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Algal-tube Dwelling Amphipods in the Genus *Cerapus* from Australia and Papua New Guinea (Crustacea: Amphipoda: Ischyroceridae)

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ABSTRACT. Three new species of ischyrocerid amphipods in the genus *Cerapus (C. bundegi, C. murrayae,* and *C. volucola*) are described from Australia and Papua New Guinea. Although these species have all of the morphological characteristics of *Cerapus*, they differ from other species in the genus in the construction of their tubes which are wrapped and parchment-like and sometimes elaborately covered with pieces of cut algae and seagrasses.

Within Australia about 20 species (described and undescribed) occur in the *Cerapus* clade of Lowry & Berents, 1996 (*Bathypoma, Cerapus, Notopoma, Paracerapus* and *Runanga*). These species can be grouped by the type of tube they build. The most common tube type is made of minute sand grains and detritus held together with amphipod silk, known as detrital-tubes. The ends may be straight or fluted. In other species the females attach coarse sand grains to one end of the tube to form a holdfast that is buried in the substrate, known as anchor-tubes. The species described here make their tubes by wrapping algae into tubes, that may be simple or elaborately decorated with pieces of algae or seagrasses and these are known as algal-tubes. These species live on algae and the tubes are assumed to form an effective camouflage. Although the tubes are bizarre compared with those of other species of *Cerapus*, the morphology of the species in this group is similar to the type species *C. tubularis* Say, 1817 (Lowry & Berents, 1989), which build their tubes of minute sand grains. In this paper we describe three new species (*C. bundegi, C. murrayae*, and *C. volucola*) that build algal-tubes.

J.L. Barnard (1973) placed *Ericthonius* and related genera and *Cerapus* and related genera in the Ischyroceridae, but not *Siphonoecetes* and related genera, which he placed in the Corophiidae. Bousfield (1979; 1982) and Just (1983) maintained the classification of J.L. Barnard (1973). Lowry & Berents (1996) were able to demonstrate the monophyly of the combined *Ericthonius, Cerapus* and *Siphonoecetes* clades, but they were not able to link the group with a known family level taxon. Myers & Lowry (2003), in their revision of the corophiidean amphipods, confirmed that the siphonoecetin clade (including the above three clades) is a sister taxon to the ischyrocerin clade which makes up the subfamily Ischyrocerinae.

Diagnosis are generated with the aid of Intkey (Dallwitz *et al.*, 1993 onwards; Dallwitz *et al.*, 1998). Characters in bold face distinguish each taxon in at least two respects from every other taxon in the genus *Cerapus*. Material used in this study is lodged in the Australian Museum, Sydney (AM). The following abbreviations are used on the plates: *A*, antenna; *D*, dactylus; *G*, gnathopod; *P*, pereopod; *PL*, pleopod; *UR*, urosome.

Superfamily Photoidea Boeck, 1871
(Myers & Lowry, 2003)

Family Ischyroceridae Stebbing, 1899

Subfamily Ischyrocerinae Stebbing, 1899
(Myers & Lowry, 2003)

Tribe Siphonoecetini Just, 1983
(Myers & Lowry, 2003)

Cerapus bundegi n.sp.

Figs. 1–2

Type material. HOLOTYPE, ♂, 4.77 mm, AM P62291; PARATYPE, ♀, 3.85 mm, AM P62385; 41 PARATYPES, AM P62381; PARATYPE, ♂, 3.54 mm, AM P62383; PARATYPE, ♂, 2.74 mm, AM P62384; north of jetty, Cottesloe Beach, Perth, Western Australia, Australia, 31°59'S 115°45'E, just outside limestone reef, sand with scattered seagrass, 4 m, J. Just, 3 April 1984, AU 28. 21 PARATYPES, AM P62382, off end of South Mole, Arthur Head, Fremantle, Western Australia, Australia, 32°3'S 115°44'E, brown & red algae, 6 m, R.T. Springthorpe, 25 December 1983, WA 274.

Additional material. 2 specimens, AM P62292, *Sargassum* sp. and sand, 2.3 m; 6 specimens, AM P62332, broad-leaf *Sargassum* sp., sand & algal bottom, 2.8 m; 3 juveniles, AM P62334, fine *Dictyota* sp. and sand, 2.6 m; 2 specimens, AM P62338, broad-leaf *Sargassum* sp. and sand, 2.9 m; 1♂, AM P62339, fine *Sargassum* sp. and sand, 2.9 m; 1♂, AM P62340, *Padina* sp., *Lobophora* sp. and sand, 2.7 m; 1♀, AM P62341, fine *Dictyota* sp. and sand, 2.3 m; 3 juveniles, AM P62387, *Padina* sp. and sand, 2.3 m; 1♂, AM P62392, *Dictyotales* and sand, 2.8 m; 4 specimens, AM P62395, *Sargassum* sp. and sand, 2.7 m; 3 specimens, AM P62397, *Dictyotales* and sand, 2.8 m; 2 specimens, AM P62404, *Sargassum* sp. and sand, 2.9 m, west side of Malus Island, Dampier Archipelago, Western Australia, Australia, 26°30.61'S 116°38.92'E, R.A. Peart, 27 September 1999, WA 661. 1♂, AM P62388, south side of Kendrew Island, Dampier Archipelago, Western Australia, Australia, 20°20.63'S 116°31.99'E, *Sargassum* sp. and sand, 3.8 m, R.A. Peart, 30 August 1999, WA 694. 4 specimens, AM P62389, mixed brown algae, 17 m, M. Hewitt; 3 juveniles, AM P62391, *Dictyopteris* sp., 17 m, P. Morrison, Nelson Rocks, Dampier Archipelago, Western Australia, Australia, 20°26.51'S 116°40.23'E, 7 September 1999, WA 715. 4♂♂, AM P62386, *Dictyopteris* sp., intertidal zone, 0.5 m; 1♀, AM P62394, *Padina* sp., intertidal, 0.5 m, Tish Point, Rosemary Island, Dampier Archipelago, Western Australia, Australia, 20°29.67'S 116°35.89'E, R.A. Peart, 30 August 1999, WA 685. 11 specimens, AM P62335, beach at north end of Bundegi Reef, Exmouth Gulf, Western Australia, Australia, 21°49'S 114°11'E, rocky rubble, coralline algae with green epiphyte, 2 m, H.E. Stoddart, 4 January 1984. Many specimens, AM P62336, seagrass with bases and sand, 2 m; 12 specimens, AM P62398, mixed algae, 2 m, J.K. Lowry; many specimens, AM P62393, south Ned's Camp, Cape Range National Park, Western Australia, Australia, 22°00'S 113°55'E, seagrass, 2 m, R.T. Springthorpe, 31 December 1983. many specimens, AM P62337, Ned's Camp, Cape Range National Park, Western Australia, Australia, 21°59'S 113°55'E, green algae, 1.5 m, R.T. Springthorpe, 2 January 1984, WA 380. 6 specimens, AM P62290, 4 m, R.T. Springthorpe; 3 specimens, AM P62333, mixed coralline algae, 4 m, J.K. Lowry, Red Bluff, Kalbarri, Western Australia, Australia, 27°42'S 114°9'E, 10 January 1984. 4 specimens, AM P62286, 16 specimens, AM P62285, reef close to shore, Champion Bay, Geraldton, Western Australia, Australia, 28°45.88'S 114°36.83'E, *Ecklonia radiata* on shallow rocky reef at low tide, 0.5 m, R.A. Peart, 28 November 2000. 4 specimens, AM P62396, Seven Mile Beach, Western Australia, Australia, 29°11'S 114°53'E, *Amphibolis* sp. (seagrass), 1 m, G.J. Edgar, 6 June 1987. 2 specimens, AM P62402, 10 specimens, AM P62406, 5 specimens, AM P62403, 2♀♀, AM P62405, Cottesloe Beach, Perth, Western Australia, Australia, 31°59'S 115°45'E, sand patch on limestone reef with algae & seagrass (*Amphibolis* sp.), 2 m, J. Just, 2–3 March 1984. 1♂, AM P62390, reef west of groyne, 2 km south of Cape Peron, Western Australia, Australia, 32°16'S 115°41'E, *Caulerpa* sp. in deep channels in limestone reef, 6 m, J.K. Lowry, 26 December 1983, WA 302. 1♀, AM P62399, sponges, 6 m, R.T. Springthorpe; 5 specimens, AM P62400, *Caulerpa* sp., 6 m, J.K. Lowry; 2 juveniles, AM P62401, orange gorgonacean, 6 m, R.T. Springthorpe, end of South Mole, Arthur Head, Fremantle, Western Australia, Australia, 32°3'S 115°44'E, 25 December 1983, WA 286.

Diagnosis. Head, rostrum long, apically acute; anteroventral corner subquadrate. **Antenna 1 peduncular article 1 longer than article 3, swollen along posterior margin. Pereonite 2 with sternal keel.** Pereopod 5 merus posterior lobe with 4 plumose setae.

Description. Based on holotype male, 4.77 mm. **Head**, rostrum long, apically acute, length 0.4× head; lateral cephalic lobe with ventral corner rounded, subocular margin weakly recessed, anteroventral corner subquadrate, ventral margin horizontal, posterior margin vertical. *Antenna 1* long, length 0.5× body length; peduncular article 1 longer than (1.2×) peduncular article 3, not produced anterodistally and anteromedially, swollen along posterior margin, posterodistal corner not produced; flagellum 6-articulate; article 1 short. *Antenna 2* length 0.9× antenna 1; flagellum 5-articulate; article 1 short. *Epistome and upper lip* fused, straight. *Mandible* with palp article 2 long and slender, length 3.1× breadth, 1.2× article 3; palp article 3 slender, blade-like, long, 3.3× breadth.

Pereon. *Pereonite 1* without lateral keel; without sternal keel. *Pereonite 2* with sternal keel. *Pereonite 3* without sternal keel. *Pereonite 5* length 2.1× depth.

Gnathopod 1 coxa not fused to pereonite 1, length 1.4× depth, without anteroventral lobe; basis length 1.6× depth; carpus, length 1.2× depth with setose posterior lobe, broad; palm extremely acute, with barbed robust setae. *Gnathopod 2* carpochelate; coxa not fused to pereonite 2, length 1.7× depth, without anteroventral lobe or cusp; basis short, broad, length 1.3× breadth; carpus long, broad, length 1.2× breadth; palm shallowly excavate, anterodistal tooth small, located near articulation with propodus, posterodistal tooth well defined, medium, length 1.2× width; propodus broad, slightly curved, length 3.2× width, without proximal tooth on posterior margin, posterodistal corner smooth, without tooth; dactylus, length 0.7× propodus. Male gnathopod 2 changes significantly through growth stages. Figure 1 illustrates these changes for specimens ranging in size from 2.74 to 4.77 mm.

Pereopod 3 coxa not fused to pereonite 3, length 2.2× depth, without anteroventral lobe; basis, length 1.7× breadth, evenly rounded, with simple setae along anterior margin, without denticles along anterior margin; ischium long, length 1.6× breadth; merus short, length 0.8× breadth, without ridges. *Pereopod 4* coxa not fused to pereonite 4, length 2× depth, without anteroventral lobe; basis length 1.3× breadth, with simple setal group midway along anterior margin; ischium long, length 2× breadth; merus short, length 1× breadth. *Pereopod 5* coxa length 1.3× depth, without patches of small setae, without setae along ventral margin; merus with anterior lobe not extending beyond anterior margin of carpus, posterior lobe with 4 plumose setae; propodus with 1 seta along posterior margin; dactylus short, uncinate with one accessory hook. *Pereopod 6* coxa without setal fringe ventrally, without patch of small setae near anterior margin; basis without patch of small setae near anterior margin; merus, length 1.2× breadth; dactylus short, uncinate, with two accessory hooks. *Pereopod 7* coxa without posterodorsal lobe, without patch of small setae; merus, length 1.7× breadth; dactylus, short, uncinate, with two accessory hooks.
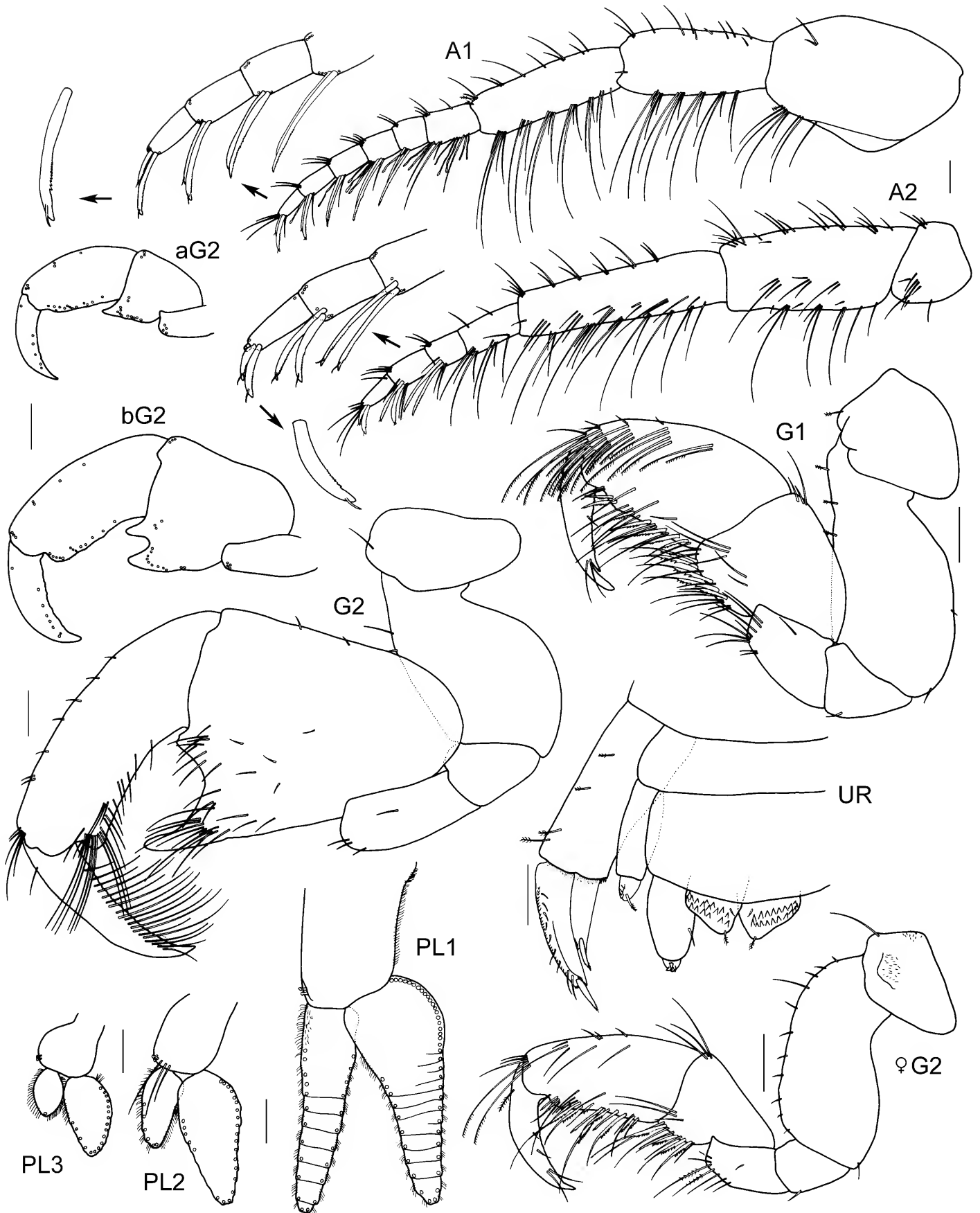
Fig. 1. *Cerapus bundegi* n.sp., holotype male, 4.77 mm (P62291), paratype female, 3.85 mm (P62385), paratype male "a", 2.74 mm (P62384), paratype male "b", 3.54 mm (P62383). South Mole, Arthur Head, Fremantle, Western Australia. Scales represent 0.1 mm.
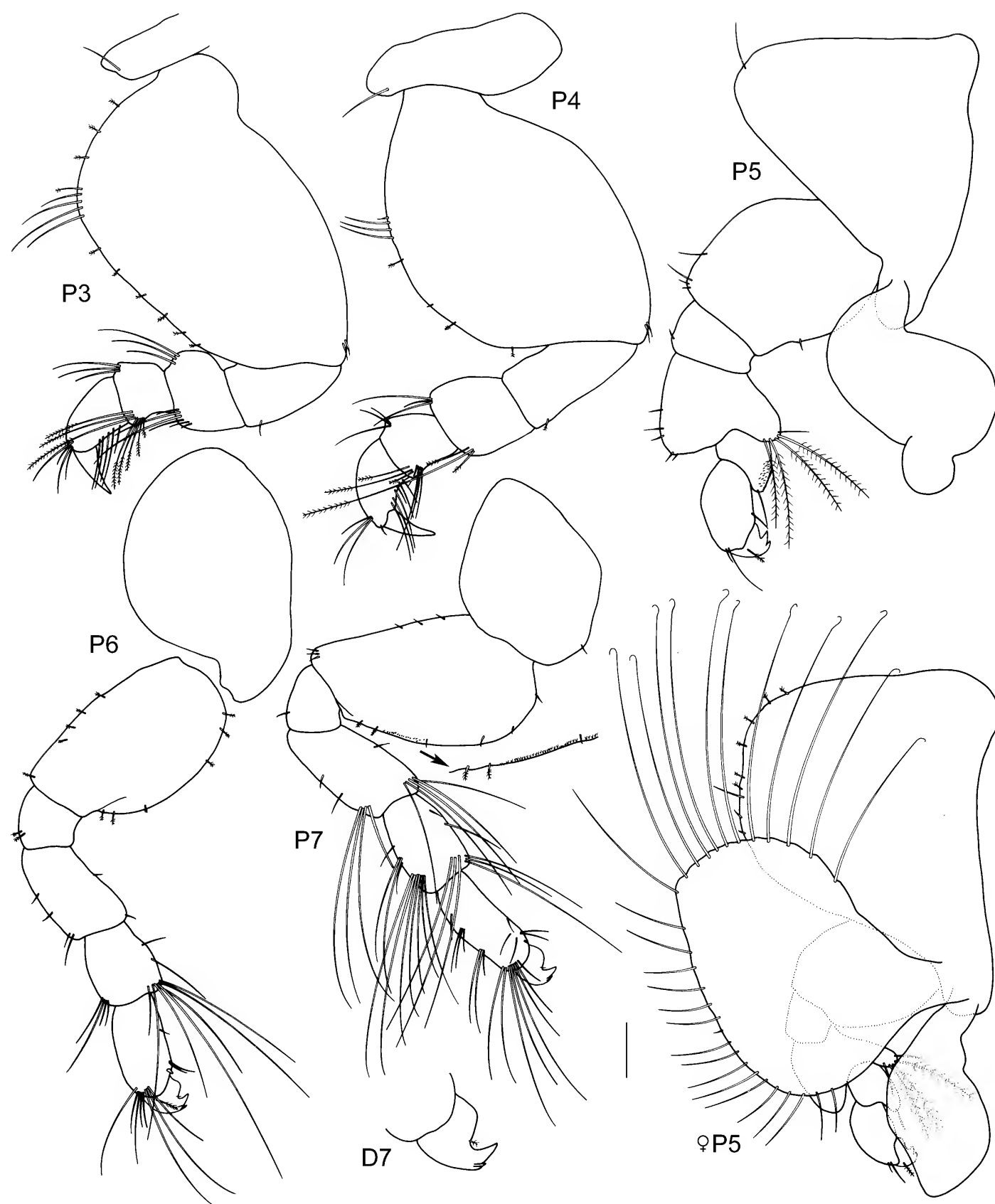
Fig. 2. *Cerapus bundegi* n.sp., holotype male, 4.77 mm (P62291), paratype female, 3.85 mm (P62385). South Mole, Arthur Head, Fremantle, Western Australia. Scales represent 0.1 mm.

Pleon. *Pleopods 1 to 3* decreasing in size. *Pleopod 1* inner ramus 8-articulate; outer ramus 8-articulate, article 1 evenly swollen. *Pleopod 2* biramous; inner ramus reduced, 1-articulate; outer ramus, broad, 1-articulate. *Pleopod 3* present; inner ramus present, reduced; 1-articulate. *Uropod 1* biramous, peduncle with distoventral corona of cuticular teeth, length 1.4× outer ramus; rami with distoventral corona of cuticular teeth; outer ramus with lateral row of denticles, without medial setae, with 9 lateral setae, with large apical robust seta without smaller slender setae; inner ramus, length 0.5× outer ramus, without medial or lateral setae, with large apical robust seta without smaller slender setae. *Uropod 2* uniramous, length of

peduncle 2.4× breadth, 3.8× ramus; ramus small, with 4 denticles and 1 apical seta. *Uropod 3* uniramous, peduncle length 1.5× breadth; ramus with 3 curved hooks. *Telson* length 0.5× breadth, moderately cleft, 0.6× length, each lobe with 17–18 anteriorly directed hooks, in 2 rows.

Female (sexually dimorphic characters). Based on paratype female, 3.85 mm (P62385). *Antenna 1* flagellum 4-articulate. *Pereonite 2* without sternal keel. *Pereonite 5* length 1.5× depth. *Gnathopod 1* coxa length 1.7× depth; basis length 2.3× depth; carpus, length 1.1× depth with setose posterior lobe. *Gnathopod 2* subchelate; coxa length 1.9× depth; basis slender, length 1.8× breadth; carpus short, compressed, length 1.3× breadth. *Pereopod 5* coxa length 1.5× depth, with setae along ventral margin. *Oostegites* from gnathopod 2 to pereopod 5.

Etymology. The species is named after Bundegi Reef, in the northern part of its range.

Tube. Wrapped, parchment-like; seagrass and algae "wrapped" to form a tube.

Habitat. Littoral, 0.5 to 6 m depth.

Life-style. Epifaunal sediment, algal or seagrass dwellers.

Remarks. *Cerapus bundegi* is a common, widespread species along the western Australian coast. The tubes of *C. bundegi* and *C. volucola* are almost identical, but morphologically the species differ in many ways. The most obvious differences are the shape of male gnathopod 2, and the number of dorsal recurved hooks on the telson (17–18 in *C. bundegi* and 14–15 in *C. volucola*).

Distribution. *Western Australia*: Malus Island, Kendrew Island, Nelson Rocks, Tish Point, Rosemary Island, all in the Dampier Archipelago; Bundegi Reef, Exmouth Gulf, Ned's Camp, Cape Range National Park; Red Bluff, Kalbarri; Champion Bay, Geraldton; Seven Mile Beach; Cottesloe Beach, Perth; Cape Peron; South Mole, Arthur Head, Fremantle (20°S to 32°S).

Cerapus murrayae n.sp.

Figs. 3–6

Type material. HOLOTYPE, ♂, 7.04 mm, AM P31037; PARATYPE, ♀, 4.64 mm, AM P51220; PARATYPE, ♂, 4.32 mm, AM P51218; PARATYPE, ♂, 3.04 mm, AM P51219; PARATYPE, ♂, 6.08 mm, AM P61568; PARATYPE, ♂, 8.9 mm, AM P62508; 36 PARATYPES, AM P61567; near bridge, Queenscliff Lagoon, Queenscliff, New South Wales, Australia, 33°47.1'S 151°16.8'E, washed in at high tide on drift algae *Lobophora variegatus* or *Zonaria*, intertidal, A. Murray, 26 October 1980. PARATYPE, ♂, 5.08 mm, AM P61569, Balmoral Beach, New South Wales, Australia, 32°49.6'S 151°15.2'E, C. Short, 3 m, sand, 7 September 1978. PARATYPE, ♂, AM P61570, 150 m N of Horseshoe Bay, Trial Bay, New South Wales, Australia, 30°53'S 153°03'E, sediment and detritus from around reef edge, hand dredge, 7 m, R.T. Springthorpe, 15 June 1986. PARATYPE, ♂, AM P61571, Split Solitary Island, New South Wales, Australia, 30°14.61'S 153°10.73'E, *Zonaria* sp., soft corals, bryozoans and sponges, 18 m, P.B. Berents, J.K. Lowry and R. Peart, 12 February 2000.

Diagnosis. Head, rostrum short, apically acute; anteroventral corner subquadrate. Antenna 1 peduncular article 1 longer than article 3, slightly swollen along posterior margin. Pereonite 2 without sternal keel. **Pereopod 5 merus posterior lobe with 7 plumose setae**.

Description. Based on holotype male, 7.04 mm (P31037). **Head**, rostrum short, apically acute, length 0.2× head; lateral cephalic lobe with ventral corner rounded, subocular margin deeply recessed, anteroventral corner subquadrate, ventral margin horizontal, posterior margin vertical. *Antenna 1* long, length 0.5× body length; peduncular article 1 longer than (1.2×) peduncular article 3, not produced anterodistally and anteromedially, slightly swollen along posterior margin, posterodistal corner not produced; flagellum 6-articulate; article 1 short. *Antenna 2* subequal in length to antenna 1; flagellum 6-articulate; article 1 long. *Epistome and upper lip* fused, straight. *Mandible* with palp article 2 long and slender, length 3.4× breadth, 1.4× article 3; palp article 3 slender, blade-like, long, 3.1× breadth.

Pereon. *Pereonite 1* with lateral keel; without sternal keel. *Pereonite 2* without sternal keel. *Pereonite 3* without sternal keel. *Pereonite 5* length 2× depth.

Gnathopod 1 coxa not fused to pereonite 1, length 1.4× depth, without anteroventral lobe; basis length 1.8× depth; carpus length 1.3× depth with setose posterior lobe, broad; palm extremely acute, with simple robust setae. *Gnathopod 2* carpochelate; coxa not fused to pereonite 2, length 1.6× depth, without anteroventral lobe or cusp; basis short, broad, length 1.3× breadth; carpus long, broad, length 1.2× breadth; palm shallowly excavate, anterodistal tooth small, located near articulation with propodus, posterodistal tooth well defined, medium in size, length 1.4× width; propodus very broad, slightly curved, length 2.2× width, without tooth on posterior margin, posterodistal corner smooth, without tooth; dactylus, length 0.7× propodus.

Pereopod 3 coxa fused to pereonite 3, with broad anteroventral lobe; basis, length 1.7× breadth, evenly rounded, with simple setae along anterior margin, without denticles along anterior margin; ischium long, length 2.8× breadth; merus short, length 1× breadth, without ridges. *Pereopod 4* coxa fused to pereonite 4, with anterior lobe; basis length 1.3× breadth, with simple setal group midway along anterior margin; ischium long, length 2.1× breadth; merus short, subequal in length 1 to breadth. *Pereopod 5* coxa length 1.2× depth, without patches of small setae, with setae along ventral margin; merus with anterior lobe extending beyond anterior margin of carpus, posterior lobe with 7 plumose setae; propodus with 3 setae along posterior margin; dactylus short, uncinate with one accessory hook. *Pereopod 6* coxa without setal fringe ventrally, without patch of small setae near anterior margin; basis without patch of small setae near anterior margin; merus, length 2× breadth; dactylus short, uncinate, with two accessory hooks. *Pereopod 7* coxa without posterodorsal lobe, without patch of small setae; merus, length 1.6× breadth; dactylus, short, uncinate, with two accessory hooks.

Pleon. *Pleopods 1 to 3* decreasing in size. *Pleopod 1* inner ramus 9-articulate; outer ramus 3-articulate, article 1 with medial lobe. *Pleopod 2* biramous; inner ramus reduced, 1-articulate; outer ramus, broad, 1-articulate. *Pleopod 3* present; inner ramus present, reduced; 1-articulate; outer ramus broad, 1-articulate. *Uropod 1* biramous, peduncle with distoventral corona of cuticular teeth, length 1.5× outer ramus; rami with distoventral corona of cuticular teeth; outer ramus with lateral row of denticles, without medial setae, and with 5 lateral setae, with large apical robust seta without smaller slender setae; inner ramus, length 0.7× outer ramus, without medial or lateral setae, with large apical robust seta without smaller slender setae. *Uropod 2* uniramous, length of peduncle 2.8× breadth, 5.8× ramus; ramus small, with 4 denticles and 1 apical seta. *Uropod 3* uniramous, peduncle
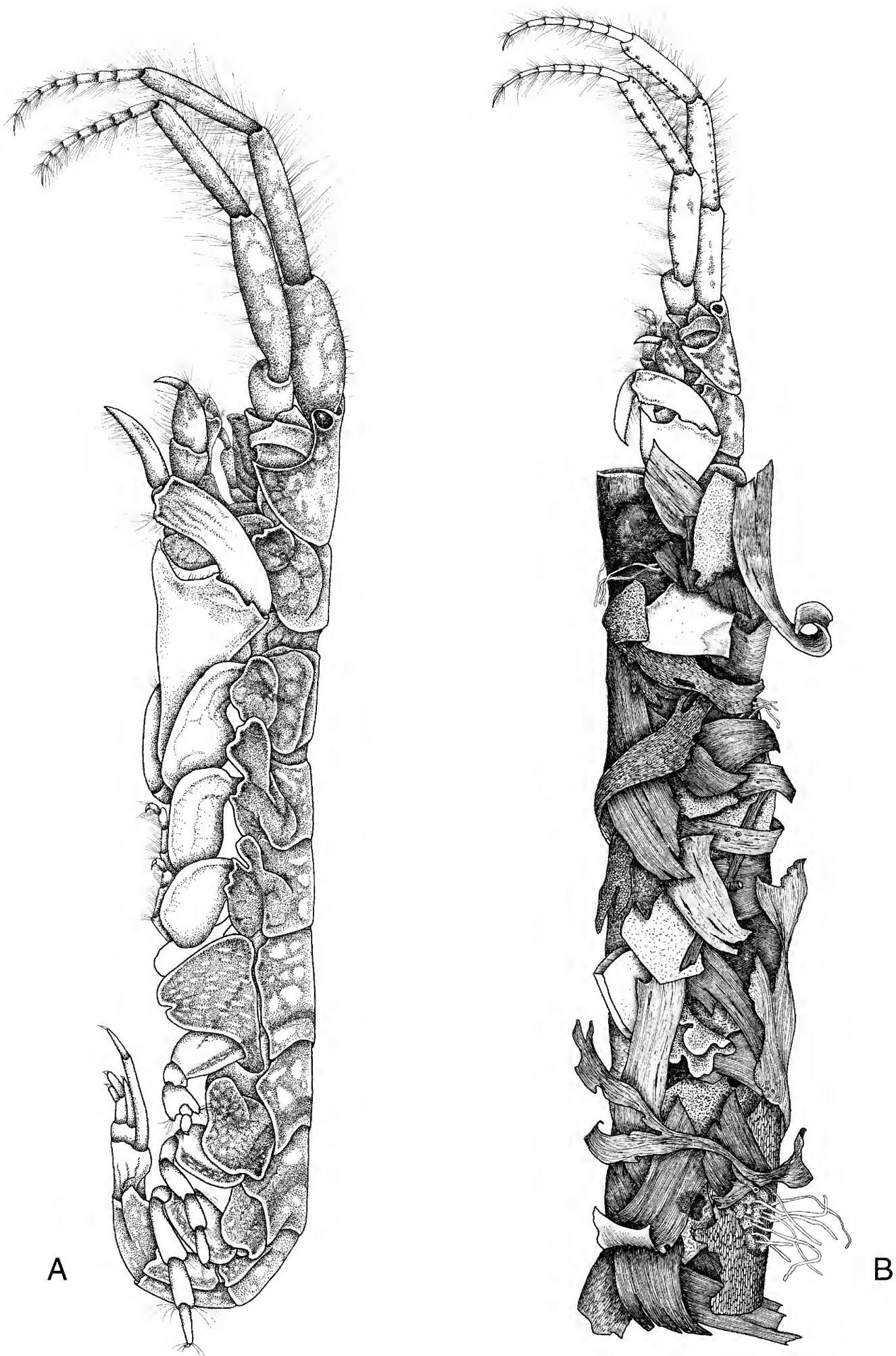
Fig. 3. *Cerapus murrayae* n.sp., Queenscliff Lagoon, New South Wales: (*A*), adult male; (*B*), tube with male protruding.
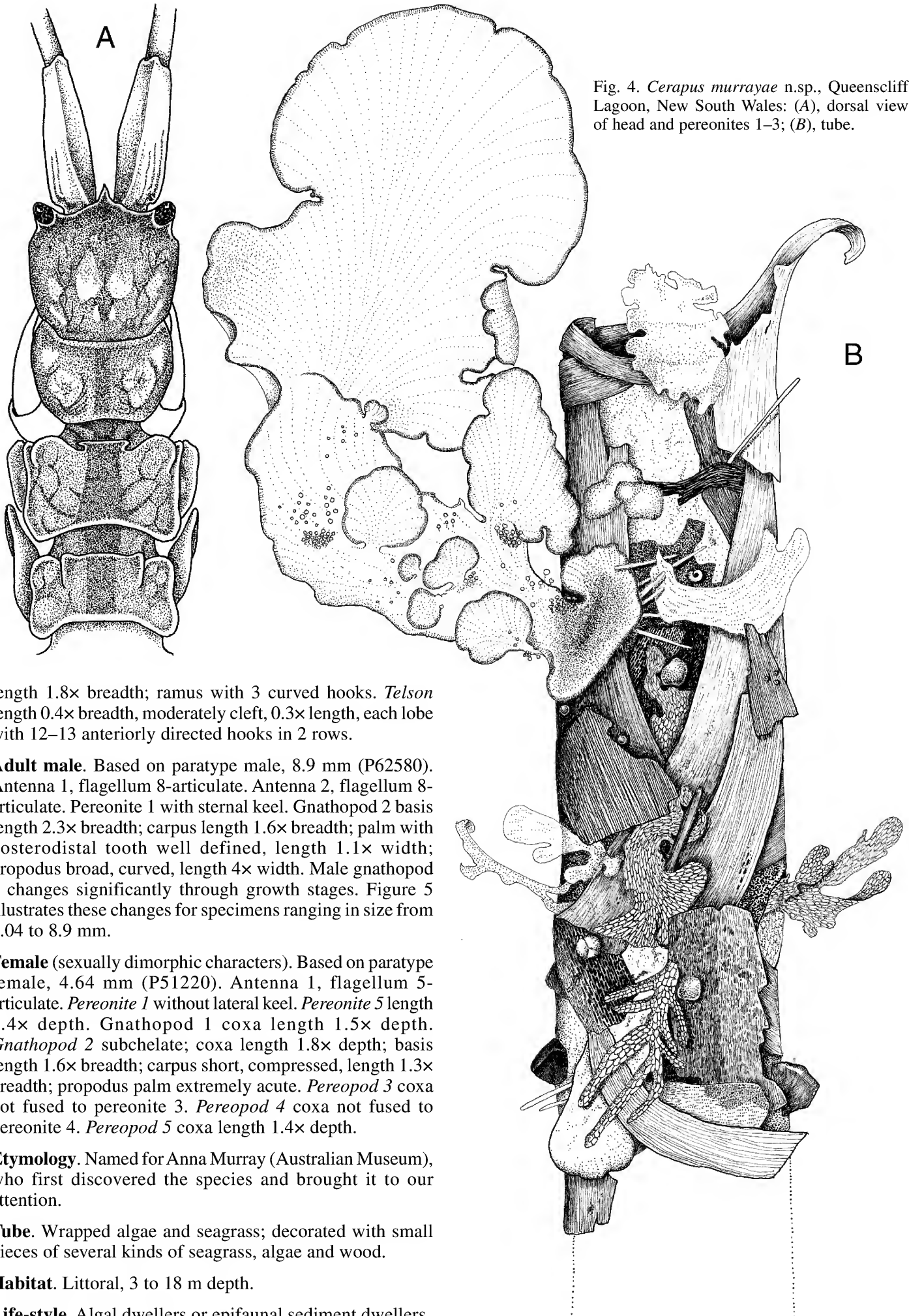
Fig. 4. *Cerapus murrayae* n.sp., Queenscliff Lagoon, New South Wales: (*A*), dorsal view of head and pereonites 1–3; (*B*), tube.

length 1.8× breadth; ramus with 3 curved hooks. *Telson* length 0.4× breadth, moderately cleft, 0.3× length, each lobe with 12–13 anteriorly directed hooks in 2 rows.

Adult male. Based on paratype male, 8.9 mm (P62580). Antenna 1, flagellum 8-articulate. Antenna 2, flagellum 8-articulate. Pereonite 1 with sternal keel. Gnathopod 2 basis length 2.3× breadth; carpus length 1.6× breadth; palm with posterodistal tooth well defined, length 1.1× width; propodus broad, curved, length 4× width. Male gnathopod 2 changes significantly through growth stages. Figure 5 illustrates these changes for specimens ranging in size from 3.04 to 8.9 mm.

Female (sexually dimorphic characters). Based on paratype female, 4.64 mm (P51220). Antenna 1, flagellum 5-articulate. *Pereonite 1* without lateral keel. *Pereonite 5* length 1.4× depth. Gnathopod 1 coxa length 1.5× depth. *Gnathopod 2* subchelate; coxa length 1.8× depth; basis length 1.6× breadth; carpus short, compressed, length 1.3× breadth; propodus palm extremely acute. *Pereopod 3* coxa not fused to pereonite 3. *Pereopod 4* coxa not fused to pereonite 4. *Pereopod 5* coxa length 1.4× depth.

Etymology. Named for Anna Murray (Australian Museum), who first discovered the species and brought it to our attention.

Tube. Wrapped algae and seagrass; decorated with small pieces of several kinds of seagrass, algae and wood.

Habitat. Littoral, 3 to 18 m depth.

Life-style. Algal dwellers or epifaunal sediment dwellers.
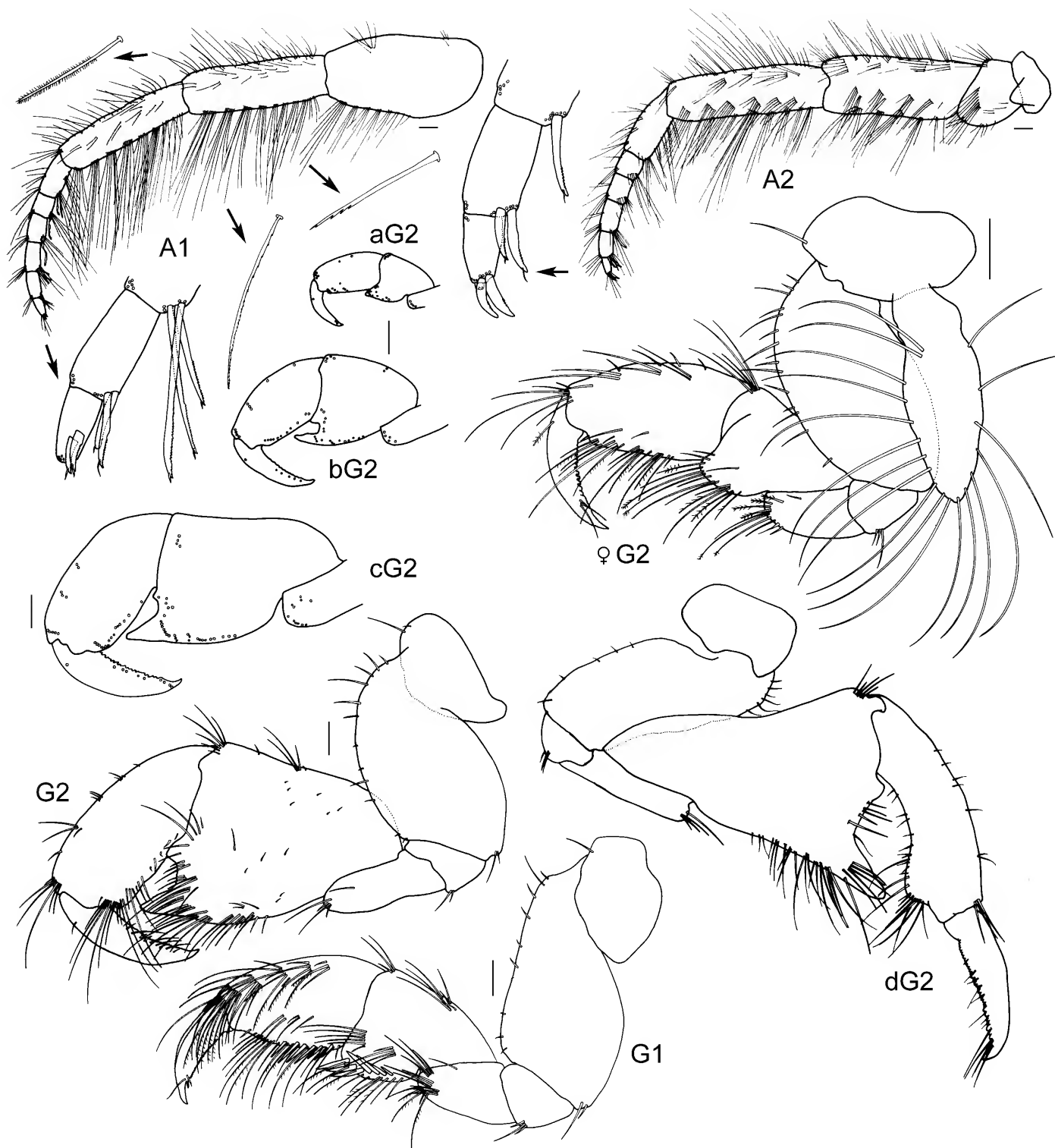
Fig. 5. *Cerapus murrayae* n.sp., holotype male, 7.04 mm (P31037), paratype female, 4.64 mm (P51220), paratype male "a", 3.04 mm (P51219), paratype male "b", 4.32 mm (P51218), paratype male "c", 6.08 mm (P61568) and paratype male "d", 8.9 mm (P62508), Queenscliff Lagoon, New South Wales. Scales for MD represent 0.05 mm; remainder represent 0.1 mm.

Remarks. *Cerapus murrayae* is currently known only from the New South Wales central coast, the most restricted distribution of the three known species that make parchment-like tubes. These spectacular tubes, decorated with pieces of algae, distinguish *C. murrayae* from *C. bundegi* and *C. volucola*. Morphologically *C. murrayae* can be distinguished from both *C. bundegi* and *C. volucola* by the shape of the male gnathopod 2 and the number of dorsal recurved hooks on the telson (17–18 in *C. bundegi* and 14–15 in *C. volucola*) is different.

Distribution. *New South Wales*: Horseshoe Bay, Trial Bay;

Split Solitary Island; Queenscliff Lagoon, Queenscliff; Balmoral Beach, Middle Harbour.

Cerapus volucola n.sp.

Figs. 7–9

Type material. HOLOTYPE, ♂, 3.20 mm, AM P62408; 12 PARATYPES, AM P62407; PARATYPE, ♂, 2.84 mm, AM P62409; PARATYPE, ♀, 3.92 mm, AM P62410; False Orford Ness, northeast of Cape York, Queensland, Australia, 11°23'S 142°52'E, rock, brown algae and sand, 4 m, D. Blake, 18 February 1979.

Fig. 6. *Cerapus murrayae* n.sp., holotype male, 7.04 mm (P31037), Queenscliff Lagoon, New South Wales. Scales represent 0.1 mm.

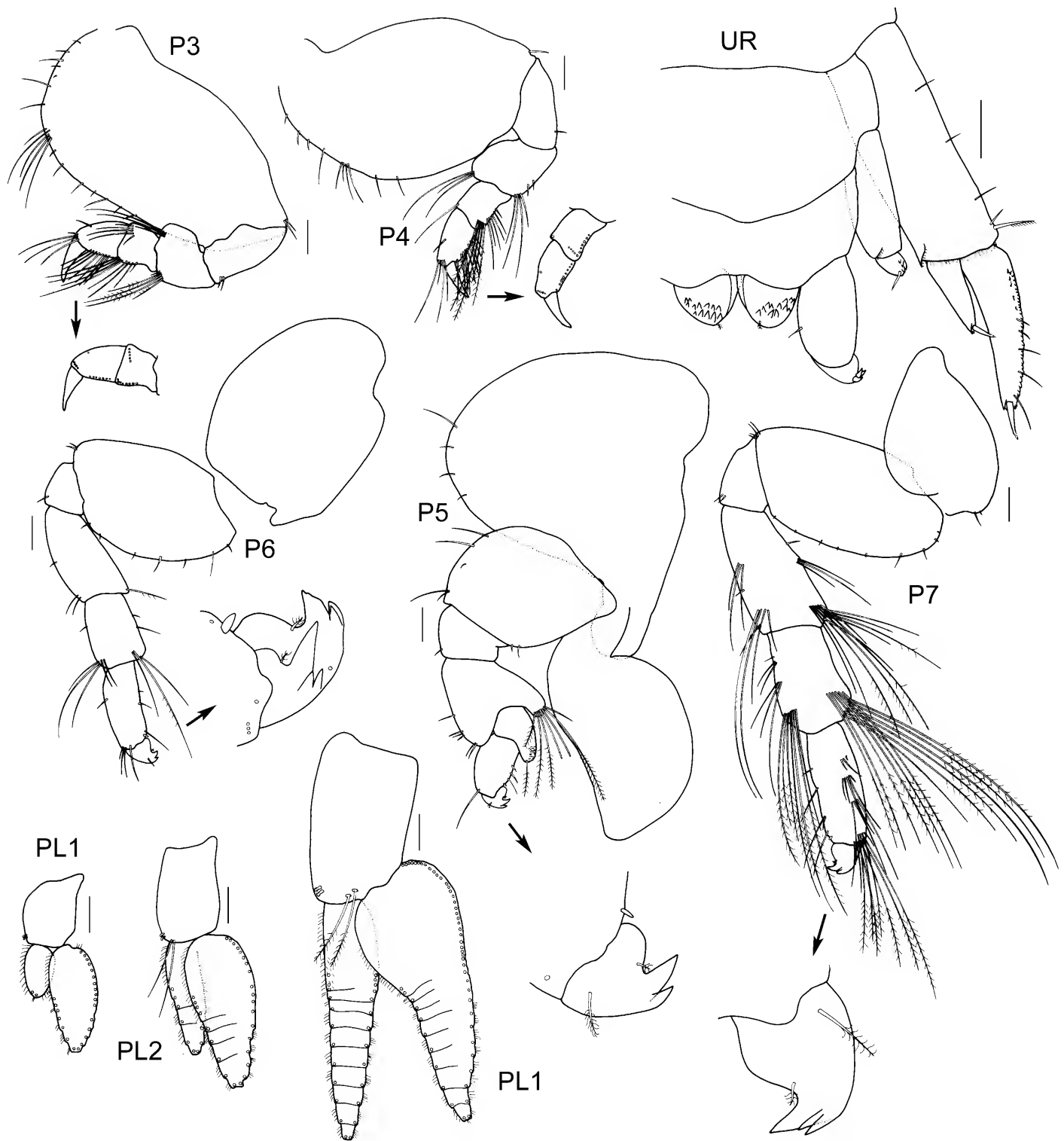**Additional material**. 1♂, AM P62419; 2 specimens, AM P62413, Padoz Natun reef, Madang Lagoon, Papua New Guinea, 5°09.60'S 145°48.77'E, *Halimeda* & epiphytic algae on rubble consolidated by sponges, 8 m, D. Gochfeld, 15 December 1993; 1♀, AM P62414, Padoz Natun reef, Madang Lagoon, Papua New Guinea, 5°09.60'S 145°48.77'E, *Halimeda* & epiphytic algae on rubble consolidated by sponges, 8 m, D. Gochfeld, 2 January 1994. 3 specimens, AM P62411, half way between Lizard Island and Carter Reef, Queensland, Australia, 14°37'S 145°33'E, 38 m, J.Leis, 26 November 1981. 5 specimens, AM P62417, Magnetic Island, Queensland, Australia, 19°8'S 146°50'E, among *Sargassum*, 3 m, G. Edgar 13 August 1981. 1 ovigerous female, AM P62415, north Wistari Reef, Capricorn Group, Great Barrier Reef, Queensland, Australia, 23°29'S 151°53'E, coral sand, 24 m, D. Fisk, 11 November 1978; 1♀, AM P62416, northwest Wistari Reef, Great Barrier Reef, Queensland, Australia, 23°29'S 151°53'E, sand, 24 m, D. Fisk, 16 December 1978. 1♀, AM P62418, Middle Reef, North Stradbroke Island, Queensland, Australia, 27°24.4'S 153°32'E, *Zonaria*, 20 m, K.B. Attwood and E.L.A. Ho, 4 June 1993.

Diagnosis. Head, rostrum long, apically acute; **antero-ventral corner rounded. Antenna 1 peduncular article 1 longer than article 3, swollen along posterior margin.** Pereonite 2 without sternal keel. Pereopod 5 merus posterior lobe with 2 plumose setae.

Description. Based on holotype male, 3.20 mm (P62408) and paratype female, 3.92 mm (P62410). With chocolate-coloured stripe around margin of head and dorsal surface of peduncle of antenna 1. **Head**, rostrum long, apically acute, length 0.3× head; lateral cephalic lobe with ventral corner rounded, subocular margin weakly recessed, anteroventral corner rounded, ventral margin horizontal, posterior margin vertical. *Antenna 1* long, length 0.5× body
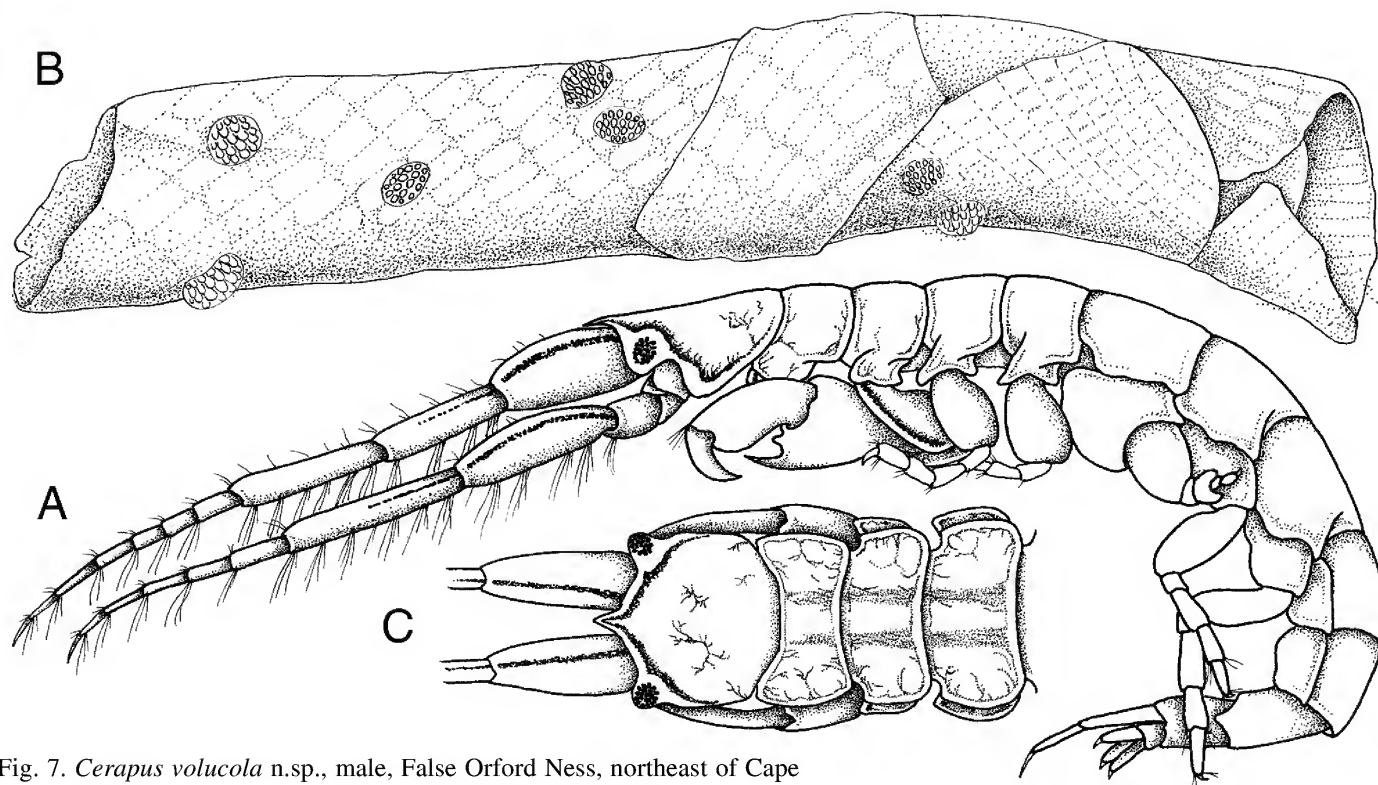
Fig. 7. *Cerapus volucola* n.sp., male, False Orford Ness, northeast of Cape York, Queensland: (*A*), whole animal; (*B*), tube; (*C*), dorsal view of head.

length; peduncular article 1 longer than (1.2×) peduncular article 3, not produced anterodistally and anteromedially, swollen along posterior margin, posterodistal corner not produced; flagellum 6-articulate; article 1 short. *Antenna 2* length 1× antenna 1; flagellum 6-articulate; article 1 short. *Epistome and upper lip* fused, straight. *Mandible* with palp article 2 long and slender, length 2.7× breadth, 1.1× article 3; palp article 3 slender, blade-like, long, 3.5× breadth.

Pereon. *Pereonites 1 to 3* without lateral or sternal keels. *Pereonite 5* length 1.6× depth.

Gnathopod 1 coxa fused to pereonite 1, without anteroventral lobe; basis length 1.75× depth; carpus, length 1.25× depth with setose posterior lobe, broad; palm extremely acute, with barbed robust setae. *Gnathopod 2* carpochelate; coxa fused to pereonite 2, without antero-ventral lobe or cusp; basis short, broad, length 1.35× breadth; carpus long, broad, length 1.1× breadth; palm deeply excavate, anterodistal tooth large, located distal to articulation with propodus, posterodistal tooth well defined, medium, length 1.3× width; propodus very broad, slightly curved, length 2.5× width, without tooth on posterior margin, posterodistal corner smooth, without tooth; dactylus, length 0.7× propodus.

Pereopod 3 coxa fused to pereonite 3, with narrow anteroventral lobe; basis, length 1.5× breadth, evenly rounded, with plumose setal group and simple setae along anterior margin, without denticles along anterior margin; ischium long, length 1.6× breadth; merus short, length 1× breadth, without ridges. *Pereopod 4* coxa fused to pereonite, with anterior lobe; basis length 1.3× breadth, with plumose setal group midway along anterior margin; ischium long, length 1.8× breadth; merus short, length 1× breadth. *Pereopod 5* coxa length 1.3× depth, without patches of small setae, without setae along ventral margin; merus with anterior lobe extending beyond anterior margin of carpus, posterior lobe with 2 plumose setae; propodus with 1 seta

along posterior margin; dactylus short, uncinate with one accessory hook. *Pereopod 6* coxa without setal fringe ventrally, without patch of small setae near anterior margin; basis without patch of small setae near anterior margin; merus, length 1.6× breadth; dactylus short, uncinate, with two accessory hooks. *Pereopod 7* coxa without postero-dorsal lobe, without patch of small setae; merus, length 2.2× breadth; dactylus, short, uncinate, with two accessory hooks.

Pleon. *Pleopods 1 to 3* decreasing in size. *Pleopod 1* inner ramus 7-articulate; outer ramus 5-articulate, article 1 evenly swollen. *Pleopod 2* biramous; inner ramus reduced, 1-articulate; outer ramus, broad, 2-articulate. *Pleopod 3* present; inner ramus present, reduced; 1-articulate. *Uropod 1* biramous, peduncle with distoventral corona of cuticular teeth, length 1.3× outer ramus; rami with distoventral corona of cuticular teeth; outer ramus with lateral row of denticles, without medial setae, with 5 lateral setae, with large apical robust seta without smaller slender setae; inner ramus, length 0.6× outer ramus, without medial or lateral setae, with large apical robust seta without smaller slender setae. *Uropod 2* uniramous, length of peduncle 2.5× breadth, 4.6× ramus; ramus small, with 4 denticles and 1 apical seta. *Uropod 3* uniramous, peduncle length 1.5× breadth; ramus with 3 curved hooks. *Telson* length 0.4× breadth, moderately cleft, 0.6× length, each lobe with 14–15 anteriorly directed hooks in 2 rows.

Female (sexually dimorphic characters). Based on paratype female, 3.92 mm (P62410). *Gnathopod 1* coxa not fused to pereonite 1, length 1.5× depth; basis length 2.3× depth; carpus, length 1.1× depth with setose posterior lobe, narrow. *Gnathopod 2* subchelate; basis length 1.6× breadth; carpus length 1.3× breadth; propodus palm extremely acute; dactylus length 0.8× propodus. *Oostegites* from gnathopod 2 to pereopod 5.

Etymology. The species name is derived from the Latin words *volumen* for scroll and *cola* for inhabit.

Fig. 8. *Cerapus volucola* n.sp., holotype male, 3.20 mm (P62408), paratype female, 3.92 mm (P62410). False Orford Ness, northeast of Cape York, Queensland. Scales represent 0.1 mm.

Tube. Wrapped, parchment-like; seagrass and algae "wrapped" to form a tube.

Habitat. Littoral, 3 to 38 m depth.

Life-style. Algal or seagrass dwellers.

Remarks. *Cerapus volucola* is a widespread species known from Madang Lagoon in northern Papua New Guinea, all along the Great Barrier Reef in northeastern Australia, to North Stradbroke Island in southern Queensland. The tubes of *C. bundegi* and *C. volucola* are almost identical, but morphologically the species differ in many ways. The most obvious differences are the shape of male gnathopod 2, and the number of dorsal recurved hooks on the telson (17–18 in *C. bundegi* and 14–15 in *C. volucola*).

Distribution. *Papua New Guinea*: Padoz Natun reef, Madang Lagoon. *Australia, Queensland*: False Orford Ness, northeast of Cape York; Lizard Island and Carter Reef; Magnetic Island; Wistari Reef, Capricorn Group; Middle Reef, North Stradbroke Island (5°S to 27 °S).
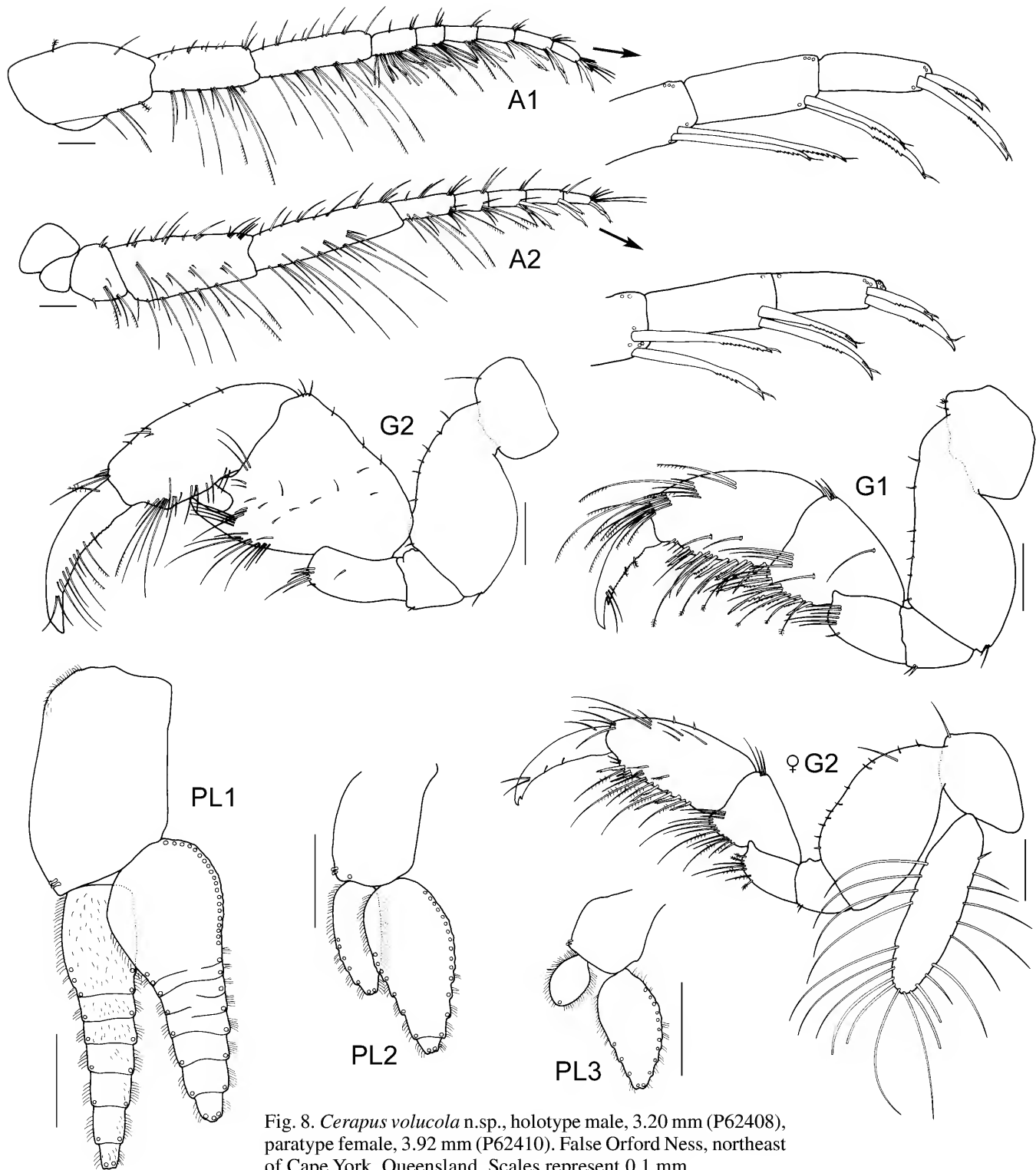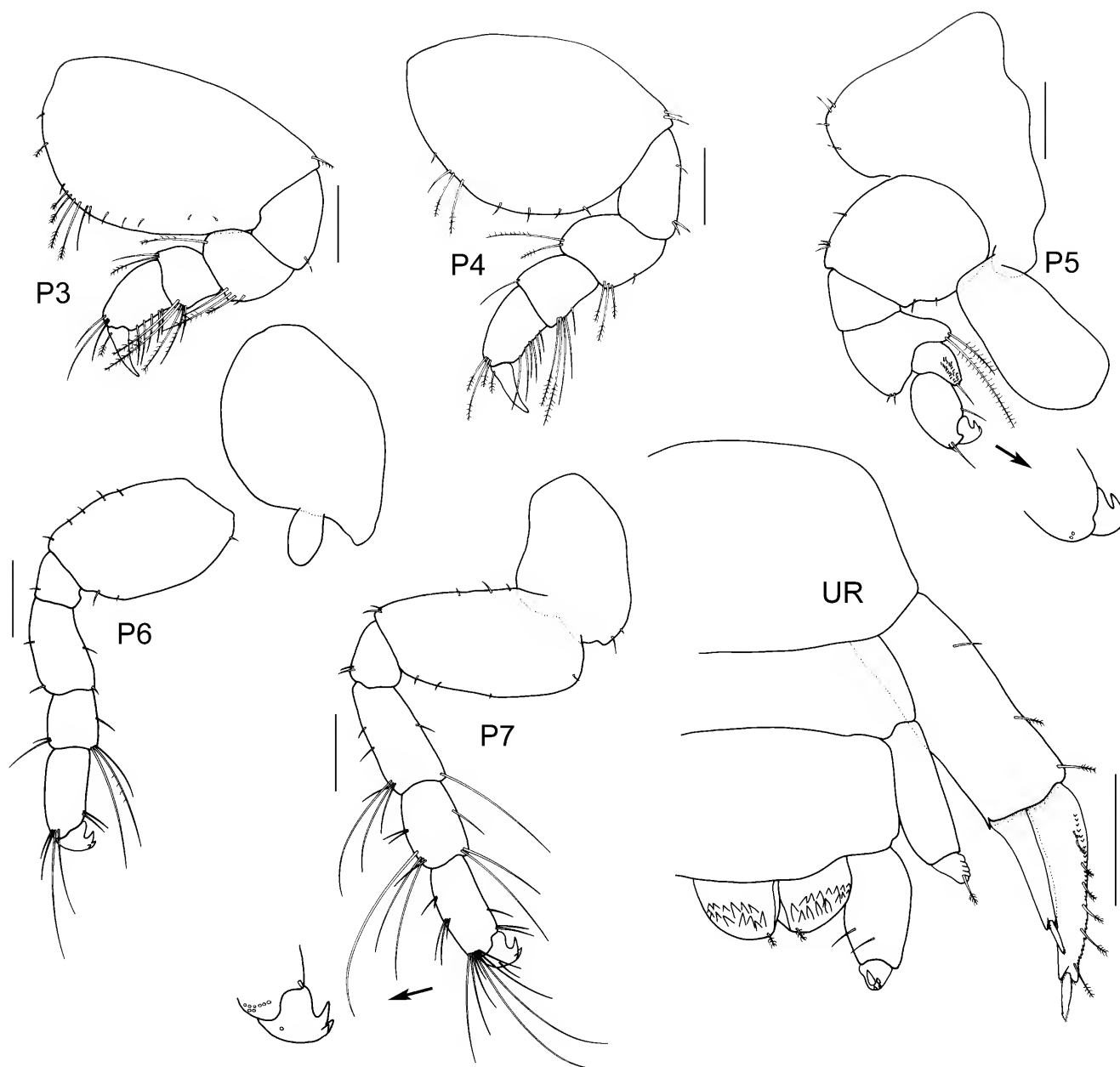
Fig. 9. *Cerapus volucola* n.sp., holotype male, 3.20 mm (P62408). False Orford Ness, northeast of Cape York, Queensland. Scales represent 0.1 mm.

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A Review of the Australian Fossil Storks
of the Genus *Ciconia* (Aves: Ciconiidae),
With the Description of a New Species

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ABSTRACT. Only a single species of stork, the Black-necked Stork *Ephippiorhynchus* (= *Xenorhynchus*) *asiaticus*, occurs in Australia today, and is known from several fossil localities from the Early Pliocene. Two species of smaller fossil storks are also known, one previously named and one described here. The former, found in the Darling Downs, southeastern Queensland, was named *Xenorhynchus nanus* De Vis, 1888. Some later authors suggested that this species should be transferred to the living genus *Ciconia*; this decision is confirmed here, the name for this species becoming *Ciconia nana*. The second species of small stork comes from several Late Oligocene and Early Miocene sites at Riversleigh, northwestern Queensland. This taxon is referred to the genus *Ciconia* and distinguished as a new species, *C. louisebolesae*. It constitutes the earliest record of the Ciconiidae from Australia.

The classification of living storks (Ciconiidae) by Kahl (1979) admitted 17 species in six genera in three tribes, whereas that of Hancock *et al.* (1992) recognized 19 species in six genera in two tribes. The family is represented in Australia by a single living species, the Black-necked Stork, or Jabiru, *Ephippiorhynchus* (= *Xenorhynchus* auct.) *asiaticus* (Latham, 1790).

Storks are rather well represented in the world fossil record, although no comprehensive review of them has been attempted. The earliest records come from the Late Eocene of Egypt (Ciconiidae gen. and sp. indet. and *Leptoptilos* sp. indet.) (Miller *et al.*, 1997). After taxa incorrectly referred to this family were removed (Olson, 1985), the earliest named species became *Palaeoephippiorhynchus dietrichi* Lambrecht, 1930 (Late Oligocene; Egypt). The identity of

the older *Eociconia sangequanensis* Hou, 1989 (Middle Eocene; China) as a stork needs to be confirmed (Unwin, 1993). Other Tertiary-aged storks are known from North America, Europe and Asia (references in Olson, 1985; Bickart, 1990). Quaternary-aged palaeospecies are known for several extant genera.

The fossil record of this family in Australia has not been studied in detail. Much of the Australian fossil stork material is comparable in size and morphology to *E. asiaticus*. Specimens assigned to this species are known from Pliocene and Pleistocene localities in northeastern and southeastern Queensland and northeastern South Australia (Archer, 1976; Baird, 1991a; Boles & Mackness, 1994; Molnar & Kurz, 1997; Vickers-Rich, 1991).

The first stork reported from Australia was described by C.W. De Vis, who named several species (De Vis, 1888, 1892, 1905); however, all but *Xenorhynchus nanus* are now known to have been misidentified to family (amended family identifications summarized by van Tets & Rich, 1990). Material of a new species of stork from Oligo-Miocene deposits at Riversleigh, northwestern Queensland, was mentioned briefly in the literature with little elaboration (Boles, 1991, 1997; Vickers-Rich, 1991). It is the purpose of this study to review *X. nanus* and the undescribed Riversleigh stork. Both are here considered to belong to the extant genus *Ciconia*. This genus has an extensive fossil record. Three of the living species of *Ciconia* have been recorded from Quaternary deposits (Brodkorb, 1963). Several fossil taxa have been assigned to *Ciconia*, but many are based on single specimens. A large, but unnamed species of *Ciconia* from the Late Miocene-Early Pliocene of Arizona is known from numerous skeletal elements (Bickart, 1990), as is another large form, *C. maltha* L. Miller, 1910, from the Quaternary of North America and Cuba (Miller, 1910; Howard, 1942; Feduccia, 1967). Other palaeospecies include *C. stehlini* Jánossy, 1992 (Early Pleistocene, Hungary, tarsometatarsi, tibiotarsi, ulna, phalanges), *C. gaudryi* Lambrecht, 1933 (Late Pliocene of Greece, humerus), *C. minor* Harrison, 1980 (Late Miocene, Kenya, distal femur) and *C. sarmatica* Grigorescu & Kessler, 1977 (Late Miocene, Romania, proximal carpometacarpus). Lambrecht (1933) cited records of indeterminate species of *Ciconia* from the Pleistocene of California and Late Pliocene of France, and Olson & Rasmussen (2001) recorded two indeterminate species from North Carolina, one Middle Miocene in age, the other Early Pliocene. Late Pleistocene or Quaternary reports of this genus include those by Ono (1984; Honshu, Japan; *Ciconia* sp.), Steadman *et al.* (1994; northeast Mexico; *Ciconia* sp. or *Mycteria* sp.) and Suarez & Olson (2003; Cuba; *Ciconia* sp.).

Species of *Ciconia* and *Mycteria* are rather generalized in their morphology compared to the large, long-legged *Ephippiorhynchus* and *Jabiru*, the heavy-bodied *Leptoptilos* and somewhat aberrant *Anastomus*. Any fossil stork remains not exhibiting characters of these more distinctive genera were frequently allocated to one of the more "typical" ones. The problem of deciding whether a fossil form based on single or fragmentary elements has been correctly assigned to genus is compounded by the heavy reliance by the current taxonomy on behavioural (Kahl, 1972, 1979; Slikas, 1998) or molecular characters (Slikas, 1997).

Materials and methods

Taxonomic nomenclature follows Kahl (1979). Osteological terminology follows Baumel & Witmer (1993), except that as terms of position and direction anterior is used rather than rostral or cranial and posterior rather than caudal. Most of the measurements follow the methods of Steadman (1980) or van den Driesch (1976), and were made with digital calipers and rounded to the nearest 0.1 mm.

Several factors hamper the ease of using the fossil record of storks from elsewhere for evaluating that of Australia. Generic-level taxonomy of the Ciconiidae has changed substantially, with several formerly monotypic genera now merged with others. New palaeogenera were often based on material that exhibited some morphological intermediacy

between two nominal genera that have since been synonymised; this is particularly so in the expanded concept of *Ciconia*. The more inclusive generic concepts result in a broader morphological range across the constituent species, into which the palaeospecies may fit comfortably. Published diagnoses of such fossil forms must be assessed with caution because some of the characters may no longer apply to the genus *sensu lato*.

Another difficulty is that many of the species of fossil storks have been based on isolated fragments, confounding comparison between nominal taxa for which common osteological elements are not known. Moreover, many extant taxa are poorly represented in skeletal collections and of those specimens that do exist, individuals from zoos form a high proportion. In addition to any developmental abnormalities the latter may have, most likewise lack provenance and are frequently unsexed.

Osteological diagnosis of Ciconiidae

The skeletal elements can be recognized as belonging to this family on the basis of the following suites of characters. Diagnoses are restricted to those portions of the elements represented by the fossils, both here for the family and subsequently for generic level taxa in the respective species accounts.

Cranium. The lateral indentations at the orbits are shallow (in dorsal view); fossae glandulae nasalis are absent. The processus postorbitalis is long, and the temporal fossae well defined and rather extensive posteriorly. There is a single small circular fontanelle orbitocranialis situated at the posterior border of septum interorbitalis where it joins the braincase.

Quadrate. The anterior and posterior borders of the blade-like processus orbitalis are straight or slightly tapering through most of its length. The process is more or less straight (in posterior view) but not strongly flattened, with the distal end somewhat inflated; it is not incised posteriorly, twisted nor inflected medially or ventrally. The processus oticus is broad and not compressed laterally; the processus mandibularis is deep mediolaterally (in ventral view). The condylus medialis and combined condyli lateralis and caudalis are long and thin, and converge laterally at an acute angle; the sulcus intercondylaris is moderately large, particularly on its medial half. The short, broad projection of the condylus lateralis extends anteriorly along the lateral side, at its anterior end supporting the cotyla quadratojugalis, which is located just above the posteroventral border of the element; the part of the projection between the cotyla and the posterior end of the quadrate comprises about half of its length.

Humerus. The element has a pronounced sigmoid curvature, with a particularly marked anterior bend in the distal end (in dorsal view). *Proximal end*. In anterior view, the long axis and distal border of the caput humeri are oriented dorsodistally-ventroproximally; the caput humeri is moderately short. The sulcus ligamentum transversus and incisura capitis are deep. The tuberculum dorsale is distinct and triangular. The fossa pneumotricipitalis is large. The distal margin of the crista bicipitalis forms a nearly right

angle with the shaft. The intumescentia humeri is inflated, particularly distally. The crista deltopectoralis is prominent, with its apex more or less level with the distal end of the crista bicipitalis. *Distal end*. The fossa musculus brachialis is large and deep, particularly ventrodistally, and is angled sharply dorsoproximally-ventrodistally relative to the shaft. The tuberculum supracondylare ventrale is elongate and situated along a prominent ridge. The epicondylus ventralis is strongly produced as a triangular projection. The epicondylus dorsalis and processus flexorius are rudimentary. The ventral side of the distal end is flat (in anterior view) with the processus supracondylare dorsalis prominent, angling moderately to very abruptly to shaft. The fossa olecrani is broad and shallow, and extends proximally from, and dorsoventrally across, the condylus ventralis humeri.

Ulna. *Proximal end*. The proximal end is straight in relation to the shaft, i.e. there is no inflection from the midline of the shaft. The margins of the impressio m. brachialis are pronounced, with the anterior margin the more extensive distally. The tuberculum lig. collateralis ventralis is slightly bulbous but does not overhang the impressio m. brachialis and has a relatively short distal extension along its border. The incisura radialis is more proximodistally oval (narrower, longer) than circular and the impressio m. scapulotricipitalis is small with little distal extension.

Tibiotarsus. *Proximal end*. The proximal end is deeper than wide because the region level with the incisura tibialis between the cristae cnemialis and the facies articularis is elongated. The surface is mostly level, with a small to at most moderate rise towards the cristae cnemialis. The cristae cnemialis are not strongly developed proximally, but are rather broad (in proximal view). They form a more or less 90° angle, and from this junction, the crista cnemialis lateralis is about twice the length of the crista cnemialis cranialis. The crista cnemialis cranialis is situated towards, but not at, the medial edge, with only a slight indentation separating them; it is long distally, angling smoothly into the shaft (in medial view). There is an expanded articular surface at the end of the crista cnemialis lateralis with a flattened anterolateral face, which projects both anteromedially and posterolaterally (in proximal view). *Distal end*. The shaft is long, thin and straight, with the posterior surface rounded and the anterior surface flattened for most of its length, taken up by a very broad and shallow sulcus extensorius, which deepens for a short extent just proximal of the pons supratendineus. There is a large, prominent papilla for M. tibialis cranialis centred directly proximal to the area intercondylaris and level with the distal border of the pons supratendineus. The pons supratendineus is restricted to the medial half of shaft, with its distal border strongly developed into a ridge. The scar on the lateral face of the shaft is large and proximodistally elongated. The sulcus m. fibularis is moderately deep. The distal end of the element has little mediolateral expansion, and the medial border of the shaft does not flare strongly outwards proximal to the condylus medialis. The condyli lateralis and medialis are more or less parallel and directly distal to the respective borders of the shaft, are longer anteroposteriorly than proximodistally, and have about the same distal extension; the condylus lateralis extends further proximally. The condylus medialis is notched distally. The area inter-

condylaris is a deep circular pit centred on the midline of shaft, extending between the pons supratendineus and the condylus medialis. The sulcus intercondylaris is deep (in distal view) and the trochlea cartilaginis tibialis is shallow with prominent borders.

Tarsometatarsus. *Proximal end*. The eminentia intercotylaris is narrow, with the lateral border abrupt and the medial one sloping (in dorsal view). In proximal view, the rims of the cotylae are rounded and (in dorsal view) the medial rim of cotyla medialis is blunt or rounded. The hypotarsi comprises two parallel cristae hypotarsi separated by a single large sulcus hypotarsi, which is deep throughout its length; it is centred mediolaterally on the plantar face. There is no small secondary groove within the sulcus hypotarsi. *Distal end*. The sulcus extensorius occupies the greater part of the length of the anterior surface, making the distal third of the shaft relatively flat, and then angling from the midline of the shaft to the lateral side at the distal end, extending into the foramen vasculare distale but not beyond that into the incisura intertrochlearis lateralis. The fossa metatarsi I is a long proximodistally elongated oval, terminating distally on a ridge extending towards the trochlea metatarsi II. The fossa supratrochlearis plantaris is markedly excavated lateral to this ridge. The trochleae are not inflated proximally nor do they join the shaft abruptly; the shaft bulges laterally just proximal to the trochlea metatarsi IV, meeting it with relatively little demarcation. The trochleae form a shallow but obvious curve (in distal view). The trochleae metatarsi II and IV are more or less equal in length and shorter than trochlea metatarsi III.

Genus *Ciconia* Brisson, 1760

Ciconia Brisson (1760). *Ornithologia sive Synopsis Methodica*, 1: 48, 361—type species: *Ciconia = Ardea ciconia* Linnaeus, 1758.

In the original concept of *Ciconia*, the genus comprised two species, *C. ciconia* Linnaeus, 1758 (Eurasia, Africa) and *C. nigra* Linnaeus, 1758 (Eurasia, Africa). The generic limits were expanded by Kahl (1979) and Wood (1983, 1984) to incorporate three species that were long kept in monotypic genera: *(Sphenorhynchus) abdimii* Lichtenstein, 1823 (Africa), *(Dissoura) episcopus* Boddaert, 1783 (Africa, southern Asia), and *(Euxenura) maguari* Gmelin, 1789 (South America). This has considerably expanded the size range of the species in both directions and added variability in the morphology.

The represented elements can be diagnosed as *Ciconia* and separated from those of other genera of storks by the following suites of characters:

Cranium. Most of the characters on which a generic diagnosis might be based are missing in the fossil. It does permit separation from *Ephippiorhynchus* by having the fossae temporalis moderately shallow and moderately concealed by the cristae temporalis, rather than deep and unconcealed (in dorsal view); the nuchal area (supra-occipital) is slightly convex around the prominentia cerebellum, rather than somewhat concave; and the crista nuchalis transversus is low and does not project posteriorly beyond the extent of the prominentia cerebellum. In these characters, the fossil agrees with *Ciconia*.

Quadrate. The processus oticus is thin (in lateral view). The processus orbitus is thin. The sulcus between the processus mandibularis and condylus pterygoideus is moderately deep. The processus mandibularis is markedly longer mediolaterally than anteroposteriorly, the condyli form an acute angle and the sulcus intercondylaris is relatively narrow.

Humerus. The tuberculum ventrale is situated distal to the caput humeri. The fossa pneumotricipitalis does not extend proximally well beyond the attachment for M. scapulohumeralis caudalis nor as far distally past the midpoint of the crista bicipitalis. The intumescentia humeri is moderately inflated distally. There is a slight notch where the distal end of the crista bicipitalis joins the shaft, but the sulcus nervus coracobrachialis is obsolete. The impressio m. coracobrachialis is flat, not depressed. The dorsal edge of the crista deltopectoralis is generally straight, not concave. The attachment for M. scapulohumeralis cranialis is situated at the proximal end of the linea m. latissimus dorsi rather than ventral to it and directly distal to the fossa pneumotricipitalis. In dorsal view, the dorsal side of the shaft posterior to the condylus dorsalis is shallow, with the anterior and posterior sides straight and roughly parallel, forming a rectangular surface; the anterior face of the shaft meets anteroproximal corner of the processus supracondylaris dorsalis gradually; and the tuberculum supracondylare dorsale is not strongly developed. The epicondylus ventralis is moderately produced (in anterior view). The scar for M. pronator profundus is moderately short and shallow and that for M. flexor carpi ulnaris is moderately small; thus the area of the ventral side distal to the epicondylus ventralis is not markedly excavated (in ventral view) and the epicondylus ventralis is less undercut (in anterior view). The sulcus humerotricipitalis is moderate in width. The condylus ventralis humeri extends further distally relative to the condylus dorsalis humeri (in anterior view); in distal view, its posterior surface faces more posteriorly and less distally. The ventrodistal corner, distal to the epicondylus ventralis, is only slightly to moderately excavated.

Ulna. The condition of the ulnar fragment considered in this study is not suitable for useful comparisons between taxa. This element is not diagnosed further.

Tibiotarsus (taken in part from Howard, 1942 and Olson, 1991). There are limited characters of the proximal end that are useful in separating the genera of storks, and most of these are related to the angles and extent of the cristae and articular surfaces. On the distal end, the tuberculum retinaculi m. fibularis proximal to the condylus lateralis forms a prominent triangular ridge, which is pointed proximally and broadens distally (prominent papilla in *Ephippiorhynchus*); the proximomedial corner of the condylus lateralis is not incised by expansion of the area intercondylaris; the proximomedial border of the condylus medialis lacks a prominent round fossa; the posterior sides of the condyli extend prominently and are more oval than circular (in lateral view); the distal border of pons supratendineus is horizontal (tilted or arched in *Ephippiorhynchus*); the distal opening of the canalis extensorius is moderately to strongly horizontally elongate (rounded in *Ephippiorhynchus*); and the incisura intercondylaris is broad and relatively flat at its base (in distal view).

Tarsometatarsus (taken in part from Howard, 1942). The hypotarsus is slender relative to the proximal width of the cotylae and to the length of crista hypotarsi lateralis, the longer of the cristae; the cristae hypotarsi are slender. The eminentia intercotylaris is situated on the proximodistal midline rather than medial to it, and the lateral side of its base is only slightly excavated, if at all. The area between the cotylae and the hypotarsus consists of a gradual drop with a pit of moderate depth proximal to the cristae hypotarsi. The ridge leading to the distal end of the hypotarsus is generally low and broad. The cotyla lateralis is elongate; the cotyla medialis much more circular (in proximal view). The trochlea metatarsi II is situated dorsally and is little rotated laterodorsally-medioplantarly. The fossa metatarsi I is flush with the surface of the bone or only slightly elevated.

Ciconia nana (De Vis, 1888)

Fig. 1

Xenorhynchus nanus De Vis, 1888. *Proc. Linn. Soc. N.S.W.* 3: 1287, Qld: Darling Downs: Condamine River: Chinchilla.
Ciconia nana (De Vis, 1888). Rich & van Tets, 1982: 306A; van Tets, 1984: 470; van Tets & Rich, 1990: 166; Vickers-Rich, 1991: 752.

De Vis (1888) based *Xenorhynchus nanus* on material from the Condamine River, near Chinchilla, in the Darling Downs of Queensland. The material comprised a distal tibiotarsus, collected by J. Daniels, and a proximal ulna, a later acquisition but described at the same time. Subsequently De Vis (1905) reported this species from Wurdulumankula, Cooper Creek, South Australia, based on a distal tibiotarsus, collected by Professor J. Gregory. The original tibiotarsal fragment was designated as the lectotype by Brodkorb (1963). Similarities in size and shape to species of *Ciconia* were noted by Rich & van Tets (1982), who provisionally transferred this form to this genus, where it has been listed in subsequent reviews (e.g., van Tets, 1984; van Tets & Rich, 1990; Vickers-Rich, 1991), although no detailed comparisons had been made.

The Darling Downs, southeastern Queensland, feature deposits of two discrete periods. Pleistocene deposits occur on the east side of the Condamine River (26°48'S 150°41'E), producing the Darling Downs Local Fauna (Molnar & Kurz, 1997). The older, Pliocene-aged assemblage, the Chinchilla Local Fauna, which yielded the holotype of *X. nanus*, comes from the fluviatile Chinchilla Sands along the western banks of the Condamine River, near Chinchilla. On the basis of closer faunal resemblances of this fauna to the Early Pliocene Bluff Downs Local Fauna than to the Pleistocene Darling Downs Local Fauna, its age has been put at Early to Middle Pliocene (T. Rich *et al.*, 1991).

Many important specimens from Gregory's trip along Cooper Creek have their locality listed as Wurdulumankula, although no similar place name has been found on Gregory's maps (Gregory, 1906), and the exact location of this site is uncertain (Tedford & Wells, 1990). It is considered to be located in the Piranna Soakage of Cooper Creek, in the eastern Lake Eyre basin, South Australia, and to be one of a number of sites from which fossils of the Malkuni Fauna have been recovered, one of two faunas in the fluviatile deposits of the Katipiri Formation (Tedford & Wells, 1990).
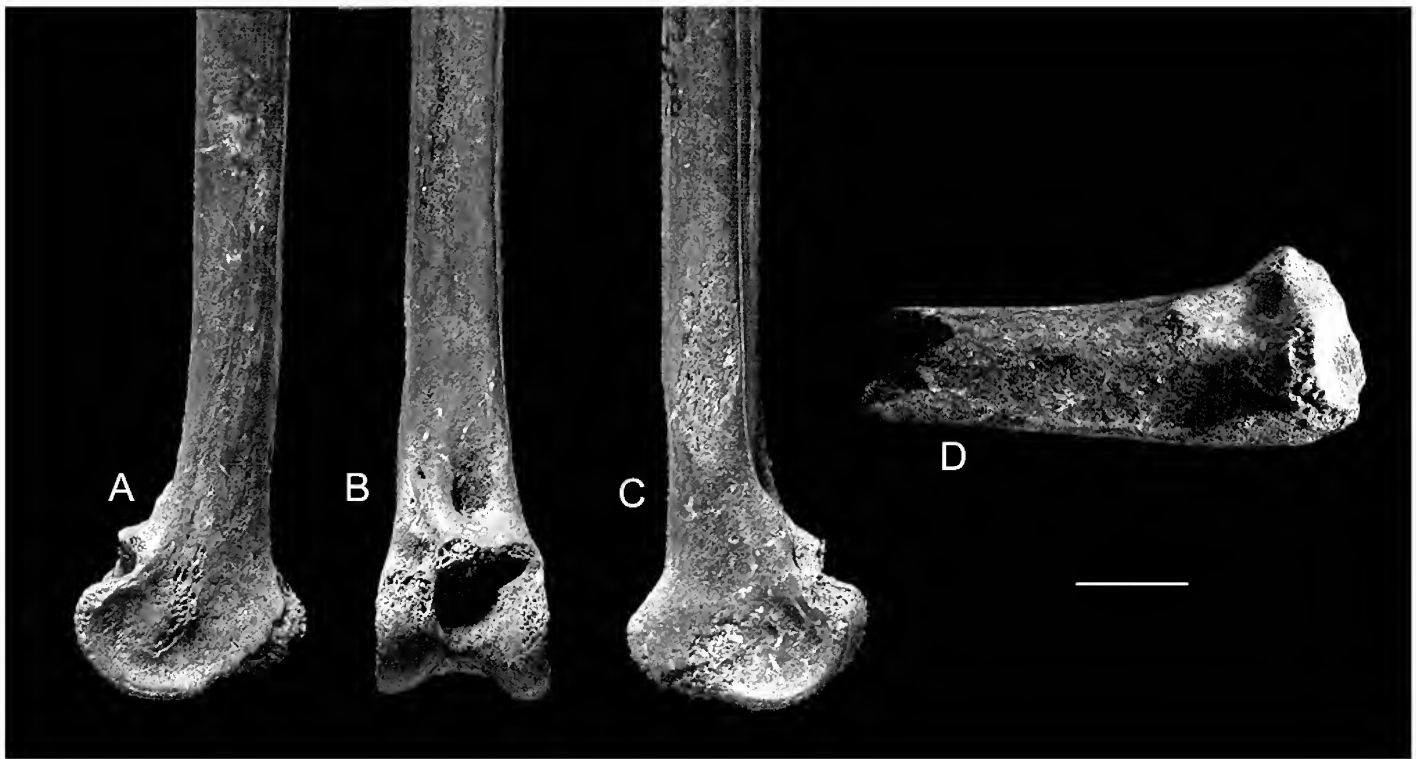
Fig. 1. Specimens of fossil stork *Ciconia nana*. (*A–C*) lectotype (QM F1131), distal right tibiotarsus; (*A*) anterior view; (*B*) lateral view; (*C*) medial view; (*D*) paralectotype (QM F5514), proximal right ulna, anterior view. Scale = 10 mm.

These assemblages represent fluviatile/lacustrine faunas in the Great Artesian basin that predate the formation of inland dunes and are probably Late Pleistocene in age (Woodburne *et al.*, 1985). The fossils are found as "float" or in place.

Lectotype. Distal tibiotarsus (QM F1131; Fig. 1a–c; Brodkorb, 1963).

Type locality. North bank of the Condamine River, 5 km from Chinchilla, Darling Downs, Queensland.

Paralectotype. Proximal ulna (QM F5514, Fig. 1d).

Etymology. *Nanus* (Latin, a dwarf), in reference to the small size of this bird in comparison with its putative congener, *E. (X.) asiaticus*.

Diagnosis. *Ciconia nana* is diagnosed from other living species in the genus by the following combination of characters: the anterior extension of the condylus lateralis relative to the condylus medialis is greater; the ridge from the papilla for M. tibialis cranialis to the condylus medialis is only slightly incised by a furrow; and the tuberculum retinaculi m. fibularis is nearly confluent with the lateral border of the shaft (in anterior view).

Of the fossil forms, few can be compared with *C. nana* for lack of common elements. *Ciconia maltha* was much larger (Table 1), as was the unnamed Mio-Pliocene species from Arizona, which Bickart (1990) characterized as a "giant, equalling in size large individuals of the extant *Jabiru mycteria*". The somewhat younger *Ciconia stehlini* had a tibiotarsus of comparable proximal width to *C. nana*. Jánossy (1992) did not provide any characters that serve to separate these species morphologically. Of living species, *C. ciconia* and *C. nigra* are similar to *C. nana* in proximal width of the tibiotarsus but the condyli of *C. nana* are deeper.

Referred material. Distal tibiotarsus (QM F5513), Wurdulumankula, Cooper Creek, South Australia.

Measurements. Table 1.

Description

De Vis' (1888) description of the original tibiotarsus (QM F1131) was detailed, and identified diagnostic characters at family, generic and specific levels. Descriptions of the other specimens amounted to just a few adjectives. The second tibiotarsus "adds nothing to our information about the smaller Jabiru than that it attained a rather larger size than the tibia already described". Its distal width was greater and "all parts of the bone are proportionately larger" (De Vis, 1905). About the ulna De Vis (1888) remarked only that it was of compatible size with the first tibiotarsus but "unfortunately its worn condition unfits it for description".

Tibiotarsus. The lectotypical tibiotarsal fragment QM F1131 consists of the distal end with the shaft broken distal to the crista fibularis (length 118.6 mm as preserved). It is abraded on the proximal borders of both condyli, the cristae of trochlea cartilaginis tibialis, the epicondylus medialis and the papilla for M. tibialis cranialis. The anterior face of the shaft is flattened, with the linea extensorius developed into a low ridge along its distal end. The posterior face is strongly rounded. The tuberculum retinaculi m. fibularis is confluent with the lateral border of the anterior face of the shaft; a nutrient foramen is proximal to this. There is a large, broad, elongate scar on the lateral face of the shaft; the distal end is level with the tuberculum. The tuberositas retinaculi extensorius on the linea extensorius is small but obviously elongate. The sulcus extensorius is of uniform depth, not deepening markedly proximal to the pons supratendineus. The distal border of the pons supratendineus is developed

Table 1. Measurements (mm) of the tibiotarsus of *Xenorhynchus nanus* and other fossil and living species of storks, giving mean, standard deviation, range and sample size (in parentheses). † indicates fossil taxa; values for *Ciconia stehlini* and *C. maltha* from Jánossy (1992) and Howard (1942), respectively. *QM*, Queensland Museum, Brisbane.

		distal width across condyli	depth, condylus lateralis	depth, condylus medialis
†	*Ciconia nana*			
	QM F1131 (lectotype)	14.3	19.5	18.5
	QM F5513	16.1	20.6	20.5
	Ciconia ciconia	15.3; 0.7	18.5; 0.8	18.1; 1.0
		14.5–16.2 (4)	17.4–19.2 (4)	16.6–18.9 (4)
	Ciconia nigra	14.8 (1)	18.4 (1)	17.5 (1)
	Ciconia maguari	18.2; 1.3	21.8; 1.0	21.7; 0.7
		17.0–19.5 (3)	20.9–22.9 (3)	20.9–22.3 (3)
	Ciconia episcopus	11.6; 0.5	13.5; 0.8	13.4; 0.7
		11.0–12.0 (3)	12.3–14.2 (3)	12.4–13.6 (3)
	Ciconia abdimii	10.9; 0.8	12.6; 0.6	12.7; 0.7
		9.7–12.1 (6)	11.8–13.7 (6)	11.8–13.9 (6)
†	*Ciconia stehlini*	14.5	—	—
†	*Ciconia maltha*	18.0–21.5	—	—
	Anastomus lamelligerus	11.3; 0.6	13.0; 0.5	13.0; 0.5
		10.6–11.8 (3)	12.6–13.5 (3)	12.7–13.6 (3)
	Anastomus oscitans	10.8 (1)	11.8 (1)	12.0 (1)
	Mycteria ibis	13.3; 0.5	17.1; 0.6	17.2; 1.0
		12.6–14.2 (6)	16.1–18.3 (6)	16.2–18.9 (6)
	Mycteria leucocephala	13.1; 0.4	16.6; 1.4	16.9; 1.0
		12.7–13.4 (3)	15.3–18.1 (3)	16.0–18.0 (3)
	Mycteria cinerea	13.2 (1)	18.1 (1)	18.0 (1)
	Mycteria americana	13.5; 0.6	17.0; 1.2	16.9; 1.4
		12.6–13.8 (4)	16.0–18.5 (4)	15.6–18.6 (4)
	Leptoptilos dubius	20.3; 0	26.5; 0.4	25.9; 0
		20.3 (2)	26.2–26.8 (2)	(2)
	Leptoptilos javanica	16.4 (1)	20.5 (1)	19.6 (1)
	Leptoptilos crumeniferus	19.1; 0.8	23.4; 0.8	23.8; 0.6
		18.1–20.1 (4)	22.3–23.7 (4)	22.9–24.3 (4)
	Jabiru mycteria	21.1; 0.2	27.4; 0.1	28.4; 0.3
		20.9–21.3 (3)	27.3–27.5 (3)	28.1–28.7 (3)
	Ephippiorhynchus senegalensis	18.1; 1.1	25.0; 1.6	25.4; 1.3
		17.1–19.5 (4)	23.7–27.3 (4)	24.5–27.3 (4)
	Ephippiorhynchus asiaticus	17.1; 0.9	23.0; 1.5	22.9; 1.2
		15.6–18.4 (9)	21.5–25.2 (9)	21.6–24.8 (9)

anteriorly into a strong ridge. The condyli are similar in shape and size, with the condylus medialis extending slightly further distally and more markedly anteriorly. The depressio epicondylus lateralis is deeper and more extensive than the depressio epicondylus medialis; both have prominent rims anteriorly. Despite abrasion, the cristae of the trochlea cartilaginis tibialis are prominent, extending well away from the shaft. Measurements, Table 1.

The other tibiotarsal fragment, QM F5513, is slightly larger and has less abrasion of the distal end. It retains about half the length of the shaft, as does the lectotype (length 62.6 mm as preserved) and the medial half is missing for much of this. It agrees closely with the lectotype in morphology other than that the sulcus extensorius is slightly deeper, the tuberositas retinaculi extensorius is more raised, the tuberculum retinaculi m. fibularis is a small distance from the lateral border rather than confluent with it, and the distal opening of the canalis extensorius is somewhat larger and rounder.

Ulna. Specimen QM F5514 consists of the proximal end of a right ulna. It is rather damaged, with the olecranon missing, and moderate to heavy abrasion on the cotyla dorsalis, facies articularis radialis and crista intercotylaris. It is broken distal to the proximalmost papilla. The impressio m. brachialis is long, moderately deep proximally and shallow distally. It is bounded posteriorly by a broad, rounded tuberculum lig. collateralis ventralis and anteriorly by a heavy ridge, which separates it from a prominent incisura radialis. Although, because of the abrasion, measurements of this element cannot be compared directly with those of other taxa, overall the specimen is slightly smaller than the ulna of *Ciconia ciconia*. The measurements of the specimen as preserved are, length 46.0 mm; proximal width 16.6 mm; proximal depth 11.8 mm.

De Vis (1888) placed this species in the same genus as the living *Ephippiorhynchus asiaticus*, "noting further its strong resemblance to the Jabiru's tibia in the massiveness, direction, and sculpture of the bridge traversing the

intercondylar space, we cannot but admit congeneric affinity between the two". A comparison of the distal tibiotarsal fragments with other living species of the Ciconiidae, and *E. asiaticus* in particular, demonstrates that De Vis' generic allocation for these specimens is not supported. The comparative material available to De Vis was limited to selected taxa, almost all of Australian origin. Thus, his placement of the fossil specimens in the same genus as the only Australian species is not surprising; it is doubtful that he had access to osteological representatives of any other genera of storks.

De Vis (1888) noted size differences between the fossil tibiotarsus and that of *E. asiaticus*: "the fossil tibia ... is in the mean two-ninths less in its dimensions than the recent bone, indicating a bird but little more than half the bulk of the jabiru of the present day". The morphological differences he mentioned were that "the rotular channel is shallower; there is considerably less intercondylar space behind the posterior edge of the bridge, the canal under the bridge is relatively much wider, the ectocondylar tubercle is not prominent, and the double flexure inwards and forwards apparent in the living jabiru between the shaft and the articular end is scarcely appreciable". Most of these are either actually differences between *Ciconia* and *Ephippiorhynchus* or have no generic significance.

The condition of the ulnar fragment is not suitable to permit a useful comparison. The shallow, round impressio m. scapulotricipitalis may be of generic significance but it is also likely that the possible slight morphological differences between the fossil and recent specimens are due to abrasion.

Riversleigh stork

The presence of a new species of stork from Oligo-Miocene deposits at Riversleigh, was briefly mentioned by Vickers-Rich (1991). Boles (1991) noted that it "was not close to the living ... *Xenorhynchus*" without further elaboration, and subsequently (Boles, 1997) stated that the material was "probably referable to *Ciconia*". This taxon is described below.

The Riversleigh deposits are located 5 km west of the Riversleigh homestead (19°02'S 138°45'E), 200 km north of Mt Isa, northwestern Queensland, where they occur as an outcrop of Tertiary limestone overlying the Cambrian Thorntonia Limestone. There are now over 200 named Oligo-Miocene deposits at Riversleigh. An informal system of grouping has been used (Systems A–C). These systems are "regionally clustered sites that appear to be superpositionally-related (differing in age but not significantly in position) and/or space-related (spatially isolated but approximately contemporaneous)" (Archer *et al.*, 1989). The principal accumulations are thought to have occurred in several episodes involving large lakes, shallow pools and cave deposits. Undoubted stork material has been recovered from three sites and a referred specimen comes from a fourth.

White Hunter Site, Hal's Hill Sequence, D-Site Plateau, is considered to be part of System A, of Late Oligocene/Early Miocene age (Creaser, 1997; Myers & Archer, 1997). The White Hunter Local Fauna also contains other birds, including the small casuariid *Emuarius gidju* (Patterson & Rich, 1987) (Boles, 1992), the dromornithid *Barawertoris tedfordi* Rich, 1979, a flightless rail (Boles, 2005) and several passerines. Wayne's Wok Site is in the central section

of the D-Site Plateau. Its age is still unclear, but may be System A or B (?Early to Middle Miocene) (Black, 1997; Cooke, 1997a; Creaser, 1997). Birds found here also include *Emuarius*, dromornithids and passerines. Bitesantennary Site is a cave deposit in the Verdon Creek Sequence, on the northern section of the D-Site Plateau, where it intrudes into the widespread D-Site layer. It is possibly a System B site (Cooke, 1997a).

Specimens of five skeletal elements were obtained at Bitesanntennary Site in close proximity and are assumed to have been associated. Proximal tarsometatarsal fragments from White Hunter Site and Wayne's Wok Site allow direct comparison with each other but not with a distal tarsometatarsal fragment from Bitesantennary Site. Because the tarsometatarsal fragments all come from storks of comparable size and morphology, they are referred to the same taxon. A cervical vertebra from Neville's Garden Site (Early Miocene) is tentatively referred to this species because of its size and morphological similarity to that of living storks.

Ciconia louisebolesae n.sp.

Fig. 2

Holotype. QM F30290, right distal humeral fragment with surface damage to the anterior face of the condylus dorsalis, tuberculum supracondylare ventrale and dorsal border of sulcus humerotricipitalis.

Type locality. Bitesantennary Site, Riversleigh, northwestern Queensland, currently considered to be Early Miocene; Bitesantennary Local Fauna.

Paratypes. All from Bitesantennary Site. *Cranium*—QM F20910, neurocranium, lacking skull roof; *quadrate*—QM F20893, complete right element; *humerus*—QM F20911, proximal right element broken through distal to the midpoint of the crista bicipitalis and to the fossa pneumotricipitalis, and missing the tuberculum dorsalis and processus deltopectoralis; *tibiotarsus*—QM F31350, extreme proximal left element broken through the shaft through proximal end of the foramen interosseum proximale; damage to most projecting features, including both the cristae cnemialis, particularly the crista cnemialis caudalis, the medial edge of the facies articularis medialis, and extensively on the posterior edge along the area of contact between the facies articularis medialis and lateralis; *Tarsometatarsus*—QM F36446, right distal fragment broken through the shaft proximal to the fossa metatarsi I.

Etymology. Dedicated with love and respect to my mother, Louise Boles, for her guidance in my development as a person and her tolerance of my many transgressions.

Diagnosis. Similar in size to *C. ciconia* and *C. nigra*, but sufficiently different to recognize as a new species. It differs by the following suite of characters of the distal humerus: the condylus ventralis humeri is proportionally smaller, not extending as far ventrally; the epicondylus ventralis is closer to the distal end; the muscle scars distal to the epicondylus ventralis are more extensive (in ventral view) and more excavated (in anterior view), although less than in genera such as *Ephippiorhynchus*; and the posterodorsal corner is
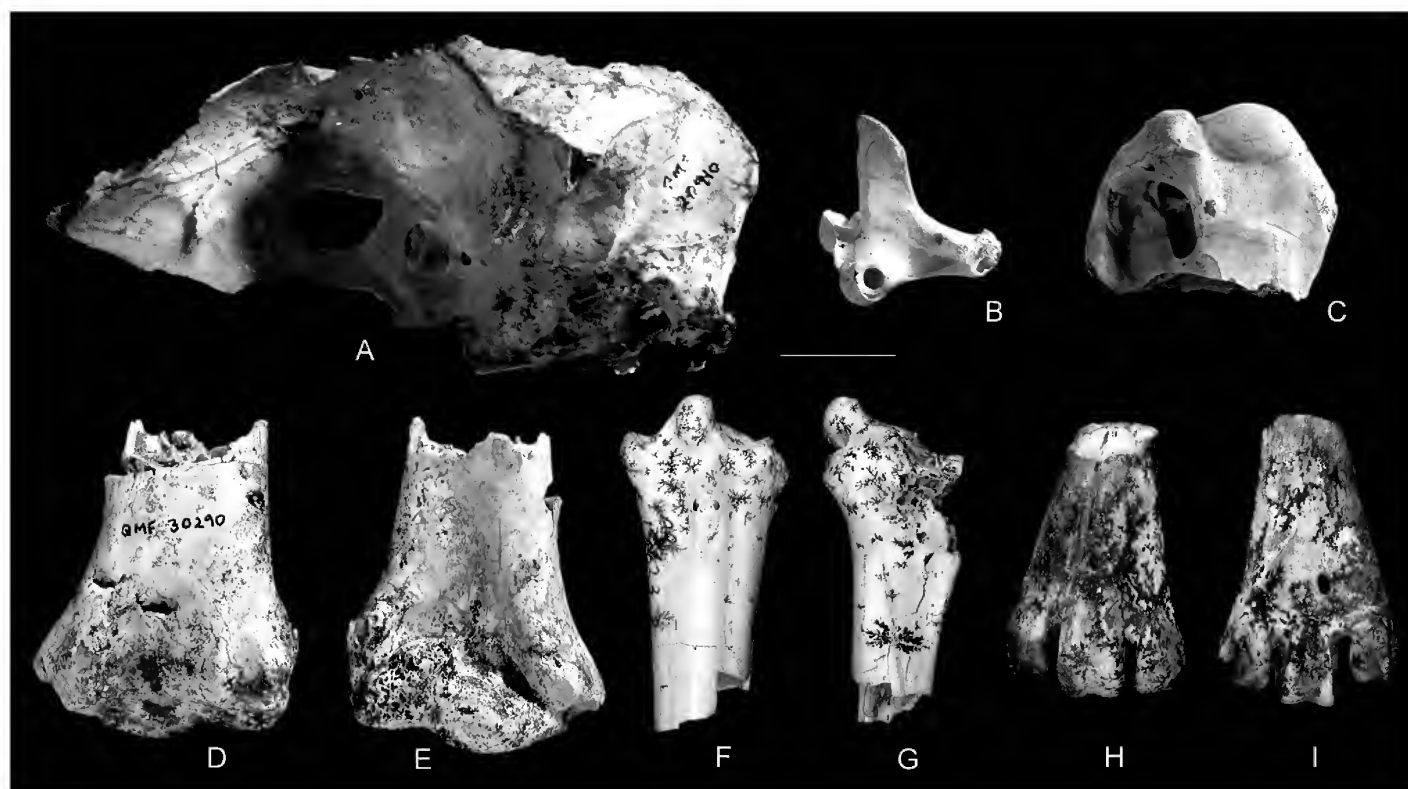
Fig. 2. Specimens of the fossil stork *Ciconia louisebolesae*. (*A*) partial skull (QM F20910, Bitesantennary Site), lateral view; (*B*) right quadrate (QM F20893, Bitesantennary Site), lateral view; (*C*) proximal right humerus (QM F20911, Bitesantennary Site), posterior view; (*D–E*) distal right humerus (holotype: QM F30290, Bitesantennary Site), (*D*) anterior view, (*E*) posterior view; (*F–G*) proximal left tarsometatarsus (QM F36447, Wayne's Wok Site), (*F*) anterior view, (*G*) lateral view; (*H–I*) distal right tarsometatarsus (QM F36446, Bitesantennary Site), (*H*) dorsal view, (*I*) plantar view. Scale = 10 mm.

more rounded (in dorsal view). The crista bicipitalis is not short (as in *C. maguari*) and is prominently extended. In its size and comparative narrowness of the incisura tibialis, the tibiotarsus more closely resembles that of the small species of *Ciconia* (e.g., *episcopus* and *abdimii*) rather than *C. ciconia* or the larger taxa.

Referred material. QM F50428 (Neville's Garden Site) cervical vertebra with only minor damage; QM F36445 (Wayne's Wok Site) left proximal tarsometatarsus with damage to the crista hypotarsi medialis and plantar face of cotyla lateralis; QM F36447 (White Hunter Site) proximal left tarsometatarsus missing most of hypotarsus.

Measurements. Tables 2–4.

Description

Cranium. Measurements as preserved: 31.7 mm width of parietal; 40.1 mm width at midline of orbits (front of specimen as preserved); 40.7 mm width at processes temporalis. The specimen comprises the rear of the skull missing the dome of skull dorsal to the fossa temporalis and in a line just across top of the orbitae, retaining most of the parietal and frontal on a level with the orbital rims; the lamina parasphenoidalis is present but palatal elements are missing; the interorbital septum is present to in front of the fontaculi interorbitales and about half way through the orbits. Many of the external structures are damaged, with the processus postorbitalis lost and the posteroventral border of the processus paraoccipitalis and edges of the lamina parasphenoidalis slightly to strongly abraded; a large opening in the centre of the septum interosseus is a post-

mortem artefact. The orbitae are broad and rounded. The fossa temporalis is broad, with the crista temporalis nuchalis strongly developed. The processus zygomaticus is short and blunt. The foramen magnum is squarish oval, with the dorsal border broken. The condylus occipitalis is hemispherical, with the dorsal border abraded. The recessus tympanicus dorsalis is moderately small and round; the fenestra vestibule, foramen pneumaticum caudale and fenestra cochleae are tightly grouped in a small recess. The cotylae quadratica otici and squamosi are of similar circular shape and size. The interior of the cranial cavity is largely intact. The fossa cranii caudalis and fossa tecti mesencephale are broad and circular, with the crista tentorialis prominent.

Quadrate. Viewed anterodorsally, the element is very transversely expanded across the processus mandibularis and less so across the processus oticus; the midbody is comparatively thin between these processes, with the lateral side markedly concave. The crista tympanicum is low. The processus orbitalis is straight on its anterior border; its posterior border is straight until dorsal end, which curves to meet the anterior border at the apex. The capitula squamosum and oticum are elliptical, their long axes converging anteriorly (in posterodorsal view). The incisura intercapitularis is broad but shallow; it extends to a large round foramen pneumaticum located centrally on the posterodorsal surface. The region from the base of the capitulum squamosum, through this foramen, diagonally towards the base of the condylus lateralis is anteroposteriorly compressed compared to the rest of the element. The posterior surface between the processus mandibularis and processus oticus is very slightly concave (in lateral view).

Table 2. Measurements (mm) of the quadrate of *Ciconia louisebolesae* and living species of storks, giving mean, standard deviation, range and sample size (in parentheses). *QM*, Queensland Museum, Brisbane.

	greatest length, processus oticus through processus mandibularis	greatest depth, processus orbitalis through processus mandibularis
Ciconia louisebolesae		
QM F20893	20.2	20.2
Ciconia ciconia	22.3; 0.8	20.5; 1.0
	21.7–23.2 (3)	19.3–21.7 (4)
Ciconia niger	20.6; 0.2	19.3; 0.1
	20.4–20.7 (2)	19.2–19.4 (2)
Ciconia maguari	24.2; 0.5	23.7; 2.7
	23.7–24.6 (3)	21.8–26.8 (3)
Ciconia episcopus	19.2; 1.0	17.4; 1.0
	18.8–20.8 (5)	15.8–18.6 (6)
Ciconia abdimii	17.5; 0.5	15.1; 0.6
	17.0–18.0 (4)	14.5–15.8 (4)
Anastomus lamelligerus	20.1 (1)	17.5; 0.4
	17.2–17.8 (2)	
Mycteria ibis	23.5; 0.3	24.7; 0.7
	23.3–23.9 (3)	24.5–25.3 (4)
Mycteria leucocephala	23.8; 0.7	24.9; 0.6
	23.3–24.3 (2)	24.5–25.3 (2)
Mycteria americana	23.4; 1.3	25.2; 2.0
	22.5–24.3 (2)	23.8–26.8 (2)
Leptoptilos crumeniferus	35.1 (1)	34.0 (1)
Jabiru mycteria	35.6; 0.1	39.1; 0.2
	36.5–36.6 (3)	38.9–39.3 (3)
Ephippiorhynchus senegalensis	29.6; 1.9	28.6; 2.1
	28.2–30.9 (2)	26.7–31.1 (4)
Ephippiorhynchus asiaticus	29.2; 2.1	2.3; 1.5
	26.9–31.5 (4)	25.8–29.1 (4)

The condylus medialis is the most medially projecting part of the element, while the projection of the condylus lateralis is the greatest laterally, exceeding that of the processus oticus. The condyli lateralis/caudalis lie perpendicular to the processus orbitalis. The small, oval condylus pterygoideus stands discrete from the condylus medialis, separated by a small sulcus.

Cervical vertebra. This is very elongate (greatest length 39.7 mm, proximal width 26.2 mm, proximal depth 19.8 mm, distal width 18.6 mm, distal depth 19.5) and agrees with modern *Ciconia ciconia* in morphology. It is not diagnosed further.

Humerus. In anterior view, the caput humeri is rounded, sloping dorsally from the apex more steeply than on the ventral side; it is moderately broad, becoming expanded at its anteroposterior midpoint. Its distal border on the posterior surface is obscure. The sulcus lig. transversus is broad and deep but short, confined to the ventral third of the anterior face, barely reaching the ventral border of the caput; it ends abruptly at the edge of the anterior face of the element. Its depth is augmented by a bordering ridge on its proximal side and the intumescentia humeri on the distal. The proximal surface of the intumescentia is flat and smooth and (in proximal view) is little inflated; it is tilted dorsally to join smoothly with the shallow, indistinct impressio coracobrachialis.

On the posterior surface, the broad incisura capitis separates the caput humeri from a long, deep and thickened area along the proximoventral border of the element, proximal to the fossa pneumotricipitalis, before merging with the proximal end of the posterior shaft surface without an obvious demarcation. Ventrally the prominent proximal section attenuates towards the crista bicipitalis, but protrudes substantially more posteriorly than the crista. On its ventral end, it supports the elongate scar for M. biceps brachii.

The tuberculum ventrale is relatively large, triangular-trapezoidal in shape and oriented proximodorsally. In proximal view, it sits at the apex of a triangular block bounded along its dorsal base by the sulcus lig. transversus. This triangular block protrudes posteriorly well beyond the rest of the proximal end of the element. The deep but moderately thin crus dorsale fossae runs distally from this, forming the dorsal border of the fossa pneumotricipitalis. The fossa is elliptical and highly pneumatic. The area between it and the crus ventrale fossae is excavated as a broad concave basin. The thick crus has a well marked, elongate scar for the attachment of M. scapulohumeralis caudalis. The crista bicipitalis is not well-developed ventrally.

The ridges bordering the sulcus scapulotricipitalis are short but moderately pronounced; they do not extend to the distal border. The ridge on the ventral side of the sulcus humerotricipitalis is broader and longer but about the same height as those defining the sulcus scapulotricipitalis. The sulcus humerotricipitalis is broad and shallow, with no obvious separation from the flat posterior surface of the shaft proximal to it; it is apparent only because of the bordering ridges. The fossa m. brachialis becomes confluent with the shaft on its dorsal and proximal sides and is poorly demarcated on its ventral side. The ridge along the ventral border supporting the tuberculum supracondylare ventrale is strongly developed and rather broad. In distal view, the condylus dorsalis humeri extends further anteriorly than does this ridge, which is turn projects only slightly more than the condylus ventralis humeri. The distal border of the condylus dorsalis humeri just reaches the dorsodistal corner. The condylus ventralis humeri is a rounded oval without obvious inflation. The incisura intercondylaris is moderately broad but shallow. The scars for M. flexor carpi ulnaris and M. pronator profundus face distally; they are adjacent, separated by only a thin ridge. The scars for M. ectepicon-dylo-ulnaris and M. extensor digitorum communis are shallower and less extensive.

Tibiotarsus. The specimen is too damaged to permit standard measurements for comparison with other taxa. The following measurements, taken from the specimen as preserved, give an indication of the general size: proximal width 15.5 mm; proximal depth (measured from the facies articularis medialis to the crista cnemialis lateralis in a direct anteroposterior line) 20.2 mm; in both cases, the actual value would be considerably greater, particularly for the latter measurement.

The crista cnemialis cranialis is broken; the remaining base is straight and does not extend far distally, although some distance further than the crista cnemialis lateralis. Their junction, at about a right angle, is marked by a shallow sulcus intercnemialis. The crista patellaris is straight, in both proximal and lateral views. The incisura tibialis is deeply incised, concave and moderately narrow; at its proximal

Table 3. Measurements (mm) of the humerus of *Ciconia louisebolesae* and other fossil and living species of storks, giving mean, standard deviation, range and sample size within parentheses. † indicates fossil taxa; values for *Ciconia maltha* from Howard (1942). *QM*, Queensland Museum, Brisbane.

	proximal width	distal width	depth, condylus dorsalis humeri
Ciconia louisebolesae			
QM F20911	32.9	—	—
QM F30290	—	28.2	14.9
Ciconia ciconia	39.6; 1.7	30.6; 0.8	16.1; 1.0
	37.2–40.9 (6)	28.8–31.5 (10)	15.2–17.3 (10)
Ciconia boyciana	—	33.8 (1)	18.9 (1)
Ciconia nigra	40.1;1.1	30.6; 0.6	16.4; 0.8
	38.9–40.9 (3)	30.0–31.2 (2)	15.6–17.2 (2)
Ciconia maguari	43.7; 1.0	33.5; 1.8	17.9; 0.8
	42.7–44.7 (4)	31.6–36.1 (5)	16.6–18.5 (5)
Ciconia episcopus	32.2; 2.8	23.9; 1.2	12.8; 0.8
	28.2–35.6 (6)	22.1–24.6 (4)	11.7–13.6 (4)
Ciconia stormi	—	21.9 (1)	11.4 (1)
Ciconia abdimii	28.3; 1.4	22.9; 0.5	12.3; 0.1
	26.5–30.0 (5)	22.4–23.2 (3)	12.2–12.4 (3)
Ciconia maltha †	46.2–53.3	38.7–40.7	—
Anastomus lamelligerus	26.5; 0.0	21.6; 0.9	11.5; 0.2
	26.3–26.6 (2)	20.6–22.3 (3)	11.3–11.7 (3)
Anastomus oscitans	—	20.0; 1.3	11.4; 0.6
		18.6–21.1 (3)	10.9–12.0 (3)
Mycteria ibis	34.6; 2.1	26.3; 1.2	14.3; 0.7
	33.1–38.2 (5)	24.5–27.5 (4)	13.8–15.3 (4)
Mycteria cinerea	—	27.2; 2.2	15.0; 1.1
		25.6–28.7 (2)	14.2–15.8 (2)
Mycteria leucocephala	31.9; 2.1	28.9; 0.9	14.9; 0.7
	31.7–32.0 (2)	28.2–29.5 (2)	15.4–16.4 (2)
Mycteria americana	34.1; 2.9	27.6; 1.6	14.9; 0.8
	31.0–36.7 (3)	25.9–29.7 (18)	13.0–16.5 (18)
Leptoptilos dubius	53.0 (1)	46.8 (1)	24.7 (1)
Leptoptilos crumeniferus	48.8; 0.7	47.7; 3.3	25.4; 1.6
	48.4–49.6 (3)	43.5–51.9 (7)	23.5–28.1 (7)
Leptoptilos javanicus	45.0; 3.9	36.1; 2.3	19.7; 0.9
	42.6–49.5 (3)	34.4–38.7 (3)	19.0–20.8 (3)
Jabiru mycteria	54.1; 1.4	40.8; 3.2	22.4; 1.9
	52.9–55.7 (3)	34.6–45.7 (10)	18.2–25.5 (10)
Ephippiorhynchus senegalensis	46.6; 2.2	36.1; 1.3	18.7; 0.5
	44.0–48.9 (4)	35.1–37.0 (2)	18.3–19.0 (2)
Ephippiorhynchus asiaticus	44.1; 1.8	35.9; 2.7	19.2; 1.6
	42.7–47.0 (9)	32.9–37.6 (9)	18.0–20.8 (9)

end, it merges with a shallow excavation on the proximal surface. Its posterior border flares abruptly medially as the anterior side of the rather narrow and strongly rounded facies articularis lateralis. Much of the proximal surface of the facies is missing but what remains indicates that this was markedly raised. The circular fossa retropatellaris is deeper and smaller than the flattened and shallowly concave facies articular medialis. The circular attachment for M. femorotibialis medialis is on the end of the crista medialis, facing posteromedially. The facies gastrocnemialis is relatively flat from the medial side of the crista cnemialis cranialis along the medial side of the shaft, before curving smoothly into the posterior face.

General agreement in morphology and the association of the Riversleigh tibiotarsal fragment with other stork material from Bitesantennary Site are used as the basis for allocating it to this taxon.

Tarsometatarsus. The eminentia intercotylaris is directed anteroproximally at about 50° from the horizontal, projecting further anteriorly than the cotylae. The rounded anterior side is elliptical (in anterior view) with its long axis directed proximodistally; from the apex, it slopes posterodistally on its posterior side. The lateral side drops directly to the cotyla lateralis; the medial side extends as a long sloping ridge, confluent with the anterior rim of the cotyla medialis to past its mediolateral midpoint. The apex is slightly broader than the base (in medial view).

The cotylae are roughly equal in both their anterior and posterior extents and thus in overall depth. In proximal view, the cotyla medialis is roughly circular over most of its border, with the anterior side flattened. Posterior to the anterior rim, the cotyla meets medial side of the eminentia intercotylaris in a smooth, gradual slope. The medial rim projects strongly proximally to a narrow edge. In anterior

Table 4. Measurements (mm) of the tarsometatarsus of *Ciconia louisebolesae* and other fossil and living species of storks, giving mean, standard deviation, range and sample size (in parentheses). † indicates fossil taxa; values for *Ciconia maltha* from Howard (1942). *QM*, Queensland Museum, Brisbane.

| | proximal width across cotylae | depth, cotyla lateralis | depth, cotyla medialis | distal width | medial depth, trochlea | | | greatest distal depth |
					metatarsi II	metatarsi III	metatarsi IV	
Ciconia louisebolesae								
QM F36445	c. 18.2	—	9.2	—	—	—	—	—
QM F36447	16.3	7.9	9.4	—	—	—	—	—
QM F36446	—	—	—	19.6	9.6	9.0	8.5	14.3
Ciconia ciconia	17.4; 1.5	9.0; 0.9	9.1; 0.6	19.9; 1.3	8.8; 0.4	9.3; 0.6	8.5; 0.5	15.3; 1.0
	14.2–19.3 (9)	7.4–10.1 (9)	8.4–9.8 (9)	17.7–21.7 (9)	8.3–9.6 (9)	8.3–10.2 (9)	7.8–9.3 (9)	13.5–16.6 (9)
Ciconia nigra	16.2; 0.4	8.6; 0.4	8.4; 0	18.9; 0.5	7.0; 0.3	8.9; 0.3	7.6; 0.2	15.1; 0.2
	15.9–16.7 (3)	8.2–8.9 (3)	8.4 (3)	18.4–19.3 (3)	6.6–7.3 (3)	8.5–9.1 (3)	7.5–7.8 (3)	14.9–15.2 (3)
Ciconia maguari	21.3; 0.4	11.2; 0.5	10.1; 0.7	23.2; 0.9	10.0; 0.8	10.9; 0.3	10.0; 0.3	18.0; 1.2
	20.7–21.6 (4)	10.7–11.7 (4)	9.3–10.8 (4)	22.2–24.2 (4)	9.4–11.2 (3)	10.5–11.2 (3)	9.5–10.3 (3)	17.0–19.7 (3)
Ciconia episcopus	14.4; 1.3	7.8; 0.8	7.8; 0.7	16.7; 1.1	7.2; 0.3	8.0; 0.6	7.2; 0.6	12.2; 0.7
	12.8–16.2 (6)	7.1–8.9 (6)	6.7–8.9 (6)	15.7–18.5 (6)	6.4–7.5 (6)	7.3–8.9 (6)	6.5–8.0 (6)	11.5–13.0 (6)
Ciconia abdimii	12.5; 0.9	7.0; 0.4	6.6; 0.4	14.9; 1.1	6.8; 0.6	7.3; 0.4	6.3; 0.4	10.7; 0.8
	11.1–13.5 (5)	6.6–7.4 (5)	6.2–7.1 (5)	13.9–15.6 (5)	6.2–7.7 (5)	6.7–7.5 (5)	5.9–7.0 (5)	9.6–11.8 (5)
†*Ciconia maltha*	20–24.5	—	—	23–28	—	—	—	—
Anastomus	13.4; 0.2	7.0; 0.6	7.4; 0.1	14.9; 0.6	7.1; 1.3	7.0; 0.5	5.7; 1.3	10.6; 1.3
lamelligerus	13.2–13.5 (2)	6.5–7.4 (2)	7.3–7.5 (2)	14.4–15.3 (2)	6.2–8.0 (2)	6.6–7.3 (2)	4.8–6.6 (2)	9.7–11.5 (2)
Mycteria ibis	15.4; 0.8	8.8; 0.9	8.9; 1.0	18.9; 0.8	8.4; 0.9	9.1; 0.6	7.8; 0.5	16.1; 1.5
	14.6–16.2 (4)	7.7–9.6 (4)	7.8–9.9 (4)	18.2–19.9 (4)	7.4–9.3 (4)	8.4–9.7 (4)	7.1–8.4 (4)	14.1–17.4 (4)
Mycteria	14.8; 0.7	9.3; 0.8	9.3; 0.3	17.8; 0	7.8; 1.3	8.8; 0	8.0; 0.2	15.4; 0.4
leucocephala	14.3–15.3 (2)	8.7–9.9 (2)	9.1–9.5 (2)	17.8 (2)	6.9–8.7 (2)	8.8 (2)	7.8–8.1 (2)	15.1–15.7 (2)
Mycteria	15.5; 0.3	9.3; 0.2	9.2; 0.1	18.7; 1.5	8.4; 0.7	8.8; 0.9	8.1; 0.4	16.4; 0.8
americana	15.2–15.9 (2)	9.1–9.4 (2)	8.7–9.2 (2)	17.4–19.7 (2)	7.2–8.9 (2)	7.9–9.1 (2)	7.6–8.8 (2)	14.5–18.2 (2)
Leptoptilos dubius	23.8 (1)	12.8 (1)	12.9 (1)	28.1 (1)	12.4 (1)	14.0 (1)	11.7 (1)	22.9 (1)
Leptoptilos	22.0; 0.9	13.1; 0.3	12.1; 0.9	26.6; 1.0	12.1; 1.0	13.5; 0.4	11.3; 0.9	20.7; 1.4
crumeniferus	20.8–23.2 (5)	12.8–13.6 (5)	11.1–13.0 (5)	25.0–27.6 (5)	10.9–13.2 (5)	13.1–14.0 (5)	10.3–12.2 (5)	18.2–21.4 (5)
Jabiru mycteria	24.8; 0.1	13.3; 0.5	13.5; 0.4	30.0; 0.1	12.2; 0.1	13.2; 1.3	12.6; 0.1	21.9; 0.9
	24.7–24.8 (3)	12.8–13.7 (3)	13.1–13.8 (3)	29.5–29.6 (3)	10.7–13.1 (3)	13.1–13.3 (3)	11.8–13.5 (3)	20.7–23.0 (3)
Ephippiorhynchus	21.1; 1.6	12.4; 1.6	11.4; 0.7	23.6; 1.6	10.3; 1.1	11.4; 0.1	10.5; 1.1	18.1; 1.6
senegalensis	19.6–23.3 (4)	11.0–14.6 (4)	10.9–12.4 (4)	22.3–22.6 (4)	9.8–11.8 (4)	10.5–12.7 (4)	9.8–12.0 (4)	17.0–20.5 (4)
Ephippiorhynchus	19.4; 1.3	11.5; 1.0	10.7; 0.7	22.4; 1.1	10.5; 1.1	10.8; 0.6	10.2; 0.6	19.4; 1.4
asiaticus	18.1–21.6 (9)	10.4–12.8 (9)	10.0–12.0 (9)	21.3–24.0 (9)	9.3–11.2 (8)	9.7–11.4 (9)	9.1–10.7 (9)	17.3–21.7 (9)

view, the cotyla medialis is situated more proximally than the cotyla lateralis.

The area intercotylaris immediately posterior to the eminentia intercotylaris has a shallow depression between the eminentia intercotylaris and the borders of the cotylae. It then slopes posteriorly to another, much more extensive depression just anterior to the hypotarsus. The medial side of this section is higher than the lateral side.

The hypotarsus has two cristae hypotarsi separated by a broad, open, moderately deep sulcus hypotarsi. There is a very thin, low ridge running through the sulcus parallel to the crista lateralis hypotarsi. On the lateral side of this low ridge, the sulcus slightly excavates the base of the crista lateralis hypotarsi such that this is narrower than the posterior margin. The configuration of the crista medialis hypotarsi cannot be assessed. The main axis of the hypotarsus runs through the eminentia intercotylaris about 20° medial to the anteroposterior midline. The hypotarsus is separated from the ridge of the lateral shaft surface by a moderately deep furrow and from the medial shaft surface by broader and shallower furrow; both furrows contain a small nutrient foramen.

The anterior face is excavated at the proximal end by a deep fossa infracotylaris dorsalis, which continues distally as a wide sulcus extensorius. The deepest part of this basin

contains two foramina vasculare proximale at the same level, immediately proximal to the round tuberositas m. tibialis cranialis. On their medial side, the sulcus extensorius is prominent, bordered both medially and laterally by narrow ridges.

Viewed anteriorly, the lateral and medial margins of the proximal fragment of shaft converge distally. Distal to the rim on the medial side, the shaft curves medially to a projection level with the cotyla, before angling proximally into the medial rim of the cotyla. The lateral side also swings outwards to meet the rim of cotyla lateralis, but not as strongly. The curvature of the anterior shaft face to the eminentia intercotylaris is greater on the lateral side because of an anterior projection distal to the cotyla lateralis. A rounded projection lateral to the cotyla lateralis originates just distal to the rim, then collapses to a low, flat, broad ridge forming the lateral shaft surface. There is a thin, low ridge on the lateral shaft surface that starts near the midpoint of the cotyla, trending posterodistally towards the midline of the shaft, then more distally. On the medial side, the projection on the proximal end of the medial shaft face continues distally as the broad, rounded shaft margin.

On the distal end, the small portion of shaft that is retained is narrow before flaring to meet the trochleae. Its lateral margin is straight, the medial more curved to join trochlea

metatarsi II (in dorsal view). There is a deep groove running proximodistally proximal to, and level with, the lateral border of the trochlea metatarsi III. It meets the foramen vasculare distale, which is obscured on the dorsal surface. The medial side of the dorsal face slopes to join the medial surface; the junction of the dorsal and lateral faces is rather abrupt.

On the plantar surface, the sulcus supratrochlearis plantaris is moderately shallow. It is not strongly demarcated laterally, but medially is confined by a moderately high, narrow ridge connecting the base of the trochlea metatarsi II and the fossa metatarsi I. This long, elliptical fossa is situated on the proximal end of the ridge. There is a low, very thin ridge running lateral to the midline and meeting the foramen vasculare distale, which is prominent on this side.

This fragment is markedly compressed dorsoplantarly. The dorsal surface is more or less straight (in medial view), with the dorsal side of the trochlea metatarsi III projecting beyond it. The ridge supporting the fossa metatarsi I protrudes further plantarly than does the rest of the plantar shaft surface. The sulcus intertrochlearis lateralis is broader and deeper than the sulcus intertrochlearis medialis.

The trochleae are arranged in a curve, viewed distally. The trochlea metatarsi II lies at an angle of about 10° medial to the dorsoplantar midline; the trochleae metatarsi III and IV are tilted laterally about 10° and 20° from this midline, respectively. The trochlea metatarsi IV projects further dorsally and distally than does the trochlea metatarsi II, but neither projects as far as the trochlea metatarsi III. The trochlea metatarsi II extends further plantarly than the trochlea metatarsi IV. The trochlea metatarsi II is rounded dorsally and distally; its plantar border comprises a triangular projection, with a wide fovea lig. collateralis occupying much of the medial surface. The trochlea metatarsi III is grooved on its dorsal surface, with the lateral side projecting slightly further distally. The other trochleae lack grooves on their dorsal surfaces, although the trochlea metatarsi IV has a shallow groove on its distal surface. The dorsal surface of the trochlea metatarsi IV is tilted laterally. The distoplantar corner forms a triangular projection, projecting beyond the rest of the trochlea, but it and the fovea lig. collateralis are less prominent than on the trochlea metatarsi II.

The two proximal fragments differ in size, but share the same morphology. The magnitude of the morphometric differences are within that exhibited by modern taxa (Table 4; see also Hancock *et al.*, 1992 for measurements of living species).

Taphonomy

The occurrence of a stork in Wayne's Wok and White Hunter Sites is not surprising. Both support rich local faunas comprising species of a range of vertebrate groups, including many indicative of aquatic environments. In contrast, Bitesanntennary Site is an initially unlikely source of such a bird. It has also yielded many species (almost all bats with 11 species recorded; Hand, 1997), but on both faunistic and geological bases it is considered to be a cave-fill deposit. The other somewhat anomalous occurrence found here is that of the bulungamayine kangaroo *Ganguroo bilamina* (Cooke, 1997b).

There are several explanations for the presence of the non-bats *Ciconia louisebolesae* and *G. bilamina* in this cave deposit (see Baird, 1991b). It is possible that they used the cave as a shelter (*Ganguroo*) or there may have been a pool or other suitable foraging habitat within its immediate entrance. Otherwise the cave may have served as a predator's lair and these species represent prey items, or their carcasses may have been washed into the cave from outside after death. An entrance of the cave may have opened upward through the roof rather than to the side and thus served as a pitfall trap for unwary animals. The skeleton of a Yellow-billed Spoonbill *Platalea flavipes*, a bird of roughly similar size, shape and habits as *Ciconia* storks, has been recovered from Weekes Cave, South Australia; van Tets (1974) considered that it "may have become trapped in the sink hole after blundering into it" in search of residual water after a wet period in the usually dry environment.

Discussion

Despite the number of putative palaeospecies assigned to *Ciconia*, it is difficult to interpret the fossil history of this genus. The fragmentary nature of many of the remains makes comparisons troublesome; these do not lend themselves to clarifying any trends. The only species that are well represented are the large *C. maltha* and unnamed *Ciconia* of North America.

As currently construed, the genus *Ephippiorhynchus* occurs in equatorial Africa, represented by *E. senegalensis*, and in southern and southeastern Asia (but not Malaysia or Indonesia), southern New Guinea and northern and eastern Australia, represented by *E. asiaticus*. Its entry into Australasia from the north is unlikely to have been possible until Australia approached Asia and the New Guinean landmass was formed during the Late Miocene. Its current fossil record in Australia is compatible with this timetable and suggests that congeneric storks should not be recovered from earlier deposits. The Australasian and Asian populations are considered only subspecifically different and are separated by a substantial distributional gap. It seems unlikely that *E. asiaticus* was preceded into Australia by an earlier and now extinct congener. As there is no evidence of other large storks, such as marabous, all ephippio-rhynchine-like storks in Australia should be expected to belong to this species.

The distribution of neospecies of *Ciconia* is throughout Eurasia, Africa and South America. During the Pleistocene, this extended to North America (*C. maltha*) and Australia (*C. nana*). It is not clear why the latter landmasses lost their representatives of this genus. In Australia, *Ciconia* had a rather long history (late Oligocene-Pleistocene). Species of *Ciconia* and *Ephippiorhynchus* are sympatric across much of their ranges in Africa and Asia, so there is no reason to believe that the arrival of *E. asiaticus* in Australia was a contributing factor to the extinction of *C. nana*. There are also marked differences in size and presumably in ecology, which would have precluded any direct competition. Possible competition might be more likely between *C. nana* and ibises of the genera *Threskiornis* and *Plegadis*. *Threskiornis* cf. *T. molucca* has been recorded from the Early Pliocene Bluff Downs Local Fauna, so it and *C. nana* would have co-existed, at least in time, if not in space.

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A New Flightless Gallinule (Aves: Rallidae: *Gallinula*) from the Oligo-Miocene of Riversleigh, Northwestern Queensland, Australia

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ABSTRACT. Flightlessness in birds occurs in a taxonomically diverse array of families, but is best exemplified in the rails (Rallidae). Most flightless species of rails live on islands, where the absence of native mammalian predators may make flight superfluous. Fossil rails from Oligo-Miocene sites at Riversleigh, northwestern Queensland, Australia, are considered to represent a single species of gallinule *Gallinula*, described here as new. Compared with four Quaternary species of *Gallinula* from Australasia (two volant, two non-volant), it shows similarities with the flightless species in the development of the fore- and hindlimb elements and in other characteristics of limb bone morphology associated with flightlessness. These indicate that the Riversleigh species was non-volant. Its relationships with the Quaternary species, including the flightless *Gallinula mortierii*, now restricted to Tasmania, but known from Plio-Pleistocene deposits in eastern mainland Australia, are considered.

Flightlessness in birds occurs in a taxonomically diverse array of families. Flightlessness per se probably conveys no adaptive value; instead, it is an consequence of morphological changes that convey other selective advantages to the bird (Livezey & Humphrey, 1986). The general consensus is that the loss of volancy results as the flight muscles and pectoral assemblage become reduced as energy-saving processes during ontogeny (Olson, 1973a). Such modifications are advantageous when they do not render the birds more susceptible to predation. The presence of flightless birds on islands is strongly correlated with the absence of predators, particularly mammalian ones. Other factors can moderate this relationship, such as the availability of sufficient cover to avoid or reduce predation,

allowing birds to exist in the presence of predators, and the stability of resources, removing the need for far-ranging mobility (dispersal) (Worthy, 1988).

The developmental mechanisms involved in the loss of flight have been explored in greatest depth in the rails (Rallidae) (Olson, 1973a), the family that best exemplifies the phenomenon. About a fourth of the world's 125 or so living or recently extinct species have lost the power of flight. Most, but not all, of these are populations on islands, where the absence of native mammalian predators has reduced the benefit of the ability to fly. Those species that have become extinct usually did so at least in part from the inability to cope with the introduction of exotic predators. Prominent among the few instances of flightlessness in rails

on larger landmasses are the three species of native-hens of Australia and New Zealand (*Gallinula*, subgenus *Tribonyx*) (Fig. 1). The Black-tailed Native-hen *G. ventralis*, a volant species, is widespread through mainland Australia except for the east coast and far tropical north, but does not occur in Tasmania, to where the much larger and flightless Tasmanian Native-hen *G. mortierii* is restricted. The extinct *G. hodgenorum* of New Zealand, well represented in subfossil deposits, was also flightless (Olson, 1975a). The living volant Dusky Moorhen *G. (G.) tenebrosa* is common in both Australia and New Zealand.

The remains of rails have been recovered from several Oligo-Miocene sites at Riversleigh, northwestern Queensland (Fig. 1). These are considered to represent a single species, a new gallinule of the genus *Gallinula*. Although only one skeletal element is represented by an intact specimen, there is adequate material of the wings, legs and coracoid to indicate that this form was flightless.
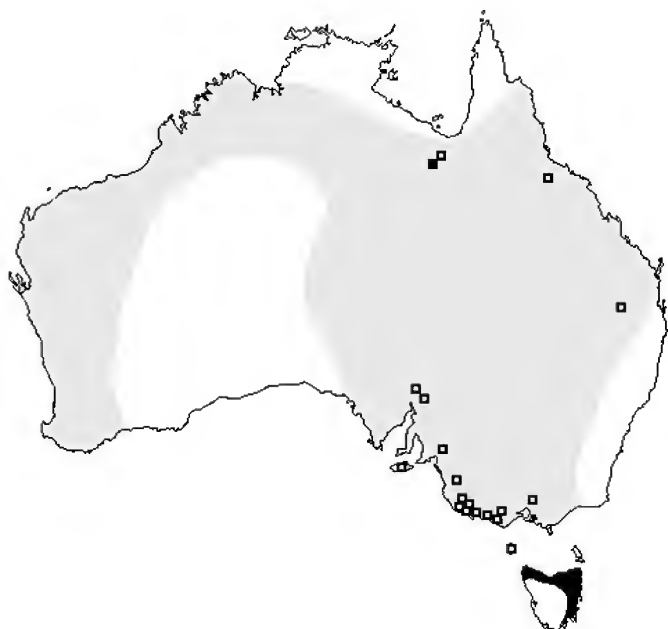

Fig. 1. Distribution of Recent and fossil Australian species of *Gallinula*. Key: black shading, current distribution of *G. mortierii*; grey shading, current distribution of *G. ventralis*; ■ Riversleigh (*G. disneyi*); □ Quaternary mainland sites producing *G. mortierii* (taken from De Vis 1888, 1892; Baird 1984, 1985, 1986, 1991b, 1992; McNamara & Baird 1991; Olson 1975b; and this work).

Materials and methods

Measurements were made with digital callipers and rounded to the nearest 0.1 mm. Length measurements of bones of *G. hodgenorum* were taken from specimens and from Olson (1975a); all other measurements were taken from specimens. Weight, wing chord and tarsus measurements of living species of *Gallinula* were taken from Marchant & Higgins (1993) and represent means for adult males. Osteological nomenclature follows Baumel & Witmer (1993), except that as terms of position and direction anterior is used rather than cranial and posterior rather than caudal. Olson (1973b) placed *Tribonyx* as a subgenus of the gallinules *Gallinula*; this was accepted by Condon (1975) and Christidis & Boles (1994), and is followed here.

Ratio-diagrams of the log differences between measurements of compared taxa were constructed following the method of Simpson (1941), wherein measurements are converted to logarithms, and one taxon is arbitrarily chosen as a standard. The difference between its converted measurements and the corresponding ones for each taxon are calculated (the logarithms of the ratios). The standard taxon thus has all ratios of 0 (zero difference in logarithms), which when plotted along a vertical axis on arithmetic graph scale, form a straight line. The logarithmic ratios for each taxon are plotted such that the points on a single horizontal line represent different values of the same variable across the taxa. Those values larger than the standard fall to the right of the standard line, the smaller ones to the left of it. The points of each taxon are connected with a line. Taxa with proportions identical to those of the standard taxon will have lines parallel to that of the standard. Variations from a parallel line are indicative of variations in the proportions from that of the standard taxon. Because only one of the fossil elements is complete, measurements of other features of the bones were used in lieu of total lengths because these should also reflect the changes in overall sizes of the elements. For the purposes of these comparisons, the values used were the means in Table 1 unless otherwise indicated.

Geology and geographical setting

The fossils described in this study were collected from the Riversleigh deposits, which are located 5 km west of the Riversleigh homestead (19°02'S 138°45'E), 200 km north of Mt Isa, northwestern Queensland, where they occur as an outcrop of Tertiary limestone overlying the Cambrian Thorntonia Limestone. There are now over 200 named Oligo-Miocene sites at Riversleigh. An informal system of grouping has been used (Systems A–C). These systems are "regionally clustered sites that appear to be super-positionally-related (differing in age but not significantly in position) and/or space-related (spatially isolated but approximately contemporaneous)" (Archer *et al.*, 1989). The principal accumulations are thought to have occurred in several episodes involving large lakes, shallow pools and cave deposits.

Rail material has been recovered from six sites, ranging from Late Oligocene to Middle Miocene in age. Current understanding of the age of these sites is taken from Creaser (1997); other birds represented at these sites are taken from Boles (1995, 1997). White Hunter Site, Hal's Hill Sequence, D-Site Plateau, considered to be part of System A (Late Oligocene), has yielded the greatest diversity of rail specimens. The White Hunter Local Fauna also contains other birds, including the small casuariid *Emuarius gidju* (Patterson & Rich, 1987) (Boles, 1992), the dromornithid *Barawertornis tedfordi* Rich, 1979, a stork (Boles, 2005) and several passerines. LSO Site (LSO Local Fauna), from the Verdon Creek Sequence, in the northern section of the D-Site Plateau, is also regarded as System A. Another site from the D-Site Plateau, but considered part of System B (Early Miocene), is Camel Sputum Site, Godthelp Hill Sequence (Camel Sputum Local Fauna). In addition to rails, it has also provided *Emuarius, Barawertornis*, another new genus and species of dromornithid, a swift *Collocalia buday* (Boles, 2001) and several passerines. Creaser's Ramparts

Site and Dirks Towers Site are in the central and northern sections of the D-Site Plateau, respectively. Both occur at about the same level and are possibly correlated. The ages are still unclear, but may be System A or B. Other birds recovered from Dirks Towers Site are *Emuarius* and passerines. Ringtail Site forms part of the Ray's Amphitheatre Sequence on Gag Plateau. This site is included in System C, considered to be of Middle Miocene age. The Ringtail Local Fauna includes waterfowl and a number of passerines.

Systematic palaeontology
Order Gruiformes Bonaparte, 1854
Family Rallidae Rafinesque, 1815

The fossils are referred to the Rallidae and subordinate taxa on the following suites of characters (adapted in part from Baird, 1992; Gilbert *et al.*, 1981; McCoy, 1963; Olsen, 1979; and Worthy, 1997).

Coracoid. The tuberculum brachiale is not undercut. The processus procoracoideus is pronounced, extending further medially than the processus acrocoracoideus. The cotyla scapularis is large and deep. The facies articularis humeralis is round, about as wide as long, and flares strongly laterally. The impressio m. sternocoracoidei is deep, extending far anteriorly.

Humerus. The incisura capitalis is deep and forms a shallow angle with the main axis of the shaft. The fossa pneumotricipitalis is shallow. The long axis of the caput humeri is roughly parallel with that of the incisura capitis. The sulcus ligamentosus transversus is shallow. The crista deltopectoralis is high, triangular and directed anteriorly. The processus supracondylaris dorsalis is small and blunt. The distal end of the element is narrow, not markedly produced laterally or medially. The processus flexorius extends further than the condylus ventralis. The fossa m. brachialis is shallow.

Carpometacarpus. The processus extensorius tends slightly proximoventrally (in anterior view). The dorsal rim of the trochlea carpalis extends far proximally and is acute at its proximalmost point. The fossa infratrochlearis is distinct, deep and circular. The os metacarpale minus is slightly curved. The facies articularis digitalis major and minor extend distally to the same extent.

Femur. The crista trochanteris is low but strongly developed proximolaterally and curves medially; there are strong ridges extending distally from its distal edge onto the anterolateral face of the shaft, where it joins the linea intermuscularis cranialis, and from near the anteriormost projection to the anterior border of the facies articularis antitrochanteris. The impressio m. iliotrochantericus caudalis is restricted to the extreme proximal end of the trochanter femoris. The collum trochanteris is distinctly narrowed both anteriorly and posteriorly. The shaft curves to meet the caput femoris in a broad, gentle curve (in anterior view). The proximal half of the shaft has a distinctive posterior inflection (in lateral view). The linea intermuscularis cranialis extends far distally from the ventral side of the crista trochanteris. The sulcus intercondylaris is moderately shallow. The fossa poplitea is shallow.

Tibiotarsus. The cristae cnemialis are strongly developed. The crista cnemialis lateralis is flattened proximodistally. The crista fibularis is well developed. The pons supratendineus is well developed. The condylus lateralis is much broader than the condylus medialis. The incisura intercondylaris is narrow and displaced medially by a broad condylus lateralis. The facies lateralis of condylus lateralis is rounded.

Tarsometatarsus. The hypotarsus is an elongated triangle (in proximal view). The crista lateralis hypotarsi is prominent, extending distally. There are two sulci hypotarsi (usually one or both enclosed), and a proximal pons tendineus on the medial side of the dorsal face. The dorsal surface of the shaft is flat, not concave. The trochlea metatarsi IV is shorter than the trochlea metatarsi III. Another useful character, which cannot be assessed on the fossil, is that the trochlea metatarsi II is much shorter than the trochlea metatarsi IV and is recessed plantarly.

Genus *Gallinula* Brisson, 1760

Gallinula Brisson, 1760, *Ornithologia sive Synopsis Methodica* vol. 1, Paris: Ad Ripam Augustinorum [50], vol. 6[2]—type species: *Gallinula* Brisson = *Fulica chloropus* Linnaeus, 1758.

Tribonyx has been distinguished from *Gallinula* by the shorter, heavier toes, longer tails, absence of white on the undertail coverts (Olson, 1973a) and short, wide bills with very short premaxilla (Olson, 1975a), all characters that cannot be assessed from the available fossil material. Osteological comparisons of a "typical" gallinule, *G. tenebrosa*, and two species of native-hens *Gallinula (Tribonyx), G. ventralis* and *G. mortierii*, found few useful characters that might permit separation of skeletal elements to subgeneric level. In the humerus of *Gallinula (Gallinula)*, the proximal end of the condylus dorsalis extends over the condylus ventralis. Brodkorb (1967) used this character to distinguish *Gallinula* (s.s.) from *Fulica*, in which the ventral extent of the condylus dorsalis is less, just reaching the dorsal border of the condylus ventralis. The species of *Gallinula (Tribonyx)* are somewhat intermediate between typical *Gallinula* and *Fulica* in this character, with a shorter, but still overlapping ventral extent of the condylus ventralis. The condylus dorsalis on the one distal humeral fossil fragment is abraded and the state of this character is equivocal. In the tarsometatarsus of *Gallinula* (s.s.), the lateral border of the shaft is about even with that of the trochlea metatarsi IV and they thus join smoothly with little lateral flaring. In contrast, species of *Gallinula (Tribonyx)* have the trochlea metatarsi IV curving outwards laterally, away from the border of the shaft. This character cannot be evaluated for the fossil material. Until skull material is recovered, it cannot be ascertained with certainty whether the Riversleigh flightless rail was indeed a native-hen.

This taxon is here diagnosed only as *Gallinula*. In the following discussion, however, extensive reference and comparisons are made to native-hens *Gallinula (Tribonyx)* because these are the only gallinules in Australia and New Zealand in which flightlessness occurs and the only ones well represented in the fossil record.

Gallinula (s.l.) can be diagnosed on the material available by the following suite of characters.

Coracoid. The processus procoracoideus extends about half way along the shaft posteriorly, joining it gradually. The impressio m. sternocoracoidei is deeply excavated mediodistally, and has a rounded border to the facies articularis sternalis.

Humerus. The crista bicipitalis extends distally only ½–⅔ as far as the crista deltopectoralis. The border of the epicondylus ventralis is concave (in anterior view). The proximal end of the condylus dorsalis extends over the proximal end of the condylus ventralis.

Carpometacarpus. The processus alularis is broad (in proximal view). The os metacarpale minus is somewhat curved proximally, less so distally, but overall more than in *Fulica*. The distoposterior corner of the symphysis metacarpalis distalis is obliquely angular, rather than square.

Femur. The junction of the impressiones obturatoriae and trochanter femoris forms an acute angle of c. 50°. The trochanter femoris is deep, flaring from the shaft both anteriorly and posteriorly (in lateral view). There is general agreement in the size and location of the impressiones iliotrochanteria. The condylus lateralis is well produced (in lateral view). The sulcus intercondylaris is situated near the midline of the element. The condylus medialis is moderately robust (in posterior view) and well produced posteriorly (in medial view).

Tibiotarsus. The impressio lig. collateralis medialis is deep. The crista fibularis is short. There is a deep U-shaped notch on the posterolateral margin of the area interarticularis. The crista cnemialis lateralis extends to a point well proximal to the proximal end of the crista fibularis. The crista cnemialis cranialis continues as a crest along the anterior medial edge of the shaft. The fossa retropatellaris is moderately deep. The anterior surface of the proximal end is slightly convex. The condylus lateralis extends far proximally, overlapping the distal ⅓–½ of the pons supratendineus.

Tarsometatarsus. The hypotarsus extends distally, rather than being truncate (in posterior and lateral views). The shaft has roughly parallel sides throughout its length. The foramen vasculare distale is situated far distally. Other useful characters, which cannot be assessed on the fossil, are that the dorsal margin of the trochlea metatarsi II is roughly even with the plantar margin of the trochlea metatarsi III; the area proximal to the trochlea metatarsi III, medial to the foramen vasculare distale and lateral to the trochlea metatarsi II, is broad with parallel sides; and the incisura intertrochlearis lateralis is wide.

Gallinula disneyi n.sp.

Fig. 2

Holotype. Queensland Museum, QM F20906, right proximal humeral fragment, broken through the shaft, with minor damage to the tuberculum ventrale.

Fig. 2. Specimens of the fossil gallinule *Gallinula disneyi*. (*A*) coracoid, shoulder end (QM F31470; White Hunter Site); (*B*) coracoid, sternal end (QM F31477; Camel Sputum Site); (*C*) humerus, proximal end (QM F20906: holotype; White Hunter Site); (*D*) humerus, proximal end (QM F31471; White Hunter Site); (*E*) humerus, distal end (QM F31472; White Hunter Site); (*F*) carpometacarpus (QM F31478; Camel Sputum Site); (*G*) femur, proximal end (QM F36452; LSO Site); (*H*) femur, distal end (QM F31479; Ringtail Site); (*I*) tibiotarsus, proximal end (QM F31473; White Hunter Site); (*J*) tibiotarsus, distal end (QM F31475; White Hunter Site); (*K*) tibiotarsus, distal end (QM F31474; White Hunter Site); (*L*) tarsometatarsus, proximal end (QM F20799; Ringtail Site); (*M*) tarsometatarsus, distal end (QM F31476; White Hunter Site). Scale equals 10 mm.

Type locality. White Hunter Site, Hal's Hill Sequence, Riversleigh, northwestern Queensland.

Age and local fauna. Late Oligocene/Early Miocene (System A); White Hunter Local Fauna.

Paratypes. *Coracoid*. QM F30692 (Dirks Towers), right shoulder fragment broken through the processus procoracoideus on the sternal side of the cotyla scapularis; QM F31469 (White Hunter), left shoulder fragment, broken on the sternal side of the foramen n. supracoracoidei; QM F31470 (White Hunter), right shoulder fragment, broken on the sternal side of the foramen n. supracoracoidei; QM F31477 (Camel Sputum), left element, missing shoulder end beyond the sulcus m. supracoracoidei, with some damage to the medial margin. *Humerus*. QM F31471 (White Hunter), right proximal fragment, broken through the shaft, with damage to the caput humeri and the tuberculum ventrale, and abrasion to the crista deltopectoralis; QM F31472 (White Hunter), left distal fragment, broken through the shaft. *Tibiotarsus*. QM F31473 (White Hunter), right proximal fragment, broken through the shaft distal to the proximal end of the crista fibularis, with abrasion to the proximal edge of the crista cnemialis medialis; QM F31474 (White Hunter), right distal fragment, broken through the shaft, with abrasion to the rims of the condyli; QM F31475 (White Hunter), right distal fragment, broken through the shaft. QM F24130 (Camel Sputum), left proximal fragment, broken through the shaft proximal to the distal end of the crista fibularis, with damage to the crista cnemialis medialis and edges of the facies articularis medialis; QM F31480 (Dirks Towers), right distal fragment, broken through the shaft proximal to the crista fibularis, missing the crista cnemialis cranialis and much of the facies articularis medialis. *Tarsometatarsus*. QM F23723 (White Hunter), proximal right fragment, broken through shaft; QM F20799 (Ringtail), proximal left fragment, broken through shaft; QM F30720 (Creaser's Ramparts), proximal right fragment, broken through shaft.

Referred specimens. *Carpometacarpus*. QM F30908 (Dirks Towers), left element lacking the distal end and the distal half of the os metacarpale minus; QM F31478 (Camel Sputum), complete left element. *Ulna*. QM F30693 (Dirks Towers), proximal left fragment with some abrasion to the rims of the articular surfaces. The olecranon is low and the processus cotylaris dorsalis is hooked (Olsen, 1979). Its proximal width is 6.3 mm. Although this specimen agrees in configuration with ulnae of the Rallidae and of *G. ventralis* in particular, it is only tentatively assigned to this taxon. It is not considered further. *Femur*. QM F36542 (LSO), proximal left fragment, broken through the shaft about ¾ of way to the distal end; complete except for slight damage to the proximal border of the crista trochanteris; QM F 31479 (Ringtail), left distal fragment, broken through the shaft, with damage to the medial side of the condylus medialis. *Tarsometatarsus*. QM F31476 (White Hunter), distal right fragment, comprising the trochleae metatarsi III and IV.

Etymology. Named for Henry John de Suffren Disney, formerly Curator of Birds at the Australian Museum, in honour of his contributions to the study of Australian birds, particularly another flightless rail, the Lord Howe Island Woodhen *Gallirallus sylvestris*.

Diagnosis. *Gallinula disneyi* is distinguished from other species of the genus by the following suite of humeral characters. It agrees with *G. mortierii*, and differs from other species, by having the proximal end round rather than elongate proximodistally (in posterior view); it is broader than in *G. hodgenorum*. The tuberculum ventrale is situated distal to the tuberculum dorsale, and is more pronounced than in *G. mortierii*. The crista deltopectoralis is short distally; it is more produced anteriorly compared to *G. hodgenorum*. The crista bicipitalis is short distally, joining the shaft more abruptly; ventrally it is rounder than in *G. mortierii* and more produced anteriorly than in *G. hodgenorum*. The condylus lateralis is thinner, not bulbous distally, and does not extend to the lateral margin of the bone (in anterior view). The tuberculum supracondylare is narrow, not round. Compared to that of *G. hodgenorum* the condylus dorsalis does not extend as far either distally or dorsally, relative to the shaft, and the fossa olecrani is shallower with less sharply defined edges.

Measurements. See Table 1.

Description

Coracoid. The processus acrocoracoideus is flattened, more so than in the other species, and is rotated such the tip is directed ventrally, more so than in *G. ventralis*; it is not directed anteriorly but is directed more laterally than in *G. hodgenorum*. The processus procoracoideus is broader distally and more rectangular than in the other species with a blunter tip (this is pointed in *G. hodgenorum*). The facies articularis humeralis and facies articularis clavicularis are smaller. Compared with the other species, the anterior end is more gracile while the sternal end is larger and more robust, with the area encompassing impressio m. sternocoracoidei broader, particularly anteriorly, than it is in *G. ventralis*. The sulcus m. supracoracoidei is more rounded (in ventral view) than in *G. ventralis*.

Carpometacarpus. The element is rather stout; it is between those of *G. mortierii* and *G. hodgenorum* in size and robustness. The os metacarpale minus is curved posteriorly; in this it resembles *G. mortierii* and *G. hodgenorum* and differs from *G. ventralis*, in which it is straight. The symphysis metacarpalis proximalis is shortened, agreeing with *G. mortierii*. The dorsal surface is flattened, more so than in *G. hodgenorum*. Compared to *G. ventralis*, the symphysis metacarpalis distalis is broader and shorter and the spatium intermetacarpale shorter. The distal end is narrower than in *G. mortierii*.

Femur. The collum trochanteris is rather short and deep (in anterior view). The distal end of the medial branch of the linea muscularis caudalis is prominent, more so than in *G. ventralis* and *G. hodgenorum*. The trochlea fibularis is broad and robust (in posterior view), with the distolateral corner square (in posterior view) and only moderately produced laterally compared to *G. hodgenorum*. The condylus medialis is well produced posteriorly. The ridge extending proximolaterally from the condylus lateralis is slightly pronounced, less so than in *G. hodgenorum*.

Tibiotarsus. Both cristae cnemialis are proportionally deeper than in *G. hodgenorum*. The foramen interosseum

Table 1. Measurements (mm) of fossil and Recent species of Australasian *Gallinula*. Values used for *G. disneyi* are indicated in bold type. For Recent species, the mean, (standard deviation) and range are given. Means for Recent species were used for constructing log-ratio diagrams (Figs. 4–5).

	Gallinula disneyi		*Gallinula ventralis* n=6	*Gallinula hodgenorum*	*Gallinula mortierii* n=3	*Gallinula tenebrosa* n=3
Coracoid						
anterior tip of processus	QM F30692	6.6	7.9 (0.3)	4.1	9.1 (0.4)	8.3 (0.1)
acrocoracoideus to	QM F31469	6.0	7.1–8.8		8.4–9.8	8.1–8.5
posterior border of facies	QM F31470	**6.0**				
articularis humeralis						
Humerus						
proximal width	QM F20906	**11.4**	12.2 (0.4)	7.8	14.2 (0.4)	13.3 (0.2)
	QM F31471	c.11.0	11.3–13.0		13.5–14.6	13.0–13.7
distal width	QM F31472	**9.7**	8.8 (0.2)	5.2	9.9 (0.1)	9.6 (0.2)
			8.0–9.5		9.7–10.1	9.3–9.9
Carpometacarpus						
total length	QM F31478	**28.6**	39.2 (1.0)	19.5	35.5 (0.4)	38.7 (0.5)
			35.8–42.4		35.1–36.4	37.8–39.4
proximal depth	QM F30908	8.3	8.2 (0.2)	4.9	9.1 (0.2)	8.2 (0.2)
	QM F31478	**7.3**	7.6–8.2		8.9–9.5	8.0–8.6
Femur						
proximal width	QM F36542	**10.5**	10.8 (0.3)	10.3	15.5 (1.2)	11.6 (0.2)
			10.0–11.4		13.2–16.9	11.2–11.9
proximal depth	QM F36542	**7.9**	8.5 (0.3)	8.1		9.5 (0.4)
			7.8–9.3		14.3–14.5	9.1–10.2
distal width	QM F31479	**>13**	10.2 (0.3)	9.7	16.8 (0.4)	11.2 (0.3)
			9.1–11.2		16.2–17.5	10.6–11.6
depth, condylus lateralis	QM F31479	**11.2**	8.8 (0.2)	8.1	14.7 (0.3)	9.6 (0.2)
			8.3–9.3		14.4–15.4	9.4–9.9
depth, condylus medialis	QM F31479	**>9.5**	7.9 (0.1)	7.3	13.3 (0.2)	8.9 (0.2)
			7.5–8.2		13.1–13.7	8.6–9.2
Tibiotarsus						
proximal width	QM F24130	9.7	9.0 (0.3)	7.9	15.6 (1.1)	9.8 (0.2)
	QM F31473	9.5	8.1–9.8		14.1–17.7	9.6–10.2
		9.6				
distal width	QM F31474	8.0	7.9 (0.3)	6.8	12.9 (0.1)	8.8 (0.1)
	QM F31475	8.2	7.0–8.5		12.6–13.0	8.6–8.9
		8.1				
depth, condylus lateralis	QM F31474	c.7.8	7.7 (0.2)	6.7	12.2 (0)	8.9 (0.2)
	QM F31475	8.0	7.0–8.3		12.2	8.5–9.3
		7.9				
depth, condylus medialis	QM F31474	>7.0	8.4 (0.3)	7.1	13.1 (0)	9.4 (0.1)
	QM F31475	**8.6**	7.5–8.9		13.0–13.1	9.1–9.6
Tarsometatarsus						
proximal width	QM F20799	10.4	8.5 (0.3)	7.4, 7.7	13.5 (0.1)	9.3 (0.1)
	QM F23723	9.6	7.5–9.4		13.4–13.8	9.1–9.5
	QM F30720	10.3				
		10.1				
proximal depth	QM F20799	9.5	8.3 (0.2)	7.6, 8.0	13.1 (0.1)	9.4 (0.2)
	QM F23723	9.2	7.5–9.0	13.0–13.2		9.1–9.7
	QM F30720	10.6				
		9.8				
depth, trochlea metatarsi III	QM F31476	c. **4.3**	4.6 (0.2)	4.1, 4.5	7.9 (0.2)	5.5 (0.2)
			4.2–5.1		7.6–8.1	5.3–5.8
depth, trochlea metatarsi IV	QM F31476	c. **4.4**	5.1 (0.1)	4.7, 5.1	7.7 (0.2)	6.4 (0.2)
			4.6–5.8		7.4–7.9	6.1–6.7

proximale is moderately long, extending proximally and cutting into the distal side of the facies articularis lateralis, which is consequently shortened. The impressio lig. collateralis mediale is situated more proximally than in the other species. The mediodistal portion of the shaft is not as curved medially as in the other species, while being more robust distally than in *G. ventralis*. The distal end of the sulcus extensorius is narrower and both it and the pons supratendineus are situated more medially than in the other species. The condylus lateralis is moderately flattened on the distal and anterodistal borders, and there is a greater difference between its anterior extension and that of the condylus medialis than in *G. hodgenorum*.

Tarsometatarsus. The proximal end is broader than in *G. ventralis*. The proximal end is broader relative to the shaft compared to *G. mortierii*. The hypotarsus is placed more medially than in the other species and the plantar apex is rounded. Both canales hypotarsi are enclosed. The shaft is more robust than that of *G. ventralis*. Compared to that of *G. hodgenorum*, the ridge extending distally from the hypotarsus is higher, longer and more centrally situated, thus making the plantar surface of the shaft more angular and less flattened.

Discussion

Comparison of *Gallinula disneyi* with other species

Three species of *Gallinula* live in Australia today: the typical *G. tenebrosa* and the two native-hens (*Tribonyx*), the volant *G. ventralis* and flightless *G. mortierii*. *Gallinula tenebrosa* is a heavier bird (male weight: 570 gm) than *G. ventralis* (410 gm), yet the legs are only slightly longer (male tarsus: *tenebrosa*, 63 mm; *ventralis*, 61 mm) and the wings are shorter (male wing: *tenebrosa*, 208 mm; *ventralis*, 218 mm). The wings of the much larger *G. mortierii* (males: weight, 1334 gm; tarsus, 84 mm) are both actually and proportionally small compared to those of the two volant species (wing: 202 mm).

The differences evident in external measurements are for the most part mirrored in the long bones (Fig. 2). The elements of *G. ventralis* are shorter than those of *G. tenebrosa*, except for the carpometacarpus, which is about the same length. The leg elements are more gracile in *G. ventralis* than in *G. tenebrosa*. The coracoid and hindlimb elements in *G. mortierii* are longer and more robust than both these species, whereas the ulna and carpometacarpus are shorter; the humerus is somewhat intermediate, approaching *G. tenebrosa* most closely. *Gallinula hodgenorum* is consistently smaller in all length measurements except for the femur, which is midway between the values for *G. ventralis* and *G. tenebrosa*. The carpometacarpus is the only complete element known for *G. disneyi*. It is larger than in *G. hodgenorum* but substantially smaller than in any of the living species (Table 1).

Because no direct comparisons of element lengths can be made between *G. disneyi* and the other taxa (other than for carpometacarpus), a number of measurements were taken from the fragments available for *G. disneyi*, with comparable ones from the living species. The measurements are given in Table 1 and comparisons of the elements between the taxa are shown in Fig. 4. The wing elements of *G. disneyi* are smaller than in the volant species, somewhat approaching those of *G. mortierii* and being of similar robustness. The legs of *G. mortierii* are considerably more robust. The femur of *G. disneyi* is larger and the lower leg elements are roughly intermediate between those of *G. tenebrosa* and *G. ventralis*. Its coracoid is particularly reduced, both actually and proportionally, compared to all living species. *Gallinula hodgenorum* is smaller and more gracile overall than *G. disneyi*, most markedly in the coracoid and elements of the wing (Table 1).

Using a log ratio diagram for the long bones lengths of Quaternary species of *Gallinula* (Fig. 2) shows that *G. ventralis* is similar to *G. tenebrosa*, with the major differences being the former's proportionally shorter coracoid and longer distal wing elements and tarsometa-

tarsus. The trend in the wing is not unexpected owing to the more pronounced mobility of this highly nomadic bird. *Gallinula mortierii* and *G. hodgenorum* resemble each other (except for size), but differ from the other taxa by having the forelimb elements much shorter relative to those of the
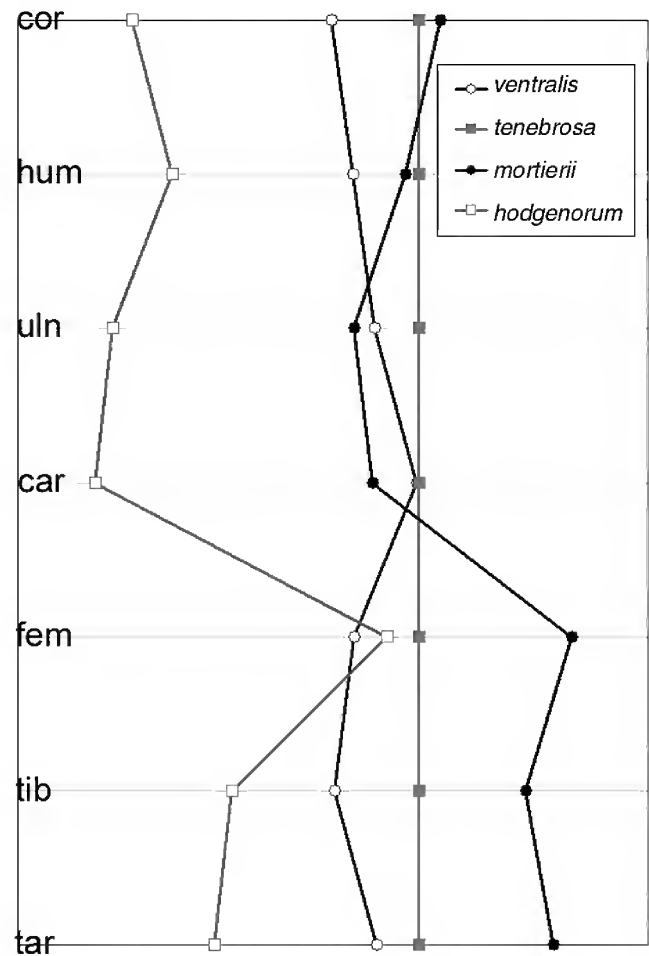

Fig. 3. Log-ratio plot of long bone lengths (coracoid, fore- and hindlimbs) of living and recently extinct Australasian species of *Gallinula*. The standard species is *Gallinula tenebrosa*. Abbreviations: *cor*, coracoid; *hum*, humerus; *uln*, ulna; *car*, carpometacarpus; *fem*, femur; *tib*, tibiotarsus; *tar*, tarsometatarsus.

hindlimb; the femur, in particular, is proportionally long. There are slight differences between the flightless species in the relative lengths of some outer limb elements.

Plots of the measurements from Table 1 produce overall patterns reminiscent of that in Fig. 3. Figure 5, based on the living species of *Gallinula*, is more indicative of relative robustness of elements than relative lengths, but the congruence in patterns supports the use of these measurements as indicators of major trends in the analysis. The relationship between proportions of *G. ventralis* and *G. tenebrosa* is similar to that in Fig. 3. Likewise, *G. mortierii* shows the less robust forelimbs and more robust hindlimbs.

A comparison of *G. disneyi* with the three species of *Gallinula (Tribonyx)* (Fig. 6), using *G. ventralis* as the standard taxon, exhibits roughly parallel tendencies of the three flightless species, with similar trends in the pattern of reduction of the wings and coracoid and increase in the robustness of the hindlimb elements. *Gallinula disneyi* differs from the other flightless forms in proportionally narrower proximal end of the carpometacarpus, smaller
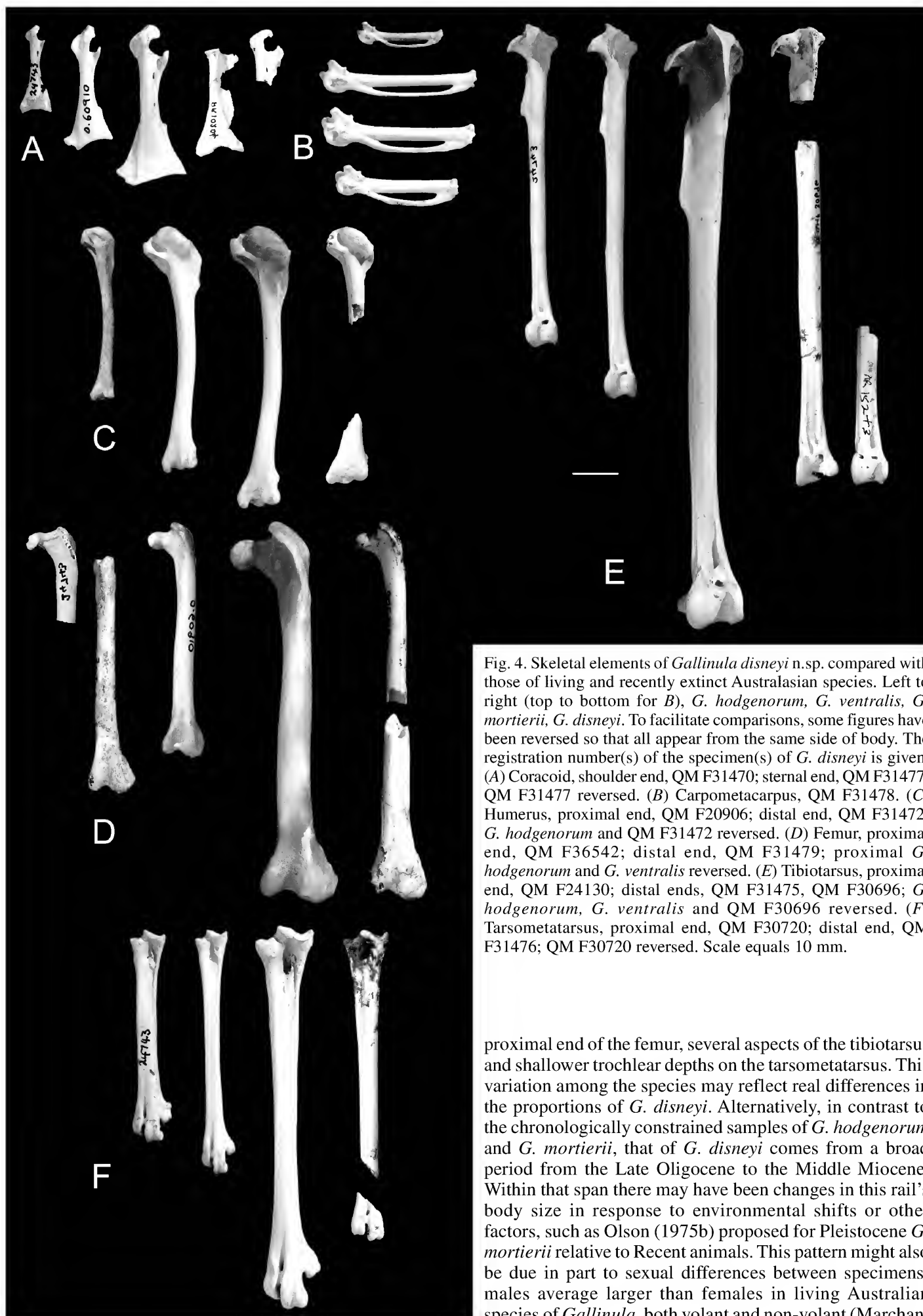
Fig. 4. Skeletal elements of *Gallinula disneyi* n.sp. compared with those of living and recently extinct Australasian species. Left to right (top to bottom for *B*), *G. hodgenorum, G. ventralis, G. mortierii, G. disneyi*. To facilitate comparisons, some figures have been reversed so that all appear from the same side of body. The registration number(s) of the specimen(s) of *G. disneyi* is given. (*A*) Coracoid, shoulder end, QM F31470; sternal end, QM F31477, QM F31477 reversed. (*B*) Carpometacarpus, QM F31478. (*C*) Humerus, proximal end, QM F20906; distal end, QM F31472; *G. hodgenorum* and QM F31472 reversed. (*D*) Femur, proximal end, QM F36542; distal end, QM F31479; proximal *G. hodgenorum* and *G. ventralis* reversed. (*E*) Tibiotarsus, proximal end, QM F24130; distal ends, QM F31475, QM F30696; *G. hodgenorum, G. ventralis* and QM F30696 reversed. (*F*) Tarsometatarsus, proximal end, QM F30720; distal end, QM F31476; QM F30720 reversed. Scale equals 10 mm.

proximal end of the femur, several aspects of the tibiotarsus and shallower trochlear depths on the tarsometatarsus. This variation among the species may reflect real differences in the proportions of *G. disneyi*. Alternatively, in contrast to the chronologically constrained samples of *G. hodgenorum* and *G. mortierii*, that of *G. disneyi* comes from a broad period from the Late Oligocene to the Middle Miocene. Within that span there may have been changes in this rail's body size in response to environmental shifts or other factors, such as Olson (1975b) proposed for Pleistocene *G. mortierii* relative to Recent animals. This pattern might also be due in part to sexual differences between specimens; males average larger than females in living Australian species of *Gallinula*, both volant and non-volant (Marchant
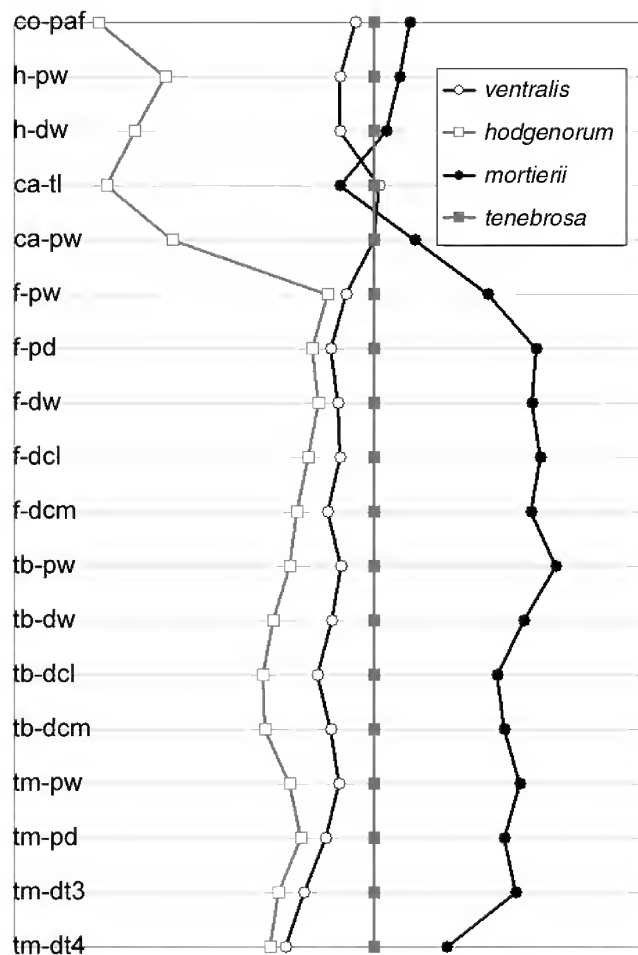
Fig. 5. Log-ratio plot of selected osteological measurements (see Table 62) of living and recently extinct Australasian species of *Gallinula*. The standard species is *Gallinula tenebrosa*. Abbreviations are *co*, coracoid; *h*, humerus; *ca*, carpometacarpus; *f*, femur; *tb*, tibiotarsus; *tm*, tarsometatarsus; *dlc*, depth of condylus lateralis; *dmc*, depth of condylus medialis; *dt3*, depth of trochlea metatarsi III; *dt4*, depth of trochlea metatarsi IV; *dw*, distal width; *paf*, processus acrocoracoideus to facies articularis humeralis; *pd*, proximal depth; *pw*, proximal width; *tl*, total length.

& Higgins, 1993). The most likely cause(s) cannot be identified until more material of common skeletal elements is available from the same sites.

Worthy (1997) pointed out exceptions to the assertion that "in all flightless birds, flightlessness is associated with increased body size" (Livezey & Humphrey, 1986). This contradiction is also demonstrated by the gallinules. While *G. mortierii* is consistent with this statement relative to other members of the genus, the flightless *G. hodgenorum* is the smallest member of *Gallinula (Tribonyx)*.

Flightlessness in *Gallinula disneyi*

The major morphological consequence of flightlessness is a reduction of the pectoral assemblage and forelimb. Concurrent with this is an increase in the size of the pelvic limb. The most obvious morphological change in the legs is an increase in the robustness of the elements. In the wing there are several structures that undergo obvious and characteristic modifications with the loss of flight.

Olson (1975a) and Rich *et al.* (1985) presented a range of features that characterize the humerus of non-volant birds.

These are evident in a comparison between the Riversleigh fossils and the similar-sized humerus of *Gallinula ventralis*. In the fossils, the incisura capitis is directed more proximodistally, bringing it more in line with the shaft; this is caused by the entire proximal end of the humerus being tilted laterally relative to the rest of the element. By virtue of this tilting, the tuberculum ventrale becomes on the same proximal level as the caput humeri. The caput itself is considerably flattened and elongate. The crista delto-pectoralis is thickened, reduced and rotated proximo-medially in respect to the shaft. The crista bicipitalis is reduced. The shaft is curved and stout; however, this has not been preserved in the fossils. Other changes are seen in the fossil carpometacarpus. Compared to this element in the volant species, it is reduced, becoming shorter as well as stouter, os metacarpale majus is bowed in anterior view, and os metacarpale minus is more curved. Changes in the coracoid related to flightlessness include a more robust processus acrocoracoideus and a broader and more medially directed processus procoracoideus lacking the ventrally directed twist of the tip.

The proportional reduction in length is not uniform across the wing elements. There is a gradient in this proportion, with increased reduction from the proximal to the distal elements (Livezey, 1995). This is characteristic of flightless birds, not just rails (see, for example, Gadow, 1902; Livezey, 1989, 1990, 1992; Livezey & Humphrey, 1986; Worthy, 1988). Direct comparison of the fossils with comparable elements of the volant *Gallinula ventralis* demonstrates that the fossil rails also exhibit this trend (Fig. 6). The proximal end of the fossil humerus is slightly smaller than that of *G. ventralis*, primarily through the reduction of the caput humeri and cristae deltopectoralis and bicipitalis, while the distal end is larger. The carpometacarpus of the fossil is substantially shorter (78% of length) and more robust. In contrast, all fragments of the fossil's hindlimb elements are considerably larger than the comparable sections of the bones of *G. ventralis*. Its larger legs and smaller wings compared to *G. ventralis* are a good indication that it was unable to fly.

Although *Gallinula hodgenorum* had greater reduction of the wings and pectoral apparatus, and more pronounced morphological differences from *G. ventralis* than had *G. mortierii* (Olson, 1975b), it showed trends in the hindlimb that are also evident in the Riversleigh bird. The shafts of both the tibiotarsus and tarsometatarsus are heavier those of *G. ventralis*. The crista cnemialis lateralis of the tibiotarsus is thicker. The proximal end of the tarsometa-tarsus is more expanded, as are the trochleae, which are also heavier. It is difficult to compare these usefully with the trochleae of *G. disneyi* because abrasion to the latter gives an underestimate of their size (see Fig. 6).

Distribution of *Gallinula disneyi*

Gallinula disneyi, like *G. mortierii*, is unusual because of its continental distribution. *Gallinula mortierii*, now restricted to Tasmania, once extended well into eastern mainland Australia, where it has been recorded from Pleistocene and possible Pliocene deposits (Fig. 1), with the youngest record at 4670±90B.P. (Baird, 1991a). It is extensively represented in deposits in southeastern Australia in the Murray-Darling River system, with a northernmost record from Wyandotte Creek, northeastern Queensland
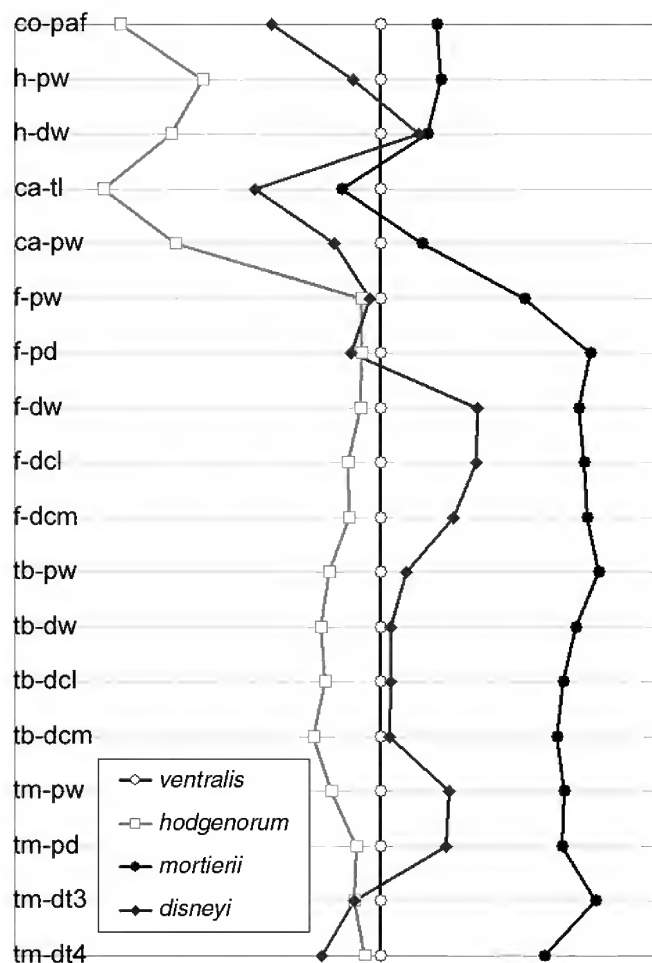
Fig. 6. Log-ratio plot of selected osteological measurements (see Table 62) of *Gallinula disneyi* and living and recently extinct species of native-hens *Tribonyx*. The standard species is *Gallinula ventralis*. Abbreviations are *co*, coracoid; *h*, humerus; *ca*, carpometacarpus; *f*, femur; *tb*, tibiotarsus; *tm*, tarsometatarsus; *dlc*, depth of condylus lateralis; *dmc*, depth of condylus medialis; *dt3*, depth of trochlea metatarsi III; *dt4*, depth of trochlea metatarsi IV; *dw*, distal width; *paf*, processus acrocoracoideus to facies articularis humeralis; *pd*, proximal depth; *pw*, proximal width; *tl*, total length.

(Olson, 1975b; Baird, 1984, 1986; McNamara & Baird, 1991). A new record from the Plio-Pleistocene Floraville Local Fauna (west of Leichhardt River, south of Floraville Homestead, northwestern Queensland; 18°17'S 139°52'E), represented by a tarsometatarsus (QM F24605), extends the western edge of the known distribution (unpublished data). During the Plio-Pleistocene, *G. mortierii* persisted despite the presence of native marsupial carnivores, even as it does today in Tasmania in the company of the Tasmanian Devil *Sarcophilus harrisii* and, previously, the Thylacine *Thylacinus cynocephalus*. Baird (1984, 1986, 1991a,b) hypothesized that its extinction on the mainland was probably due to a combination of changing environmental conditions and the introduction of the Dingo *Canis familiaris dingo* (earliest known occurrence 3450±95B.P.; Milham & Thomson, 1976). Ridpath (1972) noted that the native marsupial species were/are nocturnal, and the diurnally active *G. mortierii* has evolved several methods of avoiding ground predators. The Dingo, in contrast, forages extensively during the day when the native-hens

would receive no benefit from darkness. *Gallinula disneyi* also co-existed with numerous native marsupial carnivores (large Dasyuridae, Thylacinidae, Thylacoleonidae), and it is doubtful that any of these could have caused its eventual extinction (see Baird, 1991a). As discussed below, it is possible that rather than becoming extinct, *G. disneyi* may have evolved into the living *G. mortierii*.

Species relationships in *Gallinula (Tribonyx)*

The pattern and sequence of speciation in the native-hens *Gallinula (Tribonyx)* are unclear. The progenitor of *G. hodgenorum* would have colonized New Zealand from Australia (Olson, 1975a,b). Olson (1975b) considered that *G. hodgenorum* "probably arose from an ancestor closer to the common ancestor of both *mortierii* and *ventralis* than to *ventralis* itself". In bill structure it more closely resembled *G. mortierii* than *G. ventralis*, and was more divergent from *G. ventralis* than *G. mortierii* in morphology of the fore- and hindlimbs (Olson, 1975a). *Gallinula disneyi* obviously could not have been ancestral to either *G. ventralis* or *G. hodgenorum*, but it is possible that this species was in the direct lineage of *G. mortierii* (see below).

It is known that *G. mortierii* is not an insular derivative of *G. ventralis*; these species have been separated for a long time (Olson, 1975b). Olson (1975b) considered that *G. mortierii* was not a Tasmanian autochthon, instead probably having colonized Tasmania from the mainland during a period of low sea level. Tasmania has been alternately connected and separated from mainland Australia by changes in sea levels during the Tertiary. Although oscillations during the Quaternary are well documented, there have been other periods in the Tertiary during which lower sea levels would have exposed the intervening land. Thus the loss of flight in this lineage could have occurred in Tasmania before the Quaternary. Both *G. disneyi* and *G. mortierii* may have evolved in insular Tasmania while that island was isolated and then subsequently invaded the mainland when the connection to the mainland was re-established. The fossil record of Tasmania is thus far inadequate to determine whether a species of flightless *Gallinula* occurred there in the Tertiary.

Another possibility is that there was but a single event of this kind, which gave rise to *G. disneyi*. This species, in turn, was the direct ancestor of *G. mortierii*. Retreat and restriction of the latter to Tasmania was a Quaternary event. This scenario has other possible ramifications. Represent-atives of many lineages, across a variety of vertebrate groups, exhibited marked increases in body size through the latter half of the Pliocene, peaking during the Pleistocene. These were usually the largest members of their respective lineages (megafauna). Subsequently, the megafauna elements either died out about 40–50,000 years ago or became smaller (dwarfing), continuing as the modern representatives. It is possible that the transition of *G. disneyi* to the much larger *G. mortierii* was part of this phenomenon. Any Late Quaternary dwarfing of *G. mortierii* was minimal, however, leaving this species a large-bodied animal.

Olson (1975b) recognized a chronosubspecies (*G. m. reperta*) for specimens from Chinchilla, Queensland, on the basis of their overall smaller size than modern birds. Baird (1984) found considerable overlap in measurements between modern and Late Pleistocene specimens of *G.*

mortierii, and consequently synonymized the Chinchilla material with the living form. A more refined temporal division of specimens may yet demonstrate that size differences do exist between Pliocene and Late Pleistocene/ Holocene specimens. The Chinchilla deposit is now considered to be of Early to Middle Pliocene age (Woodburne *et al.*, 1985), earlier than previously thought. If *G. mortierii* evolved directly from *G. disneyi*, then such smaller *mortierii*-type birds would not be unexpected.

If *G. disneyi* gave rise to *G. mortierii*, the rate of such a change would have been very marked between the Late Miocene and the Pliocene. *Gallinula disneyi* is known from a time span of about 15 million years. The sample size is too incomplete to track major morphological changes across this period; however, there is no indication of any noticeable increase in size. The tarsometatarsus shows no shift towards *mortierii*-like size or robustness between the System A White Hunter Site and System C Ringtail Site. Between these widely separated times, sufficient anagenetic change in this lineage might be expected such that samples would exhibit recognisable morphological differences. In *G. disneyi-mortierii*, sudden changes in size might have been related to the onset of the aridification of Australia, starting in the Late Miocene. A possible argument against a *G. disneyi-G. mortierii* ancestor-descendant relationship is that there is no evidence of an ongoing decrease in the coracoid and forelimb, as might be expected in a flightless lineage of such long duration.

Other Riversleigh rails

Two additional specimens of rails have been recovered at Riversleigh. One shows differences from the comparable elements of *G. disneyi* and may belong to a different species. The other is tentatively referred to this family and represents a considerably smaller animal. Both are considered Rallidae indeterminate at this time.

A tibiotarsus (QM F30696) of a rail from Camel Sputum Site, from where material referred to *G. disneyi* has been recovered, consists of a left distal fragment retaining much of shaft (length as preserved 77.5 mm). It has damage to its posterodistal face and most of the condylus medialis. The shaft is of comparable in width to that of *G. disneyi* as retained on a proximal fragment (QM F24130). Compared with the two distal tibiotarsal fragments of *G. disneyi* (QM F31474, QM F31475) the distal end of this specimen is more robust, with a greater width, both actually and proportionally relative to the shaft; the condylus lateralis is deeper. Morphological differences between this specimen and the other tibiotarsi include the position of the condyli; rather than being more or less parallel and in line with the margins of the shaft, the condyli of the Camel Sputum specimen are placed further laterally and medially, respectively. This makes the distal end flare outwards from the shaft much more. The condylus lateralis is inclined more proximomedially-distolaterally. Distal width > 9.3 mm; depth of condylus lateralis 8.6 mm. In view of these differences in size and morphology, this tibiotarsus is not placed with *G. disneyi*. It may be that these features fall within the variation of that species, although it is not evident from the other specimens, nor is there an indication of such a range of differences in modern species.

A small, damaged left carpometacarpus (QM F40203), still attached to the rocky matrix, from Dunsinane Site (System A; Arena, 1997), appears to be that of a rail. Because sections of the proximal end are missing, a definite identification is precluded. This specimen is substantially smaller than the carpometacarpus of *G. disneyi*, and is comparable in size to the living *Rallus pectoralis*; there is no indication that it represents a juvenile It is tentatively assigned to the Rallidae.

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Revision of the Genera
Sphodropoda, Trachymantis and *Zopheromantis*
(Mantodea: Mantidae: Mantinae)

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ABSTRACT. The genera *Sphodropoda* Stål, *Trachymantis* Giglio-Tos and *Zopheromantis* Tindale are revised. Aspects of their biology are discussed and distributions given. One new species of *Sphodropoda, S. lepida*, is described. *Sphodropoda moesta* Giglio-Tos, *S. mjobergi* Sjöstedt and *S. papua* are new synonyms of *S. tristis* (Saussure). *Sphodropoda dentifrons* Stål is transferred to *Trachymantis. S. loripes* Tindale is transferred to *Zopheromantis. Z. trimaculata* Tindale is a new synonym of *Z. loripes*.

Sphodropoda Stål, *Trachymantis* Giglio-Tos and *Zophero-mantis* Tindale are three closely related mantid genera, known only from mainland Australia and, in the case of *Sphodropoda*, Papua New Guinea, the Solomon Islands and possibly Fiji. All are shrub and tree dwellers, and most of the species inhabit drier regions.

Stål (1871) erected *Sphodropoda* as a subgenus of *Hierodula* Burmeister and included a single species, *H. (Sphodropoda) tristis* (Saussure). Westwood (1889) elevated *Sphodropoda* to generic level. *Trachymantis* was erected by Giglio-Tos (1917) for *T. obesa* Giglio-Tos and *Zopheromantis* by Tindale (1924) for *Z. trimaculata* Tindale. Beier (1935) incorrectly synonymized *Zopheromantis* with *Hierodula* without giving reasons. *Zopheromantis* is recognized here as a valid genus.

Materials and methods

Methods and terminology follow Milledge (1990, 1997). The following abbreviations are used for male genitalia: *apr*, apical process of left phallomere; *dpr*, distal process of ventral phallomere; *pa*, phalloid apophysis. Measure-ments are in mm and range from the smallest specimen examined to the largest, except where an insufficient range of material was available, when single measurements are given. Abbreviations used for institutions where material is held are as follows: AM, Australian Museum, Sydney; ANIC, Australian National Insect Collection, Canberra; BMNH, The Natural History Museum, London; NHRM, Swedish Museum of Natural History, Stockholm; NMV, Museum Victoria, Melbourne; SAM, South Australian Museum, Adelaide; WAM, Western Australian Museum, Perth; ZMHU, Zoologisches Museum der Humbolt-Universitat, Berlin.

Relationships

These three genera appear to form a closely related group, sharing a number of characters including well-developed preacetabular spine, facial shield as wide as high, denticules between teeth on outer margins of fore femora and bifurcate distal process in the male genitalia. Beier (1964) placed *Sphodropoda* and *Trachymantis* in his Miomantini, a tribe
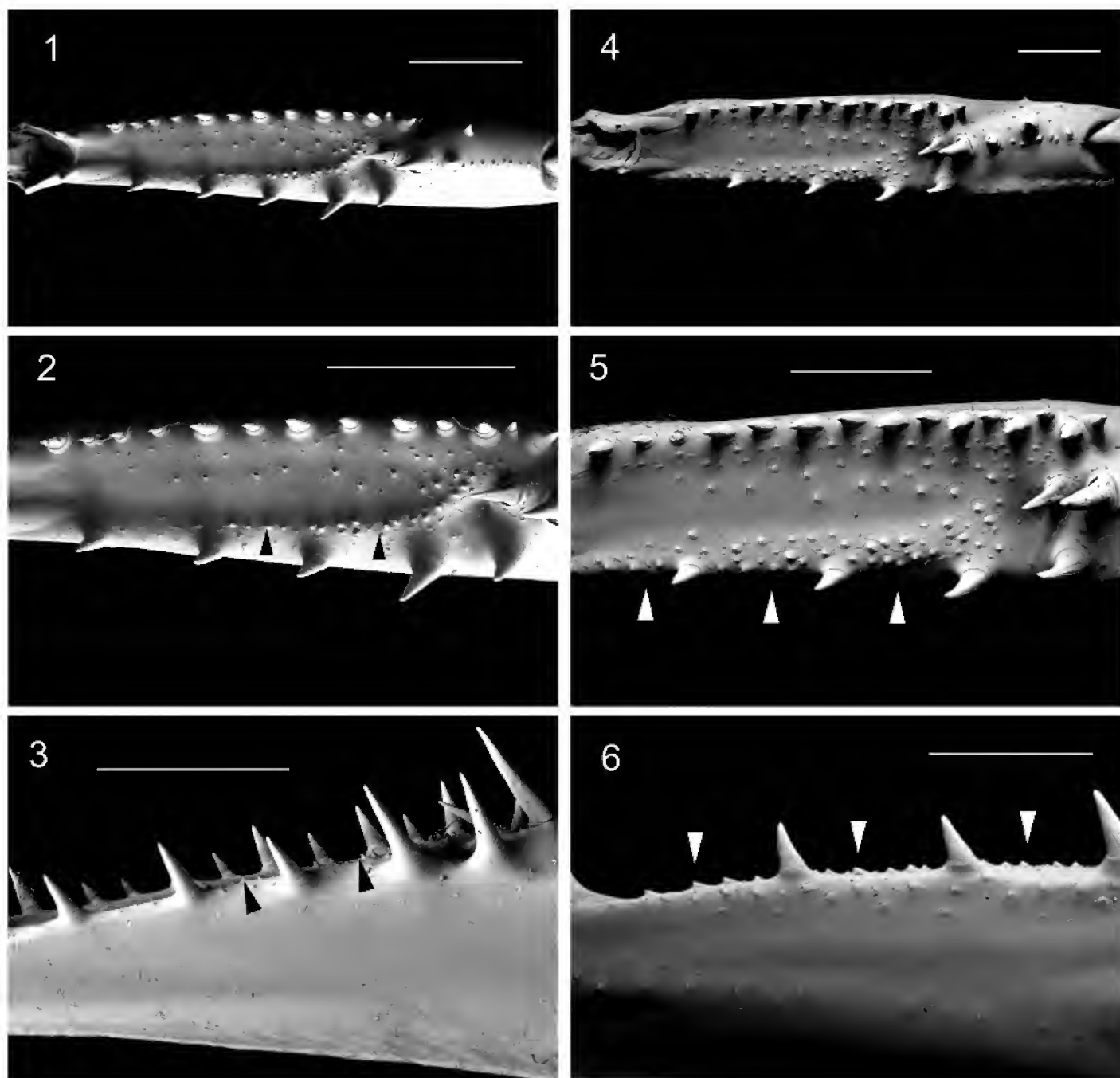
Figs. 1–6. Right fore femur, females, arrows indicate denticles. (1) *Iris* sp., ventral view; (2) same, ventral view, distal two thirds; (3) same retrolateral view, distal two thirds. (4) *Sphodropoda quinquedens*, ventral view; (5) same, ventral view, distal two thirds; (6) same retrolateral view, distal two thirds. Scales = 2 mm

sharing only the single synapomorphy of denticules between the outer spines of the fore femora. He obviously had not examined specimens of *Zopheromantis* as he considered it to be a synonym of *Hierodula* (Mantini), which lacks this feature. There is some doubt as to whether the Miomantini is monophyletic, as the genera within it display a wide variety of forms. The denticules between the outer spines in the three genera considered here are really only small tubercules, and could be interpreted as a manifestation of the relatively tuberculate cuticle they possess. I have examined specimens of the European genus *Iris* Saussure, which Beier also included in his Miomantini. The pattern of denticles (Figs. 1–3) is different from that found in the genera considered here (Figs. 4–6). In fact, the denticles are not between the outer spines but on the ventral surface of the femur. The original authors (Stål, Giglio-Tos and Tindale) considered the genera

revised here to be related to *Hierodula*. Although this seems more likely than Beier's grouping, as noted elsewhere (Milledge, 1997), further work is required on the mantid fauna of other parts of the world before the relationships of the Australian fauna can be fully understood.

Sphodropoda Stål

Sphodropoda Stål, 1871: 399. Type species *Sphodropoda tristis* Saussure, by original designation.

Diagnosis. Head about as high as wide, frontal shield without dorsal extensions; preacetabular spine strong; inner face of first tarsal segment partly or wholly black, ventral face of fore femur tuberculate, especially toward outer margin; both sexes macropterous (some females slightly brachypterous), ventral face of costal area of tegmen at least

partly red. Can be distinguished from *Trachymantis* by the lack of a tooth on the apex of the frontal shield and from *Zopheromantis* by the hind femur being only about half the length of the abdomen.

Description. Small to moderately large, body robust, male macropterous, female macropterous to slightly brachypterous. Head about as wide as high, not significantly compressed anteroposteriorly, apical margin gently arched; eyes rounded, not particularly prominent; frontal shield slightly wider than high, flat, with distinct ridge laterally and apically but not produced into a tooth at apex.

Pronotum moderately elongate, supracoxal expansion slight to distinct, dorsal surface finely to moderately coarsely granulate, margins finely denticulate, ventral surface with preacetabular spine prominent. Fore coxa as long as or longer than metazone of pronotum, often with distinctive pattern on inner face and a number of prominent tubercles on anterior margin. Fore femur finely tuberculate on ventral surface, particularly toward outer margin; with four discoidal spines, relative length from longest to shortest 3-2-1-4; with four outer and 15 inner spines, claw groove

situated at about a third the total distance from base. Inner face of tarsus largely black.

Tegmen with costal area opaque, partially red beneath; discoidal area entirely opaque to mostly hyaline. Hind wing with costal and discoidal area pigmented, anal area largely hyaline. Mid and hind legs relatively short, hind femur about half the length of abdomen. Abdomen moderately elongate, cerci short, slender and cylindrical. Male genitalia with *dpr* bifurcate.

Notes. All the species in this genus have relatively short legs, a feature that appears to be associated with the behavioural adaptation of depressing the body against the substrate when threatened. This behaviour has been observed in three of the species recognized here (*S. tristis, S. quinquedens* and *S. viridis*), the behaviour of the other (*S. lepida*) has not been observed. If the substrate is a branch or twig this behaviour includes moving to the side of the branch facing away from the threat. Similar behaviour appears to have evolved independently in other genera of Mantidae, e.g., *Tarachodula* (Preston-Mafham 1990, plate 33) and *Galepsus* (Hevers & Liske 1991, plate 21).

Key to species of *Sphodropoda*

1   Internal face of fore coxa with 5–6 transverse white bands anteriorly (Fig. 15) .... *S. quinquedens*

—— Internal face of fore coxa lacking bands 2

2   Anterior margin of fore coxa internally with six to seven whitish tubercles (Fig. 12) .... *S. tristis*

—— Anterior margin of fore coxa without such tubercles 3

3   Major veins of discoidal area of tegmina uniformly green .... *S. viridis*

—— Major veins of discoidal area of tegmina flushed reddish brown .... *S. lepida*

Sphodropoda tristis (Saussure)

Figs. 7–8, 11–13, 17, 42

Mantis tristis Saussure, 1871: 93.
Hierodula (Sphodropoda) tristis (Saussure).–Stål, 1871: 399.
Sphodropoda tristis (Saussure).–Westwood, 1889: 13.
*Sphodropoda moesta* Giglio-Tos, 1911: 20; **new synonym.**
Sphodropoda mjobergi Sjöstedt, 1918: 25; **new synonym.**
Sphodropoda papua Beier, 1965: 489–90; **new synonym.**

Type material examined. Syntype female of *Sphodropoda moesta*, Cape York, Daemel, cat. no. 3883 (ZMHU). Syntype male and syntype female of *Sphodropoda mjobergi*, Kimberley district, N.W. Australia, Mjöberg (NHRM).

Other specimens examined. Queensland. 1♂, Armstrong Creek crossing, 13 km NNW of Guthalungra, 26 Jan 1982, M.S. & B.J. Moulds. 1♀, Biggenden Bluff, Mt. Walsh National Park, 10 Jan 1984, D. Rugg. 1♂, 1♀, 7 km S of Biggenden, Mt. Walsh National Park, 9–12 Apr 1971, H. Frauca. 5♀, Bluff Range, near Biggenden, 2–12 May 1971, H. Frauca. 2 juv, Bluff Range, 8 km S of Biggenden, 9 Jan 1971, H. Frauca. 1♀, 20 km NE of Bundaberg, Apr 1971, H. Frauca. 1♂, Byfield, 10 May 1955, Common & Norris. 2♂, 1♀, Carnarvon National Park (Tourist Lodge), 25°05'S 148°15'E, 27 & 29 Apr 1979, K.H.L. Key. 1♂, Clermont, 15 Feb 1975, R.A. Farrow. 3♂, 7 km SSW of Clermont, 2 Apr 1977, R.C. Lewis. 1♀, 1 juv, near Clohesy River 12 km SW of Kuranda, 7 Feb 1988, 16°54'S 145°34'E, D.C.F. Rentz. 1 juv, 52 km SE of Cloncurry, 25 Aug 1960, M.J.D. White. 1 juv, Desailly Creek, 10 km NW of Mt.

Carbine, 16°30'S 144°55'E, 19–21 May 1981, D.C.F. Rentz. 1♂, 1 juv, 8 km W of Dimbulah, 17°09'S 145°02'E, 22 Mar 1988, D.C.F. Rentz. 1♂, 42 km N of Emerald, 20 Apr 1955, Norris & Common. 1♀, Forty Mile Scrub, 55 km SSW of Mt. Garnet, 18°06'S 144°50'E, 8 Dec 1985, J. Balderson. 1♂, 3 km N of Greenvale HS, W of Ingham, 5 Apr 1962, K.H.L. Key & E.L. Corby. 1 juv, Isla Gorge Lookout, Isla Gorge National Park, SSW of Theodore, 25°10'S 150°00'E, 21 Apr 1982, D.C.F. Rentz. 1♂, 3 km SE of Mary Kathleen, 21 Apr 1962, K.H.L. Key & E.L. Corby. 1♂, Moondoo, 26 Feb 1963, A.L. Dyce & M.D. Murray. 1 juv, 10 km SE of Mt. Carbine, 16°37'S 145°12'E, 24 Nov 1981, J. Balderson. 1 juv, 17 km WSW of Mt. Faulkner, Clermont district, 7 Jan 1965, M.J.D. White. 1♂, Mt. Larcom, 18 Apr 1955, Norris & Common. 2♂, Running River, 22 km W of Paluma, 11 Feb 1971, J.G. Brooks. 1♂, near Poona Lake, Cooloola National Park, 25°58'S 153°07'E, 4 Apr 1978, D.C.F & B.G.F. Rentz. 1♀, 1 km N of Rounded Hill, near Cooktown, 15°17'S 145°13'E, 5–7 May 1981, D.C.F. Rentz. 1♂, 23 km NNE of Taroom, 29 Mar 1977, R.C. Lewis. 1♂, 9 km WNW of Taroom, 25°34'S 149°45'E, 1 Feb 1981, D.C.F. Rentz & D.T. Gwynne. 1 juv, 7 km E of Toowoomba, 2 Jan 1956, M.J.D. White. 1♂, Townsville, 7 Jan 1968, P. Ferrar. 1♂, Townsville, 31 Dec 1967, P. Ferrar. 1♀, Watalgan Range, near Bundaberg, 3 Jul 1971, H. Frauca. 1♀, Watalgan Range, S of Rosedale, Mar 1971, H. Frauca. 1♂, Waverley Creek, Bruce Highway, 10 km S of St. Lawrence turnoff, 27 Jan 1988, M.S. & B.J. Moulds (All ANIC). 1♀, Augathella, 25°48'S 146°35'E, 18 Jan 1993, G. Milledge. 1♀, 16 km ESE of Burke & Wills Junction, 19°17'S 140°29'E, 15 Jan 1993, G. Milledge. 1♂, 2♀ 1 km NNE of Collins Weir, W of Atherton, 17°15'S 145°17'E, 10 Feb 1989, G. Milledge. 1♂, 8 km E of Emuford, 30 Dec 1989, M.S. & B.J. Moulds. 5♀, Georgetown, 12–14 Apr 1991, G. Milledge. 1♂, Georgetown, 16 Apr 1991, G. Milledge. 1♂, 12 km E of Georgetown, 12 Apr 1991, G. Milledge. 1♀, 6 km S of Normanton,
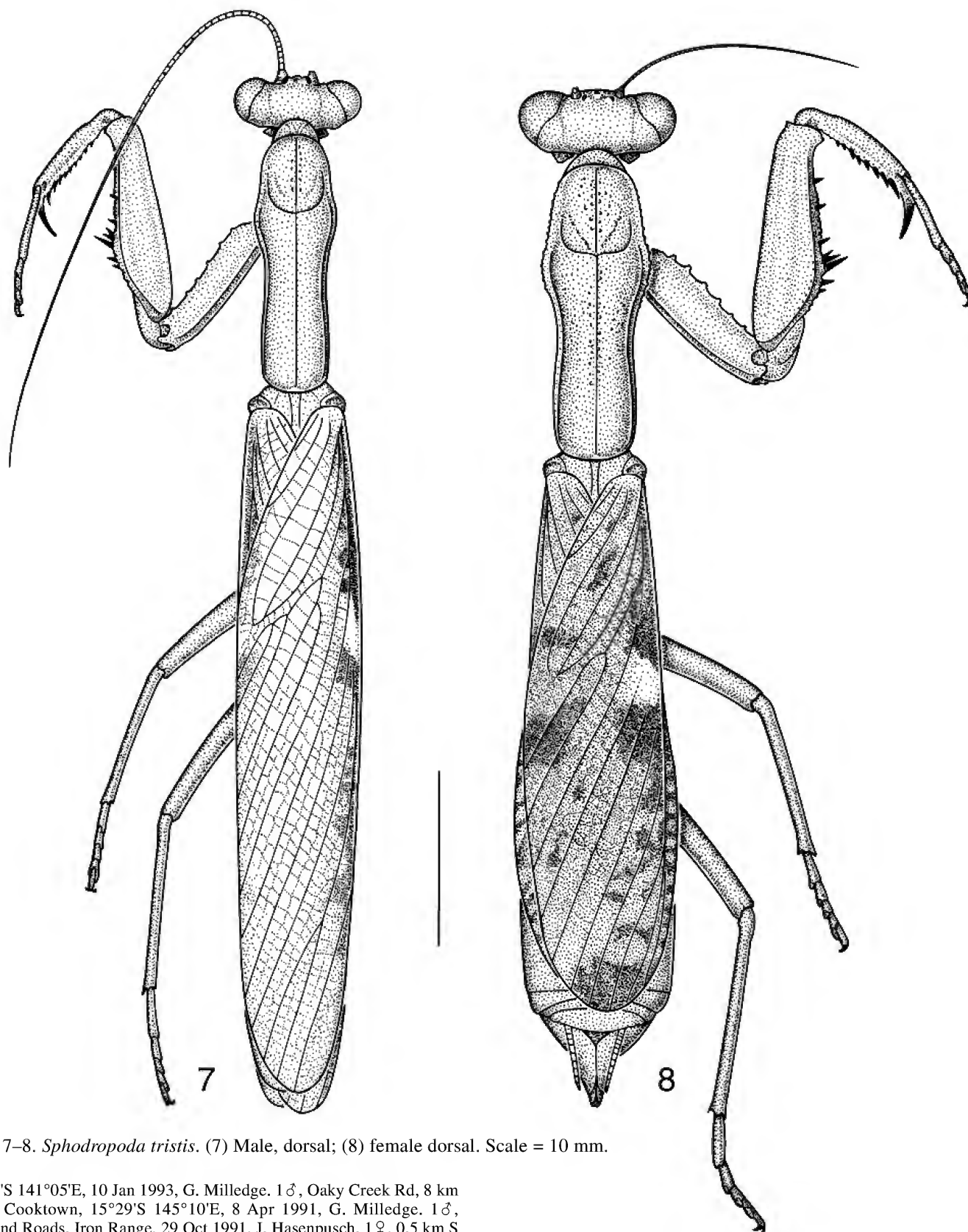
Figs. 7–8. *Sphodropoda tristis*. (7) Male, dorsal; (8) female dorsal. Scale = 10 mm.

17°44'S 141°05'E, 10 Jan 1993, G. Milledge. 1♂, Oaky Creek Rd, 8 km W of Cooktown, 15°29'S 145°10'E, 8 Apr 1991, G. Milledge. 1♂, Portland Roads, Iron Range, 29 Oct 1991, J. Hasenpusch. 1♀, 0.5 km S of Wills Creek, 9.5 km NE of Normanton, 17°38'S 141°09'E, 11 Jan 1993, G. Milledge (all NMV).

New South Wales. 1 juv, 29 km ENE of Coonabarabran, 31°08'S 149°33'E, 25 Nov 1983, D.C.F. Rentz & M.S. Harvey. 1♀, Dungay Creek, 13 km W of Kempsey, I.H. Parberry. 1 juv, 5 km SE of Merrygoen, 18 Jan 1961, M.J. D.White. 1♂, 15 km WNW of Monia Gap, 2 Feb 1964, M.J.D. White. 1 juv, 10 km W of Temora, 12 Jan 1955, M.J.D. White (all ANIC). 1♀, Clarence River, Mr Wilcox (NMV).

Northern Territory. 1♀, 43 km SE of Adelaide River, 4 Nov 1966, A. & R. Mesa. 2♂, Barrow Creek Telegraph Station, 20 Mar 1955, K.H.L. Key. 1 juv, Berrimah, 10 Mar 1972, J.C. Wombey. 1♀, 38 km ENE of Birrindudu HS, 18°15'S 129°45'E, 11 Jul 1969, C. Simpson. 1 juv, Blackfellows Station

to Burnside, 2–3 Apr 1929, T.G. Campbell. 1♀, Borroloola, McArthur River, 16 Jun 1929, T.G. Campbell. 1♂, 22 km WSW of Borroloola, 16°08'S 136°06E, 16 Apr 1976, Key & Balderson. 1♂, 36 km SW of Borroloola, 16°19'S 136°05'E, 4 Nov 1975, M.S. Upton. 1♂, 46 km SSW of Borroloola, 16°28'S 136°09'E, 28 Oct 1975, M.S. Upton. 1 juv, Caiman Creek, Coburg Peninsula, 11°14'S 132°12'E, 13 Feb 1977, R.C. Lewis. 1♀, Caranbirini Waterhole, 33 km SW of Borroloola, 16°16'S 136°05'E, 21 Apr 1976, Key & Balderson. 1 juv, 7 km SW of Coolibah HS, 15°34'S 30°54'E, 28 Jun 1968, M. Mendum. 1♀, Darwin, 25 Apr 1972, E.C. Abbey. 1♂, 8 km NNW of Elliott, 17°29'S 133°30'E, 14 Oct 1972, M.S. Upton. 1♀, Howard Springs, 30 Dec 1986, M.S. & B.J. Moulds. 1♂, Humpty Doo, 29–30 Jan 1939, E.B. Boerema. 1♂, Mataranka, 26 Mar 1955, K.H.L. Key. 1♀, McArthur
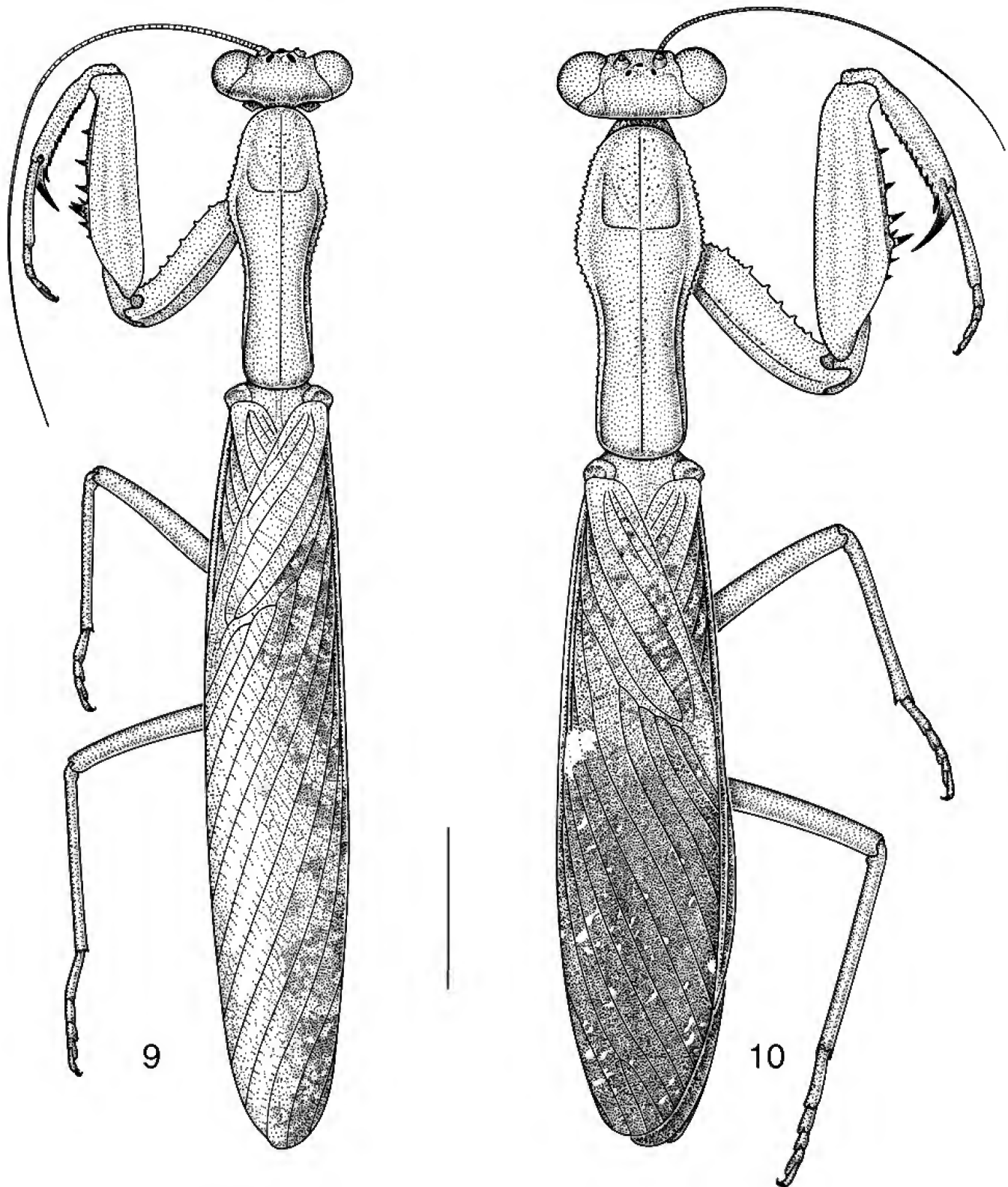
Figs. 9–10. *Sphodropoda quinquedens*. (9) Male, dorsal; (10) female dorsal. Scale = 10 mm.

River HS, 80 km SW of Borroloola, 16°39'S 135°51'E, 13 May 1973, M.S. Upton & J.E. Feehan. 1♀, 16 km WSW of McArthur River HS, 16°45'S 135°44'E, 13 May 1975, Balderson & Freeman. 1♂, 15 km E of Mt. Cahill, 12°52'S 132°50'E, 7 Mar 1973, K.H.L. Key. 1♂, October Creek, Carpentaria Hwy, 180 km E of Daly Waters, 11 Jan 1986, M.S. & B.J. Moulds. 1♂, Plenty Hwy, 268 km ENE of Alice Springs, 22°47'S 136°18'E, 14 Oct 1978, M.S. Upton. 1♂, 30 km ENE of Soudan HS, 19°55'S 137°15'E, 25 Apr 1976, Key & Balderson. 1♂, Standley Chasm, 43 km W of Alice Springs, 9 Feb 1966, Britton, Upton & McInnes. 1♂, Stuart Hwy, 58 km NW of Alice Springs, 23°11'S 133°44'E, 28 Oct 1988, D.C.F. Rentz. 1 juv, Tanami Borehole, 19°59'S 129°42'E, Jul–Sep 1971, J. Hodgson. 2♂, Tindal, 14°31'S 132°22'E, 1–20 Dec 1967, W.J.M. Vestjens. 1♂, Tindal, 2 Dec 1967, W.J.M. Vestjens. 1♂, 13 km W of Top Springs, 24 Oct 1965, Blackith & Mesa. 1♂,

Uluru Motel, Ayers Rock, 25°21'S 131°03'E, 4 Nov 1980, K.H.L. Key (all ANIC). 1♂, 31 km S of Alice Springs, 27 Sep 1987, G. Milledge. 1♀, Darwin, Jul–Aug 1912, Prof Spencer. 1♀, Uluru Camp Site, Horn Centenary Expedition, 25°23'10"S 131°00'46"E, 24 Oct 1994, G. Milledge, 1♀, Watarrka National Park, Mar 1995, G. Milledge (all NMV).

South Australia. 3♂, 8.5 km WSW of Calperum HS, 34°05'S 140°38'E, 2 Mar 1995, Cardale, Colloff & Pullen (ANIC).

Victoria. 1♀, Inglewood. 1♂, Mallee District, 3 Mar 1914, C. French. 1♂, Mallee District. 1♀, 22.3 km N of Millewa South Bore, 34°35'S 141°03'E, 17–21 Feb 1987, G. Milledge. 1♀, 16.8 km SSW of Murrayville, 35°25'S 141°09'E, 23 Feb 1986, G. Milledge. 1♀, Wyperfield National Park, 3 Mar 1964, H.E. Tarr (all NMV).
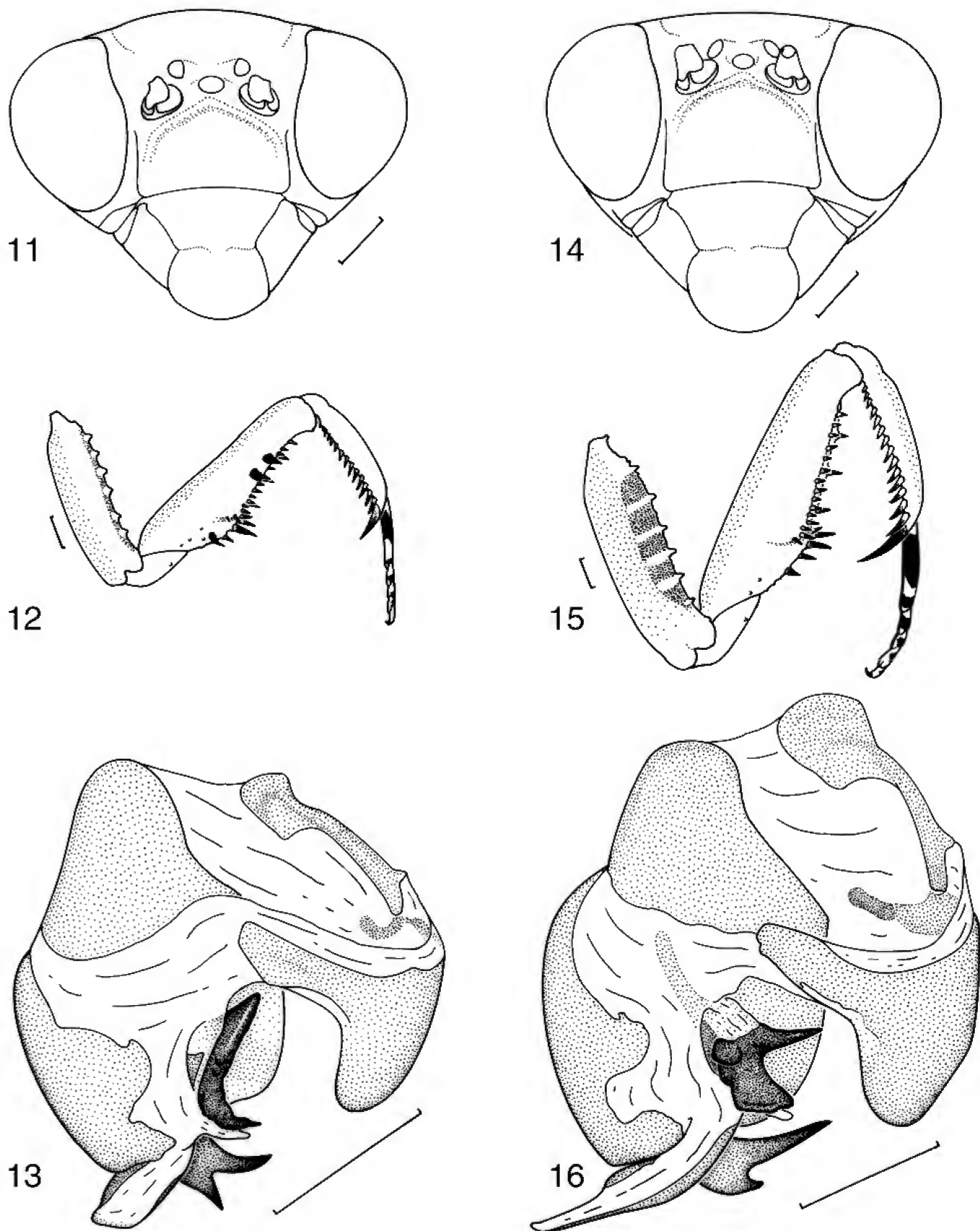
Figs. 11–16. *Sphodropoda* spp. (11) *S. tristis*, female head, anterior view; (12) same, fore femur, internal view; (13) same, male genitalia, dorsal view. (14) *S. quinquedens*, female head, anterior view; (15) same, fore leg, internal view; (16) same, male genitalia, dorsal view. Scales = 2 mm.

Western Australia. 1♀, Balgo Hills, 13 Oct 1985, M. Golding. 3♂, 38 km WNW of Balladonia Motel, 22 Feb 1980, D.C.F. 7 B.G.F. Rentz. 1♂, Brogo Hill, 160 km S of Halls Creek, 10 Sep 1985, M. Golding. 1♂, 42 km ESE of Broome, 16 Apr 1963, L.J. Chinnick. 1♂, 145 km ESE of Broome, 18°55'S 123°27'E, 8 Aug 1976, I.F.B. Common. 1♀, 186 km ESE of Broome, 18°53'S 123°43'E, 11 Aug 1976, I.F.B. Common.

1♂, 5 km SSW of Cape Bertholet, 17°17'S 122°10'E, 21 Apr 1977, D.H. Colless. 1♂, 8 km S of Cape Bertholet, 17°19'S 122°10'E, 16 Apr 1977, D.H. Colless. 1♀, Halls Creek, 29 Sep 1953, Brittan. 1♂, Kimberley Research Station, via Wyndham, 15 Aug 1955, E.C.B. Langfield. 1♂, Kimberley Research Station, via Wyndham, 28 Dec 1956, E.C.B. Langfield. 1♀, Kimberley Research Station, 21–22 Apr 1958, L.J. &
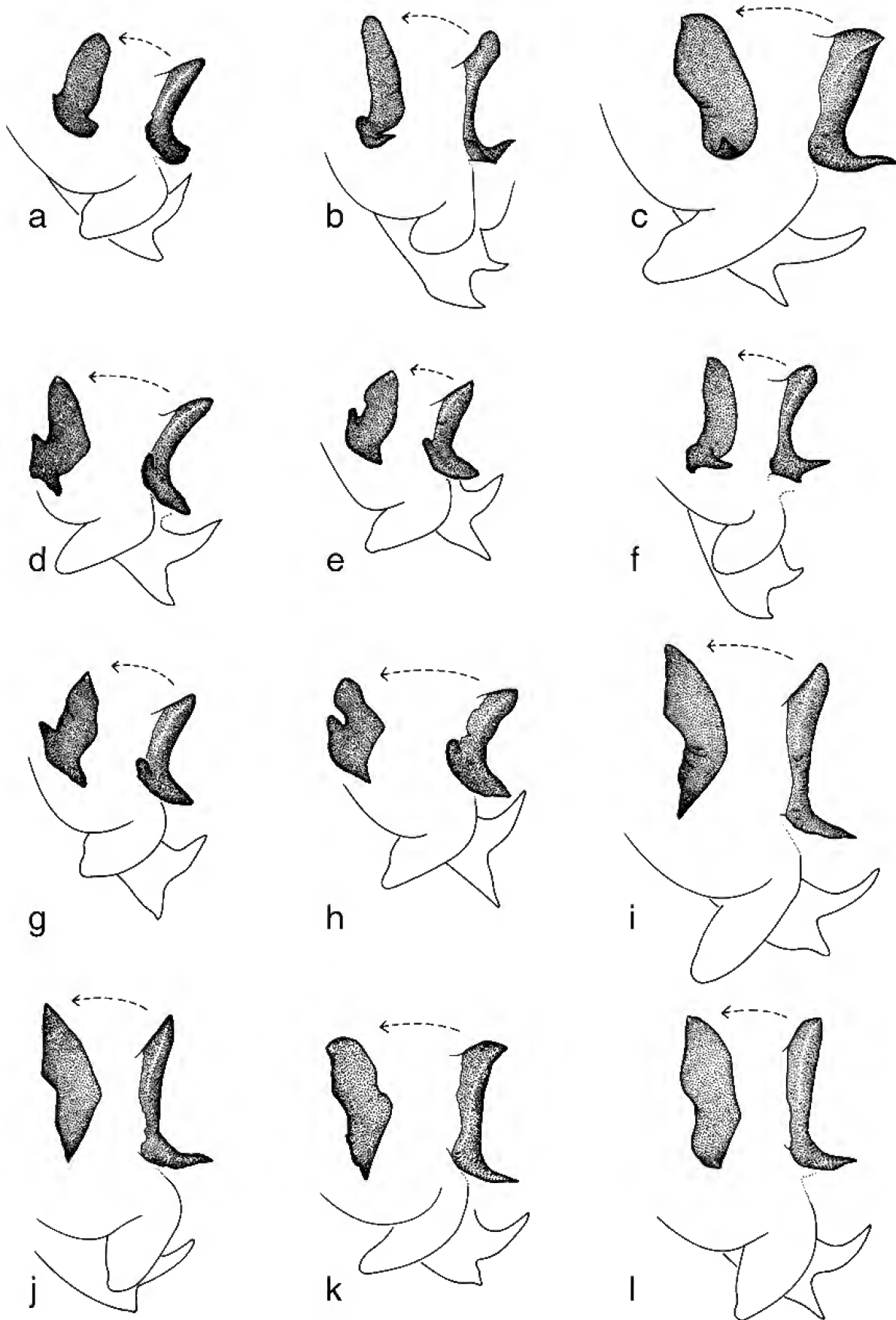
Fig. 17. *Sphodropoda tristis*, variation in male genitalia, cf figure 13, arrows indicate *pa* rotated to lateral view. (*a*) WA—near Wyndham; (*b*) Qld—near Cooktown; (*c*) Qld—near Greenvale HS; (*d*) WA—near Broome; (*e*) NT—October Ck; (*f*) Qld—Townsville; (*g*) WA—near Millstream HS; (*h*) NT—near Alice Springs; (*i*) Qld—Byfield; (*j*) WA—near Balladonia; (*k*) Vic—Mallee district; (*l*) Qld—near Taroom.

M.F. Chinnick & J. Walker. 1♂, 1 km NNE of Millstream HS, 21°35'S 117°04'E, 3 Apr 1971, Upton & Mitchell. 3♂, 2 km ENE of Millstream HS, 21°35'S 117°04'E, 22 & 30 Oct & 4 Nov 1970, M.S. Upton & J.E. Feehan. 1♀, Mining Camp, Mitchell Plateau, Kimberley district, 14°49'S 125°50'E, 9–19 May 1983, D.C.F. Rentz & J. Balderson. 1♀, 50 km SW of Sandfire Flat, Broome–Port Hedland Rd, 29 Oct 1978, M.S. & B.J. Moulds. 1 juv, 8 km SW of Walsh Point, Admiralty Gulf, 14°37'S 125°48'E, 17 May 1983, D.C.F. Rentz & J. Balderson. 1♀, 2 km NNE of Wyndham Port P.O., 15°27'S 128°06'E, 16 Apr 1985, K.H.L. Key. 1♂, Wyndham, 25 Apr 1930, T.G. Campbell (all ANIC). 1 juv, 217 km SE of Broome, 15 Sep 1924, A.S. Cudmore. 1 juv, Forrest River Mission, 8–12 Sep 1953 (both NMV). 1♂, Bamboo Creek, 20°56'S 120°13'E, 22 Jan 1974, A.M. & M.J. Douglas. 1♀, Beverley Springs HS, 16°43'S 125°27'E, 19 May 1979, B.G. Muir. 1♂, Cape Range, May 1965, G.W. Kendrick. 1♂, Derby, 1962, G. Beamish. 1♂, Greys Camp, Rudall River, near Larrys Creek, May 1971, K. Clarke & P. Moore. 1♂, 13 km ESE of Mooka HS, 24°58'S 114°49'E, 9–11 May 1981, B. Hanich & T.F. Houston. 1♂, 51 km SSW of Norseman, 8 Mar 1984, T.F. Houston. 1♀, Salmon Gums. 1♂, Walganna Rock, Austin Downs, 27°43'S 117°28'E, 27 Aug 1987, R.P. McMillan. 1♀, Winjana Gorge, campsite 13, 12 Apr 1970, Lemley Expedition (all WAM).

Diagnosis. This species can be distinguished from others in the genus by the pattern of tubercles and colouration on the inner face of the foreleg (Fig. 12).

Description. Body (Figs. 7–8) smallish to moderately large. Colour brown with mottled tegmina, green with mottled tegmina or uniform green. Ridge on frontal shield with blunt point at apex. Prothorax with numerous scattered tubercles on dorsal surface, particularly in female; lateral margin finely denticulate; metazone dark grey ventrally, sometimes with orange patch between coxal insertions. Fore leg (Fig. 12) with inner face of coxa dark grey with 6–7 contrasting cream tubercles on anterior margin; inner face of femur orange, with 3–4 small black spots at bases of spines; inner face of first tarsal segment mostly black, of other tarsal segments black apically. Wings of male longer than abdomen, as long as or slightly shorter than abdomen in female; ventral surface of costal area of tegmen rosy red, at least in basal half; discoidal area completely opaque in female, only partly so in male, usually with dark patch on distal margin of stigma (absent in uniformly green specimens and small males of other colour forms); hind wing with costal and discoidal area reddish to yellowish, anal area slightly smoky, particularly toward apex, in female, mostly hyaline in male. Abdomen with median black spot on proximal margin of ventral sclerites 2–5. Male genitalia (Figs. 13, 17) with relatively short stout *apr*; *pa* and *dpr* rather variable, *pa* compact, shagreened, L to C shaped when viewed dorsally, with pointed, laterally directed posterior process and sometimes with blunt pointed, dorsally directed process; *dpr* terminated with two short, pointed projections of variable form.

Measurements (mm). Body length, ♂ 38–68, ♀ 41–72. Head width, ♂ 7–9, ♀ 8–10. Head depth, ♂ 4–7, ♀ 6–9. Pronotum length, ♂ 9–18, ♀ 11–19. Pronotum width, ♂ 3–6, ♀ 4–8. Fore coxa length, ♂ 6–11, ♀ 8–13. Fore femur length, ♂ 7–13, ♀ 10–15. Hind femur length, ♂ 7–13, ♀ 9–14. Hind tibia length, ♂ 7–13, ♀ 9–14. Tegmen length, ♂ 26–46, ♀ 26–37.

Immature stages. First two instars dark coloured and ant-like in appearance and behaviour, the abdomen being curled dorsally when active. Later instars more like adult in behaviour and appearance. Ootheca pale grey or cream, and squat looking. Chapman & Balderson (1984) recorded a female of this species from Brisbane as laying its oothecae

in the ground. This behaviour may not be obligatory however, as I have collected oothecae from the "paper" bark of melaleuca trees in the Cairns region. I have also had females in captivity which laid oothecae on the roof and sides of the container, although oviposition was not observed.

Distribution and habits. Found through most of mainland Australia (Fig. 42), also southeast Papua New Guinea and the Solomon Islands (Beier 1965). The locality of the female type specimen, which cannot be located (Balderson 1984), is recorded as the Fiji Islands (Saussure 1871). This record, however, must remain doubtful until further specimens are obtained. This species is a shrub and tree dweller, usually found on stems or trunks. When disturbed, individuals move to the other side of the stem and flatten themselves against the substrate. Females are capable of at least short flights.

Remarks. This widespread species is quite variable in size and to some extent in the form of the male genitalia (Fig. 17). Specimens from the north west of the continent tend to be smaller (*S. mjobergi* form) while those from the northeast tend to be larger (typical *S. tristis*). However, after examining numerous specimens I cannot find any group of characters that would separate one population from the rest. Morphological characters useful in delineating other species within the genera considered here (e.g., pattern on inside of foreleg, head shape) show little or no variation. Thus *S. mjobergi* is considered a synonym of *S. tristis*. I have not been able to locate the holotype of *S. papua*. It is apparently not in the New Guinea Dept. of Agriculture & Livestock collection, although several paratypes are (F. Dori, pers. comm.), nor is it in the Bishop Museum collection (G. Nishida, pers. comm.). Beier's (1965) description and photograph suggests this species falls well within the range of variation observed for Australian *S. tristis* and it is therefore considered synonymous. I have examined a syntype of *S. moesta* Giglio-Tos and there is nothing to indicate his species is different from *S. tristis*. As suggested by Tindale (1923), it is merely the brown colour form of *S. tristis*. The syntype specimen of *S. moesta* examined was listed as the holotype by Balderson (1984). The original description by Giglio-Tos, however, clearly lists two specimens, the second from "the Island of Australia". This second specimen cannot be located in the ZMHU (M. Ohl, pers. comm.). I have also examined two syntypes of *S. mjobergi* and it is obviously the north western form of *S. tristis*. There has been some confusion as to the authorship of the name of this species. Although Saussure described the species he attributed the name *tristis* to Brunner. Up until recently all subsequent authors except Westwood (1889) attributed the name to Saussure. Balderson *et al.* (1998), however, attributed the name to Brunner in Saussure, but, as there is no indication that Brunner was responsible for the description, Saussure must be considered the author.

Sphodropoda quinquedens (Macleay)

Figs. 4–6, 9–10, 14–16, 43

Mantis quinquedens Macleay, 1826: 454.
Hierodula quinquedens (Macleay).–Saussure, 1871: 78.
Sphodropoda quinquedens (Macleay).–Kirby, 1904: 242.

Material examined. Lectotype female, Australia (ANIC).

Other specimens examined. Queensland. 1♀, Black Mountain NP, 15°39'05"S 145°13'13"E, 16 May 2000, G. Milledge (AM). 1♂, Albatross Hotel, Weipa, 12°38'S 141°52'E, 6 May 1981, K.H.L. Key. 1♀, Annan River, 3 km SW of Black Mt., near Cooktown, 15°41'S 145°12'E, 26–27 Apr 1981, D.C.F. Rentz. 1♂, 44 km N of Cairns, 10 Dec 1982, J.T. Doyen. 1♀, 8 km W of Dimbulah, 17°09'S 145°02'E, 22 Mar 1988, D.C.F. Rentz. 1♂, Emu Creek, 27 km SW of Dimbulah, 17°20'S 144°57'E, 25–26 Nov 1981, J. Balderson. 1♀, Iron Range, 12 Jul 1969, J.C. Le Souëf. 1♂, McKenzie River crossing, 75 km NNE of Dingo, 17 Jan 1987, M.S. & B.J. Moulds. 1 juv, Shiptons Flat, near Cooktown, 15°47'S 145°14'E, 16–18 May 1981, D.C.F. Rentz. 1♂, Silver Plains HS, Cape York Pen., 25 Apr 1968, J.L. Wassell (all ANIC). 1♂, Annan River crossing, 2 km S of Cooktown, 4 Apr 1991, G. Milledge. 1♀, Brisbane, 12 Oct 1914, J. Frost. 1♂, 1 km NNE of Collins Weir, W of Atherton, 17°15'S 145°17'E, 10 Feb 1989, G. Milledge. 1♂, 8 km E of Emuford, 30 Dec 1989, M.S. & B.J. Moulds. 1♂, Jardine River ferry crossing, 50 km S of Bamaga, 11°05'S 142°18'E, K. Walker. 1♀, Poison Creek Rd, 10 km W of Cooktown, 4 Apr 1991, G. Milledge (all NMV).

Western Australia. 1 juv, 8 km SW of Walsh Point, Admiralty Gulf, 14°37'S 125°48'E, 17 May 1983, D.C.F. Rentz & J. Balderson (ANIC).

Diagnosis. *Sphodropoda quinquedens* can be separated from the other species of this genus by the distinctive pattern on the inside face of the fore leg (Fig. 15), the colour markings on the ventral surface of the costal area of the tegmen and the form of the male genitalia (Fig. 16).

Description. Body (Figs. 9–10) moderately large. Colour brown with mottled tegmina, green with mottled tegmina or uniform green. Ridge on frontal shield with blunt point at apex. Prothorax with numerous scattered tubercles on dorsal surface, particularly in female; lateral margin finely denticulate, slightly lamellate in prozone. Fore leg (Fig. 15) with inner face of coxa purplish in posterior half, anterior half orange brown with 6 contrasting pointed cream tubercles on anterior margin which extend basally as ridges across surface; inner face of femur without markings; inner face of first tarsal segment mostly black, of other tarsal segments black apically. Wings of both sexes longer than abdomen; ventral surface of costal area of tegmen rosy red on inner half, outer half black, whole area crossed with slender white bands and spots; discoidal area completely opaque in female, only partly so in male; hind wing with costal and discoidal area yellowish, anal area slightly smoky, particularly toward apex, in female, mostly hyaline in male. Male genitalia (Fig. 16) with *apr* relatively elongate and narrow distally; *pa* compact, shagreened, with anterior pointed lateral projection and broad blunt posterior projection; *dpr* with anterior projection much longer than posterior one.

Measurements (mm). Body length, ♂ 64, ♀ 70. Pronotum length, ♂ 16, ♀ 21. Pronotum width, ♂ 6, ♀ 9. Fore coxa length, ♂, 11, ♀ 15. Fore femur length, ♂ 13, ♀ 18. Hind femur length, ♂ 10, ♀ 14. Hind tibia length, ♂ 10, ♀ 16. Tegmen length, ♂ 46, ♀ 46.

Immature stages. Early stages and ootheca unknown.

Distribution and habits. Found in north eastern Queensland and one record from north Western Australia (Fig. 43). This species displays cryptic behaviour similar to that described above for *S. tristis*. This behaviour has been noted previously in *S. quinquedens* (Heath & Cowgill, 1989).

Sphodropoda viridis Tindale

Figs. 18–19, 36–38, 44

Sphodropoda viridis Tindale, 1923: 446.

Material examined. Holotype male, Mount Painter, Flinders Range, South Australia, H.G. Stokes, I 14061 (SAM).—QUEENSLAND. 2♂, 27 km SE of Cunnamulla, 27 Mar 1972, R.C. Lewis (ANIC). 1♂, Gilbert River, 27 Mar 1990, J. Hasenpusch. 2♂, Georgetown, 13 & 14 Apr 1991, G. Milledge (all NMV). 1♀, Cunnamulla, H. Hardcastle (SAM).—NEW SOUTH WALES. 1♂, 1♀, Trangie, 21 Apr 1956, L.J. Chinnick (ANIC).—NORTHERN TERRITORY. 1♀, Barrow Creek Tel.Sta., 20 Mar 1955, K.H.L. Key. 5♂, Clay Pan Well, 38 km NW of Tanami, 12 Apr 1963, L.J. Chinnick. 1♀, 7 km SW of Coolibah HS, 15°34'S 130°54'E, 6 Jul 1968, M. Mendum (all ANIC). 1♂, Tourist Camp site, Ormiston Gorge National Park, Horn Centenary Expedition, 23°38'03"S 132°43'23"E, 10 Mar 1995, P. Swinkels (NMV).—SOUTH AUSTRALIA. 1♂, Mt. Painter, Flinders Range, H.G. Stokes (SAM).—VICTORIA. 1♀, Mildura Gun Club, 27 Mar 1990, P. Robertson (NMV).—WESTERN AUSTRALIA. 1♂, 17 km NE of Cane River HS, 21°56'S 115°39'E, 27 Apr 1971, Key, Upton & Mitchell. 1♂, 3 km NNW of Mandora HS, SSW of Broome, 17 Apr 1963, L.J. Chinnick. 1♂, 1 km N of Millstream HS, 21°35'S 117°04'E, 15 Apr 1971, Upton & Mitchell. 1♂, 1♀, 43 km NW of Wittenoom, 22 Apr 1963, L.J. Chinnick. 1♀, 5 km N of Wittenoom, 21 Apr 1963, L.J. Chinnick. 1♀, 48 km ESE of Wittenoom, 25 Apr 1963, L.J. Chinnick (all ANIC). 1♂, Hancock Gorge, 15 km S of Wittenoom, 15 May 1980, G. Marney & P. Duncan. 1♀, Minilya. 1♀, 2.5 km E of Marandoo Camp, 22°38'S 118°06'E, 5–19 May 1980, T.F. Houston (all WAM).

Diagnosis. This species can be distinguished by the uniform green colouration, lack of markings on the inner face of the fore coxa (Fig. 37) and the form of the male genitalia (Fig. 38).

Description. Body (Figs. 18–19) medium to rather large. Colour uniform green. Ridge on frontal shield with blunt point at apex. Prothorax with a few scattered tubercles on dorsal surface, more so in female; lateral margin finely denticulate. Fore leg (Fig. 37) with inner face of coxa without markings, anterior margin with 7–10 denticles; inner face of femur with two small dark spots at base of spines; inner face of all tarsal segments black. Wings of male longer than abdomen, those of female as long as or longer than abdomen; ventral surface of costal area of tegmen reddish; discoidal area completely opaque in female, only partly so in male; hind wing with costal and discoidal area yellowish, anal area mostly hyaline. Abdomen with median black spot on proximal margin of ventral sclerites 2–5. Male genitalia (Fig. 38) *apr* of moderate length; *pa* with smooth, pointed elongate anterior projection, shagreened and blunt posteriorly; distal projections of *dpr* short and broad, one directed anterolaterally, the other posterodorsally.

Measurements (mm). Body length, ♂ 48–64, ♀ 44–60. Pronotum length, ♂ 12–18, ♀ 14–19. Pronotum width, ♂ 3.5–6, ♀ 5–6.5. Fore coxa length, ♂ 9–11, ♀ 9–12.5. Fore femur length, ♂ 9–12, ♀ 10–14. Hind femur length, ♂ 8–12, ♀ 9–12. Hind tibia length, ♂ 8.5–14, ♀ 11–14. Tegmen length, ♂ 36–47, ♀ 30–40.

Immature stages. Immature stages and ootheca unknown.

Distribution and habits. Found across the drier parts of the continent (Fig. 44). This species displays cryptic behaviour similar to that described for *S. tristis* and *S. quinquedens*.
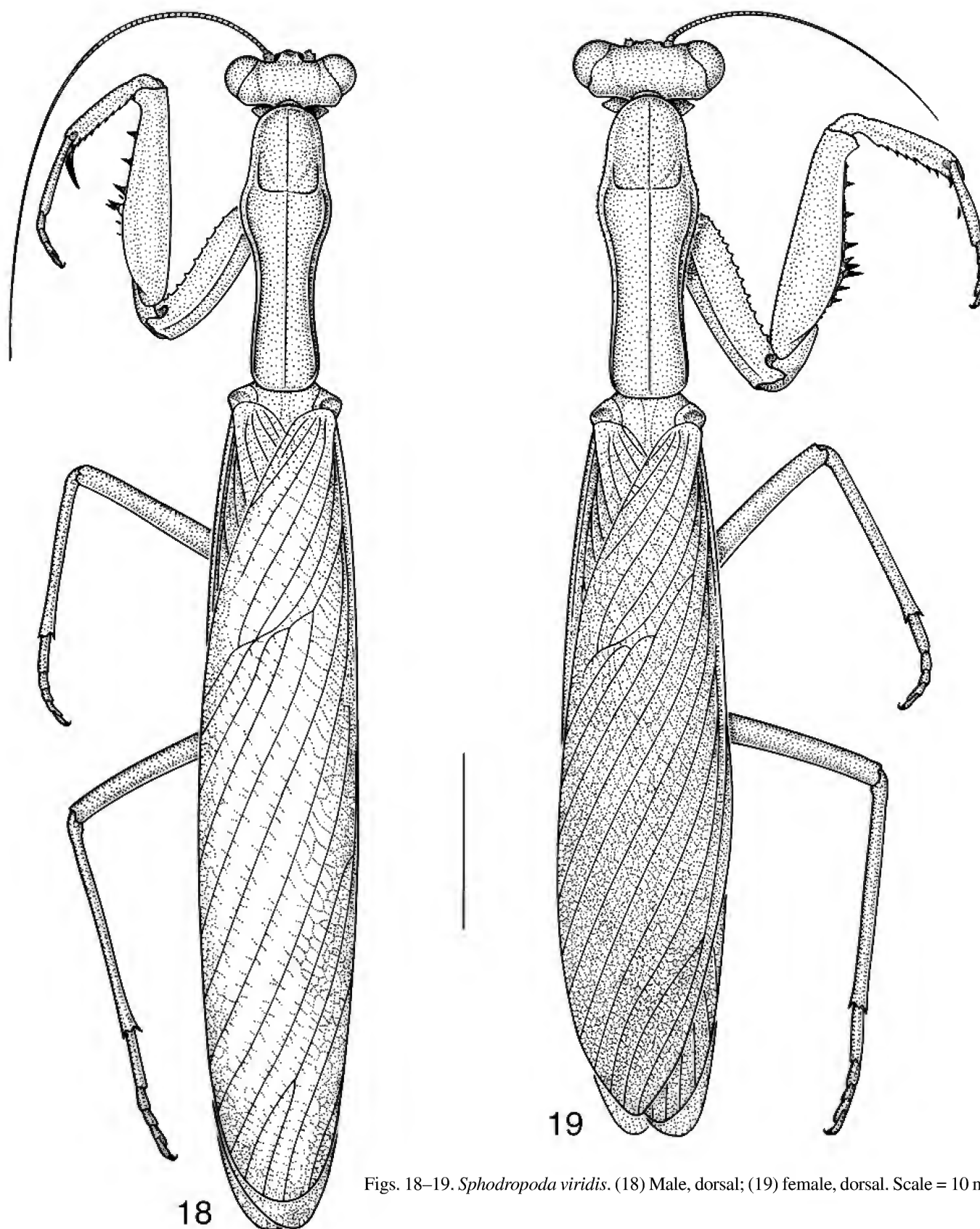
Figs. 18–19. *Sphodropoda viridis*. (18) Male, dorsal; (19) female, dorsal. Scale = 10 mm.
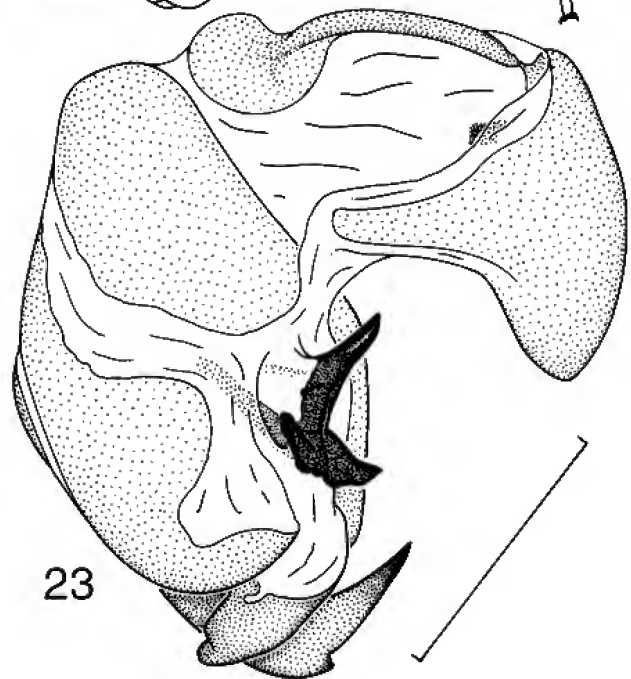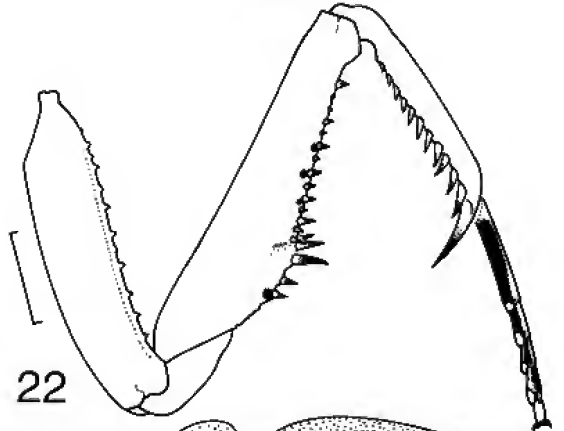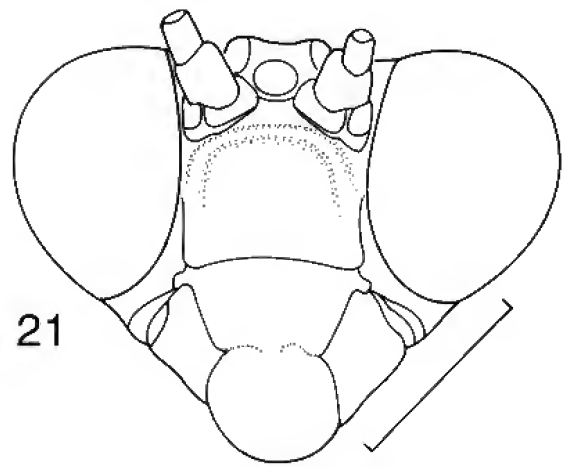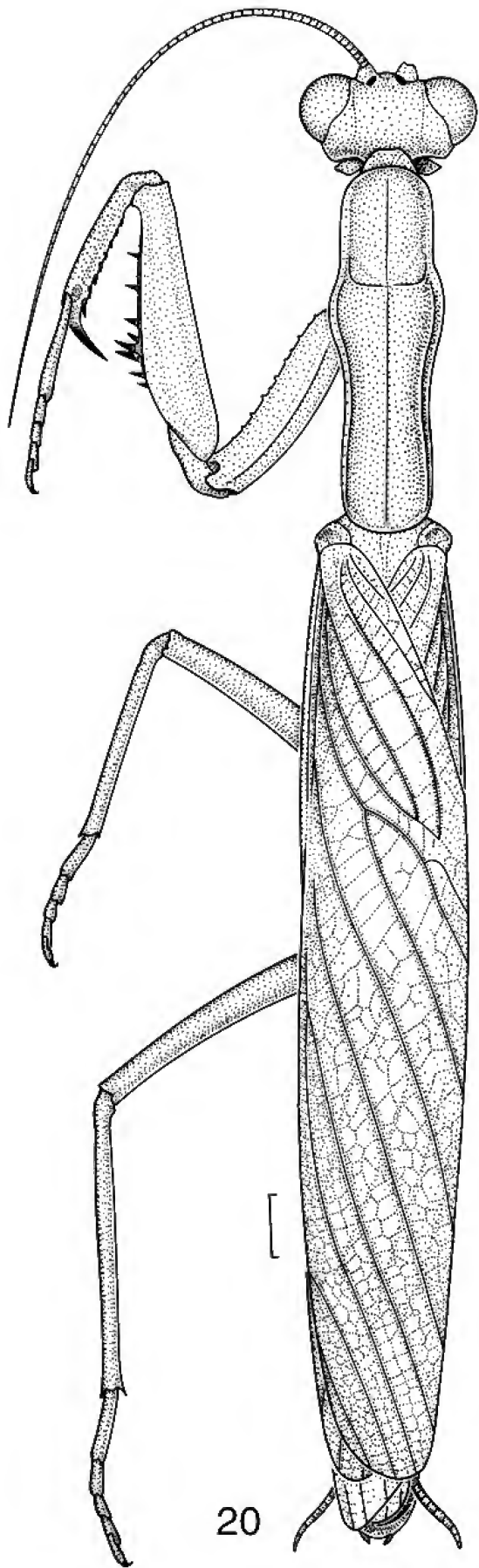
Sphodropoda lepida n.sp.

Figs. 20–23, 43

Material examined. HOLOTYPE ♂, Uluru campsite, Horn Centenary Expedition, 25°23'10"S 131°00'46"E, Northern Territory, 25 Mar 1995, G. Milledge (NMV). PARATYPES (7♂♂): 1♂, Ayers Rock, Northern Territory, 16 Feb 1967, M.S. Upton; 6♂♂, 56 km W of Amata, Musgrave Ranges, 26°09'S 130°35'E, South Australia, 20–21 Jan 1982, D.C.F. & B.G.F. Rentz & R. Honeycutt (all ANIC).

Diagnosis. This species can be distinguished by the lack of markings on the inner face of the fore coxa (Fig. 22), the banded tegmina (Fig. 20) and the form of the male genitalia (Fig. 23).

Description. Male only, female unknown. Medium sized species. Body colour partly green and partly purplish brown. Head (Fig. 21) purplish brown; narrower than other species in the genus, ridge on frontal shield without blunt point at apex. Prothorax purplish brown, paler at margins; with a few scattered tubercles on dorsal surface; lateral margin

Figs. 20–23. *Sphodropoda lepida*, male. (20) Dorsal view; (21) head, anterior view; (22) fore leg, internal view; (23) genitalia, dorsal view. Scales = 2 mm.

finely denticulate. Fore legs green; inner face of coxa without markings (Fig. 22), anterior margin with 7 denticles; inner face of fore femur with three small dark spots at base of spines; inner face of all tarsal segments black. Mid and hind legs green. Wings about as long as abdomen; dorsal and ventral surface of costal area of tegmen purplish, stronger beneath, with narrow whitish marginal band; discoidal green along anterior margin, major veins flushed with purplish brown giving banded appearance, remainder hyaline; hind wing with costal and discoidal area greenish, anal hyaline. Abdomen with median black spot on proximal margin of ventral sclerites 2–5. Male genitalia (Fig. 23) with short, broad *apr*; *pa* with smooth, pointed anterior projection, shagreened posteriorly with pointed lateral and blunt dorsal projections; *apr* with anterior projection moderately elongate, posterior one extremely short.
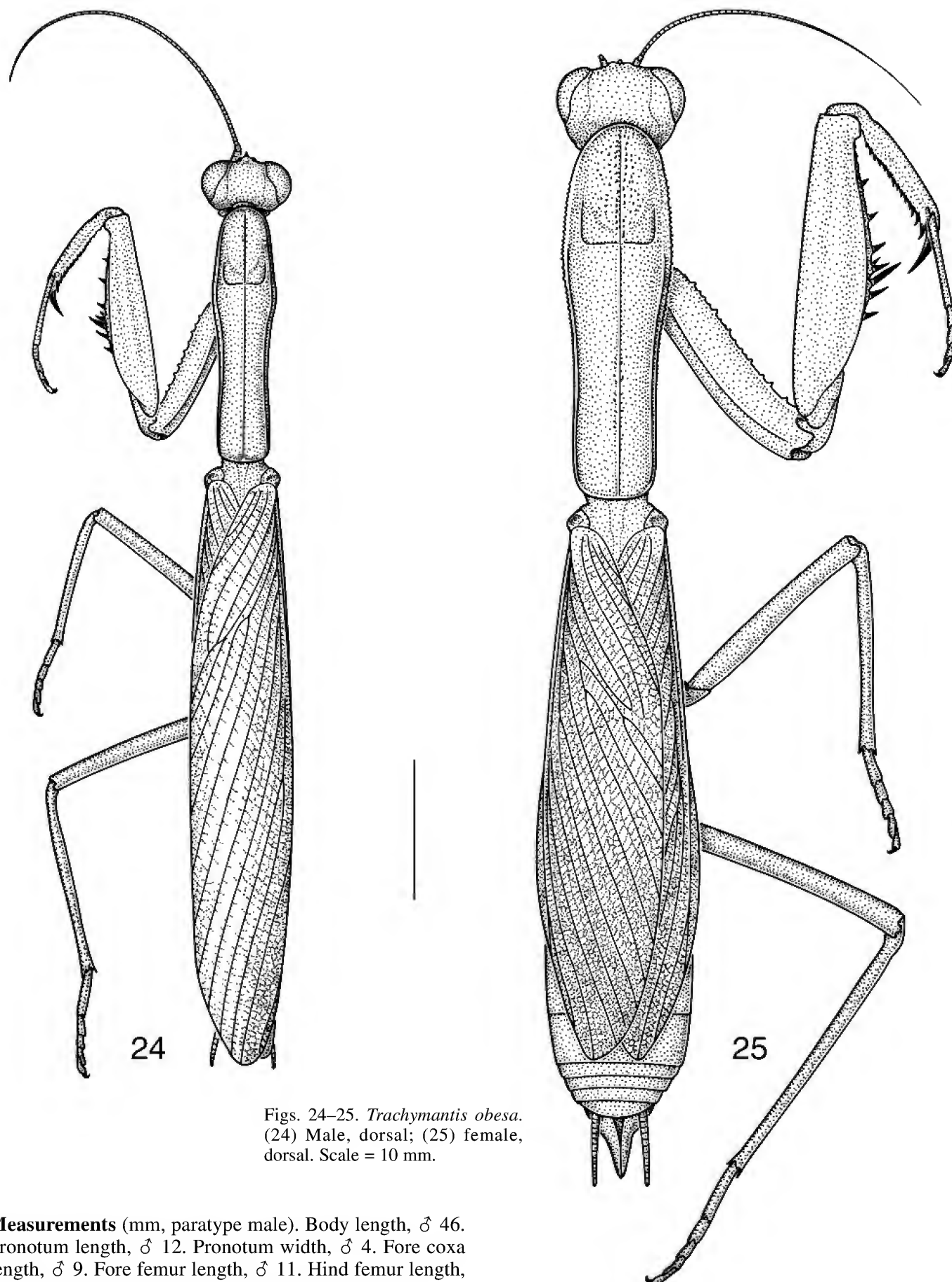
Figs. 24–25. *Trachymantis obesa.* (24) Male, dorsal; (25) female, dorsal. Scale = 10 mm.

Measurements (mm, paratype male). Body length, ♂ 46. Pronotum length, ♂ 12. Pronotum width, ♂ 4. Fore coxa length, ♂ 9. Fore femur length, ♂ 11. Hind femur length, ♂ 8.5. Hind tibia length, ♂ 10. Tegmen length, ♂ 32.

Immature stages. Immature stages and ootheca unknown.

Distribution and habits. At present, only known from central Australia (Fig. 43). Habits unknown but likely to be similar to other members of the genus.

Trachymantis Giglio-Tos

Trachymantis Giglio-Tos, 1917: 47. Type species *Trachymantis obesa* Giglio-Tos, by monotypy.
Ngawala Tindale, 1923: 447. Type species *Ngawala dentifrons* (Stål), by original designation.
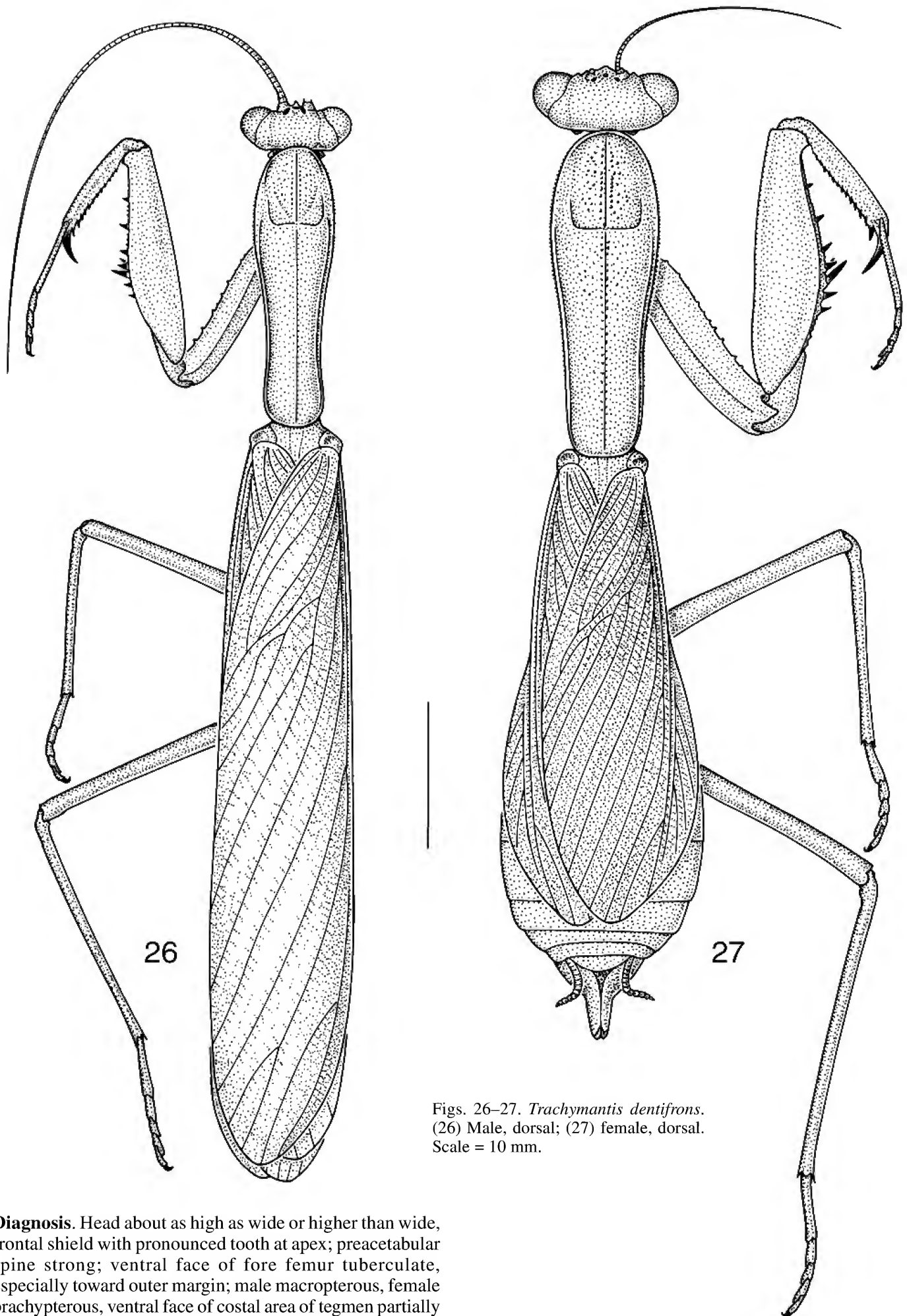
Figs. 26–27. *Trachymantis dentifrons.*
(26) Male, dorsal; (27) female, dorsal.
Scale = 10 mm.

Diagnosis. Head about as high as wide or higher than wide,
frontal shield with pronounced tooth at apex; preacetabular
spine strong; ventral face of fore femur tuberculate,
especially toward outer margin; male macropterous, female
brachypterous, ventral face of costal area of tegmen partially
dark grey, mid and hind legs normal. Can be distinguished
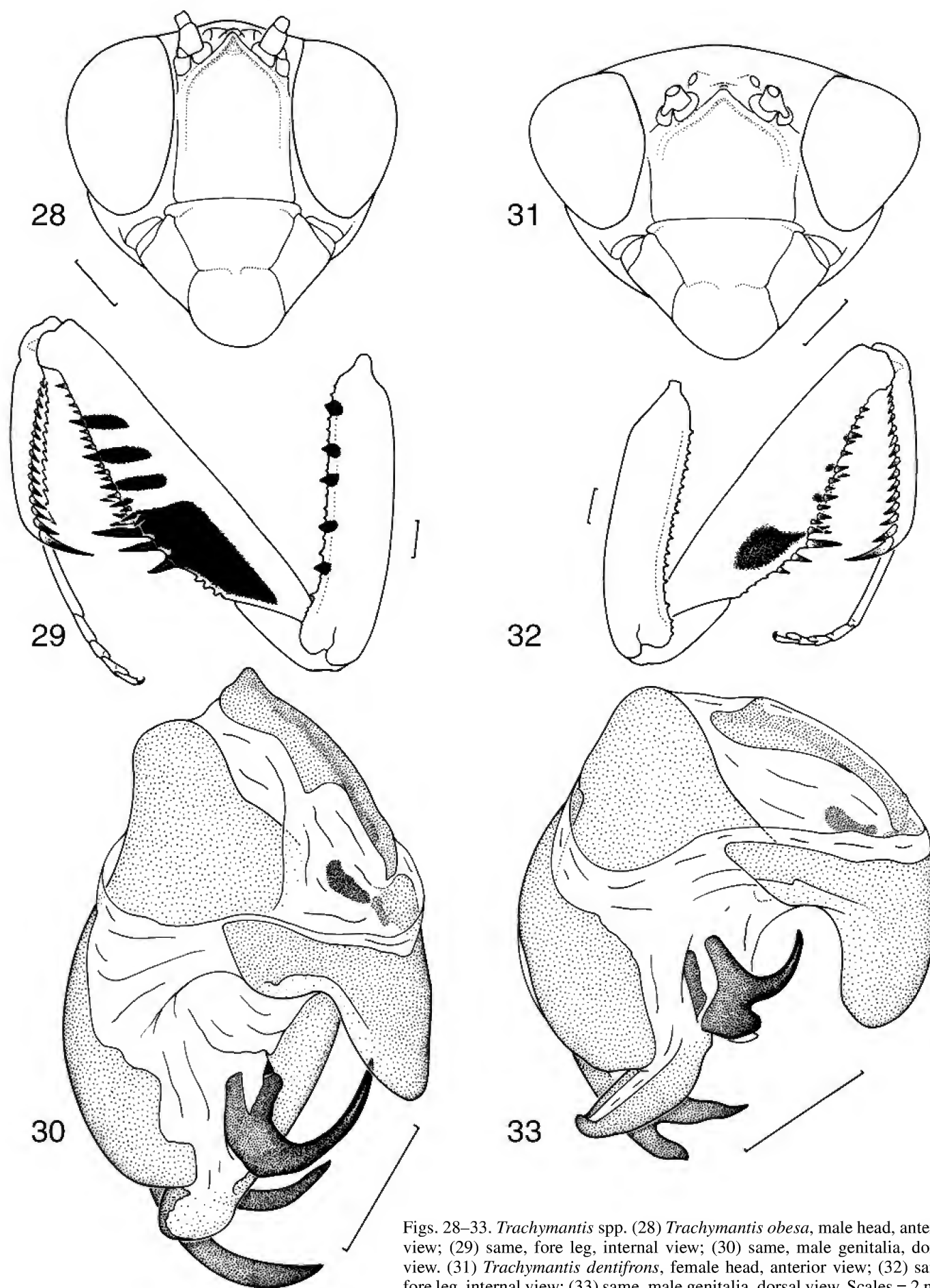
Figs. 28–33. *Trachymantis* spp. (28) *Trachymantis obesa*, male head, anterior view; (29) same, fore leg, internal view; (30) same, male genitalia, dorsal view. (31) *Trachymantis dentifrons*, female head, anterior view; (32) same, fore leg, internal view; (33) same, male genitalia, dorsal view. Scales = 2 mm.
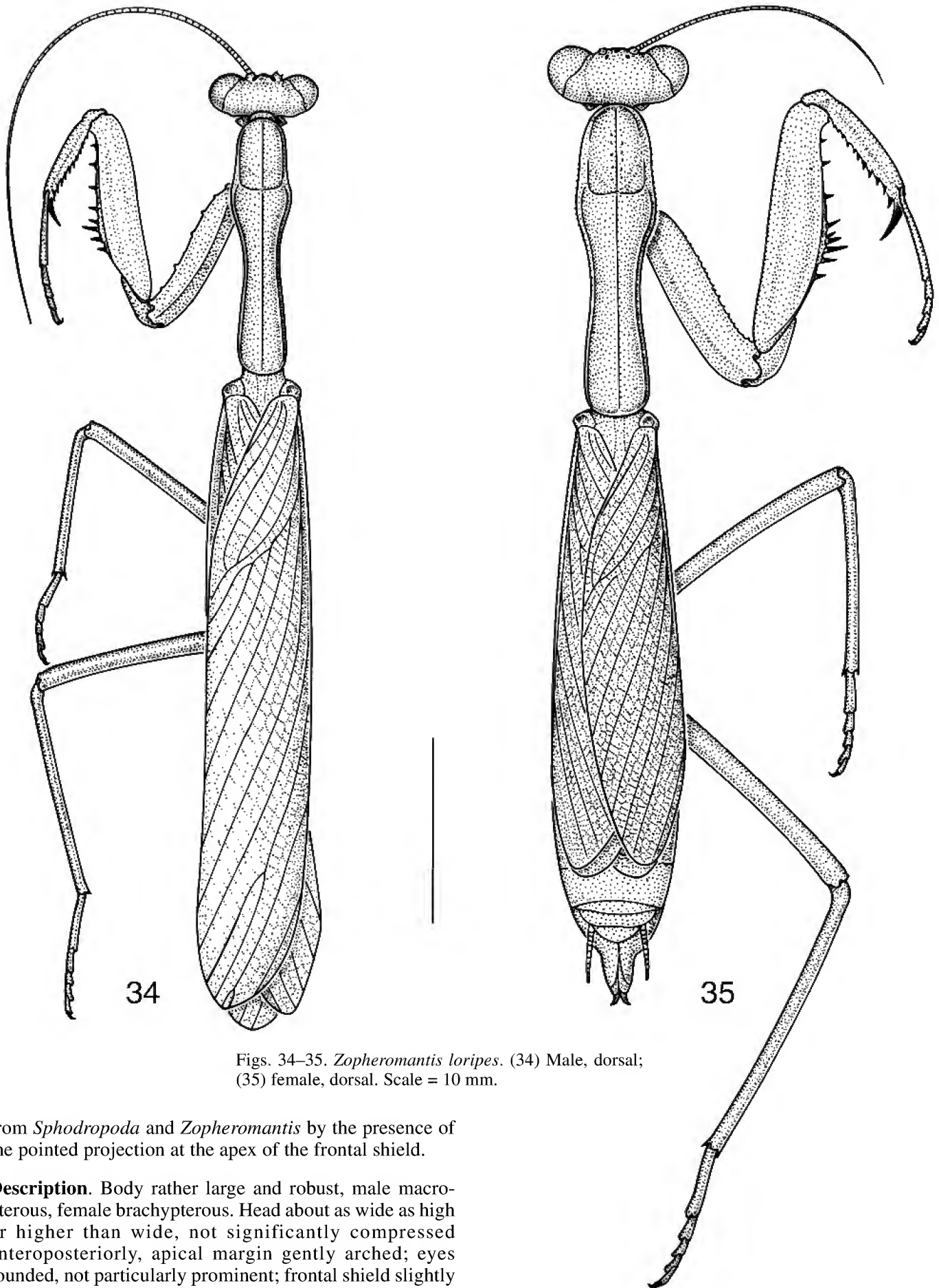
Figs. 34–35. *Zopheromantis loripes*. (34) Male, dorsal;
(35) female, dorsal. Scale = 10 mm.

from *Sphodropoda* and *Zopheromantis* by the presence of the pointed projection at the apex of the frontal shield.

Description. Body rather large and robust, male macropterous, female brachypterous. Head about as wide as high or higher than wide, not significantly compressed anteroposteriorly, apical margin gently arched; eyes rounded, not particularly prominent; frontal shield slightly to considerably wider than high, flat, with distinct ridge laterally and apically produced into a tooth at apex. Pronotum moderately elongate, supracoxal expansion distinct, dorsal surface finely granulate, mostly in prozone,
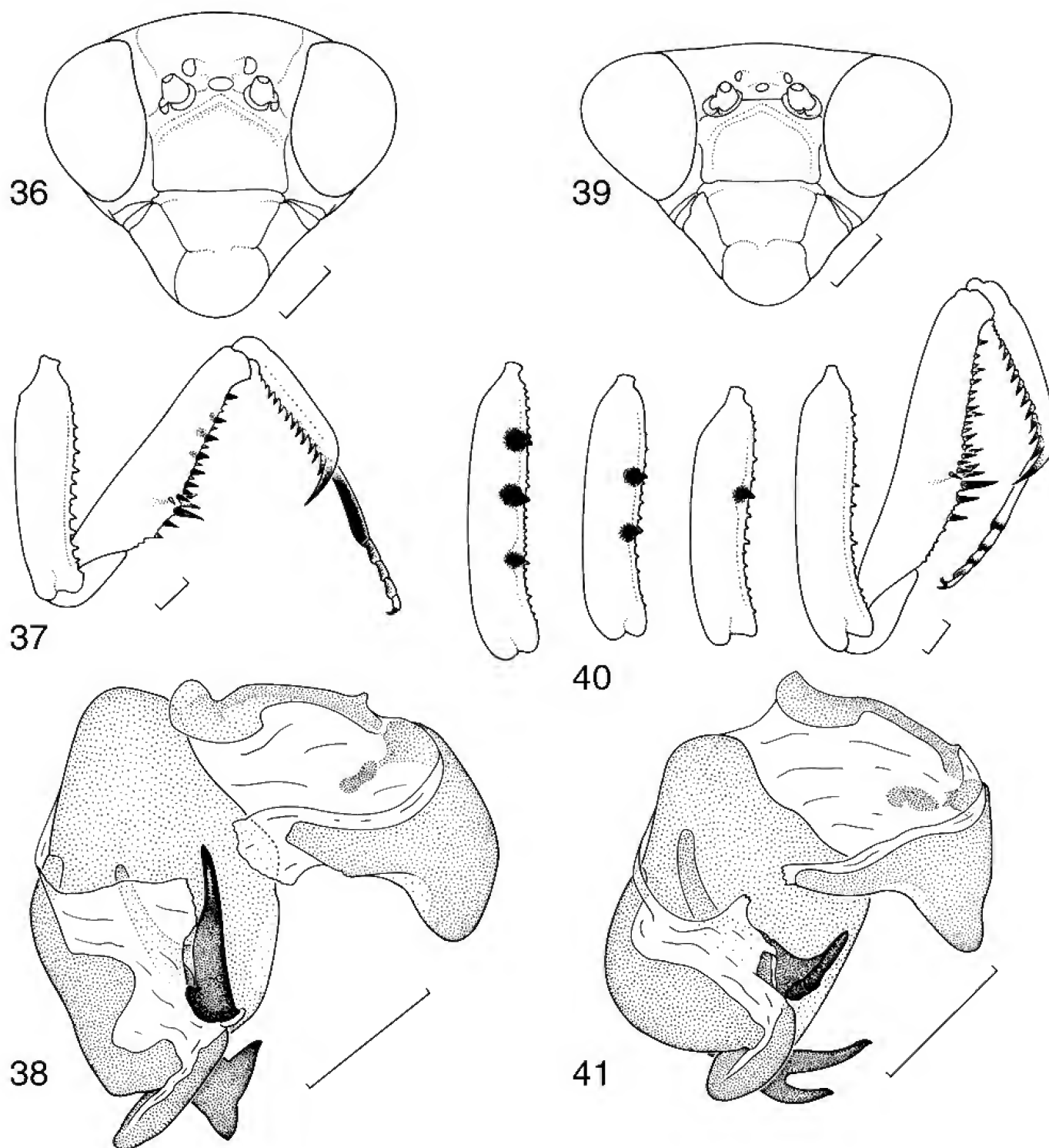
Figs. 36–41. *Sphodropoda viridis* and *Zopheromantis loripes*. (36) *Sphodropoda viridis*, female head, anterior view; (37) same, fore leg, internal view; (38) same, male genitalia, dorsal view; (39) *Zopheromantis loripes* female head, anterior view; (40) same, fore leg, internal view showing variation in coxal pattern; (41) same, male genitalia, dorsal view. Scales = 2 mm.

margins finely denticulate, ventral surface with preacetabular spine prominent. Fore coxa as long as metazone of pronotum, with or without markings, a number of denticles on anterior margin. Fore femur finely tuberculate on ventral surface, particularly toward outer margin; with four discoidal spines, relative length longest to shortest 3–2–1–4; with four outer and 15–18 inner spines, claw groove situated at about a third the total distance from base. Tegmen with costal area opaque, partially grey beneath; discoidal area entirely opaque to mostly hyaline. Hind wing with costal and discoidal area pigmented, anal area largely hyaline. Mid and hind legs normal, hind femur more than half the length of abdomen. Abdomen moderately elongate, cerci short, slender and cylindrical. Male genitalia with *dpr* bifurcate.

Key to species of *Trachymantis*

1   Facial shield much higher than wide .... *T. obesa*

—— Facial shield about as high as wide .... *T. dentifrons*

Trachymantis obesa Giglio-Tos

Figs. 24–25, 28–30, 45

Trachymantis obesa Giglio-Tos, 1917: 47.

Material examined. Holotype female, Hermannsburg, Central Australia, H.J.Hillier, 1911–311 (BMNH).—QUEENSLAND: 2♂, 3 km W of Bundeena HS, SW of Quilpie, 12 Feb 1972, R.C. Lewis. 1♀, 14 km S of Quilpie, 14 Nov 1971, R.C. Lewis. 1♂, 5 km N of Eromanga, 3 Nov 1967, R.C. Lewis (all ANIC).—NEW SOUTH WALES: 2♂, 18 km WNW of Bourke, 9 Feb 1972, R.C. Lewis (ANIC).—NORTHERN TERRITORY: 1♂, Wigley Waterhole, 8 km N of Alice Springs, 16 Feb 1966, Britton, Upton & McInnes. 1♀, 22 km NNW of Kulgera HS, 8 Oct 1955, L.J. Chinnick. 1 juv, 37 km N of Alice Springs, 17 Nov 1966, White, Blackith & Blackith (all ANIC). 1♀, Kathleen Creek, Watarrka National Park, 24°20'38"S 131°40'54"E, 21 Oct 1994, G. Milledge (NMV).—WESTERN AUSTRALIA: 2♂, 10 km NE of Menzies, 14 Jan 1989, M.S. & B.J. Moulds. 1♂, 55 km ESE of Mount Magnet, 18 Jan 1989, M.S. & B.J. Moulds. 1♂, 110 km S of Mount Magnet, 19 Jan 1989, M.S. & B.J. Moulds. 2♂, 25 km E of Sandstone, 17 Jan 1989, M.S. & B.J. Moulds.

Diagnosis. Can be distinguished from *T. dentifrons* by the facial shield being higher than wide.

Description. Body (Figs. 24–25) rather large. Colour uniform green or bluish green. Head (Fig. 28) higher than wide; frontal shield distinctly higher than wide with ridge produced into prominent point at apex. Prothorax with fine scattered tubercles on dorsal surface, mostly in prozone, more so in female; lateral margin finely denticulate. Fore leg (Fig. 29) with inner face of coxa bluish, apricot on distal quarter, anterior margin with five black spots and 11–12 small denticles; inner face of fore femur apricot in lower half with large black patch proximally and three narrow black bands distally; inner face of fore tibia orange. Wings of male longer than abdomen, those of female slightly shorter than abdomen; ventral surface of costal area of tegmen dark bluish grey with narrow apricot marginal band; discoidal area completely opaque in female, only partly so in male; hind wing with costal and discoidal area yellowish green, anal area mostly hyaline. Male genitalia (Fig. 30) with very short blunt *apr*; *pa* with single, elongate hook-like projection; distal projections of *dpr* elongate, narrow and of similar length.

Measurements (mm). Body length, ♂ 54–70, ♀ 72–75. Pronotum length, ♂ 17–20, ♀ 24–26. Pronotum width, ♂ 4.5–6, ♀ 8. Fore coxa length, ♂ 14–17, ♀ 16–18. Fore femur length, ♂ 12–14, ♀ 21–22. Hind femur length, ♂ 11–15, ♀ 18. Hind tibia length, ♂ 12–16, ♀ 20. Tegmen length, ♂ 34–46, ♀ 34–37.

Immature stages. Later instar nymphs similar in appearance to adults, early instars and ootheca unknown.

Distribution and habits. Recorded (Fig. 45) from the drier parts of Queensland, New South Wales, Northern Territory and Western Australia. The single specimen I have collected was found in a large *Acacia* shrub. Whilst in captivity it did not display cryptic behaviour as found in *Sphodropoda*.

Trachymantis dentifrons (Stål, 1877) n.comb.

Figs. 26–27, 31–33, 46

Hierodula (Sphodropoda) dentifrons Stål, 1877: 56.
Sphodropoda dentifrons (Stål), Kirby, 1904: 242.
Ngawala dentifrons (Stål), Tindale, 1923: 447.

Material examined. Two syntype females, Australia, Boucard (NHRM).

Other material. NEW SOUTH WALES: 1♂, 3 km NW of Bramah HS, NW of Balranald, 34°24'S 143°14'E, 24 Oct 1983, D.C.F. Rentz & M.S. Harvey. 1♂, 26 km S of Pooncarie, 21 Jan 1980, M.J.D. White (both ANIC).—NORTHERN TERRITORY: 1♂, 17 km SSE of Mt. Harris, 25 Aug 1955, L.J. Chinnick (ANIC). 2♂, Uluru Camp Site, Horn Centenary Expedition, 25°23'10"S 131°00'46"E, 24 & 25 Oct 1994, G. Milledge. 1♂, Uluru Mallee site, Horn Centenary Expedition, 25°24'07"S 130°59'19"E, 26 Mar 1995, G. Milledge. 1♂, Kathleen Creek, Mallee site, Horn Centenary Expedition, Watarrka NP, 24°20'54"S 131°40'36"E, 24 Mar 1995, P. Lilywhite (all NMV).—SOUTH AUSTRALIA: 2 juv, Lowan Stn., 7 km S of Sherlock, 4 Mar 1953 & 20 Dec 1954, L.J. Chinnick. 2 juv, Lowan Stn., 7 km S of Sherlock, 9 Mar 1953. 1♂, 56 km W of Amata, Musgrave Ranges, 26°09'S 130°35'E, 20–21 Jan 1982, D.C.F. Rentz & R. Honeycutt. 2♂, 1♀, 20 km NE of Kimba, 33°07'S 136°38'E, 5 Oct 1982, D.C.F. Rentz. 1♂, Brachina Gorge, Flinders Ranges, 9 Nov 1987, J.C. Cardale. 2 juv, 13 km WNW of Minnipa, 22 Oct 1968, J. Balderson & M.S. Upton. 1 juv, 5 km SSE of Minnipa, 30 Oct 1969, Key & Upton. 1♂, 18 km SSW of Pinnaroo, 35°24'S 140°48'E, 25 Oct 1983, D.C.F. Rentz & M.S. Harvey. 1♂, 1.5 km ESE of Ooldea, 3 Oct 1968, Key, Upton & Balderson (all ANIC). 1♀, Overland Railway, 40 km W of Kychering Soak, Dec 1908, Mr Chandler (NMV). 1♂, Darke's Peak, R.G. Walsh (SAM).—VICTORIA: 1♀, Big Desert, P. Robertson. 1♀, Big Desert, 35°46'S 140°58'E, 15 Apr 1987, P. Johnson. 1♀, N of Chinamans Well, Big Desert, 2 Mar 1982, A.J. Coventry. 1 juv, Grampians, Nov 1885. 1♀, 5.4 km E of Hattah, 34°47'S 142°20'E, 24 Jan 1986, G. Milledge. 1♂, 15 km SSW of Hattah, 34°54'S 142°15'E, 24 Jan 1986, G. Milledge. 1♀, 19.2 km SW of Hattah, 34°54'S 142°09'E, 21 Jan 1987, G. Milledge. 1♀, 20.8 km SE of Hattah, 34°52'S 142°28'E, 25 Jan 1987, G. Milledge. 1♂, Inglewood. 1 m, 0.5 km W of Lake Hattah, 28 Jan 1986, G. Milledge. 1♀, Lake Hattah, 18 Oct 1985, G. Milledge. 1♀, Lake Hattah, 8 Apr 1982, G. Milledge. 1♂, Mallee District, 3 Mar 1914, C. French. 1♀, 12.8 km N of Millewa South Bore, 34°40'S 141°04'E, 27 Mar 1986, G. Milledge. 1♀, 3.1 km N of Millewa South Bore, 34°45'S 141°04'E, 14 Nov 1985, G. Milledge. 1♀, 0.6 km N of Millewa South Bore, 34°46'S 141°04'E, 21 Feb 1986, G. Milledge. 1♂, 7 km SSW of Morkalla, 34°26'S 141°08'E, 15 Nov 1985, G. Milledge. 1♀, 6 km SW of Murray Valley Hwy & Annuello Rd junction, 34°50'S 142°35'E, 10 Feb 1986, G. Milledge. 2♂, 16.8 km SSW of Murrayville, 35°25'S 141°10'E, 18 Feb 1987, G. Milledge. 2♀, 16.8 km SSW of Murrayville, 35°25'S 141°10'E, 23 Feb 1987, G. Milledge. 1♀, 16.8 km SSW of Murrayville, 35°25'S 141°10'E, 19 Feb 1986, G. Milledge. 1♀, 7 km SW of Nowingi, 34°39'S 142°16'E, 16 Oct 1985, G. Milledge. 1♀, 1 juv, Ouyen, 26 Jun 1912, W.A. Hall. 1♂, Ouyen, 26 Apr 1911, S.S. Scaree. 1♂, Round Swamp, Big Desert, 35°42'S 141°43'E, 28 Mar 1985, G. Milledge. 1♂, 6.9 km N of Round Swamp, Big Desert, 35°41'S 141°43'E, 28 Mar 1983, G. Milledge. 3♀, The Springs, Murrayville Track, Big Desert, 28 Mar 1985, G. Milledge. 2♀, Waithe Fauna Reserve, 19 & 22 May 1986, G. Milledge. 1♀, 4 km N of Wedderburn, 36°23'S 143°37'E, 18 Nov 1989, G. Milledge. 1♂, Woomelang, 4 Dec 1902, Mr Hill (all NMV).—WESTERN AUSTRALIA: 1♀, Nedlands, Jan 1941, K.R. Norris. 1♂, Eyre Tower Microwave Station, 22 km ESE of Cocklebiddy, 32°08'S 126°17'E, 7 Oct 1982, D.C.F. Rentz. 1 juv, 23 km ESE of Cocklebiddy, 32°08'S 125°18'E, 25 Oct 1977, M.S. Upton & J.E. Feehan. 1♂, Cocklebiddy Repeater Stn., 36 km SW of Caiguna, 3 Nov 1984, D.C.F. Rentz. 2♂, Lake Douglas, 12 km SW of Kalgoorlie, 13 Jan 1989, M.S. & B.J. Moulds. 1♂, Kununurra, 16–19 Sep 1979, L.P. Kelsey. 2♀, 13 km SSE of Dongara, 28°21'S 115°00'E, 12 Sep 1981, D.C.F. Rentz. 1♀, Cape Naturaliste Lighthouse, 33°32'S 115°01'E, 15 Feb 1980, D.C.F. Rentz. 1♀, 19 km S of Menangina HS, 85 km E of Menzies, 24 Feb 1983, M.J. Whitten. 1♀, 27 km S of Balladonia Motel, 32°35'S 123°36'E, 13 Feb 1978, D.C.F. Rentz & M.J.D. White. 1♀, 31 km S of Balladonia Motel, 9 Feb 1980, D.C.F & B.G.F. Rentz. 1♂, 36 km WNW of Balladonia Hotel, 5 Mar 1982, M.J.D. White. 1♂ 60 km SSW of Norseman, 32°38'S 121°29'E, 17 Nov 1969, Key & Upton. 1♀, Cockleshell Gully, 19 km NNE of Jurien, 30°09'S 115°07'E, 25 Oct 1984, D.C.F. Rentz. 1♀, Crawley, 15 Mar 1934, K.R. Norris. 2♂, 33 km ENE of Perth, 30 Jan 1967, M.S. Upton. 1 juv, 37 km SW of Mt. Ragged, 33°40'S 123°11'E, 2 Nov 1977, M.S. Upton & J.E. Feehan. 2♂, 5 km SW of Mt. Ragged, 12 Nov 1969, Key & Upton. 1♂, 20 km SSE of Yanchep, 9 Sep 1981, D.C.F. Rentz. 1♀, 15 km WSW of Fraser Range HS, 32°04'S 122°39'E, 6 Sep 1981, D.C.F. Rentz. 1♀, 27 km W of Eneabba, 29°49'S 114°59'E, 9 Sep 1981, D.C.F. Rentz. 1♂, Fitzgerald National Park, 12 km NE of Hopetoun, 33°51'S 120°09'E, 10 Feb 1980, D.C.F. & B.G.F. Rentz (all ANIC). 1♂, Junga Dam, 23 km ESE of

Kalbarri, 6 Jan 1969, Kalbarri Survey. 1♂, Miling, Jan 1976, T. Verbakel. 1♂, 7.5 km E of Yuinmery HS, 28°34'S 119°01'E, 11–19 Feb 1980, T.F. Houston *et al.*, 1 juv, Roebourne, 1922. 1 juv, Cunderdin, Jul–Aug 1913. 1 juv, Fitzgerald River Reserve, Jul 1970, A. Baynes. 1 juv, 13.6 km SSW of Mt Jackson, 30°59'S 119°07'E, 5–11 Sep 1979, T.F. Houston *et al.*, 1 juv, Corrigin. 1 juv, 1.6 km W of Mundaring Weir, 6 Mar 1963, J.Dell. 1 juv, 30 km N of Bullfinch, 30°59'S 119°07'E, 7 Sep 1979, T.F. Houston *et al.*, 1 juv, Kanowna, 30°36'S 121°36'E, 16 Oct 1968, R.P. McMillan. 1 juv, Carollgouda Well, Kalbarri area, 30 Nov 1968, Hale School (all WAM).

Diagnosis. Can be distinguished from *T. obesa* by the facial shield being approximately as high as wide.

Description. Body (Figs. 26–27) rather large. Colour uniform green or bluish green. Head (Fig. 31) and frontal shield approximately as high as wide with ridge of frontal shield produced into prominent point at apex. Prothorax with fine scattered tubercles on dorsal surface, more so in female; lateral margin finely denticulate. Fore leg (Fig. 32) with inner face of coxa without markings, anterior margin with 9–11 small denticles; inner face of fore femur with large dark patch proximal to claw groove (not apparent in some specimens) and three small dark spots distal of claw groove; femora of mid and hind legs often orange red in proximal half. Wings of male longer than abdomen, those of female shorter than abdomen; ventral surface of costal area of tegmen dark bluish grey in anterior half; discoidal area completely opaque in female, only partly so in male; hind wing with costal and discoidal area yellowish green, anal area hyaline. Abdomen of female with posterior margin of fourth and particularly fifth sternite curved ventrally. Male genitalia (Fig. 33) with moderately elongate *apr*, narrowed distally; *pa* with anterior hook-like projection and posterior knob-like projection; distal projections of *dpr* of moderate length, anterior one longer than posterior one.

Measurements (mm). Body length, ♂ 53–75, ♀ 59–75. Pronotum length, ♂ 19–20, ♀ 21–26. Pronotum width, ♂ 5.5–6, ♀ 7–9. Fore coxa length, ♂ 12–15, ♀ 15–19. Fore femur length, ♂ 13–16, ♀ 18–22. Hind femur length, ♂ 14.5–15, ♀ 17–22. Hind tibia length, ♂ 15–16, ♀ 17–23. Tegmen length, ♂ 42–54, ♀ 28–38.

Immature stages. First two instars dark coloured and ant-like in behaviour and appearance. Ootheca squat, cream to sandy orange in colour. Appears to be mostly laid on the ground, usually attached to a piece of timber. The peculiar form of abdominal sternites 4–5 in the female may play a role in ootheca deposition.

Distribution and habits. Found across the arid regions of southern and central Australia (Fig. 46). Appears to be most commonly associated with mallee vegetation where the blue green body colour blends well with the leaves of certain mallee eucalypts. I have observed numerous individuals of this species, in nature and captivity, and never seen the cryptic behaviour displayed by members of the genus *Sphodropoda*. Adult females are commonly caught in pitfall traps, probably in the process of seeking oviposition sites. This would also suggest they are not capable of effective flight.

Remarks. The original description appears to be based on one specimen although this is not specified. One of the two female syntypes is labelled type, the other cotype. These are printed labels and there is no indication that they were placed there by the author. Therefore, I have decided not to

designate a lectotype. A syntype specimen is illustrated by Sjöstedt (1930, plate 8, fig. 1)

Zopheromantis

Zopheromantis Tindale, 1924: 550. Type species *Zopheromantis trimaculata* Tindale, by monotypy.

Diagnosis. Head approximately as high as wide, frontal shield without pronounced tooth at apex; preacetabular spine strong; ventral face of fore femur tuberculate, especially toward outer margin; male macropterous, female brachypterous, ventral face of costal area of tegmen red, mid and hind legs normal. Can be distinguished from *Trachymantis* by the absence of the apical tooth on the frontal shield and from *Sphodropoda* by the length of the mid and hind legs, the femur of the hind leg being distinctly longer than half the length of the abdomen.

Description. Body small to medium in size, male macropterous, female brachypterous. Head about as wide as high, not significantly compressed anteroposteriorly, apical margin gently arched; eyes rounded, not particularly prominent; frontal shield slightly wider than high, flat, with distinct ridge laterally and apically, forming blunt point at apex. Pronotum moderately elongate, rather slender, supracoxal expansion distinct, dorsally sparsely granulate in prozone, metazone almost smooth, margins finely denticulate in female largely entire in male, ventral surface with preacetabular spine prominent. Fore coxa as long as metazone of pronotum, with or without markings, a number denticles on anterior margin. Fore femur finely tuberculate on ventral surface, particularly toward outer margin; with four discoidal spines, relative length longest to shortest 3214; with four outer and 16–17 inner spines, claw groove situated at about a third the total distance from base. Tegmen with costal area opaque, red beneath; discoidal area entirely opaque to mostly hyaline. Hind wing with costal and discoidal area pigmented, anal area largely hyaline. Mid and hind legs normal, hind femur more than half the length of abdomen. Abdomen moderately elongate, cerci short, slender and cylindrical. Male genitalia with *dpr* bifurcate.

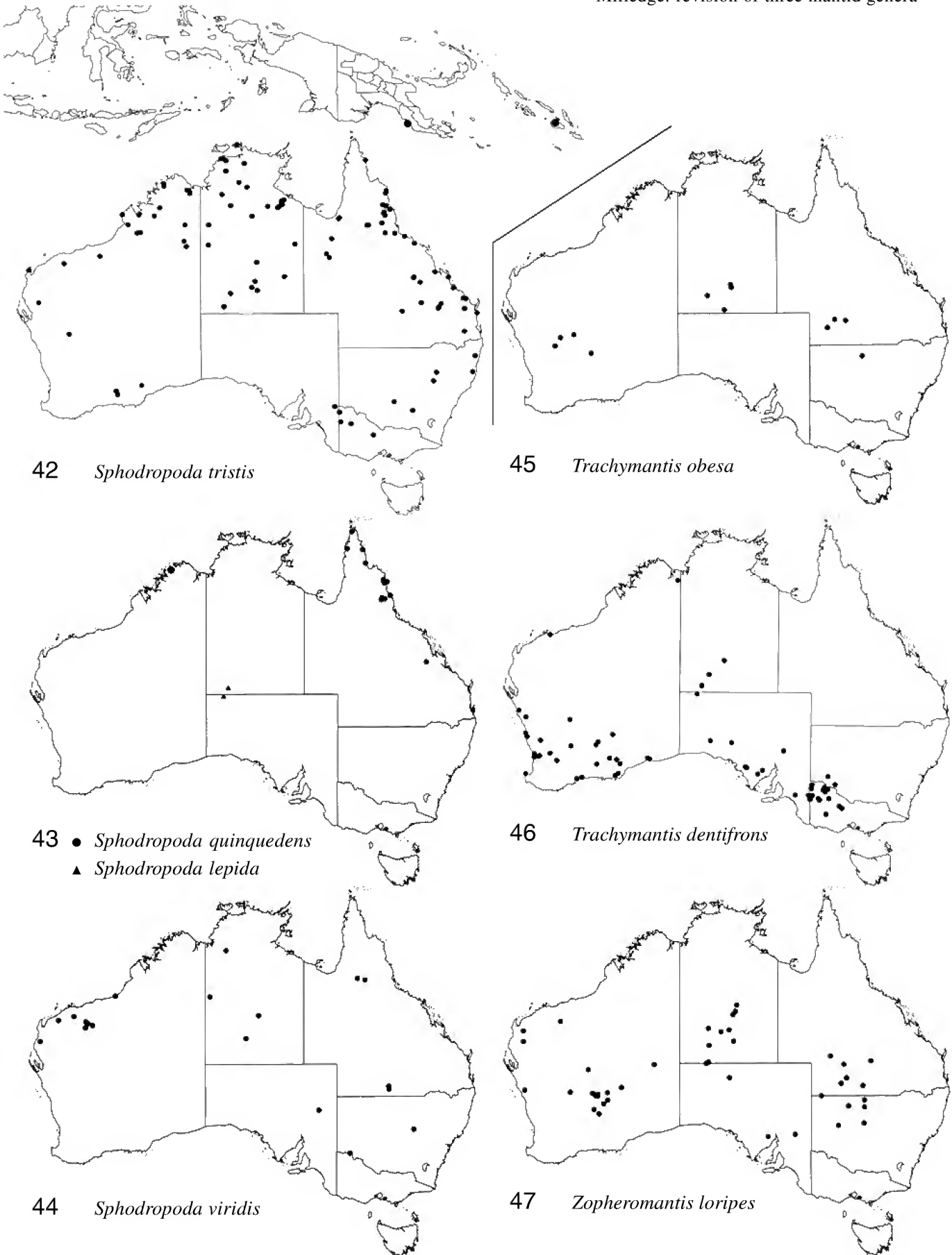### *Zopheromantis loripes* (**Tindale, 1923**) **n.comb.**

Figs. 34–35, 39–41, 47

Sphodropoda loripes Tindale, 1923: 446.
Zopheromantis trimaculata Tindale, 1924: 551, **new synonym**.
Hierodula trimaculata Beier, 1935: 82.

Material examined. Lectotype male (here designated) of *Sphodropoda loripes*, Cunnamulla, Queensland, H. Hardcastle, I–14071 (SAM). Holotype female of *Zopheromantis trimaculata*, Teetulpa, South Australia, Jan. 1904, G. Farrand, I–14590 (SAM).—QUEENSLAND: 1♂, Coopers Creek, 10.7 km NE of Windorah, 25°22'18"S 142°44'41"E, 4 Apr 1991, G.V. Maynard & G. Davis. 1♂, 33 km W of Quilpie, 16 Mar 1964, L.J. Chinnick. 1♂, 18 km NE of Thargomindah, 15 Mar 1964, L.J. Chinnick. 1♂, 23 km SW of Toompine, 10 Apr 1970, R.C. Lewis (all ANIC). 1♀, Augathella, 25°48'S 146°25'E, 18 Jan 1993, G. Milledge (NMV).—NEW SOUTH WALES: 3♂, 18 km WNW of Bourke, 9 Feb 1972, R.C. Lewis. 5♀, 6 km W of Cobar, 23 Mar 1972, White & Jaworska. 1♀, 7 km W of Cobar, 20 Feb 1963, L.J. Chinnick. 1♂, 2 juv, 7 km W of Cobar, 1 Feb 1964, M.J.D. White. 1♀, 15 km SW of Enngonia, 14 Jan 1965, M.J.D. White. 1♂, 37 km SE of Wanaaring, 10 Feb 1972, R.C. Lewis. 1♂, 1 km W of Warri gate, 11 Feb 1972, R.C. Lewis. 1 juv, 17 km SE of Wilcannia, 31 Jan 1964, M.J.D. White (all ANIC).—NORTHERN TERRITORY: 2♂, 37 km S of Alice Springs, 15 Feb 1966, Britton, Upton & McInnes. 1♂, 103 km NNW of Alice Springs, 12 Feb 1966, Britton,

42   *Sphodropoda tristis*

45   *Trachymantis obesa*

43   ● *Sphodropoda quinquedens*
     ▲ *Sphodropoda lepida*

46   *Trachymantis dentifrons*

44   *Sphodropoda viridis*

47   *Zopheromantis loripes*

Figs. 42–47. Distributions of Australian mantids: (42) *Sphodropoda tristis*; (43) ● *S. quinquedens*, ▲ *S. lepida*; (44) *S. viridis*; (45) *Trachymantis obesa*; (46) *T. dentifrons*; (47) *Zopheromantis loripes*.

Upton & McInnes. 1♂, Barrow Creek Tel.Sta., 20 Mar 1955, K.H.L. Key. 1♂, 3 km S of Barrow Creek, 13 Feb 1966, Britton, Upton & McInnes. 1♀, 25 km NW of Mount Wedge HS, 10 Apr 1963, L.J. Chinnick. 1♂, 5 km W of Mulga Park HS, 24 Mar 1963, L.J. Chinnick. 1♂, 26 km WSW of Mulga Park HS, 26°00'S 131°25'E, 18 Jan 1982, D.C.F., B.G.F. Rentz. 1♂, 25 km NE of Narwietooma HS, 9 Apr 1963, L.J. Chinnick & R. Honeycutt. 1♂, Taylors Creek, 47 km N of Barrow Creek township, 22 Jan 1984, M.S. & B.J. Moulds. 1♂, Wauchope, 21 Mar 1955, K.H.L. Key (all ANIC). 2♂, Kathleen Creek, Watarrka National Park, Horn Centenary Expedition, 24°20'38"S 131°40'54"E, 14 Mar 1995, G. Milledge (both NMV).—SOUTH AUSTRALIA: 1♀, 7 km W of Iron Knob, 28 Mar 1964, M.J.D. White. 1♂, Marla Bore, 50 km W of Welbourne Hill, 23 Mar 1963, L.J. Chinnick (both ANIC).—WESTERN AUSTRALIA: 2♂, 23 km WSW of Barradale, 22°56'S 114°45'E, 30 Mar

1971, Upton & Mitchell. 1♀, Canegrass, 8 Feb 1981, M.J.D. White. 1♀, 5 km NE of Kanowana ruins, near Broad Arrow, 18 Feb 1981, M.J.D. White. 1♂, 5 km NE of Kanowana ruins, near Broad Arrow, 24 Feb 1981, M.J.D. White. 1♀, Malcolm, 21 Feb 1979, M.J.D. White. 1♀, 1 km S of Malcolm, 28°47'S 121°31'E, 19 Feb 1978, D.C.F. Rentz & M.J.D. White. 1♂, 6 km SE of Mt. Boyce, near Yerilla HS, SE of Leonora, 15 Feb 1983, M.J.D. White. 2 juv, Mt. Leonora, near Leonora, 13 Feb 1981, M.J.D. White. 1♀, Mt. Leonora, near Leonora, 10 Feb 1983, M.J.D. White. 1♀, 3 km NNE of Mt. Ross, NW of Leonora, 28°41'S 121°03'E, 18 Feb 1978, D.C.F. Rentz & M.J.D. White. 1♂, New Yamarna HS, S of Minnie Creek, near Virginia Range, 31 Jan 1967, M.J.D. White. 1♀, 43 km NW of Wittenoom, 22 Apr 1963, L.J. Chinnick (all ANIC). 1♀, Middalya, 4 Feb 1902, T. Watt (NMV). 2♂, Kathleen Valley, 1963, T. Moriarty. 1♂, Lake Violet. 1♂, Laverton. 1♂, 2.5 km N of Mt. Linden, 29°19'S 122°25'E, 17–23 Mar 1979, T.F. Houston. 1♂, 1♀, Nolba, 28°22'S 114°52'E. 1♂, Warburton Ranges, 25 Mar 1963, H. De Graff. 1♂, 7.5 km E of Yuinmery HS, 28°34'S 119°01'E, 11–19 Feb 1980, T.F. Houston. 1♂, 9 km SE of Yuinmery HS, 28°34'S 119°01'E, 25 Mar 1979, T.F. Houston (all WAM).

Description. Body (Figs. 34–35) size varies from small to medium. Body colour uniform green or bluish green. Head (Fig. 39) approximately as high as wide; frontal shield slightly wider than high, more so in male. Fore leg (Fig. 40) with inner face of coxa without markings or with one to three dark spots, anterior margin with 7–8 small tubercles; inner face of femur without markings; inner face of tarsal segments dark at distal end. Wings of male longer than abdomen, those of female slightly shorter than abdomen; ventral surface of costal area of tegmen red with narrow pale band on anterior margin; discoidal area completely opaque in female, only partly so in male; hind wing with costal and discoidal area yellowish green, anal area hyaline. Male genitalia (Fig. 41) with short, stout *apr*, *pa* with single, blunt pointed anterolateral projection, dorsal edge slightly folded; distal projections of *dpr* moderately elongate and narrowed.

Measurements (mm). Body length, ♂ 37–50, ♀ 39–58. Head width, ♂ 6–7, ♀ 7–8. Head depth, ♂ 3.5–5, ♀ 4.5–6.5. Pronotum length, ♂ 11–13, ♀ 15–22. Pronotum width, ♂ 3–4.5, ♀ 4–6. Fore coxa length, ♂ 7–9, ♀ 11–14. Fore femur length, ♂ 8.5–12, ♀ 12–16. Hind femur length, ♂ 8.5–12, ♀ 12–18. Hind tibia length, ♂ 9.5–12, ♀ 13–19. Tegmen length, ♂ 27–35, ♀ 19–29.

Immature stages. Juveniles similar in appearance to adults, ootheca unknown.

Distribution and habits. Found in the arid regions of the continent (Fig. 47). The few specimens of this species that I have collected have been found in *Acacia* shrubs. None displayed the cryptic behaviour associated with *Sphodropoda*.

Remarks. The female syntype of *Sphodropoda loripes* described by Tindale is, in fact, a female of *Sphodropoda viridis*. Therefore I have designated the male syntype as the lectotype.

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A New Middle Devonian Arthrodire (Placoderm Fish) from the Broken River Area, Queensland

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ABSTRACT. Associated bones of the trunk-armour belonging to a large brachythoracid arthrodire are described as *Confractamnis johnjelli* n.gen. and n.sp. The specimen comes from strata of probable Eifelian age in the Broken River Group of Queensland. It shows a range of derived brachythoracid features including reduction of dermal ornament, and strong development of the dermal neck joint articulation. The posterior dorsolateral and posterior lateral plates of the trunk armour were high and narrow, and the anterior lateral plate had a distinctive narrow bilobed dorsal angle as indicated by the shape of its overlap area on the anterior dorsolateral plate. A provisional reconstruction suggests that the bones came from a large fish over 2 m in length. A cross section of the trunk armour is compared with the large arthrodire *Taemasosteus* from the Early Devonian of Burrinjuck, New South Wales. A possible close relative of this new taxon has been illustrated from the Early Devonian of Morocco, supporting other indications of resemblance in placoderm fish assemblages between these regions of east and north Gondwana during the Early-Middle Devonian.

Over 20 years ago Professor J.S. Jell (University of Queensland) made a small collection of limestone samples apparently containing bones from several localities in the Devonian outcrops of the Broken River area of Queensland (Fig. 1). They were sent to Professor K.S.W. Campbell (Australian National University), who passed on remains of placoderms (Devonian armoured fishes) to the author for preparation and study.

Acetic acid preparation, which completely removes bones (calcium phosphate) from limestone (calcium carbonate), revealed a small collection of six placoderm specimens from the ten original samples. Two samples belonged to one specimen (ANU V1028, described below). Three other samples contained only vertebrate microfossils (small scales and plates), which have been well documented from many horizons in the Broken River Devonian sequence by other authors (e.g., De Pomeroy, 1995, 1996; Turner *et*

al., 2000). The six placoderm specimens belong to two orders, the Antiarchi and the Arthrodira, which were the most successful of some seven orders within the class Placodermi (Denison, 1978; Young, 1986; Goujet & Young, 1995). The two antiarch specimens from Broken River were the best preserved, with articulated armours and some small bones of the jaws, cheek, and sclerotic ring surrounding the eye, not previously well documented for the group. They were described as two new genera (*Nawagiaspis* and *Wurungulepis*) by Young (1990).

The other four specimens can be assigned to the Arthrodira, by far the most diverse placoderm order, with its major subgroup, the Brachythoraci, comprising nearly 60% of about 170 genera within the Arthrodira (Carr, 1995). These specimens are much more fragmentary, probably because they belonged to considerably larger fishes, all representatives of the
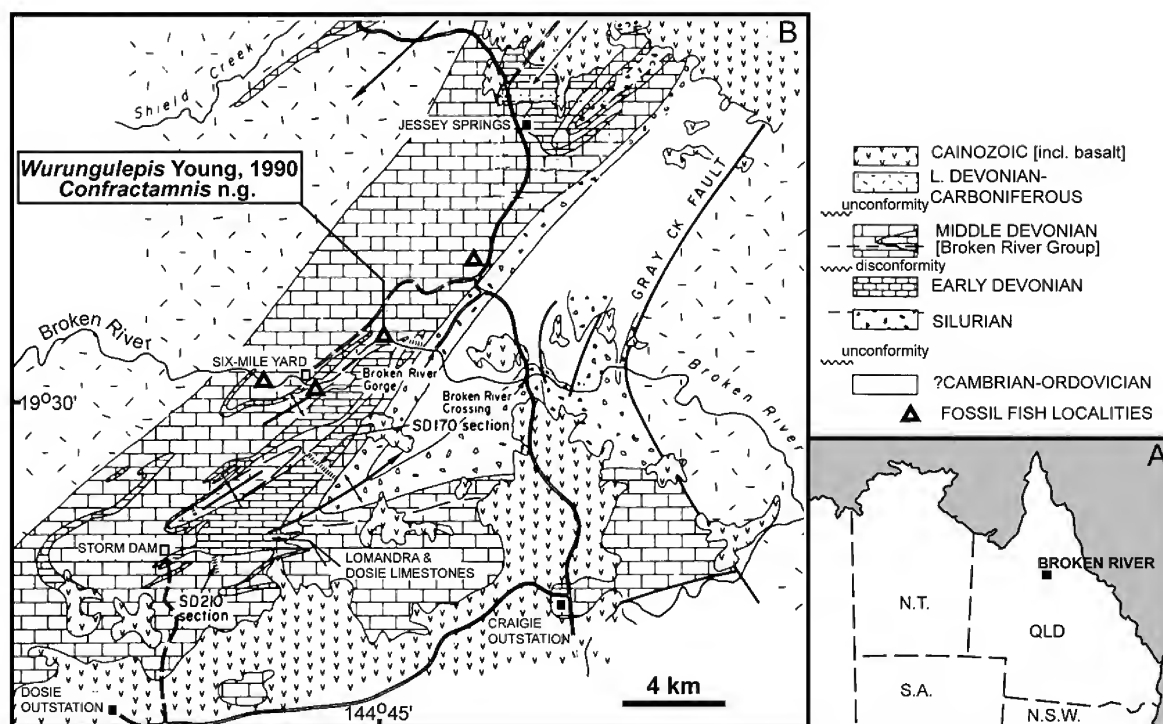
Fig. 1. (*A*) Location of the Broken River area in Queensland, Australia. (*B*) Geological map of the collecting area (modified from Turner *et al.*, 2000: fig. 2), showing the locality (Grid Reference 640 460) for the specimens described in this paper.

brachythoracid arthrodires. In marine environments of the Late Devonian the brachythoracids included probably the largest predators of their time (Young, 2003c).

The major radiation of brachythoracid subgroups had apparently already occurred by the Middle Devonian, and the diverse faunas that occupied shallow marine environments of eastern Australia during the Early-Middle Devonian have revealed primitive representatives that are important in resolving the origins and interrelationships of major brachythoracid subgroups (e.g., Lelièvre, 1995; Mark-Kurik & Young, 2003; Young *et al.*, 2001; Young, 2004a).

Two other brachythoracid specimens from the Broken River Devonian sequence have recently been described: a new species of the genus *Atlantidosteus* Lelièvre, 1984a, a large brachythoracid first recorded from the Early Devonian of Morocco (Young, 2003a), and a new genus and species *Doseyosteus talenti* Young, 2004b. The two specimens documented in this paper are the last to be described from the original J.S. Jell collection. An isolated suborbital plate of another arthrodire was illustrated by Turner *et al.* (2000: fig. 8.7), and an isolated toothplate was ascribed to ?*Ptyctodus* sp. (placoderm order Ptyctodontida) by Turner & Cook (1997). Other vertebrate macro-remains documented from the Broken River Devonian sequence include a lungfish skull (S. Turner, pers. comm.) and jaw remains of an onychodontid (Turner *et al.*, 2000: fig. 6). Apart from these osteichthyan (bony fish) remains, placoderm bones, mainly from brachythoracid arthrodires, seem to be most common amongst unprepared vertebrate samples from Broken River (S. Turner, pers. comm.).

Locality and age of the samples

The stratigraphic occurrence of various placoderm remains in the Broken River sequence was documented by Young (1993, 1996), De Pomeroy (1995, 1996), and Turner *et al.* (2000). Dating the sedimentary sequence is based mainly

on conodonts (Mawson & Talent, 1989; Sloan *et al.*, 1995). Locality and age information for all previously described placoderm taxa from the original J.S. Jell collection was reviewed by Young (2004b), to clarify conflicting information previously published.

The specimens described below were sent to Canberra as three samples, two with the field number 58/L1 (ANU V1028), and one labelled 58/L2 (ANU V1031). According to information provided by J.S. Jell (letter of 17 April, 1980), they both came from University of Queensland locality L4399, north bank of the Broken River, Grid Reference 640 460 on the Burges 1:100 000 sheet (see Fig. 1). He suggested a Middle Devonian (?Eifelian) age for this locality. On the map of the area published by Sloan *et al.* (1995: fig. 2) the locality lies within the outcrop referred to as "undifferentiated Broken River Group".

The antiarch *Wurungulepis denisoni* Young, 1990 came from the same locality (erroneously given as L4339 by Young, 1990: 45). On this evidence, a "*Wurungulepis-Atlantidosteus* fauna", of assumed Eifelian age, was listed in the macrovertebrate zonation of Young (1993, 1996). However De Pomeroy (1995: 480) assigned *Wurungulepis* an older age—the late Emsian *serotinus* Conodont Zone—citing a personal communication of J.A. Talent. This information was repeated by Turner *et al.* (2000: 498).

No conodont data were obtained during acid preparation of the specimens described below, so their precise position relative to the standard conodont zonation is uncertain. Young (2004b) concluded that the original age assessment of Eifelian for the antiarch *Wurungulepis*, from the same locality, was most consistent with current knowledge of the stratigraphic distributions of the Antiarchi, a large and diverse group comprising some 45 named genera and 154 species. Various advanced features of the brachythoracid arthrodire described below are consistent with this interpretation.

Abbreviations

Repositories for material are indicated by specimen prefixes as follows: **ANU V**, Department of Earth and Marine Sciences, Australian National University, Canberra; **MCD**, Moroccan specimens in Muséum national d'Histoire naturelle, Paris.

Standard abbreviations for placoderm dermal bones are used in the text and figures, with bone overlap areas designated as "contact face" (*cf*) on the inner surface, or "overlap area" (*oa*) on the outer surface. These and other anatomical abbreviations used in the figures are as follows: *ADL*, anterior dorsolateral plate; *AL*, anterior lateral plate; *cd*, glenoid condyle of dermal neck-joint; *cf.ADL*, area overlapping ADL plate; *cf.PDL*, area overlapping PDL plate; *cf.PL*, area overlapping PL plate; *dla*, dorsolateral axis separating dorsal and lateral walls of the trunk armour; *fo.PL*, fossa on PDL plate receiving dorsal corner of PL plate; *gr.AL*, anterior groove for AL plate; *IL*, interolateral plate; *laf*, articular fossa for dermal neck-joint; *llc*, main lateral line sensory canal; *MD*, median dorsal plate; *oa.ADL*, area overlapped by ADL plate; *oa.AL*, area overlapped by AL plate; *oa.MD*, area overlapped by MD plate; *oa.PDL*, area inserting into fossa of PDL plate; *o.PDL*, area of PDL plate overlapped by ADL; *o.PL*, area of PL plate overlapped by ADL plate; *pap*, para-articular process; *PDL*, posterior dorsolateral plate; *PL*, posterior lateral plate; *pr.sg*, subglenoid process; *ri.cd*, ridge crossing inner surface of articular condyle; *ri.p*, posterior ridge; *ri.vt*, vertical ridge; *SP*, spinal plate; *th*, thickening; *vg*, vascular grooves; *vs.cd*, ventral surface of articular condyle.

Systematic palaeontology

Class Placodermi McCoy, 1848

Order Arthrodira Woodward, 1891

Suborder Brachythoraci Gross, 1932

Confractamnis johnjelli n.gen. and n.sp.

1992   eubrachythoracid nov.–Young *et al.*, 1993: 247 (*pars*).

Name. From the Latin *confractus* (broken) and *amnis* (stream or river), with reference to the Broken River. The species name recognizes the collector, Prof. John Jell, University of Queensland, who has conducted research in the Devonian of the Broken River area over many decades.

Diagnosis. A large brachythoracid attaining a length of at least 2 m; trunk armour high, with anterior lateral, posterior dorsolateral, and posterior lateral plates all dorsoventrally elongated. Median dorsal plate enclosing a midline angle of about 150° between left and right laminae. Anterior dorsolateral plate crossed by single sensory canal groove close and subparallel to the lateral margin of the median dorsal plate. Dorsal corner of anterior lateral plate narrow, rounded, and bilobed, with 25–30° angle between main margins. Posterior dorsolateral plate extensively overlapped by anterior dorsolateral plate; posterior lateral plate with high and narrow exposed part, and elongate anterior overlap for the anterior dorsolateral plate. External surface of dermal bones smooth, or with very fine, closely spaced tuberculation of low relief.

Remarks. Because the skull roof is unknown in this new taxon, only trunk armour characters are available for assessing its affinities. It is clearly not a coccosteid, in which the ADL plate is crossed by an additional ventral sensory canal groove. The absence of the ventral sensory groove is one of four characters by which Carr (1991: 382) characterized the most derived pachyosteomorph subgroup within the Brachythoraci (comprising the Dinichthyidae and Aspinothoracidi). Within the former family, *Eastmanosteus* differs from the new taxon in possessing tubercular ornament, and both *Eastmanosteus* and *Dunkleosteus* have an extensive exposed part of the ADL plate above the sensory groove. *Levisosteus* Otto, 1999 is a poorly known brachythoracid showing possible affinity with *Dunkleosteus*, and indicating that ornament reduction may have occurred by the Eifelian, but its trunk armour is completely unknown, so no other comparisons are possible with the specimens described here. The aspinothoracids are characterized by various skull features in addition to the absence of a spinal plate in the trunk armour (Carr, 1991). There is no information on whether this small bone was present in *Confractamnis* n.gen., but it is likely that the spinal was lost independently in several groups, as suggested by Denison (1984). One group in which this had occurred by the Middle Devonian is the Heterostiidae. *Heterostius* resembles *Confractamnis* n.gen. in large size, reduction of ornament, and position of the lateral line groove near the dorsal exposed edge of the ADL plate. *Heterostius*, however, differs in extreme trunk armour reduction, with the AL plate fused to the ADL plate, whereas the AL was clearly a separate bone in *Confractamnis* n.gen. The Emsian forms *Tityosteus, Taemasosteus* and *Antineosteus* also resemble *Confractamnis* n.gen. in the dorsal position of the sensory groove on the ADL plate, but differ in the dorsal configuration of the AL plate (as indicated by the shape of its overlap on the ADL), in the shape of the PDL and PL plates, in the much flatter MD plate (*Tityosteus* and *Antineosteus*), and in the transversely elongate articular condyle attached along its length to the ADL plate (*Antineosteus*; a character defining the Homostiidae). Close affinity with *Atlantidosteus* (known from two species, one in Morocco and one in the Broken River sequence) can be excluded on the assumption that this taxon was a homostiid, with a dorsoventrally compressed trunk armour. One isolated ADL plate from the Emsian of Morocco resembles *Confractamnis* n.gen. in its pointed articular condyle, the narrow rounded dorsal angle of the overlap area for the AL plate, and the position of the sensory groove close and subparallel to the lateral margin of the MD. This specimen may represent a closely related taxon, but it differs from *Confractamnis* n.gen. in its smaller size, coarse tubercular ornament, more acute angle between the dorsal lamina of the ADL plate and the long (transverse) axis of the articular condyle, and the lack of a bilobed dorsal corner on the AL plate.

Material. ANU V1028 (holotype), a large left ADL plate with part of the MD plate attached, associated with left PDL and PL plates (all incomplete); ANU V1031, a very incomplete MD plate.

Locality. University of Queensland locality L4399, north bank of the Broken River, Grid Reference 640 460 on the Burges 1:100 000 sheet (see Fig. 1); field numbers 58/L1 (V1028) and 58/L2 (V1031).
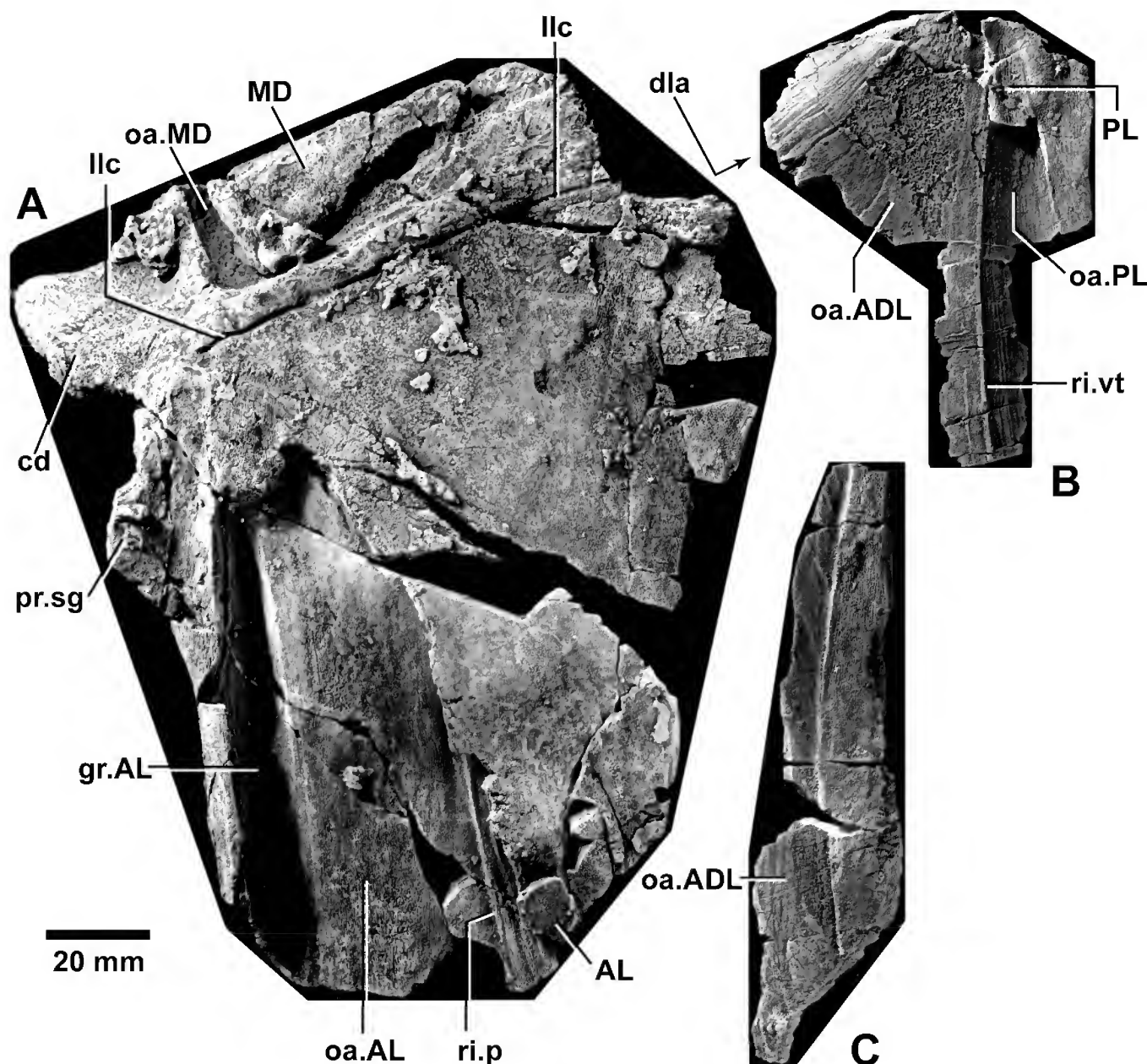
Fig. 2. *Confractamnis johnjelli* n.gen. and n.sp. ANU V1028 (holotype). Bones of the trunk armour in external view (all incomplete). (*A*) Left ADL plate, with part of the MD plate and a fragment of the AL plate attached; (*B*) left PDL plate, with part of the PL plate attached; (*C*) left PL plate. All specimens acid-prepared, and whitened with ammonium chloride for photography.

Horizon and age. According to information provided by Prof. J.A. Talent to A. Basden (pers. comm., 28 August 1995), the holotype of *Wurungulepis*, from the same locality as the material described here, came from strata that were pre-Dosey Limestone in the sequence, and equivalent to the Bracteata Formation and Lomandra Limestone. Outcrop in this vicinity is referred to as "undifferentiated Broken River Group" on the most recent published geological map (Sloan *et al.*, 1995: fig. 2). Prof. J.S. Jell (letter of 17 April, 1980) suggested a Middle Devonian (?Eifelian) age for this locality, and the sequence is shown spanning the Emsian-Eifelian boundary by Sloan *et al.* (1995: fig. 3).

Description. The holotype (ANU V1028) includes remains of four bones from the trunk armour of a very large brachythoracid. The left anterior dorsolateral (ADL) plate is particularly massive (Figs. 2A, 3), with the bone some 35 mm thick at the base of the articular condyle (cd) for the dermal neck-joint. The ventral part of the ADL is missing,

and the posterior margin is broken and incomplete, but the fragmented posterior parts reduce in thickness to a little more than 1 mm, with part of the actual margin preserved. Together with the evidence of adjacent bones it is possible to determine the general shape of the ADL plate, except for the extent of the ventral margin.

The external surface of the ADL (Fig. 2A) shows two deeply incised overlap areas for the median dorsal (MD) and anterior lateral (AL) plates (oa.MD, oa.AL). A broken fragment of the left anterolateral corner of the MD plate is still attached to the specimen, but slightly displaced. Its thickness (13 mm), so close to the lateral margin, gives some indication of the large size of this bone (cf. ANU V1031 below). The rest of this normally massive bone was either weathered away, or perhaps was contained in another uncollected limestone block. The external surface of the MD fragment appears smooth, as does the exposed surface of the ADL. On close examination, some parts show a faint tuberculation of closely spaced fine tubercles (about 15 per
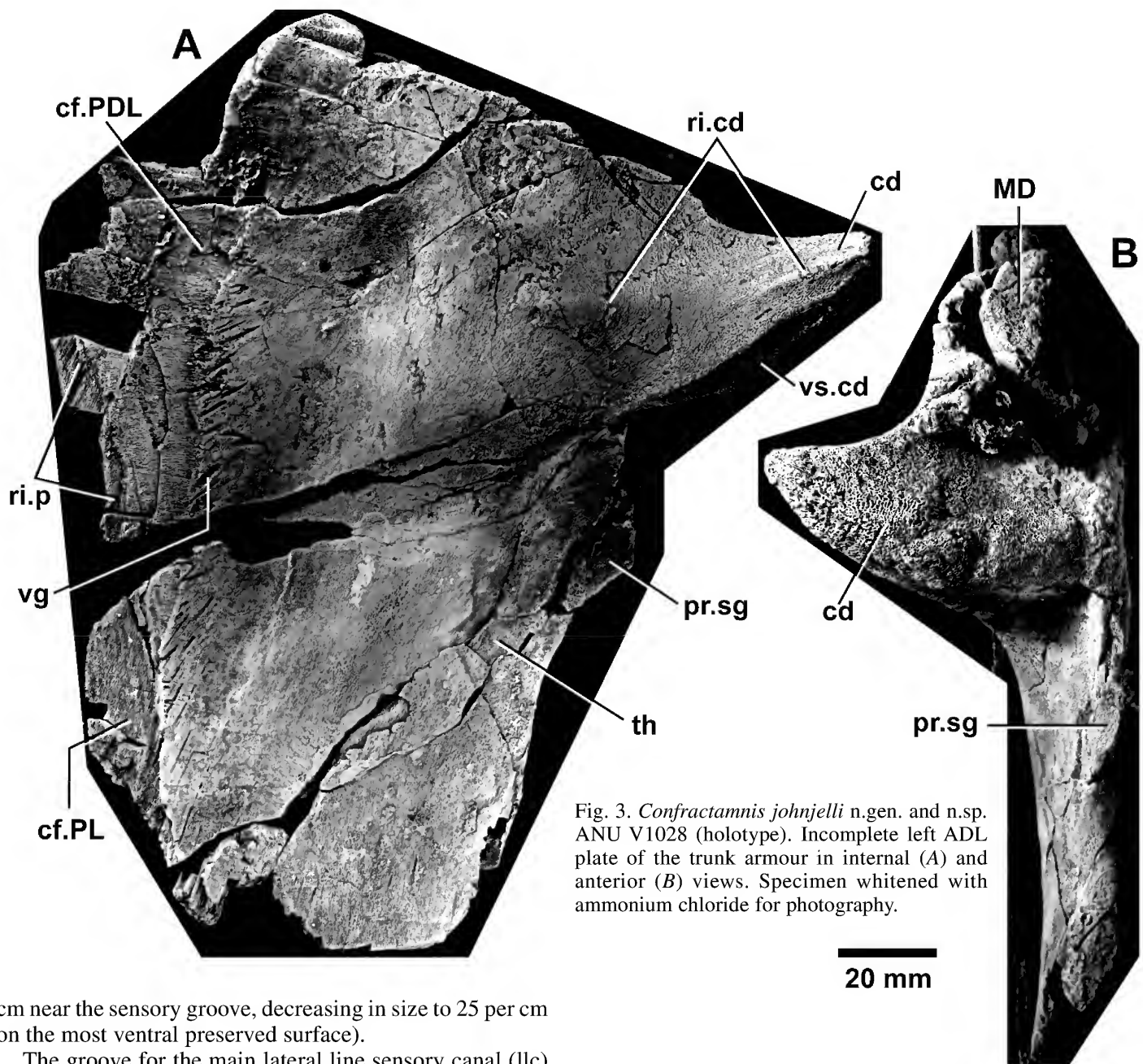
Fig. 3. *Confractamnis johnjelli* n.gen. and n.sp. ANU V1028 (holotype). Incomplete left ADL plate of the trunk armour in internal (*A*) and anterior (*B*) views. Specimen whitened with ammonium chloride for photography.

20 mm

cm near the sensory groove, decreasing in size to 25 per cm on the most ventral preserved surface).

The groove for the main lateral line sensory canal (llc) crosses the ADL plate from the region of the articular condyle, as in all arthrodires with a developed dermal neck-joint. It runs, however, close and subparallel to the edge of the overlap for the MD, which is a point of difference to many other brachythoracids. The overlap area for the AL plate is set in about 10 mm along a deep anterior groove, which braced the AL against the anterior edge of the ADL plate (gr.AL, Fig. 2A). The overlap shows that the AL had a narrow rounded bilobed dorsal corner, which forms a much more acute angle (about 25–30°), and is quite different in shape to the triangular overlap of *Eastmanosteus* or *Dunkleosteus* (dorsal angle 45–50°). Near the ventral preserved edge the overlap area expands as a posterior embayment, in which a fragment of the overlying AL plate is preserved (AL, Fig. 2A). At its margin, this embayment slopes gradually to the external surface, in contrast to the thick and undercut margins of the deeply incised main part of the overlap area (oa.AL). These show that immediately dorsal to the embayment the posterior edge of the AL was enclosed by the ADL to a depth of about 6 mm. The undercut surface is exposed by the broken margin of the overlap area, to reveal a strong ridge (ri.p, Fig. 2A).

The articular condyle for the dermal neck-joint in *Confractamnis* n.gen. is a very strongly developed projection from the anterior margin of the ADL (cd, Figs. 2, 3). In mesial view, the condyle shows a triangular cross-section. The ventral side of the triangle, with typical "siebknochen" texture of spongy bone (invested with articular cartilage in life), is partly visible in internal view (vs.cd, Fig. 3A). The posterior side of the triangle forms the smooth inner surface, which is slightly convex about a low ridge crossing the condyle from near the mesial termination to the thickened part of the ADL (ri.cd). An anterior view of the ADL plate (Fig. 3B) shows the strong dorsal support for the condyle (the "condylus ridge" of Heintz, 1934: 73), and the mesial termination of the condyle as a rounded point, with its anterodorsal surface (anterior side of triangle) being flat to slightly concave, and also with "siebknochen" texture (sieve-like bone). The actual articular surface is higher laterally than mesially (see Fig. 5C), a condition also noted in both *Dunkleosteus* and *Homostius* by Heintz (1934: 73). Lelièvre (1995) used this as a character to group some primitive brachythoracids from Morocco. Beneath the condyle is a prominent subglenoid process

(pr.sg), which would have articulated against the para-articular process of the skull roof.

The inner surface of the ADL plate shows extensive posterior contact faces for the PDL and PL plates (cf.PDL, cf.PL, Fig. 3A). The distinct anterior margin of the very extensive PDL contact face is marked by vascular grooves (vg) with radiating orientation from the ossification centre of the bone (situated anteriorly in the region of the articular condyle attachment). Ventrally this margin becomes the anterior margin for the PL contact face. A fainter ridge near the posterior border of the ADL plate (ri.p) represents the anterior margin for the more dorsal part of the PL contact face. The anterior half of the inner ADL surface is convex, where the bone is massively thickened (th) to form a broad dorsoventral ridge, decreasing ventrally where the internal convexity lies beneath the deeply incised overlap for the AL plate on the external surface. The posterior part of the inner surface in ANU V1028 is flat to concave, and inflected dorsoventrally at an angle of about 140° about the dorsolateral ridge, at the level of the sensory groove on the external surface. The PDL plate has a similar inflection ("dla" arrow, Fig. 2B).

Associated left PDL and PL plates of *Confractamnis* n.gen. are also partly preserved in the holotype. They can be placed against the ADL plate to confirm their life position. The PDL (Fig. 2B) is missing much of its dorsal part, which was overlapped by the MD plate. Only a narrow posterior strip of the external bone surface is preserved, and most of the bone comprises an internal lamina overlapped extensively by both ADL and PL plates. A thin vertical ridge (ri.vt), which was entirely internal, separates the two overlaps (oa.ADL, oa.PL). The edges of the bone are extremely thin, with many fine fractures which collapsed during acid preparation, and could be only partly reconstructed from fragments. The margins of the bone, however, are indicated by the extent of the contact face inside the ADL plate (cf.PDL, Fig. 3A), which shows that the degree of overlap was more extensive than in many other brachythoracids. The external surface of the PDL plate may have expanded dorsally (PDL, Fig. 4A), and presumably was crossed by a posterior continuation of the lateral line groove (llc). Its distinctive shape can be inferred from the marked dorsoventral elongation of the internal ridge (ri.vt, Fig. 2B), and the extensive overlap surfaces (o.PDL, Fig. 4A). The narrow dorsal corner of the PL plate is still attached to the PDL (PL, Fig. 2B). There is no sign of the internal fossa which received this corner in *Dunkleosteus* (fo.PL, Fig. 6B).

The inner surface of the PDL plate is smooth and concave, inflected about the dorsolateral angle at a level that corresponds to that on the ADL (dla, Fig. 2B). The bone margins show inner vascular grooves like those on the inside of the ADL (vg, Fig. 3A), which may indicate increased blood supply adjacent to the bone margins during periods of growth. The PDL fits inside the ADL such that the vertical ridge (ri.vt, Fig. 2B) abuts against a slight ridge inside the posterior margin of the ADL plate (ri.p, Fig. 3A).

The incomplete PL plate of *Confractamnis* n.gen. (Fig. 2C) is a remarkably high and narrow splint of bone, comprising an anterior overlap area, and high and narrow posterior exposed part. The posterior margin of the preserved part is partly broken, but the form of the inner surface shows that not much is missing. The PL plate slots into the grooved overlap behind the vertical ridge on the PDL (where part of
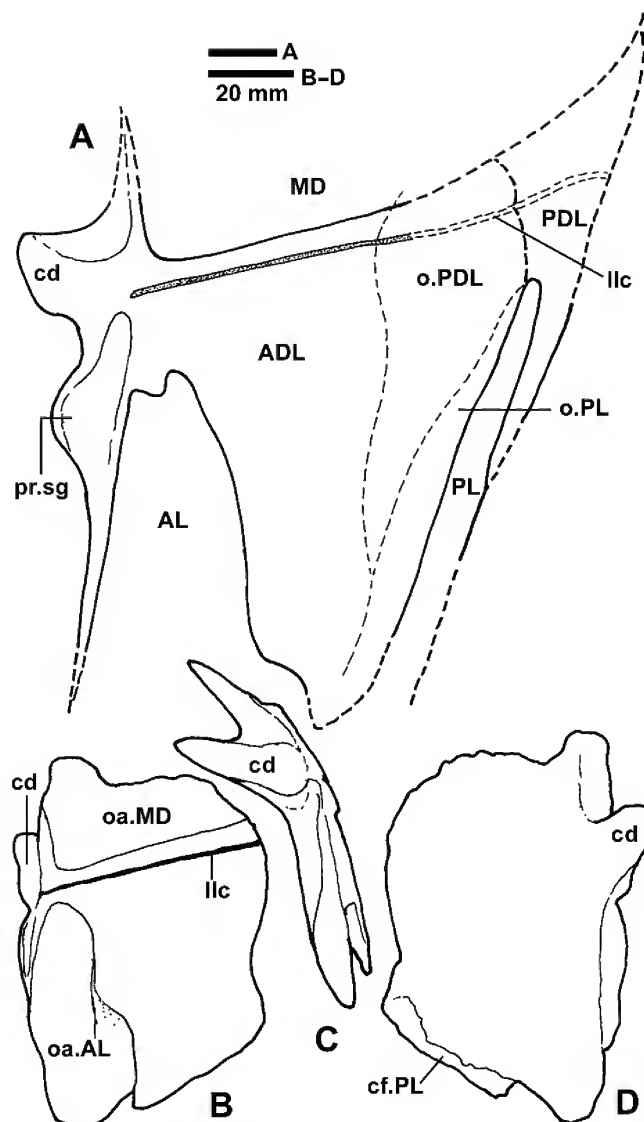

Fig. 4. (A) *Confractamnis johnjelli* n.gen. and n.sp. Reconstruction of left lateral side of the trunk armour, based on ANU V1028 (holotype). (B–D) Isolated left ADL plate from the Early Devonian of Morocco, in external (B), anterior (C), and internal (D) views. Specimen MCD 62, figured by Lelièvre (1984b: pl. 6F–H).

the PL is still attached; oa.PL, Fig. 2B). With both bones in place inside the ADL, the convex internal surface of the PL forms a thickened posterior border to the articulated armour. Its overlap area is sandwiched between the PDL and ADL plates, with its anterior edge against the posterior ridge dorsally (ri.p, Fig. 3A), and ventrally extending past the PDL to fit into a more deeply incised contact face (cf.PL). This arrangement is summarized in Fig. 4A. The ventral part of the PL plate is unknown.

One small fragment of the AL plate is also preserved attached to the external surface of the ADL in ANU V1028. Otherwise this bone is unknown, except for the distinctive shape of its dorsal part (AL, Fig. 4A), as indicated by the overlap area on the ADL.

The only other arthrodire specimen from locality UQL 4399 also belonged to a brachythoracid, and is provisionally referred to *Confractamnis* n.gen. ANU V1031 is an incomplete MD plate that lacks most diagnostic characters. However the external surface is largely smooth, with similar texture to the small portion of MD attached to the ADL plate in ANU V1028, which is consistent with it belonging to a smaller individual of the same taxon. The more complete
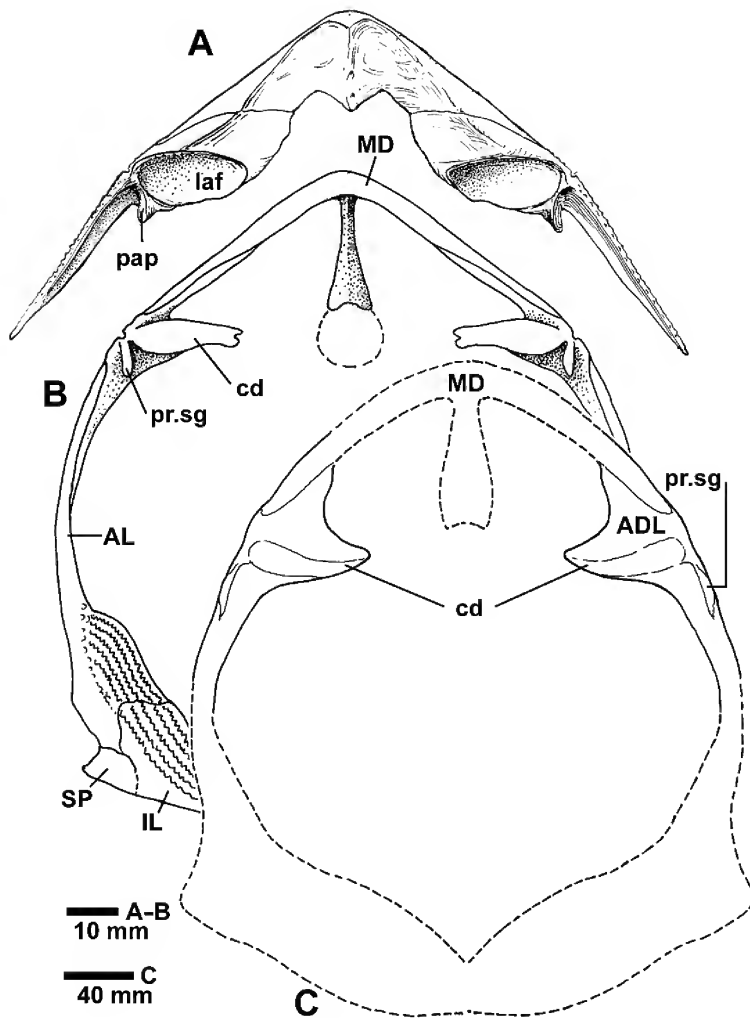
Fig. 5. Brachythoracid trunk armour restorations. (*A,B*) *Taemasosteus* (Early Devonian, Burrinjuck, NSW). (*A*) Posterior view of skull (from White, 1978: fig. 79); (*B*) anterior view of trunk armour, restored from individual bones, using *Harrytoombsia* as a model, as illustrated by Miles & Dennis (1979: fig. 9). (*C*) *Confractamnis johnjelli* n.gen. and n.sp.; trunk armour restoration, anterior view, based on *Taemasosteus* and *Harrytoombsia*.

Reconstruction

Arriving at a reliable three-dimensional reconstruction of the trunk armour of a brachythoracid from isolated bones is difficult. It took over 120 years from the first attempts (Miller, 1841) for a reliable reconstruction of the armour of *Coccosteus* (Miles & Westoll, 1968: fig. 44), this reconstruction depending on earlier attempts for other forms (e.g., *Dunkleosteus* Heintz, 1932: fig. 68; *Homostius* Heintz, 1934: fig. 45).

With the discovery of exceptional three-dimensional preservation in the acid-prepared arthrodires from Gogo, Western Australia, it was possible to check the reliability of such restorations with actual specimens. Trial and error in the Natural History Museum, London, showed that if bones were glued together with a tight fit on the clearly defined overlap areas, the left and right sides did not join up—only by leaving a small space around the edges of bone overlaps could a symmetric reconstruction be achieved (Dr R.S. Miles, pers. comm.). The first illustration of an actual reconstructed specimen from the uniquely preserved Gogo fauna was the holotype of *Harrytoombsia* by Miles & Dennis (1979: fig. 9).

The ADL plate on its own is one of the most informative in attempting a reconstruction from isolated bones, because the axis of articulation on the condyle must have been horizontal for the dermal neck-joint to function in the living animal. This provides some constraint on the cross-sectional shape of the trunk armour, a point first exploited by Heintz (1934: fig. 47) in comparing *Dunkleosteus* with the dorsoventrally compressed armour of *Homostius*. There is, however, always a degree of uncertainty regarding the precise orientation of the axis of articulation, because the condyle in life was invested with articular cartilage, so its true shape is not preserved. Thus, it is possible that the ADL may have been slightly more steeply inclined (implying a higher trunk armour) than depicted in the reconstruction (Fig. 5C), although the preserved angles of the MD plate in ANU V1031 are generally consistent with this reconstruction.

Using the trunk armour in the holotype of *Harrytoombsia* as a model (Miles & Dennis, 1979: fig. 9), the armour of *Confractamnis* n.gen. may have been some 37 cm in height, and over 30 cm across. As there is no control of the width across the articular condyles of the ADL, the armour could have been considerably larger by comparison with *Harrytoombsia* (which has proportionately smaller condyles), but it is unlikely to have been any smaller. Such a fish would have been at least 206 cm long, judging by proportions in *Coccosteus cuspidatus*, where whole animals including the tail are preserved, and total length of the fish is some 5.5 times trunk armour height (see Miles & Westoll, 1968: figs. 44, 48).

Discussion

The trunk armour bones of *Confractamnis* n.gen. just described reveal many characters by which they can be distinguished from other arthrodires. On the ADL plate, the groove for the main lateral line sensory canal (llc, Fig. 4A) crosses the bone close and subparallel to the edge of the overlap for the MD, which is a point of difference to many other brachythoracids. In *Coccosteus* and *Harrytoombsia* (Miles & Westoll, 1968: fig. 30; Miles & Dennis, 1979: fig. 4) there are two branches, the main one passing postero-ventrally across the ADL plate. In *Dunkleosteus* and
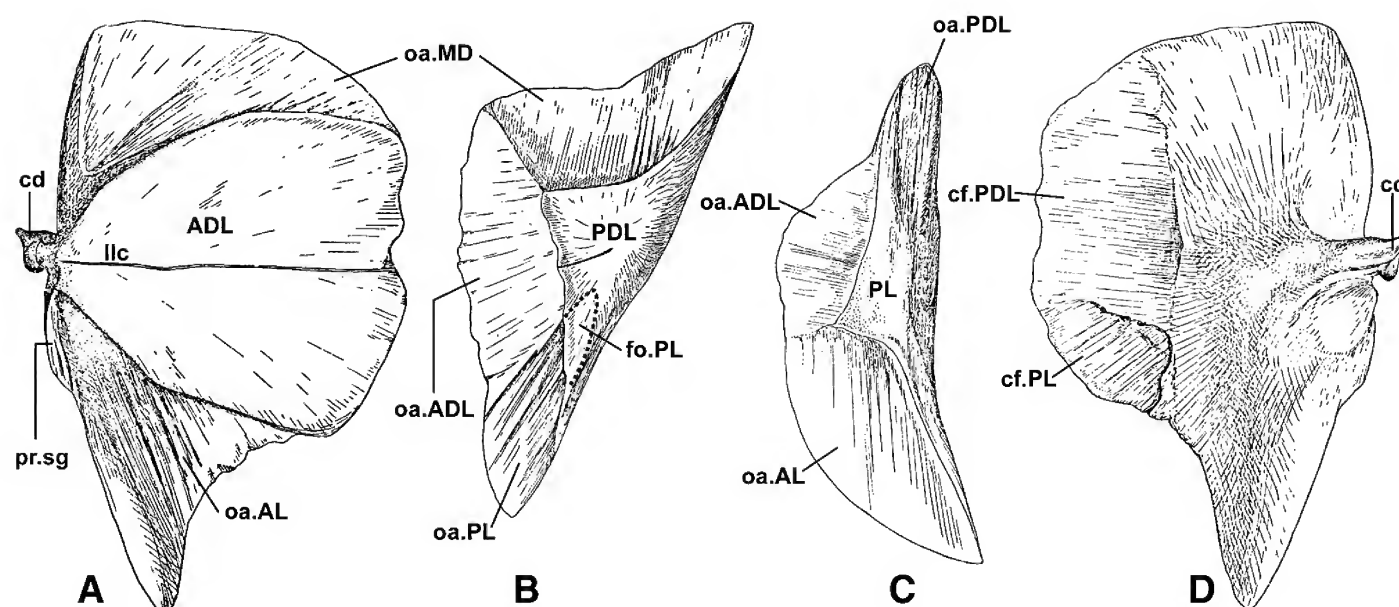
left lamina is gently curved, 95 mm from the midline to the preserved lateral edge, and 50 mm across between broken anterior and posterior margins. As all margins are incomplete, and no contact faces for the ADL and PDL plates can be discerned on the internal surface, there is insufficient information for a reasonable estimate of total length and overall shape. The bone may have been slightly broader than long, consistent with the shape of the MD overlap area on the ADL plate of the holotype (MD, Fig. 4A). This suggests a somewhat angular shape, and a straight to gently curved lateral margin.

The MD plate of ANU V1031 evidently came from an individual only about half the size of the holotype, but the bone reaches about 10 mm thickness close to the midline. The incomplete carinal process is 70 mm long and 50 mm deep as preserved. Its anteroventral edge thins to about 1 mm, and probably not much is missing. The posteroventral edge is expanded to a thickness of about 8 mm, but is incomplete in lacking the knob-like or grooved termination that is normally developed on the carinal process. The angle between the carinal process and the left lamina is about 75°.

Fig. 6. Left trunk armour bones of the Late Devonian brachythoracid *Dunkleosteus*, arranged to show overlap relations (not to scale). (*A,D*) ADL plate in lateral and internal views (reversed images from Heintz, 1932: figs. 46–n>47); (*B*) PDL plate, and (*C*) PL plate, both in external view (from Heintz, 1932: figs. 49, 54).

Eastmanosteus (Heintz, 1932: fig. 46; Dennis-Bryan, 1987: fig. 22A), there is some distance between the groove and the MD overlap, with similar exposed areas of the ADL plate both above and below the groove (Fig. 6A). In *Holonema*, the arrangement is different again, with the straight sensory groove crossing the ADL close to and subparallel with the ventral overlap for the AL plate (Miles, 1971: figs. 62, 63).

The forms most similar to *Confractamnis* n.gen. in the position of the sensory groove are *Taemasosteus* and *Tityosteus* from the Early Devonian (White, 1978: fig. 102; Gross, 1960: fig. 1B), in which it passes straight back from the level of the condyle, running subparallel to the edge of the MD overlap. However the ADL plate in both of these taxa has a triangular ventral overlap area for the AL plate, of similar shape to that of *Dunkleosteus* (Fig. 6A). The large Middle Devonian brachythoracid *Heterostius* also has a dorsally placed sensory groove on the ADL (Denison, 1978: fig. 48B), but in this case the AL plate is reduced to a massive splint of bone fused to the ADL, a unique specialization of this family. The prominently projecting articular condyle in ANU V1028 shows that *Confractamnis* n.gen. could not have had a dorsoventrally compressed armour, thus excluding a close relationship with *Atlantidosteus*, another large arthrodire documented from both Morocco and the Broken River Sequence, and referred to the Homostiidae (Lelièvre, 1984a; Young, 2003a).

Two examples of the ADL plate from the late Emsian of Morocco resemble *Confractamnis* n.gen. in the unusual shape of the AL overlap area. In the holotype of *Antineosteus*, the ADL has a sensory groove that is more ventrally placed with respect to the MD overlap (Lelièvre, 1984b: fig. 16A). The articular condyle in this form is developed completely differently, with an elongate attachment to the front margin of the bone indicating a depressed body form typical of the family Homostiidae. Another left ADL (MCD 62), from the same locality (near Akka), was figured without further comment as "Homostiid sp." by Lelièvre (1984b, pl. 6F–H). It is closely similar to ANU V1028 in the highly angular overlap for the AL, and

the orientation of the sensory groove, which has a straight course, running close to and subparallel with the ventral edge of the overlap for the MD plate (Fig. 4B). This taxon is clearly not conspecific with *Confractamnis* n.gen., since the specimen has much coarser tuberculate ornament, even though it is only about half the size of the ADL plate in the holotype. It also probably differs in having the exposed ornamented part extending ventrally past the edge of the AL overlap (but the corresponding margin is broken in ANU V1028). The articular condyle in the Moroccan specimen (cd, Fig. 4B–D) has a similar pointed mesial end in anterior view to *Confractamnis* n.gen., but is more elongate.

The thickened dorsal attachment of the condyle to the main body of the ADL plate in *Confractamnis* is quite different to that of *Taemasosteus* (Fig. 5), and a range of other brachythoracids where this has been illustrated (e.g., Heintz, 1932: fig. 68, 1934: fig. 45; Lelièvre *et al.*, 1981: figs. 7, 15). The thickenings on the inner surface of the ADL in *Confractamnis* (Fig. 3A) are similarly developed to a much smaller ADL plate belonging to the homostiid *Cavanosteus* from Burrinjuck (Young, 2004c: fig. 6), but it is not clear if this is a general or primitive brachythoracid feature.

The PDL plate of *Confractamnis* n.gen., although incompletely preserved, also demonstrates a distinctive morphology compared to other brachythoracids. Its margins, as indicated by the extent of the contact face inside the ADL, show that the degree of overlap was much more extensive than in forms like *Taemasosteus, Antineosteus* or *Heintz-ichthys* (White, 1978: fig. 105; Lelièvre, 1984b: fig. 16B; Carr, 1991: fig. 6B). *Heintzichthys, Coccosteus* and *Eastmanosteus* have a typical brachythoracid PDL plate of approximately equilateral triangular shape, with three overlap surfaces, essentially as in *Dunkleosteus* (Fig. 6B). An internal fossa for the dorsal corner of the PL plate (fo.PL) was interpreted by Carr (1991: 383) as one of five characters uniting *Eastmanosteus* and *Dunkleosteus* in the family Dinichthyidae, but this is absent in all Emsian-Eifelian brachythoracid taxa known so far.

Only the dorsal part of the PL plate is preserved in *Confractamnis* n.gen., but again it indicates a distinctive

shape. In most other brachythoracids this bone has more equilateral proportions, but with similar overlap relations to surrounding bones. In *Heintzichthys* for example (Carr, 1991: fig. 10), the PL plate overlaps the PDL, and the ADL plate overlaps its anterodorsal part, which is sandwiched between the ADL on the outside, and the overlap surface of the PDL on the inside, essentially as in *Dunkleosteus* (Fig. 5C). Brachythoracids typically show a similar connection dorsally with the PDL plate, which carries a narrow dorsal notch to receive the dorsal angle of the PL, in *Eastmanosteus* and *Dunkleosteus* developed as a fossa (fo.PL, Fig. 6B). In *Antineosteus* the PL is only known from a small narrow dorsal part in the type specimen (H. Lelièvre, pers. comm.), and from its contact face on the PDL plate, which shows a narrow dorsal notch. It is clear that the overlapped area of ANU V1028 was much more extensive, indicating that the PL plate of *Confractamnis* n.gen. was much higher and narrower than in *Antineosteus*. In *Taemasosteus*, as restored by White (1978: figs. 103–105), the PL plate overlaps the PDL, but sits entirely behind, and is not overlapped by, the ADL plate. It therefore has only one ventral overlap area, for the AL plate.

In some derived brachythoracids the PL plate may be much reduced, or completely lost. This was assumed to be the case for *Homostius* by Heintz (1934), until it was recorded (with a SP plate, also assumed to be missing in this taxon) from a new Estonian locality (Karski). The PL of *Homostius*, as described by Mark-Kurik (1993), resembles that of *Confractamnis* n.gen. in its high and narrow shape, but differs in the fact that the external part expands rather than narrows dorsally. It also carries a sensory groove, even though the normal condition in brachythoracids is for the sensory groove to cross the ADL and PDL plates. A shift in the position of the sensory canal may relate to the broad, dorsoventrally compressed body form of *Homostius* (Heintz, 1934: fig. 49).

The MD plate in *Confractamnis* n.gen. is interpreted, mainly from its overlap on the ADL plate of the holotype, to have been slightly broader than long, somewhat angular in shape, and with a straight to gently curved lateral margin. Several other brachythoracids have similar MD plates, including *Homostius* and *Antineosteus* (Heintz, 1934; Lelièvre, 1984b). In *Dunkleosteus, Taemasosteus* and *Tityosteus* the MD plate has a more elongate and rounded lateral profile (Heintz, 1932: fig. 44; White, 1978: fig. 94; Otto, 1992: fig. 6a). The 75° angle between the carinal process and the left lamina is less arched than in *Taemasosteus* (about 50°; White, 1978: fig. 95), but not as flat as in *Homostius* or *Tityosteus* (e.g., Heintz, 1934; Gross, 1960). Krasnov & Mark-Kurik (1982) identified an isolated MD plate from the Emsian of the Minusinsk area of Russia as a new species *Tityosteus orientalis*. This was also less arched than in *Confractamnis* n.gen., with an angle of about 60° between the carinal process and one lamina of the MD.

The attempted reconstruction of the trunk armour of *Confractamnis* n.gen. (Fig. 5C) can be compared with a similar reconstruction of the Emsian form *Taemasosteus* from Burrinjuck, where additional information from the skull roof (White, 1978: fig. 79) provides a constraint on the width between the articular condyles (Fig. 5A–B). Both these taxa may have had bodies with an overall fusiform shape, in contrast to the dorsoventrally compressed shape of *Homostius* and related taxa. However it is possible that relative height of the neck-joint articulation varied, and was carried higher on the armour in *Coccosteus* or *Harrytoombsia*, which may be the reason that the main sensory groove across the external surface of the ADL plate has a characteristic downward course in these taxa, presumably to align with the middle part of the flank as it ran back onto the tail of the fish (cf. Miles, 1971: fig. 108).

Conclusions and summary

The new taxon *Confractamnis* n.gen., from assumed Eifelian strata in the Broken River sequence of Queensland, shows closest affinity amongst known forms to some arthrodire material from the late Emsian of Morocco. This suggests the same distribution pattern as that indicated for the homostiid arthrodire *Atlantidosteus*, represented by two species with a disjunct distribution in the Devonian of Morocco and Queensland (Young, 2003a). Faunal connections, and continuity of shallow tropical to subtropical marine environments along the eastern and northern margins of the Gondwana supercontinent, are indicated by this pattern. On most current reconstructions the northern Gondwana margin had a palaeolatitude between 0–30°S (e.g., Young, 2003b: fig. 2). The only other likely connection (constrained by palaeolatitude) would be across the proto-Pacific Ocean, assuming this large ocean existed in the early-middle Palaeozoic (cf. Nur & Ben-Avraham, 1981). An alternative proposal, based on the evidence of Devonian fish distributions, is that palaeogeographic change during the middle Palaeozoic involved increasing proximity between Gondwana and Laurussia (Euramerica), with first shallow marine, and then non-marine fish dispersal between the two continental blocks during the Middle and Late Devonian (Young et al., 2000a,b; Young & Moody, 2002; Young, 2003b).

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Amphipods of the Genera
Ceradocus, Dulichiella, Melita and *Nuuanu*
(Crustacea: Melitidae)
from Mauritius, Indian Ocean

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ABSTRACT. Taxonomic descriptions and figures are provided for five new species of Melitidae (*Ceradocus greeni* n.sp., *Dulichiella cuvettensis* n.sp., *Melita corticis* n.sp. *Melita setimera* n.sp. and *Nuuanu rectimana* n.sp.) from collections made in the shallow coastal waters of Mauritius.

In the current study a new species of *Ceradocus, C. greeni* n.sp. is described, bringing the number of species of the genus known from Mauritius to three. The two other species, *C. hawaiensis* J.L Barnard (1955) and *C. mahafalensis* var. *incisa* Ledoyer (1978), were reported by Ledoyer (1978). A new species of *Dulichiella, D. cuvettensis* n.sp. is recognized, previously wrongly ascribed to *D. appendiculata* (Say, 1818) by Ledoyer (1978) as well as by Appadoo & Steele (1998) and *Nuuanu rectimana* n.sp. is described bringing the number of species of this genus known from the island to two, the other being *Nuuanu amikai* J.L. Barnard, reported by Ledoyer (1978). Only one species of the genus *Melita* was previously recorded from Mauritius, *Melita zeylanica* (Appadoo & Steele, 1998), here attributed to a new species, *Melita corticis* n.sp. A second new species *Melita setimera* n.sp. is now known.

Material and methods

Amphipods were collected from algae, seagrass and coral rubble from 24 sites around the island of Mauritius (19°59'–20°32'S 57°18'–57°47'E, Indian Ocean) and from Ile D'Ambre (20°01'–20°02.2'S 57°41'–57°42.2'E), a small island on the northeast coast within the lagoon from February 1998 to February 2000. The sites were visited at low tide and samples were collected from the intertidal and shallow subtidal zones. Algae and rubble were collected by scraping them off their substrates using a small hand trowel. Amphipods were extracted using the formalin-wash method as formalin is an irritant that causes the animals to release hold of the substrates (Barnard, 1976).

Some of the substrates were also collected by snorkelling and diving from depths not exceeding 2 to 3 m. The

substrates were then transferred to a plastic bag as soon as they were scraped off and amphipods were extracted using the above mentioned method once on shore.

Prior to dissection the body length of amphipods was recorded by holding it straight and measuring the distance along the dorsal side of the body from the base of the first antennae to the base of the telson. A stereomicroscope with a micrometer scaled eyepiece was used to take the measurement. Drawings were made using a Nikon compound microscope equipped drawing tube attachment. Type material is deposited in the Australian Museum (AM). All other material is kept in the first author's collection. The terminology for cuticular extensions and setae follows that of Watling (1989). Geo-spatial coordinates were read from a map of scale 1:25 000.

Abbreviations used in figures. A, Antenna (1–2); C, Coxa; D, Dactylus (3–7); Ep, Epimeron; G, Gnathopod (1–2); L, Lower lip; Md, Mandible; Mx, Maxilla (1–2); Mxp, Maxilliped; P, Pereopod (3–7); Pl, Pleonite (1–3); p, palp; T, Telson; U, Uropods (1–3); lt, left; r, right.

Fig. 1. *Ceradocus greeni* n.sp., male, 6.2 mm, female, 4.9 mm, AM P60866, Flic-en-Flac. Scales: a = 1 mm (whole animal), b = 0.2 mm (U1, U2 and U3), c = 0.2 mm (female G1 and G2), d = 0.1 mm (T), e = 0.05 mm (outer margin of U2).

Taxonomic section

Ceradocus (Denticeradocus) greeni n.sp.

Figs. 1–3

Ceradocus sp. 1 Appadoo & Steele 1998: 639.

Type material. HOLOTYPE ♂, 5.2 mm, AM P60865, at depths of 0.5–2 m living on coral rubble and *Pocockiella variegata*, Flic-en-Flac (20°16.5'S 57°21.7'E), Mauritius, C. Appadoo, 9 November 1998. PARATYPES: 2♂♂, 2♀♀, AM P60866, same data as holotype; 1♀ from
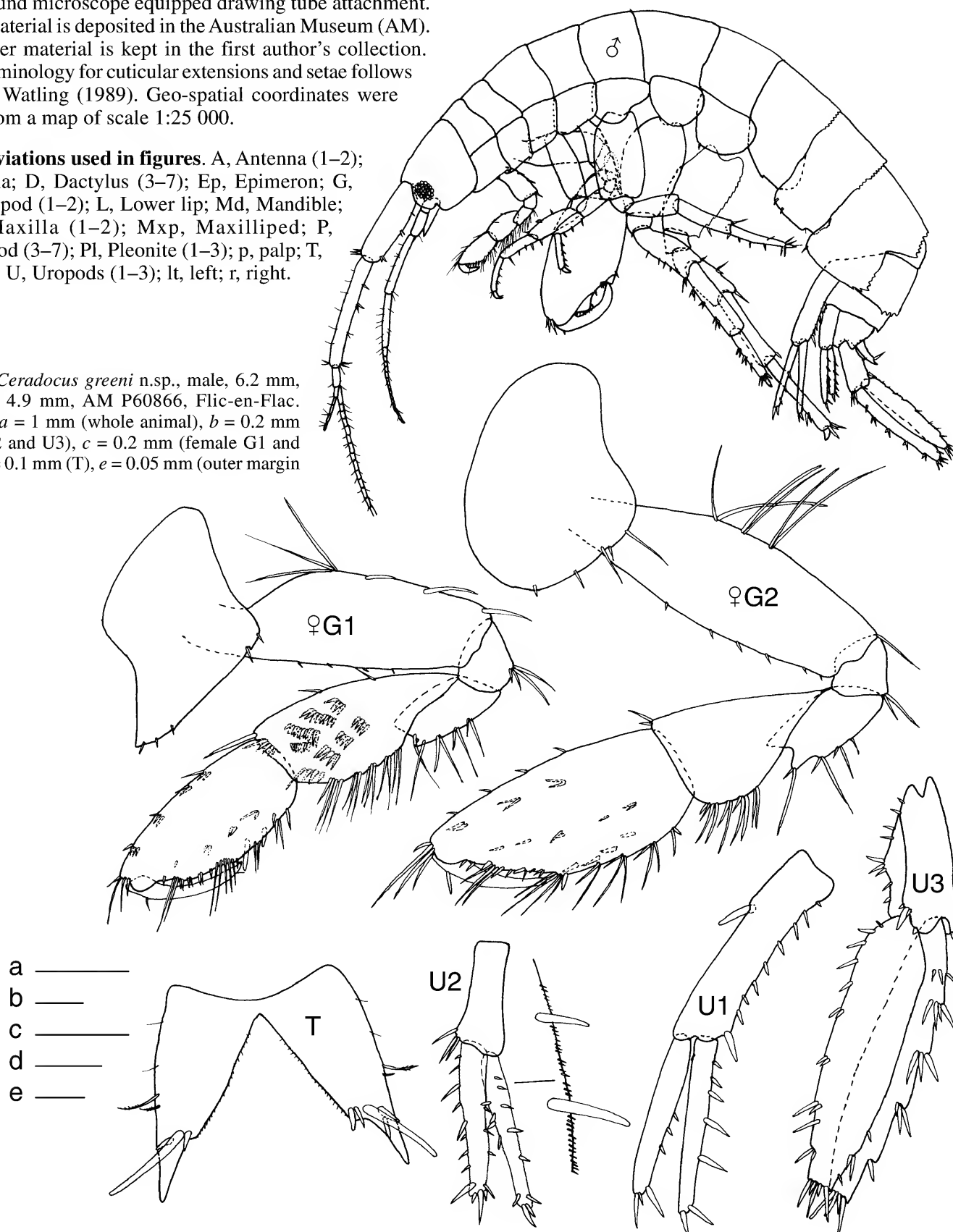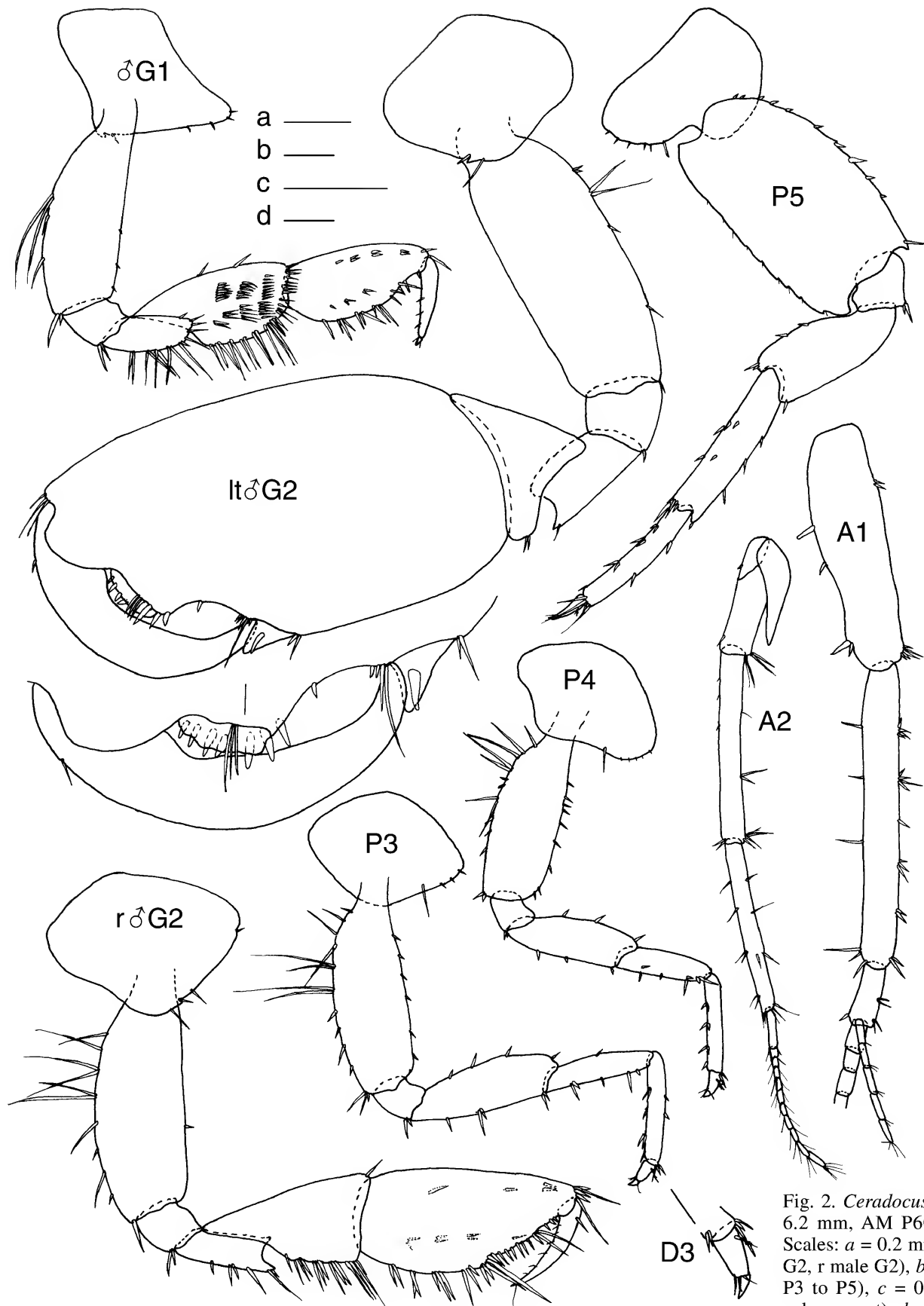
Fig. 2. *Ceradocus greeni* n.sp., male, 6.2 mm, AM P60866, Flic-en-Flac. Scales: *a* = 0.2 mm (male G1, lt male G2, r male G2), *b* = 0.2 mm (A1, A2, P3 to P5), *c* = 0.1 mm (lt male G2 enlargement), *d* = 0.1 mm (D3).

coral rubble and *Pocockiella variegata*, Flic-en-Flac, 3 March 1998; 1 juv. from coral rubble and *Pocockiella variegata*, Flic-en-Flac, 9 November 1998; 1♂, 4♀♀, 2 juv. from coral rubble, *Padina* sp. and *Pocockiella variegata*, Flic-en-Flac, 5 April 1999; 7♂♂, 5♀♀ from coral rubble, *Padina* and *Pocockiella variegata*, Flic-en-Flac, 10 December 1999; 3♂♂, 3♀♀, 1 juv. from coral rubble, *Padina* sp., *Pocockiella variegata* and *Turbinaria ornata*, Flic-en-Flac, 27 January 2000.

Description. Male length, 6.2 mm. Head with subocular notch; eyes round with discrete ommatidia. Antenna 1

peduncle article 1 with stout robust setae on posterior margin; article 2 longer than 1; article 3, 0.3× article 1; accessory flagellum 5-articulate; primary flagellum 14-articulate. Antenna 2 peduncle 3× as long as flagellum; gland cone of article 2 extending to 0.7× the length of article 3; article 4 slightly longer than article 5; flagellum 11-articulate. Mandible palp 3-articulate, article 1 with medial cusp, article 2 longest and 2.5× article 1, with long setae on
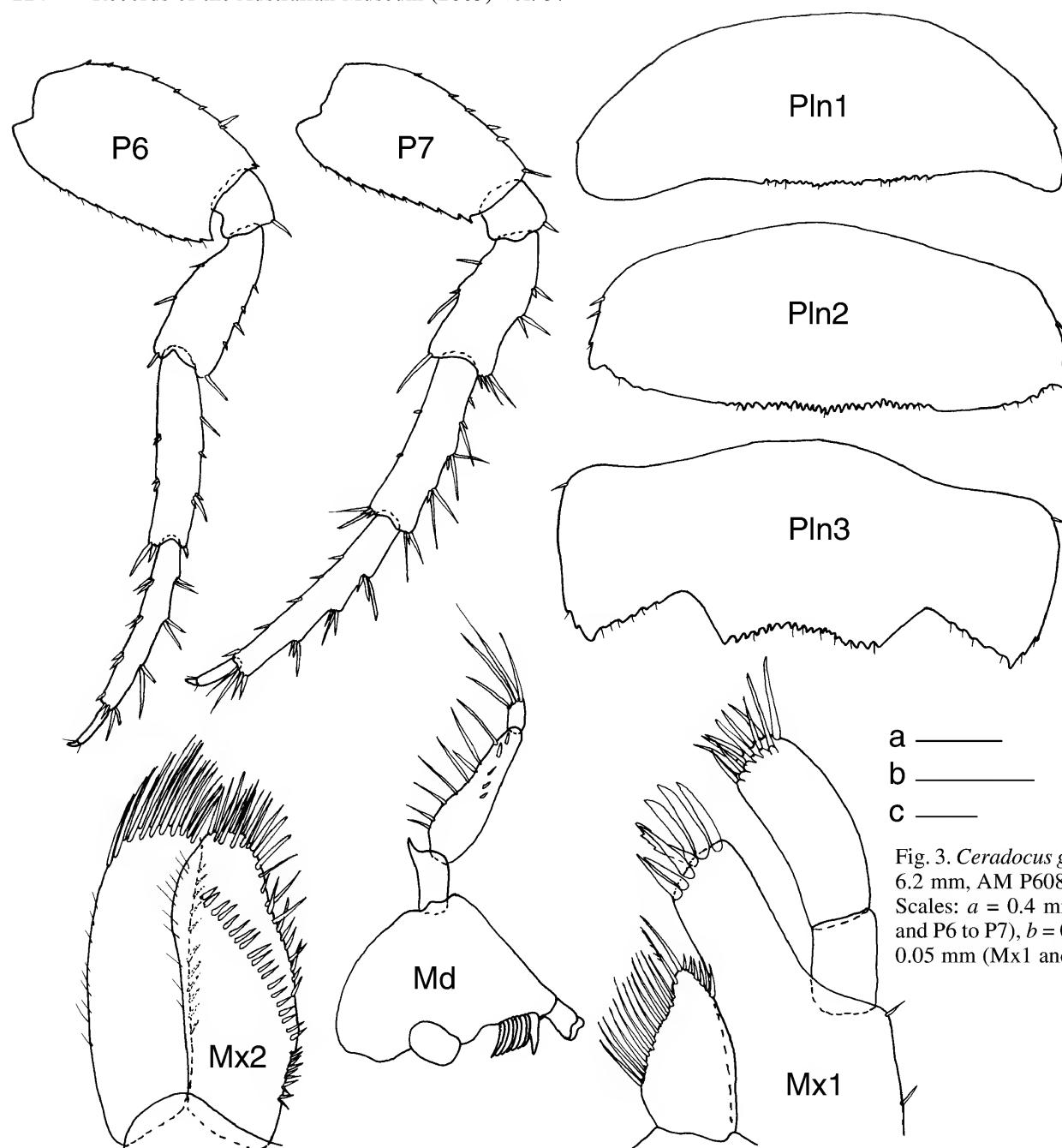
Fig. 3. *Ceradocus greeni* n.sp., male, 6.2 mm, AM P60866, Flic-en-Flac. Scales: *a* = 0.4 mm (Pln1 to Pln 3 and P6 to P7), *b* = 0.2 mm (Md), *c* = 0.05 mm (Mx1 and Mx2).

lateral margins and short setae on medial face, article 3 shortest and 0.6× the length of article 1. Maxilla 1 inner plate triangular with plumose setae; outer plate with terminal serrated robust setae; palp 2-articulate with double-row of terminal setae. Maxilla 2 outer plate with distal setae, inner plate with distal setae, inner marginal setae and an oblique row of setae. Lower lip with rounded mandibular lobes. Maxilliped palp 4-articulate, article 2 longest and 2.2× article 1. Gnathopod 1 coxa 1.3× as long as broad, anterodistal margin produced into a lobe, posterodistal margin notched; basis slender, slightly less than three times as long as broad, anterior margin with short robust setae, posterior margin with long setae; carpus with groups of medial setae, anterior margin sparsely setiferous, posterior margin densely setose; propodus subequal in length to carpus with a few medial patches of setae, palmar margin oblique with short setae; dactylus with short setae on inner margin. Gnathopod 2 asymmetrical. Small gnathopod 2 (left or right) coxa subrectangular, slightly longer than broad, distal margin with a notch and a few setae; basis 2.5× as long as broad, posterior margin with strong patches of setae;

merus anteroventral and posterodistal corners sharply produced; propodus 2× as long as broad, 1.3× carpus, palm oblique with short robust setae and a few groups of long setae; dactylus slender, inner margin with short setae. Large gnathopod 2 (left or right) coxa subrectangular, ventral margin notched and with 2 setae; basis 2.5× as long as broad; merus posterodistal corner sharply produced; carpus triangular, slightly more than 1.5× as broad as long; propodus robust, slightly over 1.5–1.75× as long as broad, palm oblique, distal margin with a process close to base of dactylus with stout robust setae followed by an excavation and a triangular process with fine setae and robust setae at the posterodistal margin; dactylus robust and fitting into the triangular process of propodus. Pereopod 3 coxa subrectangular, almost as broad as long, ventral margin with 1 long seta and a few short-setae at the anteroventral corner; basis slender with short robust setae on anterior margin and groups of long setae on posterior margin; propodus subequal to carpus; dactylus with a distinct unguis and anterior margin with one plumose seta and posterior margin with 3 setae. Pereopod 4 coxa posteriorly excavate, 0.7× as long as broad

with one long seta and a few short setae on the anterodistal corner, other features similar to pereopod 3. Pereopod 5 slender, coxa bilobed; basis 1.8× times as long as broad, anterodistal and posterodistal margins sharply produced, anterior margin with robust setae, posterior margin weakly serrated and with small setae; propodus subequal to carpus; dactylus slender. Pereopod 6 slender; basis similar to that of pereopod 5, but posterior margin more deeply serrated; propodus subequal to carpus, anterior margin with strong patches of setae; dactylus slender and similar to that of pereopod 5. Pereopod 7 similar to pereopod 6, but basis is distally less produced and narrower than basis of pereopod 6; propodus slightly longer than carpus. Pleonites 1–3 strongly toothed. Epimeron 2 with one tooth on posterodistal margin and a few irregular teeth on distal margin. Epimeron 3 with 2 teeth on posterodistal margin and 5 teeth on distal margin. Urosomite 1 and 2 each with 7 dorsal teeth. Uropod 1 peduncle, 1.3× outer ramus with a stout robust seta on medial outer margin; outer ramus slightly shorter than inner ramus. Uropod 2 peduncle 0.7× inner ramus; inner and outer rami subequal, armed with robust setae, margins of rami with very short fine robust setae. Uropod 3 peduncle inner margin with numerous robust setae; rami spatulate, equal in length to each other, twice as long as peduncle; outer ramus outer margin with long robust setae; inner ramus outer margin with numerous robust setae; rami with stout terminal robust setae. Telson deeply cleft; telsonic lobes well separated, with a pair of plumose setae on outer margin, notched at apex, with outer tooth produced and inner tooth vestigial, apices with one long and a few short setae.

Female: length, 4.9 mm. Gnathopod 1 coxa 1.2× as long as broad, anterodistal margin produced, posterodistal margin with a notch; basis slender, posterior margin with long setae, anterior margin with short robust setae; merus produced at posterodistal corner; carpus subequal to propodus with groups of medial setae, ventral margin setose; propodus 2.3× as long as broad, anterior margin with 5 groups of setae, palm oblique with fine setae and short robust setae and stout robust setae on medial face. Gnathopod 2 coxa 1.2× as long as broad, distal margin with a notch and a few setae; basis 3.1× as long as broad, anterior margin with robust setae, posterior margin with groups of long setae; carpus 0.75× length of propodus; propodus 2.2× as long as broad, palm with short robust setae and patches of fine setae, with stout robust setae on inner medial face.

Habitat. In the subtidal at depths of 0.5 to 2 m, occurring mostly on coral rubble and the associated brown alga, *Pocockiella variegata*.

Remarks. *Ceradocus greeni* n.sp. is assigned to the subgenus *Denticeradocus* because pleonites 1–3 are multidentate dorsally. This species is distinguished from *Ceradocus hawaiensis* J.L. Barnard (1955) recorded from Mauritius by Ledoyer (1978), by having the larger male gnathopod 2 with an oblique palm lacking many tooth-like processes. The species differs from *Ceradocus mahafalensis* Ledoyer (1978) var. *incisa*, reported from Mauritius, which also has an oblique palm in the larger male gnathopod 2, by the broadly sinuous palmar border, with a distal process with robust setae as opposed to a palmar margin with a deep medial incision. Urosomites 1 and 2 each have 7 teeth in *Ceradocus greeni* n.sp. instead of 5 and 4 respectively in *Ceradocus mahafalensis* var. *incisa* and *C. mahafalensis*

from Madagascar (Ledoyer, 1979).

Ceradocus greeni shares with *C. spiniferus* Ledoyer (1973), *C. tattersalli* Ledoyer (1982) and *C. serratus* (Bate, 1862), the multidentate pleonites and oblique palm in the large male gnathopod 2. However, the shape of the larger gnathopod 2 propodus palm separates it from these three species. *Ceradocus serratus* lacks the smooth excavation and the triangular process, *C. spiniferus* has a convex palmar margin and a small U-shaped excavation and *C. tattersalli* lacks the triangular process and has a palm with numerous robust setae.

Two other species of *Ceradocus* with multidentate pleonites 1–3 and oblique palm in the male gnathopod 2 are *Ceradocus (Denticeradocus) oxydus* Berents (1983) and *Ceradocus (Denticeradocus) yandala* Berents (1983). The shape of the large male gnathopod 2 is the distinguishing feature. *Ceradocus oxydus* lacks an excavation in the palmar margin which is convex with numerous robust setae. *Ceradocus greeni* differs from *C. yandala* by having a gentle excavation on the male gnathopod 2 without any mid-palmar sinus, *C. yandala* has a quadrate mid-palmar sinus.

Type locality. Flic-en-Flac, Mauritius.

Distribution. Mauritius.

Etymology. This species is named after Prof. John Green of Memorial University of Newfoundland for his help in the field to one of authors (CA) during an initial study on amphipods from Mauritius in 1995.

Dulichiella cuvettensis n.sp.

Fig. 4

Melita appendiculata.–Ledoyer, 1978: 282; Appadoo & Steele, 1998: 639. (Not *Gammarus appendiculatus* Say, 1818: 377–379).

Type material. HOLOTYPE ♂, 3.3 mm, AM P67233, from *Sargassum* sp. at depth less than 1 m, La Cuvette (20°00'S 57°34.2'E), Mauritius, C. Appadoo, 12 October 1999. PARATYPES: 1♂, 1♀, from *Sargassum* sp., La Cuvette (20°00'S 57°34.2'E), 14 May 1998. 1♀ from *Turbinaria* sp., Bain Boeuf (19°59'S 57°36'E), 15 May 1998; 1♂, 3♀♀ from *Acanthophora spicifera*, Anse la Raie (19°59.5'S 57°37.5'E), 15 May 1998; 5♂♂, 3♀♀ and 4 juv. from *Sargassum binderi*, Bain Boeuf, 16 June 1998; 1♂, 2♀♀ from *Sargassum* sp. and *Padina* sp., Ile D'Ambre (20°02'S 57°40'E), 12 November 1998; 1♂ from *Sargassum* sp. and *Ulva reticulata*, La Cuvette, 5 May 1999; 1♂ from *Padina* sp. and *Halimeda* sp., Grand Baie (20°0.5'S 57°34'E), 5 May 1999; 1♂, 1♀, from mixture of *Padina* sp., *Pocockiella variegata* and *Sargassum* sp., Bain Boeuf; 2♂♂ and 1♀, AM P67234, from *Sargassum* sp. and *Pocockiella variegata*, Bain Boeuf, 12 October 1999.

Description. Male length, 4 mm. Head without subocular notch; eyes round with well-developed ommatidia. Antenna 1 poorly setiferous, peduncle article 1 with 3 stout robust setae on ventral margin; article 2 longest, 1.5× article 1; article 3, 0.3× the length of article 1; accessory flagellum 4-articulate, primary flagellum 35-articulate. Antenna 2 weakly setiferous, peduncular article 4 subequal to 5, flagellum 14-articulate. Mandible palp slender, article 1 with a small tooth; article 3 slightly longer than article 2. Maxilla 1 palp, article 1 with long setae on distal margin; inner plate with 2 apical plumose setae. Gnathopod 1 coxa 1.6× as long as broad, posterodistal margin with a notch; basis slender, 4× as long as broad; propodus slightly 0.7× length of carpus, palmar margin with short and long setae; dactylus normal. Gnathopods 2 dissimilar (left and right). Larger gnathopod
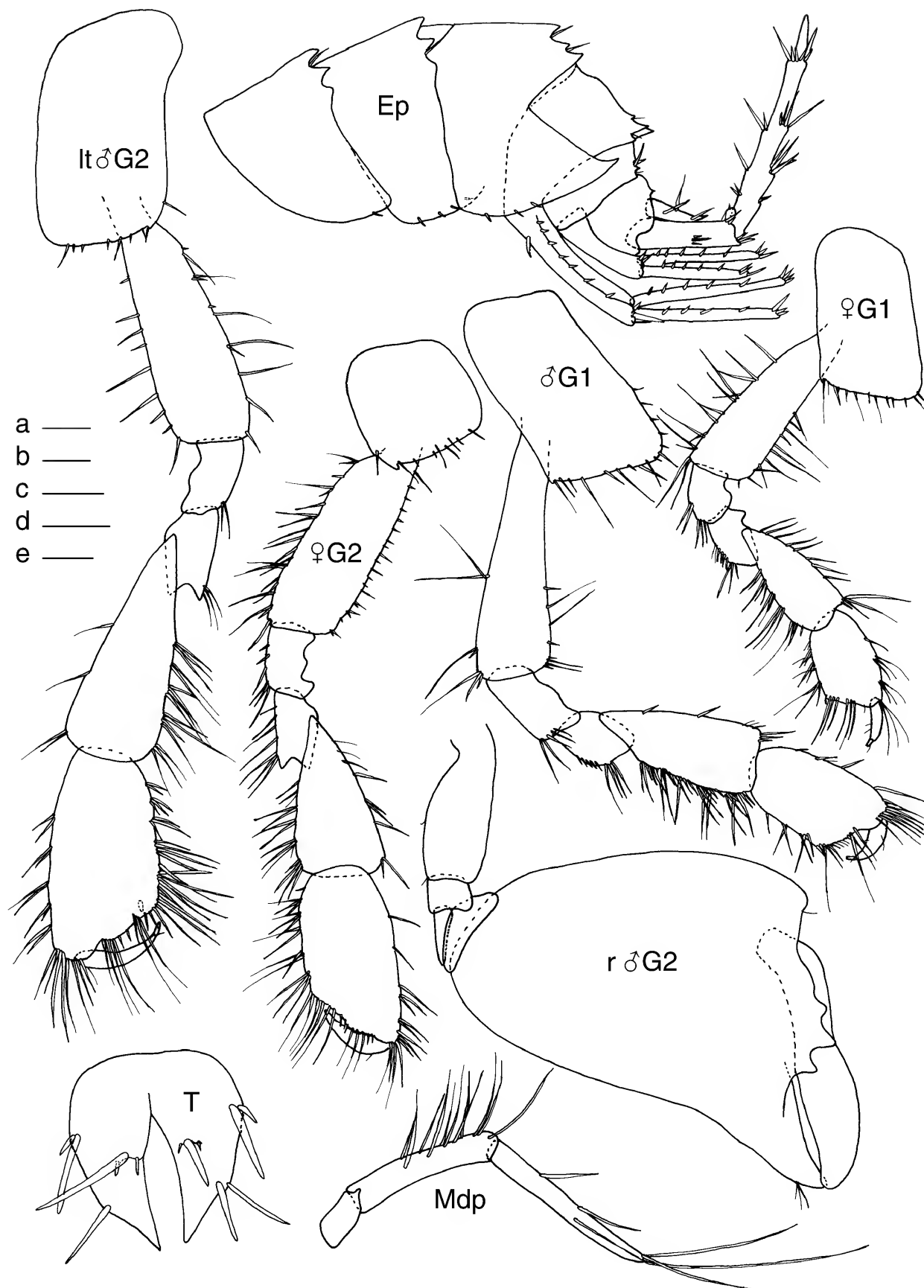
Fig. 4. *Dulichiella cuvettensis* n.sp., male, 4 mm, female, 4.8 mm, La Cuvette. Scales: *a* = 0.2 mm (Ep and r male G2), *b* = 0.1 mm (male G1 and lt male G2), *c* = 0.2 mm (female G1 and G2), *d* = 0.1 mm (T), *e* = 0.05 mm (Mdp).

2 basis without setae, and 2.3× as long as broad; carpus reduced, 3.3× as long as broad; propodus robust, distally expanded, palmar margin transverse, with 3 well-developed medial protuberances; dactylus broad throughout its length. Small gnathopod 2, coxa slightly less than 2× as long as broad, distal margin with short setae; basis slender, 3.5× as long as broad, with setae on anterior and posterior margins; merus posterodistal margin acute; propodus slightly shorter than carpus, subrectangular, palm oblique, dactylus fitting palm. Pereopod 3 coxa subrectangular with a small notch on posterodistal margin; basis anterior margin with stout short setae; propodus 1.5× length of carpus; dactylus with

bifid tip. Pereopod 4 similar to pereopod 3, but coxa without posterodistal notch and weakly excavate posteriorly. Pereopod 5 basis subrectangular, slightly more than 2× as long as broad, anterior and posterior margins parallel, anterior margin with numerous robust setae, posterior margin weakly serrated with short setae; dactylus bifid. Pereopod 6 similar to pereopod 5 but basis more slender; merus and propodus with strong groups of setae on anterior and posterior margins. Pereopod 7 basis anterior margin straight, posterior margin slightly convex; other features similar to pereopod 6. Pleonites 1 and 2 with 7 teeth, median tooth and the last tooth on either side shorter than others. Pleonite 3 with 7 teeth, median tooth small, other teeth on either side of this median tooth are successively longer than one another. The concavities of the teeth of pleonites have small setae. Urosomite 1 produced into acute teeth on dorsal surface. Urosomite 2 with a small robust seta and small tooth on dorsal surface. Urosomite 3 with a small dorsal tooth. Epimeron 1 with one robust seta on distal margin, posterodistal margin rounded. Epimeron 2 posterodistal margin slightly produced, posterior margin smooth, distal margin bears 3 robust setae. Epimeron 3 posterodistal margin produced into an acute tooth, posterior margin with a very small tooth, distal margin with three robust setae. Uropod 1 slender, with robust setae, rami subequal to each other and slightly longer than peduncle; inner margin of inner ramus with very fine short setae. Uropod 2 outer ramus slightly shorter than inner ramus; peduncle 0.75× inner ramus; inner margin of inner ramus similar to that of uropod 1. Uropod 3 outer ramus 1.8× peduncle, 2-articulate, article 1 truncate, article 2 pointed; inner ramus vestigial consisting of a small oval lobe with one robust seta. Telson cleft to about three-quarter its length, telsonic lobes produced at apex. Telson with three groups of robust setae, located subapically and medially on inner and outer margins.

Female: length, 4.8 mm (mature, with eggs). Gnathopod 1 coxa 0.75× as long as broad, posterodistal margin with notch and setae; basis with setae on anterior and posterior margins; merus with a triangular process at anterodistal margin; propodus palm oblique, palm with long setae. Gnathopod 2 coxa subrectangular about as long as broad; basis anterior and posterior margins setose; ischium anterior margin sinuous; propodus slightly longer than carpus, palm oblique with setae on margins.

Remarks. *Dulichiella cuvettensis* n.sp. differs from *D. appendiculata* (Say, 1818) in having epimeron 1 with a smoothly rounded posteroventral margin (rather than with a small acute spine) and the propodus disto-lateral margin with three (as apposed to two) subacute teeth. *Dulichiella cuvettensis* n.sp. is most similar to *D. australis* (Haswell, 1879) but differs from that species in the strongly setose uropod 3 outer ramus as well as in the rounded postero-ventral corner of epimeron 1.

Habitat. This species was collected in depths of less than 1 m. It occurs mostly on brown algae especially *Sargassum* sp. and was collected from sites on the north coast of the island.

Type locality. La Cuvette, Mauritius.

Distribution. Mauritius.

Etymology. Named after the type locality.

Melita corticis n.sp.

Figs. 5–6

Melita zeylanica Appadoo & Steele, 1998: 639.

Type material. HOLOTYPE ♂, 4.3 mm, AM P60867, 0–1 m depth, living on a mixture of *Ulva lactuca* and *Ulva reticulata*, le Bouchon (20°28'S 57°40.5'E), C. Appadoo, 27 October 1998. PARATYPES: 1♂, 3♀♀, AM P60868, same data as holotype; 2♂♂, 16♀♀, and 10 juv. from *Ulva lactuca* and *Ulva reticulata*, Le Bouchon, 16 May 1998; 2♂♂, 2♀♀, 3 juv. from *Ulva lactuca* and *Ulva reticulata*, Le Bouchon, 27 October 1998.

Description. Male length, 6.2 mm. Head with subocular notch, eyes round, a ring of clear ommatidia surrounding a dark central core. Antenna 1 weakly setiferous, article 2, 1.3× article 1, article 3, 0.5× article 1; accessory flagellum 3-articulate; primary flagellum 16-articulate (possibly regenerating in this specimen), flagellum can be 27-articulate (observed from additional material). Antenna 2 weakly setiferous, peduncular article 5 subequal to 4, flagellum 8-articulate. Mandible palp article 3 slightly longer than 2, article 1, 0.3× article 3; article 2 with two groups of setae on posterior margin, article 3 with a few lateral and terminal setae. Maxilla 1 inner plate with 8 plumose apical setae; Lower lip with rounded mandibular lobes. Gnathopod 1 coxa 1.4× as long as broad with short setae on ventral margin; basis 3× as long as broad with a strong patch of setae on anterodistal margin; carpus 1.5× length of propodus; propodus with transverse palm and forming a hood above dactylus; dactylus with medial protrusion on posterior margin. Gnathopod 2 coxa subrectangular 1.5× as long as broad, with setae on distal margin; basis 2.9× as long as broad, with a few groups of long setae on anterior margin; merus slightly produced ventrodistally; carpus 1.2× as broad as long; propodus subrectangular, 1.6× as long as broad, palmar margin weakly convex, palm rounded, with short stout setae and slender setae; dactylus broad throughout its length and slightly tapered at tip and closing across inner face of propodus. Pereopod 3 coxa subrectangular, 1.6× as long as broad, with very short setae on ventral margin; propodus and carpus subequal; dactylus with distal unguis. Pereopod 4 coxa deeply excavate posteriorly; other features similar to pereopod 3. Pereopod 5 coxa about 1.2× as long as broad, anterior margin with robust setae, posterior margin weakly serrated with short setae; dactylus short and robust with terminal unguis. Pereopod 6 coxa lobular; basis subovate, 1.4× as long as broad, anterior margin with stout setae, posterior margin serrated with stout setae; propodus 2× length of carpus; other features similar to pereopod 5. Pereopod 7 basis, 1.3× as long as broad, anterior margin with numerous robust setae, posterior margin more convex and weakly serrated; other features similar to pereopod 6. Epimera 2 and 3 posterior margin weakly serrated, distal margins with a few stout setae. Urosomite 1 smooth. Urosomite 2 with two stout robust setae on each side. Uropods 1–2, rami subequal to each other and shorter than peduncle. Uropod 3 inner ramus rudimentary, with one robust seta; outer ramus 1-articulate, spatulate, 2.5× the length of peduncle, with robust setae and slender setae. Telson cleft to base, lobes with pointed apex; each lobe with two robust setae on distal inner margins and one on the outer margin; 1 or 2 robust setae present about half-way along inner margin.
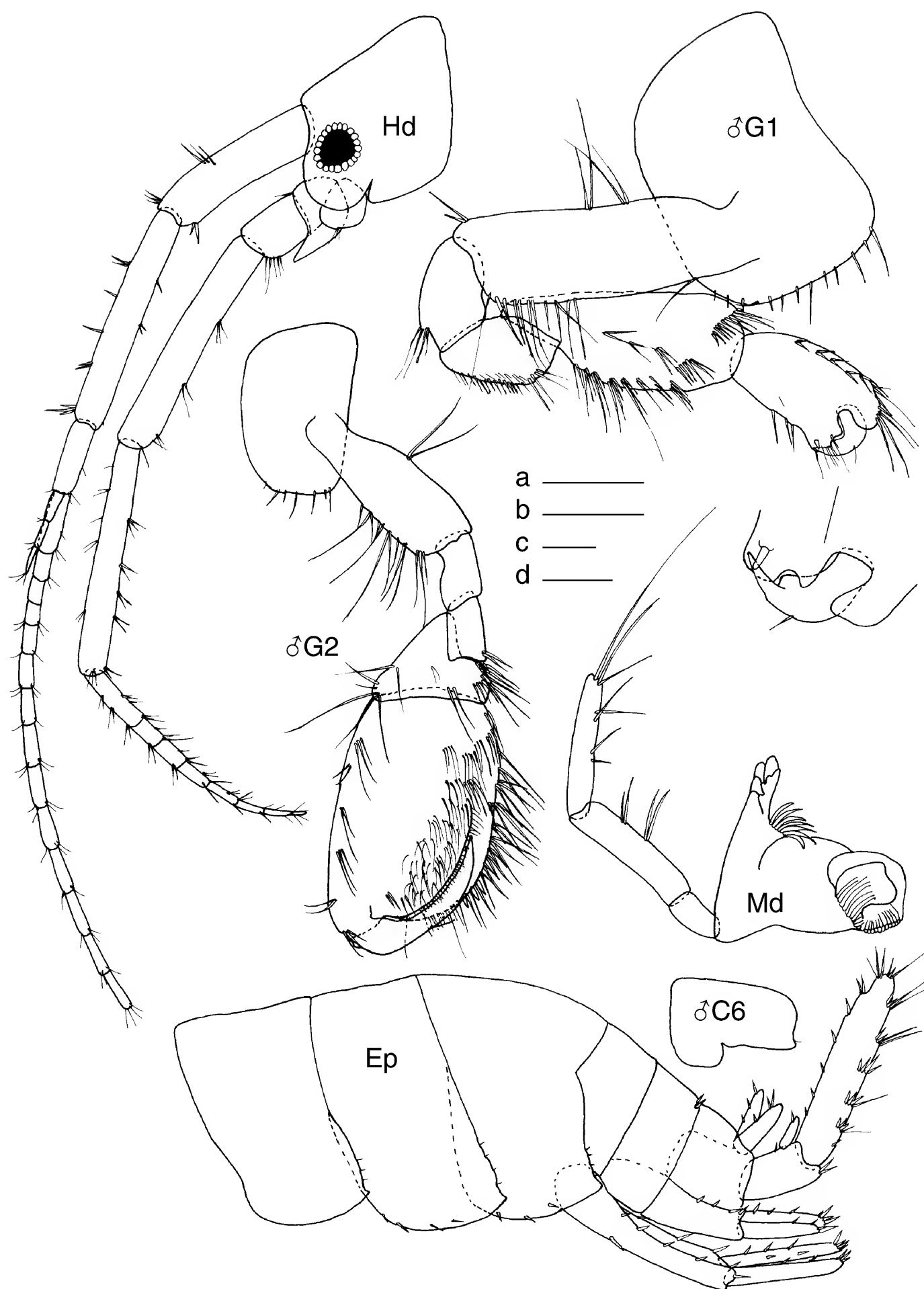
Fig. 5. *Melita corticis* n.sp., male, 6.2 mm, AM P60868, Le Bouchon. Scales: *a* = 0.4 mm (Hd, Ep, male G2, male C6), *b* = 0.2 mm (male G1, enlargement of male G2), *c* = 0.05 mm (enlargement of male G1), *d* = 0.1 mm (Mdp).
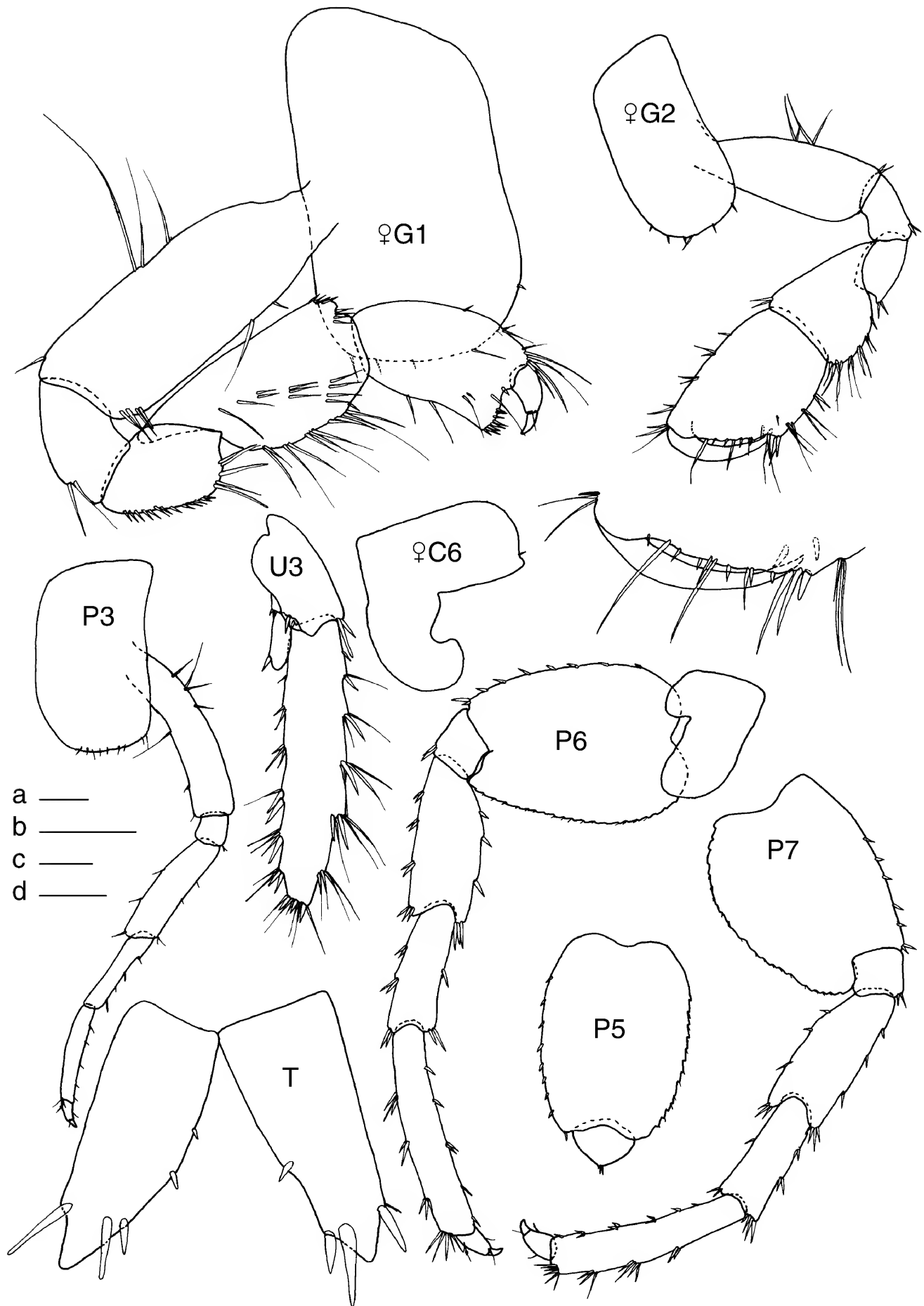
Fig. 6. *Melita corticis* n.sp., male, 6.2 mm, female, 3.3 mm, AM P60868, Le Bouchon. Scales: *a* = 0.2 mm (P3 and P5-P7), *b* = 0.2 mm (female G2 and female C6), *c* = 0.05 mm (female G1 and T), *d* = 0.2 mm (U3).

Table 1. The character states in the *Melita zeylanica* group of species.

	Antenna 2	Gnathopod 1 (male) dactylus proximal process	Gnathopod 2 carpus	U1 peduncle basofacial robust seta	U3 inner ramus terminal robust setae	Urosomite 2 dorsal robust setae
M. zeylanica Stebbing, 1904	weakly setose	not swollen	compressed	absent	1	4–6
M. zeylanica kauerti Barnard, 1972	weakly setose	swollen	not compressed	present	3–4	6
M. setiflagella Yamato, 1988	densely setose	swollen	not compressed	present	3	6
M. corticis n.sp.	weakly setose	swollen	not compressed	present	1	4

Female: length, 3.3 mm (mature with eggs). Gnathopod 1 coxa subrectangular, 1.6× as long as broad; basis about three times as long as broad; carpus 1.3× length of propodus; propodus palm transverse, palmar margin with short setae; dactylus large at base and tapered at tip. Gnathopod 2, coxa 2× as long as broad; propodus subrectangular, 1.3× length of carpus with stout setae and slender setae on palm. Pereopod 6, coxa with a large hook-like anterior lobe.

Remarks. The present material falls into the group of *Melita* that lacks a second article on the outer ramus of uropod 3 (see Ledoyer, 1982: 568). It resembles *M. pahuwai* Barnard (1970) from Hawaii in having only one robust seta instead of 3 in the inner face of male gnathopod 1 propodus; in having the robust setae on the palmar margin of the female gnathopod 2 shorter than the inner facial robust setae rather than vice-versa and in lacking robust setae on the proximal outer margins of the telson.

It appears to be particularly closely related to *Melita zeylanica* Stebbing, 1904, *M. zeylanica kauerti* J.L. Barnard 1972 and *M. setiflagella* Yamato 1988.

It can be distinguished from *M. setiflagella* Yamato (1988) by the well-developed circular eyes (smaller, slightly reniform eyes in *M. setiflagella*) by antenna 2 peduncular articles 5 and 4 being subequal (peduncular article 5 shorter than 4 in *M. setiflagella*) by antenna 2 being poorly setiferous and 8-articulate (densely setiferous and 15-articulate in *M. setiflagella*), and by female coxa 6 being without scale-like denticles.

It differs from *Melita zeylanica* Stebbing (1904) in the presence of an anterodistal bulge near the base of the dactylus in the male gnathopod, in the non-compressed carpus of the gnathopod 2 in females, and in the presence of a robust basofacial seta on the peduncle of uropod 1, the latter feature, however, may have been overlooked by Stebbing (1904). Unlike *Melita zeylanica kauerti* Barnard (1972: 235, fig. 139–140) it has 2 (rather than 3) dorsolateral robust setae on urosomite 2 and one (rather than four) robust seta in the apex of the inner ramus of uropod 3. Barnard (1972) notes that Sri Lankan material of *Melita zeylanica* has one robust seta on uropod 3 inner ramus as in present material.

These four species form a group of related forms. The current material compares most closely with *Melita zeylanica kauerti* but that species is closer to *M. setiflagella* than it is to the present material. Also *Melita zeylanica kauerti* differs more from *Melita zeylanica* than it does from the present material. This material is considered to represent a new species that can be distinguished from its close congeners by the combination of characters shown in Table 1.

Habitat. Known only from Le Bouchon at depths of less than 1 m. The site is characterized by low salinity, green-algal growth and some estuarine conditions, which is in agreement with the general occurrence of the genus in brackish waters (Bousfield, 1973).

Type locality. Le Bouchon, Mauritius.

Distribution. Mauritius.

Etymology. From the Latin *cortex* meaning a cork, in reference to the name of the type locality.

Melita setimera n.sp.

Figs. 7–8

Type material. HOLOTYPE ♂, 4.1 mm, AM P60869, 0–1 m depth, living on a mixture of *Centroceras clavulatum, Hypnea* sp., *Gracilaria corticata, Enteromorpha flexuosa* and *Sargassum densifolium*, Tamarin (20°19.5'S 57°22'E), Mauritius, C. Appadoo, 11 October 1999. PARATYPES: 2♂♂, 4♀♀, AM P60870, same data as holotype; 1♀ from *Acanthophora spicifera*, Souillac (20°31'S 57°30.7'E), 10 November 1998; 1♂, 1♀ from *Padina* sp. and *Halimeda* sp., Grand Baie (20°0.5'S 57°34'E), 5 May 1999; 2♂♂, 1♀, 1 juv. from mixture of *Padina* sp., *Enteromorpha flexuosa, Hypnea* sp., *Amphiroa* sp. and *Caulerpa sertulariodes*, Tamarin, 18 June 1999; 1♂, 3♀♀, 3 juv. from *Amphiroa flagellisima* and *Padina, Ulva lactuca* and *Enteromorpha* sp. and ash-coloured sand, Tamarin, 2 August 1999; 9♂♂, 12♀♀, 9 juv. from mixture of *Centroceras clavulatum, Hypnea* sp., *Gracilaria corticata, Enteromorpha flexuosa* and *Sargassum densifolium*, Tamarin, 11 October 1999.

Description. Male length, 4.3 mm. Head lacking subocular notch; eyes subround. Antenna 1 peduncle article 1 with stout robust setae on ventral margin; article 2, 1.2× article 1; article 3 slightly less than half length of article 1; accessory flagellum 2-articulate, primary flagellum 20-articulate. Antenna 2 article 5 subequal to 4, flagellum 9-articulate. Mandible palp article 3 slightly longer than article 2, article 1, 0.5× the length of article 3. Maxilla 1 inner plate with 6 apical plumose setae. Lower lip with rounded mandibular lobes. Gnathopod 1 coxa subrectangular, 1.6× as long as broad, distal margin with very short setae; basis slender, 2.9× as long as broad, with very dense patches of setae on anterior margin; propodus 0.6× length of carpus, with a hood over the dactylus; dactylus broad at base, with a small medial expansion and tapering tip. Gnathopod 2 coxa subrectangular, 1.4× as long as broad; basis slightly expanded about 2.2× as long as broad, with dense long setae on anterior margin and a few patches of setae on posterior margin; carpus cup-shaped, 1.5× as broad as long; propodus 1.3× times as long as broad, palmar margin slightly oblique, palmar border broadly sinuous; dactylus slender and 0.6× the length of propodus, dactylus closing across the medial face of propodus. Pereopod 3 coxa subrectangular, 1.5× as long as broad with short setae on ventral margin; basis slender, anterior margin concave, 3.5× as long as broad;
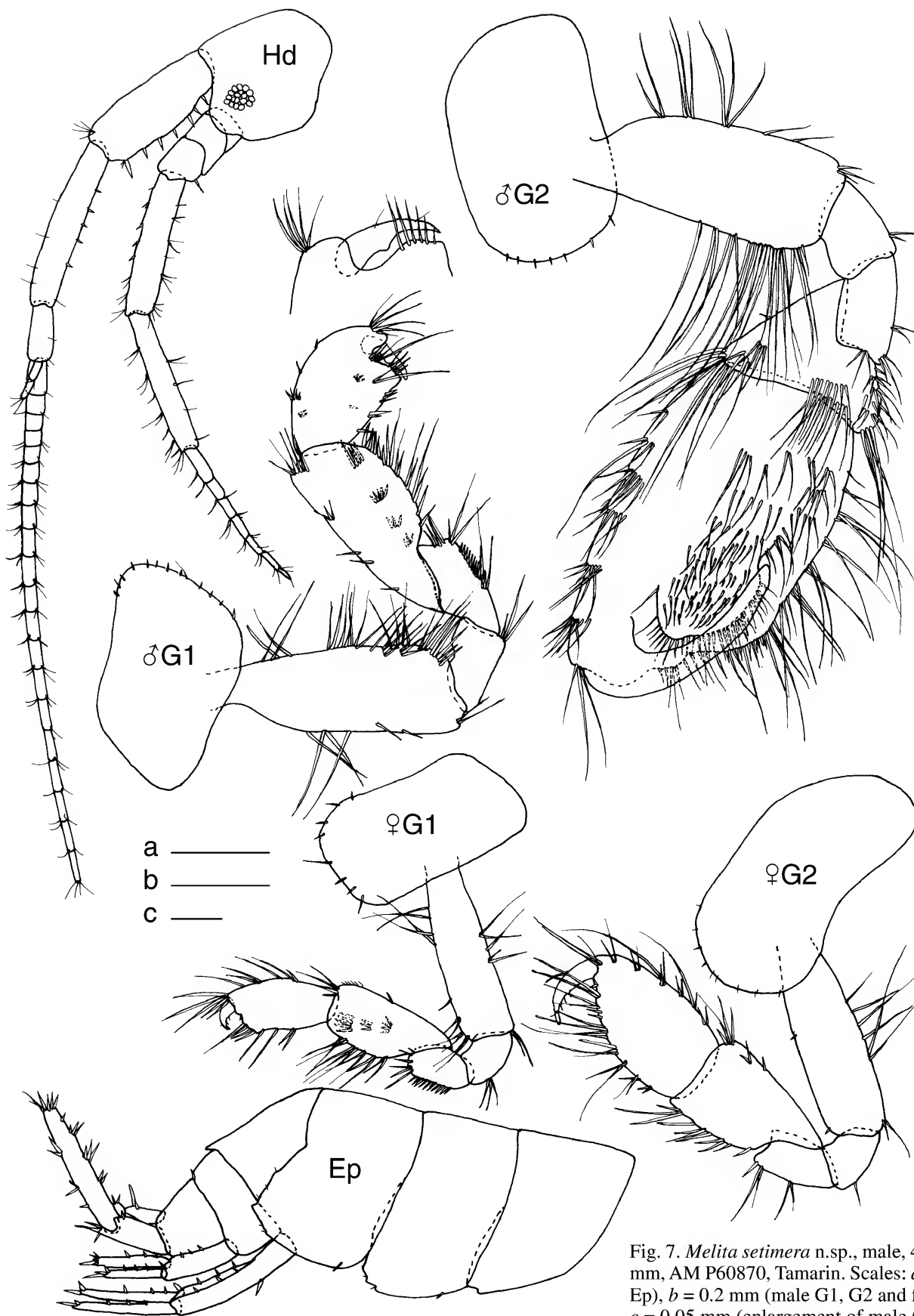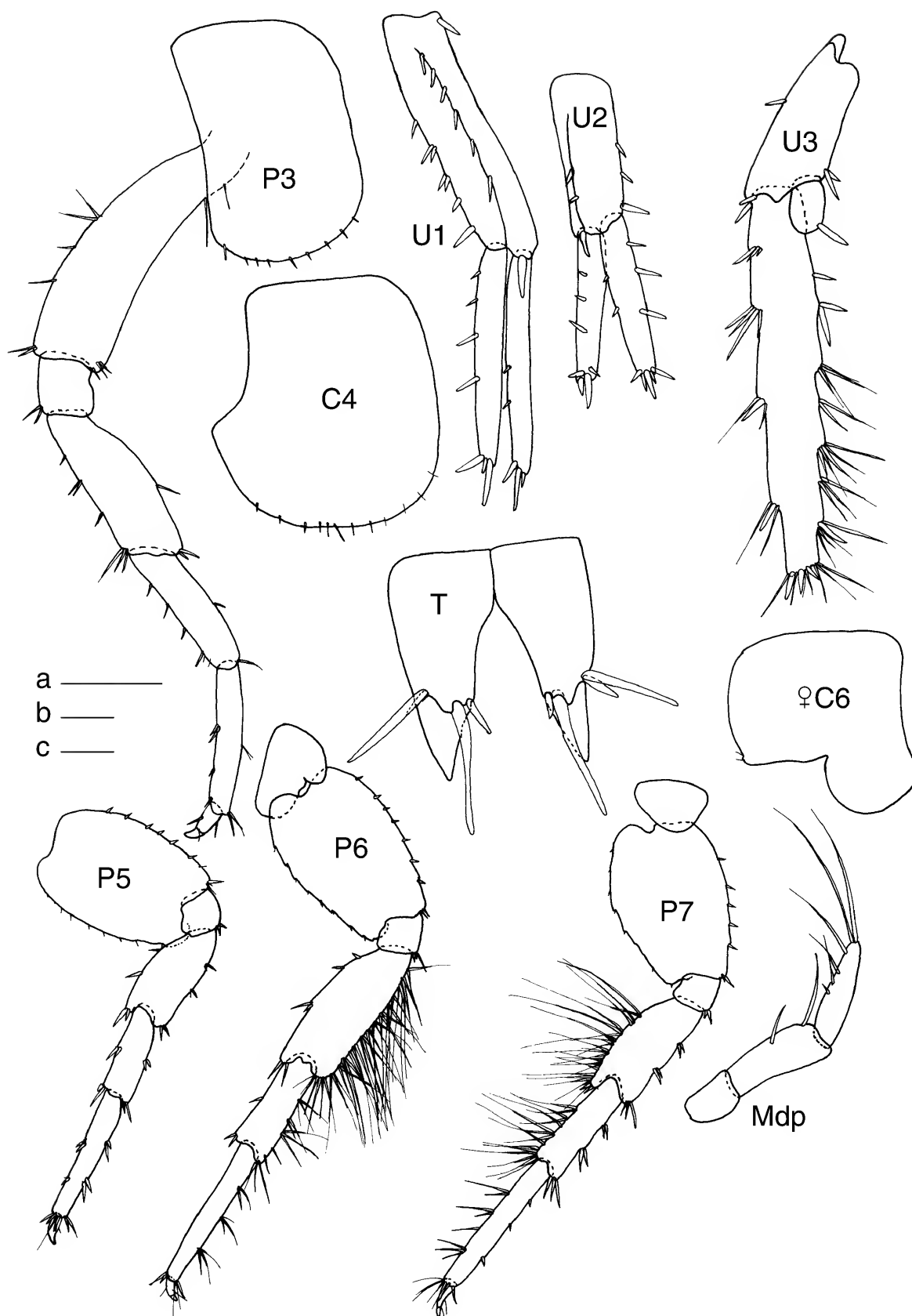
Fig. 7. *Melita setimera* n.sp., male, 4.3 mm, female, 3.8 mm, AM P60870, Tamarin. Scales: *a* = 0.4 mm (Hd and Ep), *b* = 0.2 mm (male G1, G2 and female G1 and G2), *c* = 0.05 mm (enlargement of male G1).

propodus subequal to carpus; dactylus with terminal unguis and one seta on anterior margin. Pereopod 4 coxa excavate on posterior margin; other features as pereopod 3. Pereopod 5 basis, 1.5× as long as broad, anterior margin with stout robust setae, posterior margin weakly serrated and with short setae; dactylus with 1 seta on anterior margin. Pereopod 6 basis 1.4× as long as broad, otherwise like that of pereopod 5; merus and

carpus with dense patches of long setae on anterior margins and short robust setae on posterior margin. Pereopod 7 similar to pereopod 6 except dense patches of setae on merus and carpus on the posterior margins and short robust setae on anterior margins. Epimeron 1 with small posterodistal tooth. Epimeron 2 weakly toothed at posterodistal margin. Epimeron 3 weakly toothed on posterodistal margin. Urosomite 1 with

Fig. 8. *Melita setimera* n.sp., male, 4.3 mm, female, 3.8 mm, AM P60870, Tamarin. Scales: a = 0.2 mm (P3, C4, U1,2, and female C6), b = 0.2 mm (P5 to P7), c = 0.05 mm (U3, T).

acute dorsal tooth, urosomite 2 with one robust seta on mid-dorsal surface. Uropod 1 peduncle with basofacial robust seta, rami slender, 0.9× peduncle. Uropod 2 rami subequal to peduncle. Uropod 3 inner ramus rudimentary, with one or two terminal robust setae; outer ramus 1-articulate, 2× length of peduncle, spatulate, and with short robust setae and long

fine setae. Telson apices pointed, each lobe with two robust setae on outer margin and two on medial hump.

Female: length, 3.8 mm (mature, with eggs). Gnathopod 1 coxa 2× as long as broad; basis slender, with patches of setae on proximal and distal anterior margins and on medial posterior margin; propodus palm transverse; dactylus
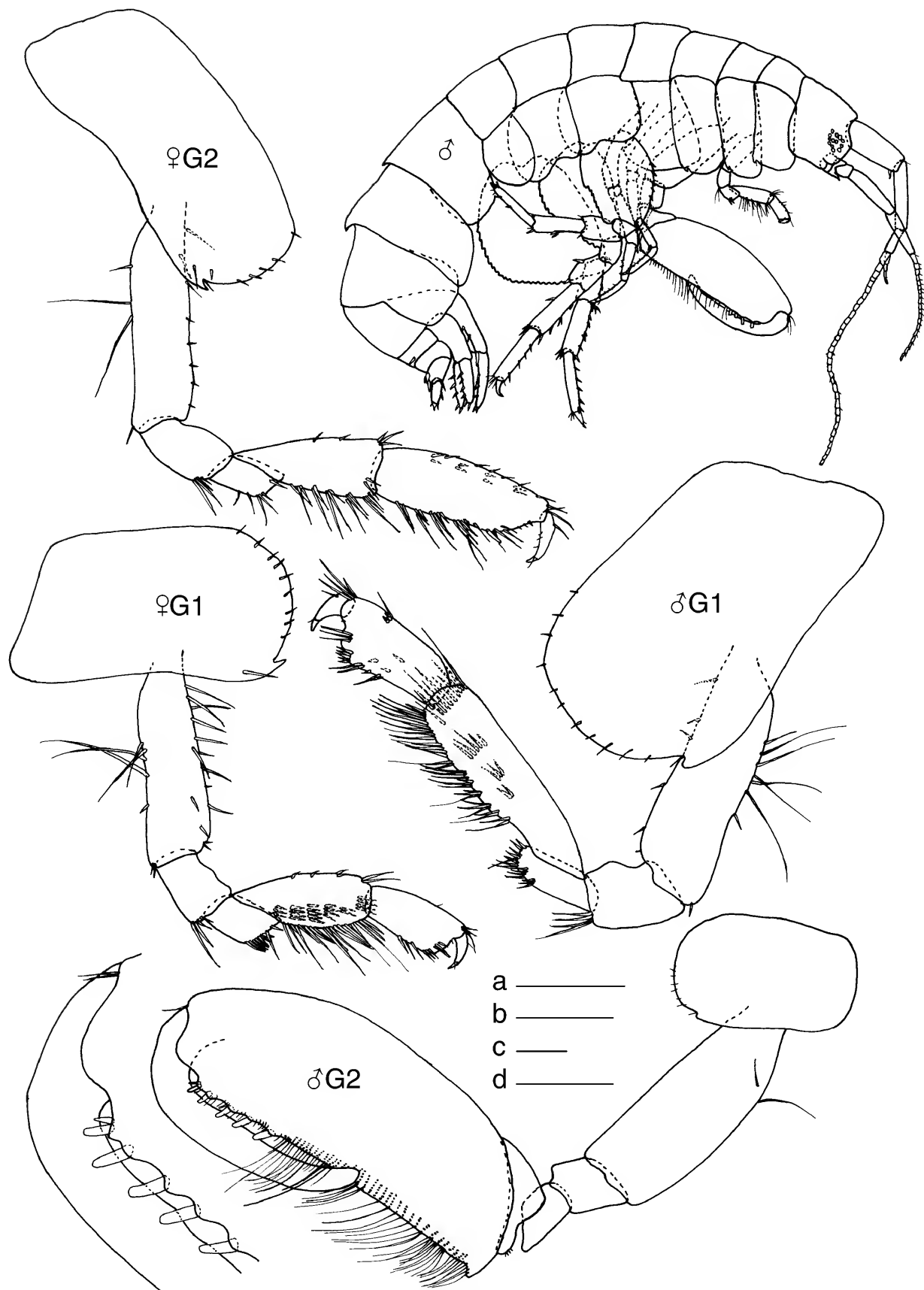
Fig. 9. *Nuuanu rectimana* n.sp., male, 5.2 mm, female, 4.2 mm, AM P60906, Albion. Scales: *a* = 1 mm (whole animal), *b* = 0.2 mm (female G1 and male G1 and G2), *c* = 0.2 mm (male G2) and *d* = 0.2 mm (enlargement of male G2).

normal. Gnathopod 2 coxa 2.1× as long as broad; basis slender, 3× as long as broad; propodus slightly longer than carpus, palm oblique, with long setae on palmar margin and anterior margin. Pereopod 6, coxa bilobed without any finger-like protuberance. Female pereopods 6 and 7 without dense setae on merus and carpus.

Remarks. This species most closely resembles *Melita simplex* Myers (1985) from Fiji, in having an acute dorsal tooth on urosomite 1 and a non sexually-dimorphic female coxa 6. *Melita setimera* male gnathopod 1, however, has a densely setose distal margin on the basis, the propodus is shorter than the carpus and it has a lobe above the dactylus.
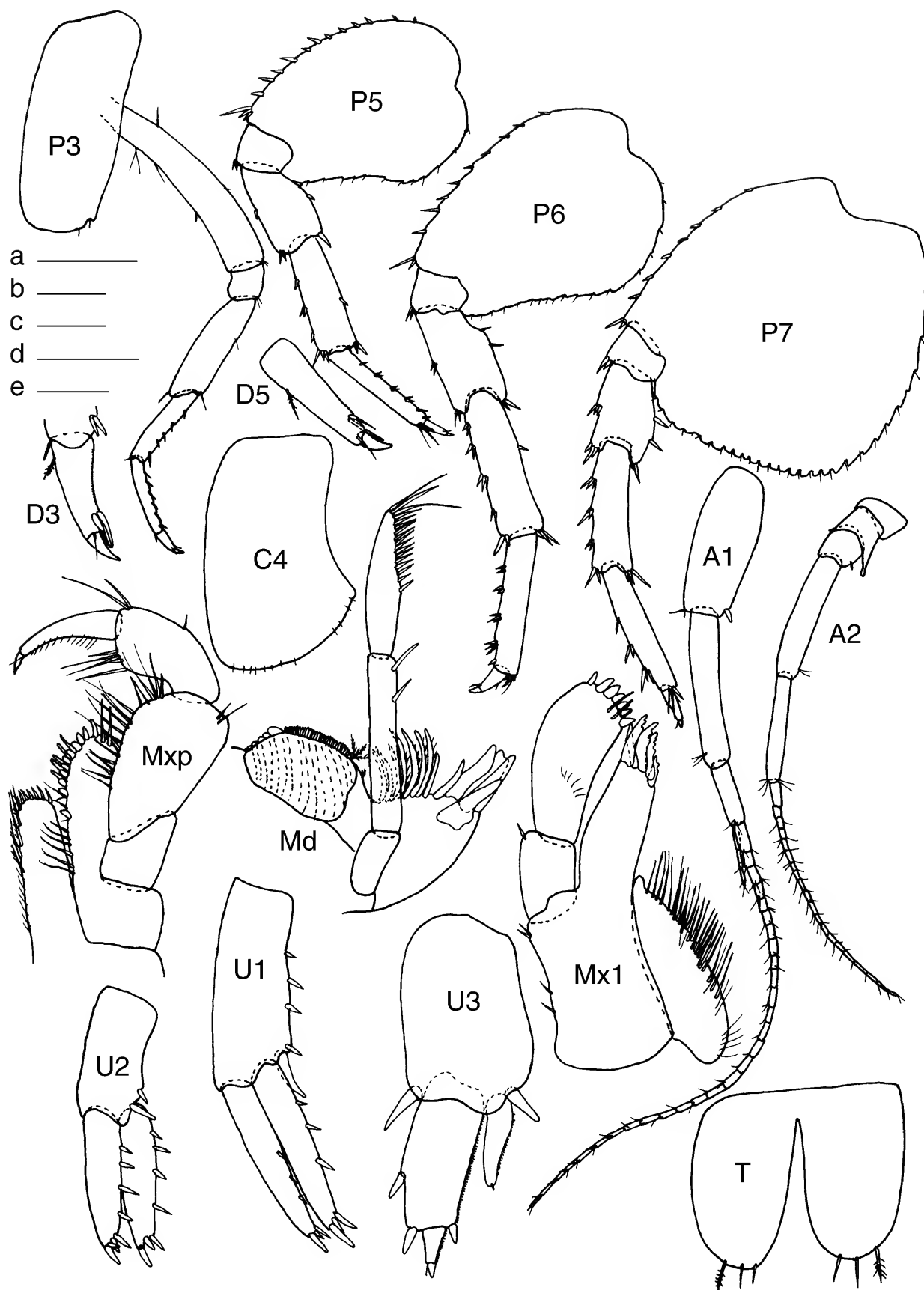
Fig. 10. *Nuuanu rectimana* n.sp., male, 5.2 mm, AM P60906, Albion. Scales: *a* = 0.4 mm (P3, C4, P5 to P7, A1 to A2), *b* = 0.2 mm (U1 to U3), *c* = 0.1 mm (Mxp), *d* = 0.1 mm (Md, Mx1, D3, D5), *e* = 0.05 mm (T).

The male gnathopod 2 propodus of *M. setimera* has parallel margins and the palmar border is broadly sinuous whereas the ventral margin of male gnathopod 2 of *M. simplex* is evenly convex. Pereopods 6 and 7 merus and carpus are densely setose in *M. setimera*, but this character state is unknown in *Melita simplex*. The telson apices of *M. simplex* have a terminal robust seta that is lacking in *M. setimera*.

Melita setimera can be distinguished from all other species of *Melita* from Mauritius, by the presence of the dorsal tooth on urosomite 1 on both males and females.

Males are easily distinguished by the broadly sinuous palmar margin of gnathopod 2 and the presence of dense long setae on merus of pereopods 6 and 7.

Habitat. *Melita setimera* was collected only at Tamarin at depths of less than 1 m. The site has some freshwater influence due to a river flowing in the vicinity.

Type locality. Tamarin, Mauritius.

Distribution. Mauritius.

Etymology. From the Latin *saeta* = bristle coupled with *merus* referring to the strongly setose merus of male pereopods 6 and 7.

Nuuanu rectimana n.sp.

Figs. 9–10

Nuuanu sp. 1 (Appadoo & Steele, 1998).

Type material. HOLOTYPE ♂, 4 mm, AM P60905, 0.5–1 m depth, living on mixture of *Enteromorpha flexuosa, Laurencia papillosa, Halodule uninervis*, Poste La Fayette (20°08.2'S 57°44.5'E), Mauritius, C. Appadoo, 7 February 2000. PARATYPES: 1♂, 3♀♀, AM P60906, 0.5 m, living among *Gracilaria salicornia*, Souillac (20°31'S 57°30.7'E), Mauritius, 25 March 1999; 1♂, 1 juv. from green filamentous algae and *Halodule uninervis* Albion (20°13'S 57°23.7'E), 12 May 1998; 1♂ from *Sargassum* sp., Bain Boeuf (19°59'S 57°36'E), 15 May 1998; 1♂ from *Sargassum* sp., Bain Boeuf, 16 June 1998; 1 juv. from *Jania* sp. and *Valonia* sp., Bain Boeuf, 28 July 1998; 1 juv. from *Pocockiella variegata* and *Valonia* sp., Balaclava (20°03.7'S 57°30.7'E), 10 September 1998; 1 juv. from *Gracilaria salicornia*, Souillac, 25 March 1999; 2♂♂, 11♀♀, 5 juv. from *Laurencia papillosa* and *Cladophora* sp., Albion, 20 April 1999; 1 juv. from *Sargassum* sp., *Amphiroa* sp., *Pocockiella variegata* and *Cymodocea* sp., Bain Boeuf, 16 June 1999; 1♂, 2 juv. from *Sargassum* sp., La Cuvette, 12 October 1999; 1♀ from coral rubble, *Padina* sp. and *Pocockiella variegata*, Flic-en-Flac, 10 December 1999; 1♀ from mixture of *Padina* sp., *Turbinaria* sp., *Sargassum* sp., *Pocockiella variegata*, Bain Boeuf, 24 January 2000; 1 juv. from mixture of *Enteromorpha flexuosa, Laurencia papillosa* and *Halodule uninervis*, Poste La Fayette, 7 February 2000.

Description. Male length, 4.0 mm. Head with lateral cephalic lobe notched; ommatidia of eyes sparse. Antenna 1 poorly setiferous, peduncle article 2 slightly longer than article 1; article 3, 0.5× article 1; accessory flagellum 4-articulate, primary flagellum 30-articulate. Antenna 2 poorly setiferous, article 5, 0.8× article 4, flagellum 20-articulate. Mandible palp slender, subfalcate, article 2 longest; article 3, 0.8× article 2 and 2.1× article 1; article 3 with short setae on medial margin and three long terminal setae. Maxilla 1 palp 2-articulate, article 2 with stout blunt robust setae at tip; inner plate with a small protuberance at apex and with long marginal setae. Maxilla 2 inner plate with oblique setal row. Gnathopod 1 coxa 1.5× as long as broad, posterodistal margin with a notch and distal margin with very short setae; basis slender, 3× as long as broad, posterior margin with a strong patch of setae; carpus slender, subrectangular, 3.5× as long as broad; propodus 0.6× length of carpus; palmar margin oblique with few setae; dactylus short, fitting palm. Gnathopod 2 coxa subrectangular 1.6× as long as broad, posterodistal margin with notch and distal margin with very few short setae; basis 2.5× as long as broad; carpus over three and half times as broad as long; propodus subrectangular, posterior margin straight, defined by a small hump at the proximal end and well-developed blunt projections embedded at the distal end, densely setose, palm obsolete, dactylus 0.6× length of propodus, robust and broad

throughout its length. Pereopod 3 coxa subrectangular, 2.2× as long as broad, posterodistal margin with notch; dactylus with two long stout setae and one small slender seta close to apical unguis. Pereopod 4 coxa 1.7× as long as broad, posterior margin excavate; other features similar to pereopod 3. Pereopod 5 basis 1.3× as long as broad, anterior margin convex and with stout robust setae, posterior margin serrated, convex proximally and concave distally; propodus subequal to carpus; dactylus with 2 long setae and one slender seta at unguis. Pereopod 6 basis about 1.5× as long as broad, similar to that of pereopod 5 except posterior margin is more castelloserrate. Pereopod 7 basis broadly expanded, about as long as broad, anterior margin with robust setae, posterior margin strongly convex, castellate with short setae; propodus slightly longer than carpus. Pleonites 1 and 2 with well-developed dorsal tooth. Epimera 1 to 3 subrectangular, distal margins smooth. Uropod 1 rami subequal to each other and 0.8× the length of peduncle. Uropod 2 rami subequal to each other, and slightly longer than peduncle, with stout robust setae. Uropod 3 peduncle 1.5× as long as broad; outer ramus 2-articulate, article 1 truncate with a stout robust setae on mid-lateral margin and two stout distal robust seta; article 2 produced with a stout robust seta; inner ramus short and sub-falcate; inner margins of both rami with very fine short setae. Telson cleft to 80% its length; telson lobes with broadly rounded apex, each with one plumose seta and two short slender setae.

Female: length, 4.2 mm (mature, oostegites with setae). Gnathopod 1 coxa 1.7× as long as broad, posterodistal margin with a notch and short setae; basis slender, 3.5× as long as broad; anterior margin with patches of setae, posterior margin with one strong patch of setae; propodus 0.7× length of carpus; palmar margin oblique, with short setae; dactylus stout, fitting palm. Gnathopod 2 coxa 2.1× as long as broad, posterodistal margin with notch and short setae; basis slender and 3.6× as long as broad; propodus 1.2× length of carpus; propodus slightly less 3.5× as long as broad, palmar margin oblique, defined by a stout robust seta; dactylus stout, fitting palm.

Remarks. The genus *Nuuanu*, established by Barnard (1970), belongs to the "*Gammarella*" group, recently revised by Lowry & Watson (2002). Males of *Nuuanu rectimana* n.sp. can easily be distinguished from *Nuuanu amikai* Barnard (1970), recorded by Ledoyer (1978) from Mauritius, by the presence of a well-developed flat-topped processes on the propodus of gnathopod 2. Other differences include the shape, setation and spination of the telson. *Nuuanu rectimana* n.sp. telson is symmetrical with two robust setae and one plumose seta on each lobe whereas in *Nuuanu amikai* Barnard (1970: 167, fig. 105) the telson is asymmetrical, with one robust seta and two plumose setae on one lobe and one plumose seta on the other. In addition in *Nuuanu rectimana* n.sp. the inner lobe of uropod 3 is slender, subfalcate and about half the left of the outer lobe whereas in *N. amikai* (Barnard 1970: 168, fig. 106) the inner lobe is triangular and less than half the length of the outer ramus. Nuuanu rectimana n.sp. differs from *Nuuanu numbadi* Barnard (1974: 39, fig. 27) from Australia by having more distally tapered telson lobes with one robust and two plumose setae as compared to more distally broad telson lobes with two robust and one plumose seta. Another difference is that epimera 2 and 3 are less acute in *N. rectimana* n.sp. than in *N. numbadi*.

Habitat. *Nuuanu rectimana* was collected in depths of less than 1 m, from seagrass (*Halodule uninervis* or *Cymodocea* sp.) mixed with other algae and coral rubble at Albion, Poste La Fayette and Bain Boeuf.

Type locality. Poste La Fayette, Mauritius.

Distribution. Mauritius.

Etymology. The species is named from the Latin *rectus* meaning straight and *manus* meaning hand, referring to the straight posterior margin of the propodus of the male gnathopod 2.

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New and Little-known Melitid Amphipods
from Australian Waters
(Crustacea: Amphipoda: Melitidae)

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ABSTRACT. During a recent review of Australian melitid amphipods (Lowry, Berents & Springthorpe, 2001), a number of problems and undescribed species were revealed. These problems and others uncovered during the course of this study are addressed here. The Melitidae, as currently conceived, is considered to contain at least five natural groups: the *Ceradocopsis* group; the *Ceradocus* group; the *Eriopisa* group; the *Nuuana* group and the *Melita* group. In the *Ceradocus* group *Austromaera* n.gen. is established for *Maera mastersii* Haswell, 1879a, that is redescribed based on syntype material and new collections from Port Jackson. *Ceradocus circe* n.sp. is described based on specimens from Tasmania, originally reported by Chilton (1921b) as *C. rubromaculatus* (Stimpson, 1856). *Maera boecki* Haswell, 1879 and *Maera hamigera* Haswell, 1879 (*sensu stricto*), both originally described from Port Jackson, are redescribed and these species as well as *Maera octodens* Sivaprakasam, 1968 are transferred to the genus *Linguimaera* Pirlot, 1934, recently re-established by Krapp-Schickel (2003). *Linguimaera schickelae* n.sp. is described from the Sydney area. *Maera griffini* Berents, 1983, is tentatively placed in the genus *Maeropsis* Chevreux, 1919. *Mallacoota subcarinata* is redescribed based on syntypes and new collections and four new Australian species (*M. chandaniae* n.sp., *M. euroka* n.sp., *M. kameruka* n.sp. and *M. malua* n.sp.) are described, two of which have previously been mis-identified as *M. subcarinata*. *Mallacoota nananui* Myers, 1985, is reported from Australia for the first time. *Miramaera thetis* n.gen., n.sp. is established for the specimens mis-identified by Stebbing, 1910a as *Maera inaequipes*. We describe a new species of *Parelasmopus, P. sowpigensis* n.sp., from Port Jackson, New South Wales. *Quadrivisio sarina* n.sp. is described from near McKay, Queensland, the first record of *Quadrivisio* Stebbing, 1907 in Australian waters. In the *Eriopisa* group *Victoriopisa australiensis* (Chilton, 1923) is redescribed and illustrated. A second species, *Victoriopisa marina* n.sp., is described from estuarine and marine habitats in New South Wales and Victoria. In the *Melita* group *Dulichiella australis* (Haswell, 1879a) is redescribed based on syntype material and *D. pacifica* n.sp. is described based on collections from the Great Barrier Reef, the southwestern Pacific Ocean and the South China Sea. *Melita ophiocola* n.sp. is described from Port Jackson, living in association with the brittlestar *Ophionereis schayeri*.

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Melitid amphipods are a diverse and abundant part of the Australian amphipod fauna. Including this work and the recent work of Krapp-Schickel (2003), there are 86 known Australian marine and freshwater species (Table 1). The majority of the marine component comes from the southeastern and southwestern parts of the country. Many species are yet to be discovered from tropical areas. Nearly 75% of the Australian melitid fauna has been described since the early 1970s and many of the earlier species were redescribed during this time. Lowry *et al.* (2001) reviewed the marine component of this fauna and provided redescriptions, pictures and an interactive key to all marine species at http://www.crutacea.net. The new species from that review are described here and some of the more problematical species are redescribed.

The Haswell species

The first descriptor of the Australian amphipod fauna, W.A. Haswell, described 10 species of melitids (Table 1), mainly from Port Jackson (Haswell, 1879a,b). Based on the original descriptions, these amphipods have never been easy to identify, and the status of his types, which could be used for redescriptions, has always been a problem (Springthorpe & Lowry, 1994). Sheard (1936) and J.L. Barnard (1972a) redescribed *Ceradocus ramsayi* (Haswell, 1879a) and *Maera mastersii* (Haswell, 1879a), but the material Sheard (1936) considered to be *M. mastersii* has recently been described as *Linguimaera tias* Krapp-Schickel, 2003 and the material of J.L. Barnard (1972a) has been described as *Linguimaera leo* Krapp-Schickel, 2003. J.L. Barnard (1972a) redescribed *Mallacoota diemenensis* (Haswell,

Table 1. Australian Melitidae, * freshwater species.

***Ceradocopsis* group**
    Ceradocopsis hamondi Moore, 1988
***Ceradocus* group**
    Austromaera mastersii (Haswell, 1879a)
    Ceradocus circe n.sp.
    Ceradocus dooliba J.L. Barnard, 1972a
    Ceradocus hawaiensis J.L. Barnard, 1955
    Ceradocus oxyodus Berents, 1983
    Ceradocus ramsayi (Haswell, 1879a)
    Ceradocus rubromaculatus (Stimpson, 1856)
    Ceradocus sellickensis Sheard, 1939
    Ceradocus serratus (Bate, 1862)
    Ceradocus woorree Berents, 1983
    Ceradocus yandala Berents, 1983
    Elasmopus alalo Myers, 1986
    Elasmopus bollonsi Chilton, 1915
    Elasmopus crenulatus Berents, 1983
    Elasmopus hooheno J.L. Barnard, 1970
    Elasmopus menurte J.L. Barnard, 1974
    Elasmopus pocillimanus (Bate, 1862)
    Elasmopus spinicarpus Berents, 1983
    Elasmopus warra Kelaher & Lowry, 2002
    Elasmopus yunde J.L. Barnard, 1974
    Hoho carteta (J.L. Barnard, 1972a)
    Hoho hirtipalma Lowry & Fenwick, 1983
    Hoho marilla (J.L. Barnard, 1972a)
    Linguimaera boecki (Haswell, 1879b)
    Linguimaera bogombogo Krapp-Schickel, 2003
    Linguimaera caesaris Krapp-Schickel, 2003
    Linguimaera garitima Krapp-Schickel, 2003
    Linguimaera hamigera (Haswell, 1879b)
    Linguimaera kellissa Krapp-Schickel, 2003
    Linguimaera leo Krapp-Schickel, 2003
    Linguimaera octodens (Sivaprakasam, 1968)
    Linguimaera schickelae n.sp.
    Linguimaera thomsoni (Miers, 1884)
    Linguimaera tias Krapp-Schickel, 2003
    Maeracoota sp. Krapp-Schickel & Ruffo, 2001
    Maeropsis griffini (Berents, 1983)
    Mallacoota balara Berents, 1983
    Mallacoota chandaniae n.sp.
    Mallacoota diemenensis (Haswell, 1879a)
    Mallacoota euroka n.sp.
    Mallacoota kameruka n.sp.
    Mallacoota malua n.sp.
    Mallacoota nananui Myers, 1985

    Mallacoota subcarinata (Haswell, 1879b)
    Miramaera thetis n.sp
    Parapherusa crassipes (Haswell, 1879b)
    Parelasmopus echo J.L. Barnard, 1972a
    Parelasmopus sowpigensis n.sp.
    Parelasmopus suensis (Haswell, 1879b)
    Parelasmopus ya J.L. Barnard, 1972a
    Premaera thetis n.sp.
    Quadrimaera quadrimana (Dana, 1852)
    Quadrimaera reishi (J.L. Barnard, 1979)
    Quadrimaera serrata (Schellenberg, 1938)
    Quadrimaera viridis (Haswell, 1879b)
    Quadrivisio sarina n.sp.
***Eriopisa* group**
    *Nedsia chevronia Bradbury, 2002
    *Nedsia douglasi Barnard & Williams, 1995
    *Nedsia fragilis Bradbury & Williams, 1996
    *Nedsia halletti Bradbury, 2002
    *Nedsia humphreysi Bradbury & Williams, 1996
    *Nedsia hurlberti Bradbury & Williams, 1996
    *Nedsia macrosculptilis Bradbury & Williams, 1996
    *Nedsia sculptilis Bradbury & Williams, 1996
    *Nedsia stefania Bradbury, 2002
    *Nedsia straskraba Bradbury & Williams, 1996
    *Nedsia urifimbriata Bradbury & Williams, 1996
    *Norcapensis mandibulis Bradbury & Williams, 1997
    *Nurina poulteri Bradbury & Eberhard, 2000
    Victoriopisa australiensis (Chilton, 1923)
    Victoriopisa marina n.sp.
***Nuuana* group**
    Gammarella berringar (J.L. Barnard, 1974)
    Nuuanu merringannee (J.L. Barnard, 1974)
    Nuuanu mokari J.L. Barnard, 1974
    Nuuanu numbadi J.L. Barnard, 1974
***Melita* group**
    *Brachina invasa Barnard & Williams, 1995
    Dulichiella australis (Haswell, 1879a)
    Dulichiella pacifica n.sp.
    Melita festiva (Chilton, 1884)
    Melita kauerti J.L. Barnard, 1972a
    Melita matilda J.L. Barnard, 1972a
    Melita myersi Karaman, 1987
    Melita oba J.L. Barnard, 1972a
    Melita ophiocola n.sp.
    *Melita plumulosa Zeidler, 1989

1879a) and *Quadrimaera viridis* (Haswell, 1879b) and Berents (1983) redescribed *Parelasmopus suensis* (Haswell, 1879b). *Parapherusa crassipes* (Haswell, 1879b) is considered to be a well known, distinctive species. In this paper we redescribe *Austromaera mastersii* (Haswell, 1879a), *Dulichiella australis* (Haswell, 1879a), *Linguimaera boecki* (Haswell, 1879b), *Linguimaera hamigera* (Haswell, 1879b) and *Mallacoota subcarinata* (Haswell, 1879b).

The *Dulichiella* complex

Once LeCroy (2000) redescribed *Dulichiella appendiculata* (Say, 1818) from near the type locality (LeCroy, pers. comm.), it was clear that material from Australia did not belong to that species. Ledoyer (1986) gave an excellent summary of the problems associated with available names for species of *Dulichiella*. Based on this information we were able to locate and borrow material of *D. appendiculata* (Say, 1818), St Catherines Island, Georgia, USA, *D. fresnelii* (Audouin, 1826), Great Bitter Lake, Suez Canal and *D. anisochir* (Kroyer, 1845) Rio de Janeiro, Brazil. Dana's types are lost and his species (*Dulichiella validus* (Dana, 1852), Singapore; *Dulichiella setipes* (Dana, 1852), Rio de Janeiro; *Dulichiella pilosus* (Dana, 1852), Rio de Janeiro) are only identifiable at generic level. Comparison of our material with these species showed that *D. australis* is a valid species and that an undescribed species (*D. pacifica* n.sp.) occurred in northeastern Australia, the southwest Pacific and the South China Sea. A separate paper (Lowry & Springthorpe, in prep.) revises *Dulichiella* on a world-wide basis.

The *Maera* complex

Krapp-Schickel & Ruffo (2000) recently established the genus *Quadrimaera* and transferred four of the nine Australian species, previously considered to be *Maera*, to this genus (Table 1). Krapp-Schickel (2003) recently re-established the genus *Linguimaera* Pirlot, 1936 and described seven new Australian species in the genus. But five remaining Australian species are still unassigned.

In the original description of *Maera mastersii* Haswell, 1879a, the illustrations of uropod 3 and the telson differ significantly from those presented by Sheard (1936) and J.L. Barnard (1972a). We examined syntype material and new material, both from Port Jackson, that agree with the description and illustrations of Haswell (1879a). Based on this material we redescribe the species and place it in the new genus *Austromaera*. Within Australia, the material considered by Sheard (1936) as *Maera mastersii* has been described as *Linguimaera tias* Krapp-Schickel, 2003 and that of J.L. Barnard (1972a) has been described as *Linguimaera leo* Krapp-Schickel, 2003. Krapp-Schickel (2003) has also re-established the Torres Strait species, *Maera thomsoni* (Miers, 1884) (synonymized with *M. mastersii* by Haswell, 1885), and transferred it to *Linguimaera*.

Two main characters define *Linguimaera* Pirlot, 1936 (Krapp-Schickel, 2003). The first is the second gnathopods of the male that are always asymmetrical, so that one is similar to the female second gnathopod and the other is enlarged and morphologically dissimilar, as is typical of mate-guarding amphipods. The second character is a serrate posterior margin on epimeron 3 (weakly serrate in *M. hamigera*). Among the Australian species in our study, *Maera boecki* Haswell, 1879, *M. hamigera* Haswell, 1879

and *M. octodens* Sivaprakasam, 1968, all have these characteristics. They are here transferred to the genus *Linguimaera*. In addition, a new species, *Linguimaera schickelae* n.sp., is described from the Sydney area.

The original description of *Maera boecki* Haswell, 1879b, was inadequate and the type material is apparently lost (Springthorpe & Lowry, 1994). As a result the species has been unidentifiable. Della Valle (1893) referred to it as *?Maera boeckii*. Stebbing (1899) transferred it to *Elasmopus* in his world monograph (Stebbing, 1906). K.H. Barnard (1916) appears to have erroneously reported *E. boecki* from South Africa. Since Sheard (1937) placed it in his catalogue of Australian Gammaridea, there have been no further records or new material. While studying material for the Australian Amphipod Project, we discovered material from Port Jackson that we are referring to this species. The species has all the characteristics of a *Linguimaera*, except for an emarginate telson, which appears to be independently derived.

The name *Maera hamigera* Haswell, 1879b (type locality Port Jackson), has not been used for an Australian species since Stebbing (1910a), but it has been used for species living in the Red Sea (Walker, 1909; Lyons & Myers, 1993), southern Africa (K.H. Barnard, 1916), Micronesia (J.L. Barnard, 1965), the Mediterranean Sea (Karaman & Ruffo, 1971), Madagascar (Ledoyer, 1982) and Western Samoa (Myers, 1997). A microscope slide from the syntype series shows the unusual gnathopod 2 of this species. Using this evidence we discovered many specimens of this species in collections from Twofold Bay on the south coast of New South Wales. We redescribe the species here, based on the syntypes and the newly discovered material. These results indicate that *L. hamigera* is currently confined to southeastern Australia. Material from other areas that also appears to be in the genus *Linguimaera*, and has been attributed to this species, needs to be re-examined. Krapp-Schickel (2003) recently renamed material, identified as *M. hamigera*, from the Mediterranean, the Red Sea, Madagascar and Western Samoa as *L. caesaris*, but left the material from southern Africa and Micronesia unresolved.

Stebbing (1910a) identified material from the *Thetis* Expedition as *Maera inaequipes* (Costa, 1851). Even as he did, he stated that "the specimens … do not justify the specific name". We establish the new genus and species *Miramaera thetis* based on material in the Australian Museum collections and transfer the New Zealand species, *Maera tepuni* J.L. Barnard, 1972b, to *Miramaera*.

Based on the key in Krapp-Schickel (2000) and unpublished phylogenetic analyses (JKL) we tentatively place *Maera griffini* Berents, 1983, in the genus *Maeropsis* Chevreux, 1919. Krapp-Schickel & Ruffo (2001) deduced that *Maera tenella* of Tattersall, 1922 (Wooded Island, Abrolhos Islands) is actually a species of *Maeracoota* Myers, 1997. Unfortunately material of this species is not available for study.

The *Mallacoota* Complex

Mallacoota J.L. Barnard, 1972, was established for six species: *M. carteta* J.L. Barnard, 1972, *M. diemenensis* (Haswell, 1879), *M. insignis* (Chevreux, 1901), *M. marilla* J.L. Barnard, 1972, *M. odontoplax* (Pirlot, 1936) and *M. subcarinata* (Haswell, 1879). At the same time Barnard demonstrated several "phenotypes" for *M. subcarinata* and *M. carteta*. Lowry & Fenwick (1983) subsequently removed

M. marilla and *M. carteta* to a new genus, *Hoho*, and described a third species, *H. hirtipalma*.

Since then Ortiz has described *M. carausui* Ortiz, 1976, Ledoyer has described *M. subinsignis* Ledoyer, 1979, *M. latidactylus* Ledoyer, 1982 and *M. schellenbergi* Ledoyer, 1984 and transferred (Ledoyer, 1982) *Elasmopus latibrachium* Walker, 1905 to *Mallacoota*. Berents (1983) has described *M. balara* and Myers (1985) has described *M. nananui*. Myers (1985) summarized the status of *Mallacoota* and concluded that an in-depth study using a wide range of material was needed. Appadoo *et al.* (2002) began this process by redescribing *M. insignis, M. latibrachium* and *M. schellenbergi* and describing the new species *M. caerulea* from Mauritius. They also excluded *M. subcarinata* of Ledoyer (1978) from that area.

The original description of *Mallacoota subcarinata* (Haswell, 1879b) was apparently based on a series of small adult specimens from Port Jackson. These syntypes are lodged in the Australian Museum, but are in poor condition. All have the unusual gnathopod 2 palmar shape indicated by Haswell's (1879b) illustrations. Unfortunately this is not one of the species with which the name has been subsequently associated. To add to this confusion J.L. Barnard (1972) described three "phenotypes" in his redescription of *M. subcarinata*. In this paper we re-establish the original species concept of *M. subcarinata* by redescribing and illustrating the types and new material from near the type locality. We describe new Australian species (*M. chandaniae* n.sp., *M. euroka* n.sp., *M. kameruka* n.sp. and *M. malua* n.sp.) some of which have in the past been mis-identified as *M. subcarinata* and comment on records of *M. subcarinata* from geographic areas outside of Australia. We also report *M. nananui* Myers, 1985 from Australian waters for the first time.

Currently *Mallacoota* contains 16 species (Table 2) half of which occur in Australia. The genus is essentially Indo Pacific with one species, *M. carausui*, in the tropical western Atlantic.

Parelasmopus, Quadrivisio and *Victoriopisa*

J.L. Barnard (1972a) redefined *Parelasmopus* and established *Ifalukia* for a species that did not quite fit the *Parelasmopus* mould. In the same paper he described two Australian species and synonymized *P. suensis* (Haswell, 1879b) with *P. setiger* Chevreux, 1901. Strangely he continued to use the later name, *P. setiger*. J.L. Barnard (1974) reassessed his position and considered *P. suensis* and *P. setiger* to be separate species. Finally, Berents (1983) redescribed *P. suensis* from a lectotype male. In this paper we describe the fourth Australian species and the first species from the southeastern part of the country. This species, *Parelasmopus sowpigensis*, also does not quite fit the *Parelasmopus* or *Ifalukia* moulds, but it is placed in a slightly expanded concept of the genus *Parelasmopus*.

Quadrivisio currently contains five species: *Q. aviceps* K.H. Barnard, 1940; *Q. bengalensis* Stebbing, 1907; *Q. bousfieldi* Karaman & Barnard, 1979; *Q. lobata* Asari, 1983; and *Q. lutzi* (Shoemaker, 1933) none of which are known from Australian waters. We describe a new species, *Q. sarina*, from the Queensland coast.

Stock & Platvoet (1981) revised the genus *Victoriopisa* and described a new species from Mauritania in the eastern North Atlantic. Including the new species described here, *Victoriopisa* now contains seven species: *V. atlantica* Stock & Platvoet, 1981;

Table 2. Species of *Mallacoota*.

> *M. balara* Berents, 1983
> *M. caerulea* Appadoo, Myers & Fagoonee, 2002
> *M. carausui* Ortiz, 1976
> *M. chandaniae* n.sp.
> *M. diemenensis* (Haswell, 1879)
> *M. euroka* n.sp.
> *M. insignis* (Chevreux, 1901)
> *M. kameruka* n.sp.
> *M. latibrachium* (Walker, 1905)
> *M. latidactylus* Ledoyer, 1982
> *M. malua* n.sp.
> *M. nananui* Myers, 1985
> *M. odontoplax* (Pirlot, 1936)
> *M. schellenbergi* Ledoyer, 1984
> *M. subcarinata* (Haswell, 1879b)
> *M. subinsignis* Ledoyer, 1979

V. australiensis (Chilton, 1923); *V. chilkensis* (Chilton, 1921a); *V. epistomata* (Griffiths, 1974a); *V. marina* n.sp.; *V. papiae* Asari, 1983 and *V. ryukyuensis* Morino, 1991. In a phylogenetic analysis of the *Eriopisa* group van der Ham & Vonk (2003) affirmed the monophyly of *Victoriopisa*.

The original description and illustrations of *Victoriopisa australiensis* (Chilton, 1923) were inadequate and the type was thought to be lost (Springthorpe & Lowry, 1994). When Karaman & Barnard (1979) established the genus *Victoriopisa* they included *V. australiensis*, but did not redescribe it. This is a very distinctive species that lives in a restricted habitat. For these reasons we redescribe and illustrate this species, based on material from Boambee Creek, Sawtell, New South Wales, near the type locality, Trial Bay. After our illustration of the Boambee Creek specimens were completed the type was located, too late to be incorporated into this study. A second species (*Victoriopisa marina* n.sp.) is described, from estuarine and marine habitats in New South Wales and Victoria.

Methods

The taxonomic descriptions presented in this paper were generated from a DELTA (Dallwitz *et al.*, 1993; Dallwitz *et al.*, 1998) database of Australian melitid species. Unless indicated otherwise, the following attributes are implicit throughout the descriptions, except where the characters concerned are inapplicable.

Head. Eyes present; one pair. *Antenna 1* peduncular article 2 not geniculate. *Mandible* palp present, well developed.

Pereon. *Gnathopod 1* not sexually dimorphic; carpus about 2× as long as broad; carpus without anterodistal swelling; propodus without anterodistal projection, posterodistal margin not swollen. *Gnathopod 2* left and right gnathopods subequal in size; propodus without strong concentration of setae, distolateral margin without spines; dactylus closing along palm, reaching end of palm, inner margin smooth. *Pereopod 5* dactylus unguis anterior margin without accessory spines; carpus and propodus with few (or none) long, slender setae along anterior margin. *Pereopod 6* coxa anterior lobe ventral margin not produced ventrally; carpus and propodus with few (or none) long, slender setae along anterior margin; propodus not expanded posterodistally; dactylus unguis anterior margin without accessory spines. *Pereopod 7* basis with posterior

margin smooth or minutely castelloserrate; merus posterodistal margin narrowly rounded or subquadrate; propodus not expanded posterodistally; dactylus unguis anterior margin without accessory spines.

Pleon. *Pleonite 1* without dorsal serrations, without dorsodistal spines, not dorsally bicarinate. *Pleonite 2* without dorsal serrations, without dorsodistal spines, not dorsally bicarinate. *Pleonite 3* without dorsal serrations, without dorsodistal spines, not dorsally bicarinate. *Epimeron 1* anteroventral corner without curved spine. *Epimeron 3* posteroventral margin smooth. *Urosomite 1* without dorsal carina, without a small dorsal hump, without dorsal serrations, without spines or gape, not dorsally bicarinate, without posterodorsal spine. *Urosomite 2* posterior margin smooth, without dorsolateral robust setae. *Urosomite 3* without dorsal robust setae. *Uropod 1* peduncle with basofacial robust seta; without distoventral spur. *Telson* cleft, without robust setae on inner margins.

A separate generic level DELTA database to species in the *Maera* complex was used to generate generic diagnosis and to generate nexus files. A preliminary phylogenetic analysis was generated using PAUP 4.0 win10 in order to analyse relationships among genera and species in this complex.

Material used in this study is lodged in the Australian Museum, Sydney (AM). The following abbreviations are used on the plates: *A*, antenna; *C*, coxa; *E*, epimeron; *G*, gnathopod; *H*, head; *MD*, mandible; *MP*, maxilliped; *MX*, maxilla; *p*, palp; *P*, pereopod; *PLN*, pleonite; *T*, telson; *U*, uropod; *UR*, urosomite; *L*, left; *R*, right.

Taxonomy
Melitidae Bousfield, 1973

Lowry & Watson (2002) reviewed the discussion of informal groups within the Melitidae. They found a *"Maera-Elasmopus* group" and a *"Melita-Eriopisa"* group recognized by Bousfield (1977) and a *"Nuuanu* group" recognized by McKinney & Barnard (1977). Barnard & Barnard (1983) recognized a *Ceradocus* group (*Maera-Elasmopus* group of Bousfield, 1977), a *Ceradocopsis* group, an *Eriopisa* group, a *Nuuana* group (*Nuuanu* group of McKinney & Barnard, 1977), a *Melita* group (*Melita-Eriopisa* group of Bousfield, 1977) and a *Parapherusa* group.

The Melitidae as conceived by Bousfield (1973) is not well defined and we can find no synapomorphy to define the whole group. In fact there appears to be very few widespread synapomorphies within the group. The extremely unequal rami of uropod 3 (the inner ramus is scale-like and the outer ramus is at least 3× longer than wide) appears to be a synapomorphy that defines a *Melita* and an *Eriopisa* group. The *Eriopisa* group has an extremely well-developed second article on the outer ramus of uropod 3, another strong synapomorphy that separates this group from the *Melita* group. A third synapomorphy (two groups of small setae guarded by spines on the dorsum of urosomite 2) occurs throughout the *Melita* group and the *Nuuana* group, but not in the *Eriopisa* group.

The *Ceradocopsis, Ceradocus* and *Parapherusa* groups all appear to be paraphyletic assemblages at best, with no defining synapomorphies. In this paper, for practical reasons, we recognize a *Ceradocopsis* group, a *Ceradocus* group (including *Parapherusa*), an *Eriopisa* group, a *Nuuana* group and a *Melita* group.

Ceradocus group
Austromaera n.gen.

Type species. *Maera mastersii* Haswell, 1879a.

Diagnosis. *Head* with anteroventral slit; eye ovate. *Antenna 1* accessory flagellum short, significantly less than half length of primary flagellum. *Mandible palp* article 1 not produced distally; article 3 short, tapering distally; article 2 longer than article 3. *Maxilla 1* inner plate with mainly apical setae. *Gnathopod 1* coxa anteroventral corner produced, acute. *Gnathopod 2* significantly enlarged in male and female; left and right gnathopods symmetrical in male (right slightly bigger than left); palm acute in male and female, male both propodi with well defined corner (greater than 90°), female both propodi with well defined corner (greater than 90°); dactylus with 1 or 2 setae on anterior margin. *Pereopods 5–7* dactyli simple. *Epimeron 2* posteroventral corner with 1 small spine. *Epimeron 3* posterior margin smooth. *Uropod 3* rami about 2× peduncle, distally subacute, without apical robust setae; outer ramus 1-articulate. *Telson* deeply cleft, lobes apically subacute, with robust setae on inner margins, without robust setae on outer margins, without apical robust setae.

Etymology. A combination of the Latin word *auster*, meaning southern, with the Latin stem *Maera*.

Species composition. *Austromaera mastersii* (Haswell, 1879a).

Remarks. *Austromaera* is part of the large *Maera* group, in which gnathopod 2 is symmetrical and significantly enlarged in males and females, the palms are acute with well defined corners and the rami of uropod 3 are distally acute or subacute. The main defining characters of the genus are: the weakly produced first article of the mandibular palp and the distally acute margins of the rami of the third uropods. *Austromaera* is the only member of the *Maera* complex with such strongly setose inner margins on the telson. It is excluded from *Maera* and *Miramaera* because of its ovate eyes, its short accessory flagellum and its weakly produced first mandibular palp article. It is excluded from *Maera* and Lupimaera because of its sparsely setose gnathopod 2 dactylus. *Austromaera* occurs in the *Maera* group, but appears to be most similar to the Indian Ocean species of *Zygomaera* that apparently have symmetrical second gnathopods. The main difference between these taxa is the telson that is emarginate in the Indian Ocean species. Currently *Austromaera* is confined to Australian waters.

Distribution. Australia.

Austromaera mastersii (**Haswell, 1879a**)
Figs. 1–4

Megamaera mastersii Haswell, 1879a: 265, pl. 11, fig. 1.–Haswell, 1882: 258.–Haswell, 1885: 105.
Maera mastersii.–Stebbing, 1899: 426.–Stebbing, 1906: 439.–Stebbing, 1910a: 642.–?Chilton, 1921b: 72 (southern Australia).
Not *Moera mastersii.*–Chilton, 1911: 564 (Kermadec Islands) (=*L. tias* Krapp-Schickel, 2003, according to Krapp-Schickel, 2003).
Not *Maera mastersi.*–Thomson, 1882: 235 (in part, part = *M. quadrimana*) (New Zealand).–Sheard, 1936: 177, fig. 3 (South Australia) (= *L. tias* Krapp-Schickel, 2003, according to Krapp-Schickel, 2003).–Sheard, 1937: 24 (South Australia) (=*L. tias* Krapp-Schickel, 2003, according to Krapp-Schickel, 2003).–
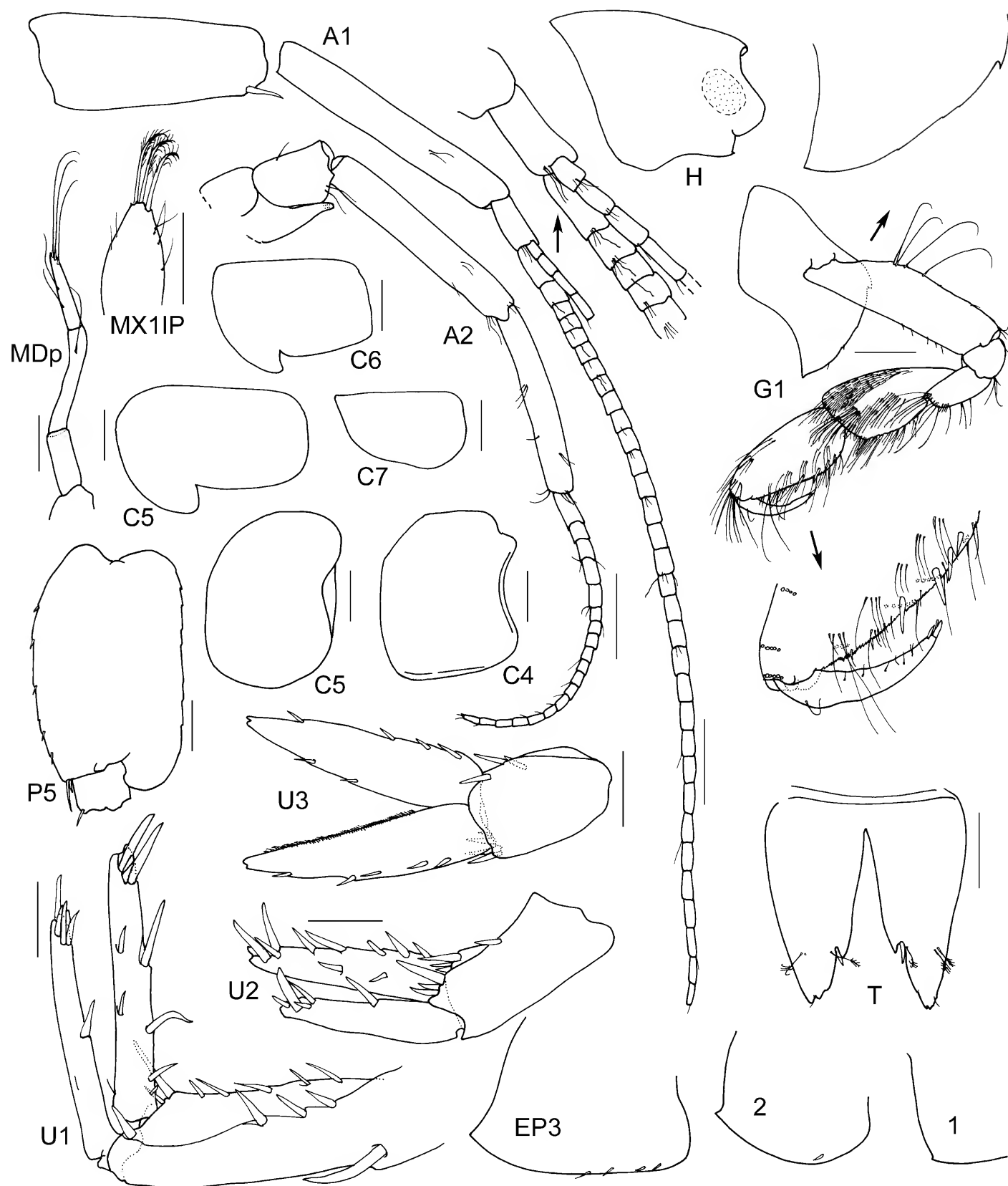
Fig. 1. *Austromaera mastersii* (Haswell, 1879a), syntype, ♀, AM P3487. Port Jackson, New South Wales, Australia.
Scales for MDp and MX1IP represent 0.1 mm, remainder represent 0.2 mm.

Sivaprakasam, 1969: 36, fig. 1 a–g [=*L. mannarensis* (Sivaprakasam, 1970), according to Krapp-Schickel, 2003].– J.L. Barnard, 1972a: 226, fig. 132 (southern Australia) (=*L. leo* Krapp-Schickel, 2003, according to Krapp-Schickel, 2003).– J.L. Barnard, 1972b: 109, figs 55–56 (New Zealand) (=*L. tias* Krapp-Schickel, 2003, according to Krapp-Schickel, 2003).– Ledoyer, 1979: 77, fig. 44 [=*Zygomaera pseudemarginata* (Ledoyer, 1982) (Madagascar)].–Lowry & Fenwick, 1983: 236 (New Zealand subantarctic) (=?*L. tias* Krapp-Schickel, 2003,

according to Krapp-Schickel, 2003).
Not *Maera mastersii*.–Chevreux, 1908: 481 (French Polynesia).– Stebbing, 1910b: 457 (South Africa).–Chilton, 1916: 367 (New Zealand).–Chilton, 1925: 317 (Chatham Islands, New Zealand).– Hale, 1929: 215, fig. 213 (figure = *L. thomsoni* of Miers, 1884) (South Australia) (=*L. tias* Krapp-Schickel, 2003, according to Krapp-Schickel, 2003).–Hurley, 1954: 603 (New Zealand) (=*L. tias* Krapp-Schickel, 2003, according to Krapp-Schickel, 2003).– Griffiths, 1974b: 291 (South Africa).–J.L. Barnard, 1962: 99 (key).
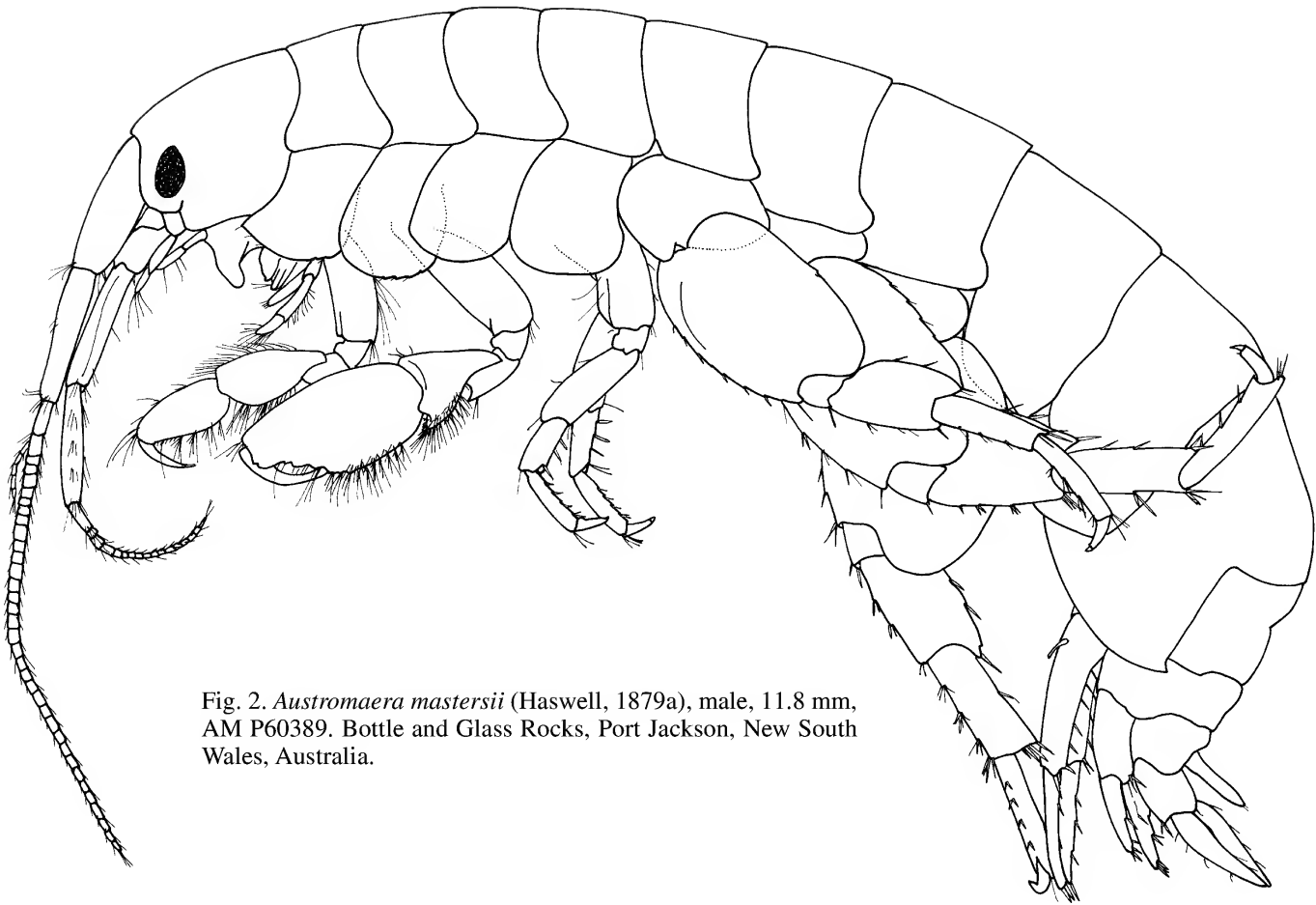
Fig. 2. *Austromaera mastersii* (Haswell, 1879a), male, 11.8 mm, AM P60389. Bottle and Glass Rocks, Port Jackson, New South Wales, Australia.

Type material. Syntype, female, ovigerous, AM P3487, Port Jackson, New South Wales, Australia, [approx. 33°50.9'S 151°16.2'E], [from AM Old Collection].

Additional material examined. New South Wales: male, 11.8 mm, AM P60389; female, 12.5 mm, AM P27286, Bottle and Glass Rocks, Port Jackson, 33°50.9'S 151°16.2'E, in and among dense tubes on sediment covered rocks, G.D. Fenwick, 29 Aug 1977. 1♂, AM P60390; 5 specimens, AM P60391, off Wy-ar-gine Point, Port Jackson, [approx. 33°49'S 151°15.1'E], sand and shell, dredge, Malacological Society, 8 May 1971. 1 specimen, AM P60392, northeast of Marys Rock, Cook Island, 28°11.42'S 153°34.79'E, orange bryozoan, 19 m, R.T. Springthorpe, 8 June 1993, stn NSW-816.

Type locality. Port Jackson, New South Wales, Australia, [approx. 33°50.9'S 151°16.2'E].

Description. Based on syntype female, AM P3487, male, AM P60389 and female AM P27286.

Head. Lateral cephalic lobes broad, rounded, with anteroventral slit, anteroventral corner subquadrate, with acute/subacute spine. *Antenna 1* longer than antenna 2; peduncular article 1 subequal in length to article 2, with 1 distal robust seta on posterior margin; flagellum with 34 articles; accessory flagellum with 6 articles. *Antenna 2* peduncular article 2 cone gland reaching at least to end of peduncular article 3; article 4 longer or subequal to article 5; flagellum with 20 articles *Mandible* palp article 3 rectolinear, setose along straight medial margin, longer than article 1; article 2 longer than article 3; article 1 not produced, shorter than article 2, about twice as long as broad. *Maxilla 1* inner plate with about 3 setae mainly terminal.

Pereon. *Gnathopod 1* coxa anteroventral corner produced, acute, posteroventral corner notch absent; merus without posterodistal spine; palm extremely acute, slightly convex,

without posterodistal corner, defined by posterodistal robust setae. *Gnathopod 2* not sexually dimorphic; subchelate; coxa posteroventral corner notch absent; merus with sharp posteroventral spine; carpus compressed; propodus without medial depression, palm acute, straight, sculptured, with sparse robust setae, defined by posterodistal robust setae, defined by posteroventral corner; apically acute/subacute. *Pereopod 5* basis posterior margin straight, posteroventral corner broadly rounded. *Pereopod 6–7* basis posterior margin convex, posteroventral corner broadly rounded.

Pleon. *Epimeron 1* posteroventral corner broadly rounded, or with small acute spine. *Epimera 1–2* posteroventral margin without spines above posteroventral corner. *Epimeron 3* posterior margin smooth, posteroventral corner with small acute spine. *Uropod 3* inner ramus subequal in length to outer ramus; outer ramus longer (1.2 to 2× length) than peduncle, 1-articulate. *Telson* with robust setae on inner margins (1 or 2 per lobe), without apical robust setae, apical conical extension absent.

Habitat. Marine; littoral; in and among dense tubes on sediment covered rocks, bryozoans, sand and shell, 7 to 19 m depth.

Remarks. Although there are many records of *A. mastersii* in the literature from inside and outside Australia, only Haswell (1879a: 265, pl. 11, fig. 1), Sheard (1936: 177, fig. 3), J.L. Barnard (1972a: 226, fig. 132), J.L. Barnard, 1972b: 109, figs 55–56 and Ledoyer (1979: 77, fig. 44) illustrated their material. Neither Sheard (1936), nor J.L. Barnard (1972a,b) showed the distinctive third uropods and telson illustrated by Haswell (1879a). Their misidentified species have recently been studied by Krapp-Schickel (2003). The
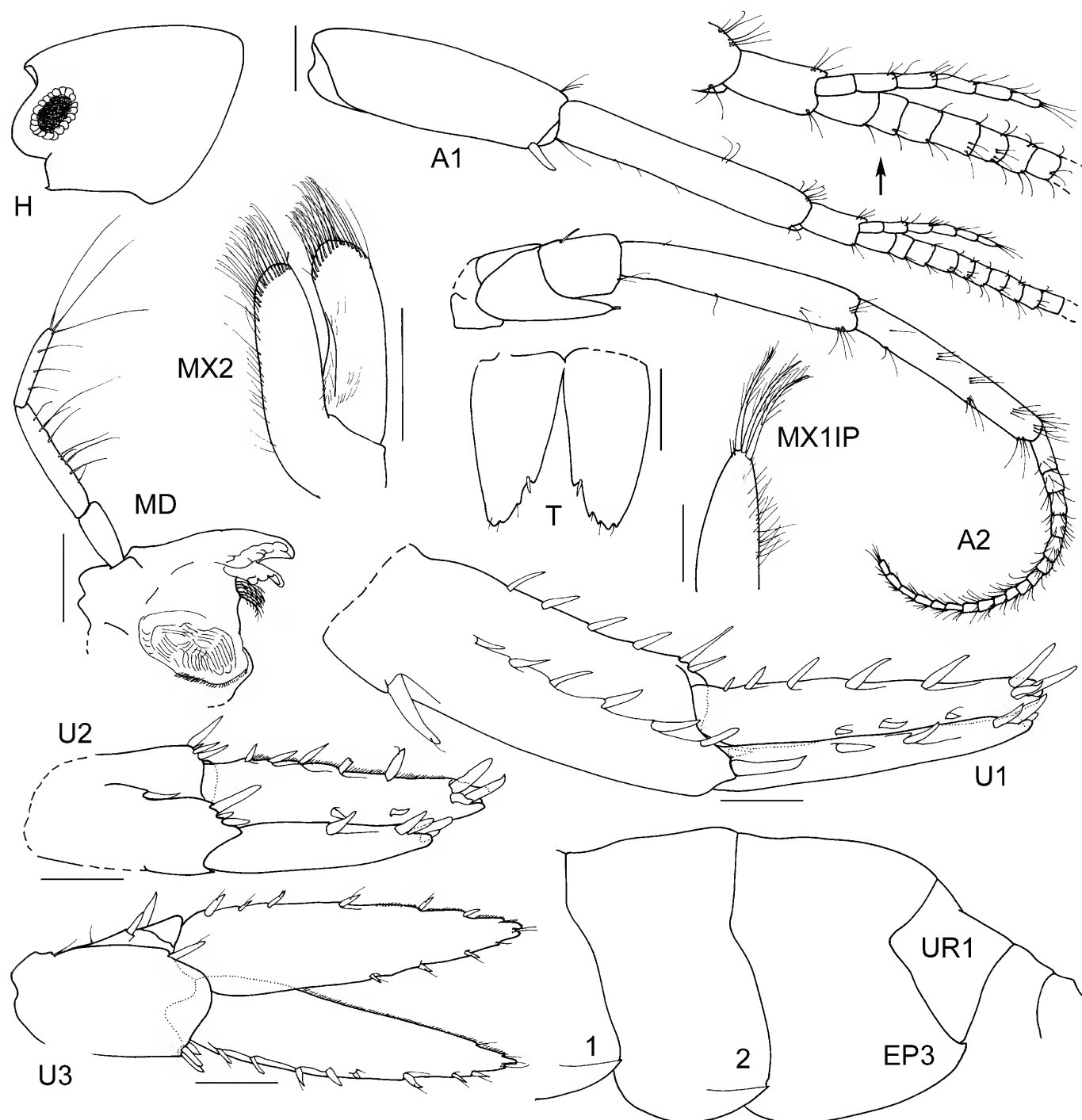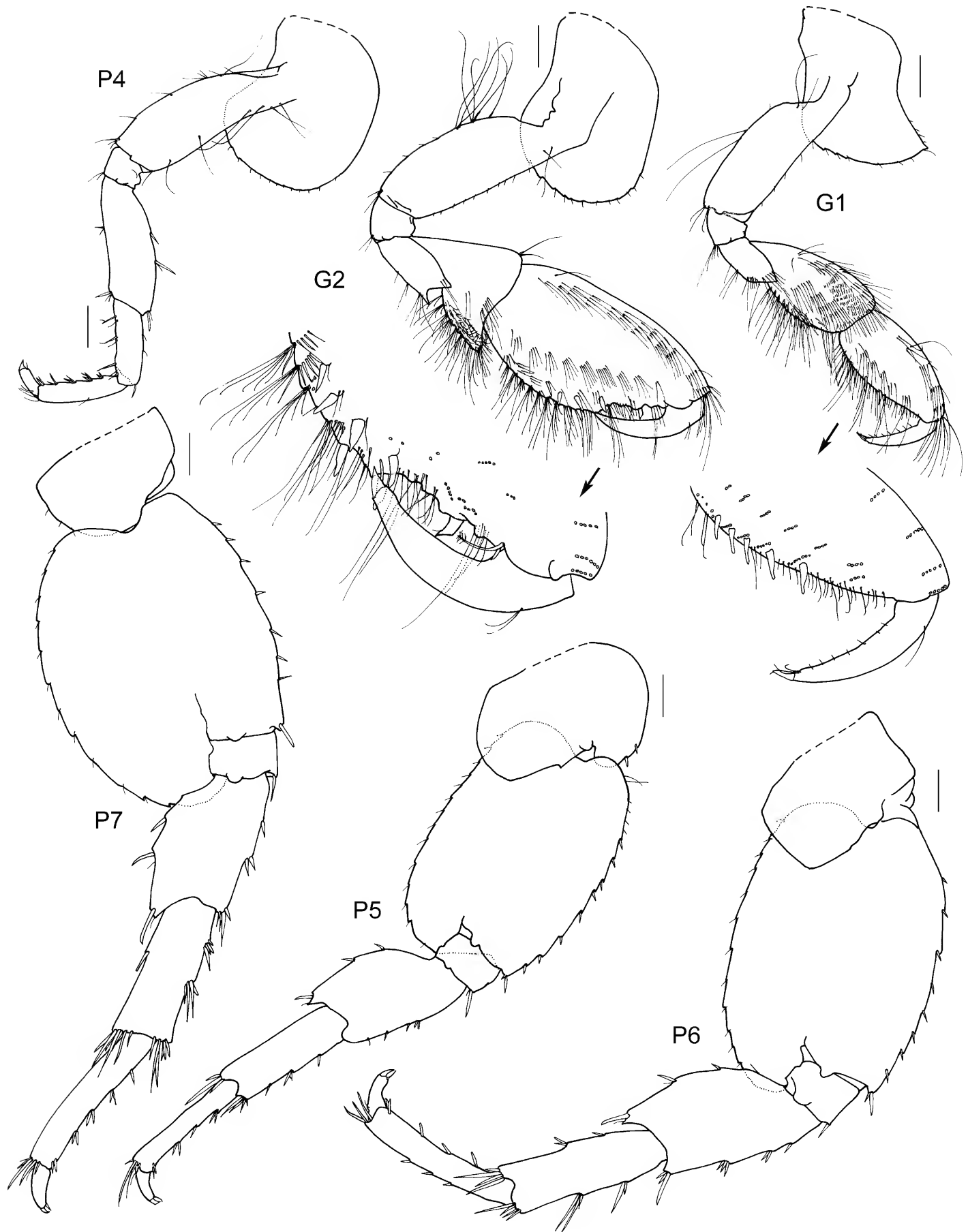
Fig. 3. *Austromaera mastersii* (Haswell, 1879a), male, 11.8 mm, AM P60389. Bottle and Glass Rocks, Port Jackson, New South Wales, Australia. Scale for MX1IP represents 0.1 mm, remainder represent 0.2 mm.

material of Ledoyer (1979) was later shown to be a different species, now known as *Zygomaera pseudemarginata* (Ledoyer, 1982). Based on currently available information, *A. mastersii* appears to be confined to southeastern and possibly southern Australia. Other records attributed to this species (at least since Haswell [1885] synonymized *L. thomsoni* with *A. mastersii* and certainly since the illustrations of Sheard [1936]) represent *Linguimaera leo* and *L. tias* of Krapp-Schickel (2003) plus several unknown species.

Distribution. *New South Wales*: Bottle and Glass Rocks and Wy-ar-gine Point, Port Jackson; Marys Rock, Cook Island (all AM).

Australian geographic areas. Southeastern Australia.

Ceradocus **Costa, 1853**

Ceradocus circe **n.sp.**

Figs. 5–7

Ceradocus rubromaculatus.–Chilton, 1921b: 71, fig. 9a–c.

Type material. HOLOTYPE ♂ "a", 24.3 mm, AM P60564; 1 PARATYPE, ♀ "a", 18.6 mm, AM P60565; 1 PARATYPE, ♂ "b", 22.9 mm, AM P5915; 8 Paratypes, AM E6543, 16 kms north of Circular Head, Tasmania, Australia, [approx. 40°46'S 145°18'E], FIS *Endeavour*, 1909–1914. 1 PARATYPE, female, AM E6542, Tasmanian Coast, Australia, FIS *Endeavour*, 1909–1914

Type locality. 16 kms north of Circular Head, Tasmania, Australia, [approx. 40°46'S 145°18'E].

Description. Based on holotype ♂ "a", AM P60564, paratype ♀ "a", AM P60565, and paratype ♂ "b", AM P5915.

Fig. 4. *Austromaera mastersii* (Haswell, 1879a), male, 11.8 mm, AM P60389. Bottle and Glass Rocks, Port Jackson, New South Wales, Australia. Scales represent 0.2 mm.

Head. Lateral cephalic lobes broad, rounded, with anteroventral notch or slit, anteroventral corner with acute/subacute spine. *Antenna 1* longer than antenna 2; peduncular article 1 subequal in length to article 2, with 4 or more robust setae along posterior margin; flagellum with at least 30 articles; accessory flagellum with 11 articles. *Antenna 2* peduncular article 2 cone gland not reaching to end of peduncular article 3; article 4 subequal to article 5; flagellum

with about 20 articles. *Mandible* palp article 3 cone-like, setose on distomedial margin, subequal to article 1; article 2 longer than article 3; article 1 produced distally, shorter than article 2, about as long as broad. *Maxilla 1* inner plate setose along entire inner margin.

Pereon. *Gnathopod 1* coxa anteroventral corner produced, acute, posteroventral corner notch absent; merus with sharp posterodistal spine; propodus palm acute, straight, defined by posterodistal corner, defined by posterodistal robust setae. *Gnathopod 2* sexually dimorphic; subchelate; coxa posteroventral corner notch absent; merus with sharp posteroventral spine; carpus compressed; propodus without medial depression, without strong concentration of setae, palm acute, straight, sculptured, with group of anterodistal robust setae, without posterodistal robust setae, defined by posteroventral spine; apically acute/subacute. *Pereopod 5* basis posterior margin straight, posteroventral corner narrowly rounded or subquadrate. *Pereopod 6* coxa anterior lobe ventral margin slightly produced, rounded; basis posterior margin straight, posteroventral corner with acute or subacute process. *Pereopod 7* basis posterior margin straight, posteroventral corner with acute or subacute process.

Pleon. *Pleonites 1–3* with dorsal serrations. *Epimeron 1* posteroventral corner with small acute spine. *Epimera 1–2* posteroventral margin with 3 large or small spines above spine defining posteroventral corner, or without spines above posteroventral corner. *Epimeron 3* posterior margin serrate, posteroventral corner with strongly produced acute spine, posteroventral margin serrate. *Urosomite 1* with dorsal serrations, with spines at midline, no conspicuous medial gape. *Urosomite 2* posterior margin serrate. *Uropod 3* inner ramus subequal in length to outer ramus; outer ramus much longer (more than 2× length) than peduncle; 1-articulate. *Telson* each lobe with 3 or more apical/subapical robust

setae, apical conical extension reaching at least halfway along longest seta.

Female (sexually dimorphic characters). *Gnathopod 2* convex, smooth, without robust setae, defined by posterodistal robust setae, defined by posterodistal spine.

Habitat. Marine; continental shelf.

Etymology. Named for the wooden schooner *Circe*, which went ashore in 1892, between Entrance Island and the North Spit, while attempting to pass through Hells Gates and enter Macquarie Harbour, Tasmania.

Remarks. Among Australian species of *Ceradocus, C. circe* occurs in the group with sparse serrations along the posterior margins of epimera 1 and 2. Within this group *C. circe* appears to be the only species with the rami of uropod 3 more than twice as long as the peduncle (not known for *C. yandala* Berents, 1983 from tropical northeastern Australia).
    Ceradocus orchestiipes A. Costa, 1853 from the Mediterranean Sea, has sparse serrations along the posterior margins of epimera 1 and 2, long rami on uropod 3 and the second gnathopods in the male and the female are very similar to those of *C. circe*. But *C. orchestiipes* does not have dorsal serrations on urosomites 1–3, nor does it have a strongly serrate posterodistal corner on epimeron 3.

Distribution. *Tasmania*: north of Circular Head; eastern slope of Bass Strait (Chilton, 1921b).

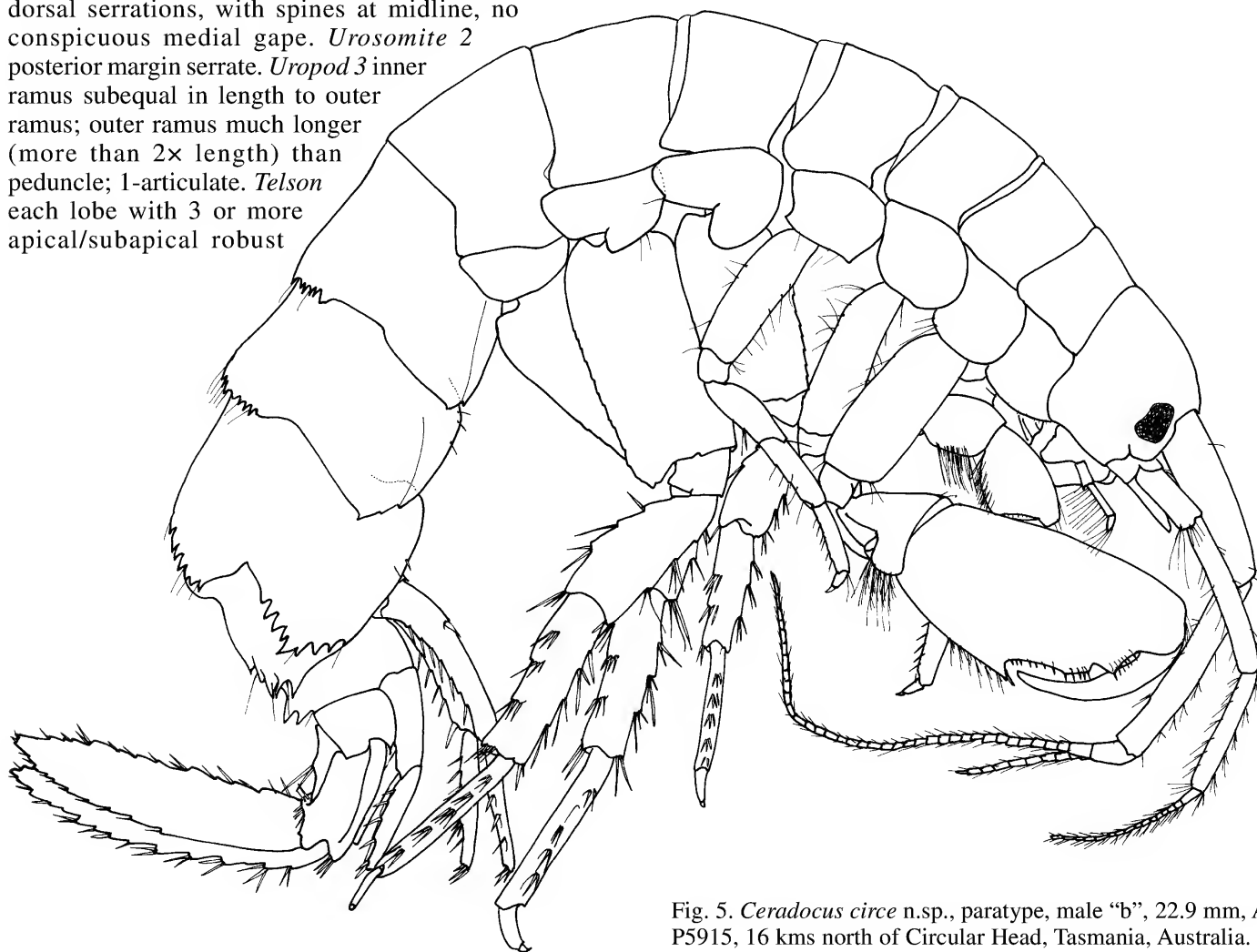**Australian geographic areas**. Southeastern Australia.

Fig. 5. *Ceradocus circe* n.sp., paratype, male "b", 22.9 mm, AM P5915, 16 kms north of Circular Head, Tasmania, Australia.
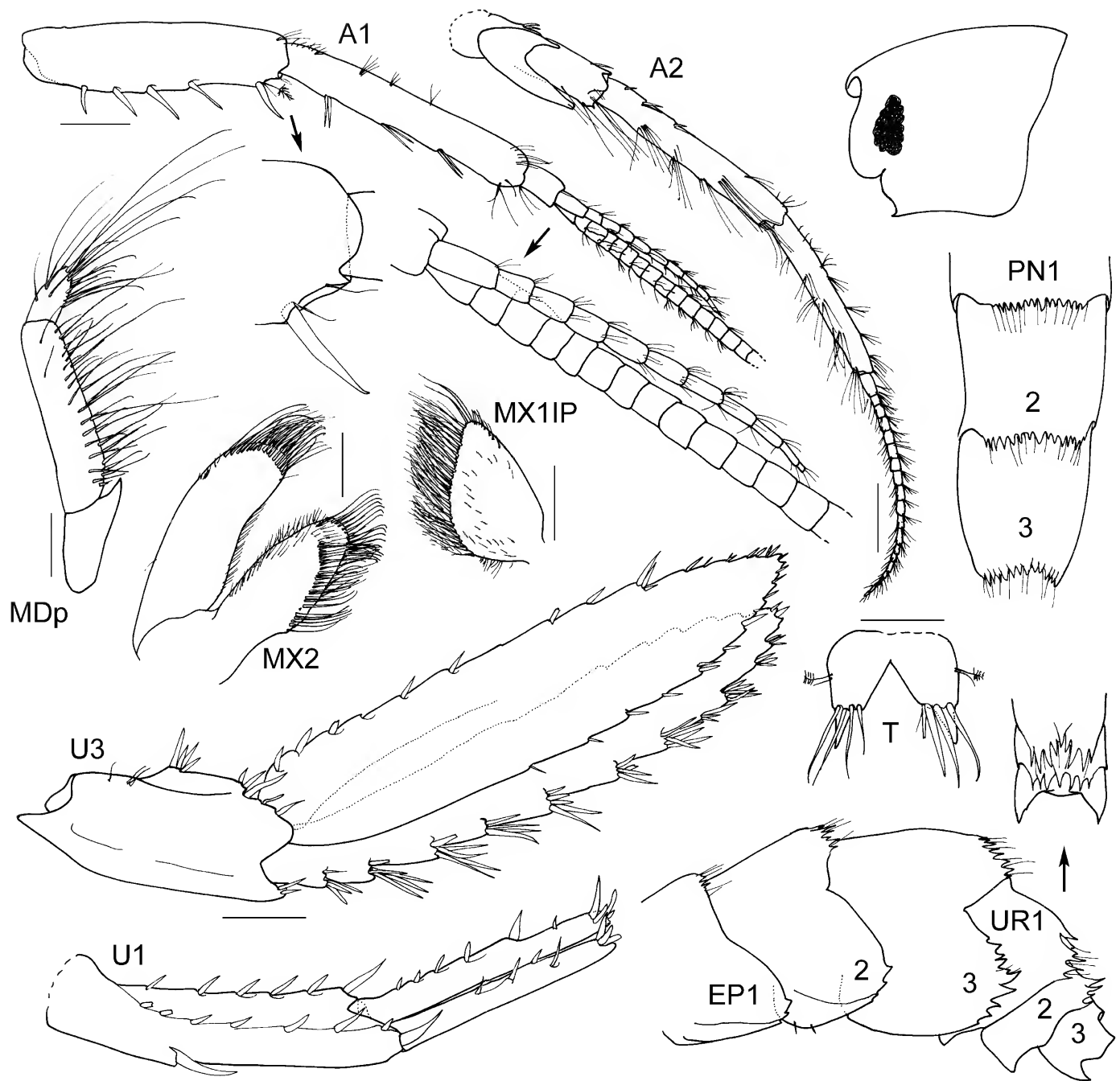
Fig. 6. *Ceradocus circe* n.sp., holotype, male "a", 24.3 mm, AM P60564, 16 kms north of Circular Head, Tasmania, Australia. Scales for A1, A2, U1, U3, T represent 0.5 mm, remainder represent 0.2 mm.

Linguimaera Pirlot

Linguimaera Pirlot, 1936: 309.–Krapp-Schickel, 2003: 258.

Type species. *Linguimaera pirloti* Krapp-Schickel, 2003, replacement name for misidentified type species.

Diagnosis. *Head* with anteroventral slit; eye ovate to reniform. *Antenna 1* accessory flagellum short, significantly less than half length of primary flagellum. *Mandible palp* article 1 not produced distally; article 2 longer than article 3; article 3 long, rectolinear. *Maxilla 1* inner plate with mainly apical setae. *Gnathopod 1* coxa anteroventral corner produced, acute or subacute. *Gnathopod 2* significantly enlarged in male, not in female; left and right gnathopods asymmetrical in male; palm acute in male and female, male one propodus with well defined corner, the other propodus with poorly defined or no corner, female with poorly defined corner or no corner in either propodus; dactylus with 1 or 2

setae on anterior margin. *Pereopods 5–7* dactyli simple. *Epimeron 3* posterior margin serrate. *Uropod 3* rami about 2× peduncle, distally truncated, apical robust setae short; outer ramus 1-articulate. *Telson* emarginate, without robust setae on outer margins, with apical robust setae, apical robust setae long.

Species composition. *Linguimaera boecki* (Haswell, 1879b); *L. bogombogo* Krapp-Schickel, 2003; *L. caesaris* Krapp-Schickel, 2003; L. *eugeniae* Schellenberg, 1931; *L. garitima* Krapp-Schickel, 2003; *L. hamigera* (Haswell, 1879b); *L. kellissa* Krapp-Schickel, 2003; *L. leo* Krapp-Schickel, 2003; *L. mannarensis* Sivaprakasam, 1970; *L. octodens* (Sivaprakasam, 1968); *L. pirloti* Krapp-Schickel, 2003; *L. schickelae* n.sp.; *L. thomsoni* (Miers, 1884); *L. tias* Krapp-Schickel, 2003.
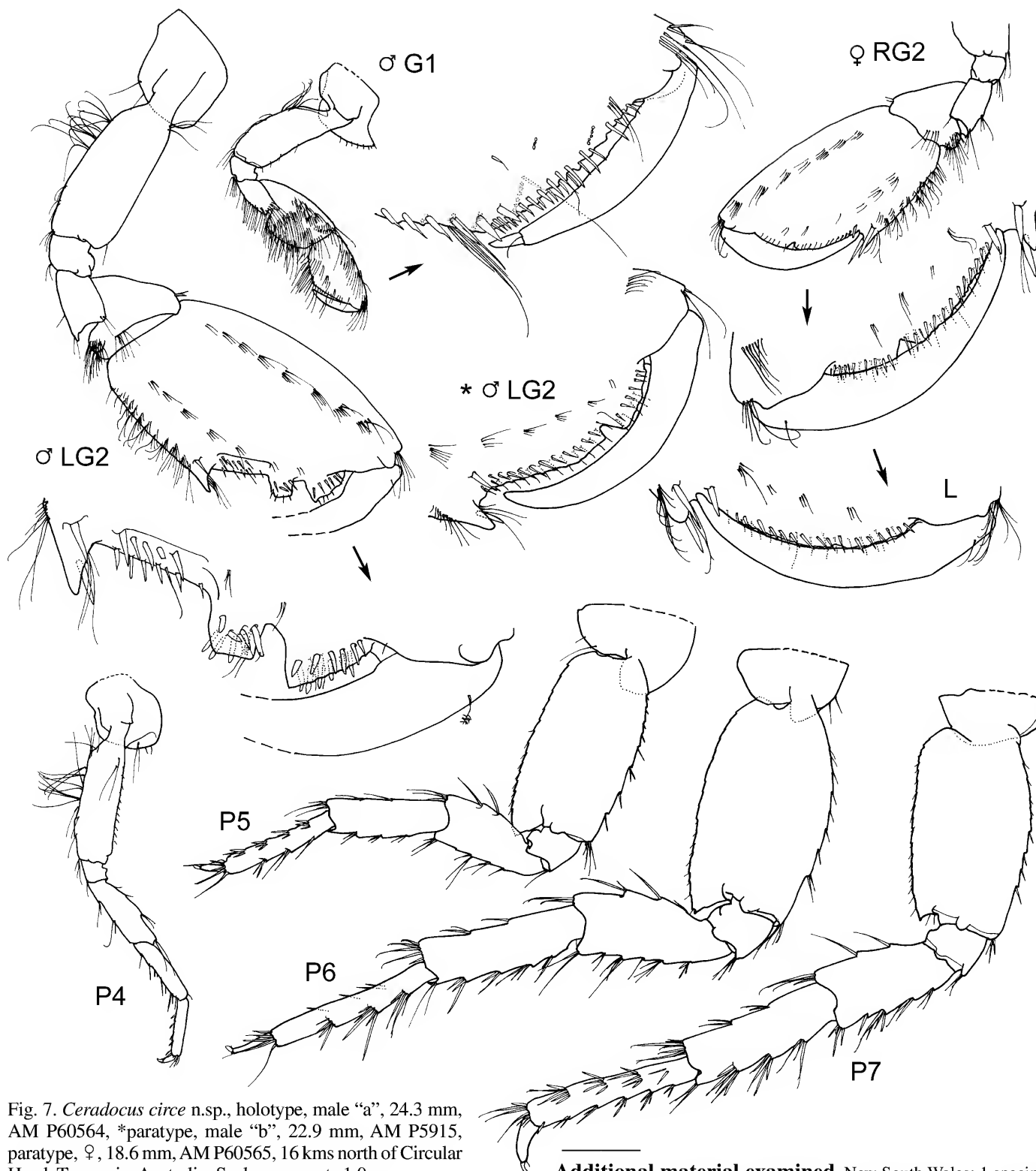
Distribution. Indo-Pacific and Mediterranean.

Fig. 7. *Ceradocus circe* n.sp., holotype, male "a", 24.3 mm, AM P60564, *paratype, male "b", 22.9 mm, AM P5915, paratype, ♀, 18.6 mm, AM P60565, 16 kms north of Circular Head, Tasmania, Australia. Scale represents 1.0 mm.

Linguimaera boecki (Haswell)

Figs. 8–10

Megamoera boeckii Haswell, 1879b: 336, pl. 21, fig. 6.
?*Maera boeckii*.–Della Valle, 1893: 732.
Elasmopus boeckii.–Stebbing, 1899: 426.–Stebbing, 1906: 445.– Stebbing, 1910a: 643.
Maera boecki.–Barnard & Barnard, 1983: 623.
Not *Elasmopus boeckii*.–K.H. Barnard, 1916: 199: pl. 27, figs 13–14.

Type material. Neotype: male, 7.5 mm, AM P60619, off Sow and Pigs Reef, Port Jackson, New South Wales, 33°50.3'S 151°16.2'E, shelley sand, 5 m, benthic grab, J.K. Lowry & A.R. Jones, 30 Sep. 1976, stn NSW-184.

Additional material examined. New South Wales: 1 specimen, AM P60763; 1♀, 7.9 mm, AM P60947, type locality.

Type locality. Sow and Pigs Reef, Port Jackson, New South Wales (33°50.3'S 151°16.2'E), shelley sand, 5 m depth.

Description. Based on neotype male, AM P60619 and female, AM P60947.

Head. Lateral cephalic lobes broad, rounded, with anteroventral notch or slit, anteroventral corner subquadrate. *Antenna 1* longer than antenna 2; peduncular article 1 subequal in length to article 2, with 2 robust setae along posterior margin; flagellum with 20 articles; accessory flagellum with 4 articles. *Antenna 2* peduncular article 2 cone gland not reaching to end of peduncular article 3; article 4 longer than article 5; flagellum with 10 articles.
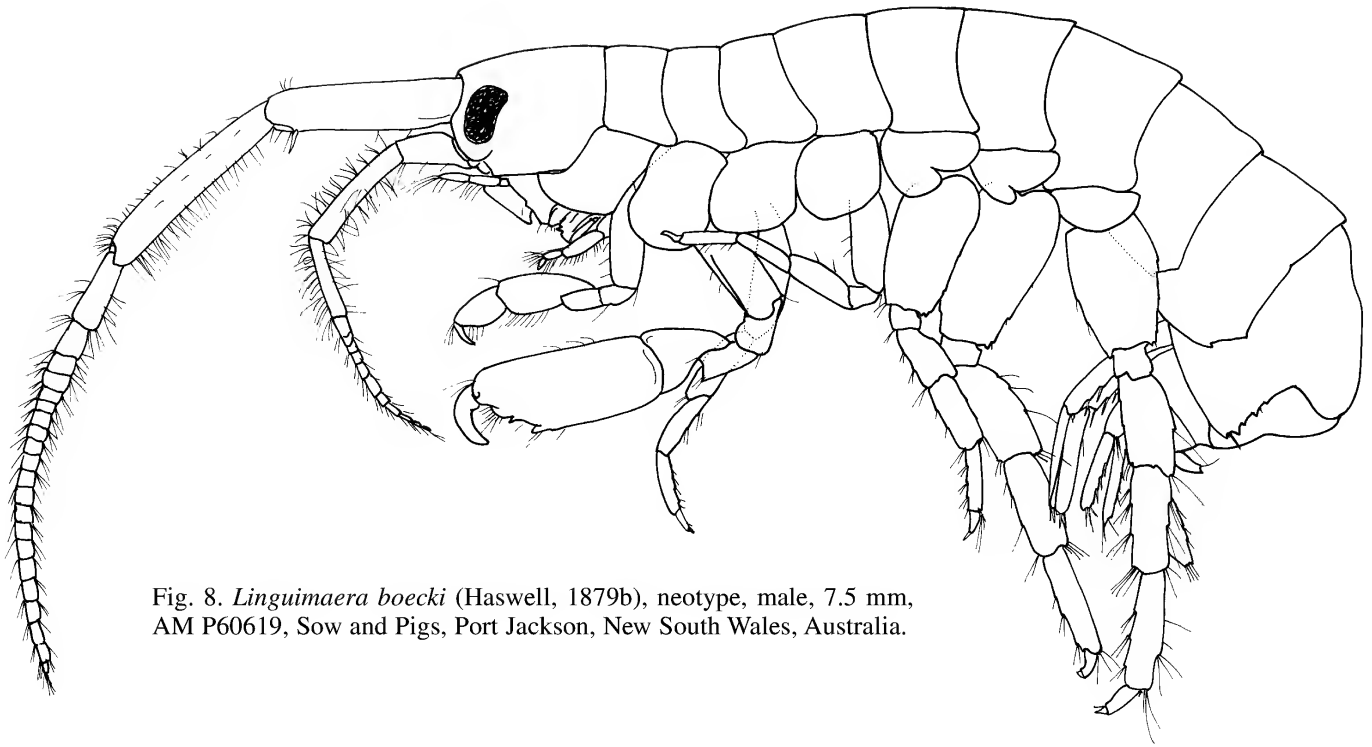
Fig. 8. *Linguimaera boecki* (Haswell, 1879b), neotype, male, 7.5 mm, AM P60619, Sow and Pigs, Port Jackson, New South Wales, Australia.

Mandible palp article 3 rectolinear, setose on distomedial margin, longer than article 1; article 2 longer than article 3; article 1 not produced, shorter than article 2, about twice as long as broad. *Maxilla 1* inner plate with 3 setae mainly terminal.

Pereon. *Gnathopod 1* coxa anteroventral corner produced, acute, posteroventral corner notch absent; merus without posterodistal spine; propodus palm acute, straight, without posterodistal corner, defined by posterodistal robust setae. *Gnathopod 2* sexually dimorphic; left and right gnathopods unequal in size, subchelate; coxa posteroventral corner notch absent; (larger) merus with sharp posteroventral spine; carpus compressed; propodus palm angle acute, straight, defined by posterodistal spine, with robust setae; dactylus apically blunt; (smaller) merus with sharp posteroventral spine; carpus long; propodus palm straight, without posteroventral spine. *Pereopod 5* basis posterior margin straight, posteroventral corner narrowly rounded or subquadrate. *Pereopod 6* coxa anterior lobe ventral margin slightly produced, rounded; basis posterior margin straight, posteroventral corner narrowly rounded or subquadrate. *Pereopod 7* basis posterior margin straight, with posterior margin smooth or minutely castelloserrate, posteroventral corner narrowly rounded or subquadrate.

Pleon. *Epimeron 1* posteroventral corner with small acute spine. *Epimera 1–2* posteroventral margin with 1 to 2 large or small spines above spine defining posteroventral corner. *Epimeron 3* posterior margin minutely serrate, postero-ventral corner with small acute spine. *Urosomites 1–3* dorsally smooth. *Uropod 3* inner ramus subequal in length to outer ramus; outer ramus longer (1.2 to 2× length) than peduncle, 1-articulate. *Telson* deeply emarginate, each lobe with 1 apical/subapical robust seta, apical conical extension reaching scarcely one third along longest seta.

Female (sexually dimorphic characters). *Gnathopod 2* carpus long; propodus without medial depression, setose, palm acute, straight or slightly concave, smooth, lined with

robust setae, defined by posterodistal robust setae, defined by posteroventral corner; dactylus apically acute/subacute.

Habitat. Marine; littoral, shelley sand, 5 m depth.

Remarks. *Linguimaera boecki* appears to be most similar to *L. hamigera*. They differ from other members of the genus in having rather short rami on uropod 3 and *L. boecki* is the only species of *Linguimaera* with an emarginate telson.

Distribution. *New South Wales*: Port Jackson (Haswell, 1879b; AM).

Australian geographic areas. Southeastern Australia.

Linguimaera hamigera (Haswell)

Figs. 11–13

Moera hamigera Haswell, 1879b: 333, pl. 21, fig. 1.
Maera hamigera.–Stebbing, 1888: 1790.–Della Valle, 1893: 723.– Stebbing 1906: 437.–Barnard & Barnard, 1983: 623.
Not *Maera hamigera*.–Walker 1909: 335, pl. 43, fig. 5, pl. 3.– Stebbing 1910a: 600.–K.H. Barnard, 1916: 196, pl. 27, figs 11–12.–Chilton, 1921b: 73.–J.L. Barnard, 1965: 507, fig. 16 (in part).–Karaman & Ruffo, 1971: 152, figs 21–23.–Ledoyer, 1982: 523, figs 196–197.–Karaman, 1982: 312, fig. 211.– Lyons & Myers, 1993: 587, fig. 10.–Myers, 1997: 109.

Type material. Syntype, ♂, AM P3477, Port Jackson, New South Wales, Australia, [approx. 33°51'S 151°16'E], [AM Old Collection].

Type locality. Port Jackson, New South Wales, Australia, (33°51'S 151°16'E).

Additional material examined. New South Wales: 1 specimen, AM P57328, 100 m north west of Split Solitary Island, 30°14.0'S 153°10.8'E, sponge, 15–17 m, R.T. Springthorpe, 7 March 1992, stn NSW-683. 1 specimen, AM P57329, 50 m west of Split Solitary Island, 30°14.0'S 153°10.8'E, rocks with brown & red algae (coralline & *Halimeda* sp.), 15–17 m, P. Hutchings & C. Rose, 7 March 1992, stn NSW-692. 1 specimen, AM P56712, Coffs Harbour Jetty, Coffs Harbour, 30°18.4'S 153°08.5'E, arborescent sponge on jetty pilings, 7 m, S.J. Keable, 9 March 1992, stn NSW-735. 1 specimen, AM P25467, 5.5–6.5
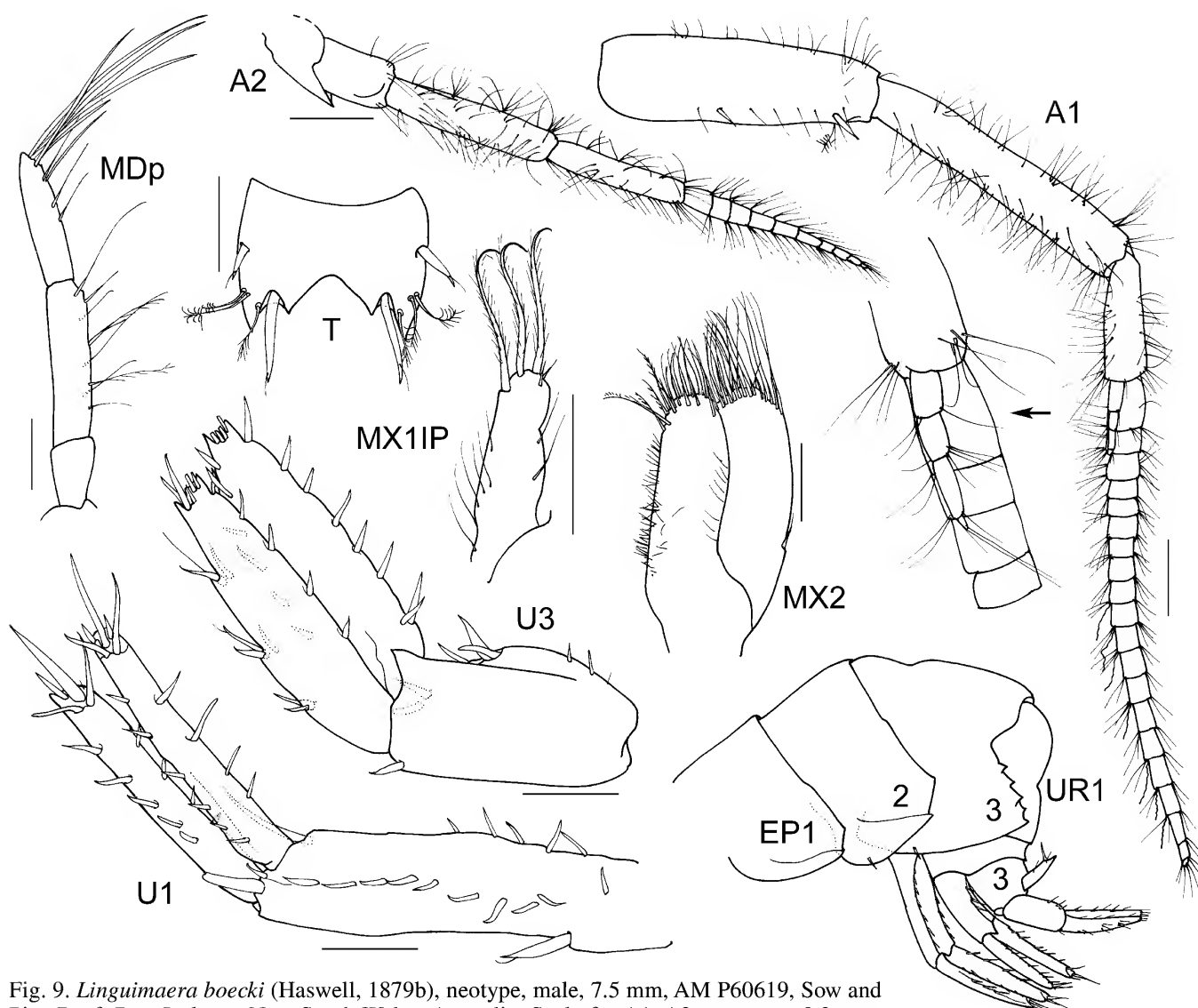
Fig. 9. *Linguimaera boecki* (Haswell, 1879b), neotype, male, 7.5 mm, AM P60619, Sow and Pigs Reef, Port Jackson, New South Wales, Australia. Scale for A1, A2 represents 0.2 mm, remainder represent 0.1 mm

km off Wattamolla, 34°10'S 151°11'E, mud, 99–108 m, E.R. Waite on HMCS *Thetis*, 22 March 1898, stn 57. 1♂, AM P60608, Munganno Point, Twofold Bay, 37°06.2'S 149°55.7'E, subtidal rock platform, wharf pile, S.J. Keable & E.A. Bamber, 12 December 1984, stn M2,3. 1♀, AM P60609, same locality. Tasmania: 1 specimen, E6546, eastern slope of Bass Strait, [approx. 39°00'S 148°40'E], FIS *Endeavour*, 1909–1914. 1 specimen, AM P25468, same locality.

Description. Based on syntype, ♂, AM P3477, ♂, AM P60608, and female, AM P60609.

Head. Lateral cephalic lobes broad, rounded, with anteroventral notch or slit, anteroventral corner subquadrate. *Antenna 1* longer than antenna 2; peduncular article 1 slightly longer than or subequal in length to article 2, with 1 robust seta on posterior distal margin; flagellum with 26 articles; accessory flagellum with 4 articles. *Antenna 2* peduncular article 2 cone gland not reaching to end of peduncular article 3; article 4 slightly longer than article 5; flagellum with 9 articles. *Mandible* palp article 3 rectolinear, setose along straight medial margin, longer than article 1; article 2 longer than article 3; article 1 not produced, shorter than article 2, about as long as broad. *Maxilla 1* inner plate with setae mainly terminal.

Pereon. *Gnathopod 1* coxa anteroventral corner produced, acute, posteroventral corner notch absent; merus without posterodistal spine; propodus palm acute, slightly convex,

defined by posterodistal corner, defined by posterodistal robust setae. *Gnathopod 2* sexually dimorphic; subchelate; left and right gnathopods unequal in size; coxa posteroventral corner notch absent; (larger) merus with subquadrate posteroventral corner; carpus compressed; propodus palm angle nearly transverse, concave, defined by posterodistal spine, with robust setae; dactylus apically blunt; (smaller) merus with sharp posteroventral spine; carpus short, or long; propodus palm straight, without posteroventral spine. *Pereopod 5* basis posterior margin slightly convex, posteroventral corner broadly rounded. *Pereopod 6* coxa anterior lobe ventral margin slightly produced, rounded, or not produced ventrally; basis posterior margin straight, posteroventral corner broadly rounded. *Pereopod 7* basis posterior margin slightly convex, with posterior margin smooth or minutely castelloserrate, posteroventral corner broadly rounded.

Pleon. *Epimeron 1* posteroventral corner broadly rounded. *Epimera 1–2* posteroventral margin without spines above posteroventral corner. *Epimeron 3* posterior margin smooth or minutely serrate, posteroventral corner with strongly produced acute spine. *Uropod 3* inner ramus subequal in length to outer ramus; outer ramus longer (1.2 to 2× length) than peduncle, 1-articulate. *Telson* each lobe with 3 or more apical/subapical robust setae, apical conical extension reaching scarcely one third along longest seta.
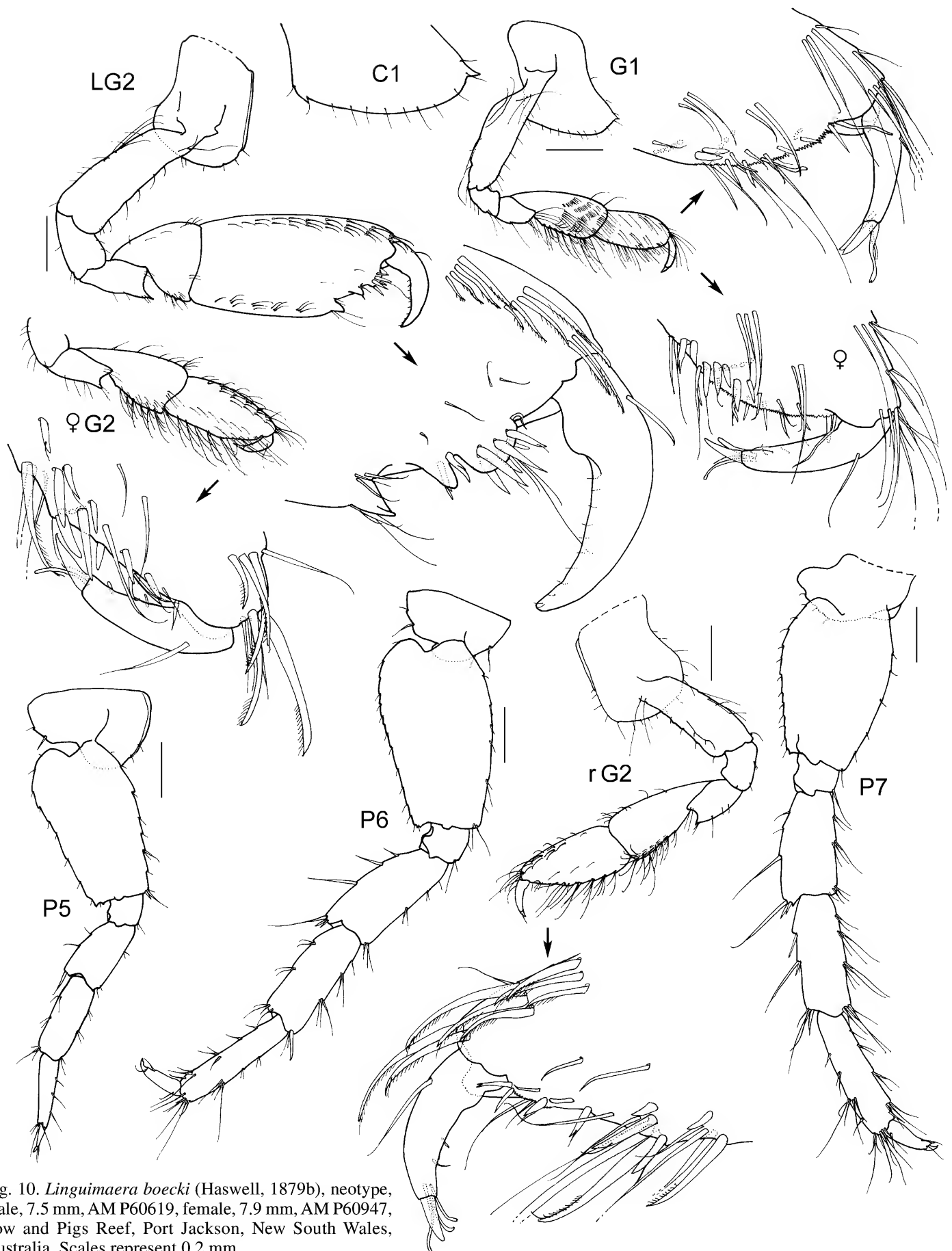
Fig. 10. *Linguimaera boecki* (Haswell, 1879b), neotype, male, 7.5 mm, AM P60619, female, 7.9 mm, AM P60947, Sow and Pigs Reef, Port Jackson, New South Wales, Australia. Scales represent 0.2 mm.

Female (sexually dimorphic characters). *Gnathopod 2* merus with sharp posteroventral spine; carpus short, or long; propodus without medial depression, palm acute, straight, sculptured, with sparse robust setae, defined by posterodistal robust setae, defined by posteroventral corner; dactylus apically acute/subacute.

Habitat. Marine; littoral; subtidal rock platforms, 0 to 7 m depth.

Remarks. Since Haswell (1879b) described *Linguimaera hamigera* (as *Maera hamigera*) from Port Jackson, only Stebbing (1910a) has reported it from Australian waters—several specimens of about 5 mm length from off Wattamolla, which he unfortunately did not illustrate. However, it has been reported by Walker (1909) from the Red Sea, K.H. Barnard (1916) from Southern Africa, J.L. Barnard (1965) from Micronesia, Karaman & Ruffo (1971) from the Mediterranean Sea, Myers (1997) from Western Samoa and Ledoyer (1982) from Madagascar. Ledoyer (1982) completely illustrated and described his material. Based on this species concept he suggested that the *Maera* sp. A of J.L. Barnard, 1970, is also *L. hamigera*, extending its distribution to Hawaii and that *L. mannarensis* (Sivaprakasam, 1970) is a synonym of *L. hamigera*, thus extending its distribution into India, a proposition not accepted by Krapp-Schickel (2003).

All reports subsequent to Stebbing (1910a) must be considered as erroneous. As currently known, *A. hamigera* is confined to southeastern Australia. Illustrated species in the literature (Walker, 1909; K.H. Barnard, 1916; J.L. Barnard, 1965; Karaman & Ruffo, 1971; Ledoyer, 1982) refer to one or more unnamed species. For instance Karaman & Ruffo (1971) illustrated a cleft telson without setae on the inner margins, whereas Ledoyer's (1982) specimens have well-developed robust setae along the inner margins.

Linguimaera hamigera is most similar to *L. boecki*, but easily distinguished from that species by its cleft telson.

Distribution. *New South Wales*: Coffs Harbour (AM); Port Jackson (Haswell, 1879b); Munganno Point, Twofold Bay (AM). *Tasmania*: eastern slope of Bass Strait.

Australian geographic areas. Southeastern Australia.

Linguimaera schickelae n.sp.

Figs. 14–16

Type material. HOLOTYPE, ♂, 15.4 mm, AM P60620, Little Bay, New South Wales, Australia, [approx. 33°59'S 151°15'E], under stones between tide marks, G.P. Whitley, 18 April 1924. 2 PARATYPES, AM P60618; 1 PARATYPE ♀, 14.1 mm, AM P60948; Clovelly Pool, Clovelly, New South Wales, Australia, [approx. 33°55'S 151°16'E], from under stones, 7 m, P.C. Terrill, 12 June 1979.

Type locality. Little Bay, New South Wales, Australia, [approx. 33°59'S 151°15'E].

Additional material examined. New South Wales: 1 specimen, AM P62902, northern cove of Boondelbah Island, Port Stephens, 32°42.28'S 152°13.47'E, airlift under small boulders, 19.6 m, R.T. Springthorpe, P.B. Berents & A. Murray, 28 May 1998, stn NSW-1401.

Description. Based on holotype male, AM P60620 and paratype female, AM P60948.

Head. Lateral cephalic lobes broad, rounded, with anteroventral notch or slit, anteroventral corner subquadrate, with acute/subacute spine. *Antenna 1* longer than antenna 2; peduncular article 1 subequal in length to article 2 or shorter than article 2, with 1 robust seta on posterior margin (distal); flagellum with about 26 articles; accessory flagellum with 7 articles. *Antenna 2* peduncular article 2 cone gland not reaching to end of peduncular article 3; article 4 longer than article 5; flagellum with about 14 articles. *Mandible* palp article 3 rectolinear, setose
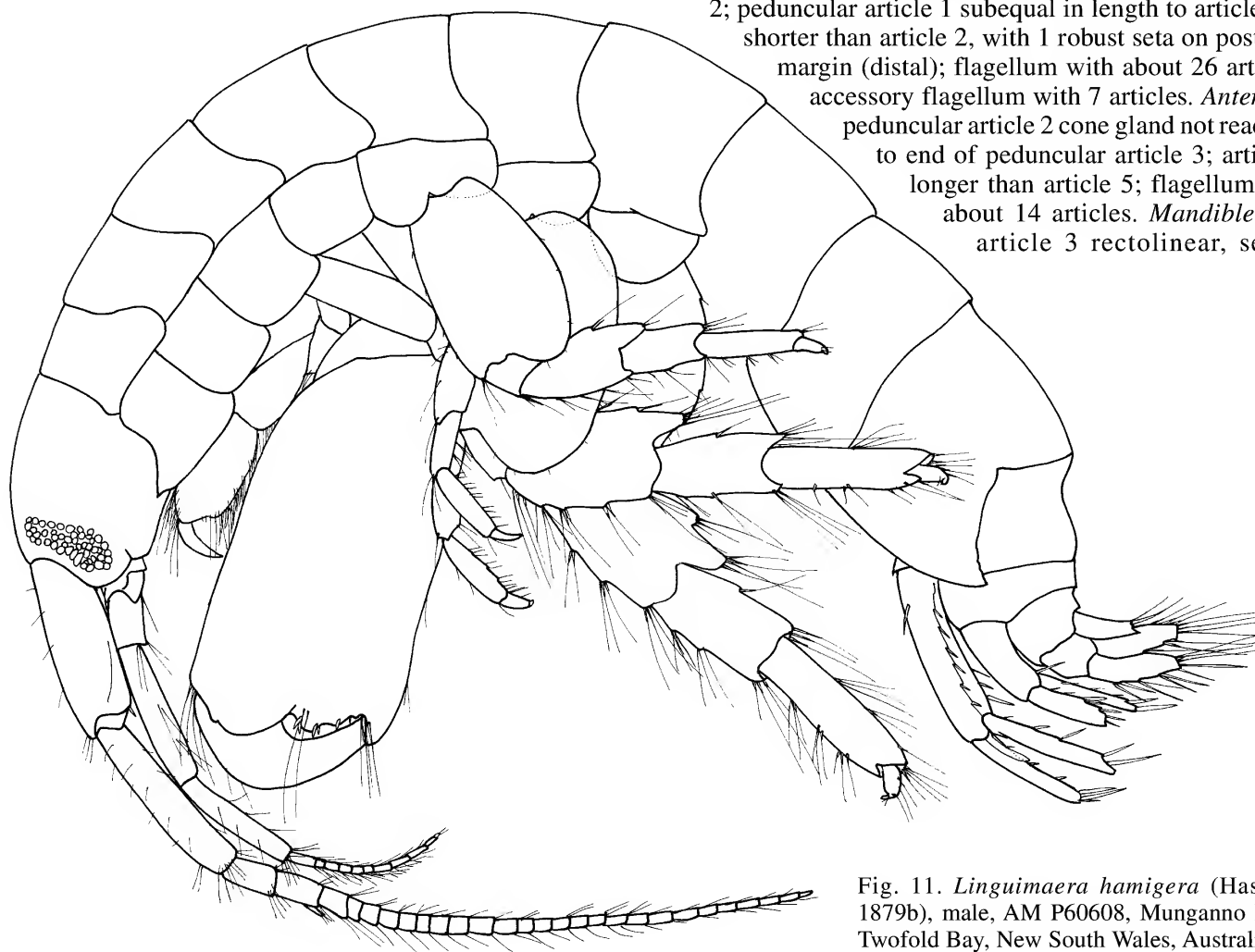
Fig. 11. *Linguimaera hamigera* (Haswell, 1879b), male, AM P60608, Munganno Point, Twofold Bay, New South Wales, Australia.
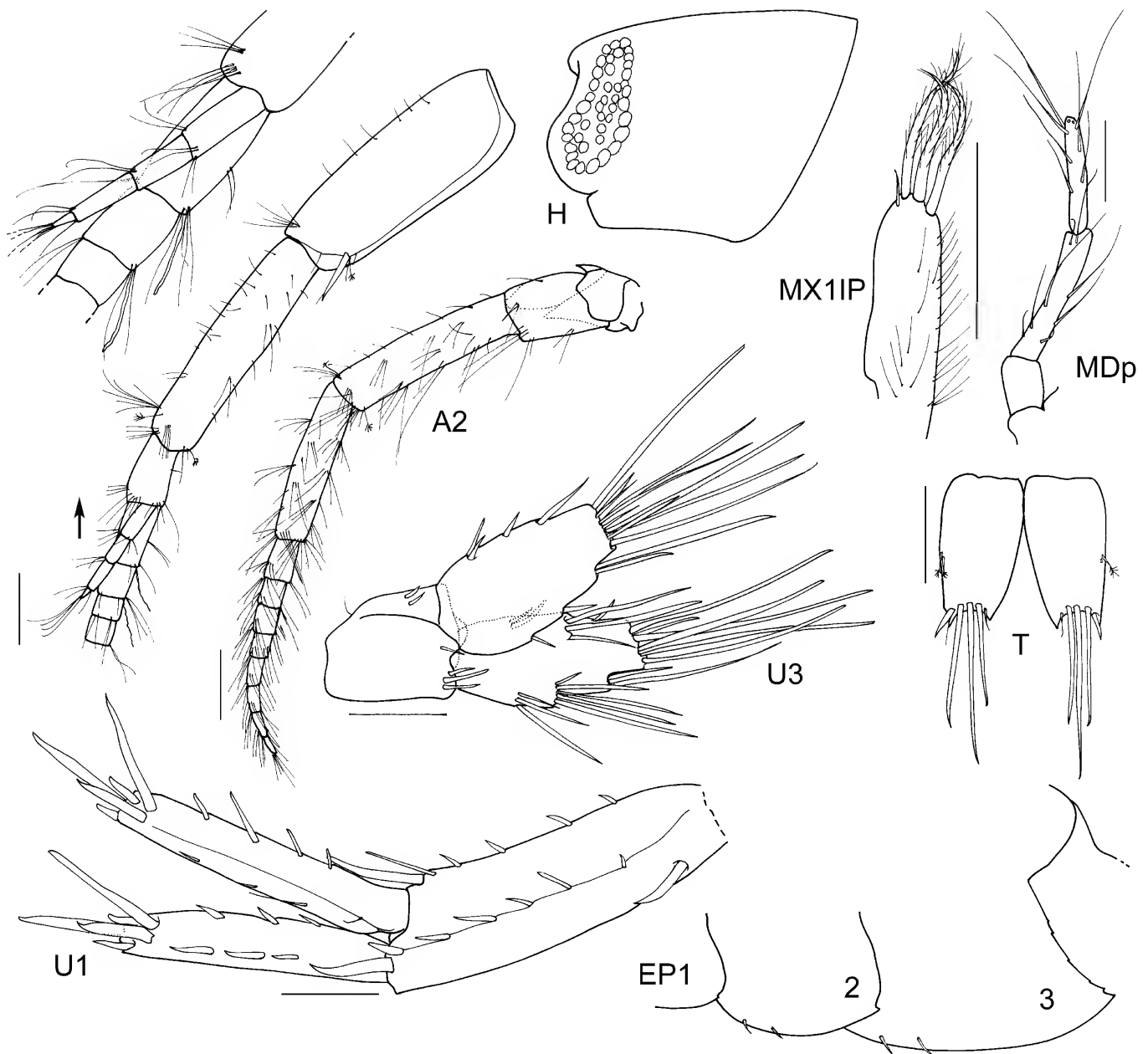
Fig. 12. *Linguimaera hamigera* (Haswell, 1879b), male, AM P60608, Munganno Point, Twofold Bay, New South Wales, Australia. Scales for MDp, MX1IP represent 0.1 mm, remainder represent 0.2 mm.

along straight medial margin, longer than article 1; article 2 longer than article 3; article 1 not produced, shorter than article 2, about as long as broad. *Maxilla 1* inner plate with setae mainly terminal.

Pereon. *Gnathopod 1* coxa anteroventral corner produced, acute, posteroventral corner notch present; merus with sharp posterodistal spine; carpus about 3× as long as broad; palm acute, straight, defined by posterodistal corner, defined by posterodistal robust setae. *Gnathopod 2* sexually dimorphic; left and right gnathopods unequal in size; coxa posteroventral corner notch absent; (larger) subchelate; merus with sharp posteroventral spine; carpus short; palm angle acute, concave, defined by posterodistal spine, with robust setae; dactylus apically acute; (smaller) subchelate; merus with sharp posteroventral spine; carpus short; palm slightly concave, defined by posteroventral spine. *Pereopod 5* basis posterior margin slightly concave or straight, posteroventral corner with acute or subacute process. *Pereopod 6* coxa anterior lobe ventral margin slightly produced, rounded;

basis posterior margin slightly concave, basis posteroventral corner narrowly rounded or subquadrate. *Pereopod 7* basis posterior margin straight, posteroventral corner narrowly rounded or subquadrate.

Pleon. *Epimeron 1* posteroventral corner with small acute spine. *Epimera 1–2* posteroventral margin with 1 to 2 large or small spines above spine defining posteroventral corner. *Epimeron 3* posterior margin serrate, posteroventral corner with small acute spine. *Uropod 3* inner ramus subequal in length to outer ramus; outer ramus longer (1.2 to 2× length) than peduncle; 1-articulate. *Telson* with robust setae on inner margins (about 4 per lobe), each lobe with 2 apical/subapical robust setae, apical conical extension reaching scarcely one third along longest seta.

Female (sexually dimorphic characters). *Gnathopod 2* propodus palm straight, sculptured, lined with robust setae.

Etymology. Named for Traudl Krapp-Schickel, who has contributed greatly to the revision of the *Maera* complex.
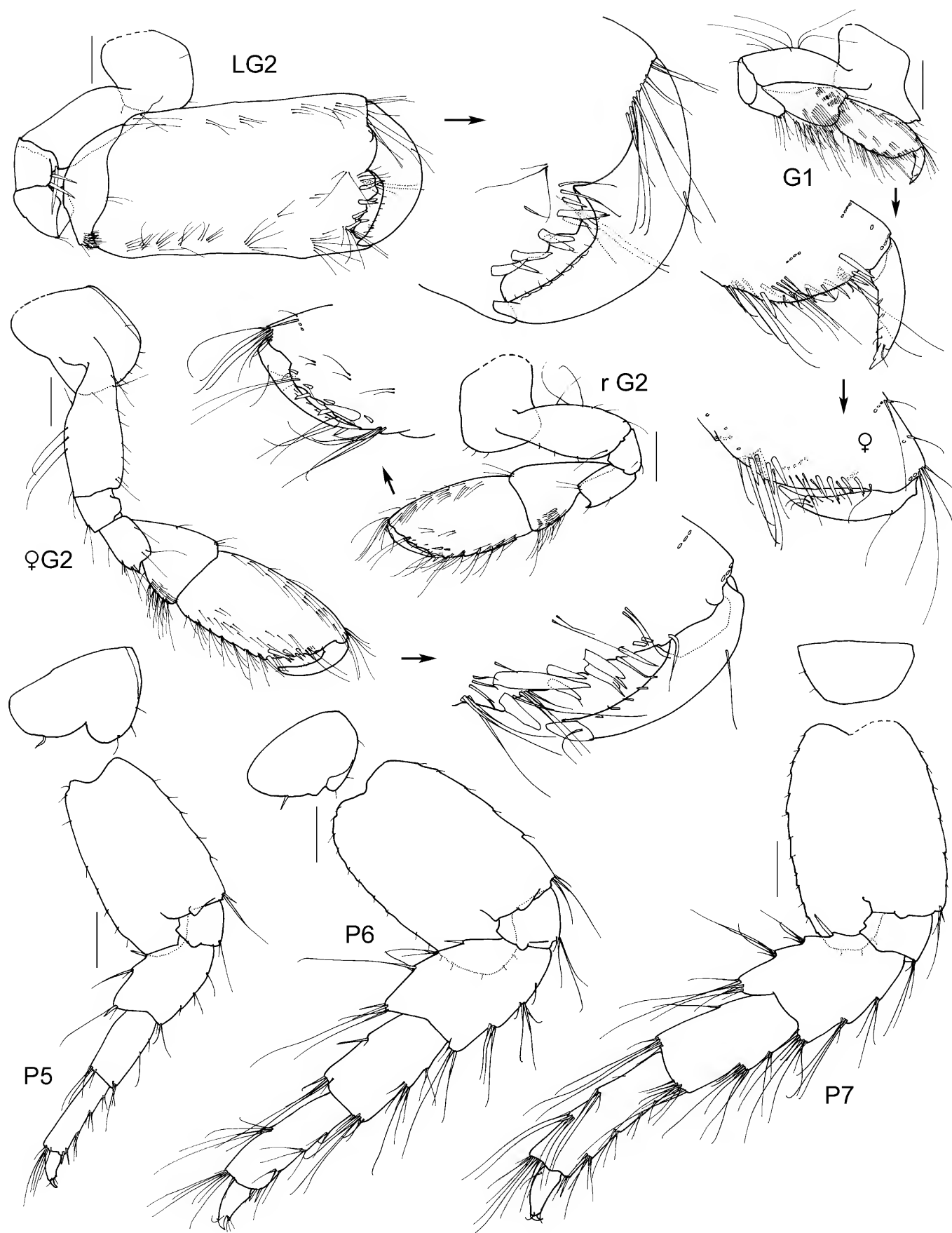
Fig. 13. *Linguimaera hamigera* (Haswell, 1879b), male, AM P60608, female, AM P60609 Munganno Point, Twofold Bay, New South Wales, Australia. Scales represent 0.2 mm.
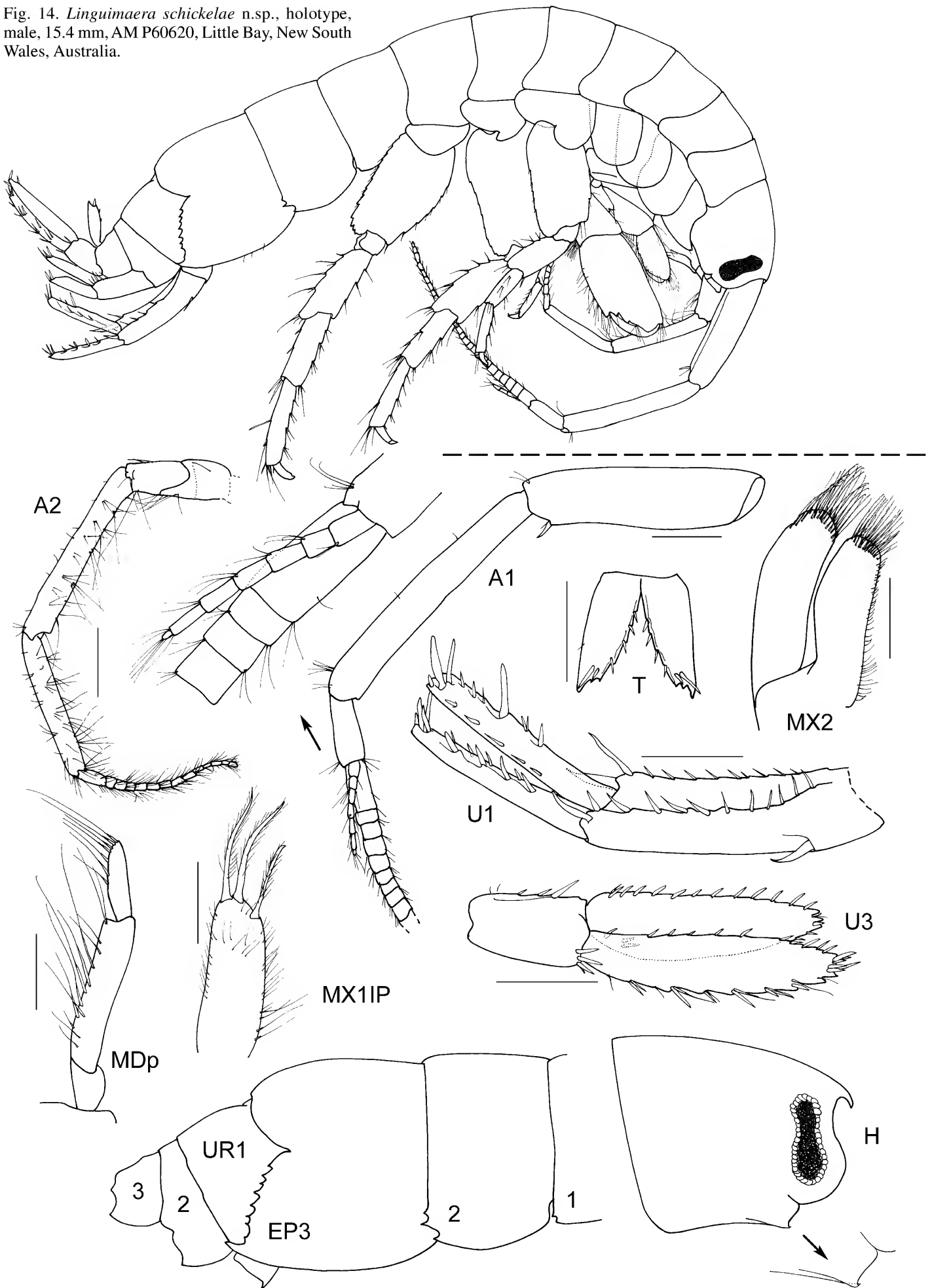
Fig. 15. *Linguimaera schickelae* n.sp., holotype, male, 15.4 mm, AM P60620, Little Bay, New South Wales, Australia; scales for MDp, MX1IP, MX2 represent 0.2 mm, remainder represent 0.5 mm.
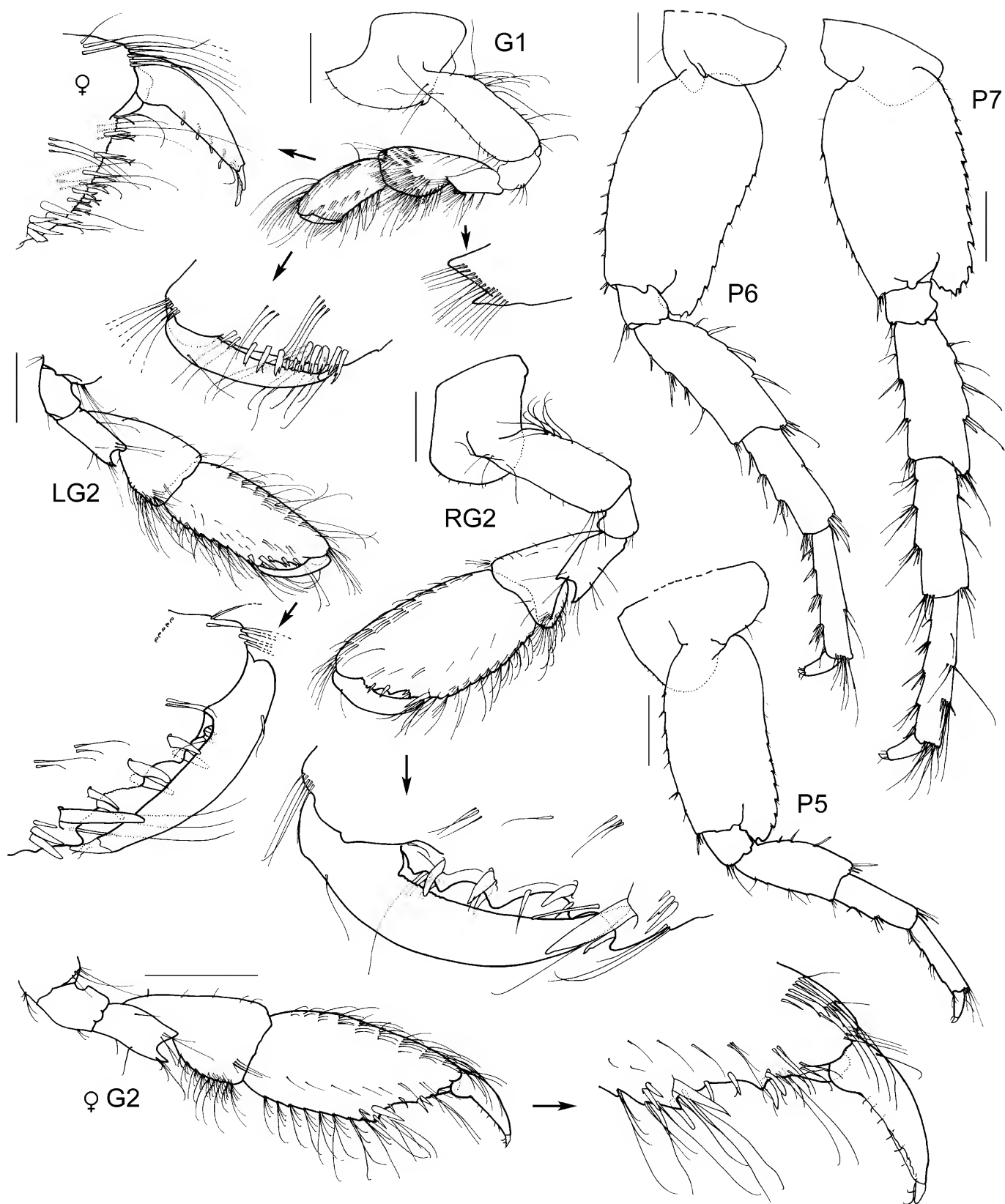
Fig. 16. *Linguimaera schickelae* n.sp., holotype, male, 15.4 mm, AM P60620, paratype, female, AM P60948, Little Bay, New South Wales, Australia. Scales represent 0.5 mm.

Habitat. Marine; littoral; under stones between tide marks and from 7 m depth.

Remarks. *Linguimaera schickelae* appears to be most similar to *L. mannarensis* (Sivaprakasam, 1970) and *L. tias* Krapp-Schickel, 2003. They all have the short tapering third article of the mandibular palp and the well defined corner of gnathopod 2 palm that is greater than 90°. *Linguimaera schickelae* and *L. mannarensis* are the only species in which the posterodistal corner of epimeron 2 has three small spines.

Distribution. *New South Wales*: Boondelbah Island, Port Stephens; Little Bay; Clovelly (all AM).

Australian geographic areas. Southeastern Australia.

Linguimaera thomsoni (Miers, 1884)

Megamaera thomsoni Miers, 1884: 318, pl. 34, fig. B.
Maera mastersii Haswell, 1885: 105 (in part).

Type material. Apparently lost.

Type locality. Torres Strait.

Description. Based on Miers, 1884: 318, pl. 34, fig. B.

Head. Lateral cephalic lobes broad, rounded. *Antenna 1* longer than antenna 2; peduncular article 1 shorter than article 2, with 1 robust seta on posterior margin; flagellum with 30+ articles. Article 4 subequal to article 5; *antenna 2* flagellum with 10+ articles.

Pereon. *Gnathopod 1* coxa anteroventral corner produced, rounded; merus with sharp posterodistal spine; carpus about 3× as long as broad; palm extremely acute, concave, without posterodistal corner. *Gnathopod 2* subchelate; merus with sharp posteroventral spine; carpus long; propodus without medial depression, setose, palm acute, convex, sculptured, with sparse robust setae, defined by posteroventral spine; apically acute/subacute. *Pereopod 5–7* basis posterior margin concave or straight, posteroventral corner narrowly rounded or subquadrate.

Pleon. *Epimeron 1* posteroventral corner with small acute spine. *Epimera 1–2* posteroventral margin with 1 to 2 large or small spines above spine defining posteroventral corner. *Epimeron 3* posterior margin serrate, posteroventral corner with small acute spine. *Uropod 3* rami distally acute/subacute; inner ramus subequal in length to outer ramus; outer ramus longer (1.2 to 2× length) than peduncle, 1-articulate. *Telson* with robust setae on inner margins, each lobe with 1 apical/subapical robust seta, apical conical extension absent.

Habitat. Marine; 7 to 16 m depth.

Remarks. *Linguimaera thomsoni* is a poorly described species. Krapp-Schickel (2003) was able to separate *L. thomsoni* from *L. pirloti* by the first coxa that is anteroventrally rounded (acute in *L. pirloti*) and the palm of gnathopod 2 that has a large excavation in *L. thomsoni* (two smaller excavations in *L. pirloti*).

Distribution. *Queensland*: Albany Island, Prince of Wales Channel, Thursday Island, Torres Strait (Miers, 1884).

Australian geographic areas. Northeastern Australia.

Mallacoota J.L. Barnard, 1972

Mallacoota chandaniae n.sp.

Figs. 17–19

Type material. HOLOTYPE, ♂ "a", 11 mm, AM P59021; 1 PARATYPE, ♂ "b", 9.1 mm, AM P62996, at end of sugar loading jetty 5 km long, Lucinda, Queensland, Australia, [approx. 18°31'S 146°19'E], pylon scrapings, 7 m, Frank Hoedt, CRIMP survey, August 1999, stn A138. 5 PARATYPES, ♂ "c", 9.5 mm, ♀ "a" 10.8 mm, 3♀♀, AM P59020, Evans Landing, Weipa, Queensland, Australia, [approx. 12°35'S 141°36'E], pylon scrapings, 0.5 m, Frank Hoedt, CRIMP survey, October 1999, stn A220.

Type locality. At end of sugar loading jetty 5 km long, Lucinda, Queensland, Australia, [approx. 18°31'S 146°19'E], pylon scrapings.

Description. Based on holotype male, AM P59021, paratype male, AM P62996 and paratype female, AM P59020.

Head. Lateral cephalic lobes broad, truncated, with anteroventral notch or slit, anteroventral corner rounded. *Antenna 1* longer than antenna 2; peduncular article 1 subequal in length to article 2, with 4 or more robust setae along posterior margin; flagellum
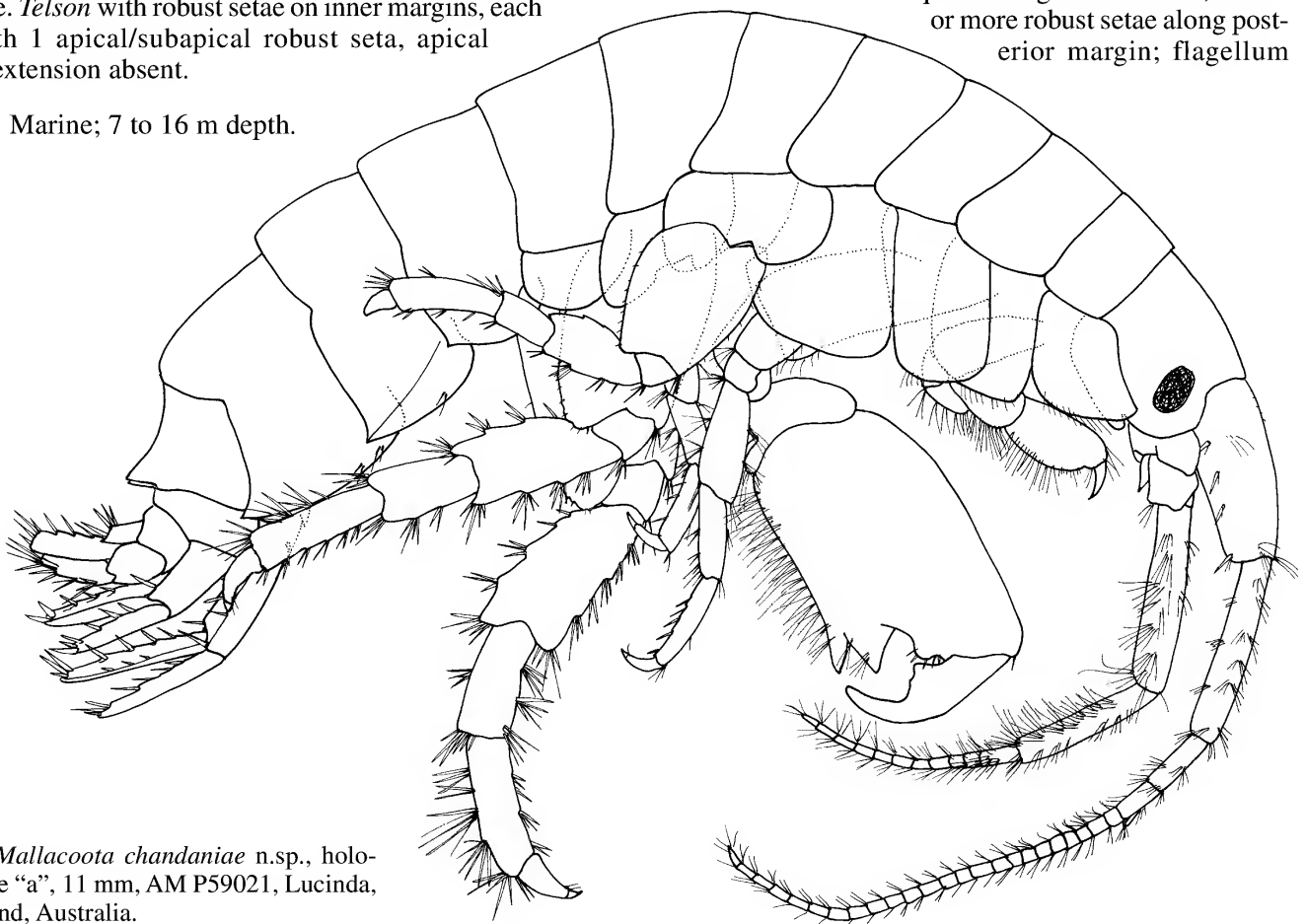

Fig. 17. *Mallacoota chandaniae* n.sp., holotype, male "a", 11 mm, AM P59021, Lucinda, Queensland, Australia.
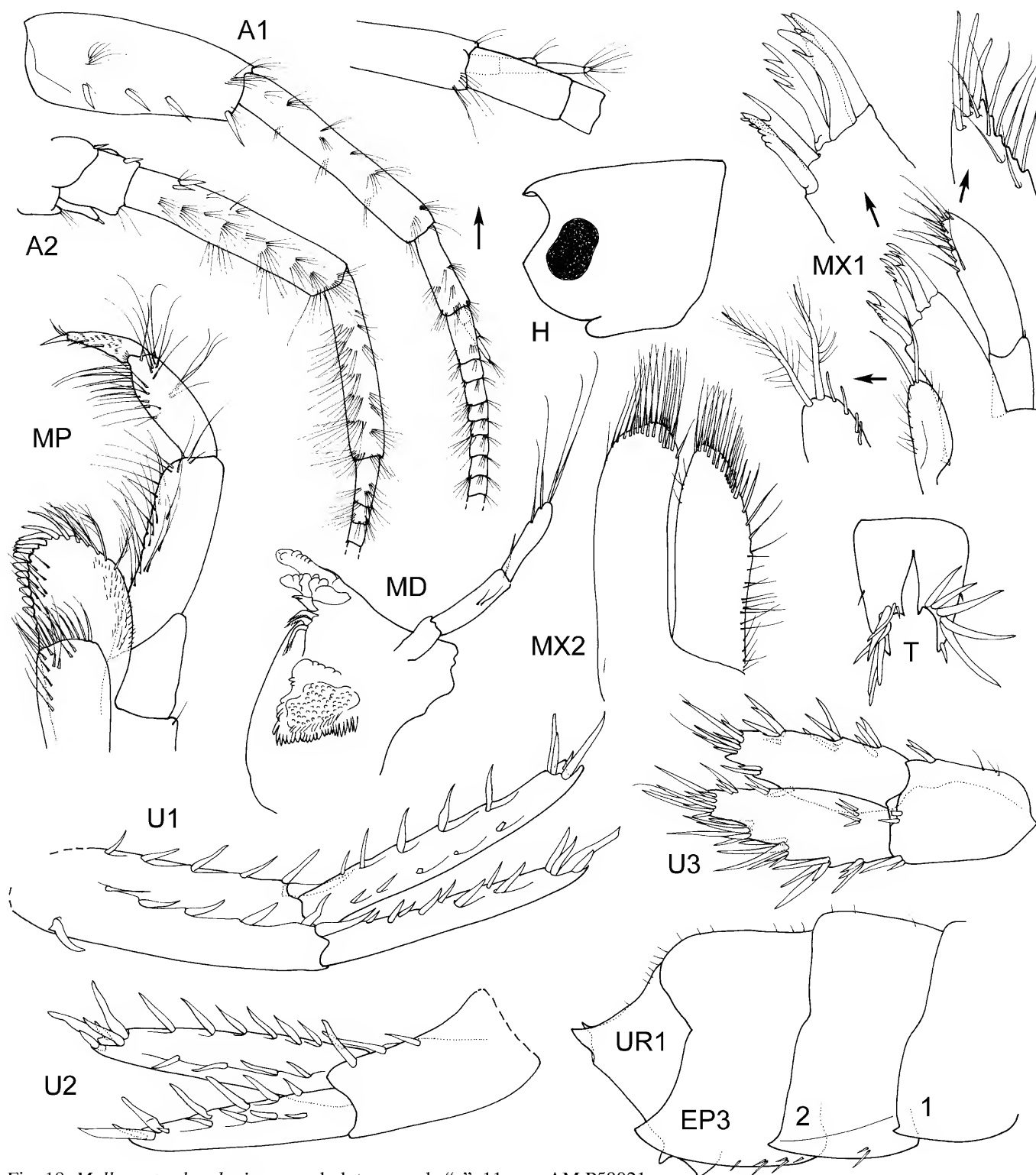
Fig. 18. *Mallacoota chandaniae* n.sp., holotype, male "a", 11 mm, AM P59021, Lucinda, Queensland, Australia.

with about 26 articles; accessory flagellum with 4 articles. *Antenna 2* peduncular article 2 cone gland not reaching to end of peduncular article 3; article 4 longer than article 5; flagellum with about 11 articles. *Mandible* palp article 3 rectolinear, with setae mostly terminal, longer than article 1; article 2 subequal to article 3; article 1 not produced, shorter than article 2, about twice as long as broad. *Maxilla 1* inner plate with 2 terminal setae.

Pereon. *Gnathopod 1* coxa anteroventral corner produced, slightly rounded, posteroventral corner notch absent; merus without posterodistal spine; palm acute, convex, without posterodistal corner, defined by posterodistal robust setae.

Gnathopod 2 sexually dimorphic; subchelate; coxa posteroventral corner notch absent; merus with subquadrate posteroventral corner; carpus compressed; propodus without medial depression, with strong setal bunch, palm slightly acute, sinusoidal, sculptured, with group of anterodistal robust setae, without posterodistal robust setae, defined by posteroventral spine; dactylus apically blunt. *Pereopod 5* basis posterior margin straight, posteroventral corner broadly rounded. *Pereopod 6* coxa anterior lobe ventral margin slightly produced, rounded; basis posterior margin straight, posteroventral corner broadly rounded. *Pereopod 7* basis posterior margin straight, posteroventral corner narrowly rounded or subquadrate.
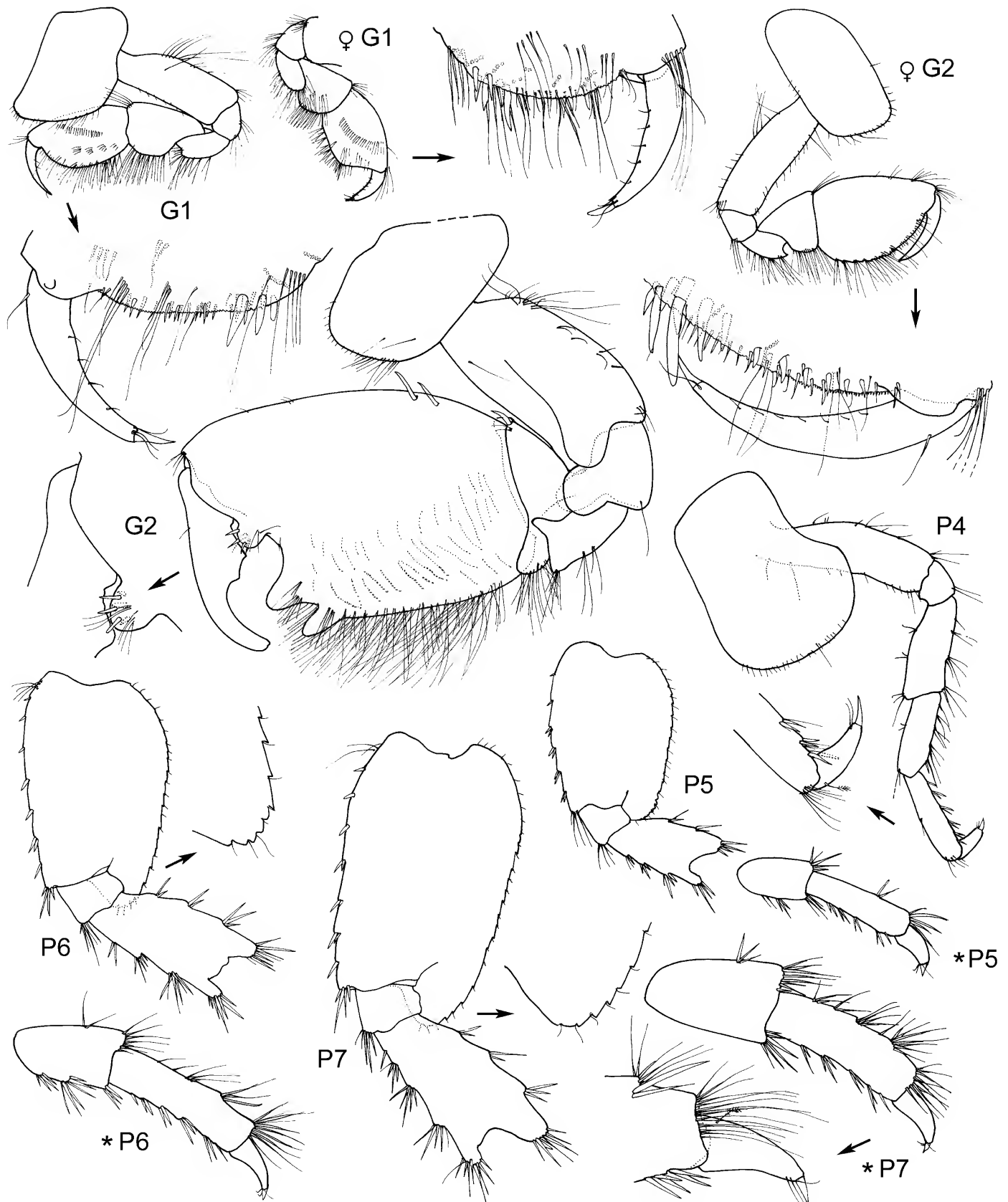
Fig. 19. *Mallacoota chandaniae* n.sp., holotype, male "a", 11 mm, AM P59021, * paratype, male "b", 9.1 mm, AM P62996, Lucinda, Queensland, Australia; paratype, female, "a" 10.8 mm, AM P59020, Weipa, Queensland, Australia.

Pleon. *Epimeron 1* posteroventral corner with small acute spine. *Epimera 1–2* posteroventral margin without spines above posteroventral corner. *Epimeron 3* posterior margin smooth, posteroventral corner subquadrate. *Urosomite 1* dorsally bicarinate. *Uropod 3* rami distally truncated; inner ramus subequal in length to outer ramus; outer ramus longer (1.2 to 2× length) than peduncle, 1-articulate. *Telson* each lobe

with 3 or more apical/subapical robust setae, apical conical extension reaching at least halfway along longest seta.

Female (sexually dimorphic characters). *Gnathopod 2* merus with sharp posteroventral spine; carpus short; setose, convex, smooth, with sparse robust setae, defined by posterodistal robust setae, without posteroventral corner; dactylus apically acute/subacute.

Habitat. Marine; littoral; living on encrusted wharf pilings.

Etymology. Named for Chandani Appadoo, in recognition of her work on the melitid amphipods of the Indian Ocean.

Remarks. *Mallacoota chandaniae* is a very distinctive species. For instance no Australian species has a strictly subquadrate epimeron 3 whereas seven species outside of Australia have this characteristic. Only two species within this group, *M. schellenbergi* Ledoyer, 1984 and the *M. subcarinata* of Myers, 1985 have a deeply cleft telson similar to *M. chandaniae*, but neither of these has the almost transverse palm of the male gnathopod 2.

Distribution. *Queensland*: Weipa; Lucinda (both AM).

Australian geographic areas. Northeastern Australia.

Mallacoota euroka n.sp.

Figs. 20–22

Mallacoota subcarinata.–J.L. Barnard, 1972a: 247, fig. 144.– Barnard & Barnard, 1983: 632 (in part).

Type material. HOLOTYPE, ♂, 10.1 mm, AM P60561; 1 PARATYPE, ♀, AM P60562; 8 PARATYPES, AM P27034, between Troubridge Light and Cape Jervis, South Australia, [approx. 35°20'S 137°40'E], sponges on mud bottom, 20 m, D. Blake & H. Larsen, 14 March 1978.

Type locality. Between Troubridge Light and Cape Jervis, South Australia, [approx. 35°20'S 137°40'E], sponge on mud bottom, 20 m.

Description. Based on holotype male, AM P60561 and paratype female, AM P60562.

Head. Lateral cephalic lobes broad, rounded, with anteroventral notch or slit, anteroventral corner rounded. *Antenna 1* longer than antenna 2; peduncular article 1 subequal in length to article 2, with 4 or more robust setae along posterior margin; flagellum with about 29 articles; accessory flagellum with 3–4 articles. *Antenna 2* peduncular article 2 cone gland reaching at least to end of peduncular article 3; article 4 longer than article 5, or article 4 subequal to article 5; flagellum with about 10 articles. *Mandible* palp article 3 rectolinear, with setae mostly terminal, longer than article 1; article 2 shorter than article 3; article 1 not produced, subequal to article 2, about twice as long as broad. *Maxilla 1* inner plate with setae mainly terminal.

Pereon. *Gnathopod 1* coxa anteroventral corner produced, rounded, posteroventral corner notch present; merus without posterodistal spine; propodus palm acute, convex, defined by posterodistal corner, without posterodistal robust setae. *Gnathopod 2* sexually dimorphic; subchelate; coxa posteroventral corner notch present; merus with sharp posteroventral spine; carpus compressed; propodus without medial depression, with strong setal bunch, palm acute,
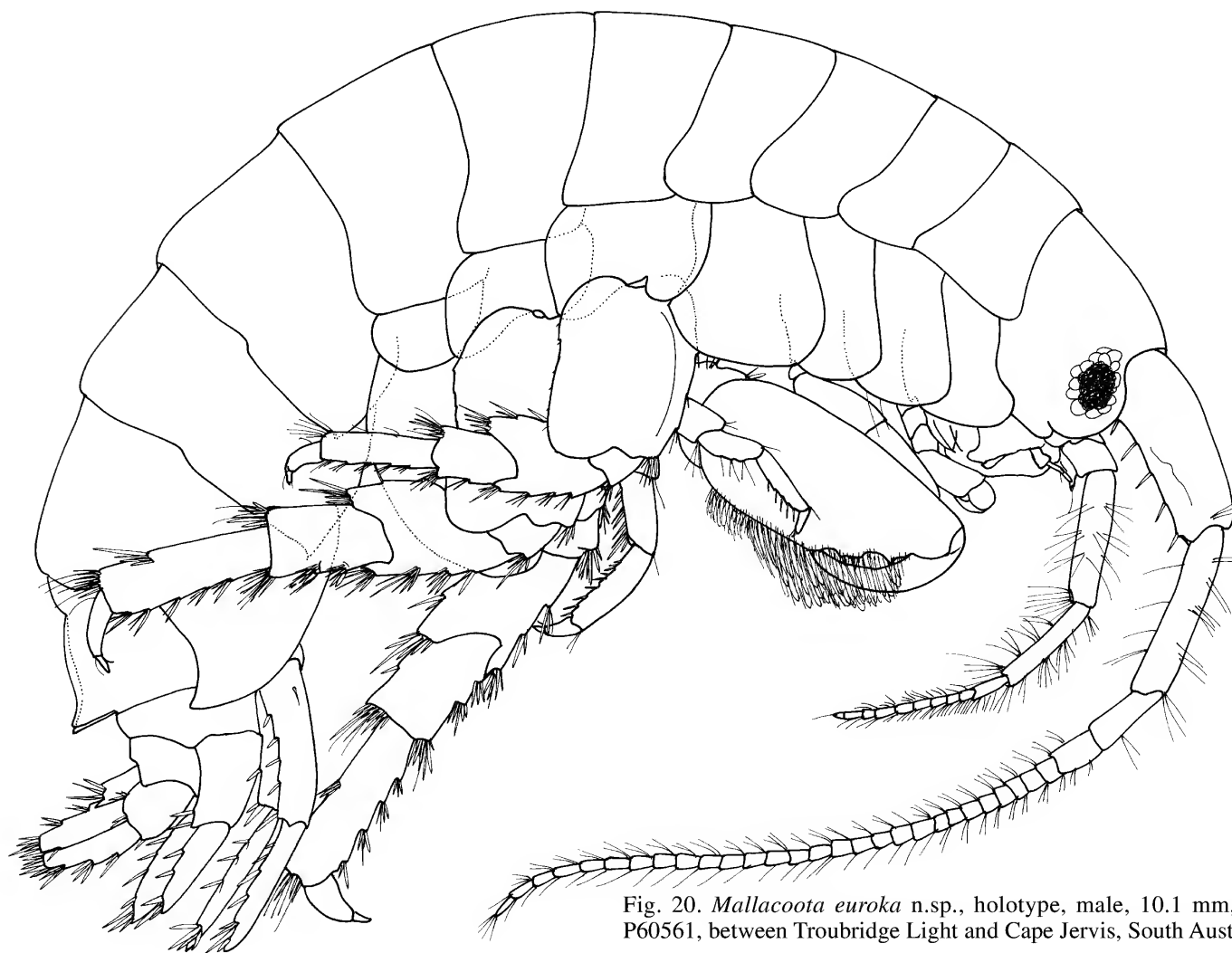

Fig. 20. *Mallacoota euroka* n.sp., holotype, male, 10.1 mm, AM P60561, between Troubridge Light and Cape Jervis, South Australia.
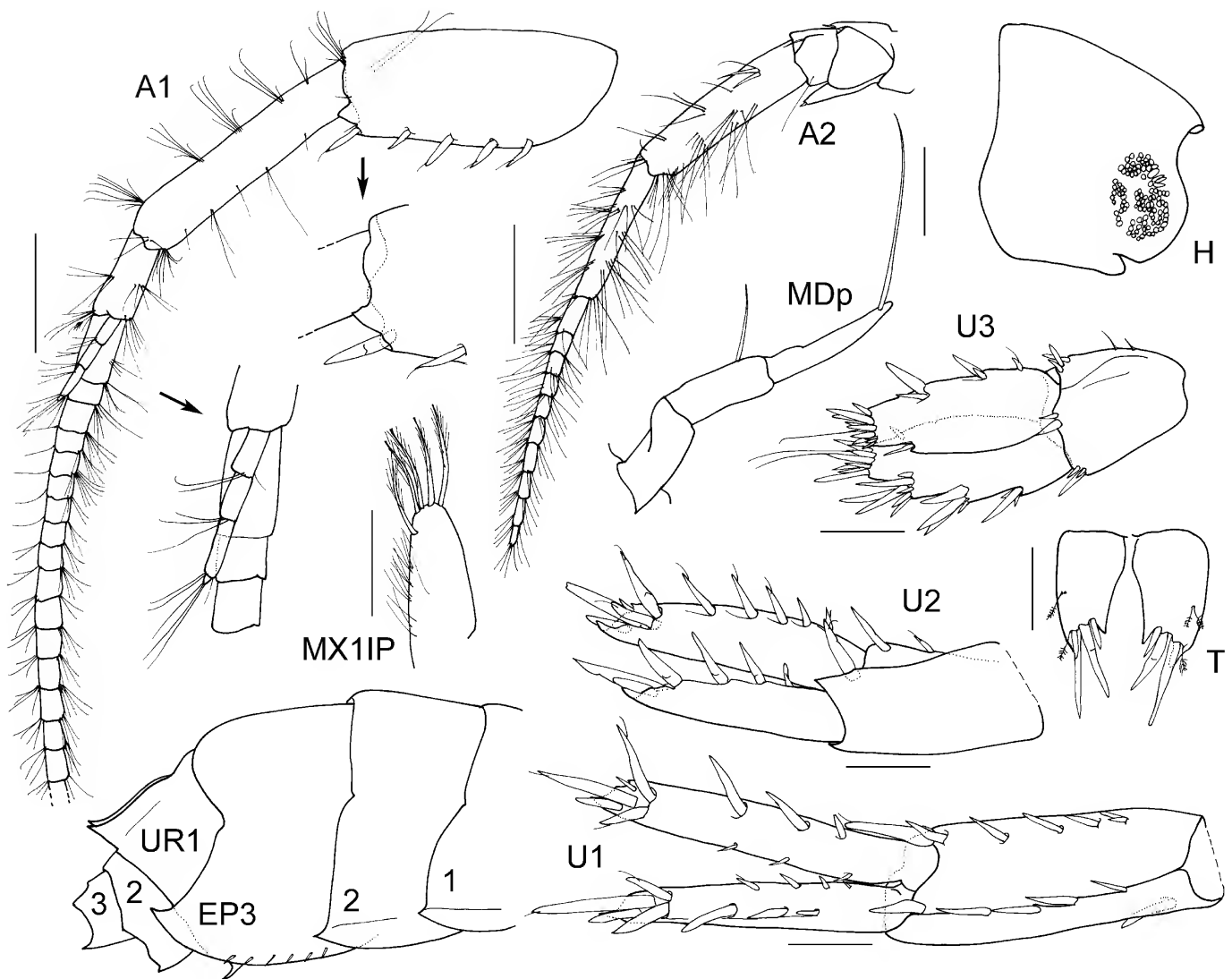
Fig. 21. *Mallacoota euroka* n.sp., holotype, male, 10.1 mm, AM P60561, between Troubridge Light and Cape Jervis, South Australia. Scales for MDp, MX1IP represent 0.1 mm, scales for A1, A2 represent 0.5 mm, remainder represent 0.2 mm.

straight, sculptured, with sparse robust setae and with group of anterodistal robust setae, without posterodistal robust setae, defined by posteroventral spine; dactylus apically blunt. *Pereopod 5* basis posterior margin concave, postero-ventral corner narrowly rounded or subquadrate. *Pereopod 6* coxa anterior lobe ventral margin slightly produced, rounded; basis posterior margin concave, posteroventral corner narrowly rounded or subquadrate. *Pereopod 7* basis posterior margin convex, with posterior margin smooth or minutely castelloserrate, posteroventral corner broadly rounded.

Pleon. *Epimeron 1* posteroventral corner with small acute spine. *Epimera 1–2* posteroventral margin without spines above posteroventral corner. *Epimeron 3* posterior margin smooth, posteroventral corner with strongly produced acute spine. *Urosomite 1* dorsally bicarinate. *Urosomite 2* posterior margin smooth. *Uropod 3* inner ramus subequal in length to outer ramus; outer ramus longer (1.2 to 2× length) than peduncle, 1-articulate. *Telson* each lobe with 3 or more apical/subapical robust setae, apical conical extension reaching scarcely one third along longest seta.

Female (sexually dimorphic characters). *Gnathopod 2* carpus short; setose, smooth, without robust setae, defined

by posterodistal robust setae, defined by posteroventral corner; dactylus apically acute/subacute.

Habitat. Marine; littoral; sponges on mud bottom, 20 m depth.

Etymology. Named for the schooner *Euroka*, built in Brisbane Waters and sunk off the Sandon River mouth, south of Clarence Head, New South Wales, in 1875.

Remarks. This species was originally described as *Mallacoota subcarinata* phenotype A by J.L. Barnard (1972a). It has a large posteroventral spine on epimeron 3, like *M. subcarinata* and *M. diemenensis*. *Mallacoota euroka* differs from *M. diemenensis* in having no dorsal spines on pleonites 1 to 3. It differs from *M. subcarinata* in the number of robust setae on the first peduncular article of antenna 1 (five in *M. euroka* and one to three in *M. subcarinata*), in having posteroventral notches on coxae 1 and 2 and in having a convex posterior margin on the basis of pereopod 7.

Distribution. *Victoria*: Port Phillip (J.L. Barnard, 1972a). *South Australia*: Cape Jervis (AM).

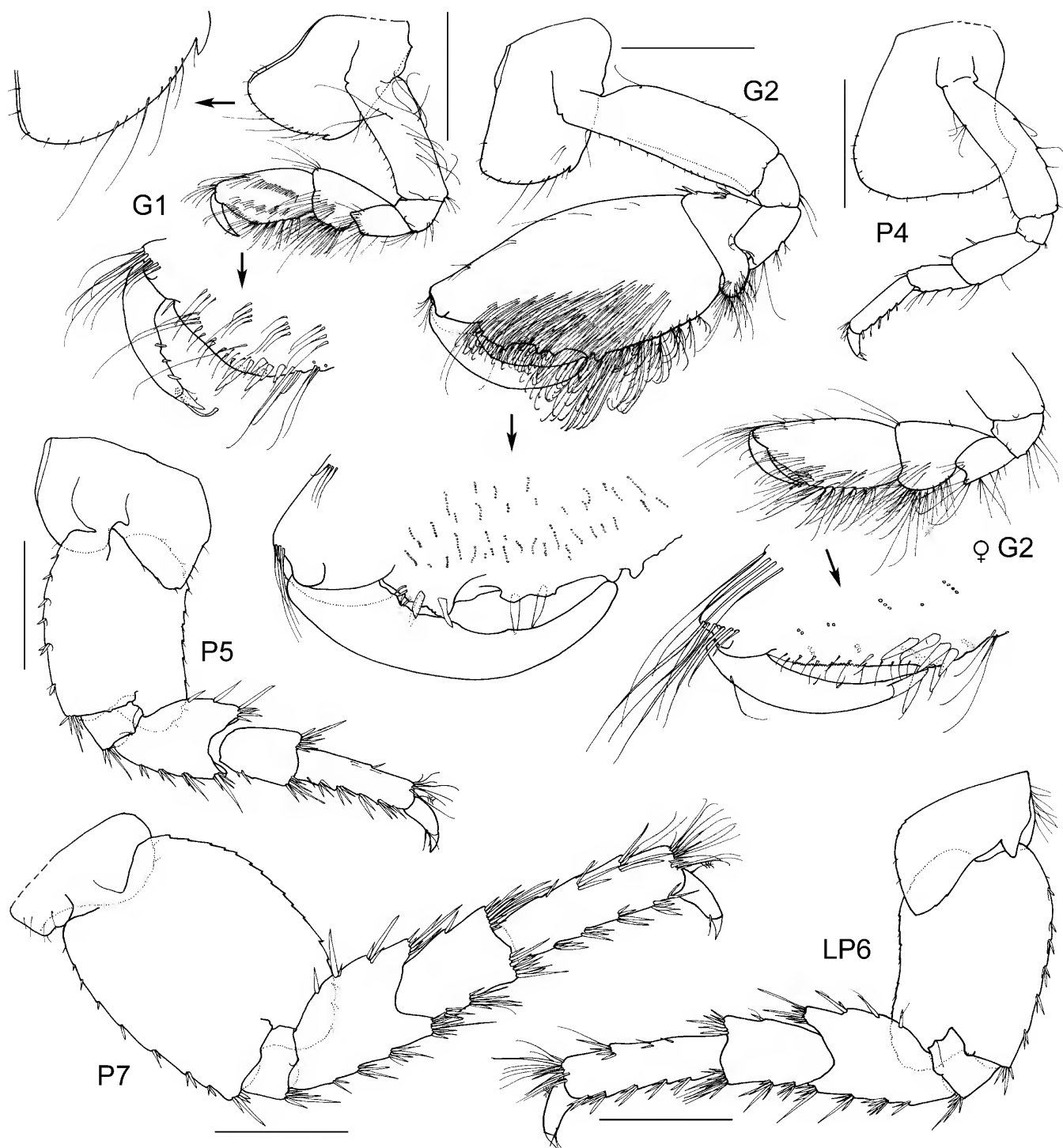**Australian geographic areas**. Southern Australia.

Fig. 22. *Mallacoota euroka* n.sp., holotype, male, 10.1 mm, AM P60561, paratype female, AM P60562, between Troubridge Light and Cape Jervis, South Australia. Scale represents 0.5 mm.

Mallacoota kameruka n.sp.

Figs. 23–25

Elasmopus subcarinatus.–Stebbing, 1888: 1019, pl. 98 (plates labelled as *E. persetosus*).

Mallacoota subcarinata.–J.L. Barnard, 1972a: 247, fig. 145.–Barnard & Barnard, 1983: 632 (in part).–Hutchings *et al*., 1989: 362.

Type material. HOLOTYPE, ♂ "a", 10.0 mm, AM P60491; 1 PARATYPE, ♀, 10.0 mm, AM P60492; 10 PARATYPES, 5♂♂, 5♀♀, AM P60493; 1 PARATYPE, ♂ "b", AM P60494, northeast of Marys Rock, Cook Island, New South Wales, Australia, 28°11.42'S 153°34.79'E, orange bryozoan, 19 m, R.T. Springthorpe, 8 June 1993, stn NSW-816.

Additional material examined. New South Wales: 41♂♂ (including juveniles), 80♀♀ (incl. juveniles), AM P54972, type locality.

13 specimens, AM P57672, 100 m north west of Julian Rocks, Byron Bay, 28°36.8'S 153°37.8'E, red algae *Delisea pulchra*, 16 m, S.J. Keable, 4 March 1992, stn NSW-648. 1 specimen, AM P56677, hand collected at low tide northern shore under Fred Hansen Bridge, Boambee Creek, Sawtell, 30°20.4'S 153°05.5'E, exposed mud flat, Australian Museum party, 8 March 1992, stn NSW-717. 4 specimens, AM P5724, Port Stephens, [approx. 32°42'S 152°06'E], dredged, A. Musgrave, 30 August 1920. 1 specimen, AM P47047, west side of Box Head, Broken Bay, 33°33'S 151°21'E, coralline algae in low intertidal zone exposed to the south, A. Murray, R.T. Springthorpe & H.E. Stoddart, 11 April 1981, stn NSW-2. 2♂♂, 2♀♀, AM P60495, Port Jackson, [approx. 33°51'S 151°16'E]. 15 specimens, G926, Jervis Bay, [approx. 35°03'S 150°44'E], T. Whitelegge. 1♂, AM P52785, Moe's Rock, South of Jervis Bay, 35°09'S 150°45'E, foliose bryozoan, 18 m, R.T. Springthorpe & J.K. Lowry, 29 June 1981, stn NSW-55. 3♀♀, AM P52784, southern end of Lighthouse Reef, Ulladulla, New South Wales, 35°22.14'S 150°29.31'E, bryozoan ?*Orthoscuticella* sp., 16 m, P.B. Berents, K.B. Attwood, 30
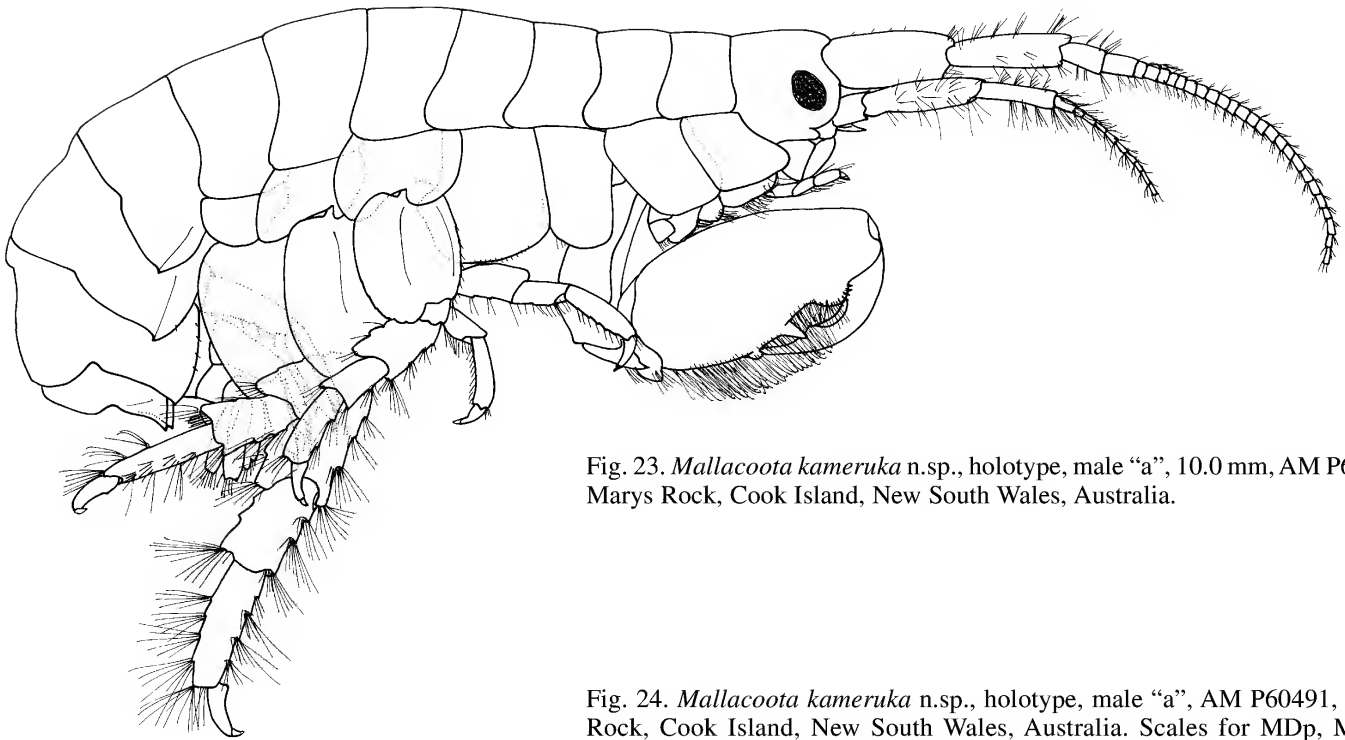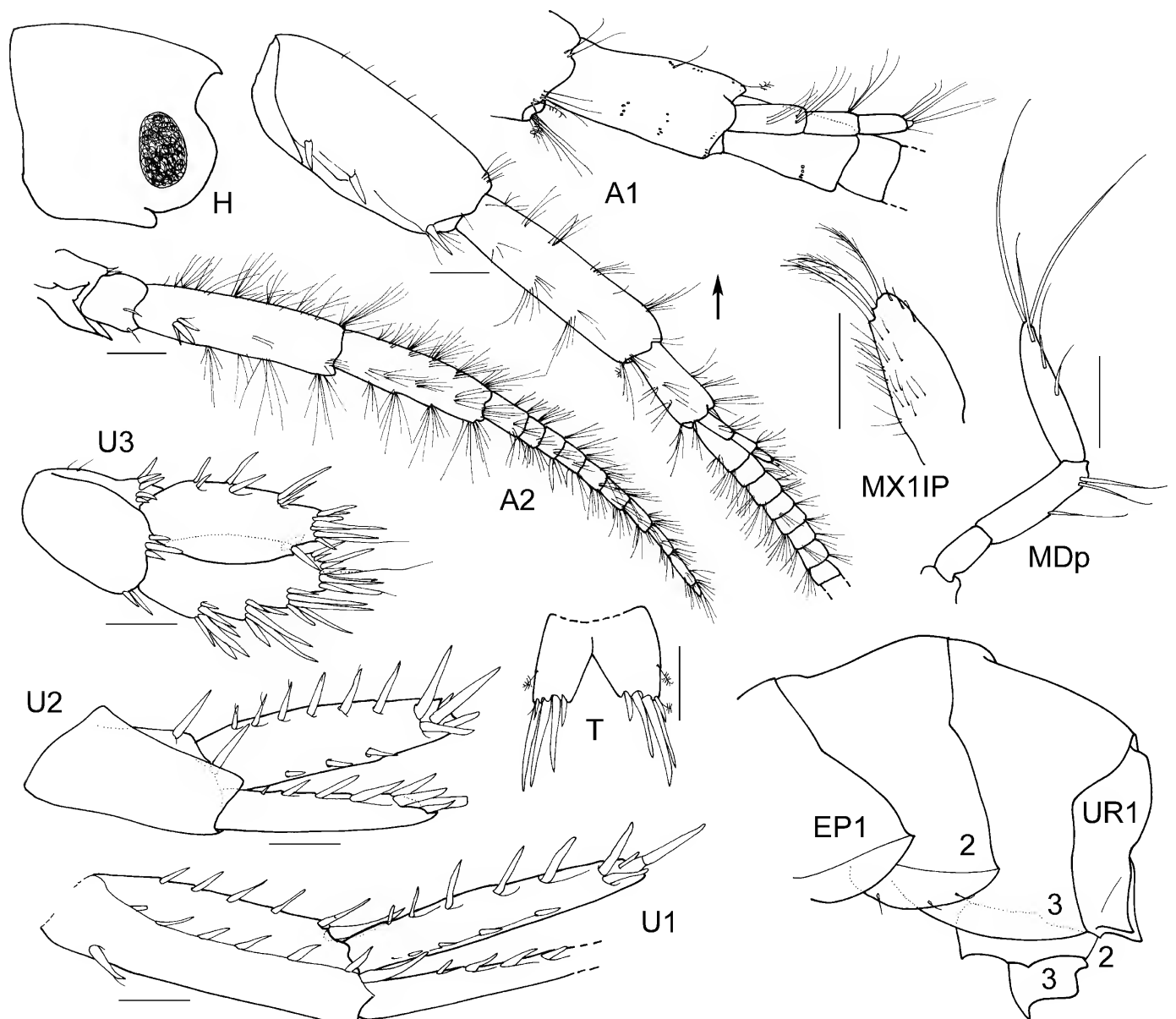
Fig. 23. *Mallacoota kameruka* n.sp., holotype, male "a", 10.0 mm, AM P60491, Marys Rock, Cook Island, New South Wales, Australia.

Fig. 24. *Mallacoota kameruka* n.sp., holotype, male "a", AM P60491, Marys Rock, Cook Island, New South Wales, Australia. Scales for MDp, MX1IP represent 0.1 mm, remainder represent 0.2 mm.
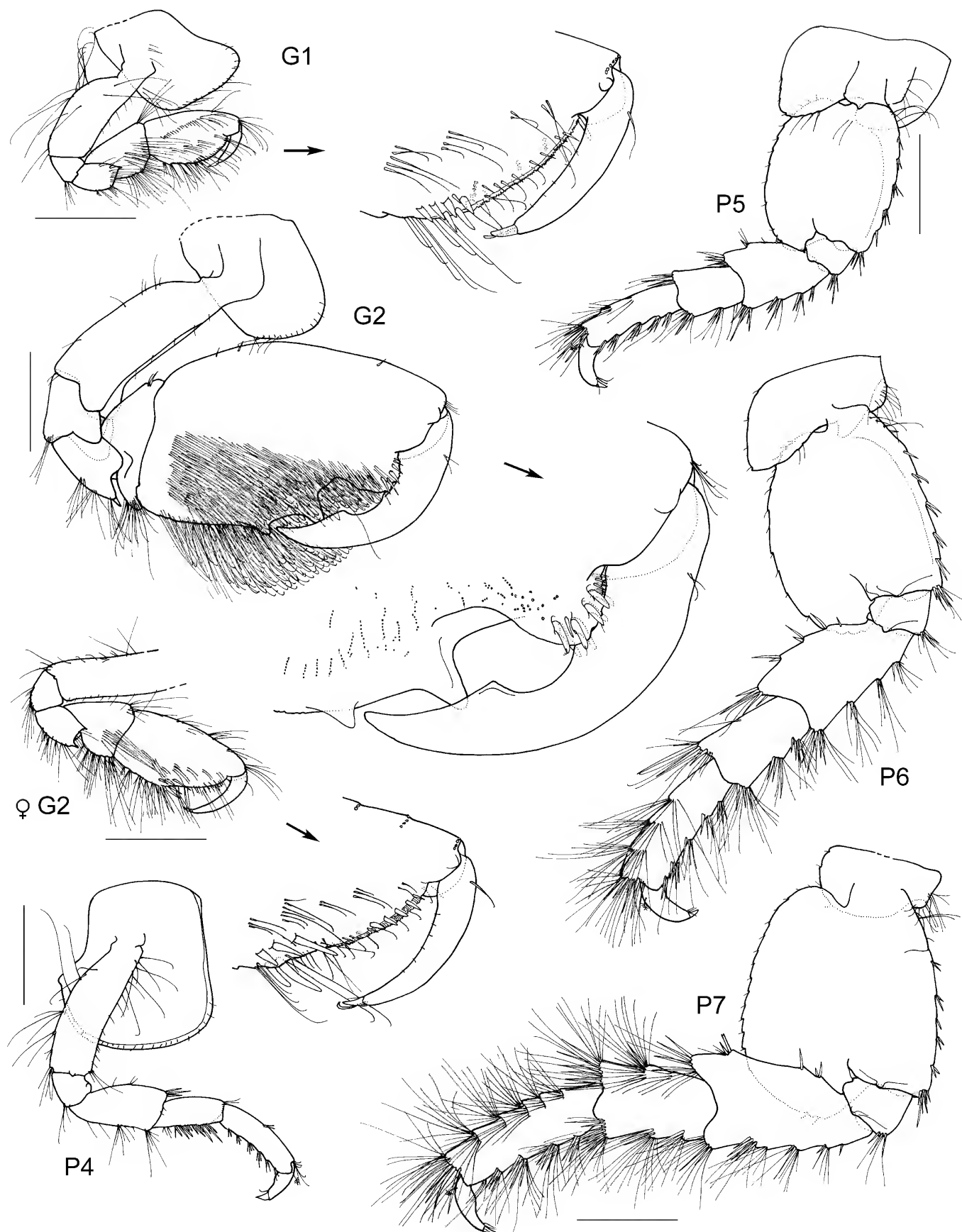
Fig. 25. *Mallacoota kameruka* n.sp., holotype, male "a", AM P60491, paratype female, 10.0 mm, AM P60492, Marys Rock, Cook Island, New South Wales, Australia. Scales represent 0.5 mm.

April 1997, stn NSW-1267. 1♂, AM P47054, Merimbula Wharf, Merimbula, 36°53.92'S 149°55.64'E, mixed red and brown algae, 8 m, K.B. Attwood, 18 May 1995, NSW–1103. 7 specimens, AM P63381, Murrumbulga Point, Twofold Bay, New South Wales, 37°04.7'S 149°53.1'E, subtidal rock platform, S.J Keable, A. Paul, L. Walker, 29 March 1985, stn Q8/9. Queensland: 2♀♀, AM P3493, Port Denison,

[approx. 20°03'S 148°15'E], [AM Old Collection]. 1♀, P 47055, Boat Rock, North Stradbroke Island, 27°25.1'S 153°33.28'E, bryozoans, hydrozoans & brown algae, 28 m, R.T. Springthorpe, 3 June 1993, stn QLD-853. Victoria: 1♂, AM P3494, Griffiths Point, [approx. 38°32'S 145°22'E], [AM Old Collection]. Western Australia: 2 specimens, AM P41234, 300 m southeast of Penguin Island, Warnbro Sound, 32°18.5'S

115°41.6'E, seagrass: *Amphibolis griffithii*, 3.5 m, P. Hutchings *et al.*, 7–9 November 1990, stn A.

Type locality. Marys Rock, Cook Island, New South Wales, Australia, 28°11.42'S 153°34.79'E, on a bryozoan, 19 m.

Description. Based on holotype male, AM P60491 and paratype female, AM P60492.

Head. Lateral cephalic lobes broad, rounded, with anteroventral notch or slit, anteroventral corner rounded. *Antenna 1* longer than antenna 2; peduncular article 1 subequal in length to article 2, with 3 robust setae along posterior margin; flagellum with at least 24 articles; accessory flagellum with 3–4 articles. *Antenna 2* peduncular article 2 cone gland reaching at least to end of peduncular article 3; article 4 longer than article 5; flagellum with about 11 articles. *Mandible* palp article 3 rectolinear, setose along straight medial margin, longer than article 1; article 2 shorter than article 3; article 1 not produced, shorter than article 2, about twice as long as broad. *Maxilla 1* inner plate with about 3 setae mainly terminal.

Pereon. *Gnathopod 1* coxa anteroventral corner produced, rounded, posteroventral corner notch absent; merus without posterodistal spine; propodus palm acute, convex, without posterodistal corner, defined by posterodistal robust setae. *Gnathopod 2* sexually dimorphic; subchelate; coxa posteroventral corner notch absent; merus with sharp posteroventral spine; carpus compressed; propodus without medial depression, with strong setal bunch, palm acute, straight, sculptured, with group of anterodistal robust setae, without posterodistal robust setae, defined by posteroventral spine; dactylus apically falcate. *Pereopod 5* basis posterior margin convex, posteroventral corner broadly rounded; carpus and propodus with many long, slender setae along anterior margin. *Pereopod 6* coxa anterior lobe ventral margin slightly produced, rounded; basis posterior margin convex, posteroventral corner broadly rounded; carpus and propodus with many long, slender setae along anterior margin. *Pereopod 7* basis posterior margin convex, with posterior margin smooth or minutely castelloserrate, posteroventral corner broadly rounded.

Pleon. *Epimeron 1* posteroventral corner with small acute spine. *Epimera 1–2* posteroventral margin without spines above posteroventral corner. *Epimeron 3* posterior margin smooth, posteroventral corner subquadrate or with small acute spine. *Urosomite 1* dorsally bicarinate. *Uropod 3* inner ramus subequal in length to outer ramus; outer ramus longer (1.2 to 2× length) than peduncle, 1-articulate. *Telson* each lobe with 3 or more apical/subapical robust setae, apical conical extension absent.

Female (sexually dimorphic characters). *Gnathopod 2* carpus short; propodus setose, smooth, with sparse robust setae, defined by posterodistal robust setae, defined by posteroventral corner; dactylus apically acute/subacute.

Habitat. Marine; littoral; living among bryozoans and red algae, 16 to19 m depth.

Etymology. Named for the coastal steamer *Kameruka*, wrecked on Pedro Reef, off Moruya, New South Wales, in 1897.

Remarks. This species was originally described as *Mallacoota subcarinata* phenotype B by J.L. Barnard (1972a). It appears to be the same as the Challenger specimens Stebbing (1888) described from off Melbourne. *Mallacoota kameruka* is similar to *M. subcarinata* and *M. malua* in the absence of posteroventral notches on coxae 1 and 2. It differs from all Australian species in having convex posterior margins of pereopods 5–7.

Distribution. *Queensland*: Port Denison; North Stradbroke Island (both AM). *New South Wales*: Marys Rock, Cook Island; Julian Rocks, Byron Bay; Boambee Creek, Sawtell; Port Stephens; Broken Bay; Port Jackson; Jervis Bay; Ulladulla; Merimbula (all AM); Munganno Point, Twofold Bay (Hutchings *et al.*, 1989). *Victoria*: Off Melbourne (Stebbing, 1888); Griffiths Point (AM); Port Phillip (J.L. Barnard, 1972a). *Western Australia*: Point Peron; Rottnest Island; Cottesloe Beach (all J.L. Barnard, 1972a); Warnbro Sound (AM).

Australian geographic areas. Northeastern, southeastern, southern and southwestern Australia.

Mallacoota malua n.sp.

Figs. 26–28

Type material. HOLOTYPE, ♂ "a", 10 mm, AM P56679; 10 PARATYPES, 3♂♂, 7♀♀, AM P60485; Coffs Harbour Jetty, Coffs Harbour, New South Wales, 30°18.4'S 153°08.5'E, arborescent sponge on jetty pilings, 7 m, S.J. Keable, 9 March 1992, stn NSW-735; 22 PARATYPES, 8♂♂, 14♀♀, AM P56678, type locality, *Pyura praeputialis* on jetty pilings, 8 m, P.B. Berents & S.J. Keable, 9 March 1992, stn NSW 733; 1 PARATYPE, ♀, 8.5 mm, AM P60486; 1 PARATYPE, ♂ "c", 7.1 mm, AM P60490, type locality, coral scrapings on jetty pilings, 6 m, R.T. Springthorpe, 9 March 1992, stn NSW 726.

Additional material examined. New South Wales: 1♂, 2♀♀, AM P56674, 50 m west of Split Solitary Island, 30°14.0'S 153°10.8'E, *Herdmania momus*, rocks, sponges & ascidians, 15–17 m, P.A. Hutchings & C.L. Rose, 7 March 1992, stn NSW-677. 1♀, AM P56676, Boambee Creek, Sawtell, 30°20.8'S 153°05.6'E, silty sand submerged at low tide, 0.3 m, E. Albertson & S. Keable, 8 March 1992, stn NSW-714. 4♂♂, 12♀♀, AM P57220, Coffs Harbour Jetty, Coffs Harbour, 30°18.4'S 153°08.5'E, worm tubes encrusted with sponge on jetty pilings, 6 m, R.T. Springthorpe, 9 March 1992, stn NSW-725. 1 specimen, AM P57221, same locality, coral scrapings on jetty pilings, 6 m, R.T. Springthorpe, 9 March 1992, stn NSW-738. 5♂♂, 6♀♀, AM P57301, same locality, finger sponge on jetty pilings, 4 m, R.T. Springthorpe, 9 March 1992, stn NSW-734. 1♂, 4♀♀, AM P57302, same locality, coral scrapings on jetty pilings, 6 m, R.T. Springthorpe, 9 March 1992, NSW 726. 7♀♀, AM P58230, outer end of Kurnell Pier, Botany Bay, 34°00.2'S 151°12.5'E, pylon scrapings, 7 m, NSW Fisheries/CRIMP Survey, 21 October 1998, stn BB KP1 P1–7. 1♂ ("b"), AM P60487, same locality. 2♂♂, 1♀, AM P63071, same locality, pylon scrapings, 3 m, NSW Fisheries/CRIMP Survey, 21 October 1998, BB KP1 P2–3. 1♂, AM P58231, Kurnell Pier (near shoreline), Botany Bay, 34°00.5'S 151°12.7'E, pylon scrapings, 3 m, NSW Fisheries/CRIMP Survey, 21 October 1998, stn BB KP2 P3–3. 2♂♂, 1♀, AM P60488, north east corner of Clark Island, Port Jackson, 33°51.85'S 151°14.47'E, red alga, 2 m, I. Takeuchi & D. Bray, 17 April 1996, stn NSW-1250. 6♂♂, 5♀♀, AM P60623, Port Jackson, 33°51'S 151°16'E, [AM Old Collection].

Type locality. Coffs Harbour Jetty, New South Wales, Australia, 30°18.4'S 153°08.5'E, sponges, ascidians on pilings, 7 m.

Description. Based on holotype male "a", AM P56679, paratype female, AM P60486, paratype male "c", AM P60490 and male "b", AM P60487.

Head. Lateral cephalic lobes broad, truncated, with anteroventral notch or slit, anteroventral corner rounded. *Antenna 1* longer than antenna 2; peduncular article 1 subequal in length to article 2, with 3 robust setae along posterior margin; flagellum with at least 23 articles; accessory flagellum with 3–4 articles. *Antenna 2* peduncular article 2 cone gland reaching at least to end of peduncular article 3; article 4 longer than article 5, or article 4 subequal to article 5; flagellum with about 12 articles. *Mandible* palp article 3 rectolinear, with setae mostly terminal, longer than article 1; article 2 subequal to article 3; article 1 not produced, shorter than article 2, about twice as long as broad. *Maxilla 1* inner plate with about 4 setae mainly terminal.

Pereon. *Gnathopod 1* coxa anteroventral corner produced, rounded, posteroventral corner notch absent; merus without posterodistal spine; propodus palm acute, convex or straight, defined by posterodistal corner, defined by posterodistal robust setae. *Gnathopod 2* sexually dimorphic; subchelate; coxa posteroventral corner notch absent; merus with sharp posteroventral spine; carpus compressed; propodus without medial depression, with strong setal bunch, palm acute, straight, sculptured, with sparse robust setae and with group of anterodistal robust setae, without posterodistal robust setae, defined by posteroventral spine; dactylus apically falcate. *Pereopod 5* basis posterior margin slightly concave, posteroventral corner narrowly rounded or subquadrate. *Pereopod 6* coxa anterior lobe ventral margin slightly produced, rounded; basis posterior margin slightly concave or straight, posteroventral corner narrowly rounded or subquadrate; propodus expanded posterodistally to from a hood-like projection. *Pereopod 7* basis posterior margin straight, with posterior margin smooth or minutely castelloserrate, posteroventral corner narrowly rounded or subquadrate; propodus expanded posterodistally to from a hood-like projection.

Pleon. *Epimeron 1* posteroventral corner with small acute spine. *Epimera 1–2* posteroventral margin without spines above posteroventral corner. *Epimeron 3* posterior margin smooth, posteroventral corner subquadrate or with small acute spine. *Urosomite 1* dorsally bicarinate. *Uropod 3* inner ramus subequal in length to outer ramus; outer ramus longer (1.2 to 2× length) than peduncle, 1-articulate. *Telson* each lobe with 3 or more apical/subapical robust setae, apical conical extension absent.

Female (sexually dimorphic characters). *Gnathopod 2* carpus short; propodus setose, slightly convex, smooth, with sparse robust setae, defined by posterodistal robust setae, without posteroventral corner; dactylus apically acute/subacute.

Habitat. Marine; littoral; among ascidians, sponges and red algae on wharf pilings, 0 to 17 m depth.

Etymology. Named for the wooden steamer *Malua*, built in Botany Bay and sunk at the mouth of Port Hacking, New South Wales, in 1886.

Remarks. *Mallacoota malua* is most closely related to *Mallacoota kameruka*. They differ in the shape of the bases of pereopods 5–7, and in the sculpturing on the palm of gnathopod 2. *Mallacoota malua* is the only species with posterodistal hood-like projections on pereopods 6 and 7.
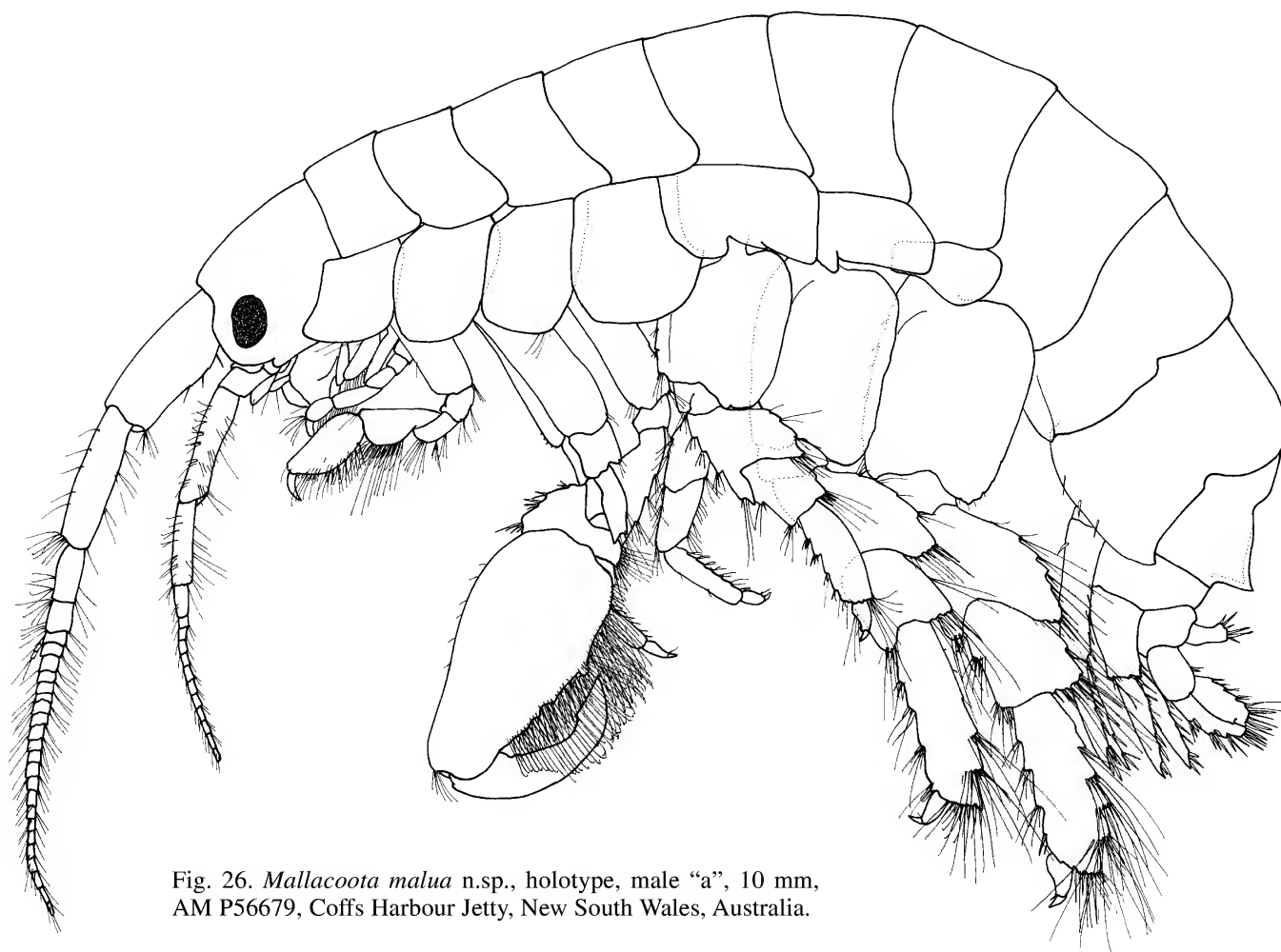

Fig. 26. *Mallacoota malua* n.sp., holotype, male "a", 10 mm, AM P56679, Coffs Harbour Jetty, New South Wales, Australia.
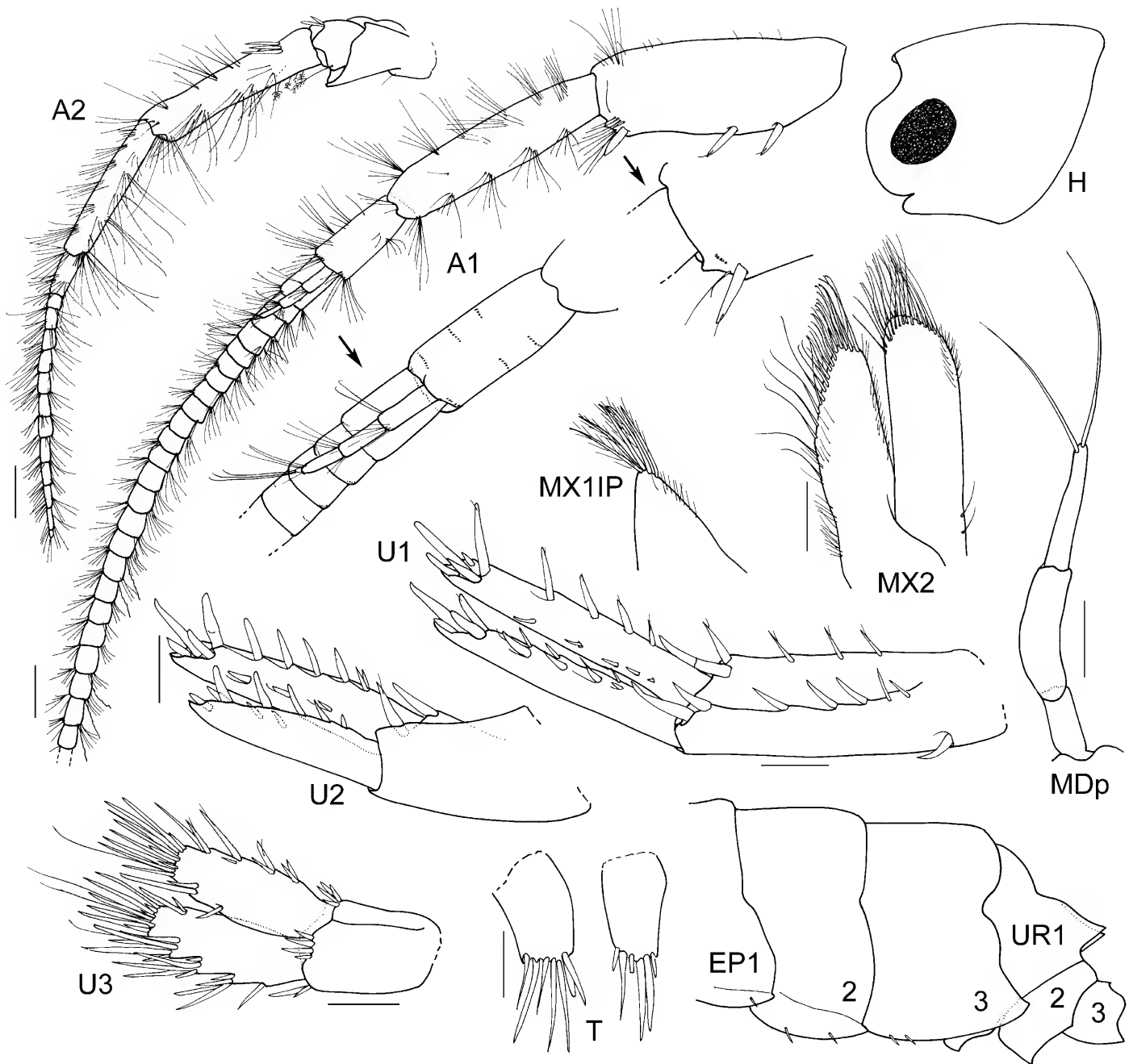
Fig. 27. *Mallacoota malua* n.sp., holotype, male "a", 10 mm, AM P56679, Coffs Harbour Jetty, New South Wales, Australia. Scales for MDp, MX1IP, MX2 represent 0.1 mm, remainder represent 0.2 mm.

Distribution. *New South Wales*: Split Solitary Island; Coffs Harbour; Boambee Creek, Sawtell; Clark Island, Port Jackson; Kurnell, Botany Bay (all AM).

Australian geographic areas. Southeastern Australia.

Mallacoota nananui Myers

?*Elasmopus subcarinatus*.–Chilton, 1915 (in part), 325, fig. 5.
Mallacoota subcarinata.–J.L. Barnard, 1972b: 114, figs 59–60.
Mallacoota nananui Myers, 1985: 121, fig. 95.–Myers, 1986: 1389, fig. 8.

Type material. HOLOTYPE: ♂, 5.7 mm, AM P35209; PARATYPES, 7♂♂, 15♀♀, AM P35210; lagoon, Nananui Ra, Viti Levu, Fiji [17°15'S 178°12'E], on *Halimeda* sp., A.A. Myers, 7 October, 1979, stn 53.

Material examined. New South Wales: about 95 specimens, AM P64661, between Comet Hole and the reef, Lord Howe Island lagoon,

[approx. 31°30.5'S 159°03'E], associated with red and brown algae, 2–3 m, J.K. Lowry & G.D. Fenwick, 10 May 1977, stn LHA-11.11 specimens, AM P64662, reef front west of Signal Point, Lord Howe Island Lagoon, [approx. 31°30.5'S 159°03'E], *Caulerpa*, 1.5–2.0 m, G.D. Fenwick, 11 May 1977, stn LHA–15.

Type locality. Lagoon, Nananui Ra, Viti Levu, Fiji [approx. 17°15'S 178°12'E].

Habitat. Marine; littoral; among red and brown algae in lagoons, 0 to 3 m depth.

Remarks. This is the first record of *M. nananui* from Australian waters.

Distribution. *New South Wales*: Lord Howe Island (AM).

Extrinsic distribution. Fiji; Nuie; New Zealand.
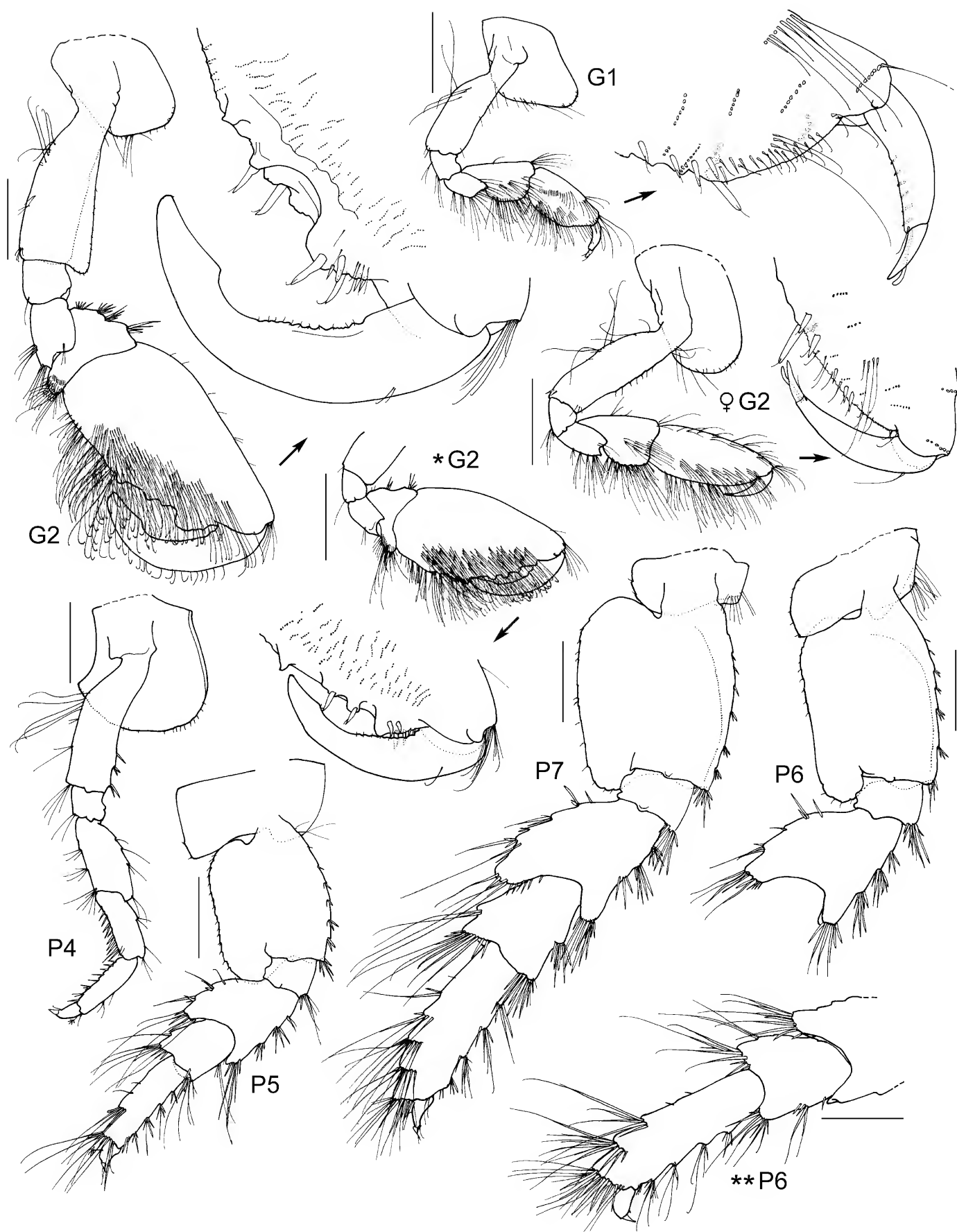
Australian geographic areas. Southeastern Australia.

Fig. 28. *Mallacoota malua* n.sp., holotype, male "a", 10 mm, AM P56679, paratype, female, 8.5 mm, AM P60486, *paratype, male "c", 7.1 mm, AM P60490, Coffs Harbour Jetty, New South Wales, Australia; ** male "b", AM P60487, Botany Bay, New South Wales Australia. Scales represent 0.5 mm.

Mallacoota subcarinata (Haswell)

Figs. 29–33

Megamoera sub-carinata Haswell, 1879b: 335, pl. 21, fig. 4.
Elasmopus subcarinatus.–Stebbing, 1906: 441.–Stebbing, 1910a: 602.–Chilton, 1921b: 76.
Not *Megamoera sub-carinata.*–Chilton, 1885: 1039.
Not *Moera petriei* Thomson, 1882: 236, pl. 18, fig. 3.–Chilton, 1883: 82, pl. 2, fig. 4.–Chilton, 1885: 1039.
Not *Moera sub-carinata.*–Chilton, 1884: 230.–Thomson & Chilton, 1886: 146.
Not *Moera subcarinata.*–Chilton, 1885: 1039.–Thomson, 1889: 261.
Not *Elasmopus subcarinatus.*–Stebbing, 1888: 1019, pl. 98 (plate labelled as *E. persetosus*). Chilton, 1892: 261.–Walker, 1904: 275, pl. 5, fig. 34.–Stebbing, 1906: 441.–Walker, 1909: 335.–Stebbing, 1910a: 602.–Stebbing, 1910b: 457.–Thomson, 1913: 243.–Chilton, 1915: 321, figs 1–6.–Stephensen, 1931: 11.–K.H. Barnard, 1935: 286.–Pirlot, 1936: 317, figs 136–145.–K.H. Barnard, 1937: 160.
Not *Maera subcarinata.*–K.H. Barnard, 1940: 460.–Nayar, 1966: 149.

Not *Mallacoota subcarinata.*–J.L. Barnard, 1972a: 247, figs 144–145.–J.L. Barnard, 1972b: 114, figs 59–60.–Lowry, 1974: 112, 125 figs 9b,d (key).–Ledoyer, 1978: 281, fig. 32.–Barnard & Barnard, 1983: 632.–Ledoyer, 1984: 71,72 figs 34–35.–Myers, 1985: 121, fig. 96.–Myers, 1986: 1390, fig. 9.–Hutchings *et al.*, 1989: 362.–Myers, 1995: 38.

Additional material examined. New South Wales: 2 specimens, AM P22484, east of Mona Vale, 33°41'S 151°19'E, 16 m, Australian Museum Shelf Benthic Survey, 11 May 1972. 2 specimens, AM P22479, east of Long Reef, 33°44'S 151°22'E, 38 m, Australian Museum Shelf Benthic Survey, 24 Aug 1972. 5 specimens, AM P22480, same locality, 36 m, Australian Museum Shelf Benthic Survey, 11 May 1972. 2 specimens, AM P22481, same locality, 32 m, Australian Museum Shelf Benthic Survey, 28 May 1972. 1 specimen, AM P22482, same locality, 15 m, Australian Museum Shelf Benthic Survey, 28 April 1972. 2
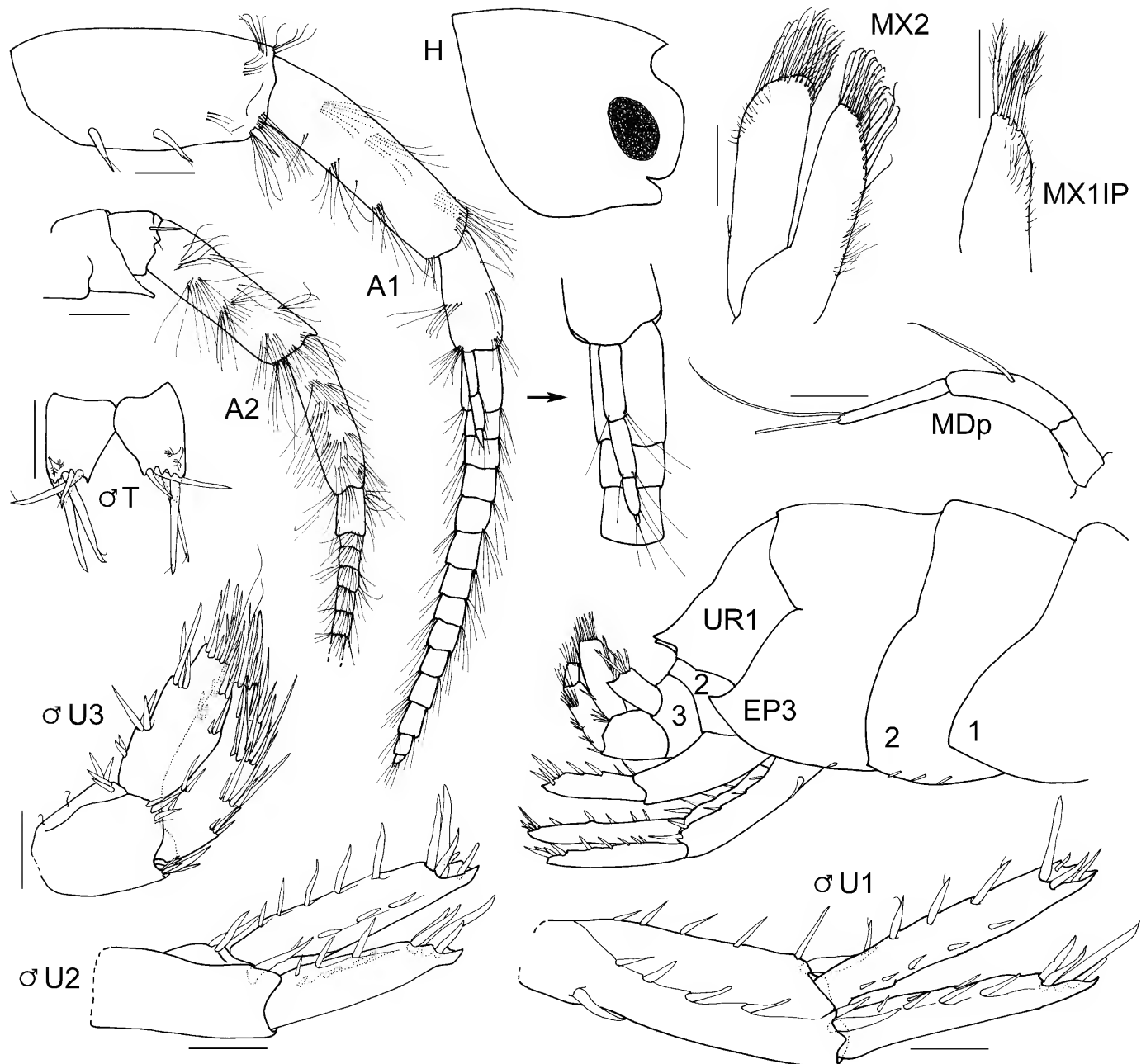

Fig. 29. *Mallacoota subcarinata* (Haswell, 1879b), syntype male, 9.6 mm, syntype, female, 10.4 mm, AM G5390, Port Jackson, New South Wales, Australia. Scales represent 0.2 mm.
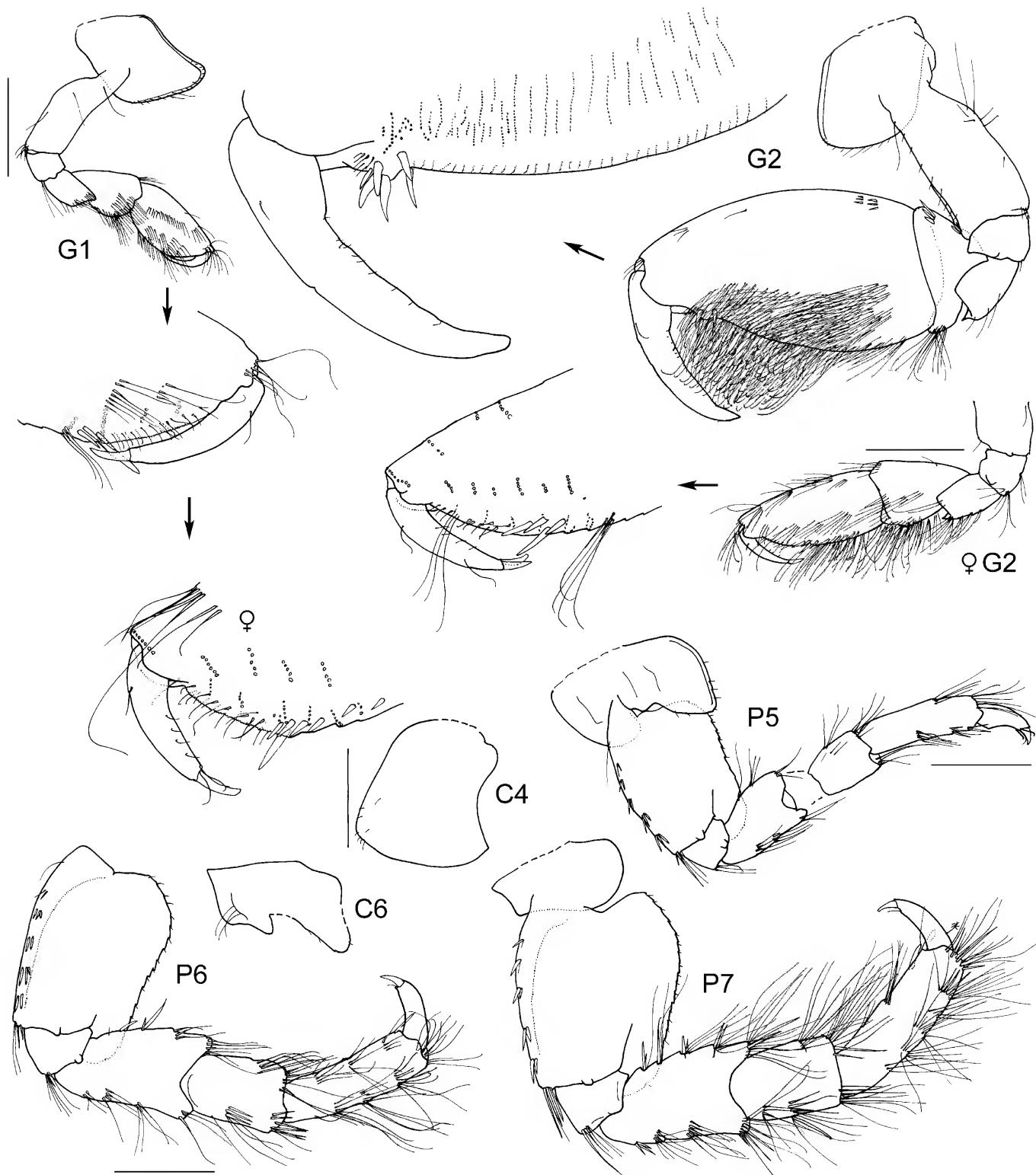
Fig. 30. *Mallacoota subcarinata* (Haswell, 1879b), syntype, male, 9.6 mm, AM G5390, syntype, female, 10.4 mm, AM P63972, Port Jackson, New South Wales, Australia. Scales represent 0.5 mm.

specimens, AM P22483, same locality, Australian Museum Shelf Benthic Survey, 1972. 1♂ "a" 10.4 mm, AM P22487, east of Long Reef, 33°44'S 151°22'E, 40 m, Australian Museum Shelf Benthic Survey, 29 June 1972. 1♂ "b" 5.7 mm, AM P60563, same locality. 9 specimens, AM P22476, east of North Head, Port Jackson, 33°49'S 151°18'E, host sponge: *Halme gigantea*, 25 m, Australian Museum Shelf Benthic Survey, 26 February 1974, transect 07. 1 specimen, AM P22477, east of North Head, Port Jackson, 33°49.5'S 151°18'E, 32 m, Australian Museum Shelf Benthic Survey, 23 May 1972. 5 specimens, AM P5860, Balmoral, Port Jackson, [approx. 33°49.7'S 151°15.1'E], T. Whitelegge, [AM Old Collection]. 1 specimen, AM P22485, east of South Head, Port Jackson, 33°50'S 151°18'E, host sponge: *Halme gigantea*, 21 m, Australian Museum Shelf Benthic Survey, February 1972, transect 11. 5 specimens, AM P63072, outer end of Kurnell Pier, Botany Bay, 34°00.2'S 151°12.5'E, pylon

scrapings, 7 m, NSW Fisheries/CRIMP Survey, 21 October 1998, stn BB KP1 P2–7. 3 specimens, AM P63073, Kurnell Pier (near shoreline), Botany Bay, 34°00.5'S 151°12.7'E, pylon scrapings, 3 m, NSW Fisheries/CRIMP Survey, 21 October 1998, stn BB KP2 P2–3. 6 specimens, AM P2497, 3–4 km off Botany Bay, [approx. 34°05'S 151°15'E], mud, 91–95 m, E.R. Waite on HMCS *Thetis*, 11 March 1898, stn. 37. 1 specimen, AM P2498, 4.5–5 km off Jibbon Point, [approx. 34°07.5'S 151°12'E], sand, mud, 84–101 m, E.R. Waite on HMCS *Thetis*, 12 March 1898, stn. 38. 8 specimens, AM P2494, 5.5–6.5 km off Wattamolla, [approx. 34°10'S 151°11'E], mud, 99–108 m, E.R. Waite on HMCS *Thetis*, 22 March 1898, stn 57. 1 specimen, AM P2499, 11–12.5 km off Wollongong, [approx. 34°27'S 151°04'E], sand, mud, rock, 102 m, E.R. Waite on HMCS *Thetis*, 18 March 1898, stn. 48. 1♂, AM P63117, Jervis Bay, [approx. 35°03'S 150°44'E], T. Whitelegge. 2 specimens, AM P62905,
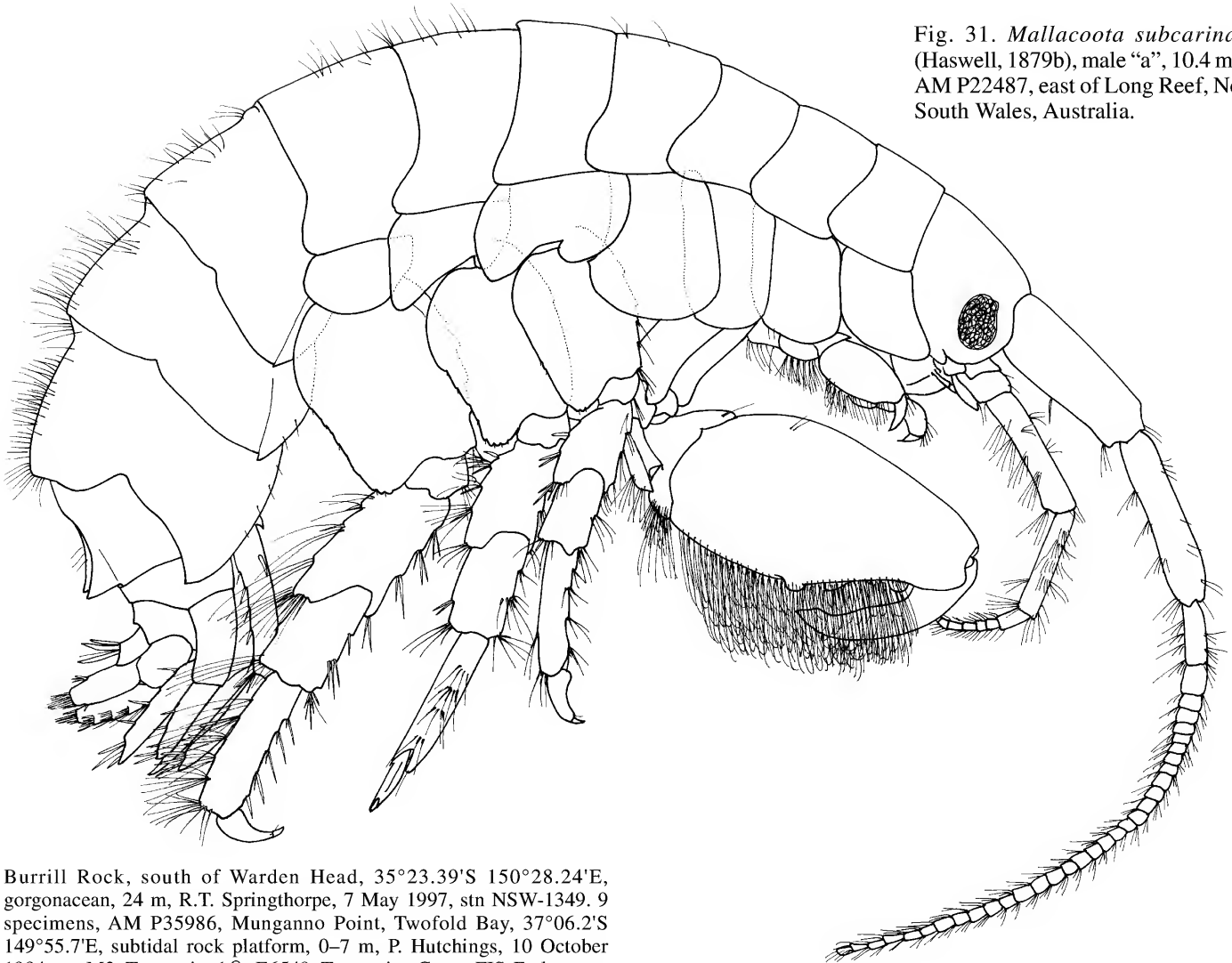
Fig. 31. *Mallacoota subcarinata* (Haswell, 1879b), male "a", 10.4 mm, AM P22487, east of Long Reef, New South Wales, Australia.

Burrill Rock, south of Warden Head, 35°23.39'S 150°28.24'E, gorgonacean, 24 m, R.T. Springthorpe, 7 May 1997, stn NSW-1349. 9 specimens, AM P35986, Munganno Point, Twofold Bay, 37°06.2'S 149°55.7'E, subtidal rock platform, 0–7 m, P. Hutchings, 10 October 1984, stn M3. Tasmania: 1 ♀, E6549, Tasmanian Coast, FIS *Endeavour*, 1909–1914. 2 specimens, E6550, eastern slope of Bass Strait, [approx. 39°00'S 148°40'E], FIS *Endeavour*, 1909–1914. 3 specimens, AM P5936, same locality.

Type locality. Port Jackson, New South Wales (33°51'S 151°16'E) and Port Stephens, New South Wales, Australia, (32°42'S 152°06'E).

Description. Based on male syntype, AM G5390, female syntype, AM P63972, male "a", AM P22487 and male "b", AM P60563.

Head. Lateral cephalic lobes broad, truncated, with anteroventral notch or slit, anteroventral corner rounded. *Antenna 1* longer than antenna 2; peduncular article 1 subequal in length to article 2, with 1–3 robust setae on posterior; flagellum with about 31 articles; accessory flagellum with 4–5 articles. *Antenna 2* peduncular article 2 cone gland reaching at least to end of peduncular article 3; article 4 subequal to article 5; flagellum with about 12 articles. *Mandible* palp article 3 rectolinear, with setae mostly terminal, longer than article 1; article 2 subequal to article 3; article 1 not produced, shorter than article 2, about twice as long as broad. *Maxilla 1* inner plate with 4–5 setae mainly terminal.

Pereon. *Gnathopod 1* coxa anteroventral corner produced, rounded, posteroventral corner notch absent; merus without posterodistal spine; propodus palm acute, convex, without posterodistal corner, defined by posterodistal robust setae. *Gnathopod 2* sexually dimorphic; subchelate; coxa

posteroventral corner notch absent; merus with sharp posteroventral spine; carpus compressed; propodus without medial depression, with strong setal bunch, palm extremely acute, convex or sinusoidal, sculptured, with group of anterodistal robust setae, without posterodistal robust setae, with or without posteroventral corner; dactylus apically blunt or falcate. *Pereopod 5* basis posterior margin straight or slightly concave, posteroventral corner narrowly rounded or subquadrate. *Pereopod 6* coxa anterior lobe ventral margin slightly produced, rounded; basis posterior margin concave, posteroventral corner serrate. *Pereopod 7* basis posterior margin slightly concave or straight, with posterior margin smooth or minutely castelloserrate, posteroventral corner narrowly rounded or subquadrate.

Pleon. *Epimeron 1* posteroventral corner narrowly rounded or subquadrate. *Epimera 1–2* posteroventral margin without spines above posteroventral corner. *Epimeron 3* posterior margin smooth, posteroventral corner with strongly produced acute spine. *Urosomite 1* dorsally bicarinate. *Uropod 3* inner ramus subequal in length to outer ramus; outer ramus longer (1.2 to 2× length) than peduncle, 1-articulate. *Telson* each lobe with 3 or more apical/subapical robust setae, apical conical extension reaching scarcely one third along longest seta or absent.

Female (sexually dimorphic characters). *Gnathopod 2* carpus short; propodus setose, convex, smooth, with sparse robust setae, defined by posterodistal robust setae; dactylus apically acute/subacute.
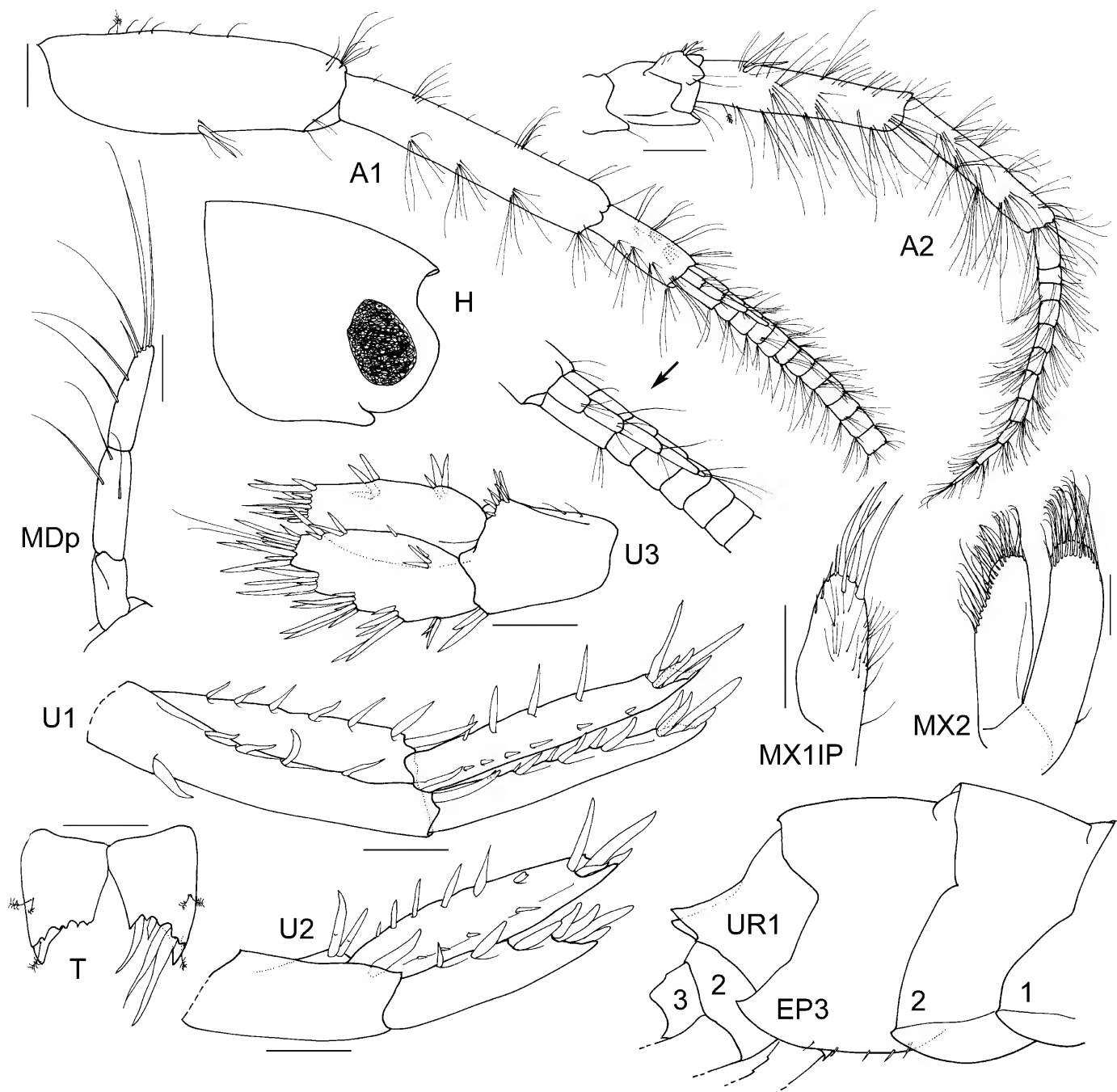
Fig. 32. *Mallacoota subcarinata* (Haswell, 1879b), male "a", 10.4 mm, AM P22487, east of Long Reef, New South Wales, Australia. Scales for MDp, MX1IP, MX2, represent 0.1 mm, remainder represent 0.2 mm.

Habitat. Marine; littoral and continental shelf; subtidal rock platforms, sand, mud, sponges and from jetty pilings, 3.5 to 108 m depth.

Remarks. *Mallacoota subcarinata* Haswell, 1879b appears to be confined to Australian waters. All extrinsic records need to be carefully studied. The species appears to be most similar to those species with a strong posteroventral corner spine on epimeron 3. In Australian waters this includes *M. diemenensis* and *Mallacoota euroka*. *Mallacoota diemenensis* differs from all other Australian species in having dorsal carinae on pleonites 1 to 3. *Mallacoota subcarinata* differs from *Mallacoota euroka* in having only one to three robust setae along the posterior margin of antennal peduncular article 1 and in the posterior margin of the basis of pereopod 7 that is straight in *M. subcarinata* and convex in *M. euroka*.

Distribution. *New South Wales*: east of Long Reef; east of Port Jackson (both AM); Port Jackson (Haswell, 1879b); off Botany Bay; off Jibbon; off Wattamolla; off Wollongong (all Stebbing, 1910a); Jervis Bay; Ulladulla; Munganno Point, Twofold Bay (all AM). *Tasmania*: Bass Strait (Chilton, 1921b).

Australian geographic areas. Southeastern Australia.

Miramaera n.gen.

Type species. *Miramaera thetis* n.sp.

Diagnosis. *Head* without anteroventral notch; eye ovate to reniform. *Antenna 1* accessory flagellum long, nearly half to more than half length of primary flagellum. *Mandible palp* article 1 strongly produced distally; article 2 longer than article 3; article 3 long, rectolinear. *Maxilla 1* inner plate with mainly apical setae. *Gnathopod 1* coxa anteroventral corner produced, acute or subacute.
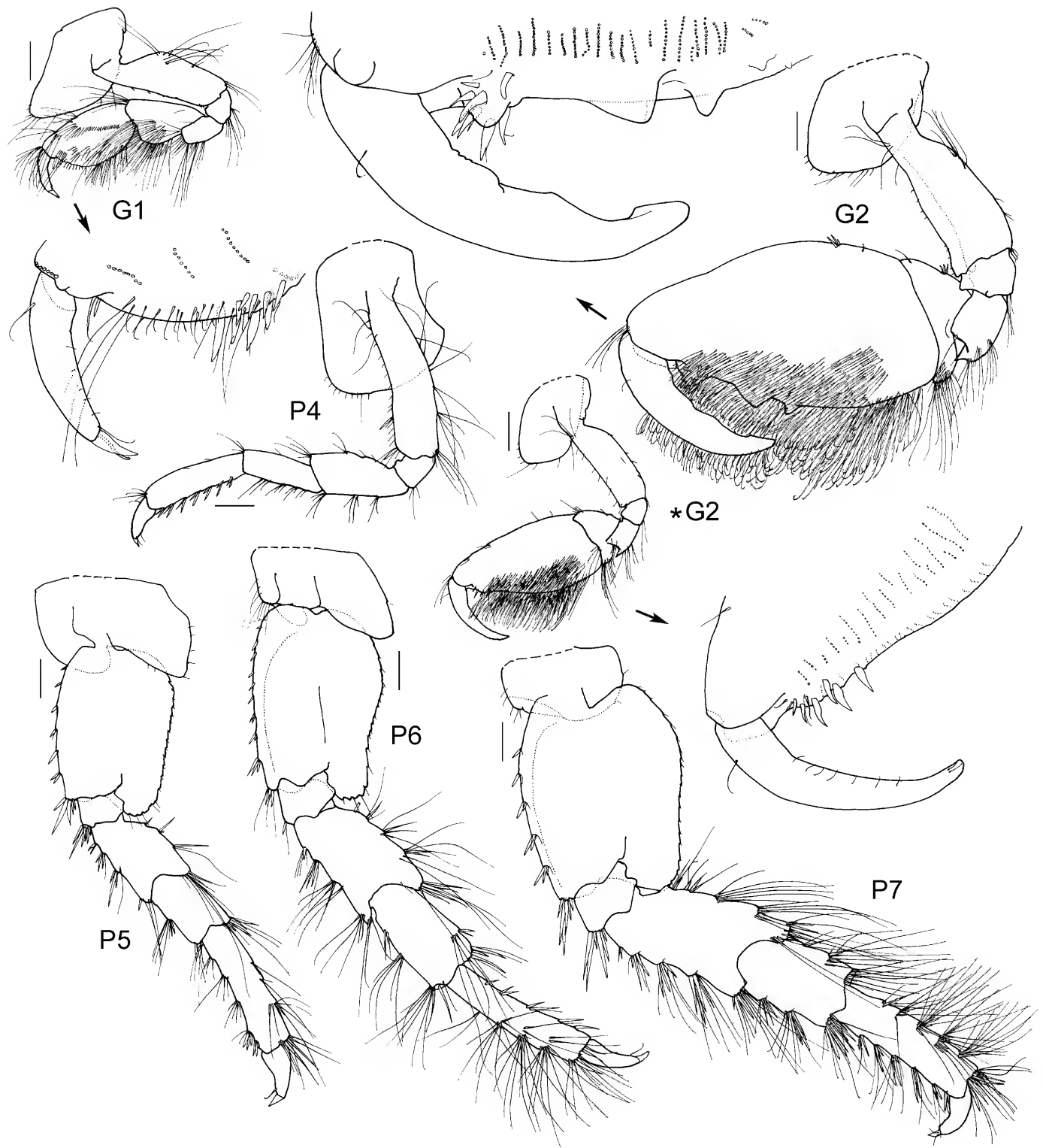
Fig. 33. *Mallacoota subcarinata* (Haswell, 1879b), male "a", 10.4 mm, AM P22487, *male "b", 5.7 mm, AM P60563, east of Long Reef, New South Wales, Australia. Scales represent 0.2 mm.

Gnathopod 2 significantly enlarged in male and female; left and right gnathopods symmetrical in male; palm acute in male and female, both male propodi with well defined corner (greater than 90°), both female propodi with well defined corner (greater than 90°); dactylus with 1 or 2 setae on anterior margin. *Pereopods 5–7* dactyli simple. *Epimeron 3* posterior margin smooth. *Urosomite 1* dorsal and posterior margins smooth. *Uropod 3* rami distally truncated, about 1.5× to 3 or more times peduncle, apical robust setae long or short; outer ramus 1-articulate. *Telson* deeply cleft, lobes truncated with apical cusps, with or without robust setae on outer margins, with short apical robust setae.

Species composition. *Miramaera tepuni* (J.L. Barnard, 1972b); *Miramaera thetis* n.sp.

Etymology. A combination of the Latin word *mirus*, meaning wonderful, with the Latin stem *Maera*.

Remarks. *Miramaera* is excluded from the *Linguimaera* group because of its symmetrical second gnathopods. It is excluded from *Quadrimaera* because of the strong apical notch on the anteroventral margin of the head, the acute palms on the propodi of male gnathopod 2, the simple dactyli on pereopods 5–7 and the telsonic lobes that are truncated with apical cusps. It may be most similar to genera

in the *Maera* group (*sensu stricto*), but it differs from that group in the setation of the dactyli of the second gnathopods. The significant differences between *Miramaera* and *Lupimaera* are that in *Miramaera* the posterior margin of epimeron 3 is smooth, the rami of uropod 3 are longer than the peduncle and the telsonic lobes have apical cusps and short robust setae. *Miramaera* differs from *Maeropsis* in having acute palms and a well defined corner of more than 90° on both male and female propodi of gnathopod 2.

Distribution. Australia; New Zealand.

Miramaera thetis n.sp.

Figs. 34–36

Maera inaequipes.–Stebbing, 1910a: 599.–Sheard, 1937: 24.

Type material. HOLOTYPE, ♂ "a", 7.9 mm, AM P62798; many PARATYPES, AM P27035; 1 PARATYPE, ♀, 6.7 mm, AM P62799; 1 PARATYPE, ♂ "b", 7.8 mm, AM P62800; 10 PARATYPES, AM P62801, between Troubridge Light and Cape Jervis, South Australia, 35°20'S 137°40'E, sponges on mud bottom, 20 m, D. Blake & H. Larsen, 14 March 1978.

Additional material examined. New South Wales: 1 specimen, AM P2492, 8–9.5 km off Coogee, 33°57'S 151°21.5'E, fine sand, 91 m, E.R. Waite on HMCS Thetis, 15 March 1898, stn 44. South Australia: 1 ovigerous female, E6544, 24 km north west of Cape Jervis, [approx. 35°26'S 137°55'E], 31 m, FIS Endeavour, 1909–1914.

Type locality. Between Troubridge Light and Cape Jervis, South Australia, [approx. 35°20'S 137°40'E], sponges on mud bottom, 20 m.

Description. Based on holotype male, AM P62798 and paratype female, AM P62799.

Head. Lateral cephalic lobes broad, rounded, without notch or slit, anteroventral corner with acute/subacute spine. *Antenna 1* longer than antenna 2; peduncular article 1 slightly shorter than article 2, with 4 or more robust setae along posterior margin; flagellum with 16 articles; accessory flagellum with 9 articles. *Antenna 2* peduncular article 2 cone gland not reaching to end of peduncular article 3; article 4 longer than article 5; flagellum with 8 or 9 articles. *Mandible* palp article 3 rectolinear, setose on distomedial margin, longer than article 1; article 2 longer than article 3; article 1 produced distally, shorter than article 2, about twice as long as broad. *Maxilla 1* inner plate with 3 setae mainly terminal.

Pereon. *Gnathopod 1* coxa anteroventral corner produced, acute, posteroventral corner notch absent; merus without posterodistal spine; carpus with anterodistal swelling; palm acute, convex, without posterodistal corner, defined by posterodistal robust setae. *Gnathopod 2* sexually dimorphic; subchelate; coxa posteroventral corner notch absent; merus with sharp posteroventral spine; carpus compressed; propodus without medial depression, palm acute, convex, sculptured, lined with robust setae, defined by posterodistal robust setae, defined by posteroventral spine; apically acute/subacute. *Pereopod 5–6* basis posterior margin slightly concave, posteroventral corner broadly rounded. *Pereopod 7* basis posterior margin slightly convex, with posterior margin castelloserrate, posteroventral corner broadly rounded.

Pleon. *Epimeron 1* posteroventral corner broadly rounded. *Epimera 1–2* posteroventral margin without spines above posteroventral corner. *Epimeron 3* posterior margin smooth, posteroventral corner subquadrate. *Uropod 3* rami distally truncated; inner ramus subequal in length to outer ramus; outer ramus longer (1.2 to 2× length) than peduncle, 1-articulate. *Telson* each lobe with 2 apical/subapical robust setae, apical conical extension reaching scarcely one third along longest seta.

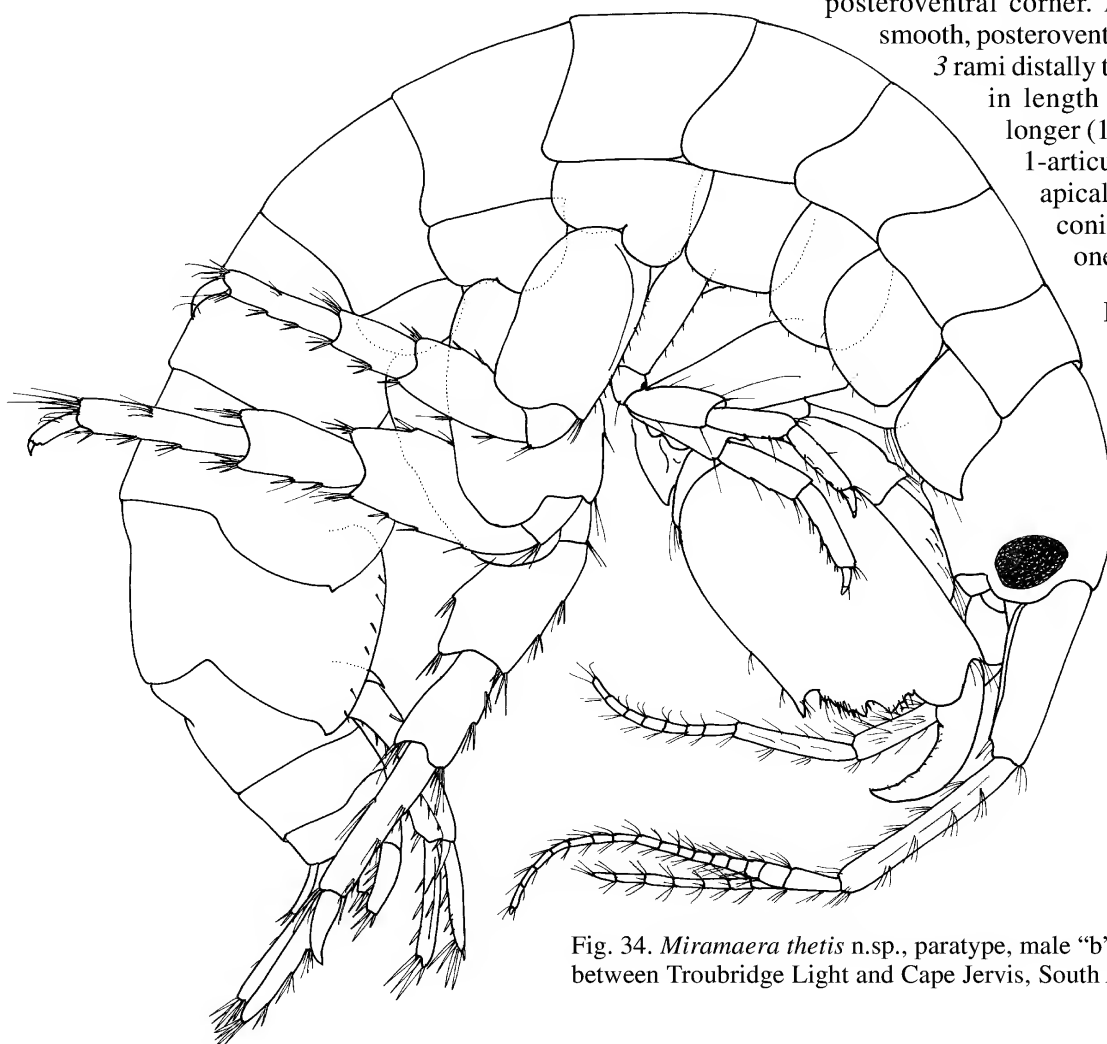**Female** (sexually dimorphic characters). *Gnathopod 2* palm smooth.

Fig. 34. *Miramaera thetis* n.sp., paratype, male "b", 7.8 mm, AM P62800, between Troubridge Light and Cape Jervis, South Australia.
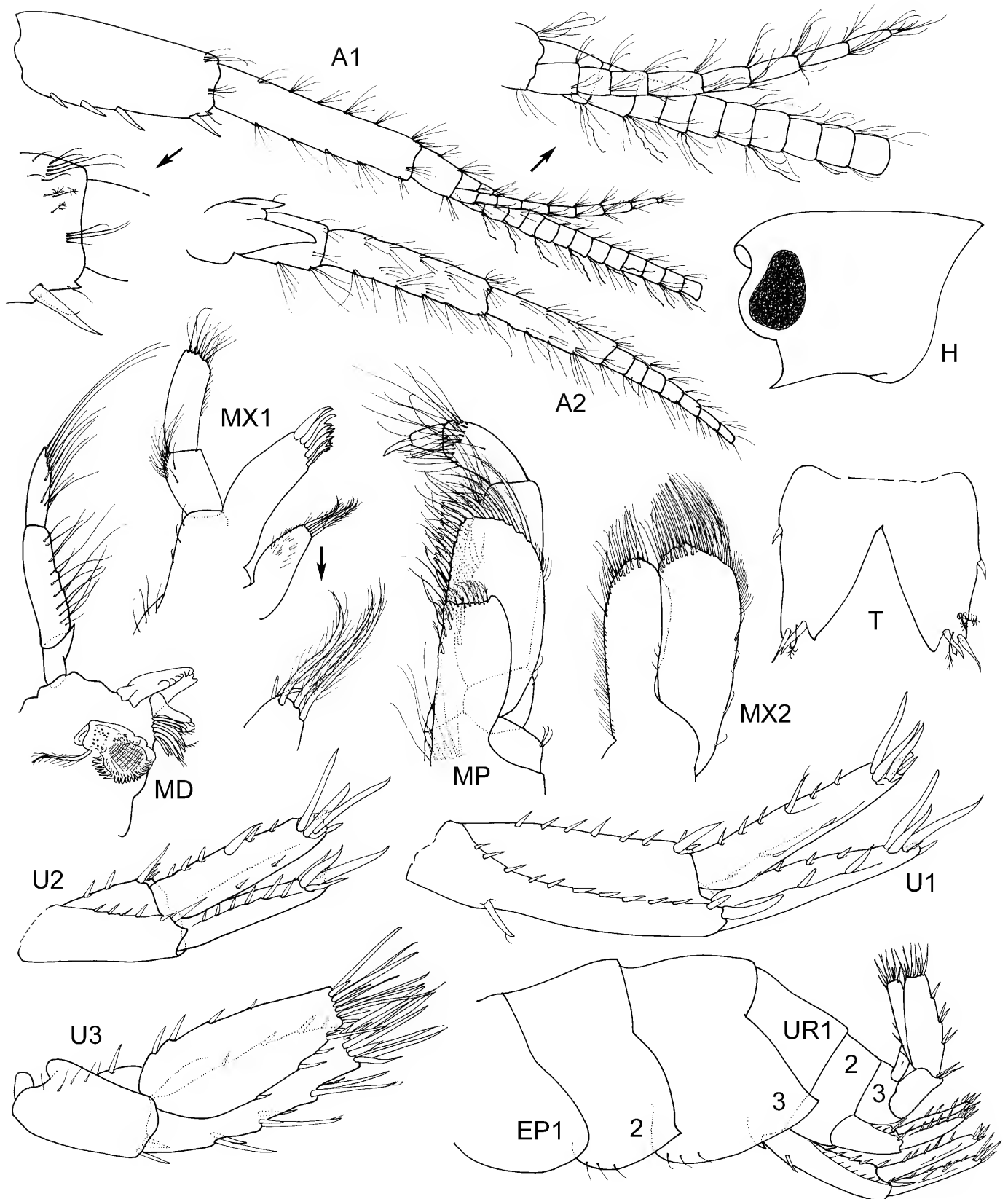
Fig. 35. *Miramaera thetis* n.sp., holotype, male, 7.9 mm, AM P62798, between Troubridge Light and Cape Jervis, South Australia.

Habitat. Marine; sponges on mud bottom, sand; littoral, continental shelf; 20 to 100 m depth.

Etymology. Named for the *Thetis* Expedition, which collected the marine fauna off the coast of Sydney during 1898.

Remarks. *Miramaera thetis* differs significantly from *Miramaera tepuni* (J.L. Barnard, 1972b), the only other species in the genus, in the rami of uropod 3 that are only half the length of those of *P. tepuni*.

Distribution. *New South Wales*: off Coogee and off Wollongong (both Stebbing, 1910a). *South Australia*: Cape Jervis (AM)

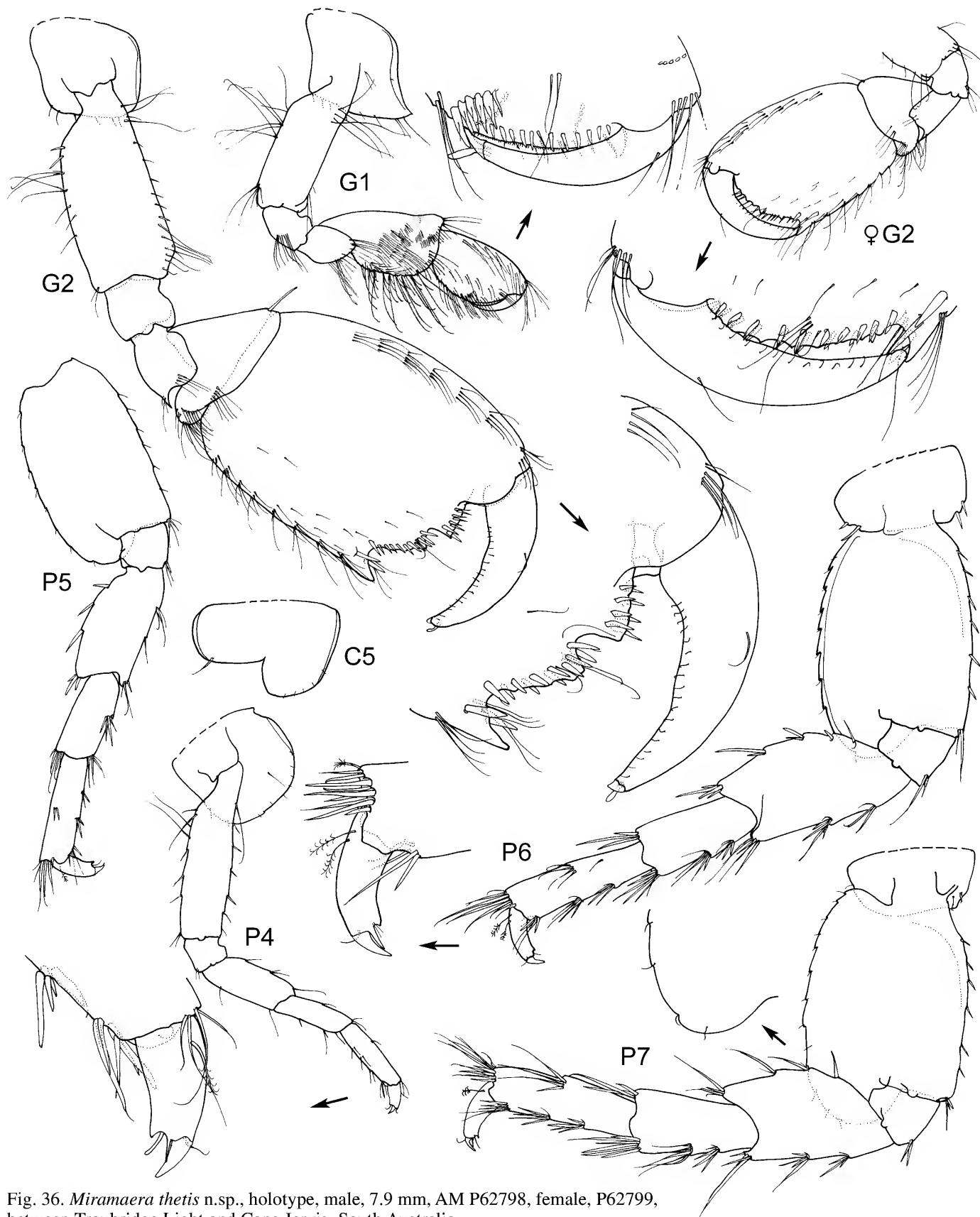**Australian geographic areas**. Southeastern and southern Australia.

Fig. 36. *Miramaera thetis* n.sp., holotype, male, 7.9 mm, AM P62798, female, P62799, between Troubridge Light and Cape Jervis, South Australia.

Parelasmopus Stebbing, 1888

Parelasmopus sowpigensis n.sp.

Figs. 37–40

Type material. HOLOTYPE, ♂, 8.9 mm, AM P60496; 1 PARATYPE, ♀, 7.1 mm, AM P60497; 16 PARATYPES, 3♂♂, 13♀♀, AM P60498; 21 PARATYPES, 13♂♂, 8♀♀, AM P60499, off Sow and Pigs reef, Port Jackson, New South Wales, Australia, 33°50.3'S 151°16.2'E, shelley sand, 5 m, benthic grab, J.K. Lowry & A.R. Jones, 30 September 1976, stn NSW-184.

Type locality. Sow and Pigs Reef, Port Jackson, New South Wales, 33°50.3'S 151°16.2'E, shelley sand, 5 m.

Description. Based on holotype male, AM P60496 and paratype female, AM P60497.

Head. Lateral cephalic lobes broad, rounded, with anteroventral notch or slit, anteroventral corner with acute/subacute spine. *Antenna 1* longer than antenna 2; peduncular article 1 subequal in length to article 2, with 3 robust setae

along posterior margin; flagellum with 22 articles; accessory flagellum with 4 articles. *Antenna 2* peduncular article 2 cone gland reaching at least to end of peduncular article 3; article 4 longer than or subequal to article 5; flagellum with 6 articles. *Mandible* palp article 3 rectolinear, setose on distomedial margin, subequal to or shorter than article 1; article 2 shorter than article 3; article 1 curved, swollen distally, longer than article 2, at least 3× as long as broad. *Maxilla 1* inner plate with 2 setae mainly terminal.

Pereon. *Gnathopod 1* coxa anteroventral corner not produced, posteroventral corner notch absent; merus without posterodistal spine; propodus palm acute, convex, without posterodistal corner, defined by posterodistal robust setae. *Gnathopod 2* sexually dimorphic; subchelate; coxa posteroventral corner notch absent; merus with sharp posteroventral spine; carpus short; propodus without medial depression, without strong concentration of setae, palm nearly transverse, straight, smooth, with group of anterodistal robust setae, defined by posterodistal robust setae, without posteroventral corner; dactylus apically blunt. *Pereopod 5* basis posterior margin straight, posteroventral corner narrowly rounded or subquadrate. *Pereopod 6* coxa anterior lobe ventral margin slightly produced, rounded; basis posterior margin slightly concave, posteroventral corner broadly rounded, narrowly rounded or subquadrate. *Pereopod 7* basis posterior margin straight, with posterior margin smooth or minutely castelloserrate, posteroventral corner narrowly rounded or subquadrate.

Pleon. *Epimeron 1* posteroventral corner narrowly rounded or subquadrate. *Epimera 1–2* posteroventral margin without spines above posteroventral corner. *Epimeron 3* posterior margin smooth, posteroventral corner with small acute spine. *Urosomite 1* dorsally bicarinate. *Uropod 3* inner ramus subequal in length to outer ramus; outer ramus longer (1.2 to 2× length) than peduncle, 1-articulate. *Telson* each lobe with 3

or more apical/subapical robust setae, apical conical extension reaching scarcely one third along longest seta.

Female (sexually dimorphic characters). *Gnathopod 2* carpus long; propodus palm acute, convex, lined with robust setae, defined by posteroventral corner; dactylus apically acute/subacute.

Habitat. Marine; littoral; shelley sand, 5 m depth.

Etymology. Named for the Sow and Pigs Reef, the type locality.

Remarks. This species fits *Parelasmopus* because of the highly distinctive mandibular palp with its very long first article and very short second article, but it differs from the generic definition in not having a serrate posteroventral margin on epimeron 3, nor does it have dorsally bicarinate first and second pleonites. J.L. Barnard (1972a) established *Ifalukia* for one species of *Parelasmopus* that lacked dorsal carinae on the pleonites and urosomites, and lacked posteroventral serrations on epimeron 3. *Parelasmopus sowpigensis* is most similar to *Ifalukia*, but differs in having a dorsally bicarinate first urosomite. It therefore strictly fits neither genus. If the mandibular palp is the main synapomorphy defining *Parelasmopus*, then it appears that some species in the complex have either lost or never had dorsal carinae or serrate ventral margins. Until the phylogenetic implications of these questions can be analysed it is best to maintain a broad concept of the genus.

Parelasmopus sowpigensis is therefore a distinctive species differing from other Australian species in having dorsally smooth first and second pleonites and smooth ventral margins on epimeron 3.

Distribution. *New South Wales*: Sow and Pigs Reef, Port Jackson (AM).

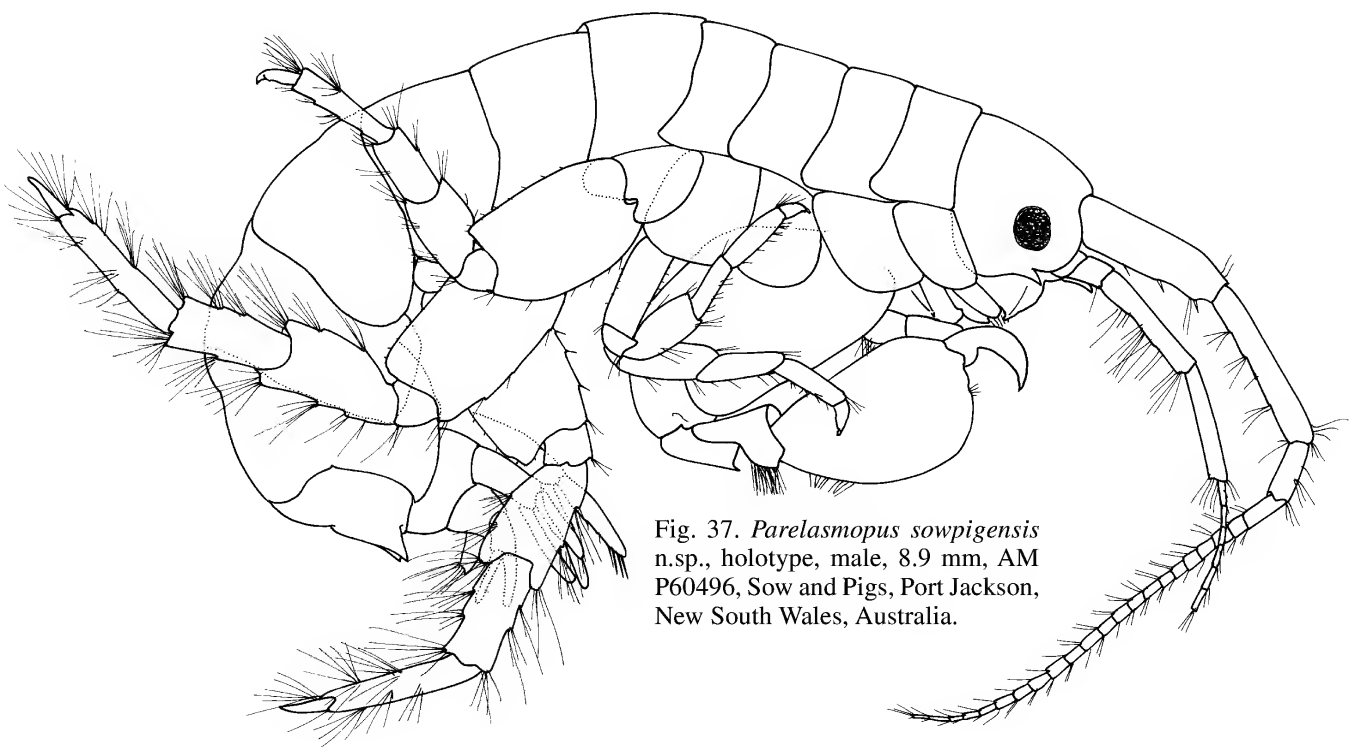**Australian geographic areas**. Southeastern Australia.

Fig. 37. *Parelasmopus sowpigensis* n.sp., holotype, male, 8.9 mm, AM P60496, Sow and Pigs, Port Jackson, New South Wales, Australia.
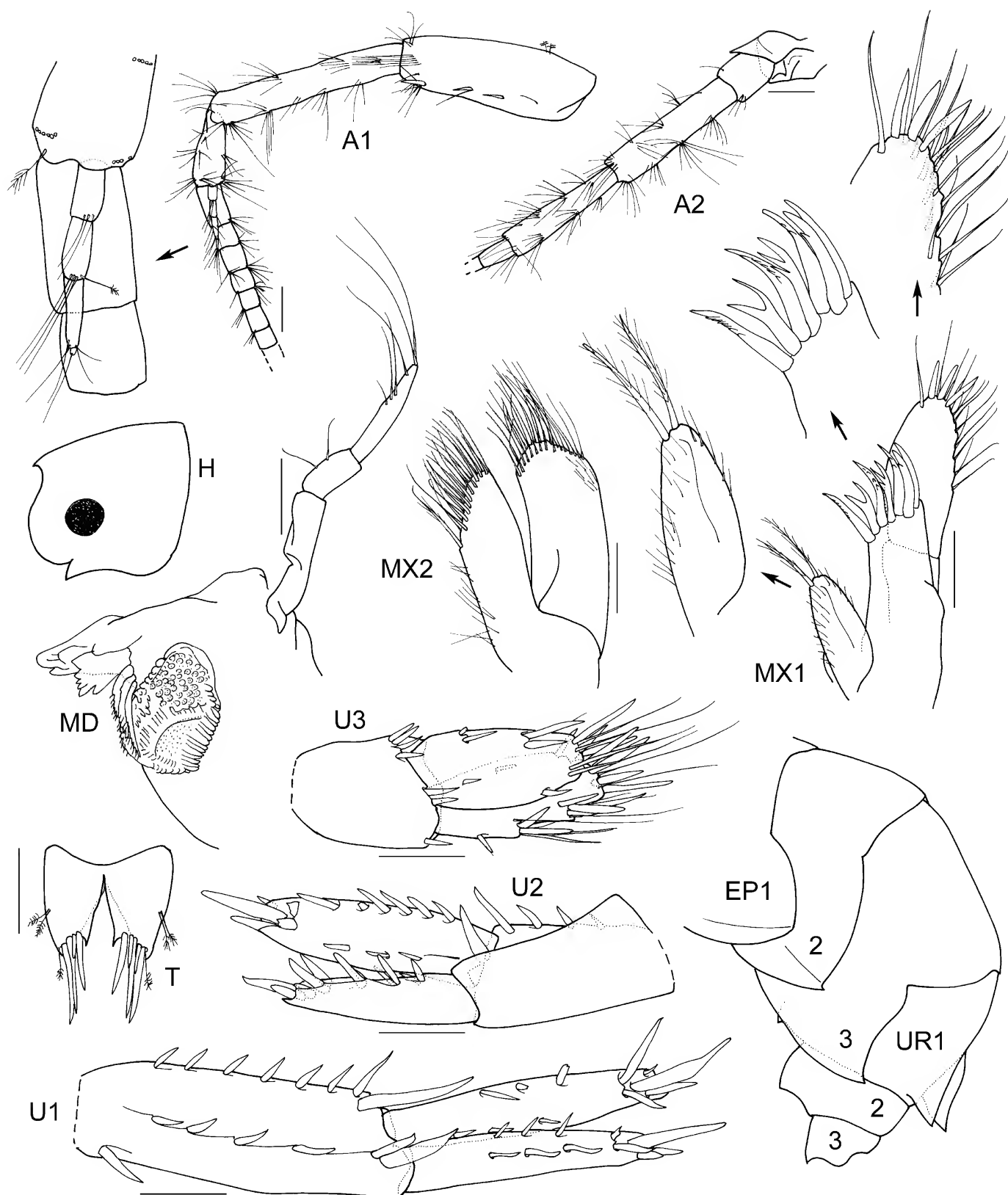
Fig. 38. *Parelasmopus sowpigensis* n.sp., holotype, male, 8.9 mm, AM P60496, Sow and Pigs, Port Jackson, New South Wales, Australia. Scales for mouthparts represent 0.1 mm, remainder represent 0.2 mm.

Quadrivisio Stebbing, 1907

Quadrivisio sarina n.sp.

Figs. 41–43

Type material. HOLOTYPE, ♀, 7.4 mm, AM P60482; 1 PARATYPE, ♂, 8.1 mm, AM P60484; 1 PARATYPE, ♀, AM P60483, Armstrong Beach, Sarina, Queensland, Australia, [approx. 21°46'S 149°29'E], sand beach, mid-tide level, N. Hacking, 18 December 1994.
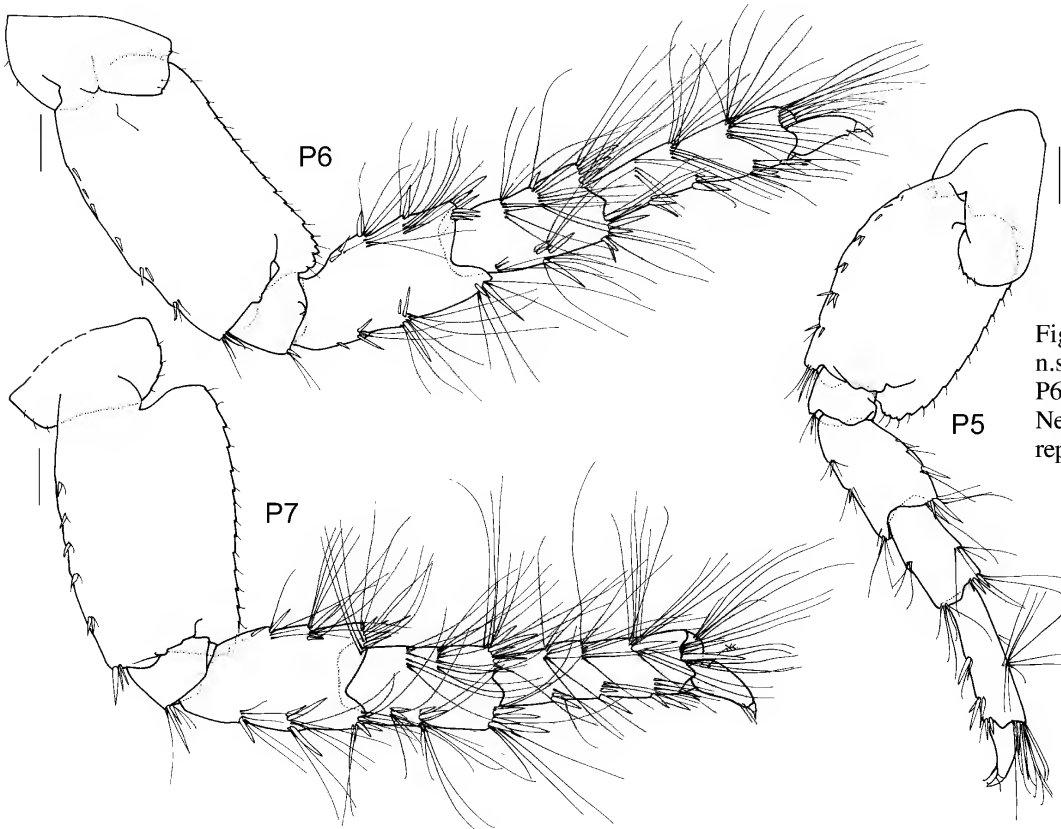
Type locality. Armstrong Beach, Sarina, Queensland, Australia, [approx. 21°46'S 149°29'E], sand beach, mid-tide level.

Description. Based on holotype female, AM P60482 and paratype male, AM P60484.

Head. Lateral cephalic lobes broad, rounded, with anteroventral notch or slit, anteroventral corner rounded. *Antenna 1* shorter than antenna 2; peduncular article 1 longer than article 2, with 2 robust setae along posterior margin;

Fig. 39. *Parelasmopus sowpigensis* n.sp., holotype, male, 8.9 mm, AM P60496, female, 7.1 mm, AM P60497, Sow and Pigs, Port Jackson, New South Wales, Australia. Scales represent 0.2 mm.

Fig. 40. *Parelasmopus sowpigensis* n.sp., holotype, male, 8.9 mm, AM P60496, Sow and Pigs, Port Jackson, New South Wales, Australia. Scales represent 0.2 mm.
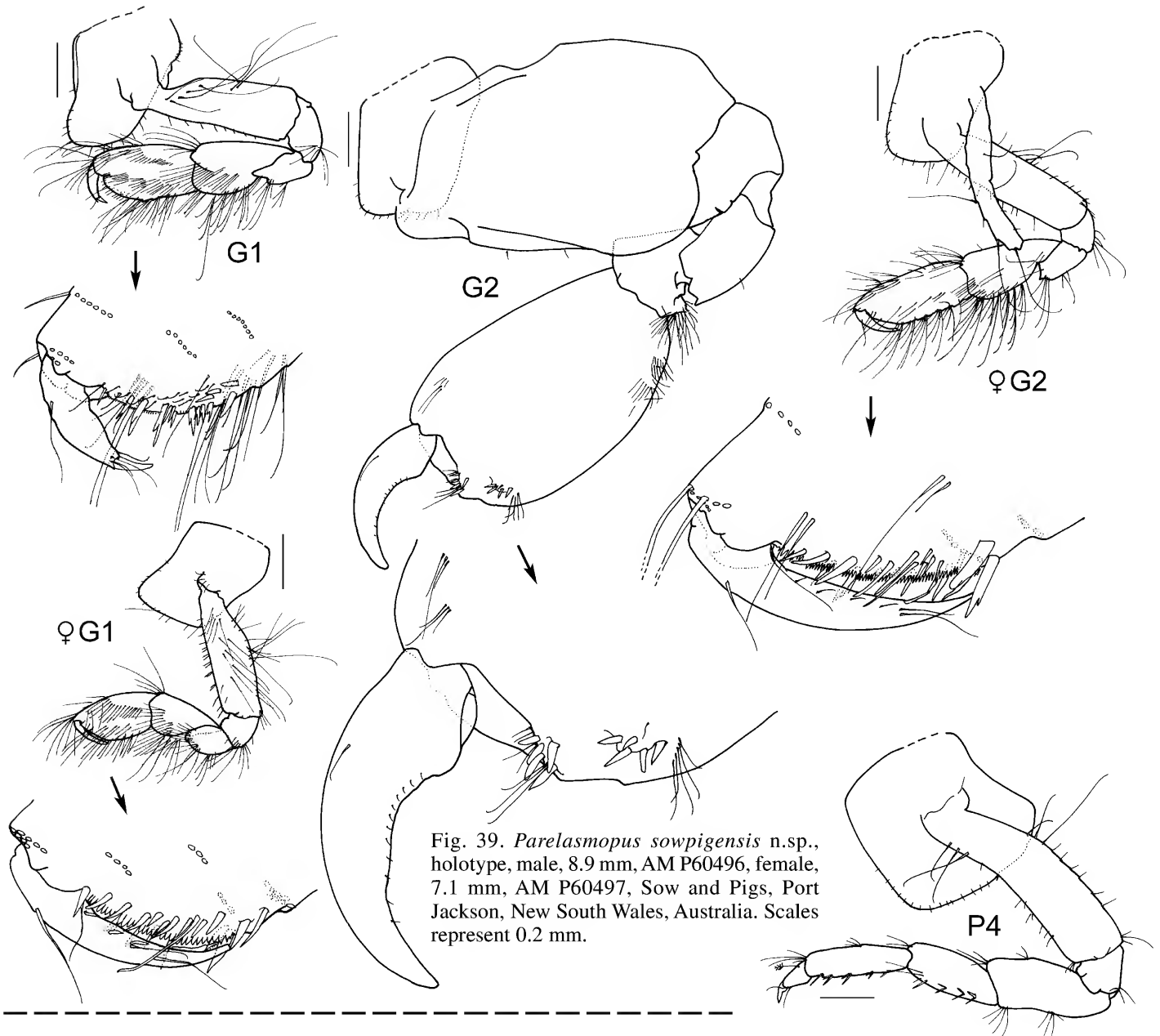
flagellum with at least 14 articles; accessory flagellum with 6 articles. *Antenna 2* peduncular article 2 cone gland reaching at least to end of peduncular article 3; article 4 subequal to article 5; flagellum with 15 articles. *Mandible* palp article 3 rectolinear, with setae mostly terminal, longer than article 1; article 2 subequal to or shorter than article 3; article 1 produced distally, shorter than article 2, about as long as broad. *Maxilla 1* inner plate setose along entire inner margin.

Pereon. *Gnathopod 1* coxa anteroventral corner not produced, posteroventral corner notch absent; merus without posterodistal spine; propodus palm nearly transverse, convex, without posterodistal corner, defined by postero-distal robust setae. *Gnathopod 2* sexually dimorphic; subchelate; coxa posteroventral corner notch absent; merus with rounded posteroventral corner, or with subquadrate posteroventral corner; carpus compressed; propodus with medial depression, without strong concentration of setae, palm extremely acute, convex, smooth, lined with robust setae, defined by posterodistal robust setae, without posteroventral corner; dactylus apically acute/subacute. Pereopod 5–6 basis posterior margin convex, posteroventral corner narrowly rounded or subquadrate. *Pereopod 7* basis posterior margin convex, with posterior margin smooth or minutely castelloserrate, posteroventral corner narrowly rounded or subquadrate.

Pleon. *Epimeron 1* posteroventral corner with small acute spine. *Epimera 1–2* posteroventral margin without spines above posteroventral corner. *Epimeron 3* posterior margin smooth, posteroventral corner with small acute spine. *Urosomite 1* with posterodorsal spine. *Urosomite 2* with two groups of 1–3 small dorsolateral robust setae. *Uropod 3* inner ramus subequal in length to outer ramus; outer ramus longer (1.2 to 2× length) than peduncle, 1-articulate. *Telson* with 1 robust seta per lobe on inner margins, each lobe with 3 or more apical/subapical robust setae, apical conical extension absent.

Female (sexually dimorphic characters). *Gnathopod 2* merus with sharp posteroventral spine or with subquadrate posteroventral corner; propodus without medial depression, defined by posteroventral corner or without posteroventral corner.

Habitat. Marine; littoral; intertidal sand beach, mid-tide level.

Etymology. Named for the Queensland town of Sarina, near the type locality of the species.

Remarks. This is the first record of *Quadrivisio* in Australian waters. It is most similar to *Q. bengalensis* Stebbing, 1907, in having robust setae on the inner margins of the telson. *Quadrivisio sarina* differs from that species in the shape of the basis of pereopod 7 and in the shape of the palm of gnathopod 2. The antennae and rami of uropod 3 are generally less setose in *Quadrivisio sarina*.

Distribution. *Queensland*: Armstrong Beach, near Sarina (AM).

Australian geographic areas. Northeastern Australia.

Eriopisa group
Victoriopisa Karaman & Barnard, 1979
Victoriopisa australiensis (Chilton)
Figs. 44–46

Niphargus australiensis Chilton, 1923: 80, fig. 1.–Sheard, 1937: 24.
Victoriopisa australiensis.–Stock, 1980: 383.–Stock & Platvoet, 1981: 30 (key).–Barnard & Barnard, 1983: 670.–Karaman, 1984: 58.–Jones, *et al*., 1986: 541.–Jones, 1987: 623.–Hutchings *et al*., 1989: 362.

Type material. Holotype, AM P5852, in South West Creek, 400 m from the sea, Macleay River, South West Rocks, Trial Bay, New South Wales, [approx. 30°53'S 153°03'E], tidal lagoon, J.R. Kinghorn, 1920.

Additional material examined. New South Wales: 4 specimens, AM P63955, near boat ramp, Hickey Island, Clarence River, New South Wales, Australia, 29°26.039'S 153°21.552'E (GPS), sand silt, van Veen grab, 3 m, P. Hutchings *et al*., 25 February 2003, stn NSW-2120. 1 specimen, AM P56683, near Fred Hansen Bridge Boambee Creek, Sawtell, 30°20.8'S 153°05.6'E, seagrass (*Zostera*) and mud, 0.2 m, Australian Museum party, 8 March 1992, stn NSW-718. 1♂, 11.1 mm, AM P56684, 50 m upstream from Fred Hansen Bridge, Boambee Creek, Sawtell, New South Wales, Australia, 30°20.8'S 153°05.6'E, seagrass (*Zostera*), 0.5 m, sweep net at low tide, Australian Museum party, 8 March 1992, stn NSW-719. 1 specimen, AM P60599, 50 m upstream from Fred Hansen Bridge, Boambee Creek, Sawtell, 30°20.8'S 153°05.6'E, seagrass (*Zostera*), 0.5 m, sweep net at low tide, Australian Museum party, 8 March 1992, stn NSW-719. 2 specimens, AM P54276, Wallis Lake, [approx. 32°17'S 152°30'E], M. Lincoln-Smith, stn Zostera Bay 5. Many specimens, AM P30831-P30971, near mangroves, north west side Fullerton Cove, Hunter River, [approx. 32°50'S 151°46.5'E], soft mudflat, 0–3.5 m, Australian Littoral Society, NSW Division, between 8 June 1975 and 12 November 1977, transects A1–4, B1–3, C6–7. 1 specimen, AM P54283, Ermington Bay, Parramatta River, 33°49.2'S 151°04.1'E, Coast and Wetlands Society
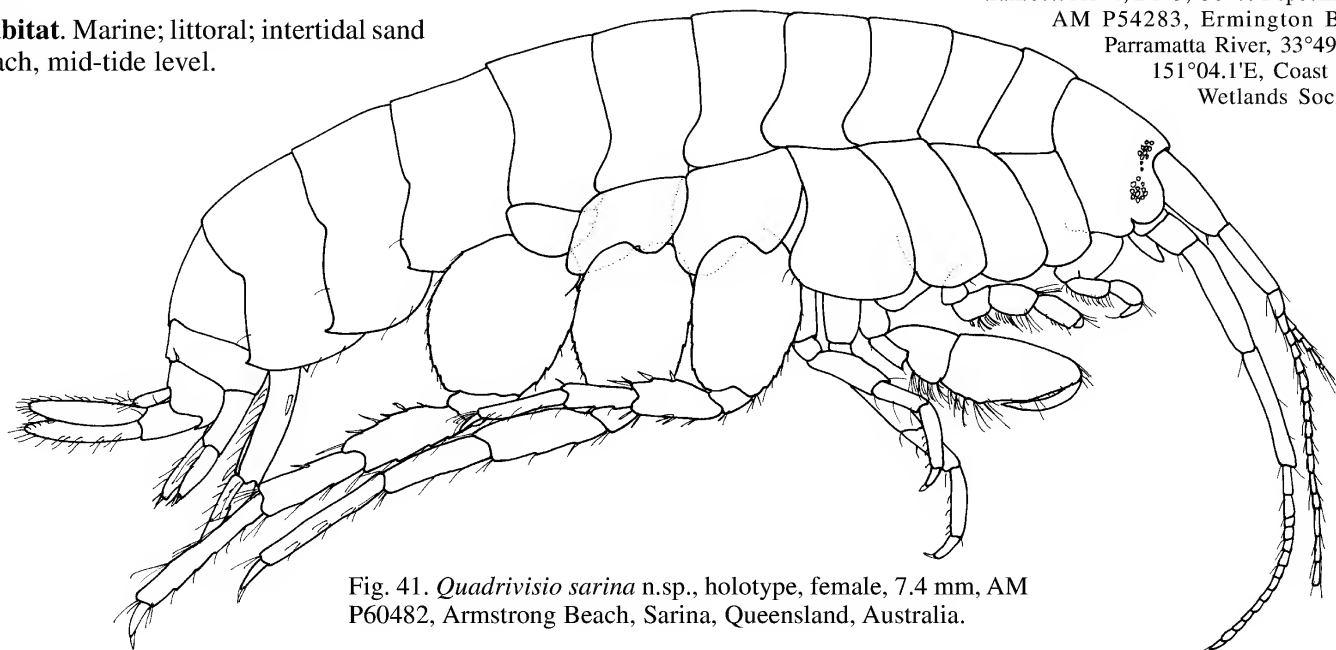

Fig. 41. *Quadrivisio sarina* n.sp., holotype, female, 7.4 mm, AM P60482, Armstrong Beach, Sarina, Queensland, Australia.
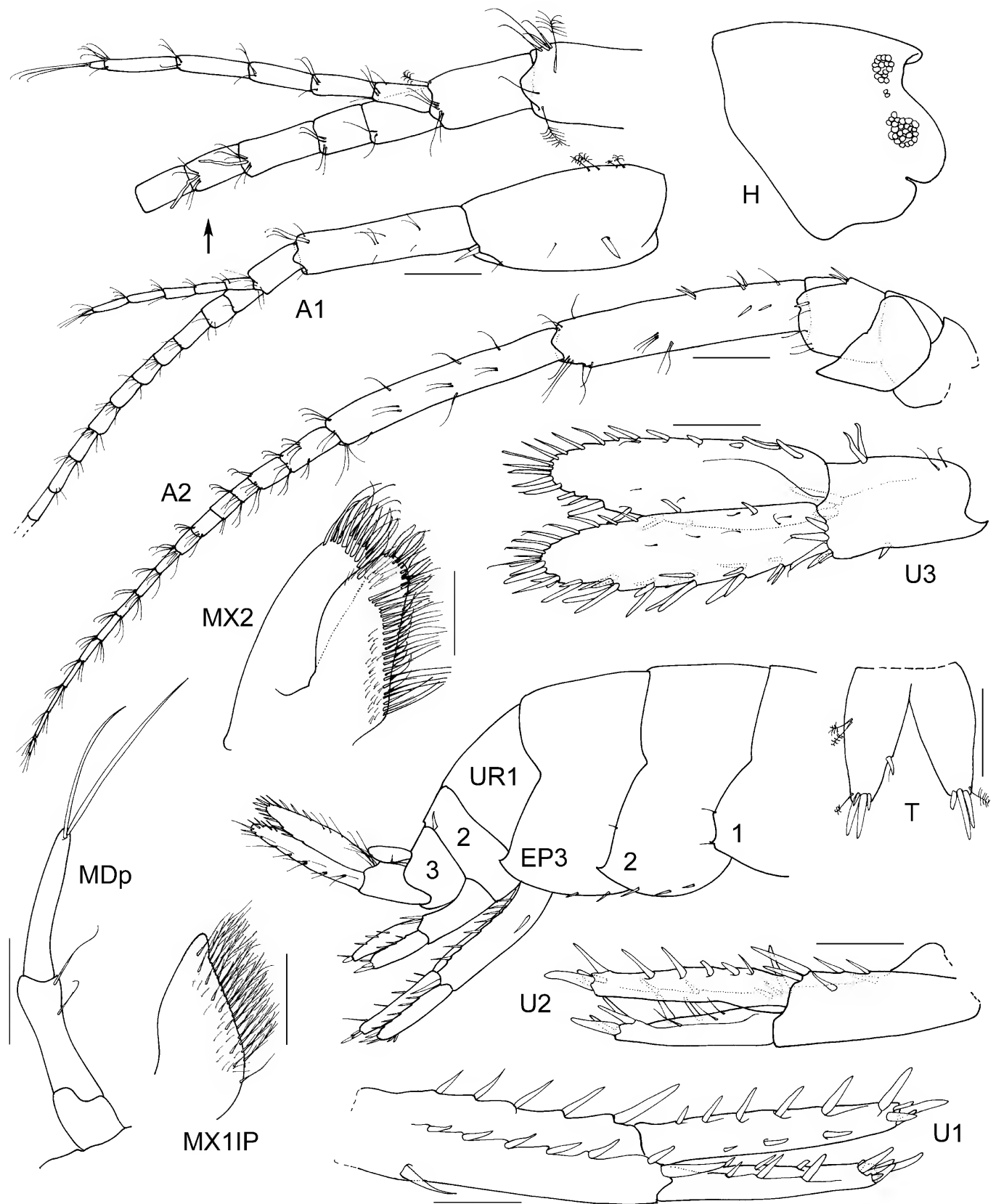
Fig. 42. *Quadrivisio sarina* n.sp., holotype, female, 7.4 mm, AM P60482, Armstrong Beach, Sarina, Queensland, Australia. Scales for mouthparts represent 0.1 mm, remainder represent 0.2 mm.

Survey, 8 October 1985, stn 6, 6. 5 specimens, AM P55282, 1 km upstream of Thackeray Street footbridge, Parramatta River, New South Wales, 33°49.24'S 151°02.17'E, muddy sand, 3.3 m, P. Berents & party, 7 December 1994, Site 2, Rep 1, Upper Parramatta River Dredging Survey, 1992–1994. 4 specimens, AM P54282, Brays Bay, Parramatta River, 33°50.0'S 151°05.5'E, Coast & Wetlands Society Survey, 8 October 1985, stn 1, 8. 2 specimens, AM P54284, Homebush Bay, Parramatta River, 33°50'S 151°05'E, Coast & Wetlands Society Survey, 8 October 1985, stn 5, 6. 50 specimens, AM P41818, south end of Homebush Bay, New South Wales, 33°50.03'S 151°04.73'E, 2.5 m, Van Veen grab, P.

Berents & party, 26 November 1992, site 25. 2 specimens, AM P54277, Cabarita, Parramatta River, 33°51'S 151°07'E, L. Garcia, 8 September 1988, stn D7.r1. 1 specimen, AM P55249, Back Creek mangrove, Tuross Lake, 36°03.67'S 150°06.43'E, mud, Australian Museum Eurobodalla Shire Estuary Survey, 16 September 1974. 2 specimens, AM P36699, Shadrachs Creek, Twofold Bay, 37°04.8'S 149°52.5'E, *Zostera*, infauna, S. Keable & A. Reid, 26 June 1985, stn L2.

Type locality. South West Rocks, Trial Bay, New South Wales, [approx. 30°53'S 153°03'E], tidal lagoon.
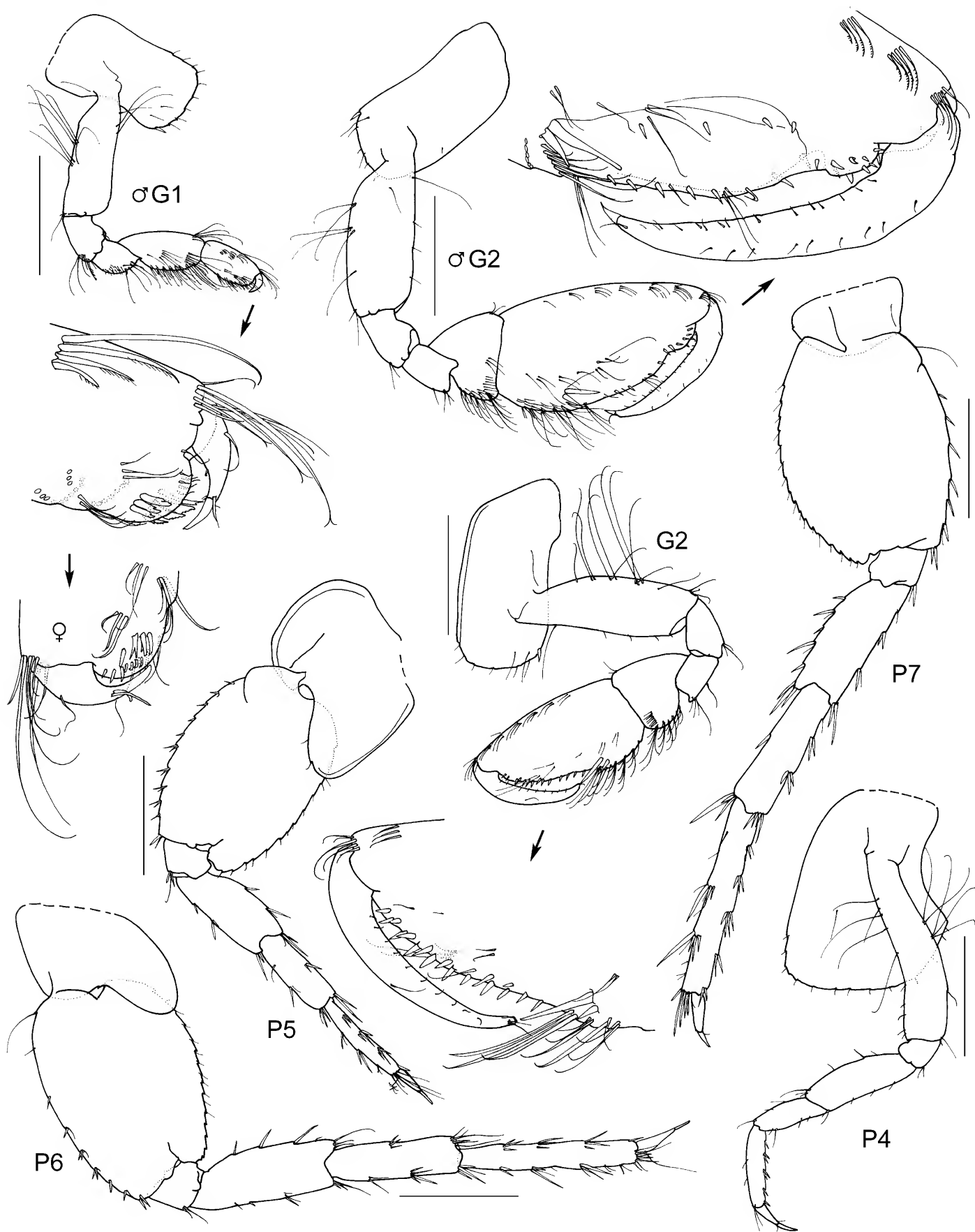
Fig. 43. *Quadrivisio sarina* n.sp., holotype, female, 7.4 mm, AM P60482, paratype male, 8.1 mm, AM P60484, Armstrong Beach, Sarina, Queensland, Australia. Scales represent 0.5 mm.

Description. Based on male, AM P56684.

Head. Eyes absent; lateral cephalic lobes absent, lacking notch or slit, anteroventral corner rounded. *Antenna 1* longer than antenna 2; peduncular article 1 subequal in length to article 2, without robust setae along posterior margin; peduncular article 2 geniculate with article 3; flagellum with 33 articles; accessory flagellum with 2 articles. *Antenna 2* peduncular article 2 cone gland not reaching to end of peduncular article 3; article 4 shorter than article 5;

Fig. 44. *Victoriopisa australiensis* (Chilton, 1923), male, 11.1 mm, AM P56684, Boambee Creek, Sawtell, New South Wales, Australia.
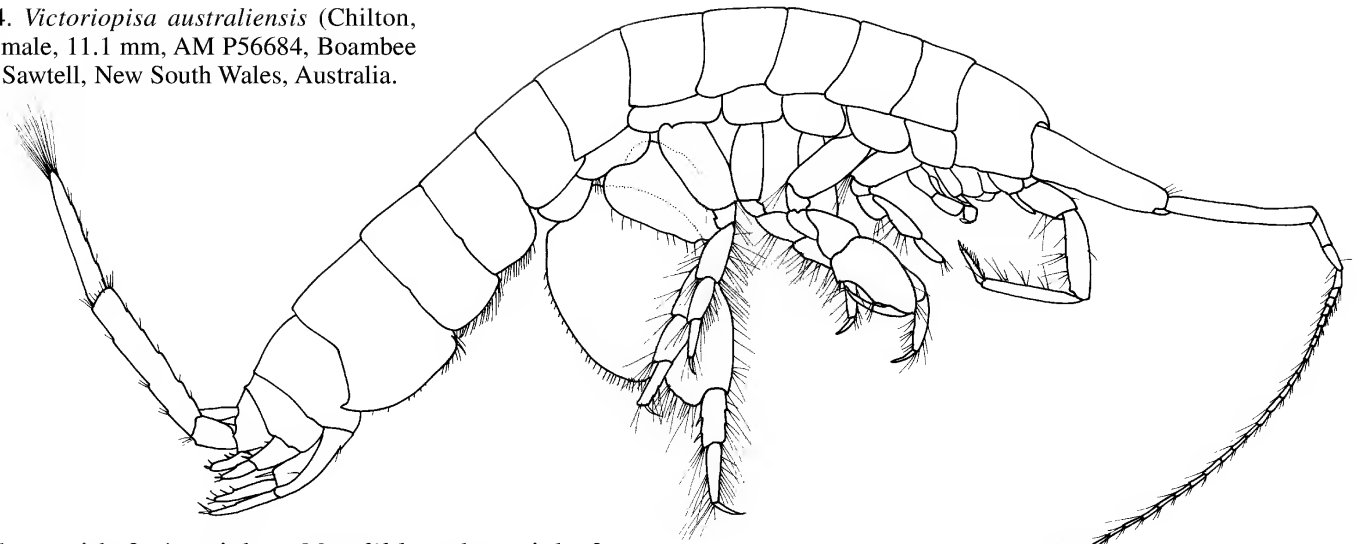
flagellum with 3–4 articles. *Mandible* palp article 3 rectolinear, setose along straight medial margin, with setae mostly terminal, longer than article 1; article 2 longer than or subequal article 3; article 1 produced distally, shorter than article 2, about as long as broad. *Maxilla 1* inner plate setose along entire inner margin.

Pereon. *Gnathopod 1* coxa anteroventral corner produced, rounded, posteroventral corner notch absent; merus without posterodistal spine; propodus palm nearly transverse, convex, defined by posterodistal corner, defined by posterodistal robust setae. *Gnathopod 2* not sexually dimorphic, subchelate; coxa posteroventral corner notch absent; merus with rounded or

subquadrate posteroventral corner; carpus short; propodus without medial depression, palm acute, concave, smooth, with sparse robust setae, defined by posterodistal robust setae, defined by posteroventral corner; dactylus apically acute/subacute. *Pereopods 5–6* basis posterior margin straight, posteroventral corner narrowly rounded or subquadrate; carpus and propodus with many long, slender setae along anterior margin. *Pereopod 7* basis posterior margin convex, with
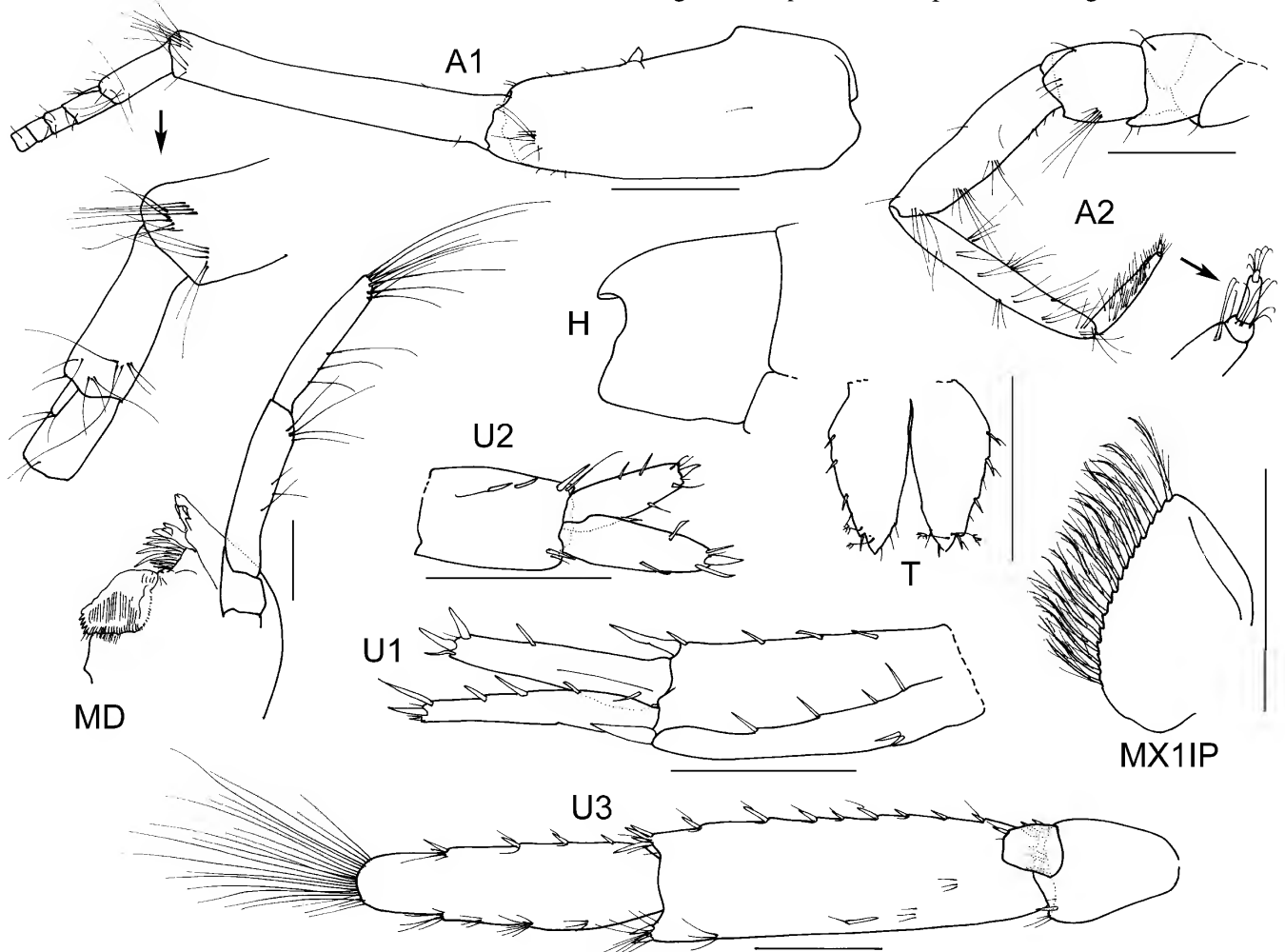

Fig. 45. *Victoriopisa australiensis* (Chilton, 1923), male, 11.1 mm, AM P56684, Boambee Creek, Sawtell, New South Wales, Australia. Scales for MD, MX1IP represent 0.2 mm, remainder represent 0.5 mm.
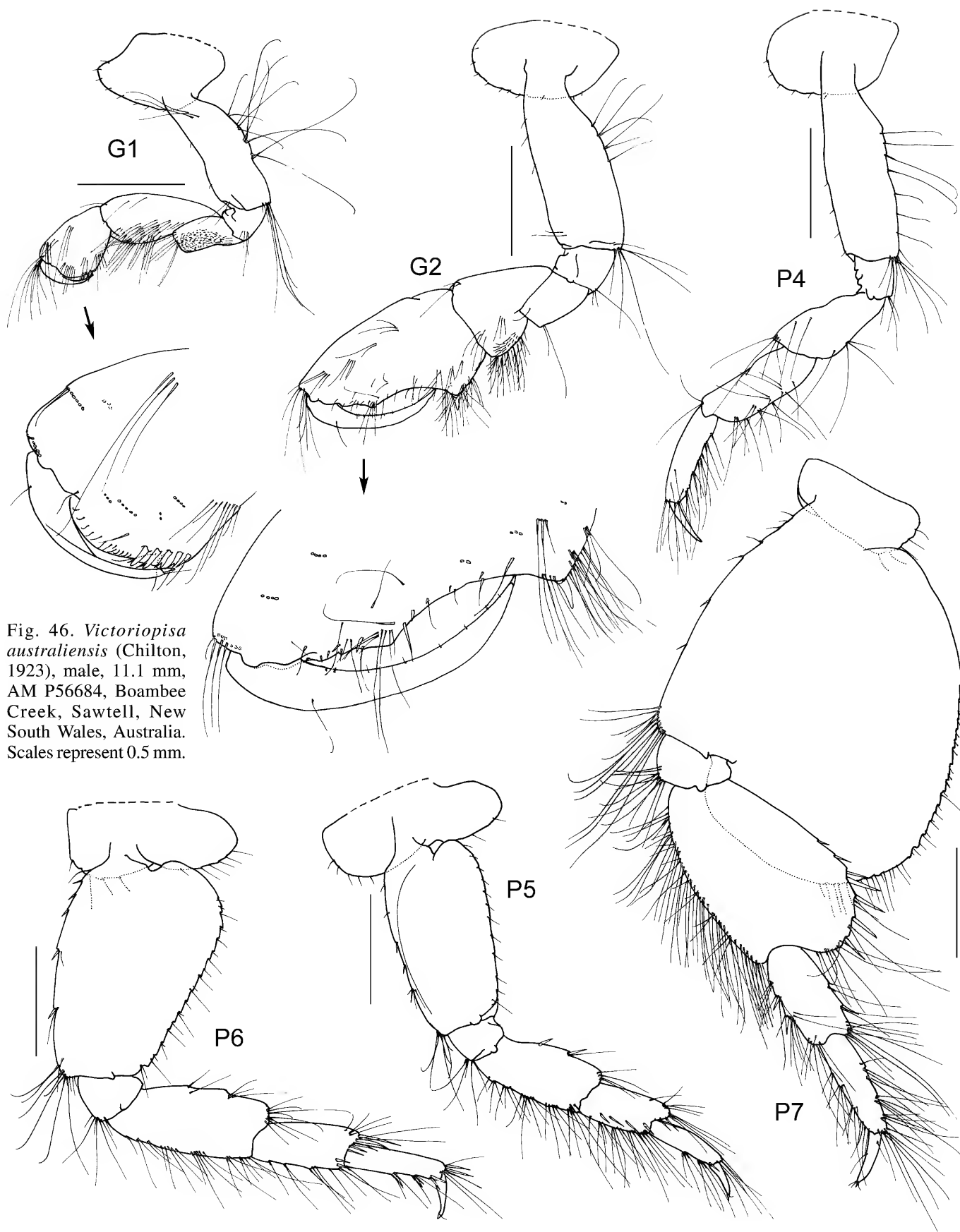
Fig. 46. *Victoriopisa australiensis* (Chilton, 1923), male, 11.1 mm, AM P56684, Boambee Creek, Sawtell, New South Wales, Australia. Scales represent 0.5 mm.

posterior margin smooth or minutely castelloserrate, posteroventral corner broadly rounded; merus posterodistal margin broadly rounded.

Pleon. *Epimeron 1* posteroventral corner narrowly rounded or subquadrate. *Epimera 1–2* posteroventral margin without spines above posteroventral corner. *Epimeron 3* posterior margin smooth, posteroventral corner with small acute spine or with strongly produced acute spine. *Uropod 1* peduncle with 2 basofacial robust setae. *Uropod 3* inner ramus scale-like, much shorter than outer ramus; outer ramus much longer (more than 2× length) than peduncle, 2-articulate. *Telson* without apical robust setae, apical conical extension absent.

Habitat. Estuarine; littoral; mangrove mud flats and seagrasses; 0 to 3 m depth.

Remarks. The holotype (AM P5852) was originally deposited in Australian Museum, but assumed to be lost (Springthorpe & Lowry, 1994). Consequently another specimen from near the type locality (AM P56684) was illustrated and used for the description. Since then the type specimen has been located.

Victoriopisa australiensis and *V. marina* differ most obviously from each other as follows. In *V. australiensis* the male gnathopod 2 has a short carpus and the palm of the propodus is broadly excavate and not bordered by robust setae, whereas in *V. marina* the carpus is compressed and the palm is narrowly excavate and bordered by robust setae. *Victoriopisa australiensis* has a large, broadly expanded basis and merus on pereopod 7 with many slender setae distally. In *V. marina* the basis and merus are narrower and the distal part of the pereopod is not nearly as setose.

Distribution. *New South Wales*: Southwest Creek, Trial Bay (Chilton, 1923); Boambee Creek, Sawtell; Wallis Lake; Fullerton Cove, Hunter River; Hawkesbury River (Jones *et al.*, 1986; Jones, 1987); Pittwater; Parramatta River; Botany Bay; Tuross; Twofold Bay (all AM).

Australian geographic areas. Southeastern Australia.

Victoriopisa marina n.sp.

Figs. 47–49

Victoriopisa sp. 2 Jones *et al.*, 1986: 541
Victoriopisa sp. Jones, 1987: 623.

Type material. HOLOTYPE, ♂, 8.1 mm, AM P61227, Cobblers (Bate Bay), New South Wales, Australia, [approx. 34°07'S 151°10'E], 65–70 m, grab, Ecology Lab, October 1990, stn T3-135. 1 PARATYPE, ♀, 7.4 mm, AM P41961, 800 m southwest of airport runway, Botany Bay, New South Wales, Australia, 33°58.33'S 151°10.22'E, 7 m, Australian Museum party, 7 April 1992, stn NSW-771.

Additional material examined. New South Wales: 1♂, 1♀, AM P53976, Royal Motor Yacht Club, Pittwater, 33°39.2'S 151°18.0'E, fine mud, 12 m, C. Rose, December 1992, stn RMYC A5. 1♂, AM P61360, between Juno Head and Hungry Beach, Hawkesbury River, 33°34'S 151°16'E, muddy sand, 10 m, Smith-McIntyre grab, A.R. Jones & C. Watson-Russell, 7 August 1979, stn HES 1–3.

Type locality. Cobblers (Bate Bay), New South Wales, Australia [approx. 34°07'S 151°10'E], 65–70 m.

Description. Based on holotype male, AM P61227 and paratype female, AM P41961.

Head. Eyes absent; lateral cephalic lobes absent, lacking notch or slit, anteroventral corner rounded. *Antenna 1* longer than antenna 2; peduncular article 1 shorter than article 2, without robust

setae along posterior margin; peduncular article 2 geniculate with article 3; flagellum with 30 articles; accessory flagellum with 2 articles. *Antenna 2* peduncular article 2 cone gland not reaching to end of peduncular article 3; article 4 shorter than article 5; flagellum with 2–3 articles. *Mandible* palp article 3 rectolinear, with setae mostly terminal, longer than article 1; article 2 subequal to or longer than article 3; article 1 produced distally, shorter than article 2, about twice as long as broad. *Maxilla 1* inner plate setose along entire inner margin.

Pereon. *Gnathopod 1* coxa anteroventral corner produced, rounded, posteroventral corner notch absent; merus without posterodistal spine; propodus palm acute, convex, defined by posterodistal corner, defined by posterodistal robust setae. *Gnathopod 2* not sexually dimorphic; subchelate; coxa posteroventral corner notch absent; merus with subquadrate posteroventral corner; carpus compressed; propodus without medial depression, without strong concentration of setae, palm acute, concave or sinusoidal, sculptured, with sparse robust setae and with group of anterodistal robust setae, defined by posterodistal robust setae, defined by posteroventral corner; dactylus apically acute/subacute. *Pereopod 5* basis posterior margin straight, posteroventral corner narrowly rounded or subquadrate. *Pereopod 6* coxa anterior lobe ventral margin slightly produced, rounded; basis posterior margin straight, posteroventral corner narrowly rounded or subquadrate. *Pereopod 7* basis posterior margin convex, with posterior margin smooth or minutely castelloserrate, posteroventral corner broadly rounded.
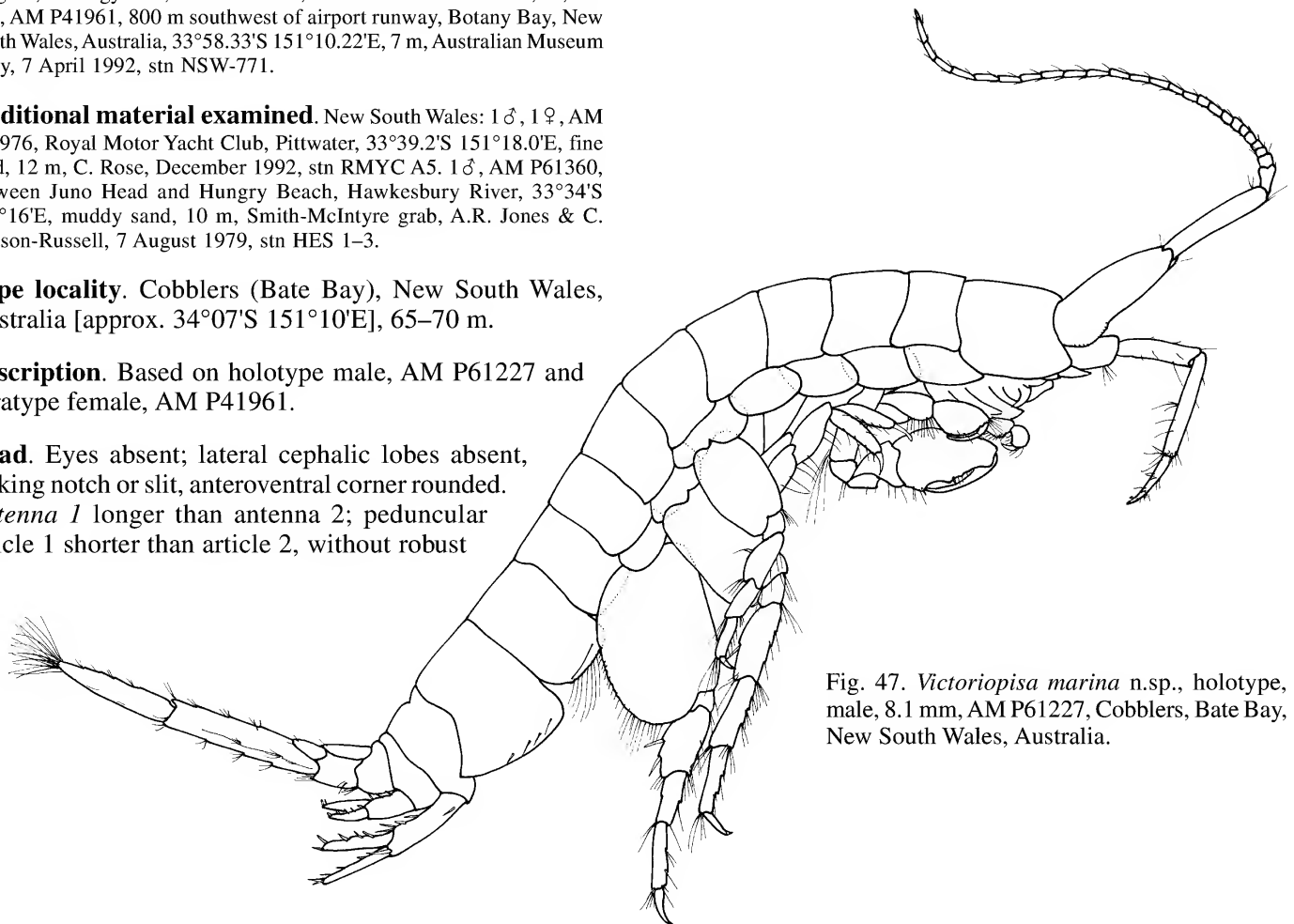

Fig. 47. *Victoriopisa marina* n.sp., holotype, male, 8.1 mm, AM P61227, Cobblers, Bate Bay, New South Wales, Australia.
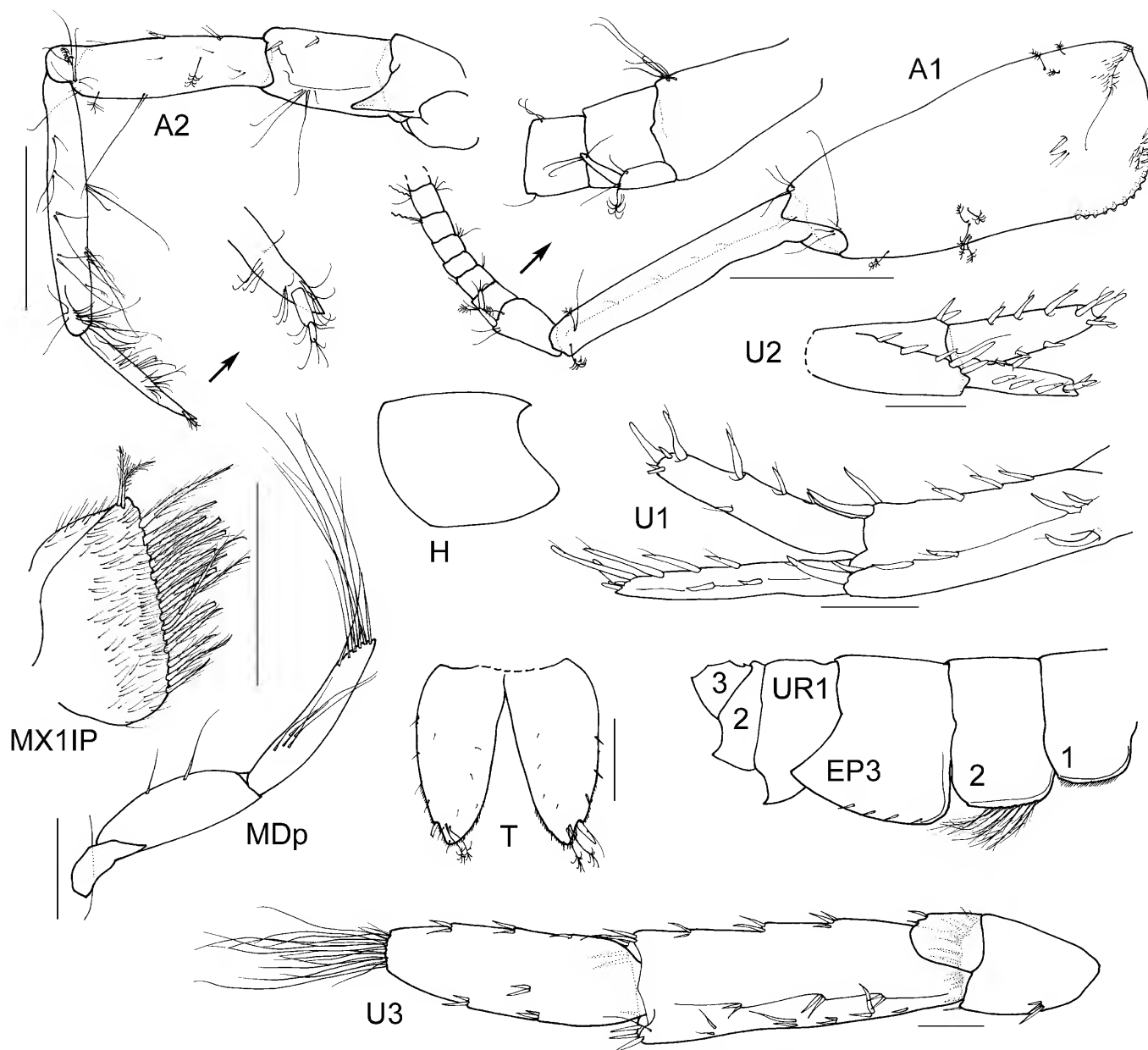
Fig. 48. *Victoriopisa marina* n.sp., holotype, male, 8.1 mm, AM P61227, Cobblers, Bate Bay, New South Wales, Australia. Scales for A1, A2, U3 represent 0.5 mm, remainder represent 0.2 mm

Pleon. *Epimeron 1* posteroventral corner broadly rounded. *Epimera 1–2* posteroventral margin without spines above posteroventral corner. *Epimeron 3* posterior margin smooth, posteroventral corner with small acute spine or with strongly produced acute spine. *Urosomite 1–3* dorsally smooth. *Uropod 3* inner ramus scale-like, much shorter than outer ramus; outer ramus much longer (more than 2× length) than peduncle, 2-articulate. *Telson* without apical robust setae, apical conical extension absent.

Habitat. Marine and estuarine; littoral and continental shelf; fine to sandy mud, 7 to 70 m depth.

Remarks. *Victoriopisa marina* is most similar to species of *Victoriopisa* with slender seventh pereopods. It differs from all of these species in the extremely broadened palm of gnathopod 1 and the shape of the palm of gnathopod 2.

Distribution. *New South Wales*: Hawkesbury River (Jones *et al.*, 1986; Jones, 1987); Pittwater; Botany Bay; Cobblers, Bate Bay (all AM).

Australian geographic areas. Southeastern Australia.

Melita group

Dulichiella Stout, 1912

Dulichiella australis (Haswell)

Figs. 50–53

Melita australis Haswell, 1879a: 264, pl. 9, figs 6–7.–Haswell, 1882: 252.
Melita fresnelii.–Stebbing, 1906: 423 (in part).–Stebbing, 1910a: 596–597, 642.–Chilton, 1921b: 70.–Hale, 1927: 314.
Melita appendiculatus.–Stebbing, 1906: 428 (in part).
Dulichiella australis.–Karaman & Barnard, 1979: 152.–Barnard & Barnard, 1983: 668.–Hutchings *et al.*, 1989: 362.

Type material. 5 SYNTYPES, AM G5393; 1 Syntype, AM P3495, Port Jackson, New South Wales, Australia, [approx. 33°51'S 151°16'E], [AM Old Collection]

Additional material examined. Queensland: many specimens, AM P61134, Lizard Island, Queensland, 14°40'S 145°28'E, October 1978. New South Wales: 3 specimens, AM P55002, northeast of Marys Rock, Cook Island, 28°11.42'S 153°34.79'E, tan sponge with large osculi, 18 m, G.D.F. Wilson, 8 June 1993, stn NSW-810. Several specimens, AM P56651; 1 specimen, AM P57284, 100 m north west of Julian Rocks,
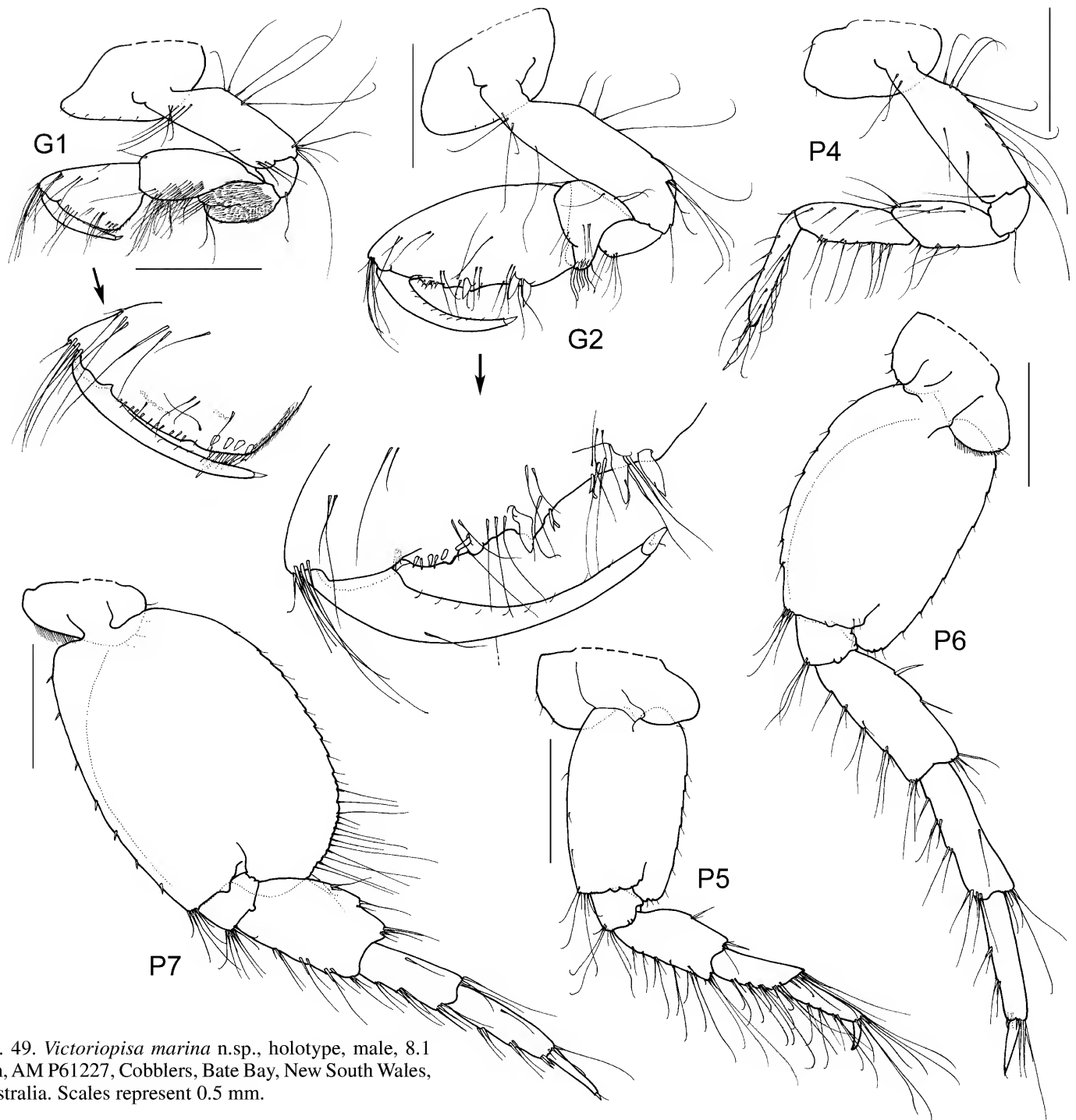
Fig. 49. *Victoriopisa marina* n.sp., holotype, male, 8.1 mm, AM P61227, Cobblers, Bate Bay, New South Wales, Australia. Scales represent 0.5 mm.

Byron Bay, 28°36.8'S 153°37.8'E, rock with finger sponge, 15 m, E.L. Albertson, R.T. Springthorpe & G.D.F. Wilson, 3 March1992, stn NSW-635. 2 specimens, AM P57684, same locality, erect plate sponge, 15 m, E.L. Albertson, R.T. Springthorpe & G.D.F. Wilson, 3 March1992, stn NSW-639. 5 specimens, AM P57285, same locality, mixed sponges, 17 m, stn NSW-642. 7 specimens, AM P56650, 100 m north west of Split Solitary Island, 30°14.0'S 153°10.8'E, plate coral, solitary ascidian, gorgonian & sponges, 15–17 m, G.D.F. Wilson, 7 March 1992, stn NSW-687. 4 specimens, AM P57105, same locality, under rock ledges, 15–17 m, R. Gentle (URG), 7 March 1992, stn NSW-697. 4 specimens, AM P57286, same locality, lace bryozoan, 17 m, R.T. Springthorpe & S.J. Keable, 7 March 1992, stn NSW-681. 5 specimens, AM P57287, same locality, sponge, 15–17 m, R.T. Springthorpe, 7 March 1992, stn NSW-683. 1 specimen, AM P57288, same locality, mixed red algae, 17 m, S.J. Keable, 7 March 1992, stn NSW-693. 3 specimens, AM P27266, Split Solitary Island, [approx. 30°15'S 153°12'E], 10 m, J. Marshall, 23 March 1978. 5 specimens, AM P56653, Coffs Harbour Jetty, Coffs Harbour, 30°18.4'S 153°08.5'E, orange sponge on jetty pilings, 6 m, R.T. Springthorpe, 9 March 1992, stn NSW-729. Several specimens, AM P56654, same locality, *Pyura praeputialis* on jetty pilings, 8 m, P.B. Berents & S.J. Keable, 9 March 1992, stn NSW-733. Many specimens, AM P56655, same locality, arborescent sponge on jetty pilings, 7 m, S.J. Keable, 9 March 1992, stn NSW-735. 24♂♂, 26♀♀, AM P57103, same locality, worm tubes encrusted with sponge on jetty pilings, 6 m, R.T. Springthorpe, 9 March 1992, stn NSW-725. 1♂, AM P57104, same locality, coral scrapings on jetty pilings, 6 m, R.T. Springthorpe, 9 March 1992, stn NSW-738. 11♀s, 5♂♂, AM P57289, same locality, coral scrapings on jetty pilings, 6 m, R.T. Springthorpe, 9 March 1992, stn NSW-726. 2 specimens, AM P57290, same locality, *Diopatra* tubes at base of jetty pilings, 6.5 m, S.J. Keable & R.T. Springthorpe, 9 March 1992, stn NSW-730. 28♀♀, 16♂♂, AM P57291, same locality, finger sponge on jetty pilings, 4 m, R.T. Springthorpe, 9 March 1992, stn NSW-734. Many specimens, AM P61141, same locality, *Diopatra* tubes at base of jetty pilings, 8.5 m, S.J. Keable, 9 March 1992, stn NSW-728. 1 specimen, AM P56652, 150 m downstream of Fred Hansen Bridge, Boambee Creek, Sawtell, 30°20.4'S 153°05.5'E, exposed flat of sandy mud, 1.2 m, van Veen grab, Australian Museum party, 8 March 1992, stn NSW-724. 25 specimens, AM P3496, Port Stephens, [approx. 32°42'S 152°06'E], [AM Old Collection]. 1 specimen, AM P23158, 500 m east of Burwood Beach, 32°57.52'S 151°44.72'E, coarse sand bottom, 14 m, Shipek collection, Australian Museum Hunter District Water Board Survey, 18 December 1975, stn HDWBS06030101, transect 3. 1♂, AM P53923, west side of Box Head, Broken Bay, 33°33'S 151°21'E, bryozoan on rocky substrate with small crinoid *Antedon*
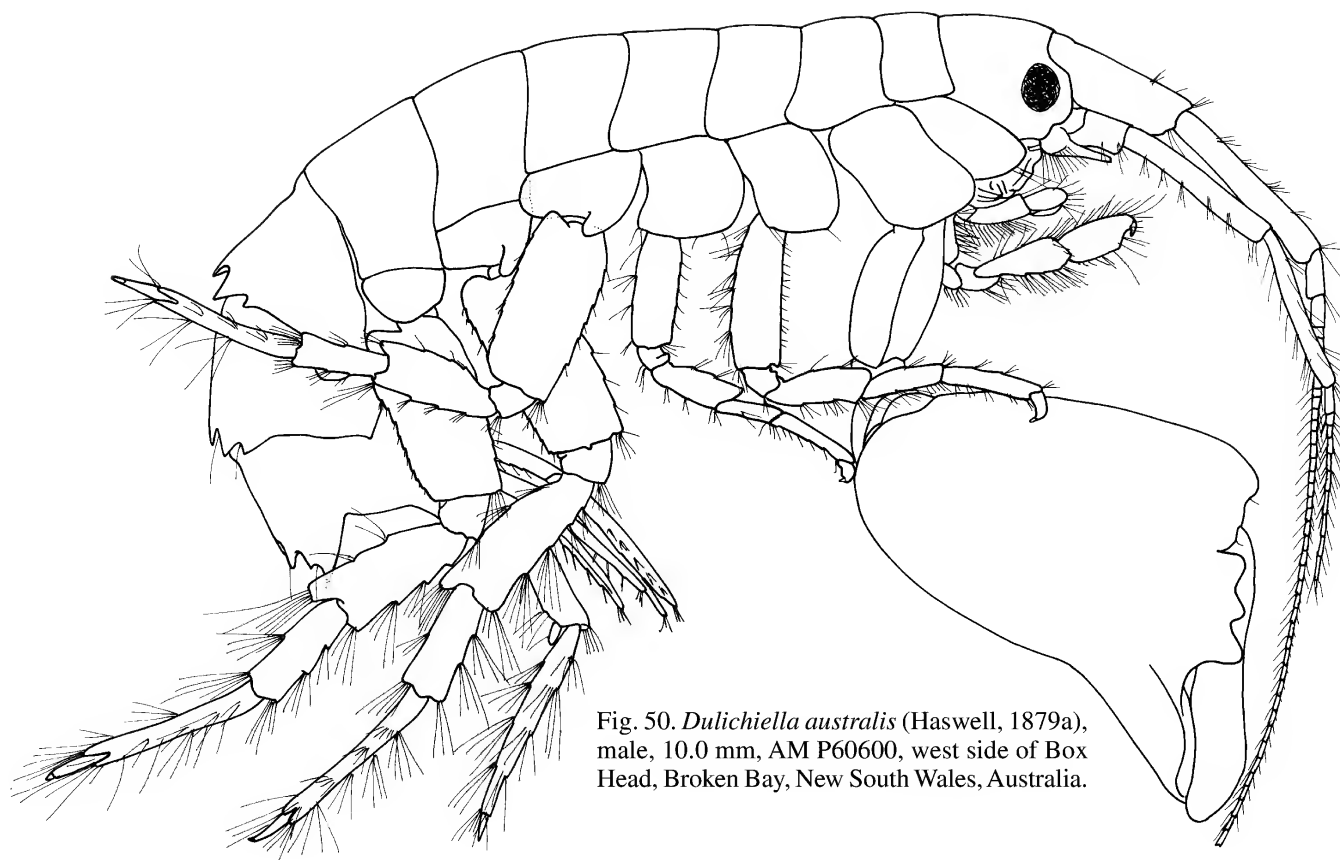
Fig. 50. *Dulichiella australis* (Haswell, 1879a), male, 10.0 mm, AM P60600, west side of Box Head, Broken Bay, New South Wales, Australia.

incomoda, 15 m, J.K. Lowry & R.T. Springthorpe, 22 November 1982, stn NSW-158. Many specimens, AM P53924, same locality, bryozoan, stn NSW-159. Many specimens, AM P53925, same locality, sponges, stn NSW-165. 4 specimens, AM P53926, same locality, sponge, stn NSW-166. Several specimens, AM P53927, same locality, stn NSW-167. Many specimens, AM P53928; 1♂, AM P60600; 1♀, AM P60601, same locality, sponge *Echinoclathria* sp., stn NSW-173. 4 specimens, AM P22493, east of Long Reef, [approx. 33°44'S 151°22'E], 40 m, Australian Museum Shelf Benthic Survey, 29 June 1972. 2 specimens, AM P22494, same locality, 36 m, 11 May 1972. 5 specimens, AM P22495, same locality, 38 m, 24 August 1972. Many specimens P22488, east of North Head, Port Jackson, [approx. 33°49'S 151°20'E], host sponge: cf *Teichonella labrinthica*, 21 m Australian Museum Shelf Benthic Survey, 20 February 1973, transect 9. 1 specimen, AM P22489, same locality, host sponge: *Polymastea craticia*. 1 specimen, AM P22490, same locality, host sponge: *Halme gigantea*, 25 m, 26 February 1974, transect 07. 3 specimens, AM P22497, same locality, host sponge: *Polymastea craticia*, 19 m, 19 February 1973, transect 10. 3 specimens, AM P22498, same locality, host sponge: *Halme gigantea*, 19 m, 19 February 1973 transect 10. 1 specimen, AM P22499, same locality, sponge 19 m, 19 February 1973 transect 10. Many specimens, AM P22501, same locality, host sponge: cf *Teichonella labrinthica*, 19 m, 19 February 1973 transect 10. 20 specimens, AM P22491, east of North Head, Port Jackson, [approx. 33°49.5'S 151°18'E], 28 m, Australian Museum Shelf Benthic Survey, 13 December 1971. 1 specimen, AM P22492, same locality, among sewage outfall, 12 May 1972. Several specimens, AM P18198, off Sydney Heads, [approx. 33°50'S 151°28'E], 119 m, [AM Old collection]. Many specimens, AM P22496, east of South Head, Port Jackson, [approx. 33°50'S 151°18'E], host sponge: *Halme gigantea*, 21 m, Australian Museum Shelf Benthic Survey, February 1974, transect 11. 3 specimens, AM P5334, Port Jackson, [approx. 33°51'S 151°16'E], W.A. Haswell, 1918. 8 specimens, AM P61140, north east corner of Clark Island, Port Jackson, 33°51.85'S 151°14.47'E, red algae, 2 m, I. Takeuchi & D. Bray, 17 April 1996, stn NSW-1250. 2♂♂, AM P63067, Brotherson Dock Berth 2, Botany Bay, 33°58.2'S 151°12.6'E, pylon scrapings, 7 m, NSW Fisheries/CRIMP Survey, 22 October 1998, stn BB BD2 P2–7. 1 specimen, AM P63068, Bulk Liquids Berth, Botany Bay, 33°58.5'S 151°12.6'E, pylon scraping, 7 m, NSW Fisheries/CRIMP Survey, 19 October 1998, stn BB BLB P3–7. 2♀♀, AM P63069, Channel Marker 4, Botany Bay, 33°59.3'S 151°12.6'E, pylon scraping, 7 m, NSW Fisheries/CRIMP Survey, 21 October 1998, stn BB CH4 P1–7. 2 specimens, AM P63083, same locality, pylon scraping, 3 m, NSW Fisheries/CRIMP Survey, 21 October 1998, stn BB CH4 P1–3. 3 specimens, AM P58236, outer end of Kurnell Pier, Botany Bay, 34°00.2'S

151°12.5'E, pylon scrapings, 7 m, NSW Fisheries/CRIMP Survey, 21 October 1998, stn BB KP1 P1–7. 1♀, AM P63070, Kurnell Pier (near shoreline), Botany Bay, 34°00.5'S 151°12.7'E, pylon scrapings, 3 m, NSW Fisheries/CRIMP Survey, 21 October 1998, stn BB KP2 P2–3. 1 specimen, AM P2486, 3–4 km off Botany Bay, [approx. 34°05'S 151°15'E], mud, 91–95 m, E.R. Waite on HMCS *Thetis*, 11 March 1898, stn 37. 1 specimen, AM P2487, 5.5–6.5 km off Wattamolla, [approx. 34°10'S 151°11'E], mud, 99–108 m, E.R. Waite on HMCS *Thetis*, 22 March 1898, stn 57. 2 specimens, AM P63548, Boat Basin, Wollongong Harbour, 34°25.35'S 150°54.4'E, pylon scrapings, 3 m, NSW Fisheries/CRIMP Survey, 17 May 2000, stn PK WHB P1–3. 1 specimens, AM P63549, same locality, pylon scrapings, 0.5 m, NSW Fisheries/CRIMP Survey, 17 May 2000, stn PK WHB P2–0. Many specimens, AM P63550 same locality, pylon scrapings, 3 m, NSW Fisheries/CRIMP Survey, 17 May 2000, stn PK WHH. 1 specimens, AM P44306, off Wollongong, 34°26.54'S 150°57.98'E, *Globigerina* ooze, 50 m, baited trap, J.K. Lowry & K. Dempsey on MV *Robin E*, 27–28 March, 1994, SEAS project, stn NSW-939. Many specimens, AM P63543, Inflammable Liquids Berth, Port Kembla Outer Harbour, 34°27.95'S 150°54.25'E, pylon scrapings, 7 m, NSW Fisheries/CRIMP Survey, 13 May 2000, stn PK ILB P2–7. 4 specimens, AM P63546, east end No.6 Jetty, Port Kembla Outer Harbour, 34°28.25'S 150°54.1'E, pylon scrapings, 3 m, NSW Fisheries/CRIMP Survey, 14 May 2000, stn PK J6O P1–3. 2 specimens, AM P63547, same locality, pylon scrapings, 7 m, NSW Fisheries/CRIMP Survey, 14 May 2000, stn PK J6O P1–7. Many specimens, AM P63544, south end No.3 Jetty, Port Kembla Outer Harbour, 34°28.6'S 150°54.5'E, pylon scrapings, 3 m, NSW Fisheries/CRIMP Survey, 16 May 2000, PK J3O P2–3. 2 specimens, AM P63545, same locality, pylon scrapings, 7 m, NSW Fisheries/CRIMP Survey, 16 May 2000, stn PK J3O P2–7. 1♂, 1♀, AM P53870, off Moona Moona Creek, Jervis Bay, 35°02.9'S 150°41.0'E, from surface of ascidian *Herdmania momus*, in *Ecklonia* bed, 4.5 m, P.B. Berents, 13 November 1981, stn NSW-249. 2 specimens, AM P53871, same locality, *Ecklonia* holdfasts, 5 m, P. Berents, 15 August 1981, stn NSW-87. 1 specimen, AM P54274, Jervis Bay, 35°03'S 150°44'E, sponge, scallop beds, 17 m, P. Berents, 13 August 1981. Many specimens, AM P30799; many specimens, AM P30800, south east of Tathra Head, 36°45–48'S 150°02–03'E, 64 m, trawl, FRV *Kapala*, 10 June 1980, stn K80-07-02. 2♂♂, AM P36221, Murrumbulga Point, Twofold Bay, 37°04.7'S 149°53.1'E, subtidal rock platform, 2–9 m, S. Keable & E. Bamber, 11 December 1984, stn Q1. 1 specimen, AM P18318, Twofold Bay, 37°05'S 149°55'E, W.A. Haswell. 108♀♀, 92♂♂, AM P35980, Munganno Point, Twofold Bay, 37°06.2'S 149°55.7'E, subtidal wharf pile, 6 m, S. Keable, 10 October 1984, stn M5. Tasmania: 1♂, AM P60602; many specimens, AM P61142, north side of Esperance
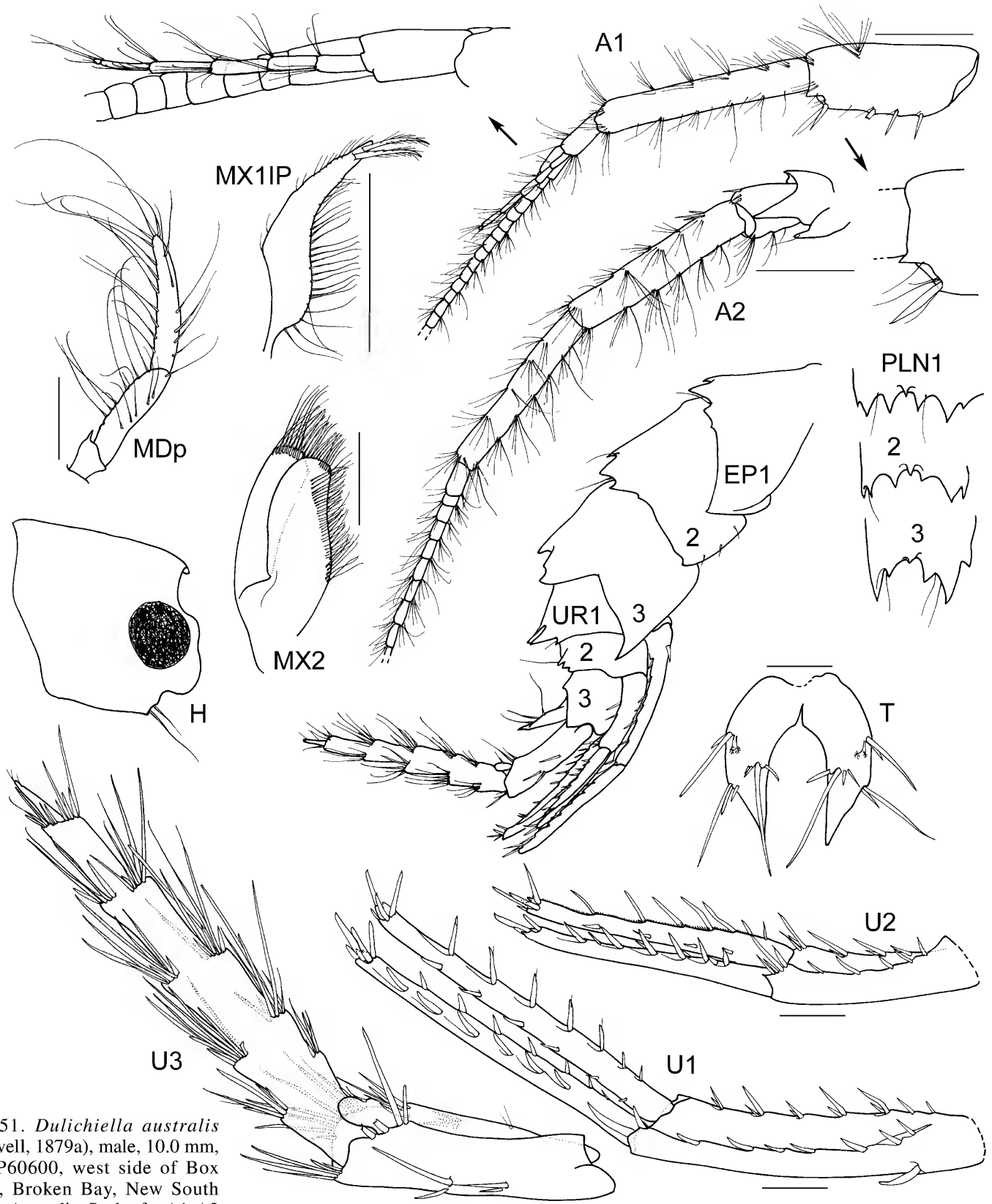
Fig. 51. *Dulichiella australis* (Haswell, 1879a), male, 10.0 mm, AM P60600, west side of Box Head, Broken Bay, New South Wales, Australia. Scales for A1, A2 represent 0.5 mm, remainder represent 0.2 mm.

Point, D'Entrecasteaux Channel, Tasmania, 43°19.5'S 147°05.5'E, lace bryozoan, 13 m, S.J. Keable, J.K. Lowry & R.T. Springthorpe, 18 April 1991, stn TAS-186. 3 specimens, AM P61143, same locality, 13 m, S.J. Keable, J.K. Lowry & R.T. Springthorpe, 18 April 1991. 3♀♀, AM P60603, same locality, sponges, lace bryozoan, red algae and ?*Vittaticella* sp., 13 m, S.J. Keable, J.K. Lowry & R.T. Springthorpe, 18 April 1991, stn TAS-187. South Australia: E6541, 3 specimens, Sanders Bank, Kangaroo Island, [approx. 35°50'S 137°15'E], 51 m, FIS *Endeavour*, 1909–1914. 3 specimens, AM P5923, same locality. 1 specimen, E4849, Spencer's Gulf, [approx. 34°00'S 137°00'E], FIS *Endeavour*, 1909–1914.

Type locality. Port Jackson, New South Wales, Australia, [approx. 33°51'S 151°16'E].

Description. Based on a male, 10 mm, AM P60600 and a female, AM P60601.

Head. Lateral cephalic lobes broad, truncated, lacking notch or slit, anteroventral corner subquadrate. *Antenna 1* longer than antenna 2; peduncular article 1 shorter than article 2, with 4 or more robust setae along posterior margin;
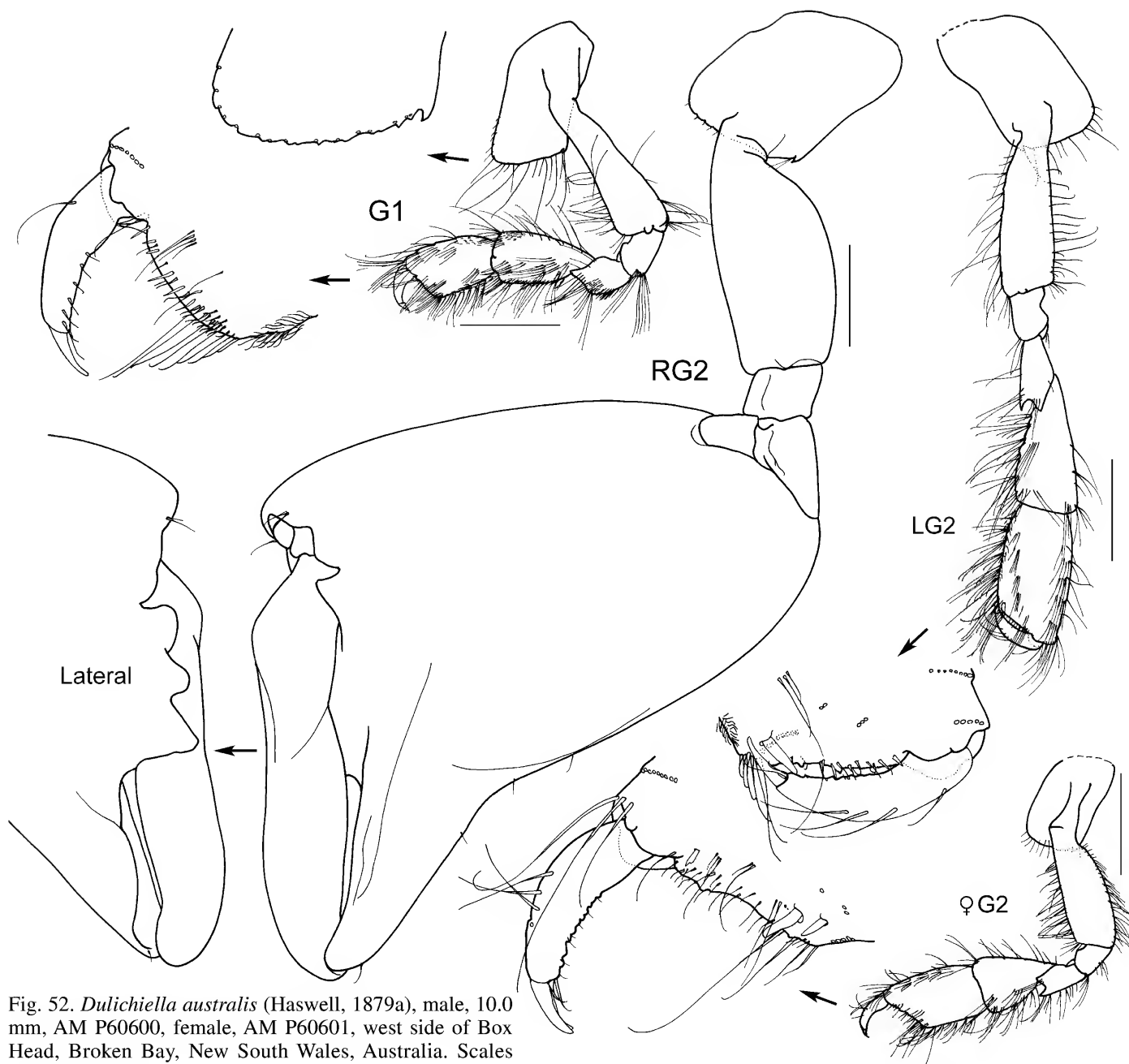
Fig. 52. *Dulichiella australis* (Haswell, 1879a), male, 10.0 mm, AM P60600, female, AM P60601, west side of Box Head, Broken Bay, New South Wales, Australia. Scales represent 0.5 mm.

flagellum with at least 40 articles; accessory flagellum with 6 articles. *Antenna 2* peduncular article 2 cone gland reaching at least to end of peduncular article 3; article 4 subequal to article 5; flagellum with about 12 articles. *Mandible* palp article 3 rectolinear, setae along both margins and terminal, longer than article 1; article 2 shorter than article 3; article 1 produced distally, shorter than article 2, about as long as broad. *Maxilla 1* inner plate with setae mainly terminal.

Pereon. *Gnathopod 1* coxa anteroventral corner not produced, posteroventral corner notch present; merus without posterodistal spine; propodus palm nearly transverse, slightly convex or straight, defined by posterodistal corner, without posterodistal robust setae. *Gnathopod 2* sexually dimorphic; left and right gnathopods unequal in size; coxa posteroventral corner notch present; (larger) chelate; merus with rounded posteroventral corner; carpus compressed; propodus, distolateral margin with 3 rounded indistinct spines; palm angle obtuse, straight, posterodistal spine absent, without robust setae; dactylus apically blunt; (smaller) subchelate; merus with sharp

posteroventral spine; carpus long; propodus palm straight, without posteroventral spine. *Pereopod 5* basis posterior margin straight, posteroventral corner narrowly rounded or subquadrate; carpus and propodus with many long, slender setae along anterior margin; dactylus unguis anterior margin with accessory spine. *Pereopod 6* coxa anterior lobe ventral margin slightly produced, rounded; basis posterior margin straight, posteroventral corner narrowly rounded or subquadrate; carpus and propodus with many long, slender setae along anterior margin; dactylus unguis anterior margin with accessory spine. *Pereopod 7* basis posterior margin straight or slightly subsigmoidal, with posterior margin smooth or minutely castelloserrate, posteroventral corner narrowly rounded or subquadrate; dactylus unguis anterior margin with accessory spine.

Pleon. *Pleonites 1–3* with dorsal serrations, with dorsodistal spine. *Epimeron 1* posteroventral corner with small acute spine. *Epimera 1–2* posteroventral margin without spines above posteroventral corner. *Epimeron 3* posterior margin smooth, posteroventral corner with strongly produced acute
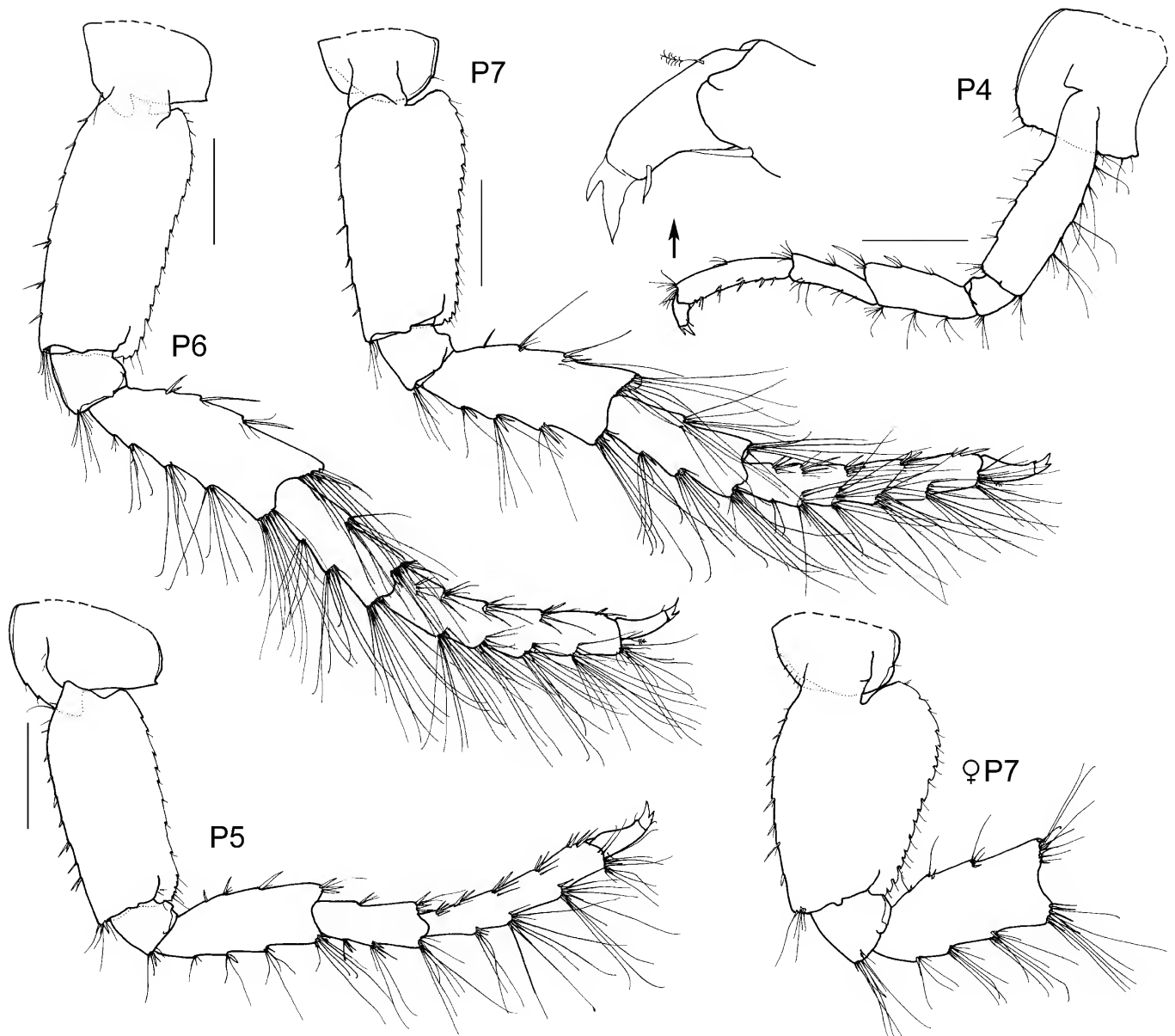
Fig. 53. *Dulichiella australis* (Haswell, 1879a), male, 10.0 mm, AM P60600, female, AM P60601, west side of Box Head, Broken Bay, New South Wales, Australia. Scales represent 0.5 mm.

spine. *Urosomite 1* with broad dorsal midline gape, rarely bearing midline spines, dorsally bicarinate. *Urosomite 2* posterior margin serrate, with two groups of 1–3 small dorsolateral robust setae. *Uropod 3* inner ramus scale-like, much shorter than outer ramus; outer ramus much longer (more than 2× length) than peduncle, 2-articulate. *Telson* without apical robust setae, apical conical extension absent.

Female (sexually dimorphic characters). *Gnathopod 2* subchelate; merus with sharp posteroventral spine; carpus short; propodus without medial depression, palm slightly acute, straight or slightly concave, smooth, without robust setae, defined by posterodistal robust setae, defined by posteroventral corner; dactylus apically acute/subacute. *Pereopod 7* basis posterior margin straight.

Habitat. Marine; littoral and continental shelf; living among bryozoans, sponges, ascidians and algae, 4.5 to 120 m depth.

Remarks. There are at least two distinctive species of *Dulichiella* along the east coast of Australia. Their ranges overlap along the Great Barrier Reef. *Dulichiella australis* and *D. pacifica* are easily distinguished by the spines on the distolateral margin of male gnathopod 2. In *D. australis* there are 3 rounded, rather indistinct spines and in *D. pacifica* there are 4 acute distinct spines. In addition pereopods 6 and 7 are more setose in *D. australis*.

Distribution. *Queensland:* Lizard Island (AM). *New South Wales*: Julian Rocks, Byron Bay; Marys Rock, Cook Island; Split Solitary Island; Coffs Harbour; Boambee Creek, Sawtell (all AM); Tacking Point (Haswell, 1879a); Manning River (Stebbing, 1910a); Port Stephens; off Burwood Beach; Box Head, Broken Bay; off Long Reef (all AM); Port Jackson (Haswell, 1879a); Clark Island, Port Jackson; Botany Bay; off Wattamolla; off Wollongong; Jervis Bay (all AM); Twofold Bay (Hutchings *et al.*, 1989). *Victoria*: Western Port (NMV). *Tasmania*: Esperance Point, D'Entrecasteaux Channel (AM). *South Australia*: Sanders Bank, Kangaroo Island (Chilton, 1921b); Spencers Gulf (AM).

Australian geographic areas. Northeastern Australia, southeastern Australia, southern Australia.

Dulichiella pacifica n.sp.

Figs. 54–57

Dulichiella appendiculata.–Berents, 1983: 111, fig. 9.–Ledoyer, 1986: 187, fig. 9S.

Type material. HOLOTYPE, ♂ "a", 4.4 mm, AM P61112; 1 PARATYPE, ♀, 5.9 mm, AM P61113; 9 PARATYPES, 1♂, 5 ovigerous females, 3 non-ovigerous females, AM P61117, between Tandai Point and Koilo Point, Guadalcanal, Solomon Islands, 9°22.5'S 159°52.2'E, coral rubble, 10 m, R.T. Springthorpe, 24 September 1991, SI-3; 1 PARATYPE, ♂ "b", 4.1 mm, AM P61114; 4 PARATYPES, males, AM P61115, Tandai Point, Guadalcanal, Solomon Islands, 9°23'S 159°52.5'E, sand with low algal turf, 20 m, hand dredge, R.T. Springthorpe, 11 October 2001, SI-36; 1 PARATYPE, ♂, AM P61116, same locality, black finger sponges from rubble bottom, 16 m, R.T. Springthorpe, 11 October 2001, SI-38.

Additional material examined. Queensland: 1 specimen, AM P30123, outer slope, Yonge Reef, 14°36'S 145°38'E, reef rock with *Halimeda* and *Lithothamnion*, 36 m, P.B. Berents & P.A. Hutchings, 9 January 1975, stn 75 LIZ D–1. 6 specimens, AM P30124, Watsons Bay, Lizard Island, 14°40'S 145°28'E, *Halophila, Caulerpa, Udotea* & drift algae, 7 m, J.K. Lowry & P.A. Hutchings, 29 September 1978, stn LI-2. 5 specimens, AM P30125, fringing reef between Bird Islet and South Island, Lizard Island, 14°40'S 145°28'E, *Halophila*, mixed algae, sediment from grass beds off reef, 24 m, J.K. Lowry, 9 October 1978, stn LI-27. 2 specimens, AM P30126, same locality, P.C. Terrill, 9 October 1978, stn LI-28. New Caledonia: 1 specimen, AM P47550, off Ilot Maitre, New Caledonia, 22°19.35'S 166°25.85'E, dead branching coral, 21 m, ORSTOM divers, 10 November 1995, stn NCL-72. 3 specimens, AM P47556; 7 specimens, AM P47563, same locality, large sea fan covered in sponges & other epiflora & epifauna, air lift, 21 m, J.K. Lowry, 10 November 1995, stn NCL-65. 1 specimen, AM P47522, Ilot Maitre, New Caledonia, 22°19.61'S 166°24.07'E, *Padina*-like alga, 10.5 m, G. Bargibant, ORSTOM, 14 November 1995, stn NCL-98. Several specimens, AM P47528, same locality, coralline algal "reef", 10.5 m, G. Bargibant, ORSTOM, 14 November 1995, stn NCL-99. 5 specimens, AM P48322, Ilot Maitre, New Caledonia, 22°20.57'S 166°25.43'E, red alga, 20 m, I. Takeuchi, 7 November 1995, stn NCL-38. 3 specimens, AM P48332, same locality, dead coral, 20 m, ORSTOM divers, 7 November1995, NCL-40. 10 specimens, AM P47334; 2 specimens, AM P47347, between Ilot Maitre and Croissant reef, New Caledonia, 22°19.7'S 166°23.3'E, *Sargassum* sp., 10 m, I. Takeuchi, 6 November 1995, stn NCL-28, 30. 1 specimen, AM P47506, between Ilot des Goelands and Grand Recif Abore, New Caledonia, 22°24.10'S 166°20.90'E, *Halimeda* sp. fine red alga, 10 m, J.K. Lowry, 16 November 1995, stn NCL-111. 1 specimen, AM P47590, between Ile Ngé & Sèche Croissant, New Caledonia, 22°19.41'S 166°20.89'E, purple bryozoan, *Iodyctium buchneri*, 20 m, ORSTOM divers, 9 November 1995, stn NCL-

57. 1 specimen, AM P47967, same locality, sediment sample (sand), 20 m, J.K. Lowry, 9 November 1995, stn NCL-56. 1 specimen, AM P48354, 200 m off Poé Plage, New Caledonia, 21°36.41'S 165°22.73'E, *Sargassum*, 1–2 m, J.K. Lowry, 19 November 1995, stn NCL-212. 4 specimens, AM P48379, fringing reef Thio, New Caledonia, dead coral, 1 m, A.A. Myers, 20 November 1995, stn NCL-217. Several specimens, AM P48460, same locality, "felt like" alga, 1 m, A.A. Myers, 20 Nov 1995, NCL-218. Singapore: 1♂, AM P61135, Pulau Sakia, Singapore, [approx. 01°16'N 103°42'E], Smith-McIntyre grab, C.S.C. Lee, University of Singapore, 23 May 1991, stn E, ZRC–1991–16108. Many specimens, AM P61136, Changi Floating Fish Farm, Singapore, [approx. 01°24'N 103°58'E], 1 m, J.B. Sigurdsson, 7 May 1997, associated with biofouling.

Type locality. Between Tandai Point & Koilo Point, Guadalcanal, Solomon Islands, (9°22.5'S 159°52.2'E), coral rubble.

Description. Based on holotype male "a", AM P61112, paratype female, AM P61113, and paratype male "b", AM P61114.

Head. Lateral cephalic lobes broad, truncated, lacking notch or slit, anteroventral corner subquadrate. *Antenna 1* slightly longer than antenna 2; peduncular article 1 shorter than article 2, with 3 robust setae along posterior margin; flagellum with about 28 articles; accessory flagellum with 4 articles. *Antenna 2* peduncular article 2 cone gland reaching at least to end of peduncular article 3; article 4 subequal to article 5; flagellum with 12 articles. *Mandible* palp article 3 rectolinear, setae along both margins and terminal, longer than article 1; article 2 subequal to article 3; article 1 produced distally, shorter than article 2, about as long as broad. *Maxilla 1* inner plate with setae mainly terminal.

Pereon. *Gnathopod 1* coxa anteroventral corner not produced, posteroventral corner notch present; merus without posterodistal spine; propodus palm acute, convex, without posterodistal corner, defined by posterodistal robust setae. *Gnathopod 2* sexually dimorphic; left and right gnathopods unequal in size; coxa posteroventral corner notch present; (larger) chelate; merus with rounded posteroventral corner; carpus compressed; propodus, distolateral margin with 4 acute distinct spines; palm angle
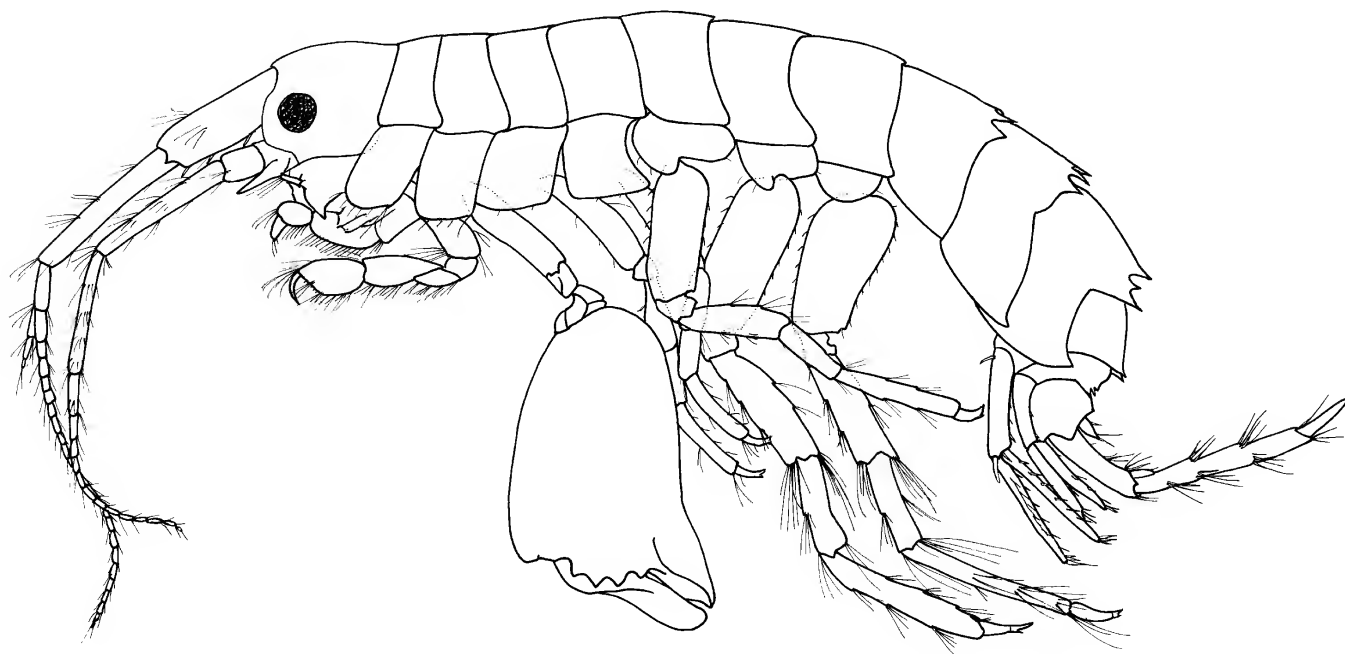

Fig. 54. *Dulichiella pacifica* n.sp., paratype, male "b", 4.1 mm, AM P61114, Tandai Point, Guadalcanal, Solomon Islands.
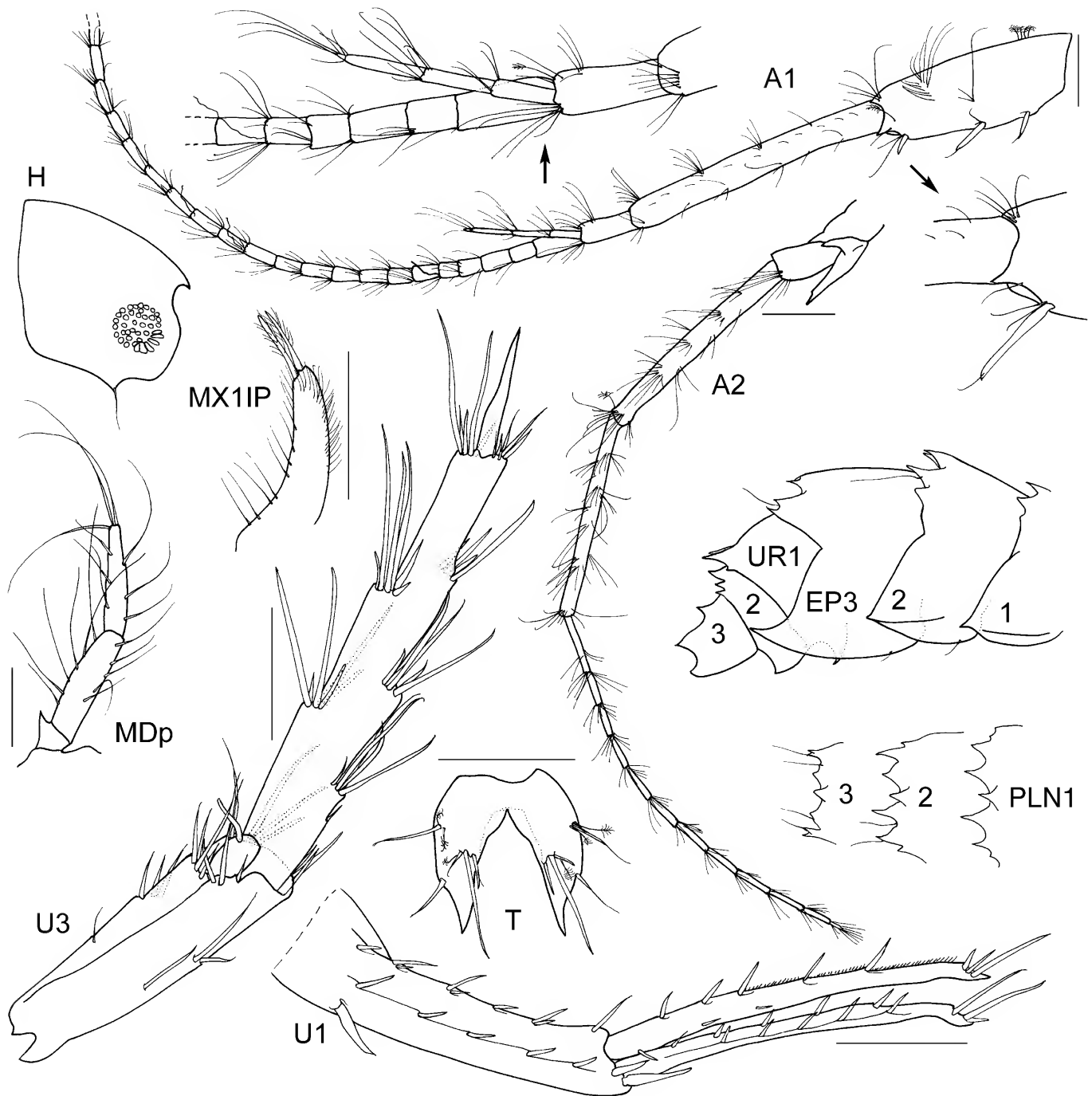
Fig. 55. *Dulichiella pacifica* n.sp., holotype, male "a", 4.4 mm, AM P61112, Tandai Point, Guadalcanal, Solomon Islands. Scales for MDp, MX1IP represent 0.1 mm, remainder represent 0.2 mm.

obtuse, straight, posterodistal spine absent, without robust setae; dactylus apically blunt; (smaller) subchelate; merus with sharp posteroventral spine; carpus long; propodus palm straight, without posteroventral spine. *Pereopod 5* basis posterior margin straight, posteroventral corner narrowly rounded or subquadrate; dactylus unguis anterior margin with accessory spine. *Pereopod 6* coxa anterior lobe ventral margin slightly produced, rounded; basis posterior margin slightly concave, posteroventral corner narrowly rounded or subquadrate; dactylus unguis anterior margin with accessory spine. *Pereopod 7* basis posterior margin straight, with posterior margin smooth or minutely castelloserrate, posteroventral corner narrowly rounded or subquadrate; dactylus unguis anterior margin with accessory spine.

Pleon. *Pleonites 1–3* with dorsal serrations, with dorsodistal spine. *Epimeron 1* posteroventral corner with small acute

spine. *Epimera 1–2* posteroventral margin without spines above posteroventral corner. *Epimeron 3* posterior margin smooth, posteroventral corner with strongly produced acute spine. *Urosomite 1* with broad dorsal midline gape, rarely bearing midline spines, dorsally bicarinate. *Urosomite 2* posterior margin serrate. *Uropod 3* inner ramus scale-like, much shorter than outer ramus; outer ramus much longer (more than 2× length) than peduncle, 2-articulate. *Telson* without apical robust setae, apical conical extension absent.

Female (sexually dimorphic characters). *Gnathopod 2* subchelate; merus with sharp posteroventral spine; carpus long; propodus without medial depression, palm acute, concave, smooth, with sparse robust setae, defined by posterodistal robust setae, defined by posteroventral corner; dactylus apically acute/subacute. *Pereopod 7* basis posterior margin subsigmoidal.
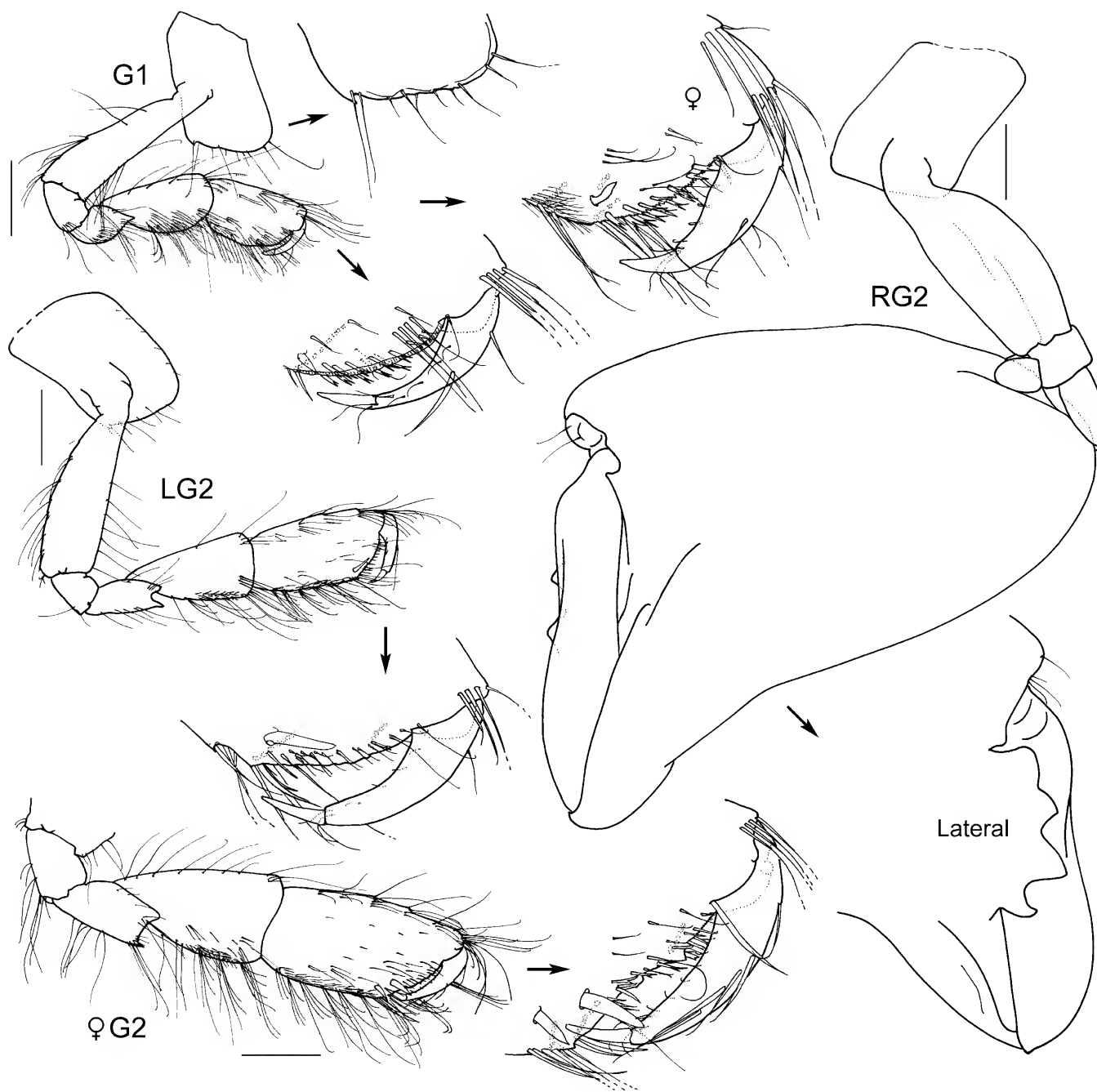
Fig. 56. *Dulichiella pacifica* n.sp., holotype, male "a", 4.4 mm, AM P61112, paratype, female, 5.9 mm, AM P61113, Tandai Point, Guadalcanal, Solomon Islands. Scales represent 0.2 mm.

Habitat. Marine; littoral; coral rubble, sponges, sand with low algal turf, 10 to 20 m depth.

Etymology. Named for its widespread distribution in the Pacific Ocean.

Remarks. This distinctive species was illustrated from Senegal by Ledoyer (1986). It is common in Singapore and occurs along the archipelago that runs from New Guinea to Fiji. A closely related, undescribed species has been reported from Florida and Bermuda by LeCroy (2000). See remarks under *D. australis* for differences between these species.

Distribution. *Queensland*: Yonge Reef, Great Barrier Reef; Lizard Island (Berents, 1983; AM).

Extrinsic distribution. Senegal, Singapore, New Guinea, Solomon Islands, New Caledonia.

Australian geographic areas. Northeastern Australia.

Melita Leach, 1814

Melita ophiocola n.sp.

Figs. 58–61

Type material. HOLOTYPE, ♀, 9.6 mm, AM P55192, west side, Bottle and Glass Rocks, Port Jackson, 33°50.9'S 151°16.15'E, 4 m, J.K. Lowry & R.T. Springthorpe, 23 March 1982, stn NSW-100. PARATYPES (114): 1 paratype, ♂, AM P46263; 1 paratype, ♀, AM P46264, type locality, 10 m, J.K. Lowry & R.T. Springthorpe, 21 January 1982, stn NSW-97; 8 paratypes, AM P25456, type locality, 9 m, G.D. Fenwick, 29 August 1977; 1 paratype, AM P55193; 1 paratype, AM P55194; 4 paratypes, AM P55199; 9 paratypes, AM P55200, type locality; 27 paratypes, AM P55195; 5 paratypes, AM P55196; 4 paratypes, AM P55197; 1 paratype, AM P55198, type locality, 4 m, 23 April 1982, stn NSW-101; 2 paratypes, AM P55236, type locality, 26 Feb 1982, stn NSW-99; 18 paratypes, AM P55241; 18, AM paratypes, AM P55242, type locality, 4 m, 26 November 1982, stn NSW-177; 11 paratypes, AM P55245, type locality, 4 m, R.T. Springthorpe & P.N. Weber, 24 December 1982, stn NSW-267; 3 paratypes, AM P55240, south of Vaucluse Point, Port Jackson, New South
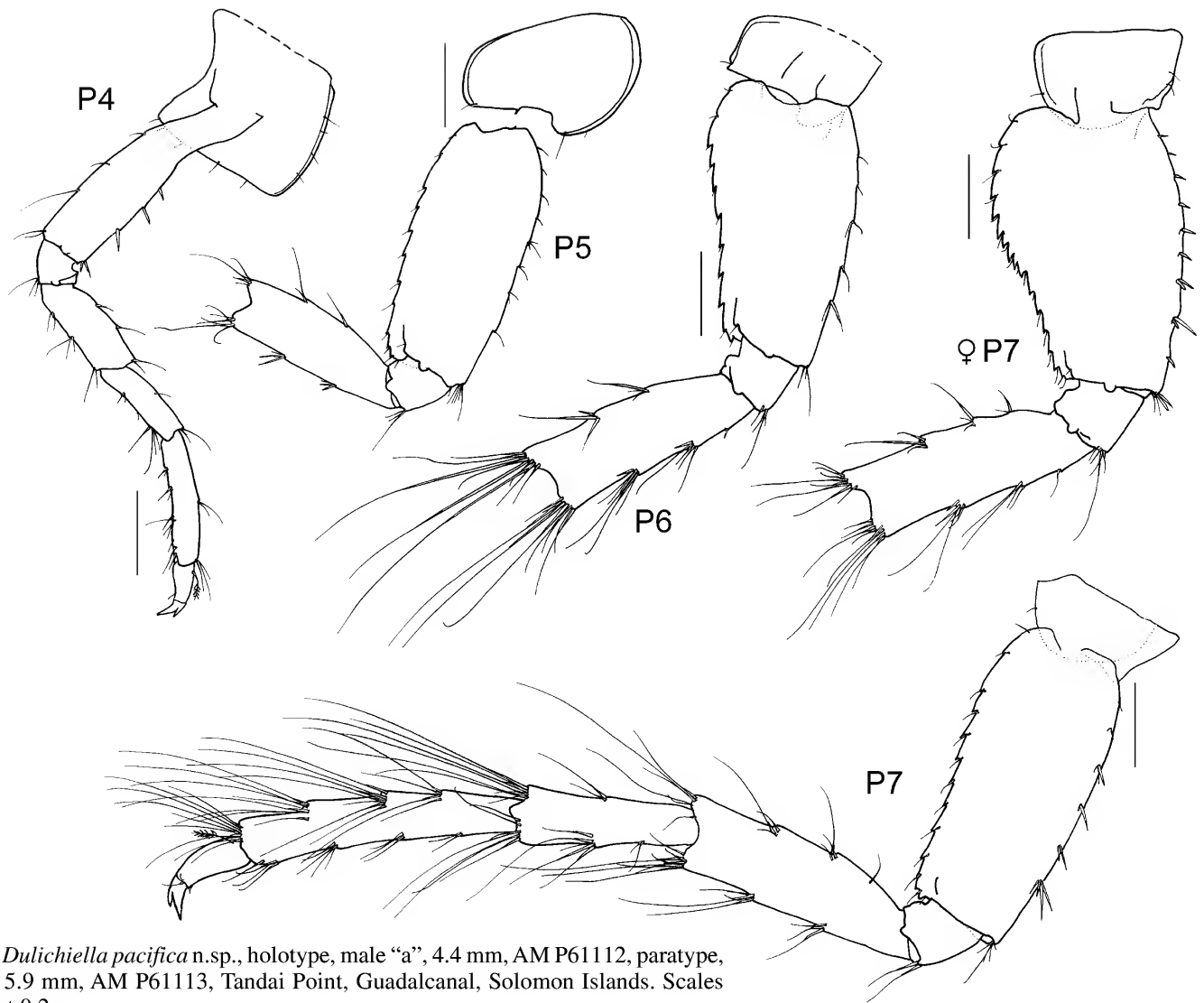
P4

P5

P6

♀ P7

P7

Fig. 57. *Dulichiella pacifica* n.sp., holotype, male "a", 4.4 mm, AM P61112, paratype, female, 5.9 mm, AM P61113, Tandai Point, Guadalcanal, Solomon Islands. Scales represent 0.2 mm.

Wales, Australia, 33°52'S 151°17'E, under rocks, shelley substrate, in association with ophiurid *Ophionereis schayeri*, 2 m, J.K. Lowry & R.T. Springthorpe, 22 June 1982, stn NSW-107.

Additional material examined. New South Wales: 1 ♀, AM P62903, northern cove of Boondelbah Island, Port Stephens, 32°42.28'S 152°13.47'E, under small boulders, 19.6 m, airlift, R.T. Springthorpe, P.B. Berents & A. Murray, 28 May 1998, stn NSW-1401. 92 specimens,

AM P31161 (4); AM P31162 (3); AM P31163 (1); AM P31164 (1); AM P31165 (2); AM P31166 (15); AM P31167 (14); AM P31168 (2); AM P31169 (1); AM P31170 (1); AM P31171 (4); AM P31172 (2); AM P31173 (11); AM P31174 (7); AM P31175 (8); AM P31176 (12); AM P31177 (2); AM P31178 (2), Little Box Head, Broken Bay, [approx. 33°33'S 151°16'E], sandy-muddy, very fine silt, 13 m, S. Arnam & R. Springthorpe, 18 November 1980. 68 specimens, AM P31142 (7); AM P31143 (5); AM P31144 (2); AM P31145 (2); AM P31146 (1); AM P31147 (3); AM P31148 (5); AM P31149 (1); AM P31150 (2); AM P31151 (3); AM P31153 (1); AM P31154 (2); AM P31155 (1); AM P31156 (10); AM P31157 (5); AM P31158 (8);
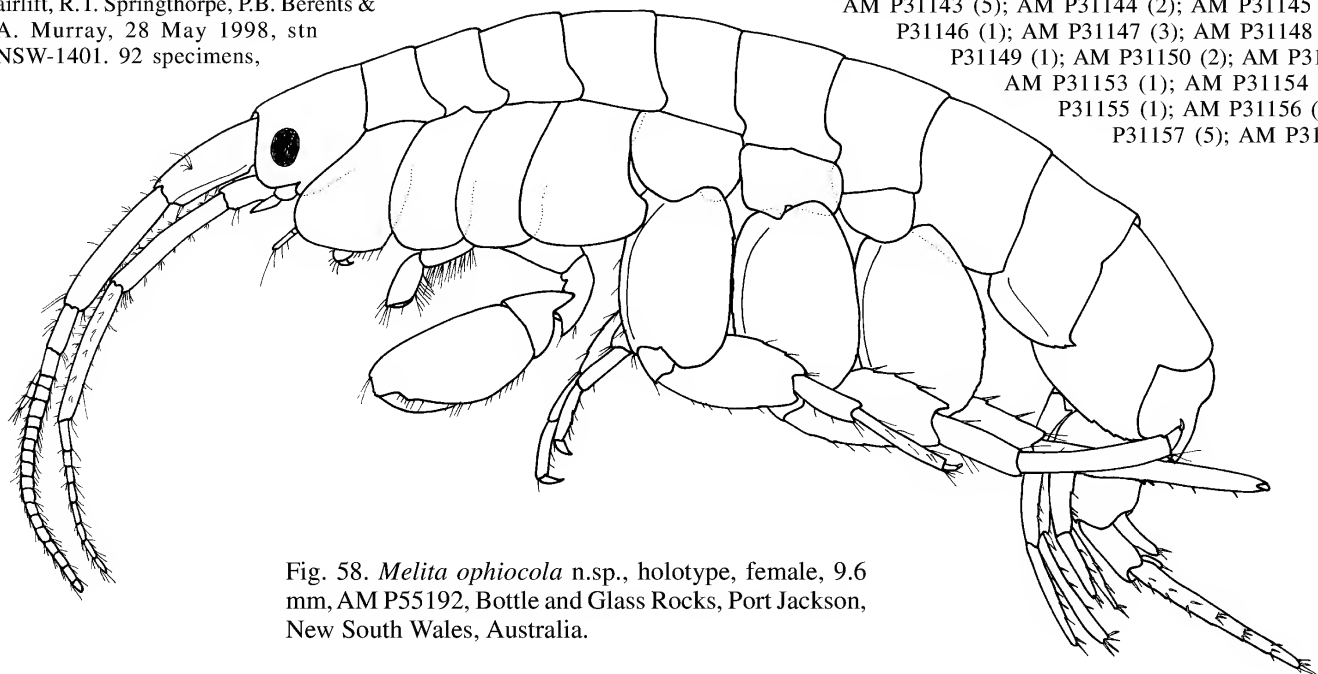
Fig. 58. *Melita ophiocola* n.sp., holotype, female, 9.6 mm, AM P55192, Bottle and Glass Rocks, Port Jackson, New South Wales, Australia.
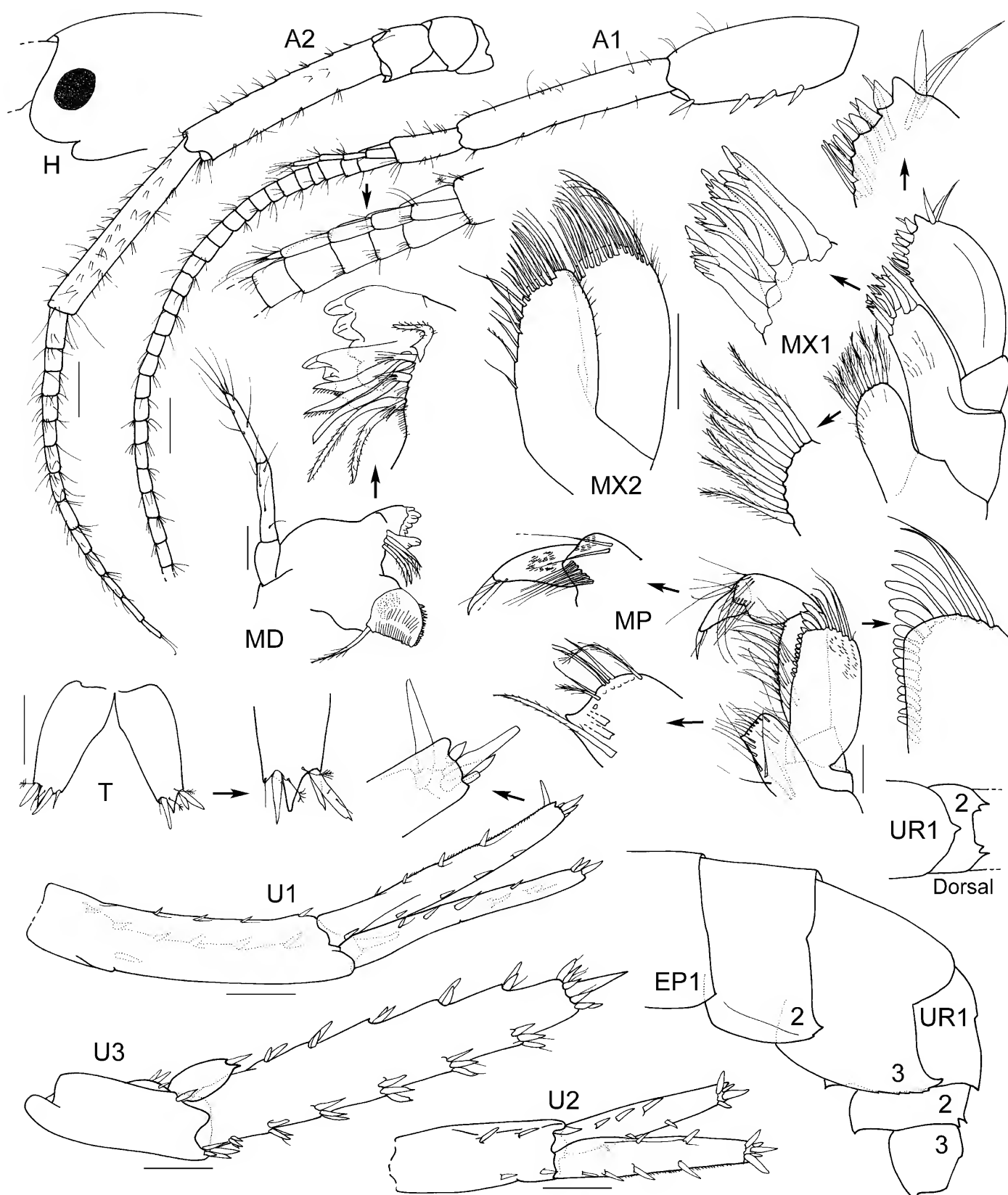
Fig. 59. *Melita ophiocola* n.sp., holotype, female, 9.6 mm, AM P55192, Bottle and Glass Rocks, Port Jackson, New South Wales, Australia. Scales for MD, MX1, MX2, MP represent 0.1 mm, remainder represent 0.2 mm.

AM P31159 (4); AM P31160 (6), 90 m south of Fairlight Pool, Port Jackson, 33°48.1'S 151°16.3'E, under stones, muddy sand, shell, in association with ophiuroid *Ophionereis schayeri*, 10 m, S. Arnam & R. Springthorpe, 13 October 1980. 2♀♀, AM P45267, 50 m north of Cannae Point, Port Jackson, 33°49'S 151°, on brittle star: *Ophionereis schayeri*, 5 m, P.B. Berents, P. Castro, G. Towner, 21 June 1995, stn NSW-1138. 67 specimens, AM P31134 (8); AM P31135 (2); AM P31136 (47); AM P31137 (1); AM P31138 (1); AM P31139 (5); AM P31140 (1); AM P31141 (2), type locality, 0.5 m, S. Arnam, J.K. Lowry & R.T. Springthorpe, 29 September 1980. 19 specimens, AM P55243 (17); AM P55244 (2), south of Vaucluse Point, Port Jackson, 33°50.9'S

151°16.15'E, rocky with sediment patches, in association with ophiuroid *Ophionereis schayeri*, 2 m, J.K. Lowry & R.T. Springthorpe, 27 May 1982, stn NSW-105. 7 specimens, AM P55234 (4); AM P55235 (3), South of Vaucluse Point, Port Jackson, 33°52'S 151°17'E, under rocks on soft substrate, in association with ophiuroid *Ophionereis schayeri*, 4 m, R.T. Springthorpe & A. Murray, 30 September 1982, stn NSW-156. 1♂, AM P55233, type locality. 2 specimens, AM P55237, type locality, 26 February 1982, stn NSW-99. 4 specimens, AM P55238 (2); AM P55239 (2), type locality, 10 m, 21 January 1982, stn NSW-97. 6 specimens, AM P55246, type locality, 4 m, R.T. Springthorpe & P.N. Weber, 24 December 1982, stn NSW-267. 6 specimens, AM P36648,
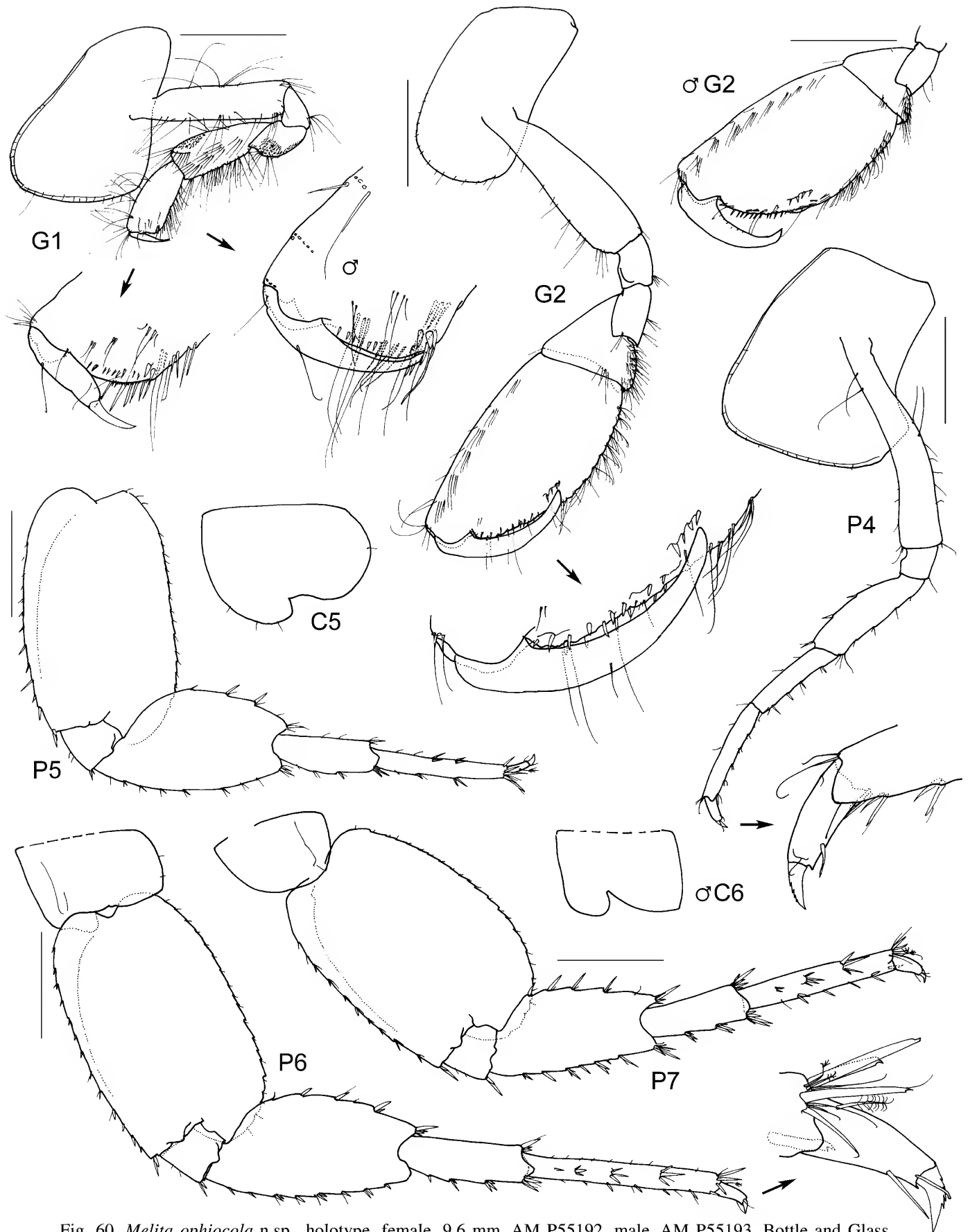
Fig. 60. *Melita ophiocola* n.sp., holotype, female, 9.6 mm, AM P55192, male, AM P55193, Bottle and Glass Rocks, Port Jackson, New South Wales, Australia. Scales represent 0.5 mm.

Murrumbulga Point, Twofold Bay, 37°04.7'S 149°53.1'E, subtidal rock platform, 3 m, S. Keable, 9 October 1984, stn Q2. 1♂, AM P55117, Munganno Point, Twofold Bay, 37°06'S 149°56'E, subtidal rock platform, 6 m, S.J. Keable, 10 October 1984, stn M6.

Type locality. Bottle and Glass Rocks, Port Jackson, New South Wales, Australia, 33°50.9'S 151°16.15'E, living in

association with the ophiuroid *Ophionereis schayeri* under rocks, 4 m.

Description. Based on holotype female, AM P55192 and paratype male, AM P55193.

Fig. 61. *Melita ophiocola* n.sp., paratype male and female, AM P55240, in association with ophiuroid *Ophionereis schayeri*, south of Vaucluse Point, Port Jackson, New South Wales, Australia. Illustration by Sharne Weidland.

Head. Lateral cephalic lobes broad, rounded, with anteroventral notch or slit, anteroventral corner rounded. *Antenna 1* longer than antenna 2; peduncular article 1 longer than article 2, with 4 or more robust setae along posterior margin; flagellum with about 30 ar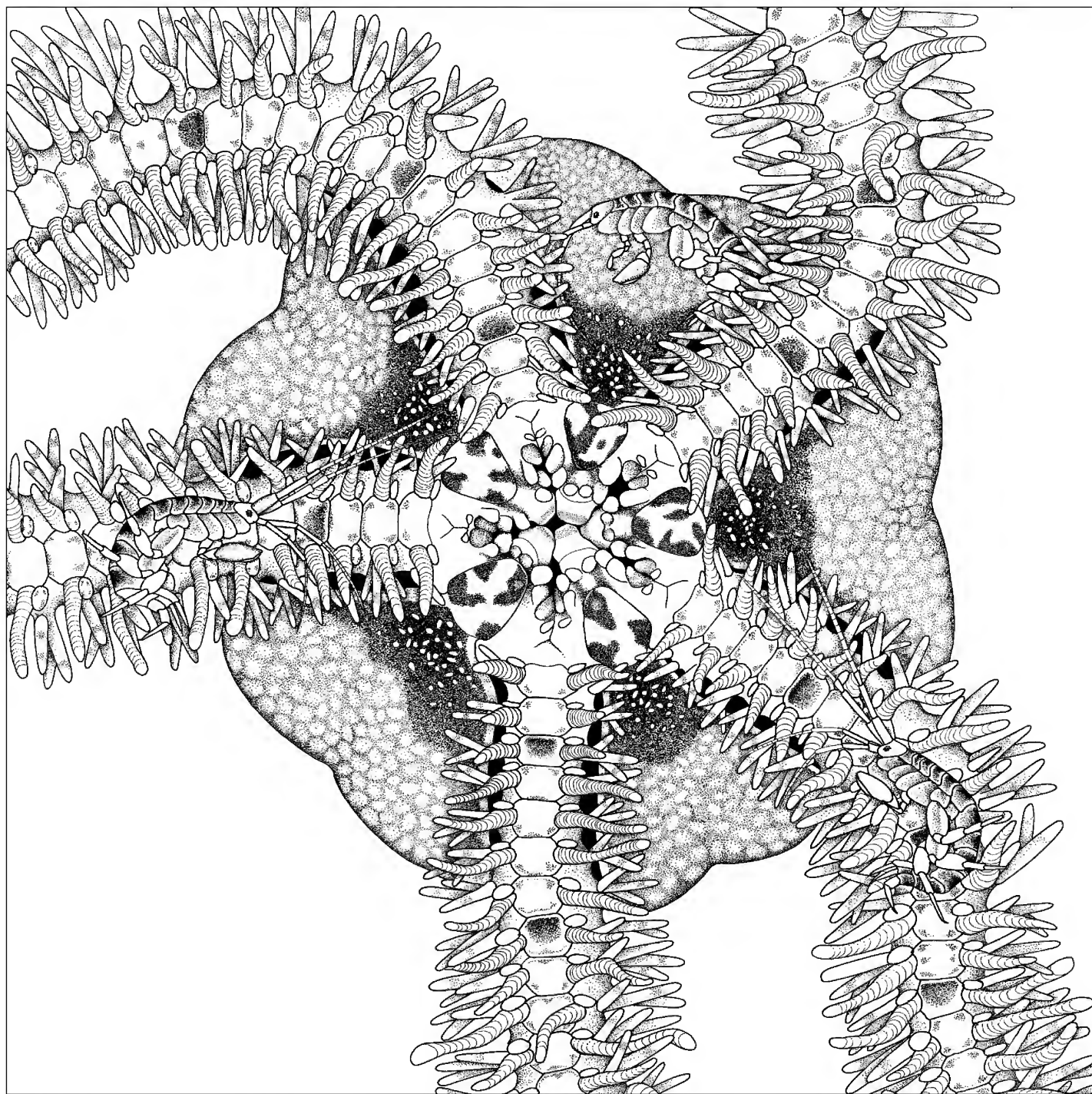ticles; accessory flagellum with about 5 articles. *Antenna 2* peduncular article 2 cone gland not reaching to end of peduncular article 3; article 4 subequal to article 5; flagellum with about 13 articles. *Mandible* palp article 3 rectolinear, setose along straight medial margin, longer than article 1; article 2 subequal to article 3; article 1 not produced, shorter than article 2. *Maxilla 1* inner plate with setae mainly terminal.

Pereon. *Gnathopod 1* coxa anteroventral corner produced, rounded, posteroventral corner notch absent; merus without posterodistal spine; carpus about 3× as long as broad; propodus palm acute, slightly convex, defined by posterodistal corner, defined by posterodistal robust setae. *Gnathopod 2* not sexually dimorphic; subchelate; coxa posteroventral corner notch absent; merus with sharp posteroventral spine; carpus compressed; propodus without medial depression, without strong concentration of setae, palm broadly rounded, convex, smooth, with sparse small robust setae, defined by posterodistal robust setae, without posteroventral corner; dactylus apically acute/subacute.

Pereopod 5-6 basis posterior margin straight, posteroventral corner broadly rounded; dactylus unguis anterior margin with 2 or more accessory spines. *Pereopod 7* basis posterior margin slighlty convex, with posterior margin smooth or minutely castelloserrate, posteroventral corner broadly rounded; dactylus unguis anterior margin with 2 or more accessory spines.

Pleon. *Epimeron 1* posteroventral corner with small acute spine. *Epimera 1–2* posteroventral margin without spines above posteroventral corner. *Epimeron 3* posterior margin smooth, posteroventral corner with strongly produced acute spine, posteroventral margin smooth or minutely serrate. *Urosomite 1* with spines at midline, no conspicuous medial gape, with posterodorsal spine. *Uropod 3* inner ramus scale-like, much shorter than outer ramus; outer ramus much longer (more than 2× length) than peduncle, 2-articulate. *Telson* each lobe with 3 apical/subapical robust setae, apical conical extension reaching at least halfway along longest seta.

Female (sexually dimorphic characters). *Pereopod 6* coxa anterior lobe ventral margin slightly produced, rounded.

Habitat. Marine; living in association with the ophiuroid *Ophionerieis schayeri* under rocks.

Depth zone. Littoral (1 to 13 m).

Remarks. *Melita ophiocola* is an unusual and distinctive species of the genus. It is an obligate commensal of the brittle star *Ophionereis schayeri* (Muller & Troschel). Preliminary results of experimental data indicate that the largest adult amphipods tend to occur in heterosexual pairs on the host and occasionally more than one pair may occur. Over 80% of individuals sampled were juveniles and there can be as many as 50 young per host. Juveniles occur throughout the year.

Mate selection experiments involving live animals showed that a significant number of large adults initially released on an overcrowded host move to another host and form heterosexual pairs (Peter Castro, pers. comm.). This apparent mobility may explain the high infection rates of over 90% observed in the field.

In a highly unusual situation for species of *Melita*, there is virtually no sexual dimorphism between males and females. We assume that this is because the female and male are always present together on the host and so there is no need for precopulatory amplexus and its associated morphological modifications.

Ophionereis schayeri is found in shallow water beneath large rocks and in crevices. It is more active at night when it may forage in the open. It moves by sinuous flexing of its arms and feeds on detritus that is transported to the mouth by the tube feet. It is assumed that *M. ophiocola* feeds on the detritus collected by its host. *Melita ophiocola* has a banded colour pattern of purple and cream dorsally with purple gnathopods and pereopods tending to cream distally. This is similar to the colour pattern of the aboral surface of its host. *Melita ophiocola* is able to move freely over the body and arms of the brittle star but lives mostly on the oral surface of the arms between the two rows of tube feet.

Distribution. *New South Wales*: Boondelbah Island, Port Stephens; Broken Bay; Port Jackson; Twofold Bay (all AM).

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Revision of Two Prioniodontid Species (Conodonta) from the Early Ordovician Honghuayuan Formation of Guizhou, South China

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ABSTRACT. The septimembrate conodonts *Acodus triangularis* (Ding in Wang, 1993) and *Prioniodus honghuayuanensis* n.sp., are described and illustrated from Guizhou, South China where both species are widely distributed in Lower Ordovician strata. The adenticulate *A. triangularis*, which ranges through the middle and upper parts of the Honghuayuan Formation, is morphologically more primitive than the denticulate *P. honghuayuanensis*, which is present from the uppermost Honghuayuan Formation into the lower part of the succeeding Dawan Formation. *Prioniodus honghuayuanensis*, elements of which were previously ascribed to *Oepikodus communis* (Ethington & Clark, 1964), appears to be closely related to a species of *Prioniodus* from the basal Whiterockian of Utah, North America.

Conodonts from the Honghuayuan Formation of Guizhou Province, South China were first studied by An (1987) in the Honghuayuan and Ganxi sections (Fig. 1). In the Honghuayuan section, An (1987) recognized three conodont assemblages with the lowermost consisting only of coniform species. The middle assemblage is characterized by the occurrence of *Serratognathus diversus* An, 1981. The upper assemblage is much higher in diversity, with the appearance of a number of pectiniform species of *Prioniodus, Bergstroemognathus* and *Rhipidognathus*. Similar faunas were also recorded from the Honghuayuan Formation of

Yanhe, northern Guizhou (An, 1987; X.Y. Chen *et al.*, 1995), and are widely distributed in the Honghuayuan Formation and age equivalent units in South China (An *et al.*, 1985; An, 1987; Wang, 1993).

More recently, conodont samples were collected from Lower Ordovician sections in Guizhou and other parts of South China with the aim of revising the faunas to provide support for a more precise biostratigraphic correlation and age alignment, both regionally and internationally. This revision will assist our understanding of the origin, radiation and phylogeny of the prioniodontid and related clades
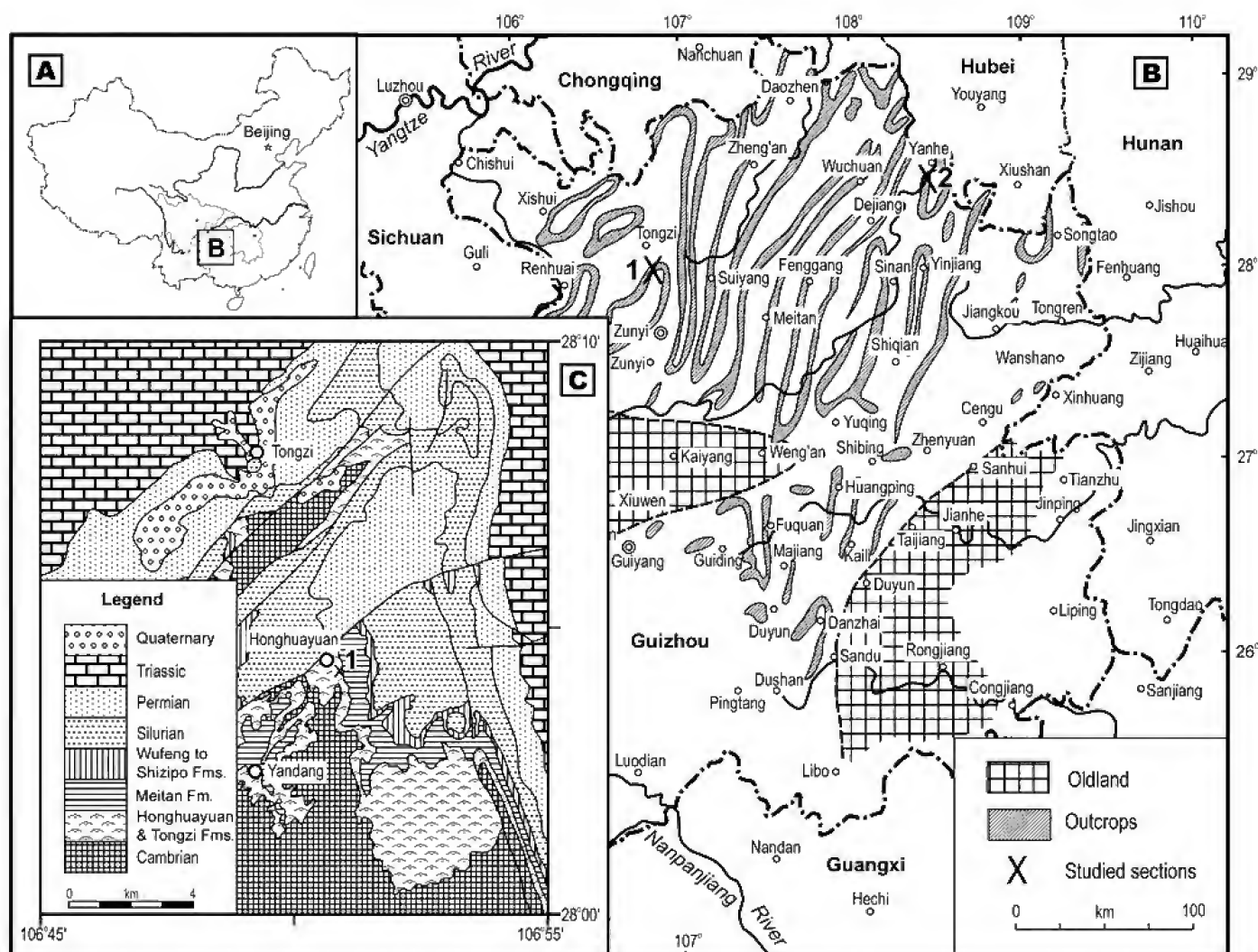

Fig. 1. Locality maps of the study areas. (*A*) China showing the location of Guizhou Province. (*B*) northeast Guizhou showing the distribution of the Ordovician rocks (after Gao, 1976) and the locations of two sampled sections for this study: 1) Honghuayuan Section of Tongzi; 2) Ganxi Section of Yanhe. (*C*) simplified geological map of the area in the vicinity of Honghuayuan village, showing the location of the Honghuayuan Section (Geology information modified from 1:200 000 Geology Map of Tongzi by Guizhou Regional Geological Survey, 1978).

through the late Early Ordovician. The present contribution is the first of several publications arising from this ongoing research project.

Regional geological setting and lithostratigraphy

The Honghuayuan Formation was initially named the Honghuayuan Limestone by Chang & Sheng (1958) based on 40 m of grey, thick-bedded limestone at Honghuayuan, 7 km south of Tongzi County town, Guizhou (Fig. 1B,C). Zhang *et al.* (1964) renamed the unit the Honghuayuan Formation, which has been widely used to describe upper Lower Ordovician strata in South China (Wang *et al.*, 1996). The formation conformably overlies the Tongzi Formation. The contact with the overlying Meitan Formation is conformable and gradational (Fig. 1C).

The Honghuayuan Formation in the type section is a medium- to thick-bedded skeletal grainstone and packstone with thin-bedded to nodular skeletal wackestone (Fig. 2). Lime mudstone and shales are rare. Skeletal debris is mostly composed of cephalopods, brachiopods, trilobites, *Archaeoscyphia*, and bryozoans. The high biotic diversity suggests deposition in a well-circulated neritic environment.

Abundant skeletal grainstones and cross bedding indicate that the formation was mostly deposited in a shoreward environment in the high-energy, shallow subtidal zone (Fig. 2), although lower-energy, deep subtidal sediments, e.g., nodular argillaceous lime mudstone, are also present. Deposition of carbonates of the Honghuayuan Formation ceased due to sea level rise, to be replaced by an increasing supply of terrigenous muds, and then greyish green mudstone (the Meitan Formation) was deposited in Guizhou (Fig. 1C).

The Honghuayuan Formation is widely distributed in Guizhou (Fig. 1B) as well as on the Yangtze Platform with similar lithofacies in the Honghuayuan section (Wang *et al.*, 1996). Near shore facies of the formation deposited adjacent to eroded land (or island) areas are more dolomitic than the type section. Some patch reefs, which are mainly formed by abundant *Calathium* and less common *Archaeoscyphia* (Zhu *et al.*, 1995) were reported from the Huanghuachang section in Yichang, Hubei. The thickness of the Honghuayuan Formation on the Yangtze Platform is commonly 20 to 50 m, varying from a few metres to more than one hundred metres. In Guizhou, the thickness increases to more than 130 m northeastwards from the "Qianzhong Oldland" (an erosional land area at the time) (Fig. 1B).
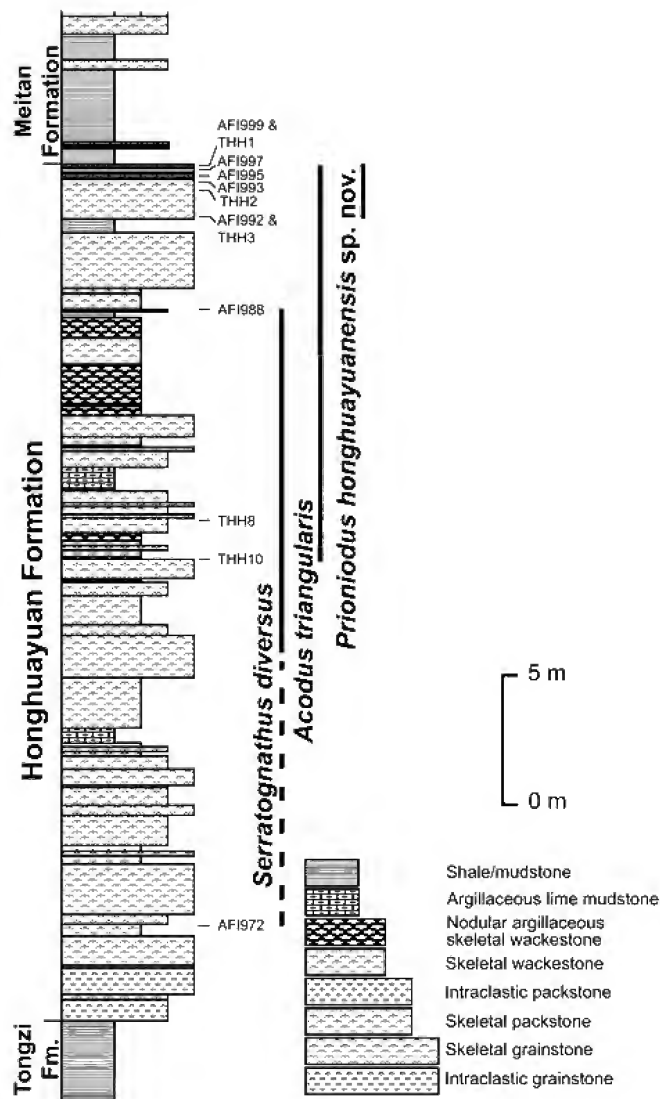
Fig. 2. Stratigraphic section through the Honghuayuan Formation at Honghuayuan, Tongzi, Guizhou Province showing the sampling positions and the stratigraphic ranges of *Serratognathus diversus* and the two species studied.

Age and correlation of the Honghuayuan faunas

The most characteristic feature of the conodont faunas from the Honghuayuan Formation is the abundance of *Serratognathus diversus* in the middle part of the formation (Fig. 2). This distinctive conodont species is apparently restricted in distribution to South China, the Tarim Basin (Zhao *et al.*, 2000), and probably Australia (R.S. Nicoll, pers. comm.) and other biogeographically related tectonic units (Zhen *et al.* in Webby *et al.*, 2000; Zhen & Percival, 2003). An (1981, 1987) proposed the *S. diversus* Zone (divided into lower and upper subzones) based on the wide distribution of this species in South China, and correlated the lower subzone to the *P. proteus* Zone and the upper subzone to the *P. elegans* Zone of Baltoscandian successions. The *S. diversus* Zone was also approximately correlated with the *T. approximatus* graptolite Zone, evidenced by the occurrence of the *T. approximatus* fauna in deeper water clastic graptolitic facies laterally equivalent to the carbonate facies of the Honghuayuan Formation (X. Chen *et al.*, 1995).

An (1981, 1987) also recognized the *communis* Zone ranging from the top of the Honghuayuan Formation to the basal part of the overlying Dawan Formation in South China,

and correlated it with the *communis* Zone of North American Mid-continent successions. Although the age determination for the Honghuayuan Formation established by An (1981, 1987) is still current, the present study has demonstrated that the so-called "*Baltoniodus communis*" from South China of previous authors represents a new species of *Prioniodus, P. honghuayuanensis* named herein. It is neither conspecific nor congeneric with *Oepikodus communis* (Ethington & Clark, 1964), an index zonal species of North American Mid-continent successions. *Prioniodus honghua-yuanensis* in fact exhibits close relationships with a younger unnamed species of *Prioniodus* from the basal Whiterockian succession of the Ibex area, Utah. The morphological changes (documented herein) from adenticulate *Acodus* species to denticulate *Prioniodus* indicate the likely origin of Prioniodontid clade. *Prioniodus honghuayuanensis* may have evolved from an adenticulate species revised herein as *Acodus triangularis* (Ding in Wang, 1993), which first occurs in the middle of the Honghuayuan Formation (THH10, Fig. 2) and is also associated with *P. honghua-yuanensis* at the top of the Formation. Morphologically *Acodus triangularis* resembles *A. longibasis* McTavish, 1973 from the Emanuel Formation of Western Australia, which also represents the primitive adenticulate prionio-dontid species, but is probably of slightly younger age.

Material and methods

Twenty conodont samples (with prefix THH) were collected in 2000 from the Honghuayuan Formation in a 32 m thick limestone succession exposed on the hill slope to the southeast of Honghuayuan village (Fig. 1), about 10 km south of the Tongzi County. *Acodus triangularis* occurs in four samples (out of fifteen which yielded conodonts), whereas *Prioniodus honghuayuanensis* n.sp. was recovered from two samples at the top of the Formation (Table 1). All samples were completely dissolved in 10% acetic acid, with residues separated and concentrated using sodium polytungstate. Subsequently, 38 large samples (with prefix AFI) were recollected from the Honghuayuan Formation on this section (location coordinates: 28°04.27'N 106° 50.91'E) to the southeast of the village. Both species were recovered from five samples at the top of the Honghuayuan Formation (Table 1).

In the Ganxi Section, measured along the road from Ganxi village to Shichangao, southwest of Yanhe County Town (Fig. 1, location coordinates: 28°22.72'N 108° 25.70'E), the Honghuayuan Formation consists of 71.8 m of thick-bedded limestones. Out of 27 productive samples collected from this section (with prefix YTH), only one from the top of the Honghuayuan Formation yielded *Acodus triangularis* and *Prioniodus honghuayuanensis* (Table 1).

All photographic illustrations shown in Figs 3–9 are SEM photomicrographs captured digitally (numbers with the prefix IY are the file names of the digital images). Figured specimens bear the prefix AMF and are deposited in the collections of the Palaeontology Section at the Australian Museum in Sydney. Authorship of the new species is attributable solely to Zhen. Conodont terminology and notation employed in this contribution are conventional as defined in the Treatise Part W (Clark *et al.*, 1981), except for the M elements (makellate), whose orientation, morphology and terminology was introduced by Nicoll (1990, 1992).

Table 1. Distribution of *Acodus triangularis* and *Prioniodus honghuayuanensis* n.sp., in ten samples of the Honghuayuan Formation at the Honghuayuan Section of Tongzi, and in one sample from the top of the Honghuayuan Formation at the Ganxi Section of Yanhe, Guizhou Province, South China.

Samples	*Acodus triangularis*								*Prioniodus honghuayuanensis*								
	Pa	Pb	M	Sa	Sb	Sc	Sd	Total	Pa	Pb	?Pc	M	Sa	Sb	Sc	Sd	Total
AFI999	2	—	1	—	—	—	—	3	2	1	1	2	2	4	3	4	19
AFI997	13	5	6	5	4	2	7	42	9	4	—	7	13	12	11	16	72
AFI995	6	—	—	2	1	1	3	13	1	1	—	1	2	2	6	9	22
AFI993	26	26	18	7	2	3	11	93	34	11	—	38	26	53	27	103	292
AFI992	1	1	2	6	7	9	2	28	3	—	—	2	—	4	—	2	11
THH1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	1
THH2	—	—	4	1	—	—	—	5	—	—	—	—	—	—	—	—	—
THH3	5	4	2	3	2	2	4	22	—	—	—	1	1	—	—	1	3
THH8	1	1	—	—	—	—	1	3	—	—	—	—	—	—	—	—	—
THH10	4	—	1?	2	1	2	1	11	—	—	—	—	—	—	—	—	—
YTH1	1	—	—	—	—	1?	—	2	3	1	—	—	1	5	2	3	15
Total	59	37	34	26	17	20	29	222	52	18	1	51	45	80	50	138	435

Systematic palaeontology
Class Conodonta Pander, 1856
Acodus Pander, 1856

Type species. *Acodus erectus* Pander, 1856.

Remarks. The generic definition of *Acodus* and other related genera like *Tripodus* Bradshaw, 1969 and *Tropodus* Kennedy, 1980 has been a subject of disagreement among conodont workers (e.g., Lindström in Ziegler, 1977; Sweet, 1988, Kennedy, 1980; Albanesi in Albanesi *et al.*, 1998; Johnston & Barnes, 2000; X.H. Chen *et al.*, 2003). It seems likely that there are more than one genus involved in these species embraced under a rather broad definition of *Acodus* given by Zhen *et al.* (2004). However, a serious revision of this species group, which will certainly need a monographic treatment, is far beyond the scope of the present project, and the level of our current understanding of these species does not yet support such a major revision. *Acodus*, defined as a multielement genus by Lindström (in Ziegler, 1977), is deeply entrenched in the Ordovician conodont literature. It was widely distributed in the Early and Middle Ordovician, and played a crucial part in the origin and early evolution of several major pectiniform clades like prioniodontids and balognothids (Stouge & Bagnoli, 1999). We retain *Acodus* as a valid genus, although Pander's original specimens of the genotype, *A. erectus*, are irretrievably lost.

The type species of *Tripodus, T. laevis* Bradshaw, was originally defined as a form species on the basis of three specimens which show sharp anterior and posterior margins, a sharp blade-like costa on the outer lateral face situated more towards anterior margin, and a broad carina on the inner lateral face (Bradshaw, 1969). Based on material from the Ibex area of Utah, Ethington & Clark (1982) revised the type species of *Tripodus* as consisting of a quinquimembrate apparatus. This is interpreted herein as including geniculate M (oistodiform element, see Ethington & Clark, 1982, fig. 33A,B), alate triform Sa (trichonodelliform element, their fig. 33C), asymmetrical tetra-costate Sb (distacodiform element, their fig. 33F,G), asymmetrical laterally compressed Sc (drepanodiform element, their fig. 33H), and asymmetrical multi-costate Sd (paltodiform element, their fig. 33D,E) elements. Apparently the type

material of *T. laevis* would fall into the definition of the Sb element of the multi-element concept of the species, and the types of *Scolopodus alatus* Bradshaw, 1969, which Ethington & Clark (1982) regarded as part of the *T. laevis* apparatus, include both Sa (Bradshaw, 1969, pl. 132, fig. 4, paratype) and Sd (Bradshaw, 1969, pl. 132, figs 1–3, holotype) elements. Ethington & Clark (1982) also regarded *Triangulodus* van Wamel, 1974 as a junior synonym of their revised *Tripodus*. This raised the question as to whether *Tripodus* is likely a senior synonym of *Triangulodus* or a junior synonym of *Acodus*.

Based on material from western Newfoundland, Stouge (1984) regarded *Tripodus* as a junior synonym of *Acodus*, and suggested that *Acodus combsi* Bradshaw, 1969, *T. laevis* Bradshaw, and *S. alatus* Bradshaw represented different elements of one species apparatus which he called *A. combsi*. By assigning the prioniodiform P element represented by the form species *A. combsi* to the species apparatus, Stouge (1984) expanded the definition of *T. laevis* given by Ethington & Clark (1982), although at the time he was unaware of their work. Further differentiation of the prioniodiform Pa and Pb elements has completed the species apparatus as septimembrate (Albanesi in Albanesi *et al.*, 1998). Acodiform specimens assignable to the form species, *A. combsi* Bradshaw, 1969 were also reported from the Ibex area of Utah under the name "*Scandodus*" *robustus* Serpagli, 1974 (Ethington & Clark, 1982, pl. 10, fig. 25). This species definition for *T. laevis* has been more or less accepted by many Ordovician conodont workers (Sweet, 1988, Stouge & Bagnoli, 1988; Albanesi in Albanesi *et al.*, 1998; Bergström & Albanesi, 2001; Pyle *et al.*, 2003), although others (Johnston & Barnes, 2000; X.H. Chen *et al.*, 2003) retained the original concept of oistodiform M and costate S elements only as defined by Ethington & Clark (1982).

By taking *A. combsi* as the name bearer of the species, Stouge's work (1984) raised two questions: firstly, should *T. laevis* or *A. combsi* be the name bearer of the revised multi-element species, and secondly, to which genus should this species be assigned? In a recent documentation, Bergström & Albanesi (2001) reviewed the validity of the species name *Tripodus laevis*, and concluded that based on the most recent edition of ICZN rules, *T. laevis* is the valid name and *A. combsi* is a junior synonym of *T. laevis*. As for

the second question, some conodont workers follow Sweet (1988) in maintaining *Tripodus* as a valid genus and assigning *Acodus* as a *nomina dubia*, whereas others (e.g., Stouge & Bagnoli, 1988; Johnston & Barnes, 2000) utilize both *Acodus* and *Tripodus* by consigning species to the respective genus on historical reasons or on the details of the P and S elements. Based on the definitions of *Acodus* given by Lindström (in Ziegler, 1977) and of *Triangulodus* given by van Wamel (1974), both bear costate S and geniculate M elements, but *Acodus* has prioniodiform (acodiform) P elements instead of scandodiform P elements without costa on lateral faces as in *Triangulodus*. However, as discussed above, the form species of *T. laevis* may represent the Sb element of the multi-element species apparatus adopted herein. If Stouge's (1984) revision of *T. laevis* is accepted, *Tripodus* is likely a junior synonym of *Acodus*. Ethington (pers. comm., 2004) suggested that the S elements of *Tripodus* were much more ornate in their surface morphologies than typical *Acodus* as demonstrated by *A. deltatus* Lindström, 1955 and *A. triangularis* Ding described herein, and the P elements of *T. laevis* (*A. combsi* s.f. of Bradshaw) were deeply albid with very shallow basal cavities and without prominent carinae on the cusps. Until the type species of *Tripodus* can be revised in detail the taxonomic relationship of these two genera remains uncertain.

In the type sections of the Marathon Basin of Texas, all three form species (*T. laevis, A. combsi* and *S. alatus*) were established based only on a few specimens, and *T. laevis* and *A. combsi* were not found in association (Bradshaw, 1969). Furthermore, co-occurrence of *Histiodella sinuosa* (Graves & Ellison) and *Periodon aculeatus* Hadding, 1913 in the Fort Peña fauna also suggests a younger age (Middle Ordovician, Yapeenian equivalent). Considering that the FAD (first-appearance datum) of *T. laevis* is a potential candidate for defining the base of the Middle Ordovician, detailed revision of this species at the type locality is urgently needed.

Acodus triangularis (Ding in Wang, 1993)

Figs 3–5

?*Triangulodus* cf. *alatus* Dzik.–An *et al.*: 1985: pl. 8, figs 1, 4, 8.
?*Tripodus alatus* (Dzik).–An, 1987: p. 193, pl. 16, figs 3–6.
Oistodus triangularis Ding in Wang 1993: p. 185, pl. 19, figs 1, 2.

Material. 222 specimens from ten samples (Table 1).

Diagnosis. A species of *Acodus* consisting of a septimembrate apparatus including pastinate Pa and Pb, makellate M, triform alate Sa, triform asymmetrical Sb, modified cordylodiform Sc, and tetra-costate Sd elements; elements mostly albid and small in size, all bearing short adenticulate processes; P elements with a triangular base bearing a large, open basal cavity; S elements bearing a longer posterior process typically with a thin, blade-like crest along the upper edge.

Description. The pastinate Pa element has a reclined to suberect cusp and a large, triangular base (Fig. 3A–O). The cusp is triangular in cross section (Fig. 3F) with a sharp costa along the anterior and posterior margins, a mid-costa on the convex outer lateral face, and a smooth, more or less flattened inner lateral face. Three costae extend basally to merge with the upper margin of the anterior, posterior and

outer lateral processes respectively (Figs 3A,G,K,I,M, 4 O). Fine striations are best developed in the area posterior to the outer lateral costa on the outer lateral face (Fig. 3L). All three processes have a blade-like upper edge (Fig. 3E,G) and an expanded base with posterior and anterior processes extending in the same plane (Fig. 3H) or with anterior process slightly turned inner laterally (Fig. 3M–O). The outer lateral process extends basally and outer laterally in a direction nearly normal to the anteroposterior plane in upper or basal view (Fig. 3B,F), and is triangular in outline in anterior view (Fig. 3C,I) or posterior view (Fig. 3E). Posterior process extends posteriorly and typically longer than the other two (Fig. 3G,K). The anterior process is anticusp-like, triangular in outline in the lateral view (Fig. 3D,I–K). Basal cavity is pyramidal, large and moderately deep, with more or less straight basal margin or with both sides of the outer lateral process slightly restricted inward (Fig. 3B,H).

The Pb element is similar to the Pa element, but with a slightly proclined cusp (Fig. 4C,F,G,J,M), a shorter and less basally extended anterior process (Fig. 4A,B,G), a shorter and anterolaterally located outer lateral process (Fig. 4A,E,F,N), and a more open basal cavity (Fig. 4D,H). The side between the anterior process and the outer lateral process is less inwardly restricted, and the basal margins on both sides of the outer lateral process are less restricted inward in upper or basal view (Fig. 4B,D,E).

The M element is geniculate, anteroposteriorly compressed, with a low and well-developed outer lateral process and a short, anticusp-like inner lateral process, which is triangular in outline in anterior (Fig. 4K) or posterior view (Figs 3P, 4L). The anterior face is broadly convex and smooth, while the posterior face bears a broad carina and a weakly developed basal buttress. The basal margin is gently arched (Figs 3P, 4K,L).

The Sa element is triform and symmetrical with a robust cusp, a short adenticulate posterior process, and a blade-like adenticulate lateral process on the anterolateral corner of each side (Figs 4P–U, 5A). The cusp is isosceles triangular in cross section with a broad anterior face (Fig. 5A), a sharp costa along the posterior margin, and a sharp costa on each lateral side (Figs 4R,T, 5A). The three costae extend basally to form short, blade-like posterior and lateral processes (Fig. 4R,Q). Basal cavity is triangular in outline with moderate depth (Fig. 4R,U). Some specimens show a few small, rudimentary denticles along the thin upper edge of the posterior process (Fig. 4S).

The Sb element resembles the Sa element in being tricostate, but is distinguished by being markedly asymmetrical (Fig. 5B–J). The cusp is proclined, scalene triangular in cross section with a sharp costa along the anterior and posterior margins and a costa on the outer lateral face. The inner lateral face is concave and smooth or bearing a broad carina, with anterior margin prominently curved inwards (Fig. 5B,C,G). The outer lateral face is divided into a broadly convex area defined by the anterior costa and the outer lateral costa, and a gently concave area between the outer lateral costa and the posterior costa (Fig. 5D,F,H,I). The base is triangular in outline when posterior process is shorter (Fig. 5J), but in more advanced forms, it is strongly laterally compressed (Fig. 5E) as a long, adenticulate blade with a straight basal margin and a straight or weakly arched upper margin. The anterior process is anticusp-like, triangular in outline in the lateral view (Fig. 5I). The outer

Fig. 3. *Acodus triangularis* (Ding in Wang, 1993): (*A–D*) Pa element, AMF126732, AFI993, (*A*) outer lateral view (IY52005), (*B*) basal view (IY64002), (*C*) antero-outer lateral view (IY52007), (*D*) inner lateral view (IY64001); (*E–G*) Pa element, AMF126733, AFI993, (*E*) upper-posterior view (IY52003), (*F*) outer lateral view (IY52004), (*G*) upper view (IY52001); (*H–K*) Pa element, AMF126734, AFI993, (*H*) basal view (IY52009), (*I*) antero-outer lateral view (IY64005), (*J*) inner lateral view (IY52008), (*K*) outer lateral view (IY64003); (*L–O*) Pa element, AMF126735, THH8, (*L*) outer lateral view showing the fine striae in the area posterior to the outer lateral costa (IY64027), (*M*) antero-outer lateral view (IY64026), (*N*) outer lateral view (IY64025), (*O*) inner lateral view (IY59016). (*P*) M element, AMF126736, AFI992, posterior view (IY65034). Scale bars 100 µm unless otherwise indicated.

[*Fig.4 caption continued*] … (*K,L*) M element, AMF126740, AFI993, (*K*) anterior view (IY64009), (*L*) posterior view (IY52017). (*M,N*) Pb element, AMF126741, THH3, (*M*) outer lateral view (IY66032), (*N*) antero-outer lateral view (IY66034). (*O*) Pa element, AMF126742, THH10, outer lateral view (IY66037). (*P–R*) Sa element, AMF126743, AFI993, (*P,Q*) posterolateral views (IY66013, IY66014), (*R*) basal-posterior view (IY66012). (*S–U*) Sa element, AMF126744, AFI997, (*S*) lateral view (IY66010), (*T*) posterior view (IY66009), (*U*) basal view (IY66011). Scale bars 100 µm.

Fig. 4. *Acodus triangularis* (Ding in Wang, 1993): (*A–E*) Pb element, AMF126737, AFI992, (*A*) outer lateral view (IY53026), (*B*) upper view (IY53025), (*C*) inner lateral view (IY65016), (*D*) basal view (IY65017), (*E*) antero-outer lateral view (IY53027); (*F,G*) Pb element, AMF126738, AFI997, (*F*) outer lateral view (IY64010), (*G*) inner lateral view (IY52050); (*H–J*) Pb element, AMF126739, AFI993, (*H*) basal-inner lateral view (IY52011), (*I*) outer lateral view (IY64006), (*J*) inner lateral view (IY52010)… [*continued p. 308*]

Fig. 5. *Acodus triangularis* (Ding in Wang, 1993): (*A*) Sa element, AMF126745, AFI992, upper view (IY66022). (*B–D*) Sb element, AMF126746, AFI992, (*B*) basal-inner lateral view (IY65013), (*C*) inner lateral view (IY65012), (*D*) outer lateral view (IY53036); (*E–H*) Sb element, AMF126747, AFI992, (*E*) posterior view (IY53037), (*F*) antero-outer lateral view (IY65015), (*G*) basal-inner lateral view (IY53038), (*H*) outer lateral view (IY65014); (*I*) Sb element, AMF126748, AFI992, outer lateral view (IY65032); (*J*) Sb element, AMF126749, AFI992, outer lateral view (IY66029). (*K,L*) Sc element, AMF126750, THH10, (*K*) outer lateral view (IY66040), (*L*) inner lateral view (IY66041); (*M*) Sc element AMF126751, AFI992, inner lateral view (IY66027); (*N*) Sc element, AMF126752, THH3, upper view (IY66031); (*O*) Sc element, AMF126753, AFI992, inner lateral view (IY66026). … [*continued p. 311*]

lateral process is also anticusp-like extending basally and outer-laterally with blade-like upper margin curved posteriorly. Basal cavity is moderately deep and triangular in outline and extends as narrow grooves underneath the posterior and anterior processes (Fig. 5B).

The Sc element is asymmetrical, strongly compressed laterally with a robust, proclined to suberect cusp, a posterior process varying from short (Fig. 5K,L) to relatively long (Fig. 5 O), and a short, anticusp-like anterior process (Fig. 5K–O). The cusp is convex lens-like in cross section, slightly bent inward with a sharp costa along its anterior and posterior margins, and with smooth outer and inner lateral faces, or with a weakly developed broad carina on the inner lateral face (Fig. 5 O). The inner lateral face is less convex with anterior margin gently curved inward. Basal cavity is convex lens-like in outline with gently arched basal margin in lateral view (Fig. 5M).

The Sd element is tetra-costate and asymmetrical, with a sharp costa along the anterior and posterior margins, and a sharp costa on each lateral side (Fig. 5P–AA). The outer lateral side is more convex with a broad convex area between the anterior process and the outer lateral process, and a less convex to concave area defined by the outer lateral process and the posterior process (Fig. 5P,U). The inner lateral side is less convex to concave with an inner laterally curved anterior margin (Fig. 5R,T,Y). Costae extend basally to merge with the upper margin of four corresponding short, blade-like processes. Small rudimentary denticles may occur along the upper edge of the posterior process of some specimens (Fig. 5P). However, the broken upper edge in some specimens superficially exhibits a denticulate appearance (Fig. 5U).

Remarks. *Oistodus triangularis* was originally proposed as a form species with the type material from the Honghuayuan Formation of Anhui Province (Ding in Wang, 1993). The two figured specimens are both pastinate with a large, triangular base and a robust cusp which bears a sharp costa along its anterior and posterior margins, and a third costa on the outer lateral face (Ding in Wang 1993, p. 185). The holotype has a reclined cusp and less downwardly extending anterior process (Wang, 1993, pl. 19, fig. 1), whereas the other figured specimen (Wang, 1993, pl. 19, fig. 2), with a suberect cusp and a longer and more downwardly extending anterior process, is identical with the Pa element described herein from Guizhou.

Specimens previously referred to *Triangulodus alatus* Dzik, 1976 from the lower Dawan Formation of South China (An *et al.*, 1985; An, 1987) possibly represent the S elements of *Acodus triangularis*. The type material of *T. alatus*, consisting of large-sized hyaline elements, occurs in late Darriwilian erratic boulders of NW Poland. The holotype (Dzik, 1976, p. 433, fig. 20k) is a scandodiform P element with an adenticulate posterior process and a short adenticulate anticusp-like anterior process. Dzik (1983, 1994) re-assigned this Baltic species to *Eoneoprioniodus*

Mound, 1965, which is likely a senior synonym of *Triangulodus* van Wamel, 1974 (see Clark *et al.*, 1981). *Triangulodus alatus* was also reported from the upper Darriwilian (*serra* Zone) of the Tarim Basin (Zhao *et al.*, 2000), and from the upper Darriwilian (*serra* Zone) of Oklahoma (Bauer, 1987).

Specimens referred to *Acodus deltatus* Lindström, 1955 from the Emanuel Formation of Western Australia (McTavish, 1973) are reassigned herein to *A. longibasis* which differs from *A. deltatus* mainly in having a more extended posterior process. This species from the Canning Basin shows some resemblance to *A. triangularis* from South China, in particular the Pa and S elements. Based mainly on the length of posterior process of the S elements in the Emanuel Formation, McTavish (1973) split this species into several subspecies of *A. deltatus* including *A. deltatus longibasis* McTavish with long posterior process, *A. deltatus deltatus* with a shortest posterior process, and *A. deltatus tortus* McTavish with an inwardly twisted cusp of the S elements. Similar variations are also observed in the species from South China with the posterior process of the S elements varying from short (Fig. 5J,L,K) to relatively long (Fig. 5B–H,M,O).

Prioniodus Pander, 1856

Type species. *Prioniodus elegans* Pander, 1856.

Remarks. The type species of *Oepikodus* Lindström, 1955, *O. smithensis* Lindström, 1955, was originally proposed as a form species based on the oepikodiform elements (Lindström, 1955, pl. 6, figs 1–3). Subsequently, Lindström (1971) considered *Oepikodus* as a junior synonym of *Prioniodus*, 1856, and its type species, *O. smithensis*, along with *Oistodus longiramis* Lindström, 1955 to be parts of the revised multi-element species *Prioniodus evae* Lindström, which was also originally proposed as a form species based on the prioniodiform elements (Lindström, 1955, pl. 6, figs 4–10). Hence Lindström (1971) defined *P. evae* as consisting of a trimembrate apparatus including prioniodiform, oepikodiform and oistodiform elements. However, Bergström & Cooper (1973, pp. 323–324) pointed out that "the apparatus of *P. evae* differs from that of *P. elegans*", the type species of *Prioniodus*, and "no element clearly homologous to the hibbardelliform element" existed in the latter. They further considered *Oepikodus* to be a subgenus of *Prioniodus*. This suggestion was formalized by Serpagli (1974). However, van Wamel (1974) and Lindström (in Ziegler, 1975) restored *Oepikodus* as a separate multi-element genus consisting of a trimembrate apparatus. Bergström (in Clark *et al.*, 1981) and Stouge & Bagnoli (1999) categorized *Oepikodus* and *Prioniodus* as belonging to different families.

Serpagli (1974) and Lindström (in Ziegler, 1975) redesignated the form species *P. evae* Lindström, 1955 as the type species of *Oepikodus*, since the originally

[*Fig. 5 caption continued*] ... (*P–R*) Sd element, AMF126754, AFI997, (*P*) outer lateral view (IY53002), (*Q*) posterior view (IY53001), (*R*) inner lateral view (IY53003); (*S*) Sd element, AMF126755, AFI997, basal-posterior view (IY66006); (*T*) Sd element, AMF126756, AFI997, inner lateral view (IY66001); (*U,V*) Sd element, AMF126757, AFI993, (*U*) outer lateral view (IY66017), (*V*) anterior view (IY66016); (*W–Y*) Sd element, AMF126758, THH3, (*W*) upper view (IY58017), (*X*) outer lateral view (IY58019), (*Y*) inner lateral view (IY58018); (*Z,AA*) Sd element, AMF126759, AFI993, (*Z*) inner lateral view (IY66018), (*AA*) posterior view (IY66020). Scale bars 100 μm.

designated type species *O. smithensis* became a synonym of *Prioniodus evae* (see Lindström in Ziegler, 1975, p. 237). As correctly pointed out by van Wamel (1974, p. 74), the form species *O. smithensis* is not a junior synonym of the form species *P. evae*, and the form species *O. smithensis* must therefore remain as the type species of *Oepikodus*. Although *O. smithensis* has page priority among the three form species erected by Lindström in the same publication for three different genera, they (*O. smithensis* Lindström, 1955, *P. evae* Lindström, 1955, and *Oistodus longiramis* Lindström, 1955) form the apparatus of a multi-element species, which was named as *P. evae* by Lindström (1971). With Lindström (1971) as the first reviser (see Article 24.2.2, ICZN of 1999 edition), *O. evae* (Lindström, 1955) emend. Lindström (1971) is recognized as a valid and proper name of the species with this multi-element apparatus.

Following the definition of *Oepikodus* as trimembrate (van Wamel, 1974) and then quadrimembrate (Bergström in Clark *et al.*, 1981), Stouge & Bagnoli (1988) suggested that *Oepikodus* consisted of a seximembrate apparatus that could be distinguished from *Prioniodus* by lack of the Sa element. Albanesi (in Albanesi *et al.*, 1998) concurred with this concept.

Oepikodus, as most recently revised by Nicoll & Ethington (2004), was defined as consisting of a septimembrate apparatus including pastinate Pa and Pb, makellate M and quadriramate S (Sa, Sb, Sc and Sd) elements. *Prioniodus* consists of a similar septimembrate apparatus that includes a triform alate Sa element, rather than a quadriform alate Sa element as in *Oepikodus*. Therefore, occurrence of the triform alate Sa element in the new species from the Honghuayuan Formation confirms its generic assignment to *Prioniodus*.

Prioniodus honghuayuanensis n.sp.

Figs 6–8

Baltoniodus communis (Ethington & Clark).–An, 1981: pl. 4, figs 20–23, 25, 27–29, ?24.
Baltoniodus communis (Ethington & Clark).–An & Ding, 1985: p. 8, 9, pl. 1, figs 1–5, 8, ?9.
Baltoniodus? communis (Ethington & Clark).–An, 1987: p. 125, 126, pl. 19, figs 1–11.
Baltoniodus communis (Ethington & Clark).–Ding *et al.* in Wang, 1993: p. 161, pl. 23, figs 1–12.

Etymology. After Honghuayuan Village, where the type section of the Honghuayuan Formation is exposed on the hill slope located to the southeast of the village.

Material. 435 specimens, including holotype (AMF126760, from sample AFI993) and 19 paratypes (AMF126761–AMF126779), from eight samples (Table 1).

Diagnosis. Species of *Prioniodus* consisting of a septimembrate apparatus, including pastinate Pa and Pb elements with denticulate posterior and outer lateral process and adenticulate (or with rudimentary denticles) anterior process which curves distally outer laterally; makellate M element with low but long inner lateral and outer lateral processes; alate triform Sa, triform asymmetrical (modified quadriramate) Sb, bipennate (modified quadriramate) Sc, and quadriramate Sd elements; all S elements with a proclined cusp, a long denticulate posterior process, and adenticulate (or rudimentarily denticulated) lateral and anterior processes.

Description. All elements are small, mostly albid, thin and fragile; the long denticulate posterior process of the P and S elements is broken in most specimens. Pastinate P elements bear a robust, laterally compressed cusp, with a sharp costa along its anterior and posterior margins, and with a prominent costa on the outer lateral face (Fig. 6). Surface of the cusp is ornamented with fine striation, which are best developed posterior to the outer lateral process on the outer lateral face (Fig. 6P). The posterior process is laterally compressed as a long blade with closely spaced, basally confluent, and more or less equal-sized denticles along its upper margin. The anticusp-like anterior process extends downward with its anterior margin strongly curved outwards and occasionally with confluent and small rudimentary denticles along its edge (Fig. 6F). The outer lateral costa extends downward to merge with the upper margin of the outer lateral process, which is long and bearing small, closely spaced denticles (Fig. 6B,M,N). The outer lateral process that extends downward laterally outward with an angle slightly >90° (Pb, Fig. 6O) or nearly normal (Pa, Fig. 6D,G) to the posterior process is often broken in the present collection. Basal cavity is triangular in shape extending underneath the three processes as narrow grooves (Fig. 6E,F,Q,O). The Pa element has a suberect cusp with anterior process curved laterally outward and with the outer lateral process extending nearly normal to the posterior process in the upper view (Fig. 6D,G). The Pb element resembles the Pa, but with a reclined cusp and an inner-laterally bent posterior process (Fig. 6K–S).

The M element has a robust and strongly outer laterally reclined cusp, and adenticulate, low and long outer lateral and inner lateral processes (Fig. 7A–D). The cusp is sightly curved posteriorly and anteroposteriorly compressed, with a weak costa on the broad anterior face, and a broad carina on the posterior face. The outer lateral process has gently arched upper and basal margins, while the inner lateral process has nearly straight upper and basal margins. Basal cavity is relatively narrow, without prominent basal buttress (Fig. 7B,C).

The Sa element is triform and symmetrical with a proclined cusp, a long denticulate posterior process, and an anticusp-like lateral process on each side (Fig. 7E–S). The cusp is triangular in cross section with a broad anterior face (Fig. 7M, O), a sharp blade-like costa along the posterior margin, and a sharp costa along the anterolateral corner of each side (Fig. 7J, S). The posterior process is long, straight and strongly compressed laterally bearing small, closely spaced denticles (Fig. 7P–R). The blade-like costa on each side is gently curved posteriorly and extends basally to merge with the upper margin of the lateral process, which often bears rudimentary denticles (Fig. 7J,R). The basal cavity is an isosceles triangle in outline with moderate depth (Fig. 7E,J).

[*Fig.6 caption continued*] ... AMF126762, (*K*) inner lateral view (IY63005), (*L*) outer lateral view (IY63006), (*M*) upper view (IY63007), (*N*) anterior view (IY63004), (*O*) basal view (IY50035), (*P*) close up of outer lateral view, showing the fine striae in the area posterior to the outer lateral costa (IY50036); (*Q–S*) Pb element, paratype, AMF126763, (*Q*) basal view (IY50027), (*R*) inner lateral view (IY63011), (*S*) outer lateral view (IY50028). All from sample AFI993; scale bars 100 μm unless otherwise indicated.

Fig. 6. *Prioniodus honghuayuanensis* n.sp.: (*A–E*) Pa element, paratype, AMF126761, (*A*) antero-outer lateral view (IY50030), (*B*) basal-outer lateral view (IY50032), (*C*) outer lateral view (IY50033), (*D*) upper view (IY63010), (*E*) inner lateral view (IY63009); (*F–J*) Pa element, **holotype**, AMF126760, (*F*) basal view (IY50039), (*G*) upper view (IY63003), (*H*) outer lateral view (IY50038), (*I*) inner lateral view (IY63001), (*J*) postero-outer lateral view (IY50040). (*K–P*) Pb element, paratype, … [*continued p. 312*]
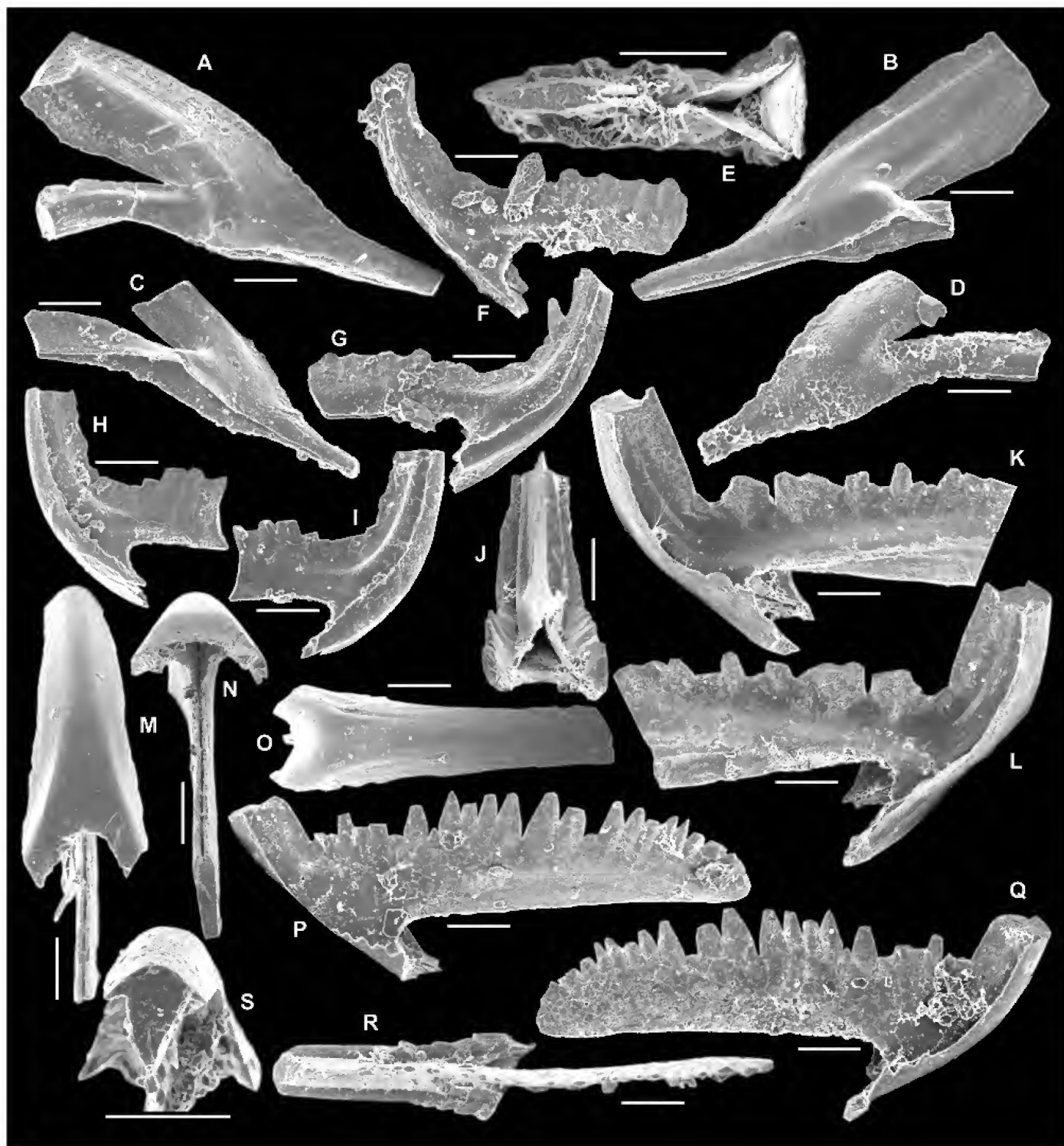
Fig. 7. *Prioniodus honghuayuanensis* n.sp.: (*A,B*) M element, paratype, AMF126764, AFI993, (*A*) anterior view (IY51011), (*B*) posterior view (IY63016); (*C,D*) M element, paratype, AMF126765, AFI993, (*C*) basal-posterior view (IY51015), (*D*) anterior view (IY63018). (*E–G*) Sa element, paratype, AMF126766, AFI993, (*E*) basal view (IY51003), (*F,G*) lateral views (IY51002, IY63012); (*H,I*) Sa element, paratype, AMF126767, AFI993, lateral views (IY63013, IY51005); (*J–N*) Sa element, paratype, AMF126768, AFI993, (*J*) basal-posterior view (IY51009); (*K,L*) lateral views (IY51010, IY51008), (*M*) anterior view (IY63014); (*N*) basal view (IY63015); (*O*) Sa element paratype, AMF126769, AFI993, anterior view (IY51006); (*P–S*) Sa element, paratype, AMF126770, AFI997, (*P,Q*) lateral views (IY51046, IY51048), (*R*) upper view (IY51045), (*S*) upper view showing the cross section of the cusp (IY63026). Scale bars 100 μm.

[*Fig.8 caption continued*] … AMF126774, AFI993, (*I*) inner lateral view (IY63021), (*J*) outer lateral view (IY51026), (*K*) basal view (IY51025); (*L–P*) Sc element, paratype, AMF126775, AFI997, (*L*) basal view (IY51050), (*M*) inner lateral view (IY51049), (*N*) outer lateral view (IY63028), (*O*) upper view (IY51051), (*P*) close up of the upper view showing the cross section of the cusp (IY51052); (*Q*) Sc element, paratype, AMF126776, AFI993, outer lateral view (IY51022). (*R–T*) Sd element, paratype, AMF126777, AFI993, (*R*) outer lateral view (IY63025), (*S*) inner lateral view (IY51037), (*T*) posterior view (IY51036); (*U–X*) Sd element, paratype, AMF126778, AFI993, (*U*) inner lateral view (IY63023), (*V*) outer lateral view (IY51033), (*W*) posterior view (IY51035), (*X*) postero-outer lateral view (IY51034); (*Y–AA*) Sd element, paratype, AMF126779, AFI993, (*Y*) postero-inner lateral view (IY51032), (*Z*) outer lateral view (IY63022), (*AA*) inner lateral view (IY51031). Scale bars 100 μm unless otherwise indicated.

Fig. 8. *Prioniodus honghuayuanensis* n.sp.: (*A–C*) Sb element, paratype, AMF126771, AFI993, (*A*) inner lateral view (IY51013), (*B*) basal-inner lateral view (IY51014), (*C*) outer lateral view (IY63017); (*D–F*) Sb element, paratype, AMF126772, AFI993, (*D*) basal view (IY51020), (*E*) inner lateral view (IY51021), (*F*) outer lateral view (IY63020); (*G,H*) Sb element, paratype, AMF126773, AFI993, (*G*) inner lateral view (IY63019), (*H*) outer lateral view (IY51017). (*I–K*) Sc element, paratype, … [*continued p. 314*]

The Sb element is strongly asymmetrical with a proclined and laterally compressed cusp, which bears a sharp costa along the anterior and posterior margins, and the third costa on the outer lateral face (Fig. 8A–H). The anterior costa is inner laterally curved and extends basally to merge with the upper margin of the anticusp-like downwardly extending adenticulate anterior process (Fig. 8A,E,G). The long posterior process is laterally compressed as a high blade bearing small, closely spaced denticles of similar sizes along its upper margin. The costa on the outer lateral face extends downward to merge with the upper margin of the downward extended, shorter, adenticulate outer lateral process. The inner lateral face is less convex, and bears a broad carina (Fig. 8A,B,E,G).

The Sc element is bipennate with a broad carina on each lateral face (more prominent on the inner lateral face), a short, adenticulate anterior process, and a long, laterally compressed, denticulate posterior process (Fig. 8I–Q). The cusp is proclined (Fig. 8Q), and laterally compressed with a sharp blade-like costa along its posterior and anterior margins (Fig. 8 O,P), which extends basally to merge respectively into the upper margin of the anterior process and the posterior process (Fig. 8I,M). The anterior process is anticusp-like, and curved laterally inward (Fig. 8I,M). The posterior process bears small, closely spaced denticles of more or less similar sizes (Fig. 8Q). The basal cavity is biconvex in outline, and extends as a narrow groove underneath the anterior and posterior processes (Fig. 8K,L).

The Sd element is quadriramate and asymmetrical, with an anterior process, a posterior process, and a lateral process on each side (Fig. 8R–AA). The cusp is proclined with a sharp blade-like costa along the anterior and posterior margins and on each lateral side (Fig. 8T,W,Y,AA). Anterior costa is inner laterally curved (Fig. 8S,U,Y), and extends basally to merge into the upper margin of the anticusp-like anterior process which is adenticulate or has small, fused rudimentary denticles along its distal edge (Fig. 8Y). As in the other S elements, the posterior process is long, laterally compressed, and blade-like bearing small, closely spaced denticles of similar sizes. The area defined by the anterior costa and the outer lateral costa is more broadly convex (Fig. 8R,V). The lateral costa on each side extends basally to merge respectively with the upper margin of the short inner and outer lateral processes. Both lateral processes extend downward and often bear small rudimentary denticles along their distal edges (Fig. 8S–U,W,X,AA).

Remarks. Although P elements of the new species show some resemblance to those of *Oepikodus communis* (Ethington & Clark, 1964), they differ in having denticulate outer lateral processes, and an anterior process which bears rudimentary denticles along its distal edge. The anterior process of *P. honghuayuanensis* extends strongly downward as an anticusp, and curves strongly outer laterally (Fig. 6F,J,Q). The Pb element of *O. pincallyensis* Zhen in Zhen *at al*., 2003 has denticulate anterior, outer lateral and posterior processes, but the anterior process of the Pa element is adenticulate. However, the P elements of *O. pincallyensis* are distinctively curved inner laterally (Zhen *et al*., 2003, fig. 19E,K) rather than outer laterally as in *P. honghuayuanensis* (Fig. 6D,M). Furthermore, the S elements of the new species can be easily distinguished from those of *O. communis, O. pincallyensis* and other species of *Oepikodus*. The Sa element is triform and alate with a

wide anterior face (Fig. 7M,O) and the open basal cavity is an isosceles triangle in outline (Fig. 7E,J). The Sb element can be described as asymmetrical triform (or modified quadriramate of some authors) with a strongly developed costa on the outer lateral face, which extends basally as a short but prominent adenticulate outer lateral process. The quadriramate Sd element of *P. honghuayuanensis* differs from that of *O. communis* in having more strongly developed costae, in having more prominent lateral processes, and in tending to develop rudimentary denticles along the distal edge of the anterior and lateral processes (Fig. 8S–U,W–Y,AA).

Oepikodus communis was originally proposed as a form species based on pastinate elements (Ethington & Clark, 1964). The type material shows a long denticulate posterior process with small, closely spaced denticles, and adenticulate anterior and outer lateral processes (Ethington & Clark, 1964, pl. 114, figs 6, 14, text-fig. 2F). Subsequently, Ethington & Clark (1982) revised *O. communis* in multielement taxonomy by accommodating another three form species which were reported in association with the type material of the form species *Gothodus communis* Ethington & Clark, 1964 in the El Paso Formation of Texas. These include *Oepikodus equidentatus* Ethington & Clark, 1964 with typical quadriramate ramiform elements (including symmetrical and asymmetrical), *Subcordylodus* sp. aff. *S. delicatus* (Branson & Mehl) with modified quadriramate ramiform elements (bearing only a weakly developed broad carina on the lateral faces), and *Oistodus longiramis* Lindström, 1955 comprising a makellate element with a long and slender outer lateral process. Ethington & Clark (1982) recognized the symmetry transition among the ramiform elements of four morphotypes, symmetrical quadriramate element, asymmetrical quadriramate element, modified quadriramate element with costa on one side, and modified quadriramate element without lateral costa. Therefore, they indicated a seximembrate apparatus for the species, although no formal notation was made. Repetski (1982) also suggested a seximembrate apparatus for *O. communis*, including prioniodiform, falodiform and four types of ramiform (belodiform, tetraprioniodiform, hibbardelliform, and cordylodiform) elements. Nicoll & Ethington (2004) defined *Oepikodus* as consisting of a septimembrate apparatus of a geniculate makellate M, four types of quadriramate or modified quadriramate S, and two types of pastinate P elements.

We also interpret *Oepikodus communis* as consisting of a septimembrate apparatus. The pastinate Pa element is represented by the holotype (Ethington & Clark, 1964, pl. 114, fig. 6) with a suberect cusp, and the pastinate Pb element by the other figured specimen of *G. communis* (Ethington & Clark, 1964, pl. 114, fig. 14) with a reclined cusp. The Sa and Sd elements are represented by the form species *O. equidentatus* Ethington & Clark (1964, pl. 113, figs 6, 8, 10, 11, 14). The Sa element is symmetrical or nearly symmetrical with a straight anterior margin, while the Sd element is markedly asymmetrical with a curved anterior margin (e. g. Ethington & Clark, 1964, pl. 113, fig. 14). The Sc element of *O. communis* is represented by those described and illustrated by Ethington & Clark (1964, p. 701, pl. 115, figs 1, 5, 7, 10) as *Subcordylodus* sp. aff. *S. delicatus* (Branson & Mehl, 1933). The makellate M element of *O. communis* is represented by those described and illustrated by Ethington & Clark (1964, p. 693, pl. 114, figs 2, 7) as *Oistodus longiramis* Lindström, 1955. The

Fig. 9. *A–P, Prioniodus* sp.: (*A,B*) Pa element, AMF126781, 100 feet above base of Kanosh Fm., Utah, (*A*) inner lateral view (IY66053), (*B*) upper view (IY66054). (*C–E*) Pb element, AMF126782, 83 feet above base of Kanosh Fm., Utah, (*C*) basal view (IY66051), (*D*) antero-outer lateral view (IY66052), (*E*) outer lateral view (IY66050). (*F,G*) Sd element, AMF126783, 78J-23, 150 feet above base of Juab Fm., Utah, (*F*) basal view (IY66061), (*G*) inner lateral view (IY66062). (*H*) Sa element, AMF126784, 78J-23, 150 feet above base of Juab Fm., Utah, lateral view (IY66060); (*I–K*) Sa element, AMF126785, 78J-16, top ledge of Wah Wah Fm., Utah, (*I*) antero-upper view (IY66042), (*J,K*) lateral views (IY66045, IY66043). (*L*) M element, AMF126786, 78J-16, top ledge of Wah Wah Fm., Utah, posterior view (IY66049). (*M,N*) Sb element, AMF126787, 100 feet above base of Kanosh Fm., Utah, (*M*) outer lateral view (IY66065), (*N*) inner lateral view (IY66066). (*O*) Sc element, AMF126788, 57 feet above base of Kanosh Fm., Utah, inner lateral view (IY66063); (*P*) Sc element, AMF126789, 78J-16, top ledge of Wah Wah Fm., Utah, outer lateral view (IY66047). (*Q–U*) *Prioniodus ?honghuayuanensis* n.sp.: ?Pc element, AMF126780, AFI999, (*Q*) inner lateral view (IY53012), (*R*) outer lateral view (IY65010), (*S*) upper view (IY53010), (*T*) outer-basal view (IY65008), (*U*) close up of outer lateral view showing fine striae in the area posterior to outer lateral costa (IY65009); Scale bars 100 μm unless otherwise indicated.

asymmetrical Sb element is a modified quadriramate element with a more prominent costa on the outer lateral face (Albanesi in Albanesi *et al.*, 1998, pl. 6, fig. 22).

Oepikodus intermedius Serpagli, 1974, from the San Juan Formation of the Argentine Precordillera, is regarded herein as conspecific with *O. communis*; it was originally described as consisting of a trimembrate apparatus (prioniodiform, oistodiform and oepikodiform). In more recent revisions of the San Juan faunas, both Lehnert (1995) and Albanesi (in Albanesi *et al.*, 1998) did not recognize symmetrical Sa elements in any of the three species (*O. communis, O. intermedius* and *O. evae*) they ascribed to *Oepikodus*.

Lindström (in Ziegler, 1975) considered the form species *Gothodus microdentatus* van Wamel, 1974 from the Glauconitic Limestone of Sweden as part of *O. communis* species apparatus. However, not only have the well-recognized elements of *O. communis* apparatus not been recorded in association with this form species in Sweden, but also the triform, asymmetrical *G. microdentatus* shows rather different morphology in comparison with the ramiform elements of *O. communis* from North America. Based on the original description and illustrations (van Wamel, 1974), the form species *G. microdentatus* more likely represents the Sb element of a multi-element species of *Prioniodus* rather than of *Oepikodus*.

Oepikodus communis is widely distributed in North America (Ethington & Clark, 1964, 1982; Repetski, 1982; Stouge, 1982; Stouge & Bagnoli, 1988; Johnston & Barnes, 2000), Argentine Precordillera (Serpagli, 1974; Lehnert, 1995; Albanesi in Albanesi *et al.*, 1998), Australia (McTavish, 1973; Zhen *et al.*, 2003), and Greenland (Smith, 1991). However, as the result of inclusion of a triform alate Sa element in this species apparatus by An and other Chinese authors (An, 1981, 1987; An *et al.*, 1985; Ding *et al.* in Wang, 1993), the occurrence of *O. communis* in South China needs to be re-examined.

Specimens referable to the Pa, Pb, Sa, Sb, Sc and Sd elements of the present new species were first recorded from the top of the "Honghuayuan Formation" of Hexian, Anhui Province as *Baltoniodus communis* (An, 1981, 1987; An & Ding, 1985). An (1987) noted the abundant occurrence (up to 80% in some samples) of this species at the top of the Honghuayuan Formation in Guizhou, Hunan, Hubei and Anhui provinces, and correlated this interval at the top of the Honghuayuan Formation with the *communis* Zone of North America and with the *elegans* Zone of Baltoscandia. Although he recognized the occurrence of triform alate element as part of this species apparatus, An (1981, 1987) included this material into his rather broad interpretation of *O. communis* (Ethington & Clark, 1964). However, as the triform Sa element occurring in the material from South China had not been recognized at the type locality of *O. communis* in North America, An (1981, 1987) doubtfully assigned *O. communis* to *Baltoniodus* rather than *Oepikodus*.

Specimens previously referred to as aff. *Oepikodus? minutus* (McTavish, 1973) from the upper Wah Wah Formation, and the overlying Juab and Kanosh formations in the Ibex area of Utah (Ethington & Clark, 1982) somewhat resemble *P. honghuayuanensis*. Prof. R. Ethington kindly provided sixty specimens of this Utah species from nine samples for comparative study. Stratigraphically the Ibex species (designated herein as *Prioniodus* sp.; Fig. 9A–P) occurs at a slightly younger level

(basal Whiterockian, *victoriae* graptolite Zone) than the new species from South China. Similarities include the prioniodiform Pb element of *Prioniodus* sp. (Fig. 9C–E) that bears a denticulate outer lateral process with anterior margin curved outer laterally towards outer lateral process, and the ramiform S series that includes alate triform Sa (Fig. 9H–K), asymmetrical triform Sb (Fig. 9M,N), bipennate Sc (Fig. 9 O,P), and quadriramate Sd (Fig. 9F,G) elements. However, the associated M element of the Ibex species shows a much shorter inner lateral process, and the Pa element has an adenticulate and weakly developed outer lateral process and a more or less straight anterior process. Bagnoli & Stouge (1997) referred this Ibex species to *Gothodus* Lindström, 1955. Based on the recent revision of *Gothodus* (Bagnoli & Stouge, 1997, and Stouge & Bagnoli, 1999), it has prioniodiform P elements comparable with those of *Oepikodus* and *Prioniodus*, but the S elements are more related to *Phragmodus* Branson & Mehl, 1933. However, most other conodont authors regard it as a junior synonym of *Prioniodus* (e.g., Bergström in Clark *et al.*, 1981) or *Baltoniodus* (Bagnoli *et al.*, 1988).

The new species from the Honghuayuan Formation shows some resemblance to *P. elegans* documented from Sweden by van Wamel (1974, p. 87–89, pl. 6, figs 1–6) and by Löfgren (1978, pl. 9, figs 1–6), but Swedish material of *P. elegans* has the M element with a denticulate inner lateral process and the P and S elements with better developed denticles on the lateral and anterior processes. *Prioniodus elegans* described from the Leningrad region of Russia and Tulubäcken of Sweden by Bergström (1988, pl. 3, figs 33–38), and from western Newfoundland by Stouge & Bagnoli (1988, pl. 13, figs 1–9) and Johnston & Barnes (2000, pl. 3, figs 1, 5–7, 11, pl. 16, fig. 17) has an even stronger development of denticulation with P elements bearing a longer, fully denticulated anterior process, and with S elements displaying well-denticulated anterior and lateral processes. The multi-element species definition of *P. elegans* followed herein conforms to the concept of Bergström (1971, 1981 in Clark *et al.*, 1981), van Wamel (1974), and Stouge & Bagnoli (1988). Stouge & Bagnoli (1988, p. 134) noted that this species displayed a large degree of morphological variation and might be polymorphic. Some of the material of *P. elegans* documented by Bergström (1988, pl. 3, figs 33–37) came from Popowka to the south of the Leningrad region, from where Pander's original type material (now lost) was collected. In comparison with those figured specimens of *P. elegans*, the P elements of *P. honghuayuanensis* display a more prominent cusp and smaller and less developed anterior and outer lateral processes (Fig. 6H,L), the P and S elements show less development of denticles on the anterior and lateral processes (Figs 6–8), and the M element lacks denticles on the inner lateral process (Fig. 7A–D). Also, the anterior process of the P elements in *P. elegans* is distinctively curved inner laterally (Bergström, 1988, pl. 3, fig. 33) rather than outer laterally (Fig. 6D,F,G) as in *P. honghuayuanensis*. In South China, *P. elegans* has only been recorded from the Jinshan Formation (biostratigraphically coeval with the Honghuayuan Formation) in Zhejiang Province of southeast China (An, 1987). It was also recorded from sub-surface core samples of the Tarim Basin, northwest China (Zhao *et al.*, 2000).

One specimen from the very top of the Honghuayuan Formation at the Honghuayuan Section (AFI999, Fig. 2) is

similar to the Pb element of *P. honghuayuanensis*, but is stellate in outline with an additional sharp, blade-like costa on the inner side of the cusp, which extends basally into a short process with a few small rudimentary denticles. It is tentatively referred to herein as a Pc element of *P. honghuayuanensis* (Fig. 9Q–U).

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Authors submitting hardcopy—option (*b*) above—should retain **original artwork** until it is called for. Previously published illustrations will generally not be accepted. Artwork may be submitted either as **digital images** or as hard copy. The author and figure number must be clearly marked on each piece of artwork or in the name of each file. Extra costs resulting from **colour** production are charged to the author. All artwork must (*a*) be rectangular or square and scalable to a width of 83 mm (one text column) or 172 mm (both text columns) and any depth up to 229 mm (the number of lines in a caption limits depth); (*b*) have **lettering** similar to 14 point, upper case, normal, Helvetica, in final print; (*c*) have no unnecessary white or black space; and (*d*) have vertical or horizontal **scale bars**, with the lengths given in the caption and with the thickness of an upper case 14 point letter "i".

Hard copy artwork submissions must meet the following requirements: (*a*) they must be no larger than A3; (*b*) the dimension of artwork should not be less than the desired final size; (*c*) **halftones** and **line-drawings** must be mounted separately; (*d*) lettering, scales and edges—especially of halftone artwork—must be sharp and straight (images or maps should not be enclosed within a box); (*e*) photographic **negatives** can be used in production, but positive images with labels are, of course, required by referees.

Halftone, colour or black and white line images may be submitted electronically; all such images must be presented as TIFF, or as multilayered PSD files suitable for *Adobe Photoshop* version 5.0 or later. Halftone and colour images must be at a minimum **resolution** of 300 dpi at final size (2040 pixels = width of page) and all labelling must be sharp (with *anti-aliased* active). Black and white line images (bitmaps) must be at a minimum resolution of 1200 dpi at final size (8160 pixels = width of page).

When reference is made to **figures** in the present work use Fig. or Figs., when in another work use fig. or figs.; the same rule applies to tables. Figures should be numbered and referred to in numerical order in the text.

Authors should refer to recent issues of the *Records of the Australian Museum* to determine the correct format for listing **references** and to *The Chicago Manual of Style* to resolve other matters of style.

Certain **anthropological manuscripts** (both text and images) may deal with culturally sensitive material. Responsibility rests with authors to ensure that approvals from the appropriate person or persons have been obtained prior to submission of the manuscript.

Stratigraphic practice should follow the *International Stratigraphic Guide* (second edition) and *Field Geologist's Guide to Lithostratigraphic Nomenclature in Australia*.

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