

Redescription of the tintinnid ciliate *Tintinnopsis fimbriata* MEUNIER, 1919 (Spirotricha, Choreotrichida) from coastal waters of Northern Germany*

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Abstract: The tintinnid ciliate *Tintinnopsis fimbriata* MEUNIER, 1919 is mainly distributed in mesohaline coastal waters of Arctic, temperate, and subtropical regions. Since its cytological features were unknown, the species is redescribed and neotypified from material collected in coastal waters of the North Sea near the Island of Sylt (Northern Germany), using live observation and protargol impregnation. The species diagnosis is improved to include the new characteristics, e.g., the somatic ciliary pattern comprising a ventral, dorsal, and posterior kinety as well as a right, left, and lateral ciliary field. Due to the complex somatic ciliary pattern, *T. fimbriata* belongs to a diverse group of highly developed tintinnids with which it shares the hypoapokinetal development of the oral primordium posterior to the lateral ciliary field.

Key words: Biogeography, ciliary pattern, morphology, neotypification, ontogenesis, taxonomy, Tintinnina.

Introduction

The genus *Tintinnopsis* STEIN, 1867 comprises about 190 species, which were often established, using minute differences in the lorica shape, size, and structure (e.g., KOFOID & CAMPBELL 1929, 1939). However, the tintinnid loricae are polymorphic due to environmental factors and the life cycle (BIERNACKA 1965, 1968; GOLD & MORALES 1974, 1975; BAKKER & PHAFF 1976; DAVIS 1978, 1981; BERNATZKY et al. 1981; LAVAL-PEUTO 1981; LAVAL-PEUTO & BROWNLEE 1986; BOLTOVSKOY et al. 1990). Therefore, DADAY (1887), BRANDT (1907), ENTZ (1909), and HOFKER (1931) emphasized the significance of cytological features for a natural tintinnid taxonomy and classification. Although silver impregnation techniques are widely used in ciliate taxonomy to study the ciliary pattern and the nuclear apparatus, merely 18 tintinnid species were redescribed after application of such methods (FOISSNER & WILBERT 1979; SONG & WILBERT 1989; BLATTERER & FOISSNER 1990; FOISSNER & O'DONOGHUE 1990; SNIEZEK et al. 1991; SNYDER & BROWNLEE 1991; CHOI et al. 1992; WASIK & MIKOŁAJCZYK 1994; PETZ et al. 1995; FOISSNER et al. 1999; AGATHA & RIEDEL-LORJÉ 2006; CAI et al. 2006; AGATHA 2007; AGATHA & TSAI 2008). Hence, a fur-

ther species, viz., *Tintinnopsis fimbriata* MEUNIER, 1919, is redescribed in the present paper.

Materials and methods

Collection: The samples were collected by bucket at high tide from the entrance to List Harbour on the Island of Sylt, North Sea, between September and December 1995. The salinity was about 31 ‰ and the water temperature about 9 °C. All observations are from field material as attempts to culture the species failed, using a temperature of about 12 °C, a cycle of 12 h light to 12 h dark with an irradiance of about 10 $\mu\text{E}/(\text{m}^2\cdot\text{s})$, and a mixture of flagellates from the sampling site as prey.

Morphological investigations: Cell movement was studied in a Petri dish (about 6 cm across; water depth about 2.5 cm) under a dissecting microscope at about 20 °C. Cell morphology was investigated under a compound microscope equipped with a high-power oil immersion objective as well as bright-field and interference contrast optics. Protargol impregnation followed the protocol of SONG & WILBERT (1995). Counts and measurements on protargol-impregnated cells were performed at $\times 1000$; in vivo measurements were made at $\times 40$ – 1000 . The kinetal density index is the ratio of kinety number to cell circumference posterior to the membranellar zone (kineties/ μm) in protargol-impregnated cells (SNYDER & BROWNLEE 1991). Usually, it was

* In occasion of his sixtieth birthday, I dedicate this article to Prof. Dr. Wilhelm (Willi) FOISSNER in acknowledgement of his contribution to protist taxonomy and systematics and as small token of appreciation for his support.

impossible to count all somatic kineties in a specimen as the curved and densely spaced ciliary rows could not be discerned in the laterally orientated fields; hence, the kinetal density index was not calculated.

Drawing of live specimen summarizes information and is based on mean measurements, while those of protargol-impregnated specimens were made with a drawing device. The kinetal map depicts the ciliary pattern of a protargol-impregnated morphostatic specimen in two dimensions (FOISSNER & WILBERT 1979; CHOI et al. 1992), that is, the cortex is drawn as cut longitudinally along the dorsal kinety; it is also based on mean measurements. Horizontal bars symbolize the collar membranelles, diagonal bars those membranelles that are partially or entirely in the buccal cavity, namely, the elongated collar membranelles and the buccal membranelle. Cell circumference is proportional to length of kineties. Kinetids are equidistantly arranged in the ciliary rows, and the kinety curvature is neglected, except for the ventral and last kinety, whose course might be of taxonomic significance. The somatic cilia are symbolized by perpendicular lines, differences in their length are not considered.

Terminology follows AGATHA & RIEDEL-LORJÉ (2006).

Neotype material: Slides with protargol-impregnated material, including the neotype, further specimens, and the illustrated divider, are deposited with the relevant cells marked in the Biology Centre of the Museum of Upper Austria (LI) in A-4040 Linz (Austria). The specimens are not from the original type locality, but from coastal waters of the North Sea near the Island of Sylt (Northern Germany). Nevertheless, a neotype is provided to ensure stability in tintinnid taxonomy as (i) no type material is available, (ii) the original description lacks many morphologic and morphometric features, and (iii) the species has several proposed subjective synonyms. For a detailed discussion of neotypification in ciliates, see FOISSNER (2002), FOISSNER et al. (2002), and CORLISS (2003).

Results

Tintinnopsis fimbriata MEUNIER, 1919

- 1894 *Codonella ventricosa* CLAP. & LACH. – LEVANDER, Acta Soc. Fauna Flora fenn. **12**: 91. [misidentification]
- 1906 *Tintinnopsis* spec. – BRANDT, Ergebn. Plankton-Exped. Humboldt-Stiftung **3** La: Plate 17, Fig. 5, 7, Plate 18, Fig. 10 (figures and figure explanations).
- 1907 *Tintinnopsis* spec. – BRANDT, Ergebn. Plankton-Exped. Humboldt-Stiftung **3** La: 180 (description).
- 1919 *Tintinnopsis fimbriata* sp. nov. – MEUNIER, Mém. Mus. r. Hist. nat. Belg. **8**: 31.
- 1929 *Tintinnopsis meunieri* nom. nov. – KOFOID & CAMPBELL, Univ. Calif. Publs Zool. **34**: 40 (not a replacement name but a new species).
- 1931 *Tintinnopsis fimbriata* MEUNIER – HOFKER, Arch. Protistenk. **75**: 321.
- 1948 *Codonaria fimbriata* (MEUNIER) nov. comb. – BALECH, Comun. Mus. argent. Cienc. nat. “Bernardino Rivadavia” (Zool.) **7**: 15 (incorrect generic affiliation).
- 1961 *Stenosemella fimbriata* – SCHULZ, Arch. Hydrobiol. Suppl. **26**: 84 (incorrect generic affiliation).
- 1998 *Tintinnopsis fimbriata* MEUNIER, 1919 – AGATHA, J. Euk. Microbiol. **45**: 9A (description of somatic ciliary pattern).
- 2005 *Tintinnopsis baltica* – VERWEIJ, ESSELINK, FOCKENS & KOEMAN, Biomonitoring van microzoöplankton in de Nederlandse zoute wateren **2004**: 31. (new synonym).

Taxonomy and nomenclature: Although *Tintinnopsis* spec. described by BRANDT (1906, 1907) strongly resembles *Tintinnopsis fimbriata* MEUNIER, 1919, KOFOID & CAMPBELL (1929) established the species *T. meunieri* for BRANDT’s specimens. Accordingly, HOFKER (1931), BALECH (1948), as well as BAKKER & PHAFF (1976) synonymized *T. meunieri* with *T. fimbriata*. Additionally, BALECH (1948) assigned *T. fimbriata* to the genus *Codonaria* KOFOID & CAMPBELL, 1939; however, this transfer was not justified as the species lacks the genus-specific cylindrical lorica cone projecting beyond the obconical collar.

Type locality: The species was discovered in the Bight of Nieuwendamme at the North Sea coast of Belgium. The neotype is from the pelagial off the Island of Sylt at the German North Sea coast (55°00’59”N, 08°26’28”E).

Remarks: The diagnosis of *Tintinnopsis fimbriata* is improved as the previous one by MEUNIER (1919) does not include cell features.

Improved diagnosis (based on data from the type and neotype population): Lorica on average 65–70 µm long, stout campanulate, consisting of (i) an obconical collar about 10 µm high and 45–50 µm wide anteriorly and (ii) a globular bowl about 40–50 µm wide merging into a pointed posterior end or a cylindroidal posterior process 12–14 × 5–7 µm in size; densely agglomerated. Extended cell on average in vivo 55–65 × 20–30 µm, elongate obconical, and highly contractile. Two macronuclear nodules and two micronuclei. Ventral kinety commences anterior to first or second kinety of right ciliary field. On average six kineties in right and five in left ciliary field, all composed of monokinetids and one anterior dikinetid, except for second kinety with two or three anterior dikinetids. Lateral ciliary field comprises about 12 monokinetidal kineties. About 17 dikinetids in dorsal kinety and eight in posterior kinety, with a cilium only at each posterior basal body. On average 17 collar membranelles of which four extend into buccal cavity; one buccal membranelle.

Description of Sylt specimens: Lorica 48–74 µm long after protargol impregnation; stout campanulate, i.e., composed of an obconical collar separated by a constriction from a globular bowl (36–50 µm wide) merging at an angle of 75–110° into a posterior process (Fig. 1a, g, 2a–f, 3a–j). Collar highly variable in length, viz., 6–20 µm long, with irregular rim 38–56 µm across. Constriction between collar and bowl usually more distinct in optical section of lorica than in surface view due to projecting agglomerated particles; inner diameter 15–31 µm. Posterior process cylindroidal, apparently hollow, with usually obliquely truncate open end, about 7 µm wide, but highly variable in length (8–18 µm long) possibly because it easily breaks off (Tab. 1). Incrustation very dense, matrix and live cell thus invisible, comprises particles of abiotic (silt grains about 5 µm across, seldom up to 20 µm across) and, rarely, biotic (diatom frustules and their fragments) origin; spiralled or annulated structures not recognizable.

Fully extended cells in vivo 35–65 × 10–25 µm; elongate obconical, i.e., cell proper gradually merges ventrally into slender, wrinkled, and highly contractile stalk up to 20 µm long, attached to bottom of bowl (Fig. 3i, j). Disturbed or preserved cells contracted by about 38 % and broadly ellipsoidal (Fig. 1h, i, 3a–h; Tab. 1). Macronuclear nodules usually in posterior three quarters of cell proper, each associated with a globular, usually faintly impregnated micronucleus; anterior nodule ellipsoidal, posterior nodule broadly ellipsoidal (Fig. 1h, k, 3a–j). Nucleoli globular to ellipsoidal, 1–2 µm across. Contractile vacuole and cytophyge not recognizable due to agglomerated lorica. Myonemes rarely and faintly impregnated. Accessory combs, striae, and tentaculoids

not recognizable, but argyrophilic granules about 0.5 µm across (probably capsules) on collar membranelles and in intermembranellar ridges. Cytoplasm colourless, finely granulated, contains food vacuoles with coccal organisms of various taxa (3–8 µm across) as well as pennate (11–12 × 3 µm) and centric diatoms (4–7 µm across). Swims by rotation about main cell axis, twitches back on obstacles. Disturbed specimens retract quickly into lorica, with motionless membranelles bent to centre of peristomial field; lorica abandonment never observed. When disturbance stops, specimens slowly extend and spread the collar membranelles almost perpendicularly to main cell axis.

Somatic ciliary pattern of most complex type (AGATHA & STRÜDER-KYPKE 2007), i.e., comprises a ventral, dorsal, and posterior kinety as well as a right, left, and lateral ciliary field (Fig. 1h, i, 2g). Length of kineties and number of kinetids usually highly variable possibly due to basal body proliferation or resorption in late dividers and/or postdividers. Kinetids of each ciliary row connected by an argyrophilic fibre. Ventral kinety commences about 1 µm posterior to collar membranelles and anterior to first or second kinety of right ciliary field, curves slightly leftwards and extends more or less parallel to kineties of lateral ciliary field, but terminates somewhat posteriorly; composed of monokinetids densely spaced in anterior portion, but more widely spaced in posterior (Fig. 1h, 2g); cilia about 3 µm long after impregnation. Kineties of right ciliary field commence about 2 µm posterior to collar membranelles, increase in length from left to right, composed of monokinetids and one anterior dikinetid, except for first kinety starting with two or three dikinetids about 1 µm posterior to remaining kineties and terminating about 9 µm posterior to collar membranelles (Fig. 1h, 2g). Cilia of right ciliary field about 3 µm long after impregnation, except for anterior cilium of dikinetids (soies; FAURÉ-FREMIET 1924) measuring 15–20 µm (Fig. 1a). Dikinetidal dorsal kinety commences about 2 µm posterior to collar membranelles and about 4–6 µm apart from left and right ciliary field, extends in leftwards curvature to posterior end of cell proper and posterior kinety, accompanied by argyrophilic granules (Fig. 1i, 2g). Cilia of dorsal kinety associated only with each posterior dikinetidal basal body, about 7 µm long after impregnation. Kineties of left ciliary field commence about 2 µm posterior to collar membranelles, increase in length from right to left, composed of monokinetids and one anterior dikinetid (Fig. 1i, 2g, 3j); last kineties difficult to separate from those of lateral ciliary field when peristomial rim hides structure and position of anterior kinetid. Cilia of left ciliary field about 3 µm long after impregnation, except for anterior cilium of dikinetids

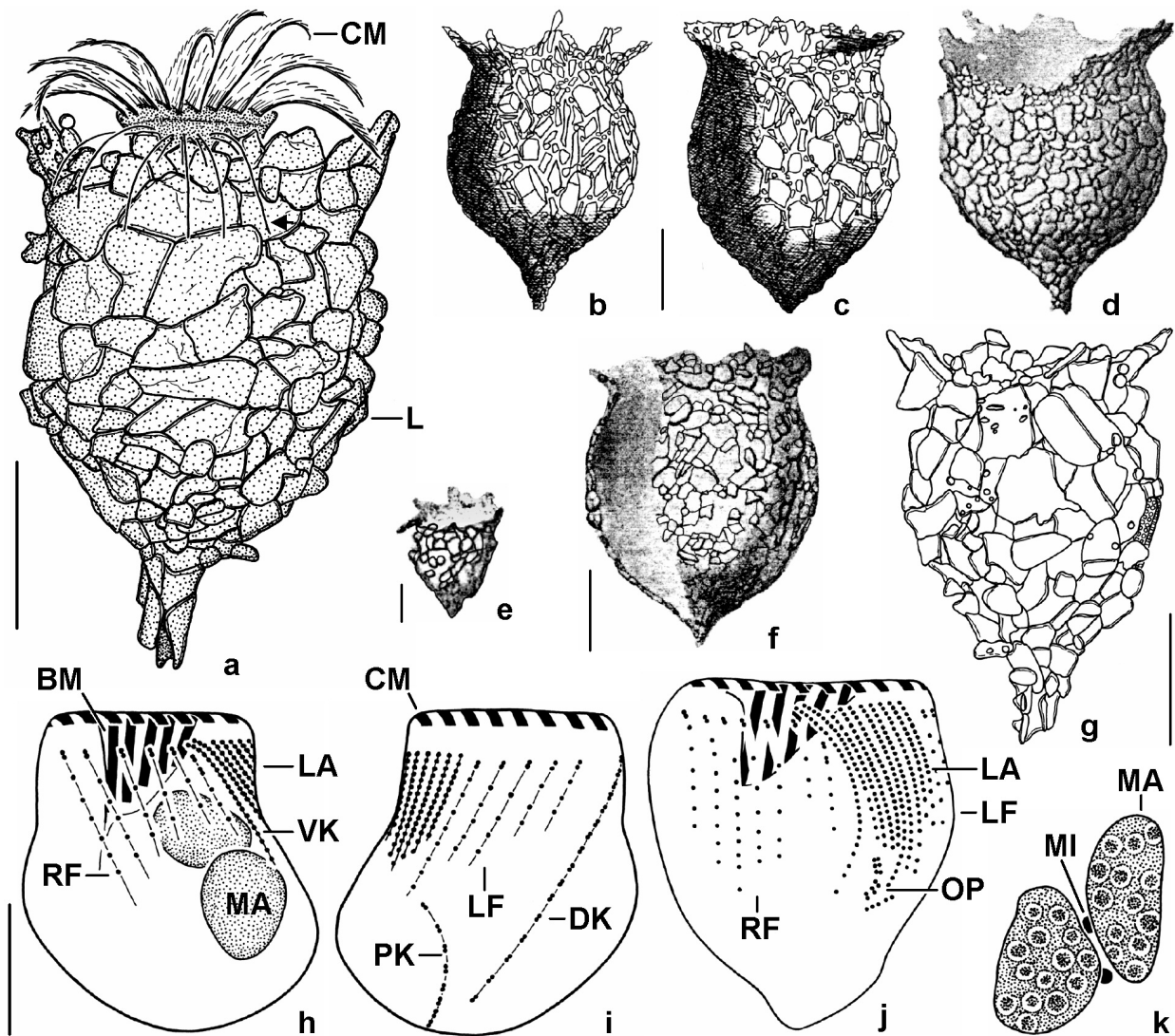


Fig. 1a-k: *Tintinnopsis fimbriata* from life (a), after preservation (b-f), and after protargol impregnation (g-k). **a:** Lateral view of a representative specimen from the neotype population collected at the German North Sea coast. Arrow marks elongated cilia of the anterior dikinetids in the right ciliary field. **b, c:** Loricae from the type population (from MEUNIER 1919). **d-f:** Loricae of the synonymous species *Tintinnopsis meunieri* KOFOID & CAMPBELL, 1929 (from BRANDT 1906). **g-i:** Lateral view of a lorica as well as a ventrolateral and dorsolateral view of its owner. **j, k:** Ventral view of a very early divider and its nuclear apparatus. BM – buccal membranelles; CM – collar membranelles; DK – dorsal kinety; L – agglomerated lorica; LA – lateral ciliary field; LF – left ciliary field; MA – macronuclear nodules; MI – micronuclei; OP – oral primordium; PK – posterior kinety; RF – right ciliary field; VK – ventral kinety. Scale bars 20 µm (a-g) and 10 µm (h-k).

(soies; FAURÉ-FREMIET 1924) measuring 15–20 µm. Kineties of lateral ciliary field commence about 1 µm posterior to collar membranelles (i.e., about 1 µm anterior to left and right ciliary field), densely spaced and clockwise inclined, composed of densely spaced monokinetids, 4–17 µm long (Fig. 1h, i, 2g); cilia about 3 µm long after impregnation. Dikinetidal posterior kinety commences about 4 µm posterior to third, occasionally fourth kinety of left ciliary field and extends almost longitudinally to posterior end of cell proper, accompanied by argyrophilic granules (Fig. 1i, 2g, 3j); cilia associated only with each posterior dikinetidal basal body, about 6 µm long after impregnation.

Adoral zone of membranelles closed and horizontally orientated (Fig. 1a, h, i, 2g). Collar membranelles up to 15–20 µm long, with cilia increasing in length from inner to outer end of membranelles. Bases (polykinetids) of collar membranelles extend obliquely across peristomial rim, separated by shallow ridges 1–2 µm wide, structure not recognizable; four bases successively elongated, terminating 1–6 µm posterior to apical cell end in buccal cavity (Fig. 1h, 2g, 3b). Single buccal membranelle, with base about 7 µm long, structure not recognizable. Several argyrophilic fibres associated with oral apparatus: (i) a horizontally orientated circular fibre underneath the membranelar zone; (ii) two fibres

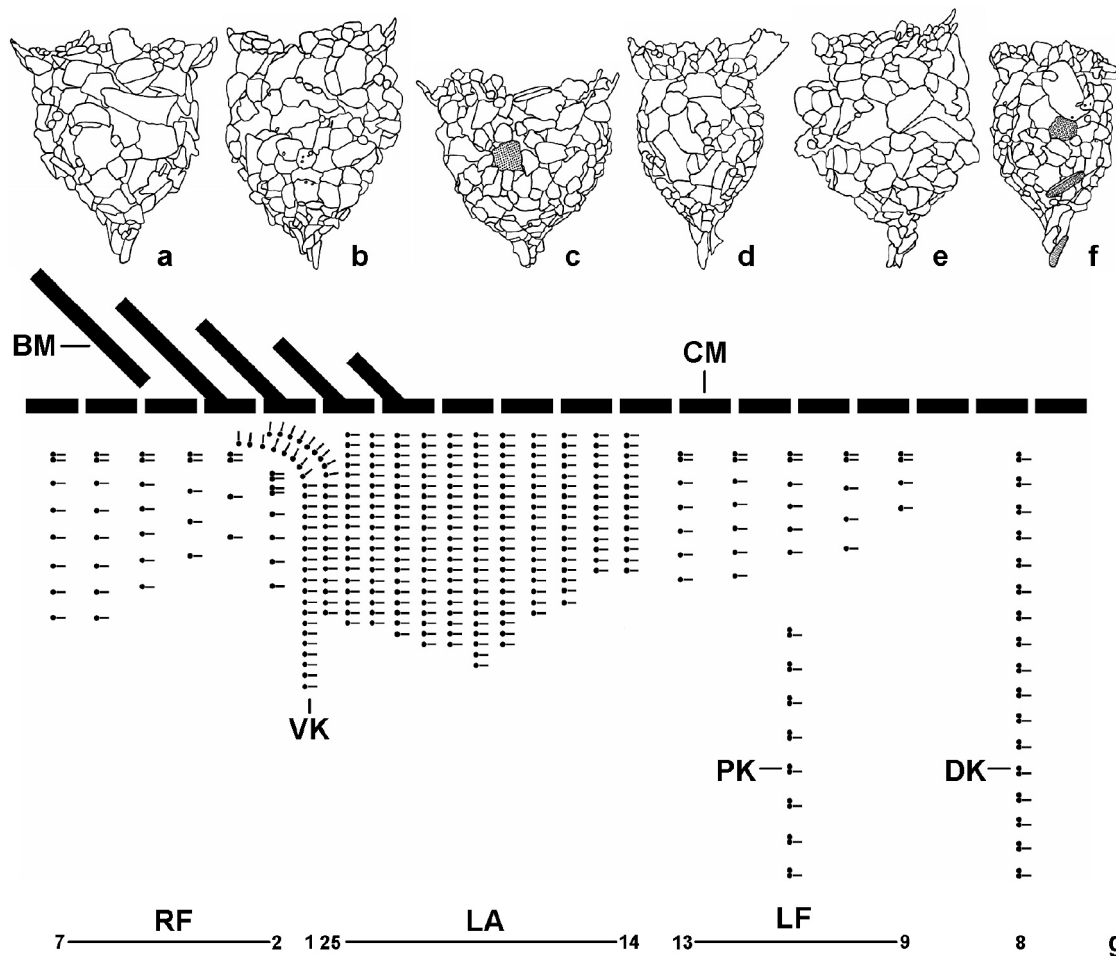


Fig. 2a–g: *Tintinnopsis fimbriata* after protargol impregnation. **a–f:** Lateral view of loricae showing variability of shape and size. Note that the constriction between collar and bowl is often less distinct in these surface views than in optical sections of the loricae (cp. Fig. 3a–j). **g:** Kinetal map of a morphostatic specimen. The numbering of the somatic kineties commences with the ventral kinety and continues in clockwise direction (top view). BM – buccal membranelles; CM – collar membranelles; DK – dorsal kinety; LA – lateral ciliary field; LF – left ciliary field; PK – posterior kinety; RF – right ciliary field; VK – ventral kinety. Scale bar 20 μm .

extending from each collar membranelle rightwards and leftwards and merging into the circular fibre; (iii) a longitudinal fibre extending from dorsal portion of circular fibre to posterior end of cell proper; and (iv) five longitudinal fibres extending from proximal end of elongated collar membranelles and buccal membranelle to posterior end of cell proper. Endoral membrane extends across peristomial field and right wall of buccal cavity, composed of a single row of basal bodies, probably with monostichomonad structure. Pharyngeal fibres about 13 μm long after protargol impregnation, rarely recognizable.

Enantiotropic division with hypoapokinetal formation of oral primordium left of ventral kinety and posterior to lateral ciliary field (Fig. 1j, k). Each macronuclear nodule has a replication band. Lorica formation neither observed in live nor in preserved specimens.

Discussion

Comparison with original description: Since the cell features of the type population described by MEUNIER (1919) are unknown, species identification is based on lorica morphology only. The loricae of the Sylt spec-

imens match the dimensions estimated from the original illustrations very well (Fig. 1b, c; lorica length: 48–74 μm vs. 68–75 μm ; bowl width: 36–50 μm vs. 50–52 μm ; diameter of anterior opening: 38–56 μm vs. 52–54 μm ; constriction: 15–31 μm inner diameter vs. 38–42 μm outer diameter), and their shape is similar to at least one illustration (Fig. 1b) provided by MEUNIER (1919) showing a lorica with a distinct posterior process. Hence, the Sylt population is regarded as conspecific with *Tintinnopsis fimbriata* MEUNIER, 1919, although it is from marine and not from brackish waters.

Comparison with further populations: The posterior lorica process is open and rather pronounced in the Sylt specimens. Loricae with a similar-shaped and similar-sized (7–20 μm vs. 8–18 μm), but apparently closed process were described by BRANDT (1906, 1907; Fig. 1d), HOFKER (1931), BALECH (1948), BIERNACKA (1948), BAKKER & PHAFF (1976), and VERWEIJ et al. (2005). All other populations possess exclusively loricae with a pointed end, like the specimens genetically analyzed by STRÜDER-KYPKE & LYNN (2003). The loricae of the Sylt specimens fall into the size range of most populations: lorica length 47–90 μm , bowl width 41–68 μm , and opening diameter 30–68 μm (LEVANDER 1894;

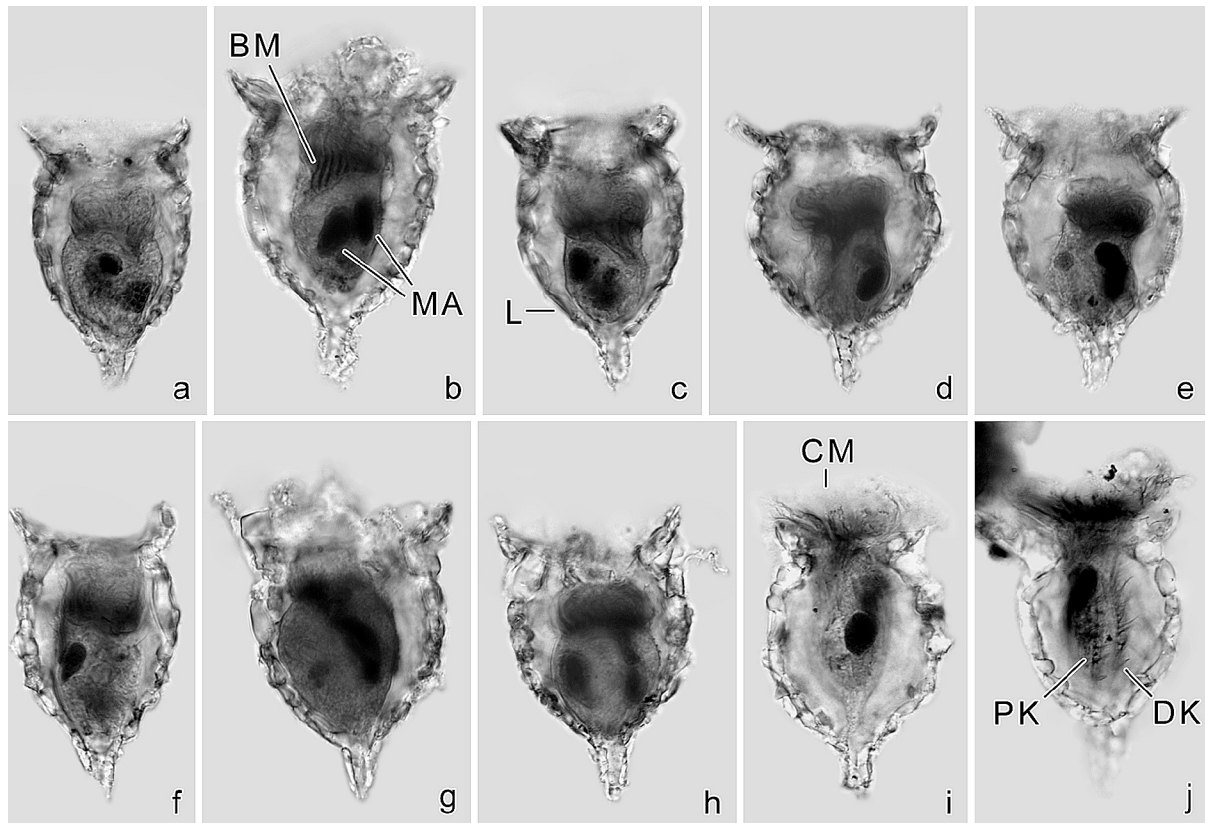


Fig. 3a–j: *Tintinnopsis fimbriata* after protargol impregnation showing the variability of lorica shape and size. Note that the posterior process is apparently hollow and has an open end. BM – buccal membranelles; CM – collar membranelles; DK – dorsal kinety; L – agglomerated lorica; MA – macronuclear nodules; PK – posterior kinety.

BRANDT 1906; HOFKER 1922, 1931; KOFOID & CAMPBELL 1929; BALECH 1948; BIERNACKA 1948, 1956, 1968; SCHULZ 1964; MOROZOVSKAYA & POLISHCHUK 1969; BAKKER & PHAFF 1976; PAULMIER 1995; VERWEIJ et al. 2005). Likewise, the inner constriction diameter of the Sylt loricae roughly corresponds to the outer constriction diameter (15–31 μm vs. 45–58 μm) measured in the other populations, while the lorica collar is usually longer (6–20 μm vs. 6–10 μm ; BALECH 1948; PAULMIER 1995). According to BAKKER & PHAFF (1976), the average lorica dimensions decrease with increasing water temperature. Additionally, HOFKER (1931) and BIERNACKA (1952, 1968) observed a positive correlation between lorica length and salinity. However, culture studies and/or gene sequence analyses are required to prove the conspecificity of the exceptionally large specimens from the White Sea (length: 80–150 μm ; bowl width: 70–100 μm ; anterior collar diameter: 70–100 μm ; BURKOVSKY et al. 1974) and the extraordinarily small specimens from Antarctic waters (length: 27 μm ; anterior collar diameter: 25 μm ; HADA 1970).

The features of cells collected in the brackish waters of the IJsselmeer (HOFKER 1931) and the Baltic Sea (BIERNACKA 1952), viz., an adoral zone composed of 18 membranelles and a nuclear apparatus with two

macronuclei and two micronuclei, match those of the Sylt specimens; however, a contractile vacuole in the posterior cell half was not found in the marine specimens collected near the Island of Sylt.

Comparison with similar species: The present results and literature data are insufficient to estimate the entire polymorphism of *Tintinnopsis fimbriata*. Accordingly, any synonymization is premature, especially, as the cytological features of most congeners are unknown. Nevertheless, *T. acuta* MEUNIER, 1910 was synonymized by KOFOID & CAMPBELL (1929), and HOFKER (1931) even added *T. denticulata* KOFOID & CAMPBELL, 1929 and *T. baltica* BRANDT, 1896. Further species with a similar lorica shape are *T. amoyensis* (length: 45–50 μm ; opening diameter: 25–27 μm ; NIE 1934), *T. brevicollis* (length: 63–95 μm ; bowl width: 55–66 μm ; opening diameter: 53–65 μm ; broadly rounded posterior end without process; rim continuous; HADA 1937), *T. meunieri* forma *minima* (length: 35–45 μm ; width: 30–32 μm ; without collar; GAJEWSKAJA 1933), *T. schotti* (length: 100–110 μm ; bowl width: 70–80 μm ; opening diameter: 90–100 μm ; BRANDT 1906, 1907), *T. tentaculata* (length: 52–63 μm ; width: 35–40 μm ; rim with five or six finger-like processes; NIE & CH'ENG 1947), *T. uruguayensis* (length: 54–63 μm ; bowl width: 23–26 μm ; opening diameter:

Table 1: Morphometric data on *Tintinnopsis fimbriata*.

Characteristics ^a	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Lorica, total length	65.0	64.0	5.6	1.2	8.6	48.0	74.0	21
Lorica, collar length	12.4	13.0	3.0	0.7	24.1	6.0	20.0	21
Lorica, anterior collar diameter	46.3	46.0	5.8	1.3	12.6	38.0	56.0	21
Lorica, inner constriction diameter	24.0	25.0	4.3	0.9	18.0	15.0	31.0	21
Lorica, bowl length	40.5	40.0	5.2	1.1	13.0	24.0	48.0	21
Lorica, bowl width	43.1	43.0	4.4	1.0	10.2	36.0	50.0	21
Lorica, length of bowl plus collar	53.0	53.0	5.9	1.3	11.1	34.0	62.0	21
Lorica, posterior process length	12.0	11.0	2.5	0.5	20.7	8.0	18.0	21
Lorica, posterior process width	7.3	8.0	1.0	0.2	13.1	5.0	8.0	21
Lorica length:anterior collar diameter, ratio	1.5	1.5	0.1	0.0	8.6	1.3	1.8	21
Cell proper, length	31.4	29.0	5.4	1.2	17.3	24.0	40.0	21
Cell proper, width	20.1	20.0	3.4	0.7	16.7	15.0	28.0	21
Cell proper, length:width ratio	1.6	1.5	0.5	0.1	28.7	1.0	2.7	21
Anterior cell end to buccal vertex, distance	10.7	11.0	1.0	0.2	9.4	9.0	13.0	21
Anterior cell end to anterior macronuclear nodule, distance	7.5	6.0	2.2	0.5	30.1	5.0	11.0	21
Macronuclear nodules, number	2.0	2.0	0.0	0.0	0.0	2.0	2.0	21
Anterior macronuclear nodule, length	11.0	10.0	2.3	0.5	21.3	8.0	18.0	21
Anterior macronuclear nodule, width	5.2	5.0	1.0	0.2	19.0	4.0	8.0	21
Posterior macronuclear nodule, length	9.5	10.0	1.0	0.2	10.8	7.0	11.0	21
Posterior macronuclear nodule, width	6.4	6.0	1.3	0.3	20.0	5.0	9.0	21
Micronuclei, diameter	1.7	2.0	0.6	0.1	37.5	1.0	3.0	21
Micronuclei, number	2.0	2.0	0.0	0.0	0.0	2.0	2.0	13
Ventral kinty, length ^b	12.5	12.5	1.3	0.6	10.3	11.0	14.0	4
Dorsal kinty, length	22.4	21.0	3.2	0.7	14.2	16.0	28.0	21
Dorsal kinty, number of kinetids	17.4	17.0	3.6	0.9	20.7	13.0	24.0	15
Posterior kinty, length	13.4	14.0	3.5	0.8	26.1	9.0	19.0	20
Posterior kinty, number of kinetids	7.6	7.0	1.9	0.4	25.5	5.0	12.0	19
Right ciliary field, number of kineties	6.2	6.0	0.4	0.1	6.7	6.0	7.0	19
Kinty 1 in right ciliary field, length	5.9	6.0	0.7	0.3	11.8	5.0	7.0	7
Kinty 1 in right ciliary field, number of kinetids	6.3	6.0	1.9	0.7	30.1	4.0	9.0	7
Kinty 2 in right ciliary field, length	4.5	4.5	1.3	0.3	28.6	3.0	8.0	14
Kinty 2 in right ciliary field, number of kinetids	3.6	3.0	0.8	0.2	21.2	3.0	5.0	14
Kinty 3 in right ciliary field, length	5.6	5.0	1.9	0.5	34.3	4.0	11.0	17
Kinty 3 in right ciliary field, number of kinetids	4.4	4.0	1.5	0.4	34.4	2.0	8.0	17
Kinty 4 in right ciliary field, length	7.2	7.0	2.1	0.5	28.6	5.0	12.0	21
Kinty 4 in right ciliary field, number of kinetids	5.7	5.0	1.6	0.4	28.6	4.0	10.0	21
Kinty 5 in right ciliary field, length	8.8	9.0	1.8	0.4	20.5	6.0	13.0	21
Kinty 5 in right ciliary field, number of kinetids	7.2	7.0	1.6	0.3	21.8	5.0	10.0	21
Kinty 6 in right ciliary field, length	8.8	9.0	1.6	0.4	18.7	5.0	11.0	20
Kinty 6 in right ciliary field, number of kinetids	7.1	7.0	1.5	0.3	20.9	5.0	9.0	20
Kinty 7 in right ciliary field, length	8.5	8.0	1.9	1.0	22.5	7.0	11.0	4
Kinty 7 in right ciliary field, number of kinetids	7.3	7.5	1.0	0.5	13.2	6.0	8.0	4
Lateral ciliary field, length ^b	11.0	11.0	0.9	0.4	8.1	10.0	12.0	6
Lateral ciliary field, number of kineties	12.0	11.5	1.4	0.7	11.8	11.0	14.0	4
Left ciliary field, number of kineties	5.3	5.0	0.6	0.2	11.6	4.0	6.0	15
Kinty 1 in left ciliary field, length	2.9	3.0	0.9	0.2	31.9	1.0	5.0	15
Kinty 1 in left ciliary field, number of kinetids	2.9	3.0	1.1	0.3	37.0	1.0	6.0	15
Kinty 2 in left ciliary field, length	4.9	5.0	1.6	0.4	33.2	1.0	8.0	14
Kinty 2 in left ciliary field, number of kinetids	4.3	4.0	1.2	0.3	28.1	2.0	7.0	14
Kinty 3 in left ciliary field, length	5.3	5.5	0.8	0.2	14.6	4.0	6.0	12
Kinty 3 in left ciliary field, number of kinetids	5.3	5.0	0.8	0.2	14.6	4.0	7.0	12
Kinty 4 in left ciliary field, length	6.6	6.0	1.7	0.5	26.3	4.0	10.0	11
Kinty 4 in left ciliary field, number of kinetids	6.0	6.0	1.2	0.4	19.7	4.0	8.0	11

Tab. 1: continued

Characteristics ^a	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Kinety 5 in left ciliary field, length	6.9	6.0	1.5	0.5	22.1	5.0	10.0	10
Kinety 5 in left ciliary field, number of kinetids	6.4	6.5	1.4	0.5	22.3	4.0	8.0	10
Kinety 6 in left ciliary field, length	7.3	7.5	1.2	0.5	16.5	6.0	9.0	6
Kinety 6 in left ciliary field, number of kinetids	7.3	7.5	1.8	0.7	23.9	5.0	10.0	6
Adoral zone of membranelles, diameter	17.7	18.0	1.5	0.3	8.6	15.0	21.0	21
Collar membranelles, number ^c	17.4	17.5	1.2	0.3	6.7	16.0	20.0	12
Buccal membranelle, number	1.0	1.0	0.0	0.0	0.0	1.0	1.0	21

^a Data are based on protargol-impregnated (method of SONG & WILBERT 1995), mounted, and randomly selected specimens from field material. Measurements in μm . CV – coefficient of variation in %; M – median; Max – maximum; Min – minimum; n – number of individuals investigated; SD – standard deviation; SE – standard error of arithmetic mean; $\bar{x}$ – arithmetic mean.

^b Kinetids could not be counted, as organelles are too densely spaced.

^c Counted in oral primordia of middle and late dividers.

22–27 μm ; outer constriction diameter: 19–21 μm ; process: 14–15 $\times$ 6–7 μm ; BALECH 1948), *Tintinnopsis* sp. from the Black Sea (length: 92–120 μm ; width: 60–68 μm ; ROSSOLIMO 1922), *Tintinnopsis* sp. from the Kara Sea (length: 118–134 μm ; width: 92–96 μm ; ROSSOLIMO 1927), and *Codonella amphorella* (length: 90 μm ; width: 50 μm ; process length: 25 μm ; without agglomerated particles; rim continuous; BIEDERMANN 1893).

According to cladistic and small subunit rRNA analyses, *T. fimbriata* belongs to a diverse group of highly developed tintinnids with entirely agglomerated, entirely hyaline, or partially agglomerated loricae (AGATHA & STRÜDER-KYPKE 2007).

Ontogenetic comparison: Ontogenesis was at least partially studied after protargol-impregnation in four species with a similar somatic ciliary pattern: *Codonella cratera* (PETZ & FOISSNER 1993), *Cymatocylis convallaria* (PETZ et al. 1995), *Favella* sp. (LAVAL-PEUTO 1994), *Stenosemella pacifica* (AGATHA & TSAI 2008), and *Tintinnopsis cylindrica* (AGATHA & RIEDEL-LORJÉ 2006). *Tintinnopsis fimbriata* matches these species in the position of the oral primordium posterior to the lateral ciliary field.

The samples from the coastal waters off the Island of Sylt were taken in the daytime. They contained many early and middle dividers, while late dividers were very rare, indicating that the late division stages take place mainly during night, as already supposed by HOFKER (1931) and BIERNACKA (1952). According to the latter author, cell division of *T. fimbriata* lasts 3–4 h at a water temperature of 18 °C. In the three populations, one replication band each traverses the macronuclear nodules, which afterwards fuse to an elongate ellipsoidal mass that divides. While HOFKER (1931) observed two macronuclear nodules each in the proter and opisthe of late dividers, BIERNACKA (1952) found only three nodules, viz., two in the proter and one in the opisthe, each accompanied by a micronucleus. The material for the proter's new lorica is secreted at the cytostome and

transported posteriorly by cell movement, while foreign particles adhere to it (BIERNACKA 1952).

Occurrence and ecology: The following compilation is restricted to *Tintinnopsis fimbriata* and the synonyms mentioned above. Due to the problematic taxonomy, however, the species might possess further synonyms and hence a much larger distribution.

Records substantiated by illustrations and/or morphological data are available for the Arctic Sea (LEVANDER 1894), the temperate and subtropical North Atlantic (this study; AGATHA 1998; STRÜDER-KYPKE & LYNN 2003; VERWEIJ et al. 2005), and the subtropical South Atlantic (BALECH 1948). Further, but uncorroborated records exist for the Arctic sea ice (IKÄVALKO 2003), saline lakes at the coast of the Kara Sea (BERNSTEIN 1931), the temperate North Atlantic (HARGRAVES 1981; PARANJAPPE 1987; EDWARDS & BURKILL 1995; Interstate Commission on Potomac River Basin 1998), the tropical South Atlantic (ARTIGAS et al. 2003), the temperate North Pacific (KONOVALOVA & ROGACHENKO 1974), and the subtropical Indian Ocean (DORGHAM & ABDEL-AZIZ 2001). Besides the records from marine waters, the species was frequently found in mesohaline waters. Substantiated records are available for the Baltic Sea and adjacent lagoons (LEVANDER 1894; BIERNACKA 1948, 1956, 1968), the Black Sea and an adjacent estuary (MOROZOVSKAYA & POLISHCHUK 1969), as well as waters and estuaries at the temperate North Atlantic coast (BRANDT 1906, 1907; MEUNIER 1919; HOFKER 1922, 1931; SCHULZ 1964; BAKKER & PHAFF 1976; PAULMIER 1995). Further, but uncorroborated records exist for the brackish waters of the Baltic Sea (SCHWARZ 1961; SPITTLER 1973; BOIKOVA 1984; KIVI 1986; JÖNSSON et al. 1997), the Black Sea and adjacent lagoons (KURILOV 2006), waters and estuaries at the temperate North Atlantic coast (VERSCHAFFELT 1929; REDEKE 1935; SCHULZ 1961; BAKKER & DE PAUW 1975; MIDDLEBROOK et al. 1987; DOLAN & GALLEGOS 2001), Arctic waters influenced by freshwater discharge

(ECHOLS & FOWLER 1973; ROGERS et al. 1981; FETZER et al. 2002), an estuary at the subtropical South Atlantic coast (SOUTO 1974), a pond associated with an Argentinian lowland river (GABELLONE et al. 2001), and a lake at the Mediterranean Sea coast (DALY YAHIA et al. 2005). BIERNACKA (1956) discovered the species even in oligohaline waters of a lagoon at the Baltic Sea coast. The preceding records indicate that the species prefers mesohaline coastal waters in Arctic, temperate, and subtropical regions.

A mass occurrence of *T. fimbriata* with an abundance of 1.08×10^6 individuals per litre caused a yellowish colouration in the Kiel Bight, Baltic Sea, at a salinity of about 15 ‰ in March 1999 (J. GÖBEL, pers. comm., Landesamt für Wasserhaushalt und Küste, Kiel). During autumn, *T. fimbriata* dominated not only the tintinnid community, but the whole ciliate plankton in the coastal waters of Sylt (this study). *Tintinnopsis fimbriata* was found to feed on pennate and centric diatoms, coccal organisms (this study), and the chrysophyte *Ebria tripartita* (HOFKER 1931). In experiments, SPITTLER (1973) observed a filtration rate of 8.5 µl per individual and hour. On the other hand, the tintinnid is lethally infected by a non-dinoflagellate protozoan parasite (HOFKER 1931).

According to BIERNACKA (1952), *T. fimbriata* forms resting cysts at low salinities and high temperatures. Encystment follows a cell division during which the macronuclear nodules do not fuse although they were traversed by replication bands; one nodule each simply migrates in the proter and opisthe. Subsequently, the opisthe forms a cyst wall, while the proter dies. Excystment, including the formation of a new oral apparatus, is accompanied by the division of the macronucleus and micronucleus (BIERNACKA 1952).

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