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Redescription of the Sub-Antarctic tardigrade *Mopsechiniscus imberbis* (RICHTERS, 1908) (Tardigrada)

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ABSTRACT. – The tardigrade *Mopsechiniscus imberbis* (RICHTERS, 1908) from Sub-Antarctic South Georgia is redescribed and a neotype designated. The species is compared with other congeners, particularly *M. granulatus* MIHELČIČ, 1967, a later often confused with *M. imberbis*.

KEYWORDS: Tardigrada, *Mopsechiniscus imberbis*, redescription, South Georgia, Sub-Antarctica.

Introduction

The genus *Mopsechiniscus* was established by DU BOIS-REYMOND MARCUS (1944) for tardigrades of the family Echiniscidae which characteristically lack anterior head sensory cirri (Fig. 3, 5). Another unique generic character is the decreasing number of trunk cirri from juvenile to adult, a trend contrary to that of other echiniscids (*i.c.*, RAMAZZOTTI 1962b, 1965, 1972, RAMAZZOTTI & MAUCCI 1983, KRISTENSEN 1987).

The type species, *M. imberbis*, is the most often recorded *Mopsechiniscus* spp. According to the literature, the taxon is notable by its remarkable individual variability (e.g. RAMAZZOTTI 1972, RAMAZZOTTI & MAUCCI 1983), and has been reported from South Georgia (RICHTERS 1908, OTTESEN & MEIER 1990), and several localities throughout South America (*i.c.*, ROSSI & CLAPS 1989, DASTYCH & MOSCAL 1992). The genus includes four nominal taxa, *i.e.* *M. imberbis* (RICHTERS, 1908), *M. granulatus* MIHELČIČ, 1967, *M. tasmanicus* DASTYCH & MOSCAL, 1992 and *M. frenoti* DASTYCH, 1999.

In studying *M. frenoti* from South Indian Province (SIP) Sub-Antarctic Îles Crozet (Dastych 1999), confusion and contradictions were found in the original descriptions of *M. imberbis* and *M. granulatus*. This paper redescribes *M. imberbis*, clarifies and reconciles confusion surrounding the species, as a first stage in the revision of *Mopsechiniscus*.

Taxonomic history of the genus *Mopsechiniscus*

RICHTERS (1908) officially described *Echiniscus imberbis*, based on seven individuals, from South Georgia in the the Sub-Antarctic, but omitted the exact locality. He recognized the special status of the species vis-à-vis the lack of anterior head sensory cirri and head papillae. The species *E. imberbis* was first informally introduced by RICHTERS (1907) (*nomen nudum*) when he discussed the occurrence of tardigrades in the Antarctic. Later, THULIN (1911) transferred *E. imberbis* to the new genus *Pseudechiniscus*.

MARCUS (1928, 1929, 1936) restated the original description of the species (temporarily transferring the taxon to *species inquirenda* in 1929) and provided a line drawing based on the photomicrograph published by RICHTERS (1908: Fig. 3). MARCUS (*i.c.*) accentuated the presence of appendages (projections) on median plate 2 (= *m2d*) as an unusual character for the family Echiniscidae.

DU BOIS-REYMOND MARCUS (1944) examined 12 specimens from Sao Paulo, Brazil, identifying the species as *imberbis*, and established the new genus *Mopsechiniscus*. The taxon was defined on the absence of the anterior head sensory cirri and papillae, with *imberbis* as its type species. Though several morphological differences were noted between the Brazilian individuals and RICHTERS' original description, these were concluded to be infraspecific variability. DU BOIS-REYMOND MARCUS (*l.c.*) also reported, 1). the presence of a pair of large flat 'buttons' („botões largos e chatos“), 2). the median cephalic projection on the head segment, 3). a spine at the base of leg I, and 4). the progressive reduction in number of trunk cirri from juveniles to adults.

RAMAZZOTTI (1962a) formally accepted the decision to unite the morphologically divergent specimens from South Georgia and Brazil under the name of *M. imberbis*, but expressed doubts to the correctness of this placement, suggesting the morphological differences between the two populations indicated two distinct species. Nevertheless RAMAZZOTTI remained undecided and underlined how few specimens were examined by RICHTERS and DU BOIS-REYMOND MARCUS, as well as the absence of detail, e.g. the lack of data about the presence of cephalic 'buttons' (“bottoni” cephalici) and the cephalic median projection, in RICHTERS (1908) original description. Later, RAMAZZOTTI (1962b, 1965) examined and identified 65 individuals from Chile as *M. imberbis*. Based on this material the description of the species, including juveniles, was supplemented with notes on morphological differences and discrepancies within the taxon. Though continuing to combine the specimens from South Georgia (RICHTERS 1908), Brazil (DU BOIS-REYMOND MARCUS 1944) and Chile (RAMAZZOTTI 1962b) under *M. imberbis*, RAMAZZOTTI (*l.c.* 1972, RAMAZZOTTI & MAUCCI 1983) considered and listed each population separately. In these monographs (*l.c.*) a shortened diagnosis for the genus was presented and, with the addition of the new species *M. granulatus* MIHELČIČ, 1967, a key was provided.

SUDZUKI (1964) re-iterated these data on *M. imberbis* reported by RICHTERS (*l.c.*) when surveying the literature on Antarctic tardigrades.

MIHELČIČ (1967) described *M. granulatus* from 62 individuals from Tronador and Bolson in the Argentinian Andes. The description is however confused and lacks a differential diagnosis. MIHELČIČ restated the lack of cirri and papillae on the head segment, noted these were replaced by an „elongated oval ring“, and reported claws without spurs. However, no information was given on the repository of the type specimens. MIHELČIČ (1971) subsequently supplemented his original description with additional information and illustrations from new material, corrected some errors and compared this new species with *M. imberbis*. In addition, he noted the presence of a „short cone-shaped button“ within the „ring“ on the head segment which he suggested was homologous with cephalic papilla.

GRIGARICK, SCHUSTER & NELSON (1983) reported six specimens of *M. imberbis* from the Venezuelan Andes, the northernmost locality of the genus. A wide range of morphological variability was noted in the specimens examined, but no further detail beyond the accepted generic characters for *Mopsechiniscus*.

BINDA & KRISTENSEN (1986) recorded *M. imberbis* from Argentina (El Sagrario Puerto) and KRISTENSEN (1987) revised the family Echiniscidae. This included an emended diagnosis and critical description of *Mopsechiniscus*, based on an unspecified number of specimens identified as *M. imberbis* from Aguas Calientes in Chile (not in Argentina, as erroneously stated: *l.c.*, p. 293; KRISTENSEN, pers. comm.). KRISTENSEN (*l.c.*) clearly indicated the head „buttons“ in *Mopsechiniscus* as homologous with cephalic papillae (secondary clavae), and identified, 1). the presence of a small depression in the middle of head plate, 2). small plates associated with main segmental plates, 3). a triangular papilla at the base of legs I-IV, 4). an asymmetry of the feet ('tarsi'), resulting from the occurrence of a cusp

and cushion shaped structure on the foot. KRISTENSEN also provided new information about the buccal apparatus and reported the presence of at least two juvenile instars. The note by KRISTENSEN of adults of *M. imberbis* without trunk cirri, a potential new species (KRISTENSEN, *l.c.*: p. 291), was erroneously attributed to RAMAZZOTTI (1972).

ROSSI & CLAPS (1989) reported *M. imberbis* from Monte Tronador in the Argentinian Andes, which probably represents "Tronador (Ventisqueros...)" *sensu* MIHELČIČ (1967), as one of two type localities for *M. granulatus*. Unfortunately, ROSSI & CLAPS gave no morphological information about their material. Similarly, OTTENSEN & MEIER (1990) reporting *M. imberbis* from South Georgia, its *terra typica*, provided neither comments or morphological data.

In describing a new species, *M. tasmanicus* from Tasmania, DASTYCH & MOSCAL (1992) compared the new taxon with unpublished samples from the Chilean Andes that were identified as *M. imberbis*. McINNES (1994) summarized from the literature the distribution of three *Mopsechiniscus* species (*imberbis*, *granulosus*, *tasmanicus*).

Material and methods

The paper is based on material of *M. imberbis* from three different tardigrade microslide collections: (A) Dr. R. D. KATHMAN, deposited in the Zoologisches Museum Hamburg (ZMH), (B) the British Antarctic Survey (BAS, Cambridge) and (C) T. MEIER M. Sc. (Oslo). All animals were collected in Sub-Antarctic South Georgia, the *terra typica*. Specimens are mounted on microscope slides in HOYER's or polyvinyl-lactophenol medium and are listed in the "Redescription".

Five specimens from slides in the KATHMAN Collection (see DASTYCH 1997) were recovered for SEM examination using the method for mites (DASTYCH & RACK 1993). Specimens were washed in distilled water, transferred to hot BOUJIN's medium, dehydrated in ethanol, critical-point-dried, gold-coated and examined with a CamScan S4 SEM.

Examples of the poorly defined species, *M. granulatus*, (originally published as *M. imberbis*) from Argentina and Chile (RAMAZZOTTI 1962b, 1964, KRISTENSEN 1987, ROSSI & CLAPS 1989, DASTYCH & MOSCAL 1992) were also analysed and compared with the South Georgian specimens of *M. imberbis*. In addition, specimens from the Venezuelan Andes identified as *M. imberbis* by GRIGARICK *et al.* (1983) were also examined.

Unless otherwise indicated, all specimens illustrated originate from the KATHMAN Collection (ZMH). Interference contrast photomicrographs were taken with ZEISS "Axiomat". Measurements in parentheses are those of the neotype.

The following abbreviations are used in text and illustrations:

A- lateral appendage (cirrus) *A*, *an*- anus, *B*- lateral appendage (spine) *B*, *bc*- claw basal cusp, *bp*- basal leg plate, *C*- lateral appendage (spine) *C*, *c1*- primary clava (= clava), *c2*- secondary clava (= cephalic papilla), *D*- lateral appendage (cirrus) *D*, *de*- cuticular depression on leg IV, *E*- lateral appendage (spine) *E*, *e*- eye spot, *ec*- external cushion on leg, *ex*- external claw, *fd*- lateral folds on median plate 2, *g*- male gonophore, *ga*- granular area (pillars) on leg, *hs*- head shield, *i*- triangular insertion of the paired plate II, *ic*- internal cushion on leg, *l*- lateral 'plates' in the male genital area, *m*- male genital 'median' plate, *mc*- mouth cone, *m2*- median plate 2, *m2d*- dorsal projections on median plate 2, *n*- notch, *np*- neck plate, *pa*- sensory papilla IV, *pl 1-4*: platelet 1-4, *ps*- pseudosegmental plate, *psd*- projections on pseudosegmental plate, *s*- leg spur, *sp*- shoulder plate, *su*- sub-cephalic median plate, *I*, *II*- the first and the second paired plate.

Redescription

Mopsechiniscus imberbis (RICHTERS, 1908)

(Figs 1–32)

Echiniscus imberbis RICHTERS, 1908: p. 4, Fig. 3; RICHTERS 1907, p. 916 (*nomen nudum*).

Pseudechiniscus imberbis,— THULIN 1911, MARCUS 1928, 1929 (as *species inquirendum*), 1936.

Mopsechiniscus imberbis. — DU BOIS-REYMOND MARCUS 1944 (in part); SUDZUKI 1964; RAMAZZOTTI 1962, 1972 (in part); RAMAZZOTTI & MAUCCI 1983 (in part); OTTESEN & MEIER 1990; McINNES 1994 (in part).

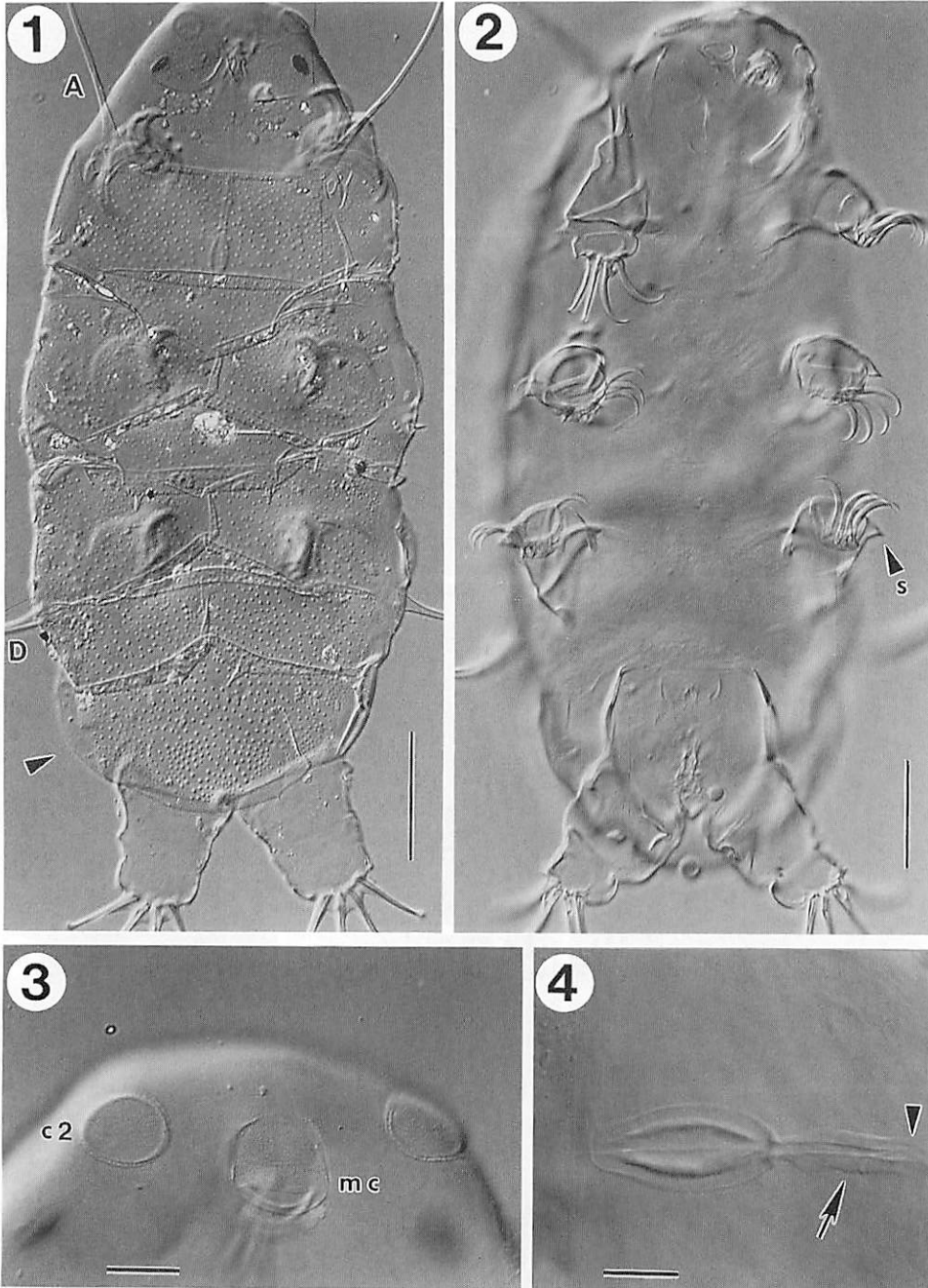
Mopsechiniscus imberbis (misidentification for *M. granulosis* MIHELČIČ), — ? DU BOIS-REYMOND MARCUS 1944 (in part); RAMAZZOTTI 1962b, 1964, 1965, 1972 (in part); RAMAZZOTTI & MAUCCI 1983 (in part); ? GRIGARICK *et al.* 1983; BINDA & KRISTENSEN 1986; KRISTENSEN 1987; ROSSI & CLAPS 1989; DASTYCH & MOSCAL 1992; McINNES 1994 (in part).

Material examined. — Sub-Antarctic South Georgia: (1) "Husvik, South Valley near Temp. Site", 21 January 1988, leg. R. RING; det. et ded. R. D. KATHMAN; 12 slides with 23 specimens mounted in HOYER's medium: 9 ♀, 10 ♂, 3 juveniles and one of undetermined sex (ZMH Reg. No. A62/95: 268–279). One specimen (slide ZMH No. A62/95: 279) from this locality (♂, 321 µm long) designated as the NEOTYPE is deposited in the Zoological Museum Hamburg. The neotype, positioned dorso-ventrally (Fig. 1), mounted with a second specimen, under separate cover glass, positioned dorso-laterally. Five specimens were recovered from three slides (Nos. A62/95: 268, 271, 273) used for SEM examination. (2) Three slides from the MEIER Collection (Nos. 12/100, 14/102, 19/100: HOYER's medium): Husvik, scree-field with some mosses, ca 30 m a.s.l. From moss, 11–13 March 1988, 3 ♂, det. T. MEIER (see OTTESEN & MEIER 1990). (3) Four slides with specimens collected in the region of Husvik Whaling Station, Stromness Bay, labelled: (A) "S. Georgia, H. DARTNALL 1992/93, 2 Dec 1992" (♂: PVL); (B) "S. Georgia, H. DARTNALL 1992/93, 5 Dec 1992" (and larva: PVL); (C) "S. Georgia, pool x2" (♂ and larva: HOYER's); (D) "S. Georgia, H. DARTNALL, 1993" (♀ and specimen of undetermined sex: HOYER's) (from the BAS Tardigrada Collection: det. S. J. McINNES).

Diagnosis. — A median sized to large *Mopsechiniscus* with long filamentous lateral appendages *A*, *D*, short spines *B*, *C* and tiny (if any) tooth in *E*. Posterior edge of median plate 2 with a pair of short dorsal spines *m2d*. Legs I–III with distinct conical spur. Adults and larvae with the same number of trunk cirri.

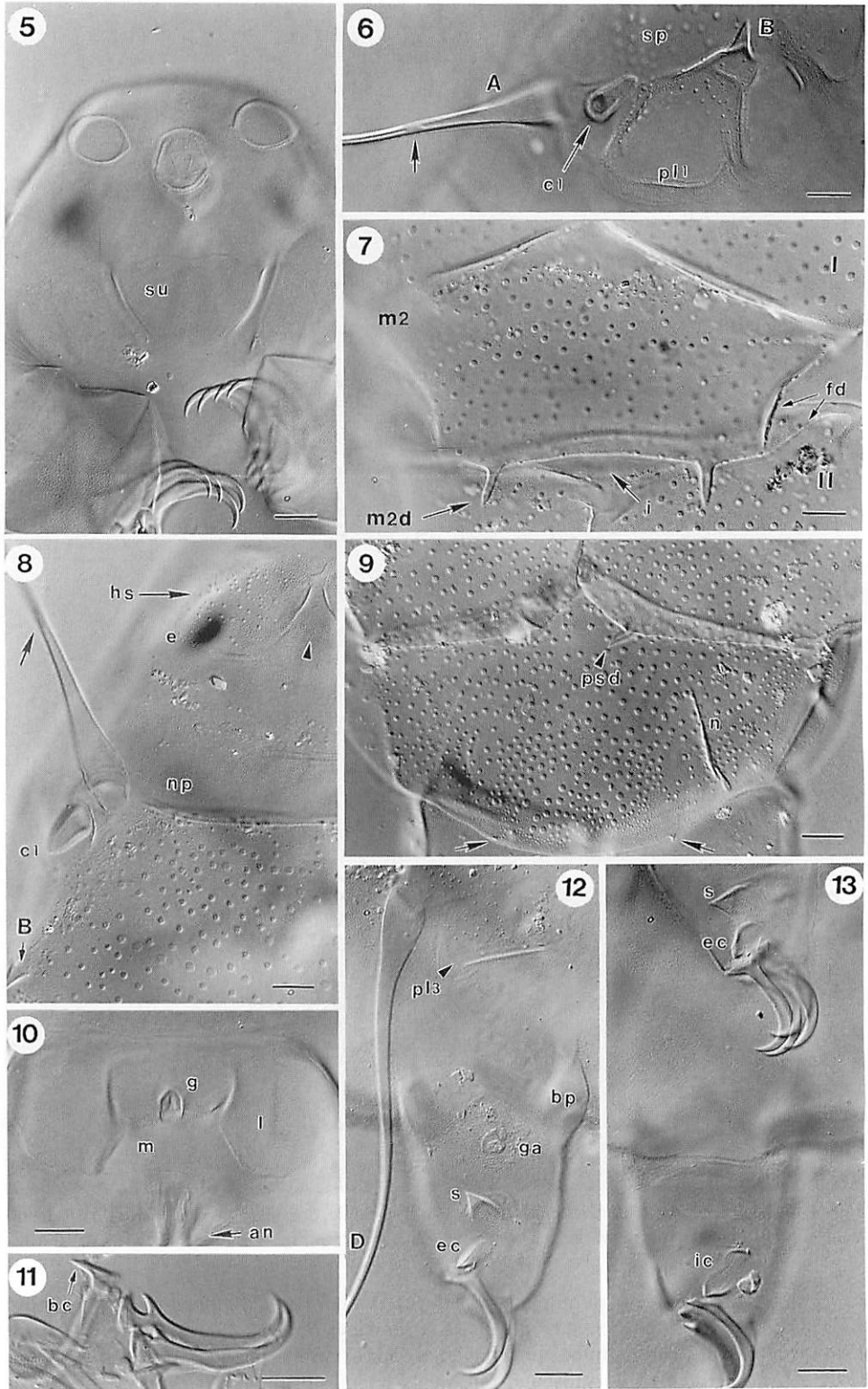
Description. — Median sized to large species, its body length between 310–466 µm (neotype 321 µm). Females larger (381–466 µm) than males (319–396 µm), two-clawed juvenile ('larva') 160 µm long. Body colour of living animals not known (presumed red), as it was not reported in the original description (RICHTERS 1908). In the slide preparations, animals yellowish-gray. Eye-spots large, dark-brown, oval and bowl-shaped.

Dorsal plates well developed (Figs 1, 21, 26, 28). Head segment with two anteriorly (dorso-frontally), slightly depressed (concave) oval areas, characteristic of most echiniscids, seen as two lobe-shaped symmetrical structures in slide preparations (Fig. 8: *hs*), or small shields in SEM (Fig 21: *hs*), that form the distinct head faceting. Usually only the rounded posterior edge of each shield distinctly marked, resembling two closely positioned wide letter "U" 's (Fig 8). The area between the shields (Fig. 8: arrowhead) is triangular and appears slightly raised above the surface of the surrounding shields, particularly in its narrower (apical) region. This apparent elevation, an optical illusion caused by the concavity of the adjacent shields, was over-schematised when drawn by DU BOIS-REYMOND MARCUS (1944: Fig. 9c) and inaccurately designated as an important generic character. The depression in the middle of the head plate *sensu* KRISTENSEN (1987) was not observed, yet in some preparations, the head shields were slightly convex and the area between them appeared, by comparison, depressed. Neck plate wide but poorly marked (Figs 8, 21, 22: *np*). Shoulder plate medially with more or less distinct vertically directed keel (Fig. 21). Trunk segments II and III with well sclerotized and vertically subdivided (paired) plates I and II (Figs 1, 21). Anterior median part of the paired plate II with a small triangular shield-like insertion (Figs 7, 26: *i*), the apex of which is directed posteriorly, so that its base borders with the median plate II (Figs 7, 21, 26). Trunk segment IV with pseudosegmental and terminal plate, the former being vertically subdivided. Terminal plate short and wide, with two long notches (incisions) but without faceting (Figs 1; 9, 25: *n*).



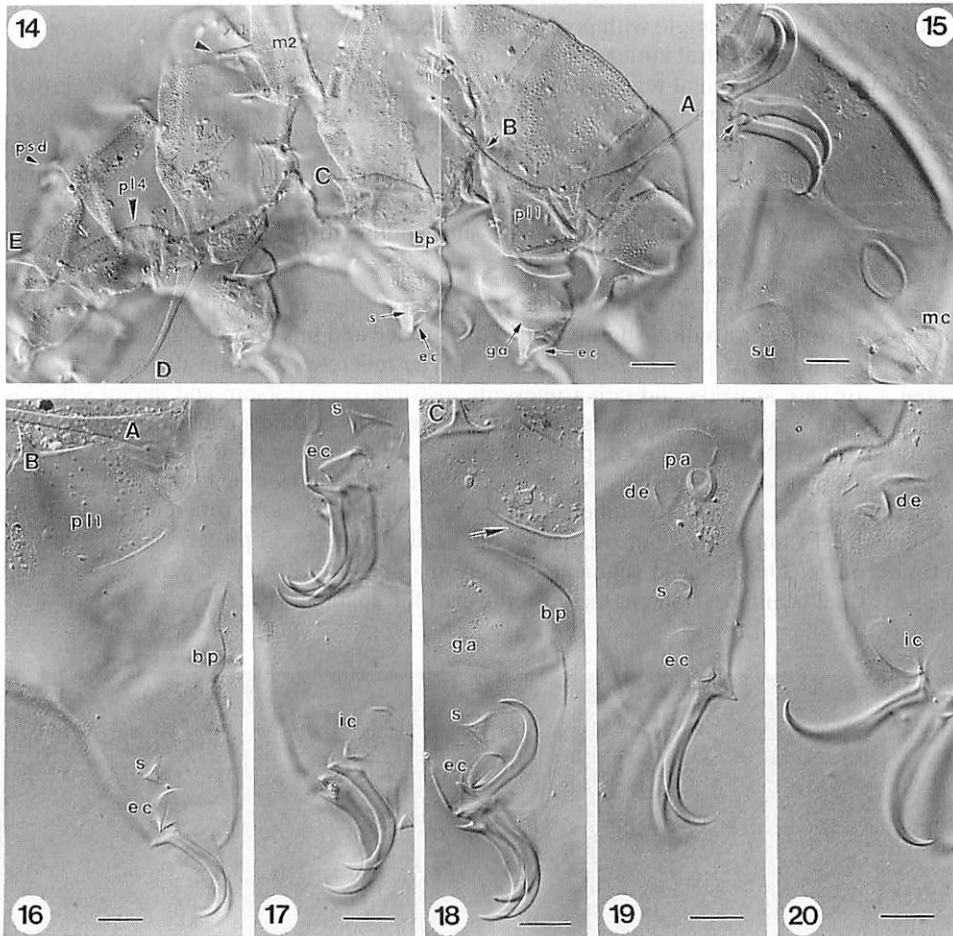
Figs 1–4: *Mopsechiniscus imberbis* (RICHTERS, 1908): 1- male, dorsally; 2- male, ventrally; 3- head, ventrally; 4- pharyngeal region (Figs 1, 3: neotype. Scale bar for Figs 1, 2: 50 μ m, Figs 3, 4: 10 μ m).

Small, closely placed lateral plate (platelets I-IV) border each dorsal trunk plate (Fig. 21). Platelets I-III are associated with lateral appendages *B*, *C* and *D*, respectively. Platelet I (at the shoulder plate) is trapezium shaped, its apex terminating as a short distinct tooth (Fig. 22: *pl1*), directed dorsally and represents lateral appendage *B* (Figs 6, 8, 22: *B*).



Platelet II is quadrangular in shape, and the spine (appendage *C*), directed obliquely dorso-posterior (Figs 21, 23), is distinctly separated from the remaining shield. Platelet III (at the paired plates II) rectangular and associated with a long lateral cirrus *D* (Figs 21, 24: *pl3*, 25). Platelet IV is situated at the border between pseudosegmental and terminal plate, and is the longest of all the accompanying shields (Figs 21, 25: *pl4*). The platelets are often poorly marked in the slide preparations, and the short tooth *B* and spine *C* are sometimes barely visible when observed dorsally.

Median plates 1–3 well marked, with plate 1 large and triangular, its apex directed posteriorly (Figs 1, 21). Median plate 2 (*m2*) the largest, is trapezoidal with the longest, basal side directed anteriorly (Figs 1, 7). Posterior part of plate 2 characteristically



Figs 14–20: *Mopsechiniscus imberbis* (RICHTERS, 1908): 14- larva, laterally; 15- male, head fragment, laterally; 16- leg I in (lateral) external view; 17- leg I in lateral view: external (upper) and internal (lower) aspect; 18- leg II, lateral (external) view; 19- leg IV, lateral (external) view; 20- leg IV, lateral (internal) view (Fig 14: BAS Collection. Scale bar = 10 μ m).

Figs 5–13: *Mopsechiniscus imberbis* (RICHTERS, 1908): 5- male, body anterior, ventrally; 6- fragment of 1st trunk segment, laterally; 7- median plate 2; 8- fragment of head and shoulder plate, dorsally; 9- pseudosegmental and terminal plate; 10- male, genital plate; 11- claws IV, laterally; 12- leg III, lateral (external) view; 13- legs III in lateral view – external (upper) and internal (lower) aspect (Figs 8, 9: neotype; 6, 7, 10: Meier's Collection; 11- BAS Collection. Scale bar = 10 μ m).

folded over the anterior margin of the (segmental) paired plates II and almost covering more or less the triangular median insertion of the latter plate. This long transversal fold of median plate 2 has two posteriorly directed, sharp, short spines (*m2d*) (Figs 7: *m2d*, 21, 26–28). Cuticle of the plate tucked under this fold (Fig. 27), borders with the anterior margin of the paired plate II and its median triangular insertion. This folding additionally forms two characteristic small folds on the lateral sides of the median plate (Figs 7, 21, 26–28, 31: *fd*). Median plate 3, visible as a triangular structure in ‘normal’ (slightly contracted) animals (Figs 1, 28), but is more rhomboid in elongated individuals (Fig. 21).

Ventral plates absent, except for poorly marked subcephalic and male genital plates. Subcephalic region with two elongated, obliquely directed cuticular thickenings, which delimit a median subcephalic plate and two accompanying small lateral areas (Figs. 2, 5), forming an inverted triangle with poorly defined base and no apex (Figs. 5, 15: *su*), as the apex is fused with ventral cuticle. These often barely visible subcephalic structures, also occur in juveniles. Genital region on both sides of a male gonophore with a thin, vertical and elongated cuticular thickening, which delimit a median area (*m*) with a gonophore (*g*) and two lateral (*l*), more or less small roughly round ‘plates’ (Figs 2, 10). The small male gonophore is oval (4.5 μm wide in the neotype) and located centrally on a small median ‘plate’ (Fig. 10: *g*, *m*). Female genital papilla (15 μm diameter in a specimen 392 μm long), composed of six rosette-like lobes surrounding the gonopore, is located on a smooth ventrum without plates.

Body sculpture composed of double ‘granulation’ of small, hemispherical cuticular tubercles (knobs) protruding slightly above the surface and tiny, closely-spaced and barely visible punctation (Figs 1, 7–9, 21, 26, 27). The tubercles ($\leq 2 \mu\text{m}$ diameter, usually about 1 μm) are sparsely and rather unevenly distributed on dorsum and lateral sides, as well as surface between the plates, and are covered with a thin, outer cuticular stratum (deformed in SEM: Fig. 30). On plate margin the tubercles are smaller and less numerous, on platelets solitary or absent (Figs 6, 22–25), and absent from legs and ventrum. The neck plate is smooth, with few tubercles (Figs 8, 22). The size of the tubercles is relatively similar on all trunk plates, but smaller on the head, platelets and posterior margin of the terminal plate. On the head segment they are mainly to the anterior part of the (lobe-shaped) shields, almost none in the posterior part the segment (Fig. 8).

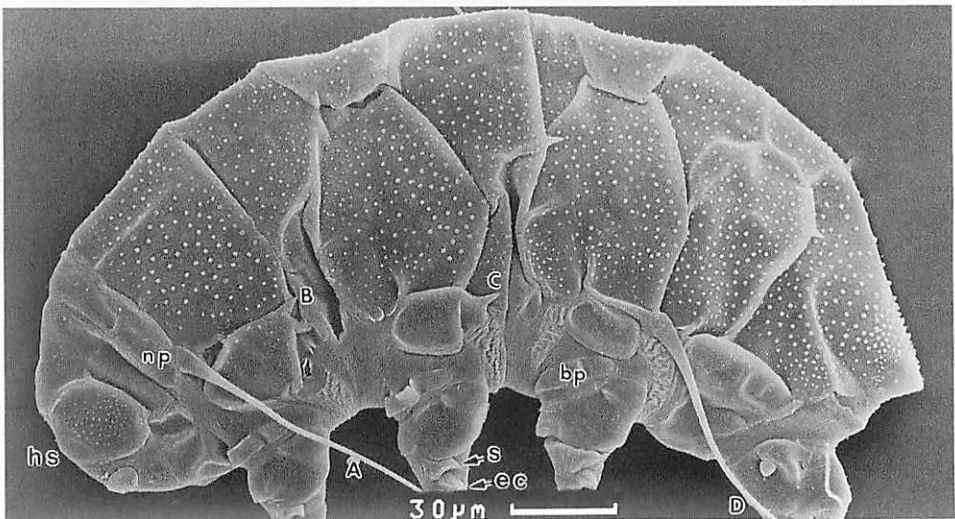


Fig. 21: *Mopsechiniscus imberbis* (RICHTERS, 1908): whole animal, latero-dorsal view.

Cuticular punctation (the dense granulation) comprises of tiny, barely visible epicuticular pillars (0.2-0.3 μm in diameter), appearing as spaced points when observed dorsally (Figs 7, 27). These pillars occur over most of the body, but are absent from the ventrum and, under SEM, absent from around tubercles, thus forming there a characteristic 'empty' ring visible (Figs 27, 30: arrowheads). The pillars are distinct under SEM, when the thin outer cuticular stratum is damaged or dissolved by fixatives (Figs 29, 30).

Mouth cone large and wide based (Figs 2, 3: *mc*, 5). Buccal apparatus large, but damaged by mounting media and thus poorly visible. Mouth tube with thin, double cuticular wall (primarily incrustated with CaCO_3) outside pharynx (Fig. 4: arrowhead). Pharyngeal unit of mouth tube with a single, thick, i.e. strongly sclerotized wall (Fig. 4: arrow). Placoids curved and wide.

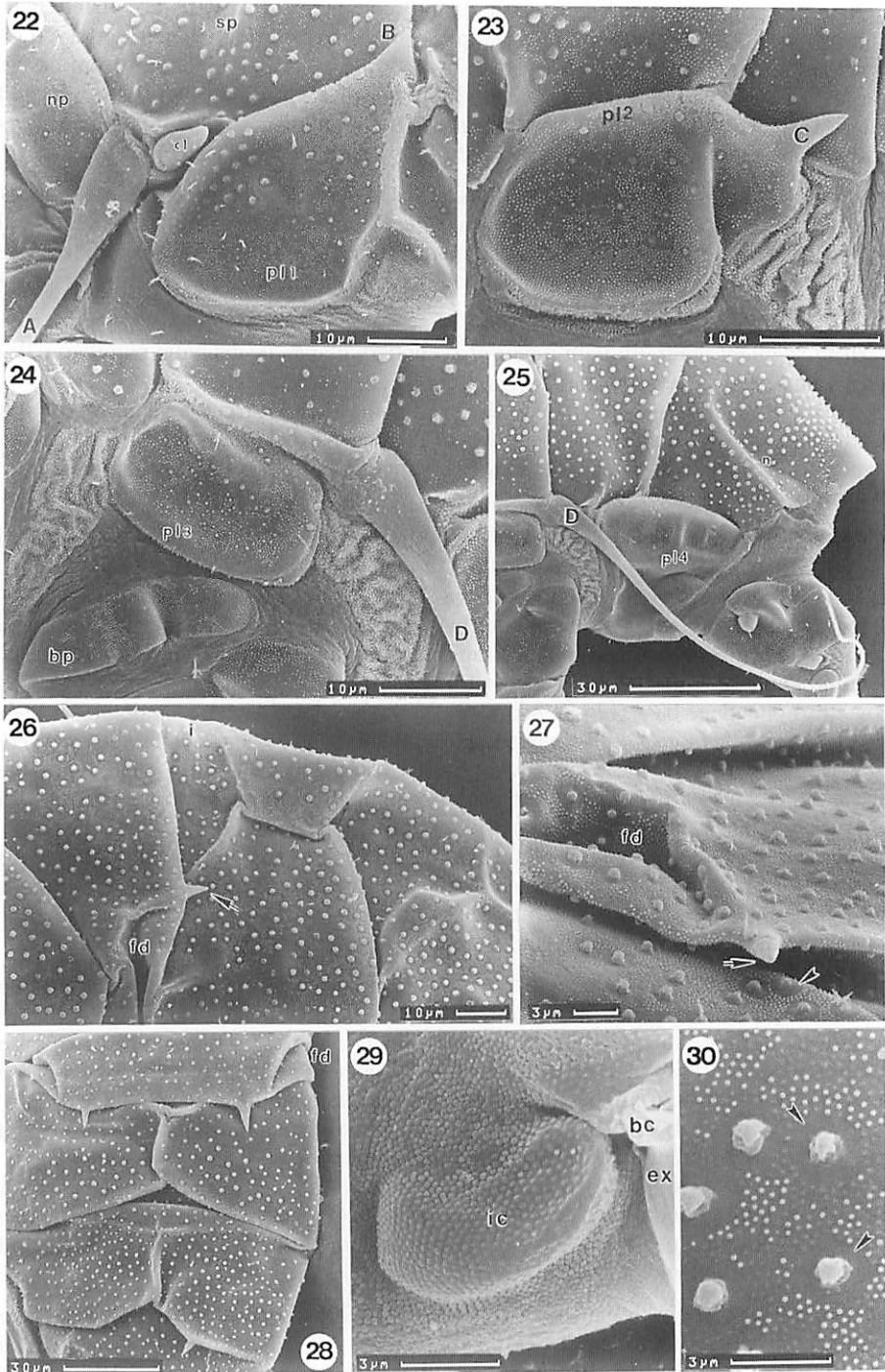
Head segment ventrally with a pair of secondary clavae (= cephalic papillae: *c2*); no internal and external sensory cirri (Figs 3, 5). The secondary clavae large (10-15 x 7-13 μm ; 13 x 11 μm in the neotype), oval, flattened dome-shaped structures and slightly larger in males than in females. The reduction of the anterior head sensory cirri, the primary clavae and the more medial, slightly lower distinct mouth cone, give the animal's head a distinct appearance (see Fig. 5).

Lateral appendages *A*, *B*, *C*, *D* and usually (tiny) *E* present, *A* and *D* as long cirri, with *A* (134-242 μm (183 μm)) usually 10-20% longer than *D* (132-220 μm (202 μm)), are one to two thirds body length. Base of cirrus *A* and *D* characteristically bulbous (Figs 8, 12, 22, 24), but without a distinct border between cirrophore and flagellum. The interior (lumen) of the cirrus base and its flagellum not sclerotized. In slide preparations the cirri resemble capillary tubes, empty except for a short internal cuticular unit situated well above the appendage base (Fig. 6, 8: arrow). At the base of cirrus *A* a small, cone-shaped clava (primary clava: *c1*) with rounded apex (Figs 6, 8, 22: *c1*). Clava slightly curved in distal part towards posterior, in the neotype 10.5 μm long and 6 μm wide at the base. Lateral appendages *B* and *C* are short tooth- or spine-like cuticular projections 5-9 μm long (in neotype, 7 and 7.5 μm , respectively). Usually a small tooth-like projection, 1-5 μm (on average 2-3 μm) long, is at the base of each notch (incision) on the terminal plate (= location *E*). In the neotype these are 1 and 1.5 μm , and aberrantly situated more terminally (Fig. 9: arrow). Spurs at *E* maybe of different size (as in neotype), or more rarely, situated unilaterally in one notch, and were absent in 12 of 28 specimens.

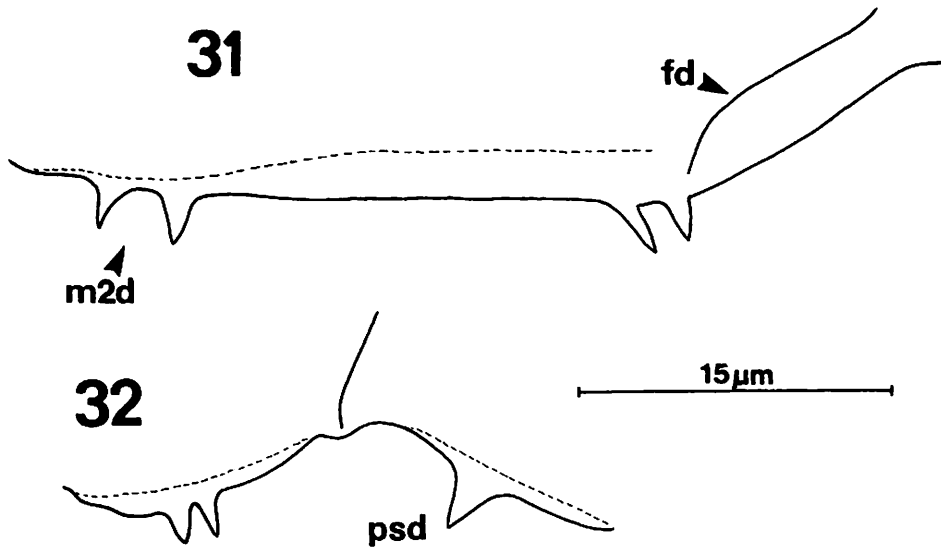
A pair of short, sharp projections (spines) occur on the median 2 and pseudosegmental plates. Spines of median plate 2 (*m2d*) are attached to the edge of its posterior fold (Figs 7: *m2d*; 26, 27: arrow) and are slightly thinner and longer than those on the pseudosegmental plate (*psd*). The spines at *m2d* are variable in number, e.g. completely absent (in one specimen: $n=26$); uneven, with two on one side and three on the other or 2:1; or even with two on each side (Fig. 31). Spine length variable at 4-14 μm (neotype 5 and 7 μm), and often different on the same plate (Fig. 28). Projections on posterior margin of pseudosegmental plate (*psd*) usually in the form of wide based, short teeth (Figs 9: *psd*, 32), 2-9 μm long (5 and 6 μm), and often of unequal length in the same specimen. Teeth were absent in three specimens (Fig. 28), a double complement located more unilaterally in one specimen and another was asymmetric with 2:1 spines on each side (Fig. 32: *psd*).

Legs, particularly IVth pair, long (Figs 1, 2, 12, 20). Externally on the basal (proximal) part of each leg, below each segmental platelet, is a small, strongly sclerotized and elongated plate (Figs 12, 14, 16, 18, 24: *bp*), that is more distinct on legs I-III but poorly developed on legs IV.

A roundish granulated area composed of relatively large epicuticular pillars occurs below the basal plate (Fig. 18: *ga*). The distal part of the leg (the foot) is asymmetric, caused by two cushion-like cuticular structures located each side of the claw row (Figs



Figs 22–30: *Mopsechiniscus imberbis* (RICHTERS, 1908): 22- fragment of 1st trunk segment with platelet I, laterally; 23- platelet II, laterally; 24- platelet III, laterally; 25- the body posterior, laterally; 26- dorsal plates, latero-dorsal view; 27- fold of median plate 2 and spine *md2*: frontal view; 28- dorsal plates, dorsally; 29- internal cushion-shaped foot structure at the external claw IV, ventrally; 30- cuticular knobs and pillars on paired plate II, dorsally.



Figs 31, 32: *Mopsechiniscus imberbis* (RICHTERS, 1908): aspects of the variability found in plate spines (31- median plate 2; 32- pseudosegmental plate).

13, 17); the internal cushion (*ic*) slightly larger than external (*ec*). Both cushions with distinct dorsal keel, terminate distally in a well formed cusp (Figs 16–18), that is less distinct (Fig. 20) or absent from internal cushion of leg IV (Fig. 29). The presence of these cushion-like structures is unique for echiniscids. A distinct characteristic spine (*spur*: *s*) is situated on all legs above the external cushion. The spurs increase in size from leg I to III and have well developed, conical, wide base and sharp tip directed posteriorly (Figs 2, 12–14, 16–19, 21: *s*). Spur on leg IV smaller and papilla- or cusp-shaped (Fig. 19). Sensory spine on leg I absent. Leg IV with a small hemispherical sensory papilla (Fig. 19: *pa*) closely associated with cuticular depression of unknown function (Figs 19: *de*; 25). A similar depression also occurs on the internal basal side of leg IV, well above the cuticular cushion (Fig. 20: *de*). Leg IV without spine fringe.

All claws long, relatively narrow and with an elongated base formed by a well defined basal cusp (Figs 11: *bc*, 13, 16–19). Claws IV distinctly (*c.* 30%) longer than the claws III. Internal claws with distinct spur, situated slightly above the base of the claw, directed moderately towards the base. Space caused by spur and basal cusp almost round on (internal) claw IV (when the claw is observed laterally) and oval on (internal) claws I–III (Figs 13; 15: arrow). External claws slightly shorter than the internal ones. External claw on legs IV 27–40 μm (31 μm), the internal one 27–40 μm (33 μm).

Juveniles (4-clawed instars) smaller (310–317 μm) than adults. Their body similarly sculptured, with identical arrangement and comparable size of the body appendages to that of adults, with anus but without gonophore.

Larva (2-clawed instar) with dorsal and lateral plates (Fig. 14) of similar shape to that of adults. One of the only two available specimens, slightly shrunk, with length of 160 μm . Body sculpture comprising very small, densely placed subcuticular pillars, which are largest (*c.* 0.5 μm in diameter) on shoulder and terminal plate and shaped like small tubercles (knobs). The distinctly differentiated double-shaped cuticular sculpture of adults was not found in larvae. The cirrotaxy (= the arrangement of the body appendages) is also identical to that of adults, i.e. no dorsal projections on median plate 1 (= *m1d*). However,

some of larval appendages are proportionally larger, e.g. on median plate 2 (Fig. 14, *m2d*, arrowhead: 7 μm), the pseudosegmental spines (*psd*: 9 μm), and the spurs at *E* (8 μm) are particularly well developed and project from the distinctly enlarged base of each notch (Fig. 14: *E*). Basal plate of each leg more sclerotized (Fig. 14: *bp*) in larvae, and the granulated area on external side of the leg relatively larger. Legs with external spur and their feet with two cushion-like structures. Sensory spine on leg I absent, leg IV sensory papilla present. Claws of same shape as in adults, with claws IV distinctly longer (20 μm) than claws III (14 μm).

Variability: *M. imberbis* is characterized by a relatively small individual variability with respect to examined characters. The presence of appendages *A*, *B*, *C*, *D*, of platelets I-IV and the structures of the leg are constant. Some variability occurs in the presence or absence of the dorsal appendages and size and number of appendages (see above). The dorsal projections *m2d* were absent in only one of the 26 examined specimen (= 3.8%), *psd* in three specimens (11.5%) and the lateral projections *E* in 12 of 28 animals (43%). The projections *m2d*, *psd* and *E* can vary sometimes markedly in size.

Differential diagnosis. — *M. imberbis* is distinguished from the poorly and insufficiently described *M. granulatus* (see below) by its cirrotaxy and external spur on legs I-III. The taxa differ in, 1). the shape of appendages *C* (short spines in *M. imberbis* versus long filamentous cirri in *M. granulatus*), 2). the presence of dorsal projections *m2d* (present v. absent), and 3). the external projection (spur) on legs I-III (relatively large, short, sharp tipped, cone shaped and wide based versus distinctly smaller, often barely visible, inconspicuous, round tipped tubercle that is only present on leg II and III).

M. imberbis can be separated from *M. tasmanicus* by, 1). lateral appendages *B*, *C* and *D* (present versus absent), 2). appendages *E* (short spines, v. very long filamentous cirri) and, 3). dorsal projections *m2d* and *psd* (present, at least one type of them, v. absent).

M. imberbis can be distinguished from *M. frenoti* by, 1) dorsal appendages *m2d* (short spines v. long filamentous cirri), 2). the presence of appendages *B* (present v. absent), 3). external projection (spur) on legs I-IV (large, sharp tipped on legs I-III and papilla-like on legs IV v. small indistinct cuticular elevation only on legs II and III), 4). different pattern of sculpturing (widely spaced knobs v. closely spaced).

M. imberbis differs from the Brazilian specimens described by DU BOIS-REYMOND MARCUS (1944) by the presence of lateral appendages *D* and dorsal *psd*, which are absent in (adult) individuals from Sao Paulo (*l.c.*). The latter specimens could thus represent an undescribed species, but unfortunately there is no information about platelets, lateral appendages (spines) *B*, leg structures and some other characters for this material. Thus, the real taxonomic status of the Brazilian taxon must remain unsolved until new material from that region can be examined.

Specimens from Venezuela described in GRIGARICK *et al.* (1983) may represent another undescribed taxon. *M. imberbis* differs from this material by, 1). the presence of lateral appendages (spines) *B* (present v. absent), 2). the dorsal projection *m2d* (present v. absent), and 3). the shape of appendages *A* (long and filamentous in *M. imberbis* v. medium sized, stiff and spine-like).

The morphology of the juvenile instars in *M. imberbis* also differs from other *Mopsechiniscus* spp., particularly that of the two-clawed larva. MIHELČIČ (1967, 1971) gave no description for the larvae of *M. granulatus*, though they have been described by RAMAZZOTTI (1962b, 1965, 1972), RAMAZZOTTI & MAUCCI (1983) and KRISTENSEN (1987) under the name of *M. imberbis*. With only two larval specimens (only one well preserved), no conclusions can be drawn on the morphological variability. Nevertheless, the larva of this species differs distinctly from that larvae of other taxa, particularly the instars of

M. granulosus (see RAMAZZOTTI, KRISTENSEN, *l.c.*) through, 1) · the lack of dorsal projections *m1d*, 2), the presence of long filamentous lateral appendages *D*, and 3), possessing the same number of appendages as the adults. All these characters contradict the descriptions given for larvae of other *Mopsechiniscus* species.

Comment

The present taxonomic confusion at species level in *Mopsechiniscus* results mainly from the unavailability of type material for the type species, *M. imberbis*. The difficulties begun when DU BOIS-REYMOND MARCUS (1944) attributed a new Brazilian species to the original description, and the following redescriptions artificially expanded of the morphological variability of *M. imberbis*. Further confusion was caused by poor and, in several significant instances, incorrect description of *M. granulosus* (see MIHELČIČ 1967, 1971), for which there is no preserved type material (DASTYCH 1993). As a consequence, RAMAZZOTTI (1962b, 1964, 1965, 1972) and RAMAZZOTTI & MAUCCI (1983) were unable to distinguish between *M. granulosus* and *M. imberbis*, and therefore expanded even more the range of individual morphological variability of the latter species. Other authors followed the description and diagnosis of *M. imberbis* emended and compiled by RAMAZZOTTI (*l.c.*), thus misidentified their specimens collected from various localities in South America (GRIGARICK *et al.* 1983, BINDA & KRISTENSEN 1986, KRISTENSEN 1987, ROSSI & CLAPS 1989, DASTYCH & MOSCAL 1992). Only from the Sub-Antarctic South Georgia there been recent correctly identified records of *M. imberbis* (OTTESEN & MEIER 1990; and BAS Tardigrade Collection).

The availability of type material is the main factor which could resolve taxonomic chaos. Unfortunately for most tardigrades type specimens do not exist. RICHTERS (1908) designated no types for *M. imberbis* (this being a common practice at that time), nor any specimens survive in the remnants of RICHTERS microslide collection. MARCUS (1928, 1929, 1936), who examined microslides from the RICHTERS collection, makes no mention of *M. imberbis* type material, and as specimens have not been examined by other authors, the slides must now be considered lost. Consequently, a neotype of *M. imberbis* is designated in this paper.

Considering the period and quality of optics, RICHTERS (1908) provided a relatively accurate description and a useful photo of *M. imberbis*, overlooking only a few of the specific characters, including the presence of cephalic papillae and the lateral appendages (spines) *B*. Similarly, the interpretation of the description by MARCUS (1928, 1929, 1936) and the drawing, based on the Richters original photo (see RICHTERS 1908: Fig. 4 and MARCUS 1928: Fig. 135) are still sufficient for a correct identification of the taxon.

Current knowledge about other species of *Mopsechiniscus* is still limited and confused. Future contributions, including redescriptions of already published material, should help clarify the taxonomy and relationships between members of this genus. This new information also provide more information data on phylogeny of this widely distributed and probably Gondwanan faunal element, that also represents at the same time one of the most derived taxa within the ancient family Echiniscidae.

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