaryon* and the *Dimacrocaryon-Rimaleptus* clade. However, the molecular data indicate that the unsegmented macronucleus of *Monomacrocaryon* evolved from a binucleate state by fusion of the macronuclear nodules.

Dimacrocaryon, *Rimaleptus*, and *Microdileptus* share a combination of two distinct features not found in any other dileptid genus: (i) two macronuclear nodules with a single micronucleus in between and (ii) an usually two-rowed dorsal brush. Thus, we suppose that the three genera have a common ancestor. *Rimaleptus* and *Microdileptus* maintained the ancestral oral apparatus, while *Dimacrocaryon* developed several specialties.

Key to Genera

1 Macronucleus unsegmented and accompanied by a single micronucleus ..... *Monomacrocaryon* (p. 143)
– Macronucleus in two nodules with a single micronucleus in between 2
2 Oral opening lined by strongly refractive granules impregnating deeply with protargol ..... *Dimacrocaryon* (p. 161)
– Oral opening without such granules 3
3 Oral opening usually > 10 µm. Preoral kineties composed of at least two obliquely arranged cilia ..... *Rimaleptus* (p. 179)
– Oral opening < 5 µm. Preoral kineties arranged in a single row with more or less grouped cilia ..... *Microdileptus* (p. 242)

Monomacrocaryon Vďačný, Orsi, Bourland, Shimano, Epstein & Foissner, 2011

2011 *Monomacrocaryon* gen. n. Vďačný, Orsi, Bourland, Shimano, Epstein & Foissner, Eur. J. Protistol. **47**: 310

Diagnosis: Small- to very large-sized Dimacrocaryonidae with narrow to cylindroidal body. Macronucleus oblong to rod-shaped. Dorsal brush staggered and multi-rowed. Right branch of circumoral kinety accompanied by a perioral kinety, left branch by many slightly to strongly oblique preoral kineties. Oral

bulge opening dileptid, i.e., roundish or ovate and located ventrally, length about 15 µm. Oral basket bulbous or obconical.

Type species (by original designation): *Dileptus terrenus* FOISSNER, 1981.

Etymology: Composite of the Greek numeral *mono* (one), the adjective *makros* (large), and the noun *karyon* (nucleus), referring to the unsegmented macronucleus. Neuter gender.

Remarks: *Monomacrocaryon* differs from all dileptids, except for *Trachelius*, by the unsegmented macronucleus. *Monomacrocaryon* is distinguished from *Trachelius* by the narrow body without lateral fossa (vs. broad with lateral fossa) and the oral ciliature (hybrid vs. dikinetidal circumoral kinety). Beginners may confuse *Monomacrocaryon* with *Rimaleptus*, in which the two macronuclear nodules are usually close together or sometimes abutting, thus appearing as a single, oblong structure.

Key to Species

1 Distinctly contractile, body length < 110 µm ..... *M. tenue* (p. 144)
– Not contractile, body length > 180 µm 2
2 Only dorsal contractile vacuoles ..... *M. terrenum* (p. 145)
– Ventral and dorsal contractile vacuoles 3
3 Body length 1000–1600 µm, proboscis occupies 1/5 of body length ..... *M. gigas* (p. 154)
– Body length 300–400 µm, proboscis occupies 1/3 of body length ..... *M. polyvacuolatum* (p. 157)

Monomacrocaryon tenue (PENARD, 1922) VĎAČNÝ et al., 2011 (Figs 48a–f)

1922 *Dileptus tenuis* sp. n. PENARD, Études Infusoires: 79

1931 *Dileptus tenuis* PENARD, 1922 – KAHL, Tierwelt Dtl. **21**: 209 (first taxonomic reviser)

1963 *Dileptus tenuis* PÉNARD, 1922 – DRAGESCO, Bull. biol. Fr. Belg. **97**: 123 (second taxonomic reviser; without figures)

2011 *Monomacrocaryon tenue* (PENARD, 1922) comb. n. – VĎAČNÝ, ORSI, BOURLAND, SHIMANO, EPSTEIN & FOISSNER, Eur. J. Protistol. **47**: 310

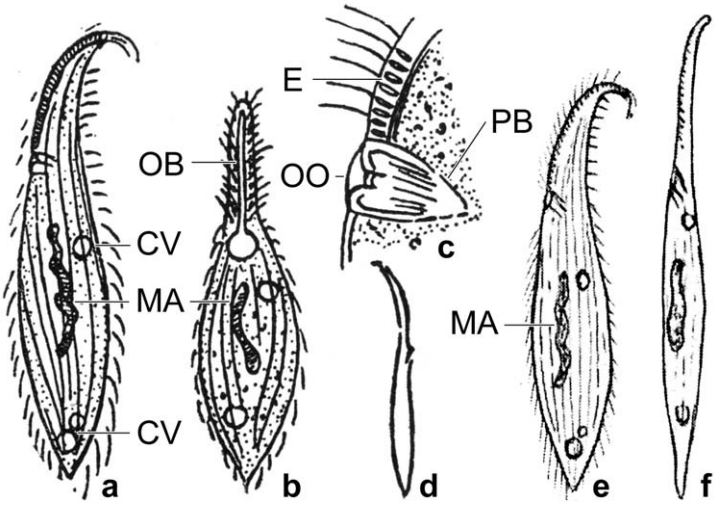
Diagnosis: Length about 85 µm, contracts up to 50%. Shape narrowly to very narrowly dileptid with acute posterior end, proboscis about 1/3 of body length. Macronucleus cylindroidal to rod-shaped, usually curved or twisted. Two diagonally arranged dorsal contractile vacuoles. Extrusomes broadly fusiform and short. Oral bulge opening roundish.

Type locality: Mosses from the surroundings of the town of Geneva, Switzerland, E6°08' N46°12'.

Type material: Not available.

Etymology: Not given in original description. The Latin adjective *tenuis* (thin) obviously refers to body shape.

Description: Length 60–110 µm, contracts up to 50%. Shape narrowly to very narrowly dileptid, that is, length:width ratio 4–9.5:1, according to the figures provided. Proboscis motile, occupies about one third of body length, not set off from trunk, thus providing cells with an *Arcuospathidium* or pleurostomatid appearance; trunk unflattened, bluntly fusiform, pointed posteriorly (Figs 48a, b, d–f). Macronucleus cylindroidal to rod-shaped with a length:width ratio of 10–15:1, usually twisted or curved. Two diagonally arranged dorsal contractile vacuoles: anterior vacuole posterior to oral bulge opening, posterior one subterminal and sometimes accompanied by a smaller vacuole (Figs 48a, b, e, f). Extrusomes attached to proboscis oral bulge, short and bluntly fusiform as described and figured by PENARD (Fig. 48c); of typical toxicyst structure when exploded. Number of ciliary rows not studied, but PENARD (1922) figured seven



Figs 48a–f: *Monomacrocaryon tenue* from PENARD 1922 (a–d) and KAHL 1931 (e, f). **a** – left side view of a stout specimen, showing, inter alia, the twisted macronucleus and the two contractile vacuoles, length 60–110 µm; **b** – ventral view, showing the roundish oral bulge opening, the oblong macronucleus, and the two diagonally arranged contractile vacuoles; **c** – detail of oral region. Note the bluntly fusiform extrusomes and the short, bulbous oral basket; **d** – left side view of a slender specimen; **e, f** – redrawn by KAHL (1931) from PENARD (1922). CV – contractile vacuoles, E – extrusomes, MA – macronucleus, OB – oral bulge, OO – oral bulge opening, PB – pharyngeal basket.

rows on one side. Oral bulge opening roundish (Fig. 48b). Pharyngeal basket bulbous and short (Fig. 48c).

Occurrence and ecology: PENARD (1922) found *Monomacrocaryon tenue* exclusively in mosses from old walls in the surroundings of the town of Geneva, Switzerland. Later records not substantiated by illustrations: decaying wood mass from the Erlangen area in Bavaria, Germany (WENZEL 1953); various soils in Belgium (CHARDEZ 1967, 1987); bog pond in France (GROLIÈRE & NJINÉ 1973); mosses from various localities in Slovakia (ROSA 1957; TIRJAKOVÁ & MATIS 1987, TIRJAKOVÁ 2005); and in a soil sample from Abaco Island, Bahamas (CAIRNS & RUTHVEN 1972).

Remarks: Within the congeners, *M. tenue* is outstanding in having (i) a highly contractile body (vs. not contractile), (ii) only two dorsal contractile vacuoles (vs. at least five), and (iii) bluntly fusiform extrusomes (vs. rather fine and rod-shaped or slightly ovate). There are only two other contractile dileptids, viz., *Pseudomonilicaryon dimorphum* and *Rimaleptus lacazei*. However, *Pseudomonilicaryon dimorphum* has four macronuclear nodules in series, and *Rimaleptus lacazei* has two globular, abutting nodules. As mentioned by DRAGESCO (1963), *Monomacrocaryon tenue* is very similar to *Pseudomonilicaryon anguillula* and *P. gracile*. However, both have a moniliform macronucleus and rod-shaped or very narrowly ovate extrusomes. Additionally, *P. anguillula* differs from *Monomacrocaryon tenue* by the contractile vacuole pattern (a dorsal row of vacuoles vs. two diagonal vacuoles).

Monomacrocaryon terrenum (FOISSNER, 1981) VĎAČNÝ, ORSI, BOURLAND, SHIMANO, EPSTEIN & FOISSNER, 2011 (Figs 49a–o, 50a–w; Table 24)

1981 *Dileptus terrenus* nov. sp. FOISSNER, Zool. Jb. Syst. **108**: 286

1984 *Dileptus terrenus* FOISSNER, 1981 – FOISSNER, Stapfia **12**: 96 (supplementary observations on another Austrian population)

1985 *Dileptus terrenus* FOISSNER – TIRJAKOVÁ & MATIS, Acta Fac. Rerum Nat. Univ. Comenianae, Bratisl. (Zool.) **28**: 80 (notes on a Mongolian population)

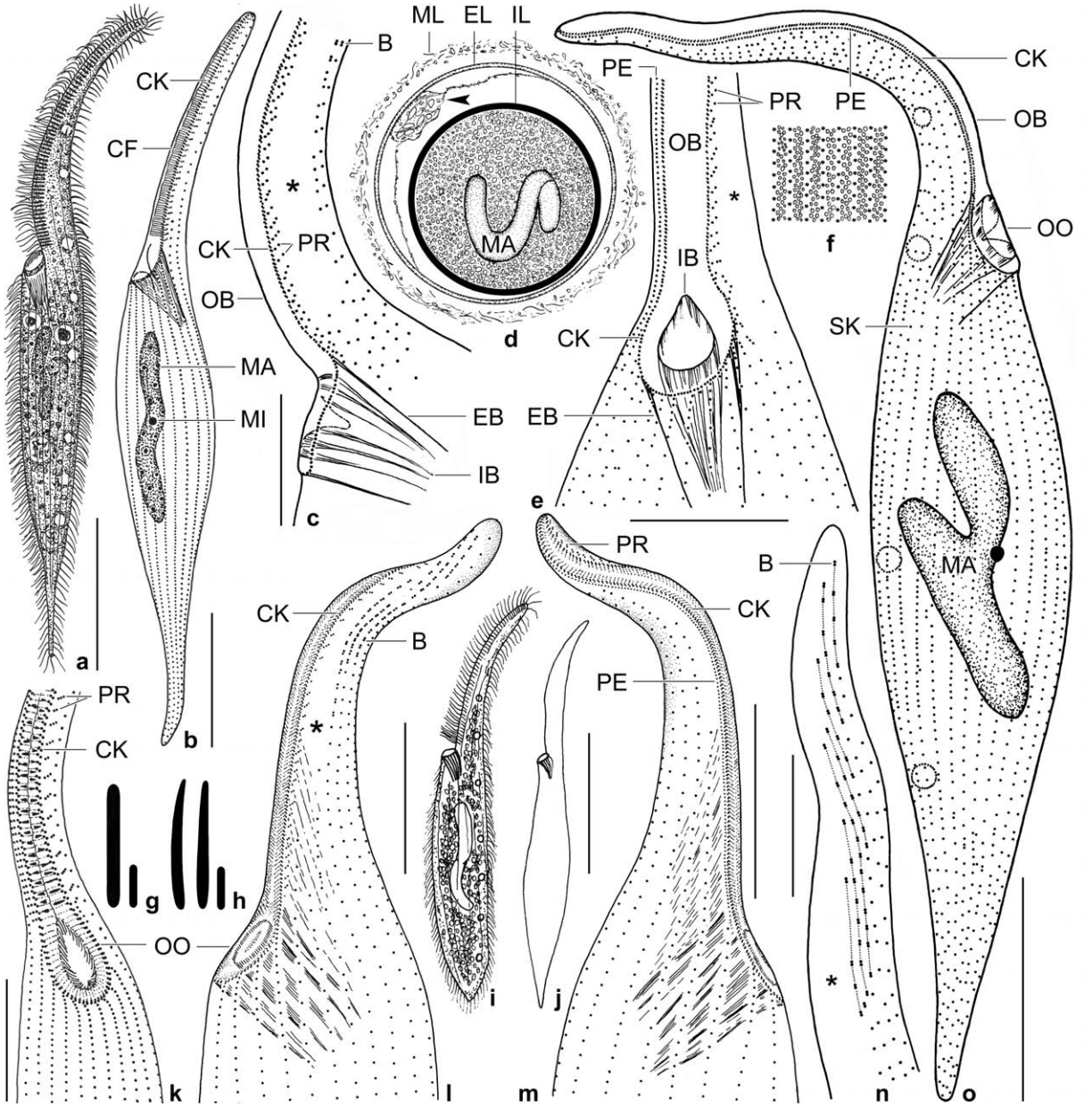
2009 *Dileptus terrenus* FOISSNER, 1981 – VĎAČNÝ & FOISSNER, J. Eukaryot. Microbiol. **56**: 232 (description of a Peruvian population and its ontogenesis)

2011 *Monomacrocaryon terrenus* (FOISSNER, 1981) comb. n. – VĎAČNÝ, ORSI, BOURLAND, SHIMANO, EPSTEIN & FOISSNER, Eur. J. Protistol. **47**: 297 (18S rRNA gene sequence of an Upper Austrian population)

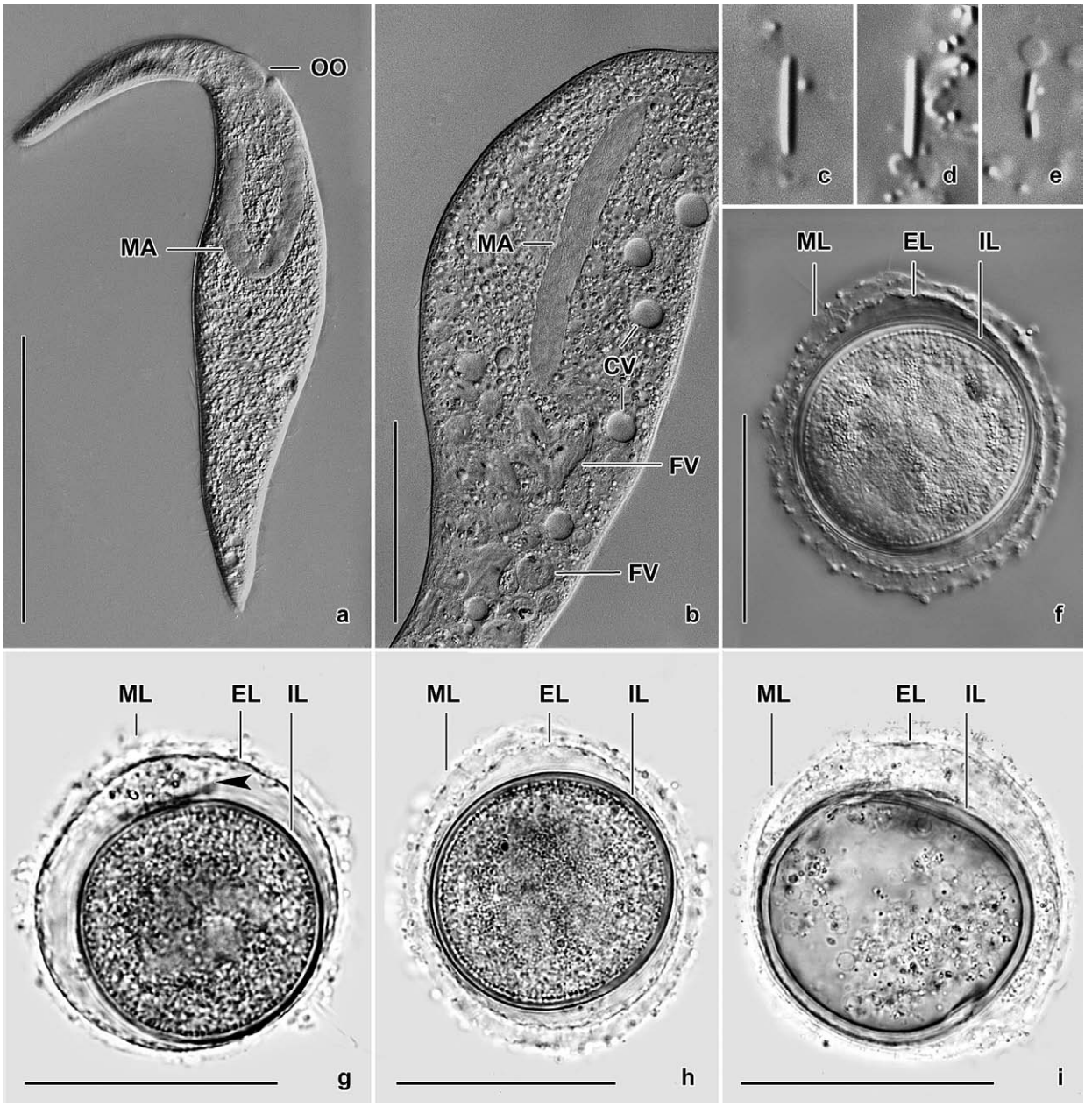
Table 24: Morphometric data on three populations (Pop) of *Monomacrocaryon terrenum* and on resting cysts of an Upper Austrian population from the outskirts of the town of Selker (S; original data). F – type from Fusch an der Glocknerstraße, Austria (from FOISSNER 1981); T – voucher from the Tullnerfeld in Lower Austria (from FOISSNER 1984); P – voucher from the coast of the Titicaca Lake in Peru (from VĎAČNÝ & FOISSNER 2009). Data based, if not stated otherwise, on mounted, protargol-impregnated (Foissner's method), and randomly selected specimens from non-flooded Petri dish cultures. Measurements in µm. CV – coefficient of variation in %, M – median, Max – maximum, Mean – arithmetic mean, Min – minimum, n – number of specimens investigated, Pop – population, SD – standard deviation, SE – standard error of mean.

Characteristics	Pop	Mean	M	SD	SE	CV	Min	Max	n
Body, length	F[a]	251.2	255.0	15.8	7.1	6.3	227.0	267.0	5
	T	263.9	273.0	67.1	21.2	25.4	152.0	350.0	10
	P	278.4	282.5	23.1	5.0	8.3	226.5	315.0	21
Body, width	F[a]	36.0	35.0	4.1	1.8	11.3	32.0	42.0	5
	T	42.5	42.0	7.1	2.2	16.6	32.0	56.0	10
	P	47.8	48.5	5.8	1.3	12.2	34.5	56.0	21
Body length:width, ratio	F[a]	7.1	7.5	1.1	0.5	15.4	5.8	8.1	5
	T[a]	6.3	6.5	1.7	0.5	26.5	2.7	8.0	10
	P	5.9	5.7	0.6	0.1	11.0	4.7	7.3	21
Anterior body end to oral bulge opening, distance	F[a]	96.6	98.0	10.3	4.6	10.6	80.0	105.0	5
	T	93.8	96.5	18.1	5.7	19.3	70.0	122.0	10
	P	94.0	93.5	12.3	2.7	13.1	78.0	113.0	21
Proboscis, % of body length	F[a]	38.7	37.4	5.9	2.6	15.3	31.4	46.3	5
	T[a]	37.6	34.5	13.3	4.2	35.4	25.0	73.7	10
	P	33.7	33.0	2.9	0.6	8.6	29.0	38.3	21
Nuclear figure, length	F[a]	58.0	59.0	10.1	4.5	17.5	46.0	73.0	5
	T	78.2	77.5	13.7	4.3	17.6	53.0	98.0	10
Macronucleus, total length	P	81.5	79.5	17.1	3.7	21.0	61.5	128.0	21
Macronucleus, width	F[a]	7.1	7.0	–	–	–	6.7	7.9	5
	T	8.8	8.5	1.2	0.4	13.7	7.0	11.0	10
Macronucleus nodules, number	F[a]	1.0	1.0	0.0	0.0	0.0	1.0	1.0	5
	T	1.0	1.0	0.0	0.0	0.0	1.0	1.0	10
	P	1.0	1.0	0.0	0.0	0.0	1.0	1.0	21
Micronucleus, largest diameter	F[a]	2.0	2.0	0.0	0.0	0.0	2.0	2.0	3
	T	2.9	2.8	–	–	–	2.7	3.2	10
	P	3.6	4.0	–	–	–	3.0	4.0	14
Micronucleus, number	F[a]	1.0	1.0	0.0	0.0	0.0	1.0	1.0	5
	T	1.0	1.0	0.0	0.0	0.0	1.0	1.0	10
	P	1.0	1.0	0.0	0.0	0.0	1.0	1.0	21
Ciliary rows, number	F[a]	29.0	28.5	3.2	1.6	10.9	26.0	33.0	4
	T	26.8	27.0	–	–	–	26.0	27.0	5
	P	26.9	27.0	2.0	0.4	7.4	24.0	31.0	21
Preoral kineties, number	P	47.1	46.0	5.1	1.1	10.9	41.0	58.0	21
Resting cysts, diameter including external layer (in vivo)	S	59.0	60.0	5.0	1.0	8.5	50.0	70.0	24
Resting cysts, diameter without external layer (in vivo)	S	49.3	50.0	4.6	0.9	9.3	40.0	60.0	24

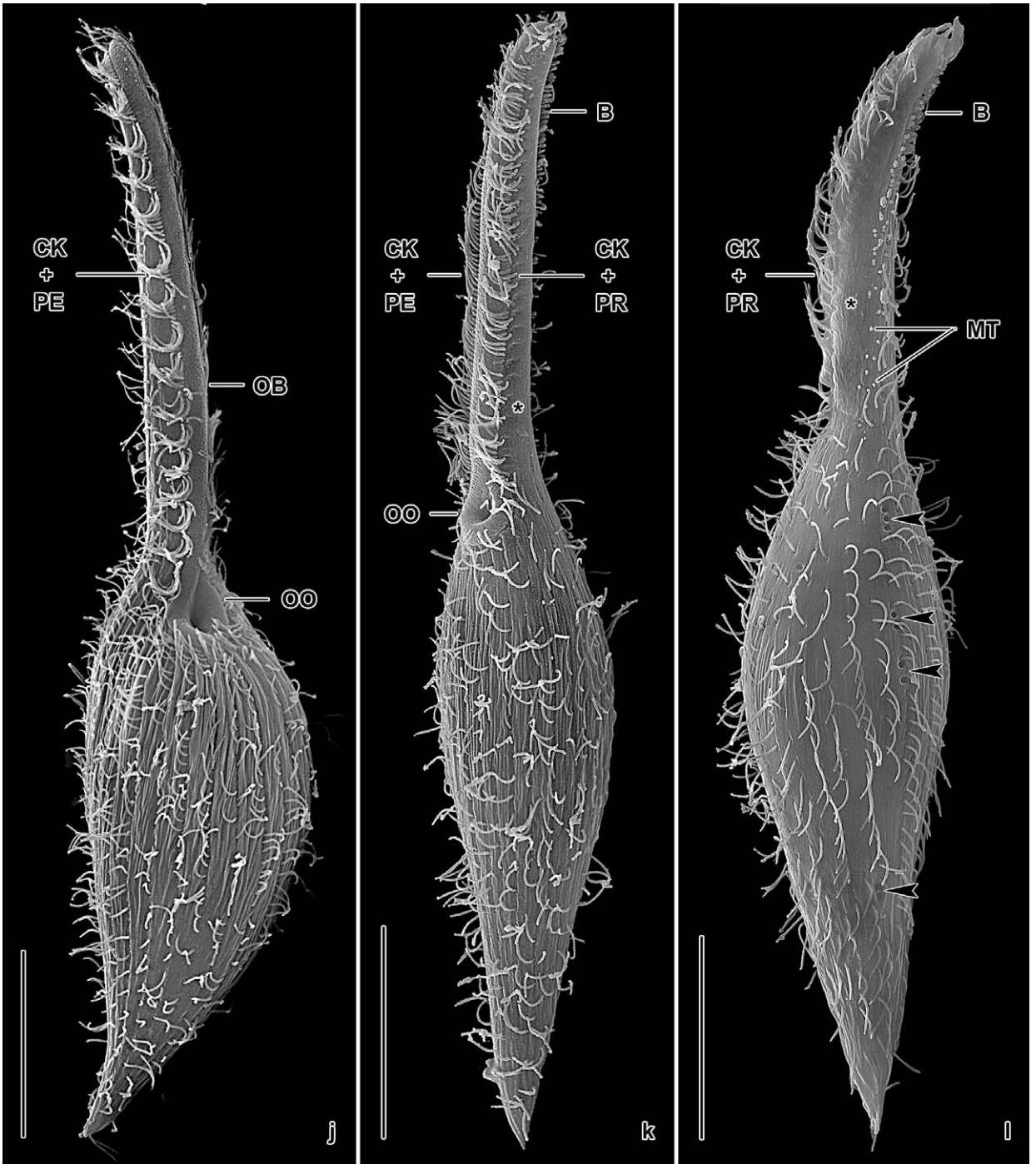
[a] Calculated from original data.



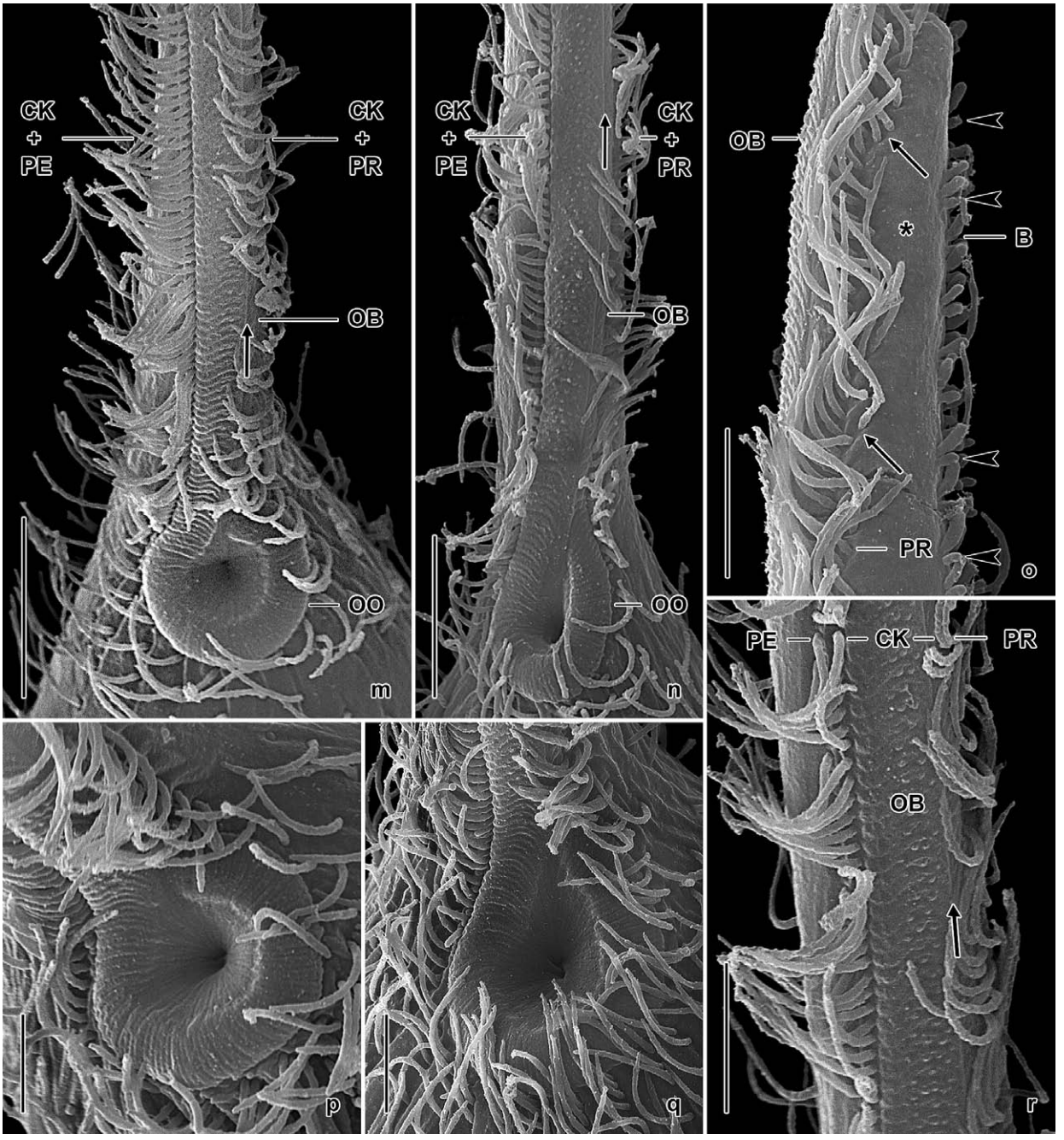
Figs 49a-o. *Monomacrocaryon terrenum* from life (a, d, f, g-j) and after protargol impregnation (b, c, e, k-o). From Foissner 1981 (a, b, f, k) and 1984 (l, m), Tirjaková & Matis 1985 (i, j), Vďačný & Foissner 2009 (c, e, n, o), and originals (d, g, h). Asterisks denote blank stripe on left side of proboscis. **a** – left side view of a representative Austrian specimen, length 425 µm; **b** – ciliary pattern of left side and nuclear apparatus of holotype specimen, length 267 µm; **c** – left side ciliary pattern of proximal proboscis area; **d** – resting cysts are about 60 µm across and have two distinct layers. Arrowhead marks an accumulation of granular material in the external cyst layer; **e, k** – ventral view of oral ciliature; **f** – cortical granulation; **g** – Austrian, Namibian and Peruvian specimens have two size types (4–8 µm and 2 µm) of rod-shaped extrusomes; **h** – in a Galapagian, North American and another Namibian population, the type I extrusomes are very narrowly ovate and 5–7 µm long; **i, j** – Mongolian specimens, length 530 µm and 560 µm; **l, m** – left and right side view of proboscis' ciliary pattern; **n** – dorsal view of proboscis, showing the staggered brush rows connected by minute dots; **o** – ciliary pattern of right side and nuclear apparatus of a Peruvian specimen, length 318 µm. B – dorsal brush, CF – central fibre, CK – circumoral kinety, EB – external basket, EL – external cyst layer, IB – internal basket, IL – internal cyst layer, MA – macronucleus, MI – micronucleus, ML – mucous layer, OB – oral bulge, OO – oral bulge opening, PE – perioral kinety, PR – preoral kineties, SK – somatic kinety. Scale bars: 20 µm (c, e, n), 30 µm (l, m), 50 µm (b, k, o), 100 µm (a), and 200 µm (i, j).



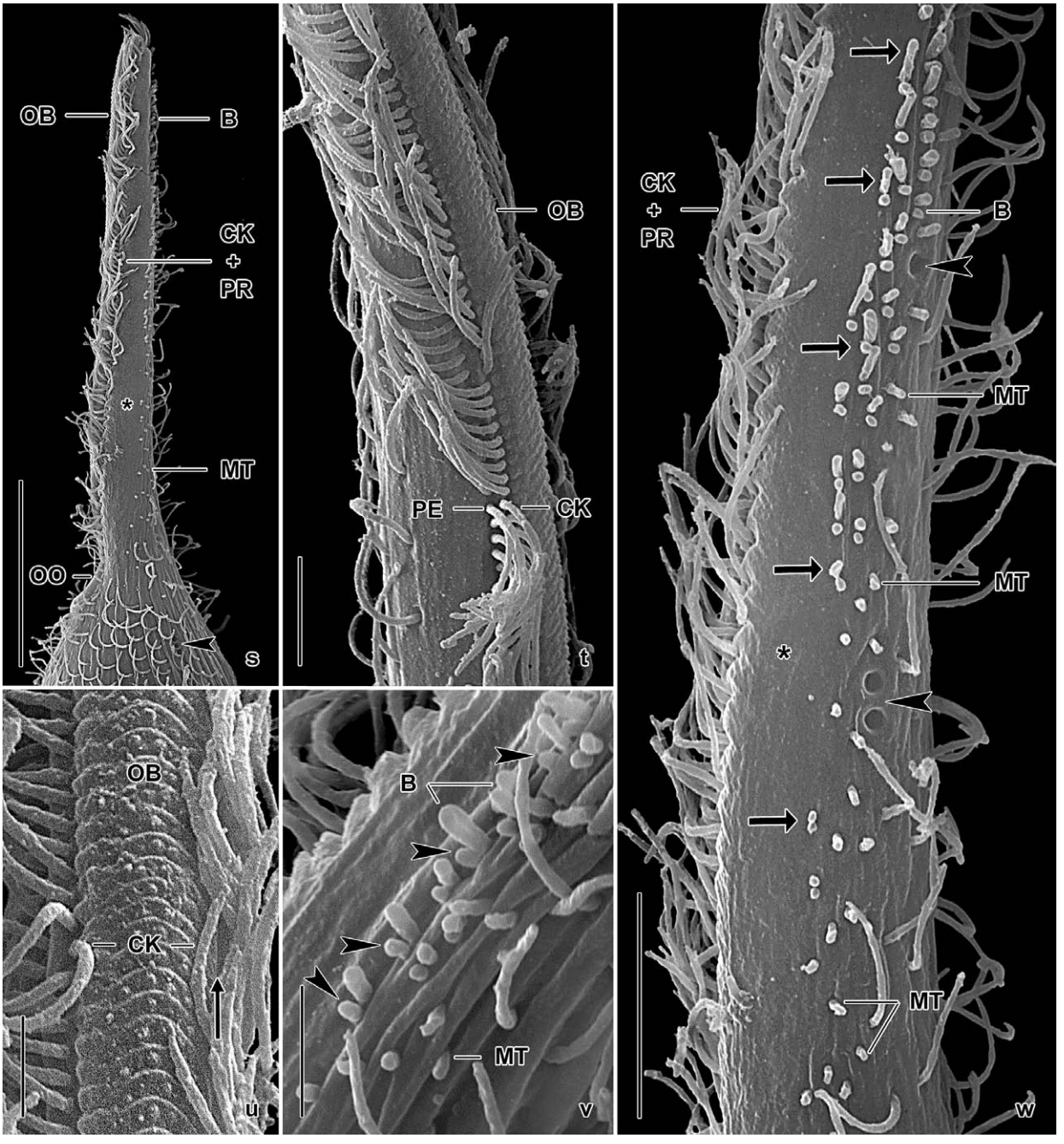
Figs 50a-i. *Monomacrocaryon terrenum*, Upper Austrian specimens from life. **a** – overview showing the narrowly dileptid body with the acute posterior end and the cylindroidal, curved macronucleus, the most important feature of the genus *Monomacrocaryon*; **b** – optical section of a squeezed specimen, showing some main cytoplasmic organelles, such as the cylindroidal macronucleus, some dorsal contractile vacuoles, and food vacuoles; **c, d** – type I extrusomes are rod-shaped with rounded ends and about 8 µm long; **e** – type II extrusomes are oblong and 2–3 µm long; **f-i** – the resting cysts are simple globes with an average diameter of about 60 µm. The cyst wall is composed of two distinct layers: the external layer is hyaline and 7–13 µm thick, while the internal layer is honey brown, compact, and 1–2 µm thick. Sometimes there is an accumulation of granular, mucous material in the external cyst layer (arrowhead). The cyst wall is covered by an up to 10 µm thick, mucous layer with adhering bacteria and debris. The cytoplasm is packed with 0.7–1 µm-sized granules becoming more or less regularly arranged underneath the cortex (f-h). The macronucleus is in cyst centre, curved or slightly tortuous, and about 55 µm long when uncoiled, and thus shorter than in vegetative specimens by about one third. Extrusomes, contractile vacuoles, cilia, and the oral basket are not recognizable. CV – contractile vacuoles, EL – external cyst layer, FV – food vacuoles, IL – internal cyst layer, MA – macronucleus, ML – mucous layer, OO – oral bulge opening. Scale bars: 50 µm (b, f-i) and 100 µm (a).



Figs 50j-l. *Monomacrocaryon terrenum*, Upper Austrian specimens in the SEM. Ventrolateral (j, k) and dorsolateral (l) overviews, showing the proboscis occupying about 37% of body length and the bluntly fusiform trunk narrowing in posterior third. Note the nice metachronal waves formed by perioral and circumoral cilia on the right side of the proboscis (j) and by preoral and circumoral cilia on the left (k). Asterisks denote the blank stripe on the left side of the proboscis, i.e., between preoral kineties and dorsal brush. Arrowheads mark the excretory pores of the contractile vacuoles. B – dorsal brush, CK – circumoral kinety, OB – oral bulge, OO – oral bulge opening, MT – monokinetidal tails of dorsal brush, PE – perioral kinety, PR – preoral kineties. Scale bars: 30 μm.



Figs 50m-r. *Monomacrocaryon terrenum*, Upper Austrian specimens in the SEM. **m, n, p, q** – oral ciliature and circular oral bulge opening. Note that the oral opening appears ovate when viewed obliquely (n, q). Arrows mark furrow separating the broad right branch of the oral bulge from the very narrow left branch; **o** – left side view of distal proboscis area, showing the preoral kineties (arrows) and the dorsal brush extending to the tip of the proboscis. The brush dikinetids are associated with an 1.3–1.8 µm long anterior bristle and an 0.8 µm long posterior stump (arrowheads). Asterisk marks the broad blank stripe between the preoral kineties and the dorsal brush; **r** – the oral bulge is dotted by the extrusome tips and transversely striated by fibre bundles, very likely transverse microtubule ribbons. Note the metachronal ciliary waves formed by the oral cilia left and right of the oral bulge. Arrow marks the furrow separating the bulge branches. B – dorsal brush, CK – circumoral kinety, OB – oral bulge, OO – oral bulge opening, PE – perioral kinety, PR – preoral kineties. Scale bars: 5 µm (o-r) and 10 µm (m, n).



Figs 50s–w: *Monomacrocaryon terrenum*, Upper Austrian specimens in the SEM. **s** – left side view of anterior body portion, showing the conspicuous blank stripe left of the oral bulge (asterisk). Arrowhead denotes excretory pores; **t** – right side view of proboscis' ciliary pattern. The circumoral and perioral kinety extend side by side and are composed of narrowly spaced cilia beating together; **u** – the oral bulge is dotted by the extrusome tips and transversely striated by fibre bundles. Arrow marks furrow separating the broader right from the narrower left branch of the bulge; **v** – the brush dikinetids are associated with an 1.3–1.8 µm long anterior bristle and an 0.8 µm long posterior stump (arrowheads); **w** – dorsolateral view of proboscis, showing the middle part of the dorsal brush consisting of staggered rows of dikinetidal bristles (arrows) anteriorly and monokinetidal bristles (MT) posteriorly. Asterisk marks the blank stripe between the preoral kineties and the dorsal brush. Arrowheads denote excretory pores of contractile vacuoles. B – dorsal brush, CK – circumoral kinety, MT – monokinetidal tails of dorsal brush, OB – oral bulge, OO – oral bulge opening, PE – perioral kinety, PR – preoral kineties. Scale bars: 3 µm (u, v), 5 µm (t), 10 µm (w), and 30 µm (s).

Nomenclature: According to Articles 30.2.4, 31.2 and 34.2 of the ICZN (1999), we emend *Monomacrocaryon terrenus* to *M. terrenum* nom. corr. because *Monomacrocaryon* is neuter gender.

Improved diagnosis (includes all information known): Size about 370 × 45 µm in vivo. Shape narrowly to very narrowly dileptid with gradually narrowed posterior region, proboscis about 37% of body length. Macronucleus cylindroidal and often curved, accompanied by a single micronucleus. A dorsal stripe of contractile vacuoles with usually two pores each. Two types of extrusomes attached to proboscis oral bulge: type I rod-shaped to slightly ovate, 4–8 µm long; type II oblong, 1.5–3 µm long. On average 28 ciliary rows, up to 7 anteriorly differentiated to a staggered, distinctly heterostichad dorsal brush with monokinetidal tails extending to second third of body. Oral bulge opening about 15 µm across. On average 47 oblique, widely spaced preoral kineties, each composed of 2–3 narrowly spaced cilia.

Type locality: Floodplain soil from a meadow in the vicinity of the village of Fusch an der Glocknerstrasse, Central Alps (Grossglockner area), Austria, E12°49' N47°13'.

Type and voucher material: Deposition of type material not mentioned in the original paper (Foissner 1981). One voucher slide (inv. no. 1984/72; mislabelled as "paratype") with protargol-impregnated specimens described by Foissner (1984) has been deposited in the Biology Centre of the Museum of Upper Austria, Linz (LI). Vďačný & Foissner (2009) have deposited four voucher slides (inv. nos 2011/319–322) with Peruvian (Titicaca Lake) protargol-impregnated morphostatic and dividing specimens in the same repository. Relevant specimens are marked by black ink circles on the coverslip.

Gene sequence: The 18S rRNA gene sequence of an Upper Austrian population (Figs 49d, 50a–w) has been deposited in GenBank (HM581674). The sequence is 1639 nucleotides long and has a GC content of 42.5%. It is a consensus sequence based on 18 clones.

Etymology: Not given in original description. The Latin adjective *terrenus* (living in soil) obviously refers to the habitat in which the species was discovered.

Description: Size in vivo highly variable in various populations, i.e., 180–560 × 35–65 µm, usually about 370 × 45 µm: Austrian type specimens 400–450 × 40–50 µm (Foissner 1981), Mongolian cells 530–560 µm long (Tirjaková & Matis 1985). Size after protargol impregnation: Austrian voucher specimens 152–350 × 32–56 µm (Foissner 1984), Peruvian cells 226–315 × 34–56 µm (Vďačný & Foissner 2009). Body very flexible but not contractile. Shape narrowly to very narrowly dileptid, i.e., length:width ratio 2.7–8.1:1 after protargol impregnation (Table 24). Proboscis about 37% of body length, usually curved dorsally; trunk bluntly fusiform with gradually narrowed posterior third, in a single Mongolian specimen posterior end abruptly narrowed (Figs 49a, b, i, j, 50a, j–l). Nuclear apparatus in mid-portion of trunk. Macronucleus oblong to rod-shaped, often curved or slightly tortuous, sometimes Y-shaped in Peruvian specimens (Fig. 49o), about 80 µm long in "uncoiled" condition; nucleoli medium-sized, globular. Micronucleus usually attached to mid-macronucleus, size similar between populations, viz., 2–4 µm across (Figs 49a, b, i, o, 50a, b; Table 24). A stripe of dorsal contractile vacuoles, first vacuole in mid-proboscis; number of excretory pores per vacuole rather variable even in a single cell, viz., one to three, usually two intrakinetal pores one after the other (Figs 49a, i, o, 50b, l, s, w). Two types of extrusomes attached to right broader branch of proboscis oral bulge: type I rod-shaped with rounded ends, 8 µm long in Austrian type specimens, 5–8 × 0.8 µm in size in Namibian cells, and 4 µm long in Peruvian specimens (Figs 49g, 50c, d), while slightly ovate and asymmetrical in populations from the Galapagos Islands (6–7 × 0.4–0.6 µm), Namibia (5–7 × 0.5–0.8 µm, another population than that mentioned above), and North America (6 × 0.8 µm, Fig. 50h); type II extrusomes oblong, 1.5–3 × 0.3–0.5 µm in size (Figs 49g, h, 50e). Cortex very flexible, slightly furrowed by ciliary rows; between each two kineties about three rows of oblong granules possibly contained in the interkinetal, oblique ridges sometimes distinct in SEM micrographs (Figs 49f, 50j, k). Cytoplasm colourless, hyaline in proboscis, opaque in trunk because packed with globules about 3

µm across and several 20 µm-sized food vacuoles with indeterminable contents. Swims slowly and roots between soil particles.

Cilia about 12 µm long in vivo, shrunken to 6 µm in SEM, narrowly spaced; in protargol preparations as typical for dileptids, i.e., with thick, deeply impregnated distal half, except for dorsal bristles. Ciliary rows ordinarily spaced, number fairly similar between populations: 26–33 in Austrian type specimens, 26–27 in voucher Austrian specimens, and 24–31 in Peruvian cells (Table 24). Right side ciliary rows gradually shortened in anterior half of proboscis; perioral kinety extends to tip of proboscis with ordinarily to narrowly spaced basal bodies (Figs 49m, o, 50t). Left side of proboscis with conspicuous blank stripe because most ciliary rows end at level of oral bulge opening (Figs 49c, e, l, 50l, o, s, w). Dorsal brush on dorsal and dorsolateral region of proboscis; staggered; distinctly heterostichad; composed of up to seven rows of loosely spaced dikinetids associated with type II bristles: anterior bristle of dikinetids 1.3–1.8 µm long, posterior bristle 0.6–0.8 µm long in SEM (Figs 49l, n, 50l, o, v, w). All brush rows continue with a monokinetidal tail extending to base of proboscis with 0.8 µm long type VI bristles (Figs 49l, s, v, w).

Oral bulge opening at beginning of second body third, projects distinctly, circular when viewed frontally (Figs 49e, 50m, p), while ovate when viewed obliquely (Figs 50n, q), about 10–13 µm across in SEM. Pharyngeal basket obconical, about 23 µm long after protargol impregnation in type specimens, without specific features (Figs 49b, c, e, l, m, o). Foissner (1984), additionally, figured fibres originating from the proboscis dikinetids and extending posteriorly to form a loose funnel (Figs 49l, m). Oral bulge distinct in SEM micrographs due to nice metachronal ciliary waves formed by perioral and circumoral cilia on the right (Figs 50j, r) and by preoral and circumoral cilia on the left (Figs 50k, r); right branch much broader than left and dotted by extrusome tips (Figs 50n, r, u). Circumoral kinety composed of ordinarily to narrowly spaced dikinetids in proboscis and narrowly spaced monokinetids around oral bulge opening (Figs 49c, e). On average 47 oblique, widely spaced preoral kineties extending in distinct furrows, each kinety composed of two to three narrowly spaced cilia (Figs 49c, e, k, l, 50k, o, w).

Resting cyst (Figs 49d, 50f–i; Table 24): All Upper Austrian specimens encysted when transferred from the non-flooded Petri dish culture onto a microscope slide with a concave depression containing Eau de Volvic. Three day-old resting cysts 60 µm across in vivo; globular to rotund, i.e., length:width ratio 1–1.2:1; honey brown; without escape apparatus. Cyst wall made of two distinct layers: external layer 7–13 µm thick, hyaline and colourless, with an extra membrane in half of cysts and with an accumulation of granular, mucous material in one third of cysts (Figs 49d, 50g, arrowhead); internal layer 1.2 µm thick, becoming 2 µm thick when cyst is pressed by the coverslip, honey brown, compact. Cyst wall covered by an up to 10 µm thick, hyaline, colourless mucous layer. Cytoplasm packed with 0.7–1 µm-sized granules becoming more or less regularly arranged underneath cortex. Macronucleus in cyst centre, curved or slightly tortuous, about 55 µm long when uncoiled, and thus shorter than in vegetative specimens by about one third. Extrusomes, contractile vacuoles, cilia, and the oral basket not recognizable.

Occurrence and ecology: *Monomacrocaryon terrenum* was discovered by Foissner (1981) in floodplain soil from a pasture meadow in the vicinity of the village of Fusch an der Glocknerstrasse, Austrian Central Alps, about 880 m above sea level. A voucher population was found in soil from the Tullnerfeld, Lower Austria (Foissner 1984). Another voucher population came from soil in the outskirts of the town of Selker, Upper Austria (Figs 49d, 50a–w; Vďačný et al. 2011b). There are several records from terrestrial and semi-terrestrial habitats all over the world: in agricultural soils and in terrestrial mosses from Slovakia (Tirjaková 1988, 2005); in soil from Apsheron Peninsula, Azerbaijan (Alekperov & Musayev 1988); in the upper 0–5 cm soil layer covered with semi-desert vegetation, Bulgansomon, Mongolia (Tirjaková & Matis 1985); in seven out of 73 sites investigated in Namibia, Southwest Africa (Foissner et al. 2002); in an up to 10 cm thick accumulation of washed-up plant debris, including filamentous algae, macrophytes, duckweeds, and

some soil at the bank of the Titicaca Lake near the town of Puno, Peru (Vďačný & Foissner 2009); in soil from the Galapagos Islands and North America (unpublished observations). *Monomacrocaryon terrenum* is possibly a cosmopolitan restricted to terrestrial and semiterrestrial habitats.

Remarks: *Monomacrocaryon terrenum* is easily distinguished from the congeners by the dorsal stripe of at least five contractile vacuoles, whereas *M. tenue* has only two vacuoles, and *M. gigas* and *M. polyvacuolatum* possess also ventral vacuoles.

After the description of Foissner (1981), this species has been studied in populations from different biogeographic regions (Foissner 1984, Tirjaková & Matis 1985, Vďačný & Foissner 2009, and unpublished observations). All are similar in body shape and size as well as the nuclear and contractile vacuole pattern. However, they differ in extrusome shape (see above), indicating two different taxa.

Monomacrocaryon gigas (Claparède & Lachmann, 1859) Vďačný, Orsi, Bourland, Shimano, Epstein & Foissner, 2011 (Figs 51a–d)

1859 *Amphileptus gigas* Claparède & Lachmann, Mém. Inst. natn. génev. **6**: 349

1881 *Amphileptus gigas*, C. & L. – Kent, Manual infusoria II: 524 (brief review; without figures)

1931 *Dileptus* (*Amphileptus*) *gigas* (Clap. u. L., 1859) – Kahl, Tierwelt Dtl. **21**: 207 (first taxonomic reviser; combining author)

1963 *Dileptus gigas* (Clap. et Lachm., 1859) – Dragesco, Bull. biol. Fr. Belg. **97**: 114 (second taxonomic reviser)

1988 *Dileptus gigas* (Claparède & Lachmann, 1859) – Foissner, Hydrobiologia **166**: 38 (saprobic classification)

2011 *Monomacrocaryon gigas* (Claparède & Lachmann, 1859) comb. n. – Vďačný, Orsi, Bourland, Shimano, Epstein & Foissner, Eur. J. Protistol. **47**: 310

non *Dileptus gigas grojecensis* – Wrześniowski, 1870, Wiss. Zool. **20**: 504 (see *Pseudomonilicaryon anser*)

non *Dileptus gigas varsaviensis* – Wrześniowski, 1870, Wiss. Zool. **20**: 504 (see *Dileptus margaritifer*)

non *Dileptus gigas* C. & L. – Conn, 1905, Fresh-water protozoa: 46 (see *Pseudomonilicaryon kahli*)

non *Dileptus gigas* – Holmes, 1907, Biol. Bull. **13**: 307 (see *Pseudomonilicaryon anser*)

non *Dileptus gigas* – Hausman, 1917, Am. Naturalist **51**: 168 (see *Pseudomonilicaryon anser*)

non *Dileptus gigas* – Visscher, 1923, Biol. Bull. mar. biol. Lab., Woods Hole **45**: 113 (see *D. margaritifer*)

non *Dileptus gigas* – Visscher, 1927, J. Morph. **44**: 373 (see *D. margaritifer*)

non *Dileptus gigas* – Visscher, 1927, J. Morph. **44**: 383 (see *D. margaritifer*)

non *Dileptus gigas* – Studitsky, 1930, Arch. Protistenk. **70**: 155 (see *D. margaritifer*)

non *Dileptus gigas* – Peschkowsky, 1931, Arch. Protistenk. **73**: 1179 (see *D. margaritifer*)

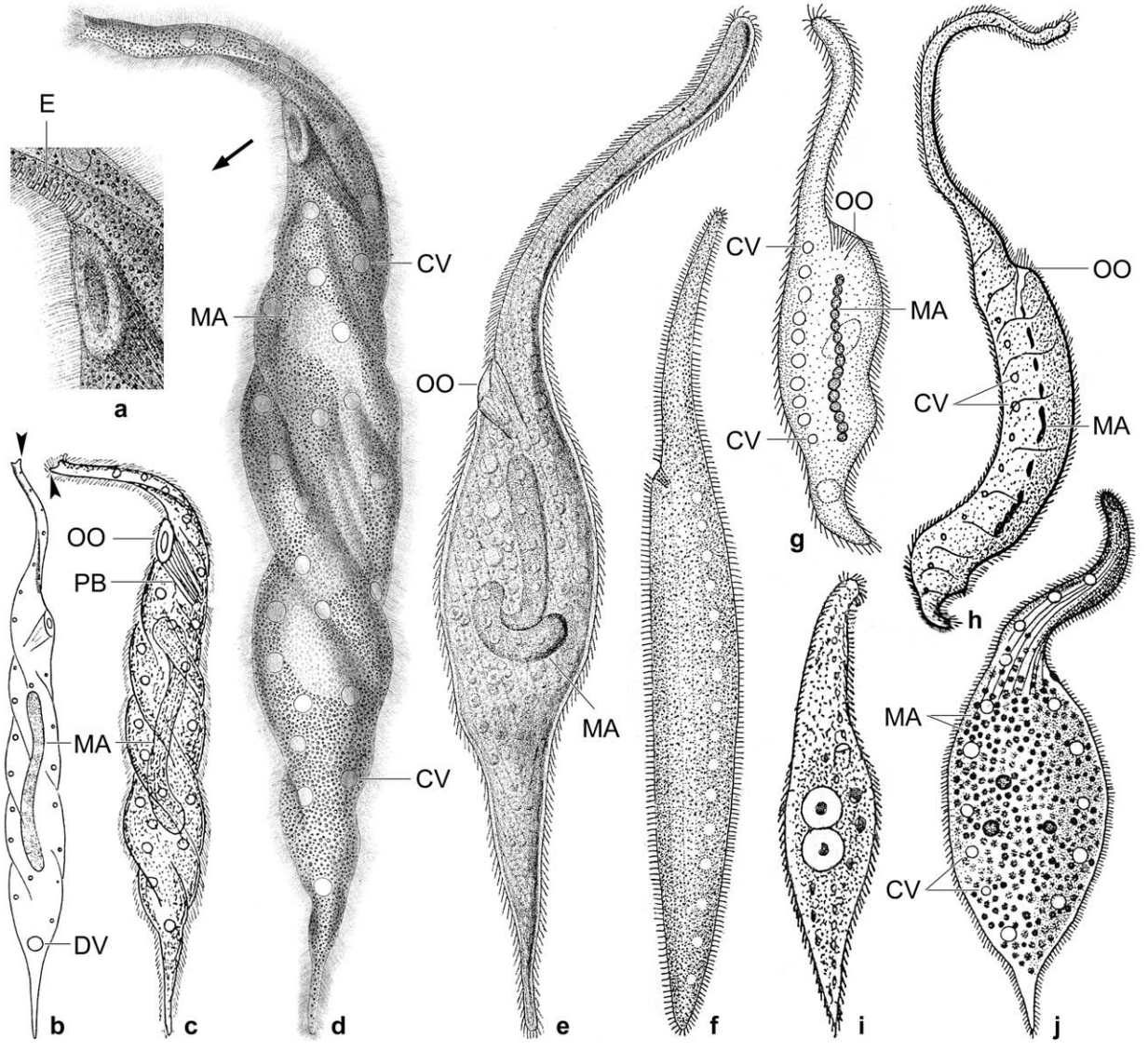
non *Dileptus gigas* (Clap. et L.) – Dragesco & Métain, 1948, Bull. Soc. Zool. Fr. **73**: 62 (see *D. margaritifer*)

non *Dileptus gigas* Claparède & Lachmann, 1859 – Lokot', 1987, Ecology of ciliated protozoa: 34 (see insufficiently described dileptids)

Generic affiliation, nomenclature, and taxonomy: *Monomacrocaryon gigas* was originally described as *Amphileptus gigas* by Claparède & Lachmann (1859). Kahl (1931) combined it with *Dileptus* due to the dileptid habitus but erroneously classified *Amphileptus* as a subgenus of *Dileptus*. Vďačný et al. (2011b) assigned it to *Monomacrocaryon* because of the unsegmented macronucleus.

Misspelled as "*D. gigus*" by Stehle (1923) and "*D. gygas*" by Aliev (1988), and thus unavailable according to Articles 33.3 and 33.5 of the ICZN (1999).

Several authors erroneously considered *D margaritifer* as a synonym of *Monomacrocaryon gigas* (see



Figs 51a–j: *Monomacrocaryon gigas* (a–d) and dileptids misidentified as *Dileptus gigas* (e–j) from life. **a** – detail of oral region, showing the oblong extrusomes attached to the proboscis oral bulge (from Claparède & Lachmann 1859); **b, c** – redrawings of German type specimen by Dragesco (1963) and Kahl (1931). Arrowheads denote the proboscis papilla; **d** – German type specimen, length 1 mm (from Claparède & Lachmann 1859); **e** – Kansas specimen, size not given (from Smith 1914); **f** – Iowan specimen, size not given (from Edmondson 1906); **g** – Michigan specimen, size not given (from Lundin & West 1963); **h** – North American specimen, size not given (from Hausman 1917); **i** – Pakistani specimen, size not given (from Gulati 1925); **j** – Chinese specimen, length 747 µm (from Tai 1931). CV – contractile vacuoles, DV – defecation vacuole, E – extrusomes, MA – macronucleus, OO – oral bulge opening, PB – pharyngeal basket.

synonymy list). However, *Dileptus margaritifer* has a much smaller (usually 450 µm vs. 1000–1600 µm), untwisted body; many scattered macronuclear nodules (vs. sigmoidal macronucleus); and only dorsal contractile vacuoles (vs. ventral and dorsal ones). Wrześniowski (1870) misidentified *D anser* (now *Pseudomonilicaryon anser*) as *Monomacrocaryon gigas*. However, *Pseudomonilicaryon anser* is much smaller (250–600 µm vs. 1000–1600 µm) and has a much longer proboscis (1/2 vs. 1/5 of body length) and

a moniliform macronucleus. Stokes (1888) suggested *Phragelliorhynchus nasutus* as a junior synonym of *Monomacrocaryon gigas*; Kahl (1931) and Dragesco (1963) followed. However, we disagree because *Ph. nasutus* is much smaller (200 µm vs. 1000–1500 µm) and has at least a dozen macronuclear nodules (vs. unsegmented macronucleus).

Monomacrocaryon gigas should be easy to identify because it is the largest dileptid known being up to 1.6 mm long! In spite of this and several unique traits (twisted body, a dorsal papilla at the tip of the proboscis, and a sigmoidal macronucleus), *M. gigas* has been never redescribed. There is only one other species with twisted body, viz., *Dileptus spiralis*, which is much smaller (300 µm vs. 1.6 mm) and whose body spiralization was possibly caused by mercuric chloride fixation. Full redescription is required.

Diagnosis (type population): Length about 1300 µm in vivo. Body twisted and very narrowly dileptid with distinct tail, proboscis about 1/5 of body length and with a papilla at tip. Macronucleus sigmoidal. Many scattered contractile vacuoles in trunk and proboscis.

Type locality: Freshwater in Berlin, Germany, E13°24' N52°31'.

Type material: Not available.

Etymology: Not given in original description. We consider the Greek *gigas* (giant) as a noun in apposition, obviously referring to the large size of the species.

Description of type population: Length 1000–1600 µm in vivo; very flexible but not contractile. Body twisted and very narrowly dileptid with a length:width ratio of about 8:1, according to the figure provided. Proboscis occupies one fifth of body length, with a dorsal papilla at the tip, slightly flattened, indistinctly set off from massive, fusiform trunk; tail distinct. Macronucleus sigmoidal with a length:width ratio of about 7.5:1, both ends slightly inflated. At least 50 contractile vacuoles scattered in trunk and dorsal side of proboscis (Figs 51b–d). Extrusomes attached to proboscis oral bulge, according to the original description similar to the trichocysts of *Paramecium aurelia*, i.e., bluntly fusiform, but figured as slightly curved rods (Fig. 51a). Pharyngeal basket obconical, conspicuous because long and composed of comparatively thick rods. Ciliature not studied. Swims majestically folding the trunk or glides slowly between algae.

Division: This was studied by Rudin (1937) in clonal cultures but the identity of this species is questionable. Depending on temperature, there were 0.3 to 1.4 divisions per day.

Occurrence and ecology: Claparède & Lachmann (1859) discovered *Monomacrocaryon gigas* in freshwater from Berlin, Germany. There are rather many unsubstantiated records, which we doubt because we never met this species. This is, for instance, obvious from several illustrations (Figs 51e–j) and the description of Holmes (1907): "*Dileptus gigas* commonly adheres to the surface of some solid object and waves its long proboscis-like anterior extremity or neck about in an anti-clockwise direction" (cp. *Pseudomonilicaryon anser* and *P. fraterculum*).

Records from limnetic habitats: in the aerobic sediment of a eutrophic lake in England (Webb 1961); water bodies of Arequipa, France (Escomel 1929; only 100–110 µm long and thus a misidentification); in a bog pond of France (Grolière & Njiné 1973); ponds in the surroundings of the town of Neuchâtel, Switzerland (Bourquin-Lindt 1919) and other Swiss localities (Baldensperger 1927); rare in the Lugana Lake in Switzerland (Fehlmann 1912); possibly in the surroundings of the town of Munich, Germany (Popoff 1908; very likely this is *D. margaritifer* because it has hundreds macronuclear nodules and a body size of 500–1000 µm); Italy (Dini et al. 1995); reported also in the databank of the Czech and Slovak Fauna (Šrámek-Hušek 1952, Matis et al. 1996); town of Budapest, Hungary (Krepuska 1917); Danube estuary (Spandl 1926); infrequent in Ukrainian reservoirs of the Seversky Donets basin (Kravchenko 1969); running waters and reservoirs in the former USSR (references in Lokot' 1987); cooling plant in Moldavia (Chorik & Vikol 1973); in the benthos of Lake Dzandar, Azerbaijan (Aliev 1988; misspelled as

D. gygas); in the summer plankton of the River Moscow, Russia (Belova 1998); saline lakes near Odessa, Russia (Boutchinsky 1895); clear pools near the River Ravi and pools in an ephemeral river in Lahore, Pakistan (Bhatia 1924, Gulati 1925, a misidentification according to the figure provided, Fig. 51i); pond in west campus of Tsing Hua University, Peiping, China (Tai 1931; a misidentification because it has many macronuclear nodules, Fig. 51j); freshwater bodies in Japan (Edmondson & Kingman 1913); in stagnant water between *Ceratophyllum* and *Utricularia*, USA (Stokes 1886, 1888); in several water bodies of the Upper Peninsula of Michigan, USA (Moore 1939; Lundin & West 1963, a misidentification according to the figure provided, Fig. 51g) and Oklahoma, USA (Gabel 1927); in summer ponds in the Tahquamenon State Park, Michigan, USA at 20 °C and pH 6.5 (Cairns & Yongue 1966); Lake Okoboji, Iowa, USA (Shawhan et al. 1947); ponds in Iowa, USA (Edmondson 1906, 1912; misidentification, possibly it is *Pseudomonilicaryon kahli*, Fig. 51f); rare in clear flowing waters with abundant plant life and in clear small pools with abundant decomposing organic sediment, USA (Hausman 1917; misidentification, very likely it is *P. anser*, Fig. 51h); pond in the Mountain Lake region, Virginia, USA (Bovee 1960); common in ponds of Kansas, USA (Smith 1914; likely a misidentification because it has a much longer proboscis as shown in Fig. 51e); pond on shore of Lake Erie, Ohio, USA (Stehle 1923; misspelled as *D. gigus*); artificial pond in the surroundings of the town of Philadelphia, USA (Wang 1928); various water bodies in Wisconsin, USA (Noland 1925); in an activated sludge plant in the USA (Lackey 1938); in a campus pond of the University of Colorado, USA (Hamilton 1943).

Unsubstantiated records from terrestrial habitats: rice fields in Italy (Coppa 1921); various soils in Russia (Yakimoff & Zérèn 1924); the tobacco region in the south of the USSR (Dixon 1937); soil of New Jersey, USA (Fellers & Allison 1920); New South Wales, Australia and South Africa (Sandon 1927, as *Amphileptus gigas*).

Saprobic classification: Foissner (1988a) classified *M. gigas* as a beta-mesosaprobic ciliate with the following valencies: b = 7, a = 3, I = 4, SI = 2.3.

Monomacrocaryon polyvacuolatum (Foissner, 1989) Vďačný, Orsi, Bourland, Shimano, Epstein & Foissner, 2011 (Figs 52a–t; Table 25)

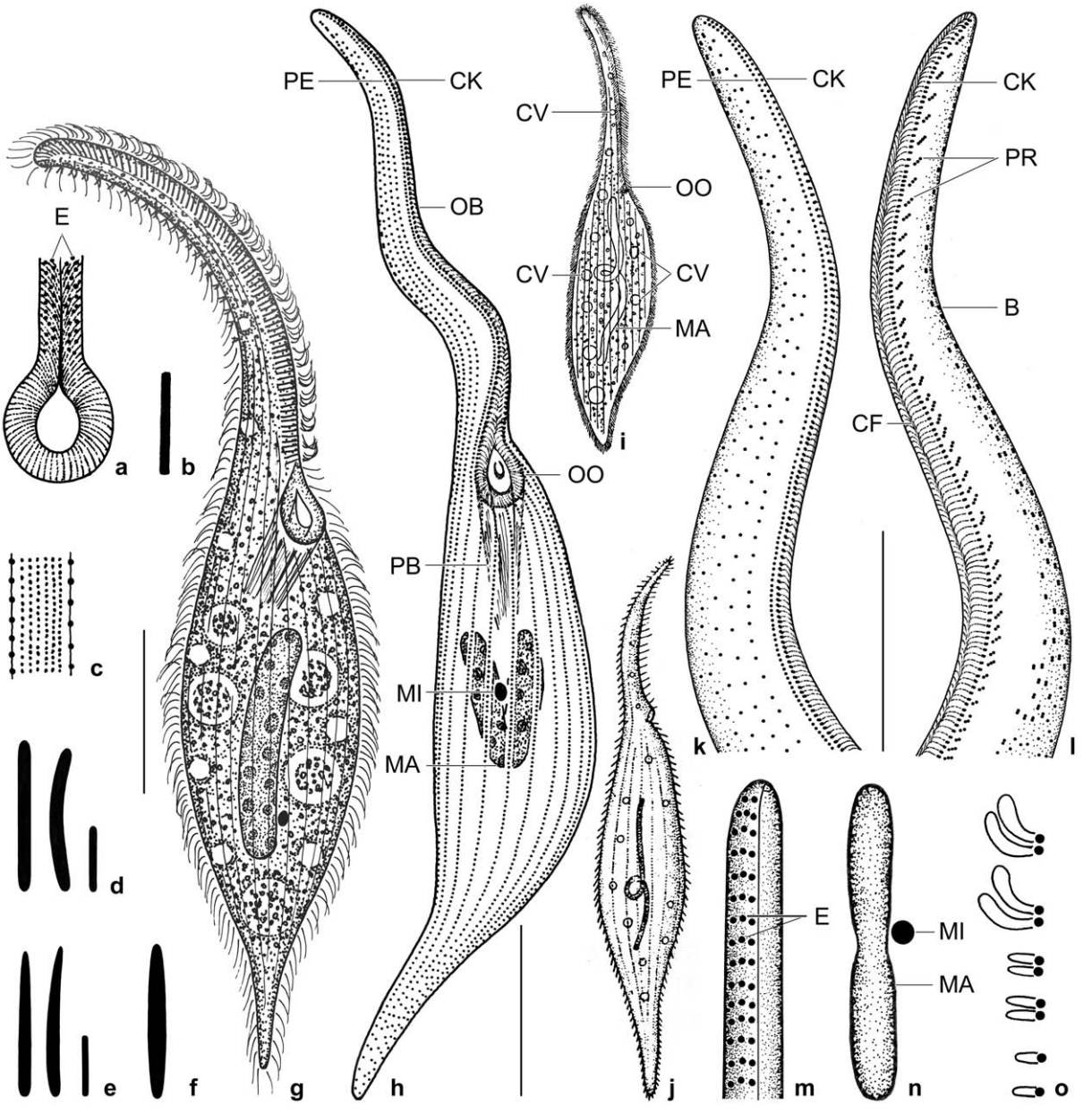
1936 *Dileptus anser* (O. F. Mueller) – Bhatia, Fauna of British India: 116 (misidentification)

1948 *Dileptus anser* O. F. Müll. – Stella, Riv. Biol. **40**: 144 (misidentification)

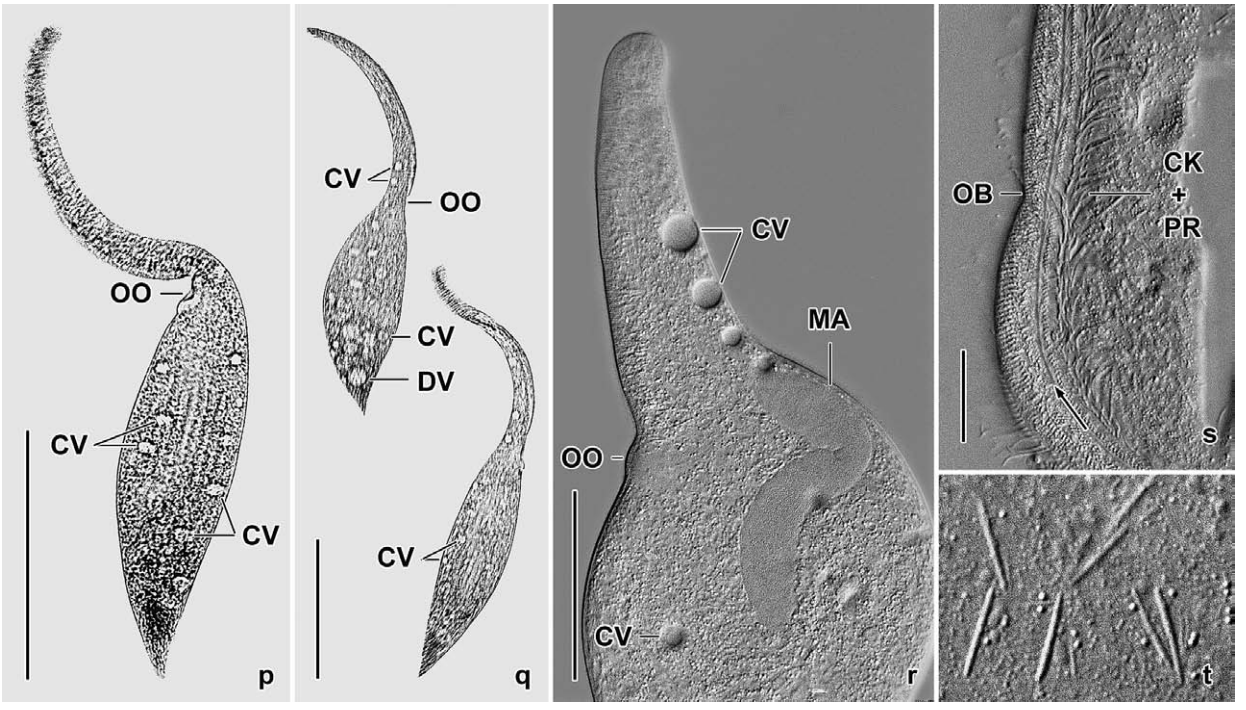
1989 *Dileptus polyvacuolatus* nov. sp. Foissner, Sber. Akad. Wiss. Wien **196**: 179

2011 *Monomacrocaryon polyvacuolatum* (Foissner, 1989) comb. n. – Vďačný, Orsi, Bourland, Shimano, Epstein & Foissner, Eur. J. Protistol. **47**: 310 (combining authors)

Taxonomy: Within the congeners, *M. polyvacuolatum* resembles only *M. terrenum*, which has, however, only dorsal contractile vacuoles (vs. also ventral ones). Bhatia (1936) described a population which resembles *M. polyvacuolatum* in body size (200–400 µm, respectively, 200–500 µm), the proportion of proboscis to body length (about 40%), and the contractile vacuole pattern (a dorsal and a ventral stripe of vacuoles). However, this population, which was found in a river from Punjab (Lahore, Pakistan), has a much longer, filiform, tortuous macronucleus (Fig. 52i). Bhatia (1936) identified the Pakistani population as *Dileptus anser*. However, this species has a moniliform macronucleus, a longer proboscis (55% vs. 40% of body length) and lacks ventral vacuoles. Possibly, Bhatia's population represents a distinct species. Stella (1948) found a population, which she also misidentified as *D. anser*, in forest soil from Italy. Stella's population matches *Monomacrocaryon polyvacuolatum* in body size (300 µm on average) and the contractile vacuole pattern, but differs in having a shorter proboscis and a much longer, filiform, tortuous macronucleus (Fig. 52j). Thus, her species is possibly also a distinct taxon. Therefore, neither Bhatia's nor Stella's observations are included in the diagnosis and description of *M. polyvacuolatum*.



Figs 52a–o: *Monomacrocaryon polyvacuolatum* (a–h, k–o) and a Pakistani (i) and an Italian (j) *polyvacuolatum*-like specimen from life (a–g, i, j, m–o) and after protargol impregnation (h, k, l). From Foissner 1989 (a–c, g, h, k, l), Bhatia 1936 (i), Stella 1948 (j), and originals (d–f, m–o). **a** – frontal view of oral bulge; **b** – extrusomes are rod-shaped and 5 µm long in Japanese type specimens; **c** – cortical granulation; **d** – African (Cotonau), Maldivian and Venezuelan specimens have two size-types (6 µm and 2 µm) of rod-shaped extrusomes; **e** – in Saudi Arabian and Austrian cells, type I extrusomes are slightly ovate and 6–7 µm long, while type II extrusomes are oblong and 2 µm long; **f** – slightly before explosion, the type I extrusomes of the African specimens become bluntly fusiform; **g** – right side view of a representative Japanese specimen, length 300 µm; **h** – ventrolateral view of ciliary pattern and nuclear apparatus of holotype specimen, length 320 µm; **i, j** – supposed *Dileptus anser*, length 200 µm and 300 µm; **k, l** – right and left side view of proboscis' ciliary pattern; **m** – in Saudi Arabian specimens, the extrusomes are attached only to the broader right branch of the proboscis oral bulge; **n** – a small portion of the Maldivian specimens has a rather pronounced constriction in the mid of the macronucleus and a single micronucleus close to that constriction; **o** – in Maldivian cells, there are three types of dorsal brush bristles. B – dorsal brush, CF – central fibre, CK – circumoral kinety, CV – contractile vacuoles, E – extrusomes, MA – macronucleus, MI – micronucleus, OO – oral bulge opening, OB – oral bulge, PB – pharyngeal basket, PE – perioral kinety, PR – preoral kineties. Scale bars: 30 µm (k, l) and 50 µm (g, h).



Figs 52p–t: *Monomacrocaryon polyvacuolatum*, Austrian (Salzburg) specimens from life (kindly supplied by Dr. Hubert Blatterer). **p, q** – overviews showing the narrowly dileptid body with a rather long proboscis and an acute posterior end. Note the ventral and dorsal contractile vacuoles, an important feature separating *M. polyvacuolatum* from *M. terrenum*; **r** – lateral view of a strongly squeezed specimen, showing the oblong macronucleus and some ventral and dorsal contractile vacuoles; **s** – ventrolateral view, showing the proboscis oral ciliature and oral bulge, which is transversely striated by fibre bundles. Arrow marks furrow separating the broader right from the narrower left branch of the oral bulge; **t** – the type I extrusomes are slightly ovate and about 8 µm long. CK – circumoral kinety, CV – contractile vacuoles, DV – defecation vacuole, MA – macronucleus, OB – oral bulge, OO – oral bulge opening, PR – preoral kineties. Scale bars: 10 µm (s), 30 µm (r), and 100 µm (p, q).

Improved diagnosis (excludes data from Bhatia 1936 and Stella 1948): Size about 300 × 45 µm in vivo. Shape narrowly to cylindroidally dileptid with distinct tail or acute posterior end, proboscis about 40% of body length. Macronucleus oblong to cylindroidal and often curved. A dorsal and a ventral stripe of contractile vacuoles. Two types of extrusomes attached to proboscis oral bulge: type I rod-shaped or slightly ovate, 4–8 µm long; type II oblong, 2–3 µm long. On average 28 ciliary rows; dorsal brush diffuse, staggered, all rows with a monokinetidal tail extending to base of proboscis. Oral bulge opening about 15 µm across. Preoral kineties oblique, ordinarily to widely spaced, each usually composed of 3 narrowly spaced cilia.

Type locality: Soil from a rice field about 30 km east of the town of Kumamoto, Japan, E130°41' N32°47'.

Type material: Foissner (1989) deposited one holotype slide (inv. no. 1988/96) and one paratype slide (inv. no. 1988/97) with protargol-impregnated specimens in the Biology Centre of the Museum of Upper Austria, Linz (LI). Relevant specimens are marked by black ink circles on the coverslip.

Etymology: Not given in original description. Composite of the Greek prefix *poly* (many) and the Latin noun *vacuola* (vacuole), referring to the many contractile vacuoles.

Description: After the original description, we studied this species in several populations from different biogeographic regions (unpublished observations). They were similar in body shape and size as well

Table 25: Morphometric data on *Monomacrocaryon polyvacuolatum* (from FOISSNER 1989). Data based on mounted, protargol-impregnated (Foissner's method), and randomly selected specimens from a non-flooded Petri dish culture. Measurements in µm. CV – coefficient of variation in %, M – median, Max – maximum, Mean – arithmetic mean, Min – minimum, n – number of specimens investigated, SD – standard deviation, SE – standard error of mean.

Characteristics	Mean	M	SD	SE	CV	Min	Max	n
Body, length	254.8	235.0	65.1	20.6	25.6	180.0	360.0	10
Body, width	39.8	38.0	8.1	2.6	20.4	29.0	56.0	10
Body length:width, ratio (calculated from original data)	6.5	6.2	1.8	0.6	27.3	3.9	9.5	10
Anterior body end to oral bulge opening, distance	104.3	99.0	28.5	9.0	27.3	63.0	145.0	10
Proboscis, % of body length (calculated from original data)	40.8	41.1	3.4	1.1	8.3	34.4	45.5	10
Oral bulge opening, diameter	15.5	15.5	1.4	0.5	9.2	14.0	17.0	10
Macronucleus, length	63.7	64.0	10.7	3.4	16.8	50.0	84.0	10
Macronucleus, width	9.6	9.5	1.0	0.3	10.1	8.0	11.0	10
Macronucleus nodules, number	1.0	1.0	0.0	0.0	0.0	1.0	1.0	10
Micronucleus, largest diameter	2.7	3.0	–	–	–	2.0	3.0	10
Micronucleus, number	1.0	1.0	0.0	0.0	0.0	1.0	1.0	10
Ciliary rows, number	28.7	28.0	3.9	1.2	13.7	24.0	39.0	10
Cilia in mid-body in 10 µm, number	6.2	6.0	1.2	0.4	19.8	5.0	9.0	10
Dorsal brush rows, number	4.0	4.0	0.0	0.0	0.0	4.0	4.0	7

as the nuclear and contractile vacuole pattern. However, they differed in extrusome shape (rod-like in Japanese, African, Maldivian and Venezuelan populations vs. slightly ovate in Saudi Arabian and Austrian populations) and arrangement (in broader right branch of Saudi Arabian and Austrian cells, while in both bulge branches of Japanese specimens which, however, might be a misobservation). Redescription with detailed morphometry and SEM observations (dorsal brush) recommended.

Size 200–500 × 30–60 µm in vivo, usually about 300 × 45 µm; very flexible but not contractile. Shape narrowly to cylindroidally dileptid, i.e., length:width ratio 3.9–9.5:1 after protargol impregnation (Table 25). Proboscis about 40% of body length, slightly flattened, usually curved dorsally, indistinctly set off from bluntly fusiform trunk; posterior end with distinct tail in Japanese type specimens, while acute in Austrian cells (Figs 52g, h, p, q). Macronucleus oblong to cylindroidal and often curved, in Maldivian specimens sometimes slightly constricted in mid, about 65 × 10 µm in size; nucleoli medium-sized, globular. Micronucleus attached to macronucleus at various positions, about 3 µm across in vivo (Figs 52g, h, n, r; Table 25). A stripe of contractile vacuoles each in ventral and dorsal side of cell, first dorsal vacuole in mid-proboscis, ventral stripe commences slightly posterior to oral bulge opening (Figs 52g, p–r). Two types of extrusomes attached to both proboscis oral bulge branches in Japanese type specimens (Fig. 52a; but see above), while only to broader right branch in Saudi Arabian and Austrian cells (Figs 52m, s): type I rod-shaped with rounded ends and slightly curved, 5 µm long in Japanese type specimens, 4–6 × 0.4 µm in African cells, 5–6 × 0.6 µm in Maldivian specimens, and 6–8 × 0.7 µm in Venezuelan individuals (Figs 52b, d), while slightly ovate and 6–7 × 0.6 µm in Saudi Arabian and Austrian specimens (Figs 52e, t); becomes bluntly fusiform before explosion in African specimens (Fig. 52f); type II oblong and 2–3 × 0.2–0.3 µm in size (Figs 52d, e). Cortex very flexible, contains about six granule rows between adjacent kineties (Figs 52c). Cytoplasm colourless, hyaline in proboscis, opaque in trunk because packed with many granules about 1 µm across and some food vacuoles containing heterotrophic flagellates (*Polytomella*). Glides moderately rapid on microscope slide.

Cilia about 8 µm long in vivo, narrowly spaced; in protargol preparations as typical for dileptids; arranged in about 28 ordinarily spaced, meridional rows (Table 25). Right side rows gradually shortened in anterior third of proboscis; perioral kinety extends to tip of proboscis with ordinarily to narrowly spaced basal bodies (Figs 52h, k). Left side of proboscis with rather broad blank stripe because most ciliary rows end at level of oral bulge opening (Fig. 52l). Dorsal brush on dorsal and dorsolateral region of proboscis; staggered; diffuse and very likely composed of four rows. Brush dikinetids very loosely spaced and associated with three types of bristles: type II bristles about 2 µm long and in anterior portion of rows, followed by some dikinetids with type III bristles and 1 µm long type VI monokinetidal tail bristles (Figs 52l, o; Table 25).

Oral bulge opening roundish, i.e., about 15 µm across in protargol preparations (Figs 52a, h; Table 25). Pharyngeal basket obconical, without specific features (Figs 52g, h). Circumoral kinety composed of ordinarily spaced dikinetids in proboscis and narrowly spaced monokinetids around oral bulge opening. Preoral kineties oblique, ordinarily to widely spaced, each composed of two to three narrowly spaced cilia (Fig. 52l).

Occurrence and ecology: Foissner (1989) discovered *M. polyvacuolatum* in soil (pH 5.7) from a rice field about 30 km east of the town of Kumamoto, Japan, where it was rather rare. Schade in Foissner (2000) found *M. polyvacuolatum* in artificial sand soil from sewage irrigation fields in Berlin-Buch and Brandenburg, Germany. Further unpublished records come from terrestrial and semiterrestrial habitats of Austria, Venezuela, Saudi Arabia, South Africa, and the Maldives, indicating that *M. polyvacuolatum* is a cosmopolitan. The Austrian population shown in Figs 52p–t is from a small road pool in the surroundings of Salzburg University.

Dimacrocaryon Jankowski, 1967

1967 *Dimacrocaryon* subg. n. Jankowski, Mater. IV Konf. uč. Sekc. zool. year **1967**: 36

1984 *Dimacrocaryon* Jankowski, 1967 – Foissner, Stapfia **12**: 90 (improved diagnosis; raise to genus level)

2001 *Dimacrocaryon* Jankowski 1967 – Aescht, Denisia **1**: 59 (catalogue of generic names of ciliates)

2007 *Dimacrocaryon* Jankowski, 1967 – Jankowski, Protista II: 571 (brief generic review)

2008 *Dimacrocaryon* Jankowski, 1967 – Lynn, Ciliated protozoa: 371 (list of genera)

Improved diagnosis: Small-sized Dimacrocaryonidae with narrow to very narrow body. Two macronuclear nodules. Dorsal brush staggered and two-rowed. Right branch of circumoral kinety accompanied by a perioral kinety, left branch by many slightly to strongly oblique preoral kineties. Oral bulge opening dileptid, i.e., ovate or elliptical and located ventrally, length ≥ 10 µm. Oral basket a sac-like structure lined by refractive granules.

Type species (by original designation): *Dileptus amphileptoides* Kahl, 1931.

Etymology: Not given in original description. Composite of the Greek numeral *di* (two), the adjective *makros* (large), and the noun *karyon* (nucleus), referring to the two macronuclear nodules. Neuter gender.

Remarks: Jankowski (1967) split *Dileptus* into several subgenera, according to the macronuclear pattern. *Dileptus amphileptoides* became type of *Dimacrocaryon*, i.e., of dileptids with two macronuclear nodules. Foissner (1984) doubted Jankowski's action but raised *D. amphileptoides* to genus level because of its special oral apparatus that did not show basket rods, not even in protargol preparations, and the oral bulge opening that was narrowly elliptical and surrounded by strongly refractive granules impregnating deeply with protargol. However, our transmission electronmicroscopical investigations showed a likely

ordinary oral basket (Figs 17a, b), but did not provide a reason for not impregnating with protargol in *D. amphileptoides* and the two new species described below. The granules covering the basket entrance are minute, oblong structures, possibly a special kind of mucocysts. Still, these granules are unique and an excellent genus identifier in vivo and in protargol preparations.

Key to Species

1 Oral bulge opening ovate ..... *D. brasiliense* (p. 162)
– Oral bulge opening very narrowly elliptical 2
2 Two types of extrusomes (oblong plus very narrowly ovate and asymmetric) ..... *D. arenicola* (p. 167)
– Only oblong extrusomes 3
3 Contractile vacuoles in ventral and dorsal side, 19 ciliary rows on average ..... *D. amphileptoides amphileptoides* (p. 169)
– Contractile vacuoles in a dorsal stripe, 27 ciliary rows on average ..... *D. amphileptoides paucivacuolatum* (p. 178)

Dimacrocaryon brasiliense nov. sp. (Figs 53a–o, 54c–h; Table 26)

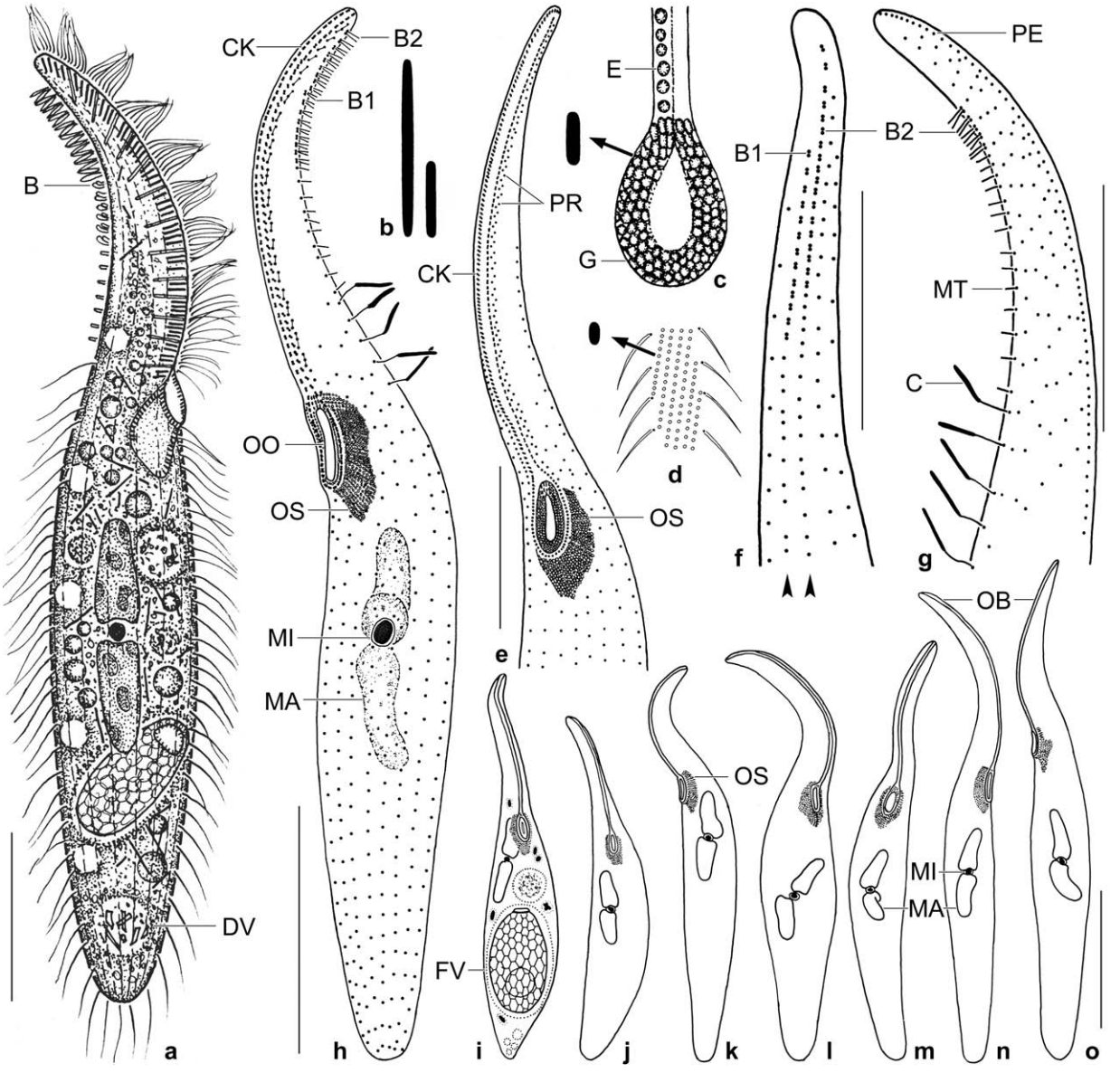
Diagnosis: Size about 170 × 30 μm in vivo. Shape very narrowly dileptid with proboscis about 37% of body length and posterior end narrowly rounded. A dorsal row of contractile vacuoles. Two size-types (7 μm and 3 μm long) of rod-shaped extrusomes attached to proboscis oral bulge. On average 19 ciliary rows, 2 staggered and differentiated into an isostichad dorsal brush: rows 1 and 2 composed of an average of 14 and 18 dikinetids, respectively; both rows with a monokinetidal bristle tail extending to base of proboscis. Oral bulge opening ovate, oral sac about 10 μm deep. Preoral kineties oblique to strongly oblique, ordinarily spaced, each usually composed of 2 ordinarily to widely spaced cilia.

Type locality: Soil from the rainforest on a small island in the Rio Negro, Anavilhanas archipelago about 40 km west of the town of Manaus, Brazil, W60° S4°.

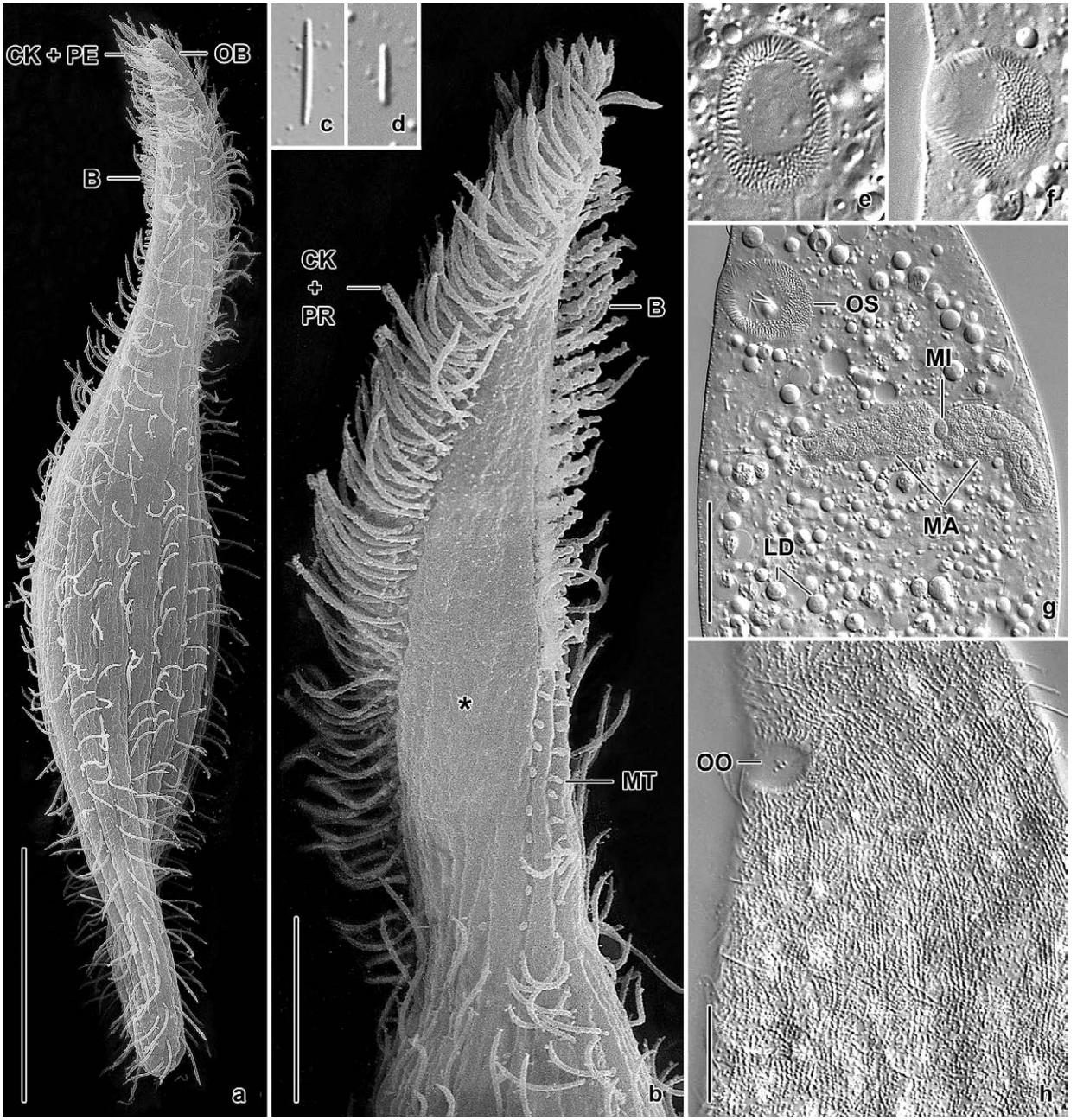
Type material: One holotype slide (inv. no. 2011/364) and five paratype (inv. nos 2011/365–369) slides with protargol-impregnated specimens have been deposited in the Biology Centre of the Museum of Upper Austria, Linz (LI). Relevant specimens are marked by black ink circles on the coverslip.

Etymology: The Latin adjective *brasiliense* refers to the country (Brazil) the species was discovered.

Description: Size 125–250 × 15–35 μm, usually about 170 × 30 μm in vivo, as calculated from some in vivo measurements and the morphometric data, assuming 15% preparation shrinkage (Table 26). Shape narrowly to cylindroidally dileptid with slightly to distinctly sigmoidal dorsal outline; proboscis crescentic, about 37% of body length, leaf-like flattened; trunk oblong to bluntly fusiform, usually widest in mid-portion, unflattened; posterior end rounded (Figs 53a, h–o). Nuclear apparatus slightly above mid of trunk, may be dislocated by large food inclusions (Fig. 53i). Two macronuclear nodules with concave proximal end surrounding micronucleus; individual nodules ovoidal to narrowly ovoidal, rarely curved; nucleoli globular to ellipsoidal, distinct both in vivo and in protargol preparations. Micronucleus in between macronuclear nodules, globular to slightly ellipsoidal, about 3 μm across, in protargol preparations surrounded by a distinct membrane (Figs 53a, h–o, 54g). A row of contractile vacuoles in dorsal side of cell, first vacuole at level of oral bulge opening; no ventral vacuoles (Fig. 53a). Two types of extrusomes arranged in a row in broader right branch of oral bulge and scattered throughout cytoplasm in considerable number: type I rod-shaped with slightly narrowed ends, about 7 × 0.8 μm in size, sparse in oral bulge, frequent in cytoplasm, rarely impregnate with protargol; type II rod-shaped with rounded ends, about 3 × 0.5 μm in size, numerous both in oral bulge and cytoplasm, does not stain with the protargol method used



Figs 53a–o: *Dimacrocaryon brasiliense* nov. sp. from life (a–d) and after protargol impregnation (e–o). **a** – right side view of a representative specimen, length 170 µm. The oral sac is well recognizable in vivo because it is up to 10 µm deep and lined with highly refractive granules; **b** – there are two size-types of rod-shaped extrusomes attached to proboscis oral bulge: type I is 7 µm long and has slightly narrowed ends, while type II is oblong and only 3 µm long; **c** – frontal view, showing the ovate oral bulge opening, the arrangement of the extrusomes, and the oral sac granules which are about 2 × 0.8 µm in size; **d** – surface view showing cortical granulation; **e** – ventrolateral view of ciliary pattern in oral region. The circumoral kinety is narrowed preorally and composed of dikinetids in the proboscis, while of monokinetids around the oral bulge opening. The preoral kineties are oblique to strongly oblique and composed of two to three ordinarily spaced basal bodies; **f** – dorsal view of proboscis. The dorsal brush is exactly on the dorsal side of the proboscis and consists of two staggered, isostichad rows both associated with a monokinetidal bristle tail (arrowheads); **g, h** – right and left side ciliary pattern and nuclear apparatus of holotype specimen, length 130 µm. Basal bodies of preoral kineties connected by lines. As typical for dileptids, the distal half of the cilia impregnates deeply with protargol; **i–o** – variability of body shape and size as well as of nuclear apparatus. The specimen shown in (i) has a large food vacuole containing a testate amoeba, the preferred food of this ciliate. Drawn to scale. B(1, 2) – dorsal brush (rows 1 and 2), C – cilia, CK – circumoral kinety, E – extrusomes, FV – food vacuole, G – granules, MA – macronuclear nodules, MI – micronuclei, MT – monokinetidal bristle tail, OO – oral bulge opening, OS – oral sac, PE – perioral kinety, PR – preoral kineties. Scale bars: 20 µm (e–g), 30 µm (a, h), and 50 µm (i–o).



Figs 54a–h: *Dimacrocaryon amphileptoides amphileptoides*, Austrian specimens (a, b) in the SEM, and *D. brasiliense* nov. sp. (c–h) from life. **a** – right side overview, showing the proboscis occupying about one third of body length and the narrowly rounded posterior body end; **b** – left side view, showing the sickle-shaped proboscis with a broad blank stripe (asterisk) between preoral kineties and dorsal brush. The strongly oblique preoral kineties extend in shallow furrows and are usually composed of two narrowly spaced cilia. The dorsal brush consists of two isostichad, staggered rows both with a monokinetidal bristle tail extending to the base of the proboscis; **c, d** – there are two types of extrusomes: type I is rod-shaped with narrowed ends and 7 µm long, while type II is oblong and 3 µm long; **e, f** – the oral sac is about 10 µm deep and lined with highly refractive granules about 2 × 0.8 µm in size; **g** – optical section showing some main cell organelles, such as macronuclear nodules, micronucleus, oral sac, and lipid droplets; **h** – the somatic and oral cortex is studded with densely spaced granules about 0.8 × 0.4 µm in size. B – dorsal brush, CK – circumoral kinety, LD – lipid droplets, MA – macronuclear nodules, MI – micronuclei, MT – monokinetidal bristle tail, OB – oral bulge, OO – oral bulge opening, OS – oral sac, PE – perioral kinety, PR – preoral kineties. Scale bars: 10 µm (b), 20 µm (g, h), and 30 µm (a).

Table 26: Morphometric data on *Dimacrocaryon brasiliense* nov. sp. (DB) and *D. arenicola* nov. sp. (DA). Data based on mounted, protargol-impregnated (Foissner's method), and randomly selected specimens from non-flooded Petri dish cultures. Measurements in µm. CV – coefficient of variation in %, M – median, Max – maximum, Mean – arithmetic mean, Min – minimum, n – number of specimens investigated, SD – standard deviation, SE – standard error of mean.

Characteristics	Species	Mean	M	SD	SE	CV	Min	Max	n
Body, length	DB	151.7	149.0	27.2	5.9	17.9	118.0	224.0	21
	DA	145.7	141.0	31.1	8.3	21.4	106.0	215.0	14
Body, width	DB	23.9	24.0	4.9	1.1	20.4	16.0	35.0	21
	DA	26.9	26.0	7.0	1.9	26.2	16.0	41.0	14
Body length:width, ratio	DB	6.5	6.5	1.3	0.3	20.2	3.6	9.2	21
	DA	5.6	5.5	0.9	0.2	16.8	4.3	7.3	14
Anterior body end to oral bulge opening, distance	DB	56.3	58.0	10.9	2.4	19.4	30.0	77.0	21
	DA	51.8	52.0	16.5	4.4	31.8	25.0	74.0	14
Proboscis, % of body length	DB	37.1	37.1	3.9	0.9	10.6	23.8	43.5	21
	DA	35.1	36.9	6.7	1.8	19.1	19.5	44.2	14
Oral bulge opening, length[a]	DB	10.5	11.0	1.5	0.3	14.0	7.0	12.0	20
	DA	12.5	11.0	5.3	1.4	42.0	9.0	25.0	14
Oral bulge opening, width[a]	DB	7.2	7.0	0.4	0.1	6.0	6.0	8.0	14
	DA	2.6	3.0	0.6	0.2	23.2	2.0	4.0	12
Oral sac, maximum depth	DB	8.0	8.0	0.7	0.3	8.9	7.0	9.0	8
	DA	2.9	3.0	1.2	0.4	39.6	2.0	5.0	8
Anterior body end to macronucleus, distance	DB	72.4	75.0	16.8	3.7	23.3	39.0	103.0	21
	DA	66.1	66.0	22.3	6.0	33.7	41.0	110.0	14
Nuclear figure, length	DB	33.0	32.0	3.9	0.9	11.9	25.0	43.0	21
	DA	29.4	30.0	7.2	1.9	24.4	19.0	41.0	14
Anterior macronuclear nodule, length	DB	17.4	17.0	3.0	0.7	17.4	12.0	25.0	21
	DA	18.4	17.0	5.7	1.5	31.0	10.0	29.0	14
Anterior macronuclear nodule, width	DB	6.8	6.0	1.3	0.3	19.0	5.0	11.0	21
	DA	6.4	6.0	1.2	0.3	19.2	5.0	9.0	14
Posterior macronuclear nodule, length	DB	16.6	17.0	2.2	0.5	13.3	13.0	23.0	21
	DA	17.6	17.0	4.3	1.2	24.5	11.0	25.0	14
Posterior macronuclear nodule, width	DB	6.6	6.0	1.3	0.3	20.1	5.0	11.0	21
	DA	6.3	6.0	1.3	0.4	20.9	4.0	9.0	14
Macronuclear nodules, number	DB	2.0	2.0	0.0	0.0	0.0	2.0	2.0	21
	DA	2.0	2.0	0.0	0.0	0.0	2.0	2.0	14
Micronucleus, largest diameter	DB	2.7	3.0	0.4	0.1	16.3	2.0	4.0	21
	DA	2.3	2.0	–	–	–	2.0	3.0	11
Micronucleus, number	DB	1.0	1.0	0.0	0.0	0.0	1.0	1.0	21
	DA	1.0	1.0	0.0	0.0	0.0	1.0	1.0	11

Characteristics	Species	Mean	M	SD	SE	CV	Min	Max	n
Ciliary rows, number	DB	18.9	19.0	1.3	0.3	6.8	17.0	22.0	21
	DA	17.4	17.5	2.4	0.6	13.9	13.0	21.0	14
Cilia in mid-body in 10 μm, number	DB	5.0	5.0	0.7	0.2	14.9	4.0	6.0	21
	DA	4.9	5.0	0.7	0.2	14.8	4.0	6.0	14
Dorsal brush rows, number	DB	2.0	2.0	0.0	0.0	0.0	2.0	2.0	20
	DA	2.0	2.0	0.0	0.0	0.0	2.0	2.0	7
Dikinetids in brush row 1, number	DB	13.7	14.0	0.9	0.3	6.9	12.0	15.0	10
	DA	10.7	10.5	1.8	0.7	16.4	8.0	13.0	6
Dikinetids in brush row 2, number	DB	18.3	18.0	3.2	0.9	17.6	15.0	26.0	13
	DA	15.8	17.0	4.5	1.9	28.6	9.0	21.0	6
Anterior body end to last dikinetid of brush row 1, distance	DB	26.8	25.0	6.2	1.9	23.0	20.0	42.0	10
	DA	22.0	25.0	6.9	2.8	31.3	10.0	28.0	6
Anterior body end to last dikinetid of brush row 2, distance	DB	22.7	22.0	5.1	1.5	22.3	17.0	35.0	12
	DA	22.0	25.0	6.9	2.8	31.3	10.0	28.0	6

[a] Measured as distances between circumoral kinety.

(Figs 53a, b, c, 54c, d). Cortex very flexible, contains dense rows of rather refractive granules with a size of about 0.8 × 0.4 μm (Figs 53d, 54h). Cytoplasm colourless and hyaline in the strongly flattened proboscis, opaque and thus dark in posterior third of proboscis and throughout trunk due to numerous lipid droplets up to 5 μm across and food vacuoles containing small testate amoebae (*Euglypha* sp., *Schoenbornia viscicula*, *Trinema lineare*), fungal spores, probably ciliates and flagellates (Fig. 53i); in posterior body end sometimes a 8 μm-sized defecation vacuole with crystalline contents. Movement without peculiarities.

Cilia about 10 μm long in vivo, ordinarily spaced; in protargol preparations as typical for dileptids, i.e., with thick, deeply impregnated distal half, except for dorsal bristles; arranged in an average of 19 narrowly to ordinarily spaced rows extending meridionally (Fig. 53h; Table 26). Right side rows shortened only in anterior fifth of proboscis, producing a short suture; perioral kinety extends to tip of proboscis with loosely spaced basal bodies (Fig. 53g). Left side of proboscis with broad blank stripe because ciliary rows end at level of oral bulge opening, except for one or two kineties extending to or above proximal half of proboscis (Figs 53e, h). Dorsal brush exactly on dorsal side of proboscis, composed of two staggered, isostichad rows each with a monokinetidal bristle tail. Brush row 1 commences more posteriorly than row 2, composed of an average of 14 widely spaced dikinetids. Brush row 2 begins subapically, composed of an average of 18 ordinarily to widely spaced dikinetids (Fig. 53f). Three types of bristles but only two types are recognizable in protargol preparations: anterior portion of rows with about 5 μm long type IV bristles followed by some 3 μm long type I bristles; posterior third composed of 2 μm long monokinetidal type VI bristles (Figs 53a, g, h). Brush structure difficult to recognize in lateral view due to the strong flattening of the proboscis.

Oral bulge opening at end of anterior body third, hardly projecting because base of proboscis almost as wide as trunk, ovate in vivo, elliptical in protargol preparations (Figs 53a, c, e). Oral sac about 10 μm deep in vivo, lined with conspicuous granules about 2 × 0.8 μm in size, well recognizable in vivo and in protargol preparations because rather deeply impregnating; granulated area roughly elliptical, usually with a minute posterior elongation recognizable only in lateral view (Figs 53a, c, e, h–o, 54e–g). Oral ciliary

pattern dileptid but with a remarkable specialization, viz., a preoral narrowing of the oral bulge/circumoral kinety. Circumoral kinety composed of ordinarily spaced dikinetids in proboscis and of narrowly spaced monokinetids around oral bulge opening; right branch curves around anterior end of proboscis, while left branch ends subapically almost touching the curved right end. Preoral kineties oblique to strongly oblique, ordinarily spaced, each composed of only two, rarely three ordinarily to widely spaced monokinetids, forming almost a line in anterior half of proboscis (Figs 53e, h).

Occurrence and ecology: As yet found only at type locality, that is, in soil of a terra firma primary (?) rainforest on one of the many small islands in the Rio Negro (black Amazon) about 10 m above low water level and thus not or rarely flooded during high water periods. The sample consisted of litter, roots, and soil from 0–10 cm. Litter layer 2–5 cm thick and with many fungal hyphae, followed by an about 5 cm thick, very dense root carpet mixed with brown, humic soil; mineral soil under root carpet loamy-sandy and brownish, yellowish down to 10 cm; pH 5.1. This species is remarkable by ingesting one to three testate amoebae up to 40 μm long, showing that the oral sac is very effective and can open widely.

Remarks: *Dimacrocaryon brasiliense* differs from *D. arenicola*, which occurs also in Brazil and is described below, by the type I extrusomes (rod-shaped vs. very narrowly ovate and asymmetric) and the shape of the oral bulge opening (ovate vs. very narrowly elliptical). *Dimacrocaryon amphileptoides* differs from *D. brasiliense* in having a very narrowly elliptical (vs. ovate) oral bulge opening and a deeper oral sac (~ 10 μm vs. < 5 μm). Further, *D. amphileptoides* possesses only one type of extrusomes which, however, are very similar to those of *D. brasiliense*.

Dimacrocaryon arenicola nov. sp. (Figs 55a–o; Table 26)

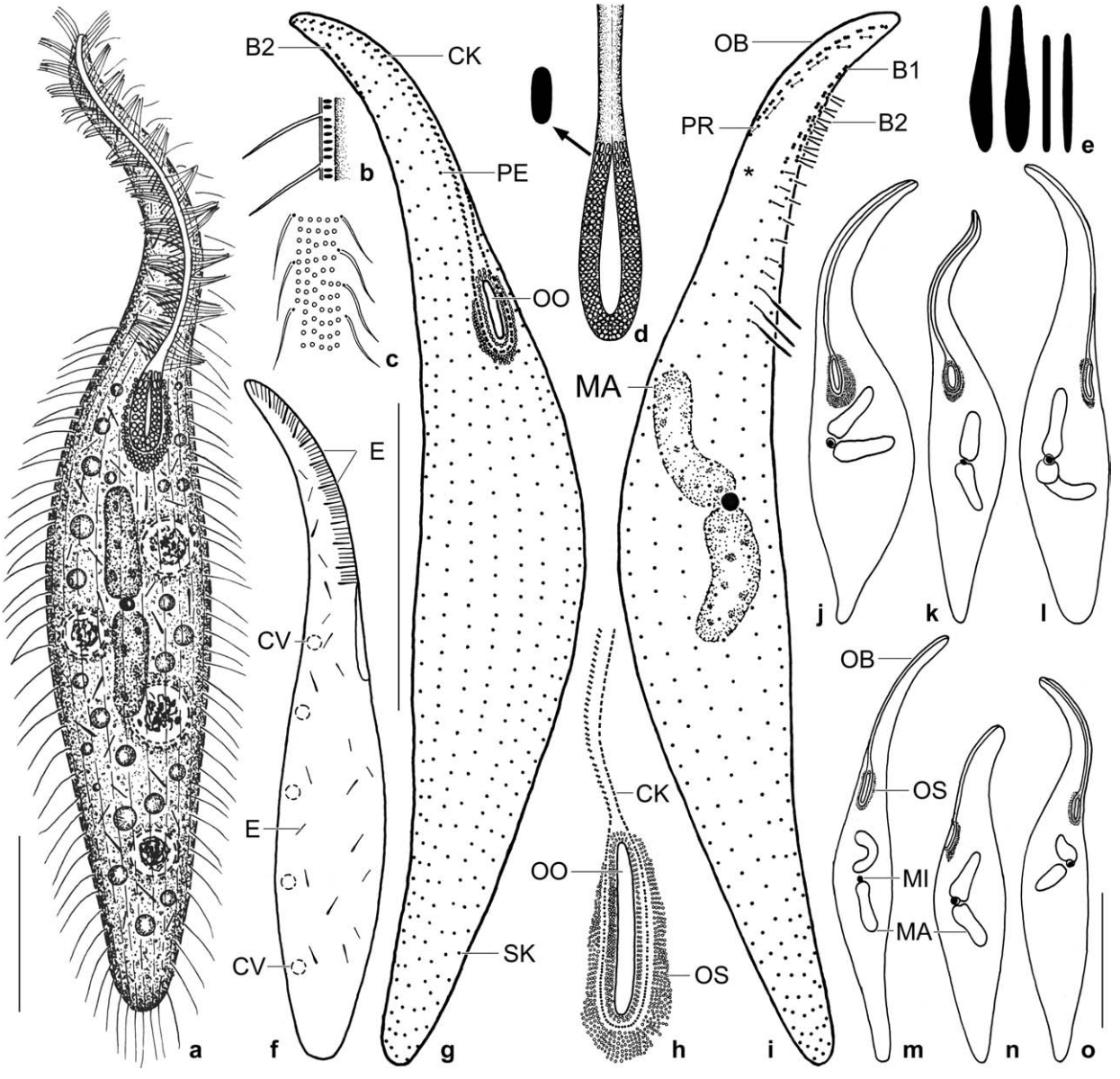
Diagnosis: Size about 170 × 30 μm in vivo. Shape narrowly dileptid with proboscis about 35% of body length and posterior end narrowly rounded. A dorsal row of contractile vacuoles. Two types of extrusomes attached to proboscis oral bulge: type I very narrowly ovate and asymmetric, about 5 × 1 μm in size; type II rod-shaped, 4 μm long. On average 17 ciliary rows, 2 staggered and differentiated into an isostichad dorsal brush: rows 1 and 2 composed of an average of 11 and 16 dikinetids, respectively; both rows with a monokinetidal bristle tail extending to base of proboscis. Oral bulge opening very narrowly elliptical, oral sac about 5 μm deep. Preoral kineties strongly oblique, ordinarily spaced, each usually composed of 2 ordinarily to widely spaced cilia.

Type locality: Sandy soil from the Restingha area in the surroundings of Rio de Janeiro, Brazil, W43° S23°.

Type material: One holotype slide (inv. no. 2011/355) and eight paratype slides (inv. nos 2011/356–363) with protargol-impregnated specimens have been deposited in the Biology Centre of the Museum of Upper Austria, Linz (LI). Relevant specimens are marked by black ink circles on the coverslip.

Etymology: The Latin word *arenicola* (living in sand) alludes to the habitat where the species was discovered.

Description and comparison with similar species: The new species has a very similar overall morphology as *D. brasiliense* described above; it matches, inter alia, in body shape, the nuclear and contractile vacuole apparatus, and the ciliary pattern (Figs 55a, f, g, i). Moreover, the morphometric features overlap considerably (Table 26). Thus, the reader is referred to *D. brasiliense* for a general description. The differences between *D. arenicola* and *D. brasiliense* are as follows: (1) type I extrusomes very narrowly ovate and asymmetric vs. rod-shaped and symmetric (cf. Fig. 55e and 53b); (2) oral bulge opening very narrowly elliptical vs. ovate (cf. Fig. 55d and 53c); (3) oral sac flat (< 5 μm) vs. deep (~ 10 μm). *Dimacrocaryon amphileptoides* has only oblong extrusomes.



Figs 55a-o. *Dimacrocaryon arenicola* nov. sp. from life (a-f) and after protargol impregnation (g-o). **a** – ventral overview of a representative specimen, length 170 μm; **b, c** – optical section and surface view showing the cortical granules embedded in an about 1 μm thick gelatinous layer; **d** – frontal view of oral bulge opening, which is very narrowly ovate and studded with granules that are about 2 × 1 μm in size; **e** – there are two types of extrusomes attached to proboscis oral bulge: type I is asymmetric and very narrowly ovate with a size of about 5 × 1 μm, while type II is rod-shaped with slightly narrowed ends and 4 μm long; **f** – lateral view showing contractile vacuole pattern and arrangement of extrusomes. The contractile vacuoles form a dorsal row; **g, i** – ventrolateral and dorsolateral view of ciliary pattern and nuclear apparatus of holotype specimen, length 109 μm. The perioral kinety is composed of comparatively loosely spaced basal bodies. Kinetosomes of preoral kineties connected by lines. Asterisk marks the blank stripe on the left side of the proboscis; **h** – ventral view showing the preoral narrowing of the circumoral kinety and the roughly elliptical, granular area around the oral bulge opening. The circumoral kinety is hybrid, i.e., composed of dikinetids in the proboscis, while of narrowly spaced monokinetids around the oral bulge opening; **j-o** – variability of body shape and size as well as of nuclear apparatus. Drawn to scale. B1, 2 – dorsal brush rows 1 and 2, CK – circumoral kinety, CV – contractile vacuoles, E – extrusomes, MA – macronuclear nodules, MI – micronucleus, OB – oral bulge, OO – oral bulge opening, OS – oral sac, PE – perioral kinety, PR – preoral kineties, SK– somatic kinety. Scale bars: 30 μm (a, g, i) and 50 μm (j-o).

Occurrence and ecology: As yet found only in the surroundings of Rio de Janeiro, namely, in the very sandy Restingha area about 100 m inshore the Atlantic coast, where the ground is covered by bushes and grass and an up to 1 cm high litter layer. The sample consisted of sandy soil, surface litter, and plant debris sieved off the very sandy soil up to a depth of 10 cm.

Dimacrocaryon amphileptoides (Kahl, 1931) Jankowski, 1967

1931 *Dileptus amphileptoides* spec. n. Kahl, Tierwelt Dtl. **21**: 208

Taxonomy: We split this species into two subspecies, mainly due to the contractile vacuoles which either form a stripe in ventral and dorsal side of trunk (*D. amphileptoides amphileptoides*) or only in dorsal side (*D. amphileptoides paucivacuolatum*). Possibly, *D. amphileptoides paucivacuolatum* is larger, has more ciliary rows, and a different extrusome pattern; however, this must be substantiated by the investigation of further populations, before they can be included into the diagnosis. Our notes indicate that *D. amphileptoides amphileptoides* is more common than *D. amphileptoides paucivacuolatum*.

Improved diagnosis (includes two subspecies and all data known): Size about 200 × 35 µm in vivo, rarely 250–400 µm long. Shape on average narrowly to very narrowly dileptid with proboscis frequently rather distinctly sickle-shaped and 1/3 of body length; posterior end narrowly rounded to acute. A dorsal and ventral stripe of contractile vacuoles or only a dorsal stripe. Extrusomes oblong, 3–5 µm long. On average about 19 or 27 ciliary rows, 2 staggered and differentiated into an isostichad dorsal brush with monokinetidal bristle tails extending to base of proboscis. Oral bulge opening very narrowly elliptical. Preoral kineties oblique to strongly oblique, ordinarily spaced, each usually composed of 3 narrowly spaced cilia.

Etymology: Not given in original description. The epithet possibly refers to the narrow mouth resembling that of the pleurostomatid genus *Amphileptus*.

Dimacrocaryon amphileptoides amphileptoides (Kahl, 1931) Jankowski, 1967 nov. stat. (Figs 7a–c, 9c, e–h, 17a–d, 54a, b, 56a–f, l, m, 57a–t; Table 27)

1931 *Dileptus amphileptoides* spec. n. Kahl, Tierwelt Dtl. **21**: 208

1953 *Dileptus amphileptoides* Kahl 1931 – Wenzel, Arch. Protistenk. **99**: 83 (some notes on morphology)

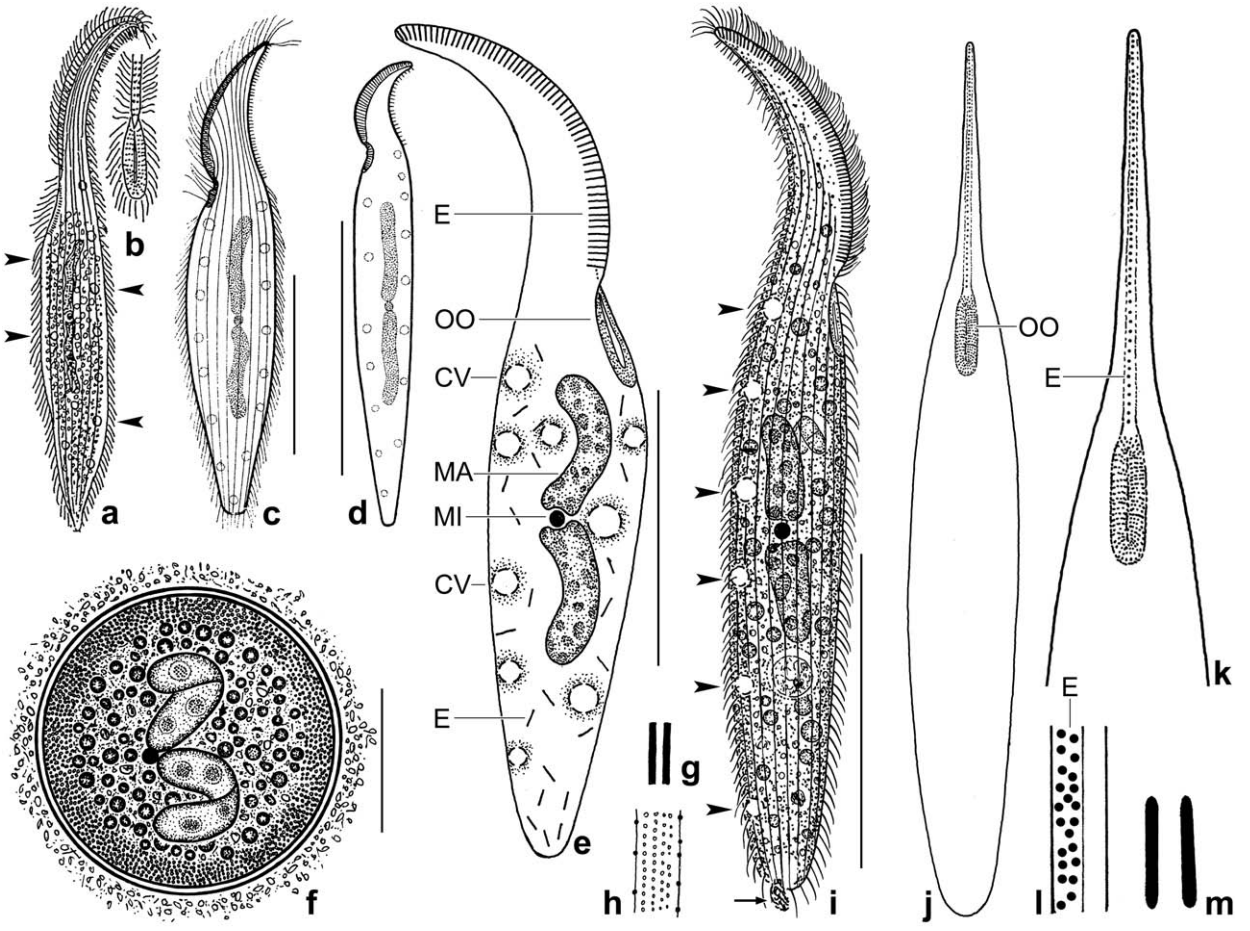
1967 *Dimacrocaryon amphileptoides* – Jankowski, Mater. IV Konf. uč. Sekc zool. year **1967**: 36 (fixation of *D. amphileptoides* as type species of the subgenus *Dimacrocaryon*)

1984 *Dimacrocaryon amphileptoides* (Kahl, 1931) – Foissner, Stapfia **12**: 92 (partim, population II)

Diagnosis: A stripe of contractile vacuoles each in dorsal and ventral side of cell.

Type locality: Kahl (1931) mentioned three sites, i.e., Mittenwald and Berchtesgaden in southern Bavaria and the Zillertal in Tyrol, Austria, but did not fix any as the type locality. The neotype is from soil of an alder stand (Alnetum viridis) on the Stubnerkogel near Bad Gastein, Salzburg, Austria E13°6' N47°7' (Foissner 1984). According to Article 76.3 of the ICZN (1999), the place of origin of the neotype becomes the type locality of the nominal species-group taxon, despite any previously published statement of the type locality.

Neotypification and voucher material: Neotypification was not explicitely mentioned by Foissner (1984), who deposited two slides (inv. no. 1982/54, mislabelled as *Dileptoides amphileptoides*; and 1984/8, mislabelled as *Rimaleptus amphileptoides*; Aescht 2008). The slide 1982/54 is declared here as a neotype for *D. amphileptoides amphileptoides*, while the slide 1984/8 is used as a holotype for *D. amphileptoides paucivacuolatum* (see below). Further, we have deposited five slides (inv. nos 2011/371–375) from the Gastein type series and four voucher slides (inv. nos 2011/376–379) of a population from a pine forest



Figs 56a-m. *Dimacrocaryon amphileptoides amphileptoides* (a-f, l, m) and *D. amphileptoides paucivacuolatum* nov. ssp. from mosses in the outskirts of the town of Giessen, Germany (g-k). From KAHL 1931 (a, b), WENZEL 1953 (c, d), FOISSNER 1984 (e, g-k), and originals (f, l, m). **a, b –** left side overview (a, length 350 µm) and frontal view of oral bulge opening (b). Arrowheads mark some of the many contractile vacuoles; **c, d –** Bavarian specimens with sickle-shaped proboscis; **e –** Austrian (Gastein area, Salzburg; FOISSNER & PEER 1985) specimen showing main body organization; **f –** resting cyst of a Norwegian specimen; **g, h –** extrusomes (g, 4 µm) and cortical granulation (h); **i –** right side view of a representative specimen, showing contractile vacuoles only in the dorsal side of the cell (arrowheads). The arrow marks fecals leaving the cell in the posterior pole region; **j, k –** ventral views, showing the very narrowly elliptical oral bulge opening and the single row of extrusomes in the proboscis oral bulge; **l, m –** arrangement and shape of the extrusomes in the proboscis of an Austrian population (Salzburg, surroundings of the town of Hüttschlag). The extrusomes are scattered in the broader right branch of the oral bulge and have a size of about 4–5 × 0.4 µm. The shape varies from perfectly oblong to very slightly widened proximally. CV – contractile vacuoles, E – extrusomes, MA – macronuclear nodules, MI – micronucleus, OO – oral opening. Scale bars: 20 µm (f), 50 µm (e), and 100 µm (c, d, i).

near Oslo, Norway. Relevant specimens are marked by black ink circles on the coverslip. All slides are deposited in the Biology Centre of the Museum of Upper Austria, Linz (LI).

The neotypification is supported here because (i) no type material is available from KAHL's (1931) specimens, (ii) the identity is treated by the subspecies *paucivacuolatum* and the rather similar *D. arenicola*, (iii) there are no doubts on the identification, (iv) the neotype is from the same biogeographic region and a similar habitat, and (v) the preparations are of good quality.

Description: The description is based on the data of KAHL (1931) and WENZEL (1953) as well as on our detailed, unpublished observations on two populations from the Austrian Central Alps (Gastein area,

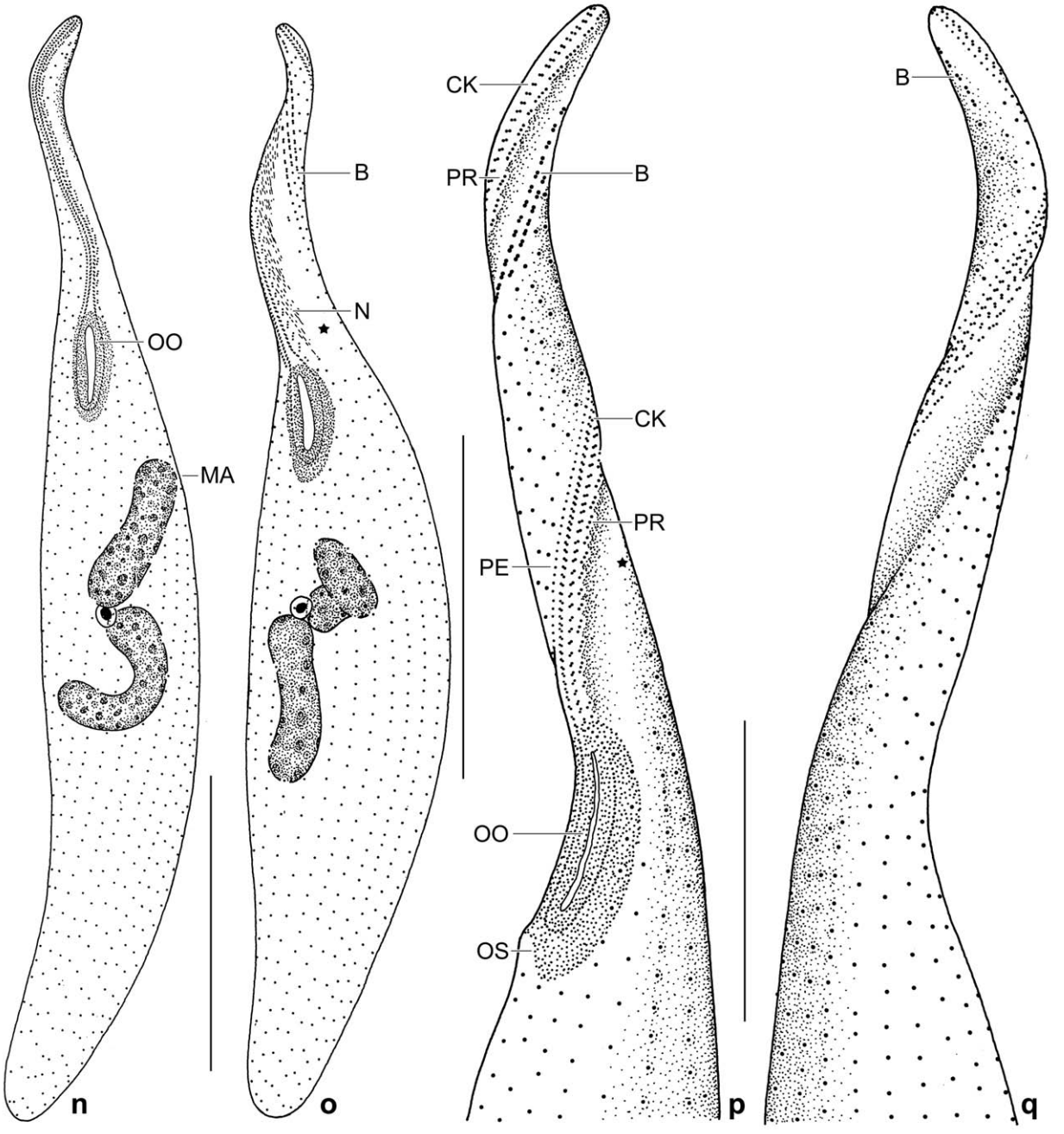
Alnetum viridis on the Stubnerkogel, Taxotop D in Foissner & Peer 1985; Bad Hofgastein area, alpine pasture on the Schlossalm). Further, selected features and morphometric data were studied in a Norwegian population found in mixed forest litter about 135 km NW of the town of Oslo.

Length in vivo 250–400 µm (Kahl 1931); 170–250 µm (on average 205 µm, n = 8) according to Wenzel (1953); 180 × 35 µm (original data from two alpine populations and three specimens); and 115–220 × 20–47 µm, on average 170 × 29 µm in two protargol-impregnated populations (Table 27), corresponding to an in vivo size of about 200 × 35 µm, if 15% preparation shrinkage is added. Kahl's length hardly reached by even the extreme values, indicating strong variability or a measurement error. Shape on average narrowly to cylindroidally dileptid with proboscis more or less distinctly sickle-shaped, occupying about one third of body length; posterior end narrowly rounded or acute, never tail-like; trunk slightly to distinctly (~ 2:1) flattened, proboscis sometimes leaf-like. Specimens often slightly, rarely fairly distinctly spiralized, especially the proboscis, and sometimes deformed by large food inclusions, mainly testate amoebae (Figs 54a, 56a, c–e, 57a, e, i–k, q). Nuclear apparatus in or near central third of trunk, may be strongly displaced by large food inclusions (Fig. 57c). Macronuclear nodules comparatively small, i.e., on avarage 20–24 × 6 µm after protargol impregnation; shape rather variable: oblong, bluntly clavate, nodulated, or slightly spiralized; nucleoli distinct, globular. Invariably a single micronucleus in between macronuclear nodules, 2–3.5 µm across in vivo (Figs 56a, c–e, 57f; Table 27). Contractile vacuoles in ventral and dorsal side of trunk, likely scattered throughout cell, except of proboscis. In rear end frequently a defecation vacuole with slimy, granular contents (Figs 56a, c–e, 57f, h, i). Extrusomes inconspicuous because oblong (rarely very slightly widened proximally) and only 3–5 µm long in four populations investigated, attached to broader right branch of proboscis oral bulge and scattered in cytoplasm; do not impregnate with the protargol method used (Figs 56a–e, l, m, 57g). Cortex very flexible and colourless, studded with minute granules, forming slightly oblique rows, as in other dileptids; rather distinctly furrowed by the ciliary rows (Figs 54a, 56h, 57a, h). Cytoplasm colourless, hyaline or studded with lipid droplets up to 5 µm across and food vacuoles with testate amoebae (Fig. 57c), silicoflagellates (Figs 7a, b), and possibly also bacteria and ciliates. Swims and glides clumsily between soil particles.

The somatic and oral ciliary pattern as well as the structure of the oral bulge opening of the two subspecies are highly similar, except of small morphometric differences (Table 27). Thus, the following description applies to both.

Cilia 8–10 µm long in vivo, widely spaced; in protargol preparations as typical for dileptides, i.e., with thick, deeply impregnating distal half, except for dorsal bristles; arranged in an average of about 19 (*D. amphileptoides amphileptoides*) or 27 (*D. amphileptoides paucivacuolata*) narrowly to ordinarily spaced rows extending meridionally. Right side rows shortened only in anterior region of proboscis; first row right of circumoral kinety extends as perioral kinety to tip of proboscis with narrowly to ordinarily spaced basal bodies. Left side of proboscis with broad and thus conspicuous blank stripe because ciliary rows end at level of oral bulge opening, except for one or two kineties extending to or above proximal half of proboscis (Figs 54a, b, 56i, n–q, 57a, e). Dorsal brush exactly on dorsal side of proboscis, composed of two staggered, isostichad rows each with a monokinetidal bristle tail extending to level of oral opening. Brush row 1 commences slightly more posteriorly than row 2, composed of an average of 14 ordinarily spaced dikinetids in Norwegian specimens; brush row 2 commences subapically, composed of an average of 17 ordinarily spaced dikinetids. Brush bristles slightly clavate, can move forward and backward, about 5 µm long in middle third of brush, gradually decreasing to about 3 µm at brush ends; tail bristles widely spaced, about 1 µm long (Figs 54a, b, 56a, c, d, i, o–q, 57e, g, m, n; Table 27).

Oral bulge opening at end of anterior body third, inconspicuous because hardly projecting from body proper and so flat that often difficult to recognize in vivo and in the scanning electron microscope (Figs



Figs 56n-q. *Dimacrocaryon amphileptoides paucivacuolatum* nov. ssp., protargol-impregnated specimens of a population from wall mosses in the outskirts of the town of Giessen, Germany (from FOISSNER 1984). **n, o –** somatic and oral ciliary pattern of the ventral side and nuclear apparatus. The asterisk denotes the blank stripe on the left side of the proboscis, i.e., between the preoral kineties and the dorsal brush. Note the narrowly elliptical oral bulge opening surrounded by a granular area, which is the main feature of this genus; **p, q –** ciliary pattern of left and right side of a spiralized proboscis. The asterisk marks the blank stripe between the preoral kineties and the dorsal brush. The preoral kineties are oblique to strongly oblique and composed of two to four narrowly spaced basal bodies. Note that the oral sac is comparatively flat, i.e., up to 5 µm deep and lined by refractive, protargol-affine granules, as typical for the genus. B – dorsal brush, CK – circumoral kinety, MA – macronuclear nodule, N – nematodesmata, OO – oral bulge opening, OS – oral sac, PE – perioral kinety, PR – preoral kineties. Scale bars: 25 µm (p, q) and 50 µm (n, o).

Table 27: Morphometric data on *Dimacrocaryon amphileptoides amphileptoides* from Austria (DA) and Norway (DN), and *D. amphileptoides paucivacuolatum* nov. ssp. from Germany (DG; from FOISSNER 1984). Data based on mounted, protargol-impregnated (Foissner's method), and randomly selected specimens from non-flooded Petri dish cultures. Measurements in µm. CV – coefficient of variation in %, M – median, Max – maximum, Mean – arithmetic mean, Min – minimum, n – number of specimens investigated, Pop – population, SD – standard deviation, SE – standard error of mean.

Characteristics	Pop	Mean	M	SD	SE	CV	Min	Max	n
Body, length	DA	168.8	166.5	31.6	11.2	18.7	120.0	220.0	8
	DN	172.1	175.0	26.7	6.9	15.5	115.0	200.0	15
	DG	200.4	203.0	32.6	9.8	16.3	145.0	250.0	11
Body, width	DA	22.1	21.0	2.0	0.7	9.2	20.0	26.0	8
	DN	36.3	35.0	8.0	2.1	22.1	23.0	47.0	15
	DG	27.4	28.0	3.5	1.1	13.0	21.0	32.0	11
Body length: width, ratio[a]	DA	7.8	8.2	1.9	0.7	23.8	4.9	10.5	8
	DN	5.0	4.9	1.5	0.4	29.8	3.3	8.5	15
	DG	7.4	7.3	1.0	0.3	13.0	5.7	8.7	11
Anterior body end to oral bulge opening, distance	DA	52.0	51.5	9.1	3.2	17.5	41.0	67.0	8
	DN	49.1	50.0	7.4	1.9	15.2	37.0	62.0	15
	DG	56.7	56.0	9.5	2.9	16.7	43.0	76.0	11
Proboscis, % of body length[a]	DA	30.5	30.0	3.9	1.4	12.8	25.0	35.0	8
	DN	28.7	28.0	2.4	0.6	8.4	24.0	33.0	15
	DG	28.4	28.3	2.9	0.9	10.2	23.3	33.0	11
Oral bulge opening, length[b]	DA	19.5	19.0	3.0	1.1	15.3	16.0	24.0	8
	DN	17.7	18.0	2.6	0.7	14.8	14.0	22.0	15
	DG	21.8	22.0	6.0	1.8	27.6	14.0	35.0	11
Oral bulge opening, width[b]	DA	6.2	6.0	–	–	–	6.0	7.0	5
	DN	4.7	5.0	0.5	0.1	10.5	4.0	5.0	15
	DG	5.4	6.0	1.2	0.4	22.3	4.0	7.0	11
Oral sac, maximum depth	DN	4.2	4.0	1.1	0.3	25.8	3.0	7.0	15
	DG	3.5	4.0	0.6	0.2	16.4	2.0	4.0	9
Nuclear figure, length	DA	41.0	41.0	5.8	2.0	14.0	30.0	48.0	8
	DN	43.0	45.0	4.3	1.1	10.0	37.0	52.0	15
	DG	45.4	46.0	9.6	2.9	21.1	30.0	60.0	11
Anterior macronuclear nodule, length	DA	20.0	20.0	2.0	0.7	10.0	17.0	23.0	8
	DN	24.1	23.0	3.6	0.9	15.1	21.0	36.0	15
	DG	27.4	28.0	5.2	1.6	19.0	20.0	35.0	11
Anterior macronuclear nodule, width	DA	5.6	6.0	0.7	0.3	13.2	4.0	6.0	8
	DN	6.4	6.0	1.0	0.3	15.4	5.0	8.0	15
	DG	7.1	7.0	0.8	0.2	11.3	6.0	9.0	11

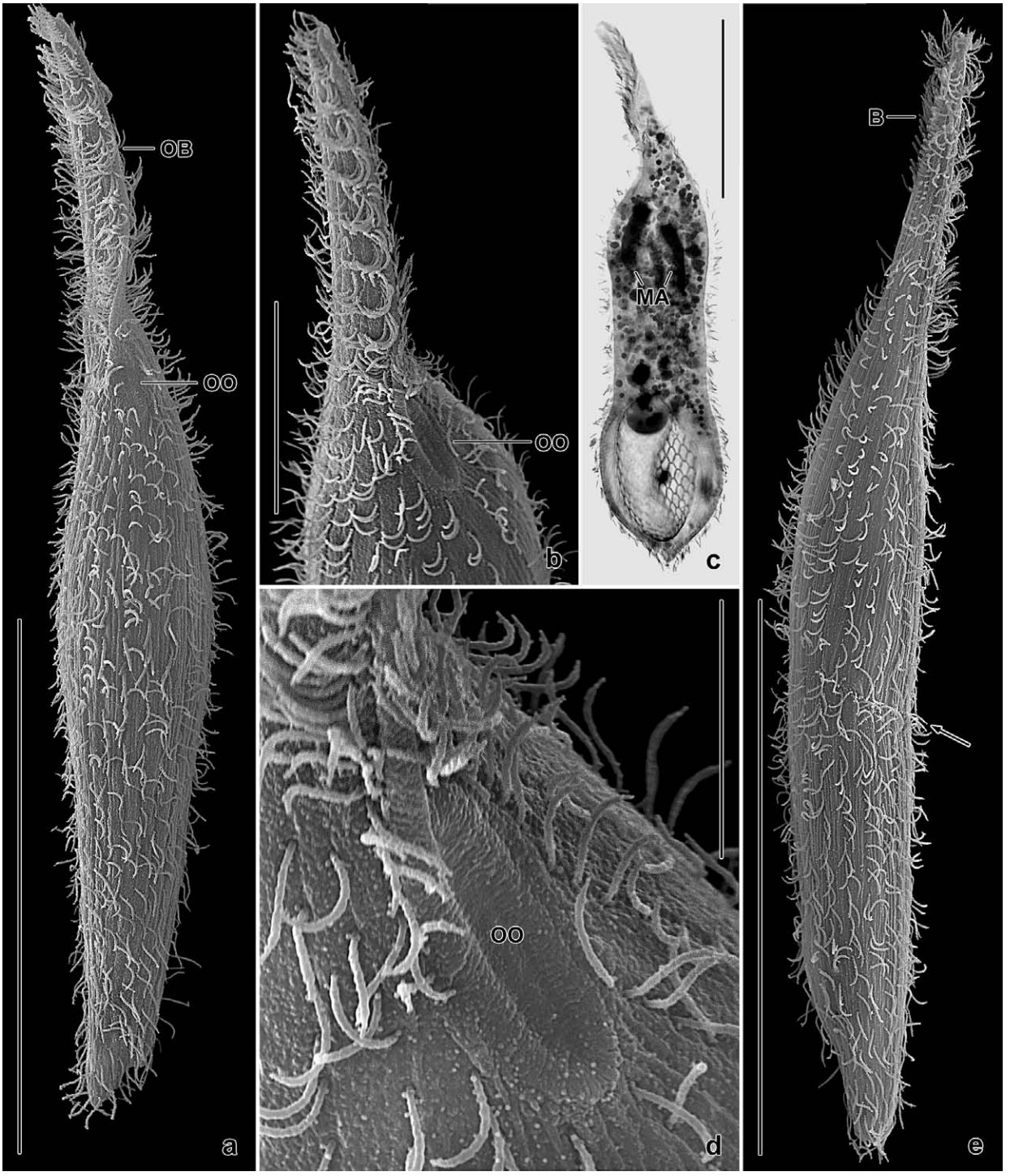
Characteristics	Pop	Mean	M	SD	SE	CV	Min	Max	n
Macronuclear nodules, number	DA	2.0	2.0	0.0	0.0	0.0	2.0	2.0	8
	DN	2.0	2.0	0.0	0.0	0.0	2.0	2.0	15
	DG	1.8	2.0	–	–	–	1.0	2.0	11
Micronucleus, longer axis	DA	1.8	1.8	0.2	0.1	13.3	1.6	2.2	8
	DN	2.8	3.0	0.4	0.1	15.1	2.0	3.0	15
	DG	3.0	3.0	0.5	0.2	16.5	2.0	4.0	9
Micronucleus, number	DA	1.0	1.0	0.0	0.0	0.0	1.0	1.0	8
	DN	1.0	1.0	0.0	0.0	0.0	1.0	1.0	15
	DG	1.0	1.0	0.0	0.0	0.0	1.0	1.0	11
Ciliary rows, number	DA	18.3	17.5	1.8	0.6	10.0	16.0	21.0	8
	DN	19.7	20.0	1.1	0.3	5.7	18.0	22.0	15
	DG	27.4	27.0	2.3	0.7	8.4	22.0	30.0	11
Cilia in mid-body in 10 µm, number	DA	5.3	5.5	0.9	0.3	16.9	4.0	6.0	8
	DN	4.5	4.0	0.6	0.2	14.1	4.0	6.0	15
	DG	5.5	5.0	1.1	0.3	20.3	4.0	7.0	11
Dorsal brush rows, number[a]	DA	2.0	2.0	0.0	0.0	0.0	2.0	2.0	8
	DN	2.0	2.0	0.0	0.0	0.0	2.0	2.0	15
	DG	2.1	2.0	–	–	–	2.0	3.0	13
Dikinetids in brush row 1, number	DN	14.3	14.0	2.6	0.7	17.8	10.0	18.0	15
Dikinetids in brush row 2, number	DN	17.4	18.0	2.5	0.6	14.4	13.0	21.0	15
Preoral kineties, number of kinetids	DN	2.7	3.0	–	–	–	2.0	3.0	15

[a] New data for *D. amphileptoides paucivacuolatum* from the German (near the town of Giessen) population studied by FOISSNER (1984).

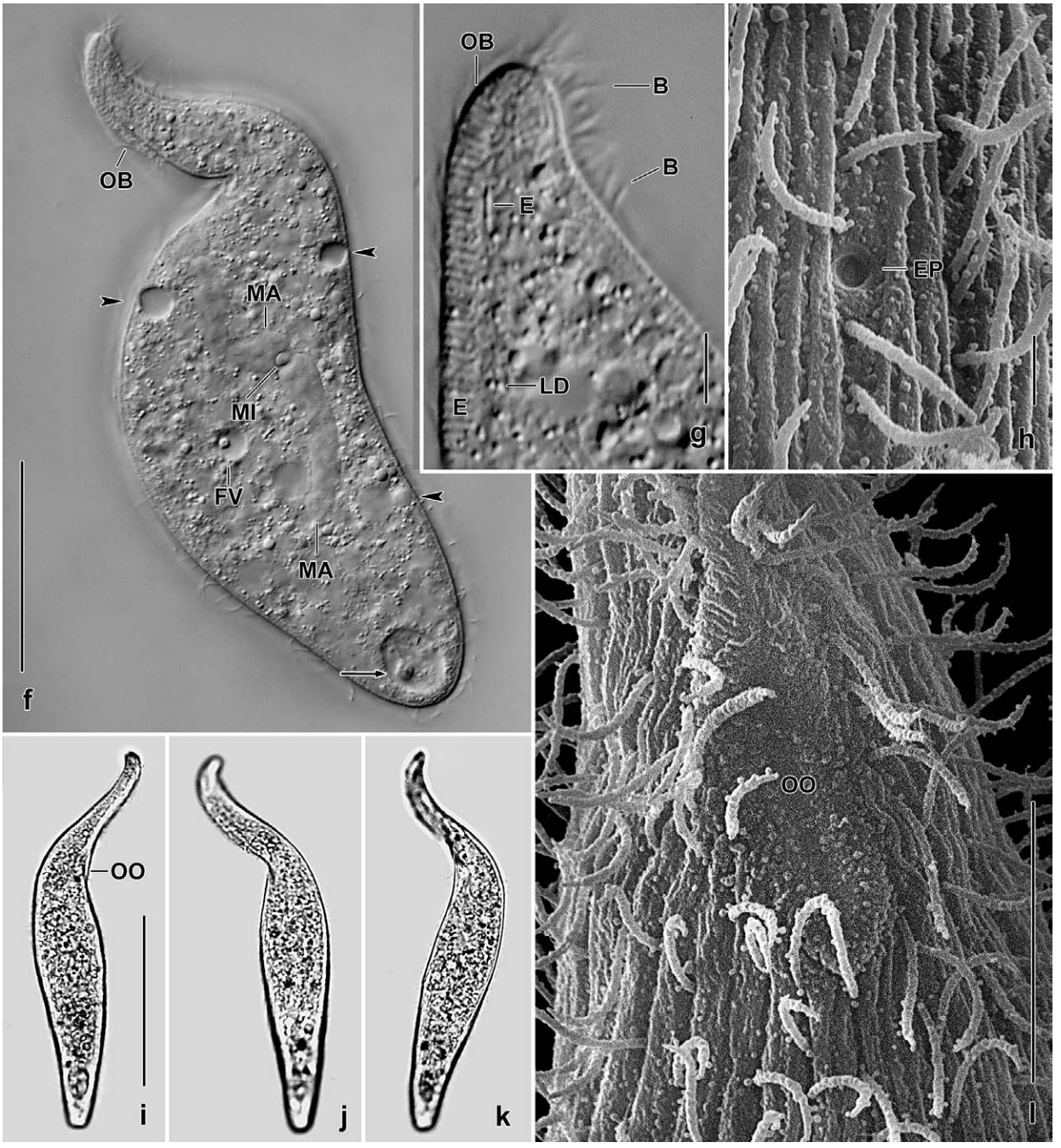
[b] Measured as distances between circumoral kinety in *D. amphileptoides amphileptoides*, while including the granular area in *D. amphileptoides paucivacuolatum*.

57a, b, d, f, i–k, l). Oral sac up to 5 µm deep, lined by refractive, protargol-affine granules about 1 × 0.5 µm in size, as typical for the genus; nematodesmata recognizable only in the electron microscope (Figs 17a, b, 56a–e, i–k, n–p, 57a, b, d). Oral cilia about 10 µm long in vivo, form nice metachronal waves (Fig. 57b), arranged in dileptid pattern, but with two remarkable specializations, viz., a preoral narrowing of the oral bulge/circumoral kinety and an only 1–2 µm wide oral bulge surface (measured between branches of circumoral kinety). Circumoral kinety composed of ordinarily to widely spaced dikinetids associated with rather distinct nematodesmata and narrowly spaced monokinetids around oral bulge opening. Preoral kineties composed of two to four ordinarily spaced monokinetids forming almost a line in anterior third of proboscis (Figs 54b, 56n–p, 57n).

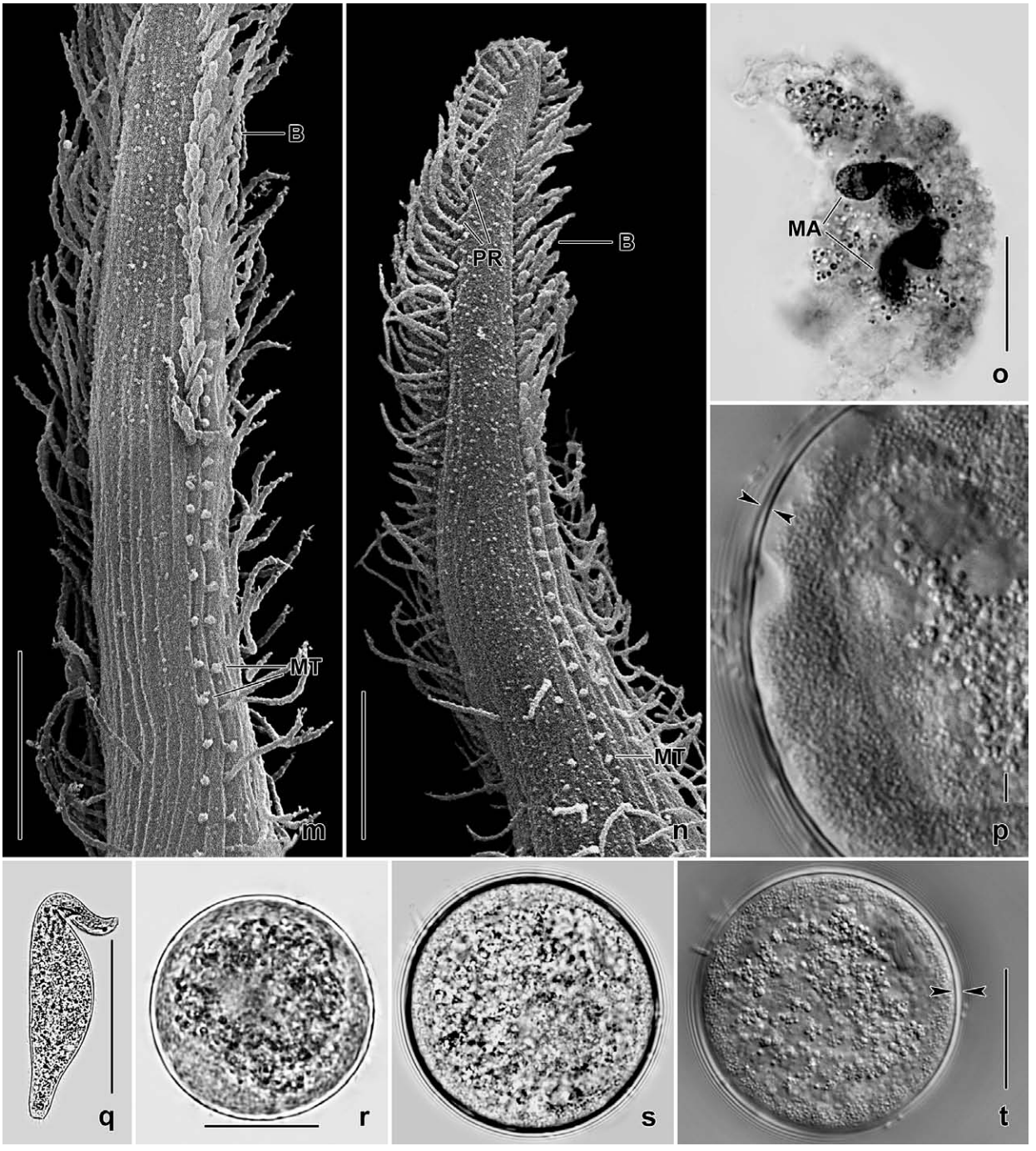
Resting cyst (Figs 56f, 57o, p, r–t): This was studied in the Norwegian population of *D. amphileptoides amphileptoides*. The spherical cysts have a diameter of 40–51 µm (on average 42.8 µm, n = 8) and are morphologically inconspicuous, i.e., have a smooth, colourless, about 1.5 µm thick wall, which stains pink with methyl green-pyronin. The cyst's periphery is packed with minute granules (≤ 0.5 µm), forming an opaque layer, while the central portion contains the nuclear apparatus, many lipid droplets 0.5–2 µm across, and some autophagous vacuoles up to 4 µm in size. The extrusomes and contractile vacuoles



Figs 57a-e. *Dimacrocaryon amphileptoides amphileptoides*, Norwegian specimens in the SEM (a, b, d, e) and an Austrian cell after protargol impregnation (c). **a –** ventrolateral overview showing the slender body with proboscis occupying about one third of body length; **b, d –** the ellipsoidal oral bulge is flat and thus inconspicuous; **c –** a specimen with a 40 µm long testate amoeba (*Euglypha*) in the rear end; **e –** dorsal overview of an early divider developing oral kinetofragments in mid-portion of trunk (arrow). B – dorsal brush, MA – macronuclear nodules, OB – oral bulge, OO – oral bulge opening. Scale bars: 10 µm (d), 30 µm (b), 50 µm (c), and 100 µm (a, e).



Figs 57f-l. *Dimacrocaryon amphileptoides amphileptoides*, Norwegian specimens from life (f, g, i-k) and in the SEM (h, l). **f –** a slightly squashed specimen showing contractile vacuoles in the ventral and dorsal side of the trunk (arrowheads), a diagnostic feature of this subspecies. The arrow marks a defecation vacuole with slimy contents; **g –** anterior region of a strongly flattened proboscis (by coverslip pressure), showing the extrusome fringe in the oral bulge and the slightly clavate dorsal brush bristles; **h –** an intrakinetal excretory pore of a contractile vacuole. The cortex is strongly furrowed, very likely by the postciliary microtubule ribbons, which are more resistant to critical point drying than the shrunken cortical membranes; **i-k –** three overviews of a freely motile specimen, showing the slender body and the slightly sickle-shaped proboscis; **l –** the oral bulge opening is only indistinctly protruding and thus difficult to discern, even in the SEM. B – dorsal brush, E – extrusomes, EP – excretory pore of a contractile vacuole, FV – food vacuole, LD – lipid droplets, MA – macronuclear nodules, MI – micronucleus, OB – oral bulge, OO – oral opening. Scale bars: 2 µm (h), 10 µm (g, l), 50 µm (f), and 100 µm (h-k).



Figs 57m-t. *Dimacrocaryon amphileptoides amphileptoides*, Norwegian specimens from life (p-t), in the SEM (m, n), and in a methyl green-pyronin stain (o). **m, n –** dorsolateral views of proboscis, showing the two-rowed dorsal brush and the broad blank stripe between the preoral kineties and the dorsal brush; **o –** a squashed resting cyst, showing the two macronuclear nodules; **p, r –** the wall of the resting cyst (opposed arrowheads) is about 1 µm thick. The cyst's periphery is studded with minute granules, while the central portion contains the nuclear apparatus, many minute lipid droplets, and some autophagous vacuoles; **q –** a freely motile specimen; **s, t –** the same resting cyst under bright field and interference contrast illumination. Note the thin, structureless cyst wall (opposed arrowheads) and the minute granules in the periphery of the cyst. B – dorsal brush, MA – macronuclear nodules, MT – monokinetidal tail bristles, PR – preoral kineties. Scale bars: 5 µm (p), 10 µm (m, n), 20 µm (o, r-t), and 100 µm (q).

disintegrated; likewise, there is only a thin mucous layer hardly attaching the cysts to the microscope slide.

Occurrence and ecology: See *D. amphileptoides paucivacuolatum*.

Dimacrocaryon amphileptoides paucivacuolatum nov. ssp. (Figs 56g–k, n–q; Table 27)

1984 *Dimacrocaryon amphileptoides* (Kahl, 1931) – Foissner, Stapfia **12**: 92 (partim, population I)

Nomenclature and taxonomy: We establish a new subspecies for population I of the *D. amphileptoides* described by Foissner (1984); for reasoning, see taxonomy of *D. amphileptoides*. This is in accordance with Article 72.3 of the ICZN (1999) because we fix a holotype below.

Diagnosis: A stripe of contractile vacuoles in dorsal side of cell.

Type locality: Wall mosses from the park of the castle Rauisch-Holzhausen, outskirts of the town of Giessen, Germany, E11°25' N47°4'.

Type material: One neotype slide [inv. no. 1984/8; mislabelled as "*Rimaleptus amphileptoides* (Genotyp) Giessen 1984"] with protargol-impregnated German specimens (population I), as investigated by Foissner (1984), is withdrawn and here used as a holotype slide for the new subspecies. Specifically, we declare the specimen shown in Fig. 56n of this monograph as the holotype of *D. amphileptoides paucivacuolatum*. This specimen and several syntype specimens are marked by black ink circles on the coverslip. Further slide (inv. no. 1984/70) belongs to this series, and is thus a paratype (Aescht 2008). The holotype and the paratype slide are deposited in the Biology Centre of the Museum of Upper Austria, Linz (LI).

Etymology: Composite of the Latin adjective *paucus* (few), the thematic vowel *i*, and the Latin noun *vacuola* (vacuole), referring to the decreased number of contractile vacuoles when compared with *D. amphileptoides amphileptoides*.

Description: Detailed data are available only for the type population (Foissner 1984). A second population has been found in a soil sample from Gough Island, Antarctica (Foissner 1996b), but was not studied in detail.

As described in the taxonomy section, the subspecies *paucivacuolatum* has contractile vacuoles only in the dorsal side of the trunk. Other differences need to be substantiated in further populations, before they can be included in the diagnosis. These are (Table 27): body size in vivo about 230 × 30 µm vs. 200 × 35 µm; number of ciliary rows 27 vs. up to 22; and the arrangement of the extrusomes (scattered in broader right branch of oral bulge vs. in a single row, Figs 56j–l). A reinvestigation of the type population showed that there are two dorsal brush rows, only one out of 16 specimens analyzed has three rows, as stated by Foissner (1984). Further, the Bavarian specimens have narrowed the circumoral kinety preorally, as the congeners and the subspecies *amphileptoides*, and the oral sac is ≤ 5 µm deep, as in *D. arenicola*.

Some other observations should be also mentioned, as far as they are different from the other subspecies: (i) contractile by about one third of body length, but possibly only under slight coverslip pressure; (ii) trunk cylindroidal, rarely slightly flattened; (iii) extrusomes only 3 µm long and thus conspicuously short; (iv) trunk usually studded with globular inclusions up to 10 µm across; (v) feeds on the testate amoeba *Euglypha rotunda*, fungal conidia, and green algae.

Occurrence and ecology: If not mentioned otherwise, the following data concern both subspecies because they were rarely separated before. According to Foissner (1998), *D. amphileptoides* is a cosmopolitan, occurring even in the Antarctic region (Foissner 1996b). Most records are from terrestrial and semi-terrestrial habitats. However, there are also several unsubstantiated records from a variety of running waters in Slovakia (Szentiványi & Tirjaková 1994; Krno et al. 1995; Matis et al. 1996; Tirjaková 1997a,

1997b; Tirjaková & Stloukal 2004). Further, it has been found in abandoned, sewage-irrigated, sandy soil in Berlin (Foissner 2000).

Kahl (1931) discovered *D. amphileptoides amphileptoides* in mosses on limestone from southern Bavaria (Mittenwald and Berchtesgaden), where it was frequent, while it was rare in mosses from granitic rocks in the Zillertal, Austria. Later, *D. amphileptoides* has been recorded from a great variety of habitats in Germany and Austria (Wenzel 1953; Foissner 1987a, 1988b, 2000; Lehle 1989; Foissner et al. 2005). The description of *D. amphileptoides paucivacuolatum* is based on a population from wall mosses of a castle in the outskirts of the town of Giessen (Foissner 1984). Further, we observed *D. amphileptoides amphileptoides* in a mixed forest about 150 km NW of the town of Oslo, Norway (Figs 7a–c, 9c, e–h, 17a–d, 57a–t).

Stout (1968) found *D. amphileptoides* infrequently in mor humus of a beech forest in Denmark, and Esteban et al. (2006) recorded it from upland grassland in England. Wang (1977) recorded it from the Tibetan Plateau, and Yang (1989) found it during winter in freshwaters of the Yuelushan area, China. Foissner (2008) found it in sandy coastal soil of Singapore; from litter and soil of the Santa Rosa National Park in Costa Rica (Foissner 1995a); and from soil of the Amazon floodplain near the town of Iquitos, Peru (Foissner 1997b). Blatterer & Foissner (1988) reported *D. amphileptoides* in 6 out of 21 litter and soil samples from Australia, viz., the Brisbane Water National Park and forests in the surroundings of the town of Adelaide. Stout (1961) found *D. amphileptoides* in lightly burnt soils from New Zealand.

Little is known on the ecology of *D. amphileptoides*. Basically, it is an omnivore, preferring small testate amoebae as food (Fig. 57c). But other matters are also ingested (Foissner 1998): green algae, autotrophic and heterotrophic flagellates (Figs 7a, b), hyphae and spores of fungi, and possibly also bacteria and ciliates. The great variety of habitats it has been reported indicates a wide ecological range.

Rimaleptus Foissner, 1984

1984 *Rimaleptus* nov. gen. Foissner, Stapfia **12**: 90

2001 *Rimaleptus* Foissner 1984 – Aescht, Denisia **1**: 143 (catalogue of generic names of ciliates)

2007 *Rimaleptus* Foissner, 1984 – Jankowski, Protista II: 573 (brief generic review)

2008 *Rimaleptus* Foissner, 1984 – Lynn, Ciliated protozoa: 371 (list of genera)

Improved diagnosis: Small- to medium-sized Dimacrocaryonidae with broad to rod-shaped, rarely rostrate body. Two macronuclear nodules. Dorsal brush staggered and two- or multi-rowed. Right branch of circumoral kinety accompanied by a perioral kinety, left branch by many slightly to strongly oblique preoral kineties. Oral bulge opening dileptid, i.e., roundish or ovate and located ventrally, length usually $\geq$ 10 μm. Oral basket bulbous or obconical.

Type species (by original designation): *Dileptus binucleatus* Kahl, 1931.

Etymology: Not given in original description. Composite of the Latin noun *rima* (cleft, gap) and the Greek adjective *leptos* (thin, slender), referring to the tiny generic gap between *Dimacrocaryon* and other binucleate species. Masculine gender.

Remarks: Although the nuclear pattern is as in *Dimacrocaryon*, Foissner (1984) established the genus *Rimaleptus* for binucleate dileptids which have an ordinary oral basket not lined by the curious granules so typical for *Dimacrocaryon*. Very likely, *Rimaleptus* and *Dimacrocaryon* are closely related because they have the same nuclear and ciliary pattern.

Foissner (1984) included only one species in *Rimaleptus*, viz., *Dileptus binucleatus*. In this monograph,

we add two new species and 15 binucleate *Dileptus* species. *Rimaleptus* contains at least two organization types, indicating that it might be polyphyletic. The first lineage, the *R. alpinus* group, comprises small to medium-sized species with two contractile vacuoles. The second lineage, the *R. mucronatus* group, collects small to middle-sized species with many contractile vacuoles. These two groups collate 12 species. The remaining six species are too incompletely described to be classified.

Life Observation-Based Key to Species of *Rimaleptus*

1 With zoochlorellae (grass green colour) 2
– Without zoochlorellae 5
2 Body broadly dileptid with rounded posterior end, about 160 µm long ..... *R. ovalis* (p. 181)
– Body narrowly to very narrowly dileptid with distinct tail or acute posterior third 3
3 A single subterminal contractile vacuole; body about 180 µm long ..... *R. nistroviensis* (p. 181)
– At least two dorsal contractile vacuoles 4
4 Macronuclear nodules globular; body about 300 µm long ..... *R. robustus* (p. 183)
– Macronuclear nodules pyriform; body about 300 µm long ..... *R. marouensis* (p. 184)
5 Strongly contractile, extended cells up to 500 µm long ..... *R. lacazei* (p. 185)
– Not or only slightly contractile 6
6 With very long tail occupying 1/4 of body length; body about 300 µm long *R. gabonensis* (p. 186)
– Posterior end narrowly rounded, acute or with short tail 7
7 Two dorsal contractile vacuoles ..... (*R. alpinus* group; p. 187) 8
– A dorsal row of contractile vacuoles, in some species also a ventral row .... (*R. mucronatus* group; p. 213) 13
8 Dileptid to narrowly dileptid with conspicuously rostrate proboscis; body about 150 µm long .... *R. conspicuus* (p. 187)
– Narrowly dileptid to rod-like with ordinary proboscis 9
9 Body length about 100 µm (up to 160 µm) 10
– Body length 150–400 µm 11
10 A single micronucleus between macronuclear nodules; body about 100 µm long .... *R. alpinus* (p. 191)
– Two micronuclei each attached laterally to macronuclear nodules; body about 125 µm long .... *R. bivacuolatus* (p. 195)
11 Extrusomes anchored both in proboscis oral bulge and oral opening; body about 180 µm long..... ..... *R. canadensis* (p. 196)
– Extrusomes anchored only in proboscis oral bulge 12
12 Extrusomes narrowly ovate; body about 175 µm long ..... *R. armatus* (p. 200)
– Extrusomes rod-like; body about 250 µm long ..... *R. binucleatus* (p. 207)
13 Proboscis about 1/5 of body length; body about 150 µm long ..... *R. brasiliensis* (p. 214)
– Proboscis 1/3–1/2 of body length 14
14 With distinct tail; body about 350 µm long ..... *R. mucronatus* (p. 217)
– Posterior body end rounded or acute 15
15 Macronuclear nodules globular; saline habitat; body about 230 µm long ..... *R. tirjakovae* (p. 228)
– Macronuclear nodules ellipsoidal to oblong; terrestrial 16
16 Ventral and dorsal contractile vacuoles; brush bristles up to 15 µm; body about 210 µm long..... ..... *R. longitrichus* (p. 232)

– Only dorsal contractile vacuoles; brush bristles short (~ 3 µm long) 17
17 Extrusomes rod-shaped, 6–10 µm long; body about 250 µm long ..... *R. similis* (p. 236)
– Extrusomes ellipsoidal to broadly fusiform, 1–2 µm long; body about 200 µm long..... ..... *R. orientalis* (p. 240)

Rimaleptus ovalis (Vuxanovici, 1959) nov. comb. (Figs 58a, b)

1959 *Dileptus ovalis* n. sp. Vuxanovici, Studii Cerc. Biol. **11**: 329

1963 *Dileptus ovalis* Vuxanovici, 1959 – Dragesco, Bull. biol. Fr. Belg. **97**: 124 (first taxonomic reviser)

Generic affiliation and taxonomy: We combine *Dileptus ovalis* with *Rimaleptus* because of the two macronuclear nodules and the ordinary oral basket. Full redescription is required although this species is easily identified by the broad body, the long proboscis, the broadly rounded posterior end, the peculiar contractile vacuole pattern, and the presence of symbiotic green algae. There are only three congeners with zoochlorellae: *R. marouensis*, *R. nistroviensis* and *R. robustus*, all having a narrowly to very narrowly dileptid body with an acute posterior third or a distinct tail.

Diagnosis: Length about 160 µm in vivo. Shape broadly dileptid with broadly rounded posterior end, proboscis about 1/2 of body length. Two globular, slightly separate macronuclear nodules. One contractile vacuole underneath oral bulge opening and three in dorsal side of trunk. With symbiotic green algae (zoochlorellae).

Type locality: Coast of Lake Floreasca, Bucharest, Roumania, E26°6' N44°28'.

Type material: Not available.

Etymology: Not given in original description. The Latin adjective *ovalis* obviously refers to the broad trunk.

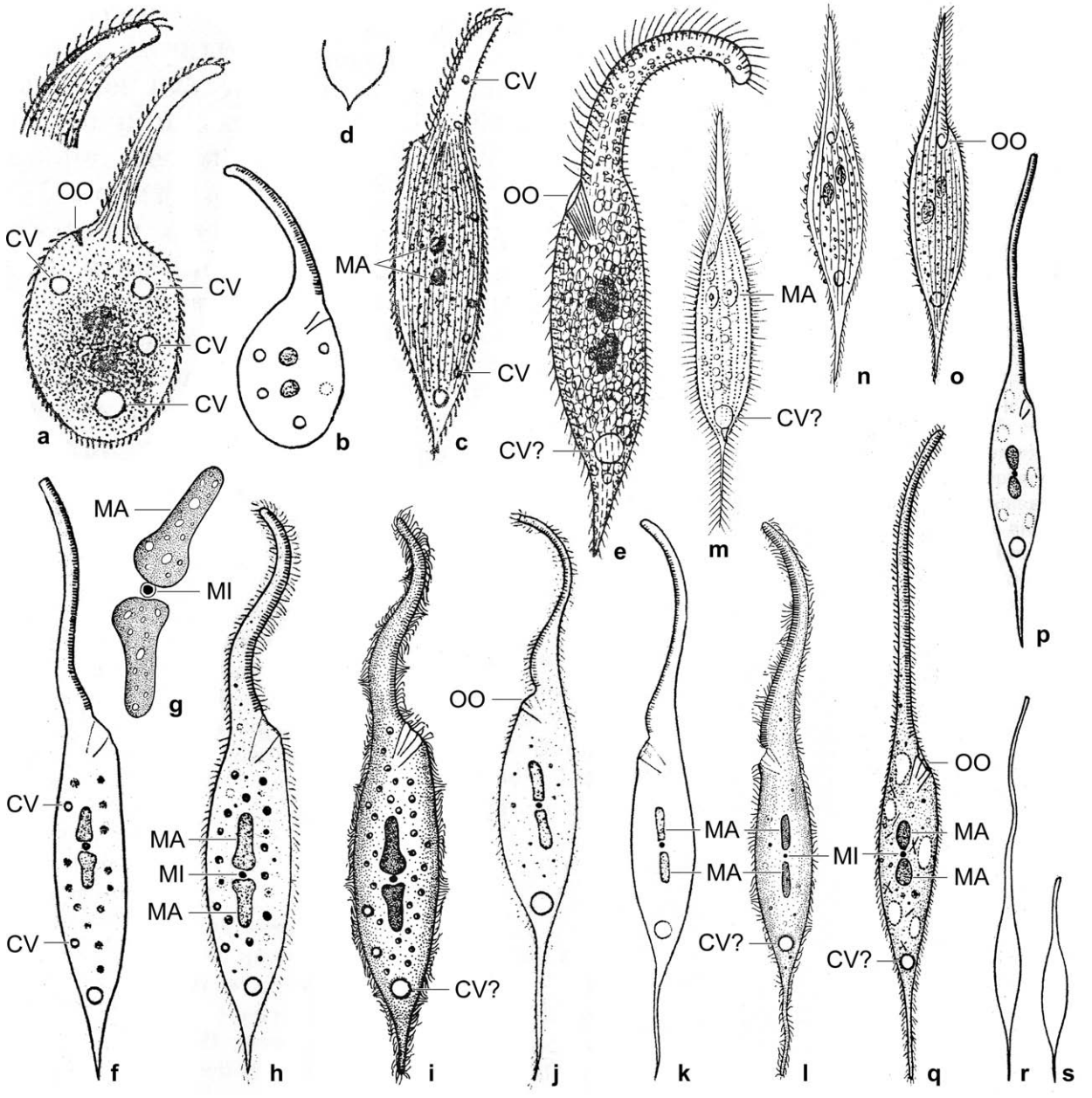
Description (type population): Length about 160 µm in vivo; slightly contractile. Shape broadly dileptid with a length:width ratio of 3:2 in extended specimens, while about 2.5:1 according to the figure provided (Fig. 58a). Proboscis half of body length or longer, distinctly set off from trunk, 8 µm wide at base and 6 µm at tip. Trunk of extended specimens broadly ellipsoidal, becoming globular in contracted (dying? authors) cells. Nuclear apparatus in middle portion of trunk; composed of two globular, slightly separate macronuclear nodules each about 11 µm across; micronuclei not studied. Contractile vacuole pattern extraordinary, that is, one vacuole posterior to oral bulge opening and three in dorsal side of trunk; first dorsal vacuole at level of ventral one. Extrusomes very fine, attached to proboscis oral bulge. Cytoplasm hyaline and transparent in proboscis, while opaque and green in trunk because packed with numerous refractile granules and globular, minute algae (zoochlorellae). Ciliature not studied. Pharyngeal basket inconspicuous as composed of fine, 9 µm-long rods. Swims slowly in circles 150–200 µm across by rotation about main body axis moving the proboscis to and fro (Figs 58a, b).

Occurrence and ecology: Vuxanovici (1959) discovered *Rimaleptus ovalis* in a sample with marsh plants from Lake Floreasca in Bucharest, Roumania during February 1958. Later, he found a single specimen on the coast of Lake Herăstrău in the vicinity of Lake Floreasca in May 1958. Very likely, this was a reorganizing cell or another species because it possessed many scattered macronuclear nodules and several ventral contractile vacuoles connected by a canal.

Rimaleptus nistroviensis (Chorik, 1967) nov. comb. (Fig. 58e)

1967 *Dileptus nistroviensis* nov. sp. Chorik, Izv. Akad. Nauk moldav. SSR **1**: 94

1968 *Dileptus nistroviensis* Chorik, 1967 – Chorik, Free-living ciliates: 71 (taxonomic revision)



Figs 58a, b: *Rimaleptus ovalis* from life, length 160 µm. **a** – left side view of type specimen and detail of anterior portion of proboscis (from VUXANOVICI 1959); **b** – redrawn type specimen (from DRAGESCO 1963). **Figs 58c, d:** *Rimaleptus robustus* from life, length 305 µm (from VUXANOVICI 1959). **c** – left side view of type specimen; **d** – detail of posterior body end of a slightly contracted specimen. **Fig. 58e:** *Rimaleptus nistroviensis* from life, length 170–190 µm (from CHORIK 1967). **Figs 58f–i:** *Rimaleptus marouensis* from life (f, h, i) and in a Feulgen preparation (g). From DRAGESCO 1963 (f, h), DRAGESCO 1966a (g), and DRAGESCO & DRAGESCO-KERNÉIS 1986 (i). **f, h, i** – left side view of specimens from Cameroun, length about 300 µm; **g** – nuclear apparatus of a French specimen. **Figs 58j–l:** *Rimaleptus gabonensis* from life, length 300 µm. From DRAGESCO 1963 (j, k) and DRAGESCO & DRAGESCO-KERNÉIS 1986 (l). **Figs 58m–s:** *Rimaleptus lacazei* from life. From GOURRET & ROESER 1886 (m), KAHL 1931 (n), and DRAGESCO 1963 (o–s). **m** – ventral view of contracted type specimen, length 200 µm; **n, o** – redrawings of type specimen; **p, q** – right side view of fully extended specimens, length about 500 µm; **r, s** – fully extended and contracted cell. CV – contractile vacuoles, MA – macronuclear nodules, MI – micronucleus, OO – oral bulge opening.

Generic affiliation and taxonomy: We combine *Dileptus nistroviensis* with *Rimaleptus* because of the two macronuclear nodules and the ordinary oral basket. Full redescription is required because many important features have not been described. *Rimaleptus nistroviensis* belongs to the small group of binucleate dileptids with symbiotic green algae, but is identified by the single subterminal contractile vacuole (very questionable, authors) and, possibly, by the extrusomes attached both to the proboscis oral bulge and the ventral side of the trunk, a unique feature as yet not found in any other dileptid, but highly reminiscent of the spathidiid genus *Cultellothrix* (Foissner & Xu 2007).

Diagnosis: Length about 180 μm in vivo. Shape very narrowly dileptid with distinct tail, proboscis up to half of body length. Two ellipsoidal macronuclear nodules each with a single micronucleus. Possibly a single contractile vacuole at base of tail. Extrusomes slightly curved rods attached to proboscis oral bulge and, possibly, to ventral side of trunk. With symbiotic green algae (zoochlorellae).

Type locality: Sand from the Dniester River, Moldavia.

Type material: Not available.

Etymology: Not given in original description. The Latin adjective *nistroviensis* refers to the Dniester River in which the species was discovered.

Description: Length 170–190 μm in vivo. Shape very narrowly dileptid with a length:width ratio of about 6.5:1, according to the figure provided. Proboscis occupies up to half of body length, slightly set off from oblong trunk; posterior end with distinct tail. Nuclear apparatus in middle portion of trunk, composed of two ellipsoidal, 15 μm-long macronuclear nodules each with a single micronucleus 4–5 μm across. A single contractile (defecation?) vacuole at base of tail. Extrusomes not described but figured as fine, slightly curved rods attached to both proboscis oral bulge and ventral side of trunk. Cytoplasm packed with symbiotic green algae (zoochlorellae). About nine meridionally arranged ciliary rows on one side of cell, according to the figure provided (Fig. 58e).

Occurrence and ecology: *Rimaleptus nistroviensis* was discovered in the sandy benthos of the Dniester River with an abundance of 20,000 ind./m^2 in October (Chorik 1967, 1968); later, it was found in the plankton from the Barnaulka River, Altai region, Russia (Èjdukajtene et al. 2004).

Rimaleptus robustus (Vuxanovici, 1959) nov. comb. (Figs 58c, d)

1959 *Dileptus robustus* n. sp. Vuxanovici, Studii Cerc. Biol. **11**: 328

1963 *Dileptus robustus* Vuxanovici, 1959 – Dragesco, Bull. biol. Fr. Belg. **97**: 125 (first taxonomic reviser)

Generic affiliation and taxonomy: We combine *Dileptus robustus* with *Rimaleptus* because of the two macronuclear nodules and the ordinary oral basket. Full redescription is required because many important features have not been described. In having symbiotic green algae, *R. robustus* is most similar to *R. marouensis*, *R. nistroviensis* and *R. ovalis*, but has conspicuously thick (vs. thin) extrusomes. Additionally, *R. marouensis* is distinguished by the shape of the macronuclear nodules (pyriform vs. globular); *R. nistroviensis* possibly differs by the contractile vacuole (a single subterminal vacuole vs. a dorsal row of vacuoles) and extrusome (attached to proboscis oral bulge and ventral side of trunk vs. only to proboscis oral bulge) pattern; and *R. ovalis* has a broadly (vs. narrowly) dileptid body and a different contractile vacuole pattern (one vacuole underneath oral bulge opening and three vacuoles in dorsal side of trunk vs. dorsal stripe of vacuoles).

Diagnosis: Length about 300 μm in vivo. Shape narrowly dileptid with acute posterior end, proboscis about 1/4 of body length. Two globular, slightly separate macronuclear nodules. A dorsal stripe of contractile vacuoles. Extrusomes thick and about 8 μm long. About 15 ciliary rows on one side of cell. With symbiotic green algae (zoochlorellae).

Type locality: Coast of Lake Herăstrău, Bucharest, Roumania, E26°05' N44°28'.

Type material: Not available.

Etymology: Not given in original description. The Latin adjective *robustus* possibly refers to the thick extrusomes.

Description: Vuxanovici's description is based on a single specimen observed in March 1958. Length 305 µm in vivo; slightly contractile. Shape narrowly dileptid with a length:width ratio of 4.8:1, according to the figure provided. Proboscis about one fourth of body length, distinctly set off from bluntly fusiform trunk, 24 µm wide at base and 15 µm at tip; posterior end acute, not disappearing when cell contracts (Fig. 58d). Nuclear apparatus in middle portion of trunk; composed of two globular, slightly separate macronuclear nodules each about 12 µm across; micronuclei not studied. A dorsal stripe of eight contractile vacuoles beginning in mid-proboscis. Extrusomes attached to proboscis oral bulge, thick and hence well recognizable at a magnification of ×280, about 8 µm long. Cytoplasm transparent, green due to many minute globular algae (zoochlorellae) 3–6 µm across. Cilia 4–5 µm long in vivo, arranged in 14–16 meridional rows on one side of cell; dorsal bristles short, recognizable in the preserved specimen. Oral basket short and fine (Fig. 58c).

Occurrence and ecology: As yet found only in a 10-day old water sample with decaying plants.

Rimaleptus marouensis (Dragesco, 1963) nov. comb. (Figs 58f–i)

1963 *Dileptus marouensis* n. sp. Dragesco, Bull. biol. Fr. Belg. **97**: 118

1966 *Dileptus marouensis* Dragesco – Dragesco, Protistologica **2**: 76 (notes on a French population)

1986 *Dileptus marouensis* Dragesco, 1963 – Dragesco & Dragesco-Kernéis, Faune tropicale **26**: 162 (taxonomic revision)

1988 *Dileptus maronensis* Dragesco, 1963 – Song, Packroff & Wilbert, Acta Protozool. **27**: 275 (incorrect subsequent spelling and therefore unavailable according to Articles 33.3 and 33.5 of the ICZN 1999)

Generic affiliation and taxonomy: We combine *Dileptus marouensis* with *Rimaleptus* because of the two macronuclear nodules and the ordinary oral basket. Full redescription is required because several important features have not been described, e.g., the extrusomes. *Rimaleptus marouensis* was studied in two populations, namely from Cameroun, Africa (Dragesco 1963) and Upper Savoy, France (Dragesco 1966a). They match very well in body shape and size and, especially, the pyriform shape of the macronuclear nodules, which are globular, ovate or oblong in most congeners. However, the French population differs from the African type by the lack of symbiotic green algae and may thus represent a distinct subspecies or species. Therefore, the diagnosis includes only data from the type population, while the description contains all observations.

Diagnosis (type population): Length about 300 µm in vivo. Shape very narrowly dileptid with distinct tail, proboscis about 40% of body length. Two pyriform macronuclear nodules with a single micronucleus in between. Two to four dorsal contractile vacuoles. With symbiotic green algae (zoochlorellae).

Type locality: Sand from a river in the village of Maroua, North Cameroun, Africa, E14°19' N10°36'.

Type material: Not available.

Etymology: Not given in original description. The Latin adjective *marouensis* obviously refers to the type locality.

Description: African type specimens about 300 µm long (Dragesco 1963, Dragesco & Dragesco-Kernéis 1986), French cells 250 µm on average (Dragesco 1966a). Shape very narrowly dileptid with a length:width ratio of about 7:1, according to the figures provided (Figs 58f, h, i). Proboscis occupies about

40% of body length, distinctly set off from bluntly fusiform trunk; posterior end with distinct tail. Nuclear apparatus in middle portion of trunk. Macronuclear nodules pyriform or bluntly clavate; many small to medium-sized nucleoli in French specimens. Micronucleus in between macronuclear nodules, globular, surrounded by a distinct membrane in Feulgen preparations (Figs 58f–i). Two to four dorsal contractile vacuoles; very likely, Dragesco (1963) and Dragesco & Dragesco-Kernéis (1986) misinterpreted the subterminal defecation vacuole as an additional contractile vacuole. African specimens green because packed with symbiotic algae, absent in French cells. French specimens with 28–30 ciliary rows (Dragesco 1966a).

Occurrence and ecology: As yet found at type locality (Dragesco 1963) and in sand from the Excenevex beach, Lake Léman, Upper Savoy, France (Dragesco 1966a).

Rimaleptus lacazei (Gourret & Roeser, 1886) nov. comb. (Figs 58m–s)

1886 *Amphileptus lacazei* (nov. sp.) Gourret & Roeser, Archs Zool. exp. gén. **4**: 468

1931 *Dileptus* (*Amphileptus*) *lacazei* (Gourr. u. R., 1886) – Kahl, Tierwelt Dtl. **21**: 208 (first taxonomic reviser, combination with *Dileptus*)

1963 *Dileptus lacazei* (Gourr. et Roes., 1886) – Dragesco, Bull. biol. Fr. Belg. **97**: 121 (second taxonomic reviser, redescription)

Generic affiliation and taxonomy: We combine *Dileptus lacazei* with *Rimaleptus* because of the two macronuclear nodules and the ordinary oral basket. Full redescription is required because important features, such as the extrusomes and morphometric data are lacking. Within the binucleate dileptids, *R. lacazei* is outstanding in having (i) a highly contractile proboscis and (ii) trunk protuberances with slightly elongated cilia. The first feature was emphasized in the original description and later confirmed by Dragesco (1963) in another French population. Interestingly, there are only two other highly contractile dileptids, viz., *Monomacrocaryon tenue* with an oblong macronucleus and *Pseudomonilicaryon dimorphum* with four macronuclear nodules. Among the congeners, *R. lacazei* resembles *R. tirjakovae*, which also lives in saline environments and possesses two globular macronuclear nodules. However, *R. tirjakovae* is acontractile and has an acute posterior body third (vs. a distinct tail).

Diagnosis (includes all information known): Length about 500 µm in vivo, contracts to less than 200 µm. Shape very narrowly dileptid to rod-like with long tail, proboscis highly contractile and about 1/2 of body length in extended cells. Two globular macronuclear nodules with a single micronucleus in between. Possibly a single contractile vacuole at base of tail. Cortex of trunk with small protuberances, bearing slightly elongated cilia.

Type locality: Brackish water from the wharf of Huiles in Marseille, France, E5°21' N43°19'.

Type material: Not available.

Etymology: Gourret & Roeser (1886) dedicated this species to Prof. H. de Lacaze-Duthiers.

Description: *Rimaleptus lacazei* was very incompletely described by Gourret & Roeser (1886). Fortunately, Dragesco (1963) found a dileptid highly resembling Gourret & Roeser's species in body shape, the pronounced contractility of the proboscis, the nuclear and contractile vacuole pattern as well as the marine habitat. Therefore, all data are put together emphasizing Dragesco's observations.

Length of contracted to semi-contracted cells about 200 µm in type population (Gourret & Roeser 1886) and 180–290 µm in Dragesco's specimens; fully extended cells over 500 µm long. Shape of contracted specimens very narrowly dileptid with a length:width ratio of 7.5–8.5:1 (Figs 58m–o, s), fully extended cells cylindroidally dileptid to rod-like with a length:width ratio of 10–16:1 (Figs 58p–r). Proboscis very conspicuous because usually occupying half or more of body length, highly contractile and flexible,

filiform and thus distinctly set off from trunk; in contracted cells shortened to a very narrowly triangular structure. Trunk bluntly fusiform, more or less flattened, only slightly broadened in contracted specimens. Tail occupies 15–25% of body length, distinctly set off from trunk, pointed posteriorly. Nuclear apparatus in middle portion of trunk, composed of two globular to broadly ellipsoidal macronuclear nodules with a single micronucleus in between; one nucleolus in centre of each nodule in type specimens. Contractile (defecation?) vacuole and cytopyge near base of tail. Extrusomes not described. Cortex of trunk with small protuberances bearing bundles of slightly elongated cilia in type population; not mentioned by Dragesco (1963). Cytoplasm colourless and hyaline, strongly vacuolated in Dragesco's specimens. Number of kineties not known, possibly few when the figure of Gourret & Roeser (1886) is assumed to be correct (Fig. 58m). Pharyngeal basket obconical, short (Figs 58m–s).

Occurrence and ecology: *Rimaleptus lacazei* was discovered in brackish water from the wharf of Huiles in Marseille, France (Gourret & Roeser 1886). Later, it was found near the type locality, i.e., the harbor of the town of Nice (Dragesco 1963). There are unsubstantiated limnetic record from the benthos of Lake Suviana, Tusco-Emilian Apennines, Italy (Madoni 1989, Dini et al. 1995) and the water bodies from the Apsheron Peninsula, Azerbaijan (Agamaliev & Aliev 1978; misspelled as *Dileptus legazei*).

Rimaleptus gabonensis (Dragesco & Dragesco-Kernéis, 1986) nov. comb. (Figs 58j–l)

1963 *Dileptus gabonensis* n. sp. (?) Dragesco, Bull. biol. Fr. Belg. **97**: 128 (unavailable)

1986 *Dileptus gabonensis* Dragesco, 1963 – Dragesco & Dragesco-Kernéis, Faune tropicale **26**: 163 (taxonomic revision)

Nomenclature: This species is not available in 1963 because it was conditionally proposed (Article 15.1 of the ICZN 1999). Thus, we use the date 1986, when Dragesco & Dragesco-Kernéis removed the question mark without providing a reason, however.

Generic affiliation and taxonomy: We combine *Dileptus gabonensis* with *Rimaleptus* because of the two macronuclear nodules and the ordinary oral basket. *Rimaleptus gabonensis* is a poorly described species, but easily distinguished from all congeners, except for *R. lacazei*, by the very long tail. *Rimaleptus lacazei* differs from *R. gabonensis* by the larger (over 500 µm vs. 300 µm) and highly contractile (vs. not contractile) body.

Diagnosis: Length about 300 µm in vivo. Shape very narrowly dileptid with long tail, proboscis about 40% of body length. Two oblong macronuclear nodules with a single micronucleus in between. Possibly a single contractile vacuole at base of tail.

Type locality: Sand from the village of Makokou, Gabon, Africa, E12°51' N33°50'. Neither Dragesco (1963) nor Dragesco & Dragesco-Kernéis (1986) specified the habitat.

Type material: Not available.

Etymology: Not given in original description. The Latin adjective *gabonensis* obviously refers to the country (Gabon) in which the species was discovered.

Description: Length about 300 µm in vivo. Shape very narrowly dileptid with a length:width ratio of about 8:1, according to the figures provided. Proboscis about 40% of body length, slightly set off from bluntly fusiform trunk, distinctly widened preorally; tail conspicuous because occupying about one fourth of body length. Nuclear apparatus in middle portion of trunk, composed of two oblong macronuclear nodules and a single micronucleus in between. Contractile (defecation?) vacuole at base of tail. Extrusomes, ciliature and oral apparatus not described.

Occurrence and ecology: As yet found only at type locality.

Table 28: Comparison of species of the *Rimaleptus alpinus* group.

Characteristics	*Rimaleptus alpinus*	*Rimaleptus armatus*	*Rimaleptus binucleatus*	*Rimaleptus bivacuolatus*	*Rimaleptus canadensis*	*Rimaleptus conspicuus*
Body size in vivo (µm)	110 × 15	175 × 25	250 × 35	125 × 25	180 × 25	150 × 55
Proboscis, % of body length (protargol)	30	27	35	25	23	48
Ciliary rows, average number	11	12	21	?	13	28
Extrusome shape	rod-shaped	narrowly ovate	rod-shaped	?	oblong	rod-shaped
Specialities	brush bristles up to 7 µm long	–	multi-rowed dorsal brush	two micronuclei	extrusomes also around oral opening	rostrate proboscis, multi-rowed dorsal brush

The *Rimaleptus alpinus* group

The six species of this group have two contractile vacuoles and two dorsal brush rows, except for *R. binucleatus* and *R. conspicuus* in which it is multi-rowed. Body shape and size as well as proboscis length and extrusome shape are rather different and thus useful species discriminators. Likewise, the number of ciliary rows and specialities separate some species easily and distinctly (Table 28).

Rimaleptus conspicuus (Kahl, 1931) nov. comb. (Figs 59a–l; Table 29)

1931 *Dileptus conspicuus* spec. n. Kahl, Tierwelt Dtl. **21**: 209

1943 *Dileptus conspicuus* Kahl – Kahl, Infusorien: 33 (taxonomic revision)

1953 *Dileptus conspicuus* Kahl 1931 – Wenzel, Arch. Protistenk. **99**: 84 (notes on a Bavarian population)

1955 *Dileptus conspicuus* var. *telobivacuolatus*, n. var. Gellért, Acta biol. hung. **6**: 84 (Hungarian variety)

1963 *Dileptus conspicuus* Kahl, 1931 – Dragesco, Bull. biol. Fr. Belg. **97**: 119 (first taxonomic reviser)

1989 *Dileptus conspicuus* Kahl, 1931 – Foissner, Sber. Akad. Wiss. Wien **196**: 175 (neotypification, authoritative redescription)

2005 *Dileptus conspicus* Kahl, 1931 – Tirjaková, Ciliates: 21 (figure of a Slovak specimen, incorrect subsequent spelling and therefore unavailable according to Articles 33.3 and 33.5 of the ICZN 1999; same mistake in Tirjaková 1997a and Tirjaková & Stloukal 2004)

Generic affiliation, nomenclature and taxonomy: We combine *Dileptus conspicuus* with *Rimaleptus* because of the two macronuclear nodules and the ordinary oral basket. Gellért (1955) described *Dileptus conspicuus* var. *telobivacuolatus* as follows (Fig. 59c): "Das Tier stimmt in jeder Beziehung mit Kahls Form überein, dennoch musste es als eine neue Varietät beschrieben werden, weil seine beiden pulsierenden Vakuolen terminal liegen, wogegen bei der typischen Form die eine Vakuole terminal, die andere in Höhe der Mundöffnung dorsal liegt. Von den beiden Vakuolen ist die ventrale stets kleiner, ihre Entleerungszeit beträgt 40 Sekunden, während die dorsal liegende Vakuole grösser ist, mit einer Entleerungszeit von 55 Sekunden. Gegenüber der 200 µm langen Form von Kahl, beträgt die Länge des vorliegenden Exemplares nur 110–120 µm. Plasma hell, bläulichgrün. Bewegung langsam, schwankend. Raubtier: ernährt sich von Protozoen. Kommt nicht häufig vor." If Gellért's observations can be confirmed, then *Rimaleptus conspicuus* should be split into two subspecies because the vacuole pattern is an important feature.

Foissner (1989) neotypified *R. conspicuus* with an Icelandic population, but did not provide the reasons.

However, we support the neotypification because (i) no type material is available from KAHL's (1931) specimens, (ii) the type locality is unclear, (iii) there are no doubts on the identification, (iv) the neotype is from the same biogeographic region and a similar habitat, and (v) the preparations are of good quality.

Within the binucleate dileptids, *R. conspicuus* is easily identified by the conspicuously rostrate proboscis. All congeners, except for *R. similis*, have a filiform or only slightly rostrate proboscis. *Rimaleptus similis* differs from *R. conspicuus* by the larger body size (on average 219 µm vs. 141 µm in protargol preparations), the less rostrate proboscis, and the higher number of contractile vacuoles (at least four vs. two).

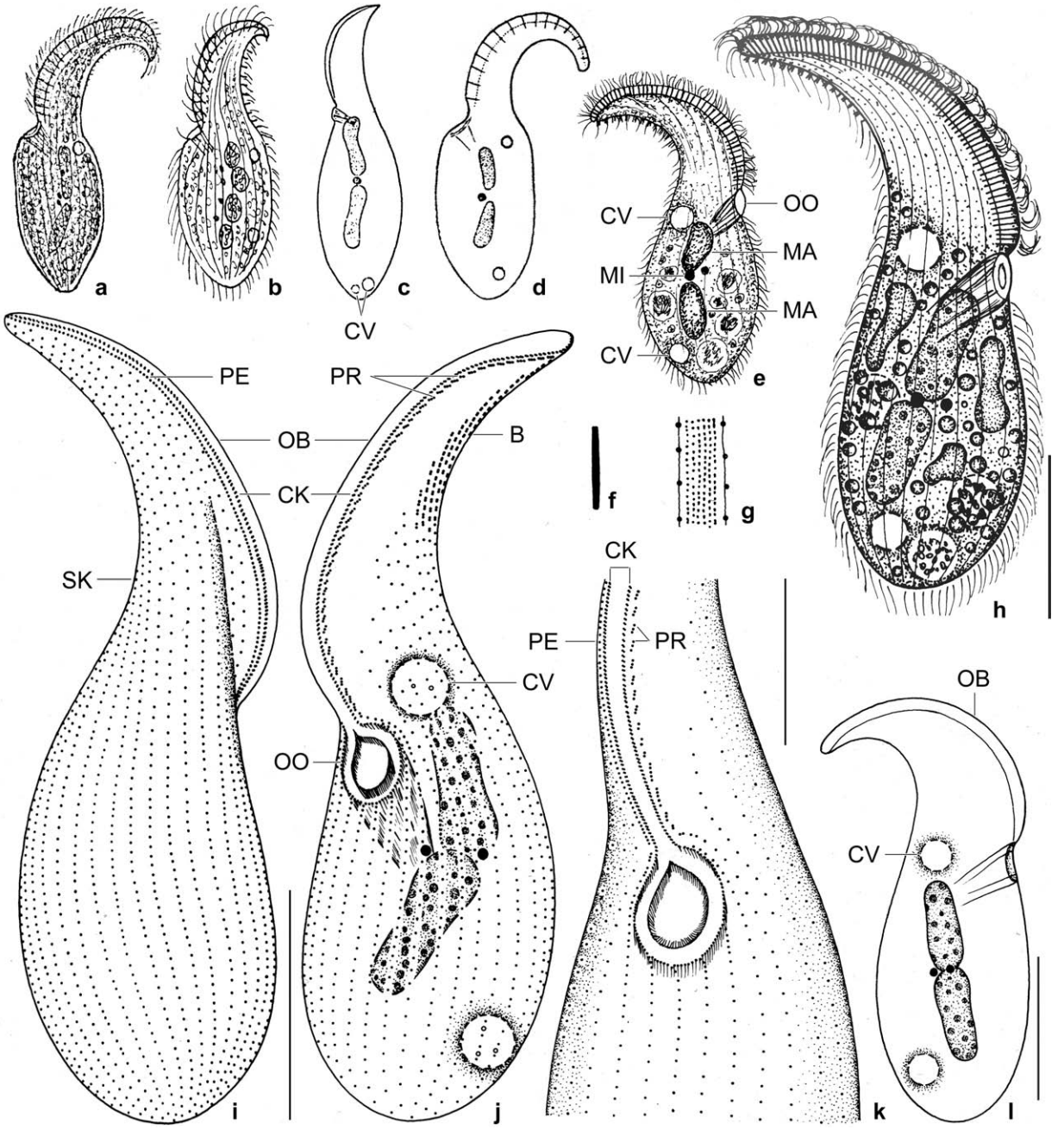
Improved diagnosis (includes all information known): Size about 150 × 55 µm in vivo. Shape dileptid to narrowly dileptid with broady rounded posterior end, proboscis conspicuously rostrate and about half of body length. Two oblong macronuclear nodules with 1–2 micronuclei in between. Two dorsal contractile vacuoles with 2–3 excretory pores each. Extrusomes rod-shaped, about 7 µm long. On average 28 ciliary rows, about 8 anteriorly differentiated into a staggered, distinctly heterostichad dorsal brush with bristles about 1.5 µm long. Oral bulge opening about 17 µm across. Preoral kineties strongly oblique, ordinarily spaced, usually composed of 3 narrowly spaced kinetids.

Type locality: KAHL (1931) did not specify any type locality, but referred to mosses from Zillertal, Austria and the Yosemite Valley, California, USA. The neotype is from the upper soil layer in the surroundings of the town of Thingvellier, SW Iceland, W21°10' N64°15'. According to Article 76.3 of the ICZN (1999), the place of origin of the neotype becomes the type locality of the nominal species-group taxon, despite any previously published statement of the type locality.

Type material: No type material is available from KAHL's specimens. FOISSNER (1989) deposited two

Table 29: Morphometric data on *Rimaleptus conspicuus* (from FOISSNER 1989). Data based on mounted, protargol-impregnated (Foissner's method), and randomly selected specimens from a non-flooded Petri dish culture. Measurements in µm. CV – coefficient of variation in %, Max – maximum, Mean – arithmetic mean, Min – minimum, n – number of specimens investigated, SD – standard deviation, SE – standard error of mean.

Characteristics	Mean	M	SD	SE	CV	Min	Max	n
Body, length	140.7	140.0	14.8	4.5	10.5	120.0	161.0	11
Body, width	41.6	41.0	5.2	1.6	12.4	34.0	52.0	11
Body length:width, ratio (calculated from original data)	3.4	3.3	0.4	0.1	12.0	2.8	4.1	11
Anterior body end to oral bulge opening, distance	67.5	70.0	5.2	1.6	7.7	56.0	75.0	11
Proboscis, % of body length (calculated from original data)	48.2	48.6	3.5	1.1	7.3	43.5	54.2	11
Oral bulge opening, diameter	12.5	12.5	1.6	0.7	13.2	11.0	14.0	6
Nuclear figure, length	47.8	48.0	4.5	1.3	9.3	42.0	56.0	11
Macronuclear nodules, length	26.5	27.0	1.6	0.5	6.2	24.0	28.0	11
Macronuclear nodules, width	10.7	10.0	1.3	0.4	11.9	10.0	14.0	11
Macronuclear nodules, number	2.0	2.0	0.0	0.0	0.0	2.0	2.0	11
Micronucleus, largest diameter	2.6	2.5	0.7	0.2	28.1	2.0	5.0	11
Micronuclei, number	2.0	2.0	0.0	0.0	0.0	2.0	2.0	11
Ciliary rows, number	28.2	28.0	1.9	0.6	6.7	25.0	32.0	11
Cilia in mid-body in 10 µm, number	6.2	6.0	1.1	0.3	17.4	5.0	8.0	11
Dorsal brush rows, number	8.1	8.0	1.1	0.3	14.0	7.0	10.0	11



Figs 59a–l: *Rimaleptus conspicuus* from life (a, b, d–h, l), after mercuric chloride fixation (c), and after protargol impregnation (i–k). From Kahl 1931 (a, b), Gellért 1955 (c), Dragesco 1963 (d), Tirjaková 2005 (e), and Foissner 1989 (h–l). **a, b** – specimens from type population, length 200 µm and 180 µm, respectively. The proboscis is very conspicuous because occupying almost half of the body length and distinctly rostrate, that is, comparatively stout, leaf-like flattened, curved dorsally, and indistinctly set off from the trunk providing cells with an *Arcuospathidium*-like appearance; **c** – *Dileptus conspicuus* var. *telobivacuolatus*; **d** – redrawing of Kahl's specimen; **e** – Slovak specimen, length 150–160 µm; **f** – extrusomes are rod-shaped and 7 µm long; **g** – surface view showing cortical granulation; **h** – representative Islandic neotype specimen, length 180 µm; **i, j** – ciliary pattern of right and left side and nuclear apparatus of main neotype specimen, length 140 µm; **k** – oral ciliary pattern; **l** – right side view showing general body organization. B – dorsal brush, CK – circumoral kinety, CV – contractile vacuoles, MA – macronuclear nodules, MI – micronucleus, OB – oral bulge, OO – oral bulge opening, PE – perioral kinety, PR – preoral kineties, SK – somatic kineties. Scale bars: 20 µm (k), 40 µm (i, j), and 50 µm (h, l).

neotype slides (inv. nos 1988/94 and 1988/95) with protargol-impregnated Icelandic specimens in the Biology Centre of the Museum of Upper Austria, Linz (LI). Relevant specimens are marked by black ink circles on the coverslip.

Etymology: Not given in original description. The Latin adjective *conspicuus* refers to the conspicuous habitus of the species.

Description: This species has been studied in several populations that match very well. Therefore, the description summarizes all observations.

Size usually about 150 × 55 μm in vivo. Type specimens up to 200 μm long (Kahl 1931), Icelandic neotype individuals 140–180 × 40–70 μm (Foissner 1989), Bavarian cells 125–180 μm (Wenzel 1953), Slovak specimens 150–160 μm (Tirjaková 2005). Body very flexible but not contractile. Shape dileptid to narrowly dileptid, i.e., length:width ratio 2.8–4.1:1, on average 3.4:1 (Table 29). Proboscis very conspicuous because occupying almost half of body length and distinctly rostrate, that is, comparatively stout, leaf-like flattened, curved dorsally, and indistinctly set off from trunk providing cells with an *Arcuospathidium*-like appearance. Trunk not flattened, ellipsoidal (Figs 59a–e, h–j, l). Typically two oblong macronuclear nodules in centre of trunk; nodules slightly pyriform in Icelandic neotype specimens, about 27 × 10 μm in size after protargol impregnation (Table 29); rarely four nodules (Kahl 1931, Wenzel 1953), a pattern typical for reorganizing exconjugants (Fig. 59b); nucleoli globular and evenly distributed in nodules. One or two micronuclei in between macronuclear nodules or near vertex formed by the abutting nodules, 4–6 μm across in vivo, while 2–5 μm in protargol preparations (Figs 59a–h, j, l; Table 29). Typically two dorsal contractile vacuoles each with two to three intrakinetal pores: anterior vacuole at level of oral bulge opening, posterior vacuole subterminal and surrounded by many small vacuoles in neotype cells (Figs 59a, b, d, e, h, j, l). Extrusomes studied only in Icelandic neotype population, inconspicuous, i.e., rod-shaped and 7 μm long, arranged in several rows in proboscis oral bulge (Fig. 59f). Cortex very flexible, colourless, contains about six oblique granule rows between adjacent kineties (Fig. 59g). Cytoplasm colourless, hyaline in proboscis, opaque in trunk because packed with globular and irregular lipid droplets 2–15 μm across and about 12 μm-sized food vacuoles containing *Leptopharynx costatus*, rarely also diatoms; in trunk end sometimes a defecation vacuole with granular contents. Cytopyge in posterior pole. Swims slowly appearing awkward.

Cilia ordinarily to narrowly spaced, arranged in an average of 28 ordinarily spaced, meridional rows following body curvature (Table 29). Right side rows gradually shortened along oral bulge; perioral kinety extends to tip of proboscis with narrowly spaced basal bodies (Fig. 59i). Blank stripe on left side of proboscis distinct, although some ciliary rows extend above proximal half of proboscis (Figs 59j, k). Dorsal brush on dorsal and left side of proboscis; staggered; distinctly heterostichad; composed of an average of eight rows with loosely to ordinarily spaced dikinetids associated with 1–1.5 μm long bristles (Fig. 59j; Table 29).

Oral bulge opening about 17 μm across in vivo. Pharyngeal basket obconical, well recognizable in vivo. Oral bulge distinct due to the nice metachronal ciliary waves. Circumoral kinety composed of narrowly spaced dikinetids in proboscis and narrowly spaced monokinetids around oral bulge opening. About 50 strongly oblique, ordinarily spaced preoral kineties, as estimated from Fig. 59j, each composed of two to four, usually three narrowly spaced kinetids, forming strongly oblique rows (Figs 59j, k).

Occurrence and ecology: *Rimaleptus conspicuus* is a rare species usually having low abundances. Typically, it occurs in mosses and soil, rarely in limnetic habitats. As yet recorded only from two main biogeographic regions: the Holarctic (both in Palearctic and Nearctic; e.g., Kahl 1931; Patrick 1961; Foissner 1989; Tirjaková 1997a, 2005; Tirjaková & Stloukal 2004) and the Australis (Blatterer & Foissner 1988), indicating that it might have restricted distribution.

Records from terrestrial habitats: eight specimens in mosses from the Zillertal in Austria and six specimens in mosses from the Yosemite Valley, California, USA (Kahl 1931); upper soil layer (0–5 cm) with moder humus covered by *Betula pubescens*, *Vaccinium uligunosum* and *Galium* sp. in the surroundings of the town of Thingvellier, SW Iceland (Foissner 1989); rare in two moss samples from the Erlangen area in Bavaria, Germany (Wenzel 1953); in mosses from the National Nature Reserve Devínska Kobyla Hill in the vicinity of the town of Bratislava, Slovakia (Tirjaková 2005); in the thin humus layer under the lichen *Parmelia saxatilis* from the Magoska Hill (737 m above sea level), NE of the village of Boldogkőváralja, Hungary (Gellért 1955); garden soil from Hungary (Biczók 1959); upper soil layer (0–5 cm) with litter and sand (pH 4.5) from a coastal forest in the Royal National Park south of Sydney, Australia, 100 m above sea level (Blatterer & Foissner 1988); lightly burnt soil in New Zealand (Stout 1961).

Records from limnetic habitats (all unsubstantiated): in a shallow streamlet covered by leaves in autumn and in the gravel substrate of a spring area below the Veľký Javorník (Little Carpathian Mts.) in the vicinity of the town of Bratislava, Slovakia (Tirjaková 1997a; Tirjaková & Stloukal 2004); in the winter fauna of the Yuelushan area, China (Yang 1989); Yellow River, Lanzhou, China (Ma 1994); in the Rock Creek, SE of Gettysburg, Pennsylvania, USA (Patrick 1961); in a campus pond of the University of Colorado, USA (Hamilton 1943); 12 ind./l in a fishless, intermittent pond in Vandorf, Ontario, Canada (Andrushchyshyn et al. 2006).

Rimaleptus alpinus (Kahl, 1931) nov. comb. (Figs 60a–j; Table 30)

1931 *Dileptus alpinus* spec. n. Kahl, Tierwelt Dtl. **21**: 209

1943 *Dileptus alpinus* Kahl – Kahl, Infusorien: 33 (first taxonomic reviser)

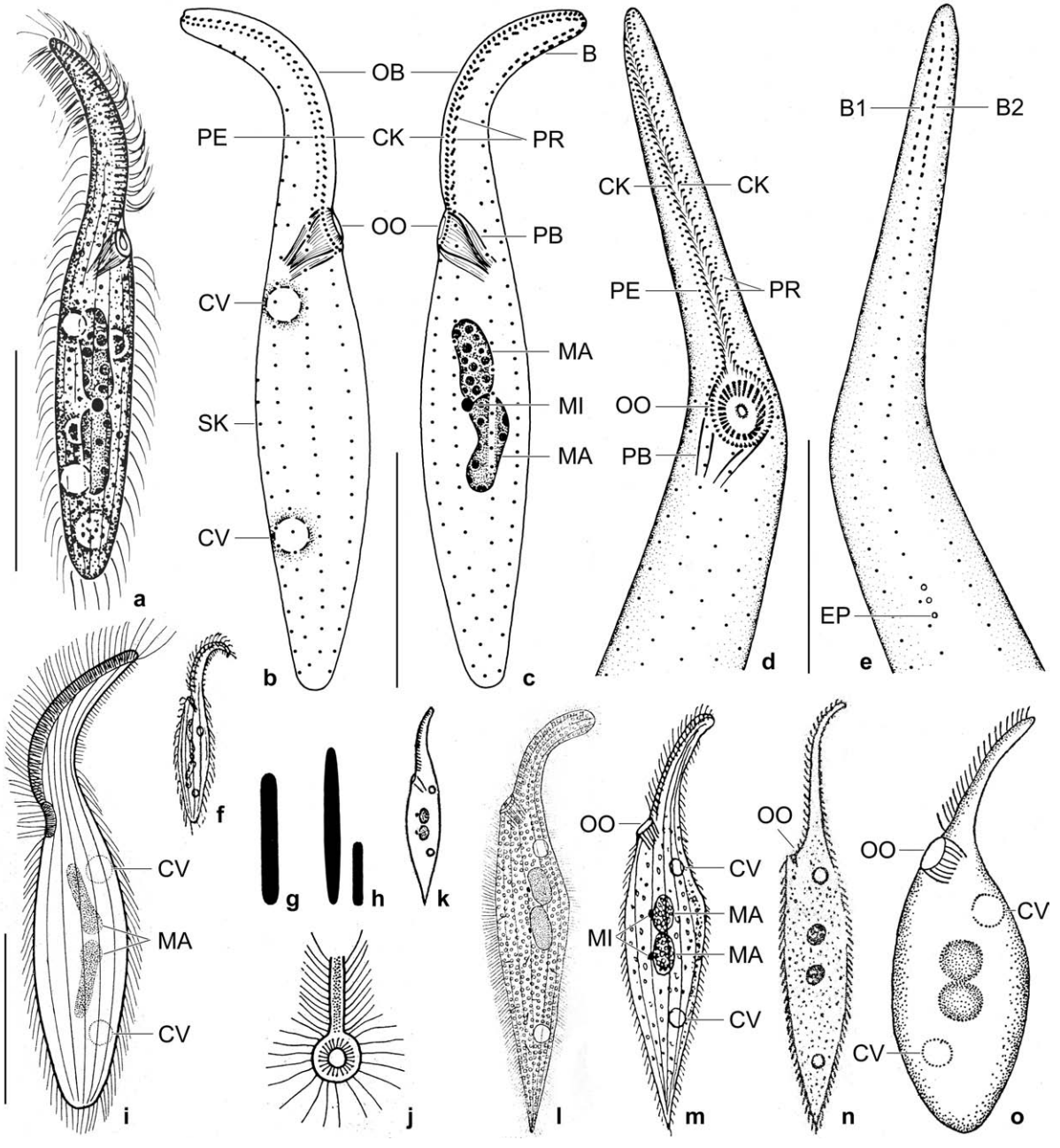
1953 *Dileptus alpinus* Kahl 1931 – Wenzel, Arch. Protistenk. **99**: 83 (description of a Bavarian population)

1963 *Dileptus alpinus* Kahl, 1931 – Dragesco, Bull. biol. Fr. Belg. **97**: 124 (second taxonomic reviser)

1989 *Dileptus alpinus* Kahl, 1931 – Foissner, Sber. Akad. Wiss. Wien **196**: 184 (neotypification, authoritative redescription)

Generic affiliation, nomenclature and taxonomy: We combine *Dileptus alpinus* with *Rimaleptus* because of the two macronuclear nodules and the ordinary oral basket. This species was established by Kahl in 1931, not 1932 as frequently listed (Blatterer & Foissner 1988, Foissner 1996b, Chrenková & Tirjaková 2000, Tirjaková 1997a, Tirjaková & Stloukal 2004, Bartošová & Tirjaková 2008). Foissner (1989) neotypified *R. alpinus* with a Bavarian population without providing the reasons. However, we support neotypification because (i) the identity is endangered by several similar species, e.g., *R. bivacuolatus*, (ii) no type material is available from Kahl's (1931) specimens, (iii) there are no doubts on identification, (iv) the neotype is from the same biogeographic region and a similar habitat, and (v) the preparations have sufficient quality.

Within the *R. alpinus* group, *R. alpinus* is outstanding in having long brush bristles (up to 7 μm vs. 2–3 μm), a feature originally mentioned by Kahl (1931) and later confirmed in two other populations (Foissner 1989, unpublished observations). Long to very long bristles occur also in *R. longitrichus* which, however, differs from *R. alpinus* in body size (210 × 30 μm vs. 110 × 15 μm) and the contractile vacuole pattern (multivacuolate vs. bivacuolate). *Rimaleptus alpinus* is most similar to *R. binucleatus* and *R. bivacuolatus*. However, *R. binucleatus* is distinguished from *R. alpinus* by the larger size (300 μm vs. 110 μm on average) and the double number of ciliary rows (19–25 vs. 10–12). The South American *R. bivacuolatus* differs from *R. alpinus*, at the present state of knowledge, only in the nuclear apparatus (each macronuclear nodule with a laterally attached micronucleus vs. a single micronucleus in between macronuclear nodules).



Figs 60a–j: *Rimaleptus alpinus* from life (a, f–j) and after protargol impregnation (b–e). From KAHL 1931 (f), WENZEL 1953 (i, j), FOISSNER 1989 (a–e), and originals (g, h). **a** – left side view of a representative neotype specimen, length 100 µm; **b, c** – right and left side ciliary and contractile vacuole pattern as well as nuclear apparatus of main neotype specimen, length 110 µm; **d, e** – ciliary pattern of ventral and dorsal side in anterior body half; **f** – type specimen, length 100 µm; **g, h** – extrusomes of Dutch (g) and Finnish (h) specimens. Type I is 5–6 µm long, while type II is only 2.5–3 µm long; **i, j** – overview and oral bulge opening of a Bavarian specimen, length 115 µm.

Figs 60k–o: *Rimaleptus bivacuolatus* from life. **k, m** – redrawn type specimen, according to DRAGESCO (1963) and KAHL (1931); **l** – type specimen, length 130 µm (from da CUNHA 1913); **n** – Roumanian specimen, length 380 µm (from VUXANOVICI 1959); **o** – Czech specimen, length 130 µm (from MORAVCOVÁ 1962).

B(1, 2) – dorsal brush (rows), CK – circumoral kinety, CV – contractile vacuoles, MA – macronuclear nodules, MI – micronucleus, OB – oral bulge, OO – oral bulge opening, PB – pharyngeal basket, PE – perioral kinety, PR – preoral kineties, SK – somatic kineties. Scale bars: 20 µm (d, e), 30µm (b, c), and 40 µm (a, i).

Table 30: Morphometric data on *Rimaleptus alpinus* (from FOISSNER 1989). Data based on mounted, protargol-impregnated (Foissner's method), and randomly selected specimens from a non-flooded Petri dish culture. Measurements in µm. CV – coefficient of variation in %, Max – maximum, Mean – arithmetic mean, Min – minimum, n – number of specimens investigated, SD – standard deviation, SE – standard error of mean.

Characteristics	Mean	M	SD	SE	CV	Min	Max	n
Body, length	103.7	100.0	15.6	4.7	15.0	85.0	130.0	11
Body, width	14.7	15.0	1.9	0.6	12.9	11.0	18.0	11
Body length:width, ratio (calculated from original data)	7.1	7.0	1.3	0.4	18.6	5.4	10.2	11
Anterior body end to oral bulge opening, distance	30.9	30.0	6.2	1.9	20.1	22.0	42.0	11
Proboscis, % of body length (calculated from original data)	29.7	31.4	2.9	0.9	9.9	24.1	32.3	11
Oral bulge opening, diameter	5.4	5.5	0.7	0.2	12.5	4.0	7.0	11
Nuclear figure, length	22.8	22.0	4.4	1.3	19.5	15.0	32.0	11
Macronuclear nodules, length	12.8	13.0	2.2	0.7	17.4	10.0	17.0	11
Macronuclear nodules, width	5.2	5.0	0.9	0.3	17.4	4.0	7.0	11
Macronuclear nodules, number	2.0	2.0	0.0	0.0	0.0	2.0	2.0	11
Micronucleus, largest diameter	1.6	1.6	–	–	–	1.4	2.0	11
Micronucleus, number	1.0	1.0	0.0	0.0	0.0	1.0	1.0	11
Ciliary rows, number	11.1	11.0	0.7	0.2	6.3	10.0	12.0	11
Cilia in mid-body in 10 µm, number	5.2	5.0	1.1	0.3	20.7	4.0	8.0	11
Dorsal brush rows, number	2.0	2.0	0.0	0.0	0.0	2.0	2.0	11

Improved diagnosis (includes all information known): Size about 110 × 15 µm in vivo. Shape narrowly to cylindroidally dileptid with narrowly rounded posterior end, proboscis about 30% of body length. Two oblong macronuclear nodules with a micronucleus in between. Two dorsal contractile vacuoles with several excretory pores each. Two size-types (5–6 µm and 2.5–3 µm) of rod-shaped extrusomes attached to proboscis oral bulge. On average 11 ciliary rows, 2 staggered and differentiated into an isostichad dorsal brush with bristles up to 7 µm long. Oral bulge opening about 6 µm across. Preoral kineties oblique to strongly oblique, ordinarily to narrowly spaced, usually composed of 2 narrowly spaced kinetids.

Type locality: KAHL (1931) discovered *D. alpinus* in moss from the Brenner pass region, i.e., the border of Austria and Italy in Tyrol, E11°30' N46°59'. The neotype is from mosses of the Schönramer Filz close to the towns of Salzburg, Austria and Freilassing, Bavaria, Germany, E12°59' N47°51' (FOISSNER 1989). According to Article 76.3 of the ICZN (1999), the place of origin of the neotype becomes the type locality of the nominal species-group taxon, despite any previously published statement of the type locality.

Type material: No type material is available from KAHL's specimens. FOISSNER (1989) deposited two neotype slides (inv. nos 1988/6 and 1988/7) with protargol-impregnated Bavarian specimens in the Biology Centre of the Museum of Upper Austria, Linz (LI). Relevant specimens are marked by black ink circles on the coverslip.

Etymology: Not given in original description. The Latin adjective *alpinus* refers to the Alps, where the species was discovered.

Description: All data are put together because the morphological conspecificity of the populations mentioned in the list of synonyms is beyond reasonable doubts. However, the review emphasizes the data of FOISSNER (1989), who provided the most detailed description.

Size in vivo similar in various populations, usually about 110 × 15 µm. Type specimens 100–120 µm long (Kahl 1931), Bavarian cells 60–160 µm, on average 113 µm (Wenzel 1953); Bavarian neotype specimens 100 × 15 µm on average in protargol preparations (Foissner 1989; Table 30). Shape narrowly to cylindroidally dileptid with a length:width ratio of an average of 7:1 after protargol impregnation (Table 30). Proboscis about 30% of body length, more or less distinctly curved dorsally; trunk oblong to bluntly fusiform, posterior end narrowly rounded (Figs 60a–c, i, f; Table 30). Nuclear apparatus in centre of trunk. Macronuclear nodules ellipsoidal to oblong, i.e., length:width ratio 2–4.5:1, on average 2.8:1, size about 13 × 5 µm in protargol preparations; nucleoli globular and evenly distributed. Micronucleus in between macronuclear nodules, possibly close to nodule vertex in some specimens, 1.4–2 µm across in protargol preparations (Figs 60a, c, i, f; Table 30). Contractile vacuole pattern very similar in all populations investigated: anterior vacuole underneath level of oral bulge opening, posterior vacuole at beginning of last fourth of trunk; number of excretory pores studied only in neotype specimens, i.e., each vacuole with three pores one after the other right of the kinety bearing brush row 2; Wenzel (1953) observed some specimens with a pair of contractile vacuoles each in anterior and posterior portion of trunk (Figs 60a, b, e, i, f). Extrusomes studied in two populations from The Netherlands and Finland (Figs 60g, h): type I rod-like with very slightly narrowed ends in Finnish specimens, about 5–6 × 0.8 µm in size; type II present only in Finnish cells, oblong and 2.5–3 µm long, possibly overlooked in the other populations. Cytoplasm colourless and hyaline; sometimes a defecation vacuole with granular material in rear body end.

Cilia ordinarily spaced; arranged in an average of 11 ordinarily spaced, meridional rows anteriorly gradually shortened along right side of oral bulge, except for perioral kinety which extends with comparatively loosely spaced basal bodies to tip of proboscis (Figs 60b, d; Table 30). Both sides of proboscis with a blank stripe, that on left side broader because some ciliary rows end at level of oral bulge opening (Figs 60b, c). Dorsal brush exactly on dorsal side of proboscis, composed of two staggered, isostichad rows (Figs 60c, e; Table 30). Brush bristles conspicuous because up to 7 µm long, as originally mentioned by Kahl (1931) in the description of *Dileptus americanus*, and later confirmed in the Bavarian neotype (Foissner 1989).

Oral bulge opening at beginning of second third of body, about 6 µm across in protargol preparations, projects indistinctly because base of proboscis almost as wide as trunk (Figs 60d, j; Table 30). Pharyngeal basket bulbous, distinct both in vivo and after protargol impregnation (Figs 60a–d). Circumoral kinety composed of loosely to ordinarily spaced dikinetids, except for narrowly spaced monokinetids around oral bulge opening. About 25 oblique to strongly oblique, ordinarily to narrowly spaced preoral kineties, as estimated from figures, each composed of two to three narrowly spaced cilia (Figs 60c, d).

Occurrence and ecology: *Rimaleptus alpinus* is a moss and soil species that has been recorded in a variety of terrestrial and semi-terrestrial habitats from all biogeographic regions (Foissner 1998). It is well adapted to terrestrial habitats by the small and highly flexible body.

Records from the Holarctis: in moss from the Brenner pass region, Austrian Alps, 2500 m above sea level (Kahl 1931); in mosses, lichens, leaf and needle litter (pH 4.8–5.2) from the Erlangen area in Bavaria, Germany (Wenzel 1953); in mosses, litter and soil from various forests in Austria and Germany (Foissner 1989, 2000; Aescht & Foissner 1993; Foissner et al. 2005); in very sandy soil and inland sand dunes from Germany and The Netherlands (Verhoeven 1999, 2001; Foissner & Al-Rasheid 2007); in soil, mosses, leaf litter, bark and decaying wood mass of various trees from several localities in Slovakia (Tirjaková & Matis 1987; Chrenková & Tirjaková 2000; Bartošová & Tirjaková 2005, 2008; Tirjaková 2005); in a shallow streamlet covered by leaves below the Veľký Javorník (Little Carpathian Mts.) in the vicinity of the town of Bratislava, Slovakia (Tirjaková 1997a, Tirjaková & Stloukal 2004); lakes around Mt. Fuji, Japan (Sudzuki 1971); Canadian grassland (Bick & Buitkamp 1976).

Records from the Australis and the Paleo- and Neotropis: in 10 out of 21 sites investigated in Australia

(Blatterer & Foissner 1988); in humic brown soil (pH 5.1) from a floodplain primary (?) forest on one of the many small islands in the Rio Amazonas, about 20 km east of Manaus, Janauari region, Brazil (Foissner 1997b); in leaf litter and soil from three sites in the Shimba Hills Nature Reserve, Kenya, equatorial Africa (Foissner 1999).

Records from Antarctica and islands in the southern oceans: in the grass sward of a sheltered, north-facing slope on Signy Island, and in moss (*Drepanocladus uncinatus*) from Sealer Hill, Byers Peninsula, Livingstone Island (Foissner 1996b).

Rimaleptus bivacuolatus (da Cunha, 1913) nov. comb. (Figs 60k–o)

1913 *Dileptus bivacuolatus* n. sp. da Cunha, Mem. Inst. Oswaldo Cruz **5**: 113

1931 *Dileptus bivacuolatus* da Cunha, 1913 – Kahl, Tierwelt Dtl. **21**: 207 (first taxonomic reviser)

1959 *Dileptus bivacuolatus* Da Cunha 1915 – Vuxanovici, Studii Cerc. Biol. **11**: 328 (misdated, very likely a misidentification)

1962 *Dileptus* cf. *bivacuolatus* Da Cunha – Moravcová, Sb. vys. Šk. chem.-technol. Praze **6**: 379 (very likely a misidentification)

1963 *Dileptus bivacuolatus* Da Cunha, 1913 – Dragesco, Bull. biol. Fr. Belg. **97**: 117 (second taxonomic reviser)

Generic affiliation and taxonomy: We combine *Dileptus bivacuolatus* with *Rimaleptus* because of the two macronuclear nodules and the ordinary oral basket. Full redescription is required because important features have not been described. *Rimaleptus bivacuolatus* is almost unique in having a micronucleus each attached laterally to the macronuclear nodules. All congeners, except for *R. nistroviensis*, have a single micronucleus between the macronuclear nodules. *Rimaleptus nistroviensis* differs from *R. bivacuolatus* by the symbiotic green algae and the contractile vacuole pattern (a subterminal vacuole vs. two dorsal vacuoles).

We doubt the observations of da Cunha (1913) because he did not stain the nucleus. Indeed, if one assumes an ordinary nuclear pattern, this species would be a senior synonym of *R. alpinus*. As concerns Vuxanovici's (1959) and Moravcová's (1962) populations, they very likely represent another species each. The Roumanian specimen is much larger (380 µm vs. up to 150 µm) and has a narrower and longer proboscis (Fig. 60n), while the Czech cell has a ventral and a dorsal contractile vacuole (vs. two dorsal vacuoles, cp. Fig. 60o with Figs 60k–m). Further, neither Vuxanovici (1959) nor Moravcová (1962) described the micronuclei, a key feature of *R. bivacuolatus*. Therefore, their observations are not included in the diagnosis and description.

Diagnosis (based on Brazilian populations): Size about 125 × 25 µm in vivo. Shape very narrowly dileptid with acute posterior end, proboscis about 1/4 of body length. Two ellipsoidal, abutting macronuclear nodules and a micronucleus each attached laterally to macronuclear nodules. Two contractile vacuoles in dorsal side of trunk.

Type locality: Da Cunha (1913) did not specify the type locality and habitat. However, the Rio de Janeiro area can be assumed to be the type locality, and the habitat was very likely freshwater, which da Cunha studied most of his life.

Type material: Not available.

Etymology: Not given in original description. Composite of the Latin numeral *bi* (two) and the noun *vacuola*, referring to the two contractile vacuoles.

Description (according to the Brazilian populations): Size 100–150 × 20–30 µm in vivo. Shape very narrowly dileptid with a length:width ratio of about 5.5:1, according to the figure provided (Fig. 60l).

Proboscis comparatively massive, occupies about one fourth of body length, slightly set off from bluntly fusiform trunk; posterior body region gradually narrowed to an acute end. Nuclear apparatus as described in the diagnosis. Two dorsal contractile vacuoles: anterior vacuole at first quarter of trunk, posterior vacuole at beginning of last quarter. Extrusomes not described but shown as fine rods attached to proboscis oral bulge and scattered throughout cytoplasm. About five meridionally arranged ciliary rows on one side of cell, according to Fig. 60l.

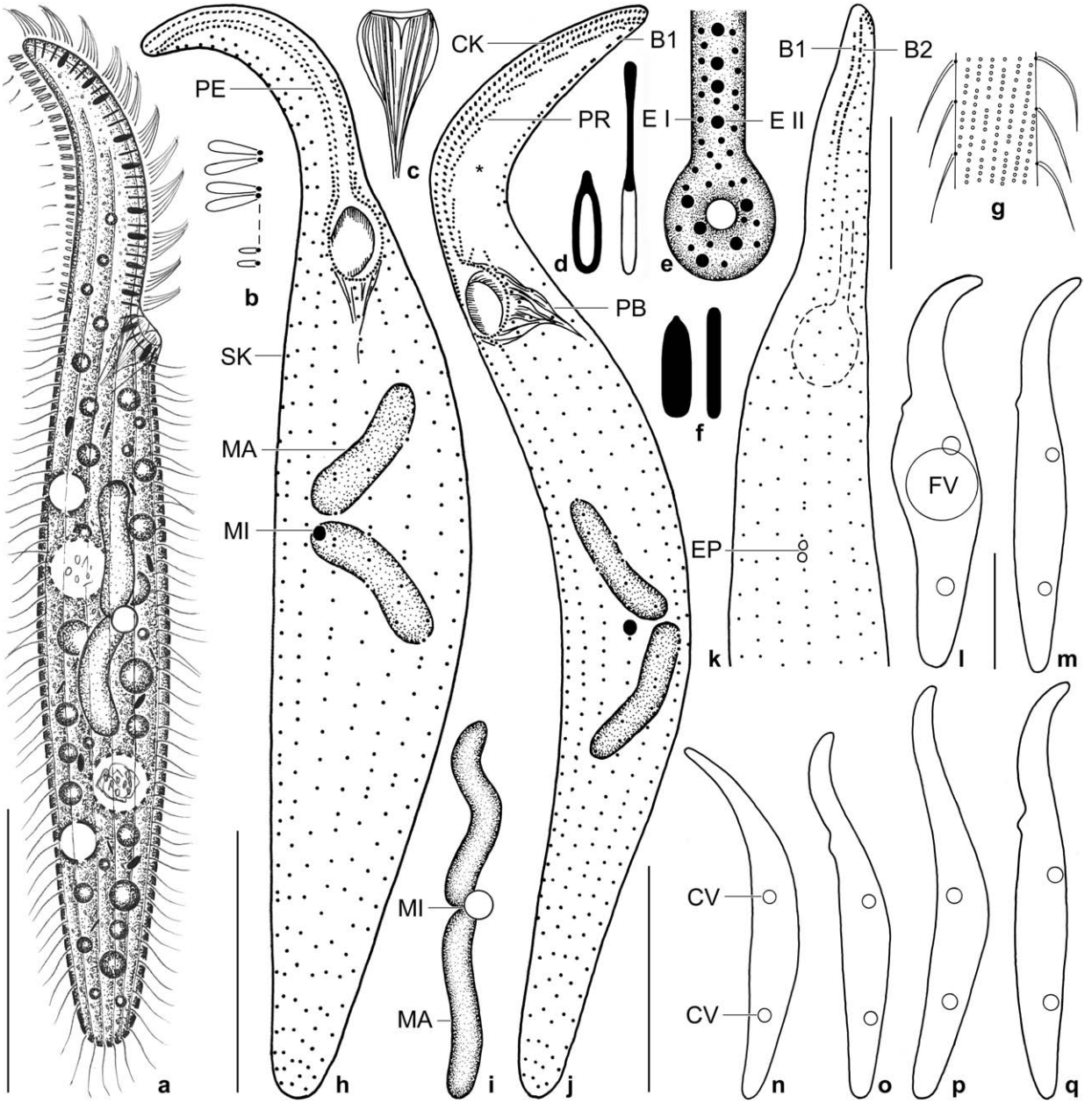
Occurrence and ecology: Da Cunha (1913) found *R. bivacuolatus* at several Brazilian localities: Manguinhos and Gavea in the town of Rio de Janeiro, Merity in the state of Rio de Janeiro, and Boituva in the state of São Paulo. Later, unsubstantiated records: possibly in a culture from a polluted river in the Czech Republic (Moravcová 1962); in "macchia" soil from Italy (Luzzatti 1938); a single specimen in a water sample from Lake Tei in the town of Bucharest, Roumania in November 1957 (Vuxanovici 1959); in the plankton of the Tisa River in Ukraine (Kovalchuk 1997b); 6–7 ind./l in fishless, intermittent ponds in Vandorf, Ontario, Canada (Andrushchyshyn et al. 2006); freshwater bodies in the Pantanal of Mato Grosso, Brazil (Lopes Hardoim & Heckman 1996).

Rimaleptus canadensis nov. sp. (Figs 61a–y; Table 31)

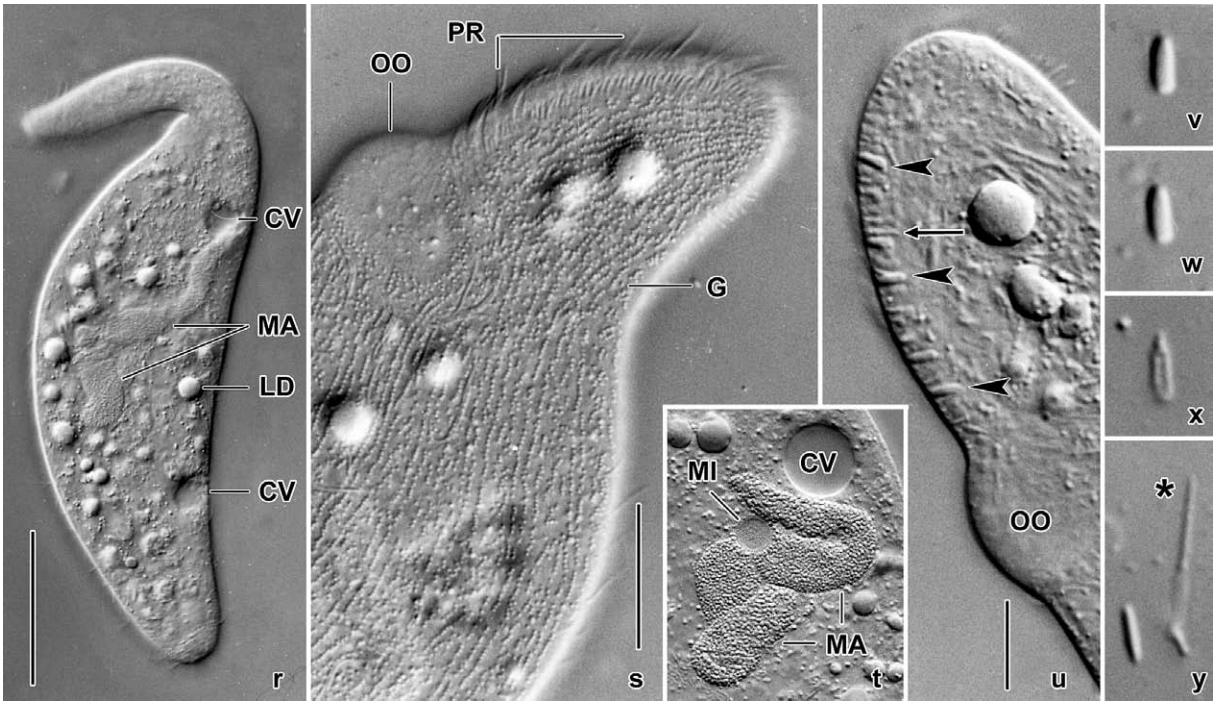
Diagnosis: Size about 180 × 25 µm in vivo. Shape narrowly to cylindroidally dileptid with posterior end narrowly rounded, proboscis about one fourth of body length. Two oblong macronuclear nodules and a

Table 31: Morphometric data on *Rimaleptus canadensis* nov. sp. Data based on mounted, protargol-impregnated (Foissner's method), and randomly selected specimens from a non-flooded Petri dish culture. Measurements in µm. CV – coefficient of variation in %, M – median, Max – maximum, Mean – arithmetic mean, Min – minimum, n – number of specimens investigated, SD – standard deviation, SE – standard error of mean.

Characteristics	Mean	M	SD	SE	CV	Min	Max	n
Body, length	157.4	160.0	18.9	4.1	12.0	127.0	203.0	21
Body, width	21.4	21.0	2.4	0.5	11.3	18.0	25.0	21
Body length:width, ratio	7.4	7.5	1.3	0.3	16.8	5.4	9.7	21
Anterior body end to oral bulge opening, distance	36.1	35.0	4.9	1.1	13.6	28.0	46.0	21
Proboscis, % of body length	23.0	22.7	1.8	0.4	7.7	20.0	25.9	21
Oral bulge opening, length	9.9	10.0	0.8	0.2	8.0	9.0	12.0	21
Oral bulge opening, width	7.7	8.0	0.9	0.2	11.2	6.0	9.0	21
Nuclear figure, length	39.6	41.0	7.1	1.6	17.9	27.0	53.0	21
Macronuclear nodules, length	21.0	20.0	2.8	0.6	13.3	18.0	27.0	21
Macronuclear nodules, width	5.2	5.0	0.7	0.2	13.4	4.0	7.0	21
Macronuclear nodules, number	2.0	2.0	0.0	0.0	0.0	2.0	2.0	21
Micronucleus, largest diameter	2.4	2.5	–	–	–	2.0	3.0	21
Micronucleus, number	1.0	1.0	0.0	0.0	0.0	1.0	1.0	21
Ciliary rows, number	12.9	13.0	1.0	0.2	8.1	11.0	16.0	21
Cilia in mid-body in 10 µm, number	4.0	4.0	0.8	0.2	20.9	2.0	6.0	21
Dorsal brush rows, number	2.0	2.0	0.0	0.0	0.0	2.0	2.0	21
Dikinetids in brush row 1, number	10.4	10.0	1.0	0.3	9.3	9.0	12.0	10
Dikinetids in brush row 2, number	17.8	18.0	1.3	0.4	7.4	16.0	20.0	10



Figs 61a–q: *Rimaleptus canadensis* nov. sp. from life (a–g, i, l–q) and after protargol impregnation (h, j, k). **a, e** – right side and ventral view of a representative specimen, length 180 µm. Extrusomes are attached both to the proboscis oral bulge and to the oral bulge opening (e), a main feature of this species; **b** – the brush dikinetids are associated with type II bristles both being 2–3 µm long and are followed by 1 µm-long monokinetidal tail bristles; **c** – the internal basket is distinctly bulbous; **d** – type I extrusome in an early stage of explosion and exploded type II extrusome; **f** – type I extrusomes are bluntly oblong with a minute anterior dome and 3 × 1 µm in size, type II extrusomes are slenderly oblong and 3–4 × 0.2–0.3 µm in size; **g** – surface view showing cortical granulation; **h** – ciliary pattern of ventral side and nuclear apparatus, length 140 µm; **i** – the nuclear apparatus consists of two abutting macronuclear nodules and a blister-like micronucleus in the nodule vertex; **j** – ciliary pattern of left side and nuclear apparatus, length 160 µm. The asterisk marks the broad barren stripe; **k** – ciliary pattern of dorsal side in anterior body half. Note dorsal brush and excretory pores; **l–q** – variability of body shape and size and the contractile vacuole pattern. From video records and drawn to scale. B1, 2 – dorsal brush rows, CK – circumoral kinety, CV – contractile vacuoles, E (I, II) – extrusomes (types), EP – excretory pores of contractile vacuole, FV – food vacuole, MA – macronuclear nodules, MI – micronucleus, PB – pharyngeal basket, PE – perioral kinety, PR – preoral kineties, SK – somatic kinety. Scale bars: 20 µm (k), 30 µm (h, j), and 50 µm (a, l–q).



Figs 61r–y: *Rimaleptus canadensis* nov. sp. from life. **r** – right side view of a squeezed specimen. Note two macronuclear nodules and two contractile vacuoles in dorsal side of trunk; **s** – the somatic and oral cortex are studded with densely spaced granules about 0.2 μm across; **t** – the blister-like micronucleus is 5 μm across and in the vertex formed by the abutting macronuclear nodules; **u–y** – there are two types of extrusomes anchored to both the proboscis oral bulge and the oral bulge opening: type I is bluntly oblong with a minute dome and 3 × 1 μm in size (arrowheads, u–x), while type II is slenderly oblong and 3–4 μm long (arrow, u, y). Asterisk in (y) marks an exploded type II extrusome. CV – contractile vacuoles, G – cortical granules, LD – lipid droplet, MA – macronuclear nodules, OO – oral bulge opening, PR – preoral kineties. Scale bars: 10 μm (u), 20 μm (s), and 30 μm (r).

blister-like micronucleus in nodule vertex. Two dorsal contractile vacuoles with 2 pores each. Two types of extrusomes attached both to proboscis oral bulge and to oral bulge opening: type I bluntly oblong with minute anterior dome, 3 × 1 μm in size; type II slenderly oblong, 3–4 × 0.2–0.3 μm. On average 13 ciliary rows, 2 staggered and differentiated into a dimorphic, isostichad dorsal brush with bristles up to 3 μm long: brush row 1 composed of an average 10 widely spaced dikinetids, row 2 composed of an average of 18 ordinarily spaced dikinetids; both rows with a monokinetidal bristle tail extending to base of proboscis. Oral bulge opening about 10 μm across. About 15 widely spaced preoral kineties each usually composed of 6 narrowly spaced kinetids, forming comparatively long, strongly oblique rows.

Type locality: Bark from trees in the Cypress Provincial Park, Vancouver, Canada, W123°12’ N49°23’.

Type material: One holotype slide (inv. no. 2011/346) and two paratype slides (inv. nos 2011/347 and 2011/348) with protargol-impregnated specimens have been deposited in the Biology Centre of the Museum of Upper Austria, Linz (LI). Relevant specimens are marked by black ink circles on the coverslip.

Etymology: The Latin adjective *canadensis* refers to the country in which the species was discovered.

Description: Size 130–230 × 20–30 μm in vivo, usually about 180 × 25 μm, as calculated from some in vivo measurements and the morphometric data (Table 31). Shape narrowly to cylindroidally dileptid, i.e., length:width ratio near 7.5:1 both in vivo and after protargol impregnation. Proboscis about one fourth of body length, slightly curved dorsally; trunk oblong to bluntly fusiform, usually slightly widened in

mid-portion, inflated in well-fed specimens (Fig. 61l); posterior end narrowly rounded, never tail-like (Figs 61a, h, j, m–q). Nuclear apparatus in mid or slightly above mid of trunk. Invariably two abutting macronuclear nodules, indidivual nodules narrowly to very narrowly ellipsoidal, more or less curved, homogenously impregnated with protargol, on average 20 × 5 μm in size. Micronucleus very near to or in vertex formed by the abutting macronuclear nodules, blister-like and hyaline, about 5 μm across in vivo, while deeply impregnated and only 2.5 μm across in protargol preparations (Figs 61a, h–j, r, t; Table 31). Invariably two dorsal contractile vacuoles each with usually two intrakinetal pores one after the other: anterior vacuole at end of first fourth of trunk, posterior one at beginning of last fourth (Figs 61a, k–r). Two types of compact extrusomes not impregnating with protargol and scattered throughout cytoplasm: type I attached to furrow separating bulge branches and scattered in oral bulge opening, bluntly oblong with minute anterior dome, 3 × 1 μm in size; type II anchored in both bulge branches and scattered in oral bulge opening, slenderly oblong with rounded ends, 3–4 × 0.2–0.3 μm in size, when exploded with a clavate granule at tip of tube emerging from the empty capsule (Figs 61a, d–f, u–y). Cortex very flexible, contains about six oblique granule rows between adjacent kineties; granules conspicuous because highly refractive and narrowly spaced in somatic and oral cortex, about 0.2 μm across in surface view (Figs 61g, s). Cytoplasm colourless, turbid due to numerous granules ~ 0.2 μm across, some lipid droplets 2–8 μm in diameter, and 10 μm-sized food vacuoles (Figs 61a, r).

Cilia about 6 μm long in vivo, ordinarily to loosely spaced; in protargol preparations as typical for dileptids; arranged in an average of 13 ordinarily spaced, longitudinal rows anteriorly gradually shortened along right side of oral bulge, except for perioral kinety which extends with ordinarily spaced basal bodies to tip of proboscis (Fig. 61h; Table 31). Left side of proboscis with conspicuous blank stripe because some ciliary rows end at level of oral bulge opening (Fig. 61j). Dorsal brush exactly on dorsal side of proboscis, composed of two dimorphic, staggered, isostichad rows: row 1 commences slightly more subapically than row 2, composed of an average of 10 loosely spaced dikinetids; row 2 begins near tip of proboscis, composed of an average of 18 ordinarily spaced dikinetids. Brush dikinetids associated with type II bristles both being 2–3 μm long. Both brush rows continue with a monokinetidal tail extending to base of proboscis with 1 μm long type VI bristles (Figs 61a, b, j, k).

Oral bulge opening at end of anterior body quarter, about 10 μm across in vivo, projects ordinarily (Figs 61a, e, l, m, o, q, s; Table 31). Pharyngeal basket short, internal basket distinctly bulbous both in vivo and after protargol impregnation (Figs 61c, j). Circumoral kinety composed of ordinarily spaced dikinetids, except for narrowly spaced monokinetids around oral bulge opening (Figs 61h, j). Preoral kineties conspicuous because widely spaced and composed of four to nine, usually six narrowly spaced kinetids, thus forming rather long, strongly oblique rows almost in parallel to circumoral kinety in anterior third of proboscis (Fig. 61j).

Occurrence and ecology: As yet found only at type locality, i.e., in a mixture of bark (pH 5.0) from Mountain hemlock trees (*Tsuga mertensiana*) and Amabilis fir trees (*Abies amabilis*).

Remarks: Within the *Rimaleptus alpinus* group, *R. canadensis* is outstanding in having extrusomes anchored to both the proboscis oral bulge and the oral bulge opening, while all congeners have extrusomes only in the proboscis. In this respect, *R. canadensis* resembles the multinucleate *Dileptus costaricanus* and *Pseudomonilicaryon falciforme*, a species with moniliform macronucleus. Other rare features, present only in *Rimaleptus tirjakovae*, are the blister-like micronucleus and its localization in the vertex formed by the abutting macronuclear nodules. However, *R. tirjakovae* is easily distinguished by the contractile vacuole pattern (a dorsal stripe vs. two dorsal vacuoles), the type I extrusomes (rod-shaped vs. bluntly oblong with minute, anterior dome), and the much higher number of ciliary rows (21 vs. 13). There are several similar bivacuolate congeners, viz., *R. alpinus*, *R. armatus*, *R. binucleatus* and *R. bivacuolatus*.

The three former species have rod-shaped or narrowly ovate extrusomes (vs. oblong and massive) and preoral kineties composed of 2–3 (vs. 4–9) basal bodies. *Rimaleptus bivacuolatus* differs by the nuclear apparatus, i.e., each macronuclear nodule has attached a micronucleus (vs. a single micronucleus in the nodule vertex).

Rimaleptus armatus (Foissner & Schade in Foissner, 2000) nov. comb. (Figs 62a–w, 63a–o, 64a–v; Table 32)

2000 *Dileptus armatus* Foissner & Schade nov. sp. – Foissner, Eur. J. Protistol. **36**: 265

Generic affiliation and taxonomy: We combine *Dileptus armatus* with *Rimaleptus* because of the two macronuclear nodules and the ordinary oral basket. Within the *R. alpinus* group, *R. armatus* is most similar to *R. canadensis* in having comparatively massive type I extrusomes. However, these are narrowly ovate and attached only to the proboscis oral bulge in the former, while bluntly oblong with a minute dome and anchored in both the proboscis oral bulge and the oral bulge opening in the latter.

Improved diagnosis (includes 3 populations): Size about 175 × 25 μm in vivo. Shape very narrowly dileptid with posterior end narrowly rounded, proboscis approximately 1/4 of body length. Two oblong macronuclear nodules with a single micronucleus in between. Two contractile vacuoles with several pores each in dorsal side of trunk. Two types of extrusomes: type I narrowly ovate, 3–6 × 1–2 μm in size; type II rod-shaped, 3 μm long. Usually about 12 ciliary rows, 2 anteriorly differentiated into an isostichad dorsal brush with bristles up to 4 μm long: brush rows 1 and 2 composed of an average of 14 and 15 dikinetids, respectively; both rows with a monokinetidal bristle tail extending to base of proboscis. Oral bulge opening ovate, about 12 × 7 μm in size. On average 18 oblique to strongly oblique, widely spaced preoral kineties, each usually composed of 2–3 narrowly to ordinarily spaced cilia.

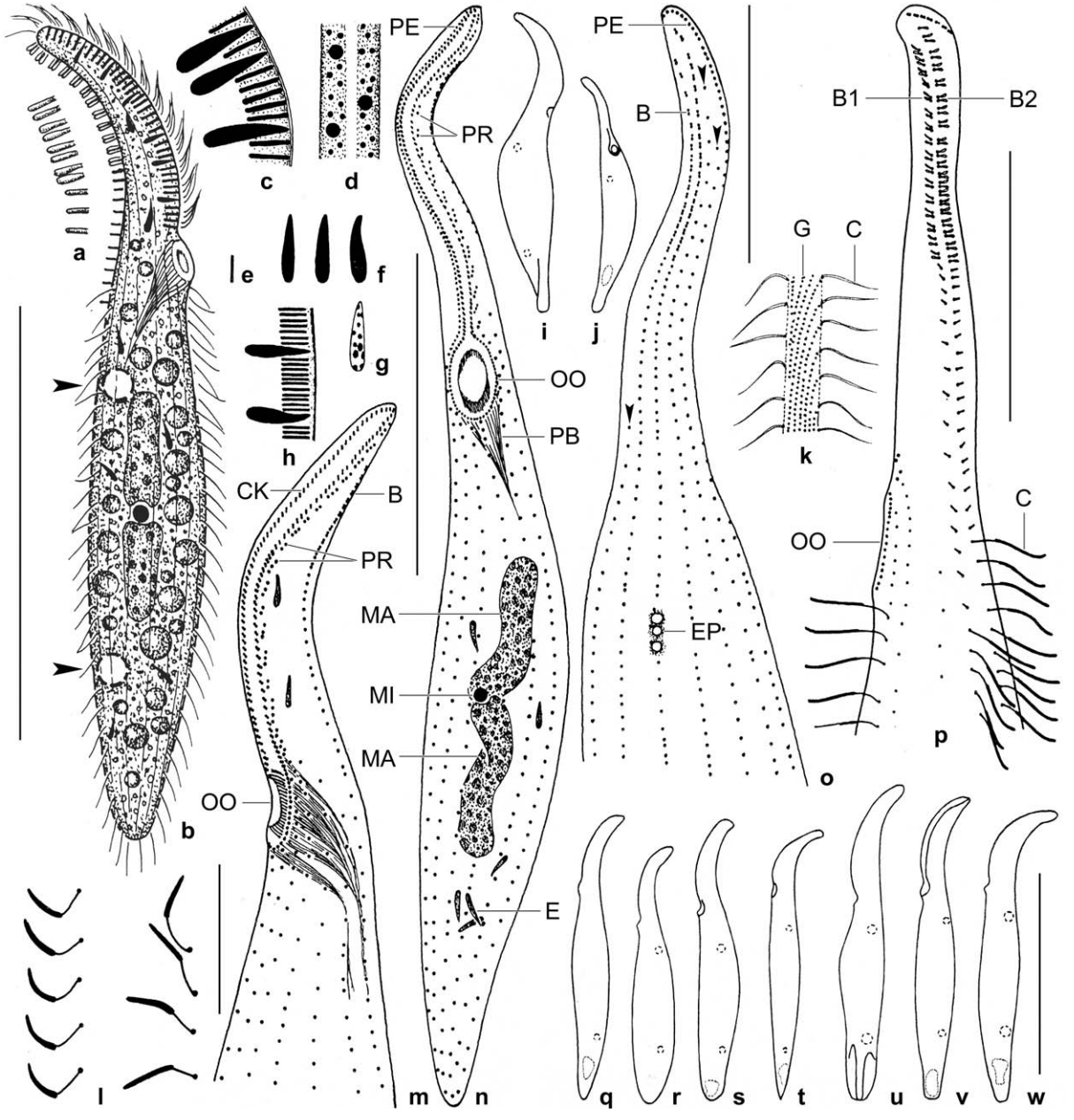
Type locality: Soil from Helgoland (Oberland), Germany, E7°53’ N54°12’.

Type and voucher material: One holotype slide (inv. no. 2000/114) and three paratype slides (inv. nos 2000/115–117) as well as fifteen voucher slides (Japanese population; inv. nos 2011/285–300) with protargol-impregnated specimens have been deposited in the Biology Centre of the Museum of Upper Austria, Linz (LI). Relevant specimens are marked by black ink circles on the coverslip.

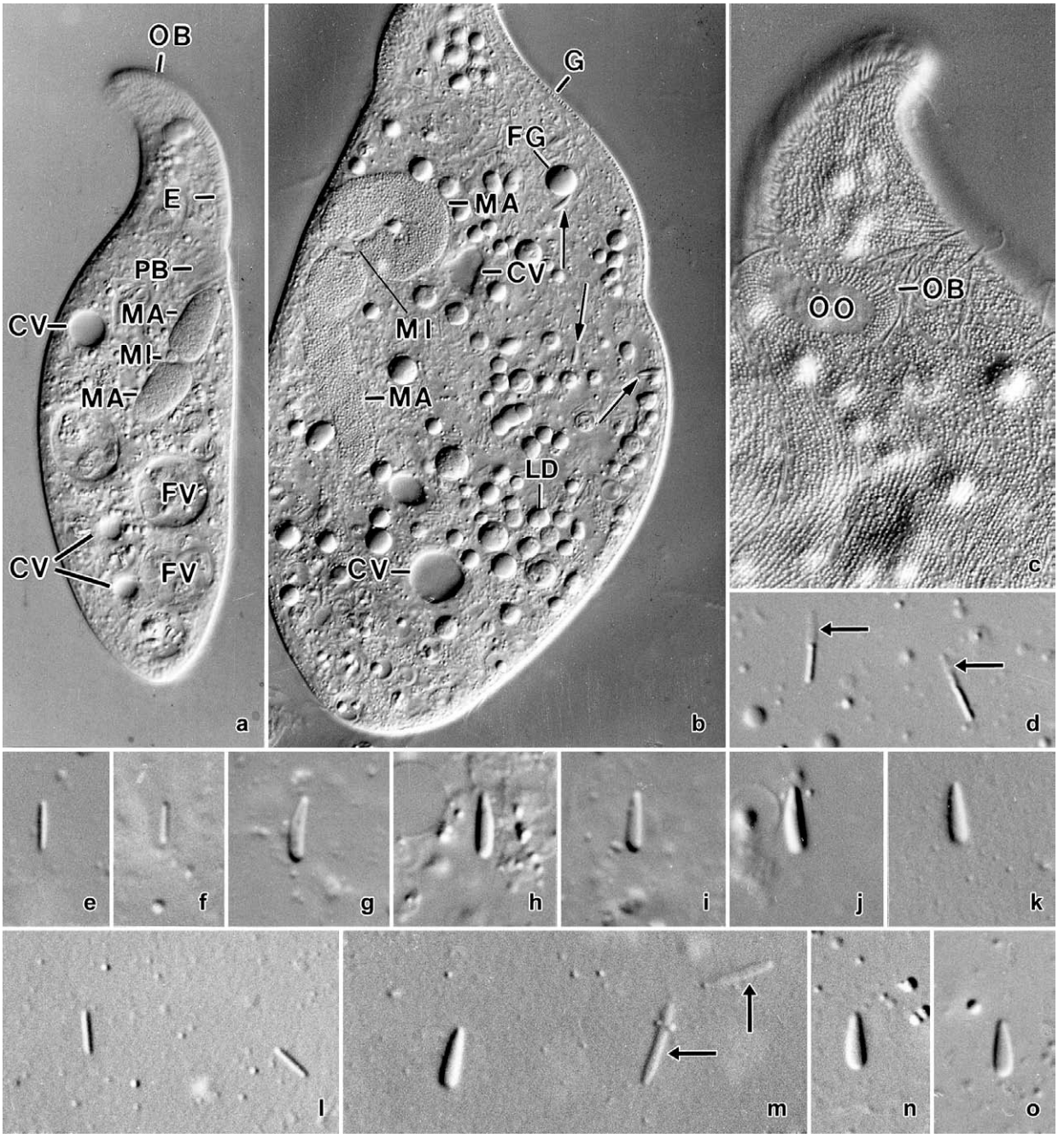
Etymology: The Latin adjective *armatus* (armed) refers to the thick extrusomes.

Description: This species has been studied in three populations, namely from Helgoland (type) and Berlin (both Germany), and from Japan. The populations match very well, therefore the diagnosis summarizes all observations. The description of the Helgoland population is followed by some additional data from the other populations.

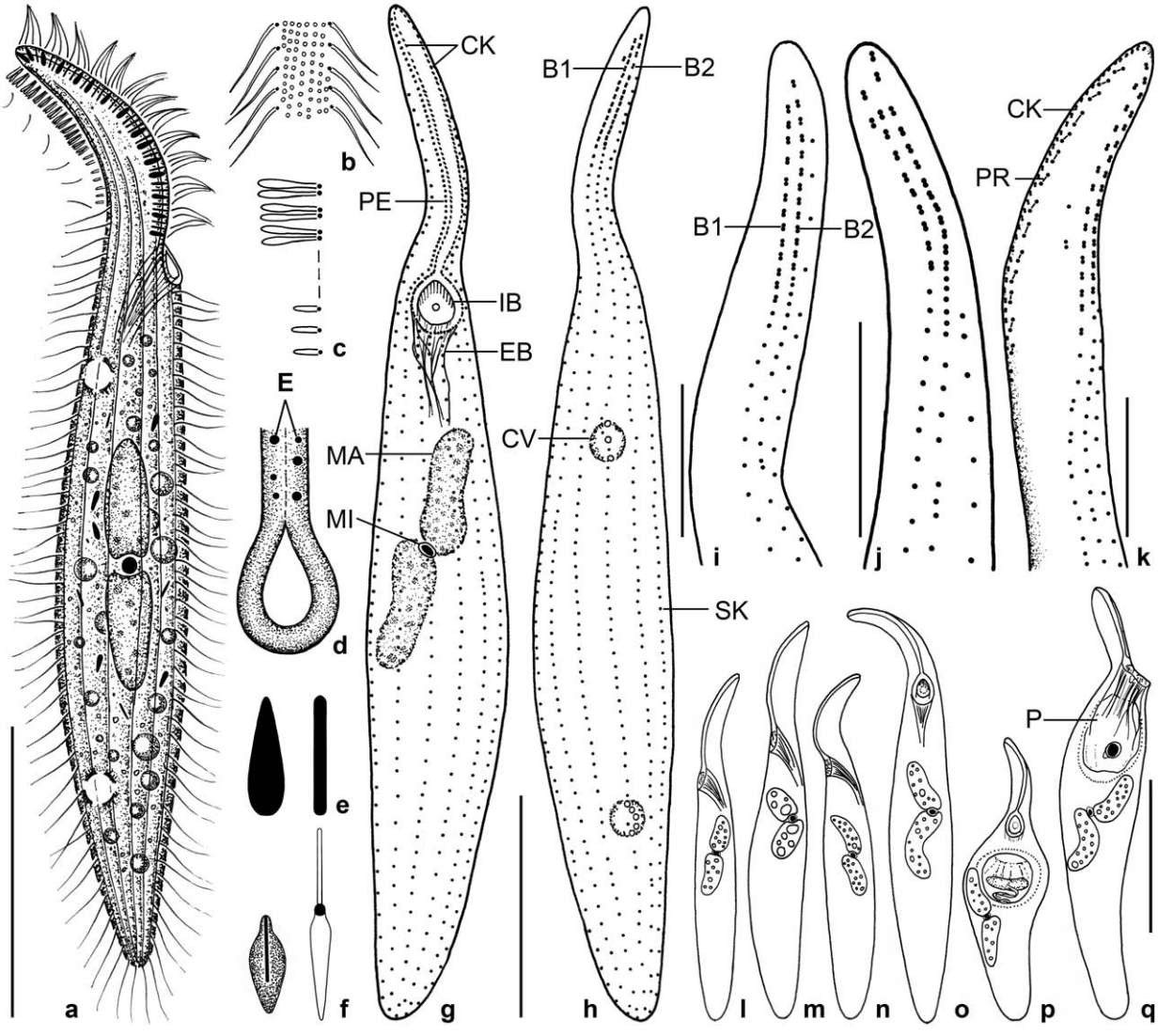
Size 140–250 × 20–40 μm in vivo, on average about 200 × 30 μm; flexible but not contractile. Shape narrowly to cylindroidally dileptid with an average length:width ratio of 7.4:1 in protargol preparations (Table 32). Proboscis leaf-like flattened, occupying about one fourth of body length; trunk cylindroidal with posterior end narrowly rounded, rarely bluntly pointed but never tail-like (Figs 62b, i, j, n, q–w). Nuclear apparatus in centre of trunk. Macronuclear nodules ellipsoidal to narrowly ellipsoidal or ovoidal, sometimes curved, with concave proximal end surrounding micronucleus; many small nucleoli. Micronucleus invariably between macronuclear nodules, about 4 × 3 μm in vivo (Figs 62b, n, 63a, b; Table 32). A contractile vacuole each in anterior and posterior quarter of trunk, each vacuole with one to six, usually three intrakinetal pores one after the other (Figs 62b, o, j, o, q–w, 63a, b). Two types of extrusomes attached to proboscis oral bulge and scattered throughout cytoplasm: type I sparse (about 15 organelles attached to proboscis) but conspicuous because highly refractive, narrowly ovate and 4–6 × 1–2 μm in size, impregnates lightly with protargol; type II numerous but inconspicuous because rod-shaped



Figs 62a–w: *Rimaleptus armatus*, Helgoland (a–d, k–o) and Berlin (e–h, i, j, p, q–w) population from life (a–f, h–k, q–w) and after protargol impregnation (g, l–p). From FOISSNER (2000). **a** – small portion of dorsal brush, bristles 2–3 µm long; **b** – right side view of a representative specimen, length 200 µm. Arrowheads mark contractile vacuoles; **c, d** – lateral and frontal view of oral bulge of a Helgoland specimen, showing two types of extrusomes: type I is narrowly ovate and 4–6 µm long, while type II is rod-shaped and 3 µm long; **e, f, h** – type I and II extrusomes of Berlin specimens; **g** – type I extrusome containing argyrophilic granules; **i–j, q–w** – variability of body shape and size and the contractile vacuole pattern. From video records and drawn to scale; **k** – surface view showing cortical granulation; **l** – two ciliary rows with cilia inflated and deeply impregnated distally; **m** – ciliary pattern of left side in anterior body portion; **n** – ciliary pattern of ventral side and nuclear apparatus of holotype specimen, length 170 µm; **o, p** – ciliary pattern of dorsal side in anterior body half. Arrowheads mark shortened somatic kineties. B(1, 2) – dorsal brush (rows), C – somatic cilia, CK – circumoral kinety, E – extrusomes, EP – excretory pores, G – cortical granules, MA – macronuclear nodules, MI – micronucleus, OO – oral bulge opening, PB – pharyngeal basket, PE – perioral kinety, PR – preoral kineties. Scale bars: 20 µm (m, p), 30 µm (o), 50 µm (n), and 100 µm (b, i, j, q–w).



Figs 63a–o: *Rimaleptus armatus*, Austrian (a), German type (b–j), and Maldivian (k–o) specimens from life in interference contrast (from FOISSNER 2000). **a** – right lateral view of a slightly squeezed specimen, showing main cell organelles, such as contractile vacuoles and two macronuclear nodules with a single micronucleus in between; **b** – dorsal view of a squashed specimen. Arrows mark type I extrusomes; **c** – surface view of anterior body half, showing the distinct rows of cortical granules which extend onto the oral bulge; **d–f** – partially or completely exploded (d) and resting (e, f) type II extrusomes, which are about 3 µm long. Extruded organelles have an about 3 µm long, hyaline extension (d, arrows); **g–j** – resting type I extrusomes are narrowly ovate and 4–6 µm long; **k–o** – resting type I (k, m–o) and type II (l) extrusomes from the Maldivian specimens are very similar in size and shape to those of the German type population (d–j). Figure (m) shows two partially or completely exploded type I extrusomes (arrows). CV – contractile vacuoles, E – extrusomes, FV – food vacuoles, G – cortical granules, LD – lipid droplets, MA – macronuclear nodules, MI – micronucleus, OB – oral bulge, OO – oral bulge opening, PB – pharyngeal basket.



Figs 64a–q: *Rimaleptus armatus*, Japanese specimens from life (a–f) and after protargol impregnation (g–q). **a** – right side view of a representative specimen, length 160 µm; **b** – surface view showing cortical granulation. There are about five oblique rows of ordinarily spaced granules between each two somatic kineties; **c** – fine structure of dorsal brush. The bristles in anterior brush portion are paired, clavate and up to 4 µm long, while those of posterior portion are monokinetidal, oblong, and only 1.5 µm long; **d** – frontal view of oral bulge and arrangement of extrusomes, which are attached to both branches of proboscis oral bulge; e – there are two types of extrusomes: type I is narrowly ovate and 3 µm long, while type II is rod-shaped with both ends rounded and 3 µm long; **f** – partially and fully exploded type I extrusome. Partially exploded extrusomes are amphoriform, while the exploded ones have the typical toxicyst structure, that is, are lanceolate and have a refractive granule at the distal end of the empty capsule; **g, h** – ciliary pattern of ventral and dorsal side as well as nuclear and contractile vacuole apparatus of main voucher specimen, length 137 µm. Each vacuole has several excretory pores in that kinety which bears brush row 2; **i–k** – dorsal and dorsolateral views of proboscis ciliary pattern. The dorsal brush consists of two staggered, isostichad rows, but often some brush irregularities occur, e.g., extra dikinetids right of brush row 1 (j, k). Basal bodies of preoral kineties connected by lines (k); **l–o** – variability of body shape and size as well as of nuclear apparatus. Drawn to scale; **p, q** – specimens having engulfed a peritrich ciliate and a naked amoebae (*Thekamoeba* sp.), respectively. Drawn to scale. B1, 2 – dorsal brush rows, CK – circumoral kinety, CV – contractile vacuole, E – extrusomes, EB – external basket, IB – internal basket, MA – macronucleus, MI – micronucleus, P – prey, PE – perioral kinety, PR – preoral kinety, SK – somatic kinety. Scale bars: 10 µm (i–k), 30 µm (g, h), and 50 µm (a, l–q).

Table 32. Morphometric data on *Rimaleptus armatus* populations (Pop) from Helgoland (H; FOISSNER 2000), Berlin (B; FOISSNER 2000), and Japan (J; original data). Data based on mounted, protargol-impregnated (Foissner's method), and randomly selected specimens from non-flooded Petri dish cultures. Measurements in µm. CV – coefficient of variation in %; M – median; Max – maximum; Mean – arithmetic mean; Min – minimum; n – number of specimens investigated; SD – standard deviation; SE – standard error of mean.

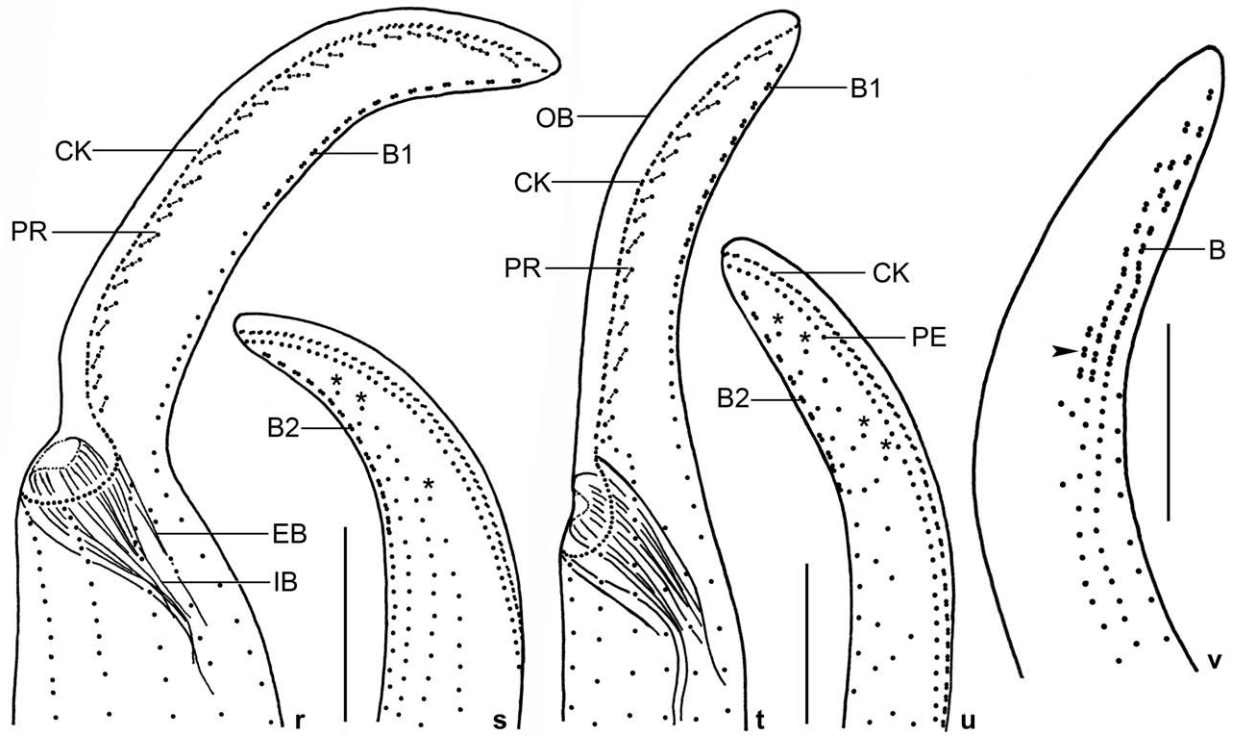
Characteristics	Pop	Mean	M	SD	SE	CV	Min	Max	n
Body, length	H	179.3	166.0	30.1	6.9	16.8	132.0	238.0	19
	B	149.0	150.0	18.5	4.8	12.4	120.0	180.0	15
	J	135.5	137.0	15.6	3.4	11.5	106.0	163.0	21
Body, width	H	24.8	24.0	4.4	1.0	17.8	17.0	32.0	19
	B	18.7	18.0	2.4	0.6	12.8	15.0	23.0	15
	J	19.2	19.0	2.2	0.5	11.4	16.0	23.0	21
Body length:width, ratio (calculated from original data)	H	7.4	7.4	1.2	0.3	16.1	5.4	9.4	19
	B	6.6	6.4	1.2	0.4	18.0	4.9	8.3	10
	J	7.1	7.0	0.7	0.1	9.5	5.6	9.1	21
Anterior body end to oral bulge opening, distance	H	48.6	50.0	8.2	1.9	16.9	29.0	60.0	19
	B	45.2	46.0	8.2	2.1	18.1	35.0	65.0	15
	J	35.4	35.0	4.3	0.9	12.0	29.0	43.0	21
Proboscis, % of body length (calculated from original data)	H	27.3	27.9	3.5	0.8	12.9	22.0	33.3	19
	B	27.4	27.5	6.6	1.9	24.0	16.0	36.7	12
	J	26.2	26.2	2.5	0.5	9.5	22.4	31.4	21
Oral bulge opening, length	H	12.2	12.0	1.7	0.4	13.8	9.0	15.0	19
	J	8.8	9.0	1.2	0.2	13.6	7.0	12.0	24
Oral bulge opening, width	H	7.5	7.0	1.1	0.3	15.0	6.0	10.0	13
	J	7.0	7.0	0.8	0.2	11.3	6.0	8.0	17
Anterior body end to macronucleus, distance	J	57.8	61.0	8.8	1.9	15.3	45.0	69.0	21
Nuclear figure, length	H	43.4	44.0	7.3	1.7	16.7	28.0	54.0	19
	B	33.6	34.0	8.4	2.1	25.1	16.0	50.0	15
	J	36.5	36.0	5.5	1.2	15.1	25.0	52.0	21
Anterior macronuclear nodule, length	H	21.5	22.0	3.3	0.7	15.1	15.0	26.0	19
	B	24.9	25.0	6.1	1.6	24.4	17.0	35.0	15
	J	18.7	18.0	2.9	0.6	15.7	13.0	27.0	21
Anterior macronuclear nodule, width	H	7.6	8.0	1.4	0.3	18.2	5.0	10.0	19
	B	4.7	5.0	0.8	0.2	17.4	3.0	6.0	15
	J	7.2	7.0	0.7	0.2	9.7	6.0	8.0	21
Posterior macronuclear nodule, length	J	20.2	20.0	3.9	0.9	19.5	16.0	33.0	21
Posterior macronuclear nodule, width	J	7.2	7.0	0.8	0.2	11.5	6.0	8.0	21
Macronuclear nodules, number	H	2.0	2.0	0.0	0.0	0.0	2.0	2.0	19
	B	2.0	2.0	0.0	0.0	0.0	2.0	2.0	15
	J	2.0	2.0	0.0	0.0	0.0	2.0	2.0	21

Characteristics	Pop	Mean	M	SD	SE	CV	Min	Max	n
Micronucleus, largest diameter	H	3.3	3.0	0.8	0.2	24.4	2.0	5.0	19
	B	1.6	2.0	0.5	0.1	29.3	1.0	3.0	12
	J	2.5	2.5	–	–	–	2.0	3.0	21
Micronucleus, number	H	1.0	1.0	0.0	0.0	0.0	1.0	1.0	19
	B	1.0	1.0	0.0	0.0	0.0	1.0	1.0	12
	J	1.0	1.0	0.0	0.0	0.0	1.0	1.0	21
Ciliary rows, number	H	14.0	15.0	1.7	0.4	12.4	10.0	17.0	19
	B	11.3	11.0	1.5	0.4	13.1	10.0	15.0	14
	J	11.7	12.0	1.1	0.3	9.8	10.0	15.0	21
Cilia in mid-body in 10 µm, number	H	4.4	4.0	1.0	0.2	21.0	3.0	6.0	19
	B	6.2	6.0	1.0	0.3	16.9	5.0	8.0	14
	J	6.3	6.0	0.9	0.2	14.4	5.0	8.0	21
Preoral kineties, number	J	18.2	17.0	2.9	0.7	15.7	15.0	26.0	18
Dorsal brush rows, number	H	2.0	2.0	0.0	0.0	0.0	2.0	2.0	19
	B	2.0	2.0	0.0	0.0	0.0	2.0	2.0	8
	J	2.0	2.0	0.0	0.0	0.0	2.0	2.0	26
Dikinetids in brush row 1, number	J	14.2	14.0	1.8	0.4	12.8	12.0	18.0	17
Dikinetids in brush row 2, number	J	15.5	15.0	1.1	0.3	6.9	14.0	18.0	17
Anterior body end to last dikinetid of brush row 1, distance	J	17.7	18.0	2.1	0.5	11.9	13.0	21.0	19
Anterior body end to last dikinetid of brush row 2, distance	J	16.9	17.0	2.0	0.5	11.7	12.0	20.0	19

and only 3 µm long, does not impregnate with protargol, composed of a 3 µm long hyaline and a 3 µm long refractive portion when exploded (Figs 62c–h, 63d–j). Oral and somatic cortex colourless, flexible and robust, cells thus withstand even strong coverslip pressure; contains innumerable, highly refractive, about 0.8 × 0.3 µm-sized granules forming six to nine narrowly spaced rows between adjacent kineties, do not impregnate with protargol (Figs 62k, 63c). Cytoplasm colourless, contains few to many lipid droplets 1–7 µm across and large food vacuoles with *Vorticella* sp. and *Thekamoeba* sp. Glides and winds on slide surface and soil particles or swims slowly, moving proboscis to and fro.

Cilia about 8 µm long in vivo, ordinarily to densely spaced; in protargol preparations as typical for dileptids, i.e., with a distinctly inflated and deeply impregnated distal half, except for dorsal bristles (Figs 62l, p); arranged in an average of 14 ordinarily spaced, longitudinal rows anteriorly gradually shortened along right side of oral bulge, except for perioral kinety extending to tip of proboscis (Figs 62n, o; Table 32). Left side of proboscis with wide blank stripe because ciliary rows end at level of oral bulge opening (Figs 62m, p). Dorsal brush exactly on dorsal side of proboscis, composed of two staggered, isostichad rows with a similar number of dikinetids associated with 2–3 µm long type II bristles. Both brush rows continue to base of proboscis with a monokinetidal tail of about 1.5 µm long type VI bristles (Figs 62a, b, o, p; Table 32).

Oral bulge opening in anterior body third, about 12 × 7 µm in size after protargol impregnation (Table 32). Pharyngeal basket of usual structure, distinct and bulbous both in vivo and in protargol preparations.



Figs 64r–v: *Rimaleptus armatus*, Japanese specimens after protargol impregnation. **r, t** – ciliary pattern of left side in anterior body third. Basal bodies of preoral kineties connected by lines; **s, u** – right side ciliary pattern of proboscis of specimens shown in (r, t). Asterisks mark gradually shortened somatic kineties; **v** – dorsolateral ciliary pattern of a specimen with a short third brush row (arrowhead). Note also the large blank area right of the dorsal brush. B(1, 2) – dorsal brush (rows), CK – circumoral kinety, EB – external basket, IB – internal basket, OB – oral bulge, PE – perioral kinety, PR – preoral kineties. Scale bars 10 μm.

Circumoral kinety composed of ordinarily spaced dikinetids, except for narrowly spaced monokinetids around oral bulge opening; with slight preoral narrowing; right branch curves around anterior end of proboscis, while left branch ends subapically almost touching the curved right end. Preoral kineties widely spaced, strongly oblique, composed of two to four, usually three narrowly spaced cilia (Figs 62m, n).

Observations on Japanese and Berlin populations: The Japanese population matches the type in all main features (Figs 64a–v; Table 32). As usual, some details differ: (i) body slightly smaller (120–190 × 20–30 μm vs. 140–250 × 20–40 μm); (ii) macronuclear nodules ranging from broadly to narrowly ellipsoidal; (iii) micronucleus surrounded by a membrane after protargol impregnation (vs. without distinct membrane); (iii) type I extrusomes shorter (3 μm vs. 4–6 μm); (iv) number of ciliary rows inconspicuously lower (on average 12 vs. 14); (v) brush bristles slightly longer (up to 4 μm vs. up to 3 μm). The Berlin population, which was also studied in detail, is very similar to the type population, except for some morphometrics (Figs 62e–h, i, j, p, q–w; Table 32).

Occurrence and ecology: There are several records of *Rimaleptus armatus* from Europe, Asia and the Indic Ocean. Foissner (2000) found *R. armatus* at three sites in Germany (litter and soil from the upper 5 cm of a beech forest about 30 km NW of the town of Kassel; artificial sand soil from sewage irrigation fields in the surroundings of the towns of Berlin-Buch and Ruhlsdorf, Brandenburg, pH 4.8–6.5), in Austria (riparian forest soil from the River Enns in Upper Austria), and on the Maldives (highly saline litter under coastal shrubs from Little Bandos, North Male Atol, pH 7.7; collected by Dr. W. Petz on 15. 12. 1990).

Foissner et al. (2005) reported *R. armatus* in seven out of 12 natural forest stands investigated in Lower Austria. The new population described here, is from the surroundings of the town of Tsukuba, Japan (soil and litter from the upper 3 cm of an abandoned field covered with up to 1 m high plants, pH 5.5). Thus, *R. armatus* is a euryhaline and likely cosmopolitan ciliate.

Rimaleptus binucleatus (Kahl, 1931) Foissner, 1984 (Figs 65a–l, 66a–g, 67a–p; Table 33)

1931 *Dileptus binucleatus* spec. n. Kahl, Tierwelt Dtl. **21**: 208

1931 *Dileptus americanus* spec. n. Kahl, Tierwelt Dtl. **21**: 209 (supposed synonym by First Reviser action herein)

1943 *Dileptus americanus* Kahl – Kahl, Infusorien: 33 (taxonomic revision)

1943 *Dileptus binucleatus* Kahl – Kahl, Infusorien: 32 (taxonomic revision)

1963 *Dileptus americanus* Kahl 1931 – Dragesco, Bull. biol. Fr. Belg. **97**: 123 (taxonomic revision; partim)

1963 *Dileptus binucleatus* Kahl, 1931 – Dragesco, Bull. biol. Fr. Belg. **97**: 117 (taxonomic revision)

1973 *Dileptus americanus* Khal, 1931 – Madrazo-Garibay & López-Ochoterena, Revta Soc. mex. Hist. nat. **34**: 64 (brief notes on a Mexican population; incorrect subsequent spelling of author name)

1984 *Rimaleptus binucleatus* (Kahl, 1931) – Foissner, Stapfia **12**: 92 (type species of genus, combining author)

2006 *Dileptus americanus* Kahl, 1931 – Vďačný, Hlúbiková & Tirjaková, Eur. J. Protistol. **42**: 183 (description of a Slovak population)

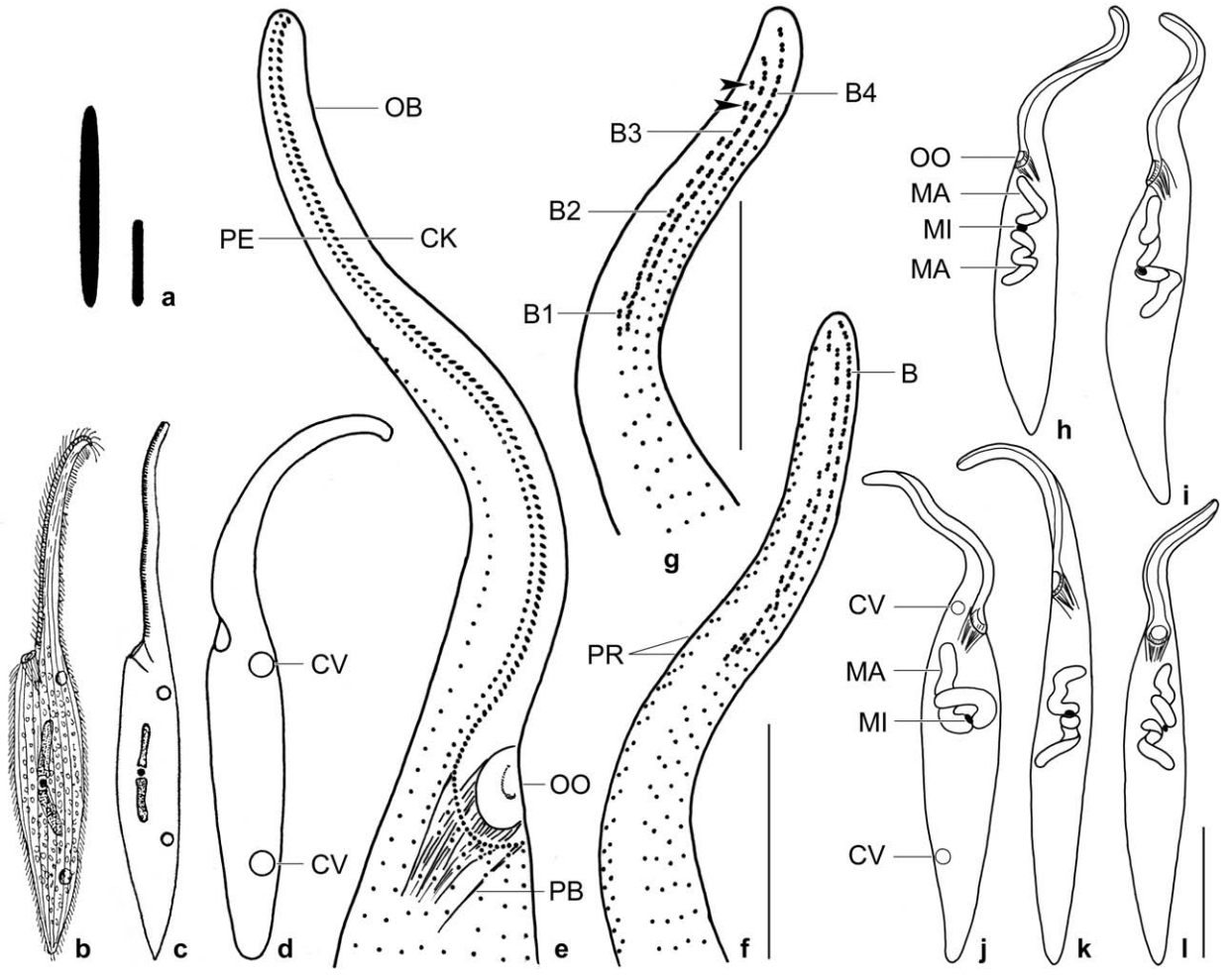
Generic affiliation, nomenclature and taxonomy: Foissner (1984) fixed *Dileptus binucleatus* as type species of the genus *Rimaleptus*. At first glance, *D. binucleatus* highly resembles *D. americanus*. According to Kahl (1931), they differ by the body size (300–400 µm vs. 190–220 µm) and shape (only slightly curved proboscis and acute posterior end vs. distinctly curved proboscis and rounded posterior end). However, our observations on populations from Slovakia (identified as *D. americanus* by Vďačný et al. 2006) and Australia (unpubl.) show transitions in body size (180–400 µm in the former and 170–250 µm in the latter) and shape (proboscis slightly to distinctly curved and posterior end acute to rounded) as well as in the shape of the macronuclear nodules (curved oblong to reniform). Both populations match very well, especially in proboscis length, the shape and size of the extrusomes as well as the number of ciliary rows (Figs 65a, 67i; Table 33).

As *D. binucleatus* and *D. americanus* were established in the same year and work by Kahl (1931), the Principle of the First Reviser applies (Article 24.2.2. of the ICZN 1999). We propose *D. americanus* as a junior synonym of *D. binucleatus* herein. Our decision is also supported in that *D. binucleatus* is the type species of the genus *Rimaleptus*.

Dragesco (1963) misidentified a French population with two ventral and three dorsal contractile vacuoles as *Dileptus americanus* (Fig. 67j). In this respect, Dragesco's specimens resemble *Rimaleptus longitrichus* which, however, has very long brush bristles (up to 15 µm vs. inconspicuous and short). Since there are no other *Rimaleptus* with ventral contractile vacuoles, Dragesco's population very likely represents a distinct species.

Rimaleptus binucleatus belongs to the *R. alpinus* group, where it is most similar to *R. alpinus* and *R. bivacuolatus* in having fine, rod-shaped extrusomes. However, *R. binucleatus* is easily distinguished by the larger size (250 µm vs. 110 µm on average) and the double number of the ciliary rows (19–25 vs. 10–12).

Improved diagnosis (includes all information known): Size about 250 × 35 µm in vivo. Shape narrowly to cylindroidally dileptid with acute or rounded posterior body end, proboscis about 35% of body length.

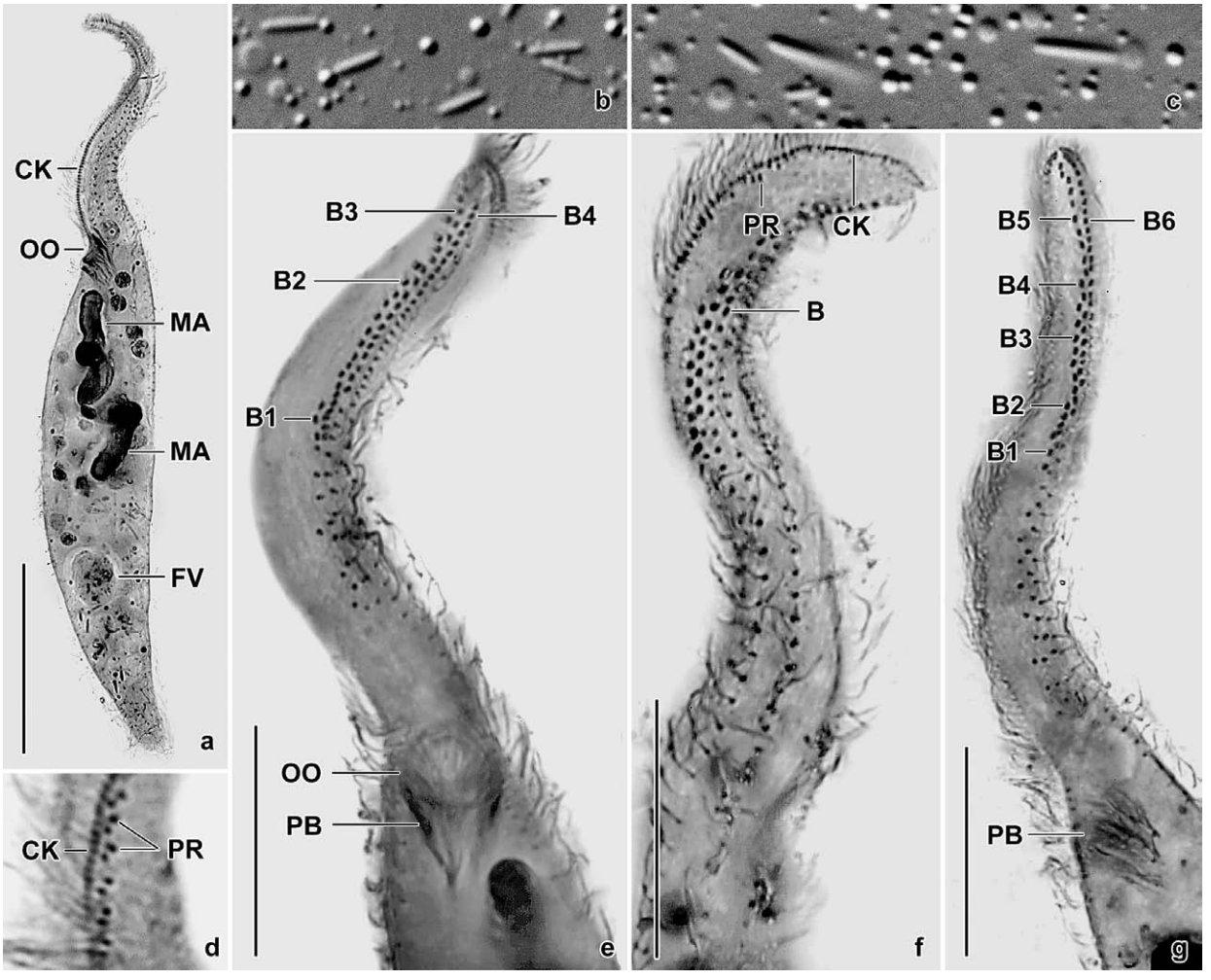


Figs 65a–l: *Rimaleptus binucleatus*, type (b, c) and Australian (a, d–l) specimens from life (a–d) and after protargol impregnation (e–l). From KAHL 1931 (b), DRAGESCO 1963 (c), and originals (a, d–l). **a** – extrusomes of an Australian specimen: type I is rod-like with slightly narrowed ends and about 6 µm long, while type II is oblong and only 2 µm long; **b** – *Dileptus binucleatus*, length 350 µm; **c** – redrawing of KAHL's *D. binucleatus*; **d** – shape variant; **e, f** – ventrolateral and dorsolateral ciliary pattern in anterior body portion; **g** – ciliary pattern of proboscis' dorsal side. Arrowheads denote some extra dikinetids right of brush row 3; **h–l** – variability of body shape and nuclear apparatus. Drawn to scale. B(1–4) – dorsal brush (rows), CK – circumoral kinety, CV – contractile vacuoles, MA – macronuclear nodules, MI –micronucleus, OB – oral bulge, OO – oral bulge opening, PB – pharyngeal basket, PE – perioral kinety, PR – preoral kineties. Scale bars: 20 µm (e–g) and 50 µm (h–l).

Two oblong macronuclear nodules with a micronucleus in between. Two dorsal contractile vacuoles with 1 excretory pore each. Two size-types (6 µm and 2 µm) of rod-shaped extrusomes attached to proboscis oral bulge. On average 21 ciliary rows, 4–6 anteriorly differentiated into a staggered, distinctly heterostichad dorsal brush with bristles up to 3 µm long. Oral bulge opening about 12 µm across. Preoral kineties oblique, ordinarily spaced, each composed of 2–3 narrowly spaced cilia.

Type locality: Moss on limestones from the Mittenwald region in Bavaria, Germany.

Type and voucher material: No type material is available from KAHL's specimens. VĎAČNÝ et al. (2006) deposited six voucher slides with Slovak protargol-impregnated specimens in the Department of Zoology, Comenius University in Bratislava, Slovakia. Later, these slides were deposited in the Biology Centre of the Museum of Upper Austria, Linz (LI). In this repository, we deposit also six voucher slides (inv.

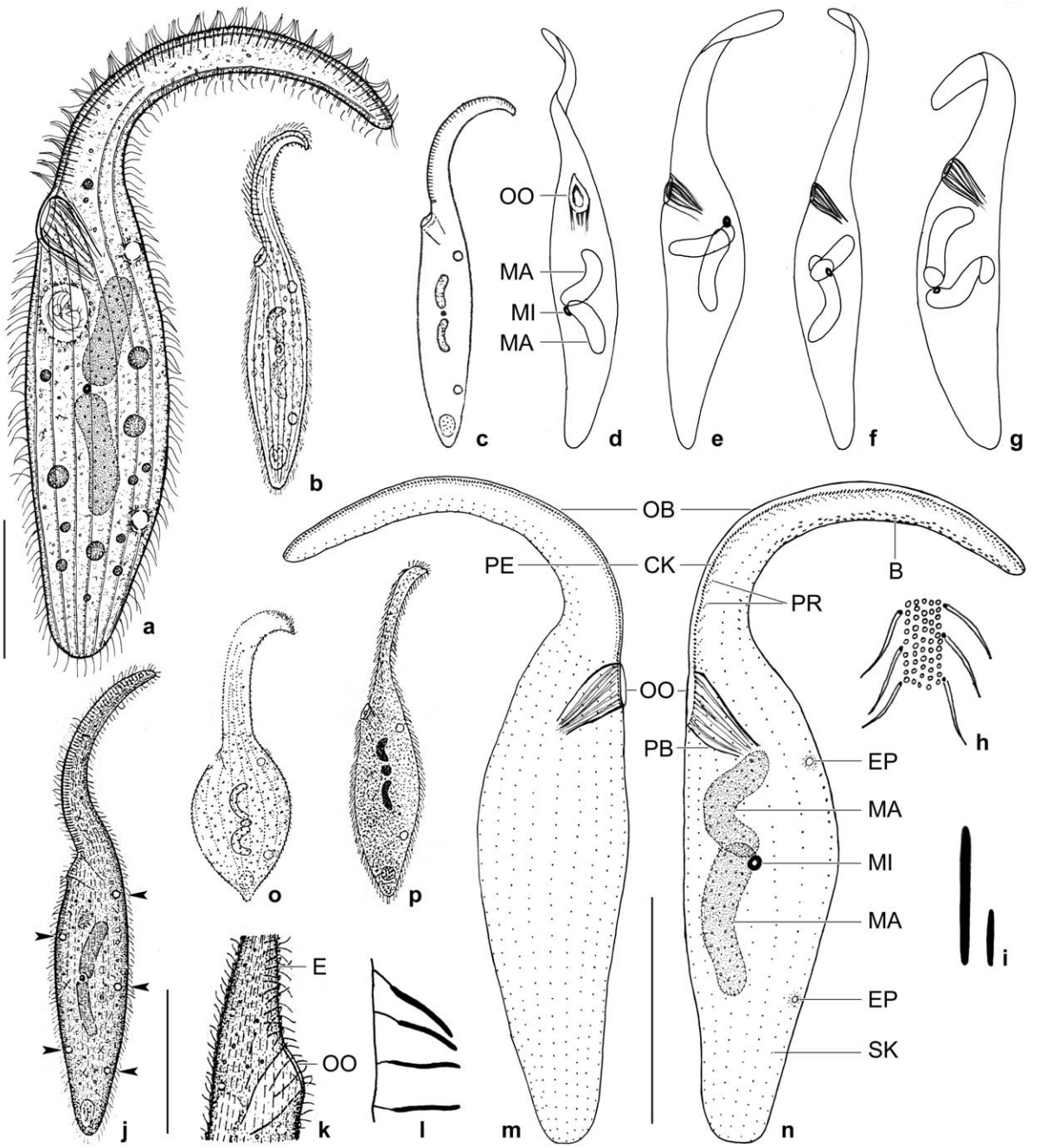


Figs 66a–g: *Rimaleptus binucleatus*, Australian specimens from life (b, c) and after protargol impregnation (a, d–g). **a** – left side view showing general organization; **b, c** – two size types (6 µm and 2 µm) of rod-shaped extrusomes are attached to the oral bulge of the proboscis; **d** – left side view of proboscis ciliary pattern, showing the preoral kineties, each usually composed of two narrowly spaced basal bodies; **e–g** – dorsal views of proboscis ciliary pattern. The dorsal brush consists of four to six staggered and distinctly heterostichad rows. Often there are some irregularities, such as breaks or some extra dikinetids, forming a short additional row. B(1–6) – dorsal brush (rows), CK – circumoral kinety, FV – food vacuole, MA – macronuclear nodules, OO – oral bulge opening, PB – pharyngeal basket, PR – preoral kineties. Scale bars: 20 µm (e–g) and 50 µm (a).

nos 2011/349–354) with Australian specimens. Relevant cells are marked by black ink circles on the coverslip.

Etymology: Not given in original description. Composite of the Latin numeral *bi* (two) and the noun *nucleus*, obviously referring to the two macronuclear nodules.

Description: Size in vivo highly variable, i.e., 170–400 × 20–40 µm, usually about 250 × 35 µm. Type specimens 300–400 µm long (Kahl 1931), Australian cells 170–250 × 20–45 µm in size. Body length/size of the supposed synonym *D. americanus*: 190–220 µm long (Kahl 1931), 200 × 40 µm (Madrazo-Garibay & López-Ochoterena 1973), 180–400 × 40–60 µm (Vďačný et al. 2006; possibly over-estimated when compared with values in Table 33). Body very flexible, Australian specimens up to 30% contractile under slight coverslip pressure. Shape narrowly to cylindroidally dileptid, i.e., length:width ratio 4.4–10:1,



Figs 67a–p: *Rimaleptus binucleatus* and its supposed synonym from life (a–c, h–k, o, p) and after protargol impregnation (d–g, l–n). From KAHL 1931 (b), DRAGESCO 1963 (c, j, k), LUNDIN & WEST 1963 (o), MADRAZO-GARIBAY & LÓPEZ-OCHOTERENA 1973 (p), and VĎAČNÝ et al. 2006 (a, d–g, h, i, l–n). **a** – *Dileptus americanus*, a representative Slovak specimen, length 300 µm; **b** – *D. americanus*, length 190–220 µm; **c** – redrawing of KAHL's specimen; **d–g** – variability of body shape and nuclear apparatus; **h** – cortical granulation; **i** – extrusomes of a Slovak specimen: type I is about 6 µm long, while type II is only 2 µm long; **j, k** – supposed *D. americanus*, overview and detail of oral apparatus, body length 175 µm. Arrowheads denote the ventral and dorsal contractile vacuoles; **l** – the distal portion of the cilia impregnates deeply; **m, n** – ciliary pattern of right and left side and nuclear apparatus of a Slovak specimen, length 193 µm; **o** – Michigan specimen, size not given; **p** – Mexican specimen, length 200 µm. B – dorsal brush, CK – circumoral kinety, E – extrusomes, EP – excretory pores, MA – macronuclear nodules, MI – micronucleus, OB – oral bulge, OO – oral bulge opening, PB – pharyngeal basket, PE – perioral kinety, PR – preoral kineties, SK – somatic kinety. Scale bars 50 µm.

Table 33. Morphometric data on a Slovak (S; from VĎAČNÝ et al. 2006) and an Australian (A; originals) population (Pop) of *Rimaleptus binucleatus*. Data based on mounted, protargol-impregnated (Foissner's method), and randomly selected specimens from non-flooded Petri dish cultures. Measurements in µm. CV – coefficient of variation in %, M – median, Max – maximum, Mean – arithmetic mean, Min – minimum, n – number of specimens investigated, SD – standard deviation, SE – standard error of mean.

Characteristics	Pop	Mean	M	SD	SE	CV	Min	Max	n
Body, length	S	210.4	207.8	47.4	15.0	22.5	150.0	295.3	10
	A	187.4	187.0	16.5	4.3	8.8	157.0	219.0	15
Body, width	S	33.1	34.4	4.4	1.4	13.4	28.1	39.1	10
	A	26.1	25.0	5.0	1.3	19.3	20.0	37.0	15
Body length:width, ratio	S	6.4	6.4	1.3	0.4	20.3	4.4	8.4	10
	A	7.4	7.2	1.4	0.4	18.7	4.9	10.0	15
Anterior body end to oral bulge opening, distance	S	78.7	80.5	25.0	7.9	31.8	40.6	117.2	10
	A	64.3	65.0	5.8	1.5	9.1	55.0	75.0	15
Proboscis, % of body length	S	37.1	34.7	7.8	2.5	21.0	27.1	48.5	10
	A	34.4	34.2	3.4	0.9	9.8	29.4	39.3	15
Oral bulge opening, length	S	12.4	12.1	1.5	0.5	11.9	10.9	14.1	10
	A	10.7	10.5	1.0	0.3	9.5	9.0	13.0	16
Oral bulge opening, width	A	10.0	10.0	0.6	0.3	6.3	9.0	11.0	6
Anterior body end to macronucleus, distance	A	85.9	84.0	8.8	2.3	10.2	73.0	103.0	15
Nuclear figure, length	S	46.3	48.0	7.1	2.2	15.4	36.7	56.3	10
	A	41.7	42.0	7.3	1.9	17.5	31.0	58.0	15
Anterior macronuclear nodule, length	S	32.3	31.3	5.0	1.6	15.6	28.1	43.8	10
	A	32.5	33.0	4.4	1.1	13.5	20.0	38.0	15
Anterior macronuclear nodule, width	S	9.6	9.8	1.5	0.5	15.6	7.0	10.9	10
	A	5.6	5.0	0.7	0.2	13.2	5.0	7.0	15
Posterior macronuclear nodule, length	A	29.4	30.0	4.5	1.1	15.1	25.0	38.0	15
Posterior macronuclear nodule, width	A	5.9	6.0	0.8	0.2	14.2	5.0	7.0	15
Macronuclear nodules, number	S	2.0	2.0	0.0	0.0	0.0	2.0	2.0	10
	A	2.0	2.0	0.0	0.0	0.0	2.0	2.0	15
Micronucleus, largest diameter	S	4.6	4.7	0.7	0.2	15.9	3.3	5.5	10
	A	3.9	4.0	0.7	0.2	19.2	3.0	5.0	15
Micronucleus, number	S	1.0	1.0	0.0	0.0	0.0	1.0	1.0	10
	A	1.0	1.0	0.0	0.0	0.0	1.0	1.0	15
Ciliary rows, number in mid-body	S	21.5	21.5	1.9	0.6	9.0	19.0	25.0	10
	A	20.6	20.0	1.7	0.4	8.2	18.0	24.0	15
Cilia in mid-body in 10 µm, number	S	6.4	6.0	0.9	0.3	14.4	5.0	8.0	10
	A	5.8	6.0	0.9	0.2	14.9	5.0	7.0	15
Dorsal brush rows, number	A	4.7	4.5	0.8	0.3	17.5	4.0	6.0	6

on average 7:1 in protargol preparations (Table 33). Proboscis about 35% of body length, usually curved dorsally; trunk bluntly fusiform, unflattened, posterior end acute to rounded, never tail-like (Figs 65b–d, h–l, 66a, 67a–g, m, n; Table 33). Nuclear apparatus in centre or slightly above mid of trunk. Invariably two macronuclear nodules in blunt to sharp angles; individual nodules reniform, oblong or cylindroidal and usually curved, some helical in Australian population; size about 32 × 7 µm after protargol impregnation; length:width ratio 3.3–7.6:1, on average 5.5:1; nucleoli 1–2 µm across, evenly distributed. Micronucleus in between macronuclear nodules, about 4.5 µm across in protargol preparations; sometimes surrounded by a distinct membrane in Australian specimens (Figs 65b, c, h–l, 66a, 67a–g, n; Table 33). Invariably two dorsal contractile vacuoles each with an intrakinetal pore: anterior vacuole slightly posterior to level of oral bulge opening, posterior vacuole at beginning of last quarter of trunk (Figs 65b–d, j, 67a–c, n). Extrusomes studied in Slovak and Australian specimens, their shape and size fairly similar (Figs 65a, 67i): type I rod-like with slightly narrowed ends, 5–7 µm long in Slovak specimens and about 6 × 0.8 µm in Australian cells; type II very fine, oblong and approximately 2 µm long. Cortex very flexible, contains five to six (Slovak specimens; Fig. 67h) or about 10 (Australian cells) rows of colourless granules between two adjacent kineties. Cytoplasm colourless, packed with lipid droplets 1–10 µm across and food vacuoles containing remnants of medium to large-sized prey ciliates. Glides rather slowly (Slovak specimens) to rapidly (Australian cells) on microscope slide, curving proboscis to and fro.

Cilia 7–8 µm long in vivo, ordinarily to narrowly spaced; in protargol preparations as typical for dileptids, i.e., 5.5 µm long and with thick, deeply impregnated distal half, except for dorsal and tail bristles (Fig. 67m). Ciliary rows ordinarily spaced, extend meridionally, number fairly stable between populations, viz., 19–25, on average 21 in Slovak specimens and 18–24, on average 20 in Australian cells (Table 33). A blank stripe on both sides of proboscis (Figs 65e–g, 66e–g, 67m, n). First row right of circumoral kinety extends as perioral kinety with ordinarily spaced cilia to tip of proboscis (Figs 65e, 67m). Dorsal brush a long, narrow field on dorsal side of proboscis; composed of four to six staggered, distinctly heterostichad rows, appearing diffuse when seen laterally; Australian specimens often with some irregularities, such as breaks or some extra dikinetids forming a short additional row (Figs 65g, f, 66e–g, 67n; Table 33). Brush dikinetids loosely to ordinarily spaced and associated with slightly clavate bristles up to 3 µm long in vivo in Australian specimens and 1.8 µm long after protargol impregnation in Slovak cells.

Oral bulge opening at beginning of second third of body, projects slightly to distinctly, roundish both in vivo and after protargol impregnation, in Slovak cells possibly sometimes ovate (Figs 65b–d, h–l, 67a–g; Table 33). Pharyngeal basket up to 20 µm long, indistinct in vivo. Circumoral kinety composed of narrowly spaced dikinetids in proboscis and narrowly spaced monokinetids around oral bulge opening. About 50 oblique, ordinarily spaced preoral kineties, as estimated from figures, each usually composed of two (Australian specimens) or three (Slovak cells) narrowly spaced cilia (Figs 65f, 66d, f, 67n).

Occurrence and ecology: *Rimaleptus binucleatus* is a moss and soil species, possibly also occurring in limnetic habitats. This species and its synonym have been reliably recorded from the Holarctis, Paleotropis and Australis, indicating cosmopolitan distribution.

Locus classicus of *R. binucleatus* are mosses on limestones from the Mittenwald region, Germany (Kahl 1931). In Australia, *R. binucleatus* occurred in a litter and soil sample (pH 5.2) from the rainforest near the town of Cairns. There are several unsubstantiated records: forest mosses from Slovenský raj (Slovak Paradise), Slovakia (Tirjaková & Matis 1987); in various soils from Abaco Island, Bahamas (Cairns & Ruthven 1972); lightly burnt soil in New Zealand (Stout 1961); Manzanares River near Madrid, Spain (Fernández-Leborans & Novillo 1995); coastal benthos of the Black Sea (Detcheva 1980, 1992; Azovsky & Mazei 2003); Volga river basin, Russia (Zhukov et al. 1998); sometimes abundant in a polluted river in Delhi, India (Kaur & Mehra 2001); Mountain Lake region, Giles County, Virginia, USA (Bovee 1960).

Terrestrial records of the synonym *Dileptus americanus*: 12 specimens in mosses from Wisconsin, USA, and in roof mosses from the town of Hamburg, Germany (Kahl 1931); leaf litter and soil of a beech forest on the "Kleinen Gudenberg" near Zierenberg, a small town about 30 km NW of the town of Kassel, Germany (Foissner 2000); calcaric fluvisol covered by mosses from the town of Bratislava, Slovakia (Chrenková & Tirjaková 2000); leaf litter (pH 4.5) from a beach forest in Vršatecké Bradlá-reef, Biele Karpaty Mts., Slovakia, 650 m above sea level (Vďačný et al. 2006); forest soil in Hungary (Gellért 1957); Thar desert, India (Das 1996); mangrove ecosystem in India (Nandi et al. 1993); in a mixture of plant litter, grass roots, and very sandy, humous soil from the Namib desert (Foissner et al. 2002); tussock grassland soils in New Zealand (Stout 1958).

Unsubstantiated limnetic records of the synonym *D. americanus*: in a eutrophic lake in England (Webb 1961); Llobregat River in Barcelona, Spain (Gracia et al. 1989); freshwater bodies on Mount Desert Island, Nebraska, USA (McCashland 1956); in Nichol's Bog at 18.5–20 ºC and pH 6.0 and in the West Branch of the Maple River, Michigan, USA (Cairns & Yongue 1966); in several water bodies of the Upper Peninsula of Michigan, USA (Lundin & West 1963; possibly a misidentification according to the figure provided, Fig. 67o); in the benthos of the slightly to moderately polluted Cape Fear River in the vicinity of Fayetteville, North Carolina, USA (Cairns & Yongue 1973); Mexico (Madrazo-Garibay & López-Ochoterena 1973, Aladro-Lubel et al. 2006).

The *Rimaleptus mucronatus* group

The six species collected in this group share multiple contractile vacuoles. Their extrusomes and dorsal brush are rather similar, but the length of the proboscis is rather different. Further, some species display curious specialities making their identification easy and reliable. For instance, *R. tirjakovae* has globular macronuclear nodules, while *R. longitrichus* possesses very long brush bristles (Table 34).

Table 34: Comparison of species of the *Rimaleptus mucronatus* group.

Characteristics	***Rimaleptus brasiliensis***	***Rimaleptus longitrichus***	***Rimaleptus mucronatus***	***Rimaleptus orientalis***	***Rimaleptus similis***	***Rimaleptus tirjakovae***
Body size in vivo (µm)	160 × 18	210 × 30	350 × 40	200 × 23	250 × 50	230 × 25
Proboscis, % of body length (protargol)	22	37	33	33	48	40
Extrusomes, number of types	2	1	2	2	2	2
Extrusomes, shape of type I	ovate to oblong with conical anterior end	rod-shaped	rod-shaped	ellipsoidal or broadly fusiform	rod-shaped	rod-shaped
Ciliary rows, average number	10	20	24	17	30	21
Dorsal brush rows, number	2	2	8	3 (?)	6	diffuse
Specialities	short proboscis	brush bristles up to 15 µm long, also ventral contractile vacuoles	posterior end with distinct tail	extrusomes minute but massive	sickle-shaped proboscis	globular macronuclear nodules, saline habitat

Rimaleptus brasiliensis nov. sp. (Figs 68a–m; Table 35)

2002 *Dileptus breviproboscis* Foissner, 1981 – Foissner, Agatha & Berger, Denisia **5**: 367 (misidentification)

Nomenclature and taxonomy: Foissner et al. (2002) misidentified the Brazilian site (30) population as *Dileptus breviproboscis* but mentioned that it could be considered as a new species, which is established here as *Rimaleptus brasiliensis* with the specimen shown in Figs 68h, j as the holotype. This is in accordance with Articles 49 and 72.3 of the ICZN (1999).

For details on taxonomy, see *Microdileptus breviproboscis*. Possibly, *R. brasiliensis* belongs to *Microdileptus*; however, the oral bulge opening is too large (9 × 5 µm).

Diagnosis: Size about 160 × 18 µm in vivo. Shape cylindroidally dileptid with acute posterior third, proboscis about 22% of body length. Two oblong macronuclear nodules with a micronucleus in between. A dorsal row of contractile vacuoles with 1–2 pores each. Two types of extrusomes attached to proboscis oral bulge: type I bluntly oblong with conical anterior end or ovate, 2–3 × 1 µm in size; type II fine, 3–4 µm long rods. On average 10 ciliary rows, 2 staggered and differentiated into an isostichad dorsal brush with bristles up to 4 µm long; both rows with a monokinetidal bristle tail extending to anterior trunk region. Oral bulge opening on average 9 × 5 µm in size. Preoral kineties ordinarily to widely spaced, each usually composed of 2 narrowly spaced kinetids, forming minute oblique rows in proximal half of proboscis, while almost a row in distal half.

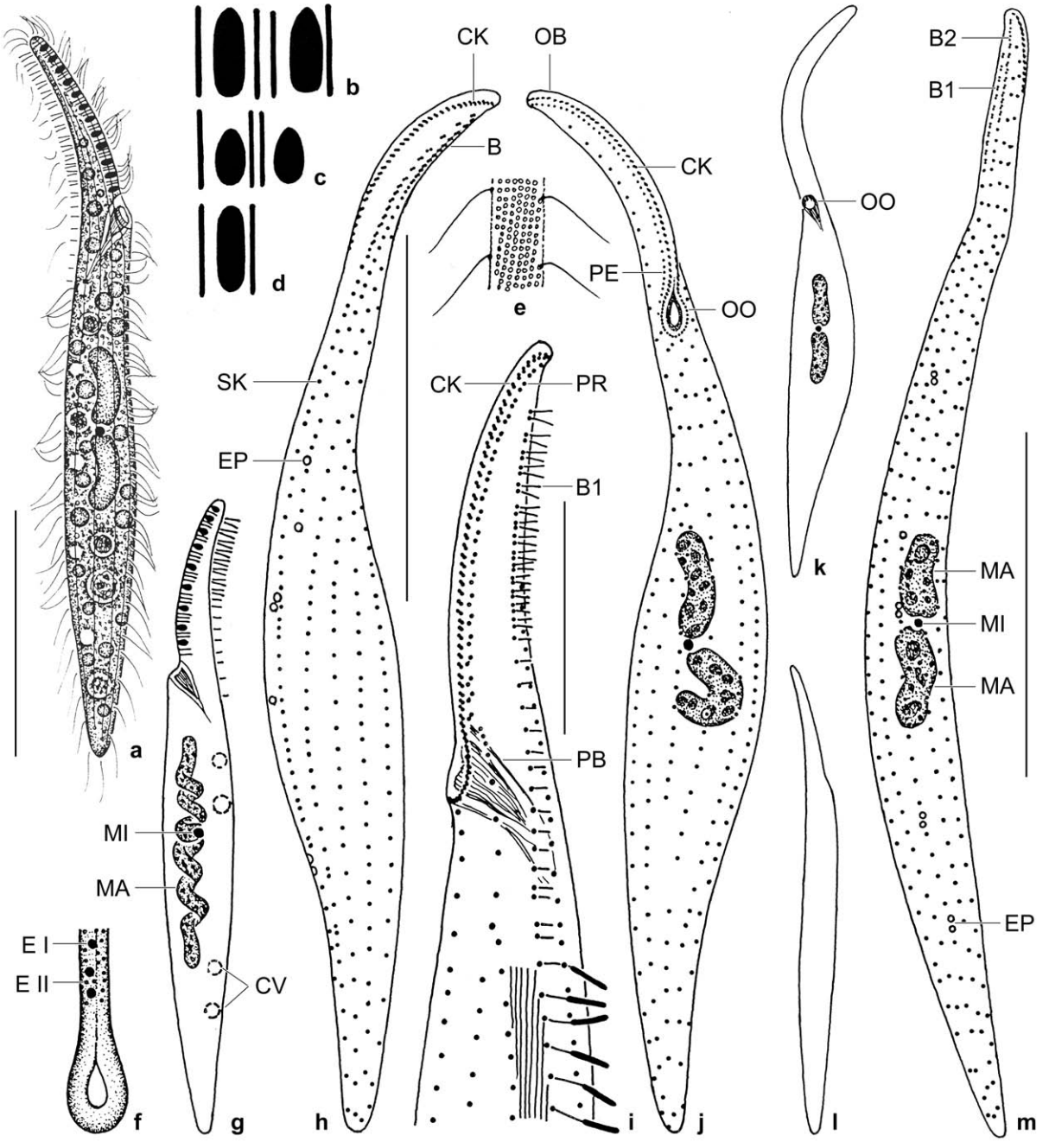
Type locality: Rain forest soil from a small island in the Amazon River, Brazil, about 20 km east of the town Manaus, Janauari region, W60° S4°.

Type material: Foissner et al. (2002) deposited five slides (inv. nos 2002/781–785) with protargol-impregnated specimens in the Biology Centre of the Museum of Upper Austria, Linz (LI), but under the name *Dileptus anguillula* (Aescht 2008). We declare the specimen shown in Figs 68h, j as the holotype of *R. brasiliensis*. This specimen and several paratype specimens are marked by black ink circles on the coverslip.

By an unfortunate mistake, the five slides were designated as neotypes in Table 1 (p. 38) of Foissner et al. (2002). We declare this as a mistake which is also recognizable from the fact that "neotypification" is not mentioned in the redescription of the species (Foissner et al. 2002: 367).

Etymology: The Latin adjective *brasiliensis* refers to the country (Brazil) in which the species was discovered.

Description: Size in vivo 120–220 × 15–25 µm, usually near 160 × 18 µm. Shape very narrowly dileptid to rod-like, length:width ratio highly variable, viz., 7–14:1, on average 9.5:1 in protargol preparations (Table 35). Proboscis indistinct because hardly set off from trunk and occupying only 22% of body length on average. Trunk oblong to bluntly fusiform, not or only slightly flattened, posterior end narrowly rounded (Figs 68a, g, h, j–m; Table 35). Nuclear apparatus in middle third of cell, invariably composed of two macronuclear nodules with a globular to slightly ellipsoidal micronucleus in between; rarely specimens, likely reorganizers, with two macronuclear groups each composed of four to six globular nodules; macronuclear nodules ellipsoidal to conspicuously spiral; nucleoli globular to irregularly lobate (Figs 68a, g, j, k, m; Table 35). A row of contractile vacuoles in dorsal side of trunk, composed of three to six, usually four small vacuoles each with one to two intrakinetal excretory pores associated with the brush kineties; occasionally, a pair of contractile vacuoles each at anterior and posterior end of trunk (Figs 68a, g, h, m; Table 35). Two types of extrusomes attached to proboscis oral bulge: type I only in broader right branch of bulge, conspicuously thick, oblong in Brazilian site (28) specimens, while ovate to oblong with conical anterior end in Brazilian site (30) individuals, about 2–3 × 1 µm in size; type II in both bulge branches, more numerous than type I and also scattered throughout cytoplasm, fine, rod-shaped, about 3–4 × ≤ 0.5



Figs 68a–m: *Rimaleptus brasiliensis* nov. sp. from life (a–f, l) and after protargol impregnation (g–k, m). From FOISSNER et al. (2002). **a** – right side view of a representative specimen, length 160 µm; **b–d** – extrusomes from populations of Brazilian sites 30 (b, c) and 28 (d). Drawn to scale, length about 3 µm; **e** – cortical granulation; **f** – frontal view of oral bulge opening; **g, k, l** – variability of body shape, nuclear apparatus and contractile vacuole pattern; **h, j, m** – dorsolateral (h, m) and ventrolateral (j) views, showing the ciliary and contractile vacuole pattern as well as the nuclear apparatus of the holotype specimen, length 140 µm. FOISSNER et al. (2002) forgot to figure preoral kineties in (h); **i** – ciliary pattern of left side in anterior body portion. Note the long, monokinetidal bristle tail associated with dorsal brush row 1. B(1, 2) – dorsal brush (rows), CK – circumoral kinety, CV – contractile vacuoles, EI, II – extrusome types, EP – excretory pores of contractile vacuoles, F – fibres, MA – macronuclear nodules, MI – micronucleus, OO – oral bulge opening, OB – oral bulge, PB – pharyngeal basket, PE – perioral kinety, PR – preoral kineties, SK – somatic kinety. Scale bars: 20 µm (i) and 50 µm (a, h, j, m).

µm (Figs 68b–d, f, g). Cortex very flexible, contains rows of colourless granules about 0.3 µm across (Fig. 68e). Cytoplasm colourless, contains many 0.5–5 µm-sized lipid droplets and food vacuoles with compact or loose contents up to 7 µm in diameter; in rear end sometimes a defecation vacuole. Swims and glides rather rapidly, showing great flexibility among soil particles.

Cilia 7–8 µm long in vivo, ordinarily to loosely spaced; in protargol preparations as typical for dileptids, i.e., with thick and deeply impregnated distal half, except for dorsal and tail bristles; somatic basal bodies associated with conspicuous (postciliary?) fibres obliquely extending backwards on right side of kineties (Fig. 68i). On average 10 ordinarily spaced ciliary rows, extending longitudinally and following body curvature (Figs 68h, j, m; Table 35). First row right of circumoral kinety extends as perioral kinety with

Table 35: Morphometric data on *Rimaleptus brasiliensis* (from FOISSNER et al. 2002). Data based on mounted, protargol-impregnated (Foissner's method), and randomly selected specimens from a non-flooded Petri dish culture. Measurements in µm. CV – coefficient of variation in %, Max – maximum, Mean – arithmetic mean, Min – minimum, n – number of specimens investigated, SD – standard deviation, SE – standard error of mean.

Characteristics	Mean	M	SD	SE	CV	Min	Max	n
Body, length	145.0	145.0	23.2	5.1	16.0	105.0	200.0	21
Body, width	15.4	15.0	2.4	0.5	15.7	12.0	20.0	21
Body length:width, ratio (calculated from original data)	9.5	9.2	2.0	0.4	21.1	7.0	13.8	21
Anterior body end to oral bulge opening, distance	32.1	32.0	6.4	1.4	19.9	23.0	45.0	21
Proboscis, % of body length (calculated from original data)	22.2	22.0	3.6	0.8	16.4	17.0	33.0	21
Oral bulge opening, length	8.4	9.0	1.5	0.3	17.4	6.0	11.0	18
Oral bulge opening, width	5.6	5.0	1.0	0.2	17.7	4.0	7.0	18
Anterior body end to macronucleus, distance	61.4	63.0	10.2	2.2	16.6	41.0	80.0	21
Nuclear figure, length	27.1	27.0	5.9	1.3	21.8	16.0	44.0	21
Macronuclear nodules, length[a]	13.8	14.0	3.0	0.7	21.6	8.0	22.0	21
Macronuclear nodules, width	4.9	5.0	0.6	0.1	12.7	4.0	6.0	21
Macronuclear nodules, number	2.0	2.0	0.0	0.0	0.0	2.0	2.0	21
Micronucleus, largest diameter	2.0	2.0	–	–	–	1.6	3.5	21
Micronucleus, number	1.0	1.0	0.0	0.0	0.0	1.0	1.0	21
Ciliary rows, number	9.9	10.0	1.0	0.2	10.3	7.0	11.0	21
Cilia in mid-body in 10 µm, number	3.8	4.0	0.8	0.2	19.7	2.0	5.0	21
Dorsal brush rows, number	2.0	2.0	0.0	0.0	0.0	2.0	2.0	21
Excretory pore groups, number	4.4	4.0	1.0	0.4	22.0	3.0	6.0	7
Excretory pores, total number	5.7	5.0	2.3	0.9	40.1	4.0	9.0	7

[a] Spiralized and/or curved nodules not straightened; actual length thus usually larger.

ordinarily to widely spaced cilia to tip of proboscis (Fig. 68j). A comparatively broad, blank stripe on both sides of proboscis (Figs 68h–j). Dorsal brush exactly on dorsal side of proboscis, composed of two staggered, isostichad rows. Brush dikinetids widely to ordinarily spaced and associated with clavate, about 4 µm long bristles anteriorly, decreasing to 2 µm posteriorly. Both brush rows extend underneath level of oral bulge opening with a tail of 1–2 µm long, monokinetidal bristles (Figs 68g–i, m).

Oral bulge opening at end of anterior body fifth, projects only slightly because base of proboscis almost as wide as trunk, ovate and about 9 × 5 µm in size after protargol impregnation (Figs 68a, f, g, i–l; Table 35). Pharyngeal basket bulbous, without specific features. Circumoral kinety composed of ordinarily spaced dikinetids, except for narrowly spaced monokinetids around oral bulge opening (Figs 68i, j). Preoral kineties ordinarily spaced, each composed of only two narrowly spaced cilia, difficult to recognize in distal half of proboscis because arranged almost in parallel with circumoral kinety (Fig. 68i).

Occurrence and ecology: As yet found at type locality and a site nearby.

Rimaleptus mucronatus (Penard, 1922) Vďačný, Orsi, Bourland, Shimano, Epstein & Foissner, 2011 (Figs 69a–t, 70a–p, 71a–p, 72a–l; Table 36)

1922 *Dileptus mucronatus* sp. n. Penard, Études Infusoires: 80

1930 *Dileptus mucronatus*, Pénard – Dumas, Les Microzoaires: 88 (description adopted from Penard 1922)

1931 *Dileptus mucronatus* Penard, 1922 – Kahl, Tierwelt Dtl. **21**: 207 (first reviser)

1960 *Dileptus mucronatus* Pénard – Dragesco, Trav. Stn biol. Roscoff **12**: 190 (notes on a French population)

1963 *Dileptus mucronatus* Pénard, 1922 – Dragesco, Bull. biol. Fr. Belg. **97**: 119 (second reviser)

1984 *Dileptus mucronatus* Penard, 1922 – Foissner, Stapfia **12**: 94 (authoritative redescription of an Austrian population)

1988 *Dileptus mucronatus* Penard, 1922 – Blatterer & Foissner, Stapfia **17**: 7 (brief note on an Australian population)

1994 *Dileptus mucronatus* Penard, 1922 – Song, J. Ocean Univ. Qingdao **24**: 17 (brief description of a Chinese population; possibly a misidentification)

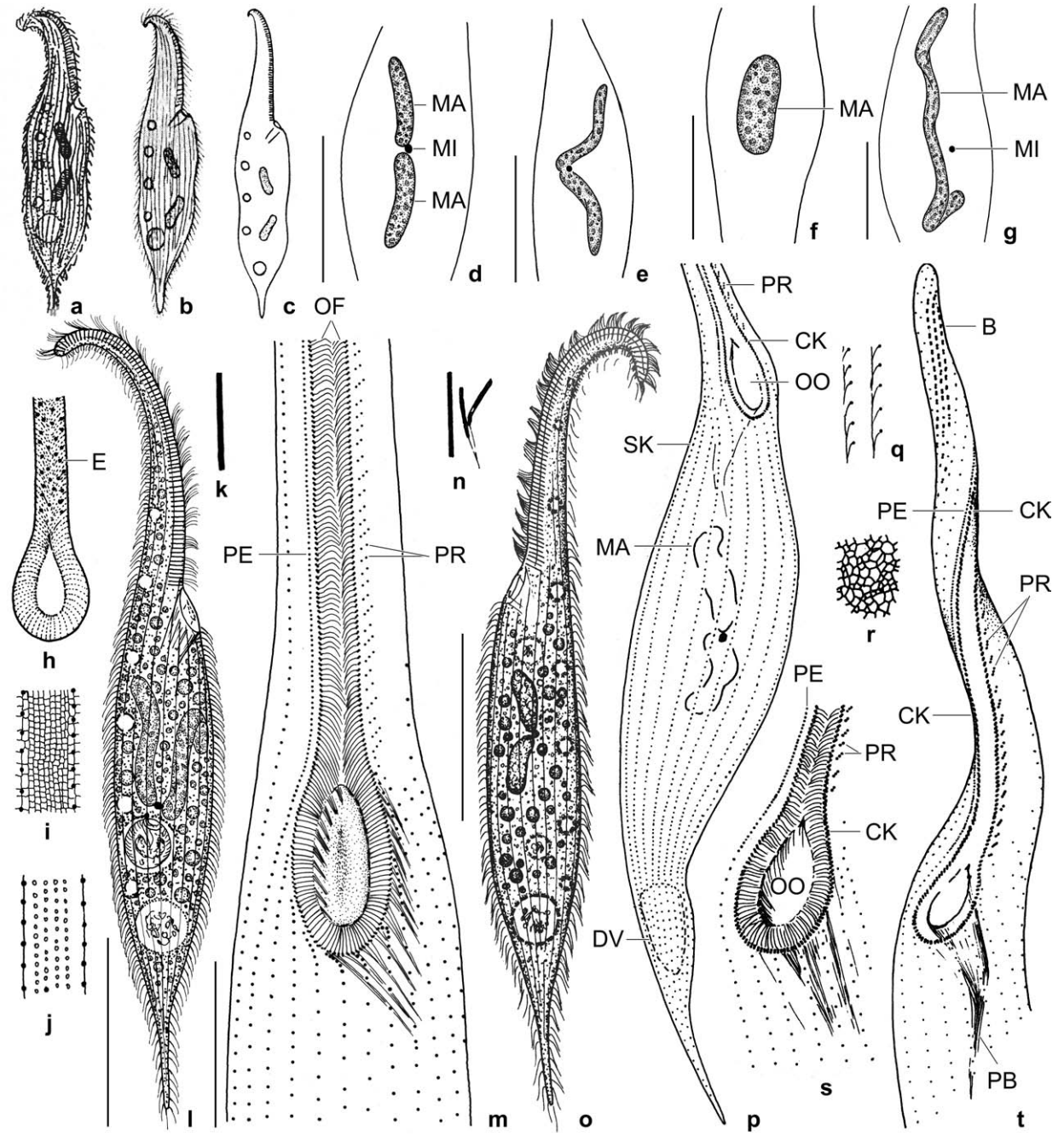
2002 *Dileptus mucronatus* Penard, 1922 – Foissner, Agatha & Berger, Denisia **5**: 370 (description of a Zanzibar population; extrusome variability)

2011 *Rimaleptus mucronatus* (Penard, 1922) comb. n. – Vďačný, Orsi, Bourland, Shimano, Epstein & Foissner, Eur. J. Protistol. **47**: **297** (18S rRNA gene sequence of a North American population)

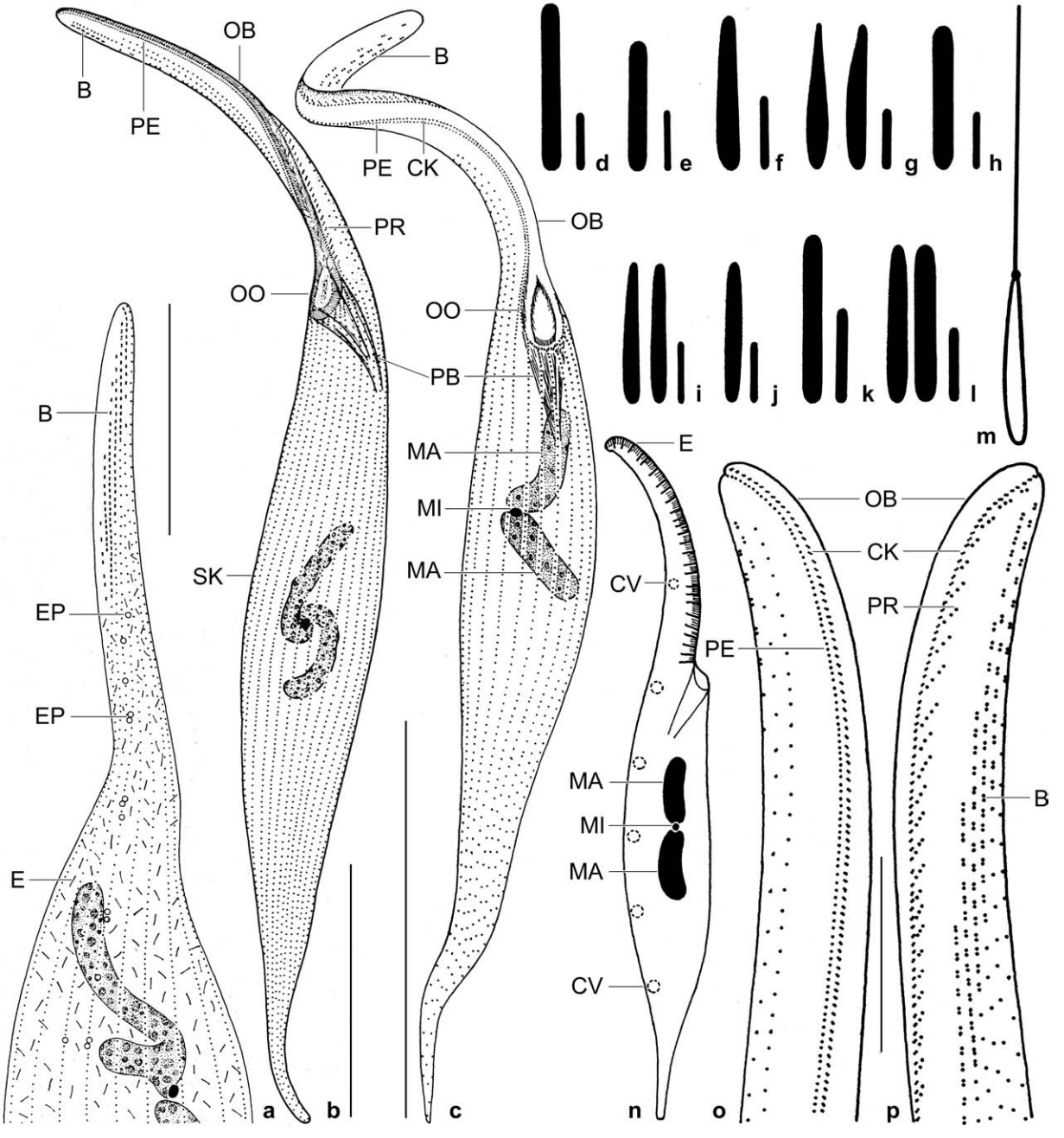
Generic affiliation, nomenclature and taxonomy: Vďačný et al. (2011b) combined *Dileptus mucronatus* with *Rimaleptus* because of the two macronuclear nodules and the ordinary oral basket. Misspelled as "*Dileptus micronatus*" by Shawhan et al. (1947), and thus unavailable according to Articles 33.3 and 33.5 of the ICZN (1999).

Neotypification was not mentioned by Foissner (1984) but one slide was designated as "paratype" (Aescht 2008). We declare this slide as a neotype of *Rimaleptus mucronatus*. Neotypification is necessary because (i) no type material is available from Penard's (1922) specimens, (ii) *R. mucronatus* possibly consists of several cryptic species, (iii) of several similar species threatining its identity, (iv) there are no doubts on the identification, (v) the neotype is from the same biogeographic region and a similar habitat, and (vi) the preparations are of good quality.

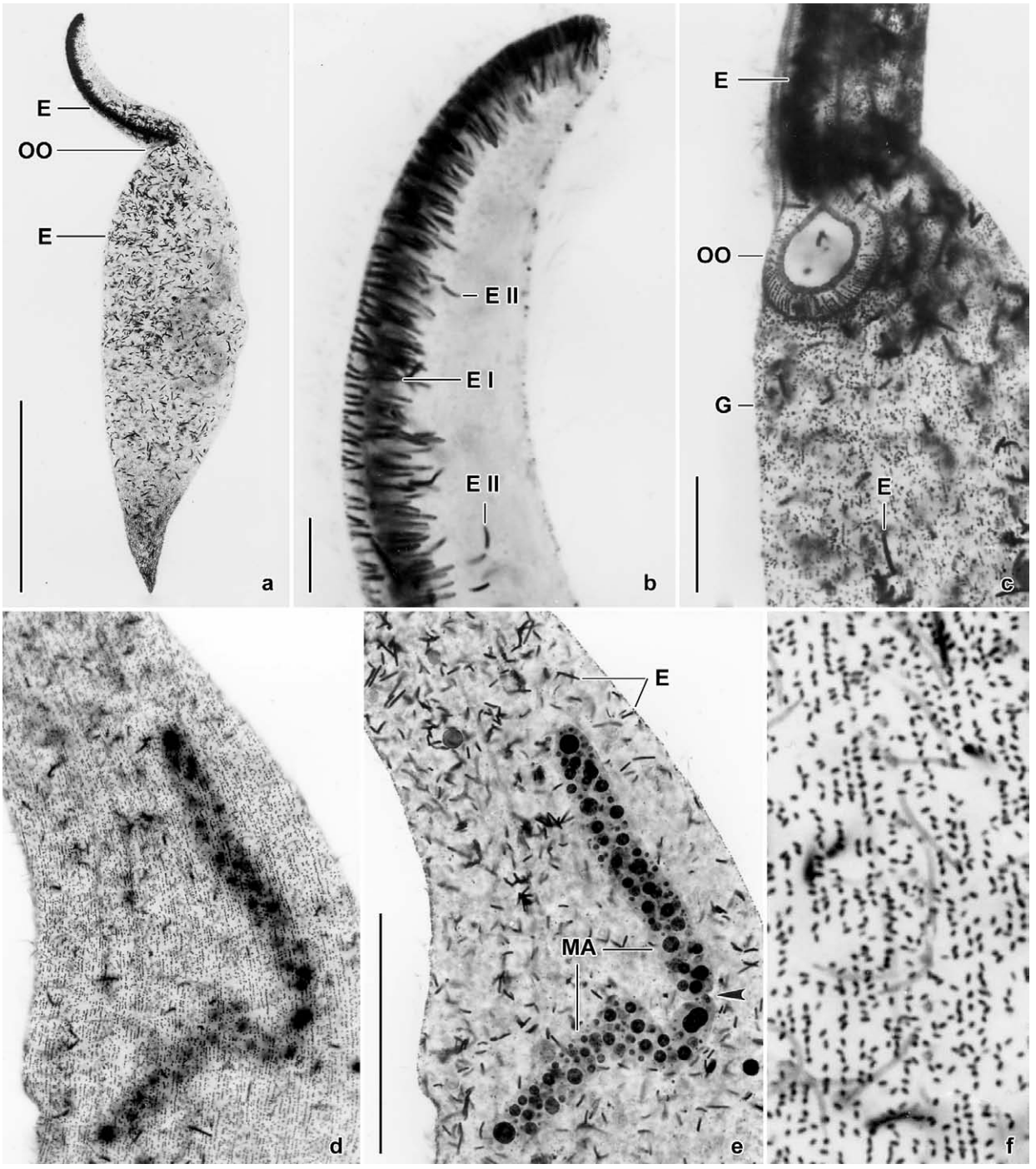
The identity of the Chinese population is questionable because it has only three dorsal brush rows and fewer ciliary rows. However, Song (1994a, b) and Song & Wilbert (1989) described only three brush rows in all dileptids they investigated, even in the large ones. Thus, we doubt their observations.



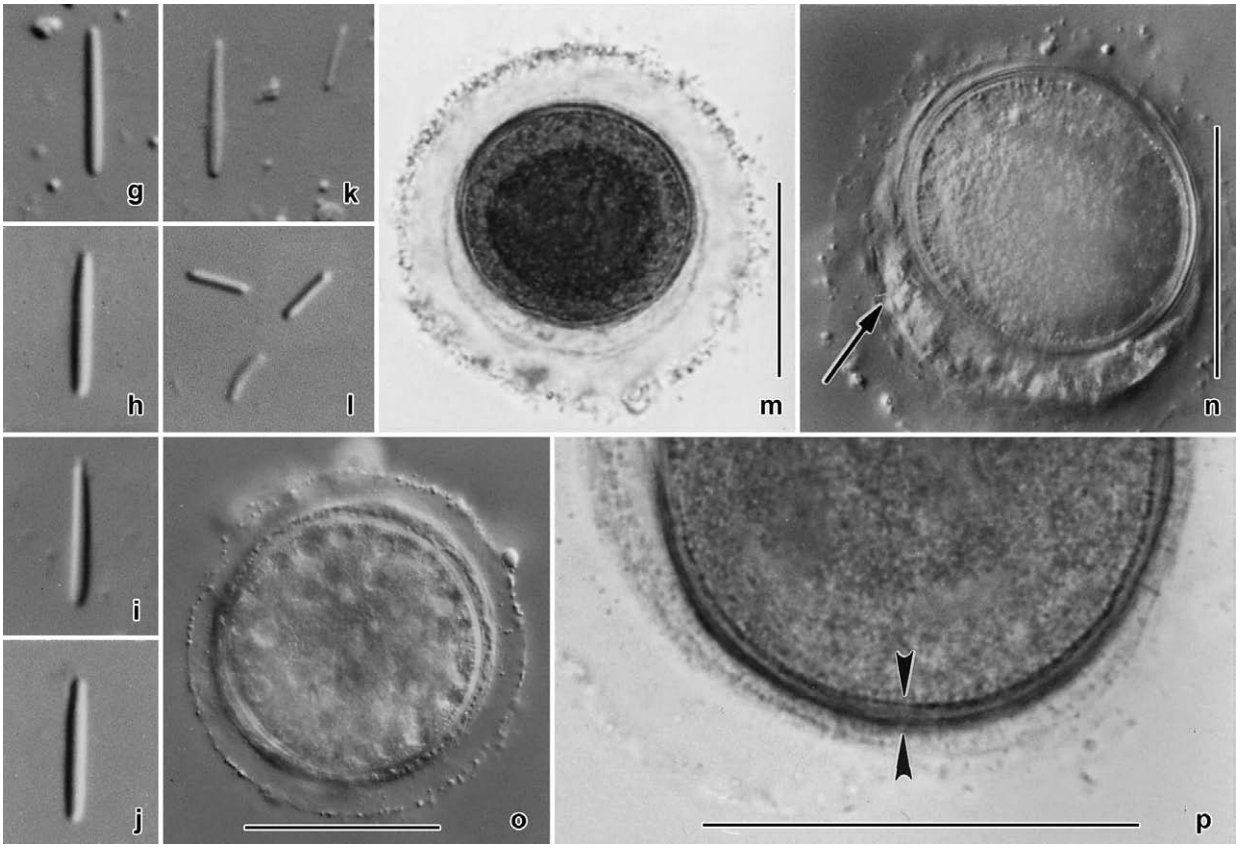
Figs 69a–t: *Rimaleptus mucronatus* from life (a–c, h, j–l, n, o) and after protargol (d–g, m, p, q, s, t) and Chatton-Lwoff silver nitrate (i, r) impregnation. From Penard 1922 (a), Kahl 1931 (b), Dragesco 1963 (c), Foissner 1984 (d–m), and Song 1994a (n–t). **a** – Swiss type specimen, length 240–275 µm; **b, c** – redrawings of type specimen; **d–g** – variability of nuclear apparatus; **h** – frontal view of oral bulge opening; **i, r** – silverline pattern; **j** – surface view showing cortical granulation; **k, n** – extrusomes are rod-shaped, about 7 µm long, and show the typical toxicyst structure when exploded; **l** – right side view of a representative Austrian specimen, length 450 µm; **m, s, t** – oral ciliary pattern, size not given for (s, t); **o** – left side view of a Chinese specimen, length 460 µm; **p** – ciliary pattern and nuclear apparatus of a Chinese specimen, size not given; **q** – surface view of cortex after protargol impregnation. B – dorsal brush, CK – circumoral kinety, DV – defecation vacuole, E – extrusomes, MA – macronuclear nodules, MI – micronucleus, OF – oral fibres, OO – oral bulge opening, PB – pharyngeal basket, PE – perioral kinety, PR – preoral kineties, SK – somatic kinety. Scale bars: 25 µm (m), 50 µm (d–g), and 100 µm (l, o).



Figs 70a–p: *Rimaleptus mucronatus* from life (d–n) and after protargol impregnation (a–c, o, p). From Foissner 1984 (a, b) and Foissner et al. 2002 (c–p). **a** – ciliary and contractile vacuole pattern of dorsal anterior body half; **b, c** – ciliary pattern and nuclear apparatus of an Austrian and a Zanzibar specimen, length 500 µm and 330 µm; **d–l** – type I (5–8 µm, usually 6 × 0.9 µm; if two are shown then it is the same organelle seen from two sides) and type II (2–4 µm) extrusomes of specimens from Kenya (d; population I), Benin (e), Zanzibar (f), Kenya (g; population II), Spain (h), Hawaii (i), St. Vincent Island in the Caribbean (j), Venezuela (k), and Austria (l; from same area as the population described in Foissner 1984). All drawn to scale; **m** – exploded type I toxicyst from a Zanzibar specimen, length 20 µm; **n** – a representative specimen from Zanzibar, length 300 µm; **o, p** – right and left side view of proboscis ciliary pattern. B – dorsal brush, CK – circumoral kinety, CV – contractile vacuoles, E – extrusomes, EP – excretory pores of contractile vacuoles, MA – macronuclear nodules, MI – micronucleus, OB – oral bulge, OO – oral bulge opening, PB – pharyngeal basket, PE – perioral kinety, PR – preoral kineties, SK – somatic kinety. Scale bars: 20 µm (o, p), 50 µm (a), and 100 µm (b, c).



Figs 71a–f: *Rimaleptus mucronatus*, Austrian specimens after silver carbonate impregnation (from FOISSNER et al. 2002). **a, b** – overview and proboscis at higher magnification. The ventral margin of the proboscis is packed with two size-types of rod-shaped extrusomes. The small extrusomes are numerous also in the cytoplasm; **c** – oral area showing cortical granulation; **d, e** – same specimen at two focal planes to show the rows of cortical granules (d), the two abutting macronuclear nodules (e, arrowhead), and the numerous small extrusomes scattered throughout the cytoplasm (e); **f** – surface view showing cortical granulation. The granules are minute (< 0.8 µm), oblong, and deeply impregnated with silver carbonate. E(I, II) – extrusome (types), G – cortical granules, MA – macronuclear nodules, OO – oral bulge opening. Scale bars: 10 µm (b), 20 µm (c), 50 µm (d, e), and 100 µm (a).

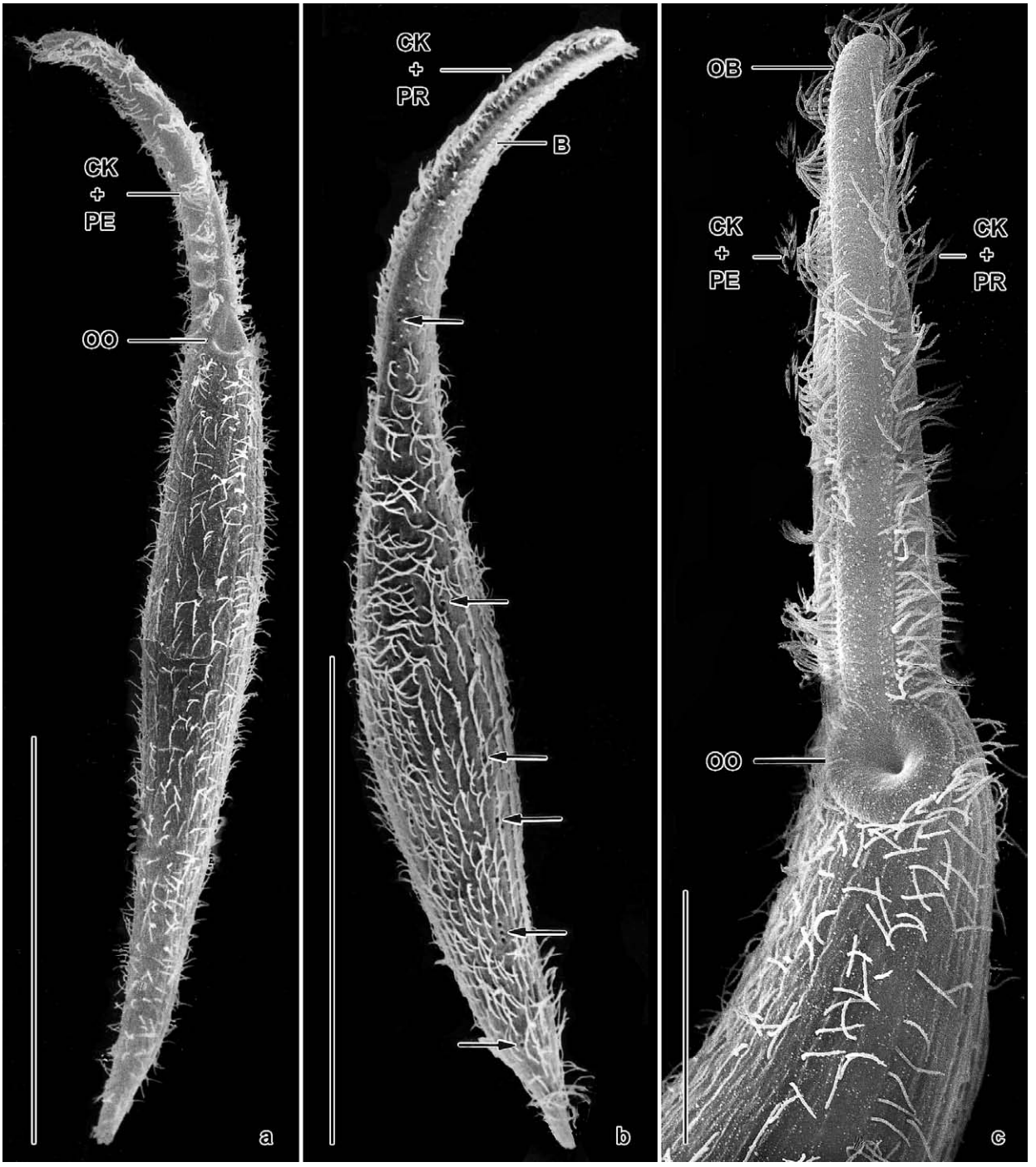


Figs 71g–p: *Rimaleptus mucronatus*, extrusomes (g–l) and resting cysts (m–p) in vivo (from FOISSNER et al. 2002). **g–l** – large (6–7 × 0.9 µm; g–k) and small (3 µm; k, l) extrusomes of a single specimen from Zanzibar. The shape of the large extrusomes varies from rod-like (g) to slightly ovate (k); **m–p** – resting cysts of Kenyan specimens. The cysts are spherical to slightly ellipsoidal, have an average size of 60 µm, and are surrounded by a conspicuous mucous layer. Arrow in (n) marks extruded cyst material, opposed arrowheads in (p) delimit the honey-brown, smooth cyst wall. Scale bars 50 µm (m–p).

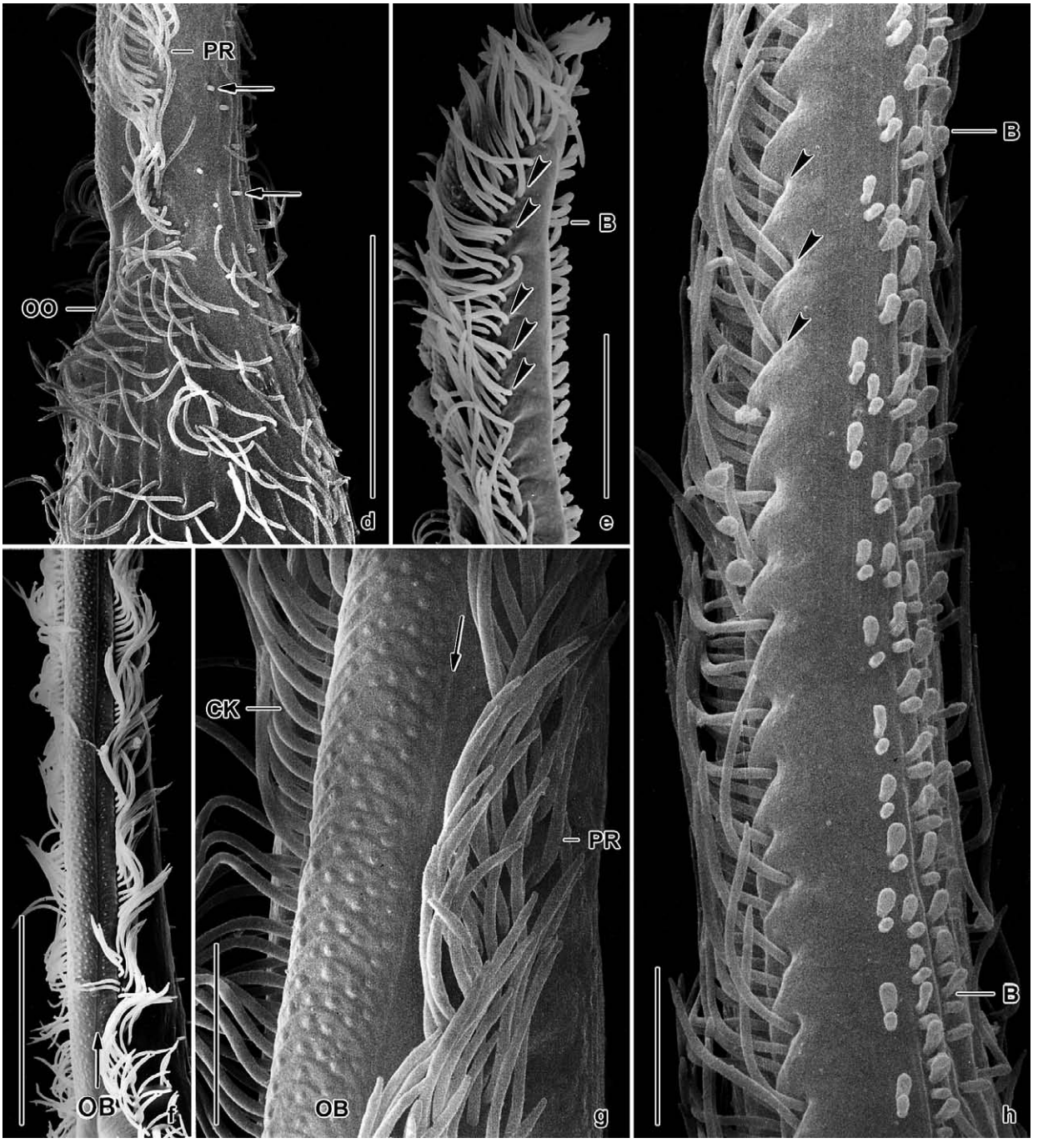
Rimaleptus mucronatus is easily identified by the moderate size (usually about 350 µm), the cylindroidally dileptid body with a distinct tail, and the dorsal stripe of contractile vacuoles. Within the *R. mucronatus* group, *R. mucronatus* most resembles *R. similis* and *R. longitrichus*. However, *R. similis* is smaller (250 µm vs. 350 µm) and has a rounded posterior end (vs. with distinct tail). *Rimaleptus longitrichus* is distinguished from *R. mucronatus* by the smaller body (210 µm vs. 350 µm), the contractile vacuole pattern (ventral and dorsal vacuoles vs. only dorsal ones), and the length of the brush bristles (up to 15 µm vs. 2–3 µm).

FOISSNER et al. (2002) studied extrusome shape and size in nine populations collected globally. They were fairly constant, i.e., 5–8 µm long and rod-shaped to slightly ovate in eight populations (Figs 70d–f, h–l, 71g–l), while very narrowly ovate in a population from Kenya (Fig. 70g). At the present state of knowledge, we cannot decide whether the Kenyan population II represents a distinct taxon or the extrusomes are considerably variable in *R. mucronatus*. Possibly, populations with very narrowly ovate extrusomes should be given subspecies rank.

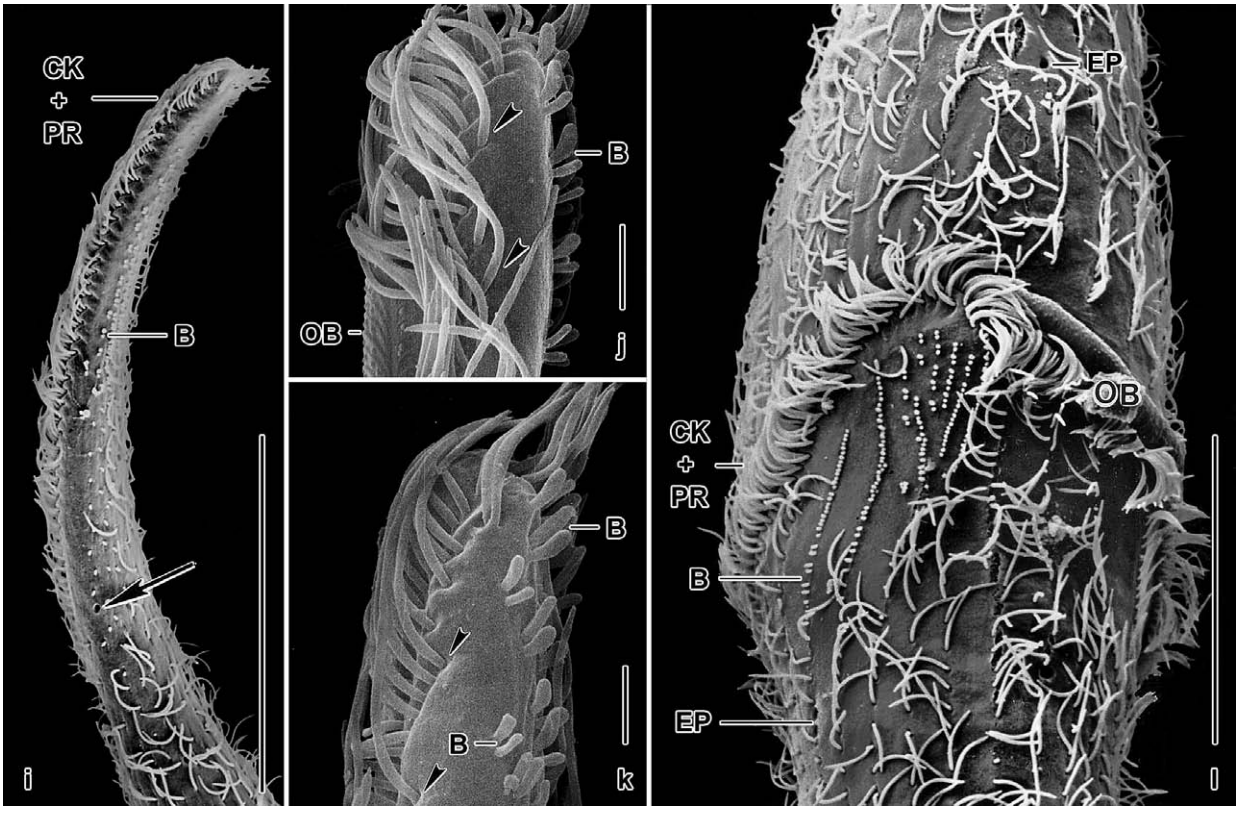
Improved diagnosis (excludes Kenyan population II): Size about 350 × 40 µm in vivo. Shape narrowly dileptid to rod-like with distinct tail, proboscis about 1/3 of body length. Two oblong macronuclear nodules with a micronucleus in between. A dorsal row of contractile vacuoles with 1–3 excretory pores each. Two types of extrusomes attached to proboscis oral bulge: type I rod-shaped to slightly ovate, usually 6–7 × 0.9



Figs 72a–c: *Rimaleptus mucronatus*, Venezuelan (a, c) and Kenyan (b) specimens in the SEM (from FOISSNER et al. 2002). **a** – overview showing the slender body with posterior end gradually narrowing to an acute end. The proboscis occupies about one third of body length; **b** – overview showing the dorsal stripe of excretory pores (arrows); **c** – ventral view of anterior body half. The oral bulge is keyhole-shaped, that is, widened in its posterior part forming an oral opening. The bulge in proboscis is delineated by the metachronal ciliary waves formed by the oral cila, i.e., by the circumoral and perioral cilia on the right of the bulge, while by the circumoral and preoral cilia left of the bulge. B – dorsal brush, CK – circumoral kinety, OB – oral bulge, OO – oral bulge opening, PE – perioral kinety, PR – preoral kineties. Scale bars: 20 µm (c) and 100 µm (a, b).



Figs 72d–h: *Rimaleptus mucronatus*, Kenyan specimens in the SEM (from FOISSNER et al. 2002). **d** – left side view showing, inter alia, the distinctly projecting oral bulge opening and the short monokinetidal tail bristles (arrows); **e** – left side view of anterior proboscis region, showing the preoral kineties (arrowheads) and the paired inflated dorsal brush bristles, extending to the tip of the proboscis; **f, g** – ventral views of proboscis. The metachronal ciliary waves, formed by the oral cilia beating together, delineate the bulge of the proboscis. Arrows mark furrow separating the broader right from the narrower left branch of the bulge, which is dotted by the large extrusomes and transversely striated by fibre bundles, very likely transverse microtubule ribbons; **h** – dorsolateral view of proboscis, showing the paired inflated dorsal brush bristles that form staggered rows. Preoral kineties (arrowheads) are oblique and each is usually composed of three narrowly spaced cilia, extending in a distinct furrow. B – dorsal brush, CK – circumoral kinety, OB –oral bulge, OO – oral bulge opening, PR – preoral kineties. Scale bars: 5 µm (g, h), 10 µm (e), and 20 µm (d, f).



Figs 72i–l: *Rimaleptus mucronatus*, Kenyan specimens in the SEM (from FOISSNER et al. 2002). **i** – dorsolateral view of proboscis showing preoral kineties extending in distinct furrows, a staggered dorsal brush, and an excretory pore (arrow) at the base of the proboscis; **j, k** – left side view of distal proboscis area, showing the preoral kineties (arrowheads) and the paired inflated dorsal brush bristles extending to the tip of the proboscis; **l** – dorsal view of dividing specimen, showing seven dorsal brush rows of highly varying length. Note the oblique division axis. B – dorsal brush, CK – circumoral kinety, EP – excretory pores, OB – oral bulge, PR – preoral kineties. Scale bars: 3 µm (j, k), 30 µm (l), and 50 µm (i).

µm in size; type II oblong, 2.5–3 µm long. On average 24 ciliary rows, about 8 anteriorly differentiated into a staggered, distinctly heterostichad dorsal brush with bristles up to 3 µm long. Oral bulge opening ovate, about 25 µm long. Preoral kineties oblique, ordinarily spaced, usually composed of 3 narrowly spaced cilia.

Type locality: PENARD (1922) discovered *R. mucronatus* in a drain in the surroundings (Pinchat) of the town of Geneva, Switzerland, E6°9' N46°10'. The neotype is from soil of a meadow near the Neusiedlersee, a soda lake in the "hell" region near Illmitz, Burgenland, Austria E16°49' N47°45' (FOISSNER 1984). According to Article 76.3 of the ICZN (1999), the place of origin of the neotype becomes the type locality of the nominal species-group taxon, despite any previously published statement of the type locality.

Type and voucher material: No type material is available from PENARD'. FOISSNER (1984) deposited one neotype slide (inv. no. 1984/34; mislabelled as "paratype") with protargol-impregnated Austrian specimens in the Biology Centre of the Museum of Upper Austria, Linz (LI). FOISSNER et al. (2002) deposited two voucher slides (inv. nos 2002/568 and 2002/569) with protargol-impregnated Zanzibar specimens in the same repository. Relevant specimens are marked by black ink circles on the coverslip.

Gene sequence: The 18S rRNA gene sequence of a North American population has been deposited in GenBank (HM581675). The sequence is 1639 nucleotides long and has a GC content of 42.5%. It is a consensus sequence based on 15 clones.

Etymology: Not given in original description. The Latin adjective *mucronatus* (sharply pointed, mucronate) refers to the distinct tail.

Description: All data are put together because the morphological conspecificity of the populations mentioned in the list of synonyms is beyond reasonable doubts, except for Song's (1994a) specimens.

Size highly variable in vivo, i.e., 240–550 µm long, usually about 350 × 40 µm. Type specimens 240–275 µm long (Penard 1922), French cells 240 µm (Dragesco 1960), Austrian individuals 300–500 × 40–60 µm in size (Foissner 1984), Chinese exemplars 350–550 µm (Song 1994a), and Zanzibar cells 250–500 µm long (Foissner et al. 2002). Australian specimens considerably smaller, i.e., 150–210 × 20–25 µm in protargol preparations (Blatterer & Foissner 1988).

Body very flexible but not contractile. Shape in vivo narrowly dileptid to rod-like, i.e., length:width ratio 5.0–13:1, on average 7:1, according to the figures available and the morphometric data. Proboscis length highly variable, viz., 20% to 41% of body length, on average about 33%, motile and flexible, anterior portion usually curved dorsally (Table 36). Trunk oblong to bluntly fusiform, unflattened, indented in mid portion in type specimen (Fig. 69a). Posterior end with distinct tail in vivo, while usually gradually narrowing to an acute end in protargol and SEM prepared cells (Figs 69a–c, l, o, p, 70b, c, n, 71a, 72a, b).

Nuclear apparatus in centre of trunk. Typically two macronuclear nodules, rarely specimens (post-dividers or reorganizers?) with nodules fused into a rod-like structure or an ellipsoidal mass (Figs 69a–g, l, o, p, 70b, c, n, 71d, e; Table 36). Individual nodules oblong to cylindroidal, curved and/or spiralized; size after protargol impregnation conspicuously variable within and between populations, viz., 42–70 × 6–9 µm, on average 53.6 × 7.5 µm in Austrian specimens (Foissner 1984), while 29–48 × 7–11 µm, on average 33.8 × 9.1 µm in Zanzibar population (Foissner et al. 2002); length:width ratio also highly variable, i.e., 3–10:1, on average 5.5:1. Nucleoli evenly distributed in macronuclear nodules, medium-sized, globular, and well recognizable after protargol and silver carbonate impregnation (Figs 71d, e). Invariably a single micronucleus between macronuclear nodules, about 3 µm across after protargol impregnation (Table 36).

Contractile vacuole pattern very similar in all populations investigated, viz., a dorsal stripe of at least four vacuoles (Figs 69a–c, l, o, 70n). First vacuole at level of oral bulge opening in Swiss specimens (Fig. 69a), while near mid of proboscis in Austrian, Chinese and Zanzibar cells (Figs 69l, o, 70a, n). Number of vacuoles: four to five in Swiss specimens (Penard 1922), about six in Austrian and Zanzibar cells (Foissner 1984, Foissner et al. 2002), and six to nine in Chinese individuals (Song 1994a). Number of excretory pores studied only in Austrian (Foissner 1984) and Kenyan (Foissner et al. 2002) specimens, viz., one to three intrakinetal pores per vacuole (Figs 70a, 72b, i).

Extrusomes studied in 11 populations (see also taxonomic section above and Figs 69k, n, 70d–l, 71g–l). Located in both branches of proboscis oral bulge (in an Austrian and Zanzibar population each) or only in right branch (Venezuelan population). Type I extrusomes "court et serrés" in type specimens (Penard 1922); rod-shaped, about 7 µm long, in several rows between circumoral kinety, and scattered in cytoplasm (Foissner 1984); "basically rod-shaped to slightly ovate and asymmetrical, 5–8 µm, usually 6–7 µm long, when exploded of typical toxicyst structure, that is, with a tube emerging from the empty capsule" (Foissner et al. 2002). Type II extrusomes oblong, 2–4 µm, usually 2.5–3 µm long; overlooked by Foissner (1984) but later found by Foissner et al. (2002) in specimens from the same area.

Cortex flexible, colourless, slightly furrowed by ciliary rows in SEM micrographs, contains several rows of granules (mucocysts) between adjacent kineties. Granules ordinarily spaced both in somatic and oral cortex, minute (< 0.8 µm) and oblong, strongly impregnate with silver carbonate (Figs 69j, 71c–f). Silverline pattern studied in Austrian (Foissner 1984) and Chinese (Song 1994a) specimens, composed

Table 36. Morphometric data on an Austrian (A; from FOISSNER 1984) and a Zanzibar (Z; from FOISSNER et al. 2002) population (Pop) of *Rimaleptus mucronatus*. Data based, if not stated otherwise, on mounted, protargol-impregnated (Foissner's method) specimens from non-flooded Petri dish cultures. Measurements in µm. CV – coefficient of variation in %, M – median, Max – maximum, Mean – arithmetic mean, Min – minimum, n – number of specimens investigated, SD – standard deviation, SE – standard error of mean.

Characteristics	Pop	Mean	M	SD	SE	CV	Min	Max	n
Body, length	A	392.0	400.0	50.0	12.9	12.8	310.0	500.0	15
	Z	286.4	300.0	33.0	10.0	11.5	220.0	330.0	11
Body, width	A	45.1	45.0	7.5	1.9	16.6	32.0	60.0	15
	Z	34.1	35.0	5.7	1.7	16.7	25.0	45.0	11
Body length:width, ratio (calculated from original data)	A	8.9	9.1	2.1	0.5	23.1	5.3	13.1	15
	Z	8.5	8.3	1.5	0.5	17.5	6.7	11.4	11
Anterior body end to oral bulge opening, distance	A	117.5	112.0	17.1	4.4	14.5	90.0	145.0	15
	Z	101.2	100.0	14.3	4.3	14.1	70.0	125.0	11
Proboscis, % of body length (calculated from original data)	A	30.3	31.3	4.9	1.3	16.3	20.5	41.4	15
	Z	35.4	35.1	3.2	1.0	8.9	31.3	40.7	11
Oral bulge opening, maximum width	A	13.2	14.0	1.4	0.4	10.8	10.0	15.0	15
	Z	12.8	13.0	1.3	0.4	9.8	11.0	15.0	11
Nuclear figure, length	A	70.3	70.0	16.6	4.3	23.7	50.0	120.0	15
	Z	57.9	55.0	10.9	3.3	18.8	45.0	85.0	11
Macronuclear nodules, length	A	53.6	50.0	9.9	2.6	18.6	42.0	70.0	15
	Z	33.8	32.0	5.7	1.7	16.8	29.0	48.0	11
Macronuclear nodules, width	A	7.5	7.0	0.8	0.2	10.9	6.0	9.0	15
	Z	9.1	9.0	1.3	0.4	14.3	7.0	11.0	11
Macronuclear nodules, number	A	1.9	2.0	–	–	–	1.0	2.0	15
	Z	2.2	2.2	0.0	0.0	0.0	2.0	2.0	11
Micronucleus, largest diameter	A	3.4	3.0	0.8	0.2	23.1	3.0	6.0	15
	Z	3.3	3.0	0.7	0.2	19.8	3.0	5.0	11
Micronucleus, number	A	1.0	1.0	0.0	0.0	0.0	1.0	1.0	15
	Z	1.0	1.0	0.0	0.0	0.0	1.0	1.0	11
Ciliary rows, number	A	25.8	26.0	2.8	0.7	10.9	21.0	30.0	15
	Z	21.6	21.0	2.2	0.7	10.0	19.0	26.0	11
Cilia in mid-body in 10 µm, number	A	6.6	6.0	0.9	0.2	13.8	5.0	8.0	15
	Z	5.6	6.0	1.3	0.4	22.8	4.0	7.0	11
Resting cysts, length including mucous layer (in vivo)	Z	87.4	86.0	10.7	2.9	12.3	72.0	104.0	14
Resting cysts, width including mucous layer (in vivo)	Z	87.1	86.0	10.8	2.9	12.4	72.0	104.0	14
Resting cysts, length excluding mucous layer (in vivo)	Z	60.7	61.0	5.8	1.6	9.6	52.0	72.0	14
Resting cysts, width excluding mucous layer (in vivo)	Z	57.8	59.0	5.0	1.3	8.7	48.0	64.0	14

of polygonal meshes about 0.4 µm in size, not yet examined in detail (Figs 69i, r). Cytoplasm colourless, hyaline in proboscis and tail, opaque in trunk due to many lipid droplets 1–3 µm across and food vacuoles containing ciliates, e.g., *Vorticella* sp. Often a defecation vacuole with granular material near base of tail. Swims rapidly, somewhat wriggly (Foissner 1984).

Cilia ordinarily to narrowly spaced, in protargol preparations as typical for dileptids. Ciliary rows ordinarily spaced, extend longitudinally following body curvature, number rather variable, viz., 22–26 in French specimens (Dragesco 1960), 21–30, on average 26 in Austrian cells (Foissner 1984), 16–19 in Chinese specimens (possibly slightly underestimated as indicated by Song's drawing), and 19–26, on average 21 in Zanzibar exemplars (Foissner et al. 2002). Details of ciliary pattern studied in three populations (Foissner 1984, Song 1994a, Foissner et al. 2002). Some right side rows shortened in proboscis area; perioral kinety extends to tip of proboscis with ordinarily to narrowly spaced basal bodies (Figs 69m, p, s, t, 70b, c, o). Both sides of proboscis with a blank stripe, that on left side broader than that on right because most rows end at base of proboscis (Figs 69m, t, 70c, o, p, 72a, b, d, e, h, i). Ventral rows distinctly curved rightwards when abutting on circumoral kinety in Austrian and Zanzibar specimens (Figs 69m, 70b, c). Dorsal brush a long field on dorsal and dorsolateral area of proboscis; staggered; distinctly heterostichad; composed of about eight rows (Figs 70a, c, o, p, 72b, h, i); as concerns Song (1994a), see taxonomy section above (Fig. 69t). Brush dikinetids loosely to ordinarily spaced, associated with type I bristles: anterior bristles about 2–3 µm long in vivo (1.0–1.7 µm in SEM), posterior bristles gradually decrease in length from about 1.5 µm to 1 µm (SEM measurements), becoming inconspicuous stumps in posterior dikinetidal brush region. All rows continue with a monokinetidal tail extending to base of proboscis with type VI bristles 0.8–1 µm long in SEM (Figs 72d, e, h, j, k).

Oral bulge opening at beginning of second third of body; projects slightly to distinctly because base of proboscis more or less narrowed; ovate in vivo, about 10 µm across in SEM preparations, sometimes ellipsoidal after protargol impregnation, possibly an artefact occurring also in other species (Figs 69h, m, p, s, t, 70b, c, 71c, 72a, c, d). Pharyngeal basket obconical, distinct both in vivo and in protargol preparations, without specific features. Oral bulge distinct in SEM micrographs because broad and limited by metachronal ciliary waves (Figs 72c, f, g). Circumoral kinety composed of ordinarily spaced dikinetids in proboscis and narrowly spaced monokinetids around oral bulge opening. Preoral kineties in distinct furrows, oblique, ordinarily spaced, each composed of two to four, usually three narrowly spaced cilia (Figs 69m, p, s, t, 70b, p, 72d, e, h, j, k).

Resting cyst: Described by Foissner et al. (2002): "The resting cysts of a cultivated Kenyan population are spherical to slightly ellipsoidal, have an average diameter of 60 µm, and are surrounded by a conspicuous mucous layer, which sometimes contains extruded cyst material. The cysts are conspicuously honey-yellow/brown because the about 2 µm thick wall has this colour, which is clearly recognizable in squashed cysts" (Figs 71m–p; Table 36).

Occurrence and ecology: Although *R. mucronatus* occurs in limnetic habitats, it is the most common middle-sized dileptid in terrestrial environments. As yet recorded from four main biogeographic regions, showing cosmopolitan distribution: Holarctic (both in Palearctic and Nearctic), Paleotropis (e.g., Benin, Kenya, Zanzibar), Neotropis (e.g., Venezuela, St. Vincent Island), and Australis.

Records from terrestrial and semi-terrestrial habitats: upper soil layer of a meadow in the surroundings of a lake (Neusiedlersee) in Burgenland, Austria (Foissner 1984, Foissner et al. 2002); with low abundance in leaf litter from the surroundings of the town of Stupava, Slovakia (unpubl. observations); in soil and litter (pH 6.0) of a leguminosae field in the Al-Hassa oasis, a few km east of the town of Al-Hofuf, Saudi Arabia (Foissner et al. 2008b); soil from the surroundings of the town of Qingdao, China (Song 1994a); wet, reddish and very sandy soil covered with a moist algal mat (pH 7.2) from a highland savannah at the

west margin of the town of Windhoek, Namibia, and in highly saline (15‰) soil and litter from decaying grass shrubbery in the Etosha National Park (Foissner et al. 2002); in floodplaid soil from Boise, Idaho, USA (Vďačný et al. 2011b); in a variety of soil samples from Benin, Kenya, Zanzibar, the Caribbean, and Venezuela (Foissner et al. 2002); upper soil layer with some sand and much litter (pH 4.2) from bush in the Brisbane Water National Park about 50 km north of Sydney, and in the upper mouldy needle and soil layer (pH 5.1) of a pine forest in a suburb of Adelaide, Australia (Blatterer & Foissner 1988).

Records from limnetic habitats: drain in the surroundings (Pinchat) of the town of Geneva, Switzerland (Penard 1922); in fine sand of the Excenevex beach, Lake Léman, France (Dragesco 1960, 1963); Priest Pot in England (Finlay & Maberly 2000); Manzanares River near Madrid, Spain (Fernández-Leborans & Antonia-García 1988); in two beta- to alpha-mesosaprobic Upper Austrian rivers (Blatterer 1994); possibly in organic mud from a tributary of the Gidra River near the village of Voderady, Slovakia (Tirjaková 2003); surroundings of the town of Sofia, Bulgaria (Detcheva 1992); Turkish inland waters (Çapar 2007); coast of Lake Okoboji, Iowa, USA (Shawhan et al. 1947); 43 ind./l in a fishless, intermittent pond in Vandorf, Ontario, Canada (Andrushchyshyn et al. 2006).

Rimaleptus tirjakovae (Vďačný & Foissner, 2008) nov. comb. (Figs 73a–o, 74a–l; Table 37)

2008 *Dileptus tirjakovae* nov. sp. Vďačný & Foissner, J. Eukaryot. Microbiol. **55**: 437

Generic affiliation and taxonomy: We combine *Dileptus tirjakovae* with *Rimaleptus* because of the two macronuclear nodules and the ordinary oral basket. *Rimaleptus tirjakovae* is almost unique in having two abutting, globular macronuclear nodules with a micronucleus in the vertex of the nodules, a highly constant pattern found in over 800 specimens. A similar pattern is found in *R. lacazei*, *R. robustus* and *R. ovalis*. The former lives in saline environments like *R. tirjakovae*, but differs by the distinct tail and the highly contractile proboscis. *Rimaleptus robustus* and *R. ovalis* are distinguished from *R. tirjakovae* by the presence (vs. absence) of endosymbiotic green algae and the habitat (freshwater vs. saline coastal soil).

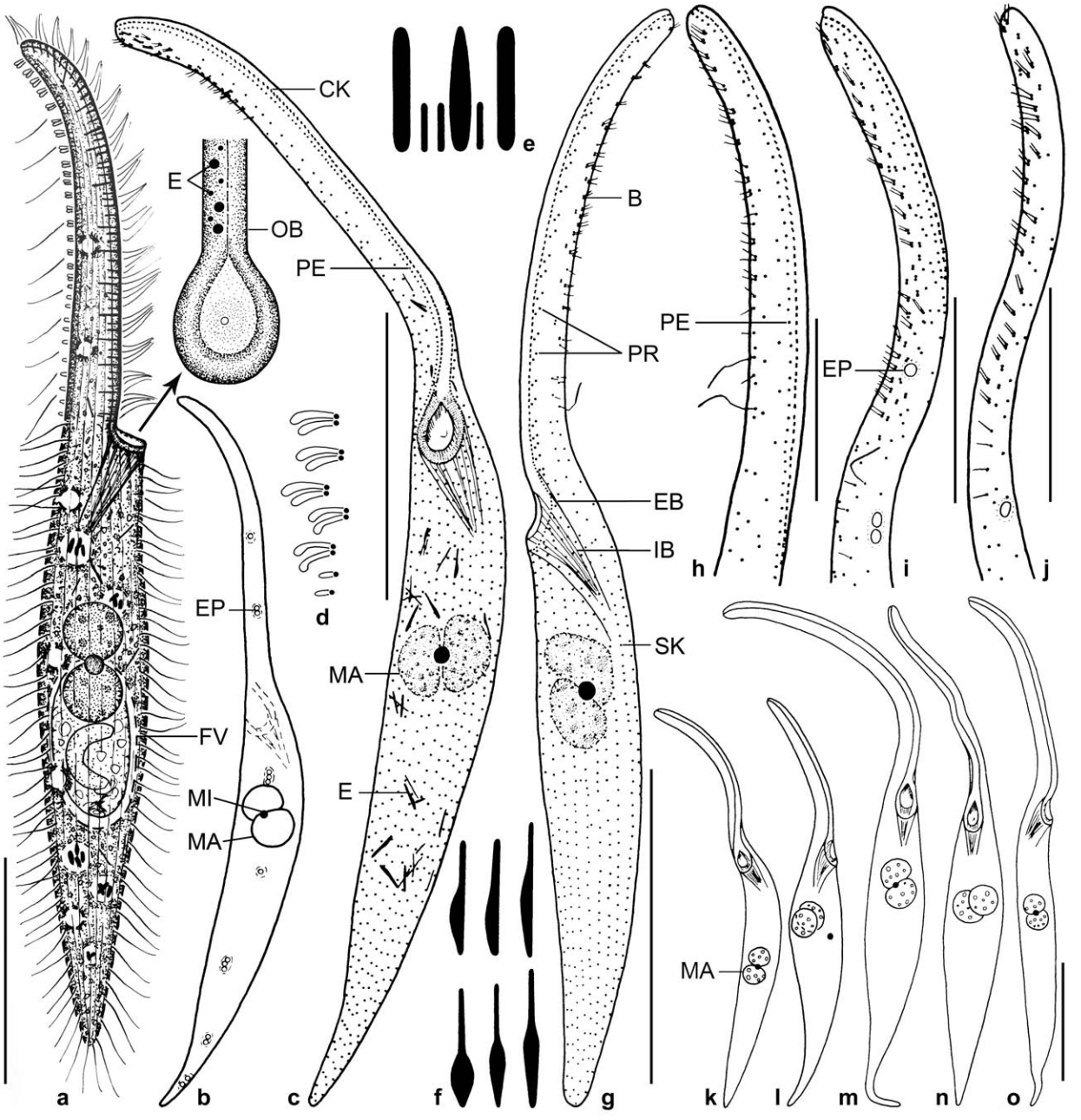
Diagnosis: Size about 230 × 25 µm in vivo. Shape very narrowly dileptid to rod-like with posterior region acute or, rarely, tail-like, proboscis about 40% of body length. Two globular, abutting macronuclear nodules with a micronucleus in nodule vertex. A dorsal row of contractile vacuoles with 1–3 pores each. Two size-types (6 µm and 2.5–3 µm) of basically rod-shaped extrusomes attached to right branch of oral bulge. On average 21 ciliary rows; dorsal brush diffuse with bristles up to 3 µm long. Oral bulge opening about 12 × 9 µm in size. Preoral kineties oblique, widely spaced, each usually composed of 2 ordinarily spaced cilia.

Type locality: Highly saline coastal soil from the bay of Nauplia, Greece, E22°43’ N37°33’.

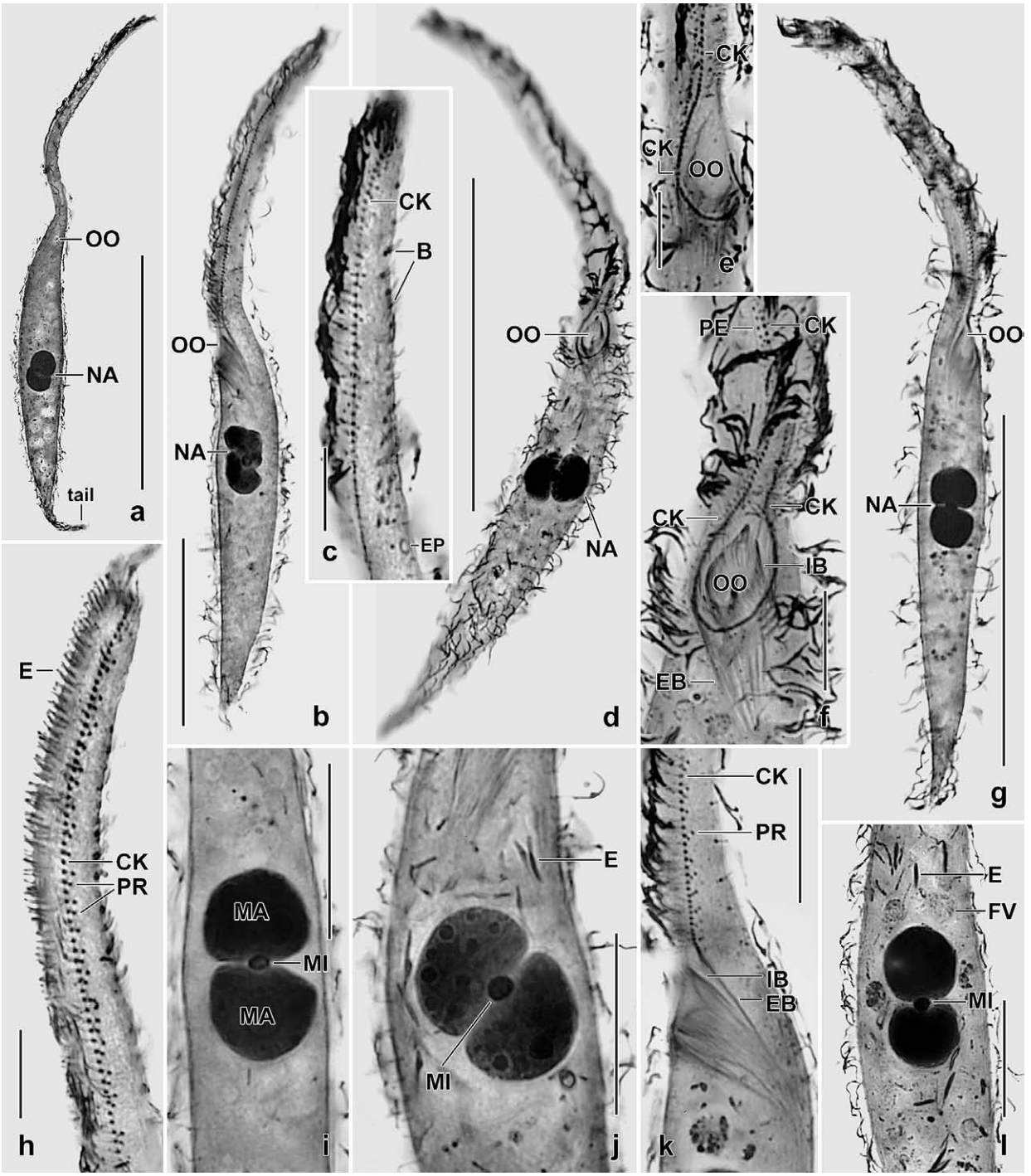
Type material: One holotype slide (inv. no. 2011/336) and seven paratype slides (inv. no. 2011/337–343) with protargol-impregnated specimens have been deposited in the Biology Centre of the Museum of Upper Austria, Linz (LI). Relevant vegetative and conjugating individuals as well as exconjugants are marked by black ink circles on the coverslip.

Dedication: Named in honour of Dr. Eva Tirjaková (Comenius University), as a small token of appreciation for guiding the junior author into ciliatology.

Description: Size 170–320 × 15–35 µm in vivo, usually about 230 × 25 µm, as calculated from some in vivo measurements and the morphometric data, assuming 15% preparation shrinkage; flexible but not contractile (Table 37). Shape very narrowly dileptid to rod-like, length:width ratio highly variable (7.5–15:1), on average near 10:1 in prepared cells. Proboscis occupies about 40% of body length, slightly to distinctly curved; trunk cylindroidal to bluntly fusiform, widest in mid-portion; posterior end elongate



Figs 73a–o: *Rimaleptus tirjakovae* from life (a, d–f) and after protargol impregnation (b, c, g–o). From Vďačný & Foissner (2008a). **a** – right side view of a representative specimen with oral area in frontal view. There are two types of extrusomes attached only to the broader right branch of proboscis' oral bulge; **b** – excretory pore and nuclear pattern; **c, g** – ciliary pattern of ventral and left side and nuclear apparatus of holotype and paratype specimen, length 215 µm and 175 µm; **d** – part of dorsal brush; **e** – two types of oral bulge extrusomes: type I is rod-shaped to very narrowly ovate and about 6 µm long, while type II is oblong and 2.5–3 µm long; **f** – when disturbed by coverslip pressure, the type I extrusomes may only partially explode, showing a variety of shapes; **h–j** – dorsal and dorsolateral ciliary pattern of proboscis. Figure (h) shows the right side of (g). Brush dikinetids are scattered on dorsal surface, forming a diffuse pattern. Brush bristles lacking or not impregnated in some dikinetids; **k–o** – variability of body shape and size as well as of nuclear apparatus. Drawn to scale. B – dorsal brush, CK – circumoral kinety, E – extrusomes, EB – external basket, EP – excretory pore(s) of a contractile vacuole, FV – food vacuole, IB – internal basket, MA – macronuclear nodules, MI – micronucleus, OB – oral bulge, PE – perioral kinety, PR – preoral kineties, SK – somatic kinety. Scale bars: 20 µm (h–j) and 50 µm (a, c, g, k–o).



Figs 74a–l: *Rimaleptus tirjakovae* after protargol impregnation (originals). **a, b, d, g –** shape and size variability. Very rarely, *R. tirjakovae* has a tail (a); **c, h, k –** left side views of proboscis and oral basket, showing an excretory pore (c) and the widely spaced preoral kineties (h); **e, f –** ventral views, showing the oral opening and the circumoral kinety which is deeply impregnated around the oral opening, where it consists of narrowly spaced monokinetids; **i, j, l –** the nuclear apparatus consists of two globular macronuclear nodules and a micronucleus in the nodule vertex. B – dorsal brush, CK – circumoral kinety, E – extrusomes, EB – external basket, IB – internal basket, MA – macronuclear nodules, MI – micronucleus, NA – nuclear apparatus, OO – oral bulge opening, PE – perioral kinety, PR –preoral kineties. Scale bars: 10µm (c, e, f, h), 20 µm (i–l), 50 µm (b), and 100 µm (a, d, g).

Table 37: Morphometric data on *Rimaleptus tirjakovae* (from Vďačný & Foissner 2008a). Data based on mounted, protargol-impregnated (Foissner's method), and randomly selected specimens from a non-flooded Petri dish culture. Measurements in µm. CV – coefficient of variation in %; M – median; Max – maximum; Mean – arithmetic mean; Min – minimum; n – number of specimens investigated; SD – standard deviation; SE – standard error of mean.

Characteristics	Mean	M	SD	SE	CV	Min	Max	n
Body, length	212.3	218.0	40.8	8.9	19.2	148.0	281.0	21
Body, width	20.4	20.0	4.2	0.9	20.8	15.0	31.0	21
Body length:width, ratio	10.6	9.9	2.2	0.5	20.7	7.5	15.0	21
Anterior body end to oral bulge opening, distance	86.4	86.0	17.3	3.8	20.0	51.0	115.0	21
Proboscis, % of body length	40.8	41.1	4.6	1.0	11.2	34.5	56.1	21
Oral bulge opening, length	12.3	12.0	1.8	0.4	14.6	10.0	16.0	21
Oral bulge opening, width	9.7	9.0	2.4	0.8	25.2	7.0	14.0	10
Oral basket, maximum length	23.4	23.0	3.8	0.8	16.3	18.0	32.0	21
Anterior body end to macronucleus, distance	119.8	116.0	25.2	5.5	21.0	70.0	159.0	21
Nuclear figure, length	19.2	20.0	3.6	0.8	18.8	14.0	31.0	21
Anterior macronuclear nodule, length	11.9	12.0	2.3	0.5	19.7	9.0	16.0	21
Anterior macronuclear nodule, width	11.9	12.0	1.9	0.4	15.9	8.0	15.0	21
Posterior macronuclear nodule, length	11.5	10.0	2.1	0.5	18.5	9.0	16.0	21
Posterior macronuclear nodule, width	11.5	12.0	1.7	0.4	15.2	8.0	15.0	21
Macronuclear nodules, number	2.0	2.0	0.0	0.0	0.0	2.0	2.0	21
Micronucleus, largest diameter	2.7	2.5	–	–	–	2.5	3.0	16
Micronucleus, number	1.0	1.0	0.0	0.0	0.0	1.0	1.0	16
Ciliary rows, number	21.3	21.0	2.5	0.5	11.8	19.0	29.0	21
Cilia in mid-body in 10 µm, number	4.7	5.0	0.6	0.1	12.4	4.0	6.0	21
Anterior body end to last dorsal brush dikinetid, distance	49.3	50.0	10.5	2.3	21.3	35.0	72.0	21
Dorsal brush dikinetids, total number	39.5	40.0	8.6	1.9	21.8	22.0	59.0	21
Dikinetidal portion of dorsal brush, % of body length	23.4	23.9	3.2	0.7	13.5	18.1	27.8	21

acute, sometimes tail-like (Figs 73a–c, g, k–o, 74a, b, d, g). Nuclear apparatus slightly above mid of trunk. Macronucleus pattern highly constant, that is, two globular nodules in over 800 specimens analyzed; very rarely cells with either a single globular or ellipsoidal nodule. Individual nodules usually close together, about 13 µm across in vivo; nucleoli globular, small to medium-sized. Micronucleus usually in vertex formed by the abutting macronuclear nodules, i.e., not in between nodules; globular, blister-like and about 3 µm across in vivo, deeply impregnated with protargol (Figs 73a–c, g, k–o, 74a, b, d, g, i–l). A row with an average of six contractile vacuoles in dorsal side of trunk and proximal half of proboscis, no ventral vacuoles; up to three excretory pores per vacuole (Figs 73a, b, i, j, 74c; Table 37). Two types of extrusomes, impregnating with protargol, attached to broader right branch of oral bulge (Figs 73a, e, 74h, j, l): type I rod-shaped to very narrowly ovate with rounded ends, about 6 × 1 µm in size, very sensitive, i.e., explode partially and become more or less distinctly clavate under even slight coverslip pressure (Fig. 73f), frequent also in cytoplasm, where certain developmental stages sometimes impregnate with

protargol; type II finely rod-shaped, about 2.5–3 µm long, more numerous than type I. Cortex very flexible, contains about ten oblique granule rows between adjacent kineties; granules inconspicuous because pale and only ~ 0.7 × 0.3 µm in size. Cytoplasm colourless, hyaline in proboscis and rear body end, opaque in trunk due to numerous granules ~ 0.4 µm across and 3–10 µm-sized vacuoles with sparse contents or some spores of bacteria, likely remnants from prey; feeds on medium-sized ciliates, such as *Metopus hasei* and *Vorticellides astyliformis* digested in large vacuoles often deforming cells. Movement without peculiarities.

Cilia about 8 µm long in vivo, ordinarily to densely spaced; in protargol preparations as typical for dileptids, i.e., with thick, strongly impregnated distal half, except for dorsal bristles; arranged in an average of 21 narrowly spaced, longitudinal rows leaving a narrow, barren area left and right of circumoral kinety (Figs 73c, g; Table 37). First row right of oral bulge extends as perioral kinety with ordinarily spaced cilia along circumoral kinety to tip of proboscis. Dorsal brush remarkable because not composed of staggered rows, as usual in dileptids, but of about 40 scattered dikinetids with 3 µm long type I bristles; followed by scattered monokinetids with 1 µm long type VI bristles (Figs 73c, d, g, h–j, 74c; Table 37).

Oral apparatus as in other dileptids, oral bulge opening slightly above mid-body; base of proboscis hardly widened and only half as wide as trunk, pharyngeal opening thus distinctly projecting. Pharyngeal basket distinct both in vivo and in protargol preparations (Figs 73a, c, g, 74d–f, k). Circumoral kinety dikinetidal, except for monokinetidal portion around oral bulge opening (Figs 74e, f, h). Preoral kineties oblique, widely spaced, each composed of two, rarely three ordinarily spaced basal bodies (Figs 73g, 74h, k).

Conjugation: See "General Part".

Occurrence and ecology: As yet found only at type locality, that is, the west coast of the Golf of Nauplia, exactly opposite to the town of Nauplia, Peloponnese, Greece. Here, the newly formed land is covered by a halophytic vegetation, especially, hemispherical, spiny colonies of rush. The soil is strongly saline, very hard when dry, and has pH 6.9 in water. The sample consisted of vegetation residues and the upper 0–2 cm soil layer which contained many fine grass roots.

Rimaleptus longitrichus (Vďačný & Foissner, 2008) nov. comb. (Figs 75a–t; Table 38)

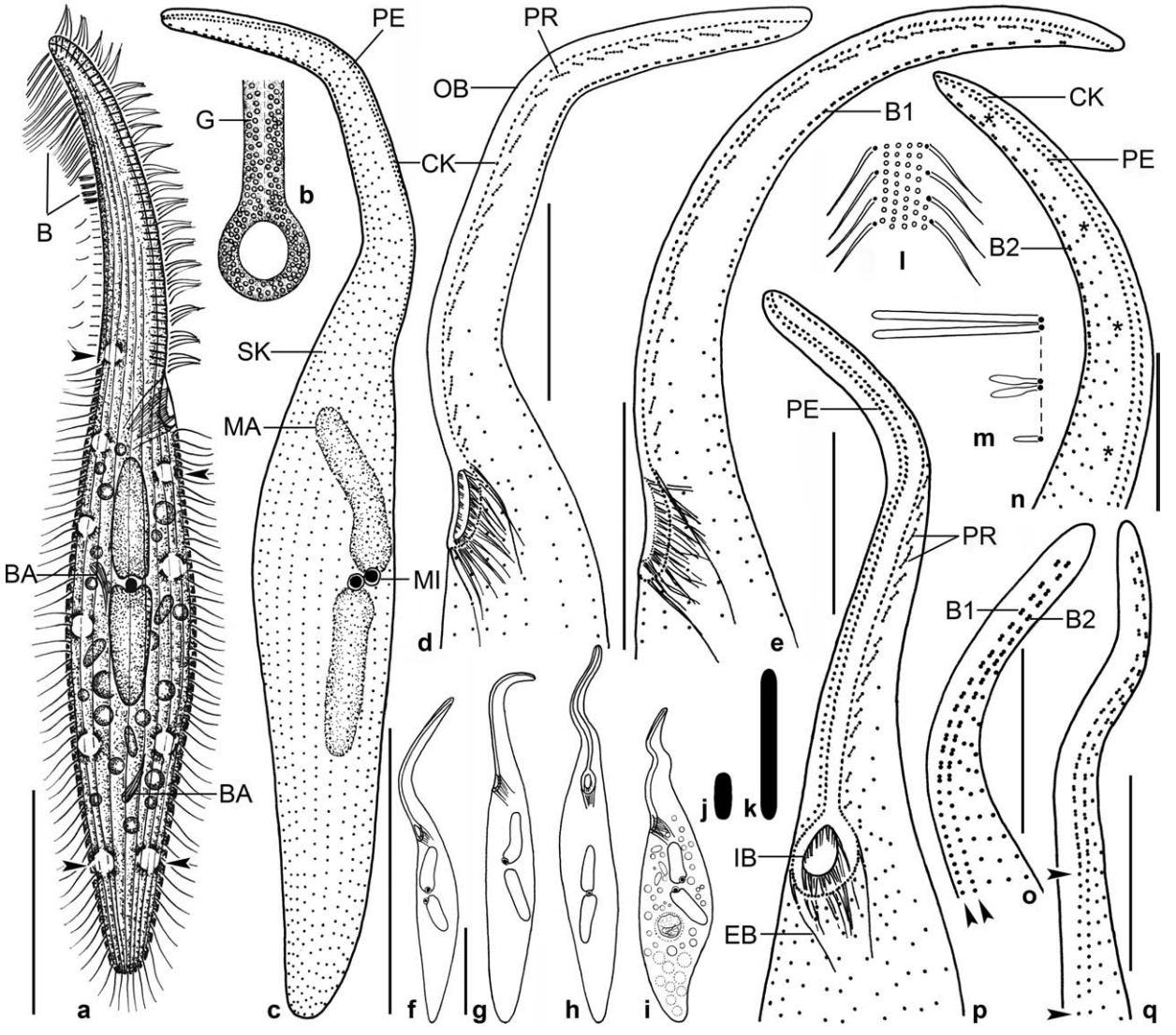
2008 *Dileptus longitrichus* nov. sp. Vďačný & Foissner, Acta Protozool. **47**: 219

Generic affiliation and taxonomy: We combine *Dileptus longitrichus* with *Rimaleptus* because of the two macronuclear nodules and the ordinary oral basket. Among the congeners, *R. longitrichus* is unique in having very long dorsal brush bristles (up to 15 µm vs. 3–4 µm) and a row of contractile vacuoles each in ventral and dorsal side of body (vs. only dorsal vacuoles).

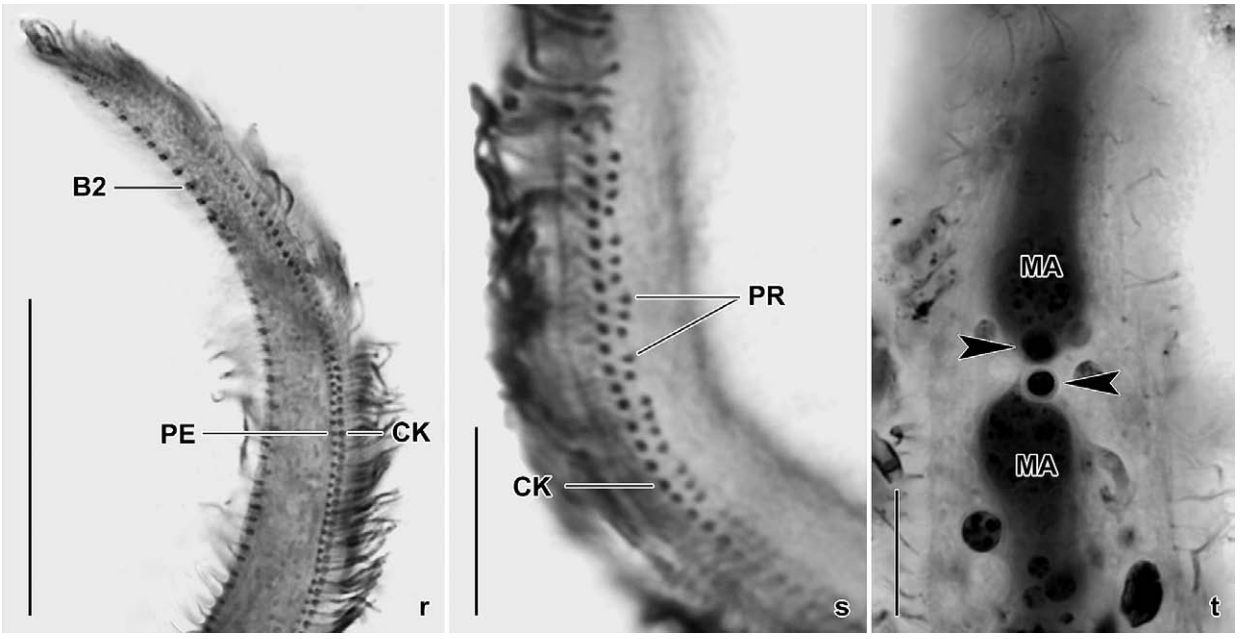
Diagnosis: Size about 210 × 30 µm in vivo. Shape narrowly to cylindroidally dileptid with narrowly rounded posterior end, proboscis about 37% of body length. Two oblong macronuclear nodules with 1–2 micronuclei in between. A row of contractile vacuoles each in ventral and dorsal side of body. Extrusomes rod-shaped, 2.5–3 µm long. On average 20 ciliary rows, 2 anteriorly differentiated into a conspicuous, isostichad dorsal brush with bristles up to 15 µm long: brush rows not staggered, composed of an average of 27 and 24 dikinetids, respectively; both rows with a monokinetidal bristle tail extending to base of proboscis. Oral bulge opening roundish, about 10 µm across. On average 25 ordinarily to widely spaced preoral kineties, each composed of 2–5 narrowly to ordinarily spaced kinetids, forming strongly oblique rows sometimes almost parallel to circumoral kinety.

Type locality: Soil from a mixed forest in the surroundings of the town of Tsukuba, Japan, E140°04' N36°02'.

Type material: One holotype slide (inv. no. 2011/272) and twelve paratype slides (inv. nos 2011/273–



Figs 75a–q: *Rimaleptus longitrichus* from life (a, b, j–m) and after protargol impregnation (c–i, n–q). From VĎAČNÝ & FOISSNER (2008b). **a** – right side view of a representative specimen, length 210 µm. Note the very long dorsal brush bristles, i.e., the main feature of this species. Arrowheads denote the two rows of contractile vacuoles, another important trait because all congeners have only dorsal vacuoles; **b** – frontal view showing the roundish oral bulge opening and the narrowly spaced cortical granules; **c, d** – ciliary pattern of right and left side and nuclear apparatus of holotype specimen, length 206 µm. Basal bodies of preoral kineties connected by lines; **e, n** – left and right side view of proboscis ciliary pattern. The right branch of the circumoral kinety is accompanied by a perioral kinety, while the left branch is associated with many strongly oblique preoral kineties. Asterisks mark gradually shortened right side somatic kineties, forming a suture on the right side of the proboscis; **f–i** – variability of body shape and size as well as of nuclear apparatus. Drawn to scale; **j** – cortical granules are about 1 × 0.5 µm in size; **k** – extrusomes are rod-shaped with both ends rounded and 2.5–3 µm long; **l** – surface view showing four oblique granule rows between adjacent kineties; **m** – fine structure of dorsal brush. The bristles in the anterior region of the brush are up to 15 µm long and are followed by about 4 µm long, clavate bristles; the tail bristles are monokinetidal, only 2 µm long, and extend to the base of the proboscis; **o, q** – dorsal views of proboscis ciliary pattern. The dorsal brush consists of two isostichad rows both associated with a monokinetidal bristle tail reaching the base of the proboscis (arrowheads); **p** – ventrolateral ciliary pattern in anterior body third. Basal bodies of preoral kineties connected by lines. BA – oral baskets of (microthoracid?) prey, B(1, 2) – dorsal brush (rows), CK – circumoral kinety, EB – external basket, G – cortical granules, IB – internal basket, MA – macronuclear nodules, MI – micronuclei, OB – oral bulge, PE – perioral kinety, PR – preoral kineties, SK – somatic kinety. Scale bars: 50 µm (a, c, f–i) and 20 µm (d, e, n–q).



Figs 75r–t: *Rimaleptus longitrichus* after protargol impregnation (from Vďačný & Foissner 2008b). **r** – right side view of proboscis; **s** – left side view of proboscis ciliary pattern, showing the preoral kineties, each composed of two to four narrowly spaced spaced monokinetids, forming strongly oblique rows almost in parallel with left branch of the circumoral kinety; **t** – the nuclear apparatus consists of two clavate to oblong macronuclear nodules and one or two micronuclei in between (arrowheads). B2 – dorsal brush row 2, CK – circumoral kinety, MA – macronuclear nodules, PE – perioral kinety, PR – preoral kineties. Scale bars: 10 µm (s, t) and 30 µm (r).

284) with protargol-impregnated specimens have been deposited in the Biology Centre of the Museum of Upper Austria, Linz (LI). Relevant specimens are marked by black ink circles on the coverslip.

Etymology: Composite of the Latin adjective *longus* (long) and the Greek noun *thrix* (hair ~ cilia), referring to the very long dorsal bristles.

Description: Size 160–260 × 20–45 µm in vivo, usually about 210 × 30 µm, as calculated from some in vivo measurements and the morphometric data, assuming 15% preparation shrinkage; length:width ratio rather variable, depending on nutrition state, on average 7:1 both in vivo and in protargol preparations (Table 38). Shape narrowly to cylindroidally dileptid with flattened proboscis occupying about one third of body length; both body ends narrowly rounded, posterior end never tail-like; dorsal outline straight to sigmoidal (Figs 75a, c, f–i). Nuclear apparatus slightly above mid of trunk. Two macronuclear nodules with concave proximal end surrounding micronucleus; individual nodules ellipsoidal to very narrowly ellipsoidal or very narrowly ovoidal, on average 25 × 8 µm in size (Table 38). One to two micronuclei (of 22 specimens investigated, 12 had one and 10 had two micronuclei) in between macronuclear nodules, about 3 µm across, in protargol preparations surrounded by a distinct membrane (Figs 75a, c, f–i, t; Table 38). A row of contractile vacuoles each in ventral and dorsal side of cell, first dorsal vacuole near base of proboscis (Fig. 75a). Extrusomes inconspicuous, i.e., rod-shaped with both ends rounded and only 2.5–3 µm long, do not impregnate with the protargol method used (Fig. 75k). Cortex very flexible, contains about four oblique granule rows between adjacent kineties; granules narrowly spaced in somatic and oral cortex, ellipsoidal, ~ 1 × 0.5 µm in size (Figs 75b, j, l). Cytoplasm colourless, hyaline in proboscis and rear body end, opaque in trunk due to numerous globular and irregular lipid droplets 2–7 µm across and food vacuoles with small ciliates, e.g., *Vorticellides astyliformis* and microthoracid (?) oral baskets (Figs 75a, i). Movement without peculiarities.

Table 38: Morphometric data on *Rimaleptus longitrichus* (from Vďačný & Foissner 2008b). Data based on mounted, protargol-impregnated (Foissner's method), and randomly selected specimens from a non-flooded Petri dish culture. Measurements in µm. CV – coefficient of variation in %; M – median; Max – maximum; Mean – arithmetic mean; Min – minimum; n – number of specimens investigated; SD – standard deviation; SE – standard error of mean.

Characteristics	Mean	M	SD	SE	CV	Min	Max	n
Body, length	187.8	188.0	24.0	5.2	12.8	145.0	223.0	21
Body, width	27.7	27.0	5.4	1.2	19.6	20.0	44.0	21
Body length:width, ratio	7.0	7.0	1.3	0.3	18.3	4.3	9.6	21
Anterior body end to oral bulge opening, distance	69.4	67.0	11.5	2.5	16.5	49.0	101.0	21
Proboscis, % of body length	36.9	36.8	3.6	0.8	9.7	30.9	46.1	21
Oral bulge opening, length	9.3	9.5	1.0	0.5	10.4	8.0	10.0	4
Oral bulge opening, width	8.0	8.0	0.8	0.4	10.2	7.0	9.0	4
Internal oral basket, length (proximal end of fibers possibly not impregnated)	5.6	6.0	1.2	0.3	21.8	4.0	8.0	19
External oral basket, length (proximal end of fibers possibly not impregnated)	9.8	10.0	2.0	0.5	20.1	8.0	14.0	17
Anterior body end to macronucleus, distance	87.0	87.0	14.1	3.1	16.2	67.0	122.0	21
Nuclear figure, length	53.4	52.0	6.7	1.5	12.5	43.0	65.0	21
Anterior macronuclear nodule, length[a]	26.0	25.0	3.4	0.7	13.0	20.0	32.0	21
Anterior macronuclear nodule, width[b]	8.4	8.0	0.9	0.2	11.0	7.0	10.0	21
Posterior macronuclear nodule, length[a]	27.6	28.0	2.9	0.6	10.6	23.0	33.0	21
Posterior macronuclear nodule, width[b]	8.2	8.0	0.9	0.2	11.3	7.0	10.0	21
Macronuclear nodules, number	2.0	2.0	0.0	0.0	0.0	2.0	2.0	21
Micronuclei, largest diameter	2.8	2.5	–	–	–	2.5	4.0	21
Micronuclei, number	1.5	1.0	0.5	0.1	35.0	1.0	2.0	22
Ciliary rows, number	19.5	20.0	1.5	0.3	7.9	18.0	22.0	21
Cilia in mid-body in 10 µm, number	5.3	5.0	0.6	0.1	10.8	4.0	6.0	21
Preoral kineties, number	26.2	25.0	3.1	1.3	11.9	23.0	30.0	6
Dorsal brush rows, number	2.0	2.0	0.0	0.0	0.0	2.0	2.0	21
Dikinetids in brush row 1, number	26.7	27.0	2.1	0.6	7.9	24.0	30.0	13
Dikinetids in brush row 2, number	24.0	24.0	1.7	0.5	7.2	21.0	26.0	13
Anterior body end to last dikinetid of brush row 1, distance	37.2	37.0	5.6	1.5	15.2	30.0	54.0	15
Anterior body end to last dikinetid of brush row 2, distance	32.9	32.0	4.7	1.2	14.3	25.0	43.0	15

[a] Spiralized and/or curved segments not straightened; actual length thus usually larger.

[b] Measured in the widest site, i.e., usually the inflated portion near to the micronucleus.

Cilia about 8 µm long in vivo, ordinarily spaced; in protargol preparations as typical for dileptids, i.e., with thick, deeply impregnated distal half, except for dorsal bristles; arranged in an average of 20 ordinarily spaced, longitudinal rows anteriorly gradually shortened along right side of oral bulge, except for perioral kinety which extends with ordinarily spaced basal bodies to tip of proboscis (Figs 75c, n, p, r; Table 38). Left side of proboscis with conspicuous blank stripe because left side ciliary rows shortened at level of oral bulge opening, except for one to two kineties extending into proximal quarter of proboscis (Figs 75d, e). Dorsal brush exactly on dorsal side of proboscis, composed of two isostichad rows with a similar number of loosely to ordinarily spaced dikinetids; both rows begin subapically and continue with a monokinetidal tail to base of proboscis (Figs 75a, d, e, o, q, r). Each brush row composed of three types of bristles (Fig. 75m): (i) anterior portion with type III bristles obliquely spread backwards in swimming specimens and highly conspicuous because of up to 15 µm long and slightly thicker than ordinary somatic cilia, decrease in length anteriorly and posteriorly or, sometimes, gradually from anterior to posterior; (ii) followed by some about 4 µm long type II bristles; (iii) posterior brush portion (tail) composed of 2 µm long type VI bristles.

Oral bulge opening at beginning of second body third, about 10 µm across, roundish both in vivo and in preparations (Figs 75b, p). Pharyngeal basket short, composed of many fine rods; internal basket about half as long as external one in protargol preparations (Table 38). Circumoral kinety composed of ordinarily spaced dikinetids, except for narrowly spaced monokinetids around oral bulge opening; right branch curves around anterior end of proboscis, while left branch ends subapically almost touching curved right end. On average 25 ordinarily to widely spaced preoral kineties, each composed of two to five narrowly to ordinarily spaced monokinetids forming strongly oblique rows sometimes almost in line with left branch of circumoral kinety (Figs 75d, e, p, s).

Occurrence and ecology: As yet found only at type locality, that is, in a slightly acidic (pH 4.9) mixture of litter, fine plant roots, and red-brown soil from a mixed forest (deciduous and cedar trees) in the surroundings of the town of Tsukuba, Japan.

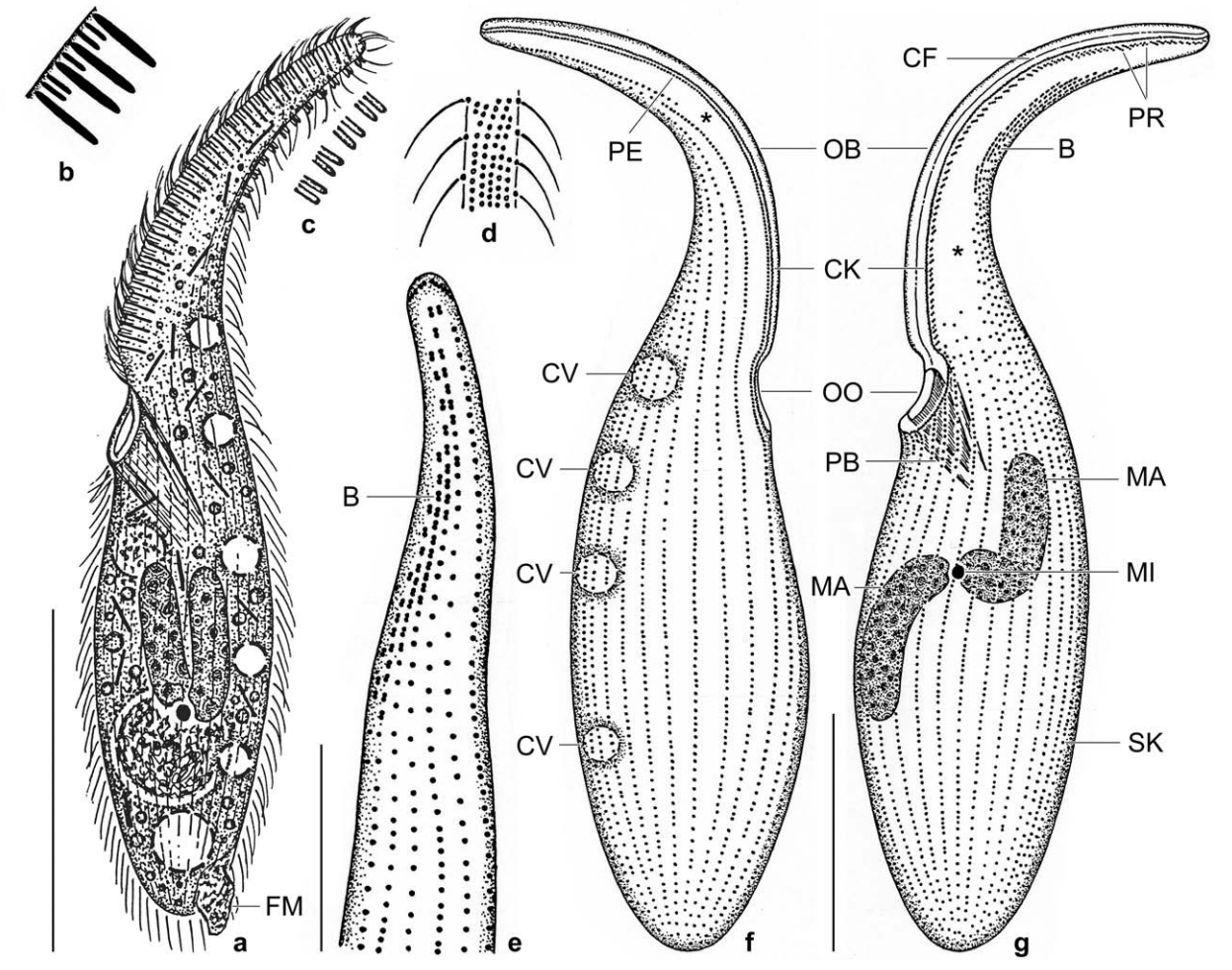
Rimaleptus similis (Foissner, 1995) nov. comb. (Figs 76a–o; Table 39)

1995 *Dileptus similis* nov. sp. Foissner, Arch. Protistenk. **145**: 43

1999 *Dileptus similis* Foissner, 1995 – Foissner, Biodivers. Conserv. **8**: 334 (description of a Kenyan population)

Generic affiliation and taxonomy: We combine *Dileptus similis* with *Rimaleptus* because of the two macronuclear nodules and the ordinary oral basket. *Rimaleptus similis* resembles *R. orientalis* and *R. conspicuus*. *Rimaleptus orientalis* differs by the proboscis (about 1/3 vs. 1/2 of body length), the number of the ciliary rows (17 vs. 30), and the shape of the extrusomes (massive and broadly fusiform to ellipsoidal vs. thin and almost rod-like). *Rimaleptus conspicuus* is considerably smaller than *R. similis* (141 µm vs. 219 µm in protargol preparations) and has only two (vs. at least four) contractile vacuoles and a strongly (vs. slightly) rostrate proboscis.

Improved diagnosis (includes all information known): Size about 250 × 50 µm in vivo. Shape narrowly to very narrowly dileptid with rounded posterior end, proboscis about 48% of body length. Two oblong macronuclear nodules with a micronucleus in between. A dorsal row of contractile vacuoles with several excretory pores each. Two types of extrusomes attached to proboscis oral bulge: type I rod-shaped, 6–10 × 1 µm in size; type II oblong, about 3 µm long. On average 30 ciliary rows, about 6 anteriorly differentiated into a staggered, distinctly heterostichad dorsal brush with bristles up to 2 µm long. Oral bulge opening about 25 µm across. Preoral kineties oblique, ordinarily to narrowly spaced, each usually composed of 3 narrowly spaced kinetids.

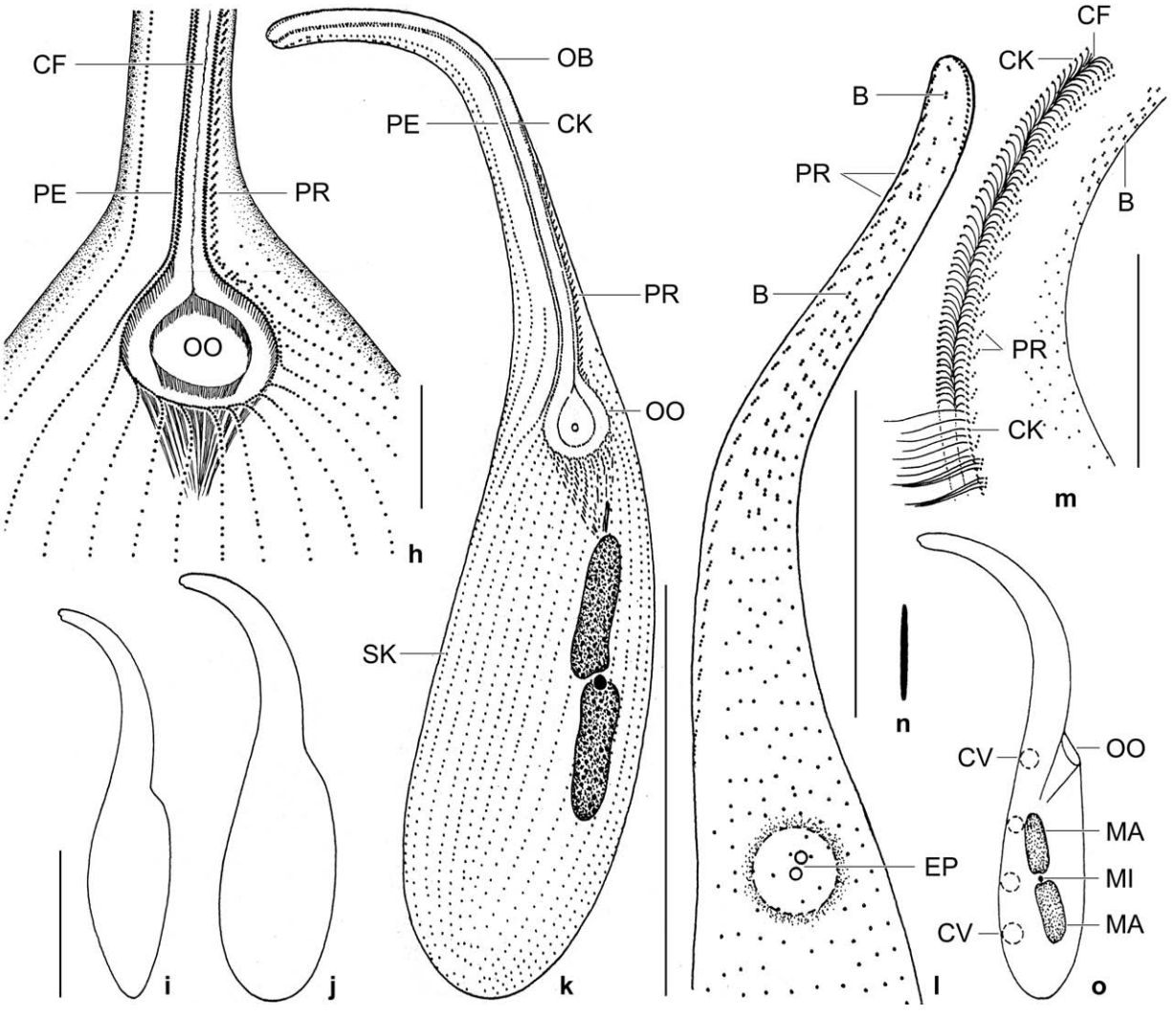


Figs 76a–g: *Rimaleptus similis*, Costa Rican specimens from life (a–d) and after protargol impregnation (e–g). From FOISSNER (1995a). **a –** left side view of a representative specimen, length 250 µm; **b** – there are two types of extrusomes attached to the proboscis oral bulge: type I is rod-shaped and 8–10 × 1 µm in size, while type II is oblong and about 3 µm long; **c** – brush bristles are up to 2 µm long; **d** – surface view showing cortical granulation; **e** – dorsal view of proboscis ciliary pattern; **f, g** – ciliary pattern of right and left side and nuclear apparatus of holotype specimen, length 225 µm. Asterisks mark broad blank stripe left and right of oral bulge. B – dorsal brush, CF – central fibre, CK – circumoral kinety, CV – contractile vacuoles, FM – fecal mass, MA – macronuclear nodules, MI – micronucleus, OB – oral bulge, OO – oral bulge opening, PB – pharyngeal basket, PE – perioral kinety, PR – preoral kineties, SK – somatic kineties. Scale bars: 20 µm (e), 50 µm (f, g), and 100 µm (a).

Type locality: Upper soil layer in the surroundings of the ranch house "La Casona", Santa Rosa National Park, Costa Rica, W85°38' N10°50'.

Type and voucher material: FOISSNER (1995a) deposited one holotype (inv. no. 1997/98) and one paratype (inv. no. 1997/99) slide with protargol-impregnated Costa Rican specimens in the Biology Centre of the Museum of Upper Austria, Linz (LI). FOISSNER (1999) deposited two voucher slides (inv. nos 1999/9 and 1999/10) with protargol-impregnated Kenyan specimens in the same repository. Relevant specimens are marked by black ink circles on the coverslip.

Etymology: The epithet refers to the supposed similarity with *R. mucronatus*. However, this has been disproved meanwhile by the detailed investigations of further populations.



Figs 76h–o: *Rimaleptus similis*, Costa Rican (h) and Kenyan (i–o) specimens from life (i, j, n, o) and after protargol impregnation (h, k–m). From Foissner 1995a (h) and Foissner 1999 (i–o). **h** – oral ciliary pattern; **i, j** – shape variants; **k** – ciliary pattern of ventral side and nuclear apparatus of main voucher specimen, length 288 µm; **l, m** – dorsolateral and ventrolateral ciliary pattern of proboscis; **n** – type I extrusomes are rod-shaped with slightly narrowed ends and 7–8 µm long; **o** – right side view showing general body organization. B – dorsal brush, CF – central fibre, CK – circumoral kinety, CV – contractile vacuoles, EP – excretory pores of contractile vacuole, MA – macronuclear nodules, MI – micronucleus, OB – oral bulge, OO – oral bulge opening, PE – perioral kinety, PR – preoral kineties, SK – somatic kineties. Scale bars: 20 µm (h, m), 30 µm (l), and 100 µm (i–k).

Description: This species has been studied in three populations from Costa Rica (type; Foissner 1995a), Kenya (voucher; Foissner 1995a), and Australia (unpubl.). They match very well, therefore the description summarizes all observations.

Size usually about 250 × 50 µm in vivo: type specimens 200–300 × 40–90 µm, Kenyan individuals 230–300 × 40–65 µm, and Australian cells 200–300 × 40–50 µm; very flexible but not contractile. Shape narrowly to very narrowly dileptid, i.e., length:width ratio 2.9–6.7:1, on average 4.8:1 (Table 39). Proboscis leaf-like flattened, slightly sickle-shaped, occupies almost half of body length on average, conspicuously widened near oral bulge opening and thus indistinctly set off from oblong to bluntly fusiform trunk; posterior end rounded, never acute or tail-like (Figs 76a, f, g, i–k, o). Nuclear apparatus in centre of trunk. Invariably

Table 39: Morphometric data on a Costa Rican (CR; from FOISSNER 1995a) and Kenyan (K; from FOISSNER 1999) population (Pop) of *Rimaleptus similis*. Data based on mounted, protargol-impregnated (Foissner's method) specimens from non-flooded Petri dish cultures. Measurements in µm. CV – coefficient of variation in %, M – median, Max – maximum, Mean – arithmetic mean, Min – minimum, n – number of specimens investigated, SD – standard deviation, SE – standard error of mean.

Characteristics	Pop	Mean	M	SD	SE	CV	Min	Max	n
Body, length	CR	218.7	210.0	27.4	7.9	12.5	170.0	280.0	12
	K	245.1	240.0	20.6	6.2	8.4	216.0	288.0	11
Body, width	CR	56.7	55.0	13.9	4.0	24.6	37.0	83.0	12
	K	43.0	44.0	4.8	1.4	11.2	36.0	50.0	11
Body length:width, ratio (calculated from original data)	CR	4.0	3.9	1.0	0.3	24.1	2.9	6.2	12
	K	5.7	5.8	0.5	0.1	8.0	5.1	6.7	11
Anterior body end to oral bulge opening, distance	CR	104.3	102.5	19.2	5.5	18.4	80.0	140.0	12
	K	121.5	120.0	11.5	3.5	9.4	112.0	152.0	11
Proboscis, % of body length (calculated from original data)	CR	47.5	47.7	5.1	1.5	10.7	39.0	58.5	12
	K	49.6	50.0	2.4	0.7	4.8	46.2	53.3	11
Nuclear figure, length (calculated from original data)	CR	69.4	70.0	13.4	4.2	19.3	44.0	90.0	10
Macronuclear nodules, length	CR	36.8	39.0	7.1	2.1	19.3	22.0	45.0	12
	K	32.1	32.0	3.9	1.2	12.0	26.0	38.0	11
Macronuclear nodules, width	CR	10.5	10.0	1.6	0.5	15.5	8.0	13.0	12
	K	9.4	10.0	0.8	0.2	8.6	8.0	10.0	11
Macronuclear nodules, number	CR	2.0	2.0	0.0	0.0	0.0	2.0	2.0	12
	K	2.0	2.0	0.0	0.0	0.0	2.0	2.0	11
Micronucleus, diameter	CR	2.8	3.0	0.6	0.2	22.6	1.5	3.5	12
	K	2.6	2.4	–	–	–	2.4	3.0	11
Micronucleus, number	CR	1.0	1.0	0.0	0.0	0.0	1.0	1.0	12
	K	1.0	1.0	0.0	0.0	0.0	1.0	1.0	12
Ciliary rows, number	CR	28.7	28.0	2.6	1.0	9.2	25.0	32.0	7
	K	31.5	31.0	2.2	0.7	7.0	28.0	35.0	11

two macronuclear nodules often side by side or one upon the other; individual nodules ellipsoidal to oblong, i.e., length:width ratio 2.2–5.2:1, on average 3.6:1 in protargol preparations; many globular nucleoli. Micronucleus between macronuclear nodules, 1.5–3 µm across after protargol impregnation (Figs 76a, g, k, o; Table 39). A dorsal row of four to eight contractile vacuoles with several excretory pores each; anteriormost vacuole near or above level of oral bulge opening, posteriormost vacuole enlarged

and slightly above cytopyge (Figs 76a, f, l, o). Two types of extrusomes attached to proboscis oral bulge and scattered throughout cytoplasm: type I rod-like with slightly narrowed ends, 8–10 × 1 μm in type specimens, 7–8 μm and 6 μm long in Kenyan and Australian cells, respectively; type II oblong, fine, about 3 μm long (Figs 76b, n). Cortex very flexible, colourless, contains about six oblique rows of 0.8 μm-sized granules between adjacent somatic kineties (Fig. 76d). Cytoplasm colourless, packed with numerous granules 1–2 μm across, up to 10 μm-sized lipid droplets, and large globular to ellipsoidal food vacuoles containing whole ciliates, e.g., *Frontonia depressa*; loose materials; or long bacteria, possibly remnants from prey.

Cilia 8–10 μm long in vivo, narrowly spaced. Ciliary rows ordinarily spaced, extend meridionally, on average 28 rows in Costa Rican specimens and 31 in Kenyan cells (Table 39). Perioral kinety extends to tip of proboscis with narrowly spaced basal bodies (Figs 76f, h, k). Both sides of proboscis with a blank stripe, that on right side narrower than that on left where most left side rows end at base of proboscis (Figs 76f–h, k, m). Dorsal brush a long field on dorsal and dorsolateral region of proboscis; staggered; distinctly heterostichad; composed of about six rows of loosely to ordinarily spaced dikinetids associated with type III bristles both being only 1–2 μm long (Figs 76c, e, g, l, m).

Oral bulge opening about 25 μm across in vivo. Pharyngeal basket obconical, distinct both in vivo and after protargol impregnation, composed of many delicate rods (Figs 76a, g, h, k). Circumoral kinety composed of narrowly spaced dikinetids in proboscis and narrowly spaced monokinetids around oral bulge opening. About 70 oblique, narrowly spaced preoral kineties, as estimated from figures, each composed of two to four, usually three narrowly spaced cilia (Figs 76g, h, k–m).

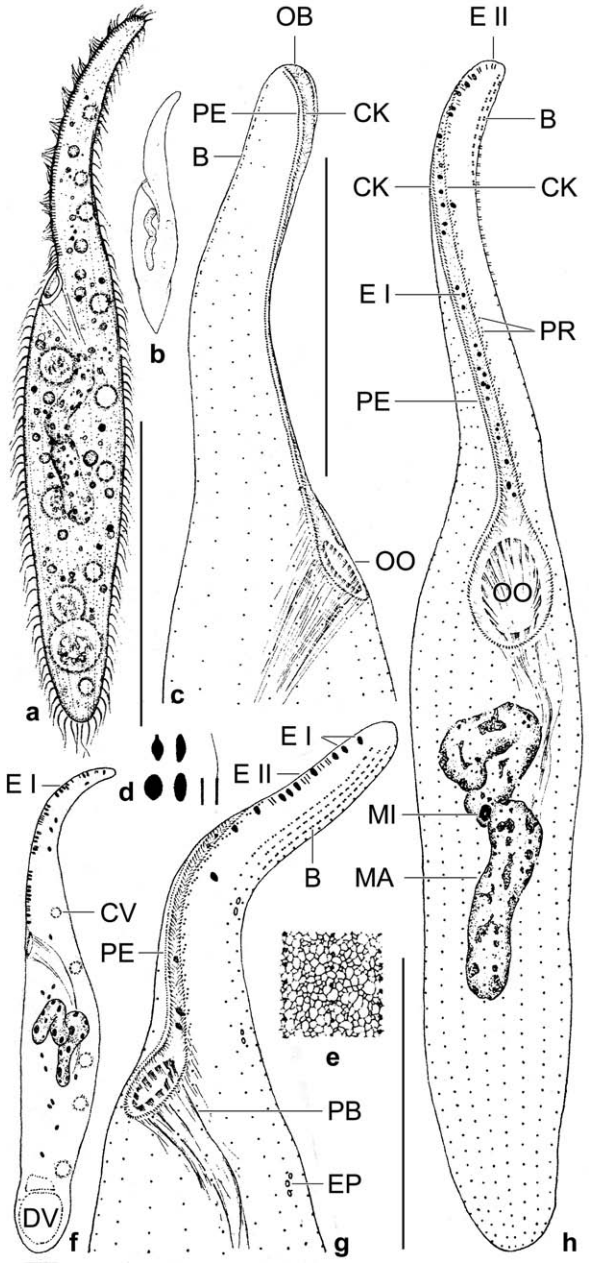
Occurrence and ecology: *Rimaleptus similis* was discovered in a tropical dry forest, viz., in the upper soil layer of the Santa Rosa National Park in Costa Rica, where it occurred together with *Dileptus costaricanus* (Foissner 1995a). In Kenya, *Rimaleptus similis* occurred in a coastal rain forest around a picnic site in the Shimba Hills Nature Reserve; the sample was a mixture of the upper 0–5 cm litter and soil layer; the brown, humic, slightly acidic (pH 6.1) soil contained a dense root carpet, as typical for rain forests (Foissner 1999). In Namibia, *R. similis* occurred in the southern escarpment of the Namib Desert, i.e., in the vicinity of the Büllsport Guest Farm; the 0–10 cm soil sample (pH 7.7) was taken from the margin of a small pond surrounded by sedges and *Ficus* trees (Foissner et al. 2002). In Australia, we found *Rimaleptus similis* in the very sandy soil under a Beef-wood (*Casuarina*) tree on Green Island near the town of Cairns, about 20 m distant from the coast. As yet, not found in Europe.

Rimaleptus orientalis (Song, Packroff & Wilbert, 1988) nov. comb. (Figs 77a–h; Table 40)

1988 *Dileptus orientalis* sp. n. Song, Packroff & Wilbert, Acta Protozool. **27**: 272

Generic affiliation and taxonomy: We combine *Dileptus orientalis* with *Rimaleptus* because of the two macronuclear nodules and the ordinary oral basket. Within the congeners, *R. orientalis* is outstanding in having minute but massive type I extrusomes. In this respect, it resembles *R. brasiliensis*, *Microdileptus microstoma* and *M. semiarmatus*. However, all differ from *Rimaleptus orientalis* by shape details of the extrusomes, the shorter proboscis (1/5–1/4 vs. 1/3 of body length), and the lower number of the ciliary rows (7–13 vs. 15–19).

Improved diagnosis: Size about 200 × 23 μm in vivo. Shape narrowly to very narrowly dileptid with rounded posterior end, proboscis about 1/3 of body length. Two oblong macronuclear nodules with a micronucleus in between. A dorsal row of contractile vacuoles with 2–3 excretory pores each. Two types of extrusomes attached to proboscis oral bulge: type I massive, broadly fusiform to ellipsoidal, 1–2 μm long; type II fine, oblong, 1–2 μm long. On average 17 ciliary rows, three (or more?) differentiated into an



Figs 77a–h: *Rimaleptus orientalis* from life (a, b, d) and after protargol (c, f–h) and silver nitrate (e) impregnation (from Song et al. 1988). **a** – left side view, length 230 µm; **b, f** – shape variants and general organization; **c, g** – ciliary pattern of proboscis; **d** – type I extrusomes only 1–2 µm long, type II is 1–2 µm long, and shows toxicyst structure; **e** – silverline pattern; **h** – ciliary pattern and nuclear apparatus of holotype specimen, length 205 µm. B – dorsal brush, CK – circumoral kinety, CV – contractile vacuoles, DV – defecation vacuole, EI, II – extrusome types, EP – excretory pores, MA – macronuclear nodule, MI – micronucleus, OB – oral bulge, OO – oral bulge opening, PB – pharyngeal basket, PE – perioral kinety, PR – preoral kineties. Scale bars: 50 µm (c, h) and 100 µm (a).

isostichad dorsal brush. Oral bulge opening about 15 µm across. Preoral kineties oblique to strongly oblique, ordinarily to widely spaced, usually composed of 3 narrowly spaced kinetids.

Type locality: Soil from the surroundings of the town of Qingdao, China, E120°43' N36°8'.

Type material: Deposition not mentioned in the original paper (Song et al. 1988) but Prof. W. Song deposits all type material in the College of Fisheries, Ocean University of Qingdao, China.

Etymology: Not given in original description. The Latin adjective *orientalis* obviously refers to the region in which the species was discovered.

Description: Length 150–250 µm in vivo; very flexible. Shape narrowly to very narrowly dileptid, i.e., length:width ratio 5–7:1, according to the figures provided, but 9.3:1 on average according to the morphometric data (Table 40). Proboscis occupies about one third of body length, slightly set off from cylindroidal to bluntly fusiform trunk; posterior end slightly to conspicuously flattened, usually rounded, rarely acute (Figs 77a, b, f, h; Table 40). Nuclear apparatus in centre of trunk. Invariably two macronuclear nodules with a globular micronucleus in between; individual nodules oblong and curved, about 25 × 7 µm in size after protargol impregnation; nucleoli ellipsoidal to lobate (Figs 77a, b, f, h; Table 40). A dorsal row of five to eight contractile vacuoles each with two to three excretory pores, posterior vacuoles sometimes larger than anterior ones (Figs 77a, f, g). Two types of extrusomes impregnate with the protargol method used, attached to proboscis oral bulge and scattered throughout cytoplasm: type I minute but massive, broadly fusiform to ellipsoidal, 1–2 µm long; type II fine, oblong, 1–2 µm long, when exploded of typical toxicyst structure, that is, with tube emerging from empty capsule (Figs 77d, f–h). Cytoplasm colourless to yellowish, often packed with food vacuoles; in rear end sometimes a defecation vacuole (Figs 77a, f). Swims slowly.

Cilia 8–10 µm long in vivo, ordinarily spaced, arranged in an average of 17 ordinarily spaced, meridional rows (Fig. 77h; Table 40). Right side ciliary rows gradually shortened along oral bulge;

Table 40. Morphometric data on *Rimaleptus orientalis* (from SONG et al. 1988). Data based on mounted, protargol-impregnated (Wilbert's method), and randomly selected specimens from a non-flooded Petri dish culture. Measurements in µm. CV – coefficient of variation in %, Max – maximum, Mean – arithmetic mean, Min – minimum, n – number of specimens investigated, SD – standard deviation, SE – standard error of mean.

Characteristics	Mean	M	SD	SE	CV	Min	Max	n
Body, length	191.6	189.0	22.3	4.9	11.6	153.0	225.0	20
Body, width	20.7	20.0	1.5	0.4	7.3	18.0	23.0	20
Anterior body end to oral bulge opening, distance	58.5	58.0	7.4	2.0	13.5	50.0	74.0	20
Macronuclear nodules, length	25.6	23.5	5.5	1.5	21.6	18.0	28.0	17
Macronuclear nodules, width	6.9	7.2	0.9	0.2	13.5	5.0	8.5	17
Macronuclear nodules, number	2.0	2.0	0.0	0.0	0.0	2.0	2.0	20
Micronucleus, number	1.0	1.0	0.0	0.0	0.0	1.0	1.0	20
Ciliary rows, number	16.7	17.0	1.1	0.2	6.5	15.0	19.0	20
Postoral ciliary rows, number	4.8	5.0	0.6	0.1	12.8	4.0	6.0	24
Cilia in mid-body in 10 µm, number	5.6	5.0	0.9	0.2	15.8	4.0	7.0	24
Dorsal brush rows, number	3.0	3.0	0.0	0.0	0.0	3.0	3.0	11
Anterior body end to last dorsal brush dikinetid, distance	24.5	24.0	2.7	0.7	11.4	20.0	28.0	15

perioral kinety extends to tip of proboscis with narrowly spaced basal bodies (Figs 77c, h). Blank stripe on left side of proboscis broad because most left side kineties end at level of oral bulge opening or slightly above (Figs 77g, h). Ventral rows slightly or indistinctly curved rightwards when abutting on circumoral kinety (Figs 77c, g, h). Dorsal brush on dorsal and dorsolateral side of proboscis, three-rowed and isostichad (Fig. 77g); observations possibly not correct (see *R. mucronatus*). Silverline pattern composed of very small, polygonal meshes; not studied in detail (Fig. 77e).

Oral bulge opening about 15 µm across in protargol preparations (Fig. 77h). Pharyngeal basket obconical, without specific features (Figs 77c, f, g, h). Oral ciliary pattern dileptid, i.e., left branch of circumoral kinety associated with many oblique to strongly oblique, ordinarily to widely spaced preoral kineties, each composed of two to three narrowly spaced cilia (Figs 77g, h).

Occurrence and ecology: SONG et al. (1988) discovered *R. orientalis* in soil from the surroundings of the town of Qingdao, China. FOISSNER (2000) recorded this species from two localities in Germany, viz., from terra fusca-rendzina soil (pH 4.3–6.8) of a beech forest about 7 km east of the town of Göttingen, and from a mixture of litter and soil of a beech forest about 30 km NW the town of Kassel.

Microdileptus nov. gen.

Diagnosis: Small-sized Dimacrocaryonidae with very narrow to rod-shaped body. Two macronuclear nodules. Dorsal brush staggered and two-rowed. Right branch of circumoral kinety accompanied by a perioral kinety, left branch by a row of widely spaced, more or less grouped preoral kinetids. Oral bulge opening dileptid, i.e., roundish and located ventrally, but conspicuously small (diameter usually < 5 µm). Oral basket bulbous.

Type species: *Dileptus microstoma* Vďačný & Foissner, 2008.

Etymology: Composite of the Greek adjective *mikros* (small) and the generic name *Dileptus*, referring to the small oral opening. Masculine gender.

Species assignable: *Dileptus breviproboscis* Foissner, 1981; *D. microstoma* Vďačný & Foissner, 2008; and *D. semiarmatus* Vďačný & Foissner, 2008.

Remarks: The three species of this new genus have two conspicuous apomorphies in common: (i) the preoral kineties are small and so strongly oblique that a more or less "grouped row" is produced left of the circumoral kinety; and (ii) a very small oral bulge opening, which, however, can open widely during prey ingestion (Figs 79j, k, 80l). A distinct genus is indicated also by the molecular trees, where *Microdileptus microstoma* forms a separate and rather long branch (Figs 34, 35). The special kind of preoral kinety occurs also in *Monilicaryon monilatum*, a member of the family Dileptidae (Figs 14, 106b, h, q–s). However, this species is very large (~ 600 µm) and has a moniliform macronucleus and only one dorsal brush row. Thus, the special preoral pattern very likely evolved convergently in *Monilicaryon* and *Microdileptus*.

The three species agree also in having a small-sized (~ 180 µm) and very slender (8–11:1) body, a short proboscis (~ 1/5–1/3 of body length), 9–10 ciliary rows, and 8–12 µm long brush bristles. They differ distinctly in the shape of the extrusomes (ampulliform in *M. microstoma*, cuneate in *M. semiarmatus*, and oblong in *M. breviproboscis*) and some specialities (contractile vacuoles lacking in mid-body in *M. microstoma*; extrusomes lacking in distal half of proboscis in *M. semiarmatus*). These are subtle differences, needing careful live observations.

Key to Species

1 Extrusomes oblong and 3 µm long; body about 150 µm long ..... *M. breviproboscis* (p. 243)
– Extrusomes massive, i.e., cuneate, bluntly fusiform, ellipsoidal, or ampulliform 2
2 Extrusomes ampulliform, along whole length of proboscis bulge; body about 170 µm long ..... *M. microstoma* (p. 252)
– Extrusomes cuneate, only in proximal half of proboscis bulge; body about 180 µm long ..... *M. semiarmatus* (p. 257)

Microdileptus breviproboscis (Foissner, 1981) nov. comb. (Figs 78a–g, 79a–p, 80a–t; Tables 41, 42)

1981 *Dileptus breviproboscis* Foissner, Zool. Jb. Syst. **108**: 281

1984 *Dileptus breviproboscis* Foissner, 1981 – Foissner, Stapfia **12**: 94 (synonymization with *D. anguillula* based on incompletely studied nuclear characteristics)

non *Dileptus breviproboscis* Foissner, 1981 – Foissner, Agatha & Berger, 2002, Denisia **5**: 367 (par lapsus as *D. anguillula* in their table on page 38; resurrection of species, based on a misidentified population here considered as a new species, *Rimaleptus brasiliensis*)

Taxonomy: This species is a typical example of the confusion produced by poorly described species. The only excuse is the insufficient experience of the senior author in 1981 and the tiny body of this species, which makes it difficult to investigate.

Foissner (1984) synonymized *Dileptus breviproboscis* with *D. anguillula* because the nuclear apparatus appeared highly variable. However, a reinvestigation of the 1984 population showed that only two out of 100 specimens are binucleate, while 98 have a distinctly moniliform macronucleus. Thus, *D. breviproboscis* and *D. anguillula* are distinct species. Based on Foissner (1984) and new data on the extrusomes, Foissner et al. (2002) resurrected *D. breviproboscis*: "Unfortunately, the original descriptions of *D. anguillula* and *D. breviproboscis* lack detailed data about the extrusomes. Thus, they cannot be assigned to any of the two types

Table 41: Comparison of *Dileptus anguillula*-like and *D. breviproboscis*-like populations[a].

Characteristics	*D. anguillula* (Kahl 1931)	*D. anguillula* (Foissner 1984)	*D. breviproboscis* (Foissner 1981)	*D. breviproboscis* (Gastein population)	*D. breviproboscis*[b] (Brazil population)	*D. breviproboscis* (Foissner et al. 2002)
Body length (µm)	120–150[c]	60–160[d] (mean = 90)	85–167[d] (mean = 118.9)	108–160[d] (mean = 125.2)	83–176[d] (mean = 133)	105–200[d] (mean = 145)
Macronuclear pattern	± moniliform	± moniliform	binucleate	binucleate	binucleate	binucleate
Extrusomes	?	oblong, 3 µm	oblong, 3 µm	?	oblong, 3 µm	oblong, 3–4 µm plus thick and ovate to oblong, 2–3 × 1 µm
Number of dorsal brush rows	?	2–(3)	?	2	2	2
Length of brush bristles (µm)	?	~ 3	?	~ 7[d]	~ 10	4
Size of oral opening (µm)	?	~ 6 × 5[d]	2.5[c]	5 × 4.4[d]	4.4 × 4.1[d]	8.4 × 5.6[d]
Preoral kineties	?	2–4 kinetids almost in line	in line	2–3 kinetids in or almost in line	in line	2 oblique kinetids
Classification in this monograph	*Pseudomonilicaryon anguillula* (Kahl, 1931)		*Microdileptus breviproboscis* (Foissner, 1981)			*Rimaleptus brasiliensis* n. sp.

[a] All have a slender body with short proboscis (1/5 to 1/3 of body length), a dorsal row of contractile vacuoles, and about 10 ciliary rows.

[b] A new population from the surroundings of Rio de Janeiro, Brazil (see description).

[c] From life.

[d] After protargol impregnation.

described above, but must be redefined. We suggest endowing *D. anguillula* with fine, rod-shaped extrusomes, while *D. breviproboscis* additionally has thick, ellipsoidal extrusomes. A detailed redescription of *D. anguillula* is in Foissner (1984). Alternatively, the Brazilian population described here as *D. breviproboscis* might be considered as a new species and *D. breviproboscis* kept in synonymy with *D. anguillula*. This, however, would unnecessarily increase the number of insufficiently described species". In the meantime, we investigated and reinvestigated several *breviproboscis* / *anguillula*-like populations, which showed that the Brazilian *breviproboscis* is, indeed, a new species differing from the original description (Foissner 1981) by four distinct features (Table 41): it has two types of extrusomes (vs. one), of which one is conspicuously thick; the dorsal bristles are considerably shorter (4 µm vs. 7–12 µm); the oral opening is much larger (8.4 µm vs. 4.5 µm); and the preoral kinetics consist of two obliquely arranged kinetids (vs. forming an unstructured or slightly structured row).

Improved diagnosis (includes all data known): Size about 150 × 15 µm in vivo. Shape narrowly dileptid to rod-like with narrowly rounded posterior end, proboscis about 1/5 of body length. Two oblong macronuclear nodules with a micronucleus in between. A dorsal row of contractile vacuoles with 1–2 pores each. Extrusomes attached to right branch of proboscis oral bulge, oblong, about 3 × 0.4 µm in size. On average 9–10 ciliary rows, 2 staggered and differentiated into an isostichad dorsal brush with bristles up to 10 µm long: rows 1 and 2 composed of an average of 12 and 16 dikinetids, respectively; monokinetidal tail of row 1 extending to second third of body and thus longer than that of row 2. Oral bulge opening 2.5–5 × 4 µm in size. Preoral kinetics each usually composed of 2 ordinarily to widely spaced kinetids, forming a row almost parallel to circumoral kinety.

Type locality: Soil from the Hochmais-Alm, i.e., an alpine pasture along the Grossglockner-Hochalpenstrasse, Hohe Tauern, Salzburg, Austria, 1850 m above sea level, E12°48' N47°7'.

Type and voucher material: FOISSNER (1981) deposited one holotype slide (inv. no. 1981/7) with a protargol-impregnated Austrian (Schloss-Alm in Gastein area) specimen in the Biology Centre of the Museum of Upper Austria, Linz (LI). However, a reinvestigation of this slide showed that it contains a single, poorly impregnated specimen from the Schloss-Alm in the Gastein area, not from the Hochmais-Alm along the Grossglockner Hochalpenstrasse, as stated in the description of the type locality by FOISSNER (1981). Very likely, FOISSNER (1981) used both, specimens from the Schloss-Alm and from the Hochmais-Alm for the description. All good slides were used as types for other new species. Thus, we investigated another population from the Gastein area, viz., from an Alnetum viridis on the Stubnerkogel, which is only a few km away from the Schloss-Alm. In these slides, there are some well-impregnated specimens which were designated as "vouchers" and stored in the Museum of Upper Austria (inv. nos 2011/372–375). A specimen of this series can be used as a neotype when the matter has been settled, i.e., the identity of *Microdileptus breviproboscis*, *Pseudomonilicaryon anguillula*, and *Rimaleptus brasiliensis* has been clarified beyond reasonable doubts.

Further, we studied a new Brazilian population in great detail. Two voucher slides (inv. nos 2011/344 and 2011/345) have been deposited in the repository mentioned above.

Etymology: Not given in original description. Composite of the Latin adjective *brevis* (short) and the noun *proboscis*, referring to the short proboscis.

Description of Austrian populations: Size 130–200 × 10–20 µm in vivo and 85–167 µm (mean =118.9, n = 8) × 8–13 µm (mean = 10.2, n = 8) in protargol preparations (FOISSNER 1981), matching sizes obtained from impregnated Stubnerkogel specimens (Table 42): 108–160 µm (mean = 125.2) × 12–20 µm (mean = 16.6). Including 15% preparation shrinkage, an usual in vivo size of 145 × 18 µm (125–185 × 14–23 µm) can be assumed. Average length:width ratio about 13:1 in FOISSNER (1981), while 8:1 in Stubnerkogel specimens (Table 42). Shape thus very narrowly to rod-like dileptid, not or inconspicuously flattened laterally (Figs 78a, b); very fragile, frequently shedding proboscis when the coverslip is put on the drop containing the specimens. Nuclear apparatus slightly above mid-trunk (Figs 78a, b); nuclear figure on average about 30 µm long in both populations (FOISSNER 1981; Table 42). Macronuclear nodules oblong to strongly spiralized, on average 3.3 µm and 5.7 µm in width, respectively (FOISSNER 1981; Table 42). Micronucleus in between macronuclear nodules, about 1.5 µm across. About six contractile vacuoles in dorsal side, one to three pores per vacuole associated with kinety bearing brush row 2 (Figs 78a, d, g). Oral bulge extrusomes oblong and about 3 µm long. Cortex and cytoplasm colourless, usually hyaline, some specimens contain many inclusions about 2 µm across; subterminally, frequently a defecation vacuole with granular contents. Feeds on flagellates and fungal spores. Swims and glides slowly and serpentinously.

Cilia about 9 µm long in vivo, ordinarily spaced on average, more loosely arranged in posterior third of trunk, longest rows with about 30 cilia (the up to 80 cilia in FOISSNER 1981 are very likely a mistake); in protargol preparations as typical for dileptids; arranged in an average of 8.7 (n = 8) and 10 (n = 11) ordinarily spaced, longitudinal rows, respectively (FOISSNER 1981; Table 42); leave blank a rather broad stripe on right and left side of proboscis because about half of kineties commence near level of oral bulge opening. First ciliary row right of circumoral kinety extends as perioral kinety to tip of proboscis with ordinarily to widely spaced cilia (Figs 78c, f). Dorsal brush exactly on dorsal side of proboscis, composed of two staggered, isostichad rows with a median of 11 widely spaced and 15 widely to ordinarily spaced dikinetids in rows 1 and 2, respectively; bristles slightly thicker than ordinary cilia, up to 6 µm long in protargol-impregnated specimens from the Stubnerkogel, possibly misinterpreted as ordinary somatic cilia by FOISSNER (1981).

Table 42. Morphometric data on *Microdileptus breviproboscis* from the Stubnerkogel, Gastein region, Austria (upper line) and Brazil (lower line). Data based on mounted and protargol-impregnated (Foissner's method) specimens, selected for "ordinary" cells in the Brazilian population. Measurements in µm. CV – coefficient of variation in %, M – median, Max – maximum, Mean – arithmetic mean, Min – minimum, n – number of specimens investigated, SD – standard deviation, SE – standard error of mean.

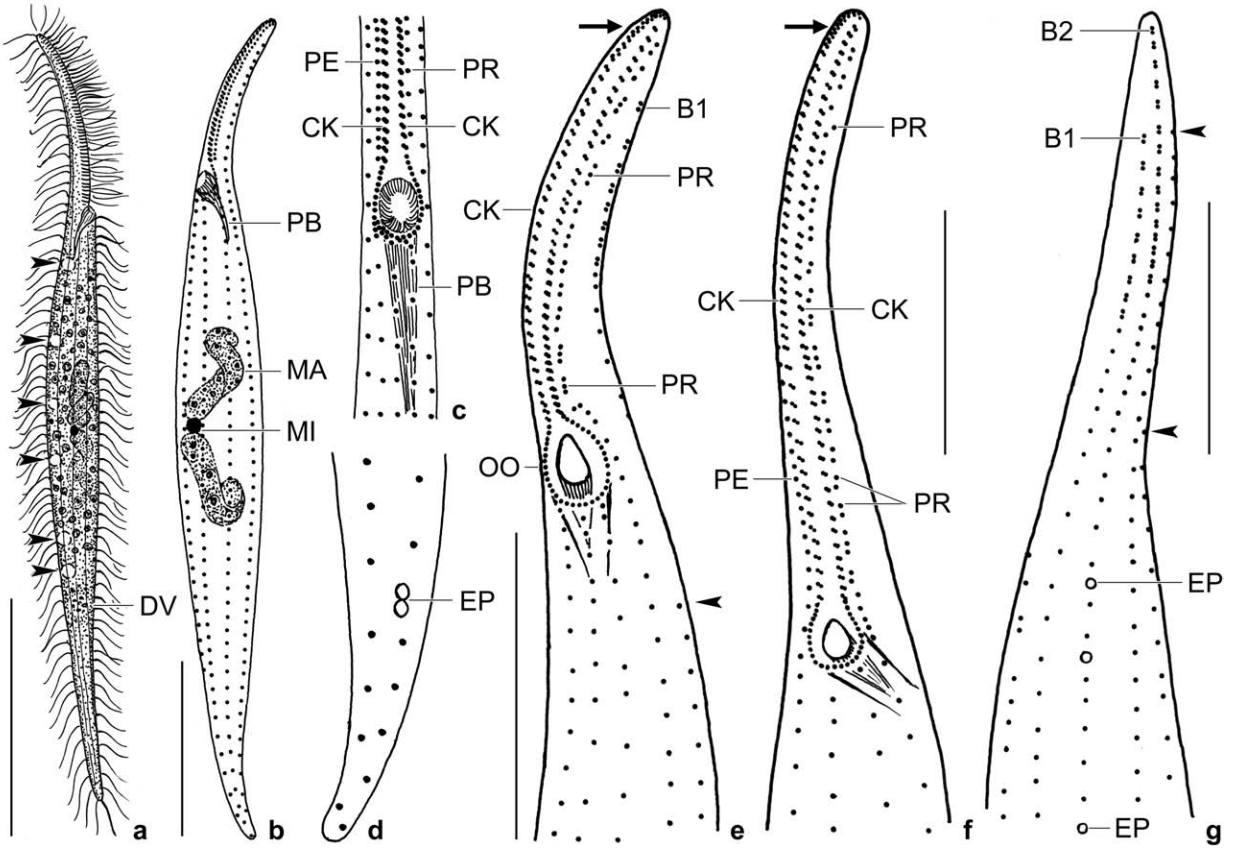
Characteristics	Mean	M	SD	SE	CV	Min	Max	n
Body, length	125.2	123.0	17.8	5.4	14.3	108.0	160.0	11
	132.8	140.0	22.7	5.0	17.1	83.0	176.0	21
Body, width	16.6	16.0	2.6	0.8	15.6	12.0	20.0	11
	15.0	13.0	4.3	0.9	28.7	9.0	23.0	21
Body length:width, ratio	7.6	7.7	1.5	0.5	20.0	5.0	10.3	11
	9.4	9.0	2.6	0.6	27.5	5.0	14.0	21
Anterior body end to oral bulge opening, distance	33.8	32.0	9.5	2.9	28.2	23.0	49.0	11
	28.6	29.0	4.3	0.9	14.8	22.0	35.0	21
Proboscis, % of body length	26.9	29.0	4.9	1.5	18.2	19.0	33	11
	21.8	21.0	2.7	0.6	12.4	18.0	30.0	21
Oral bulge opening, length	5.0	5.0	1.3	0.4	25.3	4.0	7.0	11
	4.4	4.0	0.9	0.2	19.7	3.0	6.0	21
Oral bulge opening, width	4.4	4.0	–	–	–	4.0	5.0	8
	4.1	4.0	0.7	0.2	18.3	3.0	5.0	21
Anterior body end to macronucleus, distance	56.5	60.0	12.0	3.6	21.3	37.0	80.0	11
	49.9	50.0	10.6	2.3	21.3	34.0	74.0	21
Nuclear figure, length	29.1	28.0	6.8	2.0	23.2	19.0	45.0	11
	32.0	32.0	5.9	1.3	18.3	21.0	45.0	21
Anterior macronuclear nodule, length	17.1	16.0	3.2	1.0	18.6	13.0	23.0	11
	17.1	16.0	2.6	0.6	15.4	14.0	23.0	21
Anterior macronuclear nodule, width	5.7	6.0	1.3	0.4	23.7	4.0	7.0	11
	5.5	5.0	0.8	0.2	13.6	4.0	7.0	21
Macronuclear nodules, number	2.0	2.0	0.0	0.0	0.0	2.0	2.0	11
	see text; usually two							
Micronuclei, largest diameter	2.0	2.0	–	–	–	2.0	3.0	11
	1.6	1.5	0.3	0.1	18.5	1.2	2.0	21
Micronuclei, number	1.0	1.0	0.0	0.0	0.0	1.0	1.0	11
	1.1	1.0	–	–	–	1.0	2.0	21
Ciliary rows in mid-body, number	10.3	10.0	1.0	0.3	9.8	9.0	12.0	11
	10.4	11.0	1.2	0.3	12.0	8.0	12.0	21
Cilia in mid-body in 10 µm, number	4.5	5.0	0.8	0.2	18.2	3.0	6.0	11
	5.6	5.0	1.2	0.3	21.7	4.0	9.0	21
Dorsal brush rows, number	2.0	2.0	0.0	0.0	0.0	2.0	2.0	9
	2.0	2.0	0.0	0.0	0.0	2.0	2.0	21

Characteristics	Mean	M	SD	SE	CV	Min	Max	n
Dikinetids in brush row 1, number	10.3	11.0	2.1	0.7	20.6	8.0	15.0	9
	13.6	13.0	2.1	0.5	15.3	9.0	17.0	21
Dikinetids in brush row 2, number	14.7	15.0	2.1	0.7	14.4	12.0	18.0	9
	17.8	17.0	2.8	0.6	15.9	11.0	23.0	21
Brush dikinetids, total number	25.0	25.0	4.0	1.3	16.0	20.0	33.0	9
	31.4	31.0	4.2	0.9	13.4	20.0	39.0	21
Anterior body end to last brush dikinetid, distance	21.7	23.0	4.9	1.6	22.7	15.0	29.0	10
	18.7	18.0	2.7	0.6	14.2	15.0	25.0	21
Dikinetidal portion of dorsal brush, % of body length	17.3	19.0	2.9	0.9	17.0	12.0	21.0	10
	14.3	14.0	1.9	0.4	13.5	11.0	20.0	21
Preoral kinetids, number	not counted; see text							
	27.9	27.0	5.1	1.1	18.2	18.0	36.0	21

Oral bulge opening at beginning (Foissner 1981) or at end (Table 42) of second quarter of body, inconspicuous because hardly projecting and very small, i.e., about 2.5 µm (Foissner 1981) or 5 × 4.4 µm (Table 42). Pharyngeal basket bulbous and short. Circumoral kinety composed of ordinarily to widely spaced dikinetids in proboscis and of narrowly spaced monokinetids around oral bulge opening, right branch with a conspicuous condensation of kinetids apically (Figs 78c, e, f). Preoral kineties each composed of two to three ordinarily to widely spaced cilia, forming a more or less distinct row left of circumoral kinety (Figs 78b, c, e, f).

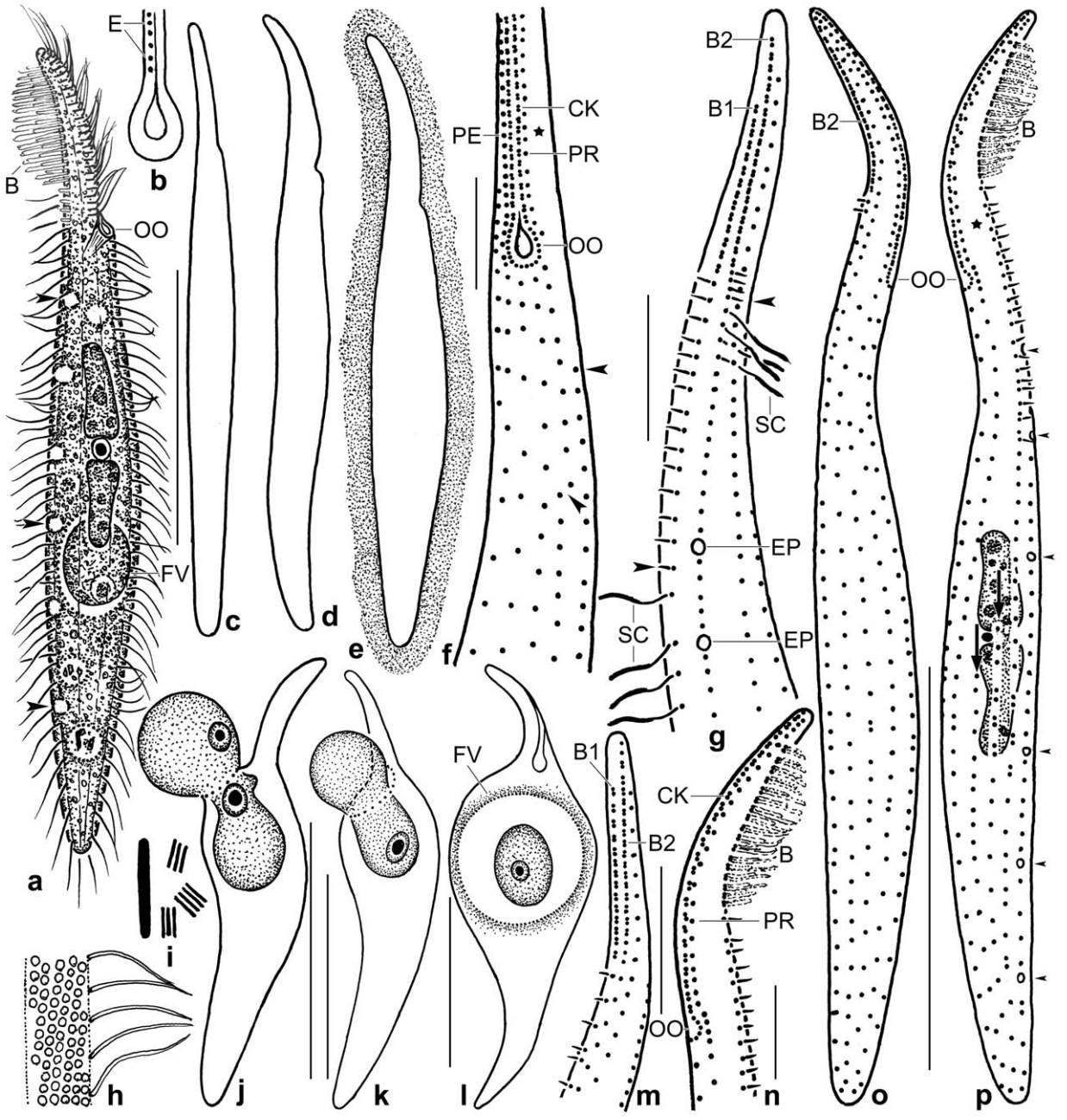
Description of a Brazilian population: High numbers of *Microdileptus breviproboscis* developed in a sample consisting of the up to 2 cm thick litter layer as well as organic debris and fine roots sieved off the upper 15 cm sand horizon from the Restingha (shrub) region in the outskirts of Rio de Janeiro, Brazil, about 1 km distant the Atlantic Ocean coast. The sample, which was slightly saline (~ 5‰) and had a pH of 5.3, contained about 40 ciliate species, several of which were undescribed. *Microdileptus breviproboscis* was possibly at the end of the logarithmic growth phase because there were many specimens, including some conjugation pairs, but few dividers.

Size 100–200 × 10–25 µm in vivo, usually about 155 × 18 µm, as calculated from some in vivo measurements and the morphometric data (Table 42). Shape narrowly to rod-like dileptid with proboscis occupying about one fifth of body length on average, posterior end narrowly rounded or acute, but never tail-like; widest in mid-trunk with ventral side usually more convex than dorsal one, proboscis flattened and slightly to distinctly curved dorsally; trunk unflattened, usually bluntly fusiform, rarely cylindroidal or distinctly winding (Figs 79a, c–e, o, p, 80a–e), strongly inflated during and after swallowing the prey (Figs 79j–l, 80l–n). Nuclear apparatus usually slightly above middle third of trunk, may be strongly dislocated by large prey, in 90% out of 214 specimens investigated composed of two macronuclear nodules and a micronucleus in between, in 10% of cells abnormal, e.g., nodules not separated or one nodule distinctly smaller than the other; some variability possibly caused by late post-dividers and injured specimens. Individual macronuclear nodules usually more or less clavate and sometimes slightly spiralized, abut with broad end on micronucleus; nucleoli ordinary, i.e., globular and rather numerous. Micronucleus in vivo surrounded by a distinct membrane rarely recognizable in protargol preparations, about 3 µm in size with membrane; after protargol impregnation broadly ellipsoidal and about 1.6 × 1.2 µm without membrane (Figs 79a, p, 80a–e, l–t; Table 42). Several minute contractile vacuoles in dorsal side, first vacuole at

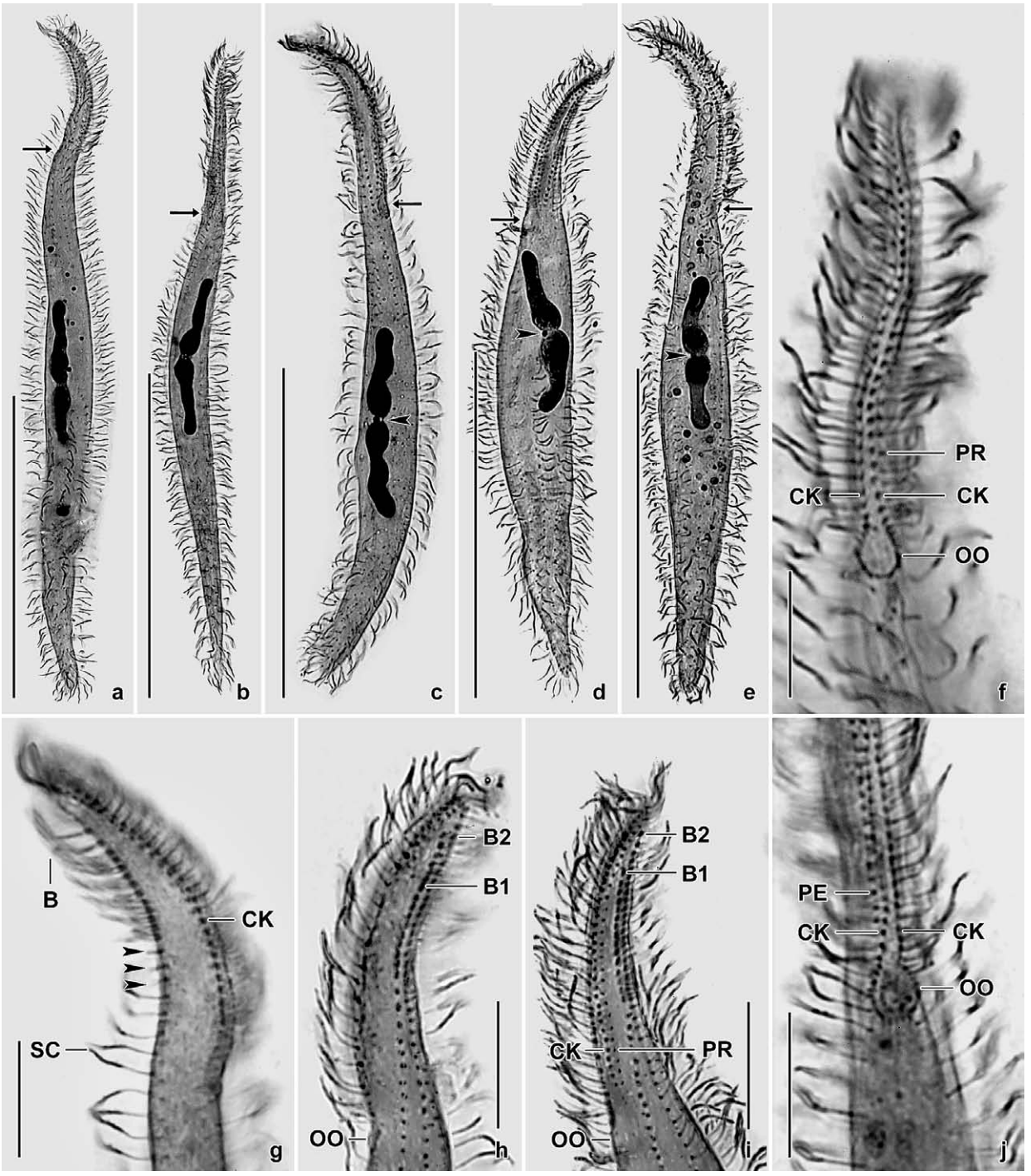


Figs 78a–g: *Microdileptus breviproboscis*, Austrian specimens from life (a) and after protargol impregnation (b–g). From Foissner 1981 (a–d, from the Hochmais-Alm along the Grossglockner Hochalpenstrasse) and originals (e–g, from the Stubnerkogel in the Gastein area). **a –** right side view. Arrowheads mark contractile vacuoles; **b –** ciliary pattern of left side and nuclear apparatus; **c –** ventral view of oral area; **d –** dorsal view of posterior body region; **e, f –** ventrolateral views, showing the variability in the arrangement of the preoral kineties, which are clearly recognizable in (e), while forming a "grouped row" in (f). The arrows mark the condensation of circumoral kinetids in the right anterior end of the proboscis. The arrowhead denotes the anterior end of a shortened somatic kinety; **g –** dorsal view, showing the dorsal brush and the excretory pores of three contractile vacuoles. Arrowheads mark kineties ending along the proboscis. B1, 2 – dorsal brush rows, CK – circumoral kinety, DV – defecation vacuole, EP – excretory pores, MA – macronuclear nodule, MI – micronucleus, OO – oral bulge opening, PB – pharyngeal basket, PE – perioral kinety, PR – preoral kineties. Scale bars: 20 µm (b, e–g) and 50 µm (a).

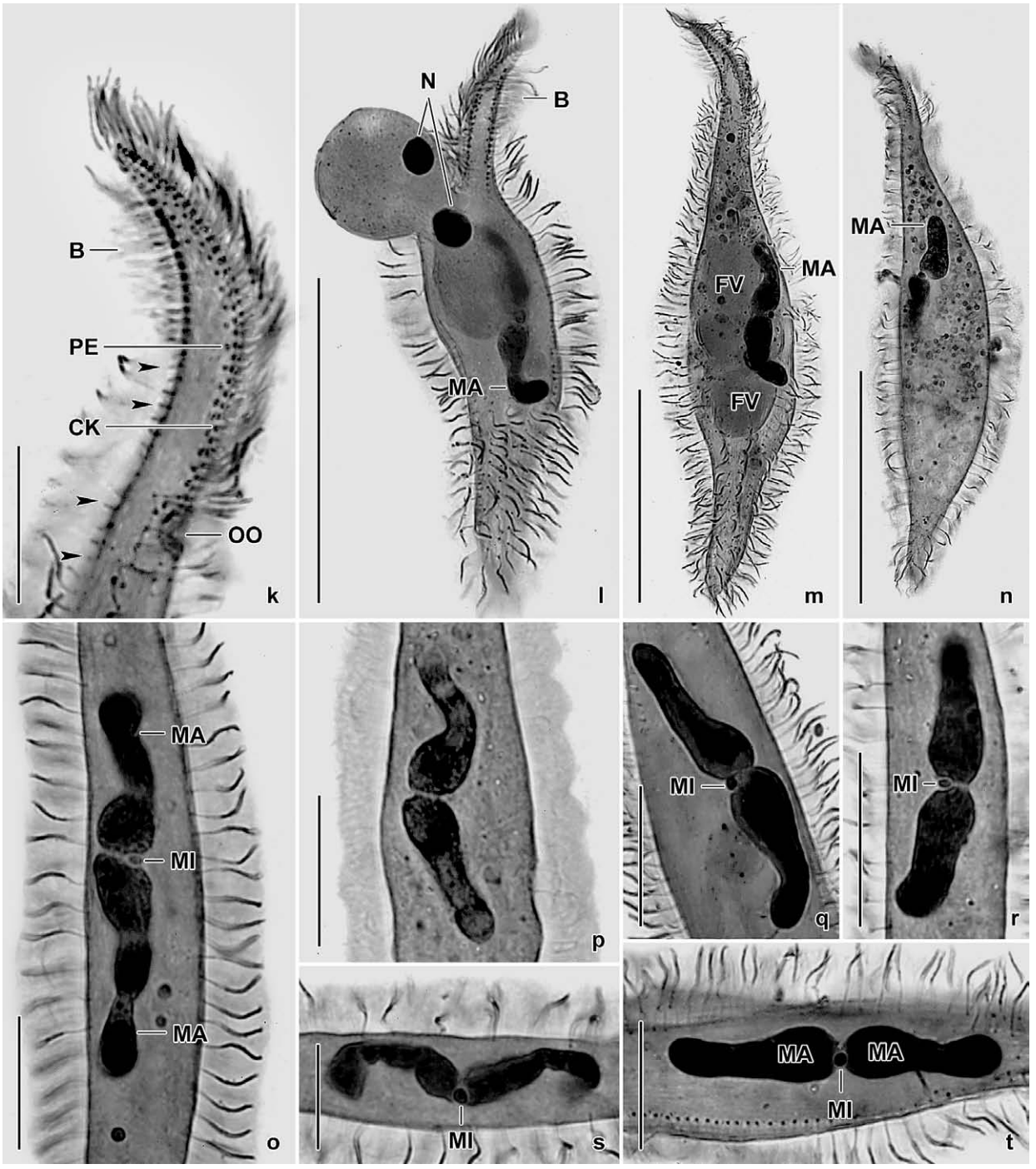
level of oral opening; each vacuole with one, very rarely with two intrakinetal excretory pores associated with kinety bearing brush row 2 (Figs 79a, g, p). Extrusomes attached to right branch of proboscis oral bulge and scattered in cytoplasm, often forming small aggregates; inconspicuous because only about 3 × 0.4 µm in size and oblong with rounded ends (Figs 79a, b, i). Cortex very flexible and soft, colourless, contains about six oblique granule rows between adjacent kineties; granules narrowly spaced in somatic and oral cortex, about 0.5 × 0.25 µm in size (Fig. 79h). All specimens covered by a 5–7 µm thick layer not recognizable in vivo but yellowishly impregnated with the protargol method used (Figs 79e, 80o, p). Cytoplasm colourless, hyaline in proboscis and rear end, while more or less opaque in trunk, depending on nutrition state. Possibly feeds only on morphostatic and dividing naked amoebae (12 cases observed) about 50 µm across, i.e., much larger than the minute oral opening, which can expand widely ingesting prey as a whole (Figs 79j, k, 80l). When inside the trunk, the prey becomes surrounded by a large vacuole deforming the cell (Figs 79l, 80m). Then, the prey disaggregates, forming many small food vacuoles 5–10 µm across (Figs 79a, 80n).



Figs 79a–p: *Microdileptus breviproboscis*, Brazilian specimens from life (a, b–d, h, i) and after protargol impregnation (e–g, j–p). **a –** right side view of a representative specimen, length 150 µm. Arrowheads mark contractile vacuoles; **b –** frontal view of oral bulge opening and arrangement of extrusomes; **c, d –** shape variants; **e –** in protargol preparations, cells are covered by a yellowish substance; **f** – ventral view of ciliary pattern in oral region. Asterisk denotes the blank stripe on the left side of the proboscis, arrowheads mark a shortened and a misaligned ciliary row; **g, m –** ciliary pattern of proboscis' dorsal side. Arrowheads mark end of bristle tails; **h –** cortical granulation; **i –** oral bulge extrusome (~ 3 × 0.4 µm) and extrusome aggregates in cytoplasm; **j–l –** feeding on a dividing and a morphostatic amoeba and its digestion in a large food vacuole, **n**–**p –** ciliary pattern of right and left side of main voucher specimen, length 137 µm. The preoral kineties are composed of widely spaced monokinetids, forming a fairly regular row along the left branch of the circumoral kinety. Asterisk marks the blank stripe on the left side of the proboscis, arrowheads denote excretory pores, and arrows note two shortened somatic kineties. B(1, 2) – dorsal brush (rows), CK – circumoral kinety, E – extrusomes, EP – excretory pores, FV – food vacuoles, OO – oral bulge opening, PE – perioral kineties, PR – preoral kinety, SC – somatic cilia. Scale bars: 10 µm (f, g, m, n) and 50 µm (a, j–l, o, p).



Figs 80a–j: *Microdileptus breviproboscis*, Brazilian specimens after protargol impregnation. **a–e** – variability of body shape and nuclear apparatus. The minute oral opening (arrows) is hardly recognizable. The arrowheads mark the micronucleus; **f, j** – ventral views of oral area, showing the minute oral opening and the oral ciliary pattern; **g–i** – right and left side views of proboscis, showing the up to 12 µm long dorsal bristles (g), the two staggered isomorphic dorsal brush rows (h, i), and the cilia whose distal half is deeply impregnated. The preoral kineties are composed of widely spaced monokinetids, forming a fairly regular row along the left branch of the circumoral kinety. The arrowheads in (g) mark the three monokinetidal bristles of brush row 2. B(1, 2) – dorsal brush (rows), OO – oral bulge opening, PE – perioral kinety, PR – preoral kineties, SC – somatic cilia, SK – somatic kinety. Scale bars: 10 µm (f–j) and 80 µm (a–e).



Figs 80k–t: *Microdileptus breviproboscis*, oral ciliature, feeding and nuclear apparatus of Brazilian specimens after protargol impregnation. **k** – right side view of proboscis ciliary pattern. Arrowheads mark monokinetidal bristles of brush row 1; **l–n** – *Microdileptus breviproboscis* feeds on morphostatic (m) and dividing (l) naked amoebae, greatly expanding the minute oral opening (l). When the prey is in the cytoplasm (m), it disintegrates into many minute vacuoles (n); **o–t** –variability of nuclear apparatus, which consists of two clavate to oblong macronuclear nodules and a single micronucleus in between. *Microdileptus breviproboscis* is fully covered by a substance becoming yellowish in protargol preparations (o, p). B – dorsal brush, CK – circumoral kinety, FV – food vacuoles, MA – macronuclear nodules, MI – micronucleus, N – nuclei of the dividing amoeba, OO – oral opening, PE – perioral kinety. Scale bars: 15 µm (k, o–t) and 50 µm (l–n).

Cilia about 7 µm long in vivo, ordinarily spaced on average; in protargol preparations within the cover described above and with thick, strongly impregnated distal half, except for dorsal and tail bristles (Figs 80a–o); arranged in an average of 10 ordinarily spaced, longitudinal rows leaving a blank stripe on right and left side of proboscis, that on left side usually broader than that on right, about half of kineties commence at or below level of oral bulge opening (Figs 79f, n–o; Table 42). First ciliary row right of circumoral kinety extends as perioral kinety to tip of proboscis with ordinarily to widely spaced cilia (Figs 79f, o, 80k). First ciliary row left of circumoral kinety composed of widely spaced preoral kinetids (Figs 79f, n, p, 80f, i). Dorsal brush exactly on dorsal side of proboscis, composed of two staggered, isostichad rows. Brush bristles conspicuous because up to 12 µm long and slightly thicker than ordinary cilia, length distinctly decreases at both ends of rows. Brush row 1 commences subapically, composed of an average of 14 ordinarily spaced dikinetids with anterior bristle about half as long as posterior one, continues to second third of body with a long, monokinetidal tail of about 1.5 µm long bristles. Brush row 2 commences apically with some monokinetids, composed of an average of 18 ordinarily spaced dikinetids, each associated with two bristles of similar length, continues with a very short, monokinetidal tail of two to five 1.5 µm long bristles (Figs 79a, g, m–p, 80g–i, k; Table 42).

Oral apparatus basically as in other dileptids, but with several specializations. Oral bulge opening at end of anterior body fifth, broadly ovate to circular, only about 4 µm wide and thus difficult to recognize. Pharyngeal basket hardly recognizable both in vivo and in protargol preparations because composed of very fine and faintly impregnated rods (Figs 79a, b, f, o, p, 80a–k). Circumoral kinety composed of ordinarily to widely spaced dikinetids, except for narrowly spaced monokinetids around oral bulge opening, becoming very widely spaced when large prey is ingested (Figs 79j, k); right and left branch only 1–2 µm apart, likely due to the small, rather distinctly flattened proboscis; right branch with a rather conspicuous condensation of kinetids apically. Preoral kineties composed of widely spaced monokinetids, forming a fairly regular row along left branch of circumoral kinety (Figs 79f, n, p, 80f, i).

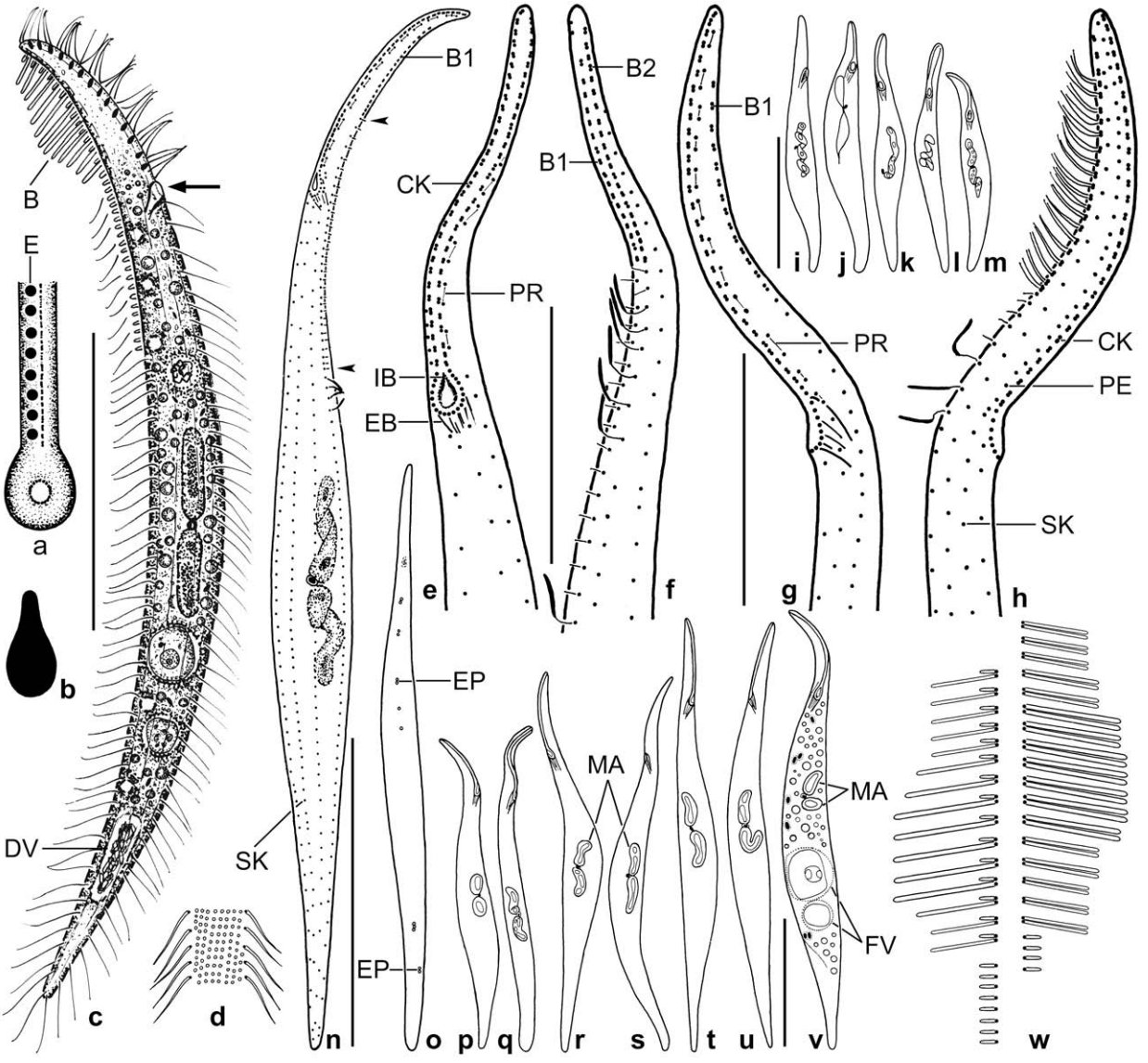
Occurrence and ecology: According to Foissner (1998), *M. breviproboscis* has been recorded from all main biogeographic regions, except Antarctica. However, when considering the identification problems, most records must be doubted, except of the type locality and the Brazilian population described here. And even this is not entirely sure because the voluminous cover of the Brazilian population could well serve as a character for a distinct species.

Microdileptus microstoma (Vďačný & Foissner, 2008) nov. comb. (Figs 81a–w, 83a, b, f, g; Tables 43, 44)

2008 *Dileptus microstoma* nov. sp. Vďačný & Foissner, Acta Protozool. **47**: 212

2011 *Rimaleptus microstoma* (Vďačný & Foissner, 2008) comb. n. – Vďačný, Orsi, Bourland, Shimano, Epstein & Foissner, Eur. J. Protistol. **47**: 297 (combination with *Rimaleptus*; 18S rRNA gene sequence of a North American population)

Diagnosis: Size about 170 × 15 µm in vivo. Shape very narrowly dileptid to rod-like with acute posterior body third, proboscis about 1/5 of body length. Two oblong macronuclear nodules with a micronucleus in between. Contractile vacuoles absent from middle third of trunk. Extrusomes attached to right branch of proboscis oral bulge, ampulliform, about 1.5 × 1 µm in size. On average 9 ciliary rows, 2 staggered and differentiated into a conspicuous, isostichad dorsal brush with bristles up to 10 µm long: rows 1 and 2 composed of an average of 15 and 19 dikinetids, respectively; monokinetidal tail of row 1 extending to second third of body and thus longer than that of row 2. Oral bulge opening about 4 × 3 µm in size. Preoral kineties each usually composed of 2 ordinarily to widely spaced kinetids, forming a single row almost parallel to circumoral kinety.



Figs 81a–w: *Microdileptus microstoma*, African type population (a–d, g, h, n, o, w) and Singapore voucher specimens (e, f, i–m, p–v) from life (a–d, w) and after protargol impregnation (e–v). From Vďačný & Foissner (2008b). **a** – frontal view of oral bulge opening and arrangement of extrusomes that are attached only to the right branch of the proboscis oral bulge; **b** – extrusomes are ampulliform and 1.5 × 1 µm in size; **c** – right side view of a representative specimen, length 170 µm. Arrow denotes the very small oral bulge opening, a main feature of the genus *Microdileptus*; **d** – surface view showing cortical granulation; **e, f** – ventrolateral and dorsolateral view of ciliary pattern in anterior body portion. Preoral kineties are difficult to recognize because composed of only two widely spaced monokinetids (connected by lines), forming a fairly regular row along the left branch of the circumoral kinety; **g, h** – left and right side view of ciliary pattern in anterior body portion. Basal bodies of preoral kineties connected by lines; **i–m** – variability of body shape and size as well as of nuclear apparatus in post-dividers. Drawn to scale; **n** – ciliary pattern of left side and nuclear apparatus of holotype specimen, length 180 µm. Note that brush row 1 is associated with a monokinetidal bristle tail (arrowheads) extending to second third of body; **o** – excretory pore pattern, showing that contractile vacuoles are absent from mid-body, thus forming a short row each in anterior and posterior third of trunk; **p–v** – variability of body shape and size as well as of nuclear apparatus of morphostatic specimens. Drawn to scale; **w** – structure of dorsal brush. The bristles are up to 10 µm long and gradually decrease to about 6 µm in end regions of rows. B(1, 2) – dorsal brush (rows 1, 2), CK – circumoral kinety, DV – defecation vacuole, E – extrusomes, EB – external basket, EP – excretory pores, FV – food vacuoles, IB – internal basket, MA – macronuclear nodules, PE – perioral kinety, PR – preoral kineties, SK – somatic kinety. Scale bars: 50 µm (c, i–m, n, p–v) and 20 µm (e–h).

Table 43: Morphometric data on two populations of *Microdileptus microstoma*: type from Africa (1st line); voucher population from Singapore (2nd line); and post-dividers from Singapore (3rd line). From VĎAČNÝ & FOISSNER (2008b). Data based on mounted, protargol-impregnated (Foissner's method), and randomly selected specimens from non-flooded Petri dish cultures. Measurements in µm. CV – coefficient of variation in %; M – median; Max – maximum; Mean – arithmetic mean; Min – minimum; n – number of specimens investigated; SD – standard deviation; SE – standard error of mean.

Characteristics	**Mean**	**M**	**SD**	**SE**	**CV**	**Min**	**Max**	**n**
Body, length	143.2	140.0	24.8	5.4	17.3	98.0	203.0	21
	152.0	154.0	23.2	5.1	15.3	109.0	209.0	21
	91.6	96.0	14.2	4.3	15.5	64.0	108.0	11
Body, width	13.0	13.0	1.8	0.4	14.2	10.0	17.0	21
	11.7	12.0	2.2	0.5	18.9	8.0	15.0	21
	11.4	11.0	1.8	0.5	15.6	8.0	15.0	11
Body length:width, ratio	11.3	10.9	2.9	0.6	25.9	6.1	20.3	21
	13.5	13.2	3.6	0.8	26.8	9.5	21.8	21
	8.2	8.3	1.5	0.4	17.9	4.6	10.3	11
Anterior body end to oral bulge opening, distance	28.5	29.0	3.1	0.7	10.8	23.0	35.0	21
	28.4	30.0	3.5	0.8	12.2	19.0	34.0	21
	16.1	16.0	3.8	1.1	23.6	9.0	24.0	11
Proboscis, % of body length	20.4	20.1	3.7	0.8	18.3	14.5	27.6	21
	18.9	19.5	2.7	0.6	14.0	14.3	23.4	21
	17.6	18.0	2.8	0.9	16.2	12.8	22.1	11
Oral bulge opening, length	4.2	4.0	0.8	0.2	19.8	3.0	7.0	21
	4.1	4.0	0.8	0.2	20.0	3.0	5.0	21
	4.4	5.0	0.8	0.3	19.3	3.0	6.0	11
Oral bulge opening, width	2.7	3.0	0.5	0.1	17.1	2.0	4.0	11
	2.8	3.0	0.4	0.1	14.0	2.0	4.0	13
	3.3	3.0	0.4	0.2	11.9	3.0	4.0	6
Anterior body end to macronucleus, distance	65.1	62.0	10.7	2.5	16.5	47.0	82.0	19
	64.6	65.0	9.5	2.1	14.7	48.0	85.0	21
	32.4	33.0	8.3	2.5	25.6	19.0	46.0	11
Nuclear figure, length	26.3	26.0	6.1	1.4	23.4	15.0	38.0	19
	24.9	25.0	4.2	0.9	16.9	17.0	33.0	21
	21.3	21.0	4.5	1.3	20.9	14.0	30.0	11
Anterior macronuclear nodule, length	15.3	14.0	4.0	0.9	25.9	10.0	24.0	19
	13.8	13.0	3.6	0.8	26.3	8.0	23.0	21
	11.8	12.0	1.8	0.7	15.0	9.0	15.0	7
Anterior macronuclear nodule, width	4.9	5.0	1.3	0.3	26.7	3.0	8.0	19
	4.3	4.0	0.7	0.1	15.6	4.0	6.0	21
	3.7	4.0	0.5	0.2	14.2	3.0	5.0	7

Characteristics	Mean	M	SD	SE	CV	Min	Max	n
Posterior macronuclear nodule, length	15.4	14.0	4.1	1.0	26.8	10.0	24.0	19
	14.6	15.0	3.4	0.7	23.0	8.0	21.0	21
	13.2	12.0	1.9	0.7	14.1	11.0	16.0	7
Posterior macronuclear nodule, width	5.1	5.0	1.1	0.3	21.8	3.0	7.0	19
	4.4	4.0	0.7	0.2	16.1	3.0	5.0	21
	3.6	4.0	0.4	0.1	10.4	3.0	4.0	7
Macronuclear nodules or moniliform beds, number	2.0	2.0	0.0	0.0	0.0	2.0	2.0	19
	2.0	2.0	0.0	0.0	0.0	2.0	2.0	21
	2.3	2.0	2.0	0.6	86.0	1.0	8.0	11
Micronucleus, largest diameter	1.8	2.0	0.3	0.1	18.4	1.5	2.5	10
	1.6	1.5	0.3	0.1	18.8	1.0	2.5	21
	2.1	2.5	0.4	0.1	18.6	1.0	2.5	9
Micronucleus, number	1.0	1.0	0.0	0.0	0.0	1.0	1.0	10
	1.0	1.0	0.0	0.0	0.0	1.0	1.0	21
	1.0	1.0	0.0	0.0	0.0	1.0	1.0	9
Ciliary rows, number	8.8	9.0	0.9	0.2	9.9	7.0	11.0	21
	8.8	9.0	1.1	0.2	12.2	7.0	11.0	21
	8.0	8.0	0.8	0.2	9.7	7.0	9.0	11
Cilia in mid-body in 10 μm, number	5.6	5.0	1.3	0.3	22.8	3.0	8.0	21
	3.7	3.0	0.9	0.2	23.4	3.0	6.0	21
	4.7	5.0	0.9	0.3	19.1	3.0	6.0	11
Dorsal brush rows, number	2.0	2.0	0.0	0.0	0.0	2.0	2.0	21
	2.0	2.0	0.0	0.0	0.0	2.0	2.0	21
	2.0	2.0	0.0	0.0	0.0	2.0	2.0	10
Dikinetids in brush row 1, number[a]	15.2	14.0	3.5	1.0	23.2	10.0	21.0	12
Dikinetids in brush row 2, number[a]	18.5	19.0	3.4	1.0	18.5	13.0	24.0	12
Anterior body end to last dikinetid of brush row 1, distance[a]	20.2	21.0	2.9	0.8	14.5	15.0	25.0	12
Anterior body end to last dikinetid of brush row 2, distance[a]	19.0	20.0	3.1	0.9	16.4	14.0	23.0	12

[a] Counted/measured only in morphostatic specimens from Singapore population.

Type locality: Soil from the University Campus in Abomey-Calavi, Benin, Africa, E2°21' N6°27'.

Type and voucher material: One holotype slide (inv. no. 2011/249) and six paratype slides (inv. no. 2011/250–255) as well as eight voucher slides (Singapore population; inv. nos 2011/256–263) with protargol-impregnated specimens have been deposited in the Biology Centre of the Museum of Upper Austria, Linz (LI). Relevant specimens are marked by black ink circles on the coverslip.

Gene sequence: The 18S rRNA gene sequence of a North American population has been deposited in GenBank (HM581676). The sequence is 1642 nucleotides long and has a GC content of 43.1%.

Etymology: Composite of the Greek adjective *mikros* (small) and the Greek noun *stoma* (mouth), referring to the very small oral entrance.

Description: This species was studied in two populations, namely from Benin (type) and Singapore (voucher). They match very well (Table 43), therefore the diagnosis and description summarize all observations. The living morphology was studied mainly in the type population.

Size 130–250 × 15–20 μm in vivo, usually about 170 × 15 μm, as calculated from some in vivo measurements and the morphometric data (Table 43). Shape very narrowly dileptid to rod-like with proboscis occupying about one fifth of body length; anterior and posterior third gradually narrowing to acute ends, posterior end never tail-like; widest in mid-portion of trunk, anterior quarter of body flattened about 2:1, trunk unflattened; dorsal outline curved to slightly sigmoidal (Figs 81c, p–v, 83a). Nuclear apparatus in mid of trunk, may be dislocated by large food items (Fig. 81v). Macronuclear nodules highly variable in shape, that is, ellipsoidal, reniform, spiralized or, very rarely, moniliform (Figs 81n, p–u, 83g; Table 44); nucleoli large, ellipsoidal or lobate, well recognizable both in vivo and in protargol preparations. Micronucleus in between macronuclear nodules, globular to broadly ellipsoidal, about 2 μm in size, usually surrounded by a distinct membrane in protargol preparations (Figs 81c, n, p–v, 83g). Contractile vacuoles in dorsal side of trunk, remarkable because lacking in mid-body, thus forming a short row each in anterior and posterior third of trunk; one to two, rarely three intrakinetal excretory pores per vacuole (Figs 81c, o). Extrusomes attached only to right branch of oral bulge; ampulliform and minute, that is, about 1.5 × 1 μm in size, rather refractive and thus distinct in vivo (Figs 81a, b); developing cytoplasmic extrusomes broadly fusiform, rarely impregnating with protargol. Cortex very flexible, contains about eight oblique granule rows between adjacent kineties; granules narrowly spaced in somatic and oral cortex, about 0.5 × 0.3 μm in size (Fig. 81d). Cytoplasm colourless, hyaline in flattened proboscis and rear end, opaque throughout trunk due to numerous lipid droplets 1–3 μm across and food vacuoles containing naked amoebae and fungal spores (Fig. 81v); in rear end sometimes a defecation vacuole with crystalline contents. Movement without peculiarities.

Cilia about 8 μm long in vivo, ordinarily spaced; in protargol preparations as typical for dileptids, i.e., with thick and strongly impregnated distal half, except for dorsal and tail bristles; arranged in an average of nine ordinarily spaced, longitudinal rows leaving a barren area on left side of proboscis (Figs 81e, g, n; Table 43). First row right of circumoral kinety extends as perioral kinety with widely spaced cilia to tip of proboscis (Figs 81h, 83b). Invariably only one ciliary row between perioral kinety and brush row 2 (Fig. 81h). Dorsal brush exactly on dorsal side of proboscis, composed of two staggered, isostichad rows. Dorsal bristles conspicuous because long and thick, that is, up to 10 × 1 μm in size. Brush row 1 commences slightly more subapically than row 2, composed of an average of 15 loosely to ordinarily spaced dikinetids each having an about 1.5 μm long anterior bristle and an up to 10 μm long posterior bristle gradually decreasing to about 6 μm in end regions of row. Brush row 2 begins near tip of proboscis, composed of an

Table 44: Comparison of macronucleus in several populations of *Microdileptus microstoma* and *M. semiarmatus* (from Vďačný & Foissner 2008b).

Species / population	Shape of macronuclear nodules (proportion, %)					Number of specimens analyzed
	Ordinary with ellipsoidal or ovoidal nodules	Ordinary with reniform nodules	Moniliform	Ordinary with helical nodules	Strand-like	
M. microstoma from Benin	19	47	4	30	–	21
M. microstoma from Singapore	33	52	9	4	–	21
M. semiarmatus from Austria	13	15	–	19	53	38

average of 19 loosely to ordinarily spaced dikinetids each associated with bristles similar to those of row 1, but anterior bristle not shortened. Both rows continue with a monokinetidal tail composed of about 1.5 µm long bristles, tail of row 1 conspicuously longer than that of row 2 and extending to second third of body; row 2 tail composed of less than five bristles (Figs 81a, f–h, n, w, 83f).

Oral apparatus basically as in other dileptids. Oral bulge opening at end of anterior body fifth, broadly ovate, only about 4 × 3 µm in size and thus difficult to recognize in vivo (Figs 81a, c; Table 43). Pharyngeal basket difficult to recognize both in vivo and in protargol preparations because composed of very fine and faintly impregnated rods. Circumoral kinety composed of ordinarily to widely spaced dikinetids, except for narrowly spaced monokinetids around oral bulge opening (Figs 81e, g, h, 83b). Preoral kineties difficult to recognize because composed of only two, rarely three widely spaced monokinetids almost in line with left branch of circumoral kinety (Figs 81e, g, n).

Notes on post-dividers: Post-dividers differ from morphostatic cells by the smaller size (90 × 11 µm vs. 150 × 12 µm), the stouter body (8.2:1 vs. 13.5:1), and the shorter (16 µm vs. 30 µm long) and broader proboscis, while the number of ciliary rows (8 vs. 9) and the proportion of body and proboscis length (18% vs. 19%) is quite similar (Table 43). Early post-dividers have a fibre-like elongation of the posterior end of the macronucleus and the dorsal brush dikinetids are very close together, especially in row 2. Further, post-dividers are highly variable in number and pattern of the macronuclear nodules: a moniliform strand composed of about 8 nodules; a single, highly spiralized strand; or, rarely, two ordinary macronuclear nodules with the micronucleus in between (Figs 81i–m; Table 43).

Occurrence and ecology: To date found at type locality and in a very sandy coastal soil (pH 7.0 in water) from Singapore, Asia (Foissner 2008); in floodplain soil from Boise, Idaho, USA (Vďačný et al. 2011b); possibly occurs also in Kenya and in the Monte Verde National Park of Costa Rica. The sample from type locality consisted of hard, red, circumneutral (pH 7.3 in water) soil mixed with some leaf litter and grass roots. *Microdileptus microstoma* was rather abundant in the non-flooded Petri dish cultures and is well adapted to the soil environment by the very slender, highly flexible body (Vďačný & Foissner 2008b).

Remarks: *Microdileptus microstoma* differs from *M. breviproboscis* and *M. semiarmatus* by the shape of the extrusomes (ampulliform vs. oblong, cuneate, or ellipsoidal) and the contractile vacuole pattern (a dorsal row of vacuoles interrupted in mid of trunk vs. a continuous dorsal row).

Microdileptus semiarmatus (Vďačný & Foissner, 2008) nov. comb. (Figs 82a–p, 83c–e, h, i; Tables 44, 45)

2008 *Dileptus semiarmatus* nov. sp. Vďačný & Foissner, Acta Protozool. **47**: 217

Diagnosis: Size about 180 × 17 µm in vivo. Shape very narrowly dileptid to rod-like with acute posterior body third, proboscis about 1/5 of body length. Two oblong macronuclear nodules with a micronucleus in between. A dorsal row of contractile vacuoles. Two types of extrusomes attached to only right posterior half of proboscis oral bulge: type I cuneate, about 2–3 × 1 µm in size; type II rod-shaped, 3 µm long. On average 10 ciliary rows, 2 staggered and differentiated into a conspicuous, isostichad, posteriorly heteromorphic dorsal brush with bristles up to 10 µm long: rows 1 and 2 composed of an average of 13 and 20 dikinetids, respectively; monokinetidal bristle tail of row 1 extending to second fourth of body and thus much longer than that of row 2. Oral bulge opening about 5 × 3 µm in size, hardly broader than oral bulge. Circumoral kinety in U-shaped pattern, composed of very widely spaced kinetids. Preoral kineties each composed of 2 very widely spaced kinetids, forming a single row almost parallel to circumoral kinety.

Type locality: Soil from a beech forest in the surroundings (Neuhaus area) of the town of Salzburg, Austria, E13° N47°.

Type material: One holotype slide (inv. no. 2011/264) and seven paratype slides (inv. nos 2011/265–271) with protargol-impregnated specimens have been deposited in the Biology Centre of the Museum of Upper Austria, Linz (LI). Relevant specimens are marked by black ink circles on the coverslip.

Etymology: Composite of the Latin prefix *semi* (half) and the adjective *armatus* (armed), referring to the extrusomes, which are restricted to the posterior half of the proboscis, a curious feature of this species.

Description: Size 130–230 × 10–25 μm, usually about 180 × 17 μm, as calculated from some in vivo measurements and the morphometric data (Table 45). Shape very narrowly dileptid to rod-like, on average about 11:1 both in vivo and in protargol preparations. Proboscis indistinct because hardly set off from body proper and occupying only one fifth of body length; anterior and posterior end acute, i.e., gradually narrowed, posterior end never tail-like; dorsal outline slightly sigmoidal or concave (Figs 82a, k–p, 83c; Table 45). Nuclear apparatus in mid of trunk. Macronuclear nodules highly variable in shape: cylindroidal (53%), spiralized (19%), reniform (15%), ellipsoidal or ovoidal (13%; Table 44); nucleoli small to medium-sized. Micronucleus in between macronuclear nodules, globular to broadly ellipsoidal, about 2 μm across, usually surrounded by a distinct membrane in protargol preparations (Figs 82a, b, k–p, 83c). A dorsal row of contractile vacuoles, first vacuole slightly underneath level of oral bulge opening. Two types of extrusomes attached to right posterior half of proboscis oral bulge (Figs 82a, h, arrows), do not impregnate with the protargol method used: type I cuneate to narrowly cuneate, about 2–3 × 1 μm in size; type II rod-shaped with both ends rounded, about 3 μm long (Fig. 82i). Cortical granulation not studied. Cytoplasm colourless and hyaline in flattened proboscis, rather opaque in trunk due to numerous lipid droplets 1–5 μm across and food vacuoles possibly containing flagellates, naked amoebae, and small ciliates; sometimes a defecation vacuole with crystalline contents in posterior body portion. Movement without peculiarities.

Cilia about 8 μm long in vivo, ordinarily spaced, have the same impregnation properties as in congeners; arranged in an average of ten ordinarily spaced, longitudinal rows leaving a rather narrow, blank stripe left of oral bulge (Figs 82b, c, g; Table 45). First row right of circumoral kinety extends as perioral kinety with very loosely spaced cilia to tip of proboscis (Figs 82d, f, 83e, i). Invariably only one ciliary row between perioral kinety and brush row 2 (Fig. 82f). Dorsal brush as described in *M. microstoma*, but remarkable because heteromorphic in posterior third, where bristles are mixed with ordinary cilia. Dorsal bristles conspicuous because about 10 μm long in central brush region, gradually decreasing in length anteriorly and posteriorly; posterior bristle of dikinetids slightly shorter than anterior one. Tail of brush row 1 extends to second fourth of body and is composed of up to ten bristles, tail of row 2 much shorter or lacking (Figs 82e, g, j, 83d, e).

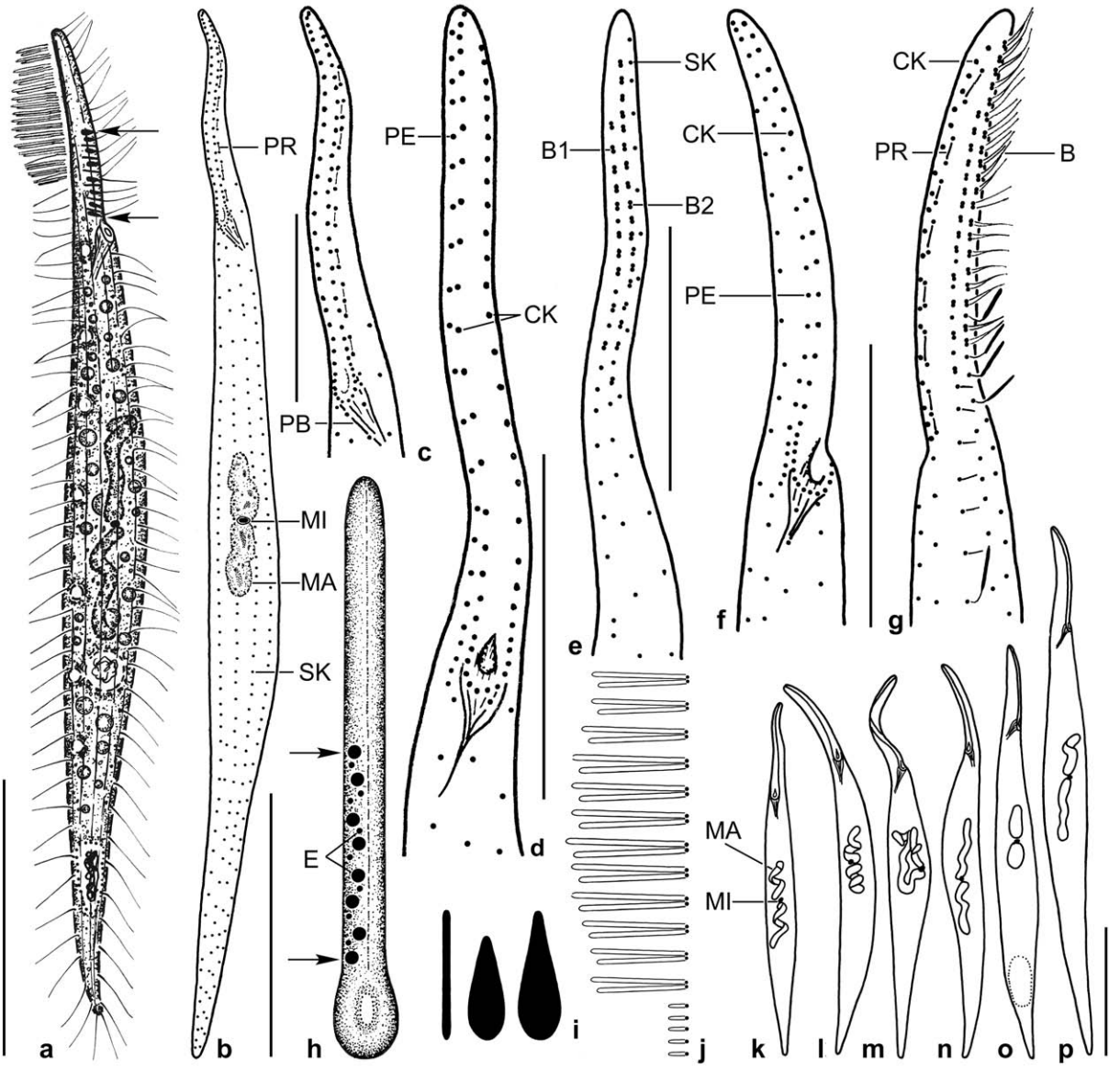
Oral bulge opening at end of anterior body fifth, broadly elliptical and very small, i.e., about 5 × 3 μm (Fig. 82h). Pharyngeal basket inconspicuous both in vivo and in protargol preparations because composed of very fine and faintly impregnated rods. Oral apparatus basically dileptid, but with several strange specializations: (i) oral bulge opening hardly broader than oral bulge, thus forming a U-shaped pattern; (ii) circumoral kinety probably monokinetidal, that is, composed of basal bodies with similar size as those of somatic cilia; (iii) circumoral, perioral, and preoral kinetids very widely spaced; (iv) right and left branch of circumoral kinety comparatively widely separated, right branch curves around anterior end of proboscis, while left branch ends subapically; (v) preoral kineties each composed of two, rarely three monokinetids, forming minute rows almost in line with circumoral kinety (Figs 82b–d, f, g, 83h, i).

Occurrence and ecology: *Microdileptus semiarmatus* was rather abundant in the non-flooded Petri dish culture from the type locality. A second population was found in soil from an oak-hornbeam forest in Vienna, viz., in soil from the Johannser Kogel (see Foissner et al. 2005 for detailed site description; designated as *Dileptus* n. sp. 1). This species is well adapted to the soil environment by the slender body.

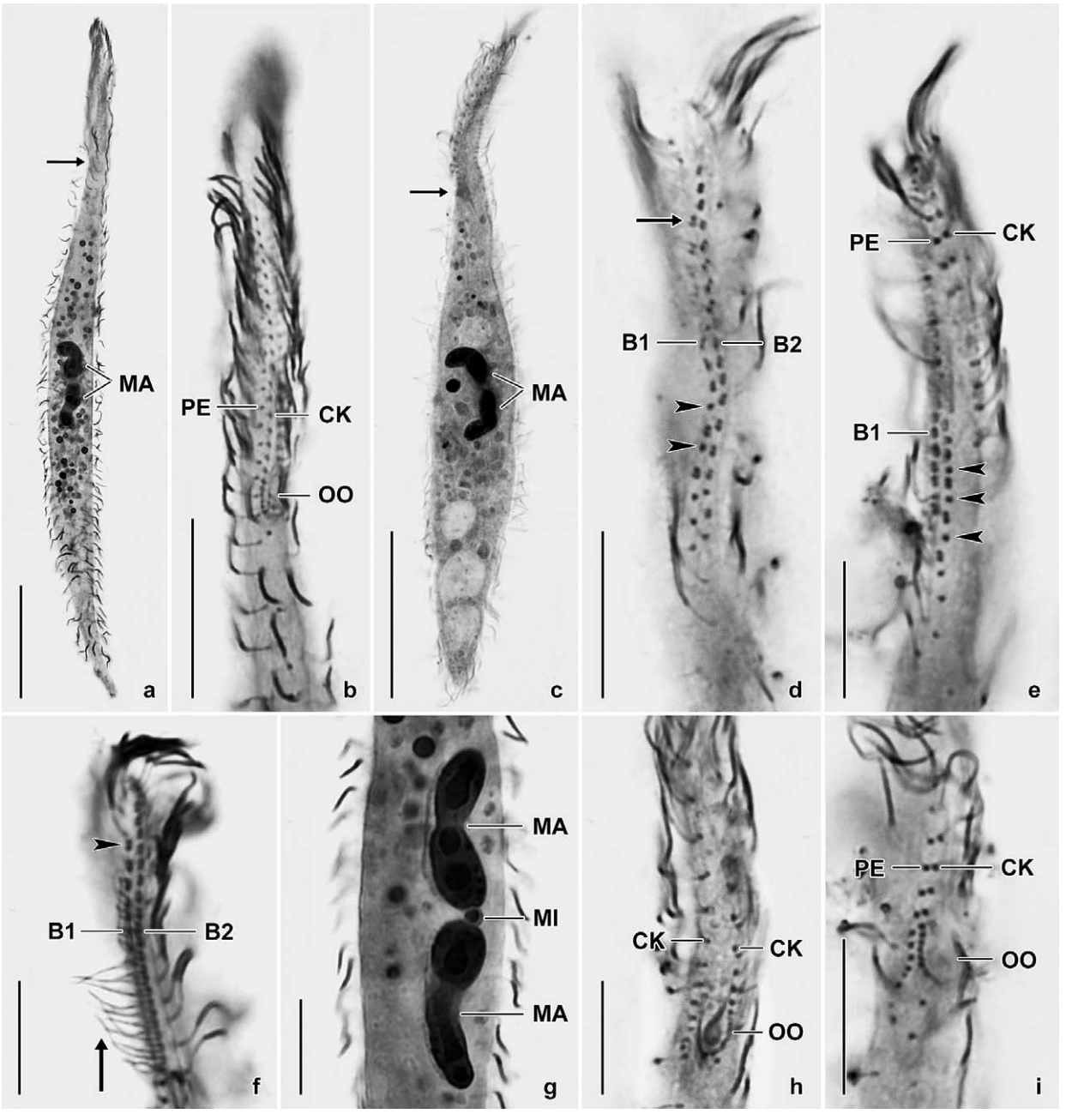
Remarks: *Microdileptus semiarmatus* differs from all described dileptids in that extrusomes occur only in the posterior half of the proboscis, a highly curious and distinct feature, which we confirmed in several specimens from both populations to exclude the possibility that it is caused by malformed or wounded specimens. *Microdileptus semiarmatus* has also two other unusual features: the oral bulge opening is hardly broader than the oral bulge, thus forming an U-shaped pattern; and the circumoral, perioral, and preoral kinetids are very widely spaced, a rare feature in dileptids.

Table 45: Morphometric data on *Microdileptus semiarmatus* (from Vďačný & Foissner 2008b). Data based on mounted, protargol-impregnated (Foissner's method), and randomly selected specimens from a non-flooded Petri dish culture. Measurements in µm. CV – coefficient of variation in %; M – median; Max – maximum; Mean – arithmetic mean; Min – minimum; n – number of specimens investigated; SD – standard deviation; SE – standard error of mean.

Characteristics	Mean	M	SD	SE	CV	Min	Max	n
Body, length	160.2	160.0	23.0	5.0	14.3	119.0	203.0	21
Body, width	14.7	15.0	3.8	0.8	25.7	9.0	23.0	21
Body length:width, ratio	11.6	11.3	3.4	0.8	29.8	6.6	21.1	21
Anterior body end to oral bulge opening, distance	30.7	30.0	4.1	0.9	13.4	25.0	39.0	21
Proboscis, % of body length	19.3	19.0	2.4	0.5	12.5	15.0	24.0	21
Oral bulge opening, length	4.2	4.0	0.8	0.2	18.9	3.0	5.0	21
Oral bulge opening, width	2.9	3.0	0.3	0.1	8.8	2.0	3.0	13
Anterior body end to macronucleus, distance	68.2	68.0	10.8	2.3	15.8	43.0	99.0	21
Nuclear figure, length	31.2	31.0	4.6	1.0	14.8	24.0	38.0	21
Anterior macronuclear nodule, length	17.1	16.0	4.7	1.0	27.2	12.0	30.0	21
Anterior macronuclear nodule, width	4.2	4.0	1.1	0.2	26.2	3.0	7.0	21
Posterior macronuclear nodule, length	18.4	18.0	5.3	1.2	28.9	12.0	36.0	21
Posterior macronuclear nodule, width	4.1	4.0	1.2	0.3	28.8	3.0	7.0	21
Macronuclear nodules, number	2.0	2.0	0.0	0.0	0.0	2.0	2.0	21
Micronucleus, largest diameter	2.0	2.0	0.4	0.1	18.2	1.5	2.5	21
Micronucleus, number	1.0	1.0	0.0	0.0	0.0	1.0	1.0	21
Ciliary rows, number	10.3	10.0	1.1	0.3	11.1	8.0	13.0	21
Cilia in mid-body in 10 µm, number	4.0	4.0	0.6	0.1	14.9	3.0	5.0	21
Dorsal brush rows, number	2.0	2.0	0.0	0.0	0.0	2.0	2.0	21
Dikinetids in brush row 1, number	13.8	13.0	2.3	0.6	16.4	10.0	18.0	17
Dikinetids in brush row 2, number	19.5	20.0	3.2	0.8	16.5	15.0	27.0	17
Anterior body end to last dikinetid of brush row 1, distance	23.8	24.0	2.4	0.6	10.0	18.0	27.0	18
Anterior body end to last dikinetid of brush row 2, distance	25.0	25.0	2.3	0.6	9.4	18.0	28.0	18



Figs 82a–p: *Microdileptus semiarmatus* from life (a, h–j) and after protargol impregnation (b–g, k–p). From Vďačný & Foissner (2008b). **a** – right side view of a representative specimen, length 180 µm. Note that extrusomes are attached only to the right posterior half of the proboscis (arrows), a main feature of this species; **b, c** – ventrolateral ciliary pattern and nuclear apparatus of holotype specimen, length 200 µm. The preoral kineties are difficult to recognize because they are composed of only two widely spaced monokinetids (connected by lines) almost parallel to left branch of circumoral kinety; **d, e** – ciliary pattern of ventral and dorsal side in anterior body portion of same specimen. The circumoral kinety is composed of very loosely arranged basal bodies with similar size as those of ordinary cilia. The oral bulge opening is hardly broader than the proboscis oral bulge, thus forming a U-shaped pattern, another unique feature of this species; **f, g** – ventrolateral and dorsolateral ciliary pattern in anterior body portion. The dorsal brush is heteromorphic in the posterior third, where bristles are mixed with ordinary cilia. Basal bodies of preoral kineties connected by lines; **h** – frontal view of oral bulge and arrangement of extrusomes. Arrows denote the two types of extrusomes attached to only right posterior branch of proboscis oral bulge; **i** – there are two types of extrusomes: type I is cuneate and 2–3 × 1 µm in size, while type II is rod-shaped and 3 µm long; **j** – dorsal brush bristles are conspicuous because about 10 µm long in central brush region, gradually decreasing in length anteriorly and posteriorly; **k–p** – variability of body shape and size as well as of nuclear apparatus. Drawn to scale. B(1, 2) – dorsal brush (rows), CK – circumoral kinety, E – extrusomes, MA – macronuclear nodules, MI – micronucleus, PB – pharyngeal basket, PE – perioral kinety, PR – preoral kineties, SK – somatic kinety. Scale bars: 50 µm (a, b, k–p) and 20 µm (c–g).



Figs 83a–i: *Microdileptus microstoma* (a, b, f, g) and *M. semiarmatus* (c–e, h, i) after protargol impregnation (from Vďačný & Foissner 2008b). **a, c** – lateral views of representative specimens, showing the slender body and the short proboscis above the oral bulge opening (arrows); **b** – ventrolateral view of ciliary pattern of proboscis. Note the very small oral opening, a main feature of the species and genus; **d, e** – dorsal and dorsolateral ciliary pattern of proboscis. The dorsal brush is heteromorphic in posterior third, where bristles are mixed with ordinary cilia (arrowheads). Arrow denotes brush row 1, which commences slightly more subapically than row 2; **f** – dorsal ciliary pattern of proboscis. The dorsal brush consists of two staggered rows, that is, row 1 commences slightly more subapically than row 2 (arrowhead). Note the long dorsal bristles (arrow); **g** – the nuclear apparatus consists of two clavate to oblong macronuclear nodules and a single micronucleus in between; **h, i** – ventral and ventrolateral oral ciliary pattern. The circumoral and perioral kinetids are very widely spaced in the proboscis, while very narrowly around the minute oral bulge opening. B1, 2 – dorsal brush rows, CK – circumoral kinety, MA – macronuclear nodules, MI – micronucleus, PE – perioral kinety, PR – preoral kineties, OO – oral bulge opening. Scale bars: 10 µm (e–i), 20 µm (b, d), and 30 µm (a, c).

Family Dileptidae Jankowski, 1980

1978 Dileptidae Jankowski, Morfologiâ, sistematika i èvolûciâ životnyh: 89 (a nomen nudum due to lack of description or definition)

1980 Dileptidae fam. nov. Jankowski, Trudy zool. Inst., Leningr. **94**: 120 (very brief characterization)

2011 Dileptidae Jankowski, 1980 – Vďačný, Orsi, Bourland, Shimano, Epstein & Foissner, Eur. J. Protistol. **47**: 310 (improved diagnosis)

Diagnosis: Dileptida with macronucleus in at least four moniliform or scattered nodules. Dorsal brush typically composed of more than three rows, rarely of one or two rows. Oral apparatus dileptid or paradileptid.

Type genus (by original designation): *Dileptus* Dujardin, 1841.

Remarks: Jankowski (1980) briefly diagnosed the family as follows: "with agile proboscis different from that of tracheliids". Vďačný et al. (2011b) used the macronuclear pattern, the dorsal brush, and the oral apparatus as diagnostic features. In knowledge of this monograph, the Dileptidae comprise two groups of genera. The first group includes *Dileptus* and *Apodileptus*, which have many macronuclear nodules scattered throughout the cytoplasm, but differ in the macronuclear division mode. In *Dileptus*, each nodule divides individually, while in *Apodileptus* the nodules fuse in mid-dividers and the multinucleate condition is obtained via an extensive reticulum that breaks into nodules post-divisionally.

The second group comprises four genera that share a moniliform macronucleus: *Monilicaryon*, *Pseudomonilicaryon*, *Paradileptus*, and *Pelagodileptus*. The first two genera have a dileptid oral ciliary pattern: the right branch of the circumoral kinety is accompanied by a single perioral kinety and the left branch by many slightly to strongly oblique preoral kineties, which became linearly arranged in *Monilicaryon*, producing a perioral-like kinety, as independently discovered by Dragesco (1972b) and Foissner (1997a). *Paradileptus* and *Pelagodileptus*, have a paradileptid oral ciliary pattern, i.e., the right branch of the circumoral kinety is accompanied by two perioral kineties and the left branch by many slightly oblique preoral kineties.

Key to Genera

Proper generic classification requires knowledge of the macronuclear division mode and details of the dorsal brush and oral ciliary pattern. Based on the macronuclear pattern, there are two groups of genera: one with many scattered nodules and another with a moniliform strand. Life observation keys to the species of these two groups are provided below.

1 Macronucleus in many nodules scattered throughout cytoplasm 2
– Macronucleus a moniliform strand composed of at least four nodules 3
2 Macronuclear nodules divide individually during ontogenesis ..... *Dileptus* (p. 265)
– Macronuclear nodules fuse into a mass during ontogenesis ..... *Apodileptus* (p. 323)
3 One perioral kinety right of oral bulge. Limnetic bottom dwellers or terricolous 4
– Two perioral kineties right of oral bulge. Planktonic 5
4 Preoral kineties linearly arranged to form a perioral-like kinety, dorsal brush as a single staggered row ..... *Monilicaryon* (p. 343)
– Preoral kineties slightly to strongly oblique, at least two staggered brush rows ..... *Pseudomonilicaryon* (p. 350)
5 Oral bulge opening paradileptid, i.e., located laterally, roundish and inverted ..... *Paradileptus* (p. 437)

– Oral bulge opening dileptid, i.e., located ventrally and very narrowly elliptical .... *Pelagodileptus* (p. 451)

Key to Dileptids with Many Scattered Macronuclear Nodules

The sole feature distinguishing *Dileptus* and *Apodileptus* is the division mode of the macronucleus (see above). Thus, we prepared the key with other features recognizable also in live interphase specimens.

1 With zoochlorellae (grass green colour) 2
– Without zoochlorellae 3
2 Proboscis occupies 1/4 of body length, posterior end tail-like; body about 245 µm long..... ..... *D. viridis* (p. 267)
– Proboscis occupies 1/2 of body length, posterior end rounded; body about 115 µm long..... ..... *D. dubius* (p. 268)
3 Ventral and dorsal contractile vacuoles 4
– Only dorsal contractile vacuoles 6
4 Proboscis occupies 1/5 of body length, extrusomes acicular and 20 µm long; body length about 450 µm ..... *D. sphagnicola* (p. 269)
– Proboscis occupies 1/3 to 1/2 of body length, extrusomes rod-shaped or very narrowly ovate and up to 10 µm long; body length about 300 µm or 1000 µm 5
5 Extrusomes clavate, anchored both in proboscis oral bulge and oral bulge opening; body about 280 µm long ..... *D. costaricanus* (p. 277)
– Extrusomes rod-shaped, anchored only in proboscis oral bulge; body about 1000 µm long ..... *D. anatinus* (p. 281)
6 Two dorsal contractile vacuoles; body about 185 µm long ..... *D. multinucleatus* (p. 290)
– A dorsal stripe of > 5 contractile vacuoles (see also Table 50) 7
7 Proboscis occupies 1/5 of body length; brackwater; body about 950 µm long..... ..... *D. estuarinus* (p. 290)
– Proboscis occupies 1/3 to 1/2 of body length; limnetic or terrestrial; body usually < 700 µm long 8
8 Extrusomes rod-shaped 9
– Extrusomes narrowly ovate 12
9 About 50 ciliary rows; body about 400 µm long ..... *D. margaritifer* (p. 292)
– Less or about 30 ciliary rows 10
10 Body rod-shaped, body about 470 µm long ..... *A. edaphicus* (p. 339)
– Body usually very narrowly dileptid 11
11 Producing a mucous secretion or thread serving as an anchor; body about 450 µm long..... ..... *D. jonesi* (p. 314)
– Not forming a mucous thread; body about 250 µm long ..... *A. visscheri rhabdoplites* (p. 334)
12 Less or about 100 macronuclear nodules, about 25 ciliary rows; body about 280 µm long..... ..... *A. visscheri visscheri* (p. 324)
– More than 100 (200–500) macronuclear nodules, about 50 ciliary rows; body about 670 µm long... .....*D. beersi* (p. 317)

Key to Dileptids with Moniliform Macronucleus

The key is intended for the identification of live specimens. In the last two species, determination should be checked in protargol preparations because they differ, especially, by the dorsal brush and preoral kinety pattern.

1 Planktonic 2
– Marine and/or halophilous 3
– Freshwater (not planktonic, i.e., in benthos or periphyton), semiterrestrial, and/or terrestrial 5
2 With zoochlorellae (grass green colour); body usually 300–600 µm long ..... *Pelagodileptus trachelioides* (p. 452)
– Without zoochlorellae; body usually 100–450 µm long ..... *Paradileptus elephantinus* (p. 438)
3 Proboscis occupies 1/3–1/2 of body length, posterior region acute or with short tail; body usually > 700 µm long ..... *Pseudomonilicaryon massutii* (p. 350)
– Proboscis occupies 1/5–1/3 of body length, posterior end with long, spine-like tail; body usually < 700 µm long 4
4 Body length 450–700 µm ..... *Pseudomonilicaryon marinum marinum* (p. 357)
– Body length about 200 µm ..... *Pseudomonilicaryon marinum minimum* (p. 359)
5 Proboscis very conspicuous occupying half or more of body length and helically rolling up when disturbed 6
– Proboscis occupies less than half of body length 7
6 Only dorsal contractile vacuoles, 50–70 ciliary rows; body about 500 µm long ..... *Pseudomonilicaryon anser* (p. 359)
– Ventral and dorsal contractile vacuoles, 70–90 ciliary rows; body about 600 µm long ..... *Pseudomonilicaryon fraterculum* (p. 371)
7 Four macronuclear nodules 8
– More than five nodules 10
8 Distinctly but slowly contractile; body about 300 µm long ..... *Pseudomonilicaryon dimorphum* (p. 384)
– Not contractile 9
9 Posterior end with long, spine-like tail, only dorsal contractile vacuoles; body about 300 µm long.. ..... *Pseudomonilicaryon aculeatum* (p. 387)
– Posterior region acute, never tail-like, ventral and dorsal contractile vacuoles; body about 250 µm long ..... *Pseudomonilicaryon edaphoni* (p. 377)
10 Extrusomes anchored both in proboscis oral bulge and oral bulge opening; body about 350 µm .... long ..... *Pseudomonilicaryon falciforme* (p. 388)
– Extrusomes anchored only in proboscis oral bulge 11
11 Two dorsal contractile vacuoles 12
– At least 3 dorsal contractile vacuoles, in some species also ventral vacuoles 15
12 Anterior contractile vacuole far underneath oral bulge opening 13
– Anterior contractile vacuole at level of oral bulge opening 14
13 Posterior end rounded; body about 110 µm long ..... *Pseudomonilicaryon gracile gracile* (p. 396)
– Posterior region acute or tail-like; body about 140 µm long ..... *Pseudomonilicaryon gracile singulare* (p. 396)
14 Extrusomes rod-shaped; body about 150 µm long ..... *Pseudomonilicaryon gracile antevacuolatum* (p. 397)
– Extrusomes very narrowly ovate; body about 230 µm long ..... *Pseudomonilicaryon gracile oviplites* (p. 399)
15 Body length < 400 µm 16
– Body length > 400 µm 18
16 Proboscis occupies 1/3 of body length, about 20 ciliary rows; body about 270 µm long ..... *Pseudomonilicaryon thononense* (p. 404)

– Proboscis occupies 1/5 of body length, about 10 ciliary rows 17
17 Extrusomes oblong and massive; body about 140 µm long ..... *Pseudomonilicaryon brachyproboscis* (p. 408)
– Extrusomes rod-shaped and thin; body about 140 µm long ..... *Pseudomonilicaryon anguillula* (p. 413)
18 Oral bulge opening elliptical, *Dimacrocaryon*-like; body about 400 µm long..... *Pseudomonilicaryon angustistoma* (p. 418)
– Oral bulge opening roundish 19
19 Ventral and dorsal contractile vacuoles (ventral vacuoles sparse!); body about 400 µm long..... *Pseudomonilicaryon japonicum* (p. 426)
– Only dorsal contractile vacuoles 20
20 One dorsal brush row, preoral kineties form a perioral-like row; body about 600 µm long ..... *Monilicaryon monilatum** (p. 343)
– Three brush rows, preoral kineties distinctly separated, each composed of 3 cilia; body about 700 µm long ..... *Pseudomonilicaryon kahli** (p. 433)

* Identification requires silver impregnation for analysing the dorsal brush and the oral ciliary pattern.

Dileptus Dujardin, 1841

1840 *Dileptus* Dujardin, C. r. hebd. Séanc. Acad. Sci., Paris **11**: 285 (a nomen nudum because without description or definition)

1841 *Dileptus* Dujardin, Zoophytes: 404

1853 *Liosiphon* Ehrenberg, Monatsber. Berliner Akad. Wiss. **1853**: 186 [cited by Jankowski (2007) as supposed synonym of *Dileptus*. However, Ehrenberg's (1853) description of *L. strampfii*, type species of the genus, shows that it is a limnetic nassulid or colpodid.]

1865 *Dileptus* – Diesing, Sber. Akad. Wiss. Wien **52**: 508 (taxonomic revision)

1875 *Dileptus* – Fromentel, Études Microzoaires: 176 (fixation of type species: *Dileptus folium*)

1884 *Phragelliorhynchus* Herrick, Science **4**: 73 [cited by Bütschli (1889), Kahl (1931), Aescht (2001), and Jankowski (2007) as synonym of *Dileptus*. Should be considered as indeterminable because too briefly described without figure.]

1889 *Dileptus* (Dujard. 1841) – Bütschli, Protozoa: 1693 (brief review)

1895 *Dileptus* Duj. – Blochmann, Mikroskopische Thierwelt: 93 (brief review)

1896 *Dileptus* Duj. – Schewiakoff, Zap. imp. Akad. Nauk **4**: 219 (taxonomic revision)

1901 *Dileptus* Duj. – Roux, Mém. Inst. natn. génev. **19**: 41 (brief review)

1911 *Dileptus* (Duj. 1841) emend. Wrzesn. 1870 – Hamburger & Buddenbrock, Nord. Plankt. **7**: 34 (brief review)

1931 *Dileptus* Dujardin, 1841 – Kahl, Tierwelt Dtl. **21**: 204 [first authoritative taxonomic revision; type species (?): *Dileptus anser* (Mueller) Dujardin]

1936 *Dileptus* (Dujardin, 1841), emend. Wrzesniowski, 1870 – Bhatia, Fauna of British India: 115 (brief review)

1963 *Dileptus* Dujardin, 1841 – Dragesco, Bull. biol. Fr. Belg. **97**: 103 [second authoritative taxonomic revision; type species: *Dileptus anser* (O. F. Mueller, 1786)]

1967 *Dileptus* Duj., 1840 – Jankowski, Mater. IV Konf. uč. Sekc. zool. year **1967**: 36 [split of genus; type species: *Dileptus anser* (Müll., 1786)]

1979 *Dileptus* Dujardin, 1841 – Corliss, Ciliated protozoa: 216 (characterization, classification)

1980 *Dileptus* Dujardin 1840 – Jankowski, Trudy zool. Inst., Leningr. **94**: 120 (misdated)

2001 *Dileptus* Dujardin 1841 – Aescht, Denisia **1**: 59 (catalogue of generic names of ciliates)

2007 *Dileptus* Dujardin, 1841 – Jankowski, Protista II: 570 (brief generic review)

2008 *Dileptus* Dujardin, 1841 – Lynn, Ciliated protozoa: 371 (list of genera)

Nomenclature: Dujardin (1841) established the genus *Dileptus* with three nominal species: *Dileptus anser* (a misidentified *D. margaritifer*), *D. folium* (now *Litonotus cygnus*), and "*Dileptus* (*Amphileptus margaritifer*, Ehr. Infus. Pl XXXVII, fig. 5: 355)", adopting the description from Ehrenberg (1838). He did not fix a type species. This was done by Fromentel (1875), using *D. folium*. Kahl (1931) overlooked Fromentel's typification and synonymized *D. folium* with *Litonotus cygnus*. Further, in his characterization of *Dileptus* on page 205, Kahl (1931) stated "typical species: *D. anser*". Dragesco (1963) and Jankowski (1967) followed. However, under the Code, *D. anser* cannot be considered as type species of *Dileptus* because (i) the first author who subsequently designates one of the originally included nominal species validly designates the type species of that genus or subgenus (type by subsequent designation), and no later designation is valid (Article 69.1 of the ICZN 1999), and (ii) the term "designation" in relation to fixation of a type species [Arts. 68, 69] must be rigidly construed (Article 67.5 of the ICZN 1999). Thus, *D. folium* is the validly fixed type species of *Dileptus*, according to Articles 67.1.2 and 69.1 of the ICZN (1999). Unfortunately, *D. folium* is a junior synonym of *Litonotus cygnus*, a pleurostomatid ciliate belonging now to a different subclass, Haptoria (Vďačný et al. 2011a). Thus, recognition of Fromentel's forgotten typification would cause changes in many well established ciliate names. Therefore, we shall bid the International Commission on Zoological Nomenclature to use its plenary power (i) to suppress Fromentel's (1875) typification of *Dileptus*, and (ii) to fix *D. margaritifer* as the type species of *Dileptus* because it is a well-known species (see description below), matching Jankowski's characterization of *Dileptus* and having slides deposited in an international repository.

Improved diagnosis: Medium- to large-sized Dileptidae with narrow to rod-like body. Many scattered macronuclear nodules dividing individually during ontogenesis. Dorsal brush multi-rowed. Right branch of circumoral kinety accompanied by a perioral kinety, left branch by many slightly to strongly oblique preoral kineties. Oral bulge opening dileptid, i.e., roundish or elliptical and located ventrally.

Type species (by subsequent designation): *Dileptus folium* Dujardin, 1841. However, *Amphileptus margaritifer* Ehrenberg, 1833 will be proposed to be fixed as the type species of *Dileptus* under the plenary power of the International Commission on Zoological Nomenclature (see discussion above).

Etymology: Not given in original description. Composite of the Greek numeral *di* (two) and the Greek adjective *leptos* (thin, slender), possibly referring to the two narrowed body ends. Masculine gender.

Remarks: In this monograph, *Dileptus* unites thirteen species and subspecies usually having more than 50 dispersed macronuclear nodules that divide individually. Although we "cleaned" the genus by transferring two species to *Apodileptus*, in which the macronuclear nodules fuse into a mass in mid-dividers, *Dileptus* still contains several organization types, for instance, a species with extrusomes anchored both in the oral bulge opening and the proboscis bulge (*D. costaricanus*); a species having a *Spathidium*-like appearance and anterior brush tails (*D. sphagnicola*); and a species forming a caudal thread to attach to the substrate (*D. jonesi*). On the other hand, most *Dileptus* species share a combination of distinct features some of which are found, however, also in other large dileptids: (i) the right side ciliary rows are shortened only in the anterior portion of the proboscis, (ii) the dorsal brush is multi-rowed, and (iii) the resting cysts are globular with the wall composed of a rather thick, hyaline external layer and a thin, honey brown internal layer, providing the cysts with a characteristic colour.

Dileptus viridis (Ehrenberg, 1833) Foissner, 1987 (Figs 84a–d)

1833 *Amphileptus viridis* n. sp. Ehrenberg, Abh. dt. Akad. Wiss. Berl. year **1833**: 229 (without figure)

1838 *Amphileptus viridis* – Ehrenberg, Infusionsthierchen: 356 (taxonomic revision)

1841 *Amphileptus viridis* Ehr. – Dujardin, Zoophytes: 485 (brief review; without figure)

1876 *Amphileptus viridis* – Fromentel, Études Microzoaires: 287 (supposed synonym)

1987 *Dileptus viridis* (Ehrenberg, 1833) nov. comb. – Foissner, Arch. Protistenk. **133**: 224 (combining author)

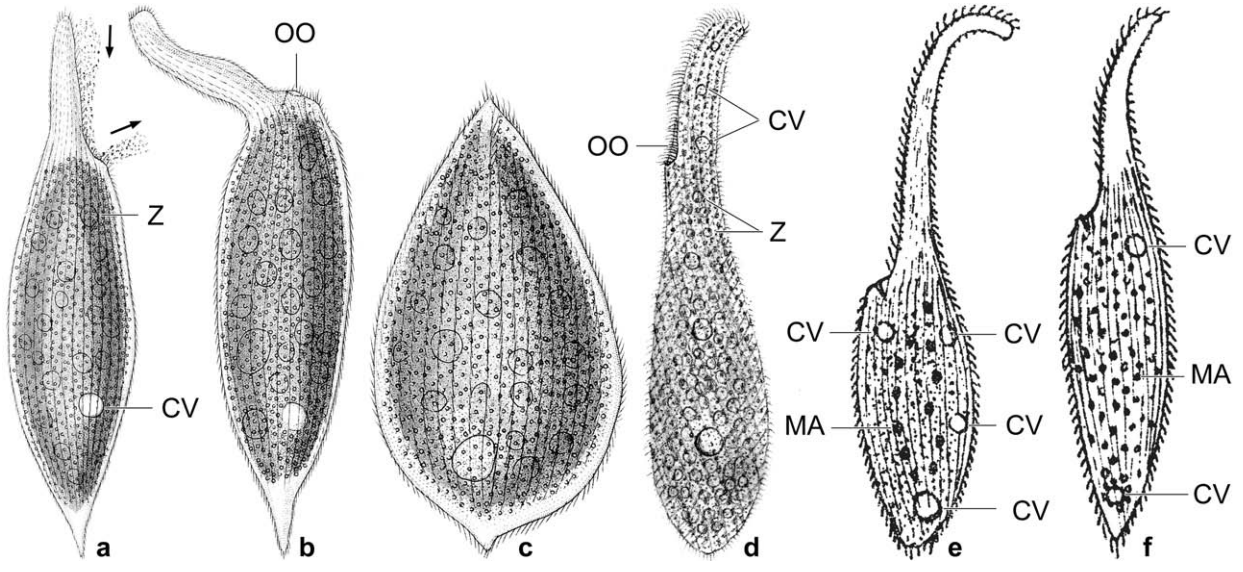
Diagnosis (type population): Length about 245 µm in vivo. Shape narrowly dileptid with short tail, proboscis about 1/4 of body length. Possibly several scattered macronuclear nodules. A single contractile vacuole subterminal on ventral side of cell. With symbiotic green algae (zoochlorellae). About 30–40 ciliary rows.

Type locality: Pond in the Zoological Garden of Berlin, Germany, E13°19' N52°30'.

Type material: Not available.

Etymology: The Latin adjective *viridis* refers to the green colour of the species due to the symbiotic algae.

Description (type population): Length about 220–270 µm in vivo. Shape narrowly dileptid with a length:width ratio of 4.5:1, according to the figures provided. Proboscis comparatively massive (three times longer than wide), about one fourth of body length, distinctly set off from oblong to bluntly fusiform trunk; posterior end with short tail. Many rather large globules scattered throughout trunk, possibly macronuclear nodules and/or food vacuoles. A single contractile vacuole described by Ehrenberg (1838) as "a bright, contractile blister in rear body region". Extrusomes not studied. Cytoplasm opaque and green in trunk due to many globular symbiotic green algae about 2.5 µm in diameter, while hyaline and



Figs 84a, b: *Dileptus viridis* from life, length about 245 µm (from Ehrenberg 1838). Arrows show the water current generated by the oral ciliature. **c: –** "Retracted" state of the specimen shown in (a, b). In our opinion, the specimen lost the proboscis, as is frequent in *Dileptus*. **d: –** *Amphileptus viridis* from life, length 300 µm (from Fromentel 1876). **e: –** *Dileptus dubius* from life, length 116 µm (from Vuxanovici 1959). **f: –** *Dileptus multinucleatus* from life, length 185 µm (from Vuxanovici 1959). CV – contractile vacuoles, MA – macronuclear nodules, OO – oral bulge opening, Z – zoochlorellae.

colourless in proboscis and tail where zoochlorellae are absent. Creeps and swims slowly by rotating about main body axis. EHRENBERG (1838) mentioned 15–20 ciliary rows on one side of cell (Figs 84a–c).

Notes on supposed synonym: FROMENTEL's population resembles EHRENBERG's species in having symbiotic green algae and a short, massive proboscis, but differs by the dorsal row of contractile vacuoles (vs. a single subterminal vacuole) and the rounded posterior body end (vs. tail-like). Thus, FROMENTEL's population possibly represents a distinct species (Fig. 84d).

Occurrence and ecology: As yet found only at type locality, i.e., in a small pond among *Lemna minor*.

Remarks: Within the multinucleate dileptids, *D. viridis* is almost unique in having symbiotic green algae, like *D. dubius*. However, *D. dubius* has a shorter body (116 µm vs. 220–270 µm) with longer proboscis (occupying 1/2 vs. 1/3 of body length) and a rounded posterior end (vs. short tail). The single contractile vacuole, which EHRENBERG (1838) definitely mentioned, is possibly a misobservation. Full redescription is required before *D. viridis* can be considered as a valid species.

Dileptus dubius VUXANOVICI, 1959 (Fig. 84e)

1959 *Dileptus dubius* n. sp. VUXANOVICI, Studii Cerc. Biol. **11**: 329

1963 *Dileptus dubius* VUXANOVICI, 1959 – DRAGESCO, Bull. biol. Fr. Belg. **97**: 127 (first taxonomic reviser)

Diagnosis: Length about 116 µm in vivo. Shape narrowly dileptid with rounded posterior end, proboscis about 1/2 of body length. Many (several?) elliptically arranged macronuclear nodules. One contractile vacuole underneath oral bulge opening and three vacuoles in dorsal side of trunk. With symbiotic green algae (zoochlorellae). About 24 ciliary rows.

Type locality: Coast of Lake Herăstrău, Bucharest, Roumania, E26°05' N44°28'.

Type material: Not available.

Etymology: Not given in original description. The Latin adjective *dubius* (doubtful) refers to VUXANOVICI's doubts about the validity of the species.

Description: VUXANOVICI's description is based on a single specimen. Length 116 µm in vivo; slightly contractile. Shape narrowly dileptid with a length:width ratio of 5:1, according to the figure provided. Proboscis about one half of body length, distinctly set off from trunk, 7 µm wide at base and 4 µm at tip, anterior portion curved dorsally, slightly flattened, moves to and fro like a flagellum; trunk bluntly fusiform; posterior end rounded. Many (several?) elliptically arranged macronuclear nodules, individual nodules oblong and only 1.5–1.8 µm long. Micronuclei not studied. Contractile vacuole pattern extraordinary, that is, one vacuole posterior to oral bulge opening and three vacuoles in dorsal side of trunk, first dorsal vacuole at level of ventral one. Extrusomes attached to proboscis oral bulge, short and fine. Cytoplasm transparent, green due to many minute globular algae (zoochlorellae), at high magnification (×600) hyaline in proboscis, while opaque in trunk due to numerous granules. About 12 meridionally arranged ciliary rows on one side of cell; brush bristles about 2 µm long. Oral basket short and fine (Fig. 84e).

Occurrence and ecology: As yet found only at type locality in a sample containing swamp plants. Only one specimen was observed in February 1958.

Remarks: The validity of this species may be questioned because the single specimen observed shows several features whose combination is a property of proter post-dividers, viz., the rounded posterior end and the comparatively short and stout body with the proboscis occupying about half of body length. Thus, we cannot exclude that *D. dubius* is a junior synonym of *D. viridis*. VUXANOVICI (1959) mentioned that *D. dubius* resembles *Pseudomonilicaryon falciforme* which, however, lacks symbiotic algae and has a dorsal row of contractile vacuoles commencing in mid-proboscis (vs. one ventral vacuole and three dorsal vacuoles, the first at level of oral bulge opening). Full redescription is required.

Dileptus sphagnicola nov. sp. (Figs 85a–r, 86a–w; Tables 46, 47)

Diagnosis: Size about 450 × 70 µm in vivo. Shape narrowly to very narrowly dileptid with acute posterior end or a short tail, proboscis rostrate and about 1/5 of body length. Many scattered macronuclear nodules and several globular micronuclei. A dorsal and a ventral stripe of contractile vacuoles with 1 pore each. Two types of extrusomes attached to right branch of proboscis oral bulge: type I acicular, 20 × 1.2 µm in size; type II slightly fusiform, 4–5 × 0.3 µm in size. On average 40 ciliary rows, up to 8 anteriorly differentiated into a staggered, distinctly heterostichad dorsal brush with monokinetidal tails extending anteriorly and posteriorly. Oral bulge opening elliptical, about 25 µm long. Preoral kineties oblique to slightly oblique, narrowly spaced, each usually composed of 3 narrowly spaced cilia.

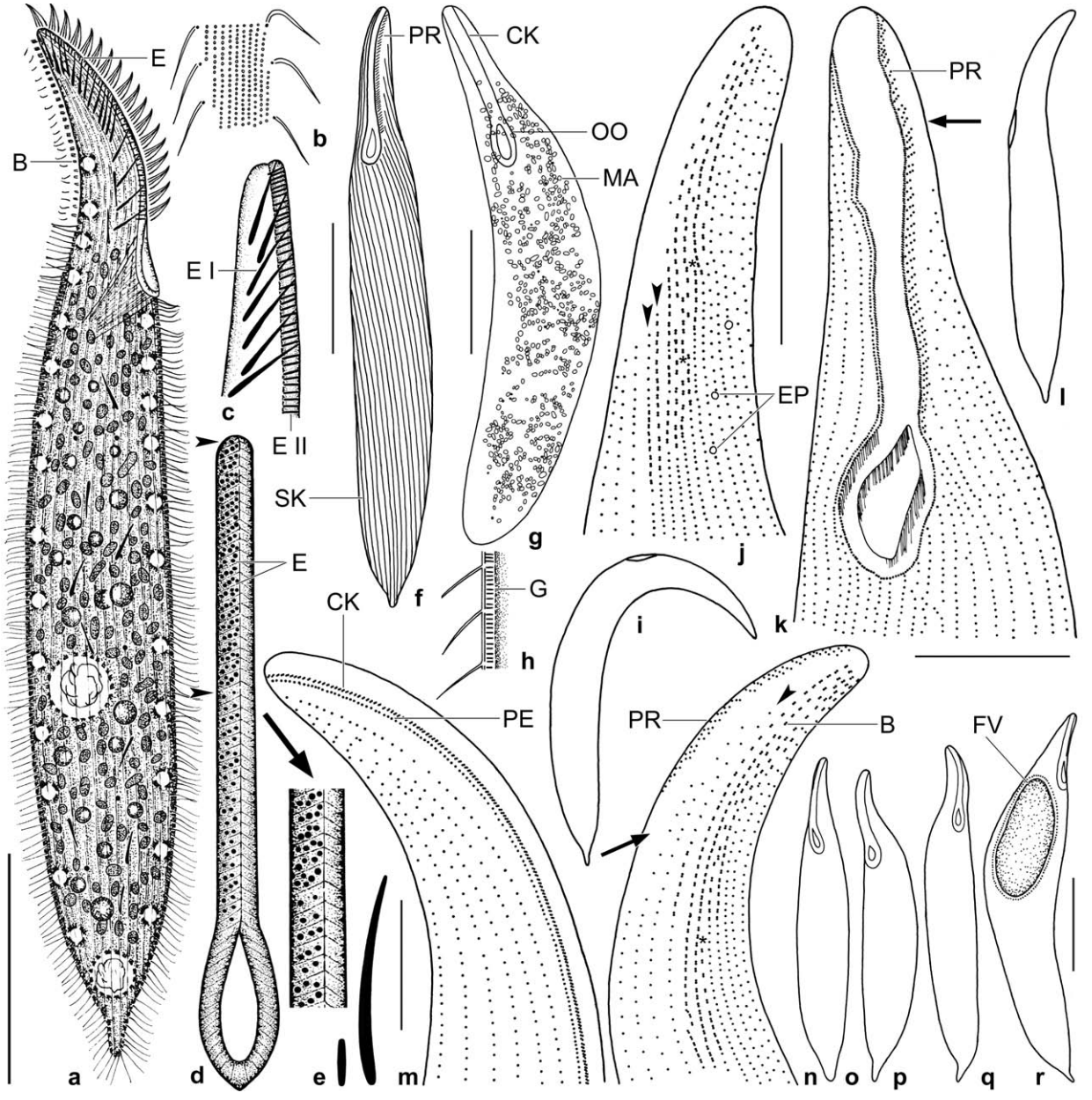
Type locality: Simmelried mire near the village of Hegne, surroundings of the town of Constance, Germany, E09°05' N47°42'.

Type material: One holotype slide (inv. no. 2011/301) and seventeen paratype slides (inv. nos 2011/302–318) with protargol-impregnated specimens have been deposited in the Biology Centre of the Museum of Upper Austria, Linz (LI). Relevant specimens are marked by black ink circles on the coverslip.

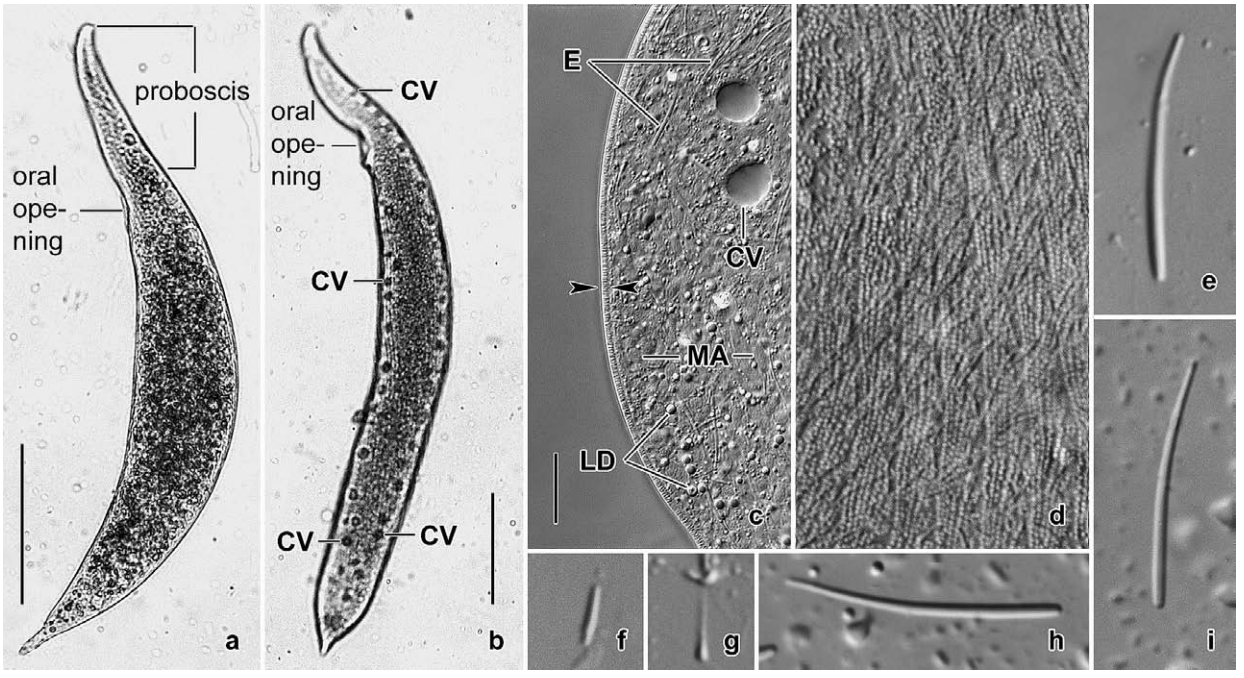
Etymology: The Latin *sphagnicola* (living in *Sphagnum*) refers to the habitat in which the species was discovered.

Description: *Dileptus sphagnicola*, an outstanding, massive species, is easily recognizable in vivo due to the large, comparatively stout body; the short, broad proboscis; the many macronuclear nodules; the ventral and dorsal stripe of contractile vacuoles; and the 20 µm long, acicular extrusomes (Figs 86a, b, c, e, h, i). This is fortunate because it is difficult to fix and to impregnate with protargol, making morphometry and observation of the ciliary pattern difficult. The latter problems were solved by using various fixatives and scanning electron microscopy. The description is based on specimens from a semi-pure culture, where *D. sphagnicola* reached considerable abundance at several small sites.

Size 350–650 × 55–90 µm in vivo, usually about 450 × 70 µm, as calculated from some in vivo measurements and the morphometric data, showing 20–40% preparation shrinkage (see above and Table 47); very flexible but not contractile. Shape narrowly to very narrowly dileptid, length:width ratio near 6:1 both in vivo and in good preparations; anterior end bluntly pointed, posterior region gradually narrowed to an acute end in about half of specimens, while tail-like set off from trunk in the other half. Proboscis rostrate, short and stout, occupies merely one fifth of body length; indistinctly set off from trunk and thus providing cells with a spathidiid appearance, flattened only in distal half. Trunk cylindroidal to bluntly fusiform, not flattened (Figs 85a, f, g, i, l, n–r, 86a, b, j–m, s; Tables 46, 47). Nuclear apparatus in trunk and proximal proboscis half, absent from tail. About 300 scattered macronuclear nodules giving cytoplasm a smooth, opaque appearance; individual nodules globular to very narrowly ellipsoidal or, rarely, dumbbell-shaped, about 4 × 2.5 µm in size; divide individually; usually one to two minute nucleoli in centre of each nodule. About 11 micronuclei scattered between or attached to macronuclear nodules, 2 µm across in protargol preparations (Figs 85a, g, 86c; Table 46). A stripe of contractile vacuoles each in ventral and dorsal side of cell, first dorsal vacuole in mid-proboscis; invariably a single intrakinetal excretory pore per vacuole (Figs 85a, j, 86b, j, k, m, v). Two types of extrusomes, not impregnating with protargol, in cytoplasm and attached to right broader branch of oral bulge conspicuously concentrated in its anterior half: type I obliquely attached, acicular, 20–22 × 1.2 µm in size, certain cytoplasmic developmental stages (16 µm long wrinkled rods) impregnate with protargol; type II perpendicularly attached, slightly fusiform, 4–5 × 0.3 µm in size, much more numerous than type I (Figs 85a, c–e, 86c, e–i). Cortex flexible, about 1.5 µm thick and distinctly separate from cytoplasm, contains about ten rows of rod-shaped, very narrowly spaced granules about 1.5 × 0.2 µm in size between each two kineties (Figs 85b, h, 86c, d). Cytoplasm



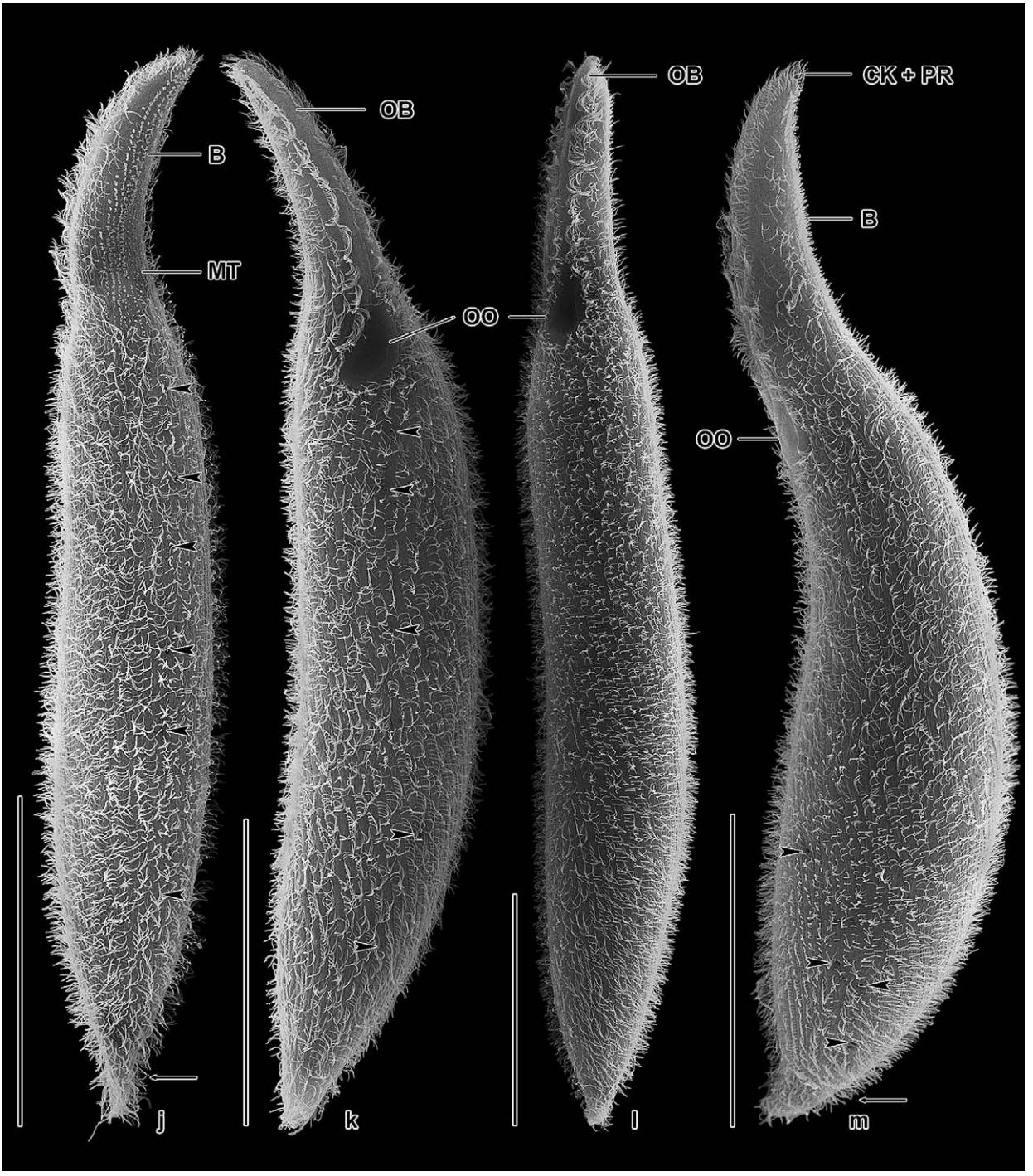
Figs 85a–r: *Dileptus sphagnicola* nov. sp. from life (a–e, h, i, l) and after protargol impregnation (g, j, k, m–r). **a** – right side view of a representative specimen, length 450 µm; **b, h** – surface view and optical section showing innumerable granules embedded in the about 1.5 µm thick cortex; **c** – lateral view of anterior half of proboscis where both types of extrusomes are conspicuously concentrated; **d** – frontal view of oral bulge and oral bulge opening. Arrowheads denote extrusomes concentrated in right anterior branch of bulge; **e** – two types of oral bulge extrusomes: type I acicular and 20 × 1.2 µm in size, type II slightly fusiform and 4–5 × 0.3 µm in size; **f** – scheme of ciliary pattern of ventral side (drawn from a SEM micrograph); **g** – nuclear pattern of holotype specimen, length 450 µm; **i, l** – a curved and a straight specimen; **j** – ciliary pattern of dorsal side of proboscis of holotype specimen. Arrowheads denote the anterior monokinetidal tail of brush rows 1 and 2. Asterisks mark brush irregularities; **k** – ciliary pattern of ventral side of holotype specimen. Arrow marks the comparatively short, narrow blank stripe left of the oral bulge; **m, n** – ciliary pattern of right and left side of proboscis. Arrowhead denotes the long anterior monokinetidal tail of brush row 1; arrow indicates narrow blank stripe; asterisk marks a shortened brush row; **o–r** – variability of body shape and size. Drawn to scale. B – dorsal brush, CK – circumoral kinety, E(I, II) – extrusome (types), EP – excretory pores, FV – food vacuole, G – cortical granules, MA – macronuclear nodules, OO – oral bulge opening, PE – perioral kinety, PR – preoral kineties, SK – somatic kineties. Scale bars: 20 µm (j, k, m, n), 50 µm (g), and 100 µm (a, f, o–r).



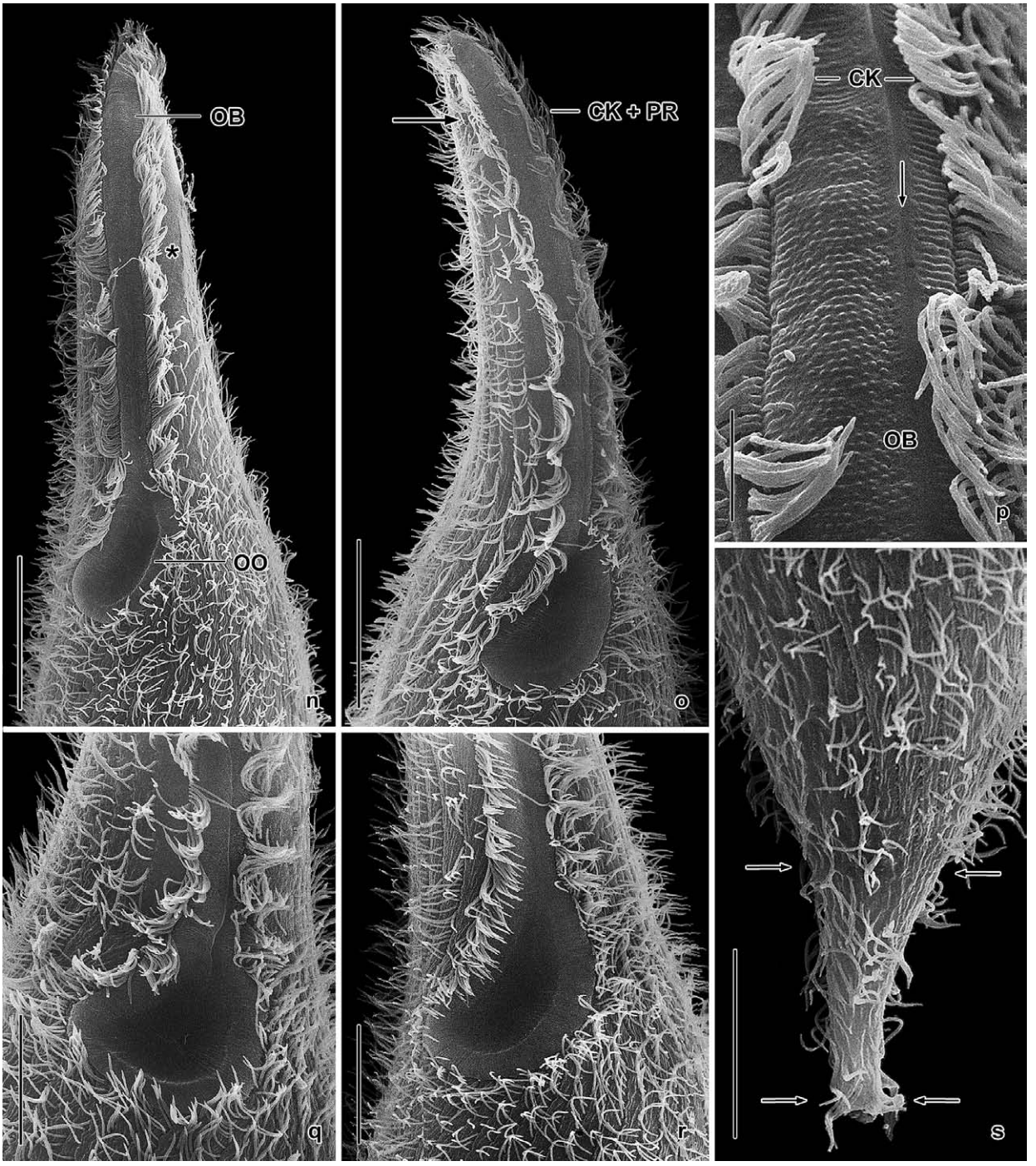
Figs 86a–i: *Dileptus sphagnicola* nov. sp. from life. **a, b** – lateral view of a stout and a slender specimen, showing the short proboscis and the stripe of contractile vacuoles each in ventral and dorsal side of cell; **c** – optical section showing the rather thick cortex (marked by opposed arrowheads) and some main cell organelles (macronuclear nodules, contractile vacuoles, lipid droplets, and extrusomes); **d** – the cortex is studded with densely spaced granules about 1.5 × 0.2 µm in size; **e, h, i** – type I extrusomes are acicular and about 20 × 1.2 µm in size; **f** – type II extrusomes are slightly fusiform and 4–5 × 0.3 µm in size; **g** – exploded type II toxicyst with some toxin remaining in the capsule. CV – contractile vacuoles, E – extrusomes, LD – lipid droplets, MA – macronuclear nodules. Scale bars: 20 µm (c) and 100 µm (a, b).

colourless, at low magnification (×40) bright to dark brown, depending on nutrition, sometimes green due to prey zoochlorellae; hyaline in proboscis and rear body end, opaque in trunk due to many macronuclear nodules, numerous food vacuoles, and lipid droplets 1–13 µm across; near posterior end sometimes a brownish faecal mass (Figs 86a, b). Sits almost motionless in masses of organic debris, when disturbed swims slowly but soon goes down to the bottom of the Petri dish gliding rather rapidly to and fro.

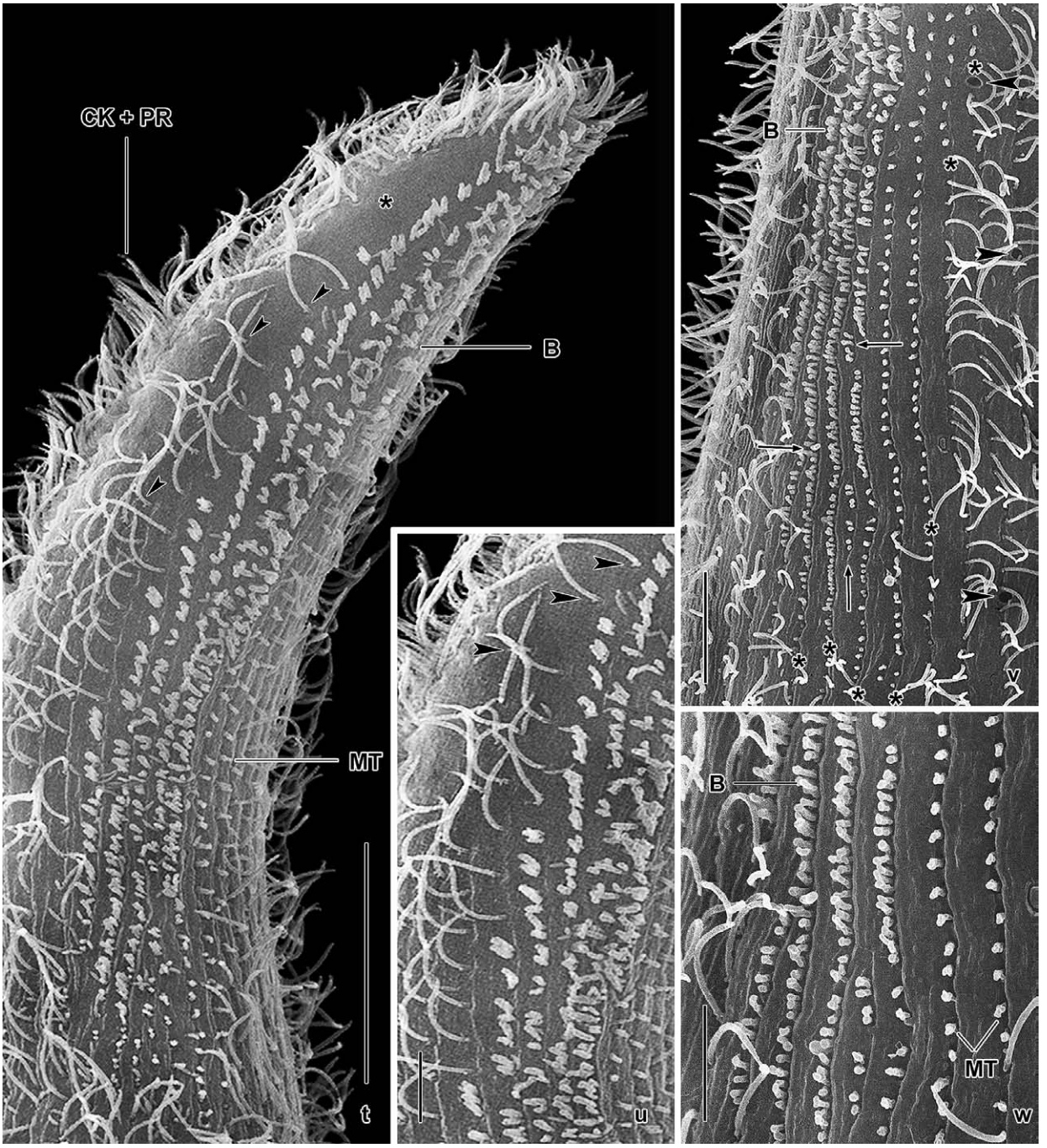
Cilia about 9 µm long in vivo, narrowly spaced; with same impregnation properties as in congeners; arranged in an average of 40 ordinarily spaced rows extending meridionally to rather distinctly helically (Figs 85f, 86j–m; Table 46); frequently with irregularities, e.g., some rows shortened anteriorly or posteriorly, and/or with short breaks (Fig. 85k). Right side ciliary rows gradually shortened only near anterior end of oral bulge, a feature difficult to recognize (Figs 85j–m, 86o). First row right of circumoral kinety extends as perioral kinety with narrowly spaced cilia to tip of proboscis (Figs 85k, m). Blank stripe on left side of proboscis comparatively short and narrow because some ciliary rows extend above proximal half of proboscis (Figs 85k, n, 86j, m, n, t). Dorsal brush a triangular field extending on dorsal and left side of proboscis; staggered; distinctly heterostichad; composed of an average of 7 (6–8) rows with loosely to ordinarily spaced dikinetids associated with 3 µm long, slightly inflated type II bristles; frequently with irregularities, such as breaks or some extra dikinetids forming a short additional row (Figs 85j, n, 86t–w; Table 46). Some ventralmost brush rows (1–3) commence in distal proboscis third with a monokinetidal tail of one to ten ordinary cilia, while the more dorsally located rows 4–7 (8) begin, as usual, with dikinetidal bristles (Figs 86t, u). Posteriorly, all rows continue with 2 µm long type VI bristles



Figs 86j–m: *Dileptus sphagnicola* nov. sp. in the SEM. Left side (j, m) and ventrolateral (k, l) overviews, showing body shape variability. The proboscis is short and comparatively stout, indistinctly set off from the oblong to bluntly fusiform trunk, thus providing cells with an *Arcuospathidium*-like appearance. The posterior region is gradually narrowed to an acute end in about half of specimens (k, l), while tail-like set off from trunk in the other half (j, m, arrows). Arrowheads denote excretory pores of contractile vacuoles on ventral and dorsal side, an important feature because most congeners have only a dorsal stripe of vacuoles. B – dorsal brush, CK – circumoral kinety, MT – monokinetidal tails of dorsal brush, OB – oral bulge, OO – oral bulge opening, PR – preoral kineties. Scale bars: 100 µm.



Figs 86n–s: *Dileptus sphagnicola* nov. sp. in the SEM. **n, o, q, r** – oral body portion, showing ciliature and shape variability of the oral bulge opening. Note the beautiful metachronal ciliary waves formed by the oral cilia, i.e., by the circumoral and perioral cilia right of the bulge, while by the circumoral and preoral cilia left of the bulge. Asterisk (n) denotes the short and narrow blank stripe on the left side of the proboscis. Arrow (o) marks a shortened ciliary row right of the oral bulge; **p** – the oral bulge is dotted by the extrusome tips and transversely striated by fibre bundles, very likely transverse microtubule ribbons. Arrow marks furrow separating the broader right from the much narrower left branch of the oral bulge; **s** – rear body end with short tail marked by opposed arrows. CK – circumoral kinety, OB – oral bulge, OO – oral bulge opening, PR – preoral kineties. Scale bars: 5 μm (p), 20 μm (q–s), and 30 μm (n, o).



Figs 86t–w: *Dileptus sphagnicola* nov. sp. in the SEM. **t, u** – dorsolateral view of proboscis. The dorsal brush is a triangular field composed of about eight staggered, distinctly heterostichad rows. Some right brush rows commence in the distal third of the proboscis with a monokinetidal tail of one to ten ordinary cilia (arrowheads), while the left rows begin, as usual, with dikinetidal bristles. Posteriorly, all rows continue with 2 μm long, oblong bristles forming monokinetidal tails ending at the base of the proboscis. Asterisk marks the short and narrow blank stripe between the preoral kineties and the dorsal brush; **v, w** – posterior brush portion showing ordinary cilia and two kinds of brush kinetids with very short bristles: dikinetids with paired, slightly inflated bristles and oblong bristles forming the monokinetidal tails (asterisks). Arrows mark some brush irregularities, such as breaks or short additional rows; arrowheads denote excretory pores of contractile vacuoles. B – dorsal brush, CK – circumoral kinety, MT – monokinetidal tails of dorsal brush, PR – preoral kineties. Scale bars: 5 μm (u, w), 10 μm (v), and 20 μm (t).

Table 46: Morphometric data on *Dileptus sphagnicola* nov. sp. Data based on mounted, protargol-impregnated (Foissner's method with Stieve fixation), and randomly selected specimens from a semi-pure culture. Measurements in µm. CV – coefficient of variation in %, M – median, Max – maximum, Mean – arithmetic mean, Min – minimum, n – number of specimens investigated, SD – standard deviation, SE – standard error of mean.

Characteristics	Mean	M	SD	SE	CV	Min	Max	n
Body, length	364.2	355.0	47.7	8.3	13.1	277.0	479.0	33
Body, width	60.8	60.0	8.2	1.4	13.5	43.0	80.0	33
Body length:width, ratio	6.1	6.2	1.3	0.2	21.7	3.9	11.1	33
Anterior body end to oral bulge opening, distance	65.4	66.0	10.6	2.3	16.1	50.0	82.0	21
Proboscis, % of body length	20.5	20.5	2.3	0.5	11.2	17.5	24.7	21
Oral bulge opening, length	24.2	23.0	3.8	0.8	15.8	19.0	31.0	21
Oral bulge opening, width	18.4	19.0	4.5	2.0	24.5	12.0	23.0	5
Anterior body end to first macronuclear nodule, distance	47.2	47.0	8.6	1.9	18.2	30.0	63.0	21
Nuclear figure, length	248.6	238.0	46.6	10.2	18.7	168.0	355.0	21
Macronuclear nodules, length	4.3	4.0	1.9	0.4	44.4	2.0	8.0	21
Macronuclear nodules, width	2.5	2.5	0.5	0.1	19.3	2.0	4.0	21
Macronuclear nodules, number (approximate)	290.7	300.0	–	–	–	160.0	438.0	21
Micronuclei, diameter	2.2	2.0	–	–	–	2.0	2.5	21
Micronuclei, number (approximate)	10.8	11.0	–	–	–	8.0	13.0	5
Ciliary rows, number	40.2	40.0	2.8	0.6	7.1	36.0	47.0	21
Cilia in mid-body in 10 µm, number	11.2	11.0	1.6	0.4	14.5	9.0	14.0	18
Dorsal brush rows, number	7.3	7.5	1.0	0.5	13.2	6.0	8.0	4

producing monokinetidal tails ending at level of oral bulge opening; tails of rows 6 and 7 (8) in some specimens extend only to mid-proboscis (Figs 86t–w).

Oral bulge opening at end of anterior body fifth, hardly projecting because base of proboscis almost as wide as trunk, elliptical to narrowly elliptical and about 25 µm long in vivo, while frequently broadly elliptical or ovate in protargol and SEM preparations, possibly due to shrinkage processes (Figs 85a, d, f, g, k, 86k–o, q, r; Table 46). Pharyngeal basket obconical, inconspicuous both in vivo and in protargol preparations due to comparatively short fibres impregnating only in distal portion (Fig. 85k). Oral bulge distinct due to nice metachronal ciliary waves (Figs 86n, o, q, r) and masses of short extrusomes in broader right branch, dotted by extrusome tips in SEM micrographs (Fig. 86p). Circumoral kinety composed of narrowly spaced dikinetids in proboscis and narrowly spaced monokinetids around oral bulge opening. About 50 oblique to slightly oblique, narrowly spaced preoral kineties, each composed of two to four, usually three narrowly spaced cilia (Fig. 85k).

Occurrence and ecology: As yet found only at type locality, i.e., in an about 70 cm wide hole filled with *Sphagnum* mud to a depth of over 2 m (for details, see Kreutz & Foissner 2006). A rich population developed in a Petri dish culture with site water, crushed wheat grains, and *Paramecium* as a prey.

Table 47: Body length and width of *Dileptus sphagnicola* nov. sp. in vivo, in the scanning electron microscope (SEM), and after protargol impregnation using various fixatives. Measurements in µm. CV – coefficient of variation in %, M – median, Max – maximum, Mean – arithmetic mean, Min – minimum, n – number of specimens investigated, SD – standard deviation, SE – standard error of mean.

Characteristics	Mean	M	SD	CV	Min	Max	n
In vivo specimens							
Body, length	490.0	450.0	–	–	420.0	600.0	3
Body, width	71.7	70.0	–	–	70.0	75.0	3
Body length:width, ratio	6.9	6.0	–	–	6.0	8.6	3
SEM prepared specimens							
Body, length	367.0	351.5	48.7	13.3	326.0	460.0	6
Body, width	58.7	58.5	7.2	12.3	49.0	70.0	6
Body length:width, ratio	6.3	6.3	0.9	14.2	4.9	7.7	6
Stieve solution							
Body, length	364.2	355.0	47.7	13.1	277.0	479.0	33
Body, width	60.8	60.0	8.2	13.5	43.0	80.0	33
Body length:width, ratio	6.1	6.2	1.3	21.7	3.9	11.1	33
Bouin solution							
Body, length	256.9	262.0	47.9	18.6	179.0	341.0	12
Body, width	55.6	55.0	11.6	20.8	39.0	78.0	12
Body length:width, ratio	4.8	4.7	1.3	26.2	2.7	7.0	12
Ethanol (70%)							
Body, length	294.8	296.0	42.0	14.3	208.0	374.0	25
Body, width	56.0	57.0	8.4	15.1	41.0	72.0	25
Body length:width, ratio	5.4	5.2	1.3	23.8	3.7	9.1	25

Remarks: The generic affiliation of this population may be questioned because it has several outstanding features, viz., the massive, *Arcuospathidium*-like body; the long (20 µm!), acicular extrusomes; the anterior tails in the rightmost brush rows; and the comparatively short, narrow blank stripe on the left side of the proboscis. Nevertheless, we assign the German population to *Dileptus* because of the many macronuclear nodules which divide individually and the oral ciliary pattern. If molecular data show comparable differences, the species should be referred to a new genus.

Within the group of large, multinucleate dileptids, *D. sphagnicola* resembles *D. costaricanus* and *D. anatinus* in having a stripe of contractile vacuoles each in ventral and dorsal side of body. However, *D. costaricanus* has a much smaller body (280 × 40 µm vs. 450 × 70 µm) and extrusomes anchored both in the proboscis oral bulge and in the oral bulge opening (vs. only in proboscis bulge). *Dileptus anatinus* has different extrusomes (rod-shaped and 12 µm long vs. acicular and 20 µm long) and a larger, less stout body (800–1200 µm × 100–120 µm vs. 350–650 × 55–90 µm) with the proboscis occupying one third or more of body length (33–50% vs. 17–25%). Beginners may confuse *D. sphagnicola* with *Monilicaryon monilatum*, which has a similar size and shape (very short proboscis!). However, *M. monilatum* has a moniliform macronucleus and lacks ventral contractile vacuoles. Further, it is usually much more slender (~ 10:1 vs. 6:1).

Dileptus costaricanus Foissner, 1995 (Figs 87a–v; Table 48)

1962 *Dileptus margaritifer* Ehrenberg, 1838 (*magna*-Form) – Dingfelder, Arch. Protistenk. **105**: 557 (misidentification, possibly a distinct species)

1995 *Dileptus costaricanus* nov. sp. Foissner, Arch. Protistenk. **145**: 40

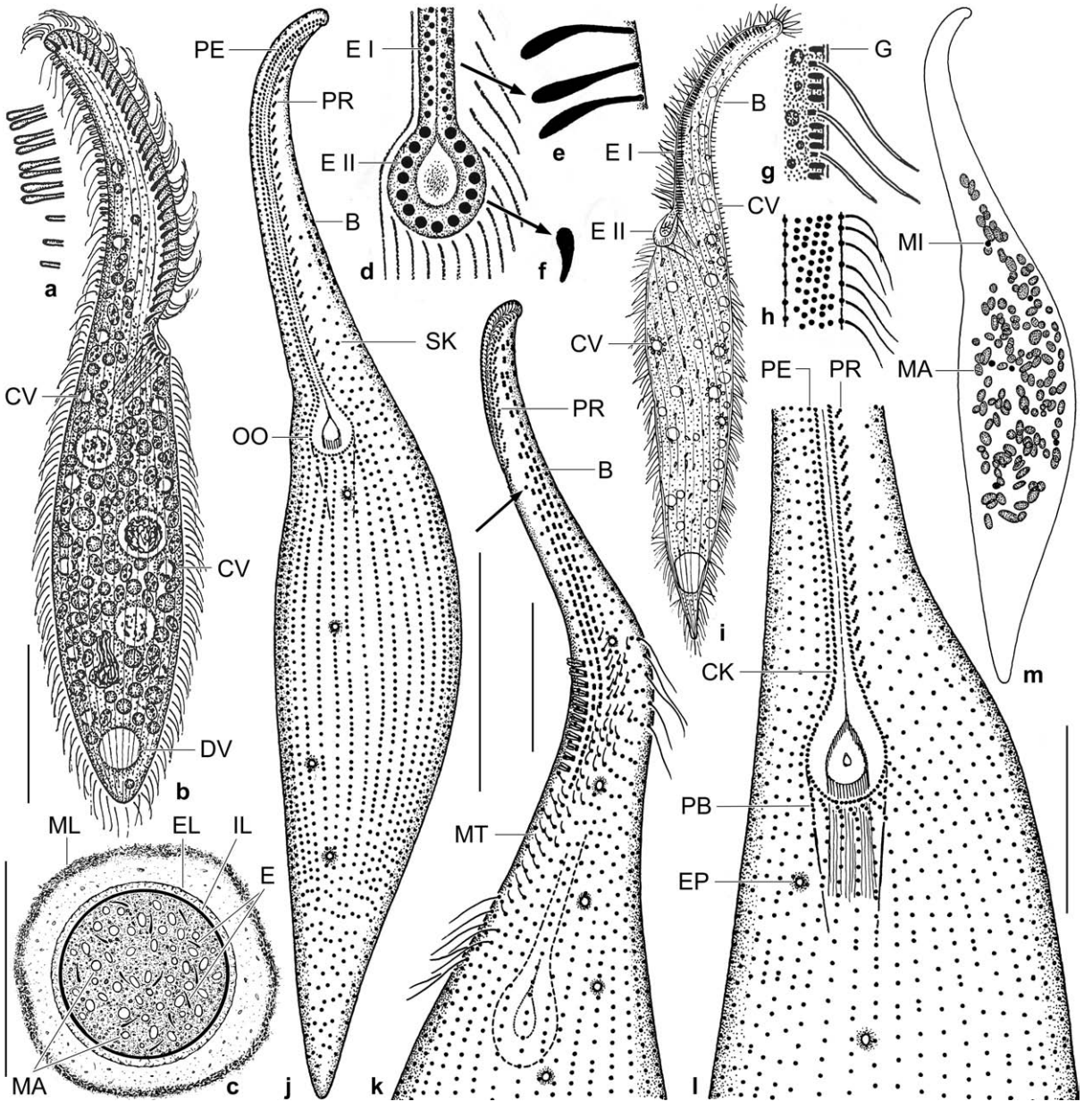
2011 *Dileptus costaricanus* Foissner, 1995 – Vďačný, Orsi, Bourland, Shimano, Epstein & Foissner, Eur. J. Protistol. **47**: 297 (18S rRNA gene sequence of a Botswanan population)

Improved diagnosis (type population): Size about 280 × 45 µm in vivo. Shape narrowly dileptid with rounded or gradually narrowed posterior region, proboscis about 1/3 of body length. Many scattered macronuclear nodules and several globular micronuclei. A dorsal and a ventral stripe of contractile vacuoles with 1 pore each. Two types of extrusomes: type I attached to proboscis oral bulge, clavate and curved, 5–7 × 1 µm in size; type II forms a ring anchored in oral bulge opening, narrowly obovate and slightly curved, about 3 × 1 µm in size. On average 38 ciliary rows, about 6 anteriorly differentiated into a staggered, distinctly heterostichad dorsal brush with monokinetidal tails extending anteriorly and posteriorly. Oral bulge opening about 10 µm across. Preoral kineties oblique, ordinarily spaced, each usually composed of 3 narrowly spaced cilia.

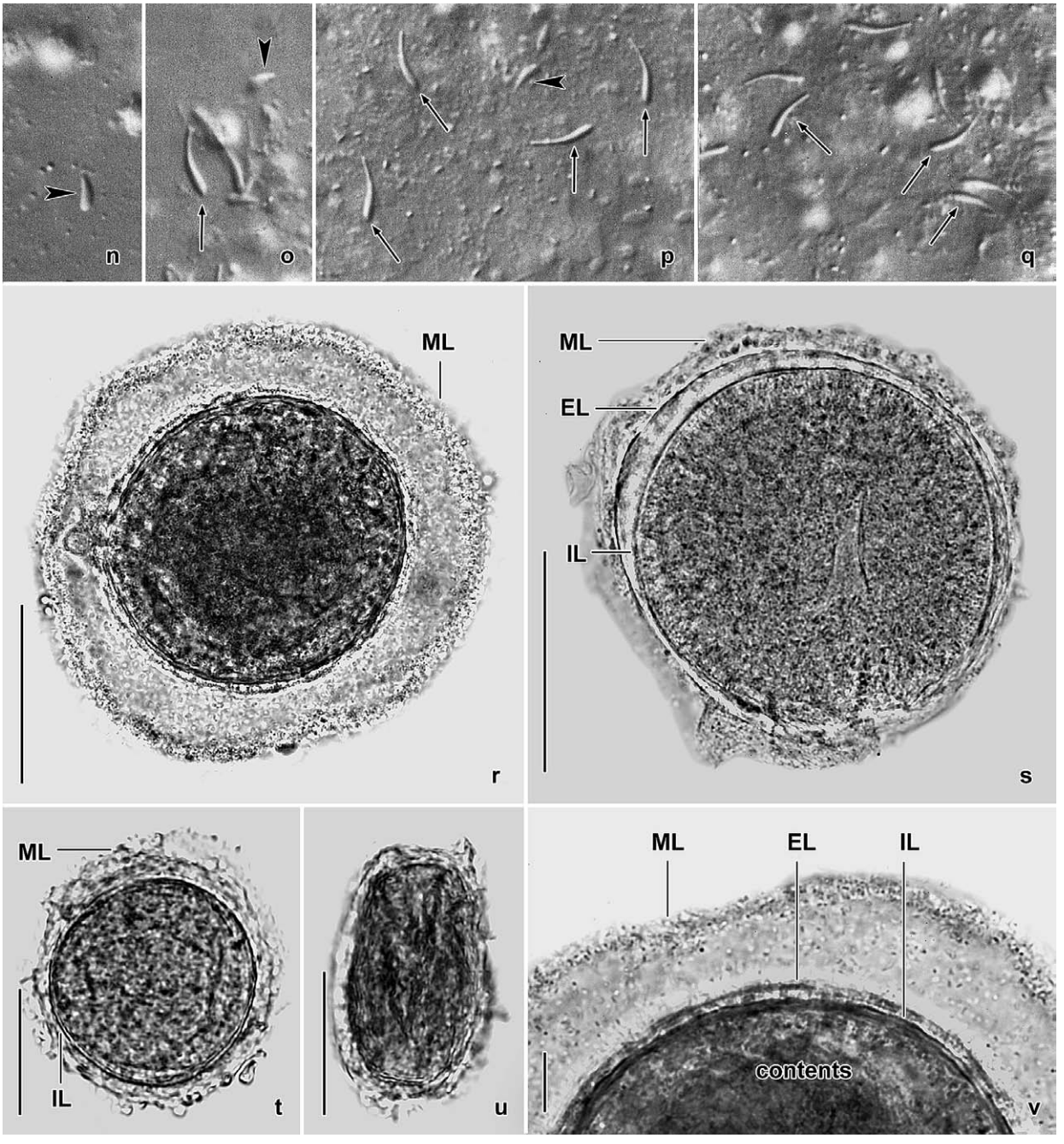
Type locality: Upper soil layer near the ranch house "La Casona" in the Santa Rosa National Park, Costa Rica, W85°38' N10°50'.

Table 48: Morphometric data on *Dileptus costaricanus* (from Foissner 1995a) and on resting cysts of a population from Botswana (original data). Data based, if not stated otherwise, on mounted, protargol-impregnated (Foissner's method), and randomly selected specimens from a non-flooded Petri dish culture. Measurements in µm. CV – coefficient of variation in %, M – median, Max – maximum, Mean – arithmetic mean, Min – minimum, n – number of specimens investigated, SD – standard deviation, SE – standard error of mean.

Characteristics	Mean	M	SD	SE	CV	Min	Max	n
Body, length	247.1	245.0	37.3	10.8	15.1	185.0	310.0	12
Body, width	38.8	37.5	6.1	1.8	15.7	33.0	55.0	12
Body length:width, ratio (calculated from original data)	6.4	5.9	1.1	0.3	16.4	5.3	8.6	12
Anterior body end to oral bulge opening, distance	76.4	75.0	12.9	3.9	16.8	60.0	95.0	11
Proboscis, % of body length (calculated from original data)	31.9	33.3	5.3	1.6	16.4	20.0	37.8	11
Macronuclear nodules, length	4.8	5.0	1.1	0.3	23.1	3.0	7.0	12
Macronuclear nodules, width	2.9	3.0	–	–	–	2.5	3.0	12
Macronuclear nodules, number	about 150 to 500							
Micronuclei, diameter	2.0	2.0	–	–	–	1.8	2.2	12
Micronuclei, number	many							
Ciliary rows, number	38.4	38.0	2.2	0.7	5.6	36.0	42.0	11
Dorsal brush rows, number	6.0	6.0	0.8	0.4	13.6	5.0	7.0	4
Resting cysts, length (in vivo)	79.9	81.5	12.0	3.2	15.0	50.0	90.0	14
Resting cysts, width (in vivo)	76.4	79.0	12.1	3.2	15.9	50.0	90.0	14
Resting cysts, diameter including mucous layer (in vivo)	102.1	100.0	24.2	6.5	23.7	60.0	140.0	14



Figs 87a–m: *Dileptus costaricanus*, Costa Rican specimens (a, b, d–h, j–m; from Foissner 1995a), resting cyst of a cell from Botswana (c; original), and a *costaricanus*-like specimen from Germany (i; from Dingfelder 1962) from life (a–i) and after protargol impregnation (j–m). **a** – the dorsal brush bristles are clavate and 2–3 µm long in the dikinetidal region of the brush, while oblong and 1–2 µm long in the monokinetidal tails; **b** – right side view of a representative specimen, length 280 µm; **c** – resting cysts are about 85 µm across and have a conspicuous mucous cover; **d** – frontal view of oral bulge opening and arrangement of extrusomes; **e** – type I extrusomes are obliquely attached to both bulge branches. They are clavate, curved, and 5–7 × 1 µm in size; **f** – type II extrusomes form a ring in the oral bulge opening. They are narrowly obovate, only slightly curved, and about 3 × 1 µm in size; **g, h** – optical section and surface view showing cortical granules; **i** – left side view of a *costaricanus*-like German species, length 670 µm; **j** – ventrolateral view of ciliary pattern; **k** – dorsal view of proboscis' ciliary pattern. Arrow denotes the anterior monokinetidal tail of brush row 1; **l** – ciliary pattern in oral region; **m** – nuclear pattern of the specimen shown in (j). B – dorsal brush, CK – circumoral kinety, CV – contractile vacuoles, E(I, II) – extrusome (types), EL – external cyst layer, EP – excretory pore of a contractile vacuole, G – cortical granules, IL – internal cyst layer, MA – macronuclear nodules, MI – micronucleus, ML – mucous layer, MT – monokinetidal tail, OO – oral bulge opening, PB – pharyngeal basket, PE – perioral kinety, PR – preoral kineties, SK – somatic kineties. Scale bars: 20 µm (k, l), 50 µm (b, j), and 100 µm (c).



Figs 87n–v: *Dileptus costaricanus* from life, extrusomes from Costa Rican type specimens (n–q, interference contrast; from Foissner 1995a) and resting cysts of a population from Botswana, Africa (r–v, bright field; originals). **n–q** – *Dileptus costaricanus* has a very special extrusome pattern. The proboscis extrusomes (type I) are clavate, curved, and 5–7 × 1 µm in size (arrows). The extrusomes attached to the oral bulge opening (type II) are narrowly obovate, only slightly curved, and about 3 × 1 µm in size (arrowheads); **r, s** – the resting cysts are on average 85 × 80 µm in size, globular to rotund and lack an escape apparatus. The cyst wall has a colourless mucous cover, which is well recognizable because up to 60 µm thick and densely populated by bacteria; **t, u** – same cyst in broad side and oblique view, showing cyst flattening, a peculiar feature as yet not found in any other dileptid cyst; **v** – the cyst wall is made of two layers and a conspicuous mucous cover colonized by bacteria: the external layer is hyaline, colourless, somewhat granular, and up to 5 µm thick, while the internal layer is honey brown, compact and only 1–1.5 µm thick. EL – external cyst layer, IL – internal cyst layer, ML – mucous layer. Scale bars: 20 µm (v) and 50 µm (r–u).

Type material: One holotype slide (inv. no. 1997/96) and one paratype slide (inv. no. 1997/97) with protargol-impregnated specimens have been deposited in the Biology Centre of the Museum of Upper Austria, Linz (LI). Relevant specimens are marked by black ink circles on the coverslip.

Gene sequence: The 18S rRNA gene sequence of a Botswanan population has been deposited in GenBank (HM581679). The sequence is 1641 nucleotides long and has a GC content of 41.7%. It is a consensus sequence based on 21 clones.

Etymology: Named after the country where it was discovered.

Description of Costa Rican population: Size 200–340 × 35–60 μm in vivo, usually about 280 × 45 μm, as calculated from some in vivo measurements and the morphometric data, assuming 10% preparation shrinkage; very flexible but not contractile (Table 48). Shape narrowly dileptid, i.e., length:width ratio near 5:1 both in vivo and after protargol impregnation. Proboscis about one third of body length, leaf-like flattened, stout and indistinctly set off from trunk, providing cells with an *Arcuospathidium*-like appearance; trunk oblong to bluntly fusiform; posterior end rounded in specimens collected from the young non-flooded Petri dish culture, while acute, but never tail-like in most cells found in the old culture (Figs 87b, j, m; Table 48). Nuclear apparatus in trunk and proximal third of proboscis. About 150–500 scattered macronuclear nodules, difficult to count since narrowly spaced and of similar size as some cytoplasmic inclusions; individual nodules highly variable, that is, globular to oblong and 3–7 × 2.5–3 μm in size; few to many nucleoli. Many micronuclei scattered between or attached to macronuclear nodules, about 2 μm across in protargol preparations (Fig. 87m; Table 48). A stripe of contractile vacuoles each in ventral and dorsal side of cell, first dorsal vacuole in mid-proboscis, ventral stripe commences slightly posterior to oral bulge opening; invariably a single intrakinetal excretory pore per vacuole (Figs 87b, j–l). Two types of extrusomes, not impregnating with protargol and scattered throughout cytoplasm: type I obliquely attached with thin end to both oral bulge branches, clavate and curved, 5–7 × 1 μm in size; type II forms a conspicuous ring in oral bulge opening, anchored with thick end to bulge cortex, narrowly obovate and only slightly curved, about 3 × 1 μm in size (Figs 87b, d–f, n–q). Cortex flexible, contains about five granule rows between adjacent kineties; granules colourless and ~ 1 × 0.5 μm in size (Figs 87g, h). Cytoplasm colourless, hyaline in proboscis, opaque in trunk because packed with 3–8 μm-sized lipid droplets and food vacuoles with indiscernible contents, possibly ciliates; in posterior end of trunk sometimes a defecation vacuole with sparse contents.

Cilia about 10 μm long in vivo, narrowly spaced, arranged in about 38 narrowly spaced rows (Table 48). Right side rows gradually shortened along oral bulge; perioral kinety extends to tip of proboscis with ordinarily spaced basal bodies (Figs 87j, l). Blank stripe on left side of proboscis comparatively short and narrow because most ciliary rows extend to distal half of proboscis (Figs 87j–l). Dorsal brush a long, narrow field on dorsal and dorsolateral region of proboscis; staggered; distinctly heterostichad; composed of about six rows with loosely to ordinarily spaced dikinetids associated with type II bristles both being 2–3 μm long. All brush rows continue with a monokinetidal tail extending to base of proboscis with 1–2 μm long type VI bristles; an anterior tail common in some rows (Figs 87a, b, j, k).

Oral bulge opening at beginning of second body third, hardly projecting because base of proboscis almost as wide as trunk, roundish both in vivo and in preparations, about 10 μm across (Figs 87b, d, j, l). Pharyngeal basket obconical, inconspicuous (Figs 87b, l). Circumoral kinety composed of ordinarily to narrowly spaced dikinetids in proboscis and narrowly spaced monokinetids around oral bulge opening. About 35 oblique, ordinarily spaced preoral kineties, as estimated from figures, each usually composed of three, rarely two narrowly spaced cilia (Figs 87j, l).

Resting cyst (Botswanan population): Mature cysts about 80 μm across in vivo, globular to rotund and flattened 2:1, a peculiar feature as yet not found in any other dileptid cyst; honey yellow; without escape

apparatus; does not break when strongly pressed by coverslip because the wall is very tough (Figs 87c, r–u; Table 48). Cyst wall composed of two distinct layers: external layer up to 5 µm thick, hyaline and colourless, somewhat granular, becomes thicker and denser in old cysts; internal layer only 1–1.5 µm thick, honey brown, compact (Figs 87c, s, v). Cyst covered by an up to 60 µm thick, hyaline, colourless mucous layer well recognizable due to adhering bacteria and debris (Figs 87c, r, s, t, v). Cytoplasm packed with 3–6 µm-sized macronuclear nodules, extrusomes, and granules up to 2 µm across (Fig. 87c).

Notes on supposed German population: Dingfelder (1962) described a "*magna*-form of *Dileptus margaritifer*", which highly resembles *D. costaricanus* in several important features, such as body shape and the peculiar extrusome pattern (Fig. 87i). On the other hand, the German and the Costa Rican populations differ so strongly in body length (670–846 µm vs. 200–340 µm) that conspecificity can be excluded. Thus, the German population, which Dingfelder (1962) found year-round in meadow rainwater puddles from the surroundings of the town of Forchheim, Germany, very likely represents a distinct species.

Occurrence and ecology: *Dileptus costaricanus* was discovered in a tropical dry forest, viz., in the upper soil layer from the Santa Rosa National Park in Costa Rica, where it occurred together with *Rimaleptus similis*. The population was rather weak but present for four weeks. Further records: soil from a woodruff-beech forest in the surroundings of the town of Vienna, Austria (Foissner et al. 2005); floodplain soil from Botswana (see resting cyst); and Amazon floodplain soil from the surroundings of the town of Manaus, Brazil. All populations were highly similar.

Remarks: *Dileptus costaricanus* is peculiar in having extrusomes anchored both to the proboscis oral bulge and to the oral bulge opening, while all congeners have them attached only to the proboscis bulge; in this respect, *D. costaricanus* resembles *Pseudomonilicaryon falciforme*, a species with moniliform macronucleus, and the binucleate *Rimaleptus canadensis*. Another rare feature of *Dileptus costaricanus* is the ventral and dorsal stripe of contractile vacuoles, a pattern found only in three other multinucleate species, viz., *D. anatinus*, *D. dubius*, and *D. sphagnicola*. *Dileptus anatinus* is much larger (1000 × 110 µm vs. 280 × 40 µm) and has rod-shaped extrusomes (vs. clavate). *Dileptus dubius* possesses only one ventral contractile vacuole underneath the oral bulge opening (vs. a ventral stripe) and is considerably smaller (116 µm vs. 280 µm). *Dileptus sphagnicola* is distinctly larger (450 × 70 µm vs. 280 × 40 µm) and has different extrusomes (acicular and 20 µm long vs. clavate and 5–7 µm long).

Dileptus anatinus Golińska, 1971 (Figs 88a–u, 89a–u, 90a–l; Table 49)

1971 *Dileptus anatinus* sp. n. Golińska, Acta Protozool. **8**: 367

1974 *Dileptus anatinus* Golińska, 1971 – Golińska, Acta Protozool. **12**: 289 (experimental study)

1995 *Dileptus anatinus* – Foissner, Berger, Blatterer & Kohmann, Informationsberichte des Bayer. Landesamtes für Wasserwirtschaft **1/95**: 197 (brief report and figures of an Austrian population)

Improved diagnosis (based on literature and the population from Austria mentioned above): Size about 1000 × 110 µm in vivo. Shape narrowly dileptid to rod-like with acute or tail-like posterior region, proboscis about 37% of body length. More than 200 scattered macronuclear nodules and several globular micronuclei. A dorsal and a ventral stripe of contractile vacuoles. Two types of extrusomes attached to right branch of proboscis oral bulge: type I rod-shaped, 10–12 µm long; type II oblong, 3–4 µm long. Oral bulge opening roundish. Preoral kineties slightly oblique, narrowly spaced, each composed of 5 narrowly spaced cilia.

Type locality: Small pond in Zaborów near Warsaw, Poland, E20°40' N52°15'.

Type and voucher material: Deposition of type slides not mentioned in the original paper (Golińska 1971). Four voucher slides with protargol-impregnated Austrian specimens have been deposited in the

Biology Centre of the Museum of Upper Austria, Linz (LI).

Etymology: Not given in original description. Possibly, the specific epiteth *anatinus* (duck, waterfowl) refers to the similarity with *D. anser*, as the Latin noun *anser* means goose.

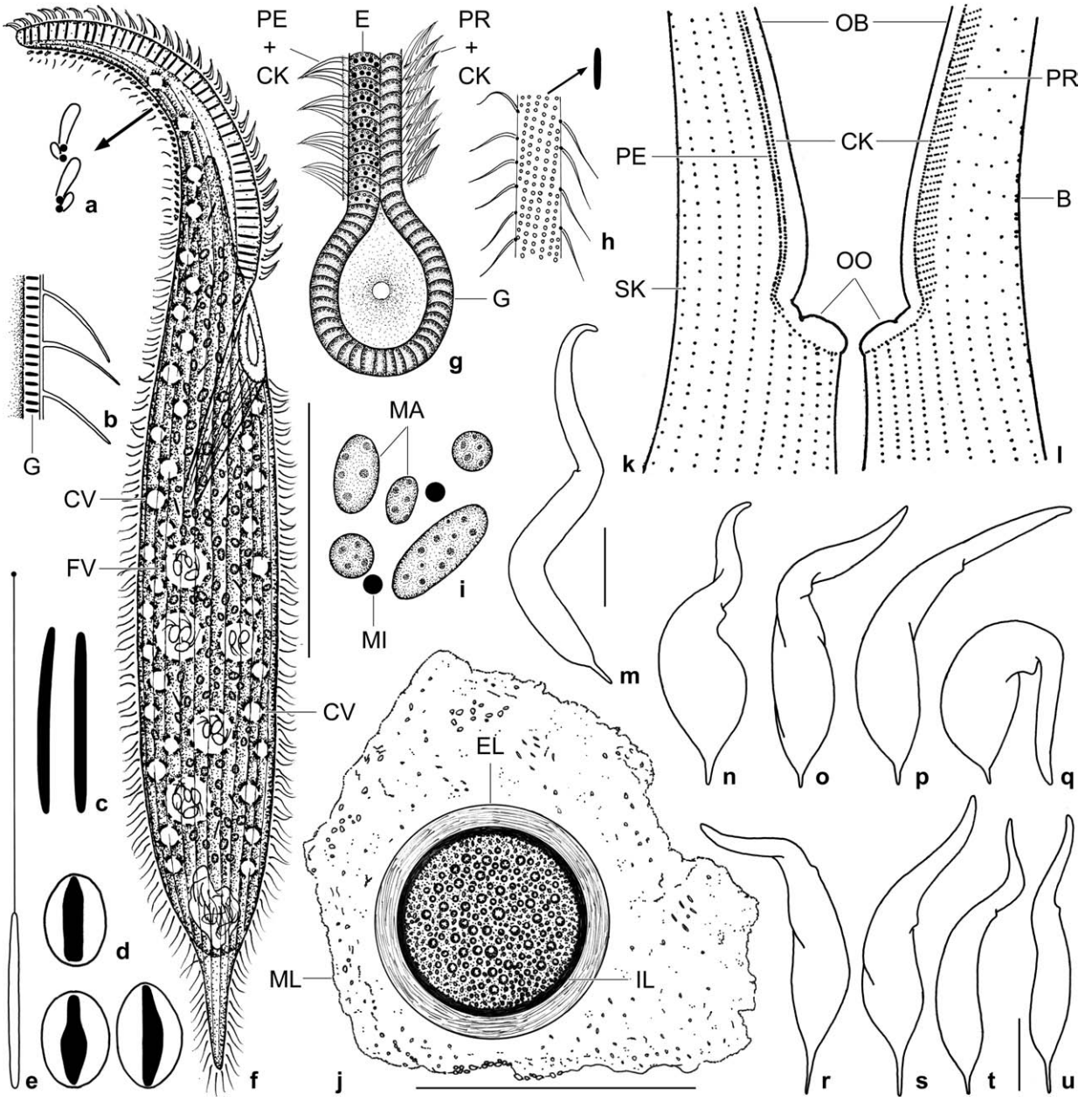
Description: *Dileptus anatinus* is difficult to impregnate with protargol, making morphometry and observation of the ciliary pattern difficult. We solved the latter problem by using scanning electron microscopy. The description is based on Polish specimens from a thriving semi-pure culture (Golińska 1971) and Austrian specimens from an ephemeral meadow puddle in Salzburg, Austria (Foissner et al. 1995 and some unpublished data). The populations match very well, therefore the diagnosis and description combine all observations; live data are mainly from the Salzburg specimens.

Size in vivo fairly similar in the two populations investigated: Polish specimens 990–1200 μm long and Austrian cells 600–1000 × 70–120 μm, showing 20–40% preparation shrinkage in protargol preparations (see Table 49); very flexible and contractile by about 10%. Shape very narrowly dileptid to rod-like, that is, length:width ratio 4–11:1 according to in vivo micrographs, while only 4.4–6.7:1 in protargol preparations due to strong shrinkage of body length. Proboscis about one third to one half of body length, slightly rostrate, that is, comparatively stout and indistinctly set off from trunk providing cells with an *Arcuospathidium*-like appearance; trunk massive and cylindroidal with a tendency to fold (Figs 89n, r), in well-fed specimens fusiform; posterior end acute or usually with short tail recognizable also in specimens inflated by food inclusions (Figs 88f, m–u, 89a, b, h, j–m). Nuclear apparatus in trunk and base of proboscis, absent from tail. About 200–500 scattered macronuclear nodules; individual nodules highly variable, that is, globular to oblong and 4–10 × 3–4 μm in size; divide individually (Golińska 1971); many small, globular nucleoli in each nodule. Several micronuclei scattered between or attached

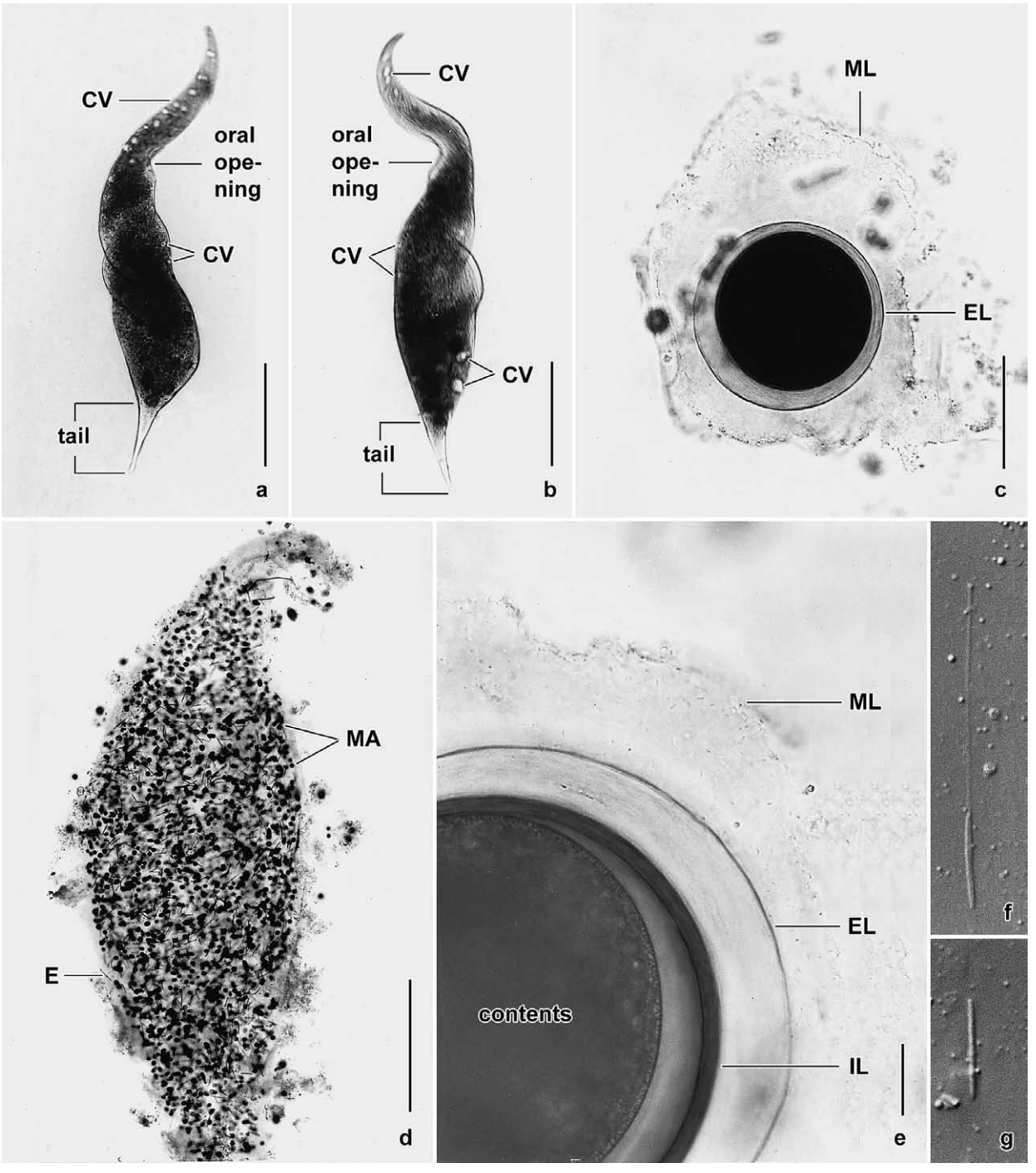
Table 49: Morphometric data on *Dileptus anatinus* from Austria. Data based, if not stated otherwise, on mounted, protargol-impregnated (Foissner's method), and randomly selected specimens from a semi-pure culture. Measurements in μm. CV – coefficient of variation in %, M – median, Max – maximum, Mean – arithmetic mean, Min – minimum, n – number of specimens investigated, SD – standard deviation, SE – standard error of mean.

Characteristics	Mean	M	SD	SE	CV	Min	Max	n
Body, length	527.4	524.0	63.1	19.0	12.0	400.0	620.0	11
Body, width	102.3	107.0	13.8	4.2	13.5	82.0	125.0	11
Body length:width, ratio	5.2	5.1	0.7	0.2	12.9	4.4	6.7	11
Anterior body end to oral opening, distance	193.5	199.0	28.9	8.7	14.9	125.0	234.0	11
Proboscis, % of body length	36.7	37.1	3.3	1.0	8.9	31.3	40.8	11
Oral bulge opening, largest diameter	30.0	30.0	2.0	1.2	6.7	28.0	32.0	3
Macronuclear nodules, number	about 200 to 500							
Ciliary rows, number on one side	28.2	29.0	3.5	1.0	12.3	23.0	33.0	11
Ciliary rows, total number	56.4	58.0	6.9	2.1	12.3	46.0	66.0	11
Resting cysts, length (in vivo)	169.3	160.0	24.6	6.4	14.5	140.0	210.0	15
Resting cysts, width (in vivo)	162.0	160.0	24.0	6.2	14.8	120.0	200.0	15

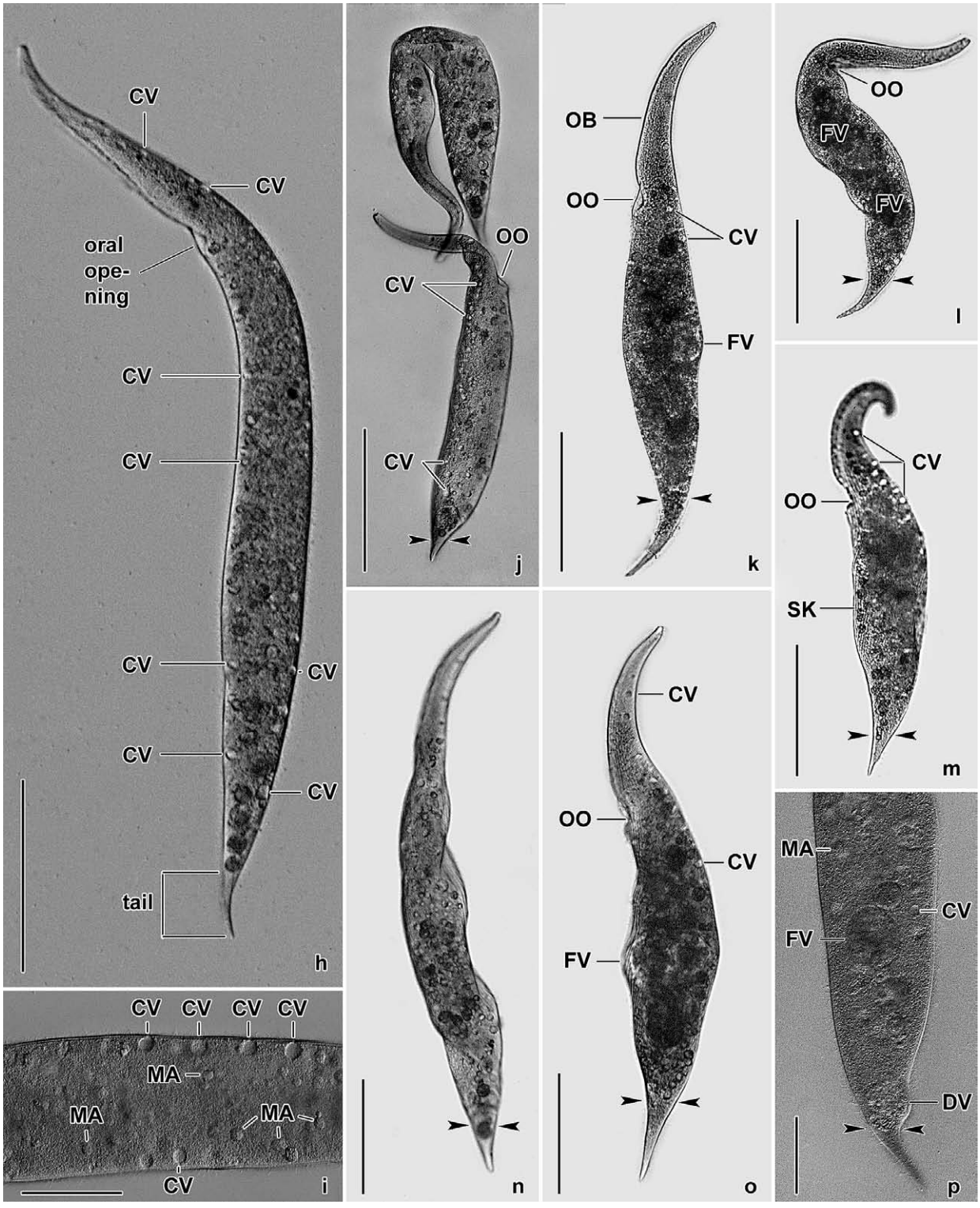
[a] Approximations because of insufficient impregnation. The total number of ciliary rows was calculated by doubling the value from one side, assuming an unflattened trunk.



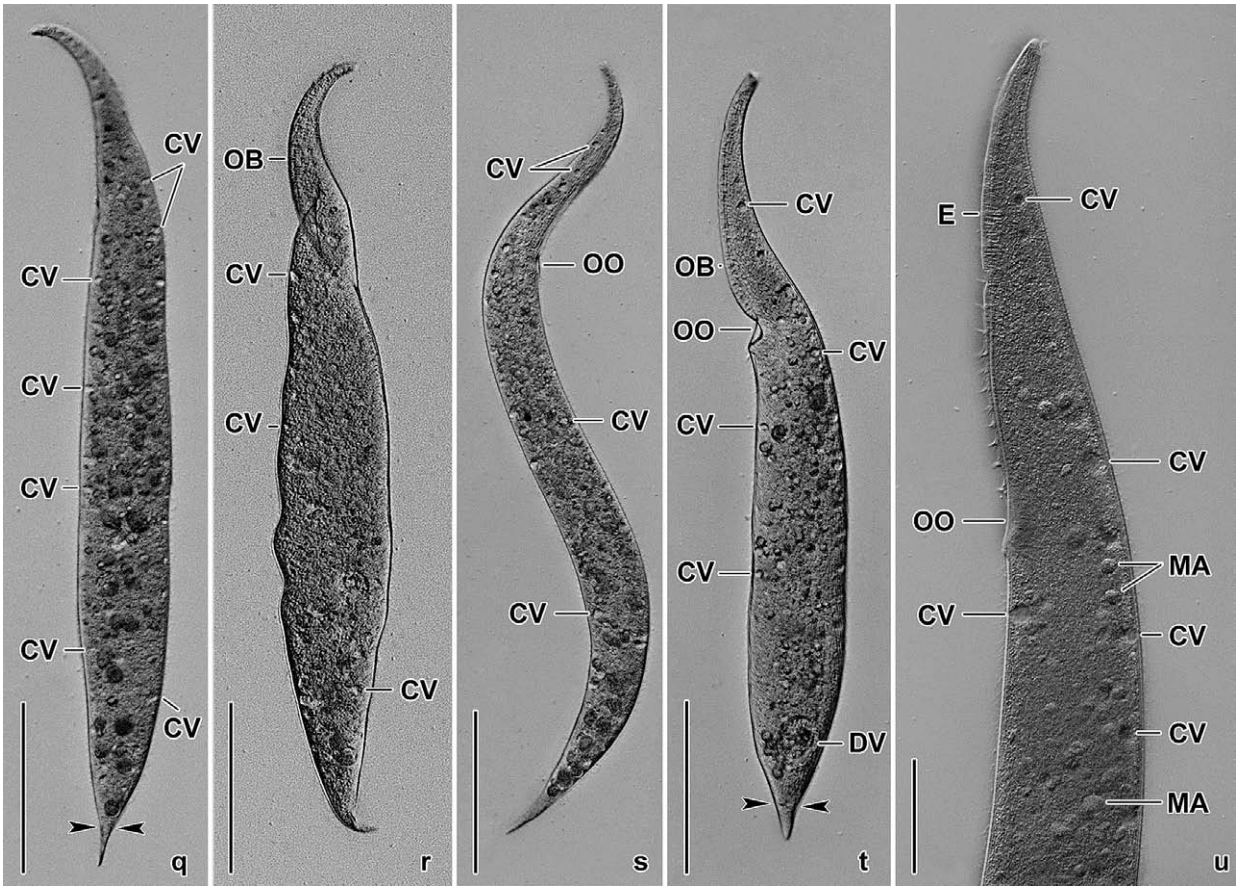
Figs 88a–u: *Dileptus anatinus*, Austrian (a–j, n–u; originals) and Polish (k–m; from Golińska 1971) specimens from life (a–j, m–u) and after protargol impregnation (k, l). **a** – the brush dikinetids are associated with type I bristles: the clavate anterior bristle is 3 μm long, while the posterior one is an 0.5 μm long stump; **b, h** – optical section and surface view showing the cortical granules which are about 2 μm long; **c** – type I extrusomes are slightly asymmetrical rods 10–12 μm long; **d** – extrusomes develop in vacuoles about 5 μm across; **e** – exploded extrusomes are about 50 μm long and display the typical toxicyst structure: a refractive granule at the tip of the tube emerging from the empty capsule; **f** –right side view of a representative specimen, length 900 μm; **g** – frontal view of oral bulge opening and arrangement of extrusomes and cortical granules; **i** – the nuclear apparatus consists of many macronuclear nodules and globular micronuclei interspersed; **j** – resting cysts are about 170 μm across and covered by an up to 50 μm thick, mucous layer; **k, l** – right and left side ciliary pattern in oral region; **m** – a specimen from type population (drawn from a micrograph provided by Golińska 1971); **n–u** – variability of body shape (drawn from micrographs). B – dorsal brush, CK – circumoral kinety, CV – contractile vacuoles, E – extrusomes, EL – external cyst layer, FV – food vacuole, G – cortical granules, IL – internal cyst layer, MA – macronuclear nodules, MI – micronucleus, ML – mucous layer, OO – oral bulge opening, PE – perioral kinety, PR – preoral kineties, SK – somatic kinety. Scale bars: 200 μm (f, j, m–u).



Figs 89a–g: *Dileptus anatinus*, Austrian specimens in vivo (a–c, e–g) and after protargol impregnation (d). From Foissner et al. (1995). **a, b** – lateral view of representative specimens showing a stripe of contractile vacuoles each in ventral and dorsal side of cell; **c, e** – resting cysts are about 170 µm across and have two distinct layers: the external layer is 20 µm thick and yellowish, while the internal layer is 5 µm thick, honey brown, and compact. The wall is covered by an up to 50 µm thick, colourless mucous layer, becoming recognizable due to the adhering materials; **d** – the nuclear apparatus consists of hundreds of scattered macronuclear nodules and many micronuclei; **f, g** – exploded (50 µm) and resting (12 µm) type I extrusome. CV – contractile vacuoles, E – extrusomes, EL – external cyst layer, IL – internal cyst layer, MA – macronuclear nodules, ML – mucous layer. Scale bars: 20 µm (e), 100 µm (c, d), and 200 µm (a, b).



Figs 89h–p: *Dileptus anatinus*, Austrian specimens in vivo. **h, j–o** – variability of body shape and size. Opposed arrowheads mark base of tail; **i, o –** optical section showing some main cell organelles. CV – contractile vacuoles, DV – defecation vacuole, FV – food vacuoles. MA – macronucler nodules, OB – oral bulge, OO – oral opening, SK – somatic kineties. Scale bars: 50 µm (i, p) and 200 µm (h, j–o).



Figs 89q–u: *Dileptus anatinus*, Austrian specimens in vivo. **q–t** – variability of body shape and size. The proboscis is indistinctly set off from the oblong massive trunk. The posterior region is gradually narrowed to an acute end (r, s) or tail-like set off from the trunk (q, t). The contractile vacuoles form a stripe each in ventral and dorsal side of cell, an important feature of *D. anatinus* because most congeners display only a dorsal stripe. Opposed arrowheads mark base of tail; **u –** optical section in anterior body portion showing indistinctly projecting oral bulge opening and some main cell organelles (macronuclear nodules, contractile vacuoles and extrusomes). CV – contractile vacuoles, DV – defecation vacuole, E – extrusomes, MA – macronucler nodules, OB – oral bulge, OO – oral opening. Scale bars: 50 µm (u) and 200 µm (q–t).

to macronuclear nodules, about 1.5 µm across in vivo (Figs 88i, 89d, u). A stripe of contractile vacuoles each in ventral and dorsal side of cell: ventral stripe commences slightly posterior to oral bulge opening and is composed of 5–15 vacuoles, dorsal stripe begins subapically and is composed of 20–35 vacuoles (Figs 88f, 89a, b, h–u). Two types of extrusomes attached only to broader right branch of oral bulge: type I rod-shaped with slightly narrowed, rounded ends, slightly asymmetric, 10–12 µm long, when exploded up to 50 µm long and of typical toxicyst structure, i.e., with a refractive granule at tip of tube emerging from empty capsule (Figs 88c, e, g, 89f, g, u); type II oblong, 3–4 µm long; developing extrusomes of various stages about 5 µm long, each enveloped in a vacuole (Fig. 88d). Cortex flexible, about 2 µm thick and distinctly separated from cytoplasm, contains about six oblique granule rows between each two kineties; granules narrowly spaced in somatic and oral bulge cortex, oblong, comparatively large, i.e., about 2 × 0.3 µm in size and thus easily mistaken for type II extrusomes in oral bulge, when exploded form a conspicuous spongious cover (Figs 88b, g, h, 90b–d). Cytoplasm colourless, at low magnification (×40) bright to dark brown, depending on nutrition; hyaline in proboscis and tail, opaque in trunk due to many

macronuclear nodules and numerous food vacuoles containing heterotrophic flagellates and euglenids in Austrian cells; near posterior end sometimes a defecation vacuole (Figs 88f, 89a, b, h–u).

Cilia about 9 µm long in vivo; number of ciliary rows not studied by Golińska (1971), about 46–66 meridionally to rather distinctly helically extending rows in Austrian specimens (Figs 90a, e, f; Table 49). Right side rows very likely shortened only near anterior end of oral bulge and thus not leaving a blank stripe right of oral bulge; perioral kinety extends to tip of proboscis with narrowly spaced basal bodies (Figs 88k, 90h, k). Blank stripe on left side of proboscis comparatively short and narrow because most ciliary rows extend to or above proximal half of proboscis (Figs 88l, 90e–g, i, j, l). Dorsal brush on dorsal and dorsolateral region of proboscis; multi-rowed, i.e., composed of at least 12 distinctly heterostichad rows with loosely spaced dikinetids associated with type I bristles: anterior bristle clavate and up to 3 µm long in vivo (1.5–2 µm in SEM), posterior bristle stump-like and about 1–1.5 µm long in vivo (0.6–0.8 µm in SEM). All rows continue with a monokinetidal tail of type VI bristles 0.6–0.8 µm long in SEM (Figs 88a, l, 90g, i, j, l).

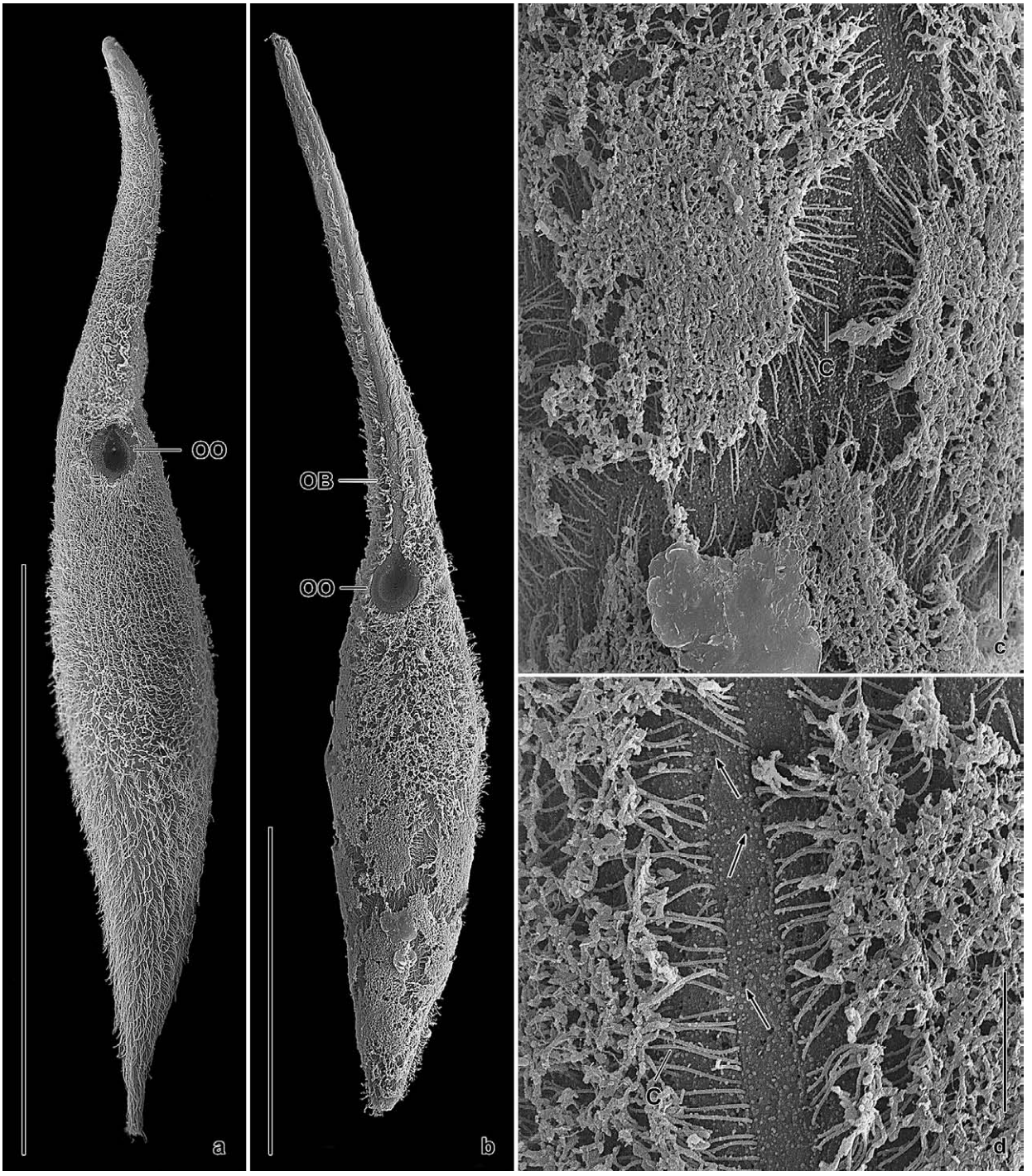
Oral bulge opening at beginning of second body third, hardly projecting because base of proboscis almost as wide as trunk, roundish both in vivo and in protargol as well as in SEM prepared specimens where about 30 µm across (Figs 88f, g, 89a, b, h, k, m, o, q, s–u, 90a, b, f, k; Table 49). Pharyngeal basket obconical and comparatively long. Circumoral kinety composed of narrowly spaced dikinetids in proboscis and narrowly spaced monokinetids around oral bulge opening. Preoral kineties slightly oblique, narrowly spaced, each composed of five narrowly spaced cilia (Figs 88k, l, 90h–l).

Resting cyst (Austrian population): Cysts conspicuous because about 170 µm across in vivo and globular to rotund, dark at low magnification (×40), yellowish brown at higher magnification, without escape apparatus. Cyst wall composed of two distinct layers: external layer abou 20 µm thick, yellowish, with distinct lamination; internal layer about 5 µm thick, honey brown, compact. Cyst wall covered by an up to 50 µm thick, colourless mucous layer becoming recognizable due to adhering bacteria, flagellates and debris; fragile and thus easily lost when cysts are transferred onto the slide. Cytoplasm colourless, studded with globules 1–5 µm across (Figs 88j, 89c, e). Unfortunately, we did not note whether the macronuclear nodules remain separate or fuse.

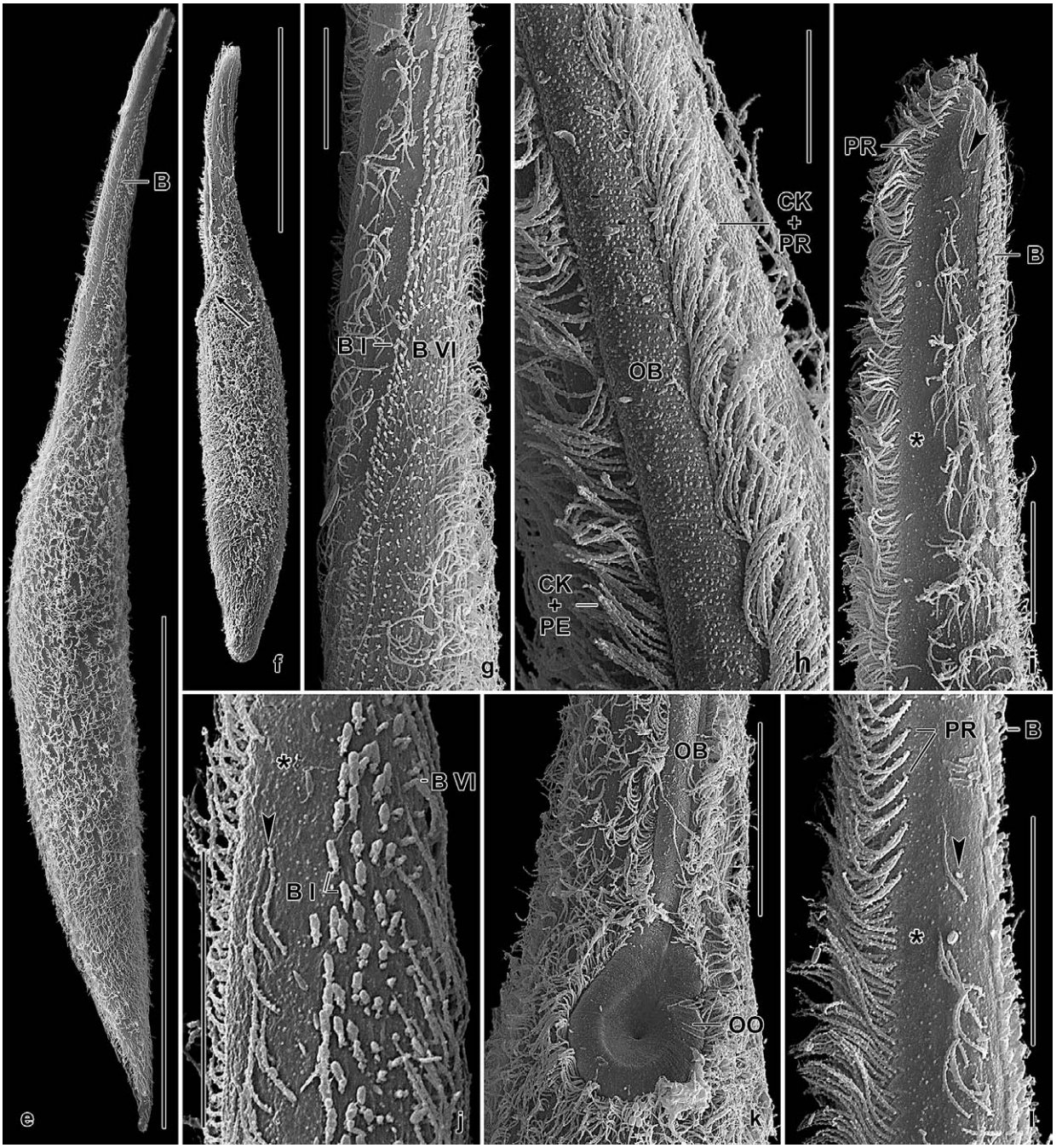
Occurrence and ecology: *Dileptus anatinus* was discovered in a small pond with low water level due to a prolonged draught in the town of Zaborów near Warsaw, Poland. It grew well in Petri dish cultures with tap water or Pringsheim's solution as a medium and *Colpidium* and *Tetrahymena* as a prey (Golińska 1971). Foissner et al. (1995) found *Dileptus anatinus* in a shallow, eutrophic meadow puddle near the so-called Henkerhaus in the Donnersberg Park (a municipal park near Salzburg city centre).

Remarks: *Dileptus anatinus* is difficult to preserve and to impregnate with protargol, making observations on the ciliary pattern difficult as already mentioned by Golińska (1971). However, it is easily recognizable in vivo due to the large, massive body; the more than 200 scattered macronuclear nodules; the ventral and dorsal stripe of contractile vacuoles; and the 12 µm long, rod-shaped extrusomes (Figs 88a, b, g).

Dileptus anatinus is most similar to *D. costaricanus* and *D. sphagnicola* in having a stripe of contractile vacuoles each in ventral and dorsal side of body. However, *D. costaricanus* is much smaller (280 × 40 µm vs. 1000 × 110 µm) and has clavate extrusomes (vs. rod-shaped) anchored to the proboscis oral bulge. *Dileptus sphagnicola* is smaller (350–650 × 55–90 µm vs.800–1200 µm × 100–120 µm) and has 20 (vs. 12 µm) µm long, acicular (vs. rod-shaped) extrusomes.



Figs 90a–d: *Dileptus anatinus*, Austrian specimens in the SEM. **a, b –** ventral views, showing the variability of body shape and length of proboscis (35% and 50% of body length). On the ventral side of the proboscis, there is the oral bulge that widens posteriorly to form a more or less roundish oral opening. The cells are densely ciliated and that shown in (b) has extruded the mucocysts; **c, d –** *Dileptus anatinus* has 2–3 µm long mucocysts which can be released very rapidly, i.e., even during osmium fixation (b). When discharged, the mucocysts swell to a slimy mass covering the body. The arrows mark minute holes where the mucocysts left the cell. C – somatic cilia, OB – oral bulge, OO – oral bulge opening. Scale bars: 10 µm (c, d) and 200 µm (a, b).



Figs 90e–l: *Dileptus anatinus*, Austrian specimens in the SEM. **e, f –** dorsolateral overviews showing variability of body shape. Arrow in (f) marks the site of the oral bulge opening; **g, j –** parts of the dorsal brush, which is multi-rowed and staggered. There are two types of dorsal brush bristles. The anterior bristle of type I is slightly inflated and 1.5–2 µm long, while the posterior bristle is a minute, conical stump. The type VI bristles are monokinetidal, conical, 0.6–0.8 µm long, and form the posterior tail of the brush rows. On the left side of the proboscis, there is a comparatively narrow blank stripe (asterisk) because several left side ciliary rows extend above proximal half of the proboscis (arrowhead); **h, k –** ventral views, showing the broad right branch of the oral bulge (h) and the roundish oral bulge opening (k); **i, l –** left side views of anterior region of proboscis, showing the blank stripe left of the preoral kineties (asterisk) and the tapering end of the left side somatic ciliary rows (arrowheads). B(I, VI) – dorsal brush (bristle types), CK – circumoral kinety, OB – oral bulge, OO – oral bulge opening, PE – perioral kinety, PR – preoral kineties. Scale bars: 10 µm (h), 20 µm (g, i, j, l), 40 µm (k), and 200 µm (e, f).

Dileptus multinucleatus Vuxanovici, 1959 (Fig. 84f)

1959 *Dileptus multinucleatus* n. sp. Vuxanovici, Studii Cerc. Biol. **11**: 328

1963 *Dileptus multinucleatus* Vuxanovici, 1959 – Dragesco, Bull. biol. Fr. Belg. **97**: 125 (first taxonomic reviser)

Diagnosis: Length about 185 µm in vivo. Shape narrowly dileptid with acute posterior end, proboscis about 1/3 of body length. Many scattered macronuclear nodules and several micronuclei. Two contractile vacuoles in dorsal side of trunk. About 20 ciliary rows.

Type locality: Coast of Lake Herăstrău, Bucharest, Roumania, E26°05' N44°28'.

Type material: Not available.

Etymology: Not given in original description. Composite of the Latin numeral *multi* and the noun *nucleus*, obviously referring to the many macronuclear nodules.

Description: Vuxanovici's description is based on a single specimen. Length 185 µm in vivo; slightly contractile. Shape narrowly dileptid with a length:width ratio of 5.5:1, according to the figure provided. Proboscis ordinary, about one third of body length, distinctly set off from trunk; trunk bluntly fusiform; posterior region gradually narrowed to an acute end. Many small macronuclear nodules and several micronuclei scattered in trunk. Two contractile vacuoles in dorsal side of trunk: anterior vacuole slightly posterior of oral bulge opening, posterior vacuole subterminal. Extrusomes not studied. Cytoplasm transparent, yellowish. About ten meridionally arranged ciliary rows on one side of cell (Fig. 84f).

Occurrence and ecology: As yet found only at type locality in a sample containing swamp plants. Only one specimen was observed in January 1958.

Remarks: Poorly described, thus needing complete redescription. The main distinguishing feature of *D. multinucleatus* is the two contractile vacuoles in the dorsal side of the trunk, a pattern as yet not found in any other congener.

The *Dileptus margaritifer* group

The seven species and subspecies collected in this group look very similar at first glance because they have a slender, medium to large-sized body, a dorsal stripe of contractile vacuoles, and a multi-rowed dorsal brush. However, on more detailed investigation considerable differences become obvious (Table 50). Reliable identification requires careful in vivo observation and silver preparations.

Dileptus estuarinus Dragesco, 1960 (Figs 90m–p)

1960 *Dileptus estuarinus* n. sp. Dragesco, Trav. Stn biol. Roscoff (N. S.) **12**: 186

1963 *Dileptus estuarinus* Dragesco, 1960 – Dragesco, Bull. biol. Fr. Belg. **97**: 108 (first taxonomic reviser)

Diagnosis: Length about 1000 µm in vivo. Shape very narrowly dileptid to rod-like with short tail, proboscis slightly rostrate and about 1/4 of body length. About 70–80 scattered macronuclear nodules and many globular micronuclei. A dorsal stripe of contractile vacuoles. About 40 ciliary rows.

Type locality: Slightly brackish sand from the mouth of a small river, Goulven, France, W4°18' N48°38'.

Type material: Not available.

Etymology: Not given in original description. The Latin adjective *estuarinus* refers to the habitat (estuary) in which the species was discovered.

Description: Length 800–1100 µm in vivo; very flexible and slightly contractile; yellowish (Dragesco 1960) or pale pink (Dragesco 1963). Shape very narrowly dileptid to rod-like, length:width ratio about

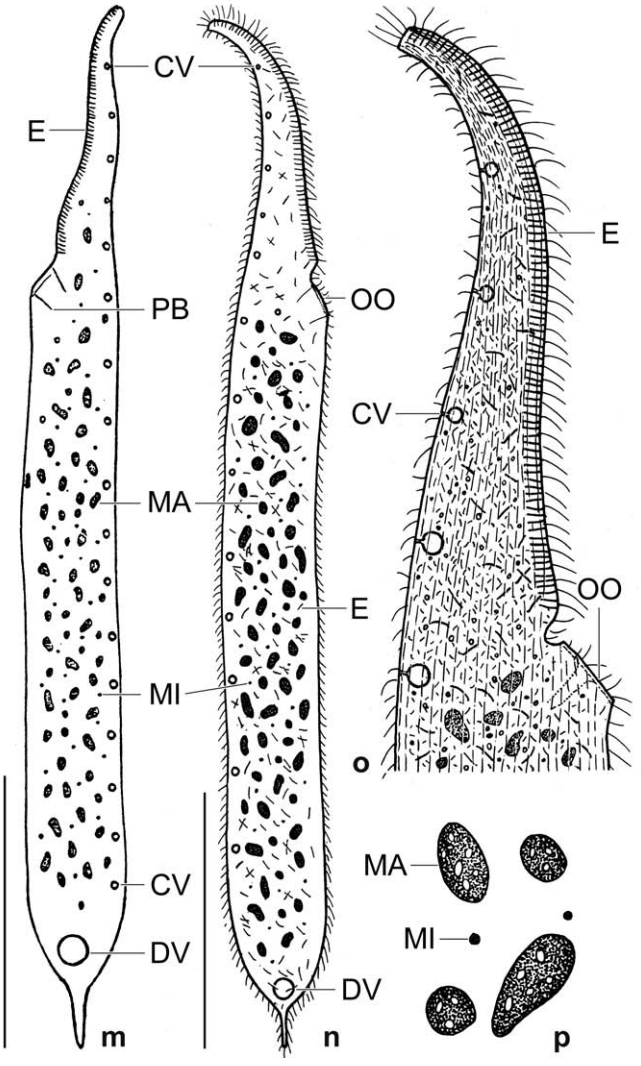
Table 50: Comparison of species of the *Dileptus margaritifer* group and the genus *Apodileptus*.

Species / Characteristics	Average size in vivo (µm)	Proboscis, % body length	Number of macronuclear nodules	Type I extrusomes, shape and size	Ciliary rows, number	Specialities
Dileptus beersi sensu JONES (1956)	670 × 65	40	200–500	narrowly ovate, 10 × 0.6 µm in size	?	–
Dileptus beersi (Venezuelan population)	450 × 50	35	130–500	narrowly ovate, 8 × 1–1.2 µm in size	36–56 (mean = 48)	–
Dileptus estuarinus	1000 × 100	25 (short)	70–80	?	about 40	brackish sand
Dileptus jonesi sensu JONES (1951, 1956)	425 × 60	40	more than 100	?	?	attaches to substrate by a mucous thread
Dileptus jonesi sensu SONG & WILBERT (1983)	400 × 80	33	70–100	rod-shaped, 5 µm long	28–34	–
Dileptus margaritifer	400 × 50	34	200–500	rod-shaped, 10 µm long	40–50 (mean = 45)	–
Apodileptus edaphicus	470 × 30	30	130–220	rod-shaped, 6 µm long	18–23 (mean = 20)	rod-shaped body, elliptical oral opening
Apodileptus visscheri visscheri	280 × 30	30	40–140	narrowly ovate, 6 µm long	19–29 (mean = 22)	–
Apodileptus visscheri rhabdoplites	230 × 35	33	35–70	rod-shaped, 4 µm long	22–29 (mean = 26)	–

10:1, according to DRAGESCO's figures. Proboscis short and stout, occupies one fifth to third of body length, indistinctly set off from trunk and thus providing cells with a spathidiid appearance; trunk massive, cylindroidal, slightly flattened, with a tendency to fold; posterior end with short but distinct tail (Figs 90m, n). About 70–80 scattered macronuclear nodules, individual nodules globular to oblong, comparatively large, i.e., about 8 µm across; several small nucleoli in each nodule. About 30 micronuclei scattered between macronuclear nodules, 0.6–0.8 µm across in methyl green stains (Fig. 90p). A stripe of 12–30 contractile vacuoles in dorsal side of proboscis and trunk. Extrusomes attached to proboscis oral bulge and scattered throughout cytoplasm; their shape not described but figured as slightly curved rods (Figs 90m–o). Cortex with many refractive granules between adjacent kineties. Cytoplasm transparent, packed with macronuclear nodules, extrusomes, food vacuoles, lipid droplets 1–13 µm across, and innumerable bacterial rods (endosymbionts?); near posterior end sometimes a defecation vacuole. Swims slowly hardly moving the proboscis. About 40 meridionally arranged ciliary rows. Oral bulge opening hardly projecting because base of proboscis almost as wide as trunk. Pharyngeal basket obconical, inconspicuous as composed of comparatively short and fine fibres (Figs 90m–o).

Occurrence and ecology: As yet found at type locality, where it was rather abundant; in the interstitium of the Øresund in Denmark (FENCHEL 1968); and in the western Baltic Sea (TELESH et al. 2008).

Remarks: *Dileptus estuarinus* differs from all other multinucleate dileptids, except for *D. sphagnicola*, in having a very short to short proboscis. However, *D. sphagnicola* has a much smaller body (350–650 µm vs. 800–1100 µm), a different contractile vacuole pattern (a dorsal and a ventral row vs. a dorsal row only), and a much higher number of macronuclear nodules (about 300 vs. 70–80). Another similar species is *Monilicaryon monilatum* which possesses, however, a moniliform macronucleus.



Figs 90m–p: *Dileptus estuarinus*, French type specimens from life (m–o) and after acetic methyl green stain (p). From Dragesco 1960 (n–p) and Dragesco 1963 (m). **m, n –** lateral views showing the massive body with short proboscis occupying one fourth of body length; **o –** detail of oral region; **p –** the nuclear apparatus consists of many macronuclear nodules and several globular micronuclei interspersed. CV – contractile vacuoles, DV – defecation vacuoles, E – extrusomes, MA – macronuclear nodules, MI – micronuclei, OO – oral bulge opening, PB – pharyngeal basket. Scale bars 250 μm.

Dileptus margaritifer (Ehrenberg, 1833) Dujardin, 1841 (Figs 91a–r, 92a–z, 93a–k, 94a–z, 95a–w, 96; Tables 51, 52)

The many "misidentifications" are due to Dujardin 1841 and Kahl 1931, who confused *D. margaritifer* and *D. anser*; see below.

1833 *Amphileptus margaritifer* Ehrenberg, Abh. dt. Akad. Wiss. Berl. year **1833**: 230 (without figure)

1838 *Amphileptus margaritifer* Ehrenberg, 1833 – Ehrenberg, Infusionsthierchen: 355 (description with figures)

1841 *Dileptus anser* – Dujardin, Zoophytes: 407 (misidentification)

1841 *Dileptus* (*Amphileptus margaritifer*, Ehr. Infus. Pl XXXVII, fig. 5: 355) – Dujardin, Zoophytes: 410 (combining author; description adopted from Ehrenberg 1838)

1841 *Dileptus granulosus* – Dujardin, Zoophytes, Pl. 11, fig. 7 (mentioned only in figure explanation; here Fig. 91g and considered as nomen nudum)

1852 *Dileptus anser* D. – Perty, Zur Kenntnis kleinster Lebensformen: 152 (misidentification)

1859 *Amphileptus margaritifer* Ehr. – Claparède & Lachmann, Mém. Inst. natn. génev. **6**: 350 (description adopted from Ehrenberg 1838)

1869 *Dileptus anser* Duj. – Quennerstedt, Acta Univ. Lund **6**: 4 (a very detailed description, but in Swedish; further, the figures are so faint that a good reproduction is impossible)

1870 *Dileptus gigas varsaviensis* Wrześniowski, Wiss. Zool. **20**: 504 (junior synonym, description of a Polish population)

1881 *Amphileptus margaritifer*, Ehr. – Kent, Manual infusoria II: 525 (brief review)

1887 *Amphileptus irregularis* sp. nov. Maskell, Trans. Proc. N. Z. Inst. **20**: 9 (poor description, junior synonym)

1889 *Dileptus anser* O. F. Mueller sp. – Schewiakoff, Biblthca zool. **1**: 22 (misidentification; brief review; partim)

1896 *Dileptus anser* O. F. Müll. sp. – Schewiakoff, Zap. imp. Akad. Nauk **4**: 221 (misidentification; taxonomic revision; partim)

1923 *Dileptus gigas* – Visscher, Biol. Bull. mar. biol. Lab., Woods Hole **45**: 113 (misidentification, feeding behavior)

1927 *Dileptus gigas* – Visscher, J. Morph. **44**: 373 (misidentification, morphological study)

1927 *Dileptus gigas* – Visscher, J. Morph. **44**: 383 (misidentification, conjugation)

1930 *Dileptus gigas* – Studitsky, Arch. Protistenk. **70**: 155 (misidentification)

1931 *Dileptus gigas* – Peschkowsky, Arch. Protistenk. **73**: 1179 (misidentification, morphological study)

1931 *Dileptus* (*Vibrio*) *anser* (O. F. Mueller, 1786) – Kahl, Tierwelt Dtl. **21**: 205 (misidentification, first taxonomic reviser)

1938 *Dileptus anser* – Hayes, Trans. Am. microsc. Soc. **57**: 11 (misidentification, morphological study)

1948 *Dileptus gigas* (Clap. et L.) – Dragesco & Métain, Bull. Soc. Zool. Fr. **73**: 62 (misidentification, feeding behavior)

1953 *Dileptus anser* (O. F. Mueller 1786) – Wenzel, Arch. Protistenk. **99**: 84 (misidentification)

1957 *Dileptus anser* O. F. Mueller, 1786 – Šrámek-Hušek, Věst. Čsl. zool. spol. **21**: 5 (misidentification, saprobic characterization)

1959 *Dileptus anser* (O. F. Mueller, 1786) – Vuxanovici, Studii Cerc. Biol. **11**: 330 (misidentification, description of a Roumanian population)

1961 *Dileptus anser* – Dumont, J. Protozool. **8**: 392 (misidentification, fine structure)

1962 *Dileptus margaritifer* Ehrenberg, 1838 – Dingfelder, Arch. Protistenk. **105**: 555 (taxonomic revision; description of a small form, possibly a just excysted specimen)

1962 *Dileptus anser* O. F. Mueller, 1786 – Liebmann, Handbuch der Frischwasser- und Abwasser-Biologie I: 475 (misidentification, saprobic characterization)

1963 *Dileptus anser* (O. F. Mueller, 1786) – Dragesco, Bull. biol. Fr. Belg. **97**: 104 (misidentification, second taxonomic reviser)

1968 *Dileptus anser* (O. F. Mueller, 1786) – Chorik, Free-living ciliates: 69 (misidentification, brief description of a Moldavian population)

1970 *Dileptus anser* (cf. Mueller, 1786) ? – Dragesco, Fac. Sci. Univ. féd. Cameroun (Numéro hors-série) year **1970**: 11 (misidentification; with symbiotic green algae and thus possibly *D. viridis*)

1971 *Dileptus anser* – Golińska, Acta Protozool. **8**: 370 (misidentification, silver impregnation and comparison with *D. anatinus* and *D. cygnus*)

1972 *Dileptus anser* (O. F. Mueller) – Bick, Ciliated protozoa: 56 (misidentification; ciliate key)

1973 *Dileptus anser* (O. F. M.) – Golińska & Jerka-Dziadosz, Acta Protozool. **12**: 1 (misidentification, experimental study)

1974 *Dileptus anser* (O. F. M.) – Vinnikova, Acta Protozool. **12**: 275 (misidentification, conjugation)

1974 *Dileptus anser* O. F. M. – Vinnikova, Acta Protozool. **13**: 97 (misidentification, fine structural changes of macronuclei during conjugation)

1976 *Dileptus anser* – Vinnikova, Protistologica **12**: 7 (misidentification, fine structural changes of micronuclei during conjugation)

1977 *Dileptus anser* – Bohatier, Protistologica **13**: 77 (misidentification, experimental study)

1977 *Dileptus anser* – Bohatier & Kink, Protistologica **13**: 509 (misidentification, experimental study)

1978 *Dileptus anser* O. F. M. – Golińska, Acta Protozool. **17**: 47 (misidentification, remodelling of injured oral apparatus)

1979 *Dileptus anser* O. F. Mueller – Golińska, Wilhelm Roux Arch. Dev. Biol. **187**: 307 (misidentification, experimental study)

1979 *Dileptus anser* Mueller, 1786 – Foissner, Acta Protozool. **18**: 418 (misidentification, silverline pattern)

1979 *Dileptus anser* O. F. Mueller, 1786 – Mamaeva, Infuzorii bassejna Volgi: 31 (misidentification, ecology)

1982 *Dileptus anser* – Golińska, J. Embryol. exp. Morph. **69**: 99 (misidentification, regulation of ciliary pattern)

1983 *Dileptus anser* – Golińska, J. Cell Sci. **62**: 459 (misidentification, regulation of ciliary pattern)

1984 *Dileptus anser* – Golińska, J. Cell Sci. **70**: 25 (misidentification, experimental study)

1984 *Dileptus margaritifer* Ehrenberg, 1838 – Wirnsberger, Foissner & Adam, Arch. Protistenk. **128**: 314 (comparison with *D. anser*, nomenclature)

1986 *Dileptus anser* (O. F. Mueller, 1786) – Dragesco & Dragesco-Kernéis, Faune tropicale **26**: 161 (misidentification, brief review)

1986 *Dileptus anser* – Golińska, J. Embryol. exp. Morph. **93**: 85 (misidentification, experimental study)

1987 *Dileptus margaritifer* – Golińska, J. Cell Sci. **87**: 349 (experimental study)

1988 *Dileptus margaritifer* – Golińska, Protoplasma **147**: 125 (experimental study)

1988 *Dileptus margaritifer* (Ehrenberg, 1833) – Foissner, Hydrobiologia **166**: 38 (saprobic classification)

1989 *Dileptus margaritifer*– Golińska, Protoplasma **152**: 156 (experimental study)

1991 *Dileptus margaritifer* Ehrbg., 1838 – Golińska, Protoplasma **162**: 160 (fine structure)

1993 *Dileptus margaritifer* – Golińska & Afon'kin, Protoplasma **173**: 144 (pre-conjugation changes and development of conjugation junction)

1995 *Dileptus margaritifer* (Ehrenberg, 1833) Dujardin, 1841 – Foissner, Berger, Blatterer & Kohmann, Informationsberichte des Bayer. Landesamtes für Wasserwirtschaft **1/95**: 185 (ecolocical and morphological review; description of a population from Benin, Africa; saprobic classification)

1995 *Dileptus margaritifer* – Golińska, Acta Protozool. **34**: 101 (ontogenesis)

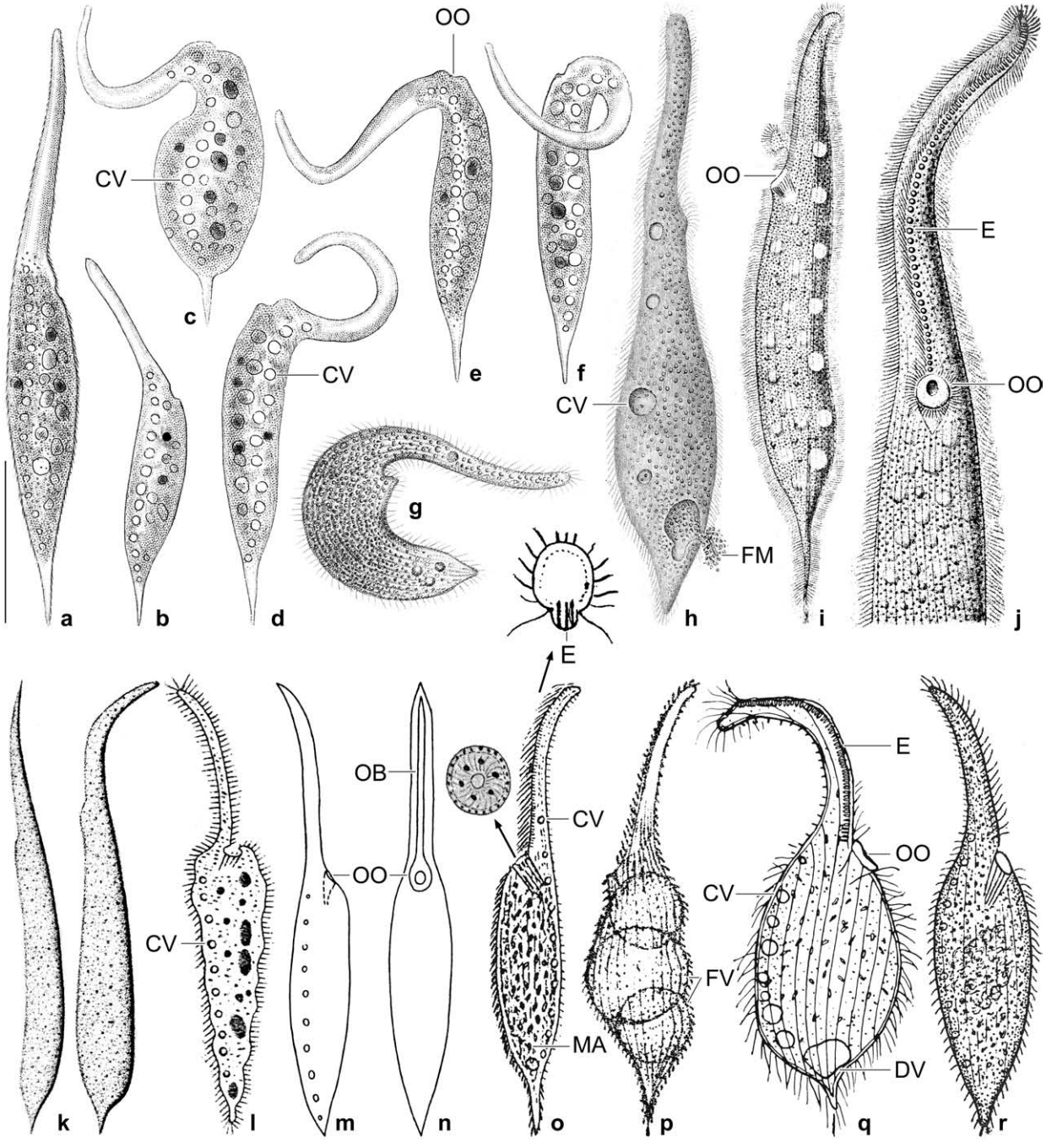
1996 *Dileptus margaritifer* – Golińska, Acta Protozool. **35**: 183 (experimental study)

2002 *Dileptus anser* – Yudin & Uspenskaya, Protistology **2**: 142 (misidentification, experimental study)

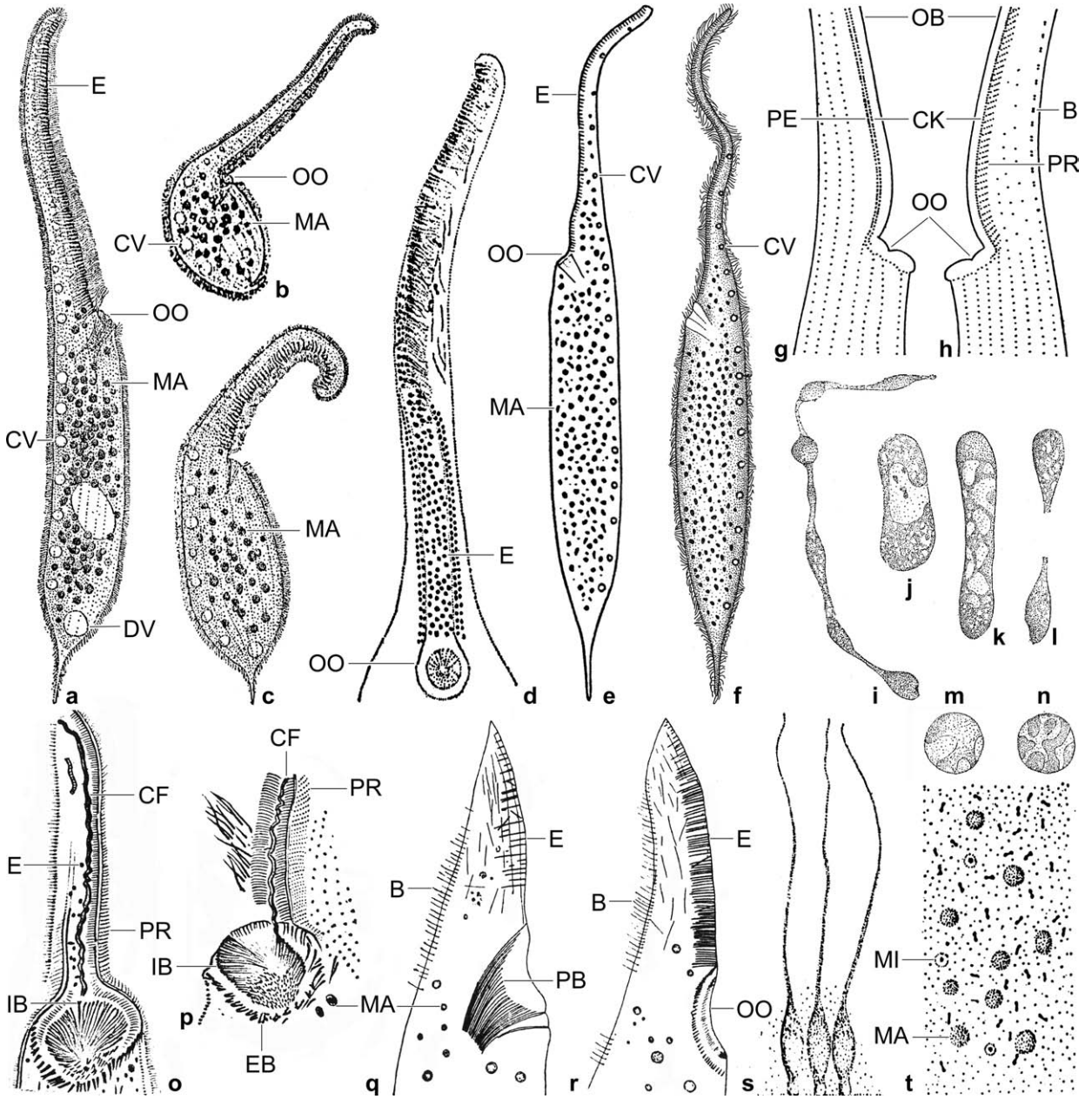
non *Dileptus margaritifer* Ehrenberg, 1838 (*magna*-Form) – Dingfelder, 1962, Arch. Protistenk. **105**: 557 (see *D. costaricanus*)

Nomenclature and taxonomy: *Dileptus margaritifer* was originally described as *Amphileptus margaritifer* by Ehrenberg (1833). Eight years later, it was combined with the genus *Dileptus* by Dujardin (1841). As mentioned by Hayes (1938), it is apparent from the descriptions and illustrations provided by Prowazek (1904), Visscher (1923, 1927a, b) and Studitsky (1930) that these authors considered *D. gigas* (now *Monomacrocaryon gigas*) as a synonym of *D. margaritifer*. Since Kahl (1931), *D. margaritifer* was usually misidentified as *D. anser* which has, however, a much longer proboscis and a moniliform macronucleus with only 10–20 nodules. According to Schewiakoff (1896) and Kahl (1931), *Dileptus margaritifer* has two further synonyms: *D. gigas varsaviensis* Wrześniowski, 1870 and *Amphileptus irregularis* Maskell, 1887; we agree. Dragesco (1963) and Dragesco & Dragesco-Kernéis (1968) proposed a further synonym: *D. beersi* Jones, 1956 which differs, inter alia, in the shape of the extrusomes (very narrowly ovate vs. rod-shaped), a feature definitely mentioned and illustrated by Jones (1956). Foissner et al. (1995) speculated that *D. jonesi* Dragesco, 1963 may be another synonym of *D. margaritifer*. However, *D. jonesi* has far fewer macronuclear nodules, ciliary rows, and forms a caudal thread, an outstanding feature never found in *D. margaritifer* as emphasized by Dragesco (1963). Considering the difficulties in separating *D. margaritifer* from *D. jonesi* and *D. beersi*, the species should be neotypified from a European population.

As concerns the other populations listed in the synonymy, most important features match: body narrowly to very narrowly dileptid, usually 450 × 50 μm in size, proboscis 1/3 to 1/2 of body length, tail distinct, many



Figs 91a–r: *Dileptus margaritifer* and its supposed synonyms from life. **a–f** – specimens from type population, drawn to scale, bar 100 µm (from Ehrenberg 1838); **g** – *D. granulosus*, length 190 µm (from Dujardin 1841); **h** – *D. anser*, length 390 µm (from Dujardin 1841); **i–k** – *D. gigas varsaviensis*, a wounded specimen, length 495 µm; ventral view with proboscis, 240 µm long; and two representative specimens, length 935 and 715 µm (from Wrześniowski 1870); **l** – *Amphileptus irregularis*, length 166 µm (from Maskell 1887); **m, n** – *D. gigas*, length 600 µm (from Visscher 1923); **o** – left side view, frontal view of oral bulge opening, and optical section through proboscis, length 450 µm (from Kahl 1931); **p** – a specimen with three large food vacuoles, length 320 µm (from Vuxanovici 1959); **q** – small form, length 158 µm (from Dingfelder 1962); **r** – a Moldavian specimen, length 375 µm (from Chorik 1968). B – dorsal brush, CK – circumoral kinety, CV – contractile vacuoles, DV – defecation vacuole, E – extrusomes, FM – faecal mass, FV – food vacuoles, MA – macronuclear nodules, OB – oral bulge, OO – oral bulge opening.



Figs 92a–t: *Dileptus margaritifer* and its supposed synonyms from life (a–c, e, f), after protargol impregnation (g, h), and in stains with iron hematoxylin (i–n, o–r), acid fuchsin (s), and Feulgen (t). (a–d, i–n, s, t from Hayes 1938). **a** – left side view, length 345; **b** – just excysted specimen, length 168 µm; **c** – post-divider, length 215 µm; **d** – ventral view with proboscis 115 µm long; **e** – semi-schematic view, length 535 µm (from Dragesco 1963); **f** – an African specimen, length 575 µm (from Dragesco & Dragesco-Kernéis 1986); **g, h** – right and left side oral ciliary pattern (from Golińska 1971); **i** – during cell division, the macronuclear nodules divide individually forming an enormously elongated, distinctly nodulated strand; **j–l** – in vegetative specimens, some macronuclear nodules increase in size becoming dumbbell-shaped and later on divide into two oblong pieces; **m, n** – the vegetative macronuclear nodules are about 5 µm across; **o, p** – ventral view showing oral apparatus (from Peschkowsky 1931); **q, r** – lateral view showing proboscis' armature (from Visscher 1923); **s** – the toxicysts become swollen and show three distinct parts after acid fuchsin stain; **t** – the nuclear apparatus consists of over 200 macronuclear nodules and many micronuclei. B – dorsal brush, CF – central fibre, CK – circumoral kinety, CV – contractile vacuoles, DV – defecation vacuole, E – extrusomes, EB – external basket, IB – internal basket, MA – macronuclear nodules, MI – micronucleus, OB – oral bulge, OO – oral bulge opening, PB – pharyngeal basket, PE – perioral kinety, PR – preoral kineties.

scattered macronuclear nodules, contractile vacuoles in a dorsal stripe. At the present state of knowledge, it appears wise to consider them as conspecific, especially because data on the extrusomes and the number of ciliary rows are usually lacking.

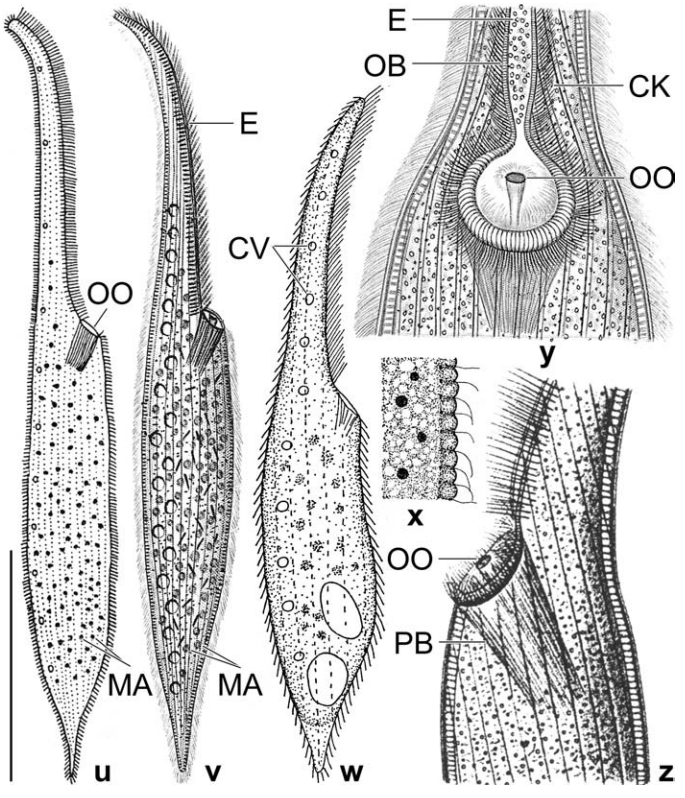
Improved diagnosis (includes all information known): Size of environmental specimens about 400 × 50 µm in vivo, in cultures up to 1000 µm. Shape narrowly to cylindroidally dileptid with distinct tail, proboscis 1/3 to 1/2 of body length. At least 200 scattered macronuclear nodules and several globular micronuclei. A dorsal stripe of contractile vacuoles with 1 pore each. Two types of extrusomes attached to proboscis oral bulge: type I rod-shaped with slightly narrowed ends, about 10 × 0.7 µm in size; type II oblong, about 3 µm long. On average 46 ciliary rows, up to 12 anteriorly differentiated into a staggered, distinctly heterostichad dorsal brush with monokinetidal tails extending to second third of body. Oral bulge opening about 30 µm across. Preoral kineties oblique, ordinarily to narrowly spaced, each usually composed of 4 narrowly spaced cilia.

Type locality: Pond in the Zoological Garden of Berlin, Germany, E13°19' N52°30'.

Type and voucher material: No type material is available from Ehrenberg's specimens. Foissner et al. (1995) deposited six voucher slides (inv. nos 2011/330–335) with protargol-impregnated specimens in the Biology Centre of the Museum of Upper Austria, Linz (LI; deposition not mentioned in the 1995 monograph). Relevant specimens are marked by black ink circles on the coverslip.

Etymology: Not given in original description. Composite of the Latin noun *margarita* (pearl ~ contractile vacuole) and the Latin suffix *fer* (carrying), referring to the dorsal stripe of contractile vacuoles.

Description: All known and some new data are put together because the morphological conspecificity is beyond reasonable doubts for most populations mentioned in the list of synonyms. In spite of the many



Figs 92u–z: *Dileptus margaritifer* and its supposed synonyms from life (u–w, y, z) and after acid fuchsin stain (x). From Schewiakoff 1889 (v, y, z), Wetzel 1925 (x), Lundin & West 1963 (w), and Bick 1972 (u). **u, v, w** – left side views, showing general body organization, length 250–600 µm; **x** – histological section of cortex and underlying cytoplasm; **y, z** – ventral and lateral view, showing oral apparatus. CK – circumoral cilia, CV – contractile vacuoles, E – extrusomes, MA – macronuclear nodules, OB – oral bulge, OO – oral bulge opening, PB – pharyngeal basket. Scale bar 100 µm.

studies available, detailed data on *D. margaritifer* are rare. Thus, the review must emphasize our own data from an African population first published by Foissner et al. (1995).

Size in vivo similar in most environmental populations, usually about 400 × 50 µm: type specimens 365 µm long on average (Ehrenberg 1833, 1838), French specimens 200–400 × 50–100 µm (Dujardin 1841), Russian cells 470–600 × 48–57 µm (Schewiakoff 1889, 1896), German cells usually 250–400 µm, rarely up to 600 µm long (Kahl 1931, Wenzel 1953, Bick 1972), North American specimens 200–600 × 30–40 µm (Visscher 1927b, Hayes 1938, Dumont 1961), Roumanian exemplar 320 µm long (Vuxanovici 1959), Moldavian specimen 375 µm long (Chorik 1968), and African cells 250–600 × 40–70 µm in size (Dragesco & Dragesco-Kernéis 1986, Foissner et al. 1995). Postdividers or rapidly dividing specimens only 100–155 × 40–50 µm in size (Hayes 1938), possibly explaining the small individuals (100–200 µm) observed by Dujardin (1841), Maskell (1887), Mermod (1914), Dingfelder (1962) and Matis (1977). Wrześniowski's (1870) specimens remarkably large, viz., 605–935 µm long, which matches our observations from the African population, where specimens reached 1 mm long.

Body very flexible but not contractile. Shape in vivo narrowly to cylindroidally dileptid, that is, length:width ratio on average 7:1 (4.5–12:1), according to the figures available in the literature and our own data based on micrographs and protargol preparations with Foissner's method, while 8.6–18.2:1 in preparations made with Wilbert's method, which caused strong shrinkage of body width (Table 51). Proboscis one third to one half of body length, slightly flattened, highly motile and flexible. Trunk cylindroidal to bluntly fusiform, unflattened, usually widest in mid-portion rarely in distal third. Posterior end with short or long tail preserved also in prepared cells and even in specimens inflated by food inclusions (Figs 91a–i, k–r, 92a, e, f, u, v, w, 93a, g, 94a–e, j, t).

Many macronuclear nodules and several micronuclei scattered in trunk and proximal third of proboscis, absent from tail. Macronuclear nodules difficult to count because numerous and of similar size as some cytoplasmic inclusions (Figs 92a, c, e, f, u, v, 94g, j, k, m, s): several hundreds to several thousands (Visscher 1927b), 180–400 in German specimens (Studitsky 1930), over 200 in North American cells (Hayes 1938), about 500 to 800 in Benin specimens (Fig. 94j), and 200–500 nodules according to Dragesco (1963). Maskell (1887) misinterpreted a defecation or food vacuole as a macronucleus, as evident from his illustration (Fig. 91l) and description: "nucleus globular, close to the posterior extremity", a pattern not found in any other species. Individual nodules highly variable in size and shape: globular to ellipsoidal, 0.1–1 µm across in Visscher's specimens (likely a mistake), about 5 µm across in Hayes' specimens, and 7 × 4 µm on average in Benin cells (Table 51). During cell division, each nodule divides by forming an enormously elongated, distinctly nodulated strand (Fig. 92i), as observed by Calkins (1926, 1933), Studitsky (1930), and Hayes (1938). Nodules may divide also in vegetative specimens (Hayes 1938), first increasing in size and becoming dumbbell-shaped before separating into two oblong pieces (Figs 92j–l). One central nucleolus in each nodule of Polish cells (Golińska 1971), while several nucleoli in African specimens (Fig. 94k). After Feulgen stain, chromatin as a cup over one half of nodule, as bands in irregular pattern over the nodule surface, or as irregular masses (Hayes 1938; Figs 92m, n). Micronuclei globular, inconspicuous both in vivo and in preparations (Fig. 94k): about 0.3–1.2 µm across according to Dragesco (1963), while 1.7–3.0 µm in Benin specimens after protargol impregnation (Table 51); surrounded by a distinct membrane in Feulgen stains (Hayes 1938); often difficult to distinguish from similarly sized and stained cytoplasmic inclusions or small macronuclear nodules, number thus difficult to determine: approximately 20 (Hayes 1938), while 6–12 according to Dragesco (1963).

Contractile vacuole pattern fairly similar in all populations mentioned in the synonymy list, viz., a dorsal stripe usually composed of usually more than 10 (4–20) vacuoles; no ventral vacuoles. First vacuole usually slightly anterior to level of oral bulge opening, in Dragesco's specimens also subapically and in

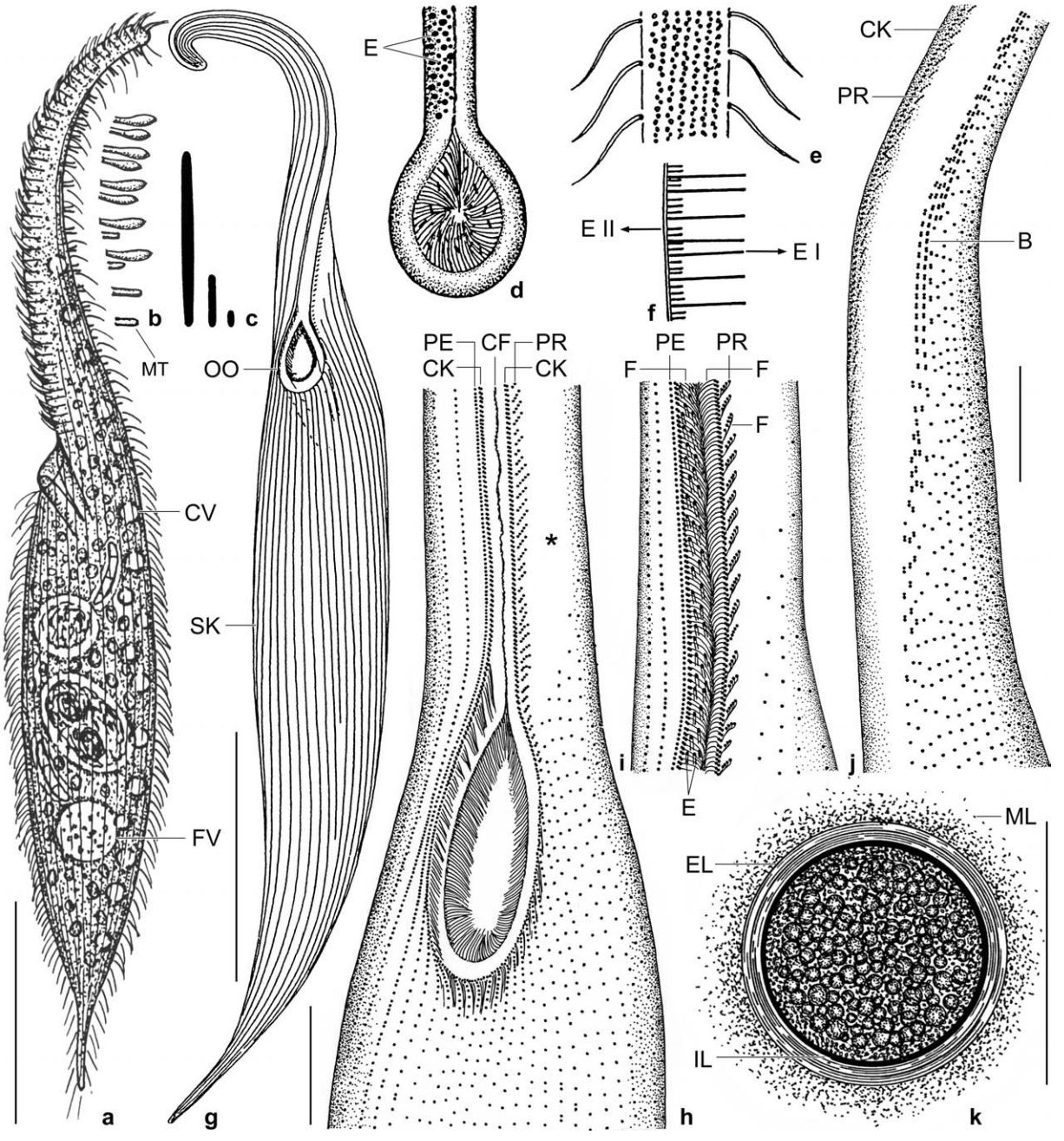
mid-proboscis. Number of excretory pores known only in Benin specimens, viz., one intrakinetal pore per vacuole (Figs 91a–f, h, i, l, m, o, q, r, 92a, e, f, u, v, w, 93a, 94a, r).

Extrusomes of toxicyst type, as speculated by Visscher (1923) and later confirmed by TEM studies (Dumont 1961, Grain & Golińska 1969). Toxicysts studded in broader right branch of oral bulge in Polish and Benin specimens (Figs 91j, 93d, i, 94o, p), while in both bulge branches in North American and Russian cells (Figs 92d, y), which is either a misobservation or an indication that these populations could be a different taxon. Shape and size studied only by us, but Visscher (1923) already recognized two types in preparations (Figs 92q, r). Type I rod-shaped with slightly narrowed ends, 9–12 × 0.5–0.8 µm in size; type II oblong, only 2–3 µm long and thus easily overlooked, more numerous than type I (Figs 93c, f, 94l, n, s). Kahl (1931), additionally, figured a ring of extrusomes (granules?) in the oral bulge opening, but did not mention this in the description (Fig. 91o). Developing toxicysts scattered throughout cytoplasm, of similar shape and size as oral bulge ones (Figs 94k, o, p, s). Toxicysts become swollen and tripartrite when fixed in Schaudinn's fluid and stained with acid fuchsin (Fig. 92s): neck, bulb, and terminal thread. Ultrastructure not yet studied in detail (Dumont 1961).

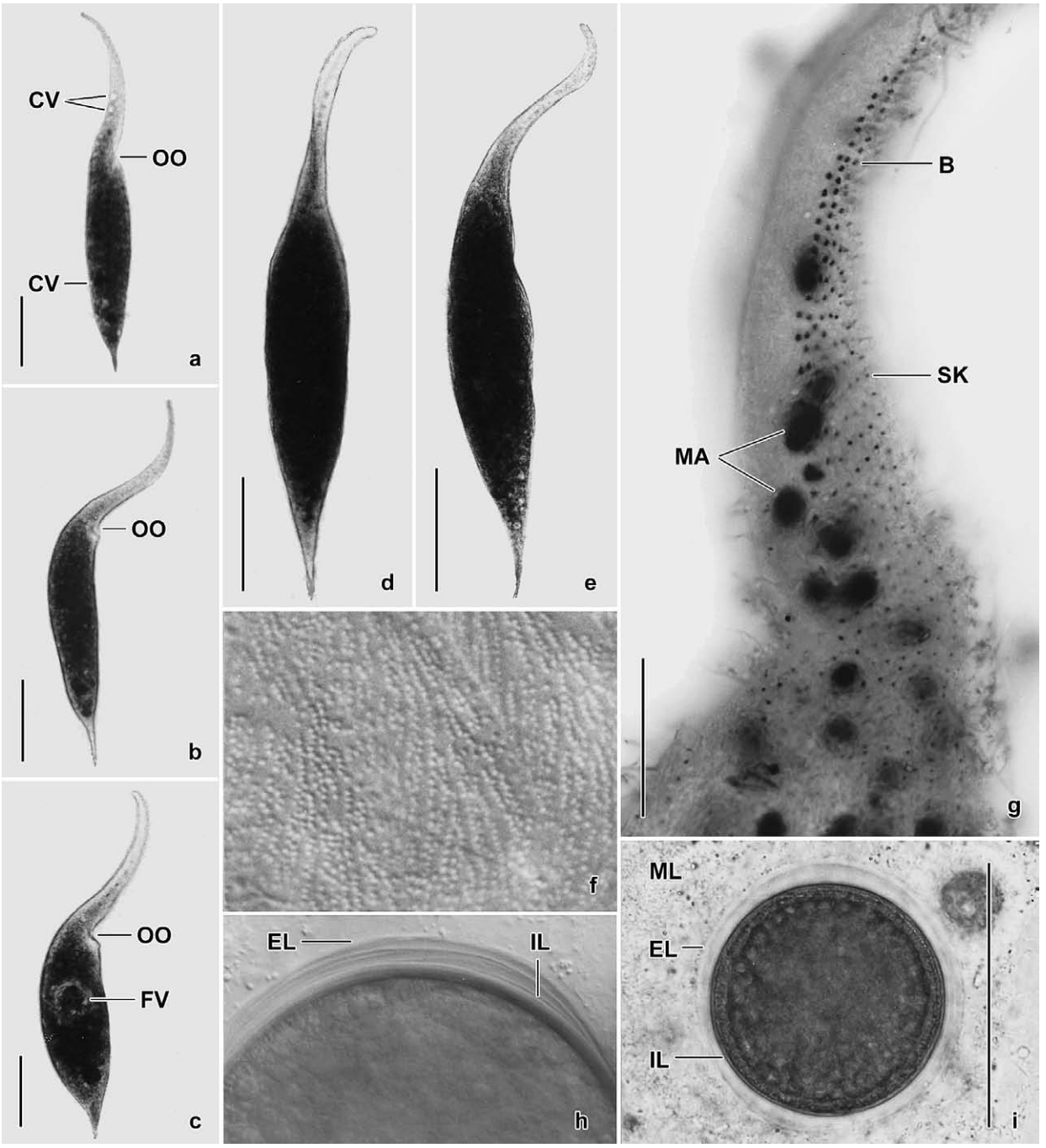
Cortex flexible, slightly furrowed by ciliary rows in SEM micrographs, contains about eight rows of very narrowly spaced, 1 µm-long, highly refractive granules between each two kineties (Figs 92x, 93e, 94f, r, t–y); granules of mucocyst type according to TEM studies (Grain & Golińska 1969). Silverline pattern composed of very small polygonal meshes about 0.5 µm in size, not yet studied in detail (Fig. 8g). Cytoplasm colourless; hyaline in proboscis and tail, opaque in trunk due to many food vacuoles. Often a defecation vacuole near base of tail, contains crystalline and granular material, empties ventrally (Fig. 91h). Movement slow, frequently restricted to the proboscis; spirals clockwise, about one rotation/length of body; ventral ciliature more active when swimming, dorsal ciliature more active during backward swimming after strong disturbance (Ludwig 1929).

Cilia about 10 µm long in vivo, narrowly spaced; in protargol preparations as typical for dileptids, i.e., with thick, strongly impregnated distal half, except for dorsal bristles. Ciliary rows narrowly spaced, with longitudinal to slightly helical course, number studied only in African populations, viz., 42–46 according to Dragesco (1963) and Dragesco & Dragesco-Kernéis (1986) and 40–50 according to Foissner et al. (1995; Figs 93g, 94t; Table 51). Details of ciliary pattern available only from Golińska (1971) and Foissner et al. (1995): (i) right side rows not shortened or only near anterior end of oral bulge, a feature difficult to recognize (Fig. 93g); (ii) first row right of circumoral kinety extends as perioral kinety with narrowly spaced cilia to tip of proboscis (Figs 92g, 93g–i, 94o, p); (iii) left side of proboscis with conspicuous blank stripe because several ciliary rows terminate slightly above oral bulge opening (Figs 92h, 93h–j, 94g, x). Dorsal brush already recognized by Quennerstedt (1869), forms a rather wide field on dorsal and dorsolateral area of proboscis, staggered, distinctly heterostichad, composed of up to twelve rows. First brush row begins usually in second third of proboscis, while last row commences subapically (Figs 93j, 94g, t). Brush dikinetids loosely to ordinarily spaced, associated with type II bristles: anterior bristles about 3 µm long in vivo (1.5 µm in SEM), posterior bristles gradually decreasing in length from about 1.3 µm to 0.7 µm (SEM measurements) becoming a conical stump in posterior dikinetidal brush region (Figs 93b, 94z). All rows continue with a monokinetidal tail extending to second third of body with type VI bristles 2–2.5 µm long in vivo (0.9–1.5 µm in SEM; Figs 93b, 94r, t, x, z).

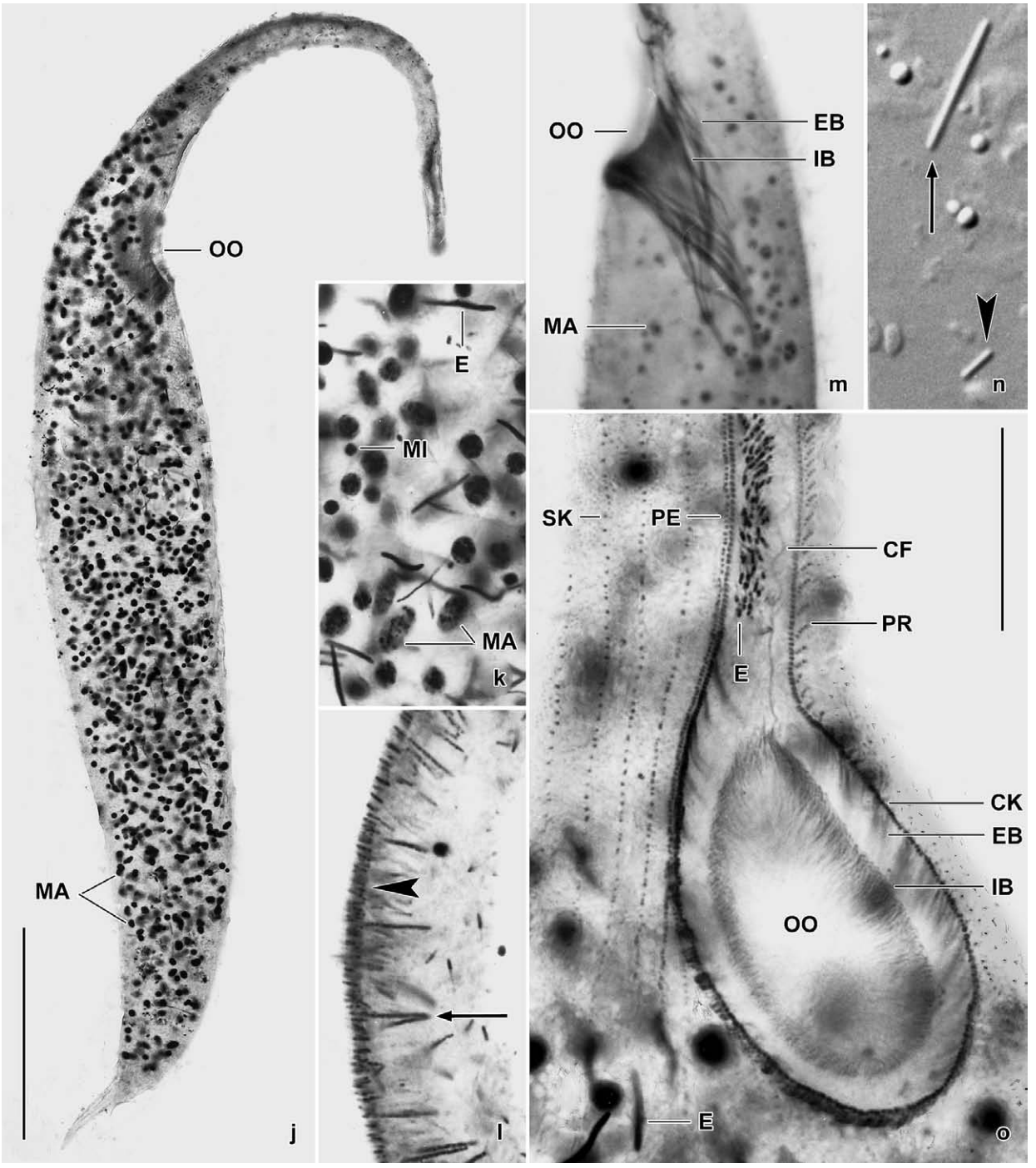
Oral bulge opening at beginning of second body third, projects distinctly because proboscis only half as wide as trunk, about 30 µm across in vivo, ovate to broadly ovate in Polish, North American, and Benin specimens, while narrowly elliptical in cells prepared with Wilbert's protargol method, a conspicuous artefact possibly occurring also in other species prepared with that method (cp. Figs 91j, n, 92d, o, p, y, 93d, g, 94u, y with Fig. 93h). Pharyngeal basket obconical, distinct both in vivo and in protargol



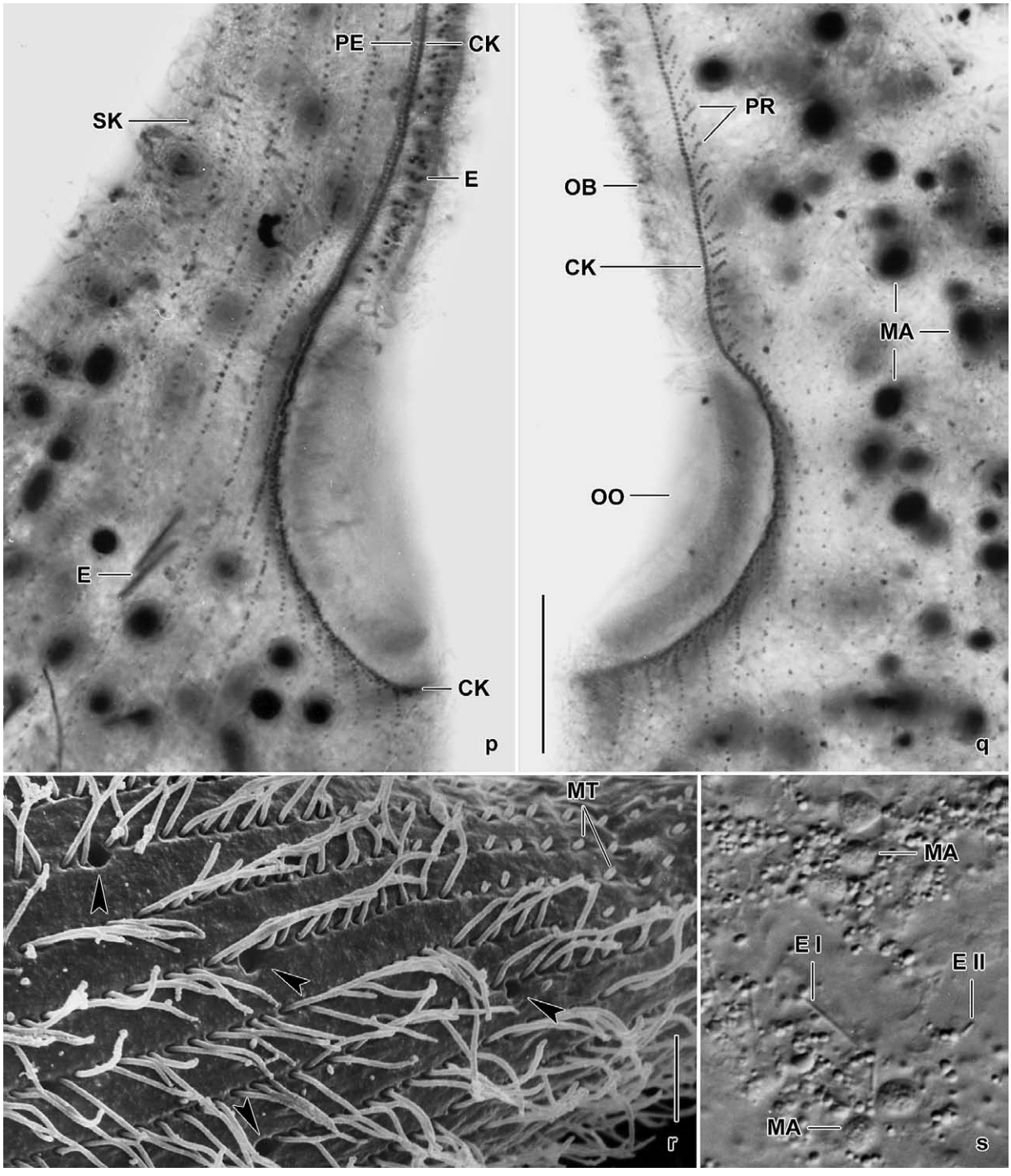
Figs 93a–k: *Dileptus margaritifer*, African specimens from life (a–f, k) and after protargol impregnation (g–j). From Foissner et al. (1995). **a** – right side view of a representative specimen, length 500 μm; **b** – the brush dikinetids are associated with clavate bristles, the posterior ones gradually decrease in length from anterior to posterior. All brush rows continue with monokinetidal tail bristles extending to the base of the proboscis; **c, f** – extrusome types: type I rod-shaped with slightly narrowed ends and 10 μm long, type II oblong and 3 μm long, cortical granules ellipsoidal and 1 μm long; **d** – frontal view of oral bulge and arrangement of extrusomes; **e** – surface view showing cortical granulation; **g** – semi-schematic view of ciliary pattern of ventral side, length 525 μm; **h, i** – ciliary pattern in oral region. Asterisk marks the blank stripe; **j** – dorsolateral view of proboscis' ciliary pattern; **k** – resting cysts are about 100 μm across and have a mucous cover. B – dorsal brush, CF – central fibre, CK – circumoral kinety, CV – contractile vacuoles, E(I, II) – extrusome (types), EL – external cyst layer, F – oral fibres, FV – food vacuole, IL – internal cyst layer, ML – mucous layer, MT – monokinetidal brush tail, OO – oral bulge opening, PE – perioral kinety, PR – preoral kineties, SK – somatic kineties. Scale bars: 20 μm (h, j) and 100 μm (a, g, k).



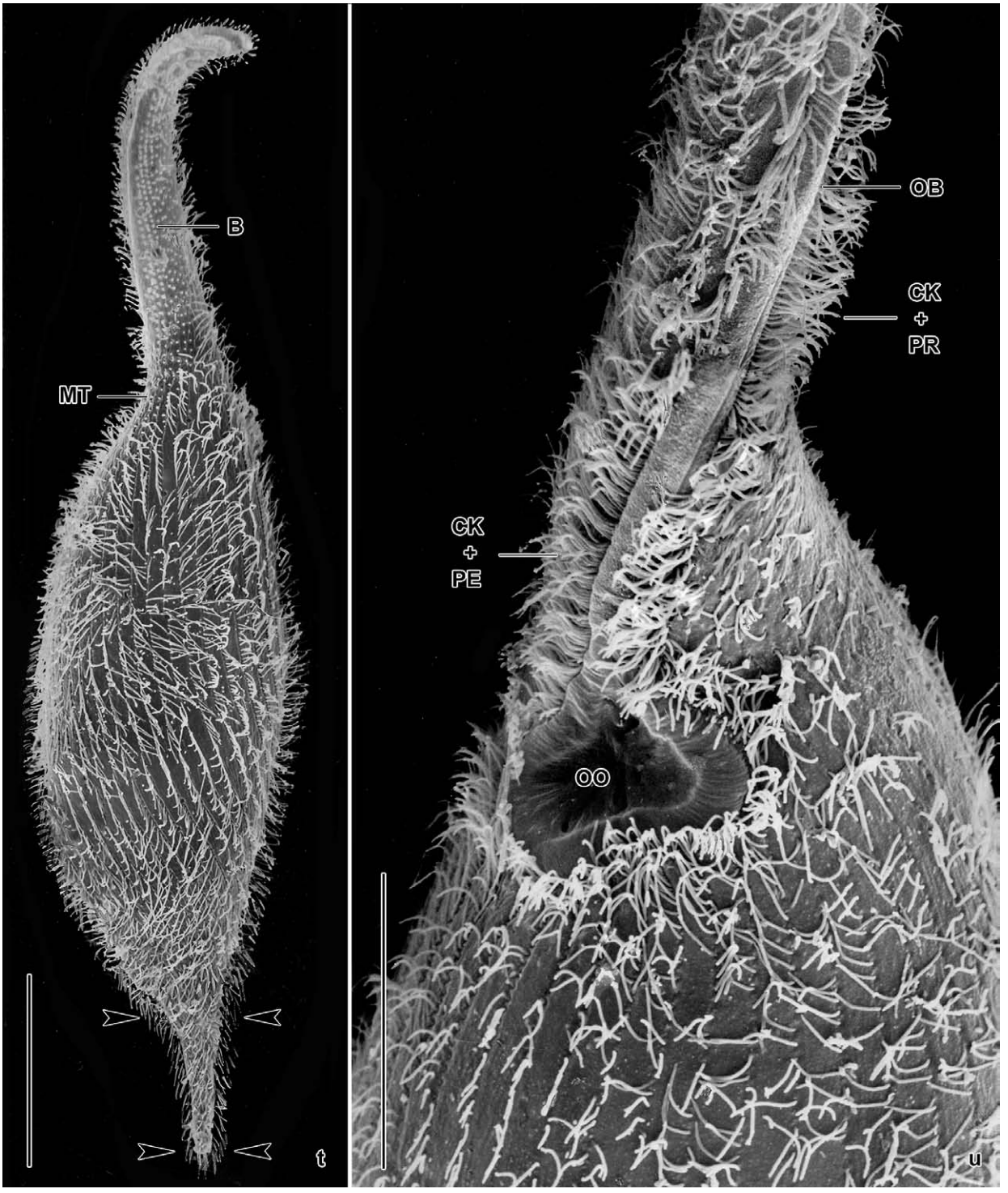
Figs 94a–i: *Dileptus margaritifer*, African specimens from life (a–f, h, i) and after protargol impregnation (g). From Foissner et al. (1995). **a–c** – right side view of two slender specimens (a, b) and a stout specimen having engulfed a *Paramecium* digested in a large vacuole; **d, e** – ventral and dorsal view of same specimen, showing the flattened, highly motile proboscis and the distinct tail; **f** – the cortex is studded with highly refractive, about 1 µm-long granules, forming about eight rows between each two somatic kineties; **g** – dorsolateral view of proboscis' ciliary pattern, showing the staggered, multi-rowed, and distinctly heterostichad dorsal brush; **h, i** – resting cysts are about 100 µm across and have two distinct layers: the external layer is hyaline, 3–5 µm thick, and has a fine lamination, while the internal layer is honey yellow, 2–3 µm thick, and compact. B – dorsal brush, CV – contractile vacuoles, EL – external cyst layer, FV – food vacuole, IL – internal cyst layer, MA – macronuclear nodules, MI – micronucleus, ML – mucous layer, OO – oral bulge opening, SK – somatic kinety. Scale bars: 20 µm (g) and 100 µm (a–e, i).



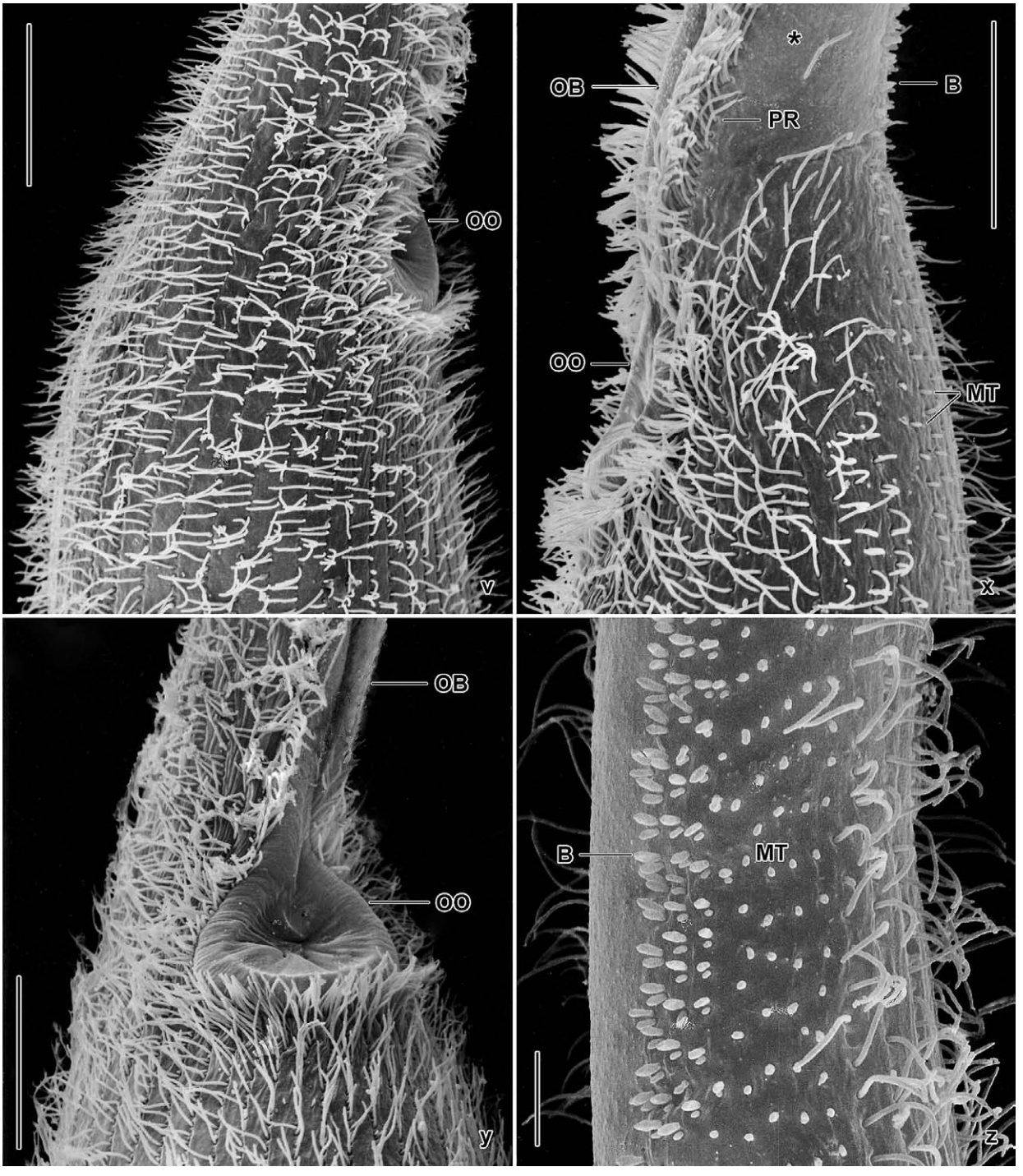
Figs 94j–o: *Dileptus margaritifer*, African (j–l, n, o; from Foissner et al. 1995) and Polish (m; from Golińska 1979) specimens from life (n) and after protargol impregnation (j–m, o). **j, k** – the nuclear apparatus consists of about 500 macronuclear nodules and many micronuclei; **l, n** – there are two types of rod-shaped extrusomes attached to proboscis oral bulge: type I (arrow) is 10 µm long, while type II (arrowhead) is only 3 µm long; **m** – lateral view showing internal and external oral basket; **o** – extrusome and oral ciliary pattern. Extrusomes are attached only to the broader right branch of the proboscis oral bulge. CF – central fibre, CK – circumoral kinety, E – extrusomes, EB – external basket, IB – internal basket, MA – macronuclear nodules, MI – micronucleus, OO – oral bulge opening, PB – pharyngeal basket, PE – perioral kinety, PR – preoral kineties, SK – somatic kinety. Scale bars: 20 µm (o) and 100 µm (j).



Figs 94p–s: *Dileptus margaritifer*, African specimens from life (s), after protargol impregnation (p, q), and in the SEM (r). From Foissner et al. (1995). **p, q** – right and left side ciliary pattern in oral region. The right branch of the circumoral kinety is accompanied by a perioral kinety, while the left branch is associated with many oblique preoral kineties; **r** – dorsal view of proboscis' posterior portion, showing scattered excretory pores (arrowheads); **s** – many extrusomes and macronuclear nodules are scattered throughout the cytoplasm. CK – circumoral kinety, E(I, II) – extrusome (types), MA – macronuclear nodules, MT – monokinetidal brush tails, OB – oral bulge, OO – oral opening, PE – perioral kinety, PR – preoral kineties, SK – somatic kinety. Scale bars: 5 μm (r) and 20 μm (p, q).



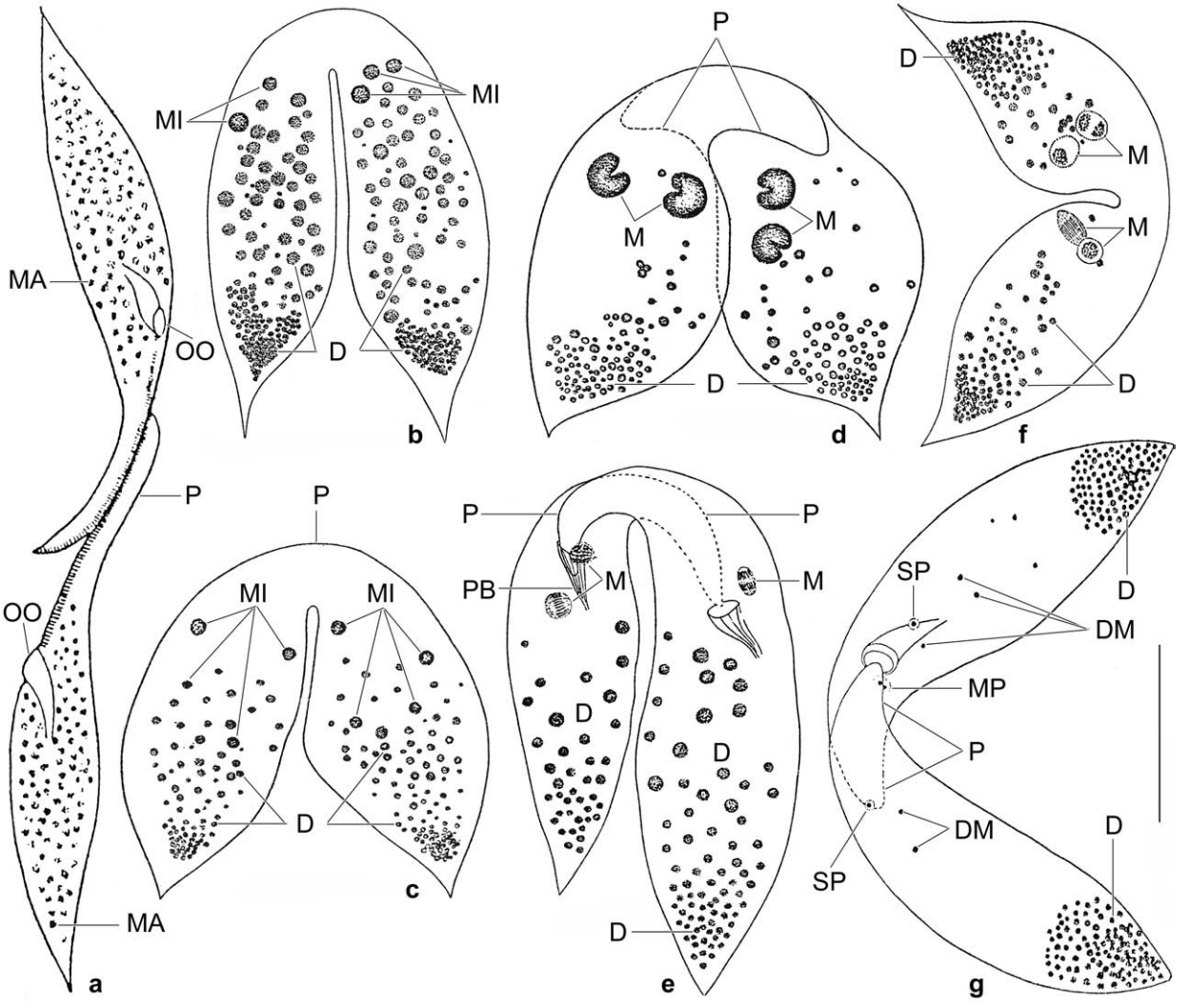
Figs 94t, u: *Dileptus margaritifer*, African specimens in the scanning electron microscope. From FOISSNER et al. (1995). **t** – left lateral view showing body shape, including the distinct tail (opposed arrowheads). The dorsal brush forms a conspicuous bristle field on the left and dorsal side of the proboscis; **u** – oral ciliature and roundish oral bulge opening. B – dorsal brush, CK – circumoral kinety, MT – monokinetidal tail, OB – oral bulge, OO – oral bulge opening, PE – perioral kinety, PR – preoral kineties. Scale bars: 30 μm (u) and 50 μm (t).



Figs 94v–z: *Dileptus margaritifer*, African specimens in the SEM. From FOISSNER et al. (1995). **v, x** – right and left side view of oral body portion.On the left side, many ciliary rows end slightly above the oral opening, producing a blank stripe on the proboscis (asterisk and Figs 93h, j); **y** – ventral view showing the roundish oral bulge opening; **z** – dorsal view of proboscis' posterior portion. The brush dikinetids are associated with type II bristles: the anterior bristles are longer than the posterior ones, which slightly decrease in length from anterior to posterior. All rows continue with a monokinetidal tail having type VI bristles. B – dorsal brush, MT – monokinetidal tails of dorsal brush, OB – oral bulge, OO – oral bulge opening, PR – preoral kineties. Scale bars: 5 μm (z) and 20 μm (v–y).

preparations, internal and external basket clearly separate (Figs 92o, p, y, z, 93h, 94m, o). Circumoral kinety composed of narrowly spaced dikinetids in proboscis and of narrowly spaced monokinetids around oral bulge opening (Figs 92g, h, 93h, i, 94o–q). Preoral kineties oblique to slightly oblique, ordinarily to narrowly spaced, each composed of three to six, usually four narrowly spaced cilia (Figs 92h, o, p, 93h–j, 94o, q, x), as first described by PESCHKOWSKY (1931) and later confirmed by GOLIŃSKA (1971) and FOISSNER et al. (1995).

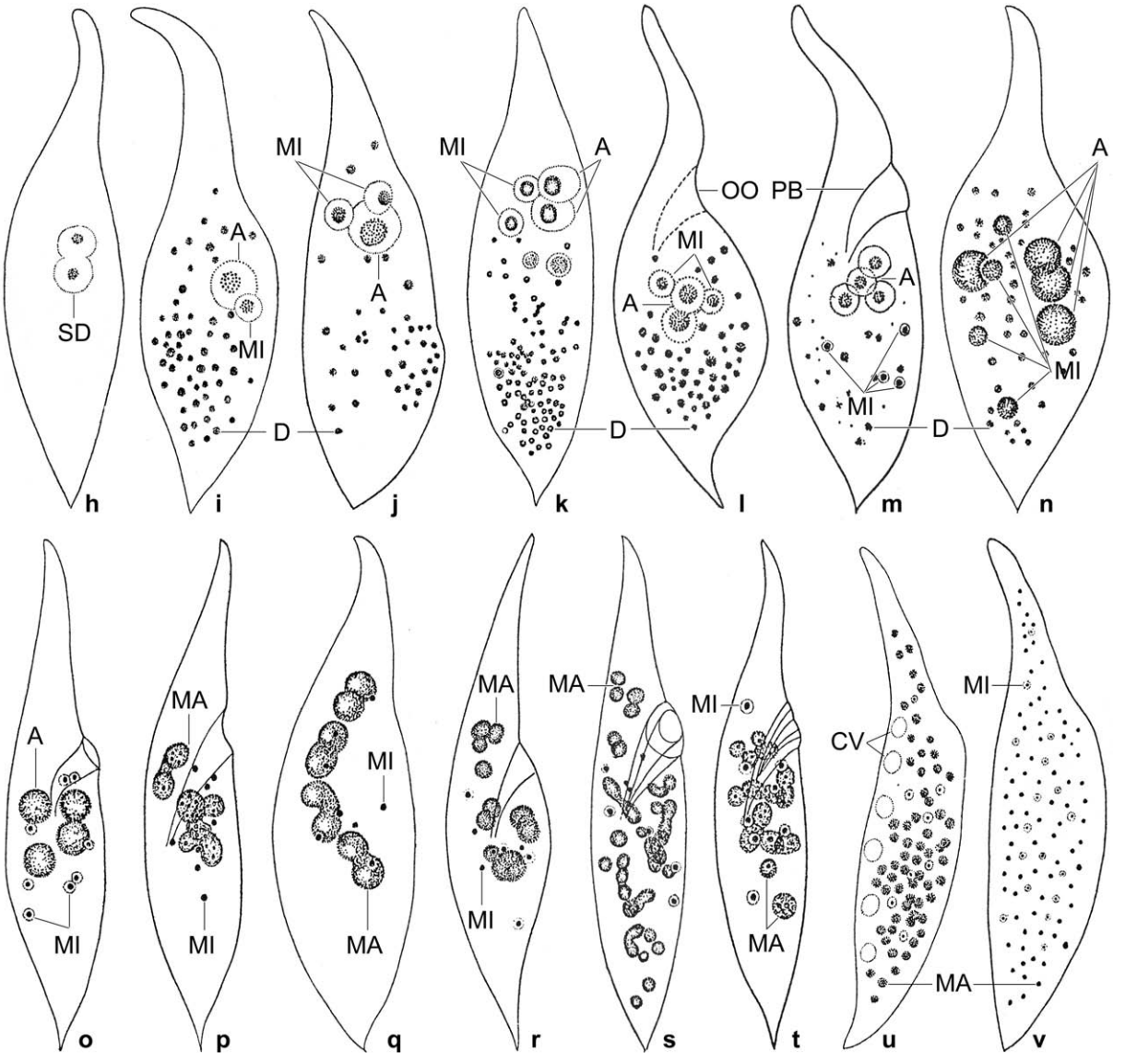
Resting cyst (Figs 93k, 94h, i; Table 51): Resting cysts of Benin specimens about 100 µm across in vivo, globular to rotund, honey yellow, without escape apparatus. Cyst wall made of two distinct layers:



Figs 95a–g: *Dileptus margaritifer* conjugants after acid borax carmine stain (from VISSCHER 1927b). **a** – very early stage showing uniting partners; **b, c** – fully developed pairs, where several micronuclei move into the anterior portion of the trunk and conspicuously increase in size, while the macronuclear nodules migrate to the posterior part of the body and start to degenerate; **d** – prophase of second maturation division; **e** – occasionally, the longer partner shows the metaphase of the first maturation division, while the shorter partner shows the metaphase of the second maturation division; **f** – ordinary second maturation division; **g** – exchange of the migratory pronuclei. D – degenerating vegetative macronuclear nodules, DM – degenerating maturation derivatives, M – maturation derivatives, MA – macronuclear nodules, MI – micronuclei, MP – migratory pronuclei, OO – oral bulge opening, P – proboscis, PB – pharyngeal basket, SP – stationary pronuclei. Drawn to scale, bar 50 µm.

external layer 3–5 µm thick, hyaline and colourless, finely laminated; internal layer 2–3 µm thick, honey yellow, compact. Cyst wall covered by an up to 50 µm thick, hyaline, colourless mucous layer distinct under interference contrast while easily overlooked in bright field. Cyst contents partited into a 4–6 µm wide peripheral, finely granular layer and a large central area packed with globules 3–6 µm across. Macronuclear nodules fused into an ellipsoidal, central mass.

Conjugation and postconjugational processes (Figs 95a–w): Conjugation and postconjugational events



Figs 95h–v: *Dileptus margaritifer* exconjugants after acid borax carmine stain (from VISSCHER 1927b). The processes shown need at least two days. **h, i** – derivatives of the first synkaryon division, body length 137 µm and 143 µm; **j–l** – derivatives of the second synkaryon division, body length 156 µm, 164 µm, and 104 µm; **m–o** – derivatives of the third synkaryon division, body length 186 µm, 135 µm, and 145 µm; **p–v** – the macronuclear anlagen divide amitotically, while the micronuclei divide mitotically until the vegetative nuclear pattern is obtained, body length 145 µm, 145 µm, 125 µm, 162 µm, 125 µm, 322 µm, and 148 µm. A – macronuclear anlagen, CV – contractile vacuoles, D – degenerating vegetative macronuclear nodules, MA – macronuclear nodules, MI – micronuclei, OO – oral bulge opening, PB – pharyngeal basket, SD – synkaryon derivatives.

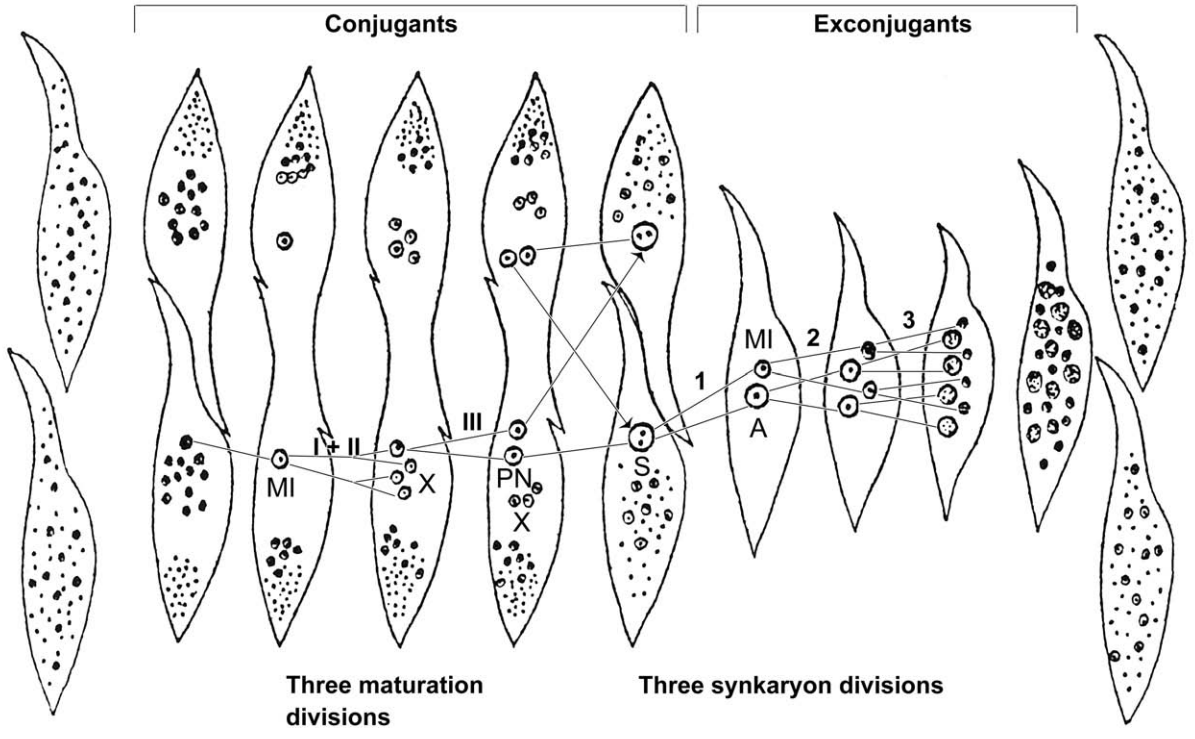


Fig. 95w: Scheme of the nuclear processes during and after conjugation of *D. margaritifer* (from VISSCHER 1927b). There are three maturation and three synkaryon divisions, which produce four macronuclear anlagen and four new micronuclei. The macronuclear anlagen divide amitotically, while the micronuclei divide mitotically until the vegetative nuclear pattern is obtained. I, II, III – maturation divisions, 1–3 – synkaryon divisions, A – macronuclear anlagen, MI – micronuclei, PN – pronuclei, S – synkaryon. Crosses mark degenerating maturation derivatives.

were excellently described by VISSCHER (1927b), using cultivated specimens from the Creve Coeur Lake near St. Louis, Missouri, USA. Both processes are similar to those described for *Rimaleptus tirjakovae* (VĎAČNÝ & FOISSNER 2008a) and *Pseudomonilicaryon thononense* (present study), however, with some variation.

There are two preconjugation divisions making the cells distinctly shorter (175 µm) than vegetative specimens (400 µm). The union mode is temporary. Pair formation is heteropolar, and the partners unite bulge-to-bulge with the proboscis (Fig. 95a). During the initial stages, the proboscis shortens markedly providing maturating conjugants with an *Enchelyodon*- or *Protospathidium*-like appearence, i.e., they resemble "polar" haptorids without proboscis (Figs 95b–f). After synkaryon formation, which occurs about twelve hours after union, the shape of the partners becomes *Spathidium*-like, and subsequently they separate (Fig. 95g). About twelve hours after separation, the vegetative body shape is regained, while attainment of the vegetative size takes about four days.

The nuclear processes are as follows (Fig. 95w): (i) several micronuclei move into the anterior portion of the trunk and conspicuously increase in size but only one of them enters the first maturation division (Figs 95b, c); (ii) the second maturation division generates four maturation derivatives that start to degenerate, except for one which undergoes the third maturation division producing two pronuclei (Figs 95d–g); (iii) a synkaryon each is formed in the partners by fusion of the migratory pronucleus with the stationary one; (iv) there are three synkaryon divisions producing four macronuclear anlagen and four new micronuclei (Figs 95h–o); (v) the macronuclear anlagen and the micronuclei divide until the vegetative nuclear pattern is obtained (Figs 95p–v); (vi) in early conjugants, the vegetative macronuclear nodules migrate into the

posterior part of the body and degenerate. The resorption of the nodules is completed about two days after separation of the partners (Figs 95b–g, i–n); (vii) unlike in *Rimaleptus tirjakovae*, there are no degenerating synkaryon derivatives and the degenerating macronuclear nodules do not fuse.

Notes on ontogenesis (see also general part): The formation of the opisthe's infraciliature was studied by Golińska (1995), using transmission electron microscopy and protargol impregnation. Basically, the process agrees with data from *Monomacrocaryon terrenum* recently published by Vďačný & Foissner (2009): (i) stomatogenesis is holotelokinetal; (ii) small anarchic fields, formed at the anterior end of the broken ciliary rows, develop into circumoral kinetofragments growing and uniting as the circumoral kinety; (iii) the ventral circumoral kinetofragments are composed of monokinetids, while the kinetofragments originating from the lateral and dorsal kineties are composed of dikinetids; (iv) all oral fibres are at first directed anteriorly, later on they orientate towards the centre of the oral bulge opening; (v) the perioral kinety is formed by alignment of the densely ciliated anterior region of the right side ciliary rows; (vi) the preoral kineties are produced by splitting of the anterior region of the dorsal and some left side ciliary rows into several minute pieces that migrate rightwards along the circumoral kinety; (vii) the dorsal brush develops after the production of the preoral kineties.

Occurrence and ecology (mainly from Foissner et al. 1995): Pure cultures of *Dileptus margaritifer* can be obtained with tap water or Pringsheim's solution as a medium and *Colpidium colpoda* and/or a species of the *Tetrahymena pyriformis* complex as food. The washed food organisms are added daily. For review and references on how to cultivate the food ciliates, see Chapter 9.1.3. Cultivation.

In most studies, this species is called *Dileptus anser* because the determination usually followed Kahl (1931). *Dileptus margaritifer* occurs year-round with frequency peaks in spring (Fig. 96); common but rarely abundant in organic mud and between algae and water plants of eutrophic puddles and ponds (Liebmann 1962, Bick & Kunze 1971); rare in plankton (e.g., Korniyenko 1972, Beaver & Crisman 1989). Also in ephemeral habitats, such as shallow meadow puddles, rainwater pools (Dingfelder 1962, Detcheva 1972), mosses (*Bryum argenteum*, *Ceratodon purpureus*, and *Brachythecium albicans*) and soil, showing the ability to produce resting cysts (Foissner et al. 1995, Andelová & Tirjaková 2000). Rare in activated sludge plants (Marco et al. 1991), percolating filters (Curds 1975), and rotating biological contactors (Madoni 1981). Eurytherm (Gajewskaja 1933), but a large data set from German rivers suggests a preference for cold water (Fig. 96). The Upper temperature limit is 25 °C according to Bick & Bertram (1973). However, Gittleson & Ferguson (1971) found *D. margaritifer* in relatively hot waters (15–17 °C), and Matis & Straková-Striešková (1991) reported it from thermal waters of Slovakia at 19–42 °C and pH 5–6.8. Rapid cooling from room temperature to 3 °C does not cause encystment (Rammelmeyer 1931). Agamaliev (1986) reported it from freshwater and brackish bays (0.2–0.34% salinity) of the Caspian Sea;

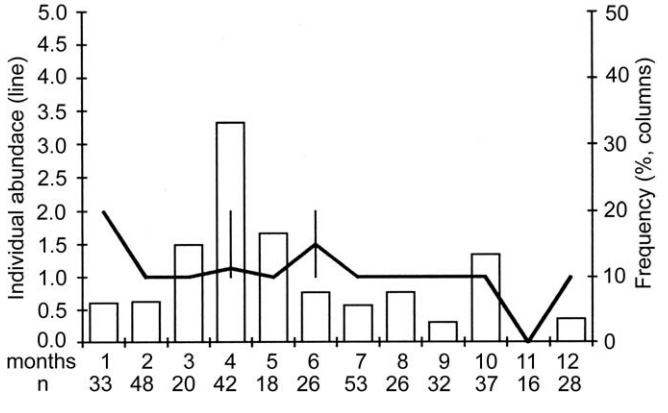


Fig. 96: Ecogram of *Dileptus margaritifer* (from Foissner et al. 1995). Frequency (%) and average estimated abundance (bars = minimum, maximum according to the Zelinka & Marvan scale: 1, 2, 3, 5, 7, 9) in the beta- to alpha-mesosaprobic Amper River and Vils River in Bavaria during the years 1987–1991. The average abundance (line) was calculated from the estimated abundance per record. n – number of samples per month.

Table 51: Morphometric data on *Dileptus margaritifer* from soil of Benin, Africa (calculated from original data of FOISSNER et al. 1995). Data based, if not stated otherwise, on mounted, protargol-impregnated (Wilbert's method), and randomly selected specimens from a non-flooded Petri dish culture. Measurements in µm. CV – coefficient of variation in %, M – median, Max – maximum, Mean – arithmetic mean, Min – minimum, n – number of specimens investigated, SD – standard deviation, SE – standard error of mean.

Characteristics	Mean	M	SD	SE	CV	Min	Max	n
Body, length	723.8	730.0	72.9	20.2	10.1	600.0	810.0	13
Body, width	52.6	50.0	8.9	2.5	17.0	40.0	70.0	13
Body length:width, ratio	14.1	14.6	2.6	0.7	18.7	8.6	18.2	13
Body length:width, ratio (from in vivo micrographs)	7.0	7.0	1.0	0.2	14.3	5.2	8.5	21
Anterior body end to oral bulge opening, distance	290.4	300.0	35.7	9.9	12.3	210.0	340.0	13
Proboscis, % of body length	40.3	39.5	5.4	1.5	13.3	33.8	52.5	13
Macronuclear nodules, length	5.8	6.0	1.4	0.4	24.3	3.5	8.0	13
Macronuclear nodules, width	3.3	3.0	0.5	0.1	14.2	3.0	4.5	13
Macronuclear nodules, number	about 500							
Micronuclei, diameter	2.2	2.2	0.3	0.1	14.2	1.7	3.0	13
Micronuclei, number	many							
Ciliary rows, number	45.5	46.0	3.8	1.1	8.4	40.0	50.0	12
Resting cysts, length (in vivo)	97.9	100.0	10.3	2.4	10.5	80.0	110.0	19
Resting cysts, width (in vivo)	95.2	100.0	11.6	2.7	12.2	75.0	110.0	19

DUMITRACHE (2003) from the psammon of the Black Sea; KRIEG (2000) from brackish water (Isebekkanal) in Hamburg, Germany; and TELESH et al. (2008) from the eastern Baltic Sea. ALBRECHT (1984) classified *D. margaritifer* as a holoeuryhaline freshwater species on base of literature data and his investigations of oversalted rivers in Germany (salinity 0 to > 3%); PATTERSON et al. (1989) did not mention it in their review of ciliates from marine sands. Feeds on flagellates (e.g., *Euglena*, *Chilomonas paramecium*, *Trachelomonas*), amoebae, ciliates (e.g., *Blepharisma japonicum*, *Coleps hirtus*, *Colpidium colpoda*, *Colpoda*, *Didinium nasutum*, *Halteria*, *Lacrymaria olor*, *Paramecium*, *Spirostomum ambiguum*, *Stentor*, *Tetrahymena pyriformis*, *Urocentrum turbo*, *Vorticella* and hypotrichs), and small metazoans, such as rotifers, planarians and oligochaetes (VISSCHER 1923, RAMMELMEYER 1931, GAJEWSKAJA 1933, HAYES 1938, DRAGESCO 1962, JANOVY 1963, KHLEBOVICH 1976, SERAVIN & ORLOVSKAJA 1977, BICK 1972a, FOISSNER 1980, TOŁŁOCZKO 1980, ORLOVSKAJA et al. 1984, own observations). Diatoms, coccal green algae, fungal spores and bacteria are also consumed (KALMUS 1928, DINGFELDER 1962, FOISSNER 1980, GRACIA & IGUAL 1987b). When fed on pieces of planarians (*Dugesia tigrina*), gigantism and monster formation occurred (JANOVY 1963). Generation time about 17 h at an uptake rate of 10–13 *Tetrahymena* cells/h (KHLEBOVICH 1976); about 11 h at 20 °C according to PETROVA et al. (1976); one to three divisions within 24 h, depending on temperature (POPOFF 1908; misidentified as *Dileptus gigas*). Biomass of 10^6 specimens: 1876 mg (DILLON & HOBBS 1973), about 500 mg when an average size of 400 × 50 µm is assumed (FOISSNER et al. 1995), 170 mg (FOISSNER 1987a). At an average of 12 mg/l O_2 and 4.7 mg/l BSB_5 in a Spanish river (IGUAL 1990); at 0.7–5.1 mg/l DOC in Swiss running waters with increased occurrence under moderate organic

Table 52: Autecological data on *Dileptus margaritifer*. Column 1 from BICK (1972a) and BICK & KUNZE (1971; summary of data from literature); column 2 from DETCHEVA (1978, 1983a, b; many analyses from Bulgarian running waters); column 3 from MIHAILOWITSCH (1989; 15–16 analyses from salt-polluted running waters in Germany); column 4 from BERECZKY (1975; many analyses from the mesosaprobic Danube River in Hungary); column 5 from FOISSNER et al. (1982; 31 analyses from various small, to some extent dystrophic, alpine waters in Austria); column 6 from PATRICK et al. (1967; many analyses from the Savannah River in the USA); column 7 from FOISSNER et al. (1995; 5–6 analyses from various Austrian rivers).

Parameters	References						
	1	2	3	4	5	6	7
Saprobity	–	b, a	–	–	b-a	–	2.1–2.5[b]
Frequency (%)	–	0.95–1.80	–	–	–	–	5.00
Temperature (°C)	0.0–22.0	11.2–25.0	4.2–20.0	8.0–21.0	5.0–19.5	14.5–25.5	5.0–13.0
pH	7.8–8.6	7.2–7.6	7.2–8.0	7.2–7.8	4.7–5.8	–	7.0–8.5
O_2 (mg/l)	2.5–18.0	5.5–8.2	2.9–3.5	7.8–14.4	3.0–12.8	–	7.7–12.8
O_2 (saturation %)	–	67–83	–	–	37–161	–	65–128
BSB_5 (mg/l)	–	5.4–11.2	–	4.0–6.8[a]	–	0.5–<5.0	1.1–4.6
$KMnO_4$ (mg/l)	–	–	–	–	9–76	–	5–17
CO_2 (free, mg/l)	0.0–16.0	–	9.1–89.4	–	0.0–7.9	>1–10	–
NH_4^+-N (mg/l)	0.0–1.4	0.02–0.31	0.09–4.8	≤0.46	0.0–6.2	0.005–0.04	<0.02–0.13
NO_3^--N (mg/l)	–	0.0–12.8	1.1–13.4	0.58–5.0	0.0–0.68	≤0.2	0.38–2.9
NO_2^--N (mg/l)	–	0.0–0.36	0.03–0.1	0.0–0.025	0.0–3.9	–	<0.03
Cl^- (mg/l)	–	–	39–8225	–	–	1–<8	3–56
Number of bacteria/ml ($\times 10^6$)	–	–	–	–	0.22–10[c]	–	<0.0027[d]

a O2-used.

b Calculated saprobic index.

c Direct counting.

d Counted using plate method (22 °C).

pollution (STÖSSEL 1979); in the mud-water contact zone (-1 to +1 cm sediment depth) of stagnant waters in the surroundings of the town of Bonn, Germany under the following conditions (REINNARTH 1979): pH 7.2–7.3, -76 to +173 mV redox potential, 0.15–2.43 mg/l NH_4^+-N, and 1–11.2 mg/l NO_3^--N. Further abiotic parameters, see Table 52. LD_{50} 20–30 minutes with the detergent SDS (sodium dodecyl sulfate) at 5×10^{-6} g/ml; LD_{50} three minutes with the detergent CTAB (cetyl trimethyl ammonium bromide) at 5×10^{-6} g/ml; in 0.1 g/ml of neutral Tween 40 (sorbitol monopalmitate), the cells survived more than 24 h (BRUTKOWSKAYA & ORLOVSKAJA 1981). The effects of various surfactants on food uptake were studied by ORLOVSKAJA & BRUTKOWSKAYA (1985). SAROJINI & NAGABHUSHANAM (1967) provided the following data for respiration: volume 0.000212 mm^3, square area 0.032 mm^2, S/V 150, on average 84 (76–98) mm^3 O_2/hr/million ind., (S/V)/resp. rate 1.7 (denoted as *Dileptus granulosus*).

There are over 500 further records. We did not include all of them but selected for biogeographic regions and interesting habitats. Further, most of the records of *Dileptus gigas* likely belong to this species.

Records from running waters: rather rare in the periphyton of beta-mesosaprobic and beta- to alpha-mesosaprobic rivers in Austria and Germany (HASLAUER & HAIDER 1976; BERNERTH 1982; AUGUSTIN et al. 1987; FOISSNER et al. 1992a, 1992b; AOÖLR 1993a, 1993b; BLATTERER 1994); in the periphyton of

polysaprobic mountain brooks in Germany (Bauer 1987); up to 8 ind./cm^2 in mesosaprobic north Italian rivers (Madoni & Ghetti 1977, 1980, 1981; Madoni 1979, 1980, 1993, 2005); in the water-sediment interface of the polluted Stirone and Mincio rivers, Italy (Madoni & Bassanini 1999, Madoni & Braghiroli 2007); Taro River, Italy (Madoni & Zangrossi 2005); in an alpha-mesosaprobic part of a Spanish river (Gracia & Igual 1987a, b); Llobregat River in Barcelona, Spain (Gracia et al. 1989); in beta-metasaprobic brooks and rivers of the former Czechoslovakia (Šrámek-Hušek 1956a, 1957; Buchar 1957; Matis 1967; Matis & Tirjaková 1992, 1995; Szentiványi & Tirjaková 1994; Tirjaková 1998, 1997a, 1997b, 2001, 2003; Tirjaková & Stloukal 2004); in the seston and sediment of beta-mesosaprobic and beta- to alpha-mesosaprobic parts of Polish rivers (Czapik 1975, 1982; Hul 1987; Wiąckowski 1981); in the Raba River, southern Poland (Komala 2000); in October rare in the free water and on artificial substrates in the mesosaprobic Danube River in Hungary (Bereczky 1977b, Bereczky et al. 1983); Roumanian part of the Danube River (Enăceanu and Brezeanu 1970); frequent in the periphyton of oligosaprobic karst waters in the former Yugoslavia (Primc-Habdija & Habdija 1991, Primc-Habdija et al. 2000); in rivers with tufa deposition, Croatia (Primc-Habdija et al. 2001); various rivers in Bulgaria (Russev et al. 1994); in the periphyton and plankton of the Tisa River in the Ukraine (Kovalchuk 1997a, 1997b); in Ukrainian streams and rivers (Kravchenko 1969); in summer in the Lielupe River, Latvia (Liepa 1973); in the benthic mud of the Volga and the Oka River as well as in various Latvian and Ukrainian rivers (Neiswestnowa-Shadina 1935; Mamaeva 1976b, 1979c; Veylande & Liepa 1985; Kovalchuk & Kovalchuk 1992); Souxiyu Nature Reserve area, Hunan Province, China (Shen & Gong 1989); Changjiang River, China (Shen et al. 1994); in two out of eight stations in the South River, Virginia, USA (Cairns & Dickson 1972); in the benthic mud of the Amazon River (Cairns 1966); in January and March in an Argentinian river in the root area of water plants (Pettigrosso & Cazzaniga 1987).

Records from slowly running and stagnant waters: worldwide in oligo- to hypertrophic puddles, ponds, lakes, and backwaters (e.g., Bovee 1960; Levander 1984, Švec 1897, Schmidt 1916, Wang & Nie 1935, Matis 1961, Kwiatkowska-Grabacka 1964, Cairns & Yongue 1966, Wilbert 1969, Njiné 1977, Kusano 1985); in bog ponds and wet and dry mosses (Jacobson 1928, Wenzel 1953, Messikommer 1954, Tirjaková & Matis 1987); rare in puddles with litter, temporary forest puddles, and in the sediment of fishponds (Bick 1958, Kramer 1964, Kwiatkowska-Grabacka 1965, Siemińska & Siemińska 1967, Grabacka 1971); in a strongly slurry-polluted and in three slightly polluted process waters (Lieb et al. 1956); in sewage (Nishimura et al. 2001) and trickling filters (Lackey 1938); in aquariums (Günkel 1997); sometimes numerous between *Vorticella* colonies on *Lemna* and *Ceratophyllum* in Berlin (Ehrenberg 1838); caves in Germany (Gittleson and Hoover 1969); on various substrates and in the plankton of a slightly mesotrophic and strongly siderotrophic lake (Plußsee) in Germany (Ehlers 1965, Mücke 1979); rarely in the periphyton of the Poppelsdorfer Weiher (pond) in the town of Bonn, Germany (Wilbert 1969); infrequent in a mesosaprobic region of a lowland brook in Lower Rhineland, Germany (Heuss 1976); scant in the sediment of the Hamburg harbour (Bartsch & Hartwig 1984); in the sandy hyporheic zone of a lowland stream in Germany (Cleven 2004); Polderwater, The Netherlands (Verschaffelt 1930); in the littoral of Lake Majeur, Switzerland (André, 1915); many sites, including *Sphagnum* ponds, in Switzerland (André 1912, Mermod 1914, Bourquin-Lindt 1919); various water bodies in the surroundings of the town of Basle, Switzerland (Riggenbach 1922); widespread in various small, mesosaprobic alpine water bodies (Wolff 1948, Foissner & Adam 1979, Foissner 1980); surroundings of the town of Bologna and other sites in Italy (Enriques 1913, Dini et al. 1995); in an Italian rice-field irrigated with sewage water (Madoni 1988); in the plankton of Lake Massaciuccoli in Western Tuscany, Italy (Mori et al. 1996); in a bog pond in France (Grolière & Njiné 1973); in the aerobic sediment of a eutrophic lake in England (Webb 1961; Bryant & Laybourn 1974); Clare Island, Ireland (Dunkerly 1913); together with *Paramecium bursaria* and *Halteria* in a Finnish lake at pH 7.4 and 15 °C (Kościuszko & Prajer 1988); in a dystrophic lake in the

Wigry National Park, Poland (Czapik & Fyda 1995); in the Goczałkowice reservoir in Poland (Krzyżanek & Krzyżanek 1986); in the plankton of an aritificial pond in the Botanical Garden of the University in Kraków, Poland (Komala & Przyboś 2001); in the periphyton of lakes in Poland (Mieczan 2005); frequent in various beta-mesosaprobic running and stagnant waters of the Czech Republic (Šrámek-Hušek 1952); on the strongly polluted coast of a water reservoir in Slovakia (Matis 1977); Turiec river basin in the West Carpathians, Slovakia (Tirjaková 1993, Tirjaková & Degma 1996); Kalános stream in Hungary (Vörösváry 1950); alkaline ponds in the Hortobágy National Park, Hungary (Szabó 1999); in tributaries to the Black Sea, Bulgaria (Detcheva 1979); aquatic biotopes of the Rhodopes Mts. and many sites in Bulgaria (Detcheva 1992, 2004); ponds on the island of Corfu, Greece (Stephanides 1948); Palestine (Bodenheimer 1937); 6 ind./cm^2 in the muddy, sandy sediment of a nutrient-poor lake in Israel (Madoni 1990); surroundings of the town of Kiev, Ukraine (Dobrovliansky 1914); in the pelagial of beta- and alpha-mesosaprobic reservoirs in Azerbaijan, and in October with up to 76 ind./l in the pelagial of a lake close to the town of Gorki (Petrova et al. 1976; Alekperov 1982, 1984); lakes in Azerbaijan (Aliev 1982, 1988); cooling plant in Moldavia (Chorik & Vikol 1973); various water bodies in Armenia (Zharikov 1982); Volga river basin (Zhukov et al. 1998); in the summer plankton of the River Moscow, Russia (Belova 1998); delta of the Volga River, former USSR (Kosova 1965); Divichinskyi estuary of the Caspian Sea (Agamaliev & Aliev 1983); in the plankton and periphyton of various lakes and water reservoirs of the former USSR (Korniyenko 1972; Mamaeva 1974; Arslanova 1980; Oleksiv 1985; Alekperov 1980, 1988, 1989; Myl'nikova 1992a, 1993; Zharikov & Rotar 1992); in the periphyton of the Glubokoje Lake, Kossino, Russia (Duplakoff 1933); 2–4 ind./l in summer plankton of lakes in the Baikal region (Lokot' 1987); Lake Baikal (Obolkina 1995); Thar desert, India (Das 1996; misspelled as *Dileptus answer*); North and South India and in West Pakistan (Naidu 1965); in freshwaters of Thailand (Charubhun & Charubhun 2000); freshwaters in Hengshui, Japan (Han & Hao 1995); putrid water from the city of Hakodate, Japan (Muramatsu 1957); in strongly polluted waters in Japan, together with *Colpidium colpoda* and *Trithigmostoma cucullulus* (Hayashi 1959); in a campus pond of the University of Colorado, USA (Hamilton 1943); freshwater bodies on Mount Desert Island, Nebraska, USA (McCashland 1956); in a slowly running river in the USA (Patrick 1961); in many water bodies of the Upper Peninsula of Michigan, USA (Lundin & West 1963); Conestoga drainage basin, Pennsylvania, USA (Cairns 1965); Douglas Lake, Michigan, USA (Cairns & Yongue 1966); numerous at 5 °C and pH 6 in the mud of tundra puddles in Alaska (Sullivan 1957, Fenchel 1975); common in Lake Cromwell, Quebec, Canada (Puytorac et al. 1972); 12 ind./l in a fishless, intermittent pond in Vandorf, Ontario, Canada (Andrushchyshyn et al. 2006); Mexico (Aladro-Lubel et al. 2006); pool in Madagascar (Sondheim 1929).

Records from terrestrial habitats: "macchia" soil from Italy (Luzzatti 1938); soil from the Rila Mountains, Bulgaria (Detcheva 1970); in sandy soil from the floodplain of the Oka River in the European part of Russia (Sassuchin 1931); Central Asia (Brodsky 1935); Calcutta, India (Bhattacharya et al. 1977); grassland in the surroundings of the Mt. Fuji, Japan (Sudzuki 1978b); Cameroon, Africa (Foissner et al. 1995).

Dileptus margaritifer is likely a cosmopolitan because it has been recorded from, e.g., Europe (Kahl 1931), Asia (Alekperov 1982, 1984), North America (Cairns 1965), South America (Pinto 1925, Pettigrosso & Cazzaniga 1987), and Africa (Dragesco & Dragesco-Kernéis 1986, Foissner et al. 1995). No records are available from the Australis and Antarctica.

Saprobic classification: Sládeček et al. (1981) and Foissner (1988a) classified *D. margaritifer* as a beta- to oligosaprobic ciliate with the following valencies: o = 4, b = 6, I = 3, SI = 1.6. Wegl (1983): o = 3, b = 7, I = 4, SI = 1.7. Bick & Kunze (1971): o = 2, b = 8, I = 4. Moravcová (1977): b = 10, I = 5, SI = 2.5 (apparently incorrectly calculated). Mauch et al. (1985): SI = 2.0. Friedrich (1990): betasaprobic; o–b = 4, b = 10, b–a = 6, I = 8, SI = 2.1. According to Šrámek-Hušek (1956b, 1958) rare in oligo- and beta-

mesosaprobic waters. The faunistic and ecological data match the index proposed by FRIEDRICH (1990): betamesosaprobic; o = 2, b = 5, a = 3, I = 2, SI = 2.1. In stagnant waters also at higher pollution levels and in the microaerobic sediment. Most frequent in spring.

Dileptus jonesi DRAGESCO, 1963 (Figs 97a–n, 99v, w)

1951 *Dileptus anser* (MUELLER) DUJARDIN – JONES, J. Elisha Mitchell scient. Soc. **67**: 205 (misidentification; description of encystment, excystment, and nuclear cycle)

1953 *Dileptus anser* (O. F. MUELLER, 1786) – JONES & BEERS, J. Elisha Mitchell scient. Soc. **69**: 47 (misidentification, comparison with several multinucleate species)

1956 *Dileptus anser* – JONES, J. Elisha Mitchell scient. Soc. **72**: 71 (misidentification; comparison with *D. beersi*)

1963 *Dileptus jonesi* nom. nov. DRAGESCO, Bull. biol. Fr. Belg. **97**: 107 (not a replacement name but a new species)

1966 *Dileptus jonesi* DRAGESCO – DRAGESCO, Protistologica **2**: 76 (notes on a French population)

1984 *Dileptus jonesi* DRAGESCO, 1963 – ARCHBOLD & BERGER, Trans. Am. microsc. Soc. **103**: 58 (description of behavior and comparison with *D. beersi*)

1989 *Dileptus jonesi* DRAGESCO, 1963 – SONG & WILBERT, Lauterbornia **3**: 41 (description of a German population)

1994 *Dileptus jonesi* DRAGESCO, 1963 – BLATTERER, Kataloge des O. Ö. Landesmuseums Linz, N. F. **71**: 154 (brief notes on an Austrian population)

non *Dileptus* cf. *jonesi* – VĎAČNÝ, ORSI, BOURLAND, SHIMANO, EPSTEIN & FOISSNER, 2011, Eur. J. Protistol. **47**: 297 (see *Apodileptus visscheri rhabdoplites*)

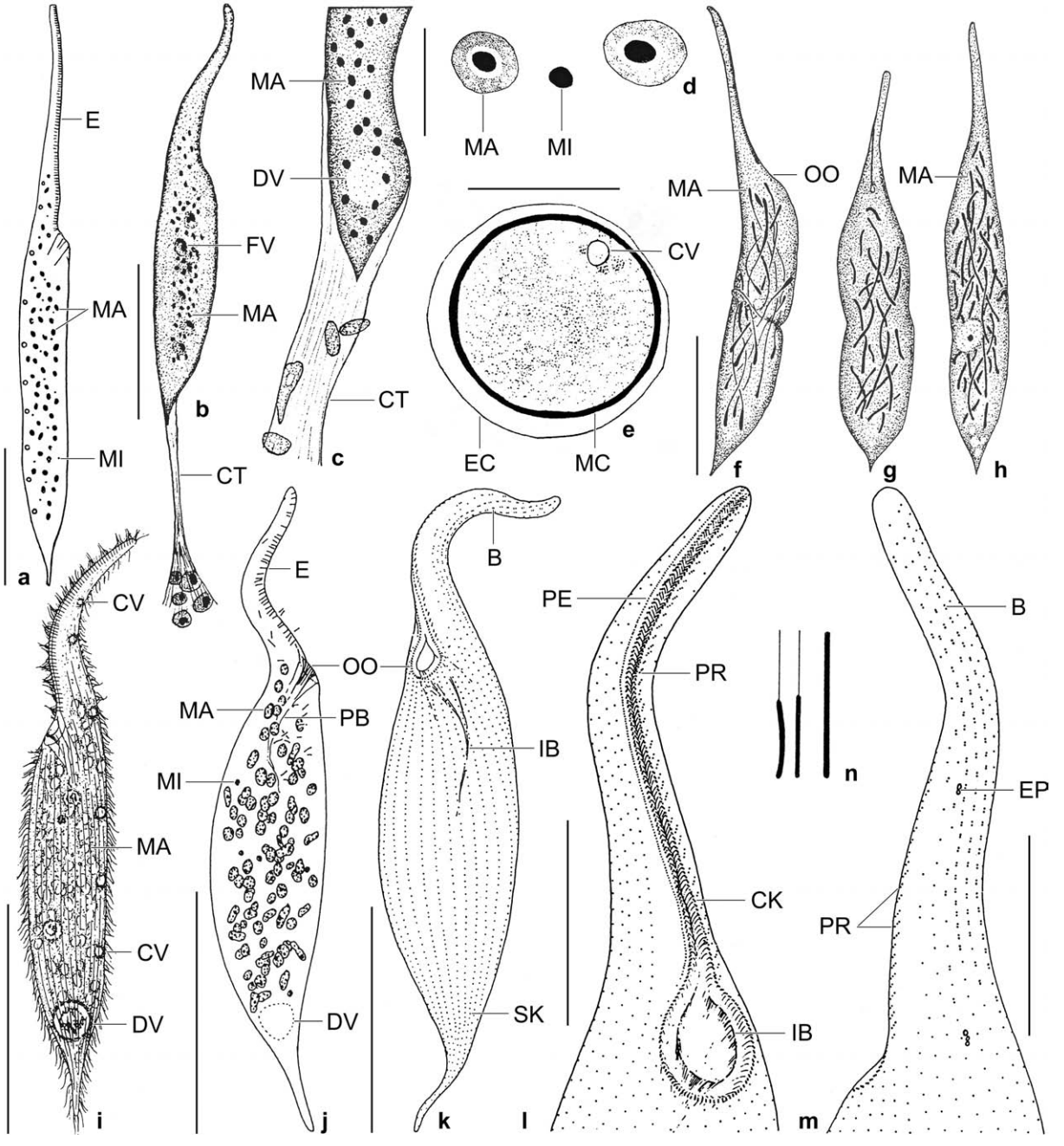
Taxonomy and typification: DRAGESCO (1963) recognized that JONES (1951, 1956) and JONES & BEERS (1953) misidentified their populations as *Dileptus anser* sensu KAHL (1931), who also misidentified *D. margaritifer* as *D. anser* (DINGFELDER 1962, WIRNSBERGER et al. 1984). JONES' specimens differed from *D. margaritifer* in the much lower number of macronuclear nodules and the ability to form a mucous thread attaching to the substrate. Accordingly, DRAGESCO (1963) established a new species, *D. jonesi*, for the *D. anser* described and illustrated by JONES (1951, 1956) and JONES & BEERS (1953).

Although neotypification is highly recommendable, we suggest to wait for a redescription of a North American population because the original data are too incomplete to be entirely sure about conspecificity of the German population studied by SONG & WILBERT (1989). Further, neither DRAGESCO (1966) and BLATTERER (1994) or SONG & WILBERT (1989) described or commented on the mucous thread, the most specific feature of *D. jonesi*.

Improved diagnosis (includes all information known): Size about 450 × 80 µm in vivo. Shape very narrowly to cylindroidally dileptid with distinct tail associated with a mucous thread, proboscis usually 1/3 of body length. About 100 scattered macronuclear nodules and several globular micronuclei. A dorsal stripe of contractile vacuoles with 2–3 pores each. Two size-types (5 µm and 2–3 µm) of rod-shaped extrusomes attached to proboscis oral bulge. On average 31 ciliary rows, several anteriorly differentiated into a staggered, anteriorly heteromorphic dorsal brush with monokinetidal tails extending anteriorly and posteriorly. Oral bulge opening about 25 µm across. Preoral kineties oblique, ordinarily spaced, each composed of 2–3 narrowly spaced cilia.

Type locality: Not mentioned by JONES (1951). Possibly, a pond on the campus of the University of North Carolina, Chapel Hill, USA, W79°02' N35°55'.

Type and voucher material: Deposition of type or voucher material not mentioned in the original or subsequent papers (JONES 1951, 1956; JONES & BEERS 1953; DRAGESCO 1964; SONG & WILBERT 1989). However, JONES (1951) made permanent slides when he was at the Duke University Marine Laboratory,



Figs 97a–n: *Dileptus jonesi* from life (a, e, i, n), after protargol impregnation (j–m), and in Schaudinn-iron hematoxylin stains (b–d, f–h). From Jones 1951 (b–h), Dragesco 1963 (a), and Song & Wilbert 1989 (i–n). **a, b, i, j** – lateral views showing general body organization; **c** – detail of rear body end showing mucous thread, an important feature separating *D. jonesi* from all other dileptids; **d** – part of nuclear apparatus: one micronucleus and two macronuclear nodules; **e –** early resting cyst still showing the contractile vacuole; **f–h** – various aspects of mid-dividers, showing individually dividing macronuclear nodules; **k** – ventrolateral view of ciliary pattern; **l, m** – ventrolateral and dorsolateral view of proboscis' ciliary pattern; **n** – there are two size-types (5 µm and 2–3 µm) of rod-shaped extrusomes. The type II displays the typical toxicyst structure when exploded. B – dorsal brush, CK – circumoral kinety, CV – contractile vacuoles, CT – caudal thread, DV – defecation vacuole, E – extrusomes, EC – ectocyst, FV – food vacuole, IB – internal oral basket, MA – macronuclear nodules, MC – mesocyst, MI – micronuclei, OO – oral bulge opening, PB – pharyngeal basket, PE – perioral kinety, PR – preoral kineties, SK – somatic kineties. Scale bars: 50 µm (c, e, l, m), 100 µm (a, b, f–h, j, k), and 200 µm (i).

North Carolina, USA, where they are probably still deposited.

Etymology: Dragesco (1963) dedicated this species to Dr. Edward Eugene Jones, Jr. of the University of North Carolina.

Description: Size in vivo fairly similar in all populations investigated: 250–600 µm in North American specimens (Jones 1956, Archbold & Berger 1984), 350–600 µm in French cells (Dragesco 1963), about 400 µm in Austrian individuals (Blatterer 1994), and 300–500 × 70–90 µm in the German ones (Song & Wilbert 1989); very flexible and slightly contractile. Shape very narrowly to cylindroidally dileptid, that is, length:width ratio about 7–12:1 according to the micrographs and drawings available in the literature. Proboscis one to two thirds of body length, straight or curved dorsally, highly motile; trunk cylindroidal in vivo, while bluntly fusiform in protargol preparations (Figs 97j, k); posterior end with indistinct to distinct tail (Figs 97a, b, i–k, 99v, w). Nuclear apparatus in trunk and base of proboscis, absent from tail. Number of macronuclear nodules similar in North Carolinan, French, Austrian and German populations, viz., about 70–100 nodules, while 130–390 nodules in starving Canadian specimens; individual nodules globular to oblong, about 3–4.5 µm across; divide individually (Figs 97f–h); nucleoli small and globular, one nucleolus in centre of each nodule in Jones' specimens, while several nucleoli in German cells. About 16 micronuclei scattered between or attached to macronuclear nodules and approximately 1.5 µm across (Figs 97a–d, j). A stripe of contractile vacuoles in dorsal side of cell, first vacuole in mid-proboscis, two to three excretory pores per vacuole; no ventral vacuoles (Figs 97a, i, m). Extrusomes studied only in German population (Song & Wilbert 1989): rod-shaped forming two size-types (5 µm and 2–3 µm long) attached to proboscis oral bulge and scattered throughout cytoplasm, impregnate with the protargol method used; exploded type II extrusomes with typical toxicyst structure (Fig. 97n). Cytoplasm colourless, packed with food vacuoles and macronuclear nodules; in posterior trunk sometimes a defecation vacuole. Swims by rotation about main body axis with proboscis held at an acute angle; frequently attaches to substrate by a mucous thread, which appears to be exuded by the entire body and passed by ciliary action to the posterior end where it spun into a tether by body rotation (Jones 1951, Archbold & Berger 1984).

Cilia ordinarily spaced, arranged in about 31 (28–34) longitudinal, ordinarily to narrowly spaced rows. Right side rows shortened only along anterior fifth of oral bulge; perioral kinety extends to tip of proboscis with narrowly spaced basal bodies (Fig. 97l). Left side of proboscis with comparatively broad blank stripe because several ciliary rows end at level of oral bulge opening, except for one to two kineties extending into proximal third of proboscis (Figs 97k, m). Dorsal brush on dorsal and dorso-lateral region of proboscis, remarkable because (i) slightly heteromorphic, especially, in anterior portion of rows where monokinetids are mixed with dikinetids, and (ii) because some rows begin with a monokinetidal tail composed of one to four basal bodies (Figs 97k, m); possibly more diffuse than shown by Song & Wilbert (1989).

Oral bulge opening at beginning of second body third, about 25 µm across, projects distinctly because proboscis only half as wide as trunk (Figs 97a, b, i). Pharyngeal basket obconical, internal basket impregnates more distinctly than external one with the protargol method used. Oral ciliary pattern dileptid, i.e., left branch of circumoral kinety associated with oblique to strongly oblique, ordinarily spaced, preoral kineties, each composed of two to three narrowly spaced cilia (Figs 97k, l).

Resting cyst: The description by Jones (1951) reads as follows (Fig. 97e): "In the living condition, the cysts are spheroidal; they have a light tan color which becomes darker as the cyst ages. There are three cyst membranes, ecto-, meso-, and endocyst; the color is present only in the mesocyst. Hayes (1938) found the diameter of dilepti cysts to be 80 µm. This is a good average, though cysts vary somewhat in over-all size and shape. Cysts measuring as little as 65 µm have produced normal, viable animals upon excystment".

Occurrence and ecology: *Dileptus jonesi* feeds preferably on small ciliates and flagellates, for instance,

Halteria, *Euglena* and *Chilomonas* (Jones 1951, Archbold & Berger 1984). The cytostome does not open until the prey reaches it, and then only enough for the prey item to be ingested (Fig. 99w; Archbold & Berger 1984). *Dileptus jonesi* is essentially an active, swimming species forming a mucous thread which allows attachment to the substrate, as definitely stated by Jones (1951, 1956) and confirmed by Archbold & Berger (1984). During locomotion, the thread may be seen trailing behind and serves as a sea anchor (Jones 1951).

Dileptus jonesi was probably discovered in a pond of the University campus in North Carolina, USA, where Jones (1951) taught. Other North American populations come from two small ponds in the centre of the woodlot north of the Farquharson Biology Building, York University, Downsview, Ontario, Canada (Archbold & Berger 1984). There are several unsubstantiated records from Europe and China: eutrophic pond in Bonn, Germany, where it occurred rarely during the winter season (Song & Wilbert 1989); eu- to polytrophic lake in Germany during winter and spring (Packroff & Wilbert 1991); Eifel maar lake in Germany (Packroff 1992); benthos of the beta- to alpha-mesosaprobic Pram River in Upper Austria (Blatterer 1994); pond in the surroundings of the town of Qingdao, China (Song & Chen 1999).

Remarks: As mentioned by previous authors and recognizable in the micrographs (Figs 99u–y), *D. jonesi* is very similar to *D. margaritifer* and *D. beersi* in body shape, the nuclear and contractile vacuole pattern, and several morphometrics. The main distinguishing feature is the ability to form a mucous thread which is, however, a difficult feature possibly not present all the time. Thus, we used the lower number of ciliary rows (about 31 vs. 45) and macronuclear nodules (≤ 100 vs. ≥ 200) for keying out the species. Possibly, the higher number of excretory pores per contractile vacuole (2–3 vs. 1) is also a good feature. *Dileptus jonesi* is also similar to *Apodileptus visscheri* and *A. edaphicus*. However, *A. visscheri* is smaller (280 µm vs. 400 µm), and *A. edaphicus* is more slender (> 12:1 vs. < 10:1) and has a lower number of ciliary rows (18–23 vs. 28–34).

Dileptus beersi Jones, 1956 (Figs 98a–f, 99a–u; Table 53)

1956 *Dileptus beersi* n. sp. Jones, J. Elisha Mitchell scient. Soc. **72**: 68

1984 *Dileptus beersi* Jones, 1956 – Archbold & Berger, Trans. Am. microsc. Soc. **103**: 58 (description of behavior)

Improved diagnosis (based on literature and a new population from Venezuela): Size about 670 × 60 µm in vivo. Shape very narrowly dileptid to rod-like with distinct tail, proboscis about 1/3 of body length. Usually more than 200 scattered macronuclear nodules and several globular micronuclei. A dorsal stripe of contractile vacuoles with 1 pore each. Two types of extrusomes attached to proboscis oral bulge: type I very narrowly ovate, 8–10 × 0.6–1.2 µm in size; type II oblong, about 2.5 × 0.4 µm in size. About 48 ciliary rows, up to 8 anteriorly differentiated into a staggered, distinctly heterostichad dorsal brush with monokinetidal tails extending to second third of body. Oral bulge opening about 20 µm across. Preoral kineties oblique, ordinarily spaced, each usually composed of 3 narrowly spaced cilia.

Type locality: Slightly brackish (3‰) Mullet Pond, Shackleford Island, North Carolina, USA, W76°39' N34°41'.

Type and voucher material: Jones (1956) made permanent slides when he was at the Duke University Marine Laboratory, North Carolina, USA but he did not provide any information about their deposition. Jones' slides are not mentioned in the catalogue of the Smithsonian Institution, Washington D.C., USA (Corliss 1972). Seven voucher slides (inv. nos 2011/323–329) with protargol-impregnated Venezuelan specimens have been deposited in the Biology Centre of the Museum of Upper Austria, Linz (LI). Relevant specimens are marked by black ink circles on the coverslip.

Etymology: Jones (1956) dedicated this species to C. Dale Beers, Professor of Zoology at the University of North Carolina.

Description of North Carolinian population (Figs 98a–f): The original description by Jones (1956) reads as follows: "Length, 450–900 µm; greatest diameter, 60–70 µm; proboscis 1/3–1/2 the total length; caudal process, 35–65 µm; contractile vacuoles situated aborally, forming two rows extending on either side of the midline from tip of proboscis to caudal process; vacuoles rarely occurring as pairs, usually alternately; nuclear apparatus, 200–500 macronuclei, 6–11 micronuclei. Body spindle-shaped; anteriorly differentiated into a long, flexible proboscis which bears rows of trichocysts on its entire oral surface. Trichocyst rows bounded laterally by a row of long cilia which continues posteriorly to cytostome. Cytostome supported by numerous trichites which are 17 µm in length and lie at about 45° angle to the

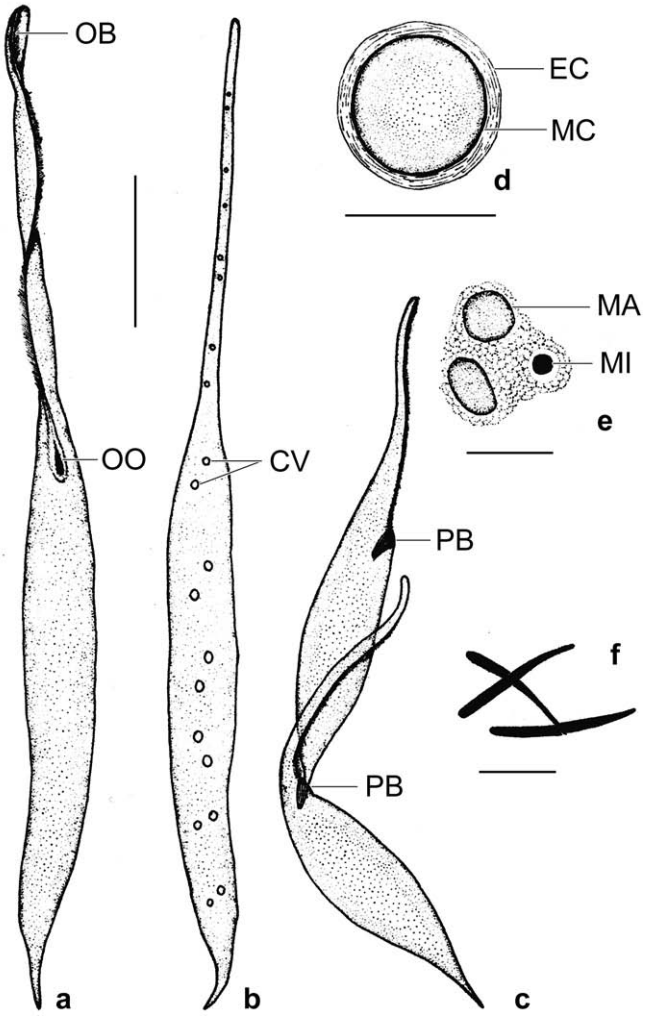
Table 53. Morphometric data on *Dileptus beersi* from soil of Venezuela. Data based on mounted, protargol-impregnated (Foissner's method), and randomly selected specimens from a non-flooded Petri dish culture. Measurements in µm. CV – coefficient of variation in %, M – median, Max – maximum, Mean – arithmetic mean, Min – minimum, n – number of specimens investigated, SD – standard deviation, SE – standard error of mean.

Characteristics	Mean	M	SD	SE	CV	Min	Max	n
Body, length	384.1	374.0	58.5	12.8	15.2	296.0	546.0	21
Body, width	45.9	46.0	11.2	2.4	24.3	28.0	70.0	21
Body length:width, ratio	8.8	8.1	2.1	0.5	24.2	6.0	13.3	21
Anterior body end to oral bulge opening, distance	133.0	133.0	16.1	3.5	12.1	105.0	164.0	21
Proboscis, % of body length	34.9	34.6	2.7	0.6	7.8	29.3	39.7	21
Oral bulge opening, length	21.9	22.0	2.0	0.5	9.2	18.0	25.0	19
Oral bulge opening, width	20.0	19.5	1.4	0.7	7.1	19.0	22.0	4
Anterior body end to first macronuclear nodule, distance	116.6	117.0	16.2	3.5	13.9	86.0	144.0	21
Nuclear figure, length	222.2	218.0	38.3	8.4	17.2	170.0	326.0	21
Macronuclear nodules, length	4.8	5.0	1.4	0.3	28.8	3.0	8.0	21
Macronuclear nodules, width	2.4	2.0	0.6	0.1	24.6	2.0	4.0	21
Macronuclear nodules, number (approximate)	214.8	208.0	–	–	–	127.0	336.0	21
Micronuclei, diameter	2.6	2.5	–	–	–	2.5	3.0	21
Micronuclei, number (approximate)	12.3	12.5	–	–	–	8.0	17.0	20
Ciliary rows, number on one side[a]	23.4	24.0	2.7	0.6	11.7	18.0	28.0	21
Ciliary rows, total number[a]	46.9	48.0	5.5	1.2	11.7	36.0	56.0	21
Cilia in mid-body in 10 µm, number	8.2	8.0	1.0	0.2	12.0	7.0	11.0	21
Anterior body end to last brush dikinetid, distance	122.0	128.0	19.6	5.9	16.1	95.0	146.0	11
Dikinetidal portion of dorsal brush, % of body length	31.4	31.0	3.5	1.1	11.2	25.5	37.6	11

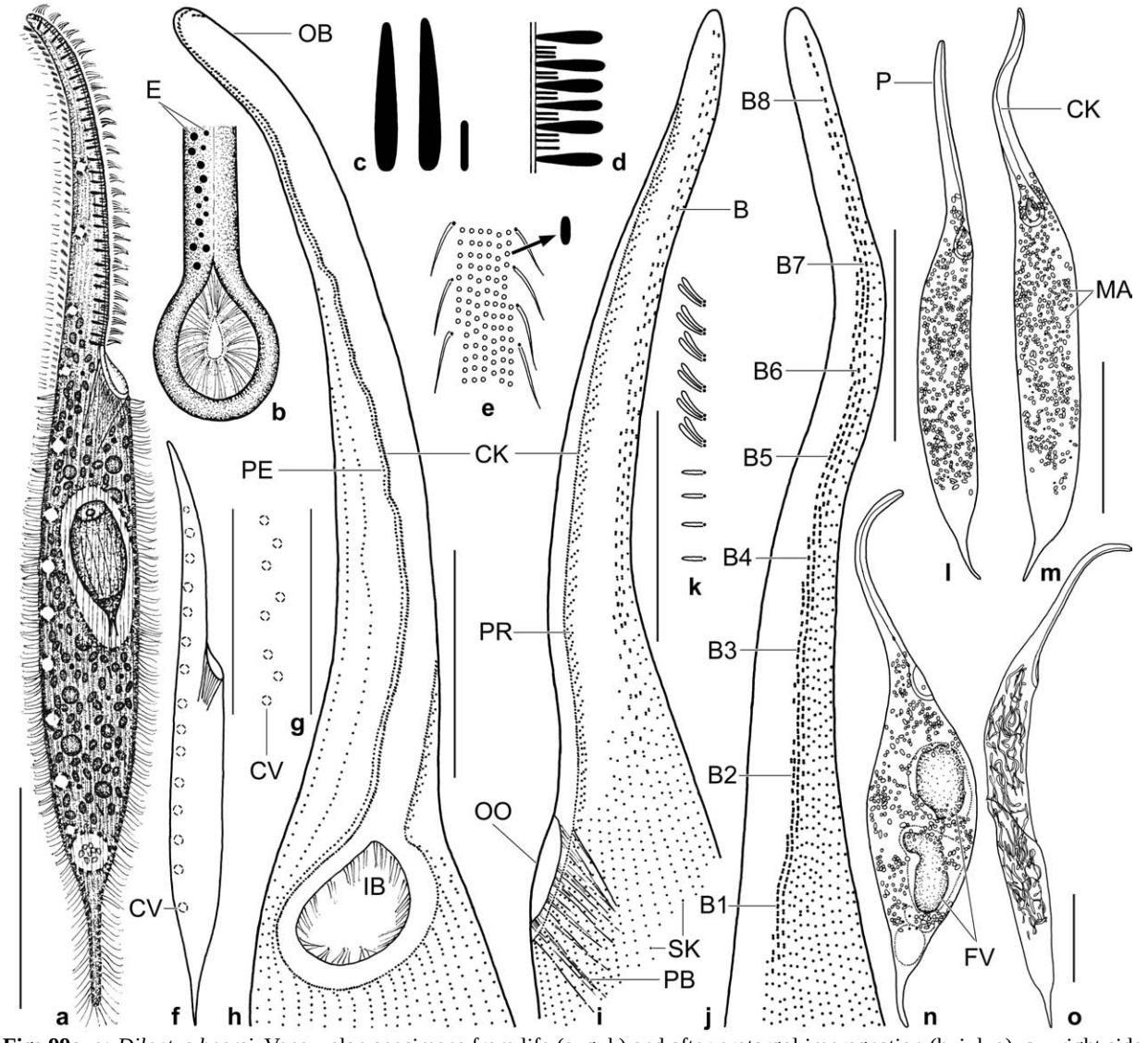
[a] Approximations because of insufficient impregnation. The total number of ciliary rows was calculated by doubling the value from one side, assuming an unflattened trunk.

longitudinal axis of the body. In a relaxed condition, cytostome circular and 19 µm in diameter. Cytopyge lying immediately anterior to caudal process and emptying toward oral surface of body. Ciliation uniform, the ciliary rows spiralling slightly, 21 µm apart and bearing cilia 6 µm in length. Spherical resting cysts formed. Cysts somewhat variable in size, but usually 100–110 µm in diameter and possessing three cyst membranes. Ectocyst colorless, laminated, sticky and of variable thickness; mesocyst tan to brown in color, 2.5 µm in thickness and inelastic; endocyst colorless and always 0.5 µm in thickness". Jones (1956) also described carefully the extrusomes (Fig. 98f): "Hundreds of trichocysts are set perpendicularly to the feeding groove and extend along its entire length. Unexploded trichocysts are blade-like structures 10 µm long and 0.6 µm wide. They not only occur in the feeding groove, but may be seen moving about in the cytoplasm of the proboscis and body. In stained preparations, protrichocysts have also been identified in the cytoplasm. The fully exploded trichocyst is 40 µm long and is composed of a shaft 12 µm in length which terminates in a 28 µm thread".

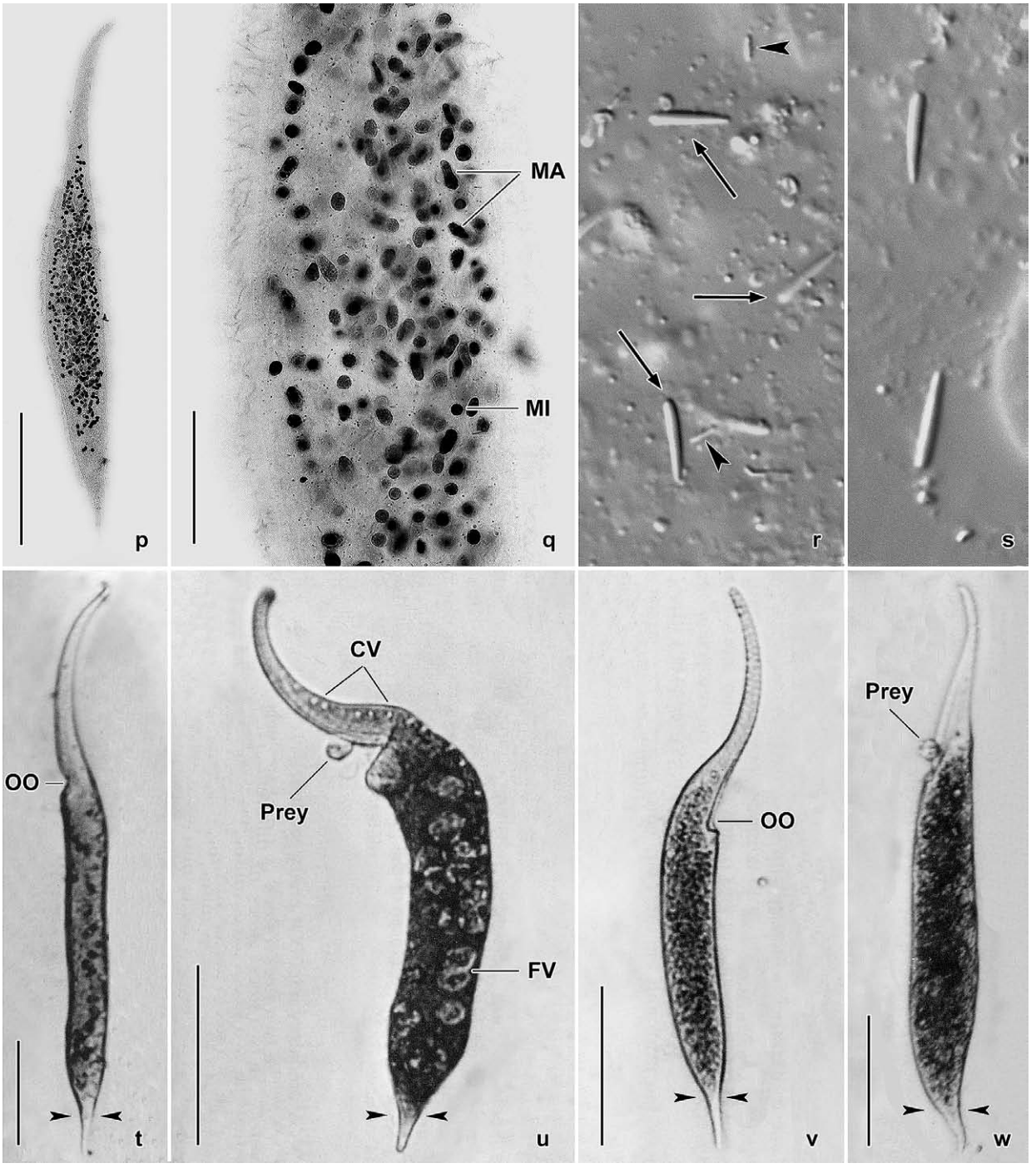
Description of Venezuelan population: Size 340–630 × 30–80 µm in vivo, usually about 450 × 50 µm, as calculated from some in vivo measurements and the morphometric data, assuming 15% preparation shrinkage; very flexible but not contractile (Table 53). Shape in vivo very narrowly dileptid to rod-like, length:width ratio near 9:1 both in vivo and after protargol impregnation. Proboscis about one third of body



Figs 98a–f: *Dileptus beersi*, North American specimens from type population in Schaudinn-alum carmine (a, b), Schaudinn-Biebrich scarlet (f), and Schaudinn-iron hematoxylin (e) stains and from life (c; from Jones 1956). Redrawn from micrographs, except for (c). **a** – ventral aspect of a mature specimen, showing the long cilia of the oral bulge. Body ciliation has been omitted; **b** – dorsal aspect of a mature specimen, showing the arrangement of the contractile vacuoles; **c** – sketch of a very late divider just prior to separation; **d** – resting cyst showing the two outer cyst layers, the endocyst cannot be seen; **e** – part of nuclear apparatus: two macronuclear nodules and one micronucleus; **f** – unexploded trichocysts from a smear. CV – contractile vacuoles, EC – ectocyst, MA – macronuclear nodule, MC – mesocyst, MI – micronucleus, OB – oral bulge, OO – oral bulge opening, PB – pharyngeal basket. Scale bars: 5 µm (d–f) and 100 µm (a, b).



Figs 99a–o: *Dileptus beersi*, Venezuelan specimens from life (a–g, k) and after protargol impregnation (h–j, l–o). **a** – right side view of a representative specimen having ingested a small rotifer, length 450 μm; **b** – frontal view of oral bulge opening and arrangement of extrusomes; **c, d** – two types of oral bulge extrusomes: type I is very narrowly ovate and about 8 × 1 μm in size, while type II is oblong and approximately 2.5 × 0.4 μm in size; **e** – surface view showing cortical granulation. The granules are 1 × 0.5 μm in size; **f, g** – the contractile vacuoles form a stripe on the dorsal side, i.e., they are not in line; **h** – ventral view of ciliary pattern in oral body portion. The circumoral kinety is composed of narrowly spaced dikinetids in the proboscis, while of monokinetids around the oral bulge opening. The first row right of the circumoral kinety extends as perioral kinety with narrowly spaced basal bodies to the tip of the proboscis. Left of the circumoral kinety, there are many oblique preoral kineties (i), each composed of two to three narrowly spaced basal bodies; **i** – left side view of proboscis'ciliary pattern of main voucher specimen. There is a broad blank stripe between the preoral kineties and the dorsal brush; **j** – dorsal view of proboscis. The dorsal brush consists of eight staggered, distinctly heterostichad rows with ordinary to loosely spaced dikinetids; **k** – in vivo, the dorsal brush bristles are 3 μm long in the dikinetidal anterior region of the brush, which is followed by 2 μm long bristles forming monokinetidal tails; **l–n** – variability of body shape and size as well as of nuclear apparatus. The nuclear apparatus consists of more than 200 macronuclear nodules and several micronuclei scattered throughout the cytoplasm. Drawn to scale; **o** – lateral view of a mid-divider, showing individually dividing macronuclear nodules, an important feature separating the genus *Dileptus* from *Apodileptus*. B(1–8) – dorsal brush (rows 1–8), CK – circumoral kinety, CV – contractile vacuoles, E – extrusomes, FV – food vacuoles, IB – internal basket, MA – macronuclear nodules, OB – oral bulge, OO – oral bulge opening, P – proboscis, PB – pharyngeal basket, PE – perioral kinety, PR – preoral kineties, SK – somatic kineties. Scale bars: 30 μm (h–j) and 100 μm (a, l–o).



Figs 99p–w: *Dileptus beersi* (p–u), Venezuelan (p–s) and North American (t, u) specimens; and *D. jonesi* (v, w), North American specimens after protargol impregnation (p, q) and from life (r–w). Figures (p–s) originals, (t–w) from ARCHBOLD & BERGER (1984). **p, q** – overview and detail of nuclear apparatus, which consists of many macronuclear nodules with several micronuclei interspersed; **r, s** – there are two types of extrusomes: type I (arrows) is very narrowly ovate and about 8 × 1 μm in size, while type II (arrowheads) is oblong and about 2.5 × 0.4 μm in size; **t, u** – a representative and a stout specimen of *D. beersi* ingesting a *Halteria* cell; **v, w** – a representative exemplar and a specimen of *Dileptus jonesi* ingesting a *Halteria*. Opposed arrowheads denote tail. CV – contractile vacuoles, FV – food vacuoles, MA – macronuclear nodules, MI – micronucleus, OO – oral bulge opening. Scale bars: 30 μm (q) and 100 μm (p, t–w).

length on average, ~ 2:1 flattened; trunk cylindroidal, slightly flattened, inflated in well-fed specimens (Fig. 99n); posterior end with distinct tail in vivo up to 70 µm long, recognizable even in specimens inflated by food inclusions (Figs 99a, l–n, p, t, u). Many macronuclear nodules scattered in trunk and base of proboscis, not in tail; individual nodules highly variable in shape, that is, globular to ellipsoidal, 3–8 × 2.5–4 µm in size; divide individually (Fig. 99o); nucleoli small and globular. On average 12 micronuclei scattered between or attached to macronuclear nodules, about 2.5 µm across in protargol preparations (Figs 99a, l–n, p, q; Table 53). A stripe of contractile vacuoles in dorsal side of trunk and proximal two thirds of proboscis; no ventral vacuoles, excretory pores not impregnated with the protargol method used (Figs 99a, f, g). Two types of extrusomes, not impregnating with protargol, attached to right branch of oral bulge: type I very narrowly ovate, about 8 × 1–1.2 µm in size, frequent also in cytoplasm, where certain developmental stages sometimes impregnate with protargol; type II oblong, about 2.5 × 0.4 µm in size (Figs 99a–d, r, s). Cortex flexible, contains about six granule rows between adjacent kineties; granules colourless but conspicuous in vivo because densely spaced and ~ 1 × 0.5 µm in size (Fig. 99e). Cytoplasm colourless, hyaline in proboscis and tail at low magnification (×40), opaque and brownish in trunk due to numerous granules, up to 10 µm-sized lipid droplets, and several food vacuoles; in posterior end of trunk sometimes a defecation vacuole with crystalline contents. Some specimens with one or two large food vacuoles containing small rotifers (Figs 99a, n). Swims rather rapidly; a mucous thread or tether was not observed.

Cilia about 8 µm long in vivo, narrowly spaced; in protargol preparations as typical for dileptids, i.e., with thick, strongly impregnated distal half, except for dorsal bristles; arranged in about 48 narrowly spaced rows extending meridionally to slightly helically (Table 53). Right side rows shortened only in anterior proboscis fifth, except for perioral kinety which extends to tip of proboscis with narrowly spaced basal bodies (Fig. 99h). Left side of proboscis with conspicuous blank stripe because of shortened ciliary rows left of oral bulge opening (Figs 99i, j). Dorsal brush on dorsal side of proboscis, staggered, distinctly heterostichad, composed of up to eight rows with loosely to ordinarily spaced dikinetids associated with 3 µm long, slightly inflated type I bristles; frequently some extra dikinetids anywhere along right brush margin. First brush row begins in third fourth of proboscis, while last row commences subapically. Each brush row continues with a monokinetidal tail extending to base of proboscis with 2 µm long, rod-shaped bristles (Figs 99i–k).

Oral bulge opening at beginning of second body third, projects distinctly because proboscis only half as wide as trunk, about 20 µm across in protargol preparations, roundish both in vivo and in good preparations (Foissner's method), while elliptical in specimens prepared with Wilbert's method, an artefact known also for *D. margaritifer* (Figs 99a, b, h; Table 53). Pharyngeal basket obconical, impregnated only in distal portion (Figs 99h, i). Circumoral kinety composed of narrowly spaced dikinetids in proboscis and narrowly spaced monokinetids around oral bulge opening; right branch curves around anterior end of proboscis, while left branch ends subapically almost touching the curved right end (Fig. 99h). Preoral kineties oblique, ordinarily spaced, each composed of two to three narrowly spaced cilia (Fig. 99i).

Occurrence and ecology: Jones (1956) discovered *D. beersi* in a slightly brackish (3‰) pond on the western end of Shackleford Island, which is about 3.2 km off the coast of North Carolina (USA) opposite to the city of Beaufort. Mullet Pond is approximately 90 m in diameter and has a maximum depth of about 1.2 m. The Venezuelan population is from a non-flooded Petri dish culture of soil from a *Tachypogon* savannah about 60 km north of Puerto Ayacucho, the capital of Amazonas state. The savannah belongs to the farm of Señor Pedro Cortez and is close to the Orinoco River, but is never flooded because it is about 20 m above the river level. The very sandy soil is covered with an algal (or cyanobacterial) crust and contains little organic matter. *Dileptus beersi* is a rather large species and thus probably not a typical

soil inhabitant. Some of our specimens contained one or two ingested rotifers. This matches observations from Jones (1956), who, additionally, observed small ciliates (e.g. *Halteria*), flagellates, green algae, and zoogleal masses as further food sources. The cytostome opens before the prey reaches it; frequently the oral bulge opening is wider than the prey item (Fig. 99v; Archbold & Berger 1984). *Dileptus beersi* is a bottom-dweller not forming a mucous thread or tether, and hence does not attach itself to a surface or to an accumulation of debris, as definitely stated by Jones (1956) and Archbold & Berger (1984).

Remarks: The Venezuelan population matches the North American type in the following characteristics: very narrowly dileptid to rod-like with a distinct tail, proboscis one third to half of body length; contractile vacuoles in a dorsal stripe; extrusomes very narrowly ovate and of similar length (8 μm and 10 μm); oral bulge opening roundish. As usual, there are some small differences, most likely caused by cultivation, i.e., Jones (1956) investigated specimens from thriving cultures, while we studied material as obtained from a non-flooded Petri dish culture set up with savannah soil. For instance, Jones' (1956) specimens were larger (450–900 × 60–70 μm vs. 340–630 × 30–80 μm) and had more macronuclear nodules (203–479 vs. 127–336). Unfortunately, Jones (1956) did not provide the number of ciliary rows, but mentioned that they are 21 μm apart (likely, this should read "2.1 μm apart"). Using this value and an average width of 65 μm, this would result in 97 kineties, a rather unlikely number not surpassed by any other species. Likewise, Jones (1956) did not mention the type II extrusomes. As these are very small and thus easily overlooked, we do not rate it as a significant difference. Although conspecificity is very likely, we do not neotypify *D. beersi* with the Venezuelan population because this is a different biogeographic region and reliable data on the number of ciliary rows are lacking from the North American population.

As mentioned by Jones (1956) and shown by our data, *D. beersi* is very similar to *D. margaritifer*. They match, inter alia, in body shape, the nuclear and contractile vacuole pattern, and several morphometric features. However, both species differ in the shape of the type I extrusomes (very narrowly ovate vs. rod-shaped), a feature definitely mentioned and figured by Jones (1956; Fig. 98f). Within the multinucleate dileptids, *D. beersi* is most similar to *Apodileptus visscheri*, which differs by the smaller size (280 × 35 μm vs. 670 × 60 μm) and the lower number of the ciliary rows (24 vs. 48). *Dileptus jonesi* is distinguished from *D. beersi* by the shape of the extrusomes (rod-like vs. very narrowly ovate), the lower number of ciliary rows (28–34 vs. 36–56), and the presence (vs. absence) of a caudal thread.

Apodileptus Vďačný, Orsi, Bourland, Shimano, Epstein & Foissner, 2011

2011 *Apodileptus* gen. n. Vďačný, Orsi, Bourland, Shimano, Epstein & Foissner, Eur. J. Protistol. **47**: 311

Diagnosis: Medium- to large-sized Dileptidae with narrow to rod-like body. Many scattered macronuclear nodules fusing during ontogenesis. Dorsal brush multi-rowed. Right branch of circumoral kinety accompanied by a perioral kinety, left branch by many slightly to strongly oblique preoral kineties. Oral bulge opening dileptid, i.e., roundish or elliptical and located ventrally.

Type species (by original designation): *Dileptus visscheri* Dragesco, 1963.

Etymology: Composite of the Greek prefix *apo* (derived from) and the generic name *Dileptus*, referring to the *Dileptus*-like general organization. Masculine gender.

Remarks: Fusion of the macronuclear nodules is the ordinary state in dividing binucleate and moniliform dileptids (e.g., *Paradileptus ovalis*, *Pseudomonilicaryon brachyproboscis*, and *P. thononense*; Vďačný & Foissner 2009, present study), while in multinucleate species (e.g., *Dileptus beersi*, *D. jonesi*, or *D. sphagnicola*) the nodules divide individually (Hayes 1938, Jones 1951, Golińska 1971, present study). Thus, *Apodileptus visscheri*, where the individual nodules fuse during cell division, is a conspicuous exception,

justifying separation at genus level. An analogy exists in the hypotrichs, where the Pseudokeronopsinae are defined by the individually dividing macronuclear nodules (for a review, see Berger 2006).

Apodileptus visscheri (Dragesco, 1963) Vďačný, Orsi, Bourland, Shimano, Epstein & Foissner, 2011

1963 *Dileptus visscheri* n. sp. Dragesco, Bull. biol. Fr. Belg. **97**: 114

2011 *Apodileptus visscheri* (Dragesco, 1963) comb. n. – Vďačný, Orsi, Bourland, Shimano, Epstein & Foissner, Eur. J. Protistol. **47**: 311 (combining authors)

Taxonomy: We split this species into two subspecies, according to the shape of the extrusomes, which was found to be constant in two populations each. Further, the dorsal brush is more diffuse in *A. visscheri rhabdoplites* than in *A. visscheri visscheri*. The sole congener, *A. edaphicus*, obviously belongs to the *A. visscheri* complex, but is sufficiently different to be considered as a distinct species.

Improved diagnosis (includes all information known): Size about 280 × 30 µm in vivo. Shape narrowly dileptid to rod-like with distinct tail, proboscis about 1/3 of body length. About 90 scattered macronuclear nodules and several globular micronuclei. A dorsal stripe of contractile vacuoles with 1 pore each. Two types of extrusomes attached to proboscis' oral bulge: type I oblong or very narrowly ovate, 4–6 × 0.5–0.8 µm in size; type II oblong, 1.5–2.5 × 0.3 µm in size. On average 22 ciliary rows, 5–7 anteriorly differentiated into a diffuse or staggered and distinctly heterostichad dorsal brush with monokinetidal tails extending to base of proboscis. Oral bulge opening about 15 µm across. On average 40 oblique to slightly oblique, ordinarily spaced preoral kineties, each usually composed of 3 narrowly to ordinarily spaced cilia.

Etymology: Not given in the original description. Dragesco (1963) dedicated this species to J. Paul Visscher (John Hopkins University, USA), acknowledging his studies on *Dileptus*.

Apodileptus visscheri visscheri (Dragesco, 1963) nov. stat. (Figs 100a–t; 101a–v, 102a–t, 105i–l; Table 54)

1963 *Dileptus visscheri* n. sp. Dragesco, Bull. biol. Fr. Belg. **97**: 114

1966 *Dileptus visscheri* Dragesco – Dragesco, Protistologica **2**: 76 (notes on a French population)

1972 *Dileptus visscheri* Dragesco – Golińska, Acta Protozool. **9**: 283 (notes on ontogenesis)

1973 *Dileptus visscheri* – Kink, Acta Protozool. **12**: 173 (fine structure of vegetative specimens and resting cyst)

1976 *Dileptus visscheri* – Kink, J. Cell Sci. **20**: 115 (excystment)

1979 *Dileptus visscheri* Dragesco, 1963 – Foissner, Acta Protozool. **18**: 418 (silverline pattern)

1986 *Dileptus visscheri* Dragesco, 1963 – Dragesco & Dragesco-Kernéis, Faune tropicale **26**: 163 (taxonomic revision)

Diagnosis: Extrusomes narrowly ovate. Dorsal brush staggered and distinctly heterostichad.

Type locality: Dragesco (1963) discovered *Dileptus visscheri* in a pond from the surroundings of the town of Thonon, France, E6°28' N46°22'. The neotype is from a shallow meadow puddle in the Donnersberg Park near the centre of the town of Salzburg, Austria, E13°02' N47°47'. According to Article 76.3 of the ICZN (1999), the place of origin of the neotype becomes the type locality of the nominal species-group taxon, despite any previously published statement of the type locality.

Neotypification, type and voucher material: We fix the Salzburg population as a neotype. Neotypification is needed because (i) no type material is available from Dragesco's (1963) specimens, (ii) the identity is endangered by several similar species, (iii) the neotype is from the same biogeographic region and

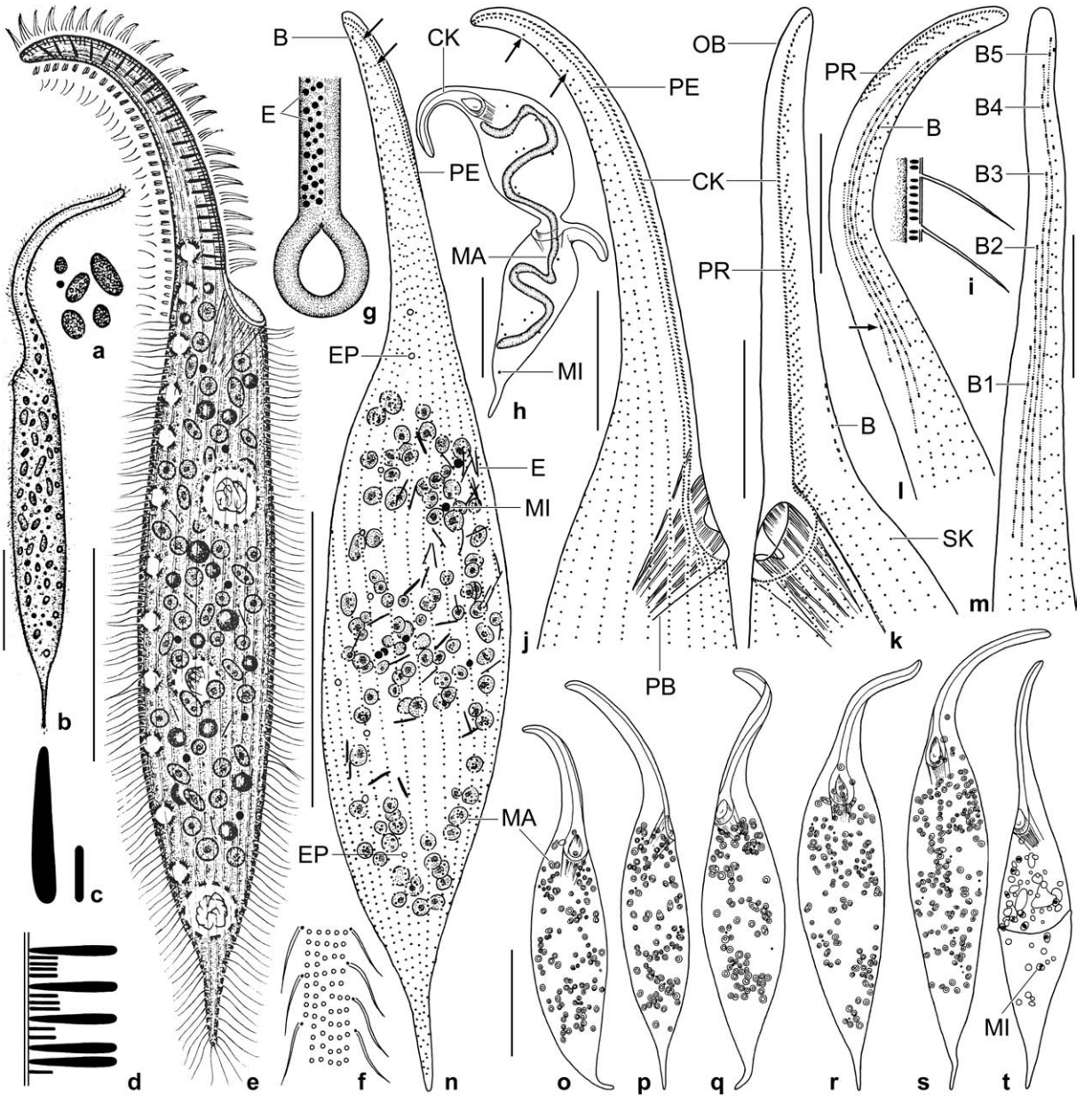
Table 54: Morphometric data on a Salzburg (S) and a Lower Austrian (Mueller boden, M) population (Pop) of *Apodileptus visscheri visscheri*, and on an alpine population of *A. visscheri rhabdoplites* nov. ssp. (R). Data based on mounted, protargol-impregnated (Foissner's method), and randomly selected specimens from semi-pure cultures. Measurements in µm. CV – coefficient of variation in %, M – median, Max – maximum, Mean – arithmetic mean, Min – minimum, n – number of specimens investigated, SD – standard deviation, SE – standard error of mean.

Characteristics	Pop	Mean	M	SD	SE	CV	Min	Max	n
Body, length	S	223.1	222.0	21.4	4.7	9.6	183.0	269.0	21
	M	271.8	274.0	51.3	10.3	18.9	170.0	378.0	25
	R	202.7	190.0	30.5	7.9	15.0	162.0	275.0	15
Body, width	S	32.6	33.0	3.3	0.7	10.2	27.0	39.0	21
	M	24.3	24.0	3.8	0.8	15.7	19.0	32.0	25
	R	29.9	28.0	4.9	1.3	16.5	24.0	40.0	15
Body length:width, ratio	S	6.9	6.9	0.9	0.2	12.7	5.7	9.0	21
	M	11.4	10.9	2.5	0.5	21.9	7.1	17.6	25
	R	7.0	6.8	1.1	0.3	15.6	5.4	8.8	15
Anterior body end to oral bulge opening, distance	S	70.5	68.0	8.9	1.9	12.6	55.0	90.0	21
	M	73.5	76.0	13.9	2.8	18.9	41.0	96.0	25
	R	66.2	62.0	9.2	2.4	13.9	55.0	80.0	15
Proboscis, % of body length	S	31.6	31.4	2.4	0.5	7.6	27.6	37.5	21
	M	27.1	26.0	2.6	0.5	9.7	23.4	31.8	25
	R	33.1	33.0	3.9	1.0	11.7	26.0	39.0	15
Oral bulge opening, length	S	13.3	13.0	1.4	0.3	10.6	11.0	16.0	21
	M	11.5	11.5	1.4	0.4	11.8	10.0	14.0	10
	R	11.5	12.0	1.0	0.3	9.0	10.0	13.0	11
Oral bulge opening, width	S	12.0	12.0	1.1	0.4	8.9	10.0	13.0	8
	M	9.7	9.5	1.6	0.5	16.2	8.0	12.0	10
	R	11.2	11.0	0.90	0.3	7.8	10.0	12.0	11
Anterior body end to first macronuclear nodule, distance	S	75.7	74.0	12.3	2.7	16.2	56.0	97.0	21
	M	82.2	84.0	15.4	3.1	18.7	47.0	111.0	25
	R	73.3	70.0	10.5	3.2	14.2	60.0	95.0	11
Nuclear figure, length	S	110.0	107.0	15.4	3.4	14.0	77.0	139.0	21
	M	150.1	141.0	34.4	6.9	23.0	92.0	222.0	25
	R	98.0	96.0	20.0	6.0	20.4	71.0	135.0	11
Macronuclear nodules, length	S	4.3	4.0	1.4	0.3	32.7	3.0	8.0	21
	M	4.5	4.0	1.6	0.3	36.2	3.0	8.0	25
	R	4.8	4.0	1.1	0.3	22.4	4.0	7.0	11
Macronuclear nodules, width	S	3.5	4.0	0.5	0.1	14.5	3.0	4.0	21
	M	3.6	4.0	0.6	0.1	17.9	3.0	5.0	25
	R	4.6	4.0	0.8	0.3	18.0	4.0	6.0	11

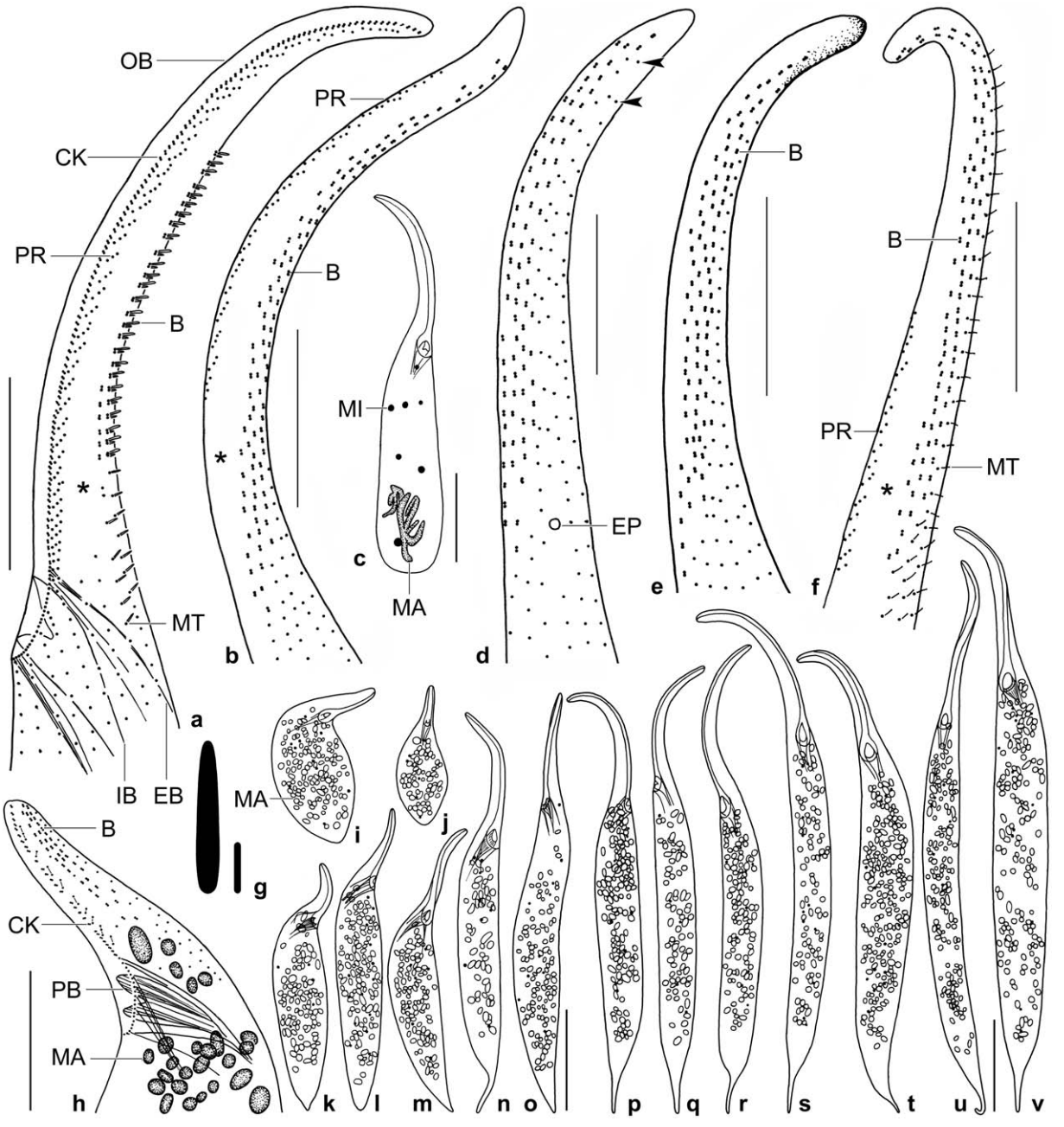
Characteristics	Pop	Mean	M	SD	SE	CV	Min	Max	n
Macronuclear nodules, number	S	87.7	89.0	8.6	1.9	9.8	71.0	102.0	21
	M	99.6	98.0	16.2	3.2	16.3	72.0	137.0	25
	R	54.9	60.0	11.7	3.5	21.3	35.0	70.0	11
Micronuclei, diameter	S	2.3	2.5	0.2	0.1	10.4	2.0	2.5	21
	M	2.4	2.5	0.2	0.0	8.7	2.0	2.5	24
	R	1.9	2.0	0.4	0.1	21.6	1.5	3.0	11
Micronuclei, number	S	7.4	6.0	2.4	0.5	32.9	4.0	14.0	21
	M	10.3	9.0	2.8	0.6	27.2	5.0	16.0	23
	R	11.8	10.0	4.1	1.2	34.2	7.0	18.0	11
Ciliary rows, number	S	24.3	24.0	2.4	0.5	9.8	20.0	29.0	21
	M	20.6	20.0	1.7	0.3	8.2	19.0	25.0	25
	R	25.9	26.0	1.7	0.4	6.4	22.0	29.0	15
Cilia in mid-body in 10 μm, number	S	8.0	8.0	1.0	0.2	12.5	7.0	10.0	21
	M	5.7	6.0	0.6	0.1	11.0	5.0	7.0	25
	R	7.0	7.0	1.1	0.3	15.7	5.0	8.0	11
Preoral kineties, number	S	44.1	43.0	4.9	1.6	11.1	37.0	51.0	9
	M	36.9	35.0	6.9	2.1	18.7	29.0	53.0	11
	R	37.4	35.0	8.2	2.7	21.9	27.0	55.0	9
Dorsal brush rows, number	S	5.3	5.0	0.5	0.1	8.6	5.0	6.0	12
	R	3.4	3.0	0.5	0.1	15.0	3.0	4.0	13
Dorsal brush dikinetids, total number	S	68.9	65.0	9.1	3.0	13.2	59.0	85.0	9
	R	67.4	65.0	11.1	3.3	16.4	55.0	88.0	11
Anterior body end to last brush dikinetid, distance	S	58.7	58.0	5.4	1.3	9.3	50.0	70.0	18
	M	62.3	61.5	15.2	3.8	24.4	35.0	86.0	16
	R	64.7	65.0	9.7	2.9	15.0	53.0	80.0	11
Dikinetidal portion of dorsal brush, % of body length	S	26.8	26.1	4.6	1.1	17.1	21.2	38.3	18
	M	23.2	22.5	3.1	0.8	13.3	17.6	28.8	16
	R	31.6	30.0	4.7	1.4	14.9	25.0	40.0	11

a similar habitat, and (iv) the protargol preparations are of sufficient quality. Eight neotype (Salzburg population; inv. nos 2011/218–225) and eight voucher (Mueller boden population; inv. nos 2011/210–217) slides with protargol-impregnated specimens have been deposited in the Biology Centre of the Museum of Upper Austria, Linz (LI). Relevant specimens are marked by black ink circles on the coverslip.

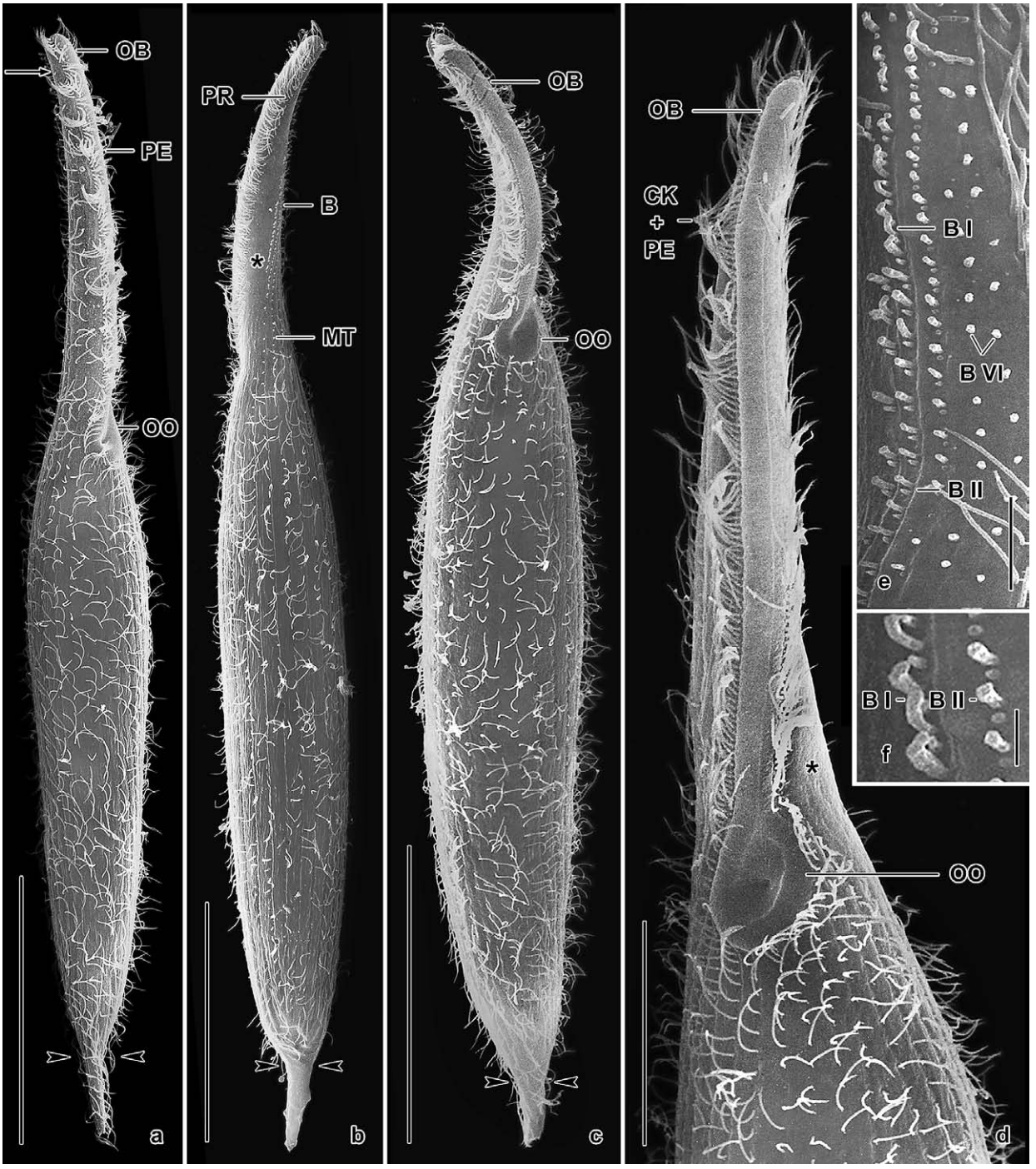
Description: The Austrian data (neotype Salzburg and voucher Mueller boden population) are based on cultivated specimens. Size usually about 280 × 30 μm in vivo, as calculated from some in vivo measurements and the morphometric data, assuming 15% preparation shrinkage (Table 54). French cells 180–320 μm (Dragesco 1963), Polish specimens 200–350 μm (Kink 1973), Salzburg individuals 210–310 × 30–40 μm, and specimens from Mueller boden 200–430 × 20–35 μm; very flexible but not contractile (Table 54). Shape in vivo narrowly dileptid to rod-like, Salzburg specimens usually fusiform in protargol preparations,



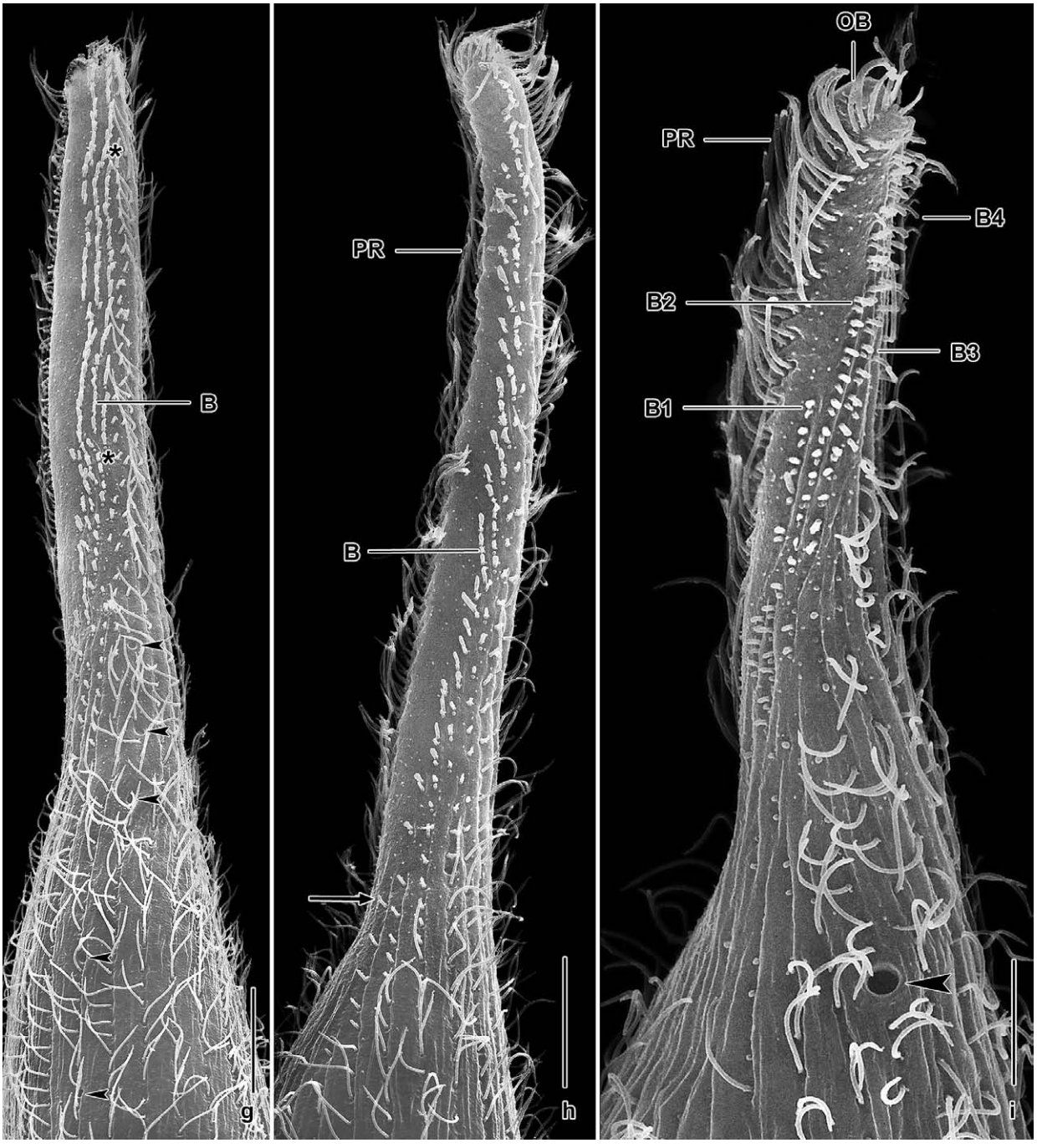
Figs 100a–t: *Apodileptus visscheri visscheri*, Salzburg neotype (c–t; originals) and French (a, b) specimens from life (b–g, i), after protargol impregnation (h, j–t), and in a Feulgen stain (a). **a, b** – part of nuclear apparatus and right side view of a French specimen, length 280 µm (from Dragesco 1963); **c, d** – two types of oral bulge extrusomes: type I very narrowly ovate and about 6 × 0.5 µm in size, type II oblong and 2–2.5 µm long; **e** – right side view of a representative Austrian neotype specimen, length 260 µm; **f, i** – surface view and optical section, showing the cortical granules; **g** – frontal view showing oral bulge opening and arrangement of extrusomes; **h** – ventrolateral view of a very late divider with a long, curved macronucleus; **j, k** – ciliary pattern of right and left side in anterior body third. Arrows mark kineties shortened anteriorly; **l, m** – dorsolateral and dorsal view of ciliary pattern of proboscis. Brush dikinetids connected by dotted lines. Basal bodies of preoral kineties connected by lines. Arrow denotes a short additional brush row right of row 1; **n** – ciliary pattern of dorsal side and nuclear apparatus of main neotype specimen, length 185 µm. Arrows mark gradually shortened somatic kineties in anterior right portion of proboscis; **o–s** – variability of body shape and size as well as of nuclear apparatus. Drawn to scale; **t** – ventrolateral view of a mid-divider, showing fusing and condensed macronuclear nodules and dividing micronuclei. B(1–5) – dorsal brush (rows), CK – circumoral kinety, E – extrusomes, EP – excretory pores, MA – macronucleus (nodules), MI – micronuclei, OB – oral bulge, PB – pharyngeal basket, PE – perioral kinety, PR – preoral kineties, SK – somatic kinety. Scale bars: 20 µm (j–m) and 50 µm (b, e, h, n–t).



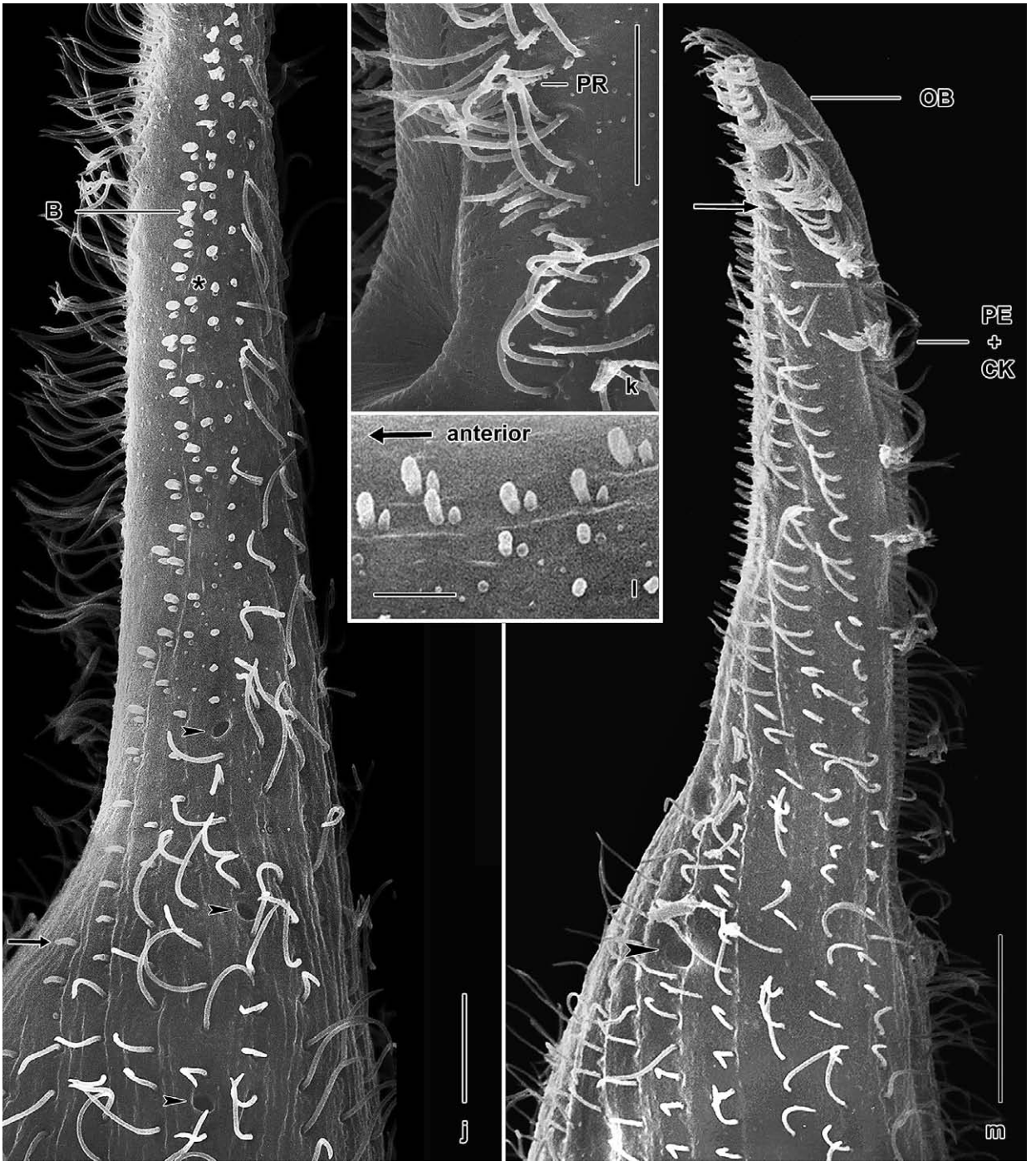
Figs 101a–v: *Apodileptus visscheri visscheri*, Mueller boden specimens after protargol impregnation (a–f, h–v) and from life (g). **a** – left side ciliary pattern of main voucher specimen. Asterisk marks the broad, blank stripe between preoral kineties and dorsal brush; **b, d–f** – dorsolateral (b, d, f) and dorsal (e) views of ciliary pattern of proboscis. Asterisks mark the blank stripe left of the oral bulge, arrowheads denote some shortened right side ciliary rows; **c** – an early post-divider developing a three-dimensional macronuclear reticulum; **g** – there are two types of extrusomes attached to the broader right branch of the proboscis: type I is very narrowly ovate and about 6 × 0.8 µm in size, while type II is oblong and 1.5–2 µm long; **h** – ciliary pattern of left side of proboscis of a very early exconjugant. Basal bodies of preoral kineties connected by lines; **i–o** – variability of body shape and size as well as of nuclear apparatus of exconjugants. Drawn to scale; **p–v** – variability of body shape and size as well as of nuclear apparatus of vegetative specimens. Drawn to scale. B – dorsal brush, CK – circumoral kinety, EB – external basket, EP – excretory pores of contractile vacuoles, IB – internal basket, MA – macronucleus (nodules), MI – micronucleus, OB – oral bulge, PB – pharyngeal basket, PR – preoral kineties. Scale bars: 20 µm (a, b, d–f, h) and 50 µm (c, i–o, p–v).



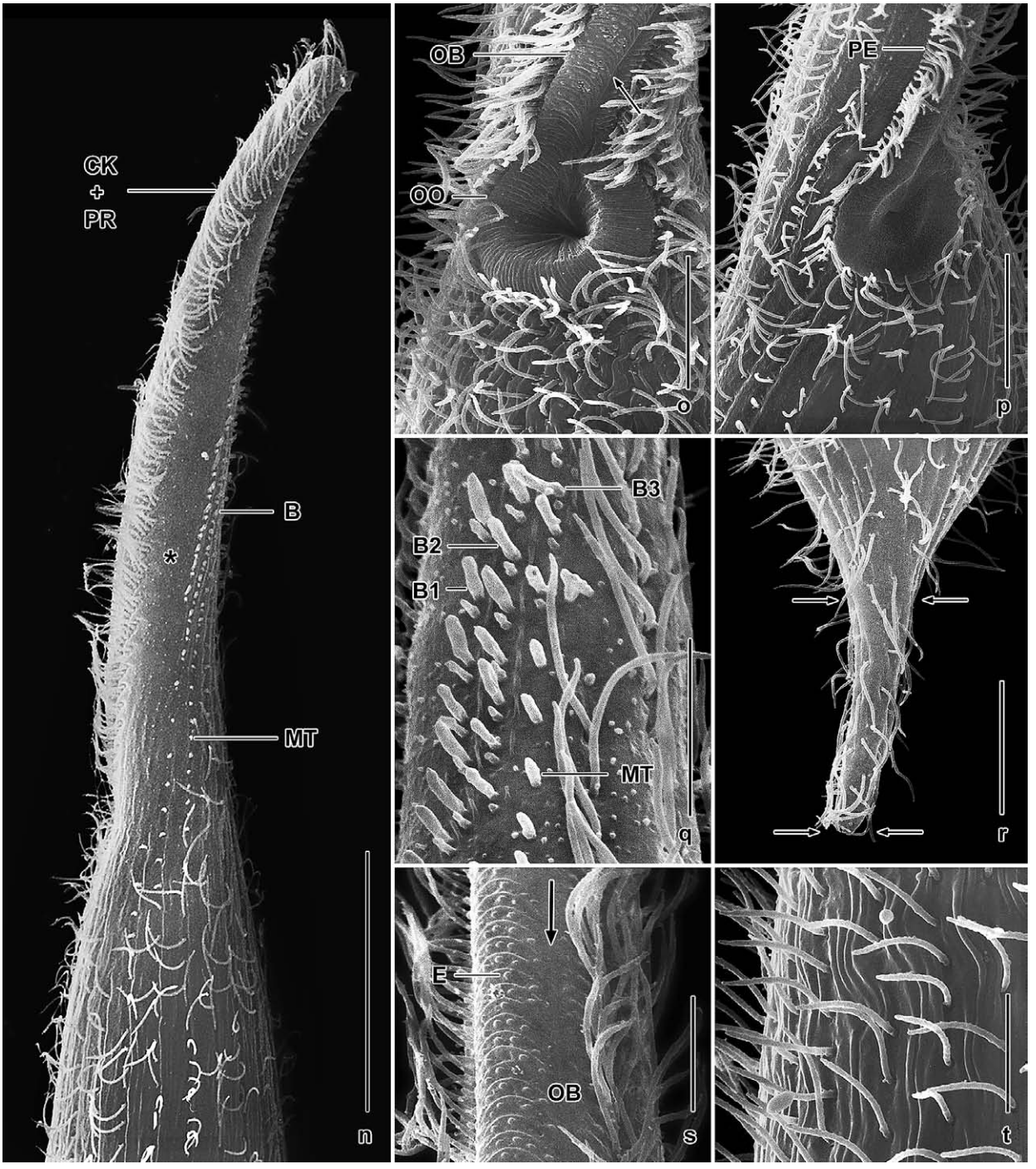
Figs 102a–f: *Apodileptus visscheri visscheri*, Mueller boden specimens in the SEM. **a–c** – ventrolateral (a, c) and dorsolateral (b) overviews, showing the very slender body. Opposed arrowheads mark the distinct tail, arrow marks a shortened ciliary row right of oral bulge, and the asterisks denote the conspicuous blank stripe on the left side of the proboscis; **d** – ventral view of anterior body portion, showing the roundish oral bulge opening and the nice metachronal waves formed by the oral cilia. There is a blank stripe (asterisk) on the left side of the proboscis; **e, f** – there are three kinds of brush bristles: type I bristles in the anterior brush row portion, type II bristles in the mid-portion, and type VI bristles in the brush tails. B(I, II, VI) – dorsal brush (bristle types), CK – circumoral kinety, MT – monokinetidal tails of dorsal brush, OO – oral bulge opening, OB – oral bulge, PE – perioral kinety, PR – preoral kineties. Scale bars: 2 μm (f), 5 μm (e), 20 μm (d), and 50 μm (a–c).



Figs 102g–i: *Apodileptus visscheri visscheri*, dorsal (g, h) and dorsolateral (i) views of proboscis of Mueller boden specimens in the SEM. The specimens show various dorsal brush deformities, such as breaks (h) or anteriorly respectively posteriorly shortened rows (g, asterisks). Possibly, these malformations are caused by the culture conditions and/or the life cycle, as there were rather many exconjugants in this population. The dorsal brush consists of several staggered rows with ordinarily to loosely spaced dikinetids associated with an about 1–2 µm long, inflated anterior bristle and an approximately 0.3–0.7 µm long conical or oblong posterior stump. All brush rows continue with a tail extending to the base of the proboscis with 0.5 µm long monokinetidal bristles. Arrow marks an anterior bristle tail of the ciliary row right of brush row 1 (h); arrowheads denote excretory pores of contractile vacuoles (g, i). B(1–4) – dorsal brush (rows 1–4), OB – oral bulge, PR – preoral kineties. Scale bars: 5 µm (i) and 10 µm (g, h).



Figs 102j–m: *Apodileptus visscheri visscheri*, Mueller boden specimens in the SEM. **j, l** – dorsal views of proboscis. The dorsal brush is multi-rowed, staggered, and all rows continue with a monokinetidal tail. Asterisk marks an anteriorly shortened row, arrow denotes an anterior bristle tail of the ciliary row right of brush row 1, and the arrowheads denote excretory pores; **k** – left side view showing the irregularly arranged preoral kineties left of the oral bulge opening; **m** – right side of view of proboscis. The circumoral and perioral kinety lie side by side and are composed of narrowly spaced cilia beating together and thus forming metachronal waves. Arrow marks a shortened ciliary row; arrowhead denotes an excretory pore. B – dorsal brush, CK – circumoral kinety, OB – oral bulge, PE – perioral kinety. Scale bars: 2 μm (l), 5 μm (j, k), and 10 μm (m).



Figs 102n–t: *Apodileptus visscheri visscheri*, Mueller boden specimens in the SEM. **n –** left side view of the specimen depicted in (b), showing the conspicuous blank stripe left of the oral bulge (asterisk); **o, p** – the oral bulge opening is roundish to broadly ovate. Arrow marks furrow separating the oral bulge branches; **q –** the posterior brush dikinetids are associated with an about 2 μm long, clavate anterior bristle and an about 0.7 μm long, conical posterior stump; **r –** opposed arrows mark tail; **s** – the oral bulge is transversely striated by fibre bundles and the broader right branch is dotted by extrusome tips. Arrow denotes furrow separating the oral bulge branches; **t** – surface view showing cortex and cilia. B(1–3) – dorsal brush (rows), CK – circumoral kinety, E – extrusome tip, MT – tails of dorsal brush, OO – oral bulge opening, OB – oral bulge, PE – perioral kinety, PR – preoral kineties. Scale bars: 5 μm (q, s, t), 10 μm (o, p, r), and 20 μm (n).

length:width ratio near 10:1 both in French (according to the figure in Dragesco 1963) and Mueller boden specimens, while 7:1 in Salzburg population. Proboscis one third to one half of body length in French specimens (Dragesco 1963) and slightly less than one third in Austrian cells, flattened, highly motile and flexible; trunk oblong, unflattened; posterior end with distinct tail preserved also in prepared cells (Figs 100b, e, n–s; 101p–v, 102a–c, r). Nuclear apparatus in trunk, rarely extending into proximal portion of proboscis, absent from tail. Number and shape of macronuclear nodules fairly similar in all populations investigated: about 40–90 nodules in French specimens (Dragesco 1963, 1966a), approximately 60 nodules in Polish cells (Kink 1973), 70–100 nodules in Salzburg specimens, and 70–140 in Mueller boden cells; individual nodules usually globular to broadly ellipsoidal, rarely ellipsoidal, 3–10 × 3–5 μm in size; fuse in mid-dividers to a globular mass (Fig. 100t), becoming rod-shaped before and during cell fission (Fig. 100h), post-dividers show a three-dimensional macronuclear reticulum (Fig. 101c); usually one, rarely two small nucleoli in centre or periphery of each nodule. On average 8 micronuclei scattered between or attached to macronuclear nodules, about 0.5–1 μm across in French specimens, while 2–2.5 μm in Austrian cells (Figs 100a, b, e, n–s, 101p–v, 105i; Table 54). A stripe of contractile vacuoles in dorsal side of body, 8–12 vacuoles in Polish cells, first vacuole slightly anterior to level of oral bulge opening; no ventral vacuoles; invariably a single intrakinetal excretory pore per vacuole (Figs 100b, e, n, 101d, 102g, i, j, m). Two types of extrusomes, not impregnating with protargol, attached to broader right branch of oral bulge (Figs 100c, d, g, n, 101g, 105k, l): type I very narrowly ovate, about 6 × 0.5–0.8 μm in size; type II oblong with rounded ends, 1.5–2.5 × 0.3 μm in size; developing cytoplasmic extrusomes sometimes impregnating with protargol, narrowly ovate to oblong or fusiform and 4 μm long. Cortex flexible, slightly furrowed by ciliary rows, about 1 μm thick and distinctly separated from cytoplasm, between each two kineties about six rows of oblong granules (~ 0.2 × 0.7 μm) possibly contained in interkinetal ridges distinct in SEM micrographs (Figs 100f, i, 102t). Silverline pattern composed of polygonal meshes about 0.5 μm in size (Foissner 1979). Cytoplasm colourless in Austrian cells, while French specimens greenish due to algal food; hyaline in proboscis and tail, opaque in trunk due to food vacuoles and numerous lipid droplets up to 10 μm across; in posterior end of trunk sometimes a defecation vacuole. Swims rather rapidly.

Cilia about 8 μm long in vivo, narrowly spaced; in protargol preparations as typical for dileptids, i.e., with thick, deeply impregnated distal half, except for dorsal bristles; arranged in an average of 22 longitudinal, ordinarily spaced rows (Figs 100n, 102a–c; Table 54). Right side rows gradually shortened in anterior fifth of proboscis; perioral kinety extends to tip of proboscis with ordinarily to narrowly spaced basal bodies (Figs 100j, n, 101d, 102a, m). Left side of proboscis with conspicuous blank stripe because some ciliary rows end at level of oral bulge opening (Figs 100k, 101a, b, 102b, d, n). Dorsal brush on dorsal and dorsolateral side of proboscis; staggered; distinctly heterostichad; composed of five to seven rows; first brush row begins usually in second third of proboscis, while last row commences subapically; all rows continue with a monokinetidal tail extending to base of proboscis (Figs 100l, m, 101a, b, d–f; Table 54). Mueller boden specimens frequently with brush malformations, such as rows broken into short straight or oblique pieces (Figs 102g, h), posteriorly shortened rows (Figs 102j, 105h), or a ciliary row right of brush row 1 anteriorly composed of rod-shaped bristles (Figs 102h, j). Type I, II, and VI brush bristles: type I anterior bristle 3–4 μm long in vivo (1.7–2 μm in SEM preparations), posterior bristle conical, about 1.5 μm long in vivo (0.7 μm in SEM; Figs 102e, f); type II anterior bristle 1–2 μm long in SEM, posterior one conical, 0.3–0.7 μm (Figs 102l, q); type VI bristles 1 μm long in SEM (Fig. 102q).

Oral bulge opening at beginning of second body third, roundish both in vivo and in preparations, about 15 μm across in vivo, projects distinctly because proboscis only half as wide as trunk (Figs 100b, e, g, k, 102d, k, o, p; Table 54). Internal and external oral basket obconical and distinct both in vivo and in protargol preparations; slightly bulbous in Mueller boden specimens. Broader right branch of oral bulge

dotted by extrusome tips in SEM micrographs (Fig. 102s). Circumoral kinety composed of ordinarily spaced dikinetids, except for narrowly spaced monokinetids around oral bulge opening (Figs 100j, k, 101a). On average 40 oblique to strongly oblique, ordinarily spaced preoral kineties, each composed of two to four, usually three narrowly to ordinarily spaced cilia; almost in parallel to circumoral kinety and composed of comparatively widely spaced basal bodies in some cells possibly regenerating the proboscis (Figs 100k, 101a, 102i, k, 105j).

Resting cyst (Polish population): Studied by KINK (1973) in vivo and in TEM (for original wording, see general part). Her observations match very well our data from *A. visscheri rhabdoplites* (see below).

Notes on ex-conjugants: Many exconjugants were found in the preparations from the Mueller boden population. They are easily distinguished from vegetative cells by the much smaller size (120 × 54 μm vs. 272 × 24 μm), the stouter body (4.7:1 vs. 11.4:1), the shorter proboscis (~ 50 μm vs. 75 μm long), and the broadly rounded or acute body end (vs. distinct tail). Further, the number of dorsal brush dikinetids and preoral kineties is much lower (cp. Fig. 101h with Figs 101a, b, d–f). In contrast, the number of macronuclear nodules (98 vs. 100) and micronuclei (9 vs. 10) is quite similar. Thus, exconjugant reorganization is associated mainly with intense proboscis and body growth as well as tail formation (Figs 101h–o).

Occurrence and ecology: *Apodileptus visscheri* was discovered by DRAGESCO (1963) in a pond from the surroundings of the town of Thonon, France, where it fed on algae and bacteria. The neotype population is from a shallow meadow puddle near the so-called Henkerhaus in the Donnersberg Park (a municipal park near Salzburg city centre). The second Austrian population was found in a floodplain forest in the surroundings of Vienna, viz., in soil from the Mueller boden (see FOISSNER et al. 2005 for detailed site description; designated as *Dileptus* n. sp. 2). Further, *A. visscheri* was recorded in the pond of Sadyba in Warsaw, Poland (KINK 1973); in the Dniester River in Ukraine (KOVALCHUK & KOVALCHUK 1992); in Benin, Africa (DRAGESCO & DRAGESCO-KERNÉIS 1986); and in the litter and upper soil layer enriched with minerals (pH 6.4) from a vegetable field irrigated with hard ground water about 40 km north of Riyadh, Saudi Arabia (FOISSNER et al. 2008b). *Apodileptus visscheri* grows well in semi-pure Petri dish cultures with *Paramecium* or small scuticociliates as a prey.

Remarks: Our observations match the rather incomplete original data (DRAGESCO 1963): body length 200–430 μm versus 180–320 μm; body shape narrowly dileptid to rod-like with distinct tail, proboscis about one third of body length; about 70–140 macronuclear nodules and 8 micronuclei versus 40–90 nodules and 8 micronuclei; and a dorsal stripe of contractile vacuoles. As usual, there are some small differences, for instance, the diameter of the micronuclei (2–2.5 μm vs. 0.5–1 μm across) and the prey (ciliates vs. algae). Unfortunately, the original description of *D. visscheri* lacks data about the extrusomes and the number of ciliary rows. Thus, without neotypification it hardly can be separated from *D. jonesi* and *D. beersi*. The former has rod-shaped extrusomes and more ciliary rows (31 vs. 22), while the latter is much larger (670 × 60 μm vs. 280 × 30 μm) and has twice the number of ciliary rows (~ 48 vs. 22).

As concerns the two Austrian populations, all important features match, except for body length and width, resulting in considerably different length:width ratios, viz., 11.4:1 vs. 6.9:1 (Figs 100o–s, 101p–v; Table 54). Possibly, this difference is caused by the culture conditions and/or the life cycle, that is, there were rather many exconjugants in the protargol slides from the Mueller boden; possibly this is also responsible for the many malformations found in the dorsal brush (Figs 102g, h).

Apodileptus visscheri rhabdoplites nov. ssp. (Figs 103a–r; Table 54)

2011 *Dileptus* cf. *jonesi* – VĎAČNÝ, ORSI, BOURLAND, SHIMANO, EPSTEIN & FOISSNER, Eur. J. Protistol. **47**: 297 (preliminary identification; 18S rRNA gene sequence)

Nomenclature: VĎAČNÝ et al. (2011b) preliminary identified this taxon as "*Dileptus* cf. *jonesi*" but

definitely stated that it differs from *D. jonesi* by the inability to form a mucous attachment thread. Our detailed morphological investigations of protargol-impregnated specimens showed that it belongs to the genus *Apodileptus* due to the fusion of the macronucleur nodules during binary fission (Fig. 103q). Further, it is similar to *A. visscheri visscheri* except for some details (see "Description" below). According to Article 49 of the ICZN (1999), the name "*jonesi*" cannot be used as an available name for that taxon. We do not denote "*Dileptus* cf. *jonesi*" sensu Vďačný et al. (2011b) with a new replacement name but establish a new subspecies, *Apodileptus visscheri rhabdoplites*, because a holotype is fixed here (Article 72.3 of the ICZN 1999).

Diagnosis: Extrusomes oblong. Dorsal brush staggered and usually diffuse.

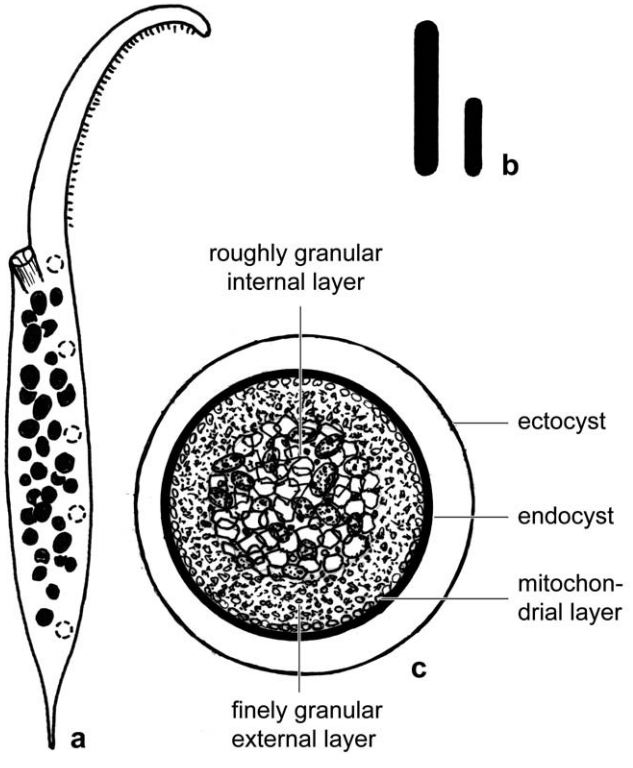
Type locality: Ephemeral pond in the Austrian Central Alps, Grossglockner-Hochalpenstrasse, surroundings of the Hochtor, E12°48' N47°6'.

Type material: One holotype slide (inv. no. 2011/226) and a series of four paratype slides (inv. nos 2011/227–230) with protargol-impregnated specimens have been deposited in the Biology Centre of the Museum of Upper Austria, Linz (LI). Relevant specimens are marked by black ink circles on the coverslip.

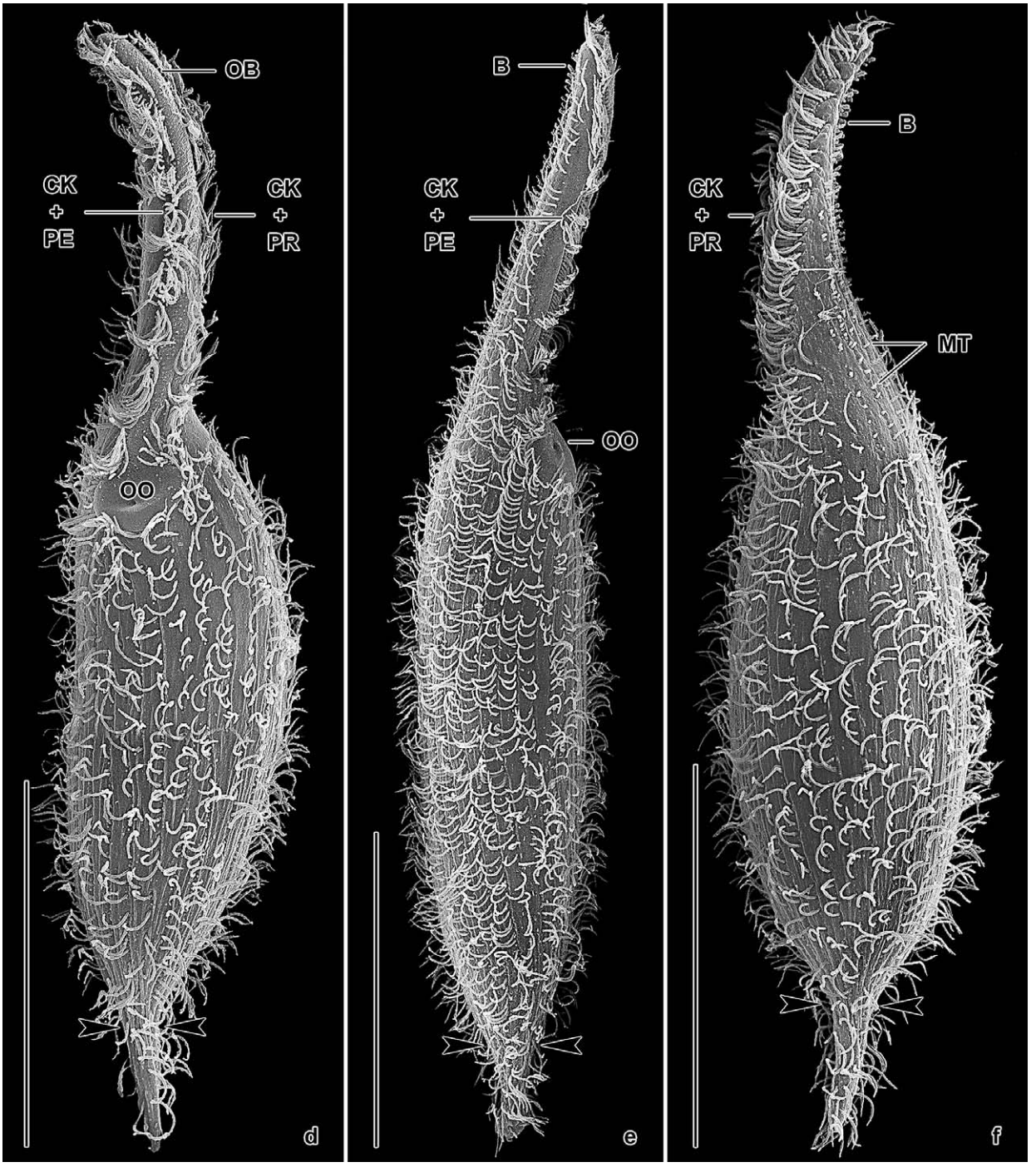
Gene sequence: The 18S rRNA gene sequence of type population has been deposited in GenBank (HM581678). The sequence is 1640 nucleotides long and has a GC content of 42.3%. It is a consensus sequence based on 19 clones.

Etymology: Composite of the Greek nouns *rhabdos* (rod) and *hoplites* (soldier ~ extrusome), referring to the rod-shaped extrusomes.

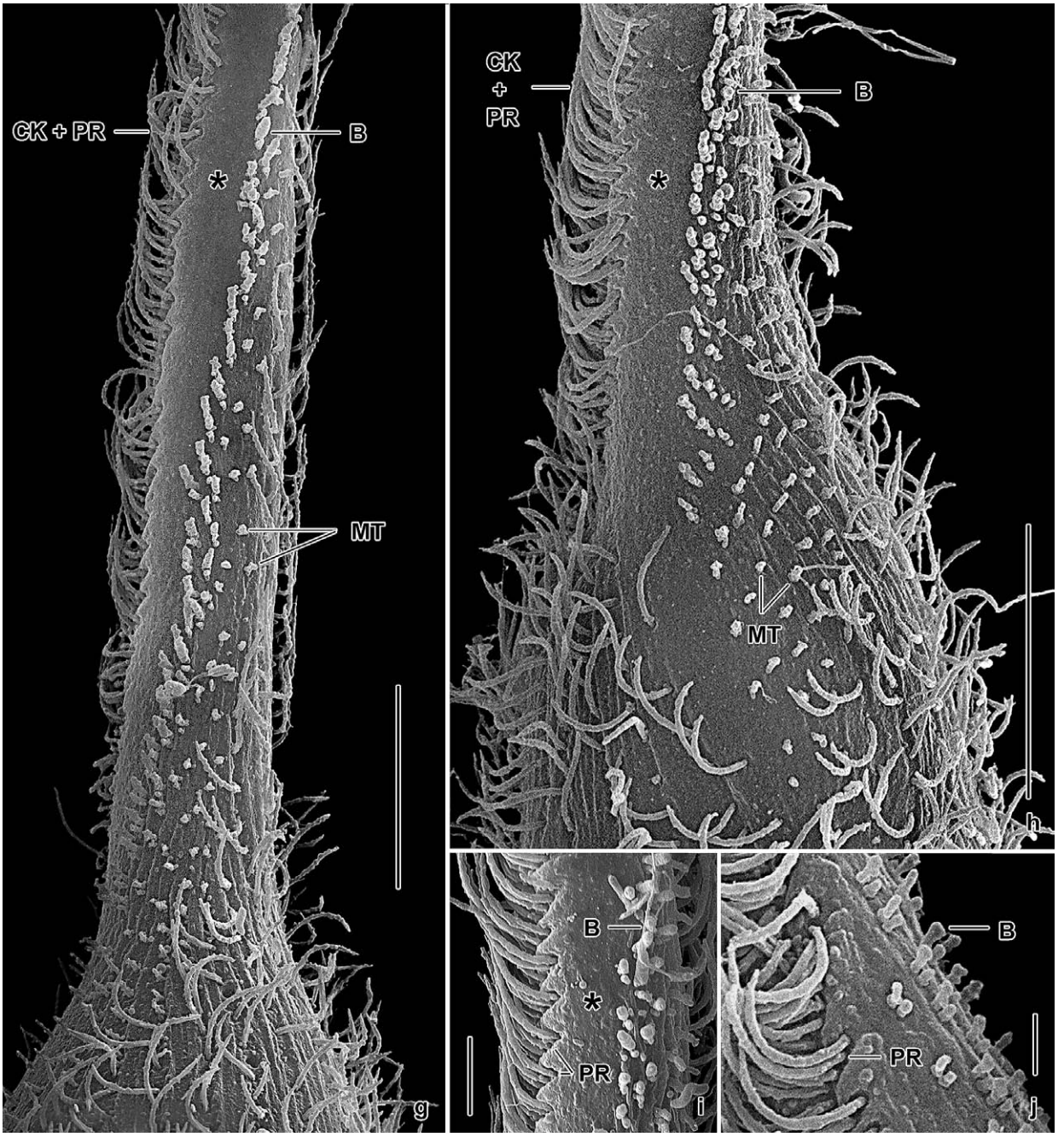
Description: This subspecies is highly similar to *A. visscheri visscheri*, except for the characteristics mentioned in the diagnosis. Thus, we provide micrographs, showing the general body organization (Figs



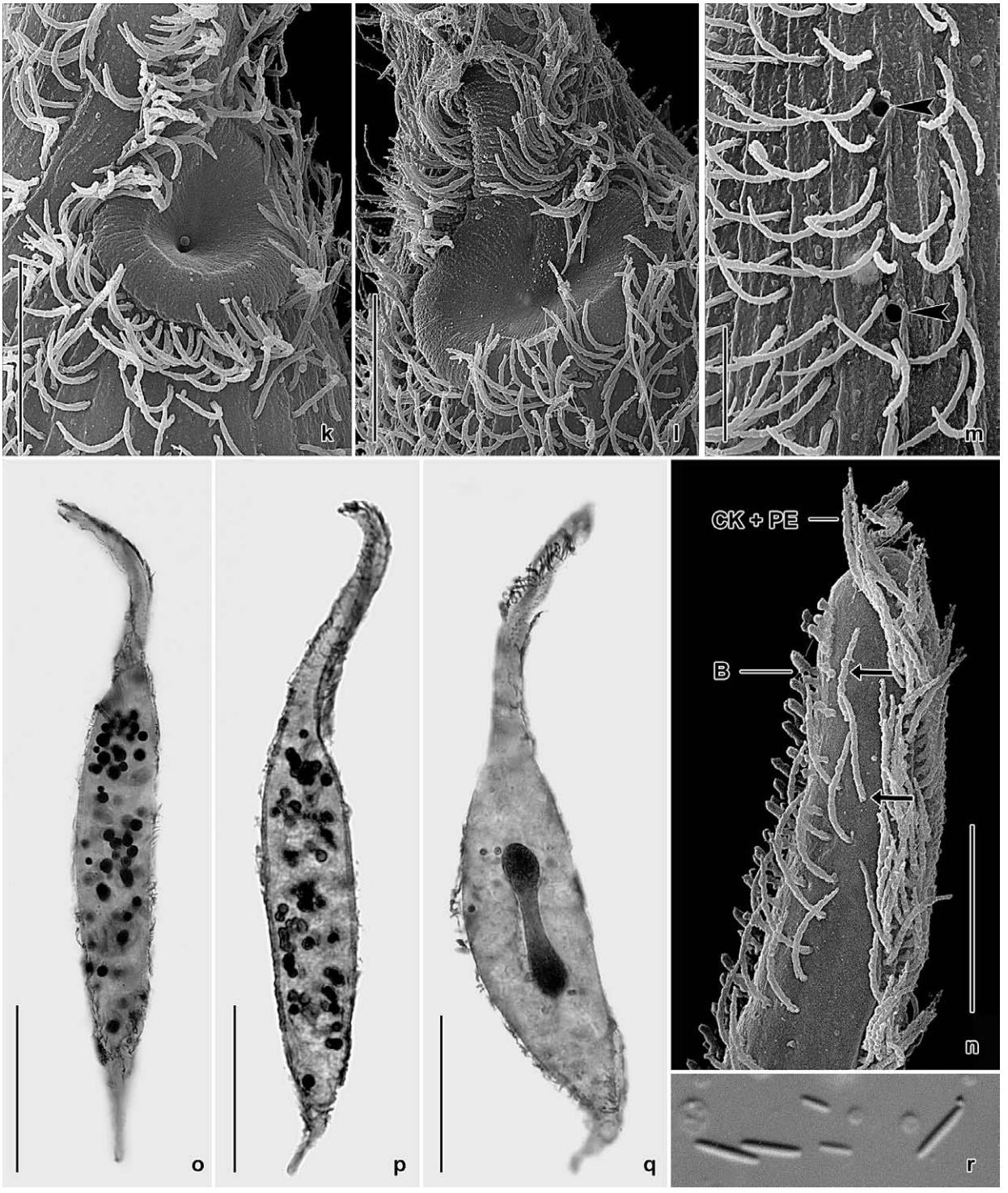
Figs 103a–c: *Apodileptus visscheri rhabdoplites* nov. ssp. from type locality in vivo. **a** – outline figure, showing the usual body shape, a dorsal stripe of contractile vacuoles, and many scattered macronuclear nodules, length 250 µm; **b** – type I and II extrusomes, size about 5 × 0.8 µm and 2.5 × 0.3 µm; **c** – the resting cyst is about 50 µm across and has a 3–5 µm thick, hyaline ectocyst; an 1–2 µm thick, compact, yellow-brown endocyst; a layer of tightly spaced mitochondria underneath the cortex; a finely granular external layer; and a roughly granular internal layer composed of macronuclear nodules and bright inclusions 2–3 µm across.



Figs 103d–f: *Apodileptus visscheri rhabdoplites* nov. ssp. from type locality in the SEM. Ventral (d) and lateral (e, f) overviews, showing the narrow to very narrow body with the proboscis occupying about one third of body length. The specimen shown in (f) is possibly malformed or just regenerating the proboscis, as indicated by the comparatively widely spaced preoral kineties in the distal portion of the proboscis. The oral bulge opening is roundish (d) and projects distinctly because the base of the proboscis is only half as wide as the trunk (e). The dorsal brush forms a triangular field extending on the dorsal and dorsolateral area of the proboscis (for details, see next plate). Opposed arrowheads mark the distinct tail. B – dorsal brush, CK – circumoral kinety, MT – monokinetidal tails of dorsal brush, OO – oral bulge opening, OB – oral bulge, PE – perioral kinety, PR – preoral kineties. Scale bars 50 μm.



Figs 103g–j: *Apodileptus visscheri rhabdoplites* nov. ssp. from type locality in the SEM. **g, h** – dorsal (g) and dorsolateral (h) view of proboscis. The dorsal brush forms a narrowly triangular field on the dorsal and dorsolateral surface of the proboscis. The brush dikinetids are ordinarily to loosely spaced and associated with an about 1 µm long, inflated anterior bristle and an approximately 0.3 µm long, conical posterior stump. All brush rows continue with a tail composed of about 0.5 µm long, monokinetidal bristles. The ventralmost brush tails reach the base of the proboscis, while some dorsalmost tails end in the mid-portion of the proboscis. The left side ciliary rows terminate at the level of the oral bulge opening, leaving a broad blank stripe (asterisks) on the proboscis; **i, j** – dorsal (i) and lateral (j) view of proboscis, showing the barren area (asterisk) between the preoral kineties and the dorsal brush; (j) is a detail of the distal portion of the proboscis of the specimen shown in (f). The preoral kineties are usually composed of three narrowly spaced cilia extending in shallow furrows. B – dorsal brush, CK – circumoral kinety, MT – monokinetidal tails of dorsal brush, PR – preoral kineties. Scale bars: 2 µm (i, j) and 15 µm (g, h).



Figs 103k–r: *Apodileptus visscheri rhabdoplites* nov. ssp. from type locality in vivo (r), after protargol impregnation (o–q), and the SEM (k–n). **k, l** – variability of oral bulge opening; **m** – surface view showing excretory pores (arrowheads); **n** – right side view of distal region of proboscis. Arrows mark shortened ciliary rows; **o–q** – in vegetative specimens (o, p), the about 90 scattered macronuclear nodules fuse into a central mass in mid-dividers (q); **r** – two size types (5 µm and 2.5 µm) of rod-shaped extrusomes. B – dorsal brush, CK – circumoral kinety, PE – perioral kinety. Scale bars: 5 µm (m), 10 µm (k, l, n), and 50 µm (o–q).

103a, d–f, l, m), the extrusomes (Figs 103b, o), and the diffuse dorsal brush (Figs 103d–g). Further, we provide morphometrics (Table 54) and show the type I resting cyst, which has an average diameter of 51 × 50 µm (40–60 × 44–55 µm, n = 6).

Apodileptus edaphicus nov. sp. (Figs 104a–p, 105a–g; Table 55)

Diagnosis: Size about 470 × 30 µm in vivo. Rod-shaped with distinct tail, proboscis about 1/3 of body length. Many scattered macronuclear nodules and several globular micronuclei. A dorsal stripe of contractile vacuoles with 1 pore each. Two size-types (6 µm and 2 µm) of rod-shaped extrusomes attached to proboscis oral bulge. On average 20 ciliary rows; dorsal brush diffuse, staggered, all rows with a monokinetidal bristle tail extending to base of proboscis. Oral bulge opening elliptical, about 22 × 11 µm in size. On average 55 oblique, widely spaced preoral kineties, each usually composed of 3 ordinarily spaced cilia.

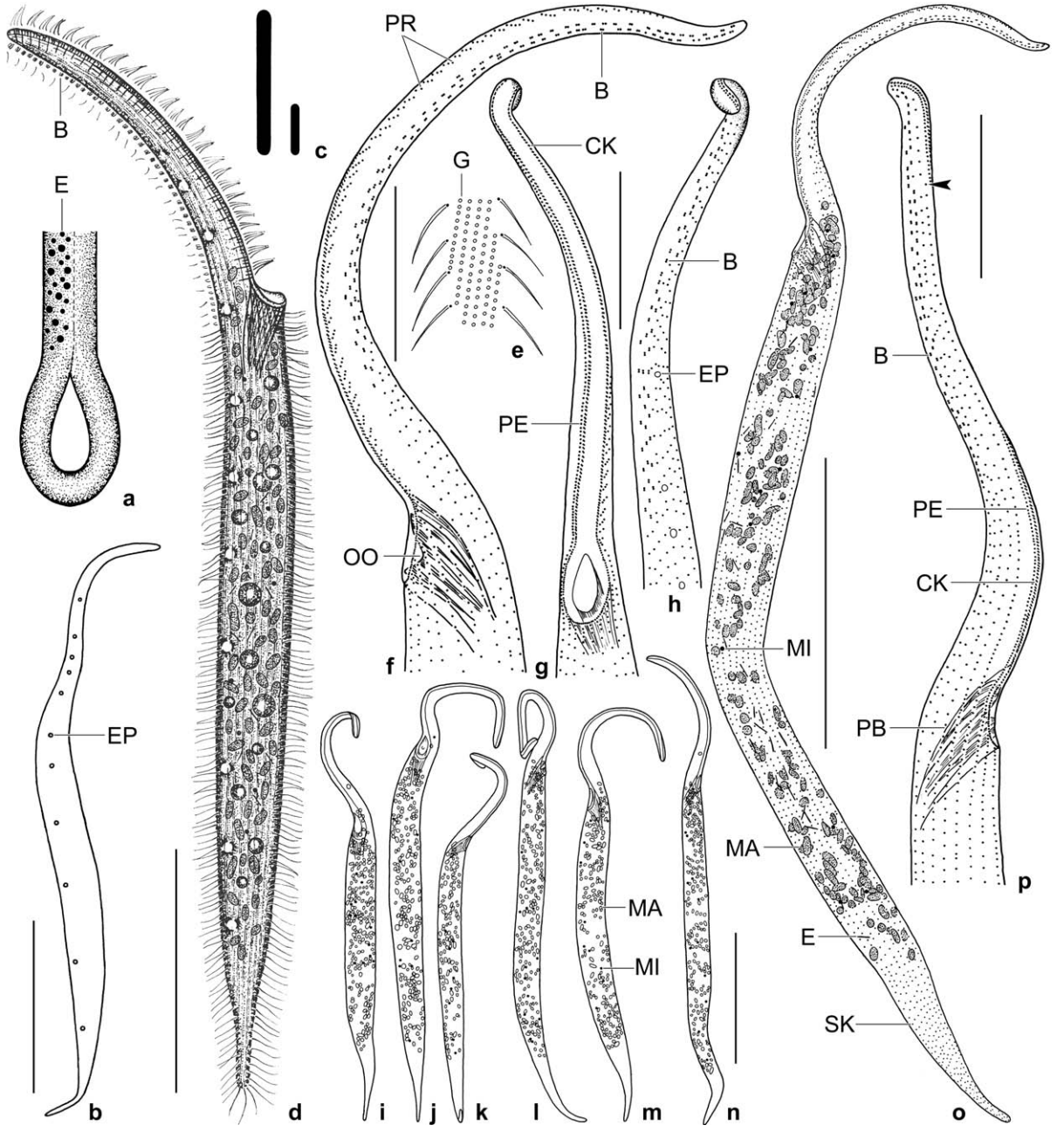
Type locality: Soil from southern Florida, USA, W81° N26°.

Type material: One holotype slide (inv. no. 2011/202) and seven paratype slides (inv. nos 2011/203–209) with protargol-impregnated specimens have been deposited in the Biology Centre of the Museum of Upper Austria, Linz (LI). Relevant specimens are marked by black ink circles on the coverslip.

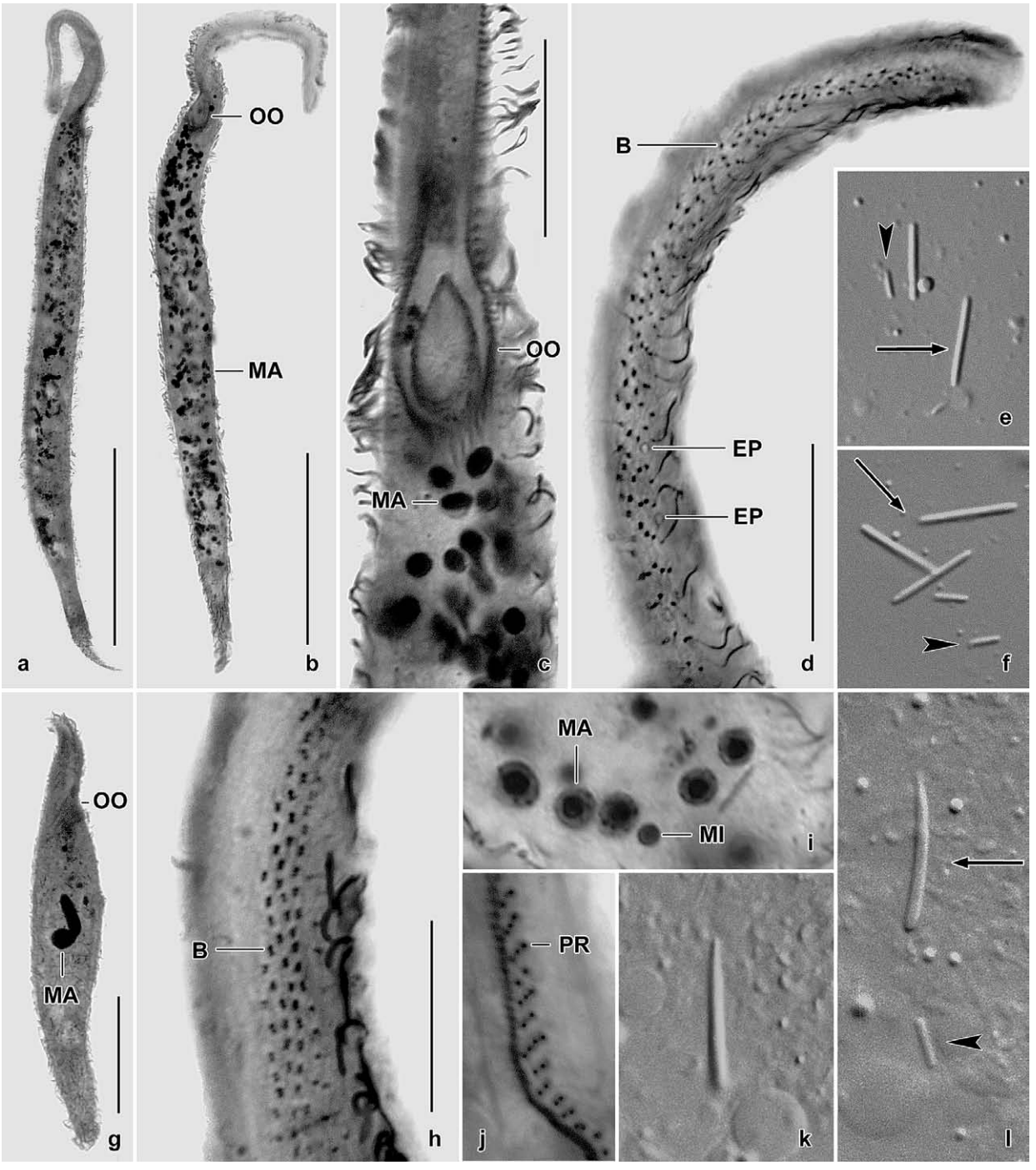
Etymology: Derived from the Greek substantive *edaphon* (soil organisms) because well adapted to the soil environment by the very slender, highly flexible body.

Description: Size 350–600 × 25–35 µm in vivo, usually about 470 × 30 µm, as calculated from some in vivo measurements and the morphometric data, assuming 15% preparation shrinkage; flexible but not contractile (Table 55). Shape rod-like, length:width ratio rather variable (12.4–23.8:1), on average near 17.4:1 in prepared cells. Proboscis slightly less than one third of body length on average, usually curved dorsally; trunk oblong, unflattened; posterior end with distinct tail in vivo sometimes becoming indistinct or acute in protargol preparations (Figs 104b, d, i–o, 105a, b; Table 55). Nuclear apparatus in trunk and base of proboscis, absent from tail region. On average 174 macronuclear nodules; individual nodules globular to narrowly ellipsoidal, about 4 × 3 µm in size on average; usually a small nucleolus in centre of each nodule. On average 13 micronuclei scattered between or attached to macronuclear nodules, 2–2.5 µm across in protargol preparations (Figs 104i–o, 105a–c; Table 55). A narrow stripe of contractile vacuoles in dorsal side of trunk and proximal half of proboscis, no ventral vacuoles; usually a single (rarely two) intrakinetal excretory pore per vacuole (Figs 104b, d, h, 105d). Two size-types (6 µm and 2 µm long) of rod-shaped extrusomes attached to broader right branch of oral bulge and scattered throughout cytoplasm, where certain developmental stages (oblong or fusiform and 4–5.5 µm long) sometimes impregnate with protargol (Figs 104a, c, o, 105e, f). Cortex flexible, contains about five granule rows between adjacent kineties (Fig. 104e). Cytoplasm colourless, hyaline in proboscis and tail, opaque in trunk due to numerous lipid droplets 1–10 µm across. Glides and wriggles like a worm.

Cilia about 8 µm long in vivo, ordinarily spaced; in protargol preparations as typical for dileptids; arranged in an average of 20 longitudinal, narrowly to ordinarily spaced rows (Table 55). Right side rows shortened only along anterior fifth of oral bulge; perioral kinety extends to tip of proboscis with ordinarily spaced basal bodies (Figs 104g, p). Left side of proboscis with a blank stripe because some ciliary rows end left of oral bulge opening (Figs 104f, o). Dorsal brush a long, narrow field on dorsal and dorsolateral region of proboscis; staggered; distinctly heterostichad; diffuse, very likely composed of four rows. First row begins in second third of proboscis, while last row commences subapically. All brush rows continue with a monokinetidal tail extending to base of proboscis with rod-shaped type VI bristles (Figs 104f, h, o, p, 105d).



Figs 104a-p. *Apodileptus edaphicus* nov. sp. from life (a, c-e) and after protargol impregnation (b, f-p). **a** – frontal view showing oral bulge opening and arrangement of extrusomes; **b** – the excretory pores of the contractile vacuoles form a narrow stripe on dorsal side; **c** – there are two size-types of rod-shaped extrusomes attached to the right branch of the proboscis' oral bulge: type I is 6 μm long and type II is about 2 μm long; **d** – right side view of a representative specimen, length 470 μm; **e** – surface view showing cortical granulation; **f, o** – ciliary pattern of left side and nuclear apparatus of holotype specimen, length 476 μm; **g, h** – ciliary pattern of ventral and dorsal side of proboscis. The dorsal brush consists of several staggered rows with loosely to very loosely spaced dikinetids; **i-n** – variability of body shape and size as well as of nuclear apparatus. Drawn to scale; **p** – right side view of ciliary pattern in oral body portion. Arrowhead denotes a shortened ciliary row right of perioral kinety. B – dorsal brush, CK – circumoral kinety, E – extrusomes, EP – excretory pores, G – cortical granules, MA – macronuclear nodules, MI – micronuclei, OO – oral bulge opening, PB – pharyngeal basket, PE – perioral kinety, PR – preoral kineties, SK – somatic kineties. Scale bars: 30 μm (f-h, p) and 100 μm (b, d, i-o).



Figs 105a-l. *Apodileptus edaphicus* nov. sp. (a-g) and *A. visscheri visscheri*, Salzburg neotype (h-l) from life (e, f, k, l) and after protargol impregnation (a-d, g-j). **a, b** – overviews of representative specimens; **c** – the oral bulge opening is elliptical; **d, h** – ciliary pattern of proboscis' dorsal side; **e, f** – two size-types (6 µm long, arrows; 2 µm long, arrowheads) of rod-shaped extrusomes; **g** – very early opisthe post-divider, showing a rather short macronuclear strand; **i** – the nuclear apparatus consists of several micronuclei and many macronuclear nodules each having a large central nucleolus; **j** – the preoral kineties are composed of two to three narrowly spaced basal bodies; **k, l** – the type I extrusomes are very narrowly ovate and about 6 × 0.5 µm in size (arrow), while type II is oblong and about 2–2.5 µm long (arrowhead). B – dorsal brush, EP – excretory pores, MA – macronuclear nodules, MI – micronucleus, OO – oral bulge opening, PR – preoral kineties. Scale bars: 20 µm (c, d, h), 50 µm (g), and 100 µm (a, b).

Table 55: Morphometric data on *Apodileptus edaphicus* nov. sp. Data based on mounted, protargol-impregnated (Foissner's method), and randomly selected specimens from a non-flooded Petri dish culture. Measurements in µm. CV – coefficient of variation in %, M – median, Max – maximum, Mean – arithmetic mean, Min – minimum, n – number of specimens investigated, SD – standard deviation, SE – standard error of mean.

Characteristics	Mean	M	SD	SE	CV	Min	Max	n
Body, length	412.3	408.0	56.0	12.2	13.6	339.0	512.0	21
Body, width	23.8	23.0	2.3	0.5	9.6	20.0	30.0	21
Body length:width, ratio	17.4	16.9	2.8	0.6	16.0	12.4	23.8	21
Anterior body end to oral bulge opening, distance	124.1	126.0	15.1	3.3	12.1	86.0	145.0	21
Proboscis, % of body length	30.3	29.6	3.7	0.8	12.2	24.0	39.2	21
Oral bulge opening, length	19.1	18.0	2.0	0.6	10.3	17.0	22.0	10
Oral bulge opening, width	9.9	10.0	1.2	0.4	12.1	8.0	12.0	10
Anterior body end to first macronuclear nodule, distance	118.6	128.0	32.5	7.1	27.4	27.0	158.0	21
Nuclear figure, length	253.2	254.0	54.1	11.8	21.4	190.0	350.0	21
Macronuclear nodules, length[a]	4.0	4.0	1.0	0.1	25.4	2.5	7.0	100
Macronuclear nodules, width[a]	2.9	3.0	0.5	0.0	16.4	2.0	4.0	100
Macronuclear nodules, number (rough values)	173.8	171.0	–	–	–	127.0	222.0	21
Micronuclei, diameter	2.1	2.0	–	–	–	2.0	2.5	21
Micronuclei, number (rough values)	12.2	13.0	–	–	–	7.0	18.0	21
Ciliary rows, number	20.4	20.0	1.2	0.3	5.9	18.0	23.0	21
Cilia in mid-body in 10 µm, number	5.1	5.0	–	–	–	5.0	6.0	21
Preoral kineties, number	54.8	56.5	6.9	2.8	12.6	43.0	62.0	6
Anterior body end to last brush dikinetid, distance	107.5	111.0	13.9	3.0	12.9	70.0	126.0	21
Dikinetidal portion of dorsal brush, % of body length	26.3	26.0	3.5	0.8	13.3	19.5	34.3	21

[a] Ten posterior nodules of ten specimens each measured.

Oral bulge opening at beginning of second body third, broadly elliptical to elliptical both in vivo and in preparations, about 22 × 11 µm in vivo (Figs 104a, d, g, 105c; Table 55). Pharyngeal basket obconical, without specific features (Figs 104d, f, g, p). Circumoral kinety composed of narrowly to ordinarily spaced dikinetids in proboscis and narrowly spaced monokinetids around oral bulge opening; right branch curves around anterior end of proboscis, while left branch ends subapically almost touching the curved right end. On average 55 oblique, widely spaced preoral kineties, each composed of two to four, usually three ordinarily spaced cilia (Figs 104f, o; Table 55).

Occurrence and ecology: As yet found only at type locality, that is, in a sample collected by Miss Gerlinde FISCHER along a "Pine Trail" in southern Florida (USA). The sample, in which the species was rather rare, was a mixture of conifer needles, mosses, lichens, and soil crumbles.

Remarks: Unfortunately, the preparations did not contain dividers making the generic affiliation uncertain. However, several post-dividers were found. They show a short macronuclear strand, very likely originating from a fused macronuclear mass, indicating that the nodules did not divide individually (Fig. 105g).

Among the large multinucleate dileptids, *A. edaphicus* is most similar to *A. visscheri*, *Dileptus jonesi*, and *D. margaritifer* (Table 55). *Apodileptus visscheri* is smaller (~ 280 µm vs. ~ 470 µm), stouter (up to 11:1

vs. 17:1), and has fewer macronuclear nodules (on average ≤ 100 vs. 174). *Dileptus jonesi* has a much stouter body (8:1 vs. 17:1) and a higher number of ciliary rows (28–34 vs. 18–23). *Dileptus margaritifer* has much more ciliary rows (40–50 vs. 18–23).

Monilicaryon Jankowski, 1967

1967 *Monilicaryon* subg. n. Jankowski, Mater. IV Konf. uč. Sekc. zool. year **1967**: 36

1989 *Monilikaryon* – Blatterer, Bufus-Info **5/89**: 9 (incorrect subsequent spelling and therefore unavailable, according to Articles 33.3 and 33.5 of the ICZN 1999)

1997 *Monilicaryon* Jankowski, 1967 stat. nov. – Foissner, Limnologica **27**: 196 (improved diagnosis; raise to genus level)

2001 *Monilicaryon* Jankowski 1967 – Aescht, Denisia **1**: 102 (catalogue of generic names of ciliates)

2003 *Monillicarion* – Tirjaková, Acta zool. Univ. Comenianae **45**: 37 (incorrect subsequent spelling and therefore unavailable, according to Articles 33.3 and 33.5 of the ICZN 1999)

2007 *Monilicaryon* Jankowski, 1967 – Jankowski, Protista II: 572 (brief generic review)

2008 *Monilicaryon* Jankowski, 1967 – Lynn, Ciliated protozoa: 371 (list of genera)

Improved diagnosis: Medium- to large-sized Dileptidae with narrow to rod-like body. Macronucleus moniliform. Dorsal brush a single row interrupted by excretory pores. Right branch of circumoral kinety accompanied by a perioral kinety; left branch associated with a perioral-like kinety formed by the linearly arranged preoral kineties. Oral bulge opening dileptid, i.e., roundish and located ventrally.

Type species (by original designation): *Amphileptus monilatus* Stokes, 1886.

Etymology: Not given in original description. Composite of the Latin noun *monile* (necklace) and the Greek noun *karyon* (nucleus), referring to the moniliform macronucleus. Neuter gender.

Remarks: Jankowski (1967) established *Monilicaryon* as a monotypic subgenus of *Dileptus*, using the moniliform macronucleus as sole character. Thirty years later, Foissner (1997a) raised *Monilicaryon* to genus rank due to two specialities of the ciliary pattern: (i) the preoral kineties are so strongly oblique that a single, perioral-like kinety is formed left of the oral bulge and (ii) the dorsal brush is a single row interrupted by excretory pores. All other dileptids have at least two brush rows and many short, oblique preoral kineties. We suppose that the perioral-like kinety of *Monilicaryon* evolved by a linear arrangement of many short preoral kineties. A similar pattern has been found in the binucleate genus *Microdileptus*, where the preoral kineties are so strongly oblique that almost a single, perioral-like kinety is formed.

Monilicaryon monilatum (Stokes, 1886) Jankowski, 1967 (Figs 106a–x; Table 56)

1886 *Amphileptus monilatus*, sp. nov. Stokes, Ann. Mag. nat. Hist. **17**: 102

1888 *Amphileptus monilatus* – Stokes, J. Trenton nat. Hist. Soc. **1**: 167 (description adopted from Stokes 1886)

1905 *Dileptus monilatus* Stokes – Conn, Bull. Conn. St. geol. nat. Hist. Survey **2**: 46 (combining author)

1931 *Dileptus* (*Amphileptus*) *monilatus* (Stokes, 1886) – Kahl, Tierwelt Dtl. **21**: 205 (first taxonomic reviser; partim)

1943 *Dileptus monilatus* Stokes – Kahl, Infusorien: 32 (taxonomic revision)

1961 *Dileptus* (*Amphileptus*) *monilatus* (Stokes) – Buck, Jh. Ver. vaterl. Naturk. Württ. **116**: 201 (ecology)

1963 *Dileptus monilatus* (Stokes, 1886) – Dragesco, Bull. biol. Fr. Belg. **97**: 109 (second taxonomic reviser)

1967 *Monilicaryon monilatus* (Stokes, 1886) – Jankowski, Mater. IV Konf. uč. Sekc. zool. year **1967**: 36 (split of *Dileptus*; fixation of *D. monilatus* as type of *Monilicaryon*)

1972 *Dileptus monilatus* (Stokes) Kahl – Dragesco, Annls Fac. Sci. Univ. féd. Cameroun **9**: 91 (brief description of an Ugandan population; without figure)

1972 *Dileptus monilatus* (Stokes) Kahl – Dragesco, Annls Fac. Sci. Univ. féd. Cameroun **11**: 77 (description of oral ciliary pattern)

1988 *Dileptus monilatus* (Stokes, 1866) – Foissner, Hydrobiologia **166**: 38 (saprobic classification)

1995 *Monilicaryon monilatus* (Stokes, 1886) Jankowski, 1967 – Foissner, Berger, Blatterer & Kohmann, Informationsberichte des Bayer. Landesamtes für Wasserwirtschaft **1/95**: 199 (brief review and description of a German population)

1997 *Monilicaryon monilatus* (Stokes, 1886) Jankowski, 1967 – Foissner, Limnologica **27**: 197 (neotypification, authoritative redescription)

2001 *Monilicaryon monilatum* nom. corr. – Aescht, Denisia **1**: 102 (mandatory change of species epithet ending)

2003 *Monillicarion monillatus* (Stokes, 1886) – Tirjaková, Acta zool. Univ. Comenianae **45**: 37 (incorrect subsequent spelling and therefore unavailable, according to Articles 33.3 and 33.5 of the ICZN 1999)

non *Dileptus monilatus* – Jones & Beers (1953), Vuxanovici (1959), Dingfelder (1962), Dragesco (1970), Dragesco & Dragesco-Kernéis (1986), and Song (1994b), who misidentified *Pseudomonilicaryon kahli* as *Monilicaryon monilatum* (see synonymy list of *Pseudomonilicaryon kahli*)

non *Dileptus monilatus* (Stokes) Kahl – Dragesco, 1966, Protistologica **2**: 76 (see *Pseudomonilicaryon japonicum*)

Nomenclature and taxonomy: Foissner (1997a) neotypified *Monilicaryon monilatum* because (i) no type material is available from Stokes' (1886) specimens, (ii) the neotype is from a similar habitat, and (iii) the protargol preparations are of sufficient quality. We add the danger of misidentifications (see below).

Monilicaryon monilatum was originally described as *Amphileptus monilatus* by Stokes (1886). Ten years later, Schewiakoff (1896) synonymized it with *Amphileptus anser* (now *Pseudomonilicaryon anser*). However, this was not accepted by Conn (1905) and Kahl (1931), who combined Stokes' species with *Dileptus*. Unfortunately, Kahl (1931) misidentified a Hamburg population of *Pseudomonilicaryon kahli* as *Dileptus monilatus*, causing a mixed description. This was recognized by Šrámek-Hušek (1957), who established a new species for Kahl's population: *D. kahli* (now *Pseudomonilicaryon kahli*). In 1967, Jankowski erected the new subgenus, *Monilicaryon*, for Stokes' species. Finally, based on a careful reinvestigation, Foissner (1997a) raised *Monilicaryon* to genus level (see genus discussion above). More detailed morphometric characterization recommended.

Monilicaryon monilatum is easily identified by its large size (about 600 µm), the very short proboscis, the moniliform macronucleus, and the dorsal stripe of contractile vacuoles. Within the large dileptids with moniliform macronucleus, *M. monilatum* most resembles *Pseudomonilicaryon kahli*, which has, however, a longer proboscis (1/3–1/2 vs. 1/5–1/4 of body length), far fewer ciliary rows (22–27 vs. 40–60), and a different oral ciliary pattern (many preoral kineties vs. a perioral-like kinety left of oral bulge).

Improved diagnosis (includes all information known): Size about 600 × 60 µm in vivo. Shape narrowly dileptid to rod-like with short tail or gradually narrowed posterior end, proboscis usually 1/5 to 1/4 of body length. Macronucleus moniliform, usually composed of about 22 ellipsoidal nodules; several globular micronuclei. A dorsal stripe of contractile vacuoles with 1 pore each. Two types of extrusomes attached to proboscis oral bulge: type I very narrowly ovate and 6–9 µm long; type II oblong and 2–3 µm long. On average 50 ciliary rows, of which usually one is differentiated into a staggered dorsal brush. Oral bulge opening about 16 µm across.

Type locality: Stokes (1886) did not specify a type locality, referring to North American stagnant freshwaters with *Ceratophyllum* and *Utricularia*. The neotype is from mud of the Amper River, near town of Fürstenfeldbruck, Bavaria, Germany, E11°15' N48°10'. According to Article 76.3 of the ICZN (1999), the place of origin of the neotype becomes the type locality of the nominal species-group taxon, despite any previously published statement of the type locality.

Type material: No type material is available from Stokes' specimens. Foissner (1997a) deposited four neotype slides (inv. nos 1998/73–76) with protargol-impregnated German specimens in the Biology Centre of the Museum of Upper Austria, Linz (LI). Relevant specimens are marked by black ink circles on the coverslip.

Etymology: Not given in original description. The Latin adjective *monilatus* (moniliform) obviously refers to the macronucleus.

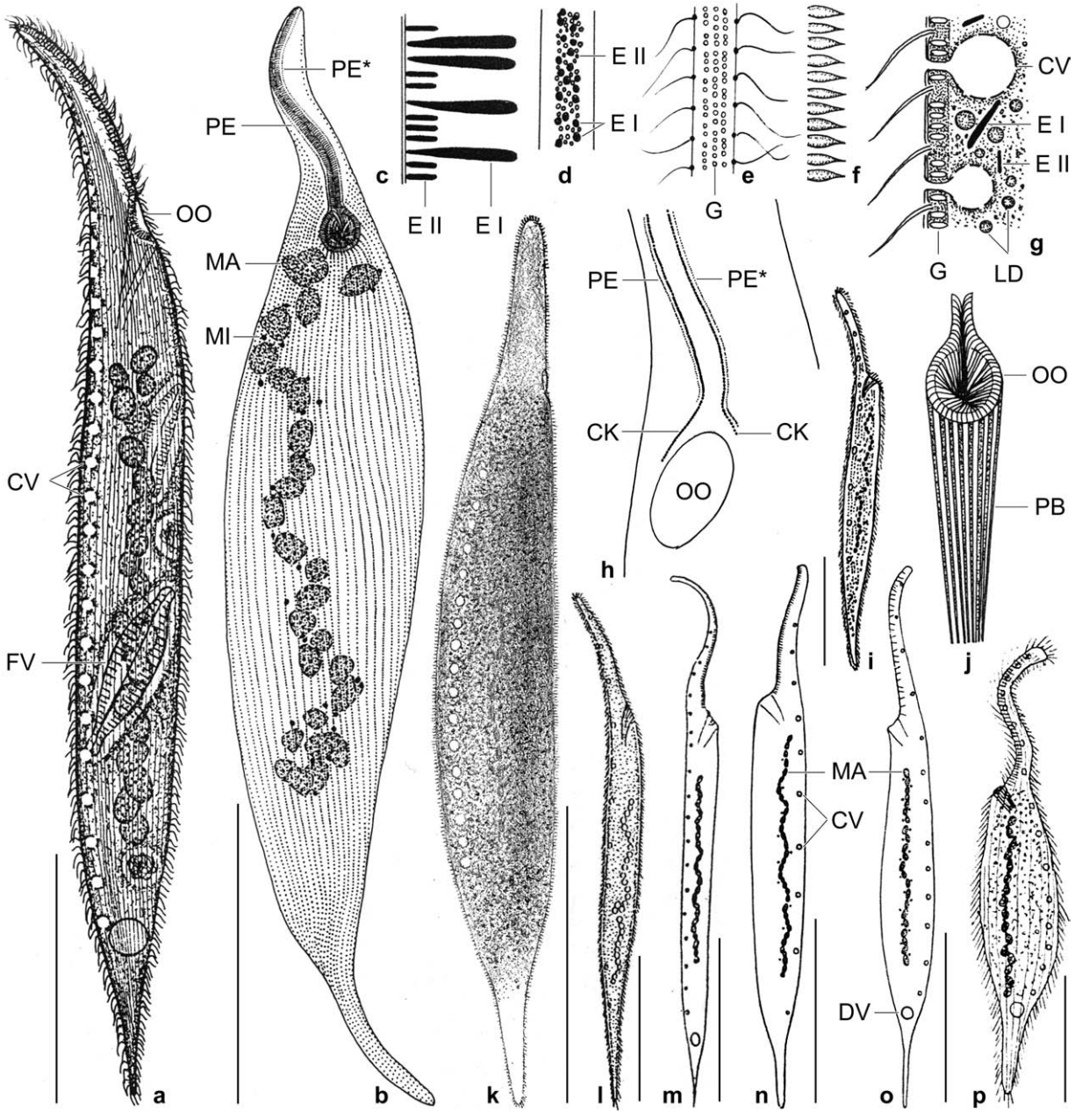
Description: All known data are put together because the morphological conspecificity is beyond reasonable doubt for most populations mentioned in the list of synonyms. This review emphasizes the authoritative redescription of Foissner (1997a), who studied both live and impregnated cells and provided neotype slides.

Size highly variable but similar in most populations, usually 400–700 × 50–80 µm in vivo: North American specimens about 700 µm long on average (Stokes 1886, 1888), Connecticut exemplar 300 µm (Conn 1905), German cells 500–900 µm (Kahl 1931, 1943; Buck 1961), Cameroon exemplar 650 µm (Dragesco 1963), Ugandan specimen 1300 µm (Dragesco 1972a), and German neotype specimens 300–1000 × 50–80 µm in size with smallest individuals possibly injured (Foissner 1997a).

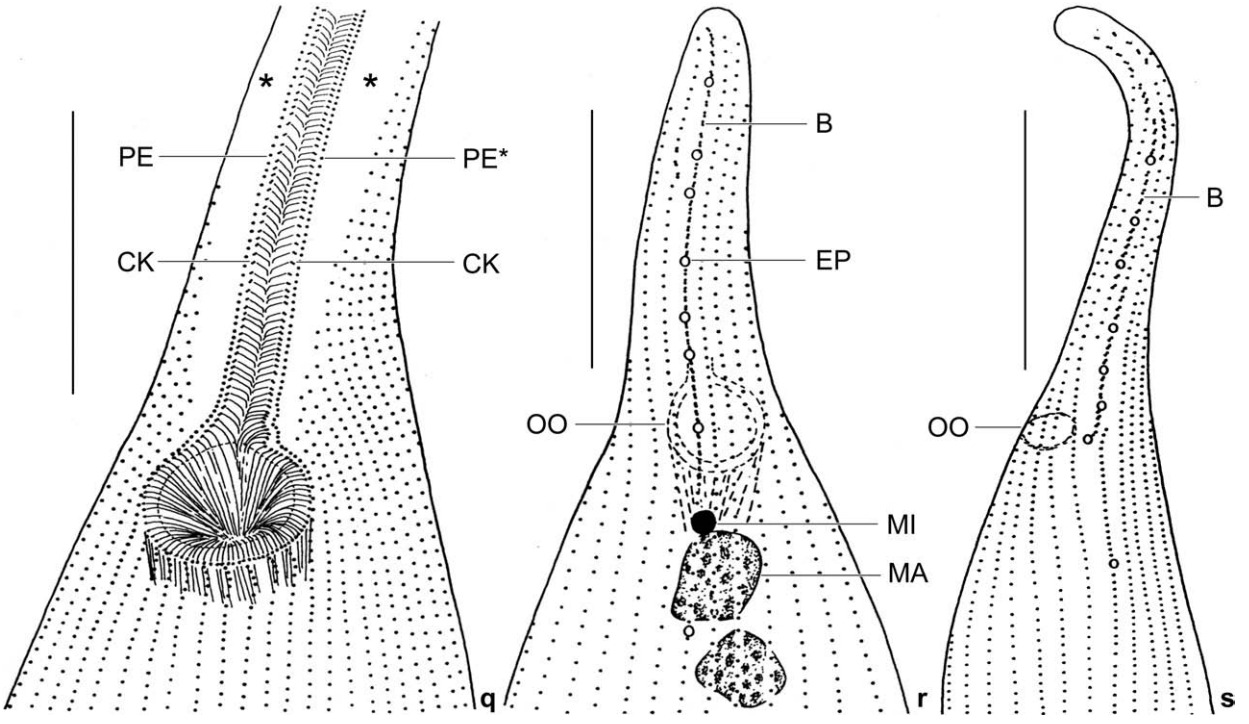
Body very flexible and slightly contractile, often helically twisted along main axis and/or curved loop-like (Fig. 106w). Shape narrowly dileptid to rod-like, that is, length:width ratio on average 8.6:1 (3.9–17.6:1), according to the figures available in the literature and our data based on protargol preparations (Table 56).

Table 56: Morphometric data on *Monilicaryon monilatum* (from Foissner 1997a). Data based on mounted, protargol-impregnated (Foissner's method), and randomly selected field specimens. Measurements in µm. CV – coefficient of variation in %, M – median, Max – maximum, Mean – arithmetic mean, Min – minimum, n – number of specimens investigated, SD – standard deviation, SE – standard error of mean.

Characteristics	Mean	M	SD	SE	CV	Min	Max	n
Body, length	389.3	375.0	85.0	20.0	21.8	258.0	534.0	18
Body, width	66.7	63.8	13.5	3.4	20.3	52.5	105.0	16
Body length:width, ratio (calculated from original data)	6.1	5.9	1.2	0.3	20.0	3.9	8.4	16
Anterior body end to oral bulge opening, distance	87.5	84.0	27.8	8.0	31.8	48.0	150.0	12
Proboscis, % of body length (calculated from original data)	22.0	21.4	6.2	1.8	28.1	11.6	32.6	12
Pharyngeal basket, largest diameter	15.8	15.8	2.1	0.5	13.5	12.0	19.5	16
Pharyngeal basket, length	35.8	36.0	9.3	2.7	26.1	22.5	52.5	12
Macronuclear nodules, length	13.3	13.5	2.3	0.5	17.2	9.0	18.0	18
Macronuclear nodules, width	8.4	9.0	1.4	0.3	16.3	6.0	10.5	18
Macronuclear nodules, number	21.8	21.0	5.8	1.4	26.7	14.0	30.0	17
Micronuclei, largest diameter	2.5	2.3	0.4	0.1	17.0	1.5	3.0	17
Micronuclei, number	18.0	18.0	4.8	1.4	26.4	11.0	26.0	11
Ciliary rows, number	51.8	50.0	5.3	1.3	10.2	40.0	60.0	17



Figs 106a–p: *Monilicaryon monilatum* from life (a, c–g, i–p) and after protargol impregnation (b, h). From Stokes 1886 (l); Conn 1905 (k); Kahl 1931 (i); Buck 1961 (p); Dragesco 1963 (m–o), 1972b (h); and Foissner 1997a (a–g, j). **a** – right side view of a well-fed specimen, length 700 µm; **b** – ciliary pattern and nuclear apparatus of main neotype specimen, length 372 µm; **c, d** – optical section and surface view of proboscis, showing two shape and size types of extrusomes: type I very narrowly ovate and 6–9 × 1 µm in size; type II oblong and 2–3 × 0.5 µm in size; **e, g** – surface view and optical section of dorsal cortex; **f** – the dorsal bristles are flame-shaped; **h** – ciliary pattern in oral region, where Dragesco (1972b) recognized the perioral-like kinety (PE*) on the left side of the oral bulge; **i** – *Dileptus monilatus*, length 700 µm; **j** – the oral basket is obconical and composed of an internal and external basket. The latter consists of many about 130 µm long rods; **k** – Connecticut specimen, length 300 µm; **l** – *Amphileptus monilatus*, length 725 µm; **m** – Cameroon specimen, length 650 µm; **n, o** – poor redrawings of Kahl's and Stokes' specimens; **p** – German specimen, length 700 µm. CK – circumoral kinety, CV – contractile vacuoles, EI, II – extrusome types, FV – food vacuole, G – cortical granules, LD – lipid droplets, MA – macronucleus (nodules), MI – micronuclei, OO – oral bulge opening, PB – pharyngeal basket, PE – perioral kinety, PE* – perioral-like kinety. Scale bars: 100 µm (b, k) and 200 µm (a, i, l–p).



Figs 106q–s: *Monilicaryon monilatum* after protargol impregnation (from Foissner 1997a). **q** – ventral view of oral infraciliature. The right branch of the circumoral kinety is accompanied by an ordinary perioral kinety, while the left branch bears a perioral-like kinety (PE*), which is very likely formed by the linearly arranged preoral kineties typical for dileptids. Asterisks mark the broad blank stripe right and left of the oral bulge; **r, s** – dorsal views of proboscis, showing the dorsal brush composed of a single row of dikinetids interrupted by pores of contractile vacuoles. Dotted lines show the oral bulge opening on ventral side. B – dorsal brush, CK – circumoral kinety, EP – excretory pore of a contractile vacuole, MA – macronuclear nodule, MI – micronucleus, OO – oral bulge opening, PE – perioral kinety, PE* – perioral-like kinety. Scale bars: 40 μm (q, r) and 80 μm (s).

Proboscis conspicuously short, i.e., occupies one fourth to one sixth, rarely up to one third of body length, slightly flattened laterally and curved dorsally, very fragile and thus mutilated and regenerating specimens frequent. Trunk massive, cylindroidal to bluntly fusiform and not flattened, posterior region gradually narrowed to an acute end or tail-like set off from trunk (Figs 106a, b, i, k–p, t, u).

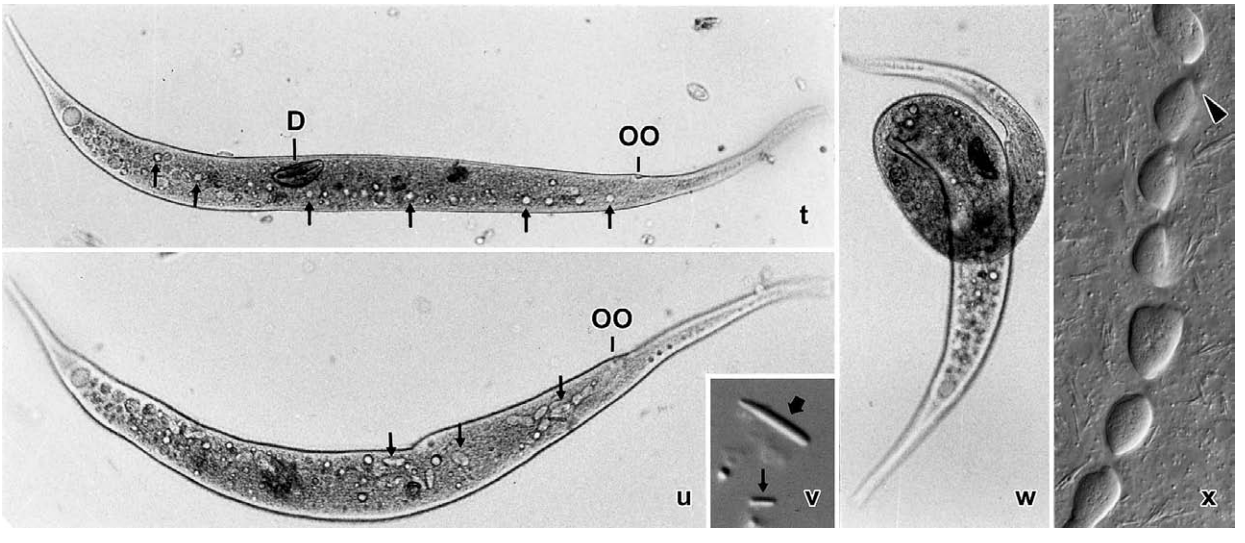
Nuclear strand extends between oral bulge opening and base of tail. Macronucleus a moniliform, basically straight strand surrounded by a slightly argyrophilic capsule (Figs 106a, b, i, l–p, u, x). Individual nodules globular to ellipsoidal, occasionally dumbbell-shaped. Number of nodules of usual variability within and between populations: 31 on average in North American specimens (Stokes 1886), 16 in German specimen (Buck 1961), 24 in Cameroon exemplar (Dragesco 1963), 16–22 in Ugandan cells (Dragesco 1972a), and 14–30 in German neotype specimens (Foissner 1997a). Size of nodules: 10–15 μm in vivo (Dragesco 1972a), 9–18 × 6–10 μm after protargol impregnation (Table 56). Nucleoli small, roundish and evenly distributed. Several (11–26 according to Foissner 1997a) micronuclei about 2.5 μm across attached to macronuclear strand but outside of capsule (Table 56).

Contractile vacuoles similar in all populations mentioned in the synonymy list, that is, arranged in a dorsal stripe beginning near tip of proboscis; no ventral vacuoles (Figs 106a, g, i, k–p, t). Number of vacuoles: 11 on average in North American specimens (Stokes 1886), 16 in a German specimen (Buck 1961), 19 in a Cameroon exemplar (Dragesco 1963), and 20–40 in German neotype cells (Foissner 1997a). Number of excretory pores studied only in neotype specimens, viz., invariably a single, intrakinetal pore per vacuole (Figs 106g, r, s).

Extrusomes studied only by FOISSNER (1997a). Two shape and size types attached to proboscis oral bulge and scattered throughout cytoplasm: type I very narrowly ovate, attached with narrower end, 6–9 × 1 µm in size; type II oblong and 2–3 × 0.5 µm in size (Figs 106c, d, g, v). Cortex gelatinous and conspicuously thick, i.e., about 2 µm; between each two kineties about three rows of bright, 1.5–2 × 1 µm-sized cortical granules, very likely mucocysts (Figs 106e, g). Cytoplasm colourless, at low magnification (< ×100) brownish due to cytoplasmic inclusions and dense granulation; usually with several large food vacuoles containing ciliates, rotifers, and diatoms possibly from ingested ciliates (Figs 106a, t). Movement slow and serpentine in organic mud.

Cilia 8–10 µm long in vivo, narrowly spaced; arranged in about 50 longitudinal, narrowly to ordinarily spaced rows gradually shortened anteriorly, leaving a rather wide, blank stripe left and right of proboscis oral bulge (Figs 106b, q; Table 56). First kinety right and left of oral bulge extends with narrowly spaced basal bodies to tip of proboscis as perioral and perioral-like kinety, respectively (Figs 106b, h, q). Anterior end of ventral ciliary rows more densely ciliated and slightly curved rightwards when abutting on circumoral kinety (Fig. 106q). Dorsal brush exactly on dorsal side of proboscis; usually composed of an ordinary or staggered row of narrowly to ordinarily spaced dikinetids associated with type IV bristles, rarely up to four brush kineties; interrupted by pores of contractile vacuoles (Figs 106f, r, s).

Oral bulge opening usually in second body fifth, projects indistinctly to ordinarily, roundish both in vivo and in preparations, where it is about 16 µm across (Figs 106a, b, h–q; Table 56). Pharyngeal basket obconical, distinct both in vivo and in protargol preparations, consists, as usual, of an internal and external basket: external basket composed of many about 130 × 2 µm-sized rods impregnated only in distal portion with the method used; internal basket made of many about 100 µm long fibres, very likely transverse microtubule ribbons originating from the oral monokinetids surrounding the bulge opening (Figs 106j, q). Circumoral kinety composed of ordinarily spaced dikinetids in proboscis, while of narrowly spaced monokinetids around oral bulge opening. Proboscis dikinetids associated with (i) about 10 µm long cilia



Figs 106t–x: *Monilicaryon monilatum* from life (from FOISSNER 1997a). **t, u, w** – a gliding specimen. Note the short proboscis and the small, not projecting oral bulge opening. Arrows in (t) mark contractile vacuoles, those in (u) denote macronuclear nodules; **v** – there are two shape and size types of extrusomes: type I is very narrowly ovate and 6–9 µm long (thick arrow) and type II is oblong and 2–3 µm long (thin arrow); **x** – part of macronucleus which consists of an average of 21 nodules in series. Arrowhead marks one of many micronuclei. D – ingested diatom, OO – oral bulge opening.

forming a distinct mane (Fig. 106a) and (ii) conspicuous fibres extending to centre of proboscis oral bulge, forming the central fibre (Fig. 106q).

Occurrence and ecology: Some of the faunistic data on *M. monilatum* very likely refer to *Pseudomonilicaryon kahli* because the determination usually followed Kahl (1931), who mixed these species.

Monilicaryon monilatum prefers beta-mesosaprobic, benthic habitats in slowly running and stagnant waters. Often found in the organic mud and between filamentous algae, rarely in the pelagial. There is a single unsubstantiated terrestrial record from "macchia" soil in Italy (Luzzatti 1938). Buck (1961) found *M. monilatum* frequently in slightly to strongly polluted running waters, especially near and in capture nets of certain trichopteran larvae (Polycentropidae), where it possibly searched for food (amoebas, ciliates and larvae of copepods). Reliably recorded from Europe, North America and Africa, thus possibly cosmopolitan. Occurs throughout the year (eurythermic), but with a distinct frequency maximum in summer (Foissner et al. 1995). Feeds on ciliates, rotifers, and small and large diatoms (*Nitzschia palea*, *N. sigmoidea*, *Synedra ulna*, *Cymbella* sp., *Rhoicosphenia curvata*), in spite of the small (~ 15 µm) oral bulge opening (Dragesco 1972a, Foissner et al. 1995, Foissner 1997a). Biomass of 10^6 specimens about 900 mg, when an average size of 600 × 60 µm is assumed (Foissner et al. 1995), while 1933 mg according to Nesterenko & Kovalchuk (1991).

Records from running waters: numerous, especially under stones in slightly to strongly polluted German rivers (Buck 1961); in the cooling water system of a conventional, large power plant fed by the beta- to alpha-mesosaprobic Main River, Germany (Bernerth 1982); rare to numerous in a beta- to alpha-mesosaprobic part of the Alb River, Germany (Mauch 1990); in beta- to alpha-mesosaprobic Austrian and Bavarian rivers (Foissner & Moog 1992; Foissner et al. 1992a, b; Blatterer 1994); in a Spanish river at BSB_5 0.7–5.1 mg/l (Fernández-Leborans et al. 1990); in the water-sediment interface of the polluted Stirone and Mincio rivers, Italy (Madoni & Bassanini 1999, Madoni and Braghiroli 2007); in the periphyton and seston of the alpha-mesosaprobic Sava River in the former Yugoslavia (Primc 1981, Primc-Habdija et al. 1996); rare in the periphyton of oligosaprobic karst waters in the former Yugoslavia (Primc-Habdija & Habdija 1991); in the littoral of the Danube River and in the organic mud of the Gidra River, Slovakia (Tirjaková 1992, 2003; Matis & Tirjaková 1995); Danube River (Enăceanu & Brezeanu 1970); with low dominance and frequency in the seston of alpha-mesosaprobic parts of a Polish river (Hul 1987); in Ukrainian streams and rivers (Kravchenko 1969, Kovalchuk 1997a); Dniester River in Ukraine (Kovalchuk & Kovalchuk 1992); Volga river basin, Russia (Zhukov et al. 1998); inner lakes of the Valamo Island, Russia (Karpov et al. 1991); winter fauna of freshwaters in the Yuelushan area, China (Yang 1989); Souxiyu Nature Reserve area, Hunan Province, China (Shen & Gong 1989); Yellow River, Lanzhou, China (Ma 1994); brooks and rivers of Middletown, Connecticut, USA (Conn 1905); in the benthos of slightly to moderately polluted North American rivers (Cairns & Yongue 1966, 1973; Cairns & Dickson 1972).

Records from slowly running and stagnant waters: in the benthos and plankton of Latvian and German oligotrophic lakes (Liepa 1984, Packroff & Wilbert 1991); Eifel maar lake in Germany (Packroff 1992); in the periphyton and sediment of a clean foothill stream in Germany (Packroff & Zwick 1996); in the benthos of Lake Suviana, Tusco-Emilian Apennines, Italy (Madoni 1989, Dini et al. 1995); up to 2 ind./cm^2 in the sediment of an Italian reservoir (Madoni 1991); in the sediment of fishponds in Poland (Kwiatkowska-Grabacka 1965, Siemińska & Siemińska 1967, Grabacka 1977); Turiec river basin in the West Carpathians, Slovakia (Tirjaková 1993, Tirjaková & Degma 1996); freshwaters in Bulgaria (Detcheva 1992); in lakes of Azerbaijan (Aliev 1982); in the benthos of a water reservoir in the former USSR (Zharikov & Rotar 1992); brackish water of the White Sea estuary (Burkovsky 1976, Burkovsky & Mazei 2001); in the periphyton of Lake Dong Hu, Wuhan, China (Shen 1980); in mesotrophic lakes of

China (Song 2000); between *Ceratophyllum* and *Utricularia*, USA (Stokes 1886); Lake Okoboji, Iowa, USA (Shawhan et al. 1947); in a slowly running river in the USA (Patrick 1961); Conestoga drainage basin, Pennsylvania, USA (Cairns 1965); in a North American pond at 24 °C and pH 6.0 (Cairns & Yongue 1966); rare in Lake Cromwell, Quebec, Canada (Puytorac et al. 1972); 36 ind./l in a fishless, intermittent pond in Vandorf, Ontario, Canada (Andrushchyshyn et al. 2006); in slightly saline sand from Douala, Cameroon, Africa (Dragesco 1963); rarely in the sand from the saprobic Kasinga channel and numerous between papyrus and other water plants in Lake George, Uganda, Africa (Dragesco 1972a).

Saprobic classification: Sládeček et al. (1981), Wegl (1983) and Foissner (1988a) classified *M. monilatum* as a beta-mesosaprobic ciliate with the following valencies: b = 7, a = 3, I = 4, SI = 2.3. Russev et al. (1976) classified this species as alpha-mesosaprobic in Bulgarian rivers.

Pseudomonilicaryon Foissner, 1997 (Key to species, see p. 263-265)

1997 *Pseudomonilicaryon* nov. gen. Foissner, Limnologica **27**: 196

2001 *Pseudomonilicaryon* Foissner 1997 – Aescht, Denisia **1**: 137 (catalogue of generic names of ciliates)

2007 *Pseudomonilicaryon* Foissner, 1997 – Jankowski, Protista II: 572 (brief generic review)

2008 *Pseudomonilicaryon* Foissner, 1997 – Lynn, Ciliated protozoa: 371 (list of genera)

Improved diagnosis: Small- to large-sized Dileptidae with narrow to rod-like body. Macronucleus moniliform. Dorsal brush usually multi-rowed, rarely two-rowed. Right branch of circumoral kinety accompanied by a perioral kinety, left branch by many slightly to strongly oblique preoral kineties. Oral bulge opening dileptid, i.e., ovate to narrowly elliptical and located ventrally.

Type species (by original designation): *Dileptus gracilis* Kahl, 1931.

Etymology: Composite of the Greek prefix *pseudo* (false) and the generic name *Monilicaryon*. Neuter gender.

Remarks: The main features of this genus, which comprises thirteen species and six subspecies, is the moniliform macronucleus and the *Dileptus*-like ciliary pattern, as diagnosed above. There are three further genera with a moniliform macronucleus but with different oral ciliary pattern: *Monilicaryon* has linearly arranged preoral kineties, forming a left perioral-like kinety, while *Paradileptus* and *Pelagodileptus* possess an additional perioral kinety to the right of the proboscis oral bulge.

With respect to the proboscis' somatic ciliary pattern, four groups are recognizable, indicating that *Pseudomonilicaryon* is polyphyletic (Figs 107, 108). Thus, this feature deserves more detailed description in future.

Pseudomonilicaryon massutii (Kahl, 1933) Foissner, Agatha & Berger, 2002 (Figs 109a–z; Table 57)

1929 *Dileptus anser* O. F. M. – Massutí Alzamora, Notas Resúmenes **32**: 3 (misidentification)

1933 *Dileptus massutii* spec. n. (Massuti 1929) Kahl 1933, Tierwelt N.- und Ostsee **23**: 63

1963 *Dileptus massutii* Kahl, 1933 – Dragesco, Bull. biol. Fr. Belg. **97**: 125 (first taxonomic reviser)

1963 *Dileptus grandis* n. sp. Dragesco, Bull. biol. Fr. Belg. **97**: 111 (synonymy proposed by Foissner et al. 2002)

2002 *Pseudomonilicaryon massutii* (Kahl, 1933) nov. comb. – Foissner, Agatha & Berger, Denisia **5**: 373 (neotypification, authoritative redescription)

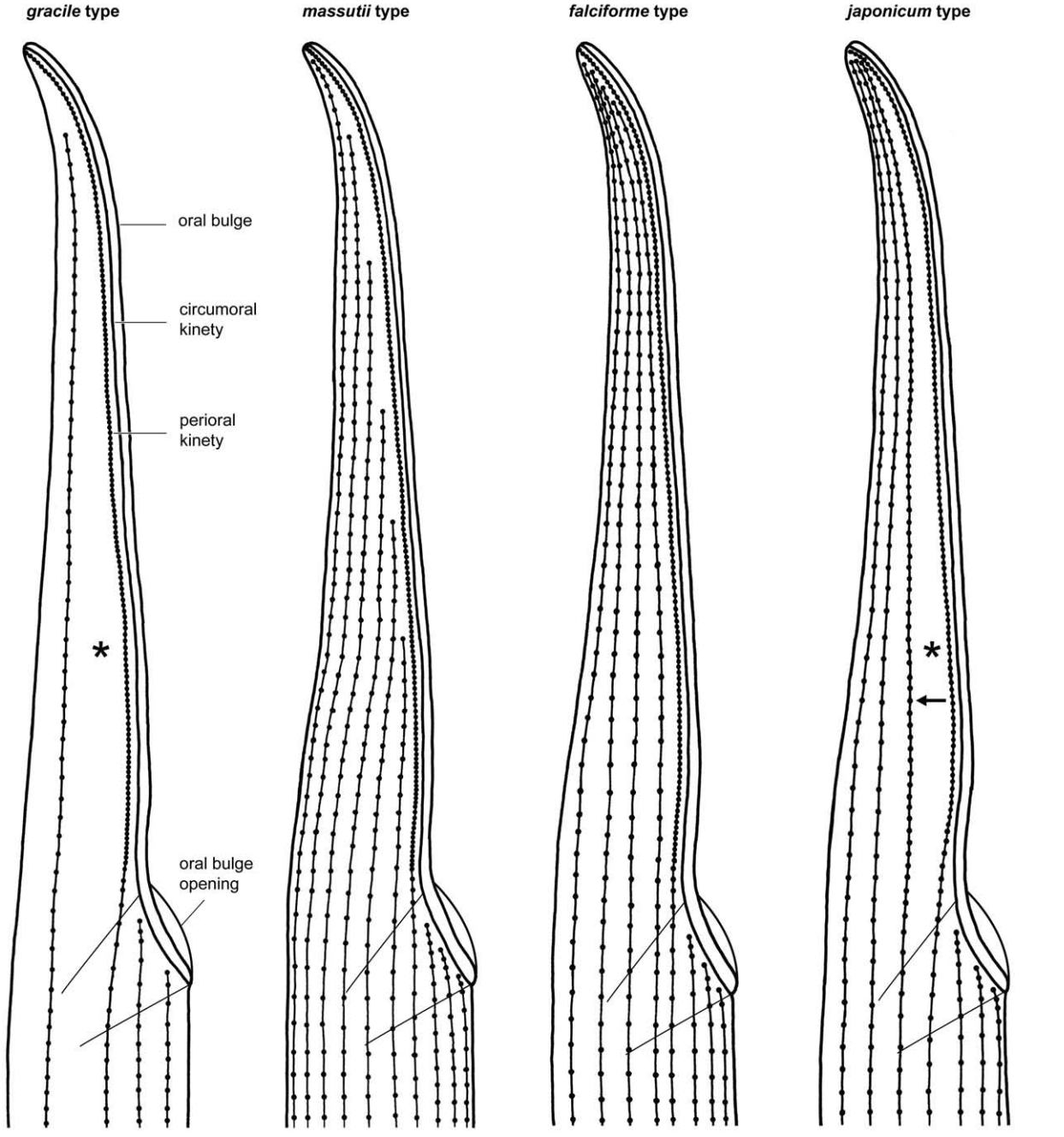


Fig. 107: Somatic ciliary pattern of *Pseudomonilicaryon* proboscis' right side.

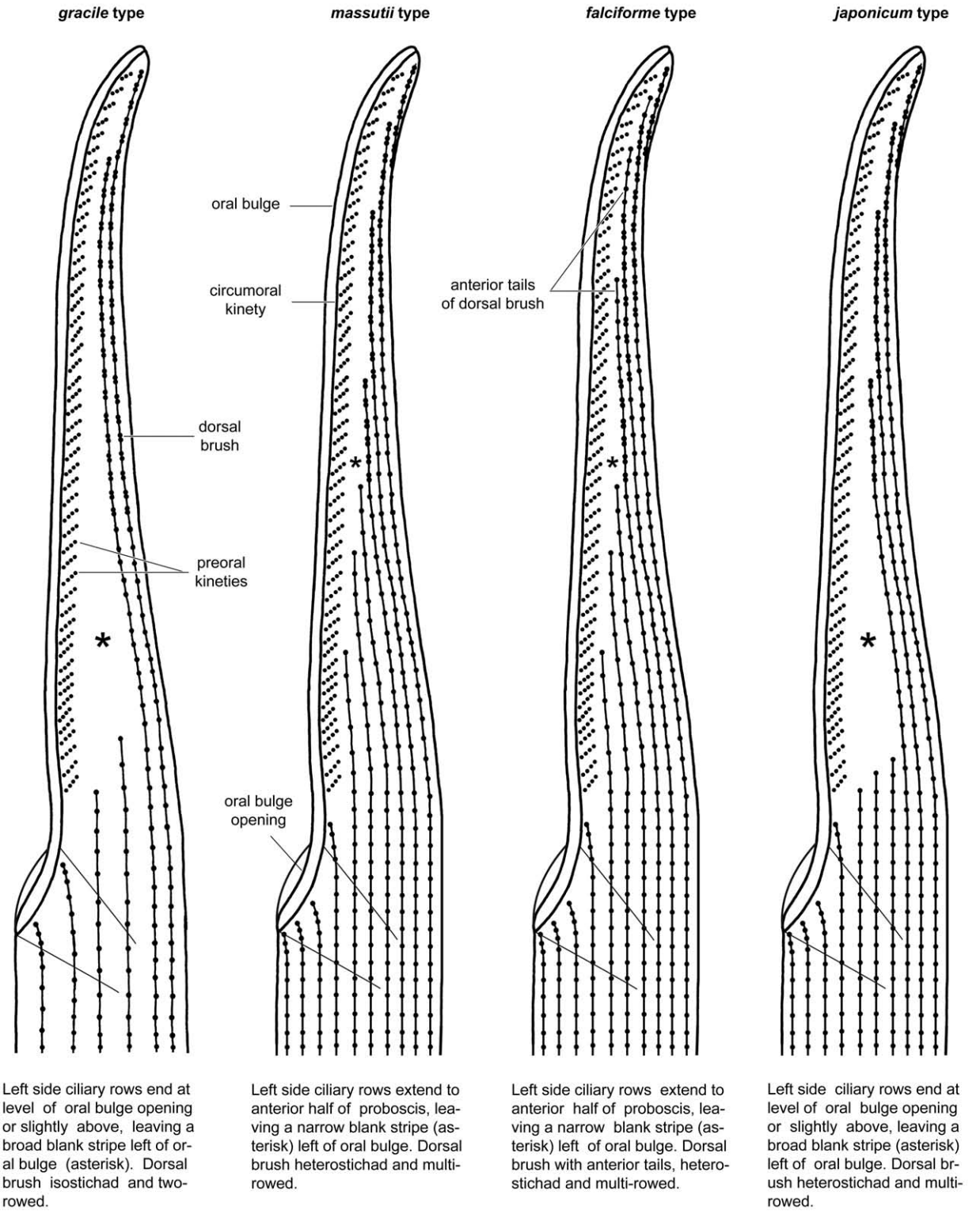


Fig. 108: Somatic ciliary pattern of *Pseudomonilicaryon* proboscis' left side. Examples, see Fig. 107.

2012 Possibly, *P. massutii* has a further synonym: *P. kahli* (for details, see that species)

Nomenclature and taxonomy: Massutí Alzamora (1929) misidentified a Mediterranean population as *Dileptus anser*. This was recognized by Kahl (1933), who classified it as a new species, *Dileptus massutii*. Almost seventy years later, Foissner et al. (2002) rediscovered this species in a saline, semiterrestrial habitat from Namibia and combined it with *Pseudomonilicaryon* on the basis of the *Dileptus*-like oral ciliary pattern and the moniliform macronucleus. Foissner et al. (2002) proposed the superficially described *Dileptus grandis* as a junior synonym because Dragesco (1963) distinguished *P. massutii* from *D. grandis* only by the stouter trunk and the slightly longer proboscis; we agree. Dragesco (1963) provided a figure (reproduced here as Fig. 109l) and the following description for *D. grandis*: "Nous avons trouvé, en 1946, dans l'eau provenant d'un terrain inondé (près la Brague, Alpes-Maritimes), un *Dileptus* gigantesque que nous avons longtemps assimilé à *D. monilatus*. En fait nous sommes bien obligés de la considérer aujourd'hui comme une espèce distincte, que nous décrivons comme suit : très volumineux (longueur moyenne 1000 µm sur 80 µm de largeur), *D. grandis* nage lentement sur le fond des godets, tout en montrant une tendance à se plisser et à s'enrouler légèrement, autour de son axe (à la manière du *D. gigas*). La trompe est assez longue (1/2–1/3 de la longueur du corps) et garnie de puissants trichocystes. La bouche est très apparente et montre une très puissante armature fibrillaire d'une longueur remarquable. L'appareil nucléaire est constitué par un macronucleus en chapelet (35 éléments ovalaires) et une trentaine de micronuclei sphériques. Les vacuoles contractiles sont nombreuses (au moins 20) et sont réparties tout le long de la région dorsale, pénétrant très en avant dans la trompe (une grande vacuole postérieure est assez fréquente). Le corps finit en une pointe très tronconique, pourvue de longs trichocystes".

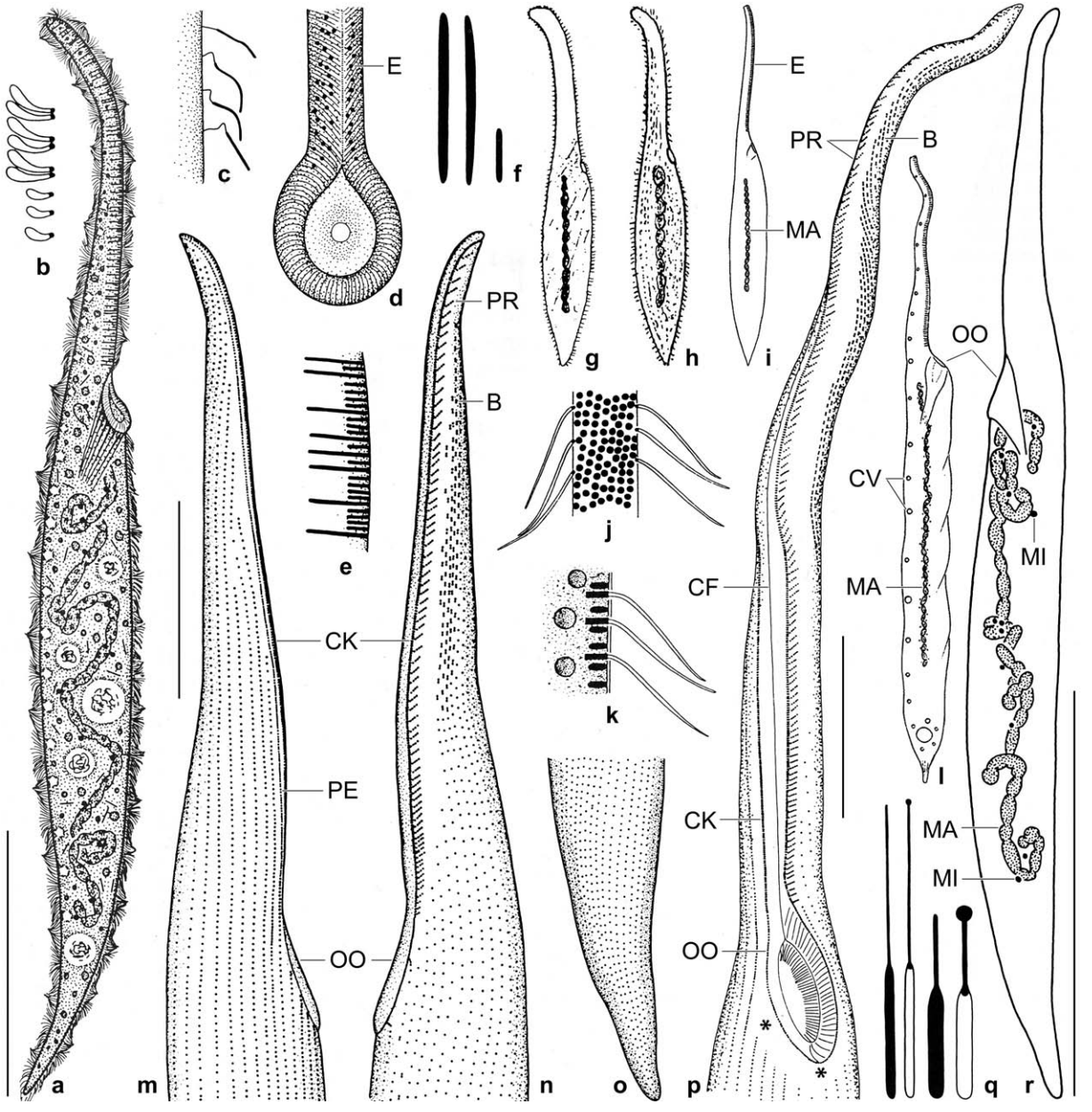
There are several species which resemble *P. massutii*, viz., *P. angustistoma*, *P. japonicum*, *P. kahli*, and *P. marinum*. The first two species differ by body length (~ 400 µm vs. ~ 800 µm), the shape of the extrusomes (very narrowly ovate vs. rod-shaped), and the ciliary pattern (right side rows not shortened vs. gradually shortened along proboscis). *Pseudomonilicaryon kahli* is distinguished mainly by the freshwater habitat (for details, see that species). *Pseudomonilicaryon marinum* differs by the short proboscis (1/5 vs. 1/3 of body length) and the spine-like tail (vs. acute posterior third).

Foissner et al. (2002) neotypified *P. massutii* because (i) no type material is available from Massutí Alzamora's (1929) specimens, (ii) the identity is endangered by several similar species (see above), (iii) the neotype is from a similar habitat, and (iv) the protargol preparations are of sufficient quality.

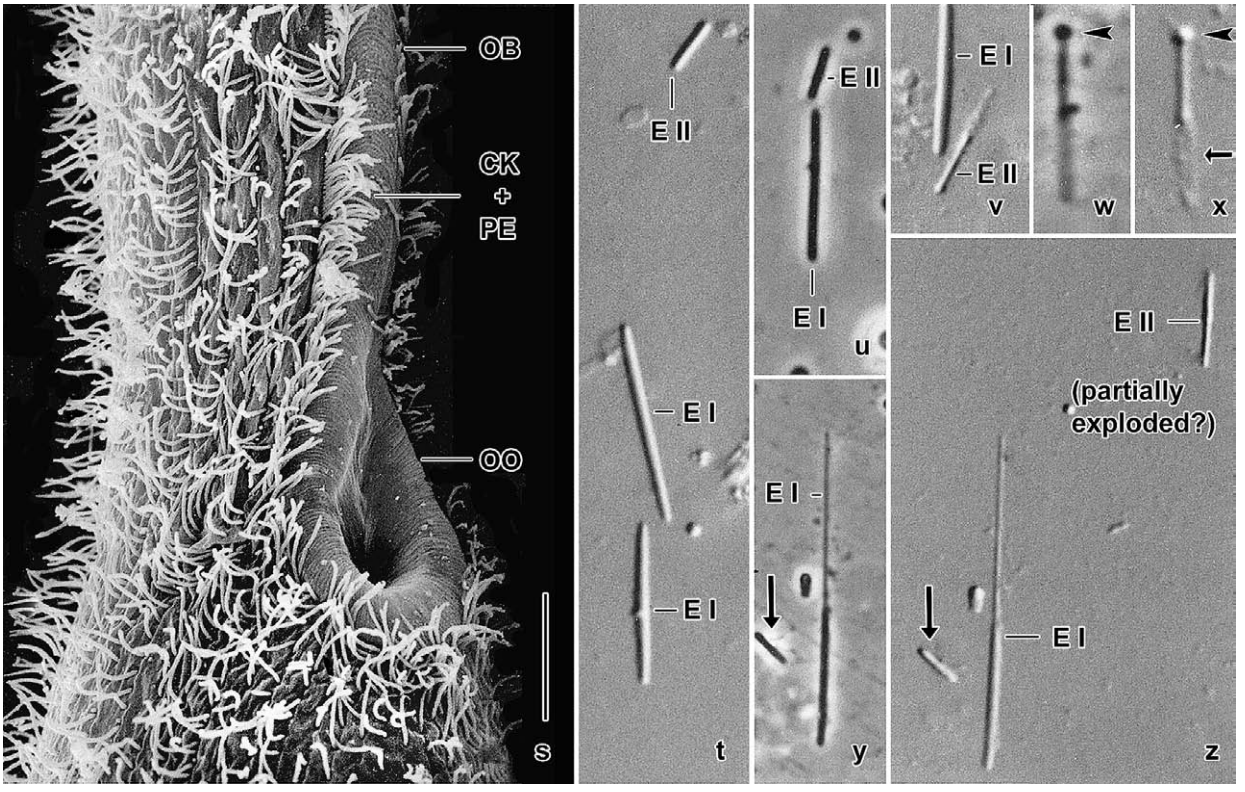
Improved diagnosis (neotype population): Size about 800 × 65 µm in vivo. Shape very narrowly dileptid to rod-like with acute posterior quarter, proboscis about 1/3 of body length. Macronucleus moniliform and tortuous, composed of an average of 47 ellipsoidal to very narrowly ellipsoidal nodules; several globular micronuclei. A dorsal stripe of contractile vacuoles with up to 3 pores each. Two size types (10 µm and 3 µm) of basically rod-shaped extrusomes attached to proboscis oral bulge. On average 44 ciliary rows, up to 15 anteriorly differentiated into a staggered, distinctly heterostichad dorsal brush with monokinetidal tails extending to second third of body. Oral bulge opening about 18 µm across. Preoral kineties slightly oblique, ordinarily spaced, each usually composed of 4 narrowly spaced cilia. In coastal waters and semiterrestrial saline inland habitats.

Type locality: Massutí Alzamora (1929) discovered this species in the Bay of Palma de Mallorca, Island of Mallorca, Spain, E2°38' N39°33'. The neotype is from a highly saline semiterrestrial habitat in the Etosha National Park, Namibia, E16°45' S18°45' (Foissner et al. 2002). According to Article 76.3 of the ICZN (1999), the place of origin of the neotype becomes the type locality of the nominal species-group taxon, despite any previously published statement of the type locality.

Type material: No type material is available from Massutí Alzamora's specimens. Foissner et al. (2002)



Figs 109a–r: *Pseudomonilicaryon massutii* from life (a, b, d–l, q) and after protargol impregnation (c, m–p, r). From Massutí Alzamora 1929 (g), Kahl 1933 (h), Dragesco 1963 (i, l), and Foissner et al. 2002 (a–f, j, k, m–r). **a** – right side view of a representative Namibian neotype specimen, length 800 µm; **b** – the brush dikinetids are associated with clavate, 2–3 µm long bristles, followed by inflated, about 1 µm long monokinetidal tail bristles; **c** – after protargol impregnation, the distal half of the cilia is thicker than the proximal half; **d, e** – surface view and optical section of oral bulge showing the arrangement of the extrusomes, which are more numerous in the right than the left bulge branch; **f** – *P. massutii* has two size types (10 µm and 3 µm) of rod-shaped extrusomes; **g –** original figure, length 400 µm (in text, 400–1000 µm); **h** – redrawing by Kahl (1933); **i** – likely an incorrect redrawing from Kahl (1933) by Dragesco (1963); **j, k** – surface view and optical section showing the cortical granules; **l** – *Dileptus grandis* is a junior synonym of *Pseudomonilicaryon massutii*, length 1100 µm; **m, n** – ciliary pattern of proboscis' right and left side; **o** – ciliary pattern of left posterior body portion; **p** – ventral view of proboscis' ciliary pattern. Asterisks mark area not clearly seen in the preparation; **q** – exploded type I (length up to 30 µm) and type II (up to 9 µm) extrusomes; **r** – left side view and nuclear apparatus of main neotype specimen, length 555 µm. B – dorsal brush, CF – central fibre, CK – circumoral kinety, CV – contractile vacuoles, E – extrusomes, MA – macronucleus (nodules), MI – micronuclei, OO – oral bulge opening, PE – perioral kinety, PR – preoral kineties. Scale bars: 50 µm (m, n, p) and 200 µm (a, r).



Figs 109s–z: *Pseudomonilicaryon massutii*, Namibian specimens in the SEM (s) and in vivo under interference (t, v, x, z) and phase contrast (u, y, w) illumination. From Foissner et al. (2002). **s –** ventrolateral view showing oral bulge opening and dense ciliation; **t, u –** resting type I and II extrusomes are rod-shaped and 10 µm and 3 µm long, respectively; **v** – a resting type I extrusome and a completely exploded type II extrusome; **w, x** – completely exploded type II extrusomes with a refractive globule, likely a toxin droplet (arrowheads), at the tip of the empty capsule (arrow); **y, z** – (partially?) exploded extrusomes of long type I and short type II with full capsule. Arrows mark a resting type II extrusome. CK – circumoral kinety, EI, II – extrusome types, OB – oral bulge, OO – oral bulge opening, PE – perioral kinety. Scale bar 10 µm (s).

deposited five neotype slides (inv. nos 2011/34, 42–45) with protargol-impregnated specimens in the Biology Centre of the Museum of Upper Austria, Linz (LI). Relevant specimens are marked by black ink circles on the coverslip.

Etymology: Kahl (1933) dedicated this species to Miguel Massutí Alzamora.

Description: Size usually about 800 × 65 µm in vivo: Mediterranean specimens 400–1000 µm (Massutí Alzamora 1929), Namibian neotype individuals 550–1100 × 50–85 µm (Foissner et al. 2002), French cells about 1000 µm (Dragesco 1963); very flexible but not contractile. Shape very narrowly dileptid to rod-like, that is, length:width ratio 6.5–19.3, according to the morphometric data (Table 57) and the figures from Massutí Alzamora (1929) and Dragesco (1963). Proboscis one fourth to almost one half of body length, anterior portion curved dorsally, flattened, rather stout in Massutí's specimens, while slender in neotype and French cells. Trunk oblong to bluntly fusiform, unflattened; posterior end acute in Massutí's and neotype specimens, while with an inconspicuous tail in French cells (Figs 109a, g–i, l, o, r). Nuclear apparatus in anterior five sixth of trunk. Macronucleus moniliform, straight in Mediterranean and French specimens, while highly tortuous in neotype cells, composed of 39–59 ellipsoidal to very narrowly ellipsoidal nodules in Namibian specimens, 35 nodules in French ones, and only 11 in the Mediterranean cells, as estimated from the illustration (Fig. 109g) of Massutí Alzamora (1929); nucleoli numerous and spherical.

Several minute, globular micronuclei attached to macronuclear strand (Figs 109a, g–i, l, r; Table 57). A dorsal stripe of contractile vacuoles, first vacuole in mid-proboscis in neotype specimens, while subapical in French cells; no ventral vacuoles; up to three excretory pores per vacuole (Figs 109a, l). Extrusomes studied only in Namibian neotype specimens, accumulated in proboscis oral bulge, especially in its right branch, numerous and scattered in cytoplasm, immature extrusomes impregnate with protargol; two shape and size types attached to bulge of proboscis: type I rod-shaped with rounded ends, slightly asymmetrical, about 10–12 × 0.7–1 µm in size; type II like type I but only 3–4 × 0.5–0.7 µm; when exploded of typical toxicyst structure, viz., a refractive granule each at proximal and distal end of tube emerging from the empty capsule, large type I up to 30 µm long, small type II up to 9 µm (Figs 109d–f, q, t–z). Cortex very flexible, furrowed by ciliary rows in SEM micrographs, contains approximately seven rows of about 1 × 0.5 µm-sized granules between each two kineties (Figs 109j, k, s). Cytoplasm colourless, contains many glossy lipid droplets 1–5 µm across and some food vacuoles with loose contents, for instance, remnants of *Condylostomides etoschensis*, which is killed and almost completely dissolved by the extrusomes before it is engulfed; usually a large defecation vacuole in rear end. Movement without peculiarities.

Cilia in protargol preparations about 7 µm long, narrowly spaced, and with deeply impregnated distal half (Fig. 109c); arranged in about 44 longitudinal, narrowly spaced rows (Figs 109m, n; Table 57). Right side ciliary rows gradually shortened along oral bulge; perioral kinety extends to tip of proboscis with narrowly spaced basal bodies (Fig. 109m). Blank stripe on left side of proboscis rather wide because most left side ciliary rows end at level of oral bulge opening or slightly above (Figs 109n, p). Dorsal brush conspicuous because occupying dorsal and half of left side of proboscis; composed of up to 15 staggered, distinctly heterostichad rows. Brush dikinetids loosely to very loosely spaced, associated with type I bristles both

Table 57: Morphometric data on a Namibian population of *Pseudomonilicaryon massutii* (from FOISSNER et al. 2002). Based on mounted, protargol-impregnated (Foissner's method) specimens from a non-flooded Petri dish culture. Measurements in µm. CV – coefficient of variation in %, M – median, Max – maximum, Mean – arithmetic mean, Min – minimum, n – number of specimens investigated, SD – standard deviation, SE – standard error of mean.

Characteristics	**Mean**	**M**	**SD**	**SE**	**CV**	**Min**	**Max**	**n**
Body, length	686.3	649.5	207.0	84.5	30.2	478.0	944.0	6
Body, width	55.2	54.5	11.2	4.6	20.4	44.0	73.0	6
Body length:width, ratio	12.6	12.2	3.6	1.5	28.9	8.3	19.3	6
Anterior body end to oral bulge opening, distance	224.8	228.5	68.8	24.3	30.6	120.0	304.0	8
Proboscis, % of body length	30.3	31.5	4.4	1.8	14.7	24.9	36.1	6
Anterior body end to first macronuclear nodule, distance	248.5	204.5	99.5	40.6	40.0	140.0	392.0	6
Macronucleus, total length (uncoiled and thus approximate)	330.7	330.5	–	–	–	228.0	433.0	6
Macronuclear nodules, maximum length	24.2	23.5	4.8	2.0	20.0	19.0	33.0	6
Macronuclear nodules, width	7.0	7.5	1.3	0.5	18.1	5.0	8.0	6
Macronuclear nodules, number	47.4	46.0	7.4	3.3	15.7	39.0	59.0	5
Micronuclei, length	2.5	2.5	–	–	–	2.0	3.0	8
Micronuclei, width	2.1	2.0	–	–	–	2.0	3.0	8
Micronuclei, number	17.8	18.0	4.4	2.0	24.6	12.0	24.0	5
Ciliary rows, number in mid-body	44.4	46.0	6.8	3.1	15.4	34.0	52.0	5
Cilia in mid-body in 10 µm, number	6.0	6.0	1.2	0.5	20.4	5.0	8.0	5
Anterior body end to last dorsal brush dikinetid, distance	172.0	172.0	67.7	32.4	37.6	114.0	230.0	4

being 2–3 μm long, followed by type VI tail bristles 1 μm long and inflated in vivo (Figs 109b, n, p).

Oral bulge opening at beginning of second body third, projects more distinctly in Namibian and French cells than in Mediterranean specimens, roundish both in vivo and in preparations, about 18 μm across (Figs 109a, d, g–i, l, s). Pharyngeal basket obconical, distinct both in vivo and after protargol impregnation, without specific features (Figs 109p, s). Circumoral kinety composed of narrowly spaced dikinetids in proboscis and possibly of narrowly spaced monokinetids around oral bulge opening. Preoral kineties slightly oblique, ordinarily spaced, each usually composed of four narrowly spaced cilia (Figs 109n, p).

Occurrence and ecology: Massutí Alzamora (1929) discovered the species in the Bay of Palma de Mallorca, Island of Mallorca, Spain, but did not specify the habitat. Possibly, it was a brackish coastal pond because he mentioned several typical limnetic species, such as *Litonotus cygnus* and *Aspidisca costata*. Agamaliev (1974) reported it from the Western shores of the Caspian Sea, and Grolière & Njiné (1973) from a bog pond in France (as *Dileptus grandis*). The neotype population is from highly saline (15‰) soil and litter collected in the surroundings of the Okerfontein water-hole in the Etosha National Park, Namibia (Foissner et al. 2002). Further record comes from an inundated area close to the town of Brague, Alpes-Maritimes, Azure Coast, France (Dragesco 1963) and the western Baltic Sea (Telesh et al. 2008).

Pseudomonilicaryon marinum (Kahl, 1933) nov. comb.

1933 *Dileptus marinus* spec. n. Kahl, Tierwelt. N.- und Ostsee **23**: 63

Generic affiliation and taxonomy: Jankowski (1967) did not combine *Dileptus marinus* with one of his subgenera. Indeed, the generic home of this species remains doubtful because its oral ciliature is not known. We suggest to combine it with *Pseudomonilicaryon* because of the moniliform macronucleus. *Dileptus marinus* var. *minimus* described by Jones (1974) is recognized here as a distinct subspecies because it is distinctly smaller than the nominotypical subspecies (200 μm vs. 450–700 μm). Full redescription of both subspecies is required because several important data are lacking.

Pseudomonilicaryon marinum occurs in saline habitats, where only three other species have been recorded: *P. massutii*, *Rimaleptus tirjakovae*, and *R. lacazei*. *Pseudomonilicaryon marinum* is easily distinguished from these species by the long, spine-like tail (vs. acute posterior body third), a feature definitely mentioned and figured by Kahl (1933) and later confirmed by Bock (1952a) and Dragesco (1960, 1963). Further, the two *Rimaleptus* species have only two macronuclear nodules (vs. a moniliform strand composed of at least six nodules).

Improved diagnosis (includes two subspecies): Size about 200–700 × 50–55 μm in vivo. Shape cylindroidally dileptid to rod-like with long tail, proboscis about 1/5–1/3 of body length. Macronucleus a moniliform strand composed of 6–17 nodules. A dorsal row of contractile vacuoles. In marine coastal waters.

Etymology: Not given in original description. The Latin adjective *marinus* (marine) obviously refers to the habitat where the species was discovered.

Pseudomonilicaryon marinum marinum (Kahl, 1933) nov. comb., nov. stat. (Figs 110a–d)

1933 *Dileptus marinus* spec. n. Kahl, Tierwelt. N.- und Ostsee **23**: 63

1935 *Dileptus marinus* Kahl, 1933 – Kahl, Tierwelt Dtl. **30**: 823 (first taxonomic reviser)

1952 *Dileptus marinus* Kahl, 1933 – Bock, Zool. Anz. **149**: 110 (description of a German population)

1960 *Dileptus marinus* KAHL – DRAGESCO, Trav. Stn biol. Roscoff (N. S.) **12**: 186 (description of a French population)

1963 *Dileptus marinus* KAHL, 1933 – DRAGESCO, Bull. biol. Fr. Belg. **97**: 114 (second taxonomic reviser)

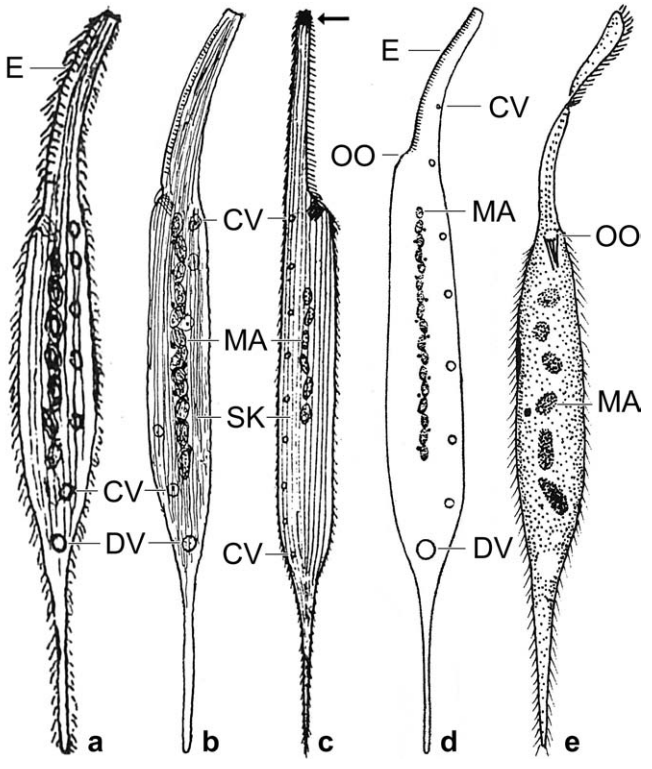
Diagnosis: Length about 450–700 µm in vivo.

Type locality: Sand from the saline bay of the town of Kiel, Germany, E10°08' N54°19'.

Type material: Not available.

Description: KAHL (1933) observed only one specimen, which supposedly lost the tip of the proboscis. Later, he included the species in his revision (KAHL 1935), but with two differences (cp. Fig. 110a with 110b): a higher number of macronuclear nodules (12 vs. 7) and the contractile vacuoles in a spiral line (vs. dorsal stripe). However, the populations observed by BOCK (1952a) and DRAGESCO (1960, 1963) match KAHL's (1933) original description. Thus, all data are put together.

Body size 420 µm (KAHL 1933), 700 × 50–55 µm (BOCK 1952a), and 450–600 µm (DRAGESCO 1960, 1963); highly flexible but not contractile. Shape cylindroidally dileptid to rod-like with a length:width ratio of 10–14:1, according to the figures provided. Proboscis occupies one fifth to one fourth of body length, about 100 µm long according to KAHL (1933), ordinarily set off from trunk, slightly curved dorsally, hyaline except for anterior end, where BOCK (1952a) observed an accumulation of refractive (dark) granules (Fig. 110c, arrow). Trunk oblong, 200 µm long in KAHL's exemplar, opaque due to many granules in BOCK's specimens. Tail conspicuous because as long as proboscis or even longer, i.e., occupies about one fourth of body length, 120 µm long in KAHL's specimen (Figs 110a–d). Macronucleus an almost rod-shaped, moniliform strand extending from underneath oral bulge opening to third quarter of trunk in type and DRAGESCO's specimens, while in middle quarters of trunk in BOCK's specimens, composed of six to seven (or 12? see above) globular nodules in German specimens (KAHL 1933, BOCK 1952a), while of 17 nodules



Figs 110a–d: *Pseudomonilicaryon marinum marinum* from life. **a** – German type specimen, length 420 µm (from KAHL 1933); **b** – redrawing of German type specimen (from KAHL 1935); **c** – German specimen, length 700 µm (from BOCK 1952a). Arrow denotes an accumulation of dark granules in tip of proboscis; **d** – French specimen, length 600 µm (from DRAGESCO 1963).

Fig. 110e: *Pseudomonilicaryon marinum minimum* from life, length 197 µm (from JONES 1974).

CV – contractile vacuoles, DV – defecation vacuoles, E – extrusomes, MA – macronucleus (nodules), OO – oral bulge opening, SK – somatic kineties.

in French cells, as estimated from Dragesco's illustration (Fig. 110d). Micronuclei and extrusomes not known. A dorsal stripe of contractile vacuoles: seven to ten in Kahl's and Dragesco's specimens, 17–19 according to Bock (1952a) but only nine are shown; first vacuole at level of oral bulge opening in German specimens (Figs 110a–c), while in proximal half of proboscis in French cells (Fig. 110d). Cortex with oblong granules, forming about three rows between each two kineties (Kahl 1933). Kahl (1933) and Bock (1952a) figured roughly ten ciliary rows on one side of cell. Creeps between sand grains, probing with the proboscis (Bock 1952a). Somatic and oral ciliature not known. Oral opening and pharyngeal basket comparatively small, according to the figures available (Figs 110a–d).

Occurrence and ecology: *Pseudomonilicaryon marinum marinum* was discovered and re-discovered in sandy sediments of the Kiel bay, a coastal town in northern Germany (Kahl 1933; Bock 1952a, 1952b; Telesh et al. 2008). Dragesco (1960, 1963) found it in the mesopsammon of Roscoff, France. Fernández-Leborans & Novillo (1993) recorded it in September from the sublittoral of the Santoña Estuary, Bay of Biscay, Spain, and Agamaliev & Aliev (1983) reported it from the Divichinskiy estuary of the Caspian Sea.

Pseudomonilicaryon marinum minimum nov. ssp. (Fig. 110e)

1974 *Dileptus marinus* Kahl, var. *minimus*, n. var. Jones, Univ. South Alabama Monogr. **1**: 25

Nomenclature and taxonomy: *Dileptus marinus* var. *minimus* is infrasubspecific because it was published after 1960 and Jones (1974) expressly used the term "var." (Article 45.6.3 of the ICZN 1999). Thus, it is not available, according to Article 45.5 of the ICZN (1999). However, we recognize Jones' variety as a reliable subspecies and fix as a holotype the figure given by Jones (1974), here reproduced as Fig. 110e.

Diagnosis: Length about 200 µm in vivo.

Type locality: Sand from the mouth of the Dog River, Mobile Bay, Alabama, USA, W87°57' N30°38'.

Type material: Not available.

Etymology: Not given in original description. The Latin adjective *minimus* (small) refers to the small body size.

Description: Length 197 µm in vivo; shape cylindroidally dileptid with a length:width ratio of 11:1, according to the figure provided. Proboscis about one third of body length, distinctly flattened, slightly set off from oblong trunk; tail occupies about one fourth of body length. Macronucleus extends between oral bulge opening and base of tail, moniliform and composed of six broadly ellipsoidal to ellipsoidal nodules. One (unlikely in our opinion) globular micronucleus close to mid of macronucleus. A dorsal stripe of contractile vacuoles. Oral bulge opening roundish, comparatively small; oral basket obconical and short. Extrusomes and ciliature not known.

Occurrence and ecology: As yet found only at type locality in July 1970.

Pseudomonilicaryon anser (Mueller, 1773) nov. comb. (Figs 111a–t, 112a–v, 113a–r, 114a–g; Table 58)

1773 *Vibrio anser* Mueller, Vermium Terrestrium et Fluviatilium: 46 (without figure)

1786 *Vibrio anser* – Mueller, Animalcula Infusoria: 73 (description with figures)

1838 *Amphileptus anser* – Ehrenberg, 1838, Infusionsthierchen: 355 (combination with *Amphileptus*)

1859 *Amphileptus anser* Ehr. – Claparède & Lachmann, Mém. Inst. natn. génev. **6**: 350 (description adopted from Ehrenberg 1838)

1859 *Amphileptus cygnus* Claparède & Lachmann, Mém. Inst. natn. génev. **6**: 350 (synonymy proposed by Schewiakoff 1896, description of a German population)

1870 *Dileptus gigas grojecensis* Wrześniowski, Wiss. Zool. **20**: 504 (synonymy proposed by Schewiakoff 1896 and Kahl 1931, description of a Polish population)

1876 *Amphileptus cygnus* – Fromentel, Études Microzoaires: 286 (synonymy proposed by Schewiakoff 1896)

1876 *Amphileptus longicollis* – Fromentel, Études Microzoaires: 288 (synonymy proposed by Schewiakoff 1896)

1881 *Amphileptus cygnus* C. & L. – Kent, Manual infusoria II: 524 (description adopted from Claparède & Lachmann 1859)

1881 *Amphileptus anser* Ehr. – Kent, Manual infusoria II: 524 (description adopted from Ehrenberg 1838)

1889 *Dileptus anser* O. F. Mueller sp. – Schewiakoff, Biblthca zool. **1**: 22 (brief review, partim)

1896 *Dileptus anser* O. F. Müll. sp. – Schewiakoff, Zap. imp. Akad. Nauk **4**: 221 (taxonomic revision, partim)

1907 *Dileptus gigas* – Holmes, Biol. Bull. **13**: 307 (misidentification; detailed description of movement)

1917 *Dileptus gigas* – Hausman, Am. Naturalist **51**: 168 (misidentification; notes on North American populations)

1930 *Amphileptus longicollis*, de Fromentel – Dumas, Les Microzoaires: 109 (brief description of a French population)

1931 *Dileptus* (*Amphileptus*) *cygnus* (Clap. u. L., 1859) – Kahl, Tierwelt Dtl. **21**: 205 (first taxonomic reviser)

1949 *Dileptus cygnus* Clap. et Lachm. 1859 – Šrámek-Hušek, Věst. Čsl. zool. spol. **13**: 330 (description of a Czech population)

1951 *Dileptus cygnus* – Canella, Annali Univ. Ferrara **1**: 156 (description of an Italian population)

1953 *Dileptus cygnus* – Jones & Beers, J. Elisha Mitchell scient. Soc. **69**: 47 (description of behaviour of a North American population)

1959 *Dileptus cygnus* (Clap. L. 1859) – Vuxanovici, Studii Cerc. Biol. **11**: 327 (description of a Roumanian population)

1962 *Dileptus anser* (O. F. Mueller 1786) nov. comb. – Dingfelder, Arch. Protistenk. **105**: 558 (brief taxonomic revision)

1963 *Dileptus anser* O. F. M. – Doroszewski, Acta biol. exper., Warsaw **23**: 3 (preliminary identification, experimental study)

1963 *Dileptus anser* O. F. M. – Doroszewski, Acta Protozool. **1**: 187 (preliminary identification, experimental study)

1963 *Dileptus cygnus* Clap. et Lachm., 1859 – Doroszewski, Acta Protozool. **1**: 313 (definitive identification, experimental study)

1963 *Dileptus cygnus* (Clap. et Lachm., 1859) – Dragesco, Bull. biol. Fr. Belg. **97**: 113 (second taxonomic reviser)

1964 *Dileptus cygnus* Clap. et Lachm. – Golińska & Doroszewski, Acta Protozool. **2**: 60 (comparison of processes during binary fission and regeneration)

1965 *Dileptus cygnus* – Golińska, Acta Protozool. **3**: 143 (description of nuclear cycle)

1966 *Dileptus cygnus* Clap. et Lachm. – Golińska, Acta Protozool. **4**: 41 (experimental study)

1966 *Dileptus cygnus* – Doroszewski & Raabe, Kosmos, Warszawa **15**: 133 (comparison of processes during binary fission and regeneration)

1967 *Dileptus cygnus* Clap. et Lachm. – Doroszewski & Golińska, Acta Protozool. **4**: 343 (experimental study)

1968 *Dileptus cygnus* Clap. et Lachm. – Doroszewski, Acta Protozool. **5**: 291 (experimental study)

1969 *Dileptus cygnus* Claparède et Lachmann, 1859 – Grain & Golińska, Protistologica **5**: 269 (fine structure)

1969 *Dileptus cygnus* Clap. et Lach., 1859 – Golińska & Grain, Protistologica **5**: 447 (experimental study)

1970 *Dileptus cygnus* (Clap. et Lachm, 1859) – Dragesco, Fac. Sci. Univ. féd. Cameroun year **1970**: 11 (description of a Cameroon population)

1970 *Dileptus cygnus* – Doroszewski, Acta Protozool. **7**: 353 (experimental study)

1971 *Dileptus cygnus* (Clap. et Lachm.) – Golińska, Acta Protozool. **8**: 369 (silver impregnation and comparison with *D. anatinus* and *D. margaritifer*)

1972 *Dileptus cygnus* Clap. et Lachm. – Doroszewski, Acta Protozool. **10**: 109 (experimental study)

1976 *Dileptus cygnus* Clap. et Lachm., 1859 – Golińska & Kink, Acta Protozool. **15**: 143 (experimental study)

1978 *Dileptus cygnus* – Doroszewski & Dryl, Acta Protozool. **17**: 561 (experimental study)

1979 *Dileptus cygnus* Clap. et L., 1859 – Mamaeva, Infuzorii bassejna Volgi: 31 (ecology)

1984 *Dileptus anser* O. F. Mueller, 1786 – Wirnsberger, Foissner & Adam, Arch. Protistenk. **128**: 313 (authoritative redescription and neotypification)

1986 *Dileptus cygnus* (Claparède et Lachmann, 1859) – Dragesco & Dragesco-Kernéis, Fauna tropicale **26**: 159 (brief review)

1987 *Dileptus cygnus* Claparède et Lachmann, 1859 – Lokot', Èkologiâ resničnyh prostejših: 33 (brief description and ecology)

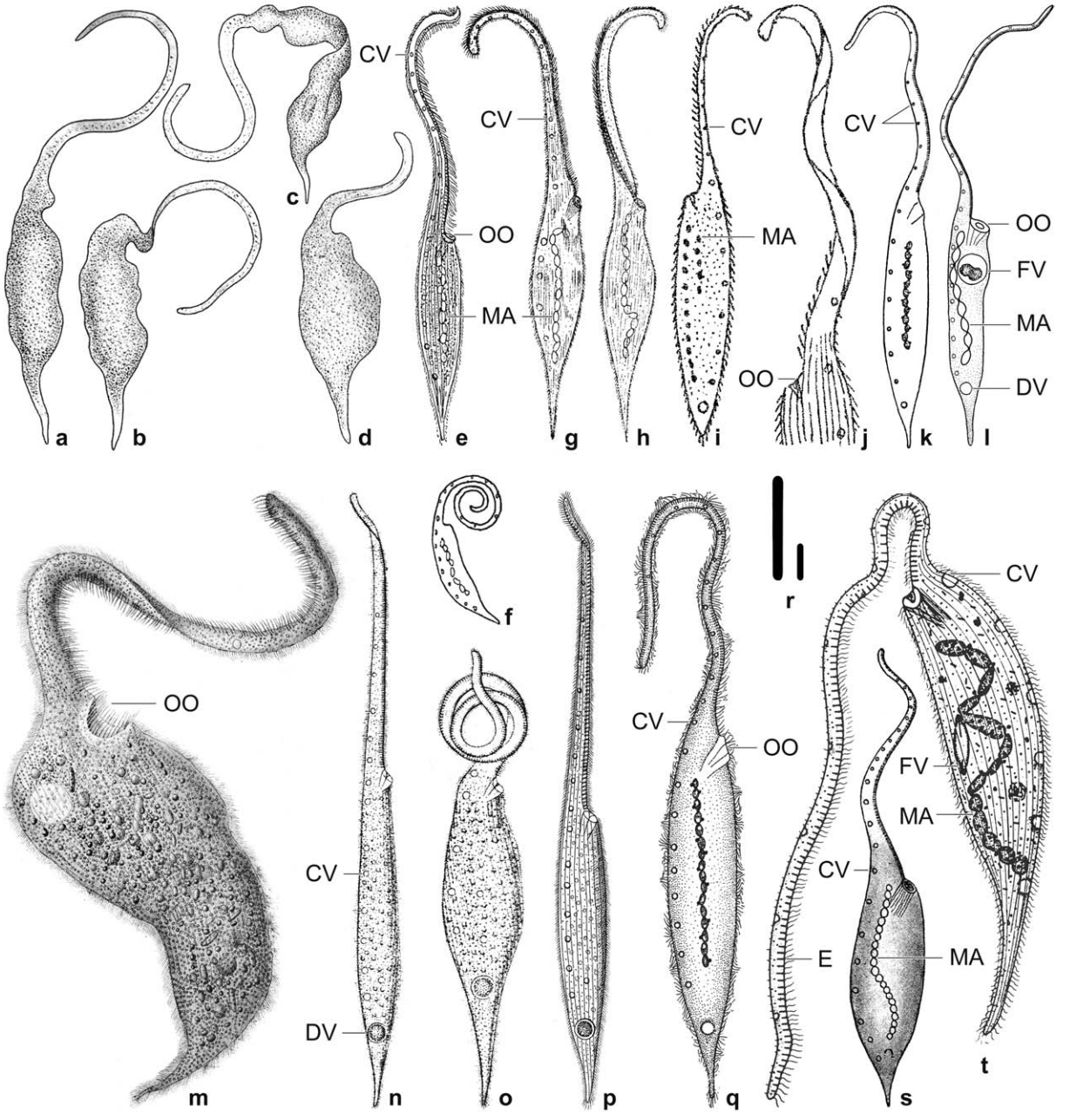
1995 *Dileptus anser* – Foissner, Berger, Blatterer & Kohmann, Informationsberichte des Bayer. Landesamtes für Wasserwirtschaft **1/95**: 198 (brief review)

non *Dileptus anser* – Dujardin (1841), Perty (1852), Kahl (1931), Hayes (1938), Vuxanovici (1959), Dumont (1961), Dragesco (1963), Chorik (1968), Golińska (1971, 1978, 1979, 1982–1984, 1986), Vinnikova (1974a, b, 1976), Dragesco & Dragesco-Kernéis (1986), Yudin & Uspenskaya (2002), who misidentified *Dileptus margaritifer* as *Pseudomonilicaryon anser* (see synonymy list of *D. margaritifer*)

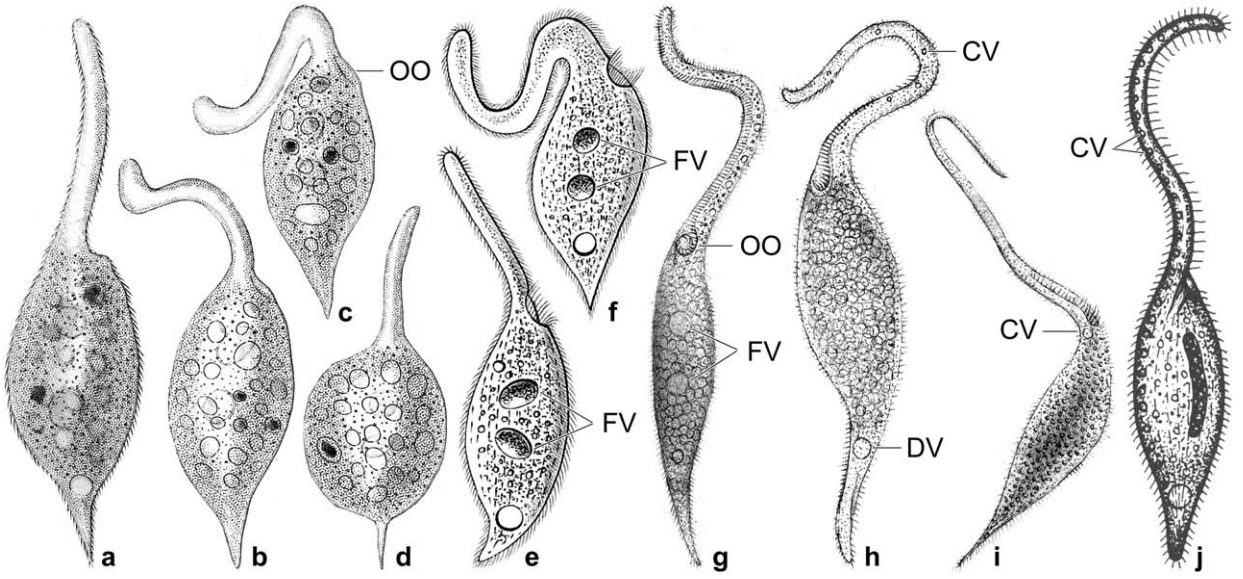
Generic affiliation, taxonomy, and nomenclature: We assign *D. anser* to the genus *Pseudomonilicaryon* because it has a *Dileptus*-like ciliary pattern and a moniliform macronucleus.

Pseudomonilicaryon anser was originally described as *Vibrio anser* by Mueller (1773). Sixty-eight years later, Dujardin (1841) assigned Mueller 's species to the genus *Dileptus*. Unfortunately, he misidentified and mixed *Dileptus margaritifer* with *D. anser*, causing many further misidentifications (see *D. margaritifer*). In 1859, Claparède & Lachmann described *Amphileptus cygnus* (*Dileptus cygnus* since Kahl 1931), a species with the proboscis occupying one half of body length, and thus highly resembling Mueller 's *D. anser*. However, Kahl (1931) and Dragesco (1963) overlooked that *D. cygnus* is a junior synonym of *D. anser* and identified *D. margaritifer* as *D. anser* and *D. anser* as *D. cygnus*. This problem was first recognized by Dingfelder (1962) and later discussed and adopted by Wirnsberger et al. (1984).

According to Schewiakoff (1896) and Kahl (1931), *P. anser* has two further synonyms, viz., *D. gigas grojecensis* Wrześniowski, 1870 and *Amphileptus longicollis* sensu Fromentel (1876); we agree. Wrześniowski (1870) and Schewiakoff (1896) considered *Amphileptus gigas* (now *Monomacrocaryon gigas*) as a synonym of *P. anser*. We disagree because *M. gigas* has a cylindroidal macronucleus (vs. a moniliform strand) and a twisted, up to 1.6 mm long body (vs. not twisted and up to 600 µm long). Schewiakoff (1896) also synonymized *Amphileptus irregularis*, *A. margaritifer* (now *Dileptus margaritifer*), *A. monilatus* (now *Monilicaryon monilatum*), *A. moniliger*, and *Phragelliorhynchus nasutus* with *P. anser*; we disagree. *Amphileptus moniliger* and *M. monilatum* have a much shorter proboscis (1/5 vs. 1/2 of body length). *Amphileptus irregularis* is a junior synonym of *D. margaritifer*, as first recognized by Kahl (1931) and accepted here. *Dileptus margaritifer* has a shorter proboscis (1/3 vs. ½ of body length) and at least 150 scattered macronuclear nodules (vs. a moniliform strand composed of 7–25 nodules). *Phragelliorhynchus nasutus* is much smaller (200 µm vs. 500 µm), thus conspecificity can be excluded.



Figs 111a–t: *Pseudomonilicaryon anser* and its supposed synonyms from life. **a–d** – Danish specimens, length not given (from MUELLER 1786); **e, f** – German specimen with straight and rolled proboscis, length 600 µm (from KAHL 1931); **g, h** – Czech specimens, length 400–600 µm (from ŠRÁMEK-HUŠEK 1949); **i, j** – Roumanian specimen, length 520 µm, and detail of oral region (from VUXANOVICI 1959); **k** – right side view showing general body organization, length 700 µm (from DRAGESCO 1963); **l** – Polish specimen, length not given (from GOLIŃSKA 1965); **m** – *Amphileptus cygnus*, length 220 µm (from CLAPARÈDE & LACHMANN 1859); **n, o** – *Dileptus gigas grojecensis*, a specimen with straight proboscis, length 615 µm, and a specimen with rolled proboscis, length 366 µm (from WRZEŚNIOWSKI 1870); **p** – *Dileptus gigas*, length 615 µm (from KENT 1881); **q** – African specimen, length 640 µm (from DRAGESCO & DRAGESCO-KERNÉIS 1986); **r** – two size-types of rod-shaped extrusomes in an Austrian specimen (original): type I is 6 µm long and type II is about 2 µm long; **s** – Italian specimen, length not given (from CANELLA 1951); **t** – representative Austrian specimen, length 455 µm (from WIRNSBERGER et al. 1984). CV – contractile vacuoles, DV – defecation vacuole, E – extrusomes, FV – food vacuole, MA – macronucleus (nodules), OO – oral opening.



Figs 112a–j: *Pseudomonilicaryon anser* and its supposed synonyms from life. **a–d** – *Amphileptus anser*, length about 220 μm (from EHRENBERG 1838); **e, f –** likely redrawings from EHRENBERG (1838) by KENT (1881), length about 220 μm; **g, i** – *Amphileptus longicollis*, length 400 μm and 490 μm (from FROMENTEL 1876); **h –** *Amphileptus cygnus*, length 410 μm (from FROMENTEL 1876); **j** – *Dileptus cygnus*, length 400 μm (from LOKOT' 1987). CV – contractile vacuoles, DV – defecation vacuole, FV – food vacuoles, OO – oral bulge opening.

Pseudomonilicaryon anser resembles only one other species, viz., *P. fraterculum*, which differs in the contractile vacuole pattern (vacuoles scattered in trunk and dorsal side of the proboscis vs. in a dorsal stripe), the higher number of ciliary rows (70–90 vs. 50–70), and the number of cilia comprising the preoral kineties (usually 3 vs. invariably 2). To be certain of these and other differences, *P. anser* should be reinvestigated in detail, preferably a European or Asian population.

WIRNSBERGER et al. (1984) neotypified *P. anser* with an Austrian population without providing any reason. However, we agree because its identity must be fixed for distinguishing it from the North American *P. fraterculum*.

Diagnosis (includes all information known): Size about 500 × 60 μm in vivo. Shape narrowly dileptid to rod-like with distinct tail, proboscis on average 55% of body length. Macronucleus moniliform, composed of 7–25 globular to oblong nodules; several globular micronuclei. A dorsal stripe of contractile vacuoles with 1–3 pores each. Two size types (6 μm and 2 μm) of rod-shaped extrusomes attached to proboscis oral bulge. About 60 ciliary rows; dorsal brush diffuse, staggered. Oral bulge opening about 20 μm across. Preoral kineties oblique, ordinarily spaced, each composed of 2 ordinarily spaced cilia.

Type locality: MUELLER (1773) did not specify the type locality, referring to Danish freshwaters ("in aquis, ubi Lemna"). The neotype is from an alpine meadow puddle on the Schlossalm in the surroundings of Bad Hofgastein, Salzburg, Austria, E13°4' N47°9' (WIRNSBERGER et al. 1984). According to Article 76.3 of the ICZN (1999), the place of origin of the neotype becomes the type locality of the nominal species-group taxon, despite any previously published statement of the type locality.

Type material: WIRNSBERGER et al. (1984) deposited two neotype slides (inv. nos 1986/14 and 1986/15) with silver nitrate-impregnated (Chatton-Lwoff method, as modified by CORLISS) specimens in the Biology Centre of the Museum of Upper Austria, Linz (LI). Relevant specimens are marked by black ink circles on the coverslip.

Etymology: Not given in original description. The apposite noun *anser* means goose.

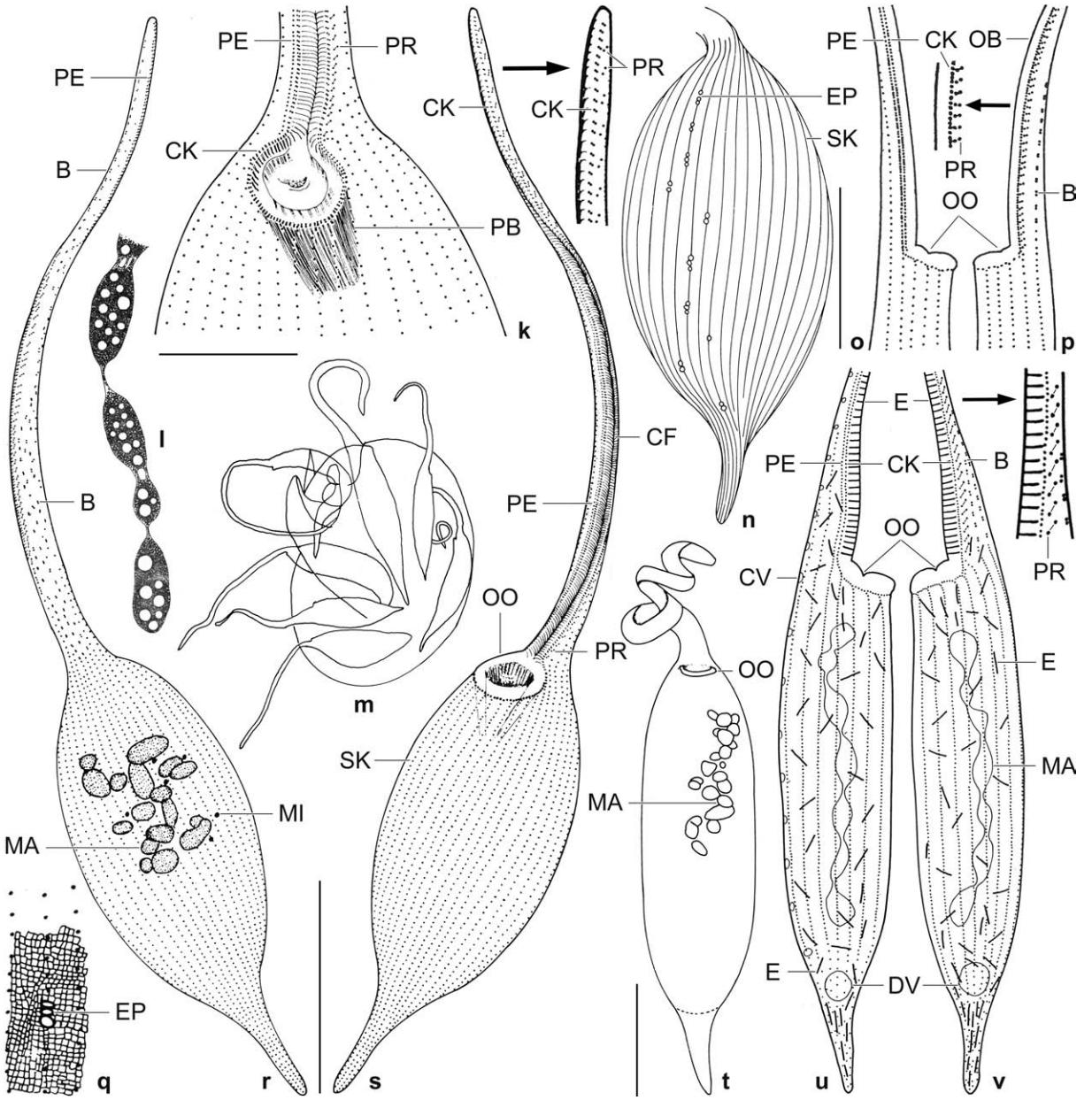
Description: All known and some new data are put together because the morphological conspecificity is beyond doubts for most populations mentioned in the list of synonyms. Redescription recommended.

Body length about 220 µm in Berlin specimens (Claparède & Lachmann 1859; possibly a measurement error), 400–490 µm in French cells (Fromentel 1876), 366–615 µm in Polish individuals (Wrześniowski 1870), up to 600 µm in Hamburg cells (Kahl 1931), 400–600 µm in Czech specimens (Šrámek-Hušek 1949), 520 µm in a Roumanian exemplar (Vuxanovici 1959), 400–600 µm in African cells (Dragesco 1970, Dragesco & Dragesco-Kernéis 1986), 250–500 µm in Austrian individuals (Wirnsberger et al. 1984), and 150–300 × 50–80 µm (but 400 µm according to Fig. 112j) in Russian specimens (Lokot' 1987). Thus, an average in vivo length of about 500 µm can be expected; when the average length:width ratio (9:1, see next paragraph) is taken into account, the size of a typical *P. anser* is about 500 × 55 µm.

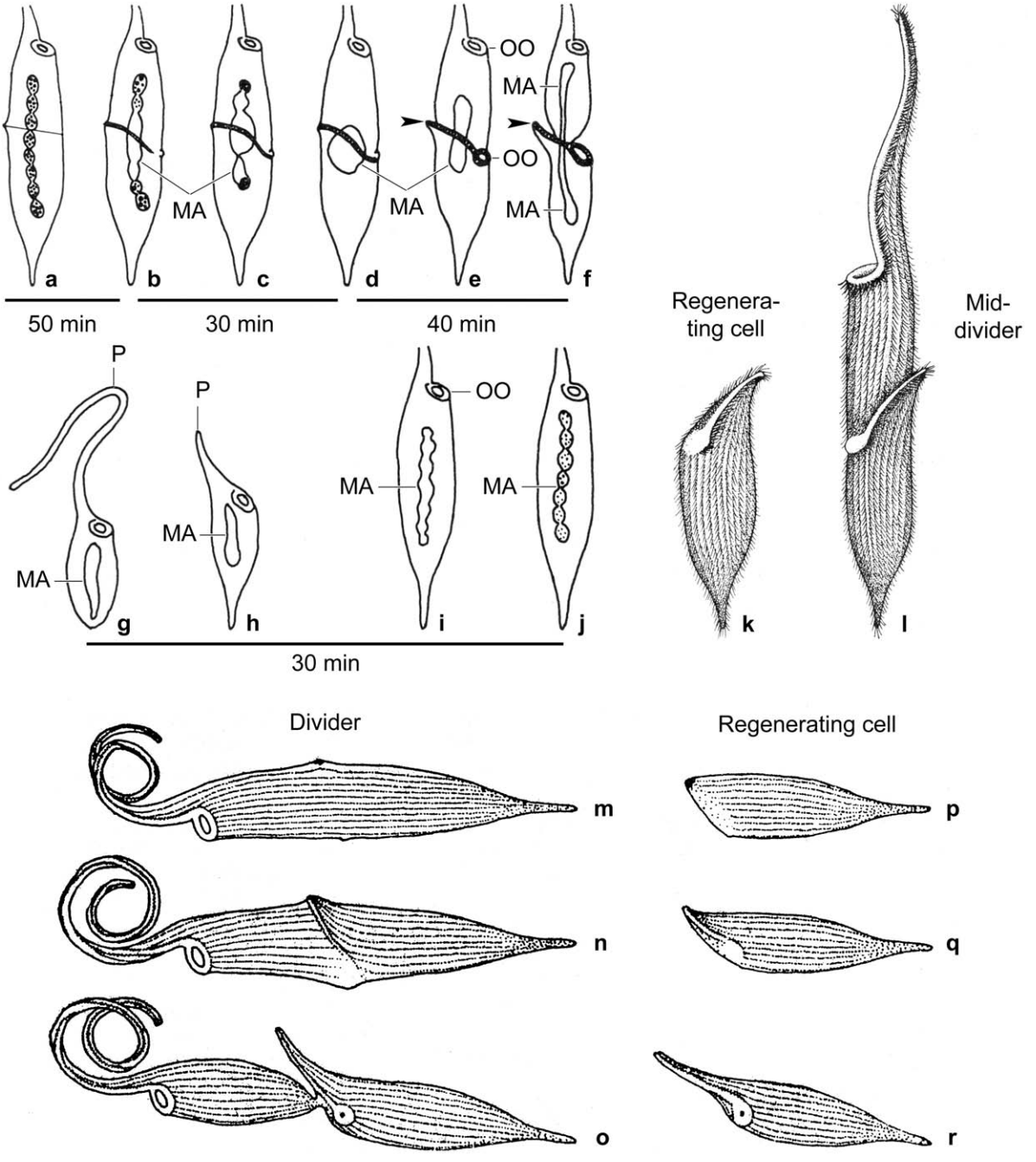
Body very flexible but not contractile. Shape in vivo narrowly dileptid to rod-like, that is, length:width ratio on average 9:1 (5–15:1), according to the figures available in the literature and our own data based on micrographs. Proboscis very conspicuous because usually occupying half or even more of body length, highly motile and flexible, 2:1 flattened, 8 µm wide at base and 6 µm on tip in Roumanian specimens, 9.7 (7–11) µm wide at base and 3.4 (2–6) µm on tip in prepared Austrian cells; with a tendency to roll up or twist (Figs 111f, o, 112t), possibly misinterpreted as contractility by several authors (Kahl 1931, Šrámek-Hušek 1949, Wirnsberger et al. 1984); very fragile and thus often lost or broken during preparation (Wirnsberger et al. 1984). Trunk almost oblong to bluntly fusiform, widest in mid-portion, about 110 × 50 µm in Austrian specimens, unflattened, with a tendency to fold (Fig. 114f). Posterior end with short or up to 40 µm long tail preserved also in prepared cells and even in specimens inflated by food inclusions or flattened by coverslip pressure (Figs 111a–h, k–q, s, t, 112a–j, n, r–v, 114a, b, d–g); acute in Roumanian specimens, which thus could be a different species (Fig. 111i).

Nuclear apparatus usually extending between oral bulge opening and base of tail. Macronucleus a moniliform, basically straight strand in most populations (Figs 111e–h, k, l, q, s, 112l, u, v), while slightly to strongly tortuous in Roumanian (Fig. 111i) and Austrian (Figs 111t, 112r, t, 114a, d) specimens; difficult to recognize under bright field illumination, and thus not seen by Claparède & Lachmann (1859) and Wrześniowski (1870), as mentioned by Kahl (1931). Fromentel (1876) and Kent (1881) possibly misinterpreted food inclusions in Ehrenberg's specimens as two macronuclear nodules (Figs 112e–g). Nodules connected with one or several short bridges recognizable in Brachet and Feulgen stains (Fig. 112l). Number of nodules of usual variability within and between populations: 11 in Hamburg specimens (Kahl 1931), up to 14 in Czech individuals (Šrámek-Hušek 1949), 21 in an Italian exemplar (Canella 1951), 16 in Roumanian specimens (Vuxanovici 1959), 7–15 in Polish cells (Golińska 1965), 9 in a North American specimen (Bovee 1979), and 12–25 in Austrian cells (Fig. 114a; Table 58). Individual nodules rather variable in shape and size: globular to narrowly ellipsoidal, 13–27 × 11–13 µm in Polish specimens (Golińska 1965), 5–8 µm long in African cells (Dragesco 1970), and 6–17 × 3–7 µm in Austrian specimens (Wirnsberger et al. 1984). Nucleoli evenly distributed, few to more than ten per nodule, when small then more numerous (Fig. 112l). Several globular micronuclei attached to macronuclear strand, about 1.5 µm across in African specimens (Dragesco 1970) and 2 µm in Austrian cells (Table 58). Number of micronuclei fairly similar in various populations: 7 in Hamburg specimens, 6–13 in Austrian cells (Table 58), and 12 according to the drawings provided by Dragesco (1963) and Dragesco & Dragesco-Kernéis (1986). Division and post-divisional reorganization of the macronucleus need 150 minutes (Golińska 1965). See explanation of Figs 113a–j for details.

Contractile vacuole pattern identical in all populations investigated, viz., a dorsal stripe of 15–20 organelles with first vacuole near distal end of proboscis; no ventral vacuoles. Number of vacuoles in proboscis:



Figs 112k–v: *Pseudomonilicaryon anser* from life (m), in a Feulgen stain (l), and after protargol (k, o, p, r–v) and Chatton-Lwoff silver nitrate (n, q) impregnation. From Golińska 1965 (l), 1971 (o, p); Grain & Golińska 1969 (u, v); and Wirnsberger et al. 1984 (k, m, n, q–t). **k** – ventral view of oral ciliary pattern. The right branch of the circumoral kinety is accompanied by a perioral kinety, while the left branch is associated with many oblique preoral kineties, each invariably composed of two basal bodies; **l** – the macronucleus is composed of about ten nodules connected by thin bridges; **m** – seven specimens gathered in an empty cladoceran shell; **n** – dorsal view showing ciliary and contractile vacuole pattern; **o, p** – scheme of right and left side oral ciliary pattern. Note that each preoral kinety is composed of two kinetosomes; **q** – silverline pattern and excretory pores of a contractile vacuole; **r, s** – dorsolateral and ventrolateral ciliary pattern and nuclear apparatus of main neotype specimen. The dorsal brush is diffuse and forms a long field occupying the dorsal and most of the left side of the proboscis; **t** – ventral view of a specimen with rolled proboscis; **u, v** – scheme of right and left side ciliary pattern, and nuclear and contractile vacuole apparatus. The preoral kineties consist of two basal bodies (connected by a line). B – dorsal brush, CF – central fibre, CK – circumoral kinety, DV – defecation vacuole, E – extrusomes, EP – excretory pores of contractile vacuoles, MA – macronuclear nodules, MI – micronucleus, OB – oral bulge, OO – oral bulge opening, PB – pharyngeal basket, PE – perioral kinety, PR – preoral kineties, SK – somatic kineties. Scale bars: 20 μm (k) and 50 μm (n, r–t).



Figs 113a–j: *Pseudomonilicaryon anser*, division and post-divisional reorganization of macronucleus takes about 150 minutes (from GOLIŃSKA 1965). **a** – in very early dividers, the macronucleus highly resembles that of morphostatic cells; **b, c** – in early dividers, the nodules begin to fuse in mid-portion of the strand; **d** – after 35 minutes, all nodules have fused to a central, globular mass; **e, f** – when the proboscis bud appears (arrowheads), the macronucleus begins to divide (e), becoming a long rod constricted in the fission area (f); **g** – a proter post-divider as evident from the long proboscis and the posteriorly tapered macronucleus; **h** – opisthe post-dividers have a very short proboscis and an anteriorly pointed macronucleus; **i, j** – after cell fission, the macronucleus elongates to a nodulated strand.

Figs 113k–r: *Pseudomonilicaryon anser*, comparison of dividing cells in various stages (l–o) with regenerating posterior fragments in the corresponding stage (k, p–r). From GOLIŃSKA & DOROSZEWSKI 1964 (k, l) and DOROSZEWSKI & RAABE 1966 (m–r). MA – macronucleus (nodules), OO – oral bulge opening, P – proboscis.

about seven in Austrian cells, 10–15 according to Jones & Beers (1953). Number of vacuoles in trunk: seven in an Italian exemplar (Canella 1951) and six to eight in Austrian specimens (Wirnsberger et al. 1984). Number of excretory pores studied only in Austrian specimens (Wirnsberger et al. 1984), viz., two to three, rarely one intrakinetal pore per vacuole (Figs 111e–l, n–q, s, t, 112n, q, u, 114a). Claparède & Lachmann (1859) misinterpreted a large food vacuole as a single contractile vacuole (Fig. 111m).

Extrusomes of toxicyst type as shown by TEM studies (Grain & Golińska 1969). Shape and size in vivo investigated only in an Austrian population (Figs 111r, 114c): type I rod-like with rounded ends, 4–6 × 0.8 µm in size; type II oblong, only 2 × 0.5 µm in size, more numerous than type I; figure 114c suggests the extrusomes to be indistinguishable from those of *P. fraterculum*. Doroszewski & Golińska (1967) observed one to several toxicyst rows in the proboscis oral bulge, but did not mention whether only in the broader right bulge branch or in both bulge branches.

Cortex flexible; contains several rows of granules (mucocysts) between two kineties each; conspicuous in TEM because 1.8 µm long and separated from cytoplasm by a *lamina corticalis* (Grain & Golińska 1969). Silverline pattern composed of polygonal meshes about 0.2 µm in size, not yet studied in detail (Fig. 112q). Cytoplasm colourless, while greenish in Austrian specimens due to food vacuoles with green algae and diatoms; hyaline in proboscis and tail, opaque in trunk (Figs 111t, 114b, d–g). Usually a defecation vacuole with crystalline contents near base of tail; often misinterpreted as a contractile vacuole (Figs 111i, k, l, n–q, 112a, c, e–h, j, u, v, 114a, b, g).

Holmes (1907), who misidentified it as *Dileptus gigas*, provided the following description of movement: "*Dileptus gigas* commonly adheres to the surface of some solid object and waves its long proboscis-like anterior extremity or neck about in an anti-clockwise direction. The surface of the body is quite sticky, as is shown by the fact that it adheres readily to any object brought in contact with it. The slender extremity in its movement about in a circle executes many twists and curls in more or less irregular ways. These movements may be very vigorous or they may be very slow, but they scarcely ever entirely cease. The slender neck is very extensile and may be elongated to three or more times when in a contracted state.

Dileptus often executes short forward and backward movements at tolerably regular intervals. During its movement forward the body elongates, and while gliding backward it widens, showing the same correlation of contractility with the direction of the beat of the cilia that occurs in *Loxophyllum meleagris*. The backward and forward excursions vary exceedingly in length. Frequently they are exceedingly short. Even when the organism remains attached in one place the body undergoes more or less regular elongations and contractions while waving about the anterior extremity. There is a rhythm here much as in the preceding species occurring quite independently of external stimulation. The posterior third of the body when severed from the rest still undergoes elongations and contractions, although in a somewhat lessened degree. In larger pieces the rhythm of movement is more manifest." These observations basically match our data from *Pseudomonilicaryon fraterculum*.

Cilia about 6 µm long in vivo, narrowly spaced; arranged in about 60 meridional, narrowly to ordinarily spaced rows (Table 58). Grain & Golińska (1969) strongly underestimated the number of ciliary rows (12–20; Figs 112u, v), as evident from one of their micrographs, which shows 13 kineties in the right side region of the oral bulge opening, suggesting about 52 rows in total. Details of ciliary pattern studied by Grain & Golińska (1969), Golińska (1971), and Wirnsberger et al. (1984): (i) first row right of circumoral kinety extends as perioral kinety to tip of proboscis (Figs 112k, o, s, u); (ii) left side rows end at level of or slightly above oral bulge opening (Figs 112k, p–s, v); (iii) left side of proboscis with comparatively narrow blank stripe due to the slender proboscis and brush kinetids extending onto left side (Figs 112p, r, v); (iv) dorsal brush a long field occupying dorsal and most of left side of proboscis, diffuse and staggered (Figs 112p, r, v); (v) brush dikinetids very loosely spaced, associated with 3 µm long bristles.

Oral bulge opening slightly underneath second body half, roundish both in vivo and in protargol preparations, about 20 µm across, usually projects distinctly because proboscis less than half as wide as trunk (Figs 111e, i, j, l–q, s, t, 112a–j, k, o, p, s–v). Pharyngeal basket obconical, almost 20 µm long in preparations, without specific features (Figs 112k, s; Table 58). Circumoral kinety composed of narrowly spaced dikinetids in proboscis and narrowly spaced monokinetids around oral bulge opening (Figs 112o, p, u, v). Preoral kinety pattern quite similar in the populations studied by GRAIN & GOLIŃSKA (1969), GOLIŃSKA (1971), and WIRNSBERGER et al. (1984): individual kineties ordinarily spaced in proximal half of proboscis while widely spaced in distal half, oblique, invariably composed of two ordinarily to loosely spaced cilia (Figs 112k, p, r, s, v).

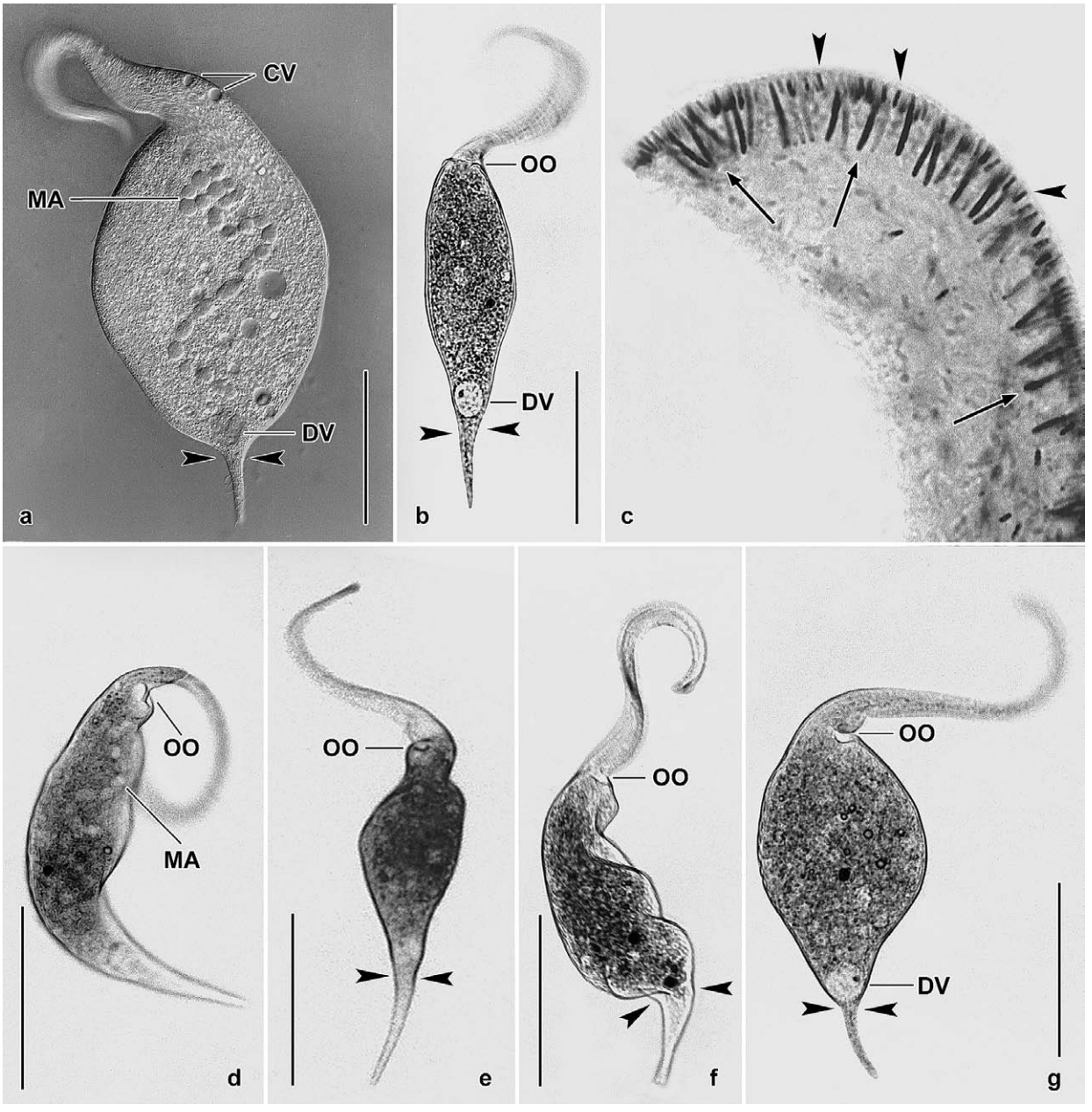
Occurrence and ecology: "*Pseudomonilicaryon anser* and *P. fraterculum* are the kings of beasts among the ciliated protozoa. They are entirely carnivorous and their appetite is apparently insatiable. The prey is stung by the well developed extrusomes which dileptids bear upon their long proboscis and if too large to be swept into the buccal cavity by the cilia is forced in by the writhings of the proboscis (HAUSMAN 1917)". We agree!

In most studies, *P. anser* is called *Dileptus cygnus* because the determination usually followed KAHL (1931). *Pseudomonilicaryon anser* is a bottom-dweller slowly moving through organic mud, constantly probing with the proboscis; rarely free-swimming. When disturbed, swims rapidly backwards but soon settles on microscope slide. Frequently, several specimens gather in masses of organic debris, in empty cladoceran shells (Fig. 112m; JONES & BEERS 1953, DOROSZEWSKI 1968, WIRNSBERGER et al. 1984), or in

Table 58: Morphometric data on *Pseudomonilicaryon anser* (from WIRNSBERGER et al. 1984). Data based on mounted, protargol-impregnated (Foissner's method), and randomly selected specimens. Measurements in µm. CV – coefficient of variation in %, M – median, Max – maximum, Mean – arithmetic mean, Min – minimum, n – number of specimens investigated, SD – standard deviation, SE – standard error of mean.

Characteristics	Mean	M	SD	SE	CV	Min	Max	n
Proboscis, width at tip	3.4	3.0	1.3	0.4	37.2	2.0	6.0	10
Proboscis, width at base	9.7	9.0	1.9	0.5	19.4	7.0	11.0	13
Trunk, length	111.2	108	25.5	7.1	22.9	85.0	182.0	13
Trunk, width at level of oral bulge opening	15.3	15.5	2.2	0.6	14.1	11.0	18.0	12
Trunk, width in widest portion	47.3	50.0	11.0	3.0	23.1	25.0	66.0	13
Tail, length	29.2	28.0	4.8	1.3	16.4	16.0	32.0	13
Tail, width 20 µm from distal end	7.2	6.0	3.6	1.0	49.6	4.0	14.0	13
Tail, width at distal end	3.5	4.0	0.8	0.2	21.9	2.0	5.0	13
Pharyngeal basket, length	19.2	18.0	3.5	1.0	18.0	16.0	26.0	11
Outer and inner oral basket, distance in between	3.1	3.0	0.8	0.2	24.7	2.0	4.0	13
Macronuclear nodules, length	10.7	10.0	3.1	0.9	29.3	6.5	17.0	12
Macronuclear nodules, width	5.1	5.0	1.1	0.3	22.9	3.0	7.0	12
Macronuclear nodules, number	17.8	17.0	3.6	1.0	20.4	12.0	25.0	13
Micronuclei, largest diameter	2.1	2.0	–	–	–	2.0	3.0	13
Micronuclei, number	9.6	10.0	2.7	0.8	27.9	6.0	13.0	10
Extrusomes, length	3.5	3.5	0.6	0.3	16.5	3.0	4.0	4
Ciliary rows, number[a]	59.5	60.0	7.2	2.2	12.2	50.0	70.0	11

[a] The total number of ciliary rows was calculated by doubling the value from one side, assuming an unflattened trunk.



Figs 114a–g: *Pseudomonilicaryon anser*, Austrian specimens from life (a, b, d–g) and after silver carbonate impregnation (c). **a** – lateral view of a strongly squeezed specimen, showing, inter alia, the moniliform macronuclear strand composed of about 23 nodules, some dorsal contractile vacuoles, and the distinct tail (opposed arrowheads); **b** – ventral view of a slender specimen with a large defecation vacuole. Opposed arrowheads denote tail; **c** – there are two size-types of rod-shaped extrusomes attached to the oral bulge of the proboscis: type I is 6 µm long (arrows) and type II is about 2 µm long (arrowheads); **d–g** – overviews showing the long proboscis, the sometimes distinctly folded trunk, and the conspicuous tail (opposed arrowheads). CV – contractile vacuoles, DV – defecation vacuole, MA – macronucleus (nodules), OO – oral bulge opening. Scale bars: 50 µm (a) and 100 (b, d–g).

the leaf rosettes of Characeae (Fig. 7d ; Fauré-Fremiet 1910). *Pseudomonilicaryon anser* is a catharobic ciliate rather common but rarely abundant in stagnant waters and ephemeral habitats, such as rain-water pools, puddles, and mosses (Hausman 1917, Kahl 1931, Dingfelder 1962, Dragesco 1963). Klekowski (1981) calculated a wet weight of 2400 mg/10^6 ind. and an oxygen consumption of 3000 pl O_2/ind./h at 23 °C (see also Fenchel & Finlay 1983); Chorik & Shubernetsky (1978) mentioned 2400 pl O_2/ind./h at 23 °C. *Pseudomonilicaryon anser* grows well in Petri dish cultures with Pringsheim's solution enriched with dried egg yolk as a medium and *Colpidium colpoda* and *Tetrahymena pyriformis* as a prey (for details, see Golińska 1965, 1966; Doroszewski & Golińska 1967; Grain & Golińska 1969).

Records from the Palearctic: among *Lemna* in Danish freshwaters (Mueller 1773, 1786); Lough Neagh, Ireland (Xu & Wood 1999); in soil and *Sphagnum* of Belgium (Chardez 1967, 1987) and France (Grolière & Njiné 1973); eastern Baltic Sea (Telesh et al. 2008; possibly a misidentification; misspelled as *Dileptus cygnis*); pond in the Zoological Garden of Berlin, Germany (Claparède & Lachmann 1859); mud of the mesosaprobic Aussenalster, a river in the surroundings of the town of Hamburg, Germany (Kahl 1931); meadow rainwater puddles in the surroundings of the town of Forchheim, Germany (Dingfelder 1962); puddle of an alpine pasture (Schlossalm) in the surroundings of the village of Bad Hofgastein, Salzburg, Austria, neotype locality (Wirnsberger et al. 1984); hole filled with peat in Grojec, surroundings of the town of Warsaw, Poland (Wrześniowski 1870); pond in Sadyba, vicinity of Warsaw, Poland (Golińska 1965); fishpond in Poland (Siemińska & Siemińska 1967); streams in Poland (Grabacka 1982); freshwater puddle with pH 5–6.5 close to Lake Velké Dářko, Českomoravská vysočina highlands (602 m a. s. l.), Czech Republic (Šrámek-Hušek 1949, 1952); submerged and wet mosses from Slovenský raj, Slovakia (Tirjaková & Matis 1987); in the littoral of the mesosaprobic Danube River and in the pelagial of the Morava River, Slovakia (Matis & Tirjaková 1995, Baláži & Matis 2002); in October rare in the free water and on artificial substrates of the mesosaprobic Danube River in Hungary (Bereczky et al. 1983); alkaline ponds in Hortobágy National Park, Hungary (Szabó 1999); among *Lemna* in three Roumanian lakes, viz., Balta Manole, Herăstrău, and Floreasca (Vuxanovici 1959); with low abundance (2–4 ind./l) and frequency in the benthos and plankton of the Volga River and various water reservoirs of the former USSR (e.g., Chorik 1968, Mamaeva 1979c, Nebrat 1980, Lokot' 1987, Zharikov 1992; Zharikov & Rotar 1992); in the summer plankton of the River Moscow, Russia (Belova 1998); in the benthos of Lake Dzhandar, Azerbaijan (Aliev 1988); in the winter fauna of the Yuelushan area, China (Yang 1989).

Records from the Nearctic: rare in clear flowing waters with abundant plant life and in clear small pools with abundant decomposing organic sediment, USA (Hausman 1917; misidentified as *Dileptus gigas*); pond in the campus of the University of North Carolina, Chapel Hill, USA (Jones & Beers 1953); in June in the Cape Fear River, North Carolina, USA (Cairns & Yongue 1973); acid-bog and forest mosses from the Lake Itasca region, Minnesota, USA (Bovee 1979); Carolina Biological Supply, USA (Stoeck et al. 2003; an obvious misidentification as shown by the short proboscis); rare in Lake Cromwell, Quebec, Canada (Puytorac et al. 1972). In the absence of detailed morphological data, one cannot exclude that the North American records refer to *Pseudomonilicaryon fraterculum*!

Records from the Paleotropis: catharobic water from the surroundings of the town of Yaoundé, Cameroon (Dragesco 1970, Dragesco & Dragesco-Kernéis 1986) and soil from South Africa (Sandon 1927).

As yet recorded only from two main biogeographic regions, viz., the Holarctic (both in the Palearctic and Nearctic; e.g., Kahl 1931, Jones & Beers 1953, Wirnsberger et al. 1984) and the Paleotropis (Dragesco & Dragesco-Kernéis 1986), indicating restricted distribution.

Experimental studies: *Pseudomonilicaryon anser* has been used for studies on regeneration and ciliary movement, especially by Marek Doroszewski, Krystyna Golińska, and Jolanta Kink. See general part and synonymy list for some key references.

Pseudomonilicaryon fraterculum nov. sp. (Figs 115a–y, 116a–u, 117a–l, 118a–g, 119a–m; Table 59)

2011 *Pseudomonilicaryon fraterculum* – Vďačný, Orsi, Bourland, Shimano, Epstein & Foissner, Eur. J. Protistol. **47**: 297 (authors disclaimed the name for nomenclatural purposes according to Article 8.3 of the ICZN 1999; 18S rRNA gene sequence)

Diagnosis: Size about 600 × 70 µm in vivo. Shape narrowly to cylindroidally dileptid with distinct tail, proboscis on average 55% of body length. Macronucleus moniliform, composed of an average of 26 globular to oblong nodules; several globular micronuclei. Many scattered contractile vacuoles, each with 1–2 pores, in trunk and dorsal side of proboscis. Two size types (10 µm and 2.5 µm) of rod-shaped extrusomes attached to right branch of oral bulge. On average 80 ciliary rows; dorsal brush multi-rowed, staggered, with monokinetidal tails extending anteriorly and posteriorly. Oral bulge opening about 30 µm across. Preoral kineties narrowly to ordinarily spaced, slightly oblique, each usually composed of 3 narrowly spaced cilia.

Type locality: Soil from a puddle in front of the Idaho Transportation Department Building, Boise, Idaho, USA, W116°13’50” N 43°38’10”.

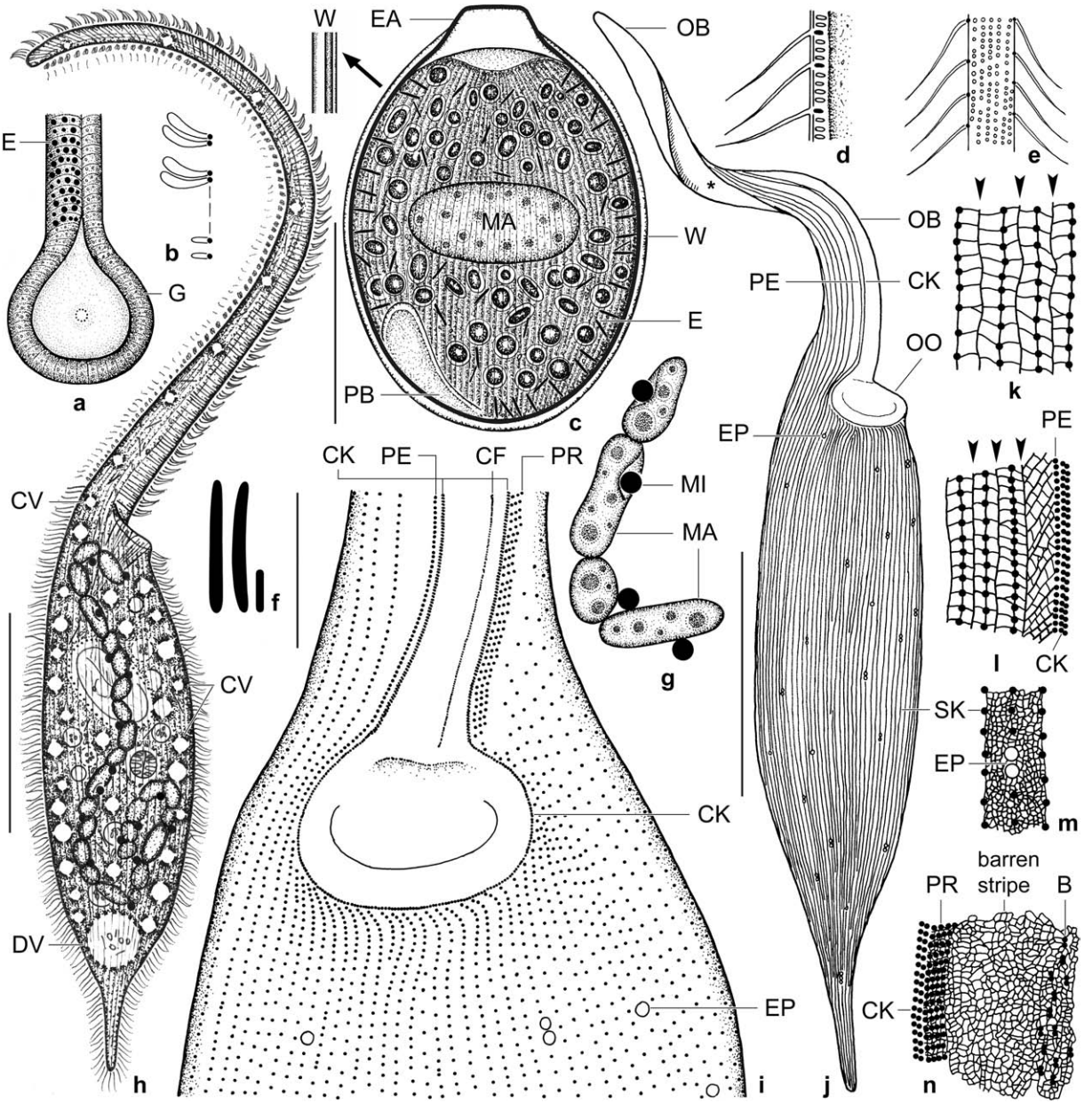
Type material: One holotype slide (inv. no. 2011/231) and 17 paratype slides (inv. nos 2007/139-144, 2011/232–248) with silver nitrate-impregnated specimens, and five paratype slides with protargol-impregnated cells have been deposited in the Biology Centre of the Museum of Upper Austria, Linz (LI). Relevant specimens are marked by black ink circles on the coverslip. (See also introduction to description.)

Gene sequence: The 18S rRNA gene sequence of type population has been deposited in GenBank (HM581677). The sequence is 1640 nucleotides long and has a GC content of 42.3%. It is a consensus sequence based on 19 clones.

Etymology: The Latin noun *fraterculum* (little brother) refers to the high similarity with the European *Pseudomonilicaryon anser*.

Description: *Pseudomonilicaryon fraterculum* was first noted in a non-flooded Petri dish culture of soil from the type locality. However, few specimens were contained. Thus, pure cultures were established with Eau de Volvic and soil eluate containing the natural protist community. Only few of the cultures did well and provided the material needed for silver and SEM preparations. Likewise, *P. fraterculum* is difficult to impregnate with protargol, usually showing only the nuclear apparatus.

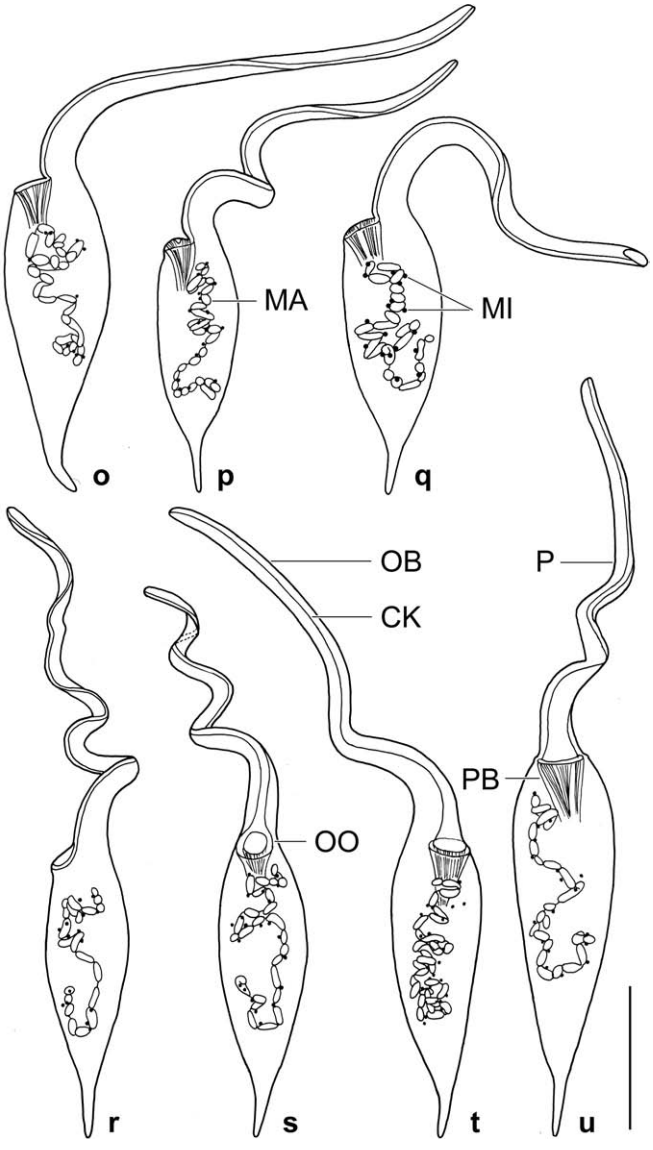
Size 470–930 × 50–85 µm in vivo, on average 648 × 71 µm (Table 59); considerably smaller in Chatton-Lwoff silver nitrate preparations, even if 5% shrinkage is added (563 × 67 µm), indicating the influence of culture conditions; very flexible but not contractile. Shape very narrowly to cylindroidally dileptid, length:width ratio near 9:1 both in vivo and in preparations. Proboscis very conspicuous because occupying an average of 55% of body length, highly motile and flexible, 2:1 flattened, rather fragile and thus sometimes lost when cells are transferred from the culture onto a microscope slide; trunk oblong to fusiform both in vivo and in preparations, widest in mid-region, unflattened, with a tendency to fold; posterior end with distinct tail up to 70 µm long in vivo and well recognizable in most prepared specimens (Figs 115h, j, o–u, 116a–f, o–q, 119a, i; Table 59). Nuclear apparatus extends between oral bulge opening and base of tail. Macronucleus a moniliform and tortuous strand composed of an average of 26 nodules; individual nodules rather variable in shape and size, that is, globular to narrowly ellipsoidal, on average 10 × 6 µm in size; several nucleoli, most 2–3 µm across. On average 17 micronuclei attached to macronuclear strand or to a concavity of the macronuclear nodules, 4 µm across in vivo, while 2.5–3 µm in prepared specimens (Figs 115h, g, o–u, 116g, s; Table 59). Many scattered contractile vacuoles in trunk and dorsal



Figs 115a–n: *Pseudomonilicaryon fraterculum* nov. sp. from life (a–h) and after Chatton-Lwoff silver nitrate impregnation (i–n). **a –** frontal view of oral bulge opening and arrangement of extrusomes; **b** – the brush dikinetids are associated with curved, inflated, 3 μm long bristles followed by 1 μm long tail bristles; **c** – resting cysts are about 105 × 75 μm in size and have an escape apparatus. The wall is composed of three distinct layers (arrow); **d, e** – optical section and surface view showing cortical granulation; **f** – two size types (10 and 3 μm long) of basically rod-shaped extrusomes; **g** – part of nuclear apparatus; **h** – right side view of a representative specimen, length 600 μm. The contractile vacuoles form a stripe each on ventral and dorsal side, a major feature separating *P. fraterculum* from *P. anser*, which has only a dorsal stripe; **i** – oral ciliary pattern of holotype specimen; **j** – ventrolateral view of ciliary and contractile vacuole pattern of a late post-divider, length 497 μm. Asterisk marks blank stripe; **k, l** – a platyophryid silverline pattern occurs in the proboscis'right side. Arrowheads denote median silverlines; **m, n** – a narrowly-meshed silverline pattern occurs in the cortex of the trunk and the proboscis' dorsal and left side. B – dorsal brush, CF – central fibre, CK – circumoral kinety, CV – contractile vacuoles, DV – defecation vacuole, E – extrusomes, EA – escape apparatus, EP – excretory pores, G – cortical granules, MA – macronuclear nodules, MI – micronucleus, OB – oral bulge, OO – oral bulge opening, PE – perioral kinety, PR – preoral kineties, SK – somatic kineties, W – cyst wall. Scale bars: 20 μm (i), 50 μm (c), and 100 μm (h, j).

side of proboscis; one to two, rarely three intrakinetal excretory pores per vacuole (Figs 115h–j, m, 116g, n, 117a, c, d, i, 119j, m). Two types of basically rod-shaped extrusomes with slightly narrowed, rounded ends, studded in cytoplasm and right broader branch of proboscis oral bulge: type I inconspicuously curved causing a slight asymmetry, anterior end slightly more narrowed than posterior, 8–10 × 1–1.5 µm in size; type II oblong, 2–2.5 µm long (Figs 115a, f, 116g–l, n, r–t). Cortex flexible, conspicuous in vivo because distinctly separated from cytoplasm and about 2 µm thick; between each two kineties about four rows of ellipsoidal (~1 × 0.4 µm), colourless, ordinarily spaced granules recognizable also in some SEM micrographs (Figs 115a, d, e, 116m, 119g). Cytoplasm colourless, hyaline in proboscis and tail, opaque in trunk due to numerous granules ~ 0.4 µm across and 10–30 µm-sized food vacuoles containing whole scuticociliates, small colpodas, remnants of small rotifers, or loose material; in trunk end sometimes a defecation vacuole with crystalline material.

Cilia about 8 µm long in vivo, shrunken to ~ 6 µm in SEM preparations, narrowly spaced; arranged in



Figs 115o–u: *Pseudomonilicaryon fraterculum* nov. sp. after Chatton-Lwoff silver nitrate impregnation. Lateral (o–r) and ventral (s–u) views, showing variability of body shape and size as well as of the nuclear apparatus. CK – circumoral kinety, MA – macronucleus, MI – micronuclei, OB – oral bulge, OO – oral bulge opening, P – proboscis, PB – pharyngeal basket. Drawn to scale, bar 100 µm.

about 80 longitudinal, narrowly spaced rows frequently having irregularities, e.g., some rows shortened anteriorly or posteriorly, and/or with short breaks (Figs 115i, j, 117a, c, d, 119a, i; Table 59). Anterior end of ventral ciliary rows more densely ciliated and slightly curved rightwards abutting on circumoral kinety (Figs 115i, 117b–d). Most left side rows end slightly above level of oral bulge opening, producing a comparatively narrow blank stripe (Figs 115i, j asterisk). Ciliature of proboscis' right side with several remarkable specializations (Figs 115i, 117e, h, j, l): (i) at base of proboscis about seven right side ciliary

Table 59: Morphometric data on *Pseudomonilicaryon fraterculum* nov. sp. from North America. Data based, if not stated otherwise, on mounted, silver nitrate-impregnated (Corliss' variation of the Chatton-Lwoff technique), and randomly selected specimens from a semi-pure culture. Measurements in µm. CV – coefficient of variation in %, M – median, Max – maximum, Mean – arithmetic mean, Min – minimum, n – number of specimens investigated, SD – standard deviation, SE – standard error of mean.

Characteristics	Mean	M	SD	SE	CV	Min	Max	n
Body, length	535.9	546.0	72.1	15.7	13.4	407.0	652.0	21
Body, length (in vivo, rough values)	648.0	642.5	–	–	–	470.0	930.0	10
Body, width	63.8	62.0	6.7	1.5	10.6	54.0	78.0	21
Body, width (in vivo, rough values)	70.5	72.5	–	–	–	50.0	85.0	10
Body length:width, ratio	8.4	8.3	1.1	0.2	12.7	6.4	10.8	21
Body length:width, ratio (in vivo, rough values)	9.3	9.0	–	–	–	7.8	11.0	10
Anterior body end to oral bulge opening, distance[a]	294.7	304.0	59.2	12.9	20.1	208.0	406.0	21
Proboscis, % of body length	54.6	54.8	5.3	1.2	9.7	42.6	62.3	21
Oral bulge opening, length[b]	24.3	23.0	3.9	1.1	16.1	20.0	31.0	12
Oral bulge opening, width	30.0	30.0	2.9	0.7	9.7	24.0	35.0	15
Anterior body end to macronucleus, distance	323.1	335.0	59.2	12.9	18.3	224.0	420.0	21
Nuclear figure, length	124.3	117.0	27.1	5.9	21.8	97.0	191.0	21
Macronucleus, total length (uncoiled and thus approximate)	275.6	278.0	–	–	–	200.0	374.0	21
Anteriormost macronuclear nodule, length	10.1	10.0	3.5	0.8	34.6	5.0	16.0	21
Anteriormost macronuclear nodule, width	6.6	6.0	1.4	0.3	21.1	4.0	10.0	21
Posteriormost macronuclear nodule, length	10.9	11.0	3.7	0.8	33.9	6.0	19.0	21
Posteriormost macronuclear nodule, width	6.0	6.0	0.9	0.2	15.2	5.0	8.0	21
Macronuclear nodules, number	26.4	26.0	4.8	1.0	18.0	20.0	35.0	21
Micronuclei, largest diameter	2.6	2.5	–	–	–	2.5	3.0	21
Micronuclei, number	17.0	16.0	4.1	0.9	24.1	11.0	24.0	21
Ciliary rows, number	80.5	80.0	5.0	1.1	6.2	70.0	90.0	21
Cilia in mid-body in 10 µm, number	8.1	8.0	1.0	0.2	11.8	7.0	10.0	21
Groups of excretory pores in ventral side of trunk, number	13.4	12.0	4.3	1.6	31.8	8.0	20.0	7
Groups of excretory pores in dorsal side of trunk, number	17.9	17.0	4.0	1.4	22.5	13.0	24.0	8
Excretory pores per vacuole, number	1.8	2.0	–	–	–	1.0	2.0	21
Resting cysts, length (in vivo)	103.8	105.0	7.5	3.8	7.2	95.0	110.0	4
Resting cysts, width (in vivo)	72.5	75.0	9.6	4.8	13.2	60.0	80.0	4

[a] If proboscis curved, than "extended".

[b] Very likely as long as wide (see Fig. 119d), but optically shortened in ventrally oriented specimens.

rows, while only two subapically, indicating gradual shortening, (ii) first row right of perioral kinety with comparatively narrowly spaced basal bodies, but never as narrow as in perioral kinety, (iii) a narrow blank stripe right of oral bulge; and (iv) a special silverline pattern (see below). First row right of circumoral kinety extends as perioral kinety with narrowly spaced cilia to tip of proboscis. Dorsal brush on dorsal and dorsolateral region of proboscis; multi-rowed; staggered. Brush dikinetids ordinarily to loosely spaced, associated with tongue-shaped type IV bristles both being 2.5–3 μm long in vivo, shrunken to about 1.8–2.5 μm in SEM preparations (Figs 115b, n, 117f, k, 119h, k, j, k, m). The ventralmost brush rows commence with a monokinetidal tail of ordinary cilia, while the more dorsally located rows begin, as usual, with dikinetidal bristles (Fig. 119h). Posteriorly, all rows continue with a monokinetidal tail of 1–2 μm long (0.8–1.3 μm in SEM), oblong type VI bristles ending at level of oral bulge opening (Figs 119j–m).

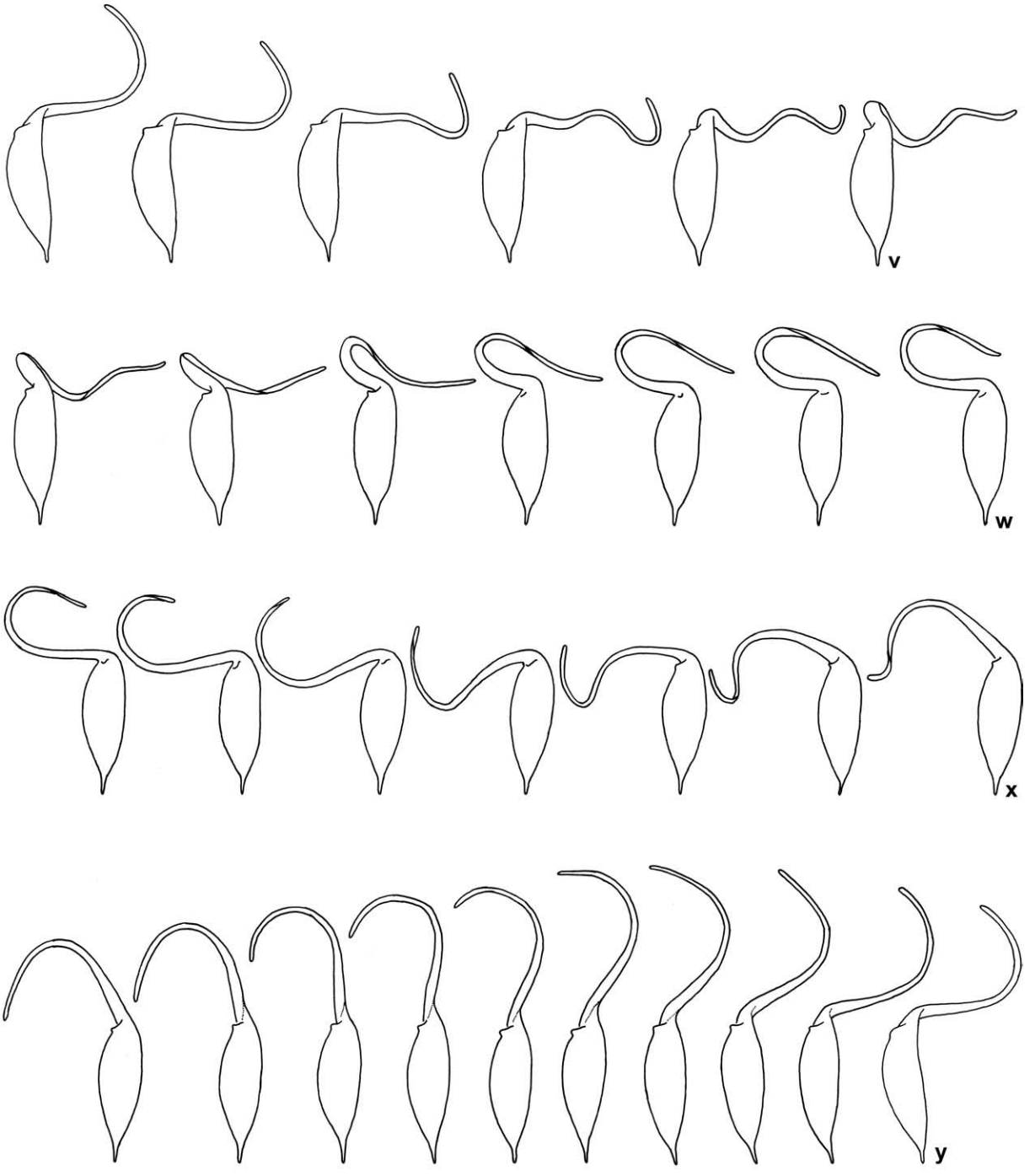
Silverline pattern narrowly and polygonally meshed, meshes 0.5–1 μm in size (Figs 115m, n, 117f, i, k); distinctly larger (2–2.5 μm) and quadrangular in right proximal half of proboscis, forming a platyophryid pattern (Foissner 1993) due to median silverlines dividing the meshes in mid (Figs 115k, l, 117g, h, j, l). Median silverlines gradually split into two to three anastomosing lines, producing the narrowly meshed pattern typical for the trunk (Fig. 117h).

Oral bulge opening slightly underneath second body half, projects distinctly because base of proboscis only half as wide as trunk, about 30 μm across both in vivo and in preparations, except for a single SEM specimen with an ovate bulge opening, possibly an artefact occurring also in other species (Figs 115a, h–j, 117a–e, 119c, d; Table 59). Pharyngeal basket obconical, distinct both in vivo and in preparations, about 50 μm long, without specific features. Oral bulge distinct in SEM micrographs due to the metachronal ciliary waves and extrusome tips in broader right branch (Figs 119b, d, e). Circumoral kinety composed of narrowly spaced dikinetids in proboscis and narrowly spaced monokinetids (possibly) around oral bulge opening (Fig. 115i). Preoral kineties narrowly to ordinarily spaced, slightly oblique; usually composed of three, rarely four or two narrowly spaced cilia each; separated by distinct ridges in SEM micrographs (Figs 115i, n, 116r, u, 119e, f).

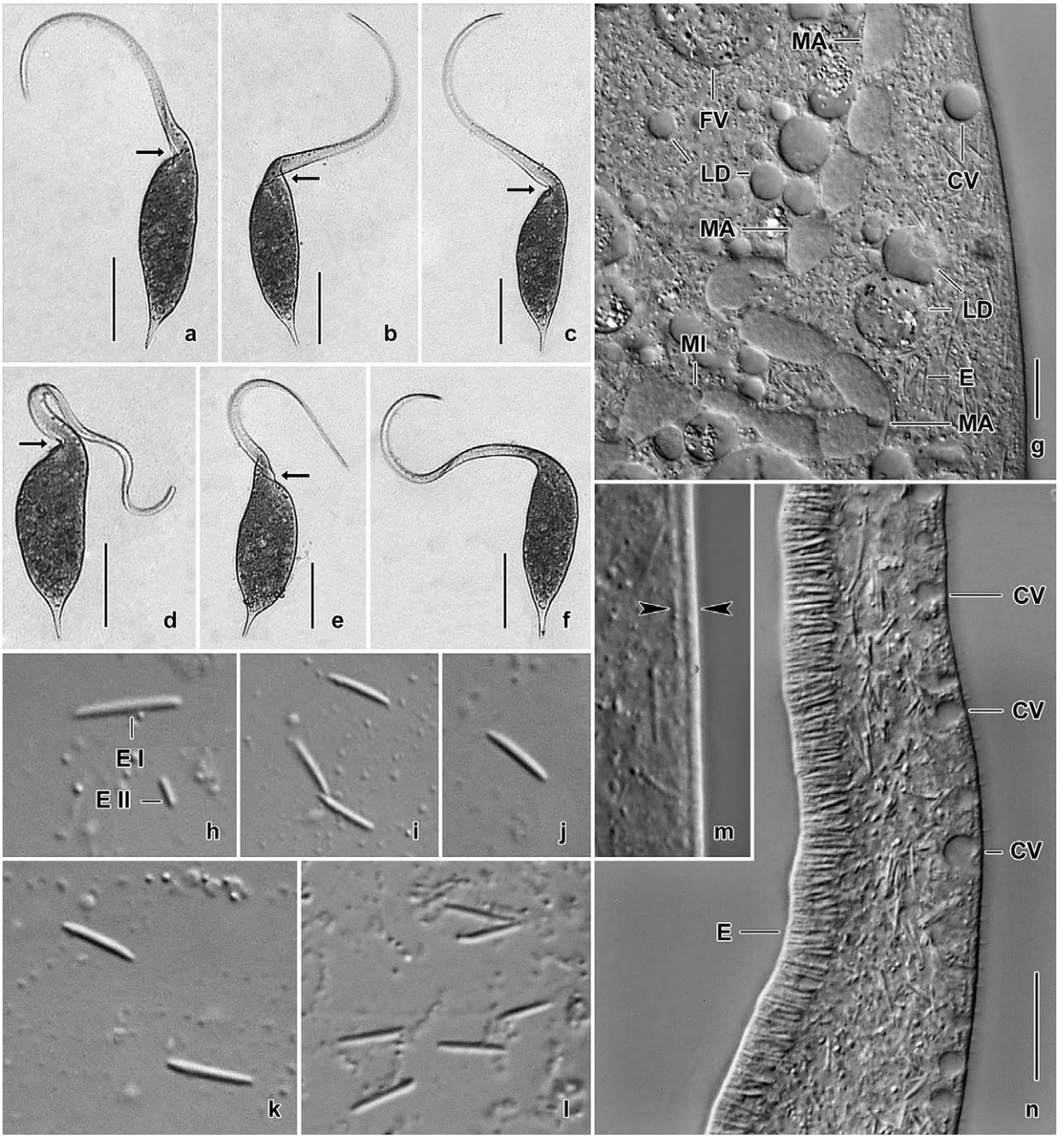
Movement and behaviour: *Pseudomonilicaryon fraterculum* is a bottom-dwelling, sluggish ciliate usually sitting in or slowly moving through masses of organic debris and vigorously probing with the proboscis. One probing cycle takes about four seconds and consists of four actions (Figs 115v–y): a dorsal stroke, a dorsal return stroke, a ventral stroke, and a ventral return stroke. During the dorsal stroke, the proboscis is behind the trunk, describing a semicircle when the tip of the proboscis reaches the level of the tail or a quarter-circle when the proboscis forms a right angle with the trunk. Then, the proboscis undulates, forming a sinusoid pattern (Fig. 115v). The dorsal return stroke follows the undulation immediately and the proboscis moves antero-ventrally in an arc-shaped pattern (Fig. 115w). The ventral stroke is performed in a similar way to the dorsal one but in front of the trunk, i.e., the tip of the proboscis reaches the level of the tail or the proboscis forms only a right angle with the trunk, and then commences undulation (Fig. 115x). Finally follows the ventral return stroke during which the proboscis moves in an antero-dorsal direction, forming an arc-shaped pattern (Fig. 115y). During probing, the cell slowly rotates about the main body axis. When disturbed, *P. fraterculum* twists but never contracts the proboscis (Figs 115r, s, 116p), swimming rapidly backwards rotating about the main body axis; however, soon slows down and sits on the slide again. Does not attach to the substrate by a mucous thread or tether.

Resting cyst (Figs 115c, 118a–g; Table 59): Encystment was induced by transferring a dozen specimens onto a microscope slide with a concave deepening containing centrifuged soil eluate. The preparation was stored in a moist chamber and checked every 24 h. Only four specimens encysted four days after setting up the preparation, while the others became very small and died.

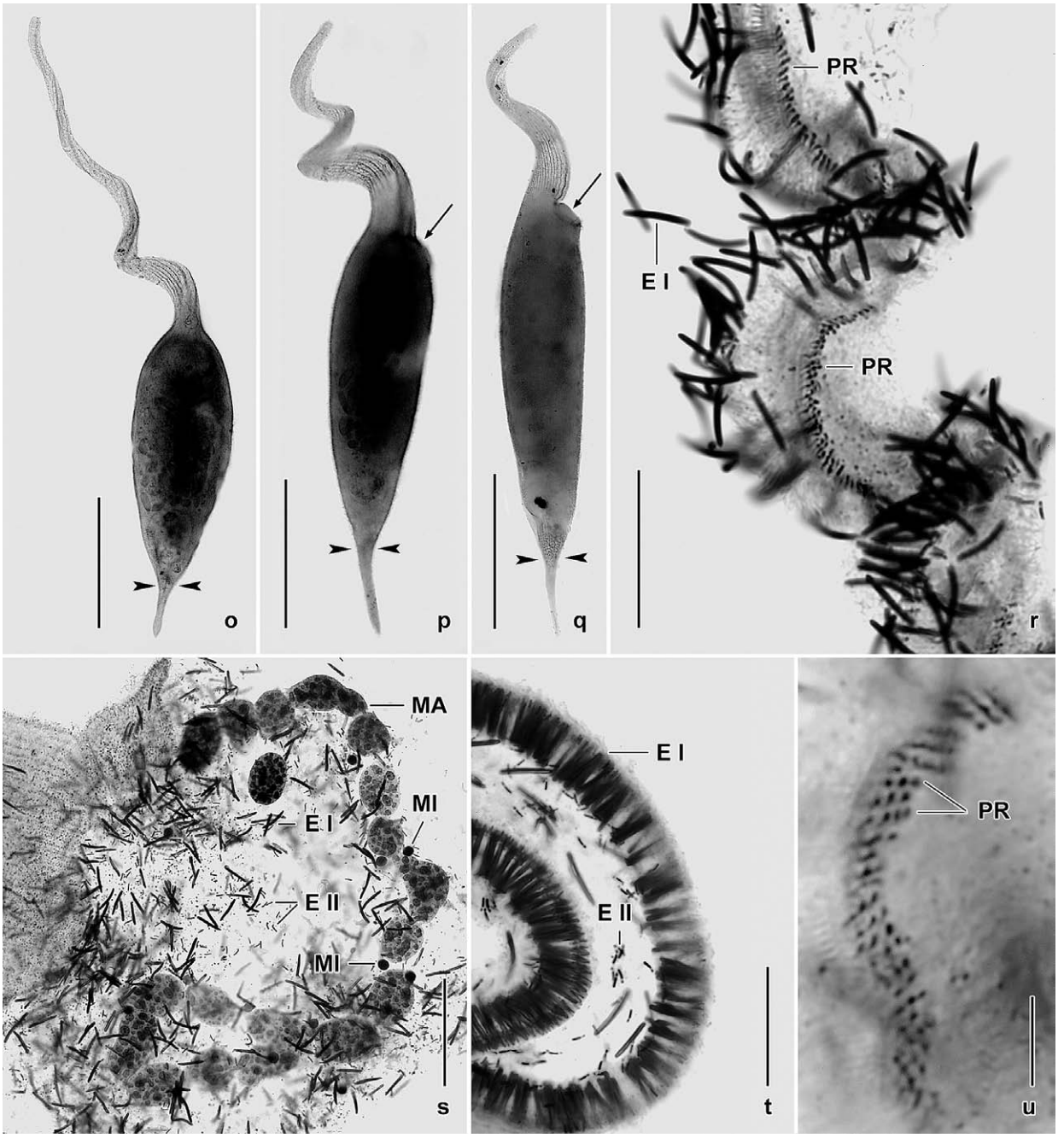
One week-old resting cysts 95–110 × 60–80 μm in size, on average 105 × 75 μm; broadly ellipsoidal with



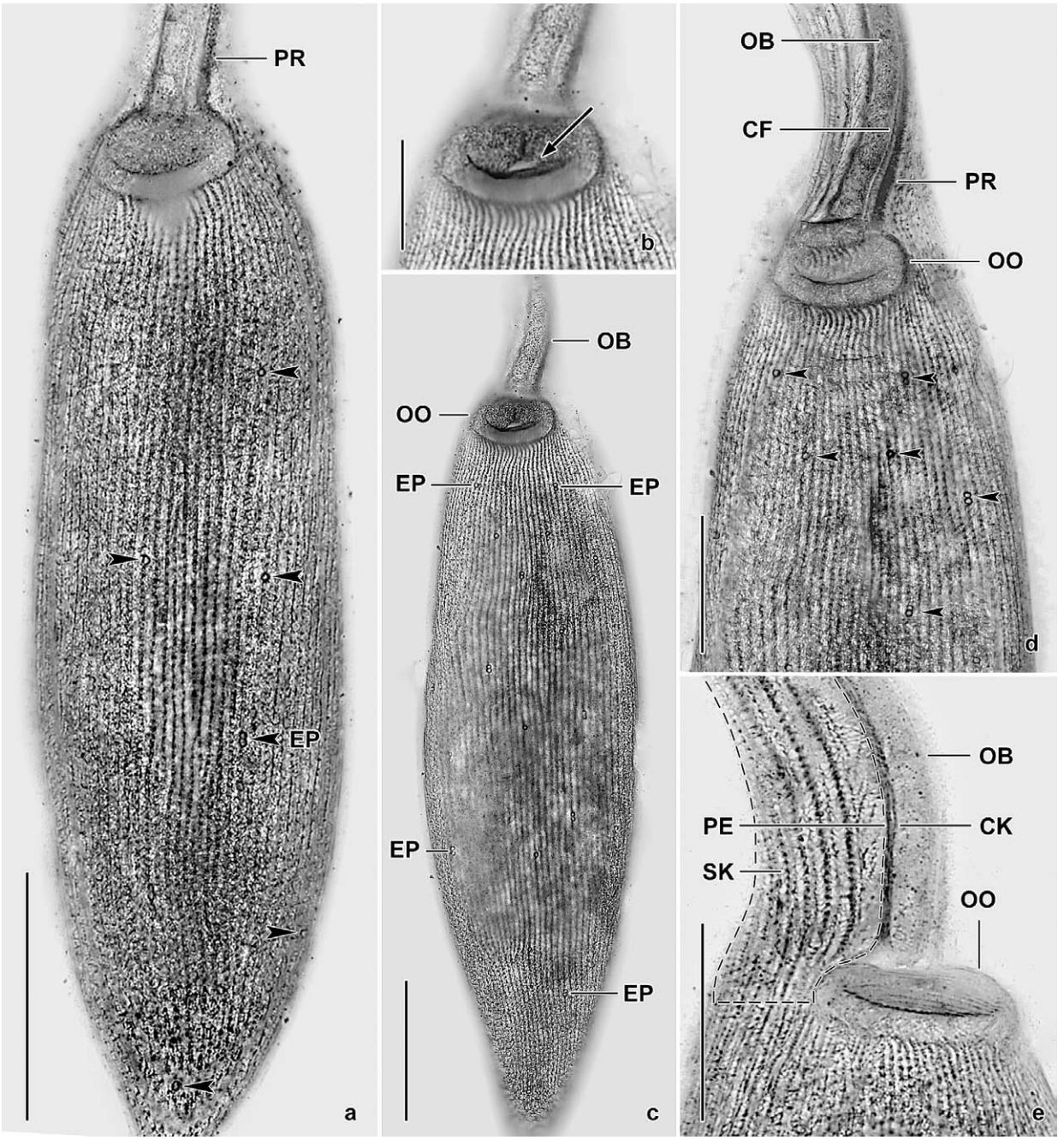
Figs 115v–y: *Pseudomonilicaryon fraterculum* nov. sp., probing cycle redrawn from video records. One probing cycle takes about four seconds and consists of four actions: a dorsal stroke, a dorsal return stroke, a ventral stroke, and a ventral return stroke. **v –** during the dorsal stroke, the tip of the proboscis is back of the trunk, describing a quarter-circle. Then the proboscis undulates, forming a sinusoid pattern; **w –** during the dorsal return stroke, the proboscis moves antero-ventrally in an arc-shaped pattern; **x –** the ventral stroke is performed in a similar way as the dorsal one but in front of the trunk, that is, the proboscis forms a right angle with the trunk and then waves; **y** – during the ventral retroaction, the proboscis moves in an antero-dorsal direction, forming an arc-shaped pattern.



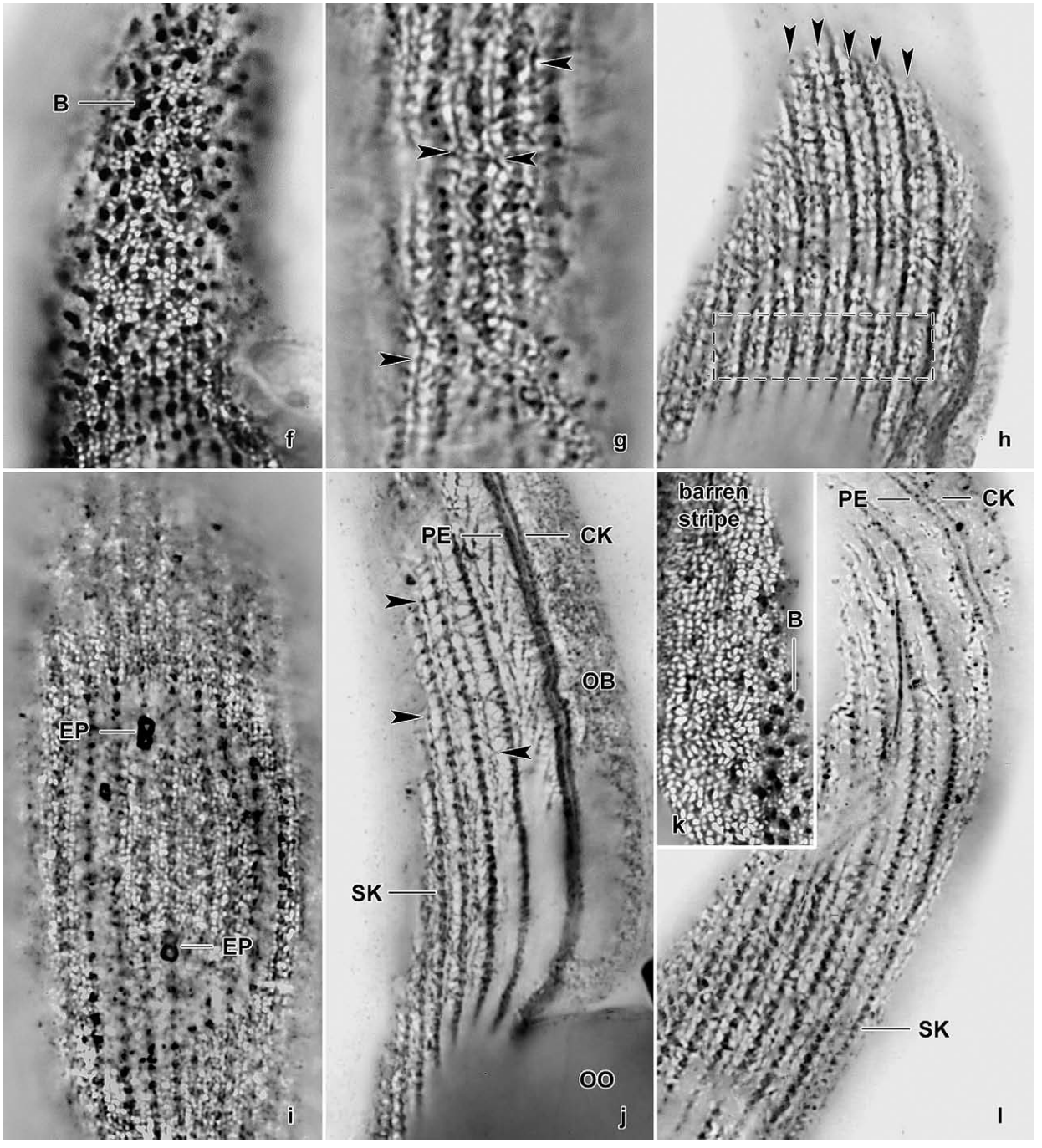
Figs 116a–n: *Pseudomonilicaryon fraterculum* nov. sp. from life. **a–f** – overviews of freely motile specimens, showing the very conspicuous proboscis occupying half or more of body length. This is an important feature shared only with *P. anser*. Arrows mark oral bulge opening; **g** – optical section showing some main cell organelles, such as macronuclear nodules forming a moniliform strand, micronuclei attached to the macronuclear nodules, developing extrusomes, lipid droplets, and food vacuoles; **h–l** – there are two types of extrusomes: type I is almost rod-shaped and slightly asymmetric with anterior end more distinctly narrowed than posterior (j), and has a size of 8–10 × 1–1.5 μm; the oblong type II is only 2 μm long (h); **m** – the cortex is distinctly separated from the cytoplasm and 1.5–2 μm thick (opposed arrowheads); **n** – lateral view of proboscis, showing some dorsal contractile vacuoles and the proboscis oral bulge studded with extrusomes. CV – contractile vacuoles, E(I, II) – extrusome (types), FV – food vacuoles, LD – lipid droplets, MA – macronuclear nodules, MI – micronucleus. Scale bars: 20 μm (g, n) and 100 μm (a–f).



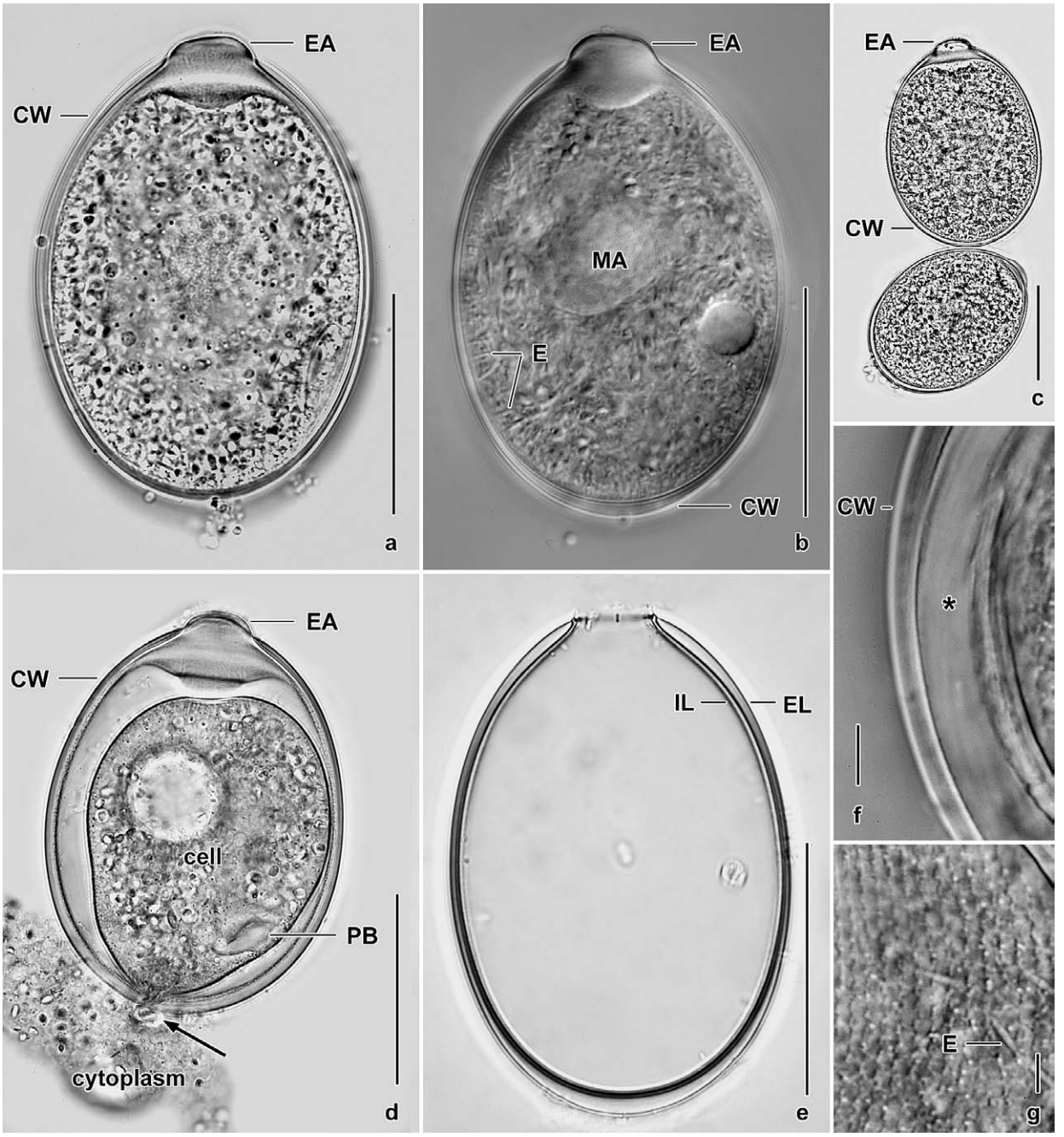
Figs 116o–u: *Pseudomonilicaryon fraterculum* nov. sp. after Chatton-Lwoff silver nitrate (o–q) and silver carbonate (r–u) impregnation. **o, p** – ventral and right side view, showing the very conspicuous proboscis and the distinct tail (opposed arrowheads). Arrow marks oral bulge opening; **q** – a late opisthe post-divider or a regenerating specimen, as indicated by the rather short proboscis. Arrow denotes the oral bulge opening, opposed arrowheads mark the distinct tail; **r, t**– there are two types of extrusomes in the proboscis: type I is basically rod-shaped with slightly narrowed, rounded ends and is 8–10 × 1–1.5 μm in size, while type II is oblong and about 2 μm long; **s** – the nuclear apparatus consists of several globular micronuclei attached to the moniliform macronuclear strand composed of about 20 nodules; **u** – in mid-portion of the proboscis, the preoral kineties are slightly oblique and composed of three to four cilia each. This is an important feature distinguishing *P. fraterculum* from the highly similar *P. anser*, whose preoral kineties are invariably composed of two cilia. EI, II – extrusome types, MA – macronuclear nodules, MI – micronuclei, PR – preoral kineties. Scale bars: 5 μm (u), 20 μm (r–t), and 100 μm (o–q).



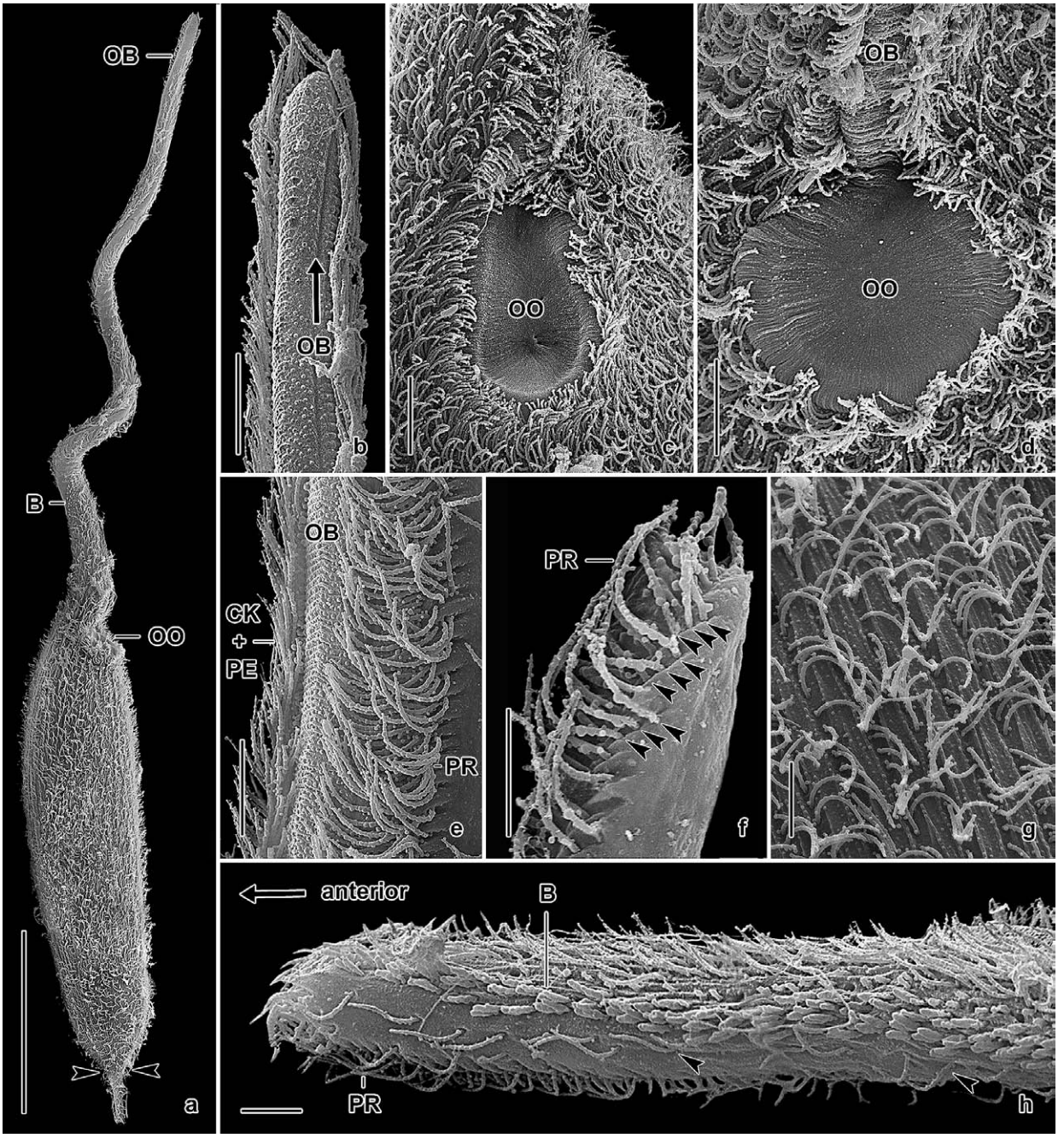
Figs 117a–e: *Pseudomonilicaryon fraterculum* nov. sp. after Chatton-Lwoff silver nitrate impregnation. **a, c, d** – ventral views of ciliary and contractile vacuole pattern (arrowheads). Note the large, roundish oral bulge opening and the central fibre separating the broader right from the narrower left branch of the proboscis oral bulge; **b** – the anterior end of the ventral ciliary rows is slightly curved rightwards abutting on the circumoral kinety. The arrow marks a central opening in the oral bulge; **e** – ciliary pattern of right side oral region. The right branch of the circumoral kinety is accompanied by a perioral kinety composed of densely spaced basal bodies. The first row right of the perioral kinety has comparatively narrowly spaced basal bodies, but never as narrow as in the perioral kinety, a rare feature found, for instance, in *P. japonicum* or *P. angustistoma*. The platyophryid portion of the silverline pattern is surrounded by a dashed line. Note the dish-like projecting oral bulge opening. CF – central fibre, CK – circumoral kinety, EP – excretory pores OB – oral bulge, OO – oral bulge opening, PE – perioral kinety, PR – preoral kineties, SK – somatic kinety. Scale bars: 20 µm (b), 30 µm (d, e), and 50 µm (a, c).



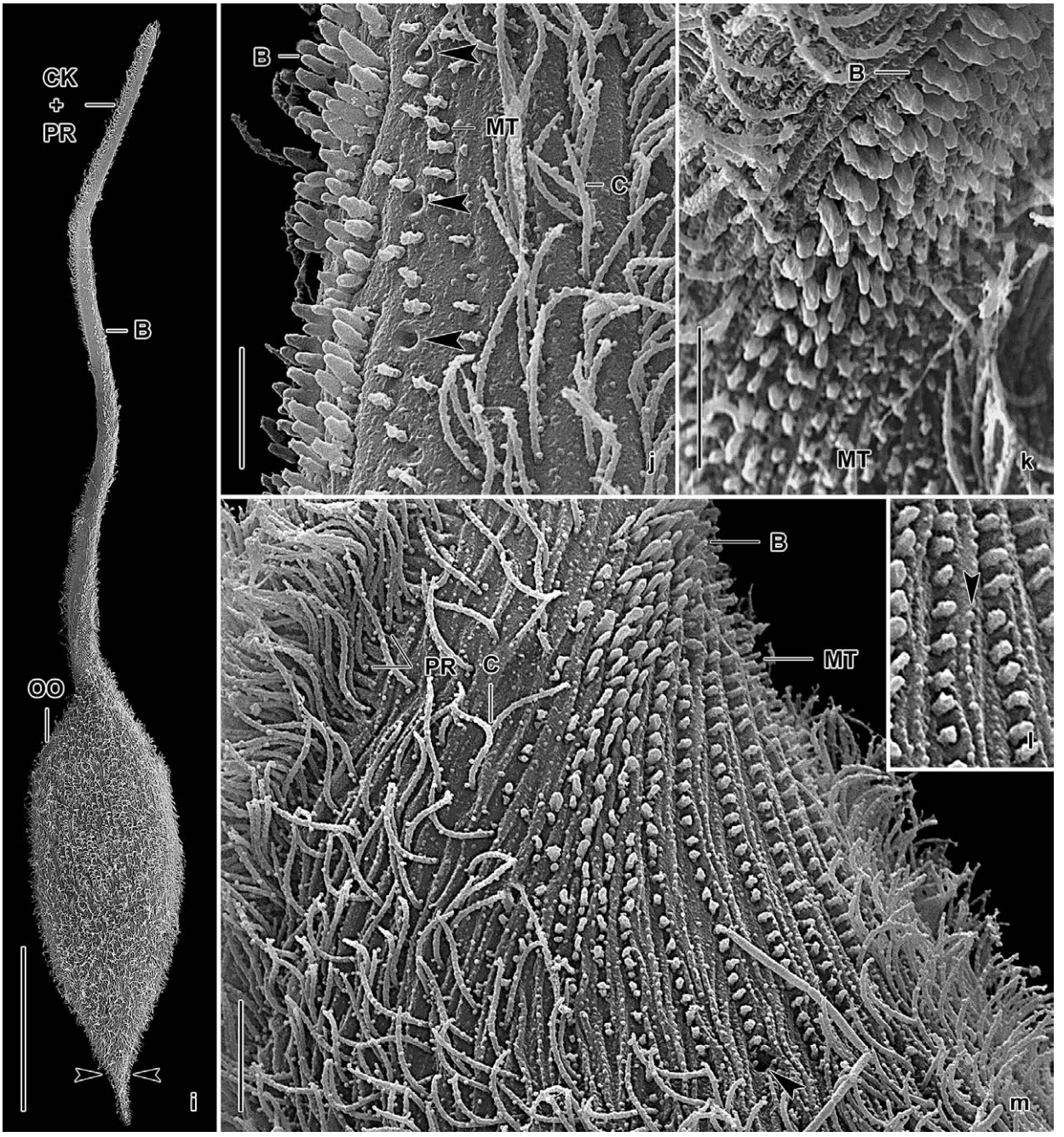
Figs 117f–l: *Pseudomonilicaryon fraterculum* nov. sp., silverline pattern after Chatton-Lwoff silver nitrate impregnation. **f** – dorsal view of proboscis showing the very narrowly-meshed silverline pattern and the staggered, multi-rowed dorsal brush; **g, j, l** – in the right side of the proximal proboscis area, there is a platyophryid silverline pattern with 2–2.5 µm large meshes between two kineties each. The meshes are divided by a median silverline (arrowheads); **h** – at the base of the proboscis' right side, each median silverline (arrowheads) gradually splits into two to three anastomosing lines (surrounded by a dashed line), producing the narrowly-meshed silverline pattern extending in the trunk cortex; **i** – the trunk has a very narrowly-meshed silverline pattern. Note the intrakinetal excretory pores; **k** – on the left side of the proboscis, there is a wide blank stripe with minute (0.5–1 µm), polygonal silverline meshes. B – dorsal brush, CK – circumoral kinety, EP – excretory pores, OB – oral bulge, OO – oral bulge opening, PE – perioral kinety, SK – somatic kineties.



Figs 118a–g: *Pseudomonilicaryon fraterculum* nov. sp., resting cysts from life in bright field (a, c, d, e) and interference contrast (b, f, g). **a–c** – the resting cysts are broadly ellipsoidal and have an average size of 105 × 75 µm. In the anterior pole area, there is a conspicuous escape apparatus, which is colourless, compact, about 20 µm in size, and very likely produced by the middle wall layer. The macronuclear nodules fuse to an ellipsoidal, central mass, and extrusomes become attached to the somatic cortex (b); **d** – when the cyst is pressed by the coverslip, the wall does not open at the escape apparatus but in the posterior pole area (arrow); **e** – an empty cyst, showing the colourless, up to 4 µm thick outer layer; the light brown, compact, 2 µm thick middle layer; and the membranous inner layer; **f** – in this cyst, the specimen is smaller than the wall, leaving an empty space (asterisk) between wall and cell; **g** – surface view showing the narrowly arranged ciliary rows and some underlying extrusomes. CW – cyst wall, E – extrusomes, EA – escape apparatus, EL – outer cyst layer, IL – inner cyst layer, MA – macrocnucleus, PB – pharyngeal basket. Scale bars: 5 µm (f, g) and 50 µm (a–e).



Figs 119a–h: *Pseudomonilicaryon fraterculum* nov. sp. in the SEM. **a** – right side overview showing the slightly helical proboscis, which occupies about 56% of body length, length 630 µm. Opposed arrowheads mark the distinct tail; **b, e** – the oral bulge is dotted by the extrusome tips and transversely striated by fibre bundles, very likely transverse microtubule ribbons. The circumoral and preoral cilia are narrowly spaced, producing metachronal waves (e). The arrow in (b) marks the furrow (central fibre) separating the broader right from the narrower left branch of the oral bulge; **c, d** – usually, the oral bulge opening is circular (d), rarely ovate (c), possibly due to some preparation artefacts; **f** – anterior end of proboscis, showing that the preoral kineties are separated by distinct ridges and usually consist of three cilia (arrowheads); **g** – surface view showing cilia and the rather distinctly furrowed cortex studded with granules; **h** – dorsal view of anterior end of proboscis, showing the dorsal brush. The right brush rows commence with a monokinetidal tail of ordinary cilia (arrowheads), while the left rows begin, as usual, with dikinetidal bristles. B – dorsal brush, CK – circumoral kinety, OB – oral bulge, OO – oral bulge opening, PE – perioral kinety, PR – preoral kineties. Scale bars: 5 µm (e–h), 10 µm (b–d), and 100 µm (a).



Figs 119i–m: *Pseudomonilicaryon fraterculum* nov. sp. in the SEM. **i** – dorsolateral overview showing the proboscis about twice as long as trunk, the most characteristic feature of *P. fraterculum* and *P. anser*, length 700 µm. Opposed arrowheads mark the short but distinct tail; **j**, **k, m** – dorsal and dorsolateral view of proboscis, showing the staggered, multi-rowed dorsal brush. The brush dikinetids are associated with about 2 µm long, tongue-shaped bristles slightly wrinkled due to the preparation procedures. All brush rows continue with a monokinetidal tail extending to the base of the proboscis with 0.8–1.3 µm long, oblong bristles. Arrowheads mark intrakinetal excretory pores of contractile vacuoles; **l** – detail of posterior brush portion of the specimen shown in (m). The monokinetidal tail bristles extend in distinct furrows to the base of the proboscis. Note also the tips of the cortical granules (arrowhead) in the ridges between the brush tails. B – dorsal brush, C – ordinary somatic cilia, CK – circumoral kinety, OO – oral bulge opening, MT – monokinetidal tails of dorsal brush, PR – preoral kineties. Scale bars: 5 µm (j, k, m) and 100 µm (i).

a length:width ratio of 1.4–1.5:1 (Table 59). Cyst wall structureless, light brown, 2–3 μm thick, increasing to 3–4 μm in cysts slightly squashed by the coverslip (Figs 118a–d, f). Wall tripartite in empty cysts from an old culture (Figs 115c arrow, 118e): outer layer colourless, 3–4 μm thick; middle layer light brown, 2–3 μm thick; inner layer membranous and colourless. Escape apparatus as a conspicuous convexity (plug) in anterior pole area, colourless, compact, and about 20 μm in size, likely produced by middle wall layer (Figs 115c, 118a–d); lacking in empty cysts, showing that cells left cysts this way (Fig. 118e); cannot be removed by mechanical pressure, causing breaks in posterior wall area (Fig. 118d arrow). Pharyngeal basket possibly preserved as an oblong, bright, 30 μm long structure opposed to escape apparatus (Figs 115c, 118d). Cyst contents partitioned into a thin peripheral layer of refractive, about 0.3 μm-sized granules and a large central area packed with 2–4 μm-sized globules (autophagous vacuoles?) not dissolving in water when cyst contents is squeezed out (Figs 115c, 118a). Macronuclear nodules fused to an ellipsoidal, central mass 23–50 × 22–35 μm in size; many small nucleoli (Fig. 118b). Numerous 5 μm long extrusomes scattered throughout cytoplasm and attached to cell cortex (Figs 118b, g). Cilia maintained, arranged in meridional rows, start beating when cyst is slightly pressed by the coverslip (Fig. 108g).

Occurrence and ecology: As yet found only at type locality, that is, in a mixture of cyanobacterial crusts, dead grass clippings and the 0–3 cm upper soil layer from a grass lawn in Idaho, USA. During the late spring and summer months, the lawn is flood-irrigated once every week by a canal system connecting with the Boise River. The water is absorbed over three to four days. The ephemeral puddles remaining just prior to complete absorption/evaporation are rich in cyanobacteria which form crusts during the fall and winter months when the lawn is not irrigated. The sample was collected on July 18, 2007 by Dr. William Bourland (Boise State University, Idaho, USA).

Remarks: Within congeners, *P. fraterculum* resembles only *P. anser*, in having a highly motile proboscis occupying half or more of body length. Both species are very similar, inter alia, in body shape and size, the nuclear apparatus, and several morphometric features. However, *P. fraterculum* has a different contractile vacuole pattern (vacuoles scattered in trunk and dorsal side of proboscis vs. only dorsal vacuoles in proboscis and trunk), a higher number of ciliary rows (70–90 vs. 50–70), and a higher number of basal bodies comprising the preoral kineties (usually 3 vs. invariably 2). The higher number of macronuclear nodules (20–34 vs. 12–25) and micronuclei (11–24 vs. 6–13) emphasize the distinctness of the North American population. Finally, *P. fraterculum* must be compared with *Phragelliorhynchus nasutus*, a poorly described North American organism also having a long proboscis. However, *Ph. nasutus* is much smaller (200 μm vs. 600 μm), thus conspecificity can be excluded.

Pseudomonilicaryon dimorphum (Wang, 1940) nov. comb. (Figs 120a–i)

1940 *Dileptus dimorphus* sp. nov. Wang, Sinensia **11**: 18

1963 *Dileptus dimorphus* Wang, 1940 – Dragesco, Bull. biol. Fr. Belg. **97**: 115 (first taxonomic reviser)

Generic affiliation and taxonomy: Jankowski (1967) did not combine *Dileptus dimorphus* with one of his subgenera. Indeed, the generic home of this species remains doubtful because its oral ciliature is not known. We suggest to combine *D. dimorphus* with *Pseudomonilicaryon* because of the moniliform macronucleus. Full redescription is required.

Pseudomonilicaryon dimorphum is similar to only two other species, viz., *P. aculeatum* and *P. edaphoni*, which also have the macronucleus composed of only four serially arranged nodules. However, *P. dimorphum* differs from these and all other dileptids, except for *Rimaleptus lacazei* and *Monomacrocaryon tenue*, in being highly contractile (vs. not contractile). This peculiarity was carefully studied and illustrated by Wang

(1940) and confirmed by Dragesco (1963) in a French population. *Rimaleptus lacazei* is distinguished from *P. dimorphum* by the number of macronuclear nodules (two vs. four) and the habitat (marine vs. freshwater). *Monomacrocaryon tenue* differs from *Pseudomonilicaryon dimorphum* in being much smaller (60–110 µm vs. 260–390 µm) and having only two dorsal contractile vacuoles (vs. a dorsal row of at least five vacuoles).

Improved diagnosis: Length about 315 × 50 µm in vivo, contracts slowly to less than 200 µm. Shape narrowly to very narrowly dileptid with long, spine-like tail, proboscis about 1/3 of body length. Macronucleus moniliform, composed of 4 oblong nodules; 4 globular micronuclei. A dorsal row of contractile vacuoles. About 16 ciliary rows.

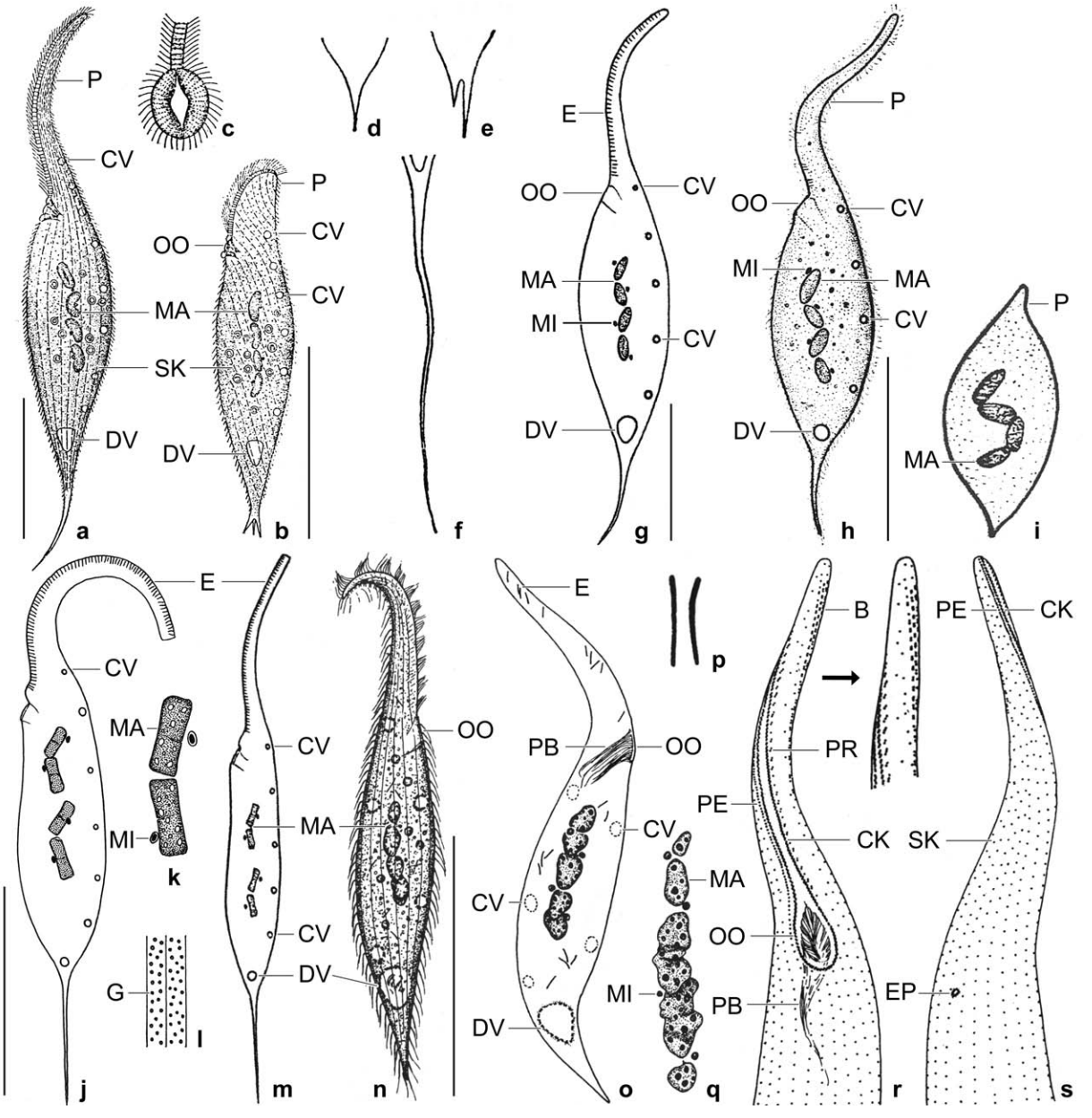
Type locality: Pond in the Campus of the Bible Institute, Nanyoh, Hunan, Japan, E139°258' N36°10'.

Type material: Not available.

Etymology: Not given in original description. Composite of the Greek numeral *di* (two) and the Greek noun *morphe* (form, shape), obviously referring to the two shapes (extended and contracted) the species may assume.

Description: Size in extended Japanese specimens 260–390 × 35–60 µm (Wang 1940) and about 300 µm in French individuals (Dragesco 1963); highly flexible and contractile to less than 200 µm; both contraction and extension occur slowly. Shape of extended specimens narrowly to very narrowly dileptid with a length:width ratio of about 5.5–7:1, according to the figures provided (Figs 120a, g, h). Proboscis about one third of body length, 90 µm long according to Wang (1940), slender and thus distinctly set off from broad trunk, usually curved dorsally, in contracted cells shortened to a triangular, massive lip (Figs 120a, b, g–i). Trunk fusiform, widest in mid-portion, more or less flattened, only slightly broadened in contracted specimens. Tail conspicuous because up to 100 µm long; without cilia in type population, while ciliated in French specimens; in fully contracted specimens a bi- or rarely trifurcated stump, attaching cells to water plants (Figs 120a, b, d–i). Nuclear apparatus in middle quarters of trunk. Macronucleus a moniliform, almost straight strand composed of four nodules; individual nodules about 18 × 11 µm in size, oblong in dorsal and ventral view, reniform when viewed laterally in Japanese specimens; only 4 µm across and lenticular according to Dragesco (1963), but about 18 × 9 µm when calculated from his illustrations. Invariably four micronuclei, usually one each in a concavity of macronuclear nodules or in between two nodules, 4 µm across in Japanese specimens (Figs 120a, b, g–i). A stripe of 7–11 contractile vacuoles in dorsal side of trunk, first vacuole near level of oral bulge opening (Figs 120a, b, g, h). Shape and size of extrusomes not known, form two rows in oral bulge of proboscis (Wang 1940). Cytoplasm brownish in Japanese cells, while orange in French specimens, possibly due to algal food; proboscis and tail hyaline, trunk opaque due to many food vacuoles and lipid droplets; in posterior end of trunk sometimes a defecation vacuole. About 16 longitudinal ciliary rows (Wang 1940) becoming helical in contracted cells (cp. Fig. 120a with 120b). Oral bulge opening at beginning of second body third, projects ordinarily, roundish with broadly fusiform opening (Fig. 120c). Pharyngeal basket obconical, short. Swims by rotation about main body axis, using the tail as a rudder (Wang 1940).

Occurrence and ecology: *Pseudomonilicaryon dimorphum* was discovered by Wang (1940) among water plants of a small pond in the Campus of the Bible Institute, Nanyoh, Hunan, Japan. Great numbers occurred during October and November, 1937. Dragesco (1963) found it in July, 1961 in fine sand from the Excenevex beach, Lake Léman, France. Both populations fed on algae.



Figs 120a–i: *Pseudomonilicaryon dimorphum* from life. From WANG 1940 (a–f) and DRAGESCO 1963 (g–i). **a, g, h** – left side view of extended specimens; **b, d, e, i** – left side view (b, i) and rear end (d, e) of contracted specimens; **c** – frontal view showing the oral bulge opening; **f** – very long tail of a fully extended specimen.

Figs 120j–m: *Pseudomonilicaryon aculeatum* from life (j, l, m) and after acetic methyl green stain (k). From DRAGESCO 1960 (j–l) and DRAGESCO 1963 (m). **j, m** – left side view of representative specimens; **k** – part of nuclear apparatus showing two macronuclear nodules, each with a micronucleus attached; **l** – surface view showing cortical granules.

Figs 120n–s: *Pseudomonilicaryon edaphoni* from life (n) and after protargol impregnation (o–s). From SONG (1994b). **n, o** – left side views showing general organization; **p** – extrusomes are 5 µm long rods; **q** – nuclear apparatus of an "abnormal" specimen; **r, s** – ventral and dorsal view of ciliary pattern in anterior body portion. The oral ciliary pattern is dileptid, i.e., the right branch of the circumoral kinety is accompanied by a perioral kinety, while the left branch is associated with many oblique preoral kineties. B – dorsal brush, CK – circumoral kinety, CV – contractile vacuoles, DV – defecation vacuole, E – extrusomes, MA – macronucleus, MI – micronuclei, OO – oral bulge opening, P – proboscis, PB – pharyngeal basket, PE – perioral kinety, PR – preoral kineties. Scale bars 100 µm.

Pseudomonilicaryon aculeatum (Dragesco, 1960) nov. comb. (Figs 120j–m)

1960 *Dileptus aculeatus* n. sp. Dragesco, Trav. Stn biol. Roscoff (N. S.) **12**: 188

1963 *Dileptus aculeatus* Dragesco, 1960 – Dragesco, Bull. biol. Fr. Belg. **97**: 118 (first taxonomic reviser)

Generic affiliation and taxonomy: Jankowski (1967) did not assign *Dileptus aculeatus* to one of his subgenera. Indeed, the generic home of this species remains doubtful because its oral ciliature is not known. We suggest to combine *D. aculeatus* with *Pseudomonilicaryon* because of the moniliform macronucleus. Full redescription is required.

There are only two similar species, viz., *P. dimorphum* and *P. edaphoni.* The former is highly contractile (vs. not contractile), the latter lacks a tail (vs. a very prominent tail) and has a different contractile vacuole pattern (ventral and dorsal vacuoles vs. only dorsal). The main features of *P. aculeatum*, i.e., the spiny tail and the curious nuclear apparatus, were checked in many specimens to exclude post-divisional and post-conjugational processes (Dragesco 1960).

Improved diagnosis: Length about 300 µm in vivo. Shape very narrowly to cylindroidally dileptid with long, spine-like tail, proboscis about 1/3 of body length. Nuclear apparatus composed of 4 oblong nodules in 2 groups and 4 ellipsoidal micronuclei. A dorsal row of contractile vacuoles.

Type locality: Lake Léman, Thonon region, France, E6°21' N46°21'.

Type material: Not available.

Etymology: The Latin adjective *aculeatus* (spiny) refers to the spine-like tail of the species.

Description: Length about 300 µm in vivo; flexible but not contractile. Shape very narrowly to cylindroidally dileptid, that is, length:width ratio 8–11:1, according to the figures provided. Proboscis about one third of body length, distinctly set off from oblong trunk; tail conspicuous because spine-like and occupying one fifth to one fourth of body length (Figs 120j, m). Nuclear apparatus in middle quarters of trunk or in anterior three quarters of trunk. Macronucleus constantly composed of four oblong nodules, forming two zigzagging groups. Invariably four ellipsoidal micronuclei attached to macronuclear nodules, micronuclei surrounded by a distinct membrane in methyl green stains (Figs 120j, k, m). A stripe of five to six contractile vacuoles in dorsal side of trunk. Cortex with yellow brown granules, forming about three rows between each two kineties (Fig. 120l). Extrusomes, oral apparatus, and ciliature not described.

Occurrence and ecology: As yet found at type locality, that is, in fine sand from the shore of the Excenevex beach, Lake Léman, France; in the interstice and pelagial of the Caspian Sea (Agamaliev 1969, 1971, 1974; Petran 1977; Alekperov & Aliev 1996) and on its islands (Agamaliev 1972); and in the upper 4 cm of the ground of the west coast of the Caspian Sea (Agamaliev 1970).

Pseudomonilicaryon edaphoni (Song, 1994) nov. comb. (Figs 120n–s)

1994 *Dileptus edaphoni* sp. nov. Song, Acta zootax. sin. **19**: 388

Generic affiliation and taxonomy: We combine *Dileptus edaphoni* with *Pseudomonilicaryon* because it has a *Dileptus*-like ciliary pattern and a moniliform macronucleus. *Pseudomonilicaryon edaphoni* belongs to the small group of dileptids with four macronuclear nodules, but is easily identified by the lack of a tail and the contractile vacuole pattern (ventral and dorsal vacuoles vs. only dorsal ones). However, a solid redescription is necessary because details of the extrusomes and dorsal brush are lacking, and most morphometrics are based on four specimens only.

Diagnosis: Size about 240 × 35 µm in vivo. Shape very narrowly dileptid with acute posterior third, proboscis about 1/3 of body length. Macronucleus moniliform, composed of 4–5 globular nodules; 4 globular micronuclei. Extrusomes 5 µm long, curved rods. Usually 3 dorsal and 2 ventral contractile

vacuoles with 1 pore each. On average 22 ciliary rows, three anteriorly differentiated into a dorsal brush. Oral bulge opening ovate. Preoral kineties ordinarily spaced, strongly oblique, each usually composed of 2 narrowly spaced cilia.

Type locality: Soil from the surroundings of the town of Qingdao, China, E120°43' N36°8'.

Type material: Deposition not mentioned in the original paper (Song 1994b) but Prof. W. Song usually deposits type material in the College of Fisheries, Ocean University of Qingdao, China.

Etymology: Composite of the Greek substantive *edaphon* (soil biota) and the inflectional ending *i*, referring to the habitat of the species.

Description: Size 180–300 × 30–40 μm in vivo; very flexible but not contractile. Shape very narrowly dileptid with a length:width ratio of about 6–7:1, according to the figures. Proboscis one third of body length, anterior fifth usually curved dorsally; trunk fusiform and unflattened; posterior third acute (Figs 120n, o). Nuclear apparatus in middle quarters of trunk. Macronucleus a moniliform strand composed of four to five nodules (possibly seven in Fig. 120q); individual nodules 7–11 × 2–3 μm in size after protargol impregnation; many small, globular nucleoli. Four micronuclei attached to macronuclear strand, 2–3 μm across in protargol preparations (Figs 120n, o, q). Usually three dorsal and two ventral contractile vacuoles in trunk, each vacuole with a single excretory pore (Figs 120n, o, s). Extrusomes not studied in vivo, 5 μm long and slightly curved in protargol preparations, attached to oral bulge and scattered throughout cytoplasm (Figs 120o, p). Cytoplasm colourless, trunk opaque because packed with lipid droplets and food vacuoles, proboscis and rear body end hyaline; sometimes a subterminal defecation vacuole.

Cilia ordinarily spaced, arranged in 21–23 longitudinal, ordinarily spaced rows. Right side rows shortened only near anterior end of oral bulge; perioral kinety extends to tip of proboscis with narrowly spaced basal bodies (Fig. 120s). Blank stripe on left side of proboscis rather narrow because one or two kineties extend almost to tip of proboscis (Fig. 120r). Dorsal brush on dorsal side of proboscis, probably three-rowed (not studied in detail and possibly too much schematized), remarkable because each row begins with a monokinetidal tail of two to three basal bodies (Fig. 120r).

Oral bulge opening at beginning of second body third, ovate, hardly projecting (Figs 120n, r). Pharyngeal basket obconical, well recognizable in protargol preparations (Figs 120o, r). Oral ciliary pattern dileptid, i.e., left branch of circumoral kinety associated with many ordinarily spaced, strongly oblique preoral kineties each composed of one to three, usually two narrowly spaced cilia (Fig. 120r).

Occurrence and ecology: As yet found only at type locality, that is, in the 0–2 cm upper soil layer in the surroundings of the town of Qingdao, China.

Pseudomonilicaryon falciforme (Kahl, 1931) nov. comb. (Figs 121a–y, 122a–m; Table 60)

1931 *Dileptus falciformis* spec. n. Kahl, Tierwelt Dtl. **21**: 208

1963 *Dileptus falciformis* Kahl, 1931 – Dragesco, Bull. biol. Fr. Belg. **97**: 116 (first taxonomic reviser)

non *Dileptus falciformis* Dumas, 1930, Les Microzoaires: 89 (see insufficiently described dileptids)

non *Dileptus falciformis* Kahl, 1932 – Alekperov, 2005, Atlas svobodnoživuŝih infuzorij: 70 (misidentification, see insufficiently described dileptids)

Nomenclature, generic affiliation and taxonomy: *Dileptus falciformis* Dumas, 1930 is a senior primary homonym of *D. falciformis* Kahl, 1931 which we, however, assign to *Pseudomonilicaryon* because it has a *Dileptus*-like oral ciliary pattern and a moniliform macronucleus. Thus, according to Article 23.9.5 of the ICZN (1999) Kahl's name must not be replaced. Moreover, *Dileptus falciformis* Dumas, 1930 is considered a nomen dubium because of the insufficient description and the lack of original material.

KAHL (1931) established *D. falciformis* with the peculiar arrangement of the extrusomes, both in the proboscis oral bulge and in the oral bulge opening, while most dileptids have extrusomes only in the bulge of the proboscis. DRAGESCO (1963) recognized KAHL's species but, unfortunately, omitted this important feature.

In Austria and Hawaii, we found populations matching *D. falciformis* in most important features, such as body shape and size, the nuclear apparatus and, especially, the peculiar extrusome pattern. The arrangement of the contractile vacuoles is, however, different: KAHL's specimens have only dorsal vacuoles, while the Austrian and Hawaiian cells show both, ventral and dorsal vacuoles. Nevertheless, it appears reasonable to emphasize the matching features and to identify both populations as *D. falciformis*, especially because the ventral vacuoles are sparse and thus possibly easily overlooked. On the other hand, the differences are too pronounced for a neotypification at the present state of knowledge.

The Austrian and Hawaiian specimens differ in body width (on average 66 µm vs. 45 µm), the length:width ratio (4 vs. 7:1), and the number of ciliary rows (45 vs. 35). While some difference in the first two features is very likely caused by the preparation procedures and culture conditions, the kinety number is considerably (22%) lower in the Hawaiian specimens, suggesting some biogeographic specialization.

Within dileptids with moniliform macronucleus, *D. falciformis* is outstanding in having (i) extrusomes anchored both in the proboscis oral bulge and in the oral bulge opening and (ii) an anterior tail in the ventralmost rows of the dorsal brush. The first feature occurs only in two other dileptids, viz., in the multinucleate *D. costaricanus* and in the binucleate *Rimaleptus canadensis*. The second feature occurs only in two congeners: *P. edaphoni* and *P. fraterculum*. However, *P. edaphoni* has only four (vs. more than ten) macronuclear nodules and 22 (vs. 40) ciliary rows, and *P. fraterculum* has a much larger body (600 µm vs. 350 µm) with very long (vs. ordinary) proboscis.

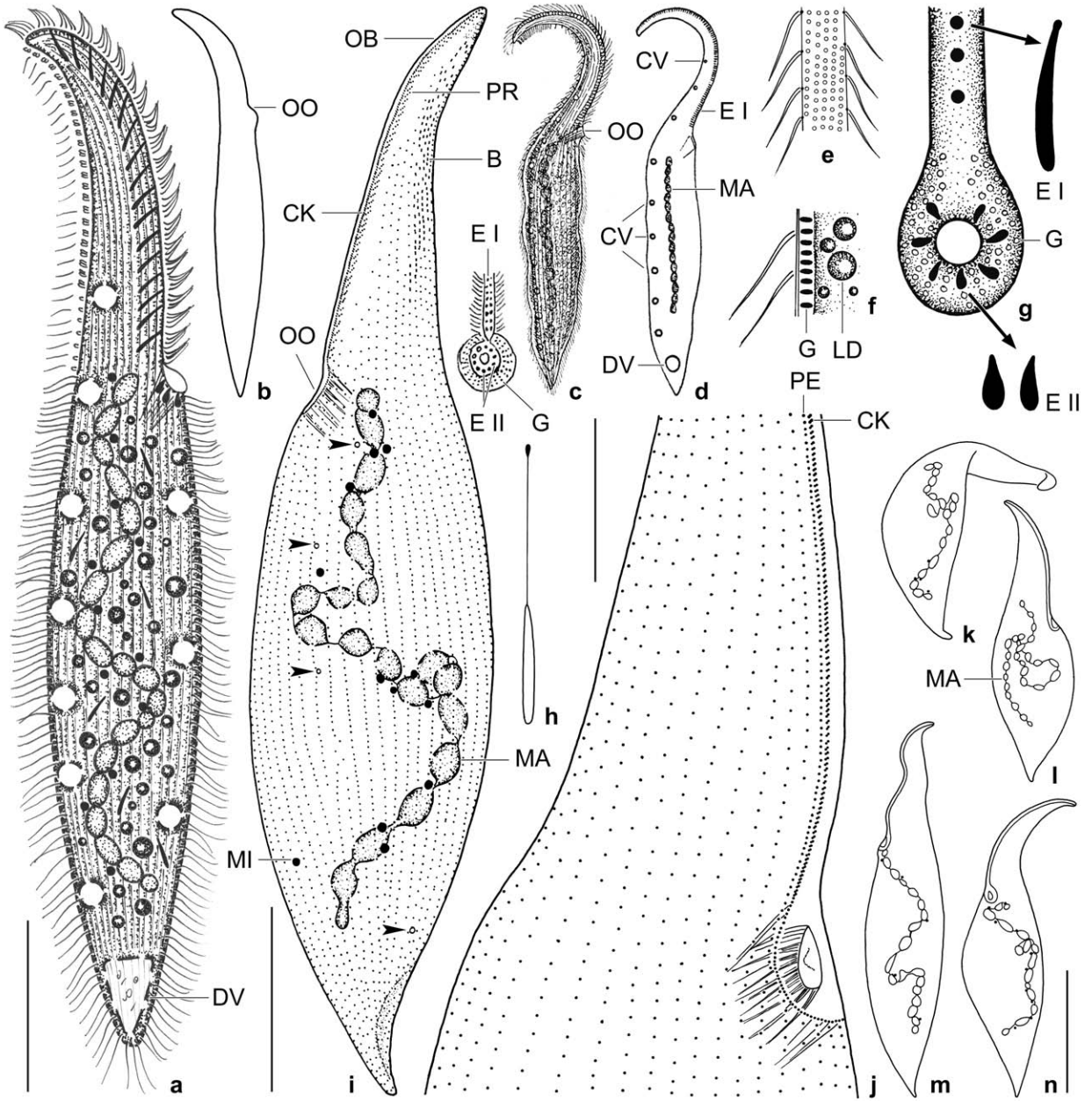
Improved diagnosis (includes all information known): Size about 350 × 50 µm in vivo. Shape narrowly to cylindroidally dileptid with acute posterior end, proboscis about 1/3 of body length. Macronucleus moniliform, usually composed of about 20 globular to oblong nodules; several globular micronuclei. A dorsal and a ventral stripe of contractile vacuoles with 1 pore each. Two types of extrusomes: type I attached to proboscis oral bulge, very narrowly ovate, slightly curved, about 7 × 0.8 µm in size; type II forms a ring in oral bulge opening, ovate and almost straight, about 1.5–2 × 1 µm in size. On average 40 ciliary rows, up to 12 anteriorly differentiated into a multi-rowed, staggered, distinctly heterostichad dorsal brush with monokinetidal tails extending anteriorly and posteriorly. Oral bulge opening about 14 µm across. On average 51 ordinarily to widely spaced, strongly oblique preoral kineties, each usually composed of 3 narrowly spaced cilia.

Type locality: Moss on limestones from the surroundings of the town of Berchtesgaden, Bavaria, Germany, E12°58' N47°37'.

Type and voucher material: No type material is available from KAHL's specimens. Two voucher slides (inv. nos 2011/185 and 2011/186) with Austrian protargol-impregnated specimens and eight protargol voucher slides (inv. nos 2011/187–194) with Hawaiian specimens have been deposited in the Biology Centre of the Museum of Upper Austria, Linz (LI). Relevant specimens are marked by black ink circles on the coverslip.

Etymology: Not given in original description. Composite of the Latin noun *falx* (sickle) and the suffix *form* (shaped), obviously referring to the sickle-like (falciform) curved proboscis.

Description: Size usually about 350 × 50 µm in vivo; German type specimens 300–450 µm long, Austrian cells 270–370 × 40–70 µm in size, and Hawaiian individuals 280–500 × 35–70 µm; very flexible but not contractile. Shape in vivo narrowly to cylindroidally dileptid, that is, length:width ratio about 7:1 in



Figs 121a–n: *Pseudomonilicaryon falciforme*, German type (c, d) and Austrian voucher (a, b, e–n; all original) specimens from life (a–h) and after protargol impregnation (i–n). **a** – right side view of a representative specimen, length 300 µm. Note the ventral and dorsal stripe of contractile vacuoles; **b** – right side view of a shape variant; **c** – frontal view of oral bulge opening, showing the arrangement of the extrusomes, and right side view of German type specimen, length 450 µm (from KAHL 1931); **d** – from DRAGESCO (1963), very likely redrawn from KAHL (1931); **e, f** – surface view and optical section showing the cortical granules; **g** – frontal view of oral bulge opening and arrangement of the extrusomes. Type I extrusomes are very narrowly ovate, slightly curved, 7 × 0.8 µm in size, and attached to the proboscis oral bulge. Type II extrusomes are ovate, almost straight, about 1.5–2 × 1 µm in size, and form a conspicuous ring in the oral bulge opening; **h** – exploded type I extrusome, 15 µm long; **i** – left side ciliary pattern and nuclear apparatus of main voucher specimen, length 304 µm. Arrowheads denote excretory pores of contractile vacuoles; **j** – right side ciliary pattern in oral region; **k–n** – variability of body shape and size as well as of nuclear apparatus. Drawn to scale. B – dorsal brush, CK – circumoral kinety, CV – contractile vacuoles, DV – defecation vacuole, EI, II – extrusome types, G – cortical granules, LD – lipid droplet, MA – macronucleus, MI – micronucleus, OB – oral bulge, OO – oral bulge opening, PE – perioral kinety, PR – preoral kineties. Scale bars: 20 µm (j), 50 µm (a, i), and 100 µm (k–n).

German specimens (according to the KAHL's figure, reproduced here as Fig. 121c), 5.5–10:1 in Hawaiian cells, and 5–8.7:1 in Austrian individuals, which are moderately inflated in the protargol preparations (Table 60). Proboscis about one third of body length, leaf-like flattened, slender, sickle-like curved dorsally in type specimen, while stout and only slightly curved dorsally in Austrian and Hawaiian cells; trunk oblong to bluntly fusiform, slightly fold in type specimen; posterior third acute (Figs 121a–d, i, k–n, t–y). Nuclear apparatus in anterior five sixth of trunk. Macronucleus moniliform, conspicuous in vivo, straight in type specimen, while slightly to strongly tortuous in Austrian and Hawaiian cells; number of nodules fairly similar in all populations: 10–20 in German specimens, 15–25 in Austrian individuals, and 18–31 in Hawaiian cells; individual nodules globular to narrowly ellipsoidal, highly variable in size, i.e., 4–16 × 4–8 µm, impregnate deeply and homogenously. On average 11 micronuclei attached to macronuclear nodules, about 2.5 µm across in prepared specimens and thus small compared to cell size (Figs 121a, c, d, i, k–n, t–y, 122a, c; Table 60). A dorsal stripe of contractile vacuoles in type specimen (Fig. 121c), while a dorsal and ventral stripe both in Austrian and Hawaiian cells, ventral vacuoles less numerous than dorsal ones; first dorsal vacuole in proximal half or third of proboscis; each vacuole with a single, intrakinetal excretory pore about 2 µm across (Figs 121a, i). Two types of extrusomes not impregnating with protargol: type I rather sparse, obliquely attached with thin end to both bulge branches in type and Hawaiian specimens, while forming a single row in Austrian cells, very narrowly ovate with minute globular dome, slightly curved, and about 7 × 0.8 µm in size; when exploded with typical toxicyst structure, viz., about 15 µm long and with a refractive granule at distal end of tube emerging from the empty capsule (Fig. 121h); type II forms a conspicuous ring in oral bulge opening, ovate and almost straight, about 1.5–2 × 1 µm in size (Figs 121a, c, g, o, 122d–h). Cortex flexible, about 1.5 µm thick and distinctly separated from cytoplasm, contains about five oblique granule rows between each two kineties; granules narrowly spaced in somatic and oral bulge cortex, 1 × 0.5 µm in size (Figs 121e, f). Cytoplasm colourless, hyaline in proboscis, opaque and brownish in trunk due to numerous lipid droplets 1–5 µm across; in posterior end of trunk sometimes a defecation vacuole with sparse contents.

Cilia about 8 µm long in vivo, narrowly spaced; in protargol preparations as typical for dileptids, i.e., with thick, strongly impregnated distal half, except for dorsal bristles; arranged in an average of 45 longitudinal, narrowly spaced rows in Austrian cells and in 35 rows in Hawaiian specimens; frequently with irregularities, e.g., some rows shortened anteriorly or posteriorly, and/or with short breaks (Fig. 121i; Table 60). Right side ciliary rows shortened only near anterior end of oral bulge; cilia of perioral kinety ordinarily spaced (Figs 121j, r, 122b). Blank stripe on left side of proboscis distinct, although most ciliary rows extend to or above proximal half of proboscis (Figs 121i, p, q, 122l, m). Dorsal brush extends on dorsal and left side of proboscis; staggered; distinctly heterostichad; composed of up to twelve rows with loosely to ordinarily spaced dikinetids associated in Hawaiian specimens with 2.5 µm long, inflated, curved type I bristles becoming rod-shaped in protargol preparations; frequently with small irregularities, such as breaks or some extra dikinetids forming short additional rows. Some ventralmost brush rows commence in distal proboscis half with a monokinetidal tail of one to ten ordinary cilia, while the more dorsally located rows begin, as usual, with dikinetidal bristles. Posteriorly, all rows continue with a monokinetidal tail of 1 µm long, oblong type VI bristles ending at level of oral opening (Figs 121i, p, q, s, 122i, k, m).

Oral bulge opening at end of anterior body third; hardly projecting in type and Hawaiian specimens, while ordinarily projecting in Austrian cells; small as compared to body size, i.e., about 14 µm across in protargol preparations and thus occupying less than 5% of body length (Figs 121a, b, c, g, o, 122a; Table 60). Pharyngeal basket difficult to recognize both in vivo and in protargol preparations because composed of very fine and faintly impregnated rods (Figs 121i, j). Circumoral kinety composed of ordinarily spaced dikinetids, except for narrowly spaced monokinetids around oral bulge opening (Fig. 121j). On average

51 ordinarily to widely spaced preoral kineties each composed of two to five, usually three narrowly spaced kinetids, forming oblique to strongly oblique rows occasionally almost in line with left branch of circumoral kinety (Figs 121i, p, q, 122j, l, m).

Occurrence and ecology: *Pseudomonilicaryon falciforme* was discovered by KAHL (1931) in moss on limestones from the surroundings of the town of Berchtesgaden, Bavaria, Germany. Further, it was found in moss from the Erlangen area, also in Bavaria, by WENZEL (1953); very rare in soil from an oak-hornbeam forest on the Johannser Kogel in the surroundings of the town of Vienna (see FOISSNER et al. 2005 for detailed site description); and in a mixture of soil, mud, and dry leaf litter from flat lava rockpools in a temporary river of the Pu'uhonua O Honau Nau area, Hawaii. WANG (1977) reported it from the Tibetan Plateau, and YANG (1989) found it during winter in freshwaters of the Yuelushan area, China.

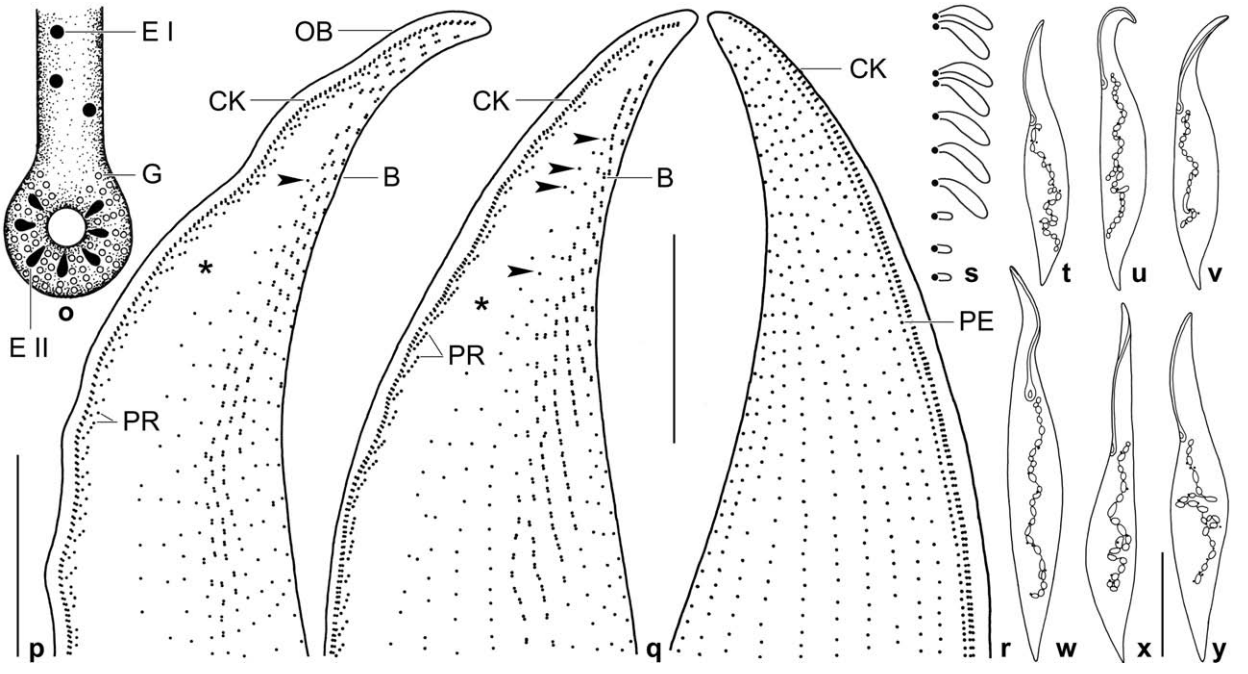
Pseudomonilicaryon gracile (KAHL, 1931) FOISSNER, 1997

1931 *Dileptus gracilis* spec. n. KAHL, Tierwelt Dtl. **21**: 209

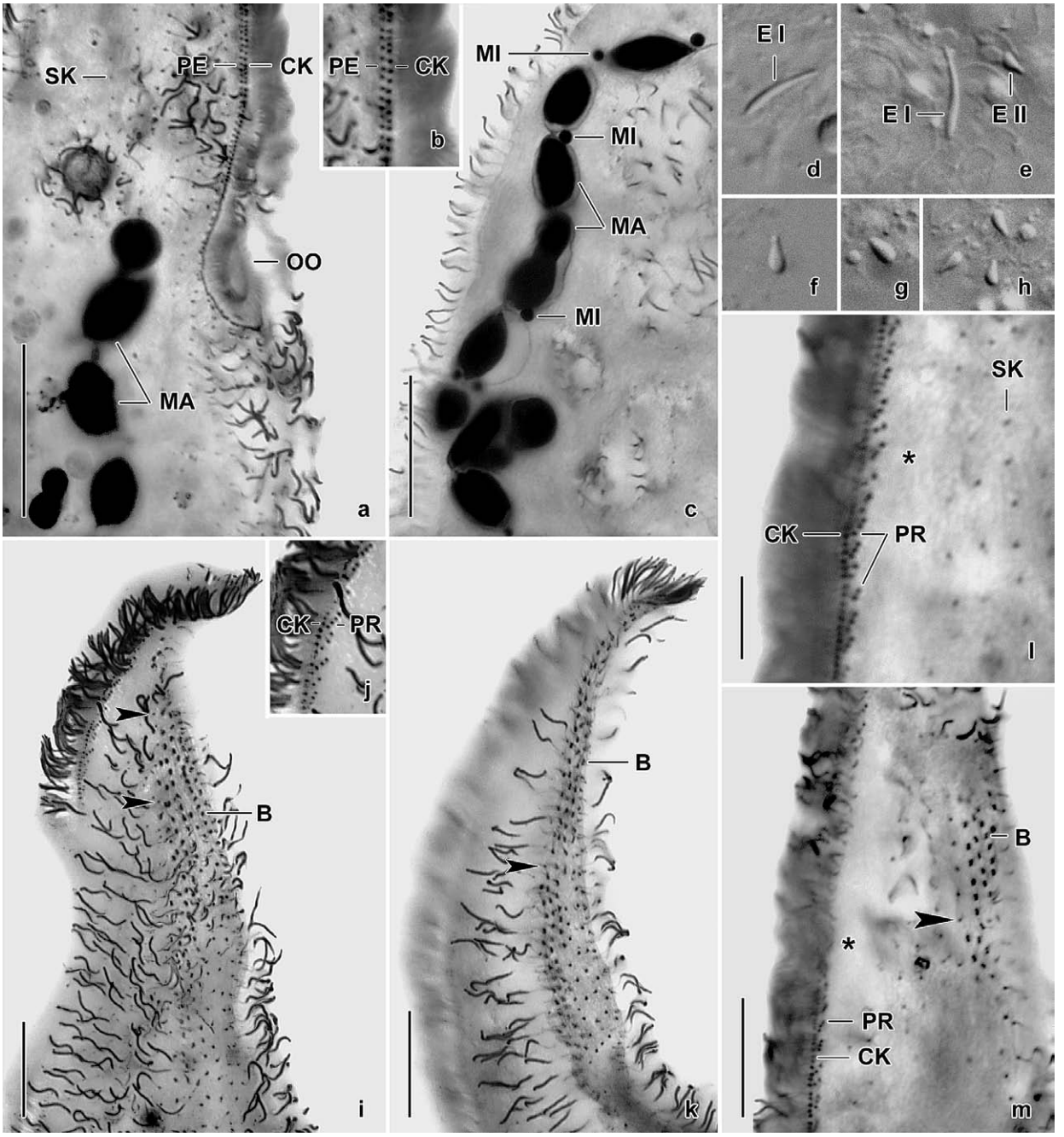
1989 *Dileptus gracilis* KAHL, 1931 – FOISSNER, Sber. Akad. Wiss. Wien **196**: 182 (neotypification)

1997 *Pseudomonilicaryon gracilis* nov. comb. – FOISSNER, Limnologica **27**: 196 (type species of genus, combining author)

2001 *Pseudomonilicaryon gracile* – AESCHT, Denisia **23**: 157 (mandatory change of species epithet ending)



Figs 121o–y: *Pseudomonilicaryon falciforme*, Austrian (p–r) and Hawaiian (o, s–y) voucher specimens from life (o, s) and after protargol impregnation (p–r, t–y). **o** – frontal view of oral bulge opening and arrangement of the extrusomes; **p, q** – left side views of proboscis' ciliary pattern. Arrowheads denote the anterior monokinetidal tail of some ventralmost brush rows, while the asterisks mark the blank stripe left of the oral bulge; **r** – right side view of proboscis' ciliary pattern; **s** –in the anterior region of the dorsal brush, the bristles are paired, curved backwards, inflated, and 2.5 µm long, while the bristles are monokinetidal, oblong, and only 1 µm long in the posterior portion; **t–y** – variability of body shape and size as well as of nuclear apparatus. Drawn to scale. B – dorsal brush, CK – circumoral kinety, EI, II – extrusome types, G – cortical granules, OB – oral bulge, PE – perioral kinety, PR – preoral kineties. Scale bars: 20 µm (p–r) and 100 µm (t–y).



Figs 122a–m: *Pseudomonilicaryon falciforme*, Austrian specimens from life (d–h) and after protargol impregnation (a–c, i–m). **a** – ciliary pattern in oral region; b – the perioral kinety extends in parallel with the circumoral kinety; c – the nuclear apparatus consists of a moniliform macronuclear strand and several globular micronuclei; **d–h** – there are two types of oral bulge extrusomes: type I is very narrowly ovate, slightly curved, and about 7 × 0.8 µm in size, while type II is ovate, almost straight, and about 1.5–2 × 1 µm in size; **i, k, m** – dorsolateral views of proboscis' ciliary pattern, showing the staggered, multi-rowed dorsal brush and the deeply impregnated distal half of the cilia. Some brush rows commence with a monokinetidal tail of ordinary cilia (arrowheads). The asterisk denotes the blank stripe on the left side of the proboscis; **j, l** – left side views, showing the preoral kineties which are composed of two to four, usually three narrowly spaced kinetids, forming oblique to strongly oblique rows. The asterisk marks the blank stripe between the somatic and oral ciliary pattern. B – dorsal brush, CK – circumoral kinety, EI, II – extrusome types, MA– macronuclear nodules, MI – micronuclei, OO – oral bulge opening, PE – perioral kinety, PR – preoral kineties, SK – somatic kineties. Scale bars: 10 µm (l) and 20 µm (a, c, i, k, m).

Table 60. Morphometric data on *Pseudomonilicaryon falciforme* from Austria (A) and Hawaii (H). Data based on mounted, protargol-impregnated (Foissner's method) specimens from non-flooded Petri dish cultures. Only five specimens were found in the slides from the Austrian site. Measurements in µm. CV – coefficient of variation in %, M – median, Max – maximum, Mean – arithmetic mean, Min – minimum, n – number of specimens investigated, Pop – population, SD – standard deviation, SE – standard error of mean.

Characteristics	Pop	Mean	M	SD	SE	CV	Min	Max	n
Body, length	A	272.6	269.0	39.0	17.4	14.3	234.0	320.0	5
	H	310.9	292.0	54.1	14.0	17.4	246.0	443.0	15
Body, width	A	66.0	67.0	2.3	1.0	3.6	62.0	68.0	5
	H	44.9	43.0	8.2	2.1	18.2	30.0	61.0	15
Body length:width, ratio	A	4.1	4.0	0.6	0.3	13.7	3.4	4.8	5
	H	7.0	6.9	1.2	0.3	17.3	5.4	9.9	15
Anterior body end to oral bulge opening, distance	A	95.8	96.0	8.8	4.0	9.2	87.0	110.0	5
	H	98.4	95.5	15.8	4.2	16.0	78.0	132.0	14
Proboscis, % of body length	A	35.4	36.2	3.2	1.4	9.0	30.0	38.1	5
	H	32.1	33.1	4.1	1.1	12.7	21.9	37.3	14
Oral bulge opening, length	A	14.6	14.0	1.9	0.9	13.4	12.0	17.0	5
	H	12.9	12.0	1.7	0.5	13.0	11.0	16.0	14
Anterior body end to macronucleus, distance	A	101.6	108.0	12.7	5.7	12.5	83.0	112.0	5
	H	107.2	107.0	16.1	4.1	15.0	82.0	139.0	15
Nuclear figure, length	A	126.8	116.0	22.2	9.9	17.5	104.0	154.0	5
	H	148.7	140.0	39.2	10.1	26.4	108.0	263.0	15
Macronucleus, total length (uncoiled and thus approximate)	A	204.8	197.0	–	–	–	172.0	246.0	5
	H	187.8	192.0	–	–	–	134.0	270.0	15
Anteriormost macronuclear nodule, length	A	6.6	6.0	1.3	0.6	20.3	5.0	8.0	5
	H	5.9	6.0	1.5	0.4	24.8	4.0	9.0	15
Anteriormost macronuclear nodule, width	A	6.0	6.0	1.2	0.5	20.4	5.0	8.0	5
	H	5.1	5.0	1.0	0.2	19.0	4.0	7.0	15
Tenth macronuclear nodule, length	A	12.4	12.0	2.2	1.0	17.7	10.0	16.0	5
	H	10.0	10.0	2.1	0.5	21.0	6.0	14.0	15
Tenth macronuclear nodule, width	A	6.8	6.0	1.1	0.5	16.1	6.0	8.0	5
	H	5.9	6.0	0.7	0.2	12.7	5.0	8.0	15
Posteriormost macronuclear nodule, length	A	7.0	6.0	2.0	0.9	28.6	5.0	10.0	5
	H	9.2	8.0	4.2	1.1	45.4	4.0	20.0	15
Posteriormost macronuclear nodule, width	A	5.8	6.0	0.8	0.4	14.4	5.0	7.0	5
	H	5.7	6.0	0.7	0.2	12.8	4.0	6.0	15
Macronuclear nodules, number	A	19.4	19.0	3.6	1.6	18.4	15.0	25.0	5
	H	22.7	22.0	3.2	0.8	14.0	18.0	31.0	15
Micronuclei, largest diameter	A	2.4	2.5	–	–	–	2.0	2.5	5
	H	2.5	2.5	–	–	–	2.0	2.5	15

Characteristics	Pop	Mean	M	SD	SE	CV	Min	Max	n
Micronuclei, number	A	10.4	11.0	2.2	1.0	21.1	7.0	13.0	5
	H	11.7	12.0	2.5	0.7	21.7	7.0	15.0	15
Ciliary rows, number	A	45.4	45.0	2.1	0.9	4.6	43.0	48.0	5
	H	34.9	36.0	3.2	0.8	9.1	30.0	40.0	15
Cilia in mid-body in 10 μm, number	A	8.2	8.0	0.8	0.4	10.2	7.0	9.0	5
	H	6.7	6.0	1.0	0.3	14.6	6.0	9.0	15
Preoral kineties, number	A	51.0	52.0	4.2	2.1	8.3	45.0	55.0	4
Anterior body end to last dorsal brush dikinetid, distance	A	70.8	70.0	11.0	4.9	15.5	60.0	86.0	5
	H	79.8	86.0	13.2	4.4	16.6	66.0	98.0	9
Dorsal brush rows, number	A	10.4	10.0	1.1	0.5	11.0	9.0	12.0	5
	H	8.4	8.0	1.2	0.4	14.2	7.0	10.0	8
Dorsal brush, % of body length	A	26.0	26.0	1.5	0.7	5.9	24.1	28.3	5
	H	25.4	24.4	3.4	1.1	13.3	20.1	32.0	9

Nomenclature and taxonomy: FOISSNER (1989) neotypified *P. gracile* with a Bavarian population without providing the reasons. However, we support neotypification because (i) no type material is available from KAHL's (1931) specimens, (ii) the identidy of the species is threatened by several similar species, such as *P. anguillula*, (iii) the neotype is from a similar habitat, and (iv) the protargol preparations are of sufficient quality. The neotype is here classified as a distinct subspecies (*P. gracile antevacuolatum*). This might pose nomenclatural problems in future, especially when *P. gracile antevacuolatum* is a distinct species; then, it would be a misidentified neotype. If further research shows that the location of the anterior contractile vacuole is variable, then *P. gracile antevacuolatum* merges into *P. gracile* and can be used as a neotype.

We split this species into four subspecies, according to the shape of the rear body end (rounded in *P. gracile gracile*, *P. gracile antevacuolatum* and *P. gracile oviplites*, acute to tail-like in *P. gracile singulare*), the shape of the extrusomes (rod-like in *P. gracile antevacuolatum*, very narrowly ovate in *P. gracile oviplites*), and the location of the anterior contractile vacuole (far underneath oral bulge opening in *P. gracile gracile* and *P. gracile singulare*, at level of oral bulge opening in *P. gracile antevacuolatum* and *P. gracile oviplites*). Two groups can be recognized: (i) *P. gracile gracile* and *P. gracile singulare* with the anterior vacuole far underneath the oral bulge opening, ≤ 10 ciliary rows, and short to ordinary proboscis and (ii) *P. gracile antevacuolatum* and *P. gracile oviplites* with anterior vacuole at level of oral bulge opening, about 16 ciliary rows, and ordinary to long proboscis.

As mentioned by KAHL (1931), *P. gracile* is very similar to *Dileptus anguillula* (now *Pseudomonilicaryon anguillula*) which has, however, a different contractile vacuole pattern (a dorsal row vs. two dorsal vacuoles) and fewer ciliary rows (8–12 vs. 14–19).

Improved diagnosis (includes four subspecies): Size about 110–230 × 20–30 μm in vivo. Shape very narrowly to cylindroidally dileptid with rounded or acute posterior end, proboscis 25–57% of body length. Macronucleus moniliform and tortuous, composed of about 13 nodules on average; 6 globular to ellipsoidal micronuclei. Two dorsal contractile vacuoles with 2–5 excretory pores each, anterior vacuole at level of oral bulge opening or far underneath. Two types of extrusomes attached to proboscis oral bulge: type I rod-shaped or very narrowly ovate, 4–6 × 0.8 μm in size; type II oblong, 2–2.5 μm long. On average 16 ciliary rows, 2 staggered and differentiated into an inconspicuous dorsal brush with bristles 2–3 μm long: brush rows 1 and 2 composed of an average of 22 and 31 dikinetids, respectively; both rows with

a monokinetidal bristle tail extending to base of proboscis. Oral bulge opening about 12 µm across. On average 32 widely spaced, strongly oblique preoral kineties, each composed of 2–3 narrowly to ordinarily spaced cilia.

Etymology: Not given in original description. The Latin adjective *gracilis* (slender) obviously refers to body shape.

Pseudomonilicaryon gracile gracile (Kahl, 1931) Foissner, 1997 nov. stat. (Fig. 123b)

1931 *Dileptus gracilis* spec. n. Kahl, Tierwelt Dtl. **21**: 209

1963 *Dileptus gracilis* Kahl, 1931 – Dragesco, Bull. biol. Fr. Belg. **97**: 120 (first taxonomic reviser)

1997 *Pseudomonilicaryon gracilis* nov. comb. – Foissner, Limnologica **27**: 196 (type species of genus, combining author)

non *Dileptus gracilis* Kahl, 1931 – Foissner, 1989, Sber. Akad. Wiss. Wien **196**: 182 (see P. *gracile antevacuolatum*)

Diagnosis: Body rounded posteriorly. Anterior contractile vacuole far underneath oral bulge opening.

Type locality: Moss from Wisconsin, USA, W88°47' N43°47'.

Type material: No material available from Kahl's specimens.

Description: Length 100–120 µm in vivo. Shape cylindroidally dileptid with a length:width ratio of 10:1, according to the figure provided. Proboscis about one fourth of body length, indistinctly set off from cylindroidal trunk; posterior end rounded. Macronucleus moniliform, composed of eight nodules, as estimated from Kahl's illustration (Fig. 123b). Two contractile vacuoles in dorsal side of trunk: anterior vacuole at beginning of second fourth of trunk, posterior vacuole at beginning of last fourth of trunk. Extrusomes attached to proboscis oral bulge, their shape not described but illustrated as short rods (Fig. 123b). Number of ciliary rows not studied, but Kahl (1931) showed five rows on one side of cell, indicating about ten rows in total. Oral basket minute and short.

Occurrence and ecology: *Pseudomonilicaryon gracile gracile* was discovered by Kahl (1931) in moss from Wisconsin, USA, where only ten specimens were found. Later records not substantiated by illustrations, possibly including *D. gracile antevacuolatum*: frequent in an activated sludge plant in London, England (Reid 1969); soil from spruce forests in Austria and Germany (Aescht & Foissner 1993, Foissner 1998); rendzic leptosol from a pine forest in the Stampfltal, Lower Austria (Foissner et al. 2005); mosses (*Bryum argenteum*, *Ceratodon purpureus* and *Brachythecium albicans*) on carbonaceous fluvisol from the town of Bratislava, Slovakia (Andelová & Tirjaková 2000); in the periphyton of the Tisa River, Ukraine (Kovalchuk 1997a); strongly rooted, reddish surface (0–5 cm) soil from the Mt. Fields National Park, Tasmania, pH 7.0 (Blatterer & Foissner 1988).

Remarks: Detailed redescription urgently needed, with special regard to the contractile vacuoles.

Pseudomonilicaryon gracile singulare (Vuxanovici, 1962) nov. comb., nov. stat. (Fig. 123a)

1962 *Dileptus singularis* n. sp. Vuxanovici, Studii Cerc. Biol. **14**: 333

Generic affiliation and taxonomy: Jankowski (1967) did not assigned *Dileptus singularis* to one of his subgenera. Indeed, the generic home of this rather poorly described species remains doubtful because its oral ciliature is not known. We suggest to combine *D. singularis* with *Pseudomonilicaryon* and as a subspecies of *P. gracile*. *Pseudomonilicaryon gracile singulare* highly resembles *P. gracile gracile* in body size, the nuclear apparatus, and the contractile vacuole pattern, but has an acute or tail-like (vs. rounded) rear end. As Vuxanovici (1962) found many specimens, the acute body end is very likely correct,

representing the typical state. Further, it is a limnetic (vs. moss) species. Full redescription is required.

Diagnosis: Body acute to tail-like posteriorly. Anterior contractile vacuole far underneath oral bulge opening.

Type locality: Coast of Lake Herăstrău, Bucharest, Roumania, in March 1960, E26°05' N44°28'.

Type material: Not available.

Etymology: Not given in original description. The Latin adjective *singularis* (single) possibly refers to its uniqueness, i.e., being a new species.

Description: Length 120–160 µm in vivo. Shape very narrowly dileptid with a length:width ratio of 6:1, according to the figure provided. Proboscis about one third of body length, distinctly set off from trunk, slightly curved dorsally; trunk obconical; posterior end tail-like. Macronucleus moniliform, composed of about 10 nodules. Micronuclei, extrusomes, and number of ciliary rows not known. Two contractile vacuoles in dorsal side of trunk: anterior vacuole at end of first fourth of trunk, posterior one at beginning of last fourth of trunk. Cytoplasm transparent, hyaline in proboscis while opaque in trunk because packed with granules. Oral basket minute and short (Fig. 123a).

Occurrence and ecology: As yet found only at type locality, where many specimens were observed.

Pseudomonilicaryon gracile antevacuolatum nov. ssp. (Figs 123c–k; Table 61)

1989 *Dileptus gracilis* KAHL, 1931 – FOISSNER, Sber. Akad. Wiss. Wien **196**: 182 (misidentification)

Taxonomy: We establish a new subspecies *P. gracile antevacuolatum*. We use "nov. ssp." instead of "*nom. nov.*" because we fix here a holotype (Article 72.3 of the ICZN 1999; see Type material).

Pseudomonilicaryon gracile antevacuolatum differs from the nominotypical subspecies by the longer proboscis (33–47% vs. 25% of body length), the location of the anterior contractile vacuole (at level vs. far underneath of oral bulge opening), and, possibly, also by the higher number of ciliary rows (~ 15 vs. ~ 10). The most important feature is possibly the location of the anterior vacuole because this is found also in the subspecies *P. gracile oviplites* (see below).

Diagnosis: Body rounded posteriorly. Anterior contractile vacuole at level of oral bulge opening. Type I extrusomes rod-shaped with rounded ends, 4–6 µm long.

Type locality: Moss from the Schönramer Filz close to the town of Freilassing, Bavaria, Germany, E12°59' N47°51'.

Type material: FOISSNER (1989) deposited two neotype slides (inv. nos 1988/98 and 1988/99; designated as *Dileptus gracilis*) with protargol-impregnated specimens in the Biology Centre of the Museum of Upper Austria, Linz (LI). Relevant specimens are marked by black ink circles on the coverslip. See, "nomenclature and taxonomy" of *Pseudomonilicaryon gracile*.

Etymology: Composite of the Latin prefix *ante* (in front) and the Latin noun *vacuola* (vacuole), referring to the anterior contractile vacuole vis-à-vis the oral bulge opening.

Description: Body size in vivo 100–200 × 25–40 µm, usually about 150 × 25 µm, according to the protargol-prepared cells (Table 61), when 15% shrinkage is added; very flexible but not contractile. Shape narrowly to cylindroidally dileptid, that is, length:width ratio 5.2–9.2:1 (Table 61). Length of proboscis highly variable, about one third of body length in small cells (100–130 µm), while almost one half of body length in large specimens (140–200 µm), usually curved dorsally; trunk elongate ellopsoidal to cylindroidal with posterior end rounded, never tail-like (Figs 123b, i–k; Table 61). Nuclear apparatus in anterior two thirds of trunk (Figs 123c, j). Macronucleus an irregularly nodulated and highly tortuous strand, consisting of an average of ten nodules connected by fine argyrophilic bridges; nucleoli globular,

Table 61: Morphometric data on *Pseudomonilicaryon gracile antevacuolatum* nov. ssp. (PGA; from FOISSNER 1989) and *P. gracile oviplites* nov. ssp. (PGO). Data based on mounted, protargol-impregnated (Foissner's method), and randomly selected specimens from non-flooded Petri dish cultures. Measurements in µm. CV – coefficient of variation in %, M – median, Max – maximum, Mean – arithmetic mean, Min – minimum, n – number of specimens investigated, SD – standard deviation, SE – standard error of mean.

Characteristics	Sspec.	Mean	M	SD	SE	CV	Min	Max	n
Body, length	PGA	129.5	128.0	19.7	6.2	15.2	94.0	165.0	10
	PGO	202.2	197.0	36.6	10.1	18.1	148.0	255.0	13
Body, width	PGA	20.4	21.0	2.0	0.6	9.6	18.0	24.0	10
	PGO	24.5	24.0	4.9	1.4	20.2	17.0	33.0	13
Body length:width, ratio	PGA[a]	6.4	6.2	1.2	0.4	18.4	5.2	9.2	10
	PGO	8.5	8.9	1.8	0.5	21.5	4.5	10.7	13
Anterior body end to oral bulge opening, distance	PGA	79.7	78.0	21.1	5.9	26.5	43.0	125.0	13
	PGO	53.0	53.0	11.1	3.5	21.0	31.0	70.0	10
Proboscis, % of body length	PGA[a]	40.7	40.0	4.6	1.5	11.4	33.0	47.6	10
	PGO	39.5	39.9	8.4	2.3	21.2	26.9	57.3	13
Oral bulge opening, length	PGA[a]	10.1	10.0	1.6	0.5	16.0	7.0	13.0	9
	PGO	12.2	12.0	1.4	0.4	11.1	9.0	15.0	13
Oral bulge opening, width	PGA[a]	8.2	8.0	1.4	0.5	17.0	7.0	10.0	9
	PGO	8.3	8.0	–	–	–	8.0	9.0	3
Anterior body end to macronucleus, distance	PGO	96.5	96.0	27.2	7.5	28.2	60.0	143.0	13
Nuclear figure, length	PGA	43.6	43.5	7.1	2.3	16.4	30.0	56.0	10
	PGO	64.2	62.0	13.9	3.9	21.6	45.0	93.0	13
Macronucleus, total length (uncoiled and thus approximate)	PGO	118.4	123.0	–	–	–	58.0	167.0	13
First macronuclear nodule, length	PGA	9.1	10.0	1.9	0.6	21.0	6.0	11.0	10
	PGO	8.1	8.0	1.7	0.5	21.1	6.0	10.0	13
First macronuclear nodule, width	PGA	5.6	6.0	1.2	0.4	21.4	4.0	7.0	10
	PGO	4.3	4.0	0.6	0.2	14.6	4.0	6.0	13
Last macronuclear nodule, length	PGO	8.1	8.0	2.0	0.5	24.5	6.0	12.0	13
Last macronuclear nodule, width	PGO	4.4	4.0	0.7	0.2	14.8	3.0	5.0	13
Macronuclear nodules, number	PGA	10.8	10.0	2.7	0.9	25.0	7.0	15.0	10
	PGO	15.4	15.0	2.9	0.8	18.9	9.0	20.0	13
Micronuclei, largest diameter	PGA	1.9	2.0	–	–	–	1.6	2.0	10
Micronuclei, length	PGO	2.4	2.5	–	–	–	1.5	3.0	11
Micronuclei, width	PGO	1.4	1.5	–	–	–	1.0	1.5	11
Micronuclei, number	PGA	5.4	5.0	–	–	–	5.0	6.0	9
	PGO	7.5	7.0	2.8	0.9	37.3	4.0	13.0	10
Ciliary rows, number	PGA	15.3	15.5	0.8	0.3	5.4	14.0	16.0	10
	PGO	16.8	17.0	1.5	0.4	8.8	14.0	19.0	13

Characteristics	Sspec.	Mean	M	SD	SE	CV	Min	Max	n
Cilia in mid-body in 10 μm, number	PGA	5.6	5.5	1.3	0.4	22.6	4.0	8.0	10
	PGO	4.4	5.0	1.0	0.3	21.9	3.0	6.0	13
Preoral kineties, number	PGO	33.9	32.0	4.8	1.7	14.2	28.0	43.0	8
Dorsal brush rows, number	PGA	2.0	–	–	–	–	2.0	2.0	2
	PGO	2.0	2.0	0.0	0.0	0.0	2.0	2.0	11
Dikinetids in brush row 1, number	PGO	22.0	22.0	3.1	1.2	13.9	19.0	27.0	7
Dikinetids in brush row 2, number	PGO	30.4	31.0	1.8	0.7	6.0	28.0	33.0	7
Anterior body end to last dikinetid of brush row 1, distance	PGO	35.6	37.0	6.9	2.2	19.4	21.0	43.0	10
Anterior body end to last dikinetid of brush row 2, distance	PGO	36.8	38.5	7.2	2.3	19.5	23.0	45.0	10

[a] Calculated from original data.

small to medium-sized. On average five micronuclei close to or attached to macronuclear strand, about 2 μm across in prepared specimens (Figs 123c, h, j; Table 61). Two dorsal contractile vacuoles each with two to three intrakinetal pores (Figs 123c, i, k): anterior vacuole at level of or slightly posterior to oral bulge opening, posterior vacuole at beginning of last fourth of trunk. Extrusomes scattered throughout cytoplasm and attached to proboscis oral bulge, quite similar in South African and German specimens, where the small type possibly has been overlooked (Figs 123f, g): type I rod-shaped with rounded ends, 4 μm and 6 μm long in German and South African specimens, respectively; type II extrusomes oblong, about 2 μm long. Cortex flexible, contains about three rows of loosely spaced, colourless, about 1 μm long granules between adjacent kineties (Fig. 123e). Cytoplasm colourless, contains few to many lipid droplets 1–5 μm across; near posterior end often a defecation vacuole. Slowly glides on microscope slide.

On average 15 longitudinal, ordinarily spaced ciliary rows leaving a wide, blank stripe left and right of oral bulge (Figs 123i, j; Table 61). First row right of circumoral kinety extends as perioral kinety with ordinarily spaced cilia to tip of proboscis. Only one ciliary row between perioral kinety and brush row 2 (Fig. 123i). Dorsal brush composed of two isostichad rows. Both rows begin subapically and continue with a monokinetidal tail. Brush dikinetids ordinarily spaced, associated with 2–3 μm long bristles (Fig. 123j; Table 61).

Oral bulge opening roundish both in vivo and in preparations, about 12 μm across, ordinarily projecting (Figs 123d, h; Table 61). Pharyngeal basket possibly bulbous, distinct both in vivo and after protargol impregnation. Circumoral kinety composed of ordinarily spaced dikinetids in proboscis and of narrowly spaced monokinetids around oral bulge opening (Figs 123h–j). Preoral kineties widely spaced, oblique to strongly oblique, each composed of two to three narrowly spaced cilia (Figs 123h, j).

Occurrence and ecology: Foissner (1989) discovered *P. gracile antevacuolatum* in moss from the Schönramer Filz close to the town of Freilassing, Bavaria, Germany. Possibly occurs also in soil from the Republic of South Africa (see extrusomes).

Pseudomonilicaryon gracile oviplites nov. ssp. (Figs 124a–s; Table 61)

Diagnosis: Body rounded posteriorly. Anterior contractile vacuole at level of oral bulge opening. Type I extrusomes very narrowly ovate, 5–6 × 0.8 μm in size.

Type locality: Soil and mud from a rockpool on granitic outgrowths (Lajas) in the surroundings of the farm of Mr. EISENBERG, about 50 km NE of Puerto Ayacucho, Venezuela, W67°20' N6°10'.

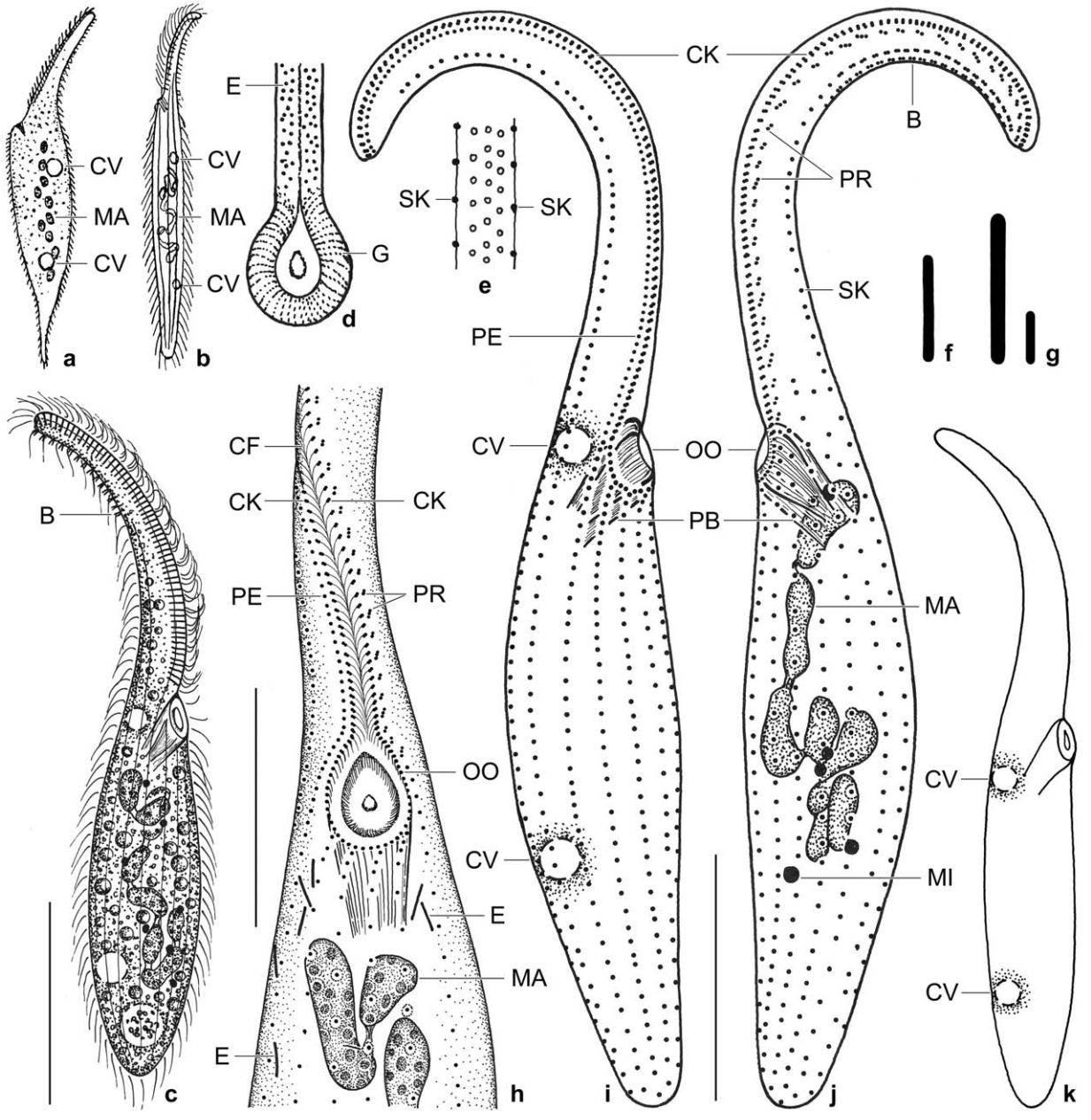
Type material: One holotype slide (inv. no. 2011/178) and six paratype slides (inv. nos 2011/179–184) with protargol-impregnated specimens have been deposited in the Biology Centre of the Museum of Upper Austria, Linz (LI). Relevant specimens are marked by black ink circles on the coverslip.

Etymology: Composite of the Latin noun *ovum* (egg), the thematic vowel *i*, and the Greek noun *hoplites* (soldier ~ extrusome), referring to the very narrowly ovate extrusomes.

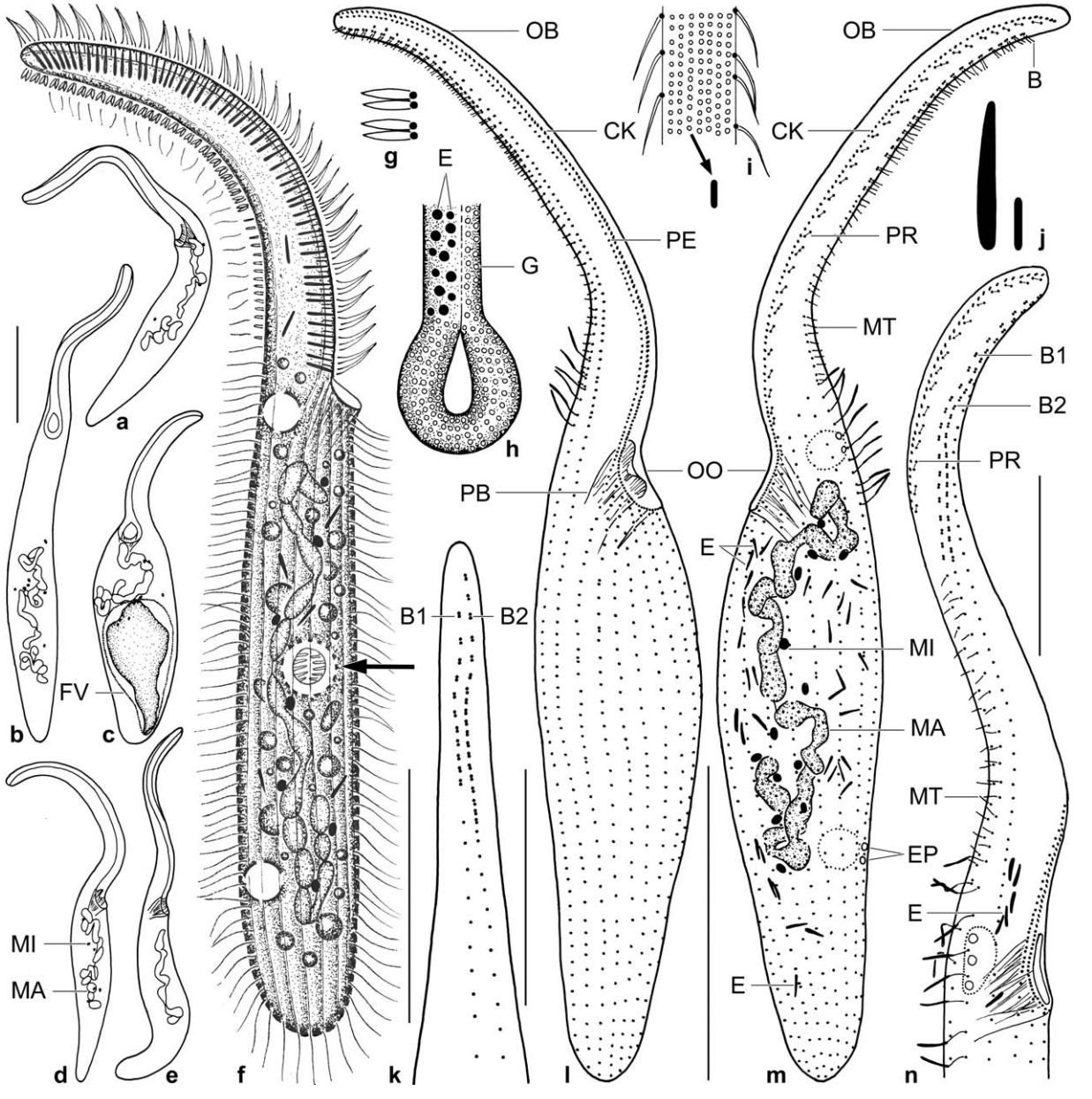
Description: Size 170–300 × 20–40 μm in vivo, usually about 230 × 30 μm, as calculated from some in vivo measurements and the morphometric data, assuming 15% preparation shrinkage; very flexible but not contractile (Table 61). Shape narrowly to cylindroidally dileptid, length:width ratio near 9:1 both in vivo and in protargol preparations. Length of proboscis highly variable, viz., 27% to 57%, on average 40% of body length, usually curved dorsally; trunk cylindroidal, broadly fusiform in some prepared specimens, distinctly inflated in cells with large food inclusions (Fig. 124c); posterior end rounded both in vivo and in protargol preparations, never tail-like (Figs 124a–f, l, m; Table 61). Nuclear apparatus usually in anterior three fourth of trunk, may be dislocated by large food items. Macronucleus moniliform, tortuous, in some specimens a mixture of nodules and distinctly nodulated strands, about 120 μm long when "uncoiled", composed of an average of 15 oblong nodules connected by argyrophilic strands; individual nodules ellipsoidal to very narrowly ellipsoidal, on average 8 × 4 μm in size; nucleoli small, globular. On average seven micronuclei attached to macronuclear strand, broadly ellipsoidal to ellipsoidal, about 2.5 × 1.5 μm in size (Figs 124a–f, m, o; Table 61). Two dorsal contractile vacuoles each with two to five intrakinetal pores one after the other: anterior vacuole at level of oral bulge opening, posterior one at beginning of last fourth of trunk (Figs 124f, m, n). Two types of extrusomes, not impregnating with protargol, attached to broader right branch of oral bulge: type I very narrowly ovate, about 5–6 × 0.8 μm in size; type II oblong with rounded ends, 2.5 μm long; developing extrusomes numerous in trunk cytoplasm, very narrowly ovate, impregnate with protargol (Figs 124h, j, m, n). Cortex flexible, contains about seven granule rows between adjacent kineties; granules narrowly spaced in somatic and oral bulge cortex, colourless and about 0.8 × 0.3 μm in size (Figs 124h, i). Cytoplasm colourless, contains few to many globular and irregular lipid droplets 1–10 μm across and large food vacuoles with small rotifers (Figs 124c, f).

Cilia about 8 μm long in vivo, ordinarily spaced; in protargol preparations as typical for dileptids, i.e., with thick, deeply impregnated distal half, except for dorsal bristles; arranged in an average of 17 longitudinal, ordinarily spaced rows leaving a wide, blank stripe left and right of oral bulge (Figs 124l–n, p–s; Table 61). First row right of circumoral kinety extends as perioral kinety with ordinarily to widely spaced cilia to tip of proboscis (Figs 124l, r). Invariably only one ciliary row between perioral kinety and brush row 2 (Figs 124l, n, p, q). Dorsal brush exactly on dorsal side of proboscis, composed of two staggered, isostichad rows. Row 1 commences slightly more subapically than row 2, composed of an average of 22 dikinetids. Row 2 begins near tip of proboscis, composed of an average of 31 dikinetids. Brush dikinetids very loosely spaced in anterior portion of rows, while loosely to ordinarily in posterior half; associated with type IV bristles being 2.5 μm long in vivo and becoming 1.5–2 μm long and rod-shaped after protargol impregnation. Both brush rows continue to base of proboscis with a monokinetidal tail composed of about 2 μm long type VI bristles (Figs 124f, g, k–n, p, q).

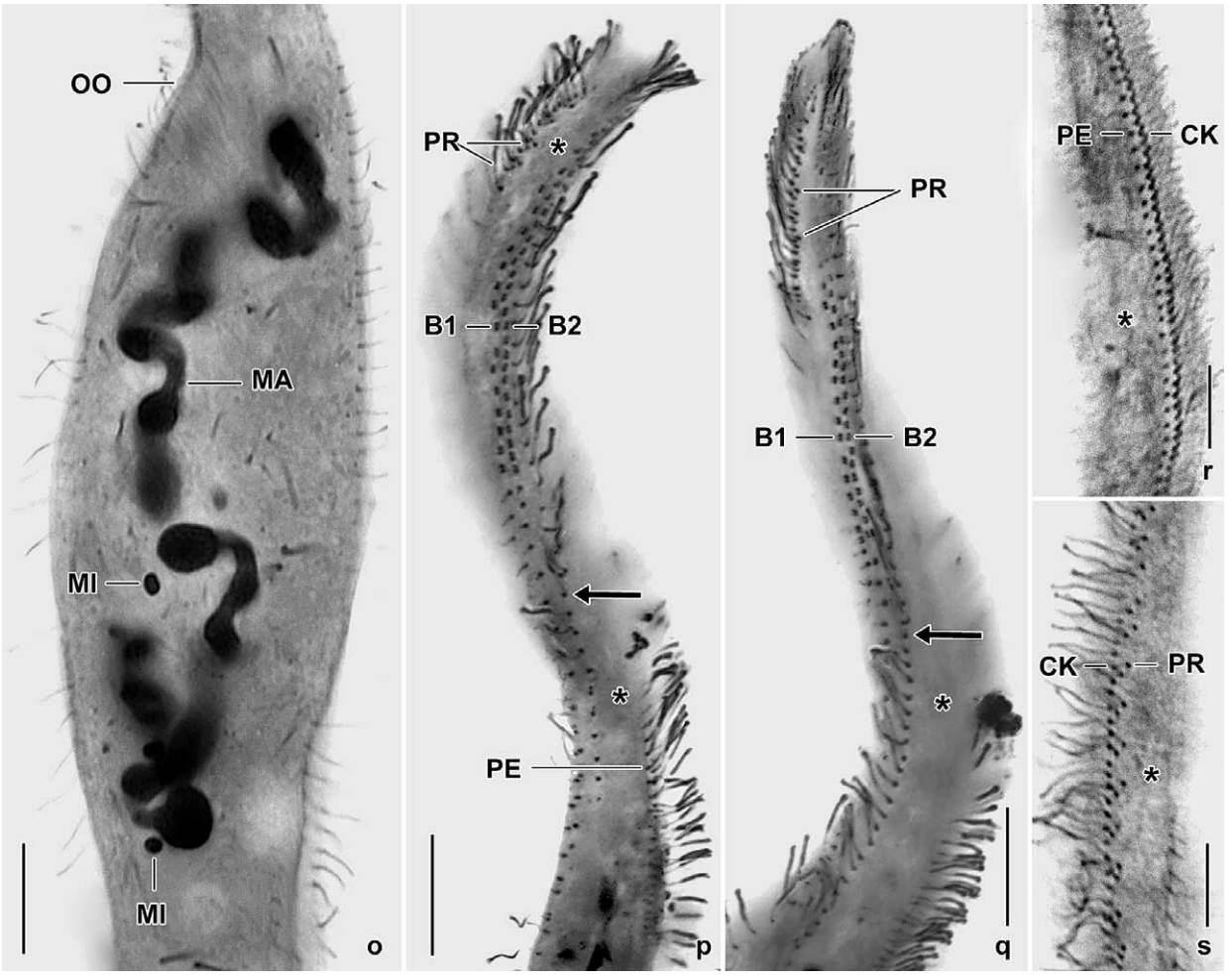
Oral bulge opening roundish both in vivo and in preparations, about 12 μm across, projects distinctly because proboscis only half as wide as trunk (Figs 124f, h; Table 61). Pharyngeal basket obconical, difficult to recognize both in vivo and in protargol preparations because composed of very fine and faintly impregnated rods (Figs 124l–n). Circumoral kinety composed of ordinarily to widely spaced dikinetids in proboscis, while of narrowly spaced monokinetids around oral bulge opening; right branch curves



Figs 123a–k: *Pseudomonilicaryon gracile singulare* (a), *P. gracile gracile* (b), and *P. gracile antevacuolatum* nov. ssp. (c–k) from life (a–g, k) and after protargol impregnation (h–j). From Vuxanovici 1962 (a), Kahl 1931 (b), and Foissner 1989 (c–f, h–k). **a** – *Dileptus singularis*, length 150 µm; **b** – *D. gracilis*, length 110 µm; **c** – right side view of a representative German specimen, length 160 µm; **d** – frontal view of oral bulge and arrangement of extrusomes; **e** – surface view showing cortical granulation; **f** – type I extrusomes are rod-shaped and 4 µm long in German specimens; **g** – there are two size-types (6 µm and 2 µm) of rod-shaped extrusomes in South African specimens; **h** – ciliary pattern in oral region. The circumoral kinety consists of ordinarily to widely spaced dikinetids in the proboscis, while of narrowly spaced monokinetids around the oral bulge opening. Right of the circumoral kinety is a perioral kinety, while at left are many strongly oblique preoral kineties, each usually composed of two narrowly spaced basal bodies; **i, j** – right and left side ciliary pattern as well as the nuclear and contractile vacuole apparatus of the holotype specimen, length 132 µm. Note the special location of the anterior contractile vacuole vis-à-vis the oral bulge opening; **k** – body shape and contractile vacuole pattern. B – dorsal brush, CF – central fibre, CK – circumoral kinety, CV – contractile vacuoles, E – extrusomes, G – cortical granules, MA – macronuclear nodules, MI – micronucleus, OO – oral bulge opening, PB – pharyngeal basket, PE – perioral kinety, PR – preoral kineties, SK – somatic kineties. Scale bars: 20 µm (h), 30 µm (i, j), and 50 µm (c).



Figs 124a–n: *Pseudomonilicaryon gracile oviplites* nov. ssp. from life (f–j) and after protargol impregnation (a–e, k–n). **a–e** – variability of body shape and size as well as of nuclear apparatus. Drawn to scale, 50 µm. Note the inflated specimen (c) containing a rotifer in a large vacuole; **f** – right side view of a representative specimen, length 230 µm. The arrow marks the mastax of a rotifer; **g** – the brush dikinetids are associated with flame-shaped, about 2.5 µm long bristles; **h** – frontal view of oral bulge and arrangement of extrusomes and cortical granules; **i** – surface view showing cortical granulation. The granules have a size of about 0.8 × 0.3 µm; **j** – two types of oral bulge extrusomes: type I is very narrowly ovate and about 6 × 0.8 µm in size, while type II is about 2.5 µm long; **k** – dorsal view of proboscis ciliary pattern of an opisthe post-divider or of a distorted specimen, showing the two staggered brush rows with very loosely spaced dikinetids in the anterior brush region and loosely to ordinarily spaced dikinetids in the posterior region; **l, m** – right and left side ciliary pattern as well as the nuclear and contractile vacuole apparatus of the holotype specimen, length 193 µm; **n** – lateral view of proboscis' ciliary pattern. B(1, 2) – dorsal brush (rows), CK – circumoral kinety, CV – contractile vacuoles, E – extrusomes, EP – excretory pores of contractile vacuole, FV – food vacuole, G – cortical granules, MA – macronucleus (nodules), MI – micronuclei, MT – monokinetidal tail of dorsal brush, OB – oral bulge, OO – oral bulge opening, PB – pharyngeal basket, PE – perioral kinety, PR – preoral kineties. Scale bars: 20 µm (k, n) and 50 µm (a–f, l, m).



Figs 124o–s: *Pseudomonilicaryon gracile oviplites* nov. ssp. after protargol impregnation. **o** – the nuclear apparatus consists of a highly tortuous, moniliform macronuclear strand and several broadly ellipsoidal to ellipsoidal micronuclei; **p, q** – dorsolateral ciliary pattern of proboscis. The dorsal brush consists of two staggered, isostichad rows composed of very loosely to ordinarily spaced dikinetids. Asterisks mark a broad blank stripe left and right of the oral bulge; arrows denote the single ciliary row between perioral kinety and brush row 2; **r** – right side proboscis' ciliary pattern, showing the circumoral kinety composed of dikinetids, the perioral kinety consisting of comparatively widely spaced basal bodies, and the broad blank stripe (asterisk); **s** – left side view of proboscis' ciliary pattern, showing, inter alia, the widely spaced preoral kineties, each usually composed of two ordinarily to widely spaced basal bodies. Asterisk marks the broad blank stripe. B1, 2 – dorsal brush rows, CK – circumoral kinety, MA – macronucleus, MI – micronuclei, OO – oral bulge opening, PE – perioral kinety, PR – preoral kineties. Scale bars 10 µm.

around anterior end of proboscis, while left branch ends subapically almost touching the curved right end (Figs 124l–n, r, s). On average 32 widely spaced, strongly oblique preoral kineties, each composed of two to three narrowly to ordinarily spaced cilia; some almost in line with left branch of circumoral kinety, especially in anterior portion of proboscis (Figs 124m, n, p, q, s; Table 61).

Occurrence and ecology: As yet found only at type locality, that is, in mud and soil of a rather large rockpool on granitic outgrowths called "Lajas" in Venezuela. The sample, which had pH 5.4 in water, consisted of the up to 3 cm deep, grey-brown, sandy mud and soil accumulated between some moss and a dense lawn of velosiaceans, a group of plants endemic to South America.

Pseudomonilicaryon thononense (Dragesco, 1960) nov. comb. (Figs 125a–d, 126a–t; Table 62)

1960 *Dileptus thononensis* n. sp. Dragesco, Trav. Stn biol. Roscoff (N. S.) **12**: 188

1963 *Dileptus thononensis* Dragesco, 1960 – Dragesco, Bull. biol. Fr. Belg. **97**: 117 (first taxonomic reviser)

Generic affiliation and taxonomy: Jankowski (1967) did not combine *Dileptus thononensis* with one of his subgenera. Our data show that it belongs to *Pseudomonilicaryon* because it has a *Dileptus*-like ciliary pattern and a moniliform macronucleus.

In Venezuela, we found a population fairly similar to *Pseudomonilicaryon thononense*: body about 250–350 µm long and very narrowly to cylindroidally dileptid with distinct tail and proboscis occupying 1/3–1/2 of body length; macronucleus moniliform, several globular micronuclei; contractile vacuoles in a dorsal stripe. Details of the nuclear apparatus are, however, rather different: Dragesco's specimens had much more micronuclei (15–16 vs. 4–9) and macronuclear nodules (60–70 vs. 20–34), each having a big central nucleolus (vs. several small nucleoli). Nevertheless, it appears reasonable to emphasize the matching features and to identify the Venezuelan population as *Dileptus thononensis*, especially because there is evidence that Dragesco (1960) strongly over-estimated the number of macronuclear nodules: if there are 60–70 of them, each about 6 µm across, they would occupy 270–315 µm, even when 25% space is added for a zigzagging arrangement. On the other hand, we do not neotypify *D. thononensis* with the Venezuelan population because this is a different biogeographic region and data about the extrusomes and the number of ciliary rows are lacking from the French population.

There are several *Pseudomonilicaryon* species which resemble *P. thononense*, viz., *P. massutii*, *P. japonicum*, and *P. angustistoma*. However, all have, inter alia, a much higher number of ciliary rows (about 40 vs. 18). Another similar species is *P. kahli* which, however, is much larger (450–900 µm vs. 250–370 µm) and possesses more ciliary rows (22–27 vs. 17–21).

Improved diagnosis (based on literature and a new population from Venezuela): Size about 250–300 × 35 µm in vivo. Shape very narrowly to cylindroidally dileptid with distinct tail, proboscis about 37% of body length. Macronucleus moniliform, composed of about 25–70 (?) globular to ellipsoidal nodules; several globular micronuclei. A dorsal stripe of contractile vacuoles with 1–3 pores each. Two size-types (6 µm and 2–2.5 µm) of rod-shaped extrusomes attached to right branch of oral bulge. On average 18 ciliary rows; dorsal brush diffuse, staggered, all rows with a monokinetidal tail extending to base of proboscis. Oral bulge opening about 15 µm across. On average 43 ordinarily spaced, oblique preoral kineties, each usually composed of 3 ordinarily spaced cilia.

Type locality: Dragesco (1960) discovered *Dileptus thononensis* in fine sand from Lake Léman, Thonon region, France, E6°21' N46°21'.

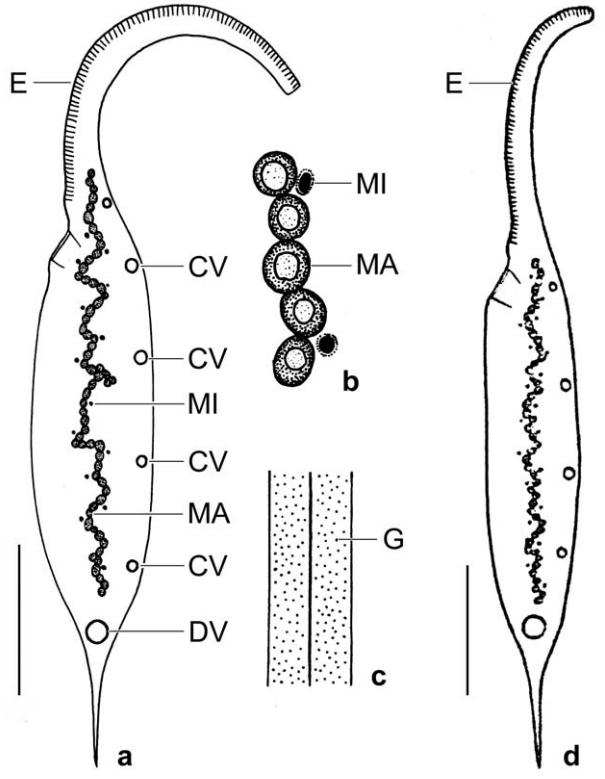
Type and voucher material: No type material is available from Dragesco's specimens. Eight voucher slides (inv. nos 2011/170–177) with protargol-impregnated Venezuelan specimens have been deposited in the Biology Centre of the Museum of Upper Austria, Linz (LI). Relevant specimens are marked by black ink circles on the coverslip.

Etymology: Dragesco (1960) named this species after the region in which the species was discovered (Thonon, France).

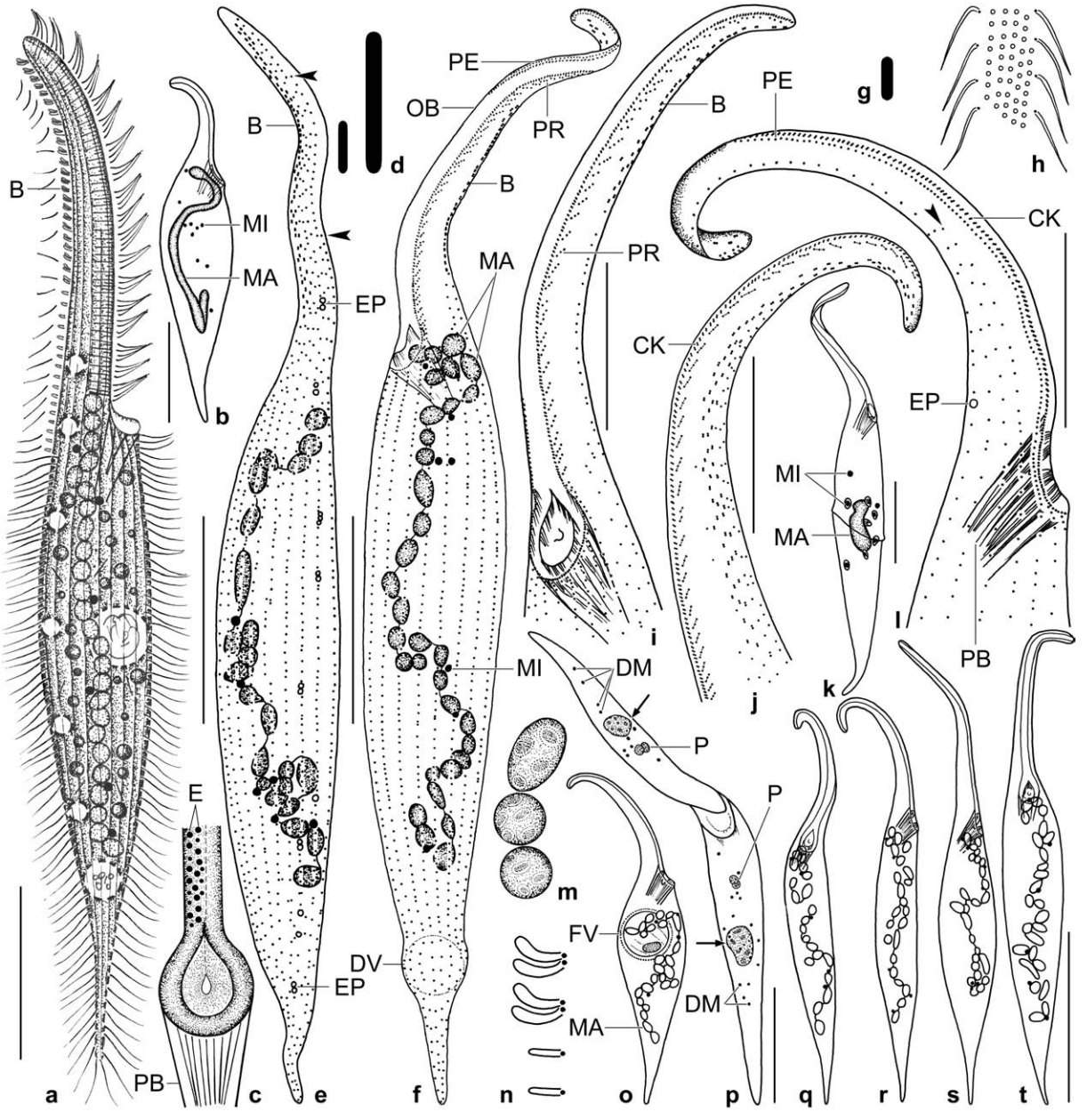
Description of Thonon population: The original description by Dragesco (1960) reads as follows (Figs 125a–c): "Cette nouvelle espèce, trouvée dans le sable fin d'Excenevex, pendand l'hiver 1955–1956, rappelled un peu *D. marinus*, mais se différencie de toutes les espèce du genre par sa petite taille (250 µm), son apareil nucléaire constitué par un chapelet de 60 à 70 petits éléments sphéroïdaux (diam. 5–7

μm) dont la structure semble être du type *Geleia* (grande zone centrale achromatique), sa pointe caudale efilée. La trompe est courte, relativement épaisse et semble peu mobile. Les vacuoles pulsatiles montrent la dispostion habituelle: grande vacuole caudale et petites vacuoles satellites dorsales. Les espaces intercinétiques sont garnis de très fins protrichocystes. La bouche, du type habituel, est armée de fines baguettes squelettiques".

Description of Venezuelan population: Size 250–370 × 25–40 μm in vivo, usually about 300 × 35 μm, as calculated from some in vivo measurements and the morphometric data, assuming 15% preparation shrinkage (Table 62). Shape very narrowly to cylindroidally dileptid, length:width ratio near 9:1 both in vivo and in protargol preparations. Proboscis about one third to one half of body length, usually curved dorsally, anterior fifth sometimes coiled; trunk fusiform both in vivo and in preparations, distinctly inflated in well-fed specimens (Fig. 126o); posterior in vivo with distinct tail often becoming indistinct or acute in protargol preparations (Figs 126a, e, f, o, q–t; Table 62). Nuclear apparatus extends between oral bulge opening and base of tail. Macronucleus a moniliform, basically straight strand composed of 20–34, on average of 25 nodules; individual nodules rather variable in shape and size, that is, globular to narrowly ellipsoidal, sometimes surrounded by a distinct membrane after protargol impregnation; in mid-dividers fuse to an ellipsoidal mass (Fig. 126k), becoming a long rod in early post-dividers (Fig. 126b); many nucleoli about 1–2 μm across, well recognizable both in vivo and in protargol preparations. On average six micronuclei attached to macronuclear nodules, about 2.5 μm across in prepared specimens (Figs 126a, e, f, m, o, q–t; Table 62). A stripe of contractile vacuoles in dorsal side of cell, first vacuole slightly anterior of oral bulge opening; no ventral vacuoles; one to three, usually two intrakinetal excretory pores per vacuole (Figs 126a, e, l). Two size-types of rod-shaped extrusomes with rounded ends, not impregnating with protargol, scattered throughout cytoplasm and attached to right broader branch of oral bulge: type I about 5–6.5 × 0.8 μm in size, certain cytoplasmic developmental stages sometimes impregnate with protargol;



Figs 125a–d: *Pseudomonilicaryon thononense*, French type specimens from life (a, c, d) and after acetic methyl green staining (b). From Dragesco 1960 (a–c) and Dragesco 1963 (d). **a, d –** lateral views showing the distinct tail and the long, moniliform macronuclear strand composed of about 60–70 nodules; **b –** the macronuclear nodules are about 5–7 μm across and have a large achromatic centre (nucleolus?). There are several globular micronuclei attached to the macronuclear strand; **c –** surface view showing cortical granules (protrichocysts). CV – contractile vacuoles, DV – defecation vacuole, E – extrusomes, MA – macronuclear nodule, MI – micronucleus, G – cortical granules. Scale bars 50 μm.



Figs 126a–t: *Pseudomonilicaryon thononense*, Venezuelan specimens from life (a, c, d, g, h, m, n) and after protargol impregnation (b, e, f, i–l, o–t). **a –** right side view of a representative specimen, length 300 µm; **b –** an early post-divider; **c –** frontal view showing oral bulge opening and arrangement of the extrusomes; **d –** two size types (5–6.5 µm and 2–2.5 µm) of rod-shaped extrusomes; **e –** ciliary pattern of dorsal side and nuclear apparatus of main voucher specimen, length 275 µm. Arrowheads mark gradually shortened somatic kineties; **f –** ventrolateral ciliary pattern and nuclear apparatus, length 296 µm; **g, h –** cortical granules are oblong (1 × 0.4 µm) and form about five rows between adjacent kineties; **i, j –** ventrolateral and dorsolateral ciliary pattern of proboscis; **k –** in mid-dividers, the moniliform macronucleus fuses to a central mass; **l –** ciliary pattern of proboscis' right side. Arrowhead denotes a shortened ciliary row; **m –** the macronucleus is composed of globular to ellipsoidal nodules; **n –** fine structure of dorsal brush; **o, q–t –** variability of body shape and size as well as of nuclear apparatus. Drawn to scale; **p –** conjugating pair with macronuclear nodules condensed to an ellipsoidal mass (arrows). B – dorsal brush, CK – circumoral kinety, DM – degenerating maturation derivatives, DV – defecation vacuole, E – extrusomes, EP – excretory pores, FV – food vacuole, MA – macronuclear nodules, MI – micronuclei, OB – oral bulge, P – pronuclei, PB – pharyngeal basket, PE – perioral kinety, PR – preoral kineties. Scale bars: 30 µm (i, j, l), 50 µm (a, b, e, f, p), and 100 µm (o, q–t).

Table 62: Morphometric data on *Pseudomonilicaryon thononense* from Venezuela. Data based on mounted, protargol-impregnated (Foissner's method), and randomly selected specimens from a non-flooded Petri dish culture. Measurements in µm. CV – coefficient of variation in %, M – median, Max – maximum, Mean – arithmetic mean, Min – minimum, n – number of specimens investigated, SD – standard deviation, SE – standard error of mean.

Characteristics	Mean	M	SD	SE	CV	Min	Max	n
Body, length	268.3	269.0	27.9	6.1	10.4	226.0	324.0	21
Body, width	29.7	29.0	3.7	0.8	12.6	24.0	37.0	21
Body length:width, ratio	9.1	9.2	1.3	0.3	14.1	7.0	11.7	21
Anterior body end to oral bulge opening, distance	100.9	101.0	12.7	2.8	12.6	80.0	129.0	21
Proboscis, % of body length	37.7	36.7	4.0	0.9	10.6	32.0	50.2	21
Oral bulge opening, length	13.5	13.0	1.4	0.3	10.1	12.0	16.0	21
Oral bulge opening, width	11.8	11.5	1.7	0.9	14.5	10.0	14.0	4
Anterior body end to first macronuclear nodule, distance	111.4	109.0	16.7	3.6	15.0	88.0	162.0	21
Nuclear figure, length	110.2	111.0	20.8	4.5	18.8	78.0	146.0	21
Anteriormost macronuclear nodule, length	8.0	7.0	2.4	0.5	30.7	5.0	13.0	21
Anteriormost macronuclear nodule, width	5.3	5.0	0.7	0.2	13.6	4.0	6.0	21
Posteriormost macronuclear nodule, length	7.4	7.0	1.6	0.4	22.2	5.0	12.0	21
Posteriormost macronuclear nodule, width	5.4	5.5	0.8	0.2	14.8	4.0	7.0	21
Macronuclear nodules, number	25.5	25.0	3.8	0.8	14.8	20.0	34.0	21
Micronuclei, largest diameter	2.4	2.5	–	–	–	2.0	2.5	20
Micronuclei, number	5.7	5.5	1.4	0.3	24.9	4.0	9.0	20
Ciliary rows, number	18.2	18.0	1.1	0.2	6.2	17.0	21.0	21
Cilia in mid-body in 10 µm, number	5.2	5.0	0.7	0.2	13.4	4.0	6.0	21
Preoral kineties, number	42.1	43.0	3.6	1.0	8.5	35.0	48.0	13
Anterior body end to last dorsal brush dikinetid, distance	87.8	86.5	11.4	2.6	13.0	70.0	116.0	20
Dorsal brush dikinetids, total number	64.0	63.0	8.6	2.0	13.4	50.0	80.0	19
Dikinetidal portion of dorsal brush, % of body length	32.7	31.5	3.6	0.8	10.9	28.2	43.6	20
Groups of excretory pores, number	6.6	6.0	1.5	0.4	22.6	5.0	10.0	14

type II about 2–2.5 µm long (Figs 126c, d). Cortex flexible, contains about five rows of granules between adjacent kineties; individual granules ~ 1 × 0.4 µm in size (Figs 126g, h). Cytoplasm colourless, hyaline in proboscis and tail, opaque in trunk because packed with globular and irregular lipid droplets 1–5 µm across and 10–20 µm-sized food vacuoles containing mainly *Protocyclidium terricola*, rarely *Vorticellides astyliformis*; in trunk end sometimes a defecation vacuole with crystalline contents (Figs 126a, f, o). Swims fairly rapidly by rotation about main body axis and roots between soil particles.

Cilia about 10 µm long in vivo, ordinarily spaced; in protargol preparations as typical for dileptids, i.e., with thick, deeply impregnated distal half, except for dorsal bristles; arranged in an average of 18 longitudinal, ordinarily spaced rows two to three anteriorly gradually shortened along right side of oral bulge; perioral kinety extends to tip of proboscis with ordinarily spaced basal bodies (Figs 126e, f, l; Table 62). Left side of proboscis with conspicuous blank stripe because some ciliary rows end left of oral bulge opening (Figs 126f, i, j). Dorsal brush a long, narrow field on dorsal and dorsolateral surface of proboscis; distinctly

heterostichad; diffuse and composed of at least four rows (Figs 126e, f, i, j). Brush dikinetids with type I bristles both being about 3 µm long; brush tails end at level of oral bulge opening, composed of 2 µm long type VI bristles (Figs 126a, n).

Oral bulge opening at beginning of second body third, roundish both in vivo and in preparations, about 15 µm across, projects distinctly because proboscis only half as wide as trunk (Figs 126a, c; Table 62). Pharyngeal basket obconical, distinct both in vivo and in protargol preparations (Figs 126c, f, i, l). Circumoral kinety composed of ordinarily spaced dikinetids in proboscis, while of narrowly spaced monokinetids around oral bulge opening; right branch curves around anterior end of proboscis, whereas left branch ends subapically almost touching the curved right end. On average 43 ordinarily spaced preoral kineties, each composed of two to four, usually three narrowly to ordinarily spaced cilia, forming oblique to strongly oblique rows sometimes almost in line with left branch of circumoral kinety, especially in anterior half of proboscis (Figs 126f, i, j; Table 62).

Notes on conjugation (Fig. 126p): The single pair found suggests that conjugation of *Pseudomonilicaryon thononense* is highly similar to that of other dileptids, especially of *Rimaleptus tirjakovae* recently described by Vďačný & Foissner (2008a): pair formation is heteropolar and the partners unite bulge-to-bulge; conjugants are distinctly shorter (the longer partner is 160 µm, the shorter is 117 µm) than morphostatic cells (~ 270 µm); the proboscis is reduced to a rounded triangular lip; the oral ciliary pattern resembles that of polar haptorids; two globular pronuclei of similar size are formed in each partner; and the vegetative macronuclear nodules condense to an ellipsoidal mass (Fig. 126p, arrows). Unlike *R. tirjakovae*, the number of ciliary rows does not change (18 in the longer partner, 16 in the shorter, and 18 in vegetative cells), and all micronuclei perform the first and second maturation division, as suggested by many degenerating maturation derivatives.

Occurrence and ecology: Dragesco (1960, 1963) discovered *Pseudomonilicaryon thononense* in fine sand from the Excenevex beach, Lake Léman, France. Our population is from rockpools on granitic outgrowths (called "Lajas") between the Agricultural Research Institute and the airport of Puerto Ayacucho, Venezuela (W75° S6°). The sample consisted of dark cyanobacterial mud mixed with aeolian soil deposits.

Pseudomonilicaryon brachyproboscis Vďačný & Foissner, 2008 (Figs 127a–w, 128a–g, 129a–r; Tables 63, 64)

2008 *Pseudomonilicaryon brachyproboscis* nov. sp. Vďačný & Foissner, Acta Protozool. **47**: 225

2009 *Pseudomonilicaryon brachyproboscis* Vďačný & Foissner 2008 – Vďačný & Foissner, J. Eukaryot. Microbiol. **56**: 241 (notes on ontogenesis)

Diagnosis: Size about 140 × 15 µm in vivo. Shape very narrowly to cylindroidally dileptid with posterior end narrowly rounded, proboscis about 1/5 of body length. Macronucleus moniliform and tortuous, composed of 11 nodules on average; usually two narrowly ellipsoidal micronuclei. Contractile vacuoles, each with 1 excretory pore, in dorsal side of trunk: two close together in anterior third of trunk and one vacuole in posterior third. Two types of extrusomes: type I oblong with conical anterior end, 2.5 × 1 µm in size; type II oblong with rounded ends, 2 µm long. On average 7 ciliary rows, 2 anteriorly differentiated into a staggered, dimorphic, isostichad dorsal brush: brush row 1 composed of an average of 7 widely spaced dikinetids, brush row 2 composed of 11 ordinarily spaced dikinetids; both rows with a monokinetidal bristle tail extending to base of proboscis. Oral bulge opening about 8 × 5 µm in size. Circumoral kinety distinctly narrowed preorally. On average 8 widely spaced, strongly oblique preoral kineties, each composed of two widely spaced cilia.

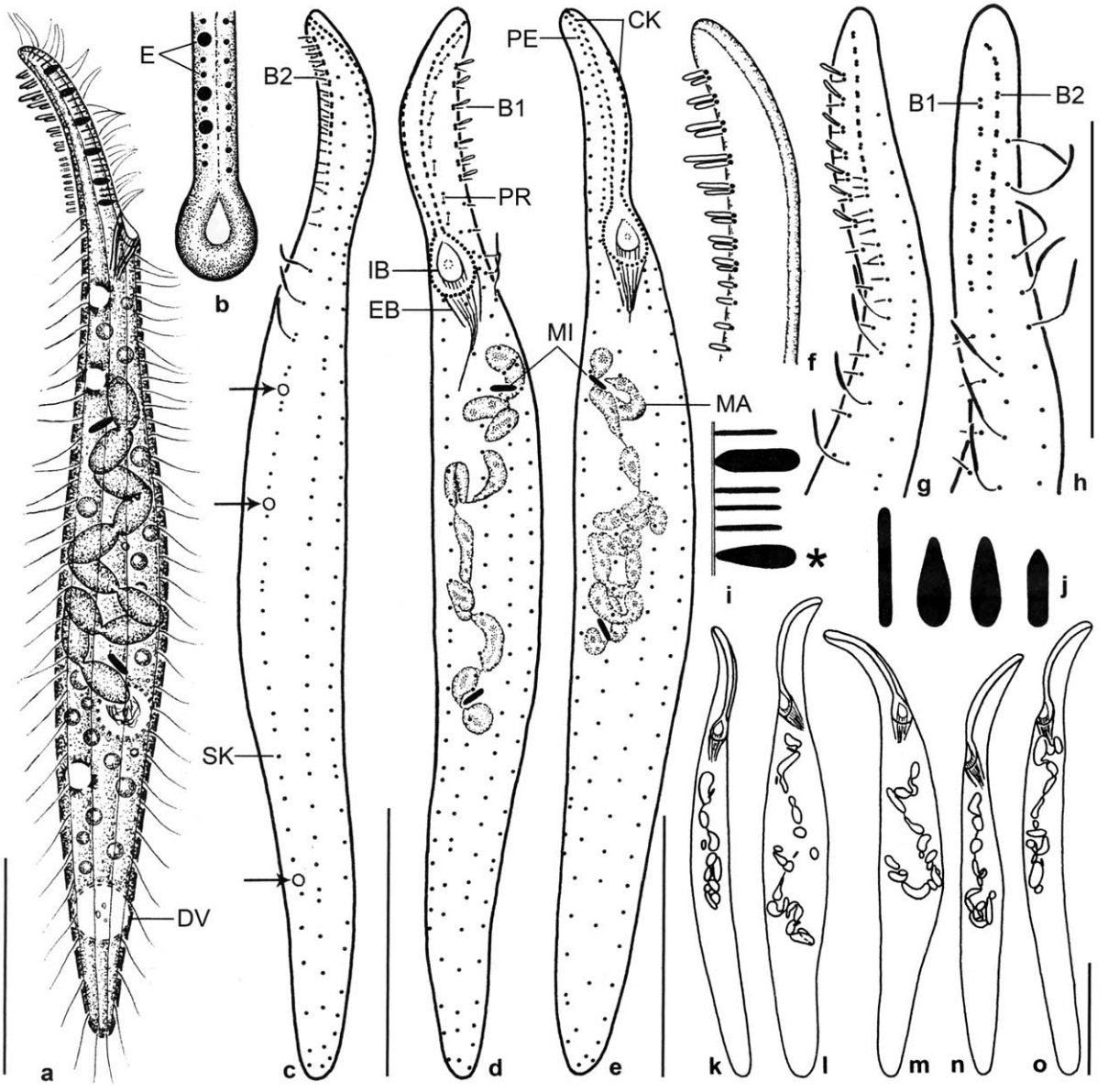
Type locality: Soil from a young *Pinus* forest between the towns of Katarraktis and Vlasia, Peloponnese, Greece, E21°57' N38°01'.

Type material: Vďačný & Foissner (2008b) deposited one holotype slide (inv. no. 2011/158) and eleven paratype slides (inv. nos 2011/159–169) with protargol-impregnated specimens in the Biology Centre of the Museum of Upper Austria, Linz (LI). Relevant specimens are marked by black ink circles on the coverslip.

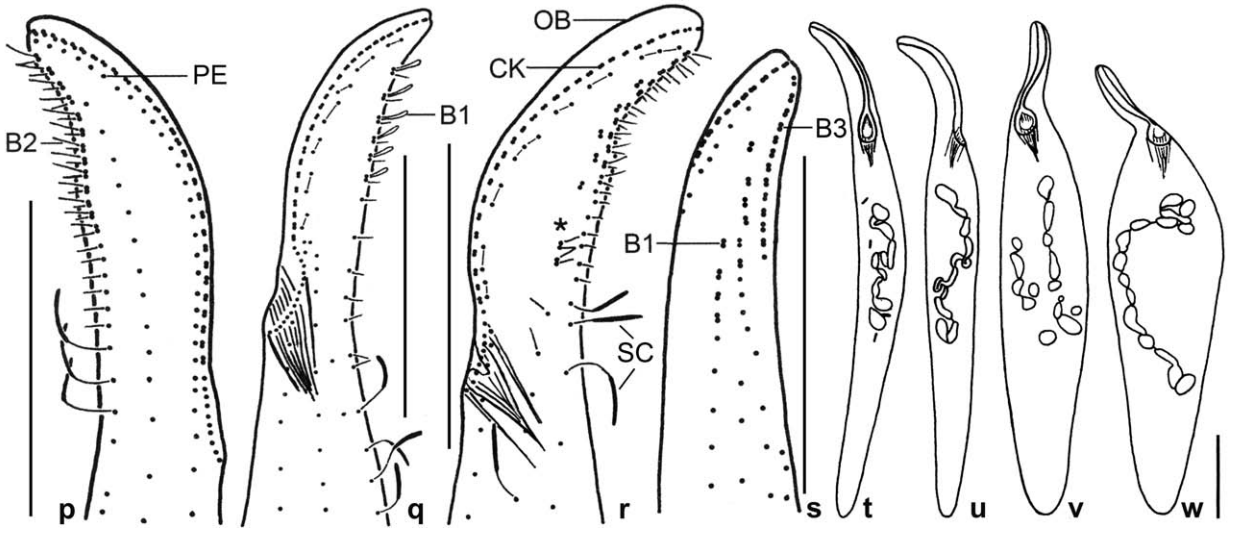
Etymology: Composite of the Greek adjective *brachy* (short) and the Latin noun *proboscis*, referring to the short proboscis, a main feature of the species.

Description: Size 120–150 × 10–20 μm in vivo, usually about 140 × 15 μm, as calculated from some in vivo measurements and the morphometric data, assuming 15% preparation shrinkage; flexible but not contractile. Shape very narrowly to cylindroidally dileptid, length:width ratio on average near 9:1. Proboscis occupies one fifth of body length on average, slightly curved dorsally, mid-region often inflated in protargol preparations; trunk cylindroidal, rarely narrowly fusiform, ventral margin often rather distinctly convex in mid of trunk, distinctly widened in well-fed specimens; posterior end narrowly rounded, never tail-like (Figs 127a, c–e, k–o, t–w, 128a, d; Table 63). Nuclear apparatus usually in anterior two thirds of trunk. Macronucleus highly variable, moniliform and tortuous, about 70 μm long in "uncoiled" condition, composed of an average of 11 oblong nodules; nucleoli medium- to large-sized, globular or ellipsoidal. One to four micronuclei, usually one micronucleus each near anterior and posterior end of macronucleus, conspicuous because narrowly ellipsoidal, that is, 3 × 1 μm in size (Figs 127a, d, e, k–o, t–w, 128a, d, g; Table 63). Contractile vacuoles in dorsal side of trunk, arranged in remarkable pattern, viz., two rather close together in anterior third of trunk and one vacuole in posterior third, vacuoles thus lacking in mid-body; rarely a third vacuole occurs in the anterior group and/or a second one in posterior third; usually a single (very rarely two) intrakinetal excretory pore per vacuole (Figs 127a, c, 128a; Table 63). Two types of extrusomes (Figs 127b, i, 128b): type I only in right branch of oral bulge, oblong with conical anterior end, appears narrowly ovate (!) when slightly out of focal plane (Fig. 127i, asterisk), about 2.5 × 1 μm in size, very rarely impregnates with protargol; type II in both bulge branches, more numerous than type I, oblong with both ends rounded, 2 μm long, does not stain with the protargol method used; developing cytoplasmic extrusomes sometimes impregnating with protargol, rod-shaped and 4 μm long or narrowly ovate to oblong and 3 μm long, and thus difficult to distinguish from micronuclei (Fig. 127j). Cortex flexible, contains about eight granule rows between adjacent kineties; granules colourless and ~ 0.5 × 0.2 μm in size. Cytoplasm colourless, in well-fed specimens packed with lipid droplets 1–3 μm across and 5 μm-sized food vacuoles with indefinable or crystalline contents; in posterior body end sometimes a defecation vacuole. Movement without peculiarities.

Cilia about 6 μm long in vivo, ordinarily spaced; in protargol preparations as typical for dileptids, i.e., with thick, strongly impregnated distal half, except for dorsal bristles; arranged in an average of seven longitudinal, ordinarily spaced rows leaving a rather wide, blank stripe left and right of oral bulge (Figs 127c–e; Table 63). First row right of circumoral kinety extends as perioral kinety with ordinarily to widely spaced cilia to tip of proboscis (Figs 127c, e, p). Invariably only one ciliary row between perioral kinety and brush row 2 (Figs 127c, p). Dorsal brush pattern highly specific and constant, that is, two dimorphic, staggered rows in over 700 specimens analyzed; a few, likely distorted cells have either three staggered rows (two specimens) or some irregularities in row 1 (one specimen; Figs 127r, s). Brush row 1 commences slightly more subapically than row 2, composed of an average of seven widely spaced dikinetids each having an about 3 μm long, slightly inflated anterior bristle and an about 2 μm long, oblong posterior bristle in protargol preparations. Brush row 2 begins near tip of proboscis, its anterior portion usually slightly curved rightwards, composed of an average of 11 ordinarily spaced dikinetids each associated with bristles similar to those of row 1, but anterior bristle not inflated (Figs 127c, d, g, h, p, q, 128c, e, f; Table 63). Bristles 4 μm long subapically, decreasing in length anteriorly and posteriorly according to the



Figs 127a–o: *Pseudomonilicaryon brachyproboscis* from life (a, b, f, i, j) and after protargol impregnation (c–e, g, h, k–o). From Vďačný & Foissner (2008b). **a** – right side view of a representative specimen, length 140 μm; **b** – frontal view of oral bulge opening and arrangement of extrusomes; **c, d** – dorsolateral and ventrolateral ciliary pattern and nuclear apparatus of holotype specimen, length 118 μm. Arrows mark the single excretory pore of the contractile vacuoles. Basal bodies of preoral kineties connected by lines; **e** – ventrolateral ciliary pattern and nuclear apparatus of a paratype specimen. Note the two narrowly ellipsoidal micronuclei, a unique feature as yet not found in other dileptids; **f** – fine structure of dorsal brush. The brush dikinetids are associated with slightly inflated bristles that are 4 μm long subapically and decrease in length anteriorly and posteriorly; **g, h** – dorsal ciliary pattern of proboscis. The dorsal brush is composed of two dimorphic, staggered, isostichad rows. Drawn to scale; **i** – there are two types of oral bulge extrusomes. Type I extrusomes are oblong with conical anterior end, 2.5 × 1 μm in size, and appear narrowly ovate when slightly out of focal plane (asterisk). Type II extrusomes are finely rod-shaped and 2 μm long; **j** – developing cytoplasmic extrusomes are rod-shaped (4 μm long), narrowly ovate to oblong (3 μm long), and oblong with conical anterior end (2.5 × 1 μm); **k–o** – variability of body shape and size as well as of nuclear apparatus. Drawn to scale. B1, 2 – dorsal brush rows, CK – circumoral kinety, DV – defecation vacuole, EB – external basket, E – extrusomes, IB – internal basket, MA – macronuclear nodules, MI – micronucleus, PE – perioral kinety, PR – preoral kinety, SK – somatic kinety. Scale bars: 30 μm (a, c–e, k–o) and 20 μm (g, h).



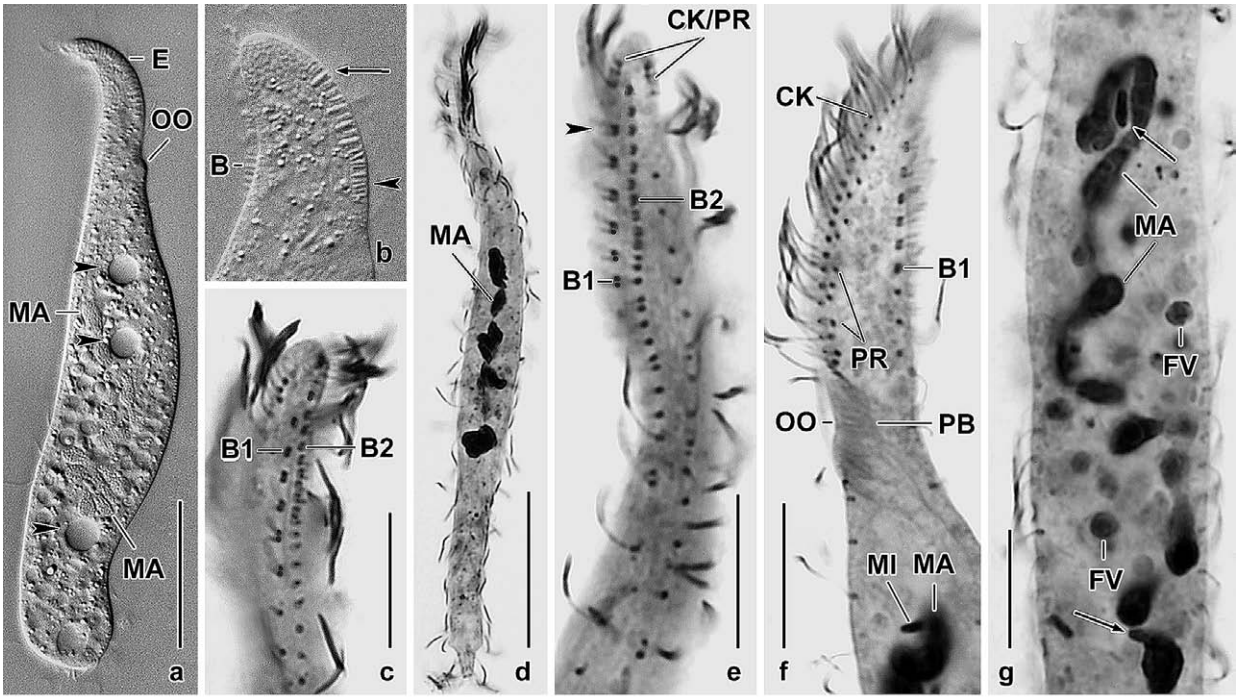
Figs 127p–w: *Pseudomonilicaryon brachyproboscis* after protargol impregnation. From Vďačný & Foissner (2008b). **p** – right side ciliary pattern of anterior body portion; **q, r** – left side ciliary pattern of anterior body portion. Asterisk marks a break in dorsal brush row 1. Basal bodies of preoral kineties connected by lines; **s** – dorsolateral view of a proboscis with three staggered brush rows; **t–w** – variability of body shape and size as well as of nuclear apparatus; Drawn to scale. B1–3 – dorsal brush rows, CK – circumoral kinety, OB – oral bulge, PE – perioral kinety, SC – somatic cilia. Scale bars: 20 μm.

live observations (Fig. 127f). Both rows continue with a short monokinetidal tail composed of about 2 μm long type VI bristles (Figs 127a, c, d, g, p–r).

Oral bulge opening at end of anterior body fifth, ovate to broadly ovate, in vivo about 6 μm across (Fig. 127b; Table 63). Pharyngeal basket small, internal basket indistinctly bulbous both in vivo and after protargol impregnation, external basket impregnated only in distal portion. Oral ciliary pattern basically as in other dileptids, but with a special feature, viz., a distinct preoral narrowing of the circumoral kinety/oral bulge (Figs 127d, e). Circumoral kinety composed of ordinarily spaced dikinetids, except of narrowly spaced monokinetids around oral bulge opening. On average eight widely spaced, strongly oblique preoral kineties, each composed of only two, rarely three widely spaced cilia (Figs 127d, q, r, 128f).

Notes on ontogenesis (Figs 129a–r; Table 64): The ontogenesis basically agrees with that of *Monomacrocaryon terrenum* (Vďačný & Foissner 2009). The following peculiarities are probably genus- or species-specific: (i) early dividers display a transient indentation in the prospective fission area, just as known from several spathidiids (Figs 129k, l, arrowheads); (ii) the anterior portion of two right side ciliary rows generates the new perioral kinety, but the more dorsally located kinety contributes fewer kinetids than the more ventrally located one (1–4 vs. ~ 10 kinetids; Figs 129e, f, j, arrowheads); (iii) the preoral kineties are very likely produced by only one kinety – the first row right of the dorsal brush (Figs 129g–i); possibly brush row 1 is also involved in this process (Fig. 129g); (iv) the staggered pattern of the dorsal brush rows and the dimorphic arrangement of the dikinetids develop post-divisionally (Figs 129e, h–i); and (v) the micronucleus massively changes its shape from narrowly ellipsoidal (3 × 1 μm in size) to globular (~ 4 μm in diameter) during early ontogenesis (cp. Figs 127d, e, 128g, 129l with Figs 129m, o–q, arrows; Table 64), and becomes narrowly ellipsoidal again in late dividers, when the fused macronuclear nodules commence division (Fig. 129r).

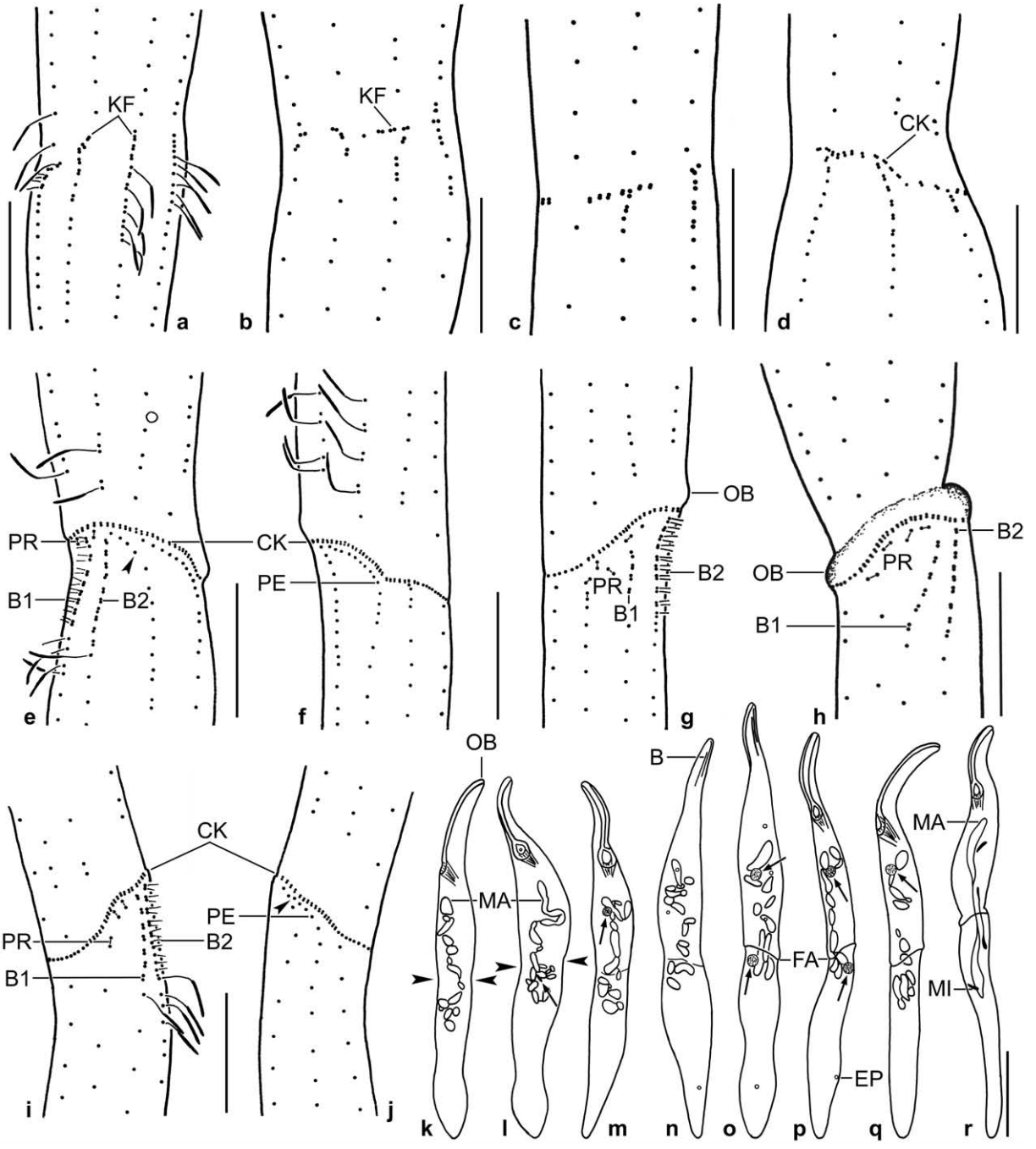
Occurrence and ecology: *Pseudomonilicaryon brachyproboscis* was rather abundant in the non-flooded Petri dish culture from the type locality, where the litter layer was thin, poorly decomposed, but locally



Figs 128a–g: *Pseudomonilicaryon brachyproboscis* from life (a, b) and after protargol impregnation (c–g). From Vďačný & Foissner (2008b). **a** – right side view of a squeezed specimen. Arrowheads mark the contractile vacuoles; **b** – there are two types of extrusomes anchored in the proboscis: type I is oblong with a conical anterior end and 2.5 × 1 µm in size (arrow), while the oblong type II is 2 µm long (arrowhead); **c, e** – dorsolateral ciliary pattern of proboscis. The dorsal brush consists of two staggered and dimorphic rows, that is, row 1 commences slightly more subapically than row 2 (arrowhead) and consists of loosely spaced dikinetids, while row 2 has ordinarily spaced dikinetids; **d** – ventral view of a representative specimen, showing the slender body and moniliform macronucleus; **f** – left side ciliary pattern in anterior body portion. The widely spaced preoral kineties are strongly oblique and composed of two to three widely spaced basal bodies; **g** – the nuclear apparatus consists of a highly tortuous, moniliform macronuclear strand and two narrowly ellipsoidal micronuclei (arrows), one each near the anterior and posterior end of the macronuclear strand. B(1, 2) – dorsal brush (rows), CK – circumoral kinety, E – extrusomes, FV – food vacuoles, MA – macronuclear nodules, MI – micronucleus, OO – oral bulge opening, PB – pharyngeal basket, PR – preoral kineties. Scale bars: 30 µm (a, d) and 10 µm (c, e–g).

penetrated by moss and masses of fungal hyphae. The sample consisted of a mixture of *Pinus* needles and terrestrial mosses; pH 6.3. A second population was found in slightly saline soil from the margin of the Zicklacke, a saline inland lake in Burgenland, Austria.

Remarks: *Pseudomonilicaryon brachyproboscis* is unique in having narrowly ellipsoidal micronuclei, an unusual shape as yet not found in other dileptids, but present in some spathidiids (e.g., *Arcuospathidium namibiense* and *A. etoschense*; Foissner & Xu 2007) and bryophyllids (e.g., *Apobryophyllum vermiforme*; Foissner et al. 2002). Further, *Pseudomonilicaryon brachyproboscis* displays a curious contractile vacuole pattern, which is rather constant and is thus possibly a reliable feature of this species. These two basic differences are not included in the following comparison. There are only two congeners similar to *P. brachyproboscis*, viz., *P. gracile* and *P. anguillula*. However, *P. gracile* differs from *P. brachyproboscis* by the much higher number of ciliary rows (15 vs. 7), and *P. anguillula* is distinguished from *P. brachyproboscis* by the shape of the extrusomes (finely rod-shaped vs. oblong with conical anterior end). A further similar species is *Microdileptus breviproboscis* which, however, is binucleate.



Figs 129a–r. *Pseudomonilicaryon brachyproboscis*, ciliary pattern (a–j) and body as well as nuclear changes (k–r) in dividers after protargol impregnation. From Vďačný & Foissner (2009). **a–d –** right side (a) and dorsal (b–d) views of early dividers developing circumoral kinetofragments; **e, f, j –** dorsolateral (e) and right side (f, j) views of mid-dividers. The perioral kinety is produced from kinetofragments developing in the anterior portion of two right side ciliary rows, but the more dorsally located kinety contributes with fewer kinetids (arrowheads) than the more ventrally located one; **g–i –** left side views of mid-dividers, showing the origin of the preoral kineties (connected by lines) by proliferation from the anterior end of the first kinety right of the dorsal brush; **k–r –** very early dividers are indented in the prospective fission area (arrowheads). In mid-dividers, the micronuclei become globular (arrows). Further explanations, see text. Drawn to scale. CK – circumoral kinety, B(1, 2) – dorsal brush (rows), EP – excretory pore of contractile vacuole, FA – fission area, KF – circumoral kinetofragments, MA – macronuclear nodules, MI – micronucleus, OB – oral bulge, PE – perioral kinety, PR – preoral kineties. Scale bars: 10 μm (a–j) and 30 μm (k–r).

Table 63: Morphometric data on *Pseudomonilicaryon brachyproboscis* (from Vďačný & Foissner 2008b). Data based on mounted, protargol-impregnated (Foissner's method), and randomly selected specimens from a non-flooded Petri dish culture. Measurements in µm. CV – coefficient of variation in %, M – median, Max – maximum, Mean – arithmetic mean, Min – minimum, n – number of specimens investigated, SD – standard deviation, SE – standard error of mean.

Characteristics	Mean	M	SD	SE	CV	Min	Max	n
Body, length	123.6	126.0	9.1	2.0	7.4	106.0	136.0	21
Body, width	13.8	14.0	2.6	0.6	18.6	10.0	19.0	21
Body length:width, ratio	9.2	9.8	1.6	0.3	16.8	6.7	11.9	21
Anterior body end to oral bulge opening, distance	23.5	24.0	3.0	0.7	12.7	16.0	29.0	21
Proboscis, % of body length	19.0	19.1	1.7	0.4	8.8	14.3	21.6	21
Oral bulge opening, length	7.7	8.0	0.7	0.1	8.8	7.0	9.0	21
Oral bulge opening, width	5.2	5.0	0.3	0.1	5.8	5.0	6.0	19
Anterior body end to macronucleus, distance	42.9	41.0	5.4	1.2	12.7	33.0	56.0	21
Nuclear figure, length	39.3	39.0	9.4	2.1	24.0	26.0	60.0	21
Macronucleus, total length ("uncoiled"; rough values)	68.8	69.0	–	–	–	44.0	92.0	21
Anteriormost macronuclear nodule, length	9.2	8.0	3.9	0.9	42.6	3.0	22.0	21
Anteriormost macronuclear nodule, width	3.7	4.0	0.7	0.2	19.4	3.0	5.0	21
Macronuclear nodules, number	11.8	11.0	2.7	0.6	23.3	8.0	19.0	21
Micronucleus, length	2.9	3.0	0.4	0.1	15.4	2.0	4.0	19
Micronucleus, width	1.0	1.0	–	–	–	0.5	1.0	19
Micronuclei, number	1.9	2.0	0.8	0.2	42.7	1.0	4.0	19
Ciliary rows, number	7.4	7.0	0.6	0.1	8.0	6.0	8.0	21
Cilia in mid-body in 10 µm, number	4.8	5.0	0.9	0.2	18.1	4.0	6.0	21
Preoral kineties, number	8.4	8.0	0.6	0.2	7.7	7.0	9.0	14
Dorsal brush rows, number[a]	2.0	2.0	0.0	0.0	0.0	2.0	2.0	21
Dikinetids in brush row 1, number	6.9	7.0	0.7	0.1	9.5	6.0	9.0	21
Dikinetids in brush row 2, number	11.1	11.0	1.0	0.2	8.6	10.0	13.0	21
Anterior body end to last dikinetid of brush row 1, distance	17.3	17.0	1.6	0.4	9.3	13.0	19.0	21
Anterior body end to last dikinetid of brush row 2, distance	13.4	13.0	1.4	0.3	10.3	11.0	16.0	21
Contractile vacuoles, number[b]	3.2	3.0	0.4	0.1	12.6	3.0	4.0	21

[a] In over 700 specimens analyzed, only two had three brush rows and one specimen had some irregularities in row 1.

[b] Usually only a single pore per vacuole; thus the number of pores corresponds with the number of contractile vacuoles.

Pseudomonilicaryon anguillula (Kahl, 1931) nov. comb. (Figs 130a–p; Tables 41, 65)

1931 *Dileptus anguillula* spec. n. Kahl, Tierwelt Dtl. **21**: 208

1963 *Dileptus anguillula* Kahl, 1931 – Dragesco, Bull. biol. Fr. Belg. **97**: 119 (first taxonomic reviser)

1984 *Dileptus anguillula* Kahl, 1931 – Foissner, Stapfia **12**: 94 (description of an Austrian population)

2002 *Dileptus anguillula* Kahl, 1932 – Foissner, Agatha & Berger, Denisia **5**: 370 (redefinition and comparison with *Microdileptus breviproboscis*; misdated)

Table 64: Morphometric data on dividing specimens of *Pseudomonilicaryon brachyproboscis*. Data based on mounted, protargol-impregnated (Foissner's method), and randomly selected specimens from a non-flooded Petri dish culture. Measurements in µm. CV – coefficient of variation in %, M – median, Max – maximum, Mean – arithmetic mean, Min – minimum, n – number of specimens investigated, SD – standard deviation, SE – standard error of mean.

Characteristics	Stage[a]	Mean	M	SD	SE	CV	Min	Max	n
Body, length	Very early divider	130.4	128.0	11.8	2.6	9.1	115.0	153.0	21
	Early divider	132.0	131.0	10.9	4.4	8.2	120.0	145.0	6
	Early mid-divider	143.2	143.0	7.6	3.1	5.3	133.0	154.0	6
Body, width	Very early divider	15.4	15.0	2.0	0.4	13.0	12.0	21.0	21
	Early divider	16.7	18.0	3.1	1.3	18.7	12.0	20.0	6
	Early mid-divider	15.0	15.0	1.0	0.4	6.7	14.0	17.0	7
Body length:width, ratio	Very early divider	8.6	8.7	1.2	0.3	13.9	6.4	10.5	21
	Early divider	8.3	7.2	2.3	1.0	28.2	6.2	12.0	6
	Early mid-divider	9.6	9.9	0.9	0.3	8.9	8.4	10.5	6
Anterior body end to oral bulge opening, distance	Very early divider	8.6	8.7	1.2	0.3	13.9	6.4	10.5	21
	Early divider	22.2	23.0	1.8	0.7	7.9	20.0	24.0	6
	Early mid-divider	24.5	25.0	4.6	1.9	18.7	17.0	31.0	6
Proboscis, % of body length	Very early divider	19.1	19.1	1.7	0.4	8.8	14.4	22.8	21
	Early divider	16.9	16.7	1.6	0.7	9.8	14.3	18.9	6
	Early mid-divider	17.2	17.7	3.3	1.4	19.5	11.4	21.6	6
Proter, length	Very early divider	69.9	70.0	7.9	1.7	11.2	60.0	84.0	21
	Early divider	72.5	73.0	5.4	2.2	7.4	67.0	79.0	6
	Early mid-divider	76.5	78.0	6.9	2.8	9.0	65.0	84.0	6
Proter, width	Very early divider	14.7	15.0	2.2	0.5	15.2	10.0	21.0	21
	Early divider	15.1	16.0	2.6	1.1	17.5	12.0	19.0	6
	Early mid-divider	14.3	14.0	1.5	0.6	10.5	12.0	17.0	7
Proter length:width, ratio	Very early divider	4.9	4.7	0.9	0.2	18.1	3.3	6.6	21
	Early divider	5.0	4.5	1.3	0.5	25.1	3.8	6.6	6
	Early mid-divider	5.2	5.4	0.5	0.2	9.9	4.6	5.9	6
Proboscis, % of proter length	Very early divider	35.7	35.8	3.0	0.6	8.3	27.5	40.3	21
	Early divider	30.7	30.8	2.9	1.2	9.4	25.9	33.6	6
	Early mid-divider	31.9	31.4	4.2	1.7	13.3	25.6	38.6	6
Opisthe, length	Very early divider	60.4	60.0	5.3	1.2	8.7	51.0	71.0	21
	Early divider	59.5	59.0	5.7	2.3	9.6	54.0	68.0	6
	Early mid-divider	66.4	64.0	7.4	2.8	11.2	59.0	81.0	7
Opisthe, width	Very early divider	14.4	14.0	2.8	0.6	19.5	10.0	21.0	21
	Early divider	15.3	15.0	3.7	1.5	24.1	10.0	20.0	6
	Early mid-divider	13.2	14.0	2.2	0.8	16.6	10.0	16.0	7

Characteristics	Stage[a]	Mean	M	SD	SE	CV	Min	Max	n
Opisthe length:width, ratio	Very early divider	4.3	4.2	0.9	0.2	20.5	3.1	6.5	21
	Early divider	4.1	3.8	1.4	0.6	34.7	2.7	6.8	6
	Early mid-divider	5.2	5.1	1.4	0.5	27.3	3.9	8.1	7
Proter:opisthe length, ratio	Very early divider	1.2	1.1	–	–	–	1.0	1.3	21
	Early divider	1.2	1.2	–	–	–	1.1	1.3	6
	Early mid-divider	1.2	1.2	–	–	–	0.8	1.3	6
Macronucleus, total length	Very early divider	67.2	70.0	7.9	1.7	11.8	47.0	79.0	21
	Early divider	73.2	75.0	5.8	2.4	7.9	62.0	78.0	6
	Early mid-divider	76.1	81.0	17.8	6.7	23.4	54.0	106.0	7
Micronucleus, largest diameter	Very early divider	3.2	3.0	–	–	–	3.0	4.0	16
	Early divider	3.2	3.0	–	–	–	3.0	4.0	5
	Early mid-divider	3.9	4.0	–	–	–	3.0	4.0	7

[a] Very early dividers are characterized by the proliferation of basal bodies in mid-body, while early dividers have developed oral kinetofragments. Early mid-dividers have a continuous circumoral kinety on both sides of the cell.

non *Dileptus anguillula* KAHL – FOISSNER, AGATHA, & BERGER, Denisia **5**: 38 (par lapsus, see *R. brasiliensis*)

Generic affiliation, taxonomy and nomenclature: JANKOWSKI (1967) did not combine *Dileptus anguillula* with one of his subgenera. Our data show that it belongs to *Pseudomonilicaryon* because it has a *Dileptus*-like oral ciliary pattern and a moniliform macronucleus. *Pseudomonilicaryon anguillula* is most similar to *P. brachyproboscis*, *Microdileptus breviproboscis*, and *Rimaleptus brasiliense* in having a slender body with short proboscis and at least three dorsal contractile vacuoles (Table 41). However, *P. anguillula* differs from them, except of *P. brachyproboscis*, by the macronuclear pattern (a moniliform strand vs. two nodules). *Pseudomonilicaryon anguillula* is distinguished from *P. brachyproboscis* mainly by the extrusomes (thin and rod-shaped vs. massive and oblong with conical anterior end) and the shape of the micronuclei (globular vs. elongate ellipsoidal).

Improved diagnosis: Size about 140 × 20 μm in vivo. Shape very narrowly to cylindroidally dileptid with acute to narrowly rounded posterior end, proboscis about 1/5 of body length. Macronucleus moniliform and tortuous, usually composed of about 9 nodules; 1–2 micronuclei. A dorsal row of contractile vacuoles. Extrusomes attached to proboscis oral bulge, rod-shaped, 3–4 μm long. On average 10 ciliary rows, 2 anteriorly differentiated into a staggered, isostichad dorsal brush with bristles up to 4 μm long. Oral bulge opening about 6 μm across. Circumoral kinety distinctly narrowed preorally. Preoral kineties widely spaced, strongly oblique, each composed of 2–3 ordinarily to widely spaced kinetids.

Type locality: KAHL (1931) did not specify the type locality, referring to Northern Germany and the Austrian calcareous and granitic Alps.

Type and voucher material: Neither KAHL (1931) nor FOISSNER (1984) deposited type or voucher material, respectively (inv. nos 2007/781-785). Thus, we reinvestigated the population studied by FOISSNER (1984) and have deposited three voucher slides with protargol-impregnated specimens in the Biology Centre of the Museum of Upper Austria, Linz (LI). Relevant specimens are marked by black ink circles on the coverslip.

Etymology: Not given in original description. The Latin *anguillula* (little eel) is a noun in apposition, obviously referring to the slender body of the species.

Description: Size about 140 × 20 μm in vivo: type specimens 120–150 μm long (KAHL 1931), Austrian cells

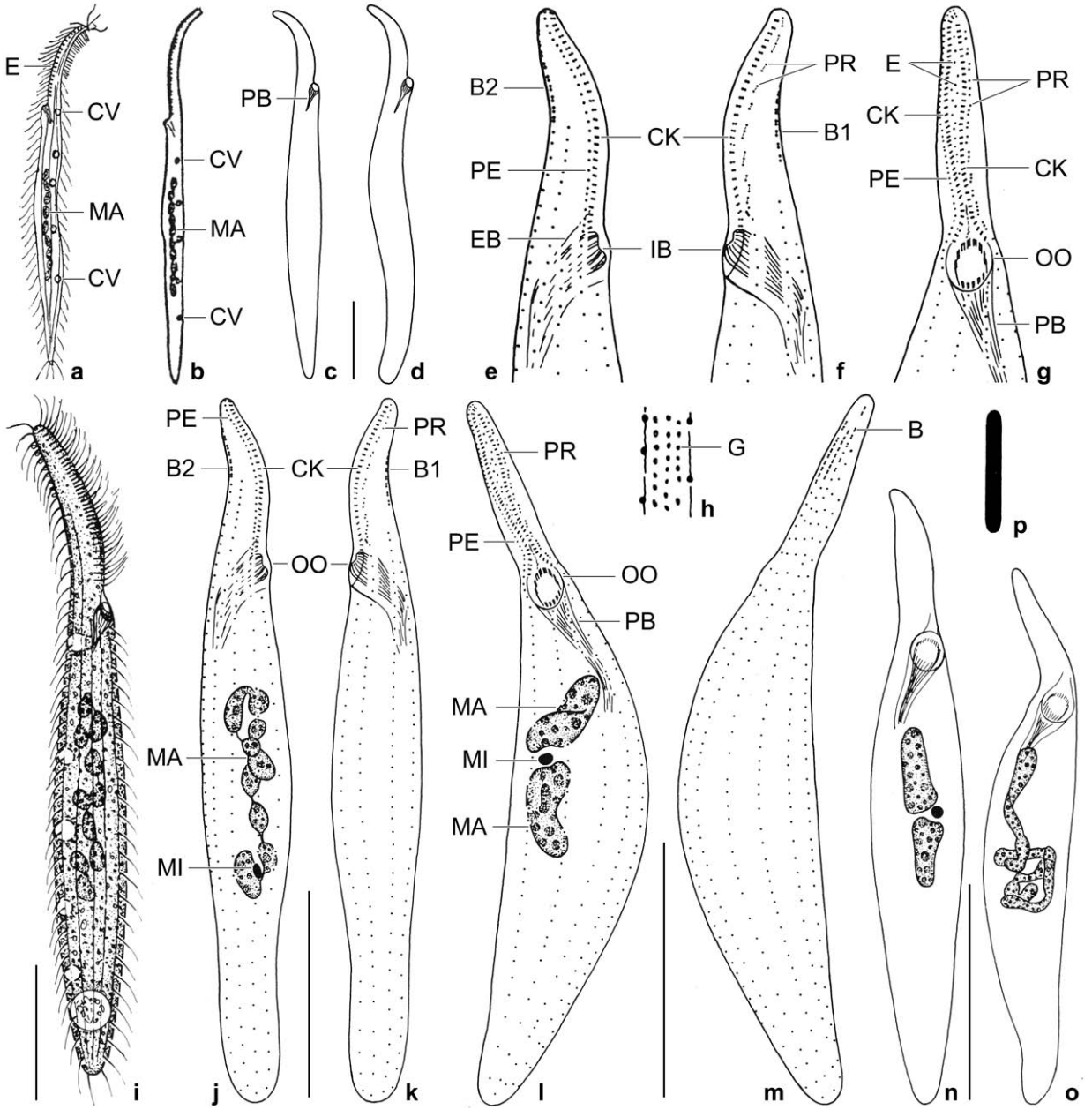
140–170 × 15–20 µm in size as calculated from the morphometric data (Table 65), Singapore specimens 110–120 × 20–25 µm. Body very flexible but not contractile. Shape narrowly dileptid to rod-like, i.e., length:width ratio in type specimen about 14:1 and in an Austrian cell about 9:1 in vivo, according to the figures provided; Austrian cells inflated in protargol preparations (Figs 130a–d, i–o; Table 65). Proboscis indistinct because hardly set off from trunk and occupying only 22% body length on average, more or less distinctly curved dorsally. Trunk oblong, sometimes widened in mid-portion after protargol impregnation, posterior end acute to narrowly rounded (Figs 130a–d, i–o). Nuclear apparatus usually in middle quarters of trunk. Macronucleus a moniliform strand of about nine oblong nodules in type specimens (Kahl 1931) and of 6–11 nodules in Austrian cells, where two out of hundred specimens had only two nodules (Foissner 1984 and new data; see *Microdileptus breviproboscis*); nucleoli globular to oblong, evenly distributed. One or two micronuclei in between macronuclear nodules or attached to macronuclear strand, about 2 µm across in protargol preparations (Figs 130a, b, i, j, l, n, o; Table 65). A dorsal row of four to five contractile vacuoles: first vacuole at or slightly posterior of level of oral bulge opening (Figs 130a, b, i); sometimes a pair of vacuoles each at anterior and near posterior end of trunk in Singapore specimens. Extrusomes studied in several populations from Singapore, Canada and Brazil, attached to proboscis oral bulge, inconspicuous, i.e., rod-shaped and only 3–4 µm long in vivo (Fig. 130p). Cortex very flexible, contains three (Austrian specimens) to six (Singapore specimens) oblique granule rows between adjacent kineties; granules about 0.2 µm across (Fig. 130h). Cytoplasm colourless, hyaline; in rear end sometimes a defecation vacuole.

Cilia 7–8 µm long in vivo, ordinarily to narrowly spaced; arranged in an average of ten longitudinal,

Table 65: Morphometric data on an Austrian population of *Pseudomonilicaryon anguillula* (from Foissner 1984). Data based on mounted, protargol-impregnated (Foissner's method), and randomly selected specimens from a non-flooded Petri dish culture. Measurements in µm. CV – coefficient of variation in %, M – median, Max – maximum, Mean – arithmetic mean, Min – minimum, n – number of specimens investigated, SD – standard deviation, SE – standard error of mean.

Characteristics	Mean	M	SD	SE	CV	Min	Max	n
Body, length	90.3	91.0	17.5	5.5	19.4	60.0	116.0	10
Body, width	16.1	14.5	1.4	0.5	9.0	13.0	21.0	10
Body length:width, ratio (calculated from raw data)	5.9	5.7	1.0	0.3	16.7	4.6	7.4	10
Anterior body end to oral bulge opening, distance	19.4	19.0	3.9	1.2	20.2	14.0	26.0	10
Proboscis, % of body length (calculated from raw data)	22.1	22.4	2.6	0.8	11.8	18.2	26.7	10
Oral bulge opening, length	5.9	6.0	0.5	0.2	8.4	5.0	7.0	10
Oral bulge opening, width	5.9	6.0	0.5	0.2	8.4	5.0	7.0	10
Nuclear figure, length	25.5	24.0	6.8	2.2	26.8	14.0	38.0	10
Macronuclear nodules, length	8.7	8.4	2.5	0.8	29.1	5.6	13.0	10
Macronuclear nodules, width	3.9	3.7	1.1	0.3	27.5	2.8	6.0	10
Macronuclear nodules, number[a]	5.8	6.5	3.3	1.1	57.4	2.0	11.0	10
Micronucleus, diameter	2.0	1.7	–	–	–	1.5	3.0	9
Micronucleus, number	1.0	1.0	0.0	0.0	0.0	1.0	1.0	10
Ciliary rows, number in mid-body	10.1	10.0	1.2	0.4	11.8	8.0	12.0	10
Cilia in mid-body in 10 µm, number	5.5	5.0	1.0	0.3	17.7	4.0	7.0	10
Dorsal brush rows, number (calculated from raw data)	2.2	2.0	–	–	–	2.0	3.0	10

[a] Only two out of hundred specimens had two macronuclear nodules.



Figs 130a-p. *Pseudomonilicaryon anguillula* from life (a-d, h, i, p) and after protargol impregnation (e-g, j-o). From Kahl 1931 (a), Dragesco 1963 (b), Foissner 1984 (c-o), and original (p). **a** – left side view of type specimen, length 140 µm; **b** – redrawn type specimen; **c, d** – shape variants; **e, f** – higher magnification of right and left side ciliary pattern of the specimen shown in (j, k); **g** – higher magnification of oral ciliary pattern of the specimen shown in (l). Note preoral narrowing (or widening of mid-proboscis) of circumoral kinety or oral bulge, a rare feature found also in *P. brachyproboscis*; **h** – surface view showing cortical granulation; **i** – right side view of a representative Austrian specimen, length 150 µm; **j, k** – ciliary pattern of right and left side of a typical specimen with moniliform macronucleus; **l, m** – ciliary pattern of ventral and dorsal side of an "abnormal" binucleate specimen with three-rowed dorsal brush; **n, o** – variability of body shape and size as well as of nuclear apparatus. Two out of hundred specimens had the macronucleus composed of two nodules (l, n). Drawn to scale; **p** – Singapore specimens have rod-shaped, 3–4 µm long extrusomes. B(1, 2) – dorsal brush (rows), CK – circumoral kinety, CV – contractile vacuoles, E – extrusomes, EB – external oral basket, G – cortical granules, IB – internal oral basket, MA – macronuclear nodules, MI – micronucleus, OO – oral bulge opening, OB – oral bulge, PB – pharyngeal basket, PE – perioral kinety, PR – preoral kineties. Scale bars 30 µm.

ordinarily spaced rows leaving a rather wide, blank stripe left and right of oral bulge (Figs 130e, f, j, k; Table 65). First row right of circumoral kinety extends as perioral kinety with widely spaced cilia to tip of proboscis (Figs 130e, g, j, l). Only one ciliary row between perioral kinety and brush row 2 (Figs 130e, j). Dorsal brush exactly on dorsal side of proboscis, usually composed of two staggered, isostichad rows both extending to base of proboscis with a monokinetidal tail of 1.5–2 µm long bristles; two out of ten specimens, possibly distorted cells, with three staggered rows (Fig. 130m; Table 65). Brush dikinetids loosely to ordinarily spaced and associated with clavate bristles both being about 2.5 µm long after protargol impregnation in Austrian specimens (re-analysis of protargol-impregnated specimens).

Oral bulge opening at end of anterior body fifth, projects only slightly because base of proboscis almost as wide as trunk, about 6 µm across in protargol preparations (Figs 130g, l, n, o; Table 65). Pharyngeal basket possibly bulbous, internal basket impregnates more distinctly than external. Oral ciliary pattern basically as in other dileptids, but with a special feature found also in *P. brachyproboscis*, viz., a preoral narrowing of the circumoral kinety or oral bulge (Figs 130g, l). Circumoral kinety composed of widely spaced dikinetids, except for narrowly spaced kinetids forming a line around oral bulge opening. About 11 widely spaced, strongly oblique preoral kineties, each composed of two to three ordinarily to widely spaced cilia (Figs 130f, g, k, l).

Occurrence and ecology: Some of the faunistic data on *P. anguillula* very likely refer to *Microdileptus breviproboscis* or vice versa because of the taxonomic problems explained in *M. breviproboscis*. Foissner (1984) found *Pseudomonilicaryon anguillula* in brown, alluvial soil of a Mesobrometum in Lower Austria, near the village of Bierbaum. Since then, it has been recorded in terrestrial habitats from all biogeographic regions, except Antarctica and the islands in the southern oceans: in soil from various forests in Austria and Germany (Aescht & Foissner 1993, Foissner et al. 2005); in inland dunes of the Hoge Veluwe National Park, The Netherlands (Foissner & Al-Rasheid 2007); in soil from Belgium (Chardez 1967, 1987); frequent in mor humus of a beech forest from Denmark (Stout 1968); mor and mull humus of beechwood soil in the Chiltern Hills, England (Stout 1963); in leaf litter from Devínska Kobyla, western Slovakia (Tirjaková 2005); in soil and mosses from Canada (Foissner et al. 2002); in leaf litter and soil from a variety of localities in the vicinity of the town of Manaus, Brazil (Foissner 1997b); in the upper soil layer (pH 3.3) from a primary rain forest in the Bukit Timah Nature Reserve, Singapore (Foissner 2008); in bark of *Eucalyptus* and in brown leaf litter with distinct signs of decomposition (pH 5.5) from Cairns, Australia (Blatterer & Foissner 1988, Foissner 1997b); in tussock and pasture soil in New Zealand (Stout 1958, 1960); and in lightly and heavily burnt soils of New Zealand (Stout 1961).

There are also a few unsubstantiated limnetic records: in a eutrophic lake in England (Webb 1961) and in the beta- to alpha-mesosaprobic Antiesen River and Gusen River in Upper Austria (Blatterer 1994, AOÖLR 1996).

Pseudomonilicaryon angustistoma Foissner, Agatha & Berger, 2002 (Figs 131a–u; Table 66)

2002 *Pseudomonilicaryon angustistoma* nov. sp. Foissner, Agatha & Berger, Denisia **5**: 382

Improved diagnosis: Size about 400 × 35 µm in vivo. Shape very narrowly dileptid to rod-like with distinct tail, proboscis about 37% of body length. Macronucleus moniliform, composed of an average of 18 ellipsoidal to very narrowly ellipsoidal nodules; several globular micronuclei. A dorsal stripe of contractile vacuoles with 1–2 pores each. Two types of extrusomes attached to proboscis oral bulge: type I very narrowly ovate, 6 µm long; type II oblong, about 2 µm long. On average 39 narrowly spaced ciliary rows, up to 10 anteriorly differentiated into a staggered, distinctly heterostichad, complex dorsal brush with three types of bristles and monokinetidal tails extending to base of proboscis. Oral bulge opening

elliptical, about 25 × 10 μm in size. Preoral kineties widely spaced, oblique, each usually composed of 3 ordinarily spaced cilia.

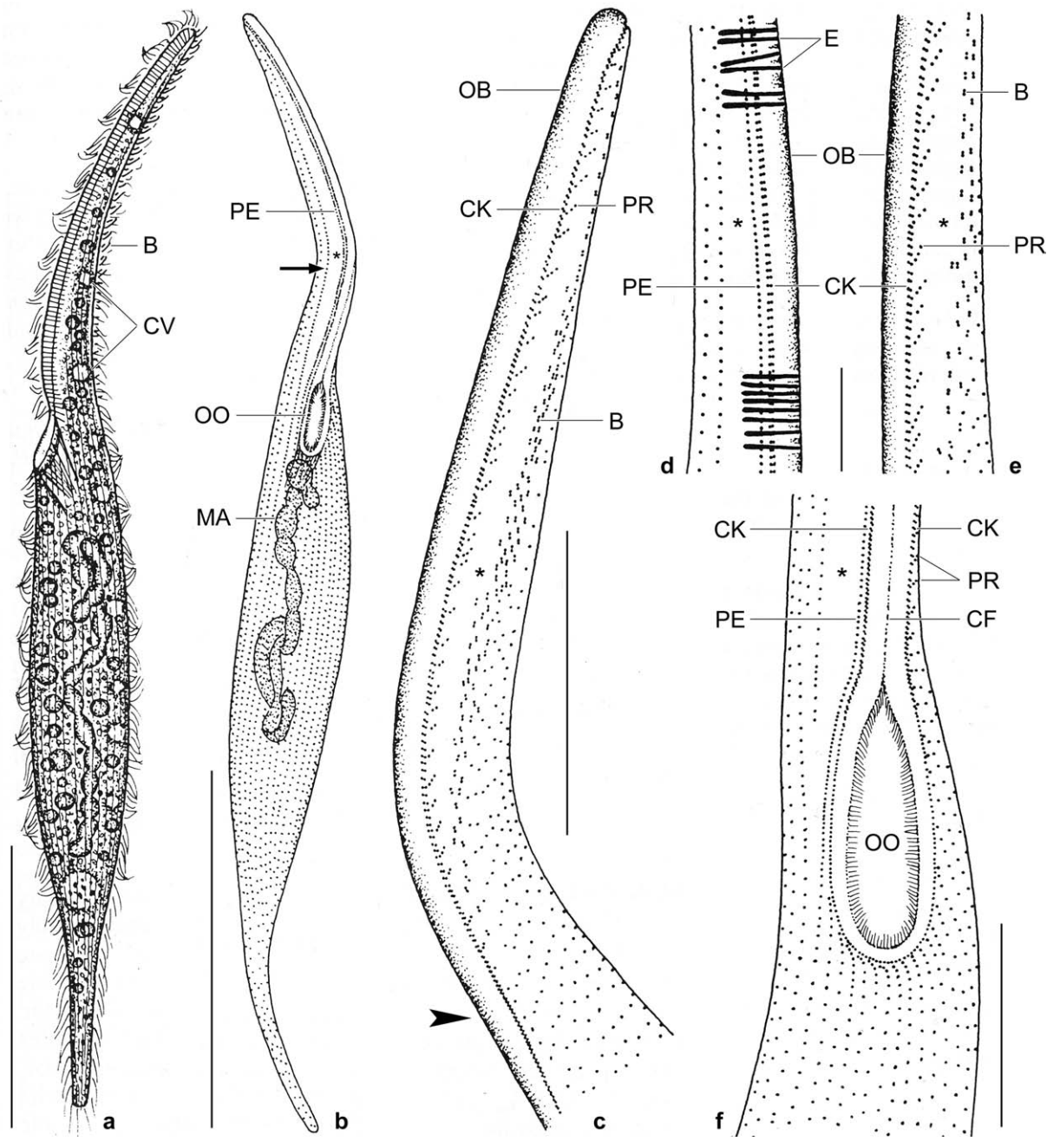
Type locality: Mud and soil from road puddles in the Bambatsi Guest Farm between the towns of Khorixas and Outjo, Namibia, E15°25' S20°10'.

Type material: Foissner et al. (2002) deposited one holotype slide (inv. no. 2002/364) and two paratype slides (inv. nos 2002/362 and 2002/363) with protargol-impregnated specimens in the Biology Centre of the Museum of Upper Austria, Linz (LI). Relevant specimens are marked by black ink circles.

Etymology: Apposite noun composed of the Latin adjective *angustus* (narrow) and the Greek noun *stoma* (mouth), meaning having a "narrow-mouth".

Description: Size highly variable, i.e., 250–650 × 25–65 μm in vivo, usually about 400 × 35 μm, as calculated from some in vivo measurements and the morphometric data, assuming about 10% preparation shrinkage (Table 66); very flexible but not contractile. Shape very narrowly dileptid to rod-like, i.e., length:width ratio 7.9–17.4:1, on average 11.4:1 in protargol preparations. Length of proboscis also highly variable, viz., 25% to 46% of body length, on average about 37%, usually curved dorsally; trunk oblong to cylindroidal, unflattened; posterior end with distinct, up to 100 μm long tail well recognizable also in prepared specimens (Figs 131a, b; Table 66). Nuclear apparatus extends between oral bulge opening and base of tail. Macronucleus moniliform and tortuous, broken into two long pieces in two out of eight specimens, composed of 8–44, on average of 18 nodules; individual nodules ellipsoidal to very narrowly ellipsoidal, homogenously impregnated. On average 8 micronuclei attached to macronuclear strand, 3 μm across (Figs 131a, b; Table 66). A dorsal stripe of contractile vacuoles beginning subapically; possibly some also on ventral side; one to two intrakinetal excretory pores per vacuole (Figs 131a, n). Extrusomes highly similar to those of *P. japonicum*, attached to broader right branch of proboscis oral bulge, impregnate faintly to distinctly with the protargol method used (Fig. 131d): type I very narrowly ovate, 6 μm long; type II oblong, only about 2 μm long. Cortex very flexible, slightly furrowed by ciliary rows in SEM micrographs (Fig. 131n); cortical granulation not studied. Cytoplasm colourless, packed with lipid droplets 1–5 μm across and some food vacuoles containing remnants of rotifers; at base of tail a defecation vacuole. Movement not studied in detail.

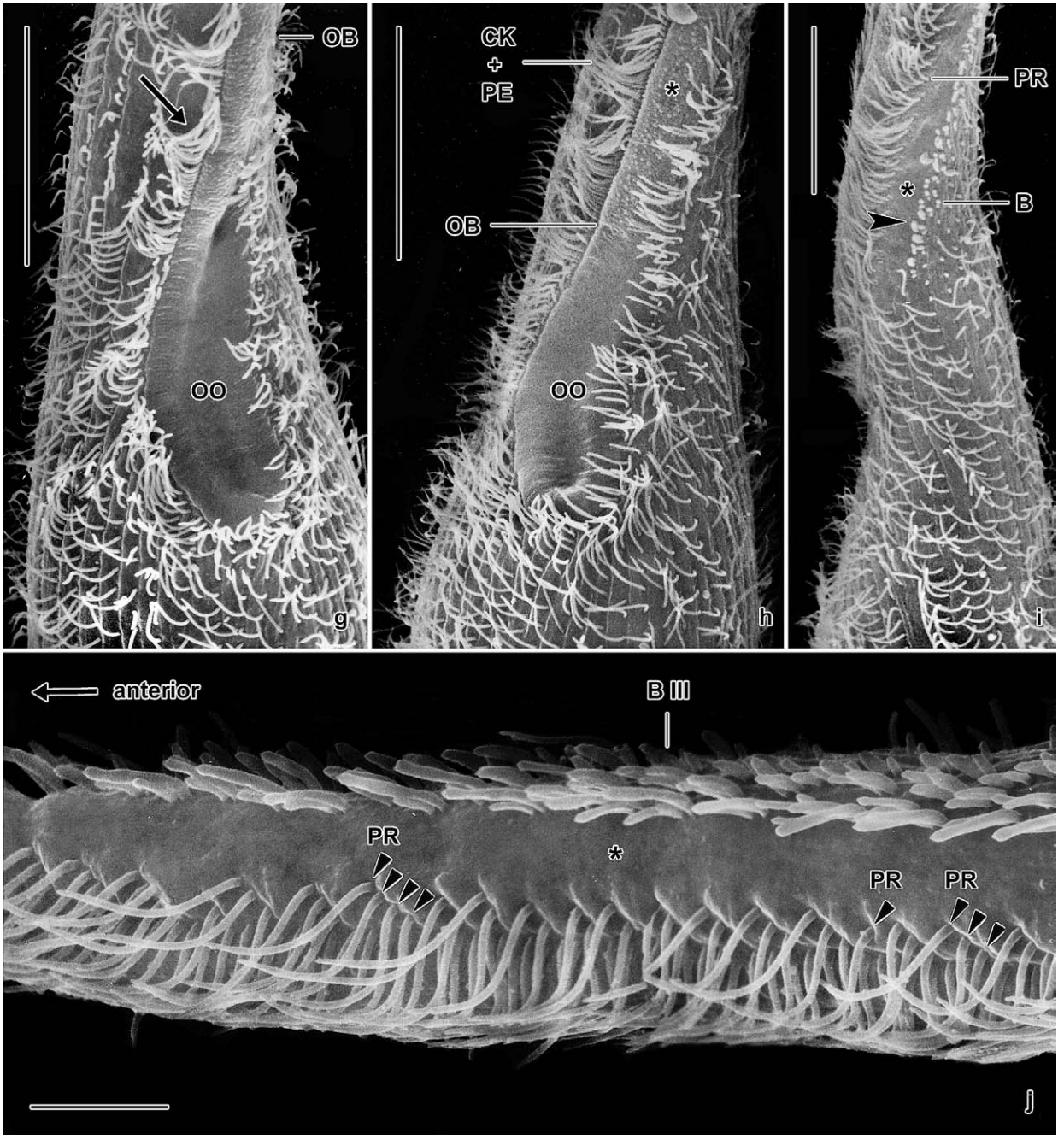
Cilia narrowly spaced; arranged in an average of 39 narrowly spaced rows (Fig. 131b; Table 66). Anterior end of ventral ciliary rows more densely ciliated and distinctly curved rightwards before abutting on circumoral kinety (Fig. 131f). Ciliature of proboscis' right side with the same peculiarities as in *P. japonicum* (Figs 131b, d, f): (i) ciliary rows not shortened, (ii) first row right of perioral kinety with comparatively narrowly spaced basal bodies in some specimens, but never as narrow as in perioral kinety, and (iii) a comparatively wide, blank stripe right of oral bulge. First row right of circumoral kinety extends as perioral kinety with narrowly spaced cilia to tip of proboscis. Left side of proboscis with comparatively narrow blank stripe because of the rather narrow proboscis and the left side brush rows (Figs 131c, e, i–m, t, u). Dorsal brush a long field on dorsal and left side of proboscis; staggered; distinctly heterostichad; composed of up to ten rows with loosely to very loosely spaced kinetids. First brush row begins usually in second third of proboscis, while last row commences subapically. All rows continue with a monokinetidal tail, those of dorsalmost rows extend to mid-proboscis, while those of ventralmost rows reach base of proboscis. Type III, V, and VI brush bristles (SEM observations and measurements): type III bristles of same length (1.5–2.5 μm) or anterior bristle shorter (1.3–1.5 μm) than posterior (2.5–3.8 μm; Figs 131j–m, o–s); type V anterior bristle strongly inflated, obovate, 1.2–1.4 μm long, posterior bristle conical, 0.6–0.8 μm long, lacking or covered by the strongly inflated anterior bristle in proximal portion of proboscis (Figs 131k, l, q–u); type VI bristles conical, 0.6–0.8 μm long, form the monokinetidal tails (Figs 131k, l, q, r, t,



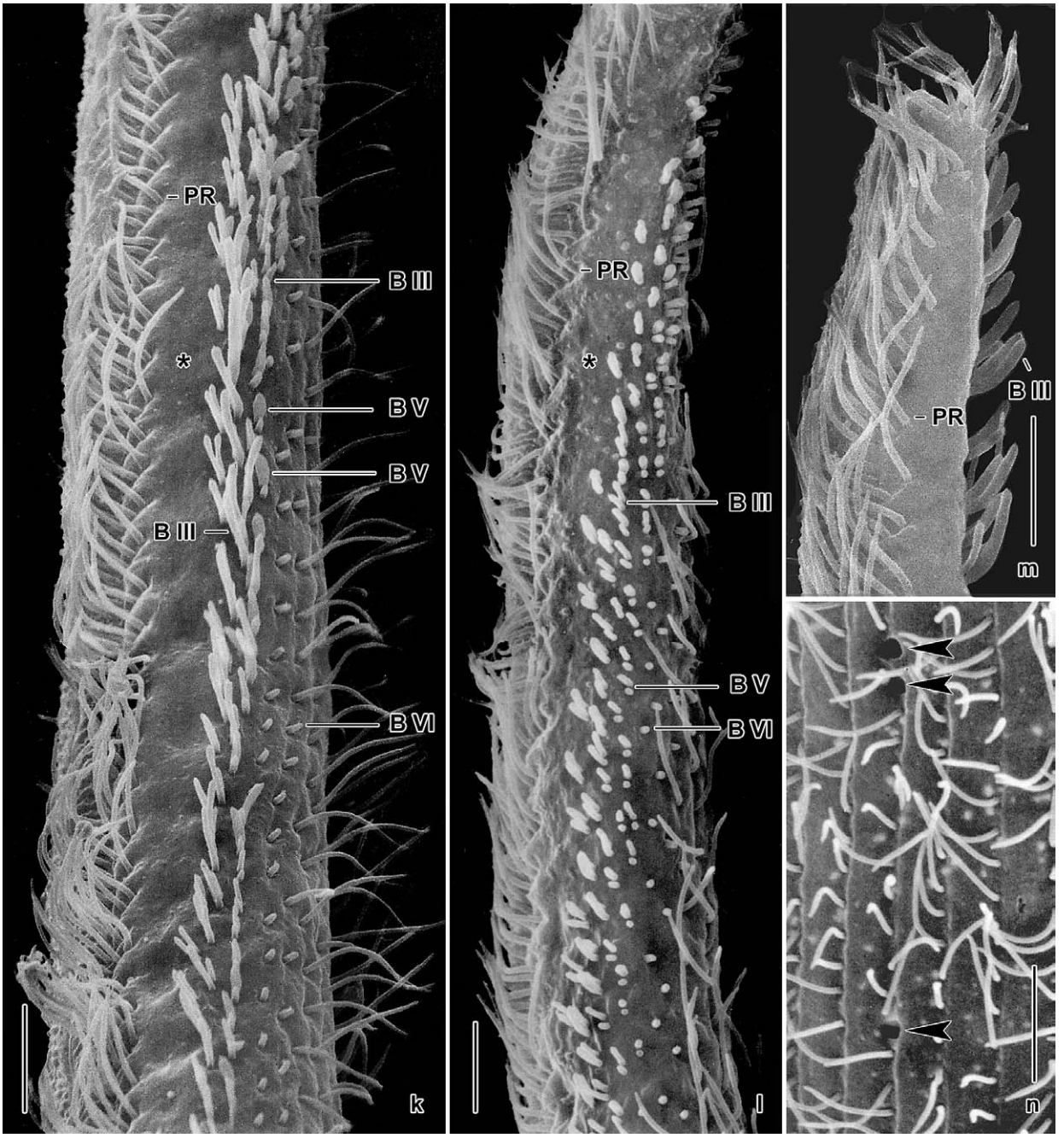
Figs 131a–f: *Pseudomonilicaryon angustistoma* from life (a) and after protargol impregnation (b–f). From FOISSNER et al. (2002). The asterisks mark the blank stripe right and left of the proboscis oral bulge. **a** – left side view of a representative specimen, length 400 µm; **b** – ciliary pattern of ventral side and nuclear apparatus of holotype specimen, length 320 µm. Note the elliptical oral bulge opening, the main feature of this species. The arrow marks a densely ciliated row right of the perioral kinety, a rare feature found also in *P. japonicum* and *P. fraterculum*; **c** – dorsolateral view, showing the staggered, multi-rowed dorsal brush and the preoral kineties which are comparatively widely spaced and composed of two to three narrowly spaced basal bodies each. Arrowhead marks site where the oral bulge opening begins; **d, e** – right and left side ciliary pattern and type I extrusomes in mid-region of proboscis. The short type II extrusomes are not impregnated; **f** – ciliary pattern in oral area of another specimen, showing that the elliptical oral bulge opening is a stable feature. B – dorsal brush, CF – central fibre, CK – circumoral kinety, CV – contractile vacuoles, E – extrusomes, MA – macronuclear nodules, OB – oral bulge, OO – oral bulge opening, PE – perioral kinety, PR – preoral kineties. Scale bars: 10 µm (d, e), 20 µm (f), 30 µm (c), and 100 µm (a, b).

Table 66: Morphometric data on *Pseudomonilicaryon japonicum* (PJ) and *P. angustistoma* (PA). From FOISSNER et al. (2002). Data based on mounted, protargol-impregnated (Foissner's method), and randomly selected specimens from non-flooded Petri dish cultures. Measurements in µm. CV – coefficient of variation in %, M – median, Max – maximum, Mean – arithmetic mean, Min – minimum, n – number of specimens investigated, SD – standard deviation, SE – standard error of mean.

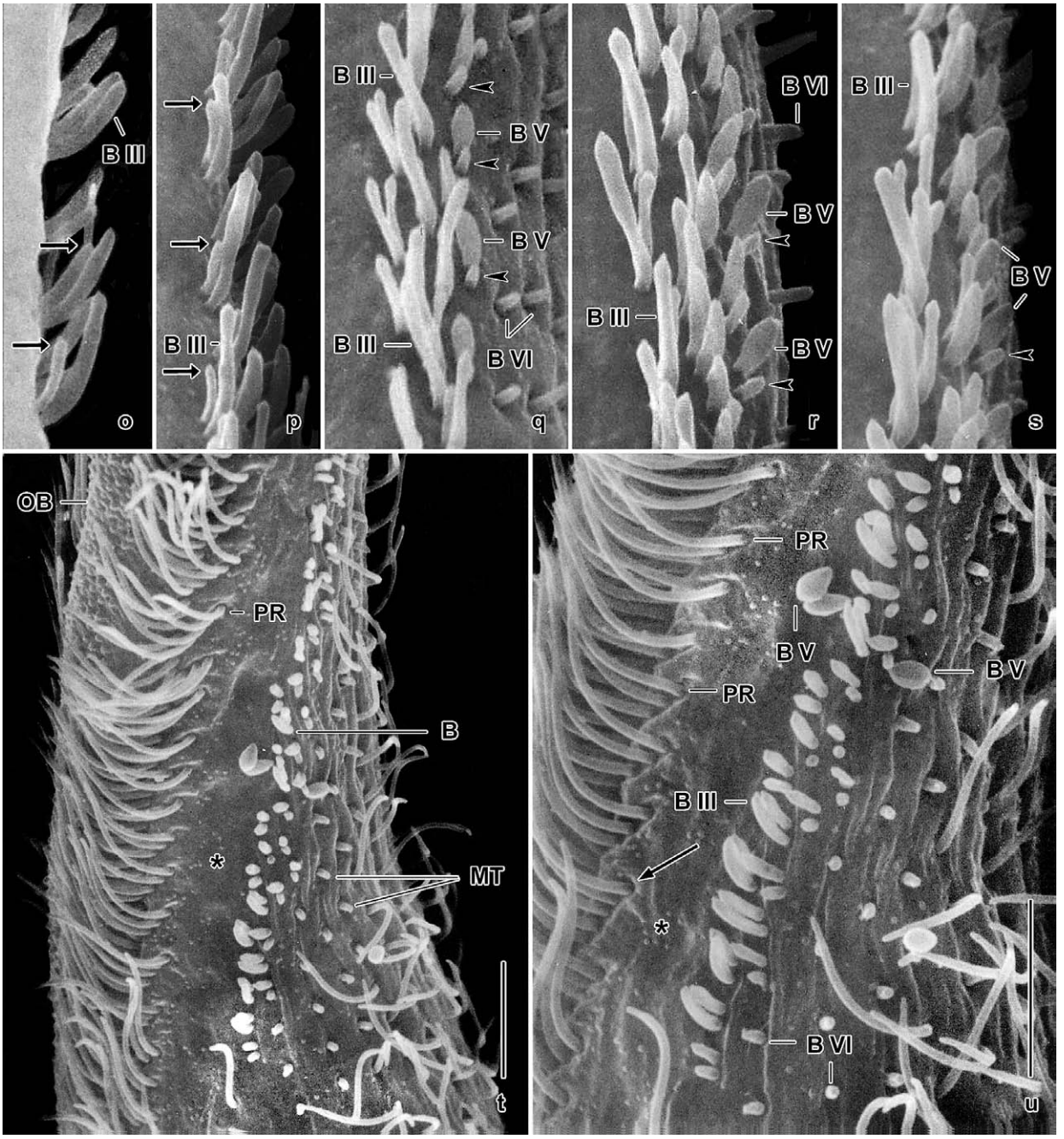
Characteristics	Species	Mean	M	SD	SE	CV	Min	Max	n
Body, length (curved proboscides not "extended")	PJ	372.7	349.0	71.5	16.4	19.2	239.0	544.0	19
	PA	354.1	350.0	91.7	22.2	25.9	230.0	600.0	17
Body, width	PJ	66.1	64.0	12.0	2.8	18.2	46.0	93.0	19
	PA	31.8	30.0	9.0	2.2	28.3	23.0	61.0	17
Body length:width, ratio	PJ	5.7	5.5	1.1	0.3	19.8	3.8	8.4	19
	PA	11.4	11.0	2.6	0.6	22.8	7.9	17.4	17
Anterior body end to oral bulge opening, distance (curved proboscides not "extended")	PJ	131.9	134.0	35.0	8.0	26.6	65.0	184.0	19
	PA	129.1	125.0	31.6	7.7	24.5	75.0	180.0	17
Proboscis, % of body length (curved proboscides not "extended")	PJ	35.5	33.5	8.1	1.8	22.7	22.0	54.9	19
	PA	36.8	36.7	5.3	1.3	14.3	25.0	45.7	17
Oral bulge opening, length	PJ	about same as width							
	PA	24.6	25.0	5.5	1.5	22.4	18.0	37.0	14
Oral bulge opening, width	PJ	18.6	18.5	2.5	0.6	13.4	15.0	25.0	18
	PA	10.3	10.0	1.6	0.5	15.9	8.0	14.0	10
Anterior body end to macronucleus, distance (curved proboscides not "extended")	PJ	166.7	166.0	40.7	9.3	24.4	86.0	231.0	19
	PA	154.5	160.0	39.0	9.5	25.2	95.0	230.0	17
Nuclear figure, length	PJ	145.8	134.0	37.6	9.1	25.8	91.0	206.0	17
	PA	108.8	94.0	54.2	13.2	49.8	45.0	250.0	17
Largest straight macronuclear nodule, length	PJ	22.4	23.0	5.9	1.3	26.2	13.0	36.0	19
	PA	16.9	15.0	6.6	1.6	38.9	10.0	40.0	17
Largest straight macronuclear nodule, width	PJ	6.8	6.0	1.6	0.4	23.0	5.0	10.0	19
	PA	6.7	7.0	1.1	0.3	16.5	5.0	9.0	17
Macronuclear nodules, number	PJ	28.1	27.0	4.5	1.0	15.9	20.0	35.0	19
	PA	17.8	16.0	8.6	2.1	48.2	8.0	44.0	17
Micronuclei, length	PJ	4.4	4.0	–	–	–	3.5	5.0	19
	PA	2.8	3.0	–	–	–	2.0	3.5	17
Micronuclei, width	PJ	2.9	3.0	–	–	–	2.0	3.0	19
	PA	2.8	3.0	–	–	–	2.0	3.3	17
Micronuclei, number	PJ	20.2	21.0	4.4	1.0	21.9	12.0	27.0	19
	PA	8.5	8.0	3.6	0.9	42.3	3.0	18.0	17
Ciliary rows in mid-body, number	PJ	39.1	40.0	4.9	1.1	12.6	28.0	48.0	19
	PA	38.9	40.0	5.2	1.3	13.3	30.0	50.0	17
Cilia in mid-body in 10 µm, number	PJ	7.5	7.0	1.2	0.3	15.6	5.0	9.0	19
	PA	4.8	5.0	1.1	0.3	23.5	3.0	7.0	17
Dorsal brush rows, number (rough values)	PJ	17.6	18.0	–	–	–	13.0	24.0	5
	PA	8.7	10.0	–	–	–	5.0	10.0	15
Anterior body end to last dikinetid of dorsal brush, distance (curved proboscides not "extended")	PJ	117.1	111.0	25.4	5.8	21.7	80.0	156.0	19
	PA	109.4	110.0	35.0	8.5	31.9	60.0	200.0	17



Figs 131g–j: *Pseudomonilicaryon angustistoma* in the SEM (from Foissner et al. 2002). **g, h** – oral ciliature and elliptical oral bulge opening, an important feature of this species because all congeners have a roundish or ovate oral opening. The broader right branch of the proboscis oral bulge is finely granulated by the tips of the extrusomes (h, asterisk). The arrow in (g) marks the dense oral ciliature caused by the cilia of the circumoral and perioral kinety; **i** – left side view of proximal proboscis area, showing the blank stripe (asterisk) between preoral kineties and dorsal brush. The arrowhead marks the brush region shown at higher magnification in Figures (t, u); **j** – left side view of anterior portion of proboscis, showing the rod-shaped type III brush bristles, which are about 2.5–3.8 µm long; the oblique preoral kineties, which are separated by distinct ridges and consist of one to four cilia (triangles); and the blank stripe (asterisk) between the preoral kineties and the dorsal brush. B – dorsal brush, B III – bristle type, CK – circumoral kinety, OB – oral bulge, OO – oral bulge opening, PE – perioral kinety, PR – preoral kineties. Scale bars: 5 µm (j) and 20 µm (g–i).



Figs 131k–n: *Pseudomonilicaryon angustistoma* in the SEM (from FOISSNER et al. 2002). **k, l** – left side view of two proboscides, showing the variability of the dorsal brush: the bristles are shorter and thus less conspicuous in the right specimen. The brush is composed of several staggered rows with loosely to very loosely spaced kinetids associated with three types of bristles (measurements from SEM micrographs): type III bristles are rod-shaped and about 2.5–3.8 µm long; the anterior bristle of type V is strongly inflated, obovate and 1.2–1.4 µm long, while the posterior bristle is conical and only 0.6–0.8 µm long; the type VI tail bristles are monokinetidal and about 0.7 µm long. Asterisks mark blank stripe on the left side of the proboscis, i.e., between the preoral kineties and the dorsal brush; **m** – left side view of distal proboscis area, showing the preoral kineties and dorsal brush extending to the tip of the proboscis. The preoral kineties are oblique, each usually composed of three ordinarily spaced cilia; **n** – part of dorsal surface, showing excretory pores (arrowheads) of two contractile vacuoles and a flat ridge left of the ciliary rows. B (III, V, VI) – types of dorsal brush bristles, PR – preoral kineties. Scale bars 5 µm.



Figs 131o–u: *Pseudomonilicaryon angustistoma*, dorsal brush in the scanning electron microscope (from FOISSNER et al. 2002). All measurements from SEM micrographs. Figures (t, u) are from the specimen shown in (i). There are three types of brush bristles, each likely with a special, as yet unknown function. The dikinetidal type III bristles are rod-shaped and of a similar length (o, q) or the anterior bristle (o, p, arrows) is slightly to distinctly shorter than the posterior one (1.3–1.5 µm vs. 2.5–3.8 µm). The anterior bristle of type V dikinetids is strongly inflated, obovate, and 1.2–1.4 µm long, while the posterior bristle is a minute, conical stump (q–s, arrowheads) lacking or covered by the strongly inflated anterior bristle found only in the proximal portion of the proboscis (t, u). The type VI bristles are monokinetidal, conical, 0.6–0.8 µm long, and form the tail of the brush rows (q, r, t, u). The asterisks mark the blank stripe between preoral kineties and dorsal brush. The arrow in (u) denotes a preoral kinety composed of five cilia. B (III, V, VI) – types of dorsal brush bristles, MT – monokinetidal tails of dorsal brush, OB – oral bulge, PR – preoral kineties. Scale bars 5 µm.

u).

Oral bulge opening at beginning of second body third, projects ordinarily, elliptical to narrowly elliptical and about 25–30 μm long in SEM (Figs 131b, f, g, h), on average 25 × 10 μm in size after protargol impregnation (Table 66). Pharyngeal basket obconical, inconspicuous in protargol preparations because basket rods impregnated only in distal portion (Figs 131a, f). Oral bulge distinct in SEM micrographs due to the nice metachronal ciliary waves and the extrusome tips in broader right branch (Figs 131g, h, t). Circumoral kinety composed of narrowly to ordinarily spaced dikinetids in proboscis and narrowly spaced monokinetids around oral bulge opening (Fig. 131f). Preoral kineties comparatively widely spaced, extend in distinct furrows, oblique and each composed of one to five, usually three ordinarily to narrowly spaced cilia (Figs 131c, e, j–m, t, u).

Remarks: The most important difference between *P. angustistoma* and other species with moniliform macronucleus is the elliptical oral bulge opening, a special feature resembling, for instance, *Dimacrocaryon amphileptoides* and, especially, *Pelagodileptus trachelioides*. Indeed, this pelagic species has remarkable similarities (size, macronuclear pattern) with *Pseudomonilicaryon angustistoma*, but is distinctly stouter (4.3:1 vs. 11.4:1), has 120–200 ciliary rows (vs. 39), and is packed with symbiotic green algae (zoochlorellae). *Pseudomonilicaryon angustistoma* is also similar to *P. japonicum*, except for the more slender body (length:width ratio 11.4:1 vs. 5.7:1), the higher number of macronuclear nodules (28 vs.18), and the more complex dorsal brush (three vs. two types of bristles). However, there are some remarkable similarities, viz., the blank stripe right of the oral bulge and the densely ciliated row right of the perioral kinety. Possibly, *P. angustistoma* and *P. japonicum* form a subgroup within the genus.

Occurrence and ecology: To date found only at type locality. The slender body indicates that *P. angustistoma* is a terrestrial species.

Pseudomonilicaryon japonicum Foissner, Agatha & Berger, 2002 (Figs 132a–p, 133a–t; Table 66)

1966 *Dileptus monilatus* (Stokes) Kahl – Dragesco, Protistologica **2**: 76 (misidentification, possibly a distinct species)

2002 *Pseudomonilicaryon japonicum* nov. sp. Foissner, Agatha & Berger, Denisia **5**: 378

Improved diagnosis (type population): Size about 400 × 75 μm in vivo. Shape narrowly to very narrowly dileptid with acute posterior third, proboscis 35% of body length. Macronucleus moniliform and tortuous, composed of an average of 28 globular to ellipsoidal nodules; several lenticular micronuclei. A dorsal and a ventral stripe of contractile vacuoles with 1–2 pores each. Two shape and size types of extrusomes attached to proboscis oral bulge: type I very narrowly ovate, 6 μm long; type II oblong, about 2 μm long. On average 39 ciliary rows, about 18 anteriorly differentiated into a staggered, distinctly heterostichad dorsal brush with monokinetidal tails extending to base of proboscis. Oral bulge opening about 20 μm across. Preoral kineties ordinarily spaced, oblique, each composed of 3 narrowly spaced cilia.

Type locality: Tree and soil mosses from the surroundings of the "Spring of Wisdom" in Kyoto, Japan, E135°45' N35°00'.

Type material: Foissner et al. (2002) deposited one holotype slide (inv. no. 2002/682) and four paratype slides (inv. nos 2002/683–686) with protargol-impregnated specimens in the Biology Centre of the Museum of Upper Austria, Linz (LI). Relevant specimens are marked by black ink circles on the coverslip.

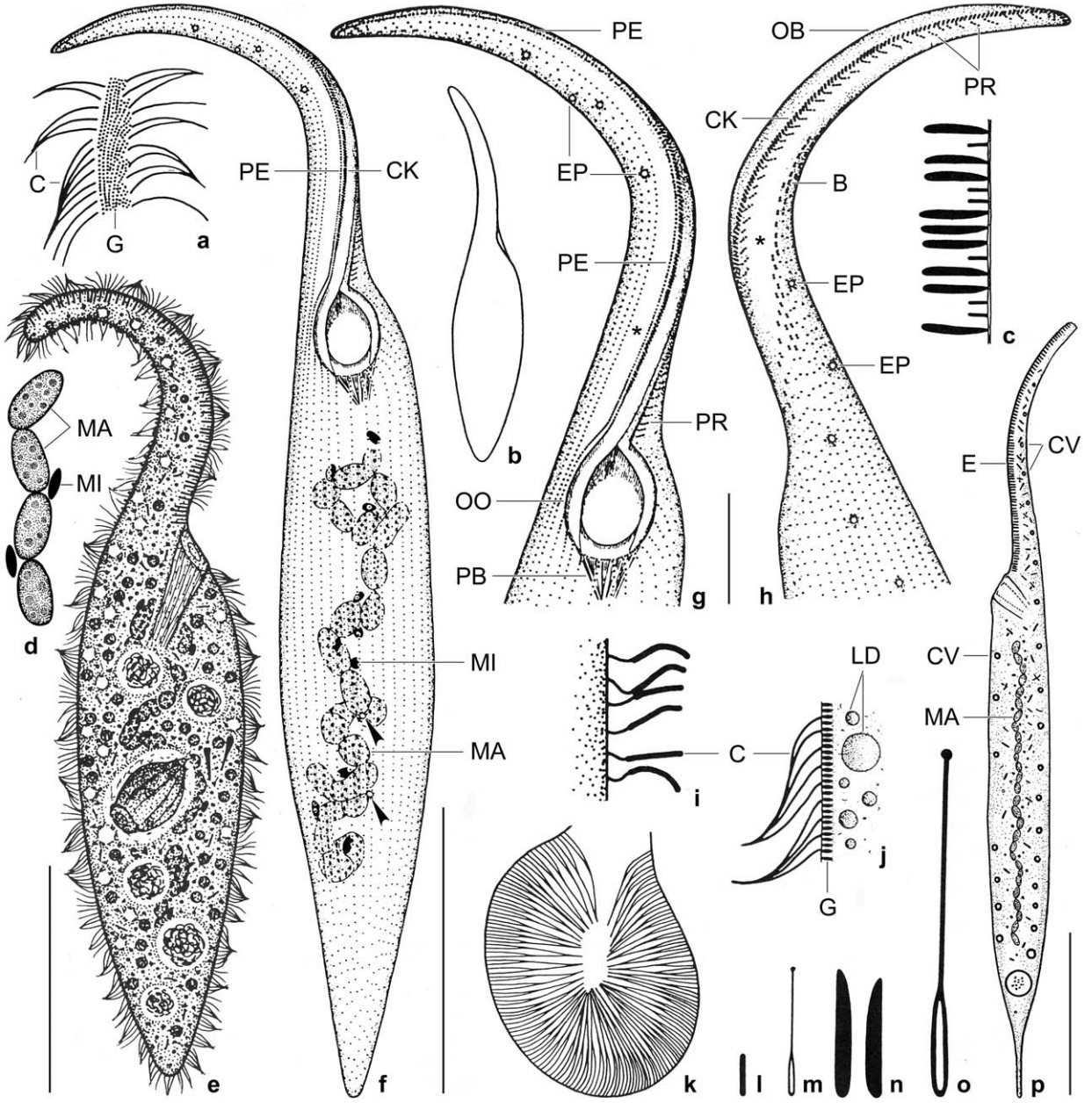
Etymology: The Latin adjective *japonicus* refers to the country in which the species was discovered.

Description of Japanese population: Size 260–580 × 50–105 μm in vivo, usually about 400 × 75 μm, as

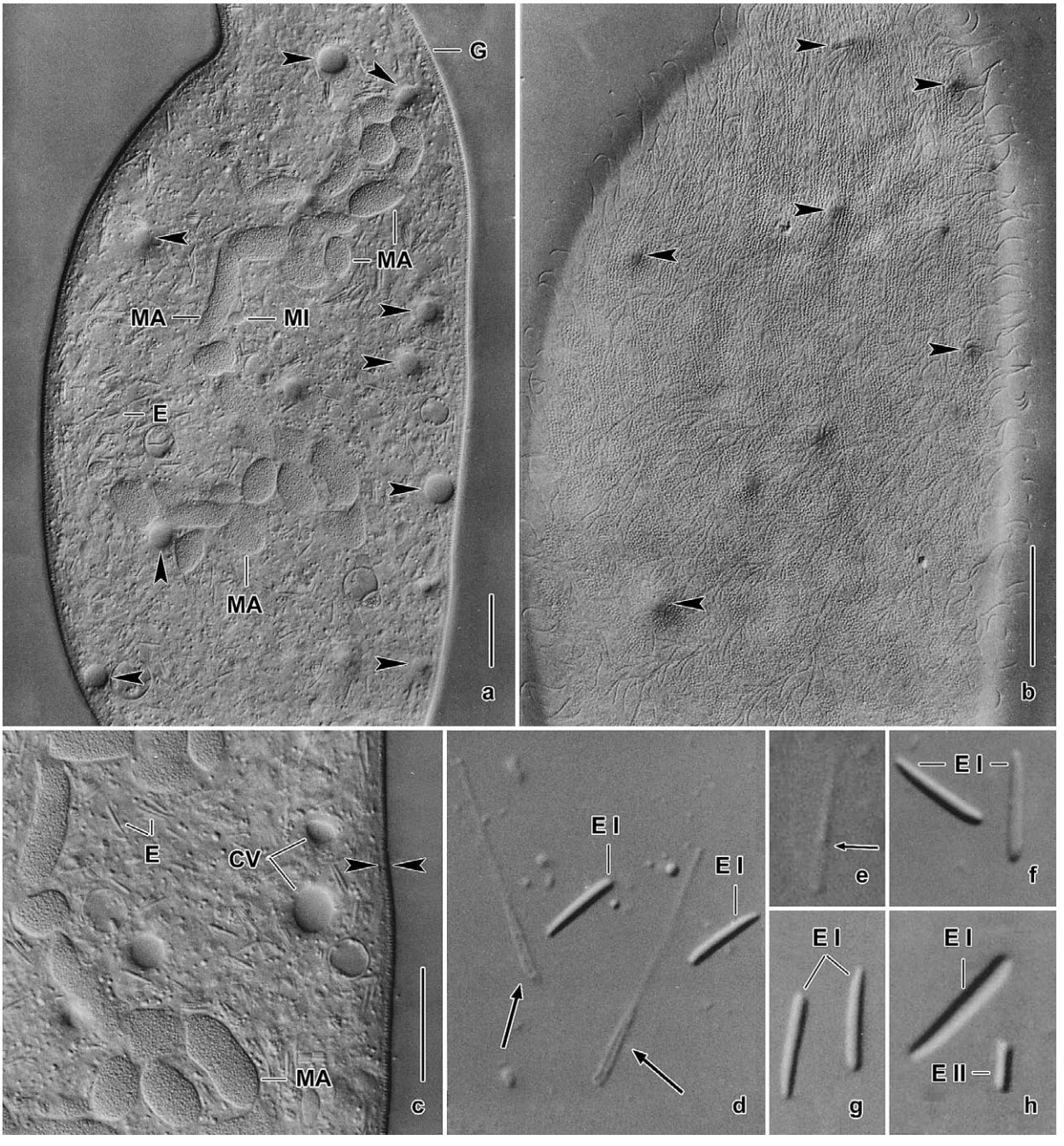
calculated from some in vivo measurements and the morphometric data, assuming about 10% preparation shrinkage (Table 66); very flexible but not contractile. Shape narrowly to very narrowly dileptid, i.e., length:width ratio 3.8–8.4:1, on average 5.7:1 in protargol preparations. Length of proboscis highly variable, viz., 22% to 55% of body length, on average about 35%, usually conspicuously curved dorsally; trunk slenderly to bluntly fusiform, widest in mid-portion; posterior end acute to narrowly rounded both in vivo and after various preparations, never tail-like (Figs 132b, e, f, 133i–k; Table 66). Nuclear apparatus usually in anterior three quarters of trunk. Macronucleus moniliform and tortuous, composed of an average of 28 nodules easily recognizable even in vivo at low magnification (Fig. 133a); individual nodules usually ellipsoidal; nucleoli small and globular. On average 20 micronuclei adjacent to macronuclear strand, conspicuous because lenticular in vivo, while ellipsoidal, ovoidal or globular in preparations, the latter possibly when viewed transversely (Figs 132d, f, 133a, c; Table 66). Contractile vacuoles numerous and conspicuous in dorsal and right side of proboscis and trunk, forming a broad stripe, while sparse and thus easily overlooked in ventral and left side of trunk; usually one, rarely two intrakinetal excretory pores per vacuole (Figs 132e–h, 133a–c, i–n, r). Two shape and size types of extrusomes attached to proboscis oral bulge: type I very narrowly ovate, 6 × 0.8 μm in size; type II oblong, about 2 × 0.3 μm in size; when exploded both of typical toxicyst structure, that is, with a refractive (toxin?) granule at top of tube emerging from the empty capsule, type I extends to 16 μm, type II to 6 μm; developing extrusomes scattered in cytoplasm and impregnating with protargol (Figs 132c, l–o, 133a, c–h). Cortex very flexible, slightly furrowed by ciliary rows in SEM micrographs, contains a layer of refractive, comparatively large (1 × 0.5 μm) granules, forming about seven oblique rows between adjacent kineties (Figs 132a, j, 133a–c, n). Cytoplasm colourless, packed with many lipid droplets 1–5 μm across, some 15 μm long pharyngeal baskets from ciliate prey (or spines for the resting cyst?), and up to seven vacuoles with remnants of rotifers, the preferred food of this ciliate; in rear end sometimes a defecation vacuole. Movement without peculiarities.

Cilia about 10 μm long in vivo, narrowly spaced; in protargol preparations as typical for dileptids, i.e., with thick, deeply impregnated distal half (Fig. 132i), except for dorsal bristles; arranged in about 40 longitudinal, narrowly spaced rows (Figs 132f, 133i–k, n; Table 66). Anterior end of ventral ciliary rows more densely ciliated and indistinctly curved rightwards abutting on circumoral kinety (Figs 132f, g, 133o, p). Ciliature of proboscis' right side with several remarkable specializations (Figs 132f, g, 133m, o, r): (i) rows not shortened or only near anterior end of oral bulge, (ii) first row right of perioral kinety with comparatively narrowly spaced basal bodies in half of specimens, but never as narrow as in perioral kinety, and (iii) a comparatively wide, blank stripe right of oral bulge. First row right of circumoral kinety extends as perioral kinety with narrowly spaced cilia to tip of proboscis (Figs 132f, g, 133j, m, o, r). Left side of proboscis with conspicuously broad, blank stripe because left side ciliary rows end at level of oral bulge opening or slightly above (Figs 132h, 133i, k, l, q, s, t). Dorsal brush on dorsal and left side of proboscis; staggered; distinctly heterostichad; composed of about 18 rows (possibly slightly overestimated, according to the SEM micrographs). Brush dikinetids loosely to ordinarily spaced, associated with type II bristles both being 3–4 μm long in vivo (1.5–1.7 μm in SEM preparations). All rows continue with a monokinetidal tail extending to second third of body with type VI bristles 1.5–2 μm long in vivo (0.8–1.2 μm in SEM preparations); tails of dorsalmost rows usually extend only to mid-proboscis (Figs 132h, 133i, k, l, q, s, t).

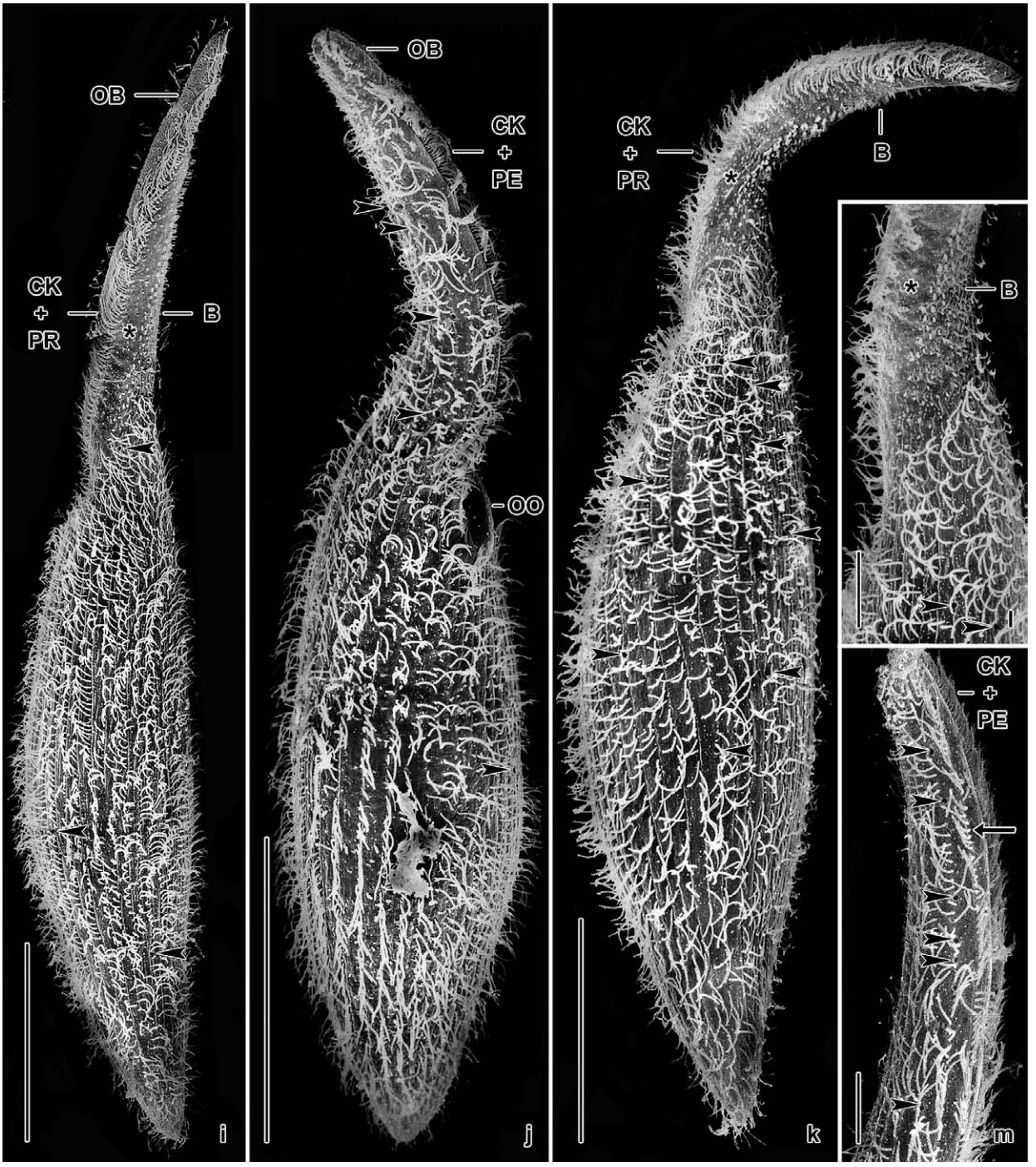
Oral bulge opening usually at beginning of second body third, projects ordinarily, roundish both in vivo and in preparations (Figs 132f, g, k, 133j, o, p), except for a single SEM specimen with an elliptical oral bulge opening and thus possibly belonging to another species. Pharyngeal basket obconical, distinct both in vivo and after protargol impregnation, without specific features (Figs 132e–g, k). Circumoral kinety composed of narrowly spaced dikinetids in proboscis and narrowly spaced monokinetids around oral



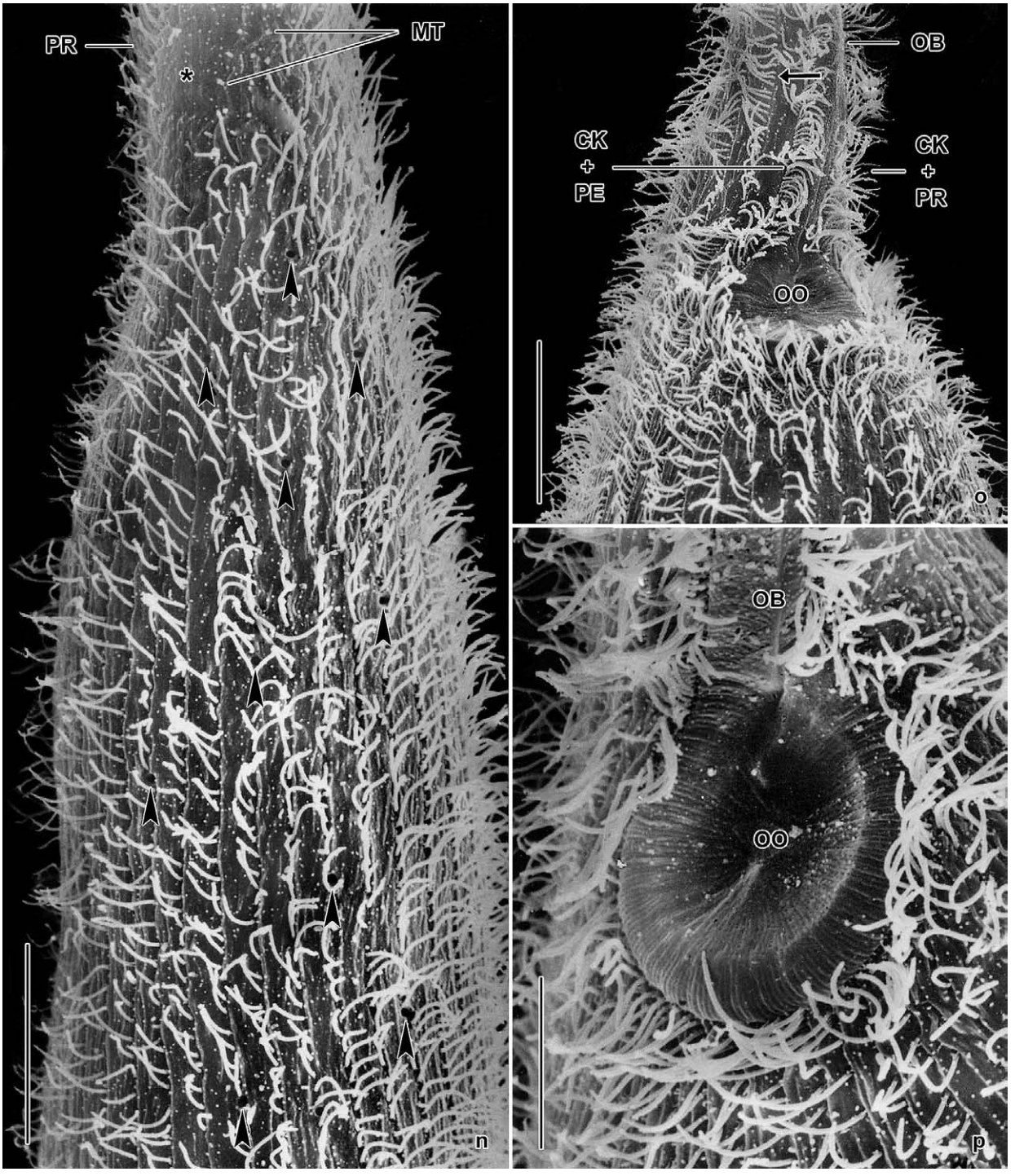
Figs 132a–p: *Pseudomonilicaryon japonicum* (a–o) and a French, *japonicum*-like specimen (p) from life (a–e, j, l–p), after protargol impregnation (f–i), and in the SEM (k). From Foissner et al. 2002 (a–c, e–o), Dragesco 1966a (p), and original (d). **a, j** – surface view and optical section showing cortical granulation; **b** – shape variant; **c** – optical section of proboscis' oral bulge, showing two shape and size types of extrusomes; **d** – the nuclear apparatus consists of a moniliform macronuclear strand and several lenticular micronuclei; **e** – right side view of a representative specimen having ingested a rotifer, length 400 µm; **f** – ventral ciliary pattern, and nuclear apparatus of holotype specimen, length 380 µm. Arrowheads denote some ventral excretory pores; **g, h** – ventrolateral and dorsolateral view of proboscis of holotype specimen. Note the excretory pores on the right side of the proboscis and a blank stripe (asterisks) right and left of the oral bulge; **i** – after protargol impregnation, the distal half of the cilia is thickened; **k** – the oral bulge opening and the basket are supported by furcated fibres; **l–o** – resting and exploded type II (2 µm and 6 µm) and type I (6 µm and 16 µm) extrusomes; **p** – *Dileptus monilatus* (?), length 1200 µm. B – dorsal brush, C – cilia, CK – circumoral kinety, CV – contractile vacuoles, E – extrusomes, EP – excretory pores, G – cortical granules, LD – lipid droplets, MA – macronuclear nodules, MI – micronucleus, OB – oral bulge, OO – oral bulge opening, PB – pharyngeal basket, PE – perioral kinety, PR – preoral kineties. Scale bars: 30 µm (g, h), 100 µm (e, f), and 250 µm (p).



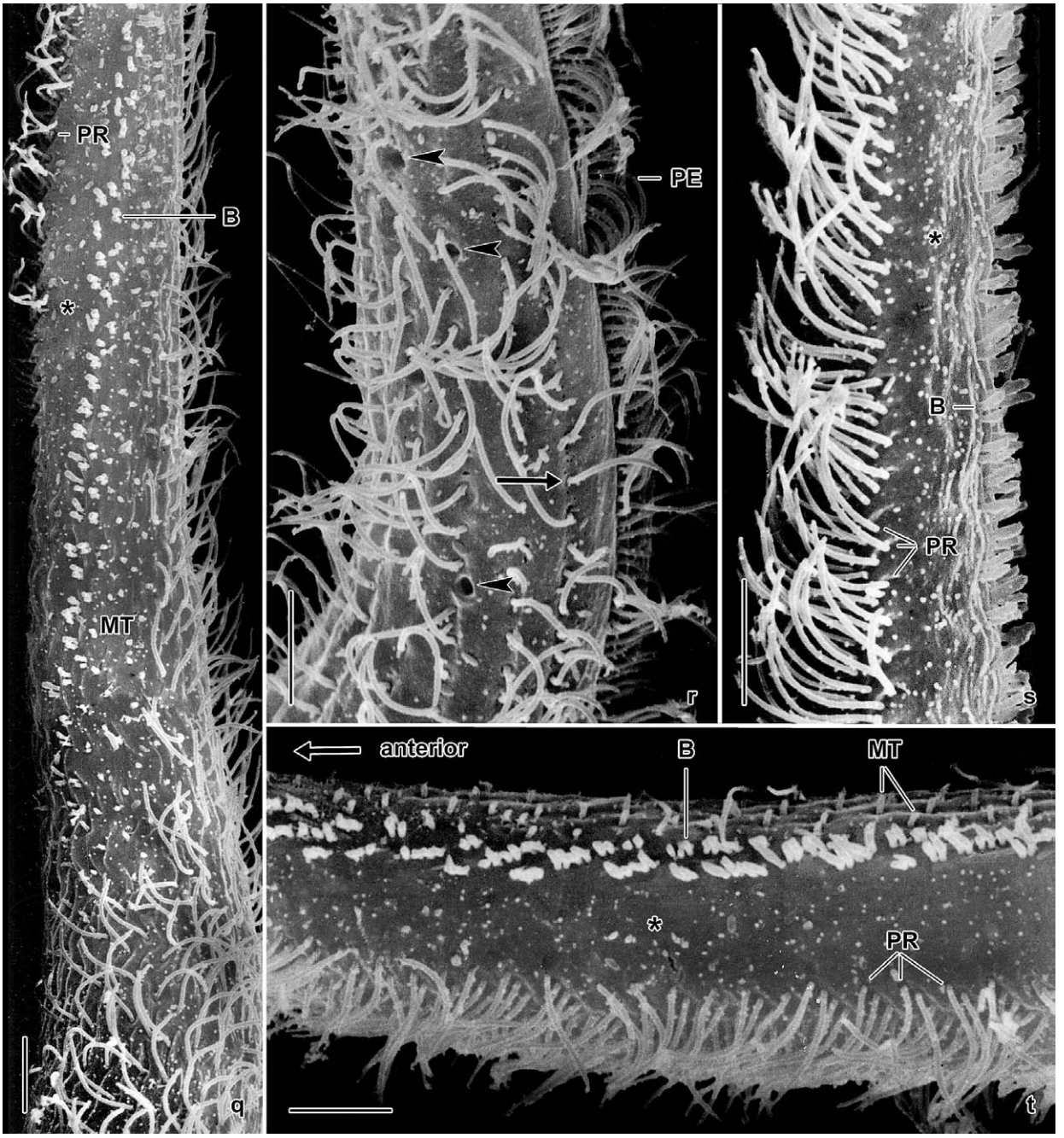
Figs 133a–h: *Pseudomonilicaryon japonicum* from life (from FOISSNER et al. 2002). **a–c** – optical sections (a, c) and surface view (b) of a heavily squeezed specimen, showing some important features: one of many micronuclei is adjacent to the moniliform macronuclear strand, and the cytoplasm is packed with granules and developing extrusomes. The arrowheads mark scattered contractile vacuoles and their excretory pores (b); opposed arrowheads (c) denote the rather thick cortex studded with narrowly spaced granules, forming about seven oblique rows between each two kineties (b). The cortical granules are colourless and about 1 × 0.5 µm in size; **d–h** – there are two shape and size types of extrusomes: type I is very narrowly ovate and 6 µm long, while type II is oblong and only about 2 µm long. Arrows mark exploded type I (d) and type II (e) extrusomes. They show the typical toxicyst structure, that is, a (toxin?) granule on top of tube emerging from the empty capsule. CV – contractile vacuoles, E(I, II) – extrusomes (types), G – cortical granules, MA – macronuclear nodules, MI – micronucleus. Scale bars 20 µm (a–c).



Figs 133i–m: *Pseudomonilicaryon japonicum* in the SEM (from FOISSNER et al. 2002). **i–k** – left side (i, k) and right side (j) overviews. Asterisks denote the blank stripe on the left side of the proboscis. Arrowheads mark excretory pores on right side of proboscis and ventral and dorsal side of trunk; **l** – dorsal view showing the dorsal brush, the broad blank stripe (asterisk), and the scattered excretory pores (arrowheads); **m** – the first row (arrow) right of the perioral kinety has comparatively narrowly spaced basal bodies in about half of specimens. Arrowheads mark the intrakinetal excretory pores on the right side of the proboscis. B – dorsal brush, CK – circumoral kinety, OB – oral bulge, OO – oral bulge opening, PE – perioral kinety, PR – preoral kineties. Scale bars: 10 μm (l, m) and 50 μm (i–k).



Figs 133n–p: *Pseudomonilicaryon japonicum* in the scanning electron microscope (from FOISSNER et al. 2002). **n** – dorsal view of trunk, showing the stripe of excretory pores (arrowheads). Most left side ciliary rows end at level of oral bulge opening, producing a conspicuous barren area (asterisk) on the proboscis; **o, p** – oral ciliature and circular oral bulge opening. The arrow marks the densely ciliated somatic kinety right of the perioral kinety. CK – circumoral kinety, MT – monokinetidal tails of dorsal brush, OB – oral bulge, OO – oral bulge opening, PE – perioral kinety, PR – preoral kineties. Scale bars: 10 μm (p) and 20 μm (n, o).



Figs 133q–t: *Pseudomonilicaryon japonicum* in the SEM (from FOISSNER et al. 2002). **q, s, t** – dorsal (q) and lateral (s, t) views of proboscis. The dorsal brush consists of staggered and distinctly heterostichad rows with widely to ordinarily spaced dikinetids. In the anterior portion of a brush row are dikinetidal type II bristles, while in the posterior portion are monokinetidal type VI bristles. Each preoral kinety is composed of three cilia. Asterisks mark broad blank stripe on the left side of the proboscis; **r** – right side view of proboscis' base. *Pseudomonilicaryon japonicum* is unique in having contractile vacuoles and excretory pores (arrowheads) not only on the dorsal, but also in the right side of the proboscis. Possibly, the right side pores belong to the ventral vacuole stripe. The first ciliary row (arrow) right of the perioral kinety is ordinarily ciliated in about half of specimens, while densely in the other half (m, o). This is another rare feature, as yet observed only in *P. angustistoma* and *P. fraterculum*. B – dorsal brush, MT – monokinetidal tails of dorsal brush, PE – perioral kinety, PR – preoral kineties. Scale bars 5 µm.

bulge opening. Preoral kineties ordinarily spaced, oblique, each composed of two to four, usually three narrowly spaced cilia (Figs 132g, h, 133s, t).

Notes on French population: Dragesco (1966a) described a population which resembles *P. japonicum* in having ventral and dorsal contractile vacuoles, a rare feature in *Pseudomonilicaryon*. However, this population, which occurred in Lake Léman near the town of Thonon, France, has a much larger body (1200 µm vs. 400 µm) and a distinct tail (Fig. 132p). Dragesco (1966a) supposed the Thonon population to be *Monilicaryon monilatum*. However, this species has a shorter proboscis (1/5 vs. 1/3 of body length) and lacks ventral vacuoles. Possibly, Dragesco's population represents a distinct species.

Occurrence and ecology: To date found at type locality and (possibly) in rain forest moss from Venezuela, where it has a short tail and thus resembles *Pseudomonilicaryon angustistoma*. These specimens fed, like those of the type population, on rotifers, suggesting *P. japonicum* as a bryophilic rotifer predator.

Remarks: *Pseudomonilicaryon japonicum* is unique in having excretory pores not only in the dorsal side but also in the right side of the proboscis rather close to the circumoral kinety (Figs 132f, g, 133j, m, r). Possibly, the right side pores belong to the ventral vacuole stripe. A further rare feature, as yet known only from *P. brachyproboscis*, *P. aculeatum*, and *P. gracile oviplites*, is the lenticular shape of the micronuclei (Figs 132d, f, 133a). Likewise, the condensation of the cilia in the first kinety right of the perioral row is rather unusual, but present in only half of specimens (Figs 132f, g, 133m, o).

Within the group of dileptids with a moniliform macronucleus, *P. japonicum* is most similar to *P. falciforme* and *P. angustistoma*. In vivo, these species are best separated by the shape of the oral bulge opening (roundish in *P. falciforme* and *P. japonicum*, distinctly elliptical in *P. angustistoma*) and the arrangement of the extrusomes (ordinary in *P. japonicum* and *P. angustistoma*, while *P. falciforme* has, additionally, short, knotty extrusomes in the oral bulge opening). In preparations, the structure of the dorsal brush (*P. falciforme* with anterior tails, *P. angustistoma* with strongly inflated type V bristles in proximal brush portion) adds further characteristics.

Pseudomonilicaryon kahli (Šrámek-Hušek, 1957) nov. comb. (Figs 134a–t)

This species is possibly a junior synonym of *Pseudomonilicaryon massutii* because the main morphological characteristics are so similar that they cannot be separated unambiguously. However, the habitats are different: saline for *P. massutii*-like populations, limnetic or terrestrial for *P. kahli*-like populations. Considering that few ciliates live in both, limnetic and saline habitats, we keep *P. massutii* and *P. kahli* separate, assigning saline records to the former and limnetic ones to the latter.

1905 *Dileptus gigas* C. & L. – Conn, Fresh-water protozoa: 46 (misidentification)

1931 *Dileptus monilatus* (Stokes, 1886) – Kahl, Tierwelt Dtl. **21**: 205 (misidentification, brief description of a Hamburg population)

1953 *Dileptus monilatus* (Stokes, 1886) – Jones & Beers, J. Elisha Mitchell scient. Soc. **69**: 42 (misidentification, description of morphology and behaviour of a North American population)

1957 *Dileptus kahli* nom. nov. Šrámek-Hušek, Věst. Čsl. zool. spol. **21**: 6 (not a replacement name but a new species)

1959 *Dileptus monilatus* (Stokes, 1886) – Vuxanovici, Studii Cerc. Biol. **11**: 328 (doubtful species with symbiotic green algae)

1962 *Dileptus monilatus* (Stokes, 1886) – Dingfelder, Arch. Protistenk. **105**: 557 (similar as depicted in Kahl)

1963 *Dileptus kahli* (nom. nov.) – Dragesco, Bull. biol. Fr. Belg. **97**: 110 (repeated "nom. nov." instead of Šrámek-Hušek, 1957)

1970 *Dileptus monilatus* (Stokes) Kahl, 1931 – Dragesco, Annls Fac. Sci. Univ. féd. Cameroun year **1970**: 11 (very likely a misidentification, possibly a distinct species)

1986 *Dileptus monilatus* (Stokes, 1886) Kahl, 1930 – Dragesco & Dragesco-Kernéis, Faune tropicale **26**: 159 (misidentification, description of African populations)

1994 *Dileptus monilatus* (Stokes, 1886) – Song, Acta zootax. sin. **19**: 388 (misidentification, description of a Chinese soil population)

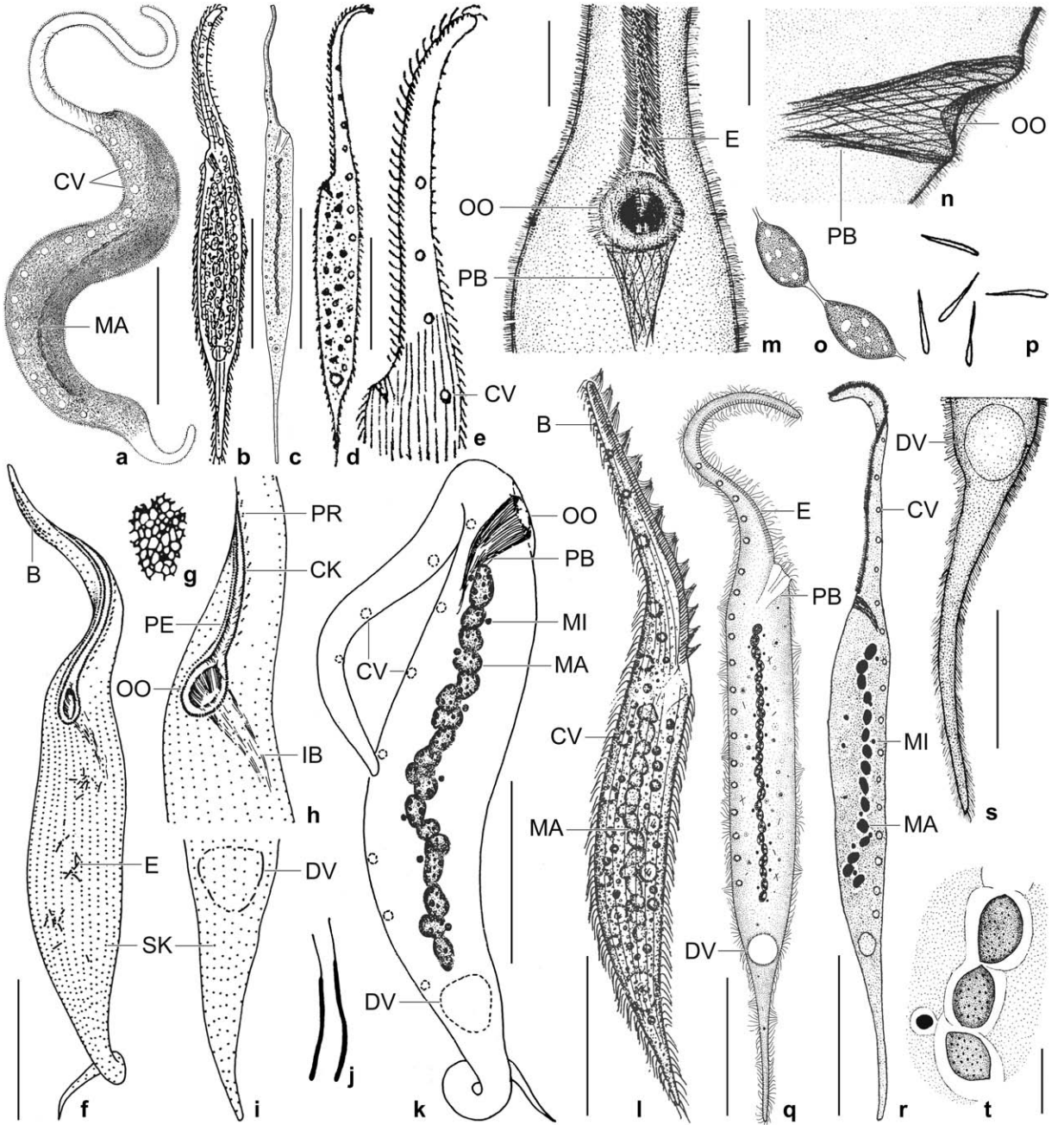
Generic affiliation, nomenclature, and taxonomy (see also above): Jankowski (1967) did not combine *Dileptus kahli* with one of his subgenera. We assign it to *Pseudomonilicaryon* because it has a *Dileptus*-like ciliary pattern and a moniliform macronucleus (Song 1994b).

Kahl (1931) misidentified a Hamburg population (Alster Lake) as *D. monilatus* Stokes, 1886, but mentioned that it considerably differs from that of Stokes (1886) in having a distinct tail (vs. acute posterior third) and a much longer proboscis occupying 1/3–1/2 vs. 1/5 of body length. Further, Kahl (1931) emphasized that it possibly represents a new species: "Sollte Stokes' Form sich als typisch erweisen, so muß die meine als selbständige Form neu benannt werden". This was done by Šrámek-Hušek (1957), who observed a single specimen matching Kahl's *Dileptus* from Hamburg, using, unfortunately, nom. nov. instead of spec. nov. Later authors (Vuxanovici 1959, Dingfelder 1962, Dragesco & Dragesco-Kernéis 1968, Song 1994b) followed Kahl's classification, neglecting Kahl's doubts and Šrámek-Hušek (1957). We declare the figure from Kahl (1931), here reproduced as Fig. 134b and used by Šrámek-Hušek (1957) for establishing *D. kahli*, as the holotype.

As concerns the populations listed, all important features match: body 400–900 μm long and cylindroidally dileptid to rod-like with distinct tail and proboscis 1/3–1/2 of body length; macronucleus moniliform and composed of 15–35 nodules; contractile vacuoles in a dorsal stripe. However, the Roumanian population studied by Vuxanovici (1959) is very likely a distinct species because it has symbiotic green algae and much smaller macronuclear nodules (3 μm vs. 15–20 μm in diameter). Vuxanovici (1959) did not describe the arrangement and number of the macronuclear nodules, and thus the generic home of his population remains doubtful. Unfortunately, the important description of Song (1994b) possibly also contains serious mistakes, i.e., some tabulated values do not fit the figures: (i) the Table gives a length of 340–440 μm (an average of 393 μm), while one of his figures shows a 540 μm long specimen (here reproduced as Fig. 134f) and another an even 630 μm long exemplar (Fig. 134k), values that match the literature data very well when some preparation shrinkage is added; (ii) the tabulated number of ciliary rows is 22–27 (on average 23), while one of his figures (here reproduced as Fig. 134f) shows 12 kineties on one side, suggesting about 30 rows in total; (iii) and the dorsal brush, which is said to be three-rowed (Fig. 134f), is not shown in detail and possibly too schematized.

As obvious from the synonymy list, *Pseudomonilicaryon kahli* was frequently confused with *Monilicaryon monilatum* which, however, is easily distinguished both in vivo and in protargol preparations by the much shorter proboscis (1/5 vs. 1/3–1/2 of body length), the acute posterior third (vs. distinct tail), the much higher number of ciliary rows (40–60 vs. 22–27), and the different dorsal brush (1 vs. 3 rows) and oral (preoral kineties form a perioral-like kinety vs. distinctly separated each consisting of 3 cilia) ciliary pattern. Another similar species is *Pseudomonilicaryon thononense*, which is much smaller (usually 300 μm vs. 700 μm) and possesses less ciliary rows (usually 18 vs. possibly 30).

Improved diagnosis (includes all information known): Size about 700 × 40 μm in vivo. Shape cylindroidally dileptid to rod-like with distinct tail, proboscis about 1/3 of body length. Macronucleus moniliform, composed of 15–35 globular nodules; several globular micronuclei. A dorsal stripe of contractile vacuoles. Possibly about 30 ciliary rows, several differentiated into a dorsal brush anteriorly. Oral bulge opening roundish. Preoral kineties strongly oblique, each usually composed of 3 narrowly spaced cilia.



Figs 134a–t: *Pseudomonilicaryon kahli* from life (a–e, l, o, q), after protargol (f, h–k) and Chatton-Lwoff silver nitrate (g) impregnation, in Schaudinn-iron hematoxylin stains (m, n, p, r, s), and in a Feulgen preparation (t). From Conn 1905 (a), Kahl 1931 (b), Jones & Beers 1953 (m, n, p, r–t), Vuxanovici 1959 (d, e), Dragesco 1970 (c), Dragesco & Dragesco-Kernéis 1986 (o, q), and Song 1994b (f–l). **a–d, k, l, q, r** – lateral views showing general body organization; **e, m, n** – details of oral region; **f, h, i** – ventrolateral ciliary pattern; **g** – silverline pattern; **j** – exploded extrusomes after protargol impregnation; **o** – the macronuclear nodules are about 15 µm long; **p** – resting extrusomes are very narrowly ovate and about 6 × 0.8 µm in size in hematoxylin stains; **s** – rear body region; **t** – the nuclear apparatus is surrounded by a gelatinous capsule in Feulgen preparations. B – dorsal brush, CK – circumoral kinety, CV – contractile vacuoles, DV – defecation vacuole, E – extrusomes, IB – internal basket, MA – macronuclear nodules, MI – micronuclei, OO – oral bulge opening, PB – pharyngeal basket, PE – perioral kinety, PR – preoral kineties, SK – somatic kineties. Scale bars: 10 µm (m, n, t), 20 µm (s), 100 µm (a, c, d, f, k, l, q, r), and 200 µm (b).

Type locality: Šrámek-Hušek (1957) discovered *P. kahli* in the Podolský potok stream, Janovice, Czech Republic, E18°06' N49°46'.

Type and voucher material: No type material is available. Song (1994b) did not mention deposition of any slides containing Chinese specimens identified as *Dileptus monilatus*.

Dedication: Šrámek-Hušek (1957) dedicated this species to the eminent German ciliate taxonomist, Alfred Kahl.

Description: Size usually about 700 × 40 µm in vivo; Hamburg specimens 500–900 µm long (Kahl 1931), Czech exemplar 650 µm (Šrámek-Hušek 1957), North American specimen 550 µm (Conn 1905); African cells 500–800 µm (Dragesco 1970; Dragesco & Dragesco-Kernéis 1986), and Chinese specimens 400–500 µm (Song 1994b, but see critic above); very flexible but not contractile. Shape distinctly fusiform, cylindroidally dileptid to rod-like, that is, length:width ratio about 10–16:1, according to the figures available. Proboscis one third to one half of body length, anterior fifth usually curved dorsally, highly motile and flexible; trunk oblong and unflattened in vivo; tail usually distinct, occupies up to one third of trunk length (Figs 134a–d, f, i, k, l, q–s). Macronucleus a moniliform, basically straight strand extending between oral bulge opening and base of tail, composed of 15–35 globular to broadly ellipsoidal nodules 15–20 µm in diameter (Figs 134a–d, k, l, q, r, t); macronucleus surrounded by a homogenous, gelatinous envelope in North American specimens in Feulgen preparations (Fig. 134t); many nucleoli about 1–2 µm across, well recognizable in vivo and in preparations (Figs 134o, t). Four to 20 micronuclei attached to macronuclear nodules, 3–5 µm across in vivo, while 2–3 µm in protargol preparations (Fig. 134k); surrounded by a distinct membrane in North American specimens (Fig. 134t). A stripe of contractile vacuoles in dorsal side of cell: about 5–10 vacuoles in proboscis and 10–15 in trunk (Figs 134a–e, k, l, q, r). Extrusomes not studied in vivo; very narrowly ovate and 6 × 0.5 µm in size in iron hematoxylin stains (Fig. 134p), while rod-shaped and 7–9 µm long after protargol impregnation, sometimes showing a typical toxicyst structure (Fig. 134j). Cytoplasm colourless, opaque in trunk because packed with lipid droplets and food vacuoles; in trunk end sometimes a defecation vacuole (Fig. 134s). Usually moves slowly through organic mud and zoogleal masses, probing with the proboscis; swims by rotation about main body axis (Jones & Beers 1953).

Cilia ordinarily to narrowly spaced, arranged in at least 22–27 longitudinal rows (Song 1994b; but see critic above). Perioral kinety extends to tip of proboscis with narrowly spaced basal bodies. Left side of proboscis with broad, blank stripe because left side ciliary rows end at level of oral bulge opening, except for one to two kineties extending to or above proximal third of proboscis (Figs 134e, f, h). Dorsal brush on dorsal and dorso-lateral region of proboscis, probably three-rowed (Fig. 134f; Song 1994b; but see critic above). Silverline pattern composed of very small, polygonal meshes about 0.5 µm in size (Fig. 134g).

Oral bulge opening at beginning of second body third, roundish and about 10 µm across in iron hematoxylin stains (Fig. 134m), appears ovate when viewed obliquely (Figs 134f, h). Pharyngeal basket obconical, well recognizable in vivo and in preparations (Figs 134b–d, f, h, k, m, n, q, r). Oral ciliary pattern dileptid, left branch of circumoral kinety associated with many short, strongly oblique preoral kineties, each usually composed of three narrowly spaced cilia (Figs 134f, h).

Occurrence and ecology: *Pseudomonilicaryon kahli* was first observed in the mud of the mesosaprobic Aussenalster Lake in the surroundings of the town of Hamburg, Germany (Kahl 1931). Later, Šrámek-Hušek (1957) reported a single specimen from the beta-mesosaprobic Podolský potok stream, Czech Republic. Further freshwater records: meadow rainwater puddles in the surroundings of the town of Forchheim, Germany (Dingfelder 1962); a doubtful record (see above) from the coast of Lake Herăstrău, Bucharest, Roumania (Vuxanovici 1959); brooks and rivers in the surroundings of the town of Middletown, Connecticut, USA (Conn 1905); Chapel Hill, North Carolina, USA (Jones & Beers 1953); and various

sandy benthic localities in tropical Africa (Dragesco 1970; Dragesco & Dragesco-Kernéis 1986). Song (1994b) recorded *P. kahli* in soil from the surroundings of the town of Qingdao, China. Possibly, *P. kahli* is a ubiquitous cosmopolite feeding on bacteria and medium-sized ciliates, such as *Euplotes* and *Colpoda* (Jones & Beers 1953).

Paradileptus Wenrich, 1929

1929 *Paradileptus*, n. gen. Wenrich, Trans. Am. microsc. Soc. **48**: 352

1931 *Tentaculífera* Sokoloff, An. Inst. Biol. Univ. Méx. **2**: 165 (synonymy proposed by Corliss 1979)

1943 *Paradileptus* Wenrich – Kahl, Infusorien: 32 (taxonomic revision)

1953 *Paradileptus* Wenrich, 1929 – Reichenow, Protozoenkunde: 1102 (brief review)

1979 *Paradileptus* Wenrich, 1929 – Corliss, Ciliated protozoa: 216 (characterization, classification)

1986 *Paradileptus* Wenrich, 1929 – Dragesco & Dragesco-Kernéis, Faune tropicale **26**: 163 (monograph)

2001 *Paradileptus* Wenrich 1929 – Aescht, Denisia **1**: 115 (catalogue of generic names of ciliates)

2002 *Paradileptus* Wenrich, 1929 – Lynn & Small, Phylum Ciliophora: 482 (guide to ciliates)

2007 *Paradileptus* Wenrich, 1929 – Jankowski, Protista II: 574 (brief generic review)

2008 *Paradileptus* Wenrich, 1929 – Lynn, Ciliated protozoa: 371 (list of genera)

Improved diagnosis: Small- to large-sized Dileptidae with narrowly dileptid. Macronucleus moniliform. Dorsal brush multi-rowed. Right branch of circumoral kinety accompanied by two perioral kineties, left branch by many oblique preoral kineties. Oral bulge opening paradileptid, i.e., inverted and located laterally, just as in numeral 6. Cyst wall radially striated.

Type species (by original designation): *Amphileptus flagellatus* Rousselet, 1890. However, *A. flagellatus* is a junior synonym of *A. moniliger* Ehrenberg, 1835 and a senior synonym of *Dileptus elephantinus* Švec, 1897 (see below). Thus, we shall propose *D. elephantinus* to be fixed as the type species of *Paradileptus* under the plenary power of the International Commission on Zoological Nomenclature.

Etymology: Not given in original description. Composite of the Latin prefix *para* (like) and the generic name *Dileptus*. Masculine gender.

Remarks: Wenrich (1929) diagnosed the genus as follows: "Body oval or conical in shape, broad and obliquely truncated at the level of the cytostome, providing a wide peristomal field with a raised border or rim which is prolonged anteriorly into a spirally wound proboscis; a narrow trichocyst–(toxicyst)–bearing zone flanked on either side by a band of longer cilia, takes origin near the cytostome and traverses the anterior edge of the rim of the peristome and the proboscis; cilia of uniform length on the remainder of the body surface; cytostome a circular opening, closed except during ingestion; pharynx with longitudinal fibrils, as in *Dileptus*; contractile vacuoles small, numerous, distributed over the body; macronucleus beaded or in segments". Foissner et al. (1999) added the perioral kineties, and we add the resting cyst, which distinctly differs from the, admittedly few, dileptid cysts known (see general part), including that of *Pelagodileptus trachelioides*.

Paradileptus comprises seven nominal species, of which only one, *P. elephantinus*, is valid. *Paradileptus* is possibly closely related to *Pelagodileptus*, as they share two strong synapomorphies: (i) the right branch of the circumoral kinety is accompanied by two perioral kineties and (ii) the planktonic way of life. The two genera differ by the structure of the resting cysts and the proboscis base, which is strongly broadened in *Paradileptus*, taking along the oral bulge and the bulge opening which becomes located

laterally and inverted, just as in numeral 6. This pattern evolved very likely convergently in one other dileptid, *Apotrachelius*, which has, however, a lateral fossa, a single perioral kinety, and many scattered macronuclear nodules.

Paradileptus elephantinus (Švec, 1897) Kahl, 1931 (Figs 135a–w, 136a–z, 137a–z)

1835 *Amphileptus moniliger* Ehrenberg, Abh. dt. Akad. Wiss. Berl. year **1835**: 165 (nomen oblitum, without figure)

1838 *Amphileptus moniliger* Ehrenberg, Infusionsthierchen: 356 (taxonomic revision, with figure)

1890 *Amphileptus flagellatus* sp. n. Rousselet, J. Quekett microsc. Club **4**: 114 (supposed synonym)

1897 *Dileptus elephantinus* Švec, Bull. int. Acad. tchéque Sci. **4**: 41 (nomen protectum)

1929 *Paradileptus conicus*, n. sp. Wenrich, Trans. Am. microsc. Soc. **48**: 353 (synonymy proposed by Krainer 1988 and Foissner et al. 1995)

1929 *Paradileptus robustus* n. sp. Wenrich, Trans. Am. microsc. Soc. **48**: 357 (synonymy proposed by Kahl 1931)

1929 *Paradileptus flagellatus* (*Amphileptus flagellatus*) (Rousselet, 1890) – Wenrich, Trans. Am. microsc. Soc. **48**: 359 (combining author)

1931 *Paradileptus* (*Dileptus*) *elephantinus* (Sveç, 1897) – Kahl, Tierwelt Dtl. **21**: 210 (taxonomic revision; combining author)

1931 *Paradileptus* (*Amphileptus*) *flagellatus* (Rousselet, 1980) – Kahl, Tierwelt Dtl. **21**: 210 (taxonomic revision)

1931 *Tentaculífera mexicana* Sokoloff, An. Inst. Biol. Univ. Méx. **2**: 165 (synonymy proposed by Kahl 1935)

1933 *Paradileptus robustus* Wenrich – Wang & Nie, Contr. biol. Lab. Sci. Soc. China **10**: 32 (description of a Chinese population)

1935 *Paradileptus elephantinus* Sveç, 1897 – Kahl, Tierwelt Dtl. **30**: 823 (taxonomic revision)

1935 *Paradileptus conicus* Wenrich, 1929 – Kahl, Tierwelt Dtl. **30**: 823 (taxonomic revision)

1943 *Paradileptus elephantinus* Sveç – Kahl, Infusorien: 32 (taxonomic revision)

1943 *Paradileptus conicus* Wenrich – Kahl, Infusorien: 32 (taxonomic revision)

1943 *Paradileptus flagellatus* Rousselet – Kahl, Infusorien: 32 (doubtful species; supposed synonym)

1945 *Paradileptus ovalis* nova species Huber-Pestalozzi, Vjschr. naturf. Ges. Zürich **90**: 123 (synonymy proposed by Foissner et al. 1999)

1945 *Paradileptus conicus* – Huber-Pestalozzi, Vjschr. naturf. Ges. Zürich **90**: 120 (description of a Swiss population)

1951 *Paradileptus estensis* Canella, Annali Univ. Ferrara **1**: 81 (synonymy proposed by Foissner et al. 1999)

1951 *Paradileptus robustus* Wenrich – Canella, Annali Univ. Ferrara **1**: 142 (description of an Italian population)

1957 *Paradileptus elephantinus* – Šrámek-Hušek, Věst. Čsl. zool. spol. **21**: 3 (ecology)

1961 *Paradileptus* (*Dileptus*) *elephantinus* Svec – Buck, Jh. Ver. vaterl. Naturk. Württ. **116**: 201 (ecology)

1965 *Dileptus elephantinus* Sveč – Kosova, Vsesoûz. Gidrobiol. Ob., Akad. Nauk Ukr. SSR year **1965**: 123 (ecology)

1969 *Paradileptus elephantinus* – Kravchenko, Vest. Zool., Akad. Nauk Ukr. SSR year **1969**: 71 (ecology)

1969 *Paradileptus elephantinus* Švec – Sládeček, Arch. Protistenk. **111**: 277 (saprobic classification)

1969 *Paradileptus elephantinus* Svec – Wilbert, Arch. Hydrobiol. **35** (Suppl.): 458 (ecology)

1972 *Paradileptus elephantinus* Sveç – Dragesco, Annls Fac. Sci. Univ. féd. Cameroun **11**: 76 (description of a Chadian population)

1972 *Paradileptus elephantinus* – Heuss, Kalthoff & Klös, SchrReihe Landesanst. Gewässerkde Nordrhein-Westfalen Heft **32**: 80 (ecology)

1972 *Paradileptus minutus* Dragesco, Annls Fac. Sci. Univ. féd. Cameroun **9**: 90 (synonymy proposed by Foissner et al. 1999; very likely an injured specimen)

1973 *Paradileptus elephantinus* (Svec.) – Liepa, Latv. PSR Zinát. Akad. Vest. year **1973**: 32 (ecology)

1975 *Paradileptus conicus* Wenrich 1929 – Fryd-Versavel, Iftode & Dragesco, Protistologica **11**: 520 (ciliature after silver impregnation)

1975 *Paradileptus elephantinus* Svec. 1897 – Fryd-Versavel, Iftode & Dragesco, Protistologica **11**: 520 (description of a French population)

1976 *Paradileptus elephantinus* Sveç – Mamaeva, Zool. Ž. **55**: 658 (ecology)

1978 *Paradileptus elephantinus* – Mamaeva & Kopylov, Citologiâ **20**: 472 (ecology)

1978 *Paradileptus elephantinus* – Zhukov & Mamaeva, Trudy Inst. Biol. vnutr. Vod **34**: 166 (ecology)

1979 *Paradileptus elephantinus* Svec., 1897 – Mamaeva, Infuzorii bassejna Volgi: 31 (brief review, ecology)

1979 *Paradileptus conicus* Wenrich, 1929 – Mamaeva, Infuzorii bassejna Volgi: 32 (brief review, ecology)

1979 *Paradileptus elephantinus* Svec – Mücke, Arb. Inst. landw. Zool. Bienenkd. **5**: 268 (ecology)

1980 *Paradileptus* (*Dileptus*) *elephantinus* (Svec) – Nebrat, Gidrobiol. Ž. **16**: 31 (ecology)

1983 *Paradileptus elephantinus* (Šveć.) – Liepa, Protozoologiâ **8**: 136 (ecology)

1983 *Paradileptus elephantinus* – Matsuoka, Matsuo, Maesako & Shigenaka, Bull. biol. Soc. Hiroshima Univ. **49**: 15 (ecology)

1984 *Paradileptus elephantinus* Sveć – Alekperov, Hydrobiol. J. **20**: 18 (ecology)

1984 *Paradileptus elephantinus* (Svec, 1897) – Schlott-Idl, Limnologica, Berlin **15**: 45 (ecology)

1985 *Paradileptus* sp. (*elephantinus* Svec.) – Kusano, Rep. Inst. nat. Stu. **16**: 105 (ecology)

1985 *Paradileptus elephantinus* (Svec) – Oleksiv, Gidrobiol. Ž. **21**: 91 (ecology)

1986 *Paradileptus elephantinus* (Sveç, 1897) – Dragesco & Dragesco-Kernéis, Faune tropicale **26**: 165 (brief taxonomic monograph)

1986 *Paradileptus minutus* Dragesco, 1972 – Dragesco & Dragesco-Kernéis, Faune tropicale **26**: 166 (brief taxonomic monograph)

1986 *Paradileptus elephantinus* Svec – Oleksiv, Lopotun & Tkač, Vest. L'vov. Univ. (Ser. Geol.) **9**: 29 (ecology)

1987 *Paradileptus elephantinus* Sveç, 1897 – Lokot', Èkologiâ resničnyh prostejših: 35 (ecology)

1987 *Paradileptus conicus* Wenrich, 1929 – Lokot', Èkologiâ resničnyh prostejših: 35 (ecology)

1988 *Paradileptus elephantinus* (Švec, 1897) – Foissner, Hydrobiologia **166**: 41 (saprobic classification)

1989 *Paradileptus elephantinus* – Barbieri & Godinho-Orlandi, Revta Hydrobiol. Trop. **22**: 282 (ecology)

1990 *Paradileptus elephantinus* (Svec.) – Belova, Gidrobiol. Ž. **26**: 21 (ecology)

1991 *Paradileptus elephantinus* Svec – Nesterenko & Kovalchuk, Acta hydrochim. hydrobiol. **19**: 25 (biomass)

1992 *Paradileptus elephantinus* Svec. – Myl'nikova, Inf. Byull. Biol. vnutr. Vod **93**: 40 (ecology)

1992 *Paradileptus elefantinus* Svec. – Nebrat, Gidrobiol. Ž. **28**: 29 (incorrect spelling, ecology)

1992 *Paradileptus elephantinus* – Zharikov, Inf. Byull. Biol. vnutr. Vod **93**: 47 (ecology)

1992 *Paradileptus elephantinus* – Zharikov & Rotar, Inf. Byull. Biol. vnutr. Vod **92**: 22 (ecology)

1993 *Paradileptus elephantinus* Svec. – Myl'nikova, Trudy Inst. Biol. vnutr. Vod **67**: 192 (ecology)

1995 *Paradileptus elephantinus* Svec, 1897 – Czapik & Fyda, Przegl. zool. **39**: 67 (ecology)

1995 *Paradileptus elephantinus* (Švec, 1897) Kahl, 1931 – Foissner, Berger, Blatterer & Kohmann, Informationsberichte des Bayer. Landesamtes für Wasserwirtschaft **1/95**: 203 (monograph)

1996 *Paradileptus elephantinus* (Swec) Kahl – Nauwerck, Ber. nat.-med. Ver. Salzburg **11**: 156 (ecology)

1999 *Paradileptus elephantinus* (Švec, 1897) Kahl, 1931 – Foissner, Berger & Schaumburg, Informationsberichte des Bayer. Landesamtes für Wasserwirtschaft **3/99**: 221 (taxonomical and ecological monograph)

2002 *Paradileptus elephantinus* (Švec, 1897) – Baláži & Matis, Biologia, Bratisl. **57**: 155 (ecology)

Nomenclature: *Paradileptus elephantinus* (Švec, 1897) Kahl, 1931 was originally described as *Amphileptus moniliger* by Ehrenberg (1835), as indicated by Fig. 143m. Unfortunately, Kahl (1931) and other authors overlooked Ehrenberg's description. In this situation, the older species epithet *moniliger* does not take precedence over the younger *elephantinus* because both conditions of Article 23.9.1 of the ICZN (1999) are met: (i) *Amphileptus moniliger* Ehrenberg, 1838 has not been used after 1899 [possibly this species was last time mentioned by Marsson 1901 as "*Dileptus moniliger* (Ehb.)"] and (ii) the junior synonym, *Paradileptus elephantinus* (Švec, 1897) Kahl, 1931, has been used at least in 25 works published by at least ten authors in the immediately preceding fifty years, encompassing a span of not less than ten years (see list of synonyms). Thus, *Amphileptus moniliger* would become a nomen oblitum and *Paradileptus elephantinus* a nomen protectum. However, the matter is complex because the type species of the genus, *P. flagellatus*, is very likely an older synonym of *P. elephantinus* and a younger synonym of *Amphileptus moniliger*. If this synonymization is anticipated, the species must be named *Paradileptus moniliger* which, however, is a forgotten name. Thus, we shall make a bid to the International Commission of Zoological Nomenclature to protect *P. elephantinus*, i.e., the name which was widely used since Kahl (1931) and which we use in the present monograph.

Synonymy and identification: This species is rather variable and more importantly, very fragile. Specifically, the trunk shape, the proboscis, and the tail are delicate and thus usually recognizable mainly in freshly collected material. The tail disappears rapidly and the cell becomes bulky, looking like *P. elephantinus*, when the environment becomes unfavourable. Therefore, Foissner et al. (1999) supposed synonymy of most or all species listed above. They differ from each other and from *P. elephantinus* in body size and/or shape and/or number of macronuclear nodules. The last character has been used by several authors, but is doubtful because it has a high intrapopulation variability (8–14, mean 11.9 nodules in Australian population; 7–20 nodules in the 1994 Salzburg population; 5–9, mean 6.9 nodules in the 1997 Salzburg population, only 1[!] nodule in half of specimens in a collection made one month later), indicating that the differences between populations must not be over-interpreted. Thus, all these taxa are inseparable, including the binucleate *P. flagellatus* (Rousselet, 1890) Wenrich, 1929, at least at the present state of knowledge; at best, some can be considered as subspecies or ecoforms. Basically, the populations need careful reinvestigation as concerns the extrusomes (in vivo!) and the number of ciliary rows.

Paradileptus elephantinus is easy to identify because it is very conspicuous due to the helical shape and proboscis, the dish-like widened proboscis base, and the obconical trunk. However, these features are frequently partially or completely lost in insufficiently preserved (fixed) cells, leaving behind an ellipsoidal mass (Fig. 137g). In this case, look for the characteristic, moniliform macronucleus, but be careful not to confuse it with *Linostomella* (a heterotrich previously named *Condylostoma*). There is only one further euplanktonic dileptid with moniliform macronucleus, *Pelagodileptus trachelioides*, which is usually distinctly larger (300–600 µm vs. 150–350 µm), has symbiotic green algae, and a narrowly elliptical oral bulge opening (vs. roundish and just as in numeral 6).

Improved diagnosis (includes all information known): Size about 300 × 150 µm in vivo. Shape dileptid to narrowly dileptid with long proboscis dish-like broadened posteriorly at left side; trunk obconical with short tail. Macronucleus moniliform, composed of about 15 globular nodules; several globular micronuclei. Many scattered contractile vacuoles, each with 1 pore, in trunk and dorsal side of proboscis. Extrusomes rod-shaped, possibly 4 µm long, attached to proboscis oral bulge. About 160 ciliary rows; dorsal brush multi-rowed, staggered, with monokinetidal tails extending to base of proboscis. Oral bulge opening about 20 µm across. Preoral kineties narrowly spaced, slightly to ordinarily oblique, each composed of about 10 narrowly spaced cilia.

Type locality: Plankton from the Počernický rybník Pond near Prague, Czech Republic, E14°49' N50°12'.

Type material: Not available.

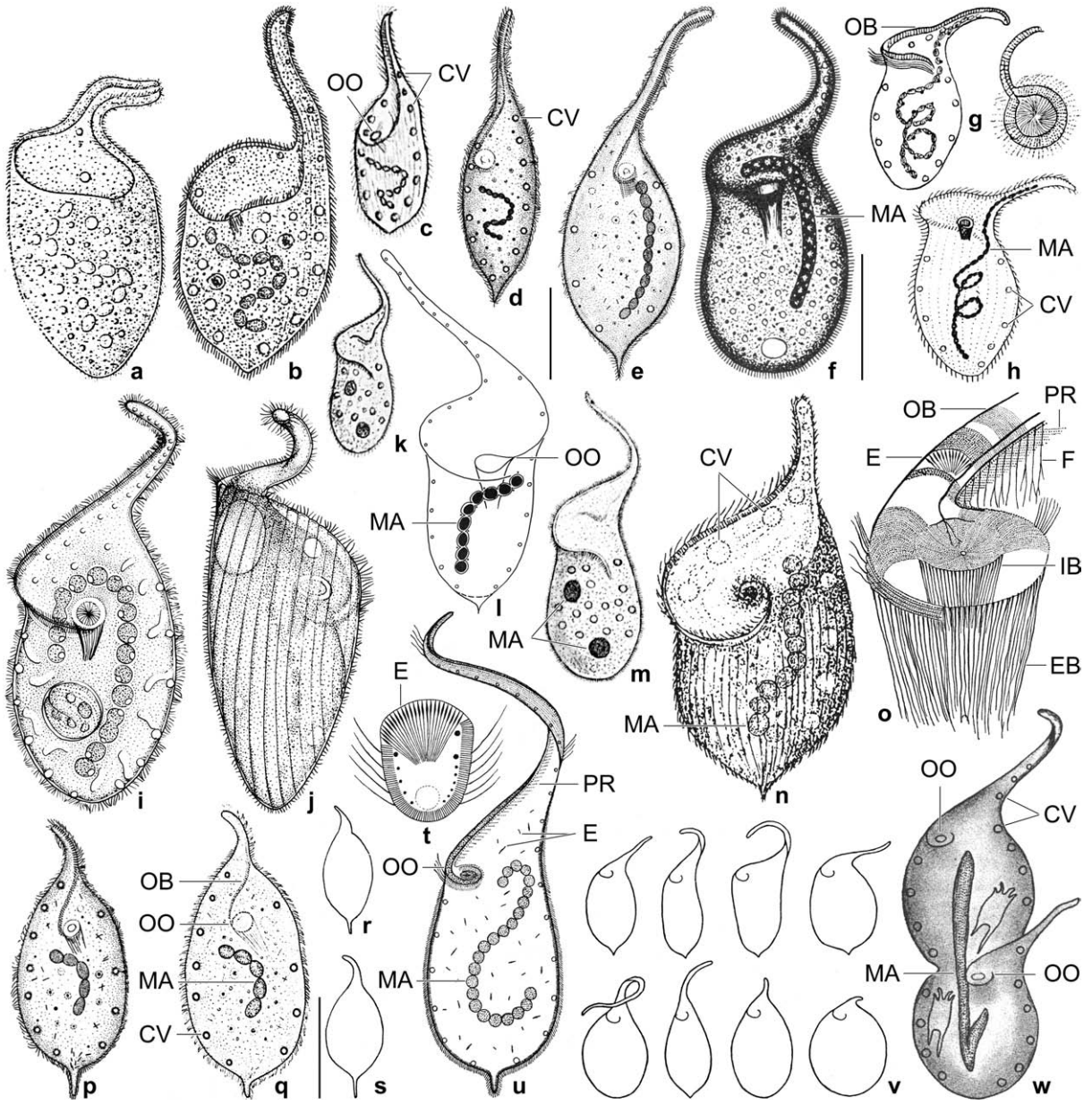
Etymology: Not given in original description. The Latin adjective *elephantinus* (elephantine) refers to the long and motile proboscis resembling that of an elephant.

Description: All known data are put together although some synonyms are still questionable. Thus, some data are kept separate.

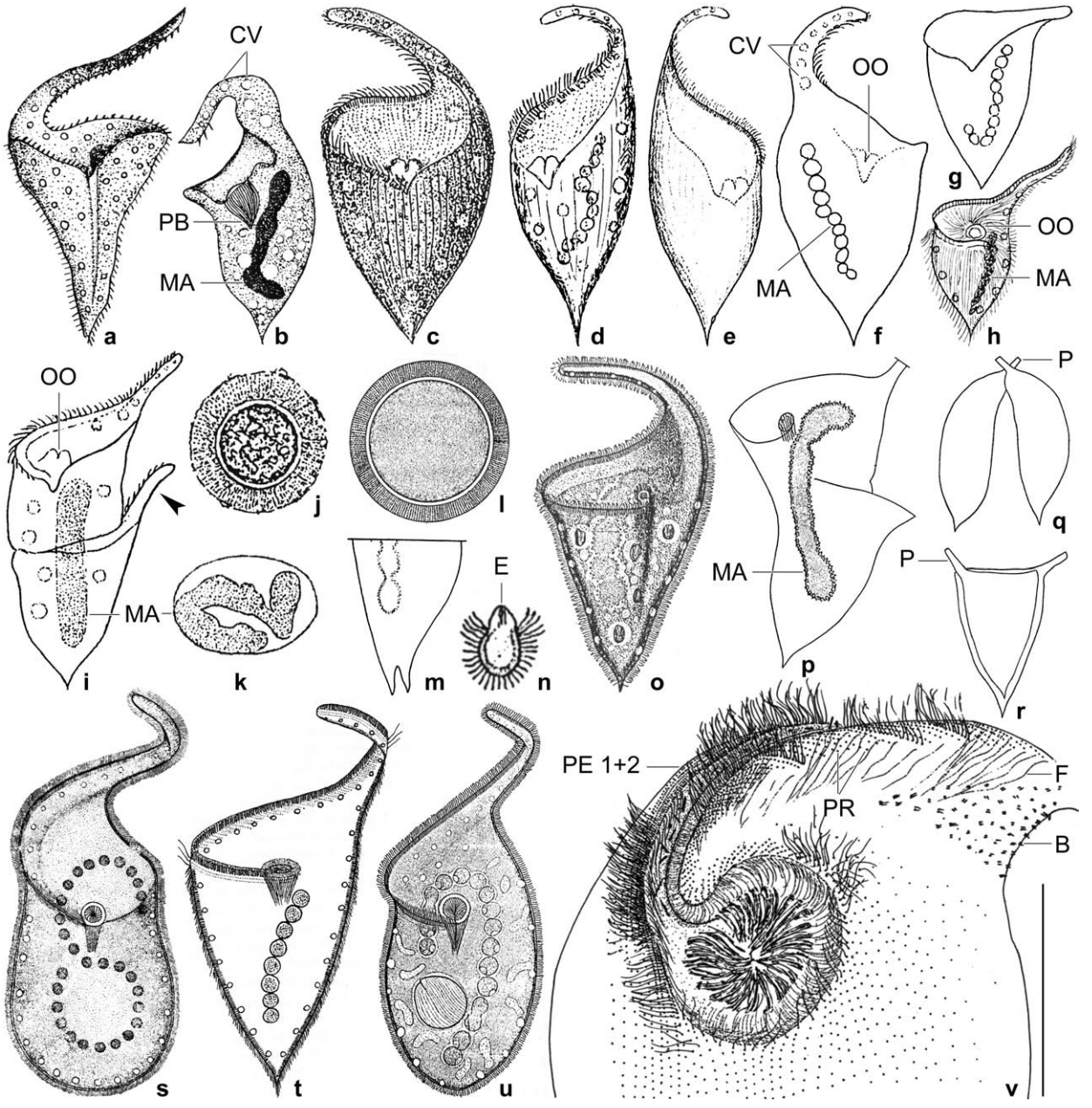
Size in vivo similar in most populations, usually about 300 × 160 µm: 200–250 × 100 µm (Švec 1897, Kahl 1931); 300–350 × 100–150 µm (Fryd-Versavel et al. 1975); 128–176 × 192–240 µm, on average 144 × 212 µm (Mamaeva 1979c); 100–150 µm (Kusano 1985); 300–350 µm, 270 µm without proboscis (Dragesco & Dragesco-Kernéis 1986); 250–600 × 100–350 µm (Lokot' 1987); 250 µm (Czapik & Fyda 1995); 500–600 µm (Diéguez & Balseiro 2000). Body length/size of supposed synonyms: *Amphileptus moniliger* 270–360 µm (Ehrenberg 1835, 1838); *Paradileptus conicus* 100–200 µm (Wenrich 1929, Kahl 1931), 140–190 × 90–115 µm (Canella 1951), 280–350 × 90–130 µm (Fryd-Versavel et al. 1975), 153 × 100 µm (Mamaeva 1979c), 200–350 ×150–200 µm (Lokot' 1987); *P. estensis* 350–800 µm (Canella 1951); *P. flagellatus* 385–455 × 210–250 µm (Rousselet 1890), about 400 µm (Kahl 1931); *P. minutus* 220–330 µm (Dragesco 1972a, Dragesco & Dragesco-Kernéis 1986); *P. ovalis* 160 µm (Huber-Pestalozzi 1945); *P. robustus* 180–450 µm, usually 250–350 µm (Wenrich 1929), 400 × 240 µm (Wang & Nie 1933), 180–450 µm, usually 250–350 µm (Huber-Pestalozzi 1945); *Tentaculifera mexicana* 100 × 60 µm (Sokoloff 1931; possibly fixed material).

Body very flexible but not contractile. Shape in vivo dileptid to narrowly dileptid, that is, length:width ratio on average 2.8:1 (M = 2.8:1, SD = 0.6:1, SE = 0.1:1, CV = 22.5%, Min = 1.3:1, Max = 4.3:1, n = 38), according to the figures available in the literature; and on average 3.3:1 (M = 3.3:1, SD = 0.6:1, SE = 0.2:1, CV = 17.4%, Min = 2.5:1, Max = 4.5:1, n = 13), according to our light microscopical and SEM micrographs. Proboscis conspicuous because helically twisted and posteriorly broadened dish-like (Figs 135a–n, u, 136a–h, o, s–u, w, x, 137a–f, o–u); highly variable in length because very fragile and thus often injured or even more or less lost; usually occupies one third to one half of body length, while distinctly longer than trunk in some specimens of *Paradileptus estensis*, which thus might be a distinct species (Figs 135u, v, 137e, f), up to 90 µm long according to Švec (1897). Trunk massive, slightly flattened and obconical in fresh material, while becoming almost globular under adverse conditions (Figs 135a–n, p–v, 136a–h, o, s–u, w, x, 137a–f, o–t). Posterior end with distinct tail present only in fresh material (Figs 135d, e, p–u, 137f, p), soon becoming acute and more or less broadly rounded (Figs 135a–c, f–j, 136a–h, s–u, w, x, 137a–e, g, l, m, q–s); rarely bifurcated in North American cells (Fig. 136m).

Nuclear apparatus usually extends between oral bulge opening and base of tail, rarely commences in anterior third of proboscis (Figs 135g, h). Macronucleus a moniliform, slightly to strongly sigmoidal or tortuous strand surrounded by a gelatinous capsule in vivo (Figs 135a–i, l, n, p, q, u, 136b, d, f–h, s–u, w, x,



Figs 135a–w: *Paradileptus elephantinus* and its supposed synonyms. **a, b** – specimens from type population, length 200–250 µm (from Švec 1897); **c** – *P. elephantinus*, length 230 µm (from Kahl 1931); **d, e** – *P. elephantinus*, length 270 µm and 430 µm (from Dragesco & Dragesco-Kernéis 1986); **f** – *P. elephantinus*, length 600 µm (from Lokot' 1987); **g** – *P. elephantinus* and frontal view of oral bulge and oral opening, length 300 µm (from Kahl 1935); **h** – *P. elephantinus*, length 250 µm (from Czapik & Fyda 1995); **i, j** – *Paradileptus* sp., ventral and dorsal view, length not given (from Curds 1982); **k** – *Amphileptus flagellatus* supposedly has only two macronuclear nodules (food vacuoles?), which is the sole difference to *P. elephantinus*, length 385–455 µm (from Rousselet 1890); **l** – *P. elephantinus*, semi-schematic view (from Krainer 1988); **m** – *P. flagellatus*, length 400 µm (from Kahl 1931); **n** – *P. ovalis*, length 160 µm (from Huber-Pestalozzi 1945); **o, t–w** – *P. estensis*, detail of oral apparatus (o), optical section of proboscis (t), total views (u, v), and mid-divider (w), length 350–800 µm (from Canella 1951); **p–s** – *P. minutus*, total views showing the short proboscis (very likely due to injury), length 220–300 µm (from Dragesco & Dragesco-Kernéis 1986 and Dragesco 1972a). CV – contractile vacuoles, E – extrusomes, EB – external basket, F – fibres, IB – internal basket, MA – macronucleus (nodules), OB – oral bulge, OO – oral bulge opening, PR – preoral kineties. Scale bars: 50 µm (d, e), 100 µm (q), and 200 µm (f).



Figs 136a–v: *Paradileptus elephantinus* and its supposed synonyms. From Wenrich 1929 (l–r, u), Sokoloff 1931 (a, b), Wang & Nie 1933 (s), Kahl 1935 (h), Huber-Pestalozzi 1945 (c–g, i–k), Canella 1951 (t), and Fryd-Versavel et al. 1975 (v). **a, b** – *Tentaculifera mexicana*, total view and longitudinal optical section, length 100 µm; **c–g** – *Paradileptus conicus*, length 140–200 µm; **h** – *P. conicus*, length 150 µm; **i** – *P. conicus*, late divider with fused macronuclear nodules and new proboscis (arrowhead) for the posterior daughter, length not given; **k** – *P. conicus*, optical section through trunk of a post-divider, showing the slightly nodulated macronuclear strand; **j, l–r** – *P. conicus*, resting cysts are 100–120 µm across and have a radially striated wall (j, l); a specimen with two-tailed rear body end (m); optical section through proboscis (n); overview, length 100–200 µm (o); late divider with macronuclear rod showing a roughened outline (p); and conjugants united bulge-to-bulge with the proboscis (q, r), length not given; **s** – *P. robustus*, length 400 µm; **t** – *P. conicus*, length l40–190 µm; **u** – *P. robustus*, length 200–350 µm; **v** – *P. conicus*, oral ciliary pattern, scale bar 50 µm. The right branch of the circumoral kinety is accompanied by two perioral kineties side by side, while the left branch is associated with many oblique preoral kineties, each usually composed of ten basal bodies. B – dorsal brush, CV – contractile vacuoles, E – extrusomes, F – fibres, MA – macronucleus (nodules), OO – oral bulge opening, P – proboscis, PB – pharyngeal basket, PE 1+2 – perioral kineties, PR – preoral kineties.

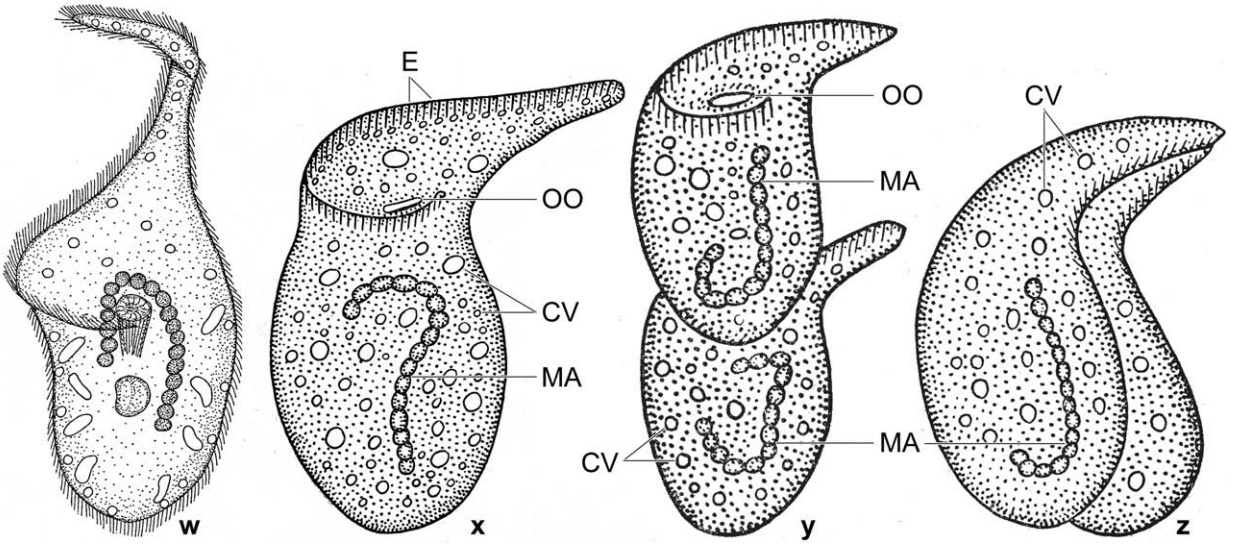
137e, g, h, l–n). Individual nodules usually conspicuously globular, rarely broadly ellipsoidal or ellipsoidal, with roughened outline in haemalum stains (Wenrich 1929). Number of nodules rather variable within and between populations: 8–12 (Švec 1897); usually 10–15 (extremes 1–20) according to Foissner et al. (1995, 1999); 8 (*Amphileptus moniliger*, Ehrenberg 1838); 8 (*Paradileptus estensis*, Canella 1951); 2 (*P. flagellatus*, Rousselet 1890); 4–6 (*P. minutus*, Dragesco 1972a); 11–14 (*P. ovalis*, Huber-Pestalozzi 1945); 4–8 (Wenrich 1929) and 23 (Canella 1951) in the synonym *P.conicus*; 10–23 (Wenrich 1929) and 29 (Wang & Nie 1933) in the synonym *P. robustus*. Size of nodules and nucleoli not yet studied. During cell division, the macronuclear nodules fuse to a globular mass, becoming a long, mid-constricted rod in late dividers (Figs 135w, 136i, p); early post-dividers have an oblong macronucleus becoming elongated and nodulated in late post-dividers (Figs 136k, y). Several globular micronuclei attached to macronuclear strand; exact number not known.

Contractile vacuole pattern identical in all populations investigated, i.e., many vacuoles scattered underneath cell surface of trunk and proboscis (Figs 135b–i, l, n, p, q, u, 136a–d, h, o, s–u, w, x, 137a, b). Number of vacuoles given only for the synonym *P. minutus*: 10–15 (Dragesco 1972a). Excretory pores studied only by Foissner et al. (1995, 1999), that is, invariably a single, intrakinetal pore per vacuole (Figs 137o–q, t, z).

Extrusomes in vivo short and rod-shaped, forming about three rows in proboscis oral bulge (Fig. 136n); should be checked in further populations. After protargol impregnation, appear as slightly curved, 4 µm long rods (Figs 137j–n, v); in other preparations tripartited into neck, bulb, and thread (Fig. 135t).

Cortex flexible, slightly furrowed by ciliary rows in SEM micrographs (Fig. 137z). Cortical granules 2–3 µm long, closely spaced and thus forming a more or less distinct fringe (Foissner et al. 1999). Cytoplasm yellow brown at low magnification due to minute cytoplasmic inclusions and food vacuoles; without symbiotic green algae. Swims rather rapidly rotating about main body axis with proboscis projecting forward in a helical pattern; when disturbed, swims rapidly backwards (Wenrich 1929).

Cilia about 10 µm long in vivo, ordinarily to widely spaced. Ciliary rows narrowly to ordinarily spaced,



Figs 136w–z: *Paradileptus elephantinus* and its supposed synonyms. From Lundin & West 1963 (w) and Mamaeva 1979c (x–z). **w** – *Paradileptus robustus*, size not given; **x** – *P. elephantinus*, length 128–176 µm; **y** – *P. elephantinus*, very late divider with already separated macronuclear strands in daughter cells, length not given; **z** – *P. elephantinus*, conjugants united bulge-to-bulge with the proboscis, length not given. CV – contractile vacuoles, E – extrusomes, MA – macronuclear strand, OO – oral bulge opening.

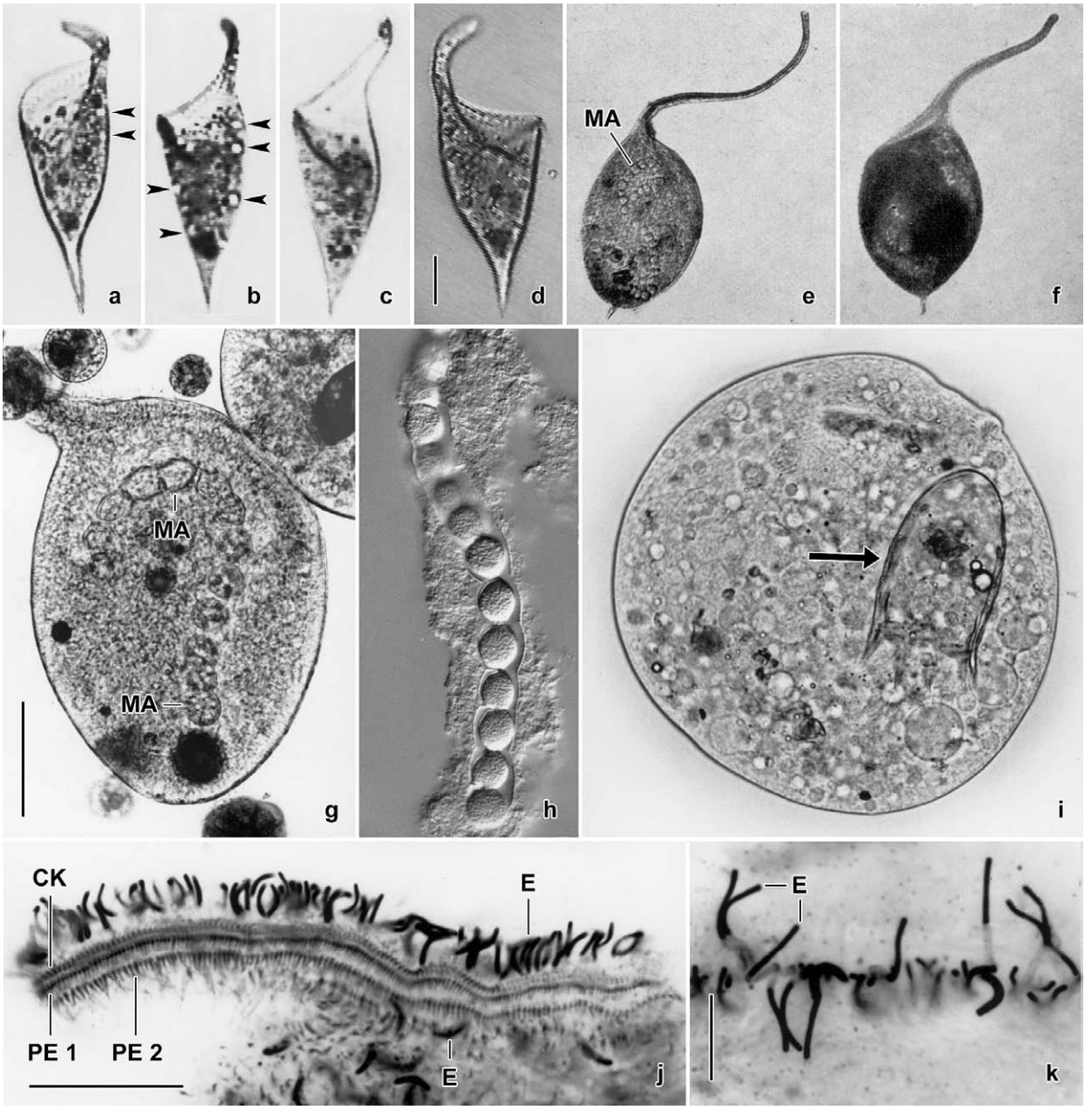
meridionally arranged, number studied only by Fryd-Versavel et al. (1975), viz., about 200 in *P. elephantinus* and 120 in the synonym *P. conicus*, a considerable difference indicative for distinct species. Details of ciliary pattern available only from Fryd-Versavel et al. (1975) and Foissner et al. (1995, 1999): (i) first two rows right of circumoral kinety extend as perioral kineties with narrowly spaced cilia to tip of proboscis (Figs 136v, 137j, l, n, s); (ii) left side of proboscis with conspicuous blank stripe (Figs 137o, r, t, u, w, y); (iii) dorsal brush a triangular field on dorsal and dorsolateral area of proboscis, multi-rowed, staggered, distinctly heterostichad, with monokinetidal tails extending to base of proboscis (Figs 136v, 137o, r, t, u, w, y); (iv) brush dikinetids loosely spaced, associated with type III bristles: anterior bristle about 1.2–1.5 µm long, posterior one stump-like and only 0.3–0.5 µm long in SEM (Figs 137w, x).

Oral bulge opening in or slightly underneath second body half; located laterally and inverted, just as in numeral 6; about 45 µm across after protargol impregnation, while 15–25 µm in vivo and in SEM (Figs 135g, n, 137o, r, u). Pharyngeal basket obconical, composed of numerous fibres (Fig. 135o). Canella (1951) and Fryd-Versavel et al. (1975), additionally, figured fibres originating from proboscis dikinetids and extending laterally or dorsally (Figs 135o, 136v). Structure of circumoral kinety not yet studied in detail. Preoral kineties conspicuous because composed of about ten narrowly to ordinarily spaced cilia and thus forming rather long, slightly to ordinarily oblique rows (Figs 136v, 137n, v, w, y).

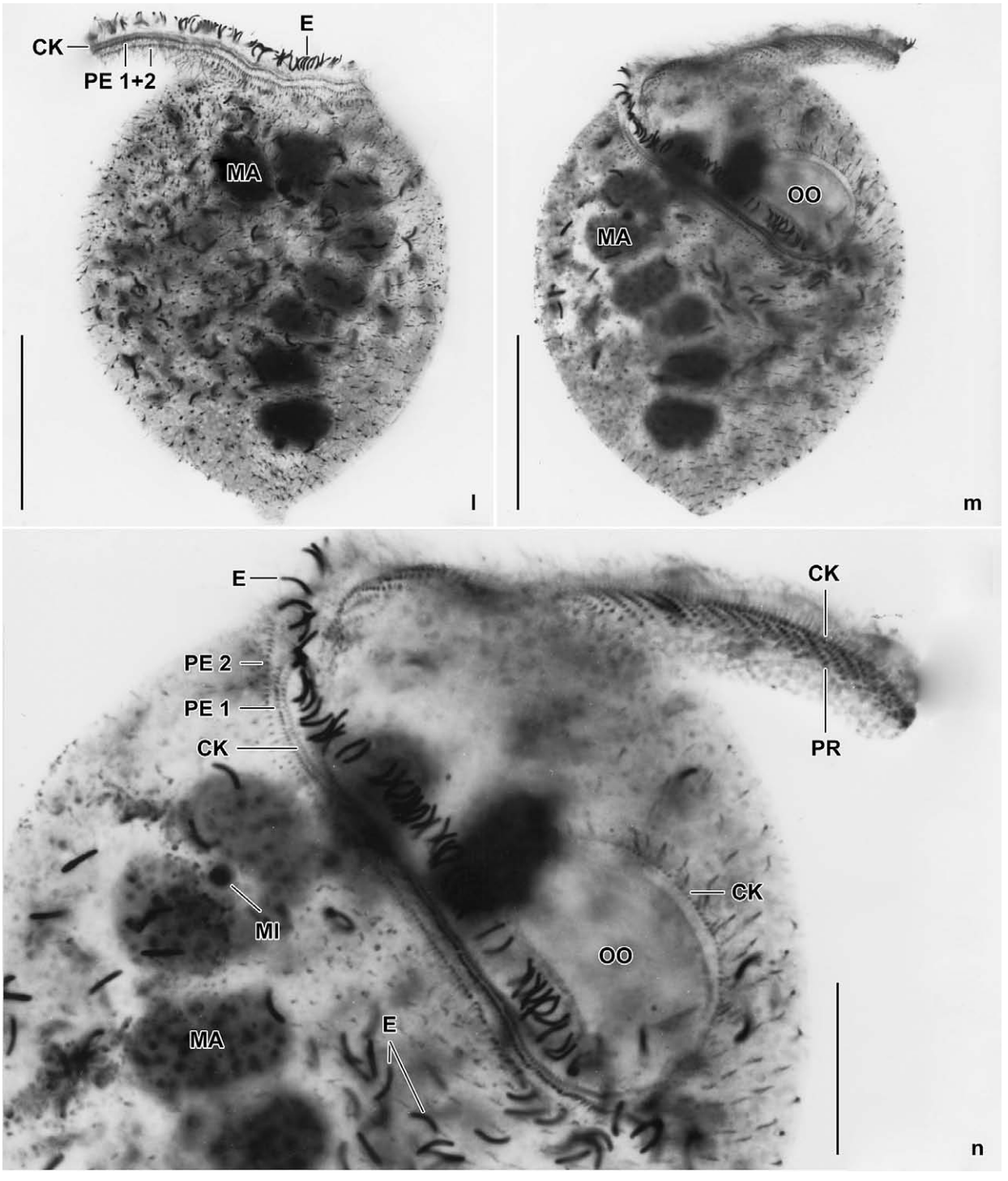
Resting cyst (Figs 136j, l): The resting cyst of the synonym *P. conicus* was studied by Wenrich (1929) and Huber-Pestalozzi (1945). Their data match well, especially in size (100–120 µm and ca. 100 µm) and the peculiar radial striation of the wall. The description by Wenrich (1929) reads as follows: "Cysts were found in watch glasses in which specimens of *D. conicus* obtained in San Francisco had been segregated. They are spherical, from 100 to 120 µm in diameter, with a relatively thick wall. Figure 4 (reproduced here as Fig. 136l) is a somewhat diagrammatic representation of one of these cysts. Others had still thicker walls. The cyst wall, besides being thick, is rather dense and is characterized by many radiating striations. These are believed to be derived from the rodlets of the ectosarc which have greatly expanded. It was not possible to make out the details of the nuclear structure, so it is not known whether or not a nuclear reorganization takes place. There was a narrow space between the cyst wall and the protoplasm".

Notes on conjugation (Figs 136q, r, z): Wenrich (1929) described it as follows: "Conjugation was observed in some of the *P. conicus* collected in San Francisco, but not in those collected in Philadelphia. As already noted, the conjugants were smaller than the average size for the species. The proboscis was also reduced in all the conjugants observed, but this may have been due to injury during the transfer from Golden Gate Park to Berkeley. The conjugants became attached to each other by their oral surfaces, as indicated in the sketches. Nuclear details have not, as yet, been worked out". Wenrich's observations basically match those of Mamaeva (1979c).

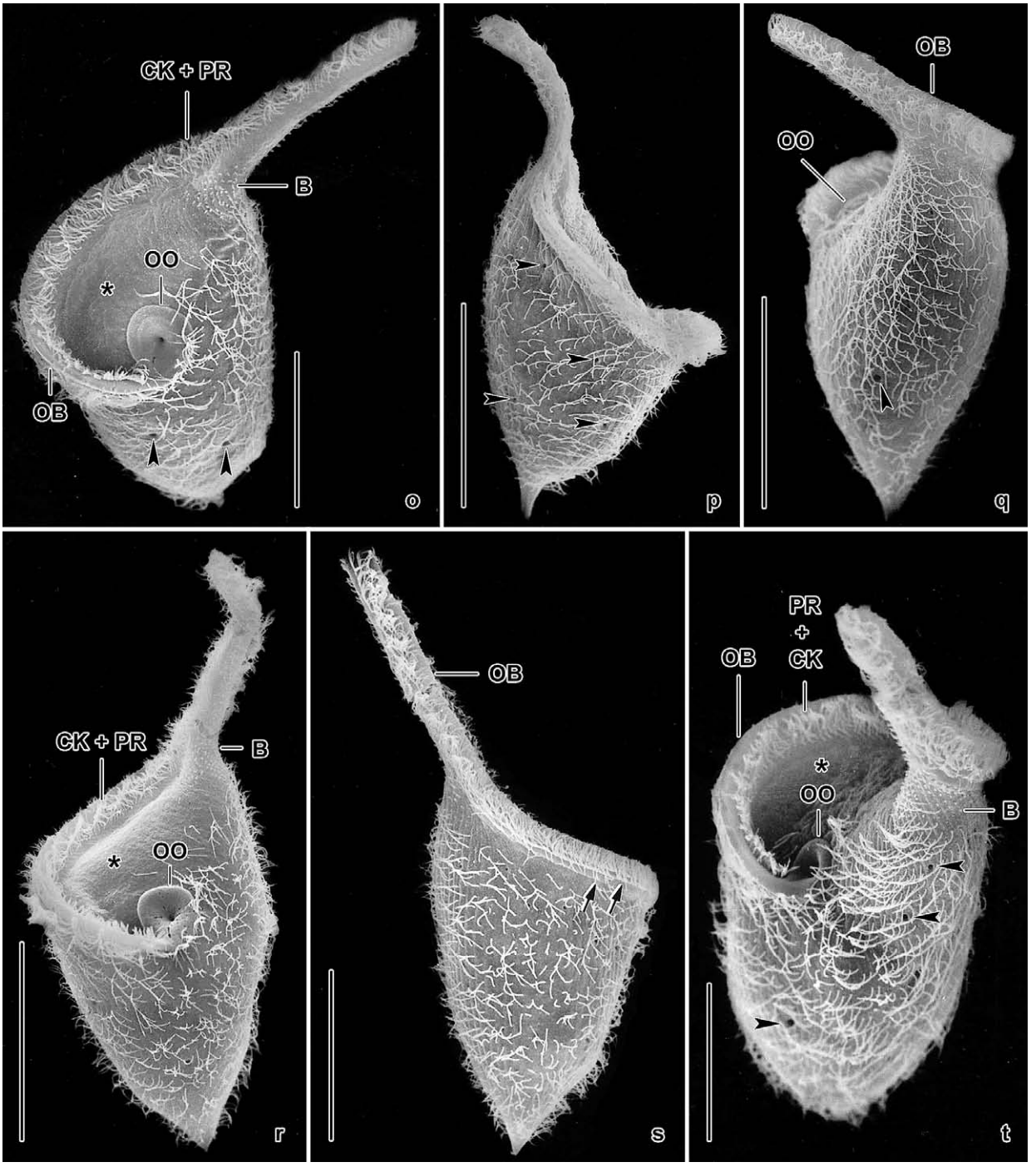
Occurrence and ecology (mainly according to Foissner et al. 1999): Common but usually not very abundant in the plankton of mesotrophic and eutrophic lakes, reservoirs, ponds, and large rivers. Numbers usually below 1000 ind./l, but contribution to total heterotrophic biomass often considerable due to the huge size. Reliably recorded from Eurasia, Africa and Australia, thus very likely cosmopolitan. Throughout the year, that is, eurytherm but possibly preferring the warm seasons (Mamaeva 1979a). This matches data of Belova (1989), who found high numbers mainly at 19–24 °C. Oligostenohaline. Omnivorous, feeds on bacteria, heterotrophic and autotrophic flagellates (*Chilomonas paramecium, Cryptomonas, Leptocinclis*), ciliates (*Ophrydium versatile*), and rotifers such as *Polyarthra, Keratella* and *Synchaeta* (Švec 1897, Wenrich 1929, Bick 1972b, Fryd-Versavel et al. 1975, Mamaeva & Kopylov 1978, Mücke 1979, Krainer 1988, Foissner et al. 1995, Diéguez & Balseiro 2000; Fig. 137i). Biomass of 10^6 specimens: 1700 mg (Schlott-Idl 1978), 2200 mg (Mamaeva 1979c), about 1000 mg (Foissner et al. 1995), 736 mg (Nestrenko & Kovalchuk 1991), 170 mg (Nesterenko & Kovalchuk 1991; for the synonym *P. conicus*,



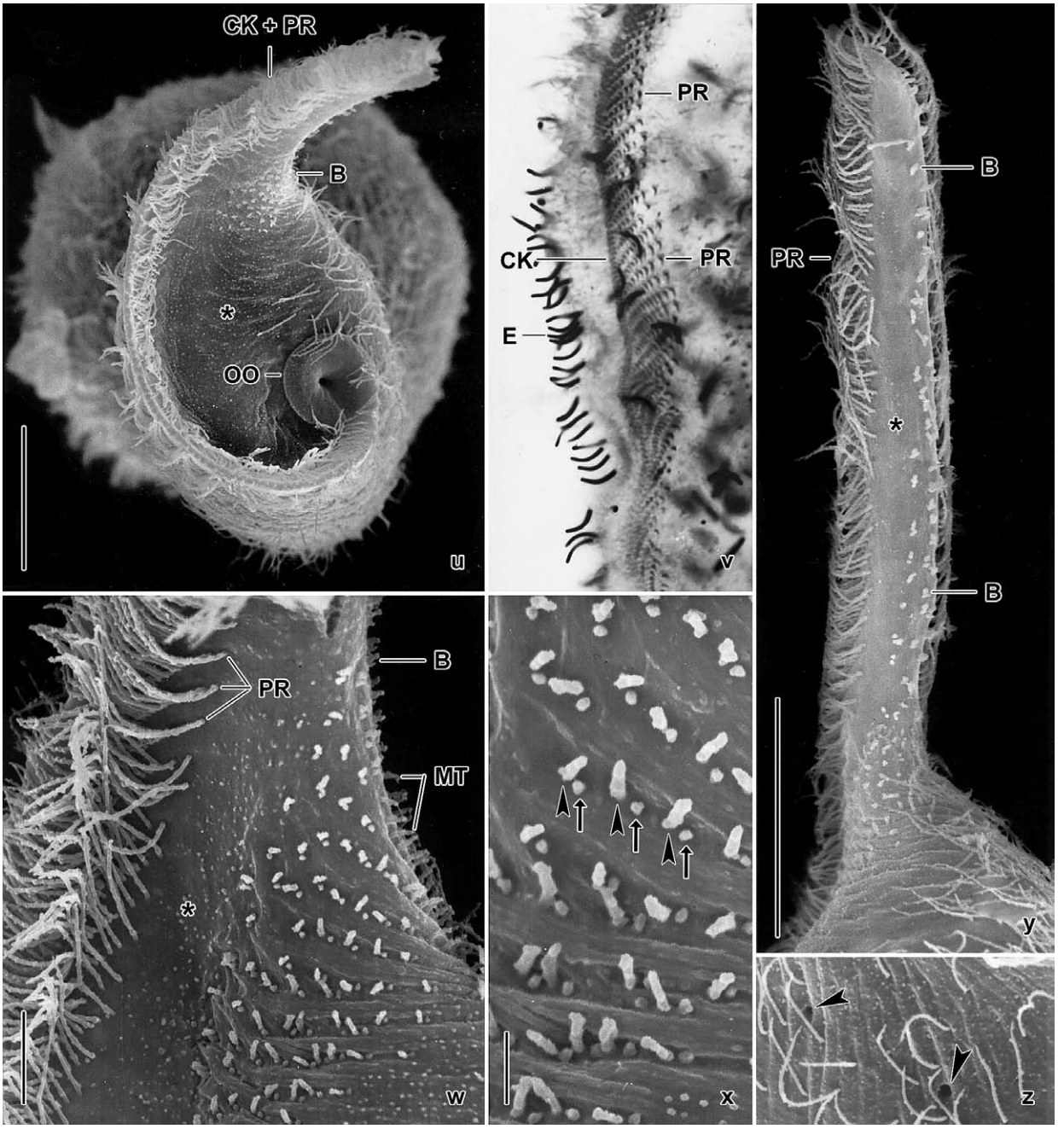
Figs 137a–k: *Paradileptus elephantinus* and its supposed synonyms from life (a–f, h, i), fixed with osmic acid (g), and after protargol impregnation (j, k). From Foissner et al. 1999 (a–d, g–k) and Canella 1951 (e, f). **a–d** – various views of a single, freshly collected specimen, showing the helical proboscis and the cone-shaped trunk. The proboscis base is broadened to a dish-like platform, causing the oral bulge opening to become located laterally. Arrowheads mark contractile vacuoles; **e, f** – total views of *P. estensis*, which is possibly a distinct species because of the large size (350–800 µm) and the long, thin proboscis (but see Fig. 135v!); **g** – *Paradileptus elephantinus* is very delicate and rounds up when fixed with osmium acid, forming the common *elephantinus* habitus; **h** – the moniliform macronucleus is enclosed in a gelatinous capsule; **i** – a squashed specimen, showing an ingested rotifer, *Keratella* (arrow); **j, k** – ciliary pattern of right side of proboscis (j) and resting and released extrusomes in proboscis oral bulge (j, k). There are two perioral kineties side by side associated with the right branch of the circumoral kinety (j). This is an important feature that occurs only in a specialized group of planktonic dileptids, viz., in the genera *Paradileptus* and *Pelagodileptus*, where the increased number of densely spaced cilia might increase the efficiency of food acquisition. CK – circumoral kinety, E – extrusomes, MA – macronucleus (nodules), PE 1, 2 – perioral kineties. Scale bars: 5 µm (k), 20 µm (j), and 50 µm (a–d, g).



Figs 137l–n: *Paradileptus elephantinus* after protargol impregnation (from FOISSNER et al. 1999). Dorsolateral (l) and ventrolateral (m, n) views of somatic and oral ciliary pattern. The right branch of the circumoral kinety is accompanied by two perioral kineties, while the left branch is associated with many slightly oblique and comparatively long preoral kineties. The proboscis base is strongly broadened, taking along the oral bulge and the bulge opening which becomes located laterally and inverted, just as in numeral 6. CK – circumoral kinety, E – extrusomes, MA – macronucleus (nodules), MI – micronucleus, OO – oral bulge opening, PE 1, 2 – perioral kineties, PR – preoral kineties. Scale bars: 20 µm (n) and 50 µm (l, m).



Figs 137o–t: *Paradileptus elephantinus* in the scanning electron microscope (from FOISSNER et al. 1999). Total views showing the obconical trunk and the long, helically twisted proboscis. The base of the proboscis is strongly broadened, taking along the oral bulge and causing the bulge opening to become located laterally and inverted, just as in numeral 6 (o, r, t). The left side ciliary rows terminate at the level of the oral bulge opening, leaving a conspicuous barren area (asterisks) on the dish-like broadened oral field (o, r, t). There are two perioral kineties side by side, an important feature of *Paradileptus* (s, arrows). Arrowheads (o–q, t) mark excretory pores of contractile vacuoles, which are scattered in the trunk and the dorsal side of the proboscis. B – dorsal brush, CK – circumoral kinety, OB – oral bulge, OO – oral bulge opening, PR – preoral kineties. Scale bars: 30 μm (o, t) and 50 μm (p–s).



Figs 137u–z: *Paradileptus elephantinus* in the scanning electron microscope (u, w–z) and after protargol impregnation (v). From FOISSNER et al. (1999). Asterisks denote the broad, blank stripe left of oral bulge (u, w, y). **u** – frontal view showing the dish-like broadened oral field surrounded by the helically extending proboscis; **v** – the left branch of the circumoral kinety is associated with many oblique, comparatively long preoral kineties, each composed of about ten basal bodies (cilia); **w** – left side view of posterior proboscis portion, showing preoral kineties and part of dorsal brush; **x** – brush dikinetids are loosely spaced and associated with type III bristles: the anterior bristle is about 1.5 µm long (arrowheads), while the posterior one is a 0.3 µm long stump (arrows); **y** – left side view of proboscis, showing the dorsal brush extending from base to tip of proboscis; **z** – surface view showing cortex slightly furrowed by ciliary rows. Arrowheads mark intrakinetal excretory pores of two contractile vacuoles. B – dorsal brush, CK – circumoral kinety, E – extrusomes, MT – monokinetidal tails of dorsal brush, OO – oral bulge opening, PR – preoral kineties. Scale bars: 2 µm (x), 5 µm (w), and 20 µm (u, y).

likely miscalculated). Generation time of *Paradileptus* sp. in Lake Constance at 8.5 °C about 210 h (Mueller 1989). Reck (1987) found *P. elephantinus* and *P. conicus* at following conditions: 3.4–11.3 °C (> 200 ind./l at 7–8.4 °C), pH 8.4–9.1 (9.1), 5.8–19.4 mg/l O_2 (14.7 mg/l), 44–176% O_2-saturation (121%), 0.03–0.06 mg/l NH_4^+-N (0.04 mg/l). Schlott-Idl (1984) recorded it at 4–20 °C (maximum at 16 °C), pH 6.6–9.0 (7.9), 2.8–13.3 mg/l O_2 (9.9 mg/l), and 0.013–0.13 mg/l NH_4^+-N (0.013 mg/l).

Locus classicus of *P. elephantinus* is a fishpond (Počernický rybník) in the vicinity of Prague, Czech Republic, where Švec (1897) discovered it during an algal bloom in July (for a review, see Šrámek-Hušek 1952). Locus classicus of *Amphileptus moniliger* is a pond in the Zoological Garden in Berlin, Germany (Ehrenberg 1835, 1838). Later it was recorded in freshwater bodies in the surroundings of the town of Berlin, Germany (Marsson 1901). The synonym *Paradileptus flagellatus* was found in Lake Cromwell, Quebec, Canada (Puytorac et al. 1972). Locus classicus of both *P. conicus* and *P. robustus* is a pond at the University of Pennsylvania, USA, where Wenrich (1929) found *P. conicus* in mid-May, reaching a maximum on May 20 and not seen after May 25. *Paradileptus robustus* was present in very small numbers in company with a few individuals of *P. conicus*, which occurred also in Mattson Lake, San Francisco, USA, from September to November and from January to March. Locus classicus of *Tentaculifera mexicana* is a pond in Bosque de Chapultepec, Mexico City (Sokoloff 1931). Huber-Pestalozi (1945) discovered *Paradileptus ovalis* in the spring plankton of a large lake (Zürichsee) in Switzerland. Locus classicus of *P. estensis* is the moat of the castle Estense, Ferrara, northern Italy (Canella 1951, Dini et al. 1995). Dragesco (1972a) discovered *P. minutus* in the Kasinga channel, Uganda.

Further records of *P. elephantinus* substantiated by illustrations: England (Curds 1982); pond in France (Fryd-Versavel et al. 1975); occasionally abundant in the spring plankton of the Alster in Hamburg, Germany (Kahl 1935); groundwater ponds in Styria, Austria, only during the warm season (Krainer 1988); abundant (360 ind./l) in a eutrophic fishpond in Salzburg, Austria, during early September (Foissner et al. 1995, 1999); in a moderately dystrophic lake in Poland (Czapik & Fyda 1995); 50 ind./l in a reservoir of the Volga River (Mamaeva 1979c); Baikal Lake area (Lokot' 1987); Lake Ho Hu, Nanking, China (Wang & Nie 1933); pond Mizutori-no-numa, Japan (Kusano 1985); freshwater of the Upper Peninsula in Michigan, USA (Lundin & West 1963); Chari River, Chad, Africa (Dragesco 1972b, Dragesco & Dragesco-Kernéis 1986); abundant in the plankton of the Murray River, Australia (Foissner et al. 1999).

There are many records of *P. elephantinus* not substantiated by illustrations. We did not include all of them but selected for biogeographic regions and interesting habitats: pond in Münster and about 1000 ind./l during summer in a eutrophic pond (Poppelsdorfer Weiher) in Bonn, Germany (Krüger 1936; Wilbert 1989, who also recorded *P. conicus* mainly during summer); rare in German running waters (Buck 1961, Heuss et al. 1972); mesotrophic lake (Heiliges Meer) in Germany (Mücke 1979); eutrophic lake (Plußsee) in Germany only from March to early May with a peak of 208 ind./l in 0–2 m (Reck 1987; she also recorded the synonym *P. conicus* during the same time); in 0–15 m almost throughout the year with peaks (142 ind./l = 241 mg/m^3 in the surface layer; 240 ind./l in 3 m; 222 ind./l = 277 mg/m^3) during May and June (Schlott-Idl 1984, Zimmermann 1989); eutrophic lake (Piburger See) in Tyrol, Austria; small lake (Höllerersee) in Upper Austria (Nauwerck 1996); former Czechoslovakia (Šrámek-Hušek 1957, Sládeček 1969, Baláži & Matis 2002); Latvian running waters (Liepa 1973, 1983); Ukrainian reservoirs, ponds, and rivers (Kravchenko 1969; Nebrat 1980, 1992; Oleksiv 1985; Oleksiv et al. 1996; in some of their papers, they recorded also the synonym *P. conicus*); Azerbaijanian reservoir (Alekperov 1980, 1984; who also recorded the synonym *P. conicus*); Volga delta, former USSR (Kosova 1965); in the Volga river basin, Russia (Zhukov et al. 1998; they also recorded the synonyms *P. conicus* and *P. flagellatus*); betamesosaprobic reservoir and other reservoirs and lakes in the former USSR (Mamaeva 1976a; Zhukov & Mamaeva 1978; Zharikov 1992: benthic record; Zharikov & Rotar 1992; Myl'nikova 1992a, 1993:

P. conicus also recorded); up to 20 ind./l at 28 °C in Java lakes (Ruttner 1952); freshwaters of Thailand (Charubhun & Charubhun 2000); water supply reservoir in Brazil throughout the year with up to 600 ind./l during March-April-May and September-October (Barbieri & Godinho-Orlandi 1989).

Records of the synonym *P. conicus* not substantiated by illustrations (see also previous paragraph): lake in the town of Zürich, Switzerland (Thomas 1964; including the synonym *P. ovalis*); Danube River and its side branches in Hungary (Bereczky & Nosek 1994); eastern Baltic Sea (Telesh et al. 2008); Latvian lakes (Liepa 1984); Azerbaijanian reservoirs with daily vertical migrations (Alekperov 1980, 1982, 1983, 1988, 1989, 1990); up to 80 ind./l in the Volga River (especially during summer), Ladoga Lake, and mesotrophic and eutrophic reservoirs and lakes in the former USSR (Korniyenko 1972; Mamaeva 1976b, 1979a, b, c; Smirnova 1987; Belova 1989, 1994; Myl'nikova 1992b); Lake Donghu (in summer, autumn and winter) and other sites in China (Shen & Gu 1965; Gong 1986, who also recorded *P. robustus* in winter; Su et al. 1988); in municipal and suburban districts of the towns of Hiroshima and Higashi-Hiroshima, Japan (Matsuoka et al. 1983); near Mexico City (Perez-Reyes & Salas-Gomez 1961); among living and dead macrophytes in the Pantanal, Brazil (Lopes Hardoim & Heckman 1996, Heckman 1998); Lake El Trébol, Río Negro, Argentina (Diéguez & Balseiro 2000).

Records of the synonym *P. robustus* not substantiated by illustrations (see also previous paragraph): Michigan, USA (West & Lundin 1963); cypress swamp in the delta plain of the Mississipi River, USA (Bamforth 1969); South River, Virginia, USA (Cairns & Dickson 1972, Ruthven 1972); Japan (Sudzuki 1978a; misspelled as *P. robostus*).

Records of *Paradileptus* sp., possibly referring to *P. elephantinus*, which is, according to the literature and our experience, much more common than *Pelagodileptus trachelioides*: wet mosses from Venezuela (Scorza & Núñez Montiel 1954) and Japan (Sudzuki 1964); Lake Oglethorpe and West Long Lake, USA (Pace 1982, Sanders et al. 1989, Pace & Vaqué 1994); Kenyan lakes (Bamforth et al. 1987); Lake Constance and a eutrophic lake in Germany (Mueller 1989, Mueller et al. 1991, Weisse & Mueller 1990, Schweizer 1994, Zimmermann 1994, Gaedke & Wickham 2004); eutrophic lakes (Windermere, Esthwaite) in England (Laybourn et al. 1990, Laybourn-Parry & Rogerson 1993); Denmark (Have 1993); mesotrophic Lake Mondsee, Austria (Salbrechter & Arndt 1994); Lake Taupo, New Zealand (James et al. 1995).

Saprobic classification: Foissner et al. (1995) classified *P. elephantinus* as a beta-mesosaprobic ciliate with the following valencies: o = 3, b = 6, a = 1, I = 3, SI = 1.8.

Pelagodileptus Foissner, Berger & Schaumburg, 1999

1999 *Pelagodileptus* nov. gen. Foissner, Berger & Schaumburg, Informationsberichte des Bayer. Landesamtes für Wasserwirtschaft **3/99**: 232

2001 *Pelagodileptus* Foissner, Berger & Schaumburg 1999 – Aescht, Denisia **1**: 121 (catalogue of generic names of ciliates)

2007 *Pelagodileptus* Foissner, Berger et Schaumburg, 1999 – Jankowski, Protista II: 574 (brief generic review)

2008 *Pelagodileptus* Foissner, Berger, & Schaumberg, 1999 – Lynn, Ciliated protozoa: 371 (list of genera; incorrect subsequent spelling of last author name)

Improved diagnosis: Medium- to large-sized Dileptidae with narrow to very narrow body. Macronucleus moniliform. Dorsal brush multi-rowed. Right branch of circumoral kinety accompanied by two perioral kineties and left branch by many slightly oblique preoral kineties. Oral bulge opening dileptid, i.e., located ventrally and narrowly to very narrowly elliptical.

Type species (by original designation and monotypy): *Dileptus trachelioides* ZACHARIAS, 1894.

Etymology: Composite of the Greek noun *pelagios* (living in the open sea = planktonic) and the generic name *Dileptus*, meaning "a *Dileptus* living in the plankton". Masculine gender.

Remarks: FOISSNER et al. (1999) established the genus *Pelagodileptus* for *Dileptus trachelioides*, although the oral ciliature is as in *Paradileptus*, because it has a slit-like oral bulge opening (vs. roundish and inverted) and lacks the dish-like widening of the oral field at the base of the proboscis. Very likely, *Pelagodileptus* and *Paradileptus* are closely related, as they share two strong synapomorphies, viz., two perioral kineties and a planktonic way of life. Further, a sister relationship is supported by the moniliform macronucleus and the contractile vacuole pattern.

Pelagodileptus trachelioides (ZACHARIAS, 1894) FOISSNER, BERGER & SCHAUMBURG, 1999 (Figs 138a–w, 139a–w, 140a–y, 141a–u, 142a–e; Table 67)

1894 *Dileptus trachelioides* ZACHARIAS, n. sp., ForschBer. biol. Stn Plön **2**: 78

1908 *Amphileptus trachelioides* ZACH. sp. – AWERINZEW, Ann. Biol. lac. **2**: 168 (combination with *Amphileptus*)

1927 *Dileptus trachelioides* ZACHARIAS – HUBER & NIPKOW, Vjschr. naturf. Ges. Zürich **72**: 312 (morphology and division; ecology)

1931 *Amphileptus* (*Dileptus*) *trachelioides* (ZACH. 1893) – KAHL, Tierwelt Dtl. **21**: 182 (taxonomic revision; incorrect dating)

1933 *Amphileptus trachelioides* ZACHARIAS – GAJEWSKAJA, Zoologica, Stuttg. **32**: 58 (morphology)

1935 *Paradileptus* (*?*) *caducus* spec. n. KAHL, Tierwelt Dtl. **30**: 823 (synonym; poorly described)

1943 *Amphileptus trachelioides* ZACHARIAS – KAHL, Infusorien: 32 (taxonomic revision)

1962 *Dileptus saaleri* SCHWARZ, Z. Fisch. (N. F.) **10**: 420 (synonym proposed by FOISSNER et al. 1999)

1963 *Dileptus tracheloides* ZACHARIAS, 1888 – DRAGESCO, Bull. biol. Fr. Belg. **97**: 125 (incorrect spelling and dating)

1964 *Amphileptus trachelioides* (ZACHARIAS) – SLÁDEČEK, Sb. vys. Sk. chem.-technol. Praze **8**: 523 (description of a Czech population)

1966 *Paradileptus canellai* n.sp. DRAGESCO, Protistologica **2**: 77 (synonym)

1966 *Paradileptus caducus* KAHL – DRAGESCO, Arch. Protistenk. **109**: 181 (redescription from life)

1975 *Paradileptus caducus* KAHL 1935 – FRYD-VERSAVEL, IFTODE & DRAGESCO, Protistologica **11**: 520 (oral ciliature after silver impregnation)

1979 *Amphileptus trachelioides* ZACH., 1893 – MAMAEVA, Infuzorii bassejna Volgi: 35 (brief review; ecology; incorrect dating)

1988 *Amphileptus trachelioides* (ZACHARIAS, 1894) – FOISSNER, Hydrobiologia **166**: 37 (saprobic classification)

1991 *Paradileptus caducus* KAHL, 1935 – PACKROFF & WILBERT, Arch. Protistenk. **140**: 125 (authoritative redescription from life and after silver impregnation)

1999 *Pelagodileptus trachelioides* (ZACHARIAS, 1894) nov. comb. – FOISSNER, BERGER & SCHAUMBURG, Informationsberichte des Bayer. Landesamtes für Wasserwirtschaft **3/99**: 232 (combining authors)

2004 *Pelagodileptus trachelioides* (ZACHARIAS, 1894) FOISSNER, BERGER & SCHAUMBURG – BUTKAY, Lauterbornia **49**: 129 (life morphology and ecology)

2007 *Pelagodileptus trachelioides* (ZACHARIAS, 1894) – SONNTAG, SUMMERER & SOMMARUGA, Freshwat. Biol. **52**: 1478 (characterization of secondary metabolites of the green symbiotic algae)

2011 *Pelagodileptus trachelioides* (ZACHARIAS, 1894) FOISSNER et al., 1999 – VĎAČNÝ, ORSI, BOURLAND, SHIMANO, EPSTEIN & FOISSNER, Eur. J. Protistol. **47**: 297 (18S rRNA gene sequence of a Japanese population)

Synonymy and identification: ZACHARIAS (1894) established this species in the genus *Dileptus* because of the dileptid habitus. AWERINZEW (1908) transferred it to *Amphileptus* because of the slit-like oral bulge opening. The redescription of the synonym *Paradileptus caducus* by FRYD-VERSAVEL et al. (1975) and PACKROFF & WILBERT (1991) confirmed ZACHARIAS' classification. Finally, FOISSNER et al. (1999) established the new genus *Pelagodileptus* for ZACHARIAS' species because of the *Paradileptus*-like oral ciliary pattern and the *Dileptus*-like habitus.

Paradileptus caducus and *P. canellai* are junior synonyms because they agree in habitat (plankton), size, nuclear apparatus, and symbiotic green algae. They are, however, much more slender, indicating profound phenotypic variation, possibly due to certain ecological factors. The number of macronuclear nodules, used by DRAGESCO (1966b) for species distinction, is highly variable (see below). FOISSNER et al. (1999) suggested *Dileptus saaleri* SCHWARZ, 1962, another poorly described planktonic dileptid, as a further synonym of *Pelagodileptus trachelioides*. The second proboscis near mid-body shows that SCHWARZ (1962) observed a divider. He did not mention zoochlorellae, possibly because only preserved specimens were studied.

Within dileptids with moniliform macronucleus, *P. trachelioides* resembles *Pseudomonilicaryon angustistoma* in having a very narrowly elliptical oral bulge opening. However, *P. angustistoma* occurs in terrestrial habitats (vs. planktonic), is much more slender (11.4:1 vs. 5:1), has far fewer ciliary rows (39 vs. 120–200), and lacks symbiotic green algae. Further, *Pelagodileptus trachelioides* has a similar size and shape as *Monilicaryon monilatum*, which is, however, usually benthic, lacks symbiotic green algae, and has a roundish oral bulge opening. There are two planktonic dileptids which look like a bulky *Pelagodileptus trachelioides*, viz., *Paradileptus elephantinus* and *Trachelius ovum*. However, both lack symbiotic green algae and have a roundish (vs. very narrowly elliptical) oral bulge opening. Further, *Paradileptus elephantinus* has a much stouter and smaller (300 × 150 μm vs. 600 × 200 μm) body with a large oral field, and *Trachelius ovum* possesses a dumbbell-shaped macronucleus.

Improved diagnosis (includes all information known): Size about 490 × 160 μm in vivo. Shape narrowly to very narrowly dileptid with rounded or tailed posterior end, proboscis about 1/3 of body length. Macronucleus moniliform, usually composed of about 15 globular nodules; several globular micronuclei. Many scattered contractile vacuoles in trunk and dorsal side of proboscis. Two size-types (6 μm and 2 μm) of rod-shaped extrusomes attached to proboscis oral bulge. About 170 ciliary rows; dorsal brush multi-rowed, staggered, with monokinetidal tails extending to base of proboscis. Oral bulge opening very narrowly elliptical, about 75 × 15 μm in size. Preoral kineties narrowly spaced, slightly oblique, each usually composed of 4–6 narrowly spaced cilia. With symbiotic green algae (zoochlorellae).

Type locality: Plankton from the Großen Plöner See, northern Germany, E10°24' N54°07'.

Type and voucher material: No type material is available from ZACHARIAS' specimens. PACKROFF & WILBERT (1991) made permanent slides at Bonn University, Germany but did not mention their deposition.

Gene sequence: The partial 18S rRNA gene sequence of a Japanese population has been deposited in GenBank (AB558117). The sequence is 1608 nucleotides long and has a GC content of 41.9%.

Etymology: Not given in original description. Composite of the generic name *Trachelius* and the Latin suffix *-oides* (similar), obviously referring to the shape similarity with *T. ovum*.

Description: All known data are put together because the morphological conspecificity is beyond reasonable doubts for most populations mentioned in the list of synonyms. Generally, *Pelagodileptus trachelioides* is a very fragile ciliate, in spite of its large size, which explains the high variability of size and shape observed by several authors and in a cultivated Japanese population (Figs 141a–c, e–u). The curious ejection of cytoplasm described by several authors is another expression of this fragility (see movement and behaviour).

Size highly variable but similar in most populations, usually about 360–620 × 110–200 µm: 230–270 × 180–200 µm (Zacharias 1894, Kahl 1931); 230–270 × 100–300 µm (Rylov 1935); 100–600 × 100–300 µm (Huber & Nipkow 1927); 600–800 µm (Gajewskaja 1933); up to 700 × 130 µm, distorted specimens 500–610 × 230 µm (Sládeček 1964); 500–600 µm (Mamaeva 1979c); usually 220–800 × 80–300 µm, extremes 120–1100 µm (Butkay 2004); size of proboscis 50–900 × 10–13 µm, usually 338 × 11 µm, size of trunk 105–420 × 45–120 µm, usually 225 × 76 µm (Sonntag et al. 2007). The data of Sonntag et al. (2007) are so different that conspecificity becomes questionable. Size of synonyms: *Dileptus saaleri* (fixed material) 300 × 75 µm (Schwarz 1962); *Paradileptus caducus* 500–800 µm (Kahl 1935), 400–650 × 150–200 µm (Fryd-Versavel et al. 1975), 400–800 × 100–200 µm (Krainer 1988), 340–700 × 80–150 µm (Packroff & Wilbert 1991); *P. canellai* up to 600 µm (Dragesco 1966a).

Body very flexible but not contractile. Shape of freshly collected specimens narrowly to very narrowly dileptid (Figs 138i, l, n, o, 139i, j, n, q–u, 140a, h, j, m, n, 141a-c), drastically changes in unfavourable environments becoming bulky, looking very much like *Trachelius ovum* (Figs 138a–d, h, j, m, p, 139a–d, e, g, h, 140k, l, 141a–c), rarely becoming globular (Fig. 138u). Length:width ratio thus highly variable, on average 4.3:1 (M = 4.5:1, SD = 1.8:1, SE = 0.4:1, CV = 41.5%, Min = 1.5:1, Max = 8:1, n = 24), according to the figures available in the literature, while 3.2:1 in SEM cells (min = 2.5, max = 3.7, n = 8). Proboscis occupying 25–50%, on average 37% of body length (Figs 138b, i, o, 139i, j, n, s–u, 140a, j, 141a-c), highly motile and flexible, shortens or even disappears when conditions become adverse (Figs 138a, d, j, p, v, w, 139a–d, q, 140k, l), which was possibly misinterpreted as contractility by Sládeček (1964). Trunk oblong, ovate, or bluntly fusiform, unflattened, usually widest in mid-portion. Posterior end with short tail, acute, or with a spike usually present only in fresh material (Figs 138b, i, l, o, 139a, b, i, j, n, t, u, 140j, s–v), soon becoming more or less broadly rounded (Figs 138a, c, d, h, j, m, p, u, w, 139c–h, 140a, k, l, q, r, 141a–c).

Nuclear apparatus usually extends in anterior four fifths of trunk, rarely between oral bulge opening and base of tail. Macronucleus a moniliform, straight or sigmoidal strand surrounded by a gelatinous capsule in German specimens (1a–d, i, l–o, w, 2j, n, s, t, 3a, j). Number of nodules rather variable within and between populations: 9–14 (Zacharias 1894, Kahl 1931); 8–15, usually 8–9 (Huber & Nipkow 1927); 12–18 (Gajewskaja 1933); 7–18 (Rylov 1935); 9 (Wesenberg-Lund 1952); 15–27 (Sládeček 1963); 6–23 (Krainer 1988; Table 67); usually 6–45 (Butkay 2004); 7–20, usually 15–17 (synonym *Dileptus saaleri*, Schwarz 1962); 11–22 (synonym *Paradileptus canellai*, Dragesco 1966a); 12 (Kahl 1935), 6–12 (Dragesco 1966b), and 7–10 (Packroff & Wilbert 1991) in the synonym *Paradileptus caducus*. Individual nodules rather stable in shape and size, viz., globular with a diameter of 20 µm (Zacharias 1894), 15–20 µm (Huber & Nipkow 1927, Schwarz 1962), 10 µm (Dragesco 1966a), 13–26 µm (Dragesco 1966b), 10–20 µm, usually about 15 µm (Krainer 1988; Table 67), and 12–24 µm (Butkay 2004). In African cells, nodules with a central nucleolus and connected by short bridges recognizable in Feulgen stains (Figs 139m, o); several nucleoli per nodule according to the figures of Krainer (1988) and Butkay (2004). Usually many globular micronuclei attached to macronuclear strand but outside of capsule, about 3 µm across in vivo (Dragesco 1966a) and 2.8 µm after protargol impregnation (Krainer 1988; Table 67). Number of micronuclei: 6–25 in African cells (Dragesco 1966a) and 6–21 in Austrian specimens (Krainer 1988; Table 67). Schwarz (1962) observed globular and dumbbell-shaped micronuclei possibly undergoing division.

Many contractile vacuoles scattered underneath cell surface of trunk and proboscis' dorsal side (Figs 139j, n, t, 140p). Individual vacuoles about 6 µm across (Butkay 2004). Vacuoles difficult to recognize due to the strongly vacuolated cytoplasm, and thus very likely overlooked by Zacharias (1894), Huber & Nipkow (1922), Gajewskaja (1933), and Krainer (1988). A single intrakinetal excretory pore per vacuole in Japanese specimens (Fig. 141q).

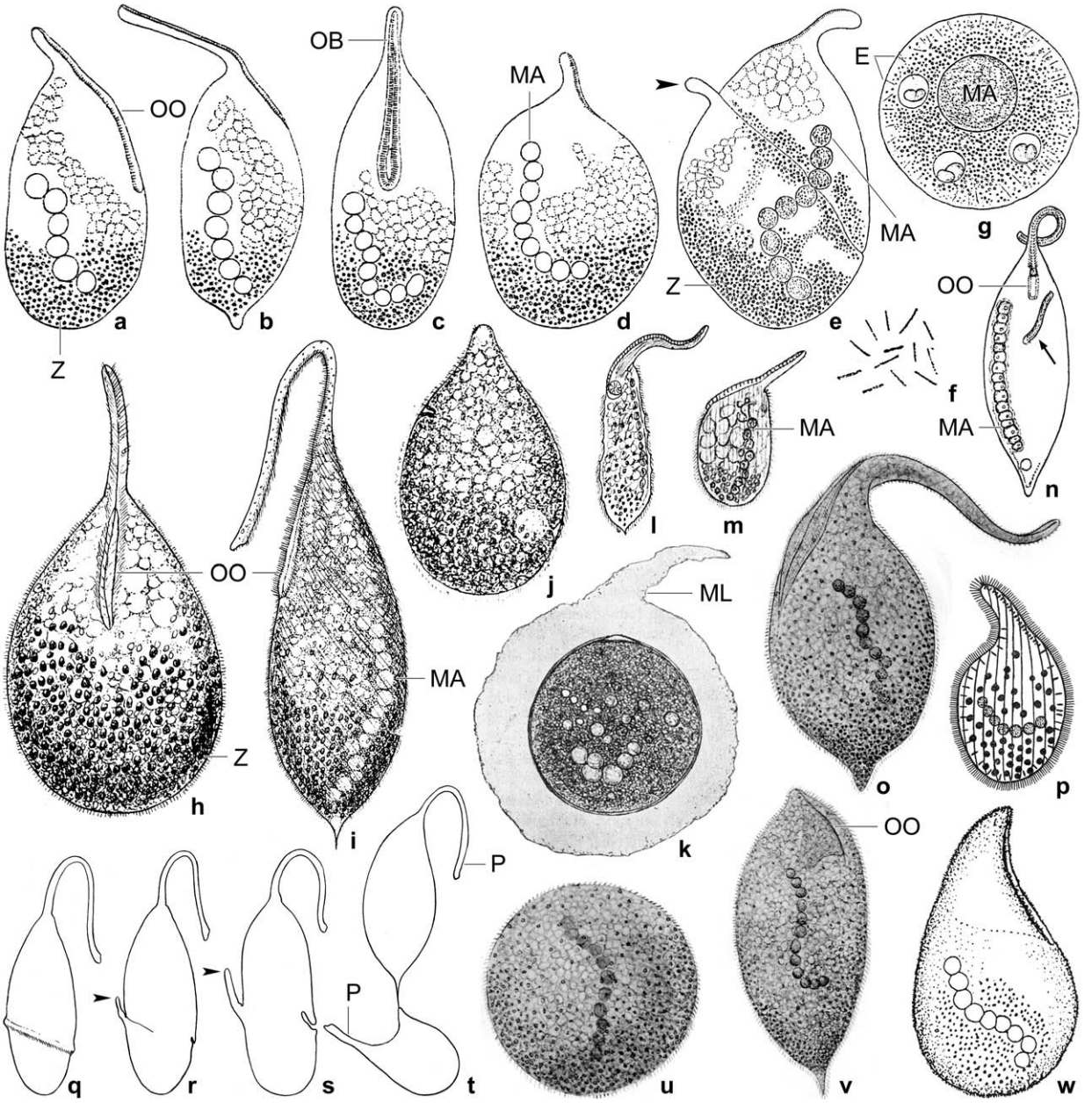
Extrusomes studded in broad right branch of proboscis oral bulge and scattered throughout cytoplasm. Quite similar in Austrian, Swiss, Japanese, and type population, where the small type has been possibly overlooked: type I in vivo 6–10 µm long and rod-shaped slightly narrowing anteriorly, acicular after protargol impregnation (Figs 138f, 140b, e, 141e); type II oblong and only 2 µm long (Figs 140e, 141d). Rylov (1935), additionally, figured rod-shaped extrusomes attached to the somatic cortex (Fig. 138p).

Cortex flexible, rather thick (Krainer 1988), and slightly furrowed by ciliary rows in SEM micrographs (Fig. 141q). Cortical granulation not yet studied in vivo; in SEM dense, individual granules oblong, about 0.8 × 0.3 µm in size (Fig. 141u). Silverline pattern narrowly meshed, meshes polygonal and 0.3–0.9 µm in size, not yet studied in detail (Fig. 140c). Cytoplasm very viscous and strongly vacuolated, thus appearing spumous (Figs 138a–e, 139j, n, t, 140a, j, p). Butkay (2004) observed how the spumous condition originates (Fig. 140o): "At a certain place of the body, small blisters accumulate from all directions. After a short while, they flow together abruptly, forming a "giant vacuole". This event occurs over and over again, causing the spumous appearance of the plasm". Cells green due to innumerable symbiotic algae 2–4 µm in diameter, accumulated in posterior third of trunk and in plasm strands separating vacuoles (Figs 138a–d, h, i, l, m, o, p, 139n, t, 140a, j, p; Table 67). Huber & Nipkow (1927) and Krainer (1988) observed specimens without zoochlorellae.

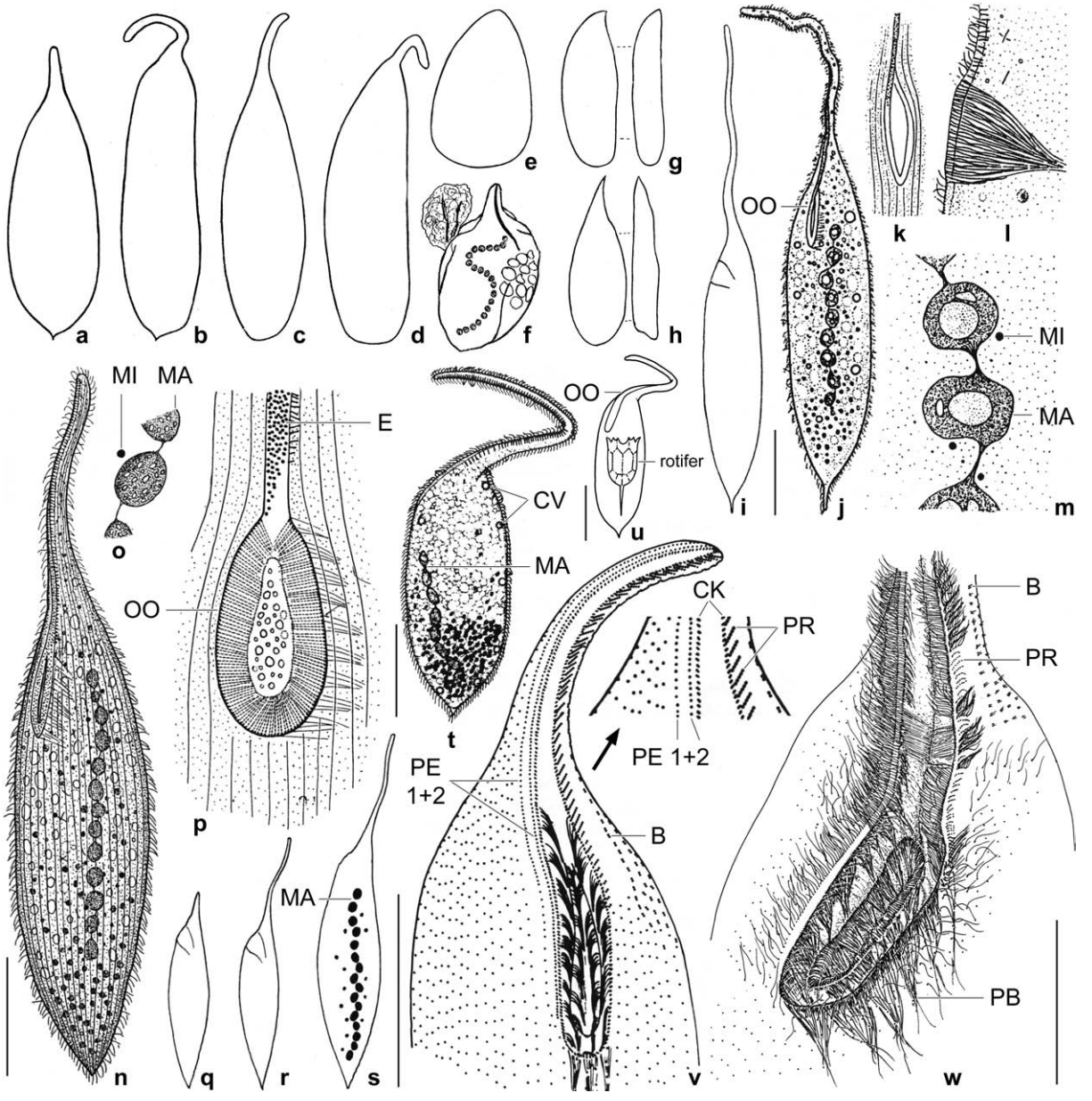
Cilia ordinarily spaced; in SEM preparations about 20 µm long (Figs 141a-c, q), after protargol impregnation with thick, strongly impregnated distal half. Ciliary rows narrowly to ordinarily spaced, meridionally arranged (Figs 141a-c), number studied only in two populations, viz, about 200 in French specimens (Fryd-Versavel et al. 1975) and 120–160 in Austrian cells (Krainer 1988). Details of ciliary pattern described by Fryd-Versavel et al. (1975), Krainer (1988), and Packroff & Wilbert (1991): (i) first two rows right of circumoral kinety extend as perioral kineties with narrowly spaced cilia to tip of proboscis; (ii) left side of proboscis with comparatively narrow blank stripe; (iii) dorsal brush a triangular field on dorsal and dorsolateral area of proboscis, multi-rowed, staggered, with monokinetidal tails extending to base of proboscis; (iv) brush dikinetids loosely spaced, associated with type II bristles: anterior bristle 1.7–2.4 µm long, posterior a 0.5–0.7 µm long stump in SEM micrographs (Figs 139v, w, 140d, 141c, j, n, r–u).

Oral bulge opening in second body third, flat, does not project; very narrowly elliptical, i.e., about 75 × 15 µm in size after protargol impregnation and in SEM micrographs (Figs 138a, c, h, i, 139j, k, n, p, v, w, 140a, d, 141a, c, g, h, p; Table 67). Pharyngeal basket obconical, composed of innumerable fibres (Figs 139l, p, v, w, 140a, d). Krainer (1988), additionally, observed long fibres originating from the oral dikinetids of the proboscis and extending laterally or dorsally to form a loose funnel (Fig. 140d). Oral bulge delineated by metachronal ciliary waves, dotted by extrusome tips, and transversely striated by fibre bundles in SEM (Figs 141j, m–o). Structure of circumoral kinety not yet studied in detail, composed of narrowly spaced kinetosomes throughout in protargol preparations (Figs 139v, w), but dense ciliature recognizable only along proboscis oral bulge in SEM, indicating that the basal bodies around oral bulge opening are barren (Figs 141i–p). Preoral kineties narrowly spaced, oblique, and each composed of four to six narrowly spaced cilia (Figs 139v, w, 141j, l); wrongly oriented in Krainer's figure (Fig. 140d).

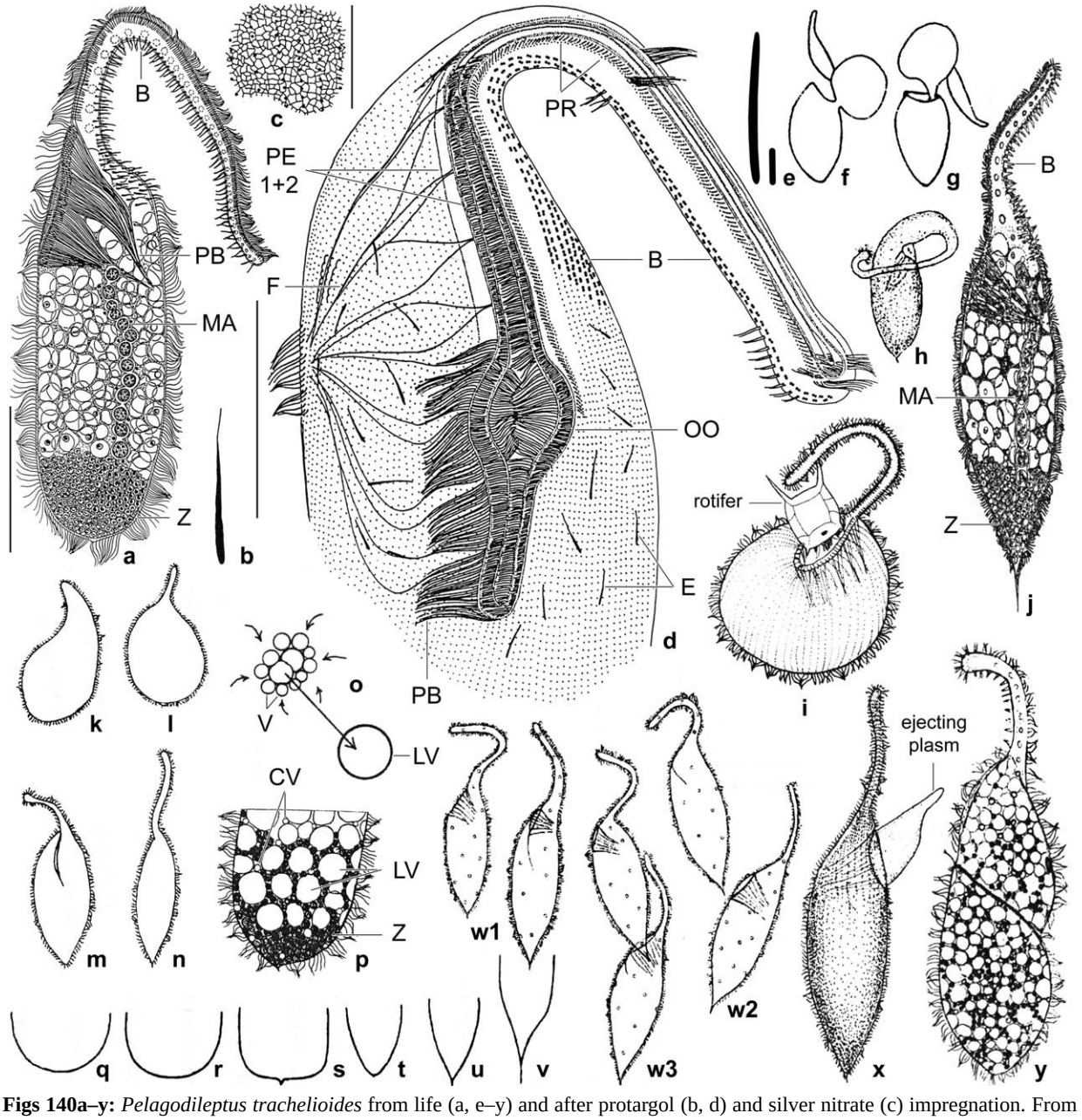
Movement and behaviour: Swims slowly to moderately fast by rotation about main body axis with proboscis projecting forward (Krainer 1988) or performing circular and dangling movements (Foissner et al. 1999). Butkay (2004) observed two specimens swimming side by side for a while (Fig. 140w1). Later on, one specimen slowly sank (Fig. 140w2) and the tail of the anterior specimen entered its oral bulge opening (Fig. 140w3). He could not decide whether this was a pre-conjugation courtship, cannibalism, or the beginning of cell fusion. When heavily disturbed, cells round up and discard the proboscis; often, autolysis follows (Packroff & Wilbert 1991).



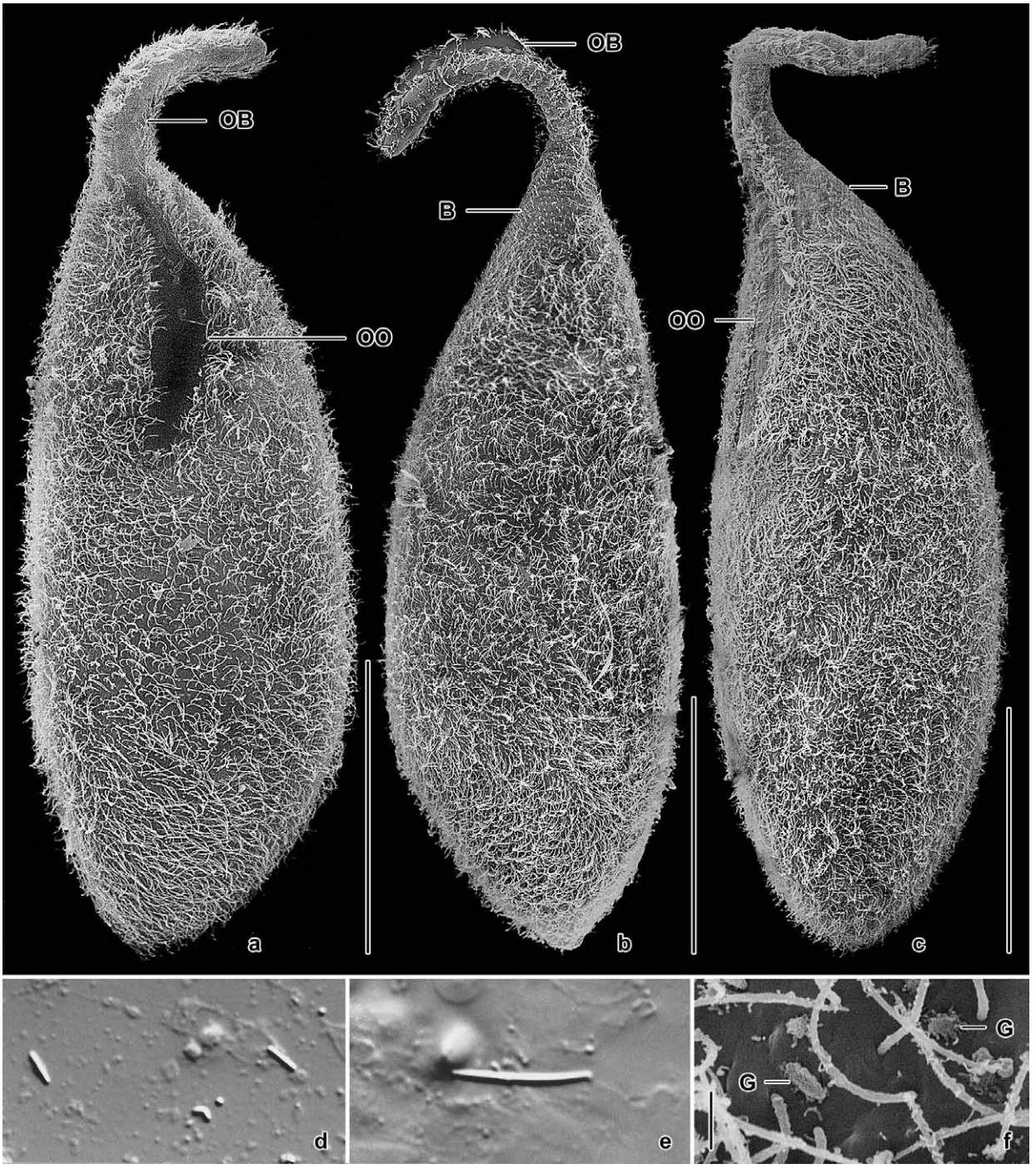
Figs 138a–w: *Pelagodileptus trachelioides* and its supposed synonyms from life (a–m, o–w) and after fixation (n). **a–g** (from ZACHARIAS 1894) – *Dileptus trachelioides*, total views of bulky specimens looking very much like *Trachelius ovum*, size 230–270 × 180–200 µm (a–d); middle divider with a new proboscis (arrowhead) for the posterior daughter (e); extrusomes, 10 µm long (f); and resting cyst with macronuclear nodules fused to a globular mass, 160–180 µm across (g); **h–k** (from HUBER & NIPKOW 1927) – *Dileptus trachelioides*, tracheliform (h), dileptid (i), and a just excysted (j) specimen, body size 100–600 × 100–300 µm, on average 300 µm long; resting cysts are 120–160 µm across, have an inconspicuous convexity (escape apparatus?), and are covered by a thick, hyaline, colourless mucous layer (k); **l** (from KAHL 1935) – *Paradileptus caducus*, length 700 µm; **m** (from KAHL 1931) – *Amphileptus trachelioides*, length 250 µm; **n** (from SCHWARZ 1962) – *Dileptus saaleri*, arrow marks the new proboscis of a mid-divider, size 300 × 75 µm; **o, u, v** (from GAJEWSKAJA 1933) – *Amphileptus trachelioides*, normal cell (o) and specimens with lost proboscis and tail (u, v), length up to 800 µm; **p** (from RYLOV 1935) – *Amphileptus trachelioides*, size 230–270 × 100–300 µm; **q–t** (from HUBER & NIPKOW 1927) – *Dileptus trachelioides*, binary fission, arrowheads mark proboscis bud; **w** (from WESENBERG-LUND 1952) – *Dileptus trachelioides*, distorted specimen, length not given. E – extrusomes, MA – macronucleus (nodules), OB – oral bulge, OO – oral bulge opening, P – proboscis, Z – zoochlorellae.



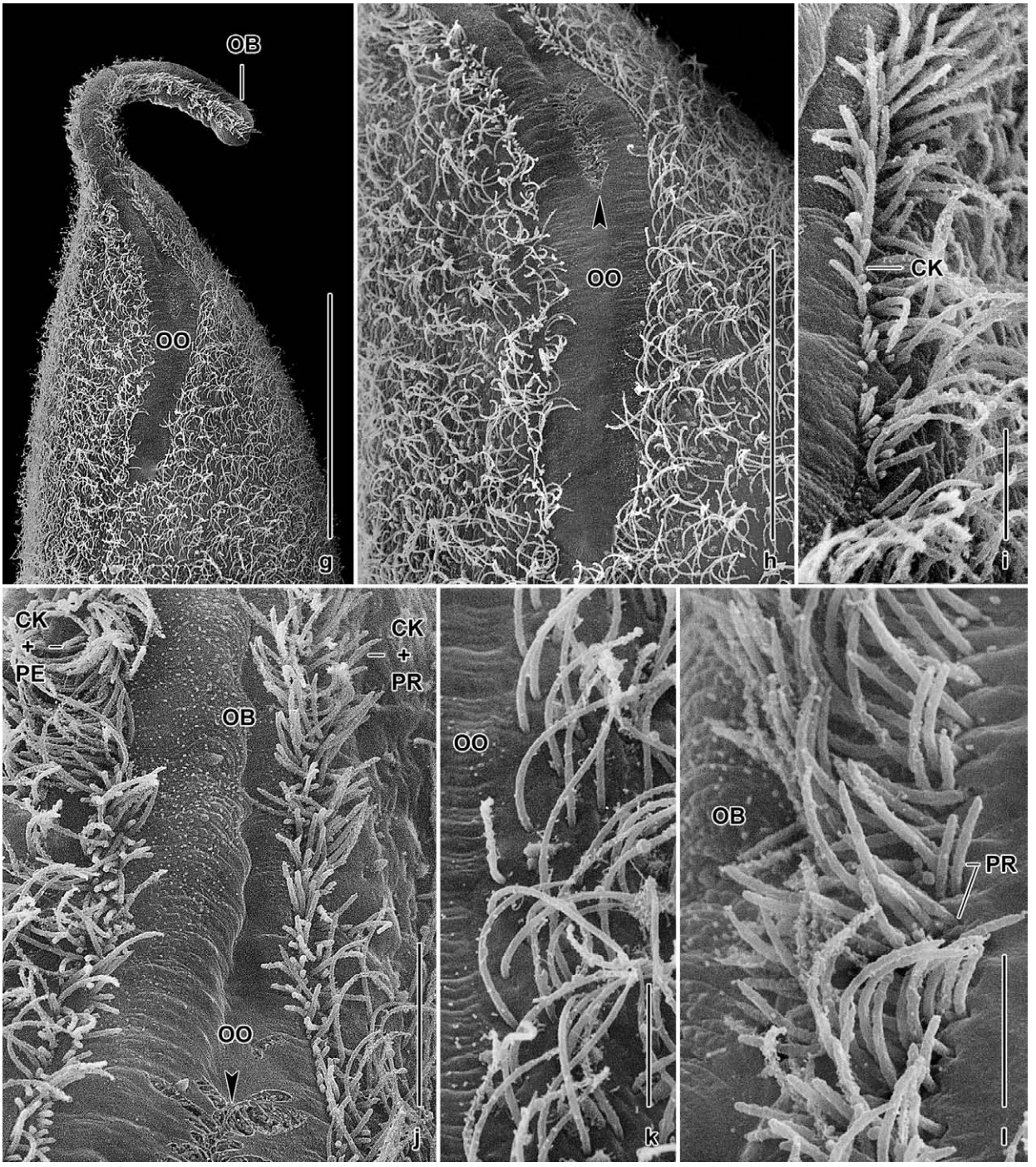
Figs 139a–w: *Pelagodileptus trachelioides* and its supposed synonyms from life (a–k, n, p–r, t, u), after protargol impregnation (v, w), and in iron-hematoxylin (l) and Feulgen (m, o, s) stains. **a–h** (from Sládeček 1964) – tracheliform (a–d) and distorted (e, g, h) specimens, and a specimen ejecting cytoplasm from the oral bulge opening (f), size up to 700 × 230 μm. In our experience, cytoplasm ejection is an expression of fragility. It is also known from other fragile ciliates, when they begin to die, are slightly pressed by the coverslip, or are insufficiently fixed; **i–m** (from Dragesco 1966b) – *Paradileptus caducus*, total views, length 400–800 μm (i, j); ventral view of oral bulge opening (k); lateral view of oral basket (l); nuclear apparatus consisting of 6–12 macronuclear nodules and several micronuclei (m); **n–s** (from Dragesco 1966a) – *Paradileptus canellai*, total views of normal (n, r, s) and distorted (q) specimens, on average 600 μm long; nuclear apparatus (o); and ventral view of oral apparatus, showing the narrowly ovate oral bulge opening (p); **t–v** (from Packroff & Wilbert 1991) – *Paradileptus caducus*, total views, size 340–700 × 80–150 μm (t, u), and oral infraciliature showing, inter alia, the two perioral kineties side by side and many oblique and comparatively long preoral kineties (v); **w** (from Fryd-Versavel et al. 1975) – *Paradileptus caducus*, oral infraciliature. B – dorsal brush, CV – contractile vacuoles, CK – circumoral kinety, MA – macronuclear strand, MI – micronuclei, PE 1+2 – perioral kineties, PR – preoral kineties. Scale bars: 50 μm (v, w) and 100 μm (i, j, n, t, u).



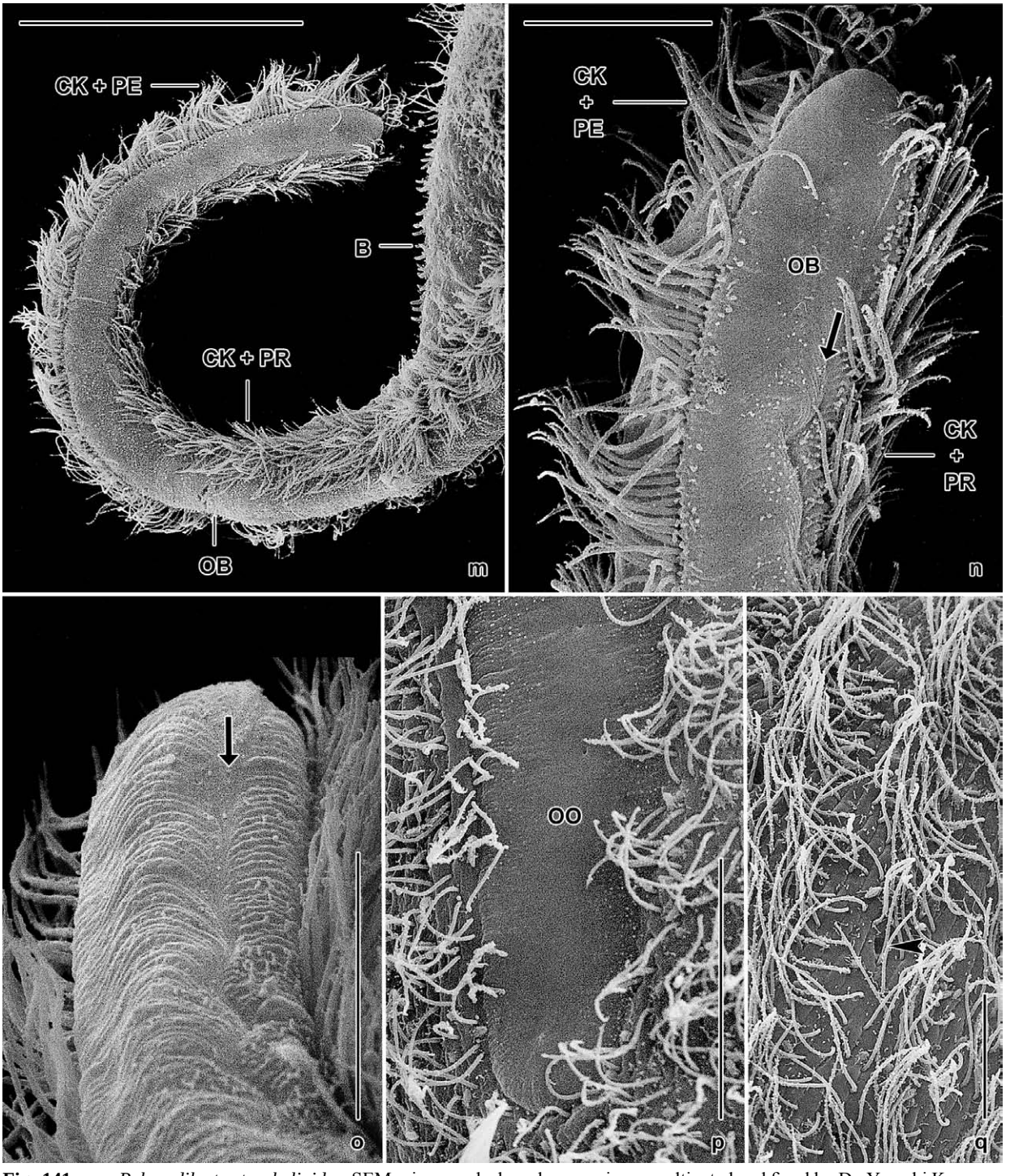
Figs 140a–y: *Pelagodileptus trachelioides* from life (a, e–y) and after protargol (b, d) and silver nitrate (c) impregnation. From KRAINER 1988 (a–d), BUTKAY 2004 (f–y), and original (e). **a, h, j** – total views, size 220–800 × 80–300 µm; **b** – after protargol impregnation the extrusomes are acicular; **c** – silverline pattern; **d** – ventral view of proboscis' ciliary pattern, showing two perioral kineties accompanying the right branch of the circumoral kinety. Note that KRAINER (1988) wrongly oriented the preoral kineties; **e** – in Austrian specimens, there are two types of extrusomes: type I is 6–10 µm long and rod-shaped slightly narrowing anteriorly, type II is oblong and only 2 µm long; **f, g, y** – binary fission; **i** – specimen ingesting a rotifer; **k–n** – tracheliform (k, l) and normal (m, n) specimens; **o** – formation of a large vacuole from small ones; **p** – rear body end, showing innumerable symbiotic green algae as well as several contractile and large empty vacuoles; **q–v** – the rear body end is tail-like (u, v) in freshly collected specimens and becomes broadly rounded (q–t) under laboratory conditions; **w1–3** – BUTKAY (2004) observed two specimens swimming side by side for a while (w1). Later on, one specimen slowly sank (w2) and the tail of the anterior specimen entered its oral bulge opening (w3); **x** – specimen ejecting cytoplasm from the oral bulge opening. The ejected material is hyaline, 80–100 µm long, swims in the medium, and dissolves after a while. B – dorsal brush, CV – contractile vacuoles, E – extrusomes, F – fibres, LV – large vacuoles, MA – macronuclear strand, OO – oral bulge opening, PB – pharyngeal basket, PE 1+2 – perioral kineties, PR – preoral kineties, V – vacuoles, Z – zoochlorellae. Scale bars: 5 µm (c), 50 µm (d), and 100 µm (a).



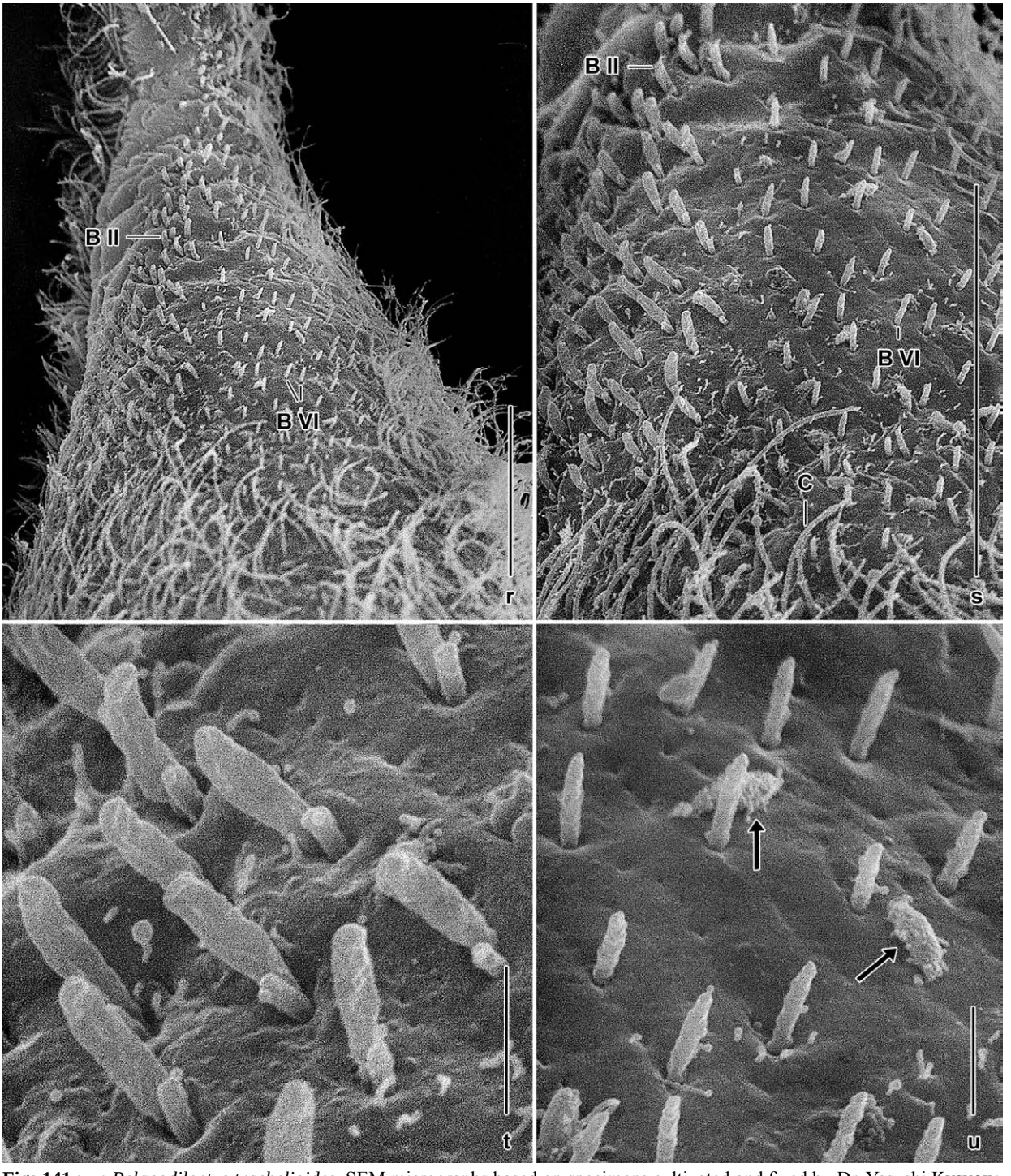
Figs 141a–f: *Pelagodileptus trachelioides* from Lake Biwa in Japan (a–c, f; originals) and a small lake (Grabensee) near the town of Salzburg, Austria (d, e; from FOISSNER et al. 1999). SEM micrographs based on specimens cultivated and fixed by Dr. Yasushi KUSUOKA (Lake Biwa Museum, Japan). **a–c** – ventral (a), dorsolateral (b), and ventrolateral (c) overviews of bulky specimens resembling *Trachelius ovum*. However, the oral bulge opening is very conspicuous in *Pelagodileptus trachelioides* because it is large, slit-like, and very narrowly elliptical; **d** – type II extrusomes are oblong, only 2 µm long, and thus easily overlooked; **e** – type I extrusomes are 6–10 µm long and almost rod-shaped, i.e., have a slightly narrowed anterior end; **f** – surface view showing cortex, cilia and some extruded cortical granules. B – dorsal brush, G – cortical granules, OB – oral bulge, OO – oral bulge opening. Scale bars: 1 µm (f) and 100 µm (a–c).



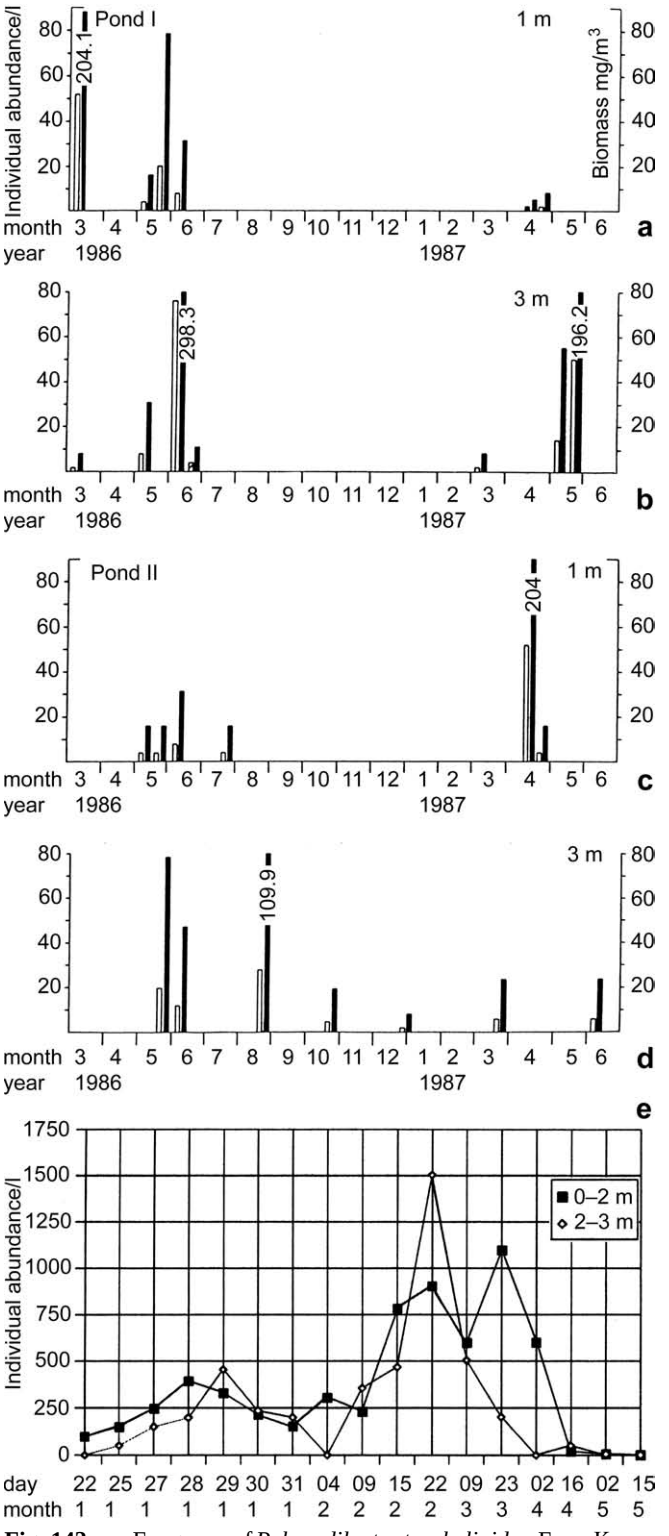
Figs 141g–l: *Pelagodileptus trachelioides*, SEM micrographs based on specimens cultivated and fixed by Dr. Yasushi KUSUOKA (Lake Biwa Museum, Japan). **g** – ventral view of anterior body portion, showing the slit-like and very narrowly elliptical oral bulge opening; **h–j** – details of oral region of the specimen shown in (g). The oral bulge is flat, i.e., only slightly protruding and delineated by dense oral ciliature. Arrowheads mark sites where the oral opening begins to burst; **k** – posterior portion of oral bulge opening, showing that the narrowly spaced circumoral basal bodies seen in protargol preparations are not ciliated; **l** – left of the oral bulge are many oblique preoral kineties, each composed of several narrowly spaced cilia. CK – circumoral kinety, OB – oral bulge, OO – oral bulge opening, PE – perioral kineties, PR – preoral kineties. Scale bars: 5 µm (i, k, l), 10 µm (j), 50 µm (h), and 100 µm (g).



Figs 141m–q: *Pelagodileptus trachelioides*, SEM micrographs based on specimens cultivated and fixed by Dr. Yasushi KUSUOKA (Lake Biwa Museum, Japan). **m** – ventral view of proboscis, showing the oral bulge and the dense oral cilia that beat together, forming metachronal waves; **n, o** – ventral views of distal proboscis area, showing the oral ciliature extending to the tip of the proboscis, and the furrow (arrows) separating the broader right from the narrower left branch of the oral bulge; **p** – posterior portion of the oral bulge and surrounding ciliature; **q** – surface view showing cortex, cilia, and an excretory pore (arrowhead). B – dorsal brush, CK – circumoral kinety, OB – oral bulge, OO – oral opening, PE – perioral kineties, PR – preoral kineties. Scale bars: 10 µm (n, o, q), 20 µm (p), and 40 µm (m).



Figs 141r–u: *Pelagodileptus trachelioides*, SEM micrographs based on specimens cultivated and fixed by Dr. Yasushi KUSUOKA (Lake Biwa Museum, Japan). All measurements from SEM micrographs. **r, s** – dorsal view of proboscis. The dorsal brush forms a comparatively broad field composed of several staggered, distinctly heterostichad rows having paired type II bristles anteriorly and monokinetidal type VI bristles posteriorly; **t** – the brush dikinetids are loosely spaced and associated with type II bristles: the anterior bristle is slighlty inflated and about 1.7–2.4 µm long, while the posterior bristle is a 0.5–0.7 µm long stump; **u** – the tail bristles are monokinetidal and 1–2 µm long. Arrows mark extruded cortical granules. BII, VI – brush bristle types, C – ordinary cilia. Scale bars: 2 µm (t, u) and 20 µm (r, s).



Figs 142a–e: Ecograms of *Pelagodileptus trachelioides*. From KRAINER 1988 (a–d) and BUTKAY 2004 (e). **a–d** – individual abundances (white bars; ind/l) and biomasses (black bars; mg/m^3) at 1 m and 3 m. **e** – individual abundances at 0–2 m and 2–3 m in the Von-Campe Lake of Germany from 22nd January to 15th May 1995.

SLÁDEČEK (1964), KRAINER (1988), and BUTKAY (2004) observed that *Pelagodileptus trachelioides* ejects cytoplasm from the oral bulge opening (Figs 139f, 140x). BUTKAY (2004) noted that the ejected material is hyaline, 80–100 μm long, swims in the medium, and dissolves after a while. KRAINER (1988) observed that such material formed an adhesive disc attaching the cell to the microscope slide. Later, the disc was resorbed and the cell detached and swam away.

Resting cyst: Resting cysts were studied by ZACHARIAS (1894) and HUBER & NIPKOW (1927). However, their data disagree in important features: (i) size (160–180 μm vs. 120–160 μm); (ii) absence/presence of a mucous layer, and (iii) the macronuclear nodules (fused vs. not fused). In our opinion, ZACHARIAS (1894) misinterpreted a dying, globularly inflated specimen as a resting cyst because he did not observe a cyst wall (Fig. 138g). Globular degradation is frequent in dying ciliates in our experience. According to HUBER & NIPKOW (1927), the cysts are 120–160 μm across in vivo, dark green, and have an inconspicuous convexity (escape apparatus?). The wall is covered by a thick, hyaline, colourless mucous layer. The cytoplasm is packed with macronuclear nodules, bright globules, and symbiotic green algae (Fig. 138k). During spring circulation, resting cysts are transported from the sediment to the water column.

Notes on division: Binary fission was studied by ZACHARIAS (1894), HUBER & NIPKOW (1927), and BUTKAY (2004). It appears quite similar to that of *Dileptus* (see general part). The data can be summarized as follows (Figs 138e, q–t, 140f, g, y): (i) cell division occurs in active (non-encysted) condition at full moon in nature and during night in the laboratory; (ii) the division furrow is oblique, i.e., makes an angle of 40° with the transverse body axis; (iii) the parental proboscis remains unchanged; (iv) the new proboscis appears in

Table 67: Morphometric data on *Pelagodileptus trachelioides* (from KRAINER 1998). Data based on mounted, protargol-impregnated (Foissner's method), and randomly selected field specimens. Measurements in µm. CV – coefficient of variation in %, Max – maximum, Mean – arithmetic mean, Min – minimum, n – number of specimens investigated, SD – standard deviation, SE – standard error of mean.

Characteristics	Mean	SD	SE	CV	Min	Max	n
Body, length	450.1	56.9	16.4	12.6	396.8	512.0	12
Body, width	129.0	25.3	7.3	19.6	76.8	166.4	12
Oral bulge opening, length	74.1	18.1	6.0	24.4	42.0	102.0	10
Oral bulge opening, width	13.1	1.6	0.5	12.1	10.8	16.8	10
Macronuclear nodules, length	15.7	3.6	1.1	23.2	10.8	20.4	10
Macronuclear nodules, width	14.0	2.3	0.7	16.1	12.0	18.0	10
Macronuclear nodules, number	12.8	3.6	0.8	28.4	6.0	23.0	18
Micronuclei, largest diameter	2.8	–	–	–	2.4	3.6	10
Micronuclei, number	10.7	3.8	1.0	35.6	6.0	21.0	15
Symbiotic green algae, diameter	2.4	0.0	0.0	0.0	2.4	2.4	10

mid-dividers as a bud in the opisthe's dorsal area and grows post-divisionally; (iv) the macronuclear nodules do not fuse, that is, the moniliform strand divides into two pieces (ZACHARIAS 1894; unlikely in our opinion); and (v) some symbiotic green algae migrate from the opisthe's posterior region to the proter's posterior region.

Occurrence and ecology: Euplanktonic throughout the year with a spring peak in lakes, reservoirs, ponds and large rivers. Reliably recorded from the Holarctis only (see below). Eurytherm, but data from Austrian and German ponds (KRAINER 1988, BUTKAY 2004) as well as BUTKAY's experiments suggest a preference for cold water (Figs 142a–e). This matches the old data from FINDENEGG (1943; 6.6–14.6 °C in Carinthian lakes) and HUBER & NIPKOW (1927), who found highest numbers at 8–15 °C. However, GAJEWSKAJA (1933) observed *Pelagodileptus trachelioides* at 0–22.2 °C, pH 7.2–7.9, 6.4–13.5 mg/l O_2, and 0–3.3 mg/l CO_2. Likewise, SCHWARZ (1962) observed a peak in summer (see below). Oligo-euryhaline. Mixotrophic, that is, can sustain periods of low food supply by using its symbiotic green algae, which are, however, sometimes lacking (HUBER & NIPKOW 1927, KRAINER 1988). In a nutrient enrichment experiment, *P. trachelioides* occurred only during the initial period (LIEPA 1984). Feeds on *Oscillatoria rubescens*, *O. limosa*, dinoflagellates, *Pandorina morum*, copepods, and planktonic rotifers, such as *Asplanchna priodonta*, *Keratella aculeata*, *K. cochlearis*, *Polyarthra* sp. and *Synchaeta* sp. (HUBER & NIPKOW 1927, SCHWARZ 1962, FRYD-VERSAVEL et al. 1975, PACKROFF & WILBERT 1991, BUTKAY 2004). Biomass of 10^6 specimens about 4500 mg, when an average trunk size of 400 × 150 µm is assumed (FOISSNER et al. 1999).

Locus classicus of *Pelagodileptus trachelioides* is a large lake (Großer Plöner See) in northern Germany (ZACHARIAS 1894a, b, 1900). The maximum abundance was 20 ind./cm^2 during May (ZACHARIAS 1896). Later, ZACHARIAS (1900, 1902) found *P. trachelioides* in many other lakes near Plön. Locus classicus of the synonym *Paradileptus caducus* is very slowly running water (Alster) in Hamburg, northern Germany, where KAHL (1935) observed a dozen specimens. The locus classicus of *Dileptus saaleri* is also in northern Germany, where SCHWARZ (1962) discovered it in brackish lakes (2.4–4.9‰ salt) near the Baltic Sea with a peak (311 ind./l) during summer. Locus classicus of *Paradileptus canellai* is Lake Geneva, where DRAGESCO (1966a) found numerous specimens in August.

Further records substantiated by illustrations: spring plankton of a large lake (Zürichsee) in Switzerland (HUBER & NIPKOW 1927); same site (THOMAS 1964; including the synonym *Amphileptus trachelioides*;

without illustration); freshwater near Paris, France (Dragesco 1966b); pond in France during October and January (Fryd-Versavel et al. 1975); Danish lakes (Wesenberg-Lund 1952); autumn and winter plankton of the Von-Campe Lake in the vicinity of the town of Hannover, Germany (Butkay 2004); eu- to polytrophic lake in Germany during winter and spring (Packroff & Wilbert 1991); very rare in a small lake (Grabensee) near Salzburg (Foissner et al. 1999); up to 52 ind./l (1 m, early March) and 76 ind./l (3 m, early June) in groundwater ponds of Styria, Austria, disappearing during summer (Krainer 1988); very abundant in a drinking water reservoir in Bohemia during late May (Sládeček 1964); summer and winter plankton of Lake Baikal but also very abundant from winter to spring and from summer to autumn (Gajewskaja 1933, see this paper for old Russian records; Eggert 1968; Kaplin 1969); in plankton from Lake Biwa, Japan (Figs 141a-c, f-u; Vďačný et al. 2011b).

Records not substantiated by illustrations (most likely correct because the species is very distinct): lakes in Finland (Järnefelt 1936a, b); Swedish lakes (Pejler 1964); in a eutrophic lake of Estonia (Kisand et al. 1998; as *Paradileptus caducus*); Lielupe River and lakes in Latvia (Liepa 1973, 1984a, b); water supply ponds in the surroundings of the town of Freiburg, Germany (Höhne 1963); occasionally abundant in an oligotrophic lake (Erdfallsee) in Germany (Ehlers 1965); slightly eutrophic drinking water reservoir (Saidenbach-Talsperre) in Germany, peaking during May (Beuschold 1961); mesotrophic lake (Pfäffikersee) in Switzerland mainly during spring and autumn (Messikommer 1952, 1954); lakes in Carinthia, Austria, mainly during May (Findenegg 1943, 1953); in the seston of the reservoirs Klíčava and Vrané fed by the River Vltava, Czech Republic (Sládeček 1962); Danube River in Hungary (Bereczky 1977a, Bereczky & Nosek 1995); brackish lake in the former Yugoslavia (Petković & Petković 1978); Moldavian and Azerbaijanian reservoirs (Chorik 1968, Alekperov 1984); up to 60 ind./l at 0–20 °C in various mesosaprobic reservoirs in the former USSR (Mamaeva 1974, 1976a, b, 1979c; Zhukov & Mamaeva 1978); Volga River, Russia (Mamaeva 1979a, b); diverse sites in the former USSR, including the cooler basin of a power station (Timofeeva 1989, Averintzeva 1899, Arslanova 1980); Onega and Ladoga lakes, Russia (Smirnova 1987, Kustovlyankina 1990); reservoir near Moscow, Russia, subdominant during summer (Belova 1994); up to 235 ind./l (surface) and 2 ind./l (92 m) in Cayuga Lake, New York, USA, during late June (Hunt & Chein 1983); freshwaters in Thailand (Charubhun & Charubhun 2000; as *P. caducus*).

Saprobic classification: Kolkwitz & Marsson (1909) classified *Pelagodileptus trachelioides* as an oligosaprobic indicator. Later, Kolkwitz (1950) emphasized that it occurs also in beta-mesosaprobic habitats. Sládeček (1964) and Foissner (1988a) classified it as oligosaprobic: o = 7, b = 3, I = 4, SI = 1.3.

Insufficiently Described and Doubtful Dileptids

Altogether there are 78 insufficiently described or doubtful dileptids, i.e., very likely non-dileptid ciliates originally or subsequently assigned to dileptids. More than half of these problematic species were described by Abbé E. Dumas, a French amateur protistologist who studied the protist fauna of the French Massif Central. He published the results in three volumes (Dumas 1929, 1930, 1937), which contain the description of 550 new species, including 45 nominal species of *Dileptus*. Unfortunately, the studies of Dumas were forgotten, though some of his new species appear well described. However, most are insufficiently described, hardly providing sufficient details for recognition (Foissner 1995b). This applies also for his dileptids, many of which are indeterminable or belong to other ciliate groups, especially to the pleurostomatid haptorians.

In the first chapter, we treat the insufficiently described and doubtful dileptids established by various authors but, especially, by Fromentel (1874–1876). In the second chapter, we discuss the dileptids described by Dumas (1929–1937). All taxa are arranged alphabetically and supplied with original figures (if available) and brief comments.

From Various Authors

Amphileptus anser – Fromentel, 1876, Études Microzoaires: 286 (Figs 143c1, c2). Based on *Vibrio anser* Mueller, 1773; *Amphileptus anser* sensu Ehrenberg, 1838; and *Dileptus anser* sensu Dujardin, 1841. Mentioned also by Dumas (1929). However, Fromentel's and Dumas' species have a proboscis occupying only 1/3 (vs. 1/2) of body length, and thus conspecificity with Mueller 's and Ehrenberg's species is not likely. Possibly, it is a poorly observed *Dileptus margaritifer*.

Amphileptus longicollis Ehrenberg, 1831, Abh. dt. Akad. Wiss. Berl. year **1831**: 115; without figure. Also in Ehrenberg (1838, Infusionsthierchen: 357) (Figs 143n–p). Mentioned in the revisions of Claparède & Lachmann (1859, Mém. Inst. natn. génev. 6: 355) and of Kent (1881, Manual infusoria II: 526). Not cited in the revisions of Kahl (1930–1935) and Dragesco (1963). Schewiakoff (1896) synonymized *A. longicollis* with *A. anser* (now *Pseudomonilicaryon anser*). Certainly, the figures show the proboscis area of a regenerating *Dileptus* specimen. Thus, the species is indeterminable.

Amphileptus massiliensis (nov. sp.) Gourret & Roeser, 1886, Archs Zool. exp. gén. **4**: 471 (Figs 143a1, a2). Kahl (1931, Tierwelt Dtl. **21**: 208) transferred it to *Dileptus* (Fig. 143b). Mentioned also in the revision of Dragesco (1963, Bull. biol. Fr. Belg. **97**: 125). This species is so poorly described that it is best considered as indeterminable.

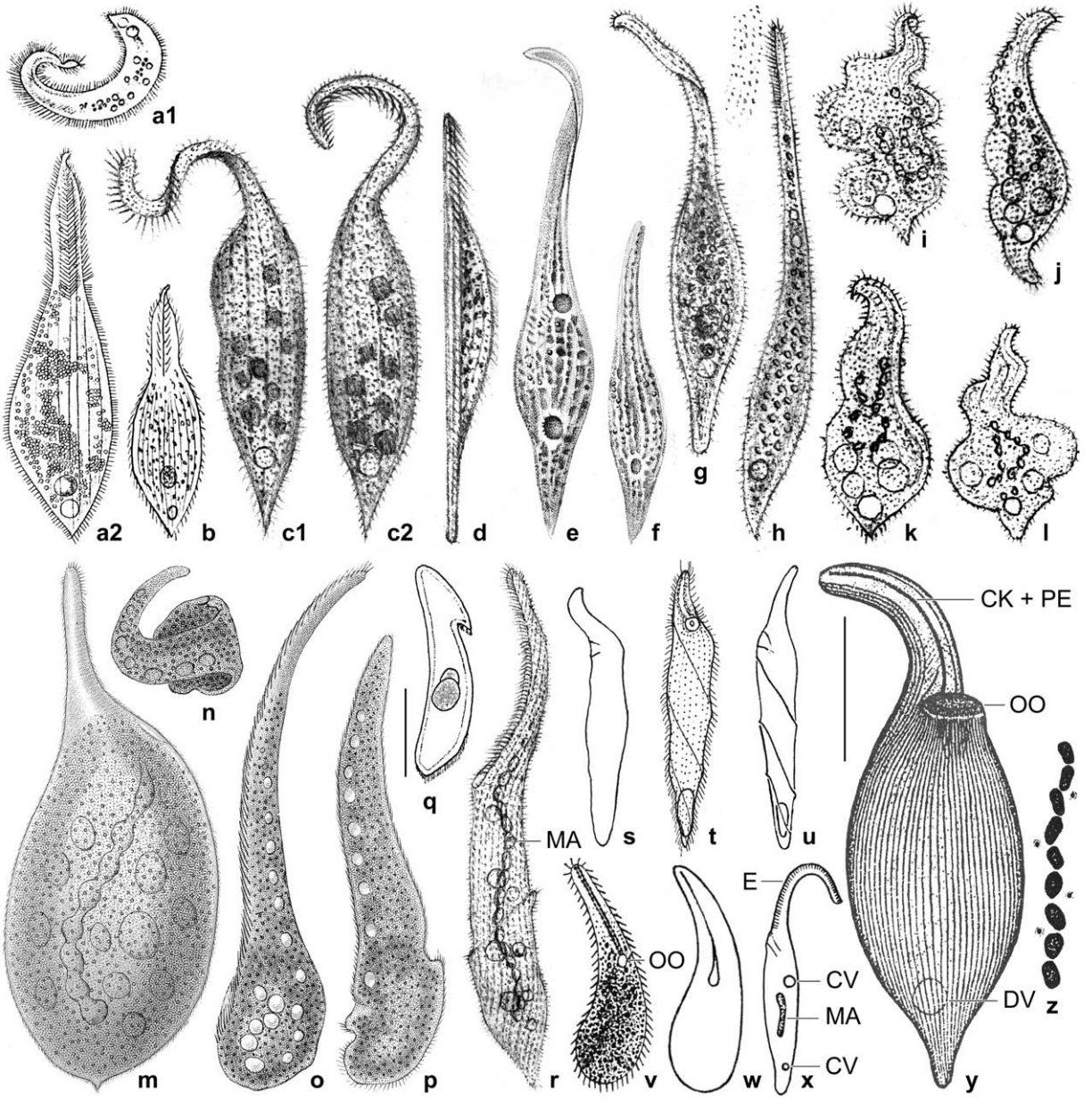
Amphileptus moniliger Ehrenberg, 1835, Abh. dt. Akad. Wiss. Berl. year 1835: 165; without figure. Also in Ehrenberg (1838, Infusionsthierchen: 356) (Fig. 143m). See *Paradileptus elephantinus*.

Amphileptus moniliger – Fromentel, 1876, Études Microzoaires: 287 (Fig. 143r). Schewiakoff (1896) synonymized it with *Amphileptus anser* (now *Pseudomonilicaryon anser*). Not cited in the revisions of Kahl (1930–1935) and Dragesco (1963). This is an indeterminable, early mid-divider of a pseudomonilicaryonid dileptid. Fromentel's species is obviously not conspecific with *A. moniliger* Ehrenberg, 1835 (see above) because the latter has a much stouter body (length:width ratio 2.5:1 vs. 8.5:1) and a shorter proboscis (1/4 vs. 1/3 of body length). See also *Paradileptus elephantinus*.

Ctenoctophrys chattoni n. g., n. sp. Weill, 1946, C. R. hebd. Séanc. Acad. Sci., Paris **222**: 683 (Figs 145a, b). Listed as incertae sedis within the family Tracheliidae by Corliss (1979, Ciliated protozoa: 216) and by Lynn (2008, Ciliated protozoa: 371). Not cited in the catalogue of generic names of ciliates (Aescht 2001). Corliss (1979) classified *Ctenoctophrys* in the family Tracheliidae because of the many tentacles which are, however, cilia forming a velum resembling that of trichodinids. Not a dileptid, and very likely not even a ciliate. It is rather frequently cited by palaeontologists as a striking example of convergence between ciliates and ctenophores (e.g., Conway-Morris 1998, 2003). Possibly, neither Corliss (1979) nor Lynn (2008) consulted the original description because the cilia can hardly be interpreted as tentacles or proboscides. In our opinion, this marine organism, which has a size of 45 × 65 µm, is a cnidarian larva.

Dileptus anas – Fromentel, 1876, Études Microzoaires: 291 (Fig. 145h). Based on *Trichoda anas* Mueller, 1773. Mentioned also by Dumas (1929, Les Microzoaires: 112; without figure). Not cited in the revision of Kahl (1930–1935). Not a dileptid.

Dileptus calceolus Fromentel, 1876, Études Microzoaires: 291 (Fig. 145c). Mentioned also by Dumas (1929, Les Microzoaires: 113) (Fig. 147k) and Escomel (1929, Faune de Arequipa: 27; without figure).



Figs 143a–z: Insufficiently described ciliates (a1, a2, b, d–l, q, v, w) and doubtful dileptids (c1, c2, m–p, r–u, x–z) from life (a–s, u–x), after mercuric chloride fixation (t), and after silver nitrate impregnation (y, z). **a1, a2** – *Amphileptus massiliensis*, a curved and a straight specimen, size not given (from Gourret & Roeser 1886); **b** – a redrawing of *A. massiliensis* by Kahl (1931); **c1, c2** – *Amphileptus anser*, length 210 µm and 240 µm (from Fromentel 1876); **d** – *Dileptus fasciola*, length 175 µm (from Fromentel 1876); **e, f** – *Dileptus folium*, an extended and a contracted specimen, length 180 µm and 120 µm (from Dujardin 1841); **g, h** – *Dileptus folium*, length 200 µm and 215 µm (from Fromentel 1876); **i–l** – *Dileptus meleagris*, length 330 µm, 400 µm, 370 µm, and 300 µm (from Fromentel 1876); **m** – *Amphileptus moniliger*, length 360 µm (from Ehrenberg 1838); **n–p** – *Amphileptus longicollis*, length up to 270 µm (from Ehrenberg 1838); **q** – *Micruncus complanatus*, length 120 µm (from Delphy 1938); **r** – *Amphileptus moniliger*, length 300 µm (from Fromentel 1876); **s, t** – *Dileptus spiralis*, lateral and ventral view, length 300 µm (from Gelei 1954); **u** – a redrawing of *D. spiralis* by Dragesco (1963); **v** – *Dileptus proboscideus*, length 105 µm (from Lepşi, 1957a); **w** – a redrawing of *D. proboscideus* by Dragesco (1963); **x** – *Dileptus* sp., length 160 µm (from Dragesco 1963); **y, z** – *Dileptus falciformis*, ventrolateral view of ciliary pattern and nuclear apparatus, length 120 µm (from Alekperov 2005). CK – circumoral kinety, CV – contractile vacuoles, DV – defecation vacuole, MA – macronucleus, OO – oral bulge opening, PE – perioral kinety. Scale bars: 30 µm (y) and 50 µm (q).

Obviously, FROMENTEL's species is a *Blepharisma*. Very likely, DUMAS' species is not conspecific with that of FROMENTEL (1876) and its identity remains obscure. Not cited in the revision of KAHL (1930–1935).

Dileptus caudatus – FROMENTEL, 1876, Études Microzoaires: 293 (Fig. 145l). Based on *Enchelys caudata* MUELLER, 1786 and *Uroleptus filum* EHRENBERG, 1833. Mentioned also by DUMAS (1929, Les Microzoaires: 122) (Figs 146u,v). Not cited in the revision of KAHL (1930–1935). Not a dileptid.

Dileptus corniger FROMENTEL, 1876, Études Microzoaires: 292, Pl. XV, fig. 6. Not cited in the revision of KAHL (1930–1935). Not a dileptid. (Figure too bleached to be reproduced.)

Dileptus crinitus – FROMENTEL, 1876, Études Microzoaires: 293 (Fig. 145m). Based on *Trichoda crinita* MUELLER, 1786. Not cited in the revision of KAHL (1930–1935). Not a dileptid.

Dileptus cylindricus FROMENTEL, 1876, Études Microzoaires: 289 (Fig. 145k). Mentioned also by DUMAS (1929, Les Microzoaires: 120) (Fig. 146w). Not cited in the revision of KAHL (1930–1935). Not a dileptid, but very likely *Pseudoblepharisma tenue* KAHL, 1926.

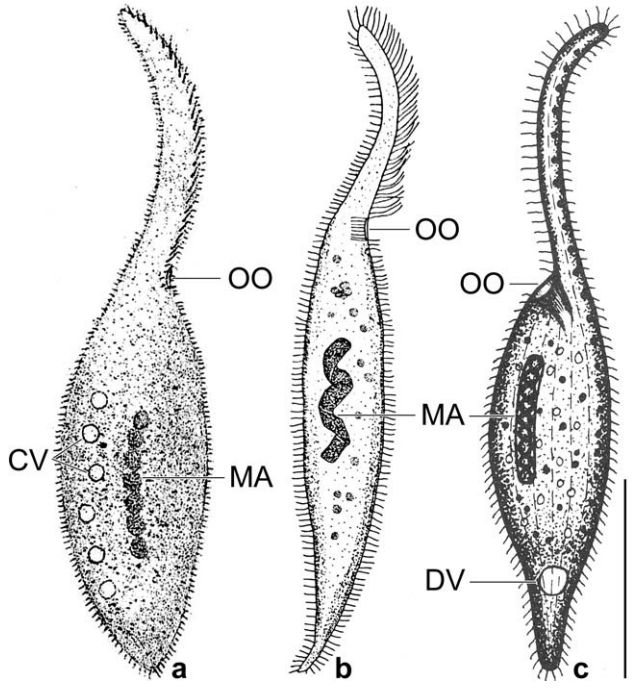
Dileptus falciformis KAHL, 1932 – ALEKPEROV (2005, Atlas svobodnoživuŝih infuzorij: 70) (Figs 143y, z). *Dileptus falciformis* (now *Pseudomonilicaryon falciforme*) was established by KAHL in 1931, not 1932 as given by ALEKPEROV (2005). Certainly, ALEKPEROV's species is not *D. falciformis* because of the much higher number of ciliary rows (70–75 vs. 30–48), the *Pseudomonilicaryon japonicum*-like (vs. *P. falciforme*-like) right side ciliary pattern of the proboscis, and the limnetic (vs. terrestrial) habitat. Length 180–220 µm in vivo, 170–200 µm after silver nitrate impregnation, only 120 µm according to the figure (Fig. 143y). Narrowly dileptid with a length:width ratio of about 3.2:1. Proboscis about one third of body length, distinctly set off from bluntly fusiform trunk; posterior end tail-like. Macronucleus moniliform, composed of 9–15 nodules; 3–5 globular micronuclei. A single contractile vacuole, very likely a misidentified defecation vacuole at base of posterior narrowing. Cytoplasm hyaline. About 70–75 narrowly spaced ciliary rows; right side ciliary rows unshortened, leaving a broad blank stripe right of oral bulge. Oral bulge opening roundish; oral basket conical, composed of 35–40 rods. ALEKPEROV (2005) found this species in the plankton and benthos of lakes in Azerbaijan and Tajikistan. Possibly, this is an opisthe post-divider of a member of the *P. japonicum* group; indeterminable with the data provided.

Dileptus fasciola – FROMENTEL, 1876, Études Microzoaires: 290 (Fig. 143d). Based on *Vibrio anas* MUELLER, 1786 and *Amphileptus fasciola* EHRENBERG, 1838, which is now *Litonotus fasciola* (EHRENBERG, 1838) WRZEŚNIOWSKI, 1870 [see SCHEWIAKOFF (1889, 1896) and KAHL (1931)]. Mentioned also by DUMAS (1929, Les Microzoaires: 110) (Fig. 147b).

Dileptus folium DUJARDIN, 1841, Zoophytes: 409 (Figs 143e, f). Mentioned also by FROMENTEL (1876, Études Microzoaires: 291) (Figs 143g, h) and DUMAS (1929, Les Microzoaires: 121) (Fig. 147c). FROMENTEL (1875) fixed it as type species of *Dileptus*. WRZEŚNIOWSKI (1870) assigned *D. folium* to the genus *Litonotus*. KAHL (1931) synonymized *L. folium* with *L. cygnus* (MUELLER, 1773); we agree.

Dileptus gallina – FROMENTEL, 1876, Études Microzoaires: 290 (Fig. 145d). Based on *Trichoda gallina* MUELLER, 1786, which is now *Uroleptus gallina* (MUELLER, 1786) FOISSNER et al., 1991. Mentioned also by DUMAS (1930, Les Microzoaires: 86) (Fig. 148g). Neither FROMENTEL's nor DUMAS' species is conspecific with *U. gallina*, and their identity remains obscure (possibly a *Loxophyllum helus*).

Dileptus gigas CLAPARÈDE & LACHMANN, 1859 – LOKOT' (1987, Èkologiâ resničnyh prostejših: 35) (Fig. 144c). Certainly, LOKOT's species is not *D. gigas* (now *Monomacrocaryon gigas*) because of the untwisted body and the much longer proboscis (40% vs. 20% of body length). The species is referred as *D. anser* in the figure legend. However, *D. anser* has a moniliform macronucleus (vs. single oblong macronucleus) and a longer proboscis (55% vs. 40% of body length). Length 1000–1500 µm in vivo, only 650 µm according to the figure (Fig. 144c). Narrowly dileptid with a length:width ratio of about 5.4:1. Proboscis about



Figs 144a–c: Insufficiently described dileptids from life (a, c) and after silver nitrate impregnation (b). **a** – *Dileptus* sp. (?), length 350 µm (from Conn 1905); **b** – *Dileptus* sp., length about 112 µm (from Thompson & Croom 1978); **c** – *Dileptus gigas*, length 650 µm (from Lokot' 1987). CV – contractile vacuoles, DV – defecation vacuole, MA – macronucleus (nodules), OO – oral bulge opening. Scale bar 200 µm.

40% of body length, ordinarily set off from bluntly fusiform trunk; posterior end tail-like. Macronucleus in middle quarters of trunk, oblong and slightly curved. Lokot' (1987) found 2–4 ind./l in the summer plankton of lakes in the Central Baikal region. Indeterminable with the data provided.

Dileptus lacrimula Fromentel, 1876, Études Microzoaires: 292 (Figs 145e–g). Not cited in the revision of Kahl (1930–1935). Not a dileptid, possibly a contracted *Lacrymaria*. Best considered as indeterminable.

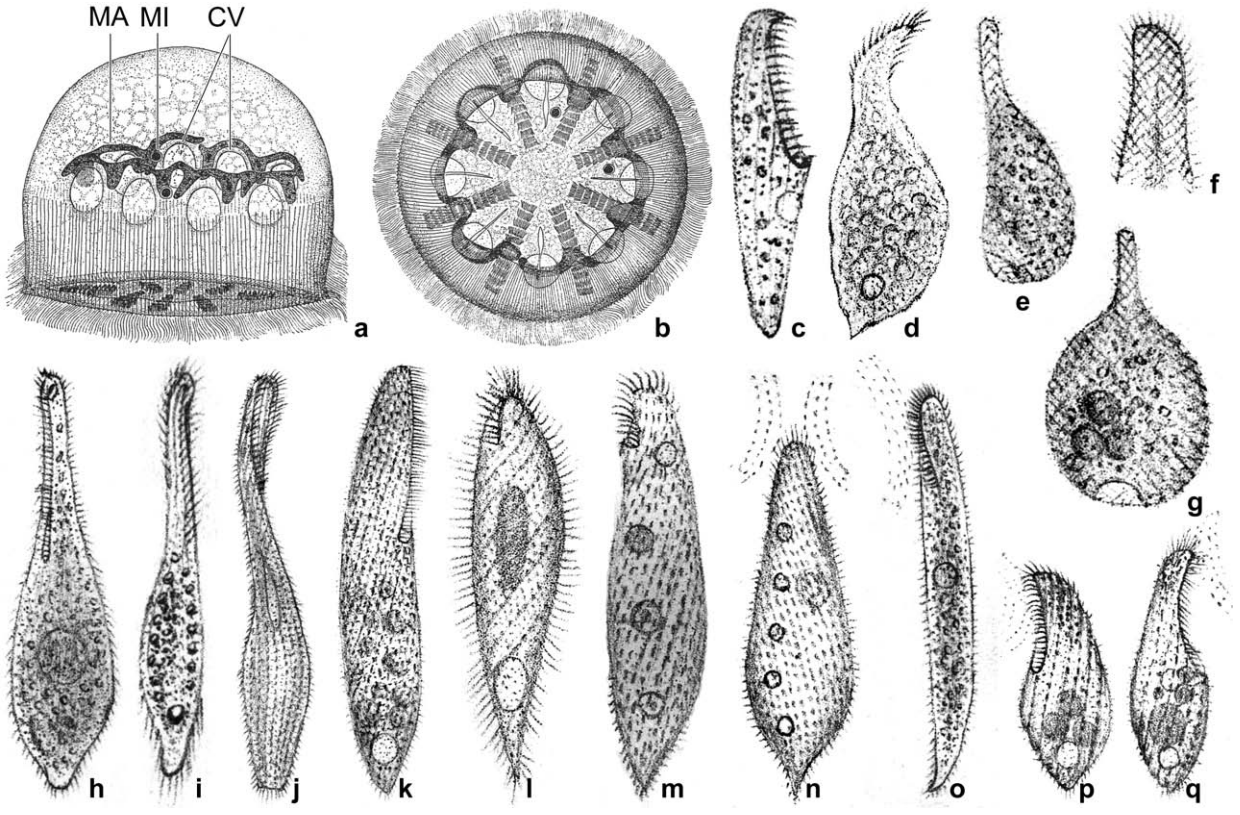
Dileptus meleagris Fromentel, 1876, Études Microzoaires: 289 (Figs 143i–l). Mentioned also by Dumas (1930, Les Microzoaires: 85) (Fig. 148e). A synonym of *Loxophyllum meleagris* (Mueller, 1773) Dujardin, 1841.

Dileptus musculus – Fromentel, 1876, Études Microzoaires: 292 (Fig. 145n). Based on *Uroleptus musculus* sensu Ehrenberg, 1838, which is a junior synonym of *U. gallina* (Mueller, 1786) Foissner et al., 1991. Mentioned also by Dumas (1930, Les Microzoaires: 87) (Fig. 148o). Neither Fromentel's nor Dumas' species is conspecific with *U. gallina*, and their identity remains obscure.

Dileptus piscis – Fromentel (1876, Études Microzoaires: 290) (Fig. 145i). Based on *Trichoda piscis* Mueller, 1773, which is now *Uroleptus piscis* (Mueller, 1773) Ehrenberg, 1831. Mentioned also by Dumas (1929, Les Microzoaires: 119) (Fig. 147u). Neither Fromentel's nor Dumas' species is conspecific with *U. piscis*, but both are very likely pleurostomatid haptorians.

Dileptus proboscideus n. sp. Lepşi, 1957, Buletin şti. Acad. Repub. pop. rom. **9**: 232 (Fig. 143v). Reviewed in Dragesco (1963, Bull. biol. Fr. Belg. **97**: 124) (Fig. 143w). Length 105 µm in vivo; not contractile. Narrowly ovoidal with a length:width ratio of about 3.5:1. Proboscis about one half of body length, flexible and motile; trunk oblong and broadly rounded posteriorly. Cytoplasm opaque due to many granules. Oral bulge opening roundish and small. Lepşi (1957a) found this species in a peatbog from the East Carpathian Mts. (900 m a. s. l.), Roumania. In our opinion, this organism is indeterminable.

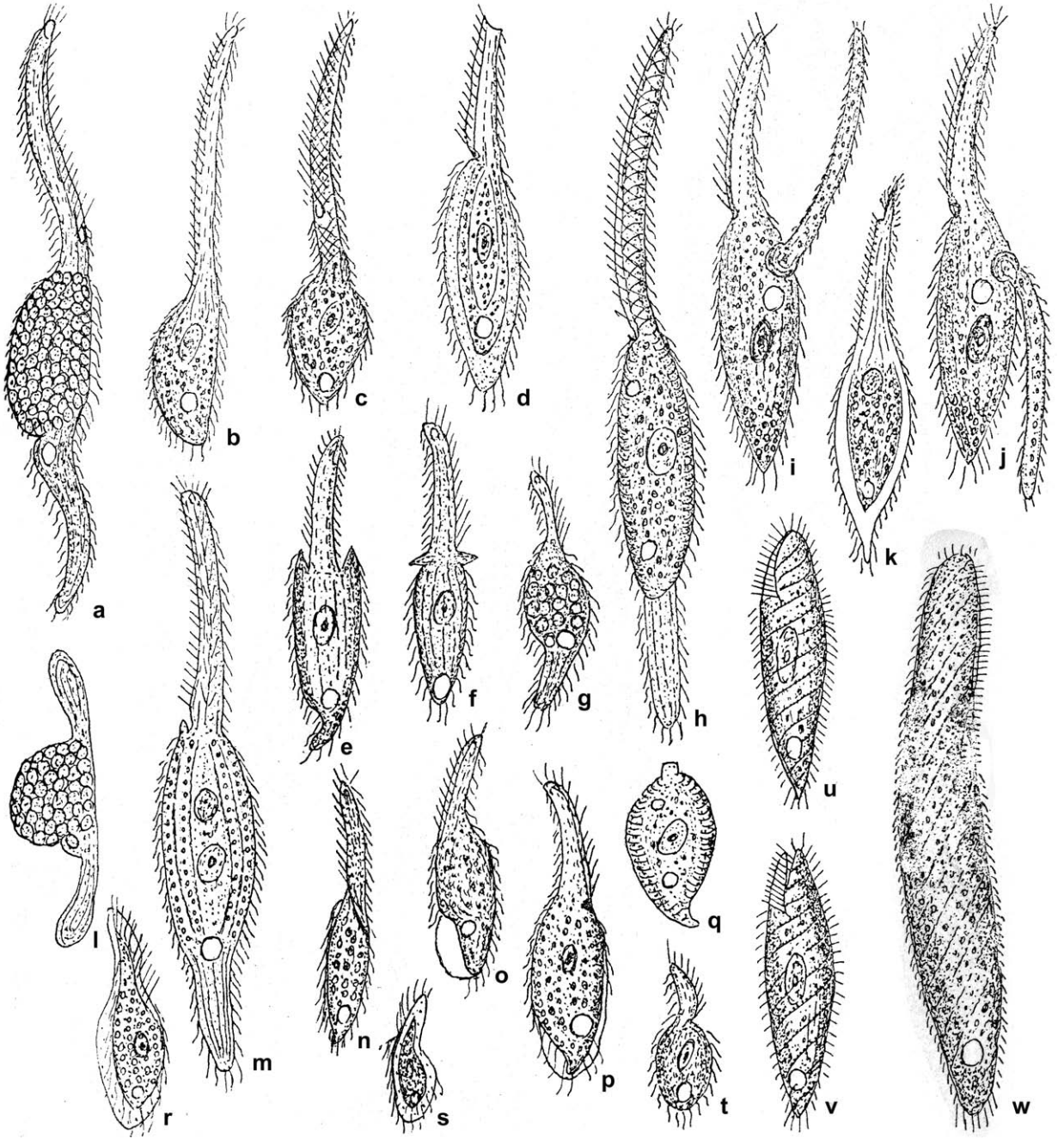
Dileptus spiralis n. sp. Gelei, 1954, Acta biol. hung. **5**: 284 (Figs 143s, t). Reviewed in Dragesco (1963, Bull. biol. Fr. Belg. **97**: 125) (Fig. 143u). Length 300 µm in vivo (?). Body twisted and very narrowly



Figs 145a–q: Ciliates referred to dileptids by several authors. From Weill 1946 (a, b) and Fromentel 1876 (c–q), all from life. **a, b** – *Ctenoctophrys chattoni*, lateral and ventral view, size about 45 × 65 µm; **c** – *Dileptus calceolus*, length 75 µm; **d** – *Dileptus gallina*, length 100 µm; **e–g** – *Dileptus lacrimula*, lateral view, detail of anterior body portion, and ventral view, size not given; **h** – *Dileptus anas*, length 130 µm; **i** – *Dileptus piscis*, length 120 µm; **j** – *Dileptus truncatus*, length 190 µm; **k** – *Dileptus cylindricus*, length 225 µm; **l** – *Dileptus caudatus*, length 110 µm; **m** – *Dileptus crinitus*, length 110 µm; **n** – *Dileptus musculus*, size not given; **o** – *Dileptus uvula*, length 140 µm; **p, q** – *Dileptus striatus*, length 80 µm and 90 µm. CV – contractile vacuoles, MA – macronucleus, MI – micronucleus.

dileptid with a length:width ratio of about 6:1. Proboscis about one fifth of body length, comparatively massive, slightly curved dorsally; trunk oblong to bluntly fusiform, with three helical crests; posterior region dorsoventrally flattened, not tail-like. Macronucleus oblong, but Gelei (1954) could not determine whether sausage-like or composed of nodules in a series. Several contractile vacuoles, their pattern not studied in detail. Cytoplasm opaque due to many food vacuoles, containing euglenid flagellates and diatoms. Ciliary rows extend meridionally, i.e., do not follow the helical body organization; number not studied, but Gelei (1954) figured eight rows on ventral side. Oral bulge opening roundish. Jerked to and fro in an empty crustacean shell, when swimming rotated about main body axis. Gelei (1954) found only a single specimen in the summer plankton of a meadow puddle in the Börzsöny Mts., Upper Hungary. Too insufficiently described to be recognized as a distinct species; body crests possibly caused by fixation. Best considered as indeterminable. There is one unsubstantiated recorded from alkaline biotopes in Hortobágy National Park, Hungary (Szabó 1999).

Dileptus striatus – Fromentel, 1876, Études Microzoaires: 289 (Figs 145p, q). Based on *Trichoda striata* Mueller, 1786. Mentioned also by Dumas (1929, Les Microzoaires: 110) (Fig. 147r). Obviously, Fromentel's species is a *Blepharisma*, while that of Dumas (1929) is very likely a pleurostomatid ciliate. Not cited in the revision of Kahl (1930–1935).



Figs 146a–w: Insufficiently described and doubtful dileptids in vivo (from DUMAS 1929). **a, l** – *Dileptus orbicularis*, length160 µm; **b, c** – *Dileptus clavipes*, both 110 µm; **d** – *Dileptus marginellus*, length 100 µm; **e** – *Dileptus bicornis*, length 85 µm; **f** – *Dileptus bicristatus*, length 75 µm; **g** – *Dileptus gibbosus*, length 65 µm; **h, q** – *Dileptus lacrymarioïdes*, length of extended cell 190 µm and of contracted cell 45 µm; **i, j** – *Dileptus brachiatus*, length 125 µm; **k** – *Dileptus fastigiatus*, length 105 µm; **m** – *Dileptus costatus*, length 155 µm; **n** – *Dileptus torquescens*, length 70 µm; **o** – *Dileptus sinuosus*, length 65 µm; **p** – *Dileptus submarginatus*, length 80 µm; **r** – *Dileptus limbatus*, length 60 µm; **s** – *Dileptus reclinis*, length 35 µm; **t** – *Dileptus arcuatus*, length 40 µm; **u, v** – *Dileptus caudatus*, length 110 µm; **w** – *Dileptus cylindricus*, length 240 µm.

Dileptus truncatus Fromentel, 1876, Études Microzoaires: 291 (Fig. 145j). Not cited in the revision of Kahl (1930–1935). Not a dileptid, possibly a pleurostomatid haptorian or a *Spirostomum*. Best considered as indeterminable.

Dileptus uvula – Fromentel, 1876, Études Microzoaires: 293 (Fig. 145o). Based on *Trichoda uvula* Mueller, 1773. Not cited in the revision of Kahl (1930–1935) and in the catalogue of hypotrich names (Berger 2001). Not a dileptid, but a hypotrich; possibly a junior synonym of *Engelmanniella mobilis* (Engelmann, 1862) Foissner, 1982.

Dileptus sp. (?) – Conn, 1905, Bull. Conn. St. geol. nat. Hist. Surv. **2**: 46 (Fig. 144a). Possibly a *Pseudomonilicaryon* species. Length 350 µm in vivo. Narrowly dileptid with a length:width ratio of about 4.7:1. Proboscis about 40% of body length, indistinctly set off from bluntly fusiform trunk. Macronucleus in middle quarters of trunk, composed of seven nodules in series. A dorsal row of contractile vacuoules in trunk. Conn (1905) found this species in brooks and rivers of Middletown, Connecticut, USA.

Dileptus sp. – Dragesco, 1963, Bull. biol. Fr. Belg. **97**: 128 (Fig. 143x). An insufficiently described *Monomacrocaryon* species. Length 120–180 µm in vivo. Very narrowly dileptid with a length:width ratio of about 6.8:1. Proboscis about one half of body length, distinctly curved dorsally; trunk oblong to bluntly fusiform and rounded posteriorly. Macronucleus in centre of trunk, oblong and curved. Two dorsal contractile vacuoles: anterior vacuole at beginning of second fourth of trunk, posterior vacuole at beginning of posterior fourth. Dragesco (1963) found this species in moss from Villefranche-sur-Mer, France. It is most similar to *Monomacrocaryon tenue*, which is, however, smaller (60–110 µm vs. 120–180 µm) and has a shorter proboscis (1/3 vs. 1/2 of body length).

Dileptus sp. – Thompson & Croom, 1978, Antarct. Res. Ser. **27**: 44 (Fig. 144b). Body size of silver nitrate-impregnated specimens 90.6–144.6 × 14.8–23.7 µm, on average 112.5 × 18.5 µm. Very narrowly dileptid with a length:width ratio of about 6.8:1. Proboscis about one third of body length; trunk oblong to bluntly fusiform and tapered posteriorly. Macronucleus in centre of trunk, twisted and nodulated. Many scattered contractile vacuoles. Thompson & Croom (1978) found this species in a small (~ 2 m^2) tidal pool with a maximum depth of 2 cm on King George Island, South Shetland Islands. Possibly, this is *Rimaleptus alpinus*, which has been found in the Antarctis by Foissner (1996b).

Micruncus nov. gen. *complanatus* nov. sp. Delphy, 1938, Bull. Stn biol. Arcachon **35**: 62 (Fig. 143q). Size 250 × 50 µm in vivo, while only 120 µm long according to the figure provided; strongly flattened, that is, less than 10 µm thick. Shape *Epispathidium amphoriforme*-like with a length:width ratio of about 5:1. Two globular inclusions (macronucleus?) in mid of trunk. Cytoplasm yellowish. Cortex thick. Ciliature holotrichous. Delphy (1938) classified *Micruncus* in the family Tracheliidae; Corliss (1979) and Lynn (2008) followed. Dragesco (1963) did not cite it in his monograph. Certainly not a dileptid, possibly a poorly observed spathidiid or pleurostomatid haptorian, or a *Remanella*. Very likely, this species is indeterminable.

Phragelliorhynchus nasutus Herrick, 1884, Science 4: 73; without figure. Schewiakoff (1896) synonymized *Ph. nasutus* with *Amphileptus anser* (now *Pseudomonilicaryon anser*). Indeed, *Phragelliorhynchus nasutus* resembles *Pseudomonilicaryon anser* and *P. fraterculum* in having a very long and highly motile proboscis, but is much smaller (200 µm vs. about 500 µm) and thus conspecificity can be excluded. Kahl (1931) considered *Phragelliorhynchus nasutus* as a junior synonym of *Dileptus gigas* (now *Monomacrocaryon gigas*). We disagree because *M. gigas* is much larger (up to 1.6 mm vs. 200 µm) and has a much shorter proboscis (1/5 vs. 1/2 of body length). This species, which Herrick (1884) found in Minnesota, USA, should be considered as indeterminable because of the weak description and the absence of a figure.

From Dumas (1929–1937)

Amphileptus anser, Mueller – Dumas (1929, Les Microzoaires: 107) (Fig. 147a). See "various authors".

Dileptus acutus Dumas, 1929, Les Microzoaires: 115 (Fig. 147p). The species is referred as *Dileptus acutatus* in the figure legend (Pl. XXIII, fig. 14). Possibly an *Acropisthium*. Best considered as indeterminable.

Dileptus aduncus Dumas, 1929, Les Microzoaires: 121 (Fig. 147e). Length in vivo 170 µm. Shape narrowly dileptid with acute posterior end. Oral opening distinct, at base of proboscis. Two globular, separate macronuclear nodules in centre of trunk. A single terminal contractile (defecation?) vacuole. Possibly a *Rimaleptus*.

Dileptus anas (Mueller, 1773) – Dumas (1929, Les Microzoaires: 112; without figure). See "various authors".

Dileptus arcuatus Dumas, 1929, Les Microzoaires: 119 (Fig. 146t). Mentioned also by Dumas (1937, Les Microzoaires: 40) (Fig. 148i). Certainly, *D. arcuatus* sensu Dumas (1929) and Dumas (1937) are not conspecific because of the very different body shape (broadly vs. cylindroidally dileptid). Their identity remains obscure. Best considered as indeterminable.

Dileptus biacuta Dumas, 1937, Les Microzoaires: 41 (Fig. 148c). Certainly not a dileptid. Best considered as indeterminable.

Dileptus bicaudatus Dumas, 1929, Les Microzoaires: 120 (Fig. 147n). The species is referred as *Dileptus caudatus* in the figure legend (Pl. XXXI, fig. 2). Length in vivo 100 µm. Shape very narrowly dileptid with proboscis occupying almost half of body length; posterior end with two unequally long tail-like projections. Nuclear apparatus not observed because cytoplasm packed with globules. A single terminal contractile (?) vacuole in shorter tail-like projection. Possibly, this is a wounded or malformed dileptid. Best considered as indeterminable.

Dileptus bicornis Dumas, 1929, Les Microzoaires: 118 (Fig. 146e). Length in vivo 85 µm. Proboscis occupies almost half of body length; trunk cylindroidal, with a triangular projection each right and left of base of proboscis; posterior end tail-like. Nuclear apparatus not described, but Dumas (1929) figured an ellipsoidal structure (macronucleus?) in centre of trunk. A single contractile (defecation?) vacuole at base of tail. Cytoplasm finely granulated. Possibly, a wounded or malformed dileptid. Best considered as indeterminable.

Dileptus bicristatus Dumas, 1929, Les Microzoaires: 118 (Fig. 146f). Length in vivo 75 µm. Proboscis occupies about half of body length; trunk bluntly fusiform, with a transverse triangular projection each right and left of base of proboscis; posterior end narrowly rounded. Nuclear apparatus not described, but Dumas (1929) figured an ellipsoidal structure (macronucleus?) in centre of trunk. A single terminal contractile (defecation?) vacuole. Cytoplasm finely granulated. Possibly, a wounded or malformed dileptid. Best considered as indeterminable.

Dileptus brachiatus Dumas, 1929, Les Microzoaires: 119 (Figs 146i, j). Length in vivo 125 µm. Shape narrowly dileptid with proboscis occupying about 40% of body length; trunk bluntly fusiform; posterior end acute. Nuclear apparatus not described, but Dumas (1929) figured an ellipsoidal structure (macronucleus?) in centre of trunk. A single contractile (?) vacuole in dorsal side of mid-body, where Dumas (1929) observed a long, mobile, finger-like projection; possibly a *Protospathidium* attacking the *Dileptus*. Best considered as indeterminable.

Dileptus calceolus Fromentel, 1876 – Dumas (1929, Les Microzoaires: 113) (Fig. 147k). See "various authors".

Dileptus caudatus Fromentel, 1876 – Dumas (1929, Les Microzoaires: 122) (Figs 146u, v). See "various authors".

Dileptus cavicaudus Dumas, 1929, Les Microzoaires: 110 (Fig. 147q). Length in vivo 90 µm. Body fusiform with proboscis occupying about one third of body length. Nuclear apparatus not described, but Dumas (1929) figured two ellipsoidal structures (macronuclear nodules?) in trunk. A single contractile (defecation?) vacuole slightly above hook-like curved, hyaline posterior body portion. Possibly, a wounded or malformed dileptid. Best considered as indeterminable.

Dileptus cilunculus Dumas, 1930, Les Microzoaires: 88 (Fig. 148a). Dumas (1930) considered this species as a variety of *D. hians* Dumas, 1930. Certainly not a dileptid; possibly a wounded ciliate. Best considered as indeterminable.

Dileptus cinereus Dumas, 1929, Les Microzoaires: 116 (Fig. 147h). Length in vivo 90 µm. Body fusiform with proboscis occupying about one third of body length. Macronucleus oblong, in centre of trunk. Two dorsal contractile vacuoles. Cytoplasm greyish. Possibly a *Monomacrocaryon* species, resembling *M. tenue* which is, however, contractile and has a cylindroidal and curved or twisted macronucleus.

Dileptus clavipes Dumas, 1929, Les Microzoaires: 117 (Figs 146b, c). Very likely, the figures show the proboscis area of regenerating *Dileptus* specimens. Thus, the species is indeterminable.

Dileptus corniculatus Dumas, 1929, Les Microzoaires: 121 (Fig. 147f). The species is referred as *D. corniculata* in the figure legend (Pl. XXVII, fig. 12). Length in vivo 160 µm. Shape crescentic with anterior and posterior third narrowing to acute ends. Oral opening small, at beginning of second body third. Macronucleus (food inclusion?) globular, in centre of trunk. A terminal contractile (defecation?) vacuole. Possibly, a poorly observed *Microdileptus* or *Monomacrocaryon*. Best considered as indeterminable.

Dileptus costatus Dumas, 1929, Les Microzoaires: 117 (Fig. 146m). Length in vivo 155 µm. Proboscis as long as broadly fusiform trunk; tail long and comparatively broadly rounded posteriorly, flattened and hyaline. Two separate macronuclear nodules in centre of trunk. A single contractile vacuole at base of tail. Five rows of shiny granules between ribs on trunk. Very likely a pleurostomatid ciliate.

Dileptus crispatus Dumas, 1930, Les Microzoaires: 85 (Fig. 148b). Certainly, the figure shows a strongly wounded ciliate. Thus, the species is indeterminable.

Dileptus cristatus Dumas, 1937, Les Microzoaires: 40 (Fig. 148p). Length in vivo 85 µm. Shape narrowly dileptid. Proboscis occupies about 35% of body length, with 7–8 dorsal papillae forming a serrate pattern; trunk cylindroidal with narrowly rounded posterior end. Dumas (1937) did not describe nuclear and contractile vacuole apparatus, but figured two globules (macronuclear nodules?) in centre of trunk and a single subterminal contractile vacuole. Possibly a distinct dileptid.

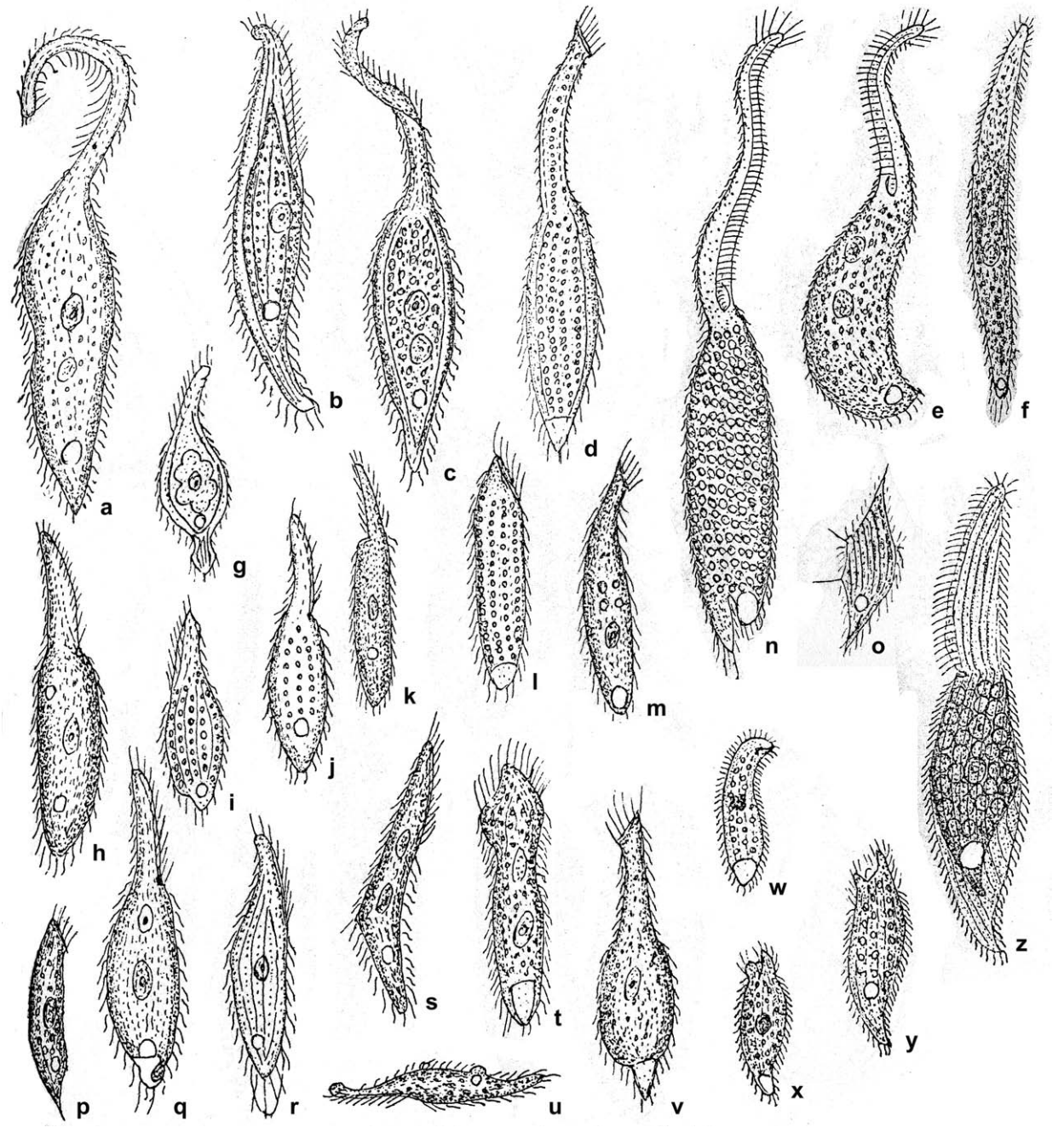
Dileptus cuspidatus Dumas, 1929, Les Microzoaires: 114 (Fig. 147v). Not a dileptid, but a wounded or malformed ciliate. Best considered as indeterminable.

Dileptus cylindricus Fromentel, 1876 – Dumas (1929, Les Microzoaires: 120) (Fig. 146w). See "various authors".

Dileptus cylindroïdes Dumas, 1929, Les Microzoaires: 114 (Fig. 147l). This is a wounded ciliate or a dileptid that supposedly lost the proboscis. Best considered as indeterminable.

Dileptus decorus Dumas, 1929, Les Microzoaires: 111 (Fig. 147g). Length in vivo 60 µm. Nuclear apparatus (food inclusions?) in form of a rosette with six lobes. A single subterminal contractile vacuole. Possibly a pleurostomatid with a large food inclusion. Best considered as indeterminable.

Dileptus diaphanus Dumas, 1929, Les Microzoaires: 110 (Fig. 147j). Length in vivo 110 µm. Body fusiform, leaf-like flattened, and transparent. Proboscis occupies about one third of body length. Nuclear



Figs 147a–z: Insufficiently described and doubtful dileptids in vivo. From DUMAS 1929 (a–v) and DUMAS 1930 (w–z). **a** – *Amphileptus anser*, length 200 µm; **b** – *Dileptus fasciola*, length 165 µm; **c** – *Dileptus folium*, length 190 µm; **d** – *Dileptus resplendens*, length 120 µm; **e** – *Dileptus aduncus*, length 170 µm; **f** – *Dileptus corniculatus*, length 160 µm; **g** – *Dileptus decorus*, length 60 µm; **h** – *Dileptus cinereus*, length 90 µm; **i** – *Dileptus vitreus*, length 55 µm; **j** – *Dileptus diaphanus*, length 110 µm; **k** – *Dileptus calceolus*, length 100 µm; **l** – *Dileptus cylindroïdes*, length 65 µm; **m** – *Dileptus truncatus*, length 72 µm; **n** – *Dileptus bicaudatus*, length 100 µm; **o** – *Dileptus difforme*, length not given; **p** – *Dileptus acutus*, length 55 µm; **q** – *Dileptus cavicaudus*, length 90 µm; **r** – *Dileptus striatus*, length 80 µm; **s** – *Dileptus gonophyllus*, length 80 µm; **t** – *Dileptus helicoïdes*, length 75 µm; **u** – *Dileptus piscis*, length 90 µm; **v** – *Dileptus cuspidatus*, length 80 µm; **w, x** – *Dileptus gulosus*, length 60 µm; **y** – *Dileptus hians*, length 80 µm; **z** – *Dileptus lineatus*, length 200 µm.

apparatus not studied. A single subterminal contractile (defecation?) vacuole. Three rows of hyaline globules in cytoplasm. Too insufficiently described to be recognized as a distinct dileptid. Best considered as indeterminable.

Dileptus difforme Dumas, 1929, Les Microzoaires, Pl. XXXIV, fig. 9 (reproduced here as Fig. 147o). Mentioned only in the figure legend without description or definition, and thus a nomen nudum according to Article 12 of the ICZN (1999).

Dileptus ectromeloïdes Dumas, 1937, Les Microzoaires: 40 (Fig. 148l). Certainly not a dileptid; possibly a poorly observed *Ileonema* or a pleurostomatid ciliate.

Dileptus exiguus Dumas, 1930, Les Microzoaires: 87 (Fig. 148j). Certainly not a dileptid; possibly a *Blepharisma*. Best considered as indeterminable.

Dileptus falciformis Dumas, 1930, Les Microzoaires: 89 (Fig. 148d). Certainly not a dileptid, possibly a wounded ciliate. This is a senior primary homonym of *D. falciformis* Kahl, 1931 which is now, however, associated with the genus *Pseudomonilicaryon*. Thus, according to Article 23.9.5 of the ICZN (1999) Kahl's name must not be replaced.

Dileptus fasciola Ehrg., 1838 – Dumas (1929, Les Microzoaires: 110) (Fig. 147b). See "various authors".

Dileptus fastigiatus Dumas, 1929, Les Microzoaires: 113 (Fig. 146k). Certainly not a dileptid; very likely a pleurostomatid. Best considered as indeterminable.

Dileptus folium Dujardin, 1841 – Dumas (1929, Les Microzoaires: 121) (Fig. 147c). See "various authors".

Dileptus gallina Mueller, 1786 – Dumas (1930, Les Microzoaires: 86) (Fig. 148g). See "various authors".

Dileptus gibbosus Dumas, 1929, Les Microzoaires: 118 (Fig. 146g). Not a dileptid; possibly a poorly observed pleurostomatid. Best considered as indeterminable.

Dileptus gonophyllus Dumas, 1929, Les Microzoaires: 116 (Fig. 147s). Certainly not a dileptid; possibly a wounded ciliate. Best considered as indeterminable.

Dileptus gulosus Dumas, 1930, Les Microzoaires: 88 (Figs 147w, x). Certainly not a dileptid; possibly a wounded ciliate. Best considered as indeterminable.

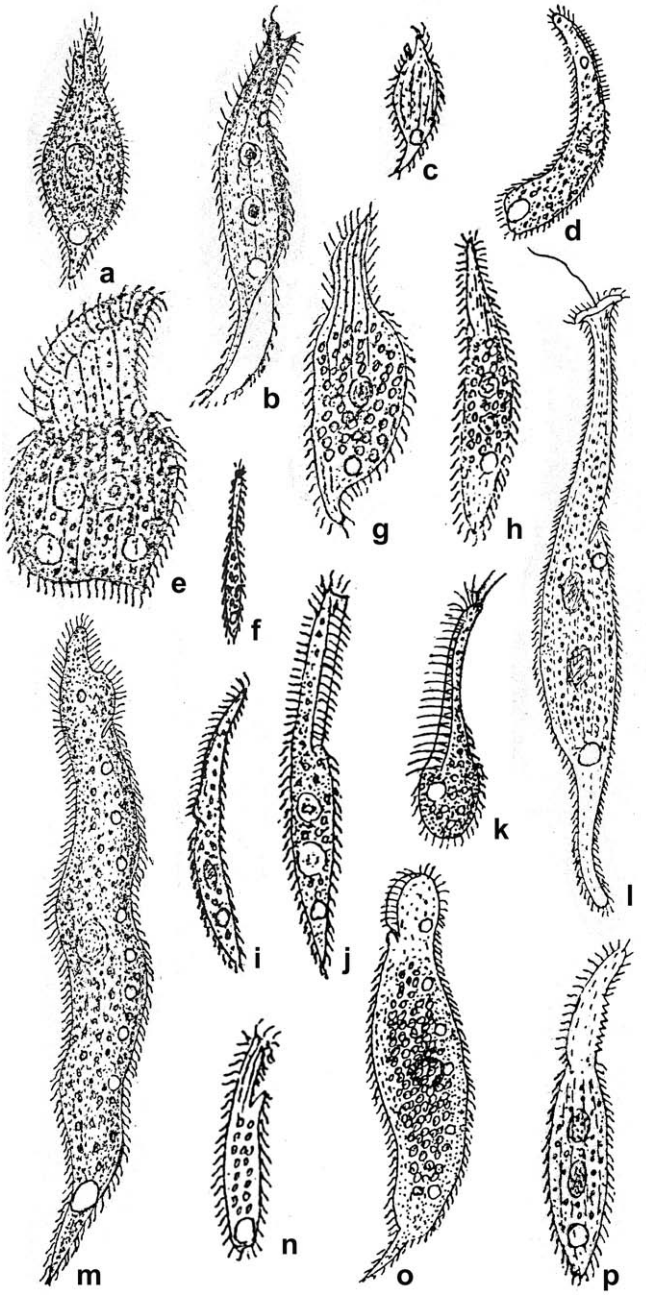
Dileptus helicoïdes Dumas, 1929, Les Microzoaires: 114 (Fig. 147t). Certainly not a dileptid; possibly a wounded or malformed ciliate. Best considered as indeterminable.

Dileptus hians Dumas, 1930, Les Microzoaires: 87 (Figs 147y, 148n). Certainly not a dileptid; possibly a wounded ciliate. Best considered as indeterminable.

Dileptus lacrymarioïdes Dumas, 1929, Les Microzoaires: 111 (Figs 146h, q). The species is referred as *Dileptus lacrymaroïdes* in the figure legend (Pl. XXII, fig. 5). Length in vivo 190 µm; contracts in a similar way as *Lacrymaria*. Shape very narrowly dileptid with proboscis occupying about half of body length; posterior body fifth tail-like, flattened and distinctly striated. Macronucleus (food inclusion?) globular and in centre of trunk. Two ventral contractile vacuoles (a pattern as yet not found in any other dileptid and thus very doubtful, authors). Cortex transversely striated. Possibly a pleurostomatid or a poorly observed *Lacrymaria*.

Dileptus limbatus Dumas, 1929, Les Microzoaires: 111 (Fig. 146r). Not a dileptid; very likely a poorly observed pleurostomatid. Best considered as indeterminable.

Dileptus lineatus Dumas, 1930, Les Microzoaires: 85 (Fig. 147z). Not a dileptid; very likely a



Figs 148a–p: Insufficiently described and doubtful dileptids in vivo. From Dumas 1930 (a, b, d–h, j, k, m–o) and Dumas 1937 (c, i, l, p). **a** – *Diletus cilunculus*, length 82 µm; **b** – *Dileptus crispatus*, length 117 µm; **c** – *Dileptus biacuta*, length 35 µm; **d** – *Dileptus falciformis*, length 80 µm; **e** – *Dileptus meleagris*, length 85 µm; **f** – *Dileptus minimus*, length 40 µm; **g** – *Dileptus gallina*, length 90 µm; **h** – *Dileptus* sp., length not given; **i** – *Dileptus arcuatus*, length 72 µm; **j** – *Dileptus exiguus*, length 95 µm; **k** – *Dileptus pistillaris*, length 70 µm; **l** – *Dileptus ectromeloïdes*, length 205 µm; **m** – *Dileptus subcylindroïdes*, length 220 µm; **n** – *Dileptus hians*, length not given; **o** – *Dileptus musculus*, length 140 µm; **p** – *Dileptus cristatus*, length 85 µm.

pleurostomatid.

Dileptus marginellus Dumas, 1929, Les Microzoaires: 113 (Fig. 146d). Length in vivo 100 µm. Body fusiform, with ribs becoming more visible during contraction. Oral opening at base of proboscis. Globular macronucleus in mid of trunk. A single subterminal contractile vacuole. Very likely not a dileptid; possibly a poorly observed pleurostomatid that lost the anterior body portion. Best considered as indeterminable.

Dileptus meleagris Fromentel, 1876 – Dumas (1930, Les Microzoaires: 85) (Fig. 148e). See "various authors".

Dileptus minimus Dumas, 1930, Les Microzoaires: 86 (Fig. 148f). Mentioned also by Escomel (1929, Faune de Arequipa: 27; without figure). Certainly not a dileptid; possibly a ciliate fragment. Indeterminable.

Dileptus musculus Mueller, 1786 – Dumas (1930, Les Microzoaires: 87) (Fig. 148o). See "various authors".

Dileptus orbicularis Dumas, 1929, Les Microzoaires: 116 (Figs 146a, l). Not a dileptid; possibly a pleurostomatid packed with food.

Dileptus paradoxus Dumas, 1937, Les Microzoaires: 41; without figure. As mentioned in the original description, it is very likely a ciliate fragment. Indeterminable with the data provided.

Dileptus piscis (Mueller, 1773) – Dumas (1929, Les Microzoaires: 119) (Fig. 147u). See "various authors".

Dileptus pistillaris Dumas, 1930, Les Microzoaires: 87 (Fig. 148k). Certainly not a dileptid, but a ciliate fragment. Best considered as indeterminable.

Dileptus reclinis Dumas, 1929, Les Microzoaires: 112 (Fig. 146s). Possibly a small pleurostome. Best considered as indeterminable.

Dileptus resplendens Dumas, 1929, Les Microzoaires: 115 (Fig. 147d). Not a dileptid; possibly a poorly observed *Lacrymaria*. Best considered as indeterminable.

Dileptus sinuosus Dumas, 1929, Les Microzoaires: 112 (Fig. 146o). Not a dileptid; very likely a wounded or malformed pleurostomatid. Best considered as indeterminable.

Dileptus striatus (Mueller, 1786) – Dumas (1929, Les Microzoaires: 110) (Fig. 147r). See "various authors".

Dileptus subcylindroïdes Dumas, 1930, Les Microzoaires: 86 (Fig. 148m). Certainly not a dileptid; possibly a poorly observed *Spirostomum* or *Homalozoon*. Best considered as indeterminable.

Dileptus submarginatus Dumas, 1929, Les Microzoaires: 112 (Fig. 146p). Length in vivo 80 µm. Body narrowly dileptid with proboscis occupying almost half of body length; trunk oblong, rounded posteriorly. Dumas (1929) did not describe nuclear and contractile vacuole apparatus, but illustrated a globule (macronucleus?) in centre of trunk and a single subterminal contractile (defecation?) vacuole on ventral side. Posterior margin of body surrounded by a distinct hyaline lamina. Possibly a pleurostome ciliate too insufficiently described to be recognized as a distinct species. Best considered as indeterminable.

Dileptus torquescens Dumas, 1929, Les Microzoaires: 118 (Fig. 146n). Length in vivo 70 µm. Body fusiform with proboscis occupying about half of body length; posterior end acute. Nuclear apparatus not studied. A single terminal contractile (defecation?) vacuole. Cytoplasm contains bright globules. Too insufficiently described to be recognized as a distinct dileptid. Best considered as indeterminable.

Dileptus truncatus Dumas, 1929, Les Microzoaires: 112 (Fig. 147m). Certainly not a dileptid; possibly a *Spathidium spathula*, as mentioned in the original description. Best considered as indeterminable.

Dileptus vitreus Dumas, 1929, Les Microzoaires: 115 (Fig. 147i). Not a dileptid; very likely a poorly observed pleurostomatid that lost the anterior body portion. Best considered as indeterminable.

Dileptus sp. – Dumas, 1930, Les Microzoaires, Pl. XXVII, fig. 7 (reproduced here as Fig. 148h). Mentioned only in the figure legend. Indeterminable with the data provided.

Acknowledgements

Financial support was provided by the Austrian Science Foundation (FWF, P-19699-B17). The technical assistance of Mag. Gudrun Fuss, Mag. Barbara Harl, Robert Schörghofer, and Andreas Zankl is greatly acknowledged. Special thanks to Dr. Erna Aescht, Dr. William Bourland, and Prof. Dr. Denis Lynn, who reviewed and improved the monograph in many ways. Likewise, the stimulating discussions with Dr. Sabine Agatha and Prof. Dr. Helmut Berger improved the manuscript. Furthermore, we greatly acknowledge Prof. Dr. Slava Epstein and Dr. William Orsi for help with the molecular investigations.

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With few exceptions, titles of journals are given in accordance with the abbreviations found in the 4th edition of the "World List of Scientific Periodicals", published by Butterworths, London, 1963–1965. Also practically without exceptions, all works cited here have been examined first-hand in order that dates, titles, names of journals or books, and complete pagination could be given with accuracy. No attempts were made to correct title mistakes, even if obvious. Several papers are from journals or books difficult to obtain and to reference. We did our best to cite them in a way that experienced librarians can locate them. The dating of Ehrenberg's works follows Corliss (1979).

Russian references are cited as follows: Author's name in Latin alphabet, using the author's own

transliteration, repeated in square brackets in ISO 9:1995 transliteration; date; title of the paper in ISO 9:1995 transliteration, followed by English title translation in square brackets; title of the journal in ISO 9:1995 transliteration; and "(in Russian)". The International Standard ISO 9:1995 is a univocal system of one character for one character equivalents for Cyrillic and Latin alphabets not requiring any knowledge of Russian language.

Some authors have used (unfortunately) several spellings of their names. For the sake of simplicity, we arbitrarily have chosen one of the spellings and used it throughout the text. This problem mainly concerns the following authors: Agamaliev F. G. (Agamaliyev F. G.), Alekperov I. K. (Alekperov I. H.), Aliev R. A. (Aliyev R. A.), Augustin H. (Augustin J.), Bereczky M. Cs. (Bereczky M.), Detcheva R. B. (Decheva R., Detcheva R., Detscheva R. B., Detschewa), Dragesco-Kernéis A. (Dragesco-Kerneis A.), Fernández-Leborans G. (Fernandez-Leborans G.), Gajewskaja N. (Gajevskaja N.), Gelei J. (Gelei J. v.), Golińska K. (Golinska K.), Grolière C.-A. (Groliere C.-A.), Jankowski A. W. (Jankowski A. V., Jankovskij A. V., Yankovskii A. V., Yankovskij A. V.), Jones E. E. Jr. (Jones E. E.), Lepşi I. (Lepsi I., Lepsi J.), Liepa R. A. (Liepa R., Liyepa R. A.), Mamaeva N. V. (Mamayeva N. V.), Njiné T. (Njine T.), Orlovskaja E. E. (Orlovskaya E. E.).

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*The monograph is part of a doctoral thesis performed at the University of Salzburg, Austria, and has been supported by the Austrian Science Fund (FWF).

Systematic Index

The index contains all names of dileptid ciliates and their food organisms as well as names of other ciliates and organisms mentioned in the monograph. The index is two-sided, that is, species appear both with the generic name ahead (for example, *Dileptus margaritifer*) and with the species name first (*margaritifer*, *Dileptus*). Valid names (in our judgment) of dileptid subspecies, species, and genera are in ***boldface italics***. Acceptable suprageneric names of dileptids are in **b o l d f a c e s p a c e d t y p e**. Invalid names (junior homonyms, synonyms, outdated combinations or misspellings) of dileptids are given in parentheses. All non-dileptid names are in ordinary font, i.e., in *italics* and without parentheses. **Boldface page number** indicates the location of the main description of a taxon.

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Table 3 continued from page 33.

Characteristics	Stage[a]	Mean	M	SD	SE	CV	Min	Max	n
Proter, oral opening to proter end, distance	Very early divider	80.7	78.0	10.6	2.3	13.1	69.0	106.0	21
	Early divider	78.8	84.0	11.6	2.5	14.7	55.0	94.0	21
	Mid-divider	77.2	75.0	9.9	2.2	12.8	67.0	98.0	21
	Late divider	85.1	88.0	13.9	5.7	16.3	61.0	100.0	6
	Very late divider	85.8	87.0	–	–	–	68.0	101.0	4
Proboscis, % of proter length	Very early divider	54.6	54.3	3.7	0.8	6.8	47.4	60.6	21
	Early divider	56.4	55.0	3.8	0.8	6.8	50.7	64.1	21
	Mid-divider	54.4	55.1	4.6	1.0	8.4	39.5	62.5	21
	Late divider	49.0	48.6	5.3	2.2	10.9	42.4	57.0	6
	Very late divider	50.9	50.8	–	–	–	47.7	54.2	4
Opisthe, length	Very early divider	133.1	134.0	13.5	2.9	10.1	110.0	152.0	21
	Early divider	142.2	141.0	16.4	3.5	11.6	110.0	171.0	22
	Mid-divider	134.0	135.0	12.3	2.7	9.2	102.0	150.0	21
	Late divider	135.7	140.0	9.1	3.7	6.7	121.0	144.0	6
	Very late divider	147.4	146.0	–	–	–	137.0	162.0	4
Opisthe, width	Very early divider	46.1	46.0	4.3	0.9	9.4	38.0	59.0	21
	Early divider	45.3	46.0	4.9	1.0	10.8	34.0	58.0	22
	Mid-divider	50.3	51.0	7.4	1.6	14.7	34.0	69.0	21
	Late divider	47.0	47.0	3.2	1.3	6.7	42.0	52.0	6
	Very late divider	53.1	54.0	–	–	–	42.0	63.0	4
Opisthe length:width, ratio	Very early divider	2.9	2.9	0.4	0.1	15.3	2.0	3.5	21
	Early divider	3.2	3.3	0.6	0.1	17.7	2.1	4.3	22
	Mid-divider	2.7	2.7	0.6	0.1	20.5	2.0	4.2	21
	Late divider	2.9	2.9	0.3	0.1	9.5	2.6	3.3	6
	Very late divider	2.8	2.9	–	–	–	2.3	3.3	4
Proter:opisthe length, ratio	Very early divider	1.3	1.3	0.1	0.0	8.3	1.2	1.6	21
	Early divider	1.3	1.3	0.1	0.0	9.4	1.1	1.5	21
	Mid-divider	1.3	1.3	0.1	0.0	10.4	1.1	1.6	21
	Late divider	1.2	1.2	0.1	0.0	9.8	1.0	1.4	6
	Very late divider	1.2	1.2	–	–	–	1.1	1.3	4
Macronucleus, total length	Morphostatic	81.5	80.0	17.1	3.7	21.0	62.0	128.0	21
	Very early divider	84.2	86.0	12.3	2.7	14.7	59.0	105.0	21
	Early divider	99.7	93.0	16.3	3.5	16.3	78.0	146.0	22
	Mid-divider	47.8	47.0	9.2	2.0	19.3	31.0	64.0	21
	Late divider	103.5	101.0	10.6	4.3	10.3	93.0	120.0	6
	Very late divider	100.4	100.0	–	–	–	87.0	116.0	4
	Proter post-divider	82.3	82.0	19.3	4.2	23.5	43.0	121.0	21
	Opisthe post-divider	70.8	65.0	26.7	5.8	37.7	30.0	124.0	21
Micronucleus, largest diameter	Morphostatic	3.6	4.0	–	–	–	3.0	4.0	14
	Very early divider	4.4	4.0	0.8	0.3	19.0	3.0	6.0	9
	Early divider	6.1	6.0	1.0	0.3	16.4	4.0	7.0	12
	Mid-divider	6.3	6.0	1.6	0.6	25.4	5.0	10.0	8
	Late divider	4.0	4.0	0.0	0.0	0.0	4.0	4.0	4
	Very late divider	4.0	4.0	–	–	–	4.0	4.0	3
	Proter post-divider	4.0	4.0	0.5	0.2	12.5	3.0	5.0	9
	Opisthe post-divider	3.9	4.0	0.9	0.3	22.3	3.0	6.0	12
Ciliary rows, number	Morphostatic	26.9	27.0	2.0	0.4	7.4	24.0	31.0	21
Preoral kineties, number	Morphostatic	47.1	46.0	5.1	1.1	10.9	41.0	58.0	21
Dorsal brush dikinetids, total number	Morphostatic	55.3	56.0	6.6	1.4	12.0	43.0	69.0	21