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Porcellidiidae of Australia (Harpacticoida, Copepoda). III. Synopsis of Genera and Species

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Abstract. Three new species belonging to the Porcellidiidae are described. A species from NSW possessing massive honeycomb-like dorsal growths of cuticle, and other features not found elsewhere in the family, has been placed in a new genus, *Cereudorsum verrucosum* gen. *et* sp. nov. A second species from Queensland, characterized by unusual features of the male antennule, has been placed in a new genus, as *Geddesia quadrata* gen. *et* sp. nov. *Porcellidium trisetosum* Geddes, 1968 does not fit the diagnosis for *Porcellidium* and is transferred to *Geddesia* gen. nov., as *G. trisetosa* (Geddes, 1968) comb. nov. A third species from the Cocos Keeling Islands is unique in having only one seta on the maxillule endopod. It has been referred to a new genus, as *Clunia cocosensis* gen. et sp. nov. This brings the total number of genera described from eastern coast of Australia to 16.

A key to the genera, a list of the apomorphic or unique characters of each genus and a check list of the identifiable species of Porcellidiidae is given. The geographical distribution of species along the east coast of Australia is outlined.

Keywords: Porcellidiidae, *Cereudorsum, Clunia, Geddesia, Porcellidium.*

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It is now recognized that the family Porcellidiidae has more than one genus, although there is some disagreement as to their number. Bodin (1997) lists eight but Wells (2007) only recognizes six and considers *Acutiramus, Kensakia, Kioloaria, Murramia* and *Mucrorostrum* synonyms for *Porcellidium* on the grounds that they were not defined according to the Hennigian system. The real problem, however, was the lack of agreement between authors over the concept of *Porcellidium*. Our knowledge of these characters is based on Brady's (1880) incomplete and inaccurate description of his *Porcellidium viride*. However, Brady does show one unique species specific feature on the male antennule that allows the species to be identified with certainty. This fact has been used to redescribe the male *Porcellidium viride* in detail and give a definitive diagnosis for the genus (Harris, 2014a). The new diagnosis highlights the fact that more than half of the species formerly placed in *Porcellidium* no longer belong to that genus and must be moved elsewhere. The five genera listed above each possess apomorphic characters, not found on the type species *P. viride*, which exclude them from the genus *Porcellidium*. By 2002 ten genera had been described and prior to this paper another three had been added (Harris, 2014a,b). The three new species described here present a similar problem: they possess characters considered apomorphic which exclude them from all previously described genera.

Based on over 60 species for which reliable data on the male antennule are now available, a reassessment of all the proposed genera can be made to determine their validity. Walker-Smith (2001) pointed out that the genera proposed by Harris & Robertson (1994), Harris (1994) and Harris & Iwasaki (1996) were defined on a collection of characters

and not autapomorphies. To overcome this problem, type material has been re-examined for each genus to assess whether the diagnostic characters chosen can be considered autapomorphic or not. This is relatively simple for genera with several species that possess the same character set as the type species, but not for genera based on a single species. The three new species described here will illustrate this problem. They do not fit the diagnosis of any existing genus, but display unique features that suggest each should be placed in a separate genus.

A revised list of the apomorphic and autapomorphic characters for each of the genera is given to bring their definition into line with Hennigian principles (Table 1). This enables the 71 species of Porcellidiidae recognized in this study to be placed in the appropriate genus. The genus to which a species excluded from Porcellidium has been placed is shown in a check list (Table 2).

The family is well represented on the eastern coast of Australia where 32 species have been described. Their distribution along the coast is discussed.

Methods and terminology

Methods and terminology follow Harris & Robertson (1994) and Harris (2014a,b). Measurements of caudal ramus and genital double-somite are taken from dissections, laid flat and the male antennule fully extended. The following method was used to extend the antennule. Seaweed was washed in a 50/50 mixture of soda water saturated with CO_2 (from soda siphon or bottled soda water) and fresh water. This appears to anaesthetize the copepods which were then fixed in 5% formalin with their antennules fully extended. Drawings and measurements were made from calibrated digital photographs of paratype specimens mounted in 50% glycerol or dissections mounted in polyvinyl lactophenol. Two measurements of length are given, L_{max} from rostrum to posterior extremity of caudal furca and L_{urs} from rostrum to posterior extremity of the genital double-somite. Scanning electron micrographs (Plates 1 and 2, pp. 172–173) were taken on an Hitachi S225 ON SEM from gold coated, formaldehyde fixed material. The abbreviation AM for Australian Museum, Sydney and NHM for the Natural History Museum, London are used.

No information is available for the manner in which the three specimens from Cocos Keeling Islands were obtained or their exact location.

Systematics

Family Porcellidiidae Boeck, 1865

Genus *Cereudorsum* gen. nov.

Type species. *Cereudorsum verrucosum* sp. nov.

Diagnosis. Dorsal organs present (trough-like depressions in cuticle), surrounded by massive honeycomb-like cuticle (Figs 1A, 4F); male antennule unique, no denticle on segment 3, segment 4 with group of four or five swollen finger-like structures in place of typical cuticular denticles; maxilliped coxal lobes wide apart; no ridge plates on labrum; male and female caudal ramus rectangular, T1 small pinnate, deeply recessed, setae T2, T3 and T4 large pinnate, equally spaced (not pinnately clavate); maxillule with six setae on endopod; male P5 trapezoid, no reduction in number of terminal setae; spermatophore elongate, ephemeral on female.

Species composition. Only the type species is known, *Cereudorsum verrucosum* sp. nov. Recorded from Sydney, NSW, Australia.

Etymology. *Cereudorsum*, (L. *cereus* = waxen, honeycomb + *dorsum* = the back).

Remarks. Dorsal organs surrounded by massive honeycomb-like growth of cuticle are not known elsewhere in the Porcellidiidae; their presence is considered an autapomorphic character that defines the genus.

Superficially, the large pinnate terminal setae (T2–T4) on the caudal rami resemble the pinnately clavate setae of *Clavigofera* but in the latter genus the pinnae arise from a flattened expansion of the seta shaft, not the shaft itself (Fig. 12R), and T1 is the same size and shape as T2–T4.

The maxillipeds of *Cereudorsum* resemble those of *Dilatatiocauda*, which do not meet in the midline or possess a fimbriate process, but the basis is elongated typical of other Porcellidiidae.

Cereudorsum verrucosum sp. nov.

Figs 1–5; Plates 1, 2

Type material. HOLOTYPE adult male, length 0.73 mm, P81216; ALLOTYPE adult female, length 0.92 mm, P81217; PARATYPE specimens 10 ♀♀, 6 ♂♂, P81218, deposited at AM, Sydney. Additional paratypes deposited at NHM, London. All collected from rotting *Ecklonia radiata* near entrance to Gunnamatta Bay, Port Hacking, Sydney, New South Wales (34°05'S 151°08'E), V. A. Harris, 1977.

Diagnosis. Female with blocks of microtubules near edge on anterior half of cephalosome, microtubules absent from male cephalosome; both male and female have two dorsal organs with honeycomb-like cuticle on cephalosome and one each on metasome segment 3 and genital double-somite; numerous dorsal sensilla (> 100) on cephalosome, metasome and genital double-somite; female caudal rami with two longitudinal ridges; internal seta absent from segment 1 of male and female P4 endopod; first (lateral) seta on male P5 with five strong ventral setules, each terminal seta with row of three setules at its base.

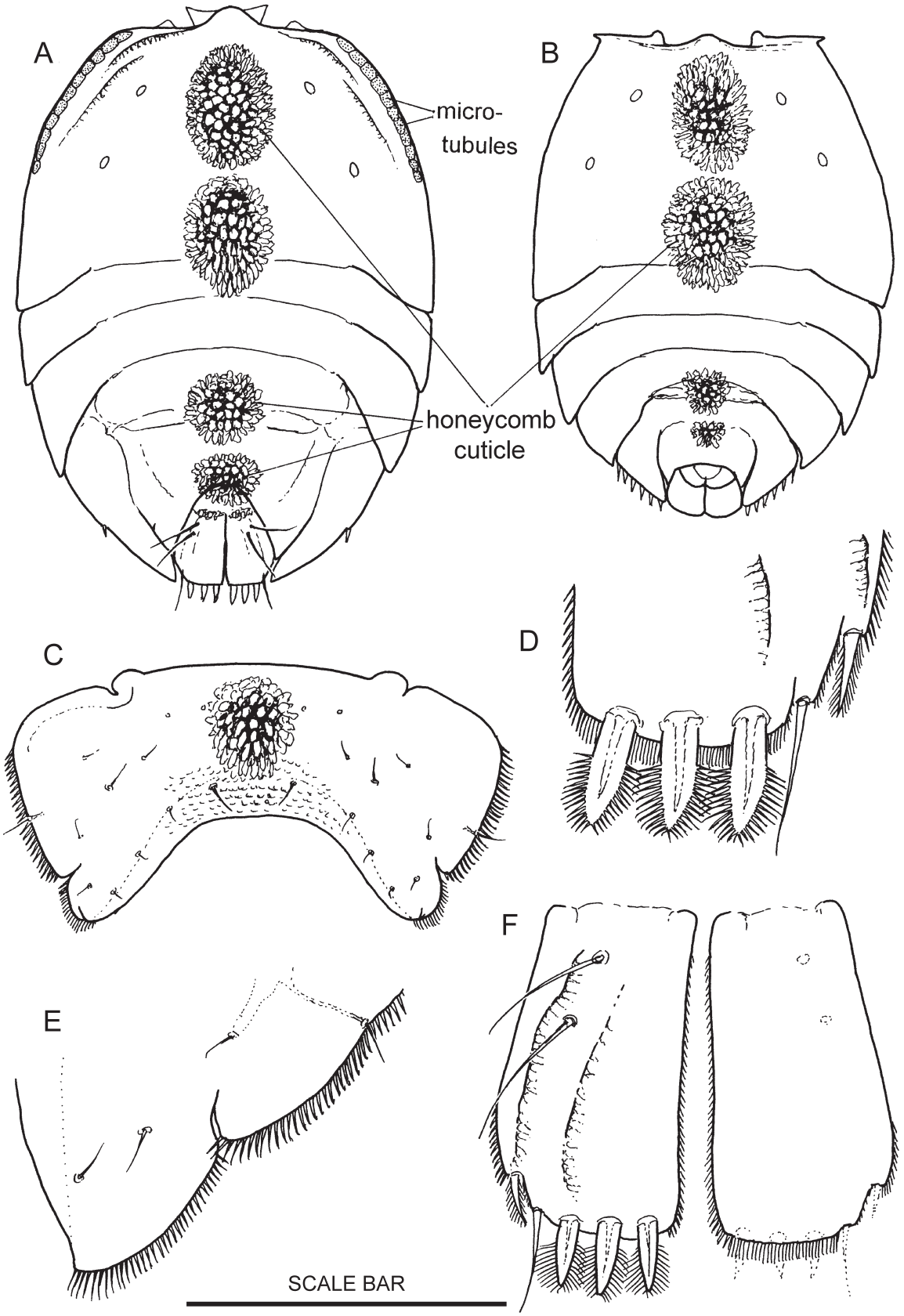

Figure 1. *Cereudorsum verrucosum* sp. nov. Female: *(A)* adult; *(C, E)* genital double-somite (*E* detail of posterior lobe); *(D, F)* caudal rami (*D* detail of terminal setae). Male: *(B)* adult. Scale bar: A, B = 0.5 mm. C = 0.03 mm. D = 0.08 mm. F = 0.14 mm.

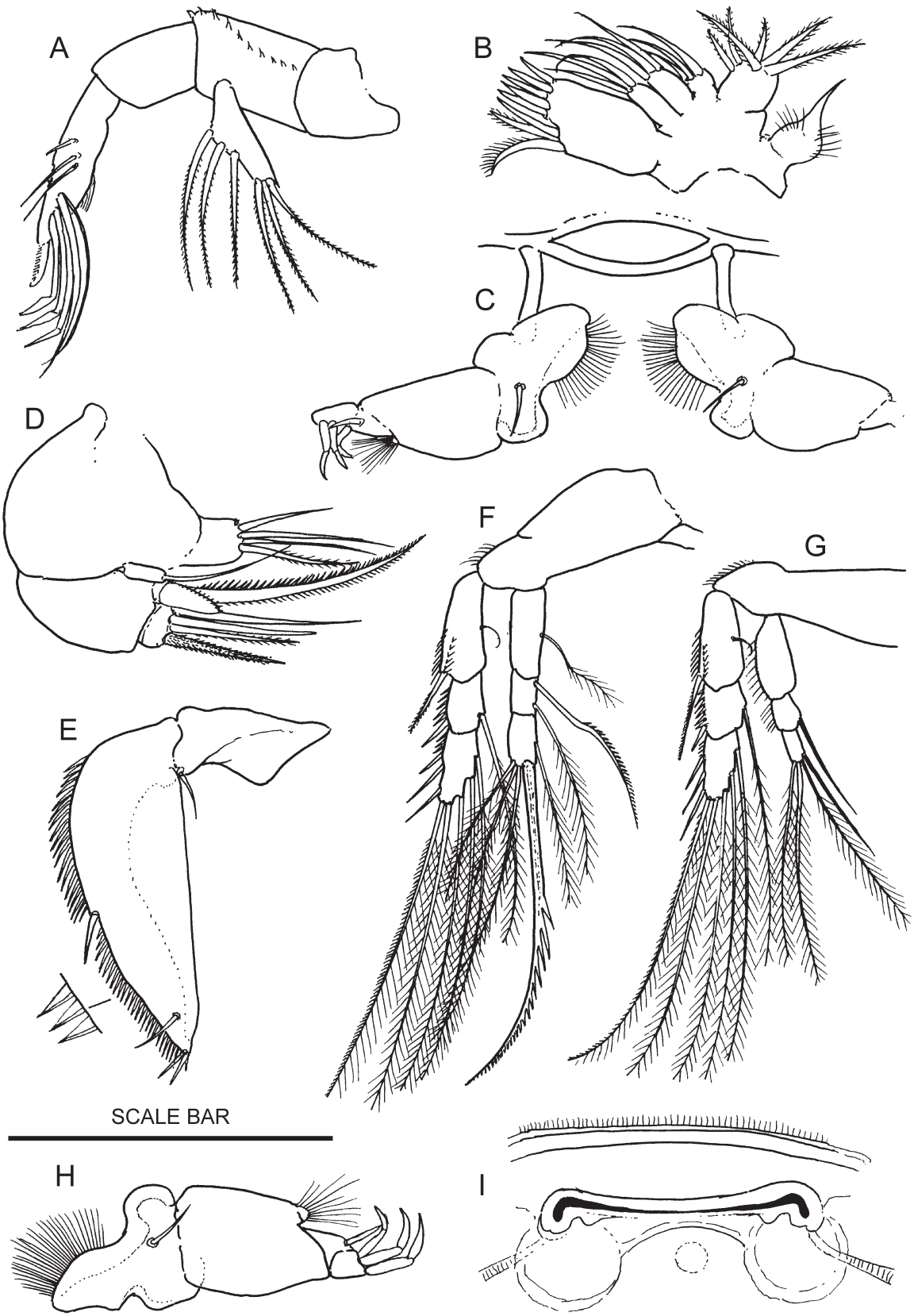

Figure 2. *Cereudorsum verrucosum* sp. nov. Female: *(A)* antenna; *(B)* maxillule; *(C)* maxillipeds (note, coxae do not touch); *(D)* maxilla; *(E)* P5 and detail of border setules; *(F)* P3; *(G)* P4; *(H)* maxilliped; *(I)* genital opening. Scale bar: A, C = 0.14 mm. B = 0.08 mm. D, H, I = 0.1 mm. E = 0.3 mm. F, G = 0.23 mm.

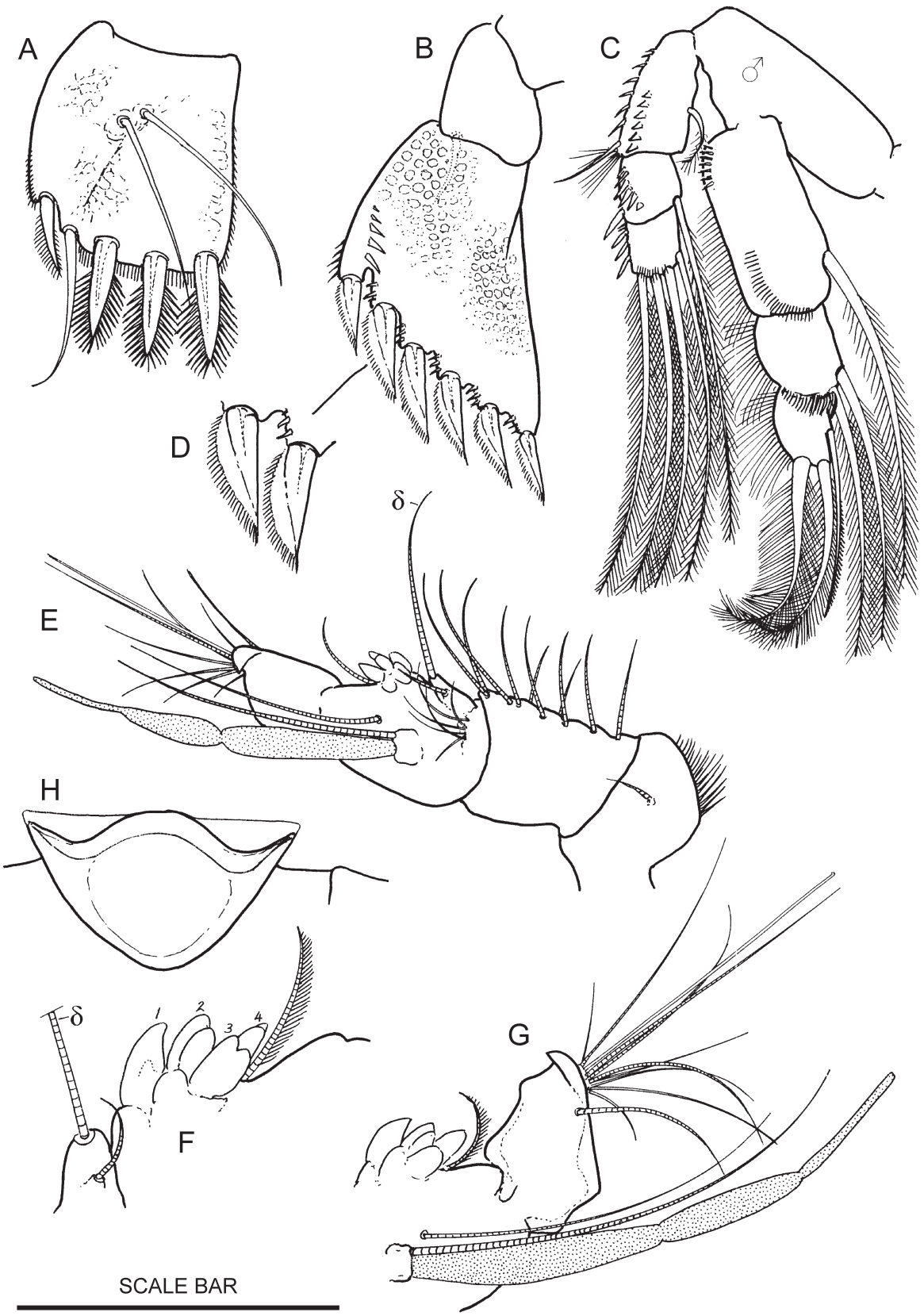

Figure 3. *Cereudorsum verrucosum* sp. nov. Male: *(A)* caudal ramus; *(B, D)* P5 ventral view (pits on dorsal side); *(C)* P2; *(E)* antennule; *(F, G)* details of coupling denticles and dactylus. Female: *(H)* rostrum (ventral). Scale bar: A = 0.1 mm. B, C, E, H = 0.14 mm. F = 0.06 mm. G = 0.08 mm.

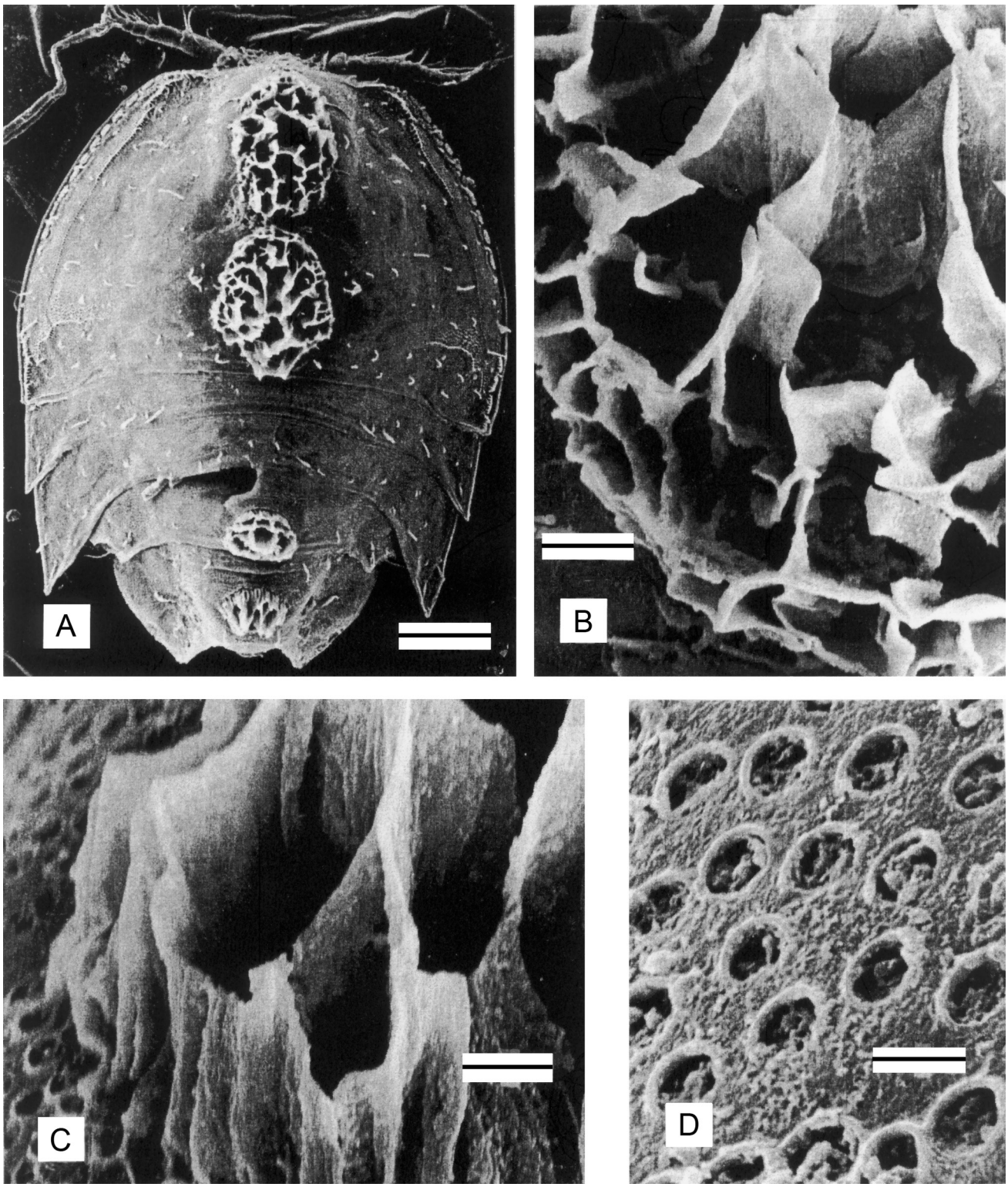

Plate 1. Scanning electron micrographs of *Cereudorsum verrucosum*. *(A)* adult female (dorsal, note caudal rami and P5 limbs missing); *(B, C)* honeycomb-like cuticle; *(D)* dorsal pits. Scale bar: A = 0.13 mm. B = 0.016 mm. C = 8.5 µm. D = 3.2 µm.

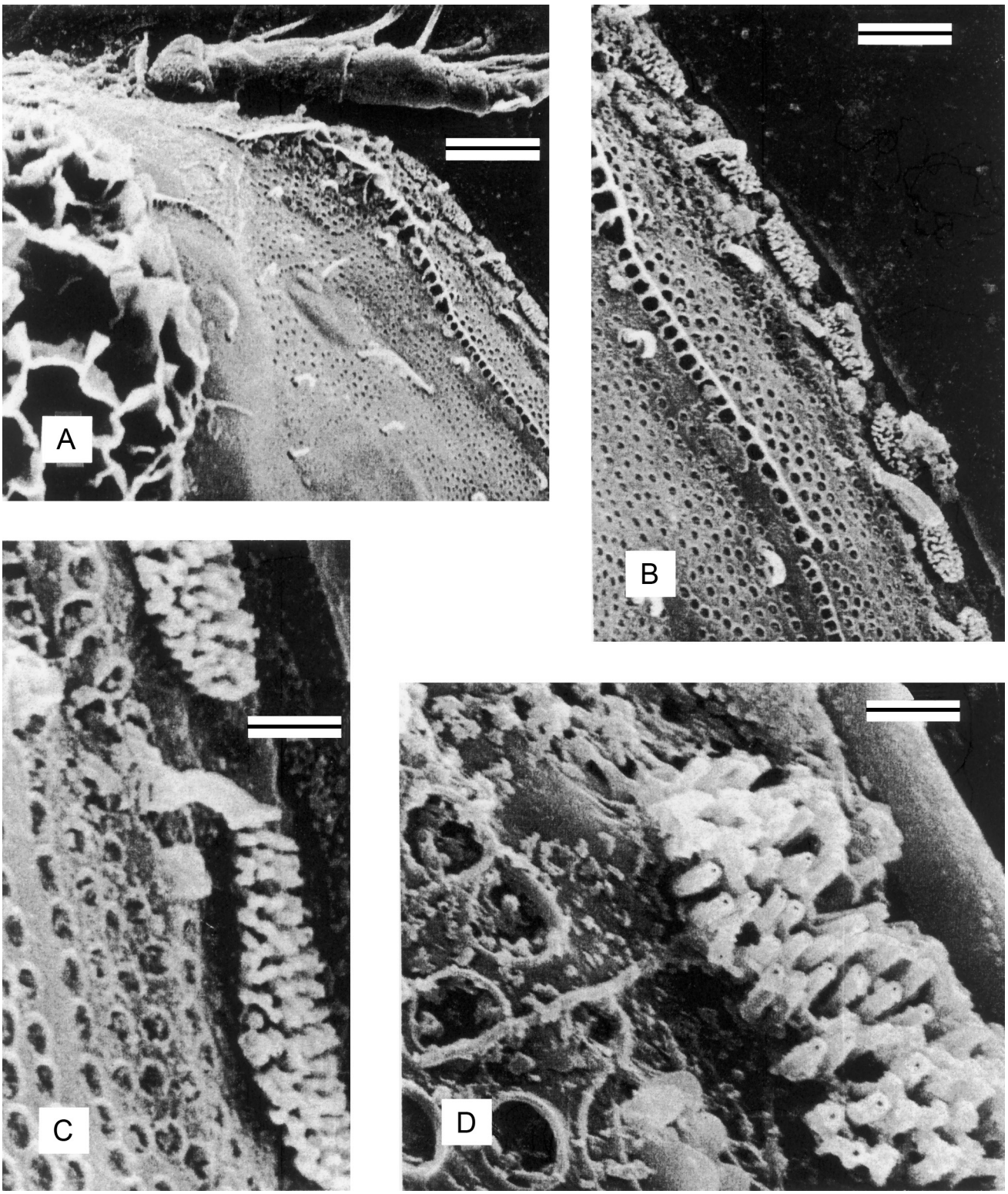

Plate 2. Scanning electron micrographs of *Cereudorsum verrucosum*. *(A)* right "shoulder" region of female cephalosome; *(B)* border of cephalosome showing blocks of micro-tubules; *(C, D)* detail of microtubules. Scale bar: A = 0.045 mm. B = 0.022 mm. C = 6.4 µm. D = 3.2 µm.

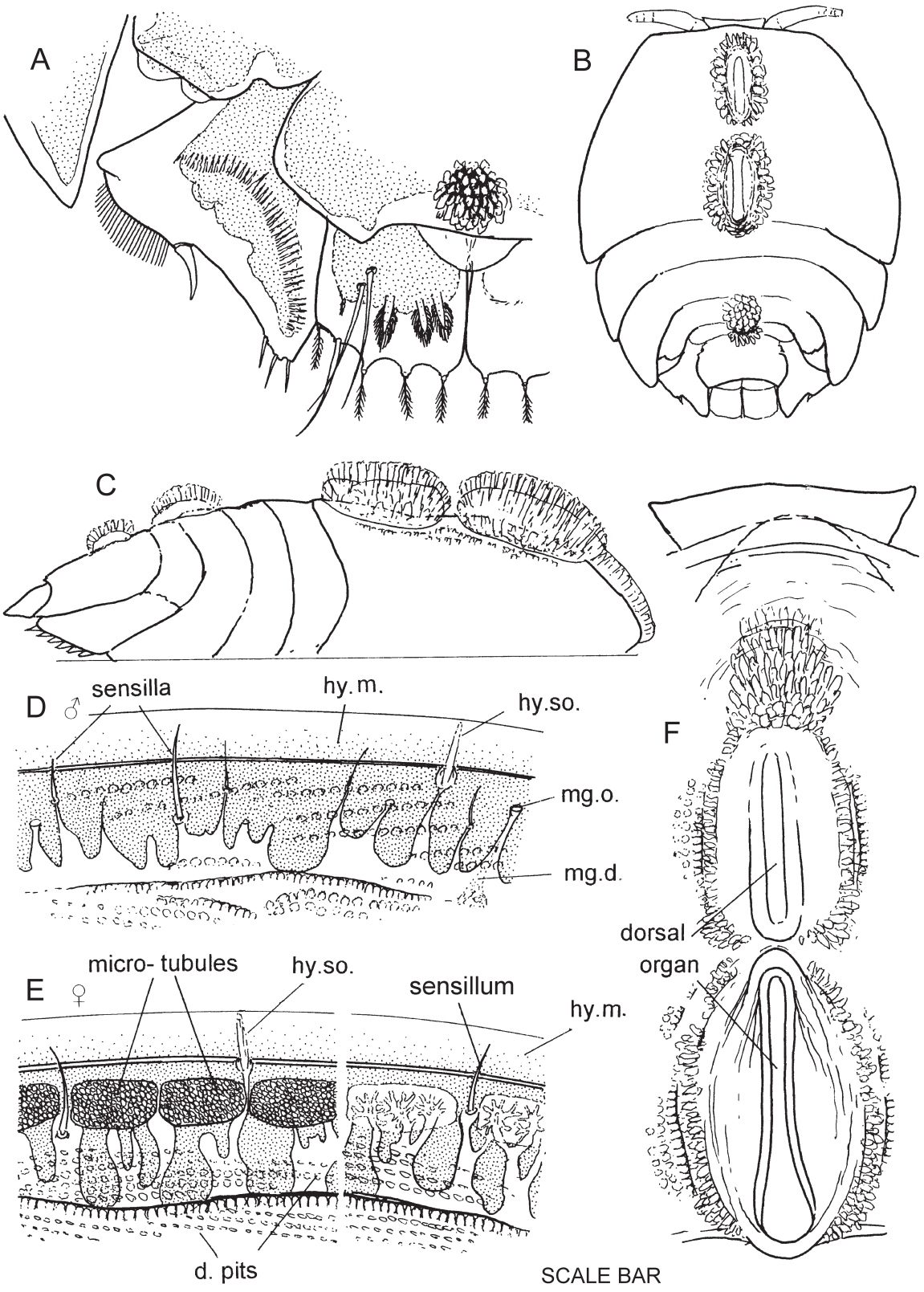

Figure 4. *Cereudorsum verrucosum* sp. nov. *(A)* P5 and caudal ramus of pharate stage V female copepodid, showing difference in type of setae between adult and juvenile; *(B)* stage V female copepodid; *(C)* lateral view of adult male; *(D)* border of male cephalosome, note absence of micro-tubules (*hy.m.* hyaline membrane; *hy.so.* hyaline sense organ; *mg.d.* duct of marginal gland; *mg.o.* opening of marginal duct); *(E)* border of female cephalosome (left superficial focus showing micro-tubules, right deep focus showing branched ducts of marginal glands, lettering as for *D*; *d.pits*, dorsal pits); *(F)* dorsal organs and cuticular honeycomb of stage V copepodid (dorsal view). Scale bar: A, F = 0.14 mm. B = 0.55 mm. C = 0.35 mm. D, E = 0.08 mm. F = 0.14 mm.

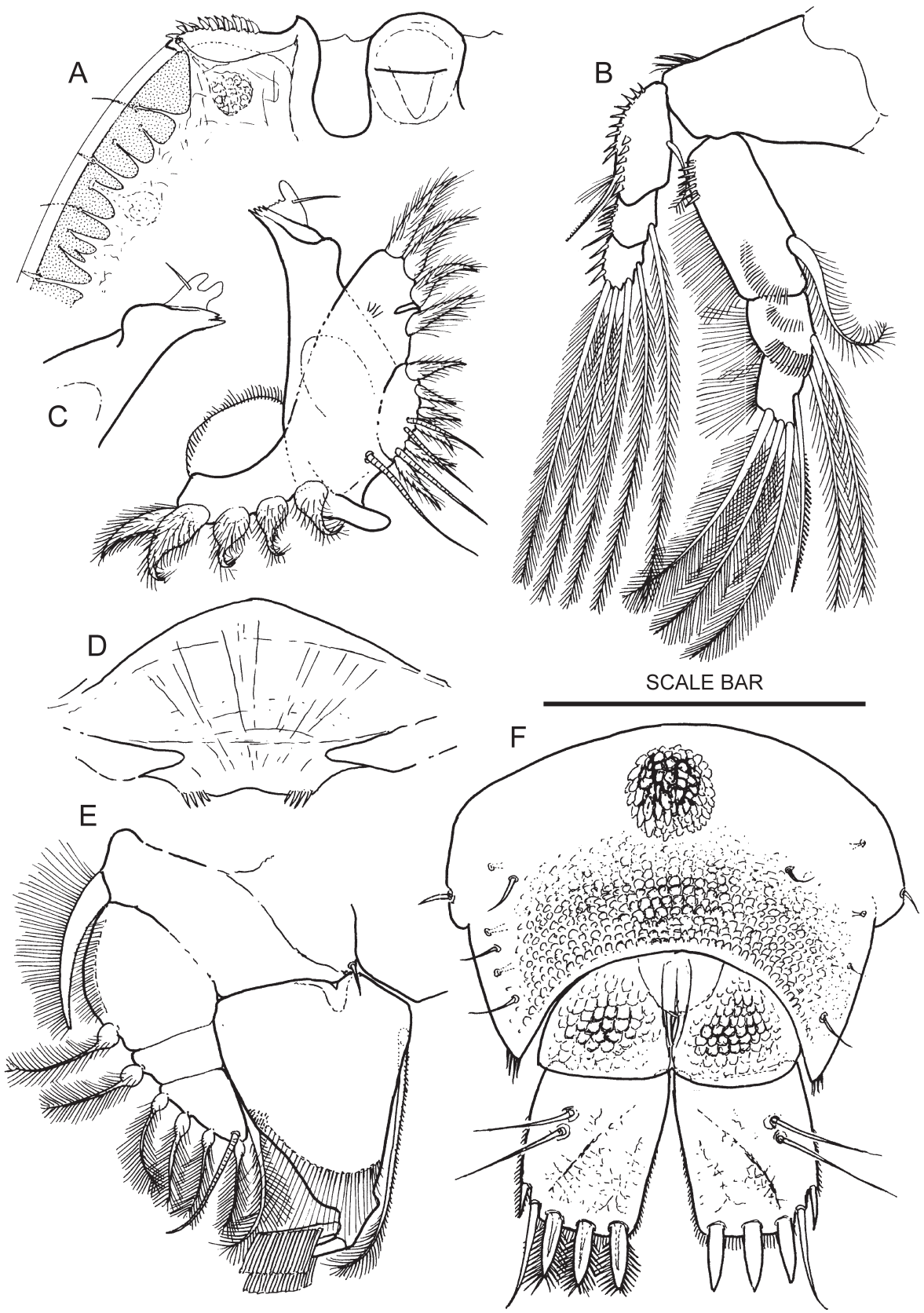

Figure 5. *Cereudorsum verrucosum* sp. nov. Male: *(A)* rostrum and "shoulder" (ventral); *(F)* genital double-somite and caudal rami. Female: *(B)* P2; *(C)* mandible and molar process; *(D)* labrum; *(E)* P1. Scale bar: A = 0.22 mm. B, C = 0.18 mm. D = 0.1 m.m. E = 0.15 mm. F = 0.14 mm.

Biometric data. *Females* (N = 6): maximum length (L_{max}) mean 0.92 mm, range 0.90–0.98 mm, body length (L_{urs}) mean 0.85 mm, range 0.82–0.86 mm; cephalosome width (W) 0.65 mm, range 0.63–0.66 mm, length 0.47 mm; rostrum width (R) 0.13 mm; genital double-somite width 0.35 mm, length 0.20 mm; caudal ramus width 0.08 mm (¾ down ramus), length 0.16 mm.

Ratios: L_{urs}/W1.3, L_{max}/W1.4, cephalosome 55% of L_{urs}, W/R5.0; genital double-somite w/l 1.75, width 54% of cephalosome, anterior lobe 77% of lateral border, posterior lobe 23% of lateral border; caudal ramus 19% of L_{urs}, l/w 2.0, Hicks' index for α 86%, for β 60%.

Males (N =8): maximum length (L_{max}) 0.72 mm, range 0.70–0.76 mm; cephalosome width (W) 0.55 mm, range 0.49–0.57 mm, length 0.32 mm; rostrum (ventral) 0.07 mm; caudal ramus width 0.055 mm, length 0.065 mm; antennule length (fully extended) 0.20 mm; spermatophore 0.18 × 0.04 mm.

Ratios: L_{max}/W 1.3, cephalosome 43% of L_{max}, W/R 7.8; caudal ramus l/w 1.15, Hicks' index for α 68%, for β 60%; antennule 27% of body length, antennule segment 2 34%, segments 3+4 34%, dactylus 24%, aesthetasc 78% of antennule length; spermatophore 25% of L_{max}.

Description. *Adult females* (Fig. 1A): colourless or very pale amber, heavily sclerotized regions brown. Body outline elliptical, truncated anteriorly with convex bulge above rostrum, rostrum (Fig. 3H) partly obscured by anterior bulge. Hyaline border clear, 12–14 µm wide. Rows of conspicuous pits (3 µm) surrounded by rim of thickened cuticle ornament dorsal surface of cephalosome, metasome, genital double-somite and P5s (Plate 1D, p. 172), conspicuous cuticular ridge runs parallel to edge of cephalosome and medial to the blocks of microtubules (Fig. 1A; Plate 2B, p. 173). Numerous (> 100) sensilla form a regular pattern on the dorsal surface of the cephalosome, metasome segments and genital double-somite (Plate 1A, p. 172; Fig. 1C). Some resemble setae, but most are short tubular structures with a basal collar that project through holes in the cuticle (Plate 2B,C, p. 173). Two massive cuticular outgrowths resembling honeycomb 30–50 µm high (Fig. 1A, 4C; Plate 1A,B,C, p. 172) are present on dorsal midline of cephalosome. Individual cells range from 5–40 µm in diameter and have very thin walls (< 0.5 µm). Similar, but smaller, cuticular outgrowths are present on metasome 3 and genital double-somite. On either side of anterior half of cephalosome there are eleven blocks of microtubules close to hyaline border (Figs 1A, 4E left side; Plate 2A–D, p. 173). Each block contains 80–100 tubules and each tubule is 0.75 µm in diameter, 2.5 µm high and has a lumen 0.15 µm in diameter (Plate 2D, p. 173). Labrum without ridge plates, posterior edge with three or four setules at lateral corner (Fig. 5D). Genital double-somite about half width of cephalosome (Fig. 1C, note that width is distorted in drawing by pressure of coverglass), a distinct notch marks boundary between anterior and posterior lobes, one sensillum mid-way along edge of anterior lobe, posterior lobe about ¼ length of genital double-somite, (in normal view posterior lobe appears pointed, but when laid flat it is rounded, Fig. 1C), setules on posterior lobe smaller than those on anterior lobe (Fig. 1E). Dorsal surface pitted, many seta-like sensilla present plus area of honeycomb cuticle in midline. Posterior arch deep, surrounds about ½ of caudal furca. Genital opening straight (Fig. 2I). Metasome segment 4 with fimbriate setules on posterior edge of sternum. Caudal rami broad, elongate (Fig. 1F), medial edge straight with setules down length, lateral edge slightly convex with few setules distally. Seta T1 small pinnate, deeply recessed, posterior border slightly convex with three very large pinnate setae (T2, T3 and T4) evenly spaced (Fig. 1D). Dorsal surface with two longitudinal ridges and some net-like markings, α and β setae very long (about ½ length of ramus).Seta on first segment of antennule pinnate. Structure and setation of mouthparts and ambulatory limbs typical of family. Basis of antenna with row of triangular setules (Fig. 2A), exopod with six plumulose setae, segment 2 of endopod with three lateral setae, geniculate setae plain, claw comb-like. Mandible with small group of setules on anterior lobe (Fig. 5C). Maxillule with single bulbous seta on exopod (Fig. 2B). Maxilla as in Fig. 2D. Maxilliped coxae do not meet in midline (Fig. 2C), coxa with fimbriate border, fimbriate process greatly reduced in size and represented by a bunch of fine fimbriate setules (Fig. 2H). Endopod of P1 with small area of denticulate setules at lateral end of fimbriate crescent (Fig. 5E). P2 endopod with strong proximal setules on segment 1, serrulate spinous seta on segment 3 ⅔ length of endopod (Fig. 5B). Serrate spinous seta on segment 2 of P3 endopod (Fig. 2F) shorter than endopod (0.7:1), large serrate spinous seta on segment 3 very much longer than endopod (1.7:1). P4 endopod segment 1 without internal seta (Fig. 2G), seta on segment 2 and first internal seta of segment 3 thin, straight spinous. Exopod of P5 lanceolate (Fig. 2E), dorsal surface with rows of pits, one sub-terminal seta and two apical setae, border setules long (25 µm). Females carry 10 eggs per brood.

Adult males (Fig. 1B). Outline of cephalosome a sharply truncated hemi-ellipse, convex in midline above rostrum, rostrum rounded (Fig. 5A), lateral angle of antennule sockets project forward, shoulder with epaulet and several cuticular serrations (in ventral view, Fig. 5A), hyaline border starts at epaulet. No microtubules on border of cephalosome (Fig. 4D), ducts from marginal glands open individually dorsal to hyaline border. Colour, pits, ridges, sensilla and massive dorsal cuticular honeycomb as described for female. Caudal rami rectangular (Figs 3A, 5F), lateral edge convex, with setules at posterior end, posterior border slightly convex with fine setules, setules down medial edge, dorsal surface with longitudinal ridge and net-like markings, α and β setae very long (almost length of ramus), inserted very close together about ⅓ way down ramus. Terminal seta T1 small, pinnate, recessed at lateral corner, T2, T3 and T4 large pinnate setae evenly spaced. Antennule (Fig. 3E) without denticle on segment 3, four or five closely grouped finger-like processes (not cuticular denticles) on segment 4 (Fig. 3F), dactylus shorter than segment 3+4, with small hook at end of segment 5 (Figs, 3E, G), aesthetasc long (about ¾ length of antennule), divided into three sections by two constrictions. Terminal segment of P2 endopod with two plumose setae and one serrulate spinous seta (Fig. 3C). Segment 1 of P4 endopod without internal seta, setae on segments 2 and 3 plumose (not spinous). P5 exopod acutely trapezoid (apical angle 50°) with rows of pits on dorsal surface (Fig. 3B), first (lateral) seta with five strong ventral setules, each terminal seta with two or three setules at its base (Fig. 3D).

Remarks. This species is remarkable for a number of unusual features. Nothing corresponding to the dorsal organs and their cuticular outgrowths has been found on any other member of the Porcellidiidae. They do not appear to be derived from any ancestral or pre-existing structure. They first appear on stage III copepodids, but after metamorphosis to adult the trough is completely obscured by the massive honeycomb cuticle. These structures occur on both sexes and first appear on stage III copepodids in a simple form. They are best interpreted from juvenile stages because the mass of cuticular honeycomb is shorter and does not obscure the dorsal organs (Fig. 4B). The dorsal organ on stage V copepodids appears as a longitudinal trough with thickened rim (Fig. 4F). This is surrounded by a clear oval area which is bounded by a ridge and pits, similar to the ridge parallel to the edge of the cephalosome but greatly extended in height to form the folds of the cuticular honeycomb. In adults the honeycomb is massive and completely obscures the dorsal trough (Fig. 1A, 4C; Plate 1A, p. 172). The function of the dorsal organ and cuticular honeycomb is not known.

Ducts from marginal glands of male animals open individually close to the hyaline border as in other porcellidiid species (Fig. 4D), but similar ducts are not found in female animals in the region of microtubule blocks (Fig. 4E, left hand side). From the body cavity passages run through the thickened cuticular border of the cephalosome and end in fine branches under the blocks of microtubules (Fig. 4E, right hand side). It is assumed that secretions from the marginal glands exit through the microtubules. Blocks of microtubules are not found on juvenile animals, but first appear at the moult from stage V copepodid to adult female.

The caudal rami of copepodid stages bear typical thin pinnate setae. The large pinnate setae with hollow shaft do not appear until the final moult to the adult stage (Fig. 4A shows a pharate stage V female copepodid with both juvenile and adult terminal setae). Unlike the clavate setae of *Clavigofera*, the pinnae do not originate from a thin lateral expansion of the shaft, but from the shaft itself.

The male antennules are also unique for they have finger-like structures on segment 4 that appear to take the place of coupling denticles found on all other species. They may perform the same function of increasing friction during mate guarding behaviour.

Etymology. The specific name refers to the wart-like appearance of the dorsal organs (L. *verruca* = a wart).

Distribution. *Cereudorsum verrucosum* has only been found on partly decomposed *Ecklonia radiata* in muddy water at the entrance to Gunnamatta Bay, Port Hacking. This is unusual for it is very rare to find porcellidiids on rotting algae and only one or two species can tolerate muddy water. Nearly all the animals in the sample are covered with diatoms, suctorian protozoa, moulds and sand particles, which make critical observation of detail difficult. The type series, Cr34. 2/77, contained 82 ♀♀, 54 ♂♂ (8 coupled to female copepodids) and 8 copepodids. V. A. Harris 1977.

Genus *Geddesia* gen. nov.

Porcellidium.—Geddes, 1968: 11.

Type species. *Geddesia quadrata* sp. nov.

Diagnosis. Male antennule unique, no denticle or comb on segment 3, two serrate denticles and two spherical structures on segment 4; female cephalosome truncated anteriorly, male deeply concave anteriorly; hyaline border to lateral edge; no dorsal organ with cuticular honeycomb; no ridge plates or setules on labrum; female caudal ramus pentagonal, medial corner 90°, posterior border between T2 and T4 straight, T3 absent; maxillule endopod with six setae; coxae of maxillipeds touch in mid-line; female P5 exopod without ventral expansion, not truncated posteriorly, dorsal and apical setae not pinnate.

Species composition. *Geddesia trisetosa* (Geddes, 1968) comb. nov.; *Geddesia quadrata* sp. nov.

Etymology. The genus is named after Dr D. C. Geddes.

Remarks. The genus is defined on the unique structure of the male antennule, number of setae on maxillule endopod and absence of T3 seta on caudal ramus (compare with *Mucrorostrum, Clunia* and *Brevifrons*).

Geddes' *Porcellidium trisetosum* is included here on the assumption that its maxillule exopod has six setae (Geddes states that "…mouthparts like those of *P. viride* (Philippi) as described by Sars (1911)", this implies six setae on the maxillule, Geddes (1968: 11).

The genus is known from Bahamas and Great Barrier Reef, Australia.

Key to species of *Geddesia*

1 Male P2 endopod with two terminal setae. Male T2 and T4 on caudal ramus short (< ⅕ ramus width). Gap between T2 and T4 > ¾ of maximum width of male caudal ramus. Colour yellow. (Plate 1D, p. 172) ..... *G. quadrata* sp. nov.

—— Male P2 endopod with three terminal setae. Male T2 and T4 on caudal ramus long (> ½ ramus width). Gap between T2 and T4 ½ maximum width of caudal ramus. Colour brown-red ..... *G. trisetosa* (Geddes, 1968)

Geddesia quadrata sp. nov.

Figs 6–9

Type material. Holotype, adult male, length 0.86 mm, P81221; allotype, adult female, length 1.06 mm, P81222 (both mounted on slide), deposited at AM, Sydney. Paratype female mounted on slide and deposited at NHM, London. All collected from seagrass (*Zostera* sp?), Green Island, Great Barrier Reef, Queensland, Australia (16°41'S 45°56'E), V. A. Harris, 1973.

Diagnosis. Female cephalosome hemi-ellipse sharply truncated, anterior edge straight, clear area (lens) above rostrum; male cephalosome deeply concave anteriorly; α and β setae on male caudal ramus and terminal setae T1, T2, T4, all very short (< ¼ width of ramus); area of denticulate setules on P1 endopod resemble maize corn cob; male P2 with two terminal setae on endopod; falciform ventral ridge on female P5 exopod with deep posterior (apical) notch; female length 1.06 mm, colour yellow.

Biometric data. *Females* (N = 4): maximum length (L_{max}) 1.06 mm, body length (L_{urs}) 0.98 mm; cephalosome width (W) mean 0.75 mm; rostrum width 0.16 mm; genital double-somite width 0.33 mm, length 0.22 mm; caudal ramus length 0.15, width 0.08 mm.

Ratios: L_{urs}/W 1.3, W/R 4.7; genital double-somite w/l 1.5, arch 50% of length; caudal ramus 15% of L_{urs}, l/w 1.8, Hicks' index for α 80%, β 50%.

Males (N = 3): length (L_{max}) 0.86 mm [0.90 mm*], body length (L_{urs}) 0.81 mm [0.85 mm*]; cephalosome width 0.70 mm, length 0.47 mm [0.50 mm*]; antennule fully extended 0.21 mm; spermatophore 0.21 × 0.09 mm. [* = Measured from shoulder. Due to the deeply concave anterior border of the male cephalosome, the length measured from the rostrum is very much shorter.]

Ratios: L_{max}/W 1.2 [1.28 mm] cephalosome length 55% of L_{max}; caudal ramus l/w 1.0; antennule 23% of L_{max}, segment 3+4 38%, dactylus 27% of antennule length; spermatophore 25% of L_{max}.

Description. *Adult females* (Fig. 6A; Plate 1D, p. 172): colour lemon yellow, cephalosome hemi-ellipse strongly truncated anteriorly with small epaulette at shoulder, rostrum prominent (Fig. 6B, C) with clear lens-like structure dorsal to rostrum. Dorsal pits very small (2 μm) near edge of cephalosome, hyaline border clear, 15 μm wide (Fig. 7C). Labrum without setules or ridge plates. Genital double-somite (Fig. 7D) narrow (less than ½ width of body), very small notch marks boundary between anterior and posterior lobes (Fig. 7F marked with *), posterior lobe about ¼ length of anterior lobe, acutely pointed posteriorly, lateral edge with very short border setules, arch less than ½ length of genital double-somite. Genital opening (Fig. 6F). Caudal ramus (Fig. 6E) pentagonal, widens posteriorly, maximum width ⅔ down ramus, dorsal surface with fine reticulation. Bevelled edge with setules, posterior edge straight, ¾ of maximum width, 90° to medial edge, posterior border setules conspicuous. Beta seta half way down ramus, T1, and γ close together near posterior end of bevelled edge, T3 absent, T4 small at medial corner. Structure and setation of mouthparts and ambulatory limbs typical of family. Antenna (Fig. 7A, B) with fine setules along edge of basis and endopod segment 1, exopod with five plumulose setae and one serrulate spinous seta, geniculate setae on endopod segment 2 with plain terminal section, claw comb-like. Setae on mandible endopod unusually long (Fig. 7D). Maxillule with six setae on endopod. Claw on maxilla with distal edge comb-like (Fig. 7H). Maxilliped (Fig. 7E). P1 (Fig. 8F), exopod segment 1 with single row of denticles parallel to edge, endopod segment 1 short, broad (w/l = 0.9) with elongate patch of denticulate setules that resemble maize corn cob at lateral end of fimbriate crescent. Setules along external edge of segment 1 on P2, P3 and P4 exopods unusually strong (Fig. 8A, C, D). Serrate spinous seta on segment 2 of P3 endopod strong, almost as long as endopod (0.9:1), large serrate spinous seta on segment 3 longer than endopod (1.35:1, Fig. 8A). Seta on endopod of P4 segment 2 and internal seta of segment 3 strong serrulate spinous setae ½ length of endopod (Fig. 8D). P5 exopod (Fig. 6G) lanceolate, apex rounded (not acute), apical end of ventral falciform ridge terminates in notch (Fig. 7G), two dorsal and one apical seta present (not pinnate), P5s extend beyond genital double-somite but are separated by full width of caudal rami. Females carry six eggs.

Adult males (Fig. 9A), colour lemon yellow, cephalosome truncated hemi-ellipse, posterior half of body semi-circular. Anterior of cephalosome strongly concave, convex medial prominence above rostrum with clear, lens-like, structure in rostrum (Fig. 9D), small epaulette present (Fig. 9B). Dorsal pits and hyaline border as for female. Caudal ramus (Fig. 8B) square (l/w = 1), dorsal surface with reticulate markings, lateral edge slightly convex with border setules along posterior half, α and β setae about ¼ width of ramus or less, β seta half way down ramus. Medial corner 90° with T4 at corner, setae T1 and γ recessed at lateral corner (no bevelled edge), T3 absent, posterior border straight with conspicuous row of setules, distance between T2 and T4 80% of ramus width. Antennule (Figs 9E, F) without denticle or comb on segment 3, prominent peg-like ventral process present (marked * on figures), segment 4 with two small serrated denticles and two bulbous structures (Fig. 9E, F). Dactylus cylindrical, as long as segment 3+4.Two plumose terminal setae on P2 endopod (Fig. 8E), setae on P4 endopod plumose (not spinous). P5 exopod (Fig. 9C) trapezoidal, lateral seta same size and shape as five terminal setae, row of 20 ventral setules, no setules at base of terminal setae. Spermatophore ¼ length of body.

Etymology. The specific name refers to the straight posterior border of the caudal ramus which makes an angle of 90° with the medial edge, (L. *quadratus* = made square).

Remarks. The female animal described by Geddes (1968) as *Porcellidium trisetosum* lacks the T3 seta on its caudal ramus and the female cephalosome is truncated anteriorly: two features that exclude it from the genus *Porcellidium*. The male antennule is not described, but the maxillule is stated to be the same as Sars (1904) described for *P. fimbriatum*, which has six setae on the endopod. Therefore, Geddes' *trisetosum* fits the diagnosis of *Geddesia* and should be moved to that genus as *Geddesia trisetosa* (Geddes, 1968) comb. nov.

The latter differs from *G. quadrata* in the following features: size of female (L_{max} 0.78 mm), colour (red-brown), male P2 endopod with three terminal setae, female Hicks' index for α 70%, length of spinous setae on female P4 endopod as long as endopod, male P5 with setules at base of each terminal seta.

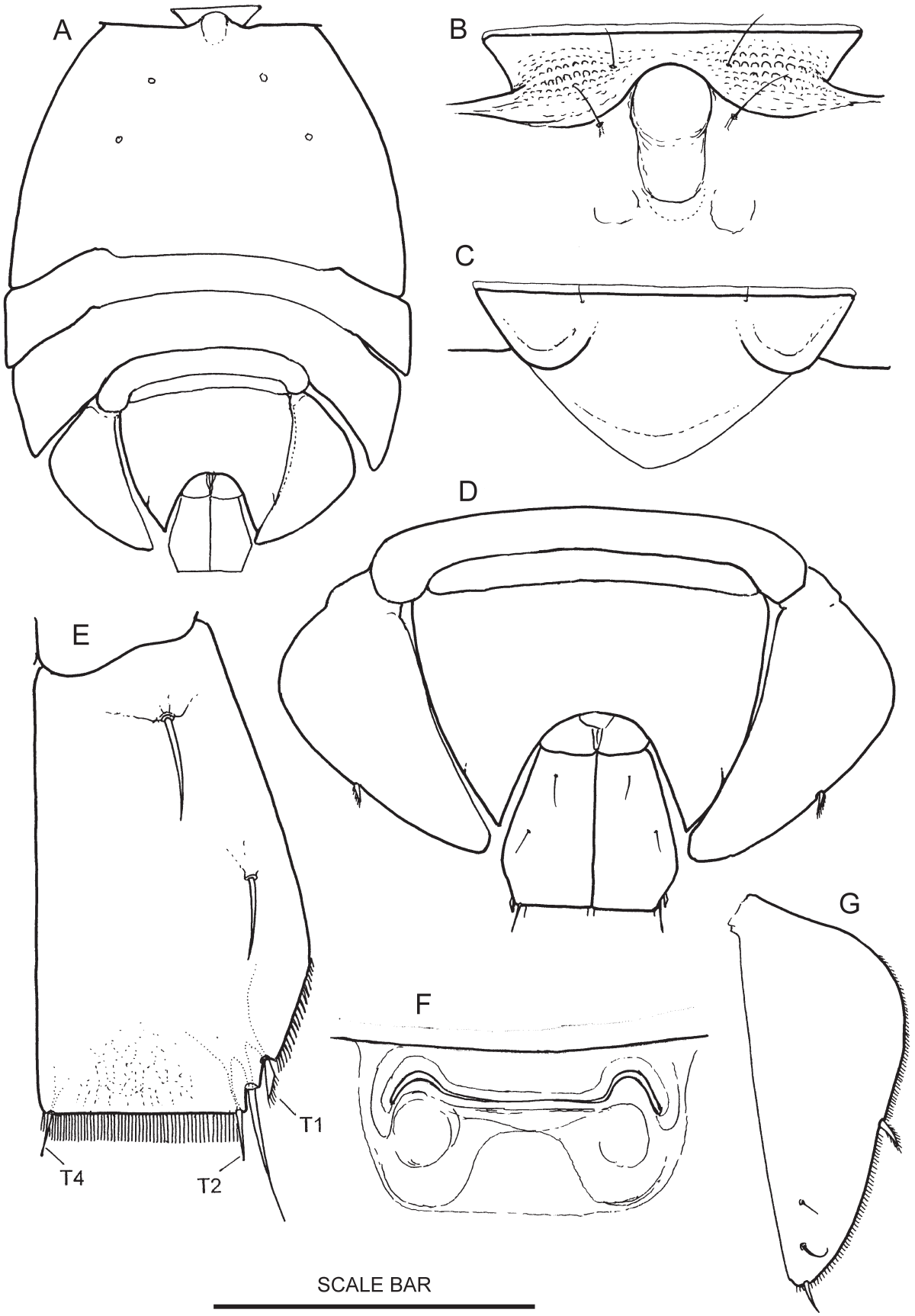

Figure 6. *Geddesia quadrata* sp. nov. Female: *(A)* adult; *(B, C)* rostrum (dorsal, ventral); *(D)* urosome and caudal furca; *(E)* caudal ramus; *(F)* genital opening; *(G)* P5 (dorsal). Scale bar: A = 0.6 mm. B, C = 0.13 mm. D = 0.3 mm. E = 0.1 mm. F = 0.08 mm. G = 0.23 mm.

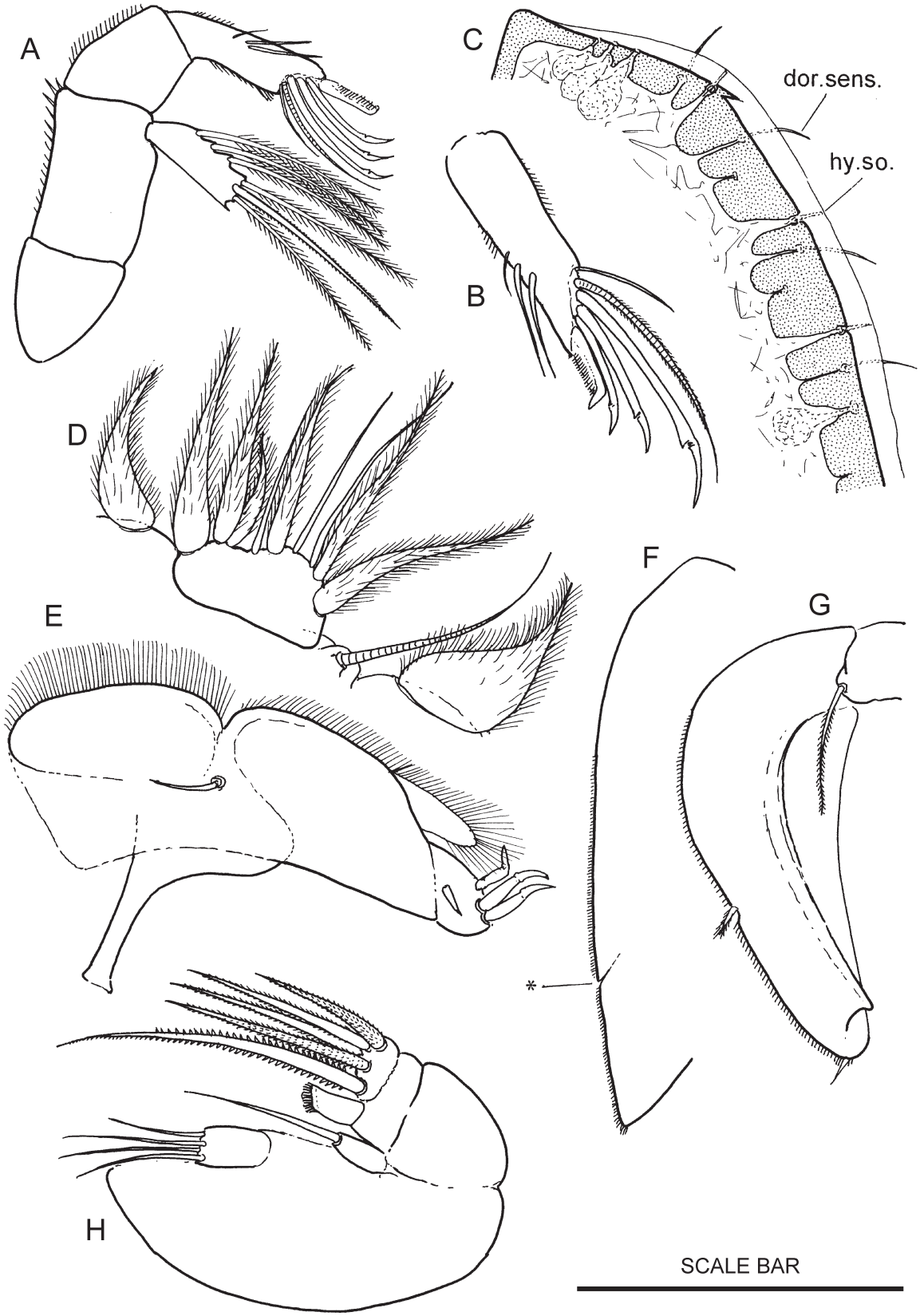

Figure 7. *Geddesia quadrata* sp. nov. Female: *(A, B)* antenna; *(C)* edge of cephalosome (*dor.sens*. dorsal sensillum; *hy.so*. hyaline sense organ); *(D)* mandible endopod; *(E)* maxilliped; *(F)* edge of urosome (* notch); *(G)* P5 (ventral); *(H)* maxilla. Scale bar: A, C, F = 0.14 mm. B, D, E, H = 0.1 mm. G = 0.37 mm.

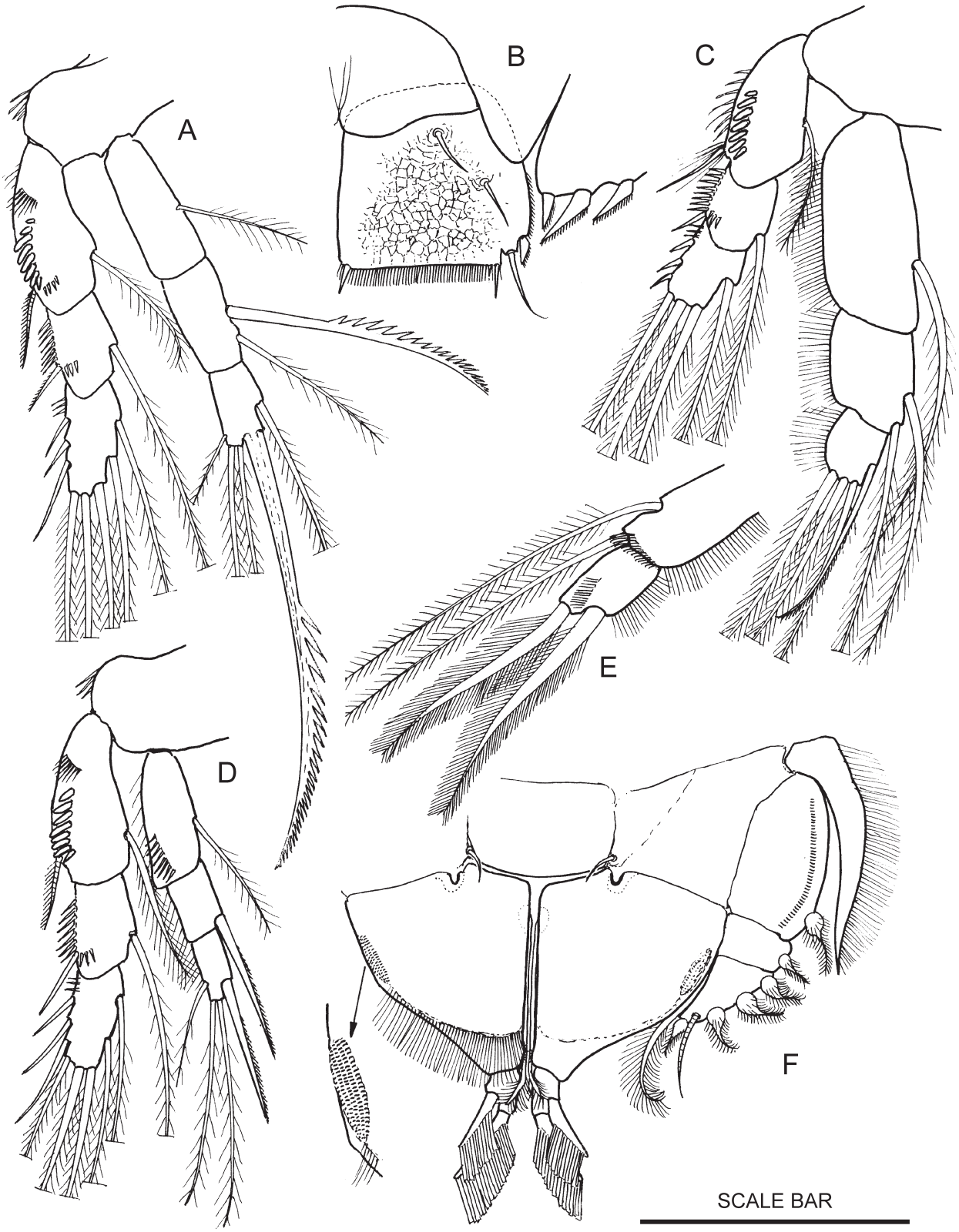

Figure 8. *Geddesia quadrata* sp. nov. Female: *(A)* P3; *(C)* P2; *(D)* P4. Male: *(B)* caudal ramus; *(E)* P2 endopod terminal setae; *(F)* P1. Scale bar: A, C, D = 0.14 mm. B, E = 0.1 mm. F = 0.15 mm.

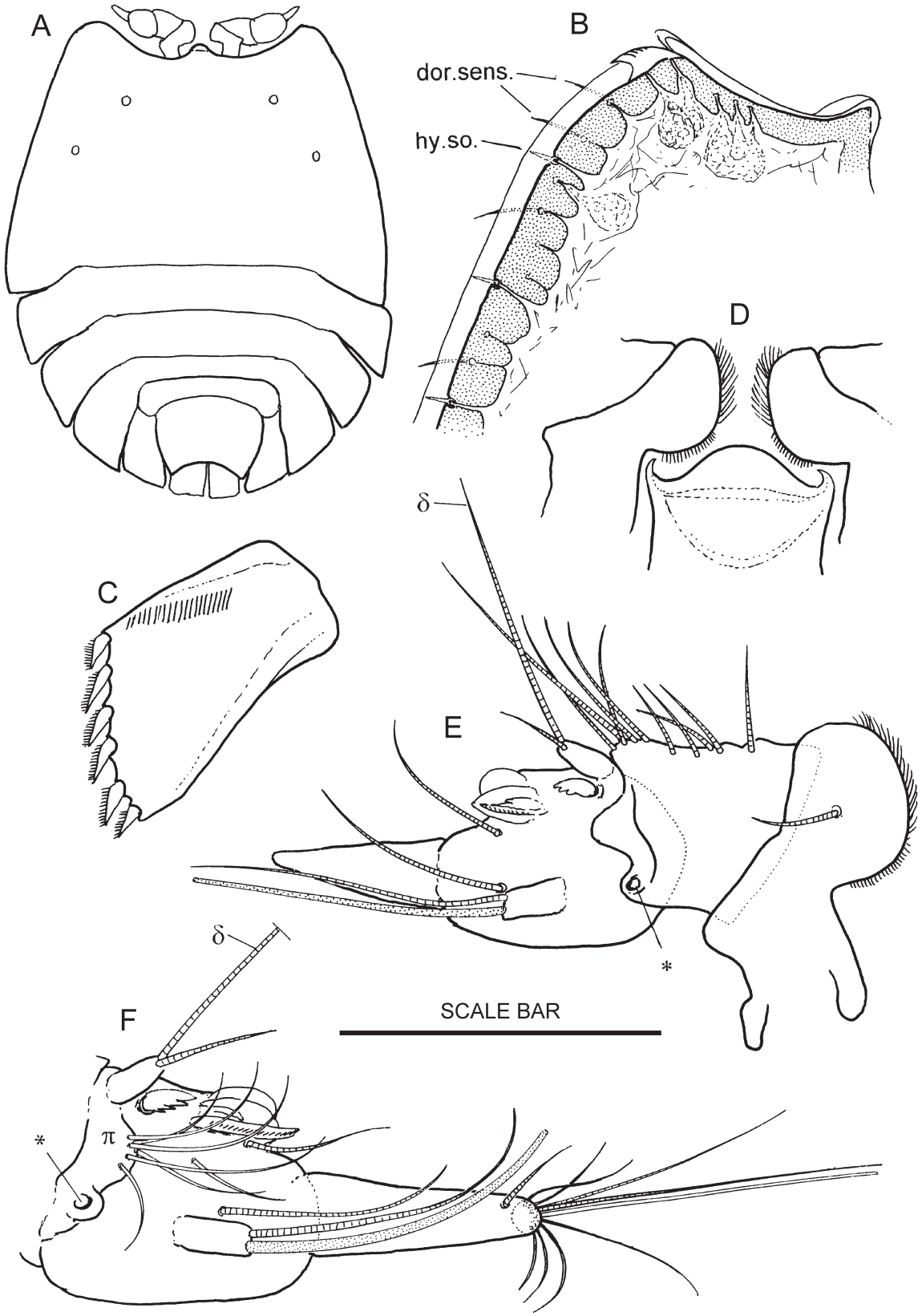

Figure 9. *Geddesia quadrata* sp. nov. Male: *(A)* adult; *(B)* edge of cephalosome; *(C)* P5 (ventral); *(D)* rostrum (ventral); *(E)* antennules; *(F)* details of coupling denticles (* ventral process or peg). Scale bar: A = 0.6 mm. B, C, D = 0.14 mm. E = 0.1 mm. F = 0.08 mm.

Distribution. Type series collected from sea grass *Zostera capricornia* on the reef side of Green Island, Cairns, Great Barrier Reef, Australia, 6 ♀♀, 2 carrying eggs, 8 ♂♂, 2 juveniles, V. A. Harris, 1973. Geddes' animals come from the Bahamas.

Genus *Clunia* gen. nov.

Type species. *Clunia cocosensis* sp. nov.

Diagnosis. Maxillule endopod with only one seta;female cephalosome not truncated; hyaline border with sensilla at lateral edge of cephalosome; no dorsal organs with cuticular honeycomb; no ridge plates on labrum; no lateral striations to anterior lobe of female genital double-somite; female caudal ramus pentagonal, median corner 90°, posterior border straight, T3 absent; coxae of maxillipeds touch in midline; no ventral expansion to female P5 exopod.

Species composition. *Clunia cocosensis* sp. nov., is the only species currently known. Recorded from the Indian Ocean.

Etymology. The genus is named *Clunia* after John Cluniess-Ross who settled on the Cocos (Keeling) group of islands in 1827.

Remarks. The shape of the caudal ramus and absence of T3 resemble *Geddesia* and *Mucrorostrum*, but the presence of only one seta on the maxillule endopod (in contrast to six on the former and two on the latter) and the endite formula are unique features that justify erection of the genus *Clunia*. No male specimen is available for male characters that would confirm this decision.

Clunia cocosensis sp. nov.

Figs 10–11

Type material. HOLOTYPE adult female, length 1.06 mm, P81219; PARATYPE specimens (adult female and dissected female on slide) P81220, deposited at AM, Sydney. All collected from Cocos (Keeling) Islands, Indian Ocean, F. H. Talbot, 1979.

Diagnosis. Female cephalosome hemi-elliptical; dorsal cuticle almost devoid of pits; anterior lobe of mandibular palp long, without ventral setules, molar process modified as a scraper; single seta on maxillule exopod long, not bulbous, endopod with one seta, endite formula 2-3-1; first dorsal seta on P5 exopod close to lateral seta, apical seta pinnate.

Biometric data. *Females* (N = 3): maximum length (L_{max}) 1.03, 1.06, 1.09 mm, body length (L_{urs}) 0.94, 0.97, 0.99 mm; cephalosome width 0.65 mm; rostrum width 0.137 mm; genital double-somite 0.35 mm wide, 0.24 mm long: caudal ramus 0.12 mm long, 0.08 mm wide.

Ratios: L_{urs}/W 1.5, L_{max}/W 1.6, W/R 4.75; genital double-somite w/l 1.46; caudal ramus 12.4% of L_{urs}, caudal ramus l/w 1.5, Hicks' index for α 80%, for β 68%.

Description. *Adult female* (P81219, Fig. 10A). Natural colour unknown, specimens have light brown oil (?) droplets in body cavity. Rostrum not prominent, no lens in rostrum, dorsal pits small (3 μm) near edge of cephalosome, metasome segments and P5. Hyaline border clear, 12 μm wide. Genital double-somite (Fig. 11D) not broad, pointed posteriorly, lateral edge almost straight with no trace of division into anterior and posterior lobes, border setules absent except at apex, posterior arch less than ½ length of genital double-somite. Caudal ramus (Fig. 10G) pentagonal, maximum width about ⅔ down ramus, posterior border straight, 90° to medial edge. A diagonal ridge runs from proximal medial corner to insertion of T2 seta. Terminal setae T1, T2, T4 pinnate, T1 and γ recessed on beveled edge, T4 at medial corner, T3 absent. Terminal fringe of setules between T2 and T4 ⅔ maximum width of ramus. Structure and setation of mouthparts and ambulatory limbs typical of family. Exopod of antenna with five plumulose setae and one spinous seta, endopod segment 2 with three lateral setae, first terminal seta short, geniculate setae with plain end section, claw comb-like (Fig. 10E). Cutting edge of mandible molar process modified into trowel-like scraping organ without anterior seta or lappet (Figs 10B, C). Precoxa of maxillule elongate, endites bear 2-3-1 setae respectively, single plain seta on endopod and exopod (Fig. 10D). Maxilla (Fig. 11F) claw on endopod not broad or serrate, maxilliped (Fig. 10F). Conspicuous crescent of setules on segment 1 of P1 exopod (Fig. 11E), endopod with small but conspicuous triangle of setules at lateral end of fimbriate crescent. Spinous setules on external edge of P2, P3 and P4 exopod segments 1 and 2 appear to lie in a double row of about 9 + 9 setules (Figs 11A, C, G), segment 1 has a proximal row of nine fine setules and segment 3 has five or six setules. Serrated spinous seta on segment 2 of P3 shorter than endopod, large serrated spinous seta on segment 3 strong (Fig. 11C) longer than endopod (1.4:1). Spinous setae on P4 endopod segments 2 and 3 plain (Fig. 11G). P5 exopod lanceolate, not truncated posteriorly, two dorsal setae (first located very close to lateral seta—a position not known elsewhere in the Porcellidiidae) and one pinnate apical seta (Fig. 11B), border setules strong, P5s reach just beyond genital double-somite. One of the specimens has four large eggs in the brood chamber.

Adult male (no specimen available).

Etymology. Named from the Cocos Islands where the species was collected.

Remarks. The absence of a male animal renders the above description incomplete. The position of the first dorsal seta close to the lateral seta on the female P5 is unusual and has not been observed on any other member of the family.

Distribution. The four female specimens were collected at a depth of 4 m from dead coral encrusted with algae in a channel at the reef crest between Direction Island and Prison Island, Cocos (Keeling) Islands, Indian Ocean, F. H. Talbot, 8 Oct. 1979.

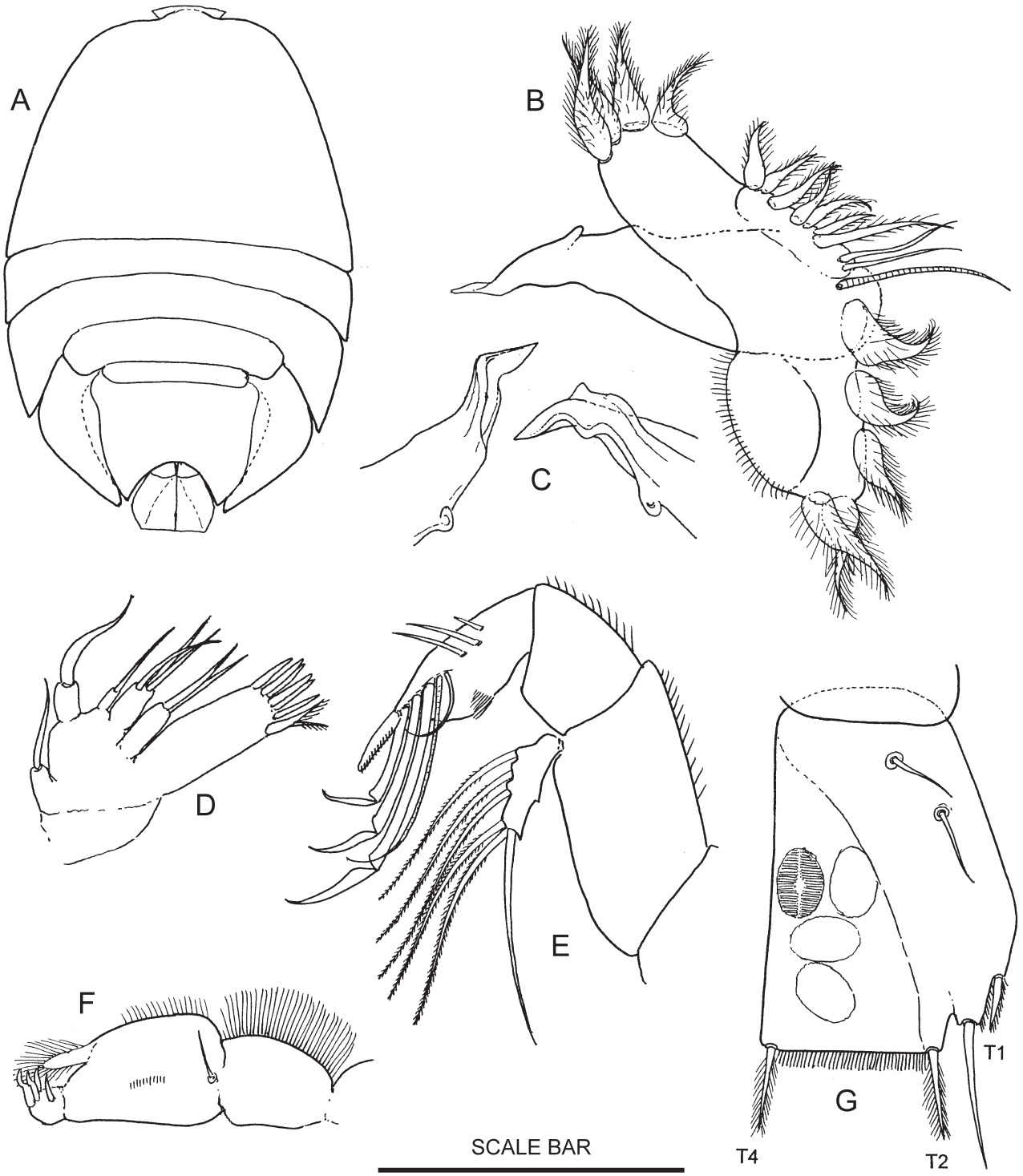

Figure 10. *Clunia cocosensis* sp. nov. Female: *(A)* adult; *(B, C)* mandible and detail of molar process; *(D)* maxilla; *(E)* antenna; *(F)* maxilliped; *(G)* caudal ramus (with diatoms on dorsal surface). Scale bar: A = 0.6 mm. B, C, D = 0.08 mm. E = 0.06 mm. F, G = 0.1 mm.

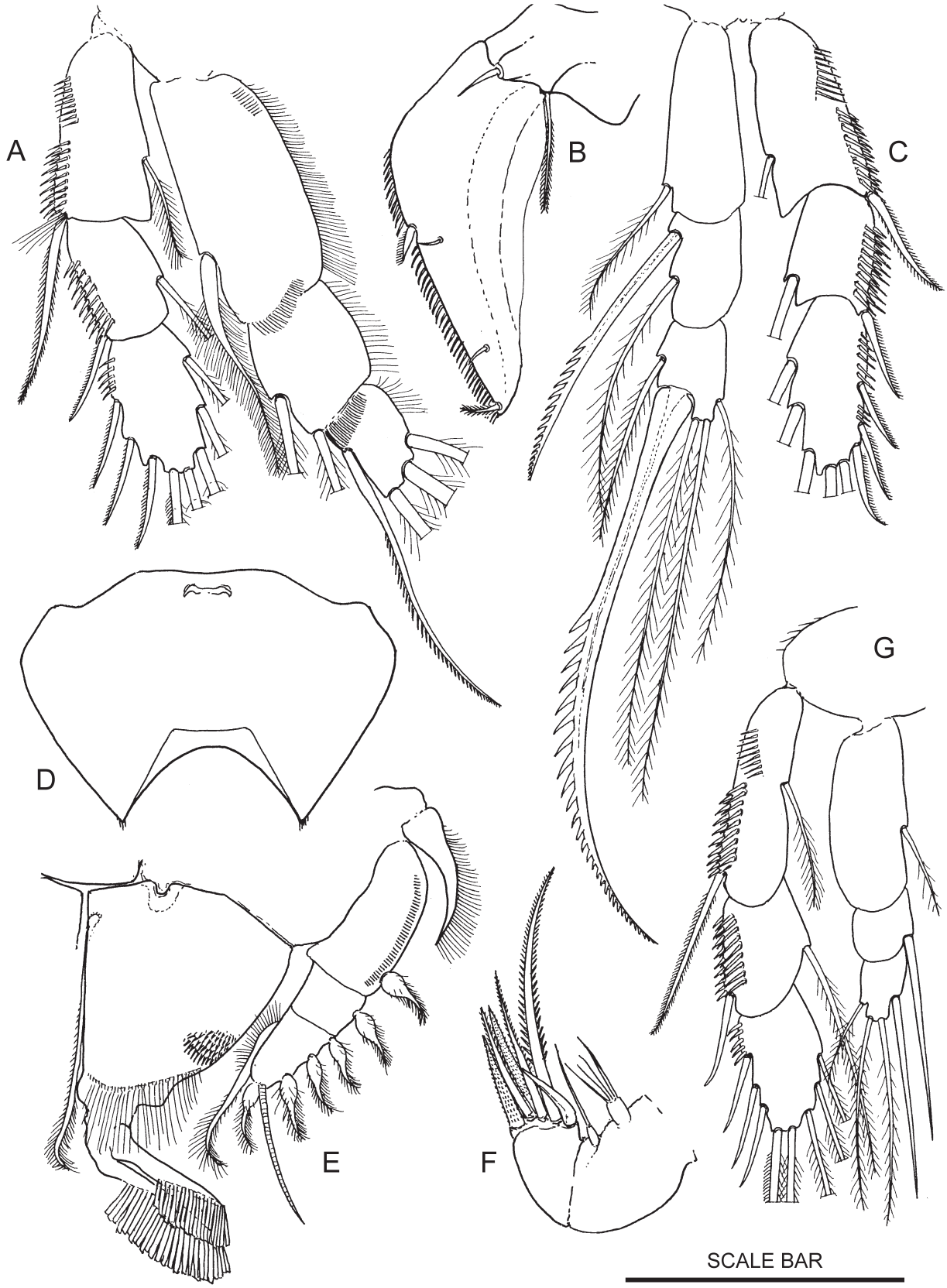

Figure 11. *Clunia cocosensis* sp. nov. Female: *(A)* P2; *(B)* P5 (ventral); *(C)* P3; *(D)* urosome; *(E)* P1; *(F)* maxilla; *(G)* P4. Scale bar: A, C, G = 0.1 mm. B = 0.23 mm. D = 0.3 mm. E, F = 0.08 mm.

Discussion

Reappraisal of the proposed genera and their validity

Sixteen genera have now been named, but not all of these have been accepted, either because the defining characters were not autapomorphic (Walker-Smith, 2001; Wells, 2007), or due to the fact that the type genus to the Porcellidiidae had not been clearly defined, resulting in a diverse assembly of very different species (Huys *et al*., 1996). The latter problem has been resolved with a definitive diagnosis for *Porcellidium* by Harris (2014a), but the first difficulty has not been addressed.

Wells (2007) objected that "… Although the ICZN neither precludes nor declares invalid taxa that are not in accord with Hennigian principles, they are now widely accepted as the ruling paradigms in systematics". Walker-Smith has pointed out that many of the genera were only defined on a unique combination of characters and not autapomorphies. However, Bodin (1997) points out that the diagnoses given "… of these genera are in accordance with the rules of the ICZN… ". It is necessary, therefore, to reconsider the grounds on which the disputed genera were based.

A careful re-examination of type material for all Australian and Japanese genera in the Porcellidiidae has been made to assess whether the unique features found were specific to only one species or to a closely defined group of species as autapomorphic characters defining a genus. The current data base contains detailed information on over 70 species. It shows certain features, such as shape of the cephalosome, caudal ramus, genital double-somite and structure of the male antennule, are extremely variable and may be useful species-specific characters. On the other hand, variation in a feature like the number of setae on the maxillule endopod, which is almost constant throughout the family, is more likely to be regarded as an autapomorphic character defining a genus. A number of other unique features, such as the brush pad of *Kensakia*, ventral hyaline membrane of *Tectacingulum* or the loss of terminal setae from the male P5 of *Synurus* are regarded as characters defining genera.

The result of this re-assessment is given in Table 1 where apomorphic and autapomorphic characters are listed for each genus except *Porcellidium* and *Acutiramus*. A total of 33 characters have been selected to define *Porcellidium*, all are present on the type species *P. viride* and appear to be plesiomorphic: none of them are considered autapomorphic. However, each of them are known to have a corresponding apomorphic state which is indicated in Table 1.

Remarks

Table 1 gives the main defining characters for each of the genera. *Porcellidium* is based on characters that are exhibited by *Porcellidium viride* and all species placed in that genus. Genera 3 to 16 are clearly defined by easily seen autapomorphic characters that separate them from *Porcellidium* and *Acutiramus*. *Acutiramus* is maintained because it is clearly excluded by the new definition of *Porcellidium* in shape of the female genital double-somite, caudal rami, P5 and details of the male antennule. It is excluded from *Ravania* by the presence of T3 on the caudal ramus and structure of the male antennule.

The case for placing *Clunia cocosensis* and *Geddesia quadrata* in separate genera is not so clear for they both have a pentagonal caudal ramus similar in shape to *Mucrorostrum yoroium*, but not found elsewhere in the family. However, the three species cannot be placed together in the same genus because of fundamental differences in the setation of their maxillule. This appendage shows remarkable uniformity in the number of setae on endites and the endopod throughout the Porcellidiidae and any deviation must be considered an autapomorphic feature. *Geddesia* has six setae on the endopod, the typical porellidiid condition, but *Mucrorostrum* has only two setae on the endopod and an endite formula 1-2-1. *Clunia* on the other hand, has only one endopod seta and an endite formula 2-3-1. These two unique differences in maxillule setation are considered autapomorphic characters defining *Mucrorostrum* and *Clunia*.

An unexpected consequence of re-describing the type species for *Porcellidium* is that about half of the species described in the literature do not belong to that genus. Either they do not share all the characters of the genus or they possess apomorphic character states that eliminate them from *Porcellidium* and place them in other genera. Of the 59 species listed in the literature, eight are inadequately described and cannot be placed in any known genus: *P. fulvum* and *P. interruptum* Thomson (1882)*, P. tuberculatum* Wolfenden (1905), *P. affine* and *P. charcoti* Quidor (1906), *P. wolfendeni* Brady (1910), *P. scotti* Pesta (1935) and *P. malleatum* Vervoort (1964). However, they may prove valid species when accurately redescribed. Another seven are synonyms for other species: *P. dentatum* Claus (1860), *P. ovatum* Haller (1879), *P. lecanoides* Claus (1889), *P. sarsi* Bocquet (1948), *P. penicilliferum,* Tiemann (1978), *P. acutum* and *P. aoifuchidorum* Harris & Iwasaki (1996, 1997) and another three are juvenile stages: *P. subrotundum* Norman (1868), *P. rotundum,* and *P. australe* Brady (1910). This leaves 41 recognized species, but only 20 of these fit the diagnosis for *Porcellidium*. The remainder must be transferred to other genera.

Table 2 gives a check list of the 71 species belonging to the Porcellidiidae recognized in the present study. It reveals the genus to which species rejected from *Porcellidium* have been moved, together with the original author, geographical distribution and the size of holotype and allotype specimens.

Distribution of Australian Porcellidiidae

A list of 32 described species and their recorded presence on the east coast of Australia is given in Fig. 14, but sampling has not been uniform along the whole coast. Knowledge of the NSW porcellidiid fauna is based on extensive collection at 17 stations over a period of two decades, whereas data on the Great Barrier Reef rests on a single sample washed from a mixture of seagrass (*Zostera capricornia* ?) and *Halimedia* sp. at Green Island, Cairns.

Despite this, there appears to be a clear distinction between the species that occur in northern Queensland and those that are found south of the Tropic of Capricorn. Of the 27 species known from NSW, only four have been recorded from Hervey Bay, southern Queensland and only two of these have been collected as far south as Eden (*Acutiramus rufolineatus* and *A. quinquelineatus*). Two species, *Clavigofera pacifica* and *Synurus ctenocheirus*, are known from Japan, but none of the other species has been recorded beyond Australian shores. No New Zealand species has been found in Australian waters. Eight species are only known from single localities.

Table 1. A summary of characters used to define genera in the Porcellidiidae (§ autapomorphic character, † apomorphic character). * For types of coupling denticle arrangement see Harris (2014b, p. 162). Characters i to xxxiii are considered plesiomorphic. Alternative (apomorphic) characters, indicated within parentheses ( ), refer to other genera, see genera numbered 2–16 in this table.

1 ***Porcellidium*** **Claus, 1860** (type species *P. viride*) [20 species]
- i Spermatophore elongate. (11).
- ii Normally deposited ventrally on the female's genital double-somite. (11).
- iii Spermatophore ephemeral, shed before egg laying starts. (11).
- iv Female receives only one spermatophore during her life span. (11).
- v Female cephalosome semicircular, not truncated anteriorly. (5, 12, 15).
- vi Male cephalosome truncated anteriorly. (9, 13).
- vii Hyaline border to cephalosome. (3).
- viii Ducts of marginal glands open dorsal to hyaline border. (3).
- ix No honeycomb-like pattern of cuticular folds on cephalosome. (5, 10, 14). Dorsal organs absent. (14).
- x Male genital somite not fused to P5 baseoendopod and segment 4 of metasome. (12).
- xi Female genital double-somite posterior lobe broad, rounded. (2, 6, 7, 8, 12, 13, 14, 15).
- xii No striations (rugosity) on anterior lobe of female genital double-somite. (6).
- xiii Anterior and posterior lobes clearly indicated by notch or cleft. (7, 8, 12, 13, 15).
- xiv 50% or more of caudal furca enclosed in posterior arch of genital double-somite.
- xv Female caudal ramus rectangular, but T1 and γ setae may be recessed at external corner. (2, 7, 8, 9, 11, 12, 13, 15, 16).
- xvi Terminal setae T1 to T4 always present on caudal ramus.(8, 9, 11, 12, 13, 15, 16). Setae never pinnate clavate, Fig. 12R. (6).
- xvii T2 and T3 very close together, never lie parallel to posterior border. (2).
- xviii α and β setae on caudal ramus never very close together (i.e., not less than width of ramus). (10).
- xix No ridge plates on labrum. (10).
- xx No denticle or comb on segment 3 of male antennule; ventral process (blade or knob) may be present. (4, 7, 8, 9, 13).
- xxi Anterior process on segment 3 of male antennule with δ and δ' setae that point forward, not laterally. (4, 10).
- xxii Segment 4 of male antennule has three coupling denticles (shape variable, but never a brush-pad). (2, 3, 4, 6, 8, 9, 12, 13, 14, 15).
- xxiii Endites on maxillule with three or four setae each. (5, 9, 16).
- xxiv Endopod of maxillule with six setae. (5, 9, 16).
- xxv Coxae of maxillipeds touch in mid-line. (10, 14).
- xxvi Fimbriate process always present on basis of maxilliped. (10, 14).
- xxvii Exopod segment 3 of P2, P3 and P4 with three external setae. (12).
- xxviii Terminal pair of setae on segment 3 of female P3 and P4 endopod plumose. (10).
- xxix Female P5 shorter than genital double-somite. (2, 5, 6, 7, 8, 9, 11, 13, 14, 15).
- xxx No ventral expansion of falciform ridge on female P5. (7).
- xxxi Male P5 trapezoid with six setae (one lateral, five terminal). (12).
- xxxii Animals dorsoventrally flattened, oval or elliptical in outline.
- xxxiii No notch at distal end of falciform ridge on female P5. (7, 8, 12).

2 ***Acutiramus*** **Harris & Robertson, 1994** [12 species]
- i Female P5s reach beyond genital double-somite and caudal rami to touch one another posteriorly.
- ii Female caudal ramus rhomboid (not rectangular).
- iii Setae T1, T2 and T3 always present on male and female caudal ramus.
- iv T2 and T3 very close, may lie parallel to posterior border.

3 ***Tectacingulum*** **Harris, 1994** [2 species]
- i Hyaline membrane on ventral side of cephalosome.§
- ii Marginal glands open on ventral side of cephalosome.§
- iii Large area of short peg-like setules on segment 1 of P1 exopod.§
- iv False (cuticular) border to cephalosome.§

4 ***Murramia*** **Harris, 1994** [2 species]
- i Male antennule segment 3 δ' absent from anterior process.§
- ii Unique arrangement of denticles on male antennule (type E*).§

5 ***Brevifrons*** **Harris, 1994** [1 species]
- i Unique arrangement of denticles and setae on male antennule (unipinnate seta associated with sensory lobe on segment 4).§
- ii Maxillule formula for endite setae 2-2-1.§
- iii Maxillule with two setae on endopod.†
- iv Low honeycomb-like ridges on dorsal surface of cephalosome.†
- v Male and female cephalosome truncated anteriorly.†

6 ***Clavigofera*** **Harris & Iwasaki, 1996b** [5 species]
- i Anterior lobe of female genital double-somite with lateral band of ridged cuticle (rugosity).§
- ii Terminal setae T1 to T4 large, pinnately clavate.§
- iii Seta T1 identical in size to T2, T1 to T4 evenly spaced across posterior border of caudal ramus.§
- iv Setae T1 and γ not recessed at lateral corner.†

Continued on next page

Table 1—*Continued*

7 *Kushia* Harris & Iwasaki, 1996b [4 species]
- i Female P5 with ventral expansion to falciform ridge.§
- ii Male antennule segment 3 with anterior comb-like denticle.§
- iii Unique arrangement of denticles on male antennule segment 4 (type C*).§

8 *Kensakia* Harris & Iwasaki, 1997 [5 species]
- i Brush-pad on segment 4 of male antennule.§
- ii Unique arrangement of denticles on male antennule (type A*).§
- iii Seta T2 absent from female caudal ramus.§
- iv Female caudal ramus trapezoid.†
- v T3 absent from male and female caudal ramus.†

9 *Mucrorostrum* Harris & Iwasaki, 1997 [1 species]
- i Unique arrangement of denticles on male antennule, four identical denticles on segment 4 (type D*).§
- ii Maxillule formula for endite setae 1-2-1.§
- iii Maxillule with two setae on endopod.†
- iv Female caudal ramus pentagonal, medial corner 90°.†
- v Animals can conglobate.†

10 *Dilatatiocauda* Harris, 2002 [7 species]
- i Labrum with two grooved plates (ridge plates).§
- ii Terminal pair of setae on female P3 and P4 endopod long, straight spinous setae (usually serrate).§
- iii Fimbriate process absent from maxilliped basis.§
- iv Coxae of maxilliped wide apart.†
- v Segment 5 of male antennule with lateral lobe.†
- vi Large areas of short peg-like setules on segment 1 of P1 endopod.†

11 *Porcelloides* Harris, 2014a [2 species]
- i Spermatophore reniform with recurrent duct.§
- ii Spermatophore deposited on dorsal surface of female P5, firmly attached by adhesive.§
- iii Spermatophore semipermanent on female, remains attached long after egg laying starts.§
- iv Deposition of more than one spermatophore on female common (1–4 may be present, implying that more than one male has deposited them).§
- v Unique arrangement of denticles on segments 4 of male antennule (type G).§
- vi Outline of male and female body ovate (egg-shaped), very little dorsoventral flattening.†
- vii Animals can conglobate.†

12 *Synurus* Harris, 2014b [2 species]
- i Male genital somite fused to metasome segment 4 and P5 baseoendopod.§
- ii Epipleural lobe of male metasome segment 4 very long (stretches back to extremity of caudal furca).§
- iii Male P5 ovate.§
- iv Male P5 with lateral seta, terminal setae atrophied or absent.§
- v Seta T1 absent from male and female caudal ramus.§
- vi Segment 3 of P2, P3 and P4 exopod with only two external setae.§
- vii Male cephalosome deeply concave anteriorly.†
- viii Anterior of female cephalosome truncated.†

13 *Ravania* gen. nov. Harris, 2014b [3 species]
- i Unique arrangement of denticles on male antennule (type B*).§
- ii Seta T3 absent from caudal ramus.†
- iii Male cephalosome semicircular anteriorly, not truncated.†

14 *Cereudorsum* gen. nov. [1 species]
- i Unique structure of male antennule (segment 4 with swollen finger-like structures in place of normal coupling denticles).§
- ii Dorsal organs.§
- iii Massive honeycomb-like cuticle surrounds dorsal organs.§
- iv Marginal glands open through numerous microtubules at edge of cephalosome (female only) §?
- v Reduction or absence of fimbriate process on basis of maxilliped.†
- vi Coxal lobes of maxillipeds wide apart.†

15 *Geddesia* gen. nov. [2 species]
- i Unique arrangement of male antennule (bulbous structures and denticles on segment 4) §?
- ii Anterior of female cephalosome truncated.†
- iii Male cephalosome deeply concave anteriorly.†
- iv Female caudal ramus pentagonal, medial corner 90°.†
- v T3 absent from male and female caudal ramus.†

16 *Clunia* gen. nov. [1 species, no male available]
- i Maxillule endopod with only one seta.§
- ii Maxillule formula for endite setae 2-3-1.§
- iii Female caudal ramus pentagonal, medial corner 90°.†
- iv T3 absent from caudal ramus.†

Key to the genera of Porcellidiidae

The following key to the above genera is based on features that can usually be seen on whole animals in dorsal and ventral view except for the denticles on the male antennule which require the antennule to be fully extended. The shape and setation of the female caudal ramus are easily seen and can be used to identify species and genera. The range in shape and setation of the female caudal ramus is extensive, but not easy to define in words. Figure 12 shows diagrammatically the basic shapes referred to in the key.

Multiple characters are given for each genus in the key, but confirmation of identity should be made by reference to Table 1 and the original descriptions of genera.

1 Body egg-shape (ovoid). Females carrying eggs may have one or more spermatophores attached to P5s. Female caudal ramus trapezoid (Fig. 12A, B), T2 always present, T3 may be present or absent. Male antennule[b] segment 4 with large denticulate pad (never brush-pad) ..... *Porcelloides*

—— Body outline oval or elliptical. Females carrying eggs never have spermatophore attached (lost before egg laying starts). Female caudal ramus trapezoid, T2 and T3 always absent (Fig. 12C). Male antennule[b] segment 4 with brush-pad. (Fig. 12Q) ..... *Kensakia*

—— Body outline oval or elliptical. Females carrying eggs never have spermatophore attached (lost before egg laying starts). Female caudal ramus rectangular, pentagonal or rhomboid. Male antennule segment 4 denticles variable in shape and number but never a brush-pad 2

2 Hyaline membrane with sensilla on ventral surface of cephalosome, false cuticular border to cephalosome. Ducts of marginal glands open on ventral surface of cephalosome ..... *Tectacingulum*

—— Hyaline membrane with sensilla forms lateral border of cephalosome. Ducts of marginal glands open on dorsal surface of cephalosome 3

3 Coxal lobes of maxillipeds wide apart 4

—— Coxal lobes of maxillipeds touch in midline 5

4 T1 and γ not deeply recessed at lateral corner of female caudal ramus, setae T1–T4 slender, T2 and T3 very close together. Terminal pair of setae on P3 and P4 endopod long, straight spinous (not plumose). No massive dorsal cuticular honeycomb ..... *Dilatatiocauda*

—— T1 and γ setae deeply recessed at lateral corner of female caudal ramus, T1 slender, T2, T3 and T4 large, pinnate, equally spaced. Massive cuticular honey-comb on back ..... *Cereudorsum*

5 Female caudal ramus rectangular, setae T1 and γ not recessed, T1, T2, T3 and T4 large, pinnately clavate (Fig. 12D, R), equally spaced across posterior edge. Lateral ridges (rugosities) on anterior lobe of female genital double-somite ..... *Clavigofera*

—— Setae T1–T4 on female caudal ramus never pinnately clavate or equally spaced across posterior edge. No rugosities on female genital double-somite. Caudal rami may be rectangular, pentagonal or rhomboid 6

6 Female caudal ramus rectangular, may widen posteriorly, T1 and γ setae may *or* may not be recessed at lateral corner, T2, T3 and T4 attached to posterior edge, (Fig. 12E, F, G, H) 7

—— Female caudal ramus pentagonal, medial corner 90°, lateral corner with T1 and γ on sloping (bevelled) edge, T2 and T4 on straight posterior edge. (Fig. 12I), T3 absent 9

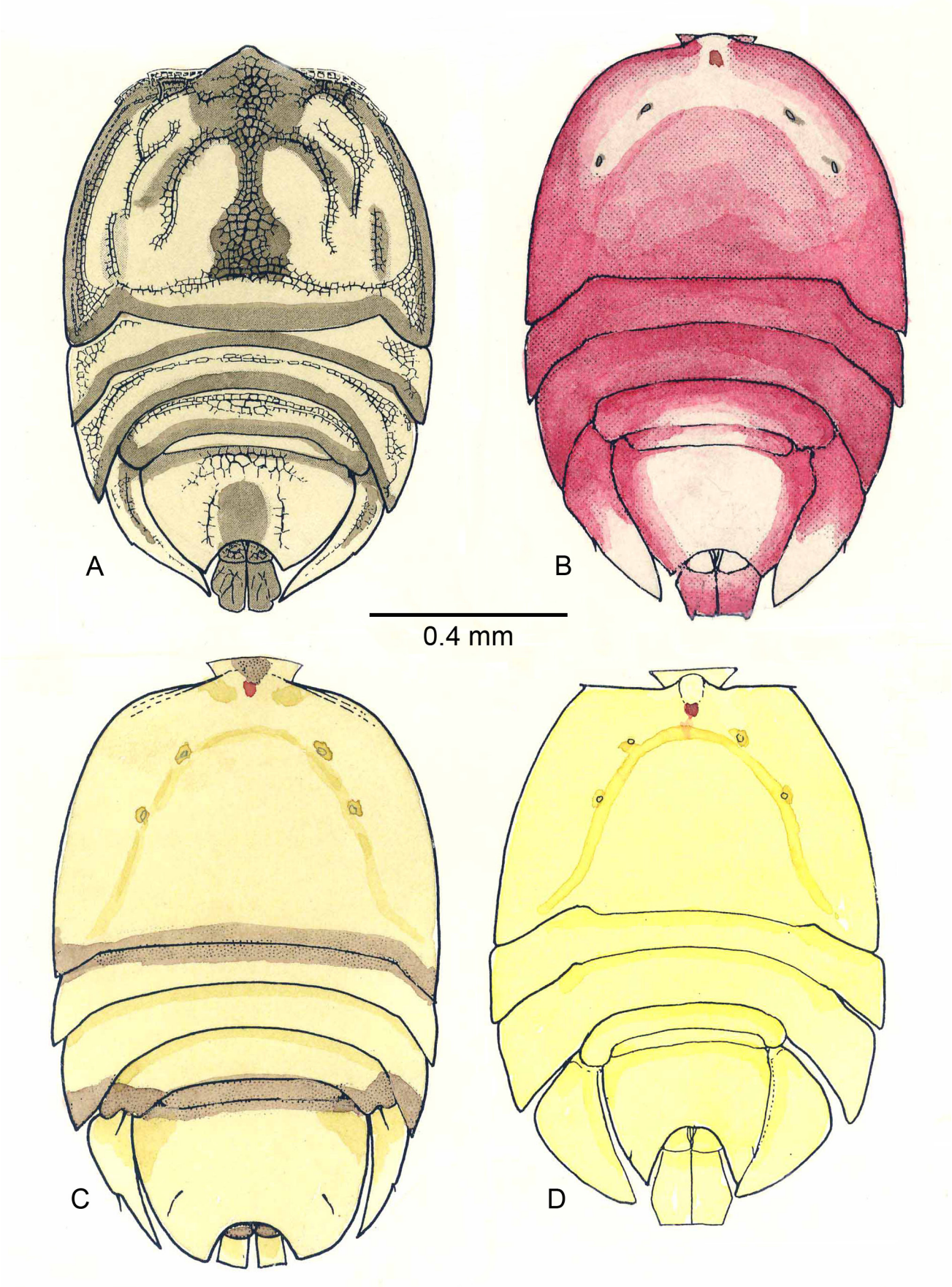

Plate 3. *(A) Brevifrons faviolatum* Harris, 1994, female. *(B) Mucrorostrum yoroium* Harris & Iwasaki, 1997, female, Japan. *(C) Murramia bicincta* Harris, 1994, female. *(D) Geddesia quadrata* sp. nov., female. All Australian species.

—— Female caudal ramus rhomboid or rounded posteriorly; terminal seta T2 always present, T1 or T3 may be absent (Fig. 12J or K, L); posterior edge straight at acute angle with medial edge (bevelled) and T4 at apex (Fig. 12M, N) *or* posterior edge convex with T4 at apex (Fig. 12K) *or* posterior edge may be rounded, no apex (Fig. 12 O) 10

7 Female caudal ramus lateral corner deeply recessed or bevelled bearing T1 and γ. T2 and T3 very close, T4 near medial corner, (Fig. 12G). Anterior comb on segment 3 of male antennule[b]. Falciform ridge of female P5 extended as ventral expansion (Fig. 12P). Maxillule[a] endopod with six setae ..... *Kushia*

—— Female caudal ramus with T1 and γ deeply recessed at lateral corner. T2, T3 and T4 evenly spaced across posterior border (Fig. 12H). Female genital double-somite narrow, pointed posteriorly. No comb on segment 3 of male antennule. No ventral expansion on female P5. Maxillule[a] with two setae on endopod. (Plate 3A, p. 190) ..... *Brevifrons*

—— Female caudal ramus may *or* may not be recessed (Fig. 12E, F).T2 and T3 very close, T4 near medial corner. Female genital double-somite broad, rounded posteriorly. No comb on segment 3 of male antennule. No ventral expansion on female P5. Maxillule[a] with six setae on endopod 8

8 Male antennule[b] δ' seta absent from anterior lobe, δ seta and one coupling denticle present on segment 3, ventral lobe (blade or knob) absent, segment 4 with four denticles (large denticulate pad plus three serrated denticles). (Plate 3C, p. 190) ..... *Murramia*

—— Male antennule[b] setae δ and δ' always present on anterior lobe of segment 3 but no coupling denticle, a ventral lobe (blade or knob) may be present, segment 4 with three denticles (shapes variable but never a brush-pad) ..... *Porcellidium*

9 Maxillule[a] endopod with six setae. Anterior of male cephalosome concave. Male antennule[b] segment 3 without a coupling denticle, segment 4 with two denticles. (Plate 3D, p. 190) ..... *Geddesia*

—— Maxillule[a] endopod with two setae. Anterior of male cephalosome semicircular (not truncated). Male antennule[b] with one denticle on segment 3, segment 4 with four denticles. (Plate 3B) ..... *Mucrorostrum*

—— Maxillule[a] endopod with one seta. (Male characters not known) ..... *Clunia*

10 Male P5 oval with one lateral seta, terminal setae absent or reduced to very small spines. Anterior of male cephalosome deeply concave. Seta T1 absent from caudal ramus, T3 present, (Fig. 12J). Female genital double-somite not divided into anterior and posterior lobes ..... *Synurus*

—— Male P5 trapezoid with six terminal setae. Anterior of male cephalosome semicircular. Seta T1 present, T3 absent from caudal ramus, (Fig. 12K, L). Female genital double-somite not divided into anterior and posterior lobes ..... *Ravania*

—— Male P5 trapezoid with six terminal setae. Anterior of male cephalosome truncated. Seta T1 and T3 present on caudal ramus, (Fig. 12M–O). Female genital double-somite divided into anterior and posterior lobes by notch, cleft or indentation ..... *Acutiramus*

[a] Study of maxillule setation requires dissection, but a maxillule with six setae on the endopod can usually be identified without dissection (see Fig. 13 for position of maxillule).

[b] The male antennule must be viewed from ventral aspect fully extended (see *Methods and terminology*). For different "types" of coupling denticle arrangement, see Harris (2014b, pp.161–162).

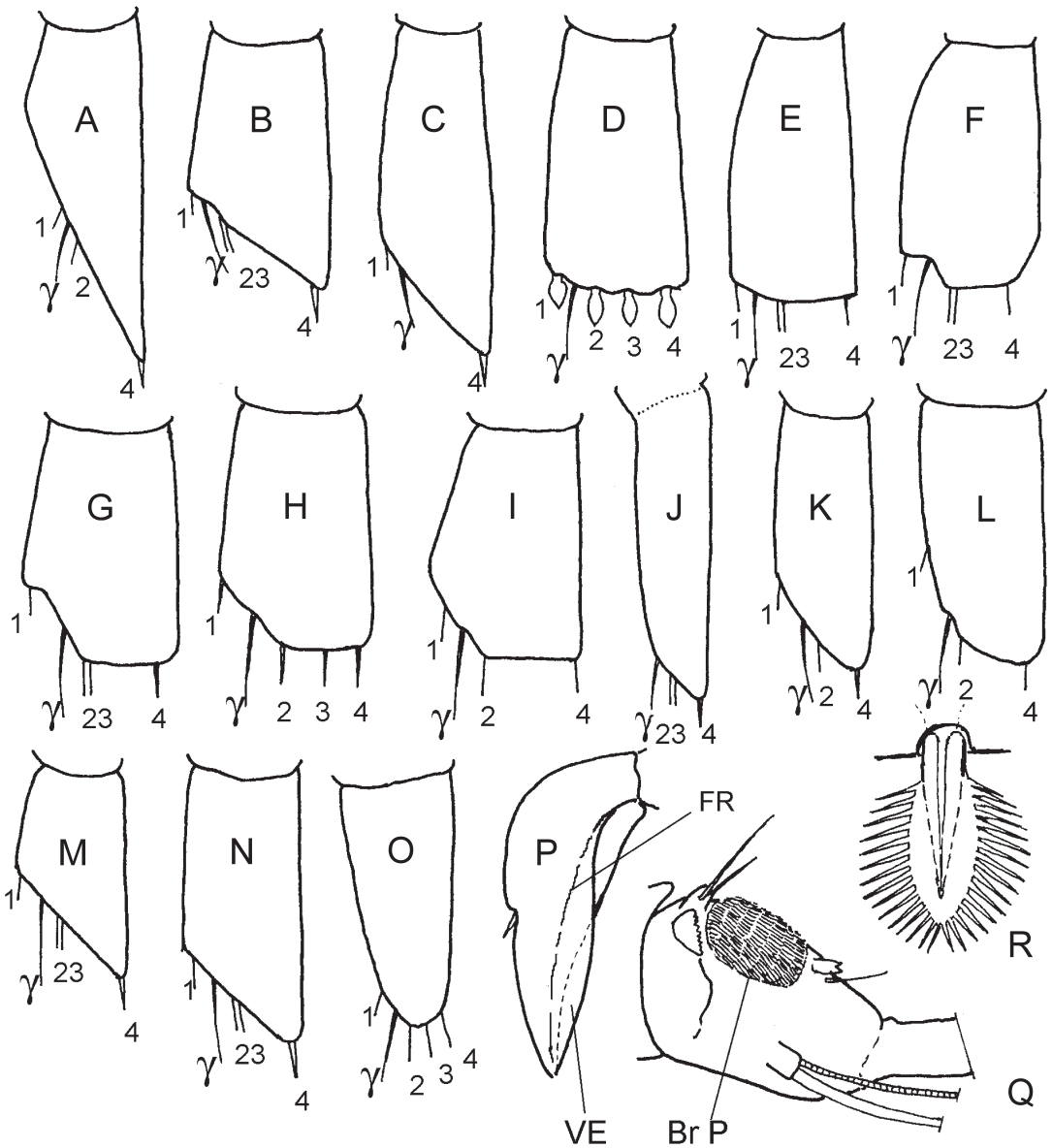

Figure 12. Types of female left caudal ramus and terminal setae found in the Porcellidiidae (α and β seta not shown). *(A, B) Porcelloides. (C) Kensakia. (D) Clavigofera. (E, F) Porcellidium, Tectacingulum, Murramia* and *Dilatatiocauda*. *(G) Kushia*. *(H) Brevifrons* and *Cereudorsum. (I) Mucrorostrum, Geddesia* and *Clunia. (J) Synurus. (K, L) Ravania. (M, N, O) Acutiramus*. *(P) Kushia,* female right P5 ventral view (*VE*, ventral expansion; *FR*, falciform ridge). *(Q) Kensakia*, male antennule (ventral view; *Br P,* Brush-pad). *(R) Clavigofera,* pinnate clavate terminal seta from caudal ramus.

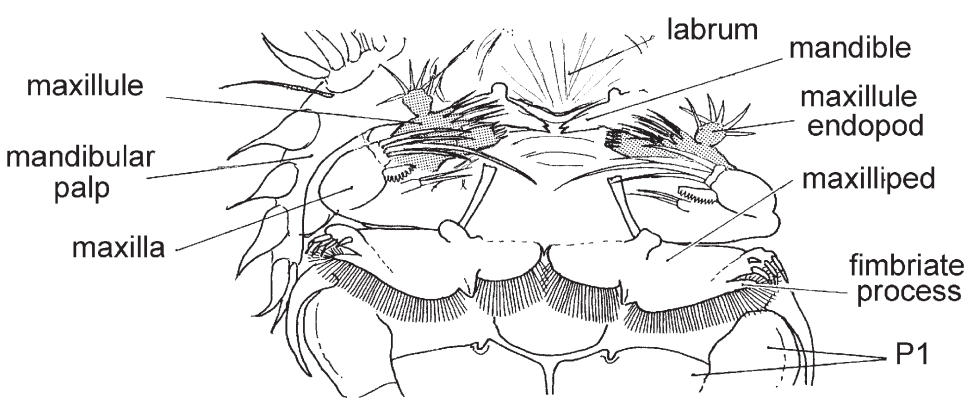

Figure 13. Ventral view of mouth region showing position of maxillule endopod, (*Mx1*, maxillule; *END*, maxillule endopod; *Mx2*, maxilla; *MXP*, maxilliped; *MDP*, mandibular palp; *MP*, molar process; *LAB*, labrum).

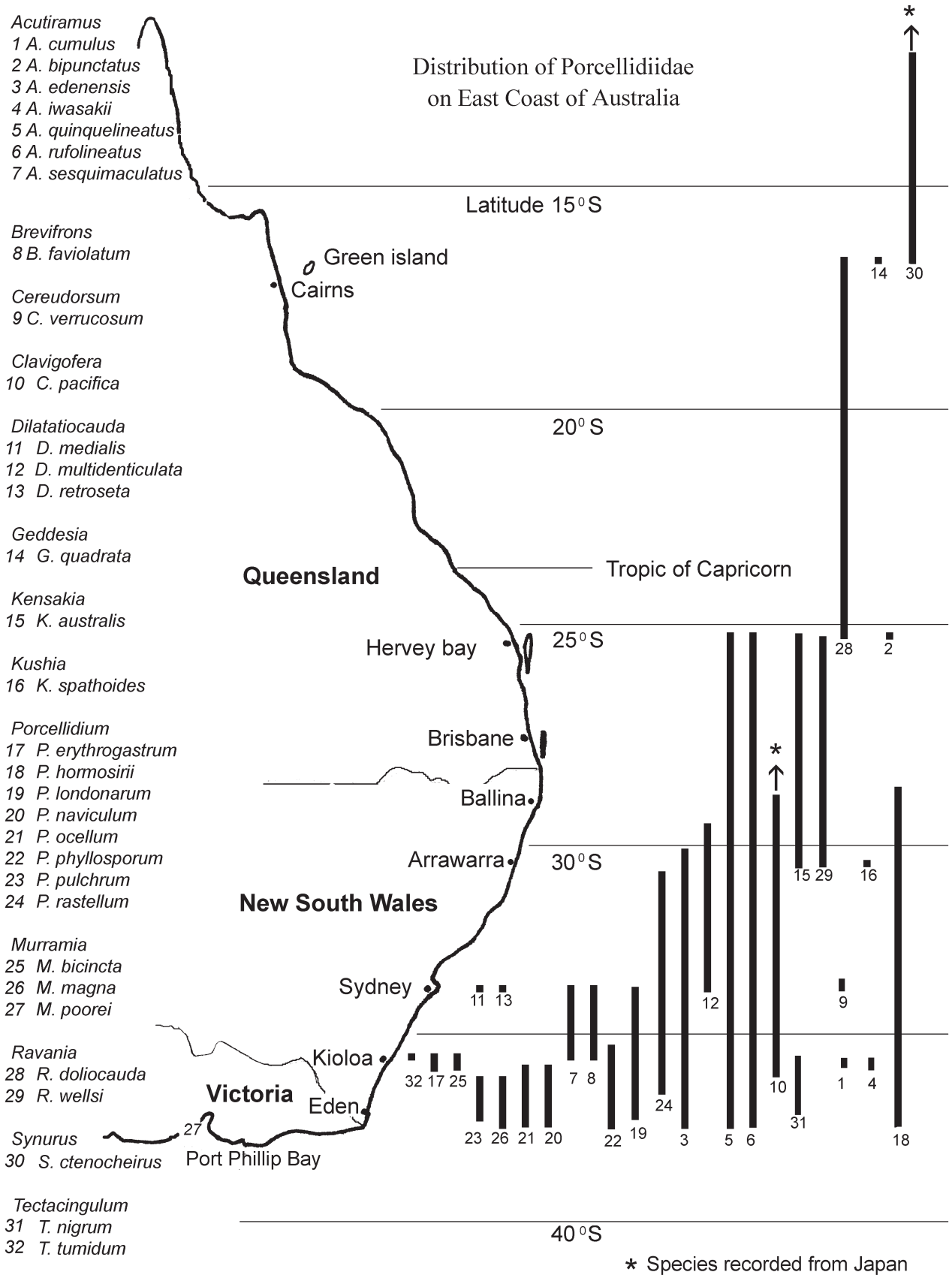

Figure 14. Australian Porcellidiidae. List of species and their known distribution.

Table 2. List of species sufficiently well described to be placed in a genus (in alphabetical order).

genus/species		original name and author	locality	size in mm female	male
PORCELLIDIDAE					
Acutiramus Harris & Robertson, 1994					
A. bipunctatus	1	Harris, 2014b	Qld[a] Australia	0.63	0.56
A. brevicaudatus	2	*Porcellidium brevicaudatum* Thompson & Scott, 1903	Sri Lanka/Madagascar/ Korea	0.78	0.53
A. cumulus	3	Harris, 2014b	NSW[a] Australia	0.78	0.55
A. edenensis	4	Harris, 2014b	NSW[a] Australia	0.67	0.49
A. geddesi	5	*P. ovatum* Geddes, 1968	W. Indies	0.62	0.51
A. iwasakii	6	Harris, 2014b	NSW[a] Australia	0.70	0.54
A. paguri	7	*P. paguri* Ho, 1986	Japan	0.56	0.46
A. quinquelineatus	8	Harris & Robertson, 1994	NSW/Qld Australia	0.55	0.43
A. rufolineatus	9	Harris & Robertson, 1994	NSW/Qld Australia	0.52	0.48
A. sesquimaculatus[b]	10	*Kioloaria sesquimaculata* Harris, 1994	NSW Australia	0.76	0.59
A. similis	11	*P. similis* Kim & Kim, 1996	Korea	0.76	0.50
A. tapui	12	*P. tapui* Hicks & Webber, 1983	New Zealand	0.69	0.51
Brevifrons Harris, 1994					
B. faviolatum	13	Harris, 1994	NSW Australia	1.00	0.83
Cereudorsum gen. nov.					
Cer.verrucosum	14	sp. nov.	NSW Australia	0.92	0.72
Clavigofera Harris & Iwasaki, 1996b					
Cla. clavigofera	15	*P. clavigerum* Pesta, 1935	Honolulu	0.5	?
Cla. echinophila	16	*P. echinophilum* Humes & Gelerman, 1962	Madagascar	0.57	0.43
Cla. laurencia	17	*P. laurencium* Hicks, 1982	South Africa	0.80	0.53
Cla. pacifica	18	Harris & Iwasaki, 1996b	Japan/NSW Australia	0.58	0.42
Cla. ulva	19	*P. ulvum* Hicks, 1982	South Africa	0.80	0.53
Clunia gen. nov.					
Clu. cocosensis	20	sp. nov.	Cocos Keeling Islands	0.97	—
Dilatatiocauda Harris, 2002					
D. bipartita	21	*P. bipartitum* Kim & Kim, 1997	Korea/Japan	1.70	1.00
D. dilatata	22	*P. dilatatum* Hicks, 1971	New Zealand	0.92	0.63
D. medialis	23	Harris, 2002	NSW Australia	0.92	0.70
D. multidenticulata	24	Harris, 2002	NSW Australia	0.84	0.58
D. plana	25	*P. planum* Tiemann, 1977	Mozambique	1.07	0.79
D. retroseta	26	Harris, 2002	NSW Australia	0.93	0.67
D. tristanensis	27	*P. tristanense* Wiborg, 1964	SW Africa	0.89	0.77
Geddesia gen. nov.					
G. quadrata	28	sp. nov.	Qld Australia	1.06	0.86
G. trisetosa	29	*P. trisetosum* Geddes, 1968	Bahamas	0.78	0.63
Kensakia Harris & Iwasaki, 1997					
Ke. acuta	30	*P. acutum* Kim & Kim, 1997	Korea/Japan	0.90	0.74
Ke. acuticaudata[c]	31	*P. acuticaudatum* Thompson & Scott, 1903	Sri Lanka/Maldives	0.65	0.50
Ke. australis	32	Harris, 2014b	Qld Australia	0.61	0.55
Ke. parva	33	Harris & Iwasaki, 2009	Malaysia	0.54	0.45
Ke. shimodensis	34	Harris & Iwasaki, 2009	Japan	1.06	0.81
Kushia Harris & Iwasaki, 1996b					
Ku. gamoi	35	Harris & Iwasaki, 1996b	Japan/Korea	0.64	0.62
Ku. igaguria	36	Harris & Iwasaki, 1996b	Japan	0.78	0.66
Ku. spathoides	37	Harris, 2014b	NSW Australia	0.74	0.68
Ku. zosteraphila	38	Harris & Iwasaki, 1996b	Japan	0.93	0.76
Mucrorostrum Harris & Iwasaki, 1997					
Muc. yoroium	39	Harris & Iwasaki, 1997	Japan	1.08	0.86
Murramia Harris, 1994					
Mur. bicincta	40	Harris, 1994	NSW Australia	1.07	0.86
Mur. magna	41	Harris, 1994	NSW Australia	1.38	1.21
Mur. poorei[d]	42	*P. poorei* Walker-Smith, 2001	Victoria[a] Australia	0.81	0.62

Continued on next page

Table 2—*Continued*

genus/species		original name and author	locality	size in mm female	male
Porcellidium Claus, 1860					
P. akashimum	43	Harris & Iwasaki, 1996a	Japan	0.84	0.69
P. algoense	44	Hicks, 1982	South Africa	0.61	0.46
P. brevicavum	45	Kim & Kim, 1997	Korea/Japan	0.73	0.63
P. erythrum	46	Hicks, 1971	New Zealand	0.57	0.48
P. erythrogastrum	47	Harris & Robertson, 1994	NSW Australia	0.83	0.61
P. fimbriatum	48	Claus, 1863	Europe	0.76	0.56
P. hartmannorum	49	Tiemann, 1978	SW Africa	0.76	0.55
P. hormosirii	50	Harris & Robertson, 1994	NSW Australia	0.68	0.50
P. kiiroum	51	Harris & Iwasaki, 1996a	Japan	0.81	0.58
P. londonarum	52	*P. londonii* Harris, 1994	NSW Australia	0.75	0.57
P. naviculum	53	Harris & Robertson, 1994	NSW Australia	0.72	0.57
P. ocellum	54	Harris & Robertson, 1994	NSW Australia	0.67	0.56
P. ofunatense	55	Harris & Iwasaki, 1996a	Japan/Korea	0.94	0.68
P. phyllosporum	56	Harris & Robertson, 1994	NSW Australia	0.93	0.73
P. pulchrum	57	Harris & Robertson, 1994	NSW Australia	0.71	0.55
P. rastellum	58	Harris, 2014a	NSW Australia	0.77	0.54
P. roscoffensis	59	*P. lecanoides* var. *roscoffensis* Bocquet, 1948	Europe	0.85	0.70
P. rubrum	60	Pallares, 1966	Argentina	0.69	0.61
P. viride	61	Philippi, 1840	Europe	0.91	0.62
P. wandoensis	62	Kim & Kim, 1997	Korea/Japan	0.69	0.61
Porcelloides Harris, 2014a					
Poi. scutatus	63	*Porcellidium scutatum* Claus, 1889	Europe	0.84	0.78
Poi. tenuicaudus	64	*Porcellidium tenuicauda* Claus, 1860	Europe	1.40	0.78
Ravania Harris, 2014b					
R. doliocauda	65	Harris, 2014b	Qld Australia	0.75	0.66
R. ravanae	66	*P. ravanae* Thompson & Scott, 1903	Sri Lanka	0.64	0.55
R. wellsi	67	Harris, 2014b	Qld Australia	0.57	0.51
Synurus Harris, 2014b					
S. ctenocheirus	68	Harris, 2014b	Qld Australia/Japan	0.68	0.48
S. unicus	69	*P. unicus* Ummerkutty, 1970	Sri Lanka	0.75	0.63
Tectacingulum Harris, 1994					
T. nigrum	70	Harris, 1994	NSW Australia	0.95	0.68
T. tumidum	71	Harris, 1994	NSW Australia	1.14	0.76

[a] NSW = New South Wales, Qld = Queensland.

[b] Transferred to *Acutiramus*, see Walker-Smith (2001).

[c] Placed in *Acutiramus* by Harris & Robertson (1994). Specimens labelled *Porcellidium acuticaudatum* in the NHM collection (1928.4.2.43) from Lake Timsâh, Ismalia do not have T2 or T3 on the trapezoid caudal ramus—diagnostic characters for *Kensakia*.

[d] Walker-Smith confirms that the male antennule is characteristic of *Murramia* (personal communication).

· The following may be valid species, but are omitted from this list because their description does not allow them to be placed in a genus; they require redescription, (*fulvum* and *interruptum* Thomson, 1882, *tuberculatum* Wolfenden, 1905, *scotti* Pesta, 1935 and *malleatum* Vervoort, 1964).

· The species recorded from South Australia by Nicholls (1941) cannot be identified from his descriptions and are not considered here.

Many species occur in large populations on particular species of algae or sea grass, for example *Porcellidium hormosirii* is abundant on *Hormosira banksii*, the dominant mid-littoral alga on the NSW coast, but neither species are found at Hervey Bay. *P. phyllosporum* has only been found on *Phyllospora commosa* and *P. naviculum* on *Cystophora moniliformis*. *Tectacingulum nigrum* and *Murramia bicincta* are only found on other species of *Cystophora* common on the southern coast of NSW. From Sydney to the northern coast of NSW *Dilatatiocauda multidenticulata* is abundant on *Sargassum* which replace the *Cystophora* species. This shows that porcellidiid copepods tend to select particular seaweeds, consequently their distribution will be influenced by the distribution of algal species.

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