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Front cover: Plate VIII of P.H. MacGillivray's "Monograph of the Tertiary Polyzoa of Victoria" published in 1895 in *Transactions of the Royal Society of Victoria*. Some of the bryozoans depicted are re-examined by P.E. Bock and P.L. Cook in two papers in this issue.

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Wilson, B.R. and Allen, G.R., 1987. Major components and distribution of marine fauna. Pp. 43–68 in: Dyne, G.R. and Watson, D.W. (eds). *Fauna of Australia. General articles.* Vol. 1A. Australian Government Publishing Service: Canberra.

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Memoirs of Museum Victoria 58(2): 179–189 (2001)

REVISION OF TERTIARY SPECIES OF *ANASKOPORA* WASS (BRYOZOA: CRIBRIMORPHA)

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Abstract

Bock, P.E. and Cook, P.L., 2001. Revision of Tertiary species of *Anaskopora* Wass (Bryozoa: Cribrimorpha). *Memoirs of Museum Victoria* 58(2):179–189.

The subgenus *Anaskopora* Wass, 1975 is raised to generic rank, separated from the genus *Corbulipora*, and redefined. The type species, *Cribrilina elevata* MacGillivray, 1895, is a Tertiary fossil from Victoria with small globular colonies formed principally by a special kind of interzooidal frontal budding. Other Tertiary fossil species with a similar colony structure, here assigned to *Anaskopora*, are *Cribrilina cornuta* MacGillivray, 1895 and *Lepralia rotundata* MacGillivray, 1895. Two further new Tertiary species, *A. simplex* and *A. mesa*, from Victoria and South Australia have small encrusting colonies. A key to species is given.

Introduction

Revision of the cribrimorph genus *Corbulipora* MacGillivray, 1895 means that its subgenus *Anaskopora* Wass, 1975 also requires redefinition (Bock and Cook, 2001). *Anaskopora* is considered here to be generically distinct from *Corbulipora* and to include *Cribrilina cornuta* MacGillivray, 1895, a species which Wass (1975) referred to *Corbulipora*.

Frontal budding is unusual in the Cribrimorpha. It occurs in *Corbulipora* principally as a result of expansions of cuticle and coelomic tissue derived from the pelmatidia on the frontal surface of the costae which form the calcified frontal shield or pericyst. Pelmatidia are usually absent in *Anaskopora* and if present are infrequent and restricted to the margins of the horizontal median area of costal fusion of the pericyst. Frontal buds are however commonly present and these arise in a series, often surrounding each autozooid and originate from a special type of pore-chamber. These also occur in *Corbulipora* and are termed chambered pores (Bock and Cook, 2001). Chambered pores consist of a calcified chamber arising around one or more septular pores in a vertical zooid wall. The chamber is uncalcified frontally and usually expands to form an interzooidal kenozooid. These pores somewhat resemble the pore-chambers found in *Celleporella* and *Hippothoa* (Gordon and Hastings, 1979) but are larger and less regularly positioned. Avicularia occur in series with these pores which are also the origin of rhizoids in Recent species (Arnold and Cook, 1997).

All the species described here are fossils from Victoria and South Australia and the specimens are from the collections of Museum Victoria (NMV). All species are illustrated by SEM, in many cases for the first time.

Key to species of *Anaskopora*

1. Autozooids large (Lz >1 mm). Costae curved, median area of costal fusion narrow, lacunae rare .... *A. simplex* sp. nov.

— Autozooids smaller (Lz <0.75mm). Costae with vertical marginal, and horizontal median elements, median area of costal fusion wide 2

2. Vertical costal components distinct, well separated 3

— Vertical costal components very short, closely apposed 4

3. Colony usually a globular ectoproctolith. Costae <11, median area with 8–12 large, rounded lacunae. Pelmatidia absent .... *A. elevata*

— Colony encrusting minute substrata. Costae >14, marginally raised with a single series of pelmatidia; medially horizontal with >15 scattered lacunae. .... *A. mesa* sp. nov

4. Median area of fusion with 12–24 regularly radiating costae, alternating with rows of 6–8 lacunae……*A. cornuta*
— Median area of fusion with no obvious costae but with numerous scattered minute lacunae with intervening tubercles……*A. rotundata*

Anaskopora Wass

Corbulipora (*Anaskopora*) Wass, 1975: 170.

Type species. *Cribrilina elevata* MacGillivray, 1895.

Description. Colonies encrusting, usually on very small substrata, with subsequent interzooidal frontal budding and overgrowth forming globular ectoproctoliths. Basal zooid walls calcified only peripherally, autozooids with marginal gymnocyst and extensive, costate pericyst. Peripheral, vertical component of costae without lateral fusions; central, horizontal component constituting the median area of fusion. Lacunae present, sometimes numerous; pelmatidia absent or rare, marginal only. Secondary calcified orifice with or without lateral condyles; peristome raised distally, forming a curved plate which is often marginally fimbriated. Oral spines paired, sometimes wide and flattened, or inflexed and fused medially above the secondary calcified orifice. Chambered pores large, forming kenozooids surrounding each autozooid; 1–3 distally and 2–4 laterally; calcification becoming extrazooidal later in ontogeny. Avicularia interzooidal, budded in series with kenozooids, usually distal or distolateral and single, occasionally proximal and even paired. Rostrum raised, palate rounded or subtriangular, orientated distally or laterally, with paired condyles. Dimorphic brooding zooids and ovicells unknown.

Remarks. The principal characters separating *Anaskopora* from *Corbulipora* s.s. are the regular presence of small interzooidal kenozooids surrounding autozooids, the distal or distolateral interzooidal avicularia present beside each autozooid and the raised distal oral fimbriated plate. The chambered pores resemble those of *Corbulipora* but are more regularly placed surrounding each autozooid and are presumably in communication with both neighbouring autozooids. In the globular colonies, nearly all budding after the earliest encrusting stages, is interzooidal and frontal. Each new layer of autozooids is derived from enlarged kenozooids of the previous layer. The virtual absence of pelmatidia and the apparent complete absence of multiphase growth also distinguishes *Anaskopora* from *Corbulipora*.

In nearly all species of *Anaskopora* the median area of fusion of each autozooid is delineated sharply from the peripheral component of the costae, making a distinct angle at the margin of the shield where there is occasionally a single pelmatidium. The vertical component is often elongated and never bears any costal fusions although the costae may be closely apposed in some species. The species described here form a series. In *A. simplex* sp. nov. the costae have no distinct vertical element and are curved with only terminal lateral fusions. At the other extreme, in *A. rotundata*, costae are hardly discernable and the median area is wide, consisting of numerous scattered lacunae and small tubercles. In contrast, *A. cornuta* has regular rows of costae with numerous costal fusions whereas in *A. elevata* and *A. mesa* sp. nov. the median area consists of scattered lacunae. The constant occurrence of a distal avicularium and a distal plate, together with the distinctive kenozooids arising from chambered pores, suggests that although the frontal shield shows a great diversity of structures these species all form a fairly natural grouping. All species appear to encrust minute substrata early in astogeny. *A. elevata* and *A. rotundata* are known only with globular frontally budded colonies; *A. simplex* and *A. mesa* have few or no frontally budded zooids. Colonies of *A. cornuta*, however, occur in both states. All these species occur in the Tertiary deposits of Victoria and South Australia. Living species assignable to *Anaskopora* have only recently been been recognised; they occur from Queensland and New South Wales, and were described by Arnold and Cook (1997) as *A. doliaris* (Maplestone) and *A. parkeri*. These Recent colonies are small and globular and are anchored by well-developed rhizoids.

The complete absence of ovicells or of any zooid with modified skeletal morphology which might be interpreted as a brooding zooid raises the suspicion that some kind of multiphase growth may occur in *Anaskopora* as it does in *Corbulipora* (Bock and Cook, 1994). However if this were true any alternative growth phase or phases which might have had a reproductive function have not as yet been recognised in any fossil or Recent assemblage. One species which was referred to *Anaskopora* by Wass (1975; *A. ampulla*, p. 170, pl. 8, figs 5, 6) remains unrecognised in the material examined here. Maplestone (1901: 207, pl. 37, fig. 9) originally described *Corbulipora ampulla* from Mornington and the type slide (NMV P10156) was examined by Wass together with one of the specimens described as *C.* sp. aff. *ampulla* by Brown (1958: 54). The type material consists of a few isolated zooids only, one of which was presumably that figured by Wass (1975). None of the zooids has a distal avicularium which was, however, mentioned by Brown in his specimens, and which are therefore assumed to belong to *Anaskopora*. The peripheral vertical component of the costae forms an angle with the median area which has approximately 20 large rounded lacunae but no regularly placed costal fusions. There are also about 20 costae, the vertical components being closely apposed; according to Wass (1975) the distal pair are elongated to form a hood over the orifice. *Anaskopora ampulla* has some characters similar to those of *A. mesa* sp. nov. but differs in several respects from that species.

Brown (1958: 55, fig. 33) also described as *Corbulipora pennata* an encrusting Tertiary species with costae raised and extended laterally. A large distal avicularium was described but not figured by Wass who redescribed and figured the unique holotype. The encrusting habit and distal avicularium suggest that *C. pennata* may be referable to *Anaskopora* but as the specimen is no longer present in the NMV collection its assignment must remain uncertain.

Anaskopora elevata (MacGillivray)

Figures 1–2, Table 1

Cribrilina elevata MacGillivray, 1895: 59, pl. 8, fig. 19.—Maplestone, 1904: 201 (listed).

Corbulipora elevata.—Brown, 1958: 54.

Corbulipora (Anaskopora) elevata.—Wass, 1975: 170, pl. 8, figs 1, 2, 4.

Material examined. Lectotype. NMV P27641, Schnapper Point, Victoria, Miocene (selected by Wass, 1975).

Other material. Balcombe Bay, Bairnsdale, Fyansford, Warrambine Creek, Muddy Creek.

Distribution. Additional records given by Maplestone (1904) include Shelford, Griffins, Campbells Point, Mornington and Mitchell River; records in Brown (1958) include Localities XI and XIV on the Glenelg River at Werrikoo (south-western Victoria), and at Mount Gambier, South Australia. All records are Miocene (Appendix).

Description. *Anaskopora* with globular colonies formed by interzooidal frontal budding from an early stage encrusting a very small substratum. Autozooids with a distinct gymnocyst, frontal shield with 8–10 costae, the vertical components widely spaced, inflexed sharply to form a median area of fusion. Costae bifurcate terminally, and with some lateral fusions produce 8–12 relatively large lacunae. Secondary calcified orifice not greatly raised distally, with a pair of short oral spines. Recessed junction of suboral costae forming a proximally sinuate secondary orifice. Distal avicularium fairly large, length of rostrum equal or exceeding that of autozooid orifice; rostrum rounded and directed distally.

Remarks. The secondary orifice is distinctly sinuate. Many zooids communicate directly through septular pores and the chambered pores are small, forming kenozooids at the corners of the autozooids. The calcification becomes extrazooidal late in ontogeny surrounding the autozooids.

Powell (1967: 223) suggested that *C. elevata* might be 'closely allied' to the type species of *Cribralaria* Silén, *C. curvirostris* Silén (1941: 122, figs 182–183) from the north-western Pacific. *Cribralaria curvirostris* has autozooids with numerous, rounded lacunae and no chambered pores. The ovicell is partially immersed in the subrostral chamber of the large distal avicularium which has a raised acute rostrum. The only feature superficially similar to the avicularium of *A. elevata* is its distal position (see also Gordon, 1989: 15). *Anaskopora elevata* differs from the other globular species in its small number of widely spaced costae and scattered median lacunae.

Table 1. Measurements in mm of species of *Anaskopora*. Lz, lz, length and width of zooid; Lo, lo, length and width of orifice; Lav, lav, length and width of avicularium; Lr, length of rostrum.

	Lz	lz	Lo	lo	Lav	lav	Lr
A. elevata	0.46–0.54	0.37–0.50	0.14–0.15	0.13–0.17	0.17–0.23	0.10–0.12	0.09–0.15
A. cornuta	0.66–0.78	0.45–0.66	0.15–0.18	0.12–0.16	0.12–0.18	0.08–0.10	0.08–0.10
A. rotundata	0.60–0.70	0.41–0.51	0.10–0.14	0.12–0.13	0.08–0.10	0.06–0.08	0.05–0.07
A. simplex sp. nov.	0.95–1.40	0.58–0.70	0.18–0.23	0.23–0.25	0.13–0.19	0.12–0.14	0.07–0.10
A. mesa sp. nov.	0.53–0.88	0.40–0.50	0.09–0.13	0.17–0.23	0.10–0.18	0.06–0.09	0.07–0.10

Anaskopora simplex sp. nov.

Figures 3–4, Table 1

Material examined. Holotype. NMV P140964, Balcombe Bay, Victoria, Miocene.

Other material. Princetown, Cape Otway, Victoria.

Distribution. See above, Miocene to Oligocene (Appendix).

Etymology. Simplex (Latin) — simple, referring to the pericyst.

Description. Colonies encrusting minute substrata, with occasional isolated frontal buds arising from small chambered pores at the corners of the autozooids. Autozooids large, gymnocyst marginal; pericyst formed by 18–28 flattened costae, widely spaced and curved over the frontal with no sharp angle of inflexion. Median area of fusion narrow, formed by apposition and fusion of terminal and subterminal costal bifurcations, with very few lateral fusions. Secondary calcified orifice raised to form fimbriated distal plate. Suboral bar raised and swollen; with 1 pair of oral spines. Distal avicularium relatively small, the rostrum less than half length of autozooid orifice, subtriangular to rounded, with large paired condyles. Chambered pores include more than 1 septular pore and tend to occur at corners of autozooids, forming small kenozooids and extrazooidal calcification late in ontogeny.

Remarks. The specimens from Princetown and Cape Otway include only a few isolated groups of zooids but the material from Balcombe Bay is plentiful comprising more than 250 zooids most of which encrust fragments of the bryozoans *Porina* and *Laminopora*. The largest specimen has more than 80 autozooids. The relative simplicity of the costal shield resembles those of *Figularia* and *Membraniporella* and the apposed ends of the costae are raised in small tubercles similar to those of of the species illustrated as *M. bifurca* Powell by Gordon (1984: pl. 19A).

Anaskopora cornuta (MacGillivray)

Figures 5–7, Table 1

Cribrilina cornuta MacGillivray, 1895: 58, pl. 8, figs 10–12.—Maplestone, 1904: 201 (listed).

Corbulipora cornuta.—Brown, 1958: 55.—Wass, 1975: 168, pl. 7 figs 3–6, pl. 8 fig. 3.

Material examined. Lectotype. NMV P27635, Schnapper Point, Victoria, Miocene (selected by Wass, 1975).

Other material. Balcombe Bay, Warrambine Creek, Muddy Creek, Cooriemungle, Princetown, Victoria and Mount Schanck, South Australia.

Distribution. Additional records given by MacGillivray (1895) include Corio Bay and Gellibrand; by Maplestone (1904) include Spring Creek, Shelford, Griffins, Campbells Point, Mornington and Mitchell River; and by Brown (1958) include localities XI, Glenelg River at Werrikoo, and XVI, Crawford River at Glenaulin, all in Victoria. All records are Miocene, except Spring Creek and Glenaulin which are Oligocene (Appendix).

Description. Colonies encrusting minute substrata, or cylindrical to globular, principally formed by interzooidal frontal budding. Autozooids with a narrow gymnocyst and a pericyst formed by 12–24 costae; vertical components short and closely apposed. Median area of fusion very regular, with radiating rows of small lacunae between the costae, which overlap or abut terminally. Secondary calcified orifice small with a slight but distinct distal plate, paired oral spines and condyles. Recessed junction of the suboral costae forming a proximal sinus. Avicularium distal or distolateral, sometimes in pairs or triads, with a short, rounded, raised rostrum about two-thirds length of autozooidal orifice. Chambered pores not obvious but small interzooidal kenozooids are numerous surrounding each autozooid and becoming extrazooidal in older colonies.

Remarks. Like *A. rotundata*, the globular colonies have randomly orientated zooids and are almost completely composed of frontal buds. *Anaskopora cornuta* differs from *A. elevata* in its dimensions and much more numerous straight rows of costae and lacunae. It differs from *A. rotundata* in the regularity of the rows of costae and lacunae and its slightly larger avicularia. A significant number of the many specimens examined encrust small shell and bryozoan fragments like the colonies of *A. simplex* and *A. mesa*.

Anaskopora rotundata (MacGillivray)

Figures 8, 12–16, Table 1

Lagenipora rotundata MacGillivray, 1895: 78, pl. 10, fig. 18.

Lagenipora morningtoniensis Maplestone, 1902: 24, fig. 15.— Maplestone, 1904: 216 (listed).

Material examined. Holotype. NMV P27688, Lake Bullenmerri, Victoria, Miocene.

Holotype of *L. morningtoniensis*. NMV P10205, Mornington, Victoria, Miocene.

Other material. Balcombe Bay, Bairnsdale, Fyansford, Cooriemungle, Victoria and Mount Schanck, South Australia.

Distribution See above, Miocene (Appendix).

Description. Colonies globular, formed principally by interzooidal frontal budding and some overgrowth, from zooids encrusting very small substrata. Autozooids with distinct, narrow gymnocyst, pericyst formed by 20–24 closely apposed costae with very little vertical component. Horizontal area of fusion formed by random and repeated bifurcations and lateral fusions, producing a finely punctate shield, with small tubercles among lacunae formed where various costal elements have met and fused. Tubercles may occur in central longitudinal series in some zooids. Secondary calcified orifice has raised fimbriated distal plate and paired oral spines which are often flattened and curved. Proximal sinus formed by recessed costae of suboral bar together with paired condyles. Distal avicularium is small, rounded rostrum less than half length of autozooid orifice. Autozooids become surrounded by kenozooids late in ontogeny.

Remarks. MacGillivray's (1895) account and figure did not adequately describe this species which he noted was represented by a 'single minute fragment'. The type specimen consists of approximately 15 worn zooids encrusting and almost completely enclosing a minute shell fragment on both sides. Most of the zooid orifices and the avicularia are so worn that few characters remain. The minutely tuberculate frontal shields are, however, better preserved and can be seen to be identical with those of the lectotype of *Lagenipora morningtoniensis*. MacGillivray's (1895) figure did not show the distal avicularium which he had not recognised as being present but did illustrate the frontal shield and the distal plate of a single zooid. Not surprisingly, Maplestone (1902) did not consider that his material had been described before. He referred *L. morningtoniensis* to the ascophoran genus *Lagenipora* because he considered that the finely punctate and tuberculate pericyst was a 'granulated' frontal shield and that the distal plate and flattened curved oral spines which tend to surround the secondary orifice constituted an 'irregularly elevated peristome.' This structure he thought was 'very similar to *L. simplex*, MacG.' *Lagenipora simplex* MacGillivray (1890: 109, pl. 5 fig. 8) is a Recent species from Western Port, Victoria, referable to *Celleporina bidenticulata* Busk, 1881 (Busk, 1881, 1884; Bock, personal observation).

Anaskopora rotundata occurs frequently together with *A. elevata* and *A. cornuta* from a wide range of Victorian and South Australian localities. It has not been reported since its description and neither has *L. morningtoniensis*, probably because the colonies have not been recognised as distinct from those of *A. cornuta* which they greatly resemble. The autozooids and avicularia are very similar in size and shape but the structure of the zooidal frontal shields of *A. cornuta* and *A. rotundata* are totally dissimilar.

Anaskopora mesa sp. nov.

Figures 9–11, Table 1

Material examined. Holotype. NMV P140965, Balcombe Bay, Victoria , Miocene.

Other material. Balcombe Bay, Bairnsdale, Victoria; Mount Schanck, South Australia.

Distribution. See above, Miocene (Appendix).

Etymology. Mesa (Spanish) — a plateau at the summit of a mountain, referring to the shape of the autozooid pericyst.

Description. Colonies encrusting minute substrata. Autozooids with distinct vertical gymnocyst and peripheral component of 16–24 costae. Median area of fusion wide, with crenulated peripheral rim formed by spinous processes bordering single marginal series of pelmatidia. Horizontal component of costae not obvious, shield formed by calcification surrounding 25–35 large, often irregular lacunae, some with raised rim. Secondary calcified orifice rounded, distal plate distinct, sometimes with paired spinous processes. Oral spines large, paired, occasionally with additional distal spine and often raised and inflexed above orifice and fused medially. Distal avicularium small, length of rostrum less than that of orifice. Rostrum subtriangular to rounded, not raised, with paired condyles. Chambered pores and kenozooids present at corners of autozooids, small pore-chambers and septular pores also present.

Remarks. The material from Mount Schanck is not well preserved and none of the autozooids shows the raised, inflexed and fused oral spines present in the Victorian specimens. These spines are remarkably similar to those which sometimes occur in *Corbulipora ornata* (encrusting and kenozooidal phases only, Bock and Cook, 2001).

One specimen from Balcombe Bay differs from all the others. It comprises only a few, rather worn zooids (Fig. 11). Although the frontal shield resembles those of the other colonies, the secondary calcified orifice differs in having little or no raised distal plate but a large square tooth projecting proximally into the orifice from the distal wall. In a few zooids the suboral bar is raised above the orifice, forming a partial peristome similar to that described by Wass (1975) in material he assigned to *A. ampulla*. Until this and additional specimens become available for examination it is not possible to decide whether this specimen represents a species distinct from *A. mesa* sensu stricto or is identical with *A. ampulla*.

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Appendix. Details of Tertiary localities mentioned in the text

Bairnsdale (Skinners): Mitchell River bank, about 12 km W of Bairnsdale, Vic. 37°47.9′S, 147°29.5′E.

Balcombe Bay: Also known as Fossil Beach, Mornington, Mount Martha and possibly 'Schnapper Poin' (MacGillivray); on coast of Port Phillip Bay, about 3 km S of Mornington, Vic. 38°14.5′S, 145°01.7′E. Fyansford Clay. Balcombian; Middle Miocene, (Langhian).

Batesford Quarry: Upper levels of limestone Quarry, 7 km W of Geelong. Vic. 38°06.5′S, 144°17.3′E, Fyansford Clay. Middle Miocene (Balcombian).

Bird Rock: Coastal section, about 3 km W of Torquay, Vic. 38°21.4′S, 144°17.8′E. Jan Juc Formation. Janjukian; Late Oligocene, (Chattian). Also known as Spring Creek.

Campbells Point: On Lake Connewarre, 12.5 km SE of Geelong, Vic. 38°13.7′S, 144°26.7′E. Middle Miocene.

Cape Otway: Also Point Flinders, Locality AW1. Coastal section 2 km NW of Cape Otway, Vic. 38°51.1′S, 143°29.5′E. Glen Aire Clay. Early Oligocene (Rupelian/Latorfian).

Cooriemungle area: Road cuttings about 18 km N of Princetown. 38°32.4′S, 143°08.1′E. Gellibrand Marl. Balcombian.

Corio Bay: Coastal exposures between 2 and 6 km N of Geelong, Vic. Middle to Late Miocene.

Fyansford: This locality was mentioned by Maplestone (1904) and is almost certainly in the same area as the Batesford Quarry (see above).

Gellibrand: This locality was mentioned by MacGillivray (1895) and is in the same area as Princetown.

Glenaulin: Locality XVI of Brown (1958). Limestone, South landslip, Allotment 1, Parish of Glenaulin, south-western Vic. Janjukian, Late Oligocene (Chattian).

Glenelg Group: Locality XI of Brown (1958). Limestone Creek cliff. Allotment 16, and Locality XIV, near base of section at Caldwells Cliff, Allotment 68b, both Parish of Werrikoo, south-western Vic. Myaring Beds, upper Gambier Limestone. Longfordian, Early Miocene (Burdigalian).

Griffins: This locality is listed in Maplestone's checklist (1904). The locality was one of the limestone quarries on the Moorabool River, about 8 km NW of Gee. This is close to the Batesford Quarry (above).

Lake Bullenmerri: One of the rare inland outcrops of the uppermost Gellibrand Marl. 38°16.9´S, 143°06.2´E. Middle Miocene.

Mount Gambier: Abandoned quarry on road to Port MacDonnell, about 7 km S of Mount Gambier, SA. 37°53.5´S. 140°43.2´E. Gambier Limestone. Longfordian(?) Early Miocene.

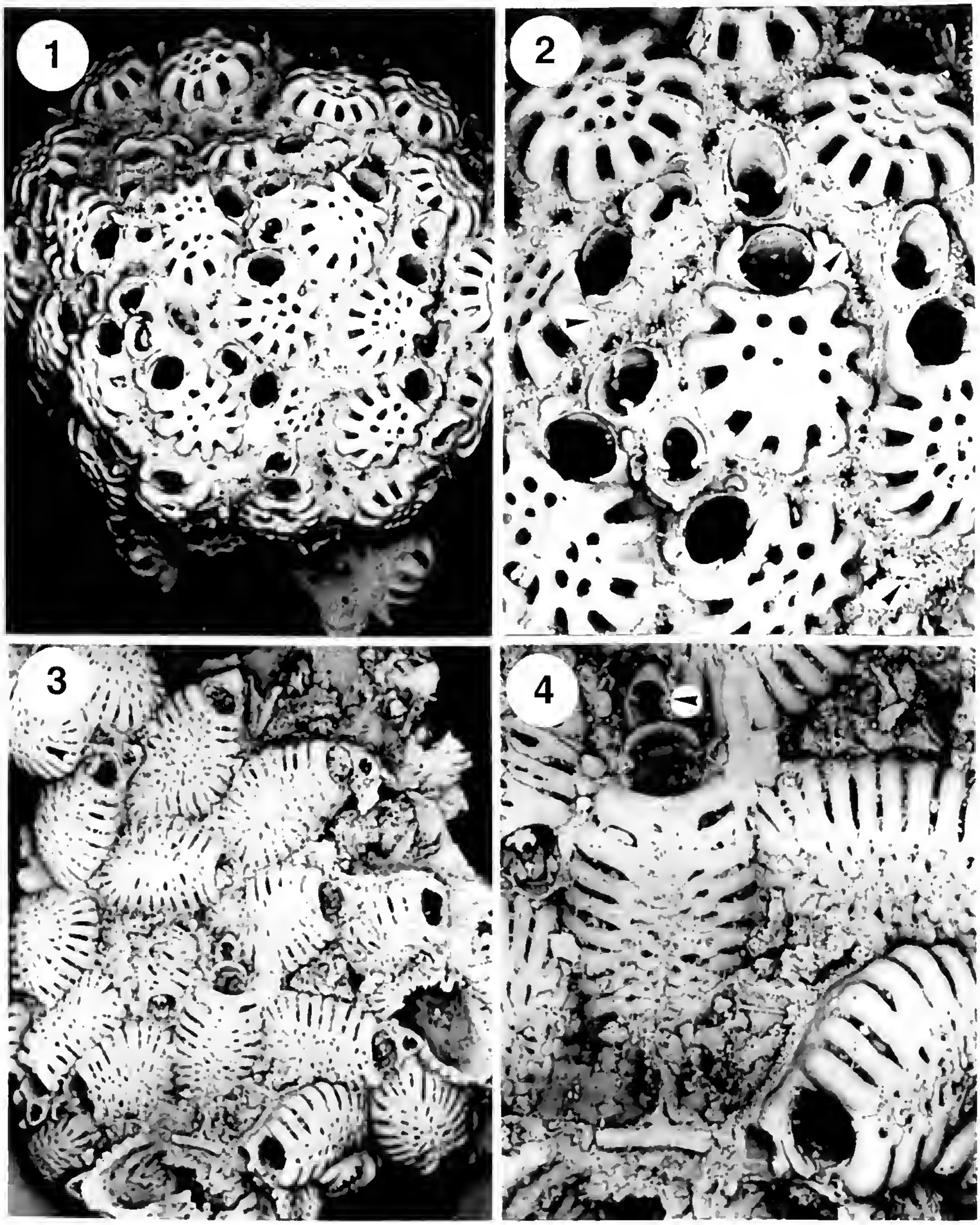
Mount Sebanck: Limestone quarry about 1 km W of Mount Schanck, about 15 km S of Mount Gambier, SA. 37°57´S, 140°43.2´E. Gambier Limestone. Longfordian; Early Miocene.

Muddy Creek: Clifton Bank, Muddy Creek, 8 km W of Hamilton, Vic. 37°44.6´S, 141°56.4´E, Muddy Creek Marl (= Gellibrand Marl). Balcombian.

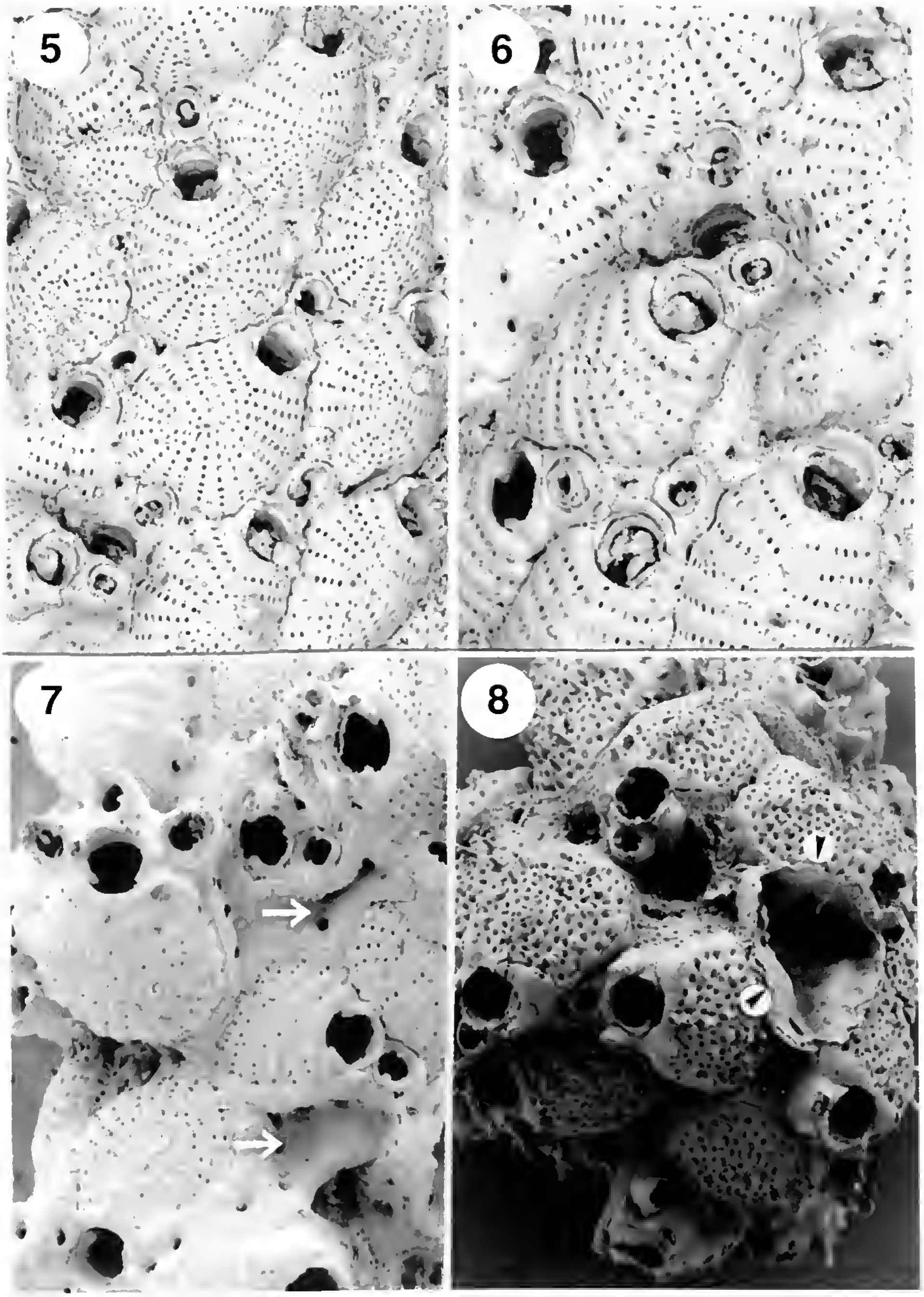
Princetown (Gigantocypraea locality): Coastal section, about 2 km W of Princetown, Vic. 38°41.9´S, 143°08.3´E. Gellibrand Marl. Balcombian.

Shelford (Red Bluff): Road cutting 35 km WNW from Geelong, Vic., 38°3.1´S, 143°59.2´E. Middle Miocene.

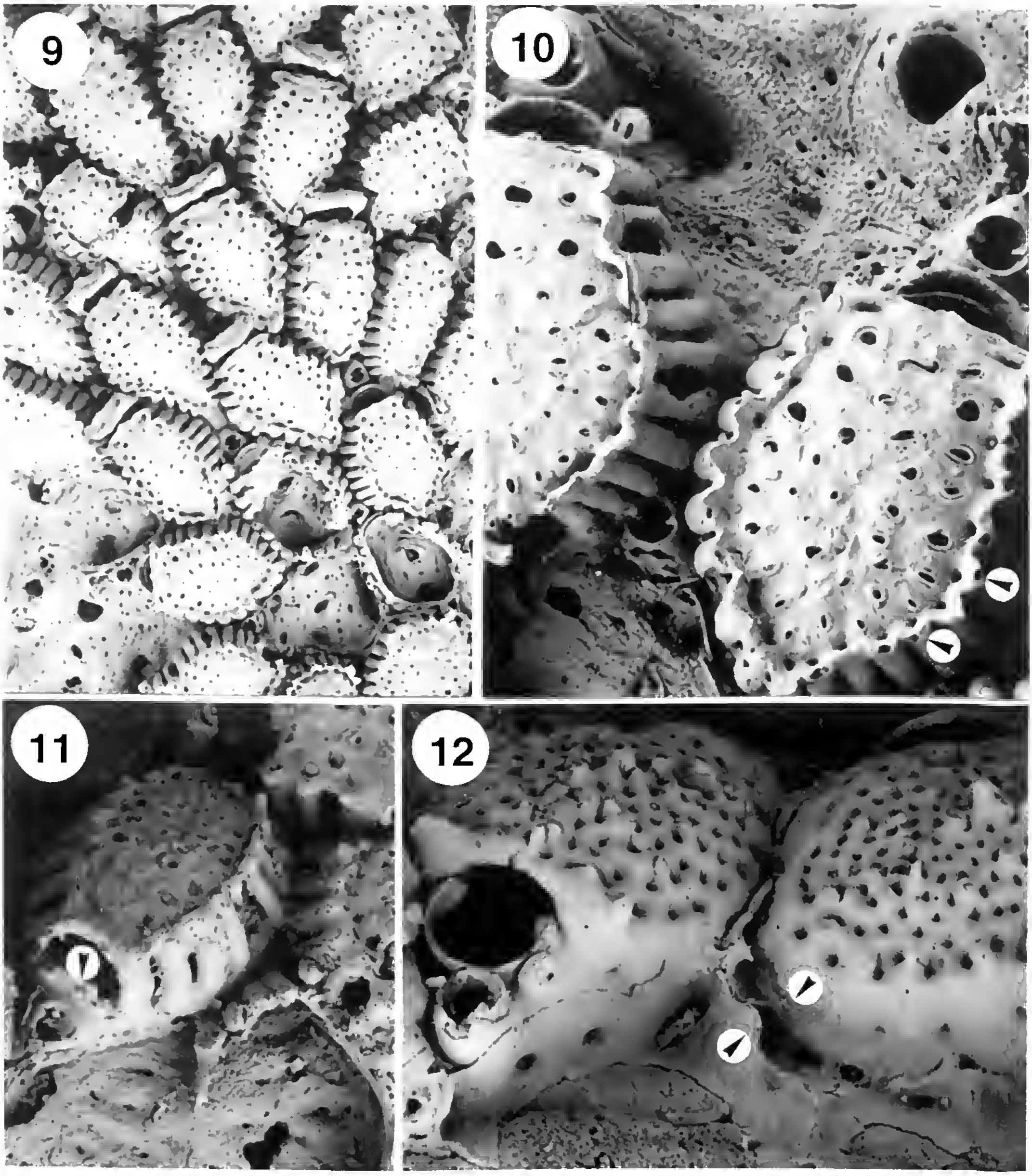
Warrambine Creek: Stream section beside the bridge on the Inverleigh-Winchelsea Road, 31 km W of Geelong, Vic. 38°7.0´S, 144°00.4´E. Middle to Late Miocene.



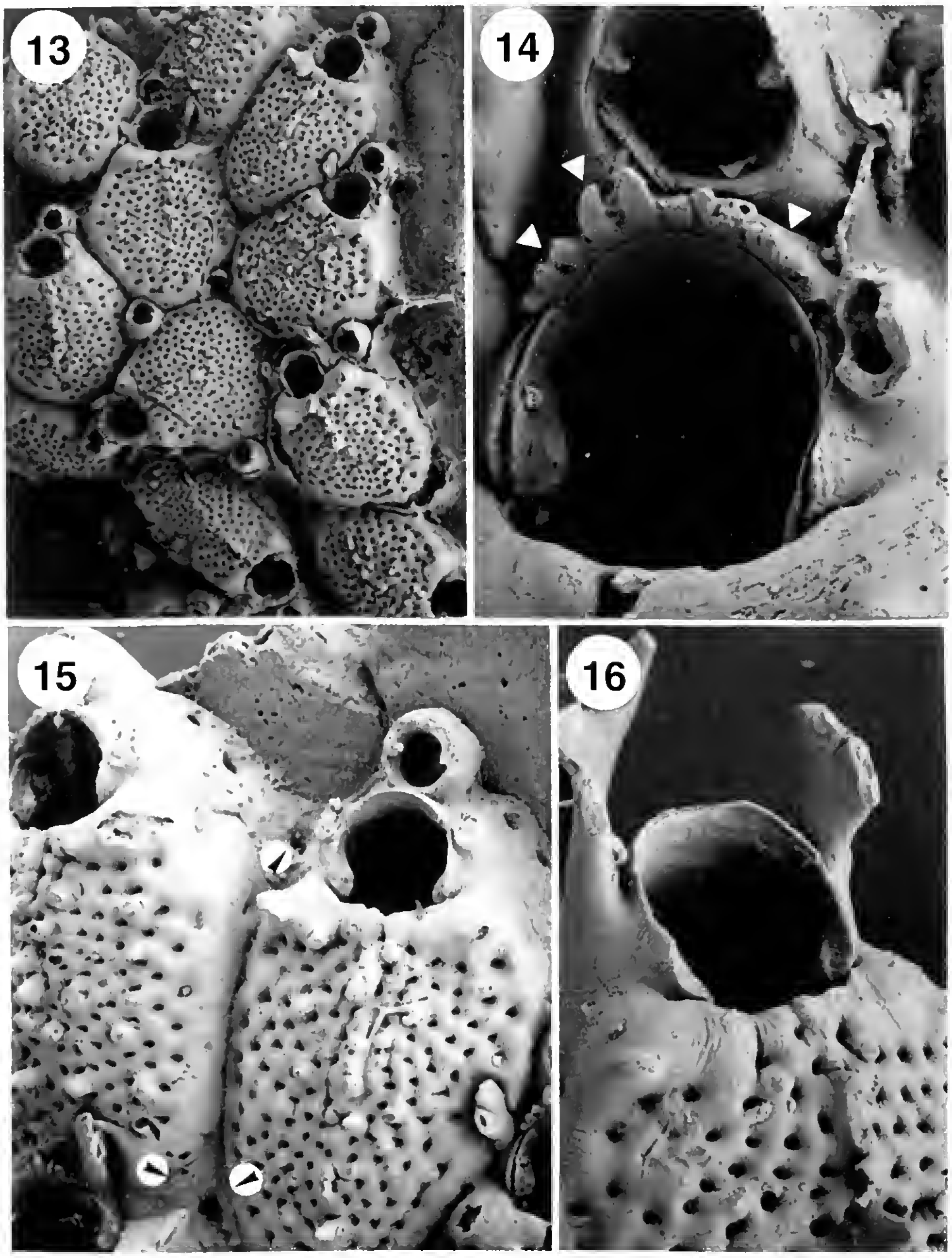
Figures 1–4. *Anaskopora elevata*. Balcombe Bay, Vic. Fig. 1, globular colony, showing frontal buds (×40). Fig. 2, enlargement of zooids from the same colony. Note distal avicularia and large area of extrazooidal calcification surrounding zooids (arrowed) (×80). Figures 3–4. *Anaskopora simplex* sp. nov. Balcombe Bay, Vic. Fig. 3, part of a small encrusting colony (×23). Fig. 4, enlargement of zooids from the same colony, distal avicularium arrowed (×50).



Figures 5–8. *Anaskopora cornuta*. Balcombe Bay, Vic. Fig. 5, slightly worn zooids, showing regular rows of intercostal lacunae (×52). Fig. 6, enlarged zooids (×70). Fig. 7, frontally budded zooids and avicularia. Interzooidal kenozooids and developing frontal buds arrowed (×60). Fig. 8. *Anaskopora rotundata*. Balcombe Bay, Vic. Globular colony with developing frontal bud (arrowed) (×65).



Figures 9–12. *Anaskopora mesa* sp. nov. Balcombe Bay, Vic. Fig. 9, encrusting colony; zooids with raised medially fused oral spines (×37). Fig. 10, enlargement of zooids from the same colony, marginal pelmatidia arrowed (×128). Fig. 11, zooid of *A.* aff. *mesa* showing distal oral tooth (arrowed) (×72). Figure 12. *Anaskopora rotundata* Balcombe Bay, Vic. Zooids from growing edge of encrusting colony, showing lateral septular pores and developing chambered pore (arrowed) (×125).



Figures 13–16. *Anaskopora rotundata*. Balcombe Bay, Vic. Fig. 13, colony encrusting basal side of erect bryozoan (×48). Fig. 14, Secondary calcified orifice, showing condyles and fimbriated distal plate (arrowed) (×360). Fig. 15, zooids showing tuberculate frontal shield and chambered pores developing as kenozooids at 'corners' of zooids (arrowed) (×127). Fig. 16, orifice, showing distal plate and oral spines (×240).

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REVISION OF THE MULTIPHASED GENUS *CORBULIPORA* MACGILLIVRAY (BRYOZOA: CRIBRIMORPHA)

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Abstract

Bock, P.E. and Cook, P.L., 2001. Revision of the multiphased genus *Corbulipora* MacGillivray (Bryozoa: Cribrimorpha). *Memoirs of Museum Victoria* 58(2): 191–213.

Corbulipora MacGillivray is redefined to include only species which occur in successive growth phases. The fossil type species, *Corbulipora ornata* MacGillivray, occurs in an encrusting ancestrulate phase, an erect quadriserial, ovicellate phase, and a frontally-budded partially kenozooidal phase. The encrusting ancestrulate phase of the Recent species, *C. tubulifera* (Hincks), is the type species of the genus *Acanthocella* Canu and Bassler, which is a junior synonym of *Corbulipora*. The succeeding, ovicellate, flustrine phase, known as *Watersia militaris* (Waters), is the type species of *Watersia*, another junior synonym of *Corbulipora*. It produces a third bilaminar phase known as *C. oriparma*, a synonym of *C. tubulifera*. This has rhizoids and develops further flustrine phases. Fossil specimens assigned to *Acanthocella tubulifera* in the past are here considered to be the primary encrusting phase of a bilaminar phase, known as *Corbulipora suggerens* (Waters), from which it has become separated. A thinly calcified intervening erect phase similar to the flustrine phase of *C. tubulifera* is inferred to have existed but not to have been preserved as a fossil. Some species previously referred to *Watersia* are assigned to *Klugeflustra* Moyano which, like *Neoflustra* Lopez Gappa, has flustrine colonies with large, hyperstomial ovicells, unlike those of the family Flustridae sensu stricto. A key to species of *Corbulipora* and their various phases is given.

Introduction

The superfamily Cribrilinoidea Hincks, as redefined and interpreted by Gordon (1984: 60), includes not only all the genera usually assigned to the family Cribrilinidae Hincks (for example, Bassler, 1953: G184), but all those referred to the Cribrimorpha by Lang (1916). Many of the Cretaceous genera described by Lang were included in the family Pelmatoporidae by Larwood (1962: 51). Voigt (1993) also assigned Cretaceous species to this family.

'Cribrimorphs' are characterized by the presence of a frontal shield of hollow calcified spines which overarch a membranous frontal wall with contiguous, uncalcified primary orifice and operculum. Obviously, many 'anascan' genera share these characteristics and the resulting shifts in systematic position of various species of *Callopora* and *Membraniporella* (Ryland and Hayward, 1977), emphasise Levinsen's (1909: 156) opinion of the 'unnaturalness' of the family Cribrilinidae. Gordon (1984: 60–61) noted the similarities among some species of Calloporidae with those of *Membraniporella* and *Figularia* and remarked 'at present it is difficult to define positively the boundaries between the two families.' Moyano (1984, 1991) suggested some preliminary groupings of cribrimorphs based on frontal shield structures. These include some with umbonulomorph affinities but do not deal with some intermediate forms. It remains difficult to define any polythetic boundaries among superfamily and family groups, which are themselves almost certainly non-homogeneous.

However difficult it may be to define cribrimorphs exclusively, many species with distinctive characteristics have been described. Detailed examination of some apparently ubiquitous taxa has recently yielded much more information on ovicell ontogeny and on kinds and degrees of polymorphs, which have revealed many exclusive groups of character correlations, and have greatly increased the number of described species (Ristedt, 1985; Bishop and Househam, 1987; Harmelin and Aristegui, 1988).

Briefly, the frontal shield (pericyst) is formed by spinous outgrowths (costae) which are hollow outfoldings of the calcifying marginal frontal wall (gymnocyst). The costae extend over the flexible part of the frontal wall (frontal membrane) and fuse centrally (median area of fusion, Larwood, 1962). The central coelomic space of each costa is in contact, at its origin, with the perigastric (or visceral) coelom of the zooid (Wass, 1975). Small uncalcified areas regularly spaced along the lateral vertical faces of each costa have the potential to expand their overlying cuticle intussusceptively and to calcify and form fusions with those of neighbouring costae leaving holes between successive costae (lacunae). Other small uncalcified areas, equally regularly distributed along the upper (frontal) surface of each costa (lumen pores or pelmatidia), allow similar expansions of cuticle and underlying coelom frontally. These may also calcify forming spinous processes. Sometimes the most marginal pelmatidia, which are usually the largest, extend as spinous processes which meet those of neighbouring zooids, forming interzooidal fusions quite late in ontogeny. This may produce secondary calcification and even tertiary interzooidal shields or extrazooidal expanses (Wass, 1975). In some species frontally budded zooids arise from expansions originating from enlarged pelmatidia, which then function very like the frontal septular pores of many ascophorans allowing transfer of coelom and nutrients to the developing buds.

Interzooidal communication through both septular pores, pore-chambers and a special kind of pore-chamber (here called a chambered pore) all occur in species of *Corbulipora*. The chambered pores allow another form of frontal budding. They originate as a fairly simple uniporous or multiporous pore-plate at the base of a vertical wall. This rapidly develops a large calcified chamber with a window covered by cuticle on the upper and outer side. These chambers may encompass more than one septular pore. Some zooids of the same astogenetic generation may communicate directly through septular pores, others through septular pores on both sides of a chambered pore. This often expands frontally between the vertical zooid walls, forming a kenozooid with an uncalcified window at its frontal side. These kenozooids tend to occur at the 'corners' between autozooids and are very evident at the growing edges of colonies; they are also the origin of rhizoids and 'stalk' kenozooids. Somewhat similar kinds of pore-chambers have been described in the family Hippothoidae by Gordon and Hastings (1979) but these are much more regular in size, shape and distribution than the chambered pores. It is interesting, however, that Gordon (1989) noted that an ability to produce frontal buds from the windows of such pore-chambers was a definitive character of his Infraorder Hippothoomorpha and he considered that there was a 'kind of conceptual linkage, from the Cribrilinoidea through Catenicelloidea to Hippothooidea'.

The potential for considerable astogenetic and ontogenetic change within a colony is thus present in cribrimorph morphology. Although almost every possible resultant structure seems to be produced in *Corbulipora*, in general, this potential does not seem to be realized among other cribrimorph genera. Pelmatidia are not always present, or are little-developed, and interzooidal frontal buds are rare. Species may thus be defined by such characters as the proportion of the gymnocyst to the pericyst, the number and form of costae, and the extent and nature of the median area of fusion. Patterns of kenozooids and ovicells, together with avicularia, also seem to define many taxa in detail and to have character consistency (Ristedt, 1985; Bishop and Househam, 1987). The species of *Corbulipora* described below pose problems precisely because they display a wide range of ontogenetic changes, coupled with the occurrence of multiple astogenetic phases in which the contributing zooids are often completely unlike one another; in one case being totally 'un-cribrimorph' in appearance (Bock and Cook, 1994).

Colonies in which the zooids exhibit zones or areas of totally differing morphologies are not unknown in other Bryozoa. Frequently isolated zones or areas have been assigned to completely unrelated taxa and Voigt (1975) has illustrated several examples drawn principally from the Late Cretaceous of Northern Europe. Among these, one cribrimorph, *Castanopora bipunctata* (Goldfuss), shows remarkable autozooidal heteromorphy. Colonies are bilaminar, unilaminar, or occasionally encrusting. In all these colony forms, entire fragments or large areas within colonies have membraniporine zooids with no trace of a calcified costal shield frontally. In other specimens, all or most of the zooids have a shield composed of 10–18 costae with pelmatidia, which alternate with rows of small lacunae. Both types of autozooid bear identical ovicells, and like some phases of *Corbulipora tubulifera*, identical kinds of large avicularia occur in both kinds of colony. *Castanopora bipunctata* does not, however, seem to occur in isolated subcolonies, each representing a distinct phase, and thus differs from *Corbulipora*.

Specimens from the collection of Dr Shizuo Mawatari, and from the following institutions have been examined: Australian Museum, Sydney (AM), Natural History Museum, London (BMNH), Museum of Victoria, Melbourne (NMV) and the Zoological Museum, Copenhagen (ZMC).

Corbulipora MacGillivray

Corbulipora MacGillivray, 1895: 60.—Wass 1975: 168.
Watersia Levinsen, 1909: 94.
Acanthocella Canu and Bassler, 1917: 35.

Type species. Corbulipora ornata MacGillivray, 1895.

Description. Complete colonies consisting of subcolonies with encrusting, erect and/or semi-erect phases of growth. Each phase with zooids of consistent morphologies, which may differ completely from those of a preceding or succeeding phase. Each species including at least 1 cribrimorph phase, usually more. Growth sequences always beginning with an encrusting ancestrulate phase but other sequences may alternate or co-exist, although sometimes in physical isolation. All phases are known, or assumed, to be capable of a separate existence. Ancestrula tatiform, with marginal spines. Zooids of all cribrimorph phases with gymnocyst and pericyst of costae with pelmatidia and lacunae. Oral spines 1–3. Ovicells often confined to 1 phase only but not necessarily the same phase in different species. Ovicells are prominent, hyperstomial, closed by operculum, with median suture and paired entooecial frontal areas. Brooding zooids of flustrine phase with flattened spines or with exposed frontal membrane and enlarged oral spines only. Avicularia interzooidal, large, with distally orientated rostrum, rounded or expanded terminally.

Remarks. Multiphased growth is known or may be reliably inferred to occur in each of the three species here referred to *Corbulipora*. In *C. ornata*, all zooids of the three phases recognized have costate pericysts. The first phase is encrusting, the second erect and quadriserial, and this phase develops both avicularia and ovicells. The third phase is frontally budded from the pelmatidia of the second erect phase zooids and is often purely kenozooidal. In *C. suggerens*, two cribrimorph phases have been recognized and inferred to belong to one taxon. One phase is encrusting, the other is bilaminar. Its colony and zooid morphologies are so akin to those of the third, bilaminar phase of *C. tubulifera*, that it seems almost certain that it represents a third phase, and that a missing, intervening, erect second phase, with very thin calcification, and perhaps flustrine or cellularine growth, once occurred, but was not preserved in the fossil material. The bilaminar phase of *C. suggerens* occasionally bears ovicells, unlike that of *C. tubulifera*. This last species has been observed with its three phases growing from one another. The ancestrulate encrusting phase gives rise to several flustrine subcolonies which alone bear ovicells. Large avicularia occur in this phase and in the third phase, which develops from the tips of the flustrine fronds. These two phases may alternate (Bock and Cook, 1994). Recently a further living species of *Corbulipora*, *C. inopinata*, has been described from southwestern Australia by Bock and Cook (1998). It closely resembles *C. tubulifera* and also occurs in three subcolony phases. The flustrine, second phase differs in having zooids with frontal spines, somewhat resembling those of the earlier ontogenetic stages of the second, quadriserial phase of *C. ornata*.

The genus *Corbulipora* was introduced for *C. ornata* alone. Wass (1975) redefined the genus and assigned some species to a new subgenus, *Anaskopora*. These species, together with *Cribrilina cornuta* MacGillivray (1895), which Wass (1975) referred to *Corbulipora*, are now regarded as generically distinct and are discussed elsewhere (Bock and Cook, 2001).

Corbulipora collaris Canu and Bassler (1920: 308, pl. 43 fig. 14), from the North American Eocene was also redescribed by Wass (1975: 170, pl. 8, figs 7–9). It has medially orientated adventitious oral avicularia and an endozooidal ovicell. It is therefore excluded here from *Corbulipora* which is considered to have a Tertiary to Recent, Australasian distribution only. When Wass (1975) revised *Corbulipora*, *C. collaris* was the only species assigned to the genus in which an ovicell had been described. This was probably the reason why he used the term 'entozooidal' for the ovicell type, which he then applied to the whole genus. All ovicells now observed in species referred to *Corbulipora* are hyperstomial, with paired, entooecial frontal areas.

Key to species and phases of *Corbulipora*

1. Subcolony flustrine, autozooids with exposed frontal membrane and 1 pair of oral spines. Ovicells and large interzooidal avicularia present ....*C. tubulifera* phase 2

— Subcolony not flustrine, autozooids with costal frontal shield.......................2

2. Subcolony encrusting a substratum, mostly single layered.......................... 3

— Subcolony erect, suberect and bilaminar or formed by frontal budding 5

3. Autozooids large (Lz >0.75 mm), costae 16–24, with 3–4 concentric series of long, sometimes branched, spinous processes arising from pelmatidia ....*C. suggerens* phase 1

— Autozooids smaller, costae 10–18, with 1–2 concentric series of blunt tubercles arising from pelmatidia.. 4

4. Autozooids very small (Lz <0.50 mm), orifice small (lo 0.10 mm). Lateral oral spines raised, inflexed and fused above the orifice......*C. ornata* phase 1

— Autozooids larger (Lz >0.60 mm), orifice larger (lo >0.11 mm). Oral spines not raised or fused...*C. tubulifera* phase 1

5. Subcolony erect, quadriserial; autozooids with long gymnocyst and small costal shield. Avicularia rare, ovicells present.....................*C. ornata* phase 2

— Subcolony composed of autozooids and kenozooids, budded frontally from phase 2-zooids, orientation random. Gymnocyst and orifice not generally visible; avicularia and ovicells absent.................................*C. ornata* phase 3

— Subcolony bilaminar, small; autozooids orientated distally, interzooidal avicularia present...6

6. Subcolony triangular, arising from 2–4 zooids with partially calcified frontal shields, orifices not occluded by oral spines. Avicularia not raised distally, with a bar. Ovicells present...*C. suggerens* phase 3

— Subcolony rectangular, arising from 6-8 zooids with partially calcified frontal shields, orifices often occluded by growth and fusion of oral spines. Avicularia raised distally, with paired condyles. Ovicells absent, rhizoids present...*C. tubulifera* phase 3

Corbulipora ornata MacGillivray

Figures 1–9, 27, Tables 1, 2

Corbulipora ornata MacGillivray, 1895: 60, pl. 8 figs 20, 21.—Maplestone, 1904: 201 (listed).—Brown, 1958: 54.—Wass, 1975: 168, pl. 7 figs 1, 2.

Material examined. Lectotype (chosen by Wass, 1975): NMV P27642, Schnapper Point (= Balcombe Bay), Victoria. Middle Miocene, Balcombian.

Other material. Balcombe Bay; Cooriemungle, near Princetown and Princetown, Victoria (Middle Miocene, Balcombian); Bird Rock, near Torquay, Victoria (Upper Oligocene, Janjukian); Mount Schanck, S of Mount Gambier, South Australia (Lower Miocene, Longfordian).

Distribution. Additional localities given by MacGillivray (1895) and Maplestone (1904) include: Cape Otway, Spring Creek, Campbells Point, Mornington, Mitchell R. and Bairnsdale; localities given by Brown (1958) include: Localities XVI (Glenaulin Clay) and XXVI (Wataepoolan Limestone) near Crawford R.; and XXII and XXIII on Glenelg R., Nangeela, south-western Victoria. Miocene to Oligocene (see Appendix).

Description. *Corbulipora* with subcolonies of 3 growth phases; all zooids with costate pericysts. Subcolonies of encrusting phase very small, comprising at most 40 zooids; basal walls calcified only at margins. Ancestrula has 14–16 marginal spines and buds a triad of distal primary zooids. As in *C. suggerens*, appearance of some zooids differs from those budded later in astogeny. Autozooids have small, distinct gymnocyst, and pericyst with 10–16 costae, each with 2 or 3 intervening lacunae and 2 pelmatidia, raised as blunt tubercles. Secondary calcified orifice small, with paired condyles and 3 oral spines, lateral pair often raised vertically, inflexed and fused above orifice (Figs 1, 2). This condition also occurs in some zooids of third phase, which may resemble those of first phase closely. Zooids communicate through small pore-chambers at base of vertical walls.

Second phase erect and quadriserial, zooids

Table 1. Comparative measurements in mm among phases in species of *Corbulipora*. Lz, lz, length and width of zooid; lo width of orifice.

C. ornata	*C. suggerens*	*C. tubulifera*
Phase 1	Phase 1	Phase 1
Lz 0.45–0.48	Lz 0.58–0.87	Lz 0.58–0.74
lz 0.37–0.40	lz 0.37–0.54	lz 0.38–0.50
lo 0.08–0.09	lo 0.11–0.13	lo 0.12–0.13
Phase 2	Phase 2	Phase 2
Lz 0.70–1.00	—	Lz 0.78–1.32
lz 0.28–0.36	—	lz 0.25–0.33
lo 0.13–0.14	—	—
Phase 3	Phase 3	Phase 3
Lz 0.33–0.37	Lz 0.58–0.87	Lz 0.54–0.87
lz 0.33–0.37	lz 0.37–0.54	lz 0.32–0.54
lo 0.07–0.10	lo 0.06–0.12	lo 0.10–0.14

Table 2. Comparative measurements in mm among phases of *Corbulipora* and species of *Klugeflustra*. Lz, lz, length of zooid; Lav, lav, length and width of avicularium; Lp, length of palate; Lov, lov, length and width of ovicell.

	Lz	lz	Lav	lav	Lp	Lov	lov
C. ornata phase 2	0.70–1.00	0.28–0.36	0.55–0.66	0.17–0.21	0.43–0.55	0.24–0.25	0.23–0.25
C. suggerens phase 3	0.58–0.87	0.37–0.54	0.28–0.43	0.12–0.16	0.12–0.20	0.12–0.16	0.16–0.21
C. tubulifera phase 2	0.78–1.32	0.25–0.33	0.65–0.96	0.22–0.26	0.31–0.35	0.23–0.27	0.28–0.33
K. vanhoeffeni	1.23–1.56	0.40–0.50	1.03–1.25	0.25–0.33	0.40–0.50	0.50–0.60	0.44–0.48
K. kishakaensis	1.32–1.43	0.32–0.36	0.25–0.37	0.32–0.31	0.08–0.10	0.33–0.43	0.40–0.47
K. simplex	0.44–0.50	0.15–0.19	—	—	—	0.21–0.28	0.28–0.31

communicating through simple septular pores. Branches bifurcate occasionally. Intermediate developmental stages linking encrusting with quadriserial phase unknown, and in isolation, component zooids of the 2 phases totally unlike. Erect-phase autozooids have elongated, smooth gymnocyst surrounding costal shield which may be subrectangular or small and oval. Zooid length nearly twice that of those from other phases, 12–22 costae, distal pair forming suboral bar, prominent and sloping forward on distal edge (Fig. 4). Secondary calcified orifice large, almost perpendicular to frontal shield, with 1 pair of small lateral spines. Costae expanded and fused terminally; variable median area of fusion which changes its aspect with ontogeny. Costae bearing 2 or 3 small pelmatidia which alternate with 2–4 lacunae. Ovicells generally rare, narrow, with paired, crescentic, entooecial frontal areas. Oral spines of brooding zooids greatly enlarged, raised and fused above orifice, like those of phase 1 zooids; spines also bear some pelmatidia (Fig. 27). Avicularia also rare; large, with distinct gymnocyst, in series with autozooids. Rostrum rounded or expanded terminally, and orientated distally; small paired condyles (Fig. 3).

Subcolonies of third phase arise by frontal budding directly from autozooids of second phase. Zooid buds develop from greatly expanded pelmatidia; kenozooids and autozooids produced; ovicells and avicularia absent. Frontally budded zooids have random orientations; frontal shields have 10–16 costae, each with 2 or 3 pelmatidia raised into long spinous processes. These interdigitate and sometimes fuse interzooidally, especially at margins of zooids, forming continuous secondary shield in some specimens. Secondary, calcified orifice very small, with 3 oral spines. These may be long and prominent, occasionally raised, inflexed and fused above orifice, exactly as in encrusting zooids of first phase, not occluding orifices (compare *C. tubulifera*), but many zooids have no obvious orifice. Some may have been occluded by general interzooidal fusion of spinous processes but others seem to have been budded with no orifice, and are therefore true kenozooids.

Remarks. The taxonomic identity of the first and second phases of *C. ornata* can only be inferred, since zooids of intermediate morphologies have not been found linking them in situ. The ontogenetic changes in second-phase zooids leading to the third phase can, however, be traced in many specimens from Balcombe Bay and Mount Schanck. Early in ontogeny, the pericysts of the erect second-phase zooids form a small, oval area distal to an elongated gymnocyst (Fig. 3). The costae are long and virtually without lateral fusions, so that the intervening, slit-like lacunae extend to a narrow median area of fusion. Ontogenetic changes begin with a widening of this area by the development of lateral costal fusions, and a thickening of the shield by expansion of the pelmatidia and growth of spinous processes frontally (Fig. 4, 5). Some pelmatidia continue to increase in size, particularly those on the thickened suboral bar, and they become blister-like, while the more lateral spinous processes fuse interzooidally. The third-phase buds arise directly from expanded pelmatidia and some appear to develop as chambered pores or small interzooidal kenozooids (Figs 6, 7). The larger kenozooids and some autozooids have costate pericysts with numerous, long spinous processes arising from their pelmatidia. The third phase forms small, globular masses, budding from and overgrowing the second-phase zooids especially at the bifurcations of erect branches. In some specimens secondary calcification results in the third phase appearing as a globular mass of spinous or ridged costae with no orifices and no distinct zooidal structure remaining. The zooids of the second phase remain visible protruding at the proximal and distal ends of the mass (Figs 8, 9).

Corbulipora suggerens (Waters)

Figures 10–16, 28–29, Tables 1, 2

Cribrilina suggerens Waters 1881: 327, pl. 17 fig. 75.—MacGillivray, 1895: 57, pl. 8 fig. 8.—Maplestone, 1904: 201 (listed).

Cribrilina tubulifera Waters, 1883: 436 (not Hincks, 1881).

Acanthocella tubulifera.—Brown, 1958: 54 (fossil specimens only).

Cribrilina jonesi Brown 1958: 52, fig. 28.

Corbulipora sp.—Wass and Yoo, 1975: 811, pl. 2 fig. 4.

Corbulipora suggerens.—Bock and Cook, 1994: 34, fig. 6.

Material examined. NMV P73147, Holotype of *C. jonesi*, locality IX, E bank of Glenelg R., Myaring, south-western Victoria (Middle Miocene, Balcombian).

Other material. Balcombe Bay (ovicells); Cooriemungle; Princetown (ovicells); Griees Creek; Bairnsdale (all Middle Miocene, Balcombian); Narrawaturk Bore 2, near Peterborough, Victoria and Mount Schanck, South Australia (both Lower Miocene, Longfordian).

Distribution. Additional localities given by MacGillivray (1895) and Maplestone (1904) include: Campbells Point, Curdies Creek, Muddy Creek, Mitchell R. and Schnapper Point; and by Brown (1958) include Locality XIV, section at West end of Caldwell's Cliff, Glenelg R. (Miocene, Myaring beds) (see Appendix).

Description. Corbulipora with subcolonies of 2 known growth phases. Ancestrula tatiform, with 10–12 marginal spines. Autozooids of first, encrusting phase large, oval, with distinct rim of smooth gymnocyst surrounding costal shield with 16–24 costae (Fig. 10). Secondary, calcified orifice smaller than that of *C. tubulifera* (compare figs 16, 17), with 3 oral spines and paired condyles. Costae with 3, occasionally 4 pelmatidia and 3 or 4 lacunae. Median area of fusion increases in width with astogeny, and pelmatidia become raised and tuberculate, with long, sometimes branched spinous processes, which interdigitate and occasionally fuse laterally. Zooids with typical pore-chambers, with 3 distal and 1 or 2 lateral windows within gymnocyst boundary (Fig. 10). Avicularia and ovicells absent.

Bilaminar phase forming small, subtriangular subcolonies, each arising from 2–4 zooids which have frontal shields uncalcified or calcified only at distal end (Fig. 12). Subcolonies expand by bifurcation of zooid rows to 4–6 within two astogenetic generations. Basal lamina between the 2 zooid faces with few septular pores; autozooids with 2 or 3 large chambered pores or kenozooids laterally and distally (Figs 13–15). Autozooids of first 2 generations of completely calcified zooids often have elongated costal shields with little or no gymnocyst visible, and 16–22 costae. Distal pair of costae form prominent suboral bar sloping forward on distal edge, obscuring large, wide, vertical secondary calcified orifice. Costae well separated marginally with 2 or 3 intervening lacunae and 3 concentric rows of tuberculate pelmatidia. Autozooids of next 2 or 3 generations with increasingly short, rounded costal shields, with some marginal gymnocyst visible; 10–16 costae, distal pair forming suboral bar defining a minute, semicircular orifice, with paired condyles and 3 oral spines, which is visible frontally (Fig. 16). Pelmatidia arranged in 3 raised concentric series, with spinous processes which may interdigitate and fuse laterally. Oral spines often long but do not fuse above or occlude orifice. At growing margin of subcolonies, large, blister-like chambered pores or kenozooids occur in adjacent series between autozooids (Figs 13–15). Avicularia only among zooids of proximal, earlier astogenetic generations of subcolonies; large and interzooidal, with distally orientated, subspathulate rostrum and complete bar (Fig. 12). Ovicells rare, only on those zooids on proximal margin of phase 3 subcolonies, where zooids lack any calcified, costal frontal shield. Ovicells slightly flattened frontally, with paired entooecial areas, which in a few cases show signs of costate structure (Figs 28, 29). Unlike brooding zooids of *C. ornata* and *C. tubulifera*, paired oral spines not enlarged.

Remarks. The encrusting and bilaminar phases of *C. suggerens* resemble the equivalent first and third phases of *C. tubulifera* closely. The encrusting zooids are usually larger and in early astogeny exhibit a dramatic change in appearance between the generations like those of *C. ornata* at the same astogenetic stage. The vertical, marginal parts of the costae are well separated and the median area of fusion is narrow. There are only two concentric series of pelmatidia with short, but distinct spinous processes. In the next generations, zooids have wider median areas of fusion and three or more series of spinous processes. In some specimens from Princetown, a large distal pore-chamber forms an irregular distal kenozooid with a single pore in its frontal surface. The pore-chambers do not normally protrude beyond the base of the gymnocyst, unlike those of *C. tubulifera*. The zooids of the bilaminar phases of the two species resemble one another closely, but the size and shape of the subcolonies differ. The narrow origin of those of *C. suggerens* suggest that they may have been derived from the tips of a quadriserial, or very narrow, thinly calcified phase which has not been preserved. This in contrast to the much wider colonies of *C. tubulifera*, which are known to be derived from the broader, flustrine, *Watersia*-phase fronds. The orifices of the zooids of *C. suggerens* are not occluded by oral spine development, and the avicularia also differ from those of *C. tubulifera* in having a flat rostrum and a complete bar. Finally, as mentioned above, the bilaminar phase of *C. suggerens* occasionally bears ovicells proximally, unlike that of *C. tubulifera*.

Waters's (1883) record of *C. tubulifera* from Muddy Creek seems to have been based on specimens of the encrusting phase of *C. suggerens*, which he described as growing on shell (see above). He noted that the autozooids had larger orifices than those of his specimens of bilaminar *C. suggerens* where they are extremely small. Brown (1958) introduced *Cribrilina jonesi* for another bilaminar species from the Victorian Tertiary. The zooids had 16 costae and a thick suboral bar, and he noted their resemblance to *Acanthocella tubulifera*, which he regarded as a senior synonym of *C. suggerens*. Brown remarked on the small size of the orifice. The holotype of *C. jonesi* has been examined and proves to be identical with the bilaminar phase of *C. suggerens*.

Corbulipora tubulifera (Hincks)

Figures 17–26, 30–32, Tables 1, 2

Cribrilina tubulifera Hincks 1881: 8, pl. 1 fig. 7.—Waters, 1887b: 187, pl. 5 figs 2, 6.

Acanthocella tubulifera.—Brown, 1958: 52 (lectotype only, see *C. suggerens*).

Flustra militaris Waters 1887a: 93, pl. 14 fig. 2.

Watersia militaris.—Levinsen, 1909: 94, 95 (not Livingstone, 1929: 53; not Gordon, 1986: 28).

Corbulipora sp.—Wass, 1973: 361, pl. 1 figs 1–4.

Corbulipora oriparma Wass 1975: 169, pl. 9 figs 1–7, pl. 10 figs 1–6, 9–11.—Cook, 1979: 271, fig. 1D.—Wass and Yoo, 1983: 323.

Corbulipora tubulifera.—Bock and Cook, 1994: 33, figs 1–5.

Material Examined. BMNH 1899.5.1.726, photograph of lectotype of *C. tubulifera*, Bass Strait. BMNH 1887.10.21.1, ?part of type material of *W. militaris*, Port Jackson, Waters coll. BMNH 1926.6.1.2, Port Jackson, 9–15 m, label in Waters's hand 'sandy mud bottom near the Heads'. BMNH 1897.5.1.447, Port Jackson. AM U5006, 'Endeavour' Exped., T.Mortensen, S of Lakes Entrance, Victoria, 38°15′–25′S, 148°20′–43′E, 128–220 m, 8–9 Sep 1914, sand. NMV Bass Strait Survey: *Kimbla* stn 99 40°06′S, 143°16′E, 11 Oct 1980, 139 m; stn 100, as above, 158 m; stn 101, as above, 187 m. *Sarda* stn 112, 40°22′S, 145°127′E, 3 Nov 1981, 40 m. *Hai Kung* stn 135, 40°50′S, 146°31.3′E, 4 Feb 1981, 68 m. *Tangaroa* stn 155, 38°34′S, 144°54.3′E, 12 Nov 1981, 70 m; as above, 75 m; stn 164, 40°40.7′S, 148°36.9′E, 14 Nov 1981, 67 m. SLOPE stn 22, 37°0.6′S, 150°20′E 21 Jul 1986, 363 m; stn 45, 42°2.2′S, 148°38.7′E, 27 Jul 1986, 800 m; stn 46, as above, 720 m; stn 47, 41°59′S, 148°38.8′E, 27 Jul 1986, 500 m. ZMC, Port Jackson, NSW (label in Waters' hand).

Description. Corbulipora with subcolonies of 3 growth phases, 2 of which may be sequential as well as alternating. Observed sequences include encrusting (phase 1) to flustrine (phase 2); flustrine to bilaminar (phase 3); and bilaminar to flustrine (Fig. 18).

Phase 1. Subcolony encrusting small fragments of shell, dead bryozoans etc. Ancestrula tatiform with 10–14 fine marginal spines (La 0.45 mm) (Figs 23). Subcolony forming small patch of 50–100 zooids, basal walls calcified only marginally. Autozooids with marginal gymnocyst and pericyst of 10–16 stout costae. Vertical marginal part of costae well separated, inflexed and abutting centrally to form wide median area of fusion, alternating with short rows of 2 or 3 lacunae. Pelmatidia in 2 concentric circles, raised, forming blunt tubercles, occasionally spinous. Suboral bar swollen, with 3 or 4 pelmatidia. Secondary, calcified orifice semicircular with pair of small condyles and 3 oral spines. Operculum golden brown, closely apposed to the calcified orifice. 1 distal and 2 or 3 large lateral chambered pores, each enclosing several small septular pores. Each marginal chamber capable of giving rise to 1 rhizoid or stalk kenozooid. Avicularia and ovicells absent.

Phase 2. Subcolony arising from long stalk of thinly calcified kenozooids derived from chambered pores at margins of phase 1 or phase 3 subcolonies. Stalk kenozooids in apposed pairs or triads, and bud elongated autozooids by the second to fifth astogenetic generation, followed by bifurcation of zooid rows to form bilaminar flustrine frond (Fig. 18b). Fronds 6–8 rows wide, increasing to 10–12 before simple bifurcation. Largest subcolonies extend for >90 astogenetic generations, bifurcate 4 times, and include over 2000 zooids. Marginal zooids elongated, but not kenozooids. Vertical walls of opposing laminae do not correspond, and simple septular pores communicate through basal walls. Zooids also have 1 distal, and 1 or 2 lateral multiporous septular pores. Autozooids very thinly calcified, with no gymnocyst or cryptocyst; frontal membrane continuous with simple, terminal crescentic operculum. Oral spines paired, terminal, arising from lateral walls, wide at base; short and frontally directed in autozooids; massive, swollen and curved over operculum in brooding zooids. Ovicells may be developed on all zooids except marginal zooids; large, prominent, hyperstomial and closed by operculum. Frontally ovicells slightly flattened, with median suture and paired, crescentic entooecial areas (Figs 30, 31). Number of tentacles 12–14 (Lt 0.75 mm, Lt sheath 0.20 mm). Avicularia scattered, usually proximal to, or at a bifurcation of zooid rows. Gymnocyst thinly calcified, elongated, shorter in those avicularia at bifurcations; opesia uncalcified, rostrum raised and thickly calcified distally. Mandible subspathulate, hinged on paired condyles, directed distally (Fig. 3). Rhizoids arising from multiporous septular pores in walls of stalk kenozooids, or from autozooids at proximal end of fronds.

Phase 3. Subcolony bilaminar, forming subrectangular masses of 100–150 zooids, anchored by numerous rhizoids originating from enlarged marginal chambered pores. Subcolonies at tips of flustrine fronds, and proximal ends formed by 2 apposed series of 6–8 partially calcified zooids, alternating with next generation of zooids, which have frontal shield calcified at distal end only (Figs 25, 26). Following generation of 8–10 zooids elongated, with 16–18, often irregular costae, and prominent suboral bar. Subsequent 4 or 5 astogenetic generations have zooids with increasingly shorter and rounder costal shields, less prominent suboral bar, and smaller, semicircular calcified orifice. Pelmatidia in 2 concentric series, raised as blunt tubercles. 3 oral spines, becoming very large, swollen and fused, occluding orifice completely and developing large, blister-like pelmatidia on frontal surface. Large chambered pores at margins give rise to stalk kenozooids or rhizoids (Fig. 27, 28). Avicularia infrequent, occurring in earlier astogenetic generations, morphology same as those occurring in flustrine fronds. Ovicells absent.

Remarks. The nomenclatural consequences of the identity of *Cribrilina tubulifera*, *Watersia militaris* and *Corbulipora oriparma* are considerable, and are summarized in the synonymy given above. Although *Acanthocella* was introduced by Canu and Bassler (1917) with the Recent, Australian, *Cribrilina tubulifera* Hincks as type species, it was apparently their intention to erect a genus to receive the Eocene, Gulf of Mexico species, *A. erinacea* (Canu and Bassler, 1917: 36, pl. 4 fig. 1; 1920: 309, pl. 43 figs 101–103). *Acanthocella erinacea* has a frontal shield like that of *A. tubulifera* but has elongated ovicells without entooecial areas. It resembles the Recent, amphiAtlantic *Cribrilina figularis floridana* Smitt (1873), which was referred to *Reginella* by Cheetham and Sandberg (1964), Cook (1985: 125, pl. 9F) and Winston (1982: 134, fig. 59), and which does not develop ovicells. One further species of *Acanthocella*, *A. clypeata* Canu and Bassler (1928: 39, pl. 4 figs 9, 10, Fig. 5) from the

Gulf of Mexico, has complex oral spines which incorporate the suboral bar (Ristedt, 1979). No ovicells have been described. *Acanthocella erinacea*, *R. floridana* and *A. clypeata* are not known to occur in more than one phase and are excluded from *Corbulipora* here. *Acanthocella erinacea* has been made the type species of *Castanoporina*, a new subgenus of the Cretaceous genus *Castanopora* by Voigt (1993). He described a new species, together with one originally introduced by Larwood (1962) as *Castanopora voigti*. *Castanoporina voigti* was illustrated by Voigt (1993: 148, pls 7, 8, 9) having both colonies and zooids with a strong resemblance to those of erect, phase 2 *Corbulipora ornata*. However, the zooids each have paired, adventitious oral avicularia and the ovicells have no entooecial frontal areas.

Watersia Levinsen (1909: 99) was informally introduced in a key to genera of Bicellariidae. In addition, *Watersia militaris* was mentioned twice (pp. 94, 95), although with no indication of author or date. However, Levinsen seems to have thus indicated *Flustra militaris* Waters as type species, as no other taxon was assigned to the genus *Watersia*, which was not mentioned again. *Flustra militaris* was originally described by Waters (1887a) from Port Jackson, New South Wales. His figure shows three apparently verticillate rows of brooding zooids, with membranous frontals, stout, 'club-shaped' oral spines, and ovicells with a median suture and paired frontal areas. The colony was described as 'bilaminate' and Waters noted the similarities in appearance of the ovicells with those of '*Flustra episcopalis*' (= *Euthyroides*).

Some specimens (ZMC, BMNH), four of which have labels in Waters' hand, or are from his collection, and all of which are from Port Jackson, have been examined. All the subcolonies were dry and very shrunken laterally, none possessed the earliest astogenetic stages of the flustrine phase. None of the subcolonies had any avicularia, which are generally rare in flustrine subcolonies with ovicells. Waters (1887a) did not mention avicularia in his original description. The verticillate appearance of the ovicelled specimens illustrated by Waters (1887a) is explained by the considerable lateral shrinkage which occurs when flustrine colonies are dried. The ovicells are prominent, but the very thinly calcified proximal parts of the zooids almost disappear from view. The length of the zooids of the subcolonies from New South Wales is consistently greater than 1.0 mm; longer than the zooids of this phase in the specimens from Bass Strait.

The structure of the ovicells resembles that of species of *Figularia*, as well as *Euthyroides*, and the similarities have been discussed and illustrated by Gordon (1989, pls 2, 30). It is interesting that the species illustrated as *Figularia mernae* Gordon (1989: 15, pl. 2C, D) from New Zealand, occurs with an encrusting and a flustrine phase.

Corbulipora oriparma was described in detail by Wass (1973, 1975). He particularly noted the astogenetic and ontogenetic changes occurring in the small, bilaminar subcolonies. He described the increasingly early occlusion of the zooidal orifices with astogeny, and speculated on the apparent impossibility of any tentacle protrusion in these zooids. He also described the changes in zooid shape with astogeny and spinous processes arising from the pelmatidia.

Among the 94 specimens examined, 27 include the transitional stages between phases. The commonest transition is that from the bilaminar to the flustrine phase (15 examples), with the transition from the encrusting to the flustrine phase being less frequent (nine examples). The transition from the flustrine to the bilaminar phase occurs in only three examples (Fig. 24). The total number of phase 1 subcolonies is 27, the majority (18) occurring from *Tangaroa* stn 155. The small subcolonies all encrust minute shell fragments, and some have the ancestrula visible. Some have a few marginal rhizoids, and one has a flustrine phase growing from stalk kenozooids. Stalk kenozooids developing from enlarged pores also occur in subcolonies from *Kimbla* stns 99 and 100, and *Tangaroa* stn 164. The kenozooids originate from adjacent chambered pores and are closely apposed in pairs or triads; their walls become attached to each other by the first astogenetic generation, and communicate with one another through septular pores. Zooids of the following generations are just as elongated, but have traces of an operculum present, and may have been capable of feeding early in their ontogeny. Some of these zooids develop thin calcification over their frontal walls later in ontogeny, and these develop multiporous septular pores, which are the origins of rhizoids 10–20 mm long. The total number of flustrine subcolonies is 40 and the largest occur from SLOPE stn 22 and *Tangaroa* stn 164, comprising 90 astogenetic generations and bifurcating four times. Ovicells are frequent, and when they are present, avicularia are rare. The flustrine subcolonies from Kimbla stn 100 and the 'Endeavour' sample, which have bilaminar phase 3 subcolonies developing at the tips of their fronds, have numerous avicularia but few or no ovicells. The 27 bilaminar phase 3 subcolonies have the largest number of rhizoids (Cook, 1979). The number of flustrine subcolonies arising from the bilaminar phases seems to be limited only by the number of marginal kenozooidal chambers which have not already produced rhizoids. One specimen from the *Endeavour* sample has approximately 120 zooids, spanning five astogenetic generations, with partially calcified proximal zooids and nearly 60 marginal rhizoids, 10 mm long. Only one stalk kenozooid is present. On the other hand, one subcolony from SLOPE stn 22 has 11 stalks and 20 rhizoids emanating from a group of 70 zooids. If all these stalks developed into large, flustrine subcolonies, they would have the potential to produce more than 20,000 brooding zooids with ovicells. Some of the zooids from bilaminar subcolonies from *Kimbla* stns 99 and 100 have their interiors filled with orange tissue. Their orifices are completely occluded by the development and fusion of the oral spines. The tissue is reminiscent of that which fills the 'closed' zooids of some species of the genus *Conopeum* (Cook, 1985: 87), which can apparently function as hibernacula. It is inferred that if the closure of orifices is correlated with a non-feeding role for bilaminar subcolonies, the tissue-filled, closed zooids of *Corbulipora* may function as similar storage areas.

Notes on multiphased growth

Cloning by accidental fragmentation and subsequent isolation has been discussed for several colonial marine animals including Bryozoa by Jackson (1983). Cloning by specific series of astogenetic changes leading to the production of isolated subcolonies is known in the free-living, lunulitiform species of Cupuladriidae, particularly in the genus *Discoporella* (Cook, 1985; Winston, 1988). These species are components of sand fauna assemblages, and similar environments are associated with records of *Corbulipora tubulifera*, particularly those from the *Endeavour* sample (see above). Flustrine and bilaminar subcolonies were attached by their rhizoids to very large colonies of Catenicellidae and flustrine colonies of *Spiralaria*. These in turn were anchored to coelenterate colonies, and the entire mass was covered and intertwined with worm-tubes, sponges and smaller encrusting and creeping bryozoan colonies. Quantities of shell fragments and foraminiferans, together with sand grains were also present. This sample was from a locality and depth close to that from which another sample from Gabo Island originated, which was analysed by Cook (1979). This comprised a similar assemblage of animals and colony forms, including subcolonies of bilaminar *C. tubulifera*. Both assemblages probably formed a mat on the surface of the bottom sediments. The minute shell fragments encrusted by the ancestrulate phase of *C. tubulifera* suggests that these subcolonies may have lived both on the surface and within the the upper layers of the sediments. Interstitial colonies living on shell fragments were described by Winston and Håkansson (1986), and included several cribrimorph species. Although the records of *C. tubulifera* are from much deeper, and quieter waters, most from more than 50 m, and many from more than 100 m depth, an interstitial life would still be possible. The rhizoids which sometimes emanate from the growing margins of encrusting subcolonies would also help to anchor the large, erect, flustrine subcolonies as they grew, and before their own proximal rhizoids were developed later in ontogeny.

Bock and Cook (1994) have already speculated briefly on the roles of the different phases of *C. tubulifera* in establishing, extending and maintaining the colony asexually and sexually (Fig. 32). It is possible to infer similar roles among different phases of the two fossil species, *C. ornata* and *C. suggerens*. The encrusting subcolonies of both species are small; they inhabit a similar size of shell fragment substratum as those inhabited by *C. tubulifera*, and may well have lived in similar interstitial and semi-interstitial conditions. The erect, ovicellate phase of *C. ornata* is much more heavily calcified than the equivalent, flustrine phase of *C. tubulifera*, but would extend the colony and aid dispersal of larvae in the same way. Although there are numerous specimens of the small, bilaminar subcolonies of *C. suggerens* in the material examined, very few possess ovicells, and these occur only singly, near the proximal margins of the subcolonies on zooids with no costal frontal shield (Figs 28, 29). It seems reasonable to infer that, if the 'missing' cellularine or flustrine phase of *C. suggerens* existed, it too would have borne the majority of the ovicells. This inference is strengthened by the close similarity between the bilaminar phases of *C. tubulifera* and *C. suggerens*. Subcolonies of both species develop large chambered pores and kenozooids at the margins which are known to produce both stalk kenozooids and rhizoids in the Recent species. It has been inferred that the bilaminar phase is anchored by its rhizoids. After fracture of the delicate flustrine subcolonies it is isolated from the encrusting phase but stabilizes and maintains the extended colony, also producing more flustrine phases and increasing the area occupied by the clone even further. To a certain extent this stabilizing role may be enhanced by the non-feeding nature of many zooids of the bilaminar phase and it is interesting that, although quite different in origin and subcolony structure, the kenozooidal third phase of *C. ornata* may have had a similar function. The kenozooidal masses also have large chambered pores etc., at the surface which may have given rise to rhizoids. Although much more robust than the erect phase of *C. tubulifera*, the quadriserial subcolonies of *C. ornata* may have also been susceptible to fracture, especially if they had originated from stalk kenozooids.

Notes on some other records of *Watersia*

Watersia militaris has not been fully described since its introduction and the genus *Watersia* has rarely been mentioned. Mawatari (1956) referred to '*Watersia kishakaensis*'. The synonymy included two previously described taxa, *Flustra simplex kishakaensis* Okada, 1918 and *Euthyroides simplex* Okada, 1921. These species are quite distinct from one another, although both have flustrine colonies and hyperstomial ovicells. *Watersia kishakaensis* has large ovicells with paired frontal entooecial areas, and small, interzooidal avicularia with rounded mandibles, orientated distally. *Euthyroides simplex* has much smaller ovicells and no avicularia. Dr Shunsuke Mawatari has kindly lent us some preparations of *W. kishakaensis*, together with some manuscript notes on species, made by his father, Dr Shizuo Mawatari. These confirm the separate identity of the two species, and the details of Mawatari's (1956: 121, fig. 5a) description. The ancestrula and early astogeny of neither *W. kishakaensis* nor *W. simplex* have been observed and described. Both species bear several resemblances to some Antarctic forms assigned to *Klugeflustra* by Moyano (1972), who introduced the genus for two flustrine species which had large, hyperstomial ovicells with paired, entooecial frontal areas. Both the type species, *Flustra vanhoeffeni* Kluge (1914), and *Flustra drygalskii* Kluge (1914), have colonies with broad bilaminar fronds, possess interzooidal avicularia, develop numerous rhizoids, and have recently been described from the Antarctic by Rosso (1994) and by Hayward (1995). Gordon (1985) regarded *Klugeflustra* as a junior synonym of *Watersia*, and although much more robust, both the Antarctic species resemble the *Watersia*-phase of *C. tubulifera* in their colony form, thinly calcified zooids, spathulate avicularia and large ovicells. However, Ristedt (1991: 378, pl. 2 fig. 1) has described the early astogeny of *K. vanhoeffeni* in a specimen from the Weddell Sea (76°55.2′S, 40°58.9′W, 216–264 m). The ancestrula is very large (Lan 1.0 mm), encrusting and membraniporine, with no marginal or oral spines, gymnocyst or cryptocyst. The encrusting base of the colony consists of approximately 50 similar autozooids. A specimen of *K. vanhoeffeni* from the South Shetland Islands (*Discovery* stn 1872, near Clarence and Elephant Islands, 63°29.6′S, 54°03.1′W, 247 m, 12 Nov 1936), has been examined. The robust fronds are 45 mm in length, the zooids large, very thinly calcified, with no cryptocyst and two to three large, multiporous lateral septular pores. The avicularia are large, spathulate, and occur proximally to each bifurcation of zooid rows. The avicularia are raised distally and the descending part of the subrostral chamber is more heavily calcified than the rest, and appears white in contrast to the brown cuticle of surrounding walls. The proximal opesia is large and the mandible is hinged on a bar. Ovicells occur in identical bands on both sides of the fronds, five to seven astogenetic generations deep, and at intervals of about five generations apart. Ovicells are very large, are closed by the partially open operculum, and have a pair of long, irregular frontal entooecial areas flanking a central suture. These may be subdivided into four foramina in some cases.

In spite of the close similarities between *K. vanhoeffeni* and the *Watersia*-phase of *C. tubulifera*, the complete lack of a cribrimorph phase in early astogeny, suggests that the genus *Klugeflustra* should be maintained for the Japanese and Antarctic species described above.

One further Antarctic flustrine genus, *Neoflustra* Lopez Gappa (1982), is also known to have hyperstomial ovicells, but these do not have frontal entooecial areas. The avicularia are numerous but adventitious and occur on a distinct proximal zooidal gymnocyst. It is interesting that although the autozooids of the type species, *N. dimorpha*, have no spines, the brooding zooids bear several pairs of flattened, overarching, marginal spines, the distal pair being enlarged like those on the brooding zooids of the *Watersia*-phase of *C. tubulifera*. *Klugeflustra kishakaensis*, *K. simplex*, *K. vanhoeffeni* and *K. drygalskii*, together with *Neoflustra*, form a distinctive subgroup, at present classified within the Flustridae. Their ovicell structure is so unlike that found in all other members of the family, however, that it seems almost certain that a new family grouping may be eventually required to accommodate them. However, little more can be inferred without much more information about the early astogenetic stages of colonies. The relationship of these genera with *Corbulipora*, and the Cribrimorpha in general, is even more obscure and cannot be evaluated until more is known about the occurrence of multiphase growth within the Bryozoa.

The records of *Watersia* sp. (Gordon 1985) and of *Watersia militaris* from New Zealand given by Livingstone (1929) and by Gordon (1986), are not referable to the genera and species discussed here, but belong to the anascan family Calloporidae (Cook and Bock, 2000).

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We are very grateful to several colleagues for notes on, and the loan of specimens from the collections in their care. These include Drs Peter Arnold (Museum of Tropical Queensland, Townsville), Penny Berents (Australian Museum, Sydney), P.J. Chimonides and Mary Spencer Jones (Natural History Museum, London), Dennis Gordon (NIWA Wellington), Peter Hayward (University of Wales, Swansea), Shunsuke Mawatari (Hokkaido University, Sapporo), David Holloway (Museum Victoria), and Claus Nielsen (Zoological Museum, Copenhagen). We also thank Mr David McDonald for his help in preparation of this paper.

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Appendix. Details of Tertiary localities in south-eastern Australia

Bairnsdale (Skinner's): Mitchell R. bank, about 12 km W of Bairnsdale, Vic. 37°47.9'S, 147°29.5'E. Miocene.

Balcombe Bay: also known as Fossil Beach, Mornington, Mount Martha and possibly 'Schnapper Point' (MacGillivray); on coast of Port Phillip Bay, about 3 km S of Mornington. Vic. 38°14.5'S, 145°01.7'E. Fyansford Clay. Balcombian; Middle Miocene, (Langhian).

Bird Rock: Coastal section, about 3 km W of Torquay, Vic. 38°21.4'S, 144°17.8'E. Jan Juc Formation. Janjukian; Late Oligocene, (Chattian). Also known as Spring Creek.

Campbells Point: On Lake Connewarre, 12.5 km SE of Geelong, Vic. 38°13.7' S, 144°26.7' E. Middle Miocene.

Cape Otway: also Point Flinders. Locality AW1. Coastal section 2 km NW of Cape Otway. Vic. 38°51.1'S, 143°29.5'E. Glen Aire Clay. Early Oligocene (Rupelian/Latdorfian).

Cooriemungle area: road cuttings about 18 km N of Princetown. 38°32.4'S, 143°08.1'E. Gellibrand Marl. Balcombian.

Curdies Creek: this is the locality name applied to the bryozoans described by Waters (1881). The original paper mentions 'Yarra Yarra', which is the river on which Melbourne is located, and from which no bryozoan fossil localities have been recorded. Later publications (e.g. MacGillivray, 1895) have used the locality Curdies Creek for this collection. The coastal section at the mouth of the Curdies R. exposes Late Miocene limestone with a sparse bryozoan fauna. Inland sections are generally in limestone but some of the muddy sediments of the Gellibrand Marl are exposed near Timboon. However, it is believed that the sample is more likely to have come from coastal sections, which were much more accessible at that time. If the sample was obtained from the coastal exposure, it almost certainly was close to the locality listed as 'Princetown' below.

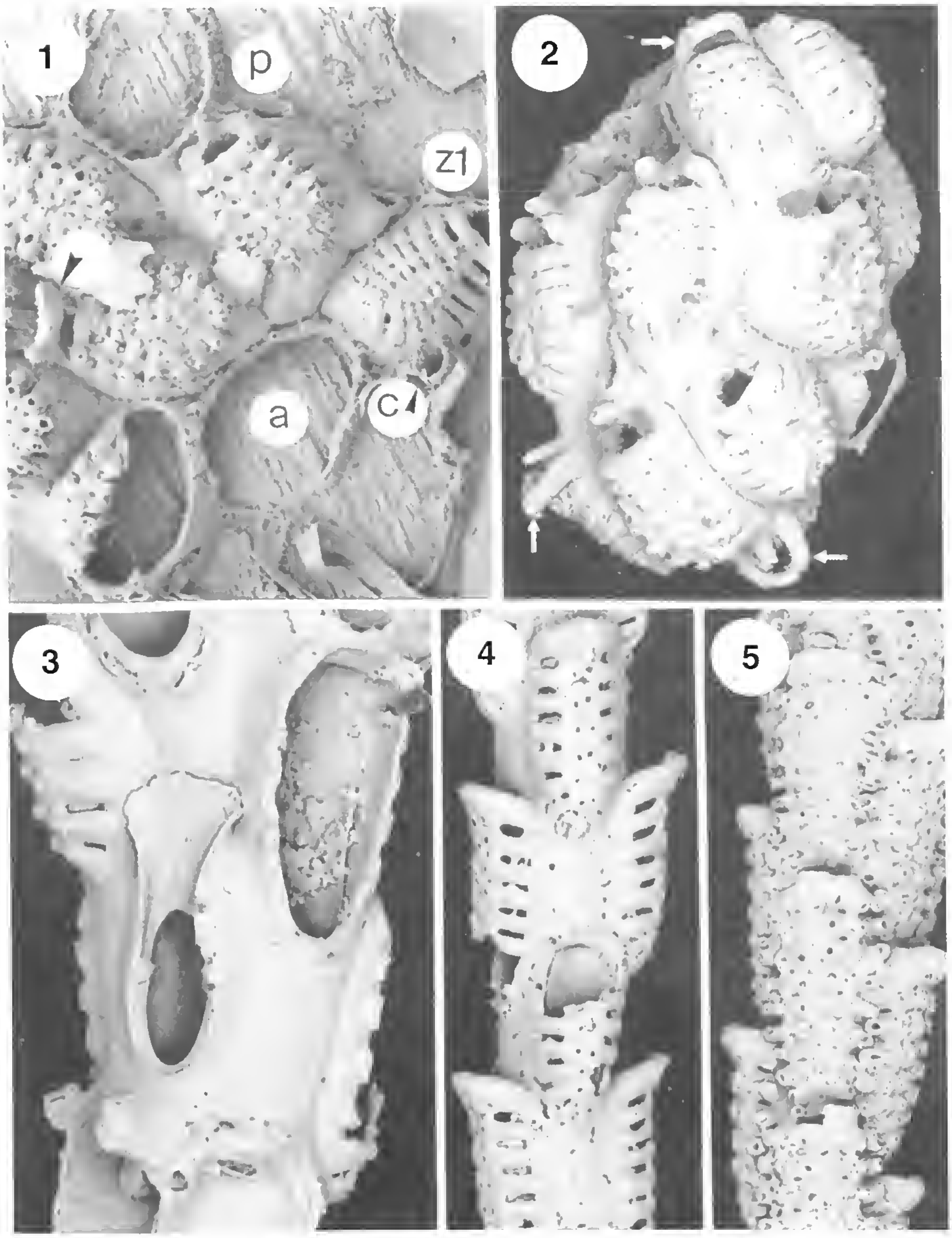
Grices Creek: also known as Gunyong Creek; on coast of Port Phillip Bay, about 8 km N of Mornington, Vic. 38°11.9'S. 145°03.9'E. Fyansford Clay. Balcombian (some material may be Bairnsdalian); Middle Miocene, (Langhian).

Mount Schanck: limestone quarry about 1 km W of Mount Schanck, about 15 km S of Mount Gambier, SA. 37°57'S, 140°43.2'E. Gambier Limestone. Longfordian; Early Miocene.

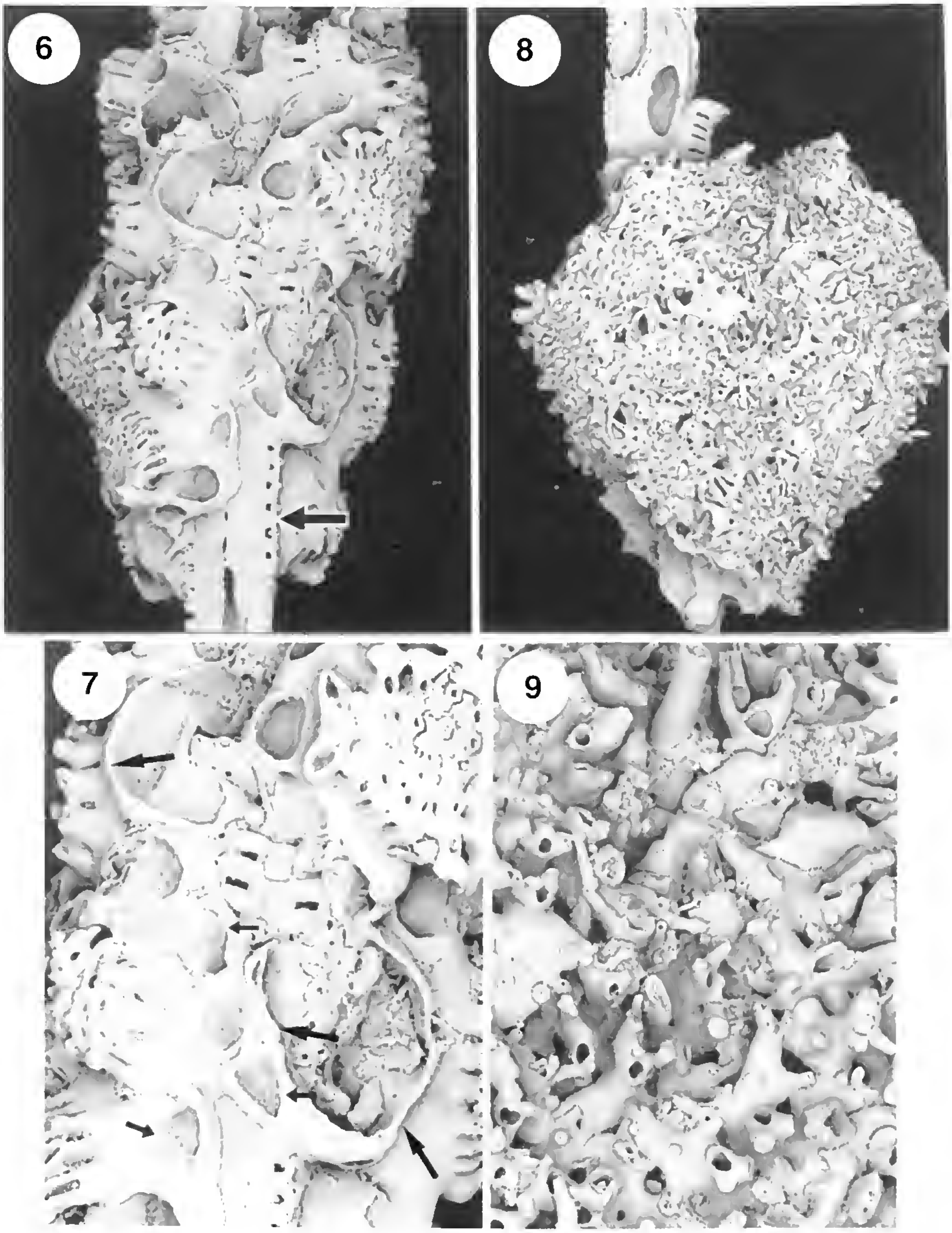
Muddy Creek: Clifton Bank, Muddy Creek, 8 km W of Hamilton, Vic. 37°44.6'S, 141°56.4'E, Muddy Creek Marl (= Gellibrand Marl). Balcombian.

Narrawaturk Bore 2: at Peterborough, Vic. 38°36.3'S, 142°52.3'E. Core 9, 522.1–526.4 m. Gellibrand Marl. Early Miocene (Longfordian).

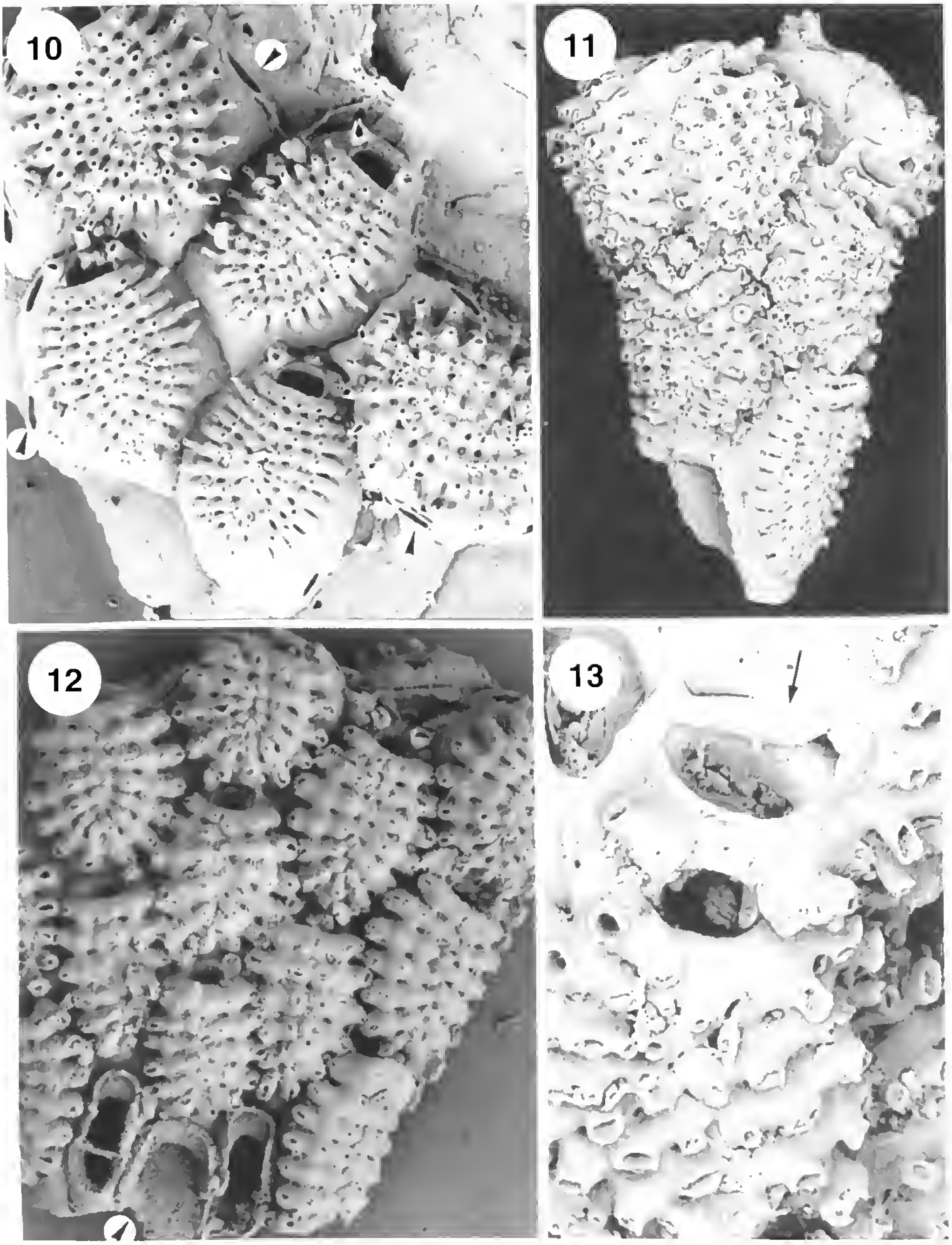
Princetown (*Gigantocypraea* locality): coastal section, about 2 km W of Princetown, Vic. 38°41.9'S, 143°08.3'E, Gellibrand Marl. Balcombian.



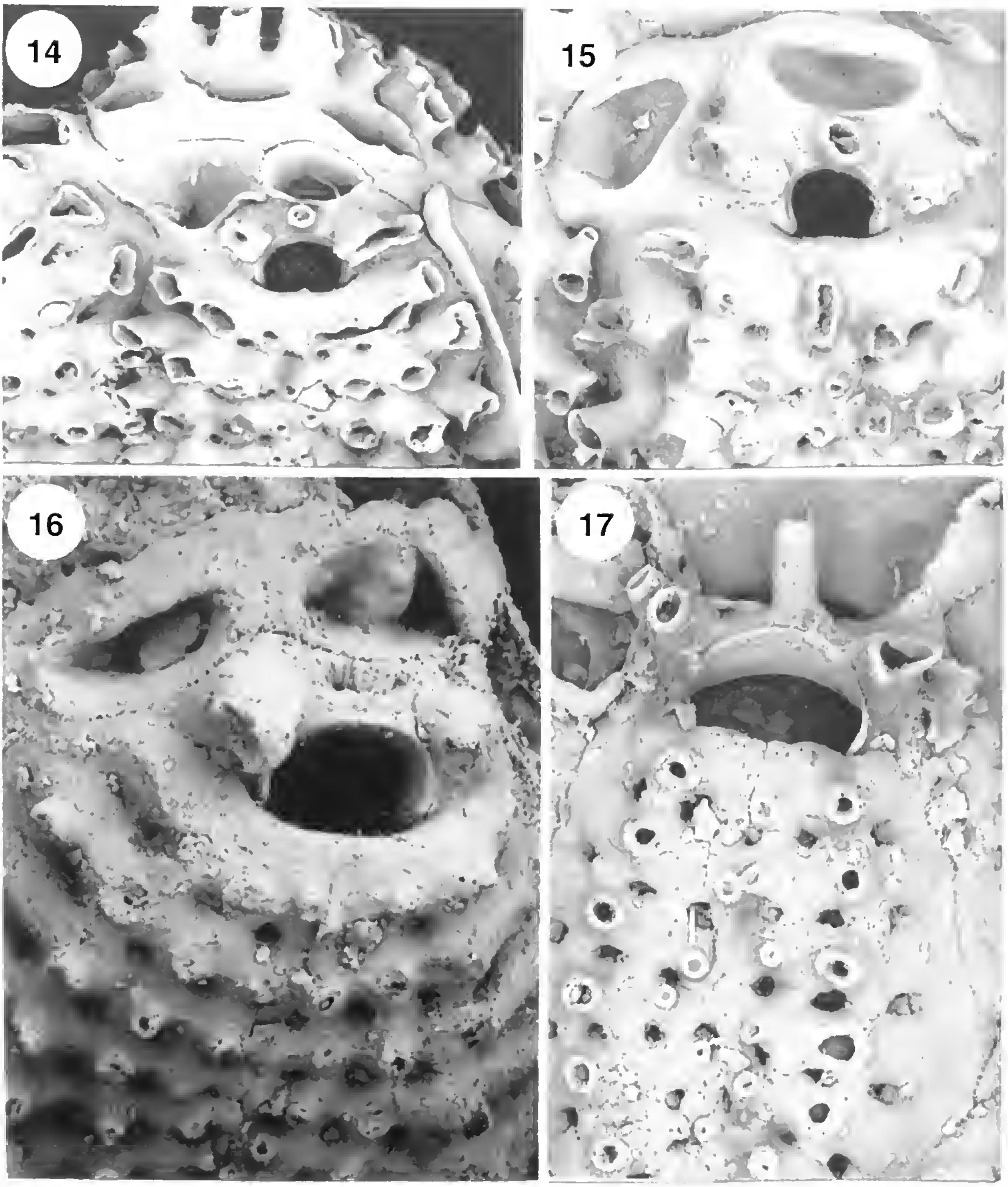
Figures 1–5. *Corbulipora ornata*. Figs 1–2, Mount Schanck, SA, encrusting, phase 1 subcolonies. Fig. 1, ancestrula (a) and primary triad of zooids. Note that the first distal zooid (z1) has costae with no lateral fusions; the second and third zooids have costae with lateral fusions and raised marginal spinous processes. Note pore chambers (p), potential frontal bud arising from raised chambered pore (c), and raised, medially fused oral spines on the third zooid (arrowed) (×70). Fig. 2, encrusting, globular subcolony, showing raised, medially fused oral spines (arrowed) (×62). Figs 3–5, Balcombe Bay, Vic., erect, phase 2 subcolonies. Fig. 3, zooids early in ontogeny with long gymnocyst and small, simple costate shield (incomplete or worn), and avicularium with distally expanded rostrum and paired condyles (×80). Fig. 4, zooids later in ontogeny with median area of frontal shield with pelmatidia (×50). Fig. 5, zooids late in ontogeny with numerous, raised pelmatidia and prominent suboral bar (×42).



Figures 6–9. *Corbulipora ornata*. Balcombe Bay, Vic., subcolonies of erect, phase 2 and kenozooidal, phase 3 zooids. Fig. 6, note central column of phase 2 zooids surrounded by frontally budded costate zooids and kenozooids (arrowed) ×45). Fig. 7, enlargement of zooids, note marginal chambered pores (small arrows), and raised walls of partially calcified kenozooids (large arrows), all originating above the pelmatidia of underlying, phase 2 zooids (×70). Figs 8–9, later astogenetic stages. Fig. 8, subcolony showing mass of spinous frontal shields of autozooids and kenozooids, the outlines of which are no longer visible. The central core of the original erect, phase 2 subcolony zooids is visible distally and proximally (×30). Fig. 9, enlarged portion of the same subcolony (×100).



Figures 10–13. *Corbulipora suggerens*. Fig. 10. Princetown, Vic., encrusting, phase 1 subcolony, zooids showing spinous, costate frontal shields: pore chambers (arrowed) (×50). Fig. 11, Balcombe Bay, Vic., bilaminar, phase 3 subcolony arising from paired, proximal zooids (×70). Fig. 12, Mount Schanck, SA, slightly wider, bilaminar, phase 3 subcolony, with paired proximal avicularia and zooid with uncalcified frontal (arrowed) (×64). Fig. 13, Balcombe Bay, Vic., enlargement of zooid from distal part of subcolony in Fig. 11, showing large, frontally uncalcified, distal kenozooid arising from chambered pore (arrowed) (×160).



Figures 14–17. *Corbulipora suggerens.* Figs 14–15. Balcombe Bay, Vic., zooids from distal margin of subcolony in Fig. 11, showing large kenozooids arising from distal chambered pores; note relatively small size of the calcified orifice. Fig. 14 (×120). Fig. 15 (×150). Compare both figures with the origin of stalk kenozooids of *C. tubulifera* illustrated in Fig.20. Fig. 16, Princetown, Vic., single zooid from encrusting, phase 1 subcolony showing frontal shield and oral spines. Note large chambered pore surrounding distal oral spine, probably derived from a pore chamber, and relatively small size of calcified orifice. Compare with *C. tubulifera*, Fig. 17 (×210). Figure 17. *Corbulipora tubulifera. Tangaroa* stn 155, Bass Strait, single zooid showing frontal shield and oral spines. Note relatively large size of calcified orifice (×200).

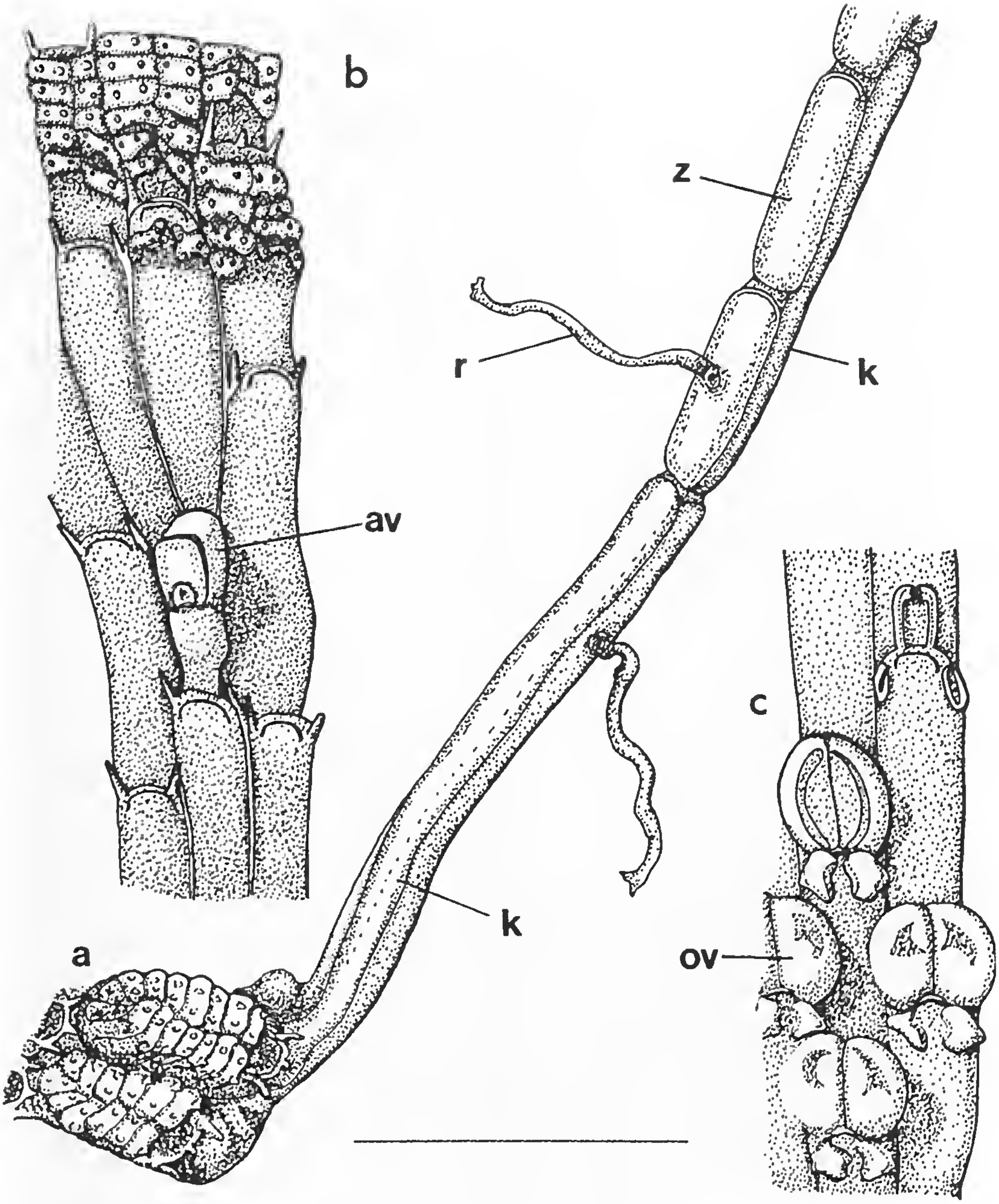
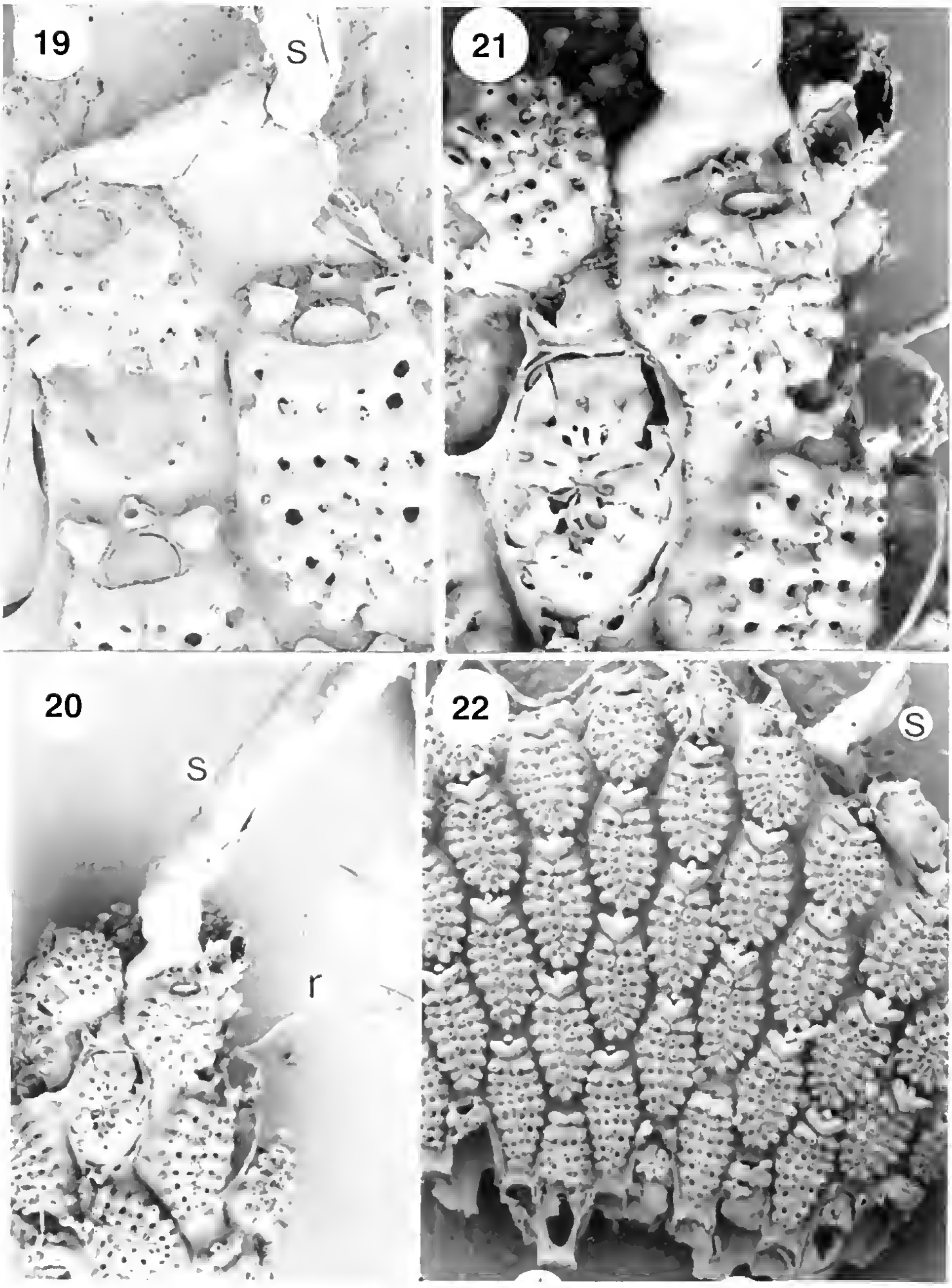
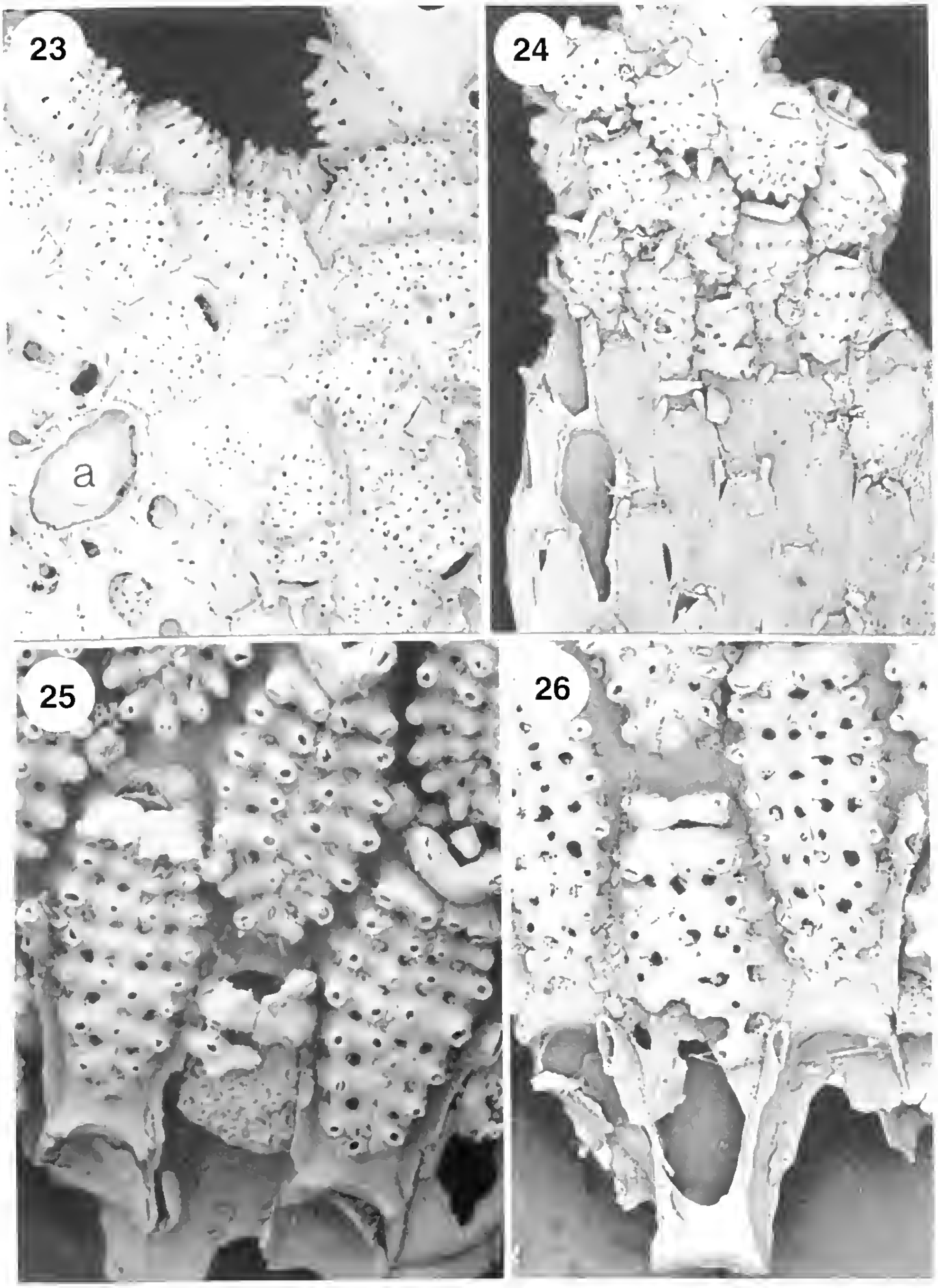


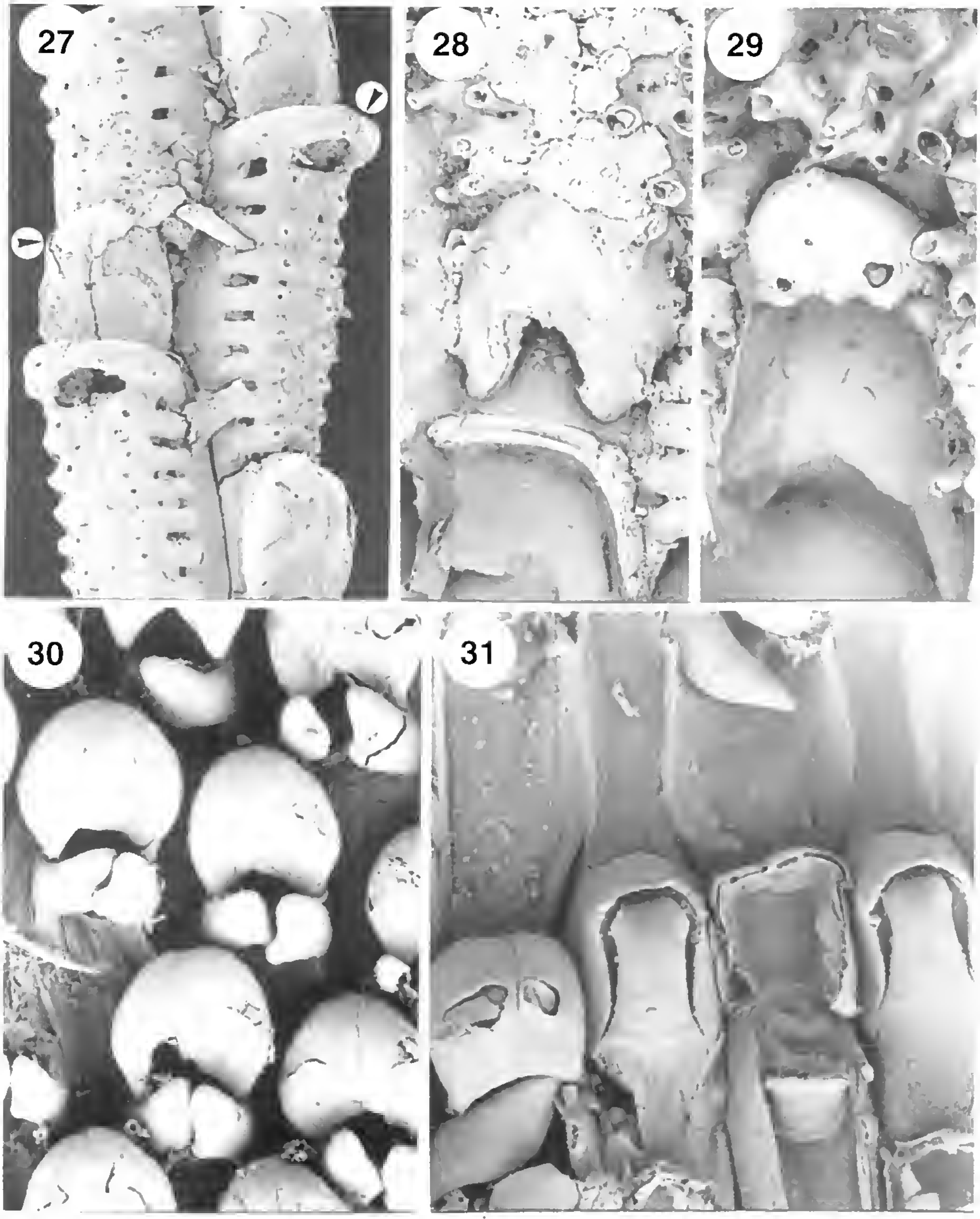
Figure 18. *Corbulipora tubulifera*, characteristics of phases. a. encrusting, phase 1 zooids with stalk kenozooids (k), arising from marginal chambered pores, developing rhizoids (r) and budding autozooids (z) at the base of an erect, flustrine phase 2 subcolony. b. tip of a frond of a flustrine, phase 2 subcolony, with an avicularium (av), and developing distal transitional zooids and bilaminar, phase 3 zooids with costate frontal shields (see also Fig. 24). c. zooids of flustrine, phase 2 subcolony with ovicells (ov) and large oral spines. Scale = 0.60 mm.



Figures 19–22. *Corbulipora tubulifera*. Bass Strait. Fig. 19. *Tangaroa* stn 155, encrusting, phase 1 autozooids with distal stalk kenozooid (s), arising from chambered pores; note autozooid frontal membranes and opercula (×80). Figs 20–22. *Kimbla* stn 100. Fig. 20, small, bilaminar, phase 3 subcolony, with rhizoids (r) and a pair of large stalk kenozooids (s), see also Fig. 21 (×35). Fig.21, enlargement of zooids from Fig. 20, showing origin of stalk kenozooids from distal chambered pores; compare with Figs 14 and 15 (×80). Fig. 22, bilaminar, phase 3 subcolony with distal rhizoids and a stalk kenozooid (s); proximal autozooids with partially calcified frontal shields (arrowed); see also Figs 25 and 26. Note progressive, distally directed closure of zooid orifices by fused oral spines (×28).



Figures 23–26. *Corbulipora tubulifera*. Bass Strait. Fig. 23, *Tangaroa* stn 155, early astogeny of an encrusting, phase 1 subcolony, on an adeonid bryozoan; ancestrula (a) (×46). Figs 24–26, Kimbla stn 100. Fig. 24, part of a flustrine, phase 2 frond, developing transitional distal zooids, and phase 3, calcified zooids at the tip (×31); compare with Fig. 18b. Figs 25 and 26, zooids with uncalcified or partially calcified frontal shields from proximal zone of transition from phase 2 to phase 3 subcolony shown in Fig. 22. (×90).



Figures 27–31. Ovicells in *Corbulipora*. Fig.27. *Corbulipora ornata*, Balcombe Bay, Vic. Brooding zooids of erect, phase 2 subcolony, showing ovicells. Crescentic entooecial area (arrowed) and raised, medially fused oral spines (arrowed) (×75). Figures 28 and 29, *Corbulipora suggerens*. Fig. 28, Balcombe Bay, Vic., brooding zooid with uncalcified frontal shield and ovicell with crescentic entooecial areas (×130). Fig. 29, Princetown, Vic., brooding zooid with uncalcified frontal shield and ovicell with paired pores (×200). Figures 30 and 31, *Corbulipora tubulifera*, Bass Strait, *Tangaroa* stn 164. Fig. 30, brooding zooids from flustrine, phase 2 subcolony, showing uncalcified frontal membranes, enlarged oral spines and ovicells with crescentic entooecial areas (×80). Fig. 31, part of a flustrine, phase 2 subcolony, showing uncalcified frontal membranes, one ovicell and two avicularia (×100).

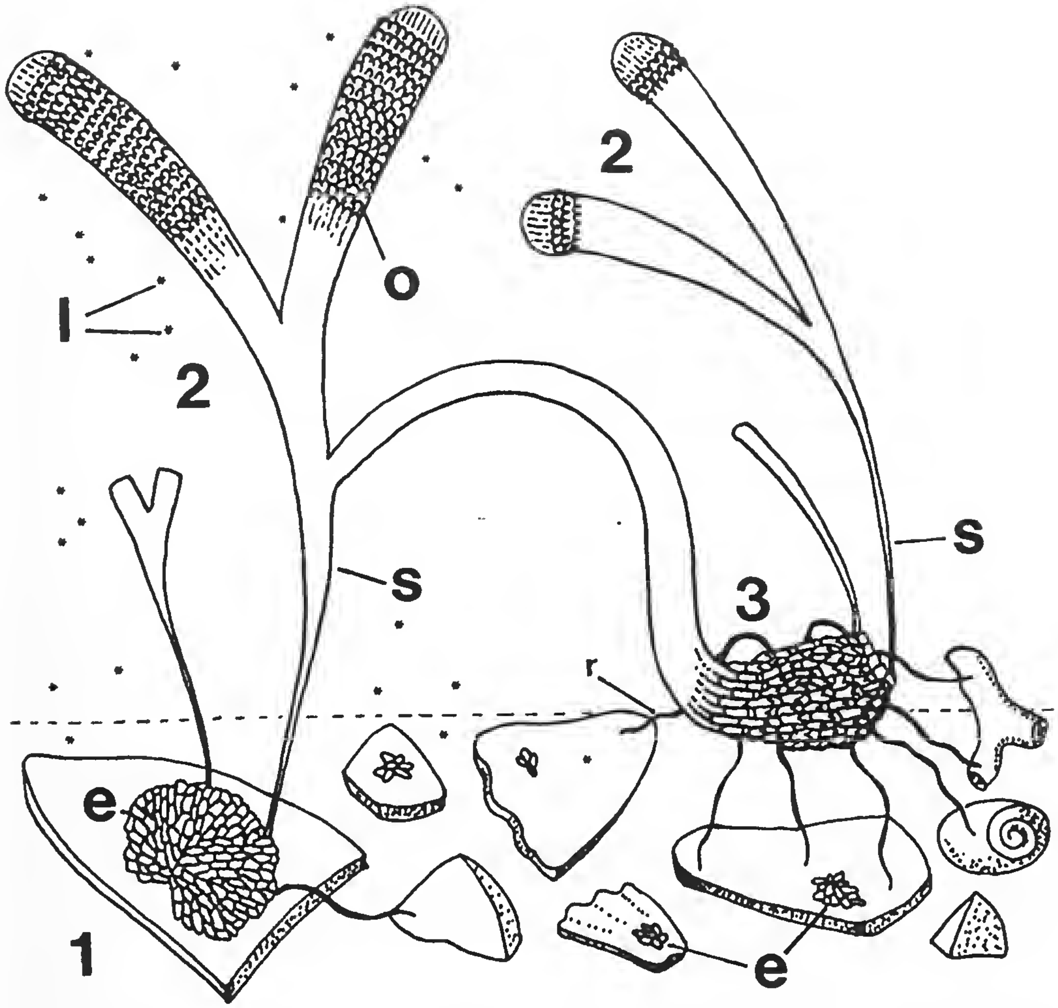


Figure 32. Diagram of inferred roles of different phases in *Corbulipora tubulifera*. 1. encrusting phase (e) establishes subcolony on shell fragment which becomes anchored by rhizoids in and on the surface layers of sediment. 2. erect flustrine phase arises from stalk kenozooids (s), budded from marginal chambered pores of phase 1 zooids. Flustrine phase produces brooding zooids with ovicells (o), which brood embryos of motile larvae (l), which disperse and settle on shell fragments, metamorphosing and producing ancestrulae, which bud new, phase 1 subcolonies (e). 3. bilaminar phase originates from the tips of fronds of the flustrine phase, and becomes anchored on surface of sediment by rhizoids (r). These subcolonies maintain the area occupied by the flustrine phase 2 subcolonies, even if they become isolated. Phase 3 subcolonies then bud further phase 2, flustrine subcolonies from marginal stalk kenozooids (s), and repeat the sexually reproductive phase. Not to scale.

Memoirs of Museum Victoria 58(1): 215–222 (2001)

NOTES ON THE GENERA *NORDGAARDIA* AND *USCHAKOVIA* (BRYOZOA: BUGULIDAE)

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Abstract

Cook, P.L., 2001. Notes on the genera *Nordgaardia* and *Uschakovia* (Bryozoa: Bugulidae). *Memoirs of Museum Victoria* 58(2): 215–222.

The rare deep-water bryozoan genera *Nordgaardia* and *Uschakovia* share important similarities in budding patterns and zooid structure together with a type of avicularium which has an extended subrostral chamber. Ovicells are known only in *Nordgaardia* and are here described in Australian specimens of *N. cornucopioides* for the first time. The remarkable spines of *Uschakovia gorbunovi* are described from a colony from the Faroe Islands; they are extensions of the frontal body wall, and each has a modified parietal muscle at its base.

Introduction

Two species of the genus *Nordgaardia* Kluge, 1962 have been described in some detail: *N. pusilla* (Nordgaard, 1907), type species, by Hayward (1978), and *N. cornucopioides* by d'Hondt (1983). The type and only species of Uschakovia Kluge, 1946, *U. gorbunovi* Kluge, 1946, has been described solely from Russian Arctic specimens by Kluge (1946, 1962). Deep-water bryozoans often have delicate colonies with thinly calcified zooids and the opportunity to examine well-preserved specimens is rare. A single almost complete colony of *U. gorbunovi*, together with 18 colonies of *N. cornucopioides*, seven of which possessed both ancestrulae and ovicells, are here compared directly from material in the collections of Museum Victoria. The relationships of the two genera with each other and with some other genera of the superfamily Buguloidea are assessed.

The specimen of *U. gorbunovi* is part of a collection including several colonies of this species, collected as part of the Undersogelsor af den marine bunddyrfauna omkring Faeroesne (BIOFAR, Investigations of the marine benthic fauna of the Faroe Islands). The other specimens are stored at the Marine Station, Vidskridvbakka, FR-180, Kaldbak, Foroyar. The figured specimen, was presented to Museum Victoria by Dr P.J. Hayward (Marine Research Group, University of Swansea, UK), who investigated the Bryozoa from this collection (Hayward, 1994). The specimens of *N. cornucopioides* were among material sorted by P.E. Bock from Museum Victoria's SLOPE stations (taken on the south-eastern Australian slope from RV *Franklin* using a WHOI epibenthic sled) and are stored in Museum Victoria (NMV).

Nordgaardia Kluge

Nordgaardia Kluge, 1962: 437.

Type species. Synnotum pusillum Nordgaard, 1907.

Diagnosis. Colony erect, arising from an ancestrula anchored by numerous rhizoids, followed by a short chain of uniserial autozooids. Autozooids thinly calcified, elongated, tubular; proximal gymnocyst expanding to surround an extensive opesia with an almost terminal operculum. Distal part of zooids free, projecting from branch surface. Autozooids arranged in alternating pairs or in triads. Avicularia arising proximal to opesia, subrostral chamber greatly extended, expanded terminally into an acute, beaked rostrum. Ovicell with partially membranous ectooecium, surrounding a thinly calcified capsule of entooecium, attached to distolateral end of the brooding zooid, with a laterally directed aperture which partially obscures the brooding zooid operculum.

Remarks. Nordgaardia pusilla, originally introduced for material from 1000 m in the northern Atlantic, was redescribed in detail by Hayward (1978: 215, Figs 3d–h), who had 12 samples from the western European continental slope from a depth range of 610–1400 m. This material included colonies with ancestrulae and ovicells which he described for the first time. D'Hondt (1983) introduced a second species, *Nordgaardia* *cornucopioides* from Brazil which differs from *N. pusilla* in having a greater proportion of each zooid freely projecting from the branch surface and in having more robust avicularia. D'Hondt's specimens possessed neither ancestrulae nor ovicells. The colonies described below from the continental slope of eastern Tasmania and Victoria appear to be referable to *N. cornucopioides* and allow description of both these features, and comparison with *N. pusilla*.

Camptoplites marchemarchadi Redier and d'Hondt (1976) was assigned to *Nordgaardia* by d'Hondt (1983: 82). Although d'Hondt (1983) distinguished the two genera from each other on the basis of their avicularian types, that of *N. marchemarchadi* having an elongated subrostral chamber, not a flexible 'stalk' as is present in *Camptoplites*, he mentioned that avicularia occurred only on the secondary branches. The development of these secondary branches is a characteristic found only in *Camptoplites*, and was fully described by Hastings (1943). The generic position of *C. marchemarchadi* is therefore equivocal. The type specimen was from West Africa, and it is possible that the fragmentary specimen from Senegal assigned to *Kinetoskias* sp. by Cook (1968: 63), which had similar avicularia, may have belonged to the same species.

Nordgaardia cornucopioides d'Hondt

Nordgaardia cornucopioides d'Hondt, 1983: 80, pl.1, figs 3–4 (off Brazil, 770–805 m).—Harmelin and d'Hondt, 1992: 31 (Gulf of Cadiz, 281 m).—d'Hondt and Gordon, 1996: 85, fig. 11D (New Caledonia, 1175–1950 m).

Material examined. Stn SLOPE-32, 38°21.90'S, 149°20'E, 23 Jul 1986, S of Point Hicks, Vic., 1000 m. stn SLOPE-33, 38°19.60'S, 149°24.30'E, 23 Jul 1986, S of Point Hicks, Vic., 930 m. stn SLOPE-34, 38°16.40'S, 149°24.30'E, 23 Jul 1986, S of Point Hicks, Vic., 800 m. stn SLOPE-45, 42°2.20'S, 148°38.70'E, 27 Jul 1986, off Freycinet Peninsula, Tas., 800 m. All NMV F74868.

Description. Nordgaardia with at least half the distal part of each zooid free and projecting from the branch surface. Avicularia expanded and truncate distally, with a hooked rostrum. Ovicells very large.

Remarks. The four colonies from Tasmania (stn SLOPE-45) and three of those from Victoria (stn SLOPE-32) have ancestrulae and rhizoids present, and branch three to four times. Ovicells are present in all these colonies, which include, on average, more than 100 zooids each. The ancestrula is tubular, attached by 10–12 proximal rhizoids, and has a narrow opesia extending nearly the whole of its length. It gives rise to one distal zooid which bears 15–20 rhizoids along its entire length. The first pair of autozooids follows. Subsequent autozooids are arranged in alternating pairs or in triads with frontals inclined to one side of the branch so that the long tubular proximal parts of the zooids tend to be visible only on the basal side. Hayward (1978) described the slightly different budding and branching patterns of *N. pusilla* in detail and also noted the difficulty in understanding the morphology of the ovicells because their delicate calcification was distorted by collection and preservation. The ovicells of *N. cornucopioides* are also very thinly calcified and are somewhat distorted. The ovicells are larger than those of *N. pusilla* (Table 1) and have an almost completely membranous ectooecium which surrounds a distinctly smaller calcified capsule of entooecium. The two layers merge at a small attachment area on the basal side of the distolateral wall of the brooding zooid which has a wider border of gymnocyst on the outer side. The large aperture of the ovicell opens laterally above the operculum of the brooding zooid which is

Table 1. Measurements in mm of *Nordgaardia pusilla*, *N. cornucopioides*, and *Uschakovia gorbunovi* from specimens and literature.

	N. pusilla	*N. cornucopioides*	*U. gorbunovi*
Length of ancestrula	1.30–1.50	1.70–1.85	1.00–1.70
Length of autozooids	1.40–1.80	0.90–1.20	0.76–0.83
Length of opesia	0.76–1.00	0.65–0.75	0.50–0.54
Length of subrostral chamber	0.54–0.85	0.67–0.74	0.45–0.66
Length of rostrum	0.12–0.19	0.19–0.30	0.12–0.27
Length of ovicell	0.36	0.45–0.50	—
Width of ovicell	0.28	0.39–0.45	—
Length of tentacles	—	0.40–0.45	0.25–0.29

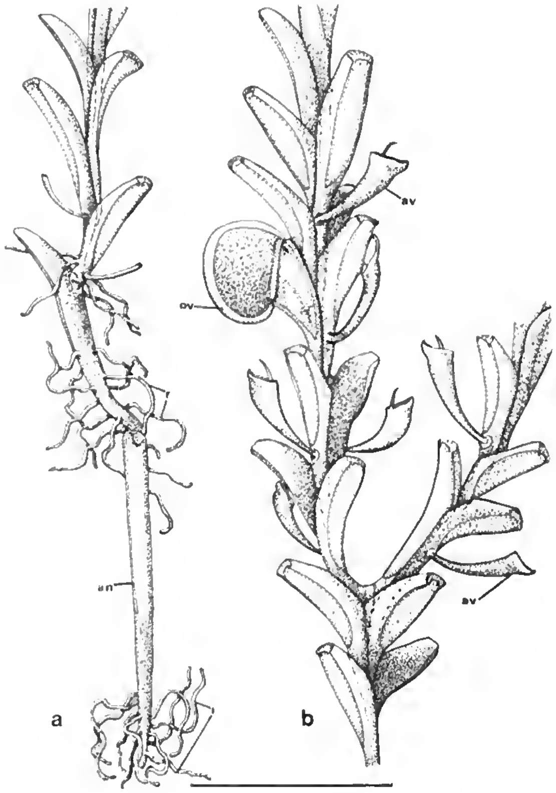

Figure 1. *Nordgaardia cornucopioides* d'Hondt, Tasmania. a, primary astogenetic zone: ancestrula (*an*), rhizoids (*r*). b, later astogenetic zone: avicularia (*av*), ovicell (*ov*). Scale = 1 mm.

therefore partially obscured (Fig. 1b). Ovicells with an uncalcified ectooecium were figured in *Bugula longissima* Busk by Hastings (1943: Fig. 39D) and ovicells with a laterally facing aperture obscuring the brooding zooid operculum were figured in *Kinetoskias mitsukurii* by Yanagi and Okada (1918: 425, Fig. 7a) and in *K. elongata* by Harmer (1926: 469, pl. 34, fig. 11). The closely similar ovicelled zooids of *Euoplozoum cirratum* (Busk) were illustrated by d'Hondt and Gordon (1996: 86, fig. 9D).

A few autozooids have partially protruded tentacle crowns. The tentacles are closely opposed and contracted in most cases but in a few zooids they are slightly expanded with an estimated total of 14–16 tentacles in the crown. The avicularia do not reach the largest rostral dimension given by d'Hondt (1983, i.e. length of rostrum 0.30 mm) but are within the range he figured. They are more robust than those of *N. pusilla* and their rostra are hooked terminally. The extensive muscle systems occupy nearly all the distal, expanded part of the elongated subrostral chamber.

D'Hondt's specific name refers to the similarity of the avicularia with those occurring in some species of the genus *Cornucopina* Levinsen. Harmer (1926) described several species including *C. moluccensis* (Busk) which has large avicularia almost exactly like those of *N. cornucopioides*. The extended proximal parts of the autozooids and the complex budding patterns of the two genera are also somewhat similar but *Cornucopina* differs completely in the expanded shape of the distal part of its autozooids and in the occurrence of numerous marginal spines.

The locality of the Tasmanian specimens of *N. cornucopioides* is remote from most other records of *Nordgaardia* which are all from the Atlantic. However, recently, specimens from very deep water from New Caledonia have been recorded by d'Hondt and Gordon (1996). It is just

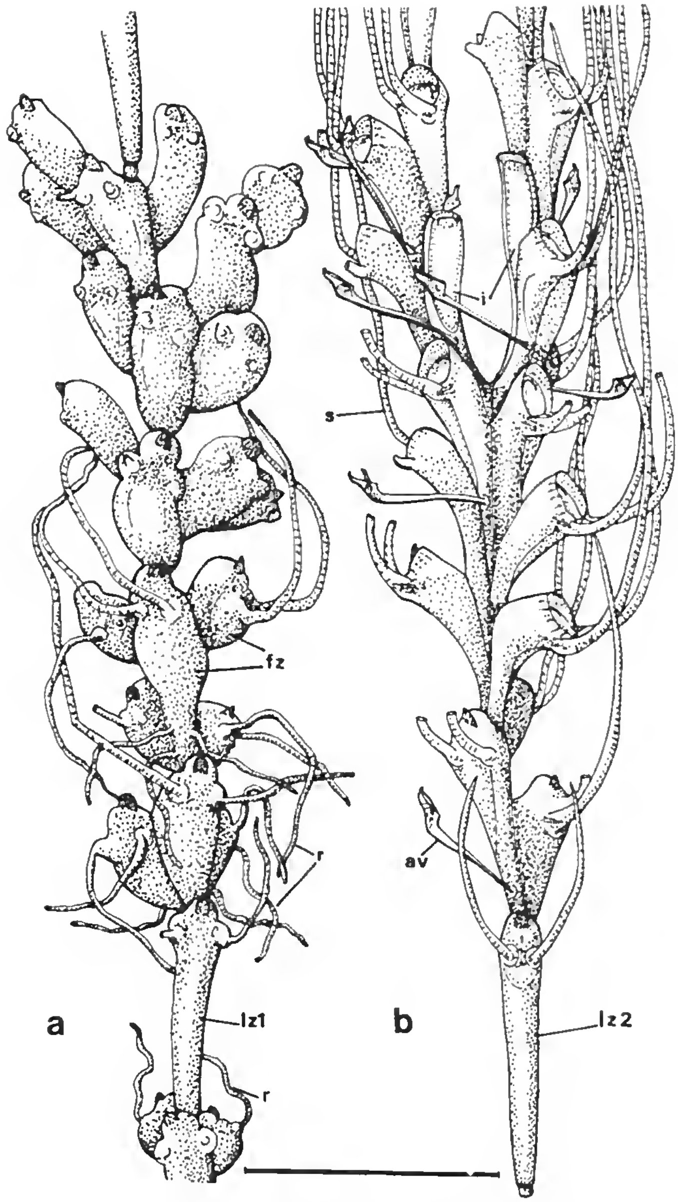

Figure 2. *Uschakovia gorbunovi* Kluge, Faroe Islands. a, primary astogenetic zone: founding zooids (fz), rhizoids (*r*), primary linking zooid (*lz 1*). b, later astogenetic zone: secondary linking zooid (*lz 2*), spines (*s*), inward-facing zooids (*i*), avicularia (*av*). Many spines not shown completely. Scale = 1 mm.

possible that a single rather variable taxon is concerned. Harmelin and d'Hondt (1992) noted that their colonies from the north-eastern Atlantic (off Cadiz, 35°43.5', 6°18.2'W, 281 m) had some avicularia which approached the more slender type found in *N. pusilla*. The avicularia of the Tasmanian population of *N. cornucopioides* are generally less robust than those originally described by d'Hondt (1983) from Brazil, and the very delicate, slender avicularia described for *N. marchemarchadi*, from Senegal, suggest that a direct comparison of all the available material might reveal a continuum of character states.

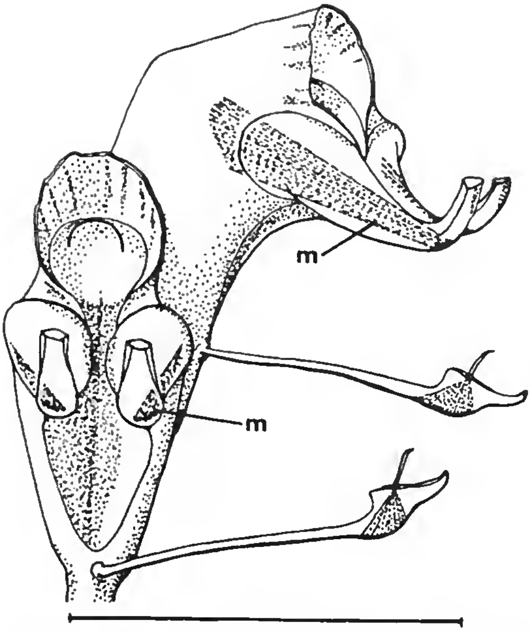

Figure 3. *Uschakovia gorbunovi* Kluge, Faroe Islands. Two autozooids and avicularia, showing modified parietal muscles (*m*). Spines not shown completely. Scale = 0.5 mm.

Uschakovia Kluge

Uschakovia Kluge, 1946: 196.

Type species. Uschakovia gorbunovi Kluge, 1946 (monotypic).

Diagnosis. As for *U. gorbunovi.*

Uschakovia gorbunovi Kluge

Uschakovia gorbunovi Kluge, 1946: 196 , pl. 1, figs 1–4.—Kluge, 1962: 438, Figs 228A–D (Arctic, Kara and East Siberian Seas, 64–648 m).—Hayward, 1994: 183 (Faroe Islands, 610–1400 m).

Material examined. BIOFAR stn 095, 060°41.51'N, 05°18.63'W, south-east Faroe Islands, 23 Jul 1987, 803 m, NMV F74869.

Description. Colony erect, arising from an ancestrula anchored by rhizoids which gives rise to a series of 'founding' zooids which also develop rhizoids. Erect branched part of colony originating from one zooid, or a short uniserial chain of 'linking' zooids which are extremely elongated. Branches of autozooids in alternating pairs and triads, becoming quadriserial before a bifurcation. Primary branch bifurcating several times to form a cluster of 4–6 branches. Autozooids with very long tubular proximal gymnocyst expanding distally to surround an elongated opesia. Outward-facing zooids with bipartite opesia, distal part covered by frontal membrane which surrounds operculum, the proximal part formed by the swollen bases of pair of long partially cuticular spines. Inward-facing zooids without spines, opesia elongated. Avicularia arising from proximal gymnocyst of both kinds of zooids; the subrostral chamber considerably elongated and expanded distally to form a terminally hooked acute rostrum. Ovicells unknown.

Remarks. The colony examined here does not differ materially from those described from the high Arctic by Kluge (1962). Colonies attain a height of 10–15 mm and a width of 5–8 mm, and are composed of two groups of distinctly different zooids, each group connected by a single elongated linking zooid (length 1.00–1.14 mm). The colony from the Faroes has no ancestrula; those figured by Kluge (1962) have ancestrulae which are more elongated than, but which otherwise resemble, the succeeding founding zooids. The groups of founding zooids (length 0.50–0.55 mm) alternate with one or two linking zooids and this succession may be repeated. The colony from the Faroes has a few founding zooids followed by a linking zooid which has no calcification. A further group of approximately 20 triserially budded founding zooids, the more proximal with rhizoids, is then followed by a second, single calcified linking zooid. The remainder of the colony is formed by bifurcation of a biserial-to-quadriserial branch which is budded distally to the linking zooid (Fig. 2). The resulting colony has six branches. All zooids are very thinly calcified early in astogeny at least. The tubular proximal gymnocysts are closely apposed and each expands distally to surround the opesia; the terminal third of this upper part of the zooid is free and projects from the branch surface. The founding zooids appear to have passed through ontogenetic changes including resorption of calcification and they have completely cuticular body walls. A line marking the presumed former position of the edge of the gymnocyst is present in some zooids and all are swollen, irregularly orientated, and have open opercula. The underlying orifices are however sealed by cuticle. The more distal zooids have paired cuticular tubercles near the distal ends of the former opesia; the more proximal zooids have long uncalcified, spinous processes, or paired rhizoids in the same position. Other rhizoids arise from the proximal part of these zooids. The more proximal of the two linking zooids is more slender and longer than the neighbouring founding zooids but also has cuticular walls. The more distal linking zooid is separated from the nearest proximal founding zooid by two cuticular nodes with an intervening small calcified internode (Fig. 2b). The gymnocyst is thinly calcified and very elongated and tubular, expanding distally to surround a bipartite opesia which is divided by lateral constrictions formed by the swollen bases of paired spinous processes. The opesia proximal to the constriction is short and both parts of the frontal membrane form an angle at the constriction. The distal part is almost circular and the small almost semi-circular operculum has a marginal sclerite. The autozooids of the next three to four astogenetic generations resemble the linking zooid but have a shorter, tubular gymnocyst and longer narrower proximal opesia. The operculum and the circular distal part of the frontal membrane are sunken with a cowl-like raised rim of semitransparent gymnocyst with a crenulated border.

After four to five astogenetic generations the first bifurcation occurs and branches become tri- to quadriserial; they are close to each other and the autozooids facing inward differ from those facing outward which are in the majority. The inward-facing zooids are flattened and have a wide elongated opesia without any trace of spines or lateral constrictions; a distal pair of parietal muscles is visible in many zooids. The outward-facing zooids all have paired spines and laterally constricted bipartite opesiae. The spines are 1.55–3.50 mm long and are direct expansions of the body wall. On the proximal face they are derived from the cuticle of the frontal membrane; on the distal face they are thinly calcified and continuous with the lateral gymnocyst which forms a curved shoulder round the base of each spine. The spines are curved at their origin but extend distally and are numerous and long enough to obscure the underlying zooids completely. Although flattened and partially calcified at first, they become tubular and completely cuticular. At the base of each spine the frontal cuticle is expanded to form a tubercle and muscles extend through this from the cuticular frontal face to the interior of the shoulder and the lateral part of the gymnocyst (Fig. 3). These muscles appear to be modified and enlarged parietal muscles. All the zooids are so thinly calcified that they are somewhat shrunken by preservation in alcohol. In life the frontal membranes would be convex especially when the tentacle crowns were retracted. The base of the spines would therefore not constrict the opesia as much as they do in the preserved state. However, contraction of the parietal and other muscles during tentacle protrusion would presumably cause the proximal part of the frontal membrane to become concave. This would alter the position and direction of the elongated frontal spines. The avicularia which arise from the proximal gymnocyst are similar to but much less robust than those of *N. cornucopioides*; the elongated proximal part of the subrostral chamber is narrower and the 'head' more elongated.

Discussion

In colony form and budding patterns, and in the possession of erect rhizoid-bearing ancestrulae and elongated avicularia, *Nordgaardia* and *Uschakovia* resemble each other closely. Kluge (1962) suggested that the founding zooids of *Uschakovia* might function in nutrient storage as well as in attachment of colonies. The swollen, cuticular zooids resemble the basal vesicular kenozooids of *Caulibugula* (Hastings, 1939) which may also function in both of these ways. The greatly extended cuticular peduncle of *Kinetoskias* (see Kluge, 1962) which has rhizoids at its base is analogous to the founding zooid of *Uschakovia* but is an extrazooidal structure in direct contact with all autozooids. It presumably expands continuously with growth in the same manner as the peduncle of the ascophoran genus *Parmularia* (Cook and Chimonides, 1985). The apparent resorption of calcification in *Uschakovia* seems to be an ontogenetic change which proceeds distally from the ancestrular region. The earliest founding zooids and the more proximal linking zooid bear only rhizoids, the more distal founding zooids bear long uncalcified spines and show traces of cuticle which may mark the former position of a gymnocyst. The distal linking zooid and first pair of autozooids have completely calcified gymnocysts but like all the founding zooids their open opercula have an underlying orifice sealed by cuticle. This gradient of ontogenetic change suggests that the resorption of calcification is a successive process which, in the larger colonies figured by Kluge (1962), may have proceeded further than in the specimens from the Faroes.

Nordgaardia and *Uschakovia* exhibit an interesting mosaic of characteristics of other genera within the Bugulidae. Both genera have similar avicularia which also closely resemble those of several species of *Cornucopina* (Harmer, 1926) as noted above. However, *Cornucopina* differs in autozooid morphology although its budding pattern does resemble that of *N. pusilla*. The avicularia of some species of *Kinetoskias* although less elongated are similar to those of *Nordgaardia* in structure and position (Yanagi and Okada, 1918; Harmer, 1926). As noted above, the ovicells of *Nordgaardia* resemble those of *Kinetoskias* which has however a very different colony form (Kluge, 1962). The modified parietal muscles at the base of the spines in *U. gorbunovi*, are, like the spines themselves, apparently unique. However, the 'flexor zooecii' muscles of both *Kinetoskias* and *Euoplozoum* (Busk, 1881; Harmer, 1926) are analogous in some ways although certainly not homologous.

An elongated ancestrula attached by long rhizoids is found in several genera of Bugulidae. Hastings (1943) illustrated the ancestrulae of several species of *Camptoplites* in detail. The zooid shape and to a certain extent the budding patterns and the avicularia of all the deep-water genera, including *Nordgaardia*, *Uschakovia*, *Kinetoskias* and some forms of *Camptoplites*, show a large number of similarities with one another which cannot all be ascribed to the common features of their environments. In all respects, the extensive continuum of character correlations found in the family Bugulidae (Gordon, 1984) seems to accommodate all four genera. Hayward (1978) considered that the budding and bifurcation patterns of *Nordgaardia* were so close to those of the genera *Epistomia* and *Synnotum* that both *Nordgaardia* and *Uschakovia* could be retained within the family Epistomiidae (Hastings, 1943; Ryland and Hayward, 1977). The members of this family do not however possess elongated avicularia or hyperstomial ovicells. Kluge (1962) introduced the family Sadkoidae to include *Nordgaardia* and *Uschakovia*. *Nordgaardia* has been included in this family by d'Hondt (1983) and by Harmelin and d'Hondt (1992). However, as noted by Ryland (1982: 760), the family name is invalid as no genus *Sadkoa*, from which the family name should have been derived, seems ever to have been described. In any case, the family is unnecessary as both genera are assignable to the Bugulidae.

Acknowledgements

I thank Dr Peter J. Hayward (Marine Research Group, Swansea University), for presenting the colony of *Uschakovia* to Museum Victoria for examination, and to Philip E. Bock for all his help and encouragement.

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Memoirs of Museum Victoria 58(2): 223–230 (2001)

FOUR NEW SPECIES AND A NEW RECORD OF *CHIMARRA* STEPHENS (TRICHOPTERA: PHILOPOTAMIDAE) FROM BOUGAINVILLE ISLAND, PAPUA NEW GUINEA

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Abstract

Cartwright, D.I., 2001. New species and a new record of *Chimarra* Stephens (Trichoptera: Philopotamidae) from Bougainville Island, Papua New Guinea. *Memoirs of Museum Victoria* 58(2): 223–230

Descriptions and keys are provided for males of five species of caddisflies of the widespread genus *Chimarra* from Bougainville Island, Papua New Guinea, including four new species. Females of four species are also keyed and described.

Introduction

The cosmopolitan caddisfly genus *Chimarra* Stephens, 1829 has not been recorded from Bougainville Island, although 21 species have been described from mainland New Guinea (Papua New Guinea and Irian Jaya, Indonesia) (Neboiss, 1986; Malicky, 1994). Two have been described from the nearby Solomon Islands, Guadalcanal Island (9°32′S, 160°12′E) (Kimmins, 1957a). Specimens of the genus were collected during 1987–1990 by Ms Cathy Yule near Arawa (6°12′S, 155°32′E) and deposited in Museum Victoria, Melbourne. A total of 21 males and 18 females were sorted to five species. Females were paired with respective males on the basis of similarities in coloration particularly on the head, and on wing venation and locality.

The Bougainville Island *Chimarra* species display the following character states: in the forewing: the curved or sinuous Rs vein basal to the discoidal cell is associated with thickened veins in four of the species; abdominal segments VIII and IX are elongate in females of three of the four known species; lateral lobe processes are present on tergum X in males of all species; and in one species, the dense brush of small spines is present on the phallus. The forewing with vein Rs curved has been cited as a key diagnostic feature for the subgenus *Chimarra* (*Chimarra*) separating it the from other subgenera of *Chimarra* in the New World (Blahnik, 1998). This feature is also present in many species from Australia (Cartwright, in prep.), several species from Asia (Kimmins, 1957b, 1964) and Africa (Kimmins, 1963). Kimmins (1957b, 1962) reported that both *C. crepidata* Kimmins from India and *C. papuana* Kimmins from New Guinea have the phallus containing numerous spines at the apex, a characteristic also of *C. pinga* sp. nov.

Both males and females are most readily distinguished by genitalic features, often requiring the clearing of the abdomen in potassium hydroxide.

Figured specimens are identified by the notebook numbers of Dr Arturs Neboiss (NMV), prefix PT-; or the author; prefix CT-. Abbreviations for genitalic parts are indicated on Figs 1–3 and 21.

Depositories are abbreviated as follows: BMNH, the Natural History Museum, London; NMV, Museum Victoria, Melbourne.

Chimarra Stephens

Chimarra Stephens, 1829: 318.—Mosely and Kimmins, 1953: 398.

Type species. Phryganea marginata. Linnaeus, 1767 by monotypy.

Remarks. A diagnosis of the genus *Chimarra* and subgenus *Chimarra* was provided by Blahnik (1998).

Key to males and females of species of *Chimarra* from Bougainville Island

1. Males 2
— Females 6
2. Inferior appendages in lateral view, long and slender, length > 3.5 times width (Figs 1, 4)..........3
— Inferior appendages in lateral view, not long and slender, length < twice width (Figs 7, 10)..........4

3. Inferior appendages, very long and slender over the whole length, length > 5 times width (Figs 1–3).. *Chimarra longpela*

— Inferior appendages, long and slender over the apical half, broadened in basal third, length < 4 times width (Figs 4–6)..................*Chimarra panguna*

4. Inferior appendages with large process present on mesal margin (Fig. 8); phallus with dense brush of pale spines apically (Figs 7–9).. *Chimarra pinga*

— Inferior appendages without process present on mesal margin; phallus without dense brush of pale spines apically (Figs 11, 14) 5

5. Inferior appendages in lateral view widely bifid (Fig. 10) ....*Chimarra biramosa*

— Inferior appendages in lateral view not bifid (Fig. 13) ....*Chimarra yuleae*

6. Abdominal segments VIII and IX short and robust (Fig. 21) ....*Chimarra biramosa*

— Abdominal segments VIII and IX long and slender (Figs 22, 23).................7

7. Abdominal segments VIII and IX in ventral view, of similar width, and not tapered apically (Fig. 22) ....*Chimarra pinga*

— Abdominal segments VIII and IX in ventral view, not of similar width, tapered apically (Figs 23, 24).. 8

8. Abdominal segment IX extended apically to form an elongated point Figs 23, 23a)...*Chimarra longpela*

— Abdominal segment IX not extended apically to form an elongated point (Fig. 24)...*Chimarra yuleae*

Chimarra longpela sp. nov.

Figures 1–3, 17, 23, 23a

Type material. Holotype male. Papua New Guinea, Bougainville I., Panguna, light trap, 7 Dec 1989, C. Yule (NMV T-17489).

Paratypes, all same locality and collector as holotype: 1 male, 13 Apr 1988 (genitalia prep. PT-1795, figured); 1 male, Mar 1989; 1 male, 19 Apr 1988; 3 males, 17 Dec 1988; 2 males, 2 females (genitalia prep. CT-284, figured), 29 Jan 1989; 1 female, Feb 1989; 1 female, Apr 1989, 1 female, 1 Oct 1988 (all NMV).

Other material examined. Papua New Guinea, Bougainville I., Konaiano Ck, Panguna, 24 Sep 1988, C. Yule, 1 female (NMV).

Description. General colour brownish, including head, mesothorax and wings; although triangular area on head between ocelli dark brownish. Wing venation: forewing veins Rs and M curved and thickened basal to discoidal and median cells (Fig. 17); forewing with forks 1, 2, 3 and 5 present; hindwing with forks 1, 2, 3 and 5 present.

Male. Genitalia dark brown. Ventral process on segment IX absent; inferior appendages in lateral view, very long and slender, length about 6 times width (Fig. 1), in ventral view, straight and slender, length about 5 times width, tapered slightly apically (Fig. 2); lobes of tergum X simple, divided dorsomedially for most of length (Fig. 3); phallus tubular with a conspicuous dark spine embedded subapically (Figs 1, 3).

Female. Abdominal segments VIII and IX elongate and slightly laterally compressed, segment IX extended apically to form an elongated point; cerci short (Figs 23, 23a).

Length of forewing: male 5.0–5.9 mm, female 4.9–5.8 mm.

Etymology. Longpela — New Guinea pidgin word for long, referring to the inferior appendages of the male.

Distribution. Papua New Guinea. Bougainville I. (males known only from the type locality).

Remarks. In the male, the extremely elongate and slender inferior appendages are distinctive. The female genitalia are also extremely elongate and similar to *C. yuleae* sp. nov. and *C. pinga* sp. nov. *Chimarra longpela* females can be distinguished by the elongated point on abdominal segment IX.

Chimarra panguna sp. nov.

Figures 4–6, 18

Type material. Holotype male, Papua New Guinea, Bougainville I., Panguna, 29 Aug 1988, C. Yule (NMV T-17503).

Paratype male, same data as holotype: genitalia prep. CT-282, figured (NMV).

Description. Male. General body colour brown, head and mesothorax dark brown contrasting with pale warts; wings brownish. Wing venation: forewing vein Rs curved anteriorly basal to discoidal cell (Fig. 18); forewing with forks 1, 2, 3 and 5 present; hindwing with forks 1, 2, 3 and 5 present.

Genitalia brown. Ventral process on segment IX absent; inferior appendages broadest basally, narrowed at about half length, apical half slender, length about 3 times width (Figs 4, 5); lateral lobes of tergum X simple, divided dorsomedially for most of length (Fig. 6), shorter than inferior appendages, slightly downturned apically; phallus tubular, inserted between lateral lobes, with 2 dark spines embedded subapically and basally (Figs 4, 6).

Female unknown.

Length of forewing: male 4.1–5.0 mm.

Etymology. Panguna — named after the type locality (Panguna), noun in apposition.

Distribution. Papua New Guinea, Bougainville I. (known only from type locality).

Remarks. The males of *C. panguna* can be distinguished from other Bougainville species by the slender apical half and robust basal half of the inferior appendages.

Chimarra pinga sp. nov.

Figures 7–9, 19, 22

Type material. Holotype male, Papua New Guinea, Bougainville I., Panguna, light trap, 17 Dec 1988, C. Yule (NMV T-17505).

Paratypes, all same locality and collector as holotype: 1 male, 20 Jan 1988 (genitalia prep. PT-1793, figured); 1 male, Feb 1989; 1 female, 19 Dec 1989 (genitalia prep. CT-286, figured) (all NMV).

Description. General body colour pale, including head and mesothorax, although triangular area on head between ocelli dark brownish; wings brownish. Wing venation: forewing discoidal cell veins R4-5 and R2-3 thickened basally, Rs curved anteriorly basal to thickening (Fig. 19); forewing with forks 1, 2, 3 and 5 present; hindwing with forks 1, 2, 3 and 5 present.

Male. Genitalia dark brown. Ventral process on segment IX absent; inferior appendages in lateral view subtriangular, length about 1.5 times width (Fig. 7) with a mesal digitiform projection subapically (Figs 8, 9); lateral lobes of tergum X simple, slightly truncated apically, divided dorsomesally for most of length (Fig. 8); phallus tubular, dilated apically with a field of small, pale spines, and with conspicuous dark spine embedded subapically (Figs 7–9).

Female. Abdominal segments VIII and IX in ventral view, long and slender, of similar width, and not tapered apically; cerci short (Fig. 22).

Length of forewing: male 5.1–5.2 mm, female 5.7 mm.

Etymology. Pinga — New Guinea pidgin word for finger, referring to finger-like mesal projection on the inferior appendages of the male.

Distribution. Papua New Guinea, Bougainville I. (known only from type locality).

Remarks. Chimarra pinga is a distinctive species in that the male has digitiform projections on the inferior appendages and a phallus with an apical 'brush' of spines, separating it from all known Australasian species. The female differs from other Bougainville species on the basis of the abdominal segments VIII and IX, having the combination long and slender, of similar width, and not tapered apically.

Chimarra biramosa Kimmins

Figures 10–12, 16, 21

Chimarra biramosa Kimmins, 1957a: 292, figs 4a, 5.—Neboiss, 1986: 108.

Type material. Holotype male, Solomon Islands, Guadalcanal I., Tapenanje, 10–15 Dec 1953, J.D. Bradley (BMNH). Type not seen.

Paratypes, 1 male, 6 females, all same data as holotype (BMNH). Paratypes not seen.

Material examined. 1 male, Papua New Guinea, Bougainville I., Arawa 10/39, 21 Dec 1989, C. Yule (NMV); 1 male, same locality and collector, 13 Jun 1988 (genitalia prep. PT-1797, figured); 1 female, same loc. and collector, 12 Mar 1988; 1 female, same loc. and collector, 14 Aug 1988 (genitalia prep. CT-283, figured); 1 female, same loc. and collector, 25 Dec 1989; 1 female, Panguna, light trap, 29 Jan 1989, C. Yule; 2 females, Panguna, 3 Dec 1987, C. Yule (all NMV).

Description (revised after Kimmins, 1957a). General body colour brown, head and mesothorax dark brown contrasting with pale warts; wings brownish. Wing venation: forewing vein Rs slightly curved basal to discoidal cell, forewing with forks 1, 2, 3 and 5 present (Fig. 16); hindwing with forks 1, 2, 3 and 5 present (Kimmins 1957a: fig. 4a).

Male. Genitalia dark brown. Ventral process on segment IX absent; inferior appendages in lateral view short with dorsal extension basally (i.e. bifid or biramous) (Fig. 10), in ventral view, broad, tapering apically (Fig. 11); lateral lobes of tergum X simple, length almost as long as inferior appendages (Fig. 12); phallus tubular, with conspicuous asymmetrical dark spine subapically (Figs 10–12; Kimmins 1957a: fig. 5a–c).

Female. Abdominal segments VIII and IX

short; segment VIII dark brownish; segment IX with pair of dark brown sub-triangular ventral plates; cerci short (Fig. 22; Kimmins 1957a: fig. 5d).

Length of forewing: male 4.1–4.5 mm, female 5.0–5.2 mm.

Distribution. Solomon Islands, Guadalcanal I. and Papua New Guinea, Bougainville I.

Remarks. Chimarra biramosa males differ from all other Australasian species in the widely bifid inferior appendages of the male (Kimmins, 1957a). The female differs from the other Bougainville species in having short abdominal segments VIII and IX. Kimmins' (1957a) figures have been redrawn to allow direct comparisons and to accompany the description that is revised in light of new interpretations of *Chimarra* genitalic structures.

Chimarra yuleae sp. nov.

Figures 13–15, 20, 24

Type material. Holotype male, Papua New Guinea, Bougainville I., Panguna, light trap, 17 Dec 1988, C. Yule (NMV T-17509).

Paratypes, all same locality and collector as holotype: 1 male, 3 Dec 1987 (genitalia prep. PT-1792, figured); 1 male, 29 Jul 1988 (genitalia prep. PT-1796); 1 male, Feb 1989; 1 female, 17 Dec 1988 (genitalia prep. CT-285, figured); 1 female, Apr 1989 (all NMV).

Description. General body colour pale, including head, mesothorax and wings. Wing venation: forewing with a heart-shaped raised thickening at the junction of veins M1-2 and M3 (Fig. 20); forewing with forks 1, 2, 3 and 5 present; hindwing with forks 1, 2, 3 and 5 present.

Male. Ventral process on segment IX absent; inferior appendages in lateral view triangular, narrowed basally, broadened apically, with apicodorsal projection, length about same as width, with mesal flange and tapering to acute apex (Fig. 13), in ventral view, basically subrectangular (Fig. 14); lateral lobes of tergum X elongate, extending further than inferior appendages, slightly upturned apically; phallus tubular, with a conspicuous ventral dark spine embedded subapically (Figs 13–15).

Female. Abdominal segments VIII and IX in ventral view, not of similar width, tapered apically; cerci short (Fig. 24).

Length of forewing: male 5.1–5.3 mm, female 6.0–6.1 mm.

Etymology. The species is named for Cathy Yule (collector).

Distribution. Papua New Guinea, Bougainville I. (known only from type locality).

Remarks. In the male, the distinctive triangular inferior appendages allow separation from other Bougainville species. The female genitalia is very similar to *C. longpela* but lacks the elongate point on segment IX.

Acknowledgements

I thank Ms Cathy Yule for collecting all the material studied, Dr Arturs Neboiss (NMV) for providing access to the specimens, and him, John Dean and two anonymous referees for comments on drafts of this manuscript.

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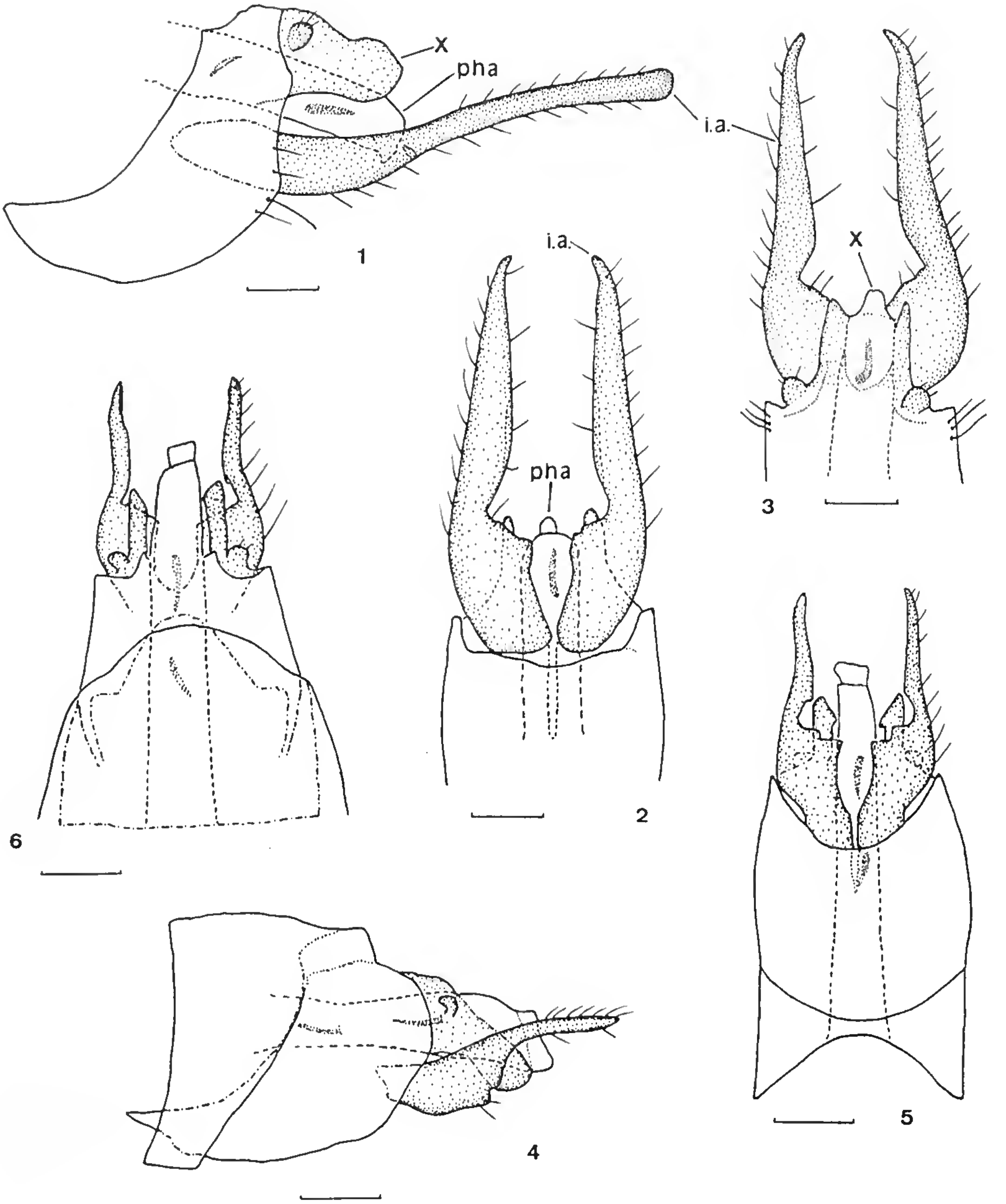
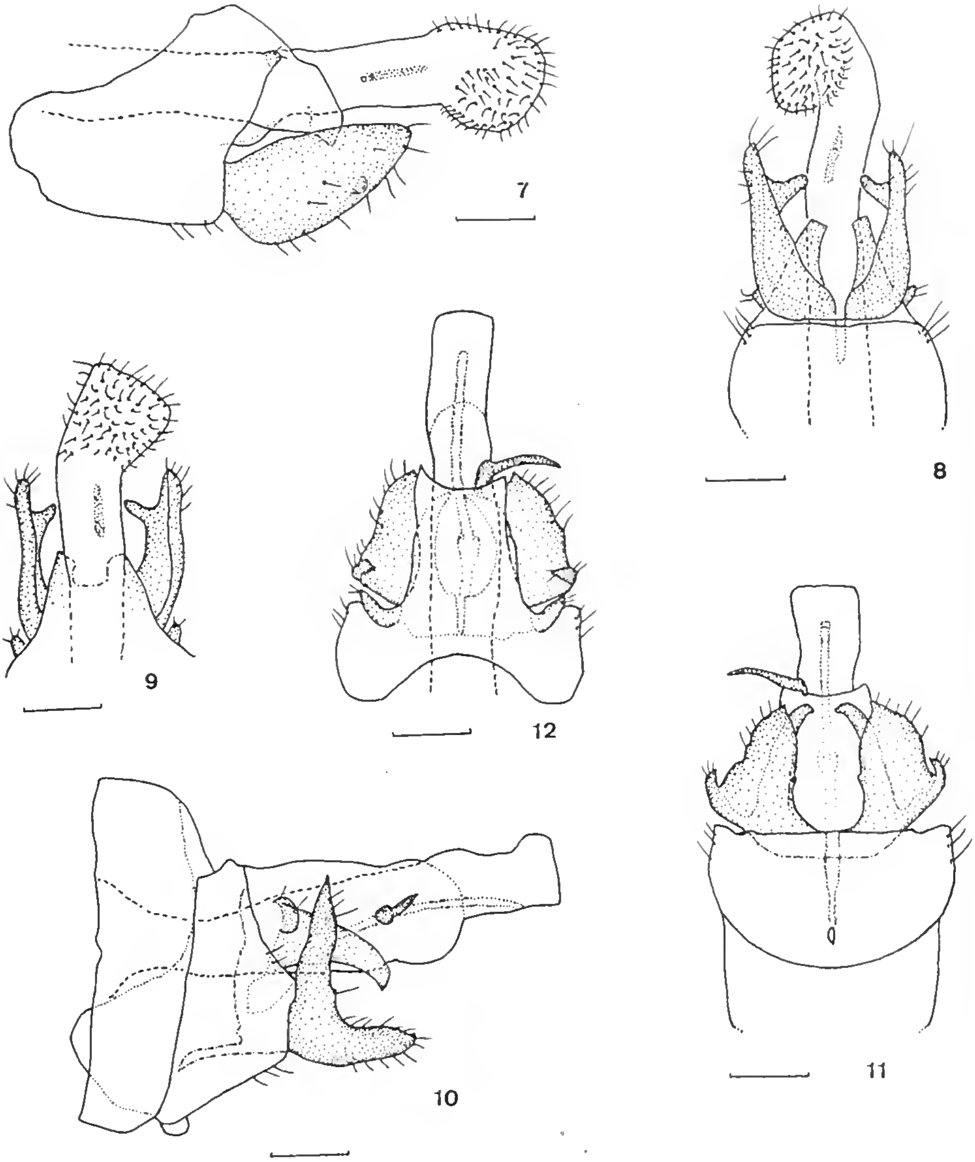
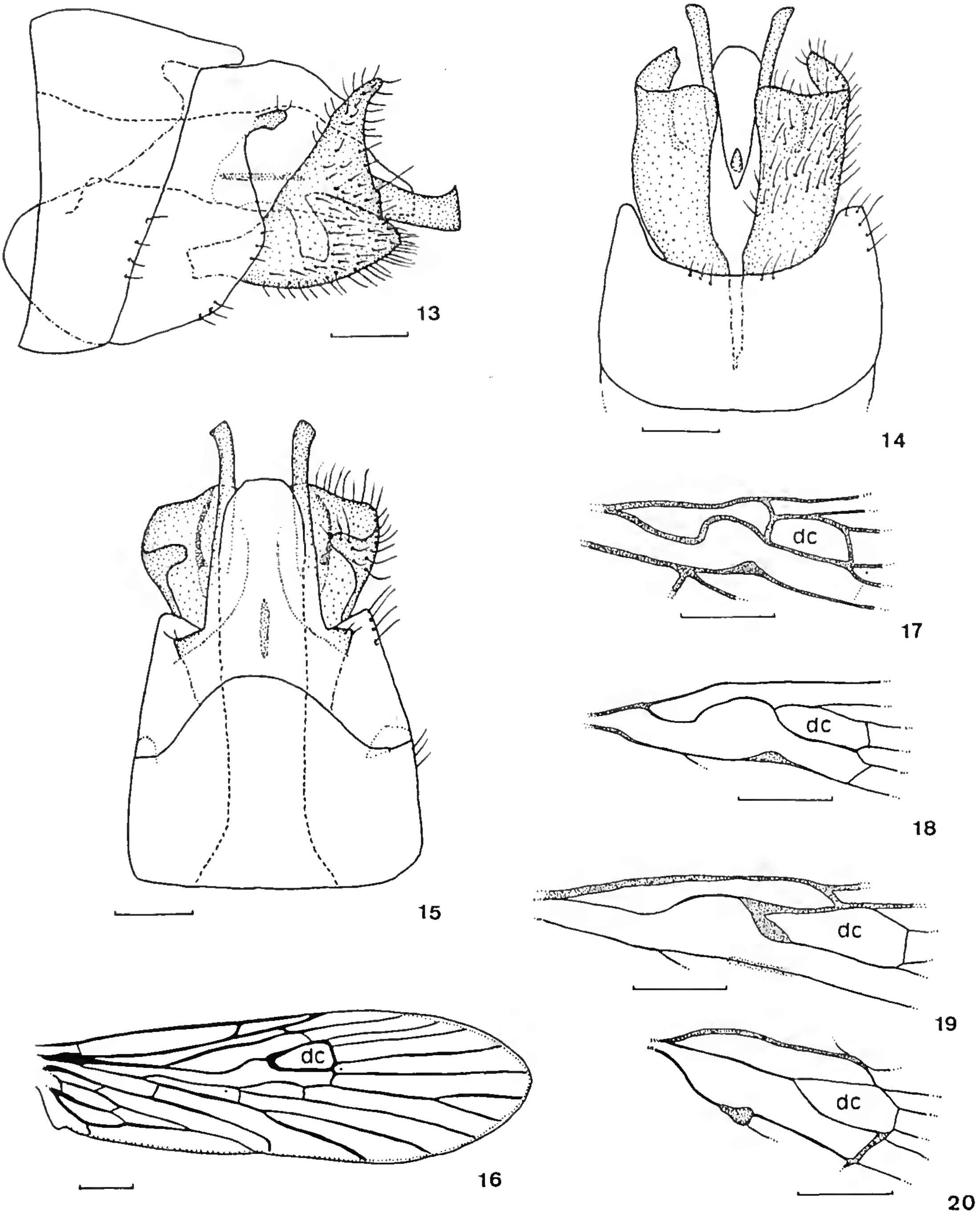


Figures 1–6. *Chimarra* spp. Male genitalia in lateral, ventral and dorsal views. 1–3: *Chimarra longpela* sp. nov. 4–6: *Chimarra panguna* sp. nov.

Abbreviations: i.a., inferior appendages; X, tergum X; pha, phallus. All scale lines 0.1 mm.

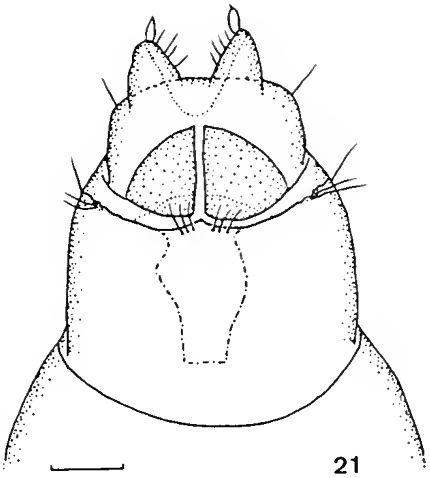


Figures 7–12. *Chimarra* spp. Male genitalia in lateral, ventral and dorsal views. 7–9: *Chimarra pinga* sp. nov. 10–12: *C. biramosa* Kimmins.
All scale lines 0.1 mm.



Figures 13–20, *Chimarra* spp. Male. 13–15: Genitalia in lateral, ventral and dorsal views. *Chimarra yuleae* sp. nov. 16: *Chimarra biramosa* Kimmins, forewing. 17–20: section of forewing. 17: *Chimarra longpela* sp. nov. 18: *Chimarra panguna* sp. nov. 19: *Chimarra pinga* sp. nov. 20: *Chimarra yuleae* sp. nov.

Abbreviation: dc, discoidal cell. Scale lines. Figs 13–15: 0.1 mm; Figs 16–20: 0.5 mm.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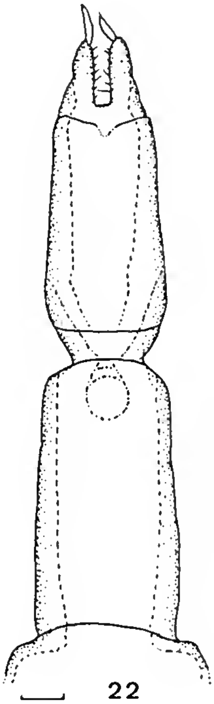
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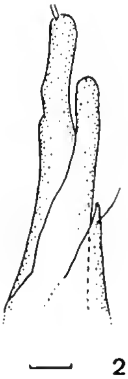
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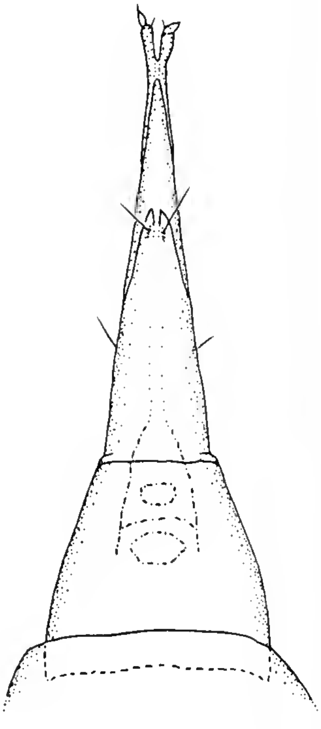
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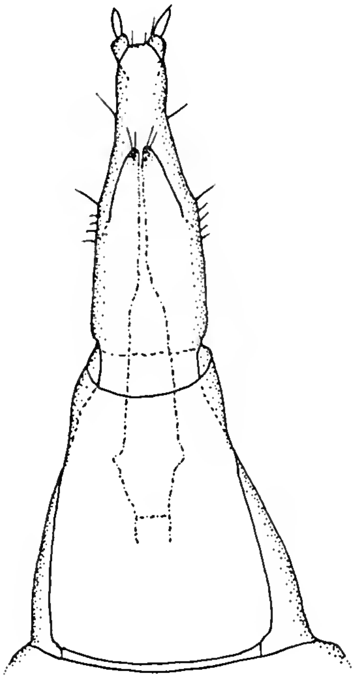
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Figures 21–24. *Chimarra* spp. Female genitalia. 21: *Chimarra biramosa* Kimmins, ventral view; 22: *Chimarra pinga* sp. nov., ventral view. 23, 23a: *Chimarra longpela* sp. nov. 23: ventral view; 23a: lateral view. 24: *Chimarra yuleae* sp. nov. ventral view.

Abbreviations: IX, abdominal segment nine; VIII, abdominal segment eight. All scale lines 0.1 mm.

Memoirs of Museum Victoria 58(2): 231–246 (2001)

NEW SPECIES OF HYDROPSYCHIDAE (INSECTA: TRICHOPTERA) FROM NORTHERN AUSTRALIA

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Abstract

Dean, J.C., 2001. New species of Hydropsychidae (Insecta: Trichoptera) from northern Australia. *Memoirs of Museum Victoria* 58(2):231–246.

Five new species of hydropsychid caddisflies of northern Australia are described from males, females and larvae: *Cheumatopsyche kakaduensis* sp. nov., *C. suteri* sp. nov., *C. wellsae* sp. nov., *C. dostinei* sp. nov. and *Asmicridea capricornica* sp. nov. *Cheumatopsyche kakaduensis* sp. nov. has thus far only been recorded from Kakadu National Park, while the remaining four species are widely distributed across northern Australia. Distribution maps are presented with keys for identification of males, females and larvae.

Introduction

Caddisflies of the family Hydropsychidae of northern Australia are poorly known. In recent years a large amount of material from the Alligator Rivers region, Northern Territory, has been accumulated and a smaller amount from north-western Australia. Four new species of *Cheumatopsyche* Wallengren, 1891 and one of *Asmicridea* Mosely, 1953 are described here from this material. Distribution records for northern Australia (including North Queensland) are presented. Additional undescribed species are known from Cape York Peninsula and the Queensland wet tropics but are outside the scope of the present study.

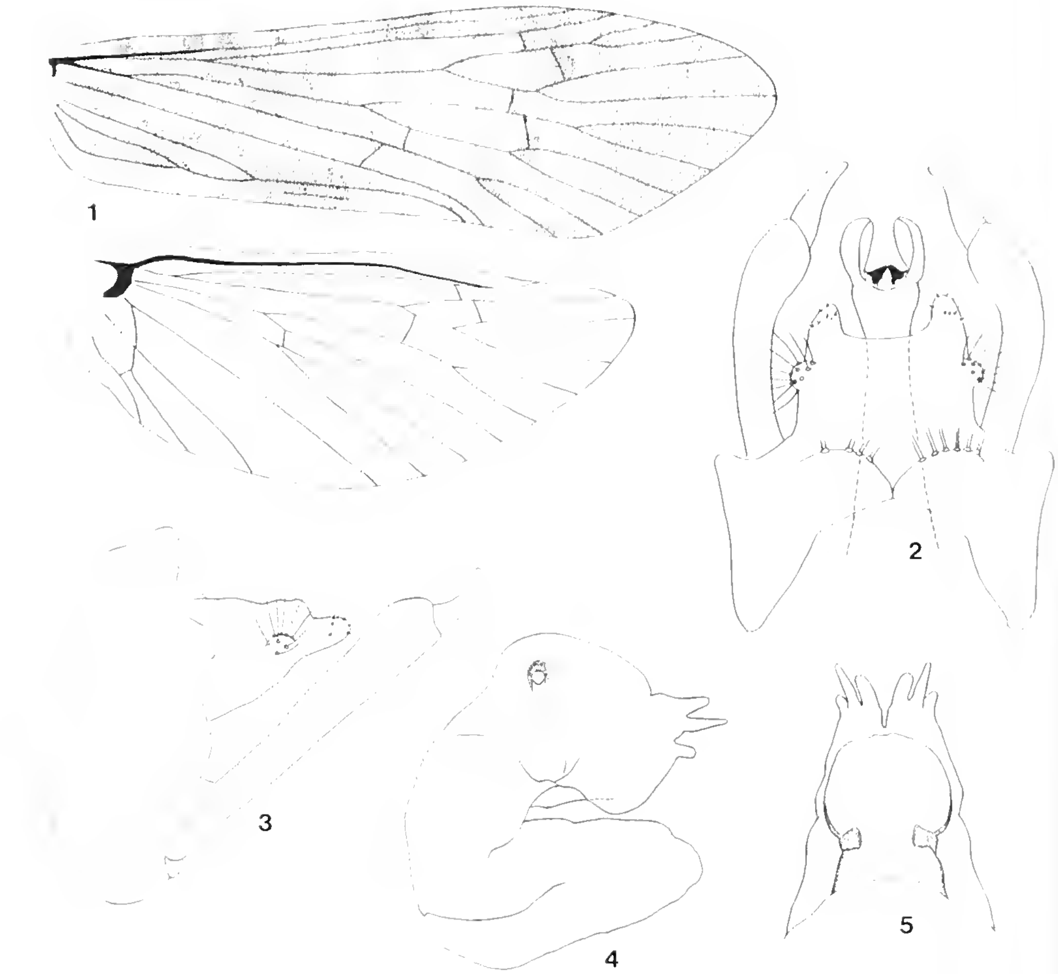
Although only one species of *Cheumatopsyche* has been described from Australia, recent examination of larval material has revealed the existence of at least 18 species (Dean, 1999). *Cheumatopsyche modica* (McLachlan, 1871) was described from material collected in Victoria. While the name has subsequently been applied to all adult Australian *Cheumatopsyche* material, probably in part a consequence of the conservative male and female genitalia, the identity of the described species has yet to be determined. Of six larval species currently known from Victoria, any one of three or four could be *C. modica*. Since none of these species occurs in northern Australia, description of northern species can proceed prior to the identity of *C. modica* being established. A similar situation exists in *Asmicridea*. Although larvae of the two described species have yet to be determined, type localities for both species are in southern Australia. The northern Australia larva described below is clearly different from all larvae known from southern Australia (Dean, 1999).

Associations of adults and larvae have been achieved by collection of pupal chambers containing pharate male pupae and associated larval sclerites. Observations on colour are based on material preserved in 70% ethanol. Adult genitalia have been prepared for examination by clearing in cold potassium hydroxide for 24–48 hours. Terminology for adults follows Nimmo (1987), while that for larvae follows Wiggins (1977) and Shefter and Wiggins (1986). Type material has been lodged in Museum Victoria, Melbourne (NMV) or the Australian National Insect Collection, Canberra (ANIC). Material without a stated repository is lodged in Museum Victoria. Not all of the material examined is listed below and a full listing is available from the author. Abbreviations for material examined are: M, adult male; F, adult female; MP, male pupa; FP, female pupa; P, unsexed pupa; L, larva. Abbreviations for collectors are: AW (A. Wells), DC (D. Cartwright), JB (J. Blyth), JD (J. Dean), JEB (J.E. Bishop), MBM (M.S. and B.J.Moulds), PD (P. Dostine), PS (P. Suter).

Cheumatopsyche kakaduensis sp. nov.

Figures 1–11

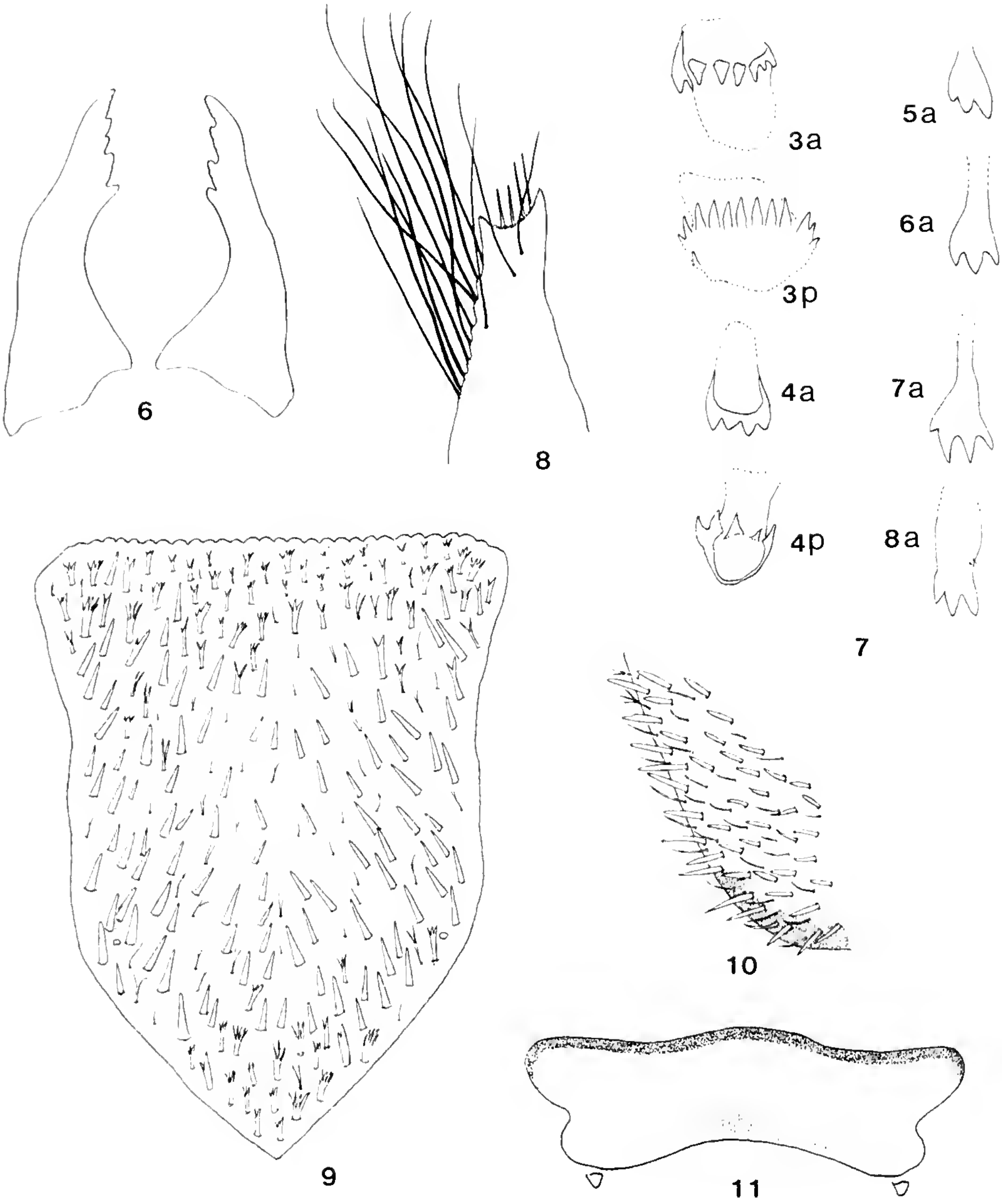
Type material. Holotype: adult male, Gulungul Creek, Radon Springs, Northern Territory (12°45′S 132°55′E), 13–14 Apr 1989, P.Suter and A.Wells (NMV T-17415). Paratypes collected with holotype: 6 males, 6 females (NMV); 5 males, 5 females (ANIC).



Figures 1–5 *Cheumatopsyche kakaduensis* sp. nov. Adult: 1, wings; 2, male genitalia, dorsal; 3, male genitalia, lateral; 4, female genitalia, lateral; 5, female genitalia, dorsal.

Other material examined. **Northern Territory.** Numerous M, F, P, and L, collected with holotype; 1M, Graveside Creek (13°18′S 132°32′E), 18 Jul 1988, PD; 2P, 1L, Little Nourlangie Rock Creek (12°52′S 132°48′E), 22 Apr 1989, PS and AW; 2L, creek 5 km W of Gimbat OSS field station (13°33′S 132°34′E), 19 Apr 1989, AW and PS; 2P, 47L, Baroalba Springs (12°49′S 132°52′E), various dates, AW and PS, DC; 2L, Magela Creek, d/s Magela Falls (12°46′S 133°6′E), various dates, AW and PS, DC; 2L, Carbo Creek (13°17′S 132°51′E), 29 May 1988, AW and PS; 1L, Barramundie Creek, d/s Falls (13°22′S 132°28′E), 26 May 1988, AW and PS; 3L, Lone Spring (12°17′S 132°36′E), 21 Aug 1999, JD.

Description. Adult. General colour dark brown, almost black. Vertex of head dark brown; antennae straw-coloured; thorax medium brown. Wings (Fig. 1): forewing dark brown, irrorate; hindwing uniformly paler brown. Length of forewing 4.9–6.1 mm (male), 5.0–6.3 mm (female). Male genitalia (Figs 2, 3): distal lobes of tergum X rounded, not turned up apically,



Figures 6–11 *Cheumatopsyche kakaduensis* sp. nov. Pupa: 6, mandibles; 7, abdominal hook plates (3–8: abdominal segment number, a: anterior hook plate, p: posterior hook plate); 8, apical process of abdomen. Larva: 9, frontoclypeus; 10, pronotum, anterolateral margin; 11, prosternites.

separated by a distance approximately 3 times their width; pre-anal appendages squat, located well forward of base of distal lobe; terminal segment of clasper about quarter length of basal segment; dorsum of abdominal segment IX broad in lateral view. Female genitalia (Figs 4, 5): clasper receptacle small, shallow; inner aperture aligned with outer aperture, clearly visible in lateral view; separation of receptacles in dorsal view 2–3 times width of each receptacle.

Pupa. Right mandible with 3 subapical teeth, left mandible with 4 (Fig. 6). Paired hook plates on abdominal segments 3–8; anterior plates on segments 3–8 and posterior plates on segments 3 and 4 only (Fig. 7); some variation in number of teeth on all plates. Apical processes of abdomen (Fig. 8) with apicolateral angles acute, separated by shallow concave surface covered by small protrubences; outer margin of each process fringed with long black setae, ventral surface with series of pale spine-like setae which protrude beyond apex.

Mature larva. Head and thoracic sclerites predominantly medium-dark brown; unpigmented area surrounding each eye; small pale region in centre of frontoclypeus. Frontoclypeus length: width ratio 1.54–1.59; anterior margin finely crenulate with about 25 lobes (Fig. 9). Head and pronotum densely covered with conspicuous spine-like setae; those near posterior angle of frontoclypeus brush-like (Fig. 9); primary seta 17 on head short, length much less than distance from setal base to apex of frontoclypeus; primary seta 22 near anterolateral margin of pronotum short, robust, not much longer than adjacent secondary setae (Fig. 10). Posterior prosternites reduced to small flecks, one adjacent to each posterolateral angle of anterior prosternite (Fig. 11). Abdominal gills present on segments 1–7.

Etymology. The name reflects the apparent restriction of the species to Kakadu National Park.

Comments. C. kakaduensis appears to have a limited distribution having been recorded only from a few small creeks close to the escarpment and from one lowland spring (Fig. 53). The larva has previously been designated *Cheumatopsyche* sp. 10 (Wells, 1991) and *Cheumatopsyche* sp. AV10 (Dean, 1999).

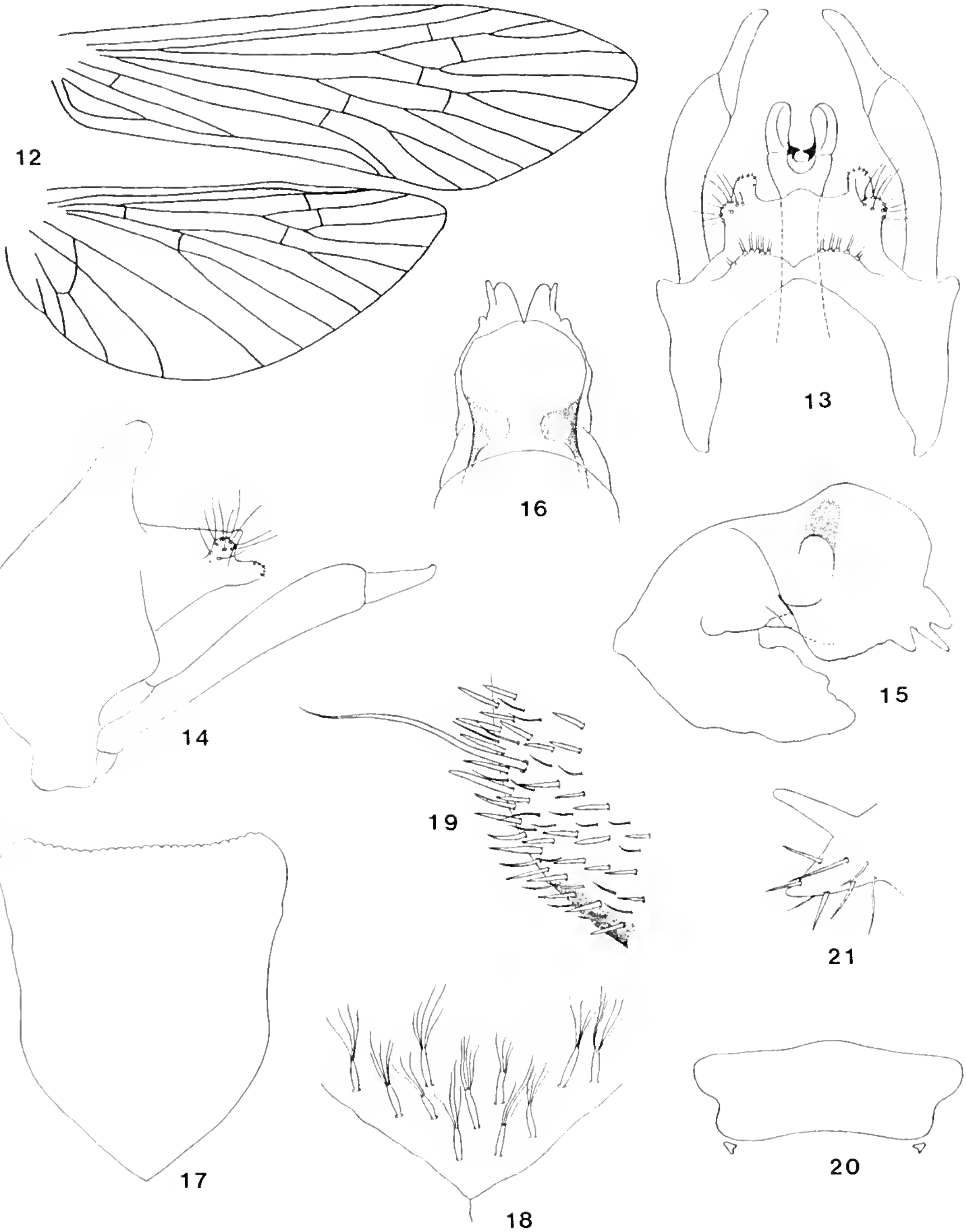
Cheumatopsyche suteri sp. nov.

Figures 12–21

Type material. Holotype: adult male, South Alligator River, Gimbat OSS Field Station, Northern Territory (13°35´S 132°36´E), 24 May 1988, A.Wells and P.Suter (NMV T-17428). Paratypes collected with holotype: 7 males, 4 females (NMV); 6 males, 2 females (ANIC).

Other material examined. **Western Australia.** 1M, 2F, Drysdale River, Kalumburu Crossing, 28 Sep 1979, JB; 20M, 35F, Camp Creek, Mitchell Plateau, various dates, JEB, PS; 4M, Barnett River Gorge, 1 Oct 1979, JB; 15L, Manning Gorge, near Gibb River Rd, Kimberley, 28 Jul 1994, DC; 10L, King Edward River, Mitchell River Rd, 25 Sep 1995, L.Metzeling; 1L, tributary of Bell Creek, Kimberley, 27 Jul 1994, DC. **Northern Territory.** 6L, South Alligator River, Kakadu Hwy crossing (13°17´S 132°19´E), 26 May 1988, PS and AW; 2M, 2F, Jim Jim Creek, 3 km d/s falls, 1 Sep 1979, JB; 1M, 1MP, 1L, Kambolgie Creek (13°32´S 132°23´E), various dates, PS and AW, DC; 15L, Magela Creek, d/s Magela Falls (12°46´S 133°06´E), various dates, AW and PS, DC; 3M, 1F, 16L, Graveside Gorge (13°18´S 132°32´E), various dates, AW and PS, PD; 3L, Baroalba Springs, Gubara (12°49´S 132°52´E), 28 Apr 1990, DC; 4 L, Koolpin Creek (13°29´S 132°35´E), 25 May 1988, PS and AW; 1L, Nourlangie Creek (12°28´S 132°44´E), 26 May 1988, PS and AW; 2L, Lone Spring, Kakadu National Park (12°17´S 132°36´E), 21 Aug 1999, JD; 1M, 2F, Howard Springs, near Darwin, 23 Jun 1969, Le Souef; 1M, Devil Devil Creek, 70 km SW of Daly River Mission, 23 Aug 1979; JB; 4M, 1F, Katherine Gorge National Park, 13 Aug 1979, JB; 2M, Roper River, Mataranka Homestead, 25 Jan 1977, MBM; 6L, Mann River, Arnhemland (12°22´S 134°08´E), 26 Aug 1999, JD; 18L, Liverpool River, Arnhemland (12°21´S 134°07´E), 26 Aug 1999, JD; 1L, Florence Falls, Litchfield National Park (13°06´S 13°047´E), 31 Aug 1999, JD. **Queensland.** 10M, 21F, 36L, Gunshot Creek, Telegraph Crossing (11°44´S 142°29´E), Feb 1992, DC and AW; 4M, 3F, 15L, Cockatoo Creek, Telegraph Crossing (11°39´S 142°27´E), Feb 1992, DC and AW; 2MP, 4L, Canal Creek, u/s Eliot Ck junction (11°23´S 142°25´E), 6 Feb 1992, DC and AW; 1L, Peaches Creek, 3 km NE of Coen (13°42´S 143°15´E), 4 Nov 1988, K.Walker; 15M, 8F, Upper Jardine River, various sites, Oct 1979, MBM; 1M, Gordon Creek, Iron Range, 19 Apr 1975, MBM.

Description. Adult. General colour dark brown, almost-black. Vertex of head dark brown; antennae straw coloured, basal segments usually with oblique darker bands; thorax medium brown. Wings (Fig. 12): forewing medium-dark brown, weakly irrorate; hindwing uniformly paler brown. Length of forewing 5.9–7.2 mm (male), 5.7–7.1 mm (female). Male genitalia (Figs 13, 14): dorsum of tergum X mesally elevated; distal lobes of tergum X rounded, not turned up apically, separated by approximately 4 times their width; pre-annal appendages raised, elongate in lateral view, situated close to base of distal lobes; terminal segment of clasper almost a third length of



Figures 12–21 *Cheumatopsyche suteri* sp. nov. Adult: 12, wings; 13, male genitalia, dorsal; 14, male genitalia, lateral; 15, female genitalia, lateral; 16, female genitalia, dorsal. Larva: 17, frontoclypeus; 18, secondary setae near apex of frontoclypeus; 19, pronotum, anterolateral margin; 20, prosternites; 21, foretrochantin.

basal segment, narrow, apically turned inwards; dorsum of segment IX narrow in lateral view. Female genitalia (Figs 15, 16): clasper receptacle large, broadly tubular; inner aperture clearly dorsal to outer aperture, outer aperture wide, semicircular; in dorsal view separation of receptacles usually less than width of each receptacle.

Pupa. Abdominal hook plates similar to *C. kakaduensis*.

Mature larva. Head and thoracic sclerites predominantly pale-medium brown; unpigmented area surrounding each eye. Dorsum of head somewhat flattened. Frontoclypeus length:width ratio 1.34–1.43; anterior margin finely crenulate with approximately 27 lobes (Fig. 17). Secondary setae numerous on posterior half of frontoclypeus, sparser on anterior half; some setae dark, but mostly pale and inconspicuous under dissecting microscope; setae of frontoclypeus hair-like with 4 or 5 apical filaments (Fig. 18). Primary seta 17 on head moderately long, about as long as distance from base of seta to apex of frontoclypeus. Pronotum with dark secondary setae restricted to anterior margin and region of middorsal line, setae towards lateral margins paler; primary seta 22 near anterolateral margin of pronotum long, tapered, about half length of pronotal sclerite (Fig. 19). Posterior prosternites reduced to small flecks, one adjacent to each postero-lateral angle of the anterior prosternite (Fig. 20). Abdominal gills present on segments 1–7.

Etymology. The species is named for Phil Suter who collected much of the material on which the present description is based.

Comments. The species is widely distributed across northern Australia with many records from the Northern Territory, north-western Australia and Cape York Peninsula in North Queensland (Fig. 54). The larva has previously been referred to as *Cheumatopsyche* sp. 12 (Wells, 1991) and *Cheumatopsyche* sp. AV12 (Dean, 1999).

Cheumatopsyche wellsae sp. nov.

Figures 22–30

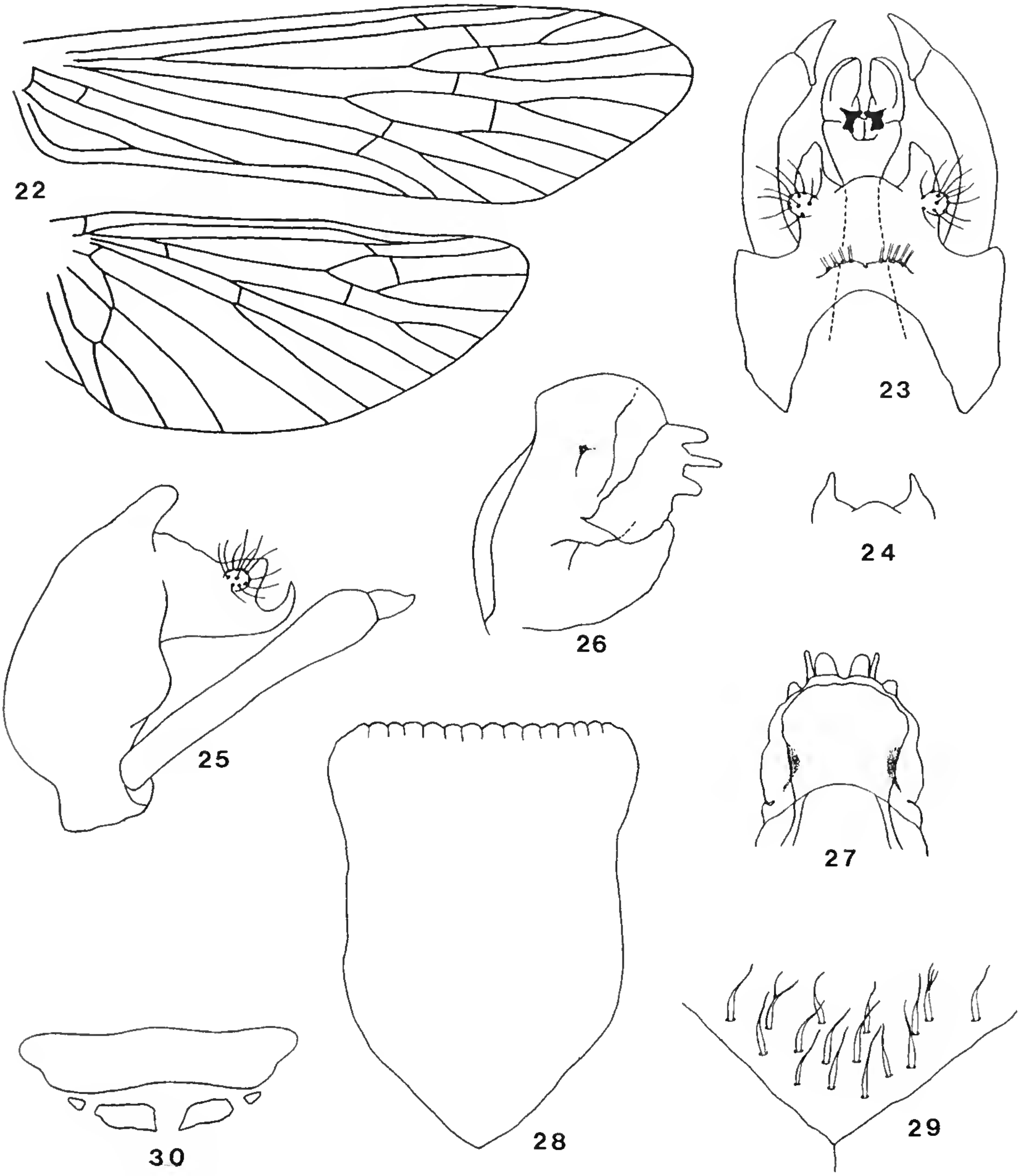
Type material. Holotype: adult male, East Alligator River, Cahills Crossing, Northern Territory (12°26'S 132°58'E), 27 May 1988, A.Wells and P.Suter (NMV T-17440). Paratypes collected with holotype: 11 males, 7 females (NMV); 4 males, 4 females (ANIC).

Other material examined. **Western Australia.** 1M, 1F, Drysdale River, Kalumburu Crossing, 28 Sep 1979, JB; 13M, 26F, Camp Creek and vicinity, Mitchell Plateau, various dates, JEB, PS; 1M, Barnett River Gorge, Kimberley, 1 Oct 1979, JB; 16M, 21F, Crossing pool, Millstream, Pilbara, 21 Oct 1979, JB; 19M, 29F, Fortescue Falls, Hamersley Range National Park, 27 Oct 1979, JB; 39M, 34F, Ord River, 9 km N of Kununurra, 19 Sep 1979, JB; numerous M and F, Spillway Creek, Ord River Dam, 2 Feb 1978, JEB. **Northern Territory.** Numerous L, East Alligator River, E of Jim Jim Falls (13°12'S 133°20'E), 29 May 1988, AW and PS; 2F, 3MP, numerous L, South Alligator River, Gimbat OSS Field Station (13°35'S 132°36'E), various dates, AW and PS, PD; 1M, 4F, Jim Jim Creek, 3 km d/s falls, 1 Sep 1979, JB; 11L, Coobamrbora Spring, Kakadu National Park (12°24'S 132°40'E), 21 Aug 1999, JD; 2M, 30L, Kambolgie Creek (13°32'S 132°23'E), various dates, PS and AW, DC; 1 MP, 8L, Magella Creek, u/s Magela Falls (12°47'S 133°06'E), various dates, AW and PS; 1M, 2F, 4L, Graveside Gorge (13°18'S 132°32'E), various dates, PD, AW and PS; 1L, Nourlangie Creek (12°28'S 132°44'E), 26 May 1988, PS and AW; numerous M, F, Katherine Gorge National Park, 13 Aug 1979, JB; 4M, Roper Bar, 15 Jul 1969, Le Souef; 4F, Groote Eylandt, Amagule Pool, 6 Feb 1984, M.Davies; 15L, Mann River, Arnhemland (12°22'S 134°08'E), 26 Aug 1999, JD; 13L, Liverpool River, Arnhemland (12°21'S 134°07'E), 26 Aug 1999, JD; 2L, Florence Falls, Litchfield National Park (13°06'S 130°47'E), 31 Aug 1999, JD. **Queensland.** 1M, 1F, 1P, 14L, Bertie Creek, Telegraph Crossing (11°50'S 142°30'E), Feb 1992, DC and AW; 2MP, 36L, Cockatoo Creek, Telegraph Crossing (11°39'S 142°27'E), Feb 1992, DC and AW; 7L, Pascoe River, 60 km W of Lockhart (12°53'S 143°01'E), 10 Nov 1988, K.Walker; 5M, 4F, Archer River Crossing, Cape York Peninsula, 9 Sep 1974, MBM; 1M, 4F, Currunda Creek, trib. of Freshwater Creek, Cairns district, 30 April 1979, AW.

Description. Adult. General colour pale-medium brown. Wings (Fig. 22): forewing golden-pale brown, without irroration; hind wing paler brown. Length of forewing 5.2–6.3 mm (male), 4.9–6.1 mm (female). Vertex of head pale-medium brown; antennae straw coloured, basal segments without darker bands. Thorax golden. Male genitalia (Figs 23–25): distal lobes of tergum X strongly upturned, apices pointed both in lateral and dorsal views; width of lobes somewhat variable. Terminal segment of clasper short, triangular, about fifth length of basal segment; inner basal angle acute. Female genitalia (Figs 26, 27): clasper receptacle small; in lateral view consisting of short, narrow chimney with circular aperture at upper end, delicate sclerotisation extended anteroventral from base of chimney; separation of receptacles in dorsal view greater than 8 times width of each receptacle.

Pupa. Abdominal hook plates similar to *C. kakaduensis*.

Mature larva. Dorsum of head medium brown, lateral margins predominantly pale yellow, venter of head extensively dark brown-black. Frontoclypeus length:width ratio 1.54–1.62, anterior margin coarsely crenulate with about 15 lobes



Figures 22–30 *Cheumatopsyche wellsae* sp. nov. Adult: 22, wings; 23, male genitalia, dorsal; 24, distal lobes of male genitalia, variant; 25, male genitalia, lateral; 26, female genitalia, lateral; 27, female genitalia, dorsal. Larva: 28, frontoclypeus; 29, secondary setae near apex of frontoclypeus; 30, prosternites.

(Fig. 28); secondary setae clear, appressed, inconspicuous under dissecting microscope, those near posterior angle of frontoclypeus predominantly simple, the apex thin and whip-like (Fig. 29). Pronotum pale-medium brown; secondary setae clear, appressed and inconspicuous; primary seta 22 near anterolateral margin of pronotum long, tapered, about half length of pronotal sclerite. Posterior prosternites consisting of pair of small lateral sclerites and pair of large mesal sclerites. (Fig. 30). Mesonotal and metanotal sclerites densely clothed with appressed fine, forward-directed dark setae, forming short fringe along anterior margin of both segments. Abdominal gills present on segments 1–7.

Etymology. The species is named for Alice Wells who collected much of the material on which the present description is based.

Comments. The species is widely distributed across northern Australia, and has been collected from the Pilbara and Kimberley regions of Western Australia, the Northern Territory, Cape York Peninsula in North Queensland and further south in eastern Queensland (Fig. 55). The larva has previously been designated *Cheumatopsyche* sp. 11 (Wells, 1991) and *Cheumatopsyche* sp. AV11 (Dean, 1999).

Cheumatopsyche dostinei sp. nov.

Figures 31–38

Type material. Holotype: adult male, Adelaide River, 15 km E of Stuart Highway, Northern Territory, 15 Aug 1979, J.Blyth (NMV T-17459). Paratypes collected with holotype: 5 males, 11 females (NMV); 3 males, 3 females (ANIC).

Other material examined. **Western Australia.** 11M, 12F, 15 km S of Windjana Gorge, 4 Aug 1989, McCubbin; 9M, 5F, Ord River, 9 km N of Kununurra, 19 Sep 1979, JB; 1M, Geiki Gorge National Park, 9 Oct 1979, JB; 1M, Dunham River, 100 km S of Wyndham, 7 Feb 1977, MBM; 3M, 10F, Fitzroy River Crossing, Derby-Broome Road, 3 Nov 1978, MBM. **Northern Territory.** 2M, 8F, 4L, East Alligator River, Cahills Crossing (12°26´S 132°58´E), 27 May 1988, AW and PS; 2MP, South Alligator River, Kakadu Hwy crossing (13°17´S 132°19´E), 26 May 1988, PS and AW; 22L, Wildman River, Arnhem Highway (12°50´S 132°02´E), 22 Apr 1989, PS and AW; 1M, 1F, 14L, Kambolgie Creek (13°32´S 132°23´E), various dates, DC, AW and PS; 1M, Jim Jim Creek, Kakadu Hwy (12°57´S 132°33´E), 28 May 1988, PS and AW; 2MP, 9L, Nourlangie Creek (12°28´S 132°44´E), 26 May 1988, PS and AW. **Queensland.** 9M, 6F, Upper Ross River, SW of Townsville, 8 May 1979, AW; 1M, 3F, Cairns, Lake Morris Rd (16°55´S 145°46´E), 16 Nov 1988, K.Walker; 2M, 20F, Forty Mile Scrub, 65 km SW of Mt Garnet, 19 Dec 1974, MBM; 1M, 2F, Archer River Crossing, Cape York Peninsula, 9 Sep 1974, MBM.

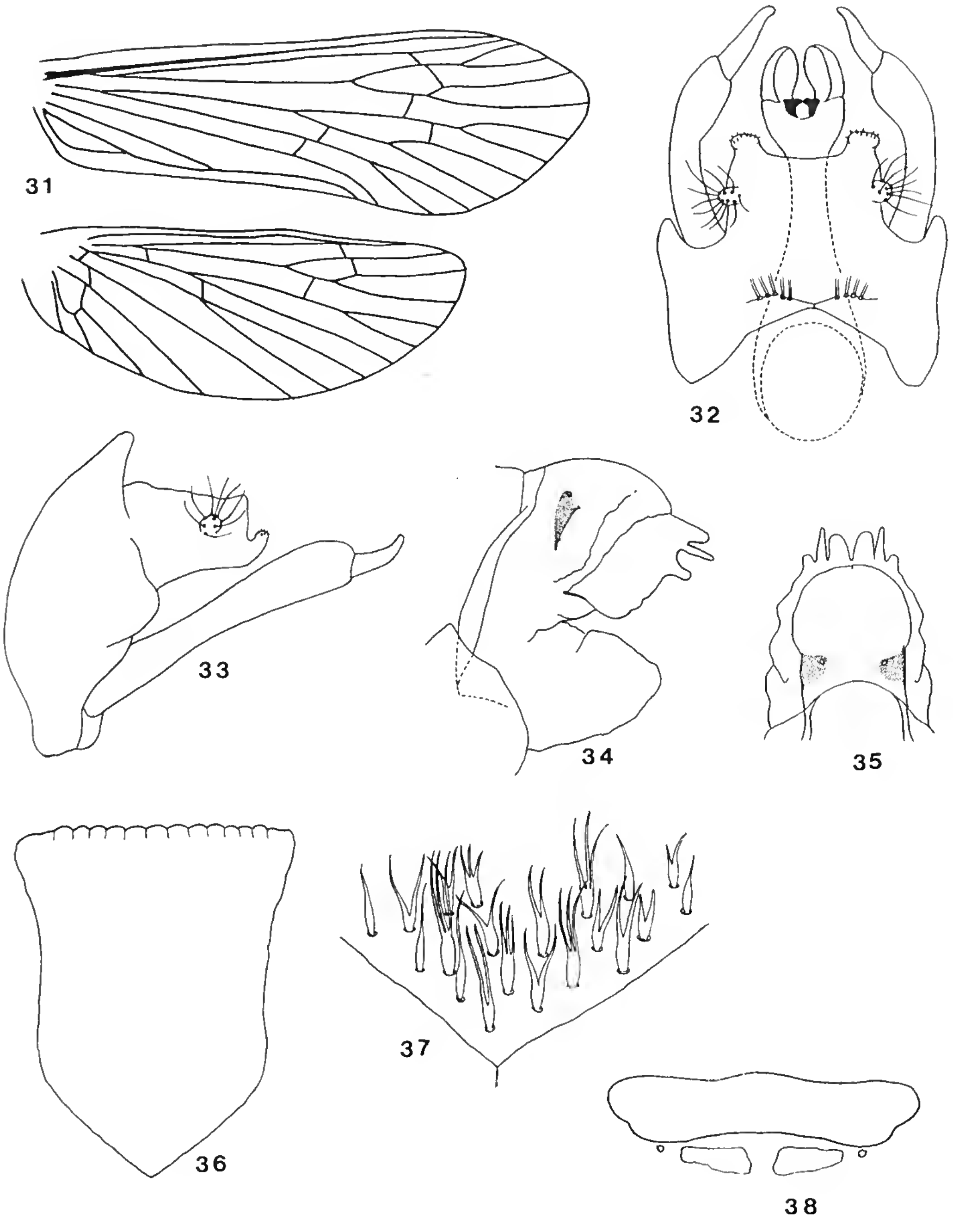
Description. Adult. General colour pale-medium brown. Wings (Fig. 31): forewing pale-medium brown, without irroration; hind wing very pale fawn, almost white. Length of forewing 4.2–5.2 mm (male), 5.0–5.5 mm (female). Vertex of head medium-dark brown; antennae with basal segments yellow, without oblique darker bands. Thorax medium brown. Male genitalia (Figs 32, 33): distal lobes of tergum X broad, somewhat truncate in dorsal view, separated by a distance about 3 times the width of each lobe; in lateral view each lobe upturned. Pre-anal appendages located well anterior of posterior margin of tergum X. Clasper with apical segment about quarter length of basal segment. Female genitalia (Figs 34, 35): clasper receptacle moderately large, subtriangular in lateral view; outer margin oblique, orientated anteroventral to posterodorsal; inner aperture small and dorsal; separation of receptacles in dorsal view about 2 times the width of each receptacle.

Pupa. Abdominal hook plates similar to *C. kakaduensis*.

Mature larva. Dorsum of head pale-medium brown, lateral margins predominantly pale yellow, venter of head pale-medium brown. Frontoclypeus length:width ratio 1.5–1.6, anterior margin coarsely crenulate with about 15 lobes (Fig. 36); secondary setae clear, appressed, inconspicuous under dissecting microscope, those near posterior angle of frontoclypeus predominantly bi- or multifurcate (Fig. 37). Pronotum pale-medium brown; secondary setae clear, appressed and inconspicuous; primary seta 22 near anterolateral margin of pronotum long, tapered, about half length of pronotal sclerite. Posterior prosternites consisting of pair of small lateral sclerites and pair of large mesal sclerites (Fig. 38). Mesonotal and metanotal sclerites densely clothed with appressed fine, forward-directed dark setae, forming short fringe along anterior margin of both segments. Abdominal gills present on segments 1–7.

Etymology. The species is named for Peter Dostine in recognition of his contribution to knowledge of the aquatic insects of northern Australia.

Comments. The larva is very similar to *C. wellsae*. The venter of the head capsule is medium brown in *C. dostinei* as opposed to dark brown, almost black in *C. wellsae*, and the primary seta on the dorsum of the pronotum is longer in *C. dostinei* than in *C. wellsae*, but these



Figures 31–38 *Cheumatopsyche dostinei* sp. nov. Adult: 31, wings; 32, male genitalia, dorsal; 33, male genitalia, lateral; 34, female genitalia, lateral; 35, female genitalia, dorsal. Larva: 36, frontoclypeus; 37, secondary setae near apex of frontoclypeus; 38, prosternites.

characters are not completely reliable. To separate the two species, setae near the posterior angle of the frontoclypeus must be examined under high magnification. *C. dostinei* is widely distributed across northern Australia (Fig.56). The larva has previously been referred to as *Cheumatopsyche* sp. 13 (Wells, 1991) and *Cheumatopsyche* sp. AV13 (Dean, 1999).

Asmicridea capricornica sp. nov.

Figures 39–52

Type material. Holotype: adult male, Graveside Creek, Northern Territory (13°18'S 132°32'E), 18 Jul 1988, P. Dostine (NMV T-17476). Paratypes collected with holotype: 6 males, 6 females (NMV); 6 males, 3 females (ANIC).

Other material examined. **Western Australia.** 1L, King Edward River, Mitchell Plateau, 25 Sep 1995, L.Metzeling; 3P, 14L, Manning Gorge, nr Gibb River Rd, Kimberley, 28 Jul 1994, DC; 2P, 12L, Bell Creek Gorge, Mt Hart Station, Kimberley, 26 Jul 1994, DC; 2L, Trib. Mitchell River, Mitchell Plateau, 19 Feb 1979, JEB. **Northern Territory.** 4M, 41F, 149L, Gulungul Creek, Radon Springs (12°45'S 132°55'E), various dates, PS and AW, JD; 7P, 143L, Magella Creek, u/s Magela Falls (12°47'S 133°06'E), various dates, AW and PS; 5P, 33L, East Alligator River, E of Magela Falls (12°47'S 133°22'E), various dates, PS and AW; 1L, South Alligator River, Gimbat OSS station (13°35'S 132°36'E), 20 Apr 1988, PS and AW; 3P, 64L, Baroalba Creek, Kubarra Pools, 12°49'S 132°52'E, various dates, AW and PS, DC, JD; 1P, 3L, Barramundie Creek, d/s Falls (13°22'S 132°28'E), 26 May 1988, AW and PS; 1L, Liverpool River, Arnhemland (12°21'S 134°07'E), 26 Aug 1999, JD. **Queensland.** 4L, Babinda Creek, The Boulders, 24 Nov 1979, DC; 1L, Little Mulgrave River, 10 km SW of Gordonvale, 16 Nov 1988, K.Walker; 3L, Millstream Creek, 1 Aug 1980, S.Bunn and Gray; 1L, Annan River, 30 km S of Cooktown, 20 Jun 1971, E.F.Riek.

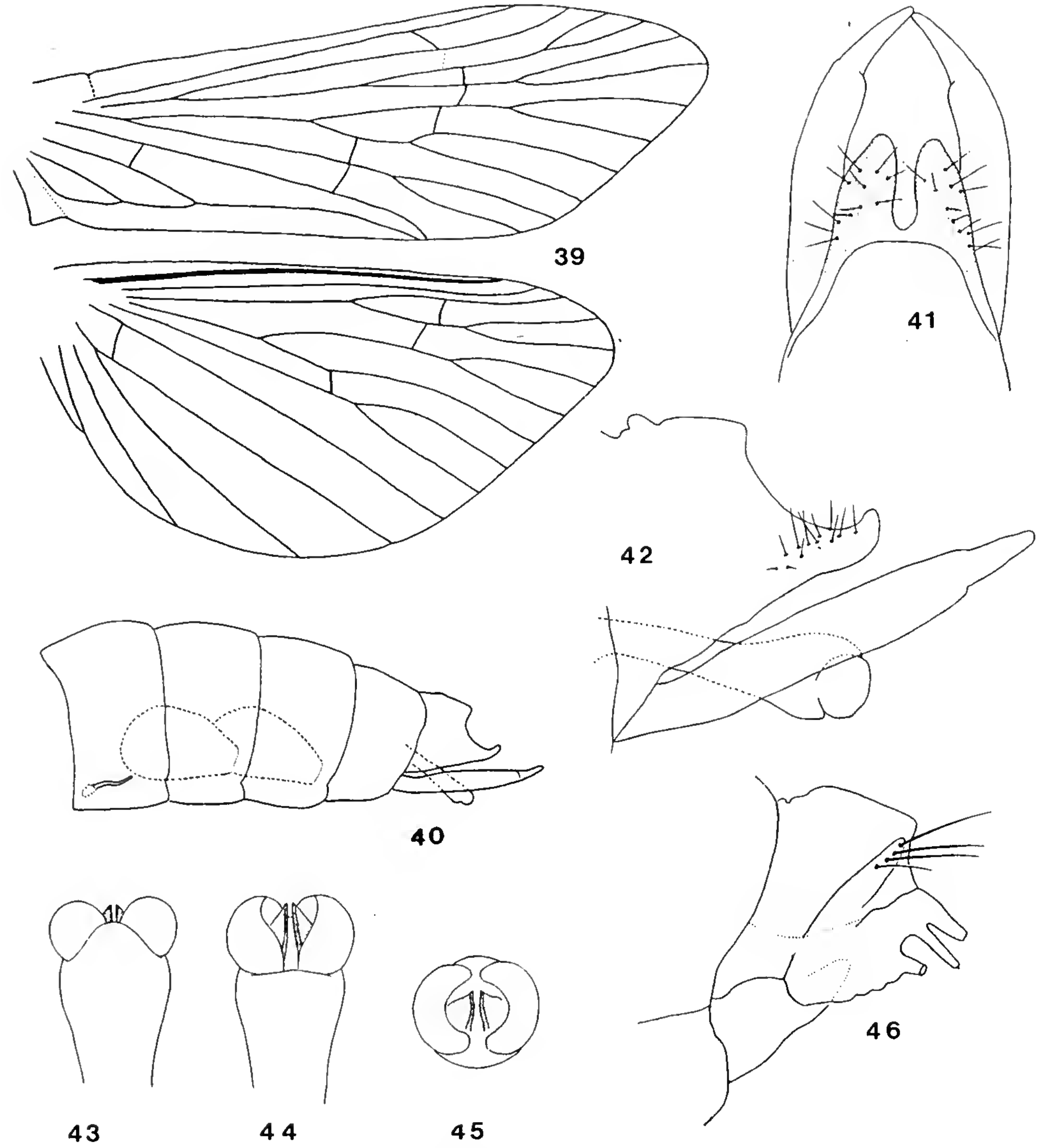
Description. Adult. General colour pale. Wings (Fig. 39): forewing whitish, with golden tinge (female more intense than male), no obvious colour pattern except for small area of medium brown near base of wing around humeral crossvein; hindwing white, almost hyaline. Length of forewing 5.8–6.9 mm (male), 6.1–7.3 mm (female). Vertex of head and thorax pale golden colour; antennae straw coloured. Abdominal sternite 5 with lateral process about half length of segment. Male abdominal segments 6 and 7 with internal membranous sacs (Fig. 40). Male genitalia (Figs 41–45): tergite X elongate, deeply cleft, apices upturned; phallus elongate, terminating in a pair of rounded endothecal processes, and between these a pair of elongate phallotremal sclerites, each sclerite with a strongly acute apex. Female genitalia (Fig. 46): simple, without obvious clasper receptors or pockets.

Pupa. Mandibles slender (Fig. 47); right mandible with 3 subapical teeth, left mandible with 4. Abdominal segment 3 with paired anterior and posterior hook plates, segments 5–7 with anterior hook plates only (Fig. 48), segment 4 without hook plates; some variation in numbers of teeth on all plates. Apical processes of abdomen with long dorsal projection at outer apical angle, inner apical angle with 2 short projections (Fig. 49); numerous long black setae apically and also along outer lateral margin.

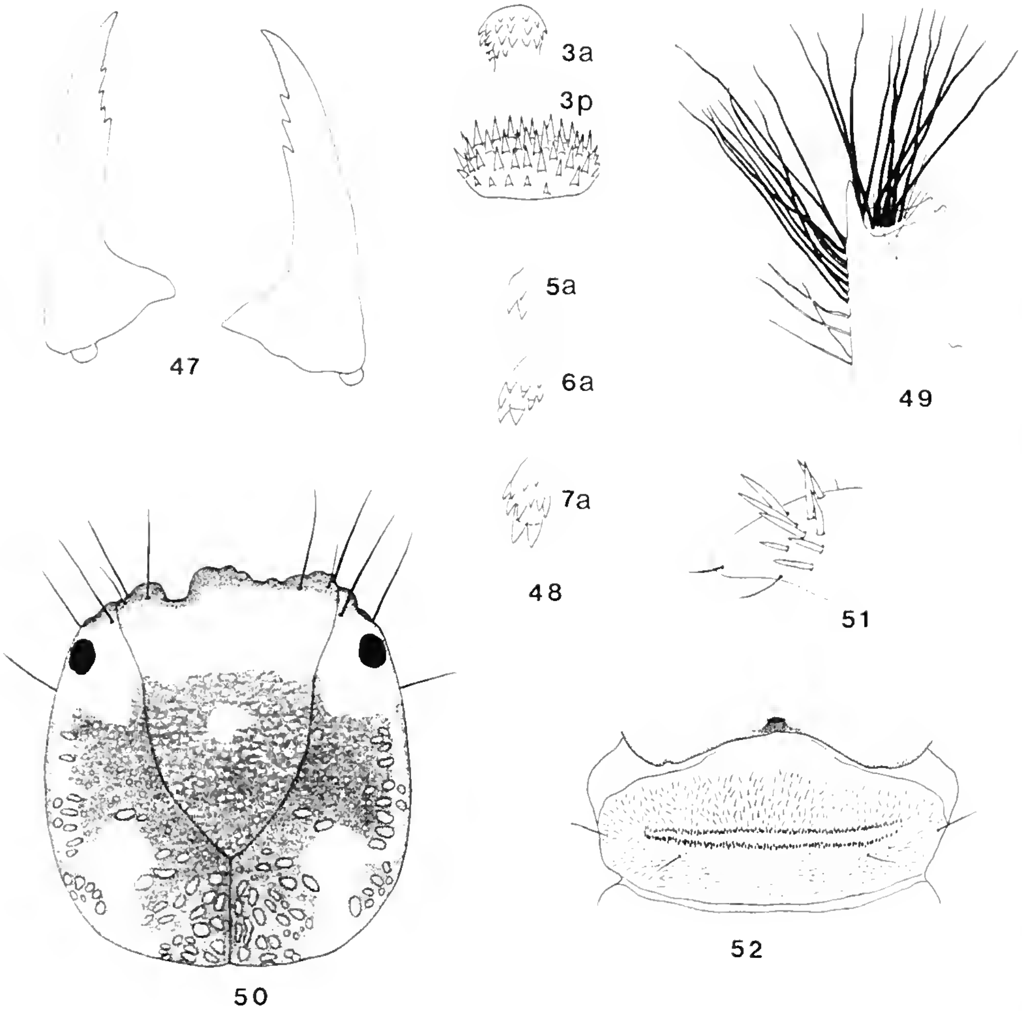
Mature larva. Head with distinctive pattern of yellow and pale brown, dorsal surface covered with numerous small pale dimples, particularly conspicuous on darker pigmented areas (Fig. 50). Head capsule broadest at or a little posterior to midlength; lateral margins rounded; posterior ventral apotome about third length of ecdysial line linking it with anterior ventral apotome. Frontoclypeus length about two-thirds head capsule length; anterior margin with deep notch on left side, mesal lobes projecting well forward of base of notch. Foretrochantin not forked (Fig. 51). Mesosternum and metasternum each with 2 gill tufts. Abdominal segments 1 and 2 with transverse double row of stout appressed setae on dorsal surface (Fig. 52).

Etymology. The name recognises the broad distribution of this species across northern Australia in latitudes north of the Tropic of Capricorn.

Comments. The structure of male genitalia within the Australian genera *Asmicridea* and *Smicrophylax* is conservative and the genitalic structure of *A. capricornica* is similar to species of both genera. *A. capricornica* can be distinguished from the two described species of *Asmicridea* by the possession of paired membranous sacks within abdominal segments 6 and 7. This character state has previously been used to distinguish adult males of *Asmicridea* and *Smicrophylax* (Neboiss, 1977) and separation of adults becomes tenuous. Fortunately, larval characters are of greater diagnostic value and enable separation of the genera and species of *Asmicridea*. *A. capricornica* is widely distributed across northern Australia (Fig. 57), and while there is some overlap the species tends to occur further upstream in river systems than do species of the genus *Cheumatopsyche*. The larva of *A. capricornica* has previously been reported as *Asmicridea* sp. AV 3 (Dean, 1999).



Figures 39–46 *Asmicridea capricornica* sp. nov. Adult: 39, wings; 40, abdominal segments 5–10, lateral; 41, male genitalia, dorsal; 42, male genitalia, lateral; 43–45, apex of phallus, dorsal, ventral and apical; 46, female genitalia, lateral.



Figures 47–52 *Asmicridea capricornica* sp. nov. Pupa: 47, mandibles; 48, abdominal hook plates (3, 5–7: abdominal segment number, a: anterior hook plate, p: posterior hook plate); 49, apical process of abdomen. Larva: 50, head capsule, dorsal; 51, foretrochantin; 52, dorsum of abdominal segment 1.

Keys to species of Hydropsychidae of north-western Australia and the Northern Territory

Adults

1. Abdominal sternite 5 with lateral processes (Fig. 40); posterior wing with Sc and R1 separate right to wing margin (Fig. 39)........*Asmicridea capricornica*
— Abdominal sternite 5 without lateral processes; posterior wing with Sc and R1 fused prior to wing margin (Figs 1, 12, 22, 31) ....*Cheumatopsyche*...2
2. Males 3
— Females 6
3. Colour pale—medium brown; distal lobes of tergum X distinctly upturned in lateral view (Figs 25, 33) 4
— Colour dark brown—black; distal lobes of tergum X rounded in both dorsal and lateral views, not upturned (Figs 3, 14)..........5
4. Distal lobes of tergum X acute in both dorsal and lateral views (Figs 23–25) ....*Cheumatopsyche wellsae*
— Distal lobes of tergum X rounded in both dorsal and lateral views (Figs 32, 33) ....*Cheumatopsyche dostinei*
5. Pre-anal appendages squat, located well anterior of base of distal lobes; dorsum of segment IX broad in lateral view (Figs 2, 3) ....*Cheumatopsyche kakaduensis*
— Pre-anal appendages elongate, located close to base of distal lobes; dorsum of segment IX narrow in lateral view (Figs 13, 14).....*Cheumatopsyche suteri*
6. Clasper receptacle in lateral view small, consisting of very short chimney (Fig. 26); separation of receptacles in dorsal view about 8 times width of each receptacle (Fig. 27) ....*Cheumatopsyche wellsae*
— Clasper receptacle moderate to large (Figs 4, 15, 34); separation of receptacles in dorsal view less than 3 times width of each receptacle (Figs 5, 16, 35)..........7
7. Inner aperture of clasper receptacle aligned with outer aperture (Fig. 4) ....*Cheumatopsyche kakaduensis*
— Inner aperture of clasper receptacle clearly dorsal to outer aperture (Figs 15, 34).......... 8
8. Outer margin of clasper receptacle semicircular; inner aperture large; separation of receptacles in dorsal view less than or equal to width of each receptacle (Figs 15, 16) ....*Cheumatopsyche suteri*
— Outer margin of clasper receptacle oblique, orientated anteroventral to posterodorsal; inner aperture small; separation of receptacles in dorsal view about twice width of each receptacle (Figs 34, 35)..*Cheumatopsyche dostinei*

Mature larvae

1. Foretrochantin simple (Fig. 51); terga of abdominal segments 1 and 2 each with 2 transverse rows of stout appressed setae (Fig. 52).......... ....*Asmicridea capricornica*
— Foretrochantin forked (Fig. 21); terga of abdominal segments 1 and 2 without transverse row of setae..........*Cheumatopsyche*....2
2. Anterior margin of frontoclypeus coarsely crenulate, fewer than 20 lobes (Figs 28, 36).......... 3
— Anterior margin of frontoclypeus finely crenulate, more than 20 lobes (Figs 9, 17) 4
3. Setae near apex of frontoclypeus predominantly simple (Fig. 29).......... .... *Cheumatopsyche wellsae*
— Setae near apex of frontoclypeus predominantly divided (Fig. 37).......... ....*Cheumatopsyche dostinei*
4. Pronotum with primary seta 22 short, less than twice length of adjacent secondary setae (Fig. 10)..........*Cheumatopsyche kakaduensis*
— Pronotum with primary seta 22 long, about half length of pronotum (Fig. 19) ....*Cheumatopsyche suteri*

Acknowledgments

The present study would not have been possible without the extensive collection and rearing of material from Kakadu National Park by Alice Wells and Phil Suter. They are thanked for making the material available. Chris Humphrey, Peter Dostine, John Hawking and ERISS provided support and assistance during my visit to the region. Ken Walker is thanked for providing access to additional material held in Museum Victoria and for preparing the distribution maps.

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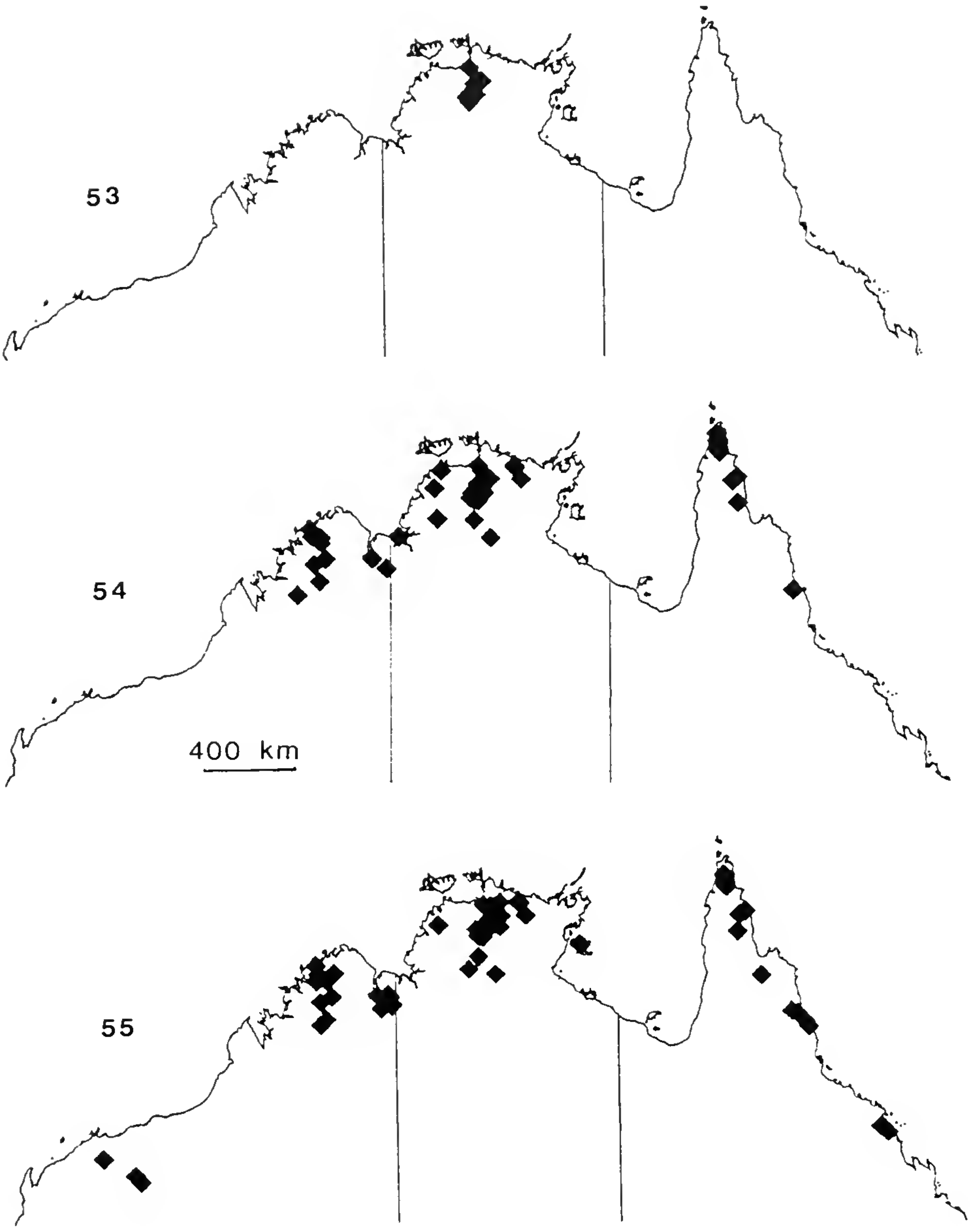
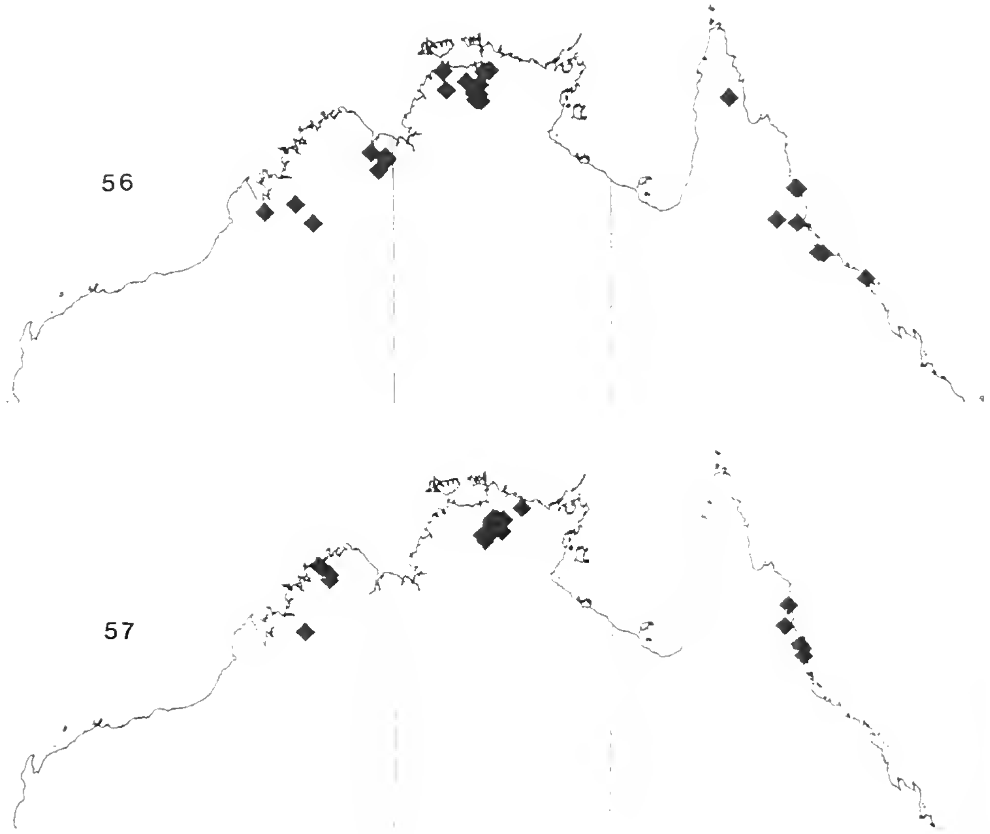


Figures 53–55. Distribution of Hydropsychidae in northern Australia. 53, *Cheumatopsyche kakaduensis* sp. nov.; 54, *Cheumatopsyche suteri* sp. nov.; 55, *Cheumatopsyche wellsae* sp. nov.



Figures 56–57. Distribution of Hydropsychidae in Australia. 56, *Cheumatopsyche dostinei* sp. nov.; 57. *Asmicridea capricornica* sp. nov.

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REDESCRIPTION OF *BUNGONA* HARKER WITH NEW SYNONYMS IN THE AUSTRALIAN BAETIDAE (INSECTA: EPHEMEROPTERA)

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Abstract

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The monospecific genus *Bungona* Harker is redefined and descriptions of the imago and nymphs of *Bungona narilla* Harker are provided. Two species described by Lugo-Ortiz and McCafferty (1998) as *Cloeodes fustipalpus* and *C. illiesi* are recognised as being conspecific and junior synonyms of *Bungona narilla*. *Bungona narilla* is distributed along the east coast of Australia from North Queensland to Tasmania and nymphs occur in shallow, slow flowing, cobble streams.

Introduction

Harker (1957) erected the genus *Bungona* and *Bungona narilla*, type species, on the basis of a nymph and adult from Coal and Candle Creek, Sydney. The adult was distinguished from the genus *Pseudocloeon* by the shape and number of segments of the forceps and the nymphs were distinguished by the shape of the labial palpi and the maxillary palpi being 3-segmented. As the Australian baetid fauna became better known through the Monitoring River Health Initiative it was clear that the original description of the nymph was inadequate to distinguish *Bungona* from other baetid genera. The British Museum of Natural History has no record of type material having been deposited in spite of assertions that types were lodged (J. Harker, pers. comm). Dean and Suter (1996) and Suter (1997) redefined the genus in terms of the nymph, and noted that a number of distinguishing characters were not recorded by Harker (1957).

Direct association of an adult and nymph from the Rose River in Victoria and adults and nymphs from the New England area in New South Wales has enabled verification that the nymphs described by Dean and Suter (1996) and Suter (1997) are conspecific with *Bungona narilla* Harker.

Lugo-Ortiz and McCafferty (1998) recorded the genus *Cloeodes* Traver, 1938 from Australia. They described two new species *C. fustipalpus* and *C. illiesi*, without citing any Australian papers. The two species clearly belong in *Bungona* as redefined by Dean and Suter (1996) and subsequently verified. *Bungona* has numerous nymphal and imaginal characteristics which distinguish it from *Cloeodes* as defined by Traver (1938) and redefined by Waltz and McCafferty (1987a, b). Character states of *C. fustipalpus* and *C. illiesi* are within the variation of *Bungona narilla* and both are treated as junior synonyms of *Bungona narilla*.

Nymphs were collected using a hand-held 250 µm mesh, dip net held downstream of disturbed substrate, or by hand picking of nymphs clinging to the under-surface of rocks. Mature nymphs were kept in 1L plastic rearing containers which had mesh lids and which contained river water and a cobble. These were maintained in the stream or in the laboratory until the subimago emerged. The subimago was then removed and placed in a dry rearing container to complete the final moult. All specimens were preserved in 75% ethanol.

Nymphs were dissected and mounted on slides in polyvinyl lacto-phenol mounting medium. Illustrations were prepared with the aid of a camera lucida. Mouthparts were viewed ventrally (except labrum) and the labium is illustrated with the ventral surface shown on the right hand side of the illustration and the dorsal surface on the left. Comparative measurements of segments of labial palpi, maxillary palpi and legs are expressed as ratios compared with the proximal segment length, which is given in parentheses. Ranges of segment lengths are also presented in parentheses. At least 20 specimens were used for nymphal morphometric parameters. All measurements are given in millimetres.

The specimens examined were collected by numerous people identified by initials, as follows; AB (Andrew Boulton), BC (Bruce Chessman) DNR (Department of Natural Resources, Queensland), DO (David Oldmeadows), JD (John Dean), MN (Mark Nelson), MP (Melanie Pearson), PM (Phil Mitchell), PS (Phil Suter), SB (Stuart Bunn) and TC (Tim Curmi).

The neotype is placed in the Australian National Insect Collection (ANIC), CSIRO, Canberra, and all other material is held in the senior author's collection.

Bungona Harker

Bungona Harker, 1957: 73.—Campbell, 1988: 9.—Dean and Suter, 1996: 22.— Suter, 1997: 2.

Cloeodes.—Lugo-Ortiz and McCafferty 1998: 122–128. (not *Cloeodes* Traver, 1938).

Type species. Bungona narilla Harker, 1957 (original designation).

Diagnosis. Male Imago (Figs 1–5). Forewings with paired marginal intercalaries from radial to cubital sectors (Fig. 3); pterostigmatal veinlets entire; base of vein MA2 attached to crossvein between MA1 and MP1. Hind wings absent. Tarsal claws dissimilar. Posterior margin of metanotum not deeply emarginate (Fig. 1); metascutellar hump lacking a dorsoposterior projection (Fig. 2). Forceps 4-segmented, segment 3 elongate, segment 4 longer than wide; segment 1 lacking long basal bristles; segment 2 with very short bristles (Figs 4 and 5).

Mature Nymph (Figs 6–22): Head hypognathous. Labrum slightly broader than long, with a shallow median notch (Fig. 13). Left mandible with incisors apically separate, prostheca robust and digitate, margin between incisors and molars lacking tuft of setae, thumb of molar area triangulate and elevated above plane of incisor base (Figs 16 and 17). Right mandible with incisors separate apically, prostheca bifid, margin between incisors and molars with tuft of setae present (Figs 14 and 15). Maxillae palpi with 3 segments, palpi subequal to length of galeolacinia, galeolacinia with 4–5 apical teeth (Figs 18–20). Labium with 3-segmented palpi, terminal segment short, bulbous, medially broader than basal width, segment 2 without inner apical lobe; glossae and paraglossae equal in length (Fig. 22).

Thorax lacking hindwing pads. Femora lack a femoral patch or villopore, with long robust blunt setae on dorsal margin, apically with a pair of contiguous setae (Fig. 6). Tibiae with subproximal arc of long fine setae, with a longitudinal row of long fine setae on dorsal margin, adjoining proximal arc (Fig. 6). Tarsi with a longitudinal row of long fine setae on dorsal margin (Fig. 6). Tarsal claw short, edentate (Fig. 7).

Abdominal terga with triangular, serrated, scales which lack fine setae (Fig. 10), posterior margins with triangular teeth (Fig. 11). Abdominal sternites with scales and a row of short, fine setae on segments 4–6; posterior margins with long triangular teeth. Abdominal colour pattern with tergites 9 and 10 dark. Gills asymmetrical, ovate to pointed apically, with serrated and ciliated inner margins (Figs 8 and 9). 3 caudal filaments; terminal filament shorter than cerci, fringed with setae on lateral margins; cerci fringed on inner margin.

Remarks. While both adults and nymphs of the type species were described, Harker (1957) did not record the edentate claws, tarsal and tibial setal fringes, sternal setae and other nymphal characters which distinguish this genus from other Australian baetids. The problem posed by the absence of type material of the type species has been overcome by successful rearing of adult material. Comparison of adults with Harker's descriptions has confirmed the identity of *Bungona narilla*.

Waltz and McCafferty (1987a, b) revised *Cloeodes* and closely related genera (Waltz and McCafferty, 1987b). Lugo-Ortiz and McCafferty (1998: 122) commented that *Cloeodes* had "edentate tarsal claws, a conspicuous arc of long, fine, simple setae on the tibiae and setal tufts on sterna 2–6." They considered the two species they described from Australia to belong in *Cloeodes*. However, the Australian species possesses a row of setae only on sterna 4–6, and can be clearly distinguished from *Cloeodes* and other closely related genera by the following combination of adult and nymphal characters:

Male imago with pterostigmatic veinlets entire, base of vein MA_2 attached to crossvein between MA_1 and MP_1. Hind wings absent. Tarsal claws dissimilar. Posterior margin of metanotum not deeply emarginate, metascutellar hump lacking a dorsoposterior projection. Forceps four-segmented, segment 3 elongate, segment 4 longer than wide, segment 1 lacking long basal bristles, segment 2 with very short bristles. Mature nymph with incisors of left mandible apically separate.

Right mandible with incisors apically separated, prostheca bifid, margin between incisors and molars with tuft of setae present. Labial palpi with terminal segment short, bulbous, medially broader than basal width, segment 2 without inner apical lobe. Maxillae with 3 segmented palpi which is subequal to length of galeolacinia. Legs with tibiae possessing proximal arc of long fine setae adjoined to longitudinal row of long fine setae and tarsi with a row of long fine setae. Scales on abdominal tergites and sternites lacking fine setae, row of fine setae on sternites 4–6. Gills with serrated and ciliated margins.

Bungona and *Cloeodes* are closely related genera, but there are at least three adult and nine nymphal characters which clearly distinguish the Australian material from the revised characterisation of *Cloeodes* given by Waltz and McCafferty (1987a, b). Lugo-Ortiz and McCafferty (1998) did not mention the distinctive characters of the Australian material which here have been used to support the maintenance of *Bungona*. The "*Cloeodes* group" is widely distributed in South America (Waltz and McCafferty (1987a, b), Africa (Waltz and McCafferty , 1994), Madagascar (Lugo-Ortiz and McCafferty, 1999), Sri Lanka, China (Waltz and McCafferty, 1987a, b) and Australia (Lugo-Ortiz and McCafferty, 1998; this paper) and all share a number of characteristics but re-examination of this material is now warranted to establish the phylogenetic relationships.

Bungona narilla Harker

Bungona narilla Harker, 1957: 73, figs 48–57.
Cloeodes fustipalpus Lugo-Ortiz and McCafferty, 1998: 123–124, figs 1–9. (syn. nov.)
Cloeodes illiesi Lugo-Ortiz and McCafferty, 1998: 124–127, figs 10–18. (syn. nov.)

Material examined. Neotype herein selected. Adult male from Gara R. at Thalgarrah Field Study Centre, NSW, 30°26'S 151°29'E, 25 Nov 1998, PS and JD, ANIC.

Adults. **Vic.** 1 male reared from Rose R. RWC Gauge Station, 35°52'S 146°03'E, 18 Jan 1997, PS and MP; 1 male, same locality, 4 Feb 1997, PS and MP. **NSW.** 1 male reared from Gara R. at Thalgarrah Field Study Centre, 30°26'S 151°29'E, 25 Nov 1998, PS and JD; 10 males, Commissioners Waters on Andersons Rd E of Armidale, 30°34'S 151°47'E, 24 Nov 1998, PS and JD; 4 males Gara R. E of Armidale on Armidale to Coffs Harbour Rd, 30°32'S 151°48'E, 24 Nov 1998, PS and JD.

Nymphs. **Qld.** 4 nymphs, Booloumba Ck, Conondale Ranges, 26°42'S 152°38'E, 4 May 1993, SB; 2 nymphs, Sunday Ck site 5, 17°55'S 145°09'E, 30 May 1992, SB; 2 nymphs, Bundaroo Ck, Conondale Ranges, 26°42'S 152°37'E, 20 May 1993, SB; 3 nymphs, Koolmoon Ck near Tully, 17°45'S 145°38'E, 31 Jul 1990, 29 Nov 1990, SB; 6 nymphs, Stony Ck, Conondale Ranges, 26°50'S 152°46'E, 15 Mar 1993, 15 Nov 1993, SB; 6 nymphs, un-named Ck, Upper Conondale Ranges, 26°52'S 152°44'E, 20 May 1993, SB; 5 nymphs, Mt Barney Ck at Mt Maroon, 28°14'S 152°44'E, 2 Nov 1998, DNR; 1 nymph, Little Yabba Ck at Sunday Ck Rd, 26°36'S 152°37'E, 18 May 1999, DNR. **NSW.** 1 nymph, Kangaroo R., Upper Kangaroo Valley, 34°42'S 150°35'E, 23 Sep 1972, JD; 1 nymph, Wollondilly R. at Murphys Crossing, 33°43'S 150°30'E, 16 Nov 1990, BC; 4 nymphs, Bellinger R. at Cool Ck, 30°27'S 152°37E, 23 Sep 1994, AB; 1 nymph, Imlay Ck/Wallaugh R. junction, 37°14'S 149°42'E, 27 Oct 1995, AB; 2 nymphs, Collombatta Ck (MACL02), 30°54'S 152°44'E, 18 Sep 1994, AB; 3 nymphs, Chandler R. at Carten, 30°44'S 152°02'E, 5 Nov 1995, AB. 6 nymphs, Goorudee Rivulet, North of Adaminaby, 35°59'E 148°46'E, 11 Mar 2000, PS and TC; 1 nymph, Commissioners Waters on Andersons Rd E of Armidale, 30°34'S 151°47'E, 24 Nov 1998, PS and JD; 2 nymphs, Gara R., E of Armidale on Armidale to Coffs Harbour Rd, 30°32'S 151°48'E, 24 Nov 1998, PS and JD; 10 nymphs, Woolomombi R. near Kilcoy Cemetery, 30°26'S 151°49'E, 25 Nov 1998, PS and JD; 10 nymphs, Gara R. at Thalgarrah Field Study Centre, 30°26'S 151°29'E, 25 Nov 1998, PS and JD; 24 nymphs, Tilbuster Ck (Commissioners Waters), 30°29'S 151°42'E, 25 Nov 1998, PS and JD; 5 nymphs, Dumaresq Ck on Weir Rd u/s Armidale, 30°29'S 151°37'E, 25 Nov 1998, PS and JD; 28 nymphs, Gara R. on Guyra-Dorrigo Rd., 30°12'S 151°4'E, 25 Nov 1998, PS and JD; 9 nymphs, Marowan Ck near Glencoe, 29°56'S 151°43'E, 26 Nov 1998, PS and JD; 5 nymphs, Maybole Ck, SW of Glen Innes, 29°53'S 151°38'E, 26 Nov 1998, PS and JD; 3 nymphs, Chandler R. on Lynock Rd, 30°18'S 152°05'E, 26 Nov 1998, PS and JD; 7 nymphs, Guy Fawkes R. at Ebor, 30°24'S 152°20'E, 27 Nov 1998, PS and JD; 1 nymph, Bellinger R., 23.7 km u/s of Thora, 30°28'S 152°35'E, 29 Nov 1998, PS and JD; 4 nymphs, Mongarlowe R. 1.8 km d/s Monga Settlement, 35°33'S 149°55'E, 1 Dec 1998, PS and JD; 1 nymph, Trib. Mongarlowe R. at Monga turnoff to Monga, 35°32'S 149°56'E, 1 Dec 1998, PS and JD; 12 nymphs, Mongarlowe R, 100 m W of turnoff to Monga, 35°32'S 149°56'E, 1 Dec 1998, PS and JD; 3 nymphs, Shoalhaven R. at Bombay Bridge, 7.7 km W of Braidwood, 35°26'S 149°43'E, 1 Dec 1998, PS and JD. **Vic.** 2 nymphs, King R. upstream of Lake William Hovell, 36o56'S 146o27'E, 7 Jun 1990, 12 Nov 1991, PM; 10 nymphs, Rose R. at "Bennies", 36°58'S 146°31'E, 6 Dec 1996, 14 Jan 1997, PS and MP; 8 nymphs, Rose R. RWC Gauge Station, 35°52'S 146°03'E, 18 Jan 1997, PS and MP. **Tas.** 1 nymph, Wilmot R. on Spellmans Rd, 41°31'S 146°10'E, 13 Oct 1994, DO and MN; 3 nymphs, Rubicon R., Smiths Rd, 41°19'S 146°34'E, 6 Oct 1994, DO and MN.

Description. Male Imago. Body length: 4.6 mm. Cerci length: 8.4 mm. Forewing length: 4.2 mm. General colour brown with cream abdominal markings, abdominal segments 1–2 with central cream marking, 3 dark brown, 4 cream, 5–6 dark brown, 7–10 light brown. Head: turbinate eyes on high stalks, separate, reddish-brown dorsally (Fig. 1). Thorax brown; posterior margin of metathorax with shallow emargination (Fig. 1), meta-scutellar hump lacking a posterior projection (Fig. 2); legs cream, ratio of fore leg segments 1.00: 1.05: 0.01: 0.58: 0.34: 0.20: 0.13 (1.0 mm); middle and hind leg measurements similar, ratio of segment lengths 1.00: 0.74: 0.09: 0.18: 0.10: 0.08: 0.15 (0.72 mm). Wings hyaline (Fig. 3), pterostigma with 4–5 cross veins, intercalaries paired from R_2 - Cu vein, MA2 extending to and beyond MA_1-MP_1 crossvein. Forceps long, 4-segmented; segment 1 and 2 subequal, third segment elongate 1.3 times as long as segment 2, with slight constriction in basal half; segment 4 longer than wide, approx half segment 3 length (Fig. 4); segment 1 lacking tufts of basal bristles, segment 2 with few short basal bristles (Fig. 5).

Female Imago. Body length: 4.5 mm. Cerci length: 6.7 mm. Forewing length: 4.7 mm. General colour brown with cream central markings on abdominal segments. Head: eyes not turbinate, smaller, placed laterally. Legs all similar in length. Wings hyaline, similar to male.

Mature nymph. (all measurements based on 21 mature specimens). Body length: 3.9 mm (3.0–6.2 mm). Cerci length: 1.7 mm (1.1–2.1 mm). Terminal filament: 1.5 mm (1.0–1.9 mm). Antennal length: 0.9 mm (0.8–1.1 mm). Females generally larger than males. The description given by Lugo-Ortiz and McCafferty (1998) for the nymph is adequate and generally well illustrated. Additions only are given below.

Thorax: Fore legs (Fig. 6) with upper margins of femora with 4–9 blunt simple setae, apically with a pair of contiguous setae, lower margin with numerous short, fringed setae; fore tibiae with proximal arc of long fine setae and a longitudinal row of long fine setae, inner margin with 2–14 short fine setae, apically with pair of short fringed setae; tarsi with longitudinal row of long fine setae, inner margin with 4–10 short fringed setae with 2 apical setae; tarsal claw short lacking teeth (Fig. 7). Middle and hind legs similar, with outer margins of femora lined with 5–10 blunt setae, apically with pair of contiguous setae; tibiae with proximal arc of long fine setae and longitudinal row of long fine setae, inner margin with 4–10 short fine setae, apically with pair of short fringed setae; tarsi with longitudinal row of long fine setae, inner margin with 5–10 short fringed setae with 2 apical setae; tarsal claw short lacking teeth.

Ratios of leg segments: fore leg, 1.00: 0.62: 0.67 (0.72 mm); middle leg, 1.00: 0.60: 0.55 (0.72 mm): hind leg, 1.00: 0.56: 0.48 (0.75 mm).

Femur length to width ratios: fore leg, 4.83 (3.55–6.62); middle leg, 4.92 (3.79–5.92); hind leg, 4.62 (3.65–6.54).

Abdominal segments 1–7 with plate-like gills with serrated and ciliated inner margins (Figs 8b, 9b), first, fifth-seventh gills narrow apically pointed (Fig. 8a), second-fourth gills ovate (Fig. 9a), rounded apically (shape of gills variable within populations from narrow-pointed to broadly ovate). Abdominal colour pattern variable but with nineth and tenth segments brown. Scales on tergites and sternites triangular and serrated (Fig. 10), posterior margins of tergites with triangular spines (Fig. 11). Paraprocts with 10–18 well developed sharp marginal spines (Fig. 12), number varies with instar.

Mouthparts. Labrum (Fig. 13) almost square length 0.8 width, anterior margin with a medial concavity, anterior margin fringed with short bifid setae, submarginal row of spine setae. Right mandible (Fig. 14) outer incisor with 3–4 teeth and small subapical tooth, inner incisor with 3 teeth, prostheca bifid (Fig. 15) with lateral section strongly serrated (damaged in specimen described and illustrated as Fig. 3 by Lugo-Ortiz and McCafferty, 1998), margin between incisors and molars smooth or serrated with tuft of setae near molars. Left mandible (Fig. 16) outer incisor with 2–4 teeth, inner incisor with 3 large teeth, prostheca robust (Fig. 17), margin between incisors and molars smooth or serrated, lacking tuft of setae. Maxilla rectangular (Fig. 18) with 4 apical teeth (Fig. 19), maxillary palpi 3-segmented, palpi length subequal to galeolacinia (Fig. 20), apical segment longer than basal segment; segment ratios 1.00: 0.66 : 1.14 (0.07 mm, 0.04–0.09 mm). Hypopharynx as in Fig. 21. Labium (Fig. 22) with glossae and paraglossae long, narrow and pointed, labial palpi with 3 segments, apical segment ovoid, basal segment 1.73 times as long as broad, ratio of segments 1.00 : 0.87: 0.56 (0.15 mm, 0.12–0.18 mm).

*Remarks.*No new material has been found from the type locality but nymphs consistent with Harker's description have been recorded from streams of the Great Dividing Range in Queensland, New South Wales, Victoria and one specimen from Tasmania. Adults reared from the Rose R. in Victoria confirmed its identity. Lugo-Ortiz and McCafferty (1998) described *Cloeodes fustipalpus* from nymphs collected from the Chandler and Bellinger Rivers near Armidale in New South

Wales. This species cannot be differentiated from *B. narilla*, and is here synonymised.

Lugo-Ortiz and McCafferty (1998) differentiated a second species (*Cloeodes illiesi*) from a single nymph from Cascade Falls near Cairns on the basis of abdominal colour pattern, bifid right prostheca and a reduced maxillary palp. They stated that the colour pattern of *C. fustipalpus* "... varies somewhat among specimens ..." . The pattern illustrated for *C. illiesi* is within the range of variation of *B. narilla*. The bifid prostheca is also consistent with *B. narilla*. The specimen they illustrated and described as *C. fustipalpus* had a broken prostheca (subsequently confirmed by McCafferty, pers. comm.). The maxillary palpi in *C.illiesi* may also be an aberration, as at least one specimen examined in this study had a short, 2-segmented maxillary palp on one side of the body, and a long, 3-segmented palp on the other. Such an aberration has also been observed in specimens of *Cloeon* in northern Australia. Although not specifically mentioned as distinguishing features in their paper, Lugo-Ortiz and McCafferty (1998) noted that the margin between the incisors and molars of the right mandible of *C. illiesi* differed from *C. fustipalpus* in that it was smooth, not serrated, the gills were narrow and less tracheated and the paraprocts had few scale bases. In the extensive material available for this study this combination of characters was not consistent even within a single population. For example, specimens with a smooth mandibular margin had broad, strongly tracheated gills and numerous paraproct scale bases, and specimens with narrow, poorly tracheated gills had numerous paraproct scales and serrated madibular margins. Early instar nymphs of the *fustipalpus* type had more pointed gills than older nymphs in the same population suggesting this character may be influenced by age and environment. *Cloeodes illiesi* is considered a junior synonym of *B. narilla*.

Distribution and ecology. North Queensland to Tasmania. Nymphs have been collected from streams of low gradient and low turbidity, mainly in foothill and lowland reaches. Large numbers have been recorded from shallow water (less than 20 cm) at the edge of cobble streams where velocities were very low. In the Conondale Ranges, southern Queensland, specimens were collected from bedrock in shallow, still, edge habitat. They were observed on the upper surface of the rock during the day and when disturbed only swam a few centimetres and then settled. Adults were not collected with UV light traps, and few were collected by sweep netting the riparian vegetation. A single specimen was collected from a swarm of baetid males at a height of 8–10m above the Rose River.

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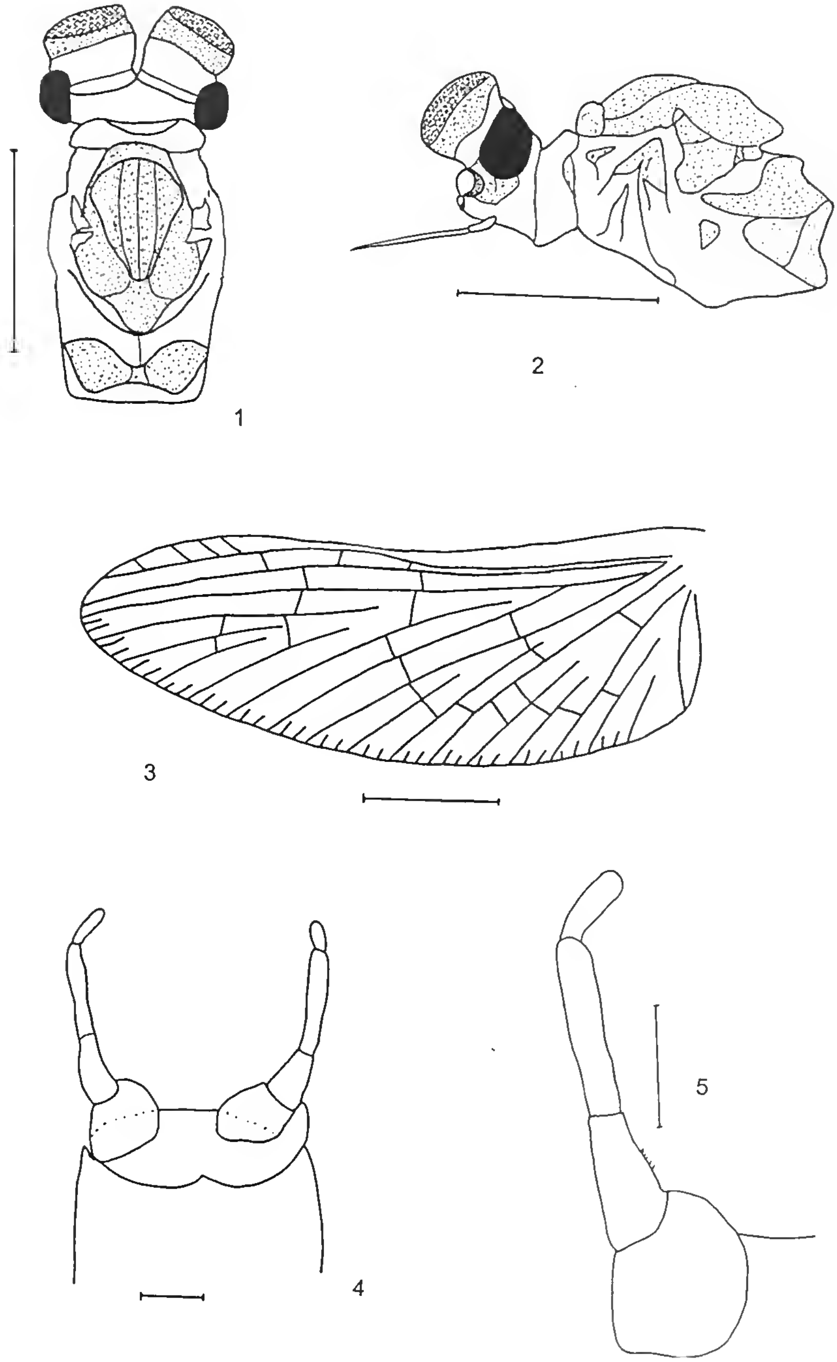
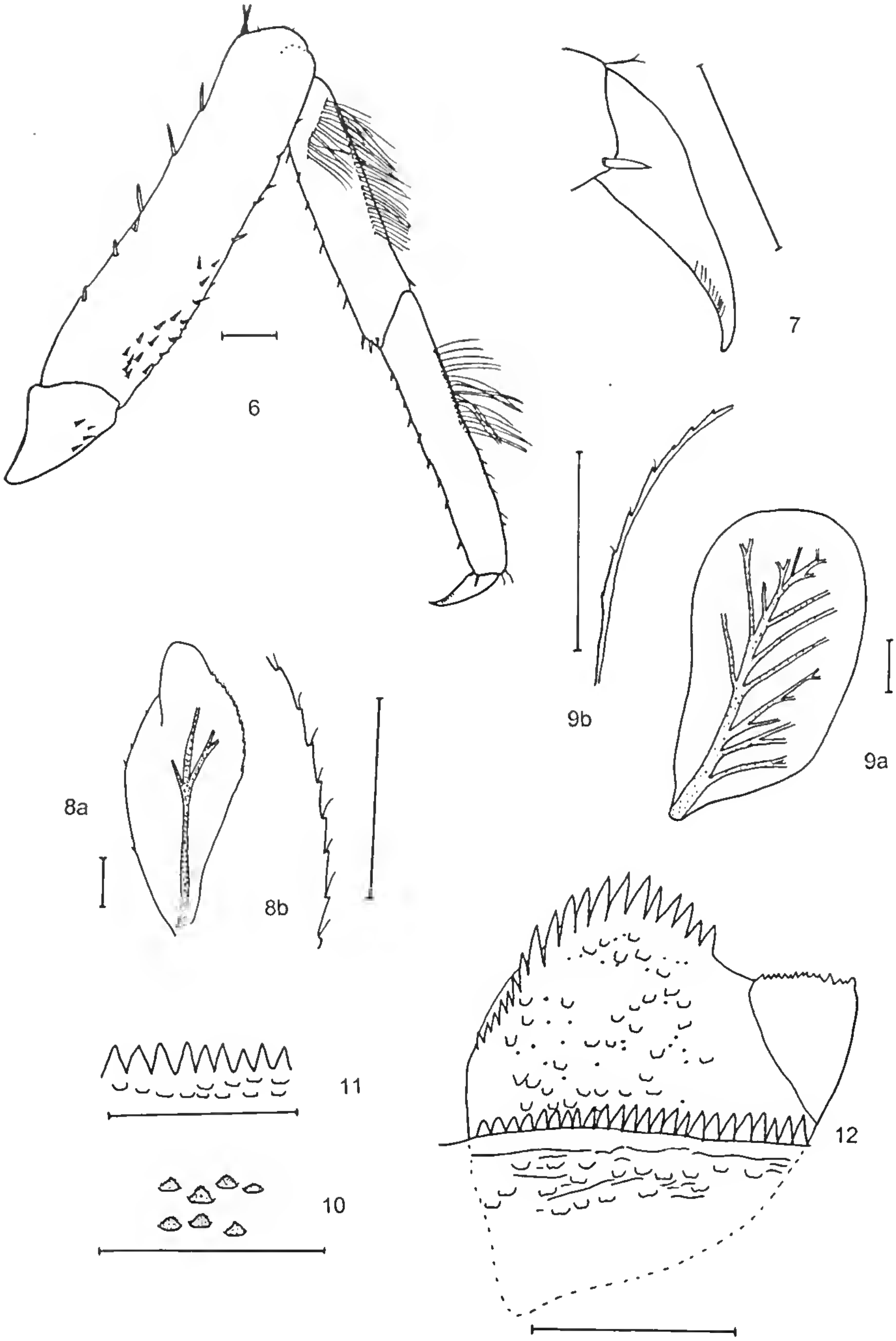
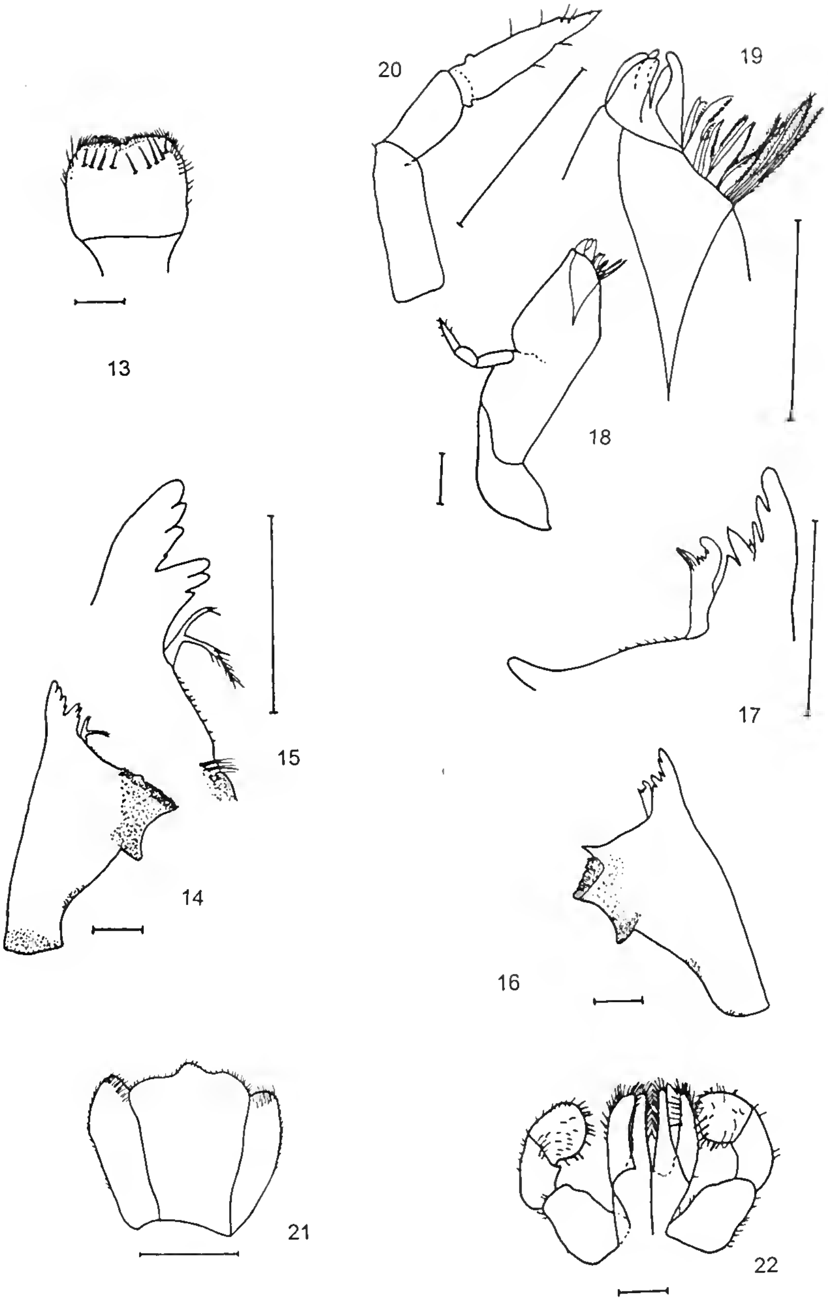


Figures 1–5. *Bungona narilla*, male imago. 1, dorsal view of head and thorax; 2, lateral view of head and thorax; 3, forewing; 4, ventral view of male forceps; 5, enlarged view of right forcep. Scale lines: 1 mm (Figs 1–3); 0.1 mm (Figs 4–5).



Figures 6–12. *Bungona narilla*, nymph. 6, foreleg; 7, tarsal claw; 8, sixth abdominal gill, (8a, whole gill; 8b, lateral margin of gill); 9, third abdominal gill, (9a, whole gill; 9b, lateral margin of gill); 10, scales on tergites; 11, posterior margin of fourth abdominal tergite; 12, paraproct. Scale lines: 0.1 mm.



Figures 13–22. *Bungona narilla*, nymph. 13, labrum; 14, right mandible; 15, incisors and prostheca of right mandible; 16, left mandible; 17, incisors and prostheca of left mandible; 18, maxilla; 19, apex of maxilla; 20, maxillary palp; 21, hypopharynx; 22, labium, dorsal (left) and ventral (right) aspects. Scale lines: 0.1 mm.

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DESCRIPTIONS OF NEW SPECIES OF *BIRUBIUS* (AMPHIPODA: PHOXOCEPHALIDAE) FROM AUSTRALIA AND PAPUA NEW GUINEA WITH COMMENTS ON THE *BIRUBIUS-KULGAPHOXUS-TICKALERUS-YAN* COMPLEX

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Abstract

Taylor, J. and Poore, G.C.B., 2001. Descriptions of new species of *Birubius* (Amphipoda: Phoxocephalidae) from Australia and Papua New Guinea with comments on the *Birubius-Kulgaphoxus-Tickalerus-Yan* complex. *Memoirs of Museum Victoria* 58(2): 255–295.

Five new species of *Birubius* Barnard and Drummond, 1976 (Crustacea: Amphipoda: Phoxocephalidae) are reported: *B. drummondae* sp. nov and *B. heislersi* sp. nov from Victoria, Australia; *B. wallisae* sp. nov. from Queensland, Australia; and *B. lowryi* sp. nov., and *B. wilsoni* sp. nov. from Papua New Guinea. The present records extend the range of the genus previously reported from Australia and Indonesia. The genus *Birubius* is discussed and compared with the Australian genera *Tickalerus* Barnard and Drummond, 1978 (monotypic), *Kulgaphoxus* Barnard and Drummond, 1978 (two species) and *Yan* Barnard and Drummond, 1978 (two species) in light of the new species exhibiting a combination of characters from all genera. Their synonymy is foreshadowed.

Introduction

Barnard and Drummond (1978) discussed the relationships between all Australian species of the Phoxocephalidae. The subfamily Birubiinae was established to include the Australian type genus *Birubius* Barnard and Drummond, 1976, Australian genera *Tickalerus* Barnard and Drummond, 1978, *Kulgaphoxus* Barnard and Drummond, 1978 and *Yan* Barnard and Drummond, 1978 and the North and South American genera *Microphoxus* J.L. Barnard, 1960 and *Metharpinia* Schellenberg, 1931. Barnard and Karaman (1991) expanded the subfamily to include the North and South American genera *Foxiphalus* J.L. Barnard, 1979 and *Grandiphoxus* J.L. Barnard, 1979. The genus *Linca* Alonso de Pina, 1993 was erected based on a single specimen from the Argentine continental shelf and although showing some convergence with the Brolginae, its similarity to *Birubius* best placed it in the Birubiinae. *Linca* differs from *Birubius* by the presence of ventral setae on uropod 1 peduncle, an autapomorphy of this monotypic genus. Jarrett and Bousfield (1994) reassessed the North and South American genera and removed them from the Birubiinae. They erected the new subfamily Metharpiniinae to include *Beringiaphoxus* Jarrett and Bousfield, 1994, *Foxiphalus* J.L. Barnard, 1979, *Grandiphoxus* J.L. Barnard, 1979, *Majoxiphalus* Jarrett and Bousfield, 1994, *Metharpinia* Schellenberg, 1931, *Microphoxus* J.L. Barnard, 1960 and *Rhepoxynius* J.L. Barnard, 1979. The genus *Linca* was not included in the new subfamily and so remains a member of the Birubiinae.

Our preliminary cladistic analysis (work in progress) of most species of Birubiinae, Brolginae, Leongathinae, Metharpiniinae, Parharpiniinae and Tipimeginae has failed to support the monophyly of any of the subfamilies or genera. We are unable to identify a synapomorphy for the subfamily Birubiinae, even in the restricted sense, nor for its type genus *Birubius*. The Birubiinae shares a broad form of the basis of pereopod 5 with all subfamilies except Harpiniinae which exhibit a narrow basis unique to that subfamily. It shares a biarticulate palp of maxilla 1 with all subfamilies except Phoxocephalinae and those members of the Harpiniinae that exhibit a uniarticulate palp. It differs from Brolginae, Harpiniinae, Phoxocephalinae and Pontharpiniinae by the medium to elongate (rather than short) length of peduncular article 2 of antenna 1, a state that it also shares with Tipimeginae, Parharpiniinae and some members of the Joubinellinae.

Examination of unidentified phoxocephalid amphipods from the Australian Museum, Museum Victoria and Queensland Museum collections revealed five new species belonging to the nominal subfamily Birubiinae. The generic placement of some of the species was uncertain using Barnard and Karaman's (1991) generic diagnoses. Although closely fitting the description for *Birubius* four species exhibited a large dorsal hook on urosomite 3, a character restricted within the Birubiinae to members of *Tickalerus* and *Kulgaphoxus*.

Barnard and Drummond (1978) defined *Kulgaphoxus*, *Tickalerus* and *Yan* only on the basis of differences from *Birubius*, the largest genus. *Tickalerus* differs from *Birubius* in the presence of a dorsal hook on urosomite 3, shortened outer ramus of uropod 3 and rectangular coxa 4. *Kulgaphoxus* differs from *Birubius* in the presence of a dorsal hook on urosomite 3, shortened outer ramus of uropod 3, proximal placement of setae on peduncular article 2 of antenna 1 and the vestigial dactyl of pereopod 7. *Yan* differs from *Birubius* in the proximal placement of setae on peduncular article 2 of antenna 1 and the vestigial dactyl of pereopod 7. The new species share some but not all of the diagnostic features of *Kulgaphoxus*, *Tickalerus* and *Yan* and could not be placed in any of the genera as presently diagnosed.

The discovery of four species exhibiting a dorsal hook on urosomite 3 is significant. Previously it was a trait observed in only five phoxocephalid species belonging to *Kulgaphoxus*, *Microphoxus* and *Tickalerus* and was partly used to split these species from *Birubius*. The trait was formerly believed to be sexually dimorphic and restricted to females with males having a reduced hump at best. Males of the new species *B. drummondae* sp. nov. and *B. wallisae* sp. nov. however exhibit a well developed dorsal hook as in females. It appears that sexual dimorphism is variable but the possibility that males without hooks belong to other species is a remote possibility.

Barnard and Drummond did not use cladistic methodology to define genera. Rather, small genera were picked off from larger clusters on the basis of few differences that may or may not be unique synapomorphies. The inevitable consequence of this is that the large genus, *Birubius* in this case, is paraphyletic because its numerous species lack a synapomorphy. We are forced to conclude that either (a) the small genera, *Kulgaphoxus*, *Linca*, *Tickalerus* and *Yan*, as presently constituted are gradal offshoots of Birubiinae which cannot be supported in a classification based on cladistic principles; or (b) the type species of the four genera represent much larger clades which may be redefined using very different character suites (synapomorphies).

Until the cladistic analysis is completed we are reluctant to complicate the taxonomy further by erecting new small genera simply because they do not comply with existing diagnoses. It is unclear whether the minor genera in question will come to encompass larger clades but it is certain that they cannot be justified as currently defined. Therefore in this contribution we describe the new taxa as members of *Birubius* in spite of their similarities to some members of *Kulgaphoxus*, *Tickalerus* and *Yan*. The synonymy of these genera with *Birubius* is foreshadowed. Our revised diagnosis of *Birubius* is written to include all species included in *Birubius*, *Kulgaphoxus*, *Tickalerus* and *Yan*.

Abbreviations are: A, antenna; H, head; rLM, right lacinia mobilis; MD, mandible; MX, maxilla; MP, maxilliped; GN, gnathopod; P, pereopod; EP, epimeron; U, uropod; PL, pleopod; T, telson; r, right; m, male; tl., total length; MAFRI, Marine and Freshwater Resources Institute, Queenscliff; NMV, Museum Victoria, Melbourne; AM, Australian Museum, Sydney, QM, Queensland Museum, Brisbane. All dissections and illustrations follow the methods of Barnard and Drummond (1978) whereby the left side of the animal is illustrated unless otherwise stated. Descriptions of the new species closely follow that of other species of the genus described in Barnard and Drummond (1978).

Birubius Barnard and Drummond

Birubius Barnard and Drummond, 1976: 543.—Barnard and Drummond, 1978: 191.—Barnard and Karaman, 1991: 635.

Type species. *Birubius panamunus* Barnard and Drummond, 1976 (by original designation).

Diagnosis. Rostrum variably constricted. Eyes present. Antenna 1 peduncular article 2 length variable, ventral setae not confined apically. Antenna 2 peduncular article 1 not or scarcely ensiform, article 3 with 2 facial setules, facial robust setae on article 4 in 2+ rows, all robust setae thick, article 5 ordinary. Right mandibular incisor with 3-4+ teeth, right lacinia mobilis bifid or simple, often flabellate or absent, molar not triturative, with 4+ splayed robust setae; palpar hump small to medium, apex of palp article 3 oblique. Maxilla 1 inner plate with 3-4 setae, palp 2-articulate. Maxillipedal plates small to ordinary, apex of palp article 3 not strongly protuberant, dactyl elongate, apical nail distinct.

Gnathopods small, similar, gnathopods 1-2 carpus length medium to elongate, not cryptic (posterior margin not concealed by the abutment of propodus and merus), palms oblique, gnathopods 1–2 propodus ordinary to narrow, ovate to rectangular, poorly setiferous anteriorly. Pereopods 3–4 carpus with (rarely without) posteroproximal robust setae, propodus with robust setae. Pereopod 5 basis of broad form (basis equal to or greater than twice width of ischium), pereopods 5–6 merus-carpus broad to narrow; pereopod 7 unreduced, article 3 not enlarged, dactyl well developed, vestigial or absent.

Epimera 1–2 with or without long facial brushes of setae, without posterior setae, epimeron 3 bearing long setae. Urosomite 3 with or without dorsal hook in females, sometimes in male only if in female. Uropod 1 peduncle without interramal robust setae, without major displaced robust seta (seta that is shifted onto the apical margin disjunctly from the true inner margin), uropods 1–2 rami occasionally continuously setose to apex (thus with minute apical robust setae or nails), uropod 1 inner ramus with 1 row of marginal robust setae. Uropod 2 inner ramus ordinary to shortened. Uropod 3 variable, either unreduced (outer ramus longer than peduncle), or reduced (outer ramus shorter than or subequal to peduncle), bearing a second article on outer ramus, with 2 long apical setae. Telson ordinary to elongate.

Species. Biribius batei (Haswell, 1879); *B. rostratus* (Dana, 1853) = *B. barnardi* Pirlot, 1932. Species described by Barnard and Drummond, 1978: *B. apari; B. babaneekus; B. booleus; B. cartoo; B. chintoo; B. eake; B. eleebanus; B. gallangus; B. gambodeni; B. gelarus; B. jirrandus; B. kabbulinus; B. kareus; B. karobrani; B. kinkus; B. kokorus; B. kyeemus; B. lorus; B. lowannus; B. maamus; B. maldus; B. mayamayi; B. muldarpus; B. munggai; B. myallus; B. nammuldus; B. narus; B. panamunus; B. quearus; B. taldeus; B. thalmus; B. ularitus; B. wirakus; B. wulgaru; B. yandus; B. yorlunus.* Species added after 1978: *B. bali* Ortiz and Lalana, 1999; *B. drummondae* sp. nov.; *B. heislersi* sp. nov.; *B. lowryi* sp. nov.; *B. murarini* Ortiz and Lalana, 1997; *B. wallisae* sp. nov.; *B. wilsoni* sp. nov.

Habitat and distribution. Marine 0–70 m. Australia; Indonesia; Papua New Guinea.

Remarks. Barnard and Karaman's (1991) generic diagnosis has been altered to accommodate the new species and to reflect the foreshadowed synonymy of *Tickalerus*, *Kulgaphoxus* and *Yan*.

Biribius drummondae sp. nov.

Figures 1–6

Material examined. Holotype. Australia, Victoria, Western Port (38°22′S, 145°32′E) no further data, NMV J47227 (1 female, tl. 3.8 mm).

Allotype. Same locality as holotype, NMV J47228 (1 male, tl. 5.25 mm).

Paratypes. Same locality as holotype, NMV J47226 (27 females, tl. 3.0–5.7 mm).

Diagnosis. Rostrum constricted. Antenna 2, article 4 without well developed dorsal setation. Right lacinia mobilis bifid, distal branch denticulate. Pereopods 3–4 carpus with 2–3 proximoposterior robust setae. Pereopod 5 dactyl fully formed. Pereopod 7 basis without long ventral setae. Coxa 1 not expanded distally. Coxa 4 lacking long ventral setae. Epimeron 3 without large tooth; without ventral setae; without long posterior seta; with oblique row of facial setae. Urosomite 3 with large dorsal hook. Uropod 1 without basofacial setae. Uropods 1–2 inner rami lacking accessory apical nails. Uropod 3 unreduced, outer ramus longer than peduncle.

Description of female. Head about 18% of total body length, greatest width about 100% of length; rostrum constricted, exceeding apex of peduncular article 1 on antenna 1. Eyes medium, clear of pigment. Antenna 1 peduncular article 1 about 1.3 times as long as wide, about 1.8 times as wide as peduncular article 2, ventral margin with 4 setules, produced dorsal apex with 1 setule; peduncular article 2 about 0.8 times as long as peduncular article 1, with 5 ventral setae; primary flagellum with 10 articles, about 0.9 times as long as peduncle, bearing long aesthetases; accessory flagellum with 8 articles. Antenna 2, peduncular article 4 robust setae formula = 1-3-4-3, dorsal margin with notch bearing 3 setae, ventral margin with 4–5 groups of 1–2 long to short setae, 1 long ventrodistal robust seta; peduncular article 5 about 0.8 times as long as peduncular article 4, facial robust seta formula = 1–2, dorsal margin naked, ventral margin with 3 sets of 1–2 long to short setae, without ventrodistal robust setae; flagellum 1.51 times as long as peduncular articles 4–5 combined, with 11 articles. Mandibles with medium palpar hump; right incisor with 4 teeth and notch; left incisor with 2 humps in 2 branches; right lacinia mobilis bifid, distal branch much shorter than proximal branch, denticulate, proximal branch simple, pointed, with facial hump; left lacinia mobilis sub-bifid; right raker 7; left rakers 7 plus 1 rudimentary; molar in form of bulbous hump, right molar with 4 long robust setae, plus 1 short robust seta strongly disjunct,

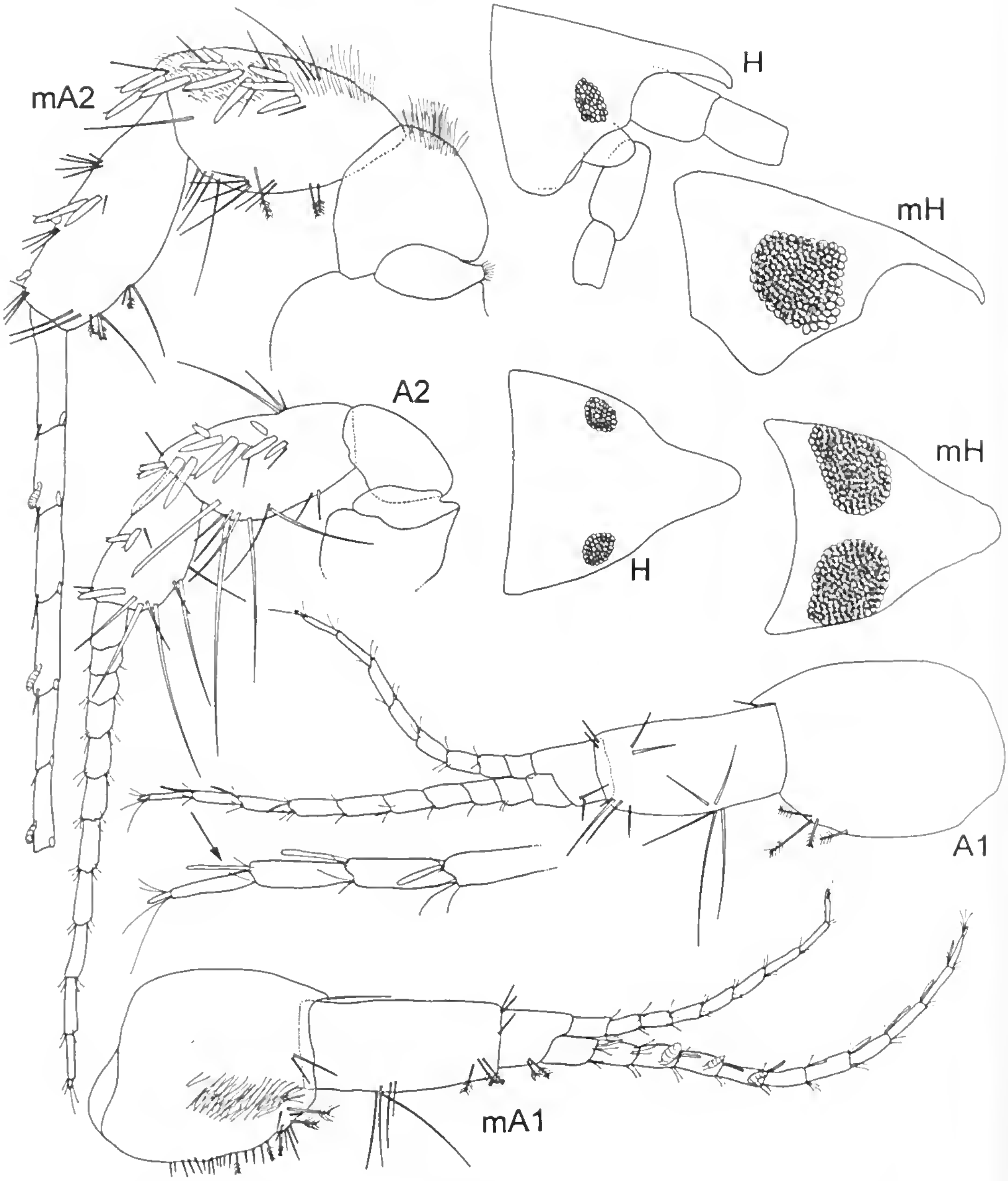

Figure 1. *Birubius drummondae* sp. nov., holotype female, tl. 3.80 mm (m = male allotype, 5.25 mm).

left molar with 5 long robust setae, plus 1 short robust seta strongly disjunct; palp article 1 slightly elongate, article 2 with 1 medium inner apical seta and 2 other shorter inner setae, article 3 about equal in length to article 2, apex oblique with 6 robust to slender setae, with 3 basofacial setae. Maxilla 1 inner plate narrow, bearing 1 long apical seta, 1 similar apicomedial seta, 2 apicolateral much shorter seta; palp article 2 with 1 apicomedial marginal robust seta, 3 apicomedial setae and 3 submarginal setae. Maxilla 2 inner and outer plates extending equally, outer not

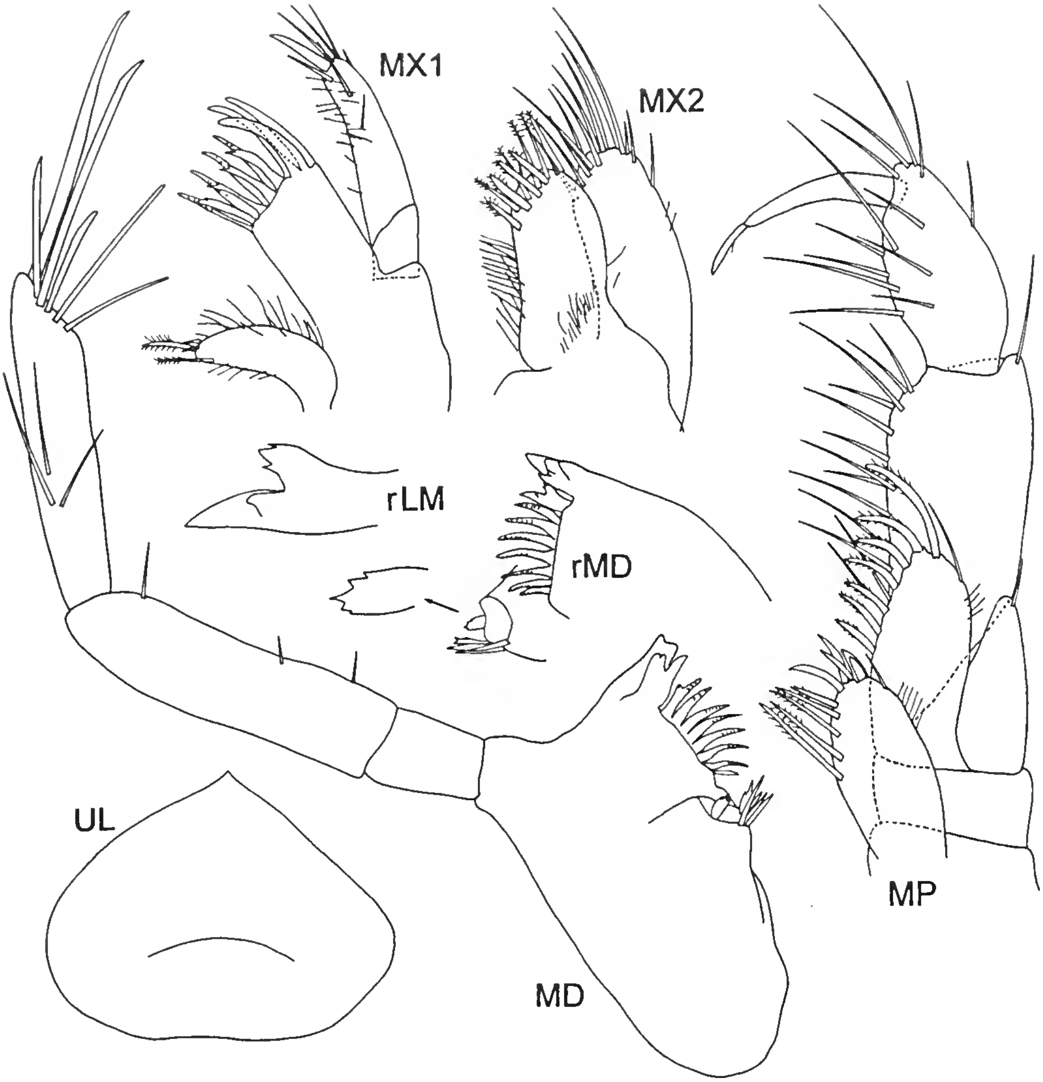

Figure 2. *Birubius drummondae* sp. nov., holotype female, tl. 3.80 mm.

broader than inner. Maxilliped inner plates with 2 large thick apical robust seta, 3 apicofacial setae, 5 medial setae; outer plate with 7 medial and apical robust setae, 1 apicolateral seta; palp articles 1–2 with 1 apicolateral seta, article 3 weakly protuberant, with 3 facial setae, 1 lateral seta, nail of article 4 medium length, with 1 accessory setule. Coxa 1 not expanded distally; main ventral setae of coxae 1–4 = 5-5-5-0, posteriormost seta of coxae 1–3 shortened; anterior and posterior margins of coxa 4 parallel, posterior margin straight, posterodorsal corner sharp, posterodorsal margin medium, width-length ratio of coxa 4 almost = 36:53. Long posterior setae on basis of gnathopods 1–2 and pereopods 3–4 = 4-1-5-7, short posteriors = 1-0-1-0 , long anteriors = 4-8-0-0, short anteriors = 2-2-0-0.

Gnathopods, width ratios of carpus-propodus on gnathopods 1–2 = 20:27 and 20:27, length ratios = 21:26 and 1:1; palmar humps ordinary, palms oblique; gnathopod 1 carpus of medium length gnathopod 2 carpus slightly elongate. Pereopods 3–4 similar, facial setae on merus = 3 and 3, on carpus = 3 and 4; main spine of carpus

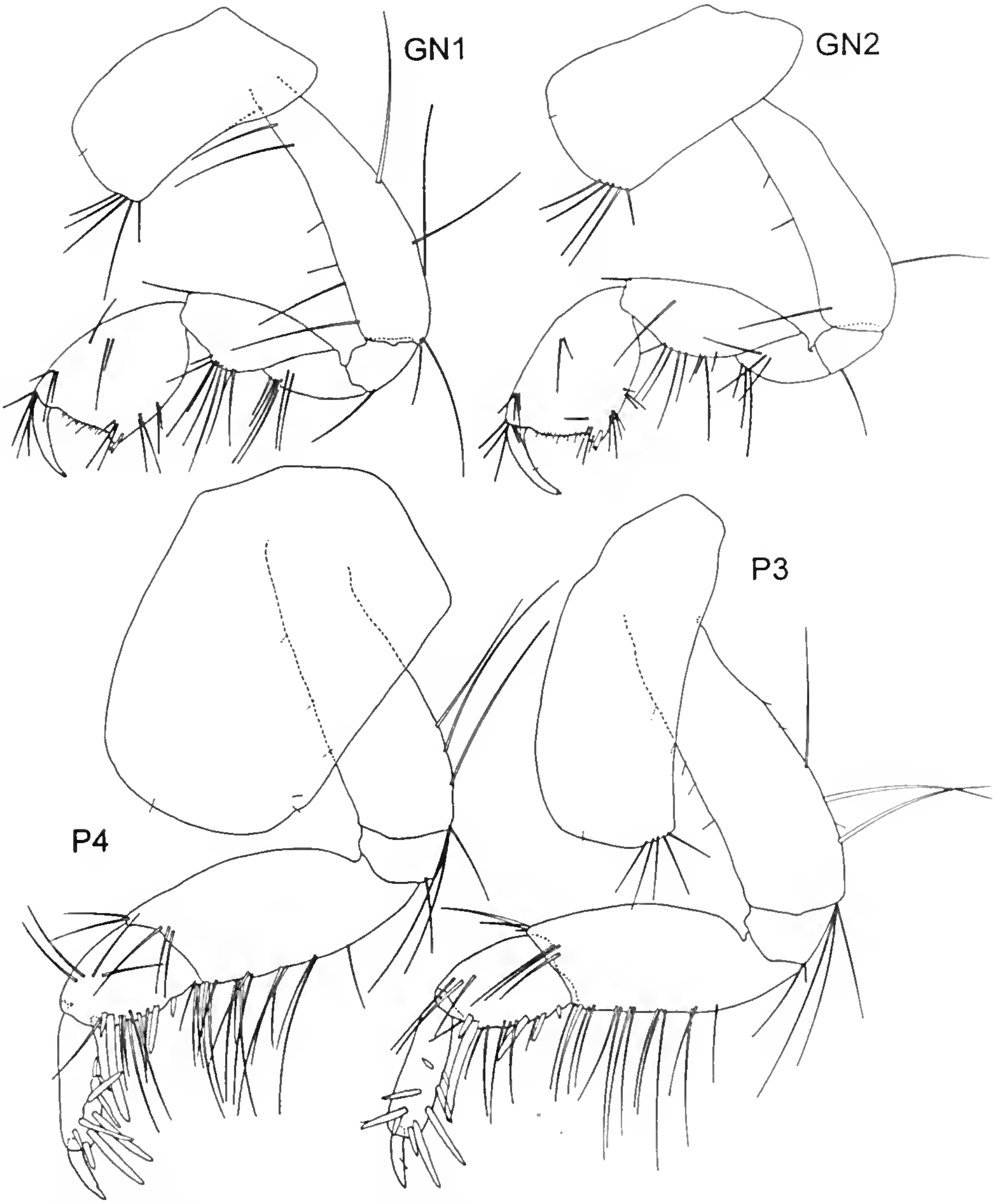

Figure 3. *Birubius drummondae* sp. nov., holotype female, tl. 3.80 mm.

extending to M. 77 on propodus, carpus with 2 and 3 proximoposterior robust setae; robust setae formula of propodus = 4 + 5 and 4 + 5; acclivity on inner margin of dactyls of pereopods 3–4 weak, midfacial seta ordinary. Coxae 5–7 posteroventral seta formula = 2-2-1; merus-carpus of pereopods 5–6 broad, facial robust setae rows dense, facial ridge formula on basis of pereopods 5–7 = 0-2-2, anterior ridge of pereopod 7 long; width ratios of basis, merus, carpus, propodus of pereopod 5 = 11:12:11:5, of pereopod 6 = 18:13:10:5, of pereopod 7 = 107:27:23:11, length

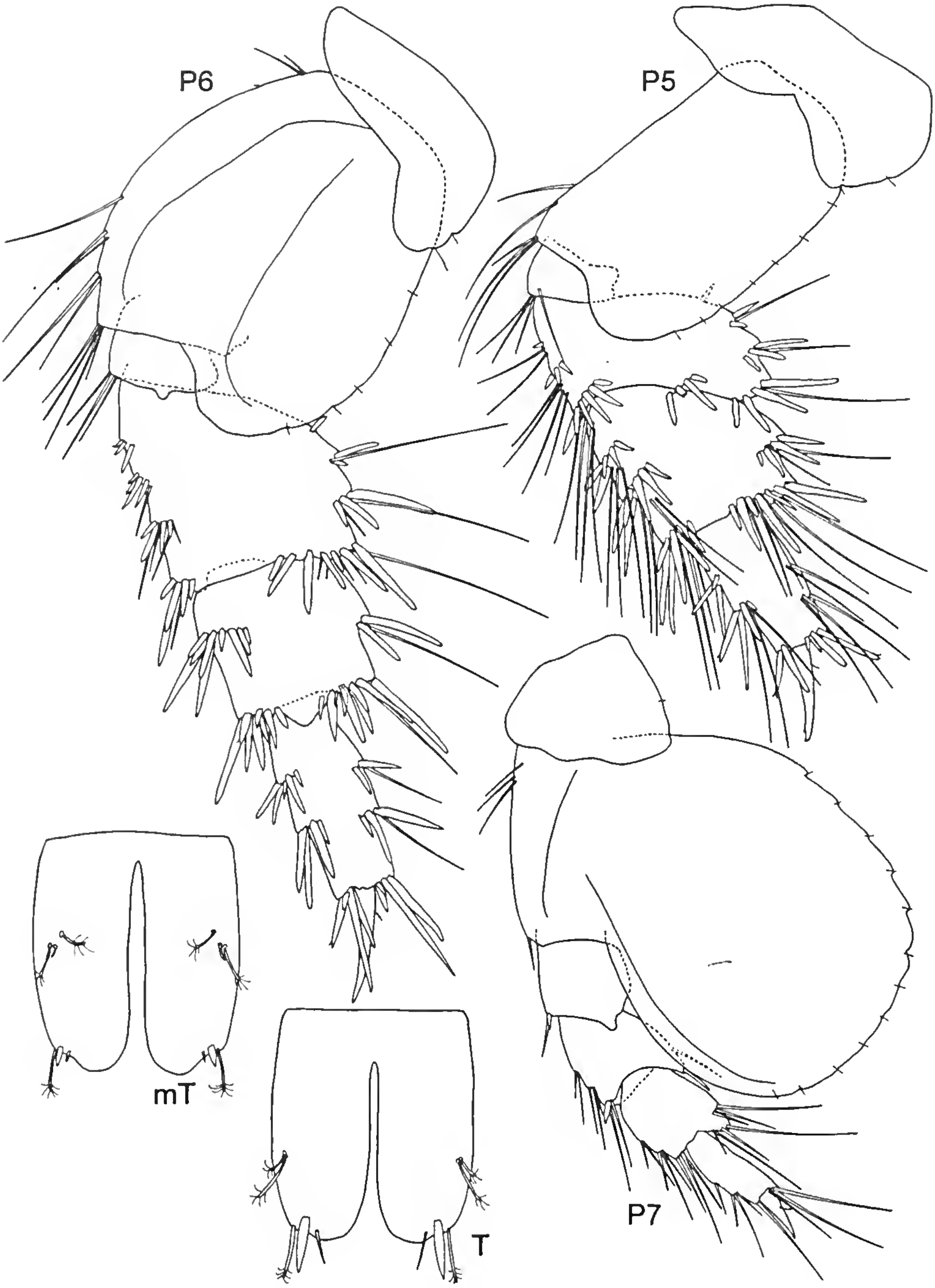

Figure 4. *Birubius drummondae* sp. nov., holotype female, tl. 3.80 mm (m = male allotype, 5.25 mm).

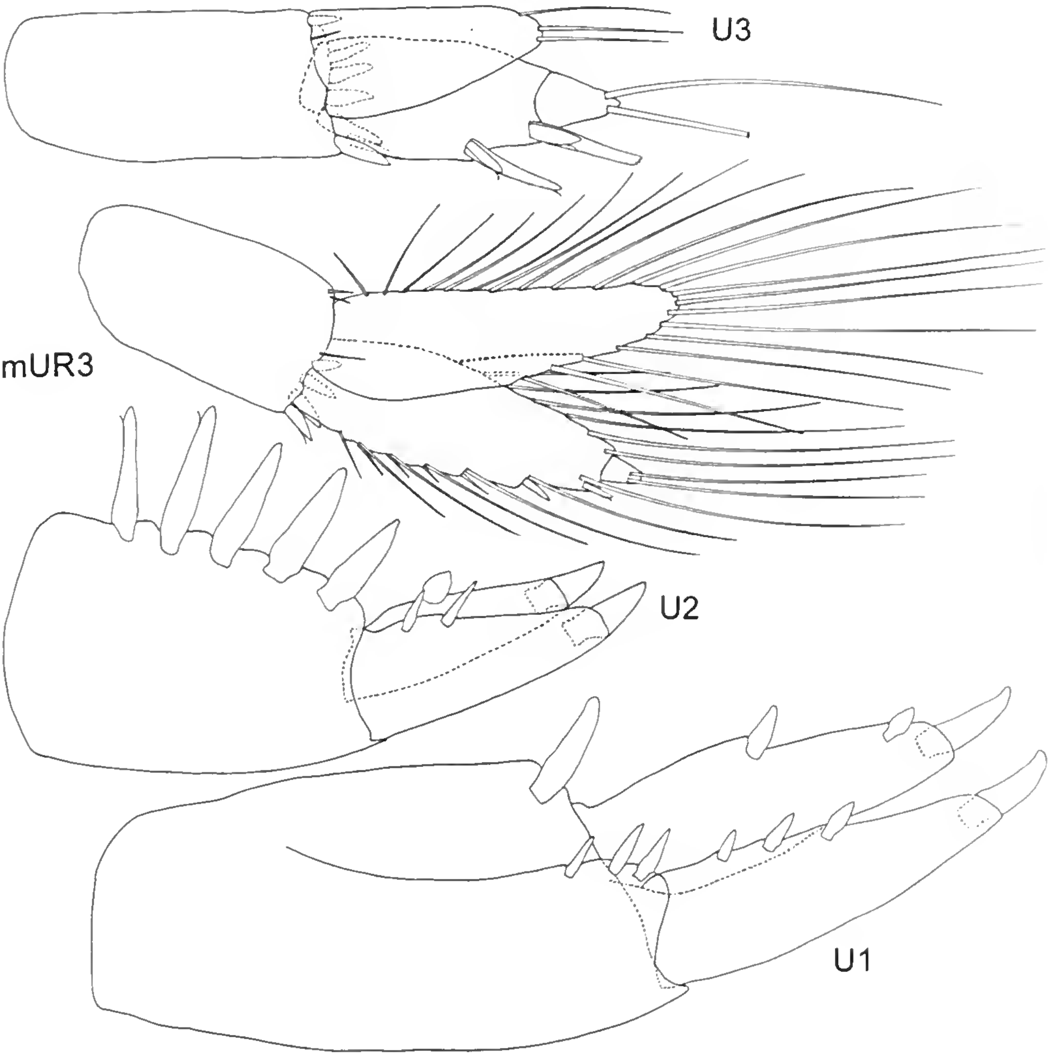

Figure 5. *Birubius drummondae* sp. nov., holotype female, tl. 3.80 mm (m = male allotype, 5.25 mm).

ratios of pereopod 5 = 45:21:24:22, of pereopod 6 = 58:32:24:29, of pereopod 7 = 63:15:13:13; basis of pereopod 7 exceeding apex of merus, naked ventrally. Pleopods 1–3 with 2 coupling hooks; rear facial setae on peduncle = 2-2-3; articles on outer rami = 11-10-11, inner rami = 7-6-6.

Epimeron 1 posteroventral corner rounded, anteroventral margin with 3 setae, posteroventral face with 2 medium setae, set vertically; epimeron 2 posteroventral corner rounded, with 5 facial setae, posteriormost pair set almost vertically; epimeron 3 posteroventral corner barely protuberant, with setule sinus, posterior margin almost straight, with 2 setule notches, ventral margin naked, midface with oblique row of 4 setae near posterior margin. Urosomite 1 naked, articulation line almost complete; urosomite 3 with large hook dorsally. Uropods 1–2 rami with articulate enlarged apical nails, uropod 1 outer ramus with 3 dorsal robust setae, inner with 1 dorsomedial and 1 subapical robust setae, uropod 2 outer ramus with 2 dorsal robust setae, inner

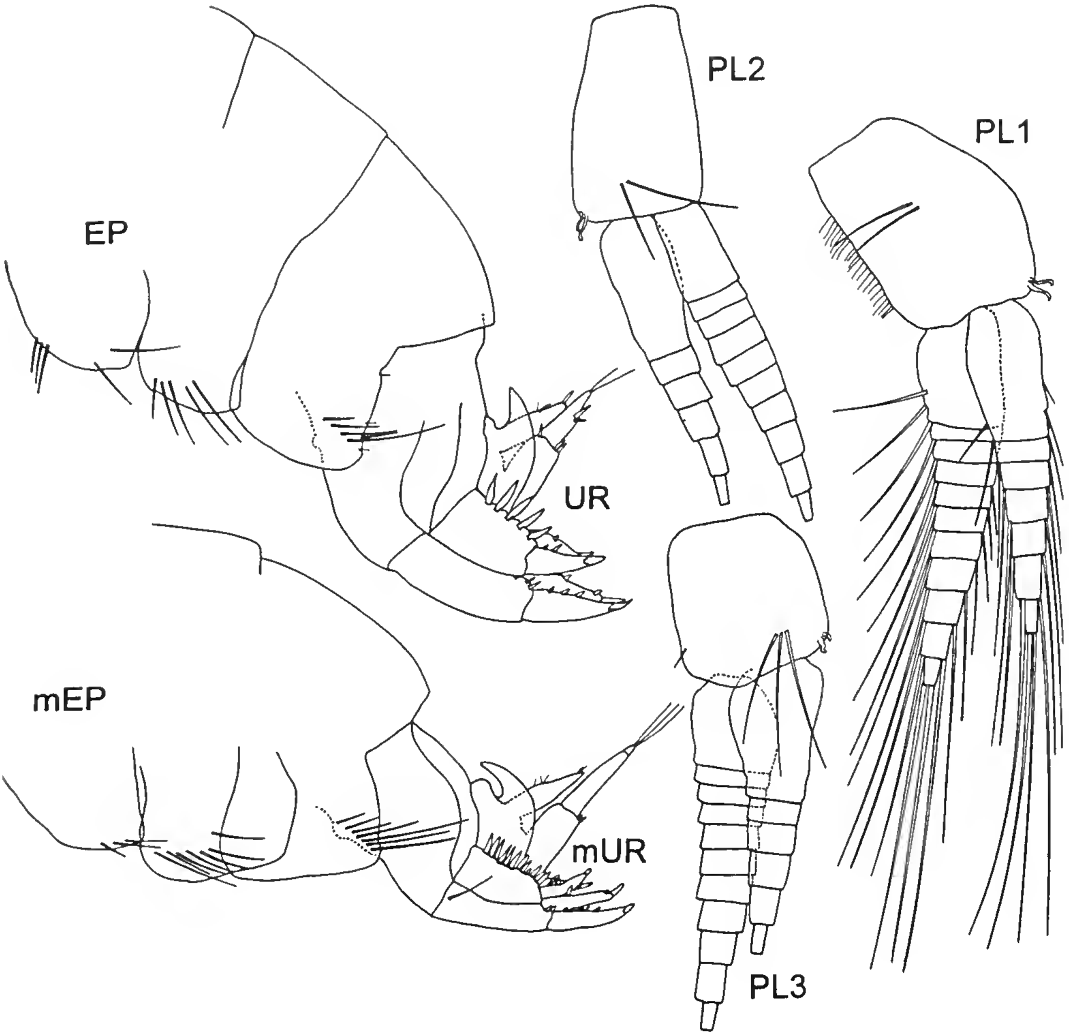

Figure 6. *Birubius drummondae* sp. nov., holotype female, tl. 3.80 mm (m = male allotype, 5.25 mm).

with 1 broad dorsomedial robust seta; uropod 1 peduncle with 3 apicolateral robust setae, without basofacial slender setae, with apical enlarged robust seta; uropod 2 peduncle with 5 dorsal robust setae; apicolateral corners of peduncles on uropods 1–2 without comb. Uropod 3 unreduced, outer ramus longer than peduncle. Uropod 3 peduncle with 6 ventral robust setae, dorsally with 1 lateral robust seta; rami masculine, inner extending to M. 100+ on article 1 of outer ramus, apex with 3 setae, medial and lateral margins naked, article 2 of outer ramus elongate, 0.38, bearing 2 long setae, apicomedial margin of article 1 naked, lateral margin with 1 acclivity, robust setal formula = 2-2, without slender setae formula. Telson long, length-width ratio = 34:29, not fully cleft, each apex wide. rounded, lateral acclivity broad, shallow, bearing ordinary lateral setule, robust setae next medial little longer than setule, midlateral setules diverse.

Description of male. Similar to female but eyes larger. Antenna 1 like female but with dense medial setation on peduncular article 1; primary flagellum bearing calceoli. Antenna 2 elongate, peduncular articles 3–4 with dense dorsal setation, peduncular article 5 about as long as article 4, dorsal margin bearing 2 calceoli and 3 groups of male setae, flagellum 28-articulate bearing calceoli. Maxilliped and maxillae 1–2 similar to female. Right lacinia mobilis bifid, distal branch much shorter than proximal branch, flabellate, proximal branch simple, pointed, with facial humps; left lacinia mobilis with 4 teeth; right raker 8; left rakers 9; right and left molars with 5 long robust setae; palp similar to female, article 3 with 6 basofacial setae. Main ventral setae of coxae 1–4 = 7-6-7-0. Gnathopods 1–2 similar to female. Urosomite 3 with large hook dorsally. Uropod 1 outer ramus with 5 dorsal robust setae, inner with 1 dorsomedial and 1 subapical robust setae, uropod 2 outer ramus with 3 dorsal robust setae, inner with 1 broad dorsomedial robust seta; uropod 1 peduncle with 2 apicolateral robust setae, with 1 basofacial slender seta; uropod 2 peduncle with 12 dorsal robust setae. Uropod 3 with inner ramus elongate, exceeding apex of article 1 on outer ramus. Telson elongate, length-width ratio = 7:6.

Etymology. For Margaret Drummond who identified this species as new from Museum Victoria collections and contributed so much to knowledge of Australian amphipods.

Remarks. The following variations from the holotype were observed in the paratypes. The main ventral setae of coxae 1–4 = (4-5)-(4-6)-(4-6)-0. Uropod 1 outer ramus with 3–4 dorsal robust setae, inner ramus with 1 dorsomedial and 1 subapical robust setae. Uropod 2 outer ramus with 1–2 dorsal robust setae, inner ramus with 1 dorsal robust setae.

Birubius drummondae shares the dorsal hook of urosomite 3 with *Tickalerus birubi*, both species of *Kulgaphoxus* and three other new species of *Birubius* described herein. This species can not be placed in the genus *Tickalerus* as it lacks both the well developed dorsal setation on article 4 of female antenna 1 and the shortened outer ramus of uropod 3, characters diagnostic of the type species, *T. birubi*. It remains distinct from both species of *Kulgaphoxus* in its lack of accessory apical nails on the inner rami of both uropods 1–2, the unreduced rostrum and the perfectly rectangular coxa 4, a character it shares with *T. birubi*. *Birubius drummondae* differs from previously described species of *Birubius* by the presence of the dorsal hook on urosomite 3, and from the other new species described herein by the combination of characters listed in the diagnoses. The species is number MoV3679 in Museum Victoria's TAXA database.

Birubius heislersi sp. nov.

Figures 7–11

Material examined. Holotype. Australia, Victoria, Ninety Mile Beach (38°30'S, 147°25.8'E), 40 m, Smith-McIntyre grab, 8 May 1998 (MAFRI stn 37C), NMV J47320 (1 female, tl. 6.8 mm).

Paratypes. Australia, Victoria, Apollo Bay, Skenes Creek (38°23.4'S, 144°15.6'E), 40 m, Smith-McIntyre grab, 3 May 1998 (MAFRI stn 18C), NMV J47321 (2 females, tl. 6.5–9.75 mm).

Diagnosis. Rostrum constricted. Antenna 2, article 4 without well developed dorsal setation. Right lacinia mobilis bifid, distal branch denticulate. Pereopods 3–4 carpus with 3–4 proximoposterior robust setae. Pereopod 5 dactyl fully formed. Pereopod 7 basis with 1 medium ventral setae, without long ventral setae. Coxa 1 expanded distally. Coxa 4 lacking long ventral setae. Epimeron 3 with small tooth; without ventral setae; without long posterior seta; with oblique row of facial setae. Urosomite 3 without dorsal hook. Uropod 1 with basofacial setae. Uropods 1–2 inner rami lacking accessory apical nails. Uropod 3 reduced, outer ramus shortened, subequal to peduncle.

Description of female. Head about 18% of total body length, greatest width about 78% of length; rostrum constricted, exceeding peduncular article 1 on antenna 1. Eyes medium, clear of pigment. Antenna 1 peduncular article 1 about 1.3 times as long as wide, about 1.6 times as wide as peduncular article 2, ventral margin with 10 setules, weakly produced dorsal apex with 3 setules; peduncular article 2 about 0.8 times as long as peduncular article 1, with 8 ventral setae; primary flagellum with 15 articles, about 0.95 times as long as peduncle, bearing aesthetases; accessory flagellum with 13 articles. Antenna 2, peduncular article 4 robust setae formula = 1-3-5-6, dorsal margin with notch bearing 3 setae, ventral margin with 6 groups of 1–2 long to medium setae, 1 ventrodistal robust seta; peduncular article 5 about 0.7 times as long as peduncular article 4, facial robust seta formula = 0-3, dorsal margin naked, ventral margin with 3 sets of 1–2 long to short setae, 3 ventrodistal long to medium robust setae; flagellum 1.6 times as long as peduncular articles 4-5 combined, with 16 articles. Mandibles with medium palpar hump; right incisor with 3 teeth; left incisor with 3 teeth in 2 branches; right lacinia mobilis bifid, distal branch shorter than proximal branch, broad, denticulate, proximal branch simple, pointed, with marginal denticles; left lacinia mobilis with 4 teeth; right raker 10; left

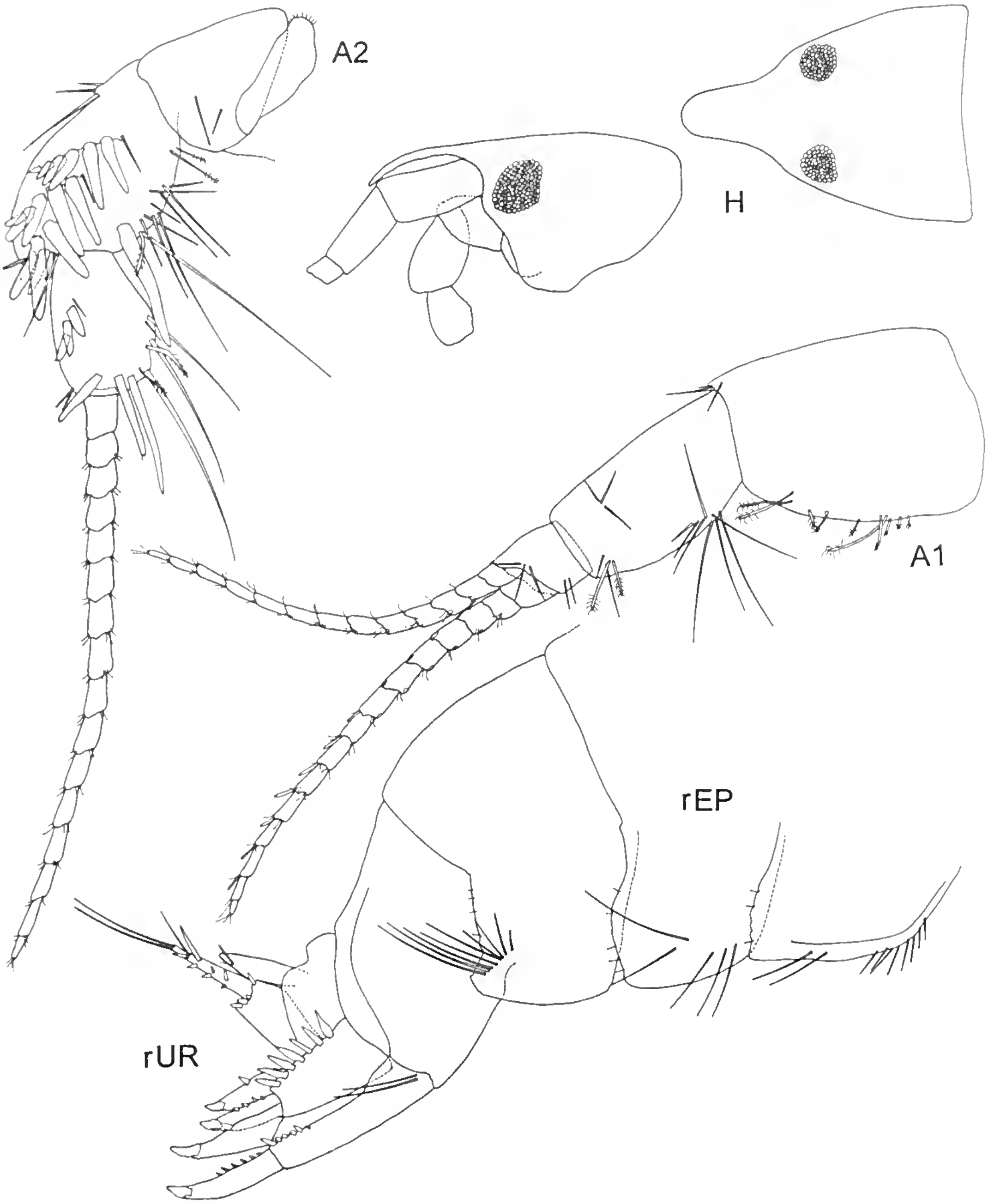

Figure 7. *Birubius heislersi* sp. nov., holotype female, tl. 6.80 mm.

rakers 7; molar in form of short protrusion demarcated mainly by robust setae, right and left molar with 5–6 long robust setae, plus 1 short robust seta strongly disjunct; palp article 1 slightly elongate, article 2 with 1 medium inner apical seta and 2 other shorter inner setae, article 3 about 0.8

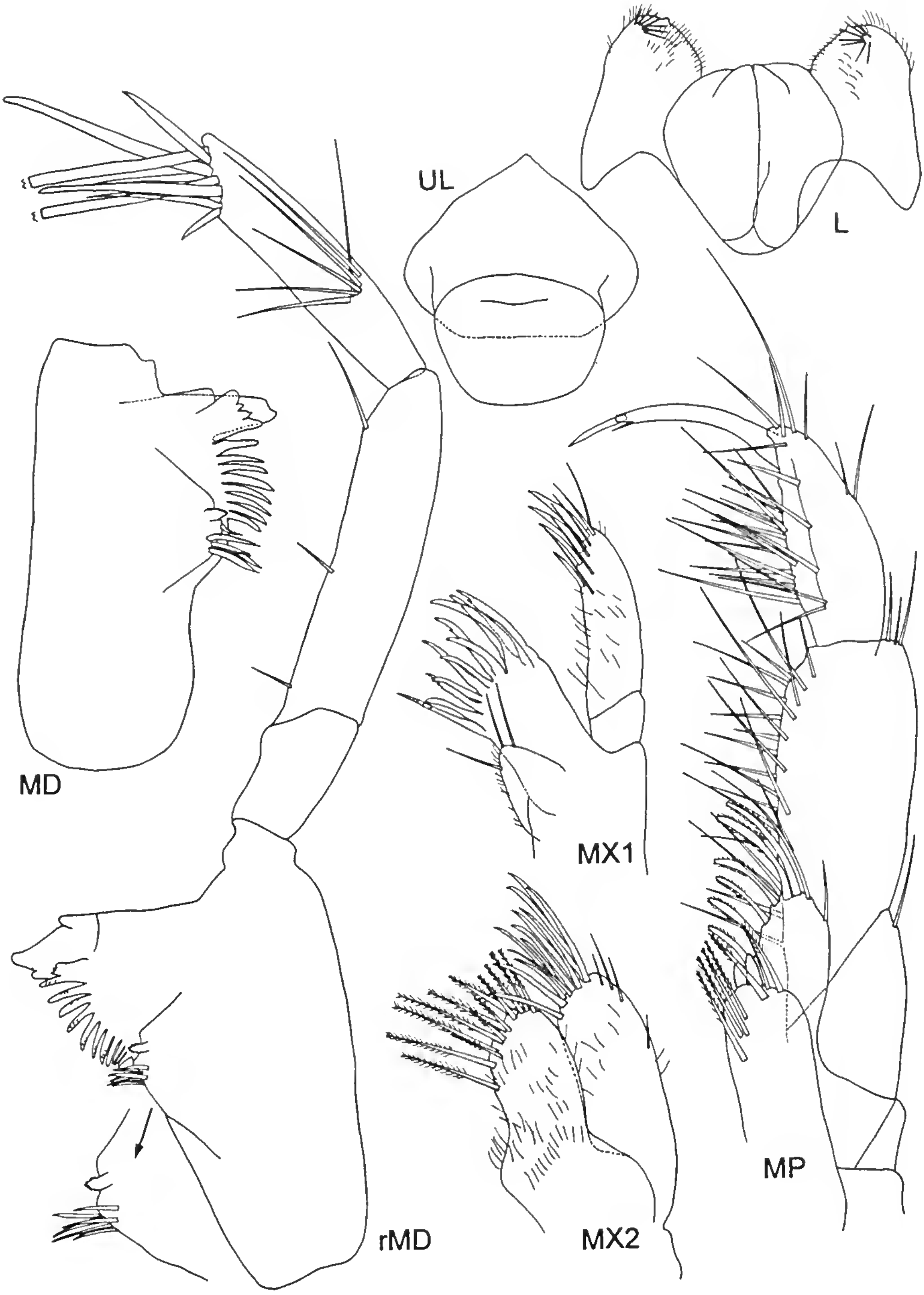

Figure 8. *Birubius heislersi* sp. nov., holotype female, tl. 6.80 mm.

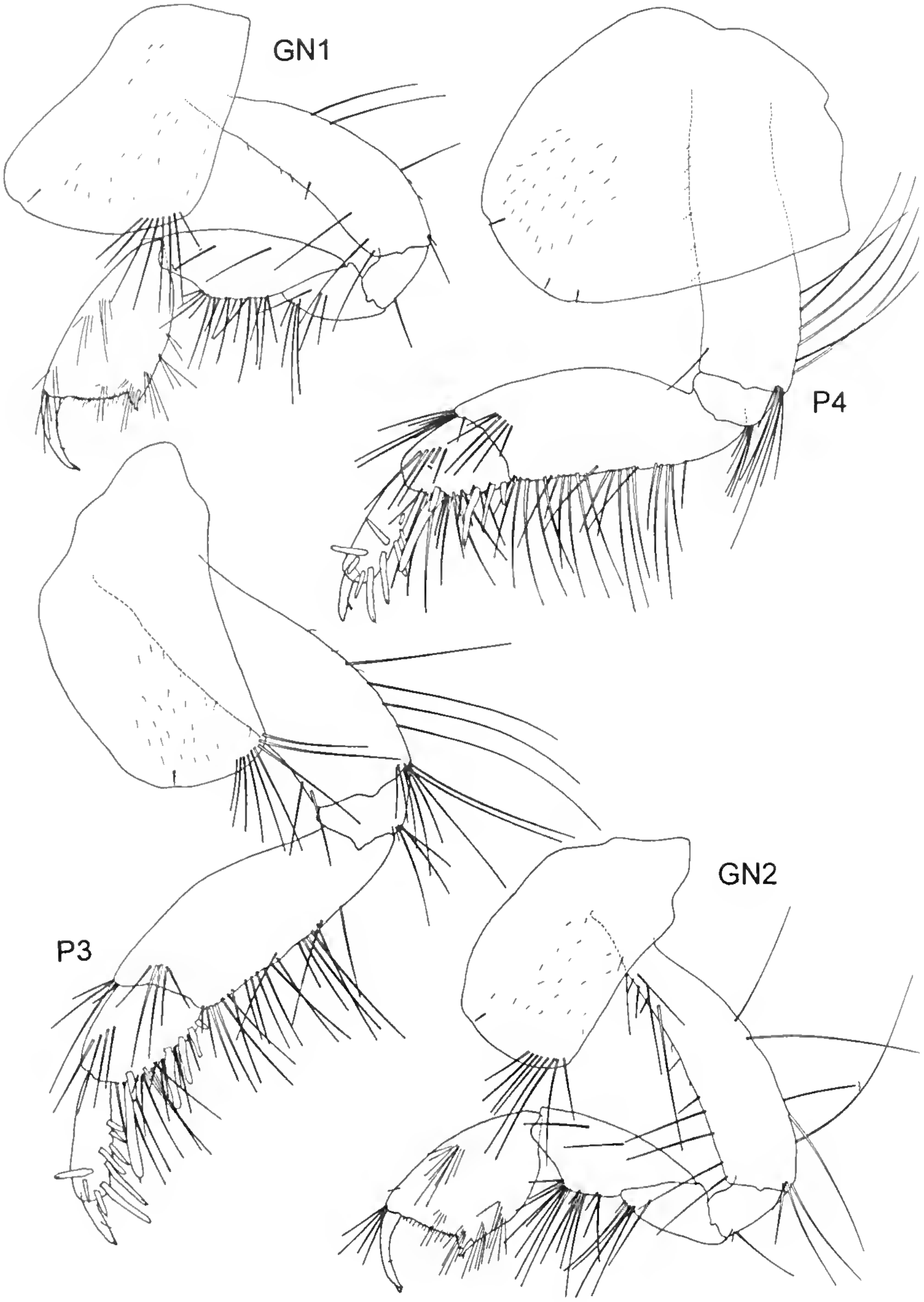

Figure 9. *Birubius heislersi* sp. nov., holotype female, tl. 6.80 mm.

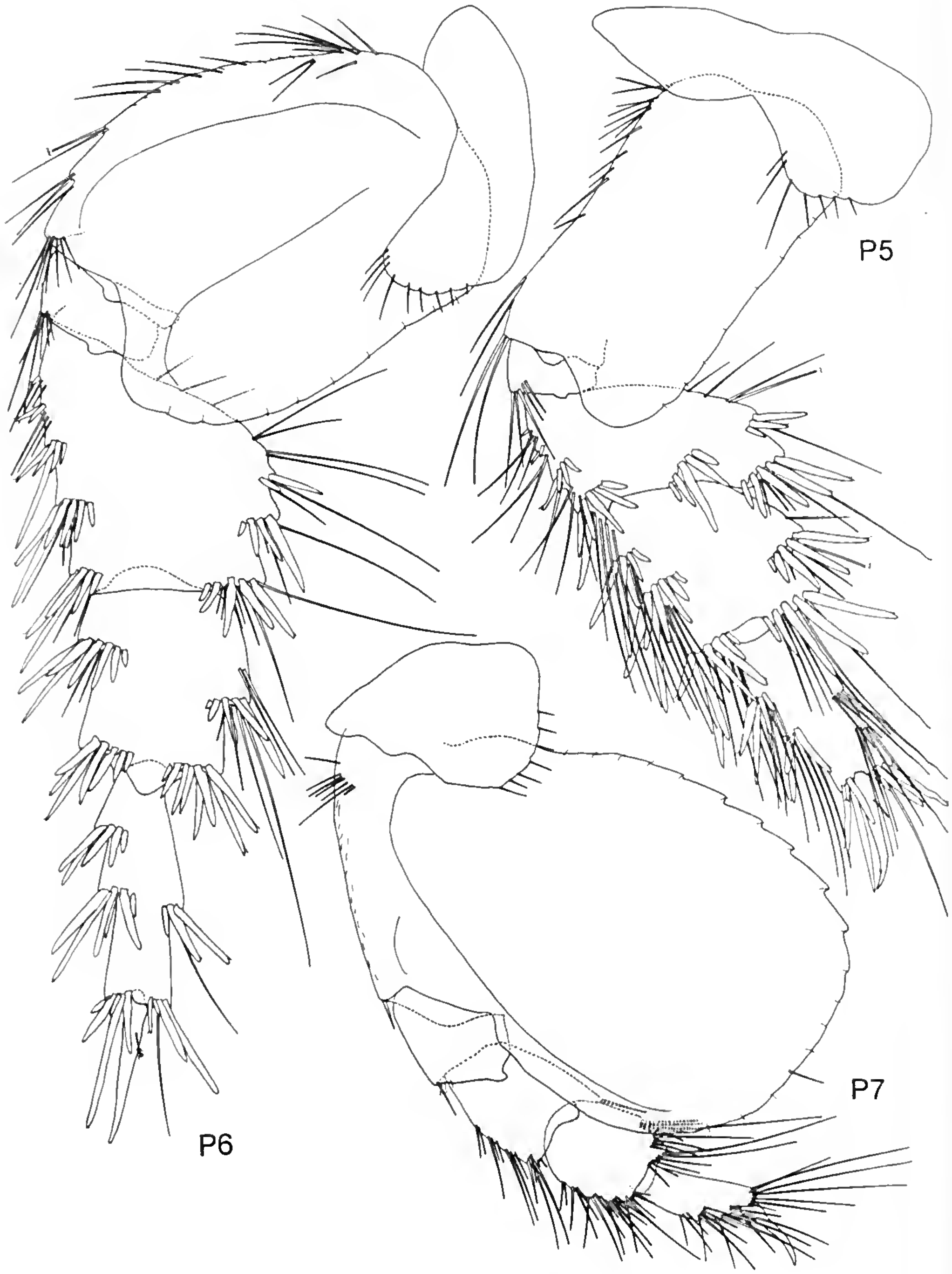

Figure 10. *Birubius heislersi* sp. nov., holotype female, tl. 6.80 mm.

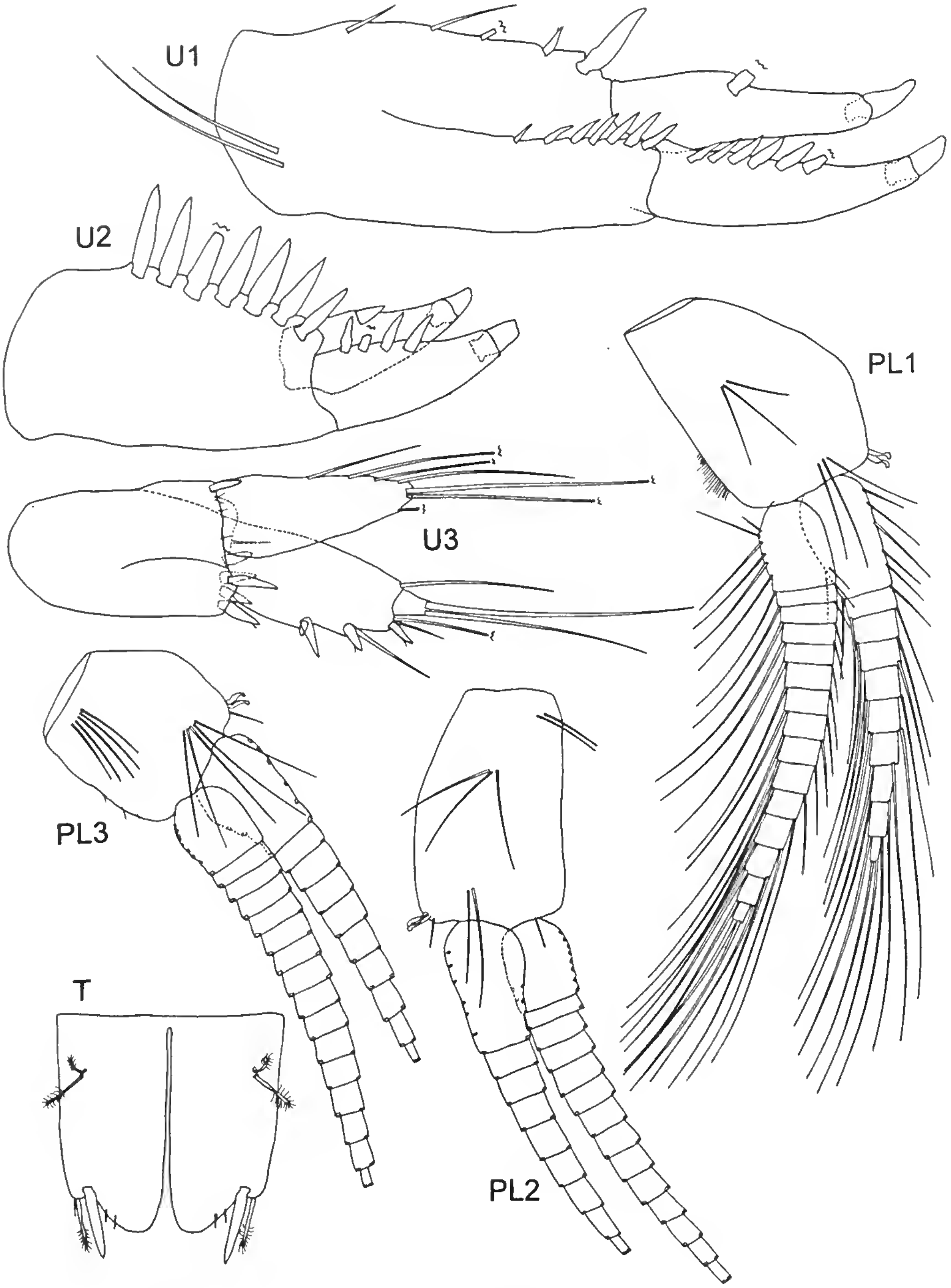

Figure 11. *Birubius heislersi* sp. nov., holotype female, tl. 6.80 mm.

times long as article 2, apex oblique with 8 robust setae, with 6 basofacial setae. Maxilla 1 inner plate large, bearing 1 long apical seta, 1 similar apicomedial seta, 1 similar apicolateral seta; palp article 2 with 4 apicomedial marginal robust setae and 6 submarginal setae. Maxilla 2 inner and outer plates extending subequally, outer not broader than inner. Maxilliped inner plates with 2 large thick apical robust seta, 3 apicofacial setae, 4 medial setae; outer plate with 6 medial and apical robust setae, 2 apicolateral setae; palp article 1 with 1 apicolateral setae, article 2 with 3 apicolateral setae, article 3 protuberant, with 5 proximal facial setae, with 2 lateral setae, nail of article 4 medium length, with 1 accessory setules. Coxa 1 expanded distally, anterior margin weakly concave; main ventral setae of coxae 1–4 = 8-8-9-0, posteriormost seta of coxae 1–3 shortened; anterior and posterior margins of coxa 4 divergent, posterior margin oblique, almost straight, posterodorsal corner sharp, posterodorsal margin short, width-length ratio of coxa 4 = 59:50. Long posterior setae on basis of gnathopods 1–2 and pereopods 3–4 = 3-8-12-12, short to medium posteriors =2-1-1-0 , long anteriors = 3-7-2-1, short anteriors = 1-6-4-6.

Gnathopod propodus narrow; gnathopods 1–2 width ratios of carpus-propodus = 5:7 and 11:15, length ratios = 1:1 and 25:26; palmar humps ordinary, palms oblique; gnathopods 1–2 carpus elongate. Pereopods 3–4 similar, facial setae on merus = 5 and 6, on carpus = 4 and 5; main spine of carpus extending to M. 75 on propodus, carpus with 3–4 proximoposterior robust setae; robust setae formula of propodus = 4 + 5; acclivity on inner margin of dactyls of pereopods 3–4 weak, midfacial seta ordinary. Coxae 5–7 posteroventral setule formula = 7-9-7; merus-carpus of pereopods 5–6 broad, facial robust setae rows dense, facial ridge formula on basis of pereopods 5–7 = 0-2-2, anterior ridge of pereopod 7 very short; width ratios of basis, merus, carpus, propodus of pereopod 5 = 29:30:26:12, of pereopod 6 = 50:33:25:13, of pereopod 7 = 65:15:14:6, length ratios of pereopod 5 = 55:23:26:29, of pereopod 6 = 62:39:31:33, of pereopod 7 = 69:19:17:17; pereopod 7 basis reaching or exceeding middle of carpus, with 1 medium ventral setae. Pleopods 1–3 with 2 coupling hooks; pleopod 1 with 3 mid and 3 proximal facial setae, pleopod 2 with 2 proximal, 3 mid and 2 distal facial setae, pleopod 3 with 5 proximal and 5 distal facial setae; articles on outer rami = 15-14-16, inner rami = 10-9-10.

Epimeron 1 posteroventral corner rounded, anteroventral margin with 8 short to medium setae, posteroventral face with 2 long setae, posterior margin with 3–5 setules in sinuses; epimeron 2 posteroventral corner rounded, with 5 facial setae, posteriormost pair set vertically, posterior margin with 5–6 setules in sinuses; epimeron 3 posteroventral corner weakly protuberant, with small tooth, posterior margin straight, with setule sinuses, ventral margin naked, face with horizontal row of 9 setae. Urosomite 1 naked, articulation almost complete; urosomite 3 weakly protuberant dorsally, without hook. Uropods 1–2 rami with articulate enlarged apical nails, uropod 1 outer ramus with 6 dorsal robust setae, inner with 1, uropod 2 outer ramus with 4 dorsal robust setae, inner with 1 dorsomedial robust seta; uropod 1 peduncle with 7 apicolateral robust setae and 2 basofacial slender setae, apically with 2 marginal robust setae, apicalmost enlarged, medially with 3 slender setae; uropod 2 peduncle with 7 dorsal robust setae; apicolateral corners of peduncles on uropods 1–2 without comb. Uropod 3 reduced, outer ramus shortened, subequal to peduncle. Uropod 3 peduncle with 5 ventral robust setae, dorsally with 1 lateral robust seta; rami masculine, inner extending to M. 100+ on article 1 of outer ramus, apex with 2 setae, medial margin with 1 seta, lateral margin with 4 setae, article 2 of outer ramus short, 0.21, bearing 2 long setae, apicomedial margin of article 1 with a single seta, lateral margin with 2 acclivities, robust setal formula = 1-1-2, slender setal formula = 2-1-0. Telson length-width ratio = 1:3, almost fully cleft, each apex wide, rounded, lateral acclivity broad, shallow, bearing ordinary lateral setule, robust setae next medial longer than setule, midlateral setules diverse.

Male. Unknown.

Etymology. For Simon Heislers, Museum Victoria, who identified this species as new from Museum Victoria collections.

Remarks. The following variations from the holotype were observed in the paratypes. The main ventral setae of coxae 1–4 = (5-8)-(5-8)-(5-9)-0. Uropod 1 outer ramus with 6–8 dorsal robust setae, inner ramus with 1 dorsal robust seta. Uropod 2 outer ramus with 3–4 dorsal robust setae, inner ramus with 1 dorsal robust seta.

Birubius heislersi conforms well to Barnard and Drummond's (1978) diagnosis of *Birubius* except that it exhibits shortened rami of uropod 3 as seen in *Tickalerus* and *Kulgaphoxus*. It differs from these genera in the lack of a dorsal hook on urosomite 3. Attempts to identify this species using Barnard and Drummond's (1978) key failed. *Birubius heislersi* appears most similar to *B. lowanus* (Barnard and Drummond, 1978) but differs on many accounts including the denticulate vs simple distal branch of the right lacinia mobilis, more ventral setae on coxae 1–3, the presence of 3–4 vs 1 proximoposterior robust seta on carpus of pereopods 3–4 and the naked ventral margin of uropod 3. The species is number MoV3671 in Museum Victoria's TAXA database.

Birubius lowryi sp. nov.

Figures 12–17

Material examined. Holotype. Papua New Guinea, NW corner of Pig I. (05°9.98'S, 145°50.45'E), 21 m, J. D. Thomas, 4 Feb 1990 (stn PNG 33K), AM P60004 (1 female, tl. 4.75 mm).

Allotype. Papua New Guinea, Barracuda Point, E of Pig I. (05°10.26'S, 145°50.61'E), 30 m, J. D. Thomas, 8 Feb 1990 (stn PNG 37K), AM P56151 (1 male, tl. 3.75 mm).

Paratypes. Same data as allotype. AM P60005 (4 females, tl 3.0–3.75 mm). Papua New Guinea, Horseshoe Reef, Bootless Inlet (09°30.05'S, 147°15.50'E), 30 m, 28 Oct 1980, AM P60006 (2 females, tl. 3.75–3.9 mm).

Diagnosis. Rostrum constricted. Antenna 2, article 4 without well developed dorsal setation. Right lacinia mobilis bifid, distal branch simple. Pereopods 3–4 carpus with 1 proximoposterior robust seta. Pereopod 5 dactyl fully formed. Pereopod 7 basis with long ventral setae. Coxa 1 strongly expanded distally. Coxa 4 lacking long ventral setae. Epimeron 3 with small tooth; with ventral setae; without long posterior seta; without facial setae. Urosomite 3 with large dorsal hook. Uropod 1 with basofacial setae. Uropods 1–2 inner rami lacking accessory apical nails. Uropod 3 unreduced, outer ramus longer than peduncle.

Description of female. Head about 16% of total body length, greatest width about 84% of length; rostrum constricted, narrow, elongate, reaching middle of peduncular article 2 on antenna 1. Eyes large, clear of pigment. Antenna 1 peduncular article 1 about 1.5 times as long as wide, about 2.0 times as wide as article 2, ventral margin with 8 setules, unproduced dorsal apex without setule; peduncular article 2 about 0.6 times as long as peduncular article 1, with 5 ventral setae; primary flagellum with 10 articles, about 0.8 times as long as peduncle, lacking aesthetases; accessory flagellum with 8 articles. Antenna 2, peduncular article 4 robust setae formula = 1-3-4-4, dorsal margin with notch bearing 2 setae, ventral margin with 6–7 groups of 1–2 long to short setae, without ventrodistal robust seta; peduncular article 5 about 0.76 times as long as peduncular article 4, facial robust seta formula = 1–2, dorsal margin naked, ventral margin with 4 sets of 1–2 long to short setae, 2 ventrodistal long to medium robust setae; flagellum 1.07 times as long as articles 4–5 of peduncle combined, with 11 articles. Mandibles with medium to large palpar hump; right incisor with 3 teeth; left incisor with 2 humps in 2 branches; right lacinia mobilis bifid, distal branch shorter than proximal branch, simple, pointed, proximal branch simple, pointed; left lacinia mobilis with 5 teeth; right raker 8; left rakers 7; molar in form of short protrusion demarcated mainly by robust setae, right molar with 6 long robust setae, left molar with 6 long robust setae, no seta disjunct; palp article 1 slightly elongate, article 2 with 2 long-medium inner apical setae and 2 other medium inner setae, article 3 about 0.86 times long as article 2, apex oblique with 6 robust to slender setae, without basofacial setae. Maxilla 1 inner plate narrow, bearing 1 long apical seta plus 1 shorter apicomedial seta; palp article 2 with 1 apicomedial marginal robust seta, 3 apicomedial setae and 3 submarginal setae. Maxilla 2 inner and outer plates extended equally. Maxilliped inner plates with 1 large thick apical robust seta, 3 apicofacial setae, 1 medial seta; outer plate with 5 medial and apical robust setae; palp article 1 with 1 apicolateral seta, article 2 with 2 apicolateral setae and 1 other lateral seta, article 3 unprotuberant, with 2 facial setae, nail of article 4 long, with 2 accessory setules. Coxa 1 strongly expanded distally; posterior setae of coxa 1–3 = 3-4-3, main ventral setae of coxae 1–4 = 6-6-8-0, posteriormost seta of coxae 1–3 elongate; anterior and posterior margins of coxa 4 strongly divergent, posterior margin oblique, posterodorsal corner rounded, posterodorsal margin medium, width-length ratio of coxa 4 almost = 1:1. Long posterior setae on basis of gnathopods 1–2 and pereopods 3–4 = 2-8-9-10, short posteriors = 5-6-6-7, long anteriors = 0-10-0-0, short anteriors = 6-6-12-12.

Gnathopods, width ratios of carpus-propodus on gnathopods 1–2 = 9:11 and 10:13, length ratios = 23:26 and 25:19; palmar humps ordinary, palms oblique; gnathopods 1–2 carpus of medium length. Pereopods 3–4 similar, facial setae on merus = 4 and 3, on carpus = 4 and 4; main spine of carpus extending to M. 91 on propodus, carpus with 1 proximoposterior robust seta; robust setae formula of propodus = 2 + 4; acclivity on inner margin of dactyls of pereopods 3–4 weak, midfacial seta short. Coxae 5–7 posteroventral seta

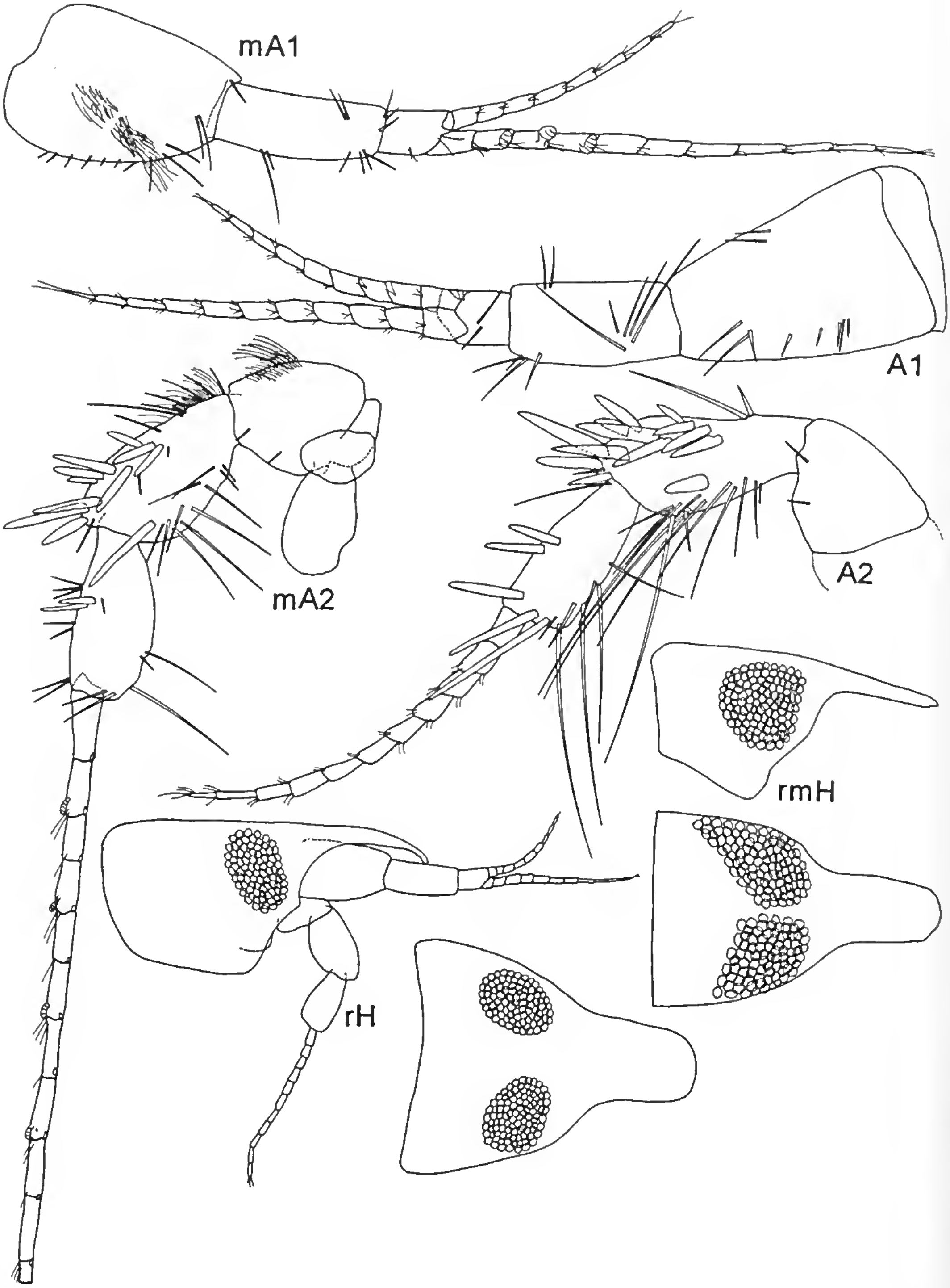

Figure 12. *Birubius lowryi* sp. nov., holotype female, tl. 4.75 mm (m = male allotype, 3.75 mm).

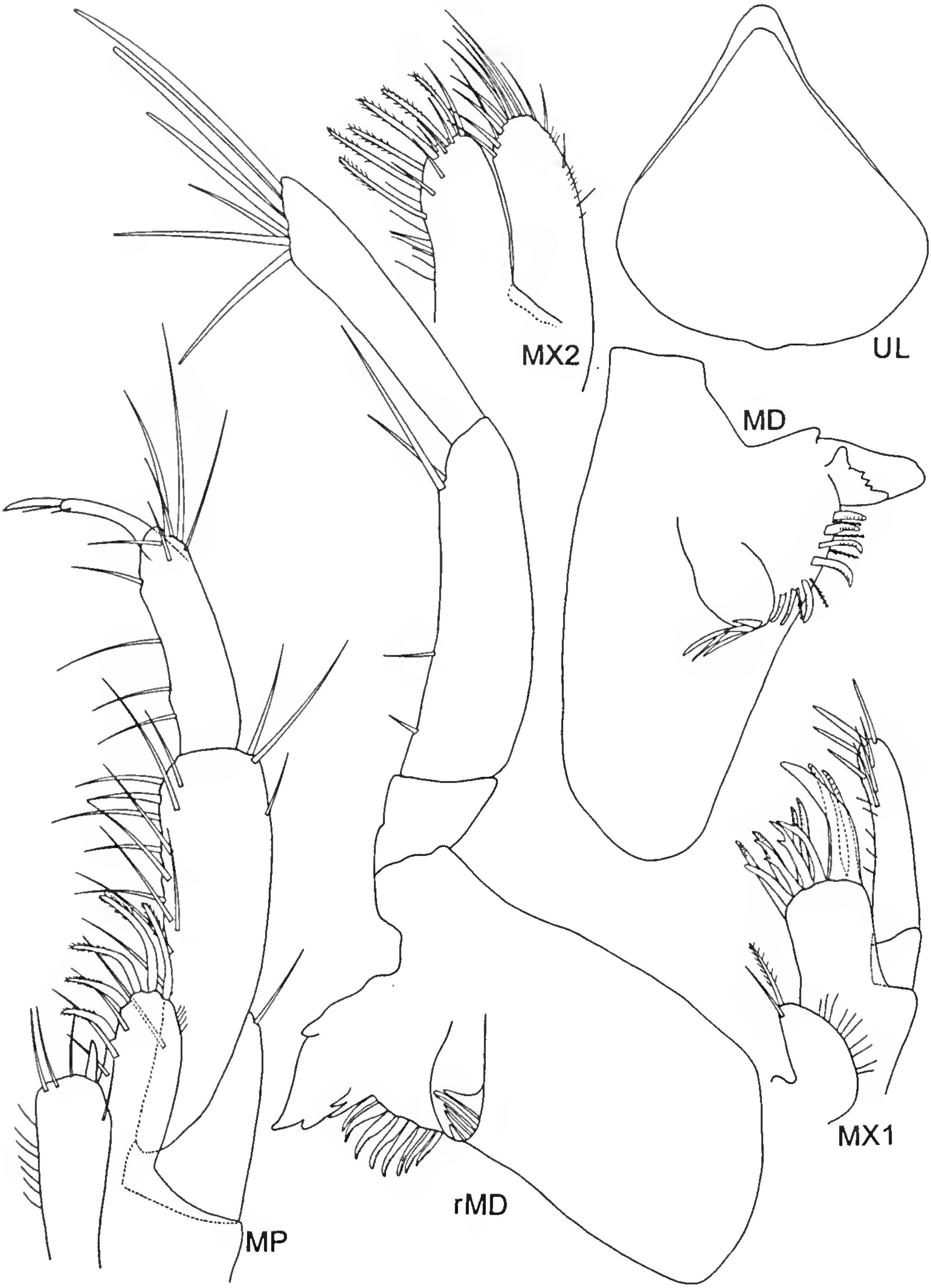

Figure 13. *Birubius lowryi* sp. nov., holotype female, tl. 4.75 mm.

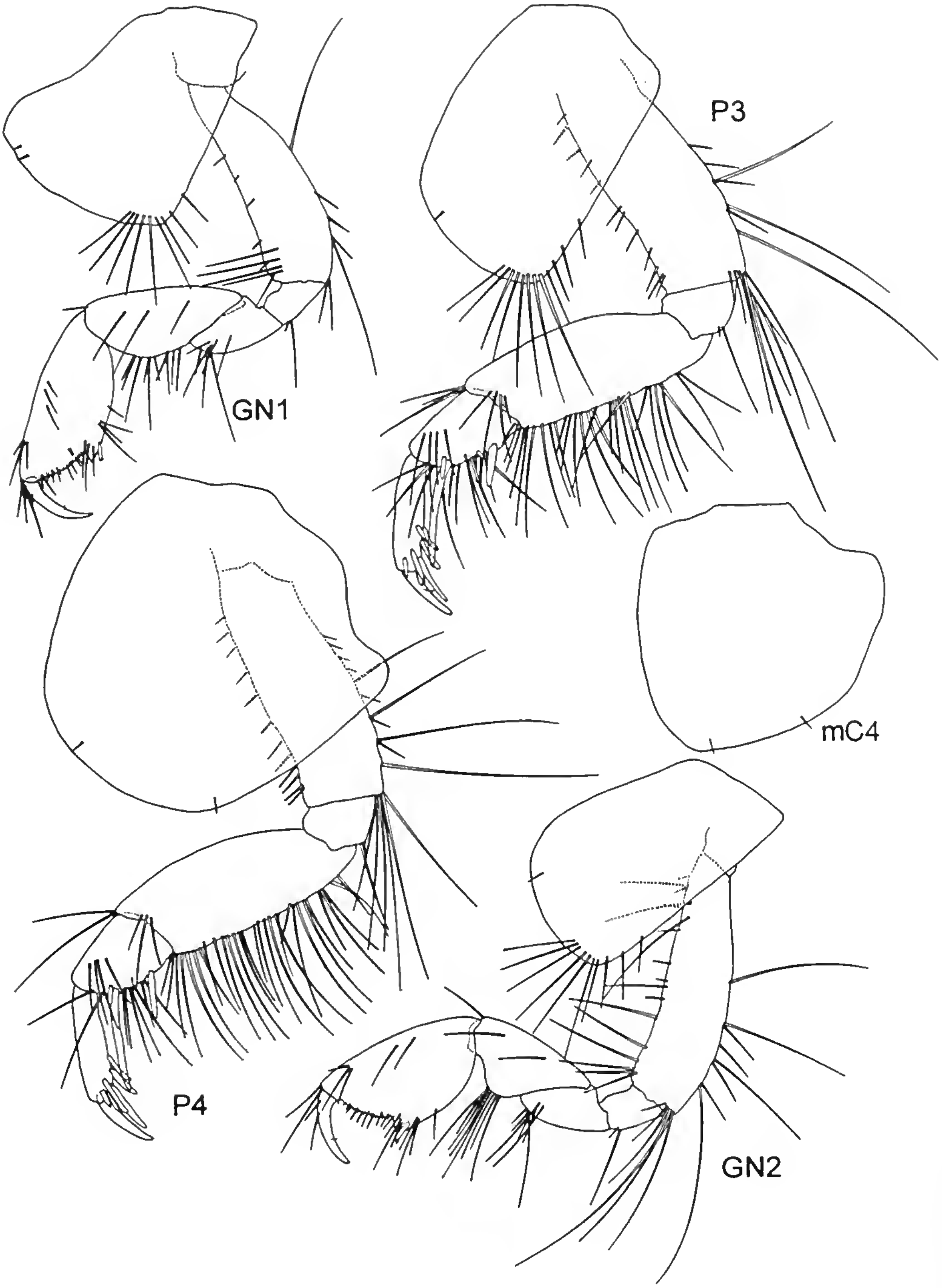

Figure 14. *Birubius lowryi* sp. nov., holotype female, tl. 4.75 mm (m = male allotype, 3.75 mm).

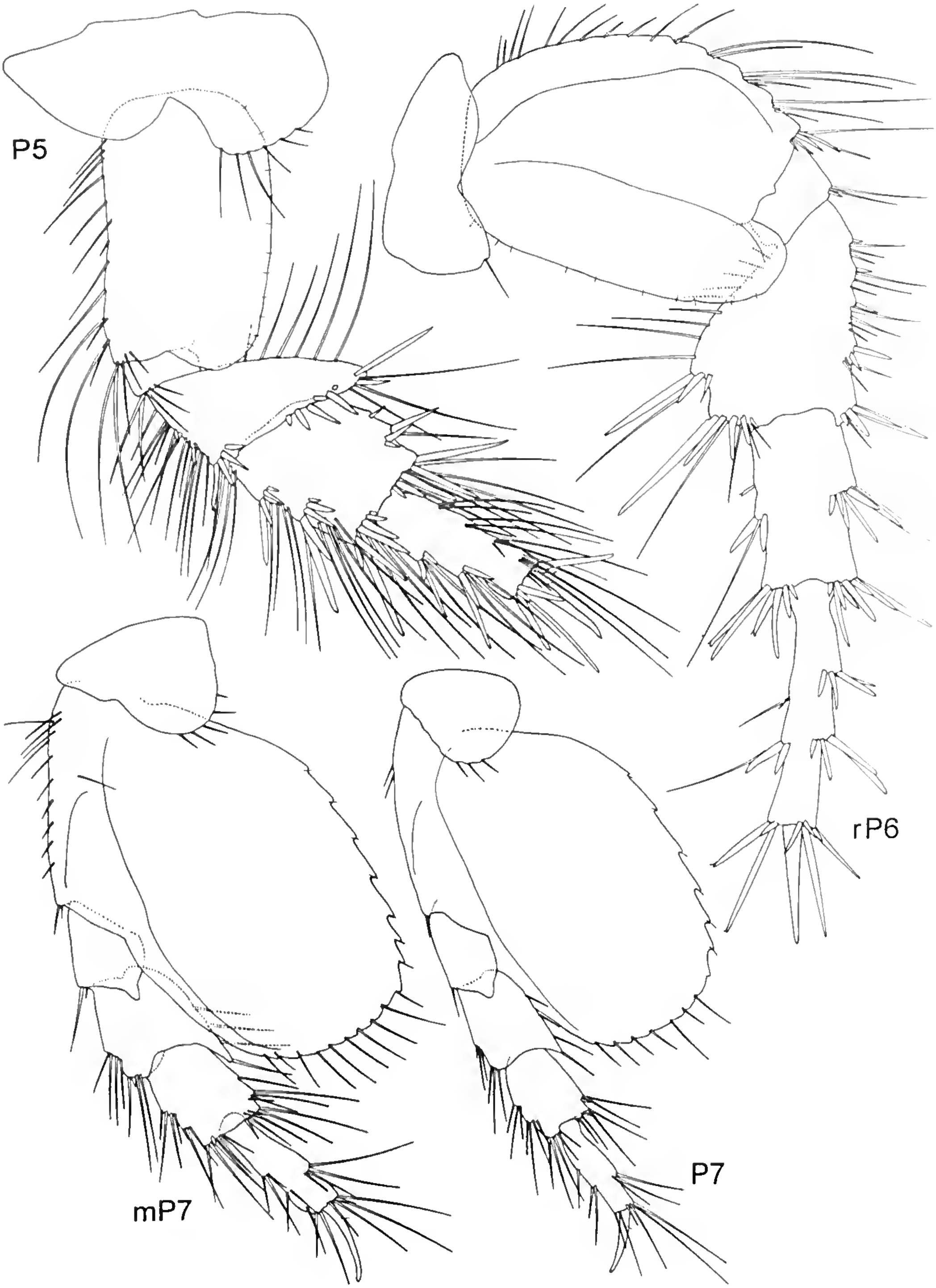

Figure 15. *Birubius lowryi* sp. nov., holotype female, tl. 4.75 mm (m = male allotype, 3.75 mm).

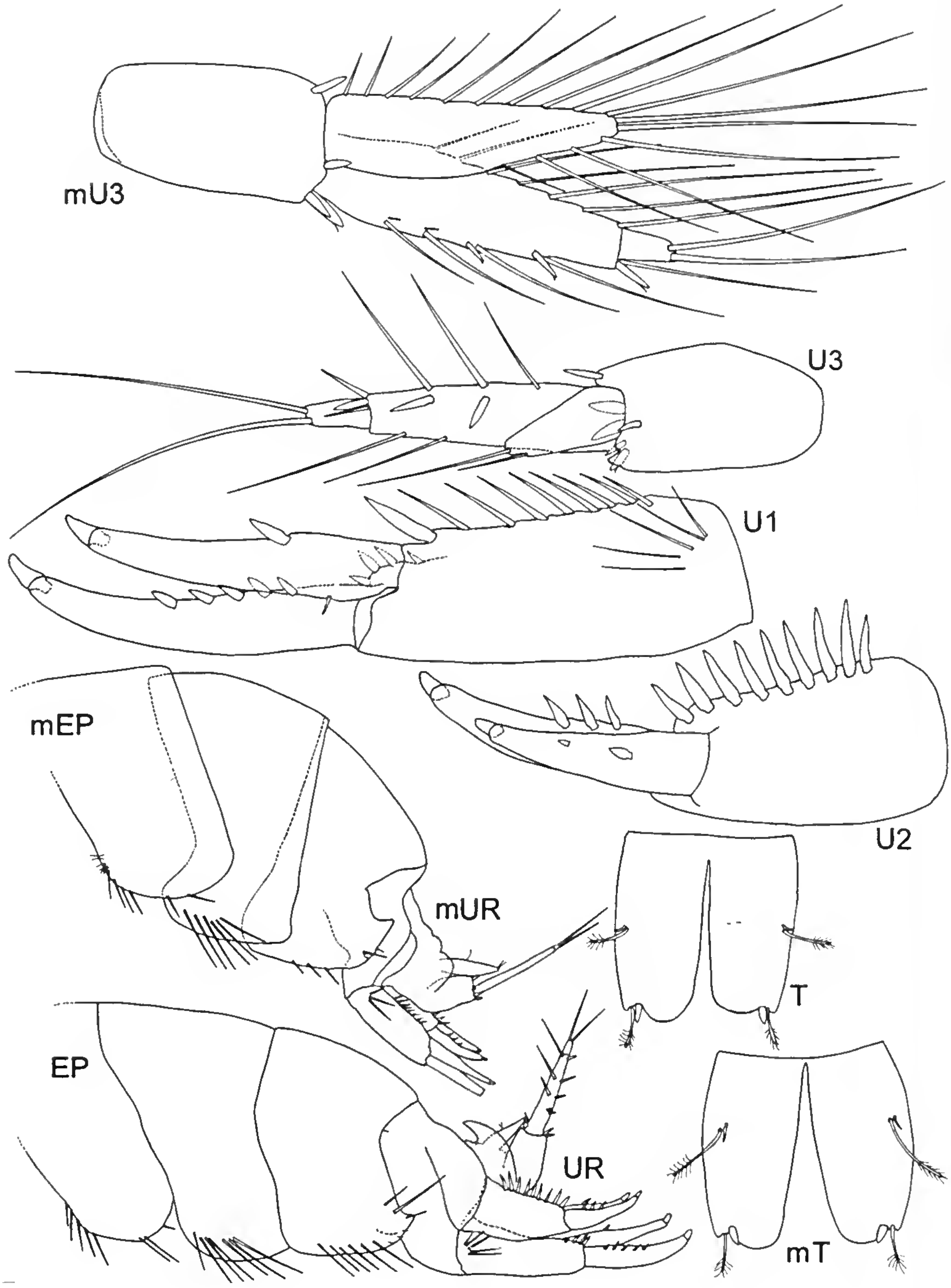

Figure 16. *Birubius lowryi* sp. nov., holotype female, tl. 4.75 mm (m = male allotype, 3.75 mm).

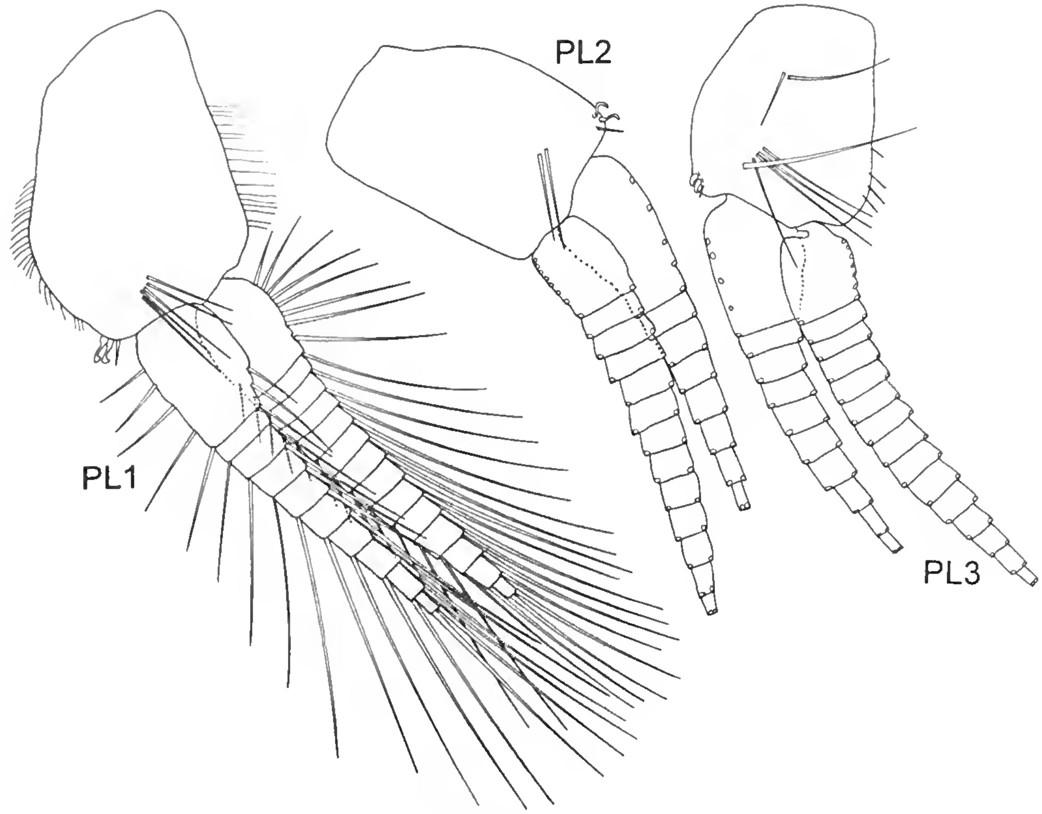

Figure 17. *Birubius lowryi* sp. nov., holotype female, tl. 4.75 mm.

formula = 6-1-3; articles 4–5 of pereopods 5–6 medium to narrow, facial robust setae rows poorly developed, facial ridge formula on basis of pereopods 5–7 = 0-2-2, anterior ridge of pereopod 7 long; width ratios of basis, merus, carpus, propodus of pereopod 5 = 24:27:20:9, of pereopod 6 = 37:23:15:8, of pereopod 7 = 25:7:6:3, length ratios of pereopod 5 = 41:17:26:24, of pereopod 6 = 49:32:26:36, of pereopod 7 = 53:14:13:15; Pereopod 7 basis of reaching apex of merus, moderately setose ventrally. Pleopods 1-3 with 2 coupling hooks; pleopod 1 with 5 distal facial setae, pleopod 2 with 2 distal facial setae, pleopod 3 with 2 mid and 5 distal facial setae; articles on outer rami = 14-13-15, inner rami = 10-8-10.

Epimeron 1 posteroventral corner rounded, anteroventral margin with 5 setae, posteroventral face with 3 medium setae; epimeron 2 posteroventral corner rounded, with 7 facial setae; epimeron 3 posteroventral corner with small to medium tooth, posterior margin almost straight with 3 medium setae, ventral margin with 6 medium setae. Urosomite 1 naked, articulation line almost complete; urosomite 3 with large hook dorsally. Uropods 1–2 rami with articulate enlarged apical nails, uropod 1 outer ramus with 5 dorsal robust setae, inner with 1 dorsomedial robust seta, uropod 2 outer ramus with 3 dorsal robust setae, inner with 2 small robust seta; uropod 1 peduncle with 4 apicolateral robust setae, and 5 basofacial slender setae, medially with many marginal setae plus apical enlarged robust seta; peduncle of uropod 2 with 9 dorsal robust setae; apicolateral corners of peduncles on uropods 1–2 without comb. Uropod 3 unreduced, outer ramus longer than peduncle. Uropod 3 peduncle with 5 ventral robust setae, dorsally with 1 lateral seta; rami feminine, inner extending to M. 41 on article 1 of outer ramus, apex with 2 setae, medial and lateral margins naked, article 2 of outer ramus elongate, 0.26, bearing 2 long setae, apicomedial margin of article 1 with 2 setae, lateral margin with 3 acclivities, robust setal formula = 1-1-1-0, slender setal formula = 1-1-1-1. Telson, length-width ratio = 27:26, not fully cleft, each apex wide, rounded, faintly setose, lateral acclivity broad, shallow, bearing ordinary lateral setule, robust setae next medial shorter than setule, midlateral setules diverse.

Description of male. Similar to female but eyes larger. Antenna 1 like female but with dense medial setation on peduncular article 1; primary flagellum bearing calceoli. Antenna 2 elongate, peduncular articles 3–4 with dense dorsal setation, peduncular article 5 about as long as article 4, dorsal margin lacking calceoli bearing 2 groups of male setae, flagellum 28–articulate bearing calceoli. Maxilliped and maxillae 1–2 similar to female. Right mandible damaged; left lacinia mobilis with 6 spines; left rakers 9, left molar with 7 long robust setae, palp similar to female, article 3 with 1 basofacial seta. Main ventral setae of coxae 1–4 = 5-7-6-0, Gnathopods 1–2 similar to female. Urosomite 3 without large hook dorsally. Uropod 1 outer ramus with 3 dorsal robust setae, inner with 1 dorsomedial robust seta, uropod 2 outer ramus with 3 dorsal robust setae, inner with 1 dorsal robust seta; uropod 1 peduncle with 3 apicolateral robust setae, with 3 basofacial slender setae; uropod 2 peduncle with 8 dorsal robust setae. Uropod 3 with inner ramus falling short of article 1 on outer ramus. Telson elongate, length-width ratio = 14:13.

Etymology. For Dr Jim Lowry, in gratitude for his assistance and advice during the first author's visit to examine Australia Museum collections.

Remarks. The following variations from the holotype were observed in the paratypes and material examined. The main ventral setae of coxae 1–4 = (5-7)-(5-7)-(5-7)-0. Uropod 1 outer ramus with 3–4 dorsal robust setae, inner ramus with 1 dorsal robust seta. Uropod 2 outer ramus with 2–3 dorsal robust setae, inner ramus with 1 dorsal robust seta.

Birubius lowryi conforms well to Barnard and Drummond's (1978) diagnosis of *Birubius* except that it exhibits a dorsal hook on urosomite 3 as seen in *Tickalerus* and *Kulgaphoxus*. It varies from these genera in the lack of a shortened outer ramus of uropod 3. It differs from the other new species described herein by the combination of characters listed in the diagnoses. It can be distinguished from *B. wilsoni*, the only other species described from Papua New Guinea, by the absence of posterior setae on coxae 1–3, long ventral setae on coxa 4 and the presence of proximoposterior setae on the carpus of pereopods 3–4. The species is number MoV3667 in Museum Victoria's TAXA database.

Birubius wallisae sp. nov.

Figures 18–24

Material examined. Holotype. Australia, Queensland, N entrance to Moreton Bay (27°02.85′S, 153°20.11′E), 19 m, Smith-McIntyre grab, G.C.B. Poore, 16 Mar 1998 (stn ASB/6/24), NMV J47236 (1 female, tl. 5.0 mm).

Allotype. Australia, Queensland, Middle Banks, Moreton Bay (27°15′S, 153°15′E), 18 November 1976 (stn 6), QM W25241 (1 male, tl 4.8 mm).

Paratypes. Australia, Queensland, N entrance to Moreton Bay, all Smith-McIntyre grab, G.C.B. Poore, 16 Mar 1998: 27°02.94′S, 153°20.04′E, 24 m, (stn ASB/6/21), NMV J47237 (3 females, tl. 3.45–4.45 mm); 27°02.34′S, 153°19.42′E, 11 m, (stn ASB/6/26), NMV J41725 (1 female, tl. 4.10 mm); 27°02.34′S, 153°19.47′E, 13 m, (stn ASB/6/28), NMV J41726 (1 female, tl. 3.0 mm). Queensland, Middle Banks, Moreton Bay (27°15′S, 153°15′E), 18 Nov 1976 (stn 6), QM W8682 (12 females, tl. 3.10–4.75 mm, 9 males, tl. 4.10–4.80 mm).

Diagnosis. Rostrum constricted. Antenna 2, article 4 without well developed dorsal setation. Right lacinia mobilis bifid, distal branch simple. Pereopods 3–4 carpus with 2–3 proximoposterior robust setae. Pereopod 5 dactyl fully formed. Pereopod 7 basis without long ventral setae. Coxa 1 not expanded distally. Coxa 4 lacking long ventral setae. Epimeron 3 without tooth; with ventral setae; without long posterior seta; with oblique row of facial setae. Urosomite 3 with large dorsal hook. Uropod 1 with basofacial setae. Uropods 1–2 inner rami lacking accessory apical nails. Uropod 3 unreduced, outer ramus longer than peduncle.

Description of female. Head about 16% of total body length, greatest width about 100% of length; rostrum constricted, narrow, exceeding apex of peduncular article 1 on antenna 1. Eyes large, occluded with pigment. Antenna 1 peduncular article 1 about 1.3 times as long as wide, about 2.1 times as wide as peduncular article 2, ventral margin with 8 setules, unproduced dorsal apex with 1 setule; peduncular article 2 about 0.75 times as long as peduncular article 1, with 6 ventral setae; primary flagellum with 12 articles, about 0.6 times as long as peduncle, lacking aesthetases; accessory flagellum with 10 articles. Antenna 2, peduncular article 4 robust setae formula = 1-2-4-5, dorsal margin with notch bearing 1 robust seta and 1 slender seta, ventral margin with 7–8 groups of 1–2 long to short setae, with ventrodistal robust seta; peduncular article 5

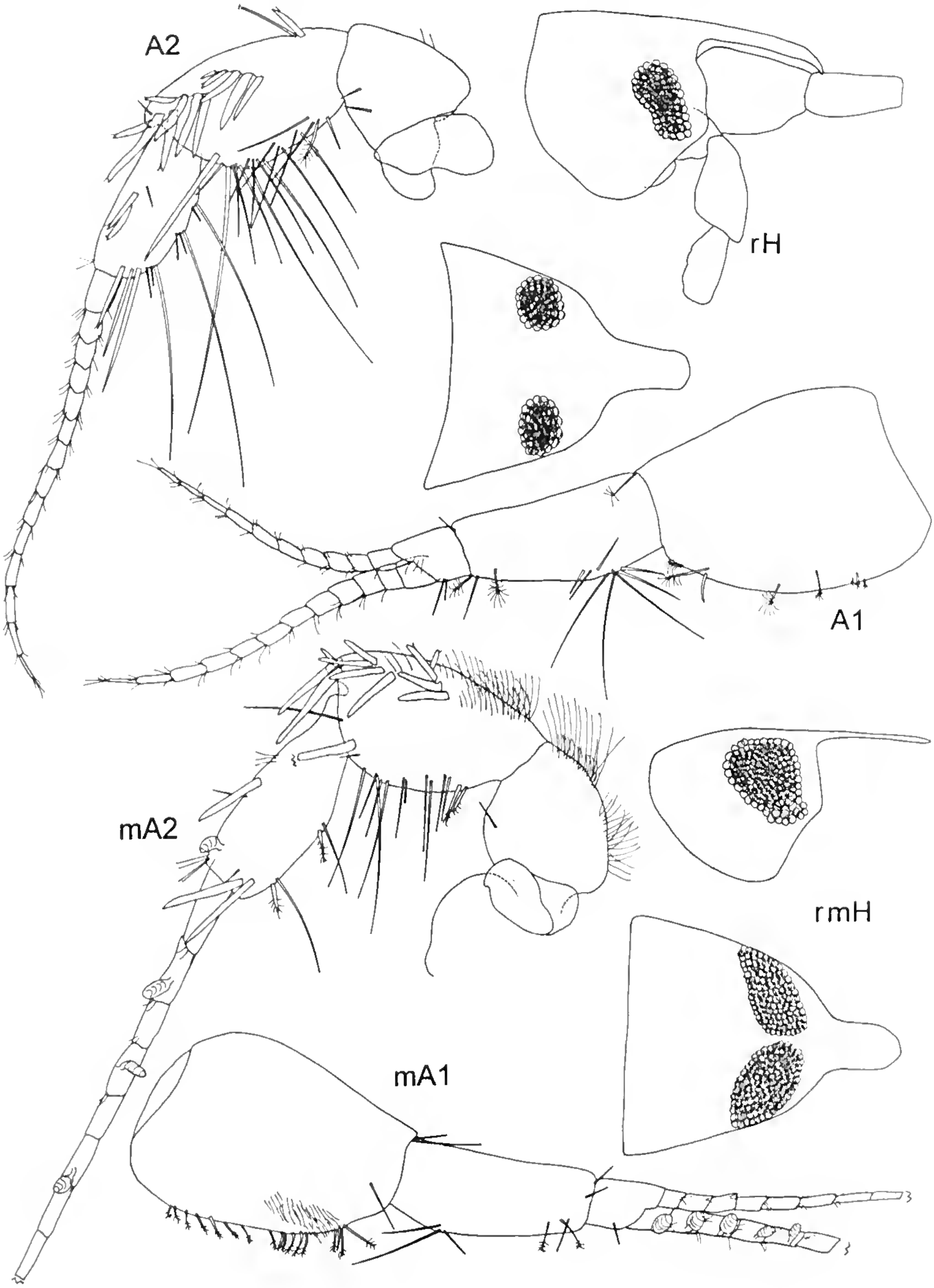

Figure 18. *Birubius wallisae* sp. nov., holotype female, tl. 5.00 mm (m = male allotype, 4.80 mm).

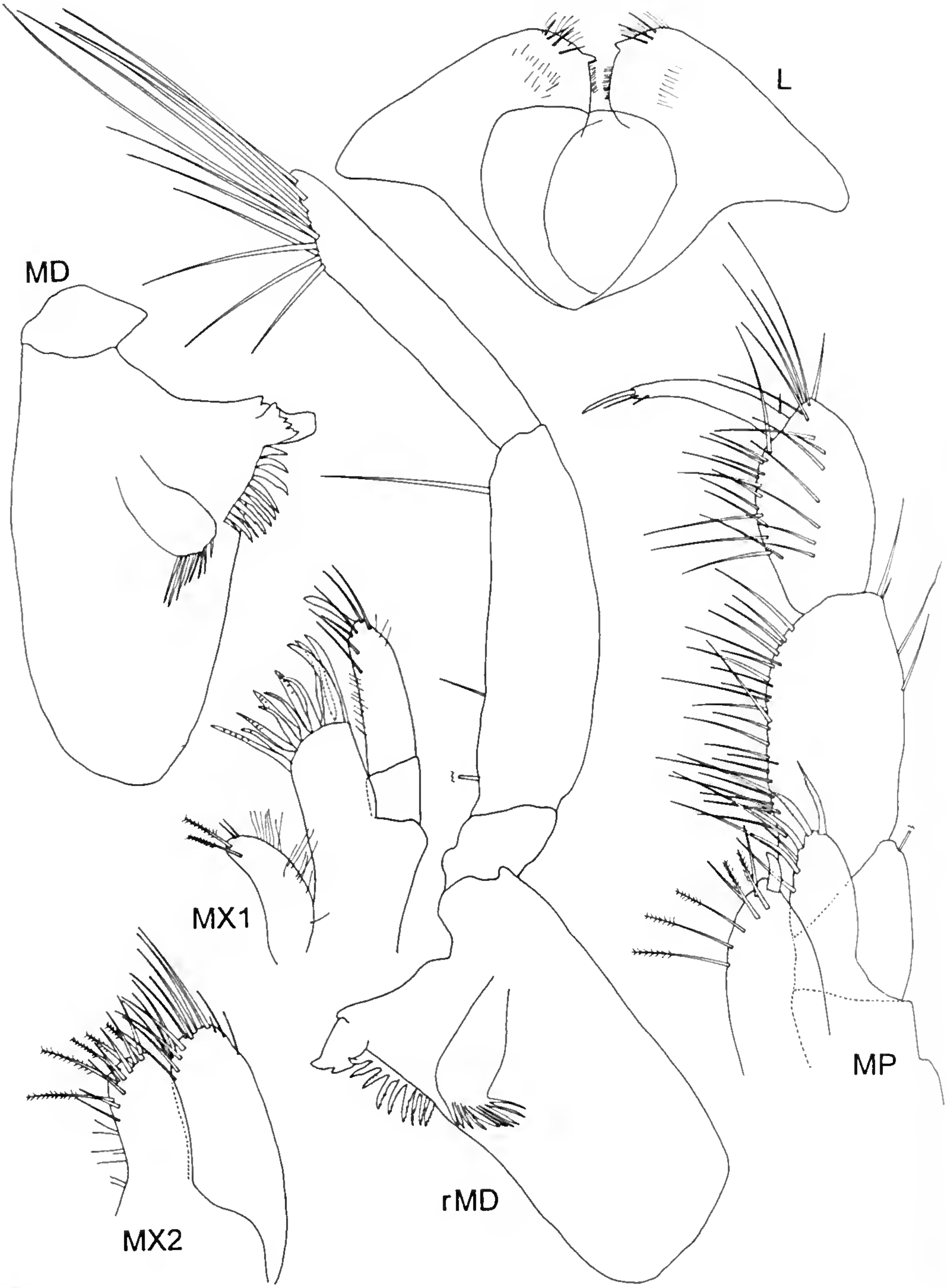

Figure 19. *Birubius wallisae* sp. nov., holotype female, tl. 5.00 mm.

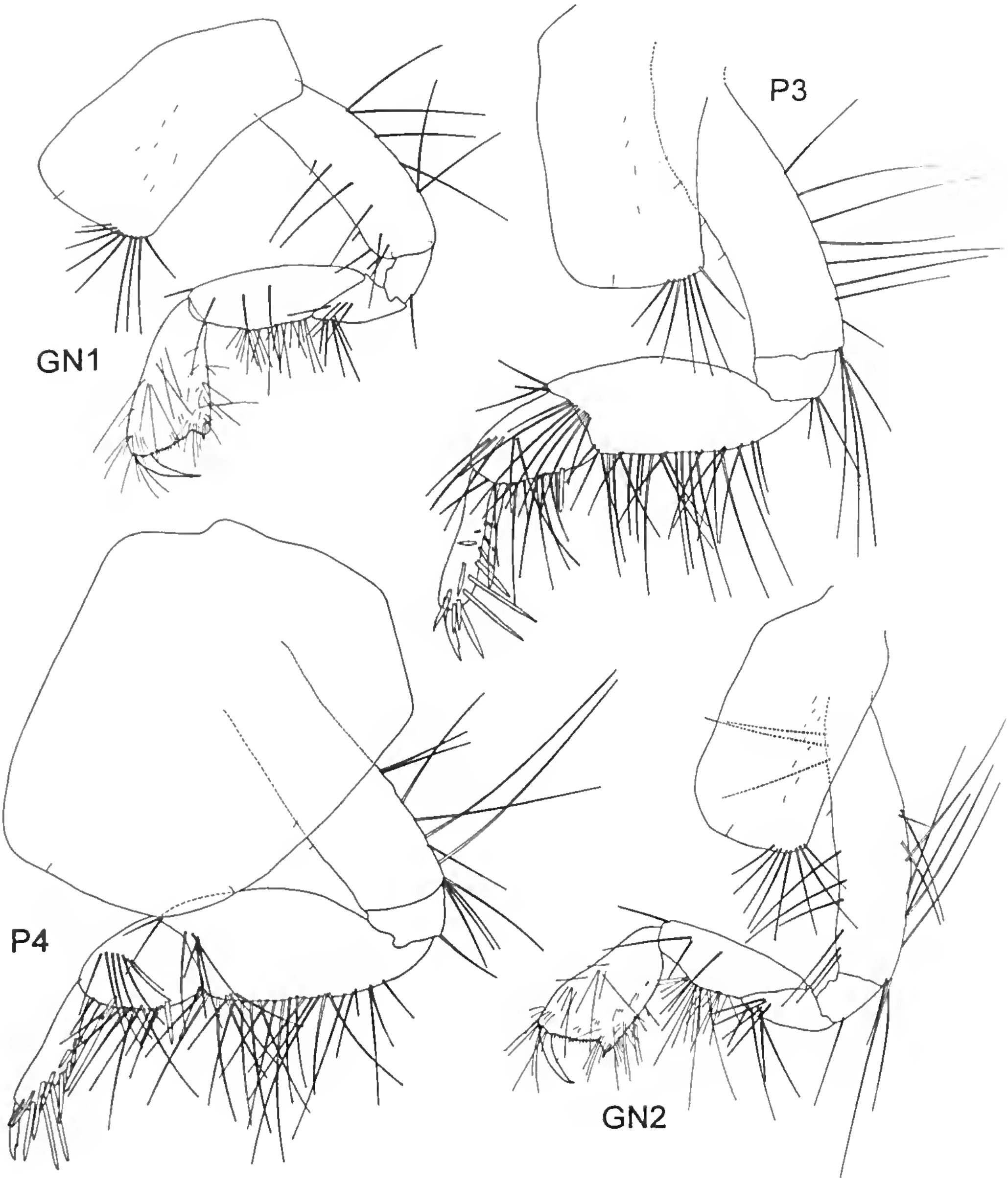

Figure 20. *Birubius wallisae* sp. nov., holotype female, tl. 5.00 mm.

about 0.7 times as long as peduncular article 4, facial robust seta formula = 0–2, dorsal margin naked, ventral margin with 3 sets of 1–3 long to short setae, 2–3 ventrodistal long to medium robust setae; flagellum 1.15 times as long as peduncular articles 4–5 combined, with 14 articles. Mandibles with medium palpar hump; right incisor with 3 teeth; left incisor with 2 humps in 2 branches; right lacinia mobilis bifid, distal branch shorter than proximal branch, simple, pointed, proximal branch simple, pointed; left lacinia mobilis with 5–6 teeth; right raker 8; left rakers 9; molar in form of short protrusion demarcated mainly by robust setae, right molar with 10

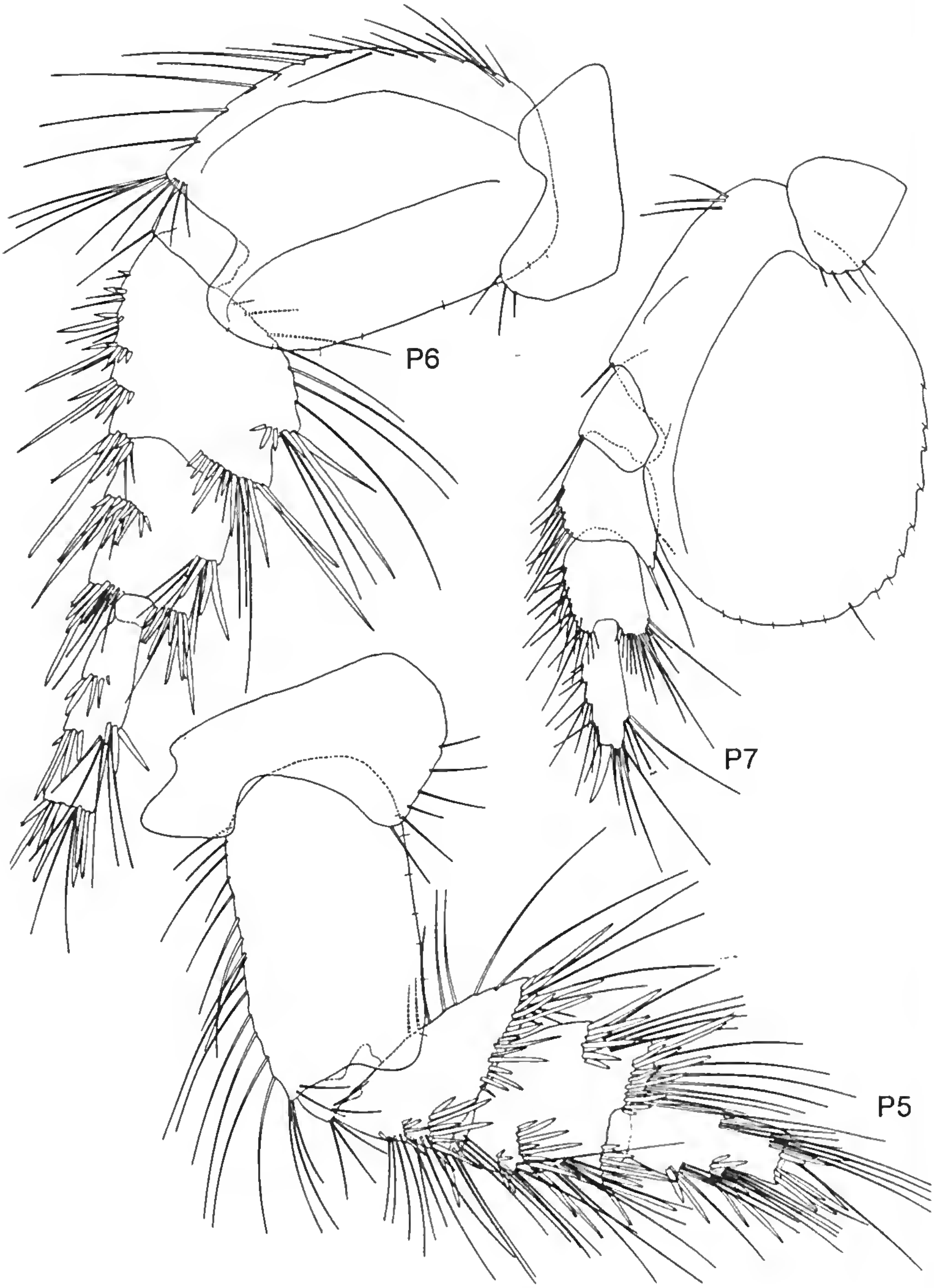

Figure 21. *Birubius wallisae* sp. nov., holotype female, tl. 5.00 mm.

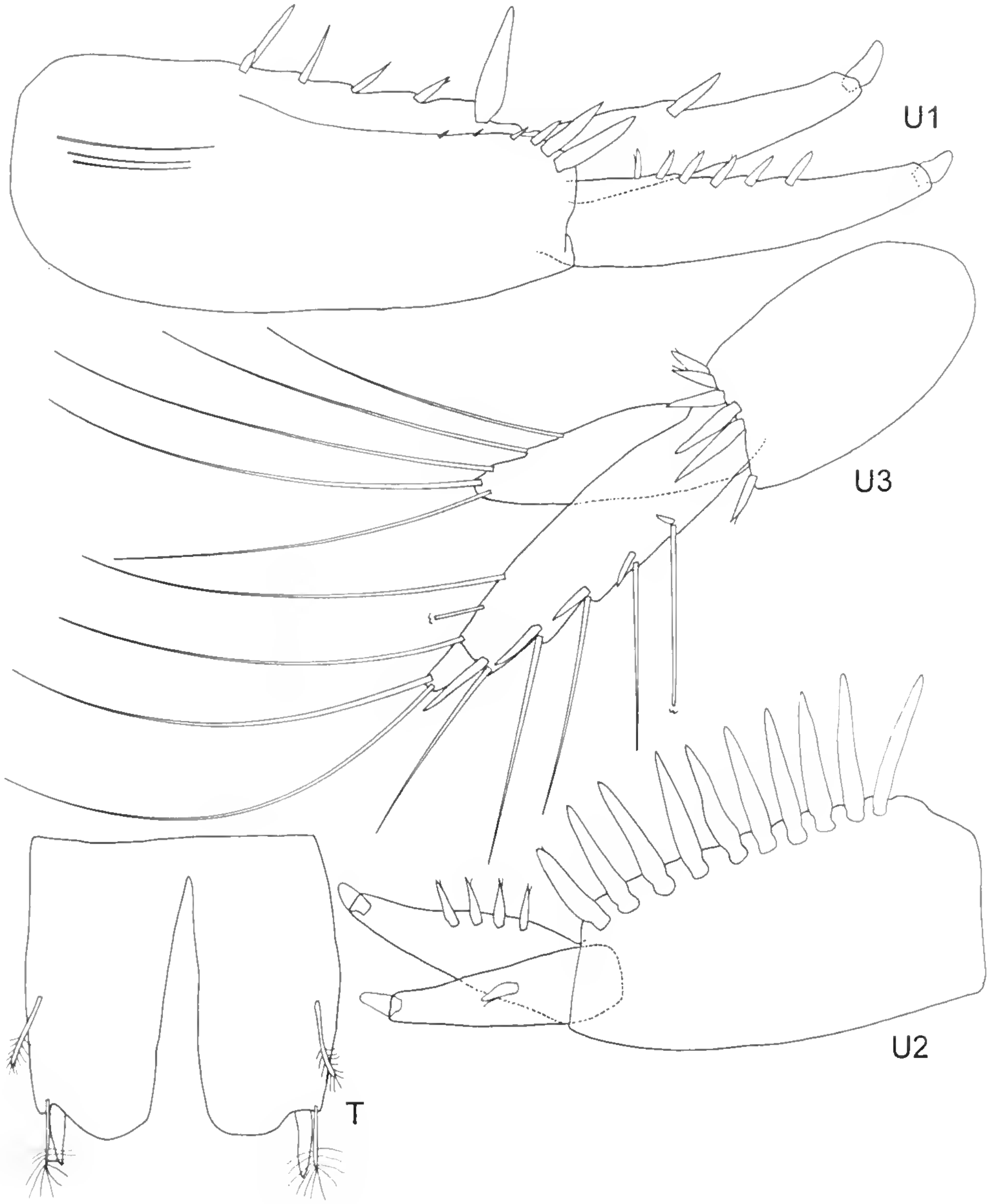

Figure 22. *Birubius wallisae* sp. nov., holotype female, tl. 5.00 mm.

long robust setae, left molar with 8 long robust setae, no seta disjunct; palp article 1 short, article 2 with 1 long inner apical seta, and 2 other medium inner setae, article 3 about 0.91 times long as article 2, apex oblique with 11 robust to slender setae, without basofacial setae. Maxilla 1 inner plate narrow, bearing 1 long apical seta, 1 shorter apicomedial seta plus 2 shorter apical setae; palp article 2 with 1 apicomedial marginal robust seta, 3 apicomedial setae and 3 submarginal setae. Maxilla 2 inner and outer plates extended equally. Maxilliped inner plates with 1 large thick apical robust seta, 5 apicofacial setae, 1 medial seta; outer plate with 6 medial and api-

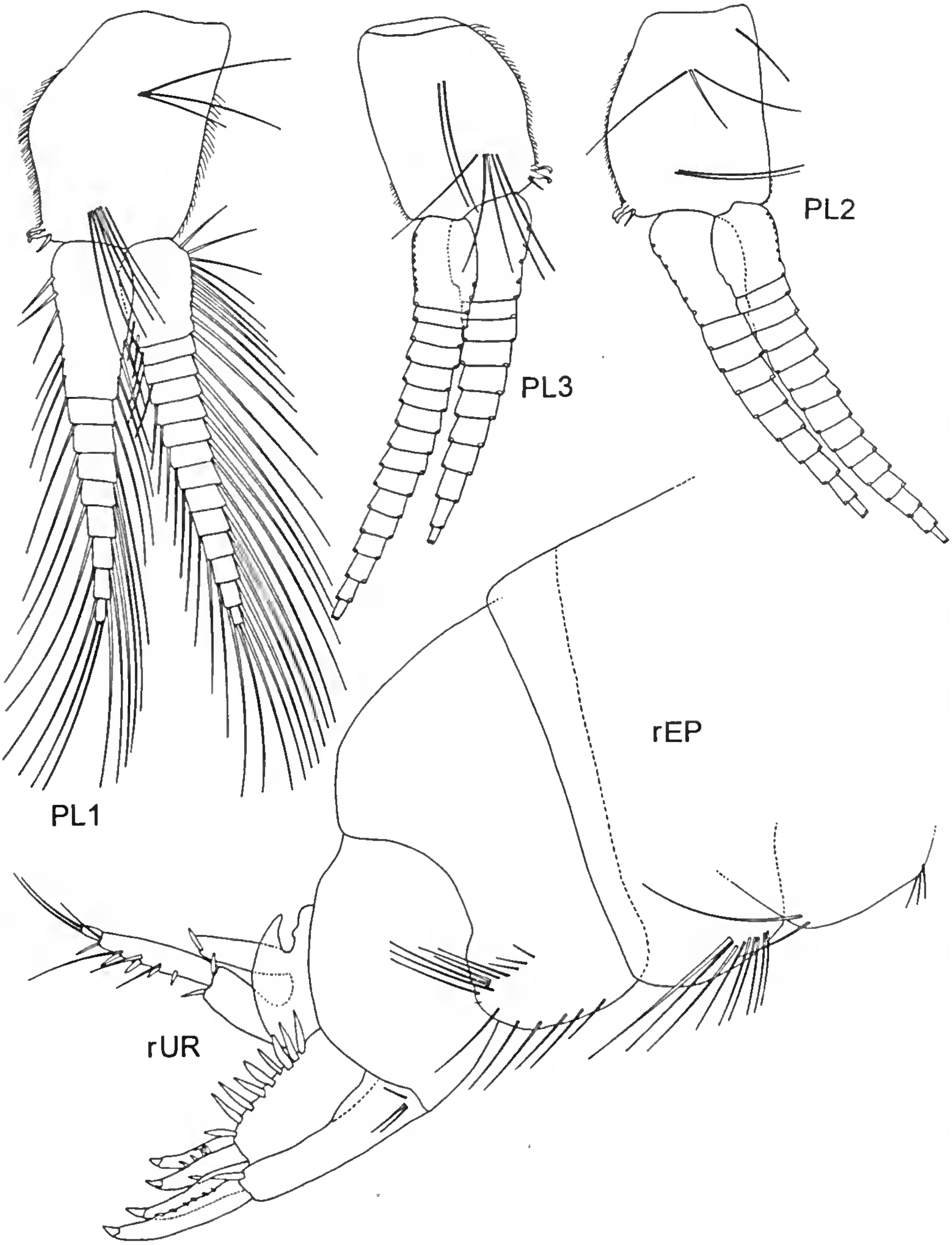

Figure 23. *Birubius wallisae* sp. nov., holotype female, tl. 5.00 mm.

cal robust setae; palp article 1 with 1 apicolateral seta, article 2 with 2 apicolateral setae and 2 other lateral seta, article 3 slightly protuberant, with 7 facial setae, nail of article 4 medium length, with 2 accessory setules. Coxa 1 unexpanded distally; main ventral setae of coxae 1–4 = 9-8-7-0, posteriormost seta of coxae 1–3 shortened; anterior and posterior margins of coxa 4 divergent, pos-

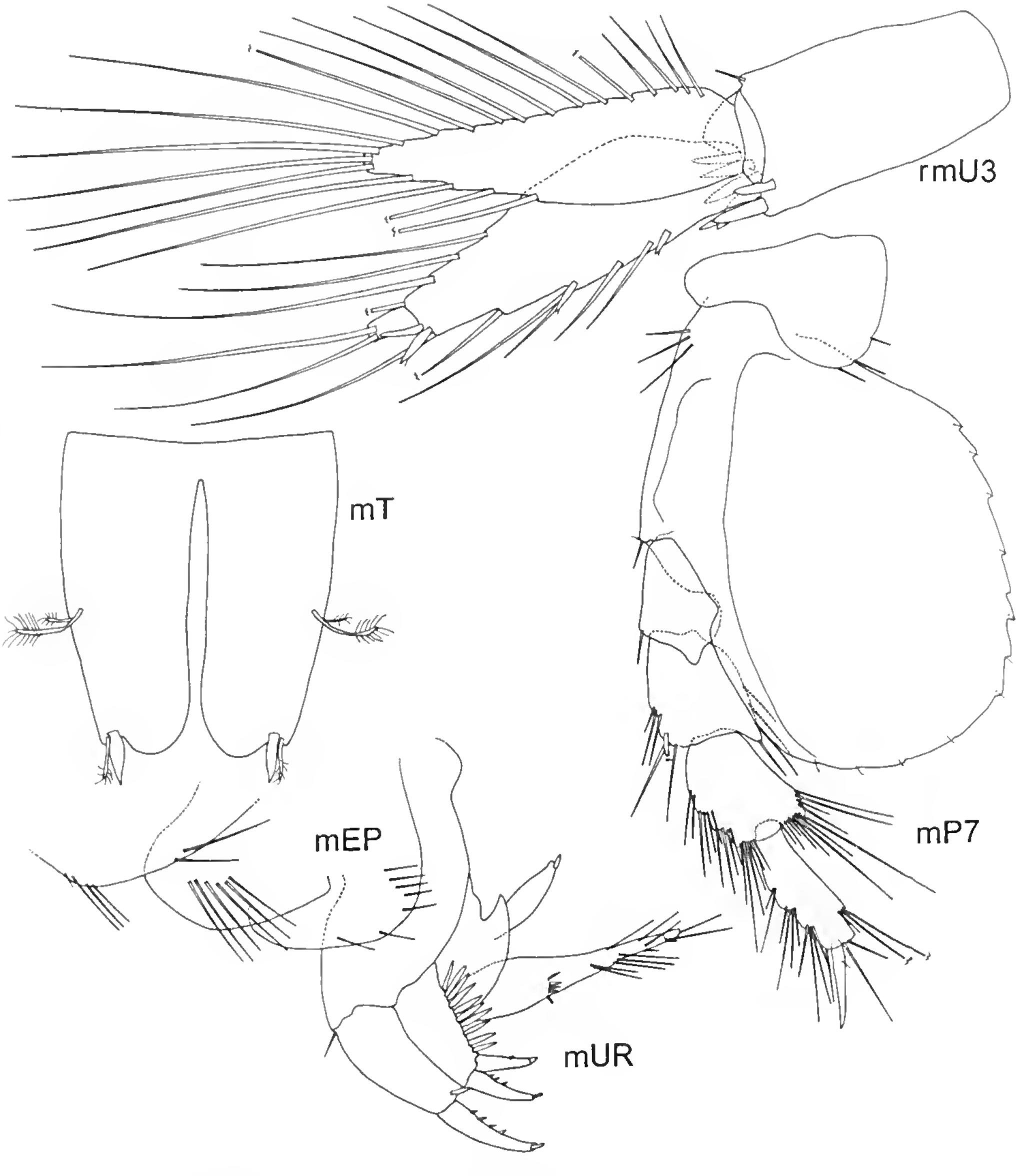

Figure 24. *Birubius wallisae* sp. nov., allotype male, tl. 4.80 mm.

terior margin oblique, posterodorsal corner rounded, posterodorsal margin medium, straight, width-length ratio of coxa 4 almost = 5:6. Long posterior setae on basis of gnathopods 1–2 and pereopods 3–4 = 6-10-11-10, short posteriors = 0-0-0-0 , long anteriors = 6-6-0-0, short anteriors = 2-1-4-2.

Gnathopods, width ratios of carpus-propodus on gnathopods 1–2 = 8:11 and 2:3, length ratios = 12:11 and 1:1; palmar humps ordinary, palms oblique; gnathopods 1–2 carpus elongate. Pereopods 3–4 similar, facial setae on merus = 7 and 5, on carpus = 5 and 7; main spine of carpus extending to M. 100+ on propodus, carpus with 1 proximoposterior robust seta; robust setae formula of propodus = 6 + 7; acclivity on inner margin of dactyls of pereopods 3–4 weak, mid-facial seta short. Coxae 5–7 posteroventral seta formula = 6-3-4; merus-carpus of pereopods 5–6 medium to narrow, facial robust setae rows poorly developed, facial ridge formula on basis of pereopods 5–7 = 0-2-2, anterior ridge of pereopod 7 short; width ratios of basis, merus, carpus, propodus of pereopod 5 = 26:28:25:11, of pereopod 6 = 41:31:19:8, of pereopod 7 = 50:15:12:6, length ratios of pereopod 5 = 47:19:23:25, of pereopod 6 = 27:15:13:16, of pereopod 7 = 60:16:15:18; pereopod 7 basis reaching apex of merus, with 1 medium ventral seta. Pleopods 1–3 with 2 coupling hooks; pleopod 1 with 3 mid and 3 proximal facial setae, pleopod 2 with 2 proximal, 3 mid and 2 distal facial setae, pleopod 3 with 5 proximal and 5 distal facial setae; articles on outer rami = 14-16-15, inner rami = 9-11-10.

Epimeron 1 posteroventral corner rounded, anteroventral margin with 3 setae, posteroventral face with 2 medium to long setae; epimeron 2 posteroventral corner rounded, with 9 facial setae, posteriormost pair set vertically; epimeron 3 posteroventral corner without tooth, posterior margin rounded, naked, midface with oblique row of 9 setae near posterior margin, ventral margin with 6 long setae. Urosomite 1 naked, articulation line barely present; urosomite 3 with large hook dorsally. Uropods 1–2 rami with articulate enlarged apical nails, uropod 1 outer ramus with 6 dorsal robust setae, inner with 1 dorsomedial robust seta, uropod 2 outer ramus with 4 dorsal robust setae, inner with 1 robust seta; uropod 1 peduncle with 3 apicolateral robust setae, 3 smaller setae, and 3 basofacial slender setae, medially with few marginal setae plus apical enlarged robust seta; uropod 2 peduncle with 9 dorsal robust setae; apicolateral corners of peduncles on uropods 1–2 without comb. Uropod 3 unreduced, outer ramus longer than peduncle. Uropod 3 peduncle with 5 ventral robust setae, dorsally with 1 lateral seta; rami feminine, inner extending to M. 76 on article 1 of outer ramus, apex with 2 setae, medial margin naked, lateral margin with 3 long setae, article 2 of outer ramus short, 0.15, bearing 2 long setae, apicomedial margin of article 1 with 2 setae, lateral margin with 4 acclivities, robust setal formula = 1-1-1-1-1, slender setal formula = 1-1-1-1-1. Telson, length-width ratio = 1:1, not fully cleft, each apex wide, rounded, lateral acclivity broad, shallow, bearing ordinary lateral setule, robust setae next medial shorter than setule, single midlateral setule.

Description of male. Similar to female but eyes larger. Antenna 1 like female but with dense medial setation on peduncular article 1; primary flagellum bearing calceoli. Antenna 2 elongate, peduncular articles 3–4 with dense dorsal setation, peduncular article 5 about as long as article 4, dorsal margin bearing 1 calceolus and 2 groups of male setae, flagellum at least 19-articulate (both broken) bearing calceoli. Maxilliped and maxillae 1–2 similar to female. Right lacinia mobilis bifid, distal branch much shorter than proximal branch, simple; proximal branch simple, pointed; left lacinia mobilis with 5 teeth; right raker 6; left rakers 9; right molar with 4 long robust setae, left molar with 6 long robust setae, palp similar to female, article 3 with 2 basofacial setae. Main ventral setae of coxae 1–4 = 6-7-7-0. Gnathopods 1–2 similar to female. Urosomite 3 with large hook dorsally. Uropod 1 outer ramus with 4 dorsal robust setae, inner with 1 dorsomedial robust seta, uropod 2 outer ramus with 3 dorsal robust setae, inner with 1 dorsal robust seta; uropod 1 peduncle with 4 apicolateral robust setae, without basofacial slender seta; uropod 2 peduncle with 10 dorsal robust setae. Uropod 3 with inner ramus elongate, reaching article 1 on outer ramus. Telson elongate, length-width ratio = 11:9.

Etymology. For Dr Elycia Wallis, Museum Victoria, in appreciation of her support during the first author's PhD candidature.

Remarks. The following variations from the holotype were observed in the paratypes and material examined. The main ventral setae of coxae 1–4 = (5-8)-(4-8)-(5-8)-0. Uropod 1 outer ramus with 2–5 dorsal robust setae, inner ramus with 1 dorsal robust seta. Uropod 2 outer ramus with 1–3 dorsal robust setae, inner ramus with 1 dorsal robust seta.

Birubius wallisae conforms well to Barnard and Drummond's (1978) diagnosis of *Birubius* except that it exhibits a dorsal hook on urosomite 3 as seen in *Tickalerus* and *Kulgaphoxus*. It differs from these genera in the lack of a shortened outer ramus on uropod 3 but shares with *Kulgaphoxus* the proximal vs widely spread placement of ventral setae on antennae 1 peduncular article 2. *Birubius wallisae* differs from the other new species in the combination of characters listed in the diagnoses. The species is number MoV3716 in Museum Victoria's TAXA database.

Birubius wilsoni sp. nov.

Figures 25–30

Material examined. Holotype. Papua New Guinea, NW corner of Pig I. (05°9.98´S, 145°50.45´E), 21 m, J. D. Thomas, 4 Feb 1990 (stn PNG 33K), AM P56149 (1 female, tl. 4.20 mm).

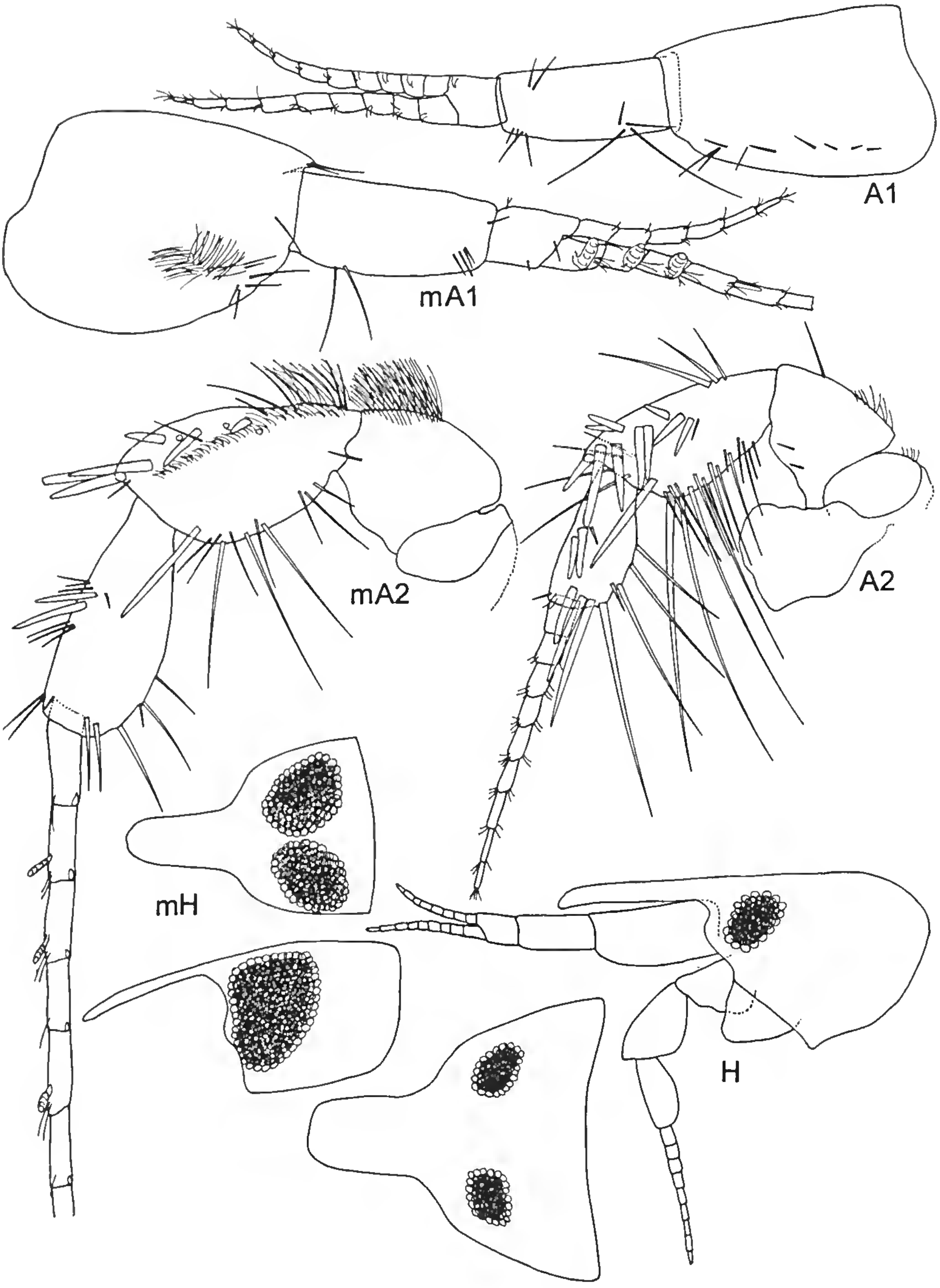

Figure 25. *Birubius wilsoni* sp. nov., holotype female, tl. 4.20 mm (m = male allotype, 3.55 mm).

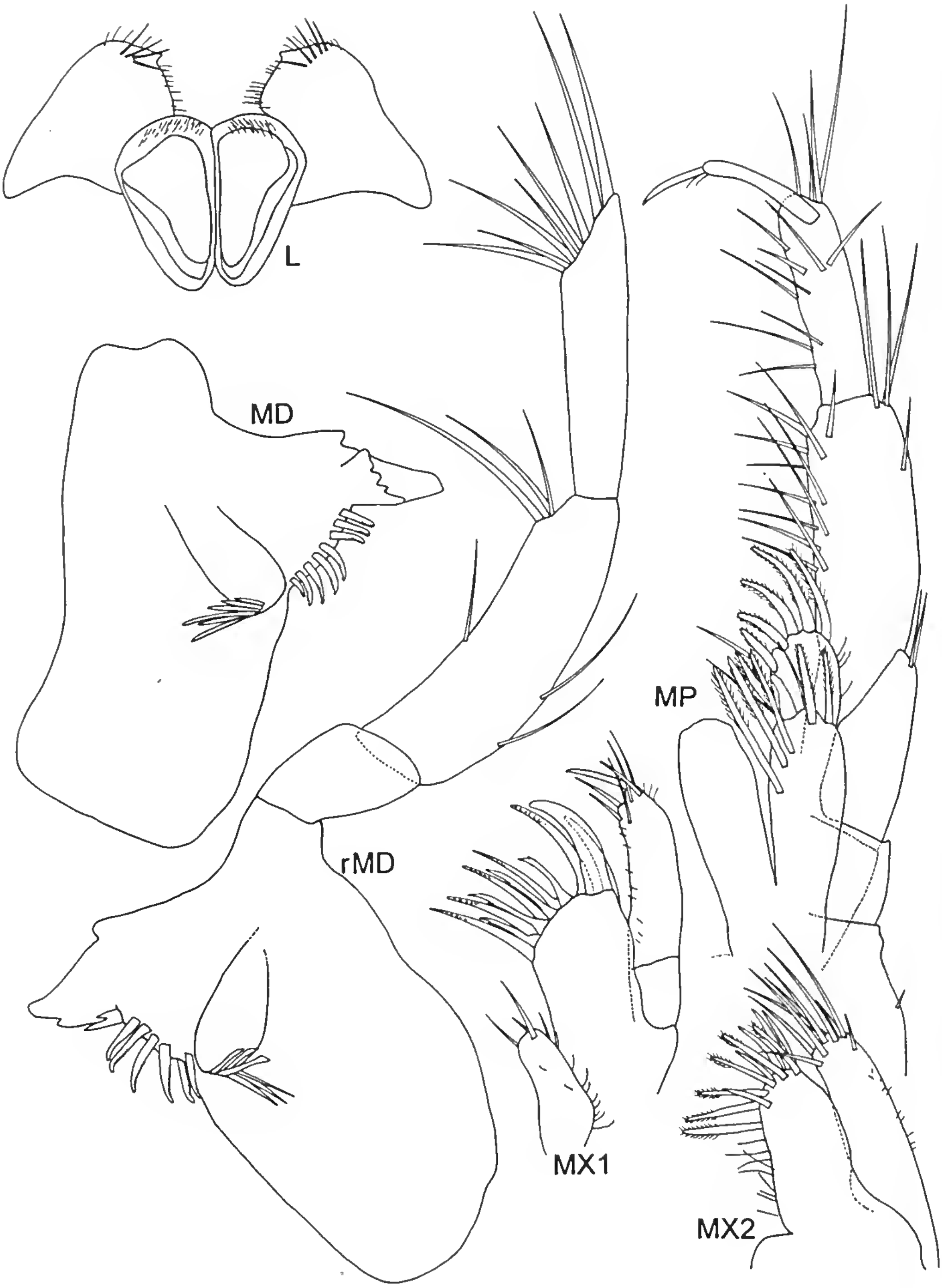

Figure 26. *Birubius wilsoni* sp. nov., holotype female, tl. 4.20 mm.

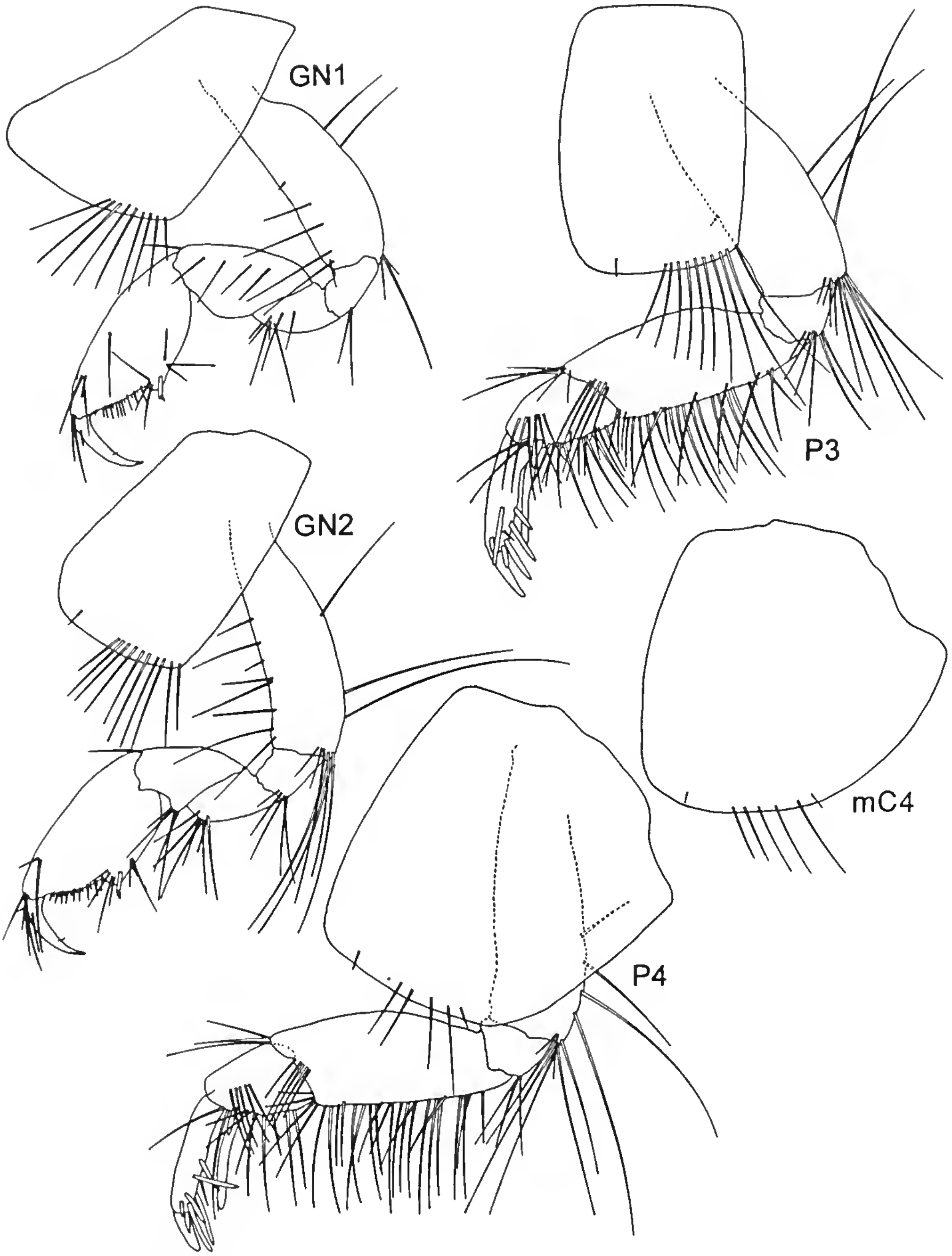

Figure 27. *Birubius wilsoni* sp. nov., holotype female, tl. 4.20 mm (m = male allotype, 3.55 mm).

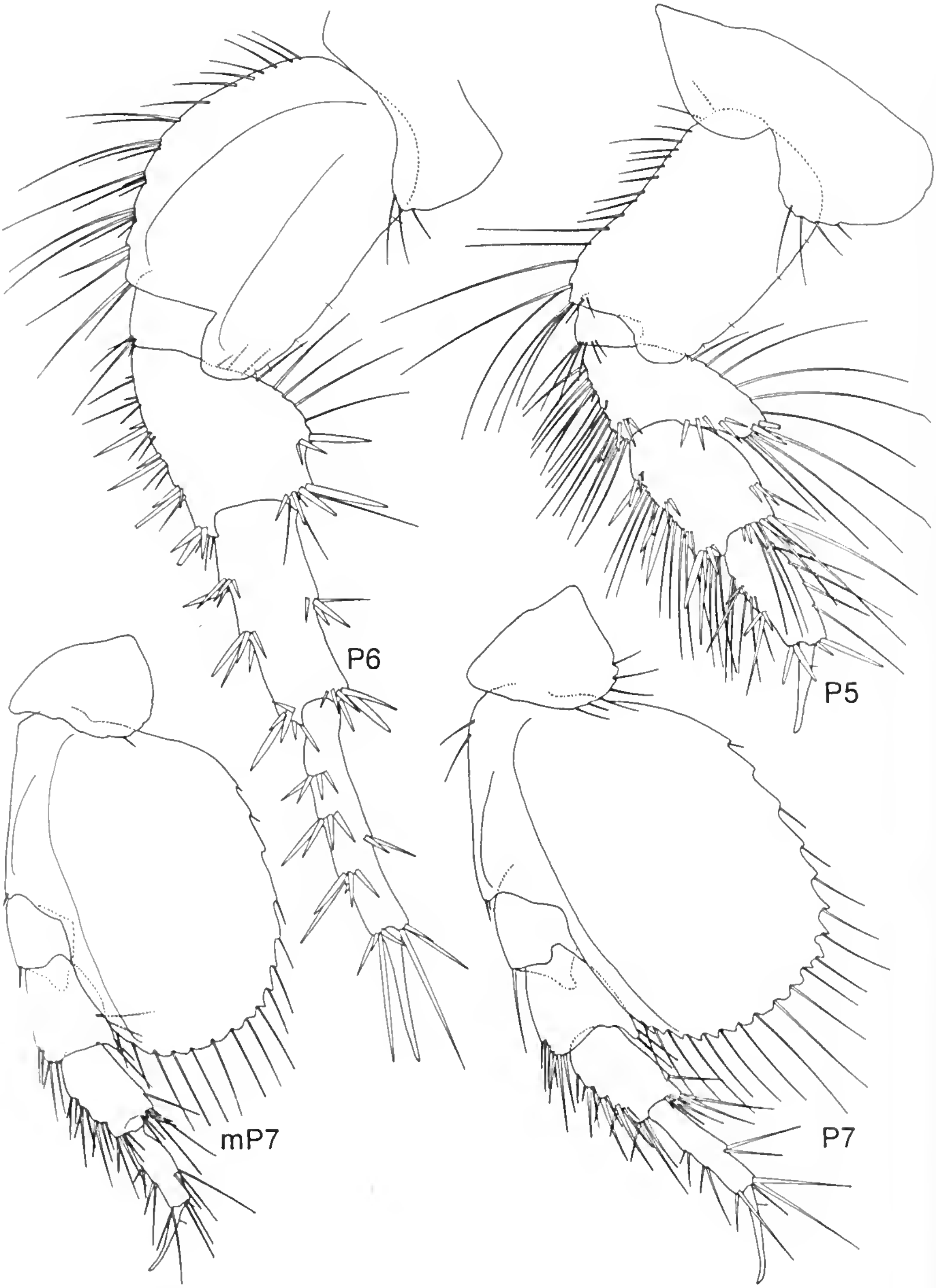

Figure 28. *Birubius wilsoni* sp. nov., holotype female, tl. 4.20 mm (m = male allotype, 3.55 mm).

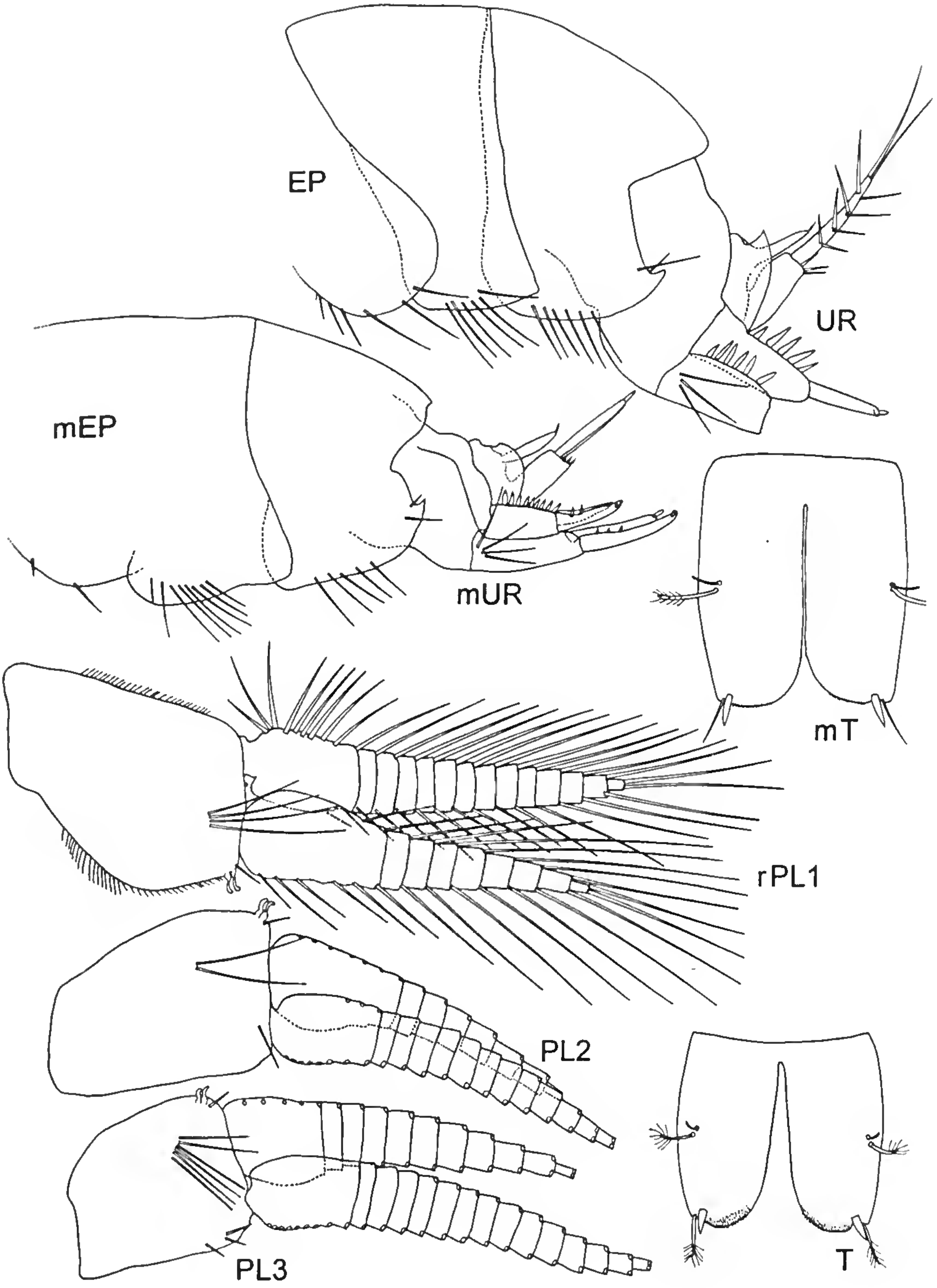

Figure 29. *Birubius wilsoni* sp. nov., holotype female, tl. 4.20 mm (m = male allotype, 3.55 mm).

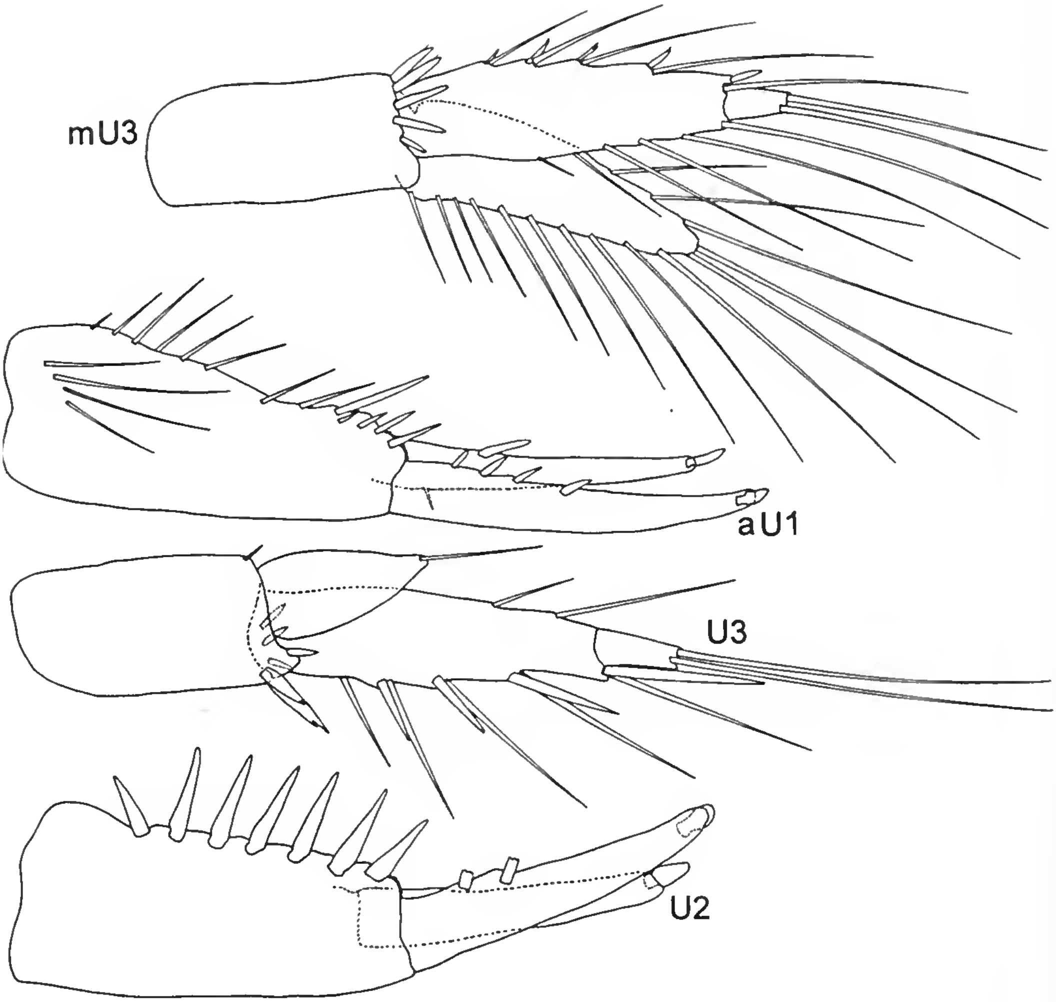

Figure 30. *Birubius wilsoni* sp. nov., holotype female, tl. 4.20 mm (m = male allotype, 3.55 mm).

Allotype. Papua New Guinea, Madang (05°9.57′S, 145°59.93′E), 4 m, J. D. Thomas, 20 Feb 1990 (stn PNG 54), AM P56150 (1 male, tl. 3.55 mm).

Paratypes. Same data as holotype, AM P60002 (1 male, tl. 3.7 mm). Papua New Guinea, Madang (05°9.57′S, 145°59.93′E), 4 m, J. D. Thomas, 20 Feb 1990 (stn PNG 54), AM P60003 (2 females, tl. 4.2–4.8 mm, 53 males, tl. 2.7–3.3 mm).

Diagnosis. Rostrum constricted. Antenna 2, article 4 without well developed dorsal setation. Right lacinia mobilis bifid, distal branch simple. Pereopods 3–4 carpus without proximoposterior robust setae. Pereopod 5 dactyl fully formed. Pereopod 7 basis with long ventral setae. Coxa 1 strongly expanded distally. Coxa 4 with long ventral setae. Epimeron 3 with small tooth; with ventral setae; without long posterior seta; without facial setae. Urosomite 3 with small dorsal hook. Uropod 1 with basofacial setae. Uropods 1–2 inner rami lacking accessory apical nails. Uropod 3 unreduced, outer ramus longer than peduncle.

Description of female. Head about 19% of total body length, greatest width about equal to length; rostrum constricted, narrow, elongate, reaching middle of peduncular article 2 on antenna 1. Eyes medium, pigmented. Antenna 1 peduncular article 1 about 1.6 times as long as wide, about 2.1 times as wide as peduncular article 2, ventral margin with 9 setules, unproduced dorsal apex without setule; peduncular article 2 about 0.66 times as long as peduncular article 1, with 9 ventral setae; primary flagellum with 9 articles, about 0.6 times as long as peduncle, lacking aesthetases; accessory flagellum with 9 articles. Antenna 2, peduncular article 4 robust setae formula = 1-2-4-3, dorsal margin with notch bearing 3 setae, ventral margin with 7–8 groups of 1–2 long to short setae, 1 long ventrodistal robust seta; peduncular article 5 about 0.68 times as long as peduncular article 4, facial robust seta formula = 1–2, dorsal margin naked, ventral margin with 3 sets of 1–2 long to short setae, 2 ventrodistal long to medium robust setae; flagellum 0.85 times as long as peduncular articles 4–5 combined, with 9 articles. Mandibles with medium palpar hump; right incisor with 3 teeth; left incisor with 2 humps in 2 branches; right lacinia mobilis bifid, distal branch much shorter than proximal branch, simple, pointed, proximal branch simple, pointed; left lacinia mobilis with 4–5 teeth; right raker 6; left rakers 8; molar in form of short protrusion demarcated mainly by robust setae, right molar with 6 long robust setae, left molar with 6 long robust setae, no seta disjunct; palp article 1 slightly elongate, article 2 with 3 long-medium inner apical setae and 1 other medium inner seta, article 3 about 0.93 times long as article 2, apex oblique with 8 robust to slender setae, without basofacial setae. Maxilla 1 inner plate narrow, bearing 1 long apical seta, 1 shorter apicomedial seta, 2 apicolateral much shorter seta; palp article 2 with oneapicomedial marginal robust seta, 3 apicomedial setae and 3 submarginal setae. Maxilla 2 inner plate shorter and broader than outer. Maxilliped inner plate with 1 large thick apical robust seta, 2 apicofacial setae, 3 medial setae; outer plate with 5 medial and apical robust setae; palp articles 1 and 2 with 2 and 3 apicolateral seta, article 3 unprotuberant, with 2 facial setae, nail of article 4 long, with 2 accessory setules. Coxa 1 strongly expanded distally; main ventral setae of coxae 1–4 = 9-9-10-6, posteriormost seta of coxae 1–2 medium, of coxa 3 elongate; anterior and posterior margins of coxa 4 strongly divergent, posterior margin oblique, posterodorsal corner rounded, posterodorsal margin medium, undulent, width-length ratio of coxa 4 almost = 29:31. Long posterior setae on basis of gnathopods 1–2 and pereopods 3–4 = 3-8-8-8, short posteriors = 2-2-4-3 , long anteriors = 4-6-0-0, short anteriors = 2-1-1-0.

Gnathopods, width ratios of carpus-propodus on gnathopods 1–2 = 21:24 and 18:25, length ratios = 8:11 and 8:13; palmar humps ordinary, palms oblique; gnathopods 1–2 carpus of medium length. Pereopods 3–4 similar, facial setae on merus = 5 and 5, on carpus = 6 and 5; main spine of carpus extending to M. 87 on propodus, carpus without proximoposterior robust setae; robust setae formula of propodus = 2 + 4 and 2 + 5; acclivity on inner margin of dactyls of pereopods 3–4 weak, midfacial seta short. Coxae 5–7 posteroventral seta formula = 4-3-6; merus-carpus of pereopods 5–6 medium to narrow, facial robust setae rows poorly developed, facial ridge formula on basis of pereopods 5–7 = 0-2-2, anterior ridge of pereopod 7 long; width ratios of basis, merus, carpus, propodus of pereopod 5 = 24:20:14:9, of pereopod 6 = 34:23:14:6, of pereopod 7 = 50:13:9:5, length ratios of pereopod 5 = 38:23:22:27, of pereopod 6 = 24:15:17:18, of pereopod 7 = 58:17:17:18; basis of pereopod 7 reaching apex of merus, heavily setose ventrally. Pleopods 1–3 with 2 coupling hooks; pleopod 1 with 4 distal facial setae, pleopod 2 with 2 distal facial setae, pleopod 3 with 6 mid facial setae; articles on outer rami = 14-13-15, inner rami = 9-8-11.

Epimeron 1 posteroventral corner rounded, anteroventral margin with 4 setae, posteroventral face with 3 medium setae; epimeron 2 posteroventral corner rounded, with 6 facial setae, posteriormost pair set vertically; epimeron 3 posteroventral corner with small to medium tooth, posterior margin almost straight with 2 medium setae, ventral margin with 6 medium setae. Urosomite 1 naked, articulation line absent; urosomite 3 with small hook dorsally. Uropods 1–2 rami with articulate enlarged apical nails, uropod 1 outer ramus with 4 dorsal robust setae, inner with 1 dorsomedial robust seta, uropod 2 outer ramus with 2 dorsal robust setae, inner without robust seta; uropod 1 peduncle with 4 apicolateral robust setae, and 4 basofacial slender setae, medially with many marginal setae plus apical enlarged robust seta; uropod 2 peduncle with 7 dorsal robust setae; apicolateral corners of peduncles on uropods 1–2 with comb. Uropod 3 unreduced, outer ramus longer than peduncle. Uropod 3 peduncle with 6 ventral robust setae, dorsally with 1 lateral seta; rami feminine, inner extending to M. 46 on article 1 of outer ramus, apex with 1 seta, medial and lateral margins naked, article 2 of outer ramus short, 0.23, bearing 2 long setae, apicomedial margin of article 1 with 2 setae, lateral margin with 4 acclivities, robust setal formula = 1-1-1-1-0, slender setal formula = 1-1-1-1-1. Telson, length-width ratio = 55:54, not fully cleft, each apex wide, rounded, setose, lateral acclivity broad, shallow, bearing ordinary lateral setule, robust setae next medial shorter than setule, midlateral setules diverse.

Description of male. Similar to female but eyes larger. Antenna 1 like female but with dense medial setation on peduncular article 1; primary flagellum bearing calceoli. Antenna 2 elongate, peduncular articles 3–4 with dense dorsal setation, peduncular article 5 about as long as article 4, dorsal margin lacking calceoli, bearing 2 groups of male setae, flagellum 24-articulate bearing calceoli. Maxilliped and maxillae 1–2 similar to female. Right mandible damaged, left lacinia mobilis with 5 spines; left rakers 7; molar in form of bulbous hump, left molar with 4 long robust setae, palp similar to female, article 3 with 1 basofacial seta. Main ventral setae of coxae 1–4 = 8-7-8-5. Gnathopods 1–2 similar to female. Pereopod 7 basis narrower than female. Urosomite 3 without hook dorsally Uropod 1 outer ramus with 3 dorsal robust setae, inner with 1 dorsal robust seta, uropod 2 outer ramus with 2 dorsal robust setae, inner without robust seta; uropod 1 peduncle with 2 apicolateral robust setae, with 4 basofacial slender seta; uropod 2 peduncle with 9 dorsal robust setae. Uropod 3 with inner ramus falling short of article 1 on outer ramus. Telson elongate, length-width ratio = 6:5.

Etymology. For Dr Robin Wilson, Museum Victoria, a good friend and colleague of both authors.

Remarks. The following variations from the holotype were observed in the paratypes. The main ventral setae of coxae 1–4 = (7-9)-(7-9)-(8-11)-(6-9). Uropod 1 outer ramus with 1–4 dorsal robust setae, inner ramus with 1 dorsal robust seta. Uropod 2 outer ramus with 2 dorsal robust setae, inner ramus without dorsal robust setae.

Birubius wilsoni conforms well to Barnard and Drummond's (1978) diagnosis of *Birubius* except that it exhibits a dorsal hook on urosomite 3 as seen in *Tickalerus* and *Kulgaphoxus*. It varies from these genera in the lack of a shortened outer ramus on uropod 3 but shares with *Kulgaphoxus* the proximal vs widely spread placement of ventral setae on antennae 1 peduncular article 2. *Birubius wilsoni* differs from the other new species described herein by the combination of characters listed in the diagnoses. It can be distinguished from *B. lowryi*, the only other species described from Papua New Guinea, in the presence of posterior setae on coxae 1–3, long ventral setae on coxa 4 and the absence of proximoposterior setae on the carpus of pereopods 3–4. The species is number MoV3666 in Museum Victoria's TAXA database.

Discussion

Birubius is by far the largest genus of phoxocephalid amphipods, now comprising 38 species from Australia (Barnard and Drummond, 1978), three species from Indonesia (Dana, 1853, Ortiz and Lalana, 1997, 1999) and two species from Papua New Guinea. Species of *Birubius* occur intertidally to 70 m in benthic sandy to muddy sediments. The new species expand the depth and geographic range of the genus from that previously known. The biogeographic relationships between the species from Australian waters and those from Papua New Guinea and Indonesia are as yet unknown but could be elucidated only by cladistic analysis of species of *Birubius*, *Kulgaphoxus*, *Tickalerus* and *Yan*.

Acknowledgements

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Memoirs of Museum Victoria 58(2): 297–333 (2001)

BATHYAL JOEROPSIDIDAE (ISOPODA: ASELLOTA) FROM SOUTH-EASTERN AUSTRALIA, WITH DESCRIPTION OF TWO NEW GENERA

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Abstract

Just, J., 2001. Bathyal Joeropsididae (Isopoda: Asellota) from south-eastern Australia, with description of two new genera. *Memoirs of Museum Victoria* 58(2): 297–333.

Fifty-three species of *Joeropsis*, listed here, have been previously described in this, until now, the only genus of the family. Characters in the Joeropsididae are tabulated and discussed to ascertain which may be diagnositic at family and genus level. *Joeropsis bicarinata* sp. nov., *Rugojoeropsis rugosa* gen. nov., sp. nov., *Scaphojoeropsis multicarinata* gen. nov., sp. nov., and *S. kimblae* sp. nov. are described from the lower shelf and upper bathyal of south-eastern Australia. All are strongly sculptured dorsally.

Introduction

Members of the Joeropsididae Nordenstam have been found around all continents and in all oceans from the North Atlantic and Pacific boreal to the subantarctic. Depths range from the intertidal to the midcontinental slope, with most species occurring on the mid to uppermost shelf. Up until now, the family included a single genus. Between them, Menzies (1962) and Wolff (1962) listed 14 species of *Joeropsis* Koehler; subsequently, 39 species have been described (Table 1).

Hale (1937) reported *J. patagoniensis* Richardson from subantarctic Macquarie I. No further records of Joeropsididae from Australia have been made, although many undescribed species exist in museum collections. The four new species described herein were collected on the lower shelf and upper slope (100–600 m, primarily below 200 m) off south-eastern Australia from south of Sydney to the east and west coasts of Tasmania. The four species differ from all other joeropsidids in having a strongly sculptured dorsum. Of the 53 species previously recognised, only *J. waltervadi* Kensley has some dorsal sculpture in the form of two low, broad, rounded, parallel dorsal ridges on the anterior pereonites. One of the new species is placed in *Joeropsis*; one in a new genus, *Rugojoeropsis*, and two in a second new genus, *Scaphojoeropsis*.

Length of specimens was measured from the tip of the pseudorostrum (see definition below) along the dorsum to the apex of the pleotelson.

Analysis of characters

The new forms of Joeropsididae encountered in this study suggested the possibility that new genera could be differentiated from *Joeropsis*. A comparative analysis of the distribution of characters in the known and new species was undertaken to ascertain what might constitute diagnostic characters at the family and genus levels (Table 2).

Most known species of *Joeropsis* have been incompletely described, which renders interspecific comparisons difficult. Exceptions are *J. mediterranea* Amar, and the redescription, by Bocquet and Lemercier (1958), of *J. brevicornis* Koehler. The description of *J. vibicaria* Barnard contains few useful details. For most species (more than 30), the following aspects are illustrated in the literature: dorsal habitus view, mandible(s), maxilla 1, maxilliped, male pleopod 1, male and female pleopod 2, pleopod 3 and uropod. Other characters are occasionally illustrated and/or described in the text. In many cases, illustrations are difficult to interpret in detail. In several instances text and illustrations do not match.

Where information could be found, the following characteristics were consistent in species of *Joeropsis* and the four new joeropsidid species: general configuration of antennae 1 and 2; presence of a pseudorostrum (see discussion below); no coxae visible in dorsal view; no free pleonites; all pereopods similar, ambulatory; shape of mandibular molar; number of articles in mandibular and maxillipedal palps; general shape of maxillae 1 and 2 (except *Scaphojoeropsis kimblae* sp. nov., maxilla 2 is strongly reduced); general shape of male and female pleopods; general shape of uropods. These characters are considered here to be diagnostic of Joeropsididae.

Table 2 compares another 21 characters potentially useful in discriminating between joeropsidid genera. Where 30 (an arbitrary selection reflecting availability of information) or more of

Table 1. Species of *Joeropsis* with area of type locality.

J. affinis Kussakin, 1961 (Sea of Okhotsk, Kurile Is)
J. antarctica Menzies and Schultz, 1968 (South Shetland Is)
J. antillensis Müller,1993 (Martinique)
J. beuroisi Kensley, 1975 (South Africa)
J. bicarinata sp. nov.(south-eastern Australia)
J. bifasciata Kensley, 1984a (Belize)
J. bourboni Müller, 1990a (Réunion)
J. brevicornis Koehler, 1885 (North-east Atlantic)
J. caboverdensis Müller, 1988 (Cape Verde Is)
J. ceylonensis Müller, 1991a (Sri Lanka)
J. concava Schultz, 1966 (Santa Cruz Canyon)
J. coralicola Schultz and McCloskey, 1967 (North Carolina)
J. curvicornis (Nicolet, 1849) (Chile)
J. dollfusi Norman, 1899 (Mediterranean)
J. dubia Menzies, 1951 (California)
J. faurei Müller, 1990a (Réunion)
J. gertrudae Müller, 1989a (Society Is)
J. hawaiiensis Miller, 1941 (Hawaii)
J. indica Müller, 1991a (Sri Lanka)
J. integra Kensley, 1984b (South Africa)
J. intermedia Nordenstam, 1933 (Argentina)
J. juvenilis Kensley, Ortiz and Schotte, 1997 (Cuba)
J. lata Kussakin, 1961 (Sea of Okhotsk)
J. legrandi Juchault, 1962 (Mediterranean)
J. letourneuri Müller, 1990a (Réunion)
J. lobata Richardson, 1899 (California)
J. marionis Beddard, 1886 (Marion I.)
J. mediterranea Amar, 1961 (Mediterranean)
J. meteor Müller, 1991b (Gulf of Aden)
J. minuta Müller, 1989a (Society Is)
J. monsmarinus Kensley, 1980 (Vema Seamount)
J. montalentii Fresi, 1968 (Mediterranean)
J. neozealanica Chilton, 1892 (New Zealand)
J. nigricapitis Kensley, 1994 (Bermuda)
J. palliseri Hurley, 1957 (New Zealand)
J. paradubia Müller, 1989b (Columbia)
J. paulensis Vanhöffen, 1914 (Antarctica)
J. patagoniensis Richardson, 1909 (Patagonia)
J. personata Kensley, 1984a (Belize)
J. polynesiensis Müller, 1989a (Society Is)
J. rathbunae Richardson, 1902 (Bermuda)
J. salvati Müller, 1989a (Society Is)
J. sanctipauli Kensley, 1989 (St Paul I.)
J. schoelcheri Müller, 1993 (Martinique)
J. serrulus Kensley, 1984b (South Africa)
J. setosa George and Strömberg, 1968 (San Juan Archipelago)
J. stebbingi Kensley, 1975 (South Africa)
J. tayrona Müller, 1989b (Columbia)
J. tobagoensis Kensley & Schotte, 1994 (Tobago)
J. unidentata Kensley, Ortiz and Schotte, 1997 (Cuba)
J. vibicaria Barnard, 1965 (Gough I.)
J. waltervadi Kensley, 1975 (South Africa)
J. wolffi Müller, 1991b (Gulf of Aden)

Table 2. Comparison of characters in *Joeropsis* and the four new species described herein.

Character	*Joeropsis* spp.[1]	*Joeropsis bicarinata*	*Rugojoeropsis rugosa*	*Scaphojoeropsis multicarinata*	*Scaphojoeropsis kimblae*
Body					
1. *Body* with subparallel margins one or more of pereonites 2–4 occasionally slightly broader than 1 and succeeding ones, particularly in brooding females	(45)[2]	x	x		
— *Body* fusiform, distinctly tapering from pereonite 2/3 to apex of pleotelson				x	x
2. *Cuticle* smooth (setae not considered)	(45)	x			
— *Cuticle* roughly calcified			x	x	x
3. Without dorsal *ornamentation* on pereon	(44)				
— With two broad, rounded longitudinal dorsal ridges on pereonites 1–4(5)	(1)				
— With two parallel, sharp longitudinal dorsal keels along entire pereon and onto pleotelson		x			
— With variety of humps and short ridges			x	x	x
Cephalon					
4. Without dorsal *ornamentation*	(45)	x			
— With middorsal humps			x		
— With anterior and dorsal ridges				x	x
5. *Anterior margin* between antennae not depressed (Fig. 2)	(45)	x	x		
— *Anterior margin* between antennae strongly depressed relative to dorsal side of cephalon (Fig. 14c)				x	x
6. *Pseudorostrum* in lateral view with apical projection (Fig. 2)	(43)	x			
— *Pseudorostrum* in lateral view without apical projection (Fig. 9e)			x		
— *Pseudorostrum* attached to depressed anterior margin of cephalon in nearly vertical position (Fig. 14c)				x	x
Eyes					
7. With *dorsolateral eyes* on low bulge	(45)	x	x		
— *Blind*, without remnants of eye bulge				x	x
Pereopods					
8. *Dactylus* with 2 claws	(11)	x	x	x	x
— *Dactylus* with 3 claws at least on pereopods 2–7	(28)				

Table 2. Continued.

Character	*Joeropsis* spp.[1]	*Joeropsis bicarinata*	*Rugojoeropsis rugosa*	*Scaphojoeropsis*	
				multicarinata	*kimblae*
Mouthparts					
9. *Upper lip* evenly rounded, less than twice as wide as long (Fig. 4 ul)	(6)	x	x		
— *Upper lip* weakly convex, more than twice as wide as long (Fig. 20 ul)				x	x
10. *Mandible cutting edge* with strong teeth in curved, regular row (Fig. 4 md)	(40)	x	x		
— *Mandible cutting edge* divided into two parts, large terminal tooth pointing forward, posterior teeth on broad flange pointing mediad to backwards (Fig. 16 md)				x	x
11. *Mandibular raker* setae long, in regular row (Fig. 4 md)	(40)	x	x		
— *Mandibular raker* setae short, sparse, in irregular or unusual configuration (Fig. 16 md)				x	x
12. *Mandibular palp article 3* with apical and subapical setae (Fig. 4 md)	(31)	x	x		
— *Mandibular palp article 3* with apical setae only (Fig. 20 md)				x	x
13. *Lower lip*, lobes longer than wide, distally tapering, pointed (Fig 4 ll)	(6)	x	x		
— *Lower lip*, lobes wider than long, rectangular, lateral corner projecting, pointed (eg. Fig. 20 ll)				x	x
14. *Maxilla 1 outer plate* with 12 dentate setae	(17)	x	x		
— *Maxilla 1 outer plate* with 11 dentate setae	(11)				
— *Maxilla 1 outer plate* with 10 dentate setae	(4)			x	x
— *Maxilla 1 outer plate* with 9 dentate setae	(1)				
— *Maxilla 1 outer plate* with 8 dentate setae	(2)				
15. *Maxillipeds* covering at least 2/3 of ventral width of cephalon, overreaching other mouthparts (Fig. 3 c)	(37)	x	x		
— *Maxillipeds* covering about 1/3 of ventral width of cephalon; do not reach anterior margin of cephalon to fully cover other mouthparts (Fig. 15 c)				x	x
16. *Maxilliped basis* reaching to apex of or beyond palp ar. 3 (Fig. 3 mp)	(37)	x	x		
— *Maxilliped basis* reaching to middle of palp ar.2 (Fig. 20 mp)				x	x

Table 2. Continued.

Character	*Joeropsis* spp.[1]	*Joeropsis bicarinata*	*Rugojoeropsis rugosa*	*Scaphojoeropsis multicarinata*	*Scaphojoeropsis kimblae*
17. *Maxillipedal palp* about 1/2 length of basis (Fig. 11 mp)	(38)	x	x		
— *Maxillipedal palp* about 80–90% length of basis (Fig. 16 mp)				x	x
18. *Maxillipedal palp article3* unproduced medially	(39	x	x		
— *Maxillipedal palp article 3* strongly produced medially				x	x
19. *Maxillipedal palp article 4* longer than 3	(40)	x	x		
— *Maxillipedal palp article 4* shorter than 3				x	x
Pleopods					
20. *Female pleopod 2* without long apical setae (Fig. 11 pl2)	(29)	x	x		
— *Female pleopod* 2 with long apical setae (Fig. 19 pl2)				x	x
21. *Pleopod 3* exopod articulation strongly oblique (Fig. 6, 3)	(33)	x	x		
— *Pleopod 3* exopod articulation transverse or nearly so (Fig. 21 pl3)				x	x

[1] Species of *Joeropsis* described prior to this study.

[2] Number in parentheses: number of species in which character condition could been confirmed.

the species of *Joeropsis* were found to share a character, with none found to differ (characters 1, 2, 4, 5, 6, 7, 10, 11, 12, 15, 16, 17, 19, 21), that character is considered to be shared by all species. Comments are presented below for remaining characters.

Character 3 (dorsal sculpture). *Joeropsis waltervadi* and the new species *J. bicarinata* differ from all other species of *Joeropsis* in having two longitudinal ridges running along the dorsum, broadly rounded and confined to the pereon in the former, and sharp keels extending to the pleotelson in the latter. The homology of these two sculptural expressions is not clear. The dorsal sculpture on the pereon and pleotelson of the other three new species differs distinctly from that in the two species of *Joeropsis*.

Character 8 (number of pereopodal claws). Eleven species of *Joeropsis* are described and/or illustrated as having two dactylar claws on all pereopods, 28 as having three claws at least on pereopods 2–7. Generally only one or two pereopods are illustrated, and in several instances text and illustrations do not match. Where three claws are illustrated, the accessory claw is distinct and of similar shape to the two terminal ones. Bocquet and Lemercier (1958), in their redescription of the type species *J. brevicornis* Koehler, state that pereopod 1 carries two dactylar claws, all other pereopods carry three claws, as shown in their illustrations of pereopods 1 and 7. Similarly, several species, e.g. *J. intermedius* Nordenstam and *J. patagoniensis* Richardson are described and illustrated (Nordenstam, 1933) as having two claws on pereopod 1 and three on the rest of the pereopods. Amar (1961) described and illustrated *J. mediterranea* as having two claws on all pereopods (pereopods 1, 2 and 6 illustrated). The four species described in this study have two claws only on all pereopods. *J. mediterranea*, as well as the four new species, carry small, simple setae on the lateral and medial surfaces of the dactylus (not known or difficult to interpret in all other species with two claws only). Homology between one such seta and a distinctive accessory claw cannot be ruled out (Wilson, 1994). While two claws on pereopod 1 and three on pereopods 2–7 may be more common in *Joeropsis* than two claws on all pereopods, the character is useful only at the species level pending further comparative studies.

I am not aware that a similar dichotomy in the number of fully developed pereopodal claws has been reported in other janiroid genera.

Character 9 (upper lip). The upper lip in *J. brevicornis* (see Bocquet and Lemercier, 1958), five other species of *Joeropsis* and two of the new species is evenly rounded, about 1.5 times as wide as long. The upper lip has not been described or illustrated for other species of *Joeropsis*. In the other two new species, the upper lip is less rounded and about 2.5 times wider than long. More information is required to fully evaluate the generic significance of these differences, but the character has been included tentatively in the diagnoses of genera.

Character 13 (lower lip). In six species, including *J. brevicornis*, plus in two of the new species, the lobes of the lower lip are longer than wide, curving mediad and tapering to a more or less acute apex (no information is available for other species of *Joeropsis*). This shape is common to most janiroids and is tentatively considered to be shared by all species in *Joeropsis*. In two of the new species, the lower lip differs significantly, lobes being rectangular, broader than long, with projecting lateral corners.

Character 14 (maxilla 1 outer plate). In 34 species of *Joeropsis* the number of apical spine-like setae on the outer plate of maxilla 1 is given in text and/or illustration. The numbers given are 12 (17 species), 11 (11), 10 (4), 9 (1) and 8 (2). It is not clear, however, whether numbers have been enumerated in a consistent manner, i.e., large denticulate setae only, or smaller simple setae included, where these occur, (cf. Fig. 4 m1: 12 dentate + 2 small simple and Fig. 16 m1: 10 + 3). In several cases, the number given in the text and the number illustrated do not agree, e.g. *J. hawaiiensis* Miller (text: 6, illustration: 8). Clear evidence of considerable interspecific variation in the number of denticulate setae occurs within *Joeropsis*, but further comparative studies are required before its significance can be ascertained. Numbers given in descriptions of the new species do not include the small simple setae.

Character 18 (maxillipedal palp article 3). In 40 species of *Joeropsis*, the third article of the maxillipedal palp is unproduced medially (see Fig. 3 mp). *J. santipauli* Kensley has a slight expansion medially on article 3. The two species referred to *Scaphojoeropsis* gen. nov. have distinctive medial lobes on article 3. This character may be useful in separating genera.

Character 20 (female pleopod 2). In 20 species of *Joeropsis* illustrations show that the distal fifth to four-fifths of the lateral margins of pleopod 2 in females are densely fringed with what has been described as 'setules' or 'setae' (see below: cuticular scales). No long true setae occur apically. In another nine species where the female pleopod 2 is not illustrated, pleopod 2 of the male is shown to carry similar lateral 'setules/setae'. Evidence from *Joeropsis bicarinata* sp. nov. (Fig. 5) suggests that the 'setal' fringe is similar in male and female in species of *Joeropsis*. Presence of this fringe, and absence of long apical setae on the female operculum, (a few short simple setae may be present), may be characteristic for all species of *Joeropsis*. *Rugojoeropsis rugosa* gen. nov., sp. nov. has a similar fringe to Joeropsis on male and female pleopods 2. *Scaphojoeropsis multicarinata* sp. nov. has an almost invisible fringe in the distalmost tenth of both female and male pleopod 2. Pleopod 2 of male *S. kimblae* sp. nov. has a fringe along nearly the entire lateral margin (not verified in females). Both species of *Scaphojoeropsis* carry a row of long simple setae apically on pleopod 2. The presence of lateral 'setules/setae' appears to be ubiquitous in Joeropsididae, whereas the presence of long apical setae appears to be confined to *Scaphojoeropsis*.

Additional remarks on morphology

Rostral projection. Wilson (1989: 130) defined the asellote rostrum as 'a projection of the cephalic frons that may also include the dorsal surface of the cephalon.' Serov and Wilson (1995: 41) proposed the following definition 'any anterior extension from the frons or vertex [midanterior dorsal cephalic margin] of the cephalon.' While a rostrum derived from the vertex generally will incorporate the upper frons along its ventral side, a projection derived from the frons normally does not involve an extension of the vertex. Whether the dorsoposterior margin of a frons-derived projection could fuse with the cephalic vertex, thus obscuring the origin of the rostrum, is not clear. For the purposes of phylogenetic analyses, discriminating between a true *rostrum*, being an extension of the cephalic vertex, and a frons-derived *pseudorostrum* may be useful. All species in Joeropsididae possess a pseudorostrum, and that term is used throughout this study. All species in *Joeropsis* and *Rugojoeropsis* have the cephalic vertex concavely recessed, with the pseudorostrum fitting into, and projecting from, the recession. In *Joeropsis*, the pseudorostrum projects straight forward over the inferior parts of the frons (see Fig. 2 habitus, lateral view). In *Rugojoeropsis* the pseudorostrum forms a box-like hump without an apical projection (Fig. 9 cl). In *Scaphojoeropsis* the pseudorostrum borders the vertex along a straight line, is broadly rounded apically, and angled downwards (see Fig. 14 c).

Cuticular scales. In most instances where pleopod 3 has been illustrated in species of *Joeropsis*, the exopod is shown with a dense fringe of thin, simple setae. The four species described here have complex, flattened, often overlapping cuticular scales (arising as outgrowths from the cuticle, not inserted into it like setae, see, e.g., Fig. 6, 3) along the entire margin of the exopod. This character is not confined to these four species because it occurs in *J. mediterranea* (Amar, 1961: fig. 3) and *J. salvati* (Müller, 1989a: fig. 75). The scales are so transparent that normally they can be seen in their entirety only with the aid of Nomarski or phase contrast. With ordinary light microscopy, only the slightly strengthened posterior edge of the individual scale usually is visible (as a thin, simple setule). These scales vary in form and size between species as evidenced by the four species described below. They are likely to be present in all species of Joeropsididae. The fringe of reported 'setules/setae' on the lateral margin of pleopod 2 in females and males in Joeropsididae consists of similar cuticular scales (e.g. Figs 5H and 11pt).

Female reproductive structures. With the exception of male pleopods 1 and 2, the literature does not provide information on reproductive structures in Joeropsididae. A preparatory female of the new species *Scaphojoeropsis multicarinata* allows some preliminary comments to be made (Fig. 1). The elongate ovaries reach from the anteriormost part of pereonite 1 through to pereonite 6. The oviduct attaches to the ventral side of the ovary in the middle of pereonite 3, curves laterad and posteriad, and opens ventrally on pereonite 5 mediad to the coxa. The spermathecal duct appears to open on the anterior surface of pereonite 5, from where it curves into pereonite 4 and runs straight to the middle of pereonite 3 to join the oviduct in a common opening to the ovary. In the specimen illustrated, the anteriormost portion of the spermathecal duct is slightly inflated and filled with denser material. A single female of the new species *Rugojoeropsis rugosa* has a similar configuration.

Conclusion

Joeropsis bicarinata sp. nov. differs from other species in the genus as currently conceived only in the presence of two sharp, longitudinal dorsal keels. A possibly intermediate condition between those keels and the normally smooth dorsum in *Joeropsis* is seen in the low, rounded ridges in *J. waltervadi*. *J. bicarinata* is referred to *Joeropsis*.

The second new species shares with *Joeropsis* all characters analysed in Table 2 except for the rough, calcified cuticle, dorsal sculpture in the form of humps and transverse ridges, and the box-shaped, unproduced pseudorostrum. Since all species of *Joeropsis* possess a smooth cuticle and straight, overhanging pseudorostrum, a new genus *Rugojoeropsis* is justified. The remaining two new species differ in many characters from *Joeropsis* and *Rugojoeropsis* (Table 2), notably in the shape of the cephalon and pseudorostrum, the shape of the entire body, and details of mouthparts. They too warrant a new genus, *Scaphojoeropsis*.

Joeropsididae Nordenstam

Jaeropsini Nordenstam, 1933: 190.

Jaeropsidae.—Menzies, 1962: 63.—Menzies and Kruczynski, 1983: 94.

Joeropsididae.—Sivertsen and Holthuis, 1980: 96 (correction of spelling).—Kussakin, 1999: 10.

Diagnosis. Janiroidea with flattened body; lateral margins normally parallel, occasionally tapering posteriorly. Pereonites of subequal length, with truncate, entire or at most finely serrate, lateral margins covering coxae. All pereopods similar, slender, ambulatory, with 2 or 3 dactylar claws. Sessile eyes normally present in dorsolateral position on cephalon. Anterior margin of cephalon with strong concavity, or rarely without concavity. Pseudorostrum present, inserted into cephalic concavity, rarely joined along straight line. Pleotelson subequal in width to pereonite 7, with no free pleonites. Antenna 1 shorter than cephalon, peduncular article 1 expanded, longer than articles 2 and 3 combined; flagellum shorter than peduncle, with 2 or 3 articles, rarely 4 (one species herein) or 5 (*Joeropsis sanctipauli* and one species herein). Antenna 2 geniculate, with peduncular article 6 and flagellum folding laterad and backwards under lateral expansion of peduncular article 5; first 4 peduncular articles short, article 4 more or less telescoped into 3, article 5 longer than 1–4 combined, greatly expanded laterally, article 6 much shorter than 5, generally widening distally; antennal scale absent; flagellum with enlarged, normally conjoint article 1. Mandible molar a long, slender, pointed projection; incisor of 5–6 large teeth, (occasional small accessory denticles not counted); lacinia mobilis absent; palp with 3 articles. Maxillipeds, palp with 5 articles, at least article 2 medially expanded. Pleopod 2 of male and female with longer or shorter lateral fringe of modified cuticular scales; pleopod 3 exopod 2-articulate, longer than endopod, with lateral fringe of modified cuticular scales, endopod with 3 plumose setae; pleopod 4 exopod vestigial. Uropods biramous, inserted ventrally on pleotelson normally within distinctive insinuation in pleotelson margin; peduncle usually broader than long and medially expanded; rami shorter than peduncle. Anus outside pleopodal chamber, between bases of uropodal peduncles, partly or entirely covered by male pleopod 1 or female pleopod 2 respectively. Oostegites on pereopods 1–5. Female spermathecal duct opening on anterior surface of pereonite 5, oviduct opening ventral on pereonite 5 mediad to coxa.

Included genera: Joeropsis Koehler, 1885, *Rugojoeropsis* gen. nov., *Scaphojoeropsis* gen. nov.

Joeropsis Koehler

Joeropsis Koehler, 1885: 1.—Sivertsen and Holthuis, 1980: 96.—Kussakin, 1999: 12.

Jaeropsis.—Nordenstam, 1933: 191.—Menzies and Barnard, 1959: 10.—Menzies, 1962: 63. (unjustified emendation).

Iaeropsis.—Nierstrasz, 1941: 288 (unjustified emendation).

Type species. Joeropsis brevicornis Koehler, 1885 (by monotypy).

Diagnosis. Joeropsididae with lateral body margins parallel, rarely with dorsal sculpture. Cuticle smooth. Cephalon with anterior margin strongly concave. Pseudorostrum inserted into concavity, flush with dorsal surface of cephalon, with overhanging apex. Dorsolateral eyes present. Upper lip evenly rounded, less than twice as wide as long. Mandibles with incisor of 5 or 6 strong subequal teeth in regular, curved row; spine row setae long, in regular row. Lower lip, lobes longer than wide, distally tapering, pointed. Maxillipeds in ventral view covering at lease two-thirds of cephalic width, and covering other mouthparts except for medioapical concavity; endite reaching to end of or beyond palp article 3; palp about half length of endite; palp article 3 without medial lobe, (*J. sanctipauli*, with a small medial lobe, appears to be an exception), article 4 much longer than 3. Pleopod 2 of female with at most a few short simple setae apically. Pleopod 3 exopod with strongly oblique articulation between articles.

Included species. See Table 1.

Joeropsis bicarinata sp. nov.

Figures 2–7

Material examined. Holotype. Vic. Bass Strait, S of Point Hicks, 38°17.70'S 149°11.30'E, 400 m, coarse sand, gravel, mud, many sponges, WHOI epibenthic sled, M.F. Gomon et al., 24 Jul 1986, ORV Franklin (stn SLOPE-40), NMV J18685 (female, 4.8 mm, with including 6 slides).

Paratypes (43 specimens). NSW. E of Newcastle, 32°53'S 152°35'E, 146–175 m, 15 Aug 1985, FRV *Kapala* (stn K85-12-23), AM P38889 (5). Off Eden, 36°57.40'S 150°18.80'E, 220 m, muddy shell, WHOI epibenthic sled, G.C.B. Poore et al., 20 July 1986, ORV *Franklin* (stn SLOPE-21), NMV J18681 (14). Off Eden, 37°0.60'S 150°20.70'E, 363 m, coarse shell, WHOI epibenthic sled, G.C.B. Poore et al., 21 July 1986, ORV *Franklin* (stn SLOPE-22), NMV J18682 (1).

Vic. Bass Strait, S of Point Hicks, 38°17.70'S 149°11.30'E, 400 m, coarse sand, gravel, mud, many sponges, WHOI epibenthic sled, M.F. Gomon et al., 24 Jul 1986, ORV *Franklin* (stn SLOPE-40), NMV J18683 (1), NMV J27641 (1 male, pleotelson and pleopods 1–5 illustrated, 2 slides), NMV J18684 (2). 50 km S of Mallacoota, 38°06.2'S 149°45.5'E, 188 m, WHOI epibenthic sled, R. Wilson, 14 Oct 1984, FRV *Soela* (stn S05/84/30), NMV J18687 (5).

Tas. 15 km E of Mistaken Cape, Maria I., 42°37'S 148°20'E, 102 m, WHOI epibenthic sled, R. Wilson, 9 Oct 1984, FRV *Soela* (stn S05/84/1), NMV J18686 (3). 30 km NNW of Cape Sorell, 42°10.9'S 144°48.9'E, 160 m, WHOI epibenthic sled, R. Wilson, 20 Oct 1984, FRV Soela (stn S05/84/54), NMV J18688 (4). 25 km W of Port Davey, 45°23.3'S 145°39.8'E, 160 m, WHOI epibenthic sled, R. Wilson, 21 Oct 1984, FRV *Soela* (stn S05/84/60), NMV J18689 (6).

Description. Cephalon about third wider than midline length; pseudorostrum as long as wide, projecting to right angled point. Body without setae, dorsally with 2 sharp, parallel, longitudinal keels running on to proximal third of pleotelson. Cephalon and pereon margins smooth. Pleotelson width about 1.5 length, with medioproximal keels in continuation of pereonite keels, low sinuous keels in distal half terminating laterad of uropods, lateral margins evenly curved, minutely serrate, distal margin strongly insinuated for uropods, apex between uropods rounded right angled.

Antenna 1 of up to 5 articles; article 1 rectangular, distomedial corner with small teeth, width 0.75 length, about twice as long and wide as article 2 which is twice as long and wide as 3, article 5 as long as 3, both longer than 4, article 5 with 2 aesthetases; lateral margins of articles 1 and 2 lined with cuticular outgrowth. Antenna 2, peduncle articles 1–4 of subequal length, article 3 widest, article 4 third embedded into 3, article 5 ovate, nearly twice as long as 1–4 combined,

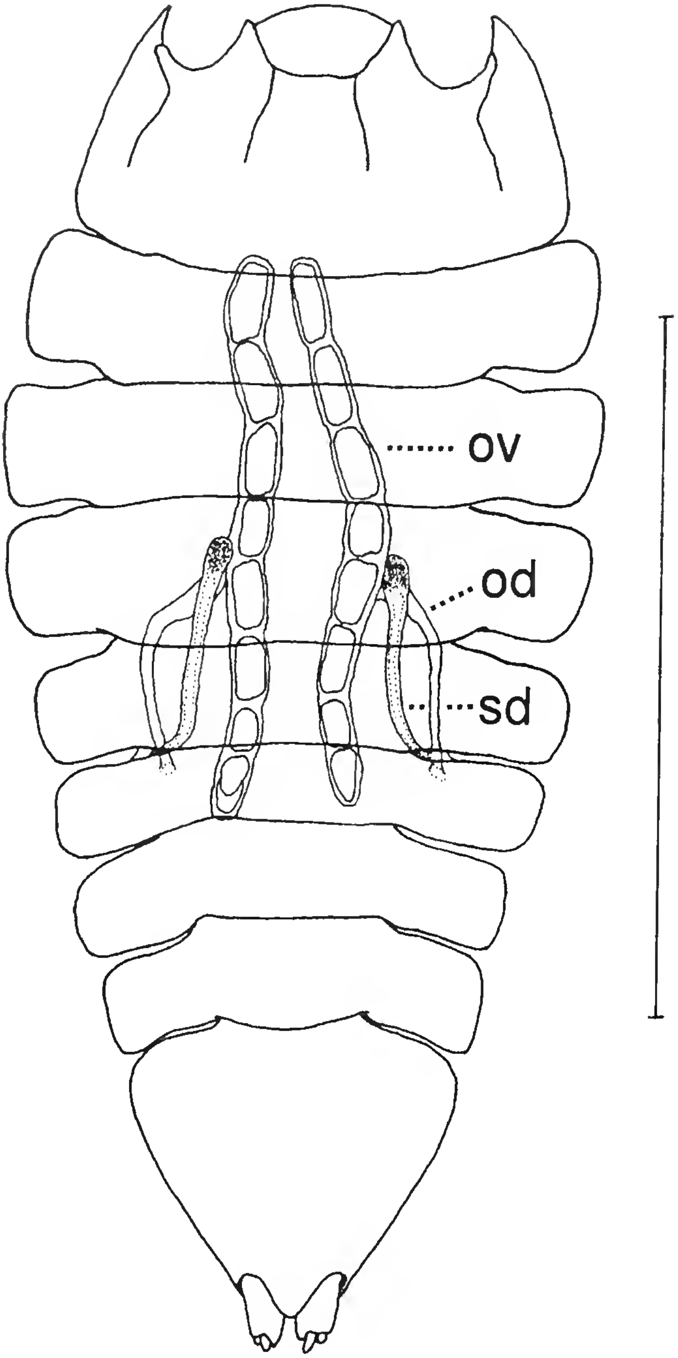

Figure 1. *Scaphojoeropsis multicarinata* gen. nov., sp. nov. Reproductive structures of preparatory female (paratype, NMV J18690), dorsal view; dorsal sculpture of body omitted; **od**, oviduct; **ov**, ovary; **sd**, spermathecal duct. Scale bar: 1 mm.

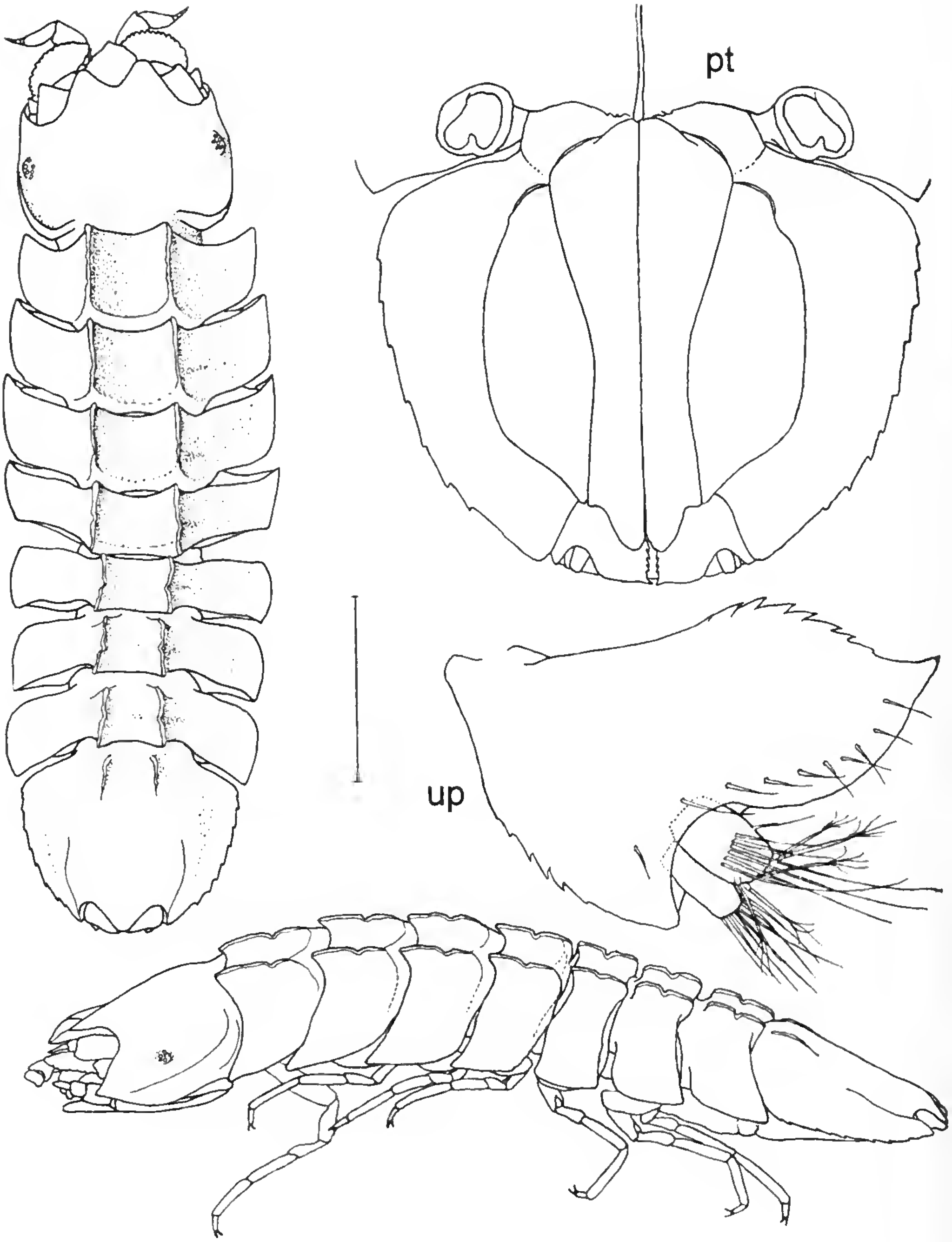

Figure 2. *Joeropsis bicarinata* sp. nov., holotype, except pt: paratype, male, (NMV J27641). **pt**, male pleotelson, ventral view, setae omitted; **up**, right uropod, ventral view. Habitus scale bar: 1 mm.

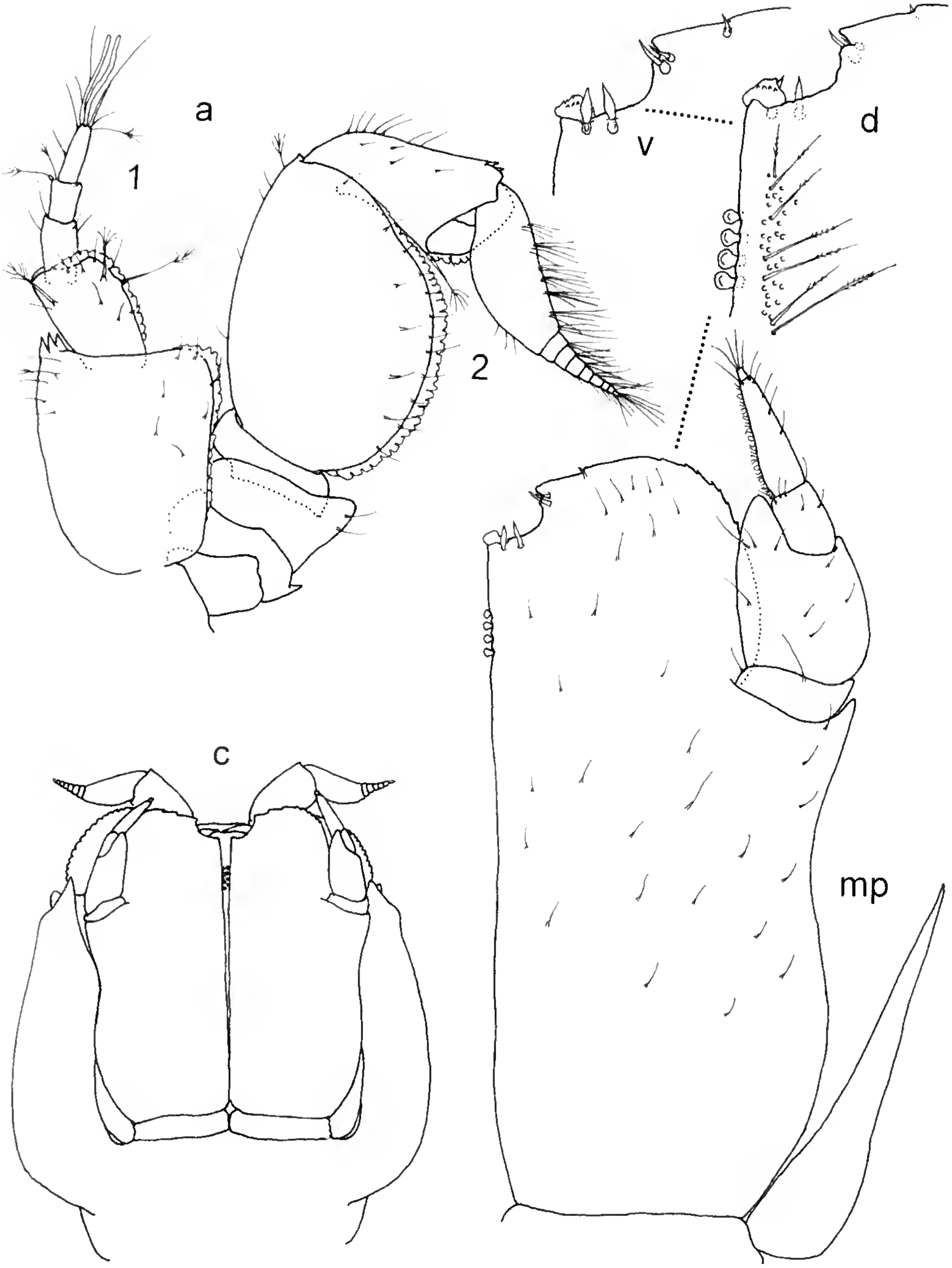

Figure 3. *Joeropsis bicarinata* sp. nov., holotype. **a**, right antennae 1 and 2, dorsal view; **c**, ventral view of cephalon, setae omitted; **mp**, maxilliped, with enlarged ventral (**v**) and dorsal (**d**) view of mediodistal part of endite.

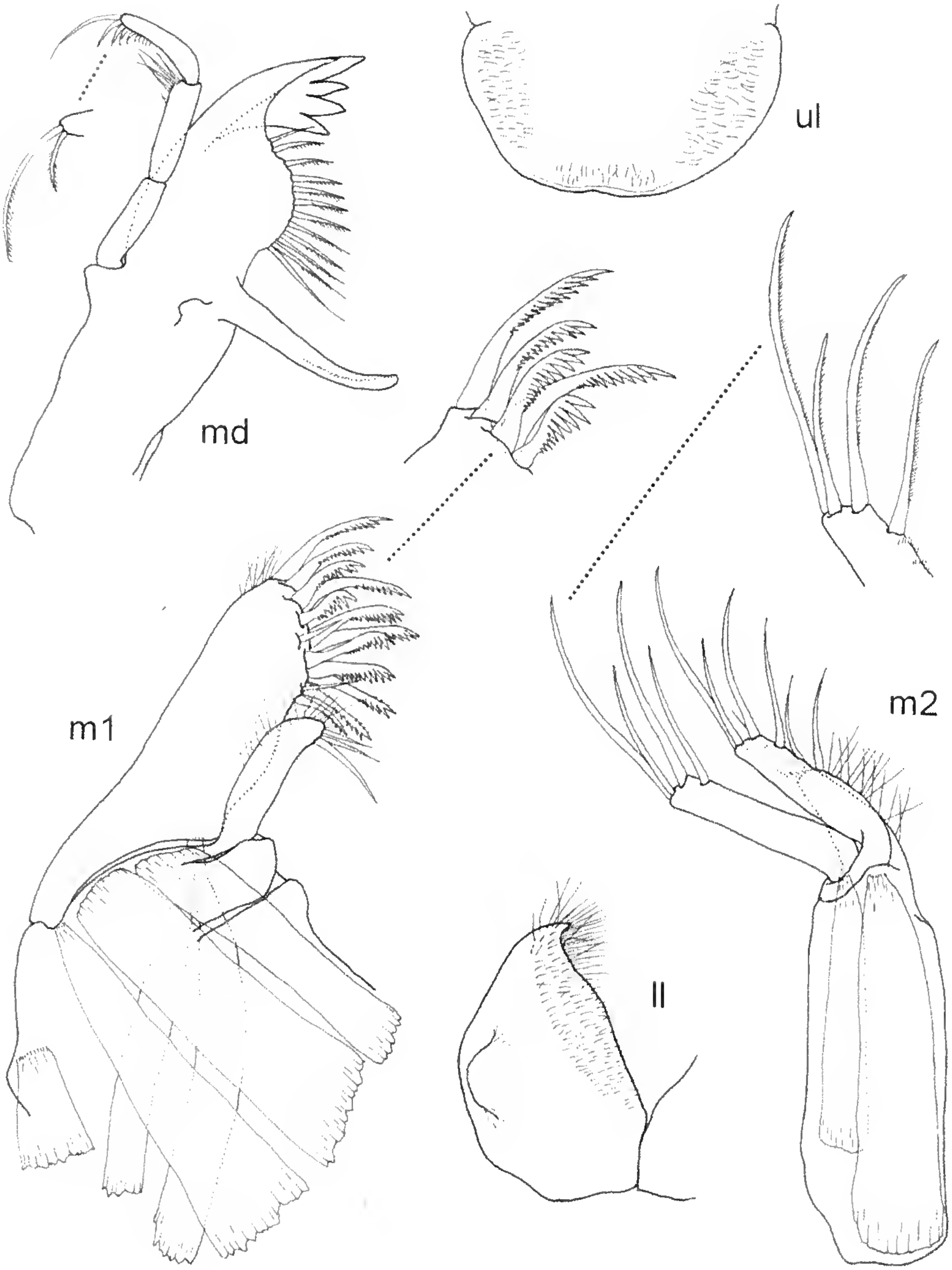

Figure 4. *Joeropsis bicarinata* sp. nov., holotype. **ll**, lower lip; **md**, mandible; **m**, maxilla (1 and 2); **ul**, upper lip.

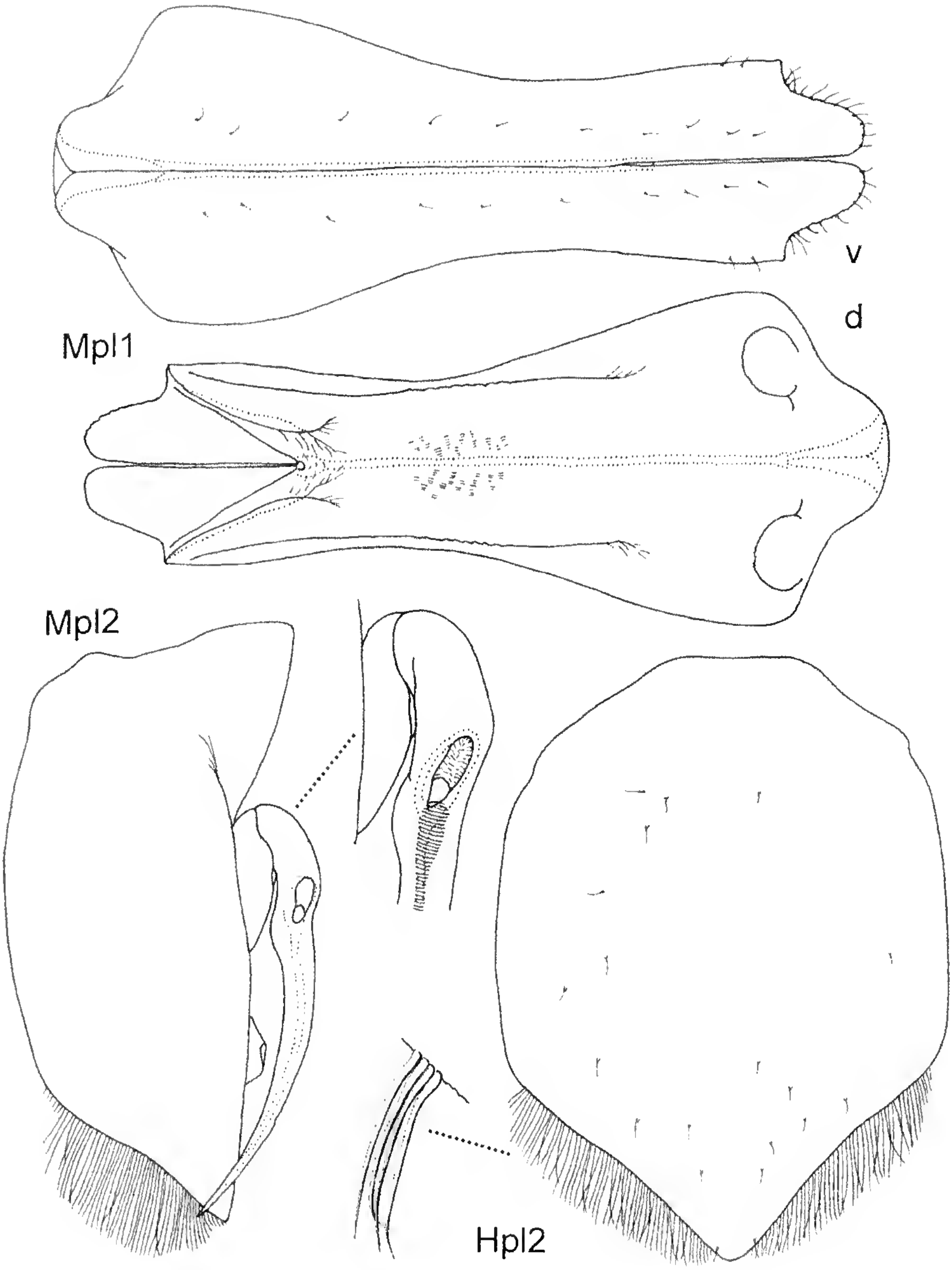

Figure 5. *Joeropsis bicarinata* sp. nov. **M**, paratype, male, (NMV J27641). **H**, holotype. **pl**, pleopod (1 and 2); **d**, dorsal and **v**, ventral view.

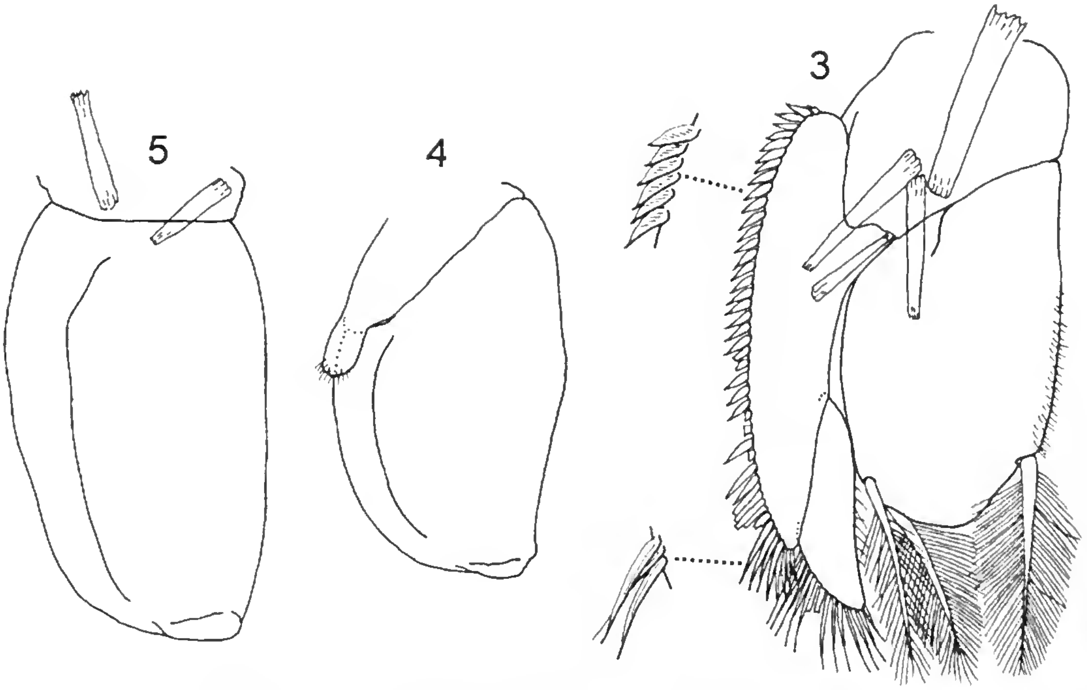

Figure 6. *Joeropsis bicarinata* sp. nov., paratype, male, (NMV J27641). Pleopods 3–5.

width two-thirds length, lateral margin fringed with cuticular outgrowth, article 6 as long as 1–4 combined, distally expanded; flagellum about fifth longer than peduncle article 6, with up to 10 articles, article 1 inflated, conjoint, twice length of remaining articles combined.

Mouthparts: Mandibles, palp reaching apex of 5-dentate incisor, articles of subequal length, article 2 with distal tuft of long pectinate setae, article 3 with terminal long pectinate seta and subapical row of successively shorter similar setae along distal half of article. Maxilla 1 outer plate with 12 coarsely dentate setae and 2 shorter, slender, simple setae; inner plate third width of outer plate, reaching to mediodistal corner of outer plate, with 3 long, simple setae and many long setules distally. Maxilla 2, all 3 plates with 4 long, curved, finely pectinate setae, outer and middle plates of similar shape and length, overreaching inner plate with about third length, inner plate with many long setules medially. Maxillipeds covering about 0.6 ventral width of cephalon, reaching forward beyond upper lip, basis twice as long as greatest width, endite reaching to proximal third of palp article 4, with scattered simple setae on ventral surface and dorsal field of slender, plumose setae inside medial margin, mediodistal concavity of endite with 1 medial lump-shaped seta and a few short spear-head-shaped setae, apical and lateral margins evenly rounded, finely serrate; palp article 2 three times longer than 1, with bluntly triangular, forward pointing medial lobe reaching apex of article 3, article 3 0.4 length of distally tapering article 4, medial surface of article 4 covered with short setules, article 5 minute; epipod about as long as palp, narrow, tapering to acute point.

Pereopods slender, similar, with 2 claws; basis about 4 times longer than wide, twice length of ischium, 2–7 with two penicillate setae in proximal half; merus about 0.8 length of ischium, dorsodistally expanded; carpus slightly wider than and of subequal length to propodus, ventrodistal corner with group of acute, forward pointing spines; propodus with 3 to 4 slender, robust setae along ventral margin, single penicillate seta dorsoapically; dactylus of pereopod 1 about quarter length of propodus, twice as long as wide, of pereopods 2–7 about third length of propodus, about 2.5 times longer than wide, dorsal and ventral claws of equal length, dorsal claw more slender.

Pleopods: Male pleopod 1 2.5 times longer than greatest width, strongly tapering towards midlength, margins only slightly diverging distal to midpoint, apical lobes broadly rounded, set off

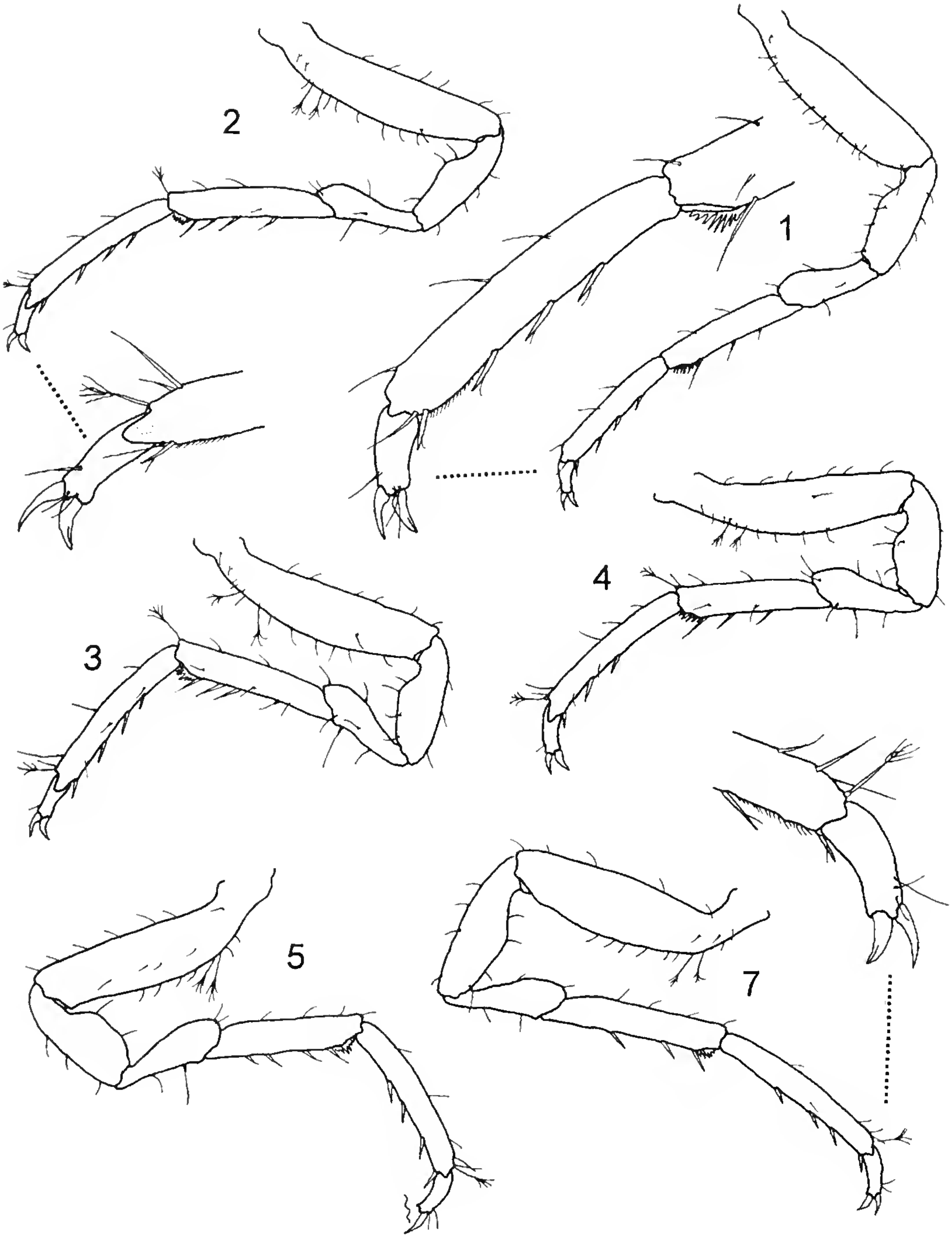

Figure 7. *Joeropsis bicarinata* sp. nov., holotype. Pereopods 1–5 and 7.

from lateral margins by pointed right angle, apical lobes fringed with short, simple setae; dorsal surface with simple stylet guides running from sperm duct opening to right-angled lateral corners; mid-dorsal surface with oval field of tiny setules, ventral surface with 2 longitudinal rows of short, simple setae. Male pleopod 2, protopod 2.5 times longer than midwidth, proximal two-thirds of lateral margin faintly convex, naked, distal third curved mediad, slightly concave, with dense fringe of long, thin cuticular scales, apex pointed; stylet evenly curved, in retracted position reaching to apex of protopod. Female pleopod 2, shaped like combined protopods of male pleopod 2, distal third triangular, lateral fringe of cuticular scales about 1.2 times longer than in male, apex rounded, ventral surface with scattered short, simple setae including a couple at apex. Pleopod 3, endopod rounded rectangular, midsurface length 1.5 times midwidth; exopod article 1 about 5 times longer than midwidth, reaching just beyond apex of endopod, lateral margin densely fringed with cuticular scales, short and broad in proximal two-thirds, longer and more slender distally; exopod article 2 articulating along medial margin of article 1, barely half length of article 1, distally tapering to blunt apex, lateral margin fringed with long, slender cuticular scales, medial margin with a few setules. Pleopod 4, endopod subequal in size and shape to endopod pleopod 3, without setae; exopod a vestigial, rounded lobe with apical setules, length about 1.3 width. Pleopod 5, similar to pleopod 4 in shape but about 1.2 times longer.

Uropods: Peduncles not reaching beyond margin of pleotelson, broadly expanded medially, mediodistal corner produced, acutely pointed, ventrodistally with row of simple submarginal setae, medial and lateral margins serrate; rami of equal length, about quarter length of lateral margin of peduncle, outer ramus twice as long as wide, with apical row of long, simple setae, inner ramus length 1.5 times width, with midventral row of long, simple setae and several apical penicillate setae.

Size. Largest male 5.5 mm; largest female 4.8 mm.

Distribution. Eastern Australia south of 33°S, eastern Bass Strait, east and west coasts of Tasmania; 102–400 m.

Etymology. The species is named for the two prominent dorsal keels.

Remarks. The dorsal keels are present in specimens as small as 2 mm, although barely raised from the dorsal surface, but they cannot be seen in specimens of 1 mm.

Rugojoeropsis gen. nov.

Type species. Rugojoeropsis rugosa sp. nov.

Diagnosis. Joeropsididae with lateral body margins parallel, with humps and ridges dorsally. Cuticle roughly calcified. Cephalon with anterior margin strongly concave. Pseudorostrum inserted into concavity, box shaped, without overhanging apical projection. Dorsolateral eye bulges without ommatidia. Upper lip evenly rounded, less than twice as wide as long. Mandibles with incisor of 5 strong subequal teeth in regular, curved row; spine row setae long, in regular row. Lower lip, lobes longer than wide distally tapering, pointed. Maxillipeds in ventral view covering at least two-thirds of cephalic width, and covering other mouthparts except for medioapical concavity; endite reaching beyond palp article 3; palp about half length of endite; palp article 3 without medial lobe, article 4 much longer than 3. Pleopod 2 of female with a few tiny simple setae apically. Pleopod 3 exopod with strongly oblique articulation between articles.

Included species. Rugojoeropsis rugosa sp. nov.

Etymology. From the Latin *rugosus* = uneven, rough, alluding to the texture of the cuticle.

Rugojoeropsis rugosa sp. nov.

Figures 8–13

Material examined. Holotype, Tas., off Freycinet Peninsula, 41°57.50′S 148°37.90′E, 400 m, coarse shell, WHOI epibenthic sled, M.F. Gomon et al., 27 Jul 1986, ORV *Franklin* (stn SLOPE-48), NMV J18678 (preparatory female, 2.8 mm, with 5 slides).

Paratypes (29 specimens). NSW, Off Eden, 37°7.30′S 150°20.20′E, 550 m, grey coarse shell, WHOI epibenthic sled, G.C.B. Poore et al., 20 Jul 1986, ORV *Franklin* (stn SLOPE-19), NMV J18676 (1).

Tas. Off Freycinet Peninsula, 41°58.60′S 148°38.80′E, 500–600 m, coarse shell, WHOI epibenthic sled, M.F. Gomon et al., 27 Jul 1986, ORV *Franklin* (stn SLOPE-47), NMV J18677 (15, maxilliped of 1 female illustrated, 1 slide). Off Freycinet Peninsula, 41°57.50′S 148°37.90′E, 400 m, coarse shell, WHOI epibenthic sled, M.F. Gomon et al., 27 Jul 1986, ORV *Franklin* (stn SLOPE-48), NMV J18679 (1 male, pleotelson and pleopods 1 and 2 illustrated, 2 slides), NMV J18680 (12, ventral view of spent female illustrated).

Description. Cephalon twice as wide as midline length, with serrate lateral margins, with a rounded hump on each side medial to eyes; lobes

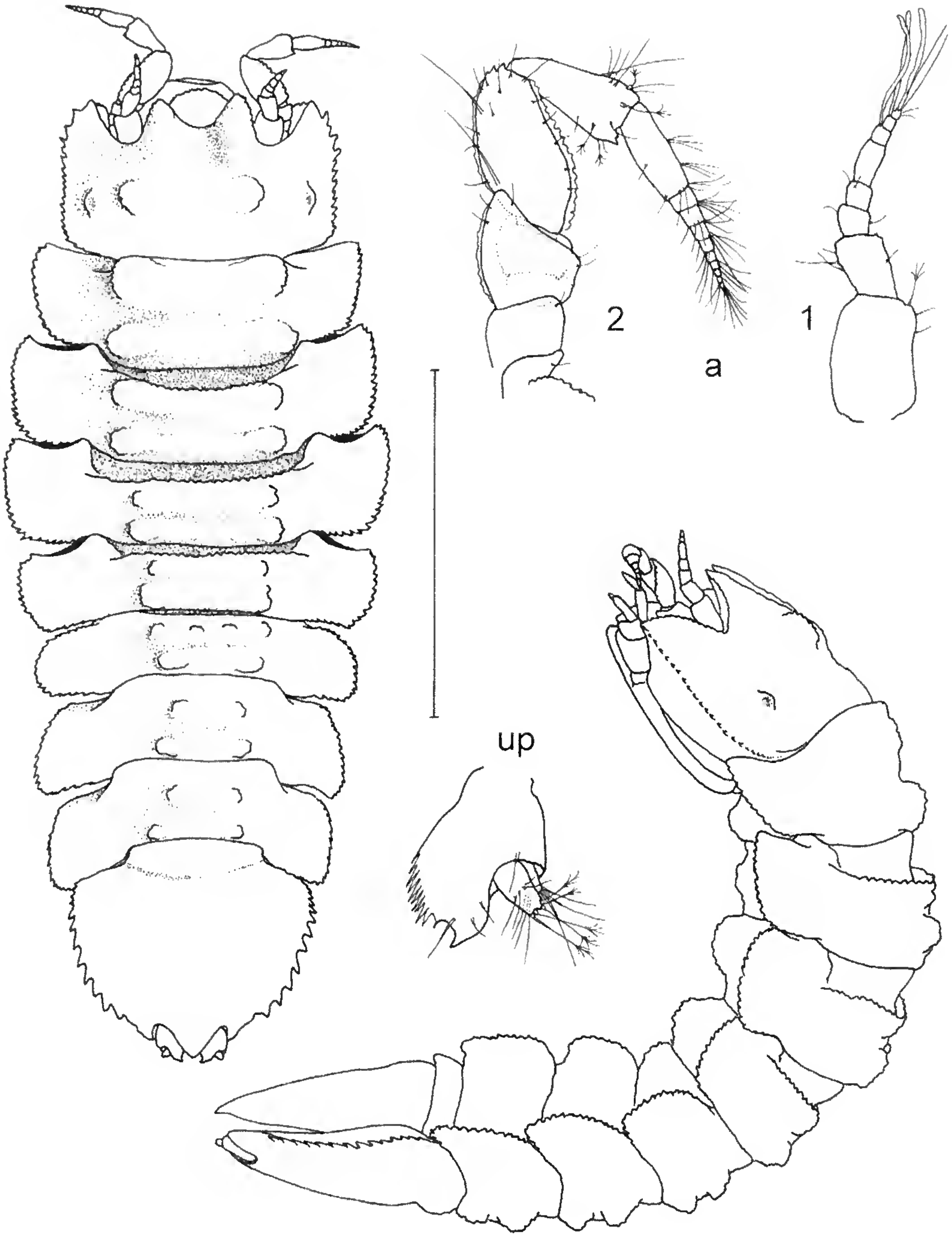

Figure 8. *Rugojoeropsis rugosa* gen. nov., sp. nov., holotype. **a**, antennae (1 and 2, right, dorsal view); **up**, uropod, left, ventral view. Habitus scale bar: 1 mm.

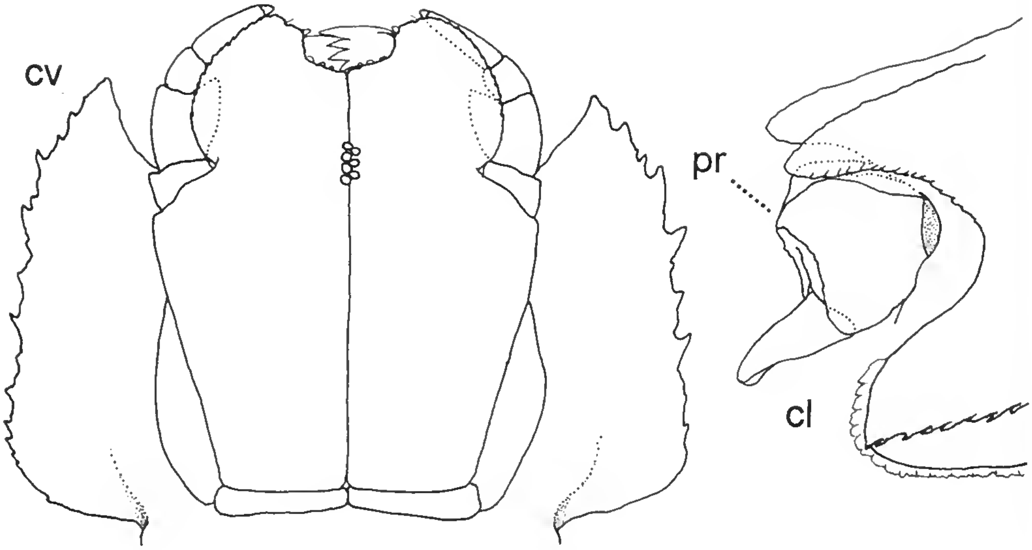

Figure 9. *Rugojoeropsis rugosa* gen. nov., sp. nov. **cl**, cephalon left lateral view (holotype); **pr**, pseudorostrum. **cv**, cephalon ventral view (paratype, spent female, NMV J18680).

surrounding midanterior sinus raised to broad, rounded keels; pseudorostrum in dorsal view with evenly convex, finely serrate anterior margin, width 1.3 length, barely reaching beyond surrounding cephalic lobes; in lateral view pseudorostrum vertically truncated, without overhanging projection.

Pereonites dorsally with 2 low, transverse, rounded ridges, lateral parts of ridges more pronounced than central parts, ridges on pereonites 1 and 2 approximately half width of segment, successively shorter on more posterior pereonites, lateral and lateroposterior margins of pereonites serrate and carrying scattered short, simple setae.

Pleotelson width about 1.1 times length, lateral margins evenly curved, coarsely serrate, distal margin strongly insinuated for uropods, apex between uropods rounded, slightly less than right angled.

Antenna 1 article 1 rectangular, reaching about halfway along cephalic sinus lobes, width two-thirds length, about twice as long as and half as wide again as article 2 which is twice as long and wide as 3; flagellum of up to 5 articles, article 1 as long as peduncular article 3, article 2 twice length of article 1 and as long as 3–5 combined, articles 3–5 each with 1 long aesthetasc. Antenna 2, peduncle articles 1–3 of increasing length, article 2 rectangular, article 3 medial margin twice as long as lateral margin resulting in strongly oblique apical margin, article 4 fully embedded into 3, subequal in size to article 2, article 5 elongate, poorly expanded laterally, as long as 1–4 combined along dorsal midline, width 0.5 length, margins fringed with cuticular outgrowth, article 6 three quarters length of 5, distally expanding; flagellum as long as peduncle articles 4 and 5 combined, with up to 10 articles, article 1 moderately inflated, conjoint, as long as remaining articles combined.

Mouthparts: Mandible palp slightly overreaching apex of 5-dentate incisor, articles 1 and 2 of equal length, article 3 two-thirds length of 2, article 2 with mediodistal row of pectinate setae, article 3 with terminal long pectinate seta and subapical row of successively shorter similar setae along distal half of article. Maxilla 1 outer plate with 12 coarsely dentate setae and 1 short, stout simple seta at midface; inner plate 0.5 width of outer plate, barely reaching mediodistal corner of outer plate, with 3 long, medioapical setae and many apical and distolateral long setules. Maxilla 2, outer and middle plates of subequal size and length about 1.3 times longer than inner plate, with 4 unequally long, straight to moderately curved, finely pectinate setae; inner plate with 3 similar setae and long medial setules. Maxillipeds covering about two-thirds of ventral width of

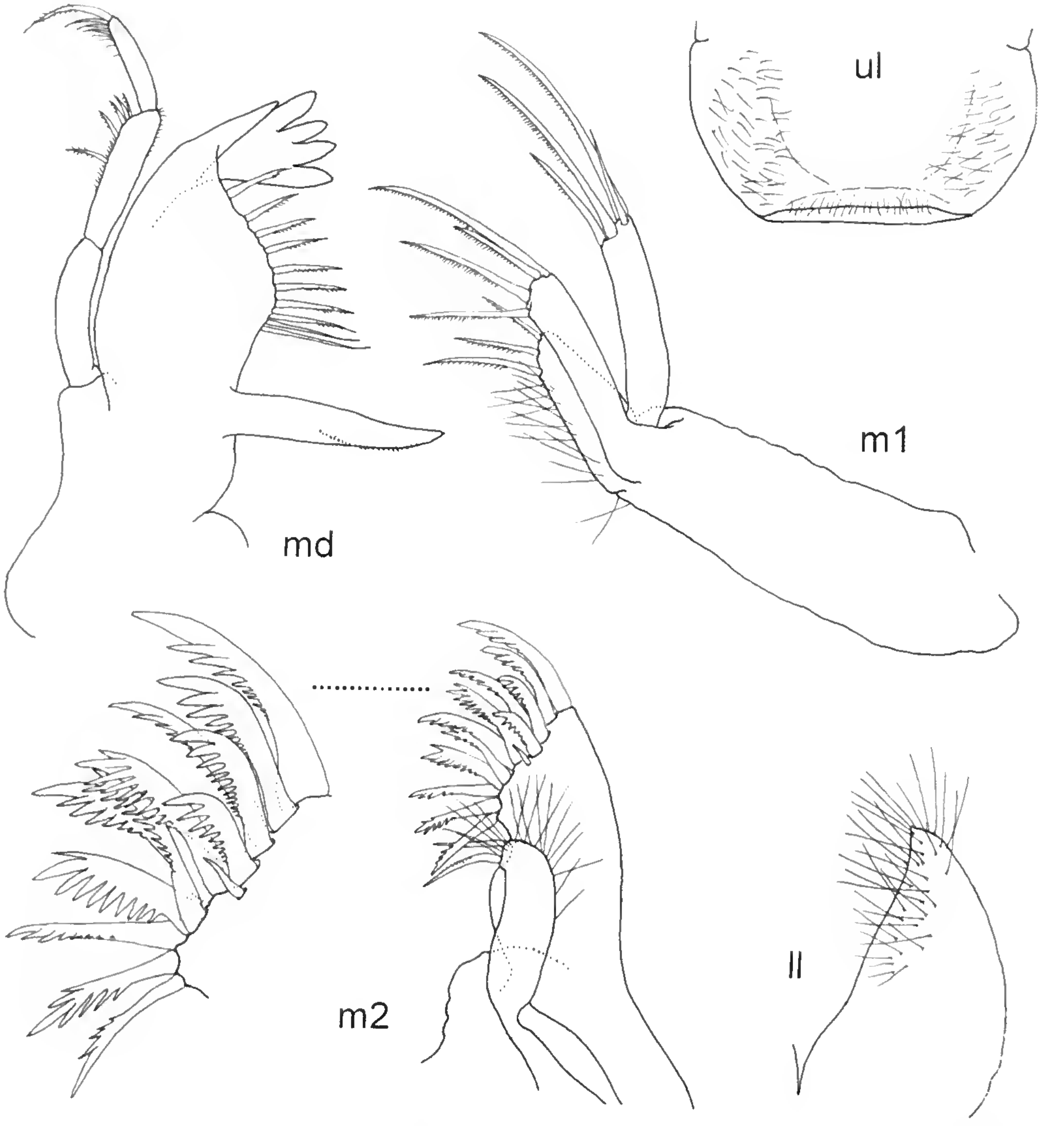

Figure 10. *Rugojoeropsis rugosa* gen. nov., sp. nov., holotype. **ll**, lower lip; **md**, mandible; **m**, maxilla (1 and 2); **ul**, upper lip (apical margin folded back artificially).

cephalon, reaching forward beyond upper lip, basis twice as long as greatest width, endite reaching to about middle of palp article 4, with dorsal field of slender setules inside medial margin, mediodistal concavity with row of 4 low, lump-shaped setae; apical and lateral margins of endite evenly rounded, finely serrate, with single slender setule in each indentation and small peg-shaped seta anterior to concavity; palp article 2 three times longer than 1 along midsurface, with forward pointing medial lobe reaching about two-thirds along article 3, apex of lobe with a few long slender setae, article 3 about half length of distally tapering article 4, medial margin of 2 and 3 fringed with cuticular outgrowth, medial surface of article 4 covered with short setules, article 5 0.2 length of 4, rounded, with tuft of long, simple setae; epipod about as long as palp, width about third length, tapering to acute point.

Pereopods similar, with 2 claws; basis about 4

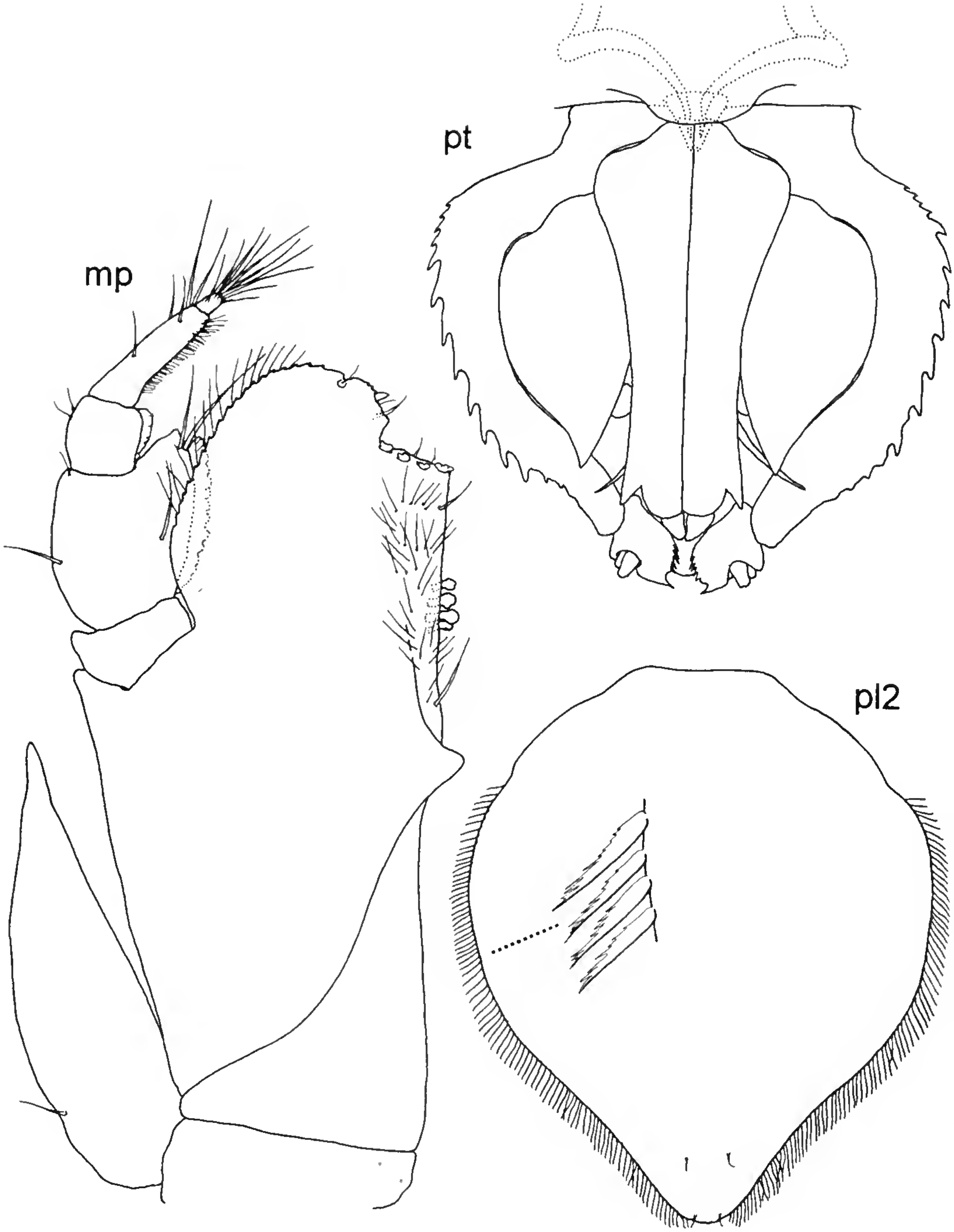

Figure 11. *Rugojoeropsis rugosa* gen. nov., sp. nov. **pt**, pleotelson, ventral view (paratype, male, NMV J18679); **mp**, maxilliped (paratype, female, NMV J18677); **pl2**, pleopod 2 (holotype).

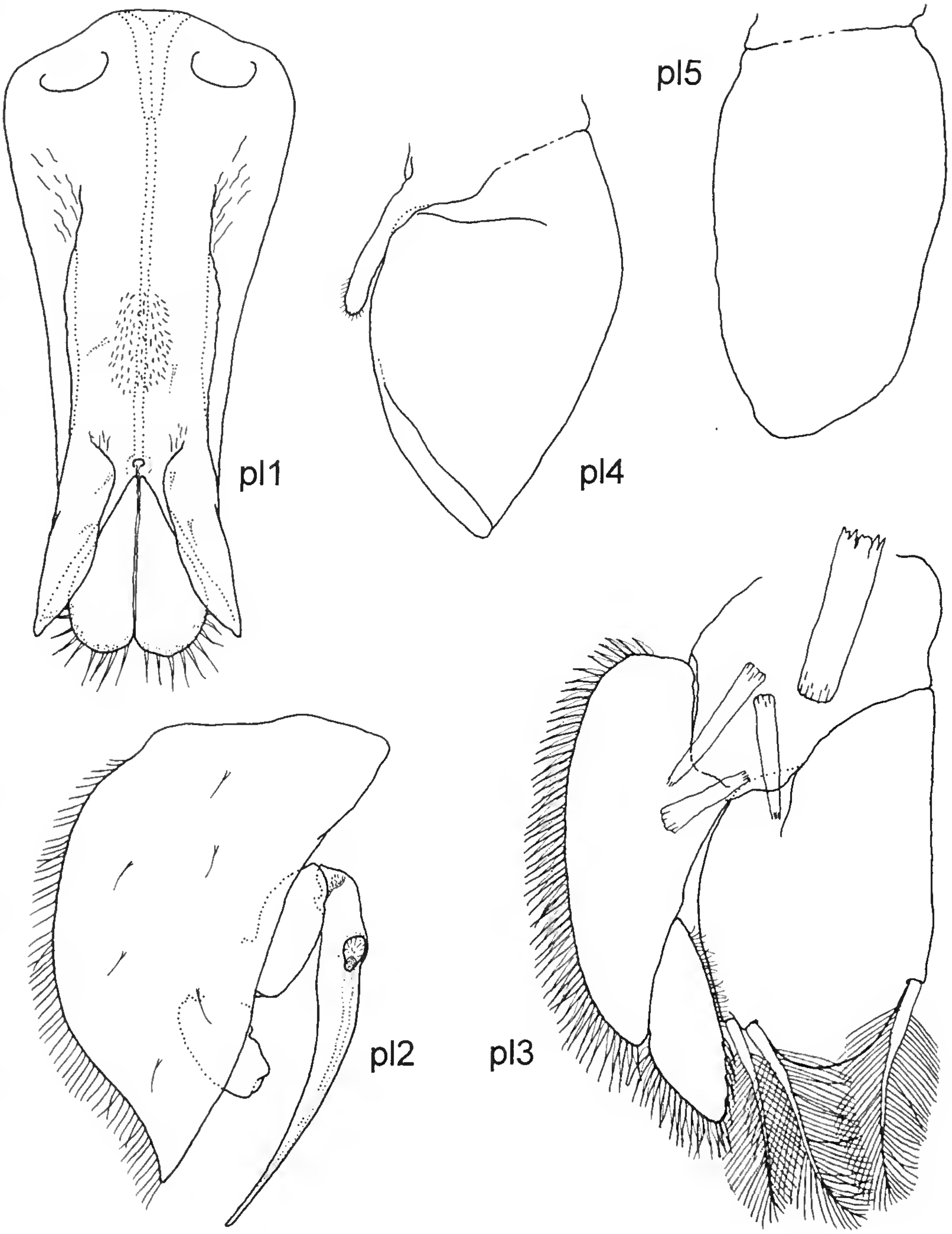

Figure 12. *Rugojoeropsis rugosa*, gen. nov., sp. nov. Paratype, male, (NMV J18679): **pl1**, pleopod 1, dorsal view; **pl2**, pleopod 2, ventral view. Holotype, **pl3–5**, pleopods 3–5, (apex of pl4 artificially folded).

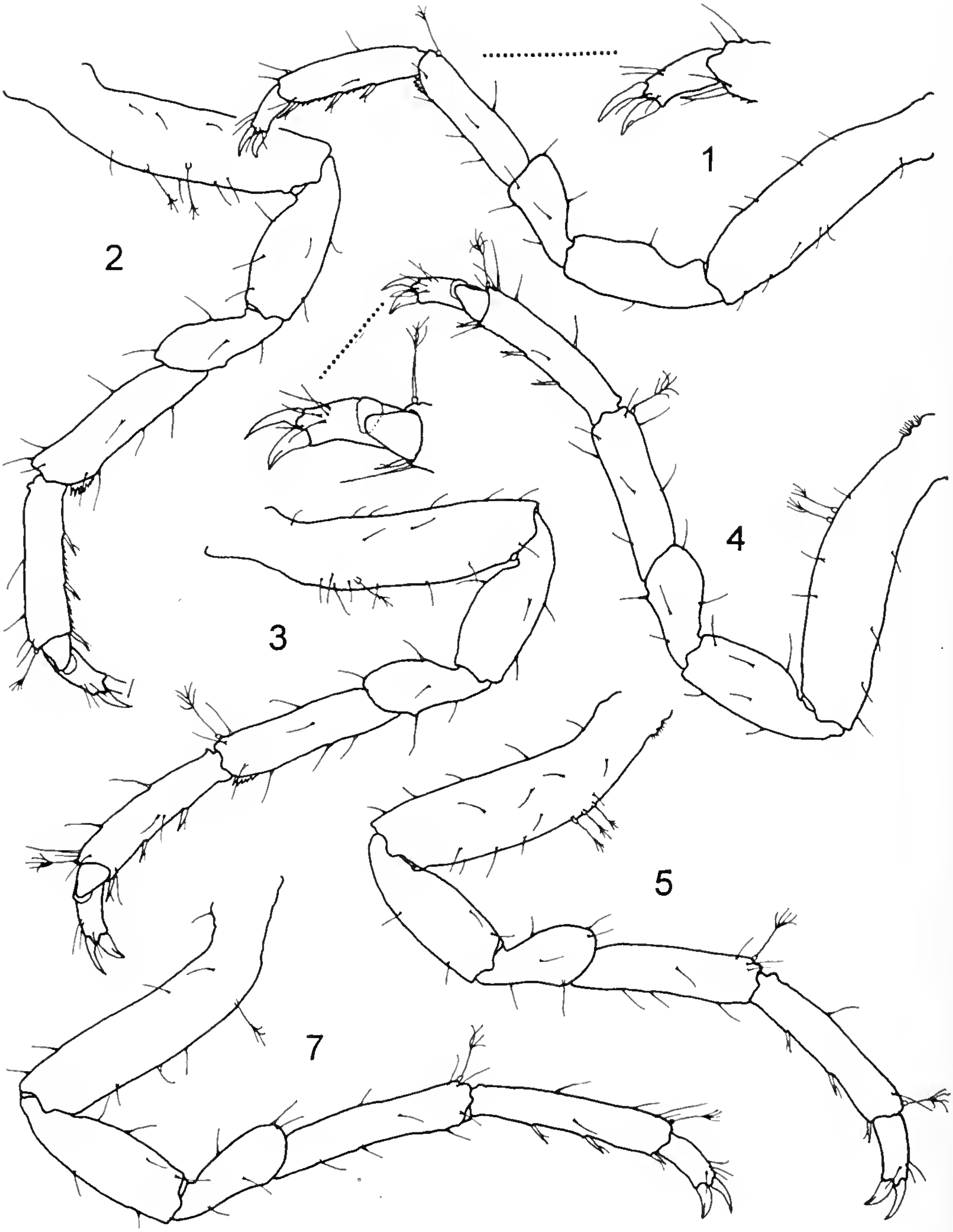

Figure 13. *Rugojoeropsis rugosa* gen. nov., sp. nov., holotype. Pereopods 1–5 and 7.

times longer than wide, twice length of ischium, with 1 or more penicillate setae on proximal half of dorsal margin (not verified in pereopod 1); merus about 0.6 length of ischium, dorsodistally expanded; carpus slightly wider than and of subequal length to propodus, single bottlebrush seta on dorsoapical margin, ventrodistal corner of carpus of some pereopods with group of acute, forward pointing spines, (verified on pereopods 1, 2 and 3 only in several specimens); propodus with 3 slender, robust seta along ventral margin, single penicillate seta dorsoapically; dactylus of pereopod 1 about third length of propodus, of pereopods 2–7 about 0.4 length of propodus, all about twice as long as wide, dorsal and ventral claws of subequal length, dorsal claw more slender.

Pleopods: Male pleopod 1 2.3 times longer than greatest width, tapering towards distal two-thirds, margins only slightly diverging in distal third, apical lobes broadly rounded, set off from lateral margins by acute backward pointing projection reaching about two-thirds along apical lobes, apical lobes fringed with simple setae; dorsal surface with simple stylet guides running from sperm duct opening to acute lateral corners, covered by extended lateral edge of stylet guide; middorsal surface with oval field of tiny setules. Male pleopod 2, protopod length 2.25 times midwidth, proximal 0.8 of lateral margin evenly convex, distal fifth concave, apex pointed, entire lateral margin with dense fringe of elongate cuticular scales serrate along anterior edge (cf. female, Fig. 11, pl2); stylet evenly curved, in retracted position reaching to apex of protopod. Female pleopod 2, shaped like combined protopods of male pleopod 2 except distolateral concavity about third length of lateral margin, lateral fringe of cuticular scales as in male, apex rounded with a few tiny simple setae. Pleopod 3, endopod rounded rectangular, width about 0.7 midsurface length; exopod article 1 about 0.9 length of endopod, barely reaching apex of endopod, lateral margin densely fringed with long, narrow cuticular scales; exopod article 2 articulating along medial margin of article 1, about half length article 1, reaching beyond endopod by third length, distally tapering to rounded apex, lateral margin fringed with long slender cuticular scales, medial margin fringed with short setules proximally and short simple setae distally. Pleopod 4, endopod of subequal size and shape to endopod pleopod 3; exopod a vestigial rounded lobe with apical setules, about six times longer than wide. Pleopod 5 similar to pleopod 4 endopod in size and shape.

Uropods: Peduncle broadly expanded medially, mediodistal corner reaching beyond apex of pleotelson, ventrodistally with a few simple submarginal setae, distal half of medial margin strongly serrate, mediodistal corner produced mediad, acutely pointed; rami of unequal length, outer ramus two-third length of inner ramus, with apical tuft of long simple setae, inner ramus about two-third length of lateral margin of peduncle, width 0.4 length, with midventral row of long, simple setae and several apical penicillate setae.

Size. Largest male 2.8 mm; largest female 2.8 mm.

Distribution. Eastern Australia south of 37°S, eastern Bass Strait, east coast of Tasmania; 400–600 m.

Etymology. From the Latin *rugosus* = uneven or rough, alluding to the texture of the cuticle.

Scaphojoeropsis gen. nov.

Type species. Scaphojoeropsis multicarinata sp. nov.

Diagnosis. Joeropsididae with body strongly tapering in dorsal view from pereonite 2 to apex of pleotelson, with variety of dorsal humps and short keels. Cuticle roughly calcified. Cephalon with midanterior dorsal surface strongly depressed, depression surrounded by sharp ridge, anterior margin straight. Pseudorostrum pointing downward, joining vertex along straight line, without apical projection. Eyes absent. Upper lip more than twice as wide as long. Mandibles with incisor divided into 2 parts, with large terminal tooth pointing forward, posterior 2–3 teeth on broad flange pointing mediad to backwards; spine row setae short, stubby, in irregular row. Lower lip, lobes wider than long, rectangular, lateral corners projecting, pointed. Maxillipeds in ventral view covering about third of cephalic width, not reaching forward to cover mandibles; endite reaching to middle of palp article 2; palp 0.8–0.9 length of endite; palp article 3 with distinctive medial lobe; article 4 shorter than 3. Pleopod 2 of female with long apical setae. Pleopod 3 exopod with transverse articulation between articles.

Included species. Scaphojoeropsis kimblae sp. nov., *S. multicarinata* sp. nov.

Etymology. From the Greek *skaphe* = boat, alluding to the body shape in dorsal view.

Scaphojoeropsis multicarinata sp. nov.

Figures 14–18

Material examined. Holotype. Vic. Bass Strait, S of Point Hicks, 38°14.80'S, 149°9.30'E, 200 m, coarse sand and gravel, WHOI epibenthic sled, M.F. Gomon et al., 24 Jul 1986, ORV *Franklin* (stn SLOPE-41), NMV J18691 (female, 2.2 mm, with 6 slides).

Paratypes (11 specimens). NSW. Off Nowra, 34°59.52'S, 151°5.94'E, 204 m, coarse shell, WHOI epibenthic sled, G.C.B. Poore et al., 14 Jul 1986, ORV *Franklin* (stn SLOPE-1), NMV J18690 (4, 1 female illustrated, see Fig. 1).

Vic. S of Point Hicks, 38°14.80'S, 149°9.30'E 200 m, coarse sand and gravel, WHOI epibenthic sled, M.F. Gomon et al., 24 Jul 1986, ORV *Franklin* (stn SLOPE-41), NMV J27719 (1 male, pleotelson and pleopods 1 and 2 illustrated, 1 slide). 50 km S of Mallacoota, 38°06.2'S, 149°45.5'E, 188 m, WHOI epibenthic sled, R. Wilson, 14 Oct 1984, FRV *Soela* (stn SO5/84/30), NMV J18694 (3).

Tas. Bass Strait, 63 km E of North Point, Flinders I., 39°44.8'S, 148°40.6'E, 124 m, fine sand and mud, SM grab, R. Wilson, 14 Nov 1981, RV *Tangaroa* (stn BSS 167), NMV J18692 (2). Bass Strait, 100 km NE of North Point, Flinders I., 38°51.58'S 148°26.5'E, 130 m, fine sand, SM grab, R. Wilson, 15 Nov 1981, RV *Tangaroa* (stn BSS 170), NMV J18693 (1).

Description. Cephalon 2.5 times wider than midline length, midanterior margin broadly concave in dorsal view, concavity rimmed by raised keel, with 2 keels reaching backwards halfway along cephalon on each side of midline, small keel present immediately lateral to posterior part of backward reaching keels, low keel present anterolaterally on each side forming recurved loop lateral to insertion of antenna 1; pseudorostrum evenly convex.

Body broadest at pereonites 2 and 3. Pereonites with middorsal longitudinal keel, that of pereonite 1 divided into short anterior and longer posterior part, pereonite 1 with small crescent shaped keels lateral to each part of midkeel, pereonites 2–7 with single middorsal keel and crescent shaped mid-lateral keels, anterior parts of midand lateral keels linked by low serrate ridge; pereonites 1–4 of equal length, pereonites 5–7 of equal length, 0.8 length of more anterior pereonites. Pleotelson width about 1.1 length, with middorsal longitudinal keel reaching to base of apical lobe; lateral margins smooth except for fringe of cuticular outgrowth, evenly tapering towards broadly rounded apex, with deep insinuation for uropods each side of apex.

Antenna 1 of 6 articles; article 1 rectangular, not reaching lateral corner of frontal sinus, width two-thirds length, about twice as long as and third as wide again as article 2 which is barely twice as long and wide as 3, articles 2 and 3 with lateral flange of cuticular outgrowth; flagellum of 3 articles, article 1 two-thirds length of peduncle article 3, article 2 as long as peduncle article 3, article 3 as long as and half width of 1, articles 2 and 3 each with 1 long aesthetasc. Antenna 2, peduncle articles 1–3 of slightly increasing length and width, article 3 distally expanded, distal width twice midlength, article 4 third length of 3, about 5 times wider than long, halfway embedded into 3, article 5 nearly twice as long as 1–4 combined, broadly expanded laterally, width, excluding broad fringe of cuticular outgrowth, two-thirds length, article 6 about 0.4 length of 5, expanded distally; flagellum as long as peduncle article 6, with up to 6 articles, article 1 not inflated, apparently not conjoint, as long as articles 2 and 3 combined.

Mouthparts: Upper lip nearly rectangular, distal margin slightly convex, fringed with setules, distolateral corners distinct, slightly projecting. Mandible palp slender, not reaching to near apex of forward pointing tooth of incisor, article 2 0.6 length of 1, article 3 six-sevenths length of 2, article 2 with 2 mediodistal pectinate setae, article 3 with 2 terminal pectinate seta; incisor with 1 large forward pointing tooth and 3 mediad to backward pointing teeth on broad flange, forward pointing tooth of right mandible with lateral serration along proximal two-thirds; spine row of few short, stout, minutely pectinate setae, left with row divided into 2 groups (distalmost slightly stouter non-pectinate seta possibly homologous with lacinia mobilis). Lower lip, about 3 times broader than long, body rectangular, distolateral parts expanded to wing-like projections with slightly acute anterior and posterior corners, lateral margins convex. Maxilla 1 outer plate with 10 unequally long finely dentate setae and 3 short simple setae on middorsal margin; inner plate with evenly rounded apex half width of outer plate, reaching to middle of medial margin of outer plate, with 2 apical simple setae and several short apical setules. Maxilla 2, inner and middle plates of equal length and width, 0.75 length and 0.6 width of outer plate with 2 subequal, straight, finely pectinate setae terminally, outer plate with 3 finely pectinate setae, apical one as long as plate, both subapicals much shorter and more slender. Maxillipeds covering about third ventral width of cephalon, endites reaching forward to cover bodies of maxillae but not mandibular incisors or upper lip; basis twice as long as midwidth, endite reaching to about middle of palp article 2, mediodistal concavity vestigial with single multidentate lump-shaped seta;

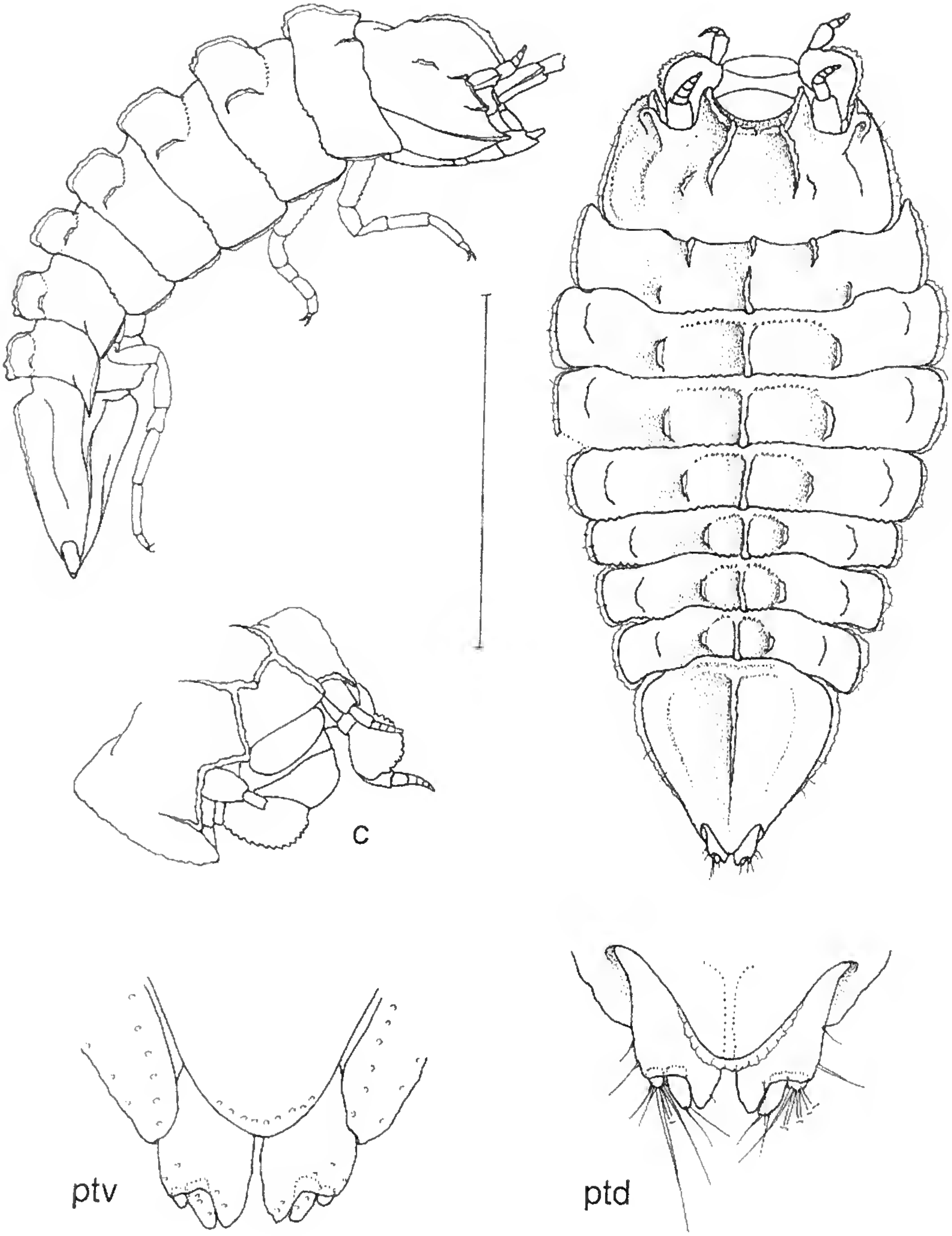

Figure 14. *Scaphojoeropsis multicarinata* gen. nov., sp. nov., holotype. **c**, cephalon, anterolateral view; **ptd**, apex of pleotelson, dorsal view; **ptv**, apex of pleotelson, ventral view, setae omitted. Habitus scale bar: 1 mm.

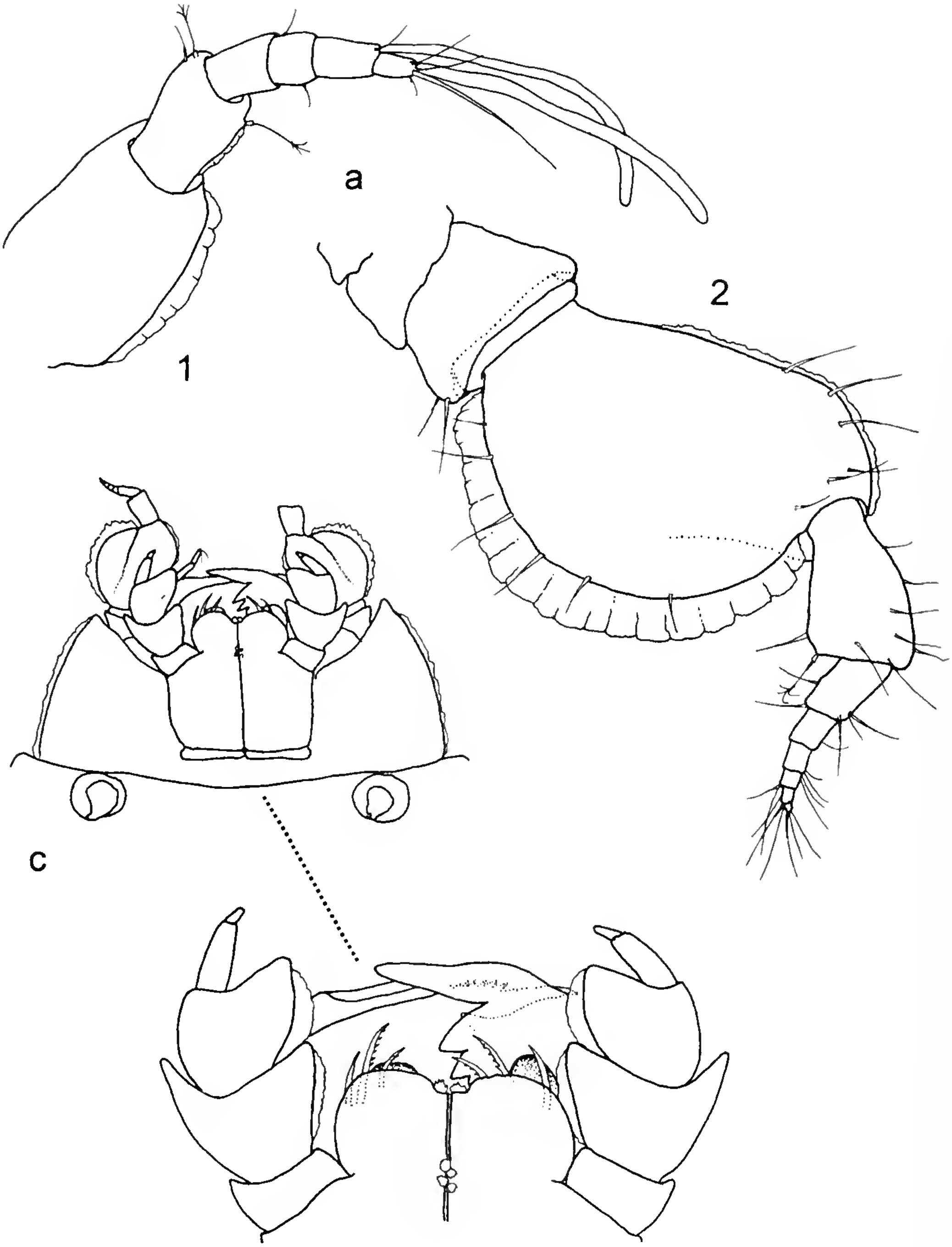

Figure 15. *Scaphojoeropsis multicarinata* gen. nov., sp. nov., holotype. **a**, antennae (1 and 2); **c**, cephalon, ventral view.

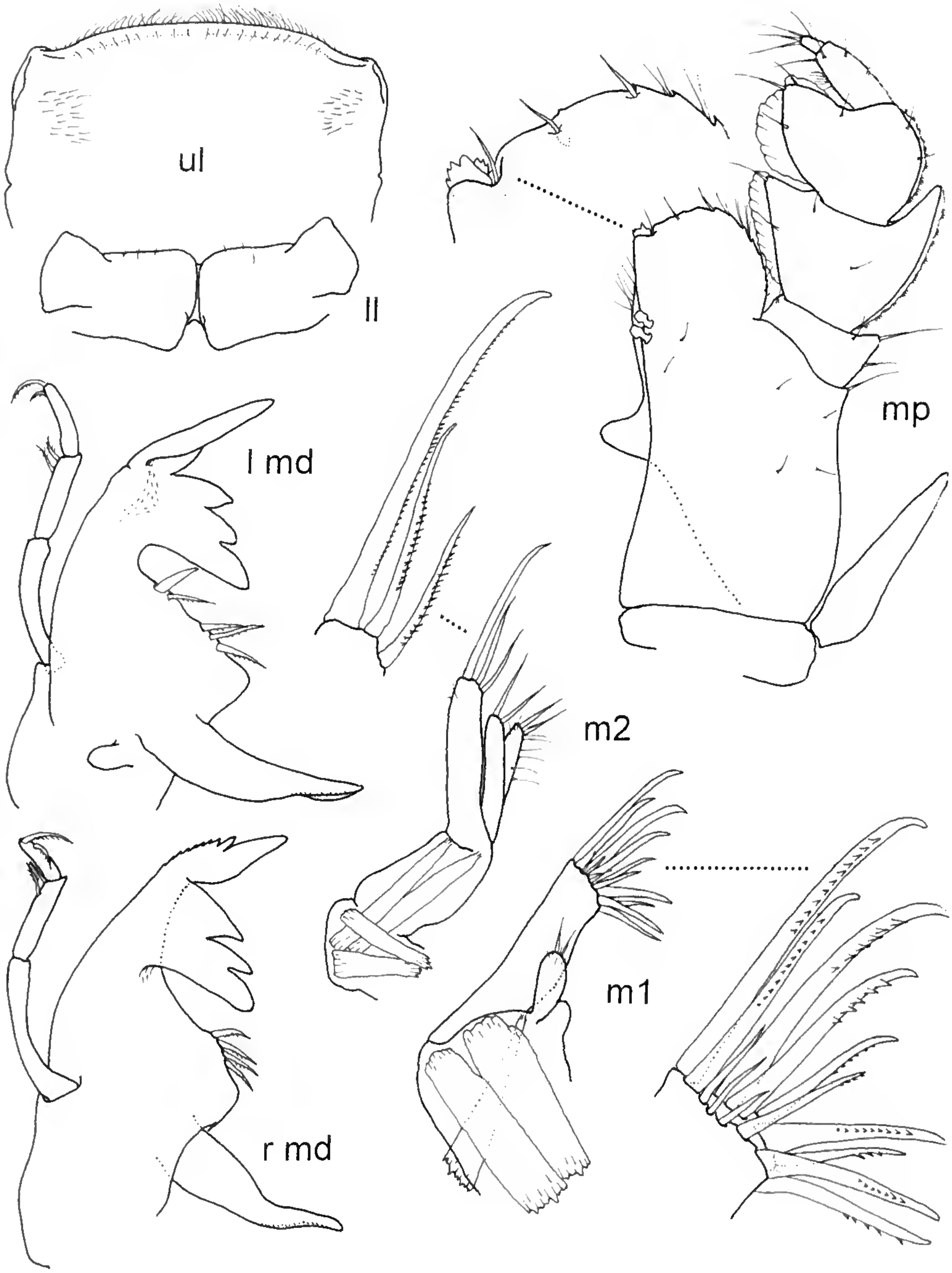

Figure 16. *Scaphojoeropsis multicarinata* gen. nov., sp. nov., holotype. **ll**, lower lip; **md**, mandible (**l**, left, **r**, right); **m**, maxilla (1 and 2), **mp**, maxilliped; **ul**, upper lip.

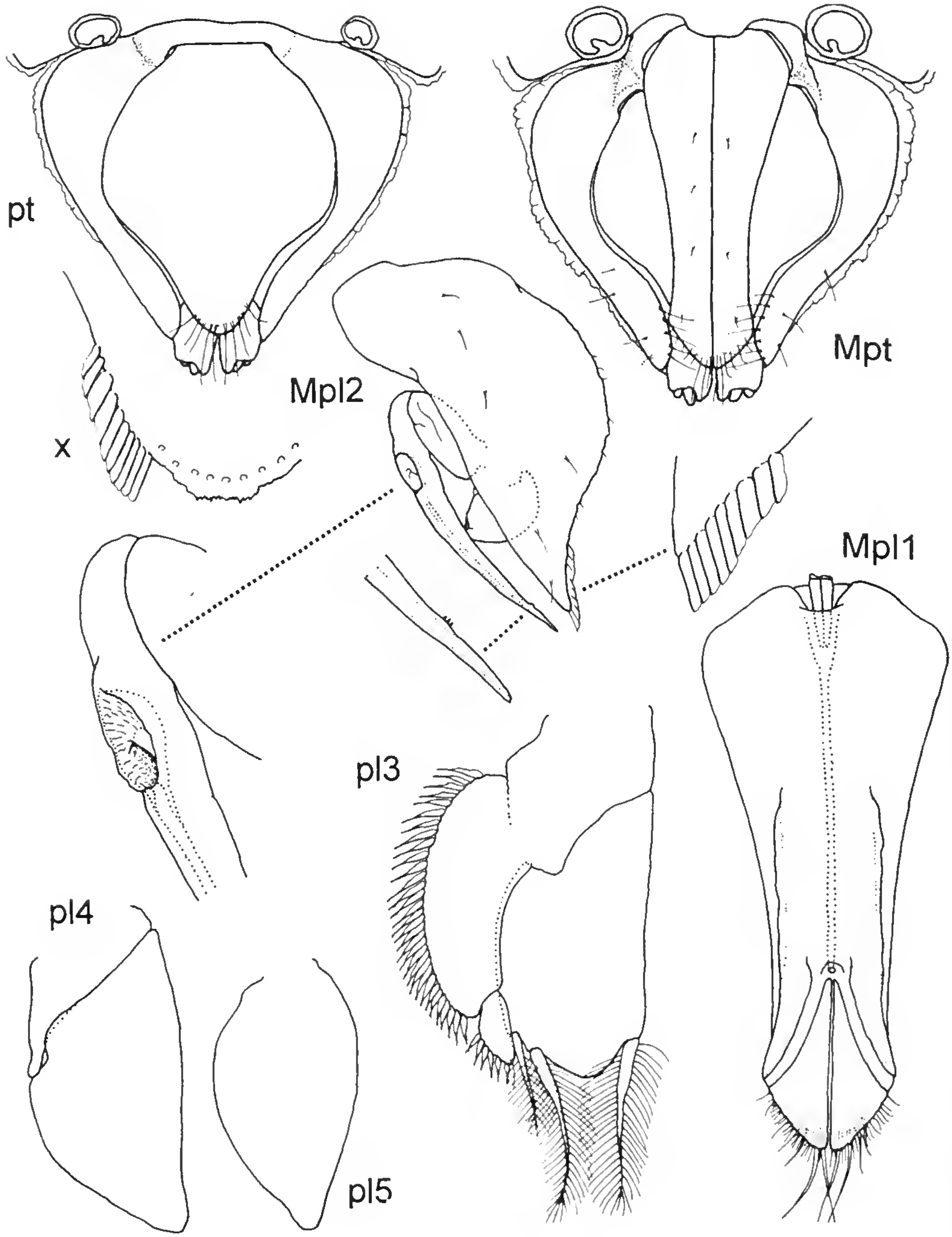

Figure 17. *Scaphojoeropsis multicarinata* gen. nov., sp. nov., holotype, except **M**: paratype, male, (NMV J27719). **pl**, pleopod (1–5); **pt**, pleotelson ventral view; **x**, apex of female pleopod 2.

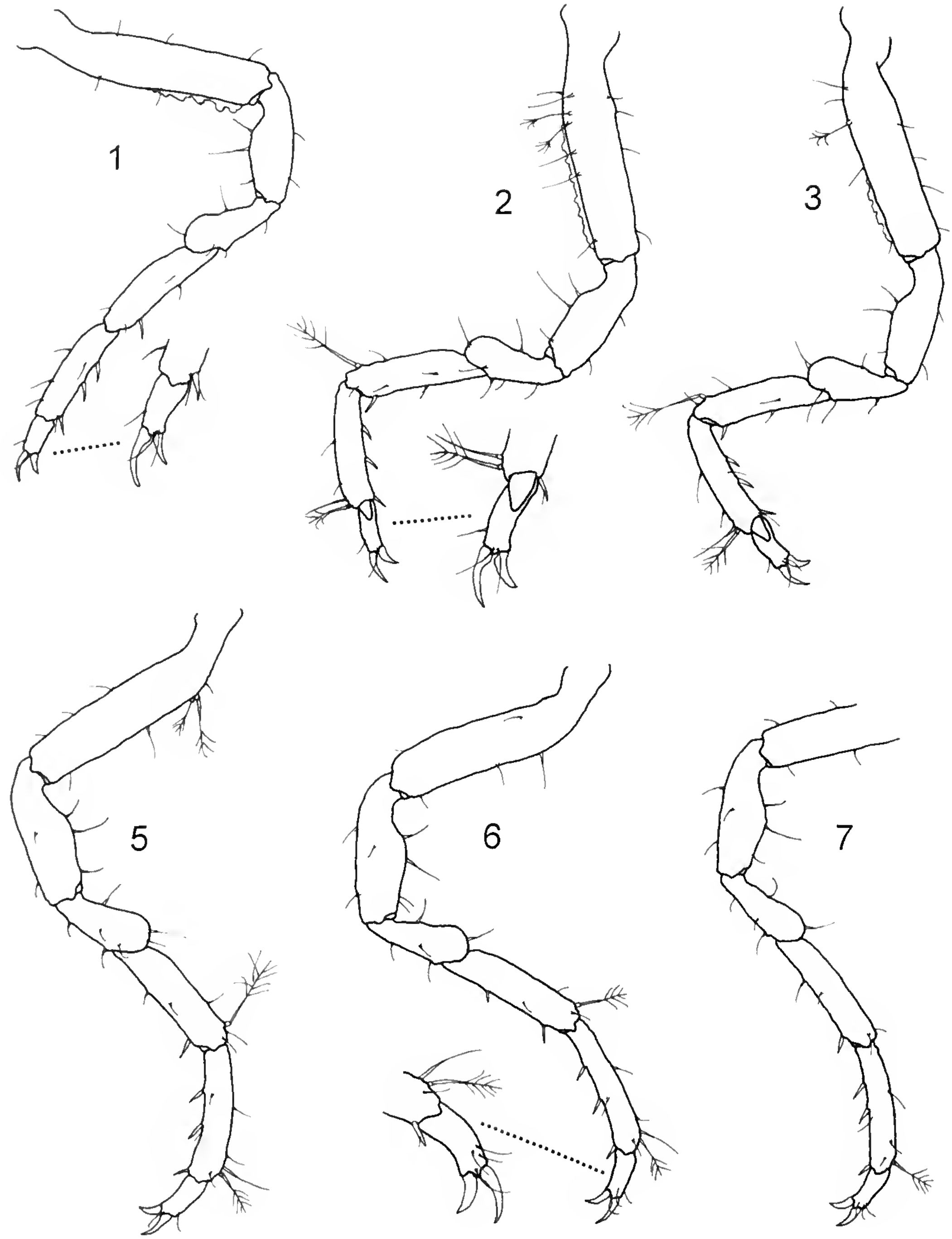

Figure 18. *Scaphojoeropsis multicarinata* gen. nov., sp. nov., holotype. Pereopods 1–3, 5–7.

distolateral margin of endite evenly rounded, finely serrate, with single slender setule in each indentation, apical margin somewhat truncate with a few short simple setae; palp articles 2 and 3 as broad as or broader than endite, palp article 2 2.5 times longer than 1 along midsurface, with acute, mediad pointing medial lobe and acute forward pointing distolateral lobe reaching halfway along article 3; article 3 subequal to 2 in length and width, medially expanded to large, forward pointing, rounded lobe, medial margins of articles 2 and 3 with coarse fringe of cuticular outgrowth, lateral margin with tiny etules; article 4 two-thirds length of 3, medial surface with setules in middle third; article 5 about third length of 4, rounded, with tuft of long, simple setae; epipod as long as palp articles 1, 2 and half of 3 combined, tapering to blunt point.

Pereopods similar, with 2 claws; basis about 5 times longer than wide, twice length of ischium, with 1 or more penicillate setae on proximal half of dorsal margin; merus about two-thirds length of ischium, with broadly rounded expansion dorsodistally; carpus and propodus length subequal to ischium, with 1 or 2 penicillate setae on dorsoapical margin (not verified on pereopod 1); propodus with 3 slender, robust setae along ventral margin; dactylus of all pereopods about two-thirds length of propodus, about twice as long as wide; dorsal claw slightly longer than ventral claw.

Pleopods: Male pleopod 1 2.3 times longer than greatest width, tapering towards distolateral corners, apical lobes evenly rounded joining lateral margins at wide angle, apical lobes fringed with short setules and medium to long simple setae; dorsal surface with simple, uncovered stylet guides running from sperm duct opening to lateral corners. Male pleopod 2 protopod 2.5 times longer than midwidth, proximal two-thirds of lateral margin evenly convex, distal third concave, apex pointed, distalmost part of lateral margin with overlapping rectangular cuticular scales; stylet evenly curved, in retracted position reaching to apex of protopod, with group of tiny teeth laterally one sixth length from apex. Female pleopod 2 shaped like combined protopods of male pleopod 2 except apex broadly rounded with fringe of long, simple setae; marginal cuticular scales as in male. Pleopod 3 endopod rectangular, width 0.6 length of medial margin; exopod barely reaching apex of endopod, article 1 as long as endopod, article 2 articulating with 1 at nearly right angle, twice as long as wide, about third length of article 1, distally tapering to blunt apex; lateral margin of both articles fringed with robust elongate cuticular scales. Pleopod 4 endopod subequal in length to endopod pleopod 3, tapering to rounded apex; exopod a tiny rounded lobe without setules. Pleopod 5 similar to pleopod 4 endopod in shape.

Uropods extending beyond apex of pleotelson by third their length; peduncle with broad, rounded medioapical, backward pointing projection covering length of inner ramus, medial length of peduncle including medial projection 1.5 midwidth; rami of unequal length, outer ramus third to half length of inner ramus, with tuft of long, simple apical seta; inner ramus width 0.5 length, with single, simple seta apically and a few setae on ventral surface.

Size. Largest male 1.6 mm; largest female 2.6 mm.

Distribution. Eastern Australia south of 35°S, to eastern Bass Strait; 124–204 m.

Etymology. The specific epithet refers to the many short dorsal keels.

Remarks. Scaphojoeropsis multicarinata is most easily distinguished from *S. kimblae* sp. nov. (condition in parentheses) by its dorsal carinae on pereon and pleotelson (no carinae), uropod peduncle with mediodistal projection (no projection), maxilla 2 with full complement of three lobes (reduced to one lobe), and male pleopod 1 with rounded apex (apex with two acute lobes).

Scaphojoeropsis kimblae sp. nov.

Figures 19–22

Material examined. Holotype. Tas. 60 km E of North Point, Flinders I., 39°41.7´S, 148°39.5´E, 115 m, muddy sand, naturalists' dredge, G.C.B. Poore, 27 Mar 1979, HMAS *Kimbla* (stn BSS 32), NMV J18695 (male, 2.1 mm, with 7 slides).

Paratypes (4 specimens). NSW. Off Eden, 37°0.60´S 150°20.70´E, 363 m, coarse shell, WHOI epibenthic sled, G.C.B. Poore et al., 21 Jul 1986, ORV *Franklin* (stn SLOPE-22), NMV J18696 (3, one without cephalon).

Tas. 60 km E of North Point, Flinders I., 39°41.7´S, 148°39.5´E, 115 m, muddy sand, naturalists' dredge, G.C.B. Poore, 27 Mar 1979, HMAS *Kimbla* (stn BSS 32), NMV J27720 (1 female, with 1 slide).

Description. Cephalon about 4 times wider than dorsal midlength, midanterior margin nearly straight in dorsal view, depressed anterior part rimmed by raised concave keel, with 2 straight keels reaching backwards from lateral parts of concave rim halfway along cephalon, small hump present on both sides posterior to insertion of

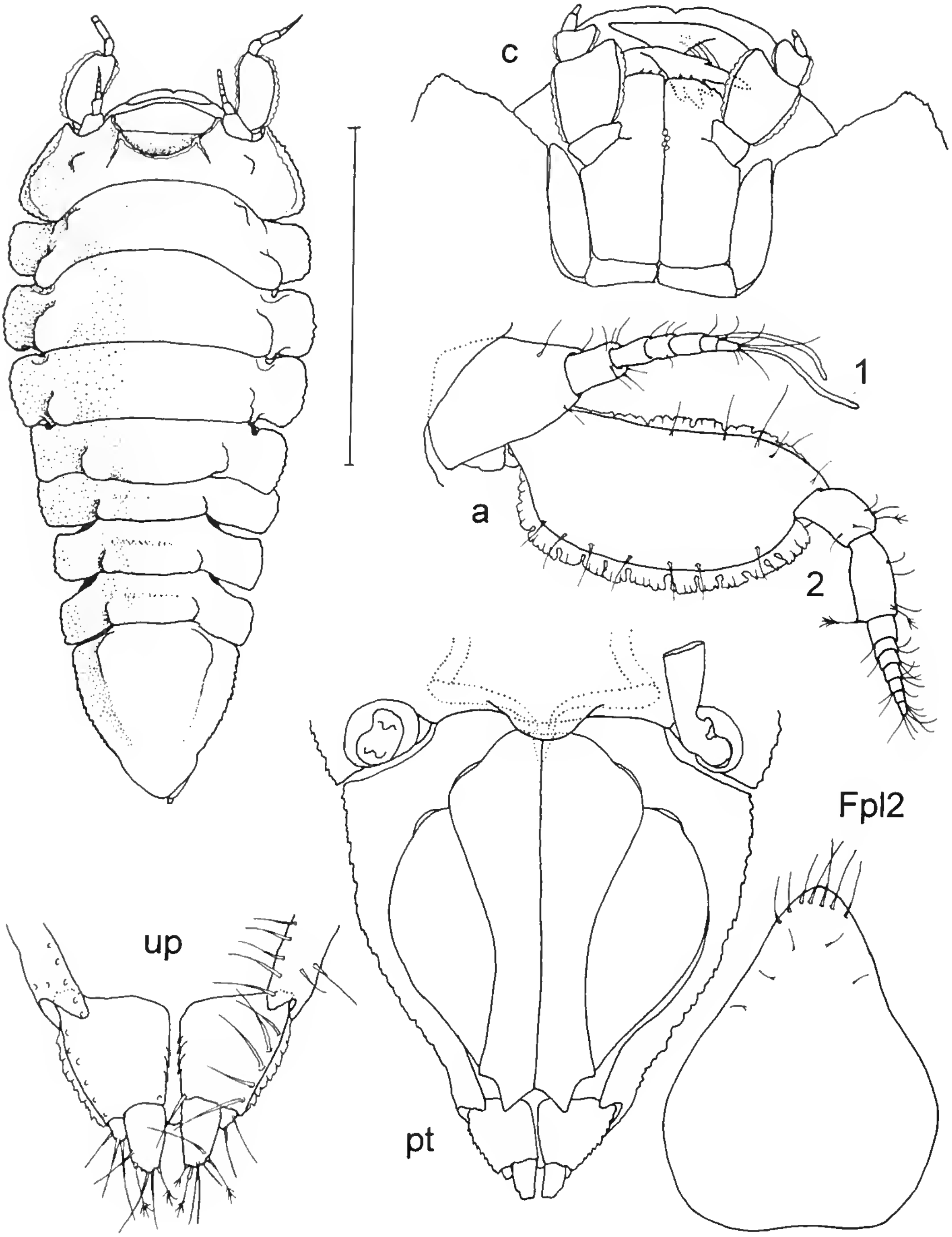

Figure 19. *Scaphojoeropsis kimblae* gen. nov., sp. nov., holotype, except **F**: paratype, female, (NMV J27720). **a**, antennae (1 and 2), right, dorsal view; **c**, cephalon, ventral view; **pl2**, female pleopod 2; **up**, uropods, ventral view; **pt**, pleotelson, ventral view, setae omitted. Habitus scale bar: 1 mm.

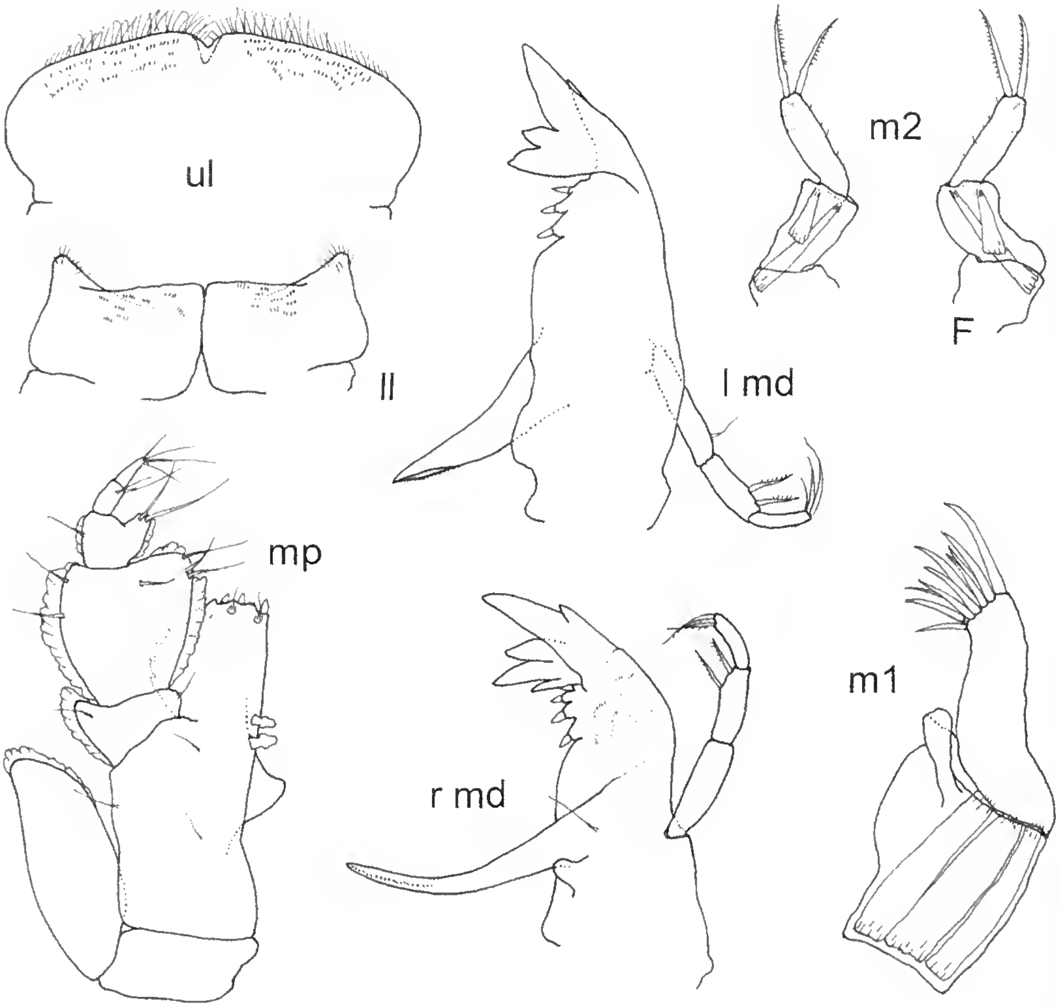

Figure 20. *Scaphojoeropsis kimblae* gen. nov., sp. nov., holotype, except **F**: paratype, female, (NMV J27720). **ll**, lower lip; **md**, mandible (**l**, left, **r**, right); **m**, maxilla (1 and 2); **mp**, maxilliped; **ul**, upper lip.

antenna 1; pseudorostrum broad, convex. Body broadest at pereonite 2. Pereonites 1, 3 and 4 of subequal length, 2 about 1.2 times longer, 1 with low midanterolateral humps, 1–4 with larger posterolateral humps; pereonites 5–7 of equal length, three-quarters length of 4, posterolateral humps joined across posterior half of pereonite to form low, rounded ridge. Pleotelson length about 1.1 width, lateral margins finely, irregularly serrate, convexly tapering to narrow point at three-quarters length and further to broadly rounded apex; apex without incisions for uropods in dorsal view, uropods barely visible in dorsal view.

Antenna 1 of 7 articles; article 1 distally tapering, reaching lateral corner of frontal ridge, width at base 0.8 length, about 2.5 times longer than article 2, articles 2 and 3 of subequal length, 3 about two-thirds width of 2; flagellum of 4 articles, article 2 length 1.25 times 1, articles 2 and 4 with 1 long aesthetase (broken off in 3?). Antenna 2, (configuration of peduncle articles 1–4 not clarified, possibly as in *S. multicarinata*, at least article 4 very short), article 5 moderately expanded laterally, width, excluding broad cuticular fringe, 2.3 times length, article 6 length 1.5 width, about 0.25 length of 5; flagellum barely 3

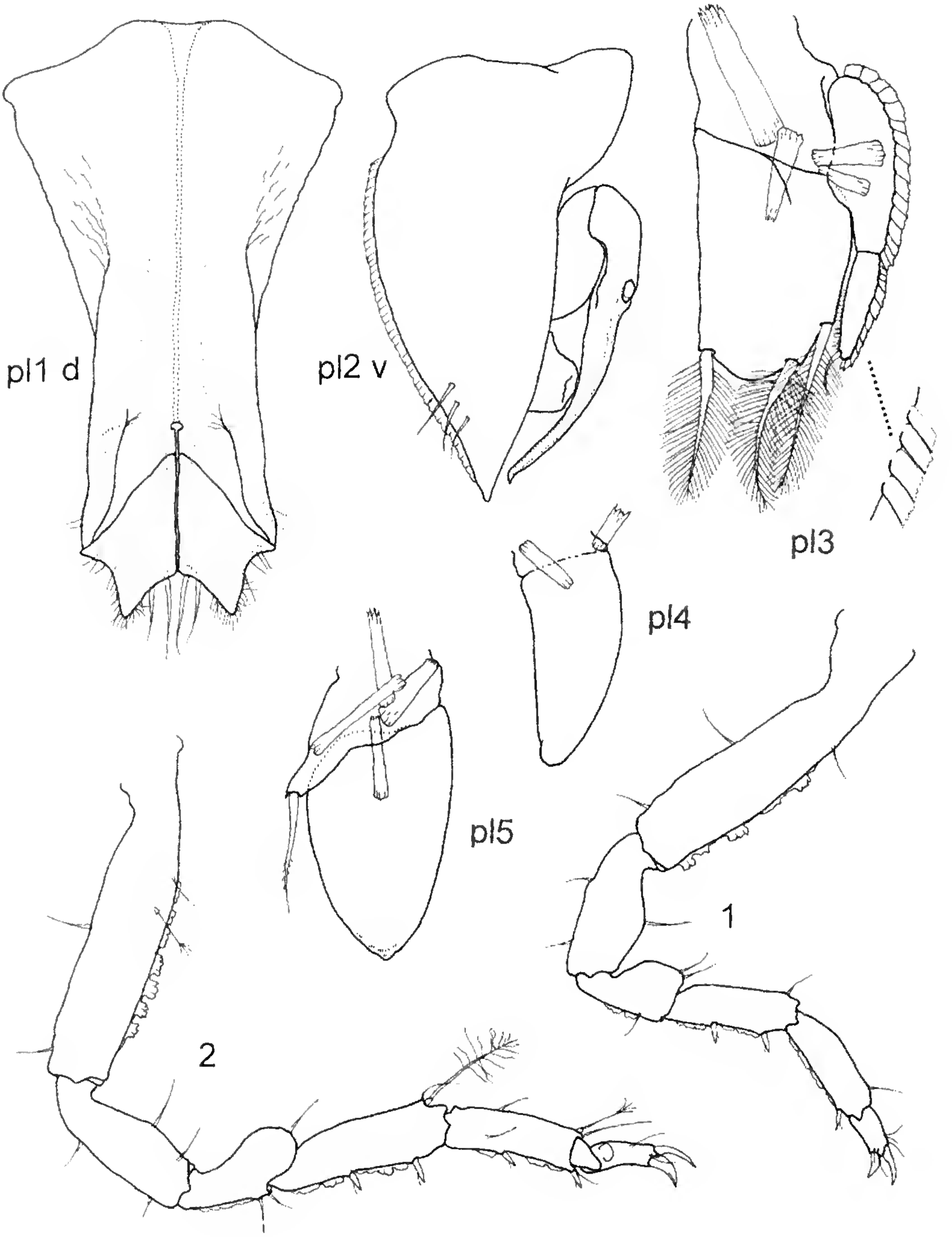

Figure 21. *Scaphojoeropsis kimblae* gen. nov., sp. nov., holotype. **pl**, pleopod (1–5); **p**, pereopod (1 and 2); **d**, dorsal view; **v**, ventral view.

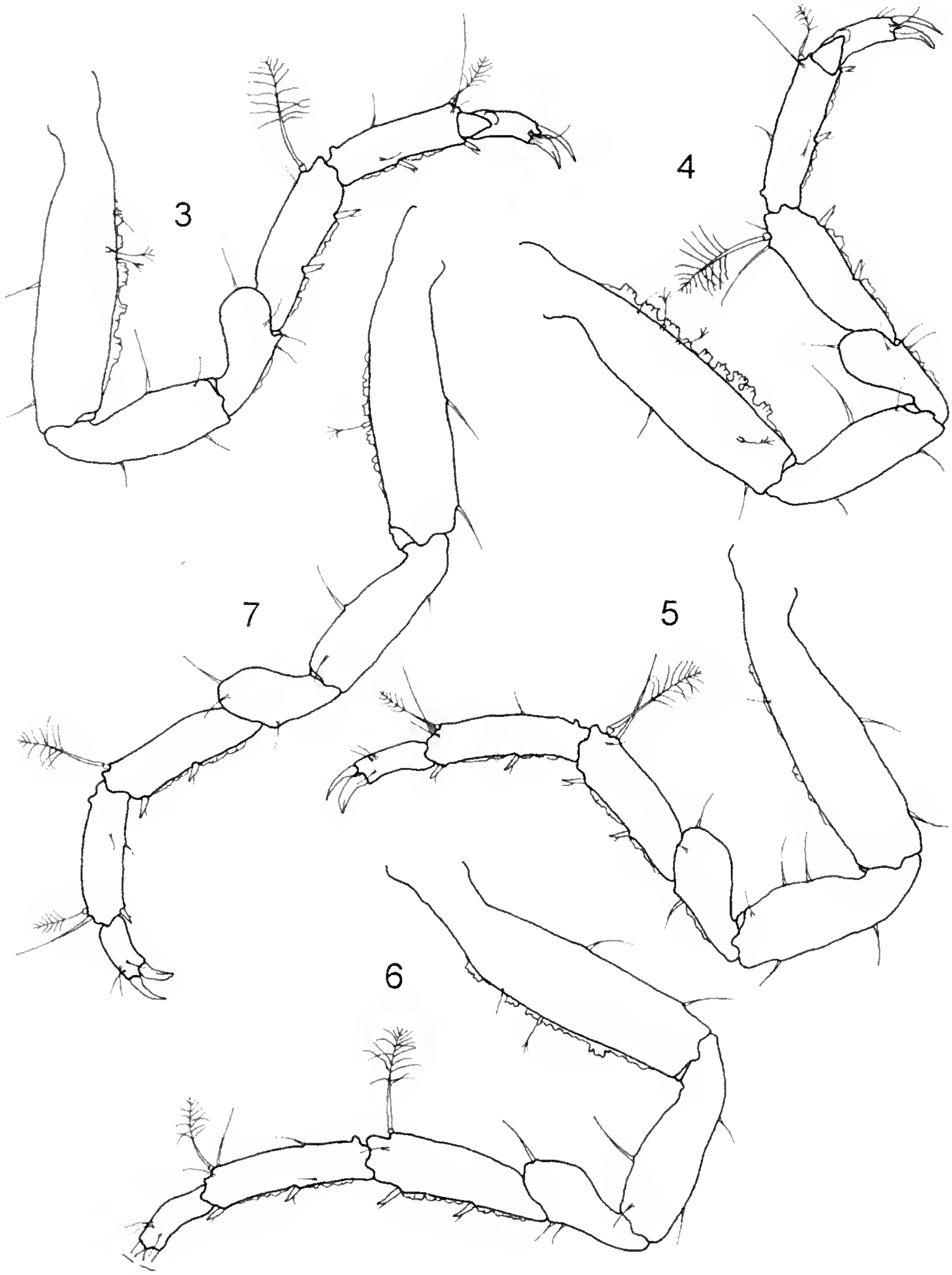

Figure 22. *Scaphojoeropsis kimblae* gen. nov., sp. nov., holotype. Pereopods 3–7.

times longer than peduncle article 6, with up to 8 articles, article 1 not inflated, apparently not conjoint, as long as articles 2–7 combined.

Mouthparts: Upper lip, length about 0.4 width, anterior margin convex, notched in middle, fringed with long setules, lateral margins rounded. Mandible palp slender, reaching to middle of incisor, article 2 about two-thirds length of 1, article 3 0.8 length of 2, article 2 with 2 mediodistal pectinate setae, article 3 with 3 terminal pectinate seta; incisor with 1 forward pointing tooth and 3 mediad pointing teeth on broad flange, forward pointing tooth of right mandible with small accessory tooth laterally; spine row composed of 4 short, peg-like setae on conical projections. Lower lip about 3 times broader than long, body rectangular, distolateral corners projecting forward to rounded apices. Maxilla 1 outer plate with 10 unequally long completely smooth setae; inner plate a vestigial rounded lobe without setae. Maxilla 2 composed of single plate, about 3 times longer than wide, with 2 pectinate robust setae apically. Maxillipeds covering about third of ventral width of cephalon, endites reaching forward to cover bodies of maxillae but not mandibular incisors and upper lip; basis length 2.5 times midwidth, reaching about two-thirds along palp article 2, mediodistal concavity vestigial with single peg like robust seta; lateral margin of endite evenly rounded, coarsely serrate, apical margin somewhat truncate with 2 peg-like robust setae and a few short simple setae; palp article 2 broader than endite; palp article 1 with short distolateral projection; article 2 broadly expanded medially, about 3 times longer than 1 along midsurface; article 3 about half length and width of 2, with medial rounded lobe; medial margins of articles 2 and 3 and lateral margin of 1, 2 and 3 with coarse fringe of cuticular outgrowth; articles 4 and 5 of subequal length and width, combined as long as 3; epipod reaching to insertion of palp, 2.3 times longer than wide, rounded apex with fringe of cuticular outgrowth.

Pereopods similar, with 2 claws; basis about 4.5 times longer than wide, twice length of ischium; 2–7 with 1 or 2 small penicillate setae midway on dorsal margin; merus about two-thirds length of ischium, with broadly rounded expansion dorsodistally; carpus and propodus of subequal length, about 0.8 length of ischium, with single large penicillate seta on dorsoapical margin; carpus and propodus with 1 or 2 slender, robust setae along ventral margin; fringe of cuticular outgrowth along dorsal margin of basis and ventral margin of merus, carpus and propodus; dactylus of all pereopods about half length of propodus, about 2.5 times longer than wide; dorsal claw subequal in length to and more slender than ventral claw.

Pleopods: Male pleopod 1 midlength about 1.7 times greatest width, tapering towards midpoint, slightly expanding in distal half towards right angled lateral corners; apical lobes acutely pointed, separated in midline at about 90 degrees, lateral margins concave, laterally with small simple setae, medially with long simple setae, apices with fringe of small setules; dorsal surface with funnel shaped, uncovered stylet guides running from sperm duct opening to lateral corners. Male pleopod 2, protopod 2.5 times longer than midwidth, apex acutely pointed, entire lateral margin with fringe of cuticular scales (details not available); stylet evenly curved, in retracted position reaching to about apex of protopod. Female pleopod 2, shaped like combined protopods of male pleopod 2 except apex broadly rounded with fringe of long, simple setae, (lateral cuticular scales not observed). Pleopod 3, endopod rectangular, width about two-thirds length of medial margin; exopod barely reaching apex of endopod; article 1 three-quarters length of endopod; article 2 articulating with 1 at right angle, 3 times as long as wide, about 0.6 length of article 1, distally tapering, apex rounded; lateral margin of both articles fringed with short, overlapping rectangular cuticular scales. Pleopod 4, endopod subequal in length to endopod pleopod 3, ovoid, without setae but with a few apical cuticular combs; exopod about quarter length of endopod, with single long pectinate seta apically. Pleopod 5 similar to pleopod 4 endopod but more slender.

Uropods: Peduncle without medial projection, medial margin as long as peduncle width at base, with acute denticles in midthird; rami of unequal length, outer ramus third length and width of inner ramus, with a few long simple setae; inner ramus two-thirds length of peduncle inner margin, width 0.6 length, with simple setae and penicillate setae apically.

Size. Largest male 2.1 mm; largest female 2.1 mm.

Distribution. Eastern Australia south of 37°S to eastern Bass Strait; 115–363 m.

Etymology. The species is named after HMAS *Kimbla*.

Remarks. See previous species for characters to separate *Scaphojoeropsis kimblae* from *S. multicarinata*.

Acknowledgments

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Memoirs of Museum Victoria 58(2): 335–345 (2001)

PLATYPROTUS PHYLLOSOMA, GEN. NOV., SP. NOV., FROM ENDERBY LAND, ANTARCTICA, AN UNUSUAL MUNNOPSIDID WITHOUT NATATORY PEREOPODS (CRUSTACEA: ISOPODA: ASELLOTA)

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Abstract

Just, J., 2001. *Platyprotus phyllosoma*, gen. nov and sp. nov., from Enderby Land, Antarctica, an unusual munnopsidid without natatory pereopods (Crustacea: Isopoda: Asellota). *Memoirs of Museum Victoria* 58(2): 335–345.

A new genus and species, *Platyprotus phyllosoma*, of munnopsidid isopod is described from Enderby Land, Antarctica. *Platyprotus* differs from all other munnopsidids, except *Microprotus* Richardson, 1910 and some species in *Storthyngurella* Malyutina, 1999, in having fully ambulatory pereopods 5–7 without natatory setae. *Platyprotus* differs from those genera primarily in body shape, lack of marginal spines on pereonites 5–7 and pleotelson, lack of a preanal ridge, and in possessing highly derived spatulate setae on article 3 of the mandibular palp. All three genera are part of the wider '*Storthyngura*' clade. If the present concept of *Storthyngurella* is confirmed, ambulatory pereopods 5–7 have been derived independently more than once within that clade. The family name is emended to Munnopsididae Hansen, 1916.

Introduction

The Munnopsididae are a highly diverse family occurring in all oceans primarily in deep water from upper slope to hadal depths, as well as at shelf depths in polar and subpolar regions. The natatory pereopods 5–7 with expanded, flattened carpi and propodi fringed with long plumose natatory setae generally have been considered the most immediately recognisable synapomorphy in the Munnopsididae (Wilson, 1989).

Wilson et al. (1989) transferred *Microprotus* Richardson, 1910 from the Janiridae to the Munnopsididae. The five known species in *Microprotus* have ambulatory pereopods 5–7 with tubular carpi and propodi without plumose natatory setae. Wilson (1989) recognised seven subfamilies in the Munnopsididae, but left several genera, including *Microprotus* and *Storthyngura* Vanhöffen, 1914 as incertae sedis. Wilson et al. (1989) considered *Microprotus* to be most closely related to the heterogeneous *Storthyngura* complex.

Malyutina (1999) described a new genus, *Storthyngurella*, with eight species from abyssal to upper hadal depth, five of which were transferred from the *Storthyngura complex*. Two of the species referred to *Storthyngurella*, *S. menzies* Malyutina and *S. triplispinosa* Menzies, have ambulatory pereopods 5–7. The remaining species, including the type species of *Storthyngurella*, *S. hirsuta* Malyutina, 1999, have slender natatory pereopods 5–7 with short plumose setae along the posterior margin of carpus and propodus.

This paper reports on a new munnopsidid species from Antarctica, *Platyprotus phyllosoma* gen. nov. and sp. nov., with ambulatory pereopods 5–7 and no natatory setae. *Platyprotus* shares with *Storthyngura* and *Microprotus* a suite of characters listed by Wilson (1989: 343) as strong indicators of a monophyletic taxon. Malyutina (1999: 269) added *Storthyngurella* to this clade. *Platyprotus* differs from the other three genera mentioned, notably in body shape, in the lack of body spines along the margins of pereonites 5–7 and the pleotelson, in the complete lack of a preanal ridge on the pleotelson, and in the uniquely spatulate setae on article 3 of the mandibular palp (Table 1). These differences are considered autapomorphic.

Wilson et al. (1989) concluded that the ambulatory pereopods 5–7 of *Microprotus* are an apomorphic reversal within the Munnopsididae, derived from the natatory pereopods of an ancestral *Storthyngura*. The presence of a group of species with ambulatory pereopods within *Storthyngurella*, and the discovery of *Platyprotus*, do not disprove this hypothesis. The question arises, however, as to whether this reversal combines *Microprotus*, *Storthyngurella* and *Platyprotus* in a monophyletic taxon. For that hypothesis to be accepted *S. menzies* and *S. triplispinosa* would have to be, a priori, recognised as a separate

Table 1. Characters of presumed generic significance among *Microprotus*, *Storthyngurella* (characters in bold refer to species without natatory pereopods), *Storthyngura* and *Platyprotus* gen. nov.

Character	*Microprotus*	*Storthyngurella*	*Storthyngura*	*Platyprotus*
Body shape	subcylindrical	subcylindrical	subcylindrical	flat
Dorsal spines on cephalon	absent	present	present/absent	absent
Lateral spines on pereonites number	2–7	4–7	1/3/4–7	3–4
Lateral spines on pleotelson	present	present	present (absent*)	absent
Apical spines on pleotelson	2	1	variable/absent	absent
Pleotelson articulation	fused	**free**/fused	fused/free	free
Preanal ridge	present	present	present	absent
Medial spine on article 1 of antenna 1	absent	present	present/absent	present
Mandibular palp article 3 setae	simple	simple	simple	complex, spatulate
Maxilliped epipod lateral tooth	present	present **or absent**	present or absent	absent
Male pleopod 2, apex of basis	acute	rounded	acute	rounded
Male/female pleopod 2 setae	simple	?	variable: no setae to short plumose	long hemiplumose
Pleopod 3, endopod setae	numerous	**3–4**	3-numerous	3

*Two of the many *Storthyngura* species, *S. eltaniae* Georges and Menzies, 1968 and *S. torbeni* George, 1987 lack pleotelson spines; both have a simple pleotelson of *Eurycope*-like shape.

(new) genus, since the remaining species in *Storthyngurella* have slender natatory pereopods 5–7. The alternative is to accept that ambulatory pereopods 5–7 were derived more than once as part of an evolutionary trend within the '*Storthyngura*' clade. This is the only possible hypothesis if the present concept of *Storthyngurella* is confirmed. Table 1 does not provide answers to these questions, which can only be addressed by a full cladistic analysis of the entire '*Storthyngura*' clade.

Munnopsididae Hansen, 1916, nom. emend.

Remarks. Most prior authors have referred to this family as Munnopsidae (or erroneously as Eurycopidae). G.D.F. Wilson (pers. comm.) has drawn my attention to the fact that the genitive of the latinised adjectival ending *-opsis* (Greek, like) of *Munnopsis* is *-opsidis* and the family name is here emended to Munnopsididae.

Platyprotus gen. nov.

Type species. Platyprotus phyllosoma sp. nov.

Diagnosis. Munnopsididae with pereopods 5–7 ambulatory, without natatory setae. Body flattened, widening from pereonite 1 to pleotelson. Pleotelson free. Middorsal spines short, triangular. Lateral spines (not coxal spines) on pereonites 3 and 4 only. Pleotelson without marginal spines. Pleotelson without preanal ridge. Antenna 1 article 1 with strong medial spine. Antenna 1 flagellum with aesthetases on distalmost half of articles. Mandible with posterior projection articulating with cephalon in short notch. Mandibular palp article 3 with highly modified spatulate setae. Mandibular incisor teeth distinct. Maxilliped epipod lateral margin smooth. Male pleopod 2 protopod with broadly rounded apex, fringed with long hemiplumose setae. Pleopod 3 endopod with 3, exopod with 9 pappose setae.

Etymology. The name combines references to the flat body and to the similarity of pereopods 5–7 to *Microprotus*.

Platyprotus phyllosoma sp. nov.

Figures 1–8

Material examined. Holotype. Off Enderby Land, Antarctica (65°50.1'S, 50°34.30'E–65°50.10'S, 50°34.90'E), 540 m–2°C, mainly rocky bottom with mud/clay patches, dominant biota: crustaceans, ophiuroids, bryozoans, hard coral, 20 Nov 1985, M. Norman on *Nella Dan*, WHOI epibenthic sled (stn. HRD-011), Museum Victoria, J47017 (male, 5 mm, with 5 slides — pleopod 1 missing, presumably lost during collecting).

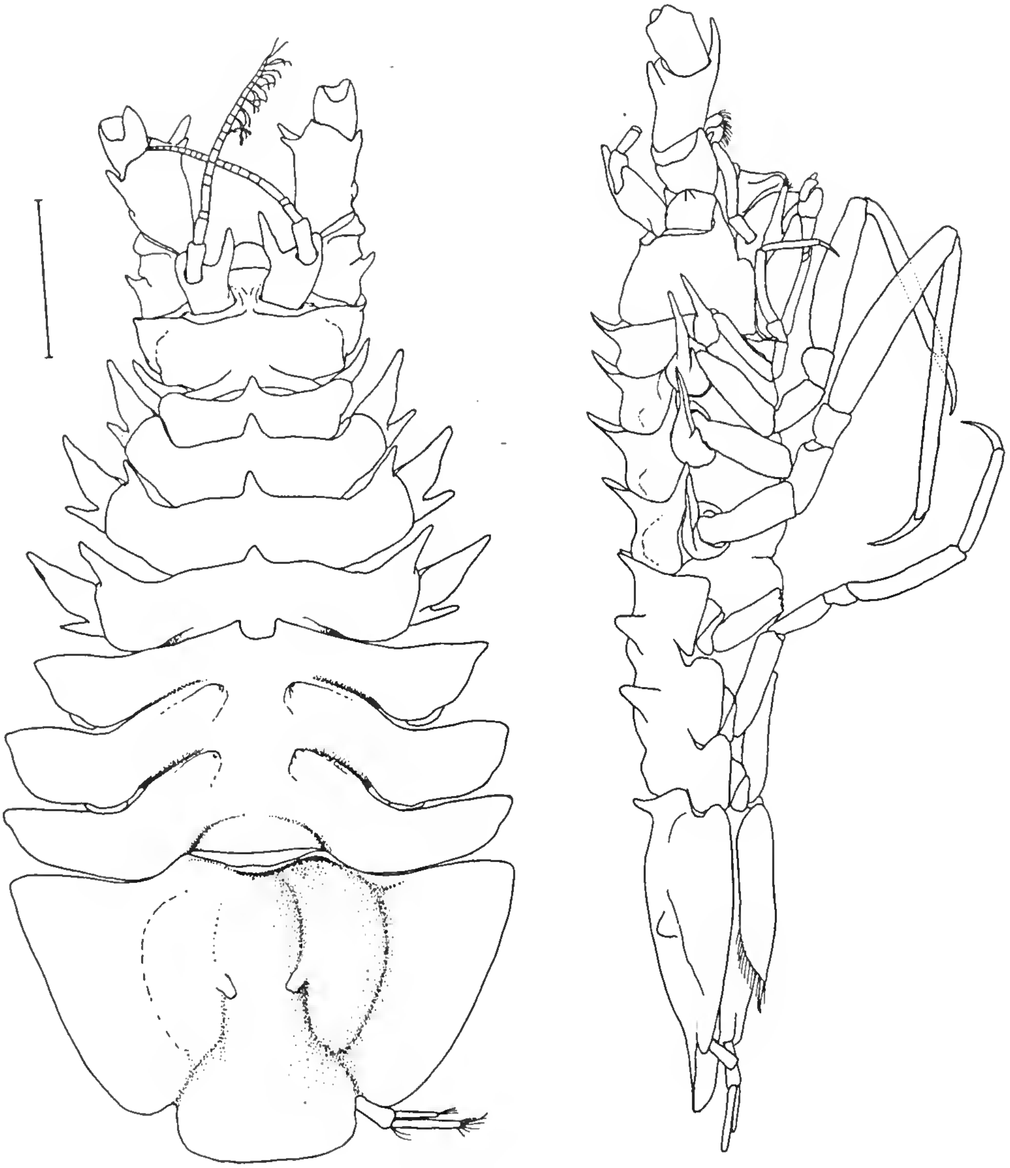

Figure 1. *Platyprotus phyllosoma* sp. nov., holotype. Scalebar: 1 mm.

Paratype. Same data as holotype, Museum Victoria, J47135 (female, 4.1 mm).

Description (holotype, male). Body broad, flattened; width increasing from pereonite 1 to 7, pereonite 7 about 2.3 times wider than 1.

Cephalon without rostrum, 2.5 times wider than long, 20% wider than pereonite 1; with strong frontal ridge, epistome broadly rounded in lateral view.

Pereon: Pereonites 1–4 with 1 short, dorsal, triangular, forward pointing spine on midanterior margin; pereonite 1 with single long coxal spine; pereonite 2–4 with bifurcate broad coxal spine, anterior part more than twice length and width of

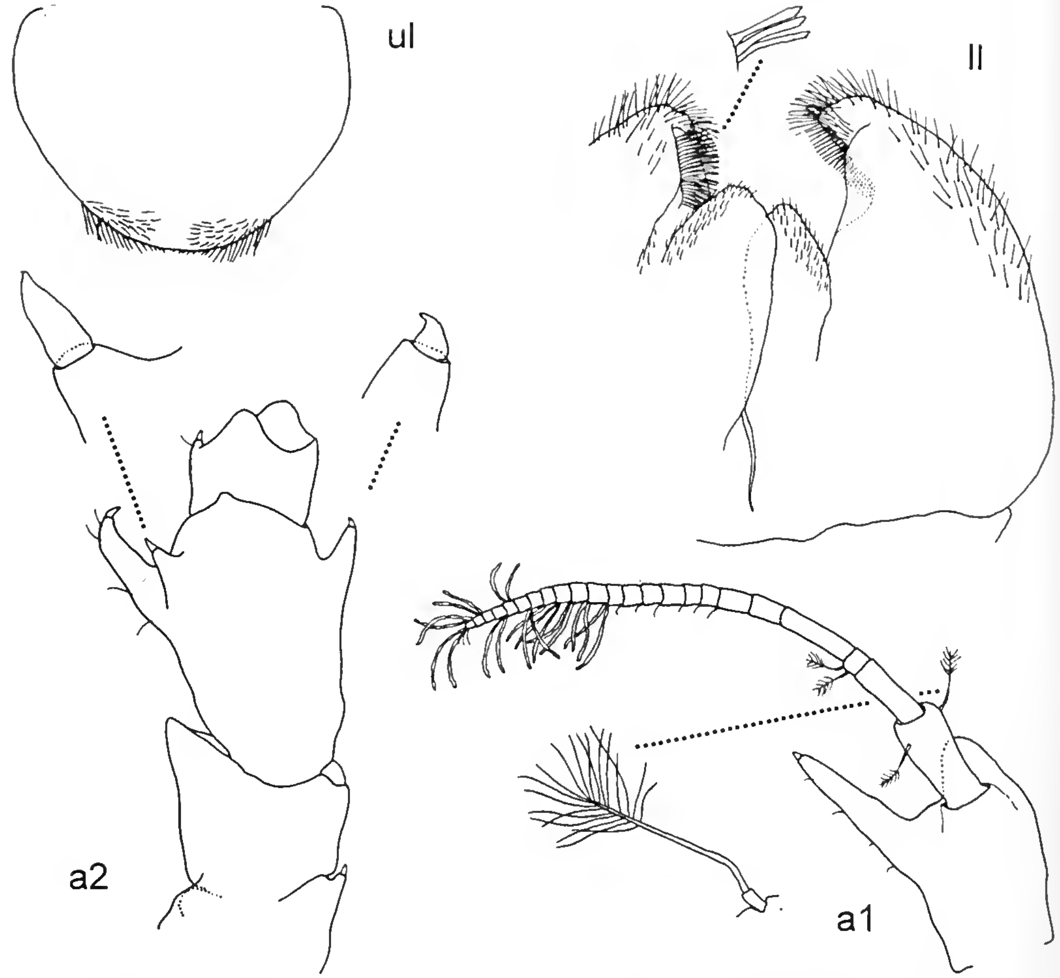

Figure 2. *Platyprotus phyllosoma* sp. nov., holotype, except ul: paratype female. a1, antenna 1; a2, peduncle of antenna 2; ll, lower lip.

posterior part; pereonites 3 and 4 with single anterolateral spine. Pereonite 1 about 75% length of 2, pereonites 2–4 of equal length; pereonites 5–7 fused, 5 with midanterior sinus flanked by 2 short, pointed spines, 6 and 7 with 2 broad, apically rounded spines near anterior margin at point of pereonite fusion, lateral margins widely over-reaching coxae, without spines. Pereonites 1–4 combined about same length as 5–7 combined.

Pleotelson free, straight and ventrally flat in lateral view, as long as pereonites 4–7 combined; as wide at base as pereonite 7, semicircular, except for triangular notches at insertion of uropods, length 60% greatest width; without preanal ridge; without lateral or apical spines; anterior dorsal margin with raised transverse keel in area of articulation with pereonite 7; dorsal surface with broad, rounded midlongitudinal ridge and rounded inflations on each side, 2 short rounded spines at midlength between middle ridge and lateral inflations; anus external to respiratory chamber, not covered by pleopods.

Antennae: Antenna 1 as long as pereonites 1–4 and half of 5 combined; article 1 with rounded projection anterolaterally and long, slender spine medially, article 2 inserted dorsally on 1, article 3 slightly shorter than 2, 4 quarter length of 3, 5 subequal to 3, with an additional 19 short articles, distal ones with aesthetases. Antenna 2 article 1

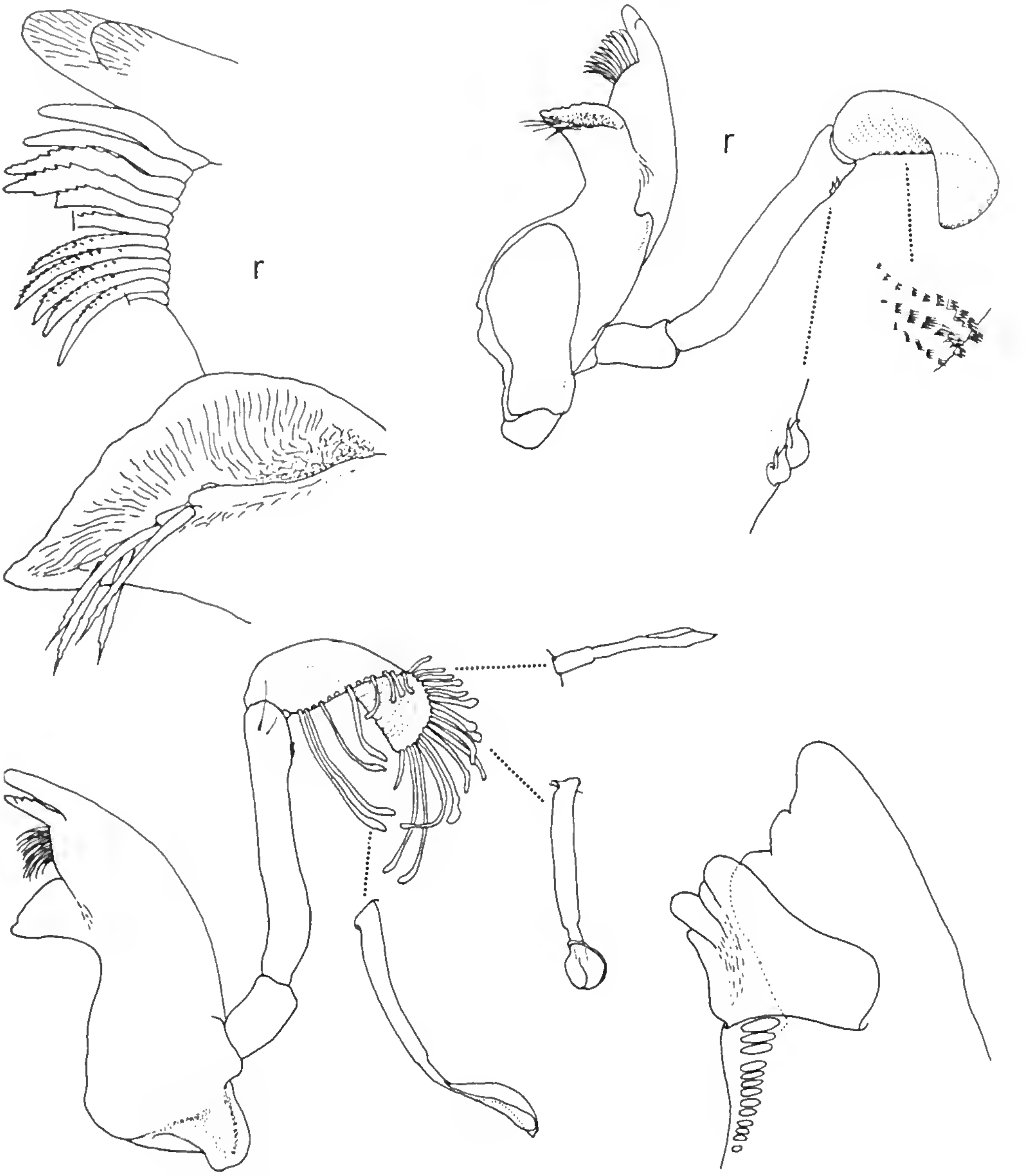

Figure 3. *Platyprotus phyllosoma* sp. nov., holotype. Mandibles: r, right; l, left.

with small distolateral spine, article 2 without spines, article 3 with 1 short and 1 long distomedial spines and 1 distolateral spine, all spines tipped by short broad seta; (flagellum not known).

Mouthparts: Upper lip evenly rounded, with 2 fields of distal setae.

Mandible with elongate cuticular projection articulating with cephalon in shallow groove (Fig. 7e); left mandible with broad, right with more narrow incisor of 3 rounded (presumably worn) teeth, left with broad, irregular lacinia mobilis with 4 rounded teeth and row of more than 10 slender setae, right with similar number but broader, microdentate setae; molar cylindrical, hollowed truncate, with short row of microdentate setae on posterior margin; palp exceeding length

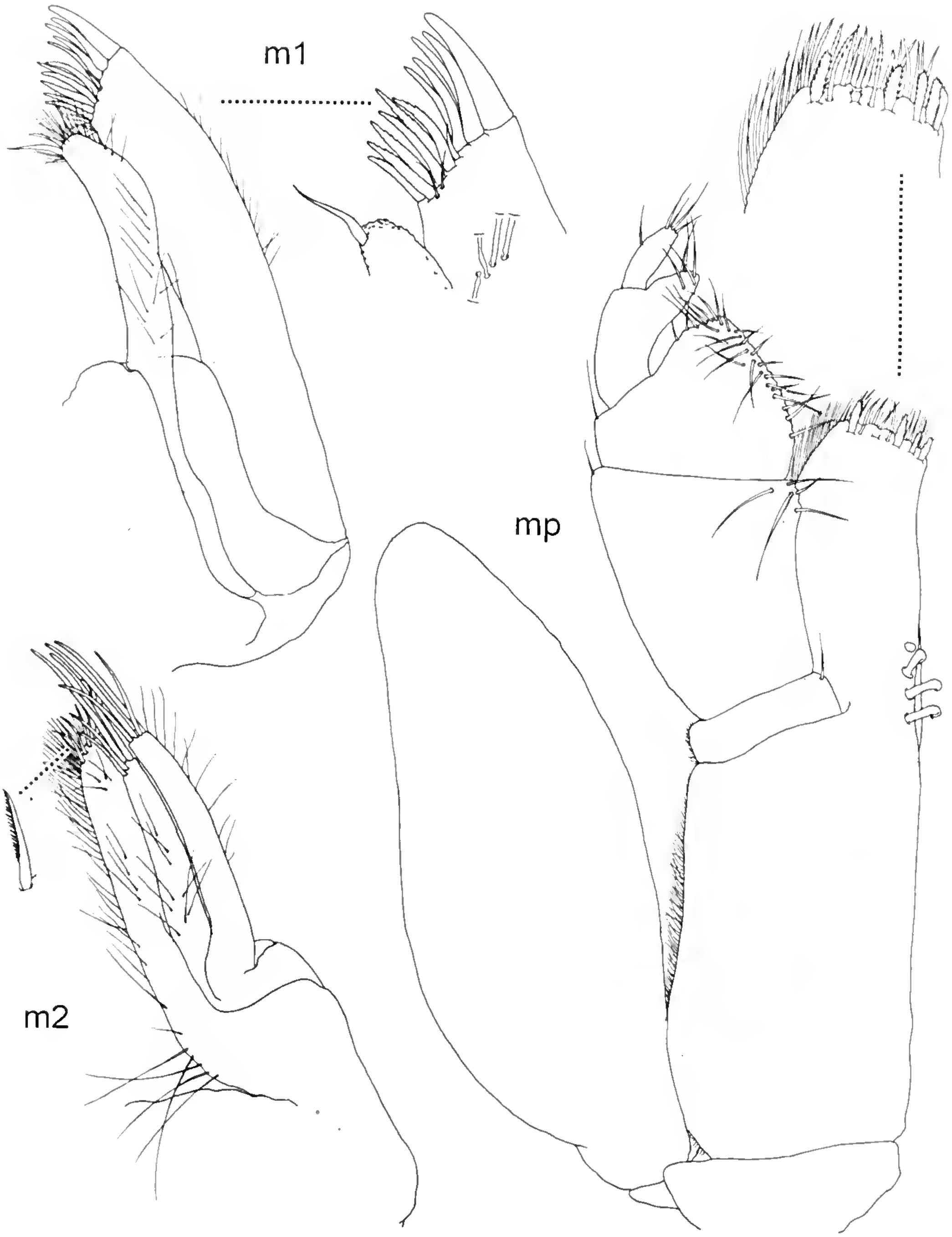

Figure 4. *Platyprotus phyllosoma* sp. nov., holotype. mp, maxilliped; m1, m2, maxillae 1, 2.

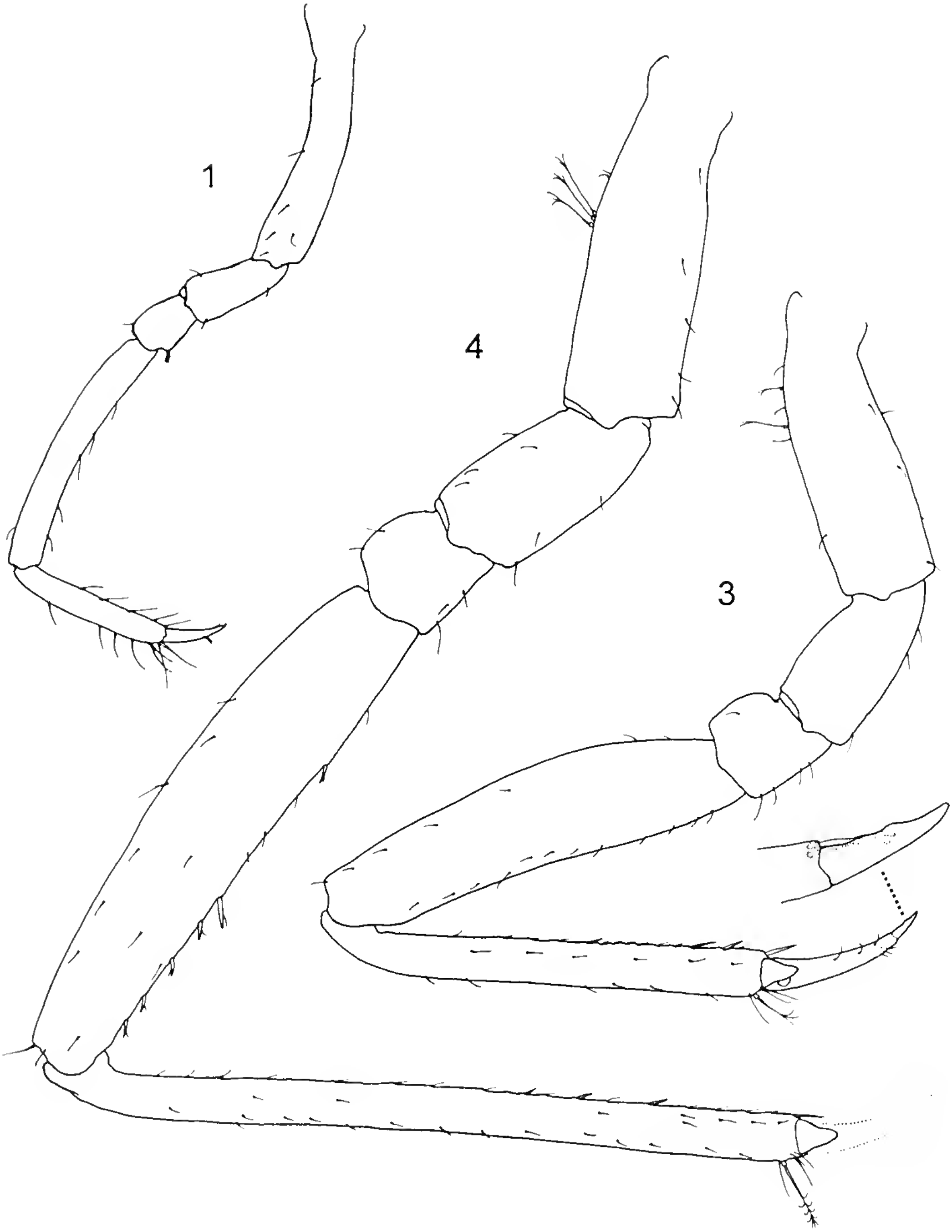

Figure 5. *Platyprotus phyllosoma* sp. nov., holotype. Pereopods 1, 3 and 4.

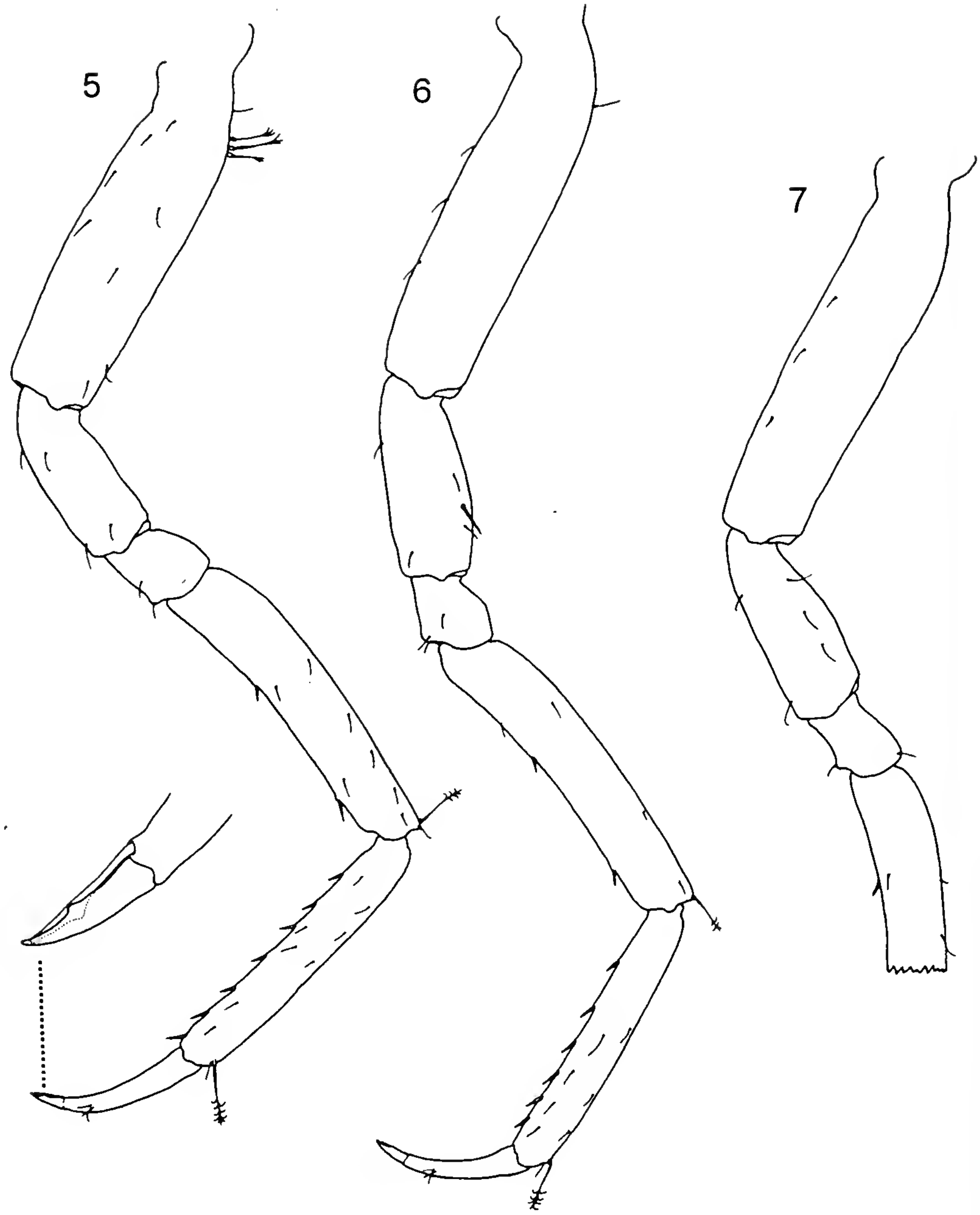

Figure 6. *Platyprotus phyllosoma* sp. nov., holotype. Pereopods 5, 6 and 7.

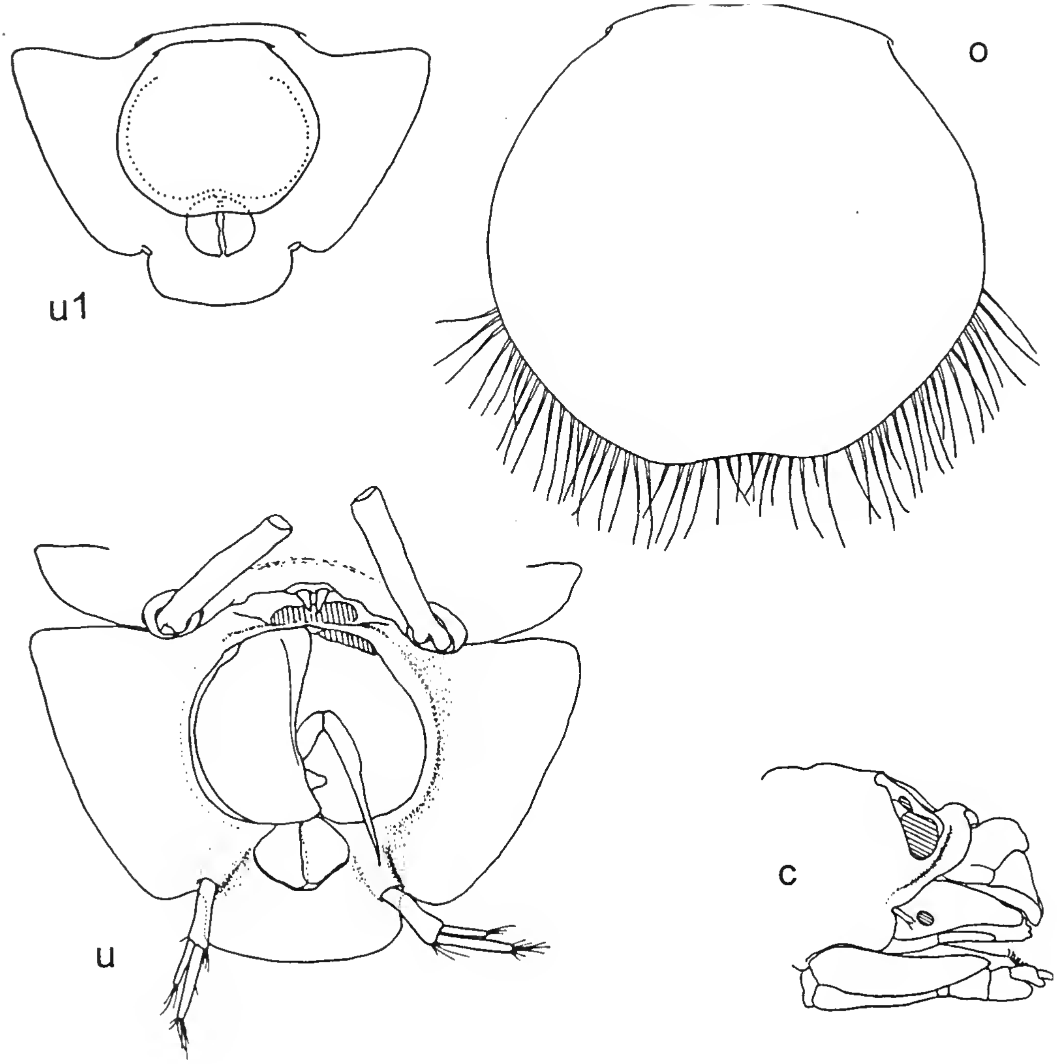

Figure 7. *Platyprotus phyllosoma* sp. nov. holotype. c, cephalon, right lateral view; u, urosome, ventral view. Paratype: u1, female urosome, ventral view; o, operculum enlarged.

of mandibular body by entire article 3, article 2 2.5 times longer than 1, with 2 tiny, curved, acute setae distolaterally, article 3 broad, of twisted spoon-shape, lateral and apical margins with highly modified spatulate setae, concave surface with densely set transverse rows of microsetules.

Lower lip outer lobes with medial row of robust setae and apical and lateral cover of setules, inner lobes rounded with lateral and apical setules.

Maxilla 1 outer lobe with 11 nearly straight spine-like setae, posterior 6 microdentate, inner lobe apically rounded, reaching to mediodistal corner of outer lobe, with 1 apical spine-like seta and many long setules. Maxilla 2 middle lobe slightly shorter than subequal outer and inner lobes, inner lobe 1.5 times width of equal width middle and outer lobes, outer and middle lobes with 2 long and 2 shorter smooth setae, inner lobe with apical row of short, pectinate setae and dense fringe of medial setules.

Maxilliped basis with 4 coupling hooks, truncate apex of endite with 6 slender fan setae, palp article 2 broadest distally, 1.5 times midwidth of endite, epipod reaching to distal end of palp

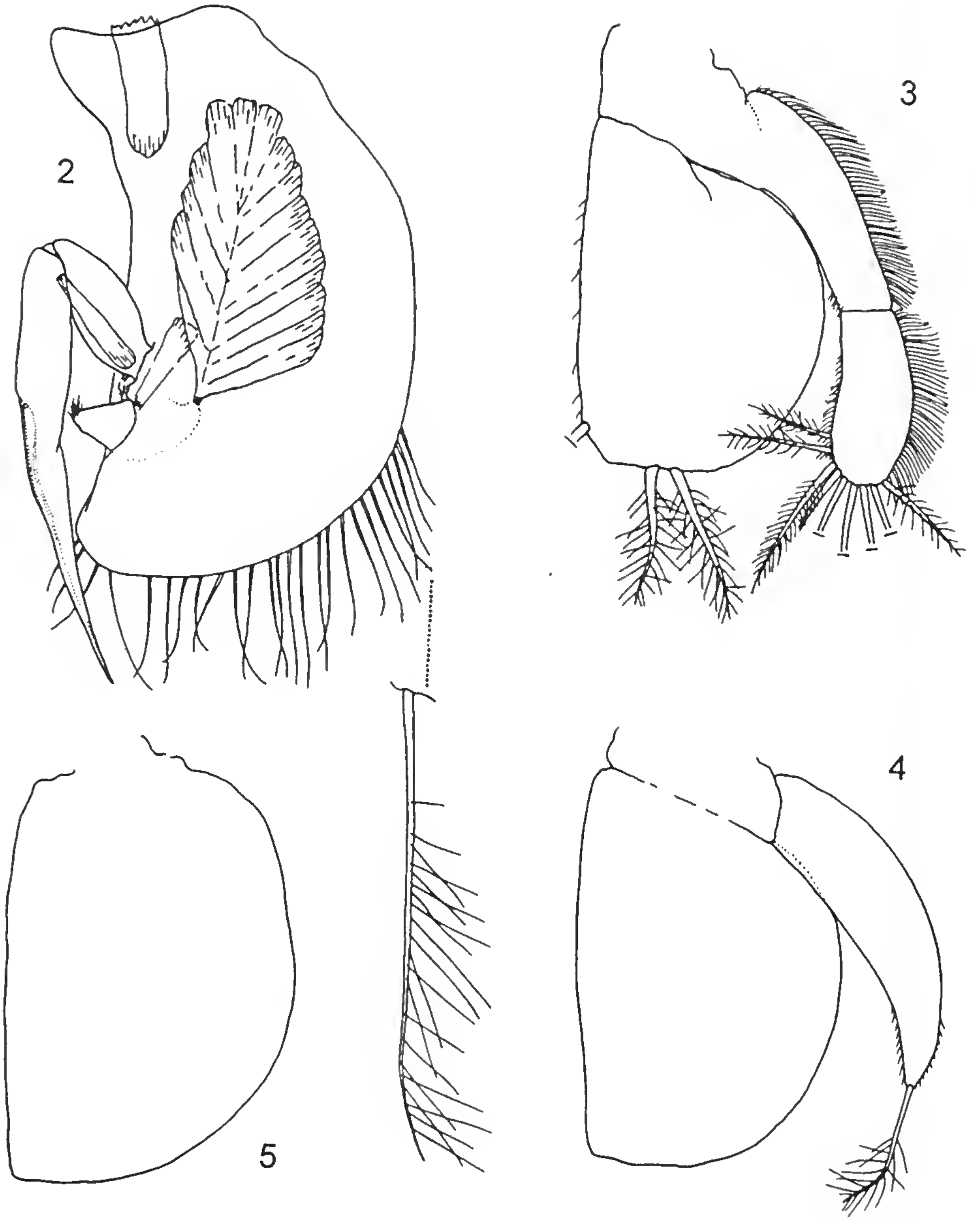

Figure 8. *Platyprotus phyllosoma* sp. nov., holotype. Pleopods 2–5 (2 viewed from above).

article 2, apex rounded, lateral margin smooth, convex in posterior half, slightly concave in distal half.

Pereopods: Pereopod 1 with scattered simple setae, much shorter and more slender than succeeding pereopods, about half length of cephalon and pereon combined; relative length of pereopods: 1 (1.0), 2 (not measured), 3 (1.9) 4 (2.5), 5 (1.7), 6 (1.7), 7 (broken); pereopods 2–3 carpus and propodus of equal length, carpus twice width of propodus, posterior margin of carpus and propodus with short simple setae and a few more robust setae; pereopod 4 propodus approximately third longer than carpus, carpus nearly 3 times wider than propodus with 6 robust setae mainly in distal half, propodus with a few robust setae among small simple setae in distal half of posterior margin. Pereopods 5–7 fully ambulatory; propodus slightly shorter than carpus, carpus little wider than propodus; pereopods 5–6 (and presumably 7) carpus anterior margin with a few robust setae, propodus with row of 6–7 robust setae. Dactylar unguis of all pereopods with midpoint tooth on concave surface, pereopods 1–4 with 2 stiff setae arising from posterodistal corner of dactylus and resting against unguis tooth, pereopods 5–6 (presumably 7) with single strong, spatulate seta in same position.

Pleopods: (pleopod 1 not known); pleopod 2 protopod about half length of pleotelson, width of combined pleopods 2 about half midwidth of pleotelson, medial margin concave, lateral margin evenly convex, apex broadly rounded, distal part of lateral margin and apex with row of long, slender hemiplumose setae; exopod a short cone with setose apex; endopod inserted about 0.6 along protopod margin, stylet in retracted position overreaching protopod apex with about third stylet length. Pleopods 3–5 endopod of similar shape and size, broad, semirectangular, 3 with 3 apical pappose setae, 4 and 5 without setae, exopod of 3 as long as and third width of endopod, apex rounded with 9 long pappose setae, entire lateral margin of exopod with dense fringe of long setules; exopod of 4 reaching about two-thirds along endopod, tapering to pointed apex carrying 1 pappose seta; 5 without exopod.

Uropods 0.4 length of pleotelson, protopod and inner ramus of equal length, outer ramus 0.6 length of inner ramus, both rami with tuft of apical setae.

Female. Generally as male. Operculum nearly circular with slightly concave apex, just covering respiratory chamber, fringed with long hemiplumose setae in distal half.

Etymology. The epithet is derived from the Greek *phyllos* = leaf and *soma* = body.

Acknowledgments

I thank Dr Gary Poore, Museum Victoria, for making the material available, and Dr G.D.F. 'Buz' Wilson, Australian Museum, for helpful discussions.

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Memoirs of Museum Victoria 58(2): 347–364 (2001)

THREE NEW SPECIES OF *CIROLANA* LEACH, 1818 (CRUSTACEA: ISOPODA: CIROLANIDAE) FROM AUSTRALIA

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Abstract

Keable, S.J., 2001. Three new species of *Cirolana* Leach, 1818 (Crustacea: Isopoda: Cirolanidae) from Australia. *Memoirs of Museum Victoria* 58 (2): 347–364.

Three new species are described from Australia. *Cirolana australis* sp. nov. off eastern and southern coasts of Tasmania, *C. comata* sp. nov. off north-eastern Queensland, and *C. dissimilis* sp. nov. off northern Western Australia, Northern Territory and northern Queensland. All appear to be associated primarily with coral or rocky reef habitat. *Cirolana comata* and *C. dissimilis* occur on the continental shelf, *C. australis* on the continental slope at depths exceeded by few other species of *Cirolana*. The species are abundant in collections made using baited traps, indicating that they are scavengers and potentially important pests of fisheries. They have nodular sculpting on the pereon, pleon and pleotelson but differ from other Australian species with similar ornamentation in having the setae on the lateral margin of the uropod endopod in a continuous row, not in discrete widely spaced groups. *Cirolana comata* and *C. dissimilis* are sexually dimorphic and have a highly sclerotized robust seta on the posterodistal angle of the basis of pereopods 4–5. These and other shared characters suggest that the two are related.

Introduction

Twenty-nine named and one unnamed species of *Cirolana* Leach, 1818 were included in the most recent key to the Australian fauna (Bruce, 1986). *Cirolana schioedtei* Miers, 1884 has subsequently been transferred to *Aatolana* Bruce, 1993 (Bruce, 1993). The juvenile specimens included in this key and discussed as *Cirolana* sp. apparently represent an undescribed species of *Plakolana* Bruce, 1993, and *C. binyana* Bruce, 1991 is also a species of *Plakolana* (Bruce, 1993). Brusca et al. (1995) listed 84 species of *Cirolana* worldwide. *Cirolana obtruncata* Richardson, 1901 was moved to *Neocirolana* Hale, 1925 by Javed and Yasmeen (1990), *C. fornicata* (Mezhov, 1981) is regarded as a species of *Metacirolana* Kussakin, 1979 (Bruce, 1996), and Keable (1999) transfered *C. porcellana* Barnard, 1936 and *C. albicauda* Nunomura, 1985 (not listed by Brusca et al., 1995) to *Dolicholana* Bruce, 1986 as suggested by Bruce (1986). These changes, and the species described by Kwon (1988), Weider and Feldmann (1992), Bruce (1995), Javed and Yasmeen (1995) and Botosaneanu and Iliffe (1997), brings the recognised species to 90 (including one species inquirenda, three incertae sedis and one fossil species). Botosaneanu and Iliffe (1997) discussed the similarities of *Anopsilana* Paulian and Delmare Deboutteville, 1956 and *Cirolana* and suggested that *Anopsilana* is a subgenus of *Cirolana*. They recognised that this is an artificial solution and it is not followed here.

Scavenging cirolanid isopods play an important role in marine foodwebs (Keable, 1995) and are significant pests of fisheries (Bird, 1981; Stepien and Brusca, 1985; Berrow, 1994; Mizzan, 1995). This study describes three new scavenging species of *Cirolana* from Australia collected with baited traps.

The terminology and procedures used follow Keable (1997). Abbreviations are: AM, Australian Museum, Sydney, Australia; BMNH, The Natural History Museum, London, United Kingdom; NMV, Museum Victoria, Melbourne, Australia; NTM, Northern Territory Museum of Arts and Sciences, Darwin, Australia; TM, Tasmanian Museum and Art Gallery, Hobart, Australia; USNM, National Museum of National History, Smithsonian Institution, Washington, D.C., USA; n, number of specimens; CE, cephalon; A1, antennule; A2, antenna; CL, clypeal region; FL, frontal lamina; MD, mandible; MP, maxilliped; MX1, maxillule; MX2, maxilla; PE, penes; PN, pleon; P1-7, pereopods 1–7; U, uropod; PL1-5, pleopods 1–5; PT, pleotelson.

Cirolana Leach, 1818

Remarks. For useful recent synonymies, diagnoses, descriptions and discussions see Bruce (1986: 139), Kensley and Schotte (1989: 132), Bruce (1993: 2), Bruce (1995: 376) and Brusca et al. (1995: 17). Revisionary work has provided increasingly narrower and more practical morphological limits to *Cirolana* with the transfer of many species to other genera (e.g. Bruce, 1981a; 1993). Three informal subgroups of *Cirolana* have also been proposed by Bruce (1986, 1995): (1) the "*C. parva* group"; (2) the "*C.* southern group"; and (3) the "*C.* tuberculate group". The new species described here (and several others) cannot be unambiguously placed in any group: the rostrum does not meet the frontal lamina and there is some sculpting on the body segments of all three species eliminating them from the "*C. parva*" group; and they cannot be members of the "*C.* southern" or the "*C.* tuberculate" groups because they have continuous setae on the lateral margin of the uropod exopod. This, combined with the character conflict which exists between these informal groups, suggests that they may be based on plesiomorphic or homoplastic characters. A phylogenetic analysis to resolve this issue is needed.

All species of Australian *Cirolana* with nodular sculpting in the form of tubercles, and that are otherwise similar to the three new species, have the uropod exopod lateral margin with discontinuous plumose setae (i.e. occurring in widely spaced groups) and fewer robust setae, or the rostrum meeting the frontal lamina.

A close relationship between *Cirolana comata* sp. nov. and *C. dissimilis* sp. nov. is suggested by many similarities, in particular corresponding sexually dimorphic characters rare in species of *Cirolana* (Bruce, 1986: 140). Both have a highly sclerotized robust seta on the posterodistal angle of the basis of pereopods 4–5 (4–6 in *C. comata*). This character does not occur in *C. australis* sp. nov., nor in *C. australiense* Hale, 1925, *C. capricornica* Bruce, 1986 or *C. similis* Bruce, 1981b (specimens AM P47660, P47668, P47669 examined). Its distribution is otherwise undocumented. Additionally, an iridescent brush formed by the aesthetascs of the antennule (Keable, 1998; Parker, in prep.) was found in both *C. comata* and *C. dissimilis* but not *C. australis*.

The three new species appear to be associated primarily with coral or rocky reefs. *Cirolana comata* and *C. dissimilis* occur on the continental shelf, *C. australis* on the continental slope. Of the species currently placed in *Cirolana* or incertae sedis, only *C. bisulcata* Hobbins and Jones, 1993, *C. bougaardti* Kensley, 1984, *C. meseda* Hobbins and Jones, 1993, *C. vanhoeffeni* Nierstrasz, 1931 and *C. stebbingi* Nierstrasz, 1931 are known from similar or greater depths than *C. australis*.

Cirolana australis sp. nov.

Figures 1–3

Cirolana new species.—Koslow and Gowlett-Holmes, 1998: 41.

Cirolana n.sp. 4.—Lowry, 1998: 63, 64.

Material examined. Holotype, Main Pedra Seamount, off southern Tasmania (44°15.6′S 147°7.8′E), baited trap, 1,312 m, 21–24 Jan 1997 (CSIRO Cruise SS01/97, stn 8), AM P59351 (male, 23 mm).

Paratypes. All same data as holotype, AM P59352 (977 specimens); BMNH 2000.2408–2409 (male, female); NMV J47153 (male, female); TM G3588 (2 females); USNM 296460 (male, female).

Additional material. E of Fortescue Bay, Tasmania (43°08.96′S 145°15.36′E), baited trap, 5.1°C, 1000 m, J. Lowry and P. Freewater, 16–17 Apr 1993 (stn SEAS TAS-365), AM P59353 (2 females, 1 male, 6 mancas); stn SEAS TAS-367, AM P59354 (7 females, 1 male, 5 mancas).

Diagnosis. Cephalon: rostrum not extending to frontal lamina, not dividing antennules; anterior margin not overriding antennules. Eyes: well developed, round. Frontal lamina: anterior margin angled. Pereonites: 1–7 with 2 transverse carinae; 4–7 with tubercles. Pleonites: 3–5 with tubercles. Pleonite 4: ventral margin free of pleonite 3; posterodorsal margin apex broadly rounded dorsally but meeting convex ventral margin at a point. Pleotelson: dorsal surface with paired tubercles in rows, (3 in each row, forming an indistinct ridge parallel to each lateral margin), conspicuous fine setae absent; anterolateral margins convex; posterolateral margins concave; apex truncate; 2–6 (usually 2 or 4) robust setae across apex. Penes: present. Pereopod 1: propodus without plumose setae. Pereopods 4–6: basis posterodistal angle robust setae absent. Pleopod 2 appendix masculina: arising subbasally; extending beyond tip of endopod, 1.46 length of endopod from insertion point; margins sinuate, tapering along entire length; slender; apex not at angle to margins, bluntly rounded. Uropods: endopod not dimorphic; lateral margin straight for proximal two-thirds, convex at distal third; exopod not dimorphic; lateral margin straight, robust and plumose setae continuous along margin.

Additional descriptive characters based on holotype. Body: length approximately 2.6 greatest width; white in alcohol; chromatophores absent; cuticular surfaces scale-like.

Cephalon: tubercles absent. Eyes: visible in ventral view; black in alcohol; partially overlapped by pereonite 1; ommatidia in rows, 7 ommatidia in horizontal diameter, 7 ommatidia in vertical diameter. Interocular furrow: distinct, not extending across cephalon. Frontal lamina: length approximately 1.9 basal width; penta-

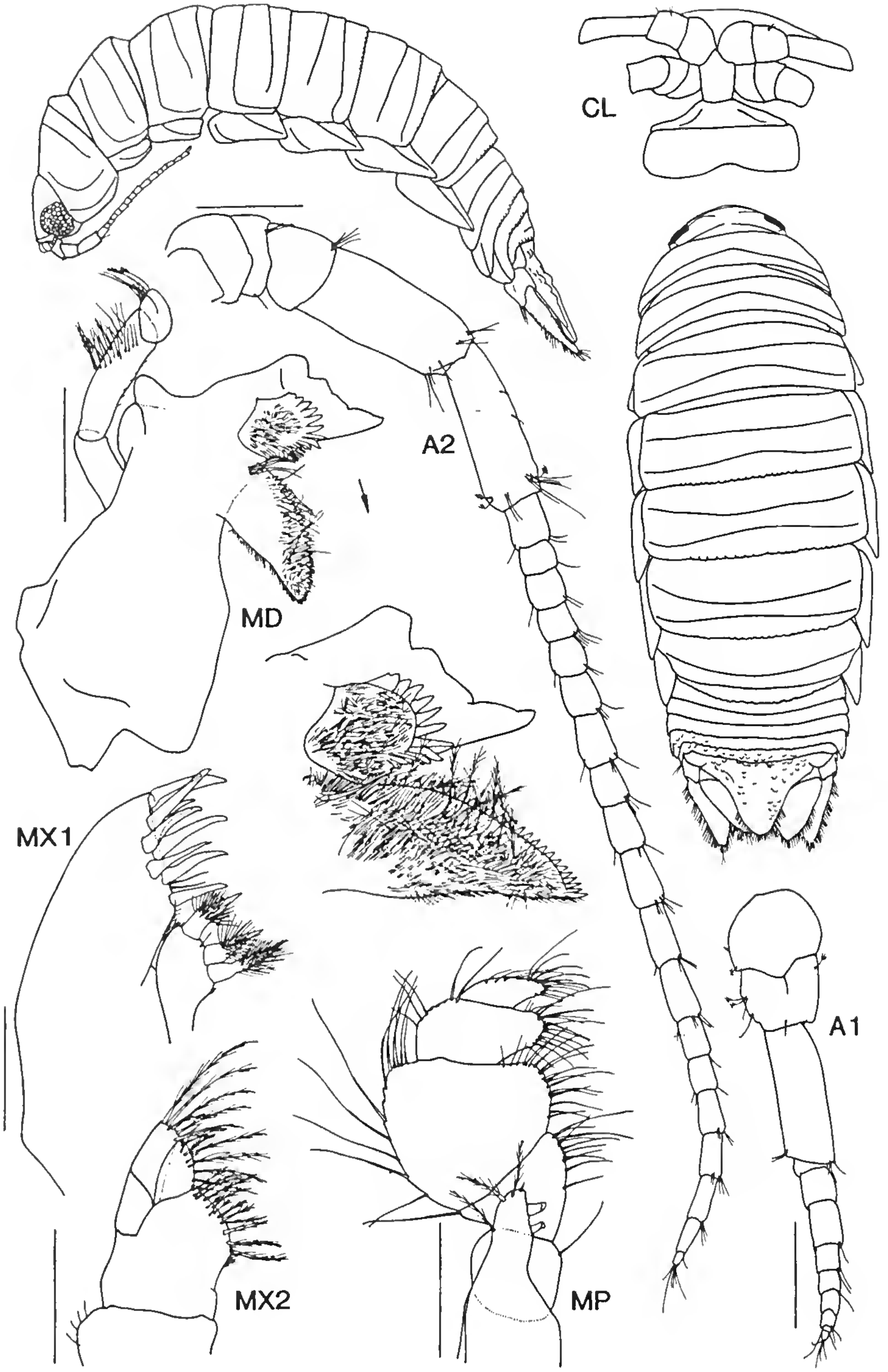

Figure 1. *Cirolana australis* sp. nov., holotype. Scales = 0.5 mm.

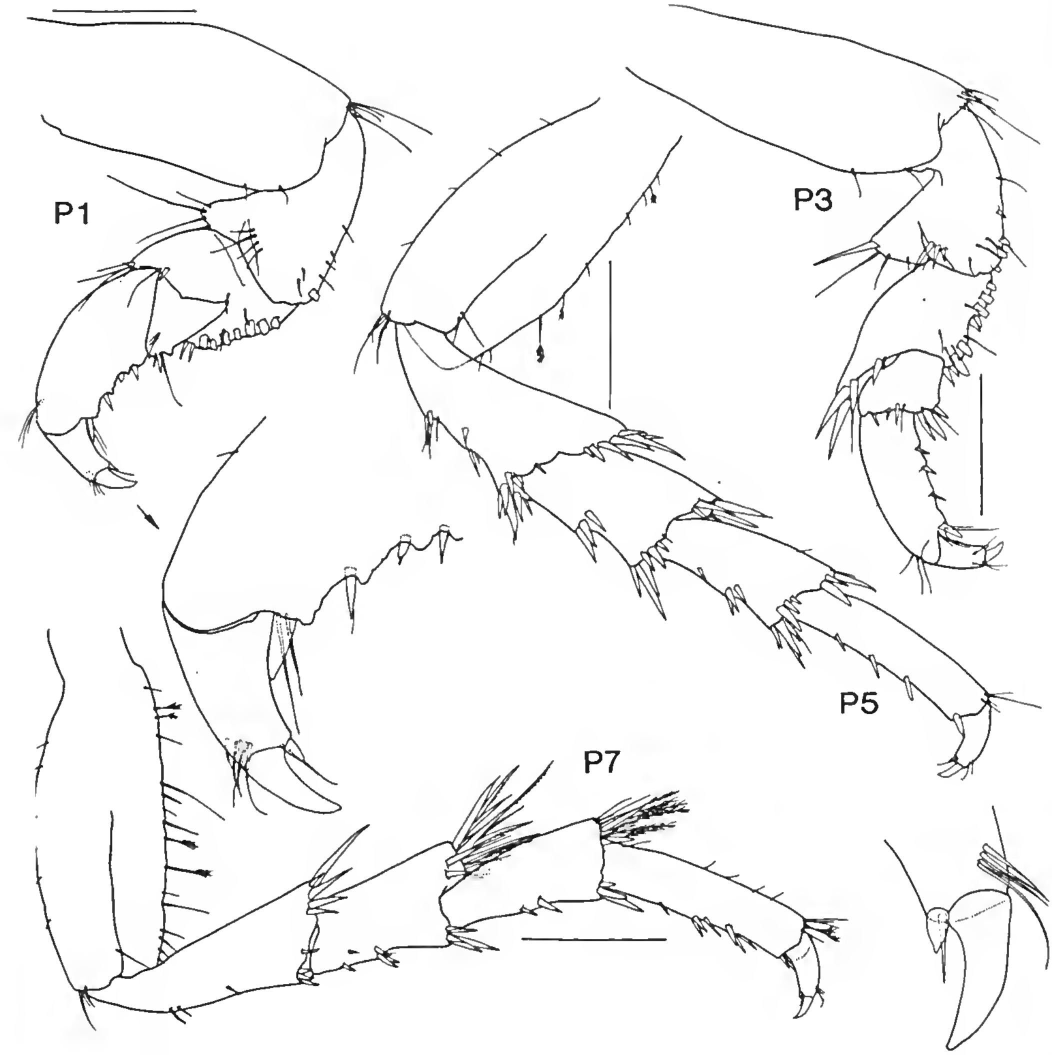

Figure 2. *Cirolana australis* sp. nov., holotype. Scales = 0.5 mm.

gonal; lateral margins divergent; apex not projecting, not visible in dorsal view, not expanded, in 1 plane (not stepped). Clypeus: triangular, not produced.

Pereonites: 4–7 length subequal and longest, 1–3 subequal; tubercles small, fine, subequal, continuous across entire posterior margin.

Pleonites: 1–5 equally visible along dorsal margin; tubercles small, subequal, continuous across entire posterior margin.

Pleotelson: length 0.85 basal width; anterodorsal uropodal sutures present; 4 robust setae across apex; plumose setae restricted to posterolateral margins, numerous proximal to robust setae.

Antennule: just reaching pereonite 1. Peduncular bases touching; articles 1–2 free; article 1 length less than width, subequal to article 2; article 2 longer than wide, with a few scattered slender and penicillate setae; article 3 longer than combined lengths of articles 1–2, length greater than width. Flagellum shorter than peduncle; articles not compressed (lengths of most greater than half width); 8-articulate; aesthetases not iridescent. Antenna: 0.3 length of body, when extended against body reaching to posterior of pereonite 3. Peduncular article 2 shorter than article 3; article 4 much longer than article 3, posterodistal angle with 4 slender setae, anterodistal angle with 5 slender setae; article 5 subequal in length to article 4, posterodistal angle with 2 penicillate and 2 slender setae, anterodistal

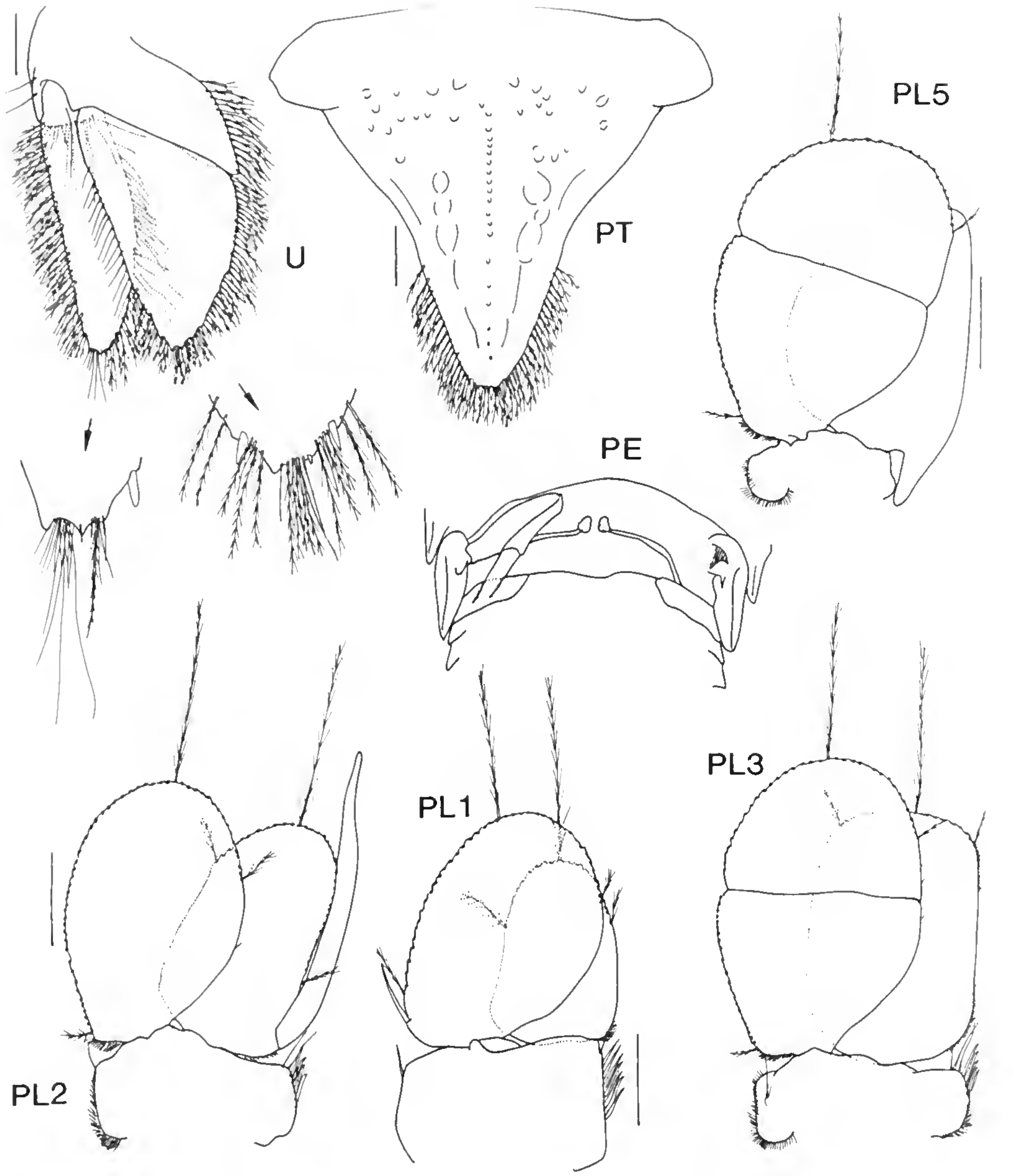

Figure 3. *Cirolana australis* sp. nov., holotype. Scales = 0.5 mm.

angle with 1 penicillate and 7 slender setae. Flagellum 19-articulate; setal brush absent.

Mandible: molar medial surface covered with short fine slender setae, cluster of long slender setae proximally present, long slender setae in submarginal row across 0.75 length of anterior margin; marginal robust setae close set. Setal row with 15 robust setae; medial surface covered in fine setae. Maxillule: medial lobe lateral margin protuberance absent; lateral lobe with 10 robust setae on distal surface and 2 slender setae. Maxilla: lateral lobe with 4 plumose and 1 slender setae; medial lobe with 14 plumose setae, medial plumose setae subequal to proximal setae; middle lobe with 4 plumose and 8 slender setae. Maxilliped: right endite with 1 coupling hook, left endite with 2 coupling hooks.

Pereopods: 1–3 merus posterior margin robust setae strongly molariform on 1 only; 2–7 coxal furrows complete. Pereopod 1: posterior margin setose fringe absent; propodus robust; dactylus shorter than 0.5 propodus length.

Penes: separated by more than width of both penes; forming flattened lobes; length approximately 1.5 basal width.

Pleopods: exopod suture complete on 3–5. Pleopod 1: exopod medial margin tapering evenly, proximolateral robust seta present; endopod shorter than exopod, lateral margin slightly concave.

Uropods: extending beyond pleotelson. Peduncle ventrolateral angle without robust setae, with 13 plumose setae; lateral margin robust seta absent; distolateral angle rounded. Endopod medial margin convex, with 5 robust setae, plumose setae along entire length; apex subbifid with lateral spine largest, with 1 minute medial robust seta, setal cluster formed by plumose and slender setae; lateral margin with 4 robust setae, plumose setae along entire length. Exopod 0.94 length of endopod; medial margin convex, with 4 robust setae, plumose setae along entire length; apex subequally bifid, without robust setae, setal cluster formed by slender setae; lateral margin with 7 large robust setae, plumose setae along entire length.

Sexual dimorphism. Females differ from males only in the primary sexual characters.

Variation. Pleotelson and uropod robust setal counts from margins (N = 20, subsample of 10 males and 10 females from AM P59352): Pleotelson: 1:1 (30%), 2:1 (40%), 2:2 (25%), 3:3 (5%). Endopod: (medial) 5 (10%), 6 (70%), 7 (20%); (lateral) 3 (65%), 4 (35%). Exopod: (medial) 4 (75%), 5 (25%); (lateral) 5 (10%), 6 (40%), 7 (45%), 8 (5%). Subadult males (19 mm, AM P59352) have the vas deferens opening almost flush to the surface of the sternite and the appendix masculina inserted submedially.

Size range. Mancas approximately 7 mm, adults to approximately 25 mm.

Etymology. Australis, Latin, southern, referring to the position of the type locality.

Distribution. Eastern and southern Tasmania; 1000–1312 metres.

Remarks. Cirolana australis is most readily differentiated by the ornamentation of the somites, coupled with the sinuate lateral margins and truncate apex of the pleotelson, low number of robust setae on the pleotelson apex, straight lateral margins of the uropod rami, and continuous distribution of the robust and plumose setae along the uropod exopod lateral margin. Other species of *Cirolana* in which robust setae occur on the margins of the pleotelson usually have six or more, but four have also been recorded in *C. rugicauda* Heller, 1861. *Cirolana rugicauda* is distinguished from *C. australis* by (in *C. rugicauda*): the rounded apex of the frontal lamina; the projecting clypeus (a character which has been used to diagnose genera and groups of genera excluding *Cirolana*, e.g. Bruce (1986)); and pleonite 3 enclosing pleonite 4 (Vanhöffen, 1914; Barnard, 1940; Kensley, 1978). *Cirolana sulcata* Hansen, 1890 and *Cirolana transcostata* Barnard, 1959 may be difficult to distinguish from *C. australis* but have a frontal lamina with a rounded apex, and uropods with lateral margins that are more convex. *Cirolana tuberculata* (Richardson, 1910) is also similar but has more prominent tubercles on the pleotelson and uropods with convex lateral margins (Delaney, 1986).

Cirolana comata sp. nov.

Figures 4–6

Material examined. Holotype. Portlock Reef, Coral Sea, Queensland (9°42.10'S 144°50.17'E), baited trap, unknown substrate, 65 m, S. Keable, 28 Jan 1993 (stn QLD-775), AM P59355 (male, 13 mm).

Paratypes. All same data as holotype, AM P39356 (298 specimens); BMNH 2000.2410–2411 (male, female); NMV J47152 (male, female); USNM 296461 (male, female).

Additional material. Off Flynn Reef, Queensland (16°41.32'S 146°18.26'E), baited trap, unknown substrate, 100 m, J. Lowry, P. Freewater and W. Vader, 7 Jun 1993 (stn SEAS QLD-937), AM P47678 (10 specimens); E of Fitzroy Reef, Queensland (23°32.53'S 152°16.45'E), baited trap, unknown substrate, 105 m, J. Lowry, P. Freewater and R. Springthorpe, 16 Jun 1993 (stn SEAS QLD-956), AM P47675 (13 specimens).

Diagnosis. Cephalon: rostrum not extending to frontal lamina, not dividing antennules; anterior margin not overriding antennules. Eyes: well developed, round with upper margin flat. Frontal lamina: anterior margin angled. Pereonites: without transverse carina; tubercles absent (except for 6 indistinct tubercles on submarginal anterior ridge of pereonite 1 in mature males). Pleonites: 3–5 with tubercles. Pleonite 4: ventral margin free of pleonite 3; posterodorsal margin apex broadly rounded dorsally but meeting convex ventral margin at a point. Pleotelson: dorsal surface with 2 paired tubercles, conspicuous fine setae forming dense patch in males; anterolateral margins almost straight and angling posteriorly toward midline; posterolateral margins straight, contiguous with anterolateral margins; apex rounded; 8–11 (usually 10) robust setae on margins. Penes: present. Pereopod 1: propodus without plumose

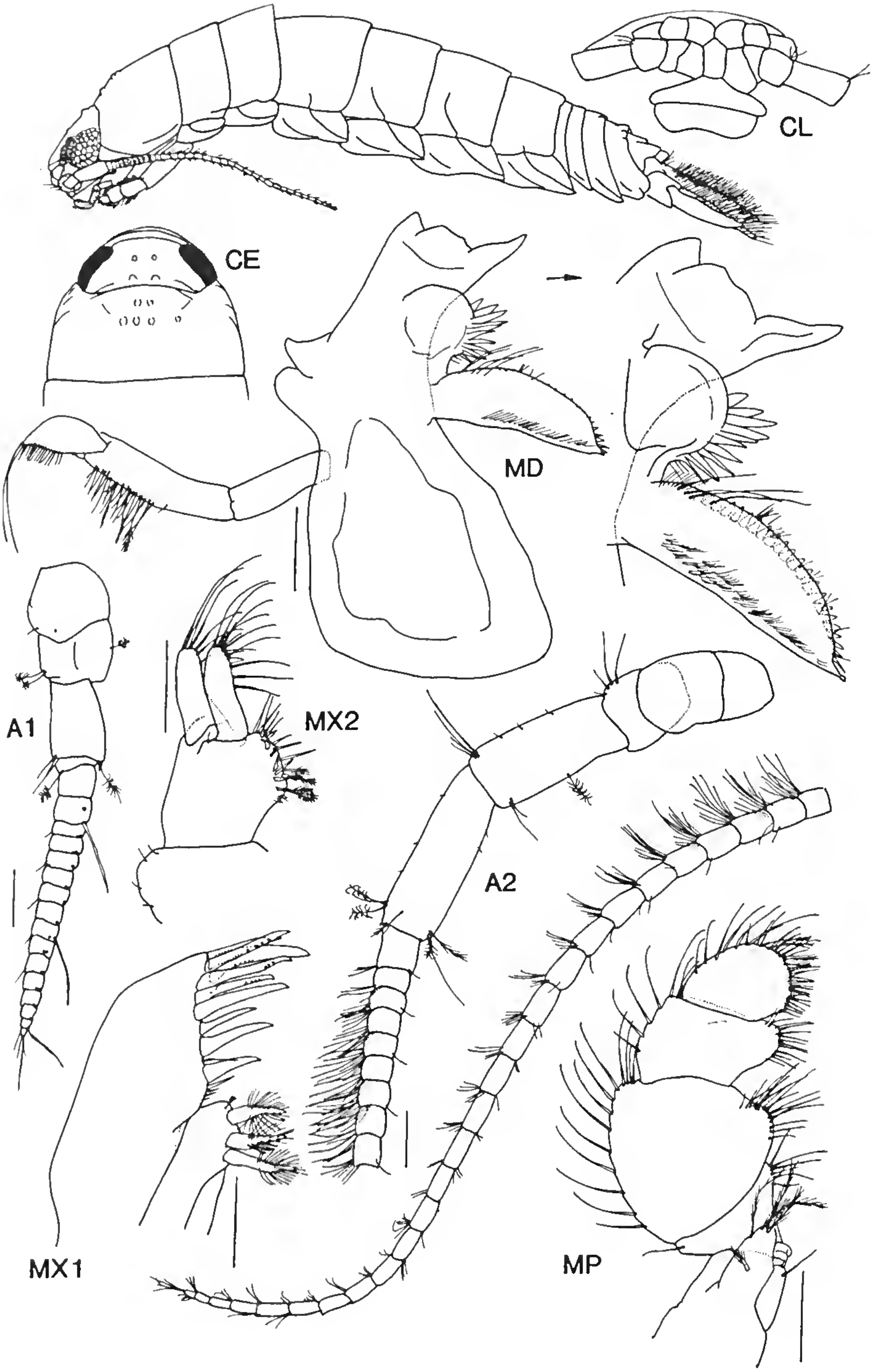

Figure 4. *Cirolana comata* sp. nov., holotype. Scales = 0.2 mm.

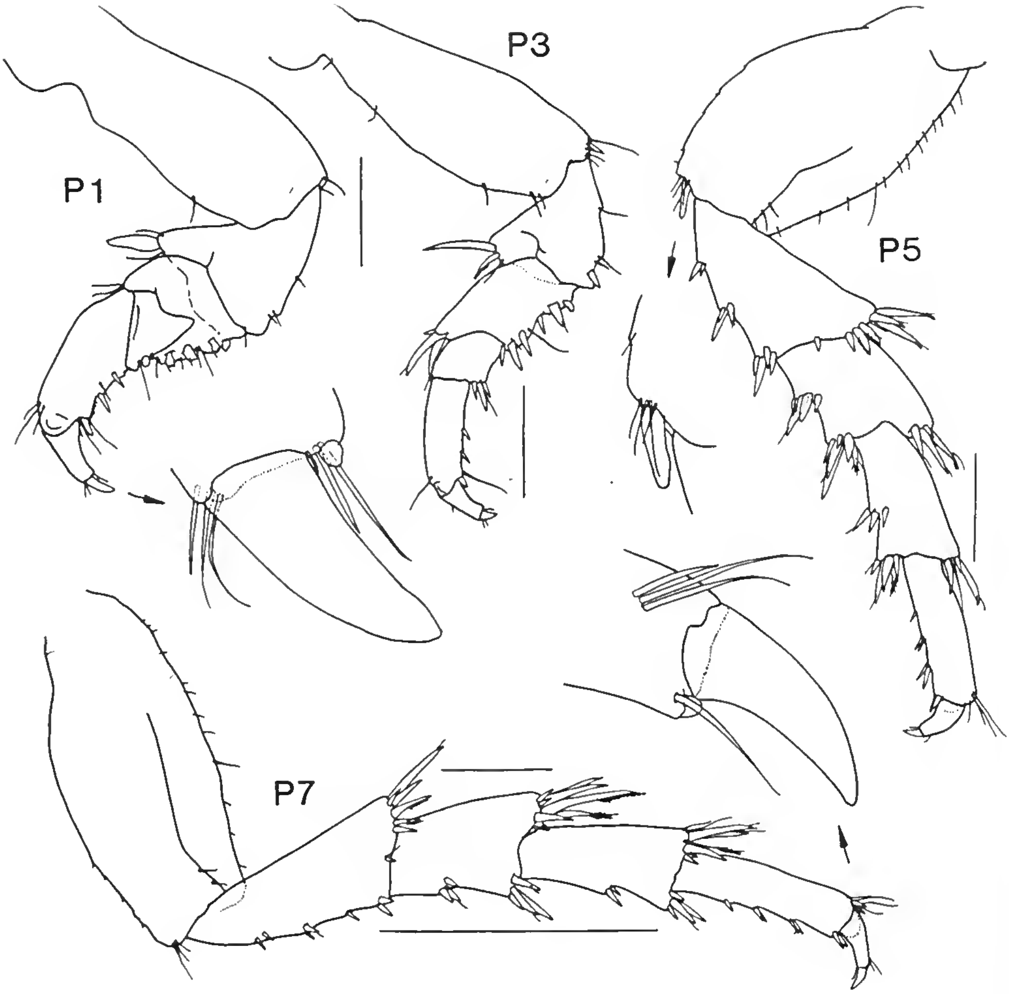

Figure 5. *Cirolana comata* sp. nov., holotype. Scales = 0.5 mm.

setae. Pereopods 4–6: basis posterodistal angle with 1 strongly sclerotized robust seta. Pleopod 2 appendix masculina: arising subbasally; extending beyond tip of endopod, 1.22 length of endopod from insertion point; margins straight, parallel along most of length, but tapering toward apex; slender; apex not at angle to margins, tapered to finely acute point. Uropods: endopod dimorphic, males with dorsal setae; lateral margin slightly convex. Exopod dimorphic, males with dorsal setae; lateral margin convex, robust and plumose setae continuous along margin.

Additional descriptive characters based on holotype. Body: length approximately 3.35 greatest width; cream in alcohol; chromatophores, small, brown in alcohol, scattered over body; Cuticular surfaces scale-like.

Cephalon: with 4 indistinct tubercles, 2 medially and 2 along posterior margin. Eyes: visible in ventral view; orange-tan in alcohol; partially overlapped by pereonite 1; ommatidia in rows, 10 ommatidia in horizontal diameter, 9 ommatidia in vertical diameter. Interocular furrow: distinct, extending across cephalon, smoothly convex. Frontal lamina: length approximately 2 basal width; pentagonal; lateral margins parallel; apex not projecting, not visible in dorsal view, not expanded, in 1 plane (not stepped). Clypeus: triangular, not produced.

Pereonites: 1 longest, 4–6 length subequal and longer than 2–3 and 7 which are subequal.

Pleonites: 1–5 visible but 1 almost completely

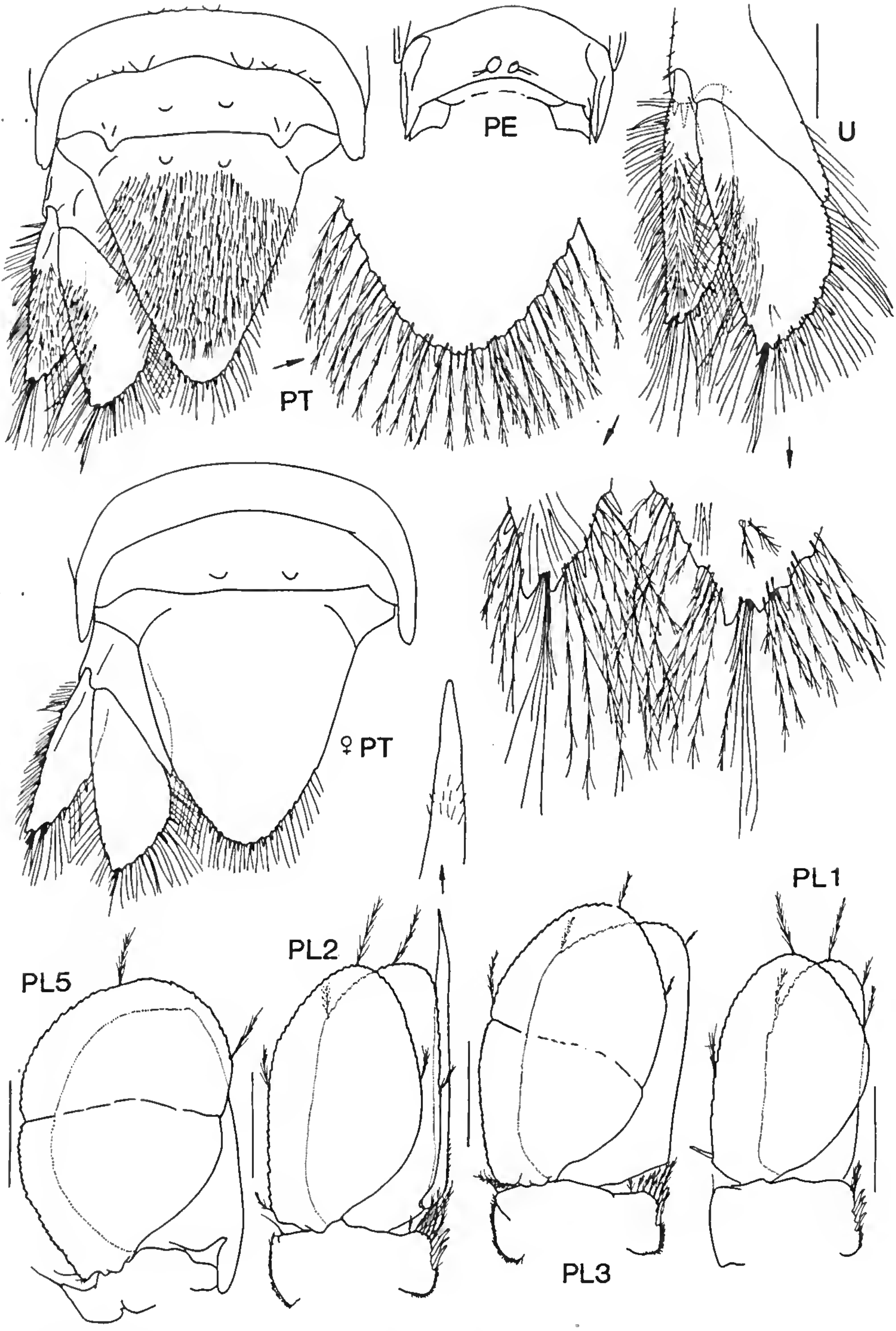

Figure 6. *Cirolana comata* sp. nov., holotype, except female = paratype, 17.5 mm, AM P59356. Scales = 0.5 mm.

concealed along dorsal margin by pereonite 7; tubercles not continuous across entire posterior margin, pleonite 3 tubercles small, subequal, pleonite 4 median tubercles prominent, pleonite 5 lateral tubercles prominent.

Pleotelson: length 0.88 basal width; anterodorsal uropodal sutures present; 5 robust setae on each posterolateral margin; plumose setae restricted to posterolateral margins, numerous proximal to robust setae.

Antennule: just reaching pereonite 1. Peduncular bases touching; articles 1–2 free; article 1 length subequal to width, greater than article 2; article 2 wider than long, anteromedial margin with 1 penicillate seta, posterodistal angle with 2 penicillate setae; article 3 shorter than combined lengths of articles 1–2, longer than article 1, length greater than width. Flagellum longer than peduncle; articles not compressed (lengths of most greater than half width); 16-articulate; aesthetases iridescent. Antenna: 0.41 length of body, when extended against body reaching to posterior of pereonite 4. Peduncular article 2 and article 3 subequal in length; article 4 much longer than article 3, with 4 slender setae at anterodistal angle, 1 penicillate seta on posteromedial margin, 2 slender setae at posterodistal angle; article 5 longer than article 4 and all other articles, with 1 slender and 2 penicillate setae at anterodistal angle, 2 penicillate and 1 slender setae at posterodistal angle. Flagellum 35-articulate; setal brush present.

Mandible: molar medial surface covered with short fine slender setae, cluster of long slender setae proximally present, long slender setae submarginal to anterior margin absent; marginal robust setae close set. Setal row with 11 robust setae; medial surface without setae. Maxillule: medial lobe lateral margin protuberance well developed; lateral lobe with 11 robust setae on distal surface. Maxilla: lateral lobe with 6 slender setae; medial lobe with 12 slender and 7 plumose setae, with 2 medial plumose setae longest and bent; middle lobe with 13 slender setae. Maxilliped: right and left endite with 2 coupling hooks.

Pereopods: 1–3 merus posterior margin robust setae strongly molariform on 1 only; 2–7 coxal furrows complete. Pereopod 1: posterior margin setose fringe absent; propodus robust; dactylus long, 0.5–1 propodus length.

Penes: separated by more than width of both penes; forming flattened lobes; length approximately 1.5 basal width.

Pleopods: exopod suture complete on 3–5 (but indistinct). Pleopod 1: exopod medial margin tapering evenly, proximolateral robust seta present; endopod length subequal to exopod, lateral margin slightly concave.

Uropods: extending beyond pleotelson. Peduncle ventrolateral angle with 2 robust setae and 1 plumose seta; lateral margin robust seta present; distolateral angle rounded. Endopod medial margin convex, with 6 robust setae, plumose setae along entire length; apex subbifid with lateral spine largest, without robust setae, setal cluster formed by plumose and slender setae; lateral margin with 2 robust setae, plumose setae along entire length. Exopod 0.86 length of endopod; medial margin convex, with 3 robust setae, plumose setae on distal two-thirds; apex subbifid with lateral spine largest, without robust setae, setal cluster formed by slender setae; lateral margin with 6 large robust setae, plumose setae along entire length.

Sexual dimorphism. Females differ from males in the primary sexual characters and do not develop the dense patches of setae found on the dorsal surface of the pleotelson, uropod endopod and uropod exopod, or the prominent lateral tubercles on pleonite 5 and dense brush of setae formed on the proximal articles of the antennal flagellum. The tubercles on the cephalon, pereonite 1, pleonites 3–4 and on the pleotelson are also absent in females.

Variation. Pleotelson and uropod robust setal counts from margins (N = 20, subsample of 10 males and 10 females from AM P39356): Pleotelson: 4:4 (5%), 4:5 (5%), 5:5 (85%) , 5:6 (5%). Endopod: (medial) 5 (70%), 6 (30%); (lateral) 1 (5%), 2 (95%). Exopod: (medial) 2 (5%), 3 (95%); (lateral): 5 (65%), 6 (35%). Males approximately 6 mm long lack tubercles, and the dorsal setae on the pleotelson and uropods.

Size range. Mancas approximately 3 mm, adults approximately 5–17.5 mm.

Etymology. Comata, Latin, hairy, referring to the dense setae found on the dorsal surfaces of the pleotelson and uropod rami in mature males.

Distribution. Off north-east Queensland; 65–105 metres.

Remarks. The prominent lateral tubercles on pleonite 5 and the dense patch of setae on the pleotelson distinguish mature males of *Cirolana comata* and *C. dissimilis* from those of other species in the genus. *Cirolana comata* differs from *C. dissimilis* in having a dense patch of setae on the dorsal surface of the uropod rami, a setal brush on the antenna in mature males and a strongly sclerotized robust seta at the posterodistal angle of the basis of pereopods 4–6 (4–5 in *C. dissimilis*). Females and immature males of *C. comata* and *C. dissimilis* are difficult to distinguish from other species but the lack of chromatophores, lack of strong tubercles or other sculpting on the somites, rostrum not extending to the frontal lamina, relatively high number of robust setae on the pleotelson, shape of the pleotelson, presence of a strongly sclerotized robust seta at the posterodistal angle of the basis of pereopods 4–5 (*C. dissimilis*), or 4–6 (*C. comata*), and the continuous distribution of the robust and plumose setae along the uropod exopod lateral margin are diagnostic. *Cirolana indica* Nierstrasz, 1931, which is only known from a single female which lacks tubercles or ridges, may be similar to *C. comata* and *C. dissimilis*. However, *C. indica* is described as having a row of plumose setae along the posterodistal angle of the propodus of pereopod 1 which is lacking in these species. *Cirolana meinerti* Barnard, 1920 apparently has a patch of setae on the dorsal surface of the pleotelson and may also be similar to *C. comata* and *C. dissimilis* in other respects. However, *C. meinerti* is described as having medial tubercles on pleonite 5 which are more prominent than the lateral tubercles. This is not the case in *C. comata* or *C. dissimilis*. Mature males of *C. pleonastica* Stebbing, 1900 develop a dense patch of setae on the dorsal surface of the uropod exopod, as in *C. comata*. However, they do not develop a similar patch on the uropod endopod or the pleotelson (Bruce, 1995). *Cirolana comata* and *C. pleonastica* are also distinct in many other features including the sculpting of the somites, and the shape and setation of the pleotelson.

Cirolana dissimilis sp. nov.

Figures 7–9

Cirolana sp. 1.—Keable, 1997: 251.

Material examined. Holotype. Just off West Point, Darwin Harbour, Northern Territory (12°26.3'S 129°46.3'E), baited trap, unknown substrate but probably rock reef, 8 m, S. Keable, 8–9 Jul 1993 (stn NT-123), NTM Cr012796 (male, 18 mm).

Paratypes. All same data as holotype, AM P44797 (40 males, 40 females); BMNH 2000.2412–2413 (male, female); NMV J47151 (male, female); NTM Cr012797 (female); USNM 296462 (male, female).

Additional material. Bet Reef, Torres Strait, Queensland (10°10.54'S 142°56.01'E), baited trap, grey clay mud with shell grit, 20 m, S. Keable, 30–31 Jan 1993, AM P44799 (many specimens). Ngalaguru (High Cliffy) I., Western Australia (15°54.77'S 124°20.68'E), baited trap, unknown substrate, unknown depth, F. Wells, 22–23 Nov 1994, AM P59357 (19 specimens).

Diagnosis. Cephalon: rostrum not extending to frontal lamina, not dividing antennules; anterior margin not overriding antennules. Eyes: well developed, round with upper margin flat. Frontal lamina: anterior margin angled. Pereonites: without transverse carina; tubercles absent (except for 4 indistinct tubercles on submarginal anterior ridge of pereonite 1 in mature males). Pleonites: 3–5 with tubercles. Pleonite 4: ventral margin free of pleonite 3; posterodorsal margin apex broadly rounded dorsally but meeting convex ventral margin at a point. Pleotelson: dorsal surface with 2 paired tubercles, conspicuous fine setae forming dense patch in males; anterolateral margins convex; posterolateral margins convex; apex rounded; 8–11 (usually 10) robust setae on margins. Pereopod 1: propodus without plumose setae. Pereopods 4–6: basis posterodistal angle with 1 strongly sclerotized robust seta on pereopods 4–5 only. Penes: present. Pleopod 2 appendix masculina: arising basally; extending beyond tip of endopod, 1.21 length of endopod from insertion point; margins straight, parallel along most of length, but tapering toward apex; slender; apex not at angle to margins, tapered to finely acute point. Uropods: endopod not dimorphic; lateral margin slightly convex; exopod not dimorphic; lateral margin straight, robust and plumose setae continuous along margin.

Additional descriptive characters based on holotype. Body: length approximately 3.6 greatest width; cream in alcohol; chromatophores absent; cuticular surfaces scale-like.

Cephalon: with tubercles, 4 indistinct along posterior margin. Eyes: visible in ventral view; black in alcohol; partially overlapped by pereonite 1; ommatidia in rows, 9 ommatidia in horizontal diameter, 8 ommatidia in vertical diameter. Interocular furrow: distinct, extending across cephalon, smoothly convex. Frontal lamina: length approximately 2 basal width; pentagonal; lateral margins concave; apex not projecting, not visible in dorsal view, not expanded, in 1 plane (not stepped). Clypeus: triangular, not produced.

Pereonites: 1, 4–6 length subequal and longest, 2–3 and 7 subequal.

Pleonites: 1–5 visible but 1 almost completely concealed along dorsal margin by pereonite 7; tubercles not continuous across entire posterior margin, pleonites 3–4 tubercles small and subequal, pleonite 5 lateral tubercles prominent.

Pleotelson: length 0.79 basal width; anterodorsal uropodal sutures present; 5 robust setae on each posterolateral margin; plumose setae restricted to posterolateral margins, numerous proximal to robust setae.

Antennule: just reaching pereonite 1. Peduncular bases touching; articles 1–2 free; article 1 length subequal to width, subequal to article 2; article 2 longer than wide, with 1 penicillate seta at posterodistal angle and on anterolateral margin; article 3 shorter than combined lengths of articles 1–2, longer than article 1, length greater than width. Flagellum longer than peduncle; articles not compressed (lengths of most greater than half width); 19-articulate; aesthetases iridescent. Antenna: 0.38 length of body, when extended against body reaching to posterior of pereonite 4. Peduncular article 2 shorter than article 3; article 4 much longer than article 3, with 1 penicillate seta on posterolateral margin, 3 slender setae at posterodistal angle; article 5

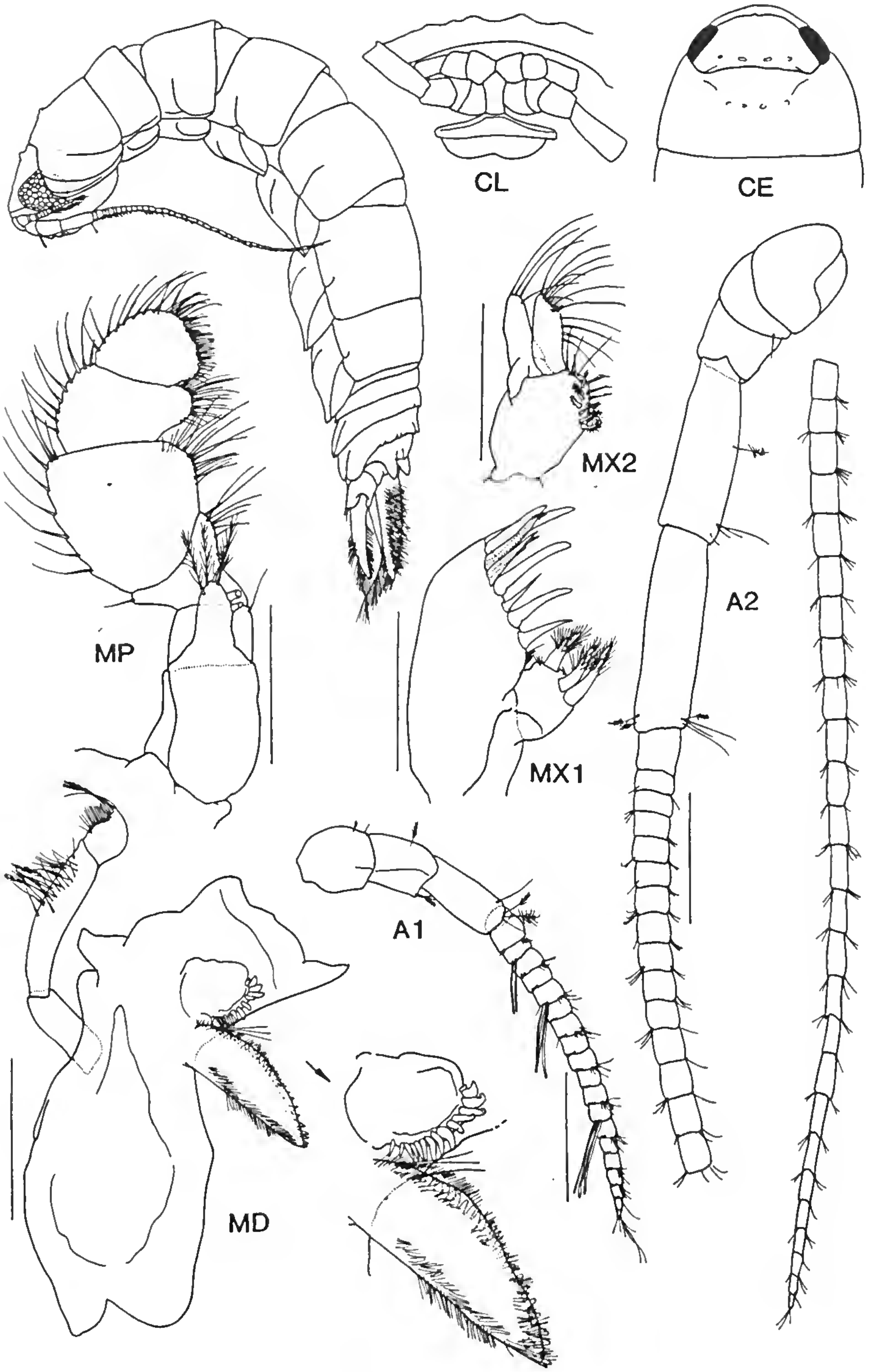

Figure 7. *Cirolana dissimilis* sp. nov., holotype. Scales = 0.5 mm.

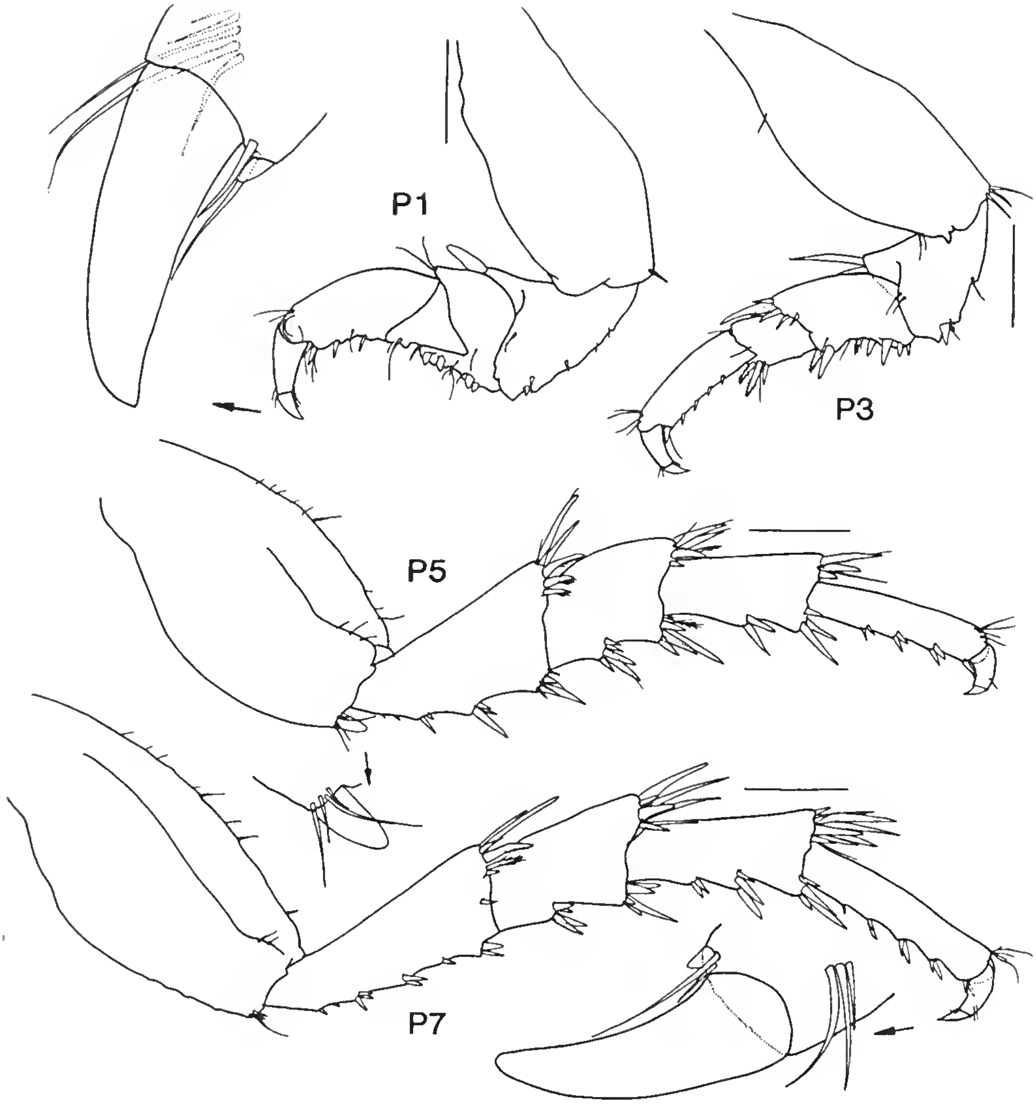

Figure 8. *Cirolana dissimilis* sp. nov., holotype. Scales = 0.5 mm.

longer than article 4 and all other articles, with 2 penicillate setae at anterodistal angle, 4 slender and 1 penicillate setae at posterodistal angle. Flagellum 41-articulate; setal brush absent.

Mandible: molar medial surface covered with short fine slender setae, cluster of long slender setae proximally present, long slender setae submarginal to anterior margin absent; marginal robust setae close set. Setal row with 15 robust setae; medial surface without setae. Maxillule: medial lobe lateral margin protuberance well developed; lateral lobe with 10 robust setae on distal surface. Maxilla: lateral lobe with 4 slender setae; medial lobe with 4 slender and 14 plumose setae, with medial plumose seta longest and bent; middle lobe with lateral row of 10 long slender setae and medial row of 10 short slender setae. Maxilliped: right and left endite with 2 coupling hooks.

Pereopods: 1–3 merus posterior margin robust setae strongly molariform on 1 only; 2–7 coxal furrows complete. Pereopod 1: posterior margin setose fringe absent; propodus robust; dactylus long, 0.5–1 propodus length.

Penes: separated by more than width of both penes; forming flattened lobes; length approximately 1.5 basal width.

Pleopods: exopod suture complete on 3–5 (but

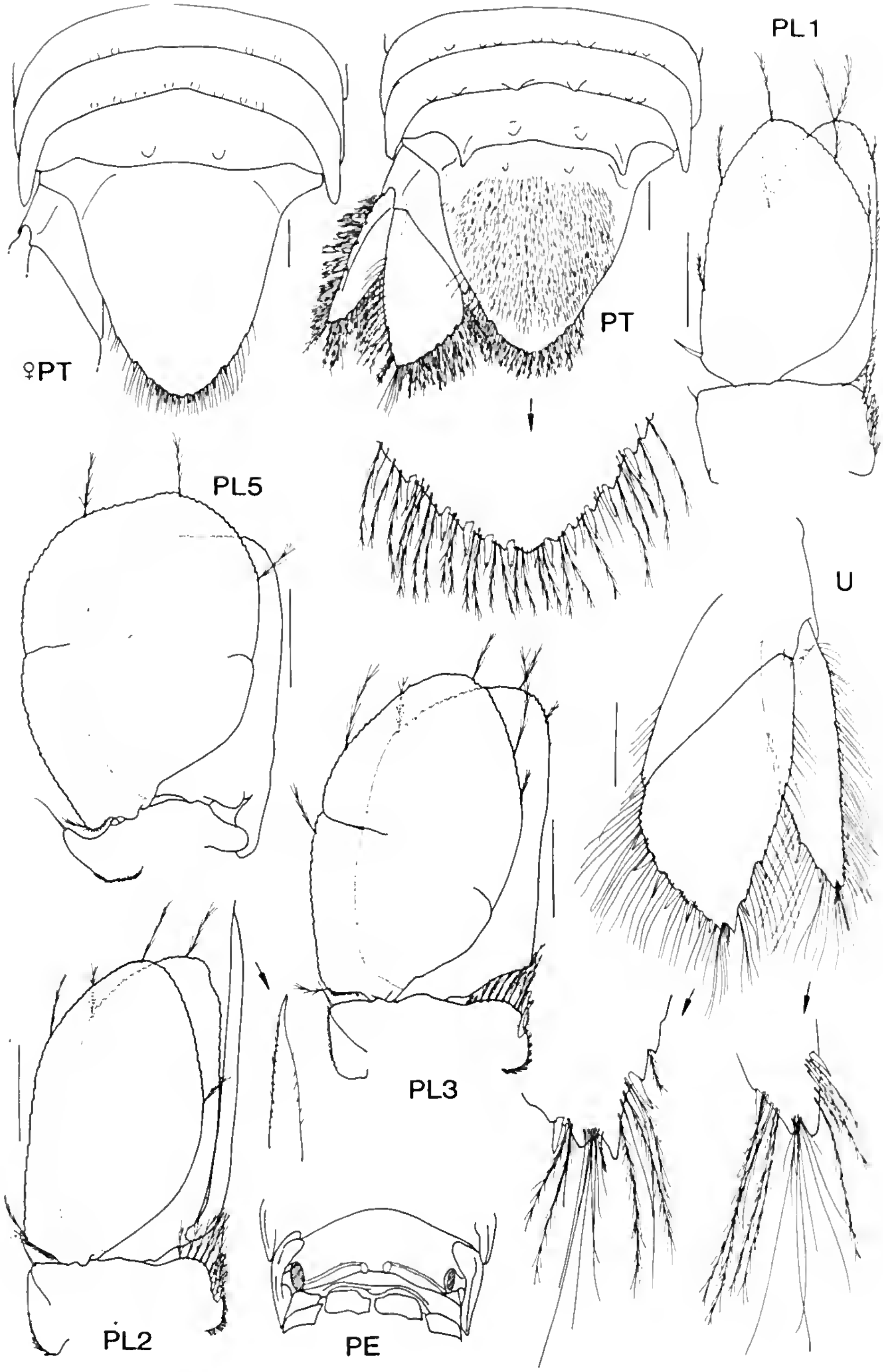

Figure 9. *Cirolana dissimilis* sp. nov., holotype, except female = paratype, 21 mm, AM P44797. Scales = 0.5 mm.

indistinct). Pleopod 1: exopod medial margin tapering evenly, proximolateral robust seta present; endopod length subequal to exopod, lateral margin straight.

Uropods: extending beyond pleotelson. Peduncle ventrolateral angle with 2 robust setae and 2 plumose setae; lateral margin robust seta absent; distolateral angle rounded. Endopod medial margin convex, with 7 robust setae, plumose setae along entire length; apex subbifid with lateral spine largest, without robust setae, setal cluster formed by slender setae; lateral margin with 2 robust setae, plumose setae along entire length. Exopod 0.83 length of endopod; medial margin convex, with 3 robust setae, plumose setae on distal two-thirds; apex subequally bifid, without robust setae, setal cluster formed by slender setae; lateral margin with 7 large robust setae, plumose setae along entire length.

Sexual dimorphism. Females differ from males in the primary sexual characters and do not develop the dense patch of setae found on the dorsal surface of the pleotelson or the prominent lateral tubercles found on pleonite 5. The tubercles on pleonites 3–4 and on the pleotelson are also less conspicuous in females and are absent in specimens smaller than approximately 20 mm. The indistinct tubercles on the cephalon and pereonite 1 are also absent in females.

Variation. Pleotelson and uropod robust setal counts from margins (N = 20, subsample of 10 males and 10 females from AM P44797): Pleotelson: 4:4 (15%), 4:5 (25%), 5:5 (55%), 5:6 (5%). Endopod: (medial) 5 (20%), 6 (55%), 7 (25%); (lateral) 2 (100%). Exopod: (medial) 3 (95%), 4 (5%); (lateral) 5 (15%), 6 (45%), 7 (40%). In males, development of tubercles on the somites and the patch of setae on the pleotelson appear to be associated with maturity. Males approximately 9 mm long lack tubercles, while males approximately 12 mm long have tubercles on the cephalon and pereonite 1, and weakly developed on the pleonites. Males of 12 mm in length, and shorter, lack the patch of setae on the pleotelson.

Size range. Adults 7.5–21 mm.

Etymology. *Dissimilis*, Latin, dissimilar, referring to the sexually dimorphic pleotelson and pleon.

Distribution. Off Kimberley region, Western Australia; Darwin Harbour, Northern Territory; Torres Strait, Queensland; 8–20 m.

Remarks. See *Cirolana comata*. Keable (1997) recorded that in Darwin Harbour *Cirolana dissimilis* (as *C*. sp. 1) was one of the numerically dominant scavengers collected among subtidal rock and coral reef habitats, and was also collected in lower numbers from the scour zone of the main channels where gravel sediments predominate.

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I thank Drs J. Lowry and P. Berents for making the material available for study, and Dr F. Wells for collecting and donating the specimens from Western Australia. Drs N. Bruce and R. Brusca kindly provided unpublished character lists for cirolanid isopods which were useful in writing the species descriptions. I am also grateful to Dr P. Berents, Dr G. Poore and an anonymous reviewer for comments on drafts of the manuscript, and to Mr R. Springthorpe who composed and inked my illustrations. This study was undertaken while in receipt of an Australian Museum Collection Visiting Fellowship.

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Memoirs of Museum Victoria 58(2): 365–371 (2001)

REDESCRIPTION OF THE TROPICAL AUSTRALIAN ISOPOD, *LYIDOTEA NODATA* HALE, 1929 (CRUSTACEA: IDOTEIDAE)

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Abstract

King, R. and Poore, G.C.B., 2001. Redescription of the tropical Australian isopod, *Lyidotea nodata* Hale, 1929 (Crustacea: Idoteidae). *Memoirs of Museum Victoria* 58(2): 365–371.

Lyidotea Hale, 1929 is rediagnosed and its only species, *L. nodata* Hale, 1929 redescribed. Membership of Idoteidae is confirmed but its relationship to other genera remains unresolved.

Introduction

Lyidotea nodata was described by Hale (1929) from a mature female (SAM C1699) and several smaller (possibly immature) specimens from Flinders I., northern Queensland. He placed the species in the valviferan isopod family Idoteidae Samouelle and believed the distinctive flagella of both pairs of antennae and the fusion of pereonite 7 with the pleotelson justified a new genus. Poore and Lew Ton (1990, 1993) omitted the genus *Lyidotea* from their reviews of the related families Holognathidae Thomson and Idoteidae of Australia and New Zealand and in the latter paper explicitly removed it from Idoteidae. They believed the species' "habitus, fusion of body segments, pereopod 1, antenna 2 and oostegite 5 are all arcturid-like." They could not decide on its family placement but their error has since been realised (Poore, 2001).

In Australia the Idoteidae are most diverse in southern latitudes with 22 species recorded south of 30°S. The only taxa recorded north of this latitude are rare: *Euidotea bakeri* (Collinge) and *Paridotea miersi* Poore and Lew Ton extending from the southern coast as far north as 22°S in WA, *Idotea brevicorna* Milne Edwards in Shark Bay, WA, and Indonesia, and *Lyidotea nodata*. Only the last two of these are essentially tropical.

Here, this rather arcturid-like valviferan is redescribed from new material in the collections of Museum Victoria and Hale's (1929) family placement confirmed. The rediagnosis is necessary as part of a wider phylogenetic study on the Arcturidae Dana (where the genus is used as an outgroup in the analysis) and to correct inaccuracies in Hale's original description. The generic diagnosis uses the characters and follows the format used by Poore and Lew Ton (1993) for other genera of Idoteidae.

The new material was collected by CSIRO and Museum Victoria on the North-west Australian shelf between Dampier and Port Hedland in 1982 and 1983 and from as far south as Rottnest I. No new material from Queensland was available. The taxonomic drawings were prepared with a camera lucida. The limbs are drawn to the same scale. The following abbreviations are used: NMV, Museum Victoria, Melbourne; WAM, Western Australian Museum, Perth; SAM, South Australian Museum, Adelaide.

Lyidotea Hale

Lyidotea Hale, 1929: 35–36.

Type species. *Lyidotea nodata* Hale, 1929 by original designation.

Diagnosis. Body semicylindrical; all pereonites with paired dorsal elevations;. Head as wide as pereonite 1; pereonite 1 fused to head with fusion indicated by a groove; pereonites 1 to 7 parallel-sided; pereonite 7 fused to pleon with no distinct suture indicated. Pleon with all pleonites fused; pleotelson apically blunt. Antenna 1 with single short flagellar article. Antenna 2 flagellum of 2 articles plus claw. Mandible with well developed truncate molar process, spine row, lacinia mobilis and toothed incisor. Maxilla 1 with 2 typical lobes. Maxilla 2 with 3 typical lobes. Maxillipedal endite with distal setae; palp with articles 2+3 and 4+5 fused. Coxa completely fused to pereonal tergites. Pereopod 1 reduced; pereopods 2 to 7 with few spiniform setae; dactylus with secondary unguis almost as large as primary unguis. Penes separate, simple and straight. Oostegites on maxilliped and pereopods 1 to 5; not thickened, oostegites 2 to 4 forming the majority of the marsupium, on fully mature female with supportive extensions on coxae 2, 3 and 4.

Remarks. The ambulatory pereopods, mouthparts with fused maxilliped palp articles, separate penes, and absence of uropodal exopods place *Lyidotea* within the Idoteidae. In Arcturidae and similar families (Poore, 2001) maxillipedal palp articles always number five, and there is a single penial plate. Pereopods are usually differentiated into different functional groups and the uropodal exopod is rarely absent.

The genus is unique among Idoteidae in fusion of all pleonites to pereonite 7. Fusion of the head to pereonite 1 is found elsewhere in this family only in *Crabyzos* Bate (sole species, *C. longicaudatus*; Poore and Lew Ton, 1993). There are many differences in body shape, pereopods and mouthparts between these two genera and the fusion is undoubtedly homoplasious. The short, compact pereopods, almost gnathopod-like pereopod 1, dorsal body sculpture, and fusion of maxillipedal palp articles 2+3 and 4+5 resemble the situation seen in species of *Synidotea* Harger (e.g., Richardson, 1905; Poore and Lew Ton, 1990). Again, profound differences are apparent between *Lyidotea* and *Synidotea*, notably in the possession of a fused penial plate in males and the absence of oostegite 5 in females of *Synidotea*. The flagellum of antenna 2 of most genera of Idoteidae is multiarticulate; the short 'clavate' condition seen in *Lyidotea* is distinct yet similar to that seen in *Parasymmerus*, *Cleantiella* and *Erichsonella* (Brusca, 1984) from America. These genera have only slight similarities to *Lyidotea* in other morphological comparisons. A further unique condition in *Lyidotea* is the presence of coxal supports under oostegites. This is parallelled in Antarcturidae Poore, Holidoteidae Wägele, Austrarcturellidae Poore and Bardsley and Rectarcturidae Poore and may be correlated with cylindrical body shape (Poore, 2001).

Relationships of *Lyidotea* to other idoteid genera remain unresolved.

Lyidotea nodata Hale

Figures 1–4

Lyidotea nodata Hale, 1929: 35–36, fig. 1.

Type material. Flinders I., Princess Charlotte Bay, Qld, SAM C1699 (female holotype). SAMA C1845 (paratype) — not examined.

Material examined. Western Australia. North-west Shelf, between Dampier and Port Hedland, CSIRO Division of Fisheries, RV *Soela*, WHOI epibenthic sled, 31 NWA stations within rectangle defined by 18°56.6′S, 119°2.4′E and 20°1.2′S, 116°57.5′E, 30–142 m, 7 Dec 1982–30 Oct 1983, (93 specimens including males, females, juveniles and mancas, 5–13 mm), NMV collections. NW of Bluff Point (27°28′S, 133°16′E), 97 m, 9 Oct 1963, WAM 636-86 (2 males, 9 mm, 10.5 mm); W of Rottnest I., (32°00′S, 115°08′E), 135 m, 28 Aug 1973, WAM 548-73 (1 female, 13 mm).

Illustrated specimens. North-west Shelf, between Dampier and Port Hedland, 19°27.2′S, 118°58.6′E, 36–46 m, 8 Dec 1982 (stn NWA 346), NMV J23702 (1 male, 8 mm); 19°29.0′S, 118°53.5′E, 40–40 m, 12 Feb 1983 (stn NWA 81), NMV J23699 (1 female, 7.5 mm). W of Rottnest I., (32°00′S, 115°08′E), 135 m, 28 Aug 1973, WAM 548-73 (1 female, 13 mm).

Description. Male. Head with 2 rounded dorsal elevations between eyes; with setae on elevations, anterolateral margins rounded, rostral point absent. Fusion of head and pereonite 1 indicated by a shallow dorsolateral groove not incised laterally. Pereonite 1 as long as head, with 2 rounded dorsal elevations. Pereonites 2 to 4 progressively longer, each with 2 rounded dorsal elevations at midlength and 2 smaller posterior dorsal elevations. Pleotelson and pereonite 7 fused; pereonite 7 with small dorsal elevations; the whole widest two-thirds along, tapering to bluntly rounded apex.

Eyes lateral, prominent. Antenna 1 extending midway along peduncular article 3 of antenna 2; flagellum a single hemispherical article with 5 aesthetases. Antenna 2, 0.46 times body length; flagellum of 2 articles and claw, article 1 with numerous short setae, 1.3 times as long as last peduncular article, article 2 minute, claw longer, almost straight.

Mandible with truncate trituritive molar; spine row of 4 spines; left lacinia mobilis with 2 teeth; incisor 4-toothed. Maxilla 1 inner lobe with 2 terminal setae; outer lobe with 10 distal robust setae. Maxilla 2 inner lobe with 10 plumose setae; middle lobe with 3 setae; outer lobe with 4 setae. Maxillipedal endite with 5 long setae; 1 coupling hook; small oostegite present; palp oval, twice as long as wide, twice as wide as article 1; articles 2 and 3 fused, with distomesial row of 11 setae, with oblique distal suture between this and more distal articles; articles 4 and 5 fused, with mesial row of 9 seate and 5 more scattered setae distally.

Pereopod 1 ambulatory, compact; basis-merus with few setae; carpus cylindrical, with 2 mesial setae near posterior margin; propodus with semicircular blade produced from palm, mesial face with curved row of 13 barbed setae; dactylus almost as long as propodus, with mesial setae, with primary and secondary unguis. Pereopods 2 to 7 similar, with scattered setae; propodi cylindrical; dactylus tapering, with rounded denticles along posterior margin, setose, with primary and secondary unguis.

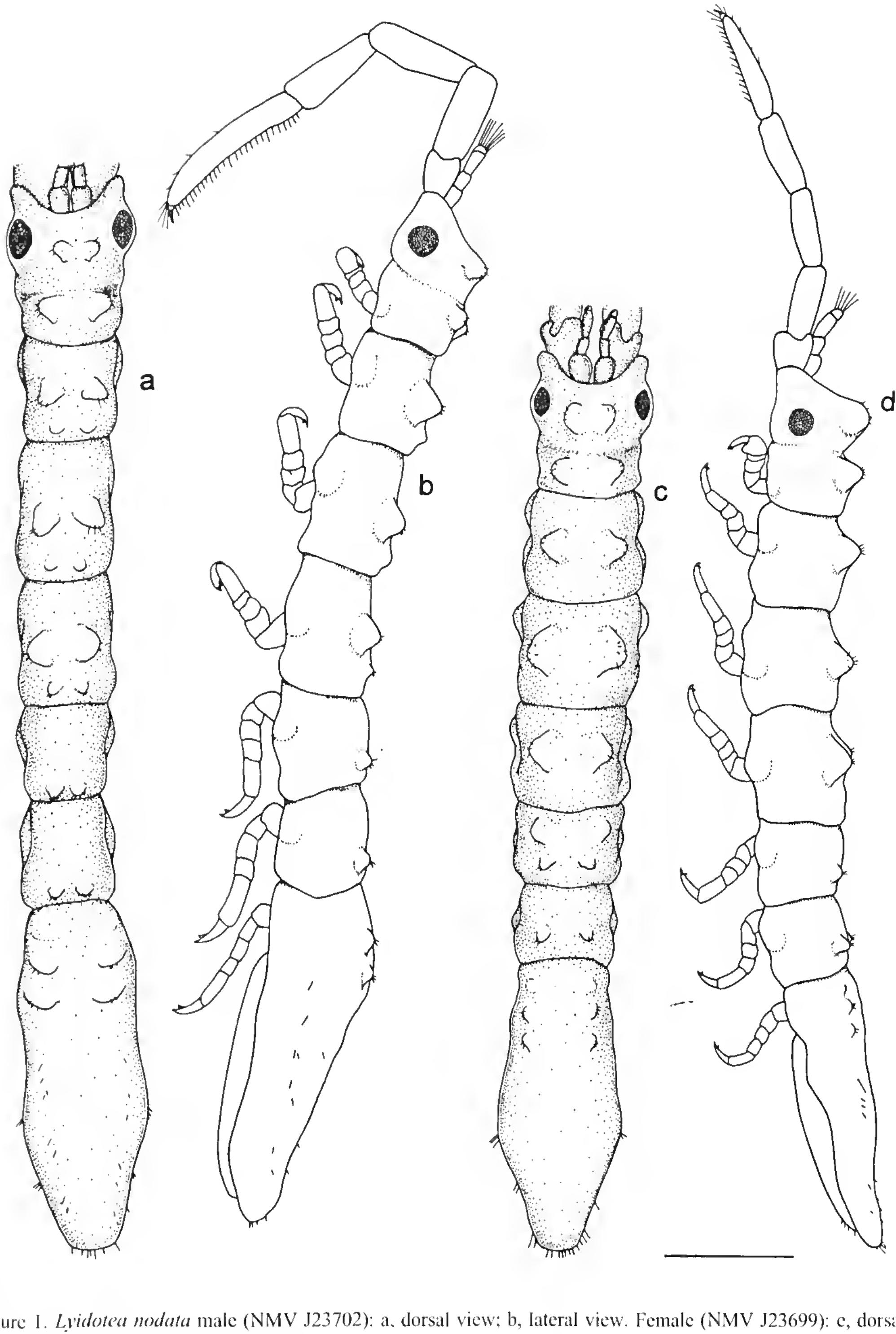

Figure 1. *Lyidotea nodata* male (NMV J23702): a, dorsal view; b, lateral view. Female (NMV J23699): c, dorsal view; d, lateral view. Scale = 1.0 mm.

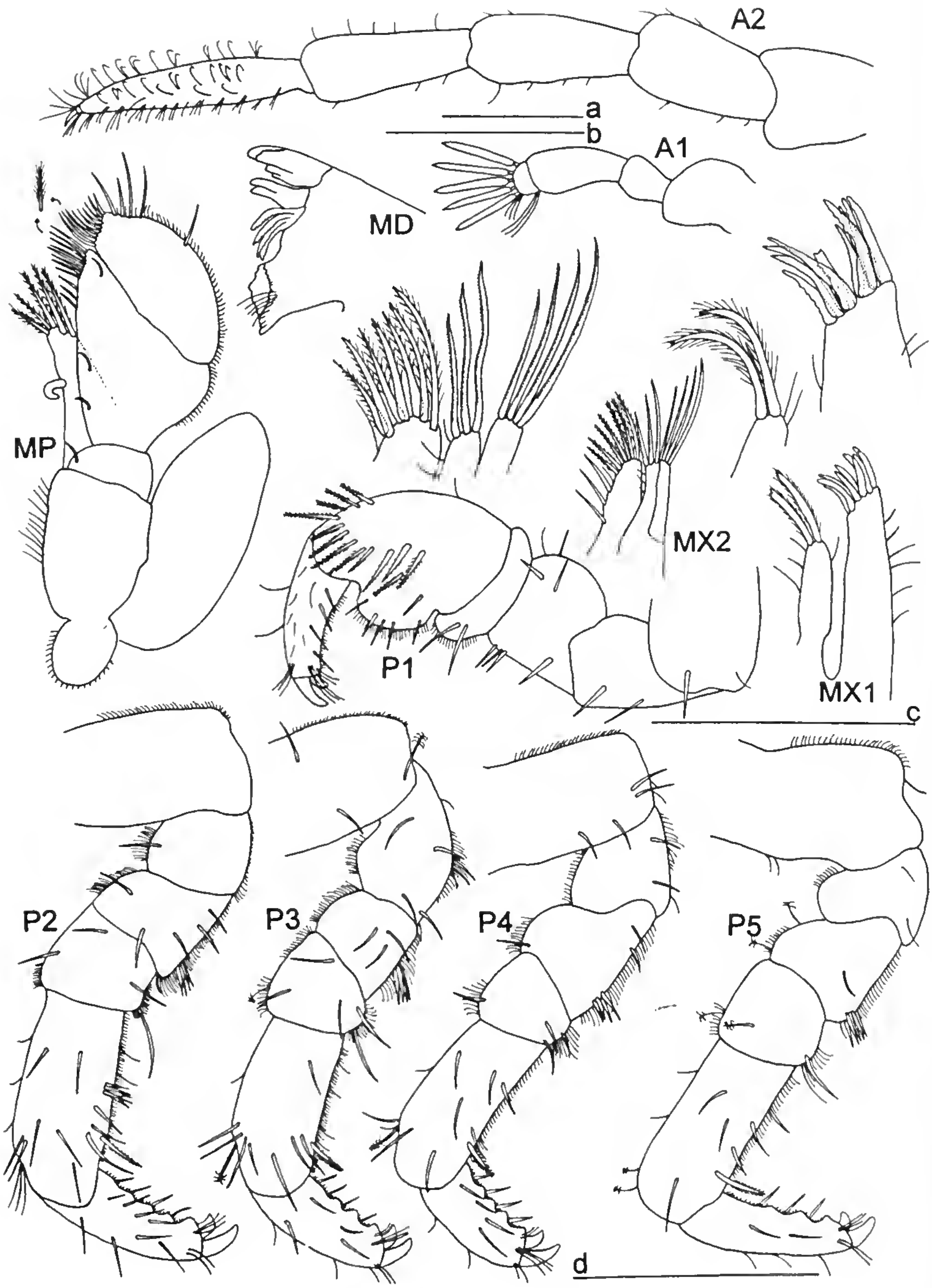

Figure 2. *Lyidotea nodata* female (NMV J23699): antennae 1 and 2, left maxilliped, left mandible, left maxillae 1 and 2, pereopods 1 to 5. Scales = 0.5 mm: a, A2; b, A1; c, MD, MX1, MX2, MP; d, P1–P5.

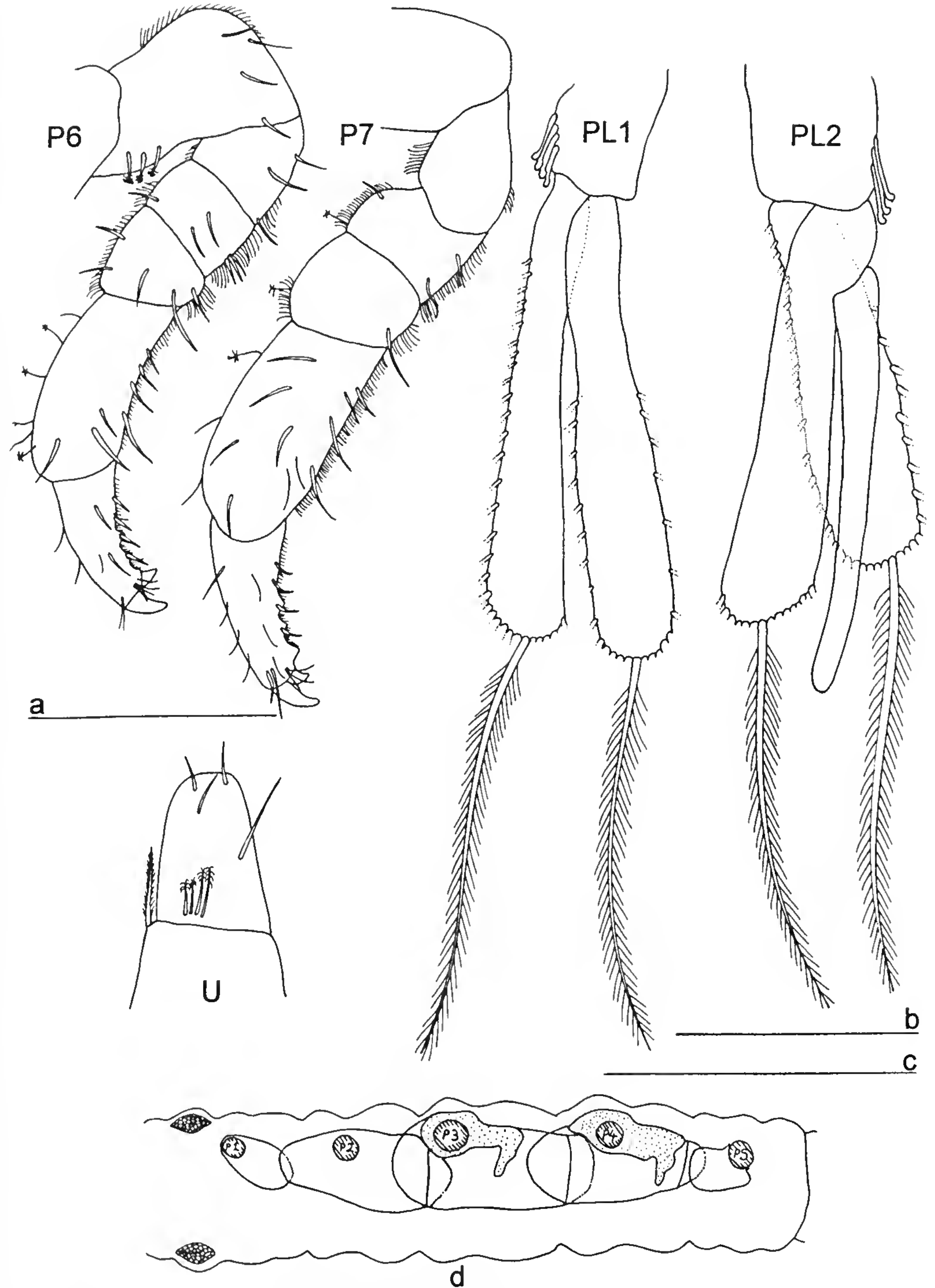

Figure 3. *Lyidotea nodata* female (NMV J23699): pereopods 6 and 7, uropod, ventral view detailing oostegites. Male (NMV J23702): pleopods 1 and 2. Scales = 0.5 mm: a, P6, P7; b, PL1, PL2; c, U. Scale = 1 mm: d, ventral view of female.

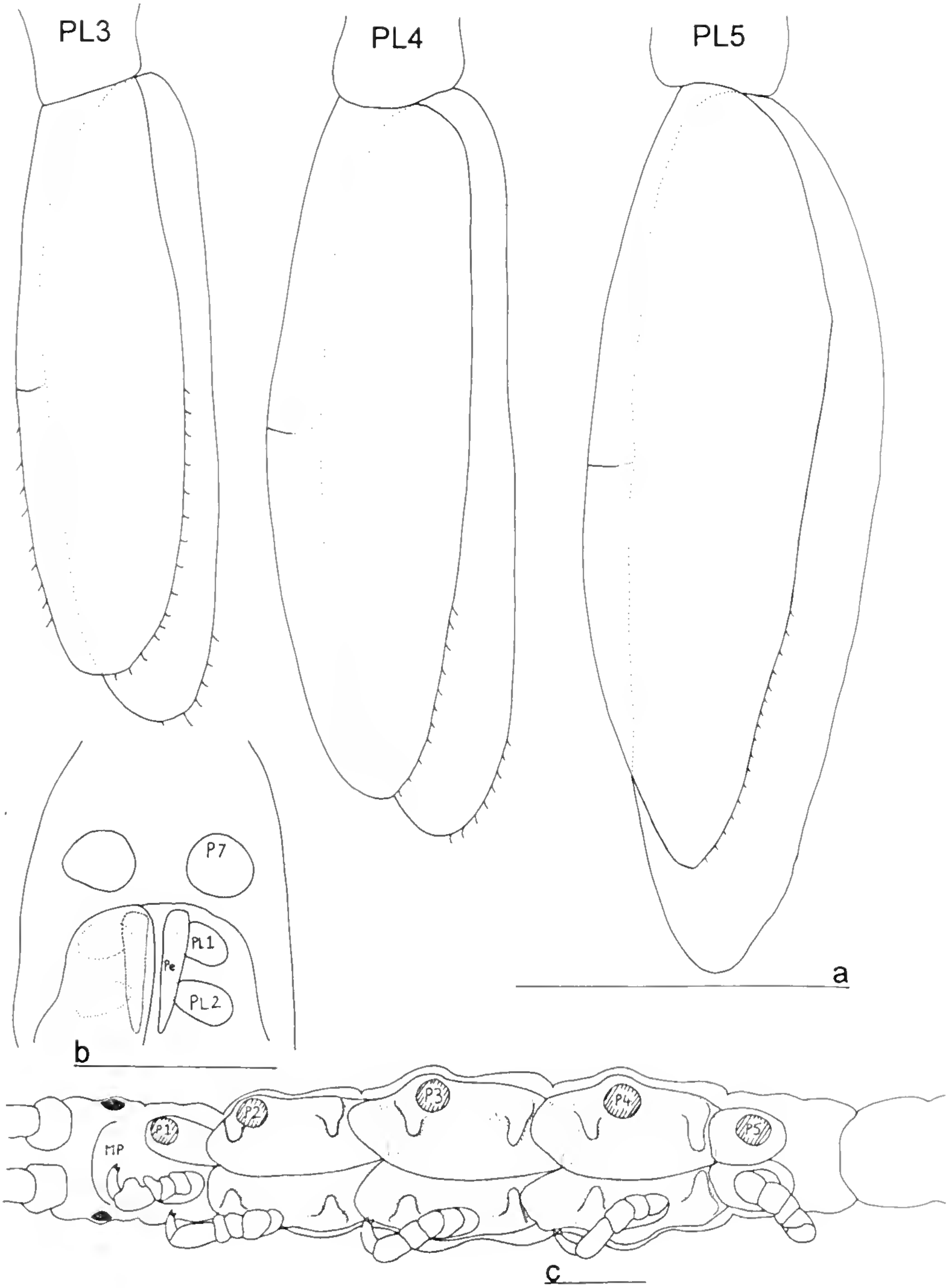

Figure 4. *Lyidotea nodata* male (NMV J23702): pleopods 3, 4 and 5, ventral view of pereonite 7 and pleon showing position of penes in situ. Female (NMV J23699): ventral view of fully mature female detailing oostegites. Female (WAM 548-73): ventral view. Scale = 0.5 mm: a, PL3–PL5. Scales = 1.0 mm; b, ventral views.

Pleopod 1 peduncle longer than wide, with 4 coupling hooks; endopod with 33 mesial and distal long plumose setae, longest as long as endopod; exopod with 27 long plumose setae concentrated distally. Pleopod 2 peduncle little longer than wide; endopod with 15 distal plumose setae, as long as endopod; appendix masculina simple, straight and blunt, reaching beyond the apex of endopod; exopod with 40 marginal plumose setae. Pleopod 3 to 5 progressively larger, without long marginal setae. Uropodal endopod 1.5 times as long as wide at base, tapering to rounded-truncate apex.

Female. Differs from the male in smaller size and wider pereonites. Small ostegite on maxilliped; oostegite on pereopod 1 small, posteriorly directed; oostegites on pereopods 2 to 4 elongated along body, with distal transverse sutures; pereopods 2 to 4 with L-shaped coxal extensions forming thickened lateral edges supporting oostegites, oostegites 5 small, meeting in midline (Fig. 3D, 4C).

Distribution. North Queensland, Western Australia; subtidal to 140 m depth.

Remarks. This redescription is the first illustration of a male, unavailable to Hale (1929), and also illustrates the oostegites for the first time. A female with slightly more developed oostegites (WAM 548-73) was found after the description of the female (NMV J23699) was completed. Both possess functional oostegites and all other appendages are the same but it was decided that the larger female be illustrated to show the slightly more developed condition. Hale failed to note the second article of the antenna 2 flagellum.

Acknowledgements

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Memoirs of Museum Victoria 58(2): 373–382 (2001)

PLAKARTHRIUM AUSTRALIENSE, A THIRD SPECIES OF PLAKARTHRIIDAE (CRUSTACEA: ISOPODA)

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Abstract

Poore, G.C.B. and Brandt, A., 2001. *Plakarthrium australiense*, a third species of Plakarthriidae (Crustacea: Isopoda). *Memoirs of Museum Victoria* 58(2): 373–382.

The Plakarthriidae share with four genera of Sphaeromatidae a flat habitus and a marginal row of setae on antenna 1, coxae and uropods, modified to maintain contact with the substrate. They do not possess areas of scales on pleopod 5, a probable sphaeromatid synapomorphy. The possibility exists that Plakarthriidae are a highly derived offshoot of a clade that also gave rise to the flattened "cassidiniine" sphaeromatids. *Plakarthrium australiense* sp. nov. is described from the southern Australian marine shelf and compared with the only two other species of the genus and family. The new species differs from *P. typicum* from New Zealand and *P. punctatissimum* from subantarctic islands of the South Atlantic and Antarctic Peninsula in having pleonite 1 fully indicated dorsally, only pleonite 2 indicated laterally and pleotelson tapering to 80% of its anterior width posteriorly.

Introduction

The Plakarthriidae Hansen, 1905 are previously known from only two species, *Plakarthrium typicum* Chilton, 1883 and *P. punctatissimum* (Pfeffer, 1887). The family is confined to shallow marine shores in cool-temperate and cold environments of the Southern Hemisphere. *Plakarthrium typicum* was described from New Zealand and has been reported as far south as The Snares islands (48°S) (Hurley, 1961; Poore, 1981) but not from Macquarie Island (GCBP collections in Museum Victoria). It has also been reported from southern Chile (Jaramillo, 1977) but this record is more likely to be the second species, *P. punctatissimum*, if not an undescribed Chilean endemic. *Plakarthrium punctatissimum* is reported from subantarctic islands of the South Atlantic and Antarctic Peninsula, namely South Georgia (type locality), South Orkneys, Petermann I., Booth-Wandel I. and Anvers I. (Richardson, 1906, 1913; Tattersall, 1921; Pesta, 1928; Wilson et al., 1976). A third species from southern Australia is here reported.

The taxonomic affinities of *Plakarthrium* Chilton, 1883 to other "flabelliferan" isopods has remained enigmatic. Hansen (1916) erected the Plakarthriinae as a subfamily of Sphaeromatidae and Menzies (1962) believed them to belong in the "platybranchiata" group of this family, a group more or less equivalent to Cassidininae Hansen, 1905 (Iverson, 1982; Harrison and Ellis, 1991; Bruce, 1994). The monophyly of this and other sphaeromatid subfamilies remains doubtful (N.L. Bruce, pers. comm.). The affinities of Plakarthriidae were reviewed with a redescription of *P. typicum* by Wilson et al. (1976) who concluded "that the Plakarthriidae are unique with no close affinities with any other family." Wägele (1989) placed the family within his suborder Sphaeromatidea, sister taxon to a clade including Serolidae, Bathynataliidae and Sphaeromatidae. Brusca and Wilson (1991) also assessed their position, placing the family as sister taxon to Serolidae, and possibly Keuphyliidae and Bathynataliidae. This paper, describing a new Australian species, also addresses some newly recognised characters which may have a bearing on plakarthriid relationships to Sphaeromatidae in particular.

Pfeffer's (1887) generic name *Chelonidium* is a junior synonym of *Plakarthrium* Chilton, 1883, a fact realised by Richardson (1904: 6; 1906: 6) who synonymised the two. Plakarthriidae (erected by Hansen (1905) as Plakarthriinae, a subfamily of Sphaeromatidae Latreille, 1825) is the family name to have been used by most authors and, under ICZN (1999) Article 40, replaces Pfeffer's (1887) family name, Chelonidiidae. Both dates should be cited for the family. Wilson et al. (1976) who incorrectly attributed the family name to Richardson (1904) reviewed later accounts of plakarthriids by Richardson (1906, 1913), Tattersall (1921), Pesta (1928), Nierstrasz (1931), Menzies (1962), Glynn (1970) and Kussakin (1973).

Material is lodged in Museum Victoria, Melbourne (NMV) and the Zoological Institute and Museum, Hamburg (ZMH).

Plakarthriidae Hansen, 1905 (1887)

Chelonidiidae Pfeffer, 1887: 85.—Pesta, 1928.

Plakarthriinae Hansen, 1905: 100.—Nierstrasz, 1931: 192.

Plakarthriidae.—Richardson, 1906: 6.—Richardson, 1913: 7.—Wilson et al., 1976: 334 (see above for other references).

Diagnosis. First coxa free and articulating. Margin of the body being defined by peduncular articles 1 and 2 of antenna 1, peduncular articles 3 and 4 of antenna 2, all coxae, uropodal rami. Pleotelson completely fused and without articulation.

Composition. There is only one genus.

Remarks. The family was rediagnosed by Wilson et al. (1976) and is recognised by the combination of characters given in the diagnosis. Only the second character, the arrangement of the marginal segmentation, is unique. Similar patterns involving an expanded peduncle of antenna 1 and uropods are seen in some genera of "cassidiniine" Sphaeromatidae, in particular, *Amphoroidella* Baker, 1908, *Leptosphaeroma* Hilgendorf, 1885, *Paraleptosphaeroma* Buss and Iverson, 1981, and *Platysphaera* Holdich and Harrison, 1981. In all four genera the body is flattened as in Plakarthriidae but antenna 2 does not contribute to the body margin and the uropodal structure is typically sphaeromatid with peduncle and endopod fused. Further, all possess the cuticular scale patches on the end of the exopod of pleopod 5 which may be a sphaeromatid synapomorphy absent in Plakarthriidae (N.L. Bruce, 1993, fig. 1F; pers. comm.). The four genera are unquestionably sphaeromatids and similarity to Plakarthriidae seems on this evidence to be convergent. Another similarity, an adaptation to maintaining a smooth profile and minimum resistance to water movement, is what Buss and Iverson (1981) have called the membrana cingula, a fringe around the edge of the body of webbed marginal setae. The membrana cingula of *Paraleptosphaeroma glynni* was illustrated in SEMs by Buss and Iverson (1981: fig. 4) and of the two other species of this genus in line drawings by Müller (1990) and Kussakin and Malyutina (1993). Bruce (1994: fig. 50B) figured the membrana cingula for *Platysphaera membranata* Holdich and Harrison, 1981. Kwon (1990) figured a similar structure in *Leptosphaeroma gottschei* Hilgendorf and we have observed the same in Museum Victoria material of *Amphoroidella elliptica* Baker. While there is a strong similarity between the membrana cingula in the four sphaeromatid genera, the equivalent structure in Plakarthriidae comprises broad separate fringed overlapping setae and is complemented by a free skirt-like flange of webbed setae underneath and parallel to the margin of the body.

Within Flabellifera the pleon fully fused to the pleotelson is seen in at least one species of Sphaeromatidae, *Maricoccus brucei* Poore, 1994. This and similar genera, *Juletta* Bruce, 1993 and *Margueritta* Bruce, 1993 (both with free pleonite 1), are placed in the Dynameninae and any similarity to *Plakarthrium* is coincidental.

The possibility exists that Plakarthriidae are a highly derived early offshoot of a clade which also gave rise to flattened "cassidiniine" sphaeromatids. In this scenario some reversals may have occurred (e.g. free coxa 1) as well as numerous synapomorphies in limbs and pleotelson.

Plakarthrium Chilton, 1883

Plakarthrium Chilton, 1883: 74.—Hansen, 1905: 115.—Menzies, 1962: 128.—Wilson et al., 1976: 334–335. (type species: *Plakarthrium typicum* Chilton, 1883 by monotypy).

Chelonidium Pfeffer, 1887: 86 (type species *Chelonidium punctatissimum* Pfeffer, 1887 by monotypy).

Remarks. The genus has the characters of the family. Only Chilton (1883) gave a diagnosis.

Plakarthrium australiense sp. nov.

Figures 1–5

Material examined. Holotype. Australia, Tasmania, Bicheno, granite reef 50 m offshore, N end of "The Gulch" (41°53′S, 147°18′E), 7 m, encrusting foliose alga, SCUBA, G.C.B. Poore and H.M. Lew Ton, 22 Mar 1988 (stn TAS-87), NMV J47067 (1 ovigerous female, 3.2 mm, with 3 slides).

Paratypes. Collected with holotype: NMV J27472 (1 male, 2.2 mm; 8 females, 1.9–2.8 mm, 1.9–3.2 mm); NMV J47021 (1 male, 2.4 mm); NMV J47068 (2 females, 3.2, 2.3 mm); ZMH K-39833 (3 females).

Other material. Tasmania, Waterhouse Point, NMV J47066 (1 juvenile, 1.9 mm). Western Bass Strait, 6 km W of Currie, King I., (39°54.7′S, 143°43.4′E), 49 m, NMV J23890 (8 specimens, 1.0–1.6 mm). Pegleg Cove, Deal I., between Pulpit Cove and Winter Cove (39°28′S, 147°22′E), 6 m, NMV J23891 (1 male, 1.7

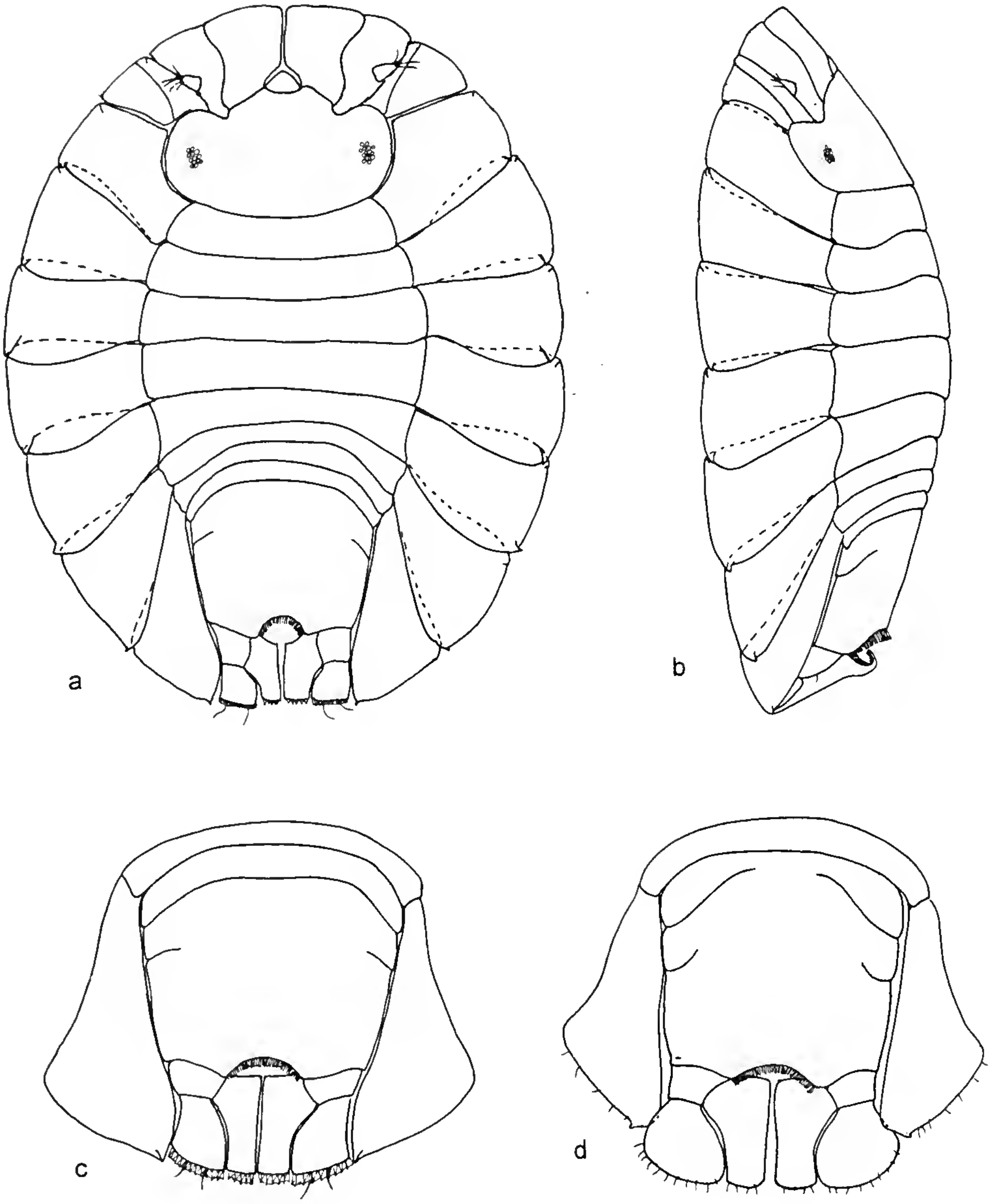

Figure 1. *Plakarthrium australiense* sp. nov. Holotype, NMV J47067: a, b, dorsal and lateral views. c, pereonite 7, pleotelson and uropods.

Plakarthrium typicum Chilton. Male, NMV J683: d, pereonite 7, pleotelson and uropods.

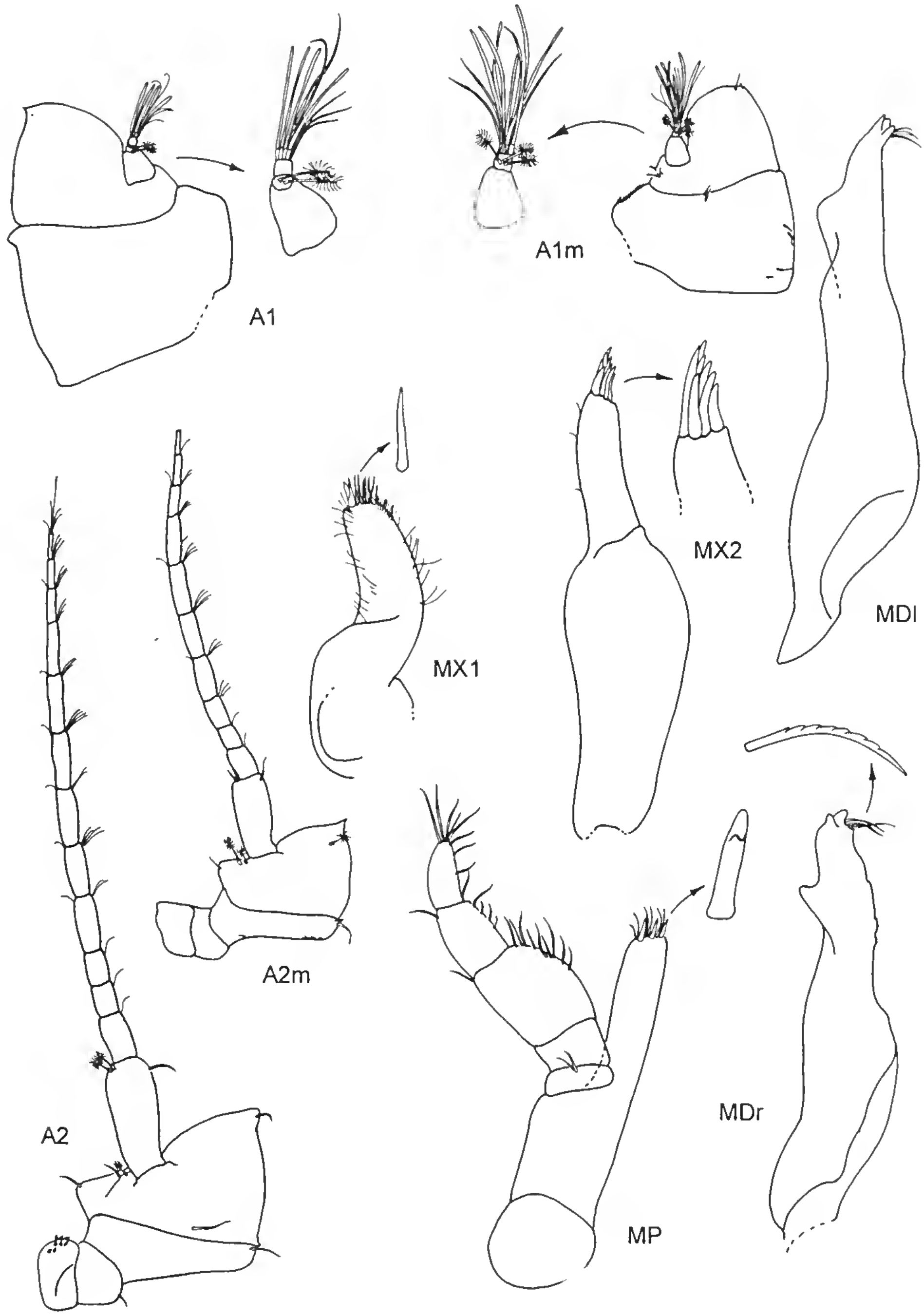

Figure 2. *Plakarthrium australiense* sp. nov. Holotype, NMV J47067: A1, A2, antennae 1, 2; MDl, MD r, left and right mandibles; MX1, MX2, maxillae 1, 2; MP, maxilliped. Paratype male, NMV J47021: A1m, A2m, antennae 1, 2.

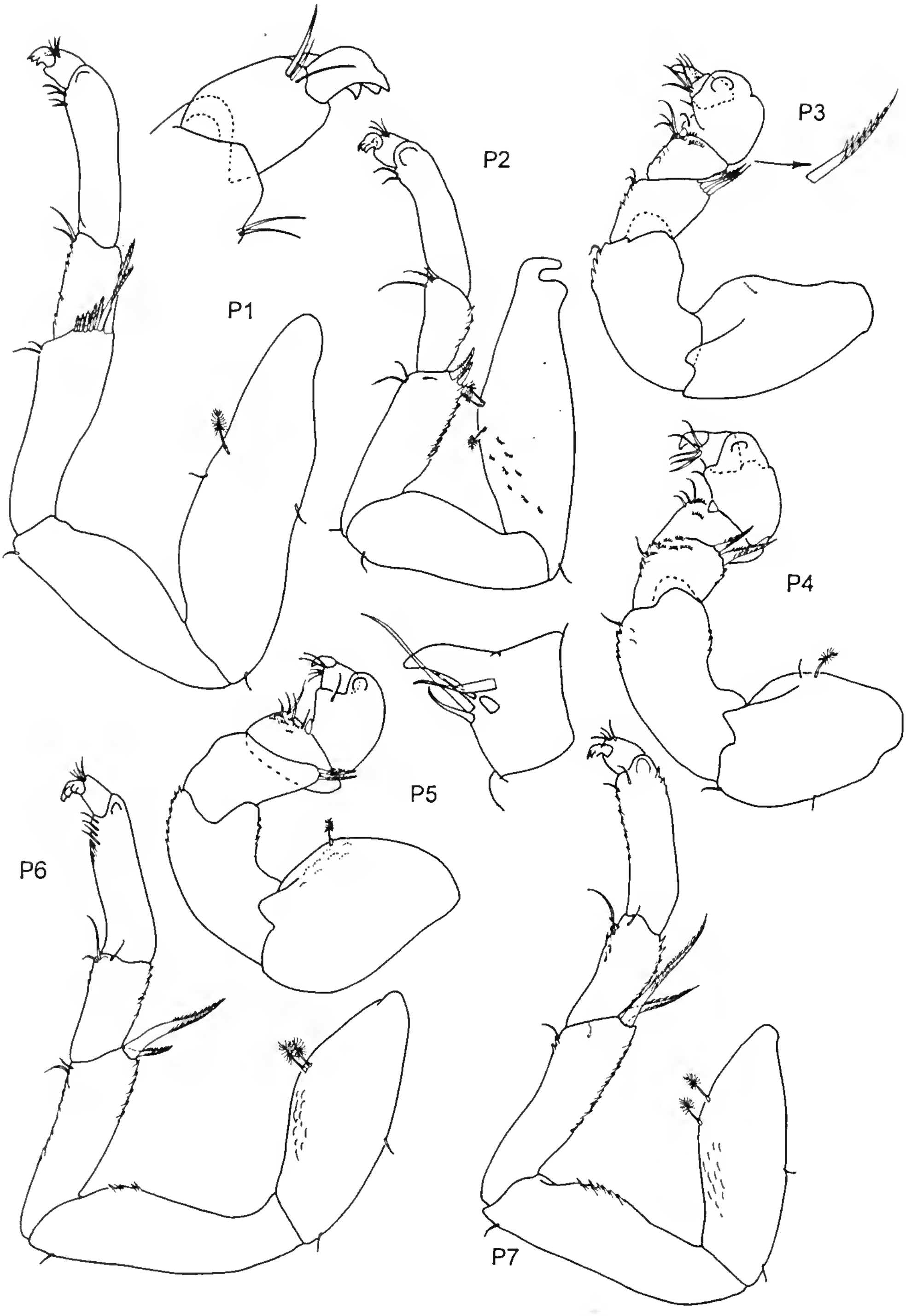

Figure 3. *Plakarthrium australiense* sp. nov. Holotype, NMV J47067: P1–P7, pereopods 1–7.

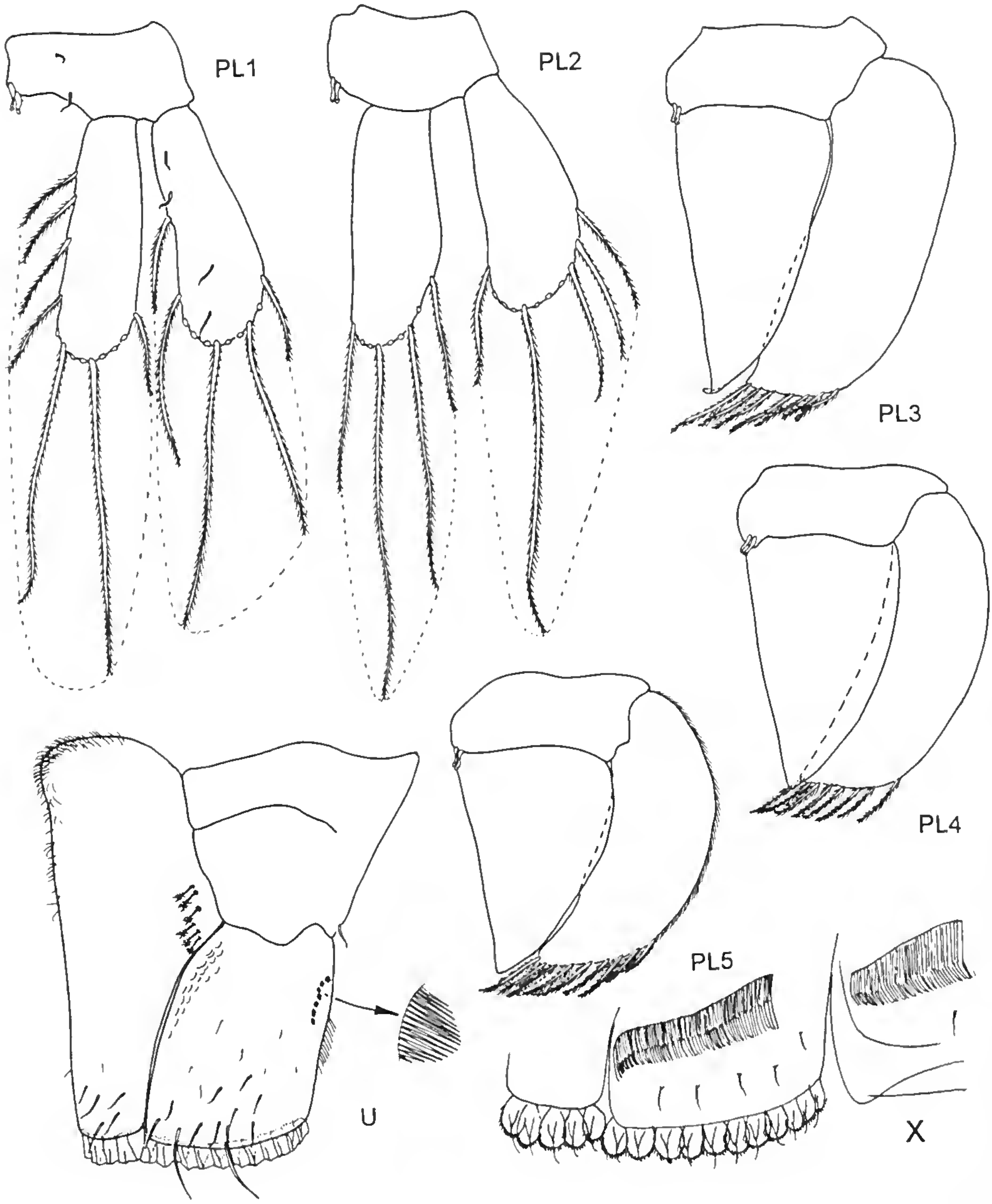

Figure 4. *Plakarthrium australiense* sp. nov. Holotype, NMV J47067: PL1–PL5, pleopods 1–5; U, right uropod; X, ventral view of margins of left uropod and coxa 7.

mm). Hogan I., Landing Beach (39°13′S, 146°59′E), ZMH K-39834 (1 male, 2.0 mm).

Victoria, 75 m SW of Eagles Nest, Venus Bay (38°40′S, 145°40′E), 8 m, NMV J23893 (1 male, 3.0 mm; 1 female, 2.0 mm, 2.0–3.0 mm). 1 km E of Harmers Haven, 500 m offshore (38°34′S, 145°40′E), 11 m, NMV J23896 (1 male, 2.1 mm; 1 female, 2.0 mm, 2.0–2.1 mm). Cape Paterson, E side (38°41′S, 145°36′E), 6–3 m, NMV J23895 (1 male, 1 female, 4 immature). 50 m S of Twin Reefs, Venus Bay (38°41′S, 145°39′E), 9 m, NMV J23894 (1 male, 2.0 mm). Wilsons Promontory, Hobbs Head, NE shore (39°2′S,

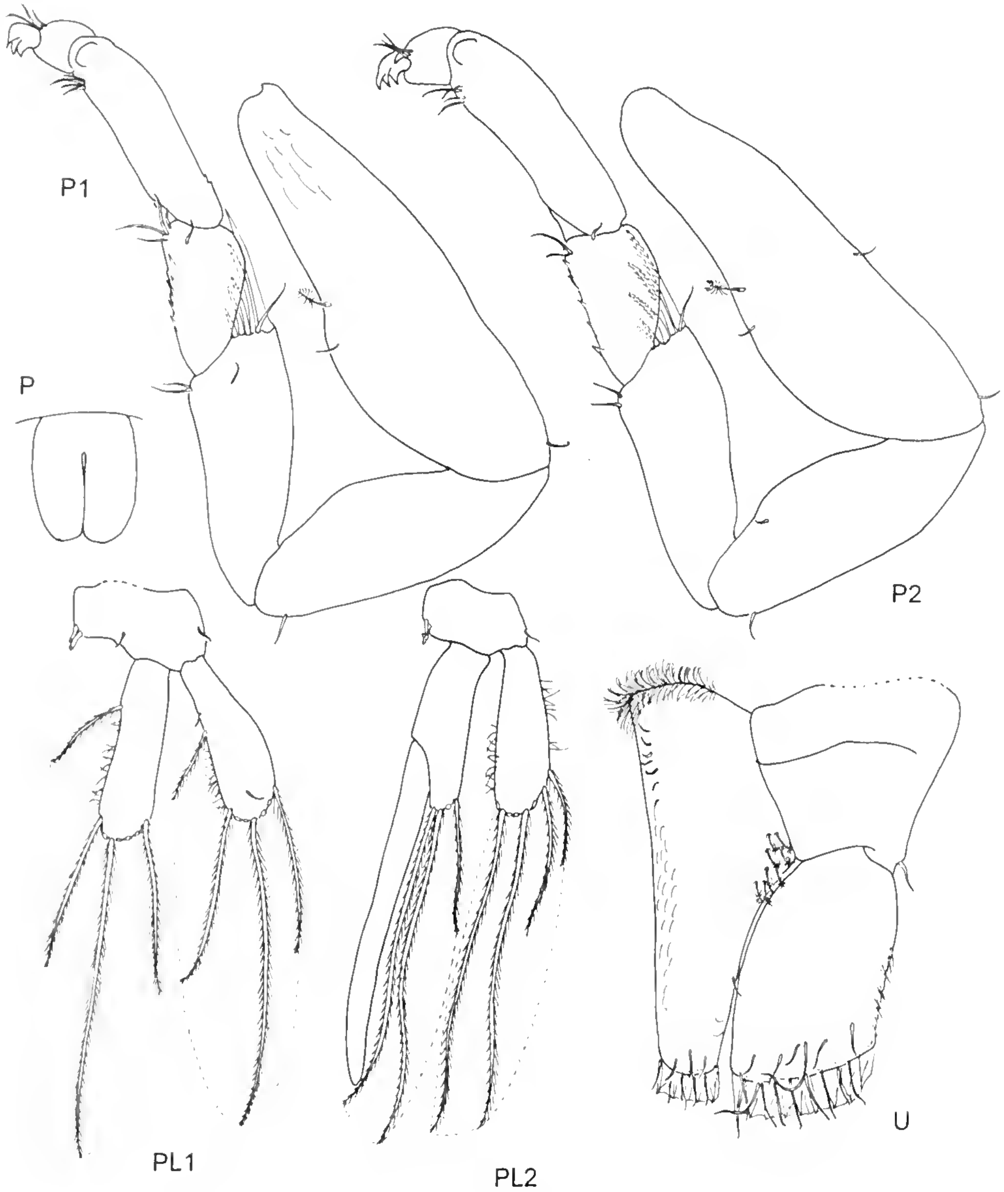

Figure 5. *Plakarthrium australiense* sp. nov. Paratype male, NMV J47021: P1, P2, pereopods 1, 2; PL1, PL2, pleopods 1, 2; P, penes; U, uropod.

146°28′E), NMV J47063 (1 female, 2.6 mm). Dutton Way, Portland (38°18.4′S, 141°36.4′E), 3 m, NMV J47065 (1 ovigerous female, 3.0 mm).

South Australia, Beachport, Snapper Point (37°29.3′S, 139°59.6′E), 6 m, NMV J20434 (1 female, 2.4 mm). NE side of Topgallant I., Investigator Group (33°43.00′S, 134°36.60′E), 12 m, NMV J23892 (1 male, 1.8 mm).

Western Australia, Breaksea I., SW corner (35°3.90′S, 118°2.50′E), 15 m, NMV J23887 (2 mancas, 1 male, 1.0–1.9 mm); NMV J23888 (1 immature; 1 female, 2.1 mm; 4 males, 1.9–2.0, 1.6–2.1 mm). King George Sound, N of False I. (35°0.70′S, 118°10.10′E), 27 m, NMV J23839 (4 males, 1.7–2.6 mm; 2 females, 1.9, 3.0 mm, 1.7–3.0 mm).

Other species. P. typicum. New Zealand. Auckland region, Tawharanui Peninsula, 6 m, *Carpophyllum flexuosum*, R. Taylor, 3 Jun 1992, NMV J37102 (14). Opposite Edward Percival Marine Station, Kaikoura (42°25′S, 173°42′E), 2 m, algae on boulders, G.C.B Poore et al., 23 Mar 1997 (stn NZ97-022), NMV J39561-J39654 (25). The Snares Islands, D.S. Horning. NMV J682 (male, with 3 slides); NMV J683 (several).

P. punctatissimum. South Georgia, Royal Bight, Moltke Harbour (54°30.58′S, 36°0.45′W), leaves of *Macrocystis*, Dr Karl von den Steinen, NMV J47311 (3 syntypes donated by Zoological Institute and Museum, Hamburg).

Diagnosis. Pleotelson with pleonite 1 fully indicated dorsally (not articulating), only pleonite 2 indicated laterally; pleotelson tapering to 80% of anterior width posteriorly. Distal margins of uropods aligned with margin of coxae. Coxae with acute posterior corners.

Description. Holotype female. Body c. 1.35 times as long as wide; ration of lengths of antenna 1 : head : pereon : pleotelson : uropod in midline = 13 : 18 : 33 : 27 : 9; widest at coxa 4 where each coxa comprises c. 27% of width. Head 1.9 times as wide as long, evenly rounded laterally, with excavated triangular front with triangular clypeus; eyes with c. 10 ommatidia. Pereonite 1 narrower than head; pereonite 3 widest; pereonites 6 and 7 shorter than others. Pleotelson with pleonite 1 fully indicated dorsally (not articulating), only pleonite 2 indicated laterally; pleotelson tapering to 80% of anterior width posteriorly; posterior notch semicircular, about third width of posterior margin, bordered by fine setae. Marginal articles of antennae 1 and 2 and coxae of pereopods 1–7 each with small triangular lobe on anterodistal and posterodistal corners; lower surface with flattened marginal surface (c. fifth of coxal length) defined proximally by a free skirt-like flange parallel to margin.

Antenna 1 peduncle with broad article 1, triangular article 2 and smaller tapering article 3 inserted in notch on lateral margin of article 2; flagellum of 2 articles, first ring-like with 2 pappose setae, second with 4 aesthetases and 5 simple setae. Antenna 2 peduncle with small articles 1 and 2; article 3 short, broad; article 4 4-sided; article 5 cylindrical, longer than wide, inserting on underside of margin of article 4; flagellum of 12 cylindrical articles.

Mandible incisor with 2–3 obscure blunt teeth; spine row of 3 spines; without palp or molar. Maxilla 1 with single lobe having 7 short apical robust setae. Maxilla 2 with single lobe with 8 short apical setae. Maxilliped without epipod; endite 4 times as long as wide, with 3 apical robust setae and 6 slender setae; palp with short article 1, longer article 2, substantially longer and broader article 3, convex and setose mesially, article 4 0.6 times as wide as article 4, article 5 as long as and shorter than article 4, with 9 mesial and distal setae.

Pereopod 1 elongate, longer than similar pereopod 2; pereopods 3–5 compact; pereopods 6–7 more elongate. Pereopod 1 merus with anterodistal row of complex setae; carpus half as long as merus, with minute tubercles on posterior margin; propodus narrow; dactylus compact with 3-toothed unguis. Pereopod 2 c. 85% length of peroopod 1; merus with 2 distal robust setae; compact dactylus with 3-toothed unguis. Pereopod 3 less than half length of pereopod 1; ischium with posterodistal denticles; merus with anterodistal row of complex setae; carpus almost triangular, with posterodistal short robust seta; propodus swollen; dactylus short, with simple curved unguis. Pereopods 4 and 5 similar to pereopod 3, 5 the most compact. Pereopod 6 about as long as pereopod 2; merus with 1 very stout and 1 shorter complex anterodistal setae; propodus with row of 4 simple posterior setae distally; short dactylus with 3-toothed unguis. Pereopod 7 longer but similar to pereopod 6.

Pleopod 1 peduncle twice as wide as long, with 2 coupling hooks on mesiodistal corner; rami attached on lateral half, not overlapping; endopod and exopod with 13 and 11 mesial and distal plumose setae respectively. Pleopod 2 peduncle wider than long, with 2 coupling hooks; rami not overlapping; endopod and exopod with 10 and 12 distal plumose setae respectively. Pleopod 3 with peduncle wider than long, with 2 coupling hooks; endopod triangular, without setae; exopod adjacent to endopod, with 7 distal plumose setae. Pleopods 4 and 5 similar to pleopod 3 but smaller and relatively wider; exopods with 8 and 9 distal plumose setae respectively.

Uropod peduncle strongly tapering; endopod attached mesially to peduncle, 2.5 times as long as greatest width, triangular in lateral view, with setose rounded margin anteriorly bordering respiratory orifice strongly produced vertically, with 6 pappose setae near articulation with peduncle, mesial margin straight, posterior margin curved and with c. 5 overlapping shingle-like scales; exopod c. 1.5 times as long as wide, with curved mesial margin against endopod, straight lateral margin, convex distal margin with c. 11 overlapping shingle-like scales.

Male. Differing slightly from female in some proportions. Pleotelson more elongate. Antenna 1 with article 2 of peduncle more rounded; flagellum with 6 aesthetases. Antenna 2 with flagellum of 10 articles. Pereopods 1 and 2 slightly more robust. Pleopod 2 endopod with appendix masculinis twice as long as endopod, attached two-thirds way along. Uropod with narrower peduncle and rami than in female. Penes oval, fused basally, attached to posterior margin of pereonite 7.

Distribution. Southern Australia, from central Victoria to southern Western Australia, including Tasmania; 6–49 m, on *Amphibolis, Ecklonia* holdfasts, red algae. No records from New South Wales (P. Berents, Australian Museum, pers. comm.).

Remarks. The Australian species differs from the other two species of *Plakarthrium* in having a clear demarcation dorsally of pleonite 1. In *P. typicum* (see Fig. 1d) and *P. punctatissimum* pleonite 1 is indicated only laterally. *Plakarthrium australiense* differs from *P. typicum*, which it most resembles, in having the pleotelson tapering rather than more or less parallel-sided, and the distal margins of the uropods aligned with the margin of the coxae. In *P. typicum*, the New Zealand species, the uropodal exopods are more oval and protrude beyond the end of coxae of pereopods 7 (Fig. 1d). *Plakarthrium typicum* lacks the acute corners of the coxae seen in the Australian species.

Plakarthrium australiense differs from *P. punctatissimum* more markedly. The latter has pleonites 1–4 indicated laterally and uropods produced more posteriorly.

The new species has a more pronounced lower marginal contact surface on coxae, antennae and uropods than the other species. This surface seals the underside of the animal and is made more effective by the skirt-like fringe along its inner edge.

Acknowledgements

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A PHYLOGENY OF THE LEPTOSTRACA (CRUSTACEA) WITH KEYS TO FAMILIES AND GENERA

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Abstract

Walker-Smith, G.K. and Poore, G.C.B., 2001. A phylogeny of the Leptostraca (Crustacea) with keys to families and genera. *Memoirs of Museum Victoria* 58(2): 383–410.

A phylogenetic analysis of the Leptostraca Claus, 1880 is undertaken using 32 of the 41 known species (including 4 undescribed species). The value of outgroups for deriving a plausible phylogeny in a group whose affinities remain contentious is discussed. A hypothetical ancestor is considered the best solution to the problem and states were scored based on general principles of crustacean evolution as evidenced by a wide variety of taxa. States of the 43 characters used in the analysis are detailed. The new phylogenetic hypothesis is compared with those of Olesen (1999). We conclude that a phylogeny based on species-level taxa and many informative characters is more likely to represent true evolutionary relationships than one based solely on genera and few characters. A new classification based on the phylogeny is derived with a new family, Paranebaliidae, being erected for *Paranebalia* Claus, 1880 and *Levinebalia* Walker-Smith, 2000. Nebaliopsididae Hessler, 1984 is supported for *Nebaliopsis* Sars, 1887. A restricted Nebaliidae Samouelle, 1819 for the remaining genera (*Speonebalia* Bowman, Yager and Iliffe, 1985, *Nebaliella* Thiele, 1904, *Dahlella* Hessler, 1984 and *Nebalia* Leach, 1814). *Sarsinebalia* Dahl, 1985 is synonomised with *Nebalia*. New keys and family and generic diagnoses are presented. All known species are listed with notes on distribution.

Introduction

Leptostracans are marine crustaceans of the malacostracan subclass Phyllocarida. Leptostracans have many derived features that separate them from other malacostraceans: the loss of ambulatory function of the thoracic limbs, which now only function in feeding, respiration and brood protection (Hessler and Schram, 1984; Dahl, 1976); a movable rostrum (Schram, 1986; Olesen, 1999); the scale-like ramus of the first antenna (Hessler and Schram, 1984; Olesen, 1999); uniramous antenna 2 (Hessler and Schram, 1984; Olesen, 1999); reduction of pleopods 5 and 6 (Hessler and Schram, 1984; Olesen, 1999); and direct larval development (Manton, 1934; Hessler and Schram, 1984).

The first species of the Order Leptostraca Claus, 1880 was described by Otto Fabricius in 1780, as *Cancer bipes* from east Greenland. Herbst (1796) later relegated this species to subspecific status, *Cancer gamarellus bipes* (cited in Sars, 1896). Leach (1814) introduced the genus *Nebalia* for *Cancer bipes* and a new British species *N. herbstii* Leach, 1814.

The genera of Leptostra are distributed differently. *Nebalia* is cosmopolitan. In contrast, *Levinebalia* Walker-Smith, 2000 has been recorded only in Australia and New Zealand. *Paranebalia* Claus, 1880 is found in central America, Bermuda, New Caledonia and Australia. *Nebaliella* Thiele, 1904 is confined to cold waters, being found in Antarctica, southern Australia and the high latitudes of the Northern Hemisphere. *Speonebalia* Bowman, Yager and Iliffe, 1985 has been recorded from only marine caves in the Turks and Caicos, and *Dahlella* Hessler, 1984 was collected from hydrothermal vents near the Galapagos. *Nebaliopsis* Sars, 1887 is a pelagic genus with a world-wide distribution. Leptostraceans have been recorded in waters from 1 m deep (Modlin, 1991) to more than 2000 metres (Fage, 1929). Most species occur in less than 200 metres. Water temperatures influence the length of time taken to reach maturity, the size at maturity and the incubation time of young (Macquart-Moulin and Castlebon, 1983).

Until now three families have been recognised: Nebaliidae Samouelle, 1819; Nebaliopsididae Hessler, 1984; and the Permian Rhabdouracidae Schram and Malzahn, 1984. Hessler's (1984) original spelling, Nebaliopsidae, is incorrect as family names based on genera ending in "*-opsis*" should end "-opsididae" (e.g. Sivertsen and Holthius, 1980). Seven nominal genera (*Nebalia;*

Paranebalia; Nebaliella; Dahlella; Sarsinebalia Dahl, 1985; *Speonebalia*; and *Levinebalia*) and 36 extant species are contained in the family Nebaliidae. Nebaliopsididae consists of the monotypic genus *Nebaliopsis*. *Rhabdouraea* Malzahn, 1962 is the monotypic fossil genus of Rhabdouraeidae.

Martin et al. (1996) reviewed the morphology and natural history of *Nebalia hessleri* Martin, Vetter and Cash-Clark, 1996 and provided a key to the extant families and genera of Leptostraca then accepted.

Olesen (1999) conducted a phylogenetic analysis of the seven extant leptostracan genera then known and described *Nebalia brucei* Olesen, 1999. Olesen questioned the monophyly of *Nebalia* and stated that as he could not find unique characters for this genus he could not exclude the possibility it is paraphyletic with *Sarsinebalia* and/or *Dahlella*. However, he maintained the status of these three genera.

The present study is a derived from an unpublished BSc(Hons) thesis (Walker-Smith, 1993) and presents a detailed phylogenetic analysis of the Leptostraca using 32 of the 41 known species (including four undescribed species). The monophyly of genera is tested and relationships between the included species deduced as far as possible. The value of certain characters in leptostracan systematics is discussed, as are the results of the phylogenetic analyses. The value of outgroups in deriving plausible phylogenies in a group whose affinities remain contentious is also discussed. A new classification based on phylogenetic principles is derived and new keys and new family and generic diagnoses are offered. All known species are listed with distributional notes.

Growth in Leptostraca

Transformations in the shape of the carapace, both pairs of antennae, pleopods, furca and other features are gradual from moult to moult in immature and subadult males and deviate from the female morphology, which generally remains unchanged except when reproductive (Dahl, 1985).

In species of Nebaliidae the terminal article of the juvenile thoracopod endopod is elliptic with thin marginal setae (Figs 4d, 4e). In sexually mature females carrying eggs or embryos, the entire endopod becomes elongated and the terminal article becomes enlarged, generally sitting at right angles to the thoracopod axis (Fig. 4l). The exterior and terminal edges of the terminal article possess a dense armature of plumose setae that are long, strong and curved, and interlock with those of opposite and neighbouring thoracopods to form the floor of the brood chamber. Embryos develop in the brood pouch and when the juveniles are ready to leave the long setae forming the floor of the chamber drop off, leaving behind a pattern of ridges and furrows that are the scars of setal attachment (Dahl, 1985). At this stage, the terminal article of the endopod differs so markedly from those of males and immature females that they could be presumed to belong to a different species (Dahl, 1985: Figs 6–10). The exopod and epipod do not change shape during this metamorphosis.

The eggs of *Nebaliopsis* are thought to be shed directly into the water (Cannon, 1931, 1960) but Brahm and Geiger (1966) reported *Nebaliopsis* with eggs developing under the carapace. These eggs appeared to be contained in a "basket formed by the large and setose posterior pair of thoracic appendages, that extend anteriad to the area of the mouth parts" (Brahm and Geiger, 1966: 41–42) and were shed when the specimens were placed in fixative.

Taxonomic confusion in Leptostraca

In the past, failure to recognise characters related to the sex and maturity of leptostracans resulted in taxonomic confusion. Thomson (1879) described *Nebalia longicornis* without taking sexual dimorphism into account and thus recognised the elongate flagellum of antenna 2 as a specific character rather than one of sexually mature males. Claus (1888) added to the taxonomic confusion by basing his identification of species on few morphological characters, most of which were growth- or sex-related and could not be used to successfully distinguish between genera or species. Claus's (1888) taxonomic concept of Leptostraca was followed by subsequent taxonomists (e.g., Thiele, 1904, 1905) and resulted in the erroneous assumption that each genus consisted of a few highly variable species. In particular, *Nebalia bipes* (Fabricius, 1780) and *N. longicornis* have been reported as geographically widespread while, in fact, each comprises several species. The subspecies described for each are likely to be separate species. Many records of nominal species in areas remote from their type locality probably refer to undescribed species. Fortunately, Dahl (1985) recognised the conservative nature of leptostracan morphology and redefined many species of *Nebalia* using new diagnostic characters. Dahl's assessment of the European shelf and Southern Hemisphere species incorporated the description of six new species of *Nebalia* (Dahl, 1985, 1990).

Analytical methods

Material for this study is deposited in Museum Victoria, Melbourne and type specimens of *Nebalia capensis* Barnard, 1914 were borrowed from the South African Museum, Cape Town. Museum Victoria collections include representative species of *Nebalia, Nebaliella, Paranebalia, Levinebalia* and *Nebaliopsis.* For most described species information relating to character states was obtained from the literature. Thirty-two species, including four undescribed species from southern Australia, were selected for phylogenetic analysis. Literature relating to six species and three subspecies of Nebaliidae was either not obtainable or provided insufficient diagnostic information; these taxa were omitted from the analysis. *Nebalia gerkenae* Haney and Martin, 2000, published later, was not included nor was the fossil family Rhabdouraeidae.

Cladistic analyses were used to generate trees of monophyletic groups as hypotheses of the relationship between the selected taxa. The relationships between genera were of greatest interest. Forty-three characters (all parsimony-informative) were scored for each taxon (Table 1) resulting in a data matrix of 32 leptostracan taxa plus a hypothetical ancestor described by 43 characters (Table 2). Characters were treated as unordered and unweighted.

The program PAUP* 4.0 (Beta 3 version for Windows) (Swofford, 1998 and updates) was used to establish relationships between taxa and produce a hypothesis from which a classification might be derived. A heuristic search was made using most of the default options in the PAUP block, except for the following commands: OUTROOT=MONOPHYL; ADDSEQ=RANDOM; NREPS=1000; NCHUCK=3; CHUCKSCORE =1; RANDOMIZE=TREES. The two most distant parsimony trees were calculated using the FILTER command and the characters states changes were mapped on one of these trees. A 50% majority-rule consensus tree of all trees was generated. Stability of the clades was assessed by bootstrap analysis (using the default settings) and a 50% majority-rule consensus tree of all bootstrap trees was constructed. Bremer support values were calculated for the two most distant trees using Auto Decay 4.0 (Eriksson, 1998) to assess the stability of the clades. Trees were illustrated using Tree View (Page, 1996).

Outgroups

Selection of an outgroup is the major problem encountered in the phylogenetic study of the Leptostraca. Leptostraca have been considered the most primitive subclass within the Malacostraca because they have a primitive caudal furca and polyramous phyllopodous (flattened, leaf-like) thoracic limbs used in filter feeding (Claus, 1888; Manton, 1934; Dahl, 1987, 1992). Hessler and Newman (1975) believed the relatively high number of segments and full complement of segmental appendages should also be regarded as primitive features. Dahl (1976) supported Hessler and Newman's (1975) view with the fact that while Phyllocarida were represented in the Lower Cambrian, no fossils of the other malacostracan subclass Eumalacostraca are known until the Devonian. However, Walossek (1999) disputed the existence of fossil malacostracans appearing in the Cambrian and stated that the only clear record appears after this time.

Other authors have placed the Leptostraca as a subclass in Phyllopoda with phyllopodous (polyramous and foliaceous) thoracopods thought to unite Branchiopoda, Leptostraca and Cephalocarida (in this class) (Milne Edwards, 1834; Schram, 1986). However Dahl (1987: 722) refuted this, stating that "polyramous thoracopods constitute a basic feature of maleostracan morphology and are therefore not a phyllopod synapomorphy." Dahl (1987) also highlighted the fact that while most genera of Leptostraca have foliaceous thoracopods those of *Paranebalia* are most similar to the stenopodous appendages of caridoid Malacostraca (e.g. Euphausiacea). Martin and Christiansen (1995) also detailed many differences between the fourth thoracopod of *Nebalia* (Leptostraca) and *Leptestheria* sp. (Branchiopoda: Conchostraca) including the size and arrangement of endites and the type and number of setae and their function. They too believed that the phyllopodous limb cannot be used as an indicator of phylogenetic affinity. This view was supported by independant evidence from an 18S rDNA study of Branchiopoda, Cephalocarida and Phyllocarida, seven other crustacean taxa and three arthropod outgroups (Spears and Abele, 1999). They concluded, with little doubt, that the presence of foliacous limbs does not define a monophyletic clade comprising branchiopods, cephalocarids and phyllocarids. They, like Dahl (1987) and Martin and Christiansen (1995), believed that foliaceous limbs have multiple origins.

While leptostracans appear to be the basal malacostracans they differ significantly from all other taxa in this class, making selection of an outgroup difficult. One potential sister taxon — the subclass Hoplocarida (Order Stomatopoda) — are morphologically so highly derived that

Table 1. Character transformations used in phyogenetic analysis of 32 species of Leptostraca. Each character is terminated by a colon and states (0, 1 …) separated by a semicolon. The 17 characters with CI=1 in tree 711 are indicated by #, those where 0.5<CI<1 by *.

1*. Rostrum, subterminal spine: absent (Fig. 1a) (0); present (Fig. 1b) (1).
2#. Rostral keel: absent (0); shorter than rostral flange (Figs 1a, d) (1); longer than rostral flange (Figs 1c, e) (2).
3*. Eye length: shorter than rostrum (0); longer than rostrum (1).
4#. Eye, supraocular scale: absent (0); longer or equal to length of eye (1); shorter than eye (Fig. 1f) (2).
5*. Eye surface: smooth (0); denticulate (Figs 1h, m) (1).
6. Eye dorsal papilla: absent (0); present (Fig. 1f) (1).
7*. Eye, ventral margin: not extremely curved (Fig. 1f) (0); extremely curved (Fig. 1k) (1).
8. Eye, dorsal margin: not dorsally convex (Fig. 1i) (0); dorsally convex (Fig. 1j) (1).
9#. Eye: not bilobed (Figs 1f, g) (0); bilobed (Fig. 1n) (1).
10. Eye: with ommatidia (Fig. 1g) (0); without ommatidia (Fig. 1i) (1).
11*. Antenna 1 anterodenticulate fourth article: absent (0); present (Fig. 1q) (1).
12#. Antenna 1 article 4: without robust setae (0); with 1 or more robust setae (Fig. 1p) (1).
13*. Antenna 1 of male: not swollen or a callynophore (0); a swollen callynophore (Figs 1c, 1d) (1); with dense field of aesthetases but not swollen (Fig. 2f) (2).
14*. Antenna 2 peduncle articles 3 and 4: not fused (Fig. 2a) (0); fused (Fig. 2b) (1).
15#. Antenna 2 peduncle articles 3 and 4: without two large cuticular outgrowths (0); with two large cuticular outgrowths (Figs 1r, 5a, b) (1).
16#. Antenna 2 peduncle surface: without denticles or minute cuticular outgrowths (0); with minute denticles or cuticular outgrowths (Figs 5a, b) (1).
17#. Antenna 2 of male: greatly elongate, reaching to the caudal furca (0); not greatly elongate, only half length of specimen (1).
18*. Antenna 2 peduncle article 2, dorsal surface: without spine (0); with spine (Fig. 2b) (1).
19. Mandible, article 2 of palp: with more than 2 setae (0); with 2 setae (1); with 1 seta (2).
20. Mandible palp, relative lengths of articles 2 and 3: 2 longer than 3 (0); 2 equal to 3 (1); 2 shorter than 3 (2).
21. Mandible, article 3 of palp: tapering distally (0); with parallel margins (1); expanded distally (2).
22. Mandible incisor teeth: 2 (Fig. 2h) (0); 1 (Fig. 2e) (1); absent (2).
23#. Molar accessory tooth/spine: absent (0); present (Fig. 2i) (1).
24#. Molar large accessory process: absent (0); present (Fig. 2e) (1).
25#. Molar process, setal brush: absent (0); present (Fig. 2e) (1).
26#. Maxilla 1 second endite: complex (Fig. 3a) (0); bilobed (Figs 3b, d) (1); elongate (Fig. 3g) (2); simple (Fig. 3c) (3); reduced (4).
27. Maxilla 2 endopod: biarticulate (0); uniarticulate (1).
28*. Maxilla 2 exopod: greater than or equal to half length of endopod (0); less than half length of endopod (1); absent (2).
29#. Thoracopod length: short, not extending well beyond the ventral margin of the carapace (Fig. 4a) (0); long, extending well beyond ventral margin of carapace (Fig. 1l) (1).
30*. Thoracopod exopod: heavily setose (Figs 4b, 4e) (0); with few setae (Fig. 4d) (1); with no setae (Fig. 4c) (2).
31#. Thoracopod exopod: without proximal lobe (Figs 4b–d) (0); with proximal lobe (Fig. 4e) (1).
32#. Thoracopod 2–5: epipod longer than exopod (Fig. 4d) (0); epipod shorter than exopod (Fig. 4b) (1); epipod absent (Fig. 4e) (2).
33#. Pleonite 4 posterior margin: smooth (0); crenate (saw-tooth) (Fig. 4a) (1).
34#. Pleonite 5 posterior margin: smooth (0); crenate (Fig. 4a) (1).
35#. Crenations on pleonites 6 and 7: absent (0); only on dorsal margin (Fig. 1l) (1); over entire margin (Fig. 4a) (2).
36. Pleonite crenation: absent (0); pointed (1); blunt (2).
37*. Pleonite size: pleonite 6 and pleonite 7, each equal in length to pleonite 5 (0); pleonite 6 and pleonite 7, each longer than pleonite 5 (1).
38. Pleopods 1–4 peduncles margins: smooth (0); crenate (Fig. 3i) (1).

Table 1. — continued.

39\. Pleopod 1, ratio of lengths of comb-row to exopod: comb-row absent (0); less than or equal to half length of exopod (1); greater than half length of exopod (Fig. 4k) (2).
40*. Pleopod 2–4 exopod lateral margin: with smooth setae not in pairs (Fig. 4i) (0); with smooth setae in pairs (Fig. 4h) (1).
41*. Pleopod 5: shorter than pleopod 6 (0); longer than pleopod 6 (1).
42*. Pleopod 6: biarticulate (0); uniarticulate (1).
43*. Carapace with: posterodorsal marginal spines (Fig. 3e) (0); without posterodorsal marginal spines (1).

Table 2. Character matrix used in phylogenetic analysis of the Leptostraca

Character numbers	1234567891	1234567892	1234567893	1234567894	123
Hypothetical ancestor	0000000000	00?000000?	?0??0?00?0	00????0000	00?
Nebaliopsis typica	0000000000	10?000?000	0200041202	0000000000	101
Levinebalia fortunata	1000000100	1011111020	?100021010	0100000001	011
Levinebalia maria	1000000100	1011111021	0100021010	0100000011	011
Paranebalia belizensis	1000100100	1011101020	010?120010	01??11?121	011
Paranebalia longipes	1000100100	1011101000	0101120010	0100111121	011
Paranebalia sp. A	1000100100	1011101021	0101121010	0100111121	011
Speonebalia cannoni	0010000101	000000?02?	?200031101	0011210101	000
Nebaliella antarctica	0210001101	0000000101	2010011000	1211211120	100
Nebaliella brevicarinata	0210001101	0000000121	0010010000	12112?11?0	100
Nebaliella caboti	0210001101	000000011?	?010011000	12112?1?20	100
Nebaliella declivatas	0210001101	0000000112	0010011000	1211211010	100
Dahlella caldariensis	0012101001	00?100?1?2	2000000101	00112?1121	011
Nebalia antarctica	0102010100	0101000112	2000000001	001121??21	011
Nebalia bipes bipes	0102000100	0101000122	2000000001	001122??21	011
Nebalia borealis	0102000100	0101000121	1000000001	001121??21	011
Nebalia brucei	0102000100	0101000110	2000000001	0011211021	011
Nebalia cannoni	0102010100	0101000102	2000000001	001122??21	011
Nebalia capensis	0102000100	0101000111	2000000001	0011221021	011
Nebalia clausi	0102000100	0101000121	2000000001	001122??21	011
Nebalia daytoni	0101000110	0121000011	2000000001	0011211?21	011
Nebalia falklandensis	0102010100	0101000110	2000000001	001122??21	011
Nebalia herbstii	0102000100	0101000122	2000000001	001122??21	011
Nebalia hessleri	0102000100	0101000121	2000000001	0011211121	011
Nebalia lagartensis	010?000100	0101000?0	1000000001	001121??21	011
Nebalia longicornis	0?02010100	0101000112	1000000001	001122??21	011
Nebalia marerubri	0102000100	0101000112	1000000001	0011211121	011
Nebalia patagonica	0?02010100	0101000112	2000000001	001122??21	011
Nebalia strausi	0102000100	0101000?2?	0000000001	001121??21	011
Nebalia sp. A	0101000110	0121000012	1000000001	0011211001	011
Nebalia sp. B	1102000000	0121000112	2000000001	0011211001	011
Nebalia sp. C	0102010100	0101000122	2000000001	0011211121	011
Sarsinebalia typhlops	1102000001	0101000?12	0000000101	00??22??01	011

sufficient characters relevant to generic differentiation in Leptostraca do not exist. Similarly, resorting to the fossil orders of Phyllocarida (e.g. Archaeostraca) provide few characters of value.

Olesen's (1999) phylogenetic anaylsis of seven leptostraean genera resulted in two hypotheses. In one, he used Anostraca (Branchiopoda) and Mysidacea (Malacostraca) as outgroups without justifying these choices. In the other, he used Mysidacea alone. Specific outgroups such as these pose real problems. The presumed shared similarities may not be homologous so it is doubtful whether the same characters are being scored for the in- and outgroups. Besides, they often do not possess relevant characters.

Olesen's (1999) use of Mysidacea as an outgroup was based on Cannon's (1927) view that the thoracopods of *Paranebalia* link malacostracans, such as mysids, with *Nebalia*. Numerous authors have viewed phyllocarids as malacostracans (27 papers cited by Spears and Abele, 1999). Mysidaceans themselves are a problematic group of two distinct clades. Although mysidaceans have until recently been treated as members of Peracarida there is now increasing morphological and molecular evidence that while one clade, Lophogastrida, is a member of Peracarida the other, Mysida, is a member of Eucarida (Watling, 1999; Jarman et al., 2000). Olesen did not differentiate the two.

Curiously, Sars (1887) suggested that body divisions, antennules, antennae, mouthparts, pleopods, caudal limbs, and development of *Nebalia* and Copepoda, especially Harpacticoida Sars, 1903 were homologues. Sars's similarities could be further evidence of the high level of convergence within the Crustacea or symplesiomorphies shared by these and possibly other groups.

Faced with the conditions that the closest relatives of leptostracans do not have similar morphologies, and that similarities between leptostracans and other less related taxa are most likely due to convergences, we were disinclined to chose any one or set of outgroups. The best alternative for polarising character states seemed to be to use a hypothetical ancestor. We used general principles of crustacean evolution as evidenced by a wide variety of taxa and were able to score 31 of 43 characters for the hypothetical ancestor. These included characters where the presence of a structure is confined to some leptostracans, characters involving fusion or loss of articles from a multiarticulate state, characters involving loss of teeth or setae which are generally numerous in the other Crustacea, and characters involving reduction in size or complexity.

Character descriptions

The 43 characters are examined in turn with its reasoned state of the hypothetical ancestor. All characters are unordered and of equal weight (Tables 1, 2). Character descriptions and figures are for females except where male characters are individually specified.

Although Dahl (1985) defined many new characters for *Nebalia*, most of these have not been used. Dahl's (1985) ratio characters (e.g. length/width characters) could only be scored from literature descriptions, generally of a single specimen. The ratios varied continously across all taxa and it was not possible to assign taxa to a few distinct classes.

Setal characters. Dahl (1985) stated that characters related to numbers of spines (= robust setae) and setae are not of primary importance as they are related to growth of the individual. He used rearing experiments to show growth related variation in the moults of six females and five males of *Nebalia pugettensis* (Clark, 1932). While his experiments show a correlation between the carapace length and the number of spines and setae on four appendages (antenna 1, pleopod 1 exopod, pleopod 5 and furca) (Dahl, 1985: Table 1), we believe that for phylogenetic purposes setae may be useful if comparisons were made between ovigerous or brooding females but none is used here.

Rostrum. Dahl (1985) recognised the presence or absence of a ventral subterminal rostral spine (character 1) as taxonomically informative. We hypothesise the possesion of a rostral spine is apomorphic as it appears to be a character unique to the Leptostraca. All species of *Paranebalia* and *Levinebalia* and *Sarsinebalia typhlops* (Dahl, 1985) and *Nebalia* sp. B possess a rostral spine (state 1: Figs 1b, d).

The presence of a keel on the ventral face of the rostrum (the rostrum minus the keel is sometimes referred to as the rostral flange; Fig. 1c arrow pointing to flange) is a character unique to leptostracans (character 2) and so is considered apomorphic. The keel is absent in *Nebaliopsis, Paranebalia, Levinebalia, Speonebalia* and *Dahlella* (state 0). Dahl (1985, 1990) did not draw the rostral keel for any of the species he described but as all other species of *Nebalia* have a keel, we assume this was an oversight. We have scored all *Nebalia* as having a keel shorter than the rostrum (state 1: Figs 1a, 1d). The possession of a keel longer than the rostrum is an autapomorphy of the genus *Nebaliella* (state 2: Figs 1c, e).

Eye. Speonebalia, Nebaliella and *Dahlella* have eyes longer than the rostrum (character 3, state 1: Fig. 1e).

The length of the supraocular scale was considered diagnostic by Dahl (1985) (character 4). *Nebaliopsis, Paranebalia, Levinebalia, Speonebalia* and *Nebaliella* all lack supraocular scales (state 0). *Dahlella* and almost all species of

Nebalia have a supraocular scale shorter than the eye (state 2: Figs 1f, i). *Nebalia daytoni* Vetter, 1996 and *Nebalia* sp. A have supraocular scales longer than the eye (state 1: Fig. 1n). Following the ontogenetic precedence criterion, the absence of the supraocular scale in juveniles of *Dahlella caldariensis* Hessler, 1984 suggests its presence is apomorphic.

Small teeth or denticles over the surface of the eye appear in *Paranebalia* (Fig. 1h) and *Dahlella* (character 5, state 1: Fig. 1m). Hessler (1984) suggested the teeth may be used by *Dahlella caldariensis* to scrape for food such as bacterial encrustations. The teeth on the surface of the eye may not be homologous in *Dahlella* and *Paranebalia*. As the teeth do not appear in the juveniles of *Dahlella* they are thought to be apomorphic.

The possession of a papilla or dorsal outgrowth on the eyestalk is a feature found in approximately one-third of species of *Nebalia* (character 6, state 1: Figs 1f, 1j) and is thought to be apomorphic.

Dahl (1985) recognised eye shape as a valuable diagnostic feature (characters 7, 8 and 9). The eyes of *Nebaliella* and *Dahlella* have an extremely curved ventral margin (character 7, state 1: Figs 1k, 1m). The eye of the first instar larva of *Dahlella* is almost square, thus the ontogenetic evidence suggests the elongate, curved eye of *Dahlella* and *Nebaliella* is the derived state.

The eyes of *Sarsinebalia typhlops*, *Nebalia* sp. B, *Dahlella* and *Nebaliopsis* are not dorsally convex like those of all other Leptostraca (character 8, state 0). The eyes of *Sarsinebalia typhlops* are almost square (Fig. 1i) (but have also been described as almost circular [Dahl, 1985]), and the eyes of *Nebalia* sp. B are triangular (Fig. 1g). The eyes of *Dahlella* are dorsally angular (Fig. 1m), while the eyes of *Nebaliopsis* are square to rectangular. The eyes of *Nebaliopsis* are very similar in shape to that of the first instar larva of *Dahlella*. *Nebalia daytoni* and *Nebalia* sp. A have an unusual bilobed eye (character 9, state 1: Fig. 1n) shared with no other species.

The presence of ommatidia in the eye is common to most species of Leptostraca (character 10, state 0). *Speonebalia*, *Nebaliella*, *Dahlella* and *Sarsinebalia typhlops* all lack ommatidia (state 1). Embryos of the genus *Nebalia* possess dark eye pigment (Sars, 1896; Manton, 1934) thus, following the ontogenetic precedence criterion, the presence of ommatidia is considered primitive.

Antenna 1. Modlin (1991) referred to the anterodenticulate fourth article of antenna 1 as a lateral flange but our observations reveal the flange lies mesially (character 11, state 1: Fig. 1q). This mesiodistal flange is found in *Levinebalia*, *Paranebalia* and *Nebaliopsis* (state 1). The flange is lacking in all other Leptostraca and assumed so for the hypothetical ancestor (state 0: Fig. 1p).

The first four articles are referred to as the peduncle. The last peduncle article (article 4) bears the scale and flagellum The arrangement of setae on the fourth peduncle article is usually linear with 1–4 simple robust setae in the anterodistal corner and a variable number of thin plumose setae (Fig. 1p). In some species and the hypothetical ancestor robust setae are absent (character 12, state 0: Fig. 1q). Rearing experiments (Dahl, 1985) showed that change in setal formula is growth related but the presence or absence of robust setae, not their number, is a valid character. Only *Nebalia* has robust setae on antenna 1 (state 1).

Mature males of *Levinebalia* and *Paranebalia* possess numerous aesthetases on a swollen flagellum of the first antenna (character 13, state 1: Fig. 2d), this chemoreceptive callynophore is found on many eucarid and peracarid Crustacea (Lowry, 1986). Immature males of *Levinebalia* and *Paranebalia* have a swollen flagellum with few aesthetases (Fig. 2c). Abundant aesthetases on a non-swollen flagellum (state 2: Fig. 2f) occur in *Nebalia daytoni*, *Nebalia* spp. A and B. This is similar to that found in *Nebalia pugettensis* (originally described as *Epinebalia pugettensis*) but this species was excluded from the analysis.

Because the callynophore is so widespread in Crustacea we were unable to score the hypothetical ancestor; the structure may be independently derived in many taxa.

Antenna 2. The peduncle of antenna 2 bears the flagellum. The peduncle has a maximum of four articles but fusion of articles does occur. The fusion of articles 3 and 4 peduncle is an apomorphic state found in *Nebalia*, *Paranebalia*, *Levinebalia* and *Dahlella* (character 14, state 1: Fig. 2b). In *Nebaliopsis*, *Nebaliella* and *Speonebalia* the articles are not fused (state 0: Fig. 2a).

Fused articles 3 and 4 of antenna 2 peduncle of *Paranebalia* possess protuberances or elongate outgrowths (usually one or two) on the anterior surface (character 15, state 1: Figs 1r, 5a and 5b; arrows point to protuberances).

Minute denticles or cuticular outgrowths appear over the surface of fused peduncle articles 3 and 4 and the flagellum in *Levinebalia* (character 16, state 1: Fig. 5a). The flagellum of male *Nebalia* and *Nebaliella* is greatly elongated, often extending past the caudal furca (character 17, state 0). The flagellum length of male *Speonebalia*, *Dahlella caldariensis* and *Nebaliopsis* is unknown as mature males have not been identified. The length of the flagellum does not differ between males and females in species of *Paranebalia* and *Levinebalia*. The presence of a dorsal spine on article 2 (character 18: Fig. 2b) is recorded for most species of *Nebalia* and *Nebaliella*.The hypothetical ancestor is assumed to have a simple peduncle of 4 articles, without cuticular outgrowths or a dorsal spine.

Mandible. The number of setae on article 2 of the mandibular palp (character 19: Fig. 2g) can be diagnostic (Hessler, 1984). However, Dahl (1985) suggested that there is a growth-related increase in the number of spines (robust setae) and setae throughout the Leptostraca. Therefore, although setal characters may be useful for supplementing other morphological features, leptostracan "chaetotaxonomy" can never be of primary importance. *Levinebalia*, most species of *Paranebalia*, *Speonebalia*, *Dahlella*, *Nebaliella brevicarinata* Kikuchi and Gamô, 1992 and half of the species of *Nebalia* have one seta on article 2 of the mandible palp.' Half of the species of *Nebalia* have two setae as does *Nebaliella caboti* Clark, 1932 and *N. declivatas* Walker-Smith, 1998. *Paranebalia longipes* (Willemöes-Suhm, 1875) has more than two setae, as does *Nebaliella antarctica* Thiele, 1904 and *Nebalia cannoni* Dahl, 1990.

The length of article 2 of mandibular palp relative to article 3 was recognised by Dahl (1985) as a diagnositic character (character 20). The plesiomorphic state is unknown.

The shape of article 3 of the mandibular palp was considered by Dahl (1985) to be a diagnostic feature of leptostracans (character 21: Fig. 2g). This is a variable character within *Nebalia*, which displays all three states. *Nebaliopsis*, *Levinebalia*, *Paranebalia*, *Speonebalia* and most species of *Nebaliella* have palps that taper distally (state 0: e.g., Fig. 2g). The palp of *Nebaliella antarctica* and *Dahlella* is expanded distally (state 2).

The mandible incisor of *Nebaliella* has two teeth (character 22, state 0: Fig. 2i). Dahl (1985, 1990) did not draw or mention the mandible incisor in his descriptions of *Nebalia*. However, as all other described species and the undescribed species of *Nebalia* from Australia have two teeth. We have scored all species described by Dahl as having two teeth (state 0: Fig. 2h). *Levinebalia*, *Paranebalia* and *Dahlella* have one tooth (state 1: Fig. 2e). The incisor is absent in *Speonebalia* and *Nebaliopsis* (state 2).

The molar of *Nebaliella* has an accessory tooth or spine (character 23, state 1: Fig. 2i; see arrow). No other leptostracan has this character state. The molar of *Paranebalia* alone has a large accessory process (character 24, state 1: Fig. 2c; see arrow). The presence of a setal brush on the molar process (character 25, state 1: Fig. 2e) is recorded only for *Paranebalia*. The hypothetical ancestor is assumed to have a setose mandibular palp, well-developed molar and toothed incisor.

Maxilla 1. In all species of Nebaliidae, including *Paranebalia* and *Levinebalia*, the palp of maxilla 1 is long and well-developed as in the hypothetical ancestor. In Nebaliopsididae it is reduced to a small stub.

There are four different types of second endites found on maxilla 1 (character 26); complex (state 0: Fig. 3a) found in *Nebalia* and *Dahlella*; bilobed (state 1: Figs 3b, d) in *Nebaliella*; elongate (state 2: Fig. 3g) in *Paranebalia* and *Levinebalia*; simple (state 3: Fig. 3e) only in *Speonebalia*. The second endite is reduced in *Nebaliopsis* (state 4). The state in the hypothetical ancestor could not be determined.

Maxilla 2. The maxilla 2 endopod is uniarticulate (character 27; state 1) in *Nebaliopsis*, *Nebaliella* (except *N. brevicarinata*), *Paranebalia* sp. A, *Levinebalia* and *Speonebalia*. This is thought to represent the derived state.

The length of the exopod of maxilla 2 relative to the endopod is informative (character 28). For *Speonebalia*, *Dahlella* and *Sarsinebalia typhlops* the maxilla 2 exopod is less than half the length of the endopod (state 1). *Nebaliopsis* does not have an exopod (state 2). All other genera have an exopod more than half the length of the endopod (state 0).

Thoracopods. The length of the thoracopods is the most obvious feature diagnosing genera of leptostracans (character 29). All genera except *Paranebalia* and *Levinebalia* have foliaceous thoracopods that do not extend well beyond the ventral margin of the carapace (state 0: Fig. 4a). The thoracopods of *Paranebalia* and *Levinebalia* extend well beyond the ventral margin of the carapace (state 1: Fig. 11).

Thoracopod exopods are densely setose (character 30) in *Paranebalia*, *Levinebalia* and *Nebaliella* (state 0: Figs 4b, 4c). The exopods have few setae in *Nebalia* (state 1: Fig. 4d), *Dahlella* and *Speonebalia* and no setae in *Nebaliopsis* (state 2: Fig. 4e).

Thoracopod exopods of *Nebaliella* have a proximal lobe (character 31, state 1: Fig. 4e) not seen in other Leptostraca.

All genera except *Nebaliella* possess thoracopodal epipods (character 32, state 2) whose length relative to that of the exopod is informative. *Paranebalia* and *Levinebalia* have relatively small epipods (state 1: Fig. 4b) compared to those of *Nebaliopsis, Speonebalia, Dahlella* and *Nebalia* which are longer than the thoracopodal exopod (state 0: e.g. Fig. 4d).

Pleonites. All species of *Nebaliella, Speonebalia, Dahlella* and *Nebalia* have a crenate posterior margin on pleonites 4 and 5 (characters 33 and 34: Fig. 4a). In his descriptions of *Nebalia* species Dahl (1985, 1990) did not mention the form of pleonites 4 and 5 but as these pleonites are crenate in all other *Nebalia* species we have assumed this is also the case in Dahl's species. The posterior margins of all pleonites of *Nebaliopsis* are smooth.

Pleonites 6 and 7 of *Paranebalia* are crenate only along the dorsal margin (character 35, state 1: Fig 1l). The pleonite margins of *Nebaliopsis* and *Levinebalia* are smooth (state 0). Pleonites 6 and 7 of *Nebaliella, Speonenbalia, Dahlella* and *Nebalia* are crenate along the entire margin (state 2).

The shape of pleonite crenations is a useful species-level character (character 36). Species of *Nebalia* may have either crenations that are pointed or blunt. *Nebalia* sp. A has both blunt and pointed crenations along the same pleonite margin (Fig. 3f), but as this is an autapomorphy for the purpose of the analysis it has been scored as having only pointed crenations.

For most Leptostraca pleonites 6 and 7 are much longer than pleonite 5 (character 37, state 1). However for *Levinebalia, Speonebalia* and *Nebaliopsis* pleonite 5 is approximately the same length as pleonites 6 and 7 (state 0).

Pleopods. The posterior margin of pleopods 1–4 of *Paranebalia, Speonebalia* and some species of *Nebalia* are crenate (character 38, state 1: Fig. 3i).

The comb-row or "spine-row", considered by Dahl (1985: pp. 142, 163) to be a generic character, consists of a row of short, pinnate setae along the exterior margin of the exopod of pleopod 1 (Figs 4k, 6a and 6b). As Dahl (1985) created a new genus for *Sarsinebalia typhlops* which does not possess a comb-row on its first pleopod. The length of the comb-row relative to the exopod is diagnostic (character 39). For all species of *Nebalia* except *Nebalia* spp. A and B the comb-row is greater than half the length of the exopod (state 2). *Nebalia* spp. A and B do not possess a comb-row (state 0: Fig. 4i). The comb-row of *Levinebalia* Walker-Smith, 2000 and *Nebaliella declivatas* is less than half the length of the exopod (state 1: Fig. 4j).

All genera except *Nebaliella* and *Nebaliopsis* have pairs of smooth setae along the exterior margin of the exopod of pleopods 2–4 (character 40, state 0 (not in pairs): Fig. 4g. state 1: Figs 3i, 4h).

For all genera except *Nebaliella* and *Nebaliopsis* the ramus of pleopod 5 is longer than the ramus of pleopod 6, measured along the midline (character 41, state 0). We have scored pleopod 5 longer than 6 as the plesiomorphic state

Pleopod 6 may be uni- or biarticulate, a character first used by Olesen (1999). *Nebaliopsis, Speonebalia* and *Nebaliella* all have a biarticulate pleopod 6 (character 42, state 0: Fig. 4l). All other Leptostraca have a uniarticulate pleopod 6 (state 1). The biarticulate condition is thought to be plesiomorphic.

Carapace. The posterodorsal margin of the carapace of *Nebaliella* has small denticles (character 43, state 0: Fig. 3e). This character state is not seen in other Leptostraca and the plesiomorphic condition is unknown.

Results

Cladograms

The phylogenetic program PAUP* 4.0 revealed 1527 equally parsimonious trees of 114 steps. Tree 711 and tree 340 were the two most distant parsimony trees (found using the FILTER command). Their statistics are: consistency index (CI) = 0.52; homoplasy index (HI) = 0.48; retention index (RI) = 0.79; rescaled consistency index (RC) = 0.41.

Bremer support values were calculated for tree 711 (Fig. 6) and tree 340. Branch lengths for tree 711 were calculated in PAUP* 4.0 and are presented diagramatically (Fig. 7). Characters with CI=1 are also plotted on this tree.

A 50% majority-rule with bootstrap values and the percentage of parsimony trees retaining nominal clades is also presented (Fig. 8).

Characters defining the clades of parsimony tree 711.

As trees 711 and 340 retain the same character state changes at the major (generic level) nodes, only tree 711 is discussed in detail (Figs. 6 and 7) with character state changes (Table 3).

Clade 63 contains all Recent Leptostraca and is supported by three synapomorphies from the characters used (plus those characters generally stated to define the taxon).

Table 3. Character transformations at all nodes in tree 711 (one of 1527 parsimonious trees). Character numbers follow each clade labelled in Fig. 6. Character numbers alone indicate a change from state 0 to state 1, – indicates a reversal from state 1 to 0, and superscripts indicate a change from one state (default 0) to another. Characters in bold have CI=1.

Clade number or taxon	Characters changing
Clade 63	11, 22^2, 27
Nebaliopsis typica	**26**^{4}, 28^2, 302, **41**
clade 62	8, 19^2, 36, 38, 40
clade 37 (Paranebaliidae)	1, 13, 14, **15**, **17**, 22$^{2>1}$, **26**^{2}, **29**, **32**, 42
clade 34 (*Levinebalia*)	**16**, –36, –38
Levinebalia maria	20, 39
clade 36 (*Paranebalia*)	5, **24**, **25**, **35**, 37, 39^2
clade 35	–27
Paranebalia longipes	19$^{2>0}$
Paranebalia sp. A	20
clade 61 (Nebaliidae)	3, 10, –11, 20^2, 30, **33**, **34**, **35**^{2}, –43
Speonebalia cannoni	**26**^{3}, 28
clade 60	7, 18, 22, 37, 39^2
clade 40 (*Nebaliella*)	**2**^{2}, **23**, **26**, 30, **31**, **32**^{2}, –40, 41
clade 38	20$^{2>1}$
Nebaliella antarctica	19$^{2>0}$, 21^2
Nebaliella brevicarinata	–27
clade 39	19$^{2>1}$, –38
Nebaliella declivatas	39$^{2>1}$
clade 59	**4**^{2}, 14, 21^2, –27, 42, 43
Dahlella calderiensis	5, –8, 28
clade 58 (*Nebalia*)	**2**, –3, –7, –10, **12**
clade 51	19$^{2>1}$
clade 43	6
Nebalia sp. C	19$^{1>2}$
clade 41	36$^{1>2}$
Nebalia cannoni	–19
Nebalia longicornis	21$^{2>1}$
Clade 49	–38
clade 45	20$^{2>0}$
clade 44	36$^{1>2}$
Nebalia capensis	20
Nebalia falklandensis	6
clade 48	13^2, 39$^{2>0}$
clade 46	**4**$^{2>1}$, **9**, –18
Nebalia daytoni	20$^{2>1}$, 39^2
Nebalia sp. A	21$^{2>1}$
clade 47	1, –8
Sarsinebalia typhlops	10, 13$^{2>0}$, 21$^{2>0}$, 28, 36$^{1>2}$
Nebalia marerubri	21$^{2>1}$
clade 57	36$^{1>2}$
clade 56	20$^{2>1}$
clade 55	36$^{2>1}$
clade 54	21$^{2>0}$
clade 53	21
Nebalia lagartensis	–20

Nebaliopsis typica Sars, 1887 (Nebaliopsididae) is defined by four apomorphies (from the characters used): maxilla 1 second endite reduced; maxilla 2 exopod absent; thoracopod exopod with no setae; pleopod 6 shorter than pleopod 5. At least 14 more character states define *Nebaliopsis typica* but these unique states are uninformative and had been excluded a priori: molar process reduced; maxilla 1 palp reduced to a small stub (but may terminate in long seta); maxilla 1, second endite reduced; maxilla 2 with endites 2–4 reduced in size and setation; maxilla 2 nearly as large as thoracopod 1; thoracopod 1 differing greatly from thoracopods 2–7, somewhat maxillipediform; thoracopod endopod not articulate; thoracopods well spaced; pleopods 2–4 exopod paddle-like, outer margin strongly curved with numerous small spinules; carapace not emarginate; carapace with network pattern of sculpturing; body cuticle and carapace thin, membranous; caudal furca leaf-like, broadest midway; entire length of mature female greater than 20 mm.

Clade 62 contains all Leptostraca except Nebaliopsididae. This clade occurs in all shortest trees and has a Bremer support value of 2 and 72% bootstrap support. Five synapomorphies define this clade although none has CI=1.

Clade 37, *Paranebalia* plus *Levinebalia*, occurs in all trees and has a Bremer support value of 3 and 85% bootstrap support. The clade is defined by ten synapomorphies, five with CI=1: antenna 2 articles 3 and 4 with two large cuticular outgrowths; antenna 2 of male not greatly elongate, only half length of specimen; maxilla 1 second endite elongate; thoracopods long, extending well beyond the ventral margin of the carapace; thoracopod 2–5 with epipod shorter than exopod. This clade is also defined by the character state — males with swollen callynophore — but as this character is multistate it has CI=0.67.

Clade 34 (*Levinebalia*), evident in 100% of trees, has Bremer support of 1 and 77% bootstrap support. It is defined by three synapomorphies: antenna 2 peduncle and flagellum surface with minute denticles or cuticular outgrowths (CI=1); pleonite margins smooth (reversal); pleopods 1–4 peduncles with margins smooth (reversal).

Clade 36 (*Paranebalia*), evident in 100% of shortest trees, has Bremer support of 5 and and 99% bootstrap support. Six synapomorphies including three with CI=1 define this clade: molar with large accessory process; molar process with setal brush; and pleonites 6 and 7 with denticles only over dorsal part of margin.

Clade 61 occurs in all trees and has Bremer support of 2 and 67% bootstrap support. This clade, all species of *Speonebalia, Nebaliella, Dahlella* and *Nebalia*, is defined by nine synapomorphies including three with CI=1. Some of the characters defining the clade are: antenna 1 without anterodenticulate fourth article (CI=0.5); thoracopod exopod not heavily setose (CI=0.67) pleonite 4 margin denticulate (CI=1); pleonite 5 margin denticulate (CI=1); with crenations over entire pleonite margin (CI=1).

Speonebalia cannoni Bowman, Yager and Iliffe, 1985 is defined by two apomorphies, one with CI=1; maxilla 1 second endite simple. *Speonebalia cannoni* also has an autapomorphy that was excluded from the analysis: maxilla 2 with marginal organelles.

Clade 60 *(Nebaliella, Dahlella* and *Nebalia*) occurs in all trees and has a Bremer support value of 1 and bootstrap support <50%. It is defined by five synapomorphies. None is unique.

Clade 40 (*Nebaliella*) is supported in all trees with Bremer support value of 6 and 100% bootstrap support. It is defined by eight synapomorphies, five with CI=1: presence of a rostral keel longer than the rostral flange; molar with accessory tooth/spine; maxilla 1 second endite bilobed; thoracopod exopod with proximal lobe; and thoracopods 2–5 without epipod. Pleopod 6 longer than pleopod 5 and pleopod 6 uniarticulate are also characters linking species in this clade.

Clades 38 and 39 relating the species of *Nebaliella* occur in all shortest trees, each clade has Bremer support of 1 and clade 39 has 50% bootstrap support.

Clade 59 (*Dahlella* and *Nebalia*), occurs in all parsimony trees and has a Bremer support value of 2 and 72% bootstrap support. Six synapomorphies define this clade but the presence of a supraocular scale is the only unique character (CI=1). All species in this clade also share: antenna 2 peduncle articles 3 and 4 not fused (CI=0.5); pleopod 6 shorter than pleopod 5 (CI=0.5) and pleopod 6 biarticulate (CI=0.5)

Dahlella has three apomorphies among the characters in this matrix but none is unique.

Clade 58 (*Nebalia*) was evident in all trees with Bremer support of 1 and <50% bootstrap support. It is defined by five synapomorphies. The presence of a rostral keel shorter than the rostral flange and article 4 of antenna 1 with robust setae are characters unique to *Nebalia*. Species in this clade also have eyes shorter than the rostrum and eyes with the ventral margin not extremely curved.

Only four clades, grouping three pairs and one group of four species of *Nebalia* appear in the 50% majority-rule tree (Fig. 8). Clade 46 (*N. daytoni* and *Nebalia* sp. A) was retained in all trees and has a Bremer support of 2 and 69% bootstrap support. Clade 47 (*S. typhlops* and *Nebalia* sp. B), retained in all trees, has a Bremer support value of 1 and <50% bootstrap support. Clade 52 (*N. bipes* and *N. herbstii*) was retained in 62% of parsimony trees but has no Bremer support and <50% bootstrap support. The clade linking *Nebalia cannoni*, Dahl, 1990, *N. falklandensis*, Dahl, 1990, *N. longicornis* and *N. patagonica* Dahl, 1990 did not occur in tree 711 but occurred in 75% of all trees. It has no Bremer support and <50% bootstrap support. The relationships of the remaining species of *Nebalia* could not be resolved.

Systematics and a new classification

Four synapomorphies used in this analysis and at least 14 other character states define *Nebaliopsis typica* (Nebaliopsididae) and differentiate it from all other Leptostraca. The sister group (clade 62) is described by robust synapomorphies so there is support for the existing family Nebaliopsididae.

All shortest trees contain a clade (clade 37), *Paranebalia* plus *Levinebalia*, sister taxon of all other species. We believe that with a Bremer support value of 3, bootstrap value of 85% and five autapomorphies for this clade, a new family can be justified for the two genera.

Clade 61, apparent in all trees, contains the remaining genera of Nebaliidae (*Speonebalia, Dahlella, Nebaliella*, and *Nebalia*). This clade is supported by nine synapomorphies, three autapomorphic for the clade (see above) and has Bremer support of 2 and 67% bootstrap support. This clade defines the restricted family, Nebaliidae.

The monophyly of *Speonebalia, Nebaliella, Dahlella*, and *Nebalia* is supported by the analysis. *Speonebalia* and *Dahlella* are monotypic and their status as genera is confirmed by the synapomorphies of their sister taxa.

Two autapomorphies for clade 58 unite all species of *Nebalia* (including *Sarsinebalia typhlops*): the presence of a rostral keel shorter than the rostrum and the presence of robust setae in the fourth article of antenna 1.

We were unable to find any characters which support separate generic status for the monotypic *Sarsinebalia* and the genus must be synonised with *Nebalia* and its species, *S. typhlops* returns to its original combination.

Table 4 lists all described species with their distribution.

Comparison with Olesen's (1999) trees

Olesen (1999) presented two equally parsimonious hypotheses of the phylogeny of the genera of Leptostraca. He used 27 mostly binary characters. The four monotypic genera are clearly monophyletic and he was convinced a priori of the monophyly of *Paranebalia* and *Nebaliella*. He entertained the possibility that *Nebalia* might be paraphyletic with respect to *Sarsinebalia* or *Dahlella* (or both). Our hypothesis differs from his. Olesen's first tree was rooted against two outgroups, Mysidacea and Anostraca, and placed *Nebaliopsis* as a sister taxon to all other Leptostraca, as in our tree. However, the position of *Nebaliella* and *Paranebalia* was directly transposed compared to our tree and *Sarsinebalia* was placed as a sister to *Dahlella* and *Nebalia*. This 3-taxon clade occurred in both of Olesen's trees (the second tree having only Mysidacea as an outgroup) and he suggested this indicated strong support. However, two of the characters linking *Dahlella* and *Nebalia* in Olesen's tree actually vary within *Nebalia* and thus are not useful (character 9: antenna 2, spine on segment 2; character 14: mandible, shape of segment 3). The third character, character 2 (the absence of a rostral spine) occurs throughout the Leptostraca and was a reversal. Our tree treats *Dahlella* as a sister taxon to *Nebalia* and synonomises *Sarsinebalia* with *Nebalia*.

Olesen's second tree (with only Mysidacea as an outgroup) suggested *Paranebalia* at the base of the Leptostraca, with the remaining taxa split into two clades. *Speonebalia* sits as a sister taxon to *Nebaliella* and *Nebaliopsis* supported by a single character (25: pleopod 6 biarticulate). A single character unites *Nebaliella* and *Nebaliopsis* (character 24: pleopod 6 longer than pleopod 5). These characters are both useful characters but, in our tree appear to have evolved twice. The second clade in Olesen's tree was the *Sarsinebalia-Dahlella-Nebalia* clade, supported by four characters, the three mentioned above and character 10 (antenna 2 with three articles), which occurred twice in this tree but only once in Olesen's other tree.

Olesen's (1999) trees lead him to question the family status of Nebaliopsididae and the monophyly of *Nebalia*. Our tree indicates the validity of the Nebaliopsididae, and more significantly of Nebaliidae and a third family. Our tree suggestes *Nebalia* is monophyletic, *Dahlella* is a separate genus and *Sarsinebalia* is a synonym of *Nebalia*.

Table 4. Taxonomic list of all families, genera and species of Recent Leptostraca with reported distributions. * indicates species omitted from phylogenetic analysis.

Order Leptostraca Claus, 1880

NEBALIOPSIDIDAE Hessler, 1984

Nebaliopsis Sars, 1887

N. typica Sars, 1887. West and south-east coast of South America, near Falkland Is, off coast of Ghana, Ivory Coast, south-west Indian Ocean, South Pacific, Scotia Sea

PARANEBALIIDAE fam. nov.

Paranebalia Claus, 1880

P. belizensis Modlin, 1991. Belize
P. longipes (Willemöes-Suhm, 1875). Bermuda, Virgin Is, southern Florida (USA), Japan, Gulf of Siam. Torres Strait (Australia)
P. sp. A. South Australia (Australia)

Levinebalia Walker-Smith, 2000

L. fortunata (Wakabara, 1976). Otago Peninsula (New Zealand)
L. maria Walker-Smith, 2000. Tasman Sea, off E coast of Tasmania (Australia)

NEBALIIDAE Samouelle, 1819

Nebalia Leach, 1814

N. antarctica Dahl, 1990. Wilhelm II Land, Adelie Land (Antarctica)
**N. bipes abyssicola* Fage, 1929. Monaco
N. bipes bipes (Fabricius, 1780). Greenland, Arctic North America, Svalbard to western Norway
**N. bipes valida* Thiele, 1904. Pribilof Is (Bering Sea)
N. borealis Dahl, 1985. Norway, Sweden, British Isles, Shetland Is, Sleat Sound (Scotland)
N. brucei Olesen, 1999. Unguja I., Zanzibar (Tanzania)
N. cannoni Dahl, 1990. South Georgia
N. capensis Barnard, 1914. South Africa
**N. chilensis* (Claus, 1888) *nomen nudum*. Chile
N. clausi Dahl, 1985. Adriatic Sea (Italy)
**N. dahli* Kazmi and Tirmizi, 1989. Karachi (Pakistan)
N. daytoni Vetter, 1996. San Diego (southern California, USA)
N. falklandensis Dahl, 1990. Falkland Is
**N. gerkenae* Haney and Martin, 2000. Monterey Bay, California (USA)
N. herbstii Leach, 1814. Shetland Is, western Bristish Isles, western France to Spanish border
N. hessleri Martin, Vetter and Cash-Clark, 1996. Southern California (USA)
**N. ilheoensis* Kensley, 1976. South-western Africa
**N. japanensis* (Claus, 1888). Japan
**N. lagartensis* Escobar-Briones, 1995. Ria Largartos, Yucatán Peninsula (Mexico)
N. longicornis longicornis Thomson, 1879. South Island (New Zealand), New Britain (Papua New Guinea), South Africa, Lifou (New Caledonia), Blanche Bay, Sandal Bay
**N. longicornis soror* Thiele, 1904. Caribbean Sea, Cuba
N. marerubri Wägele, 1983. Red Sea
N. patagonica Dahl, 1990. Magellan region
**N. pugettensis* (Clark, 1932). Friday Harbour (Washington, USA)
N. strausi Risso, 1826. Channel Is, Guernsey, France, Monaco, Italy including Sicily
N. typhlops Sars, 1870. Red Sea, Lofoten Is (Norway), Messina, Bay of Naples (Italy), North America from Davis Strait to New Jersey, Australia
N. sp. A. Eastern Bass Strait (Australia)
N. sp. B. Tasmania and eastern Bass Strait (Australia)
N. sp. C. southern Western Australia (Australia)

Table 4. continued

Nebaliella Thiele, 1904

N. antarctica Thiele, 1904. Kerguelen I., Akaroa Harbour (New Zealand)
N. brevicarinata Kikuchi and Gamô, 1992. Princess Ragnhild Coast (Antarctica), bathyal
N. caboti Clark, 1932. Cabot Strait (between Newfoundland and Cape Breton I.), New Jersey (USA), Rockall Trough
N. declivatas Walker-Smith, 1998. E coast of Victoria, New South Wales, Tasmania (Australia)
**N. extrema* Thiele, 1905. Kaiser Wilhelm II Land, Palmer Archipelago (Antarctica)

Dahlella Hessler, 1984

D. caldariensis Hessler, 1984. Galapagos I., hydrothermal vents

Speonebalia Bowman, Yager and Iliffe, 1985
S. cannoni Bowman, Yager and Iliffe, 1985. Turks and Caicos Is, marine caves

Key to families of Leptostraca

1. Maxilla 2 with endites 2–4 reduced in size and setation (Fig. 2j); thoracopods well spaced (Fig. 3h); pleopods 2–4 exopod paddle-like, outer margin strongly curved, with numerous small spinules (Fig. 4g); caudal furca leaf-like, broadest midway (Fig. 4n)........................Nebaliopsididae (monotypic)

— Maxilla 2 with at least first 3 endites well developed (Fig. 2l); thoracopods closely space (overlapping); pleopods 2–4 exopod slightly expanded midway and/or distally or outer margin parallel (Figs 4b, d, e); caudal furca tapering evenly to tip (Fig. 4m) 2

2. Antenna 1 of mature male with swollen callynophore (Figs 2d, e); thoracopods long, extending well beyond the ventral margin of carapace (Fig. 1l); thoracopods 2–5 epipod shorter than exopod (Fig. 4b).............Paranebaliidae

— Antenna 1 of mature male not swollen or with callynophore, may have a dense field of aesthetases (Fig. 2f); thoracopods short, not extending well beyond ventral margin of carapace (Fig. 4a); thoracopod 2–5 epipod longer than exopod or absent (Figs 4d, e)...Nebaliidae

Nebaliopsididae Hessler

Nebaliopsidae Hessler, 1984: 656.

Type genus. Nebaliopsis Sars, 1887 (original designation).

Diagnosis. Rostrum without spine or keel. Eye shorter than rostrum and with visual elements; without denticles; without dorsal papilla; ventral margin not extremely convex. Supraocular scale absent. Antenna 1 with anterodenticulate fourth article; article 4 without robust setae. Antenna 2, peduncle articles 3 and 4 not fused, without cuticular outgrowths, or minute denticles; without dorsal spine. Mandible without incisor process; molar process reduced, with armature. Maxilla 1 reduced to small stub. Maxilla 2 (Fig. 2j) nearly as long as thoracopod 1; endopod reduced to small, blunt distal lobe, without organelles; exopod absent; proximal endite enormously enlarged, well-armed with marginal setae; endites 2–4 reduced in size and setation. Thoracopods not extending well beyond ventral margin of carapace; well-spaced (Fig. 3h). Thoracopod 1 differentiated from thoracopod 2–8. Thoracopod (Fig. 4c) endopod blunt, featureless lobe, not articulate; exopod strongly reduced, poorly differentiated, without setae; epipod well developed, longer than exopod, somewhat maxillipediform. Posterior margins of pleonites smooth. Pleopod 1 exopod without comb-row. Pleopods 2–4 exopods paddle-like (Fig. 4g), length less than 3 times width. Pleopod 6 longer than pleopod 5 and biarticulate. Caudal rami leaf-like, broadest midway (Fig. 4n). Thorax inflated; body cuticle and carapace thin and membranous. Carapace with a network pattern of sculpturing; not emarginate; extending furthest posteriad midsagittally, without carina on anterolateral lower corner. Entire length of mature female greater than 20 mm.

Composition. Nebaliopsis Sars, 1887.

Nebaliopsis Sars

Nebaliopsis Sars, 1887: 21.

Diagnosis. With the characters of the family.

Remarks. This family, contains only the type species *N. typica* Sars, 1887. Descriptions of *N. typica* may be found in Thiele (1905), Cannon (1931) and Linder (1943). Males have not been reported.

Paranebaliidae fam. nov.

Type genus. Paranebalia Claus, 1880.

Diagnosis. Subterminal rostral spine present (Fig. 1b); keel absent. Eye shorter than rostrum; visual elements present. Eye sometimes with denticles (Fig. 1h); without dorsal papilla; ventral margin not extremely convex. Supraocular scale absent. Antenna 1 with anterodenticulate fourth article (Fig. 1q); article 4 without robust setae; male flagellum modified, either swollen (juveniles) or transformed into callynophore (Figs 2c, 2d). Antenna 2 peduncle articles 3 and 4 fused; peduncle with 2 rounded cuticular outgrowths and sometimes with minute cuticular denticles or spines (Figs 5a, b); without dorsal spine. Antenna 2 of male not greatly elongate, only half body length. Mandible incisor with 1 tooth (Fig. 2e). Molar process well developed (Fig. 2e); with or without setal brush and sometimes with large accessory process. Maxilla 1 palp (Fig. 2g), long, well developed; second endite elongate. Maxilla 2 with at least first 3 endites well developed; much smaller than thoracopod 1; endopod without organelles; exopod greater than half length of endopod. Thoracopods long, extending beyond ventral margin of the carapace; closely spaced (Fig. 1l). Thoracopod 1 differing only slightly from thoracopods 2–7. Thoracopod exopod heavily setose and without proximal lobe (Fig. 4b). Thoracopods 2–5 epipod shorter than exopod; endopods showing a degree of articulation. Pleonites 4 and 5 with smooth margins. Pleonites 6 and 7 dorsal margins sometimes crenate (Fig. 1l). Pleopod 1 exopod comb-row present. Pleopods 2–4 exopod with parallel margins; outer margins with setae in pairs. Pleopod 5 longer than pleopod 6. Pleopod 6 uniarticulate. Caudal rami tapering evenly to tip. Thorax not inflated; body cuticle and carapace firm. Carapace not sculptured; emarginate; without carina on anterolateral lower corner. Entire length of female less than 20 mm.

Composition. Paranebalia Claus, 1880; *Levinebalia* Walker-Smith, 2000.

Remarks. Six unique character states link the genera of Paranebaliidae: antenna 2, articles 3 and 4 with two large cuticular outgrowths; male antenna 1 flagellum with swollen callynophore; males without greatly elongate antenna 2; maxilla 1 second endite elongate; slender thoracopods extending well beyond the ventral margin of the carapace; thoracopods with reduced epipods. The subterminal rostral spine is a synapomorphy of the Paranebaliidae, shared with *Sarsinebalia typhlops* and *Nebalia* sp. B. The presence of an anterodenticulate fourth article on antenna 1 is found in Paranebaliidae and Nebaliopsididae.

Key to genera of Paranebaliidae

1. Eye with denticles (Fig. 1h); mandible molar with setal brush and large accessory process (Fig. 2e); antenna 2, without minute denticles or spine over ther surface of the peduncle and flagellum (Fig. 5b); pleopods 1–4, peduncle margin crenate (Fig. 2i); pleonites 6 and 7 margin dorsally denticulate (Fig. 1l)..*Paranebalia*

— Eyes without denticles; mandible molar without setal brush and accessory process; antenna 2, with minute denticles or spines over the surface of the peduncle and flagellum (Fig. 5a); pleopods 1–4, peduncle margin smooth; pleonites 6 and 7 without clearly defined crenations.....................*Levinebalia*

Paranebalia Claus

Paranebalia Claus, 1880: 576.—Thiele, 1905: 14–19, 24–25.—Verrill, 1923: 206–207.—Wakabara, 1976: 297.

Type species. Nebalia longipes Willemöes-Suhm, 1875 (by monotypy).

Diagnosis. Eyes with denticles or cuticular outgrowths (Fig. 1h). Mandible incisor with setal brush and molar large accessory process (Fig. 2e). Antenna 2 without minute denticles or spines over the surface of the peduncle and flagellum (Fig. 5b). Pleopods 1–4, peduncle margin crenate (Fig. 2i). Pleonites 6 and 7, margin dorsally crenate (Fig. 1l).

Composition. P. longipes, P. belizensis Modlin, 1991.

Remarks. This genus is distinguished most easily from *Levinebalia* by the denticulate eyes, antenna 2 without minute denticles or spines over the surface of the peduncle and flagellum, pleopods 1–4, peduncle margin crenate and pleonite 6 and 7 dorsally crenate. Undescribed species are known from Australia.

Levinebalia Walker-Smith

Levinebalia Walker-Smith, 2000: 138.

Type species. Levinebalia maria Walker-Smith, 2000 (original designation).

Diagnosis. Eyes without denticles or cuticular outgrowths. Mandible incisor without setal brush or accessory molar process. Antenna 2 peduncle and flagella with patches of minute denticles or spines (Fig. 5a). Pleopods 1–4, peduncle margin smooth. Pleonites 6 and 7, margins with ill-defined crenations.

Composition. L. maria, L. fortunata (Wakabara, 1976).

Remarks. This genus is distinguished from *Paranebalia* by smooth eyes, minute denticles or spines over the surface of antenna 2 peduncle and flagella, smooth pleonites margins and smooth pleopod peduncles. Pleonites may sometimes have tiny, ill-defined crenations.

Nebaliidae Samouelle

Nebaliadae Samouelle, 1819: 100.
Nebaliidae Baird, 1850: 31–38.—Sars, 1887: 6–7.—Verrill, 1923: 205–206.—Hessler, 1984: 656.

Type genus. Nebalia Leach, 1814 (by monotypy).

Diagnosis. Subterminal rostral spine rarely present; keel sometimes present (Figs 1a, d). Visual elements present or absent. Supraocular scale sometimes present (Fig. 1f). Antenna 1, anterodenticulate fourth article absent; male, flagellum not swollen, but may have numerous aesthetases (Fig. 2f). Antenna 2, peduncle without cuticular outgrowths or minute denticles; articles 3 and 4 sometimes fused (Fig. 2b); male antenna 2 greatly elongate, reaching to the caudal furca (unknown for *Dahlella*). Mandible incisor, present (except for *Speonebalia*). Molar process well developed (Fig. 2h), without setal brush; without accessory process; sometimes with accessory tooth/spine (Fig. 2i). Maxilla 1 palp long, well developed. Maxilla 2 (Fig. 2l) with at least first 3 endites well developed; much smaller than thoracopod 1. Thoracopods not extending well beyond ventral margin of carapace; closely spaced (Fig. 4a). Thoracopod 1 differing only slightly from thoracopods 2–7. Thoracopods 2–5 epipod longer than exopod (Fig. 4d), or absent (Fig. 4e); endopods showing a degree of articulation. Pleonites 4–7 crenate over entire margin (Fig. 4a). Pleopod 1 exopod generally with comb-row (Fig. 4k). Pleopod 2–4 exopod with parallel margins or slightly expanded medially; outer margins with setae sometimes in pairs. Pleopod 5 longer or shorter than pleopod 6. Pleopod 6 uni- or biarticulate. Caudal rami tapering evenly to tip. Thorax not inflated, body cuticle firm. Carapace strongly emarginate midsagittally. Entire body length less than 20 mm.

Composition. Nebalia Leach, 1814; *Nebaliella* Thiele, 1904; *Dahlella* Hessler, 1984; *Speonebalia* Bowman, Yager and Iliffe, 1985.

Remarks. The diagnosis for Nebaliidae has been modified since Hessler (1984) to include *Speonebalia* and exclude *Paranebalia* and *Levinebalia* (removed to Paranebaliidae). *Sarsinebalia* has been synonymised with *Nebalia*. Authorship of the family name has been attributed to Baird (1850) by other authors but Samouelle's (1819) name has precedence.

Key to genera of Nebaliidae

1. Rostrum with keel shorter than rostral flange (Figs 1a, d) or absent; molar without accessory tooth/spine (Fig. 2h); thoracopod exopod without proximal lobe (Fig. 4d); thoracopods 2–5 epipod longer than exopod (Fig. 4d); pleopods 2–4 outer margins parallel (Figs 4h–k)..2

— Rostrum with keel longer than rostral flange (Figs 1c, e); molar with accessory tooth/spine (Fig. 2i); thoracopod exopod with proximal lobe (Fig. 4e); thoracopods 2–5 epipod absent (Fig. 4e); pleopods 2–4 outer margins slightly expanded midway and/or distally (Fig. 4f)........................*Nebaliella*

2. Rostrum without keel; eye longer than rostrum; antenna 1 article 4 without robust setae 3

— Rostrum with keel shorter than rostral flange (Figs 1a, 1d); eye shorter than rostrum; antenna 1, article 4 with robust setae (Fig. 1p) ....*Nebalia*

3. Eye without denticles, narrow, tapering distally, surface smooth, without visual elements, without supraocular scale; maxilla 1 second endite simple (Fig. 3e), maxilla 2 with marginal organelles (Fig. 2k)..........*Speonebalia*

— Eye (Fig. 1m) with denticles, strongly curved (banana shape), surface with denticles, without visual elements, with supraocular scale; maxilla 1 second endite complex (Fig. 3a); maxilla 2, marginal organelles absent.......*Dahlella*

Nebalia Leach

Nebalia Leach, 1814: 99.—Thomson, 1879: 418–419.—Sars, 1896: 7–8.— Thiele, 1904: 10–12.—Thiele, 1905: 61.—Barnard, 1914: 443–446.—Fage, 1929: 41–42.—Cannon, 1931: 221–222.—Clark, 1932: 225–230.—Wägele, 1983: 127–138.— Dahl, 1985: 144–157.—Dahl, 1990: 73–91.

Epinebalia Clark, 1932: 225–230 (type species *Epinebalia pugettensis* Clark, 1932 by monotypy).

Sarsinebalia Dahl, 1985: 160–163 (type species *Nebalia typhlops* Sars, 1870 by original designation) syn. nov.

Type species. Cancer bipes Fabricius, 1780 (by monotypy).

Diagnosis. Rostrum with keel shorter than rostral flange, commonly without subterminal spine (Fig. 1a). Eyes shorter than rostrum, generally dorsally convex, sometimes with papilla (Figs 1f, j); usually with ommatidia or visual elements; surface without denticles, ventral margin not extremely convex. Supraocular scale present (Figs 1f, i). Maxilla 2 exopod at least half length of endopod (except *N. typhlops*). Antenna 1 article 4 with 1 or more robust setae (Fig. 1p). Antenna 2, article 2 with commonly with dorsal spine, articles 3 and 4 fused (Fig. 2b). Mandible palp article 3 tapering distally, with parallel margins; incisor with 2 teeth (Fig. 2h); molar process well developed without accessory tooth/spine. Maxilla 1 second endite complex (Fig. 3a). Thoracopods exopod without proximal lobe; with few setae (Fig. 4d); epipods large, well developed. Pleopod 1, exopod generally with comb-row (Fig. 4k). Pleopod 6 shorter than pleopod 5, uniarticulate.

Remarks. The two characters distinguishing *Nebalia* from other Leptostraca are the presence of a keel shorter than the rostral flange and the presence of one or more robust setae on article 4 of antenna 1. Most species of *Nebalia* are very alike and difficult to distinguish from one another. However, four species are particularly distinctive. *Nebalia daytoni* and *N.* sp. A have an unusual bilobed eye (Fig. 1n). *Nebalia* sp. A also has verticle striations on the anteroventral surface of the carapace. *Nebalia* sp. A and sp. B and *N. typhlops* all lack the comb-row on the exopod of pleopod 1. *Nebalia* sp. B has an unusual triangular shaped eye and *N. typhlops* has a rectangular to circular eye that lacks pigment. The exopod of maxilla 2 of *N. typhlops* is reduced to less than half the length of the endopod.

Sarsinebalia Dahl, 1985 is a new junior synonym.

Nebaliella Thiele

Nebaliella Thiele, 1904: 4-9, 24-25.—Cannon, 1931: 216–221.—Walker-Smith, 1998: 41.

Type species. Nebaliella antarctica Thiele, 1904 (by monotypy).

Diagnosis. Rostrum with keel longer than rostral flange, subterminal spine absent (Fig. 1c). Eyes strongly curved, extending beyond the end of the rostral keel, lacking visual elements (Fig. 1e). Antenna 1 without robust setae on article 4. Antenna 2, peduncle articles 3 and 4 not fused, without cuticular outgrowths (Fig. 2a). Mandible incisor with 2 teeth. Molar with accessory tooth/spine (Fig. 2i), without large accessory process (Fig. 2e). Maxilla 1 second endite bilobed (Figs 3b, 3d). Maxilla 2 exopod greater than half length of endopod, biarticulate, without organelles. Thoracopods without epipods (Fig. 4c). Thoracopod exopod with proximal lobe, heavily setose (Fig. 4e). Pleonites 2–7 posterior margin crenate. Pleopods 2–4 with lateral setae not in pairs (Fig. 4f). Pleopod 6 longer than pleopod 5, biarticulate. Carapace not sculptured, but may have a carina on lower anterolateral surface, posterodorsal margin with tiny denticles.

Remarks. Nebaliella occurs at depths ranging from 3 m to over 100 m. The eyes, like those of *Dahlella* and *Nebalia* typhlops, lack visual pigments; they are strongly curved and extend beyond the end of the rostrum like those of *Dahlella* but, unlike *Dahlella*, lack denticles. The rostrum is unique. Antenna 2 articles 3 and 4 are not fused in *Nebaliella*, *Nebaliopsis* and *Speonebalia*. Thoracopod epipods are absent in

Nebaliella but present in all other leptostracans. The posterior margin of the carapace of *Nebaliella* has a series of close-set spines; similar ornamentation is found in *Speonebalia*.

Dahlella Hessler

Dahlella Hessler, 1984: 656.

Type species. Dahlella caldariensis Hessler, 1984 (original designation).

Diagnosis. Rostrum without keel or subterminal spine. Eyestalks without visual elements, curved, longer than rostrum, tapering gradually to point; anterior margin denticulate (Fig. 1m); supraocular scale present. Antenna 1 without robust setae on article 4. Antenna 2, peduncle articles 3 and 4 fused. Mandible incisor with 2 teeth; molar process well developed, without accessory tooth/spine; mandible palp, distal article with 2 rows of setae. Maxilla 1 second endite complex (Fig. 3a). Maxilla 2 exopod small, less than quarter length of endopod; endopod biarticulate, without organelles. Thoracopod exopod without proximal lobe, with few setae; epipod large, approximately equal in size to exopod; proximal lobe small. Pleonites 2–7 posterior margin crenate. Pleopods 2–4 exopods with pairs of lateral setae. Pleopod 6 shorter than pleopod 5, uniarticulate. Carapace not sculptured.

Remarks. The most pronounced feature of *Dahlella* is the large, blind, toothed eye, seen only in this monotypic genus from deep-sea vent communities. Hessler (1984) suggested the eyes may be used in scraping surfaces to loosen food such as bacterial encrustations. *Dahlella* is most similar to *Nebalia*, differing in the structure of the eye, the lack of rostral keel, the small size of the exopod of maxilla 2 and the shape of the proximal lobe of the thoracic epipod. *Dahlella* shares with *Nebalia* the presence of a supraocular scale.

Speonebalia Bowman, Yager and Iliffe

Speonebalia Bowman et al., 1985: 439.

Type species. Speonebalia cannoni Bowman, Yager and Iliffe, 1985 (original designation).

Diagnosis. Rostrum without keel and subterminal spine. Eyes long and narrow, tapering distally, extending beyond tip of rostrum, without visual elements, surface smooth. Antenna 1 article 4 without robust setae. Antenna 2 peduncle articles 3 and 4 not fused, without large cuticular outgrowths or minute denticles. Mandible without incisor. Maxilla 1 second endite, simple (Fig. 3e). Maxilla 2 endopod, uniarticulate, with series of oval marginal organelles, exopod very small (Fig. 2k). Thoracopods exopod without proximal lobe, with few setae; epipods large, well developed. Pleopod peduncles with crenate lateral margin. Pleopod 1 without comb-row on lateral margin of exopod. Pleopod 2–4 exopod with parallel margins, smooth setae in pairs. Pleopod 6 shorter than pleopod 5, biarticulate. Caudal rami short and broad, tapering distally, margins densely setose, setae on medial margin very long. Carapace strongly compressed laterally, covering pleopods 1–5, more than 8 times length of rostrum, with series of close-set obtuse spines along posterior margin.

Remarks. Visual elements are also absent in *Dahlella*, *Nebaliella* and *Nebalia typhlops*. The mandibular incisor, absent in *Speonebalia*, is present in all other Nebaliidae. The mandibular palp is unusually large in *Speonebalia*, reaching the distal segment of the peduncle of antenna 2; article 3 is unusual in its slender tapered shape and its armature of three rows of complex setae. The shape of the maxilla 1 second endite (Fig. 3e) of *Speonebalia* is unique. *Speonebalia* is the only leptostracan with glands on maxilla 2. The exopod of maxilla 2 is reduced in *Speonebalia* and *Dahlella*. The posterior margin of the carapace of *Speonebalia* has a series of close-set obtuse spines; species of *Nebaliella* also show similar ornamentation on the carapace margin. The caudal rami of *Speonebalia* has a dense armature of long setae along the medial margin.

The genus is monotypic, its only species recorded from marine caves. It has been suggested the caudal setae prevent the animal from sinking and indicate a pelagic rather than a benthic life (Bowman et al., 1985). All other species of Leptostraca except *Nebaliopsis typica* are thought to be benthic.

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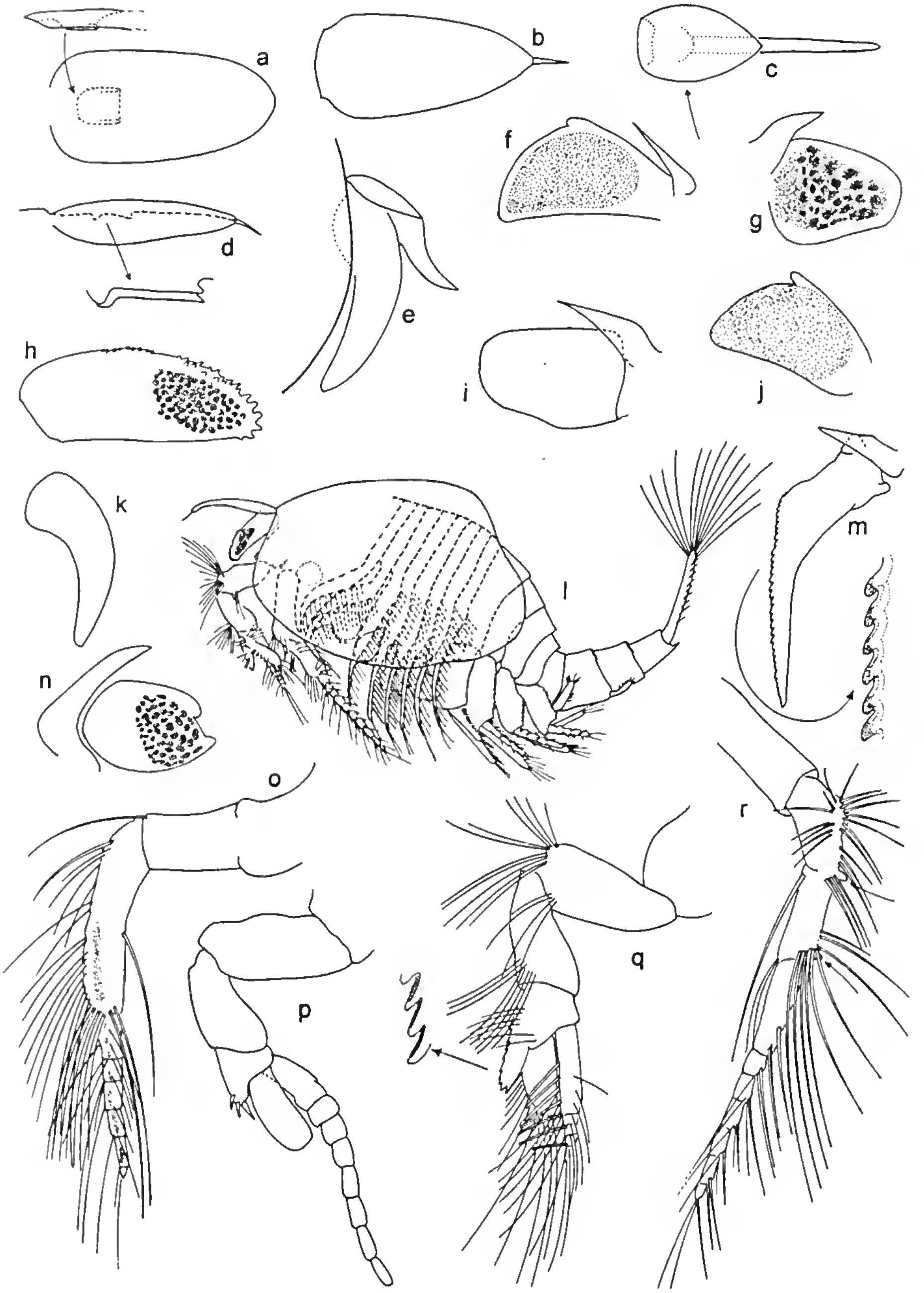

Figure 1. **a**, rostrum, dorsal and part lateral view, *Nebalia* sp. C. **b**, rostrum dorsal view, *Paranebalia* sp. A. **c**, rostrum dorsal view, *Nebaliella extrema*, after Thiele, 1905. **d**, rostrum lateral view, *Nebalia typhlops*, after Dahl, 1985. **e**, eye and rostrum, *Nebaliella extrema*, after Thiele, 1905. **f**, eye and supraocular scale, *Nebalia patagonica*, after Dahl, 1990, **g**, eye and supraocular scale, *Nebalia* sp. B. **h**, eye, *Paranebalia* sp. A. **i**, eye and suproecular scale, *Nebalia typhlops*, after Dahl, 1985. **j**, eye with dorsal papillae, *Nebalia longicornis*, after Dahl, 1990. **k**, eye, *Nebaliella declivatas*. **l**. *Paranebalia* sp. A. **m**, eye and supraocular scale. *Dahlella caldarensis*, after Hessler, 1984. **n**, eye and supraocular scale, *Nebalia* sp. A. **o**, antenna 2, *Levinebalia maria*. **p**, antenna 1, *Nebalia bipes bipes*, after Dahl, 1985. **q**, antenna 1, mesial view, *Paranebalia* sp. A. **r**, antenna 2, *Paranebalia* sp. A.

Figure 2. **a**, antenna 2, *Nebaliella declivatas*. **b**, antenna 2, *Nebalia* sp. C. **c**, immature male, *Paranebalia tippara*. **d**, mature male, *Paranebalia* sp. A. **e**, mandible incisor and molar, *Paranebalia* sp. A. **f**, antenna 2, *Nebalia* sp. A, male. **g**, mandible palp, *Levinebalia maria*. **h**, mandible incisor and molar, *Nebalia* sp. A. **i**, mandible incisor and molar, *Nebaliella declivatas*. **j**, maxilla 2, *Nebaliopsis typica* after Sars, 1887. **k**, maxilla 2, *Speonebalia cannoni*, after Bowman et al. 1985. **l**, maxilla 2, *Nebalia* sp. C.

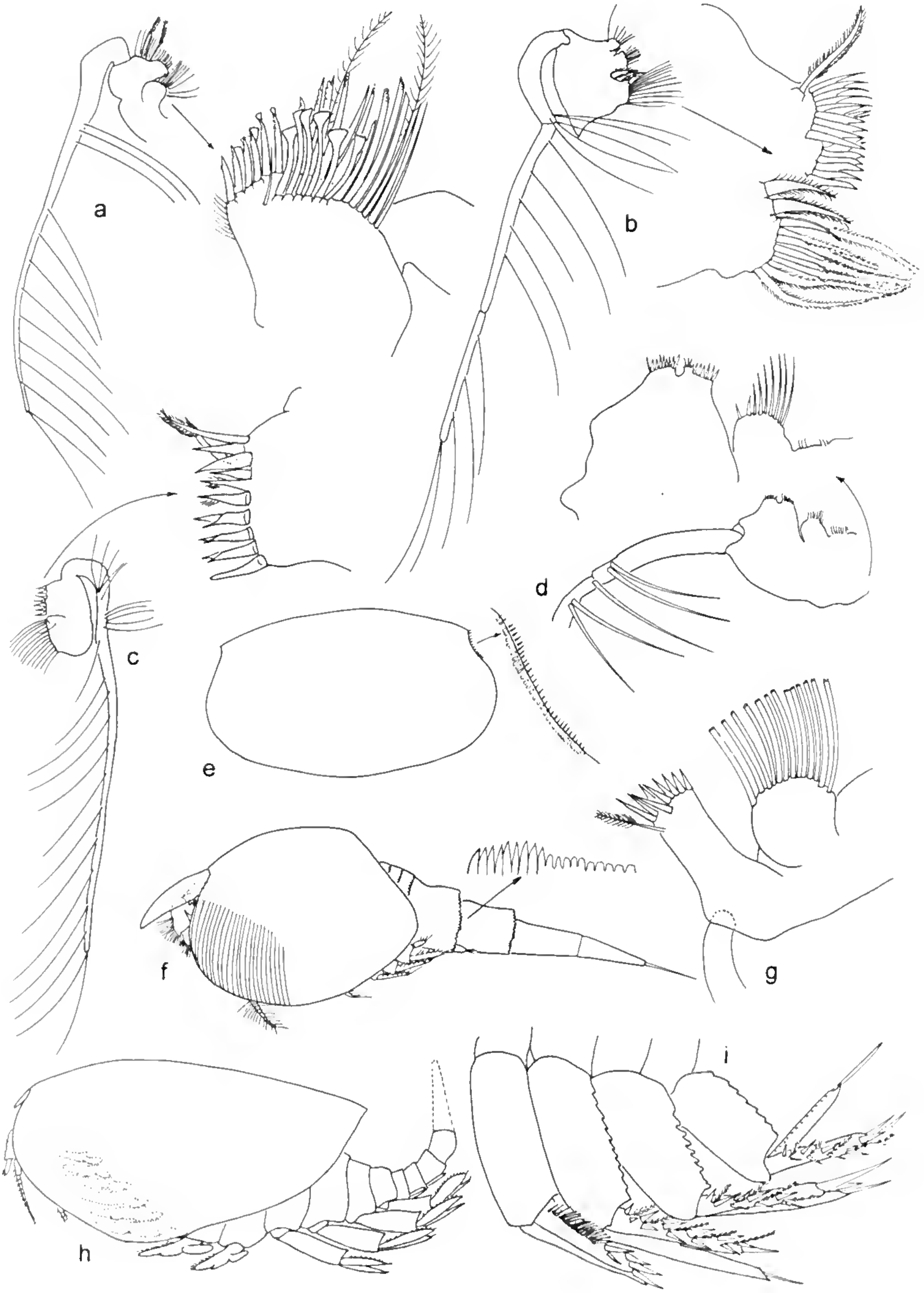

Figure 3. **a**, maxilla 1, *Nebalia* sp. C. **b**, maxilla 1, *Nebaliella declivatas*. **c**, maxilla 1, *Speonebalia cannoni*, after Bowman et al. 1985. **d**, maxilla 1, *Nebaliella declivatas*, male. **e**, carapace, *Nebaliopsis typica*, after Sars, 1887. **f**, *Nebalia* sp. A. **g**, maxilla 1 (without palp), *Paranebalia* sp. A. **h**, *Nebaliopsis typica*, after Linder (1943). **i**, pleopods 1–4, *Paranebalia* sp. A.

Figure 4. **a**, *Nebalia* sp. C. **b**, thoracopod 3, *Levinebalia maria*. **c**, thoracopod 7, *Nebaliopsis typica*, after Sars, 1887. **d**, thoracopod 3, *Nebalia* sp. C. **e**, thoracopod 3, *Nebaliella brevicarinata*, after Kikuchi and Gamô 1992. **f**, pleopod 2, *Nebaliella declivatas*. **g**, pleopod 4, *Nebaliopsis typica*, after Thiele, 1904. **h**, pleopod 2, *Nebalia* sp. C. **i**, pleopod 1, *Nebalia* sp. A. **j**, pleopod 1, *Nebaliella declivatas*. **k**, pleopod 1, *Nebalia* sp. C. **l**, end of thoracopod 3, *Nebalia pugettensis*, after Dahl, 1985. **m**, caudal furca, *Nebaliella declivatas*. **n**, caudal furca, *Nebaliopsis typica*, after Thiele, 1904.

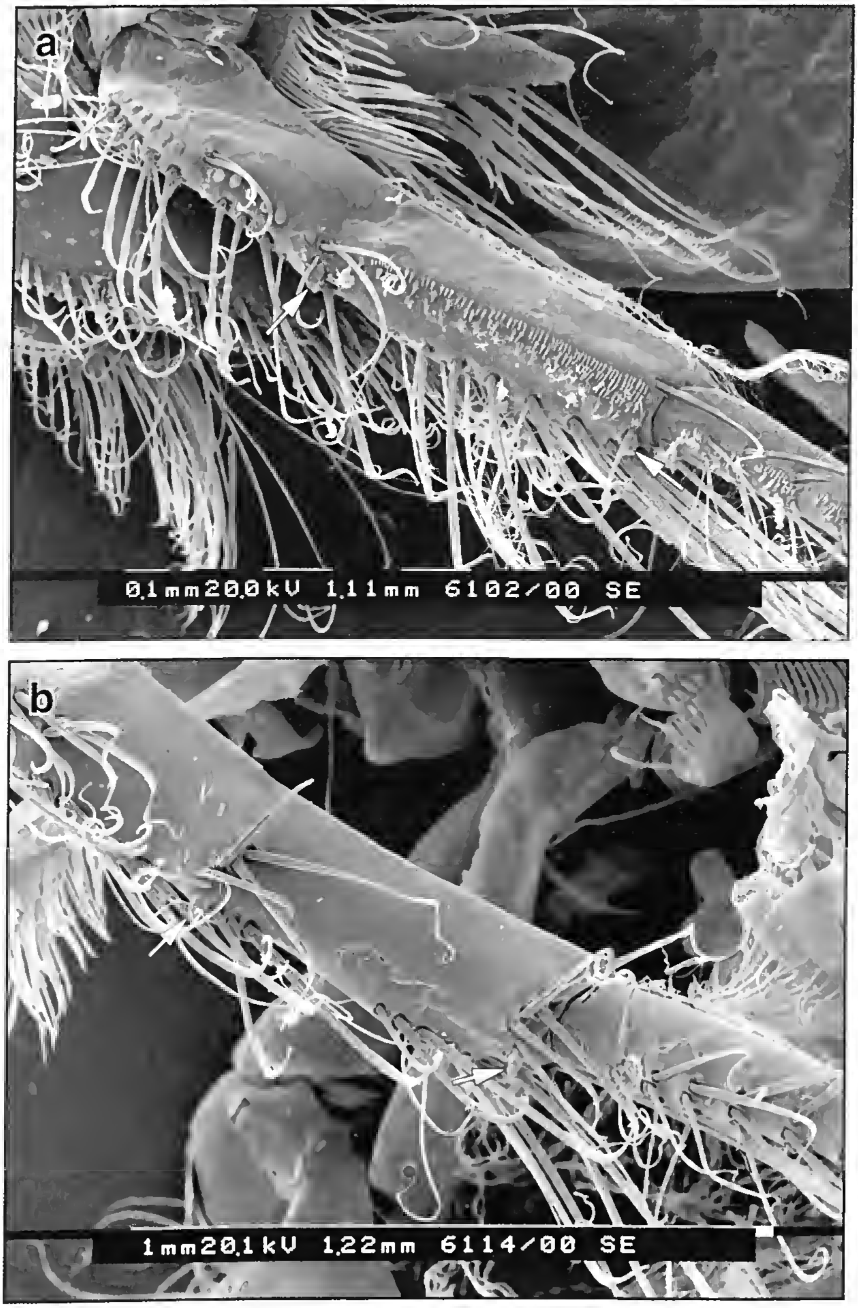

Figure 5. Antenna 2 in situ (left), peduncle article 3 and 4 (these are fused) and first article of flagellum. **a**, *Levinebalia maria*, note row of small spines. Arrows point to large cuticular outgrowths. **b**, *Paranebalia* sp. A, note absence of small spines. Arrows indicate large cuticular outgrowths.

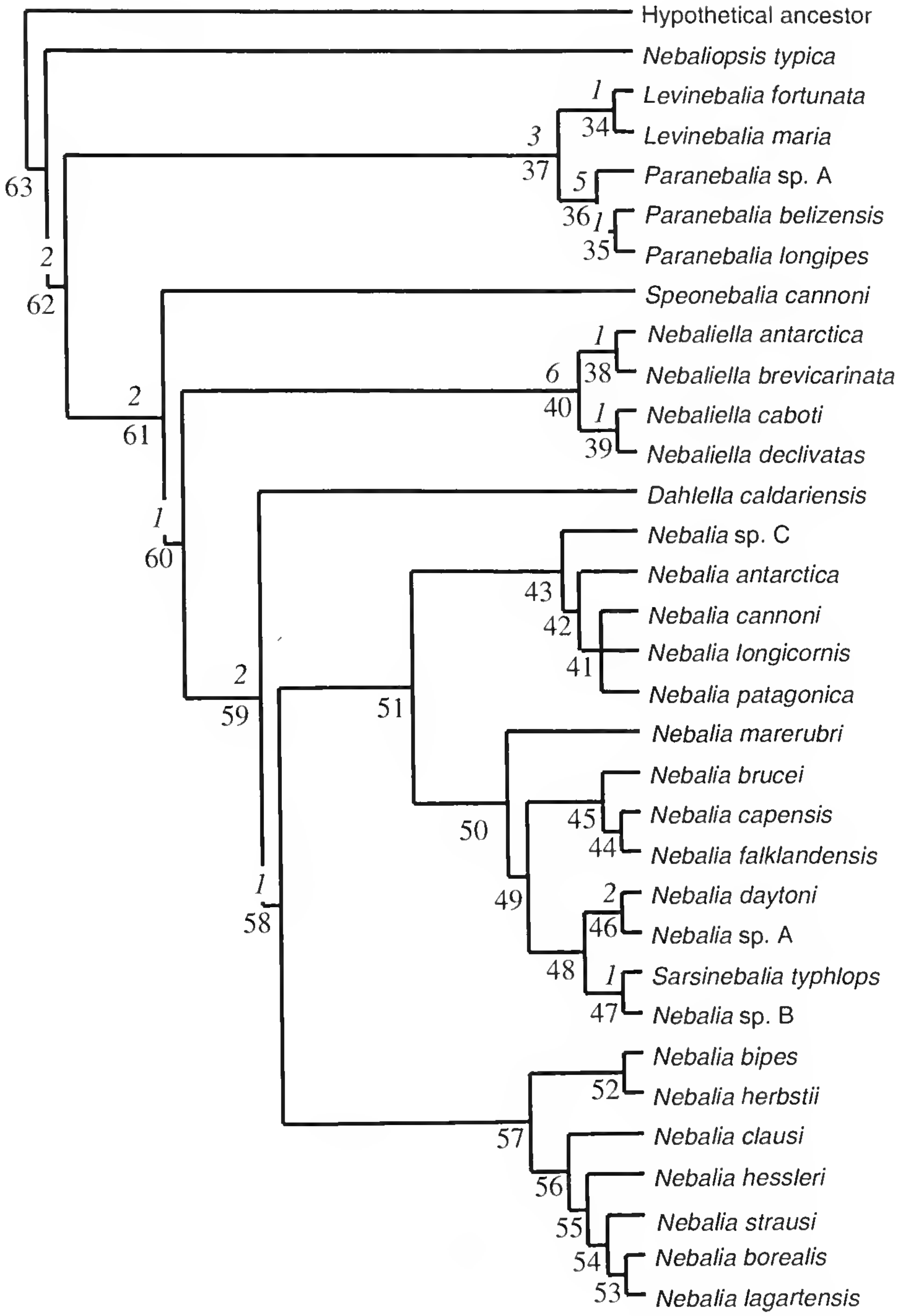

Figure 6. Hypothesis for phylogeny of Leptostraca, tree 711. Numbers above branches are Bremer values; numbers below are node numbers.

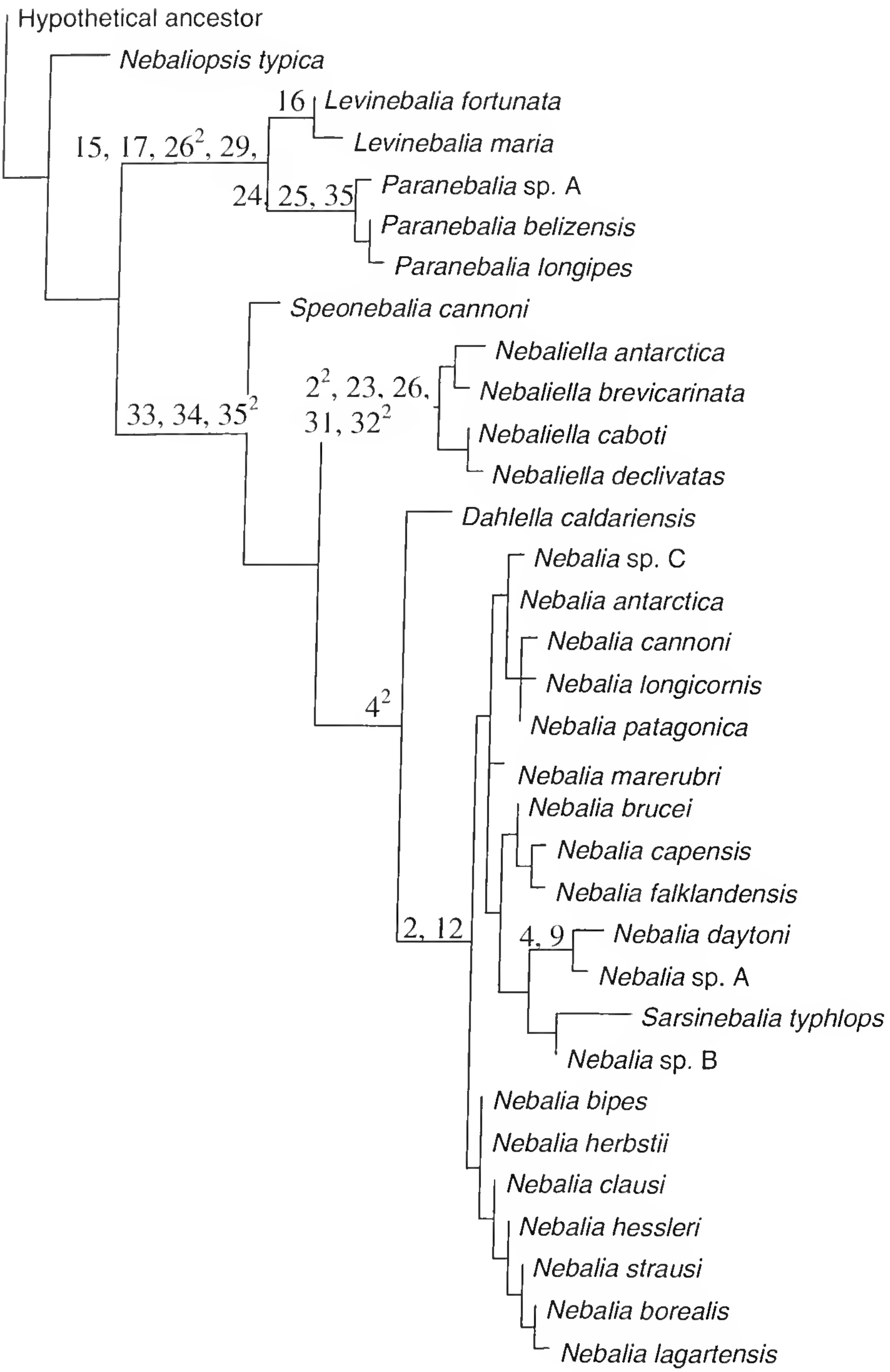

Figure 7. Tree 711 with branch lengths. Numbers are characters with CI=1 and superscripts are state changes from the plesiomorphic condition.

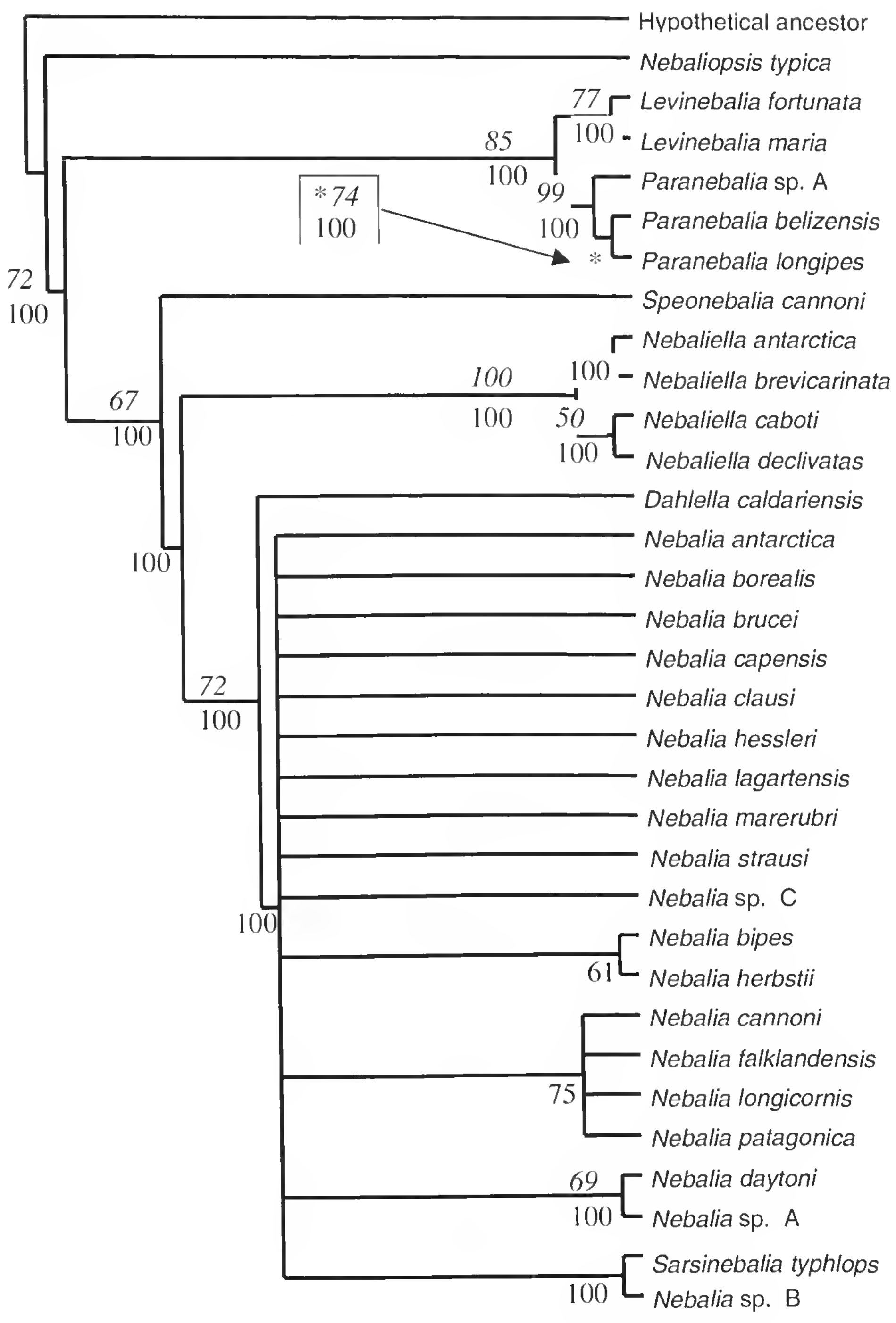

Figure 8. 50% majority-rule tree. Number above branch lines are Bootstrap values; numbers below are percentage of parsimonious trees retaining each clade (only values above 50% are included).

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