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Oreella mollis MURRAY, 1910 (Tardigrada): a redescription and revision of *Oreella*

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ABSTRACT: *Oreella mollis* MURRAY, 1910 (Oreellidae), a semi-terrestrial and primitive tardigrade is redescribed from Australian and Maritime Antarctic specimens. *Oreella vilucensis* RAHM, 1931 is recognized as a *nomen dubium*; *O. minor* RAMAZZOTTI, 1964 is a proposed new synonym of *O. mollis*, while *O. breviclava* GRIGARICK *et al.*, 1983 is a proposed synonym of *Hypechiniscus exarmatus* (MURRAY, 1907). *Oreella* is potentially important in constructing the phylogeny of terrestrial Tardigrada.

Introduction

The genus *Oreella* (Tardigrada) was established by MURRAY (1910) for *Oreella mollis* collected from the Blue Mountains, Australia. This primitive semi-terrestrial tardigrade occupies a key phylogenetic position both between the Arthrotardigrada and Echiniscoidea, and between marine and terrestrial tardigrades. Indeed ancestors of *Oreella* were probably the first terrestrial tardigrades.

The status of *Oreella*, or rather that of the parent family Oreellidae PUGLIA, 1959 (sensu RAMAZZOTTI 1962), has been the subject of much discussion (MURRAY 1910, THULIN 1928, MARCUS 1929, SCHULZ 1951, 1953, 1963, RAMAZZOTTI, 1964, RENAUD-MORNANT & ANSELME-MOIZAN 1969, RENAUD-MORNANT 1982, KRISTENSEN & HIGGINS 1984, MORONE DE LUCIA *et al.* 1984, BINDA & KRISTENSEN 1986, GRIMALDI DE ZIO *et al.* 1987, 1992, KRISTENSEN 1987, GRIMALDI DE ZIO *et al.* 1990, BERTOLANI, REBECCHI & CLAXTON 1996). The Oreellidae (*Oreella*) has been considered a basal form of Echiniscoidea, and a sister taxon to ancient *Stygarctus* (Stygarctidae); the latter taxon is recognized as a basal tardigrade family. Both these genera probably share a common ancestor.

Despite its phylogenetic importance, however, little is known about *Oreella*, or the five species ascribed to it. Species descriptions are confused and need revision. The present study is a comprehensive revision of *O. mollis* using eggs and adults recently collected from Australia and the Maritime Antarctic. The phylogeny of *Oreella* will be considered elsewhere.

Historical account

Five species have been ascribed to the genus *Oreella*:

1. *Oreella mollis* was based on types in moss, from Katoomba, Blue Mountains, c. 90 km W of Sydney, Australia. MURRAY (1910) emphasised the phylogenetic importance of *Oreella*, particularly its proximity to *Echiniscus*. Subsequent records of *O. mollis* include "Blue Bay, NS-Wales" (RICHTERS 1926); canton Freiburg: Swiss Alps (RAHM

1929) (cit. after MARCUS 1936) and "in small numbers" on Maritime Antarctic Signy Island (JENNINGS 1976a, b). The Australian *locus typicus* was confused with a site in Scotland (RAHM 1928, CUÉNOT 1932). The species was also reported from Australia as '*O.* cfr. *mollis*' in the text although it was referred as '*O. mollis*' in figure legends of adults and eggs in the same paper (BERTOLANI, REBECCHI & CLAXTON 1996).

2 i. An unidentified *Oreella* (="*Orella* spec." sic) from Rheinland, Germany (RAHM 1925a), lacked both precise locality and illustrations. RAHM (1925a) noted : "*O.* spec? I once found a species of the genus *Orella* in a moss cushion. Unfortunately, the slide was lost; thus I can give only a temporary and not exact description. Size: 300 µ. The medial terminal process was well recognizable. Apart from large cirri on the head there were also on both sides thorn-like processes: one behind the second pair of legs, the other before the third pair". Subsequent publications noted *O. mollis*: "... Hitherto in Germany found only near Bonn" (RAHM 1925b); and "...Only one genus *Oreella* with 3 species. In the area: *O. bonnensis* RAHM. With lateral head cirri, terminal medial thorn and, to differentiate from *mollis* (Fig. 861c), with thorn-like processes behind the second and before the third pair of legs (b and c). Habitat: Beuel at Bonn, the Province of Rhein" (RAHM 1932a, 1944). ("b and c" referred to the locations of projections in echiniscids). RAHM gives no further details of "*O. bonnensis*".

2 ii. *O. vilucensis* in mosses collected near Concepción ("Fundo Viluco"), Chile (RAHM 1931, 1932b). RAHM stated (1932b): "...I give a description of a new species....which seems to be identical with that from Bonn (see RAHM, 1925, Nr. 28. S.189)...", and that the new species was "...probably identical with that observed in Bonn, Beuel, Jew cemetery (see RAHM, G. 1925...)". *O. vilucensis* was characterized by "...strong [bilateral] cone-like thorns behind the second and before the third pair of legs" (*l.c.*).

3. *O. minor*, described and illustrated from Chile, provided the first account of sexual dimorphism in *Oreella* (RAMAZZOTTI 1964). *O. minor* was distinguished from *O. mollis* by its smaller size, double cuticular structure and teeth (= spurs) on the internal claws. Subsequent data from the original description of *O. minor* was restated, and both *O. mollis* and *O. vilucensis* recognized as valid species (RAMAZZOTTI 1965, 1972, RAMAZZOTTI & MAUCCI 1983), although *O. vilucensis* had two different dates of the original descriptions i.e. "1931" and "1925" in the latter two papers. *O. minor* was re-described, illustrated and the diagnosis of Oreellidae (but not *Oreella*) revised, using material rediscovered in Argentina (BINDA & KRISTENSEN 1986). They updated features, included the presence of seminal receptacles and provided a better definition of sexual dimorphism. Illustrations, notes and new records of *O. minor* were obtained from New Zealand (HORNING, SCHUSTER & GRIGARICK 1978), and the Scotia Arc (Signy Island, South Orkney Islands and South Georgia) (MCINNES 1995a, b).

4. *O. breviclava* was described as a new species from the Venezuelan Andes (GRIGARICK, SCHUSTER & NELSON 1983).

The family, Oreellidae, established by PUGLIA (1959; unpublished dissertation), was divided into two subfamilies: the Oreellinae (*Oreella* and *Echiniscoides*) and Archechiniscinae (*Archechiniscus*). RAMAZZOTTI (1962, 1972) ignored the subfamilies but accepted the taxon Oreellidae *sensu* PUGLIA as did BINDA & KRISTENSEN (1986), though RAMAZZOTTI & MAUCCI (1983) replaced PUGLIA with RAMAZZOTTI, (i.e. "Oreellidae Ramazzotti, 1962"), in accordance with ICZN rules (Article 9).

The literature contains further confusion. (1). Repeat of RAHM (1929) listing *O. mollis* in the Alps (MARCUS 1929). (2). Repeat of "*Orella* spec." from Bonn as "*O.* spec. 1" (*sensu* RAHM 1925a), though now considered to be a dubious taxon (MARCUS 1929). RAHM's identification of *O. mollis*, and thus its presence in the Alps, was subsequently questioned, whilst the two species *O. mollis* and *O. vilucensis* were recognised in the genus (MARCUS 1936). (3). *O. bonnensis*, was synonymized with *O. vilucensis* (see RAHM 1932b), based on the shared thorn-like projections and

O. vilucensis subsequently reported (MARCUS 1936) both at Beuel (Germany) and Concepción (Chile). (4). The Santiago (Chile) locality (RAHM 1932b: p. 127), was not recorded by MARCUS. (5). Both *O. mollis* and *O. vilucensis* were listed as possible taxa in Romania and Czechoslovakia (RUDESCU 1964). (6). BARTOŠ (1967) compounded reports of *O. mollis* from Italy, the Swiss Alps, Australia and *O. vilucensis* from Germany and Chile. (7). *O. vilucensis* was confirmed from Chile, whilst European records were doubted. The poorly known ecology of *Oreella* was summarised (BINDA & KRISTENSEN 1986). (8) A distribution summary of the four *Oreella* spp. (*mollis, vilucensis, minor* and *breviclava*), repeated the presence of *O. vilucensis* in Germany (MCINNES 1994).

Three phylogenetic trees have placed *Oreella* at the base of the echiniscids (THULIN 1928, MARCUS 1929, KRISTENSEN 1987). Subsequently *Parechiniscus* was placed between *Oreella* and *Echiniscus* by CUÉNOT (1926). SCHULZ, who analyzed the relationships between *Oreella* and his new genus *Stygarctus* (Stygarctidae), postulated the secondary loss of dorsal plates in *Oreella*. He also suggested a common ancestry of these genera (SCHULZ 1951, 1953, 1963). The Echiniscidae and Oreellidae are now considered as sister groups (KRISTENSEN 1987).

Material and methods

In the present study, specimens of *Oreella* from Australia, South America and especially the Maritime Antarctic were examined.

Micrometazoans were extracted from mosses and lichens collected from Signy Island (South Orkney archipelago, Maritime Antarctica) (method after DASTYCH 1985). Nineteen of these 25 extractions yielded c. 200 dead, but well preserved *Oreella*. Most (154 individuals: 46 ♀, 64 ♂, 44 juveniles, 9 eggs) were mounted on slides in FAURE's or PVL media and deposited in the Zoological Museum Hamburg (ZMH), while the remaining animals and four eggs were prepared for SEM examination. *Oreella* either dissolved or became barely visible in certain media, particularly gum chloral (e.g. HOYER, FAURE, SWAN, etc.), and polyvinyl-lactophenol (PVL), so some specimens were observed in water or glycerol temporary mounts with/without methylene blue or acid carmine staining. Tardigrades were examined via phase- and interference contrast microscopy, though most photomicrographs were taken with a ZEISS "Axiomat". For SEM examination specimens were washed, transferred to hot BOUIN's medium, dehydrated in ethanol, critical-point-dried and gold-coated for examination in a CamScan S4 SEM. Unless otherwise indicated all illustrations were prepared at ZMH from Signy Island material.

Mosses and lichens were collected from Cambewarra Mountain, New South Wales (c. 135 km S of the *locus typicus*), New England National Park, N.S.W. (425 km NE of the *locus typicus*) and from three sites in Tasmania, Australia. The 35 (13, 12, 10 juveniles, 6 eggs) extracted tardigrades were mounted in HOYER's medium for examination. The selected neotype, and an egg, are deposited in the Natural History Museum, London (NHM), while all other material is housed in the Australian Museum, Sydney or in the private collection of S. K. CLAXTON.

For comparison, specimens of *Oreella* spp. were borrowed from the following sources: the Bohart Museum, University of California, Davis (BMUC); the Museum of New Zealand Te Papa Tongarewa, Wellington (MONZ); the British Antarctic Survey, Cambridge (BAS); the Zoological Museum, Copenhagen (ZMC); the Natal Museum, Pietermaritzburg (NM); the Natural History Museum, Verona (NHMV); and the NHM, London. Many older specimens, including types, had deteriorated and were unusable. Some recent, especially Australian, specimens had also deteriorated to the extent that the cuticular granulation, head sense organs and bucco-pharyngeal apparatus were barely, if at all, discernible.

The specimen from NHM, slide labeled "Tardigrada / *Oreas* gen. n. / *mollis* n. sp." and "Australia / 1917.1.1.178 / C. ROUSSELET" was lost in an attempt to remount it. This may have been a type specimen from MURRAY's original material, extracted, mounted and labeled by ROUSSELET seven years after the description of *Oreella mollis*. ROUSSELET examined MURRAY's Antarctic rotifers (see GREAVES 1996), and may have had access to his Australian material from

the same expedition. The misspelled generic name "*Oreas*" on the slide label could confirm such an assumption.

The following abbreviations are used in text and illustrations: *A*- cirrus *A*, *an*- anus, *ap*- anal plate, *as*- anal slit, *BA*- bucco-pharyngeal apparatus, *c*- core of egg process, *c1*- primary clava (= clava), *c2*- papilla cephalica (= secondary clava), *ce*- cephalic external cirrus, *ci*- cephalic internal cirrus, *ct*- cuticle, *co*- mouth cone, *cr*- cirrophorus, *ec*- external claw, *gp*- genital papilla, *gr*- granules, *lp*- leg papilla, *m*- thin (membranous) part of the egg process, *mc*- median caudal projection, *op*- mouth opening, *os*- outermost cuticular stratum, *p*- cuticular pillars, *pe*- pedestal, *pl*- placoid, *s*- claw spur, *so*- sense organ, *sr*- seminal receptacle, *ss*- stylet sheath, *st*- stylet, *su*- stylet support, *tc*- core of the cuticular tubercle, *IV*- leg IV.

Body lengths were measured from the mouth to the tip of the median caudal projection; *pt* index (ratio) is the ratio of the length of an organ to the length of the buccal tube expressed as a percentage (PILATO 1981).

Taxonomic account

Suborder: Echiniscoidea MARCUS, 1927
Family: Oreellidae PUGLIA, 1959 (*sensu* RAMAZZOTTI 1962)

Oreellidae: PUGLIA 1959, unpublished dissertation; "Oreellidae PUGLIA 1959": RAMAZZOTTI 1962, 1972, BARTOŠ 1967, GREVEN 1980, BINDA & KRISTENSEN 1986; "Oreellidae RAMAZZOTTI, 1962": RAMAZZOTTI & MAUCCI 1983.

Emended diagnosis: Unplated semi-terrestrial Echiniscoidea with a short caudal median projection. Telescopic retractable leg with four claws in adults and two claws in larvae. Each internal claw with a downwardly directed spur. Sense organs present on legs I and IV. All head projections, except median cirrus, present. Papillae cephalica (= secondary clavae) located *under* the cuticle surface. Clavae (= primary clavae) papilla-like in females and juveniles, club-like in males. Buccal apparatus with stylet supports. Females with a pair of sack-like structures (seminal receptacles) caudo-laterally, opening directly to the exterior, but without a duct. Eggs freely laid, ornamented.

Type genus: *Oreella* MURRAY, 1910

Genus: *Oreella* MURRAY, 1910

Diagnosis: as for the family.
Type species: *O. mollis* MURRAY, 1910

Type locality: Katoomba, c. 3000 feet, Blue Mountains, New South Wales, Australia.
Composition: *O. mollis* MURRAY, 1910; *O. minor* RAMAZZOTTI, 1964 (**syn. n.?**).
Distribution: a Gondwanan element, recorded from Australian Continent, Tasmania, New Zealand, Maritime Antarctic (Signy Is.), South Georgia, and South America (Chile, Argentina).

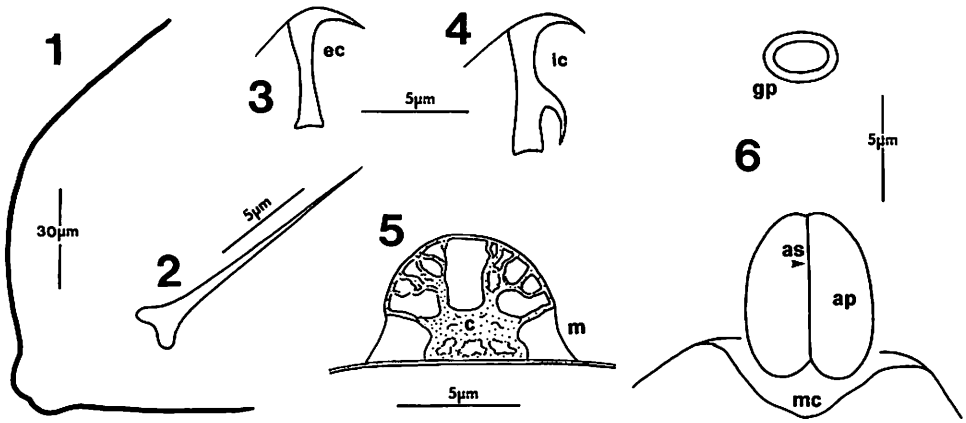
Oreella mollis MURRAY, 1910

Oreella mollis: MURRAY 1910; RAHM 1925b, 1929, 1932b, 1944; RICHTERS 1926; THULIN 1928; MARCUS 1928, 1929, 1936; CUÉNOT 1932; RUDESCU 1964; BARTOŠ 1967; RAMAZZOTTI 1962, 1964, 1972; JENNINGS 1976a, b; HORNING *et al.* 1978; RAMAZZOTTI & MAUCCI 1983; BINDA & KRISTENSEN 1986; McINNES 1994; BERTOLANI, REBECCHI & CLAXTON 1996.

Oreella cf. *mollis* BERTOLANI, REBECCHI & CLAXTON (1996: see legends for Figs 1-3).

Oreella vilucensis RAHM, 1931 (= *Oreella bonnensis* RAHM, 1932: see MARCUS 1936; = *Oreella* sp.: RAHM 1925a): RAHM 1931, 1932b, MARCUS (1936: as "*O. vilucensis* RAHM, 1925"), RUDESCU 1964, BARTOŠ 1967, RAMAZZOTTI 1962, 1965, 1972, RAMAZZOTTI & MAUCCI 1983, BINDA & KRISTENSEN 1986, McINNES 1994 (= **nomen dubium**).

Oreella minor RAMAZZOTTI, 1964: RAMAZZOTTI 1964, 1965; RAMAZZOTTI & MAUCCI 1983; BINDA & KRISTENSEN 1986; McINNES 1994, 1995a, b; DASTYCH & McINNES 1996 (= **syn. n.?**).



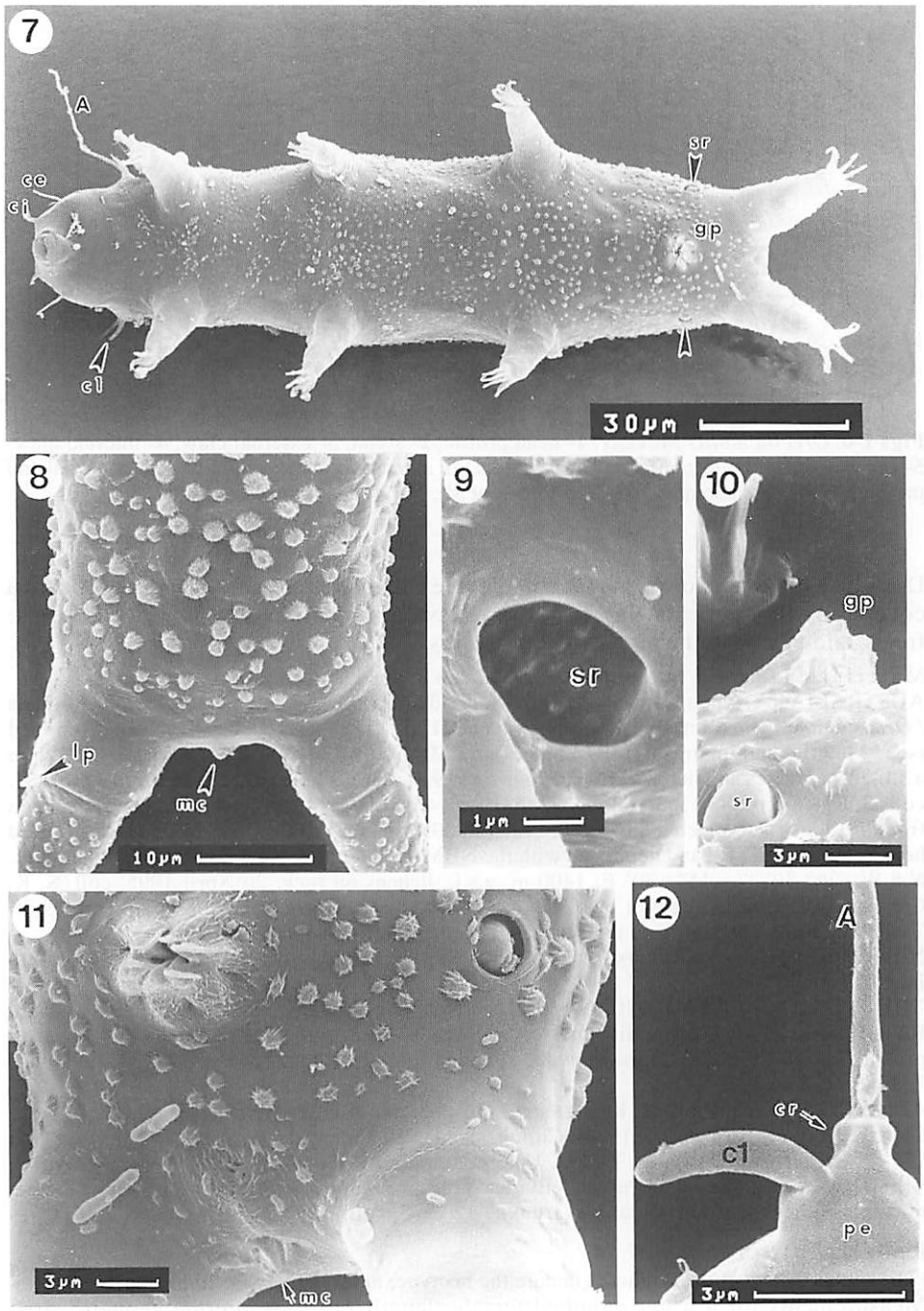
Figs 1-6. *Oreella mollis* MURRAY: **1**- head profile, **2**- stylet, **3**- external claw, **4**- internal claw, **5**- egg process, **6**- male genital and anal system (all abbreviations are explained in "Material and methods". Fig. 6: specimen from Cambewarra Mt, NSW, Australia).

Diagnosis: gonochoric *Oreella* with double cuticular granulation, papilla cephalica covered by thin cuticular layer, primary clava arising from cirrophore of cirrus *A*; freely laid eggs with hemispherical processes.

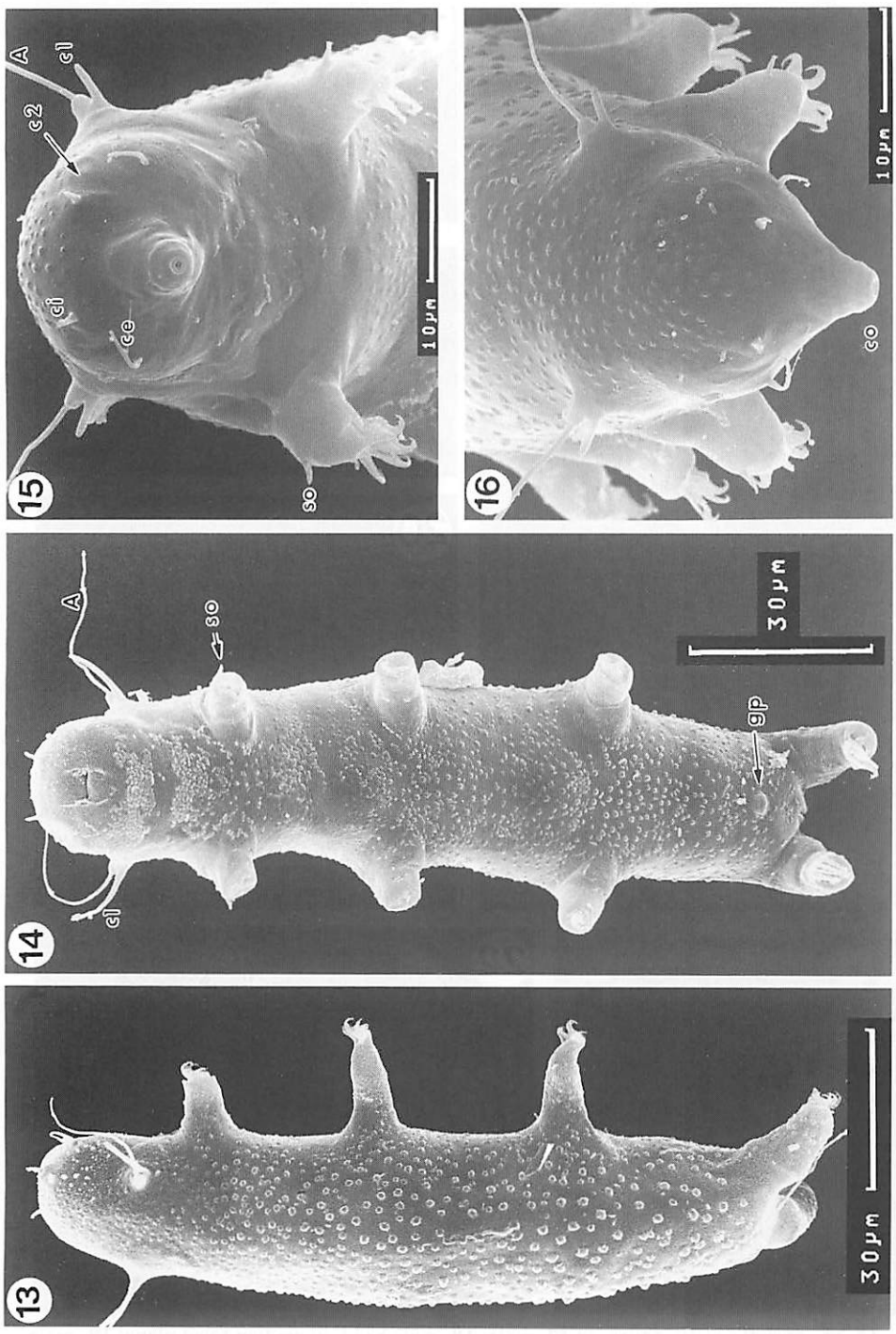
Material examined (the number of specimens studied is given in brackets):
AUSTRALIA: (A) type specimen (?): a dried individual on microscope slide labeled: "Tardigrada / *Oreas* gen. n. / *mollis* n. sp." and "Australia / 1917.1.1.178 / C. ROUSSELET", lost unexamined (see "Material and methods"); (B) Cambewarra Mt, N.S.W. 34° 48' S + 150° 35' E at 625 m a.s.l., from mosses and lichens on sandstone rock, 9 March, 19 June, 13 Sept 1986, 11 Jan. 1987, coll. S. K. CLAXTON (30 individuals: 12 ♀, 10 ♂, 4 juveniles, 4 larvae, 4 eggs): one specimen from this locality, collected on 11 Jan. 1987 (♀, 205 µm long: slide No. 1127-10) is designated here as the NEOTYPE and deposited with the NHM, London; (C) New England National Park, N.S.W., 30° 30' S + 152° 30' E, 1400 m a.s.l., lichens on rock, 20 April 1995, coll. S. K. CLAXTON (♂, 2 juv., 3 eggs) (also found in mosses on rocks and on *Nothofagus* trees); (D) Tasmania, foliose lichen from the Franklin River (no further data: ♀ and ♂).
NEW ZEALAND (see: HORNING *et al.* 1978): North Island, Trounson Kauri Park (1), South Island: Temple Basin (1);
THE MARITIME ANTARCTIC: (A) (see: JENNINGS 1976a): Signy Island (1); (B) Signy Island, Robin Plateau. East Lichen Hill, mosses and lichens from snow-free, non-calciferous stony ground, 11.2.1994, coll. M. EDWORTHY (33 slides with 154 individuals: 46 ♀, 64 ♂, 44 juveniles, 7 slides with 9 eggs).
ARGENTINA: (see: BINDA & KRISTENSEN 1986): mosses at Lago Mendez (E);
CHILE: (A) (see: RAMAZZOTTI 1964): Chiloè Island, Nal. Four syntypes of *Oreella minor*: 'Tipo 168 ♀', 'tipo 174 ♂', 'tipo 173' (♀, *simplex*-stadium), 'tipo 172 ♀'; (B) Temuco District, Villarica National Park near Pucon, Villarica Volcano, *Nothofagus* forest near its upper zone, mosses and lichens from *Nothofagus* trunk, 2.12.1987, coll. B. STUCKENBERG (2 ♀, 2 ♂).

Redescription

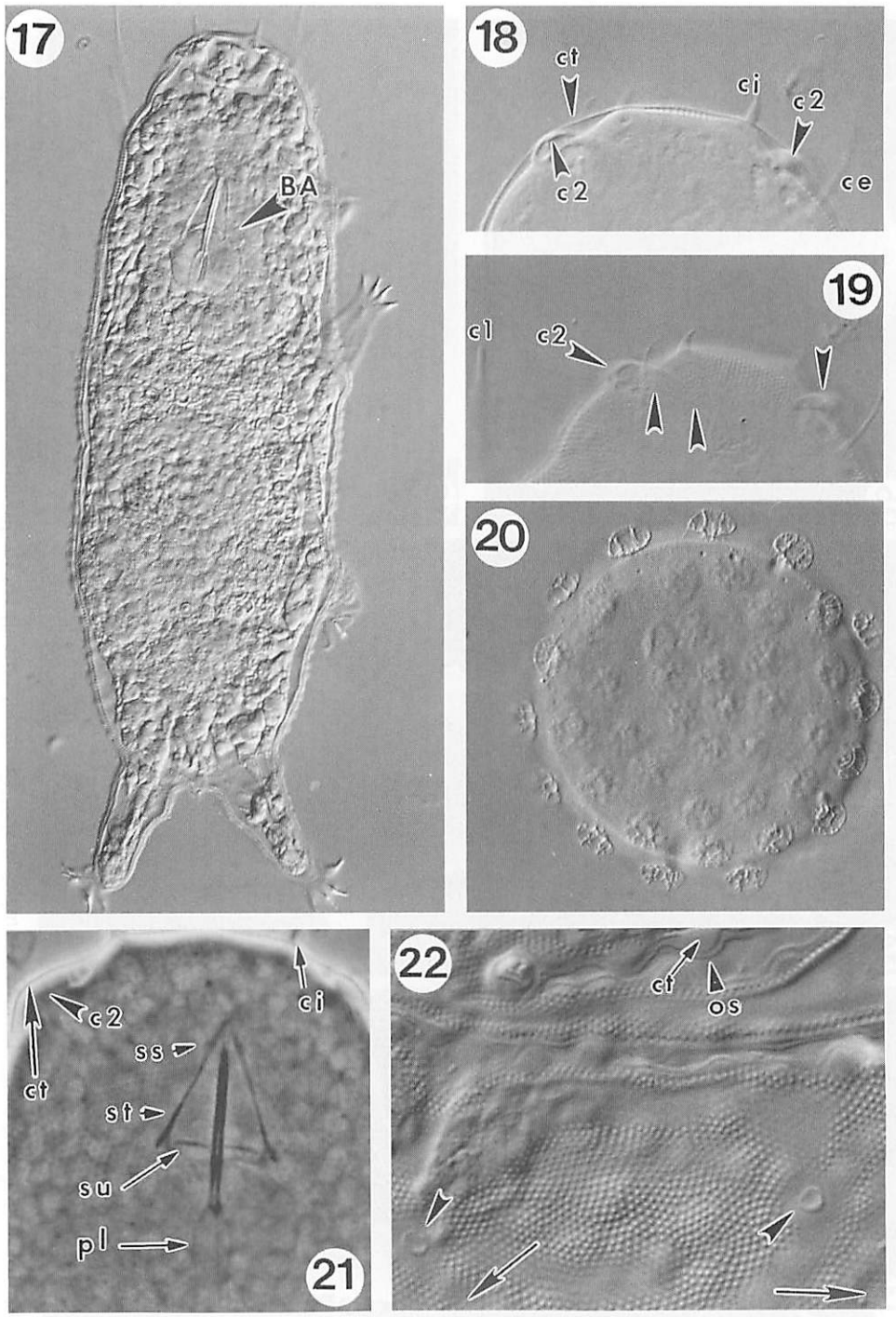
(The measurements in parentheses denote the neotype, unless otherwise indicated).
Measurements for a water mounted female: length 212 µm; internal cephalic cirri: 3 µm; external cephalic cirri: 11 µm; papilla cephalica: 9 µm; cirrus A: 43 µm; primary clava: 5.5 µm; seminal receptacle (external diameter): 6 µm; the receptacle opening (diameter): 3.5 µm; leg IV: 38 µm; external claws (leg IV): 5.5 µm; internal claws (leg IV): 6.3 µm; bucco-pharyngeal apparatus: 31 µm; mouth tube: 18 µm; its external diameter: 1.8 µm; stylet sheaths: 5.5 µm; their external diameter: 0.7 µm; stylets: 15.5 µm; pharynx (diameter): 15 µm; placoids: 6 µm; *Pt* index for stylet supports 68%.



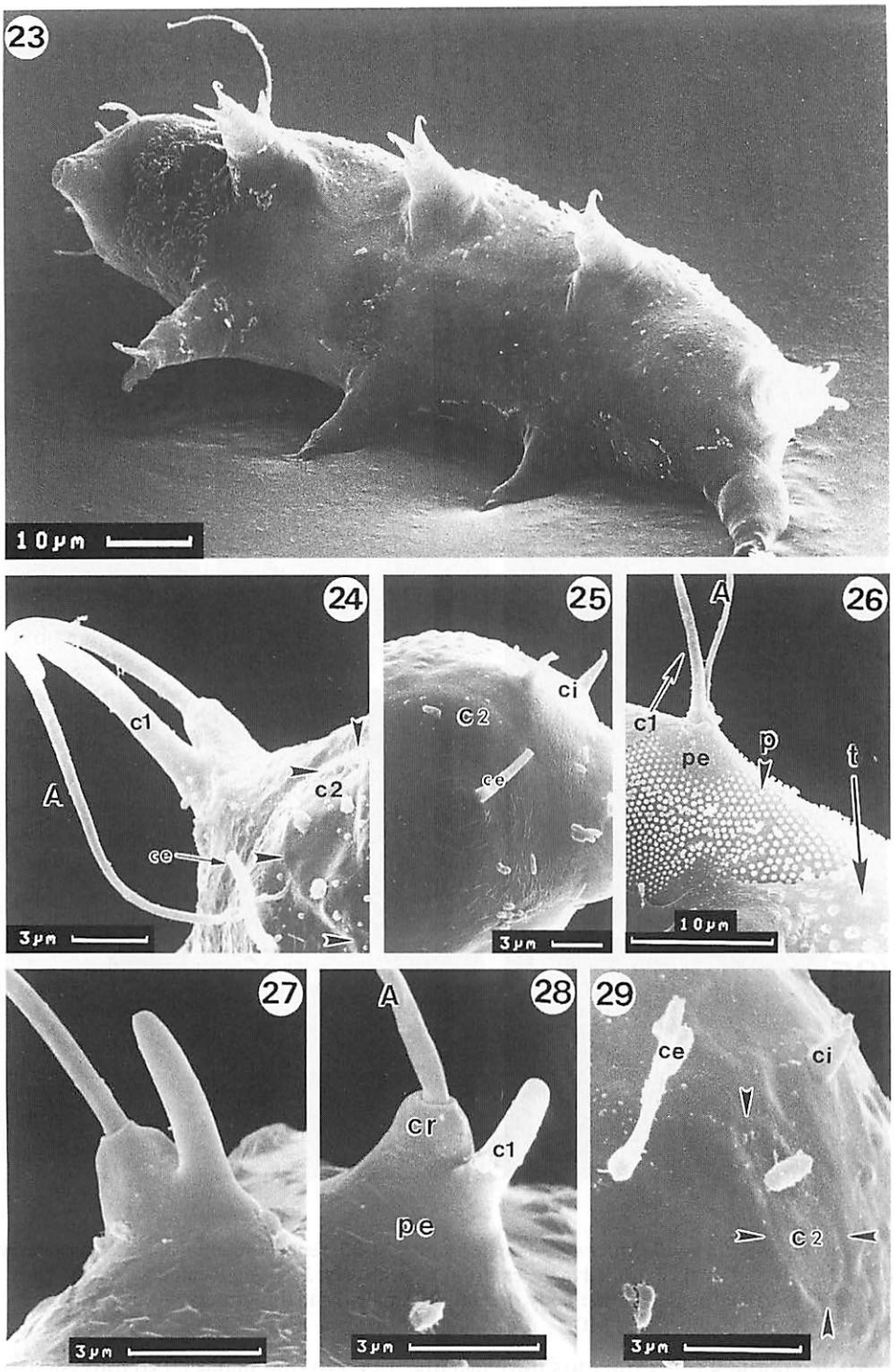
Figs 7-12. *Oreella mollis* MURRAY: **7**- female, ventral; **8**- female, caudo-dorsal; **9**- opening of seminal receptacle; **10**- female genital papilla, lateral; **11**- female, caudo-ventral; **12**- female, cirrus *A* and primary clava.



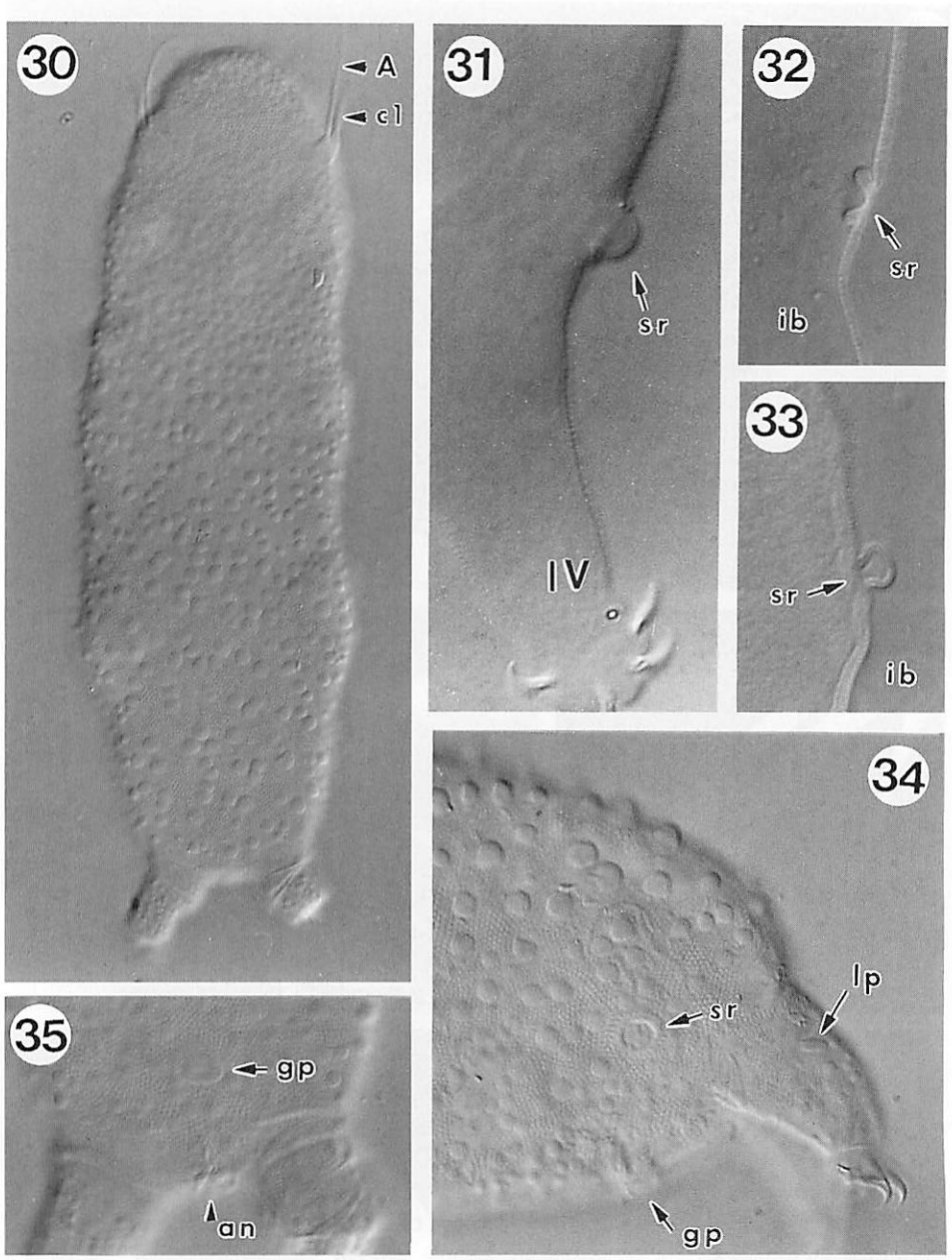
Figs 13-16. *Oreella mollis* MURRAY: **13**- male, lateral; **14**- male, ventral; **15, 16**- juvenile, frontal and dorso-frontal view, respectively.



Figs 17-22. *Oreella mollis* MURRAY: **17**- male; **18**- male head, in median focal plane; **19**- male head, ventral (arrowheads: cephalic papilla); **20**- egg; **21**- male, head segment with buccopharyngeal apparatus; **22**- female, dorso-caudal region: some cuticular tubercles in lateral view, unknown subcuticular structures [glands (?): arrowheads, dorsal view] and contours of seminal receptacles (arrows). (Fig. 21: specimen from Cambewarra Mt).

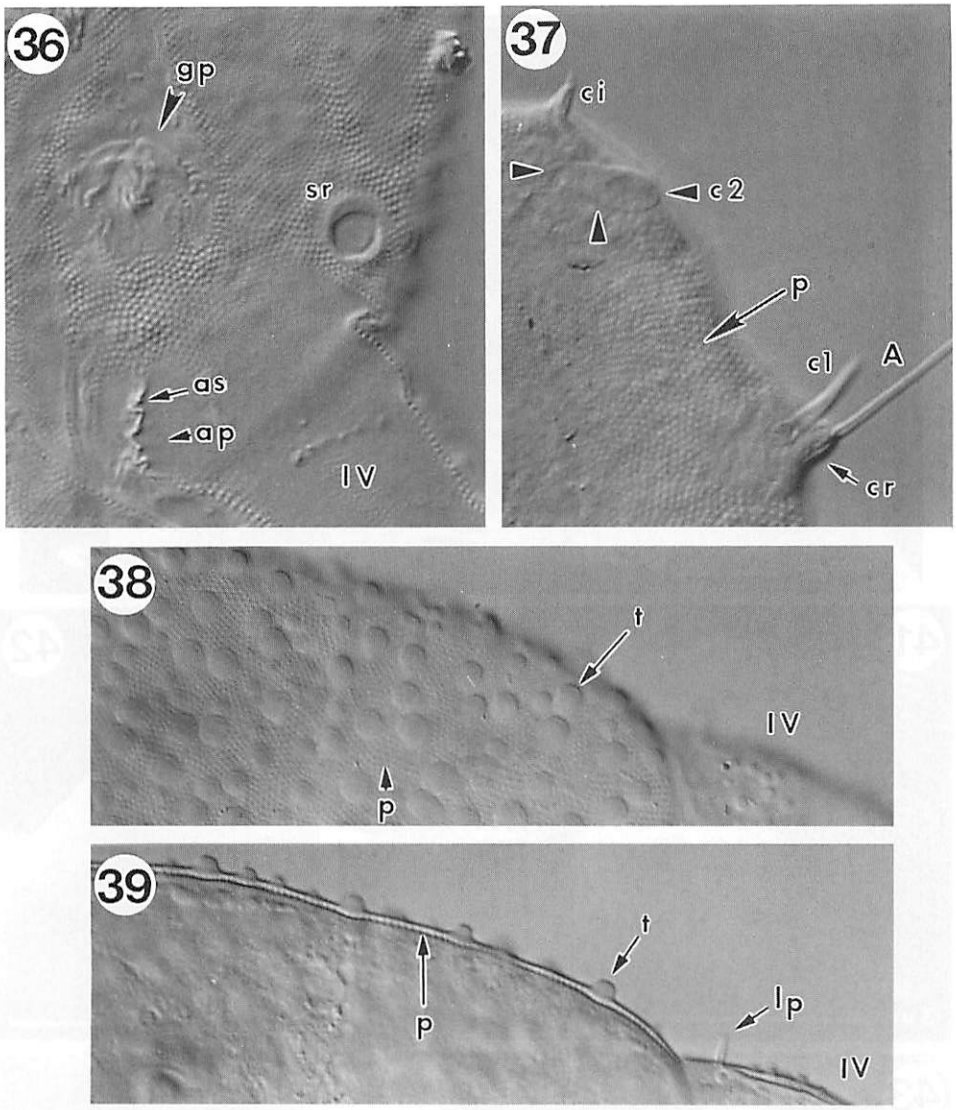


Figs 23-29. *Oreella mollis* MURRAY: **23**- larva, lateral view; **24**- male head sensory system, latero-frontal view; **25**- juvenile, fragment of head, lateral; **26**- male, cuticular pillars and tubercles at cirrus *A*; **27, 28**- cirrus *A* and primary clava: female and juvenile, respectively; **29**- juvenile, fragment of the anterior part of the head segment.



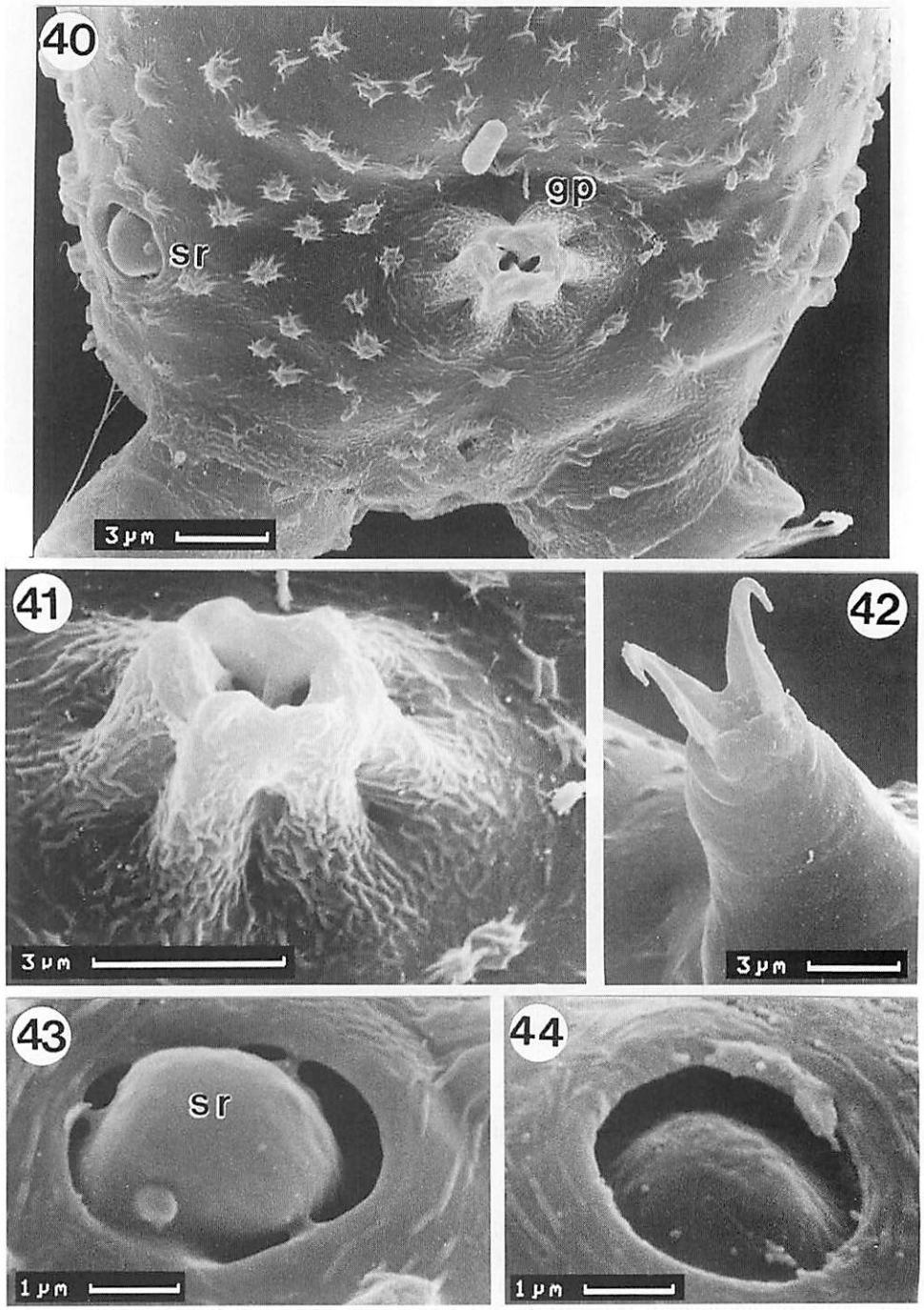
Figs 30-34. *Oreella mollis* MURRAY: **30**- male, dorsal; **31-33**: female, seminal receptacles, lateral (**31, 32**: fully and partly extruded to the exterior, respectively; **33**- fully located within the body; **34**- female, caudal region of the body, lateral; **35**- male, caudal region, ventral (Figs 31, 33: specimens from Cambewarra Mt).

Body length: 84-251 µm (205 µm), usually: 145-180 µm; males (180 µm) smaller than females; two-clawed larvae: 84-100 µm. Specimens from Australia smaller (237 µm) than those from Maritime Antarctic. Body more or less cylindrical (Figs 13, 14, 34), slightly flattened ventrally, hyaline or whitish; without dorsal or ventral plates.



Figs 36-39. *Oreella mollis* MURRAY: **36**- female, caudal region, ventral; **37**- female, head segment; **38, 39**- female, cuticular granulation: dorsolateral and lateral view, respectively.

Body cuticle with double granulation. Small, closely spaced 'pillars', hexagonally arranged, occur inside the epicuticle (Figs 26, 47, 58: *p*). These densely arranged 'dots' of uniform diameter (0.3-0.5 µm; dorsal view), slightly smaller on ventrum and legs, cover the whole body (Figs 30, 36-38). Larger, unevenly distributed, hemispherical knobs (tubercles) (Figs. 8, 13, 26, 47: *t*), with round or oval base (3.5 µm; average 1.5-2.5 µm) stand proud 2.2 µm (usually 1-2 µm) and occur over 'pillar' layer. Dorsal and lateral tubercles, increase slightly in size towards the posterior. Ventral tubercles distinctly smaller, and more sparsely distributed towards the anterior (Figs 7, 14, 23). A thin (0.3-0.5 µm), outer cuticular stratum covers the whole body, including the



Figs 40-44. *Oreella mollis* MURRAY: **40**- female, caudal region, ventral; **41**- female, genital papilla, dorsolateral; **42**- larva, leg II; **43, 44**- various degree of the extrusion of seminal receptacles.

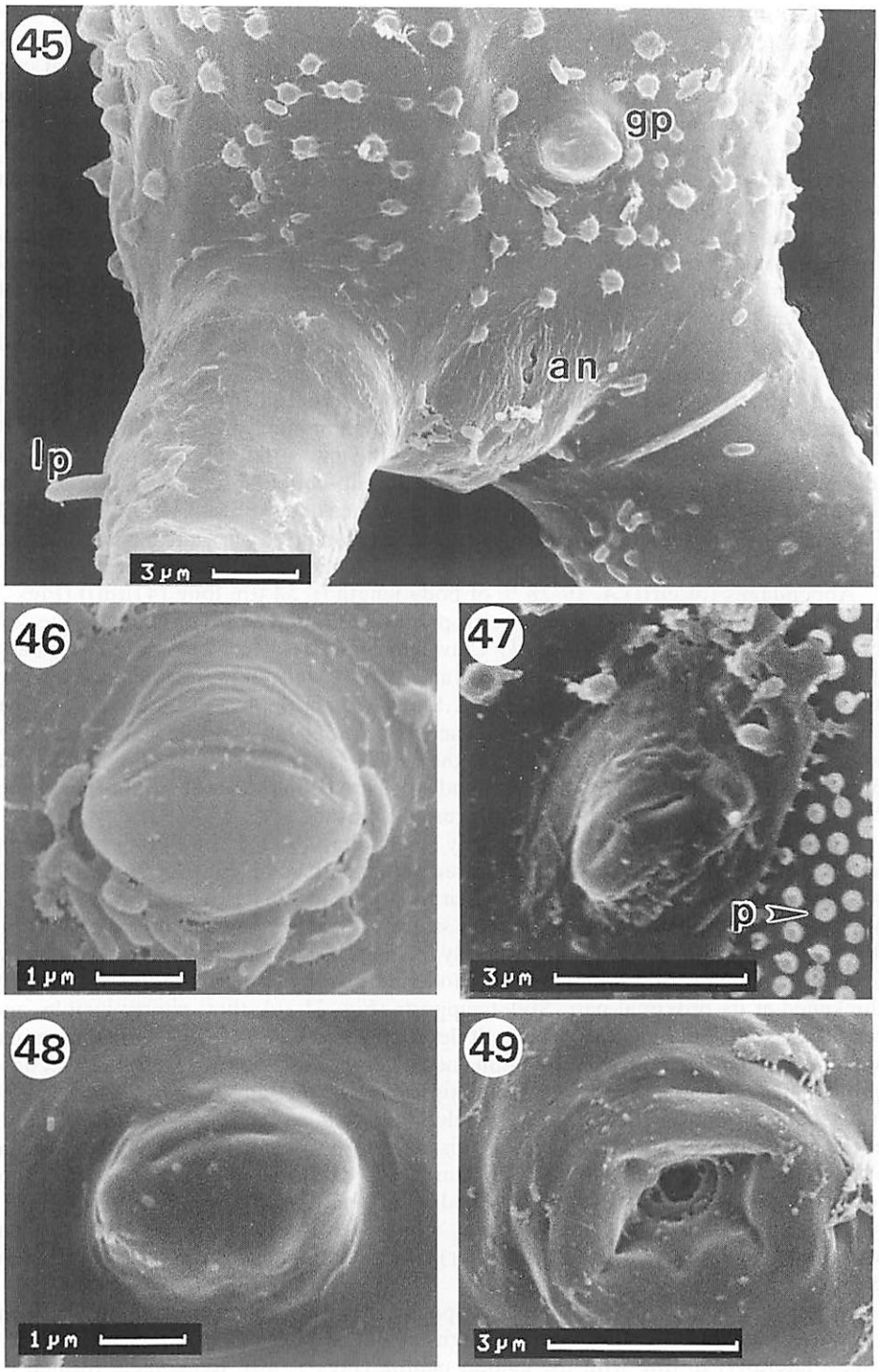
tubercles, but is only discernible in water or glycerol mounts (Fig. 22: *os*), as it dissolves (cleares) in other mounting media. This outer layer reacts with SEM fixatives, causing the tubercles to shrink and wrinkle, forming irregularly shaped stars or similar structures (Figs 11, 40, 41, 45). A pair of small (1.0-2.2 µm (1.8 µm)), round pore-like structures, occur on the caudo-dorsal surface in adults, and at least older instars (Fig. 22: arrowheads). These pores are poorly discernible, and located slightly under the cuticle, but no ducts or similar structures leading to the external environment were observed. No such structure has previously been reported in *Oreella*.

Head segment, with domed forehead (Fig. 1; comp. THULIN 1928), poorly delimited from the trunk (Figs 7, 16, 17, 30). Two pairs of cephalic cirri and a pair of cephalic papillae (= secondary clava: *c2*) present. Cephalic median cirrus, or traces, absent. Internal cephalic cirri reduced, short (3.5 ìm (2.8 µm)), and cone-shaped (Figs 7, 15, 18, 25: *ci*). External cephalic cirri, longer, setae-like, (13 µm; (11 µm)), with small poorly delimited cirrophores (Figs 7, 29, 58: *ce*). Elongated, forward pointing, cone-shaped cephalic papillae between internal and external cirri (Figs 18, 19, 21: *c2*), arising *under* the cuticle, and covered by a thin, membranous outer epicuticle (Figs 18 *ct*, 29). This is most obvious when observed at the antero-lateral margins of the head under a light microscope (Figs 18, 21), while the sub-cuticular location of the papillae is marked by a small elevation on the cuticular surface under SEM (Figs 15, 25, 29: *c2*). Papillae usually flattened dorso-ventrally, 13.5 µm long (9.5 µm), and 5.5 µm diameter (3.5 µm) at the base, with male papillae 25-50% longer than those of females.

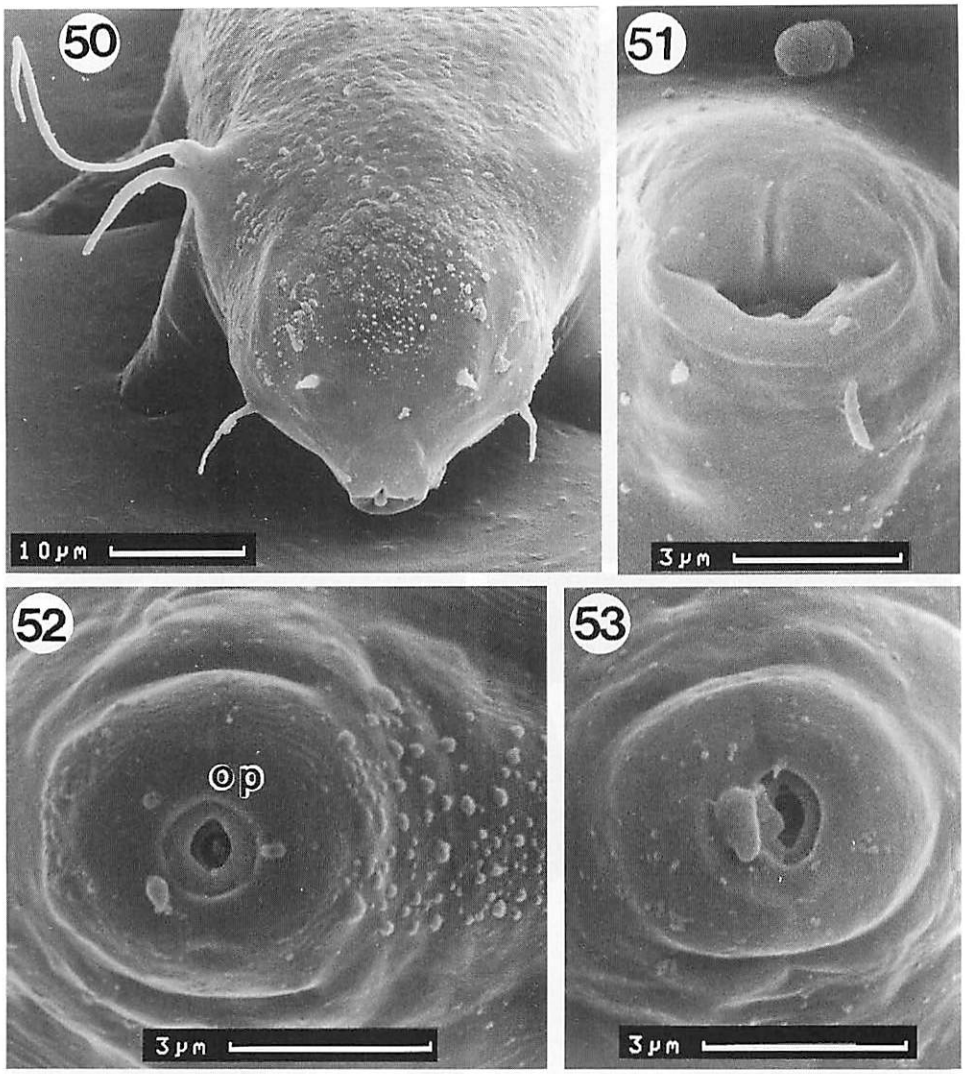
Appendages (or cirri) *A*, 19-28 % of body length (≤ 54 µm long (41µm)) (Figs 7, 14: *A*), located on a wide pedestal cirrophores, with clavae (= primary clavae, *c1*: Figs 12, 14, 15, 26, 28, 30, 37: *A*, *c1*). Clavae located laterally to cirri *A*, are a sexually dimorphic character. In females, juveniles and (two-clawed) larvae, clavae are relatively short, thin fingers (≤ 8 µm long and ≤ 1.8 µm wide at the base (7.8 µm x 1.0 µm)) (Figs 15, 23, 27, 28: *c1*). In males, clavae (27 µm long and 1.8 µm wide), distinctly longer (between 30-45% of the length of the cirri *A*), and club-shaped, (Figs 14, 24, 30, 50: *c1*). No refractive (VAN DER LAND) bodies observed in the basal part of the clavae. No other lateral or dorsal appendages present on trunk.

Bucco-pharyngeal apparatus relatively small (Figs 17, 21). Small mouth, opening antero-ventrally, located on distinct, retractable mouth cone (Fig. 15, 16, 23, 50: *co*), without lobes, papillae or lamellae when mouth cone fully extended (Figs 52, 53). When the bucco-pharyngeal apparatus is slightly retracted from the mouth cone (Figs 49-51), 'pseudolobes' which are probably artifacts, are apparent. Mouth tube narrow (external diameter ≤ 1.8 µm (1.3 µm)), moderately long (≤ 24 µm (23 µm)), distinctly thickened at its proximal part. Stylet supports (Fig. 21 *su*), thin, poorly visible, and readily dissolved in mounting media. Stylet supports *pt* index 65-70% (water mounted specimens). Stylets medium sized, thin and uniformly tapered (Fig. 2, 21). Stylet base (furca) small and slightly incised. Distal tip of stylet penetrates long (≤ 8 µm), narrow tube-shaped stylet sheath (Fig. 21 *ss*). Stylets, mouth tube, stylet supports and placoids encrusted with $CaCO_3$, which rapidly dissolve in the majority of mounting media. Pharynx round (diameter 18 µm (c. 13 µm)). Three thin, elongated placoids (5-7 µm long (7 µm)), bent and distinctly thickened at the junction with the mouth tube (Fig. 21 *pl*). Oesophagus short, and midgut large, with grayish contents, though light-brown, spherical structures (≤ 3 µm in diameter), with small, round granules within, often present.

In females, a pair of small cuticular pouches (= seminal receptacles) (≤ 5.5 µm (5 µm)), open only to the external environment. Pouches located symmetrically, caudo-laterally, in line with the genital papilla (Figs 7, 40). Receptacle formed by invagination of body wall (Fig. 33), with a relatively large opening (Figs 9, 34, 36, 43, 44). Wall of each receptacle smooth, thinner than the body wall, without cuticular



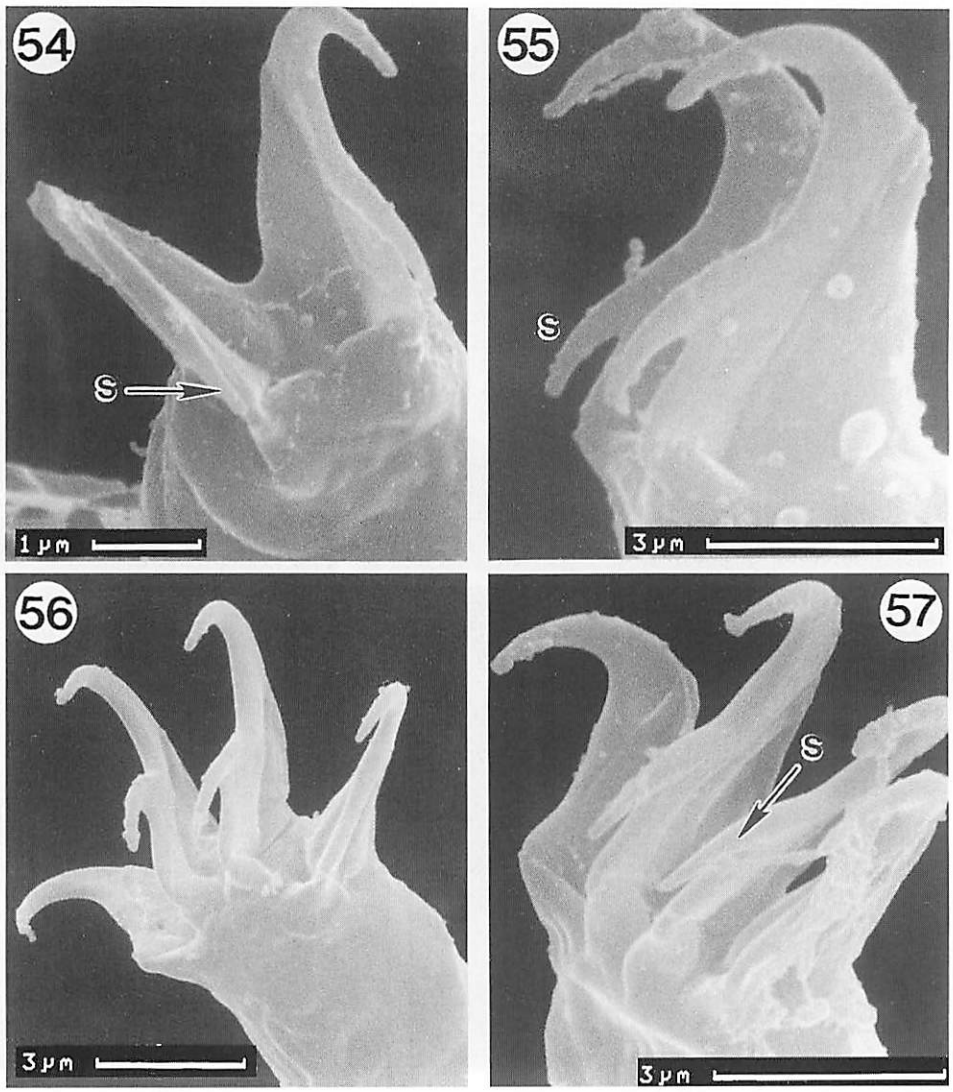
Figs 45-49. *Oreella mollis* MURRAY: **45**- male, caudal region, ventral; **46-48**: male, genital papilla; **49**- female (?), mouth opening: mouth cone slightly retracted.



Figs 50-53. *Oreella mollis* MURRAY: **50**- male, mouth cone partly retracted, dorso-frontal view; **51**- female, mouth opening: mouth cone slightly retracted; **52, 53**- female, mouth opening: mouth cone fully pulled out.

pillars (Fig. 36). In most preparations (water and permanent mounts) the receptacles are partly everted to the exterior (e.g. Figs 7, 10, 32, 40, 44), whilst in a few the pouches are fully located within the body interior (Figs 9, 33, 34, 36). However, when influenced by a stronger mounting medium, or pressure, the pouches are fully extruded to the exterior (Fig. 31). No sperm were observed within the receptacles.

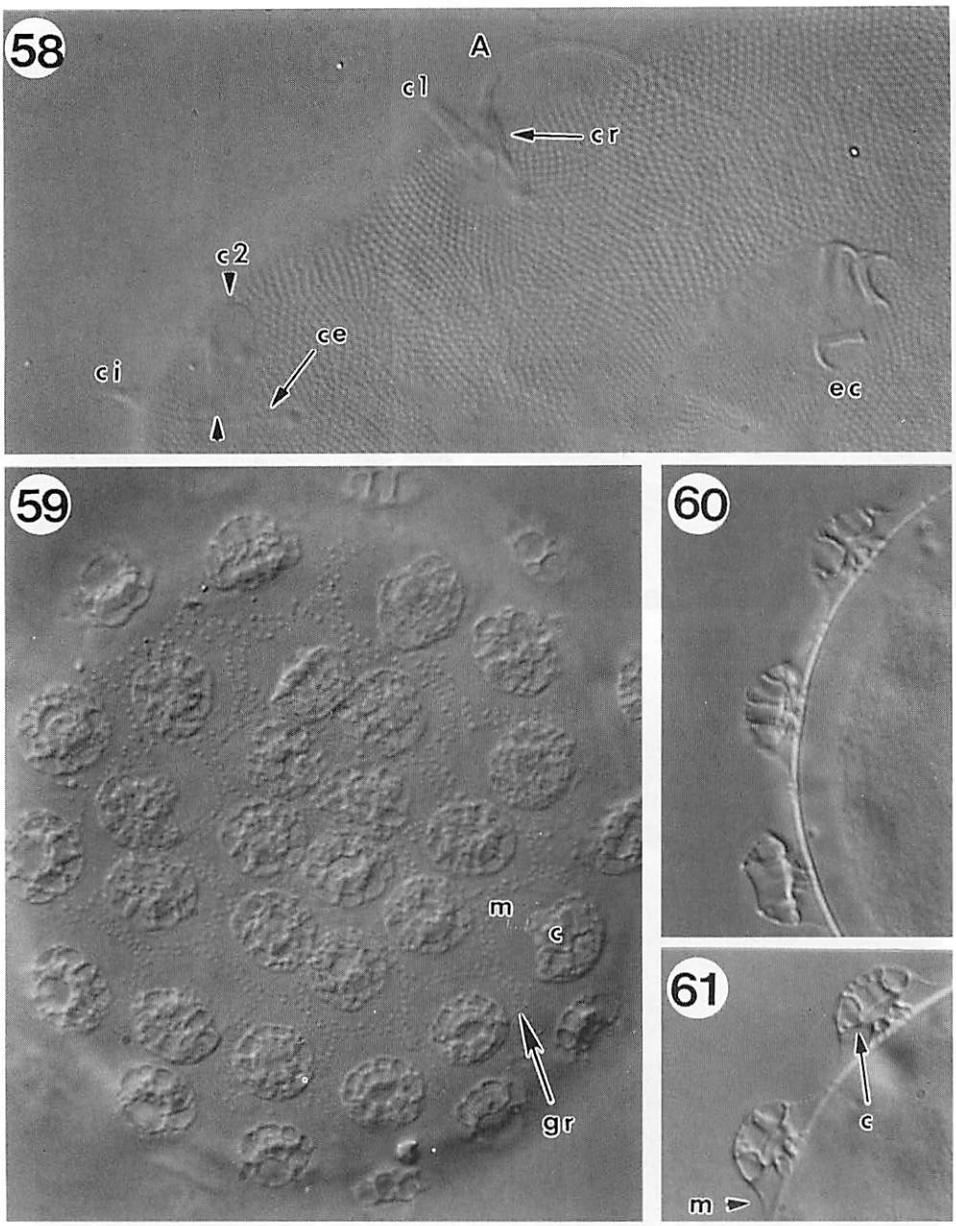
In females a large genital papilla, terminated with a gonopore, occurs caudo-ventrally at the distal part of the last trunk segment, in front of the anus, and the IVth pair of legs, but well behind the legs III (Figs 7, 34, 36, 40, 41: *gp*). Papilla with wide, round base (≤ 13 µm (11µm)), without cuticular pillars, and composed of six fused lobes arranged in a rosette, which form a crater-like structure (Figs 10, 41). Lobes arise gradually from their base and merge into six strongly sclerotized columns, which are



Figs 54-57. *Oreella mollis* MURRAY: **54, 55**- larva, claws III: frontal and lateral view, respectively; **56, 57**- female, claws IV.

also fused in their apical parts. Crown-shaped tips of these columns surround a small, transversely elongated, hourglass-shaped, gonopore (Fig. 40). In all mounted specimens, the genital opening is closed (Fig. 36).

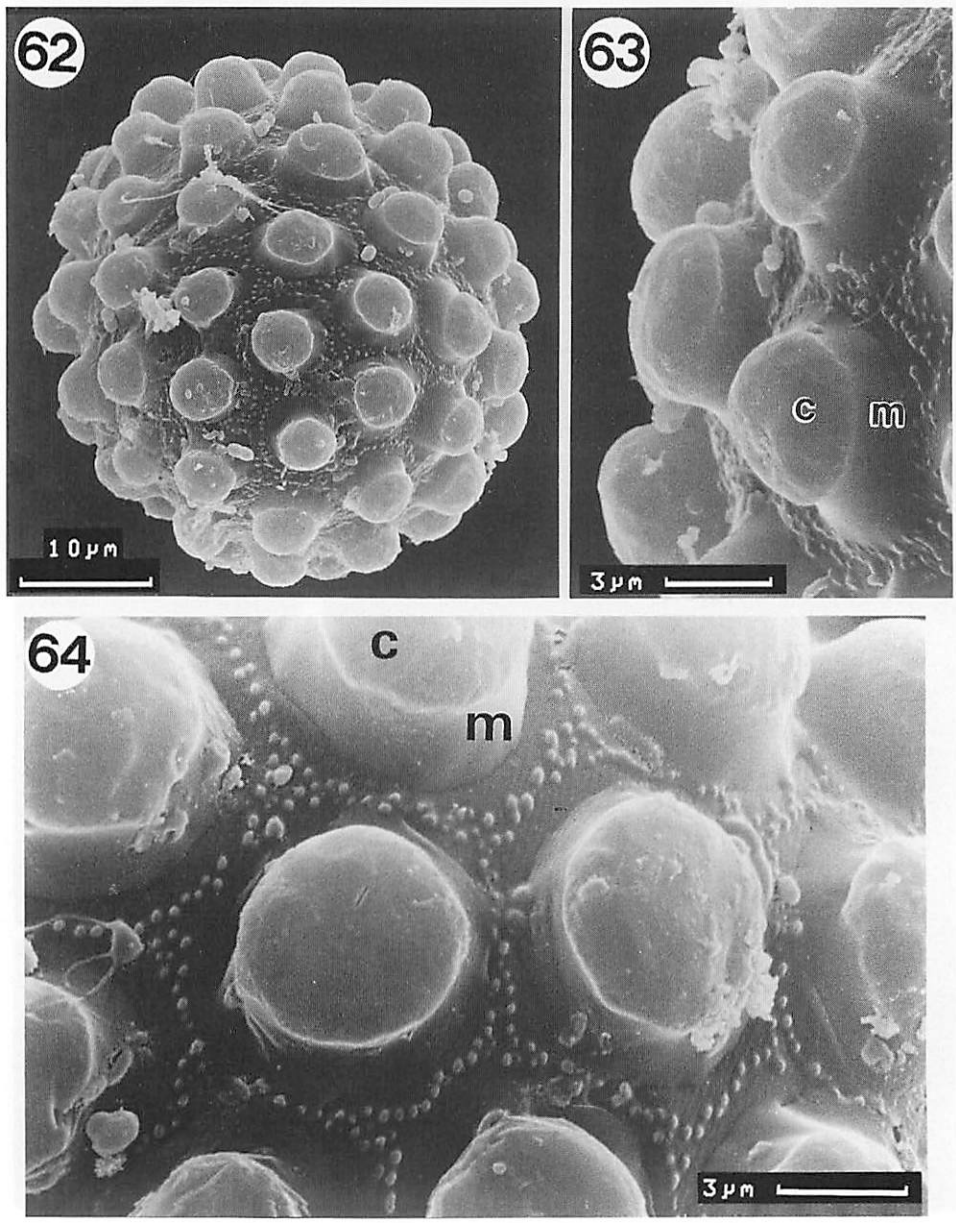
Male genital papilla, also located caudo-ventrally, distinctly smaller than female (Figs 14, 45-48: *gp*). Papilla a small, transversely directed oval structure (≤ 3.5 µm wide by ≤ 3 µm), with double walls (viewed ventrally in chloral gum mounts) (Figs 6, 35: *gp*), with a proximally sited distinct transverse, elongated crescent shaped slit (only visible in glycerol mounts or in SEM) (Figs 46, 48). In some specimens (possibly only fully mature individuals), two shorter and deeper slit-like structures occur on either side of this main slit (Fig. 47). No other openings were observed on the papilla surface,



Figs 58-61. *Oreella mollis* MURRAY: **58**- neotype, female: fragment of the anterior part of the body, latero-ventral view; **59**- surface of egg; **60, 61**- egg processes, lateral view (Figs 58, 59: specimens from Cambewarra Mt).

or in its vicinity (Figs 46-48). Distance between genital papilla and anus (measured from the posterior margins), usually about the length of the anus itself (≤ 11µm; 8 µm) (Fig. 6).

Slit-formed anus located between two elongated, round and bulbous (coffee-bean shaped, Fig. 6) anal plates (Figs 6, 35, 36: *ap, an*). Cuticular pillars absent from these plates (Fig. 36), which dissolve or deform easily in fixatives, or other mounting media,



Figs 62-64. *Oreella mollis* MURRAY: **62**- egg; **63, 64**- fragment of egg.

usually leaving a zigzag shaped slit (Figs 36, 45), surrounded by wrinkled cuticle. Undeformed anal plates were observed only in a few specimens (Fig. 6). Anal slit ≤ 11 µm (8 µm) long and located ventro-distally (i.e. almost at the level of the bases of the legs IV) (Figs 6, 11, 45). A short median caudal projection (≤ 3.5 µm) with a wide base, is located just behind the anus and between legs IV (Figs 6, 8: *mc*, 17).

Larvae (two-clawed juveniles) have neither anus nor gonophore (Fig. 23), whilst very young four-clawed instars do have an anus. Cuticular pillars cover the whole

ventrum in these instars. A small round dot, devoid of cuticular pillars, occurs in the position of the genital papilla, in sub-adults (females). A small, broad (≤ 2.5 μm wide), 'U' shaped, clear double wall structure occurs in the position of the genital papilla in sub-adult males. Though the primary clavae are still relatively short in these sub-adult males, they are distinctly longer than those of adult females (e.g. 14 μm in a specimen 150 μm: cirri *A* 38 μm), whilst the secondary clavae are of similar size or marginally larger than in adult females. Distance between papilla and anus about the length of the anus itself (≤ 11μm; 6).

Legs, particularly the IVth pair, long, thin and telescopically retractable (Figs 7, 13-15, 17, 23, 34, 42), and composed of four reasonably distinctly marked units (though they are more difficult to determine, when a small part of leg is already retracted). In arthrotardigrades these units are named coxa, femur, tibia and tarsus (Van der Land 1968: Fig. 6), but their homology with arthropod leg segments has not been proved. In this study the basal ('coxal') portion of each leg is distinctly enlarged, relatively untapered, and leads gradually to longest (though similarly shaped) 'femur' section. The 'femur' joins the short, strongly tapered, and most flexible, 'tibia', which terminates in the shortest 'tarsus' section, and claws (Fig. 13). Each leg section could be telescoped into distal portion of the previous leg unit, in any sequence. However, in the present study the 'tarsi' and 'tibiae' are most often retracted. Fully extended legs IV, measure 34 μm in a specimen 155 μm. Legs I with small, spine-like sensory organ (Figs 14, 15: *so*), ≤ 4 μm long (2 μm). A small sensory papilla, ≤ 4.5 μm long (2.5 μm) on leg IV (Figs 8, 34, 39, 45: *lp*) is located on the border between 'coxa' and 'femur'. No sensory organs on legs II and III. Small cuticular knobs cover the legs, largest on the 'femora' and progressively smaller, becoming barely visible, or completely absent, on lower leg units. Cuticular knobs absent from the base of each leg forming, particularly on legs IV, a characteristic knob-free ring (Fig. 8). Spine fringe absent. Claws small (legs IV; external ≤ 6.3 μm, the internal ≤ 8 μm), relatively thin, of echiniscid-type and increasing slightly in size towards the posterior. External claws smooth, narrow in the middle, slightly shorter than the internal ones, and effect an 'ice-hammer' shape in profile (Figs 3, 56-58: *ec*). Internal claws with distinct, steeply downward directed spur (= hook, tooth), located well above the relatively wide claw base (Figs 4, 56, 57: *s*). Tip of spur elongated and reaches almost to the base of the claw. Neotype (leg IV) internal claws slightly longer (6 μm) than external (5.5 μm).

Eggs whitish, small, spherical or slightly ovoid, with hemispherical processes (diameter with processes; 59-71 μm, without; 50-63 μm) (Figs 5, 20, 59-64). Processes, thin walled, smooth and distributed regularly (16-20 processes) around the circumference of the egg. Bases of processes round (≤ 10 μm in diameter (mostly 5.5-8.0 μm)), and each process mushroom-shaped (≤ 6 μm high (usually 4-5 μm)), with strongly sclerotized core (Figs 5, 60, 64: *c*). Core divided by septa into numerous smaller, regularly shaped, compartments or "cells", 1-3 μm long (Figs 5, 61). Core round, or oval (when viewed from the dorsal side), and ≤ 7 μm in diameter (usually 4-6 μm), with a large, round central "cell" surrounded by a ring of smaller compartments (Fig. 59). Viewed from the dorsal side, the remaining thinner "lower" part of the process wall is transparent, and not visible in slide mounts (Fig. 49, 64: *m*). Small, hemispherical granules, usually 0.3 μm or less in diameter (≤ 0.5 μm) occur between the processes in a narrow and irregularly shaped ring (Figs 59: *gr*, 63, 64). The egg processes, with internal core and septate "cells", bear some resemblance to the eggs of *Minibiotus intermedius* (PLATE, 1889).

In the Cambewarra Mt samples *Oreella mollis* occurred with an undescribed species of *Oreella* (det. S. K. CLAXTON), and with *Echiniscus curiosus* CLAXTON, 1996, *Pseudechiniscus suillus* (EHRENBERG, 1853), *Macrobiotus peteri* PILATO, CLAXTON & BINDA, 1989, *Minibiotus intermedius* (PLATE, 1889) and *Isohypsibius cameruni* (IHA-

ROS, 1969). Other species which also occurred rarely were *E. duboisi* RICHTERS, 1902, *Calohypsibius caelatus* (MARCUS, 1928) and *E.* cf. *vinculus* HORNING, SCHUSTER & GRIGARICK, 1978.

In the Signy Island samples, *Oreella* co-occurred with eight other tardigrades, namely *Echiniscus meridionalis* MURRAY, 1906, *Macrobiotus furciger* MURRAY, 1907, *Diphascon pingue* (MARCUS, 1936), *D. maucci* DASTYCH & MCINNES, 1997, *D. puniceum* (JENNINGS, 1976), *D. greveni* DASTYCH, 1984, *E. jenningsi* DASTYCH, 1984 and *Hypsibius* cf. *dujardini* (DOYÉRE, 1840), but most often with the first three taxa.

Discussion

This is the first revision of *O. mollis*. Unverified data from the original description has often been quoted (e.g. MARCUS 1928, 1929, 1936, RAMAZZOTTI 1964, 1972, RAMAZZOTTI & MAUCCI 1983, RUDESCU 1964, BARTOŠ 1967) and this has contributed considerably to the taxonomic confusion in the genus.

There are several characters which were not reported by MURRAY (1910) but which have been described in subsequent studies, including the present one (Table 1). These are (1) Seminal receptacles; (2) Spurs on internal claws; (3) Cuticular granulation on the ventral surface. Detection in later studies only is probably due to new and improved microscope techniques. MURRAY (1910) did however correctly interpret, but not adequately describe other features, most notably the cephalic papillae. These he described as: "....palps reduced to small hemispherical papillae..." (see also *op. cit.*: Fig. 26), which are distinctive when viewed on the head anterior edge in median focal plane (comp. Fig. 18). Located under the cuticle, the papillae tips do not point forward as hitherto illustrated.

All samples from the Maritime Antarctic, and mounted specimens, examined in the present study, were observed with empty seminal receptacles. However, KRISTENSEN (pers. comm.) observed spermatozoa in such pouches when he examined freshly mounted or living specimens of *O. mollis* from the Australian material in the collection of S. K. CLAXTON, and spermatozoa were drawn in the pouches of *O. minor*, examined by BINDA & KRISTENSEN (1986: Fig 1). These receptacles, appear to be homologous with the seminal receptacles of *Mesostygarctus* (KRISTENSEN, pers. comm.) and of some other Stygarctidae and Halechiniscidae: cf. GRIMALDI DE ZIO *et al.* 1992, KRISTENSEN & HIGGINS 1984, POLLOCK 1995).

Paired segmental and epidermal glands, of unknown function, have recently been reported in some marine tardigrades (KRISTENSEN 1984, KRISTENSEN & HIGGINS 1984), occurring in all segments of the body. The pair of blind pores observed in adult *Oreella* from the Maritime Antarctic and Australia, may represent similar segmental or epidermal glands (KRISTENSEN, pers. comm.), though reduced to a single pair.

The first modern description of the genus *Oreella* was established with *O. minor* (RAMAZZOTTI 1964), which was differentiated from *O. mollis by* its smaller size, the presence of spurs on internal claws, and shorter stylets (Table 1). However, such characters are insufficient for species discrimination, indeed the present study has shown that body length of *O. mollis* may be ≤ 251 µm, overlapping the key differential measurements of ≤ 170 µm for *O. minor* and ≤ 230 µm for *O. mollis* (RAMAZZOTTI 1964). Internal claw spurs (MURRAY overlooked them in *Echiniscus tessellatus* MURRAY, 1910 as well as in *O. mollis*) were found on all specimens examined in the present study and should be considered a feature of *O. mollis*.

The very short stylets in *O. minor* (c. half the length of those in *O. mollis*), described by RAMAZZOTTI (1964: Figs 1, 2: RAMAZZOTTI & MAUCCI 1983: Figs 565, 566), either represent the long, tube-like stylet sheaths, characteristic for *Oreella*, or/and the

Table 1. Some diagnostic characters of *Oreella* spp.

Characters	O. mollis (≤)	O. mollis neotype?	O. mollis (in: MURRAY)	O. minor (in: RAMAZZ.)	O. vilucensis (in: RAHM)	O. breviclava (in: G, S & N)
body length	84-251	205	230	85-167	300-430	174
dorsal plates	none	none	none	none	"pseudo-plates"	none/*present*
dorsal sculpture	double	double	papillose	double	smooth	fine/*fine*
ventral sculpture	double	double	not papillose	single/*double*	smooth	fine/*fine*
cephalic cirri internal	3.5	2.8	*	3.0-4.0	present	14.0
shape	cone	cone	cone/"spine"	spine/*cone*	"cone"	setae
cephalic cirri external	13.0	11.0	*	9.0-10.0/*9*	present	10.0
cephalic papillae length	13.5	9.5	present	present/*6*	present	5.7
diameter	5.5	3.5	*	*3.5*	*	2.0
sub-surface/ normal	sub-surface	sub-surface	reduced	*	"normal"	normal
cirrus *A*	54.0	41.0	present	15.0 - 35.0	present	19.0
clava:	present	present	present	present	absent	present
long, club-shape	27 x 1.8	-	*	11.0-18.0/*16*	*	*
short, finger-like	8 x 1.8	7.8 x 1.0	*	3.5-5.0/*3.5*	*	5.0 x 2.0
mouth tube length	24.0	23.0	*	15.0-16.0/*18*	*	*
diameter	1.8	1.3	*	*c.* 1.0	*	*
pharynx, round	18.0	*c.* 13.0	*	10.0-11.0	*	*
placoids, elongated	5.0-7.0	7.0	*	*4.5*	*	*
stylet sheath length	8.0	7.5	*	*	*	*
stylet support *pt* ratio	65-70 %	*	*	*	*	*
lateral trunk projection	absent	absent	absent	absent	present	absent
seminal receptacles	5.5	5.0	*	*	*	*
genital papillae ♀ (six fused lobes)	13.0	11.0	*	*present*	*	*
genital papillae ♂ (transverse oval)	3.5 x 3.0		*	*	*	*
anus	11.0	8.0	*	*	*	*
genital papillae to anus	11.0	8.0	*	*	*	*
median caudal projection	3.5	present	present	present	present	present
leg IV extended length	*c.* 34.0	*	*	*	*	*
leg I spine sensor	4.0	2.0	*	*c. 1.5*	"absent"	absent
leg IV papilla sensor	4.5	2.5	*	*c. 2.0*	"absent"	2.0 x 1.0
claws external	6.3	5.5	*	3.0-6.0/*4*	*	10.0
internal	8.0	6.0	*	*	*	*
internal spur	present	present	absent	present	absent	present
eggs with ornament	59-71	*	*	*	*	*
without ornament	50-63	*	*	*	*	*

(Legend: "xx"= data from original figures; *itallics* = observations on type specimens, present study; * = not recorded)

remnants of characteristic medium-long stylets. The stylets, though not the more resistant stylet sheaths, would have been partly dissolved by the mounting medium, when drawn by RAMAZZOTTI, a tenet supported by the lack of stylet supports in the original illustrations of *O. minor* (*l.c.*, 1964: Figs 1, 2). Stylets were completely cleared/dissolved in the four *O. minor* syntypes observed in the present study, while the lack of illustrated stylet supports (*l.c.*, 1964: Figs 1, 2), made it impossible to assess the real length of the stylets. *O. minor* from Argentina was described with long stylets, definite stylet supports, and short, wide stylet sheaths (BINDA & KRISTENSEN 1986).

RAMAZZOTTI (1964) noted that the "tubercoletti rotondeggianti " (= rounded tubercles) were absent from the ventral cuticle of *O. minor*. However, barely visible ventral cuticular knobs (more sparsely distributed and smaller than those on the dorsal and lateral sides of the body) could be discerned on two of the four examined syntypes using interference contrast microscopy. Though the knobs were smaller on the *O. minor* syntypes than on fresh- or water mounted specimens, these structures were found to be subject to shrinkage, or even be fully dissolved by fixing and mounting.

The status of "*Orella* sp." from Germany (RAHM 1925a), was considered dubious (MARCUS 1929), then accepted, first as *O. bonnensis* (RAHM 1932a), and synonymised with *O. vilucensis* from Chile (RAHM 1931, 1932b; MARCUS 1936). *O. vilucensis* itself was an inadequately and misleadingly described taxon (RAHM 1932b), possessing characters unique amongst terrestrial tardigrades. These include the absence of

primary clavae and the unusual position of two pairs of lateral projections between legs II and III (RAHM 1932b: Fig. 6). The location of the cirri *A*, shifted strongly towards the median body line (*op. cit.*, Fig. 6) is very unusual in Tardigrada. MURRAY (1910: Fig. 26), also moved cirri *A*, and it is not impossible that Rahm based his drawing of *Oreella* (*l.c.*, 1932b: Fig 6) on MURRAY's (1910) illustration of *O. mollis*, to supplement the vague description of his specimens from Chile and Germany. There are indeed several similarities between the two illustrations, including the caudal body outline and the similarly located segmental folds of 'pseudoplates' (MURRAY, 1910; cf. RAHM, 1932b). Neither was observed in *O. minor* by RAMAZZOTTI (1964), nor in the present study, and both were probably artifacts.

RAHM (1932b) differentiated *O. vilucensis* from *O. mollis* by its smooth, ungranulated cuticle, the lack of a clava at the cirrus *A*, and the two pairs of short lateral projections between legs II and III (Table 1). Such characters and other aspects of the incomplete description, do not allow positive identification of *O. vilucensis*. RAHM probably described, under *O. vilucensis* (and *O. bonnensis*), either aberrant Heterotardigrada specimen(s) of *Oreella*?, *Echiniscus*?, or *Pseudechiniscus*?, from Chile, and an anomalous individual of *Echiniscus* or *Pseudechiniscus*, from Germany, and/ or incorrectly interpreted normal characters in such taxa. The lack of type material, uncertainties and controversies, make it impossible to recognize *O. vilucensis* except as a *nomen dubium*.

Examination of the holotype for the recently described *O. breviclava* from subtropical Andean forest, Venezuela (GRIGARICK *et al.* 1983) revealed that this was actually *Hypechiniscus exarmatus* (MURRAY, 1907). Many holotype characters were degraded or barely visible, though appendages, plates, claws, cuticular granulation and buccopharyngeal apparatus, all conform to the *Hypechiniscus* type description (KRISTENSEN 1987) (Table 1). The "*O. breviclava*" cephalic papilla = "buccal papilla", (GRIGARICK *et al.* 1983), were not located under the cuticle. The "small hemispherical tubercles visible along margins of cuticle", are cuticular folds and probable preparation artifacts similar to those observed in mounted *H. gladiator* specimens from Nepal (DASTYCH, personal observation). There is no doubt that "*O. breviclava*" belongs in the genus *Hypechiniscus* and should be renamed *Hypechiniscus exarmatus*.

There are no significant differences between the *Oreella* specimens recently collected from Australia and Maritime Antarctic Signy I. Nor was there strong evidence for a different species in the South American and New Zealand material (Table 1). This strongly suggests that *O. mollis* and *O. minor* are conspecific, with *O. minor* as a junior synonym of *O. mollis*. This will require confirmation after the examination of new material from South America, particularly eggs which are unknown from the Neotropical region.

Oreella eggs, freely laid with ornamented shells were reported by BERTOLANI *et al.* (1996). The presence of such eggs in a heterotardigrade is unusual in that all previously described heterotardigrade eggs have been smooth and laid in an exuvium. Ornamented eggs have a key species-level significance in tardigrade taxonomy. It is expected that this character will further clarify some taxonomic problems within the Oreellidae. However, based on the available data, the present survey indicates that only *O. mollis* can be regarded as a valid species of the genus *Oreella*.

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