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Two new species of Tardigrada from the Canadian Subarctic with some notes on sexual dimorphism in the family Echiniscidae

HIERONIM DASTYCH

(With 15 figures)

Abstract

Two new terrestrial water-bears, *Pseudechiniscus alberti* sp. n. (Heterotardigrada) and *Diphascon behanae* sp. n. (Eutardigrada) are described from mosses collected in the Canadian Subarctic (Ogilvie Mtns). The latter species also occurs in West Spitsbergen. Until recently males were unknown in the genus *Echiniscus*, which was thought to be a purely parthenogenetic taxon. The description and illustration of a male *Pseudechiniscus alberti* sp. n. is given and the presence of males in four species of the genus *Echiniscus* is reported and discussed.

Introduction

The vast areas of Arctic and Subarctic zones in North America are very poorly studied with respect to the tardigrade fauna, despite the fact that the role of these animals in polar ecosystems is much greater than commonly judged. Very little has been published about tardigrades of this region (MATHEWS 1938, SCHUSTER & GRIGARICK 1965, DASTYCH 1982, MEININGER & NELSON in press, WEGLARSKA 1970, WEGLARSKA & KUC 1980) and only the papers of WEGLARSKA are devoted to the Canadian Arctic.

Through the courtesy of Dr. VALERIE BEHAN-PELLETIER I have received 130 plant samples, mainly mosses, from the mountains of Northern Canada (British and Ogilvie Mtns) which contained more than 35 species of Tardigrada. Among them several species are new records for the Canadian fauna and some others represent undescribed taxa. This paper describes two new species and includes some remarks about sexual dimorphism in the terrestrial family Echiniscidae.

Pseudechiniscus alberti sp. n. (figs 1-10, 14, 15)

D i a g n o s i s: A medium sized, bisexual *Pseudechiniscus* with strongly developed lobes on the posterior margins of the shoulder and the Ist and IInd median plates, which partly overlap adjoining plates. The paired semental plates and pseudosegmental plate have small lateral plates at their edges. Cirri externi and setae A have anchor-shaped bifurcations.

There is a spine fringe and a small spine present on the inner claws, no spines on the outer claws.

The body is 208-268 µm long (238 µm in the holotype) and red; black eyespots are 6-7 µm in diameter. The cuticle is thick, and the dorsal plates are covered with regularly distributed granulation. The ventral side is without granulation and the ventral plates are lacking. The granulation is developed as hemispherical thickenings and the cuticle between them is smooth and without striae (figs 1-4, 6, 15). The granules are 1-2 µm in size, (usually 1.3-1.5 µm) and are either slightly bigger on the shoulder plate, or almost equal in size on all dorsal plates, especially in the median line of the body.

The head plate is small and distinctly faceted. The shoulder plate is large and its anterior part has a well defined "W"-shaped sculpture, whilst the "T"-shaped pattern occurring on the posterior part of the plate is weakly marked (figs 1-3). A broad and rounded median lobe occurs on the posterior margin of the shoulder plate, which partly overlaps the Ist median plate. Similar in shape, but much lobes (B2) are developed on either side of the median lobe. Cuticular folds ("sutures") separate small, symmetrically placed lateral plates from the shoulder plate and are developed above the Ist pair of legs.

The segmental paired plates are divided and their posterior edges (C2, D2) have broad rounded lobes that terminate in minute spines, 1-2 µm long. On either side of the plates small lateral plates also occur and their posterior parts are transformed into wide, sharp spines. These plates are separated by distinct "sutures" composed of cuticular folds (figs 1, 2, 6). The vertical divisions of both paired plates are overlapped to a large degree by the lobe-like margins of the median plates.

The median plates are relatively large (figs 1-4). The first and second plates are transversely divided into two parts. The posterior margin of each plate is characteristically developed as a round and very broad lobe, which partly overlaps the paired segmental plates. The free edges of the lobes, (both the lobes on shoulder plate and spine-like parts of lateral plates) are smooth, i.e. without granulation (figs 4, 6, 14). Third median plate is undivided and without such a lobe.

The pseudosegmental plate is divided and has two broad, rounded lobes placed close to one another on the posterior margin (Ps2). The edges of these particular lobes terminate either in a small spine, about 1.5 µm long (♂♂: figs 2, 3) or are completely smooth (♀: fig. 1). At either side of the pseudosegmental plate occur small, symmetrical lateral plates, separated by "sutures" and with 2-4 small spines on the upper edges.

The terminal plate is small, without faceting but with long incisions. Spines E are 2-3 µm long.

Cirri interni are short (4-6 µm) and onion-shaped, cirri externi are much longer and with small bifurcated tips

(figs 1, 3, 7, 12). The width of these bifurcations is 1.5 µm. The papilla cephalica is hemispherical, wide (6-8 µm), but flattened and placed close to cirrus internus (figs 7, 10). The clavus is about 8 µm long.

The setae A are 40-55 µm long (about 20-25 % of the body length) and distinctly bifurcated at their tips (figs 1, 3). The anchor-shaped bifurcations are up to 4 µm wide. Other lateral appendages are short spines at B and C (3-7 µm long) developed from the posterior parts of the lateral plates. Similar spines, though more numerous (2-4), occur on both sides of the pseudosegmental plate; one specimen had these spines on the right side completely reduced and substituted by rounded protrusion (fig. 2). The dorsum has only the broad lobes at B2, C2, D2 and Ps2, mentioned above.

The first pair of legs has a small spine (3-4 µm long) which is lacking on the IInd and IIIrd pair; whilst on the IVth pair of legs there is a small papillus, 5-6 µm long. The lateral side of the body is covered with a granulation similar to that on the dorsal surface, but much smaller (fig. 3). The spine frings is composed of 1-2 teeth, which are 2-5 µm long. The inner claws have a very small spine (0.5-1.0 µm) placed very close to the bases and bent strongly downwards; the outer claws are without spines. The claws are slender and 15-18 µm long on the IVth pair of legs. One specimen had aberrantly developed outer and inner claw on the IVth pair of legs, that were strongly thickened and shorter than normal (fig. 2).

The female has a rosette-shaped gonopore, about 14 µm in diameter and composed of 6 small lobes (fig. 8); the male gonopores are oval-shaped (fig. 9) and 4-5 µm wide. Sexual dimorphism which has been observed in only 3 specimens (1 ♀, 2 ♂) was poorly defined. The female has larger body dimensions, relatively smaller papilla cephalica and shorter cirrus internus as compared with males. Moreover, no spines occur on the lobes of the paired segmental plates or the pseudosegmental plate (positions C2, D2, Ps2) and the spines of lateral plates are smaller as in the males.

L o c u s t y p i c u s. Canadian Subarctic, Ogilvie Mtns, 65° 00´N, 138° 03´W. Dry hillside, 1600 m a.s.l. Detritus among *Dryas, Phlox, Polygonum, Arenaria* and *Erigeron purpuratus*. Alkaline reaction. 5 July 1985, leg. V. BEHAN-PELLETIER (holotype and one paratype, probably also ♀). Other locality: Ogilvie Mtns, 65° 12´N, 138° 32´W. Mountain side (1800 m a.s.l.) with *Eritrichum, Dryas* and *Draba*. From moss with slightly alkaline reaction. 5 July 1985, leg. V. BEHAN-PELLETIER (two paratypes, ♂♂).

T y p e r e p o s i t o r i e s. The holotype (♀) is deposited in the Zoological Museum, University of Hamburg (ZMH), one paratype (♂) in the collection of the National Museum of Natural History, Smithsonian Institution, Washington (slide No.41). One paratype in the collection of the Biosystematics Institute (Ottawa), another one in the author's collection.

E t y m o l o g y. This species is dedicated to Dr. GERD ALBERTI, University of Heidelberg.

Discussion

The presence of characteristic lobes on the posterior margins of the shoulder and median (I, II) plates in *Pseudechiniscus alberti* sp. n. and the combination of other characters has distinctly separated this new species from all the 25 known taxa (RAMAZZOTTI & MAUCCI 1983) of this genus. In some aspects this species bears a resemblance to *P. quadrilobatus* IHAROS 1969, described from Vietnam and to *P. occultus* DASTYCH, 1980) from the Tatra Mtns.

P. quadrilobatus differs from the new species by the lack of lobes on the median plates, and the presence of lobes on paired segmental and pseudosegmental plates, occurring there, however, only singly and on the median line of the body. In *P. quadrilobatus* these lobes have a different shape, the pseudosegmental plate is undivided and the lateral plates, spine fringe, spines on inner claws and the anchor-shaped bifurcations at the appendage tips are lacking (IHAROS 1969). The latter species also has no dorsal lobes at C2 and D2.

The form of *P. alberti* sp. n. also resembles to some degree *P. occultus* and both these species have a similar shape and size of granulation (DASTYCH 1980), anchor-shaped bifurcations on the tips of cirri externi and setae A (their presence was not recorded in the original description of *P. occultus*) and two broad lobes on the posterior margins of the shoulder and pseudosegmental plate, which terminate in a small spine. However, *P. occultus* differs clearly from the new species by the lack of characteristic overlapping lobes on the median plates, the lack of a spine fringe, the presence of spines on the outer claws of the IVth pair of legs, lobes at C2, D2 and the presence of thin striae between some dorsal granules. Moreover, the lobes on shoulder plate are double, as compared with the single lobe in *P. alberti* sp. n. It should be noted that *P. occultus* also has small, symmetrical lateral plates, found during re-examination of the holotype. Unfortunately, due to the dorsal position of the type-specimen they are only clearly visible at the second paired plates. The lateral plates developed in both these species are most likely homologous to those occurring in *P. victor* (EHRENBERG, 1853).

The characteristic, but poorly visible anchor-shaped bifurcations at the tip of the head and lateral appendages (cirri, setae A and in one case setae E) are worthy of a short comment. They have been found hitherto in 5 species, namely 3 species from *Pseudechiniscus,* and the others also from genera in the family Echiniscidae, i.e. *Echiniscus* and *Bryodelphax*. BARTOS (1936) describing his *Pseudechiniscus tridentifer,* from the Tatra Mtns, first recorded this structure and named it "Dreizahn". In fact, recent studies of *P. tridentifer* from locus typicus (Rysy Mt: DASTYCH 1980) revealed that these endings are composed of two sharp spines reversed distally and that this taxon is a synonym of the Arctic-alpine species, *P. victor*. The bifurcations were reported in the latter taxon by SCHUSTER & GRIGARICK (1965). The authors also found this character in *Echiniscus becki,* and pointed out that the appendage tips can sometimes terminate in a small disc (l.c., 1966). Recently PILATO (1972) observed this structure in *Bryodelphax weglarskae*.

BARTOS described *P. tridentifer* from the mosses growing in swiftly running water and attributed these bifurcations to clinging function,

protecting the animals from being washed away from moss cushions[1]. It was due to this observation that *P. tridentifer* was recognized for a long time as the only representative of fresh-water Echiniscidae (RAMAZZOTTI 1967, 1978). As a matter of fact, this species (i.e. *P. victor*) dwells prevailingly in other habitats (and this is also true for other four taxa with the bifurcations), thus the function mentioned can only be a secondary one. The role of these structures is hitherto unknown (possibly sensory?) and its elucidation needs a separate study. It is interesting, that within the morphologically very differentiated marine Heterotardigrada the non acuminate appendages were found hitherto only in *Echiniscoides pollocki* (Echiniscodidae), which terminate with "a small bundle of rays" (HALLAS & KRISTENSEN 1982).

At present it is hard to say whether these bifurcations are homologues or not. If they are, this character should be recognized as plesiomorphy for genera *Bryodelphax, Echiniscus* and *Pseudechiniscus,* and as autapomorphy for terrestrial Echiniscidae. In this case it would have occurred in ancestral forms before their differentiation in two main phyletic lines, known within this family. However, it these bifurcations were acquired convergently, they represent yet another nonhomologous similarity in this phylum.

Diphascon beḥanae sp. nov. (figs 11-13)
(*Diphascon* sp. nov.?: DASTYCH 1985, p. 189; figs 22, 23, phot. 14d, g)

D i a g n o s i s: A medium sized *Diphascon,* without eyespots and with minute cuticular granulation. The pharynx has three macroplacoids and a microplacoid, the second macroplacoid obliquely positioned is the shortest, and the third, the longest, has small thickenings. The buccal tube is without drop-shaped structure. The claws are slender and without lunulae or cuticular bars on legs.

The body is 282 µm (310 µm)[2] long, white and without eyes. The cuticle is covered with very tiny, irregularly distributed granulation, the largest at the posterior. The granules are about 0.5 µm in size; in one specimen they were poorly developed. The buccal tube has no drop-shaped thickening and is 70 µm long. The mouth tube is 30 µm long (25 µm), and the pharyngeal tube 40 µm long (no data available from the paratype). The outer diameter of the buccal tube is 1.6 (2.0) µm. The pharyns is oval, 39 x 26 (38 x 28) µm, with large apophyses, three macroplacoids and a microplacoid (figs 11, 12). The first macroplacoid is 4.7 µm long, the IInd 4.0 µm and the IIIrd is 6.3 µm long (in the paratype these are: 4, 3 and 6 µm, respectively). The macroplacoid width is 1.5 (2.0) µm. The second macroplacoid is positioned

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[1] "Diese neue Art ist dem Wasserleben in den stark überspülten Moosen gut angepaßt. Sie hält sich in den Moosen fest ... auch mit den merkwürdigen ... Dreizähnen der beiden Cirri, sowie auch den Fäden A und E." (BARTOS 1936).

[2] Paratype measurements in brackets.

slightly oblique in relation to the first placoid, creating a characteristic arrangement for this species (Fig. 12). The third macroplacoid has small irregularities along its length, especially in the posterior region. The microplacoid is 1.5 (1.3) µm long. Mouth cavity smooth, without any granulation.

The claws are rather large, slender, and with relatively long main branches and smooth bases, i.e. without any small teeth (figs 12, 13). There are no cuticular bars at the base of the I-IIIrd inner claws or between the claws. The main branches have very small, usually poorly visible accessory spines. The claws have the characteristic, well developed structure within (fig. 13; also DASTYCH 1985: phot. 14 g). The outer claws of the IVth pair of legs are 19 µm long; the main branch being 15 µm long. The paratype has retracted claws, hence no measurements are given.

L o c u s t y p i c u s: Canadian Subarctic, Nahoni Range, 65° 42´N, 139° 38´W. Seepage area with *Lagotis, Cardamine, Dryas, Potentilla, Papaver;* from moss (1350 m a.s.l.). Acid or neutral reaction. 8 August 1985, leg. V. BEHAN-PELLETIER (holotype). Other locality: West Spitsbergen, Albert I Land, Biskayerhuken cape, 10 m a.s.l. Moss from Devonian sandstone, alkaline reaction (paratype). 31 July 1973, leg. R.W. SCHRAMM.

T y p e r e p o s i t o r i e s. The holotype is deposited in the Zoological Museum, University of Hamburg (ZMH), paratype in the author's collection.

E t y m o l o g y. This species is named for Dr. VALERIE BEHAN-PELLETIER, Biosystematics Research Institute, Ottawa.

Discussion

The combination of the main characters of *Diphascon behanae* sp. n. distinguishes this species from all known taxa within the genus. The species bears some resemblance to *D. scoticum* MURRAY, 1905 with respect to the buccal apparatus, but differs distinctly in the larger apophyses, the relatively longer macroplacoids and the oblique position of the second macroplacoid, the presence of small irregularities (thickenings) on the third macroplacoid, the rounder shape of the pharynx and the relatively thinner buccal tube. *D. scoticum* MURRAY also has well developed cuticular bars on the I-IIIrd pairs of legs and between the claws, which were absent in the new species. *D. behanae* sp. n. also has more slender claws and a granulated cuticle.

Some notes on the presence of males in the family Echiniscidae

Sexual dimorphism found in *Pseudechiniscus alberti* sp. n. gives an opportunity for some remarks on this phenomenon. Until recently the literature practically discounted the existence of such dimorphism within the terrestrial family Echiniscidae. It assumed a lack of males and as a consequence proposed parthenogenesis as the mode of reproduction for this group. This opinion referred especially to the genus *Echiniscus* which is in species the richest taxon of the whole

phylum (RAMAZZOTTI 1962, GRIGARICK et al. 1975, NELSON 1982, BERTOLANI 1982, KRISTENSEN in press).

The presence of males in the genus *Hypechiniscus* and *Bryodelphax* was recorded for the first time by BERTOLANI et al. (1984). KRISTENSEN in his fundamental revision of the Echiniscidae (in press) has reported males in several genera of this family and stated that they "have not been recorded in *Echiniscus, Bryochoerus, Parechiniscus* and many *Pseudechiniscus* species". The author (l.c.) did not mention by name in which taxa of the *Pseudechiniscus* the males were found, thus, one can suppose that the description of males in *P. alberti* sp. n. is the first such record for a definite species of this genus.

GRIGARICK et al. (1975) studied morphogenesis of two *Echiniscus* species and observed in one taxon two types of gonopores and commented: "It may be that the shape of the gonopore becomes somewhat altered following oviposition". This species was determined as *Echiniscus oihonnae* RICHTERS (l.c., 1975), but later was described as a new taxon, *Echiniscus laterculus* (SCHUSTER et al., 1980). An interesting comment on that matter was given by NELSON (1982) who stated: "... Whether the difference is due to an alternation following the oviposition or to presence of males in the population is unknown. If males were indeed present, this would be the first observation of males in any *Echiniscus* species, thus altering the view that the genus is entirely parthenogenetic". *Echiniscus laterculus* is characterized by the presence of ventral plates (GRIGARICK et al. 1975: see figs 13-16 and page 150; also SCHUSTER et al. 1980), this, with other characters, indicate its affiliation to the *Echiniscus spitsbergensis*-group. Recently, the new genus *Testechiniscus* has been estabilished for this group of species (KRISTENSEN, in press), where males were also found. In the light of this, the species studied by GRIGARICK et al. (1975) belongs to the genus *Testechiniscus* and the comment of NELSON (1982) also refers to this taxon.

Lately I have re-examined my whole *Echiniscus*-material and found males in four species of this genus. The observations of this study are probably the first as far as *Echiniscus* is concerned. The males have a well developed characteristicly round or slightly oval gonopore, 3.5-6.0 µm in diameter, depending on the species studied. Detailed analysis of the sex ratio, morphological differences and their variability between both sexes etc. is outside the scope of this paper and will be published separately. The relevant species are:

Echiniscus nepalensis DASTYCH, 1975

The species is frequent in the alpine zone of the Himalayas (DASTYCH unpublished) and males constituted about 10 % of the whole material examined.

Echiniscus aff. *testudo* (DOYÈRE, 1840)

A large population of this, probably new, species had a composition of one-third males. This taxon was collected in the vicinity of the Khumbu glacier (Nepal, 5200 m a.s.l.).

Echiniscus pseudowendti DASTYCH, 1984

The species is known from the Antarctic (DASTYCH 1984) and more than 20 males were found within a large population.

Echiniscus jenningsi DASTYCH, 1984

A taxon described from the Antarctic: only two males were found.

It should be stressed that the above-mentioned species were collected not from acquatic localities, but from mosses and lichens growing on rocks and soil, in conditions where cryptobiosis is a common phenomenon. These sites are characterized by severe climatic and rather unfavourable edaphic conditions, and represent habitats where parthenogenesis should be the preferred mode of reproduction, according to the current hypotheses on Tardigrada's cryptobiosis and dispersal in general, and the genus *Echiniscus* in particular.

The considered species belong both to a group with very strongly marked setotaxy (arrangement of the body appendages), i.e. the *blumi*-complex (*E. nepalensis, E.* aff. *testudo*), and to a group almost devoid of setae, known as the *arctomys*-complex (*E. pseudowendti, E. jenningsi*). The bisexuality found in the genus *Echiniscus,* unfortunately does not help with the assessment of the degree of relationship between these and other groups within this genus and in general constitutes one of the most controversial and difficult problem in the Echiniscidae systematics, i.e. the directions of setotaxy evolution.

Acknowledgements

I wish to thank Dr. V. BEHAN-PELLETIER, Biosystematics Research Institute (Ottawa) for valuable Tardigrada-material and Prof. Dr. H. RAHMANN and the staff of the Zoological Institute, Stuttgart University (Hohenheim) for the hospitality and kind provision of laboratory space and facilities. Finally, I wish to express my gratitude to SANDRA McINNES (British Antarctic Survey, Cambridge) for corrections to the English manuscript.

Zusammenfassung

Zwei neue terrestrische Arten von Bärtierchen aus Moosproben der kanadischen Subarktik (Ogilvie Mtns), *Pseudechiniscus alberti* sp. n. (Heterotardigrada) und *Diphascon behanae* sp. n. (Eutardigrada), werden beschrieben. *Diphascon behanae* sp. n. wurde auch in West-Spitzbergen gefunden. Bis jetzt wurde die Gattung *Echiniscus* für vollständig parthenogenetisch gehalten; Männchen waren nicht bekannt. Von *P. alberti* sp. n. werden Männchen beschrieben und abgebildet; über das Vorkommen von Männchen in vier *Echiniscus*-Arten wird berichtet und diskutiert.

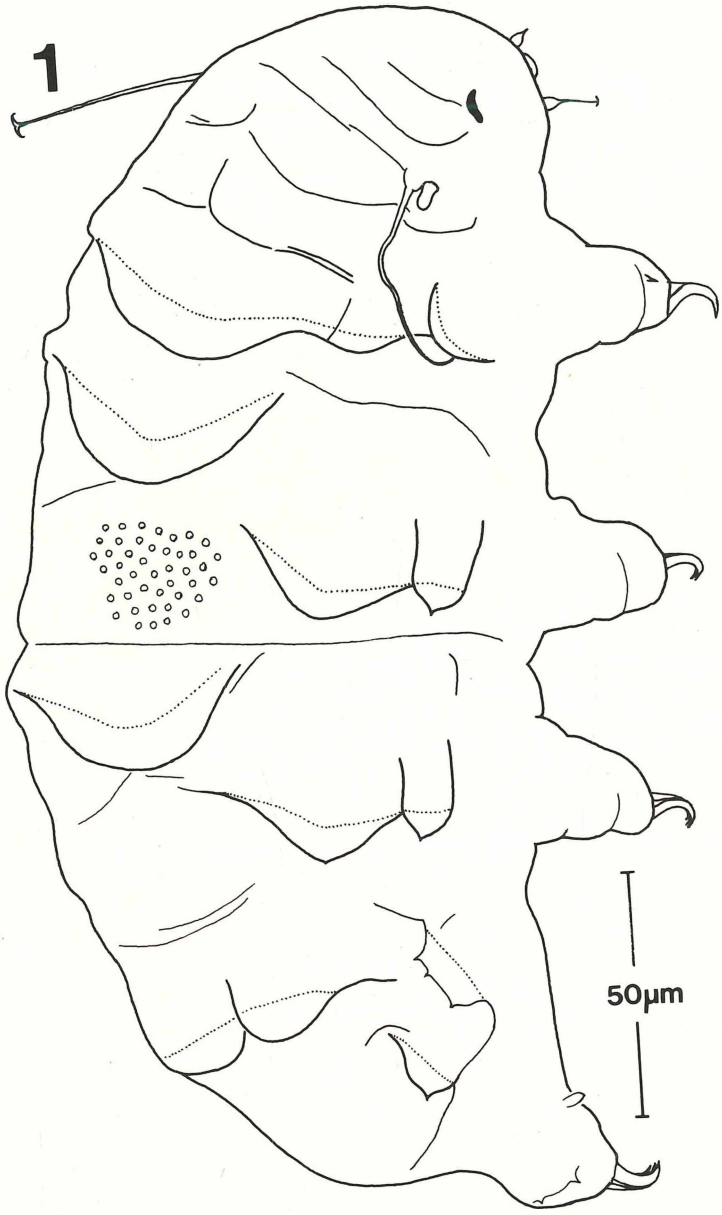


Fig. 1: *Pseudechiniscus alberti* sp. n., holotype (♀).

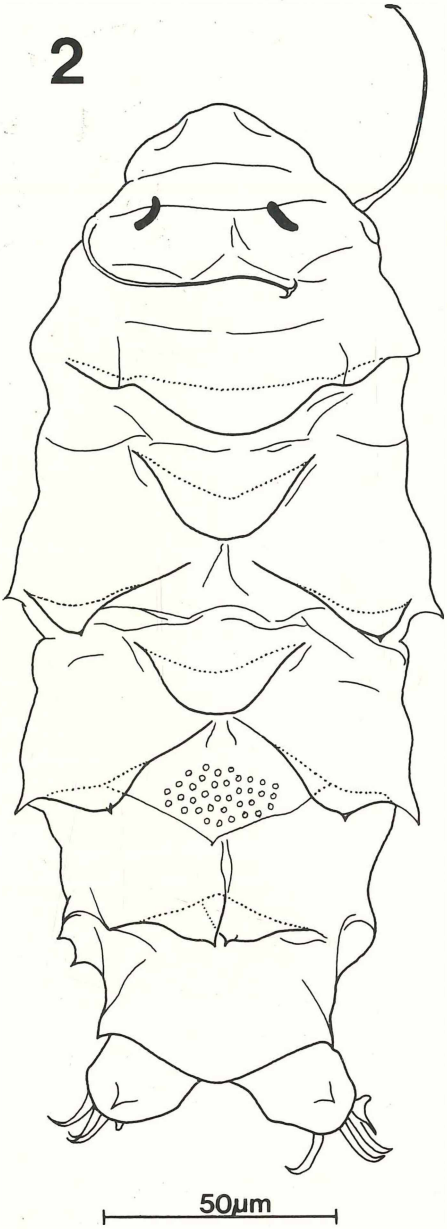


Fig. 2: *Pseudechiniscus alberti* sp. n., paratype (♂, slide No. 41).

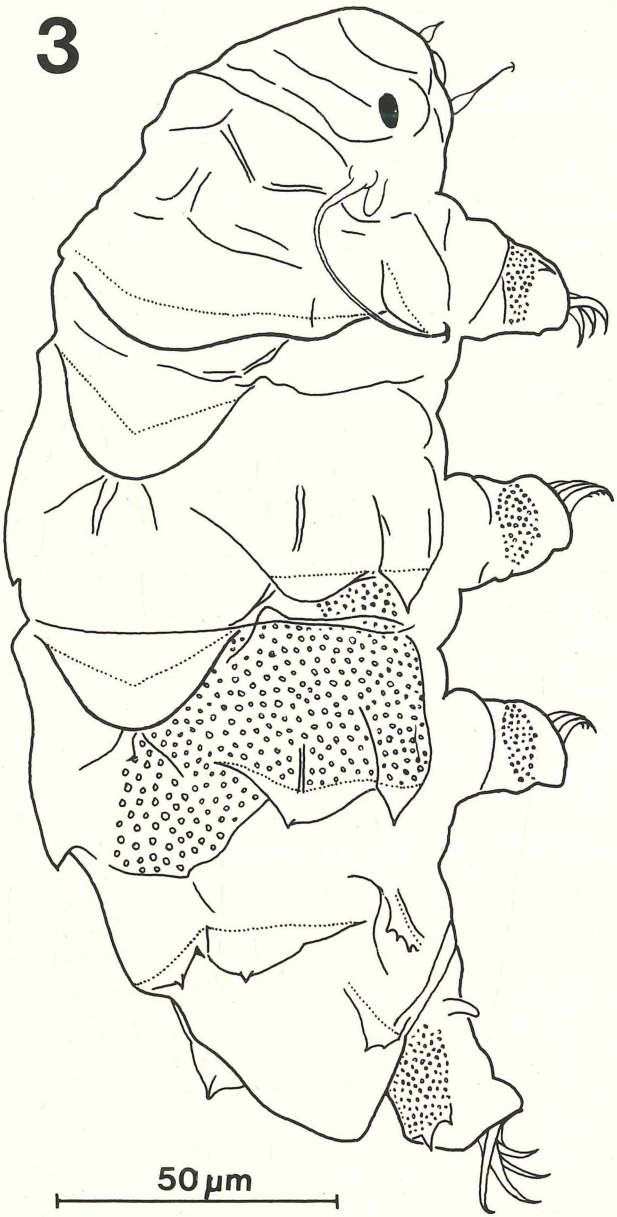
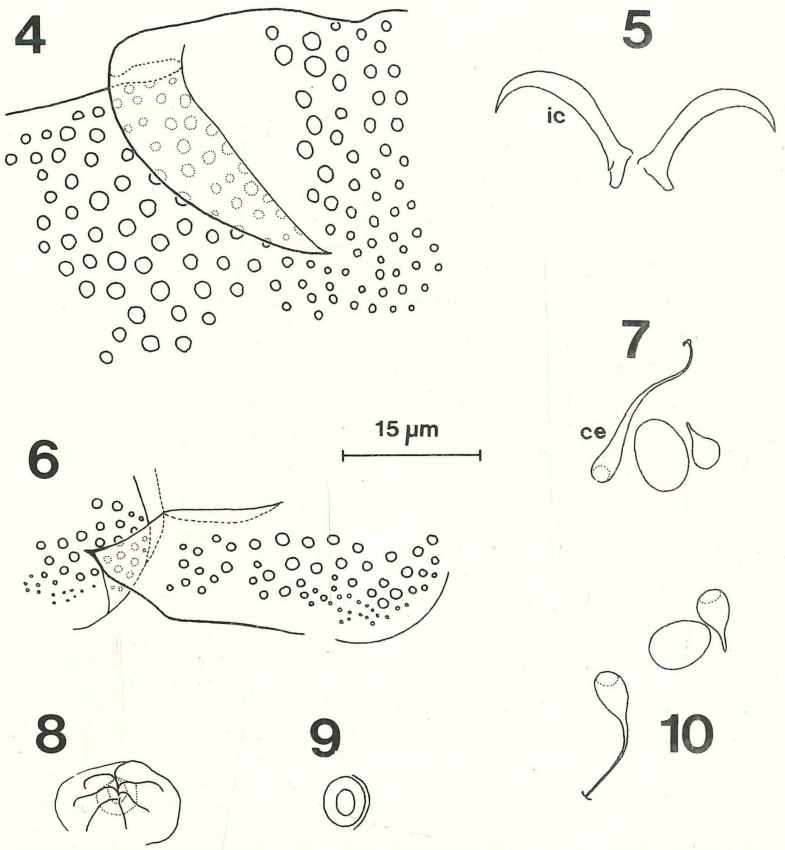
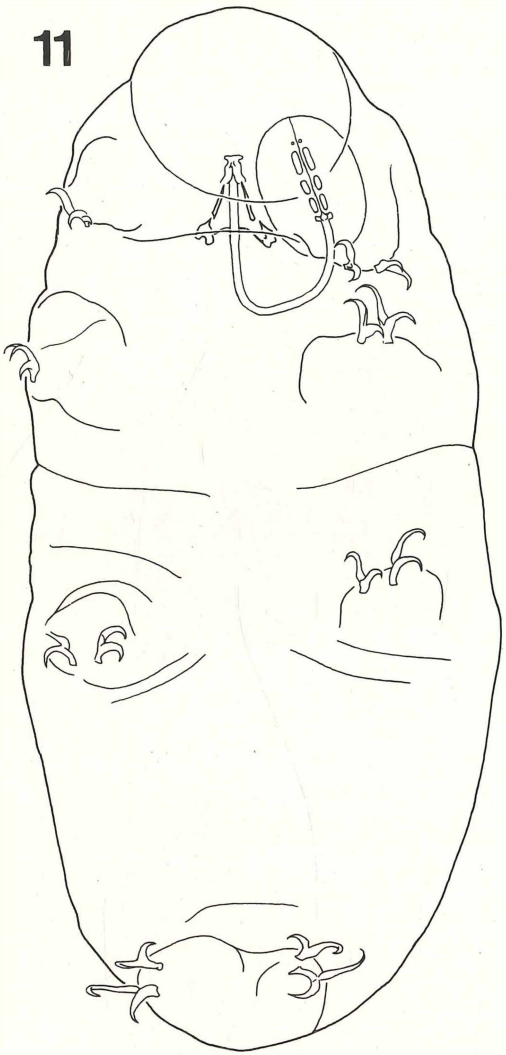
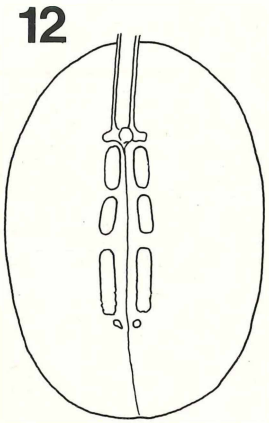


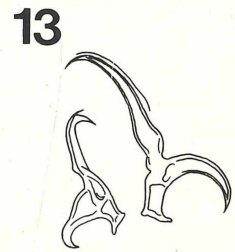
Fig. 3: *Pseudechiniscus alberti* sp. n., paratype (♂).

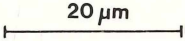


Figs 4-10: *Pseudechiniscus alberti* sp. n. - 4: first median plate, lateral view (paratype); 5: claws of the IVth pair of legs (ic = inner claw, holotype); 6: lateral plate of the IInd segmental paired plate (paratype, ♂); 7: head appendages (paratype ♂, slide No. 41); ce = cirrus externus); 8: female gonoporus (holotype); 9: male gonoporus (paratype ♂, slide No. 41); 10: head appendages (holotype).

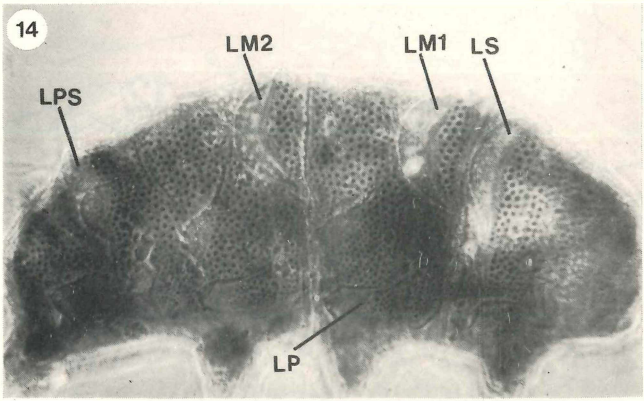


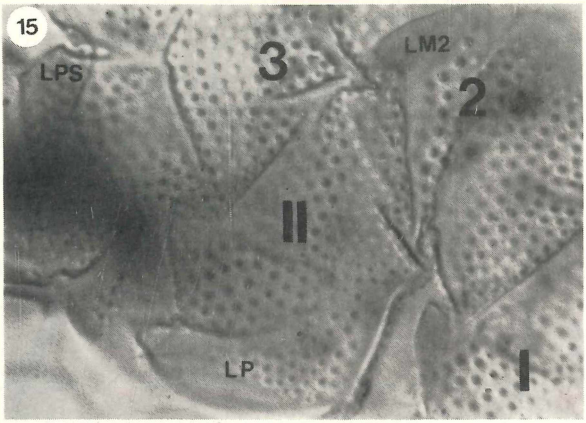






Figs 11-13: *Diphascon behanae* sp. n. - 11: ventral view; 12: pharynx; 13: claws of the IVth pair of legs (11-13: drawn from paratype).





Figs 14, 15: *Pseudechiniscus alberti* sp. n. - 14: habitus, dorsolateral view (holotype); 15: fragment of the dorsum, paratype (♂). (LS = lobe of the shoulder plate; LM1, LM2 = lobe of the Ist and IInd median plate; LSP = lobes on pseudosegmental plate; I, II = segmental paired plates; 2, 3 = second and third median plate; LP = lateral plate. Fig. 14 - phase contrast, 15 - Nomarski contrast).

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Anschrift des Verfassers:
Dr. HIERONIM DASTYCH, Krummenackerstr. 8, D-7300 Esslingen.