

## Armadillidae (Crustacea: Isopoda) from Lord Howe Island: New Taxa and Biogeography

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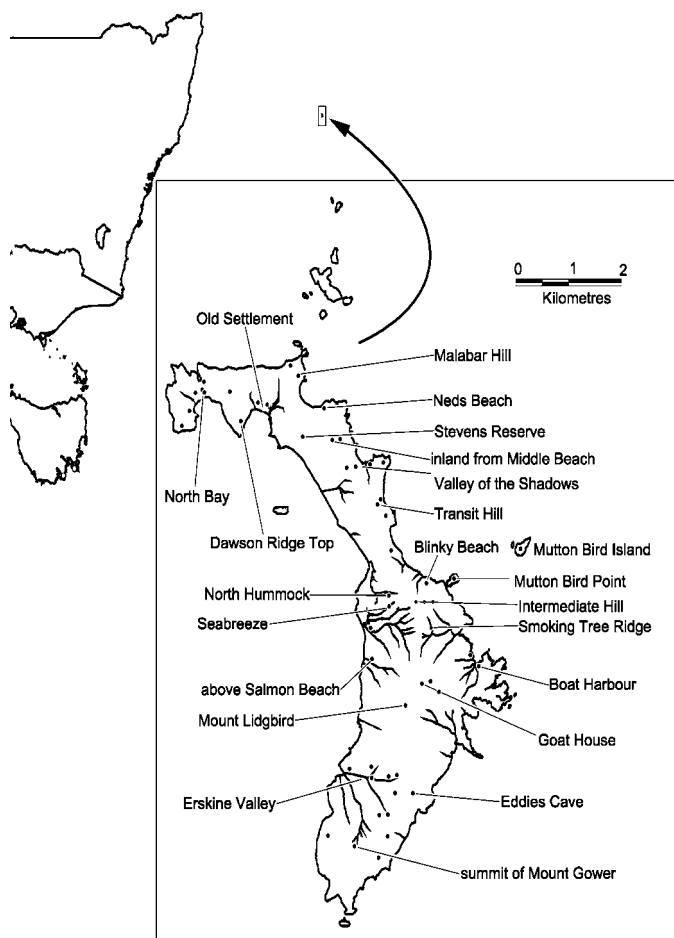
**ABSTRACT.** Lord Howe Island and associated island, Ball's Pyramid, in the Tasman Sea between Australia and New Zealand, have a surprising diversity of terrestrial isopods. New species in the genera *Pyrgoniscus*, *Cubaris* and a new genus (*Stigmops*, n.gen.) of the family Armadillidae are described from Australian Museum collections made on Lord Howe Island. Two species, formerly placed in *Anchicubaris*, are moved to the new genus. *Anchicubaris* is revised to show how it differs from the new genus. With these changes, species of *Anchicubaris* no longer occur on Lord Howe Island. A lectotype for *Anchicubaris fongosiensis* is assigned. The homonymy of *Cubaris granulatus* Lewis, 1998b is resolved with a new name and a type species for the genus *Sphenodillo* Lewis, 1998b is assigned. A key to Lord Howe Armadillidae is provided. The biogeography of Armadillidae genera on Lord Howe Island shows possible links to neighbouring regions of New Caledonia and eastern Australia. Because relationships of species in the large genera *Cubaris* and *Pyrgoniscus* are unknown, precise area relationships cannot be estimated. The high diversity and presence of armadillids on the nearby rock, Balls Pyramid, suggests that the Lord Howe fauna is a contracted remnant of a much larger Pleistocene fauna, when lowered sea levels provided interconnections and much larger areas.

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Lord Howe Island is a small, subtropical island situated on the Lord Howe Rise in the Tasman Sea approximately 700 km northeast of Sydney (31°33'S 159°05'E, Fig. 1). The island covers an area of approximately 15 km<sup>2</sup> and is the eroded remnant of volcanic activity 6–7 million years ago. The main island is dominated by two peaks, Mount Gower (875 m) and Mount Lidgerbird (777 m) in the south, hills in the north (up to 200 m high) and lowlands in the middle of the island (Hutton, 1986).

The Lord Howe Rise, upon which the island sits, was separated first from New Zealand and later from Australia approximately 80 million years ago (Hutton, 1986). The

Rise has been subject to several sea level changes during which exposed islands have acted as permanent refuges for indigenous organisms or as “stepping stones” for organisms from other landmasses (Clark & Pickard, 1977). The flora and fauna have close relatives in Australia, New Zealand, New Caledonia and Norfolk Island, but its long-term isolation has resulted in a high proportion of endemic species. These species were largely undisturbed until the first recorded human contact in 1788 when Europeans landed on the island. A permanent settlement was founded in 1834 (Hutton, 1986).



**Figure 1.** Map of Armadillidae localities on Lord Howe Island based on data from the Australian Museum invertebrate collection. Not all locality names appear in Table 1.

Ball's Pyramid is a much smaller island 25 km southeast of Lord Howe Island that consists of a 550m high steep rock (Sutherland & Ritchie, 1977). It is part of the Lord Howe Island group and connected to the main island by an underwater ridge. Some endemic species that are extinct or are close to extinction on the main island, still persist on Ball's Pyramid. For example, the only two reptiles (a skink, *Leiopisma lichenigera*, and a gecko, *Phyllodactylus guentheri*) native to the Lord Howe group (Hutton, 1986) are found on Ball's Pyramid.

Three species of Armadillidae have been reported from Lord Howe Island by Vandell (1973) and a further 16 by Lewis (1998b). These species were placed in seven different genera: *Australiodillo* Verhoeff, 1926, *Cubaris* Brandt, 1833, *Anchicubaris* Collinge, 1920, *Orthodillo* Vandell, 1973, *Pseudodiploexochus* Arcangeli, 1934, *Pyrgoniscus* Kinahan, 1859 and *Sphenodillo* Lewis, 1998b. The only published records of non-armadillid terrestrial isopods from Lord Howe Island are *Tasmanoniscus evansi* Vandell, 1973 (Oniscidae), *Trichorhina* sp. Lewis, 1998b (Platyarthridae) and *Ligia australiensis* Dana, 1853 (Ligiidae). Two cosmopolitan species of the family Porcellionidae are also recorded: *Porcellio laevis* Latreille, 1804 and *Porcellionides pruinosus* (Brandt, 1833). These latter two species have been introduced to the island, presumably from Europe.

Despite this previous taxonomic research, terrestrial isopods from Lord Howe Island held in the collections of the Australian Museum include at least 38 different species belonging to the families Actaeiidae, Armadillidae, Philosciidae, Styloniscidae, Oniscidae and Ligiidae (BL, unpubl. observations). This apparent diversity is surprising, given the isolation and small size of the islands. Island biogeography theory (MacArthur & Wilson, 1967) predicts that isolated islands, particularly young ones like Lord Howe Island, should have depressed diversity compared to the mainland regions. The observed high diversity may be a remnant from a much larger area occurring from low sea levels of previous glacial cycles. Alternatively, this level of armadillid diversity might be typical for islands, but only been brought to light by detailed surveys that have been much more extensive than on mainland Australia. If this is the case, then Australian oniscidean diversity may be enormous, requiring detailed assessments of the continental regions.

Oniscidea, the terrestrial isopods, is a monophyletic group based on the reduced triarticulate antennule and the terrestrial adaptations of the pleopods (Schmalfuss, 1989; Tabacaru & Danielopol, 1996; Erhard, 1998). Within the Oniscidea, the Armadillidae is a large family with 78 described genera and approximately 700 species. Selected genera or taxa from geographical areas have been revised, but a comprehensive revision of the entire family has not been done. The taxonomy of the family is therefore confused and in need of a global revision. Nevertheless, the Armadillidae is considered to be monophyletic owing to the dorsal insertion of the uropodal exopod, and perhaps the presence of a bilobed lamellar process on the seventh male pereonite sternite (yet to be confirmed in many species) (Taiti *et al.*, 1998).

In this paper, we describe four new species from the armadillid genera *Stigmops*, n.gen., *Pyrgoniscus* and *Cubaris* from the Australian Museum collection. Two species, formerly placed in *Anchicubaris*, are moved into the new genus. We diagnose the new genus and revise *Anchicubaris*, including assigning a lectotype for *Anchicubaris fongosiensis*. The homonymy of *Cubaris granulatus* Lewis, 1998b is resolved and a type species for the genus *Sphenodillo* Lewis, 1998b is assigned. A revised key includes all Lord Howe Armadillidae. Biogeography of the Armadillidae on Lord Howe Island is also discussed.

## Materials and methods

Specimens used in this study came from two faunal surveys of Lord Howe Island: T. Kingston and B. Miller (abbreviated K&M) for the Australian Museum "Woodhen Project" in 1978–79 and by G. B. Monteith (abbreviated GBM) as part of a Queensland Museum berlesate study in 1978–80. Table 1 provides the locality data for sample numbers used in the descriptions. Position coordinates of samples were found to have a systematic error owing to the use of an outdated chart; all positions were corrected using a recent digital map of Lord Howe Island. In some cases, no sample numbers were assigned in the original survey, so the sample may be found in Table 1 by referring to the sample date. Photos of live specimens of *Stigmops polyvelota* n.gen., n.sp. and *Stigmops odontotergina* n.sp. were taken by Kingston and Miller. Because specimens of the other species have been preserved in ethanol, live colours cannot be determined.

**Table 1.** Lord Howe Island localities of terrestrial isopods in the Australian Museum collection. Vegetation type abbreviations: Ct (*Cryptocarya triplinervis*), Cf (*Cleistocalyx fullageri*), Da (*Drypetes australascia*), Hb (*Howea belmoreana*), Hf (*Howea foresterana*), Lf (*Leptospermum flavescens*), Lq (*Linociera quadristaminea*).

place name	latitude longitude	Woodhen Site vegetation type	station number	date collected	collector(s)
Dawson Ridge Top	31°31.3'S 159°03.3'E	Rainforest	no stn. no.	05.xi.1979	GBM
Inland from Middle Beach	31°31.5'S 159°04.4'E	Hf	QMB127	06.xi.1979	GBM
Seabreeze	31°33.0'S 159°05.0'E		no stn. no.	12.ii.1979	K&M
Smoking Tree Ridge, east face	31°33.2'S 159°05.5'E	Cf, Lq (rainforest)	QMB 163	23.xi.1979	GBM
Boat Harbour	31°33.6'S 159°06.1'E	Cf, Lq (rainforest)	QMB 161	23.xi.1979	GBM
Eddies Cave on Gower Track, NE of summit	31°34.8'S 159°05.3'E		QMB 146	16.xi.1979	GBM
southern shoreline of Blinky Beach	31°32.7'S 159°05.5'E	Da, Ct, Hb	QMB 142	12.xi.1979	GBM
Old Settlement	31°31.2'S 159°03.6'E	9; Da, Ct	LHI517	2.iv.1979	K&M
			LHI544	18.iv.1979	K&M
			no stn. no.	5.xi.1979	GBM
Transit Hill (Clear Place)	31°31.5'S 159°05'E	1; Da, Ct, Hf	LHI126	19.ix.1978	K&M
			LHI139	22.ix.1978	K&M
			QMB157	xi.1979	GBM
North Bay	31°31'S 159°03'E	7; Da, Ct, Hf (rainforest)	LHI413–430	15.xi.1978	K&M
			QMB155–156,131	xi.1979	GBM
Stevens Reserve	31°31'S 159°04.5'E	2; Hf forest	LHI196	1.x.1978	K&M
			LHI596	11.vii.1979	K&M
			QMB132,127	xi.1979	GBM
Intermediate Hill	31°32.9'S 159°05.4'E	5; Cf, Lq (rainforest)	QMB123	6.xi.1979	GBM
			QMB142	12.xi.1979	GBM
			QMB163	23.xi.1979	GBM
North Hummock	31°32.9'S 159°05'E	Cf, Lq (rainforest)	QMB125,142	xi.1979	GBM
Erskine Valley	31°34.5'S 159°05'E	8; Da, Ct (rainforest)	no stn. no.	13.ix.1978	K&M
Little Slope, west side of Mount Gower	31°35.0'S 159°04.5'E	6; Hf forest	LHI351–370	22.xi.1978	K&M
			LHI371–382	22.xi.1978	K&M
			LHI385–392	20.xii.1978	K&M
			LHI178 095	30.ix.1978	K&M
			LHI610,613	11.vii.1979	K&M
Mount Gower	31°35'S 159°05'E	3; gnarled mossy forest, Lf	no stn. nos.	8.vii.1978	K&M
			no stn. nos.	21.i.1979	K&M
			no stn. nos.	28.ii.1979	K&M
			no stn. nos.	29.iii.1979	K&M
			no stn. nos.	26.iv.1979	K&M
			no stn. nos.	9.xii.1979	K&M
Ball's Pyramid	31°46'S 159°16'E	Behind exfoliating rock	no stn. nos.	21.i.1980	K&M
			no stn. nos.	24.i.1980	K&M

Some samples on loan during this study were returned only after the manuscript was finished, and were not compared with the main collection; these are referred to as “Additional material not examined”. Sex is given only for specimens that were used for the descriptions.

SEM preparation included cleaning of specimens using ultrasound and gentle brushing, where needed. The dehydration process included at least one hour in each of the following baths: 25%, 50%, 70%, 80%, 90%, 100% ethanol and 100% acetone twice followed by critical point drying using 3 cycles of 3 minutes purging and 5 minutes substitution. Images were saved in a TIF format for later processing.

Light micrographs were taken using a Leica MZ8 dissecting microscope with an attached Pixera PVC100C camera connected to a microcomputer. For calibration, an one mm grid was photographed at all scales used. Images were saved in a TIF format.

All images were modified using Adobe Photoshop (ver. 5). For assembly of the plates, the background of each image was deleted and the image was pasted into a transparent layer over a black background. The greyscale tones of each image were adjusted to standardise their appearance. In some instances, a “sharpen” filter was employed to improve visibility of features. The greyscale figures are SEM images, except where indicated.

All examined specimens are deposited in the Australian Museum (AM), Sydney with accession numbers beginning with “P”, except for Natural History Museum, London catalogue numbers (BMNH). Descriptions follow the descriptive style of Wilson (1989), wherein the word “times” or “x” is not repeated for ratios; for example, “the length is 0.88 times the width” is simply reported as “length 0.88 width”. Otherwise, terms employed follow Schmalfuss & Ferrara (1983). Dimensions of some types are given as length × width in mm.

## Taxonomy

### Armadillidae Brandt & Ratzeburg, 1831

Diagnosis modified from Schmalzfuss & Ferrara (1983). Cephalon compressed longitudinally, with a wide frontal shield; body able to conglobate; pleotelson with quadrangular distal part; antennal flagellum consisting of two articles; maxillula inner lobe with two robust plumose setae; male pereonite 7 sternite with bilobed lamellar process; pseudotracheae on all pleopodal exopods (only on the first four in *Buddelundia*); uropodal protopod flattened with concave medial margin; uropodal exopod reduced, inserted dorsally near protopod medial margin.

### Implicit characters

The following are characters found in all species of Armadillidae treated in this paper and therefore can be implicitly included into the descriptions. We use this list as a device to shorten the descriptions, while still providing comparison with taxa that do not have these features. Figures 6, 9 and 10 illustrate many of the typical limb features present in the Armadillidae treated in this paper.

*Frons* surface slightly depressed to receive antennae; clypeus lateral processes rounded. *Mandible* incisor process with 4 rounded, simple teeth, smaller and more blunt on right mandible than left; left mandible incisor process with small blunt tooth-like structure at lacinia mobilis base; right mandible lacinia mobilis small with two small blunt teeth; left mandible lacinia mobilis larger, with two sharp ridge-like teeth; molar process with fan-shaped row of long setae along thin, elongate base. *Maxillule* outer lobe medial margin with 4 apical larger robust setae, 6 smaller robust setae below; lateral margin apical half with row of setae decreasing in length towards apex. *Maxilliped* basis rectangular, distolaterally strongly rounded; endite rectangular with three thick apical setae; palp article 1 (ischium) broad, flat with one long, thick apical seta on medial side, one smaller seta on midline; article 2 larger, subtriangular, length 2–2.5 article 1, with one apical group of four setae on medial side, one group of 2–3 setae just below, one group of 2–3 setae on lateral margin; article 3 smaller, elongate and narrow, width approximately 0.25 article 2 width, length 0.67 article 2 length, with apical brush of setae, two lateral fine seta. *Male pleopod 1* endopod elongate with grooved tapering distal half, row of short, thick setae along medial side of dorsal groove. Pleopod 2 exopod “L” shaped with broad proximal portion, distal portion elongate, distal half with ventral, densely setose groove; endopod proximal article small, triangular, distal article thin, narrow, tapering, with groove. Monospiracular covered pleopodal lungs present on all five pleopod exopods. *Uropod* protopod proximal portion not visible dorsally; exopod conical, inserted dorsally, not reaching protopod posterior margin, with apical setae; endopod cylindrical, inserted along protopod proximal inner margin, not reaching pleotelson posterior margin.

**Remarks.** Many armadillid generic types are poorly documented, causing misidentifications of many species. *Anchicubaris fongosiensis* Collinge, 1920 is one such type species, which led to the misidentification of species on Lord Howe Island as members of this genus. To revise species of Lord Howe Island, we must first revisit this species. We therefore provide a new diagnosis and illustrations of the lectotype of *A. fongosiensis* for comparison with the genus *Stigmops* n.gen.

### *Anchicubaris* Collinge, 1920

**Type species.** *Anchicubaris fongosiensis* Collinge, 1920, by monotypy.

**Restricted composition.** *Anchicubaris fongosiensis* Collinge, 1920; *A. annobonensis* Schmalzfuss & Ferrara, 1983; *A. scoriformis* Collinge, 1945.

**Diagnosis.** Tergites dorsally ornamented; conglobation by folding, retaining flange along sides; epimera almost horizontal; frontal lamina raised well above level of vertex, straight and without medial incision; epimera 1 endolobes rectangular drawn out into small tooth posteroproximally, epimera 2 endolobes tooth-like; pleotelson hour-glass shaped, distal part short, posterior margin straight; uropod protopod with narrow rectangular distal part; exopod present.

**Remarks.** The composition of *Anchicubaris* Collinge, 1920 is modified to clarify the affinities of some Lord Howe Island Armadillidae. Lewis (1998b) placed the Lord Howe Island species *Anchicubaris howensis* Lewis, 1998b and *A. demiclavula* Lewis, 1998b in this African genus based on similarities in the shape and distribution of the dorsal tubercles to *A. annobonensis* Schmalzfuss & Ferrara, 1983. The large cephalic lobes of *A. annobonensis* are similar to those of *A. demiclavula* but the arrangement of pereon tubercles in *A. annobonensis* is quite different. *Anchicubaris demiclavula* has 3 pairs of tubercles on pereonite 1 and two pairs on each of pereonite 2–7. Two new species described below, *Stigmops polyvelota* n.gen., n.sp. and *S. odontotergina* n.sp., show striking similarities with *A. howensis* and *A. demiclavula*, especially the unique shape and arrangement of the dorsal tubercles and cuticular pits. Our examination of the generic type, *A. fongosiensis* Collinge, 1920 (figs. 2, 3), demonstrates that these Lord Howe Island taxa do not belong in *Anchicubaris*. The shape and distribution of tubercles in *A. fongosiensis* bear no similarity to the Lord Howe Island taxa. Furthermore, *A. fongosiensis* differs in the following features: the cuticular pits characteristic of the Lord Howe Island taxa are absent, epimera 1 endolobes are rectangular (not narrowly pointed), the uropodal exopod is not visible ventrally and pleopods 3–5 exopods are more narrow and pointed, lacking the tuft of setae present on the distal tip in *Stigmops*. Therefore *A. howensis* and *A. demiclavula* are transferred to *Stigmops* n.gen. As a result of these observations, *Anchicubaris* does not occur on Lord Howe Island, thus removing a presumed biogeographic link between Lord Howe Island and Africa.

*Anchicubaris fongosiensis* Collinge, 1920

Figs. 2, 3

*Anchicubaris fongosiensis* Collinge, 1920: 484.

**Type material.** LECTOTYPE ♂ (ex BMNH 1933.1.25.851–870). PARALECTOTYPES (BMNH 1933.1.25.851–870); 85 ind (BMNH 1919.4.26.504–518), 34 ind.

**Type locality.** Mt. Fongosi, Zululand, South Africa, E. Jones, 17.vii.1917.

**Remarks.** We designate a large male specimen (ex BMNH 1933.1.25.851–870) from the large syntypic series as lectotype, with the remaining specimens becoming paralectotypes (BMNH 1933.1.25.851–870, BMNH 1933.1.25.504–518).

*Stigmops* n.gen.

**Type species.** *Stigmops polyvelota* n.sp.

**Composition.** *Stigmops polyvelota* n.gen. n.sp., *S. odontotergina* n.sp., *S. howensis* (Lewis, 1998b) and *S. demiclavula* (Lewis, 1998b).

**Diagnosis** (with differing *A. howensis* state between parentheses). Dorsal ornamentation distinct: cephalon with 4 (2) projecting lobes, ridge above eyes, pereonite 1 with one midline anterior and two posterior lobes, pereonites 2–7 each with pair of midline lobes, increasing in size posteriorly (pereonite 7 with small pair of midline tubercles); dorsal cuticle with scales and numerous pits (Fig. 7F); body convex with nearly horizontal epimera; conglobation with imperfect folding, leaving flange along sides; frontal lamina raised well above level of vertex, cleft in midline (entire); epimera 1 thin lateral margin, dorsal surface concave, epimera 1 ventral surface with ridge close to tergite junction ending in tooth-like endolobe, epimera 2 endolobe tooth-like, endolobes not visible dorsally; pleotelson sides near parallel or hourglass-shaped, posterior margin straight (indented); uropod exopod visible ventrally through gap between pleotelson and uropod protopod distal part.

**Etymology.** “*Stigmops*” means “pitted face”, based on the Greek words “stigma” (a spot or prick) and “ops” (the face). This feminine name refers to the pits on the head and elsewhere (e.g., Fig. 7F) seen in this genus.

**Remarks.** As discussed above, several species originally included in *Anchicubaris* Collinge have been transferred to *Stigmops* n.gen. We place four endemic Lord Howe Island species in *Stigmops*: *S. polyvelota* n.sp., *S. odontotergina* n.sp., *S. howensis* (Lewis, 1998b) and *S. demiclavula* (Lewis, 1998b). As discussed above, *Anchicubaris fongosiensis*, although related, lacks synapomorphies that support the monophyly of *Stigmops* species. *Stigmops* species shares some similarities with those in *Pyrgoniscus* Kinahan, 1859, including: tooth-like endolobes, epimera 1 with ventral longitudinal ridge, raised frontal lamina, the mode of conglobation and, in *Stigmops howensis* and *Stigmops demiclavula*, the shape of the pleotelson and uropods. These two genera differ in the shape and arrangement of dorsal tubercles, highly convex body shape and presence of cuticular pits.

*Stigmops polyvelota* n.sp.

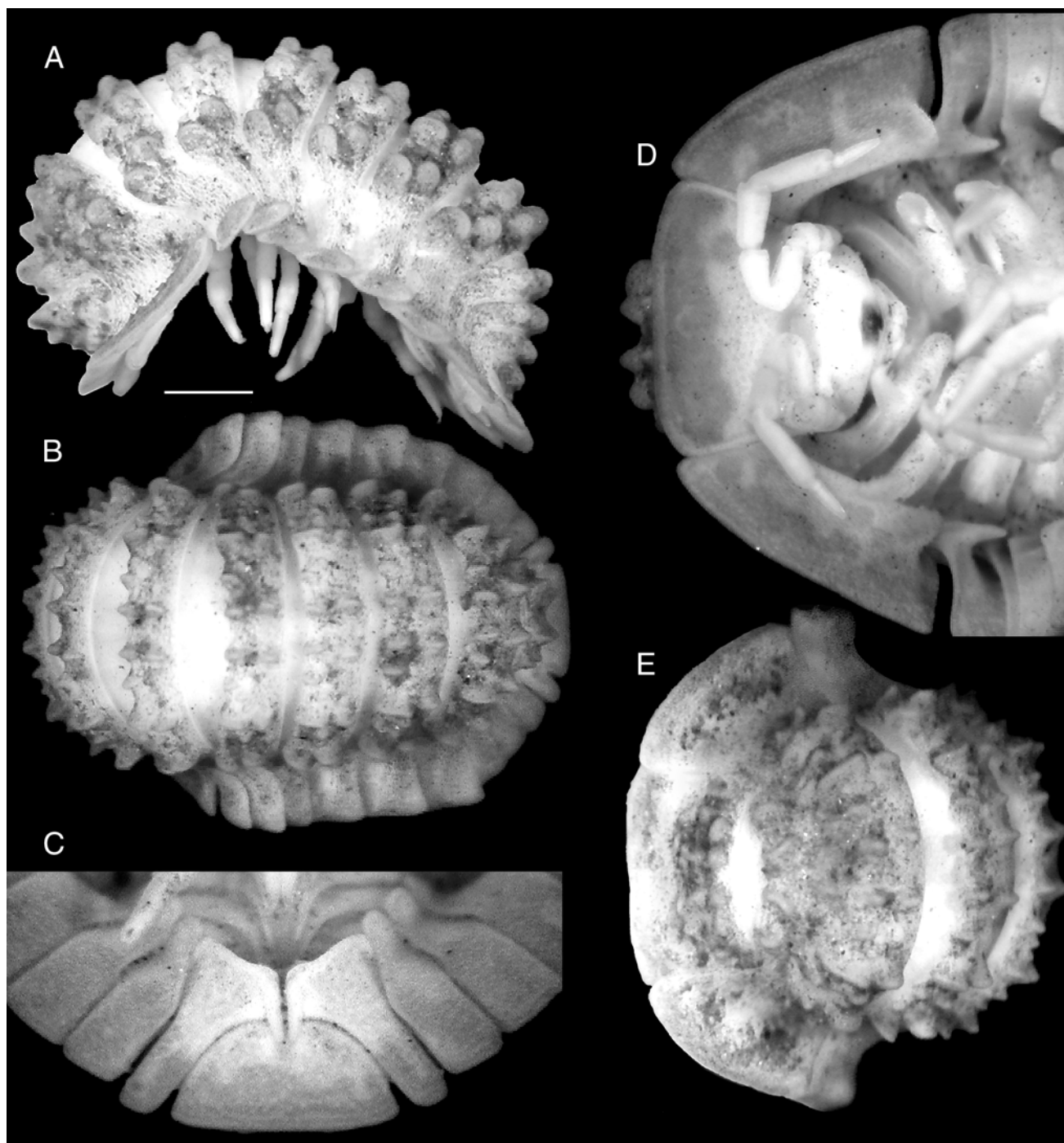
Figs. 4–6

**Type material.** HOLOTYPE ♂, P59952, 9.0 × 4.9 mm, K&M 28.ii.79. PARATYPES from K&M 26.iv.79: P59953, ♀, 8.9 × 4.5 mm, mouthparts on SEM stub, colour photograph K.1030; P59955, ♂, 3 SEM stubs; P59954, ♀.

**Type locality.** All specimens collected in pitfall traps on Mount Gower, Lord Howe Island, New South Wales, Australia, 31°35'S 159°05'E, altitude 600–650m, K&M, 28.ii.79 and 26.iv.79.

**Diagnosis.** *Cephalon* frontal lamina cleft; vertex with row of 4 lobes, not higher than pereonal lobes, middle two higher than lateral two. *Pereon* tergite 1–7 each with pair of broad laterally flattened lobes, lateral length of each near height, tergite 1 with one additional anterior transverse ridge-like lobe. *Pleonites* 3–4 dorsal surface with midline longitudinal tubercle, pleonite 3 tubercle larger than pleonite 4 tubercle. *Pleotelson* sides slightly constricted. *Uropod* protopod length 1.6 width; endopod 2.0 exopod length.

**Description.** *Colour* uniform brown in alcohol. Original photos show darker uniform brown. *Body* (Fig. 4A–C,E) convex with horizontal epimera. Cuticular pits and scales scattered on entire dorsal surface and frons. *Cephalon* (Fig. 4E) frontal lamina cleft, raised above vertex; vertex narrow with row of 4 lobes, not higher than pereonal lobes, middle two higher than lateral two, ridge above eyes; eyes small with approximately 10 ocelli. *Pereon* (Fig. 4A–D) tergite 1–7 dorsal ornamentation consisting of pair of broad laterally flattened lobes on each tergite increasing in size towards posterior, rest of each tergite with low scattered tubercles, tergite 1 with one additional anterior transverse ridge-like lobe, epimera without tubercles. Epimera 1 narrowly rounded anteriorly, lateral margin simple, posterior margin broadly rounded, dorsal surface concave, ventral surface with longitudinal ridge close to tergite junction extending from anterior margin, ending in tooth-like endolobe anterior to posterior margin; epimera 2 anterior and posterior margins rectangular, anterior margin extending in ventral tooth-like endolobe close to tergite junction; epimera 3–7 anterior margins rectangular, posterior margins grading between rectangular to increasingly rounded, endolobes absent; tergites 1–7 posterior margins slightly curved, tergite 1 length 0.2 pereon length. *Pleon* (Fig. 4D) pleura 3–5 truncated, endolobes absent; pleonites 1–5 posterior margins straight; pleonites 3–4 dorsal surface with midline longitudinal tubercle, pleonite 3 tubercle larger than pleonite 4 tubercle. *Pleotelson* (Fig. 4F,G) sides slightly constricted, distal part narrower than proximal, length 0.75 proximal width; posterior margin slightly rounded; two rounded tubercles near anterior margin, two ridge-like tubercles near posterior margin. *Antenna* (Fig. 4E) short, thick, reaching no further than epimera 1 posterior margin; flagellum length 0.75 article 5 length, flagellar article 2 length 2.0 article 1 length; all segments setose. *Mandibles* (Fig. 6A–E). Right mandible lacinia mobilis basal setose lobe with group of long fine simple setae; left mandible with longer and more simple setae, robust penicils not present. *Maxilliped* (Fig. 6L–K) basis rectangular. *Penes* broadly lanceolate; proximal bilobed lamellar process



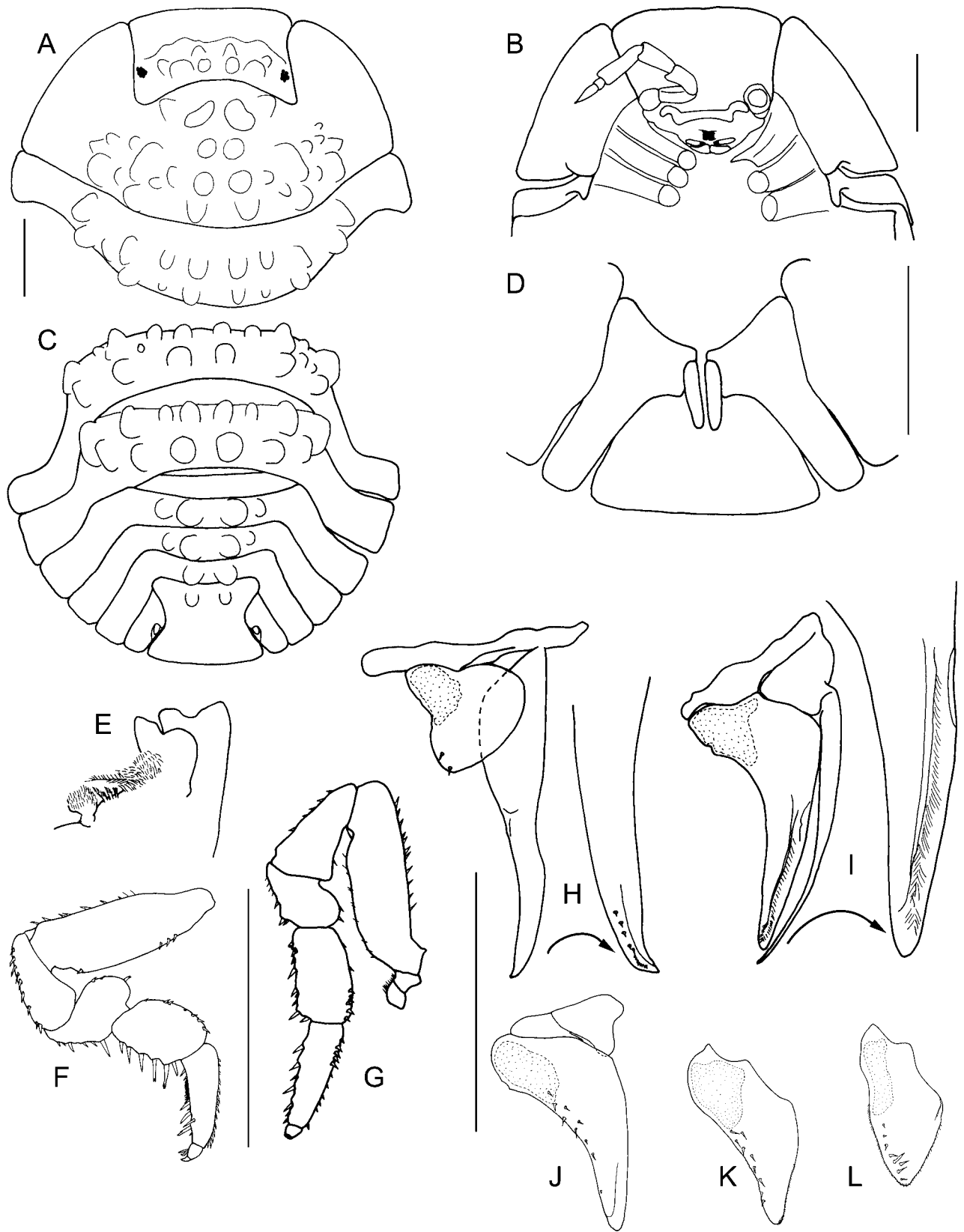
**Figure 2.** *Anchicubaris fongosiensis* Collinge, 1920, lectotype ♂ (BMNH 1933.1.25.851–870), light micrographs. A, lateral view. B, dorsal view, posterior part of body. C, pleotelson and uropods, ventral view. D,E, head and pereonites 1–2; D, ventral view; E, dorsal view. Scale bar = 1 mm.

subtriangular, small, length 0.25 penes length. *Male pleopod* (Fig. 5A,B) 1 exopod rounded triangular, pseudotrachea along proximal lateral margin, width 0.45 exopod width, length 0.5 exopod length; exopod length 0.4 endopod length. Pleopod 2 exopod proximal wide portion length 0.25 exopod length, length 2.0 exopod width, pseudotrachea along proximal lateral margin, width 0.6 exopod width, length 0.2 exopod length; one lateral long, thick two-segmented seta; endopod proximal article length 0.2 endopod length; exopod length 0.7 endopod length. *Uropod* (Fig. 4F,G) protopod subtriangular, apex rounded, length 1.6 width;

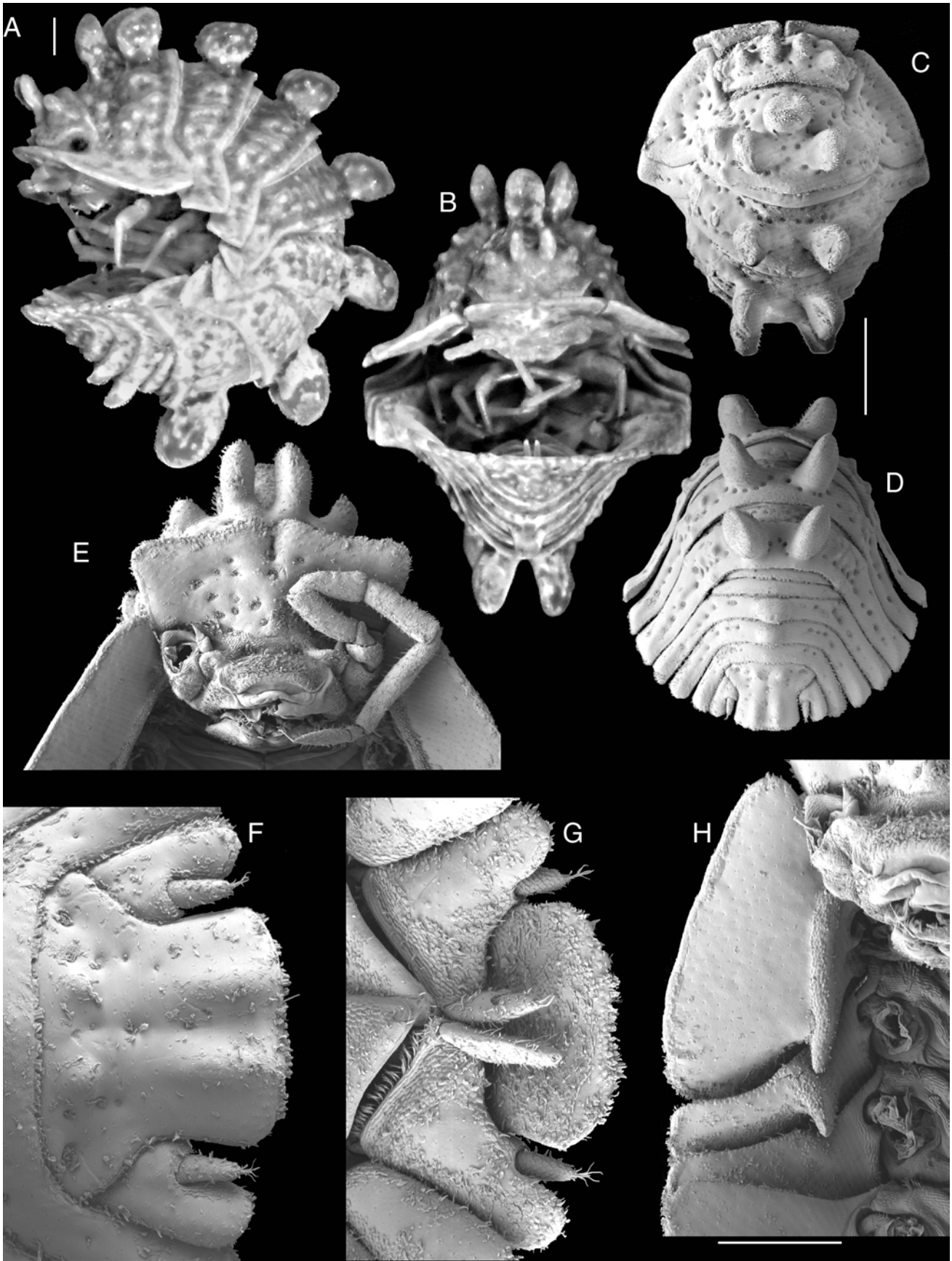
length (along inner margin of dorsally visible portion) 1.5 width (at point of exopod insertion); exopod visible ventrally through gap between pleotelson and distal part of protopod, apical setae reach posterior margin of protopod; endopod 2.0 exopod length.

**Etymology.** *Polyvelota* means “provided with many sails”, referring to the broad laterally flattened, dorsal ornamentation of this species.

**Remarks.** *Stigmops polyvelota* is distinguished from the other species of *Stigmops* by the shape and size of the dorsal

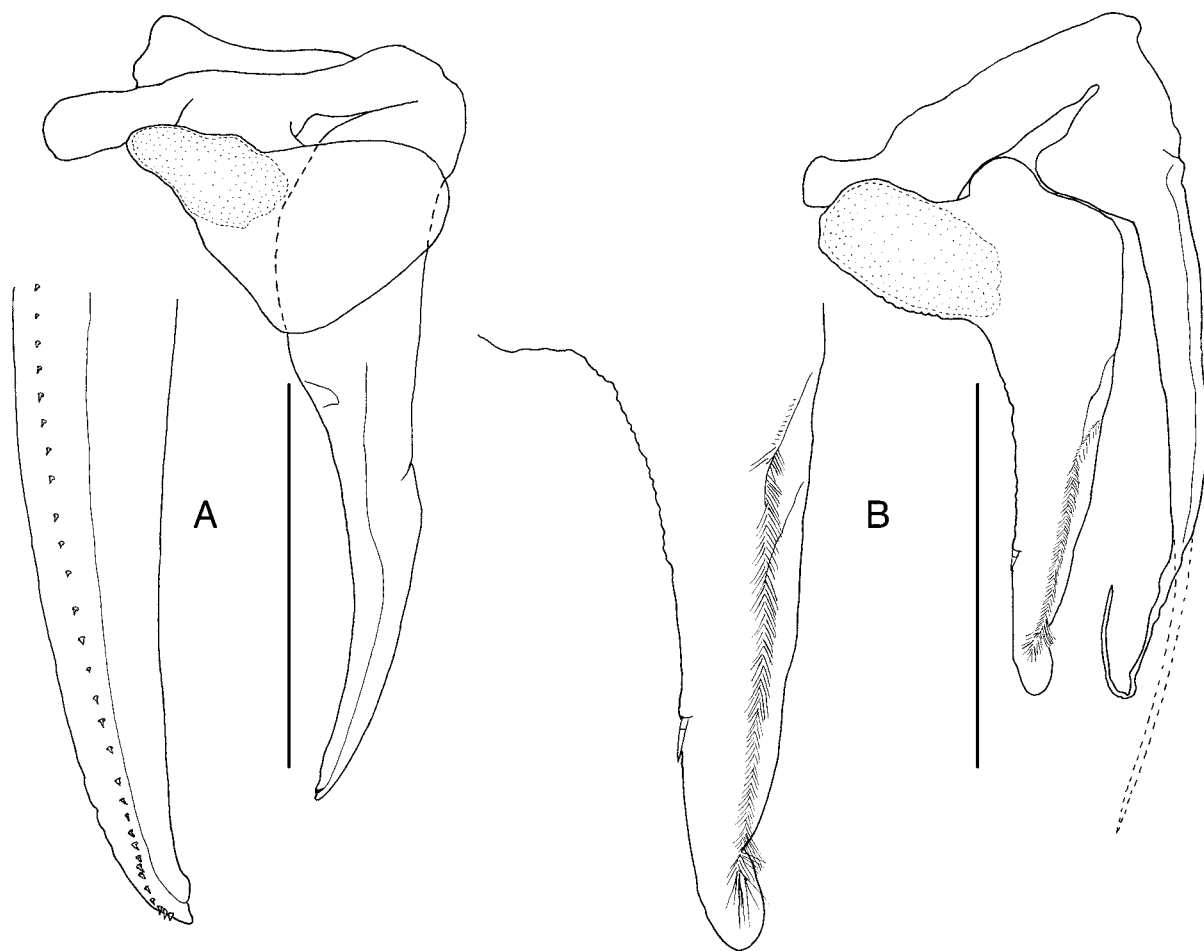


**Figure 3.** *Anchicubaris fongosiensis* Collinge, 1920. A–D, lectotype ♂ (BMNH 1933.1.25.851–870). A,B, head and pereonites 1–2; A, dorsal view; B, ventral view; C, pleon and pereonites 6–7, dorsal view; D, pleotelson and uropods, ventral view. E–L, paralectotype ♂ (BMNH 1933.1.25.851–870); E, tip of left mandible, ventral view; F, pereopod 1, lateral view; G, pereopod 7, lateral view; H, pleopod 1, ventral view, and tip, dorsal view; I, pleopod 2, and exopod tip, ventral view; J–L, pleopods 3–5, ventral view. Scale bars = 1 mm.



**Figure 4.** *Stigmops polyvelota* n.gen., n.sp. A,B, holotype ♂ (P59952), light micrographs. A, lateral view; B, ventral view. C–H, paratype ♂ (P59955). C, head and pereonites 1–3, dorsal view; D, pleon and pereonites 5–7, dorsal view; E, head, ventral view; F,G, pleotelson and uropods; F, dorsal view, G, ventral view; H, epimera 1–2 endolobes. Scale bar = 1 mm.





**Figure 5.** *Stigmops polyvelota* n.gen., n.sp. Paratype ♂ (P59955); A, pleopod 1, ventral view, and tip, dorsal view; B, pleopod 2 and exopod tip, ventral view. Scale bar = 1 mm.

lobes, especially the high cephalic lobes and the stegosaur-like pereonal lobes. This species was rarely encountered in the surveys, suggesting its general rarity in nature.

***Stigmops odontotergina* n.sp.**

Figs. 7–10

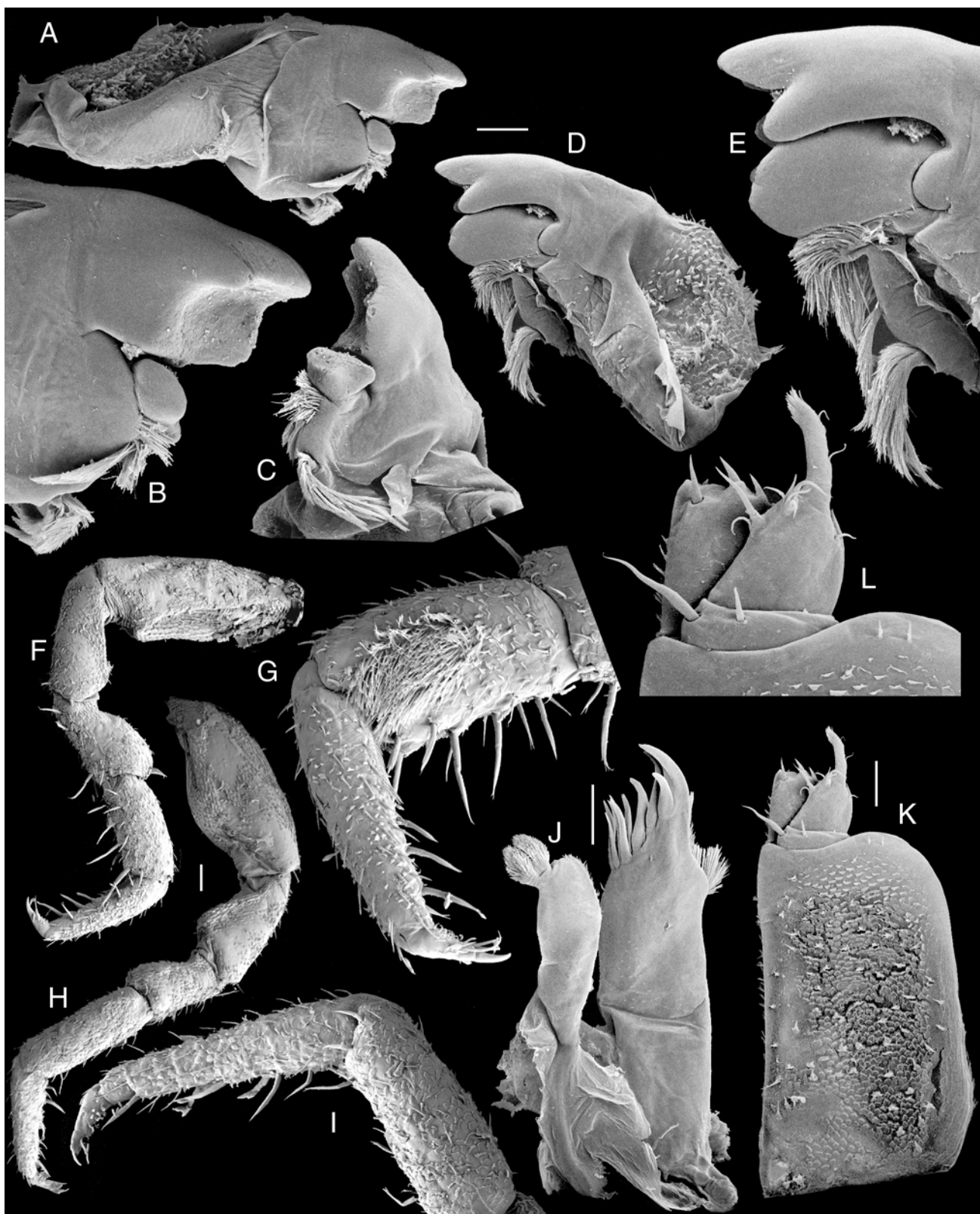
**Type material.** HOLOTYPE ♂, P59976, 4.5 × 2.5 mm, LHI386. PARATYPES: P59980, ♀, 5.4 × 2.9 mm, LHI392; P59996, ♂ on 5 SEM stubs, LHI392; P59981, ♂, 1 SEM stub, LHI392; P59979, ♀, 2 SEM stubs, LHI358; P59994, 15 inds, LHI392; P59995, ♂, SEM stub, LHI178 095; P59977, 2 specimens, LHI 178 095; P59982, 3 specimens, LHI 178 095; P59987, 1 specimen, LHI356; P59988, 2 specimens, LHI357; P59978, 1 specimen, LHI357; P59989, 7 specimens, LHI358; P59990, 2 specimens, LHI365; P59991, 1 specimen, LHI366; P59992, 1 specimen, LHI382; P59993, 3 specimens, LHI386; P59985, 1 specimen, 11.vii.79, LHI610; P59986, 2 specimens, 11.vii.79, LHI613.

**Type locality.** “Little Slope”, west side of Mount Gower, Lord Howe Island, New South Wales, Australia, 31°35'S 159°04.5'E, from pitfall traps in leaf litter, vegetation *Howea forsterana* forest, K&M 22.xi.1978 & 20.xii.1978.

**Additional material.** P59983, 1 specimen, LHI544; P59984, 1 specimen, LHI544; P34858, 7 inds, LHI 390.

**Diagnosis.** *Cephalon* frontal lamina indented, midline slightly curved; vertex with four ridge-like tubercles, middle two near longitudinal, lateral two transverse. *Pereon* dorsal ornamentation pereonite 1 with one large anterior longitudinal ridge-like midline tubercle, tergites 1–7 each with one pair of longitudinal, ridge-like midline tubercles near posterior margin, and two pairs of smaller longitudinal ridge-like tubercles lateral to midline. *Pleonites* 2–5 dorsal surface with one midline tubercle each, pleonites 2 and 5 tubercles similar size, pleonite 3 tubercle larger, pleonite 4 tubercle smaller; pleonite 3 with two small lateral tubercles. *Penes* with row of 5 medial ventral spines. *Uropod* protopod length 1.1 width; endopod 2.5 exopod length.

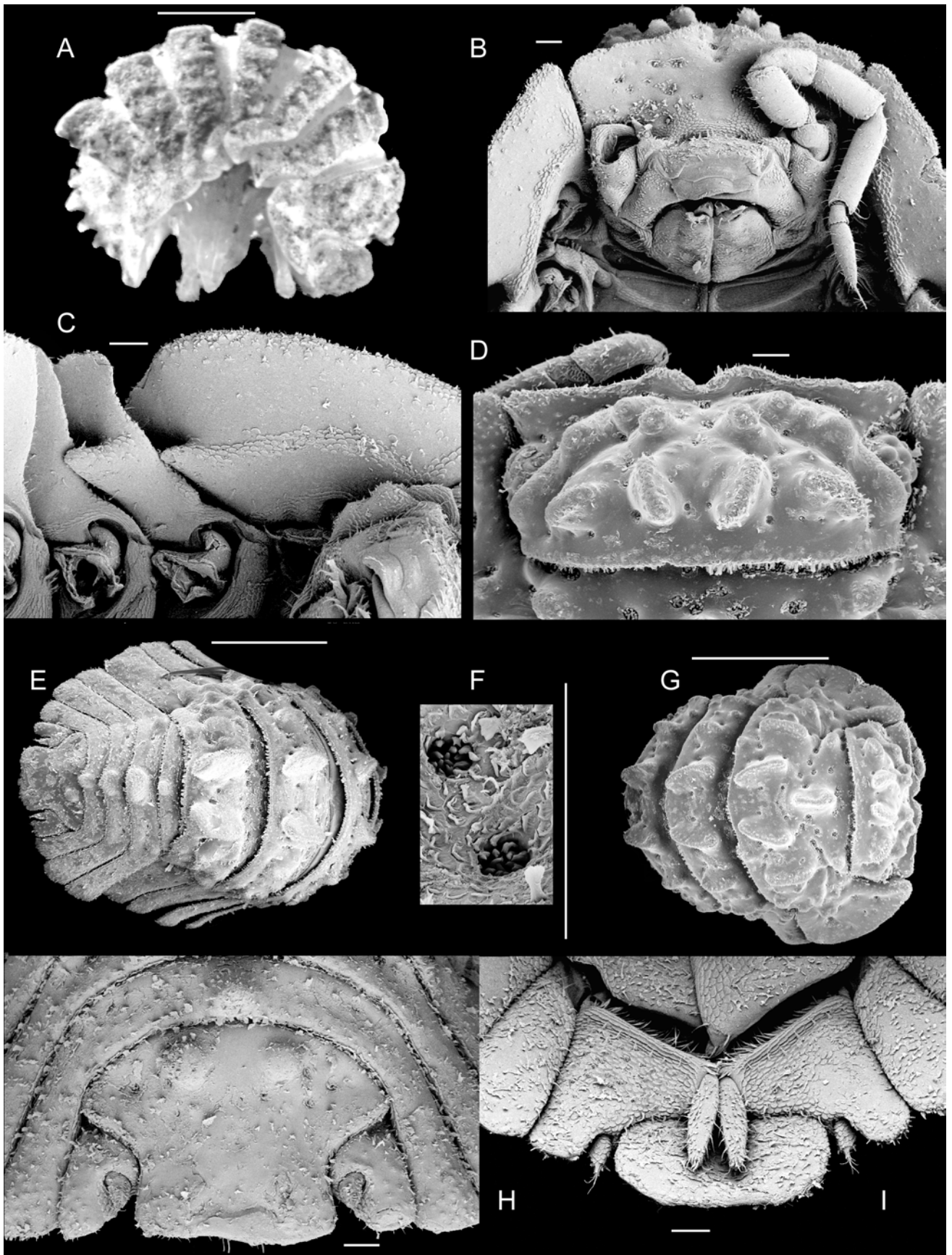
**Description.** *Colour* uniform light brown in alcohol. Original photos show darker uniform brown. *Body* (Fig. 7A,E,G) strongly convex with subhorizontal epimera. Dorsal cuticle of entire animal and frons with complex pattern of scales and pits. *Cephalon* (Fig. 7B,D) frontal lamina raised off vertex, indented, midline slightly curved, lateral margins triangular. Dorsal ornamentation four ridge-like tubercles, middle two near longitudinal, lateral two transverse along posterior margin, one pair of low round tubercles on midline near anterior margin, ridge above eyes. Head square, width 0.5 pereon width, width 2.0 length. Eyes with 6–10 ocelli in adults. *Pereon* (Fig. 7A–C,E,G) epimera 1 anterior margin narrowly rounded, extending anterior to eye, dorsal surface concave, lateral margin simple, posterior



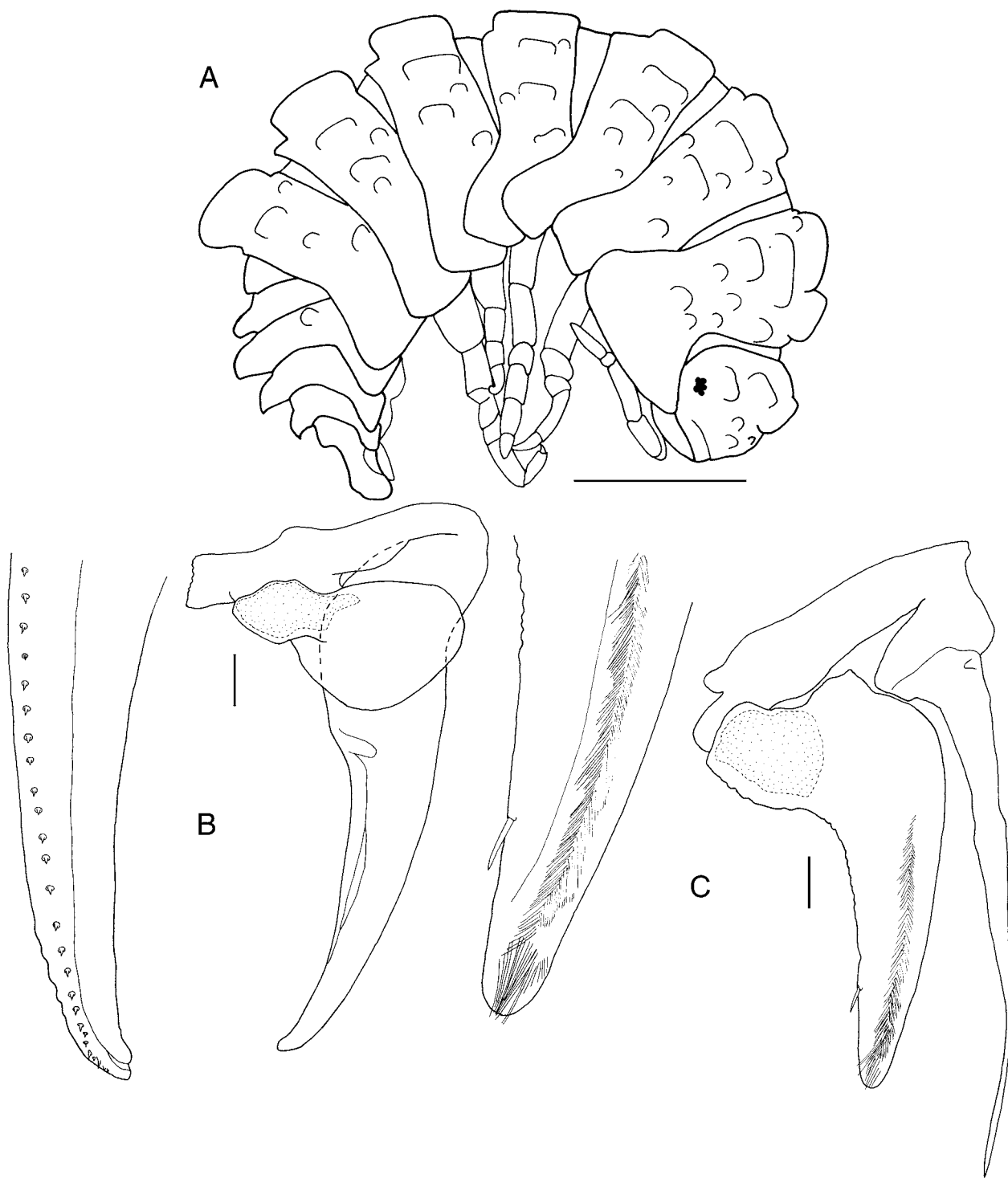
**Figure 6.** *Stigmops polyvelota* n.gen., n.sp. A–E, J–L, paratype ♀ (P59953). A–C, right mandible, A,B, ventral view, C, dorsal view; D,E, left mandible, ventral view; J, maxillule; K,L, left maxilliped. F–I, paratype ♂ (P59955); F,G, pereopod 1, F, posterior view, G, dactylus–carpus with antennal cleaning structure, anterior view; H,I, pereopod 7 lateral view. Scale bar = 100 µm.

margin broadly rounded, ventral surface with longitudinal ridge closer to tergite junction than to lateral margin extending from anterior margin, ending in tooth-like endolobe anterior to posterior margin, endolobe not visible

dorsally; epimera 2 anterior margin rectangular, posterior margin rounded, ventral surface with large tooth-like endolobe extending posteriorly from anterior margin; epimera 3–7 anterior margin rectangular, increasingly



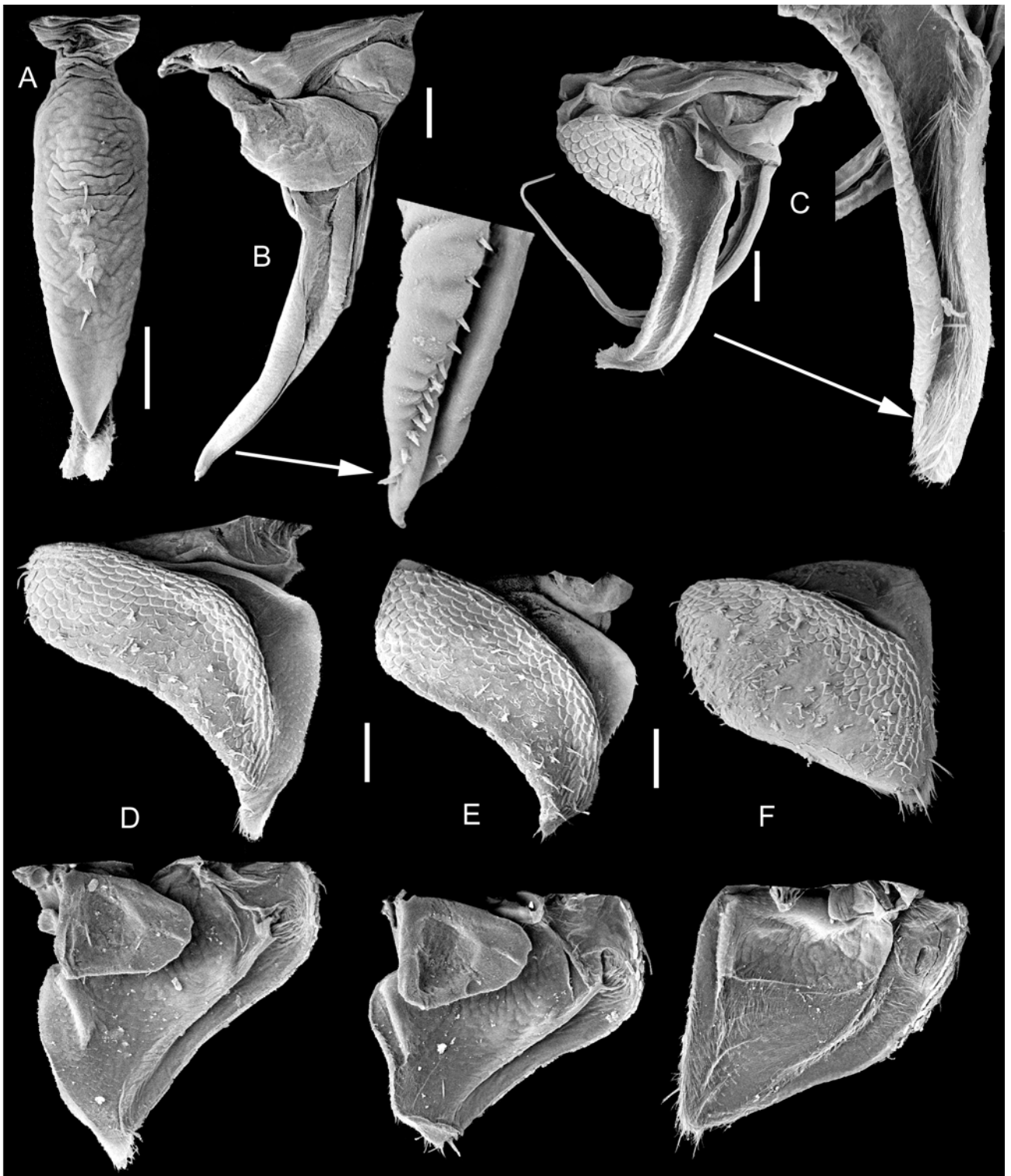
**Figure 7.** *Stigmops odontotergina* n.sp. A, holotype ♂ (P59976), light micrograph, lateral view. B–D, G, paratype ♂ (P59981); B, head ventral view; C, epimera 1–2 endolobes; D, head, dorsal view; G, head and pereonites 1–3, dorsal view. E, H, I, paratype ♂ (P59995); E, pleon and pereonites 5–7, dorsal view; H, I, pleotelson and uropods, H, dorsal view, I, ventral view. F, paratype ♀ (P59979); enlargement of cuticular pits on pereonite 1. A, E, G, scale bar = 1 mm; B–D, F, H, I scale bar = 100  $\mu$ m.



**Figure 8.** *Stigmops odontotergina* n.sp. A, holotype ♂ (P59976); lateral view. B,C, paratype ♂ (P59978); B, pleopod 1, ventral view, and tip, dorsal view; C, pleopod 2 and exopod tip, ventral view. A, scale bar = 1 mm; B,C, scale bar = 100  $\mu$ m.

rounded; epimera 3–4 posterior margin rounded, that of epimera 5–7 rectangular; epimera 3–7 endolobes absent; epimera 1–7 decreasingly angled towards posterior. Tergite 1–7 posterior margins slightly curved; tergite 1 length 0.2 pereon length. Dorsal ornamentation pereonite 1 with one large longitudinal ridge-like midline tubercle near anterior margin, one rounded tubercle on each side behind eyes; tergites 1–7 each with one pair of longitudinal, ridge-like midline tubercles near posterior margin increasing in size

posteriorly, two pairs of smaller lateral longitudinal ridge-like tubercles, decreasing in size posteriorly; low, rounded tubercles scattered above epimera tergite junction and on epimera. *Pleon* (Fig. 7E) pleura laterally truncate; pleonites 1–5 posterior margins rounded; pleonites 2–5 dorsal surface with one midline tubercle each, pleonites 2 and 5 tubercles similar size, pleonite 3 tubercle larger, pleonite 4 tubercle smaller; pleonite 3 with two small lateral tubercles. *Pleotelson* (Fig. 7H) sides slightly constricted, proximally



**Figure 9.** *Stigmops odontotergina* n.sp. Paratype ♂ (P59996); A, penes, ventral view; B, right ♂, pleopod 1 ventral view with enlargement of endopod distal tip, dorsal view; C, right ♂ pleopod 2 with enlargement of exopod distal tip, ventral view; D–F, right ♂ pleopods 3–5, ventral (top) and dorsal (below) view. Scale bar = 100  $\mu$ m.

wider than distally; length 0.75 width; posterior margin straight; dorsal surface with two proximal and two distal smaller rounded tubercles. *Antenna* (Fig. 7B) short, thick, reaching epimera 1 posterior margin, length 0.85 article 5, flagellar article length proportions 1:3; all segments setose, flagellum more densely including longer apical setae. *Mandibles* (Fig. 10A,B,E,F). Right mandible setose lobe

with shorter, thicker, less setae than left mandible, concentrated at lacinia mobilis base; simple setae only, robust penicils not present. *Penes* (Fig. 9A) lanceolate with row of 5 medial ventral spines; proximal bilobed lamellar process rectangular, covering 0.33 penes length. *Male pleopod* (Fig. 8B,C) 1 exopod rounded, pseudotrachea along proximal lateral margin width 0.5 exopod width, length 0.4



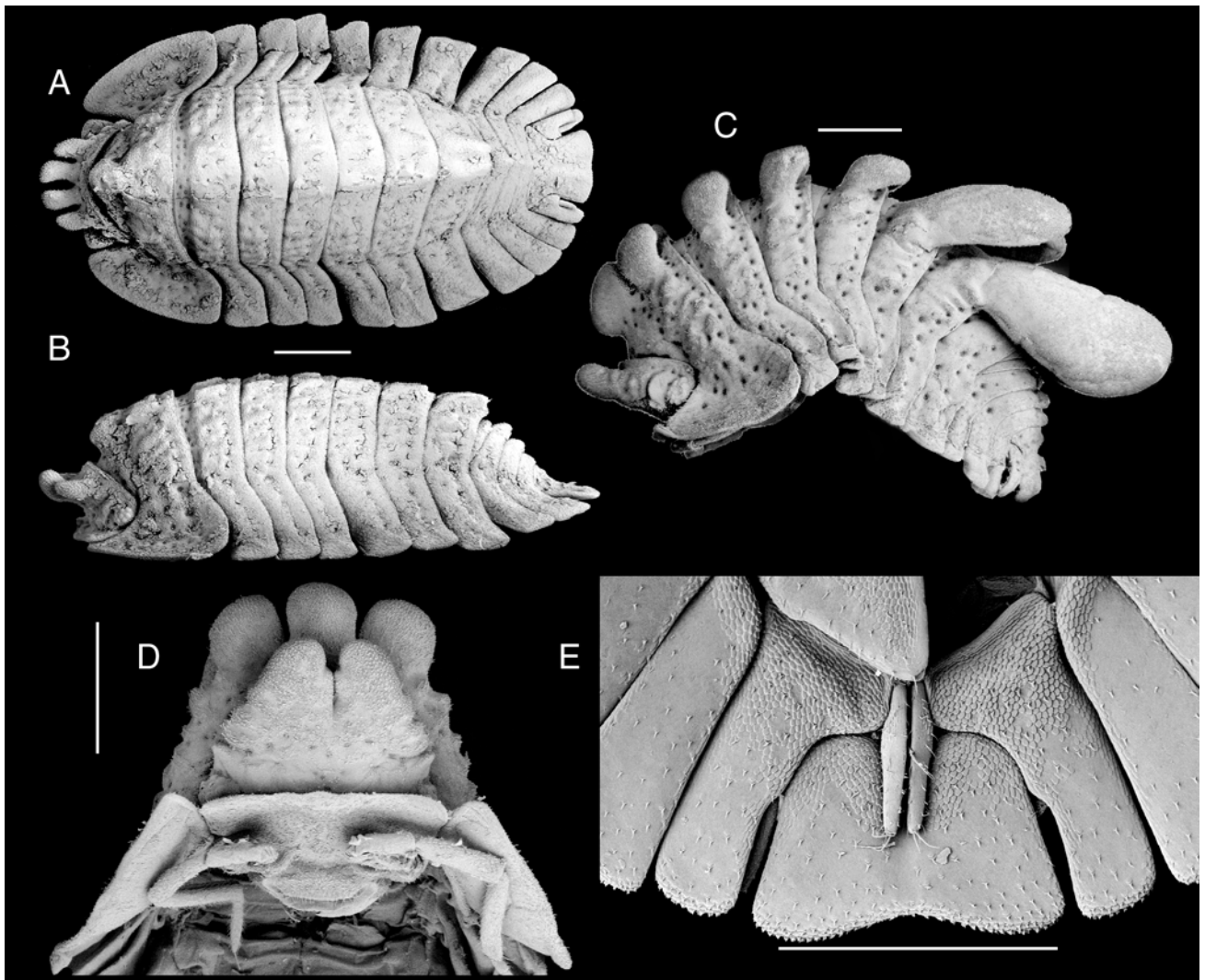
**Figure 10.** *Stigmops odontotergina* n.sp. A–F, paratype ♀ (P59979); A,B, right mandible, ventral view; C,D, left maxilliped, ventral view; E,F, left mandible, ventral view. G–J, paratype ♂ (P59996); G,H, pereopod 1: G, posterior view, H, carpus and propodus with antennal cleaning structure, anterior view; I, pereopod 4, posterior view; J, pereopod 7, posterior view. Scale bar = 100  $\mu$ m.

exopod length; exopod length 0.25 endopod length. Pleopod 2 exopod proximal wide portion length 0.3 exopod length, exopod width 0.6 exopod length, pseudotrachea along proximal lateral margin width 0.45 exopod width, length 0.2 exopod length, one lateral thick seta 0.25 exopod length from apex; endopod proximal article length 0.2 endopod length; exopod length 0.7 endopod length. Pleopods 3–5 exopods triangular with fine apical setae, ventral scales, dorsal ridge along lateral margin, ventral ridge along proximal margin, pleopod 5 exopod with three long apical setae and many short, fine setae along apex and medial

margin. *Uropod* (Fig. 7H) protopod subtriangular; length 1.1 width; median margin straight portion length 0.35 lateral margin length; dorsally visible distal portion short with rounded apex; length (along inner margin of dorsally visible portion) equal to width (at point of exopod insertion); protopod dorsally visible portion length 2.5 exopod length; endopod 2.5 exopod length.

**Etymology.** *Odontotergina* means “having a toothy back.”

**Remarks.** *Stigmops odontotergina* n.sp. is distinguished from the other species in *Stigmops* by the lower ridge-like



**Figure 11.** A,B, *Stigmops demiclavula* (Lewis, 1998b). A,B, holotype ♀ (P50141); dorsal and lateral views. C,D, *Stigmops howensis* (Lewis, 1998b) (P60001); C, lateral view; D, head anterior view. E, ♂ (P60000); pleotelson and uropods, ventral view. Scale bar = 1 mm.

cephalic tubercles, rather than large cephalic lobes, and an indented frontal lamina. This species was recorded moderately frequently on Mt. Gower, the type locality.

***Stigmops demiclavula* (Lewis, 1998b) n.comb.**

Fig. 11A,B

*Anchicubaris demiclavula* Lewis, 1998b: 751–752, fig. 4D–F.

**Type material.** HOLOTYPE ♀, P50141, on SEM stub, Stevens Reserve, Lord Howe Island, New South Wales, Australia, 31°31.5'S 159°04.5'E, clinging to under side of stone, F. Lewis, v1992.

**Additional material:** P57350, 5 ♀♀, QMB 142.

**Remarks.** *Stigmops demiclavula* (Lewis, 1998b) n.comb. is distinguished from the other species in *Stigmops* n.gen. by having four cephalic lobes much higher than the low pereonal tubercles.

***Stigmops howensis* (Lewis, 1998b) n.comb.**

Fig. 11C–E

*Anchicubaris howensis* Lewis, 1998b: 748–51, figs. 4A–C, 5A–F.

**Type material.** HOLOTYPE ♂, P41900. PARATYPE ♀, P41901.

**Type locality.** Intermediate Hill, Lord Howe Island, New South Wales, Australia, 31°32.9'S 159°05.5'E, under stone, F. Lewis, 1.v.1992.

**Additional material.** P53107, 6 ind, Intermediate Hill, 6.xi.1979; P58099, leaf litter, QMB161; P58100, 4 ind, LHI 596; P58101, 1 ind, just below summit of Intermediate Hill, QMB 123; P58102, 64 ind, QMB125; P58103, 1 ind, QMB 127; P58104, 1 ind, QMB 142; P58105, 1 ind, QMB 146; P58106, 1 ind, QMB 163; P58107, Intermediate Hill, leaf litter berlesate, GBM, 06.xi.1979; P58108, 1 ind, Dawson Ridge Top, 05.xi.1979; P58109, P58167, P58169, 10 ind, Mount Gower, pitfall, K&M 08.vii.1978; P58167–P58169, 1 ind each, Mount Gower, K&M 08.vii.1978; P58110, 1 ind, Mount Gower, pitfall, K&M 09.ii.1979; P58111,

P58160, P58161, P58163, P58165, 15 ind, Mount Gower, pitfall, K&M 29.i.1979; P58164, 1 ind, Mount Gower, pitfall, 29.iii.1979; P58166, Mount Gower, pitfall, K&M 28.ii.1979; P58162, 1 ind, Mount Gower, pitfall; P58170, 1 ind, Old Settlement; P58171, 63 ind, Seabreeze, pitfall, K&M 12.ii.1979.

**Remarks.** *Stigmops howensis* (Lewis, 1998b) n.comb. differs from the other species of *Stigmops* n.gen. by only having two large lobe-like tubercles on the cephalon, with the lateral tubercles reduced to small angular points at the base of the medial tubercles. Additionally, the dorsal pereonite tubercles show an extremely marked decrease in size from pereonite 6 to 7. The frons of this species also lacks cuticular pits that are present in the other species. Additional unusual features include an uncleft frontal lamina, a constricted pleotelson with an indented posterior margin, and long and narrow uropodal protopods. This showy species with its impressive dorsal lobes is frequently encountered in the previous surveys.

### *Pyrgoniscus* Kinahan, 1859

*Pyrgoniscus* Kinahan, 1859: 134.  
*Merulana* Budde-Lund, 1913.

**Type species.** *Pyrgoniscus cinctutus* Kinahan, 1859, by monotypy.

**Diagnosis.** Body dorsoventrally flattened with horizontal epimera; conglobation imperfect owing to folding body, leaving flange along sides; frontal lamina raised well above vertex, with or without midline cleft; epimera 1–2, sometimes 1–3, with tooth-like endolobes close to tergite junction; epimera 2–7 and pleura 3–5 ridged; pleotelson hourglass shaped; uropod protopod distally narrow rectangular, proximal part short; uropod exopod present, well developed.

**Remarks.** *Pyrgoniscus*, with an uncertain composition, includes 19 species with representatives in Africa, Madagascar and the Australasian region. The above diagnosis is derived from the original diagnosis by Kinahan (1859) and our new observations. *Pyrgoniscus* was created by Kinahan (1859) for the species *P. cinctutus* from “the Eastern Seas”. Stebbing (1900) later considered *Pyrgoniscus* a synonym of *Cubaris* Brandt, 1833. Budde-Lund (1904) placed *cinctutus* in his “section X” of *Spherillo* and later renamed the section *Merulana*, a subgenus of *Spherillo* (Budde-Lund, 1913). Verhoeff (1926) elevated *Merulana* to a genus, which was retained by Vandel (1973). Monod (1935) and Ferrara (1977) consider *Merulana* to be a junior synonym of *Pyrgoniscus*. A.J.A. Green (pers. comm. in Lewis, 1998a,b) disagreed that the described Australian species of *Merulana* belong in *Pyrgoniscus*. Our preliminary phylogenetic analysis of some species in these two genera finds *Merulana boydensis* Lewis, 1998a nested within *Pyrgoniscus*, suggesting that the two genera may not be distinct. Ultimately, an examination of the type species for both genera will allow a decision on this uncertainty. Several species currently placed in *Pyrgoniscus* are quite different from the type species, so the monophyly of the genus is uncertain. A comprehensive revision is therefore needed.

Nevertheless, the current species *Pyrgoniscus scopelicus*

n.sp. mostly agrees with the original diagnosis of the genus. This new species lacks the medial cleft of the frontal lamina indicated in the original diagnosis. Three other species without a cleft frontal lamina have previously been placed in *Pyrgoniscus*, *P. lanceolatus* Ferrara, 1977 (Kenya), *P. petiti* Monod, 1935 (Madagascar) and *P. intermedius* Lewis, 1998b (Lord Howe Island). Two separate groups occur within this genus, based on the presence or absence of a cleft frontal lamina. *Pyrgoniscus scopelicus* lacks endolobes on epimera 3, which are present in the original type species. Many species placed in *Pyrgoniscus* also lack endolobes on epimera 3, including *P. petiti* Monod, 1935 (Madagascar), *P. hispida* (Vandel, 1973) (NSW), *P. canaliculatus* (Budde-Lund, 1904) (Chatham Island), *P. intermedius* Lewis, 1998b (Lord Howe Island), *P. bicarinatus* (Budde-Lund, 1913) (NSW, Queensland) and *P. iniquus* (Budde-Lund, 1904) (Queensland).

Seven other species from the Australasian region have been placed in *Pyrgoniscus*: *P. impressifrons* (Budde-Lund, 1904) (NSW); *P. chathamensis* (Budde-Lund, 1885) (Chatham Island); *P. carinatus* (Verhoeff, 1926), *P. noduligerus* (Verhoeff, 1926), *P. translucidus gracilior* (Verhoeff, 1926), *P. translucidus translucidus* (Budde-Lund, 1885) and *P. exilis* (Budde-Lund, 1885) (New Caledonia). *Merulana rugosa* (Budde-Lund, 1913), also from Queensland, has been classified in *Pyrgoniscus* (Monod, 1935; Ferrara, 1977).

### *Pyrgoniscus scopelicus* n.sp.

Figs. 12–14

**Type material.** HOLOTYPE ♂, P59946, 10.7 × 6.0 mm, Ball’s Pyramid K&M 24.i.80. PARATYPES, all from Ball’s Pyramid, K&M 21.i.80 or 24.i.80: P59950, 14.2 × 8.6 mm.; P59997, ♂, 5 SEM stubs; P59947, ♂; P59949, ♂; P59998, ♀, 3 SEM stubs, photo K.1037; P59951, 2 ♀♀; P59948, 3 ♀♀.

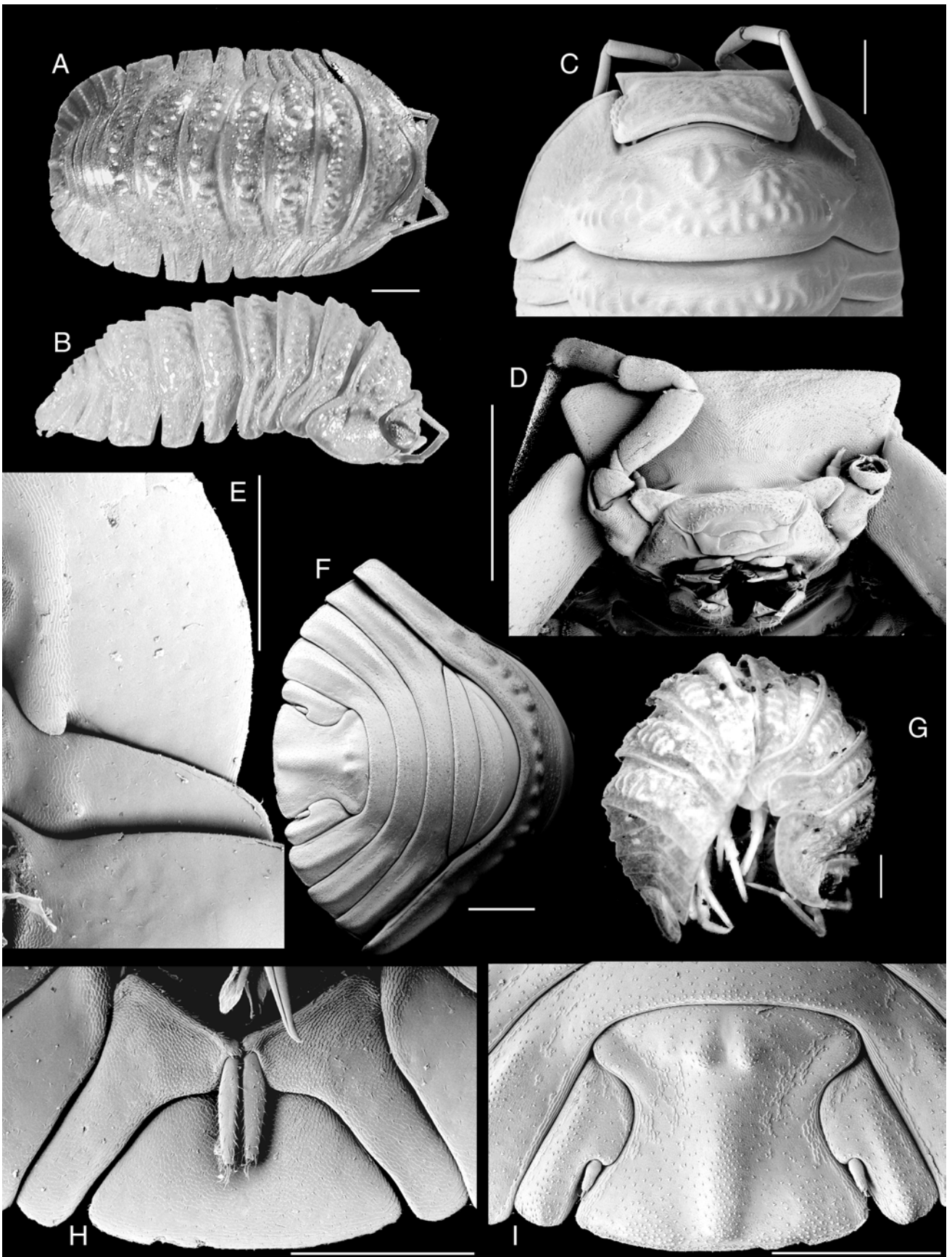
**Type locality.** Ball’s Pyramid (near Lord Howe Island), New South Wales, Australia, 31°46’S 159°16’E, collected under and behind exfoliating rock, crevice in rock face, K&M, 21 & 24 January 1980.

**Additional material.** P34877, 9 inds; P34878, 27 inds; Ball’s Pyramid, collected under and behind exfoliating rock, crevice in rock face, K&M, 24.i.80.

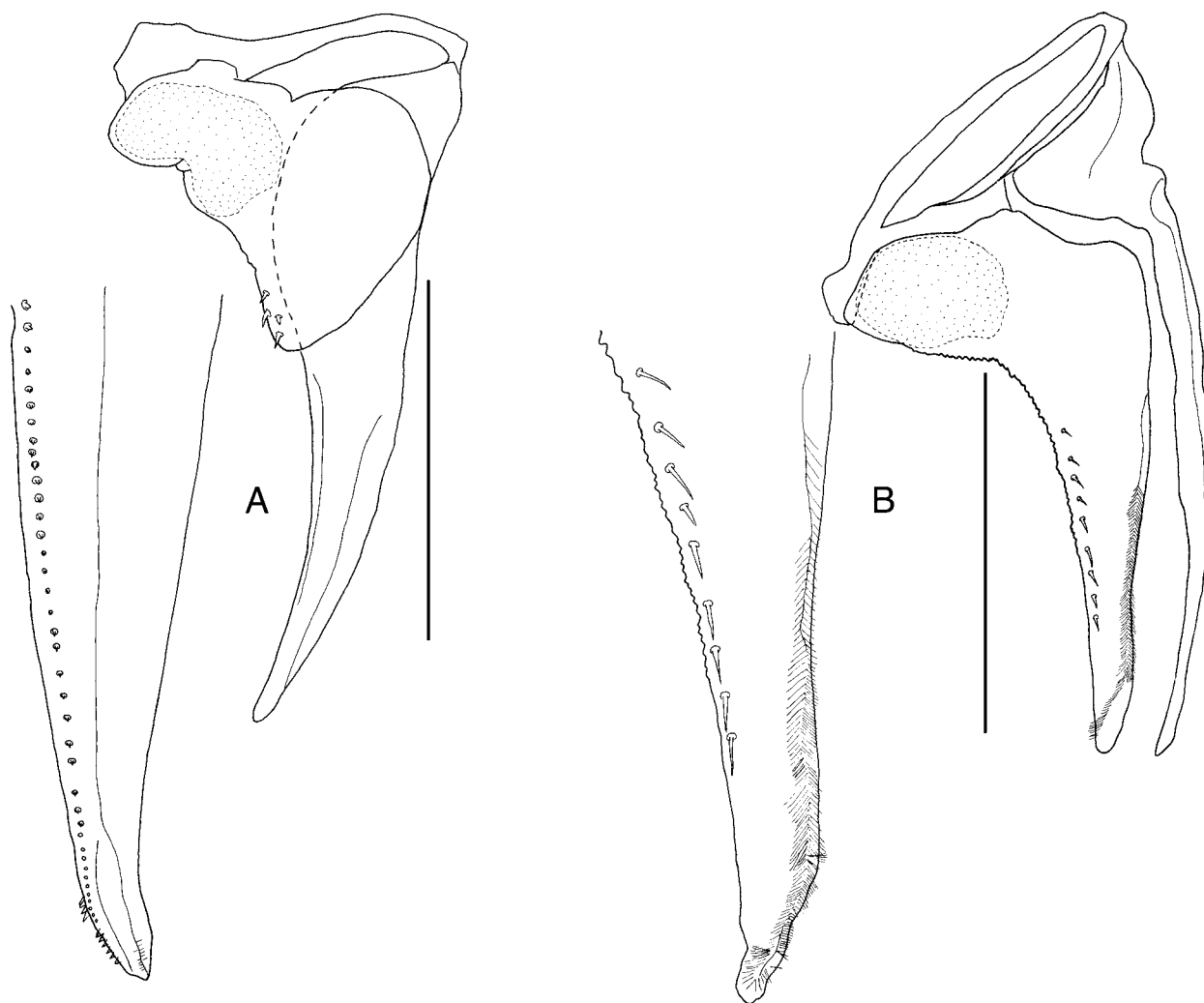
**Diagnosis.** *Cephalon* frontal lamina entire, straight; ridge-like tubercle above each eye. *Pereonite* 1 dorsal ornamentation with midline tubercles forming a “V” behind anterior margin, area around it smooth, tubercles concentrated in two round “shoulder” areas. *Pleonites* dorsal surface smooth. *Pleotelson* hourglass shape; posterior margin straight; single midline ridge distally from level of constriction, not reaching posterior margin. *Male pereopod* 1 carpus distoventrally with “brush” of setae, increasing in length distally. *Uropod* protopod length 1.9 width; dorsal surface ridged; endopod 3.0 exopod length.

**Description.** *Colour* uniform grey-brown in alcohol. *Body* (Fig. 12A,B,G) dorsoventrally flattened with expanded horizontal epimera. *Cephalon* (Fig. 12C,D) frontal lamina raised above vertex, uncleft, straight, distal lateral margins triangular; ridge-like tubercle above each eye, row of low,





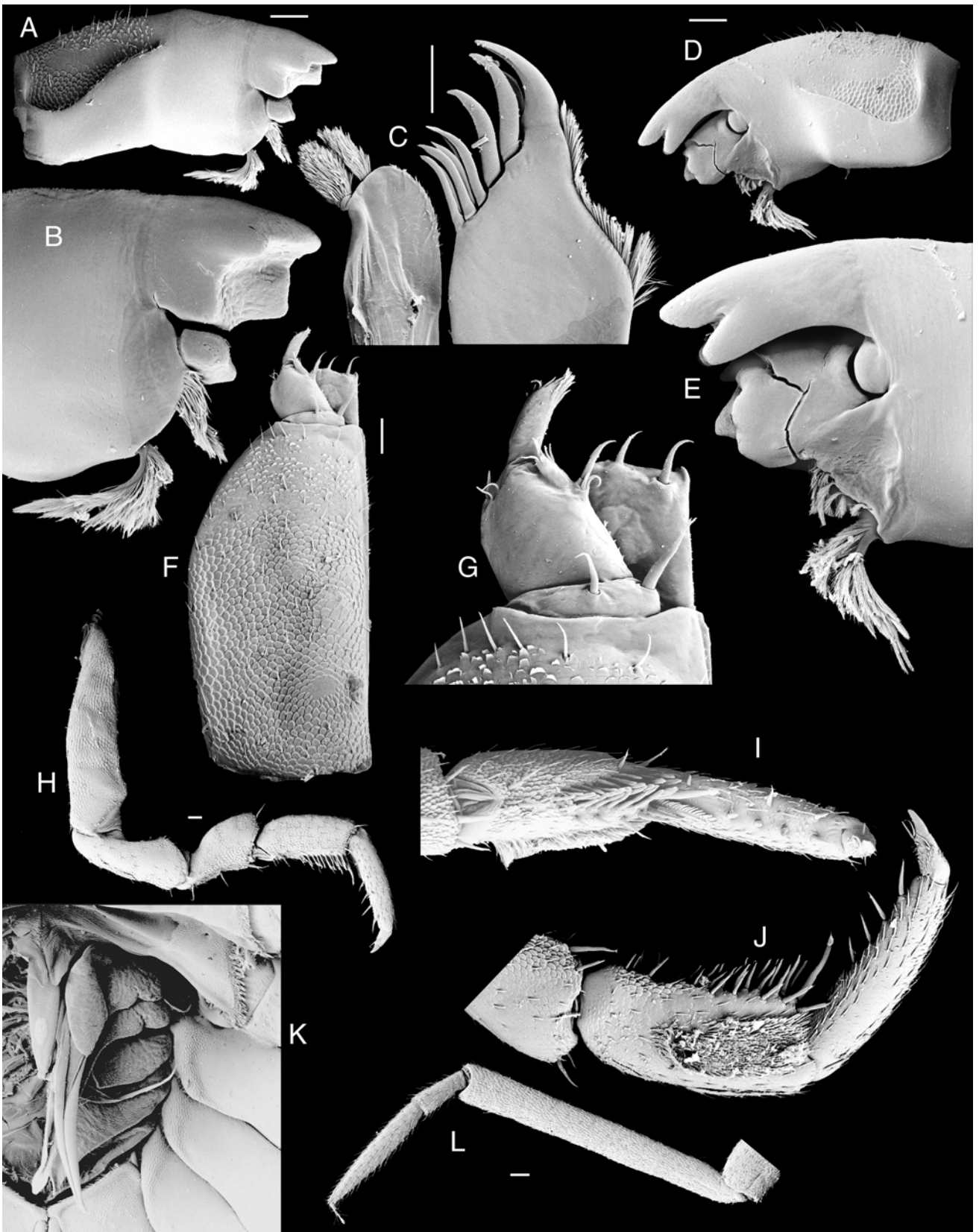
**Figure 12.** *Pyrgoniscus scopelicus* n.sp. A–C, paratype ♀ (P59998); A,B, light micrographs, A, dorsal view, B, lateral view; C, head and pereonite 1, dorsal view. D–F,H,I, paratype ♂ (P59997); D, head, ventral view; E, epimera 1–2 endolobes; F, pleon and pereonite 7, dorsal view; G, holotype ♂ (P59946), light micrograph, lateral view; H,I, pleotelson and uropods, H, ventral view, I, dorsal view. Scale bar = 1 mm.



**Figure 13.** *Pyrgoniscus scopelicus* n.sp. Paratype ♂ (P59949); A, pleopod 1, ventral view, and tip, dorsal view; B, pleopod 2 and exopod tip, ventral view. Scale bar = 1 mm.

rounded tubercles along posterior margin, scattered low rounded tubercles; head width 2.5–3.0 length. Eyes with 17–20 ocelli in adults. *Pereon* (Fig. 12A–C) epimera 1 narrowly rounded anteriorly, lateral margin simple, posterior margin rounded rectangular, dorsal surface concave, ventral surface with longitudinal ridge close to tergite epimera junction extending from anterior margin, ending in tooth-like endolobe anterior to posterior margin; epimera 2 anterior margin rectangular, posterior margin rounded rectangular, ventral surface anterior margin thickened, extending in blunt tooth-like endolobe close to tergite junction near midline; epimera 3–7 anterior margins rectangular, decreasingly angled towards posterior, epimera 7 straight; epimera 2–4 posterior margins rounded, that of epimera 5–7 rectangular; epimera 3–7 endolobes absent. Tergites 1–6 posterior margins slightly curved, tergite 7 straight; tergite 1 length 0.25 pereon length. *Dorsal ornamentation* (Fig. 12A–C) tergite 1 midline tubercles forming a “V” behind anterior margin, area around it smooth, tubercles concentrated in two round “shoulder” areas, rest of tergite with scattered tubercles, narrow band along posterior margin smooth; tergite 2–7 each with row of tubercles, smooth narrow band along posterior margin; epimera 1 with scattered tubercles, epimera 2–7 ridged; tergal cuticle with small scattered scales. *Pleon* (Fig. 12F)

pleura 3–5 truncate, ridged; pleonite 1–2 posterior margin straight, pleonite 3–5 slightly curved; endolobes absent; pleonites dorsal surface smooth. *Pleotelson* (Fig. 12I) hourglass shape, greater part posterior to constriction, proximal width 0.9 distal width, length 0.9 proximal width; posterior margin straight; two rounded tubercles near anterior margin, midline ridge distally from level of constriction, not reaching posterior margin. *Antenna* (Figs. 12C,D, 14L) long, slender, reaching epimera 2 posterior margin; flagellum length 0.6 article 5 length; flagellar articles length proportions 1:2; all segments setose, flagellum with long apical seta. *Mandibles* (Fig. 14 A,B,D,E). Right mandible lacinia mobilis base setose lobe with row of long simple setae; left mandible with 6 robust penicils. *Maxilliped* (Fig. 14F,G) palp article 2 apical group of setae on small lobe. *Male pereopod 1* (Fig. 14H,I) carpus distoventrally with “brush” of setae, increasing in length distally. *Penes* (Fig. 14K) lanceolate; proximal bilobed lamellar process triangular, length 0.4 penes length. *Male pleopod 1* (Fig. 13A,B) exopod triangular, with four separate lateral setae near apex; pseudotrachea along proximal lateral margin, width 0.5 exopod width, length 0.5 exopod length; exopod length 0.35 endopod length. Pleopod 2 exopod length 2.0 width, proximal wide portion length 0.3 exopod length, pseudotrachea along lateral margin, width 0.5



**Figure 14.** *Pyrgoniscus scopelicus* n.sp. A–G,L, paratype ♀ (P59998); A,B, right mandible, ventral view; C, maxillule, ventral view; D,E, left mandible, ventral view; F,G, right maxilliped, ventral view; L, antenna. H–K, paratype ♂ (P59997); H–J, pereopod 1: H, posterior view; I, carpus-dactylus, ventral view; J, same with antennal cleaning structure, anterior view; K, ♂ pleopods, *in situ*. Scale bar = 100 µm.

exopod width, length 0.2 exopod length, distolateral row of long, thick setae; endopod proximal article length 0.2 endopod length; exopod length 0.75 endopod length. Pleopods 3–5 exopods ridged near dorsolateral margin, ventral long thick setae along lateral margin of apical half. *Uropod* (Fig. 12H,I) protopod length 1.9 width; proximal medial margin straight portion 0.2 protopod length; protopod distally visible dorsally, length 0.67 protopod length; length (along inner margin of dorsally visible portion) 2.0 width (at point of exopod insertion); dorsal surface ridged; exopod inserted dorsally midway to apex, length 0.25 protopod dorsally visible portion length; endopod 3.0 exopod length.

**Etymology.** *Scopelicus* means “of a rocky crag projecting from the sea”, a good description of Ball’s Pyramid.

**Remarks.** We here list all species that have been recorded in Pyrgoniscus and indicate how *P. scopelicus* n.sp. differs from them. The frontal lamina is lower in *P. scopelicus* than in *P. lanceolatus* Ferrara, 1977 and *P. petiti* Monod, 1935. The straight frontal lamina differentiates it from *P. intermedius* Lewis, 1998b (also from Lord Howe Island). Unlike this species, the frontal lamina is cleft in *P. cinctutus* Verhoeff, 1926, *P. exilis* (Budde-Lund, 1885), *P. translucidus translucidus* (Budde-Lund, 1885), *P. hispida* (Vandel, 1973), *P. canaliculatus* (Budde-Lund, 1904), *P. iniquus* (Budde-Lund, 1904), *P. noduligerus* (Verhoeff, 1926), *P. translucidus gracilio* (Verhoeff, 1926), *P. bicarinatus* (Budde-Lund, 1913) and *P. chathamensis* (Budde-Lund, 1885). *Pyrgoniscus carinatus* (Verhoeff, 1926) has a straight sided pleotelson rather than an hourglass shape. A single ridge on the pleotelson separates this species from *P. impressifrons* (Budde-Lund, 1904) by a single ridge on the pleotelson, and from *P. rugosus* (Budde-Lund, 1913) by differences in dorsal ornamentation (see Fig. 12A,B).

### *Cubaris* Brandt

*Cubaris* Brandt, 1833: 189.

*Armadillo*, section VI, Budde-Lund, 1904: 118

**Type species.** *Cubaris murina* Brandt, 1833.

**Diagnosis.** Frontal lamina not raised above vertex, midline not indented; antennae slender; dorsal surface smooth, rugose or tuberculate, but without spines; epimera tergite junctions 1–6 posterior margins more or less incurved, tergite 7 junction straight or shallowly incurved; epimera 1 posterior margin entire, not cleft; epimera 1 endolobe small, not visible dorsally, not forming continuation of epimera margin; epimera 2 endolobe not projecting beyond epimera margin; tergite 1 length 0.2–0.25 pereon length; pleotelson sides parallel or constricted, dorsal surface not keeled, posterior margin bluntly rounded, straight or shallowly incurved, not deeply incised in midline; pleopods width greater than 0.3 pleon width; proximal portion length less than 0.3 protopod length, inner margin near exopod insertion smoothly concave.

**Remarks.** *Cubaris* is a large genus comprising over 100 species worldwide, 29 of which have been described from the Australia-South Pacific region. Schmalzfuss (1983) considers it to be a “heterogeneous and artificial group defined by symplesiomorphic characters”. The group is not

monophyletic and is in need of a comprehensive global revision.

The genus was created by Brandt (1833) for the pantropical species *C. murina*. Budde-Lund (1904) redefined the genus as sections of his genus *Spherillo*. Jackson (1935) later identified Verhoeff’s (1926) genus *Nesodillo* as a synonym of *Cubaris*, which was retained by Green (1961). Taiti *et al.* (1998) re-established *Nesodillo* as a distinct genus and assigned *N. sarasini* Verhoeff, 1926 as the type species. Several species originally placed in *Nesodillo* by Verhoeff may not belong here, but in *Cubaris* (Green, 1961). A revision of *Cubaris* by Green (1961) includes a key to species. A comprehensive revision of the entire genus, however, is needed. The above diagnosis is derived from Green (1961). The type specimens of *Cubaris murina* have been lost, preventing an unambiguous diagnosis. The status of *C. murina* should be stabilised by selection of a neotype, a task that is not within the scope of this paper. *Cubaris dhaliwali* does not fit any other described genera but does belong in the same group as species previously placed in *Cubaris*. Regardless of the best composition of *Cubaris* and without being able to examine the type material of *C. murina*, *C. dhaliwali* n.sp., fits the existing generic diagnosis.

### *Cubaris lewisae* nom. nov.

*Cubaris granulatus* Lewis, 1998b (not *C. granulatus* Collinge, 1915b).

**Remarks.** Lewis (1998b) described a new species of *Cubaris* from Lord Howe Island that she named *C. granulatus*. This name has already been used by Collinge (1915b) for a species from India. These species are clearly different, and the species from Lord Howe Island must be given another name. We propose the name *Cubaris lewisae* nom. nov. to replace *C. granulatus* Lewis, 1998b.

### *Cubaris dhaliwali* n.sp.

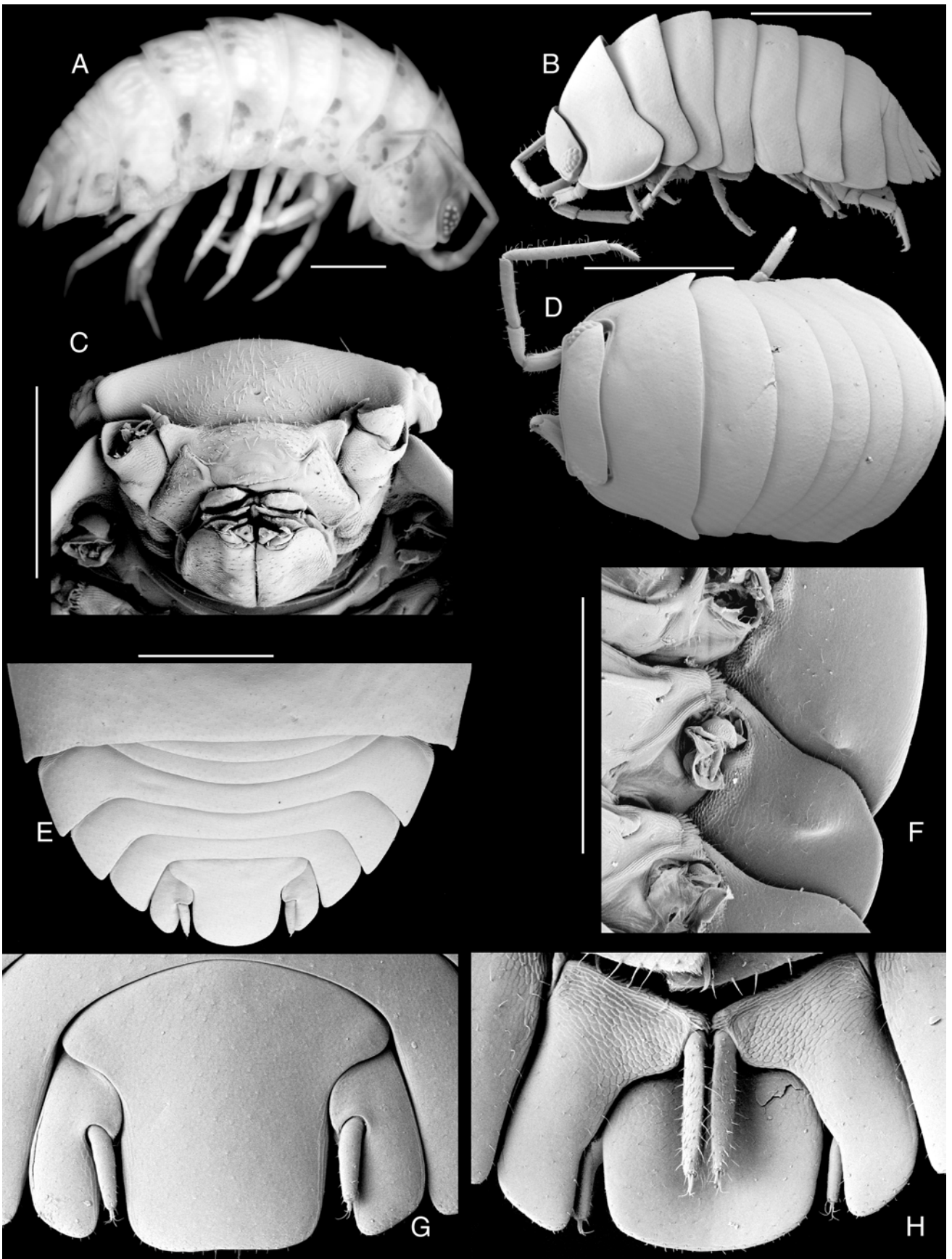
Figs. 15–17

**Type material.** HOLOTYPE ♂, P59956, 7.1 × 3.4 mm, QMB157. PARATYPES: P59960, ♀ 9.5 × 4.5 mm, QMB157; P59957, ♂, 5 SEM stubs, QMB157; P59959, ♂, 2 SEM stubs, QMB157; P59999, ♀, 3 SEM stubs, QMB157; P59958, ♂, QMB157; P59965, 1 ♀, 2 ♂♂, 6 juveniles, LHI126; P59966, 1 ♀, 1 juvenile, LHI139; P59963, 4 ♂♂, 2 ♀♀, 60 juveniles, QMB157; P59961, 7 ind., QMB157; P59962, 8 ind., QMB157.

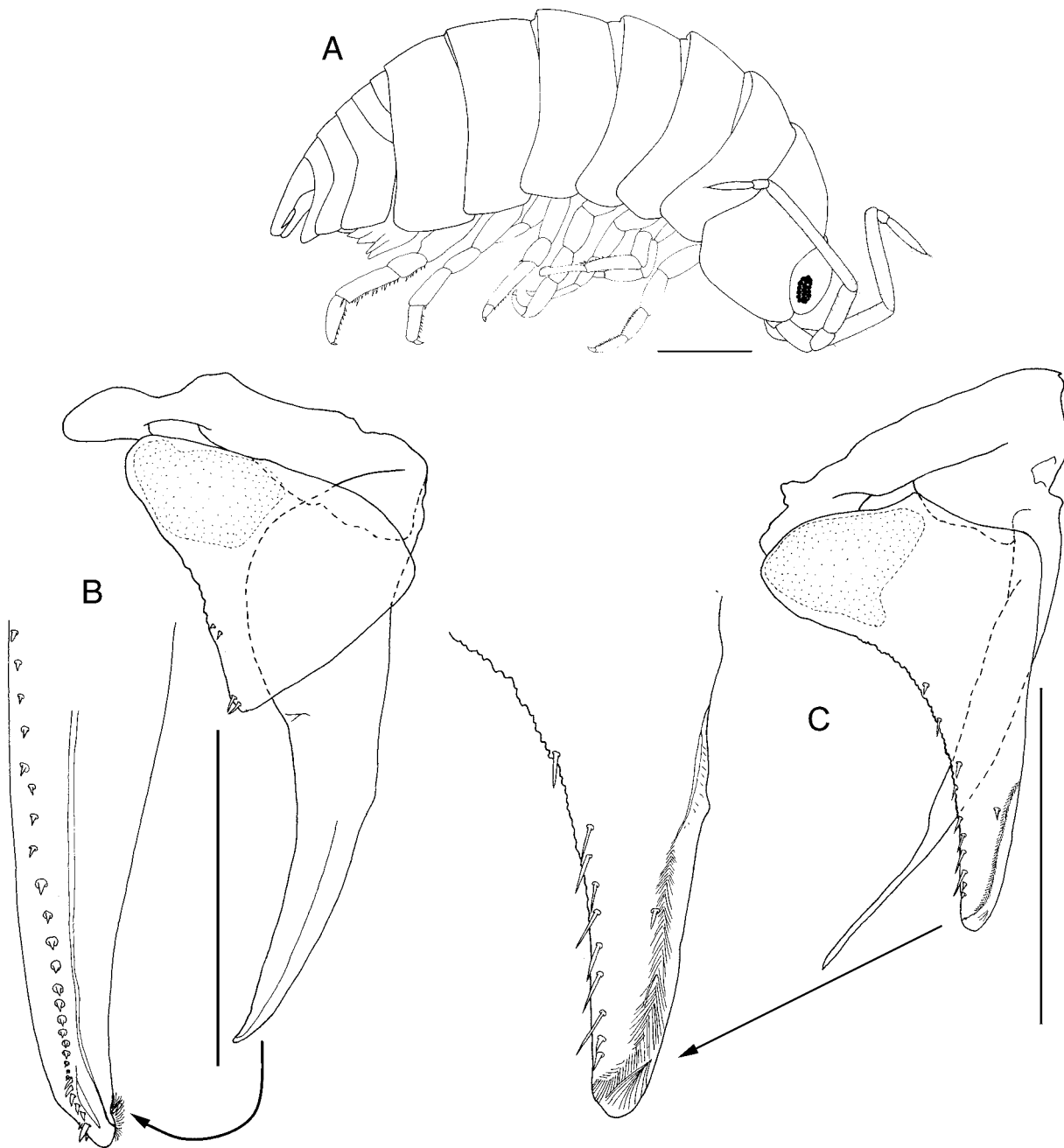
**Type locality.** Transit Hill (Clear Place), Lord Howe Island, New South Wales, Australia, 31°31.5'S 159°05'E, leaf litter, vegetation: *Drypetes australascia*, *Cryptocarya triplinervis* and *Howea forsterana*, GBM, xi1979, QMB157.

**Additional material:** P59964, ♂, QMB156; P59973, ♀, GBM, QMB131; P59974, 6 ind, QMB132; P59975, 1 ind, QMB155; P59967, 1 ind, LHI196; P59968, 3 ind, LHI413; P59969, 2 ind, LHI428; P59970, 4 ind, LHI429; P59971, 1 ind, LHI430; P59972, 1 ind, LHI517; P34902, 3 inds, LHI 122; P34903, 6 inds, LHI 533; P34904, 1 inds, LHI119.

**Diagnosis.** *Dorsal surface* smooth; frons with short setae. *Pereon* epimera 1 lateral margin simple, ventral surface



**Figure 15.** *Cubaris dhaliwali* n.sp. A, holotype ♂ (P59956); light micrograph, lateral view; B,D,E, paratype ♀ (P59999); B, lateral view; D, head and pereonites 1–6, dorsal view; E, pleon, dorsal view. C,F–H, paratype ♂ (P59959); C, head, ventral view; F, epimera 1–2 endolobes; G,H, pleotelson and uropods, G, dorsal view, H, ventral view. Scale bar = 1 mm.



**Figure 16.** *Cubaris dhaliwali* n.sp. A, holotype ♂ (P59956), lateral view. B,C, paratype ♂ (P59958); B, pleopod 1, ventral view, and tip, dorsal view; C, pleopod 2 and exopod tip, ventral view. Scale bar = 1 mm.

endolobes small, rounded, closer to lateral margin than tergite junction, no ridge anterior to endolobe; epimera 2 anterior third of ventral surface thickened, endolobes small, round, near midline. *Pleotelson* posterolateral corners rounded, posterior margin straight, lateral sides parallel. *Male pereopods* 1, 2 and 3 carpus ventral side with brush of long setae with flat spoon-like tips increasing in length distally, decreasing in length from pereopod 1–3. *Male pleopod 2* exopod row with long, thick setae along ventrolateral margin. *Uropod* protopod length 1.6 width, small gap between protopod distal portion and pleotelson.

**Description.** *Colour* pale brown with darker spots along pereonites posterior margins and epimera tergite junctions in alcohol. *Body* (Fig. 15A,B,D; 16A) strongly convex with

vertical epimera. *Cephalon* (Fig. 15C,D) frontal lamina low, not raised above vertex, straight, lateral margins rounded; dorsal surface smooth, frons with short setae; head rounded, width 3.0 length. Eyes length equal to lateral head length, with 18–20 ocelli in adults, produced laterally. *Pereon* (Fig. 15A,B,D,F; 16A) epimera 1 anterior margin narrowly rounded, dorsal surface vertical to slightly convex, lateral margin simple, slightly sinusoidal when viewed ventrally, posterior margin slightly subrectangular, ventral surface endolobes small, rounded, closer to lateral or posterior margin than tergite junction, not connected to lateral or posterior margin, no ridge anterior to endolobe; epimera 2 anterior margin broadly rounded, posterior margin rounded rectangular, anterior third of ventral surface thickened, endolobes small, round, near midline; anterior margins of epimera 3–6



**Figure 17.** *Cubaris dhaliwali* n.sp. A–I, paratype ♀ (P59999); A–C, left mandible, A,B, dorsal view, C, medial view; D,E, right mandible, dorsal view; F,G, maxillule; H,I, right maxilliped. J–L, paratype ♂, pereopod I (P59957); J, ischium–dactylus, ventral view; K, posterior view; L, carpus–dactylus with antennal cleaning structure, anterior view. Scale bar = 100 µm.

broadly rounded, of epimera 7 rectangular; posterior margins of epimera 3–4 broadly rounded, epimera 5–7 increasingly rectangular and decreasingly angled posteriorly; epimera 3–7 endolobes absent; tergites 1–6 posterior margins slightly curved, tergite 7 posterior margin straight; tergite 1 length 0.25 pereon length; dorsal surface smooth. Noduli lateralis in one straight line on all pereonites on each side. *Pleon* (Fig. 15A) pleura anterior margin slightly rounded, posterior margin pointed; pleonites 1–2 posterior margin curved, pleonites 3–5 straight; dorsal surface smooth. *Pleotelson* (Fig. 15G) posterior margin rounded, sides parallel, length 0.9 width, dorsal surface smooth. *Antenna* (Fig. 15D) long, slender, reaching middle of epimera 4; flagellum length 0.6 article 5 length; flagellar article length proportions 1:3; all segments setose, more densely on flagellum. *Mandibles* (Fig. 17A–E). Left mandible setose lobe with two robust fan-shaped penicils and row of separate long simple setae between lacinia mobilis and molar process; right mandible setose lobe with group of short simple setae confined to lacinia mobilis base. *Maxilliped* (Fig. 17H,I) palp article 2 with apical group of setae on small lobe. *Male pereopods* (Fig. 17J–L) 1, 2 and 3 carpus ventral side with brush of long setae with flat spoon-like tips increasing in length distally, decreasing in length from pereopod 1–3. *Penes* ovoid, proximal bilobed lamellar process subtriangular, covering 0.2 penes length. *Male pleopod* (Fig. 16B,C) 1 exopod triangular, apex with two long setae, lateral margin with two setae, pseudotrachea along proximal lateral margin, width 0.5 exopod width, length 0.4 exopod length; exopod length 0.4 endopod length. Pleopod 2 exopod proximal wide portion length 0.33 exopod length, pseudotrachea along proximal lateral margin, width 0.5 exopod width, length 0.3 exopod length; row of long, thick setae along ventrolateral margin; endopod proximal article length 0.2 endopod length; exopod length 0.75 endopod length. Pleopod 3 exopod lateral margin near apex with 4 large setae; exopod 4 with two large setae on lateral margin; exopod 5 apex with row of fine setae; pleopods 3–5 exopods increasingly rounded; scales along lateral margin to apex; pleopods width 0.4 pleon width. *Uropod* (Fig. 15G,H) protopod length 1.6 width, proximal width 2.0 distal width, inner margin slightly wave-like, leaving gap between pleotelson and protopod distal portion, distal tip anteriorly rounded and posteriorly pointed, half protopod length visible dorsally; length (along inner margin of dorsally visible portion) less than 2.0 width (at point of exopod insertion); exopod length 0.5 protopod dorsally visible portion length, inserted dorsally  $\frac{1}{3}$  length to apex; endopod

setose with longer apical setae than exopod, exopod length 0.6 endopod length; dorsal surface smooth.

**Etymology.** This species is named in honour of the first author's husband, Jack Dhaliwal.

**Remarks.** *Cubaris dhaliwali* n.sp. can be distinguished from the other species of *Cubaris* in the Australasian region by the following features (“\*” indicates species originally placed in *Nesodillo* and may still belong in that genus):

- smooth dorsal surface [*C. chiltoni* Vandel, 1973, *C. hickmani* Green, 1961, *C. goweri* Lewis, 1998b, *C. lewisae* nom. nov., *C. merulanoides* (Wahrberg, 1922), *C. murina* Brandt, 1833, *C. nigroflava* (Wahrberg, 1922), *C. rufoniger* (Wahrberg, 1922) and *C. tasmaniensis* Green, 1961];
- pleotelson with parallel lateral sides and rounded posterolateral corners [*C. ambitiosa* (Budde-Lund, 1885), *C. fasciata* Lewis, 1998b, *C. ferruginea* Lewis, 1998b, *C. minilobus* Lewis, 1998b, *C. hirsuta* Lewis, 1998b, *C. tasmaniensis* Green, 1961, *C. marmorata* (Wahrberg, 1922), *C. sulcifrons* Green, 1961, *C. tamarensis* Green, 1961, *C. incisa* (Verhoeff, 1926)\*, *C. plastica* (Verhoeff, 1926)\*, *C. pronyensis* (Verhoeff, 1926)\*, *C. canalensis* (Verhoeff, 1926)\*, *C. lacustris* (Verhoeff, 1926)\* and *C. pacifica* (Verhoeff, 1926)\*];
- absence of a ridge in front of the endolobe on epimera 1 [*C. miser* (Budde-Lund, 1904)];
- lateral margin of epimera 1 not grooved (*C. lundi* Stebbing, 1900), shape of the uropods [*C. tarangensa* (Budde-Lund, 1904)];
- epimera 6 posterior margin without notch (*C. crenata* Lewis, 1998b).

### *Sphenodillo* Lewis, 1998b

*Sphenodillo* Lewis, 1998b: 773.

**Type species.** *Sphenodillo agnostos* Lewis, 1998b by subsequent designation (not “*Sphenodillo howensis*”, nomen nudum).

**Remarks.** *Sphenodillo* Lewis (1998b) is monotypic as originally described and “*Sphenodillo howensis*” was designated as the type species in that publication. Lewis (1998b), however, contains no description of “*Sphenodillo howensis*”, so this name is a *nomen nudum*. Therefore, we designate *S. agnostos* Lewis, 1998b, the sole described species in the genus, as the type species of *Sphenodillo* Lewis, 1998b.

### Key to the Armadillidae of Lord Howe Island (modified from Lewis, 1998b)

1	Epimera without endolobes ( <i>Australiodillo</i> ) .....	2
—	Epimera 1–2 with endolobes .....	7
2	Dorsal surface with sharp spines .....	<i>Australiodillo primitivus</i> Vandel, 1973
—	Dorsal surface tuberculate .....	3
3	Epimera 1–2 anteroventral surface with shoulders .....	<i>Australiodillo armus</i> Lewis, 1998b
—	Epimera 1–2 anteroventral surface without shoulders .....	4



- 4 Dorsal surface densely setose ..... *Australiodillo setosus* Lewis, 1998b  
 — Dorsal surface not densely setose ..... 5
- 5 Pleonites 1–5 posterior margins without distinct midline  
 tubercle ..... *Australiodillo anomalus* Lewis, 1998b  
 — Pleonites 1–5 posterior margins with distinct midline tubercle ..... 6
- 6 Pleon dorsal tubercles sharp; body <12 mm long ..... *Australiodillo insularis* Vandel, 1973  
 — Pleon dorsal tubercles rounded; body >12 mm long ..... *Australiodillo muscosus* Lewis, 1998b
- 7 Uropodal exopods absent ..... *Pseudodiploexochus pacificus* Lewis, 1998b  
 — Uropodal exopods present ..... 8
- 8 Pleotelson divided into three parts separated by fine lines, middle  
 section with two lateral tubercles ..... *Orthodillo chiltoni* Vandel, 1973\*  
 — Pleotelson not divided into three parts ..... 9
- 9 Pleotelson with heavy dorsal keel; endolobes rounded ..... *Sphenodillo agnostos* Lewis, 1998b  
 — Pleotelson without heavy dorsal keel ..... 10
- 10 Epimera near horizontal; tooth-like endolobes ..... 11  
 — Vertical or angled epimera; rounded tubercles ..... 16
- 11 Large club-like tubercles on pereon dorsal surface; high, uncleft  
 frontal lamina ..... *Stigmops howensis* (Lewis, 1998b)  
 — Pereon dorsal tubercles not club-like; frontal lamina cleft or  
 entire ..... 12
- 12 Four high cephalic tubercles, ridge above eyes; frontal lamina  
 cleft or indented ..... 13  
 — Cephalic tubercles lower than; frontal lamina entire ..... 15
- 13 Frontal lamina indented ..... *Stigmops odontotergina* n.sp.  
 — Frontal lamina cleft ..... 14
- 14 Cephalic tubercles not higher than pereon tubercles ..... *Stigmops polyvelota* n.sp.  
 — Cephalic tubercles much higher than pereon tubercles ..... *Stigmops demiclavula* (Lewis, 1998b)
- 15 Frontal lamina straight ..... *Pyrgoniscus scopelicus* n.sp.  
 — Frontal lamina curved forming three lobes ..... *Pyrgoniscus intermedius* Lewis, 1998b
- 16 Dorsal surface densely setose ..... *Cubaris hirsuta* Lewis, 1998b  
 — Dorsal surface not densely setose ..... 17
- 17 Epimera 6 posterior margin with notch ..... *Cubaris crenata* Lewis, 1998b  
 — Epimera 6 posterior margin without notch ..... 18
- 18 Epimera 1 posterior margin sharply rectangular ..... *Cubaris goweri* Lewis, 1998b  
 — Epimera 1 posterior margin rounded/ subrectangular ..... 19
- 19 Dorsal surface granulated; epimera 1 endolobe broadly rounded ..... *Cubaris lewisae* nom. nov.  
 — Dorsal surface not granulated ..... 20

20	Pleotelson sides parallel .....	<i>Cubaris dhaliwali</i> n.sp.
—	Pleotelson hourglass-shaped .....	21
21	Pleotelson proximal width 0.95–1.05 distal width .....	<i>Cubaris ferruginea</i> Lewis, 1998b
—	Pleotelson proximally wider than distally .....	22
22	Antenna flagellar article 1 length 0.25 article 2 length .....	<i>Cubaris fasciata</i> Lewis, 1998b
—	Antenna flagellar article 1 length 0.5 article 2 length .....	<i>Cubaris minilobus</i> Lewis, 1998b

### Biogeography of Lord Howe Armadillidae

Armadillidae is a large family with 78 described genera and approximately 700 species. This family occurs mainly in the Southern Hemisphere, indicating a Gondwanan origin. Most genera are found in the southern African, Oriental and Australian-South Pacific regions with few representatives in the Neotropical region and only one in the Palaearctic (Mediterranean) region (Taiti *et al.*, 1998). The Australian-South Pacific region has the highest number of genera and highest endemism (Taiti *et al.*, 1998). Selected genera or geographical areas have been revised, but no author has yet made a comprehensive revision of the entire family. The taxonomy of the family is therefore confused and in need of a global revision. Phylogenetic relationships within the family are largely unknown and will be better understood after a revision. The following review of the biogeographic relationships of Lord Howe Armadillidae is derived from Taiti *et al.* (1998), the taxonomic references listed above for each genus and an unpublished thesis (Lillemets, 2001).

*Cubaris*, with approximately 119 nominal species found in all four Gondwanan regions (Table 2), is the largest and most widespread of the genera treated in this paper. Lord Howe Island alone has 8 species. Many species of *Cubaris* are found in the Americas (a total of c. 44 species, 11 in southern North America, 14 in Central America and the West Indies and 19 in South America). The Australian-Pacific region is also diverse with approximately 35 species. The Indian sub-continent has 19 species and 9 each in Africa and southeast Asia. One species has been described from Spain (*C. invenustus* Collinge, 1915a), although it may be an introduced species because most other *Cubaris* occur in

the southern hemisphere or are on tropical islands. *Cubaris* is not monophyletic (Lillemets, 2001) and its geographic distribution may change with a comprehensive revision. The same statement applies to the non-monophyletic *Pyrgoniscus* (Lillemets, 2001).

*Pyrgoniscus* is the second largest genus with 19 described species worldwide, with 2 on Lord Howe Island. Members of this genus are found both in the African and Australian-South Pacific regions (Table 2), though most are found in the latter region (15 species). An African link is also indicated by the presence of *Pseudodiploexochus* on Lord Howe Island. Of the 22 species in this latter genus, 16 are from Africa, two from Madagascar and one each from Mauritius, Brazil, Western Australia and Lord Howe Island (Table 2). Until this paper, *Anchicubaris* represented another link to Africa. This link is, however, removed because the two previously described species do not belong in this genus and are now placed in the new genus *Stigmops*. *Stigmops*, with 4 species, is endemic to Lord Howe Island and appears to be related to *Pyrgoniscus*, based on preliminary phylogenetic analyses (Lillemets, 2001).

The monotypic genera *Orthodillo* and *Sphenodillo* are endemic to Lord Howe Island and have only been found in small numbers. Vandel (1973) described *Orthodillo* from a single specimen and no other records of the species are known. *Australiodillo* is endemic to Lord Howe Island, New Caledonia and Queensland. Of the 9 species in this genus, 6 are endemic to Lord Howe Island, 2 found in New Caledonia and one in Queensland (Table 2). Several previously described species from Lord Howe Island are difficult to distinguish and may prove to be synonymous. Therefore, the diversity of Lord Howe *Australiodillo* may be more comparable to other regions.

**Table 2.** Worldwide distribution of Armadillidae taxa represented on Lord Howe Island.

genus	number of species	distribution
<i>Australiodillo</i>	9	Lord Howe Island, New Caledonia, Queensland
<i>Cubaris</i>	c. 119	Southern Hemisphere, southern North America, southeast Asia, Spain
<i>Orthodillo</i>	1	Lord Howe Island
<i>Pseudodiploexochus</i>	22	Lord Howe Island, Western Australia, South Africa, Tanzania, Zaire, Comoro I., Aldabra I., St. Helena I., Madagascar, Mauritius, Brazil
<i>Pyrgoniscus</i>	19	Lord Howe Island, Queensland, New South Wales, New Caledonia, Chatham I., "Eastern Seas", Madagascar, Kenya, Tanzania
<i>Sphenodillo</i>	1	Lord Howe Island
<i>Stigmops</i>	4	Lord Howe Island

The diversity of organisms on Lord Howe Island is high, much higher than what would be expected on an isolated island of its size. Many taxa possibly could have reached the island by long distance dispersal, using various biotic and abiotic methods. Some taxa present on the island, however, also have low dispersal abilities: Peloridiidae (Insecta: Hemiptera) (Evans, 1981) and Archontophoenicinae (Palmae: Areceae) (Pintaud, 1999). Armadillidae have achieved limited dispersal across large bodies of water, shown by the small number of species found on the Hawaiian Islands (Taiti & Ferrara, 1991). Never-the-less, eight different genera of Armadillidae are represented on Lord Howe Island, more than would be expected from anthropogenic introductions, as in Hawaii. Possible dispersal mechanisms of Armadillidae to oceanic islands might also include rafting on floating vegetation. For short distances, rafting may be possible, but over longer distances this method seems unlikely. An alternative hypothesis (Evans, 1981) suggests that these taxa are ancient relicts of a formerly widespread biota. Shoals of the submerged Lord Howe Plateau would have been exposed during previously low sea levels of the glacial periods, thus creating much larger terrestrial areas and possibly effective "stepping-stones" (Standard, 1961, 1963; Clark & Pickard, 1977; Hutton, 1986). Thus we would expect to see closer relationships with other land masses such as New Zealand, Australia and New Caledonia. The presence of armadillids and other non-marine fauna on tiny Ball's Pyramid supports a recent connection between this rock and Lord Howe Island, similar to the other adjacent rocks such as Mutton Bird Island. The Holocene rise in sea levels concomitantly would have caused a contraction in the ranges of the fauna of Lord Howe Island, as well as breaking any connections with nearby landmasses. In this case, we would then expect to observe vicariant distributions. Moreover, the contracting area of the island would increase species density above equilibrium levels. Whatever the cause, we are certain that the biogeographic relationships of Lord Howe Island have a historical explanation.

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