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HOLOTHURIANS OF NEW ZEALAND
Front cover: Plate 5 of A. Dendy's paper on the sea cucumbers of New Zealand published in 1897 in the *Journal of the Linnean Society*. The illustrations are of the ossicles in the skin of two species of *Calochirus*, both treated in the revision New Zealand members of the family Cucumariidae by P.M. McLoughlin and N. Alcock in this volume.
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THE NEW ZEALAND CUCUMARIIDAE (ECHINODERMATA, HOLOTHUROIDEA)

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Abstract


Three new cucumariid holothurians, Pseudocnus sentus, SquamoCnus niveus and SquamoCnus lutens, are described from Stewart Island and Fiordland. Five New Zealand and Australian cucumariid species, previously referred to the European genus Ocnus Forbes and Goodsir, are assigned to other genera. SquamoCnus brevidentis (Hutton) is a new combination. Australocnus and Psolidocnus are new genera, and Australocnus calcareus (Dendy), Australocnus occiduus (O’Loughlin and O’Hara), Psolidocnus amokurae (Mortensen), Psolidocnus farquhari (Mortensen) and Psolidocnus sacculus (Pawson) are new combinations. Ocnus brevidentis var. carneyensis (Dendy) is not recognised. The status of a syntype of SquamoCnus brevidentis (Hutton) is discussed. A neotype is established for Australocnus calcareus (Dendy). Trachythyone bollonsi (Mortensen) is synonymised with Psolidiella nigra Mortensen. The southern Australian Plesiocolochirus ignavus (Ludwig) is reported from New Zealand. S. brevidentis and S. niveus sp. nov. are brood-protecting. A key is provided for the New Zealand species of Cucumariidae.

Introduction

Recent field observations and collections by one of us (Alcock) at Stewart Island and Fiordland in southern New Zealand have yielded new species of Pseudocnus Panning, 1949 and SquamoCnus O’Loughlin and O’Hara, 1992, and provided the basis for this review.

The New Zealand cucumariid holothurians are known mainly from the works of Hutton (1872, 1878), Dendy (1897, 1909), Ludwig (1898), Dendy and Hindle (1907), Mortensen (1925), Panning (1949, 1961, 1971), Dawbin (1950) and Pawson (1963, 1968, 1970, 1983). A problem developed historically with the identity of Ocnus brevidentis (Hutton) as described in the original description, and a subsequent description by Dendy (1897) of the probable type specimen in a very poor state of preservation, points to the same species as Dendy (1909) was to later describe as a variety (brevidentis var. carneyensis). The combined evidence of the original description, and a subsequent description by Dendy (1897) of the probable type specimen in a very poor state of preservation, points to the same species as Dendy (1909) was to later describe as a variety (brevidentis var. carneyensis). When the variety was described, Dendy and Hindle (1907) wrongly assumed that another common and related but undescribed species was brevidentis. Mortensen (1925) followed the same thinking. This common undescribed species is one of two new SquamoCnus species described here. A syn-type, of uncertain status, from Stewart Island labelled Thyone brevidentis Hutton, held in The Natural History Museum in London, is the strawberry-red cucumariid described by Dendy (1909) as brevidentis var. carneyensis but confirmed here to be Hutton’s brevidentis.

Five cucumariid species and one variety from New Zealand and Australia have at times been referred to the initially European genus Ocnus Forbes and Goodsir in Forbes, 1841 – O. brevidentis (Hutton, 1872), O. calcareus (Dendy, 1897), O. brevidentis var. carneyensis (Dendy, 1909), O. farquhari (Mortensen, 1925), O. sacculus Pawson, 1983 and O. occiduus O’Loughlin and O’Hara, 1992. A review of the assignment of these species to Ocnus faces a further historical problem as to which is the type species of Ocnus. Panning (1949) revived the genus Ocnus, designating O. brunneus (Forbes ms. in Thompson, 1840) as the type species. Mortensen (1927) had synonymised O. brunneus with O. lacteus (Forbes and Goodsir, 1839). Panning (1971) accepted the synonymy by Cherbonnier (1951) of O. brunneus with O. planci (Brandt, 1835), and considered O. planci to be the type species. Rowe (1970, 1995 in Rowe and Gates) followed Mortensen’s synonymy, nominating O. lacteus as the type species. McKenzie (1984) detailed the history of the genus Ocnus; recognised O. brunneus as distinct from O. lacteus; described a neotype for O. brunneus; and discussed the possible synonymy of O. brunneus with O. planci.
McKenzie (1991) subsequently considered growing evidence that O. planci and O. brunneus were conspecific, and that characters used to separate O. brunneus from O. lacteus were not reliable. O. planci, O. lacteus and O. brunneus have all been designated type species for Oenus which is considered here to be a European genus with diagnostic characters inapplicable to the New Zealand and Australian species.

Panning (1971) restricted Oenus to five species, included O. calcareus, excluded O. brevidentis and O. farquhari, reassigned brevidentis to Pentaecta Goldfuss, 1820, but did not reassign O. farquhari. O’Loughlin and O’Hara (1992) and Rowe (in Rowe and Gates, 1995) continued to assign brevidentis to Oenus. Rowe (in Rowe and Gates, 1995) reassigned occidentis to Plesiocolochirius Cherbonnier, 1946. Panning (1971: 36), Pawson (1983: 227), O’Loughlin and O’Hara (1992: 237, 247) and Rowe (in Rowe and Gates, 1995: 279) questioned whether Oenus was the appropriate genus for New Zealand and Australian species. The five species listed above fall into three groups. Oenus brevidentis (Hutton) is reassigned to Squamocnus O’Loughlin and O’Hara, where two of the new species are assigned. O. calcareus (Dendy) and O. occidentis O’Loughlin and O’Hara are assigned to a new genus. O. farquhari (Mortensen) and O. sacculus Pawson are assigned to a second new genus, as is Trachythyone amokurae (Mortensen, 1925). Trachythyone bollonsi (Mortensen, 1925) is synonymised here with Psolidiella nigra Mortensen, 1925.

Plesiocolochirius ignavus (Ludwig, 1874), known from across southern Australia, is reported for New Zealand from NIWA specimens which had been identified as Oenus brevidentis and from an unidentified MNZ specimen from Fiordland.

O’Loughlin (1994) listed 30 brood-protecting cucumariid species, including the three New Zealand species Trachythyone amokurae (Mortensen), Psolidiella nigra Mortensen and Oenus sacculus Pawson. Two additional cases of brood-protection by the New Zealand cucumariid species Squamocnus brevidentis (Hutton) and Squamocnus niveus sp. nov. are reported here.

Abbreviations for institutions are as follows: AM, Australian Museum, Sydney, Australia; MNZ, Museum of New Zealand, Te Papa Tongarewa, Wellington, New Zealand; NIWA, New Zealand Institute of Water and Atmospheric Research, Wellington, New Zealand; USNM, US Museum of Natural History, Smithsonian Institution, Washington, USA; ZMUC, Zoological Museum, University of Copenhagen, Denmark.

The following terms are defined:

Bent and curved. Elongate tentacle and tube foot plates may be straight or bent (angular) in one plane (surface) which itself may be flat or concave or curved (Fig. 3i illustrating straight and curved, and Fig. 4i illustrating bent and curved).

Buttons. Thickened plates which are perforated, regular to irregular in outline, small (typically 0.08 mm long), discretely knobbed (Figs 3i, 5e) or lumpy (Figs 6f, 6i) or smooth, typically four perforations.

Cups. Thin plates which are perforated, concave, shallow (species in this paper) or deep, oval to rectangular, small (typically 0.04 mm long), cruciform (Figs 2g, 3f, 4d) or tripartite (Figs 5i, 5j) centrepiece, typically four large with frequently four small corner perforations, spinelets on rim and sometimes on centrepiece, sometimes with bridging connections across rim.

Denticulate. With pointed to bluntly spiny teeth-like spinelets on ossicles (Figs 1h, 1k).

Digitate. With finger-like spinelets on ossicles (Figs 1f, 4d).

Multi-layered ossicles. Ossicles which are nodular, irregularly oval in outline, large (more than 0.2 mm long), comprising a perforated knobbed base plate with additional layers built on both sides creating low domes bilaterally (Figs 2k, 3j).

Sole. Flattened, delimited, modified ventral body wall, bounded peripherally by tube feet which do not extend in series to the introvert and anus, and the place of attachment to the substrate.

Ventrum. Modified ventral body wall, bounded laterally by the lateroventral series of tube feet, not bounded peripherally by tube feet, and the place of attachment to the substrate (Figs 3b, 6b).

Order Dendrochirotida Grube, 1840

Cucumariidae Ludwig, 1894

Remarks. Thirteen species of Cucumariidae are now known for New Zealand. The two species not discussed, Amphicyclus thomsoni (Hutton, 1878) and Neocucumella bicolumnata (Dendy and Hindle, 1907), were discussed and illustrated by Pawson (1963, 1970). Ten are endemic species, while P. ignavus is a common southern Australian species. A. calcareus is reported for Macquarie and Juan Fernandez Islands, and P. nigra occurs in south-eastern Australia (O’Loughlin, 2000). A South Australian specimen, initially referred to N. bicolumnata, was
The following cucumariids are distinguished from other New Zealand holothurian species by having multiple-branching (dendritic) tentacles; by having a cylindrical and not U-shaped body form; by having a calcareous ring of ten pieces which lack posterior prolongations; and by lacking a total or dorsal cover of imbricating scales.

**Key to New Zealand Cucumariidae**

1. Cups and/or rudimentary cup ossicles and/or concave crosses present in body wall; tables and terminally spinous buttons absent. 2

2. Multilayered (nodular) ossicles present in body wall. 3

3. Body with angular dorsolateral edges; tube feet on radii only; dorsal tube feet surmount raised calcareous wreaths; some cups with bridges across rim; live colour mottled red, mauve, brown, orange, cream and white

   • Body rounded dorsolaterally; dorsal tube feet densely or sparsely scattered or absent; dorsal tube feet not surmounting raised calcareous wreaths; cups all lack bridges across rim; live colour not mottled. 4

4. Ventral tube feet radial series continuous to introvert; dorsal tube feet abundant and predominantly scattered; multilayered ossicles not macroscopically evident as scales; body wall cups with predominantly more than 4 holes; buttons with discrete rounded knobs. 5

   • Ventral tube feet radial series not continuous to introvert; dorsal tube feet sparse and scattered or absent; multilayered ossicles macroscopically evident as scales; body wall cups with predominantly 4 holes; buttons with swellings more than discrete knobs. 7

5. Tube feet present on the ventral interradii; shallow concave perforated knobbed plates about 0.1 mm long present in body wall; live colour pale-spotted strawberry-red dorsally; lacking dark brown to black coloration anteriorly and posteriorly. 8

6. Cups in body wall with predominantly finely knobbed rarely semidigitate spinelets; largest elongate tentacle plates often straight and curved; live colour predominantly white. 9

   • Cups in body wall frequently with semidigitate to digitate spinelets; largest elongate tentacle plates bent and curved, not straight; live colour yellow. 10

7. Tube feet scattered and sparse dorsally; abundant coneve multiradiate ossicles epidermally. 11

   • Tube feet absent dorsally; multiradiate ossicles absent. 12

8. Ventral tube feet in double radial series; dorsal body wall scales frequently towered, creating a knobbed surface. 13

   • Ventral tube feet in single radial series; dorsal body wall scales not towered, creating a smooth plated surface. 14

9. Distinct sole; tube feet numerous and scattered dorsally, laterally, around oral and anal cones; ventral body wall ossicles coneve crosses and rudimentary cups, perforated plates small, buttons not discretely knobbed; dorsal colour blackish. 15

   • Distinct sole; tube feet numerous and scattered dorsally, laterally, around oral and anal cones; ventral body wall ossicles coneve crosses and rudimentary cups, perforated plates small, buttons not discretely knobbed; dorsal colour blackish. 16

   2. Pseudopsolus macquariensis (Bendy)
   3. Mortensen, 1925.

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**NEW ZEALAND CUCUMARIIDAE (HOLOTHUROIDEA)**

subsequently assigned to *Neocucumella fracta* O'Loughlin and O'Hara, 1992. The continuing absence of *Pseudopsolus macquariensis* (Dendy) during recent intensive collecting at Stewart Island reinforces the probability that it is a Macquarie Island species, and it is not included in the key (Mortensen, 1925).
Lacking a distinct sole; ventral tube feet in radial series; dorsal tube feet predominantly in radial series; body wall ossicles predominantly knobbed butons with commonly 4 holes and 12 peripheral discrete knobs, cups, rare large single-layered perforated plates; live colour white with dorsal tube feet ends red.

**Australocnus calcareus** (Dendy)

10. Table ossicles present in body wall, at least anteriorly and posteriorly; 20 or 25 tentacles.  

11. Table ossicles present only anteriorly and posteriorly, irregular, predominantly more than 8 perforations; 25 tentacles; tube feet in more than 2 rows radially; tube feet discs and tentacles white. 

**Amphicyclus thomsoni** (Hutton)

12. 10 equal tentacles; body wall ossicles knobbed buttons spinous at one end; multilayered ossicles absent. 

**Pseudoants leoninoides** (Mortensen)

8 large and 2 small ventral tentacles; knobbed buttons and multilayered ossicles present, some with spinous ends. 

**Pseudocnus sentus** sp. nov.

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**Pseudocnus** Panning


**Diagnosis (emended).** Cucumariidae with body wall ossicles pear-shaped to irregular, single-layered, knobbed, perforated plates with one end denticulate (*laevigatus*-group); sometimes with knobbed buttons also present, and sometimes the denticulate plates intergrading with or replaced by multilayered ossicles some of which are denticulate (*dubiosus*-group); sometimes buttons only (*curvatus*-group); cups and tables absent.

**Remarks.** The new species described here has knobbed buttons, and multilayered ossicles some of which have a denticulate end. The latter intergrade with single-layered terminally digitate ossicles which are typical of *Pseudocnus*. The combination of ossicle types in the new species places it in the *dubiosus*-group of *Pseudocnus* categorised by Panning (1962: 58–59). Descriptions and illustrations of some members of the *dubiosus*-group by Panning (1962: 66–69) indicate the presence of multilayered ossicles. Rather than establish a new monotypic genus, the relationship with *Pseudocnus* is recognised and the diagnosis emended to explicitly include multilayered terminally denticulate ossicles. Based on morphology and mitochondrial DNA studies Lambert (1998) emended the diagnosis of *Pseudocnus* to include species with thick lobed non-denticulate buttons only, and proposed a *curvatus*-group in addition to the *dubiosus- and laevigatus*-groups of Panning (1962: 58, 70). *Pseudocnus* now embraces species with widely different ossicle types.

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**Material examined.** Holotype (MNZ EC7483). New Zealand, Stewart Island, Paterson Inlet, S side of Faith Hope and Charity Group, granite or diorite rock substrate covered in pink coralline alga, 0–4 m, N. Alcock, 30 Mar 1998.

Paratypes. Type locality and date, NMV F82784 (1); 26 Sep 1998, MNZ EC7484 (5). NMV F82781 (6), NIWA (5).

Comparative material. Syntypes of *Pseudocnus leoninoides* (Mortensen, 1925) [ZMUC (207), MNZ EC531 (16)], Auckland Islands, Masked Island, Cameron Harbour, on rock wall with Melobesia, MPE, 30 Nov 1914 (Figure 1 k–l).

**Diagnosis.** Cucumariidae with 10 dendritic tentacles, ventral 2 smaller; tube feet in zig-zag to double radial rows ventrally, less regular double to zig-zag rows dorsolaterally, rare interradially; body wall ossicles irregular knobbed buttons, single to multilayered (up to 0.6 mm long) knobbed ossicles sometimes terminally denticulate or digitate and sometimes narrowed at the denticulate end, rosettes in tentacles and introvert.

**Description.** Body up to 27 mm long, 8 mm diameter (preserved, tentacles fully withdrawn), rounded to quadrangular to pentagonal in transverse section, elongate, anal cone upturned, mouth slightly upturned, lacking distinct ventrum, oral valves well developed; body wall thin, firm, flexible, calcareous, surface rough; 10 dendritic tentacles, ventral 2 smaller; calcareous ring with narrow parallel anterior projections, deep posterior indentations (interradial) and notches (radial), lacking posterior prolongations; 1–2
polian vesicles left lateral; small free madreporite close to ring dorsally; microscopic anal scales.

Tube feet extending from introvert to anus, close zig-zag to double radial rows ventrally, less regular double to zig-zag rows dorsolaterally, rare interradially, single very extensible tube feet at introvert, tube feet not on introvert, 5 present anally.

Body wall with multilayered ossicles, sometimes imbricating anteriorly and posteriorly, some denticulate at one end, up to 0.6 mm long; intergrading with irregular finely to thickly knobbed buttons, some digitate at one end or side, typically 0.1 mm long; tube feet with endplates, thin perforated denticulate irregularly oval curved support plates 0.1 mm long, elongate bent centrally widened perforated knobbed support plates 0.24 mm long; introvert with numerous thin finely-knobbed (sometimes with connecting bridges) perforated non-denticulate plates typically 0.08 mm long with 4 central holes, intergrading with open to densely branched and knobbed rosettes typically 0.05 mm long, fewer smooth or knobbed thick perforated non-denticulate oval to triangular plates typically 0.17 mm long; tentacles with thin perforated denticulate irregularly oval convex plates 0.08 mm long, irregular elongate ossicles 0.16 mm long with large central perforations, rosettes 0.04 mm long. Ossicle form consistent through small to large specimens.

Colour (live). Body white, to white with brown spotting; intestine (preserved) cream, to cream with darker brown spotting; gonad tubules long, unbranched; stomach yellow, with or without dark brown markings; tentacles with thin finely-knobbed buttons; sometimes with tentacle rosettes.

Reproduction. Gonad tubules long, unbranched; prominent without discernible eggs in September.

Etymology. From the Latin (rough), referring to the surface of the body.

Distribution. New Zealand, Stewart Island, Paterson Inlet, rocky shallows, 0–4 m.

Remarks. This new species is distinguished from other species of *Pseudocnus* by having single and multilayered, knobbed, sometimes terminally denticulate or digitate body wall ossicles. *Pseudocnus leoninoides* (Mortensen, 1925) was reported by Dendy (1909) for the Auckland Islands (as *Cucumaria leonina* Semper var.), by Mortensen (1925) from Auckland and Campbell Islands, and by Pawson (1965) from The Snares islands (just south of Stewart Island). A specimen from the Macquarie Seamount (NIWA stn D18), identified as *P. leoninoides*, was redetermined by the authors as *Pseudocnus laevigatus* (Verrill, 1876). Pawson noted (1965: 258) that *leoninoides* could be expected for New Zealand, and while *Pseudocnus* is reported here for Stewart Island it is not *P. leoninoides*.

Numerous syntypes of *Pseudocnus leoninoides* were examined (Figures 1 k–l). With single-layered, typically 0.14 mm long, knobbed, terminally denticulate body wall ossicles only, it belongs to the *laevigatus*-group of *Pseudocnus* species. In addition to lacking knobbed non-denticulate buttons and multilayered sometimes denticulate ossicles and tentacle rosettes, *P. leoninoides* has 10 equal tentacles, has radial tube feet on the introvert, has a very thin indistinctly present calcareous ring, and has a thin relatively soft body wall. In all of these features *P. leoninoides* differs from *P. sentus*.

In body form, tentacle number and form, tube feet distribution, and ossicle combination of multilayered ossicles and knobbed buttons with an absence of cups, *Pseudocnus sentus* is similar to *Cucuvitrum rowei* O’Loughlin and O’Hara, 1992. But the monotypic genus *Cucuvitrum* lacks the distinctive pointed and digitate ossicle spinules of *P. sentus*.

*Squamocnus* O’Loughlin and O’Hara


Diagnosis (emended). Cucumariidae with calcareous body wall; body rounded to slightly angular dorsolaterally; lacking body wall growths on radii; distinct ventrum with tube feet series extending to introvert and frequently to anus, not sole; 10 dendritic tentacles, ventral 2 smaller; tube feet scattered dorsally and laterally sometimes in irregular dorsolateral series, on ventral radii sometimes extending onto ventral interradii, absent on introvert. Body wall ossicles shallow cruciform spinous cups (up to 0.05 mm long), larger cups sometimes intergrading with shallow concave finely knobbed plates (up to 0.13 mm long), regular to irregular buttons with discrete knobs, numerous large multilayered ossicles; lacking connecting bridges across cups and buttons; sometimes with tentacle rosettes.


Species. *S. aureoruber* O’Loughlin and O’Hara, 1992, *S. brevidentis* (Hutton, 1872), *S. niveus* sp. nov., *S. luteus* sp. nov..
Distribution. Coastal New Zealand, New Zealand subantarctic islands, and south-eastern Australia; 0–130 m.

Remarks. The genus *Squamocnus* comprises four closely related species characterised by a rounded dorsal body, scattered dorsal and lateral tube feet, ventral tube feet series extending to introvert, and a body wall ossicle combination of large multilayered ossicles, buttons with discrete knobs, and cruciform spinous cups without bridges. The presence of multilayered ossicles, cups that are predominantly cruciform as distinct from triradiate, and scattered dorsal and lateral tube feet distinguish *Squamocnus* from *Ocnus* Forbes and Goodsr.

*Squamocnus brevidentis* (Hutton) comb. nov.

Figure 2a–l

*Colochirus brevidentis*.—Dendy, 1897: 40–41, pl. 5 figs 54–61.—Farquhar, 1898: 325.  
*Cucumaria brevidentis*.—Perrier, 1905: 110 [uncertain *S. brevidentis*].—Dendy and Hundle, 1907: 99–100 [some, if not all, non *S. brevidentis*].—Dawbin, 1950: 38, fig. 10 [part].

*Ocnus brevidentis* var. *carnleyensis*.—Pamling, 1949: 437.


Material examined. Syntype (labelled "? Co-type") [BMNH 86.11.18.6.1 (1)]. New Zealand, Stewart Island. Other material, New Zealand, South Island, Fiordland, Preservation Inlet, exposed rock surfaces, large cluster colonies, 2–15 m, 30 Nov 1996, NMV F81958 (5); 30 Jul 1997, NMV F81957 (17); Kaikoura, 42°42′ S, 173°38′ E, 100–112 m, 14 Dec 1982, MNZ EC6915 (1); 42°38′ S, 173°40′ E, 120–130 m, 11 Dec 1982, MNZ EC6918 (15); Stewart Island, Paterson Inlet, S side of Faith Hope and Charity Group, granite or diorite rocky substrate covered in pink coralline alga, under rocks, small groups, 0–5 m, 20 Aug 1997, NMV F81956 (6); 26 Sep 1998, MNZ EC7485 (3); NIWA (3); Paterson Inlet shore and Ulva Island, MNZ EC533 (6); Bounty Platform, 49°40′ S, 178°47′ E, 63 m, 9 Nov 1962, NIWA stn A728 (4); Antipodes Islands, 73 m, 7 Nov 1962, NIWA stn A729 (1); SCUBA, 27 Nov. 1978, NMV F82779 (2).

Description of material. Body up to 55 mm long (live, tentacles partly extended); body wall thick, firm to hard; body domed dorsally, flat ventrally, distinct ventrum thin-walled in relaxed specimens, not sole; mouth anterior, slightly upturned, 5 weakly developed radial oral valves; upturned anal cone, 5 microscopic anal scales; 10 dendritic tentacles, ventral 2 smaller; calcareous ring solid, slender tapering anterior projections and posterior indentations radially and interradially, lacking posterior prolongations; single left lateral pallial vesicle.

Tube feet up to 4 rows wide on radii of ventrum, extending onto ventral interradii and ventrolaterally, radial series extending into introvert; double radial rows near introvert on oral valves, absent on introvert, very extensible prominent single radial tube feet at introvert; tube feet dorsally and laterally and around anal cone fewer, evenly scattered, with low tuberlele bases.

Body wall ossicles small, few concave finely knobbed perforated plates, buttons and multilayered ossicles; small cups regular cruciform, rarely with triradiate centrepiece, 0.025–0.048 mm long, 4–8 holes, smallest cups with bare cruciform centrepiece and digitate spinulets on rim all pointing up from cup; larger cups intergrade with regular cruciform to irregular very shallow concave plates; concave plates frequently with 8, up to 26, holes large centrally decreasing in size towards periphery, 0.09–0.13 mm long, finely knobbed over whole plate, knobs pointing in all directions; concave plates intergrade with buttons; buttons with discrete knobs predominantly irregular, about 1 in 4 may be regular with 4 holes, typically 4–7 very rarely up to 14 holes, knobs bulbous and sometimes fused and irregular, small buttons frequently with 1 oblong knob centrally less commonly 2 discrete knobs centrally, smallest buttons typically 0.1 mm long; numerous multilayered ossicles up to 0.9 mm long. Introvert with typical cups and knobbed concave plates only; concave plates frequently elongate, up to 0.13 mm long. Tentacle ossicles large elongate narrow curved thickened perforated plates (holes decreasing in size distally) up to 0.6 mm long, irregular perforated dentilecent convex plates typically 0.06 mm long, narrow centrally-enlarged perforated bent plates typically 0.15 mm long, lacking rosettes. Tube feet ossicles endplates up to 0.24 mm diameter, irregular denticle perforated enveled plates (holes decreasing in size distally) up to 0.6 mm long, irregular perforated denticle convex plates typically 0.06 mm long, narrow centrally-enlarged perforated bent plates typically 0.15 mm long, lacking rosettes. Tube feet ossicles endplates up to 0.24 mm diameter, irregular denticle perforated perforated enveled plates (holes decreasing in size distally) up to 0.6 mm long, elongate narrow centrally-widened curved bent perforated plates typically 0.15 mm long, cups, buttons. Anal ossicles typical body wall ossicles and large perforated plates; perforated plates thick, irregularly elongate or pear-shaped, single-layered not knobbed at end(s), knobs and
secondary layers extensive, frequently bluntly denticulate at narrow end, up to 0.8 mm long.

**Colour (live).** Body wall, dorsally and laterally and around oral and anal cones, and tentacles strawberry-red; ventrum cream to pale pink; and around oral and anal cones, and tentacles yellowish tips, and tube feet all over the body and twice the size of the ventral ones, and the ossicles were large reticulate nodules, irregular buttons, and papillae, bridges across knobbed ossicles, and cups similar to *S. calcareus* but with some more flat and irregular. Dendy (1897: fig. 58) illustrated these last-mentioned distinctive ossicles for the type specimen of *S. brevidentis*, and illustrated (1909: pl. 6, 2h and 2k) similar ossicles for *S. brevidentis* var. *carnleyensis*. Hutton's and Dendy's characters refer to the strawberry species described subsequently by Dendy (1909) as *S. brevidentis* var. *carnleyensis*. Mortensen (1925) followed Dendy (1909). The descriptions of var. *carnleyensis* by Dendy (1909) and Mortensen (1925) are descriptions of Hutton's *S. brevidentis*.

There are white and yellow (white preserved) undescribed species in New Zealand which are similar to the strawberry *S. brevidentis*, and one or both have been assumed to be *S. brevidentis* by Dendy and Hindle (1907), Dendy (1909), Mortensen (1925) and Panning (1949, 1971). In addition to differing from *S. brevidentis* in live colour, both species (described below) have double ventral radial series of tube feet with bare interradii, and lack the unique shallow concave knobbed plate ossicles illustrated by Dendy (1909: pl. 6, 2h and 2k). References by Panning (1949, 1971) to *S. brevidentis* are generally applicable to the strawberry, white and yellow species, but the two specimens from Cook Strait described and illustrated by Panning (1949: 437–438, fig. 32) are the white species described below.

Ludwig (1898) considered *Colochirus calcareus* Dendy, 1897 to be a junior synonym of *C. brevidentis*, and was followed by Perrier (1905), Dendy and Hindle (1907) and Dendy (1909). Mortensen (1925) and subsequent authors recognised *C. calcareus*.

In assigning the species *brevidentis* to *Pentacta* Goldfuss, 1820, and diagnosing the genus, Panning (1971: 38–39) recognised that the genus was not homogeneous and that *brevidentis* occupied an uncertain place. And in fact, he was dealing with a different species (see next species). Recently Rowe (in Rowe and Gates, 1995: 271) has discussed the diagnosis of *Pentacta*. Panning considered appendages confined to the radii, growths on the radii surmounted by tube feet or papillae, bridges across knobbed ossicles, and four or five-edged body form, to be characteristic of *Pentacta*. None of these features occurs in *S. brevidentis* which is assigned here to *Squamocnus* as diagnosed above.

Pawson (1968, 1970) did not recognise var. *carnleyensis* and in describing *S. brevidentis* referred to the strawberry species (Pawson, 1970; ossicles fig. 8C are characteristic of *brevidentis*) and white species (Pawson, 1968: dark dorsal colour occurs in the white but not red species), and included a distribution around the North Island where the red species has not been collected. Pawson (1968: 26–27) recorded *S. brevidentis* from Macquarie Island. Mortensen (1925: 335) had cast some doubt on the basis for this record. A recent study of the echiuroid fauna of Macquarie Island (O'Hara, 1999) did not confirm the occurrence of *S. brevidentis* in the Macquarie Island fauna. Mortensen (1925) reported *S. brevidentis* from the Auckland and Campbell Islands as var. *carnleyensis*.

One of the specimens from the Antipodes Islands collected on 27 November has eggs which are 0.7 mm long in the gonad tubules, while no specimen from southern New Zealand collected...
in August and November has similar macroscopically discernible eggs. This indicates a probable variation in the reproductive cycle across the geographical range of *S. brevidentis*. It was also noted that regular buttons with four holes are more common in specimens of *S. brevidentis* from the subantarctic islands than from southern New Zealand. These observations indicate that speciation may be occurring across the geographical range of this brood-protecting species.

*S. brevidentis* is distinguished from other species of *Squamosus* by its relatively large size and pale-spotted strawberry-red colour (live), by the presence of tube feet on the ventral interradii, by the presence in the body wall of shallow slightly concave and finely knobby perforated plates commonly 0.1 mm long, by the presence of digitate spinelets on the smallest cups, and by a habit of seasonal winter brood-protection under the body (Alcock, 1999). Characteristic ossicle form can be distinguished in juveniles as small as 5 mm long.

*Squamosus niveus* sp. nov.

**Figure 3a–l**

*Cucumaria brevidentis*.—Dendy and Hindle, 1907: 99–100 [probably part].—Mortensen, 1925: 331–332, fig. 26 a–b.—Dawbin, 1950: 38, fig. 10 [part].


**Material examined.** Holotype (MNZ EC7487). Stewart Island, Paterson Inlet, S side of Faith Hope and Charity Group, granite or diorite rock substrate covered in pink coralline alga, solitary under rocks, 0–1 m, N. Alcock, 30 Mar 1998.

Paratypes. Type locality and date, NMV F82783 (5), NMV F83406 (1, brood-protecting); 21 Jan 1998, NMV F82777 (3); 26 Sep 1998, MNZ EC7488 (6); NIWA (6).

Other material. North Island. Cape Maria van Diemen, MPE, 4 Jan 1915, ZMUC (58); Slipper Island, 37° S, 176° E, MPE, 20 Dec 1914, ZMUC (11); Auckland Islands, Masked Island, Carnley Harbour, MPE, 3 Dec 1914, ZMUC (105); Bounty Platform, 49°40′ S, 178°50′ E, 37 m, 9 Nov 1962, NIWA stn A743 (1); 49°40′ S, 178°47′ E, 63 m, 9 Nov 1962, NIWA stn A738 (1).

**Description.** Body up to 28 mm long (live, tentacles fully extended); body wall thick, firm to hard; body tubular, domed dorsally, flat ventrally, distinct ventrum, not sole; mouth anterior, slightly upturned, 5 weakly-developed radial oral valves; long upturned anal cone on many specimens; 5 microscopic anal scales; 10 dendritic tentacles, ventral 2 smaller; calcareous ring solid, fine tapering anterior projections radially and inter-radially, posterior notches radially, wide indentations inter-radially, lacking posterior prolongations; single left ventral polian vesicle.

Tube feet in zig-zag to double rows on ventral radii, extending from introvert to anus, ventral interradii bare; absent from introvert; irregular double dorsolateral rows or scattered dorsally and laterally in midbody, double radial rows near introvert, single very extensible radial tube feet at introvert, bases of tube feet sometimes swollen creating small tubercles.

Body wall ossicles cups, buttons and multi-layered ossicles; cups regular cruciform, rarely with tripartite centriplate, cups typically 0.028–0.056 mm long, typically 4–8 very rarely up to 14 holes (very small peripherally), cup spinelets dense and knobbled to bluntly denticulate rarely semidigitation on larger cups, spinelets always on centriplates and pointing up or in all directions from cup rim; cups intergrade with buttons; buttons with discrete knobs regular and irregular, commonly 3–6 rarely up to 14 holes, buttons typically 0.08 mm long; about 1 in 4 buttons regular, 4 uniform holes, 8–10 uniform large peripheral knobs, 2 central knobs sometimes larger, numerous multilayered ossicles up to 0.8 mm long. Introvert with typical cups and elongate very shallow concave finely knobbled perforated plates up to 0.14 mm long. Tentacle ossicles elongate, narrow, straight or bent, curved, thickened, irregularly perforated plates up to 0.4 mm long; bent curved perforated rods typically 0.15 mm long; irregular curved and convex denticulate perforated plates typically 0.06 mm long; lacking rosettes. Tube feet with endplates up to 0.22 mm diameter, irregular thin denticulate perforated curved to convex plates typically 0.07 mm long, irregularly triangular to elongate centrally-widened bent curved perforated plates typically 0.15 mm long, cups, buttons. Anal ossicles typical body wall ossicles and large perforated plates; perforated plates thick, irregularly elongate or pear-shaped, part single-layered not knobbled, extensive parts with knobs and secondary layers, frequently bluntly denticulate at end(-s), rarely sharply denticulate, plates up to 0.65 mm long.

**Colour (live).** Body white; large ossicles in body wall create greyish spotting; tentacles pink, rarely pale orange; dark brown to black on tentacle trunks, introvert, anteriorly and sometimes dorsally and anally; sometimes fine black flecking dorsally (dark markings persist on preserved material); rare brown spotting dorsally and ventrally.
Reproduction. Gonads (preserved) orange to white; long, thin, unbranched tubules; separate sexes; seasonal autumn and winter internal brood-protection in coelomic sacs; numerous eggs or embryos 0.7–0.8 mm long in sacs in March; coelomic embryos uniformly 1.0 mm long showing differentiation and osicle development by July; no brood-protection evident by September.

Etymology. From the Latin *niveus* (white as snow), referring to the live body colour.

Distribution (confirmed here). New Zealand. North, South, Stewart and Auckland Islands, Bounty Platform. 0–63 m.

Remarks. This white species was assumed to be *S. brevidentis* by Dendy and Hindle (1907), Mortensen (1925) and Panning (1949, 1971). In recognising var. *carneleyensis* (the true *brevidentis*), Mortensen (1925) distinguished it from *S. niveus* (assumed to be *S. brevidentis*). Mortensen (1925: 333) noted less scattered dorsolateral tube feet on Masked Island material and expressed doubt about referring this material to *S. brevidentis*. Panning (1949) described *S. niveus* from Cook Strait material (as *Pentacta brevidentis*). Many of the small ZMUC specimens (MPE) from Cape Maria van Diemen exhibit a deep midbody constriction, suggesting the possibility of fissiparous, but no anal body ends were present. The type species of the genus, *Squamocnus aureoruber*, is fissiparous. *S. niveus* is distinguished from the other species in *Squamocnus* by its white colour (live), grey to black anterior and posterior and sometimes dorsal coloration, absence of ventral interradial tube feet, absence in the body wall of shallow concave finely knobbed perforated plates, buttons which fairly commonly are regular with four even holes and 8–10 peripheral and two central knobs, and brood-protection in intracoelomic sacs. Characteristic osicle form can be distinguished in juveniles as small as 5 mm long.

*Squamocnus luteus* sp. nov.

Figure 4a–i


Paratypes. Type locality and date, NMV F82776 (7); type locality, 30 Jul 1997, NMV F81955 (4); Stewart Island, Paterson Inlet, S side of Faith Hope and Charity Group, 2–4 m, 30 Mar 1998, NMV F83407 (1); 0–5 m, 26 Sep 1998, MNZ EC7490 (2).

Other material. Fiordland, Preservation Inlet, Feb–Mar 1998, NIWA (8).

Description. Body up to 20 mm long, 6 mm wide (preserved, tentacles extended); thin calcareous body wall; body tubular; distinct ventrum, not sole; mouth anterior, 5 weakly developed radial oral valves; upturned anal cone, 5 microscopic anal scales; 10 dendritic tentacles, ventral 2 smaller, calcareous ring solid, slender tapering anterior projections and posterior indentations radially and interradially, lacking posterior prolongations; single left lateral perianal vesicle.

Tube feet scattered dorsally and laterally in midbody, bases slightly swollen, double radial series near introvert, sometimes also evident in irregular dorsolateral series; double to zig-zag rows on ventral radii, extending from introvert to anus, ventral interradii bare; absent on introvert; 5 radial anal tube feet.

Body wall ossicles cups, buttons, and multilayered ossicles; cups shallow, predominantly regular, cruciform, some triradiate, frequently digitate to semidigitate spinelets or fine knobs on rim pointing in all directions from rim and centrepiece, sometimes pointing up only on smallest cups, always on centrepiece, cups 0.024–0.056 mm long, typically 0.032–0.040 mm long, 4–8, very rarely up to 20 holes, holes very small peripherally, smallest cups regularly oval to rectangular, largest cups less regular around cruciform centrepiece; buttons predominantly irregular, 0.06–0.12 mm long, very rarely regular with as few as 4 holes and 2 central and 8–12 peripheral knobs, commonly 5–7, ranging 3–16 holes, peripheral knobs relatively numerous and usually discrete and not merging; numerous multilayered ossicles up to 0.8 mm long. Introvert with typical cups, some elongate up to 0.07 mm long intergrading with some very shallow concave finely knobbed plates up to 0.07 mm long. Tentacle ossicles elongate, narrow, curved, predominantly bent, some centrally widened, perforated plates up to 0.27 mm long; irregular convex denticulate perforated plates typically 0.08 mm long; lacking rosettes. Tube feet with convex endplates up to 0.16 mm diameter, irregularly oval thin curved denticulate perforated plates typically 0.08 mm long, irregularly oval to elongate narrow centrally-widened curved perforated knobbed plates typically 0.12 mm long, cups, buttons. Anal ossicles typical body wall ossicles and large perforated plates; perforated plates thick, irregularly pear-shaped, part single-layered not knobbed, part with knobs and secondary layers, bluntly denticulate in places at edges, plates up to 0.56 mm long.

Colour (live). Body and tentacles yellow; dark
grey to black markings frequently on tentacle trunks, anteriorly and posteriorly. Yellow quickly fades to white in alcohol; dark coloration persists.

**Reproduction.** Sexes separate; gonad tubules unbranched; tubules with macroscopically distinguishable eggs up to 0.6 mm long in February; no evidence of fissipary or brood-protection in February, July and October.

**Etymology.** From the Latin *luteus* (yellow), referring to the live colour of the body.

**Distribution.** New Zealand, Fiordland, Preservation Inlet; Stewart Island, Paterson Inlet. 0–15 m.

**Remarks.** After preservation in alcohol specimens quickly become white, frequently with persistent anterior and posterior dark grey to black markings, and are indistinguishable in appearance from *S. niveus*. *S. luteus* is distinguished from *S. niveus* by its smaller size and yellow colour (live), absence of a coelomic brood-protecting habit in autumn-winter, larger cups frequently with digitate to semidigitate spinesets, and largest elongate tentacle plates bent and curved but rarely straight and curved. It is distinguished from *S. brevidentis* by its smaller size and yellow colour (live), absence of interradial tube feet ventrally, absence of concave knobbed body wall plates, and presence of dark coloration anteriorly and posteriorly. Ossicle form is consistent from small to large specimens.

_Australocnus_ gen. nov.

**Comparative material examined.** *Ocnus planci* (Brandt). Western Mediterranean off Banyuls-sur-mer, 50–85 m. NMV F82971 (6) (Figure 5g–l).

**Diagnosis.** Cucumariidae with thick, firm, friable, polygonal ossicles, with reddish to black, yellow or grayish coloration anteriorly and posteriorly. Yellow quickly fades to white in alcohol; dark coloration persists.

**Reproduction.** Sexes separate; gonad tubules unbranched; tubules with macroscopically distinguishable eggs up to 0.6 mm long in February; no evidence of fissipary or brood-protection in February, July and October.

**Etymology.** From the Latin *luteus* (yellow), referring to the live colour of the body.

**Distribution.** New Zealand, Fiordland, Preservation Inlet; Stewart Island, Paterson Inlet. 0–15 m.

**Remarks.** After preservation in alcohol specimens quickly become white, frequently with persistent anterior and posterior dark grey to black markings, and are indistinguishable in appearance from *S. niveus*. *S. luteus* is distinguished from *S. niveus* by its smaller size and yellow colour (live), absence of a coelomic brood-protecting habit in autumn-winter, larger cups frequently with digitate to semidigitate spinesets, and largest elongate tentacle plates bent and curved but rarely straight and curved. It is distinguished from *S. brevidentis* by its smaller size and yellow colour (live), absence of interradial tube feet ventrally, absence of concave knobbed body wall plates, and presence of dark coloration anteriorly and posteriorly. Ossicle form is consistent from small to large specimens.

**Australocnus calcareae** (Dendy) comb. nov.

**Figure 5a–f**

_Colochirus calcareae_ Dendy, 1897: 38–40, pl. 5 figs 44–53.—Farquhar, 1898: 325.

_Colochirus brevidentis._—Ludwig, 1898: 442–444, pl. 26 figs 22–29 [non *Squamocnus brevidentis* (Hutton, 1872)].

_Cucumaria calcarea._—Mortensen, 1925: 335–337, fig. 26c–d.—Dawbin, 1950: 38, pl. 2 fig. 11.


**Material examined.** Neotype (MNZ EC7491). New Zealand, Cook Strait, Makara, rocky shallows, 0–1 m, O’Loughlin and Ayeok, 20 Sep 1998.

Other material. Neotype locality and date, NMV F83526 (1); Stewart Island, Paterson Inlet, S side of Faith Hope and Charity Group, rocky substrate, 0–5 m, 30 Mar 1998, NMV F82782 (2); 26 Sep 1998, MNZ EC7492 (6), NIWA (4), NMV F83404 (2); Cook Strait.
Description of material. Body up to 20 mm long, 5 mm wide (live, tentacles fully extended); body wall friable; rounded dorsolateral and ventrolateral edges; anal cone upturned, oral end slightly elevated; 10 dendritic tentacles, ventral 2 smaller; tube feet in double radial rows ventrally extending from introvert to anus, dorsolaterally in radial double to zig-zag rows with a few present interradially in midbody, absent on introvert, very extensively thickened, perforated, knobbed, rarely with multilayered ossicles and tentacle rosettes. Dorsal body wall ossicles predominantly buttons and cups, rare large plates; buttons oval, elongate, with discrete knobs, frequently with 2 central knobs larger than 12 peripheral ones, 2 middle holes larger than end ones, buttons typically 0.08 mm long; shallow concave cups with small knobs to blunt spines on rim and centrepiece, mostly pointing in all directions from cup rim, sometimes pointing up only, cups with predominantly 4 holes (up to 8), 0.024-0.040 mm long; large single-layered plates and multilayered ossicles) were rare or absent in A. calcareus, but present in S. brevidentis. Large multilayered ossicles are never present in A. calcareus, and this characteristic provides a diagnostic distinction between Australocnus to which A. calcareus is assigned here and Squamocnus O’Loughlin and O’Hara, 1992 to which S. brevidentis is assigned above.

Panning (1949: 438) was initially uncertain whether A. calcareus was a species distinct from S. brevidentis. Subsequently Panning (1971: 38) reassigned brevidentis to Pentacta but with reservations. Panning (1971: 30, 36) retained A. calcareus in a restricted Ocnus.

The Juan Fernandez occurrence is based on a re-determination as A. calcareus by Mortensen (1925: 337) of material referred to S. brevidentis by Ludwig (1898) who considered A. calcareus to be a junior synonym of S. brevidentis. McKnight (1984: 145) reported A. calcareus from Macquarie Island (71-433 m), but the authors were not able to confirm this record. Mortensen (1925) reported A. calcareus from Slipper Island.

A. calcareus is distinguished from the Australian species A. occiduus O’Loughlin and O’Hara by its small size, red dorsal tube feet when live, rare large perforated plates which are knobbed, and absence of tentacle rosettes. O’Loughlin and O’Hara (1992: 248) observed swollen bases of tube feet (tubercles) in calcareus specimens, but these were not evident in material examined subsequently. There is no geographical continuity for these similar species, neither occurring in south-eastern Australia.

Australocnus occiduus (O’Loughlin and O’Hara) comb. nov.

Ocnus calcareus.—Rowe, 1982: 446, fig. 10:32a.—Marsh, 1991: 472, 477.—Marsh and Pawson, 1993: 295 [non Australocnus calcareus (Dendy, 1897)].

Ocnus occiduus O’Loughlin and O’Hara, 1992: 247–248, table 1, fig. 7a–d; pls 1h, 9a–f.


Comparative material. *Plesiocolochirus spinosus* (Quoy and Gaimard, 1833), NMV F45021 (3).

**Description of material.** Body up to 32 mm long (tentacles withdrawn); rounded to slightly pentagonal in transverse section; thin-walled ventrum; double radial rows of tube feet extending from introvert to anus, irregular rows dorsolaterally, rare small dorsal and lateral ones interradially. Dorsal body wall ossicles abundant buttons and cups, rare plates; buttons with discrete knobs, commonly regular with 12 peripheral knobs uneven with midlateral and midterminal knobs often smaller, 2 central knobs not normally larger, largest buttons typically 0.09 mm long; shallow cruciform cups with small knobs on rim and centrepiece pointing in all directions, predominantly 4–8 holes, cups typically 0.04 mm long; large single-layered plates rare, irregularly oval to elongate, smooth to lumpy, perforated, not knobbed, up to 0.4 mm long; lacking multilayered ossicles. Tentacles with rosettes.

**Colour (live).** White, grey on thin ventral surface and sometimes laterally; tentacle trunks dark brown to black; fine tentacle branches pale yellow.

**Distribution.** Australia. Rottnest Island, Western Australia, to Yorke Peninsula, South Australia; 0–30 m.

**Remarks.** Rowe (1995: 277, 279) referred this species with reservations to *Plesiocolochirus Cherbonnier, 1946*, considering it to be not congeneric with *Ocnus* Forbes, 1841 but possibly requiring allocation to a new genus. The specimens of *Plesiocolochirus spinosus*, the type species for *Plesiocolochirus*, have evenly distributed radial and interradial tube feet, distinctive small paired pointed posterior projections on the radial plates of the calcareous ring, lateroventral tubercles, multilayered ossicles, and frequently bridges across the rim of cups. *Australocnus occiduus* has none of these features. *A. occiduus* is distinguished from the New Zealand *A. calceatus* by its significantly larger size, absence of red coloration of dorsal tube feet, rare large plates which are smooth to lumpy and not knobbed, and the presence of tentacle rosettes.

*Psolidocnus* gen. nov.

**Figure 61**

**Diagnosis.** Cucumariidae with contiguous body wall scales dorsally and laterally; body rounded in transverse section with flattened ventrum, mouth and anus at least slightly upturned or situated dorsally; 10 dendritic tentacles, ventral 2 smaller; tube feet in three radial series ventrally, series not extending to introvert or anus, not continuous around ventrum to create sole, absent or sparsely present dorsally; body wall ossicles large multilayered sometimes towered ossicles (seals) up to at least 0.8 mm long, irregular lumpy more than discretely knobbed buttons, regular shallow cruciform spinous cups up to 0.05 mm long with predominantly 4 holes, sometimes multiradiate concave ossicles up to 0.03 mm long.

**Type species.** *Cucumaria amokurae* Mortensen, 1925.

**Species.** *P. amokurae* (Mortensen, 1925), *P. farquhari* (Mortensen, 1925), *P. sacculus* (Pawson, 1983).

**Etymology.** From the family name Psolidae, referring to psolid-like characteristics, with *Ocnus*, the genus to which two species were referred.

**Distribution of genus.** New Zealand, South Island; Stewart Island; Auckland Islands. 9–660 m.

**Remarks.** Panning (1971: 36) did not include *P. farquhari* in *Ocnus*, but did not reassign it. Pawson (1983: 227), O’Loughlin and O’Hara (1992: 237) and Rowe (in Rowe and Gates 1995: 279) questioned whether *Ocnus* was a suitable genus for one or both of the species *P. farquhari* and *P. sacculus*. A pentagonal body form, radial rows of ventral tube feet extending to introvert and anus, numerous triradiate cups, and absence of multilayered ossicles distinguish *Ocnus* (Figure 5g–I) from *Psolidocnus*.

Panning (1949: 426) assigned *P. amokurae* to *Trachythyone Studer, 1876* with a question. O’Loughlin and O’Hara (1992: 237, 239) and O’Loughlin (1994: 542) noted that *Trachythyone* was an unsuitable genus for *P. amokurae* with its multilayered ossicles. Panning (1949, 1964) diagnosed *Trachythyone* as having cups and smooth plates in the body wall, and the absence of multilayered ossicles and lumpy to knobbed buttons distinguishes *Trachythyone* from *Psolidocnus*. In *Psolidocnus* the presence of large contiguous scales dorsally and laterally, presence of buttons and cups in the body wall, upturning of or dorsally situated oral and anal ends, and ventral radial tube feet series not extending to introvert and anus are psolid-like features, but there is not a distinct sole with peripheral tube feet as in the Psolidae. *Psolidocnus* is distinguished from *Squamocnus* and *Australocnus* by the ventral radial tube feet series not continuing to the introvert or anus, by the form of the cups which are
predominantly four-holed and up to 0.05 mm long, by the form of the buttons which are predominantly lumpy as distinct from discretely knobbed, and by the presence dorsally and laterally of macroscopically distinguishable contiguous sometimes towered scales up to at least 0.8 mm long.

*Psolidocnus* is similar to *Apsolidium* O'Loughlin and O'Hara, 1992 in having ventral radial series of tube feet not extending to introvert and anus, and by having a body wall ossicle combination of multilayered ossicles, lumpy to knobbed buttons, and cups. *Psolidocnus* differs in lacking a distinct sole; having significantly fewer tube feet dorsally, laterally and ventrally; having very large scale-like contiguous multilayered ossicles; and having shallow cups. *Apsolidium alvei* O'Loughlin and O'Hara, 1992 was assigned to its genus with reservations since it lacks a distinct sole, and the large plates with secondary layers are not typical multilayered ossicles. The form of the large plates and deep cups of *alvei* indicate that it would be no more suitably assigned to *Psolidocnus*.

**Psolidocnus amokurae** (Mortensen) comb. nov.

*Figure 6a–g*

*Cucumaria amokurae* Mortensen, 1925: 341–343, figs 29, 30a.—Dawbin, 1950: 38, pl. 2 fig. 13.


**Material examined.** Three syntypes (ZMUC). New Zealand, Auckland Islands, Camley Harbour, sandy mud, 82 m, MPE, 6 Dec 1914; syntype (MNZ EC532), type locality and date (1).

Other material. Stewart Island, Paterson Inlet, mud, 9–27 m, MPE. 17 Nov 1914, ZMUC (2); Kaikoura, 42° S, 173° E, 69 m, 7 Dec 1982, MNZ EC6951 (2); 120–130 m, 11 Dec 1982, MNZ EC6907 (2), EC6922 (11), EC7493 (2); 100–112 m, 14 Dec 1982, MNZ EC6925 (8); 95–98 m, 21 Dec 1982, MNZ EC7494 (1); Kaikoura, 91 m, 14 Jun 1961, NIWA stn C653 (1, brood-protecting); 556 m, 18 Oct 1965, NIWA stn E434 (1).

**Distinguishing features.** Body up to 17 mm long, 11 mm wide (tentacles withdrawn); body ealcareous, towered contiguous scales dorsally and laterally, smooth contiguous scales ventrally; body domed dorsally, flat ventrally, mouth antcrodorsal, anus posteriodorsal; 10 dendritic tentacles, ventral 2 smaller; tube feet sparse dorsolaterally between scales, present in 3 double radial rows on flattened ventrum, ventral rows not continuing to introvert or anus, not continuous around ventrum to create sole, lateroventral row continuous, ventrolateral row discontinuous. Dorsal body wall ossicles large contiguous multilayered ossicles, irregularly oval, up to 1.5 mm long, some bluntly towered at one edge; small, conave, shallow multiradiate ossicles in epidermis, up to 0.03 mm long, arms sometimes bifid distally, some joined at rim to form incomplete cups; conave cruciform oval cups, normally 4, rarely up to 7, perforations, knobbed cruciform centrepiece, rim with semidigitate spinules pointing up from eup rim, cups typically 0.04 mm long; lumpy to knobbed buttons, predominantly irregular, typically 6 (4–10) holes, typically 0.07 (0.07–0.12) mm long.

**Colour.** Yellow to red (live); white (alcohol) (Mortensen, 1925).

**Reproduction.** Brood-protects four juveniles up to 2.2 mm long in dorsal coelomic chamber.

**Distribution.** New Zealand, Kaikoura; Stewart Island, Paterson Inlet; Auckland Islands, Carnley Harbour. 9–556 m.

**Remarks.** O'Loughlin and O'Hara (1992) and O'Loughlin (1994) remarked that with large multilayered ossicles this species was not a *Trachythione*, but was close to both *Squamocnus* and the Psolidae. O'Loughlin (1994) described eelomiac brood-protection, by a mode similar to *P. sacculus*. Within the new genus *P. amokurae* is unique in having small concave epidermal multiradiate ossicles in addition to the common ossicle combination. It is similar to *P. farquhari* in having towered dorsal and lateral scales, but is distinguished by having dorsal tubule feet and the multiradiate ossicles. It is similar to *P. sacculus* in its mode of brood-protection, but is distinguished by having towered scales, dorsal tube feet and multiradiate ossicles.

**Psolidocnus farquhari** (Mortensen) comb. nov.

*Figure 6h–i*

*Cucumaria farquhari* Mortensen, 1925: 343–345; figs 30b, 31 a–e.—Dawbin, 1950: 38, pl. 2 fig. 12.


**Material examined.** Syntype (ZMUC). New Zealand, 2 mi E of North Cape, hard bottom, 100 m, MPE, 2 Jan 1915.

**Distinguishing features.** Body up to 17 mm long, 11 mm wide (tentacles withdrawn); body ealcareous, towered contiguous scales dorsally and laterally, smooth contiguous scales ventrally; body domed dorsally, flat ventrally, mouth antcrodorsal, anus posteriodorsal; 10 dendritic tentacles, ventral 2 smaller; tube feet sparse dorsolaterally between scales, present in 3 double radial rows on flattened ventrum, ventral rows not continuing to introvert or anus, not continuous around ventrum to create sole, lateroventral row continuous, ventrolateral row discontinuous. Dorsal body wall ossicles large contiguous multilayered ossicles, irregularly oval, up to 1.5 mm long, some bluntly towered at one edge; small, conave, shallow multiradiate ossicles in epidermis, up to 0.03 mm long, arms sometimes bifid distally, some joined at rim to form incomplete cups; conave cruciform oval cups, normally 4, rarely up to 7, perforations, knobbed cruciform centrepiece, rim with semidigitate spinules pointing up from eup rim, cups typically 0.04 mm long; lumpy to knobbed buttons, predominantly irregular, typically 6 (4–10) holes, typically 0.07 (0.07–0.12) mm long.

**Colour.** Yellow to red (live); white (alcohol) (Mortensen, 1925).

**Reproduction.** Brood-protects four juveniles up to 2.2 mm long in dorsal coelomic chamber.

**Distribution.** New Zealand, Kaikoura; Stewart Island, Paterson Inlet; Auckland Islands, Carnley Harbour. 9–556 m.

**Remarks.** O'Loughlin and O'Hara (1992) and O'Loughlin (1994) remarked that with large multilayered ossicles this species was not a *Trachythione*, but was close to both *Squamocnus* and the Psolidae. O'Loughlin (1994) described eelomiac brood-protection, by a mode similar to *P. sacculus*. Within the new genus *P. amokurae* is unique in having small concave epidermal multiradiate ossicles in addition to the common ossicle combination. It is similar to *P. farquhari* in having towered dorsal and lateral scales, but is distinguished by having dorsal tube feet and the multiradiate ossicles. It is similar to *P. sacculus* in its mode of brood-protection, but is distinguished by having towered scales, dorsal tube feet and multiradiate ossicles.
sally and laterally: 10 dendritic tentacles, ventral 2 smaller; tube feet in double series on 3 ventral radii, not extending to introvert and anus, not continuous around ventrum to form sole, absent dorsally and laterally. Dorsal body wall ossicles large multilayered perforated ossicles (scales), up to 0.8 mm long, with towers; irregular lumpy to knobbed buttons, 4–8 perforations, frequently with large central swelling, typically 0.1 mm long; cruciform concave cups, predominantly regular with 4 holes, some with 4 additional small corner holes, centrepiece lumpy, cups spinous to digitate to knobbed, spinelets mostly pointing up from cup rim, cups 0.032–0.048 mm long.

**Colour.** White, blackish dorsally especially anteriorly and posteriorly (Mortensen, 1925).

**Reproduction.** Genital tubules unbranched, few eggs linearly, ‘eggs’ up to 1.0 mm long. A few ossicles, representing early stages of cup and button development, were found in one ‘egg’ from a gonad tubule, suggesting early embryo development and vivipary.

**Distribution.** New Zealand, two miles east of North Cape; 100 m.

**Remarks.** Mortensen (1925) reported a blackish colour dorsally at the anterior and posterior ends. The syntype examined is white and lacks any black coloration. P. farquhari is similar to P. amokurae in having towered scales. It is distinguished from P. amokurae by lacking dorsal tube feet and multiradiate ossicles.

**Psolidocnus sacculus** (Pawson) comb. nov.

**Figure 6j–k**


**Material examined.** Two paratypes (USNM E27994). New Zealand, Taiaroa Canyon, 45°46’ S, 171°05’ E, 600–660 m, 25 Mar 1974.

**Distinguishing features.** Body up to 17 mm long; body calcareous, contiguous scales dorsally and laterally; body cylindrical, slightly flattened ventrally, mouth and anus slightly upturned; 10 dendritic tentacles, ventral 2 smaller; tube feet in single rows on ventral radii, zig-zag midventrally, not extending to introvert and anus, not continuous around ventrum to create sole, absent dorsally and laterally except at introvert, single radial tube feet at introvert. Dorsal body wall ossicles large thin multilayered ossicles, irregularly oval, up to 1.0 mm long, evident macroscopically as scales [about 9 longitudinally and 9 transversely (excluding ventrum) in 9 mm long specimen]; lumpy to knobbed buttons, predominantly irregular, 3–9 perforations, 0.11–0.17 mm long; cruciform concave spinous cups, predominantly regular with 4 holes, some with 4 additional small corner holes, spinelets pointed to semidigitate, pointing up only or in all directions from rim, distinct cruciform centrepiece sometimes with fine knobs, cups 0.03–0.05 mm long; ventral ossicles similar to dorsal.

**Colour (live).** White (Pawson, 1983).

**Reproduction.** Gonads comprise long unbranched tubules, sexes separate, long genital papilla slightly anterior to dorsal tentacle pair on male paratype dissected; brood-proteus in 3 anterior dorsal and lateral interradial closed internal pouches (Pawson, 1983).

**Distribution.** Taiaroa Canyon, south-eastern New Zealand; 600–660 m.

**Remarks.** P. sacculus is similar to P. farquhari in lacking dorsal and lateral tube feet. It is distinguished from P. farquhari by having multilayered ossicles without towers, single rows of ventral radial tube feet, and a closed coelomic sac mode of brood-protection. It is distinguished from P. amokurae by lacking dorsal tube feet, lacking towers on the body wall scales, and lacking multiradiate ossicles. The species is known from only the 13 type specimens.
Dusky Sound, Beach Harbour, 11–18 m, W.H. Dawbin, 5 May 1950, MNZ EC6705 (1). Southern Australia, abundant NMV material.

Comparative material. *Plesiocolochirus spinosus* (Quoy and Gaimard, 1833), NMV F45021 (3); *Leptopenacta grisea* H.L.Clarke, 1938, NMV F82972 (1).

Distinguishing features. Body up to 50 mm long; body hard, box-like, prominent raised dorsolateral edges, distinct ventrum not a sole, lateral and dorsal surfaces with lumps and ridges, smooth ventrally, oral end with 5 pointed triangular flaps (valves); 3 double radial rows of tube feet ventrally, zig-zag rows dorsolaterally, all rows extending from introvert to anus, no tube feet interradially; dorsolateral tube feet and all tube feet on tapering oral and anal ends surmount low wreaths of encircling ridges of ossicles; radial plates of the calcareous ring with posterior prolongations; body wall ossicles large multi-layered knobbed perforated scales up to 1.5 mm long, regular and irregular knobbed perforated buttons, shallow spinous cruciform cups of a plates of the calcareous ring with no posterior wreaths of encircling ridges of ossicles; radial interradially; dorsolateral tube feet and all tube feet on the radial plates of the ring, lacks connecting bridges across the rim of cup ossicles, and lacks body wall growths on any of the radii. *P. ignavus* differs in these characters. In diagnosing *Pentacta* Goldfuss, Panning (1971: 38–39) considered appendages confined to the radii, growths on the radii surmounted by tube feet or papillae, bridges across knobbed ossicles, and four- or five-edged body form to be amongst the characteristics. *P. ignavus* does have these characters, but Rowe (in Rowe and Gates, 1995: 271) has queried the diagnosis of *Pentacta*. There are affinities and discrepancies for *P. ignavus* in relation to *Leptopenacta*, *Plesiocolochirus* and *Pentacta*. A review of the assignment of *P. ignava* and related species to appropriate genera is beyond the scope of this work.

*Psolidiella nigra* Mortensen


*Trachythyone bollonsi* Mortensen, 1925: 345–346, fig. 32.—Dawbin, 1950: 38, fig. 9, syn. nov.


Material examined. Holotype, 2 paratypes [ZMUC]. New Zealand, Stewart Island, Paterson Inlet, rocky shore, 6 Apr 1924.

Other material. The Snares, Boat Harbour, covered by plant detritus in rock pools, 18 Dec 1976, MNZ EC4061 (10); AM J12281 (4).

*Psolidiella nigra* Mortensen, 1925: 345–346, fig. 32.—Dawbin, 1950: 38, fig. 9, syn. nov.


Material examined. Holotype, 2 paratypes [ZMUC]. New Zealand, Stewart Island, Paterson Inlet, rocky shore, 6 Apr 1924.

Other material. The Snares, Boat Harbour, covered by plant detritus in rock pools, 18 Dec 1976, MNZ EC4061 (10); AM J12281 (4).


Distinguishing features. Body up to 28 mm long (tentacles withdrawn), 11 mm diameter; body rounded, distinct oval sole, oral cone and upturned anal cone; oral cone wrinkled, folded, pocketed on female specimens; 5 anal scales; 10 dendritic tentacles, ventral 2 smaller. Small tube feet scattered dorsally, laterally, around oral and anal cones; tube feet in 3 radial series ventrally, not continuing to introvert and anus, bordering sole to varying degrees anteriorly and posteriorly, up to 4 rows wide lateroventrally, up to 2 rows wide midventrally; absent from introvert. Dorsal
body wall ossicles absent or sparse thick smooth buttons, typically 4 perforations, up to 0.1 mm long (tube foot endplates and support plates present dorsally). Ventral body wall ossicles abundant thick smooth perforated plates, irregularly oval, up to 16 perforations typically about 8, up to 0.24 mm long; fewer buttons similar to dorsal ones; numerous regular and irregular concave crosses, arms frequently bifid and knobbed distally, typically 0.06 mm long, rarely partly or fully closed around rim to form cups.

**Colour (preserved).** Body pale brown to very dark brown, grey, black; sole pale brown to cream; tube feet ends white; introvert and tentacles dark brown.

**Distribution.** New Zealand, North Island (Cape Maria van Diemen), South Island (Banks Peninsula and Otago Peninsula), Stewart Islands and The Snares; south-eastern Australia; rocky shallows.

**Remarks.** O’Loughlin (1994) reported numerous knobbed and concave crosses and rare cup ossicles in the type specimens of *P. nigra*, and Panning (1961) illustrated these ossicles for *P. nigra* material from Banks Peninsula. Mortensen (1925) described and illustrated these ossicles for the type specimens of *T. bollonsi*, but did not observe them in *P. nigra*. The body wall ossicle combination of rare cups, concave knobbed crosses, and smooth perforated plates and smooth buttons is the same in *P. nigra* and *T. bollonsi*, as is the tentacle number and form, dorsal black and ventral white colour, and habitat niche. The tube foot distribution described for *T. bollonsi* is consistent with the very small specimens being juveniles of *P. nigra*.

The syntype of *C. bollonsi* which was examined was 5 mm long, 2.5 mm in diameter, and a large part of the dorsal body wall had been removed. No ossicles were detected, and they have presumably dissolved from the thin body wall. The tube feet in the ventral radial series were large, did not continue to the anus, were four rows wide laterally and two rows wide medially, and single large ventral interradial tube feet were present anteriorly and posteriorly creating a distinct sole. Smaller tube feet were present around a slightly upturned anal cone (oral cone was fully withdrawn). There was some residual brown colour evident anteriorly, posteriorly and dorsally. These observations are also consistent with the small syntype of *T. bollonsi* being a juvenile of *P. nigra*.

The type specimens of *C. bollonsi* are small juveniles, and diagnostic ossicles could no longer be detected. For these reasons the authors have chosen to act under the “Principle of the First Reviser” [ICZN Article 24(a)] and make *C. bollonsi* a junior synonym of *P. nigra* although *C. bollonsi* has page precedence over *P. nigra* in Mortensen (1925). O’Loughlin (1994) has described the brood-protecting habit of *P. nigra* and has observed this species in south-eastern Australia (O’Loughlin, 2000).

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**References**


Panning, A., 1949. Versuch einer neuerordnung der familie Cucumariidae (Holothurioidea, Dendrochi-


Thompson, W., 1840. Contributions towards a knowl-
Figure 1. a–j, *Pseudocnus setus* sp. nov. (ossicles from holotype FC7483): a, right lateral body of holotype (27 mm long); b, midbody section; c, two plates of calcareous ring; d, button (0.08 mm long); e, digitate button (0.10 mm long); f, digitate button (0.10 mm long); g, digitate plate with secondary layering (0.16 mm long); h, denticulate multilayered ossicle (0.22 mm long); i, bridged introvert plate (0.09 mm long); j, tentacle rosettes.

k–l, *Pseudocnus leoninoides* (Mortensen) (ZMUC syntype), denticulate plates (0.14 mm long).
Figure 2. *Squamosus brevidentis* (Hutton) (ossicles from F81957 and F82779 and NIWA A729). a, lateral body of F81958 (36 mm long); b, left ventral; c, midbody section; d, two plates of calcareous ring; e, smallest cups (0.03 mm long); f, side of cup (0.03 mm long); g, medium cup (0.06 mm long); h, knobbed concave plate (0.1 mm long); i, knobbed concave plate (0.1 mm long); j, knobbed concave plate and buttons (0.1 mm long); k, multilayered ossicle (0.6 mm long); l, tentacle plate (0.6 mm long).
Figure 3. *Squamocnus niveus* sp. nov. (ossicles from paratypes F82777 and F82783). a, dorsal body of holotype, EC7487 (20 mm long); b, ventral; c, dorsal view of ventral coelomic brood sacs and calcareous ring and empty gonad upper left (14 mm long specimen, F83406); d, midbody section; e, two plates of calcareous ring; f, cup (0.04 mm long); g, cups (0.05 mm long); h, buttons (0.09 mm long); i, buttons (0.08 mm long); j, multilayered ossicle (0.6 mm long); k, curved and convex denticulate tentacle plates (0.06 mm long); l, straight and curved elongate tentacle plate (0.4 mm long).
Figure 4. a–i. *Squamoceans lieus* sp. nov. (ossicles from paratypes F82776). a. left lateral body and tentacles of holotype, FC7489 (20 mm long); b. midbody section; c. two plates of calcareous ring; d. cup with semidiginate spinelets (0.05 mm long); e. cup (0.05 mm long); f. button (0.08 mm long); g. buttons; h. multilayered ossicle (0.8 mm long); i. bent and curved elongate tentacle plate (0.25 mm long).

j–l. *Plesiocoloehirus ignavus* (Ludwig). j. anterior dorsolateral body of 48 mm long specimen showing radial tubercle wreaths around tube feet (F76516); k. anterior oral valves; l. bridged cups (F82775).
Figure 5. a–f, *Australocnus calcareus* (Dendy) (ossicles from F82782). a, dorsal body of F83405 (7 mm long); b, cup (0.035 mm long); c, buttons (0.08 mm long); d, button and cups; e, plate (0.3 mm long); f, plate (0.5 mm long).

g–l, *Ocnus planci* (Brandt) (F82971). g, dorsal body (40 mm long); h, ventral; i, cups (0.025 mm long); j, cups (0.025 mm long); k, buttons (0.08 mm long); l, buttons (0.08 mm long).
Figure 6. a-g, *Psolidocnus umokurae* (Mortensen) (ossicles from syntype, ZMUC and NIWA C653 specimens). a, lateral body of syntype (9 mm long); b, ventral; c, four dorsal coelomic brood juveniles in 12 mm long specimen (NIWA C653); d, concave multiradiate ossicles (0.02-0.03 mm long); e, multiradiate ossicle and cups (0.02-0.04 mm long); f, button (0.12 mm long); g, towered multilayered ossicle (1.2 mm long).

h-i, *Psolidocnus farquhari* (Mortensen) (ZMUC syntype). h, cup (0.04 mm long); i, button (0.1 mm long).

j-k, *Psolidocnus sacculus* (Pawson) (paratype E27994). j, cup (0.05 mm long); k, button (0.11 mm long).

A REVIEW OF THE CUCUMARIID GENUS *PSOLIDIELLA* MORTENSEN
(ECHINODERMATA, HOLOTHUROIDEA)

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Abstract


The holothurian cucumariid genus *Psolidiella* Mortensen is reviewed. *Psolidiella hickmani* sp. nov. and *Psolidiella maculosa* sp. nov. are described from southern Australia. *Psolidiella adhaerens* Hickman is synonymised with *Psolidiella nigra* Mortensen. *P. nigra* and *P. hickman* are external brood-protecting species. The genus *Psolidiella* is restricted to New Zealand and southern Australia. A key is provided for the described species of *Psolidiella*.

Introduction


O'Loughlin (1994) and O'Loughlin and Alcock (2000) anticipated a synonymy of *Psolidiella adhaerens* Hickman, 1962, from south-eastern Australia, with *Psolidiella nigra* Mortensen, 1925, from New Zealand. This synonymy is confirmed here. Specimens referable to *Psolidiella* have been collected from the rocky shallows across southern Australia — from Tasmania, Victoria, South Australia and Western Australia. With a narrow range of variations, specimens from the far eastern coasts of Tasmania and Victoria are identifiable as the type species *P. nigra* from New Zealand. Specimens from the Derwent estuary, from both sides of Bass Strait, and from the coast of South Australia west to Robe, differ from *P. nigra* in size and ossicle distribution and density, and represent a new and second species. Specimens from the southern coasts of Western Australia differ again in details of form of ossicles, in the arrangement of ventral tube feet, and in colour, and are a new and third species. Two small specimens from South Australia are not referable to the three species discussed below and indicate the presence of a fourth and possibly a fifth species of *Psolidiella*.

With the exclusion of *P. mollis* from *Psolidiella* by Panning (1971) the genus it is not circumpolar, as indicated by Pawson (1969), but is restricted to New Zealand and southern Australia.

Abbreviations of institutions are as follows:

AM, Australian Museum, Sydney, Australia; MNZ, Museum of New Zealand, Te Papa Tongarewa, Wellington, New Zealand; NMV, Museum Victoria, Melbourne, Australia; MPE, Dr Th. Mortensen's Pacific Expedition 1914–1916; TM, Tasmanian Museum, Hobart, Australia; WAM, Western Australian Museum, Perth, Australia; ZMUC, Zoological Museum, University of Copenhagen, Denmark.
The following terms are defined:

Bent and curved. Elongate tentacle and tube foot plates may be straight or bent (angular) in one plane (surface) which itself may be flat or curved or convex (Fig. 3i illustrating straight and curved, and Fig. 4k illustrating bent and curved).

Buttons. Thickened plates which are perforated, regular to irregular in outline, small (typically 0.08 mm long), discretely knobbed or lumpy (Fig. 4c) or smooth (Fig. 3f), typically four perforations.

Capitate. Form of cup spinelets which have a rounded head and short neck (Fig. 3g).

Crosses. Small ossicles (typically 0.05 mm long) consisting of four arms radiating from a common centre or short rod, to varying degrees bifid and distally knobbed (Figs 2d, 2f), flat or concave, sometimes intergrading with cups if concave with some distal ends joined, sometimes intergrading with multiradiate ossicles.

Cups. Thin plates which are perforated, concave, shallow (species in this paper) or deep, oval to rectangular, small (typically 0.04 mm long), cruciform (Fig. 3g) or tripartite centrepiece, typically four large with frequently four small corner perforations, spinelets on rim and sometimes on centrepiece, sometimes with bridging connections across rim.

Denticulate. With pointed to bluntly spinous to rounded teeth-like projections on the rim of ossicles (Figs 2h, 3c).

Multilayered ossicles. Ossicles which are nodular, irregularly oval in outline, large (more than 0.2 mm long), comprising a perforated knobbled base plate with additional layers built on both sides creating low domes bilaterally.

Multiradiate ossicles. Small ossicles (typically 0.05 mm long) consisting of three to five arms radiating from a common centre or short rod, including four-armed crosses, flat or concave, with the arms sometimes distally bifid and sometimes knobbed (Figs 4d, 4g).

Sole. Flattened, delimited, modified ventral body wall, bounded peripherally by tube feet which do not extend in series to the introvert and anus (Figs 1c, 3b); the place of attachment to the substrate.

Ventrain. Modified ventral body wall, bounded laterally by the lateroventral series of tube feet, not bounded peripherally by tube feet; ventrolateral tube feet series either extend to introvert and anus, or do not extend to introvert and anus and create a sole-like ventrurn (Fig. 4b); the place of attachment to the substrate.
ined but without judgement as to its universal reliability in distinguishing the Cucumariidae from the Psolidae. It is relevant to note that in their description of *Psuedocolochirus mollis* Ludwig and Heding, 1935, temporarily referred to *Psolidiella* by Panning (1949), the authors reported and illustrated the posterior part of the intestine in the right ventral interradius.

All of the southern Australian specimens referred below to two new species of *Psolidiella* are similar to *P. nigra* in having a well-defined very thin-walled sole or sole-like ventrum without an acute angular edge, ventral radial tube feet series not continuing to the introvert and anus, small tube feet scattered dorsally and laterally, up-turned anal cone, and non-calcareous thin body wall with distally knobbed concave crosses and small perforated plates but lacking scales. The three ventral radial series of tube feet do not continue to the introvert and anus in any of the three species of *Psolidiella*, and in the type species and new species from eastern Australia tube feet are to varying degrees continuous around the periphery of a sole. In the species from western Australia the three ventral series of tube feet are parallel with none occurring transversely to create a distinct sole. This condition is referred to here as a sole-like ventrum.

The presence of distally knobbed concave crosses and sometimes cups in the body wall was not reported by Mortensen (1925) or Panning (1949, 1957) or Hickman (1962) or Pawson (1970), although Panning (1961: fig. 6) did illustrate distally knobbed crosses for specimens of *P. nigra* which he examined. Panning (1971: 45) referred to the presence of crosses (as retrogressive cups) in his final diagnosis of the genus. In the light of a re-examination of type material, and the availability of further material from southern Australia referable to *Psolidiella*, the presence of concave crosses and sometimes cups is considered here to be diagnostically significant. Distally knobbed concave crosses are abundant in all southern Australian material, while cups are present but rare in the type species and abundant in south-eastern Australian material.

Panning (1949: 426, as *bollonsoni*) referred the New Zealand species *Cucumaria bollonsi* Mortensen, 1925 to *Trachythyone* Studer, 1876, and O’Loughlin and Alcock (2000) have established *T. bollonsi* as a junior synonym of *Psolidiella nigra* Mortensen, 1925. Panning (1971: 45) noted a close relationship between *Psolidiella* and *Trachythyone*. The body wall ossicle combination of cups and smooth perforated plates, and the tentacle form and number, indicate that the genera are closely related. *Psolidiella* is distinguished from *Trachythyone* by the former’s distinct sole or sole-like ventrum with the ventral radial tube feet series not continuing to the introvert and anus, upturned anal cone, and concave crosses or multiradiate ossicles in the body wall.

A single small dark grey-brown specimen from Emu Bay on Kangaroo Island in South Australia (NMV F59223), and single small dark blue-grey specimen from Waterloo Bay on the Eyre Peninsula in South Australia (NMV F59224), have the body form of *Psolidiella* and have numerous concave, distally knobbed, multiradiate ossicles dorsally and ventrally. Neither has cups dorsally or ventrally, and neither has buttons dorsally. They do not belong to any of the three species described below, and these South Australia specimens represent one or two more species of *Psolidiella*.

### Key to species of *Psolidiella*

1. Dorsal body wall normally with tube foot ossicles only; knobbed crosses and buttons absent or rare in dorsal body wall............. *Psolidiella nigra* Mortensen
    - Dorsal body wall normally with tube foot ossicles, numerous crosses or multiradiate ossicles, and numerous thickened buttons or plates............. 2

2. Dorsal body wall with numerous knobbed crosses, cups, smooth buttons and plates; lacking rosettes; midventral radial tube feet series up to two wide; lateral ventral radial series of tube feet joined to varying degrees anteriorly and posteriorly to form a distinct sole......................... *Psolidiella hickmani* sp. nov.
    - Dorsal body wall with numerous crosses and multiradiate ossicles, lumpy buttons and rosettes; lacking cups; midventral radial tube feet series up to four wide; lateral ventral radial series of tube feet parallel and never joined anteriorly and posteriorly to form a distinct sole.................................................. *Psolidiella maculosa* sp. nov.


Other New Zealand material. The Snares, Boat Harbour, covered by plant detritus in rock pools, 18 Dec 1976, MNZ EC4061 (10); ANI J12281 (4).

Syntypes of Cucumaria bollonsi Mortensen, 1925. North Island, Cape Maria van Diemen, MPE, 4 Jan 1915, ZMUC Eh 304–258 (9).


Description of material. Body up to 36 mm long (preserved, tentacles extended). 11 mm diameter. Body wall thin; body rounded, distinct very thinned walled oval sole with rim, oral cone and upturned anal cone; on female specimens oral cone wrinkled, folded, pocketed, pockets sometimes extending dorsally and laterally, rarely on male specimens; 5 small spatulate anal scales; 10 denticrate tentacles, ventral 2 smaller; ecaulear ring lacking posterior prolongations. 5 radial plates with anterior notched taper and posterior notch, 5 interradial plates with anterior pointed taper and posterior broad rounded indentation; single left ventrolateral polian vesicle; posterior intestine in left ventral interradius.

Close cover of small tube feet scattered dorsally, laterally, around oral and anal cones; tube feet in 3 radial series ventrally, not continuing to introvert and anus, bordering sole to varying degrees anteriorly and posteriorly, up to 4 rows wide lateroventrally (paired double to zig-zag rows), up to 2 rows wide midventrally; absent from introvert; 5 radial tube feet analy.

Dorsal body wall predominantly with tube foot ossicles only, rarely with a few buttons (in juveniles), very rarely with a few concave knobbed crosses or cups (in juveniles); tube foot ossicles endplates, frequently fragmentary, up to 0.16 mm wide, some with a narrow rim of support plates; tube foot support plates irregularly oval to elongate, sometimes bent and curved, perforated with large holes centrally, bluntly denticulate around margin, typically 0.10 mm long, never thickened rods; thick, smooth, irregularly oval buttons rarely present dorsally, up to 8 (typically 4) perforations, rarely marginally knobbed, frequently incompletely formed, typically 0.10–0.16 mm long.

Ventral body wall with perforated plates, buttons, very rare spinous plates, knobbed concave crosses, rare cups: plates abundant, thick, smooth, rarely lumpy, irregularly oval, typically about 8 (up to 17) perforations, frequently thickly bluntly denticulate around margin, up to 0.24 mm long; thick plates intergrade with smaller dorsal body wall type buttons; very rare irregular, spinous (surface), marginally denticulate, perforated plates; numerous shallow concave crosses, regular and irregular, arms frequently bifid and distally knobbed, knobs sometimes joined to form incomplete cups, 0.04–0.12 mm long; rare thick to thin shallow concave cups, rim smooth to capitate, 0.04–0.10 (typically 0.06) mm long.

Ventral tube feet with endplates up to 0.32 mm wide, normally with thin rim of support plates, typical ventral body wall plates: support plates irregularly oval to elongate, frequently bent and curved, marginally denticulate, largest perforations centrally, up to 0.19 mm long, very rarely rod-like.

Tentacle ossicles numerous large thick perforated narrow elongate plates and rods, straight or bent, flat or curved, rarely branched, up to 0.50 mm long; some curved to convex, marginally denticulate, perforated, irregularly oval to triangular, smooth plates up to 0.26 mm wide; bent
curved narrow denticulate perforated plates 0.08–0.18 mm long; thin perforated marginally denticulate, irregularly round, convex plates 0.05–0.08 mm wide; sometimes rosettes up to 0.12 mm long.

**Colour (preserved).** Dorsal and lateral body off-white to pale brown to very dark brown, grey, black; oral and anal cones frequently darker than dorsally; sole off-white to pale brown; tube feet ends white; introvert and tentacles off-white to dark brown.

**Reproduction.** Externally brood-protecting differentiating embryos, up to 0.8 mm long, in pockets and folds around the oral cone of female specimens (December to May; no June to August material observed). Exhibits sexual dimorphism, mature female specimens having pockets and folds around the oral cone, mature male specimens normally having a smooth oral cone. The three type specimens from Stewart Island (April) are all males with a smooth oral cone. The specimens from The Snares (December) include one brood-protecting female. All Eaglehawk Neck lots (March, May) include specimens which have: mature male and female gonads; a gonopore on the oral disc anterior to the middorsal tentacle pair; body wall thin; body rounded, distinct very small anal teeth, and very rare cups which are present in the body wall of the type material of both *P. nigra* and *P. adhaerens*. The form and distribution and size of the ossicles, the external morphology and size, and the mode and seasonality of the distinctive external brood-protective reproduction are indistinguishable for the New Zealand and Australian material referred to above.

**Psolidiella hickmani** sp. nov.

Figures 1d–f, 3a–l


**Material examined.** Holotype. Victoria, Phillip Island, Kitty Miller Bay, silt, rocky shallows, 0–1 m, J. Monaggle and M. O'Loughlin, 20 Apr 1987 (NMV F74912).

Paratypes. Type locality and date, NMV F68266 (14); 25 Oct 1987, F68259 (2); 23 Dec 1987, F68257 (4); 13 Feb 1988, F68260 (6); 22 Nov 1997, F65928 (7).

**Other material.** Victoria, Wilsons Promontory, Oberon Bay, 7 Mar 1984, F68271 (1); Cape Paterson, 29 Jan 1988, F68254 (4); Kileunda, 26 Jan 1987, F73815 (1); Harmers Haven, 27 Mar 1989, F57357 (1); Phillip Island, Cowrie Beach, 27 Nov 1985, F68263 (11); Flinders, 16 Nov 1980, F68268 (1); Port Phillip Bay, Altona, 8 Apr 1991, F73821 (2); Marengo, Hayley Point, 26 Mar 1977, F68253 (42); Crayfish Bay, 31 Dec 1980, F68270 (1); Armstrong Bay, 5 Apr 1998, F82973 (2). South Australia, Cape Northumberland, 16 May 1990, F74908 (1); Beachport, 9 Jan 1988, F74906 (5); Robe, 10 Jan 1988, F74907 (2); Tasmania. Derwent Estuary, Opossum Bay, 15 Nov 1982, F68258 (8); Bass Strait, Ludworth, 22 Nov 1982, F74910 (2); mouth of Tamar River, Greens Beach, 7 Mar 1981, F74911 (1).

**Description of material.** Body up to 17 mm long (preserved, tentacles withdrawn), 11 mm diameter; body wall thin; body rounded, distinct very thin-walled oval sole with rim, oral cone and upturned anal cone; on female specimens oral cone wrinkled, folded, pocketed, pockets sometimes extending dorsally and laterally; 5 small
spatulate scales anally; 10 dendritic tentacles, ventral 2 smaller; calcareous ring lacking posterior prolongations, 5 radial plates with anterior notched taper and posterior notch. 5 interradial plates with anterior pointed taper and posterior broad rounded indentation; single left ventrolateral polian vesicle; posterior intestine in left ventral interradius.

Close cover of small tube feet scattered dorsally, laterally, around oral and anal cones; tube feet in 3 radial series ventrally, not continuing to introvert and anus, bordering sole to varying degrees anteriorly and posteriorly, up to 4 rows wide lateroventrally (paired double to zig-zag rows), up to 2 rows wide midventrally; absent from introvert; 5 radial tube feet anally.

Dorsal body wall ossicles crosses, cups, thickened plates, thin spinous plates, tube feet endplates and support ossicles: crosses numerous, concave, some irregular and multiradiate, arms frequently bifid and knobbed distally, knobs sometimes joined to create incomplete rim or cup, typically 0.04-0.06 mm long; cups, regular, shallow, concave, rim smooth or with capitative spinelets, typically 0.05-0.06 mm long, some cups thick and large; numerous thickened smooth perforated plates, irregularly oval, frequently with small rounded denticulations marginally, up to 16 perforations, up to 0.24 mm long, intergrade with four-holed buttons; rare thin irregular perforated plates, surface spines, marginally strongly denticulate, up to 18 perforations, up to 0.19 mm long.

Ventral body wall ossicles crosses, cups, thickened plates: rare knobbed crosses; abundant cups, rim complete or incomplete, predominantly capitative spinelets on rim, cups typically 0.05-0.07 mm long; abundant thickened perforated plates similar to dorsally, up to 14 perforations, up to 0.22 mm long, intergrade with rare buttons. Tube feet ossicles endplates, tube foot support plates and rods, body wall ossicles: endplates up to 0.32 mm diameter, fairly irregular perforations, smallest centrally; support ossicles frequently curved or bent thick perforated rods and narrow elongate plates, up to 0.30 mm long.

Tentacle ossicles thickened, elongate, frequently bent and curved, perforated rods up to 0.32 mm long; frequently bent and curved elongate narrow perforated plates up to 0.22 mm long; irregularly round, marginally denticulate, concave, thin perforated plates typically 0.08-0.12 mm diameter; some rosettes up to 0.07 mm long.

Colour (preserved). Dorsal and lateral body off-white to pale brown to very dark brown, grey, black; oral and anal cones frequently darker than dorsally; sole off-white to pale brown; tube feet ends white; introvert and tentacles dark brown.

Reproduction. Externally brood-protects differentiating embryos, up to 0.5 mm long, in pockets and folds around the oral cone of female specimens (October to April). Exhibits sexual dimorphism, mature female specimens having pockets and folds around the oral cone, mature male specimens normally having a smooth oral cone. Lots from Oberon Bay, Cape Paterson, Kitty Miller Bay, Marsengo, Armstrong Bay and Opossum Bay all include at least one externally brood-protecting female, one female from Opossum Bay (November) having about 40 brood embryos in oral pockets.

Distribution. Australia, Tasmania (Opossum Bay in Derwent Estuary, and Bass Strait coast); Victoria (west of Wilsons Promontory) to South Australia (west to Robe). Rocky shallows, 0-1 m.

Etymology. Named in recognition of the contribution to our knowledge of Tasmanian holothurians by the late Prof. V.V. Hickman (formerly of the University of Tasmania).

Remarks. Psolidiella hickmani differs consistently from P. nigra by having numerous thick, smooth, perforated plates and buttons, and numerous knobbed concave crosses, in the dorsal body wall. No specimens of P. hickmani from Victoria have been observed with more than three brood embryos in pockets, while one from southern Tasmania has about 40 brood embryos in pockets. Specimens from southern Tasmania are up to 17 mm long (tentacles withdrawn) and from coastal Victoria are up to 14 mm long (tentacles withdrawn). Although based on limited evidence, these observations reflect a pattern previously noted by Materia et al. (1991) for the cucumariid holothurians Staurolithone inconspicua (Bell, 1887) and Neoamphicyclus lividus Hickman, 1962. In S. inconspicua more numerous ecolimic juveniles are brood-protected in southern Tasmanian specimens that in Victorian specimens, and in both species mature adults in southern Tasmania are larger than on coastal Victoria.

Psolidiella maculosa sp. nov.

Figures Id, f, 4a-1


Material examined. Holotype. Western Australia, Perth, Marmion Marine Park, Mettams Pool, sandy pockets on reef flat, midtidal, B.R. Wilson, 3 Jan 1987 (WAM Z4781).
Paratypes. Type locality and date, WAM Z4782 (2); Cottesloe, reef off Rosendo Street, in sand amongst Caulerpa holdfasts, 0-1 m, 6 Feb 1985, WAM Z4931 (13); Trigg Island, with Caulerpa, 22 Nov 1969, NMV F59222 (2); Quaranup, boat ramp, intertidal sand near Posidonia, 20 Jan 1988, WAM Z4932 (1).

Other material. Western Australia, Duke of Orleans Bay, Little Wharton Beach, off algae, 0-2 m, 19 Dec 1991, NMV F66253 (1).

Description of material. Up to 27 mm long (preserved, tentacles withdrawn, anal cone extended), 8 mm diameter; body wall thin; oral extension and anal cone upturned; oral cone lacking folds and pockets; 10 dendritic tentacles, ventral 2 smaller; distinct introvert, lacking tube feet; distinct sole-like ventrum, narrower than body, not extending to introvert or anus; 5 microscopic spatulate anal seales; calcareous ring solid, lacking posterior prolongations, anterior tapering projections radially and interradially, posterior notches radially; wide indentations interradially; single left ventrolateral polian vesicle; posterior intestine in left ventral interradius.

Body wall with epidermal multiradiate ossicles and crosses, buttons, rosettes, tube feet ossicles: numerous multiradiate ossicles including crosses, frequently concave, frequently irregular, 3-5 arms frequently branched and distally knobbed, up to 0.06 (typically 0.04) mm long; numerous buttons, oval to irregular, typically 0.05 mm long.

Remarks. There are no mature female specimens in the material available, and it is not possible to determine whether or not P. maculosa has the same external brood-protecting habit as P. nigra and P. hickmani.

Distribution. South-western Australia, from Duke of Orleans Bay to Perth in Western Australia; 0-2 m.

Etymology. From the Latin maculosa (spotted), referring to the body appearance.

Reproduction. The material, collected in November to February lacks mature female gonads. Long, thin, smooth, white gonad tubules are present. There are no pockets or folds around the oral cone of any specimens in the material examined.

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References


REVIEW OF PSOLIDIELLA (HOLOTHUROIDEA)


Figure 1. a-c, views of *Psolidiella* type species *P. nigra* (H2135, 26 mm long) with oral cone brood embryos. a, dorsal; b, lateral, showing oral and anal cones; c, ventral, showing sole with two rows of midventral tube feet. d, cucumariid calcareous ring of *Psolidiella* species. e, brood-protection of embryos (white, round, 0.5 mm long) around oral cone of *P. hickmani* (F68258, 15 mm long). f, dorsal view of alimentary canal of *Psolidiella* species from mouth (m) to anus (a) with posterior intestine left (l) ventral. g-k, body mount showing form and distribution of ossicles of *Psolidiella* type species *P. nigra* (H2011). g, dorsal; h, ventral interradial; i, ventral tube feet; j, tentacle trunk; k, tentacle ends.
Figure 2. a—j. *Psolidiella nigra* Mortensen. a, lateral view of holotype (ZMUC, 24 mm long). b–l, ossicles (measurements of lengths). b, ventral plate (0.19 mm, paratype); c, ventral buttons and plates (0.13–0.20 mm, paratype); d, ventral crosses (0.06–0.08 mm, EC4061); e, ventral cups (0.06 mm, EC4061); f, ventral crosses (0.05–0.06 mm, H20008); g, ventral tube foot support plates and endplate (endplate 0.32 mm, H2009); h, tentacle plate (0.24 mm, holotype); i, curved tentacle plate (0.13 mm, paratype); j, elongate tentacle plate (0.15 mm, EC4061); k, elongate tentacle plate (0.26 mm, EC4061); l, tentacle rosettes (0.10–0.12 mm, holotype).
Figure 3. a-l, *Psolidiella hickmani* sp. nov. a, lateral view of holotype (11 mm long); b, ventrolateral view of specimen showing sole with two rows of midventral tube feet (F68258, 16 mm long). c-l, ossicles from types (measurements of lengths): c, dorsal plate (0.21 mm) and crosses (0.05 mm); d, dorsal button (0.13 mm) and crosses (0.05-0.06 mm); e, dorsal spinous plate (0.17 mm); f, dorsal buttons (0.11-0.13 mm); g, dorsal cups (0.05 mm); h, dorsal tube foot endplate (0.11 mm); i, dorsal tube foot support plate (0.12 mm); j, ventral plates (0.14-0.18 mm); k, ventral tube foot ossicles (plate 0.13 mm, cross 0.06 mm); l, tentacle ossicles (0.06-0.24 mm).
REVIEW OF **PSOLIDIELLA** (HOLOTHUROIDEA)
A REVIEW OF THE TUBIFICIDAE (ANNELIDA: Oligochaeta) FROM AUSTRALIAN INLAND WATERS

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Abstract


The Australian limnic representatives of the cosmopolitan oligochaete family Tubificidae are reviewed. The four Australian species of Telmatodrilus Eisen, 1879 are placed in new genera (Breviatria and Biprostatus) and these are considered to belong to Rhyacodrilinae rather than Telmatodrilinae. Four new species, Rhyacodrilus megaprostatus, Aimidrilus nharna, Breviatria arvensis and Biprostatus duplex are described and Rhyacodrilus fultoni Brinkhurst, 1982 is transferred to Aimidrilus Finogenova, 1982. Limnodrilus clapereduensis Ratzel, 1868 and Autodrilus lianobius Bretscher, 1899 are recorded in Australia for the first time. The Australian fauna now consists of 29 described species, including 11 of the most widespread species of cosmopolitan genera (Tubifex Lamark, 1816, Potamothrix Vejdovsky and Mrazek, 1902, Limnodrilus Claparede, 1862, Autodrilus Bretscher, 1899, Rhyacodrilus Bretscher, 1901, Botriurineurum Stole, 1886 and Branchiura Beddard, 1892). Antipodrilus Brinkhurst, 1971, with five species, and the two new rhyacodriline genera, with six species, are essentially Australian genera, except that one species of Antipodrilus and possibly one of Biprostatus also occur in New Zealand. Seven endemic species belong to more widespread genera (Rhizodrilus Smith, 1900, Rhyacodrilus and Aimidrilus). The Australian tubificid fauna appears to have biogeographic affinities with northern hemisphere and marine tubificids.

Introduction

The first tubificid to be described from Australia was Branchiura pleurotheca Benham, 1907 from Blue Lake, Mt Kosciusko. Further tubificid records and descriptions from Australia were not published until Brinkhurst (1971a, b) reviewed the aquatic oligochaete faunas of the world and Australia. In these publications, Branchiura pleurotheca was synonymised with Rhyacodrilus coccineus (Vejdovsky, 1875), several other new species and a new genus (Antipodrilus) were described and the presence of numerous cosmopolitan species was recorded. Subsequent records and descriptions of new species were provided by Brinkhurst and Fulton (1979) and Brinkhurst (1982, 1984).

In this paper we list previous records and add many new ones for most species, improve some descriptions, describe four new species and address problems relating to the taxonomic position of Australian species of Telmatodrilinae by moving them to two new rhyacodriline genera. This contribution is intended to provide a foundation for future work, complementing the recent review of the Australian Phreodrilidae (Pinder and Brinkhurst, 1997). Our definition of the Tubificidae is conservative, excluding the Naididae which are generally acknowledged to be part of the same taxon (Brinkhurst, 1994; Erseus, 1990b), although a formal proposal to merge the families has yet to be made.

Materials and methods. Most specimens were stored in ethanol, often after fixation in formalin. They were then whole-mounted, dissected or serial sectioned. Dissected or whole-mounted specimens were usually first stained in Grenacher's borax carmine. Sectioned specimens were cut at 6 mm and stained in Mayer's haematoxylin and eosin.

Descriptions are limited to brief diagnoses, with important distinguishing characteristics, except for new species, or where an original description can be substantially amended.

The term chaetae is used in preference to setae, following a determination at the International
Symposium on Aquatic Oligochaete Biology, Presque Isle, Maine, USA, 1997. Roman numerals refer to segment numbers and two arabic numerals separated by a slash refer to the septum (or intersegmental furrow) separating two adjacent segments. Body lengths are for preserved specimens and are indicative of the length of mature specimens only.

Where details of the holotype are not given, as is the case for some of the earliest described cosmopolitan species, this information is unknown and not listed in Reynolds and Cook (1976, 1981, 1989, 1993).

Institutions and collections are abbreviated as follows: AMS, Australian Museum, Sydney, NSW; AMP, Adrian Pinder collection; AWT, Australian Water Technologies, Sydney, NSW; BGMJ, Barrie Jamieson collection, Brisbane, Qld; CALM, Wildlife Research Centre, Department of Conservation and Land Management, Perth, WA; ERISS, Environmental Research Institute of the Supervising Scientist, Jabiru, NT; IFC, Inland Fisheries Commission, Hobart, Tas.; (all collections now in QVM); MDFRC, Murray Darling Freshwater Research Centre, Albury, NSW (J. Hawking); MNHN, Museum National d’Histoire Naturelle, Paris, France; MON, Ecology and Evolutionary Biology, Monash University, Melbourne, Vic.; (P.S. Lake); MUR, Aquatic Ecosystems Research, Environmental Science. Murdoch University, Perth, WA (J. Davis); NMV, Museum Victoria, Melbourne, Vic.; NTM, Museum and Art Gallery of the Northern Territory, Darwin, NT; QVM, Queen Victoria Museum, Launceston, Tas.; ROB, Ralph Brinkhurst collection; SAM, South Australian Museum, Adelaide, SA; TAS, Tasmanian Museum, Hobart, Tas.; UCA, University of Canberra, Canberra, ACT (R. Norris); USNM, National Museum of Natural History, Washington, USA; WAM, Western Australian Museum, Perth, WA; ZMUH, Zoological Museum, University of Hamburg, Germany.

Abbreviations used in the figures are as follows: a, atrium; c, copulatory chamber; e, ejaculatory duct; f, female funnel; g, gut; gd, gut diverticulum; gt, glandular tissue; mf, male funnel; n, nerve cord; o, ovary; p, prostate; pa, papillae; pe, penial chaetae; pc, peritoneal tissue; s, spermatheca; sc, spermathecal chaetae; sd, spermathecal duct; t, testis; v, vas deferens.

Where possible, localities are given with latitude and longitude, Australian map grid (AMG) 1:100 000 coordinates (four digit map number followed by three castings and three northings) or Tasmaph 1: 500 000 coordinates (three castings and three northings). Australian states and territories are abbreviated as follows: Australian Capital Territory (ACT), New South Wales (NSW), Northern Territory (NT), South Australia (SA), Queensland (Qld), Victoria (Vic.), Tasmania (Tas.) and Western Australia (WA).

Tubificidae

Diagnosis. Genitalia bilaterally paired. One pair of testes and 1 pair of ovaries, usually in X and XI respectively. Spermathecae mostly in the testicular segment. Male funnels on posterior septum of testicular segment leading to vasa deferentia, atria and male pores in the ovarian segment. Female funnels leading to pores on posterior furrow of ovarian segment. Chaetae from 1 to many per bundle, hair chaetae usually restricted to dorsal bundles or absent. Reproduction normally sexual.

Tubificinae

Diagnosis. Spermathecal pores in the middle of the testes segment in most species. In all but a few genera, sperm organised as spermatozeugmata of a specific type, with non-fertile sperm encapsulating fertile sperm. Atria each with a single stalked prostate gland (prostate rarely absent). Pendant penes usually present, often with cuticle of penis sac thickened to form a penis sheath. Spermathecal chaetae, when present, usually single, enlarged, grooved distally and with large chaetal glands. Spermathecal chaetae normally absent, but when present then usually of similar form to the spermathecal chaetae. Coelomocytes not large and abundant.

Remarks. The spermatozeugmata found in tubificines are of a distinct form, with fertile sperm cells enclosed by a cortex of bound infertile sperm cells (Braidotti and Ferraguti, 1982; Ferraguti et al., 1994; Jamieson, 1992), distinct from the loosher sperm agglomerations found in the rhyacodrilinae.

Tubifex Lamarck

Type species. Lumbricus tubifex Müller, 1774.

Diagnosis. Hair chaetae usually present dorsally, accompanied by pectinate chaetae, but polymorphic forms occur. Vasa deferentia long, often of two widths. Atria comma-shaped, with vas deferentia opening close to the apex anteriorly, each with a large stalked prostate gland. Pendant penes present, each with a thin tub-shaped sheath. Genital chaetae not modified. Spermatozeugmata present.
Tubifex tubifex (Müller)

_Lumbricus tubifex_ Müller, 1774: 27 (in part).

_Tubifex rivularum_ Lamark, 1816: 225.

_Tubifex tubifex._—Michaelsen, 1900: 48.—
Brinkhurst, 1971a: 453, figs 8.1A-D, 8.3G-J.—
Brinkhurst, 1971b: 10, fig. 2.A.—Timms, 1973: 11.—

**Material examined.** NSW: Wingeecarie Creek, Berrima, 34°29'S 150°20'E, 7 Nov 1991, 4 specimens (AWT). Tas.: stream 4.9 km above Barrow Creek, 26 Nov 1978, 1 on slide (ROB); creek E of The Needles, 13 Nov 1978, 2 on slides (ROB); Arthur R., 31 Oct 1978, 1 on slide (ROB). Vic.: Beechworth Trout Hatchery, May 1994, 1 on slide (AMP) and Sep 1994, 2 on slides (NMV F77644-F77645); Thomson R. at Thompson Valley Road, 24 Nov 1976, 2 on slides and 3 in alcohol (CALM); WA: Soak NW of Corrigin, 32°10'38"S 117°49'08"E, 21 Oct 1997, several on slides and in alcohol (CALM); Parkburn Swamp, E of Corrigin, 32°24'58"S 118°02'24"E, 7 Oct 1997, 2 on slides (CALM).


**Distribution and habitat.** Cosmopolitan, including New Zealand (Brinkhurst, 1971b; Marshall and Winterbourn, 1979; Timms, 1982). Although widespread in Australia, _T. tubifex_ is not commonly encountered. In the northern hemisphere _T. tubifex_ is commonly found in marginal sites, such as those with heavy organic pollution or intense sedimentation or in highly oligotrophic waters (Brinkhurst, 1996). In sites with heavy organic pollution this species is usually associated with _Limnodrilus hoffmeisteri_ Claparedé, 1862 and these are the dominant oligochaetes or even the dominant benthic invertebrates (Brinkhurst, 1996). Studies of gross organic pollution are less common in Australia (as are ecological studies in which oligochaetes are speciated) and the Australian records of _T. tubifex_ span a wide variety of habitats. This species can tolerate salinities up to 10 ppt (Chapman et al., 1982) and mature worms are found in a variety of habitats.

**Remarks.** Mature specimens of the three species present in Australia are readily separable by examining the penial sheaths. These are usually visible through the body wall of cleared and slide-mounted specimens.

**Limnodrilus Claparedé**

_Limnodrilus_ Claparedé, 1862: 221, pl I figs 1–3, pl. III fig. 12, pl. IV fig. 6.—Michaelsen, 1900: 42.—Stephenson, 1930: 747.—Brinkhurst, 1971a: 463.

**Type species.** _Limnodrilus hoffmeisteri_ Claparedé, 1862.

**Diagnosis.** Dorsal and ventral chaetae bifid, hairs absent. Vas deferentia long, entering short bean-shaped atria apically. Prostates large, entering atria by short stalks. Atria connect, via long ejaculatory ducts, to pendant penes lying free within thick penis sheaths (formed by the thickened cuticle of the penis sac wall) of varying lengths, some longer than the body width. No modified genital chaetae. Spermatozeugmata present.

**Remarks.** Mature specimens of the three species present in Australia are readily separable by examining the penial sheaths. These are usually visible through the body wall of cleared and slide-mounted specimens.

**Limnodrilus hoffmeisteri** Claparedé


_Clitellio (Limnodrilus) hoffmeisteri._—Valliant, 1890: 424.

_Tubifex hoffmeisteri._—Ditlevsen, 1904: 422.

**Material examined.** ACT: Murrumbidgee R., 1987–1988, returned to R. Norris (UCA). NSW: Georges R. at Liverpool Weir, 1995, 1 on slide (AMS W7876); Meggarities Creek at Warrakie Rd, 33°54'S 150°36'E, 9 Feb 1993, 1 on slide (AWT); Rushy Billabong, 36°02'S 146°42'E, 5 Sep 1984, 1 on slide (MDFRC); Rylas Billabong, 36°06'S 146°58'E, 30 Jun 1981, 1 on slide and 1 in alcohol (MDFRC); Orphan School Creek, Kings Park, 3 May 1996, 1 on slide (AWT). Qld: Bulimba Creek, Brisbane, 4.8 km from mouth, 4 on slides (AMS W18081). SA: Valley Lake,
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Mt Gambier, 37°50'S 140°46'E, 26 Feb 1978, 1 on slide (AMS W18084). Vic.: La Trobe R. at Moonee—Willow Grove Bridge Rd and 100 m downstream of Moee Drain, AMG 8121-34673 and 8121-359769 respectively, Jul 1980, 2 on slides (NMV F77626–7); Mita Mita R., 2 km downstream of Dartmouth Dam, 31 Jan 1975 and Nov 1975, 3 on slides (NMV F77628, F77629, F77631) and 4 km N of Eskdale, 1 Feb 1975, 1 on slide (NMV F776230). WA: Munday Swamp, Perth, 22 Nov 1989, 1 on slide (WAM 41–95); Fire dam on Seven Day Rd, Warren R. catchment, 34°19'S 115°58'E, 4 in alcohol, 1 on slide (WAM 39–95 and 40–95); stream across Bussell Highway, 34°08'32"S 115°06'41"E, 15 Sep 1996, 1 on slide (AMP).

Ollier Australian records. Tas.: Arthurs Lake and Lake Sorrel (Fulton, 1983ab); Great Lake (Brinkhurst and Fulton, 1979); Lakes St Clair, Dove, Sorrell, Crescent, Leake and Toombs (Timms, 1978).

Distribution and habitat. Cosmopolitan, including New Zealand (Brinkhurst, 1971b; Timms, 1978). Often, though not exclusively, found in organically polluted situations.

Diagnosis. Length 20–90 mm. Anterior chaetal bundles with 3–8 bifid chaetae with the upper teeth much thicker and longer than the lower, fewer chaetae posteriorly with teeth more nearly equal. Penis sheath usually only up to 4 times as long as wide with a simple plate-like hood usually reflected back over the shaft.

**Limnodrilus udekemianus** Claparede


Clitellio (Limnodrilus) udekemianus. —Vaillant 1890: 425.

**Potamothrix Vejdovský and Mrazek**


Type species. Potamothrix moldavicus Vejdovský and Mrazek, 1902.

Distribution and habitat. Cosmopolitan (Brinkhurst, 1971b), occurring in a wide range of habitat types.

Diagnosis. Length 30–60 mm. Anterior bundles with 4–9 bifid chaetae, some with the upper teeth much longer than and as thick or somewhat thicker than the lower, fewer chaetae posteriorly. Penis sheaths up to 50 or even 80 times longer than broad with small triangular plates set at an angle to the shaft distally.

Remarks. This is the first and only record of this species from Australia. The shape of the penis sheath is normally diagnostic except in North America, where variants between this species and *Limnodrilus cervix* Brinkhurst, 1963 can be observed.
Remarks. While the genus is largely holartic, and mostly palaeartic, some of the many Pontocaspian species appear to have been introduced to North America, Africa and South America (Peru) and others are spreading through Europe (G. Milbrink, pers. comm.). The single species occurring in Australia, *Potamothrix bavaricus* (Öschmann, 1913), is a cosmopolitan species, although it may have been introduced to some parts of its current range, e.g., South America (Brinkhurst and Marchese, 1989).

**Potamothrix bavaricus** (Öschmann)

*Tubifex* (Hlyodrilus) bavaricus Öschmann, 1913: 559, figs 1–5.

*Hylodrilus* bavaricus.—Stephenson, 1930: 746.


Holotype. Type locality unknown (ZMUH 7704).

Material examined. NSW: Gowrie Creek, 54 km downstream of sewage treatment plant, 27°20’ S 151°27’ E, 28 Sep 1995, few in alcohol (AWT). Tas.: Big Waterhole Lake, 40°53’ 20” S 147°36’ 50” E, 1 Mar 1997, 2 on slide (AMP). Vic.: Curdies R., 38°20’ S 143°08’ E, 7 and 29 Feb 1992, 2 on slides (NMV F77641–2). WA: Malaga Wetlands, Perth, 2 Nov 1989, 2 on slides (WAM 76–95, 77–95); Herdsman Lake, Perth, 2 and 13 Nov 1989, 13 on slides, 8 in alcohol (slides WAM 55–95, 67–95, alcohol 54–95, 78–95); Lakes Nowergup, 31°38’ 16” S 115°44’ 42” E, Yonderup, 31°34’ S 115°41’ E, Karabooda, 31°37’ S 115°43’ E, 8 on slides (WAM 68–95 to 75–95); Coogee Springs, Perth, 9–14 Nov 1989, several on slides (MUR); Shark Lake, N of Esperance, 32°46’ S 121°51’ E, 5 Sep 1996, many specimens in alcohol (AMP); Congelin Dam, 32°49’ 07” S 116°53’ 05” E, 26 Oct 1997, 3 on slides (CALM).


**Distribution and habitat.** Eurasia, North, Central and South America, Australia and New Zealand (Brinkhurst, 1971a; Brinkhurst and Marchese, 1987; Coates and Stacey, 1994; Marshall and Winterbourn, 1979). *Potamothrix bavaricus* is quite widespread in southern Australia, occurring in both lentic and lotic sites and often very abundant when present.

**Remarks.** Antipodrilus is known only from Australia (all five species) and New Zealand (one species, *A. davidis*). In a cladistic analysis of the subfamily by Brinkhurst (1991), *Antipodrilus* appeared to group with two genera that are widely distributed in the northern hemisphere: *Psammoryctides* Hrabe, 1964 and Haber Holmquist, 1978. These northern genera have protrusible pseudopenes, with a crumpled cuticular lining to the inverted ectl part of the male duct, which forms a penis sheath when the penis is everted. *Antipodrilus* unicus Brinkhurst, 1984 and *Antipodrilus* timusi Brinkhurst, 1971, appear to have similar crumpled sheaths within the ectl part of the male duct and so the genus was coded as having protrusible pseudopenes. Unfortunately, further *Antipodrilus* specimens were not available for this study. *Antipodrilus* davidi (Benham, 1907) does appear to have both pseudopenes and the nature of the penes is not clear for the other two species (*Antipodrilus* multisetata Brinkhurst and Fulton, 1979 and *Antipodrilus* plectilus Brinkhurst and Fulton, 1979). Further anatomical study is required to confirm the presence of pseudopenes and to generally improve descriptions of *Antipodrilus* species.
**Antipodrilus davidis** (Benham)


**Holotype.** Blue Lake, Mt Kosciusko, NSW, 1906, sectioned on 4 slides (AMS G5610–11).

**Material examined.** NSW: Holotype, as above. SA: The Bubber Spring, near Lake Eyre, 3 Dec 1974, 2 on slides, 1 in alcohol (SAM E2823–E2825); Coopers Creek, southwest branch, 27 Mar 1987, 1 on slide (SAM E2817); Freeclng Springs, 1987 (AMS W198716); Davenport Spring Bore, near Hermit Hill, Lake Eyre South, 21 Sep 1989, 5 on slides (SAM E2818–E2821), WA: Spectacles Lake (North Eye), Brownmuns Swamp, Lake Marjiniup and Thomson Lake, Perth, 30 Oct and 3–9 Nov 1989, 11 on slides, 8 in alcohol (WAM 42–95 to 47–95, 49–95 to 53–95 and 81–95).


**Distribution and habitat.** Southern Australia and New Zealand (Brinkhurst, 1971b; Marshall and Winterbourn, 1979; Timms, 1982). Favours lente habitats.

**Diagnosis.** Length 25–40 mm. Anterior dorsal bundles with 2–5 non-hispid hair chaetae and 2–4 pectinate chaetae with teeth approximately equal. Ventral chaetal bundles with 3–5 bifid chaetae with the upper teeth longer and thinner than the lower, fewer posteriorly with upper teeth becoming longer and pectinations less apparent or absent. Ventrals with 3–5 chaetae anteriorly with the upper teeth markedly longer and somewhat thinner than the lower, fewer chaetae posteriorly with upper teeth less markedly longer than the lower. Spermathecal chaetae single, grooved and narrowly blade-shaped distally, slightly longer than somatic ventral chaetae. Vasa deferentia long, atria small and almost spherical, narrowing abruptly to form ejaculatory ducts. Penes present, possibly with thickened inner cuticle.

**Remarks.** The crumpled cuticle of this requires closer examination from fresh specimens.

**Antipodrilus magelensis** Brinkhurst

*Antipodrilus magelensis* Brinkhurst, 1984: 142, figs 1–2.

**Holotype.** Mudginberri Billabong, Magela Creek, NT, 4 May 1981, 1 on slide (USNM 80692).

**Material examined.** NT: Holotype, as above, and paratypes from type locality as well as Georgetown and Bowerbird Billabongs, Magela Creek, 11 on slides, 19 in alcohol (USNM 80693–80697, 80700) and several on slides (ROB); Nankeen Billabong, Magela Creek, 1 immature on slide (ROB); South Alligator R., Oct 1988 and Dec 1989, 1 on slide (NMV F77611) and 2 on slides (ERISS); SA: Charles Angus Bore, 15 km N of Alberti Creek railway siding, Lake Eyre South, 2 Dec 1974, 1 on slide (SAM E2815); Coopers Creek, north-west branch, 27 Mar 1987, 1 on slide (SAM E2816).

**Distribution and habitat.** Northern Territory (coastal riverine sites) and South Australia (few arid inland sites). The new South Australian specimens are the first to be recorded outside of the Northern Territory.

**Diagnosis.** Length up to 9 mm. Anterior bundles with 4–6 bifid chaetae with teeth equal in length and breadth, diminishing in number posteriad to 2
per bundle with upper teeth becoming shorter and thinner than the lower. Spermathecal chaetae single with grooved tips, about equal in size to somatic ventral chaetae. Vasa deferentia moderately long, joining atria subapically. Short atria terminae in coiled ejaculatory ducts, which lead to (protrusible?) penes with crumpled cuticular lining forming apparent penis sheaths.

**Antipodrilus multiseta** Brinkhurst and Fulton


*Material examined*. Tas.: Holotype and paratypes from type locality and date, four on slides (QVM:14:316–319); Lake Sorell, 3 on slides, uncertain identification (ROB).

*Other Australian records*. Tas.: Great Lake, Arthurs Lake and Lake Sorell (Fulton, 1983ab).

*Distribution and habitat*. Known only from large lakes of Tasmania’s central plateau. Collected at depths of up to 17.5 m and in both silt/sand and clay sediments (Fulton, 1983b).

*Diagnosis*. Length up to 50 mm. Chaetae 12–15 per bundle in II, gradually diminishing in number to 3 or 4 posteriorly. Anterior chaetae with blunt teeth of equal thickness, the upper slightly longer, posterior chaetae with upper teeth shorter than the lower. Spermathecal chaetae single, thin with groove tipped, twice as long as somatic ventral chaetae. Vasa deferentia moderately long and with teeth equal in width or the upper teeth thinner than the lower. Posterior chaetae with upper teeth shorter and thinner than the lower. Spermathecal chaetae single, thin and groove tipped, twice as long as somatic ventral chaetae. Vasa deferentia moderately long, atria elongate, distended where vasa deferentia and prostates attached. Ejaculatory ducts moderately long.

*Remarks*. The type specimens have all chaetae bifid, but those from Lake Sorell have pectinate chaetae posteriorly. Further investigation may be required to substantiate the unity of this taxon, although chaetal polymorphism is known for other oligochaetes (Chapman and Brinkhurst, 1986, 1987).

**Aulodrilus** Bretscher


*Type species*. *Aulodrilus limnobius* Bretscher, 1899.

*Diagnosis*. Dorsal bundles with or without hair chaetae. Often with gonads replicated and/or genital apparatus shifted forwards due to asexual reproduction. Vasa deferentia short, atria globular, bean-shaped or cylindrical with solid prostate glands. Penes pendant without cuticular sheaths. Penial chaetae (but not spermathecal chaetae) may be modified. Sperm stored as loose bundles, spermatozeugmata absent.

*Remarks*. Asexual reproduction is common in *Aulodrilus* (Brinkhurst, 1984) and most Australian records are of immature worms. However, the three species found in Australia have distinctive chaetae that permit identification of immature specimens. Finogenova and Arkhipova (1994) provide scanning electron micrographs of the distinctive chaetae of the following species.

**Aulodrilus limnobius** Bretscher


*Material examined*. NSW: Murray R. at Heyward’s Gauge, 36°06’S 147°01’E, 6 Jan 1988, 1 on slide (MDFRC). Vic.: Wentworth R., 17.7 km upstream of...
Tabberabbera, 37°31'S 147°23'E, 2 Oct 1975, 1 in alcohol (NMV F77618); Mitta Mitta R., 2 km downstream of Dartmouth Dam wall, 5 Nov 1976, 1 in alcohol (NMV F77615); Branjee Creek, Goulburn Valley, 36°42'S 148°20'E, 23 Apr 1992, 1 on slide, 3 in alcohol (NMV F77616, F77617).

**Distribution and habitat.** Recorded from Africa, Europe, Asia and North and South America (Brinkhurst, 1971a) and now southeastern Australia.

**Diagnosis.** Length 12–15 mm. Anterior dorsal and ventral chaetae similar with up to 10 bifid chaetae with upper teeth shorter and thinner than lower, the chaetae of first bundles often shorter and thicker than the rest. Chaetae of mid and posterior segments with lateral wings which appear as narrow oar-shaped blades when viewed frontally, with the upper teeth visible as a small projection beyond the blade. The wings can be discerned as a ridge on the lateral aspect of the chaetae. Vasa deferentia long, entering ovoid atria apically. Pendant penes large. Genitalia may be shifted forwards.

**Remarks.** These are the first Australian records of this otherwise widespread species.

*Aulodrilus pluriseta* (Piguet)

*Naidium pluriseta* Piguet, 1906: 218.


**Aulodrilus japonicus** Yamaguchi, 1953: 298, fig. 12, pl. VII, figs 5–7.—Finogenova and Arkhipova, 1994: 8, figs 3, 6, 9, 10.

**Material examined.** No new specimens examined.

**Other Australian records.** NT: Georgetown and Mudgeebi Billabongs, Magela Creek, Kakadu National Park (Brinkhurst, 1984). Qld: Yule Creek, Yanda Yarra (Brinkhurst, 1971b).

**Distribution and habitat.** Cosmopolitan (Brinkhurst, 1971b) but in Australia only known from the north so far.

**Diagnosis.** Length 10–25 mm. Anterior dorsal bundles with up to 8 short hair chaetae and up to 10 bifid chaetae with the upper tooth shorter and thinner than the lower and frequently replicated. Anterior ventral chaetae up to 16 per bundle with very thin, short upper teeth. Vasa deferentia long, entering ovoid atria apically. Atria with large lobate prostate gland, terminating in pendant penes. Genitalia may be shifted forwards.

**Remarks.** All Australian specimens observed so far have had replicate upper teeth on the dorsal chaetae. Specimens with replicate teeth were originally described as a separate species, *Aulodrilus japonicus* Yamaguchi, 1953, but this species was synonymised with *A. pluriseta* by Brinkhurst (1971a). Some Russian specimens, identified as *A. japonicus* by Finogenova and Arkhipova (1994), had replicate upper teeth, male pores in X and there were other minor differences in the form of the male ducts. Replicate teeth on these specimens were shown to be lateral, occurring either side of the main teeth. These may be a separate species, but forward shifting of the reproductive organs is commonly associated with asexual reproduction and other *A. pluriseta* (including other specimens described by Finogenova and Arkhipova (1994) have testes as far anterior as V (Brinkhurst, 1971a). Furthermore, the replicate teeth are essentially a form of pectination which has been shown to vary in other tubificids, including as a response to environmental conditions (Chapman and Brinkhurst, 1986, 1987).

*Aulodrilus pigueti* Kowalewski


**Distribution and habitat.** Cosmopolitan (Brinkhurst, 1971b) and widespread in Australia, occurring in a variety of habitats.

**Diagnosis.** Length 2–28 mm. Dorsal anterior bundles with 2–5 hairs and 4–5 (rarely to 10) other
The chaetae of A. limnobius are also oar-shaped, but more narrowly so than in A. pigueti and the blade-like wings of the former are in a plane perpendicular to the orientation of the teeth rather than in the same plane.

**Remarks.** The chaetae of A. limnobius are also oar-shaped, but more narrowly so than in A. pigueti and the blade-like wings of the former are in a plane perpendicular to the orientation of the teeth rather than in the same plane.

**Rhyacodrilinae** Hrabe

**Diagnosis.** Spermathecal pores close to anterior border of their segment (usually the testes bearing segment, normally X). Spermathecal ampullae containing loose or loosely bundled sperm. Atria with prostate glands diffuse or formed into distinct glands, rarely absent. Pendal penes generally absent; protrusive or eversible pseudopenes often present. Penial chaetae often modified, often numerous and typically arranged fanwise or in a row, with the blunt or bifid ectal ends close together. Spermathecal chaetae usually not modified. Coelomocytes usually large and abundant, rarely absent.

**Remarks.** Without doubt, the most problematic Australian freshwater tubificids are the four species placed in the Telmatodrilinae by Brinkhurst (1971a) and Brinkhurst and Fulton (1979) and two similar new species to be described below. The Telmatodrilinae is diagnosed by the presence of multiple prostate glands, each attached to the atria by short stalks. Telmatodrilus multiprostatus Brinkhurst, 1971 and Telmatodrilus pectinatus Brinkhurst, 1971 were placed within the Telmatodrilinae because the prostate cells are grouped into several glands, each of which appear to have a discrete connection to the atrial lumen. Later, two other Australian species, Telmatodrilus (Alexandrovia) papillatus Brinkhurst and Fulton, 1979 and Telmatodrilus? (Telmatodrilus?) bifidus Brinkhurst and Fulton, 1979, were tentatively placed here for the same reasons, although T. bifidus has only two prostates per atrium and these are not stalked. Of the two new species described below, one has prostate tissue similar to that of T. multiprostatus and the other has a pair of unstalked prostate glands, like that of T. bifidus.

Prior to the description of the Australian forms, the subfamily Telmatodrilinae consisted of three or four northern hemisphere species in two genera (or subgenera): Telmatodrilus Eisen, 1879 from western USA and Canada, and Alexandrovia Hrabe, 1962 from Alaska and Russia. This subfamily is generally considered to be closely related to the Tubificinae, based on cladistic analyses using the few characters available (Erseus, 1990b; Brinkhurst, 1994).

The Australian species differ from the holarctic forms in many respects. Their atria are ovoid to pear-shaped with apical prostates, rather than tubular with prostates along their length. In two of the Australian species the prostates lack stalks, instead being attached rather broadly to the anterior and posterior walls of the atria (Figs 9E, 11A, B). The Australian species have simple male pores, usually on the inner aspects of ventrolateral folds of the body wall, whereas the northern forms have pendal penes. Grooved spermathecal chaetae are found in two of the northern species and most of the Australian species, but all except one of the Australian forms also have modified penial chaetae which are absent in the northern forms. Coelomocytes are present in the two new species but have not been observed in the other Australian forms and appear to be absent in the holarctic species.

Before discussing the subfamilial relationships of these Australian species we should indicate that we intend to assign them to two new genera, described below. Breviatria gen. nov. will include B. multiprostatus, B. pectinatus, B. papillatus and B. arvensis sp. nov. and Biprostatus gen. nov. will include B. bifidus and B. duplex sp. nov. These names are mentioned here to facilitate the following discussion.

Erseus (1990b), in a cladistic analysis of the Naididae and subfamilies of Tubificidae, showed the two subfamilies Tubificinae and Telmatodrilinae (based on the northern species) as sharing plesiomorphic character states for modified spermathecal chaetae, absence of penial chaetae, unmodified oesophagus, absence of multiple large granular coelomocytes, lack of atrial eliation, and absence of posterior prostates. Tubificinae and Telmatodrilinae share the apomorphic states for penes and spermatozeugmata present. While these subfamilies share the presence of stalked prostates, the former has one per atrium, the latter many, and the analysis suggested that
the stalked prostates of these two groups had 'evolved independently from the diffuse prostate condition in the tubificid ancestor'. These subfamilies are also separated in that analysis by the apomorphic state of the spermathecal pore position in midsegment in Tubificinae (anterior in the Telmatodrilinae). Erseus (1990b) found that the telmatodrilines and tubificines formed a sister clade to another containing the phallodrilines, marine and freshwater rhyacodrilines and the Naididae, which share the presence of numerous coelomocytes and penial chaetae. The codings in Erseus' analysis depend on the coding of the outgroup (Phreodrilidae) adopted and are not necessarily accepted here.

We reran the analysis with the Australian forms as a separate group (AUS) using PAUP 3.1 and the original options. AUS was coded as lacking spermatozeugmata, atrial cilia and penes, but possessing coelomocytes, penial chaetae and multiple prostates (the coding was thus 10100 01101 000). Three equally parsimonious trees of 24 steps (CI 0.708) were obtained (unpublished data). In all of these, the Australian species appear within a clade which also included Phalldodrilinae and marine and freshwater Rhyacodrilinae, separate from a Tubificinae-Telmatodrilinae-Limnodriloidinae clade. This was predictable because of the coding for the presence of coelomocytes and penial chaetae, and implies that the multiple prostates of AUS are a convergent development to those of the (northern) Telmatodrilinae. Within this group, AUS was associated with the Phalldodrilinae and marine Rhyacodrilinae, rather than the freshwater Rhyacodrilinae and associated Naididae, because of the lack of hair chaetae and the apical vasa deferentia.

Brinkhurst's (1994) cladistic analysis had the broader aim of investigating the evolutionary relationships within the whole of the Clitellata and the characters and choice of states used reflected this. Again, Telmatodrilinae was coded based on the northern species, on the assumption that these were plesiomorphic within the subfamily. A clade including Tubificinae, Telmatodrilinae and Limnodriloidinae, recognised by possession of spermathecal chaetae (not unique) and stalked prostates, loss of penial chaetae (presence of which was considered plesiomorphic for the family), and organised bundles of sperm in the spermathecae, separated from a clade containing the Rhyacodrilinae and Naididae. As discussed below, the Phallodrilinae was associated with the tubificine clade rather than that including Rhyacodrilinae.

This analysis was also rerun using PAUP 3.1 and the original options and weightings and with all characters unordered. AUS was coded as lacking spermatozeugmata but having coelomocytes, penial chaetae and stalked prostates (the coding was thus 10110 11111 50010 01000 012). Twelve trees of equal length (88, CI 0.568) were produced (unpublished data). In this rerun, AUS appeared within a clade with the Tubificinae, northern Telmatodrilinae, Phalldodrilinae and Limnodriloidinae, which formed a sister group to the clade including Rhyacodrilinae and Naididae. The appearance of AUS and Phallodrilinae with the northern Telmatodrilinae, Tubificinae and Limnodriloidinae, rather than with the Rhyacodrilinae (as in Erseus' study), appears to result from the fact that this analysis saw penial chaetae as plesiomorphic for the whole family and that the prostates were coded differently by Erseus.

The lack of consistency in the above analyses requires that we consider some of the character states in detail.

Prostate. Traditionally, the prostate tissue of Rhyacodrilinae has been described as diffuse (e.g., Brinkhurst, 1971a), meaning that the prostate cells form a continuous layer over the atrium, with each cell communicating with the atrial lumen independently. More recently, this view (which focused on the freshwater forms) has been modified following the description of numerous marine forms with prostate tissue that is more clumped. Thus, Baker and Brinkhurst (1981) describe the Rhyacodrilinae as "having prostate glands forming a diffuse glandular covering; the cells communicating with the atrial lumen independently or in small clusters". Erseus (1984) describes the subfamily as having "Prostates diffuse or irregularly scattered in two or more clusters of cells broadly attached to the atrial surface, or absent". Some rhyacodrilines, including the marine *Heronidrilus* Erseus and Jamieson, 1981 and *Heterodrilus* Pierantoni, 1902, the freshwater monotypic *Macquaridrilus* Jamieson, 1968 and the Lake Baikal endemic *Rhyacodriloides Chekanovskaya, 1975, have some or all of the prostate cells formed into two or more glands (Erseus, 1981; Erseus and Jamieson, 1981; Jamieson, 1968; Martin and Brinkhurst, 1998). There are therefore precedents for including *Brevidiatria* and *Biprostatus* in Rhyacodrilinae in respect to the form of the prostates. Although most of the rhyacodrilines mentioned above have the prostate clumps broadly attached to the atrium, rather than narrowly stalked, the same is true for the two *Biprostatus* species. Furthermore,
some *Heterodrilus* (*H. inermis* (Erseus, 1981) and *H. rapidensis* Erseus, 1997) do have prostate glands that narrow into stalks like *Breviatria*. The Phalldrilinae is the only other subfamily to have more than one prostate gland per atrium and so should be mentioned here. Like *Biprostatus*, phalldrilines have a pair of prostates on each atrium, but these are almost always stalked and typically placed ental and ectal in position on the atria (Erseus, 1992), unlike the symmetrically placed prostate tissue in various tubificids to more adequately use prostate characters in phylogenetic work, as highlighted by Gustavsson and Erseus (1997).

Coelomocytes. An abundance of coelomocytes (a rhyacodriline trait) has been found in both of the new species described below but their presence in the older Australian taxa cannot be established because of the condition of the scarce material. They have recently been observed in rhyacodrilines such as *Torodrillus* Cook, 1970 and *Rhizodrillus* Smith, 1900, in which they were previously thought to be absent (Erseus, 1994). Coelomocytes have not been observed in *Rhyacodriloides*, but that genus is nonetheless now associated with the Rhyacodrilinae (Baker and Brinkhurst, 1981; Martin and Brinkhurst, 1998). Coelomocytes have not been reported for any of the northern telmatodrilines (Holmquist, 1974) and, with few exceptions, are not abundant in the Phalldrilinae (Erseus, 1992).

Genital chaetae. Groove-tipped genital chaetae are common in the Tubificinae and Limnodriloidinae and some northern Telmatodrilinae. These are generally few in number (usually 1 or 2 per bundle) and lie in enlarged chaetal glands, usually on the spermathecal segment. A few rhyacodrilines, some *Rhizodrillus* and *Rhyacodriloides*, do have similar chaetae (Baker and Brinkhurst, 1981; Erseus, 1990a; Martin and Brinkhurst, 1998), although these are on the male pore segment in the latter. The superficially similar chaetae of the rhyacodriline *Torodrillus*, appear to be a separate apomorphic development (Erseus, 1994). More typical in the Rhyacodrilinae and Phalldrilinae is modification of the penial chaetae associated with the male pores. These have bifid or simple (often club-shaped) tips, arranged in a row or fanned out with the tips close together, always on the male pore segment. Chaetae of the male pore segment are not modified in the northern Telmatodrilinae and only rarely modified in the Tubificinae (two *Virtocladorhynchus* Brinkhurst and Kathman, 1983 and the few species of *Krenedrilus* Dunniacka, 1983). *Biprostatus* and *Breviatria* are unusual within the family in possessing both grooved chaetae on the spermathecal segment (absent in two *Breviatria*) and modified penial chaetae on the male pore segment (absent in one *Breviatria*), *Krenedrilus* (Tubificinae) and some *Rhizodrillus* (Rhyacodrilinae) are the only other tubificids to have both types of genital chaetae. This means the genital chaetae may be of little help in classifying the new genera, unless grooved spermathecal chaetae are seen as plesiomorphic for the family (almost identical chaetae do occur in the Phreodrilidae) and modified penial chaetae are seen as an apomorphic development in the ancestral rhyacodriline, as tentatively suggested by Erseus (1990b). In that case, the presence of penial chaetae in the new genera might suggest their inclusion within the Rhyacodrilinae.

Somatic chaetae. Somatic chaetae are generally difficult to use in higher oligochaete taxonomy because of a lack of consistency among and within taxa. Both the northern telmatodrilines and *Breviatria* and *Biprostatus* have some unusual chaetae, but there are no chaetal features that would indicate a close relationship between the Australian and northern species. Neither do the chaetae provide evidence of a relationship to any other particular group of tubificids.

Sperm. Some *Breviatria* and *Biprostatus* appear to have sperm in the spermathecae arranged into numerous bundles with the nuclei aligned at one end, others have the sperm cells in loose masses, both arrangements typical of the Rhyacodrilinae and Phalldrilinae. The spermatozoegmata more typical of the Tubificinae, with fertile sperm encapsulated by infertile sperm (Braidotti and Ferraguti, 1982; Ferraguti et al., 1989; Ferraguti et al., 1994), are absent. Of the northern telmatodrilines, *Alexandrovia* species have some kind of sperm bundles (Holmquist, 1974), which require ultrastructural analysis to investigate homology with tubificine spermatozoegmata, and *Telmatodrilus* have loose sperm in the spermathecae. This character is thus ambiguous in terms of relationships.

Spermathecal pores. In general, tubificines have spermathecal pores near the middle of the segment (Brinkhurst, 1991) while rhyacodrilines and phalldrilines have these pores at or just
behind the anterior septa (Baker and Brinkhurst, 1981; Erseus, 1992). All *Breviatria*, at least one of the two *Biprostatus*, and the northern telmatodrilines have anterior spermathecal pores but, since this may be the plesiomorphic state for the family (Erseus, 1990b; Brinkhurst, 1991), it indicates little about the relationship between these worms.

Penes. Pendant penes may constitute an apomorphy for tubificines and northern telmatodrilines (Erseus, 1990b; Brinkhurst, 1994), although they are also present in some Phreodrilidae. Absence of penes in *Biprostatus* and *Breviatria* may be a plesiomorphic state shared by rhyacodrilines and phallodrilines.

In summary, the argument that *Breviatria* and *Biprostatus* belong within the Telmatodriinae simply because they have prostate cells formed into multiple glands is not strong, particularly considering the lack of knowledge about prostate homology and the number of rhyacodrilines that are now known to have clumped prostate tissue. *Breviatria* and *Biprostatus* have several other features, including lack of pendent penes and spermatoozeugmata and presence of penial chaetae and coelomocytes (in at least some species) which indicate a closer relationship with the Rhyacodrilinae. Therefore, as anticipated by the discussion of these and other problem taxa by Martin and Brinkhurst (1998), we now propose to consider the Australian former telmatodrilines to be properly associated with Rhyacodrilinae, described below as two new genera.

While this is undoubtedly not the last word on the position of these worms, we believe that this move represents a more parsimonious classification, pending further ontogenetic and ultrastructural analyses of some characters (especially prostate glands and organised sperm) and further phylogenetic work on the rhyacodrilines. It does seem that the Rhyacodrilinae is paraphyletic (Erseus, 1990b; Brinkhurst, 1994) and we may be trying to force the Australian ex-telmatodrilines into a group that has no phylogenetic reality. A thorough study of rhyacodriline phylogenetics is yet to be undertaken but Erseus (1990b) canvases the possibility that the Rhyacodrilinae will have to be split into a number of smaller groups to achieve monophyly, perhaps with each raised to family level. If this were to be given effect then the Australian ex-telmatodrilines may form one (or more) such groups.

*Rhyacodrilus* Bretscher


**Diagnosis.** Dorsal chaetal bundles with or without hair chaetae. Vasa deferentia moderately long, entering atria subapically, atria usually bulbous or rounded, usually covered with a diffuse layer of prostate cells. Protrusible pseudopenes present or absent. Penial chaetae usually modified, numerous with blunt tips held close together. Coelomocytes usually large and abundant.

*Rhyacodrilus coccineus* (Vejdovsky)


*Biprostatus coccineus*.—Stoliczka, 1886: 656.


*Branchiura pleurotheca* Benham, 1907: 256, pl. XLVI, figs 7–12.

*Holotype:* Type locality unknown (ZMUC 6948).

*Material examined.* NSW: Blue Lake, Mt Kosi, 36°24′23″S 148°18′50″E, Jun 1906, several on slides (2 sectioned) (AMS W5612–W5613), WA: Power Rock, Balladonna, 1 on slide, uncertain id. (ROB).

*Distribution and habitat.* Holarctic, Australia and South America (Brinkhurst, 1971a; Brinkhurst and Marchese, 1989). This species is not commonly collected in Australia.

*Diagnosis.** Length 10–35 mm. Anterior dorsal bundles with 3–5 hair chaetae and up to 5 pectinate chaetae, hairs missing in many posterior segments. Ventral chaetae 2–5 per bundle with the upper teeth thinner and not much longer than the lower (but longer in Australian specimens described as *B. pleurotheca*). Ventral chaetae of XI with 3–5 club-headed penial chaetae per bundle, equal in size to somatic ventral chaetae. Spermathecal pores ventrolateral (lateral in the *B. pleurotheca* specimens). Vasa deferentia not coiled around atria, which are globular and covered with a diffuse layer of prostate cells. Coelomocytes large and abundant.

*Remarks.* Benham (1907) described *Branchiura pleurotheca* from Blue Lake, Mt Kosi, but Brinkhurst (1971b) considered this to be synonymous with *R. coccineus*. The long upper teeth of the anterior ventral chaetae and the lateral position of the spermathecal pores of Benham's material may prove to be diagnostic of a distinct species once intra-specific variation in *R. coccineus* is better documented. Further specimens from the type locality of *B. pleurotheca* (Blue Lake, Mt Kosi) are required to substantiate the synonymy. The Power Rock specimen is dissected but not stained and little can now be seen.
of the genital anatomy. The most recent accounts of species with hair chaetae are Ohtaka (1995) and Timm (1990). The Tasmanian specimens from Southwell R., mistaken as *R. coccineus* by Pinder and Brinkhurst (1994), are attributable to *Ainudrilus fultoni* Brinkhurst, 1982. Other worms attributed to this species by Pinder and Brinkhurst (1994) are described below as a new taxon.

**Rhyacodrilus megaprostatus** sp. nov.

Figure 1

Non *Rhyacodrilus coccineus* (Vejdovský, 1875).—Pinder and Brinkhurst, 1994: 94.

**Material examined.** Holotype: Curdies R., Vic., (38°20’S 143°08’E), 7 Feb 1992, G. Quinn (MON), 1 mature on slide (NMV F81869).

Paratypes. Vic: Grassy Creek, Otway Ranges, 38°28’S 144°00’E, 6 Jun 1989, 1 mature on slide (NMV F81868); Lake Purrumbete, 38°17’S 143°14’E, 31 Jan 1992, G. Quinn (MON), 1 mature on slide (NMV F81866); Lake Purrumbete, no date, A. Glaister (MON), 1 mature on slide (NMV F81867); Branjee Creek, Goulburn Valley, 36°42’S 148°20’E, 23 Apr 1992, A. Pinder, 1 mature on slide (NMV F81870).

**Distribution and habitat.** All of the above localities are in central southern Victoria. Collected from lentic and lotic sites and from a variety of

Figure 1. *Rhyacodrilus megaprostatus* sp. nov.: A, tips of anterior dorsal chaetae with section of hair; B, tip of ventral chaeta of II; C, tip of posterior ventral chaeta; D, atrium with prostate tissue and penial chaetae of holotype; E, spermatheca of NMV F81868. Scales: A–C, 0.01 mm; D, 0.04 mm; E, 0.03 mm.
habitats including sandy sediment and rocks and bricks used for colonisation studies.

**Etymology**: Named for the size of the prostate gland in relation to the small atrium.

**Description**. Length 5–9 mm, diameter when slide mounted about 0.3 mm. Number of segments 40–70, Coelomocytes abundant.

Hair chaetae in preclitellar dorsal bundles normally 3–4 per bundle (1 long and 1 short in one Lake Purrumbete specimen), 270–300 μm long. Hairs accompanied by 3–6 pectinate chaetae, 100–110 μm long, with upper teeth slightly shorter than lower and few pectinations (Fig. 1A). Fewer dorsal chaetae posteriorly. Anterior ventral bundles with 3–5 chaetae (those from Curdies R. with as many as 7), 90–140 μm long, with upper teeth thinner than lower, teeth about equal in length on 11 (Fig. 1B), upper teeth slightly shorter than lower posteriorly (Fig. 1C). Penial chaetae in XI bluntly simple-pointed, 90–100 μm long, 1–3 per bundle, projecting medial to the line of the somatic ventral chaetae (Fig. D).

Paired male and spermathecal pores in line with ventral chaetae. Atria small, spherical (Fig. 1D), opening into smaller spherical chamber with a lobed pore. Atria enclosed by a voluminous prostate gland (Fig. 1A), concealing the vas deferens-atrial union. Prostate not closely applied to the sides of the atrium. Ovaries large and obscuring the vasa deferentia. Male funnels observed in some specimens, often closely associated with the spermathecae and a part of vasa deferentia folded and adhered to funnels. Spermathecae ovoid (Fig. 1E), containing sperm arranged in distinct masses.

**Remarks**. The apparent attachment of the prostate at the top of the atrium needs to be confirmed from sectioned material as this may indicates that the prostate is not as diffuse as is normal in *Rhyacodrilus*. Within the genus, the large volume of prostate tissue compared to the atria is unique to this new species.

According to the key to *Rhyacodrilus* in Brinkhurst (1971a) and notes in the update by Brinkhurst and Wetzel (1984), *R. megaprostatus* is closest to *R. eoeineus*, from which it differs mainly in the volume of the prostate. Several other species with hair and pectinate chaetae have been described more recently. In *Rhyacodrilus okamikae* Giani and Rodriguez, 1988 the pectinate chaetae have short upper teeth, the ventral chaetae have long upper teeth and there is only a single median spermatheca. *Rhyacodrilus caputensis* Timm, 1990 has lyre-shaped pectinate chaetae and tubular atria. *Rhyacodrilus hiemalis* Ohtaka, 1995 has voluminous spermathecae with narrow ducts, more numerous chaetae and a less voluminous prostate gland.

**Rhyacodrilus bifidus** Brinkhurst

*Rhyacodrilus bifidus* Brinkhurst, 1982; 3, pl. 6.

**Holotype**: Blue Lake, Mt Kosciusko plateau, NSW (QVM:14:232).

**Material examined**: NSW: Holotype and paratype from type locality, 36°24′24″S 148°18′50″E, 7 Feb 1977, 5 on slides (QVM:14:232–233) and 7 on slides (ROB); Lake Cootapatamba, Mt Kosciusko plateau, 37°27′59″S 148°15′48″E, 7 Feb 1977, 1 on slide (ROB); Vic.: Thomson R. at Thomson Portal Rd, 3 on slides (NMV F81671–81873); Wentworth R., 17.7 km upstream of Tabberabbera, 37°31′17″E, 2 Oct 1975, 1 on slide, tentative identification (NMV F81874). New Zealand: Lake Matheson, Canterbury Highlands, 2 Nov 1978, 2 on slides (ROB); Lake Gault, Canterbury Highlands, 5 Nov 1978, 2 on slides (ROB).

**Distribution and habitat**. Known only from the above lakes and rivers of the far southeast of mainland Australia and the lakes on the South Island of New Zealand (Brinkhurst, 1982), although the identification of the latter could not be confirmed as the genitalia are no longer visible in the specimens examined. Australian specimens have been collected from coarse sediments in rivers: sand and gravel, often between cobbles and pebbles (Ahern and Blyth, 1979; Malipatil and Blyth, 1982) but possibly in finer sediments from the Mt Kosciusko sites (Timms, 1979).

**Diagnosis**. Length up to 7 mm. Ventral and dorsal bundles with 3–8 chaetae anteriorly, bifid with upper teeth 2–3 times as long as, but thinner than, the lower. Penial chaetae 6–10 bifid per bundle in XI, about 2 times longer than somatic chaetae and slightly curved ectally. Vasa deferentia as long as atria. Atria 4 times longer than broad, ending in wide bulbs with narrow pores on the anterior face of penis sacs which open to the exterior via narrow pores. Abundant prostate tissue attached to atria subapically. Coelomocytes not abundant.

**Remarks**. The reproductive structures of the Wentworth R. specimens are not visible and so the identification cannot be confirmed. There are only three penial chaetae per bundle in XI, but these are large and bifid and the somatic chaetae are mostly four or five per bundle with the upper teeth much longer than the lower. Similarly, the identification of the whole-mounted New Zealand specimens could not be confirmed.
Ainudrilus Finogenova


**Vadicola** Baker, 1982: 3232.

**Type species.** *Ainudrilus oceanicus* Finogenova, 1982.

**Diagnosis.** Hair chaetae present or absent. Chaetae of penial segment modified, chaetae of spermathecal segment slightly modified in one species. Vasa deferentia usually wide and at least partially granulated, entering atria subapically. Atria variably shaped but more or less erect or directed posteriorly, usually consisting of an ampullae, often with spacious lumen containing sperm, usually leading to thick, and often equally large and well developed, ejaculatory ducts, often giving the appearance of a bi-partite atria. Prostate absent. Penes absent. Spermathecae with distinct, and often complex ducts. Sperm loose in ampullae. Coelomocytes large and abundant.

**Remarks.** The lack of prostate on the atria distinguishes *Ainudrilus* from almost all other rhyacodrilines, bar some other highly unusual forms such as *Jolydrilus* Marcus, 1965 and *Epirodrilus* Hrabe, 1930 (see Brinkhurst, 1971a; Baker and Brinkhurst, 1981), and one freshwater *Rhyacodrilus*. The latter, *Rhyacodrilus simplex* (Benham, 1903), lacks prostate tissue but also differs from other *Rhyacodrilus* in having vasa deferentia that coil around the atria and which join the atria apically. Further study of this species may lead to it being moved back to a resurrected *Taupodrilus*, which was established by Benham (1903) for its reception.

*Ainudrilus billabongus* (Brinkhurst, 1984).

**Ainudrilus stagnalis** Erseus, 1997

*Ainudrilus stagnalis* Erseus, 1997: 9, figs 2E–F.

**Holotype.** Bowerbird Billabong, Magela Creek, NT (NTM W00020).

**Material examined.** No new specimens examined.

**Distribution and habitat.** Known only from the freshwater type locality, in fine sand (Erseus, 1997).

**Diagnosis.** Length at least 3.2 mm (only specimen incomplete). Coelomocytes abundant. Hair chaetae absent. Anterior chaetae bifid with upper tooth much longer than lower, 4–6 per bundle anteriorly, 3–4 posteriorly. A single bifid chaeta, not larger than other ventral chaetae, near each male pore. Vasa deferentia not described. Atria with non-muscular ampullae and thick muscular ejaculatory ducts terminating in simple pores medial to the ventral chaetal line. Spermathecae absent in the only known specimen.

**Remarks.** Erseus (1997) suggested that the chaetae near each male pore is not a modified genital chaeta, but that such might be developed at a later stage.

*Ainudrilus fultoni* (Brinkhurst) comb. nov.

**Figure 2**

*Rhyacodrilus fultoni* Brinkhurst, 1982: 2, pl. 1–5.

**Holotype.** Lake Sorell, Tas. (QVM:14:230).
Material examined. Tas.: Holotype and paratypes, type locality, several sectioned specimens and others in alcohol, 2 Feb 1981 (QVM:14:230-231 and ROB); Southwell R., 41°34'50"S 145°44'04"E. 20 Dec 1988, 2 on slides (QVM:14:4201-4202); Ouse R. at Mariborough Highway, 41°59'22"S 146°38'43"E. 16 Mar 1997, 1 on slide (AMP); Lake Perry, 43°13'10"S 146°45'17"E. 11 Mar 1997, 2 on slides, 3 in alcohol (AMP).

Distribution and habitat. Known only from lakes and rivers in Tasmania. The Ouse R. and Lake Perry specimens were collected from sand between cobbles in shallow water.

Diagnosis. Length up to 15 mm. Coelomocytes large and fairly abundant. Chaetae all bifid with teeth equally long, 10–13 per bundle anteriorly, fewer posteriorly (Fig. 2A). Ventral bundles of XI with 7–9 straight penial chaetae with blunt, slightly curved tips, about equal in length to somatic ventral chaetae (Fig. 2B). Short vasa deferentia enter atria subapically (Fig. 2C). Atria consisting of a thick walled ental portion with a narrow lumen, which leads into a thinner walled ectal portion with a wide lumen which usually contains sperm in mature specimens (Fig. 2C). Spermathecae with ampullae full of loose masses of sperm, ducts short and broad opening through large pores (Fig. 2C).

Remarks. Specimens from Southwell R. were attributed to A. coccineus by Pinder and Brinkhurst (1994) but conform to the description of A. fultoni. As these specimens are dissected, rather than sectioned like the type material, the reproductive structures are illustrated here to give a different perspective (Fig. 2C). The atrium consists of a thick-walled portion in which the lumen can be seen in only one dissected specimen and a thinner walled ectal chamber (essentially an ejaculatory duct), with a sperm bundle within the latter in examined specimens.
It seems preferable to transfer *R. fultoni* from *Rhyacodrilus* to the expanding *Ainudrilus*, which includes most species without prostate glands, whereas all *Rhyacodrilus* (except *R. simplex*, discussed above) have diffuse prostate tissue. *Ainudrilus fultoni* can be distinguished from its freshwater congeners by the more numerous somatic and penial chaetae.

**Ainudrilus nharna** sp. nov.

**Figure 3**


Paratypes: Collection details as for holotype, 2 specimens serially sectioned on slides and others in alcohol (WAM 2-99 to 4-99).

Other material: WA: Collection details as for types, 7 on slides, including 1 serially sectioned (AMP); Lake Wilson at track off Scott Rd, 34°25'23"S 115°07'52"E, 14 Sep 1996, 2 on slides (AMP); Thomas Spring, Augusta, 34°21'00"S 115°09'35"E, 17 Sep 1996, A. Pinder and R. Brinkhurst, 5 on slides (AMP); stream crossing Thomson Rd, approximately 5 km N of Granite Peak, 34°40'48"S 116°42'13"E, 12 Sep 1996, A. Pinder and R. Brinkhurst, 1 on slide (AMP); northern tributary of Collier Creek on Cemetery Rd, 34°58'30"S 116°45'12"E, 11 Sep 1996, A. Pinder and R. Brinkhurst, 1 on slide (AMP); Boyndiminup Rd, Lake Muir wetland system, WA, 34°30'S 116°35'E, Jul and Oct 1993, P. Horwitz (ECU), 3 on slides and others in alcohol (WAM 90-97, 91-97).

Figure 3, *Ainudrilus nharna* sp. nov.: A, tip of dorsal chaeta; B, tip of ventral chaeta; C, tip of penial chaeta; D, genitalia, based mostly on holotype. Scales: A–C, 0.01 mm; D, 0.1 mm.
The absence of prostate tissue and the thickened vasa deferentia suggest that this new species belongs in the genus Ainudrilus. *Ainudrilus taitamensis* Erseus, 1990a, of Hong Kong, which was only tentatively included in the genus, is the only other species to have ciliated atria. The atria and pseudopenes resembles what was called a two-part atria in *A. fultoni* and the ectal part of the male duct is formed into pseudopenes or elaborate eejulatory ducts in some other species (Erseus, 1990a). The thick vasa deferentia are difficult to follow in both sectioned and dissected worms as they are tightly folded with an indistinct lumen and are obscured by the ovaries. *Ainudrilus taitamensis* and *Ainudrilus brendaee* Erseus, 1997, both marine/brackish, are the only other *Ainudrilus* to have hair chaetae. These differ from the new species in that the former has long tubular atria and the latter has only two small straight penial chaetae per bundle and ventral chaetae with upper teeth much longer than the lower.

**Rhizodrilus Smith**


**Type species.** *Rhizodrilus lacteus* Smith, 1900.

**Diagnosis.** Chaetae all bifid, hairs absent. Vasa deferentia moderately long, entering atria subapically. Atria normally tubular with diffuse prostate tissue, terminating in ejaculatory ducts which exit either on the inner aspect of large ventrolateral folds in the body wall or into a median invagination of the ventral body wall (copulatory bursa), sometimes via protrusible pseudopenes. Spermathecal chaetae and/or penial chaetae modified in mature specimens, the former associated with large glands. Some or all of the spermathecal genitalia in IX. Sperm in spermathecae in loose masses or in oriented bundles. Coelomocytes abundant.
Remarks. *Rhizodrilus* consists of a few marine and freshwater species with apparently disparate distributions (Baker and Brinkhurst, 1981; Erséus, 1990a). These are united by the presence in IX of at least some of the spermathecal genitalia. The following species was tentatively included in *Rhizodrilus* by Baker and Brinkhurst (1981).

*Rhizodrilus arthingtonae* (Jamieson)


**Holotype.** Brown Lake, North Stradbroke Island, Qld (QM G8881).

**Material examined:** Qld: Holotype and paratype, locality as above, 31 Jul 1975, dissected on slides (QM G8881-2).

**Distribution and habitat.** Known only from the type locality, a perched acidic lake. Specimens collected in organic material in sandy sediment (Jamieson, 1978).

**Diagnosis.** Length 66 mm (paratype). Coelomocytes numerous. Anterior chaetal bundles with 3–5 bifid chaetae with the upper teeth slightly longer than the lower, posteriorly teeth about equal. Hair chaetae absent. The chaetae are smaller anteriorly and posteriorly, largest in the clitellar region. Several clearly bifid penial chaetae per bundle in XI, 1.5–2 times longer than somatic chaetae and slightly curved towards the tip. Vasa deferentia narrow, coiled anteriorly, passing through the prostate before entering atria subapically. Atria fusiform to slenderly bulbous, prostate tissue compact but lobulated, enclosing the atrium and communicating with the lumen at numerous points. Spermathecal glands in IX, each with a short diagonal groove passing posteriorly from its centre to 9/10. Spermathecae in X, with indistinct ventrolateral pores at 9/10. Worm squarish in cross-section.

**Remarks.** Erséus (1994) rightly questions whether *R. arthingtonae* belongs within this genus, preferring to include only those species with large tubular atria and a clear involvement of spermathecal genitalia in IX, rather than X as is normal in the family. *R. arthingtonae* has only minor involvement of spermathecal genitalia in IX (just papillae on IX with grooves leading back to the spermathecal pores on 9/10). However, *Rhizodrilus lacteus* Smith, 1900, which has just the spermathecal chaetae and associated glands in IX but retains the spermathecae themselves in X is intermediate between *R. arthingtonae* and other *Rhizodrilus* in this respect and so *R. arthingtonae* may represent one extreme of a continuum. Arguing against this proposition is the fact that the atria are more upright and less tubular than those of other *Rhizodrilus* and Ferraguti et al. (1994) note the more plesiomorphic spermatozoal ultrastructure of *R. arthingtonae* compared to *Rhizodrilus russus* Erséus, 1990a and the related *Monopylephorus* Levinson, 1884. If *R. arthingtonae* is excluded from *Rhizodrilus*, then, short of creating a new genus, it is difficult to see a more suitable place for it. Erséus (1994) summarises the possible relationships between *Rhizodrilus* and other relevant rhyacodriline genera and, since we suggest no change to the status quo, these need not be repeated here. A more satisfactory placement of *R. arthingtonae* may have to await further phylogenetic studies of this and related rhyacodrilines.

**Breviatria** gen. nov.

**Type species.** *Telmatodrilus multiprostatus* Brinkhurst, 1971a, as the first of two species described in the original account.

**Diagnosis.** Atria ovoid to erect pear-shaped, with unciolated lumen, bearing numerous glands of prostate tissue apically, communicating independently with atrial lumen. Male pores simple on XI, on inner aspect of protruding ventrolateral folds of the body wall surrounding a broad median copulatory chamber. Spermathecal chaetae large and grooved, penial chaetae numerous with blunt or bifid tips. Spermathecae normally with ventrolateral to dorso-lateral pores, located anteriorly on X. Sperm in spermathecae in organised bundles (not spermatozeugmata) or loose. Coelomocytes abundant for at least one species, unknown in the others.

**Etymology.** *Breviatria* referring to the short atria, in contrast to the tubular atria of other genera with prostate formed into multiple clumps.

**Remarks.** Of the four species assigned to this new rhyacodriline genus, three were previously placed within the *Telmatodrilinae* and one is new. The reasons for re-assigning the earlier species were discussed above (in the *Rhyacodrilinae* remarks section). *Breviatria* is distinguished from other *Rhyacodrilinae* by the ovoid to pear-shaped atria.
with prostate tissue formed into discrete glands with separate (usually stalked) connections to the ectal part of the atria. Other rhyacodriline genera with clumped prostate tissue, mostly marine forms such as *Hermodrilus* Erseus and Jamieson, 1981 and *Heterodrilus* Pierantoni, 1902, usually have the clumps more broadly attached along the length of elongate tubular atria, although prostates are more restricted in position in a few species. The other new genus, *Biprostatus*, described below, also has small atria but these have only two large prostate glands which are broadly attached to the anterior and posterior sides of the atria. Other rhyacodrilies with short atria either have evenly distributed diffuse prostate tissue (such as most *Rhyacodrilus*) or lack prostate tissue (*Ammudrilus* and *Rhyacodrilus simplex*). *Rhizodrilus arthingtonae* (discussed above) also has ovoid atria but the lobes of prostate tissue are tightly packed over the surface of the atria and broadly attached rather than stalked. The new species described below has numerous coelomocytes but this feature needs to be re-examined when fresh material of the other species becomes available.

*Breviatria multiprostatus* (Brinkhurst) comb. nov.

Figures 4, 5


Holotype. Lake Pedder, Tas. (AMS W4178).

Material examined. Tas.: Holotype and paratypes, locality as above, 2–4 Mar 1966 (AMS W4178–W4182) and 1 on slide (ROB); Cuvier R., 10 Oct 1978, 1 on slides (ROB); Collingswood R., 4 Nov 1978, 1 on slides (ROB); trickles under the Needles, 11 Nov 1978, 1 on slides (ROB); creek in Frodshams Pass, 12 Nov 1978, 1 on slides (ROB); Lake Sorell, 2 Feb 1981, 1 sectioned (ROB); Crossing R., south of Lake Pedder, southwest Tasmania, 10 Feb 1987, 1 on slide (QVM: 14:3002) and 3 in alcohol (AMP); Lake Surprise, AMG 8112 441869, 13 Nov 1976, 1 on slide (QVM: 14:3001) and 1 in alcohol (AMP). Tentatively identified immature specimens from various sites in Tasmania listed by Brinkhurst (1982).

Other records. Tas.: Lake Pedder (Bayly, 1973); South Esk R. (Brinkhurst and Fulton, 1979); Lakes Sorell and Crescent (Timms, 1978). New Zealand: Leeston Drain, near Killinchy, 56 km S of Christchurch (Marshall, 1975; Marshall and Winterbourn, 1979); Freshwater R., Stewart Island (Cowie et al., 1978).

Distribution and habitat. Recorded from lakes, streams and rivers in Tasmania and possibly from New Zealand. The Lake Crescent specimens were collected from a variety of sediment types, including sand, detritus and mud (Timms, 1978). Specimens from Great Lake were collected at depths of up to 16.5 m (Fulton, 1983b).

Description. Length up to 16 mm. Pharyngeal glands present on either side of septa 2/3 to 4/5, gut expanded in VII to form a diverticulum which completely encircles the gut in VII and protrudes forward into VI (Fig. 4A).

Somatic chaetae all simple-pointed (Fig. 5A), up to 8 per bundle anteriorly, fewer posteriorly. Ventral chaetae missing on penial segment of mature specimens, or if present then not modified. Spermathecal chaetae (Fig. 5B) larger than somatic chaetae, with extensive musculature, projecting into an enlarged chaetal sac posteriorly on X, into which also empties a separate elongate gland (Fig. 4C). In one paratype, the spermathecal chaetal sac opens anteriorly in X, with the chaetal shaft protruding well anteriorly into IX (Fig. 4B).

Testes anteroventral in X, with sperm funnels on 10/11 feeding broad vasa deferentia which wind upwards to enter atria apically (Figs 4B, C). Atria elongate pear-shaped, may be folded over dorsally, with uncinated lumen and thick lining tissue. Atria narrow basally, opening on inner aspect of folds in the body wall lateral to a median ventral copulatory chamber. Prostate cells grouped into numerous glands which narrow basally and connect to apical third of atria (Figs 4B, C). Spermatotheca large in X with short ducts that lead to ventral pores just behind septa 9/10 (or medially in X in the Lake Sorell specimen). Sperm loose in ampulla. Ovaries attached to anterior septa of XI near sperm funnel. Female funnels large, leading to pores at intersegmental furrow 11/12 (Figs 4B, C).

Remarks. This is the only Australian tubificid to have all chaetae simple-pointed. However, many aquatic Enchytraeidae also have multiple simple-pointed chaetae in all bundles and immature forms could be confused with *B. multiprostatus*. Of the Tasmanian records, the only identifications that can be confirmed by re-examination of specimens are those from Lake Pedder and Lake Sorell. Specimens from the other sites listed above are either immature (and so are tentatively
Figure 4, *Breviatria multiprostatus* (Brinkhurst): A, anterior of specimen from Lake Sorell; B, genitalia of paratype AMS W4182; C, genitalia of Lake Sorell specimen. Scales: A–C, 0.15 mm.
identified from the chaetae only) or their identification can no longer be verified because of their poor condition. It is not known whether identifications of specimens from New Zealand were based on the genitalia of mature specimens or just the chaetae of immature worms so the identification must be considered tentative. One of the New Zealand records (Leeston Drain) is unusual in that the site was enriched with septic tank leachate and dairy effluent (Marshall and Winterbourn, 1979) whereas the Australian records are all from non-enriched sites, including minimally disturbed alpine streams.

The position of the spermathecal pores and spermathecal chaetae appears to vary. Paratypes W4180 and W4182 (Fig. 4B) both have spermathecal pores anterior in X, but spermathecal chaetae posterior and anterior (projecting forward into IX) in X respectively. The Lake Sorrel specimen has spermathecal chaetae posterior in X but the spermathecal pore medial on X (Fig. 4C). All other features of these worms seem similar and we consider the variation in spermathecal characters to be intraspecific for now. The holotype is dissected rather than sectioned and the original position of the spermathecae is unclear.

Breviatria pectinatus (Brinkhurst) comb. nov.

Figure 6


Holotype. Lake Pedder, Tas. (AMS W4176).

Material examined. Tas.: Holotype and paratypes, Lake Pedder, 2 Mar 1966, 2 on slides (AMS W4176–7) and 5 on slides (ROB).

Other Australian records. Tas.: Lake Pedder (Bayly, 1973); Lake St Clair (Timms, 1978). Vic.: Lake Tali Karng (Timms, 1974).

Distribution and habitat. Recorded only from the above lakes in Victoria and Tasmania. Bayly (1973) collected this species from Lake Pedder (in 1972) in sandy sediment but the Lake Tali Karng specimens were recovered from mud at a depth of 12 m.

Description. Length unknown, but greater than 10 mm.

Anterior bundles with 9–14 chaetae, upper teeth longer than the lower and slightly hooked. Posterior bundles with 5–8 pectinate chaetae with upper teeth not so long (Fig. 6A). Spermathecal chaetae single, thin with grooved tips (Fig. 6B), up to twice as long as somatic ventral chaetae. Penial chaetae (Fig. 6C) modified with rough, blunt to bifid tips (absent on paratype W4176), about 1.5 times longer than somatic ventral chaetae.

Vasa deferentia broad, coiled once or twice before entering atria apically (Fig. 6D). Atria pear-shaped with numerous prostates with short stalks distributed around the upper half. Stalks enveloped by the atrial muscle tissue. Individual peritoneal cells form diffuse cover over basal half of atria and some present apically (Fig. 6D). Atria narrowing to pores on the inner aspect of lateral folds in the body wall around a shallow median ventral copulatory chamber. Details of the
spermathecae difficult to decipher but possibly quite folded, with lateral or dorsolateral pores and containing loose sperm.

Remarks. Pectinate chaetae are more common in the Tubificinae than the Rhyacodrilinae and the former usually has pectinations more developed anteriorly, rather than posteriorly as in *B. pectinatus*.

Figure 6, *Breviatria pectinatus* (Brinkhurst): A, tips of pectinate dorsal chaetae of holotype; B, spermathecal chaeta of holotype; C, penial chaetae of holotype; D, male ducts and spermathecal chaetae of paratype AMS W4177. Scales: A, 0.01 mm; B–C, 0.015 mm; D, 0.05 mm.
Breviatria papillatus (Brinkhurst and Fulton) comb. nov.

Figure 7


Material examined. Tas.: Holotype and paratypes, type locality, 26 Sep 1975, 3 on slides (QVM: 14:320, 321, 326 and 327) and 1 on slide (ROB); Arthurs Lake, 4 Jul 1977, 8 on slide, 2 mature and several immature in alcohol (NMV F88870, F88871 and ROB); Lake Sorrel, no date, 4 on slides (QVM: 14:322–325).

Distribution and habitat. Recorded only from the above lakes of the central plateau of Tasmania. Collected in both sandy and clayey sediments, at depths up to 17.5m (Fulton, 1983b).

Description. Length 10–20 mm. Coelomocytes not observed. Worms encrusted with fine foreign material, body wall papillate with several rings of papillae per segment (Fig. 7A). Prostomium and segment I (and sometimes II) may be retracted into the body. Posterior segments narrow and

Figure 7. Breviatria papillatus (Brinkhurst and Fulton): A, view of body showing copulatory bursa on XI; B, tip of anterior chaeta; C–D, tips of transitional chaetae; E, tip of posterior hair chaeta; F, male ducts of NMV F88870; G, spermatheca of NMV F88870. Scales: A, 0.2 mm; B–E, 0.01 mm; F, 0.05 mm; G, 0.025 mm.
appearing highly contracted in the preserved specimens.

Anterior chaetae bifid, 5–7 per bundle, with each tooth broad and flattened (Fig. 7B). Chaetae changing to a hair-like form, some with vestiges of teeth (Figs. 7C, D) between VII and X so that postclitellar bundles have 5–9 curved hair chaetae (Fig. 7E). Penial chaetae slightly shorter than preclitellar somatic chaetae, 3–5 per bundle with bifid tips (Fig. 7F). Spermathecal chaetae not modified.

Long vasa deferentia connect to short pear-shaped atria subapically (Fig. 7F). Atria narrow gradually to enter small median copulatory chamber (which is everted in some preserved worms) near the penial chaetae which project from the protruding lateral walls of the chamber. Three or more lobes of prostate tissue on atria apically (Fig. 7F). Spermathecae small and globular (Fig. 7G) with short ducts leading to lateral pores anteriorly on X. Sperm not observed in ampullae.

Remarks. While the chaetae and papillae of *B. papillatus* are unusual, the genitalia suggest that this species is simply an apomorphic member of *Breviatria* and to exclude it would leave *Breviatria triparaphyletic*. Specimens from Arthurs Lake, some of which were dissected and illustrated for this study (Fig. 7), clearly have spermathecae with lateral pores whereas spermathecae were not seen in the type specimens from Great Lake. The spermathecae of these specimens are very small (100–150 μm) and do not contain sperm, so may not be fully developed. Unfortunately, the type specimens have become too cleared for this feature to be checked. The holotype (the only type in which the genitalia can be seen) has ‘at least 2 or 3 prostate glands’ (Brinkhurst and Fulton, 1979), but the size of these and their attachment to the atria is uncertain due to clearing and distortion during slide mounting. The prostate on one atrium of the holotype appears to be formed into two or three large, stalked lobes but on the other atrium the prostate appears to be a more cohesive mass with a number of short connections. The prostate tissue of the Arthur R. specimens is clearly formed into numerous small glands but connections to the atria are obscured. Fresh specimens from the type locality are required to determine the unity of this taxon.

*Breviatria arvensis* sp. nov.

*Material examined.* Holotype: Arve R. at Arve Rd, 43°11′20″S 146°46′05″E, Tasmania, 12 Mar 1997, R. Marchant (NMV) and A. Pinder. dissected on slide (QVM:14:3878).

Paratypes: Collection details as for holotype, 1 mature and 1 immature sagitally halved on slide, with posterior portion of 1 of these in alcohol, and 1 immature whole-mounted on a slide (QVM:14:3879–3881).

*Distribution and habitat.* Known only from the type locality, collected from sand/silt under cobble at a depth of 10–20 cm.

*Etymology.* Named *arvensis* for the type locality.

*Description.* Length at least 20 mm (none complete), width of slide mounted worms 0.25–0.3 mm. Prostomium squarish in preserved type material. Coelomocytes abundant but without consistent shape, entirely filling coelom in most of body, including the prostomium, making the worms appear quite solid when handled.

All chaetae bifid, 55–85 μm long, with upper teeth longer than lower and nodulus slightly ectal (Fig. 8A). Up to 8 chaetae per bundle anteriorly, reduced in number posteriorly. Chaetae of spermathecal segment (X) present but not modified, penial chaetae of XI 4 per bundle, straight, with bifid ectal ends and no nodulus (Fig. 8B), 150–165 μm long, projecting somewhat diagonally towards the midline to open into median copulatory chamber (Fig. 8C).

Testes anteroventral in X. Sperm funnels large, vasa deferentia wide and slightly coiled near funnel. Point of union of atria and vasa deferentia not established. Atria ovoid, thin walled, with short ejaculatory ducts leading to pores on inner aspect of folds in body wall lateral to a median ventral copulatory chamber (Fig. 8C). Prostate tissue present as numerous discreet glands, which presumably connect with atria individually, although this could not be confirmed. Spermathecae bulbous with short ducts leading to dorso-lateral pores anteriorly on X. Sperm in ampullae formed into numerous bundles. Ovaries anteroventral in XI, female pores not observed.

Remarks. Although the connections between the atria and prostate tissue are obscured in the available specimens, the numerous separate glands are similar to those of other *Breviatria*. The long straight penial chaetae with bifid tips also resemble those of other *Breviatria*. The long straight penial chaetae of *B. arvensis*, with their long upper teeth, differ from those of all other *Breviatria* but resemble those of *Biprostatus duplex*, described below.

*Biprostatus* gen. nov.

*Diagnosis.* Atria small and spherical, bearing broadly attached prostate tissue formed into
two large glands, one anterior and one posterior. Atria leading to simple pores on inner aspects of folds in body wall, lateral to a median ventral copulatory chamber. Spermathecal chaetae large and grooved, penial chaetae multiple and bluntly bifid. Spermathecal pores lateral, sperm in ampullae in loose bundles. Coelomocytes abundant in anterior segments in at least one species, to be confirmed for the rest.

*Type species:* *Telmatodrilus bifidus* Brinkhurst and Fulton, 1979.

**Remarks.** The type species of *Biprostatus* was originally placed within the telmatodriline genus *Telmatodrilus*, but is transferred to this new rhyacodriline genus for reasons already discussed above (see remarks for Rhyacodrilinae). This genus is separable from most others in the Rhyacodrilinae by virtue of the small atria with large bilobate prostate glands. Although some *Heterodrilus*, such as *H. inermis* and *H. rapidensis*, also have short atria with large paired prostate glands, these glands appear to be stalked and the chaetae of *Heterodrilus* (1 or 2 per bundle, at least some of which are trifid) are diagnostic (Erséus, 1981).
Biprostatus bifidus (Brinkhurst and Fulton) comb. nov.

Figure 9

Telmatodrilus? (Telmatodrilus?) bifidus Brinkhurst and Fulton, 1979: 3, figs 15–19.

Holotype. Great Lake, Tas. (QVM:14:328).

Material examined. Tas.: Holotype and paratypes, Great Lake, 1975, 10 on slides (QVM:14:328–339); Arthurs Lake, 4 Apr and 22 May 1977, 4 on slides (ROB).

Distribution and habitat. Recorded only from the above lakes of the central plateau of Tasmania. Collected in both sandy and clayey sediments, at depths up to 17.5m (Fulton, 1983b).

Diagnosis. Length up to 25 mm. Anterior bundles with up to 13 bifid chaetae with upper teeth longer than the broad lower. (Fig. 9A) Number of chaetae diminishing from VIII–X with upper teeth becoming shorter than the lower after the clitellar region (Fig. 9B). Chaetae of some species have groove-like markings (ornamentations) ectally. Spermathecal chaetae straight, single, with grooved tips (Fig. 9C), varying in width and length, from shorter than to 3 times longer than somatic chaetae. Pental chaetae bifid (Fig. 9D), up to 7 per bundle, twice as long and thick as somatic ventral chaetae. Atria small, elongate ovoid with short ejaculatory duets (Fig. 9E). Each atrium with a pair of broadly attached prostate glands, one anterior, which envelops the vas deferens, the other posterior, occupying much of the coelom (Fig. 9E). Male pores and penial chaetae on the lateral walls of a large median copulatory chamber. Spermathecae ovoid, with short duct-like extension entally and lateral pores. Sperm in ampullae formed into loose bundles. Coelomoocytes not recorded.

Figure 9, Biprostatus bifidus (Brinkhurst and Fulton): A, tip of anterior chaeta; B, tips of posterior chaetae; C, tips of spermathecal chaetae of Arthurs Lake specimen; D, tips of penial chaeta of holotype; E, genitalia of QVM:14:338. Scales: A–B, 0.015 mm; C, 0.015 mm; D, 0.01 mm; E, 0.12 mm.
Biprostatus duplex sp. nov.

Figures 10, 11

Telmatodrilus sp. 2.—Pinder and Brinkhurst, 1994.

Material examined. Holotype: Que R., just below Que R. Mine dam. Tasmania, AMG 8014 914956, 27 Apr 1987, Wayne Fulton and Brett Mawbey (IFC), transverse serially sectioned specimen (with the posterior whole-mounted) on 15 slides (QVM: 14:4207).


Other material. Tas: Southwell R., above Helelyr mine, AMG 8014 945960, 20 Dec 1988, S. Chilcott (IFC), 1 on slide, 5 in alcohol (AMP); Douglas Creek, AMG 8114 206692, 16–17 Feb 1990, S. Chilcott and L. Mellefont (IFC), 1 on slide (AMP); Creek at Charlie's Hill, AMG 8111 297938, 19 Feb 1990, B. Mawbey (IFC), 2 in alcohol (AMP).

Distribution and habitat. The above sites are all rivers in western Tasmania.

Etymology: Named duplex for the double prostate gland.

Description. Length up to 20 mm. Prostomium short, bluntly conical. Coelomocytes large, abundant in a few preclitellar segments.

Anterior chaetae 3–7 per bundle (Figs 10A, C), fewer posteriorly, nodulus slightly distal, upper teeth much longer than lower. Posterior chaetae 2–4 per bundle, nodulus clearly distal, upper teeth also much longer than lower. Chaetae shortest in II (75 μm) and posteriorly, otherwise about 110 μm. Spermathecal chaetae single in X and/or IX, 140–160 μm long and grooved ectally (Figs 10D, E), associated with large glands (Fig. 10G), protruding from the body wall in line with somatic ventral chaetae. Penial chaetae 4–7 per bundle, straight with notched ectal ends (Fig. 10F), no nodulus, 120–160 μm long. Penial chaetae lie medial to atria and project somewhat diagonally toward midline to open into median depression of the body wall.

Sperm funnels large, vasa deferentia thin, slightly coiled at first, then running posteriorly to enter the small globular atria subapically. Atria with prostate tissue formed into large anterior and posterior lobes (Fig. 11B). Short ejaculatory ducts lead to pores on inner aspect of folds in body wall lateral to a median copulatory chamber (Figs 11A, B). Thick glandular tissue present ventrally on either side of 10/11, more so in X (Figs 10G, 11B). Spermathecae oval (Fig. 10G), with short thick-walled ducts and pores antero-laterally in X. Sperm in ampullae formed into bundles.

Remarks. This species is similar to B. bifidus in many respects. The genitalia, bifid or notched penial chaetae and anterior somatic chaetae are similar in the two species, although the latter are less numerous in B. duplex. They differ in that the upper teeth of the posterior somatic chaetae of B. duplex are longer than the lower (like Breviatria arvensis) whereas the upper teeth are shorter than the lower on the posterior chaetae of B. bifidus. The tips of the spermathecal chaetae also appears to differ.

Bothrioneurum Stoic


Type species. Bothrioneurum vejdovskyanum Stoic, 1886.

Diagnosis. All chaetae bifid, hair chaetae absent. Prostomium with a middorsal sensory pit. Vasa deferentia short to long. Atria tubular and covered with diffuse prostate gland cells except for ectal portion, leading to protrusable pseudopenes bearing diverticula (paratria) with aecessory glands. Sperm stored within external spermatophores, attached to body wall. Spermathecae absent. Penial chaetae may be modified. Coelomocytes large and abundant.

Bothrioneurum vejdovskyanum Stoic


Other Australian records. NSW: Barrington R., Gloucester (Brinkhurst, 1982). Tas.: Arve R. (Brinkhurst, 1982).

Distribution and habitat. Cosmopolitan (Brinkhurst, 1971a) but uncommon in Australia.

Diagnosis. Length 28–35 mm. Anterior bundles with 4–6 bifid chaetae with upper teeth longer than lower, posteriorly fewer with teeth equally long. Ventrals of X1 with 4 slightly hooked, club-headed penial chaetae arranged in a fan. Vasa deferentia long, joining tubular atria apically. Atria covered with prostate gland, except for terminal portion, and leading to protrusable pseudopenes which bear paratria with aecessory glands. Spermathecae absent. Body
Figure 10, *Biprostatus duplex* sp. nov.: A, ventral chaeta of II; B, ventral chaeta of other anterior segments; C, two posterior chaetae; D, enlarged tip of spermathecal chaeta of QVM:14:4214; E, whole spermathecal chaeta of QVM:14:4214; F, tips of penial chaetae of QVM:14:4214; G, transverse section through segment X, composite from several sections of holotype. Scales: A–C, E and F, 0.01 mm; G, 0.05 mm.
Figure 11, Biprostatus duplex sp. nov.: A, transverse section through segment XI, composite from several sections of paratype QVM:14:4223; B, reconstruction of genitalia from several specimens. Scales: A–B, 0.05 mm.
wall may appear spotted or papillate, but smooth. Prostomium with dorsal sensory pit, often difficult to detect but visible as a small indentation when a slide mounted specimen viewed laterally.

Remarks. The only mature specimens examined are from Barrington R. and these matched the description of the species, except that the prostomial pit was not observed. All other identifications are of immature specimens based on the presence of the prostomial pit and the form of the somatic chaetae. An electron micrograph of the prostomial pit is provided by Brinkhurst and Gelder (1991).

Branchiura Beddard

*Branchiura* Beddard, 1892.—Michaelsen, 1900: 40.—Stephenson, 1930: 749.—Brinkhurst, 1971a: 562.

Type species. *Branchiura sowerbyi* Beddard, 1892.


*Branchiura sowerbyi* Beddard


Kawamura *japonica* Stephenson, 1917: 89, figs 1-5.


Material examined. NSW: Parramatta R., 17 Oct 1981 (AMS W197365); Wingecarribee R. at Greenstead, 14 Nov 1991, 2 in alcohol (AWT); Murray R. at Dora Dora, 24 Mar 1994 (MDFRC); Megarritys Creek, Fernsworth Avenue, 3 Feb 1993, 1 in alcohol (AWT); Rushy Billabong, 16 Jun 1981, 1 on slide (MDFRC); Ryan's Billabong, 27 Jul and 6 Dec 1982, 1 on slide, in alcohol (MDFRC). Qld: Leichhardt R., Coolullah H.S., 115 km NW Cloncurry, 25 Apr 1988, 1 on slide (SAM E2814), Vic.: junction of Thomson and MacAlister R.s, 31 Jun 1979, 1 in alcohol (NMV F77640); Mitia Mitta K., 1 Feb 1975, 2 Dec 1980 and 3 Mar 1982, 5 on slides, 3 in alcohol (NMV F77633-8), WA: Herdman Lake, 2 Nov 1989, 1 on slide (MUR); Wungong Brook, Jan 1998, 1 two-tailed worm in alcohol (AMP).


Distribution and habitat. Cosmopolitan (Brinkhurst, 1971a), widespread in Australia, occurring in a wide range of environments.

Diagnosis. Length 30-185 mm. Dorsal anterior chaetal bundles with 1-4 (or more) short hair chaetae and 5-12 (or more) chaetae that vary from simple-pointed to bifid with short upper teeth (which may be replicated). Posteriorly hairs fewer and shorter and non-hair chaetae with less replication of upper teeth. Ventral bundles with 6-11 bifid chaetae with upper teeth shorter than lower, even simple-pointed anteriorly. Gills and genital anatomy as for genus.

Other tubificid taxa

Timms (1978) records the tubificine *Peloscolex* sp. (and *'Peloscolex'* undoubtedly a misprint) from Lake St Clair, based on identifications by K. V. Naidu. These refer to some form of papillate tubificid, though presumably differing in chaetal morphology from *Breviatria papillatus*. These should not be considered definitive generic identifications since body wall papillae are characteristic of, but not diagnostic for, *Peloscolex* Leidy, 1850, now revised as *Spirosperma* Eisen, 1879, and other genera (Brinkhurst, 1979; Holmquist, 1978, 1979). We have seen several papillate immature worms from Victoria (including specimens from the Plenty, Glenelg, Curdies and La Trobe Rivers) and New South Wales (Georges R.) that have chaetae very similar to some *Spirosperma*, but mature specimens are required for identification.

The species coded *Telmatodrilus* sp. 1 in Pinder and Brinkhurst (1994) cannot yet be described from the few poorly preserved specimens. This species, which may be a *Biprostatus*, has anterior chaetae bifid (like those of *B. duplex*), posterior chaetae simple pointed, and has modified penial and spermathecal chaetae. Specimens have been collected from Que and Southwell Rivers in northwest Tasmania.

Numerous other undescribed tubificids, mostly from Tasmania and Western Australia, have been accumulated by the senior author since the preparation of this manuscript and no doubt others await discovery.

Zoogeography

Discussion of tubificid biogeography in the region is limited by the low number of specimens
that have been examined from Australia, New Zealand and Asia. No area of Australia has been thoroughly surveyed, although projects are underway to improve coverage of particular areas such as the southwest of Western Australia, Tasmania and South Australia. Nonetheless, some patterns can be discerned.

Twenty-nine species of Tubificidae, in 12 tubificine and rhyacodriline genera, have been recorded from Australian inland waters so far (Table 1). Of these, 16 species are restricted to Australia and two more are known only from Australia and New Zealand.

The nonendemic component consists of 11 common species within widespread genera (i.e. the tubificine genera *Tubifex*, *Limnodrilus*, *Aulodrilus* and *Potamodrilus* and the rhyacodrilines *Rhyacodrilus*, *Branchiura* and *Bothrioneurum*). Several of these species also occur in New Zealand (Brinkhurst and Fulton, 1979, 1982; Marshall, 1975; Timms, 1982). Of the cosmopolitan species, only *Aulodrilus pigueti*, *Aulodrilus plurisela* and *Branchiura sowerbyi* have been recorded from northern Australia (the Queensland records of *Limnodrilus* and *Tubifex* are from the southeast of the state), but this may reflect the low number of worms examined from this region. So far, records of *Aulodrilus pigueti* have been restricted to northern Australia, but other cosmopolitan species are widespread in southern Australia and seem to occur in a wide range of habitats. The endemic species appear to have more restricted distributions.

One of the three endemic genera, *Antipodrilus*, is widespread, although most of the species are not. *Antipodrilus davidis*, with the new range extensions into Western Australia and South Australia, is the most widely distributed and is now known from across southern Australia and New Zealand. By contrast, *A. magelensis* appears to be

**Table 1. Species list of Tubificidae known from Australia.** * = known only from Australia, # = known only from Australia and New Zealand, #? = New Zealand identification dubious, others cosmopolitan. NSW includes Australian Capital Territory, n = north, sw = southwest.

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A. plectilus and A. multiseta have not been known only from the south-east mainland while A. undrillus and A. multitesta have not been recorded outside a few sites in Tasmania. All species show a preference for lentic habitats.

Both species of the new genus Biprostatus are known only from Tasmania. The other new genus, Breviatria, has four species, three of which are apparently restricted to Tasmania. One of these, Breviatria multiprostatus, may also occur in New Zealand (Cowie et al. 1978; Marshall and Winterbourn, 1979) but the identifications are uncertain. The fourth, Breviatria pectinatus, is known from a few lakes in Tasmania and Victoria.

Other endemic rhyacodrilines belong to genera with disjunct global distributions. Rhizodrilus mostly consists of marine species with restricted distributions, often limited to single records from the type localities (Baker and Brinkhurst, 1981; Erseus, 1990a). The only Australian species, Rhizodrilus arthingttonae, is known only from one lake on North Stradbroke Island, Queensland (Jamieson, 1978). Ainudrilus mostly consists of coastal Pacific or Caribbean marine species (Erseus, 1990ab; 1997), except for the four freshwater Australian species. Of these, A. stagnalis and A. billabongus have been recorded only from the Northern Territory, A. uhuna only from southwest Western Australia and A. fultoni only from Tasmania.

Of the 18 species restricted to Australia and New Zealand, ten occur in Tasmania and eight are known only from that state (including most species of the new rhyacodriline genera). Similarly, about half of the 26 species of Australian Phreodrilidae are restricted to Tasmania (Pinder and Brinkhurst, 1997). By contrast, only three tubificids (Rhucodesmus megaprostatus, Rhucodesmus bifidus and Antipodrilus timmsi) and one phreodrilid (Phreodriloides notabilis Benham, 1907) are known only from southeast mainland Australia. This is despite the examination of worms from twice as many localities (and locality-dates) from Victoria and New South Wales as from Tasmania.

Of the tubificids known only from Tasmania, three (A. plectilus, A. multitesta and B. bifidus) are known only from Great Lake and Arthurs Lake on the eastern edge of the central plateau, and one (B. papillatus) is known only from these lakes and nearby Lake Sorell. While not wishing to place too much emphasis on this, because oligochaete records from other lakes are limited, it is interesting to note that two phreodrilids are also known only from these lakes (Pinder and Brinkhurst, 1997). In addition, numerous other invertebrates and fish are apparently restricted to these lakes, though mostly to Great Lake (Frankenberg, 1974; Fulton, 1983ab; Invertebrate Advisory Committee, 1994; Timms, 1985; Williams, 1974). These lakes pre-date the late pleistocene glaciations that led to the creation of most other lakes in Tasmania and lie outside earlier glacial influence (Davies, 1974). Sutherland et al. (1973) and Sutherland (1980) suggest that lacustrine environments may have existed in the Great Lake basin since the late Oligocene when basalt flows blocked the upper Ouse R. The age of Great Lake has been seen as a factor contributing to local endemity in its fauna (Timms, 1985). Other ancient lakes, such as Lake Baikal (Russia), Lake Ohrid (Europe) and Lake Tanganyikae (Africa) also have numerous endemic oligochaetes, whereas this is rare in more recent lakes (Martin, 1996). The few Tasmanian lakes of recent (Pleistocene/Holocene) origin from which oligochaetes have been identified appear to have only species that are widespread in the state. These include pre- and post-impoundment Lake Pedder as reported by Lake (1998), a few glacial lakes (Dobson, Dove and St. Clair) surveyed by Timms (1978) and a dune barrage lake in the north-east (Blackman’s Lagoon, sampled by the first author). However, records from many other Tasmanian lakes are required to confirm the apparent endemism of the oligochaeta fauna of Great Lake, Arthurs Lake and Lake Sorell.

Insufficient localities have been examined from other parts of Australia to generalise about regional diversity. The Phreodrilidae appear to be quite diverse in the southwest of Western Australia (Pinder and Brinkhurst, 1997 and unpublished data) but only one endemic tubificid is known from there so far. Three tubificids (Ainudrilus stagnalis, Ainudrilus billabongus and Antipodrilus magellenis) are known only from inland and northern Australia so far, but so few localities have been examined in these regions that it is difficult to speculate what further work will reveal.

The Australian Tubificidae seem to have a different biogeographic history to the apparently Gondwanan Phreodrilidae (Pinder and Brinkhurst, 1997). Antipodrilus appears most similar to genera that are widespread in the northern hemisphere but absent in Africa and South America (Brinkhurst, 1991). The new rhyacodriline genera, Breviatria and Biprostatus, are of uncertain affinity as the phylogenetic relationships are unclear in this possibly paraphyletic subfamily. Other endemic rhyacodrilines are members of a
cosmopolitan freshwater genus (*Rhyacodrilus* spp.) or appear to be allied to marine forms (*Ainundrillus* spp.) or are only tentatively assigned to a widespread genus whose monophyly is uncertain (*Rhzodrilus arthingtonae*). As almost nothing is known of the oligochaete fauna of southeast Asia and New Zealand, little comment can be made about affinities within the Australasian region.

**Acknowledgements**

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**References**


Invertebrate Advisory Committee, 1994. *Interim list of native invertebrates which are rare or threatened in Tasmania. Parks and Wildlife Service: Tasmania.*


Note in proof:
Recent survey work by Paul McEvoy (Australian Water Quality Centre) has revealed the presence of the cosmopolitan tubificids Potamothrix bavariensis, Aulodrilus limnobius, Aulodrilus pigueti and Branchiura sowerbyi in South Australia.
NEW AUSTRALIAN SPECIES OF OECETIS ALLIED TO O. COMPLEXA
KIMMINS (TRICHOPTERA: LEPTOCERIDAE)

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Abstract


Seven new species of long-horned caddisfly together with Oecetis complexa Kimmins form a discrete set in the Australian Oecetis fauna, here called the complexa-group, based on wings with a long footstalk on Fork 1, male inferior appendages four-lobed, and phallus with paired spiny parameres. Characteristics of this group appear to conflict with the placement of Oecetis complexa in the most recent subgeneric and species group classification of world Oecetis.

Introduction

Long-horned caddisflies of the cosmopolitan genus, Oecetis McLachlan, 1877 (Trichoptera: Leptoceridae: Leptocerinae), are diverse and often abundant in lotic and lentic waters throughout Australia. Neboiss (1986) listed 19 Australian species in the Atlas of Trichoptera of the SW Pacific — Australian Region and, in another work, described a further six (Neboiss, 1989). These last species, with several species from New Guinea and Indonesia, he placed in a ‘reticulata-group’, distinguished by males having a dorsal ‘shield’ (usually with reticulate cuticular sculpture) overhanging the terminal abdominal segments. Many additional undescribed Australian species have been represented in museum collections for several years. The present work, the first part in a review of the genus in Australia, deals with Oecetis complexa Kimmins and seven new closely allied species, here called the complexa-group. The remaining 18 described species and around 40 new species are to be reviewed in subsequent works.

Treatment of the Australian Oecetis fauna in isolation from the world fauna is insular. A classification of world Oecetis in an unpublished thesis by Chen (1992), based on a phylogenetic analysis, divided the genus into four subgenera, all further divided into species groups. According to Chen, three of the four subgenera are represented in Australia, each by one species group. Neboiss’ (1989) ‘reticulata’-group species share the derived features of the larger worldwide group to which Chen assigned them, as do also a large group of Australian species, among them the very common and widespread O. pechana Mosely, which has wings with hair short and Fork 1 sessile, and in the male, forewing bearing patches of androconia (scales), and phallus with a single internal spiny paramere. Chen’s assignment of the remaining Australian species to one subgenus is questionable. Oecetis complexa, which has males with paired spiny parameres, he grouped on the basis of putative sharing of the derived condition in which the male paramere spines are absent (and, plesiomorphically, the phallus symmetrical), with 12 other Australian species (all lacking parameres) and an assortment of Oriental, Palaearctic and Neotropical species. Within this subgenus, O. complexa was assigned to a species group sharing the feature RP1,2 divided at about one-tenth the length of the forewing (i.e., Fork 1 very short), and within the group, clustered with O. parka Mosely and O. inscripta Kimmins, on the basis of sharing the derived feature of ‘inferior appendages with basodorsal arms prominent.’ Since the basis of subgeneric placement is rejected here, for the present a new complexa-group is recognised in the Australian fauna, defined by wings with short hair on veins, the forewing (Fig. 25) with Fork 1 short, its the footstalk about as long as the fork; in males, the inferior appendages comprising four lobes, and the phallus with paired spiny, often complex and asymmetrical, parameres (Figs 26–33).

Material and methods. Specimens were prepared for study following methods used by Wells (1990) for micro-caddis flies (Hydroptilidae).
Although females have been sorted into vials with males of some species, many are so similar that until verified by breeding or rearing, the associations are considered only tentative. Thus, females are not described here.

Depositories are abbreviated as follows: ANIC, the Australian National Insect Collection, Canberra, Australian Capital Territory; BMNH, the Natural History Museum, London, England; OSS, Office of the Supervising Scientist (now ERISS, Environmental Research Institute of the Supervising Scientist), Northern Territory; NMV, Museum Victoria, Melbourne, Victoria; NTM, Northern Territory Museum and Art Galleries, Darwin, Northern Territory; and QM, Queensland Museum, Brisbane, Queensland. ‘ARR’ and ‘ARRS’ are used for Alligator Rivers Region, Northern Territory and Alligator Rivers Region Survey (conducted by the OSS), respectively. ‘WTH’ numbers are Wet Tropics Heritage numbers from the study by Walker et al. (1993).

**Key to males of the Oecetis complexa-group**

1. Preanal appendages fused with tergum IX (e.g. Figs 7, 8).............................2

2. Preanal appendages free (Figs 17, 20, 23).............................................6

3. Tergum X produced distally to form paired horn-like sclerotised spines twisted ventrally around the phallus (Figs 14, 15)........O. uptoni sp. nov.

4. Tergum X not greatly produced......................................................................3

5. Tergum X, in dorsal view, shallowly concave apically; in ventral view, mesal margins of inferior appendages obliquely slanted to form deep V (Fig. 3).............................................................................................................O. complexa

6. Tergum X with a more or less V-shaped excision (Figs 5, 8), although apices of lobes may be convergent........................................4

7. Apices of distal lobes of tergum X convergent in dorsal view (Fig. 8); in ventral view, basodorsal lobe of inferior appendages distally obliquely angled to shallow U-shaped mesal concavity (Fig. 9)........................................O. obliqua sp. nov.

8. Apices of distal lobes of tergum X divergent in dorsal view (Figs 5, 11); in ventral view, basodorsal lobes of inferior appendages separated by a deep U-shaped concavity (Figs 6, 12)..................................................5

9. Parameres terminating in a pair of equal length darkly sclerotised spines (Figs 10–12, 28); lobes formed by bisection of tergum X obliquely truncate apically (Fig. 11)..........................................................O. adelaidica sp. nov.

10. Parameres with the second distal spine subapical (Figs 4, 27); lobes formed by bisection of tergum X tapered to apices (Fig. 5)..................O. paracomplexa sp. nov.

11. Inferior appendages in ventral view with basoventral lobe forming a pair of parallel ‘pillars’ (Fig. 24); in lateral view, main body and basodorsal lobe about equal length and thickness (Fig. 22)......................O. parallela sp. nov.

12. Inferior appendages in ventral view with basoventral lobe not pillar-like (Figs 18, 21); in lateral view, main body far broader than the finger-like basodorsal lobe (Figs 16, 19)..............................................7

13. In lateral view, main body of inferior appendages about equal width throughout length, truncate apically, somewhat elasper-like in ventral view (Figs 16, 18)................................................O. blythi sp. nov.

14. In lateral view, main body of inferior appendages broad and irregular in shape, forming stout lobes in ventral view (Figs 19, 21)........O. glebula sp. nov.

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**Oecetis complexa** Kimmins

Figures 1–3, 26, 34

**Oecetis complexa** Kimmins in Mosely and Kimmins, 1953: 284.

**Material examined.** **Queensland:** holotype male, Marnewick Pk, nr Wyberba, 10 Oct 1973, A. Neboiss (NMV); male, female, Middle Cludie River, Iron Ra., 2–9 Oct 1974, M.S. Moulds (NMV); male, Iron Range, 16 Oct 1974, M.S. Moulds (NMV); male, female, 16 km W of Ravenshoe, 2 Jan 1975, M.S. Moulds (NMV WTH-1360); male, Gordon Creek, Iron Ra., 16 Oct 1975, M.S. Moulds (NMV); male, female, Alice River, Hervey Range River, 25 km W of Goodna, 29 May 1979, R. Daniels (NMV); male, Jamboree Heights, Brisbane, 6 Oct 1979, G. Daniels (NMV); 2 males, Mothar Mtn, 12 km SE of Girraween Natl Pk, nr Wyberba, 10 Oct 1973, A. Neboiss (NMV); male, female. Middle Cludie River, Iron Ra., 2–9 Oct 1974, M.S. Moulds (NMV); male, Iron Range, 16 Oct 1974, M.S. Moulds (NMV); male, female, 16 km W of Ravenshoe, 2 Jan 1975, M.S. Moulds (NMV WTH-1360); male, Gordon Creek, Iron Ra., 16 Oct 1975, M.S. Moulds (NMV); male, female, Alice River, Hervey Range River, 25 km W of Goodna, 29 May 1979, R. Daniels (NMV); male, Jamboree Heights, Brisbane, 6 Oct 1979, G. Daniels (NMV); 2 males, Mothar Mtn, 12 km SE of
Figures 1–9, *Oecetis* species, male genitalia, lateral, dorsal and ventral views: 1–3, *O. complexa* Kimmins; 4–6, *O. paracomplexa* sp. nov.; 7–9, *O. obliqua* sp. nov.

Gympie, 29 Oct 1980, A. Neboiss (NMV); male, female, Tinaroo Dam, Nov 1982, T. Hinger (NMV); male, female, Booloumba Creek, 8 km SW of Kenilworth, 26°39'S 152°39'E, 12 Dec 1984, G. Theischinger (NMV); male, female, Booloumba Creek, 8 km SW of Kenilworth, 26°39'S 152°39'E, 12 Jan 1986, G. Theischinger (NMV); male, female, Emu Creek, State Forest nr Benarken, 26°53'S 152°08'E, 15 Jan 1986, G. Theischinger (NMV); 2 males, Crows Nest Falls, N of Toowoomba, 27°14'S 152°07'E, 18 Jan 1986, G. Theischinger (NMV); 3 males, 12°44'S 145°16'E, Claudie River, Iron Range Ntl Pk, 25 km NW Lockhart River, 10 Nov 1988, K. Walker (NMV); males, females, 17°08'S 145°44'E, Mulgrave River, 8 km NW Gordonvale, 15 Nov 1988, K. Walker (NMV WTL1359). New South Wales: male, Blandford, 8 Oct 1976, M.S. Moulds (NMV); male, Clarence River, at Yates Crossing, 26 Oct 1981, Wells and Carter (NMV); male, 3 females, Swan Crossing nr Comboyne, 13 Feb 1999, G. Theischinger (ANIC). Victoria: male, Morrison, Moorabool River, 25 Mar 1953, A. Neboiss (NMV); 3 males, Greendale, 6 Jan 1956, Neboiss (NMV); male, Warrandyte, Yarra River, 1 Feb 1959, Neboiss (NMV); male, Delatite, 10 Dec 1962, Neboiss (NMV); male, female, Thurra River, Cape Everard, 22 Mar 1970, A. Neboiss (NMV); male, Tyers River, Site 22, 24 Feb 1974 (L.R.E.S.) (NMV); males, females, Otway Ra., East Branch Barwon River outflow from
Diagnosis. The male genitalia of *O. complexa* share with *O. paracomplexa* sp. nov., *O. obliqua* sp. nov., *O. uptoni* sp. nov., and *O. adelaidica* sp. nov., the derived states of preanal appendages fused with tergum X, and slender elongate lateral lobes on the inferior appendages. *O. complexa* is distinguished from these other species by other features of the male genitalia: the inferior appendages are separated ventrally by a deep, V-shaped cleft (Fig. 3) in contrast to the U-shaped separation of the other species and the basodorsal lobe is broad when viewed laterally (Fig. 1); on tergum X, the proximal part is somewhat rectangular, the distal lobes separated by a broad concavity (Fig. 2) and extended distally to form a pair of spiny structures; on the phallus, the parameres have a laterobasal spine and, more distally, a small black dorsal spine proximal to the darkly sclerotised acute apical spine.

Distribution (Fig. 34). Widespread in eastern Australia, with an anomalous record from each of South Australia and northern Western Australia.

Remarks. New figures of the male genitalia (Figs 1–3, 26) are supplied to aid comparisons.
Oecetis paracomplexa sp. nov.
Figures 4-6, 27, 35

Material examined. Holotype. Male, North Queensland, Middle Claudie River, 29 Jun 1982, Schneider and Daniels (NMV T-17393).
Paratypes. Queensland: male, same data as for holotype (NMV); male, Lockerbie area, Cape York, 13-27 Apr 1973, S.R. Monteith (ANIC); male, Dulhunty River, at Telegraph Crossing, 10 Feb 1992, D. Cartwright and A. Wells (QM).

Other material examined. Western Australia: male, 22°23'S 117°56'E GPS, 37 km NNE of Tom Price, 6 Oct 1995, D.C.F. Rentz and P.J.M. Greenslade (ANIC).

Diagnosis. O. paracomplexa sp. nov. shares with O. complexa, O. obliqua, O. uptoni and O. adelaidica, the derived states of preanal appendages fused with tergum X, and slender elongate lateral lobes on the inferior appendages. In general genital form it most closely resembles O. complexa, but differs in that the inferior appendages have a U-shaped basal separation ventrally, the basodorsal lobe narrowly digitiform in lateral view, and tergum X in dorsal view deeply divided to form 2 divergent triangular lobes.

Description. Genitalia, Figs 4-6, 27. Segment IX narrow middorsally and ventrally, broadly rounded laterally; preanal appendages slightly tapered apically, fused to tergum X. Tergum X wide at base, bifid almost throughout length, apices of lobes distally divergent. Inferior appendages in ventral view with main body slender, basoventral lobe short and obliquely truncate, in lateral view basodorsal lobe and a small median lobe digitiform. Phallus (Fig. 27) short, smoothly curved downwards, relatively simple with the fused parameres and phallobase forming a short, broad, sclerotised cover, distally divided into 2 subequal spines.

Etymology. Named for its resemblance to O. complexa; Latin — para — like.

Distribution (Fig. 35). Far northern Queensland and the Hamersley Range, Western Australia.

Oecetis obliqua sp. nov.
Figures 7-9, 28, 36


Diagnosis. Oecetis obliqua shares with O. complexa, O. paracomplexa, O. adelaidica and O. uptoni, the derived states of preanal appendages fused with tergum X, and slender elongate lateral lobes on the inferior appendages, but is distinguished by the short, spiny convergent distal lobes on segment X and the broadly oblique distal margin of the basoventral lobes of the inferior appendages in ventral view.

Description. Genitalia. Figs 7-9. Segment IX broadest ventrolaterally; preanal appendages fused with tergum X, Tergum X bifid, the short acute distal lobes being separated basally by a V-shaped cleft, their apices converging. Inferior appendages in ventral view with basoventral lobes broad-based and obliquely truncate...
apicomesally, in lateral view main body narrow, about same width as dorsobasal lobe, but longer. Phallus (Fig. 28) with parameres forming a pair of stout, sclerotised lateral spines, the base of the phallus is irregular, making interpretation difficult, but there appears to be no clear phallobase such as occurs in O. glebula sp. nov. or O. blythi sp. nov.

Etymology. Descriptive of the obliquely angled apicomesal margin of the inferior appendages; Latin — obliquus — slanting.

Distribution (Fig. 38). Northern Queensland.

Oecetis adelaidica sp. nov.

Figures 10–12, 29, 37


Paratype: Northern Territory: male, same data as for holotype.

Diagnosis. Oecetis adelaidica shares with O. complexa, O. paracomplexa, O. obliqua and O. uptoni, the derived states of preanal appendages fused with tergum X, and slender elongate lateral lobes on the inferior appendages. It is unique in having the parameres on the phallus terminating in a pair of more or less equal length darkly sclerotised spines.

Description. Genitalia, Figs 10–12, 29. Abdominal segment IX subquadrate in ventral view, the preanal appendages fused with tergum X, and inferior appendages fused with tergum X, and inferior appendages with lateral lobes slender and elongate. Inferior appendages in ventral view divided by a deep U-shaped concavity, the basoventral lobe apically truncate, the main body slender, curved; a small setate digitiform inner lobe visible in dorsal view probably represents the basodorsal lobe. Phallus (Fig. 29) relatively narrow, curved, fused parameres and phallobase forming a dorsal sheath, on each side divided apically into a pair of equal sclerotised spines, basally a small lateral spur, its tip sclerotised.

Etymology. Named for the Adelaide River, the type locality.

Distribution (Fig. 37). Adelaide River, Northern Territory.

Oecetis uptoni sp. nov.

Figures 13–15, 30, 38

Material examined. Holotype. Male, Northern Territory, 12°42′S 130°58′E, Berry Springs. 31 Mar 1992, A. Wells and J. Webber (NTM).

Paratypes. Northern Territory: 2 males, same data as for holotype (NTM); male, ARR Magela Creek at Rum pipeline, 12 Mar 1991, P. Dostine (NTM); male, ARR Magela Creek at Rum pipeline, 18/19 Mar 1991, P. Dostine (NTM); 2 males, 12°27′S 131°03′E, Howard Springs, 25 Mar 1991, de Jong, van Achtberg and Wells (NMV); 2 males, Holmes Jungle, 7 Apr 1991, Horak, Upton and Wells (ANIC); 2 males, Baroalba Springs, 12°44′S 132°49′E, 16 Jan 1992, Wells, Webber and Bickle (NTM); male, same locality, 4 Mar 1992, Wells (NTM); 2 males, Berry Springs, 12°42′S 130°58′E, 31 Mar 1992, Wells and Webber (NTM); male, 12°42′S 132°57′E, Kakadu Natl Pk, Magela Creek, OSS Site/009, 24 Apr 1992, A. Wells and J. Webber (NTM).

Other material examined. Northern Territory: female, same data as for holotype (NTM); female, Holmes Jungle, 7 Apr 1991, Horak, Upton and Wells (ANIC); female, 12°42′S 132°57′E, Kakadu Natl Pk, Magela Creek, OSS Site/009, 15 Aug 1991, A. Wells and J. Webber (NTM); female, Berry Springs, 12°42′S 130°58′E, 31 Mar 1992, Wells and Webber (NTM); 2 males, N2 ARR, Magela Creek at Rum Pipe, 30/31 Mar 1992, P. Dostine (NTM); 4 males, same loc. and collector, 6/7 Apr 1992 (NTM); male, Magela Creek, 23/24 Mar 1992, P. Dostine (NTM).

Diagnosis. Oecetis uptoni shares with O. complexa, O. paracomplexa, O. obliqua and O. adelaidica, the derived states of preanal appendages fused with tergum X, and inferior appendages with lateral lobes slender and elongate. It most closely resembles O. complexa, having tergum X modified distally to form spines, but the spines are more elaborate and curve under the phallus. Among all complexa-group species, it can be recognised immediately by the sharply down-turned paramere spines on the phallus.

Description. Genitalia, Figs 13–15, 30. Segment IX more uniform in length than other complexa-group species; preanal appendages small, club-shaped, free. Tergum X broad-based, deeply divided in distal two-thirds, forming spines that curl under the phallus. Inferior appendages broad-based, basoventral lobes almost rounded anteromesally, main body forming slender lobes distally, with a short dorsobasal lobe visible in lateral view. Phallus (Fig. 30) membranous and curving ventrally, parameres short sclerotised, each in form of a sharp down-turned spur with an acute dorsal spine.

Etymology. Named for Murray Upton, in appreciation of his support during my several years in the Northern Territory.

Distribution (Fig. 38). Northern Northern Territory.

Remarks. Oecetis uptoni was not among the numerous species of Oecetis collected in a
1988–1989 survey of the Trichoptera of the Alligator Rivers Region (Wells, 1991), and despite much subsequent collecting in the ARR, especially on Magela Creek, only very few specimens have been taken. The real or apparent rarity of this species illustrates a curious phenomenon noticed during regular sampling at a Magela Creek site over the years 1991–1993. Several species were taken once or twice only over 14 months of standardised weekly light trap-sampling, while other species were collected regularly almost throughout the period. All specimens of *O. uptoni* were taken in March and April, generally the end of the wet season in this seasonal monsoon area. This species itself may be strongly seasonal. Alternatively, our sampling successes may reflect recruitment from upstream (?escarpment) populations, and failure to establish as the water flow drops. In contrast, our sampling efforts added so much interesting material to the NMV collection.

### Oecetis blythi sp. nov.

Figures 16–18, 31, 39


Paratypes. New South Wales: male, same data as holotype (NMV); male, Clarence River at Yates Crossing, 26 Oct 1981, Wells and Carter (NMV). Queensland: 4 males, Tinaroo Dam (nr Cairrie Creek), 22 Jun 1971, E.F. Rick (ANIC); 6 males, Upper Ross River, below weir, SW Townsville, 8 May 1979, A. Wells (NMV); male, Emu Creek State Forest nr Benarkin, 26°53'S 152°08'E, 15 Jan 1986, G. Theisehinger (NMV); male, Crowe’s Nest Falls, N Townsvi, 27°14'S 152°07'E, 18.1.1986, G. Theisehinger (NMV).

Other material examined. Queensland: female, same data as holotype (NMV); male, 36 km S of Miriam Vale, 25 May 1971, E.F. Rick (ANIC); 3 females, Tinaroo Dam (nr Cairrie Creek), 22 Jun 1971, E.F. Rick (ANIC); male, South Pine River, 8 km W of Samford, 21 Oct 1980, A. Neboiss (NMV); 10 females, Clarence River at Yates Crossing, 26 Oct 1981, Wells and Carter (NMV); male, Blackdown Tableland Natl Pk, Nov 1982, T. Hinger (NMV); 3 females, Emu Creek State Forest nr Benarkin, 26°53'S 152°08'E, 15 Jan 1986, G. Theisehinger (NMV); male, 3 females, Emu Creek, State Forest nr Benarkin, 26°53'S 152°08'E, 15 Jan 1988, G. Theisehinger (NMV); male, 3 females, Tinaroo Pines Caravan Park, 10 Jun 1972, N. McFarland (NMV); 4 males, 13 females, Alice River, Hervey Range Road, 25 km W Townsville, 8 May 1979, A. Wells (NMV); males, females, Obi Obi Creek, 8 km SW Mapleton, 23 Oct 1980, A. Neboiss (NMV), Victoria: 3 males, Swan Lake, 30 km NW of Portland, 27 Feb 1976, P.A. Meyer (NMV); male, Wyperfield Natl Pk, Lake Werribee, 6 Apr 1977, J. Blyth (NMV); 3 males, 4 females, Lake Albacutya, 16 Jan 1980, J. Blyth (NMV). South Australia: male, female, North Adelaide, 28 Nov 1975, M. Davies (NMV).

**Diagnosis.** In common with *O. glebula* and *O. parallela*, *O. blythi* has the preanal appendages free and lateral lobes of the inferior appendages stout. The latter structures are somewhat intermediate in size between the form of the other two species, and the ventral lobes of the inferior appendages are subtriangular in ventral view, rather than rounded as in *O. glebula* or subrectangular as in *O. parallela*. *Oecetis blythi* can be distinguished readily in ventral view by the pair of slender processes representing the basodorsal lobe, on the inner side of the inferior appendages, lying almost parallel to the phallos.

**Description.** Genitalia, Figs 16–18, 31. Segment IX short middorsally, relatively long laterally and ventrally; preanal appendages elongate. Tergum X reduced to a short rounded lobe. Inferior appendages short and rounded mesoventrally; main body stout, short, the inner apical angle spur-like; in lateral view basodorsal lobe setate, digitiform, in ventral view, lying alongside the phallos. Phallus (Fig. 31) elongate with parameres forming a complicated set of spines, including 1 dorsal pair which almost equal in length and are membranous and free for most of the length of the phallos; basally a slender curved spine; dorsally a bract-like phallobase.

**Etymology.** Named for John Blyth whose collecting efforts added so much interesting material to the NMV collection.

**Distribution** (Fig. 39). Disjunct: mainly Townsville area of north-eastern Queensland, through north-eastern New South Wales to western Victoria; a single record from North Adelaide, South Australia (probably from the Torrens River).

### Oecetis glebula sp. nov.

Figures 19–21, 32, 40

**Material examined.** Holotype. Male, Western Australia, Ellendale, Greenough River, E of Geraldton, 11 Sep 1974, K. Carnaby (NMV T 17396).

Paratypes. Western Australia, 2 males, same data as holotype (NMV); 3 males, Millstream Crossing Pool, 21 Oct 1970, J.C. Cardale (ANIC); 5 males, 10 females, Lockyer Gorge, Harding River, Pilbara, 19 Oct 1979, J. Blyth (NMV); male, female, Fortescue Falls, Hamersley Ra. Natl Pk, 27 Oct 1979, J. Blyth (NMV).

Other material examined. Western Australia: 2 females, Millstream Crossing Pool, 21 Oct 1970, J.C. Cardale (ANIC); male, N of Carnarvon, De Grey Station Road, 29 Jun 1972, N. McFarland (NMV);

Diagnosis. In common with O. blythi and O. parallela, O. glebula has the preanal appendages free and lateral lobes of the inferior appendages stout. It is clearly distinguished from O. blythi and O. parallela by the almost parallel alignment, in ventral view, of the lobes of the inferior appendages and pair of parameres of unequal length lying dorsally along the length of the phallus.

Description. Genitalia, Figs 19–21, 32. Segment IX short laterally and dorsally; preanal appendages free, elongate. Tergum X reduced to a short truncate lobe. Inferior appendages in ventral view, and parameres in form of a set of unequal sclerotised spines ventral to the sheathing phallobase.

Etymology. Descriptive of the almost parallel alignment, in ventral view, of the lobes of the inferior appendages.

Distribution (Fig. 41). Far north-eastern Queensland, particularly in the Atherton Tableland area.
Figures 34–41, collecting sites for Oecetis complexa-group species: 34, O. complexa Kimmins; 35, O. paracomplexa sp. nov.; 36, O. obliqua sp. nov.; 37, O. adelaidica sp. nov.; 38, O. uptoni sp. nov.; 39, O. blythi sp. nov.; 40, O. glebula sp. nov.; 41, O. parallela sp. nov.
Discussion
Within the Australian Oecetis fauna, species of the complexa-group are distinct and possibly so in the world fauna too. It is apparent that these Australian taxa are not accommodated in Chen’s (1992) scheme and thus further assessment of the group in the broader context is needed.

Species of the complexa-group are found more or less peripherally on the Australian continent (Figs 34–41), although as yet they are unknown from south-western Western Australia or from Tasmania. Several species appear to be quite widespread but most have been collected in the more northerly parts of Australia. The curiously disjunct distributions seen here in O. complexa, O. paracomplexa and O. blythi are a recurrent feature among species in the Australian Oecetis fauna. The veracity of the identifications has been checked carefully. Possible explanations are gaps in sampling (real, but unlikely to be the full explanation given the intensity of collecting Australia wide), high vagility, or loss of diversity in parts of the continent as a result of aridification and/or recent agricultural or pastoral practices. An alternative explanation may lie in differences in the biology of the species.

Acknowledgements
My thanks go to Arturs Neboiss who made available to me the material from Museum Victoria and checked through a first draft of the manuscript, and to the editor, for critical comments that led to improvements.

References


THAUMATELSONINE STENOThOIDS (CRUSTACEA: AMPHIPODA): PART 1

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Abstract

The Thaumatelsonidae were separated from Stenothoidae by Walker (1906) and reduced to a subfamily of Stenothoidae by Barnard (1972). The history of the subfamily is reviewed and its included genera placed in two divisions. All genera and species of the less specialised division are revised here. Four new genera are erected, Raukumara, Ptychotelson, Pyenopyge and Yarra. Raumahara waroona and Yarra unguiserrae are described as new species. Raumahara rongo Barnard placed in the newly erected genus Raukumara. All belong to this thaumatelsonine group but it is shown that similar structures in Pyenopyge are homoplasies which developed independently. This genus is removed from Thaumatelsoninae.

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Introduction
While Walker (1906) was studying the amphipods collected during the Discovery Antarctic expedition, he noted a totally unusual telson-shape and created a new genus for which he coined the generic name Thaumatelson (from Greek "thauma", meaning "wonderful"). Gurjanova (1938) erected Parathaumatelson for Metopella nasica Stephensen, 1927. At the same time she created the family Thaumatelsonidae, comprising her genus, Thaumatelson Walker, 1906, Prothaumatelson Schellenberg, 1931 and Pseudothaumiatelson Schellenberg, 1931, all having a very unusual urosome.

Barnard (1964: 71) was clearly uneasy with the generic division within the Thaumatelsonidae (and indeed the Stenothoidae s.l.) and later (1972b: 158) opined "...the Stenothoidae being unnaturally systematised...at present signify not phyletic lines but grades of evolution..." Barnard (1972a: 318) erected Raumahara and in 1972b noted (p. 160) "...this genus bridges the differences between Stenothoidae and Thaumatelsonidae to such an extent that the two families become qualitatively inseparable. The concept of a subfamily 'Thaumatelsoninae' remains useful." Barnard had studied this mainly Australian group while having at his disposal very few specimens.
Comparison of new material, studied at Museum Victoria (Melbourne), the Australian Museum (Sydney) and the Smithsonian Institution (Washington) revealed some errors in descriptions and drawings of this group. New taxa could be erected, others removed. This paper deals with only one group of thaumatelsonines, those that share a proximally thickened, three-dimensionally inserted and spoon-shaped telson (Table 1). Others will be discussed in later contributions. Similarities and differences between the groups are discussed in Conclusions at the end of this contribution.

The habitus was observed in glycerine, under stereo- as well as phase contrast microscope; dissected parts were mounted in Faure’s medium.

Table 1. Species treated in this paper, with current generic placement.

<table>
<thead>
<tr>
<th>Original combination</th>
<th>Current generic placement</th>
</tr>
</thead>
<tbody>
<tr>
<td>Chucullha alta Barnard, 1974</td>
<td>Chucullha</td>
</tr>
<tr>
<td>Chucullha werea Barnard, 1974</td>
<td>Chucullha</td>
</tr>
<tr>
<td>Pseudolhaumatelson patagonicum Schellenberg, 1931</td>
<td>Pseudolhaumatelson</td>
</tr>
<tr>
<td>Raumahara virdurorum Krapp-Schickel and Andres, 1998</td>
<td>Ptychotelson</td>
</tr>
<tr>
<td>Prothaumatelson carinatum Shoemaker, 1955</td>
<td>Ptychotelson</td>
</tr>
<tr>
<td>Raumahara dertoo Barnard, 1972a</td>
<td>Raumahara</td>
</tr>
<tr>
<td>Raumahara judithae Moore, 1981</td>
<td>Raumahara</td>
</tr>
<tr>
<td>Raumahara noko Barnard, 1974</td>
<td>Raumahara</td>
</tr>
<tr>
<td>Raumahara waroona sp. nov.</td>
<td>Raumahara</td>
</tr>
<tr>
<td>Raumahara rongo Barnard, 1972b</td>
<td>Raumahara</td>
</tr>
<tr>
<td>Pseudolhaumatelson cyproides Nicholls, 1938</td>
<td>Thaumatelsonella</td>
</tr>
<tr>
<td>Thaumatelsonella kingelepha Rauschert and Andres, 1991</td>
<td>Thaumatelsonella</td>
</tr>
<tr>
<td>Yarra unguiserra gen. et sp. nov.</td>
<td>Yarra</td>
</tr>
</tbody>
</table>

Taxonomy

Key to thaumatelsonine species with spoon-shaped telson

1. Gnathopod 2 chelate..........................................................2
   — Gnathopod 2 subchelate..................................................7
2. Gnathopod 1 subchelate........................................................ 3
   — Gnathopod 1 chelate........................................................ 4
3. Antenna 1 article 2 swollen............................................... Raumahara
   — Antenna 1 article 2 slender, ordinary................................ Raumahara
4. Uropod 3 ramus article 2 well developed; antenna 2 article 3 subquadrate
   — Uropod 3 ramus article 2 reduced; antenna 2 article 3 ovoid...........5
5. Urosomite 1 dorsal hump reaching 50% of telson..................... Raumahara dertoo
   — Urosomite 1 dorsal hump reaching <25% telson.......................6
6. Uropod 1 rami unequal, uropod 3 ramus article 1 with 1 seta shorter than uropod 3 tip; gnathopod 2 propodus proximally bulbous...

- Uropod 1 rami subequal, uropod 3 ramus article 1 with long seta sitting upon rounded tip of uropod 3; gnathopod 2 propodus proximally slender...

7. Antenna 1 articles 1 and 2 swollen but not nasiform; gnathopods 1 and 2 rectangularly lengthened, palms similarly oblique...Chucullba warea

- Antenna 1 article 1 nasiform, lengthened, considerably or totally overlapping article 2; gnathopods not as above...

8. Gnathopods 1 and 2 propodus with parallel margins, palms much shorter than posterior margin, palmar angle on gnathopod 2 more strongly developed than on gnathopod 1...

- Gnathopods 1 and 2 propodus margins not parallel, palms not as above...

9. Antenna 1 article 1 strongly nasiform, geniculate; gnathopods 1 and 2 dactyl strongly serrate...

- Antenna 1 article 1 strongly nasiform; gnathopod 1, 2 dactyl smooth...

10. Uropod 2 rami clearly unequal...

- Uropod 2 rami scarcely different...

11. Gnathopod 1 palp corner angular; basis of gnathopod 1 with many short setae; uropod 3 peduncle shorter than ramus article 1; ramus article 2 three times as long as wide...

- Gnathopod 1 palp corner rounded; basis of gnathopod 1 with long, dense setae; uropod 3 peduncle as long as ramus article 1 and as article 2; ramus article 2 about twice as long as wide...

**Raumahara** Barnard


*Type species. Raumahara dertoo* Barnard, 1972 (original designation).

**Diagnosis.** General habitus bivalve-like (fig. 1). Antenna 1 peduncular article 2 ordinary to swollen, with dorsal process more or less overlapping article 3; accessory flagellum of 1 article. Antenna 2 article 3 rectangularly shortened, ovoid or bulbous. Mandibular palp reduced to 1 short article, or lacking. Maxilla 1 palp biarticulate. Maxilla 2 plates ordinary (tandem), or outer plate riding up on inner one. Maxilliped outer plate present, different, short. Gnathopods 1 and 2 propodochelate-forcipate. Pereopods 3–7 basis rectilinear, dactylus on inner and outer surface with a row of stiff, short setae, distally ending in a second tip. Pereopod 4 elongate, usually same as pereopod 3. Urosomite 1 dorsally thickened to a fold vaulting over urosomite 2 and reaching or overlapping telson insertion. Transparent septae (or wings) on urosomite 3. Uropod 3 ramus clearly of 2 articles, or article 2 reduced or lacking. Telson horizontal, spoon-shaped, dorsally excavated; posterior end of urosomite 1 process possibly fitting in this excavation; proximally thickened, three-dimensionally coalesced with urosomite 3.

Table 2 tabulates differences between the four species now placed in this genus.

**Raumahara dertoo** Barnard

Figures 1, 18


*Type material. Volutotype. Western Australia, Cape Naturaliste, intertidal, common seaweeds, WAM (female, 1.55 mm).*

*Material examined. Paratypes. 6 specimens (USNM 230426).*


**Diagnosis.** Antennae 1 and 2 subequal. Antenna 1 peduncular article 2 ordinary or weakly swollen; accessory flagellum of 1 article. Antenna 2 article 3 ovoid. Ocular lobes short, acute. Mandibular palp lacking. Gnathopod 1 propodochelate; gnathopod 2 propodochelate, dactylus about one-third propodus. Urosomite 1 with thick fold vaulting over urosome and half of telson (fig. 1).
Table 2. Diagnostic characters distinguishing species of *Raumahara* Barnard.

<table>
<thead>
<tr>
<th>Character</th>
<th>R. noko</th>
<th>R. dertoo</th>
<th>R. judithae</th>
<th>R. waroona</th>
</tr>
</thead>
<tbody>
<tr>
<td>Antenna 1 peduncular article 2</td>
<td>overlapping article 3</td>
<td>weakly swollen</td>
<td>overlapping article 3</td>
<td>overlapping article</td>
</tr>
<tr>
<td></td>
<td>dorsally</td>
<td></td>
<td>dorsally</td>
<td>dorsally</td>
</tr>
<tr>
<td>Antenna 1 accessory flagellum</td>
<td>2 articles</td>
<td>1 article</td>
<td>2 articles</td>
<td>1 article</td>
</tr>
<tr>
<td>Antenna 2 peduncular article 3</td>
<td>subquadrat</td>
<td>ovoid</td>
<td>bulbous</td>
<td>suboval or bulbous</td>
</tr>
<tr>
<td>Mandibular palp</td>
<td>rudimentary</td>
<td>absent</td>
<td>absent</td>
<td>absent</td>
</tr>
<tr>
<td>Gnathopod 2 dactylus</td>
<td>30-33% propodus slender</td>
<td>30-33% propodus slender</td>
<td>40% propodus</td>
<td>33-40% propodus</td>
</tr>
<tr>
<td>Gnathopod 2 propodus proximally</td>
<td>&lt; 25% telson</td>
<td>50% telson</td>
<td>&lt; 25% telson</td>
<td>Slender to bulbous</td>
</tr>
<tr>
<td>Urosomite 1 hump</td>
<td>subequal</td>
<td>subequal</td>
<td>unequal</td>
<td>subequal</td>
</tr>
<tr>
<td>Uropod 1 rami</td>
<td>strong spines</td>
<td>small spines on peduncle</td>
<td>1 distal spine on peduncle</td>
<td>lacking spines or setae</td>
</tr>
<tr>
<td>Uropod 1 peduncle + rami</td>
<td>on peduncle + rami</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Uropod 3 rami article 1 apically</td>
<td>1 short seta or weak spine</td>
<td>1 long seta surpassing uropod 3 tip</td>
<td>1 seta shorter than uropod 3 tip</td>
<td>1 long seta sitting upon uropod 3 tip</td>
</tr>
<tr>
<td>Uropod 3 ramus article 2</td>
<td>well visible, strong</td>
<td>reduced? to absent</td>
<td>reduced? to absent</td>
<td>totally absent</td>
</tr>
<tr>
<td>Telson excavated</td>
<td>weakly</td>
<td>strongly</td>
<td>strongly</td>
<td>strongly</td>
</tr>
</tbody>
</table>


Figure 1. a, general habitus of Raumahara or Ptychotelson in normal position, where most parts of legs and antennae are hidden by the enlarged coxae; on anterior end thickened peduncle antenna 1, on posterior end thickened urosome plugging or protecting the filter groove.
b. Raumahara dertoo Barnard, urosome of 1.3 mm juvenile, showing the transparent "wings" connecting telson and uropod 3.
c. Raumahara dertoo Barnard, urosome of 1.5 mm adult; wings not visible as telson adjacent to uropod 3. Scale = 0.1 mm.
Uropod 3 ramus with long, visible seta subapically on article 1; article 2 may be prolongation on article 1, surpassing insertion of seta (fig. 1). Telson spoon-like, three-dimensional, proximally thickened and coalesced with urosomite 3 ventrally, depth in proximal half about two-thirds total length; directed horizontally.

Length 1.0–1.55 mm.

**Distribution.** Cape Naturaliste to Albany, south Western Australia; intertidal, common seaweeds.

**Biology.** Female ovigerous from September to November.

**Remarks.** Barnard’s assignment of this species to Stenothoidae was probably based on the lack of a nasiform process. Antenna 1 article 2 is subquadrate to weakly swollen; antenna 2 article 3 is not rectangular-slender but ovoid (drawn but not in diagnosis of Barnard, 1972a); and uropod 3 ramus consists apparently of 1 article (although article 2 may be the minute, thin prolongation next to a long and striking seta inserted subapically on article 1). Barnard’s drawings of the urosome never show the ventral margin of the vaulting process of urosomite 1 which is a very thick fold for fortifying the whole urosome dorsally, and probably also plugs the body posteroventrally if necessary. There are some (glandular?) ducts of unknown function on the dorsal margin of this process (fig. 1). The telson can be in contact with uropod 3 but can also be in an upright position when transparent septae on the dorsal margins of urosomite 3 and uropod 3 peduncle become visible (fig. 1).

**Raumahara noko** Barnard

Figures 2, 3


**Type material.** Holotype. South Australia, Pearson Island, in algae, 18–24 m. SAM C3535 (female, 1.6 mm, in alcohol).

**Material examined.** Western Australia, Walpole, ZMH K39213, K39214 (1 adult, 1.6 mm, on 2 slides); Albany, ZMH K38204 (2); Ceduna, ZMH K38206 (1); South Australia, Port Lincoln, ZMH K38207 (7); Kangaroo Island, Hartmann, ZMH K38783 (3); Tasmania, The Gardens, St Helens, from tide pools, G.C.B. Poore, Feb 1980, NMV J3278, (1 juvenile on slide).

**Diagnosis.** Antennae 1 and 2 subequal. Antenna 1 peduncular article 2 weakly swollen, with age increasingly vaulting over article 3 proximally; accessory flagellum of 2 articles. Antenna 2 article 3 exceptionally short, subquadrate to trapezoid. Ocular lobes strong, subacute. Mandibular palp reduced to 1 short but clearly visible article. Gnathopod 1 propodochelate. Gnathopod 2 propodochelate, slender, daectylus about 30% propodus length. Urosomite 1 with fold vaulting over urosomite 2 and one third of telson, less voluminous than in type species. Uropod 3 ramus with 2 robust articles. Telson like a very flat spoon, basally thickened, three-dimensionally coalesced with urosomite 3, directed and inserted horizontally.

Length 1.0–2.0 mm.

**Redescription.** Antenna 1 subequal to shorter antenna 2. Antenna 1 subequal to head + pereiopods 1+2 (dorsal length); peduncular articles 1 and 3 without process, article 2 dorsomedially slightly vaulting over article 3, extension depending on age, reaching as far as one third article 3, process bearing a duct and 1 long seta; ratio of lengths of articles 2 : 1 ≤ 0.5; article 3 longer than article 2 ventrally, subequal dorsally; accessory flagellum short, biarticulate; article 2 much narrower than basal article and with 1 long terminal seta; flagellum longer than peduncle, of 7 articles, aesthetascs present. Antenna 2 peduncular article 3 shortened, subquadrate, article 4 shorter than 5; flagellum subquadrate to peduncle, of 7 articles.

Upper lip ventrally notched, lobes rounded. Mandibular incisor well developed, with broad cusps; lacinia mobilis on left mandible broad, with major incisions, on right mandible with distal part finely serrated; raker spine row developed, 4 strong spines; molar cusp with 3 robust curved spines; palp clearly developed, of 1 short article; 1–2 setae apically (cf. fig. 2 in juvenile with 1 seta, fig. 3 in adult with 2 setae; cf. also Barnard, 1974: fig. 71 with 1 seta, on other drawings of mandible no palp shown). Lower lip inner lobes coalesced, mandibular lobes well developed. Maxilla 1 inner plate with 1 subapical seta; outer plate mediodistally setose, apically armed with 4 serrate robust spines, 1 stout simple spine and 1 thin, short and stiff one; palp biarticulate, extending beyond outer plate, with spines apically and medioapically. Maxilla 2 plates tandem-grouped; outer plate scarcely extending beyond inner one, apically with 3 setae (cf. fig. 3 here with Barnard, 1974: fig. 71 showing 4 setae), 1 on outer margin; inner plate with 2 long apical setae, on inner margin 1 shorter, stiff one mediodistally. Maxilliped inner plate reaching half length of ischiuom, with 1 seta and 2 spines apically; outer plate reaching 50% along merus (= palp article 1); with 2 setae apically, 2 medially; palp of 4 articles; length of merus and propodus subequal.
Figure 2. *Raumahara noko* Barnard, a, habitus 1.1 mm, b, anterior body of neonatus. c, sketch of mouthparts in situ. Antennae 1, 2 at scale = 0.1 mm. Mandible at scale = 0.05 mm.
Figure 3. *Raumahara noko* Barnard. Gnathopods 1, 2 at scale $x = 0.1$ mm; urosome (from 4 different specimens and in different shape of fixation; attention to the "wings" connecting uropod 3 with telson) at scale $y = 0.1$ mm; upper lip and maxilla 2 at scale $z = 0.05$ mm.
carpus, propodus distally and dactylus with inner article 3 (propodus) much narrower than article 2; propodus with parallel margins anter- and posteriorly, with 1 strong seta anteromedially and 2 weak ones distally; posterior margin slightly concave, length : breadth > 2 : 1; propodoschelate, palm armed with short setae; palmar corner with a pair of robust spines, tip of propodus upwards curved; daetynctus as long as palm, inner margin smooth, beset with few spines. Gnathopod 2 propodoschelate-foreipate. Coxa 2 expanded, anterior margin regularly convex, posterior one nearly straight, ventrally straight to rounded; posterior margin with single spines; ischium slim, longer than merus; carpus subtriangular, lobe with dense, short setae and longer, forward-curved spines; propodus slender, length ratio of dactylus : total propodus = 33–40% (in juvenile propodus relatively shorter, thus daetynctus more than one third propodus); terminally a hooked cusp and notch; palm with stiff setae; daetynctus also terminally hooked, matching well with the propodal notch; inner margin with similar setae; outer margin with 1 long seta.

Pereopods 3 and 4 slender, subequal, but carpus in pereopod 4 longer; daetynctus about half propodus length, hind margin on inner and outer surface with dense, stiff setae, at distal end of this row a second tip, thus daetynctus seemingly bifid. Coxa 3 more than twice as deep as broad; postero-distally some spines. Coxa 4 dominant, wider than deep, getting wider with age; front margin slightly convex, ventral margin straight, posterior margin strongly convex; depth anteriorly and posteriorly subequal. Pereopods 5–7 slender, ratios of corresponding articles only slightly different; daetynctus with prominent setal comb on anterior margin inside and outside. Coxae 5–7 short; coxa 5 trapezoid, weakly produced postero-distally; coxa 6 oblong, roundly produced posteriorly; coxa 7 blunt.

Gills and ostogonites on pereopods 2–5, not found on pereopods 6 or 7.

Uropods 1–3 extending less far posteriorly in succession. All rami (and distal regions of peduncles) with very short setae dorsally. Uropod 1 peduncle subequal or longer than subequal rami; peduncle with 3 spines; inner ramus inserted much less distally; outer ramus (extending the further and more distally inserted) with 1 strong medial spine. Uropod 2 peduncle as long as longer ramus, with 1 strong spine distally, 1 medially; inner ramus very little shorter and inserted more proximally; without spination. Uropod 3 peduncle + ramus about as long as peduncle of uropod 2; peduncle distally with 1 spine, subequal to biarticulate ramus; ramus article 1 > article 2, article 1 distally with 1 spine, article 2 nail-like, well developed. Large, transparent septum on urosomite 3 dorsally; on uropod 3 peduncle dorsally also a thin, transparent "wing".

Telson not reaching end of uropod 3 rami; basis situated under the vaulted urosomite 1 and fused with urosomite 3 medially (fig. 3); distally tapering, apex rounded, spoon-like, dorsolaterally and basally with sclerotic elasps; with 1–2 pairs of setae. Telson not always in contact with body as urosomite 3 has 2 thin plates in the gap (figs 2, 3), and uropod 3 and telson may be retracted (and protected?) between them (cf. Barnard, 1974: fig. 71, uropod 3). (This may be what Barnard (1974: 113) meant by "urosomite 3 very distinct.")

Colour. Antenna 1 articles 1 and 2, eyes, and broad dorsal stripe on periconites 1–7 brick-red, mesosome and urosome orange, gnathopods 1 and 2 and pereopods 3–7 yellow-green, coxae yellow.

Distribution. South coast of Australia from extreme west to Tasmania. Littoral and sub-littoral, 18–24 m (Barnard, 1974) including tide pool.

Biology. Eggs in December to January.

Remarks. Having a well developed uropod 3 article 2, this species is the most plesiomorphic within its genus. Also, the flat spoon-like telson, rectangular antenna 2 article 3 and mandibular palp, though very reduced, confirm this impression. The other species, R. dertoo, R. judithae and R. waroona have reduced or no second article on uropod 3 ramus, an ovoid to bulbous antenna 2 article 3 and no mandibular palp. The process on antenna 1 article 2 shows a (glandular?) duct and a long sensory seta; the process on urosomite 1 has some (glandular?) duets dorsally.

This species was described from a single female of 1.6 mm and has not been reported since. As Barnard's description is very short a detailed redescription is given.

Raumahara judithae Moore
Figures 4, 5

Raumahara judithae Moore, 1981: 959, figs 14, 15.

Type material: Holotype. Tasmania, Tinderbox, from algal pool, 3–4 m, BMNH 1980:187 (female, 1.5 mm).
Figure 4. *Raumahara judithae* Moore. Habitus female, 1.8 mm; antenna 1, 2, maxilliped at scale $x = 0.1$ mm; maxillae 1, 2 at scale $y = 0.1$ mm; mouthpart-complex (mandible, upper and lower lip) at scale $z = 0.1$ mm.
Figure 5. Raumahara judithae Moore. Gnathopods 1, 2, urosome at scale = 0.1 mm; pereopods 3, 4 at scale = 0.2 mm; uropod 3 in free enlargement.
Material examined. Western Australia, Albany, ZMH K38785 (2); South Australia, Kangaroo Island, ZMH K38210 (3).

Diagnosis. Antenna 1 peduncular article 2 nasi-form, swollen; accessory flagellum with 2 articles. Antenna 2 article 3 bulbous. Mandibular palp lacking. Gnathopod 1 propodochelate. Gnathopod 2 propodochelate, propodus strongly bulging anteroproximally and less slender than in other species; dactylus about 40–50% of propodus length. Mandibular palp lacking. Gnathopod 1 propodochelate. Gnathopod 2 propodochelate, propodus strongly bulging anteroproximally and less slender than in other species; dactylus about 40–50% of propodus length. Urosomite 1 with fold vaulting over urosomite 2 and insertion of telson; uropod 3 ramus with 2 articles, article 2 minute, vanishing, spiniform, articulation between article 1 and article 2 vanishing; telson boat-like, three-dimensional, proximally coalesced with urosomite 3, inserted horizontally.

Length 1.2–2.0 mm.

Distribution. Tasmania; Kangaroo Island (South Australia), Albany (Western Australia); 3–4 m depth.

Biology. Female ovigerous in November and December.

Remarks. Gnathopod 1 propodus has 1 or 2 medial (plus 1 distal) spines anteriorly. Gnathopod 2 appears to be more powerful than in other species, the bulbous basis of propodus showing strong bundles of muscles. Because of the “wings” or septae on urosomite 3 the insertion of uropod 3 is partly hidden. Uropod 3 ramus article 2 is reduced to a tiny, spine-like peak on article 1, and the articulation is scarcely visible. But, as mentioned by Barnard (1974: 113), article 2 shows always (as in article 1) a seta at its insertion and this indicates the region of the barely observable articulation. Coxa 4 is trapezoid, anteriorly deeper than posteriorly, only little overlapping coxa 3.

The urosome is specialised compared to other members of this genus being the only species with the rami of uropod 1 clearly different in length, while in uropod 2 the rami are as in all species slightly unequal. Uropod 3 is reduced, directly in line with the lengthened urosomite 3 as a robust, solid short cone with spine-like article 2 nearly fused to article 1. Spination is extremely poor, uropod peduncles have only one spine each, rami are smooth, and the telson has 0–2 setae.

The species was described from a single specimen and has not been reported again until now.

Raumahara waroona sp. nov.

Figures 6, 7

Material examined. Holotype. Western Australia. Groyne, Cape Peron (32°16'S, 115°41'E), R. Springthorpe, AM P54514 (1 slide, sex?, 1.2 mm).

Paratype. Type locality, AM P54515 (1 specimen in alcohol, sex?, 1.2 mm).

Additional material. Type locality, AM P54516 (2 specimens in alcohol); AM P54517-P54520 (4 slides).

Diagnosis. Antenna 1 peduncular article 2 with strong process dorsally. Antenna 2 peduncular article 3 suboval to subrectangular. Mandibular palp lacking. Maxilla 1 palp of 2 articles. Maxilla 2 inner plate reduced. Maxilliped very slender, outer plate short. Gnathopod 1 propodochelate. Gnathopod 2 propodochelate-forcipate, dactylus about 33–40% length of propodus. Urosomite 1 very elongate, with large hump overlapping; urosomite 2 reduced to small triangle; urosomite 3 rectangular, fused with broad basis of telson. Uropods 1 and 2 with subequal rami, subequal to peduncle, without spines or setae; uropod 3 ramus clearly of only 1 article, semicircularly rounded, not reaching ramus insertion of uropod 2, article 2 absent; with 1 apical, centrally inserted, long seta. Hump of urosomite 1 reaching half way along telson. Telson spoon-like, deeply excavated.

Length 1.0–1.2 mm.

Description. Body smooth, very similar to most species of Raumahara. Head about as long as pereomite 1. Rostrum inequinoicuous. Eyes of stenothoid shape, normal. Lateral cephalic lobes shortly produced, rounded. Midcephalic keel and epistome developed. Pereomites 1–3 together. Urosomites 1 and 2 free; urosomites 3 broadly coalesced with telson. Urosomite 1 with large dorsal hump vaulting over urosomites 2 and insertion of telson, hump showing similar structure as nasiform process on antenna 1 article 2.

Antenna 1 shorter than antenna 2, as length as head + pereomites 1–3 together (dorsal lengths). Antenna 1 peduncular articles 1 and 3 without process, article 2 nasiform dorsomedially, with very dense aesthetases; length ratio of articles 1 : 2 : 3, about 5 : 3 : 2 on dorsally visible margin, but articles strongly overlapping; accessory flagellum short, broad, uniarticulate, 2 terminal setae; flagellum longer than peduncle, of 7 articles, with many long aesthetases. Antenna 2 peduncular article 3 suboval to subrectangular, article 3 as long as article 4, article 4 shorter than article 5; flagellum shorter than peduncle, of 7 articles.
Figure 6. *Raumahara waroona* sp. nov. Antennae 1, 2, gnathopods 1, 2 at scale 0 = 0.1 mm; maxilla 1, 2, mandible, upper lip, maxilliped at scale y = 0.1 mm; maxilla 2 in free enlargement.
Figure 7. *Raumahara waroona* sp. nov. Pereopods 3, 4, 5 at scale $x = 0.1$ mm; uroscope from 3 specimens and in different fixation, at scale $y = 0.1$ mm; uropod 3 in free enlargement.
Upper lip ventrally notched, lobes rounded. Mandible incisor on both sides well developed, left and right mandible not very different; raker spine row developed, of 3 (4–5?) spines; molar eusp with 3 robust spines; palp absent. Lower lip inner lobes coalesced, mandibular lobe present. Maxilla 1 inner plate subquadraangular, truncate, with 1 subapical seta; outer plate with 1 mediadistal long seta, apically armed with 4 serrate, robust spines, 1 stout simple spine and 1 thin, short and stiff one; palp biarticulate, ratio of lengths, 2 : 5, extending much beyond outer plate, with few spines and teeth apically and medioapically. Maxilla 2 inner plate reduced, short, and outer plate curved over inner plate (always, or artefact in slide?); outer plate apically with 3 long setae, 1 on outer margin; inner plate with 1 long apical seta, 1 shorter on inner margin mediadistally. Maxilliped inner plate reaching half length of ischiuim, with 1 seta and 1 spine apically; outer plate reaching one third of merus (= palp article 1); with 1 seta subapically, 1 medially; palp of 4 articles; article 3 (propodus) narrow like article 2; propodus distally and daetylus inner margin furry.

Gnathopod 1 shorter than gnathopod 2; coxa 1 reduced, subquadrate, covered by coxa 2; merus posterodistally rounded, about as long as triangular carpus, which is slightly produced between merus and propodus; propodus rectangular, anterior margin slightly convex, with 1 seta; posterior slightly concave; length : breadth about 2 : 1; propodocheleate, palm armed with small distal and medial spines; palmar corner curved upwards; daetylus about 40% of propodus length. Gnathopod 2 propodocheleate-foreipate; coxa 2 expanded, longer than basis, anterior margin regularly convex, posterior one nearly straight, ventrally rounded; posterior and posteroventral margin with single, short spines; ischiuim longer than merus; carpus subquadraangular, lobe with dense, short setae, distoapically some longer ones; propodus slender, length ratio of daetylus; total propodus = 33–40%: terminally a hooked eusp and notch, but no defining spines: daetylus also terminally hooked, matching well with the propodal notch.

Pereopods 3 and 4 slender, subequal; daetylus about half propodus length, hind margin on inner and outer surface with dense, stiff setae; coxa 3 more than twice as deep as wide, Coxa 4 dominant, wider than deep, front margin slightly convex, ventral margin straight or very slightly concave, posterior margin strongly convex, anteriorly deeper than posteriorly. Pereopods 5–7 slender, ratios of corresponding articles only slightly different; daetylus with prominent setal comb on anterior margin inside and outside; coxae 5–7 short; coxa 5 trapeziform, produced posterodistally; coxa 6 oblong. roundly produced posteriorly; coxa 7 blunt.

Uropod 2 extending less far posteriorly than uropod 1, uropod 3 very short. Uropod 1 peduncle subequal to subequal rami, without spines, setae or pectination. Uropod 2 peduncale as long as subequal rami, inner one inserted more proximally; no spination or pectination like uropod 1. Uropod 3 ramus consisting of 1 clear article, semicircular, not reaching ramus insertion of uropod 2, article 2 absent; with 1 apical long seta, centrally inserted. Urosomite 1 very long, large hump vaulting over urosomite 2 and shortly over telson insertion; urosomite 2 reduced to small triangle; urosomite 3 rectangular, fused with broad basis of telson.

Telson spoon-like, shorter than uropod 1 rami, about half length of hump of urosomite 1, horizontally inserted, deeply excavated and with characteristic semicircular hump proximoventrally; insertion of telson three-dimensionally thickened and fused with urosomites 2 and 3.

**Distribution.** Cape Peron, Western Australia.

**Etymology.** This material was found on Cape Peron, south of Perth. A nearby locality with an aboriginal name is Waroona, which with its double “o” reminded me of *R. dertoo*, the closest species.

**Remarks.** This species is very similar to *R. judithiae*. While in *R. noko* uropod 3 is composed of peduncale and a biarticulate ramus, in *R. dertoo* and *R. judithiae* article 2 is vanishing; in *R. waroona* sp. nov. no traces of article 2 are to be found, article 1 is as long as wide and bears apically one long seta. Thus this new species resembles the genus *Chucullla* in having uropod 3 reduced to only one article, probably the peduncle, with the — steadily present — apical long seta. Also, maxilla 2 of the present species is similar to *Chuculla* but the latter has fewer setae. Finally, reduced body length is common to both. While basic *Raumahara* females are ovigerous at 2 mm, the new species, *R. waroona*, reaches only 1.2 mm and the specialised species of *Chucullla* are also rarely longer than 1 mm. However, the morphology of the gnathopods and the nasiiform swollen antenna 1 article 2 (instead of article 1) places this new species undoubtedly in *Raumahara*. 

*THAUMATELSONINE STENOTHOID AMPHIPODA: PART 1*
Raukumara gen. nov.

Type species. Raumahara rongo Barnard, 1972b.

Diagnosis. Antenna 1 ordinary, peduncle slender. Mandibular palp lacking. Maxilla 2 plates ordinary, i.e. in tandem, but outer plate unusually slender, with 2 long setae apically. Coxa 4 trapezoid, enlarged. Gnathopod 1 subechelate-rectipalmate. Gnathopod 2 propodochele-foreipate, strong. Daetyles of pereopods unusually short. Inside and outside with comb-like row of setules; propodus to merus feeble, ischiun very long. Urosomites free, no dorsal process, but urosomites 2 and 3 triangular, dorsally much shorter than ventrally; urosomite 1 longer than urosomites 2+3 together. Uropod 3 ramus of 2 articles. Telson flat, but spoon-like and excavated dorsally, horizontally inserted, basically fused with urosomite 3.

Etymology. For the Raukumara Range on Auckland Island, New Zealand, alluding also to Raumahara which the new genus resembles (feminine).

Remarks. Barnard (1972b: 318) wrote “The retention of R. rongo in Raumahara is provisional and based on the probability that other species will be discovered that will clarify the generic partition of the thaumatelsonin stenothoids.”

Characters shared with species of Raumahara are: antenna 2 peduncular article 3 ovoid, as in R. dertoo; shape of gnathopod 2 with daetyle c. 40% of propodus as in R. judithae; a comb of setules on inner and outer sides of pereopodal daetyle; the pereopodal daetyle bifid as in all species of Raumahara; urosomite 3 and pedunule uropod 3 forming transparent “wings” dorsally; and the telson basically coalesced with urosomite 3.

Differences from specialised species of Raumahara and Ptychotelson gen. nov. are: antenna 1 peduncular article 2 ordinary, slender (even in hyperadults), and urosomite 1 ordinary, without dorsal prolongation, and not longer than urosomites 2+3 together.

One character shared with Ptychotelson is the subechelate-rectipalmate first gnathopod.

The characters unique to Raukumara are: pereopods 3-7 daetyle extremely short, their propodus to merus elongate, feeble, and ischiun very long, 3-4 times as long as wide (versus twice as long as wide in other genera).

This new genus differs from the others in the following main characters: from Raumahara and Ptychotelson gen. nov. in the shape of antenna 1 peduncular article 2; ratio of gnathopod 1 to gnathopod 2; shape of pereopods 3-7; length of urosomite 1 and spineation of uropod 1 pedunule. It differs from Raumahara in having the gnathopod 1 subechelate-rectipalmate and from Ptychotelson in having no mandibular palp.

Removal of this species from the (now monophyletic genus) Raumahara seems justified.

Raukumara rongo (Barnard) comb. nov.

Figure 8

Raumahara rongo Barnard, 1972b: 160-162, figs 91, 92.

Type material. Holotype. New Zealand, Kaikoura. NZOI 102 (female, 2.1 mm).

Material examined. Type locality. USNM 2304273 (3 ovigerous females, 1.8-2.0 mm; 2 juveniles in alcohol). USNM 230427 (1 female, 1.9 mm, on slide).

Diagnosis. Antenna 2 peduncular article 3 ovoid. Coxa 2 anterior margin more parallel to posterior one, less concave than in species of Raumahara. Gnathopod 2 propodochele, daetyle more than one third (about 40%) propodus, proximally thickened; propodus gnathopod 1 less than half as long as that of gnathopod 2. Coxa 4 trapezoidal, anteriorly deeper than posteriorly. Urosomite 3 and uropod 3 pedunule with transparent “wing” dorsally. Uropod 3 ramus with spine-like article 2, about as long as article 1. Telson like a flat spoon.

Length 1.5-2.0 mm.

Distribution. New Zealand (Kaikoura, Gisborne, Whangaparaoa Peninsula, Leigh). Canterpa brownii, 5-6 m; in crevices in Durvillaea-zone, barnacles encrusted with sponge.

Biology. Female ovigerous in January.

Remarks. The “missing seta on maxilla 1 IP” (Barnard 1972b: fig. 92c) is present as in other species. The telson is horizontally flat but not stenothoid-like, as it is dorsally excavated like a flat canoe or spoon, and — more importantly — proximally thickened and coalesced with urosomite 3. The “numerous setules” of Barnard’s description are totally lacking within his type series but are probably crystals derived during preservation.

Pycnopyge gen. nov.

Type species. Prothaumatelson carinatum Shoemaker, 1955.

Diagnosis. Antennae 1 and 2 ordinary; accessory flagellum of 1 rudimentary article. Mandibular palp lacking. Maxillal palp long, no articulation
Figure 8. *Raukumara rongo* (Barnard). Maxilla 1 (left), antenna 1, 2, gnathopod 1, pereopod 4 distally, urosome of 2 specimens, telson at scale $0 = 0.1$ mm; maxilla 1 (right) at scale $y = 0.1$ mm; mandible at scale $y = 0.05$ mm; gnathopod 1', gnathopod 2 at scale $x = 0.2$ mm.
concernable, thus of 1 article. Maxilla 2 ordinary. Maxilliped outer plate vanishing, inner plate fused. Gnathopod 1 subchelate. Gnathopod 2 propodochelate-foreipate. Peronite 4 very large. Urosomite 1 with dorsal fold, but not overlapping urosomite 2; thus uropod 2 lies over not after uropod 3. Urosomites 2 and 3 coalesced so that uropod 3 lies over, not after, uropod 3. Uropod 3 ramus article 2 well developed. Telson flat, horizontal, not coalesced with urosomite 3, not spoon-like or dorsally excavated.

Etymology. The Greek word pyge, pygaion means rump, back, while pyknos (Greek) signifies a condensed, thickened area. Together they describe the special habitus, the dorsal fold on urosomite 1 not overlapping urosomite 2, and the fusion of urosomites 2 and 3 (neuter).

Remarks. Shoemaker (1955) described, inadequately, a species from Alaska as Prothaumactelson carinatum. Barnard (1972a) removed it from that genus, assigning it provisionally to Raumahara, although he lacked information about important details.

Characters shared with Raumahara are: urosomite 1 with a dorsal fold (but only protecting urosomite 1 and not overlapping urosomite 2 as in Raumahara); propodochelate gnathopod 2.

Differences from Raumahara: antennae 1 and 2 ordinary, both with very short flagellum; accessory flagellum rudimentary article. Mandibular palp lacking. Gnathopod 1 subchelate, no palmar corner; carpus strongly and merus weakly lobed. Gnathopod 2 propodochelate, dactylus about 40% of propodus length. Pereopods 3–7 dactyli very long, longer than half propodus, smooth. Urosomite 1 dorsally thickened as a fold, not overlapping. Urosomites 2 and 3 coalesced. Uropod 1 peduncle exceeding rami. Uropod 3 ramus of 2 articles, well developed. Uropod 3 exceeding uropod 2 peduncle. Telson flat, horizontal, not coalesced with urosomite 3.

Length 1.8−3.0 mm.

Distribution. Arctic Ocean, Alaska, off Point Barrow (USA). 217 ft (66 m), perforated rocks, stones.

Remarks. Though having chelate gnathopod 2, this species does not belong to the (southern Australian-Antarctic) thaumactelsonine stenothoids, as the telson is not fused with urosomite 3, nor spoon-like or dorsally excavated, and the palp of maxilla 1 has only one article. Fortification of the urosome is created in another way, and chelation of gnathopod 2 is probably a homoplasious development in Arctic regions.

Ptychotelson gen. nov.


Diagnosis. Antenna 1 peduncular article 2 swollen, Mandibular palp of ordinary length, articulation doubtful, seemingly articles coalesced; maxilla 2 ordinary. Coxa 4 trapez-shaped, enlarged. Gnathopod 1 subchelate-receptipalmate, gnathopod 2 propodochelate-foreipate. Urosome segments free, urosomite 1 with dorsal fold vaulting over urosome, > urosomite 2 + 3; uropod 3 ramus 2 articles well developed. Telson spoon-like excavated dorsally, horizontally inserted, proximally coalesced with urosomite 3.
Figure 9. *Pycnopyge carinatum* (Shoemaker). Antennae 1, 2, gnathopods 1, 2 (detail) at scale = 0.1 mm; gnathopod 2' (complete) at scale = 0.2 mm.
Etymology. Greek *ptyx* -ychos means fold, referring to the three-dimensional, boat- or spoon-shaped telson and process of urosomite 1 overlapping the urosome like a fold or pleat.

Remarks. Krapp-Schickel and Andres (1998) were doubtful of the generic placement of *Raumahara viridurorum* and recognised that a thorough revision was needed to understand its relationship to other species with subchelate-rectipalmate gnathopod 1 or long mandibular palp. Now, after a detailed study of type material, it can be shown that the two species with similar gnathopod 1 are not closely related. *Prothaumatelson nasutum* has a vertical telson but very similar mandibular palp; *Raukimara rongo* has a less specialized urosome, a non-swollen ordinary antenna 1 peduncle and lacks a mandibular palp.

With the closely related species of *Raumahara*, *R. dertoo, R. noko, R. judithae* and *R. waroona*, the new taxon shares specialised characters of “swollen” antenna 1 peduncular article 2 (in *R. dertoo* only weakly), propodochelate gnathopod 2, a row of setae inside and outside dactyl of pereopods 3–7, special construction of the urosome with its combination of vaulting urosomite 1 and excavated telson. *Psychotelson* is less specialised in the mandibular palp being of ordinary length (probably 1–articulate) and the gnathopod 1 subchelate-rectipalmate.

This new genus differs from its nearest
relatives in the following main characters: from *Raukumara* in antenna 1 peduncular article 3 swollen and produced (versus slender, ordinary); mandibular palp long (v. absent); urosomite 1 with a thick fold fortifying the urosome (v. urosomite 1 lengthened but not thickened or folded); and from *Raumahara* in long mandibular palp (v. reduced to a short stump or absent); and gnathopod 1 subchelate-rectipalmate (v. chelate).

**Ptychotelson virdurorum** (Krapp-Schickel and Andres) comb. nov.

Figures 11, 12

*Raukumara virdurorum* Krapp-Schickel and Andres, 1998: 56-58, figs 1, 2.

Material examined. Holotype. South Australia. Steatford Bay, Port Lincoln, ZMH K38388 (ovigerous female, 1.6 mm, 1 slide). Type locality, ZMH K38389 (41 specimens in alcohol). Victoria. Point Lonsdale, ZMH K308390 (4); Cape Otway, NMV J39258, J39264, J39265 (3 slides); Port Phillip Bay, CTK (1 slide).

Diagnosis. Antenna 1 peduncular article 2 dorsally prolonged and swollen (sometimes article 1 also a little thickened). Antenna 2 peduncular article 3 subquadrate. Mandibular palp well developed, but no articulation visible. Gnathopod 1 subchelate-rectipalmate. Gnathopod 2 propodo-chelate-forcipate, dactylus c. one third propodus. Urosomite I with thick fold vaulting over urosome and insertion of telson. Uropod 3 ramus with 2 articles. Telson spoon-like, three-dimensional, proximally coalesced with urosomite 3, inserted horizontally.

Length 1.0-1.6 mm.

Distribution. South Australia to Victoria; intertidal, algae (mostly Rhodophyceae including corallines and epiphytes).

Biology. Female ovigerous in December.

Remarks. Drawings of young and adult specimens are presented to show how ratios on limbs and body segments change with age. This allometry can also be noticed in *R. judithae* and *R. waroona*. Gnathopods 1 and 2 have propodi alike and with lengthened parallel margins as is found in *Parathaumatelson*. The characteristic comb on dactyli of pereopods 3-7, inside and outside, always present in *Raumahara*, is present in one species of *Chuculiba* and absent in the other. Uropodal rami are reduced to a different degree also in *Raumahara*. However, in the latter urosomites 2 and 3 are separated, though dorsally narrowed and ventrally much wider, thus giving a triangular shape in lateral view while in *Chuculiba* articulation between urosomites 2 and 3 is scarcely visible. *C. alia* is more specialised than *C. waroona* in antenna 1, maxilla 1, nathopods, pereopodal dactyli (only one seta instead of a comb), length of uropods 1 and 2 inner rami, and length of uropod 3.

Antenna 2 peduncular article 4 is always shorter than article 5 in *Raumahara*, *Pyenopyge*, *Raukumara* and *Chuculiba*, whereas it is always longer in *Yarra*, *Pseudothaumatelson* and *Thaumatelsonella*. As the members of the first group live in shallow algae and the latter predominantly in deeper sands, this difference could be correlated with feeding behaviour.

**Chuculiba alla** Barnard


Type material. Holotype. Western Australia. Middleton Beach, Albany, intertidal, sandy rocks, coralline algae. WAM 134-71 (female, 1.41 mm).

Material examined. Western Australia (USNM, 141159; 141160 (4 specimens in alcohol); AM P43271
Figure 11. Ptychotelson viridurorum (Krapp-Schickel and Andres). a, habitus of adult female, 1.6 mm. b, middle of body of juvenile, 1.1 mm. c, sketch of mouthparts in situ. d, complete mandible and distal part seen from other side. Other figures, 4 enlargements of different views of mandible at scale = 0.025 mm.
Figure 12. Ptychotelson viridurorum (Krapp-Schickel and Andres). Antennae 1, 2, gnathopods 1, 2, pereopod 3 or 4 distally, urosome at scale = 0.1 mm; maxilla 1, 2, maxilliped, antenna 1 at scale = 0.05 mm; maxilla 1 outer plate enlarged.
Diagnosis. Midecephalic keel weak. Antenna 1 peduncular article 1 strongly nasiform, largely to totally overlapping article 2. Maxilla 1 inner plate lacking seta. Maxilla 2 in riding position but separate lobi still distinguishable. Gnathopods 1 and 2 similar, rectangularly lengthened, with parallel margins, but gnathopod 1 palm oblique and gnathopod 2 palm nearly subchelate-recipalate. P 3–7 dactylus smooth. Urosomite 1 with thick fold vaulting over urosome and insertion of telson. Uropod 3 consisting of 1 minute article and short, tiny seta.

Length 1.1–1.4 mm.

Distribution. Western Australia to Victoria. Intertidal, sandy rocks and coralline algae.

Biology. Female ovigerous at end of September.

Chuculiba warea Barnard


Type material. Western Australia. Cape Naturaliste, intertidal, algae and rocks, WAM 135-71 (female, 1.19 mm).

Material examined. Type locality, USNM 230428, USNM 141161 (2 specimens in alcohol). Cape Naturaliste, ZMH K38214 (2). South Australia, Ceduna, ZMH K38223 (2).

Diagnosis. Antenna 1 peduncular article 1 and article 2 (weakly) swollen. Maxilla 1 inner plate with seta. Maxilla 2 in riding position, lobi fused. Gnathopods 1 and 2 similar, both palms oblique. P 3–7 dactylus with comb of short setae as in Raumahara. Urosomite 1 with thick fold vaulting over urosome and insertion of telson. Uropod 3 ramus with 1 minute article (probably peduncle) and long seta apically.

Length 1.2 mm.

Distribution. Cape Naturaliste, Western Australia; Ceduna, South Australia. Intertidal, algae and rocks.

Biology. Female ovigerous in September.

Pseudothaumatelson Schellenberg


Material examined. Syntypes of Pseudothaumatelson patagonicum. Falkland Is, NHRS 738 (slide), 3603 (1 ovigerous female in alcohol). Falkland Is, MNB 22802 (1 juvenile in alcohol, partly damaged).

Other material. Prince Edward Is, MVR Cr3392-Cr3397 (slides).

The two other specimens deposited by Bellan-Santini and Ledoyer (1986: 425) in SAM could unfortunately not be found in South Africa or in Marseille.

Diagnosis. Antenna 1 peduncular article 1 nasiform, accessory flagellum of 1 article. Mandibular palp present, stout, without articulation, as long or longer than incisor. Maxilla 1 palp of 2 articles. Maxilla 2 ordinary. Gnathopods 1 and 2 subchelate, shape similar, size different. P 3–7 bases rectilinear, dactylus smooth. Pereonite 4 elongate. Urosomites 1–3 free; urosomite 1 with long process vaulting over urosomite 2 and most of telson. Telson medium, marginally scleritized, horizontally inserted, excavated, margins thickened.

Pseudothaumatelson patagonicum Schellenberg


Material examined. Syntypes of Pseudothaumatelson patagonicum. Falkland Is, NHRS 738 (slide), 3603 (1 ovigerous female in alcohol). Falkland Is, MNB 22802 (1 juvenile in alcohol, partly damaged).

Other material. Prince Edward Is, MVR Cr3392-Cr3397 (slides).

The two other specimens deposited by Bellan-Santini and Ledoyer (1986: 425) in SAM could unfortunately not be found in South Africa or in Marseille.

Diagnosis. Antenna 1 peduncular article 1 nasiform, accessory flagellum of 1 article. Mandibular palp present, stout, without articulation, as long or longer than incisor. Maxilla 1 palp of 2 articles. Maxilla 2 ordinary. Gnathopods 1 and 2 subchelate, shape similar, size different. P 3–7 bases rectilinear, dactylus smooth. Pereonite 4 elongate. Urosomites 1–3 free; urosomite 1 with long process vaulting over urosomite 2 and most of telson. Telson medium, marginally scleritized, horizontally inserted, excavated, margins thickened.

Pseudothaumatelson Schellenberg


Material examined. Syntypes of Pseudothaumatelson patagonicum. Falkland Is, NHRS 738 (slide), 3603 (1 ovigerous female in alcohol). Falkland Is, MNB 22802 (1 juvenile in alcohol, partly damaged).

Other material. Prince Edward Is, MVR Cr3392-Cr3397 (slides).

The two other specimens deposited by Bellan-Santini and Ledoyer (1986: 425) in SAM could unfortunately not be found in South Africa or in Marseille.
propodus, palmar corner rounded, with spines; basis with a few long setae anteriorly. Gnathopod 2 subchelate (rudimentarily carpochelate, as carpus acutely prolonged and propodus proximally narrowed), palm with "pearls" (Bellan-Santini and Ledoyer lacking), distally concave, defined by hump with 2 strong spines; anterior margin smooth or with 1 or 2 long setae; basis with few long setae on anterior margin. Pereonite 4 elongate, as long as pereonites 1–3. Pereopods 5–7 basis rectilinear, with about 12 short setae. Urosomites 13 free. Urosomite 1 with process vaulting over urosomites 2 and 3 and overreaching most of telson. Uropod 1 with long, spinose peduncle, longer than barely unequal rami [Rauschert and Andres (fig. 1) show the rami much shorter than peduncle but this is misleading as rami in type material are broken]; uropod 2 peduncle long, spinose, rami unequal, the longer shorter than peduncle. Uropod 3 peduncle robust, article 1 about twice as long as large, article 2 in type material broken [as long as article 1, pointed]. Telson medium, half length of urosomite 1 dorsally, marginally sclerotized, horizontally inserted, shallow excavated, coalesced with urosomite 3, with 2 setae.

Distribution. Falkland Islands; Prince Edward and Marion Islands (subantarctic), 95–197 m.

Biology. Female ovigerous in November.

Remarks. This species was first described from two individuals, reexamined by Rauschert and Andres (1991). Since the description of *Pseudothaumatelson cyprioides* by Nicholls (1938) it has always been doubtful that two species existed. Barnard and Karaman (1991: 697) stressed the "strong dissimilarity" in the sizes of gnathopods 1 and 2 (less obvious in shapes) but there are many other similarities between the two nominal species. However, their localities are not close: Schellenberg’s *P. patagonicum* comes from the Falkland Islands (subantarctic, 197 m), while Nicholls found his *P. cyprioides* in Adelie Bay, Antarctica (c. 50 m). Three additional specimens, discovered at more than 95 m depth from subantarctic Marion and Prince Edward Islands (Bellan-Santini and Ledoyer, 1986; Branch et al., 1991) were attributed to *P. cyprioides* without discussion. These probably refer to *Pseudothaumatelson patagonicum*.

Bellan-Santini and Ledoyer (1986) figured two different 1-articulate mandibular palps; one fits with the description of *P. patagonicum*, the other one is sitting under the mandible body but has a corresponding length. Their figure of maxilla 1 is misleading (Rauschert and Andres, 1991: 227) but recoloration of the slide (MVR CR3389) could confirm a normally shaped maxilla 1 with 2-articulate palp.

**Thaumatelsonella** Rauschert and Andres


**Type species. Thaumatelsonella kingelepha** Rauschert and Andres, 1991 (original designation).

**Diagnosis.** Antenna 1 peduncular article 1 nasiform, accessory flagellum of 1 article. Mandibular palp present, of 3 clearly articulated articles, article 3 slim. Maxilla 1 palp of 2 articles, Maxilla 2 ordinary. Gnathopods 1 and 2 subchelate, shapes similar, sizes different. Pereopods 3–7 bases rectilinear, dactyli smooth. Pereonite 4 elongate. Urosomites 1–3 free. Urosomite 1 with long process vaulting over urosomite 2 and most of telson. Telson medium, horizontally inserted, dorsally excavated.

**Thaumatelsonella kingelepha**

Rauschert and Andres


**Material examined.** Holotype. King George Island, Antarctica, sublittoral, sponges and bryozoans, 50 m, MNB 27271 (female 2.5 mm). Paratypes. Collected with holotype, MNB 4582–4586 (male 2.1 mm, 2 females 2.4 and 2.6 mm).

Additional material: Near Elephant Islands, Antarctica, fine sand, 260 m, ZMH K33480 (male, 1.9 mm), ZMH K33481 (male, 2.1 mm).

**Diagnosis.** Antenna 1 peduncular article 1 nasiform. Mandibular palp of 3 articles. Gnathopods 1 and 2 subchelate, ratio of lengths of propodus gnathopod 2 : 1 less than 2; bases gnathopods 1 and 2 with long, dense setae. Gnathopod 1 palmar corner rounded, carpus distally widened. Gnathopod 2 palmar corner rounded (female) or with small hump and little excavation (male), with 1–2 setae on anterior margin; carpus with triangular process, densely beset with short setae. Urosomite 1 with process vaulting over urosomites 2 and 3 and two-thirds of telson. Uropod 1 rami scarcely different, shorter than peduncle. Uropod 2 peduncle spinose, rami scarcely different, little shorter than peduncle. Uropod 3 strong, peduncle as long...
as each article of ramus, each about twice as long as wide. Telson folded, excavated, fused with urosomite 3.

Length 2.1–2.6 mm.

Distribution. King George Is and Elephant Is, sublittoral, on Porifera, Bryozoa, sandy bottom. 50–260 m.

Biology. Female ovigerous in February.

_Thaumatelsonella cyproides_ (Nicholls) comb. nov.


Type material. Syntypes. Commonwealth Bay, Antarctica, AM P18730 (1 male, 1 female, 2 mm).

Material examined: Cape Bird, AM P43242 (1 specimen, slide).

Diagnosis. Antenna 1 peduncular article 1 nasi-form. Mandibular palp of 3 articles. Gnathopods 1 and 2 subchelate, propodus of gnathopod 2 less than twice as long as gnathopod 1; basis of gnathopod 1 with many short setae; basis of gnathopod 2 with many long setae. Gnathopod 1 palmar corner angular. Gnathopod 2 palm rounded (female), distally scarcely excavated, proximally straight (male), without hump. Urosomite 1 vaulting over urosomites 2 and 3 and most of telson. Uropod 1 rami subequal, shorter than peduncle. Uropod 2 rami scarcely different, longer ramus subequal to peduncle. Uropod 3 strong, robust peduncle shorter than ramus article 1, shorter than article 2; peduncle more than twice as long as wide, ramus more than twice as long as wide, ramus article 2 more than 3 times as long as wide. Telson dorsally excavated, fused with urosomite 3.

Length: 2.0–2.1 mm.

Redescription. Body smooth. Head shorter than or equal to pereonites 1+2. Rostrum inconspicuous. Eyes of stenothoid shape, normal. Lateral cephalic lobes rounded. Perconite 4 about as long as perconites 1–3 together. Urosomites 1 and 2 free. Urosomite 3 broadly coalesced with telson. Urosomite 1 with large dorsal hump vaulting over urosomite 2 and most of telson.

Antenna 1 shorter than antenna 2, as long as head plus perconites 1–3 (dorsal lengths together); peduncular articles 2 and 3 without process, article 1 elongate, nasi-form dorsomedially; ratio of lengths of articles 1 : 2 : 3 about 7 : 4 : 3 (visible margin dorsally, but article 1 strongly overlapping); accessory flagellum short, broad, unarticulate, with 3 terminal setae; flagellum subequal to peduncle, of 7 articles, with many long aesthetases. Antenna 2 with article 4 longer than article 5; flagellum subequal to peduncle, of 10 articles.

Mandibular incisors not different, narrow and weak; with 2 broad raker spines; small molar euspir with 2 robust spines; mandibular palp well developed, of 3 articles, distal one much narrower. Lower lip inner lobes coalesced, outer ones regularly rounded. Maxilla 1 inner plate subquadangular, truncate, with 1 apical seta; outer plate with 4 serrate, robust spines, 1 stout simple spine and 1 thin, short and stiff spine; palp biarticulate, ratio of lengths of articles 2:5, extending much beyond outer plate, with spines apically and 1 seta sub-apically. Maxilla 2 ordinary, outer plate and inner plate with long setae apically. Maxilliped inner plate reaching two-thirds along ischiium, with 1 seta and 1 spine apically; outer plate reaching half along merus (palp article 1); with 1 seta apically, 3 medially; palp of 4 articles; palp article 3 (propodus) narrower than article 2; propodus distal margin and daetuelus inner margin setose.

Gnathopod 1 subchelate, much shorter than gnathopod 2. Cox 1 reduced, subquadrangular, covered by coxa 2; basis anteriorly with many dense, short setae; merus setose, posterodistally rounded, about as long as triangular carpus, which is slightly produced between merus and propodus; propodus triangular, anterior margin slightly convex, with 2–3 setae; posterior margin shorter than palm, palmar corner pronounced, with 2 robust spines; ratio length : breadth about 3 : 2, palm armed with long distal and medial spines and setae; daetuelus about half of propodus length. Gnathopod 2 subchelate. Cox 2 expanded, longer than basis, anterior margin convex with slight corner, posterior margin straight, ventrally rounded; posteroventral margin with single, short spine; basis anteriorly densely beset with many long setae; ischiium much shorter than merus, which is posterodistally pointed; carpus subtriangular, posterodistal corner reaching proximal third of propodus, moderately pointed, with dense, short setae. DISTOAPicularly some longer ones; propodus widened, hind margin regularly rounded, with 3 long setae, palm defined by 2 strong spines and a palmar corner of >150°, no defining hump or excavation; propodus on anterior margin 1 long seta; ratio of lengths of daetuelus : propodus = 33–40%; daetuelus on inner margin with many setae.
Figure 13. *Thaumotelsonella* Nicholls. Habitus ovigerous female, 2.1 mm; antenna 1' at scale $x = 0.1$ mm; maxillae 1, 2, lower lip, mandible, maxillipeds at scale $y = 0.1$ mm; antennae 1, 2, epimeral plates 1, 2 at scale $y = 0.05$ mm.
Figure 14. *Thaumotelsonella cyproides* Nicholls. Gnathopods 1, 2 (left), urosome at scale $x = 0.2$ mm; gnathopods $1', 2'$ at scale $x = 0.1$ mm; pereopods 3, 4, 5, 7 at scale $x = 0.4$ mm.
Pereopods 3 and 4 slender, subequal, bases anteriorly with dense, short setae, dactyli about half propodus length. Coxa 3 ratio of length to width 5. Coxa 4 dominant, wider than long, front margin straight, ventral margin slightly convex, posterior margin rounded, anteriorly not deeper than posteriorly. Pereopods 5-7 slender, ratio of corresponding articles only slightly different, on all bases anteriorly and posteriorly many short setae.

Uropod 2 extending less posteriorly than uropod 1. Uropod 3 extending as far as uropod 1. Uropod 1 peduncle longer than subequal rami, with many spines; rami lacking spines or setae. Uropod 2 peduncle shorter than subequal rami, without spination or pectination on rami, similar to uropods 1 and 3. Uropod 3 peduncle sub-quadrate, with 1 apical spine, ramus clearly of 2 articles, robust; article 1 with 2 apical spines, slender, about twice as long as broad; article 2 narrow, sharply pointed, smooth. Urosomite 1 very long, with large hump vaulting over urosomite 2 and most of telson. Urosomite 2 reduced, articulation not oblique as in *P. patagonicum*, but vertical to dorsal prolongation of urosomite 1. Urosomite 3 rectangular, subquadrate, fused with broad basis of telson.

Telson spoon-like, shorter than uropod 1 rami, about two-thirds length of urosomite 1 hump, horizontally inserted, excavated; insertion of telson three-dimensionally thickened and fused with urosomite 3 but not urosomite 2.

Colour. Red eyes, orange back.

**Distribution.** Cape Bird, Ross Sea (77°S) and Commonwealth Bay, Terre Adelie Coast (67°S), Antarctica, 46 m (25 fm) -130 m.

**Biology.** Female ovigerous in November.

**Remarks.** Nicholls described this species from two specimens. His figures and text are poor and the mouthparts unknown. The species was mentioned again by Bellan-Santini and Ledoyer (1986) and Braneh et al. (1991) both referring to the same material. The validity of this species was often doubted (cf. *P. patagonicum*) but important details were missing.

At the Australian Museum I was lucky to find another specimen of this species with material of *Metopoides* from Cape Bird, Antarctica. This specimen and its geographical locality correspond with Nicholls' description of *P. cyproides*. Its mandibular palp corresponds with that of *Thaumatelsonella* and its generic position is changed accordingly.

The differences between *Thaumatelsonella kingelepha* and *T. cyproides* are exceedingly small, and concern antenna 1 article 1, coxa 3, palmar corners of gnathopods 1 and 2, and setation of bases and proportions of uropod 3 articles. It is quite probable that these are due to body size as the described material of *T. kingelepha* is 2.5 mm while that of *T. cyproides* is 2.1 mm. It has been shown for *Raumahara* that allometry is present to a high degree. But before making a definite decision on the specific distinctness of these two taxa, one from the subantarctic and the other from Antarctica, I await additional material.

The essential difference between *Pseudothau-matelson* and *Thaumatelsonella* is in the structure of the mandibular palp. Jerry Barnard discussed "several examples of species with obvious gnathopodal relationships now separated from each other generically on the basis of metameric differences in mandibular and maxillary palps ..." (see Introduction). The small size of mandibular palp article 3 in *Thaumatelsonella* suggests only small steps from a 3-articulate palp to a palp with length of article 1 + article 2, but vanishing articulation between them. Having both these conditions in one genus would be analogous to having a rudimentary and absent palp as is seen in *Raumahara*.

In this complex the condition of mandibular palp of "1 article" includes species with a short stump and other with a palp of nearly full length but without articulation. Future descriptions should indicate length of the palp relative to the incisor. In *Raumahara* (and in the *Stenothoe monoculoides*-species complex) the arrangement of maxilla 2 plates varies from in tandem to a riding position, probably in response to different feeding strategies. But in *Raumahara* and *Stenothoe* more species are known from greater numbers of specimens. The division of *Pseu-dothau-matelson* and *Thaumatelsonella* is retained until a more detailed analysis of more species reveals the significance of a robust, long mandibular palp with coalesced articles versus the ordinary, 3-articulate palp or a short stump of one article.

**Yarra** gen. nov.

**Type species.** *Yarra unguiserra* sp. nov.

**Diagnosis.** Antennae 1 and 2 geniculate. Antenna 1 peduncular article 2 a nasiform process; accessory flagellum lacking. Mandibular palp lacking. Maxilla 1 palp of 2 articles. Maxilla 2 plates aberrant, in riding position. Maxilliped inner plate with apical knob, outer plate absent. Gnathopods...
1 and 2 subchelate, different in size, similar in shape. Urosomite 1 with dorsal fold, vaulting over urosomites 2 and 3 and part of telson. Uropods 1 and 2 smooth, rami unequal. Uropod 3 robust, ramus of 2 articles. Urosomites free. Telson horizontally inserted, spoon-like, dorsally excavated, marginally scleritic.

**Etymology.** Following Jerry Barnard’s habit of using local names, the genus is named for the scenic Yarra River which meanders behind the Abbotsford Annex, Museum Victoria, in whose collections this exciting animal was found.

_Yarra unguiserra_ sp. nov.

**Figures 15–18**

**Material examined.** Holotype. Australia, eastern Bass Strait, 15.5 km from Point Ricardo, 37°53.18’S, 148°28.96’E, 45 m, sand-shell, 26 Sep 1990, Smith-McIntyre grab (stn MSL-EG 44), NMV J45739 (sex?, 2 mm, slide).

Paratype. Australia, eastern Bass Strait, 7.3 km SSW of Cape Conran, 37°52.67’S, 148°42.06’E, 45 m, sand-shell, 28 Sep 1990, Smith-McIntyre grab (stn MSL-EG 60), NMV J22638 (1 specimen in alcohol, 1.2 mm).

Additional material. Type locality, NMV J45737 (1 in alcohol). Eastern Bass Strait, 24 km NNE of Eddystone Point, 40°43.9’S, 140°32.5’E, 56 m, muddy sand, 14 Nov 1981, epibenthic sled, RV Tangaroa, NMV J3767 (1 specimen, 1.2 mm, slide). Eastern Bass Strait, 15.5 km SW of Point Ricardo, 37°53.14’S, 148°28.94’E, 45 m, medium sand, 4 Jun 1991, Smith-McIntyre grab (stn MSL-EG 81), NMV J45738 (1 specimen in alcohol, sex?, 1.2 mm).

**Diagnosis.** Antenna 1 peduncle forming a knee in article 2, thus forcing article 3 to insert subrectangularly. Antenna 2 knee between peduncular articles 4 and 5. Maxilla II plates riding, each with 1 apical spine. Gnathopods 1 and 2 palmar corner well defined, palp longer than posterior margin, slightly concave, serrated; dactyl characteristically serrated inside. Gnathopod 1 dactylus with 2 sharp teeth. Gnathopod 2 dactylus with 3 huge sharp teeth, in the gaps a deep incision and a long seta inserted. Uropods 1 and 2 smooth, peduncle strong, rami unequal, dorsally pectinate. Uropod 3 robust, of 2 articles. Urosomites 1–3 free, covered with external “skin”, linking the dorsal fold of urosomite 1 with uropod 1 insertion. Telson horizontally inserted, spoon-like, dorsally excavated, margins scleritic.

Length 1–2 mm.

**Etymology:** The specific name (_unganis_ (L.), nail, _+ serra_ (L.), saw) describes the morphology of the palm and dactylus of the gnathopods (noun in apposition).**

_Description._ Body smooth, stout, coxae 2–4 dominating, coxae 3 and 4 incised on anteroventral corner. Head high, narrow. Rostrum inconspicuous. Eyes normal. Lateral cephalic lobes rounded. Perconite 4 about same width as head + perconites 1–3. Urosomites free. Urosomite 1 with large dorsal hump vaulting over urosomites 2 and 3 and great part of telson. Urosomites 2 and 3 not arranged horizontally, but vertically. Urosomite 3 broadly coalesced with telson.

Antenna 1 shorter than antenna 2, geniculate; peduncular articles 1 > 2 > 3; article 1 subquadrate, 1.5 times as long as wide; article 2 dorsally with nasiform process, ventrally with right angled margin, forcing geniculate insertion of article 3; accessory flagellum lacking; flagellum shorter than peduncle article 1, of 5 articles, with long aesthetasces. Antenna 2 geniculate between peduncular articles 4 and 5; article 3 subquadrate; article 4 on outer side of knee longer than article 5 as apical margin oblique; flagellum shorter than peduncle, of 5 articles.

Upper lip lobes asymmetrically rounded. Mandibular incisors on both sides well developed; raker spines huge, bifurcate; molar cusp well visible; palp absent. Lower lip not found. Maxilla I inner plate small, without spines or setae; outer plate with 6 robust, acute spines, arranged not bilaterally but in a crown, not very different from each other; palp biarticulate, length ratio 1: 4, extending much beyond outer plate, with 1 stout spine and 1 acute, setose spine. Maxilla II plates subequal in size but sitting in riding position, with 0 or 1 apical small spines. Maxilliped inner plate scarcely reaching half way along ischium, with 1 seta subapically, 1 knob apically; outer plate absent; palp of 4 articles, article 3 (propodus) narrow, beset with many setae as on dactylus.

Gnathopod 1 much smaller than gnathopod 2; coxa I reduced, anteroventrally with 1 seta; basis medioposteriorly with 2 long, smooth setae; merus and ischium with many short setae; ischium not reaching propodus; propodus hind margin about same length as slightly concave, serrate, oblique palm; palmar corner well defined; outer margin with group of apical, short setae, and subapical long ones, medi ally with small and short ones; dactylus with deep serration on inner margin. Coxa 2 regularly rounded anteriorly, much widened, with short setae along anterior margin; basis three-quarters length of coxa 2, with 2 long, smooth setae posteriorly; ischium to proximal propodus posterior margin beset with many short setae; merus and carpus each with 1...
Figure 15. *Yarra unguiserra* gen. and sp. nov. Habitus of 1.2 mm specimen; mouthparts at scale = 0.1 mm, except middle sketch of mandible in free scale.
Figure 16. *Yarra unguiserra* gen. sp. nov., Antennae 1, 2, gnathopods 1, 2, pereopod 3 at scale = 0.1 mm.
Figure 17. *Yarra unguiserra* gen. nov., sp. nov. Coxae 3, 4, pereopods 4, 5, 6, 7 at scale $x = 0.05$; urosome complete and epimeral plate 3 at scale $y = 0.1$ mm, telson + urosomite 3 + uropod 3 detail at scale $y = 0.05$ mm.
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Figure 18. SEM pictures. a, b, Raumahara dertoo Barnard, urosome with shallow spoon-shaped telson. Yarra unguiserr species, gnathopod 2; d, urosome with telson about as deep as wide.

long seta distoposteriorly; propodus length of palm twice hind margin; palm strongly serrate, with 10–12 teeth, deeply incised; palmar corner beset with 2 setae; propodus anterior margin smooth, anterodistally with 2 short setae; dactylus with "triple tip", created by strong and expanded dactylus, twice deeply incised on inner margin, having one long seta in each notch.

Pereopods 3 and 4 strikingly smooth and simple, only scarce and very short setae on distal end of some articles; basis, like gnathopod, posteriorly with 2 setae. Pereopod 3 (juvenile) articles similar to pereopod 4; in adult (see figures of habitus or detail) carpus swollen, while articles of pereopod 4 are similarly slender. Pereopods 5–7 slender, ratios of corresponding articles similar; length diminishing from 5 to 7.

Uropods 1–3 extending less posteriorly in succession. Uropod 1 totally unarmed; peduncle subequal to longer rami, ratio of lengths of rami 2 : 3; both rami dorsodistally finely pectinate. Uropod 2 similar in shape to uropod 1 but shorter and stouter. Uropod 3 robust, with smooth peduncle, articles of rami much shorter and narrower, of subequal length, article 2 dorsally pectinate.

Telson spoon-like, horizontally inserted, dorsally excavated, with 1–2 plumose setae on distal third; more than half length fused with urosomite 3.

Distribution. Bass Strait, Australia, 45–48 m depth, medium sand or shell-sand.

Remarks. In Barnard and Karaman's (1991: 684) key to genera of Stenothoidae this species keys out to Pseudothaumatelson in spite of having the antenna I article 2 strongly nasiform (instead of article 1) and, with article 3, geniculate. However, the mandibular palp is totally lacking and maxilla 2 is riding, both supposedly apomorphic character states shared only with Chucullba. The most striking differentiating characters are the much more specialized urosome in Chucullba, antenna 1 article 2 thickened (like Raumahara, Raumahara, Ptychotelson) instead of article 1 (Chucullba) and the very aberrant, deeply serrate dactylus in gnathopods 1 and 2 of Yarra (instead of smooth margin in all other genera of this group). This surprising species, placed here in a separate genus, may use a pair of long setae on the bases of gnathopods 1 and 2 and pereopods 3 and 4 as or in addition to
oostegites. No females with typical oostegites were found. Coxa 4 is very broad with nearly rectangular margins, like coxae 3+4 together in Cypruicideae.

Conclusions

Having studied these — until now all called thauematelsonine — genera, I feel certain that Gurjanova's idea of separating classical stenothoid genera from those ones with a "wonderful telson" is still valid. In spite of Barnard's fears (1972a: 318) there are no problems in defining a vertically inserted, hugely elevated, rudder-like telson such as in Antatelson, Ausatelson and Thaumatelson. This clade (which will be treated in Part 2 of this series) is highly aberrant, all living in the south of Australia (Bass Strait) and Antarctica, and all are reported to have a similar ecology.

Less striking are those genera which Barnard saw as bridging stenothoids and thaumatelsonids and which are better known now. Their common character is a telson with sclerified margins, basically coalesced with urosomite 3. This telson can be adjacent to the urosome (see R. rongo Barnard, 1972b: fig. 92; R. noko Barnard, 1974: fig. 71, and figures herein). It may also be separate from the urosome or upright (see Ranaulhara judithae Moore, 1981: fig. 14; *Pseudothaumatelson cyproides* Nicholls, 1938: fig. 28, and figures herein), thus appearing variously boat-, shovel- or spoon-like. In the habitus drawings of *Pseudothaumatelson cyproides* Nicholls, 1938 and *Thaumatelsonella kingelepha* (Rauschert and Andres, 1991), or in figures given in this paper, the vaulted prolongation of urosomite 1 is shown to fit in the excavation of the telson, thus strengthening the unity of the urosome.

While the bulge on urosomite 1 is differently developed, the three-dimensionally inserted, proximally thickened, folded, marginally stiffened and partly coalesced telson is always present, thus offering a well defined synapomorphy. This paper illustrates different types of telson within stenothoid genera:

1. a flat, horizontally inserted, 2-dimensional, free telson (basic Stenothoidae);
2. a proximally thickened, three-dimensionally inserted, basically coalesced, marginally stiffened and dorsally excavate telson, which is described by different authors as boat- or spoon-like (treated here); and
3. a vertically , 2-dimensionally inserted, hugely enlarged telson (treated in Part 2 of thaumatelsonine species).

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References


REDIAGNOSIS OF THE ENDEMIC SOUTHERN AUSTRALIAN GENUS
PARASTACILLA HALE, 1924 (CRUSTACEA: ISOPODA: ARCTURIDAE) WITH
DESCRIPTIONS OF TWO NEW SPECIES

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Abstract

The arcturid genus Parastacilla Hale, 1924 is rediagnosed and a key to its four species presented. All species, P. truculenta Hale, 1924; P. bakeri Hale, 1924; P. torus sp. nov. and P. tingara sp. nov. have limited distribution in southern Australia.

Introduction
The arcturid isopod genus Parastacilla was erected by Hale (1924) to include two endemic South Australian species P. truculenta and P. bakeri. Hale distinguished the new genus on the basis of the robust antennae, stout uniaxial antenna 2 flagellum, flattened anterior pereopods and unsegmented pleon.

Hale believed that Parastacilla resembled Astacilla Cordiner to which he assigned some southern Australian species; these now belong to Neastacilla Tattersall. The species of Parastacilla share many morphological similarities with species of Neastacilla from southern Australia: elongation of pereonite 4, an extremely geniculate body between pereonites 4 and 5 and similar sexual morphologies with curved, short appendix masculina and simple penial plate.

Pereopods 2 to 4 of Parastacilla are uniquely flattened and sparsely setose. The pereopods of Neastacilla species are elongate with closely spaced, long setae. In Parastacilla pereopod 2 has a small dactylus and unguis and pereopods 3 and 4 lack a dactylus. Generally, in species of Neastacilla pereopods 2 to 4 have a dactylus and unguis. In Parastacilla the body is stout and cylindrical while species of Neastacilla are elongate and slender. Antenna 2 of Parastacilla is stout with a flagellum of two articles; the distal article is very small and bears a claw. Antenna 2 of Neastacilla is slender with two or three flagellar articles of similar lengths. The fusion of the head and pereonite 1, a characteristic of the arcturid family, is extended anteriorly and incised in species of Parastacilla; this extension is evident only to a small extent in some species of Neastacilla.

The genus was partially redescribed from the types by Hale (1946) but has not been studied since. Two new species have been discovered in collections at Museum Victoria, Melbourne, and the description of these species has uncovered errors in Hale's original generic diagnosis. The types of both P. bakeri and P. truculenta have been examined to rediagnose the genus and its species. The new species described herein and a survey of museum collections has extended the known distribution of the genus from South Australia to Victoria, Tasmania and Western Australia.

Abbreviations are: NMV, Museum Victoria, Melbourne, Australia; SAM, South Australian Museum, Adelaide, Australia.

Arcturidae Bate and Westwood, 1868
Parastacilla Hale, 1924


Type species. Parastacilla truculenta Hale, 1924 (by original designation).
Diagnosis. Body cylindrical and strongly geniculate. Lateral margins of head and pereonite 1 extended anteriorly and separated by a lateral incision. Antenna 2 stout; flagellum of 2 articles, second article very small with elav and spines medially along length. Maxillipedal palp article 4 narrower than article 3. Pereopod 1 within margin of head; with dactylus barely longer than wide, without ungus, with setae on the medial and oblique distal margin. Pereopods 2 to 4 flattened and compact, with paired sparse and widely spaced setae; setae on ischium and carpus shorter than the article. Pereopod 2 with very small dactylus present on mesial surface, with ungus (sometimes with secondary ungus). Pereopods 3 and 4 dactylus absent. Pereopods 5 to 7 progressively shorter; dactylus with primary and slightly smaller secondary ungus (sometimes fused); pereopod 5 basis twice length of pereopod 6 basis. Pereonite 4 up to 9 times as long as pereonite 3; males with pereonite 4 as long as in female. Pleon with dorsolateral wings. Uropodal inner ramus with 2 setae of subequal length. Male pleopod 1 exopod laterally notched, with 2 proximal setae of unequal length on posterior face. Male pleopod 2 with appendix masculina short, reaching end of endopod, curved, with ridge on posterior face, apex simple.

Composition. Parastacilla truculenta Hale, 1924; P. bakeri Hale, 1924; P. torus sp. nov.; P. tingara sp. nov.

Remarks. The flagellum of the second antenna consists of two articles, not one as described by Hale (1924). Hale believed that all four anterior pereopods consisted of six articles, ending in a rounded setose propodus. Examination has shown that in all species the second pereopod has a small dactylus and ungus. Some specimens have a secondary ungus on the dactylus of pereopod 2.

Key to species of Parastacilla

1. Pereonites without large dorsal elevations..............P. truculenta
   — Pereonites with dorsal elevations.................................P. truculenta

2. Head without dorsal elevation; antenna 2 articles 4 and 5 with tuberculate elevations
   — Head with dorsal elevation; antenna 2 articles mostly smooth, may have some tuberculation.................................P. bakeri

3. Female pereonite 4 expanded laterally; large anteriorly directed dorsal elevations on pereonites 3 and 4; male without elevation on pereonite 3, elevation on pereonite 4 with 2 apices........................................P. torus
   — Female pereonite 4 not expanded laterally; elevations on pereonites 3 and 4 of equal size to elevation on head........................................P. tingara

Parastacilla truculenta Hale

Parastacilla truculenta Hale, 1924: 210-211, fig. 1.—Hale, 1946: 187-188, fig. 15 A.

Material examined. Holotype. South Australia, Beachport, 5-7 m, dredge, H.M. Hale, SAM C237 (1 female, 18.5 mm).
Other material. South Australia, Flinders Island, “The Hotspot” reef, 5 n. miles W of Flinders Island (33°40.80’S, 134°22.50’E), 21 m, large red algae, SCUBA, G.C.B. Poore on FV Limnos, 20 Apr 1985 (sta SA-69), NMV J16696 (manca 2, 0.6 mm).

Diagnosis. Female: 1 head with dorsal elevation. Fusion of head and pereonite 1 indicated by a dorsolateral groove with the lateral margin extended anteriorly and inersed laterally. Pereonites 2 to 7 smooth. Pereonite 4 more than 9 times as long as pereonite 3. Pereonites 5 to 7 progressively shorter. Pleon length greater than the combined lengths of pereonites 5 to 7; with small dorsolateral wings.

Eyes lateral. Antenna 1 extending to end of peduncle article 2 of antenna 2; uniarticulate flagellum with lateral and distal aesthetes. Antenna 2 stout, more than half length of body; flagellum of 2 articles and elav, with a medial row of comb-like spines full length.

Pereopod 1 dactylus barely longer than wide, without ungus, bearing 2 medial and 3 oblique setae. Pereopod 2 with dactylus and ungus, Pereopods 3 and 4 without dactylus. Pereopods 5 to 7 dactylus with ungus and secondary ungus.

Uropodal exopod oblique, not reaching mid-point of endopod, with 2 distal setae of equal length.

Distribution. South Australia; subtidal.
Remarks. This redescription was based on the holotype (SAM C237). This specimen is an immature female in which the oostegites are not fully formed. Male specimens have not been found. A specimen from Museum Victoria (NMV J16696) is a manca 2 stage: a juvenile with a developed pereopod 7 and undeveloped sexual appendages.

**Parastacilla bakeri** Hale

**Figure 1**

*Parastacilla bakeri* Hale, 1924: 211-212, fig. 2.—Hale, 1946: 187-188, fig. 15 B.

**Material examined.** Holotype. South Australia. Marino Reef, W.H. Baker, SAM C238 (1 male, 9.5 mm).

**Diagnosis.** Male: Head with small dorsal elevation. Fusion of head and pereonite 1 indicated by dorsolateral groove with lateral margin slightly extended anteriorly and incised laterally. Pereonite 2 smooth. Pereonite 3 with dorsal elevation. Pereonite 4 about 9 times as long as pereonite 3 with midlength dorsal elevation of similar height to elevation on pereonite 3. Pereonites 5 to 7 progressively shorter, smooth. Pleon longer than combined lengths of pereonites 5 to 7, with small lateral expansions, small dorsal elevation at two-thirds length and 2 dorsolateral wings.

Eyes lateral. Antenna 1 extending to end of the peduncle article 2 of antenna 2; uniarticulate flagellum with aesthetascs attached laterally and distally. Antenna 2 stout, more than half as long as body, tuberculate elevations with setae on dorsal surface of peduncle articles 3–5; flagellum of 2 articles and claw, with a medial row of spines along full length.

Pereopod 1 dactylus barely longer than wide, without unguis, bearing 2 medial setae and 3 oblique setae on the distal margin. Pereopods 2 to 4 tuberculate. Pereopod 2 with dactylus on medial surface, with unguis. Pereopods 3 and 4 without dactylus. Pereopods 5 to 7 with an unguis and a secondary unguis. Pereopods 5 and 6 dactylus denticulate; pereopod 7 dactylus smooth.

Uropodal exopod not reaching midpoint of endopod, with 2 distal setae of equal length.

Male pleopod 2 appendix masculina with ridge on posterior face, apex simple, curved and short (see Remarks).

**Distribution.** South Australia; subtidal.

**Remarks.** Hale’s original description stated that the type of *Parastacilla bakeri* (SAM C238) was ‘mounted in Balsam’ and so it was only possible to figure the whole animal and antenna 1. In 1946 Hale re-illustrated the flagellum of antenna 2 and pereopod 1 of what he recorded was the same specimen, apparently not mounted. The specimen (SAM C238) redescribed here was unmouted and undissected before being partially dissected for this redescription. It is possible that Hale’s (1946) illustrations were done without any dissecting and mounting. I assume that this is the holotype as a second specimen was never mentioned. The holotype designated by Hale was a male and is the only specimen available.

The appendix masculina was examined in situ from the holotype but not illustrated.

**Parastacilla tingara** sp. nov.

**Figures 2–4**

**Material examined.** Holotype. Tasmania, Waterhouse Point (40°49.25'S, 47°40.04'E), 5 m, seagrass: *Amphibolus antarcticus*, G. Edgar, 24 Apr 1992, NMV J39333 (1 female, 13.5 mm).

Paratype. South Australia, Edinburgh (35°05'S, 137°45'E), 3 m, red algae: *Caulocystis cephalomithos*, hand collection, R.A. King, 14 Mar 1999, NMV J39334 (1 juvenile, 8.0 mm).

**Diagnosis.** Head with dorsal elevation. Pereonite 3 with dorsal elevation, smaller than elevation on head. Pereonite 4 with some granulation on peduncular articles 3 and 4.

**Description.** Female: Anterolateral margins of head with small tubercles, rostral point very small. Head with large dorsal blunt elevation, with setae extending out of elevation. Fusion of head and pereonite 1 indicated by dorsolateral groove with lateral margin extended slightly anteriorly and incised laterally. Pereonite 2 smooth with small tuberculate anterolateral extensions, with some dorsal setae. Pereonite 3 with large dorsal elevation of a similar size to elevation on head, with dorsal setae; anterolateral extensions small and tuberculate. Pereonite 4 about 7 times as long as pereonite 3; with row of dorsolateral tubercules along anterior margin and small anterolateral expansions; not markedly wider than previous pereonites; with smaller dorsal elevation at midlength, with dorsal setae. Pereonites 5 to 7 lateral margins not expanded but slightly tuberculate, progressively shorter posteriorly, dorsal surfaces with numerous setae. Pleon longer than combined lengths of pereonites 5 to 7, with small lateral expansions, a small dorsal elevation at quarter length and 2 dorsolateral wings.

Eyes lateral. Antenna 1 extending almost to end of peduncle article 2 of antenna 2; uniarticulate...
Figure 1. *Parastacilla bakeri* male holotype (SAM C238): a, lateral view; distal end of antenna 2; pereopods 1 to 7. Scales: a = 1.0 mm; b (P1–P7) = 0.5 mm.
Figure 2. Parastacilla tingara female holotype (NMV J39333): a, dorsal view; b, lateral view; c, ventral view with oostegites detailed; antennae 1 and 2. Scales: a, b = 1.0 mm; c = 1.0 mm; A1 = 0.5 mm; A2 = 1.0 mm.
flagellum with distal aesthetases. Antenna 2 stout, more than half length of body, margins with some tuberculation; flagellum of 2 articles and claw, with medial row of comb-like spines along full length.

Maxilla 1 inner lobe with 3 terminal setae; outer lobe with 10 distal robust setae. Maxilla 2 inner lobe with 16 plumose setae; middle lobe with 4 setae; outer lobe with 3 setae. Maxillipedal endite with 19 mesial setae; 1 coupling hook present; palp article 2 with mesial setal rows; article 3 with mesial and lateral setal rows; article 4 narrower than article 3 and with mesial and lateral setal rows; article 5 with distal setae.

Pereopod 1 included within margin of head; propodus as long as carpus; dactylus barely longer than wide, without unguis, with 3 medial setae and 3 setae on the distal oblique margin. Pereopod 2 with dactylus, unguis and secondary unguis. Pereopods 3 and 4 without dactylus. Pereopods 5 to 7 with unguis and secondary unguis two-thirds length of primary unguis; dactylus barely denticulate with raised setose area close to dactylus/propodus suture; pereopod 5 basis length twice pereopod 6 basis.

Uropodal exopod oblique, not reaching midpoint of endopod, with 2 setae of subequal length. Oostegites present on pereopods 1 to 4; oostegite 4 without suture.

**Distribution.** South Australia to Tasmania; subtidal.

**Etymology.** “Tingara” is an Australian aboriginal word meaning the sea.

**Remarks.** This species most closely resembles *Parastacilla bakeri*. Males are generally only slightly smaller than females in this genus but the male specimen of *P. bakeri* is much smaller than the female of *P. tingara* (9.5 mm vs 13.5 mm) and yet both are fully mature. Ornamentation of the head, usually highly species specific, differs between *P. bakeri* and *P. tingara*. Antenna 2 of *P. bakeri* is more slender than antenna 2 of *P. tingara*. The morphology of antenna 2 is usually extremely similar between sexes of the same species. The scales on the antenna 2 flagellum in *P. bakeri* and *P. tingara* are different. *P. bakeri* has simple scales and *P. tingara* has comb-like scales as does *P. torus*. Denticulation of the
Figure 4. *Parastacilla tingara* female (NMV J39333): pereopods 1 to 7. Scale = 0.5 mm.


**Parastacilla torus** sp. nov.

**Material examined.** Holotype, Victoria, Venus Bay (38°39.57'S, 145°42.00'E), 9 m, SCUBA, 6 Mar 1982, NMV J16691 (1 female, 9.5 mm).

Paratypes. Victoria. Twin Reefs, 11 m, 4 Mar 1982, NMV J16693 (1 male, 6.0 mm), Venus Bay, 8 m, 5 Mar 1982, NMV J16695 (2 juvenile males), Cape Paterson (38°46.22'S, 145°36.53'E), 6 m, 5 Mar 1982 NMV J16692 (1 juvenile), Harmers Haven, 6 m, 6 Mar 1982, NMV J16690 (2 juveniles), Nepean Bay (38°18.26'S, 147°39.57'E), 8 Apr 1998, NMV J39297 (1 female, 8.5 mm; 1 immature female, 7.0 mm).

South Australia. Flinders Island (39°52.17'S, 148°01.02'E), SCUBA, 18 m, 19 Apr 1985, NMV J16688 (1 male, 7.0mm), “Hotspot Reef”, 5 n. miles W of Flinders Island (33°40.80'S, 134°22.50'E), 21 m, 20 Apr 1985, NMV J16687 (1 male, 8.5 mm).

Tasmania. Pegleg Cove, Deal Island (43°56.31'S, 147°18.59'E), 8 m, 13 Apr 1983, NMV J16687 (1 male, 6.5 mm).

Western Australia. North Lumps, 2 km Off Mullaloo (31°47.12'S, 115°43.54'E), 8 m, 2 May 1986, NMV J39296 (1 female, 8.0 mm).

**Diagnosis.** Head with dorsal elevation. Pereonite 3 in female with an anteriorly directed dorsal elevation. Pereonite 4 in female with large anteriorly directed elevation covering the entire dorsal surface, with anterolateral expansions. Males without the elevation on pereonite 3 or the anterolateral expansions; with a dorsal elevation on pereonite 4 with 2 apices.

**Description.** Female. Anterolateral margins of head rounded, rostral point very small. Head with large blunt elevation. Fusion of head and pereonite 1 indicated by dorsolateral groove with lateral margin extended anteriorly and incised laterally. Pereonite 2 smooth, lateral margins visible in dorsal view with small tubercles. Pereonite 3 with large anteriorly directed dorsal elevation, half height of elevation on head, lateral margins visible in dorsal view with small tubercles. Pereonite 4 about 8 times as long as pereonite 3; anterolateral expansions rounded and tuberculate, projecting around peronite 3; markedly wider than previous peronites; with large dorsal elevation; small posterior lateral projections also present. Pereonites 5 to 7 with row of tubercles along each posterior dorsal margin; progressively shorter posteriorly. Pleon longer than combined lengths of peronites 5 to 7; with small anterior lateral expansions, a small dorsal elevation and with dorsolateral wings.

Eyes lateral. Antenna 1 extending midway along peduncle article 2 of antenna 2; small tubercles on dorsal surface of peduncle article 1; flagellum uniarticulate with aesthetases along distal and lateral edge. Antenna 2 stout, more than half as long as body; flagellum of 2 articles and claw, with medial row of comb-like spines full length.

Maxilla 1 inner lobe with 3 terminal setae; outer lobe with 11 distal robust setae. Maxilla 2 inner lobe with 18 plumose setae; middle lobe with 4 setae; outer lobe with 3 setae. Maxillipeds endite with 19 mesial setae; 2 coupling hooks present; palp article 2 with mesial setal rows; article 3 with mesial setal rows; article 4 narrower than article 3, with mesial and lateral setal rows; article 5 with distal setae.

Pereopod 1 included within margin of head; propodus as long as carpus; dactylus barely longer than wide, without unguis, with 3 medial setae and 4 setae on distal oblique margin. Pereopod 2 with small dactylus with unguis and sometimes secondary unguis (see Remarks). Pereopods 3 and 4 dactylus absent. Pereopod 5 to 7 with unguis and secondary unguis, dactylus denticulate; pereopod 5 basis length twice pereopod 6 basis.

Uropod exopod oblique, not reaching midpoint of endopod, with 2 setae of subequal length. Oostegites present on pereopods 1 to 4; oostegite 4 with suture.

Male: Anterolateral lobes of head rounded, rostral point undetected. Fusion of head and pereonite 1 indicated by dorsolateral groove with lateral margin extended anteriorly and incised laterally. Head with large blunt elevation. Pereonites 2 and 3 smooth, lateral margins not expanded. Pereonite 4 around 8 times length of pereonite 3, with large forward facing dorsal elevation with 2 apices; as wide as previous peronites; lateral margins not expanded. Pereonites 5 to 7 relatively smooth, lateral margins not expanded. Pleon length greater than combined lengths of peronites 5 to 7, with small anterior lateral expansions, large dorsolateral wings present.

Eyes small, subtriangular and positioned laterally. Antenna 1 and antenna 2 as for female.
Figure 5. *Parastacilla torus*, female holotype (NMV J16691): a, lateral view; b, dorsal view; e, ventral view with oostegites detailed. Male: c, dorsal view; d, lateral view. Scale = 1.0 mm
Figure 6. *Parastacilla torus*, female holotype (NMV J16691): left maxilliped, left maxillae 1 and 2, left and right mandibles, antennae 1 and 2, distal end of uropod. Scales: a (MP, MX1, MX2, IMD, rMD, U) = 0.5 mm; b (Al) = 0.5 mm; c (A2a) = 1.0 mm; d (A2b) = 0.5 mm.
Figure 7. *Parastacilla torus*, female holotype (NMV J16691): pereopods 1 to 7. Scale = 0.5 mm
Figure 8. *Parastacilla torus*, male (NMV J16688); pleopods 1 and 2, penes. Scales: a (PL1, PL2) = 0.5 mm; b (Pe) = 0.5 mm.

Mouthparts as for female. Pereopods as for female.

Pleon 1 exopod with lateral notch and 2 plumose setae of unequal lengths on posterior face. Pleopod 2 appendix masculina with ridge on posterior face, apex simple, curved and short. Penes simple, straight.

Distribution. Tasmania, South Australia and Western Australia; subtidal.

Etymology. “Torus” is Latin for round elevation or protuberance, referring to the ornamentation of the head.

Remarks. Two specimens were found with one unguis on the dactylus of the second pereopod.

Acknowledgments

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References


LEVINEBALIA MARIA, A NEW GENUS AND NEW SPECIES OF LEPTOSTRACA (CRUSTACEA) FROM AUSTRALIA

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Abstract


The genus Paranebalia historically contained three species but with the discovery of a new species from southeastern Australia a new genus, Levinebalia, has been erected for Paranebalia fortunata Wakabara, 1976 and L. maria sp. nov. (type species). Species of Levinebalia differ from Paranebalia in: having the surface of their eyes smooth; lacking a setal brush on the mandible incisor; having smooth pleopod peduncle margins and having crenellations on the margin of pleonites 5, 6, and 7. The margin of pleonite 5 is smooth in Paranebalia. Of significance is antenna 2 of Levinebalia. It has several rows of small and medium-sized spines and patches of tiny spines on the third peduncular article and flagellum. In addition, there are conical sensory structures proximally on the third peduncle article. The conical sensory structures and spines on antenna 2 have not been observed in any other genus of Leptostraca.

Introduction

Historically there are six genera in the leptostrean family Nebaliidae: Nebalia Leach, 1814; Paranebalia Claus, 1880; Nebaliella Thiele, 1904; Dahlella Hessler, 1984; Sarsinebalia Dahl, 1985; and Speonebalia Bowman, Yager and Iliiffe, 1985. Paranebalia was recognised by Claus (1880) as being distinct from Nebalia, having thoracopods that extend beyond the ventral margin of the carapace, a greatly reduced epipod on the thoracopods and a rostrum without a keel but with a subterminal spine. Paranebalia contains three species, P. longipes (Willemoes-Suhm, 1875), P. fortunata Wakabara, 1976, and P. belizensis Modlin, 1991.

Paranebalia longipes and P. belizensis are most similar to one another having denticulate eyes, denticles or crenellations on the pleopod peduncles, and crenellations only on the dorsal margin of pleonites 6 and 7. They also share the presence of a setal brush on the mandible incisor. The setal brush is unique to P. longipes and P. belizensis.

Paranebalia fortunata and a new similar Australian species do not have denticulate eyes or crenellations on the pleopod peduncles and the dorsal margin of pleonite 5 and pleonites 6 and 7 have very small crenellations. The new species, here described as Levinebalia maria gen. et sp. nov., and Paranebalia fortunata have the unique structures on antenna 2 (Fig. 4a). Both species have several rows of small and medium spines, and patches of tiny spines, on the third peduncle article and the flagellum (Figs 5c, d, e) as well as conical structures proximally on the third peduncular article (Figs 5a, b). These may be chemosensory organs as vents can be seen around the base (Fig. 5b). Wakabara (1976: 300) observed spines on the third article of antenna 2 and the flagellum of P. fortunata and described them as "short, strong spines". She did not however, mention any conical structures on antenna 2, but my examination of a paratype revealed their existence. The conical sensory structures and spines on antenna 2 have not been observed in any other genus of Leptostraca. For these reasons the two species are placed in a new genus, Levinebalia.
Methods

All specimens examined came from the collections of Museum Victoria (NMV). Specimens were dissected and mounted in glycerol and slides were viewed under an Olympus BH-2 or BX-50 compound microscope. Whole specimens and body parts were drawn with the aid of a camera lucida. Plumose setae are numerous on many body parts, but in most cases they have been figured without their setules so as not to obscure other details. Abbreviations used in figures are: RO, rostrum; A1, antenna 1; A2, antenna 2; MD, mandible; MX1, maxilla 1; MX2, maxilla 2; T1, T3, T8, thoracopods 1, 3, and 8; P1–P6, pleopods 1–6; and CR caudal rami or furca. Scale bars are 1 mm.

Terminology. I follow the usage of Watling (1989) for setal classification. Spine has been used for a non-articulating cuticular process, seta for an articulating cuticular process and setule for a flexible extension of the shaft of a seta. A plumose seta is a seta with a regular row of long setules on each side (Watling, 1989: Fig. 4g). The comb-row consists of a row of bi-pectinate setae (Fig. 6b) and is equivalent to the spine-row of other authors (e.g., Dahl, 1985: Fig. 155). The term bi-pectinate setae refers to setae that have a comb-like row of projections along each side of the central shaft of the seta.

Scanning electron microscopy (SEM). Leptostracan specimens examined under the scanning electron microscope (SEM) were dehydrated in an ethanol series (70%–absolute EtOH, with 10% increments). Specimens were left in each alcohol concentration for 30 minutes. Specimens were then placed in a 50:50 mixture of absolute ethanol and hexamethyldisilazane (HMDS), followed by a 25:75 solution of absolute ethanol and HMDS, then placed in 100% HMDS before being air-dried. Specimens were left in each HMDS solution for 10 minutes. Specimens were mounted on SEM stubs with double-sided Scotch™ tape. Stubs were sputter-coated with gold and examined under a Phillips 505 (tungsten filament) scanning electron microscope at 20 and 20.1 kv. The SEM was linked to a computer and the program Spectrum was used to capture the images.

Levinebalia gen. nov.

Type species. Levinebalia maria sp. nov.

Diagnosis. Carapace emarginate, not sculptured. Rostrum with subterminal spine, keel absent. Surface of eyes smooth, without denticles or euticular outgrowths. Eyes elongate and with ommatidia. Antenna 1 4-articulate, article 4 without robust setae but with a variable number of teeth along anterior margin. Male flagellum modified, either swollen (in juveniles) or transformed into a callynophore. Antenna 2 with 2 rounded euticular outgrowths on peduncle article 3 and conical sensory organs (Fig. 4a), surface of peduncle article 3 and flagellum with patches of spines (Fig. 4a), dorsal spine absent. Mandible incisor without setal brush. Maxilla 1 palp long, well developed. Maxilla 2 endopod uni-articulate. Thoracopods closely spaced, long and tapering, extending beyond ventral margin of carapace; epipod small, shorter than exopod; endopods showing some articulation. Pleopods 1–4 peduncle margins smooth. Pleopod 1 exopod with or without comb-row of bi-pectinate setae (Fig. 6a). Pleonites 5, 6, and 7 margins with tiny serrations. Pleonites 5, 6, and 7 all approximately equal in size. Pleopod 5 longer than pleopod 6. Caudal furca short and stout.

Composition. Levinebalia maria sp. nov.; Levinebalia fortunata (Wakabara, 1976) comb. nov.

Etymology. Levi (Latin) means smooth, referring to the absence of denticles on the surface of the eyes.

Remarks. Levinebalia differs from Paranebalia in a number of ways. Species of Paranebalia have denticulate eyes, distinctive eurellate margins only on pleonites 6 and 7 and eurellate pleopod peduncles. They also have a setal brush on the mandibular incisor. Levinebalia species have none of these characters. The unique characters of Levinebalia are the rows of small and medium spines and patches of tiny spines on the third peduncle article and flagellum of antenna 2 (Figs 5c, d, e) and the conical structures proximally on the third peduncle article (Figs 5a, b). These may be chemosensory organs as vents can be seen around the base (Fig. 5b).

Claus (1880) used the absence of a rostral keel and the presence of a rostral spine as characters defining Paranebalia. Both species of Levinebalia also have these characters. However, Dahlella and Sponginebalia also lack a rostral keel and Sarsinebalia has a rostral spine. Their presence in species of Paranebalia and the two species assigned to Levinebalia suggests all are probably related but it is likely that these characters have arisen more than once. Indeed, Paranebalia and Levinebalia do share three unique synapomorphies: the elongate thoracopod:
**Levinebalia maria**, new genus and species of Leptostraca

Reduced epipod; and rounded cuticular outgrowths on article 3 of antenna 2 (Figs 4a, b). However, the differences between *Paranebalia* and *Levinebalia* described above, especially the unique armature of antenna 2 which is not present in any other Leptostraca, suggest more strongly that the new genus *Levinebalia* should be erected for *Levinebalia fortunata* and the new Australian species.

Unfortunately, Wakabara (1976) did not mention the comb-row on the exopod of pleopod 1. Her illustration (Fig. 2f) indicates only one type of seta on the lateral margin of the pleopod 1 exopod. However my examination of a paratype of *Paranebalia fortunata* revealed the presence of a comb-row, half as long as the exopod. The finely bi-pininate setae are approximately equal in length to the smooth setae found distally on the lateral margin of the exopod. I have also examined several other undescribed species of *Levinebalia* from the collection of Museum Victoria and all have comb-rows on the exopod of pleopod 1.

The most recent key to extant families and genera of Leptostraca (Martin et al., 1996) needs to be emended and a new key to the genera of the Leptostraca is in preparation (Walker-Smith and Poore).

*Levinebalia* is represented by *L. maria* from Tasmania, Australia and *L. fortunata* from New Zealand. Examination of material from Museum Victoria collections reveals *Levinebalia* is found throughout Australia; in New South Wales, Queensland, north Western Australia, South Australia, and Victoria but these specimens may not belong to the new species described here. *Paranebalia* has two described species: *P. longipes* originally identified from the Atlantic but also recorded from Bermuda (Willemoes-Suhm, 1975; Sars, 1887; Verrill, 1923; Clark, 1932), Virgin Islands (Thiele, 1904), southern Florida (Brattegard, 1970), West Indies (Thiele, 1905), Japan (Thiele, 1905), Gulf of Siam (Thiele, 1905) and Torres Strait (Thiele, 1905); and *P. belizensis* from Belize, Central America. The first record of *Paranebalia* in Australia was by Hale (1929: 367) as *P. longipes* "or a closely allied species" from the coast of South Australia. Dahl (1985: 135) suggested *Nebalia* and *Paranebalia* which were originally "assumed to be composed of a small number of highly variable species, with more or less cosmopolitan distribution" actually contained a considerable number of species. The existence of many undescribed species of leptostracans in Australian museum collections (Dahl's and own unpublished observations in litt.; Walker-Smith, 1998) suggest that records of *Paranebalia longipes* remote from the type locality are dubious.

*Levinebalia maria* sp. nov.

Figures 1–6

**Material examined.** Holotype. Tasman Sea, 15 km E of Maria I., Tasmania (42°37'S, 148°20'E), 102 m, WIOI epibenthic sled, R.S. Wilson, on RV Soela, 9 Oct 1984 (stn S05/84/1), NMV J34661 (1 female).

**Paratypes.** Collected with holotype, NMV J34663 (1 immature male, allotype). Australia, Tasmania, Maria I., 5 km NE of Mistaken Cape (42°37'S, 148°12.5'E), 100 m, fine muddy bryozoan sand, WIOI epibenthic sled, R.S. Wilson on RV Challenger, 23 Apr 1985 (stn TAS 31), NMV J34256 (10 females and 1 male), 15 km E of Maria I. (42°37'S, 148°20'E), 102 m, WIOI epibenthic sled, R.S. Wilson, on RV Soela, 9 Oct 1984 (stn S05/84/1), NMV J34574 (19 immature males); NMV J13282 (40 specimens; mean carapace length, 3.19±0.43 mm); NMV J34573 (1 specimen; carapace length, 3.7 mm). 20 km E of Falmouth (41°32.9’S, 148°35.0′E), 122 m, WIOI epibenthic sled, R.S. Wilson, on RV Soela, 10 Oct 1984 (stn S05/84/05), NMV J13283 (4 specimens; mean carapace length, 3.15±0.03 mm). Off Freycinet Peninsula (42°20.0′S, 148°38.70′E), 800 m, coarse shelly sand, WIOI epibenthic sled, M.F. Gomon et al. on RV Franklin, 27 Jul 1986 (stn SLOPE 45), NMV J34576 (3 specimens; mean carapace length, 3.37±0.18 mm). Off Freycinet Peninsula (41°56.60′S, 148°37.90′E), 200 m, coarse bryozoan sand, WIOI epibenthic sled, M.F. Gomon, M.F. et al. on RV Franklin, 27 Jul 1986 (stn SLOPE 49), NMV J34580 (4 specimens).

**Description of holotype.** Female (Fig. 1) with 3 embryos, entire length 4.8 mm. Carapace length 3.0 mm, depth 2.0 mm, emarginate, dorsally convex, anterior and posterior margin rounded, 3.6 times length of rostrum, posterior margin reaching pleonite 4, surface not sculptured.

Rostrum (Fig. 1) length 2.79 times width, greatest depth 0.23 times length, subterminal spine present, keel absent.

Eyestalks (Fig. 1) pigmented, ommatidial region 0.51 times length of eye. 0.69 times length of rostrum, width 0.41 times length, dorsal margin slightly convex, without denticles, dorsal papilla absent, tapering, rounded distally, supraocular scale absent.

Antenna 1 (Fig. 1) article 2 length 2.8 times width, 9 mesiodistal plumose setae; article 3 0.64 times length of article 2, with 10 distomedial plumose setae; article 4 medial flange with 19 teeth, each tooth with denticleulate surface, numerous plumose setae over lateral and medial surface;
Figure 1. Levinebalia maria. Female holotype J34661: dorsal view of rostrum; medial view of antenna 1; lateral view of antenna 2; lateral view of mandible palp.
Figure 2. *Levinebalia maria*. Female holotype J34661: thoracopod 1 anterior view; thoracopod 3 posterior view; thoracopod 8 anterior view; maxillae 1 and 2.
Figure 3. Levinebalia maria. Anterior section of male allotype J34663. Female holotype J34661: pleopods 1-4 anterior view; dorsal view of caudal furca.
swollen scale length 2.7 times width, heavily setose, with plumose setae; flagellum with 4 articles, article 1 0.8 times length of flagellum, 4 aesthetascs anteriorly.

Antenna 2 (Figs 1, 4a, 5) article 2 length 1.52 times width, without dorsal spine; articles 3 and 4 fused, combined length 2.19 times length of article 2, heavily setose on anterior surface, with 2 rounded cuticular outgrowths and a row of conical sensory organs, 1 row of spines, several rows of smaller spines and patches of tiny spines on the outer (lateral) surface of articles 3 and 4 and flagellum; flagellum with 6 articles, approximately 3 plumose setae per article.

Mandibular palp (Fig. 1) of 3 articles; article 2 with long medial seta; article 3 approximately equal in length to article 2, margins tapering, 3 rows of plumose setae along posterior and distal margin, increasing in length distally, terminal row of short setae; well developed molar process, without setal brush; mandible incisor with 1 tooth.

Maxilla 1 (Fig. 2) endite 1 rounded with 1 row of plumose marginal setae; endite 2 rectangular with 2 rows of simple robust setae and 3 plumose setae; palp long, well developed, with 12 lateral setae and 2 terminal setae.

Maxilla 2 (Fig. 2) with 5 endites; endite 1 expanded distally, margin with 3 rows of plumose setae, fine setae along proximal margin; endite 2 rectangular with 3 rows of plumose supraeucuticular setae; endite 3 approximately equal to endite 2, with 2 rows of plumose setae; endite 4 0.4 times length of endite 3, with 2 plumose setae; endite 5 same size as endite 4 with 1 long smooth seta; endopod 1.16 times length of exopod, tapering distally, of 1 article, 3 plumose setae terminally; exopod with plumose setae along lateral and terminal margins.

Thoracopod endopods and exopods tapering distally (Fig. 2); epipods reduced. Thoracopod 1, exopod lateral and distomedial margins setose, 0.52 times length of endopod; endopod anterior margin with 2 rows of plumose setae; epipod 0.31 times length of exopod. Thoracopod 3, exopod lateral margin setose, 0.65 times length of endopod; endopod anterior margin with 2 rows of plumose setae, posterior margin with several plumose setae distally; epipod 0.3 times length of exopod, dorsal lobe longer than ventral lobe, dorsal lobe tapering distally, ventral lobe rounded, margin with fine hair-like setae. Thoracopod 8 exopod lateral margin setose, 0.41 times length of endopod; endopod anterior margin with 2 rows of plumose setae, posterior margin with single row of setae distally; epipod 0.73 times length of exopod, dorsal lobe narrow and elongate, longer than ventral lobe, ventral lobe distally rounded, margin of epipod with thin hair-like setae.

Pleonites with tiny pointed denticles along dorsal margin of pleonites 5, 6, and 7; pleonite 7 0.67 times length of telson, 1.20 times length of pleonite 6, equal to pleonite 5, 1.20 times length of pleonite 4.

Pleopod 1 (Figs 3, 6) exopod 0.71 times length of peduncle, 0.67 times length of endopod, lateral margin with comb-row of bi-pectinate setae, comb-row 0.38 times length of exopod, 6 robust simple setae distally along lateral margin, 2 smooth robust setae terminally, medial margin with numerous long, fine plumose setae; endopod with long fine plumose setae on lateral and medial margins, 1 smooth seta and one short, stout spine terminally.

Pleopod 2 (Fig. 3) peduncle with 5 distal plumose setae, posterior margin not denticulate; exopod 0.82 times length of peduncle, 0.82 times length of endopod, lateral margin with 5 pairs of smooth setae, medial margin with long, fine plumose setae; endopod lateral and medial margins with long, fine plumose setae, robust smooth seta and stout spine terminally; reticulum present above endopod.

Pleopod 3 (Fig. 3) posterior margin of peduncle not serrate; exopod 0.73 times length of peduncle, 0.79 times length of endopod, 6 pairs of smooth setae, longer plumose setae between each pair, 3 terminal smooth setae, medial margin with long, fine plumose setae; endopod lateral and medial margins with long, fine, plumose setae, robust smooth setae and stout spine terminally; reticulum present above endopod.

Pleopod 4 (Fig. 3) peduncle without serrate posterior margin; exopod approximately equal to length of peduncle, 0.86 times length of endopod, lateral margin with 5 pairs of simple setae, longer plumose setae between smooth setae in each pair, 3 smooth setae terminally, medial margin with long, fine plumose setae; endopod lateral and medial margins with long, fine, plumose setae, robust smooth setae and stout spine terminally; reticulum present above endopod.

Pleopod 5 (Fig. 3) length 4.5 times width, with 8 simple setae terminally, fine plumose setae on lateral margin.

Pleopod 6 (Fig. 3) length 2.5 times width, with 9 simple setae on terminal margin, fine plumose setae on lateral margin.

Caudal furca (Fig. 3) 2.36 times long as wide, 1.44 times as long as telson, 0.17 times as long as carapace; with 9 short, subcuticular smooth setae
Figure 4. Antenna 2 in situ (left), peduncle article 3 and first article of flagellum. a. Levinebalia maria paratype J13282, note rows of small, spines. Arrows point to conical sensor organs and large cuticular projections. b. Paranebalia sp. J13278, note absence of small, spines. Arrows indicate large cuticular projections.
Figure 5. a–c. Levinebalia maria paratype J13282. a, antenna 2 (left) in situ. Arrows indicate conical sensory organs and large cuticular outgrowths. b, conical sensory organ. c, spines on article 3 of antenna 2. d–e. Levinebalia maria paratype, J34256. d, antenna 2 (right) in situ (proximal end of antenna at bottom of photo). e, area of spines, including patch of tiny spines.
Figure 6. a-b. *Levinebalia maria* paratype J13282. a, pleopod 1, exopod and endopod. Exopod with two types of marginal setae. b, proximal marginal setae, forming the comb-row (arrow in a).
on lateral margin; numerous plumose setae on medial margin and terminally, 4 denticle setae terminally.

Description of allotype. Juvenile male. Entire length 4.41 mm. Carapace length 2.84 mm, depth 1.85 mm. Antenna 1 (Fig. 3) flagellum swollen, articles fused, numerous aesthetases, article 4 as for female. Antenna 2 with small cuticular outgrowth on anteroproximal margin. All other characters same as for female.

Etymology. For Maria Island, Tasmania, type locality (noun in apposition).

Remarks. The posterior margin of the carapace of Levinebalia maria is rounded. Wakabara (1976) illustrated the carapace of Paranebalia fortunata with a straight posterior margin but my examination of a paratype of P. fortunata reveals the carapace is a similar shape to that of Levinebalia maria. The lateral margin of the exopod of pleopod 2 of L. maria possesses pairs of smooth setae and this is the setal arrangement found in P. fortunata (paratype examined). Wakabara's (1976) illustration of pleopod 2 suggested the setae occur singly along the lateral margin. No fully mature male of L. maria has been found.

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Abstract


The stegocephalid (Crustacea: Amphipoda) genus *Phippsia* Stebbing, 1906 is revised to include six species, of which three are new to science. One new species of the genus *Tetradeion* Stebbing, 1899 is also described. A key to all species of the two genera is presented.

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Introduction

In 1883, Sars described *Aspidopleura gibbosa* (the name was later changed to *Phippsia gibbosa* by Stebbing in 1906) from the west coast of Norway, and in 1925, Schellenberg described *P. roemeri*. Both species have a strictly northern distribution, found only in the North Atlantic and the Arctic (Berge and Vader, 1997). From the littoral zone in New Zealand, *Cyproidea crassa* Chilton, 1883 was placed in *Tetradeion* by Chilton (1924), and redescribed by Hurley (1955) and Barnard (1972). Although the latter species is clearly distinct from both *P. gibbosa* and *P. roemeri*, all three species do share some striking similarities that appear to have been overlooked in the literature. Pending a total revision and a phylogenetic analysis of the family (Berge and Vader, in prep.), the two genera are kept separate to minimise changes in classification. However, a preliminary cladistic analysis indicates that the eight species treated herein do form a monophyletic group but that their relationships are still unclear.

In the present paper, one new species of *Tetradeion* is described. The number of species in *Phippsia* is increased from two to six. The present study is primarily based on material from Museum Victoria, Melbourne, Australia (NMV) but additional material also comes from the Natural History Museum, London, UK (NHM), Museum fur Naturkunde, Berlin, Germany (ZMB), and Darling Marine Center, University of Maine, Walpole, USA (DMC).

All dissected appendages were mounted in polyvinyl-lactophenol, and stained with rose-bengal. Figures of these appendages were made using a Leica compound microscope. Mature and
immature females were distinguished from males by the presence of oostegites. The classification of setae follows that of Berge (in press a, b). Scales attached are all 0.1 mm. Symbols used in the figures are as follows: A1, A2; antennae 1, 2; EP3: epimeral plate 3; L: labium; LBR: labrum; LMND: left mandible; M: male; MX1, MX 2: maxillae 1, 2; MXP: maxilliped; P1-P7: pereopods 1–7; PLP: palp; RMND: right mandible; ST: setal-teeth; T: telson; U1–U3: uropods 1–3.

**Key to species of Phippsia and Tetradeion**

1. Pereopod 7 with number of articles reduced..........................Tetradeion .. 2
   — Pereopod 7 with all articles present.................................Phippsia .. 3
2. Pereopod 7 with 2 articles (plus coxa)..................................Tetradeion crassum
   — Pereopod 7 with 4 articles (plus coxa)...............................Tetradeion quatro
3. Metasome segment 3 dorsally smooth....................................4
   — Metasome segment 3 dorsally produced...............................Phippsia gibbosa
4. Telson entire.................................................................5
   — Telson cleft...........................................................................6
5. Maxilliped palp article 2 rectangular (not produced distally), labrum clongate and triangular (clearly longer than broad)......Phippsia angustipalpa
   — Maxilliped palp article 2 distally produced, labrum not longer than broad, rounded..........................Phippsia dampieri
6. Epimeral plate 3 distally without serrations.........................Phippsia roemeri
   — Epimeral plate 3 distally serrate.........................................7
7. Antenna 2 peduncle article 3 shorter than broad, epistomial plate absent..............................................Phippsia vanhoefeni
   — Antenna 2 peduncle article 3 elongate, epistomial plate large .............................................................Phippsia unihamata

**Phippsia** Stebbing

*Aspidopleurus* Sars, 1895: 203 (homonym, Pisces)

*Phippsia* Stebbing, 1906: 89 (replacement name)

**Type species.** *Stegocephalus gibbosus* Sars, 1883 (original designation).

**Species.** *Phippsia angustipalpa* sp. nov., *P. dampieri* sp. nov., *P. gibbosa* (Sars, 1883), *P. roemeri* Schellenberg, 1925, *P. unihamata* sp. nov. and *P. vanhoefeni* (Schellenberg, 1926).

**Distribution.** North Atlantic and Arctic Oceans (*P. gibbosa* and *P. roemeri*), Antarctica (*P. unihamata* and *P. vanhoefeni*), and Australia (*P. angustipalpa*, *P. dampieri* and *P. vanhoefeni*).

**Remarks.** Sars (1895) erected *Aspidopleurus* as a monotypic genus for *Stegocephalus gibbosus* mainly based on the morphology of the mouthparts. *Phippsia gibbosa* has the second article of the maxilliped palp distally produced, and its inner plate is long and rectangular. Furthermore, the setae on the outer plate of maxilla 2 have double hooks distally (referred to in the descriptions as a distal cleft, in addition to the hooks, see MX2 in Fig. 6), and the palp of maxilla 1 is reduced. All these characters, together with the conspicuous epistomial plate are characters that have, until present, separated the two northern species of the genus from all other known stegocephalid species.

However, with the inclusion of *Stegocephalopsis vanhoefeni* (Schellenberg, 1926) and the three new species, the genus no longer appears so well separated from other genera in the family. None of the last mentioned four species possesses the "doubled hooked setae" on maxilla 2, and all other character states described above vary between the different species. Furthermore, the accessory flagellum of antenna 1 varies between well developed (e.g., type species) and rudimentary (e.g., *P. dampieri*), and the telson varies between 80% cleft (e.g., *P. vanhoefeni*) and entire (e.g., *P. angustipalpa*). On the other hand, the labrum is partly fused with the epistome in all six species, and the arrangements of different maxillipedal setal-groups (Berge, in press a) indicate a strong relationship between the taxa, and between *Phippsia* and *Tetradeion*. Most species of the two genera possess an elongate and geniculate peduncle of antenna 2. The only character that separates *Phippsia* (as treated herein) from *Tetradeion* is the lower number of articles on pereopod 7. Otherwise, all characters discussed above are also (variably) present in *Tetradeion*. 
Thus, the genus appears a weakly defined group kept together mainly by a large coxa 4, short and stout antennae and narrow basis on pereopod 6. As a revision of the family and a cladistic analysis is in preparation by us, phylogenetic relationships will not be discussed further.

Stegocephalopsis pacifica (Bulycheva, 1952) probably also belongs in Phippsia, but due to the lack of material and adequate descriptions, S. pacifica is not transferred. Stegocephalopsis pacifica was originally described in Phippsia but later transferred to Stegocephalopsis by Gurjanova (1962). The maxilliped and maxilla 1 resemble those of both P. angustipalpa and P. vanhoeffeni. Furthermore, the mouthparts seem to be elongate and the species has strong affinities to P. angustipalpa.

**Phippsia gibbosa** (Sars)

*Aspidopleurus gibbous*.—Sars, 1895: 203.

**Phippsia gibbosa**.—Stebbing, 1906: 89.—Berge et al., in press.

**Phippsia angustipalpa** sp. nov.

Figures 1, 2

*Material examined.* Holotype. Australia, Tasmania, eastern Bass Strait, 100 km NE of North Point, Flinders Island (38°52.6'S, 148°25.2'E), 130-52 m, fine sand, R. Wilson on RV Tangaroa, 15 Nov 1981 (stn BSS 170), NMV J45336 (immature female, 3 mm).

Paratypes. Collected with the holotype. NMV J47018 (4 immature specimens).

**Description.** Rostrum very small. Antennae short. Antenna 1 shorter than antenna 2; flagellum 4-articulate; accessory flagellum rudimentary, Antenna 2 peduncle (articles 3-5 ) longer than flagellum; article 3 elongate, articles 3 and 4 geniculate; article 4 longer than article 5.

Epistome curved (convex) and smooth. Epistomal plate (medial keel) produced, but small.

Mouthparts elongate; pointed and narrow. Mandible incisor lateral; toothed; left lacinia mobilis powerful, laterally expanded. Maxilla 1 palp 1-articulate; rectangular; apex not reaching above the apex of outer plate; outer plate distally rectangular; ST in a pseudocrown; ST first row with 6 setae (ST 1-5, ST 7); ST 1 ordinary (similar to ST 2-4); gap between ST 5 and ST 7 present; ST A present; located distally, part of first row; ST B and C present; part of second row; inner plate with a well developed shoulder; setae pappoepispicate. Maxilla 2 gaping and geniculate; outer plate setae with distal hooks present; distal eloft absent; inner plate setal row A covering the entire margin; appressed to row B; row A setae pappoepispicate; row B setae proximally pappose; distally with cusps present; row C present; row D absent.

Maxilliped palp 4-articulate; article 2 distally unproduced; dactylus distally simple (pointed); inner plate not exceeding base of palp article 4; 2 nodular setae; medial setal-row present; not reduced; vertical; setae pappopectinate; distal setal-row present; inner setal-row present; row reduced to 1 or 2 setae; outer plate outer setal-row present; submarginal; setae attached normally; setae long; strongly curved upwards (hooks); inner setal-row absent; distal setal-group present; setae attached in a deep hollow; setae short simple. Labrum elongate; lobes symmetrical; right lobe reduced; left lobe reduced. Labium distally narrowing.

Coxal plates and basis on pereopods smooth. Coxae 1–3 contiguous. Pereopod 1 coxal plate not as deep as basis; propodus subovate. Pereopod 2 general appearance like pereopod 1; ischium not elongate, ratio length:breadth not exceeding 1.5; distal posterior margin plumose setae present; propodus subovate; palm absent. Pereopod 4 coxa posteroverentral lobe very large, reaching beyond the base of the pereopod 7; basis anterior margin with long setae absent; posterior margin with long setae present; plumose setae on distal anterior and posterior margins present; ischium plumose setae on posterior distal margin present. Pereopod 6 basis posteriorly unexpanded; with a row of long plumose setae present. Pereopod 7 basis anterior margin straight; distally rounded; medial row of setae present; setae short and robust.

Oostegites on pereopods 2–5, gills on pereopods 2–7.

**Etymology.** *Angustipalpa* describes the unproduced article 2 on the palp of the maxilliped,
Figure 1. *Phippsia augustipalpa* sp. nov. Holotype, except habitus: paratype immature female, 3 mm.
Figure 2. *Phippsia angustipalpa* sp. nov. Holotype.
a character state not found in any other species of the genus.

Distribution. Australia, Bass Strait (known only from the type locality).

Remarks. This is not a typical member of the genus in that the palp of the maxilliped is slender (hence the name) and the mouthparts are elongate and thus are more similar to those of both *Tetradeion crassum* (Chilton, 1883) and a new species of *Stegocephalina* (Berge, in press b). Based on arrangement of the different setal-groups on the maxilliped, rudimentary accessory flagellum, rounded and entire telson, and geniculated peduncle (between articles 3 and 4) on antenna 2, the species is assigned for the moment to *Phippsia*.

**Phippsia dampieri** sp. nov.

Figures 3–5

Material examined. Holotype. Australia, Western Australia, Northwest Shelf; between Port Hedland and Dampier (18°41'S, 118°39'E), 134 m, muddy sand, WHOI epibenthic sled, G.C.B. Poore and H.M. Lew Ton on RV *Soela*, 4 Jun 1983 (stn NWA 21), NMV J47019 (female, 8 mm).

Paratypes. Collected with holotype, NMV J47019 (7 specimens, male and females).

Description. Rostrum very small. Antennae short. Antenna 1 shorter than antenna 2; flagellum 6-articulate; accessory flagellum rudimentary. Antenna 2 peduncle (articles 3–5) longer than flagellum; article 3 elongate, articles 3 and 4 geniculate; article 4 longer than article 5.

Epistome curved (convex) and smooth; epistomial plate produced into a large conspicuous medial keel.

Mouthparts not elongate or pointed. Mandible incisor lateral; toothed; left lacinia mobilis powerful, laterally expanded. Maxilla 1 palp 2-articulate; rectangular; apex not reaching above the apex of outer plate; outer plate distally rectangular; ST in a pseudocrown; ST first row with 6 setae (ST 1–5, ST 7); ST 6 absent; gap between ST 5 and ST 7 present; ST A present; located distally, part of first row; ST B present; part of second row; ST C present; inner plate with a well developed shoulder; setae papposeuspitate; Maxilla 2 gaping and geniculate; outer plate setae with distal hooks present; distal cleft absent; inner plate setal row A covering the entire margin; appended to row B; row A setae papposeuspitate; row B setae proximally pappose; distally with cuspps present; row C present; row D absent. Maxilliped palp 4-articulate; article 2 distally conspicuously produced; daetynus distally simple (pointed); inner plate not exceeding base of palp article 3; 3 nodular setae; medial setal-row present; not reduced; vertical; setae pectinate; distal setal-row present; inner setal-row present; row reduced to 1 or 2 setae; outer plate outer setal-row present; submarginal; setae attached normally; setae long robust; straight; inner setal-row present; well developed; setae long robust; pappose; proximally parallel to outer, distally transverse; distal setal-group present; setae attached in a deep hollow; setae long robust. Labrum about as long as broad; lobes asymmetrical; right lobe not reduced; left lobe reduced. Labium distally narrowing.

Coxal plates and basis on pereopods covered with setae; setae very short. Coxae 1–3 contiguous. Pereopod 1 coxal plate not as deep as basis; propodus subovate. Pereopod 2 general appearance like pereopod 1; ischium not elongate, ratio length: breadth not exceeding 1.5; ischium distal posterior margin plumose setae present; propodus subovate; palm absent. Pereopod 4 coxa posteriorventral lobe very large, reaching beyond the base of the perconite 7; basis anterior margin with long setae absent; posterior margin with long setae present; plumose setae on distal anterior and posterior margins present; ischium plumose setae on posterior distal margin present. Pereopod 6 basis posteriorly unexpanded; with a row of long plumose setae present. Pereopod 7 basis anterior margin straight; distally rounded; medial row of setae present; setae short and robust.

Oostegites on pereopods 2–5, gills on pereopods 2–7.

Pleonites 1–3 dorsally smooth.

Urosome: articulation between urosomites 2 and 3 absent. Uropod 1 peduncle longer than rami; outer rami longer than inner. Uropod 2 peduncle longer than rami; outer rami longer than inner. Uropod 3 peduncle longer than half length of rami; outer rami 2-articulate, longer than inner.

Telson longer than broad; longer than peduncle uropod 3; submarginal setae on apex present; entire; apically rounded.

Males: Pereopod 2 propodus larger in males than in females; Urosome ordinary (similar to females).

Etymology. Named after the British pirate and explorer William Dampier who visited this shore.

Distribution. Northwestern Australia. Known only from type locality.

Remarks. *Phippsia dampieri* is, to the authors' knowledge, the first stegocephalid reported from
Figure 3. *Phippsia dampieri* sp. nov. Paratype male, 5 mm. except habitus: holotype female, 8 mm.
Figure 4. *Phippsia dampieri* sp. nov. Paratype male.
Figure 5. *Phippsia dampieri* sp. nov. Paratype male.
the west coast of Australia or the eastern Indian Ocean. There are records of the family from the western and northern Indian Ocean and from Papua New Guinea. The species is separated from its congeners by the combination of a entire telson and a distally produced maxilliped palp article 2.

**Phippsia roemeri** Schellenberg

Figures 6-8

_Phippsia roemeri_ Schellenberg, 1925: 197.—Stephensen, 1925: 133.

**Material examined.** About 200 specimens from BIOFAR and BIOICE programmes (Berge and Vader, 1997).

**Description.** Rostrum very small.

Antennae short. Antenna 1 as long as antenna 2; flagellum 6-articulate; accessory flagellum well developed, article 2 absent. Antenna 2 peduncle (articles 3–5) as long as flagellum; article 3 short, about as long as broad; article 4 shorter than article 5.

Epistome curved (convex) and smooth; epistomial plate produced into a large conspicuous medial keel.

Mouthparts not elongate or pointed. Mandible incisor lateral; toothed; left lacinia mobilis powerful, laterally expanded. Maxilla 1 palp 2-articulate; rectangular; apex not reaching above the apex of outer plate; outer plate distally rectangular; ST in a pseudocrown; ST first row with 6 setae (ST 1–5, ST7); ST 6 absent; gap between ST 5 and ST 7 absent; ST A present; located distally, part of first row; ST B present; part of second row; ST C present; inner plate with a well developed shoulder; setae pappoepistipulate. Maxilla 2 gaging and geniculate; outer plate setae with distal hooks present; distal cleft present; inner plate setal row A covering about two-thirds of the margin; appressed to row B; row A setae pappoepinate; row B setae proximally pappose; distally with cusps present; row C present; row D present; expanded, row elongated towards and beyond row A; with many small cusps distally. Maxilliped palp 4-articulate; article 2 distally conspicuously produced; dactylus distally simple (pointed); inner plate not exceeding base of palp article 4; 4 nodular setae; medial setal-row present; not reduced; vertical; setae pectinate; distal setal-row present; inner setal-row present; row reduced to 1 or 2 setae; outer plate outer setal-row present; submarginal; setae attached normally; setae long; straight; inner setal-row present; well developed; setae long robust; pappose; proximally parallel to outer, distally transverse; distal setal-group present; setae attached in a deep hollow; setae short simple. Labrum about as long as broad; lobes asymmetrical; right lobe not reduced; left lobe reduced. Labium distally narrowing.

Coxa plates and basis on pereopods smooth. Coxae 1–3 contiguous. Pereopod 1 coxal plate not as deep as basis; propodus subovate. Pereopod 2 longer and thinner than pereopod 1; ischiium not elongate, ratio length:breath not exceeding 1.5; ischiium distal posterior margin plumose setae present; propodus subrectangular; palm absent. Pereopod 4 coxa posteroverentral lobe very large, reaching beyond the base of the perconite 7; basis anterior margin with long setae absent; posterior margin with long setae present; plumose setae on distal anterior and posterior margins absent; ischiium plumose setae on posterior distal margin present. Pereopod 6 basis posteriorly expanded; with a row of long plumose setae present. Pereopod 7 basis anterior margin straight; distally rounded; medial row of setae absent.

Oostegites on pereopods 2–5, gills on pereopods 2–7.

**Distribution.** An abundant species in North Atlantic and Arctic Oceans that appears to be limited to cold waters (Berge and Vader, 1997).

**Remarks.** *Phippsia roemeri* appears to be close to the type species both taxonomically and zoogeographically. The two species possess a similar maxilliped and maxilla 2, in addition to the non-geniculate peduncle of antenna 2 and a cleft telson. Furthermore, they are both endemic to the North Atlantic (and subarctic), and are the only species from the Northern Hemisphere.

**Phippsia unihamata** sp. nov.

Figures 9–12

**Material examined.** Holotype. Weddell Sea, Antarctica (72°25.40'S, 16°26.63'W), 198–260 m, ZMB A 25 (female, 7 mm).
Figure 6. *Phippsia roemeri* Schellenberg, 1925. BIOFAR stn 172, female.
Figure 7. *Phippsia roemeri* Schellenberg, 1925. BIOFAR stn 172, female.
Figure 8. *Phippsia roemeri* Schellenberg, 1925. BIOFAR stn 172, female.
Figure 9. *Phippsia unihamata* sp. nov. Holotype.
Figure 10. *Phippsia unihamata* sp. nov. Holotype.
Figure 11. *Phippsia unihomata* sp. nov. Holotype.
Figure 12. Phippsia unihamata sp. nov. Holotype.
Additional material. Weddell Sea, Antarctica (72°27.28'S, 17°32.94'W), 455–473 m, ZMB A III/41 (female, 6 mm); Weddell Sea, Antarctica (72°53.10'S, 19°29.33'W), 421–429 m, ZMB A III/44 (immature, 3 mm); Antarctica (66°S, 49°E), NHM unregistered (female, 6 mm).

Description. Rostrum very small.

Antennae short. Antenna 1 shorter than antenna 2; flagellum 6-articulate; accessory flagellum rudimentary. Antenna 2 peduncle (articles 3–5) shorter than flagellum; article 3 elongate, articles 3 and 4 geniculate; article 4 longer than article 5.

Epistome curved (convex) and smooth; epistomal plate produced into a large conspicuous medial keel.

Mouthparts not elongate or pointed. Mandible incisor lateral; toothed; left lacinia mobilis powerful, laterally expanded. Maxilla 1 palp 2-articulate; rectangular; apex not reaching above the apex of outer plate; outer plate distally rectangular; ST in a pseudocrown; ST first row with 6 setae (ST 1–5, ST 7); ST 6 absent; gap between ST 5 and ST 7 present; ST A present; located distally, part of first row; ST B present; part of second row; ST C present; inner plate with a well developed shoulder; setae pappocuspitate. Maxilla 2 gaping and geniculate; outer plate setae with distal hooks present; distal eel absent; inner plate setal row A covering about two-thirds of the margin; appressed to row B; row A setae pappopectinate; row B setae proximally pappose; distally with cusps present; row C present; row D present; expanded, row elongated towards and beyond row A; with many small cusps distally. Maxilliped palp 4-articulate; article 2 distally produced; distal inner margin greatly produced; dactylus distally simple (pointed); inner plate not exceeding base of palp article 3; nodular setae 4; medial setal-row present; not reduced; vertical; setae pectinate; distal setal-row present; inner setal-row absent; outer plate outer setal-row present; submarginal; setae attached normally; setae long; straight; inner setal-row present; well developed; setae long robust; pappose; proximally parallel to outer, distally transverse; distal setal-group present; setae attached in a deep hollow; setae short simple. Labrum about as long as broad; lobes symmetrical; right lobe reduced; left lobe reduced. Labium distally narrowing.

Coxal plates and basis on pereopods covered with setae; setae very short. Coxae 1–3 contiguous. Pereopod 1 coxal plate not as deep as basis; propodus subovate. Pereopod 2 longer and thinner than pereopod 1; ischium not elongate, ratio length:breadth not exceeding 1.5; ischium distal posterior margin plumose setae present; propodus subovate; palm absent.

Pereopod 4 coxa posteroventral lobe very large, reaching beyond the base of perconite 7; basis anterior margin with long setae absent; posterior margin with long setae present; plumose setae on distal anterior and posterior margins present; ischium plumose setae on posterior distal margin present. Pereopod 6 basis posteriorly expanded; rudimentary; with a row of long plumose setae present. Pereopod 7 basis anterior margin straight; distally rounded; medial row of setae absent.

Oostegites on pereopods 2–5. gills on pereopods 2–7.

Pleonites 1–3 dorsally smooth;

Urosome: articulation between urosomites 2 and 3 absent. Uropod 1 peduncle longer than rami; outer ramus longer than inner. Uropod 2 peduncle shorter than rami; outer ramus as long as inner. Uropod 3 peduncle longer than half length of rami; outer ramus 2-articulate, longer than inner.

Telson longer than broad; longer than peduncle uropod 3; submarginal setae on apex of each lobe absent; eel; apically rounded.

Males: Unknown.

Etymology. The name refers to the fact that this was the first species we discovered without a double-hooked setae on the outer plate on maxilla 2 (MX2, Fig. 6).

Distribution. Antarctica, 198–473 m (possibly circumpolar).

Remarks. This and P. vanhoeffeni are the only species in the genus occurring in Antarctica. Both are separated from their congeners by the strongly produced and serrate hind margin of the third epimeral plate. Phippsia unihamata differs from P. vanhoeffeni in the long and geniculate peduncle of antenna 2.

Phippsia vanhoeffeni (Schellenberg, 1926) comb. nov.

Figures 13–15


Material examined. Syntype. Eastern Antarctica (Wilhelm II land), 385 m, ZMB 20388 (female, 6 mm).

Additional material. Australia, Victoria, S of Point Hicks (38°21.90'S, 149°20.00'E), 1000 m, WHOI epibenthic sled, G.C.B. Poore et al. on RV Franklin 23 Jul 1986 (stn SLOPE 32), NMV J24057 (4 males and females, 4–5 mm).
Figure 13. *Phippsia vanhoeffi* (Schellenberg, 1926). NMV J24057, female A.
Figure 14. Phippsia vanhoeffeni (Schellenberg, 1926). NMV J24057, female A.
Figure 15. *Phippsia vanhoeffeni* (Schellenberg, 1926). NMV J24057, female A.
**Description.** Rostrum very small.

Antennae short. Antenna 1 longer than antenna 2; flagellum 5-articulate; accessory flagellum well developed, article 2 absent. Antenna 2 peduncle (articles 3–5) longer than flagellum; article 3 short, about as long as broad; article 4 longer than article 5.

Epistome curved (convex) and smooth; epistomal plate (medial keel) not produced.

Mouthparts not elongate or pointed. Mandible incisor lateral; toothed; left lacinia mobilis powerful, laterally expanded. Maxilla 1 palp 1-articulate; rectangular; apex not reaching above the apex of outer plate; outer plate distally rectangular; ST in a pseudocrown; ST first row with 6 setae (ST 1–5, ST 7); ST 6 absent; gap between ST 5 and ST 7 absent; ST A present; located distally, part of first row; ST B present; part of second row; ST C present; inner plate with a well developed shoulder; setae pappocephulidate. Maxilla 2 gaping and geniculate; outer plate setae with distal hooks present; inner plate setal row A covering about two-thirds of the margin; clearly separated from row B; row A setae pappocephulidate; row B setae proximally pappose; distally with cusps present; row C present; row D present; expanded, row elongated towards and beyond row A; with many small cusps distally. Maxilliped palp 4-articulate; article 2 distally produced; distal inner margin weakly produced; dactylus distally simple (pointed); inner plate not exceeding base of palp article 3; nodular setae 2; medial setal-row present; not reduced; upper; setae pappose; setae pappose; setal row A covering about two-thirds of the margin; setae attached in a deep hollow; setae short; strongly curved upwards (hooks); inner setal-row present; well developed; setae long robust; pappose; proximally parallel to outer, distally transverse; distal setal-group present; setae attached in a deep hollow; setae short simple. Labrum about as long as broad; lobes symmetrical; right lobe not reduced; left lobe not reduced. Labium distally narrowing.

Coxal plates and basis on pereopods covered with setae; setae very short. Coxae 1–3 contiguous. Pereopod 1 coxal plate deeper than basis; propodus subovate. Pereopod 2 longer and thinner than pereopod 1; ischium not elongate, ratio length/breadth not exceeding 1.5; ischium distal posterior margin plumose setae present; propodus subrectangular; palm absent. Pereopod 4 coxa posteroventral lobe large, reaching about the base of peronite 7; basis anterior margin with long setae absent; posterior margin with long setae present; plumose setae on distal anterior and posterior margins present; ischium plumose setae on posterior distal margin present. Pereopod 6 basis posteriorly expanded; rudimentary; with a row of long plumose setae present. Pereopod 7 basis anterior margin straight; distally rounded; medial row of setae present; setae short and robust.

Oostegites on pereopods 2–5, gills on pereopods 2–7.

Pleonites 1–3 dorsally smooth.

Urosome: articulation between urosomites 2 and 3 absent. Uropod 1 peduncle longer than rami; outer rami longer than inner. Uropod 2 peduncle longer than rami; outer rami as long as inner. Uropod 3 peduncle longer than half length of rami; outer rami 1-articulate, as long as inner.

Telson longer than broad; longer than peduncle uropod 3; submarginal setae on apex of each lobe present; cleft; apically pointed.

Males: Pereopod 2 propodus equally sized in males and females; Urosome ordinary (similar to females).

**Distribution.** Eastern Antarctica (type locality) and south of Point Hicks, Victoria, Australia.

**Remarks.** This species is distinct from others of *Phippsia* in several respects, by its uniarticulate outer ramus of uropod 3, the weakly produced article 2 of the maxillipede palp, and the arrangement of setal-rows A, B and D on maxilla 2 (Berge, in press a). However, the species is transferred from *Stegocephalopsis* Sehellenberg, 1925 on the following characters: 1, articulation between labrum and epistome partly absent; 2, inner plate of maxillipede long and rectangular; 3, articulation absent between urosomites 2 and 3; and 4, epimeral plate 3 produced and strongly serrate.

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**Tetradeion Stebbing**

*Tetradeion* Stebbing, 1899: 207

**Type species.** *Cyproidea crassa* Chilton, 1883.

**Species:** *Tetradeion crassum* (Chilton, 1883); *T. quatro* sp. nov.

**Distribution.** Australia, New Zealand and subantarctic region.

**Remarks.** *Stegocephalus latus* Haswell, 1879 was described from shallow water Tasmania, Australia. Although the species was inadequately described and the two syntypes no longer exist (Springthorpe and Lowry, 1994), the descriptions by Haswell (1879, 1885) strongly resemble those of *T. crassum*. The conspicuous eyes, large coxae 1–4, reduced pereopod 7 (although all articles
appears to be present in *S. latus*), and absence of an articulation between urosomites 2 and 3 are similar. *Stegocephalus latus* was transferred to *Stegocephalopsis* by Barnard and Karaman (1991), but there are however, good reasons to suspect that it belongs in the same genus as *T. crassum*. Pending a revision of the family (Berge and Vader, in prep.), and due to inadequate information of this species' morphology, it is not herein transferred to *Tetradeion*.

**Tetradeion crassum** (Chilton)

*Cyproidea crassa* Chilton, 1883: 80.


**Material examined.** New Zealand, North Cape (precise location unknown), 3 m, 1 Sep 1911, *Terra Nova* stn 135 (see K.H. Barnard, 1930: 329), NHM 1930.8.1.95–104 (15 specimens, 2.5–3.5 mm). Auckland Islands (50°52'S, 166°42'E), 135–139 m, 9 Feb 1965, *Eltanin* Cruise 16 (stn 1425), DMC (female, 2 mm).

South Atlantic, S of Falkland Islands (54°43'S, 56°37'W), 339–357 m, 14 Mar 1966, *Eltanin* Cruise 22 (stn 1593), DMC (immature, 2 mm).

**Description.** Rostrum very small.

Antennae short. Antenna 1 shorter than antenna 2; flagellum 6-articulate; accessory flagellum rudimentary; peduncle elongate. Antenna 2 peduncle (articles 3–5) longer than flagellum; article 3 elongate, articles 3 and 4 geniculate; article 4 shorter than article 5.

Epistome curved (convex) and smooth; epistomal plate (medial keel) produced, but small.

![Figure 16. Tetradeion crassum (Chilton, 1883). NHM 1930.8.1.95–104 female.](image)
Mouthparts elongate; pointed and narrow. Mandible incisor lateral; toothed; left lacinia mobilis powerful, laterally expanded. Maxilla 1 palp 2-articulate; rectangular; apex not reaching above the apex of outer plate; outer plate distally rectangular; ST in a pseudocrown; ST first row with 6 setae (ST 1–5, ST 7); ST 6 absent; gap between ST 5 and ST 7 present; ST A present; located distally, part of first row; ST B present; part of second row; ST C present; inner plate with a well developed shoulder; setae pappoespidate. Maxilla 2 gaping and geniculate; outer plate setae with distal hooks present; distal elef present; inner plate setal row A covering about two-thirds of margin; appressed to row B; row A setae pappoesinate; row B setae proximally simple; distally with eusps present; row C present; row D present; expanded, row elongated towards and beyond row A; with many small eusps distally. Maxilliped palp 4-articulate; article 2 distally produced; distal inner margin greatly produced; dactylus distally simple (pointed); inner plate not exceeding base of palp article 3; 3 nodular setae; medial setal-row present; not reduced; vertical; setae pectinate; distal setal-row present; inner setal-row present; row reduced to 1 or 2 setae; outer plate outer setal-row present; submarginal; setae attached normally; setae long; straight; inner setal-row present; well developed; setae long robust; pappose; proximally parallel to outer, distally transverse; distal setal-group present; setae attached in a deep hollow; setae long robust. Labrum elongate; lobes asymmetrical; right lobe not reduced; left lobe reduced. Labium distally narrowing.

Coxal plates and basis on pereopods covered with setae; setae very short. Pereopod 1 coxal plate not as deep as basis; propodus subovate. Pereopod 2 general appearance like pereopod 1; ischium not elongate, ratio length:width not exceeding 1.5; ischium distal posterior margin plumose setae present; propodus subovate; palm absent.

Pereopod 4 coxal area posteroventral lobe very large, reaching beyond the base of the pereonite 7; basis anterior margin with long setae absent; posterior margin with long setae present; plumose setae on distal anterior and posterior margins present; ischium plumose setae on posterior distal margin present. Pereopod 6 basis posteriorly expanded; with a row of long plumose setae present. Pereopod 7 strongly reduced, only 2 articles present; basis anterior margin straight; distally rounded; medial row of setae present; setae short and robust.

Oostegites on pereopods 2–5, gills on pereopods 2–7.

Pleopites 1–3 dorsally smooth.

Urosome: articulation between urosomites 2 and 3 absent. Uropod 1 peduncle longer than rami; outer ramus longer than inner. Uropod 2 peduncle longer than rami; outer ramus longer than inner. Uropod 3 peduncle at least as long as rami; outer ramus 1-articulate, longer than inner. Telson longer than broad; shorter than peduncle uropod 3; submarginal setae on apex absent; entire; apically rounded.

Males: Unknown.

Distribution. Circumpolar in the subantarctic region including New Zealand, 0–357 m.

Remarks. Tetradeion crassum was thoroughly described and figured by Chilton (1924), Hurley (1955) and Barnard (1972).

The strongly reduced pereopod 7 and large red eyes are two distinctive features distinguishing this species from all other known stegocephalid species. The morphology of maxillae 1 and 2 and the maxilliped indicate phylogenetic relationships with Phippsia (see also above).

Tetradeion quatro sp. nov.

Figures 17–20

Material examined. Holotype. Australia, Victoria, eastern Bass Strait, 8 km S of Southeast Point, Wilsons Promontory, (39°12.9'S, 146°27.3'E), 65 m, medium sand, R. Wilson on RV Tangaroa, 18 Nov 1981 (stn BSS 180), NMV J47020 (female, 7 mm).

Paratypes. Collected with holotype, NMV J45337 (30 specimens, males and females, 3–8 mm).

Additional material. Australia, Victoria, eastern Bass Strait, 8 km S of Southeast Point, Wilsons Promontory, (39°12.9'S, 146°27.3'E), 65 m, medium sand, R. Wilson on RV Tangaroa, 18 Nov 1981 (stn BSS 180), NMV J45342 (female, 6 mm).

Description. Rostrum very small.

Antennae short. Antenna 1 shorter than antenna 2; flagellum 7-articulate; accessory flagellum rudimentary. Antenna 2 peduncle (articles 3–5) longer than flagellum; article 3 elongate, articles 3 and 4 geniculate; article 4 as long as article 5.

Epistome curved (convex) and smooth; epistomal plate produced into a large conspicuous medial keel.

Mouthparts not elongate or pointed. Mandible incisor lateral; toothed; left lacinia mobilis powerful, laterally expanded. Maxilla 1 palp 2-articulate; rectangular; apex not reaching above the apex of outer plate; outer plate distally rectangular; ST in a pseudocrown; ST first row...
Figure 17. *Tetdeion quatro* sp. nov. Holotype except habitus: paratype female, 4 mm.
Figure 18. *Tetradcion quatro* sp. nov. Holotype.
Figure 19. *Tetradeion quatro* sp. nov. Holotype.
Figure 20. *Tetradeon quatro* sp. nov. Holotype.
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with 6 setae (ST 1-5, ST 7); ST 6 absent; gap between ST 5 and ST 7 present; ST A present; located distally, part of first row; ST B present; part of second row; ST C present; inner plate with a well developed shoulder; setae pappoecuspidate. Maxilla 2 gaping and geniculate; outer plate setae with distal hooks present; distal elef absent; inner plate setal row A covering the entire margin; appressed to row B; row A setae pappoecinate; row B setae proximally pappose; distally with cusps present; row C present; row D present; reduced, 1-3 long setae distally; with many small cusps distally. Maxilliped palp 4-articulate; article 2 distally produced; distal inner margin greatly produced; daeytulus distally simple (pointed); inner plate not exceeding base of palp article 4; nodular setae 4; median setal-row present; not reduced; vertical; setae pectinate; distal setal-row present; inner setal-row present; row reduced to 1 or 2 setae; outer plate outer setal-row present; submarginal; setae attached normally; setae long robust; straight; inner plate not exceeding base of palp article 4; nodular setae 4; medial setal-row present; setae attached in a deep hollow; setae long robust. Labrum about as long as broad; lobes symmetrical; right lobe reduced; left lobe reduced. Labium distally narrowing.

Coxal plates and basis on pereopods covered with setae; setae very short. Coxae 1-3 contiguous. Pereopod 1 coxal plate not as deep as basis; propodus subovate. Pereopod 2 general appearance like pereopod 1; ischium not elongate, ratio length:breadth not exceeding 1.5; ischium distal posterior margin plumose setae present; propodus subovate; palm absent.

Pereopod 4 coxa posteroventral lobe very large, reaching beyond the base of pereonite 7; basis anterior margin with long setae absent; posterior margin with long setae present; plumose setae on distal anterior margin absent; plumose setae on distal posterior margin present; ischium plumose setae on posterior distal margin present. Pereopod 6 basis posteriorly unexpanded; with a row of long plumose setae present. Pereopod 7 strongly reduced, only 4 articles present; basis anterior margin straight; distally rounded; median row of setae present; setae short and robust.

Oostegites on pereopods 2-5, gills on pereopods 2-7.

Pleostegites 1-3 dorsally smooth.

Urosome: articulation between urosomites 2 and 3 absent. Uropod 1 peduncle longer than rami; outer rami longer than inner. Uropod 2 peduncle longer than rami; outer rami longer than inner. Uropod 3 peduncle longer than half length of rami; outer rami 2-articulate, longer than inner.

Telson longer than broad; longer than peduncle uropod 3; submarginal setae on apex present; entire; apically rounded.

Males: Pereopod 2 propodus larger in males than in females, urosome ordinary (similar to females).

**Etymology.** The species name reflects the presence of just four articles on pereopod 7.

**Distribution.** Eastern Bass Strait, Victoria (known only from type locality).

**Remarks.** The presence of just four articles (in addition to coxa) is a unique character state within the family; *T. crassum* has just two articles, all other stegocephalid species have six articles on pereopod 7 (in addition to coxa).

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