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The henicopid centipede *Haasiella* (Chilopoda: Lithobiomorpha): new species from Australia, with a morphology-based phylogeny of Henicopidae

GREGORY D. EDGECOMBE

Australian Museum, 6 College Street, Sydney, NSW 2010, Australia; greged@austmus.gov.au

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Paralamyctes (*Haasiella*) Pocock, 1901 (= *Wailamyctes* Archey, 1917) includes three described species from New Zealand and its Subantarctic Islands. Australian species of *P.* (*Haasiella*) include *P.* (*H.*) *subicolus* n. sp. from Tasmania and a clade composed of *P.* (*H.*) *cammooensis* n. sp. from Queensland and New South Wales, *P.* (*H.*) *ginini* n. sp. from New South Wales and the Australian Capital Territory, and an allied species from Tasmania. Monophyly of *P.* (*Haasiella*) and the membership of a *P.* (*H.*) *cammooensis* Group are supported by parsimony analysis of morphological characters. A grouping of *P.* (*Haasiella*) and *P.* (*Thingathinga*) as retrieved by molecular data analysis is also found in minimal length cladograms based on morphology. The dataset incorporates new information on several previously poorly known henicopids, including the types of *Lamyctopristus* Attems, 1928, and *Analamyctes* Chamberlin, 1955.

KEYWORDS: Myriapoda, Chilopoda, Lithobiomorpha, Henicopidae, *Paralamyctes*, *Haasiella*, Australia, taxonomy, phylogeny.

Introduction

The henicopid centipede genus *Haasiella* Pocock, 1901, was established for *Henicops insularis* Haase, 1887, from the Auckland Islands, but the peculiarities upon which Pocock (1901) based *Haasiella* are due in part to the holotype of *H. insularis* having malformed anal legs. Archey (1937) suspected that another species from the Auckland Islands, *Wailamyctes munroi* Archey, 1923, was a junior synonym of *H. insularis*, and this subjective synonymy was formalized by Johns (1964). *Wailamyctes* Archey, 1917 is based on the New Zealand species *W. trailli* Archey, 1917. Synonymy of *Wailamyctes* and *Haasiella* was first suggested by Archey (1937), and was formalized by Edgecombe (2001), who included in *Haasiella* the three described species *H. insularis*, *W. trailli* and *W. halli* Archey, 1917, all from South Island and the Subantarctic Islands of New Zealand.

The systematic position of *Haasiella* within Henicopinae has been appraised based on morphological and molecular sequence data (Edgecombe, 2001; Edgecombe *et al.*, 2002). *Haasiella* was found to be nested within the phylogenetic

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structure of the Gondwanan clade *Paralamyctes* Pocock, 1901, and accordingly classified as a subgenus of *Paralamyctes*. No species of *P.* (*Haasiella*) have been described from outside New Zealand, though Mesibov (1986) identified a species from north-western Tasmania as *Wailamyctes*. Edgecombe *et al.* (2002) included this species for morphological and molecular codings, and endorsed its membership in *Paralamyctes* (*Haasiella*). The Tasmanian species is formalized herein as *P.* (*Haasiella*) *subicolus* n. sp. Two additional new species, from Queensland/New South Wales and the Australian Capital Territory/New South Wales, are also recognized as *P.* (*Haasiella*), and a related species is reported from southern Tasmania (figure 1). The systematic position of new species of *Paralamyctes* (*Haasiella*) is evaluated with reference to morphological characters, refining the parsimony analysis of Edgecombe *et al.* (2002). Included in the analysis are a few species, including the type species of the genera *Lamyctopristus* Attems, 1928, and *Analamyctes* Chamberlin, 1955, that were previously too poorly known to code, along with additional species of other henicopid genera.

Abbreviations for repositories of specimens examined are as follow: AM, Australian Museum, Sydney; ANIC, Australian National Insect Collection, Canberra; CASENT, California Academy of Sciences, San Francisco; MNHN, Muséum national d'Histoire naturelle, Paris; QM, Queensland Museum, Brisbane; QVMAG, Queen Victoria Museum and Art Gallery, Launceston; TMAG, Tasmanian Museum and Art Gallery, Hobart. Other abbreviations are: ACT, Australian Capital Territory; NP, National Park; NSW, New South Wales; Rd, Road; SF, State Forest. Morphological terminology is as explained by Edgecombe (2001: 203). Drawings were prepared with a camera lucida attachment to a Leica MZ12. Scanning electron microscopy used a Leo 435VP with a Robinson backscatter detector, and digital images were assembled into plates with Photoshop.

CHILOPODA Latreille, 1817
Order LITHOBIOMORPHA Pocock, 1902
Family HENICOPIDAE Pocock, 1901
Subfamily HENICOPINAE Pocock, 1901
Tribe HENICOPINI Pocock, 1901
Genus *Paralamyctes* Pocock, 1901

Type species. Paralamyctes spenceri Pocock, 1901; by original designation.

Subgenus *Paralamyctes* (*Haasiella*) Pocock, 1901

= *Wailamyctes* Archey, 1917.

Type species. Henicops insularis Haase, 1887 (= *Wailamyctes munroi* Archey, 1923).

Diagnosis. Paralamyctes with median furrow on head shield extending to transverse suture, variably impressed behind suture; antenna with 17–22 articles; ocellus relatively posteriorly positioned; teeth on dental margin of maxillipede conical, decreasing in size medially, innermost tooth small; mandibular aciculae with barbs or pinnules along both margins; posterior margin of tergite 8 transverse; tarsi of legs 1–12 composed of a single article.

Assigned species. Wailamyctes halli Archey, 1917; *Wailamyctes trailli* Archey, 1917; *Paralamyctes* (*Haasiella*) *cammooensis* n. sp.; *Paralamyctes* (*Haasiella*) *ginini* n. sp.; *Paralamyctes* (*Haasiella*) *subicolus* n. sp.

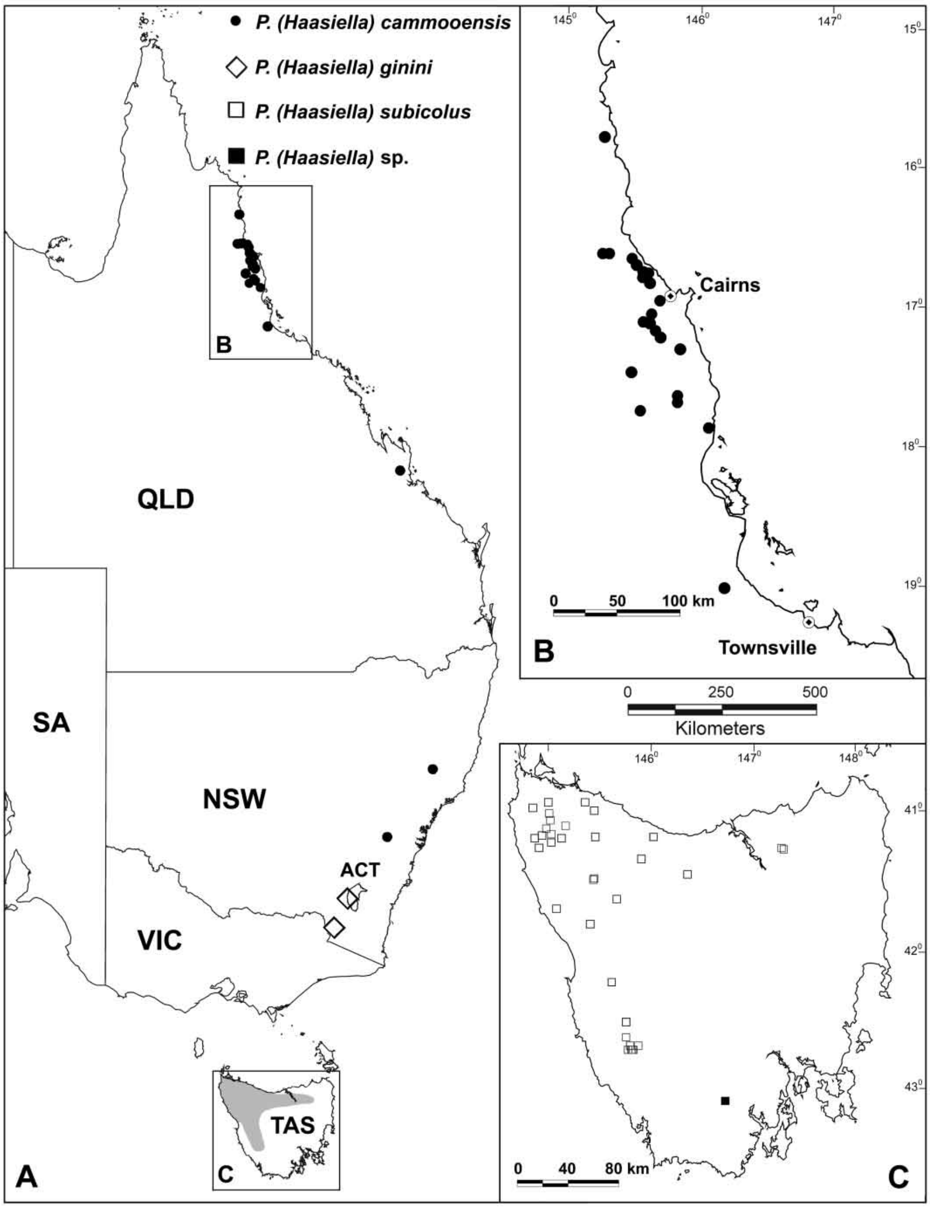


FIG. 1. Occurrences of *Paralamyctes* (*Haasiella*) species in eastern Australia. (A) Eastern Australia, showing locations of insets B and C; (B) distribution of *P.* (*H.*) *cammooensis* n. sp. in north-eastern Queensland; (C) distribution of *P.* (*H.*) *subicolus* n. sp. and *P.* (*Haasiella*) sp. in Tasmania.

Discussion. The diagnosis of the subgenus *Haasiella* above unites the three New Zealand species assigned by Archey (1917, 1923, 1937) to *Wailamyctes* with three new Australian species.

Archey (1937) cited the reduced size of the innermost tooth on the maxillipede margin in his diagnosis of *Wailamyctes*. This character is associated with a gradual reduction in the size of the teeth and their spacing medially, as seen in *P.* (*H.*) *trailli* (figure 3E of Edgecombe *et al.*, 2002), *P.* (*H.*) *cammooensis* (figure 4D) and *P.* (*H.*) *subicolus* (figure 21B). As noted in Archey's (1937) diagnosis, the teeth of *P.* (*Haasiella*) species are consistently conical, rather than the blunt bulbs of many species of *P.* (*Thingathinga*) and *P.* (*Paralamyctes*).

In New Zealand species that retain the ocellus, such as *P.* (*H.*) *halli* (figure 25 of Archey, 1917), the ocellus is positioned relatively further back than in other *Paralamyctes*. A similarly posterior position of the ocellus in observed in *P.* (*H.*) *cammooensis* (figures 2, 3) and *P.* (*H.*) *ginini* (figure 13), such that the character appears to have diagnostic value for *P.* (*Haasiella*).

P. (*Haasiella*) *cammooensis* Group

Diagnosis. *P.* (*Haasiella*) with 17 antennal articles; ocellus weakly convex; Tömösváry organ large, behind ocellus, situated relatively posteriorly on cephalic pleurite; dental margin of maxillipede moderately V-shaped, each half bearing three to five teeth; posterior margin of TT7, 9, 11 and 13 transverse, all tergites lacking projections; distal spinose projections on tibiae of legs 1–12, lacking on legs 13–15; two coxal pores on legs 12–15 in females, one or two pores on these coxae in males.

Assigned species. *Paralamyctes* (*Haasiella*) *cammooensis* n. sp.; *Paralamyctes* (*Haasiella*) *ginini* n. sp.; *Paralamyctes* (*Haasiella*) sp.

Discussion. Membership of two new Australian species, *Paralamyctes cammooensis* and *P. ginini*, in *P.* (*Haasiella*) is indicated by the following characters: a deep longitudinal median furrow on the head shield extending back to the transverse suture, and a large, bell-shaped sternite on the first maxillary coxosternite (diagnostic characters of *Paralamyctes sensu* Edgecombe, 2001); bipinnulate mandibular aciculae, a diminutive inner tooth on the dental margin of the maxillipede, and unjointed tarsi on legs 1–12 (possessed by species of *Haasiella*); and, a flattened ocellus [shared by several species of *P.* (*Thingathinga*) and *P.* (*Haasiella*)]. An enlarged Tömösváry organ situated relatively posteriorly on the cephalic pleurite in the *P.* (*H.*) *cammooensis* Group resembles that of *P.* (*Haasiella*) *trailli* (figure 1I of Edgecombe *et al.*, 2002). The dental margin of the maxillipede is more deeply V-shaped in the *P.* (*H.*) *cammooensis* Group than in other species of *P.* (*Haasiella*).

Lamyctes bipartitus Lawrence, 1960, named for a single male from Madagascar (MNHN collection), resembles *P.* (*H.*) *cammooensis* and *P.* (*H.*) *ginini* in several features of external morphology. Assessment of this species is based on study of the holotype together with two females and an additional male from Parc National d'Ankarafantsika, Mahajanga Province (CASENT 9001624). Each of these species typically possesses 17 antennal articles; elsewhere in post-larval Henicopinae, this reduced number of articles is known only in *P.* (*Paralamyctes*) *harrisi* Archey, 1922, and *P.* (*P.*) *newtoni* (Silvestri, 1917). The Malagasy and Queensland/New South Wales species in particular have similar dentition (four or five small, pointed teeth) on the maxillipede margin. Lawrence (1960) had observed *bipartitus* to be atypical of *Lamyctes* with respect to its reduced antennal segmentation, large number of teeth on the maxillipede, and undivided male first genital sternite. He speculated that additional material might reveal the species to represent a new genus. The median furrow on the head shield in '*L .*' *bipartitus* is continuous to the transverse suture, indicating membership in *Paralamyctes*. The unjointed tarsi would suggest an assignment to *P.* (*Haasiella*), and the species resembles the *P.* (*H.*) *cammooensis*

Group with respect to its lack of tergite projections and few coxal pores (1,2,2,2/1,2,2,2 in males, 2,3,3,3/2,3,3,3 in females of *P. bipartitus*). However, certain detailed characters instead suggest an alternative assignment to *P.* (*Paralamyctes*). In particular, the mandibular aciculae are developed as uniquely characteristic of that subgenus, with a row of digitiform, distally pointed pinnules confined to the dorsal edge of each acicula (figure 34A) versus both sides of the aciculae pinnulate in *P.* (*Haasiella*). As well, the Tömösváry organ is situated on the ventral margin of the head rather than on the cephalic pleurite, a condition observed only in certain species of *P.* (*Paralamyctes*) (see character 7 in the Appendix). Lawrence (1960) described an absence of distal spinose projections on the tibiae of legs 13–15 in the Malagasy species, but the holotype has a blunt projection on leg 13, and this projection is well-developed on leg 13 in the three specimens from Parc National d'Ankarafantsika. Features suggestive of the *P.* (*H.*) *cammooensis* Group, such as the lack of tergite projections, indistinct tarsal articulations, and few coxal pores, are typical juvenile traits of henicopids, and are perhaps accounted for by small size. Evidence from the mandibular aciculae and position of the Tömösváry organ makes membership of *P. bipartitus* in *P.* (*Paralamyctes*) most probable.

Paralamyctes* (*Haasiella*) *cammooensis n. sp.
(figures 2–5, 6A–D, 7–12, 38B)

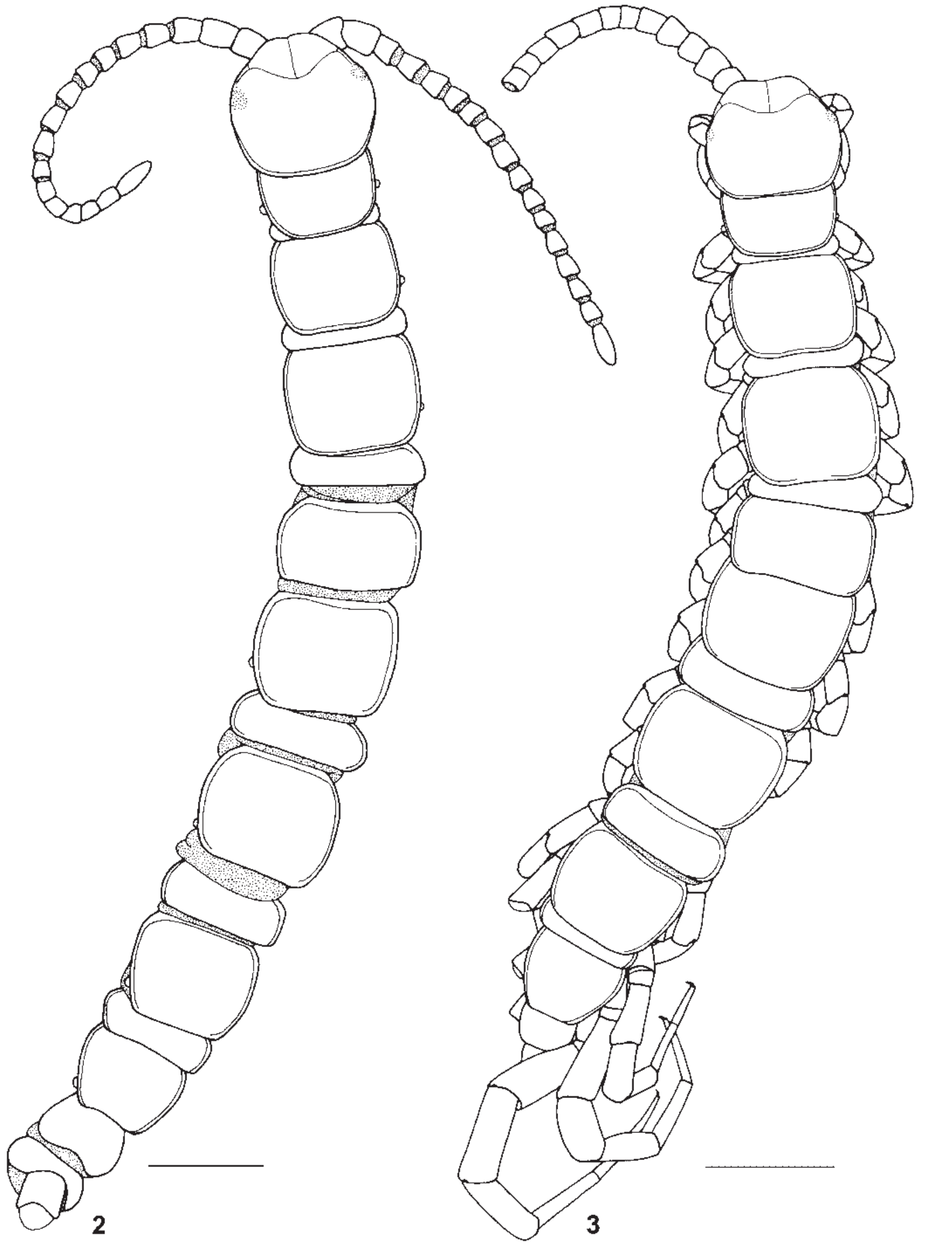
Etymology. From Cammoo Caves, the type locality.

Diagnosis. Member of *P.* (*H.*) *cammooensis* Group with four or five teeth on dental margin of maxillipede; legs finely setose, without stronger, spine-like setae on prefemur and femur; few setae on first genital sternite of female.

Holotype. ANIC-03-1, female (figure 2), Cammoo Caves (now Mt Etna Caves NP), near Rockhampton, Queensland, 23°10′S, 150°28′E, R. W. Taylor and T. A. Weir, 25 October 1976, dense, low closed forest (ex ANIC Berlesate 535). Length of head 0.56 mm; length of body 5.6 mm.

Paratypes. figured specimens ANIC-03-2–ANIC-03-4, ANIC-03-7, four females, ANIC-03-5, ANIC-03-6, two males; unfigured specimens ANIC-03-8 (five females, nine males); all from type locality, same collection.

Other material. NE Queensland rainforest: ANIC-03-9, male, Moses Creek, 4 km N by E Mt Finnigan, 15°47′S, 145°17′E, T. Weir, 14–16 October 1980; ANIC-03-10, female, Mt Lewis, 2 mi above Bushy Creek, 16°35′S, 145°18′E, J. G. Brooks, 25 November 1969; ANIC-03-11, male, Mt Lewis, 16°35′S, 145°13′E, 1010 m, R. W. Taylor and J. Feehan, 20 June 1971; ANIC-03-12, three females, five males, Black Mt Rd, 30 km N Kuranda, 16°38′S, 145°30′E, J. G. Brooks, 4 November 1969; ANIC-03-13, female, Black Mt Rd, 15 mi N Kuranda, 16°42′S, 145°31′E, A. Walford-Huggins, 6 November 1975; ANIC-03-14, three females, four males, six juveniles, larva IV, Black Mt Rd, 13.3 km N Kuranda, 16°45′S, 145°34′E, *ca* 1500 ft, J. G. Brooks, 3 January 1971; ANIC-03-15, male, 13 km NW Kuranda, 16°45′S, 145°34′E, J. Doyen, 6 December 1982; ANIC-03-16, two males, Black Mt Rd, 16°45′S, 145°35′E, 430 m, R. W. Taylor and J. Feehan, 27 June 1971; ANIC-03-17, two females, Black Mt Rd, 7 km NNW Kuranda, 16°45′S, 145°37′E, 400 m, A. Calder and T. Weir, 30 March 1984; ANIC-03-18, male, Black Mt Rd, 11.2 km N Kuranda, 16°46′S, 145°35′E, J. G. Brooks, 30 April 1970; ANIC-03-19, female, 1 km W Kuranda, 16°50′S, 145°37′E, J. Doyen, 6 December 1982; ANIC-03-20, female, Crystal Cascades, 16°57′S, 145°42′E, J. G. Brooks, 30 April 1970; ANIC-03-21,



Figs 2, 3. *Paralamyctes* (*Haasiella*) *cammooensis* n. sp. (2) Holotype, ANIC-03-1, female, Cammoo Caves, Mt Etna Caves NP, Queensland, scale 0.5 mm. (3) AM KS 74958, male, Danbulla SF, Queensland, scale 0.5 mm.

female, male, Mt Tiptree, 17°03′S, 145°38′E, 730 m, R. W. Taylor and J. Feehan, 29 June 1971; ANIC-03-22, two females, male, near Mt Haig, 17°07′S, 145°35′E, 1000 m, R. W. Taylor and J. Feehan, 30 June 1971; ANIC-03-23, male, Boar Pocket Rd, 5 mi N Gillies Hwy, 17°10′S, 145°39′E, J. G. Brooks, 9 December 1969;

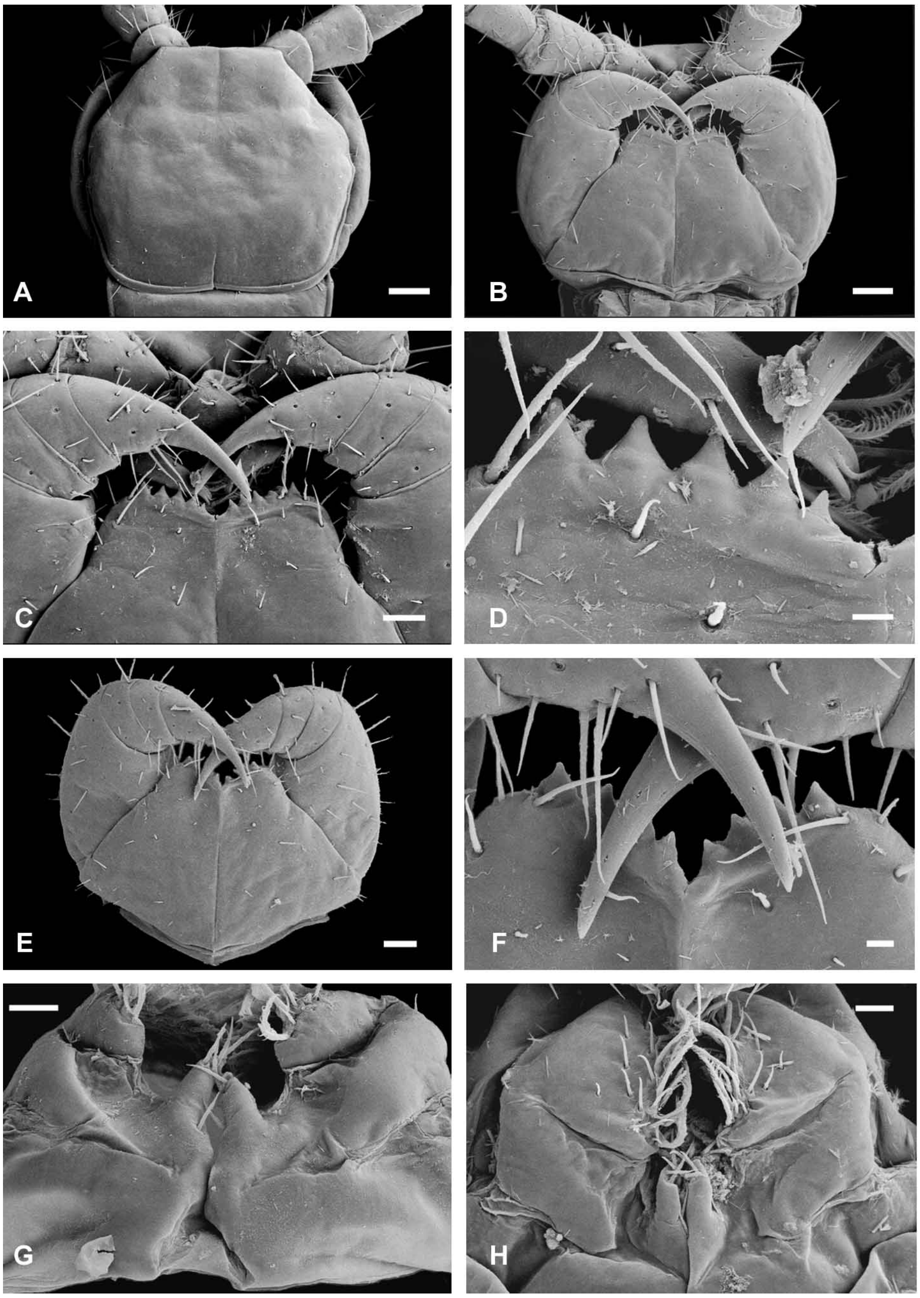


FIG. 4. *Paralamyctes* (*Haasiella*) *cammooensis* n. sp. Scanning electron micrographs. All from Cammoo Caves, Mt Etna Caves NP, Queensland. (A–D) ANIC-03-5, male. (A, B) Dorsal and ventral views of head, scales 100 μm; (C) telopodite and coxosternite of maxillipede, scale 50 μm; (D) dental margin of maxillipede coxosternite, scale 10 μm. (E–G) ANIC-03-3, female; (E, F) maxillipede and detail of dental margin of coxosternite, scales 50 μm, 10 μm; (G) first maxillae, scale 20 μm. (H) ANIC-03-2, female, coxal processes and telopods of first maxillae, scale 20 μm.

ANIC-03-24, female, Gillies Hwy, 2 km E Mt Nomico, 17°13′S, 145°42′E, 720 m, R. W. Taylor and T. A. Weir, 28 October 1976; ANIC-03-25, male, Mt Bellenden Ker, summit, 17°16′S, 145°51′E, 1560 m, R. W. Taylor and J. Feehan, 7 July 1971; ANIC-03-26, male, 27 km S Atherton, Longlands Gap Rd, 17°28′S, 145°29′E, J. G. Brooks, 11 November 1969; ANIC-03-27, two males, two larvae IV, Crawford's Lookout, 17°37′S, 145°48′E, 320 m, R. W. Taylor and J. Feehan, 5 July 1971; ANIC-03-28, four females, three males, 1.6 km SE Crawford's Lookout, 17°37′S, 145°48′E, *ca* 300 m, R. W. Taylor and J. Feehan, 10 July 1971; ANIC-03-29, two females, male, McNamee Creek, 17°40′S, 145°48′E, *ca* 400 m, R. W. Taylor and J. Feehan, 8 July 1971; ANIC-03-30, two juveniles, 1 km N Tully Falls NP, 17°45′S, 145°32′E, A. Walford-Huggins, 8 January 1976; ANIC-03-31, female, Lacey's Creek, 17°52′S, 146°04′E, *ca* 40 m, R. W. Taylor and J. Feehan, 9 July 1971; ANIC-03-32, two females, four males, 2.5 mi W Paluma, 19°01′S, 146°11′E, 2940 ft, J. G. Brooks, 13 January 1974; ANIC-03-33, two females, 2.7 mi W Paluma, 19°01′S, 146°11′E, 2920 ft, J. G. Brooks, 11 January 1975; AM KS 74958, male, Danbulla SF, Robson Creek Rd, 17°07′S, 145°37′E, G. Milledge, 27 April to 2 May 1998; QM S.45157, male, Bellenden Ker Range, summit TV station, 17°16′S, 145°51′E, 1560 m, Earthwatch/Qld. Museum, 17 October to 7 November 1981.

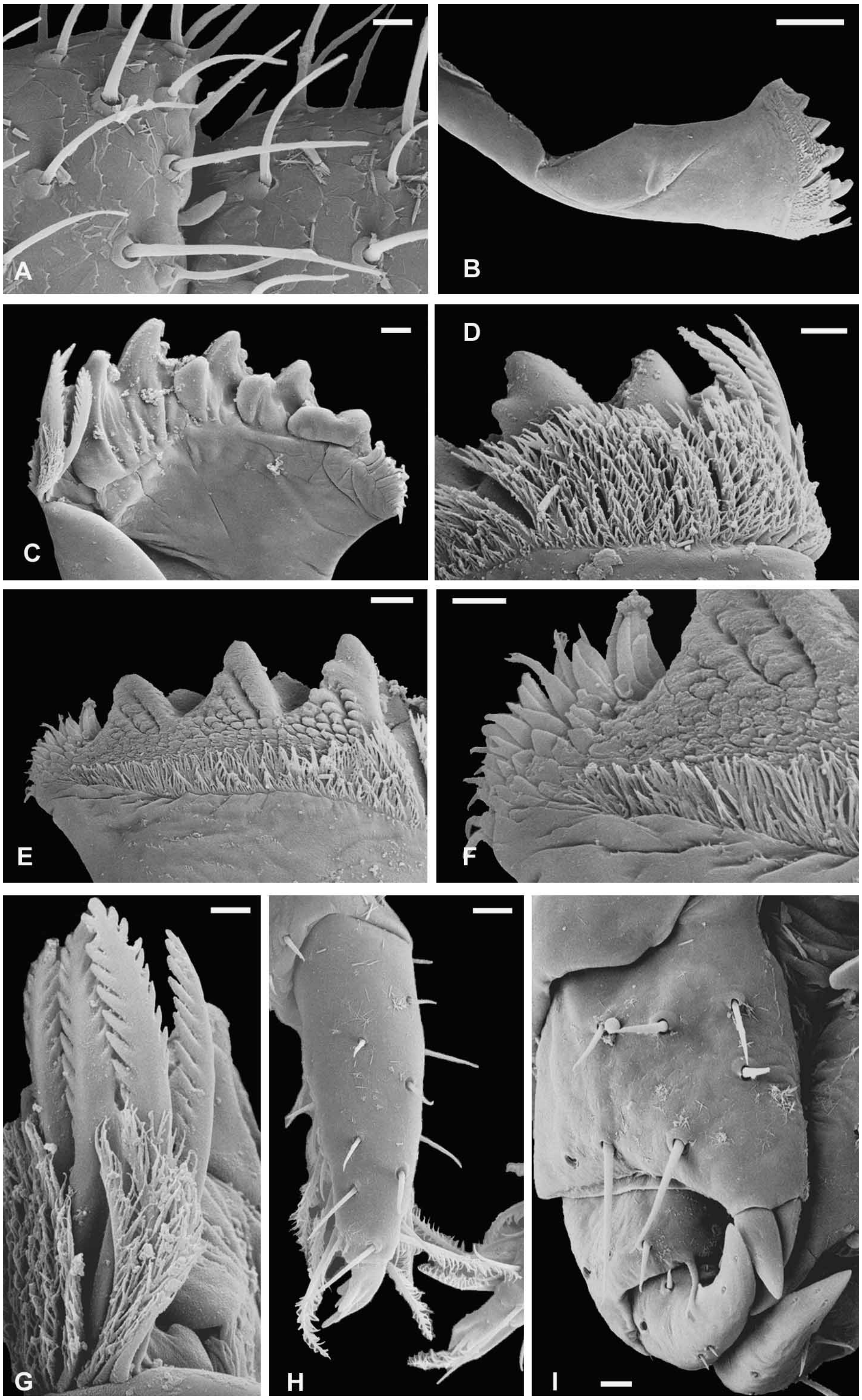
NSW: ANIC-03-34, female, male, Barrington Tops SF, Dilgry River, 31°53′S, 151°32′E, T. Weir and A. Calder, 15–16 November 1981, open forest; AM KS 67183, female, Kanangra-Boyd NP, Blood Filly Creek, 33°51′S, 150°03′E, M. Gray, G. Hunt and J. McDougall, 27 March 1976, *Eucalyptus fastigata*-*viminalis*.

Description

Length up to 7.1 mm. Head shield of subequal length and width (length 0.82 mm, width 0.80 mm in largest specimen). Head shield usually light brown; purple-black pigment concentrated around ocellus; antenna pale orange or yellow; tergites typically light brown; fresher specimens yellow to pale yellow-brown with purple-black mottling concentrated in median longitudinal band and on borders; legs pale brown; sternites occasionally pale lavender, with similar pigmentation on legs except for dull yellow tarsi.

Head shield smooth. Median notch at anterior margin moderately deep; posterior margin of head transverse or weakly convex. Median furrow well impressed to transverse suture (figure 4A), with indistinct, weak to strong continuation behind transverse suture to middle of head shield. Antenna extending back to TT5 (figure 2) or 6, usually with 17 articles, exceptionally 16, other combinations include 14/18, 17/19, 17/20, 18/18 articles; basal two articles moderately larger than succeeding articles; articles 3–16 variable in length, a few not much longer than wide; articles gently widening distally; distal article typically about 1.7 times length of penultimate article. Typical henicopid increase in abundance of trichoid sensilla from segment

FIG. 5. *Paralamyctes* (*Haasiella*) *cammooensis* n. sp. Scanning electron micrographs. (A, I) ANIC-03-2, female, Cammoo Caves, Mt Etna Caves NP, Queensland. (A) Third- and fourth-last antennal articles, scale 5 μm; (I) gonopod, scale 10 μm. (B–G) QM S45157, male, Bellenden Ker Range, Queensland. (B) Mandible, scale 50 μm; (C) inner (posterior) view of mandibular gnathal lobe, scale 10 μm; (D) aciculae and fringe of branching bristles, scale 10 μm; (E) mandibular teeth, scale 10 μm; (F) furry pad and accessory denticles, scale 5 μm; (G) aciculae, scale 5 μm. (H) ANIC-03-3, female, locality as for A, tarsus and pretarsus of second maxilla, scale 15 μm.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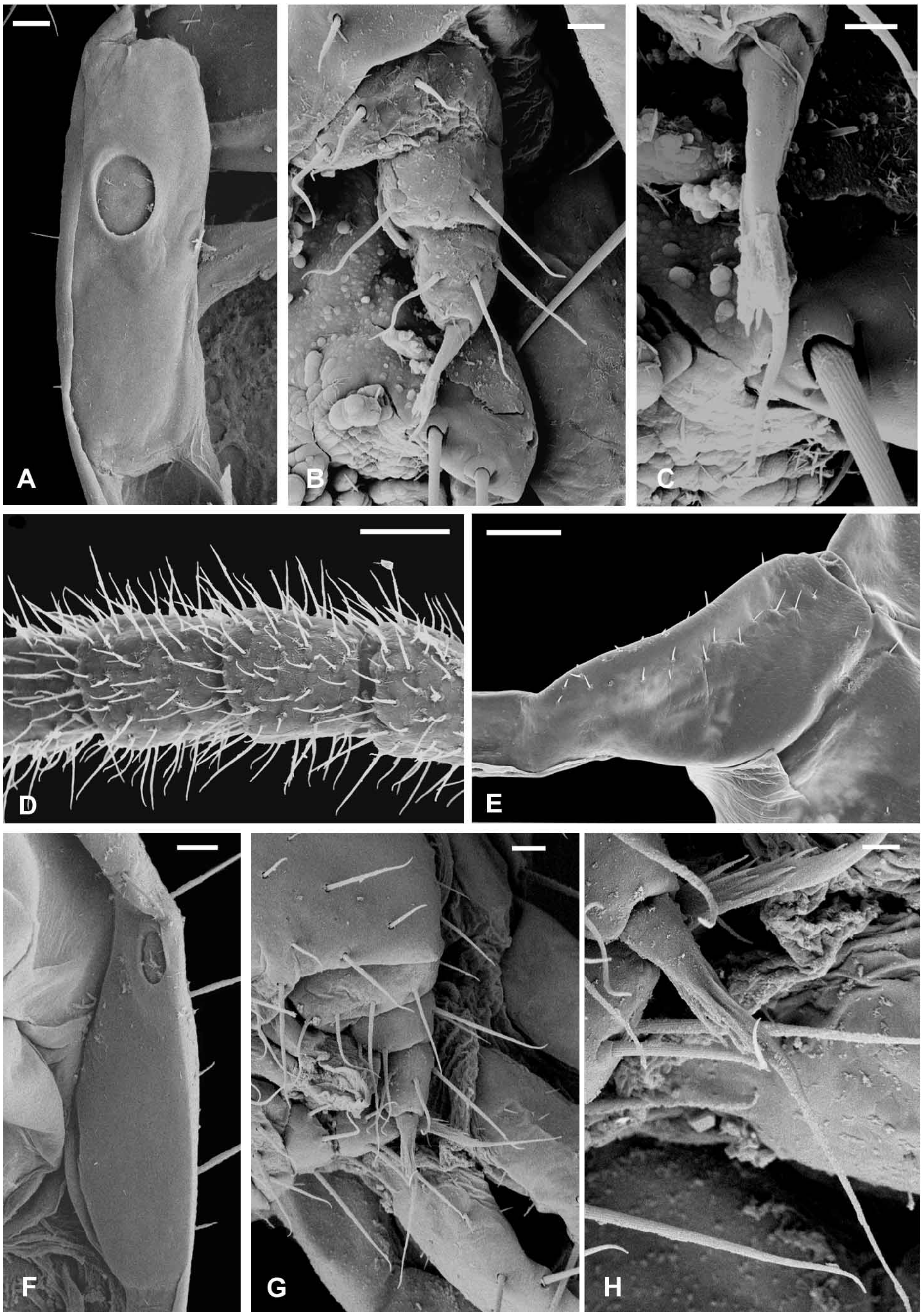
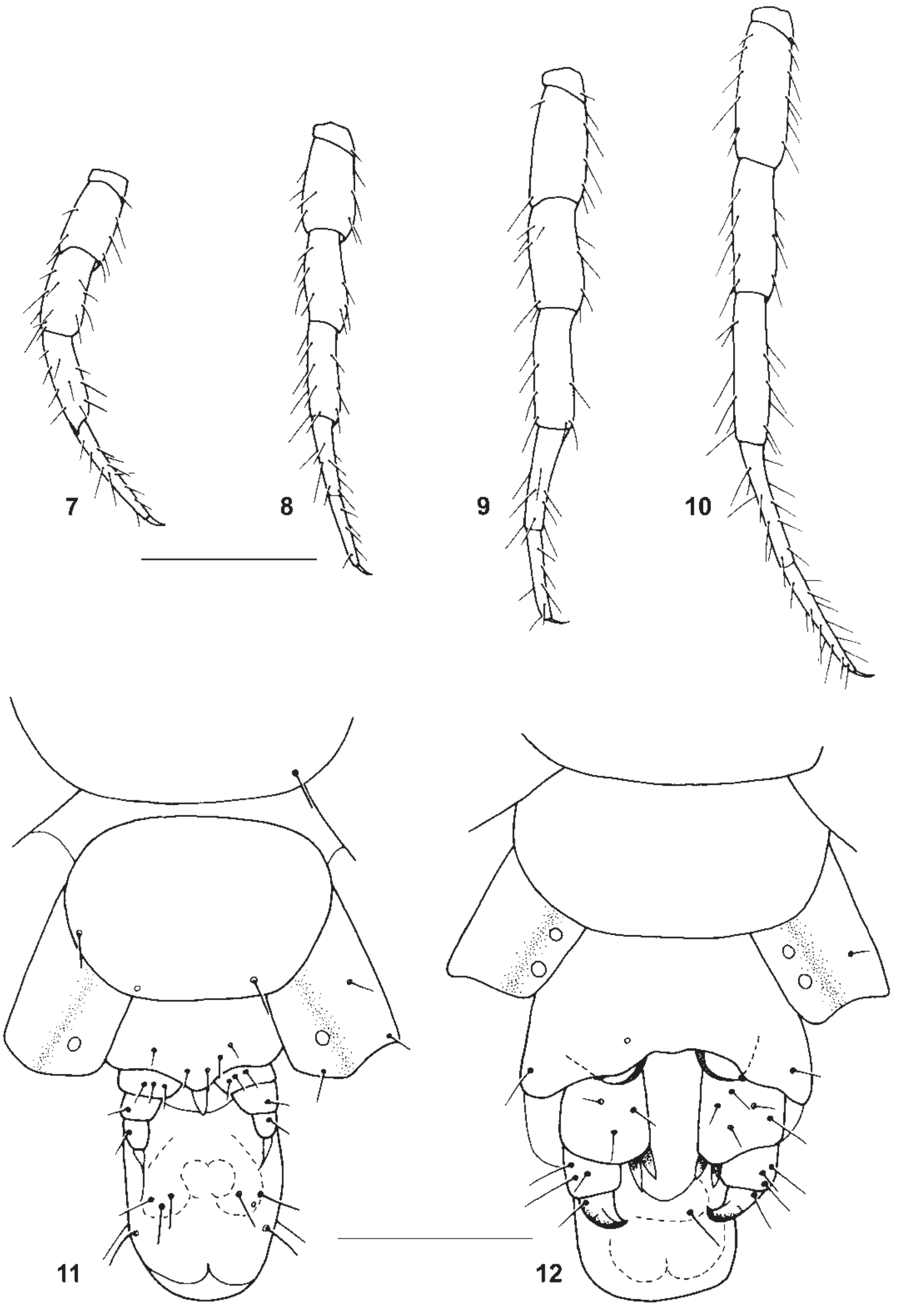


FIG. 6. (A–D) *Paralamyctes* (*Haasiella*) *cammooensis* n. sp. Cammoo Caves, Mt Etna Caves NP, Queensland. (A) ANIC-03-3, female, cephalic pleurite, showing Tömösváry organ, scale 20 μm. (B, C) ANIC-03-5, male, gonopod and detail of terminal process, scales 10 μm, 5 μm. (D) ANIC-03-7, female, articles in distal part of antenna, scale 50 μm. (E–H) *Paralamyctes* (*Haasiella*) *subicolus* n. sp. (E, F) QVMAG 23:5282, female, Christmas Hills, Tasmania. (E) Coxa of second maxilla, scale 100 μm; (F) cephalic pleurite, showing Tömösváry organ, scale 50 μm. (G, H) QVMAG 23:22969, male, Wombat Hill, Waratah, Tasmania, gonopod and detail of terminal process, scales 30 μm, 10 μm.



FIGS 7–12. *Paralamyctes* (*Haasiella*) *cammooensis* n. sp. (7–10) ANIC-03-32, male, 2.5 mi W Paluma, Queensland, scales 0.5 mm. (7) Leg 12. (8) Leg 13. (9) Leg 14. (10) leg 15. (11) ANIC-03-6, male, Cammoo Caves, Mt Etna Caves NP, Queensland. Terminal segments and gonopods, scale 0.25 mm. (12) ANIC-03-4, female, Cammoo Caves. Terminal segments and gonopods, scale as for figure 11.

3, dense from segment 5 or 6; most trichoid sensilla orientated anteriorly (figure 6D); articles 3–16 bearing a club-shaped thin-walled basiconic sensillum at anterior edge beside band of arthrodial membrane (figure 5A). Ocellus large, pale, with faint independent convexity. Tömösváry organ large, elliptical, mid-length at about 35% length of cephalic pleurite; outer margin slightly inward of lateral edge of pleurite (figure 6A).

Clypeus with row of four setae immediately in front of labrum; cluster of five setae at anteromedial apex includes two pairs along margin and single medial seta. Transverse seta projects medially from labral sidepiece; labral margin weakly curved along inner extent of sidepiece to where cluster of branching bristles overhangs; bristles branching along their entire length.

Maxillipede. Most of lateral margin of coxosternite strongly converging forwards, convergence less in anterior portion including dental margin (figure 4C); each half of dental margin sloping backwards medially, most commonly with 4+4 teeth (figure 4F), frequently with 4+5, 5+4 or 5+5 (figure 4C), one specimen with 6+6; teeth conical, pointed, gradually diminishing in size medially; porodont or pseudoporodont absent; median notch variably lacking (figure 4D) or present, V-shaped (figure 4F); setae sparsely scattered on coxosternite. Pretarsal part of forcipular tarsungulum about equal in length to tarsal part (figure 4C). Setae evenly scattered on tarsal part of tarsungulum, tibia and femur.

Mandible. Trunk with single fissure defining laminia condylifera (figure 5B). Four paired teeth (figure 5C). Five plumose aciculae; pinnules more or less symmetrical on dorsal and ventral margins of aciculae, most digitiform, with blunt tips, maximum of 9 or 10 pinnules along each side of acicula (figure 5G), as few as three along some aciculae in some specimens. Fringe of branching bristles skirts aciculae (figure 5D), shortening dorsally to narrow fringe beneath furry pad (figure 5E, F); bristles narrow-based, regularly branching along entire length, including bases (figure 5D). Three dorsal teeth bearing blunt triangular to rather scale-like accessory denticles; field of accessory denticles continuous between teeth; outer row of denticles on each tooth delineated by strong groove/grooved ridge (figure 5E). Furry pad separated from accessory denticle field on teeth by band of large, flattened scales (figure 5F); bristles of furry pad relatively short, most markedly tapering, with simple, pointed tips, occasionally bifurcate at tip.

First maxilla (figure 4G, H). As described below for *P.* (*H.*) *subicolus* except coxal process narrow, tapering, bearing three simple setae at tip, one seta medially near its base; simple setae on distal article of telopod mostly confined to membranous strip near inner margin, only a few tiny setae on more strongly sclerotized outer two-thirds of article.

Second maxilla (figure 5H). As described below for *P.* (*H.*) *subicolus* except fewer (four or five) short setae in band across anterior part of coxa.

Tergites. Tergites smooth. T1 trapeziform, 80–85% width of head, posterior angles rounded, posterior margin transverse or faintly convex backwards (figures 2, 3); T3 about 90% width of head, lateral borders subparallel; posterior angles of TT3 and 5 rounded, posterior borders faintly concave; TT1 and 3 bordered posteriorly, border on T5 variably complete; lateral borders of TT5–14 convex; T7 relatively short, posterior margin varying from weakly concave to weakly convex, posterior angle blunt to rounded; TT7–14 bordered laterally only; posterior margins of TT8–13 nearly transverse, at most weakly concave, posterior angles rounded, with no projections; posterior margin of T14 transverse to gently concave, without consistent sexual dimorphism, with blunt posterior angle; tergite of first genital segment and telson well sclerotized in both sexes. A few setae along lateral margins of tergites, longer setae anteriorly on long tergites, at posterolateral corner of short tergites; TT2, 4 and 9–14 with a few setae along posterior margin.

All setae on legs fine, none thickened or strongly pigmented, tarsal setae more slender than those on prefemur, femur and tibia; on anterior 13 legs setae on inner margin of tarsus sloping distally along distal two-thirds. Distal spinose projections on tibia of legs 1–12 (figure 7), absent on legs 13–15 (figures 8–10). Tarsal articulation undefined on legs 1–12, weak to moderately strong but unflexed on leg 13, strong and flexed on legs 14 and 15; basitarsus only slightly longer than distitarsus on legs 13–15. Pretarsal accessory claws as much as 50% length of main claw; short, distally directed ventral sensory spur beneath main claw (figure 38B).

Coxal pores. On legs 12–15, round; almost invariably two pores on each leg in females, inner pore slightly smaller, one specimen with three pores on leg 15; usually one pore on each leg in males, exceptionally two on legs 14 and 15 in larger specimens.

Female (figure 12). First genital sternite sparsely setose, in some specimens bearing only a few setae along posterior part; posterior margin concave between condylic articulations of gonopods, gently curved backwards in median part. Basal article of gonopod bearing three to seven setae; two small, conical spurs; inner spur slightly smaller; bases of two spurs nearly side by side (figure 5I). Second article of gonopod bearing three or four fairly long setae; third article bearing one or two setae. Claw simple (figure 5I).

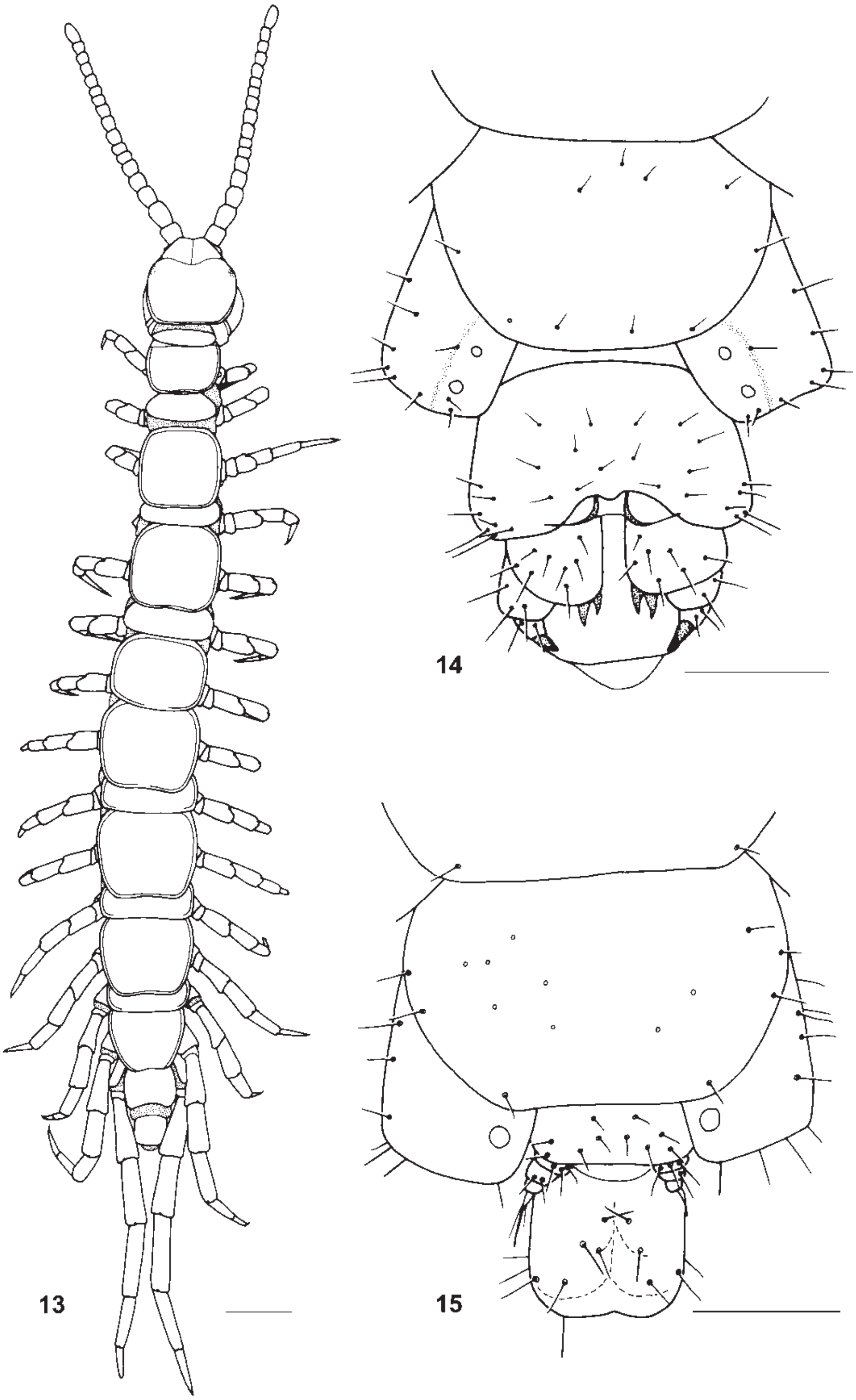
Male (figure 11). Sternite of segment 15 with transverse posteromedian margin. Sternite of first genital segment undivided, bearing a few setae that describe a shallow V across posteromedian part; posteromedian margin of sternite bulging backwards between gonopods. Gonopod of three articles and terminal process; first article bearing row of three setae at mid-length; second article bearing one or two setae just behind mid-length; third article bearing one to three setae near mid-length (figure 6B); length of terminal process as much as combined length of second and third articles of gonopod; proximal half of terminal process weakly tapering, about as long as third article of gonopod, bearing several short spines distally (figure 6C), distal half a slender flagellum. Penis small, conical.

Discussion. A few specimens from the Barrington Tops and Blue Mountains, New South Wales, are provisionally assigned to this species, all other material of which is from the Rockhampton region, Queensland, and Wet Tropics of north-eastern Queensland. The New South Wales specimens conform to Queensland material of *P.* (*H.*) *cammooensis* in having 4+4 maxillipede teeth, one pore on coxae 12–15 in the male, and two pores on these coxae in females. The samples differ only in a relatively thicker tarsus on the anal leg in the one New South Wales specimen (a female) that retains that leg.

Paralamyctes* (*Haasiella*) *ginini n. sp.
(figures 13–16)

Etymology. From Mt Ginini, one of the occurrences of this species.

Diagnosis. P. (*Haasiella*) distinguished from *P.* (*H.*) *cammooensis* by three (versus four or five) teeth on dental margin of maxillipede; numerous (up to 26) setae scattered over first genital sternite of female.



Figs 13–15. *Paralamyctes* (*Haasiella*) *ginini* n. sp. (13, 14) Holotype, ANIC-03-35, female, South Ramshead, Kosciusko NP, NSW. (13) Dorsal view, scale 0.5 mm. (14) Terminal segments and gonopods, scale 0.2 mm. (15) ANIC-03-41, male, Mt Ginini, ACT. Terminal segments and gonopods, scale 0.2 mm.

Holotype. ANIC-03-35, female (figures 13, 14), South Ramshead, Kosciusko NP, NSW [36°31′S, 148°15′E], K. Green, 2 February 1983. Length of head 0.73 mm; length of body 7.5 mm.

Paratypes. ANIC-03-36, female, ANIC-03-37, male, type locality, same collection as holotype; ANIC-03-38, female, type locality, K. Green, November 1981; ANIC-03-39, male, type locality, K. Green, January 1982; ANIC-03-40, female, type locality, K. Green, June 1986; ANIC-03-41, male (figure 15), Mt Ginini, ACT, 35°32′S, 148°46′E, 1660 m, J. F. Lawrence and T. A. Weir, 16 October 1979; ANIC-03-42, juvenile, 1 km S Mt Ginini, 35°33′S, 148°46′E, J. F. Lawrence, 11 November 1986; ANIC-03-43, male, Mt Gingera summit, ACT, 35°34′S, 148°47′E, E. Britton, Misco, 18 July 1967.

Discussion. Paralamyctes (*Haasiella*) *ginini* is identical to *P.* (*H.*) *cammooensis* in most respects. The two species have the same tergite shapes (figures 2, 3 versus 13), size and position of the Tömösváry organ (figures 6A, 16H), form of the mandibular aciculae (figures 5G, 16G), shape of the female gonopod spurs (figures 5I, 16F), distal spinose projections confined to the tibiae of legs 1–12, and both species are relatively small [maximum body length 8.4 mm in *P.* (*H.*) *ginini*]. Seven of nine specimens of *P.* (*H.*) *ginini* have 3 + 3 teeth on the dental margin of the maxillipede (figure 16D), the others having 3 + 4, whereas large specimens from Queensland have 4 + 4, 4 + 5/5 + 4, 5 + 5 or, exceptionally, 6 + 6 teeth (figure 4B–F). Juvenile specimens of *P.* (*H.*) *cammooensis* with 3 + 3 teeth (several in ANIC-03-14) have less-developed gonopods than do the larger specimens of *P.* (*H.*) *ginini* (e.g. female gonopod lacking spurs). Males of *P.* (*H.*) *ginini* have a single round coxal pore on legs 12–15 (figure 15) except for one large specimen with 1,2,2,2/1,2,2,2; the coxal pore arrangement in females is consistently 2,2,2,2/2,2,2,2. All specimens have 17 + 17 antennal articles except for a juvenile with 16/16 and one specimen with 17/18. Setation of the first genital sternite of females distinguishes the species: *P.* (*H.*) *ginini* has more numerous setae scattered on the sternite, including a group of setae at the posterolateral corner (figure 14), whereas *P.* (*H.*) *cammooensis* has few setae, generally confined to the posterior part of the sternite (figure 12).

***Paralamyctes* (*Haasiella*) sp.**

Material. Tasmania: QVMAG 23:21136, male, Tahune Bridge, DN 779 287, 43°05′38S, 146°43′42E, 60 m, K. Higgs, 14 August 1994.

Discussion. A single male from southern Tasmania belongs to the *P.* (*H.*) *cammooensis* Group. The specimen is not a juvenile of the typical northwestern Tasmanian *P.* (*Haasiella*), *P.* (*H.*) *subicolus*. It has a well-developed gonopod, typical of an adult henicopid, whereas even larger specimens of *P.* (*H.*) *subicolus* (QVMAG 23:22967, 23:22971) have undifferentiated gonopods. The maxillipede resembles *P.* (*H.*) *cammooensis* in having a narrow, V-shaped dental margin with a prominent median notch and 4 + 4 strong teeth (all as in figure 4F). These are not juvenile characters of *P.* (*H.*) *subicolus*, in which even larvae (stadium LIV: TMAG J2144, 2145) have a relatively wide, subtransverse dental margin, lack a median notch, and have smaller teeth than in the *P.* (*H.*) *cammooensis* Group, and have a long pretarsal part of the forcipular tarsungulum. The Tasmanian specimen has a coxal pore count (1,2,2,2/1,1,2,2) exceeding any males of *P.* (*H.*) *cammooensis*. The most evident distinction from *P.* (*H.*) *cammooensis* is the relative strength of the setae on the legs, many of which have a spine-like form, notably on the prefemur of the posterior legs. Additional material is required to formalize the Tasmanian species.

Paralamyctes* (*Haasiella*) *subicolus n. sp.

(figures 6E–H, 17–27, 38C, D)

Wailamyctes sp. Mesibov, 1986: 26–27.
Paralamyctes (*Haasiella*) sp. TAS Edgecombe *et al*., 2002: 60, 62.

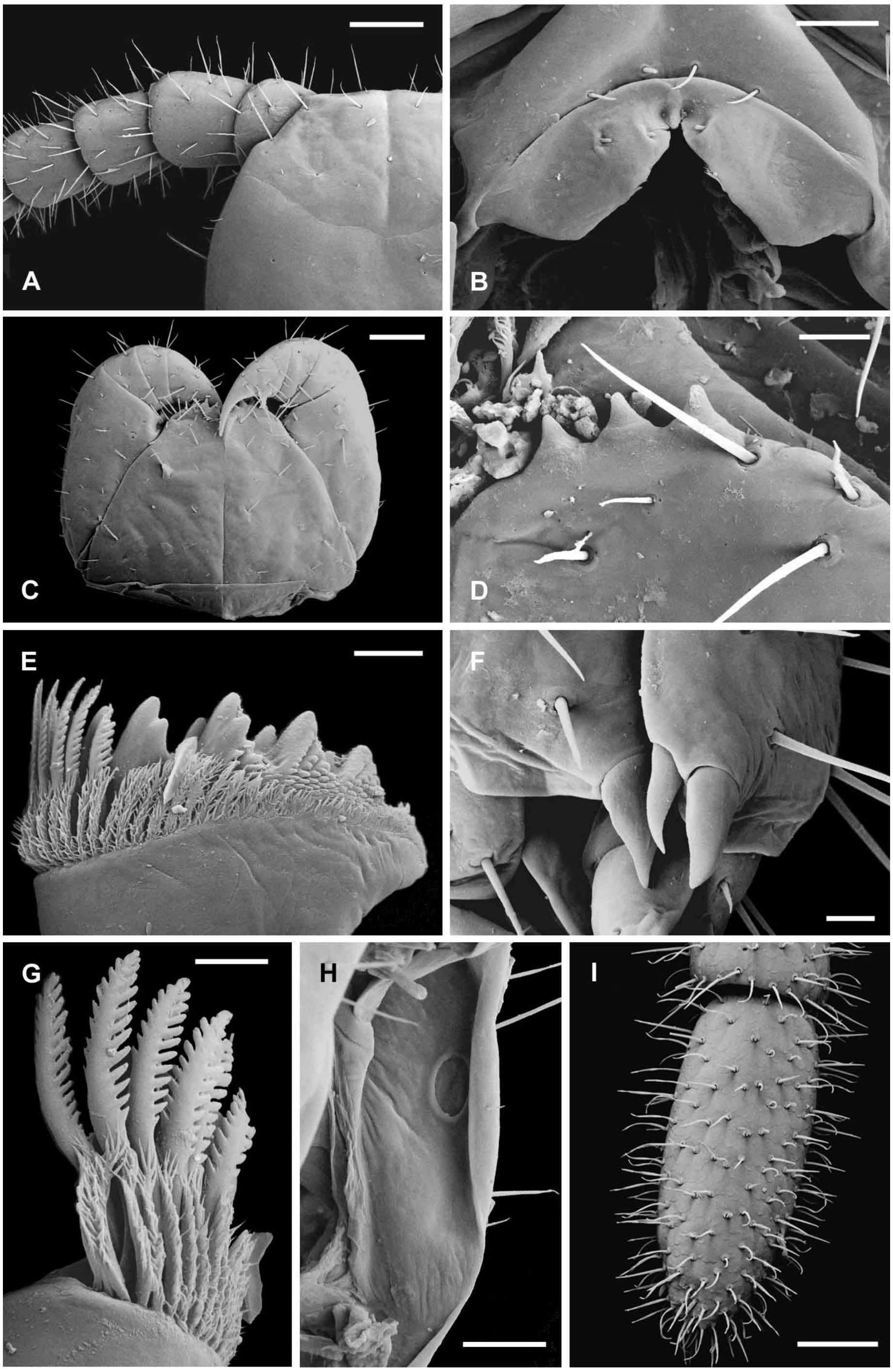
Etymology. Subex-, substratum, -*icola*, dwelling, Latin, for the typical occurrence of this species deeper in the litter than the more common, often co-occurring species, *Henicops maculatus* Newport, 1844.

Diagnosis. P. (*Haasiella*) with 19–24 (usually 22) antennal articles; ocellus flattened; 7+7 to 9+10 teeth on dental margin of maxillipede coxosternite, usually seven to nine teeth per margin; T9 and, especially, TT11 and 13, with strong projections; distal spinose projection on tibia of legs 1–14.

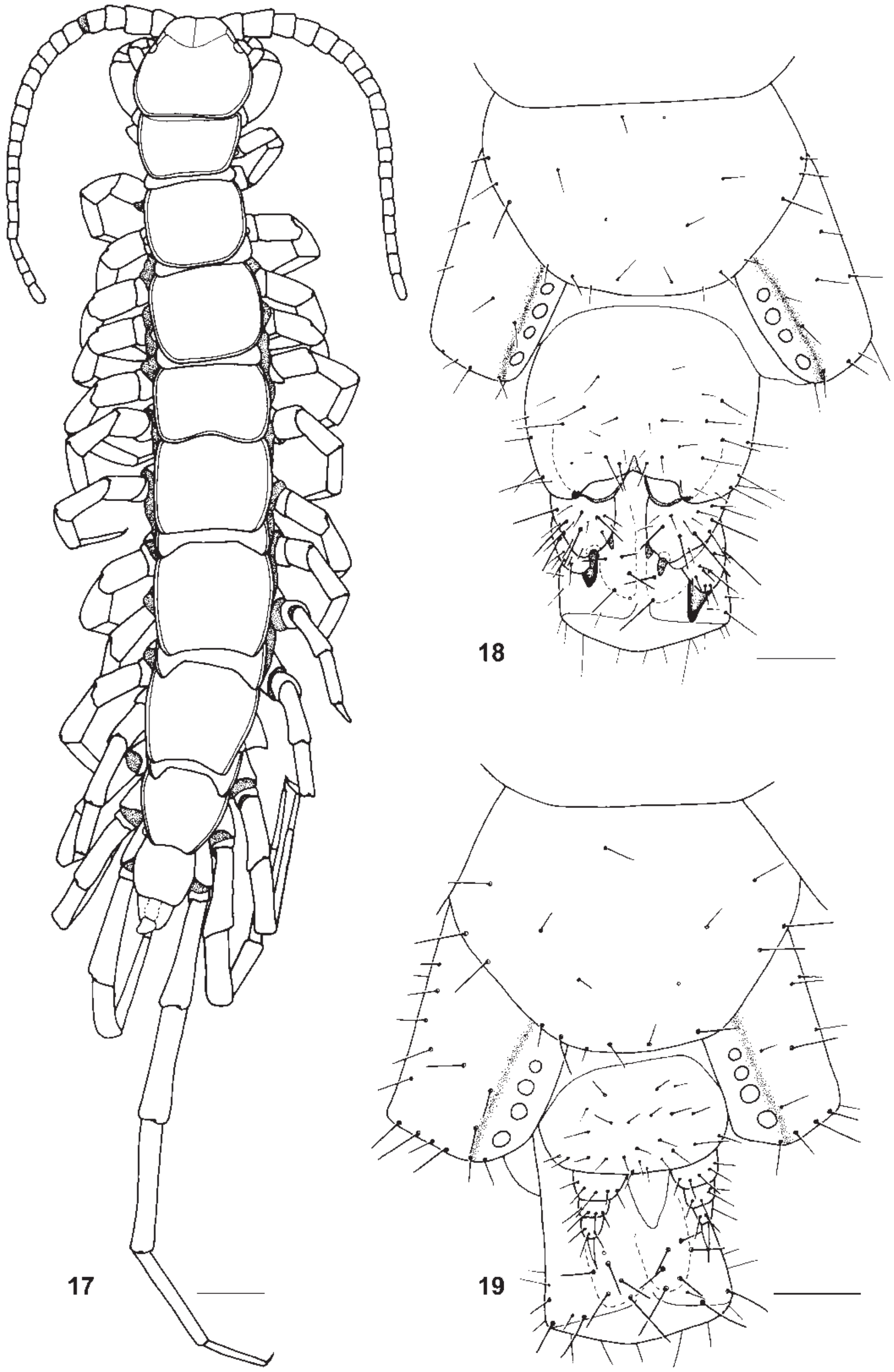
Holotype. QVMAG 23:5277, female (figure 17), Stephens Rivulet, Tasmania, CQ 275 408, 41°09′56S, 144°56′37E, 140 m, R. Mesibov, 20 November 1991. Length of head 1.6 mm; length of body 14.1 mm.

Paratypes. TASMANIA. QVMAG: all collected by R. Mesibov unless indicated otherwise. QVMAG 23:22962, male, Mt Arthur, EQ 237 322, 41°15′40S, 147°16′58E, 600 m, 17 May 1988; 23:22963, male, Mt Arthur, EQ 252 311, 41°16′15S, 147°18′03E, 620 m, 17 May 1988; 23:22964, female, Balfour, CQ 250 302, 41°15′37S, 144°54′39E, 200 m, 2 August 1990; 23:22965, female, 23:22966, female, Wombat Hill, CQ 702 064, 41°29′00S, 145°26′42E, 680 m, 20 and 22 September 1990; 23:22967, male, juvenile, 23:22968, female, Wombat Hill, CQ 703 065, 41°28′56S, 145°26′47E, 670 m, 24 and 27 September 1990; 23:22969, female, male, Wombat Hill, CQ 704 066, 41°28′53S, 145°26′51E, 690 m, 29 September 1990; 23:22970, female, Wombat Hill, CQ 700 062, 41°29′06S, 145°26′34E, 690 m, 2 December 1990; 23:22971, juvenile, Wombat Hill, CQ 704 066, 41°28′53S, 145°26′51E, 690 m, 2 December 1990; 23:22972, female, Roger River West, CQ 330 483, 41°05′57S, 145°00′40E, 210 m, 17 December 1990; 23:22973, female, male, Wombat Hill, CQ 698 060, 41°29′12S, 145°26′25E, 690 m, 26 January 1991; 23:5282, two females, Christmas Hills, CQ 321 672, 40°55′44S, 145°00′20E, 70 m, 22 June 1991; 23:5278, female, Crayfish Creek, CQ 622 674, 40°55′57S, 145°21′47E, 130 m, 12 November 1991; 23:5280, male, Arthur River, CQ 307 465, 41°06′54S, 144°59′00E, 80 m, 13 November 1991; 23:5274, two females, male, Alarm River, CQ 699 617, 40°59′07S, 145°27′12E, 140 m, 18 November 1991; 23:5276, male, Lagunta Creek, CQ 349 348, 41°13′16S, 145°01′49E, 210 m, 19 November 1991; 23:5281, male, Dodds River, CQ 435 385, 41°11′22S, 145°08′01E, 210 m, 19 November 1991; 23:5275, female, Milkshakes, CQ 462 487, 41°05′53S, 145°10′06E, 170 m, 21 November 1991; 23:5279, male, Bond Tier, CQ 194 626, 40°58′03S, 144°51′13E, 90 m, 22 November 1991; 23:5283, female, Roger River West, CQ 332 523, 41°03′47S, 145°00′53E, 50 m, 25 November 1991; 23:5620, male, Kenzies Hill, DQ 462 082, 41°28′33S, 146°21′20E, 260 m, R. Mesibov and T. Scarborough, 18 December 1991; 23:10123, female, male, Animal Creek, CP

Fig. 16. *Paralamyctes* (*Haasiella*) *ginini* n. sp. Scanning electron micrographs. All from South Ramshead, Kosciusko NP, NSW. (A–C, E, G, H) ANIC-03-37, male. (A) Dorsal view of anterior part of head, proximal part of antenna, scale 100 μm; (B) labrum and posterior part of clypeus, scale 50 μm; (C) maxillipede, scale 100 μm; (E) gnathal lobe of mandible, scale 20 μm; (G) mandibular aciculae and fringe of branching bristles, scale 10 μm; (H) cephalic pleurite, showing Tömösváry organ, scale 50 μm. (D, F, I) ANIC-03-36, female. (D) Dental margin of maxillipede coxosternite, scale 20 μm; (F) spurs on gonopods, scale 20 μm; (I) distal article of antenna, scale 50 μm.



890 910, 41°37′29S, 145°40′03E, 740 m, 24 January 1992; 23:10124, female, Frankland River, CQ 212 377, 41°11′31S, 144°52′04E, 150 m, 6 February 1992; 23:10125, female, Laurel Creek, DQ 090 230, 41°20′21S, 145°54′44E, 440 m, 12 February 1992;



Figs 17–19. *Paralamyctes* (*Haasiella*) *subicolus* n. sp. (17) Holotype, QVMAG 23:5277, female, Stephens Rivulet, Tasmania, scale 1 mm. (18) QVMAG 23:22970, female, Wombat Hill, Waratah, Tasmania. Terminal segments and gonopods, scale 0.25 mm. (19) QVMAG 23:22967, male, Wombat Hill, Waratah, Tasmania. Terminal segments and gonopods, scale 0.25 mm.

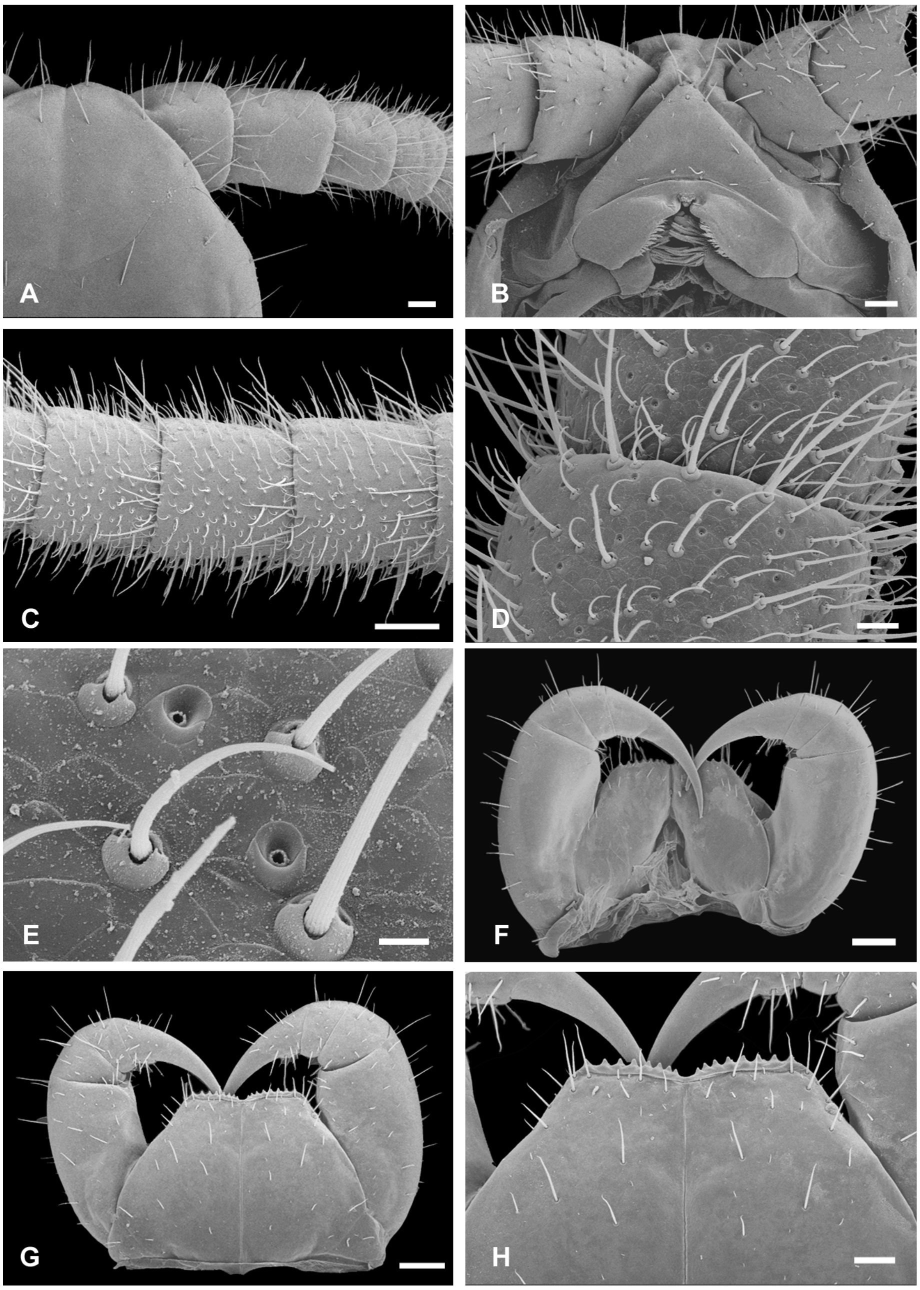


Fig. 20. *Paralamyctes* (*Haasiella*) *subicolus* n. sp. Scanning electron micrographs. (A–E) QVMAG 23:5282, female, Christmas Hills, Tasmania. (A) Dorsal view of anterior part of head, proximal part of antenna, scale 100 μm; (B) ventral view of head, scale 100 μm; (C–E) antenna, with details of sensilla, scales 100 μm, 20 μm, 5 μm. (F–H) QVMAG 23:22969, male, Wombat Hill, Waratah, Tasmania. (F, G) Dorsal and ventral views of maxillipede, scales 200 μm; (H) dental margin of maxillipede coxosternite, scale 100 μm.

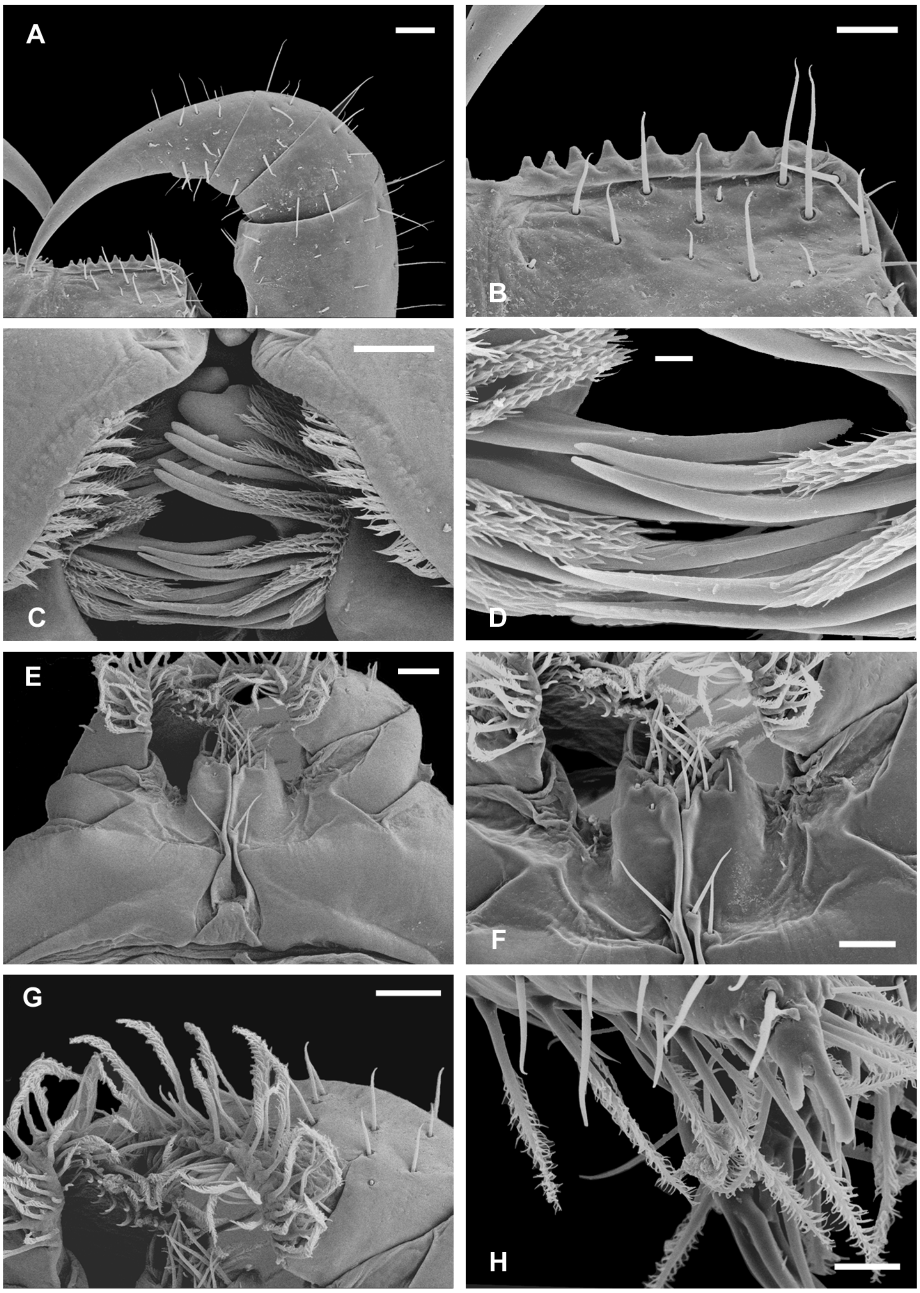


FIG. 21. *Paralamyctes* (*Haasiella*) *subicolus* n. sp. Scanning electron micrographs. QVMAG 23:5282, female, Christmas Hills, Tasmania. (A) Maxillipede telopodite, scale 100 μm; (B) dental margin of maxillipede coxosternite, scale 50 μm; (C) labral margin with mandibles *in situ*, scale 50 μm; (D) aciculae of right and left mandibles *in situ*, scale 10 μm; (E) first maxillae, scale 50 μm; (F) coxal processes of first maxillae, scale 50 μm; (G) distal article of telopod of first maxilla, scale 50 μm; (H) plumose tarsal setae and pretarsus of second maxilla, scale 30 μm.

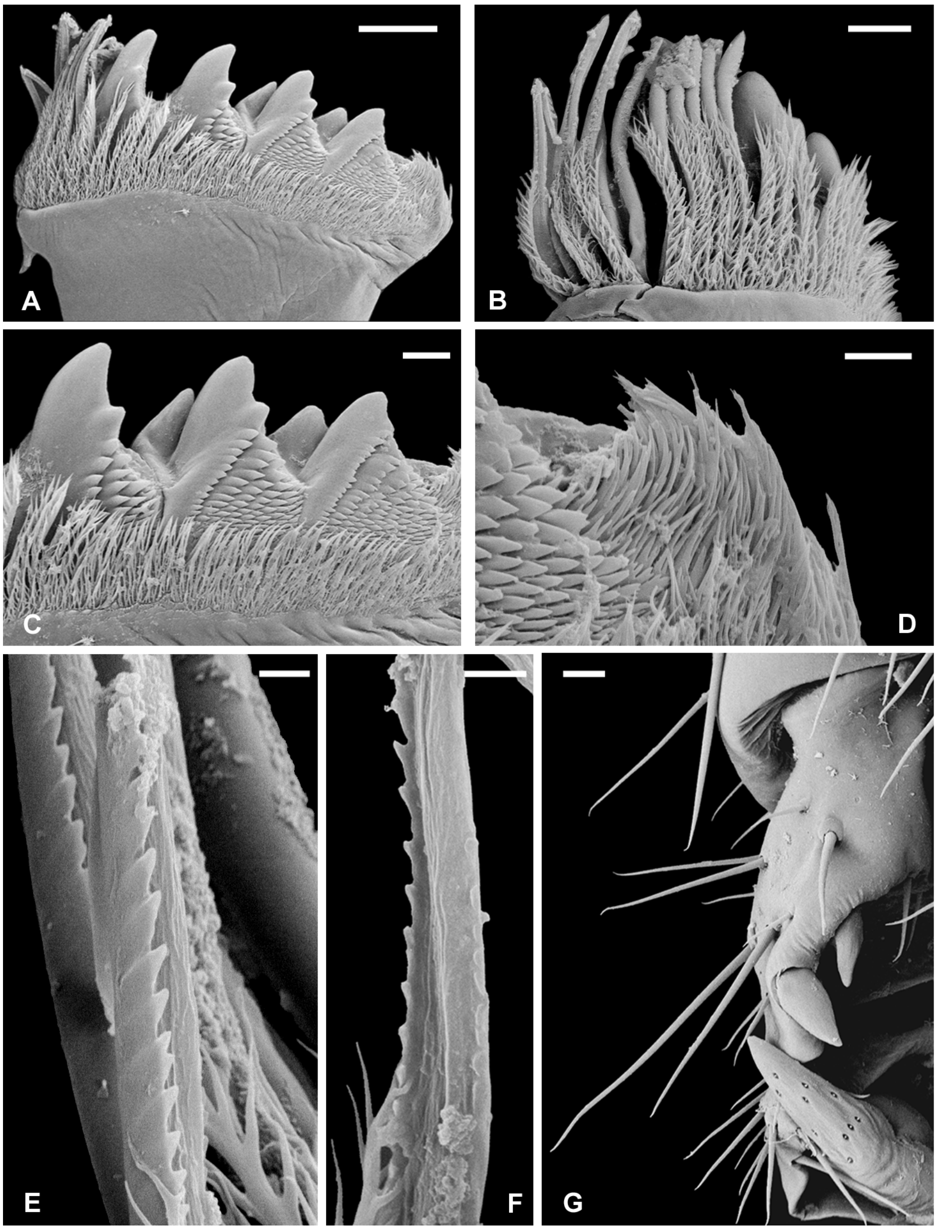
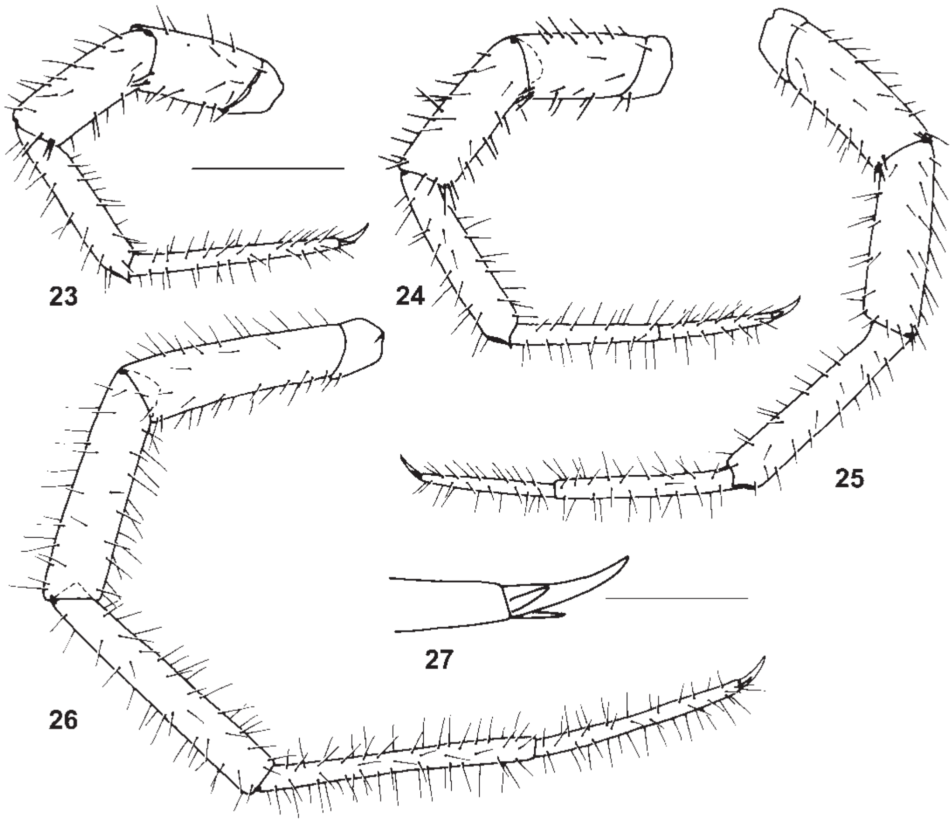


FIG. 22. *Paralamyctes* (*Haasiella*) *subicolus* n. sp. Scanning electron micrographs. AM KS 74959, female, Piemans Road, Tasmania. (A) Gnathal lobe of mandible, scale 50 μm; (B) mandibular aciculae and fringe of branching bristles, scale 25 μm; (C) mandibular teeth and fringe of branching bristles, scale 15 μm; (D) accessory denticles and furry pad, scale 10 μm; (E, F) serrated margins of mandibular aciculae, scales 3 μm; (G) gonopod, scale 25 μm.

23:16296, female, Dodds Creek, CQ 433 384, 41°11′25S, 145°07′53E, 210 m, 12 November 1993; 23:16098, female, Darwin, CP 857 239, 42°13′42S, 145°36′53E, 230 m, 27 December 1993; 23:22974, female, Mt Gnomon, DQ 185 409, 41°10′44S,



Figs 23–27. *Paralamyctes* (*Haasiella*) *subicolus* n. sp. QVMAG 23:22970, female, Wombat Hill, Waratah, Tasmania. (23) Leg 12, scale 1 mm (same for figures 24–26). (24) Leg 13. (25) Leg 14. (26) Leg 15. (27) Pretarsus of leg 15, scale 0.25 mm.

146°01′41E, 290 m, R. Mesibov and C. Brockman, 30 September 1996; 23:40730, female, Newdegate Creek, CP 406 819, 41°41′54S, 145°05′03E, 200 m, 6 March 1999; 23:41378 (DNA voucher specimen), Southern Creek, CQ 708 405, 41°10′35S, 145°27′34E, 300 m, 18 April 2000.

TMAG (rainforest unless indicated otherwise): J2145, larva IV, near confluence of Sprent and Gordon Rivers, CN 980 796, 42°37′44S, 145°45′21E, 50 m, P. Suter and C. Howard, 10 February 1976; J2213, female, Arthur River SF, Julius River, CQ 344 420, 41°09′22S, 145°01′34E, 90–110 m, R. Mesibov, 4 June 1976; J2138, female, Olga Camp, Gordon River Valley near Smith River confluence, DN 018 731, 42°41′17S, 145°48′04E, 130 m, B. Morley, 14 January 1977; J2142, larva IV, Olga Valley, DN 003 698, 42°43′03S, 145°46′56E, 40 m, C. Howard *et al.*, 28 January 1977; J2139, female, J2140, larva III, Gordon River Valley near Denison River confluence, DN 036 697, 42°43′08S, 145°49′21E, 30 m (J2139), DN 028 695, 42°43′14S, 145°48′46E, 140 m (J2140), C. Howard *et al.*, 29 January 1977; J2141, female, Gordon River Valley near Denison River confluence, DN 044 702, 42°42′52S, 145°49′57E, 90 m, C. Howard *et al.*, 1 February 1977; J2144, larva IV, near confluence of Maxwell and Denison Rivers, DN 080 729, 42°41′26S, 145°52′36E, 120 m, C. Howard *et al.*, 9 February 1977; J2214, male, Roger River State Reserve, CQ 333

524, 41°03′44S, 145°00′57E, 60 m, R. Mesibov, 15 September 1977, eucalypt over rainforest; J2143, two males, Franklin River Valley at Blackmans Bend meander, CN 981 920, 42°31′03S, 145°45′34E, 30 m, L. Hill *et al.*, 6 January 1978; J2215, male, Zeehan-Renison Bell State Reserve, CP 682 696, 41°48′51S, 145°24′47E, 280 m, R. Mesibov, 26 April 1987 [Larval stadia LIII and IV identified by comparison to leg development in *Lamyctes fulvicornis* (Andersson, 1984)].

AM: KS 74959, female, north side of Piemans Rd, 18 km from Murchison Hwy, G. Hunt, 31 January 1981, myrtle beech–*Dicksonia* stand.

Description

Length (head to telson) up to 15 mm; length of head up to 1.9 mm. Antenna and maxillipede pale orange, antenna lighter distally; head shield light orange-brown to pale purple, often with darker mottling; area surrounding ocellus usually black or dark purple; tergites pale brown, reddish brown to lavender; darker pigment irregular along lateral border; legs pale yellow-brown, tarsi darker, with orange tinge; sternites and coxae pale brown anteriorly, gradually darkening posteriorly; genital sternite and gonopods orange.

Head wider than TT1–5, about as wide as TT7 and 8. Head shield smooth. Frontal margin biconvex, with strong median notch (figure 20A); posterior margin of head gently concave. Median furrow extends back to transverse furrow, deepest in anterior half. Antenna extending back to T5, composed of 19–24 articles, usually 22. Basal two articles enlarged, relatively sparsely setose, with long trichoid sensilla; dense setation consistently developed from about fourth article; articles 4–9 of subequal length and width, with less prominent articulations than on remainder of antenna, distal to this, articles usually considerably longer than wide, barely widening distally along their length; distal article fusiform, variably longer than preceding one, typically about 1.5 times length of penultimate article. Ridged trichoid sensilla developed as about five imprecisely defined whorls, longest sensilla in whorls at posterior and anterior edges of article, all whorls directed anteriorly (figure 20C); short, curved trichoid sensilla on ventral surface of articles (figure 20D); semicircular stop (*Kragen*) on posterior side at bases of long, straight trichoid sensilla same as those of short, curved sensilla (figure 20E); pores interspersed between sensilla, with crescentic rim around posterior edge of each pore opening (figure 20E). Ocellus with weak independent convexity, moderately large, with diffuse margins, usually pale blue-white depigmented region, dark pigment surrounding ocellus sometimes extends on to ocellus. Tömösváry organ moderately large, ovate, outer edge at lateral margin of cephalic pleurite near anterior edge of pleurite (figure 6F).

Clypeus with usual row of four setae just in front of labrum, cluster of long setae at anteromedial apex (figure 20B). Transverse seta projects medially from labral sidepiece; labral margin with gentle break in curvature where fringe of branching bristles overhangs (figure 21C); fringe dense, bristles branching along their entire length.

Maxillipede. Coxosternite trapezoidal (figure 20G). Dental margin broad, about 50% maximum width of coxosternite, each half weakly convex, transverse or slightly sloping backwards medially (figure 20H); 7–10 (usually seven to nine) small, conical teeth per margin; inner teeth smaller than those more laterally (figure 21B); dental margin set off by transverse furrow; median notch lacking or shallow, rounded. Numerous setae of varied length scattered on coxosternite, lacking near median suture, concentrated anteriorly; no porodont or pseudoporodont. Tarsungulum long, slender, pretarsal part about twice length of tarsal part; setal density on outer and inner edges of tarsal part even (figure 21A).

Mandible. Four paired teeth (figure 22A). Nine aciculae; small barbs variably developed along length of aciculae (figure 22E), more pronounced on dorsal edge of each acicula (figure 22F); barbs distinct on all aciculae but more angular on those in ventral part of series (figure 22B) or represented by numerous blunt nodes along ventral aciculae and nearly nearly smooth margin in dorsal aciculae (figure 21D). Fringe of branching bristles skirts aciculae (figure 22B), evenly shortening dorsally to narrow fringe beneath furry pad; bristles narrow-based, regularly branching along entire length, with even gradation in structure along fringe (figure 22C). Three dorsal teeth bearing triangular accessory denticles; field of accessory denticles discontinuous between teeth; outer row of denticles on each tooth delineated by prominent groove/grooved ridge (figure 22C); accessory denticles nearest to fringe of branching bristles slender, pointed. Bristles of furry pad long, bifurcated, well differentiated from accessory denticles (figure 22D).

First maxilla. Bell-shaped sternite of typical size for genus (figure 21E); anterolateral margins set in arthrodial membrane, posterolateral edge meets coxa at a suture. Coxal process subquadrate, slightly narrowing anteriorly, bearing cluster of about eight simple setae on tip, separated from two setae on inner basal edge of process (figure 21F). Cluster of about four minute, barb-like basiconic sensilla between coxal process and telopod. Distal article of telopod with two rows of plumose setae along inner margin, branches developed along distal half of these setae (figure 21G); about 10 simple setae scattered over distal article of telopod, not concentrated in inner membranous strip.

Second maxilla. Sternite trapezoidal, fused to coxa. Band of about 12 short setae in single row across anterior part of coxa (figure 6E). Simple setae on outer part of tarsus, numerous plumose setae on inner part; branches on plumose setae confined to distal 50–60% (figure 21H). Claw small, composed of up to five slender, elongate digits.

Tergites. Tergites nearly smooth. T1 trapeziform, anterior width subequal to T3, about 85% width of widest tergite (T10), posterior angles rounded, posterior margin feebly concave (figure 17); lateral borders subparallel in TT3 and 5, posterior angles rounded, posterior borders transverse or faintly concave; TT1, 3 and 5 bordered posteriorly; lateral borders of TT8–14 gently convex; border of T7 incomplete posteriorly, posterior margin moderately concave, posterior angle rounded; TT8–14 bordered laterally only; posterior margin of T8 nearly transverse, those of TT10 and 12 gently and moderately concave, respectively; posterior angles of TT8, 10 and 12 blunt; TT9, 11 and 13 embayed posteriorly, with largely transverse median extent, TT11 and 13 with strong, triangular projections, T9 with shorter projection; posterior margin of T14 concave in both sexes, with abruptly rounded posterior angle. Tergite of intermediate segment elongate subhexagonal in both sexes, posterior margin concave, relatively wider in female. Anterior tergites with a few setae along lateral border, band of about four shorter setae across anterior part of tergites, a few setae anterolaterally; setation of posterior part of tergites becoming more prominent on posterior tergites such that TT10 and 12 have sparse setae scattered over tergite; row of setae along posterior margin from T9, variably as far forward as T6.

Premur and femur scattered with relatively strong, red-brown setae of varied length, including ring of setae around distal end of femur; a few short, strong setae on trochanter; tibial setae more slender; tarsal setae all slender, those on inner edge sloping distally along distal half to two-thirds of tarsus in anterior 12 legs (figure 23) and on distitarsus of legs 13 and 14 (figure 25); all tibial and tarsal setae slender, radiating on leg 15 (figure 26). Slender, sharp distal projections on tibiae of legs 1–14, absent on leg 15. Tarsal articulation entirely undefined in legs 1–12. Distitarsus 70–80% length of basitarsus on anal leg; anal leg basitarsus 11–12 times longer than broad (figure 26). Pretarsal claw slender, curved in distal third; pair of accessory claws symmetrical, 25–35% length of main claw on all legs (figures 27, 38C, D); minute, distally directed ventral sensory spur beneath main claw on all legs (figure 38C, D).

Sternites sparsely setose; a few setae along lateral margin; band of a few shorter setae across anterior part of sternites; several setae along posterior margin of posterior sternites.

Coxal pores. On legs 12–15, round, separated by less than their diameter, innermost pore typically smaller than others. Maximum 2,4,5,4/2,4,4,4 in females, 2,4,4,4/2,4,4,4 in males; usually two or three pores on leg 12 in females, one or two in male; usually three, not uncommonly four, pores on leg 13 in females, two to four in males; three or four pores on leg 14 in both sexes (occasionally five in female); usually four pores on leg 15 in female (figure 18), sometimes three, rarely five; three or four pores equally common on leg 15 in males (figure 19).

Female (figure 18). Tergite of first genital segment and telson well sclerotized except for longitudinal median band, bearing a few setae. Posterior margin of first genital sternite embayed between condylic articulations of gonopod; setae fairly evenly scattered on posterior two-thirds of genital sternite. Fifteen to 21 setae of varied length on basal article of gonopod; two small, flask-shaped spurs (figure 22G), the inner one slightly to considerably smaller with narrow, pointed tip, its base well in advance of that of the outer spur; second article of gonopod densely setose, setae short to long; third article bearing a few setae, suture separating it from claw well-defined ventrally. Claw simple (figure 22G).

Male (figure 19). Sternite of segment 15 with transverse or gently convex posteromedian margin. First genital sternite undivided, bearing about 20–25 short setae concentrated posteriorly; posterior margin of sternite approximately transverse. Gonopod bearing single band of short setae on each of three articles (five, four and three setae from proximal to distal articles, all setae of subequal size) (figure 6G); terminal process with gently tapering proximal part bearing numerous long, slender spines, flagelliform distal part that comprises more than half length of process (figure 6H). Penis prominent, conical.

Discussion

Paralamyctes (*Haasiella*) *subicolus* is most readily distinguished from other species of the subgenus by the larger number of teeth on the dental margin of the maxillipede. The pronounced projections on tergites 9, 11 and 13 allow for distinction from the other two Australian species of *P.* (*Haasiella*), but are shared with New Zealand species, e.g. *P.* (*H.*) *trailli*. The Tömösváry organ is smaller and more anteriorly situtaed on the cephalic pleurite (figure 6F) than in the *P.* (*H.*) *cammooensis* Group (figure 6A). Comparison with the best supported candidate for sister group, *P.* (*Thingathinga*), indicates that smaller size and more anterior placement are plesiomorphic states.

Phylogenetic analysis

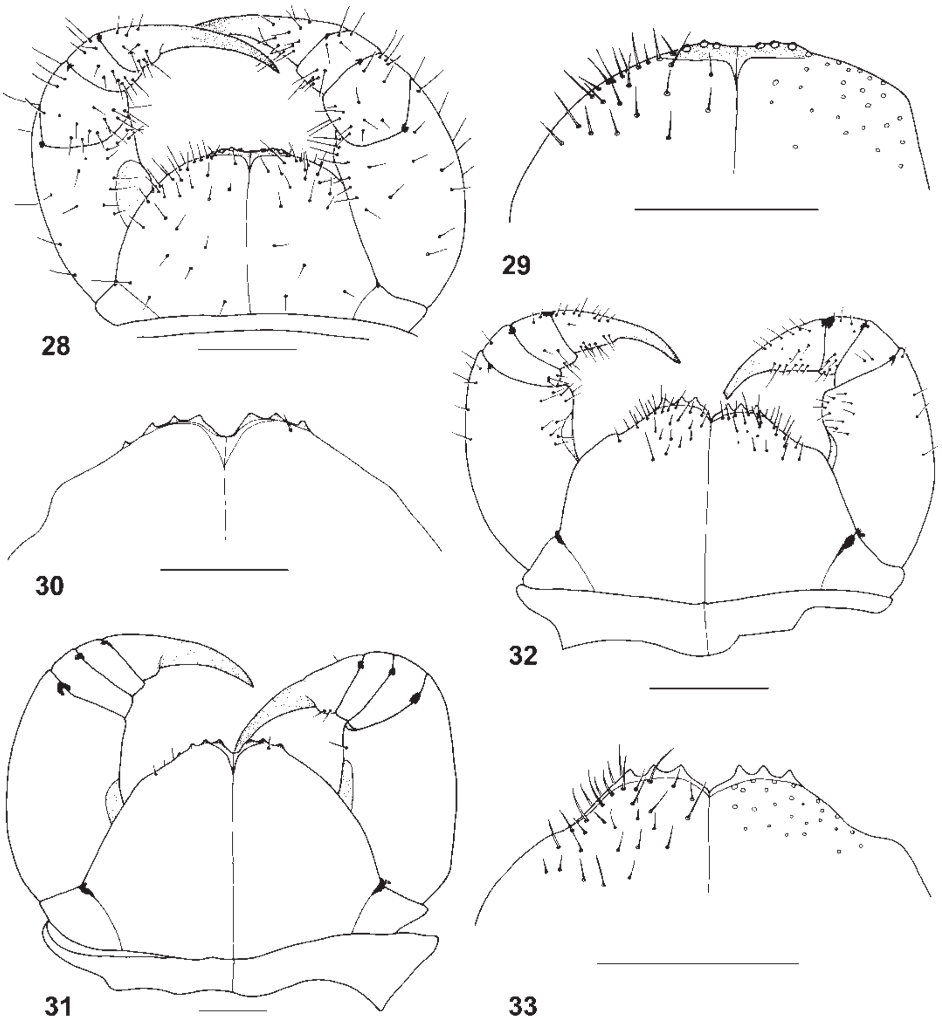
Paralamyctes (*Haasiella*) *subicolus* was included by Edgecombe *et al*. (2002) in a cladistic analysis of Henicopidae, scored for its morphological characters together with sequence data from five molecular markers. The following section updates the morphological character analysis of Edgecombe *et al*. (2002) to include *P*. (*Haasiella*) *cammooensis* and *P*. (*H*.) *ginini* n. spp. along with additional henicopids that have been studied since the previous analysis, rescore several characters to describe homologies more accurately, and add new characters (see Appendix for character list). *Paralamyctes* (*Haasiella*) *trailli* (Archey, 1917), the type species of *Wailamyctes* Archey, 1917 is used as a representative of New Zealand *Haasiella*.

Newly added taxa

Species included in the present analysis that were not analysed by Edgecombe *et al*. (2002) are *Dichelobius flavens* Attems, 1911, *Henicops dentatus* Pocock, 1901, *Lamyctopristus validus* Attems, 1928, *Paralamyctes* (*Paralamyctes*) *spenceri* Pocock, 1901, *Paralamyctes* (*Paralamyctes*) *tridens* Lawrence, 1960 and *Shikokuobius japonicus* (Murakami, 1967). *Dichelobius flavens*, *H. dentatus*, *P. spenceri* and *S. japonicus* have been studied by electron and light microscopy; *P. tridens* was scored from its slide-mounted and alcohol-preserved type material, together with a few new specimens (CASENT 9001615-9001617; figure 34C); *L. validus* was scored from light microscopy except for the mandible, which was examined with the SEM (figure 34D).

Coding for *Analamyctes* is corrected based upon examination of the holotype of its type species, *A. tucumanus* Chamberlin, 1955. This specimen (figures 32–34E–H, 35) was discovered in the United States National Museum of Natural History in 2001, and has now been transferred to the California Academy of Sciences, where Chamberlin intended to deposit it. A specimen referred to *A. tucumanus* by Edgecombe (2001, figure 2) instead represents *A. andinus* (Silvestri, 1903). The two species, now coded separately, are distinguished by the presence of two teeth and a pseudoporodont on the dental margin of the maxillipede in *A. andinus* versus three teeth and no pseudoporodont in *A. tucumanus* (figures 32, 33), and by the faint trace of joints between tarsomeres on legs 1–12 in *A. andinus* versus strong joints in *A. tucumanus*. Coding for the female of *A. tucumanus* is based on the holotype (figure 35), and coding for the male uses a specimen from La Angostura, Tucumán Province (figure 36), assigned to *Lamyctes taulisensis* Kraus, 1954, by Demange (1963). Strongly bipartite tarsi on legs 1–12 refute a referral to *Lamyctes*, and the specimen conforms to the holotype of *A. tucumanus* in all respects. Mandibular characters for *A. tucumanus* are scored from the holotype (figure 34E–H).

Lamyctopristus Attems, 1928, one of the more highly modified genera in the Henicopidae, was not included by Edgecombe *et al*. (2002), but I have now had the opportunity to study the holotype of the type species, *L. validus* Attems (figures 30, 31, 34D). Attems (1928) erected *Lamyctopristus* as a monotypic genus, the sole specimen of *L. validus* having been collected at Piquetberg, Western Cape Province, South Africa. Generic status was based principally on characters of the female gonopods, which Attems (1928: 66) described as ‘remarkable’. The basal segment of the gonopod has a hatchet-shaped inner edge that bears five and six spurs on the opposing sides. Also unique to *Lamyctopristus* is a granulation of the tergites that is not observed in other henicopids. Lawrence (1955) established a second species, *L. granulosus*, for a single male and female from Hout Bay, Cape Peninsula. Distinction from *L. validus* was made based on a single character, ‘smaller and



FIGS 28–33. Maxillipedes in ventral view, with details of dental margin of coxosternite, all scales 0.5 mm. (28, 29) *Paralamyctes* (*Parlamyctes*) *tridens* Lawrence, 1960. Syntype, MNHN, male, Manjakatompo Forest, Ankaratra, Madagascar. (30, 31) *Lamyctopristus validus* Attems, 1928. Holotype, SAM-ENW-X7515, female, Piquetberg, Western Cape Province, South Africa. (32, 33) *Analamyctes tucumanus* Chamberlin, 1955. Holotype CAS, female, Cerro San Xavier, Tucumán Province, Argentina.

more numerous teeth [spurs] of the basal joint of the female genital appendages' (seven spurs in *L. granulosus* versus five or six in *L. validus*). Given that the spur count in *L. validus* differs between the two gonopods of the single specimen, the significance of one extra spur in the only known female of *L. granulosus* is dubious. It is probable that a single species is represented. Coding is based on the holotype of *L. validus* except for characters of the male, scored from Lawrence's (1955) description and illustration of *L. granulosus*.

Study of the holotype of *Cermatobius martensii* Haase, 1885, at the Museum für

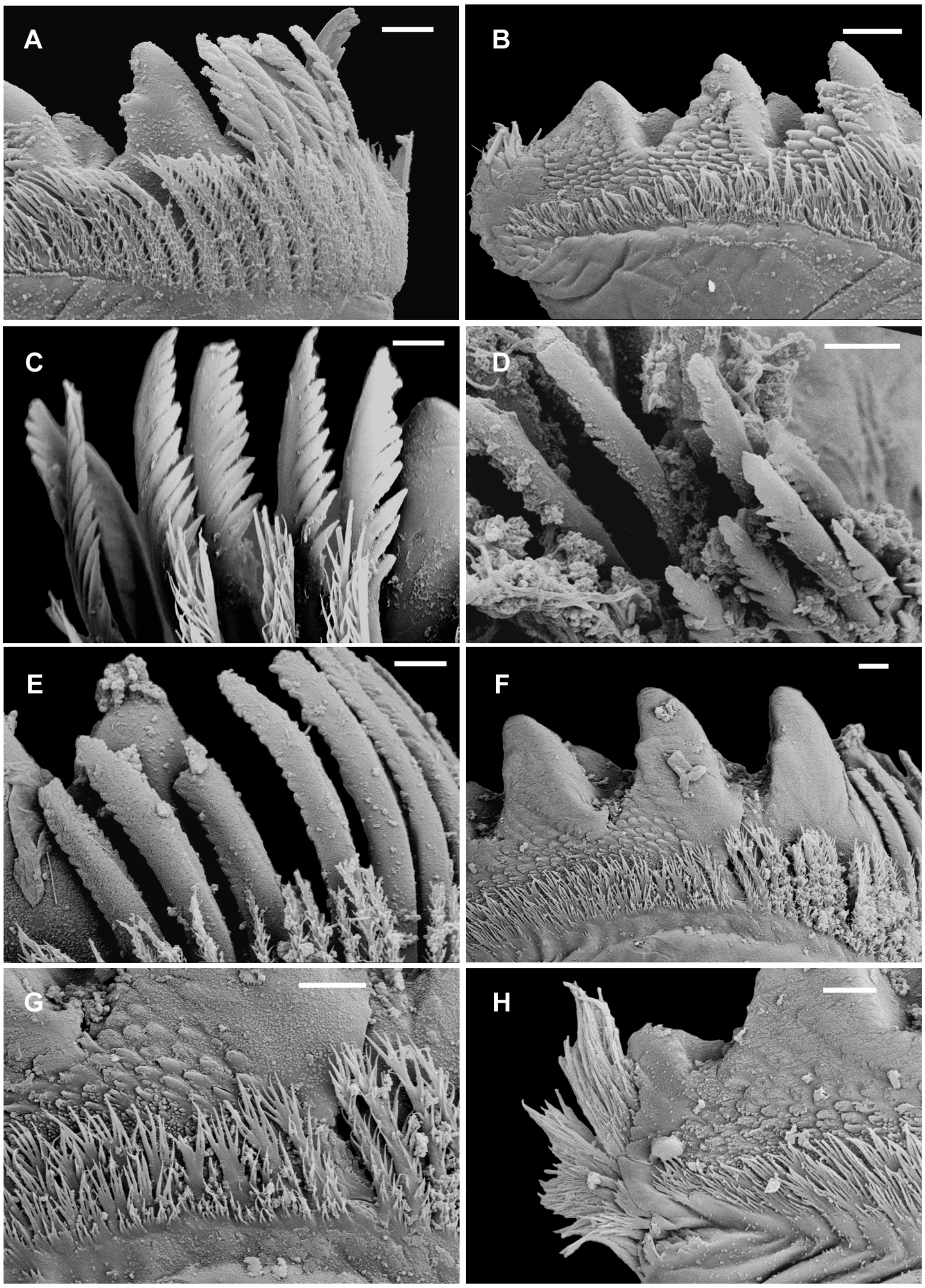
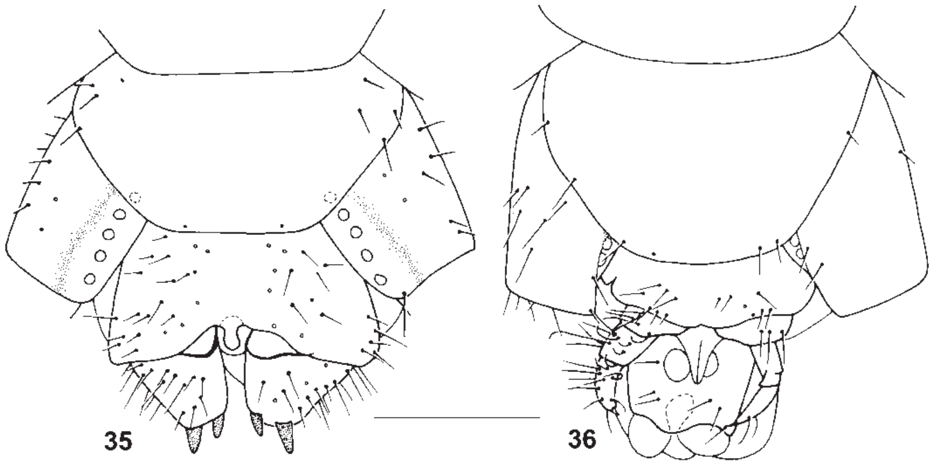


FIG. 34. Scanning electron micrographs of mandibles, all scales 10 μm. (A, B) *Paralamyctes* (*Paralamyctes*) *bipartitus* (Lawrence, 1960). Holotype, MNHN, male, Imaitso Forest, Andringitra, Madagascar. (A) aciculae and fringe of branching bristles; (B) mandibular teeth and furry pad. (C) *Paralamyctes* (*Paralamyctes*) *tridens* Lawrence, 1960. CASENT 9001616, female, 3 km NE Andranomay, Antananarivo Province, Madagascar. Aciculae. (D) *Lamyctopristus validus* Attems, 1928. Holotype, SAM-ENW-X7515, female, Piquetberg, Western Cape Province, South Africa. Aciculae in two rows. (E-H) *Analamyctes tucumanus* Chamberlin, 1955. Holotype, CAS, female, Cerro San Xavier, Tucumán Province, Argentina. (E) aciculae; (F-G) teeth and fringe of branching bristles; (H) furry pad.



FIGS 35, 36. *Analamyctes tucumanus* Chamberlin, 1955. Tucumán Province, Argentina. (35) Holotype, CAS, female, Cerro San Xavier. Terminal segments and gonopods, scale 0.5 mm. (36) MNHN, male, La Angostura. Terminal segments and gonopods, scale as for figure 35.

Naturkunde (Berlin), leads me to endorse the synonymy of *Cermatobius* Haase, 1885, and *Esastigmatobius* Silvestri, 1909 (Würmli, 1977). *Esastigmatobius japonicus* Silvestri, 1909, is accordingly assigned to *Cermatobius*.

Analytical procedures

Codings for 51 characters listed in the Appendix are presented in table 1. The data were analysed with PAUP* version 4.0b10 (Swofford, 2002). A heuristic search used tbr (tree bisection-reconnection) branch swapping, following 35 000 random stepwise addition sequences that sampled five trees per iteration. Cladograms were rooted with Lithobiidae as outgroup to Henicopidae, using four lithobiid species for which molecular data are available (Edgecombe *et al.*, 2002) as representatives of the family. Multistate characters were coded as unordered except for character 13, in which a transformation series is specified based on the observations of Demange and Silva (1976). Bremer support was computed by the 'enforce converse constraint' command in PAUP*, using MacClade version 4.0 (Maddison and Maddison, 2000) to generate the PAUP* command file with converse constraints.

Results

With the analytical procedures outlined above, 15 989 shortest cladograms of 121 steps (Consistency Index 0.55; Retention Index 0.82; Rescaled Consistency Index 0.45) were found. Figure 37 depicts the strict consensus of these cladograms. Many nodes are collapsed with a single extra step (Bremer support 1), the strongest nodes within Henicopidae being Anopsobiinae (support 5), *Henicops* (support 5), the Gondwanan Anopsobiinae *Anopsobius* + *Dichelobius* (support 4), *Paralamyctes cassisi* + *P. mesibovi* (support 3), *P. harrisi* + *P. monteithi* (support 3), *Anopsobius* (support 2), Zygethobiini (support 2) and *P* (*Haasiella*) *cammooensis* + *P.* (*H*). *ginini* (support 2).

Monophyly of *Paralamyctes sensu* Edgecombe (2001) is endorsed in most (93%)

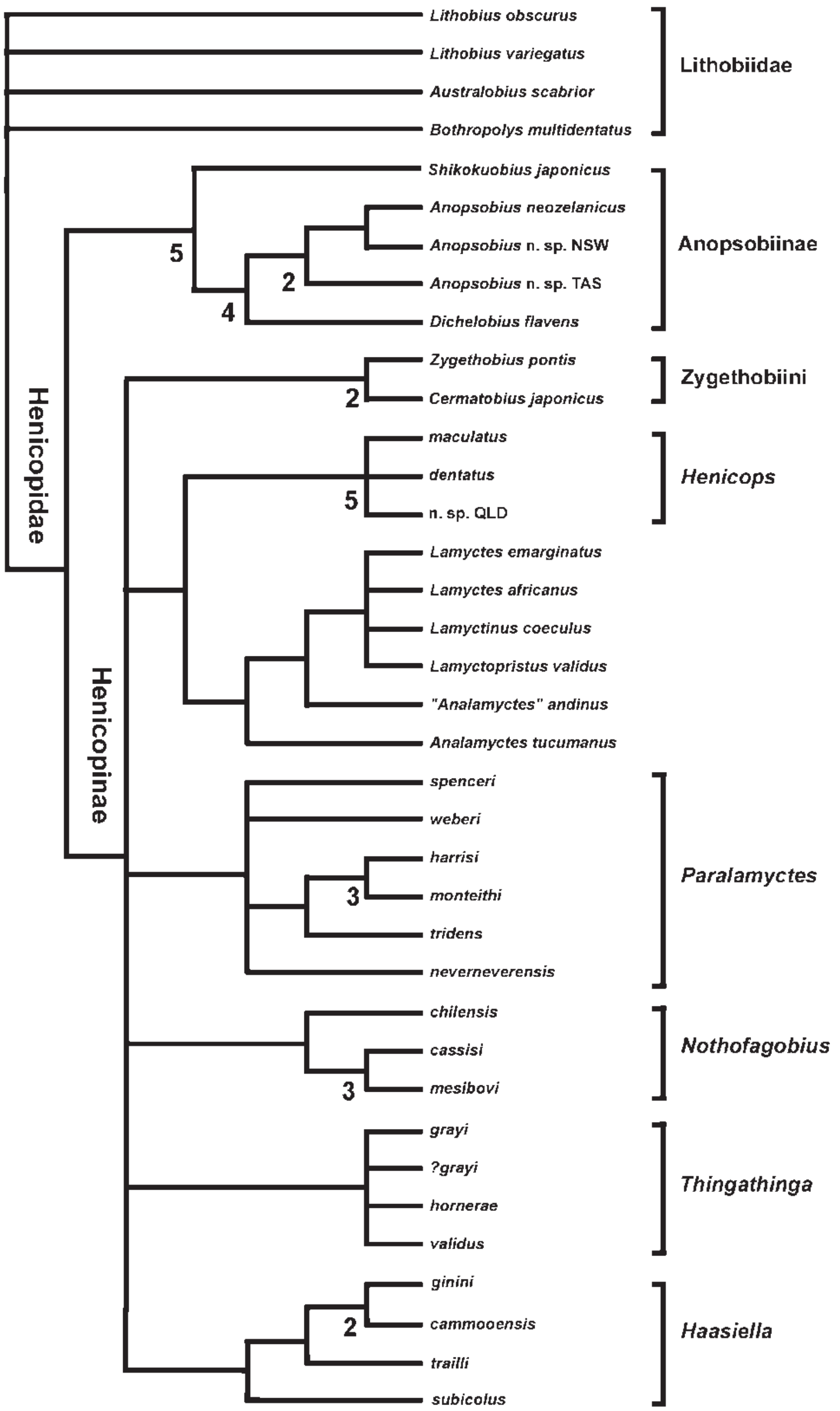


FIG. 37. Strict consensus of 15 989 minimal length cladograms (121 steps) based on morphological character data in table 1. Bremer support is indicated for nodes with support >1.

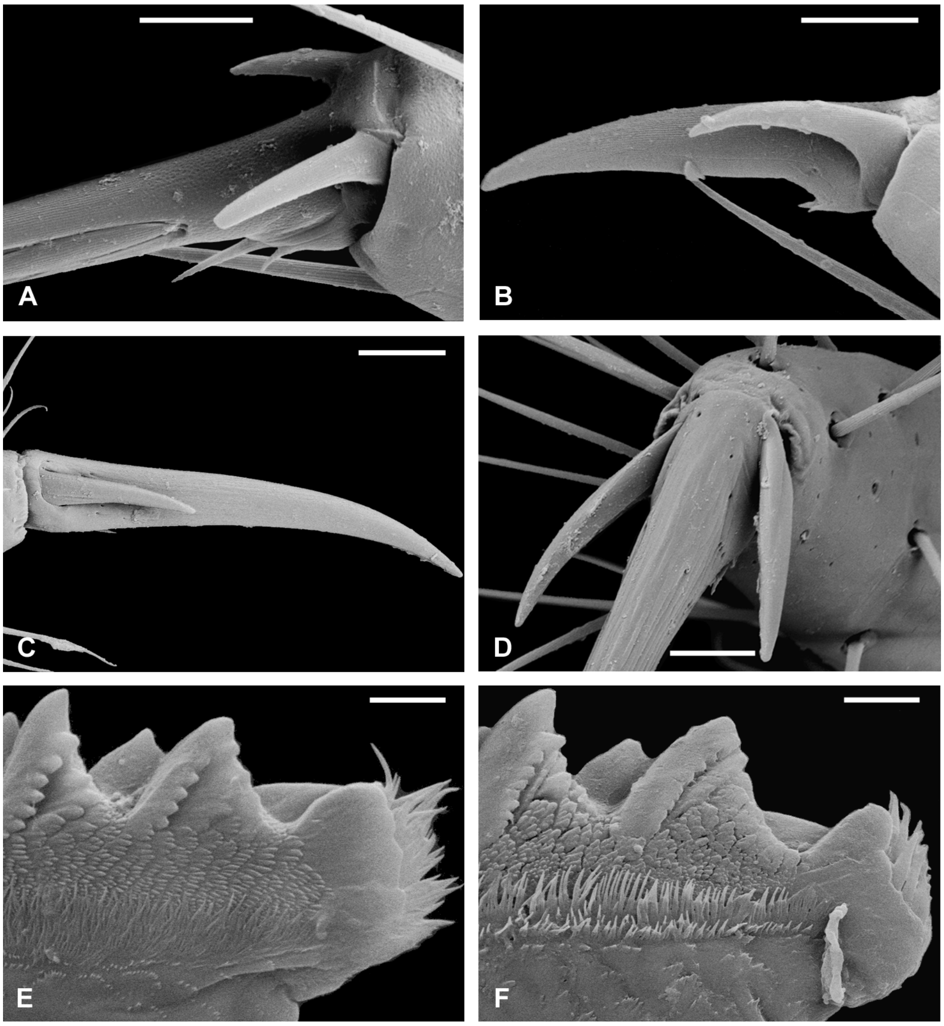


FIG. 38. (A) *Dichelobius* sp. AM, female, Monga SF, NSW. Leg 14, pretarsus, scale 10 μm. (B) *Paralamyctes* (*Haasiella*) *cammooensis* n. sp. ANIC-03-7, female, Cammoo Caves, Mt Etna Caves NP, Queensland. Leg 3, pretarsus, scale 10 μm. (C, D) *Paralamyctes* (*Haasiella*) *subicolus* n. sp. QVMAG 23:16098, female, Darwin West, Tasmania. (C) Leg 14, pretarsus, scale 50 μm; (D) leg 15, pretarsus, scale 30 μm. (E) *Lamyctinus coeculus* (Brölemann, 1889). AM, female, N Colo Heights, NSW. Mandibular teeth and furry pad, scale 10 μm. (F) *Dichelobius flavens* Attems, 1911. AM, male, Walpole-Nornalup NP, Western Australia. Mandibular teeth and furry pad, scale 10 μm.

but not all minimal length cladograms. Resolution of Zygethobiini within the group in some cladograms is affected by characters shared by *Cermatobius*, *Zygethobius* and some species of *Paralamyctes* (character 11, subsemicircular maxillipede coxosternite; character 18, embayed posterior margin of tergite 7; character 35, coxal pores in deep grooves), along with characters shared by *Cermatobius* and *Paralamyctes* (character 2, flattened ocellus; character 14, elongate maxillipede tarsungulum; character 29, large first maxillary sternite). Since *Paralamyctes sensu* Edgecombe (2001) is monophyletic in the most congruent cladogram based on

Table 1. Codings for 51 morphological characters listed in the Appendix.

Lithobius obscurus	0-0000-000	0011000000	0000000000	002200-000	0101001000	0
Lithobius variegatus rubriceps	0-0000-000	7011000000	0000000000	002200-000	0101000000	0
Australobius scabrior	0-0000-000	7010000000	0000000000	002200-000	0101101000	0
Bothropolys multidentatus	0-0010-000	2011000000	0000000000	002200-000	0101001000	0
Shikokuobius japonicus	--00010001	0010001010	0010010000	11120101-0	0000000000	2
Dichelobius flavens	--00010101	2010001010	0010010000	11100101-0	0000010000	2
Anopsobius neozelanicus	--10010101	2110001000	0010010000	11100111-0	0000010000	2
Anopsobius n. sp. NSW	--10010101	2110001010	0010010000	11100111-0	0000010000	2
Anopsobius n. sp. TAS	--10010101	2010001010	0010010000	11100111-0	0000010000	2
Zygethobius pontis	1000010001	3000000100	0010010101	1003113000	0000000000	0
Cermatobius japonicus	1100010001	3001000100	0000010111	1002112??0	0000100000	0
Lamyctes emarginatus	1001010001	0020001001	0001000001	10020101-0	0000000000	1
Lamyctes africanus	1001010001	0020001001	0001000001	10020111-0	0010000000	1
Lamyctinus coeculus	--00010001	0020001001	0001000001	10020101-0	00??000100	1
Lamyctopristus validus	1001010001	0021000001	000??00001	10020131-0	0100200001	?
Henicops maculatus	1001020001	1000000001	0001000001	2002013011	1010000001	0
Henicops dentatus	1000010001	1000000101	0001000001	2002013011	1010000001	0
Henicops n. sp. QLD	1001020001	1000000001	0001000001	2002013011	0010000001	0
Analamyctes tucumanus	1001010001	0000001001	0001000001	1002012000	0000000000	0
'*Analamyctes*' *andinus*	1001010001	0020001001	0001000001	1002013000	0000000000	1
Paralamyctes (*Paralamyctes*) *spenceri*	1000010101	4001000001	1000000111	1002012000	0000000000	0
Paralamyctes (*Paralamyctes*) *weberi*	1000010101	4001000001	1000000111	1002013000	0000000000	0
Paralamyctes (*Paralamyctes*) *tridens*	1000011101	3001000001	1000000111	1002012000	0000000000	0
Paralamyctes (*Paralamyctes*) *monteithi*	1000111111	3001100001	1000000111	1002013000	0000000000	0
Paralamyctes (*Paralamyctes*) *harrisi*	1000111111	3001100001	1000000111	1002013000	0000000000	0
Paralamyctes (*Paralamyctes*) *neverneverensis*	1000010101	4000000001	1000000111	1002014000	0000000000	0
Paralamyctes (*Nothofagobius*) *chilensis*	1000010101	4000010001	0000000011	1002013000	0000010000	0
Paralamyctes (*Nothofagobius*) *cassisi*	1000010101	4000010001	0100001011	1002014000	0000110000	0

Table 1. (*Continued*).

Paralamyctes (*Nothofagobius*) *mesibovi*	1000010101	4000010001	0100001011	1002014000	0000110000	0
Paralamyctes (*Thingathinga*) *grayi*	1100010111	5001000101	0100000011	1002113010	0000000000	0
Paralamyctes (*Thingathinga*) ?*grayi*	1100010111	5001000101	0100000011	1002014010	0000000000	0
Paralamyctes (*Thingathinga*) *hornerae*	1100010111	5001000101	0100000011	10?201?010	0000000000	0
Paralamyctes (*Thingathinga*) *validus*	1000010111	5001000001	0100100011	1002114010	0000000000	0
Paralamyctes (*Haasiella*) *trailli*	--00010101	6001000011	0000000011	10020121-0	0000000110	0
Paralamyctes (*Haasiella*) *subicolus*	1100010101	5001000011	0000000011	10020131-0	0000000010	0
Paralamyctes (*Haasiella*) *cammooensis*	1100010101	4000001011	0000000011	10020111-0	0000000110	0
Paralamyctes (*Haasiella*) *ginini*	1100010101	4000001011	0000000011	10020111-0	0000000100	0

combined molecular data of Edgecombe *et al*. (2002), it is retained in the present classification.

Relationships between the subgenera of *Paralamyctes* established by Edgecombe (2001) are unresolved in the strict consensus. However, the four subgenera, *P*. (*Paralamyctes*), *P*. (*Nothofagobius*), *P*. (*Thingathinga*) and *P*. (*Haasiella*), are each consistently resolved as monophyletic. Support for *P*. (*Haasiella*) is provided by a transverse margin of tergite 8 (character 19), unipartite tarsi on legs 1–12 (character 38) and the progressive reduction in size of the maxillipede teeth medially (character 49), each of which exhibits homoplasy. Most minimal length cladograms (as well as the Adams consensus) resolve *P*. (*Haasiella*) and *P*. (*Thingathinga*) as sister taxa. The grouping of *P*. (*Haasiella*) and *P*. (*Thingathinga*) was also retrieved across all parameters applied to combined molecular data by Edgecombe *et al*. (2002, figure 15), and is thus considered as the best supported hypothesis of sister-group relationships for *P*. (*Haasiella*).

Within *Paralamyctes* (*Haasiella*), *P*. (*H*.) *trailli* and *P*. (*H*.) *cammooensis* + *P*. (*H*.) *ginini* are united to the exclusion of *P*. (*H*.) *subicolus*. The only unambiguous synapomorphy for this grouping is the enlarged, posteriorly positioned Tömösváry organ (character 48). In all minimal length cladograms, enlargement of the Tömösváry organ within *P*. (*Haasiella*) is convergent with enlargement and similar posterior positioning in *Lamyctinus coeculus* (figure 1J of Edgecombe *et al*., 2002).

A clade including *Henicops*, *Lamyctes* and *Lamyctinus* was strongly supported in previous analysis of molecular data and combination with morphology (the latter also including *Analamyctes*), but was resolved as a grade of basal Henicopinae using the morphological data alone (figure 9 of Edgecombe *et al*., 2002). The present analysis identifies a morphological result that is congruent with the molecular signal, with these genera united as a clade that also includes *Lamyctopristus*. This results from reinterpretation of several characters (e.g. porodont/pseudoporodont; tibial projections scored as a multistate character; ocelli scored as inapplicable for blind species rather than coding blindness as a synapomorphy) as well as coding additional species within the group that have unique character combinations, such as

Henicops dentatus, '*Analamyctes*' *andinus* and *Lamyctopristus validus*. *Analamyctes tucumanus* and '*A.*' *andinus* are a paraphyletic group at the base of a *Lamyctes*–*Lamyctinus*–*Lamyctopristus* clade. No convincing autapomorphies can be specified for *Analamyctes*, even when restricted to the two Argentine species. The pseudoporodont of *A. andinus* (character 13, state 2) indicates a closer relationship to the *Lamyctes*–*Lamyctinus*–*Lamyctopristus* clade. The relationships of *Lamyctopristus* demand further attention; though the type species possesses a pseudoporodont on one side of the maxillipede (figure 30), it shares a proliferation of the mandibular aciculae and differentiation of two acicular rows (figure 34D) that is otherwise restricted to *Henicops*.

Previous morphological analysis did not retrieve the monophyly of *P.* (*Paralamyctes*) in all minimal length cladograms, though the group was unambiguously supported by molecular data (figure 15 of Edgecombe *et al.*, 2002) and combination of those data with morphology. The current dataset identifies *P.* (*Paralamyctes*) as a clade, defined by a unique structure of the mandibular aciculae (character 21: figure 34C) and the intergradation between the accessory denticles on the mandibular teeth and the furry pad (character 28). The Malagasy species *P. tridens*, included here for the first time, is most closely related to a clade composed of the Queensland *P.* (*P.*) *monteithi* and the New Zealand *P.* (*P.*) *harrisi*. This relationship is indicated by synapomorphic details of the maxillipede coxosternite (character 11, state 3) and the positioning of the Tömösváry organ in a membranous field on the ventral margin of the head (character 7, state 1). Maxillipede dentition in this group consists of few particularly blunt teeth concentrated on the inner extent of the dental margin (figures 28, 29).

Acknowledgements

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Appendix

Morphological characters

Characters 1–47 below were described by Edgecombe *et al.* (2002). Where a character has been re-evaluated, discussion is presented here.

Characters described by Edgecombe et al. (2002)

1. Ocelli: (0) cluster of ocelli; (1) single ocellus.

Edgecombe *et al.* (2002) coded blindness ('ocelli absent') as an apomorphic state; this permitted absence of ocelli to optimize at the base of Henicopidae, with the ocellus of Henicopinae having an independent derivation from those of Lithobiidae. The current coding instead treats blind taxa as inapplicable for ocellar characters.

2. Convexity of ocellus: (0) bulging; (1) flattened.
3. Antennal segmentation: (0) 17 or more segments; (1) 15 segments.
4. Change in lengths of antennomeres: (0) gradual change in length along antenna; (1) markedly uneven in proximal part of antenna, with short, paired antennomeres interspersed between longer ones.
5. Long, tubular antennomeres: (0) some antennomeres equally wide and long, proximal two antennomeres much larger than succeeding few; (1) all antennomeres longer than wide, proximal two antennomeres not substantially larger than succeeding few.
6. Tömösváry organ: (0) on small sclerotization anteroventral to ocelli; (1) near margin of cephalic pleurite; (2) near mid-width of cephalic pleurite.
7. Tömösváry organ on margin of head: (0) organ on surface of cephalic pleurite; (1) organ in membranous field on margin of head.

   Edgecombe *et al.* (2002) scored a marginal position of the Tömösváry organ (state 1) in *P.* (*Paralamyctes*) *monteithi*. A similar positioning of the organ in a membranous field on the margin of the head, rather than on the surface of the cephalic pleurite, is seen in *P.* (*P.*) *harrisi* as well as *P.* (*P.*) *tridens*.
8. Median furrow on head shield: (0) terminates in front of transverse suture; (1) deep and continuous to transverse suture.
9. Shoulder in labral margin: (0) absent; (1) present.
10. Pleurites of maxillipede segment connected ventrally, forming a continuous band between maxillipede coxosternite and sternite of first pedigerous segment: (0) pleurites discontinuous; (1) pleurites continuous.
11. Shape of maxillipede coxosternite: (0) subtriangular coxosternite with narrow, curved dental margin; (1) subtrapezoidal coxosternite with narrow, straight dental margin; (2) narrow dental margin, markedly V-shaped, with deep median notch; (3) subsemicircular coxosternite with wide, convex dental margin; (4) trapezoidal coxosternite with narrow, curved dental margin; (5) wide, subtransverse dental margin; (6) narrow, straight dental margin projected forward; (7) trapezoidal coxosternite with moderately wide, weakly V-shaped dental margin.
12. Paired cusps on teeth on maxillipede coxosternite: (0) absent (unpaired, conical teeth); (1) present.
13. Porodont: (0) absent; (1) translucent, seta-like porodont; (2) conical, tooth-like pseudoporodont.

   Edgecombe *et al.* (2002) scored porodonts as homologous in Lithobiidae, Anopsobiinae and some genera of Henicopinae. Homology between the seta-like porodont of Lithobiidae and Anopsobiinae (state 1) is least problematic, whereas some workers (Negrea and Matic, 1996) describe the tooth-like structure on the maxillipede edge in *Lamyctes* as a pseudoporodont. The latter is now scored as a separate state, but homology between the seta- and tooth-like structures is probable. Demange and Silva (1976) documented variation within and between subspecies of *Lamyctes inermipes* (Silvestri) from Argentina and Chile, which indicates a nearly complete intergradation between seta- and tooth-like forms. They considered the tooth to be derived from 'une soie qui peu à peu se transforme en un organe spécialisé' (Demange and Silva, 1976: 51). An ordered multistate coding accommodates this transformation series.

14. Proportions of maxillipede tarsungulum: (0) pretarsal section of approximately equal length to tarsal section; (1) pretarsal section much longer than tarsal section.
15. Dense setation on inner part of maxillipede tibia and femur: (0) absent; (1) present.
16. Body narrowed across anterior part of trunk: (0) T1 of similar width to head and T3; (1) T1 markedly narrower than head and T3.
17. Angulation (projections) of posterolateral corners of tergites: (0) some angular or toothed; (1) all rounded.
18. Posterior margin of tergite 7 embayed, with median sector straight and thickened ventrally: (0) absent; (1) present.
19. Course of posterior margin of tergite 8: (0) concave; (1) transverse.
20. Spiracle on first pedigerous trunk segment: (0) absent; (1) present.
21. Row of digitiform pinnules with pointed tips along dorsal edge of aciculae: (0) absent; (1) present.

    Previous coding of acicular structure (Edgecombe *et al.*, 2002: character 22) involved a multistate character. This permitted transitions between aciculae with pinnules confined to the dorsal edge and simple (apinnulate) aciculae as two of three equally parsimonious transformation series. The binary coding used here recognizes two apomorphic characters because each of these acicula types is hypothesized to be derived from the bipinnulate aciculae observed in non-henicopine lithobiomorphs. In *Paralamyctes spenceri* most aciculae are pinnulate on the dorsal side only, but the occasional bipinnulate acicula is present. In *P.* (*Haasiella*) *subicolus*, bipinnulate aciculae on the ventral part of the series grade into simple aciculae (figure 21D) on the dorsal part.
22. Entire acicula series simple: (0) absent; (1) present.
23. Fringe of branching bristles on mandible: (0) extends along entire gnathal margin, skirting aciculae; (1) terminates at aciculae.
24. Ventral bristles in fringe on mandible with a wide base: (0) absent; (1) present.
25. Differentiation of branching bristles on mandible: (0) branching structure of bristles grades evenly along fringe; (1) abrupt transition between scale-like bristles and plumose bristles.
26. Width of fringe of branching bristles dorsally: (0) fringe narrowed dorsally, not developed along all bristles of furry pad; (1) fringe wide, dense, developed along whole length of furry pad.
27. Accessory denticles on mandible all triangular, continuous between teeth, without grooved ridges on teeth: (0) absent; (1) present.

    Edgecombe *et al.* (2002) coded for presence or absence of a grooved ridge on the mandibular teeth, absence being shared by Zygethobiini and some species of *P.* (*Paralamyctes*) and *P.* (*Nothofagobius*). In some species of *P.* (*Paralamyctes*), however, the grooved ridge is faintly expressed (e.g. *P. neverneverensis*: figure 11B of Edgecombe, 2001) and presence/absence coding is rather subjective. More detailed similarities shared by *P.* (*N.*) *cassisi* and *P.* (*N.*) *mesibovi* form the basis for the present coding, in which the lack of a grooved ridge is associated with a distinctive, angular form of the accessory denticles (figures 20D, 23C of Edgecombe, 2001) and a completely uninterrupted series of accessory denticles between the teeth.

28. Furry pad intergrades with accessory denticles: (0) absent; (1) present.
29. Shape of first maxillary sternite: (0) small, wedge-shaped, with median suture; (1) large, bell-shaped, coxae not merged anterior to sternite, suture between coxa and sternite confined to posterior edge of maxilla.
30. Basal joint of telopodite of first maxilla fused on inner side to coxal process: (0) telopodite distinctly demarcated; (1) telopodite fused to adjacent part of coxa.
31. Setae on coxal process of first maxilla: (0) dense cluster of differentiated setae; (1) mostly simple setae; (2) several laciniate setae amidst simple setae. State 2 is added to describe the mix of simple and laciniate setae that is shared by all species of *Henicops* ('plumose setae' of Archey 1917, 1937). Other Henicopinae rarely possess laciniate setae, and when present they are fewer than in *Henicops*.
32. Coxa of leg 15 with long, lobate process ending in a spine: (0) absent; (1) present.
33. Prefemur of leg 15 with spurs: (0) spurs absent; (1) single ventral spur; (2) several spurs in a whorl.
34. Coxal pores: (0) on legs 14 and 15 only; (1) on legs 13–15 only; (2) on legs 12–15 only; (3) on legs 11–15.
35. Coxal pores set in deep groove, largely concealed by anteroventral face of coxa in ventral view: (0) absent; (1) present.
36. Distal spinose projections on tibiae of legs 1–11: (0) absent; (1) present.

    Edgecombe *et al.* (2002) scored for the presence of tibial projections on various legs as four separate characters. This coding is modified here because it makes unwarranted assumptions of character independence (i.e. a species with a tibial projection on leg 15 will invariably also have projections on all legs anterior to this). Tibial projections are recoded as two characters, character 36 for absence and presence (the latter uniting all henicopids), and character 37 for different distributions, scored as an unordered multistate character.
37. Distribution of distal spinose projections on tibiae: (0) strong projection on legs 1–11 only (weak projection variably distinct on leg 12); (1) strong projection on legs 1–12 only; (2) strong projection on legs 1–13 only; (3) strong projection on legs 1–14 only; (4) strong projection on legs 1–15.
38. Tarsus of legs 1–12: (0) divided into basitarsus and distitarsus; (1) undivided.
39. Articulation between basitarsus and distitarsus on anterior pairs of legs: (0) distinct on dorsal side of leg; (1) fused on dorsal side of leg, distinct ventrally.
40. Subdivision of basitarsus indicated by paired larger setae: (0) absent; (1) present.

    The larger setae on the tarsus of *Lamyctopristus validus* are positioned on the distal side of the faint joints and points of flexure that indicate the boundaries of tarsomeres. In *Henicops*, larger setae are immediately proximal, rather than distal, to the joints. The two instances are thus not coded as homologous.
41. First tarsal segment bisegmented (tripartite tarsus): (0) absent; (1) present.
42. Accessory apical claws: (0) anterior and posterior accessory claws; (1) posterior accessory claw only.

    In the holotype of *Lamyctopristus validus*, no legs are intact, but legs bearing distal spinose projections on the tibia (i.e. not the anal leg) have a posterior accessory claw but lack an anterior accessory claw. The absence of a 'spinule beneath the claw' or 'inferior claws' noted as diagnostic by Attems (1928) might refer to this absence of an anterior accessory claw which is, as recognized by Attems, peculiar within Henicopinae, which normally have symmetrical anterior and posterior accessory claws (state 0: figure 38D). Alternatively Attems

(1928) may have been indicating an absence of a ventral sensory spur (Eason, 1964, figure 486 for *Lamyctes fulvicornis*), which is prominent on legs 1–14 in Anopsobiinae (figure 38A) and present, if often small, in Henicopinae (figure 38B–D).

43. First genital sternite of male divided longitudinally into two sclerites: (0) undivided; (1) divided.

    Previous coding for *Lamyctes* treated a cleft posterior margin of the sternite as an indication of division. A deep posteromedian cleft and short median furrow are developed in *Lamyctopristus granulosus* (figure 5b of Lawrence, 1955). The coding is now restricted to species with two clearly defined sclerites, as in *Henicops* and those *Lamyctes* species transferred to *Metalamyctes* by Verhoeff (1948) [e.g. *L. africanus*; *L. castaneus* (Attems, 1909, plate 3, figure 59); *L. microporus* (Attems, 1909, plate 2, figure 51; *L. robustus* (Lawrence, 1955, figure 4b); *L. tristani* (Lawrence, 1956, figure 2)].
44. Segmentation of male gonopod: (0) four segments with a seta-like terminal process; (1) stout gonopod with one or two segments.
45. Number of spurs on female gonopod: (0) two; (1) three; (2) five to seven.
46. First article of female gonopod extended as a short process: (0) absent; (1) present.

    A gonopod process in *Paralamyctes* (*Nothofagobius*) was recognized in previous coding, but Gondwanan Anopsobiinae possess a similar extension of the spur-bearing region (Attems, 1928, text-figure 22).
47. Claw of female gonopod: (0) simple (unipartite); (1) tripartite, dorsal and ventral accessory denticles present.

New characters

48. Tömösváry organ large, positioned posteriorly on pleurite: (0) absent; (1) present.

    Edgecombe *et al*. (2002) did not employ the exceptional enlargement of the Tömösváry organ in *Lamyctinus coeculus* and *Paralamyctes* (*Haasiella*) *trailli* as an independent character because it appeared to covary with blindness, a similar enlargement also being known in blind lithobiids. However, a similarly large Tömösváry organ is also present in *P*. (*Haasiella*) *cammooensis* (figure 6A) and *P*. (*H*.) *ginini* (figure 16H), which possess ocelli. The large Tömösváry organ in *Lamyctinus* and *P*. (*Haasiella*) may be distinguished from relatively large organs in other blind henicopids (notably Anopsobiinae) by its relatively posterior position on the cephalic pleurite.
49. Maxillipede teeth progressively decreasing in size and spacing medially: (0) absent; (1) present.

    The gradual decrease in size and spacing of the maxillipede teeth medially in *Paralamyctes* (*Haasiella*) is documented in discussion of that subgenus in the systematic section above.
50. Aciculae differentiated into two (outer and inner) rows: (0) absent (single row of aciculae); (1) present.

    Lamyctopristus validus (figure 34D) resembles *Henicops* (figures 4A, 5C of Edgecombe *et al*., 2002) in having a proliferation of aciculae through the differentiation of two (inner and outer) rows. Other henicopids have the aciculae aligned in a single row.

51. Accessory denticles on dorsal part of mandible: (0) simple, triangular accessory denticles; (1) flattened, multifurcating scales; (2) tuberculate scales.
    Flattened, multifurcating, scale-like accessory denticles on the dorsalmost tooth and adjacent to the furry pad are seen in *Lamyctes* (figure 7B of Edgecombe *et al*., 2002), '*Analamyctes*' *andinus* (figure 3C, D of Edgecombe, 2001) and *Lamyctinus* (figure 38E). In other lithobiomorphs, including *Henicops*, the accessory denticles on the dorsalmost tooth are simple triangular elements (see figure 7 of Edgecombe *et al*., 2002 for examples; figure 22D herein). In Anopsobiinae (*Shikokuobius*, *Anopsobius*, *Dichelobius*) the accessory denticles are scales covered with tubercles (figure 38F).

References

Andersson, G., 1984. Post-embryonic development of *Lamyctes fulvicornis* Meinert (Chilopoda: Henicopidae), *Entomologica Scandinavica*, **15**, 9–14.

Archey, G., 1917, The Lithobiomorpha of New Zealand, *Transactions and Proceedings of the New Zealand Institute*, **49**, 303–318.

Archey, G., 1922, Notes on New Zealand Chilopoda, *Records of the Canterbury Museum*, **2**, 73–76.

Archey, G., 1923, A new Genus of Chilopoda from British Guiana, and a new species of *Wailamyctes* from Auckland Island, *Records of the Canterbury Museum*, **2**, 113–116.

Archey, G., 1937, Revision of the Chilopoda of New Zealand. Part 2, *Records of the Auckland Institute and Museum*, **2**, 71–100.

Attems, C., 1909, Myriapoda, in L. Schultze (ed.) *Zoologische und anthropologische Ergebnisse einer Forschungsreise im westlichen und zentralen Südafrika ausgeführt in den Jahren 1903–1905. Denkschriften der Medizinisch-naturwissenschaftlichen Gesellschaft zu Jena*, Vol. 14 (Jena: Gustav Fischer), pp. 1–52.

Attems, C., 1928, The Myriapoda of South Africa, *Annals of the South African Museum*, **26**, 1–431.

Chamberlin, R. V., 1955, The Chilopoda of the Lund University and California Academy of Science Expeditions. Reports of the Lund University Chile Expedition 1948–49. 18, *Lunds Universitets Årsskrift*, **51** (Lund: C.W.K. Gleerup), pp. 1–61.

Demange, J.-M., 1963. Myriapodes, in C. D. Deboutteville and E. Rapoport (eds) *Biologie de l'Amérique australe, II. Études sur la faune du sol* (Paris: Centre National de la Recherche Scientifique), pp.101–108.

Demange, J.-M. and Silva, F., 1976. Contribution à la connaissance de *Lamyctes inermipes* et *L. inermipes pacificus* Silv. par l'examen des spécimens types de la collection de F. Silvestri, *Estratto dal Bollettino del Laboratorio di Entomologia Agraria* 'Filippo Silvestri' *di Portici*, **33**, 44–52.

Eason, E. H., 1964, *Centipedes of the British Isles* (London: Frederick Warne & Co.), 294 pp.

Edgecombe, G. D., 2001, Revision of *Paralamyctes* (Chilopoda: Lithobiomorpha: Henicopidae), with six new species from eastern Australia, *Records of the Australian Museum*, **53**, 201–241.

Edgecombe, G. D., Giribet, G. and Wheeler, W. C., 2002, Phylogeny of Henicopidae (Chilopoda: Lithobiomorpha): a combined analysis of morphology and five molecular loci, *Systematic Entomology*, **27**, 31–64.

Haase, E., 1887, Die indisch-australischen Myriapoden. I. Chilopoden, *Abhandlungen und Berichte des Königlichen Zoologischen Anthropologisch-Ethnographischen Museums zu Dresden*, **5**, 1–118.

Johns, P. M., 1964, Insects of Campbell Island. Chilopoda, Diplopoda (Preliminary note on the Myriapoda of the New Zealand Subantarctic Islands), *Pacific Insects Monograph*, **7**, 170–172.

Kraus, O., 1954, Myriapoden aus Peru, I, *Senckenbergiana biologica*, **34**, 311–323.

Lawrence, R. F., 1955, Chilopoda, in B. Hanström, P. Brinck and G. Rudebeck (eds) *South African Animal Life, Vol. II. Results of the Lund University Expedition in 1950–1951* (Stockholm: Almqvist & Wiksell), pp. 4–56.

Lawrence, R. F., 1956, Chilopoda of Tristan da Cunha. *Results of the Norwegian Scientific Expedition to Tristan da Cunha 1937–1938*, Vol. 39 (Oslo: Norske Videnskaps-Akademi), pp. 1–13.

Lawrence, R. F., 1960, Myriapodes: Chilopodes, *Faune de Madagascar*, **12**, 1–122. *Publications de l'Institute de Recherche Scientifique, Tananarive-Tsimbazaza.*

Maddison, D. R. and Maddison, W. P., 2000, *MacClade. Analysis of Phylogeny and Character Evolution. Version 4* (Sunderland, MA: Sinauer Associates).

Mesibov, R., 1986, *A Guide to Tasmanian Centipedes* (Zeehan: the author), 64 pp.

Murakami, Y., 1967, Postembryonic development of the common Myriapoda of Japan XXIV. A new species of the Family Henicopidae, *Zoological Magazine*, **76**, 7–12.

Negrea, S. and Matic, Z., 1996, Contribution à la connaissance des lithobiomorphes (Chilopoda) de la région palestinienne, in J.-J. Geoffroy, J.-P. Mauriès and M. Nguyen Duy-Jacquemin (eds) *Acta myriapodologica. Mémoires du Muséum national d'Histoire naturelle*, **169**, 225–233.

Pocock, R. I., 1901, Some new genera and species of lithobiomorphous Chilopoda, *Annals and Magazine of Natural History*, **7**, 448–451.

Silvestri, F., 1917, On some Lithobioidea (Chilopoda) from India, *Records of the Indian Museum, Calcutta*, **13**, 307–314.

Swofford, D. L., 2002, *PAUP*. Phylogenetic Analysis Using Parsimony (*and Other Methods). Version 4.0b8* (Sunderland, MA: Sinauer Associates).

Verhoeff, K. W., 1948, Myriapoden der Insel Fernando Po. X. Beitrag zu den wissenschaftlichen Ergebnissen der Forschungsreise H. Eidmann nach Spanisch-Guinea 1939/40, *Zoologischer Anzeiger*, **136**, 89–98.

Würmli, M., 1977, Wiederbeschreibung und Identität von *Cermatobius martensii*, des vermeintlichen Bindegliedes zwischen Scutigeromorpha und Lithobiomorpha (Chilopoda: Cermatobiidae), *Entomologica Germanica*, **3**, 361–366.