

# Two New Species of the Henicopid Centipede *Henicops* (Chilopoda: Lithobiomorpha) from Queensland and Victoria, With Revision of Species from Western Australia and a Synoptic Classification of Henicopidae

LAUREN M. HOLLINGTON<sup>1</sup> AND GREGORY D. EDGECOMBE<sup>2\*</sup>

<sup>1</sup> School of Biological Sciences, University of Sydney NSW 2006, Australia  
lmhollington@bigpond.com

<sup>2</sup> Australian Museum, 6 College Street, Sydney NSW 2010, Australia  
greged@austmus.gov.au

**ABSTRACT.** *Henicops* Newport, 1844, is the most commonly recorded Australian genus of Henicopidae, the main southern temperate clade in Lithobiomorpha. *Henicops* is widespread throughout eastern and southwestern Australia and New Zealand, and is represented in New Caledonia by *H. brevilabiatus* (Ribaut, 1923) n.comb. New species are *H. tropicanus* n.sp. from northeastern Queensland and *H. milledgei* n.sp. from Victoria. The two nominal species from the southwest of Western Australia, *H. dentatus* Pocock, 1901a, and *H. oligotarsus* Attems, 1911, are synonymous, this species being distinguished from the Queensland *H. tropicanus* by details of the mandibular gnathal edge and female gonopod. Other characters used for diagnosing species and supraspecific groups within *Henicops* include the segmentation of the tarsi, tergite shape, and the position of the Tömösváry organ. All species of Henicopidae are listed with synonymies, generic assignments and geographic occurrences.

HOLLINGTON, LAUREN M., & GREGORY D. EDGECOMBE, 2004. Two new species of the henicopid centipede *Henicops* (Chilopoda: Lithobiomorpha) from Queensland and Victoria, with revision of species from Western Australia and a synoptic classification of Henicopidae. *Records of the Australian Museum* 56(1): 1–28.

The lithobiomorph genus *Henicops* Newport, 1844, is one of Australia's most commonly found centipede taxa, with abundant records through all eastern states and southwestern Western Australia, as well as a broad distribution in New Zealand. Despite its abundance, systematic work on *Henicops* has been limited to brief descriptions of four named species.

Excluding those species that were transferred to *Lamyctes* Meinert, 1868, after that genus was established, the nominal species of *Henicops* are the type, *H. maculatus* Newport, 1844, *H. impressus* Hutton, 1877, *H. dentatus* Pocock, 1901a, and *H. oligotarsus* Attems, 1911. *Henicops*

*maculatus* was established for Tasmanian material, and the species has also been recorded from New Zealand, Victoria and New South Wales (Pocock, 1901a; Chamberlin, 1920; Archey, 1917, 1937). *Henicops impressus*, described from Dunedin and Queenstown, New Zealand, is considered a synonym of *H. maculatus*, which is widespread and common in New Zealand (Archey, 1937). *Henicops dentatus* was erected for specimens from Perth, Western Australia, and *H. oligotarsus* from various sites in southwestern Western Australia. The possible synonymy of these Western Australian species was suggested by Archey (1937: 75). The most recent taxonomic work on *Henicops* is Archey's

\* author for correspondence

(1937) description of New Zealand material of *H. maculatus*, with a subsequent summary of that species' distribution in Tasmania (Mesibov, 1986).

The existing literature pre-dates most collections in Australian museums. These collections indicate that the distribution of *Henicops* is more extensive than previously recorded, notably ranging to the Cape York Peninsula in Queensland (Fig. 1). The present study is based on a survey of *Henicops* samples in the collections of state museums in Australia and the Australian National Insect Collection. The overwhelming majority of specimens were collected in wet sclerophyll forest and rainforest during litter invertebrate surveys, primarily since the 1970s. This study documents two new species from Queensland and Victoria, and revises Western Australian species that are considered to be closely allied to the Queensland species. To summarize the current state of henicopid taxonomy, the new species and all confamilials are placed in a synoptic classification of Henicopidae.

### Methods and terminology

Scanning electron micrographs were captured using a LEO 435VP, most using a Robinson backscatter collector.

In all species descriptions, length of specimens was measured from the anterior margin of the head shield to the

end of the telson. Because this measure is affected by telescoping, length or width of the head shield is used as a measure of body size (Andersson, 1978). Terminology used throughout species descriptions follows that used by Edgecombe (2001), with terminology pertaining to the mandible following Edgecombe *et al.* (2002). For new species, "Other material" is not part of the type series.

The following abbreviations are used for repositories of the specimens examined:

AM	Australian Museum, Sydney
ANIC	Australian National Insect Collection, Canberra
CAS	California Academy of Sciences, San Francisco
MV	Museum Victoria, Melbourne
NMW	Naturhistorisches Museum, Wien
QM	Queensland Museum, Brisbane
WAM	Western Australian Museum, Perth
ZIUh	Zoologisches Institut und Zoologisches Museum der Universität Hamburg

Abbreviations for collectors are: GBM, G.B. Monteith; JMW, J.M. Waldoock; MSH, M.S. Harvey; RWT, R.W. Taylor. Other abbreviations for label data are: ANZSES, Australian and New Zealand Scientific Exploration Society; Berl., ANIC Berlesate sample; NP, National Park; Ra, Range; rf, rainforest; SF, State Forest.

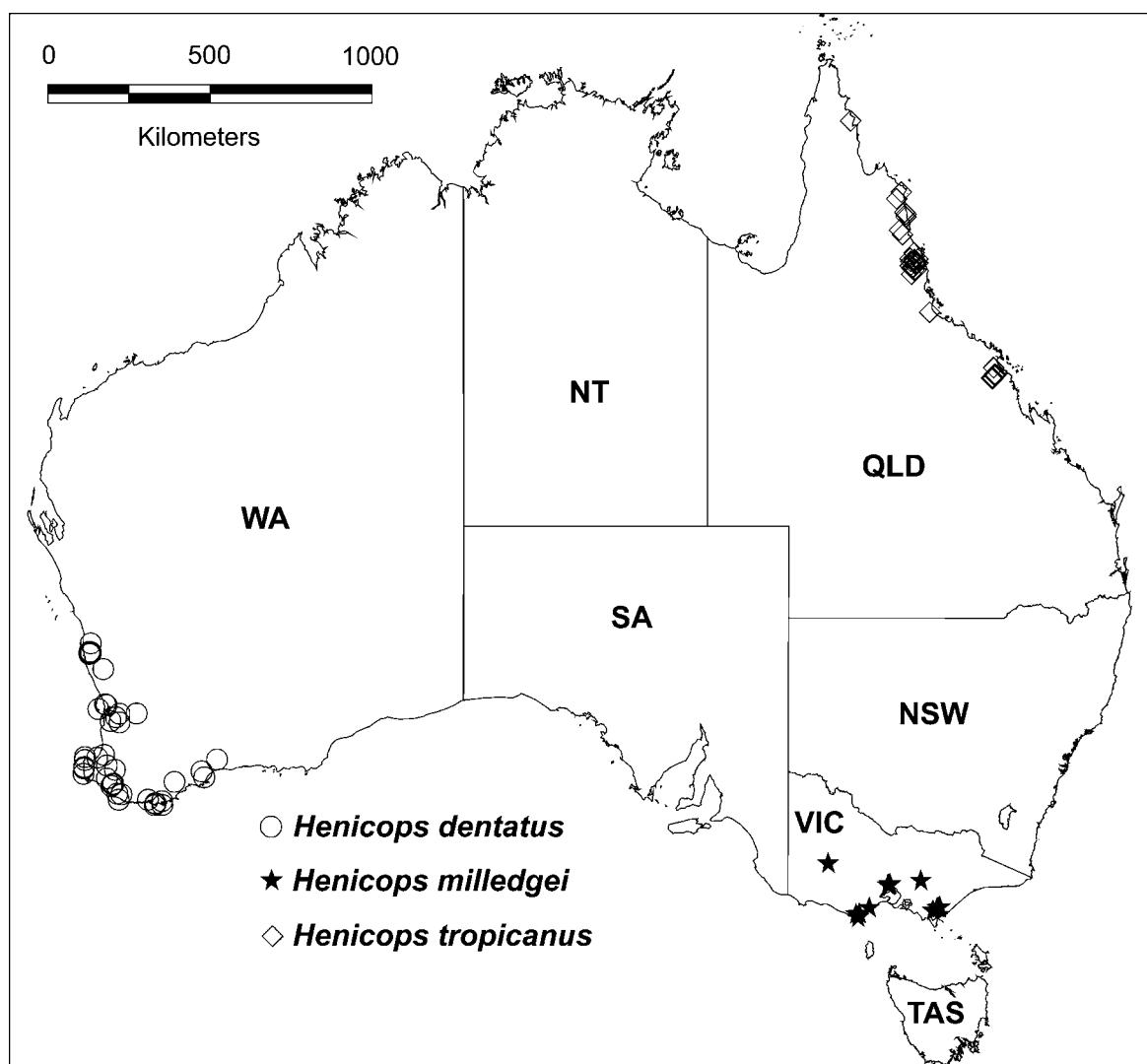


Fig. 1. Distribution of *Henicops dentatus* Pocock, 1901, *H. milledgei* n.sp. and *H. tropicanus* n.sp.

## Systematics

Chilopoda Latreille, 1817  
 Order Lithobiomorpha Pocock, 1902  
 Family Henicopidae Pocock, 1901b  
 Subfamily Henicopinae Pocock, 1901b  
 Tribe Henicopini Chamberlin, 1912

### *Henicops* Newport, 1844

**Type species.** *Henicops maculatus* Newport, 1844; by original designation.

**Diagnosis.** Member of *Lamyctes-Henicops* Group with 29–51 antennal articles; maxillipede coxosternum subtrapezoidal, dental margin moderately wide, with 3+3 or 4+4 teeth (exceptionally up to 6+6), lacking pseudopododont; mandibular aciculae abundant, arranged in two (inner and outer) rows; several laciniate or plumose setae amidst simple setae on coxal process of first maxilla; projections on (at least) tergites 9, 11 and 13; last distal spinose projection of tibia on leg 14; subdivision of basitarsus of legs 1–12 indicated by paired larger setae; tarsi of legs 13 and 14 divided into three or four tarsomeres; distitarsus of leg 15 divided into at least two tarsomeres; first genital sternite of male divided longitudinally into two sclerites; male and female gonopods abundantly setose, with numerous distally curved setae on male gonopod.

**Assigned species.** *Lamyctes brevilabiatus* Ribaut, 1923; *Henicops dentatus* Pocock, 1901a (=*H. oligotarsus* Attems, 1911, n.syn.); *H. milledgei* n.sp.; *H. tropicanus* n.sp.

**Discussion.** The genus *Henicops* was erected by Newport (1844), with his concept of *Henicops* corresponding to the modern concept of the family Henicopidae. Two species of *Henicops* were originally named, *Henicops maculatus* from Tasmania and *H. emarginatus* Newport, 1844, from New Zealand. The latter was subsequently transferred to *Lamyctes* Meinert, 1868, and is a senior subjective synonym of the type species, *L. fulvicornis* Meinert, 1868 (Eason, 1996).

In erecting a new genus, *Paralamyctes*, Pocock (1901b) rediagnosed *Henicops* with emphasis on the division of the tarsi into tarsomeres. *Henicops* was again rediagnosed by Archey (1917), who included in that diagnosis the presence of plumose setae on the coxal process of the first maxilla, a character previously used to distinguish Lithobiidae from Henicopidae (Chamberlin, 1912). The “plumose” setae on the coxal process of the first maxilla in *Henicops* vary from laciniate (Fig. 15J; Edgecombe *et al.*, 2002: fig. 8H for *H. maculatus*) to plumose, though the latter differ in detail from the complex plumose setae of lithobiids (Edgecombe & Hollington, 2002: fig. 9C,E). The present study frames the generic diagnosis around synapomorphies that identify *Henicops* as a monophyletic group within a clade that also includes *Lamyctes* (=*Lamyctinus* Silvestri, 1909a; see Edgecombe & Giribet, 2003a), *Lamyctopristus* Attems, 1928, *Analamyctes* Chamberlin, 1955, *Easonobius* Edgecombe, 2003a, and apparently *Pleotarsobius* Attems, 1909. The monophyly of this *Lamyctes-Henicops* Group is strongly supported by sequence data from multiple molecular markers (Edgecombe *et al.*, 2002; Edgecombe & Giribet, 2003b), and notably by insertions in the 18S rRNA.

*Henicops* is united with the South African *Lamyctopristus* Attems, 1928 (Edgecombe, 2004a: fig. 34D) by the mandibular aciculae being divided into inner and outer rows (Figs. 5F, 10C). This two-row arrangement is associated with a larger number of aciculae (about 20) in *Henicops* than in allied henicopines. Previous diagnoses (Archey, 1917, 1937; Attems, 1928) cited three joints in legs 1–13 as diagnostic of *Henicops*, but this is now observed to pertain to most but not all species (at least two undescribed species have only two tarsomeres on legs 1–12). A more general characterization of the *Henicops* tarsal condition is that subdivision of the basitarsus of legs 1–12 is indicated by paired larger setae. Where the tarsus has only two tarsomeres, a pair of strong, divergent setae is situated on the basitarsus in the same position as those larger setae immediately proximal to the most proximal tarsomere articulation in species with three tarsomeres, i.e., the tripartite arrangement on the tarsi of legs 1–12 in *H. maculatus* and the three species described herein occurs by subdivision of the basitarsus. Concerning the distitarsus, all species of *Henicops* uniquely share a division of the distitarsus of leg 15 into tarsomeres, a state not otherwise developed in the Henicopini (see Table 1 for a comparison of tarsal segmentation between species). The bipartite first genital sternite in males (Figs. 6I, 11B, 16F) is invariant in *Henicops*. Elsewhere in Henicopidae, the division of this sternite into two sclerites is observed only in some members of *Lamyctes*, in those mostly African species split off by Verhoeff (1941) as *Metalamyctes*. The abundance of setae on the gonopods in both sexes is added to the generic diagnosis here, the number of setae in *Henicops* substantially exceeding that in most other Henicopinae, including other members of the *Lamyctes-Henicops* Group. This abundance could be explicitly defined in terms of the male gonopod having about 15 setae on the basal article and about 10 on the second and third. Among these are many distally curved setae (Figs. 4E, 12C).

**Table 1.** Tarsal segmentation in *Henicops*, showing number of tarsomeres in basitarsus and distitarsus (e.g., 2/1 indicates two segments in basitarsus and one in distitarsus).

	1–12	13	14	15
<i>Henicops maculatus</i>	2/1	2/2	2/3	2/4(5)
<i>Henicops dentatus</i>	2/1	2/2	2/2	2/3
<i>Henicops tropicanus</i>	2/1	2/2	2/2	2/3
<i>Henicops milledgei</i>	2/1	1/2	1/3	1/4

Additional distinction from *Lamyctes* is provided by the presence of tergal projections, subdivision of the tarsi, and a wider dental margin of the maxillipede coxosternum. A species that presents incongruence is the New Caledonian *Lamyctes brevilabiatus* Ribaut, 1923. Sequences from nuclear ribosomal as well as mitochondrial markers, separately as well as in combination, indicate that this species is more closely related to *Henicops* than to *Lamyctes* (Edgecombe & Giribet, 2003a,b). The molecular data more precisely indicate an alliance with members of the *Henicops dentatus* Group as defined below. Apomorphic morphological characters shared with *Henicops* include the relatively large number of antennal articles (38–47), a

relatively wide dental margin of the maxillipede coxosternum with 3+3 teeth and no pseudopordont, laciniate setae on the coxal process of the first maxilla, and a bipartite first genital sternite in the male (AM KS82626, Mt Humboldt). The spines beneath the posterior pretarsal accessory claw are short, as in *Henicops* (Fig. 14L), rather than long and needle-like as in *Lamyctes* (Edgecombe & Giribet, 2003a: figs. 34, 36). The New Caledonian species lacks, however, several characters shared by all other members of *Henicops*. It has transverse (rather than projected) posterior margins of TT11 and 13, the last distal spinose projection is on the tibia of leg 13 (rather than 14), and the tarsi of legs 13–15 are bipartite, with no trace of a subdivision of either tarsomere. Legs 1–12 have indistinct tarsal articulations. The mandible differs from other members of *Henicops* in having relatively few (nine) aciculae in a single row (Fig. 2B,C), rather than having about 20 aciculae in two rows. Cladistic analysis of morphological evidence resolves *brevilabiatus* as sister group of *Henicops* as diagnosed above in some minimal length cladograms, but as a member of *Lamyctes* in others, whereas combination of the morphological data with molecular data favours an ingroup position within *Henicops* (Edgecombe & Giribet, 2003b). Based on strength of the molecular support together with the presence of several apomorphies of *Henicops* listed above, the species is reassigned to *Henicops*.

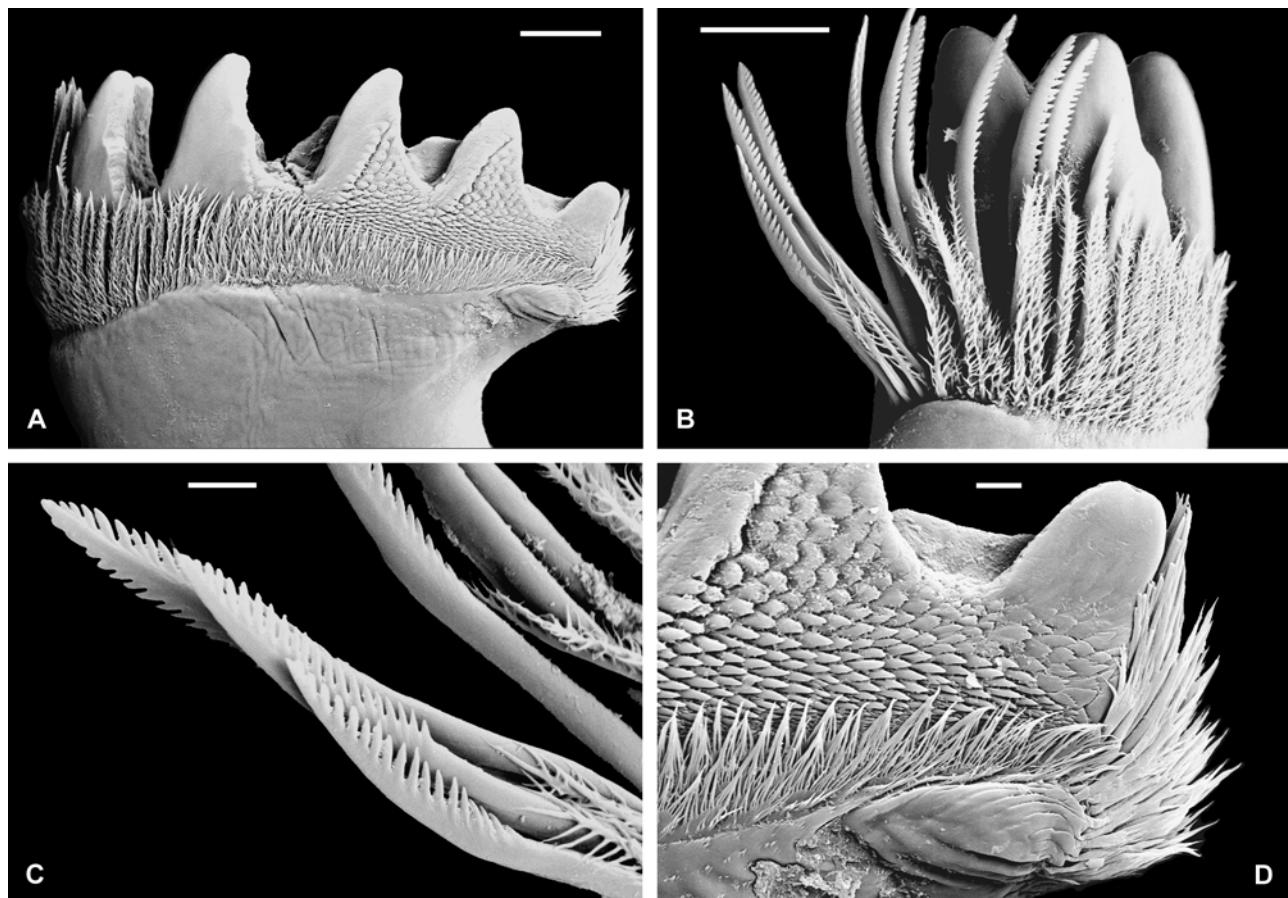


Fig. 2. *Henicops brevilabiatus* (Ribaut, 1923). QM S60651, ♀, Me Maoya, New Caledonia, mandible: (A) gnathal edge, scale 50 µm; (B) ventral part of gnathal edge, scale 50 µm; (C) aciculae, scale 10 µm; (D) dorsal teeth and furry pad, scale 10 µm.

### *Henicops dentatus* Group

**Diagnosis.** *Henicops* with 29–40 (most commonly 36) antennal articles, with a relatively gradual change in length of articles along antenna; Tömösváry organ deep, outer edge at margin of cephalic pleurite; TT7, 9, 11 and 13 with subquadrate emargination (posterior margin with transverse medial sector with independent curvature from lateral sectors); three moderate sized teeth on dental margin of maxillipede coxosternum; groove in accessory denticle field lacking on mandibular teeth; mandibular aciculae variable in structure, differentiated into some with pronounced serrations on both margins and others with a simple margin along most or all of length; ventral branching bristles of mandible lacking spine-like branches on basal part; three tarsomeres in legs 1–12; four tarsomeres in legs 13 and 14, basitarsus and distitarsus with two tarsomeres each; five tarsomeres in leg 15, basitarsus having two, distitarsus three.

**Assigned species.** *Henicops dentatus* Pocock, 1901a (=*H. oligotarsus* Attems, 1911); *H. tropicanus* n.sp.

**Discussion.** The diagnosis above lists characters that unite *Henicops dentatus* and *H. tropicanus* n.sp. that are either unique within *Henicops* or permit distinction from *H. maculatus* or other species. Several of these can be regarded as synapomorphies for *H. dentatus* and *H. tropicanus*.

Character polarity is evaluated in the context of *Henicops* being sister to a clade that includes *Lamycetes*, *Analamycetes*, *Easonobius* and *Lamyctopristus* (Edgecombe *et al.*, 2002; Edgecombe, 2003a, 2004a; Edgecombe & Giribet, 2003b) (see synoptic classification below).

Indistinct grooves in the accessory denticle field on the mandibles (Figs. 5D,I, 10A,F) are restricted to the *H. dentatus* Group within *Henicops*. Grooves or grooved ridges (see Fig. 14D,F for their presence in *H. milledgei*) are observed in most Henicopini, including other members of the *Lamycetes-Henicops* Group (Fig. 2A). The “notched”

margin of tergite 7 in the *H. dentatus* Group (Figs. 3, 7A) is distinctive for those two species within *Henicops*, though the same shape of this tergite is observed in some other Hemicopinae, e.g., within *Paralamycetes* and in Zygetobiini. Tergite shapes were noted by Pocock (1901a) as subquadrate emarginate TT7, 9, 11 and 13, serving as a distinguishing character of *H. dentatus* and *H. tropicanus* relative to *H. maculatus* and *H. milledgei*.

A differentiation of the mandibular aciculae into an outer row with serrated margins and an inner row with simple or weakly scalloped margins (Figs. 5G, 10C,D) is shared with *Henicops milledgei* (Fig. 14I). This differentiation is apparently apomorphic relative to the uniform structure of the aciculae in *H. maculatus* (Edgecombe *et al.*, 2002: fig. 5C) and *H. brevilabiatus* (Fig. 2B), the latter being shared by outgroups. Likewise, *H. milledgei* and the *H. dentatus* Group share a narrow base to the ventralmost bristles in the fringe of branching bristles along the mandibular gnathal edge. These bristles have no or few spine-like projections

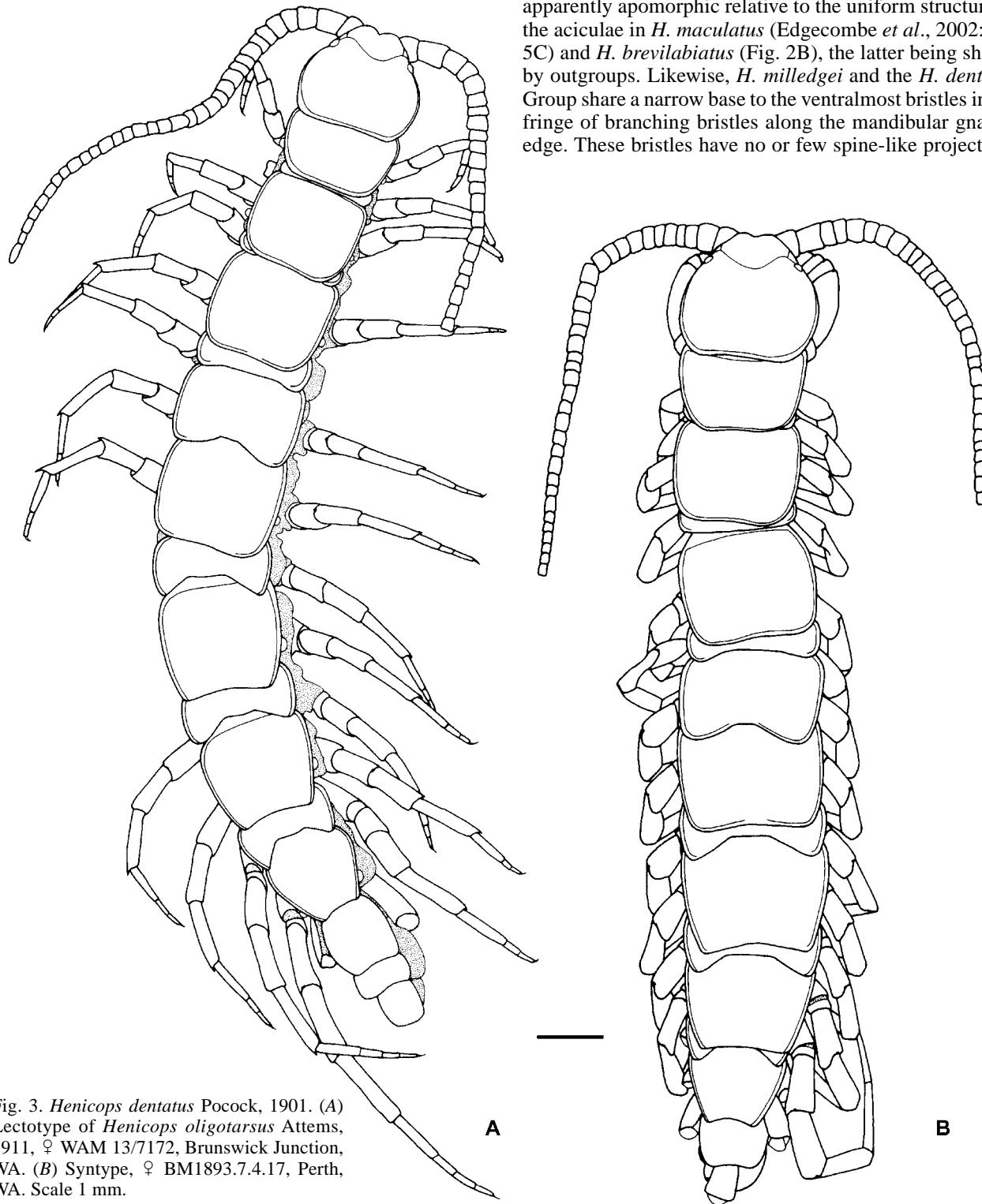


Fig. 3. *Henicops dentatus* Pocock, 1901. (A) Lectotype of *Henicops oligotarsus* Attems, 1911, ♀ WAM 13/7172, Brunswick Junction, WA. (B) Syntype, ♀ BM1893.7.4.17, Perth, WA. Scale 1 mm.

basally (the entire basal half of the bristle lacks spines in *H. dentatus*: Fig. 5H), but branch evenly along their distal part (Figs. 10E, 14H). This is also apparently apomorphic relative to the evenly spine-covered bristles in *H. maculatus* (Edgecombe *et al.*, 2002: fig. 5C), which have spines on their bases. The latter state is possessed by other taxa in the *Lamyctes-Henicops* Group (for *Lamyctes*, see Edgecombe *et al.*, 2002: fig. 6D, Edgecombe & Giribet, 2003a: fig. 27; Fig. 2B herein for *H. brevilabiatus*) and other Henicopini generally.

The relatively even length of the antennal articles in the *H. dentatus* Group is potentially apomorphic relative to the groups of shortened articles occurring in pairs in other congeners because other genera of the *Lamyctes-Henicops* Group (e.g., *Lamyctes*, *Analamyctes*, *Easonobius*, *Lamycyptopristus*) have the paired, shortened articles. The deep, submarginally positioned Tömösváry organ in the *H. dentatus* Group (Figs. 6L, 9D–F) is unique within *Henicops*, but is shared by most non-*Henicops* Henicopini. The deep, submarginal organ is thus apparently plesiomorphic relative to the shallow organ situated medially on the cephalic pleurite in *H. maculatus* (Edgecombe *et al.*, 2002: fig. 1G) and *H. milledgei* (Fig. 15D,E). This character suggests that the *H. dentatus* Group is possibly sister to all other species of *Henicops*.

### *Henicops dentatus* Pocock, 1901

Figs. 3–6

*Henicops dentatus* Pocock, 1901a: 454.

*Henicops oligotarsus* Attems, 1911: 150; **new synonymy**.

*Henicops oligotarsus*.—Borucki, 1996: fig. 102.

**Diagnosis.** Member of *Henicops dentatus* Group with female gonopod having two small, bullet-shaped or distally truncated spurs; outer spur up to 50% wider than inner spur; branching bristles on mandibular gnathal edge narrow in dorsal part of fringe; ventral bristles in fringe lacking spines on their basal third or more.

**Type material.** SYNTYPES: BM1893.7.4.17, ♀ (Fig. 3B), BM1893.7.4.18, ♂, Perth, WA, H.W.J. Turner.

**Other material.** Types of *Henicops oligotarsus* Attems, 1911: LECTOTYPE: WAM 13/7172 (Fig. 3A), ♀, Brunswick Junction, WA (station 139 of Michaelsen & Hartmeyer, 1907), 33°15'S 115°50'E, W. Michaelsen & R. Hartmeyer, 7 Oct 1905, designated here. A lectotype is selected to fix the name to a single type locality; the chosen specimen is the most intact large individual from a locality represented by both sexes in the WAM and NMV. PARALECTOTYPES: WAM, 2♂♂, from type locality. NMV: 3907, 1♀, Boyanup (station 146); 3908, 1♀, 2♂♂, Brunswick (station 139); 3909, 1♀, Albany (station 165). ZIUM: 6♀♀, 2♂♂, Lion Mill (station 99); 1♀, 1♂, Mundaring Weir (station 101); 1♂, Bridgetown (station 144); 1♀, Beverly (station 156). Attems (1911) listed additional syntypes from Wooroloo, East Fremantle, Jarrahdale, and Gooseberry Hill that we have not located.

WESTERN AUSTRALIA: WAM: 25/822, 1♀, Dandaragan, 30°40'S 115°42'E, L. Glauert, Sep 1925; 28/740, 1♂, Serpentine, 32°22'S 115°58'E, L. Glauert, Aug 1928; 14/987, 1♀, Denmark, 34°57'S 117°21'E, W.B. Alexander, May 1914; T42434, 4♀♀, 1♂, Hepburn Heights, 31°49'02"S 115°46'13"E, MSH & JMW, 13 Jul–25 Sep 1995; T42435, 3♀♀, Warwick Open Space, 31°50'34"S 115°48'50"E, MSH & JMW, 25 Sep–28 Nov 1995; T42436, 7♀♀ (Figs. 4F, 5F–I, 6H), 2♂♂ (Fig. 4E), Warwick Open Space, 31°50'33"S 115°49'00"E, MSH & JMW, 25 Sep–28 Nov 1995; T42437, 1♀, Balannup Lake, Gosnells, E.G. Cockett, 24 Dec 1968; T42438, 1♀, Bald Head, Albany, D.D. Giuliani, 10 May 1969; T42439, 1♂, Bentley, B. Anderson, 8 Sep 1976; T42440,

1♀, Boranup, G.M. Riley, 10 Sep 1965; T42441, 1♂, Peppermint Forest, 5 mi N Busselton, R.J. McKay & R.W. George, 22 Oct 1969; T42442, 1♀, T42443, 1♀, Cape Freycinet, 34°06'S 114°59'E, T.F. Houston, 15–18 Nov 1986; T42444, 1♂, Cape Naturaliste NP, catchment of Yallingup Brook, 33°38'50"S 115°02'10"E, J. Mitchell *et al.*, 1–10 Dec 2000; T42445, 1♀, Fossil Deposit SF, 4 mi W cape, G.H. Riley & G. Kendrick, 8 Sep 1969; T42446, 1♀, Cocanarup Timber Reserve, 33°38'S 119°54'E, G. Harold, Nov 1993; T42447, 1♂, Worsley Alumina Project, Collie off Fletcher Rd, D. Walford & M. Sawle, Jul 1980; T42448, 1♀, Crowea, S.J. Curry, 31 Oct 1980; T42449, 1♂, Dog Pool on Shannon River, 34°46'S 116°22'E, MSH & JMW, 27–30 Apr 1990; T42450, 1♀, 3 km N Dog Pool, 34°45'S 116°13'E, MSH & JMW, 30 Apr 1990; T42451, 4♀♀, 3♂♂, Dwellingup, J.D. Majer, 7–25 Nov 1975; T42452, 1♀, R.G.C. Mineral Sands, 10 km S Eneabba, 29°50'S 115°15'E, L.P. McMillan & P. West, 22 Jul 1997; T42456, 5♀♀, 1♂, Fitzgerald River NP, West Mt Barren, NE slope, 34°13'S 119°26'E, MSH & JMW, 28 May 1994; T42457, 1♀, Fitzgerald River NP, Twertyup, 34°01'S 119°20'E, MSH & JMW, 29 May 1994; T42458, 1♂, "Glenbourne", Old Ellens Brook Rd, 33°53'S 115°00'E, L. Marsh *et al.*, 27–28 Oct 1996; T42459, 1♂, "Glenbourne", Spring Rd S Gracetown, 33°53'S 115°00'E, 28–30 Jun 1997, L.M. Marsh *et al.*; T42460, 1♂, "Glenbourne", S Gracetown, 33°54'32"S 115°00'24"E, L. Marsh *et al.*, 30 Oct–1 Nov 1999; T42461, 1♂, Gleneagle, 32°15'S 116°10'E, J.A. Springett, 22 Oct 1971; T42463, 1♀, 12.5 mi NE Katanning, E.J. Car and G.M. Riley, 28 Oct 1964; T42464, 1♂, Leeman, R.P. McMillan, 31 Aug 1981; T42465, 1♀, T42466, 1♀, Ludlow Tuart Forest, 33°34'S 115°29'E, J.A. Springett, 31 Aug 1971; T42467, 4♀♀, Margaret River, L.E. Koch, 22–24 Aug 1973; T42468, 1♀, T42469, 1♂, 6.5 km and 5.5 km NW Meelup, 33°33'00"S 115°01'45"E, G.A. Harold, 22–27 Oct 1985; T42470, 1♂, Mt Cooke, near summit, 32°25'S 116°18'E, MSH, JMW & M. Peterson, 7 Aug 1990; T42471, 1♂, same locality, MSH & JMW, 1 Oct 1990; T42472, 1♀, same locality and collectors, 16 Dec 1990; T42473, 2♀♀, same locality, 31 Jul 1991; T42474, 1♀, same locality, 19 Sep 1991; T42475, 1♀, 1♂, base of Mt Dale, W side, 32°08'S 116°18'E, JMW *et al.*, 27 Sep 1998; T42477, 1♂, T42478, 1♀, T42479, 1♂, T42485, 1♂, c. 4 km NNE Mt Lesueur, 30°08'S 115°12'E, K. Gaull *et al.*, 9–12 Jul 1989; T42481, 1♂, 1.6 km N Mt Lesueur, 30°10'S 115°12'E, K. Gaull *et al.*, 11 Jul 1989; T42482, 1♀, c. 5 km NE Mt Lesueur, 30°09'S 115°15'E, K. Gaull *et al.*, 9 Jul 1989; T42486, 2♂♂, 7 km NE Mt Lesueur, 30°07'S 115°15'E, K. Gaull *et al.*, 1989; T42487, 1♀, 4.5 km E Mt Peron, 30°06'S 115°12'E, K. Gaull *et al.*, 7 Jul 1989; T42488, 1♂, North Tarin Rock Reserve, D. Kitchener *et al.*, 17–27 May 1971; T42489, 1♀, Pemberton, Allis Rd, 34°30'S 116°00'E, J.A. Springett, 9 Nov 1971; T42490, 1♂, Bluff Knoll, Stirling Ranges, D.D. Giuliani, 13 May 1969; T42491, 2♂♂, Stirling Range NP, Ellen Peak, 34°21'32"S 118°19'45"E, 1000 m, S. Barrett, 4 Apr 1995; T42492, 4♂♂, Swan River Dist, 15–18 Jul 1924; T42493, 1♀, The Cascades, 8 km SSW Pemberton, 34°30'S, 116°00'E, MSH & JMW, 3 May 1990; T42494, 1♂, Torbay hill, boundary track, 35°05'S 117°37'E, B.Y. Main, 20 Feb–6 Mar 1983; T42495, 1♂, Torbay Head, 35°05'S 117°38'E, B.Y. Main, 9 Aug–7 Sept 1985; T42496, 1♀, Torbay Head, B.Y. Main, 20 Jun 1986; T42497, 1♂, Torndirrup NP, Sharp Point Rd, 35°06'42"S 117°52'55"E, JMW, 14 Nov 1998; T42498, 1♀, Two People Bay, G. Smith, 15 Sep 1976; T42499, 1♀, Tutanning Reserve, Pingelly, E. Mercer, 28 Aug 1980; T42500, 1♂, Walyunga NP, M. Archer & E. Jeffreys, 4 May 1969; T42501, 1♀, Wanneroo, 33°54'32"S 115°00'24"E, R.P. McMillan, 18 Aug 1952; T42502, 1♀, West Cape Howe NP, Lake William, 35°04'S 117°37'E, B.Y. Main, 26 Mar–5 Apr 1985; T42503, 1♀, West Cape Howe NP, West Cape Howe, 35°08'S 117°36'E, B.Y. Main, 15–24 Jan 1988; WAM, 1♀, 1♂, Rottnest Island, Mt Herschell, 31°59'S 115°31'E, L. Glauert, Sep 1927.

AUSTRALIAN MUSEUM: KS15269, 3♀♀, 2♂♂, Dombalup SF, Marri Rd, 34°30'S 116°00'E, M.R. Gray, 15 Jan 1979; KS15361 (Fig. 4A–D), c. 200 individuals, Treen Brook SF, 8 km W Pemberton, 34°26'S 116°04'E, M.R. Gray, 13 Feb, 1979; KS35584, 1♀, 3♂♂, Walpole-Nornalup NP, 34°57'S 116°16'E, M.R. Gray, 15 Feb 1979; KS35644, 1♀, 2♂♂, Pine Ck, 0.5 km from Quarty Rd, Nannup-Pemberton area, 34°15'S 115°50'E, M.R. Gray, 14 Feb 1979; KS77589, 1♂, Pemberton Forest Park, Karri Bush Walk, 34°27'S 116°01'30"S E, G.D. Edgecombe & Z. Johanson, 23 Feb 2001; KS83629, 1♀ (Fig. 6G,M), KS83630, 1♂ (Figs. 5A–E,J–O, 6A–F,I–L), Gloucester NP, crossing of Bibbulmun Track and Burma Rd, 34°27'S 116°03'E, G.D. Edgecombe & Z. Johanson, 23 Feb 2001.

CALIFORNIA ACADEMY OF SCIENCES (leg. E.S. Ross & D. Cavagnaro): 2♀♀, 3♂♂, Darlington, 450 ft, 5 Sep 1962; 1♀, 20 mi S Borden, 200 m, 23 Sep 1962; 1♀, 25 mi NW Walpole, 100 m, 25 Sep 1962; 4♀♀, 2♂♂, Cape Naturaliste, 5 m, 27 Sep 1962; 1♂, 7 mi NE Busselton, 50 m, 28 Sep 1962.

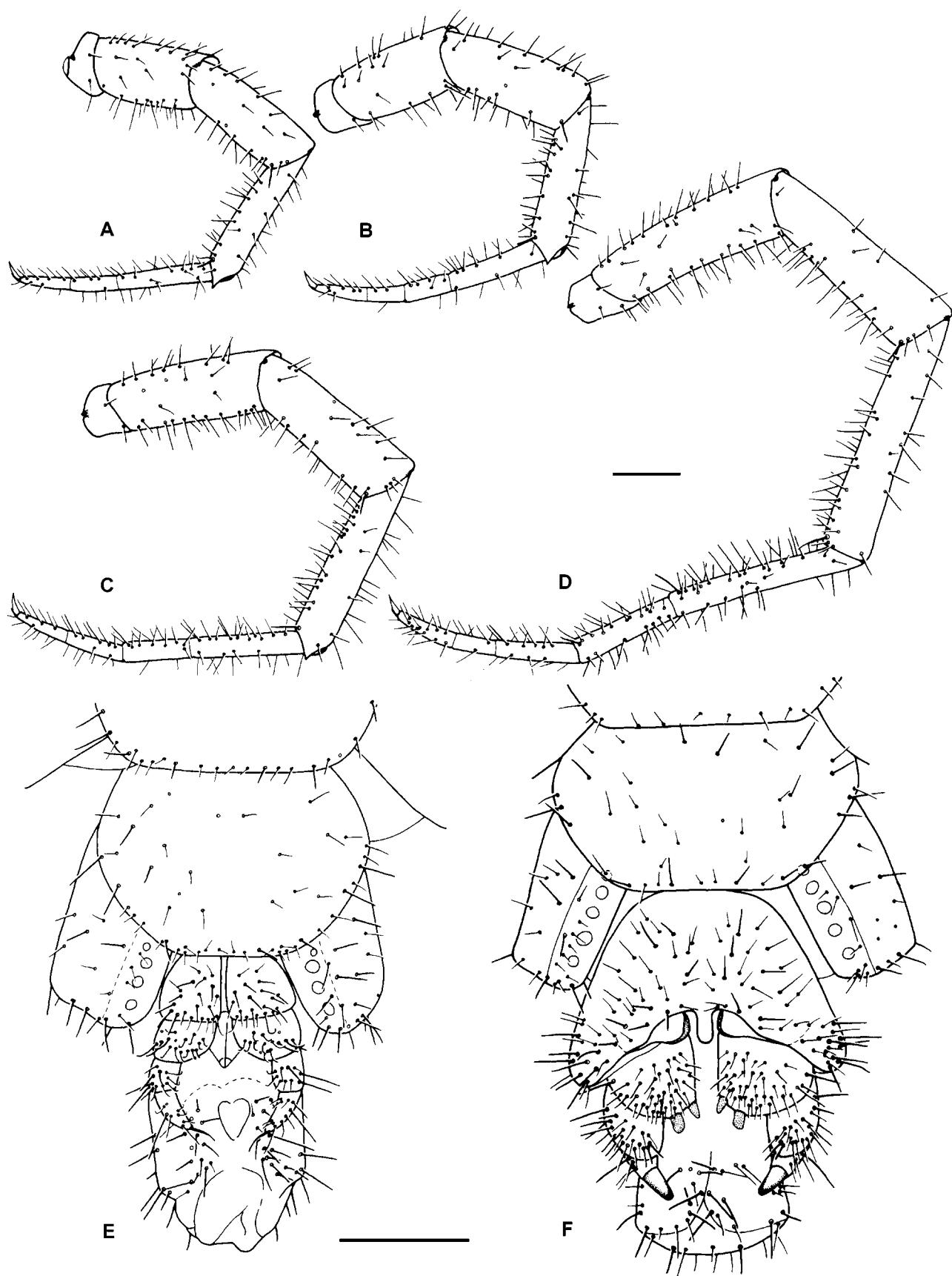


Fig. 4. *Henicops dentatus* Pocock, 1901. (A–D) ♀ AM KS15361, Treen Brook SF, W Pemberton, WA: (A) leg 12; (B) leg 13; (C) leg 14; (D) leg 15. (E,F) ♂, ♀, WAM T42436, terminal segments and gonopods, Warwick Open Space, WA. Scales 0.5 mm.

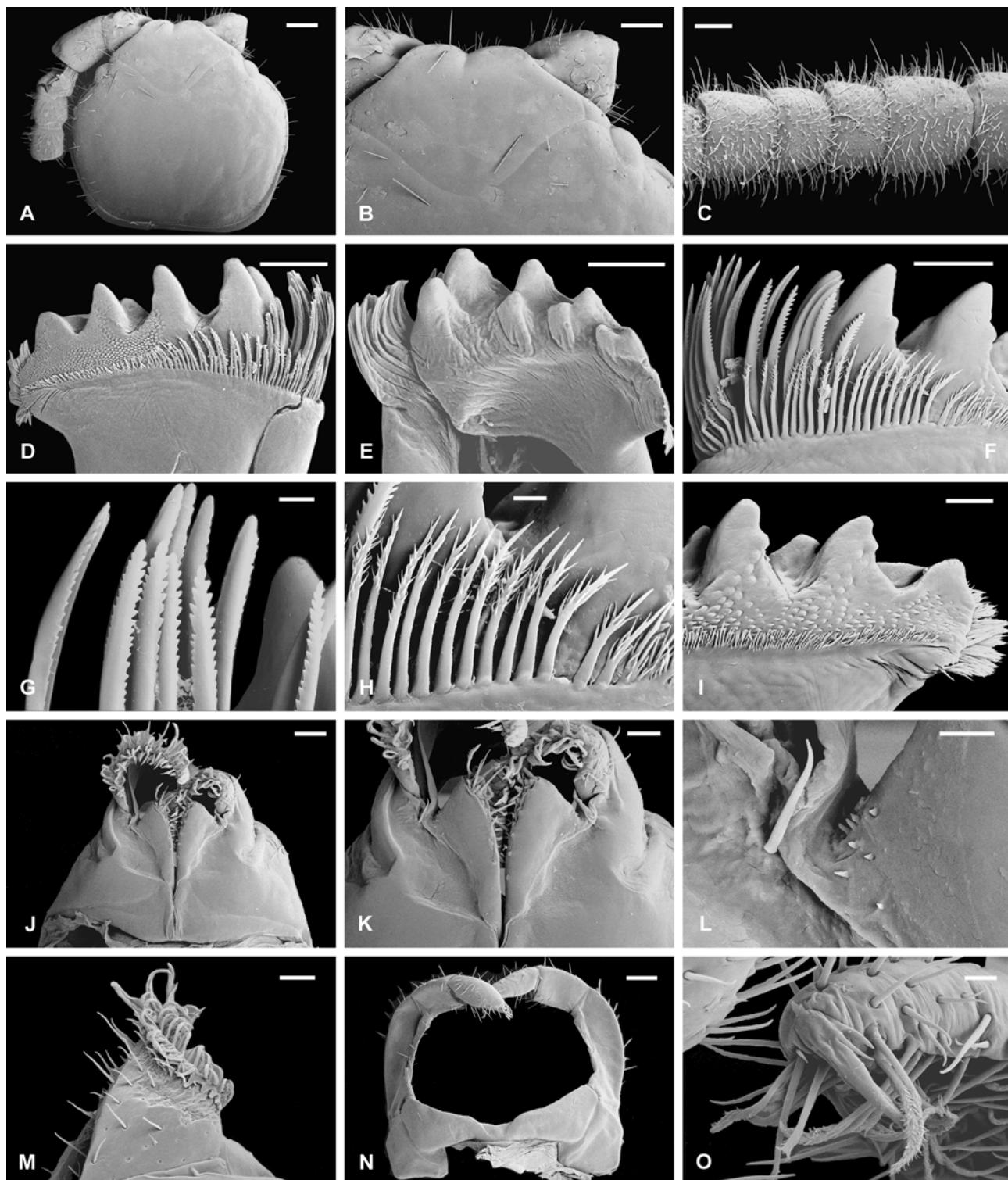


Fig. 5. *Henicops dentatus* Pocock, 1901. (A–E, J–O) ♂ AM KS83630, Gloucester NP, Pemberton, WA: (A) dorsal view of head shield, scale 60 µm; (B) anterior part of head shield, showing transverse and antennocellar sutures, scale 50 µm; (C) antennal articles, scale 100 µm; (D, E) outer (anterior) and inner (posterior) views of gnathal edge of right mandible, scales 60 µm, 50 µm; (J) first maxillae, scale 130 µm; (K) coxal processes of first maxillae, scale 60 µm; (L) cluster of sensilla microtrichoidea between telopodite and coxal process of first maxilla, scale 15 µm; (M) distal article of telopodite of first maxilla, scale 60 µm; (N) second maxillae, scale 300 µm; (O) tarsus and pretarsus (claw) of second maxilla, scale 20 µm. (F–I) ♀ WAM T42436, Warwick Open Space, WA, left mandible: (F) ventral part of gnathal edge, scale 50 µm; (G) aciculae, scale 10 µm; (H) fringe of branching bristles, scale 10 µm; (I) dorsal teeth and furry pad, scale 30 µm.

**Distribution.** Southwest Western Australia, north to Eneabba (29°50'S 115°15'E), east to Cocanarup (33°38'S 119°54'E) (Fig. 1), sclerophyll forest.

**Discussion.** *Henicops dentatus* is identical to or within the range of variation of *H. tropicanus*, described in full below, in most respects except for the female gonopods and details

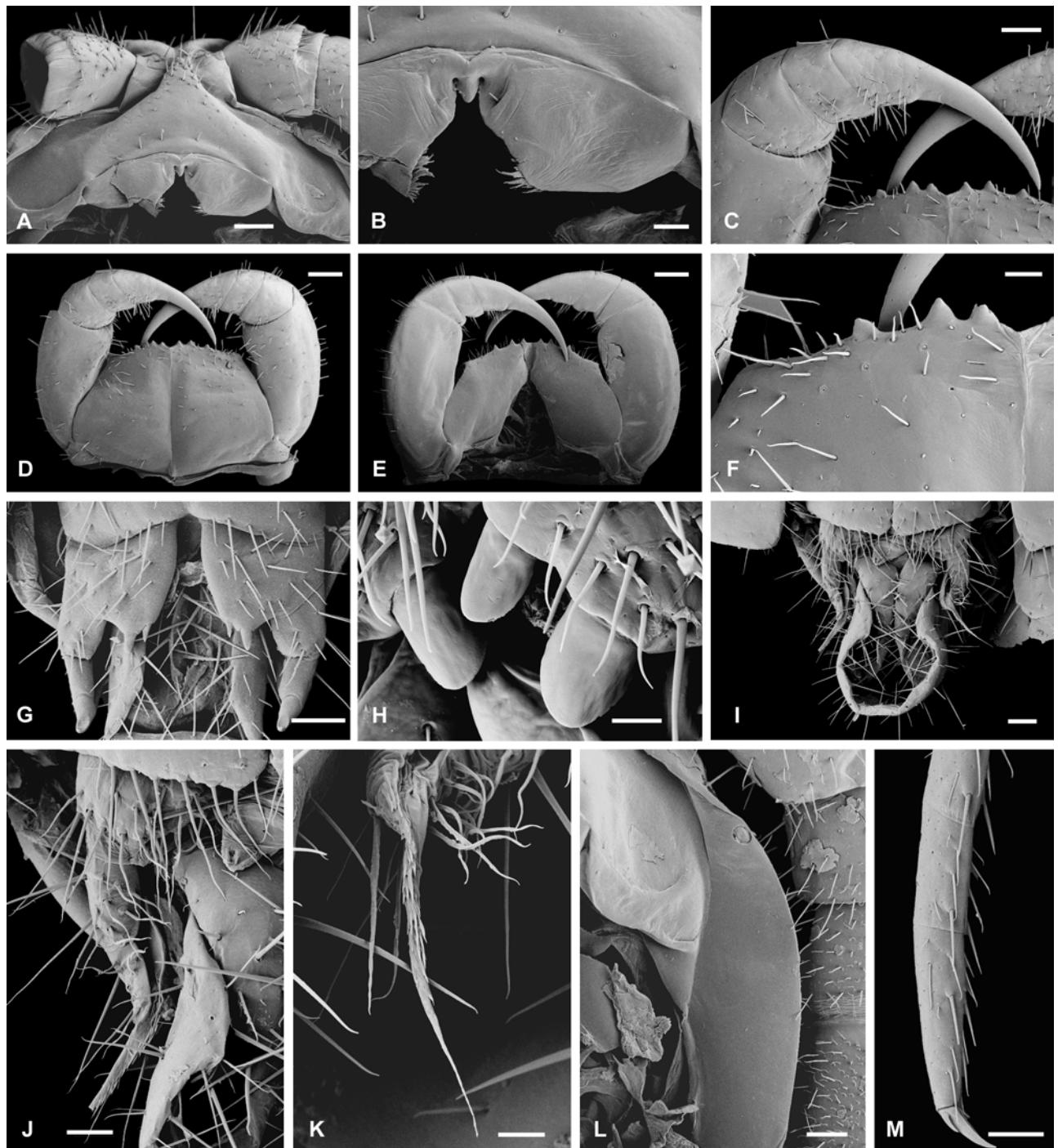


Fig. 6. *Henicops dentatus* Pocock, 1901. (A–G,I–M) Gloucester NP, Pemberton, WA. (A–F,I–L) ♂ AM KS83630: (A) clypeus and labrum, scale 180 µm; (B) labrum, scale 70 µm; (C) telopodite and dental margin of maxillipede, scale 180 µm; (D,E) ventral and dorsal views of maxillipede, scales 300 µm; (F) dental margin of maxillipede coxosternum, scale 70 µm; (I,J) gonopods and detail of right gonopod and penis, scales 100 µm, 30 µm; (K) terminal process of gonopod, scale 30 µm; (L) cephalic pleurite, showing Tömösváry organ, scale 100 µm. (G,M) ♀ AM KS83629: (G) gonopods, scale 100 µm; (M) tarsus and pretarsus of leg 12, scale 70 µm. (H) ♀ WAM T42435, Warwick Open Space, WA. Spurs on gonopods, scale 30 µm.

of the mandibular gnathal edge. Distinction between the two is discussed under the latter species.

The present study of a large sample of southwest Western Australian specimens of *Henicops*, including the syntypes of both *H. dentatus* and *H. oligotarsus*, corroborates Archey's (1937) suspicion that the two named Western Australian species are synonymous. When naming *H. oligotarsus*, Attems made no mention of the previously named *H. dentatus*. Attems (1928:63) later acknowledged

*H. dentatus* in a key to *Henicops* species. He distinguished the two Western Australian species on the basis of tergites 7, 9, 11 and 13 of *H. oligotarsus* being "toothed" and the corresponding tergites of *H. dentatus* and *H. maculatus* being "rounded", in addition to leg 15 of *H. oligotarsus* having five tarsomeres as opposed to six tarsomeres in *H. dentatus* and *H. maculatus*. Both of these alleged differences are unfounded. Description of a "toothed" condition of tergites in *H. oligotarsus* refers to the triangular projections

of the posterior angles of TT7, 9, 11 and 13. This is a more or less accurate description of the tergites of Attems' specimens (Fig. 3A), but it is identical to the condition of these tergites in the types of *H. dentatus* (Fig. 3B). Indeed, no *Henicops* specimens from anywhere in the range of *H. dentatus* (=*H. oligotarsus*) have tergites 7, 9, 11 and 13 that could be described as "rounded". Leg 15 of all Western Australian specimens has five tarsomeres (Fig. 4D) so no specific distinction can be made based on some specimens having five and others having six. The types of *H. dentatus* lack legs 14 and 15 (and seemingly lacked these legs when Pocock described the species, for no mention was made of them), so Attems' claim of a difference from *H. oligotarsus* has no basis. In the absence of any morphological characters to support the presence of multiple taxa in Western Australia, all specimens are recognized as a single species, using the older name, *H. dentatus*. The description of *H. oligotarsus* (Attems, 1911:150) stated that the species has 33–35 antennal articles but among the syntypes are large specimens with 29–36 articles. Other collections extend the range to 38 articles, though as in *H. tropicanus* the most common number is 36.

### *Henicops tropicanus* n.sp.

Figs. 7–11

**Etymology.** For the Wet Tropics of northeastern Queensland, where the species occurs.

**Diagnosis.** Member of *Henicops dentatus* Group with female gonopod having two (exceptionally three) large, elongate, bullet-shaped spurs; legs 14 and 15 relatively sparsely setose, with few setae on tibia and basitarsus of leg 15.

**Type material.** HOLOTYPE: ♀ QM S39941 (Fig. 7A), from head of Roots Creek, 12km WNW Mossman, Queensland, 16°24'46"S 145°16'03"E, 1200 m, 28 Dec 1989–11 Jan 1990, ANZSES, pitfall. PARATYPES: ♂ QM S39941, from type locality, collection data as for holotype; S39869, 3♀♀, S39873, 1♂, S39898, 2♀♀ (Figs. 8A–D, 10D–F, K, 11C,H,J), 1♂ (Figs. 9B–D,F–J, 10A–C,G–H,J,M, 11D,E,I), S39934, 2♀♀, Mossman Bluff Track, 5–10 km W Mossman, GBM, G. Thompson & ANZSES, 20 Dec 1989–15 Jan 1990.

**Other material.** QUEENSLAND: QM: S22632, 1♀, 14.4 km N Wudjl Wudjl, 15°52'S 145°19"E, R. & S. Raven, P. & E. Lawless, 28 Nov 1992–18 Apr 1993; S39861, 2♀♀, 1♂, Mt Dalrymple, 21°03'S 148°38"E, 1200 m, ANZSES, 21 Dec 1992–10 Jan 1993; S39863, 1♂, Eungella, Pease's Lkt, 21°07'S 148°31"E, 900 m, D. Cook & GBM, 17 Nov 1992–Apr 1993; S39866, 2♀♀, S39899, Maalan Rd, 2 km S Palmerston Hwy, 17°36'S 145°42"E, 750 m, GBM & J. Hasenpusch, 10 Jan–7 Mar 1995; S39870, 1♀, Wongabel SF, 17°19'30"S 145°29'45"E, R. Raven, P. & E. Lawless & M. Shaw, 23 Jul–26 Nov 1992; S39872, 2♀♀, Longlands Gap SF, 17°27'30"S 145°28'45"E, R. Raven, P. & E. Lawless & M. Shaw, 23 Jul–26 Nov 1992; S39874, 1♀, 1♂, S39875, Karnak-Devils Thumb, 8–12 km NW Mossman, 1100 m, ANZSES, 26 Dec 1989–15 Jan 1990; S39884, 2♀♀, 4♂♂, Hughes Rd, Topaz, 17°26'S 145°42"E, 650 m, GBM & Breeden, Sep–Dec 1993; S39930, 1♂, same locality, GBM, D. Cook & H. Jantekzi, 6 Dec 1993–25 Feb 1994; S39892, 4♀♀, Kjelberg Rd turnoff, 17°32'S 145°36"E, 850 m, GBM & J. Hasenpusch, 7 Mar–15 May 1995; S39961, 2♀♀, same locality, 25 Nov 1994, 10 Jan 1995; S39896, 4♀♀, Kjelberg Rd, Mt Fisher, 17°32'S 145°33"E, 1000 m, J. Hasenpusch, 1 Dec 1993–25 Feb 1994; S39902, 1♀, S39962, 1♀, Big Tableland, 15°43'S 145°17"E, 740 m, ANZSES, 20 Dec 1990–8 Jan 1991; S39906, 1♀, Eungella NP, Mt William, 21°02'S 148°36"E, 1200 m, GBM,

19 Apr 1979, rf; S39924, 1♀, 1♂, Pandanus Ck, Cathu SF, 20°48'S 148°33"E, 80 m, GBM, 22 Apr 1979; S39925, 4♂♂ (Fig. 7C), 2.5 km S Mt Hartley, 15°47'S 145°19"E, L. Roberts, 8 Dec 1993–2 Feb 1994; S39927, 2♀♀, 3 juveniles, Mt Fisher, 7 km SW Millaa Millaa, 17°33'S 145°33"E, 1000 m, GBM & D.K. Yeates, 3 May 1983, rf; S39928, 3♀♀, 3♂♂, Westcott Rd, Topaz, 17°25'S 145°42"E, 680 m, GBM, Jul–Dec 1993; S39940, 1♀, 2 km SE Mt Spurgeon via Mt Carbine, 16°27'S 145°12"E, 1100 m, GBM & G. Thompson, 20 Dec 1988, rf; S39946, 1♂, 2 juveniles, Mt Bartle-Frere, W base, 17°23'S 145°46"E, 700 m, GBM & J. Hasenpusch, 25 Nov 1994–10 Jan 1995; S39947, 2♀♀, 1♂, Lamins Hill, 17°22'S 145°42"E, 880 m, GBM & J. Hasenpusch, 1 Dec 1993–25 Feb 1994; S39954, 1♀, Eungella NP, Broken R, 21°10'S 148°30'30"E, P. Lawless, R. Raven & M. Shaw, 10 Nov 1991–29 Jul 1992; S39955, 1♀, same locality, 29 Jul–4 Dec 1992; S39956, 1♀, Maalan SF, 17°35'30"S 145°36'45"E, R. Raven, P. & E. Lawless & M. Shaw, 25 Jul–26 Nov 1992; S39967, 1♀, 1.5 km SE Mt William, 21°02'S 148°37"E, 1060 m, ANZSES, 21 Dec 1992–10 Jan 1993; S39973, 1♀, Maalan SF, V.E. Davies & R. Raven, 20–24 Apr 1978.

AUSTRALIAN MUSEUM: 1♂, Eungella NP, Broken River campsite, G.D. Edgecombe, 18 Apr 1998, rf; 1♀, KS83631, 2♂♂ (Figs. 9A,E,K–M, 10I,L, 11A,B,F,G,K), Eungella NP, Dalrymple Rd, 1.7 km and 2.9 km NE Snake Rd, G.D. Edgecombe, 21 Apr 1998, rf.

AUSTRALIAN NATIONAL INSECT COLLECTION: 2♀♀, 9 km ENE Mt Tozer (ex. Berl. 1059, 1062), 12°43'S 143°17"E, T. Weir, 10–16 Jul 1986; 2♀♀, juveniles, larval stadia LII–IV, 3 km NE Mt Webb (ex. Berl. 692, 721), 15°03'S 145°09"E, T. Weir, 1–3 Oct 1980, 3 May 1981; 1♀, 14 km W by N Hope Vale Mission (ex. Berl. 729), 15°16'S 144°59"E, A. Calder & J. Feehan, 7–10 May 1981; 2♀♀, 3♂♂, Mt Windsor Tableland (ex. Berl. 490), 16°18'S 145°05"E, 850 m, RWT, 20 Mar 1975, rf; 1♀, Mt Tiptree (ex. Berl. 1006), 17°03'S 145°37"E, B. Halliday, 13 Jul 1984, rf; 1♀, 3.2 km N Atherton (ex. Berl. 275), 17°14'S 145°29"E, J.G. Brooks, 5 May 1970, rf; 2♀♀, Mulgrave R (ex. Berl. 316), 17°15'S 145°46"E, 75 m, RWT & J. Feehan, 19 Jun 1971, rf; 1♀, Barrine NP (ex. Berl. 486), 17°16'S 145°38"E, 760 m, RWT, 21 Mar 1975, rf; 1♀, Eacham NP (ex. Berl. 484), 17°18'S 145°37"E, RWT, 23 Mar 1975, rf; 1♀, 20 km S Ravenshoe (ex. Berl. 358), 17°45'S 145°32"E, 800 m, RWT & J. Feehan, 3 Jul 1971, rf; 1♀, Paluma (ex. Berl. 207), 19°00'S 146°12"E, 810 m, E. Britton, 18 Jan 1970, rf; 3♀♀, 4♂♂, c. 3 km S Eungella (ex. Berl. 487, 488), 21°09'S 148°29"E, 780 m, RWT, 26 Mar 1975, rf; 1♀, 16 km N Eungella (ex. Berl. 493), 21°03'S 148°35"E, RWT, 13 Sep 1975.

**Distribution.** Queensland: throughout Wet Tropics, south to Eungella, north to Mt Tozer, Cape York Peninsula (Fig. 1), mostly in rainforest, 75–1200 m, mostly above 650 m.

**Description.** Length up to 24 mm; width of head shield up to 2.85 mm. Colour (based on specimens in absolute ethanol): antenna yellow to pale orange with several dark pigment spots occasionally present on dorsal side of articles in proximal third of antenna; head shield yellow with brown mottled network; tergites pale yellow to pale orange with dark (sometimes tinged with purple) mottling concentrated in longitudinal median band and near margins; dark pigment spots often present near tergal margins; maxillipedes pale orange; sternites pale yellow to pale orange with some faint purple mottling around margins; prefemur to tibia pale to moderate yellow with purple mottling, tarsi a slightly deeper orange; genital sternite and gonopods yellow.

Head shield smooth. Frontal margin with strong median notch; posterior margin transverse or weakly concave; border slightly wider posterolaterally than medially. Median furrow incised for about 1/6 length to transverse suture, shallow throughout. Antennal length 4.1–5.7 times width of head shield, usually extending back to tergite 5 (Fig. 7A); 33–40 articles, majority of specimens examined with 36; basal two articles much larger than succeeding two; relatively gradual change in length of articles along rest of antenna (Fig. 10G,H), articles 3 to 8–10 typically wider than long, gradually elongating along antenna with more

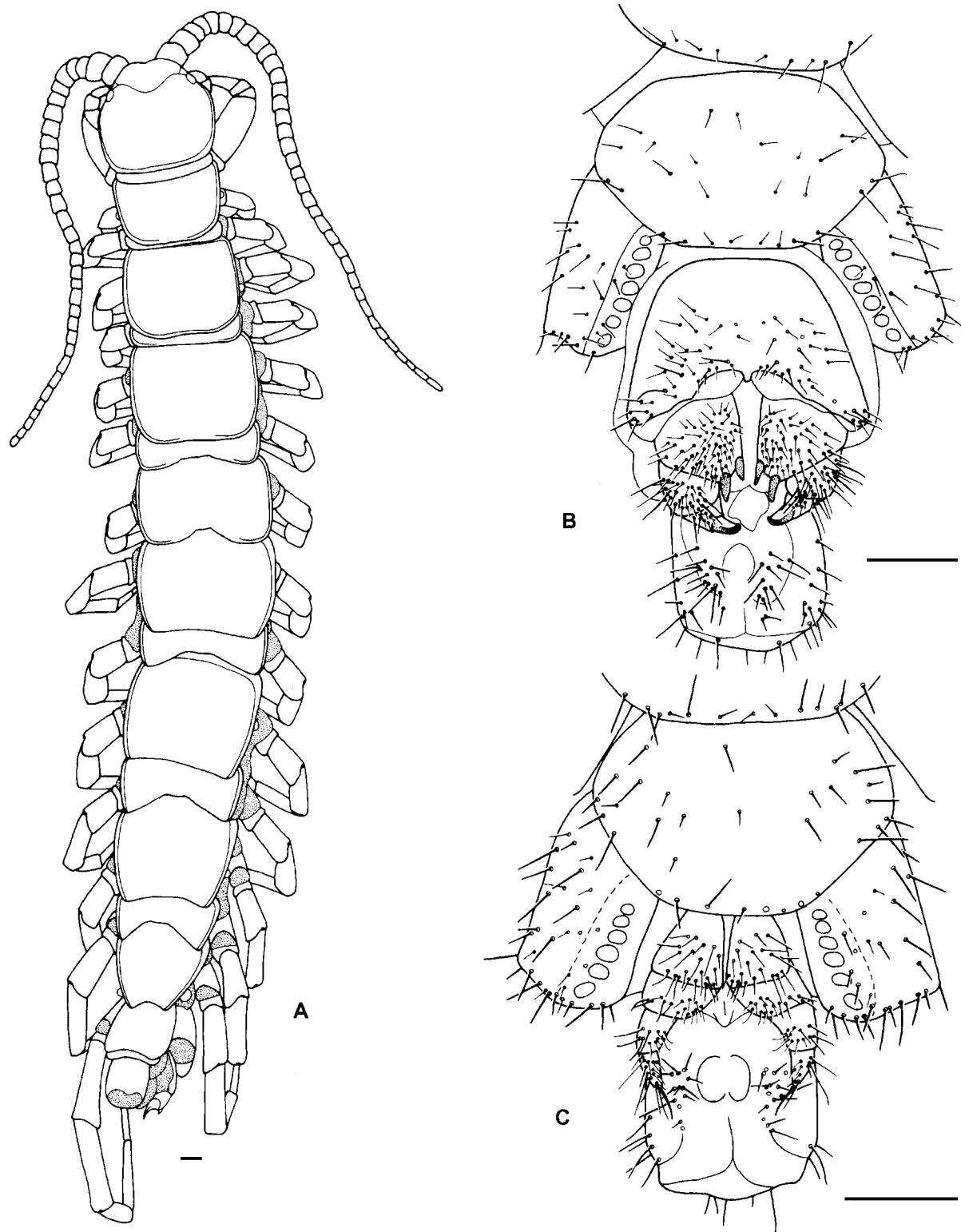


Fig. 7. *Henicops tropicanus* n.sp. (A) holotype, ♀ QM S39941, 12km WNW Mossman, QLD. (B) ♀ QM S39911, terminal segments and gonopods, Mossman Bluff camp, W Mossman, QLD. (C) ♂ QM S39925, terminal segments and gonopods, Mt Hartley, QLD. Scales 0.5 mm.

distal articles up to twice as long as wide (Fig. 10I); gradational increase in density of setae to about tenth article, then more or less constant. Ocellus moderately large, overhanging lateral margin of head (Fig. 9A), usually translucent, sometimes whitish to dark purple, domed. Tömösváry organ small, deep, longitudinally elliptical, outer edge at anterolateral margin of cephalic pleurite (Fig. 9D–F).

Small transverse seta projects medially from pit in labral sidepiece (Fig. 9C). Labral margin with rounded shoulder beside midpiece, with pronounced break in curvature where branching bristles overhang margin; fringe composed of up to 30 densely grouped bristles with many short, spine-like projections along their length, a few longer spines at distal end (Fig. 9G).

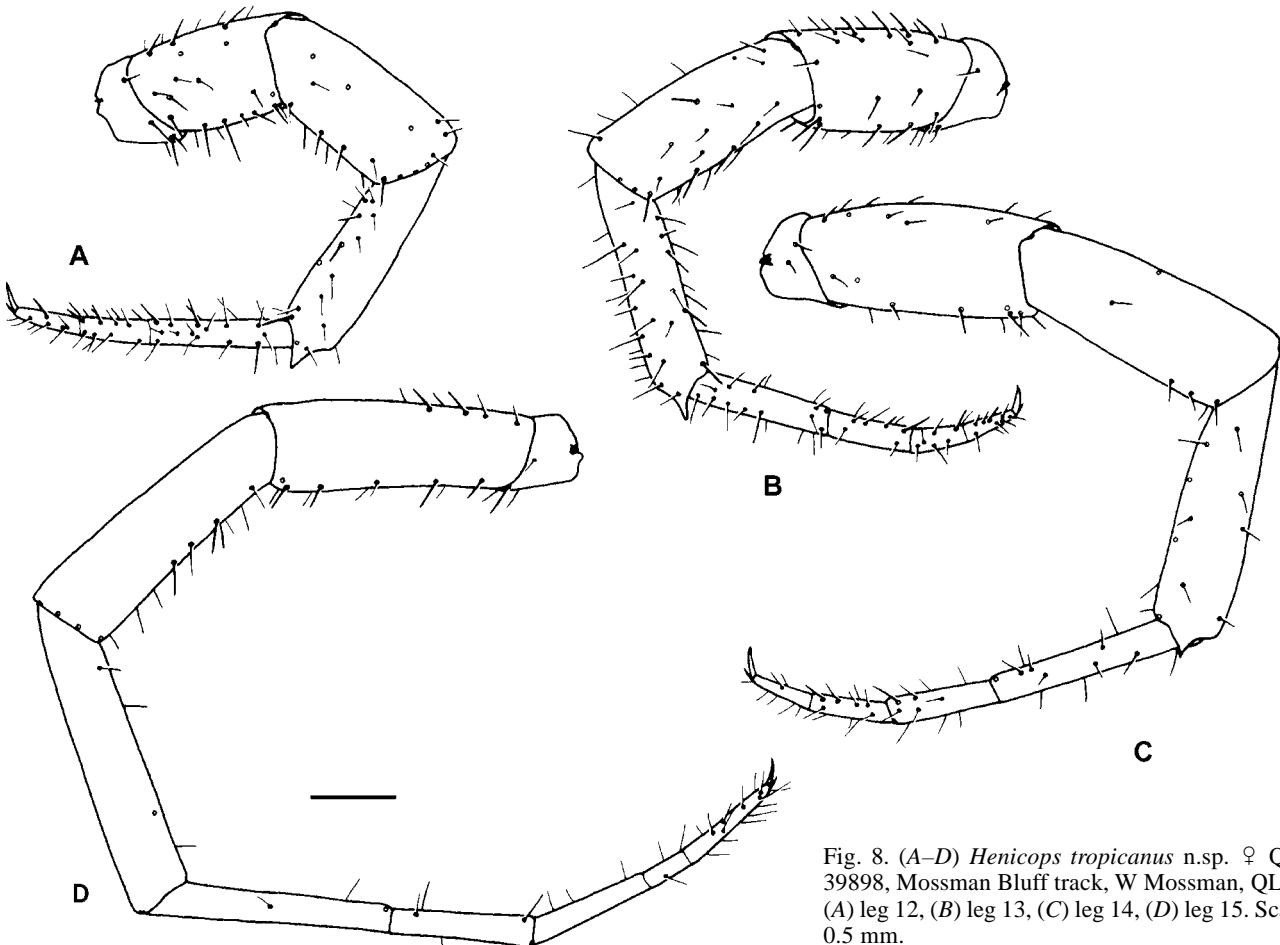


Fig. 8. (A-D) *Henicops tropicanus* n.sp. ♀ QM 39898, Mossman Bluff track, W Mossman, QLD: (A) leg 12, (B) leg 13, (C) leg 14, (D) leg 15. Scale 0.5 mm.

Maxillipede coxosternum trapezoidal to subsemicircular, dental margin broad, each half weakly convex (Fig. 9H-K); median notch lacking; teeth moderately large, triangular projections, invariably 3+3, usually with a slightly wider space between the outer tooth and middle tooth (Fig. 9K) but ranging from equidistant to space between outer and middle tooth nearly twice that between inner and middle tooth. Coxosternum bearing moderate number of large, scattered setae, usually with distinctly denser setation behind dental margin and anterolaterally (Fig. 9I,K). Tarsungulum with long, slender pretarsal section, as much as twice length of tarsal section (Fig. 9H,L). Setae on telopodite somewhat more abundant on inner part of femur, tibia and tarsal section of tarsungulum than on outer part, these setae moderately long.

Mandible: Four paired teeth on right mandible, left with smaller flattened fifth tooth adjacent to furry pad (Fig. 10A,B). Approximately 20 aciculae differentiated into two rows (Fig. 10C,D); aciculae in dorsal part of outer row with pronounced serrations on both margins along distal half, those in ventral part of outer row with a simple margin or with weak scalloping distally; aciculae of inner row with simple margin (Fig. 10C,D). Fringe of branching bristles skirts aciculae, with transition to rows of scales with multifurcating spine fringes adjacent to midpoint of the second most ventral tooth; scales gradually shortening dorsally (Fig. 10F) to terminate before reaching furry pad (Fig. 10K); ventralmost bristles in fringe narrow-based, lacking spine-like projections on basal sixth to eighth of bristle, spine-like projections abundant and even along remainder of bristle (Fig. 10E); bristles branching into a few spines distally. Accessory denticle field without grooves

between rows of denticles or at margin of denticle field (Fig. 10A,F); largest accessory denticles bluntly conical, grading into smaller triangular denticles then small elongate rods near fringe of scale-like bristles; band of unsculpted cuticle on dorsalmost tooth separates accessory denticles from furry pad; furry pad with many elongate, simple bristles (Fig. 10K), some bristles with bifid terminations.

First maxilla: Minute wedge-shaped sternite (Fig. 10L). Coxal process trapezoidal, with a few plumose setae and up to 10 simple setae on anteromedial edge (Fig. 10J), this cluster slightly separated from a few simple setae on inner edge of coxal process; plumose setae with numerous short, spine-like branches along their distal third. Cluster of about six barb-like sensilla microtrichoidea on posterolateral part of coxal process (Fig. 10J). Distal article of telopodite with two rows of about 15 plumose setae along inner margin; branches developed along distal half of these setae (Fig. 10M); shorter simple setae on membranous strip alongside inner margin; main field of distal article of telopodite bearing a few setae anteriorly.

Second maxilla: Sternite small, fused with coxae. Band of 8–11 short setae along anterior part of coxa. Tarsus bearing numerous simple setae on outer surface, cluster of many plumose setae on membranous patch on inner surface (Fig. 11D,E); branches on plumose setae mostly confined to distal half. Claw small, composed of five digits, median digit long, thick, with shorter, slender digit between median and each outer digit (Fig. 11E).

Tergites weakly wrinkled. T1 generally trapeziform, smaller than T3, slightly narrower than head shield (Fig. 7A), about 70% width of widest tergite (T8), posterior

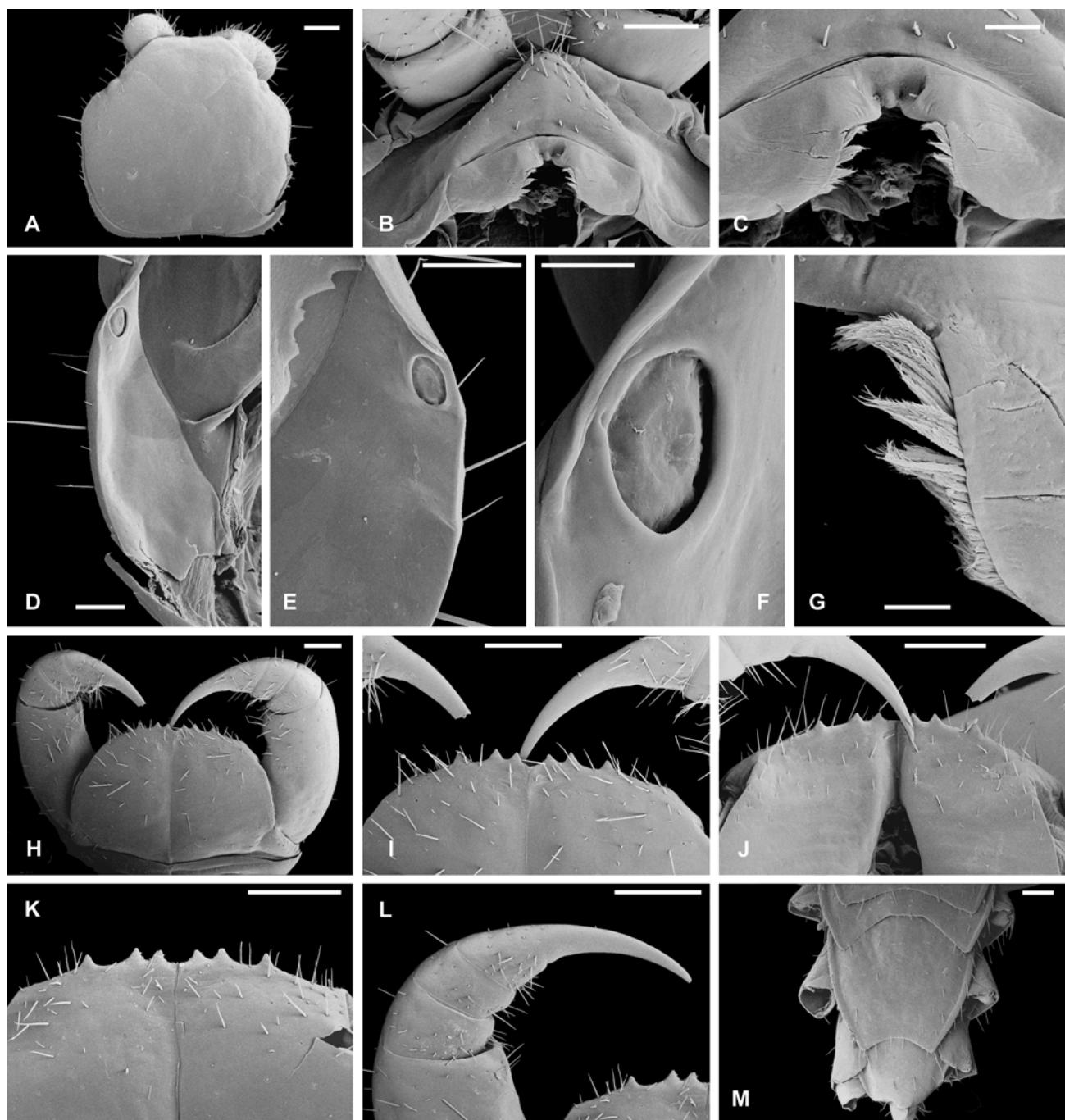


Fig. 9. *Henicops tropicanus* n.sp. (A,E,K–M) ♂ AM KS83631, Eungella NP, QLD: (A) dorsal view of head shield, scale 300 µm; (E) cephalic pleurite, scale 100 µm; (K) ventral view of maxillipede dental margin, scale 300 µm; (L) telopodite of maxillipede, scale 300 µm; (M) dorsal view of posterior tergites, scale 300 µm. (B–D,F–J) ♂ QM S39898, Mossman Bluff track, QLD: (B) ventral view of head, scale 300 µm; (C) clypeus and labrum, scale 100 µm; (D) cephalic pleurite, scale 100 µm; (F) Tömösváry organ, scale 30 µm; (G) labral margin, scale 30 µm; (H) ventral view of maxillipede, scale 300 µm; (I,J) ventral and dorsal views of maxillipede dental margin, scales 300 µm.

angles rounded, posterior margin transverse; lateral margins subparallel in T3, slightly convex in T5, posterior angles rounded in both, posterior margin faintly concave in TT3 and 5; TT1 and 3 bordered posteriorly; borders of TT5 and 7 incomplete posteriorly; posterior margin of T7 with transverse or convex medial sector, having independent curvature from lateral sectors, posterior angles gently triangular, rounded; lateral margins of TT4–14 convex, all bordered laterally; posterior margin of T8 weakly concave,

posterior angle blunt, TT10 and 12 posterior margins gently concave, posterior angles with obtuse, blunt corners; TT6, 9, 11 and 13 embayed with transverse posteromedial third, posterior angle of T6 rounded, T9 blunt, TT11 and 13 with sharp triangular projections; posterior margin of T14 concave, with blunt posterior angles.

Short to moderate, slender setae along lateral borders of all tergites, often with 3–5 longer, thicker setae concentrated on anterolateral border; often cluster of several short setae

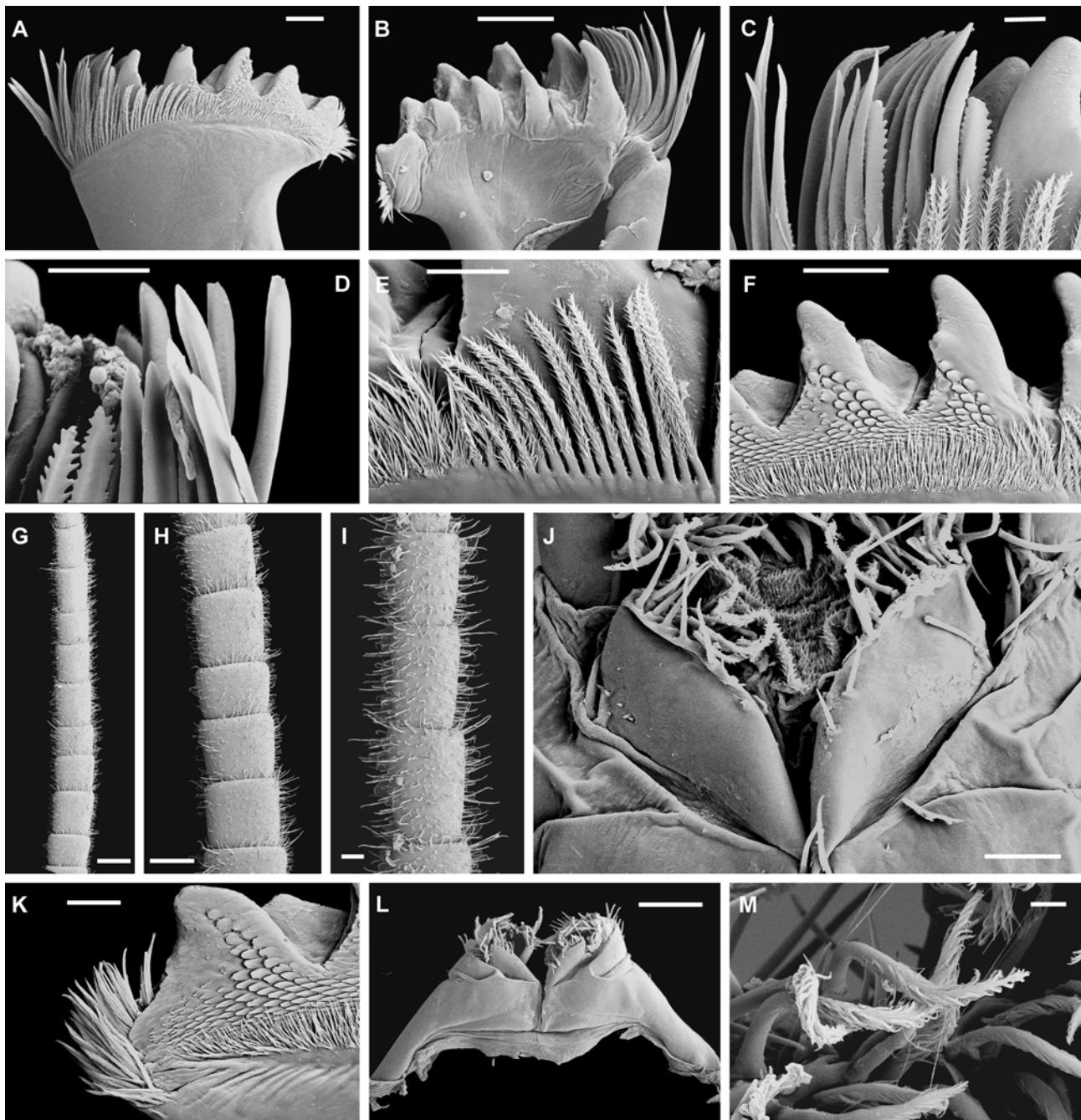


Fig. 10. *Henicops tropicanus* n.sp. (A–C,G–H,J,M) ♂ QM S39898, Mossman Bluff track, QLD: (A,B) outer (anterior) and inner (posterior) views of gnathal edge of left mandible, scale 50 µm; (C) mandibular aciculae, scale 15 µm; (G,H) antennal articles, scales 200 µm, 150 µm; (J) coxal processes of first maxillae, scale 50 µm; (M) plumose setae on inner margin of first maxillary telopodite, scale 10 µm. (D–F,K) ♀ QM S39898, right mandible: (D) aciculae, scale 30 µm; (E) fringe of branching bristles, scale 30 µm; (F) teeth, showing accessory denticles, and fringe of branching bristles, scale 50 µm; (K) dorsal tooth and furry pad, scale 30 µm. (I,L) ♂ AM KS83631, Eungella NP, QLD: (I) antennal articles, scale 100 µm; (L) first maxillae, scale 150 µm.

on posterior angles of tergites; few short, slender setae scattered sparsely over surface of most tergites. A few moderate to long setae on margins of sternites, 1–3 setae at anterolateral corner most prominent anteriorly in trunk; setae along posterolateral and posterior margins more prominent in posterior segments; posterior margin fringed by 6–10 setae on sternites 13–15; consistently strong pair of setae on anteromedial part of sternites.

Legs: Strong, pointed distal projections with sclerotized tips on tibiae of legs 1–14. Prefemur of legs 1–13 with short to moderate setae scattered on anterior and posterior faces,

some longer, thicker setae on ventral edge of prefemur, femur and tibia; longest setae on femur and tibia equal to (Fig. 8B) or shorter than (Fig. 8A) longest on prefemur; a few thickened setae encircling distal margin of femur; strong, pigmented seta at ventrodistal end of tibia on anterior face of legs 1–13; tarsus with combination of slender setae of fairly even length, and four pairs of thicker, divergent, pigmented setae on ventral side of legs 1–13 (Fig. 11K), two of these just proximal to articulations between tarsomeres, one near midlength of distal tarsomere. Setae on legs 14 and 15 more uniformly slender and sparsely

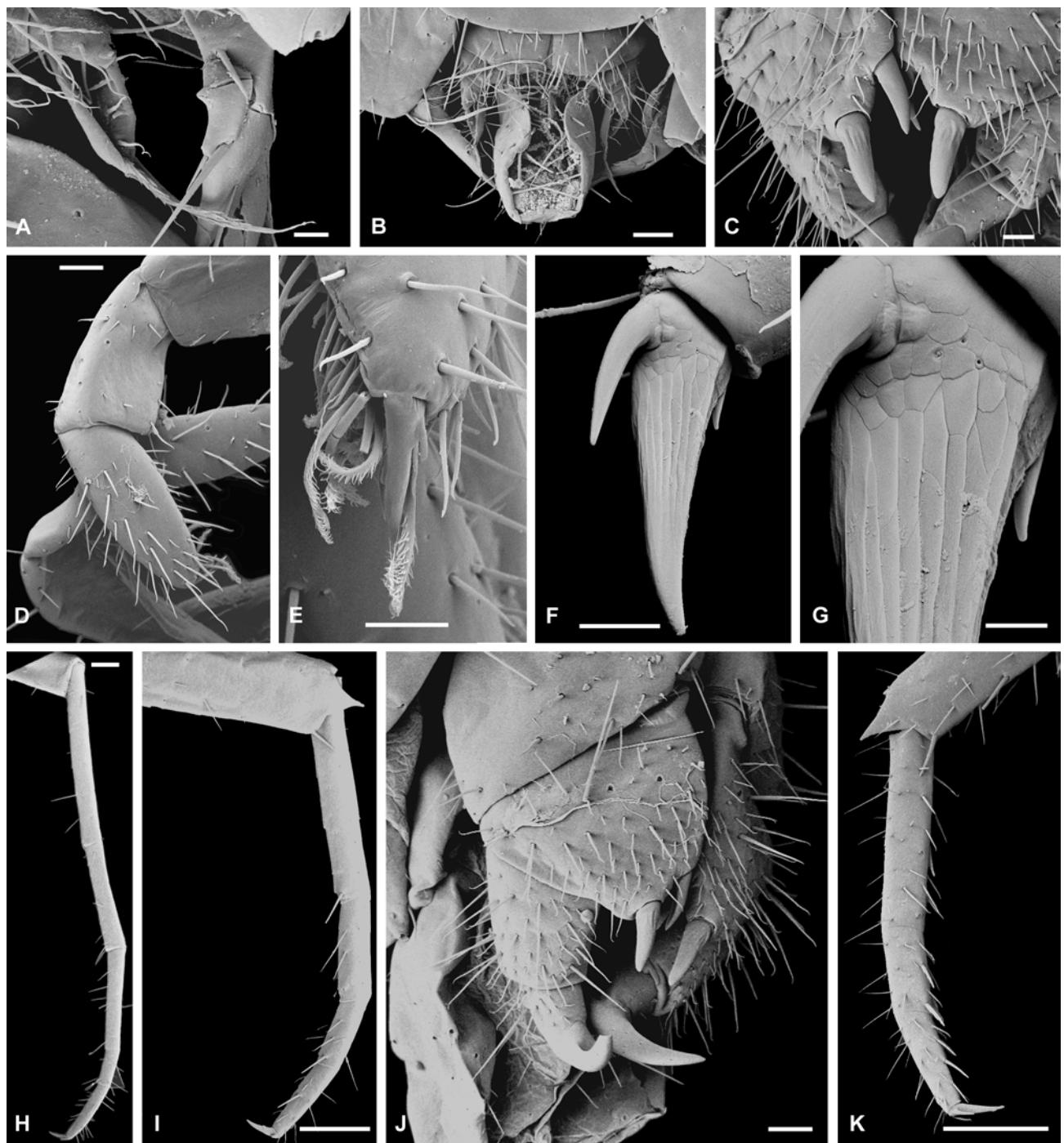


Fig. 11. *Henicops tropicanus* n.sp. (A,B,FG,K) ♂ AM KS83631, Eungella NP, QLD: (A) terminal process of ♂ gonopod, scale 30 µm; (B) ventral view of terminal segments and gonopods, scale 100 µm; (F,G) anteroventral views of pretarsus of leg 14, scales 30 µm, 10 µm; (K) tibia, tarsus and pretarsus of leg 12, scale 100 µm. (C,H,J) ♀ QM S39898, Mossman Bluff track, QLD: (C) gonopods, scale 50 µm; (H) tarsus and pretarsus of leg 15, scale 300 µm; (J) ventrolateral view of gonopods, scale 100 µm. (D,E,I) ♂ QM S39898, Mossman Bluff track, QLD: (D,E) distal part and claw of second maxilla, scales 100 µm, 50 µm; (I) tibia, tarsus and pretarsus of leg 13, scale 300 µm.

distributed than on preceding legs, especially sparse on tibia and basitarsus of leg 15. Three tarsomeres in legs 1–12 (Fig. 8A), with divided basitarsus. Condyle at joint between basitarsus and distitarsus on legs 13–15 only. Four tarsomeres in legs 13 and 14, basitarsus and distitarsus with two parts each (Figs. 8B,C, 11I); proximal tarsomere nearly 70% length of basitarsus and 55–60% length of distitarsus on leg 14. Leg 15 with five tarsomeres, basitarsus having two, distitarsus three (Figs. 8D, 11H). Distitarsus 70–80%

length of basitarsus on leg 15; basitarsus 12–14 times longer than broad; proximal tarsomere 55–65% length of basitarsus; three tarsomeres comprise about 45–50, 15–20 and 30–40% (proximal to distal) length of distitarsus. Pretarsal claws (Fig. 11F,G) as described below for *H. milledgei*.

Coxal pores round or ovate (Fig. 7B,C), commonly 5,6,6,6/5,6,6,6 in large males and females, males maximum 5,6,6,6/5,6,6,6, minimum 3,4,4,4/3,4,4,4; females maximum 7,7,7,7/7,7,7,7, minimum 3,4,5,5/3,4,5,5. Coxal

pore field set in shallow groove, distal pore(s) partly concealed by anteroventral face of coxa. Anal pores large in both sexes.

Female (Fig. 7B): Sternite of segment 15 transverse or convex posteromedially. Tergites of first genital segment and telson usually well sclerotized. Sternite of first genital segment large, posterior margin concave between condyles of gonopods except for small median projection, posterior two-thirds fairly evenly scattered with setae of varied length; short setae concentrated in a band along posteromedial margin. First article of gonopod bearing two (three in one specimen) large, bullet-shaped spurs, inner spur slightly smaller than outer; spurs gently curved such that tip points up (Fig. 11C,J); first and second articles of gonopod with mix of many short, moderate and long setae, up to 56 on first article, up to 37 on second; third article with up to 10 setae, mostly moderate, one or two long ones (Fig. 11J). Claw large, undivided.

Male (Fig. 7C): Sternite of segment 15 rounded posteriorly. Sternite of first genital segment small, divided, with transverse posterior margin, bearing numerous moderately long setae, short setae concentrated in a band near posterior margin (Fig. 11B). Gonopod of three articles and tapering, seta-like terminal process that bears many short spine-like projections (Fig. 11A), the three articles each bearing numerous short to moderately long setae, typically about 15, 10–12 and 10 for first to third articles, respectively; extended penis approximately equal in length to first article of gonopod.

Larval stadia (identified by correspondence to leg and limb-bud pairs in *Lamyctes emarginatus*: Andersson, 1979, 1984) (ANIC Berl. 1062): Stadium LII with 8 pairs of legs and two pairs of limb-buds; 14 antennal articles. Stadium LIII with 10 pairs of legs and two pairs of limb-buds; 25 antennal articles. Stadium LIII with 12 pairs of legs and three pairs of limb-buds; 25 antennal articles. Stadia LII–IV all with 3+3 teeth on dental margin of maxillipede coxosternum.

**Discussion.** As discussed above under the *Henicops dentatus* Group, *H. dentatus* and *H. tropicanus* n.sp. share numerous characters distinguishing them from other species of *Henicops*, and they appear to be sister taxa. In spite of their geographic separation, the two species are remarkably similar. They can consistently and most readily be distinguished by the morphology of the female gonopod, in particular the size and shape of the spurs on the basal article. *Henicops dentatus* has two, small bullet-shaped (Fig. 6G) or distally-truncated (Figs. 4F, 6H) spurs, with the outer spur as much as 40% longer and 50% wider than the inner spur. In contrast, the gonopods of *H. tropicanus* (Figs. 7B, 11C) bear spurs that are larger and more elongate (with the outer spur of *H. tropicanus* being approximately 40% the length of the inner margin of the first article of the gonopod, compared to approximately 20% in *H. dentatus*) and both spurs are of more nearly equal size. Though the shape of the spurs varies within *H. dentatus*, they are consistently shorter and stouter than in *H. tropicanus*. In contrast to the distinction made possible by the female gonopods, the male gonopods of the three species of *Henicops* treated herein (Figs. 4C, 7C, 12C) provide no obvious characters for specific distinction.

Two features of the mandibular gnathal edge permit distinction between *Henicops tropicanus* and *H. dentatus*. The Western Australian *H. dentatus* has a narrower fringe of branching bristles on the dorsal part of the mandible (Figs. 5D,I versus 10F), this including the entire row of scale-like bristles. As well, the branching bristles on the ventral part

of the fringe have a longer non-spinose (basal) extent (Fig. 5H versus 10E). In both of these characters, the state in *H. tropicanus* is plesiomorphic, being shared with *H. maculatus* (Edgecombe *et al.*, 2002: figs. 4A, 5C), *H. milledgei* (Fig. 14H), *H. breviliabiatus* (Fig. 2A,B,D) and outgroups.

Specimens of *Henicops tropicanus* often have a narrower medial sector to “notched” tergites 7, 9 and 11 than does *H. dentatus* (compare Fig. 3 with Fig. 7A) but this difference is inconsistent. Setation of legs 14 and 15 often also serves to distinguish between the two species: *H. tropicanus* typically has fewer setae on legs 14 and 15 (Fig. 8C,D) than *H. dentatus* (Figs. 4C,D), most notably on the tibia and basitarsus of leg 15 (Fig. 11H), and has gracile setae on the prefemur of leg 15 versus sometimes spine-like setae in *H. dentatus*.

*Henicops tropicanus* normally has two spurs on the female gonopod, only one specimen (QM S38899) having three spurs. Three-spur variants are also exceptional in other members of the Henicopinae. For example, specimens of *Lamyctes mauriesi* Demange, 1981, are recorded as normally having two conical spurs on each gonopod, but single specimens from Tenerife and Gran Canaria have two such spurs on one gonopod and three on the other (Eason & Enghoff, 1992).

### *Henicops milledgei* n.sp.

Figs. 12–16

**Etymology.** For Graham Milledge, who collected this species throughout most of its range.

**Type material.** HOLOTYPE: MV NOH-2207, ♀ (Fig. 12A), Strzelecki Ra, Tarra-Bulga NP, VIC, 0.5 km NNE Tarra Valley Picnic Area, 38°26'40"S 146°32'30"E, *Nothofagus cunninghamii* forest, G.A. Milledge, 14 Nov 1995–10 Jan 1996. PARATYPES: NOH-2208, 1♀, 3♂, from type locality, 10 Jan–5 Mar 1996; NOH-2209, 1♀, 1♂, type locality, 5 Mar–7 Mar 1995; NOH-2211, 1♀, 1♂, Tarra-Bulga NP, 0.2 km W Tarra Valley Picnic Area, 38°27'S 146°32"E, 14 Sep–14 Nov 1995; NOH-2212, 1♂, same locality, 14 Nov 1995–10 Jan 1996; NOH-2213, 1♂, same locality, 14 Nov 1995–10 Jan 1996; NOH-2214, 1♀, 3♂, same locality, 10 Jan–5 Mar 1996; NOH-2215, 1♂, same locality, 7 May–16 Jul 1996; NOH-2220, 1♀, 2♂, same locality, 5 Mar–7 May 1996; NOH-2217, 1♀, Tarra-Bulga NP, Bulga Picnic Area, 38°25'30"S 146°34'20"E, 14 Nov 1995–10 Jan 1996; NOH-2218, 1♂, same locality, 10 Jan–5 Mar 1996; NOH-2219, 2♀, 1♂, same locality, 5 Mar–7 May 1996.

**Other material.** VICTORIA: MV: OTWAY RA, leg. G.A. Milledge: NOH-1045, 2♀, 1♂, Philips Track, 0.5 km N Triplet Falls, 38°40'S 143°29"E, 6 Sep–15 Nov 1994; NOH-1046, 1♀, 1♂, same locality, 15 Nov 1994–31 Jan 1995; NOH-1047, 3♀, same locality, 31 Jan–11 Apr 1995; NOH-1048, 1♂, same locality, 11 Apr–14 Jun 1995; NOH-1049, 1♀, same locality, 14 Jun–29 Aug 1995; NOH-1050, 2♀, 2♂, Young Creek Rd, 0.4 km NW Triplet Falls, 38°40'S 143°29"E, 6 Sep–15 Nov 1994; NOH-1052, 7♀, 3♂, same locality, 15 Nov 1994–31 Jan 1995; NOH-1053, 1♀, same locality, 31 Jan–11 Apr 1995; NOH-1054, 3♀, same locality, 11 Apr–14 Jun 1995; NOH-1055, 3♀, 1♂, Young Creek Rd, 0.2 km NE Ciancio Ck Crossing, 38°40'S 143°29"E, 6 Sep–15 Nov 1994; NOH-1056, 1♀, same locality, 15 Nov 1994–31 Jan 1995; NOH-1058, 2♀, 1♂, 31 Jan–11 Apr 1995; NOH-1059, 1♀ (Figs. 14K,L, 16G–J), 2♂, same locality, 11 Apr–4 Jun 1995; NOH-1060, 1♂, Aire Crossing Tk, 0.5 km N Aire R. Crossing, 38°40'S 143°29"E, 6 Sep–15 Nov 1994; NOH-1061, 2♂, Beauchamp Falls, 38°39'S 143°36"E, 6 Sep–15 Nov 1994; NOH-1062, 7♀, 1♂, same locality, 15 Nov 1994–31 Jan 1995; MV NOH-1063, 8♀, 1♂, same locality, 31 Jan–11 Apr 1995.

CENTRAL HIGHLANDS, leg. G.A. Milledge: NOH-1778, 1 larval stadium LII, 2 larval stadia LIII, Cement Creek Reserve, 2.2 km ESE Mt Donna Buang, 37°43'S 144°42'15"E, 13 Dec 1994; NOH-1779, 2♀, 1♂ (Figs. 14B,C,H–J, 15B,D,E,G,L,M, 16A,D–F,K,L), same locality, 29 Nov 1994–20 Jan 1995; NOH-1784, 3♀, same locality, 21 Jan–7 Apr 1995; MV NOH-1782, 4♀ (Fig. 12B), 4♂, 1 larval stadium LII, Donna

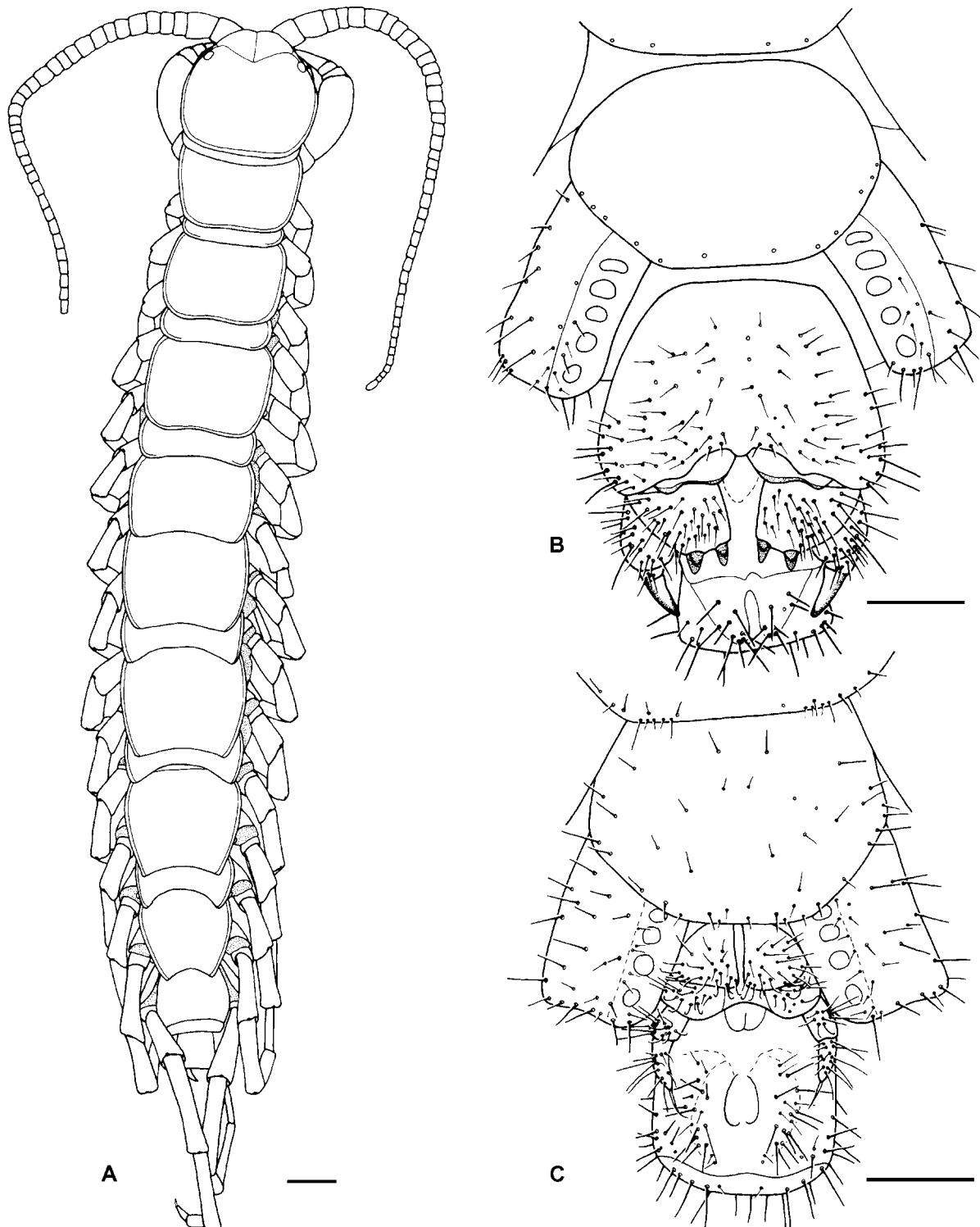


Fig. 12. *Henicops milledgei* n.sp. (A) holotype ♀ MV NOH-2207, dorsal view, Tarra-Bulga NP, Strzelecki Ranges, VIC. (B) ♀ MV NOH-1782, terminal segments and gonopods, 1km SW Mt Donna Buang, Central Highlands, VIC. (C) ♂ MV NOH-1792, terminal segments and gonopods, Acheron Gap, Central Highlands, VIC. Scales 0.5 mm.

Buang Rd, 1 km SW Mt Donna Buang, 37°43'S 144°40'E, 29 Nov 1994–20 Jan 1995; NOH-1783, 6♀♀, 1♂, same locality, 21 Jan–7 Apr 1996; NOH-1786, 2♀♀, 2♂♂, 1 larval stadium LII, Myrtle Gully Reserve, 3.4 km WSW Mt Donna Buang, 37°43'S 144°38'30"E, 29 Nov 1994–20 Jan 1995; NOH-1787, 5♀♀, 3♂♂, same locality, 21 Jan–7 Apr 1995; NOH-1788, 1♀, Road 26, 0.2 km WNW Donna Buang Rd junct., 37°43'S 144°39'30"E, 16 Feb 1995; NOH-1790, 1♀, Acheron Gap, 6 km NE Mt Donna Buang, 37°40'43"S 144°44'20"E, 20 Feb 1996; NOH-1792, 2♂♂ (Fig. 12C), same locality, 26 Oct–28 Dec 1995; NOH-1793, 2♀♀, same locality, 28 Dec 1995; NOH-1794, 4♀♀, same locality, 21 Feb–23 Apr

1996; NOH-1795, 1♀, same locality, 23 Apr–25 Jun 1996; NOH-1796, 2♀♀, 2♂♂, 0.7 km N Acheron Gap, 7 km NE Mt Donna Buang, 37°40'17"S 144°44'20"E, 21 Feb–23 Apr 1996; NOH-1797, 4♂♂, same locality, 28 Dec 1995–21 Feb 1996; NOH-1800, 1 larval stadium LIII, The Big Culvert, 2.5 km ENE Mt Observation, 37°33'36"S 145°52'15"E, 28 Dec 1995.

STRZELECKI RA, leg. G.A. Milledge: NOH-2222, 1 larval stadium LIII, Tarra-Bulga NP, Bulga Picnic Area, 38°25'30"S 146°34'20"E, 7 May–16 Jul 1996; NOH-2225, 1♀ (Fig. 13A–D), 2♂♂, Gunyah-Toora Rd, 2 km SSW Gunyah Gunyah, 38°32'30"S 146°19'E, 14 Nov 1995–10 Jan

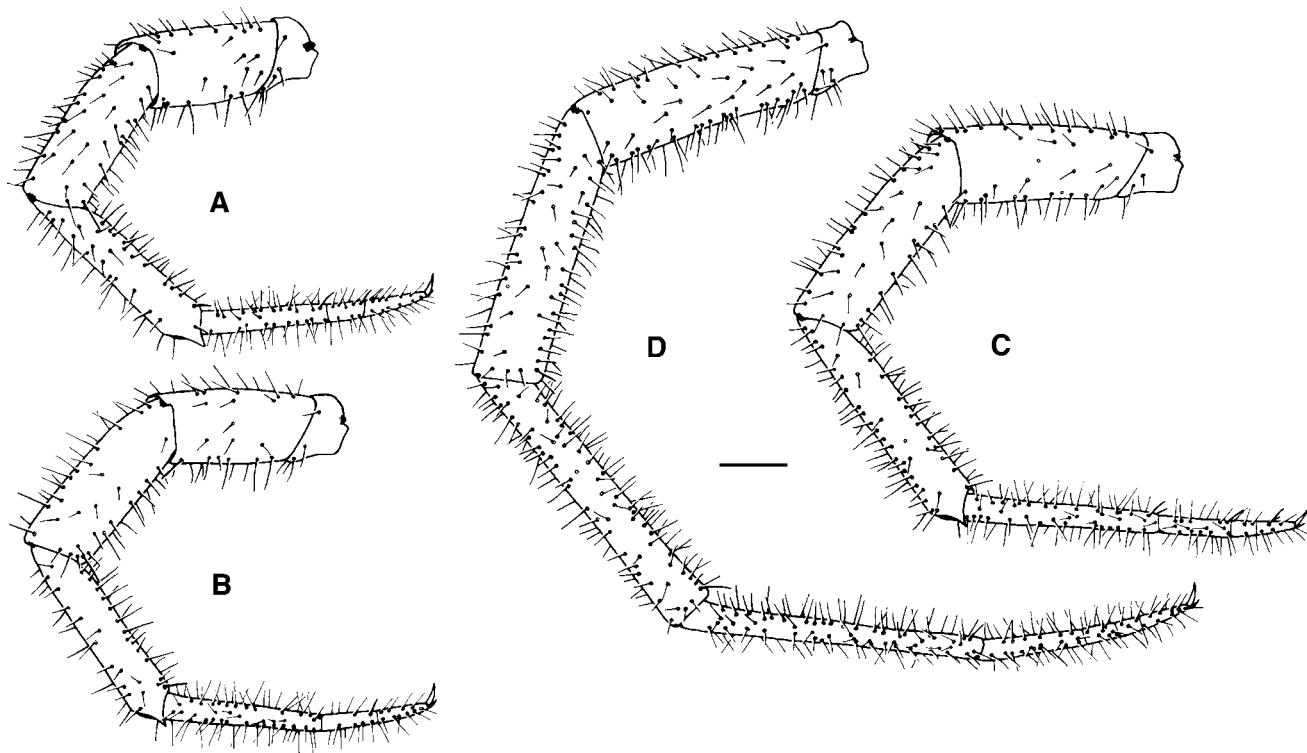


Fig. 13. *Henicops milledgei* n.sp. ♀ MV NOH-2225, Mt Donna Buang, Strzelecki Ranges, VIC: (A) leg 12, (B) leg 13, (C) leg 14, (D) leg 15. Scale 0.5 mm.

1996; NOH-2227, 1♀, Jeeralang West Rd, 0.1 km N Binns Hill Junction, 38°26'30"S 146°29"E, 10 Jan–5 Mar 1996.

AUSTRALIAN MUSEUM: KS35864, 1♀, Otway Ra, 38°27'S 143°58"E, A. Frazer, Aug 1979; KS35869, 1♂, Otway Ra, Lavers Hill, 38°41'S 143°24"E, A. Frazer, 24 Feb 1979; KS83632, 1♀, Otway NP, Sandy Ridge, Spur Road, 38°46.12"S 143°32.9"E, 278 m, G. Cassis *et al.*, 9 Nov 2002; KS83633, 2♀ (Figs. 14A,D–G, 15A,C,H,K, 16B,C), Grampians NP, Wonderland Range, Silverband Rd, 1.2 km S Rosea Campground, 37°10'28"S 142°30'29"E, G.D. Edgecombe & Z. Johanson, 15 Feb 2000, fern gully.

**Distribution.** Victoria: Otway Ranges, Strzelecki Ranges, Central Highlands, mostly from *Nothofagus cunninghamii* forest; Grampians, sclerophyll forest (Fig. 1).

**Diagnosis.** *Henicops* with 36–43 (most commonly 40 or 41) antennal articles. Uneven change in length of articles in proximal part of antenna, with short paired articles interspersed between longer articles; T7 with rounded, concave margin; Tömösváry organ small and weak, centrally located on cephalic pleurite; groove in accessory denticle field pronounced on mandibular teeth; female gonopod with two moderately large, bullet-shaped spurs (shared with *H. maculatus*). Mandibular aciculae differentiated into outer row with serrated margins and inner row with mostly simple margins; branching bristles of mandible with sparse spine-like branches on basal part of bristle (shared with *H. dentatus* Group). Uniquely: 3+3 moderate sized teeth on maxillipede coxosternum, with space between outer and middle teeth invariably more than twice the space between inner two teeth; three tarsomeres in leg 13, four in leg 14, five in leg 15, basitarsus undivided in legs 13–15; proximal coxal pores elliptical, distal pores round.

**Description.** Length up to 28 mm; width of head shield up to 3.3 mm. Colour (based on specimens in absolute ethanol): antenna dark orange, with dark pigment spots usually present, especially on dorsal side and proximally but also

common on ventral side of antenna and more distally; head shield dark orange with chestnut mottled network; tergites dark orange with dark mottling covering most of tergite, concentrated in longitudinal median band and near margins, and dark pigment spots concentrated on margins; maxillipedes orange; sternites pale orange with purple mottling around margins, becoming more concentrated in the three posterior sternites; prefemur to tibia pale to moderate yellow with purple mottling; tarsi pale to moderate yellow; genital sternite and gonopods orange with faint purple mottling on genital sternite.

Head shield smooth. Frontal margin with strong median notch and short median furrow; posterior margin transverse; border very slightly wider posterolaterally than postero-medially. Antennal length 3.1–4.7 times width of head shield, usually extending back to tergite 5 (Fig. 12A); 36–43 articles, commonly 40 or 41; basal two articles much larger than succeeding two (Fig. 14A); antenna with a markedly uneven change in the length of articles in proximal part, with short paired articles interspersed between longer articles (Fig. 14B); articles mostly substantially longer than wide in distal half of antenna; antenna densely setose along most of length, with many short, curved sensilla interspersed with long trichoid sensilla (Fig. 14C). Ocellus moderately large, overhanging lateral margin of head, usually translucent, whitish to dark purple, domed. Tömösváry organ small, fairly shallow, longitudinally elliptical, situated inward of anterolateral margin of cephalic pleurite (Fig. 15D,E).

Clypeus with transverse band of six setae medially just in front of labrum (Fig. 15B), cluster of 10 setae at clypeal apex (Fig. 15A). Labral margin with rounded shoulder beside midpiece, with gradual break in curvature where fringe of branching bristles overhangs margin (Fig. 15B); most bristles with short, spine-like projections along their length, some branching into long, slender spines distally (Fig. 15C).

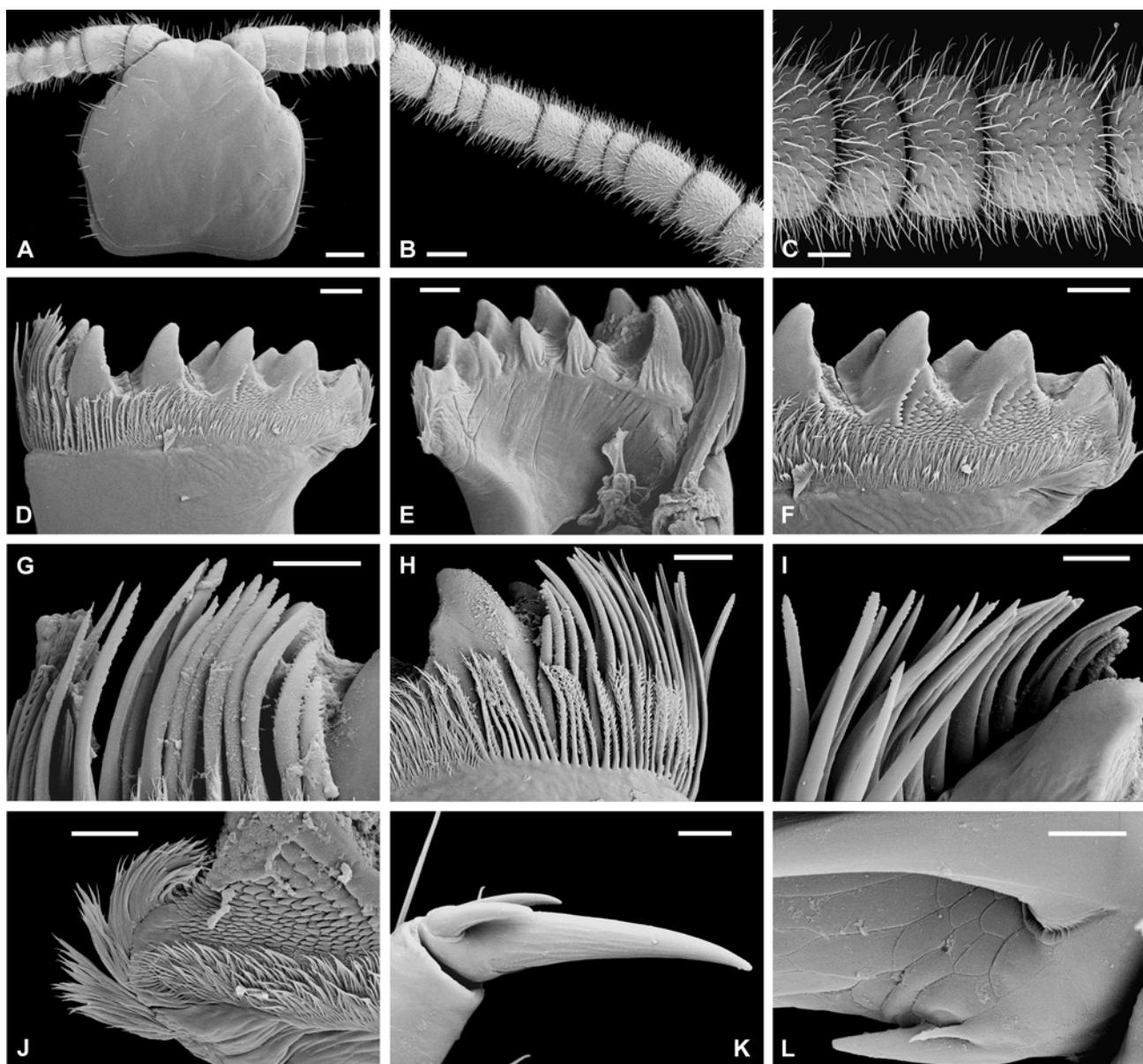


Fig. 14. *Henicops milledgei* n.sp. (A,D–G) ♀ AM KS83633, Grampians NP, VIC: (A) dorsal view of head shield, scale 100 µm; (D,E) outer (anterior) and inner (posterior) views of gnathal edge of left mandible, scales 10 µm; (F) mandibular teeth, scale 10 µm; (G) aciculae, scale 30 µm. (B,C,H–J) ♂ MV NOH-1779, Cement Creek Reserve, Central Highlands, VIC: (B,C) antennal articles, scales 30 µm, 10 µm; (H) aciculae and fringe of branching bristles of mandible, scale 50 µm; (I) inner (posterior) view of mandibular aciculae, scale 30 µm; (J) accessory denticles and furry pad of mandible, scale 30 µm. (K,L) ♀ MV NOH-1059, Otway Range, VIC: (K) anterior view of pretarsus of leg 12, scale 30 µm; (L) posterior view of pretarsus of leg 12, scale 10 µm.

Maxillipede coxosternum trapezoidal to subsemicircular, dental margin broad, each half gently convex (Fig. 16A,B); median notch at most narrow, shallow (Fig. 16D); teeth small, triangular projections, invariably 3+3, with space between outer tooth and adjacent tooth more than twice space between inner two teeth (Fig. 16C–E), inner tooth smaller than the others. Coxosternum bearing moderate number of small to moderate sized setae (Fig. 16D), mostly confined to anterior half of coxosternum (Fig. 16A,B). Tarsungulum with long, slender pretarsal section (Fig. 16A,B). Setae on telopodite denser on inner part of femur, tibia and tarsal section of tarsungulum than on outer part, especially long on tarsungulum (Fig. 16C).

Mandible as described for *H. tropicanus* except for the following: ventral aciculae in outer row of aciculae with

both margins serrated along their distal fifth to third (Fig. 14G,I); grooved ridge on accessory denticle field of all but ventralmost paired tooth (Fig. 14D,F); ventral bristles in fringe of branching bristles lacking spine-like projections on basal fifth of bristles (Fig. 14H); fringe of scale-like branching bristles extends to furry pad (Fig. 14J); bristles of furry pad curved towards dorsalmost tooth (Fig. 14F,J).

First maxilla (Fig. 15H–J) as described for *H. tropicanus* except: coxal process with a few short simple setae, several laciniate and plumose setae with intermediates between these (some with a few terminal spines, others with numerous short, slender projections along their distal halves) (Fig. 15J); distal article of telopodite with several simple setae scattered over its main field (Fig. 15I). Second maxilla (Fig. 15K–M) as described for *H. tropicanus*.

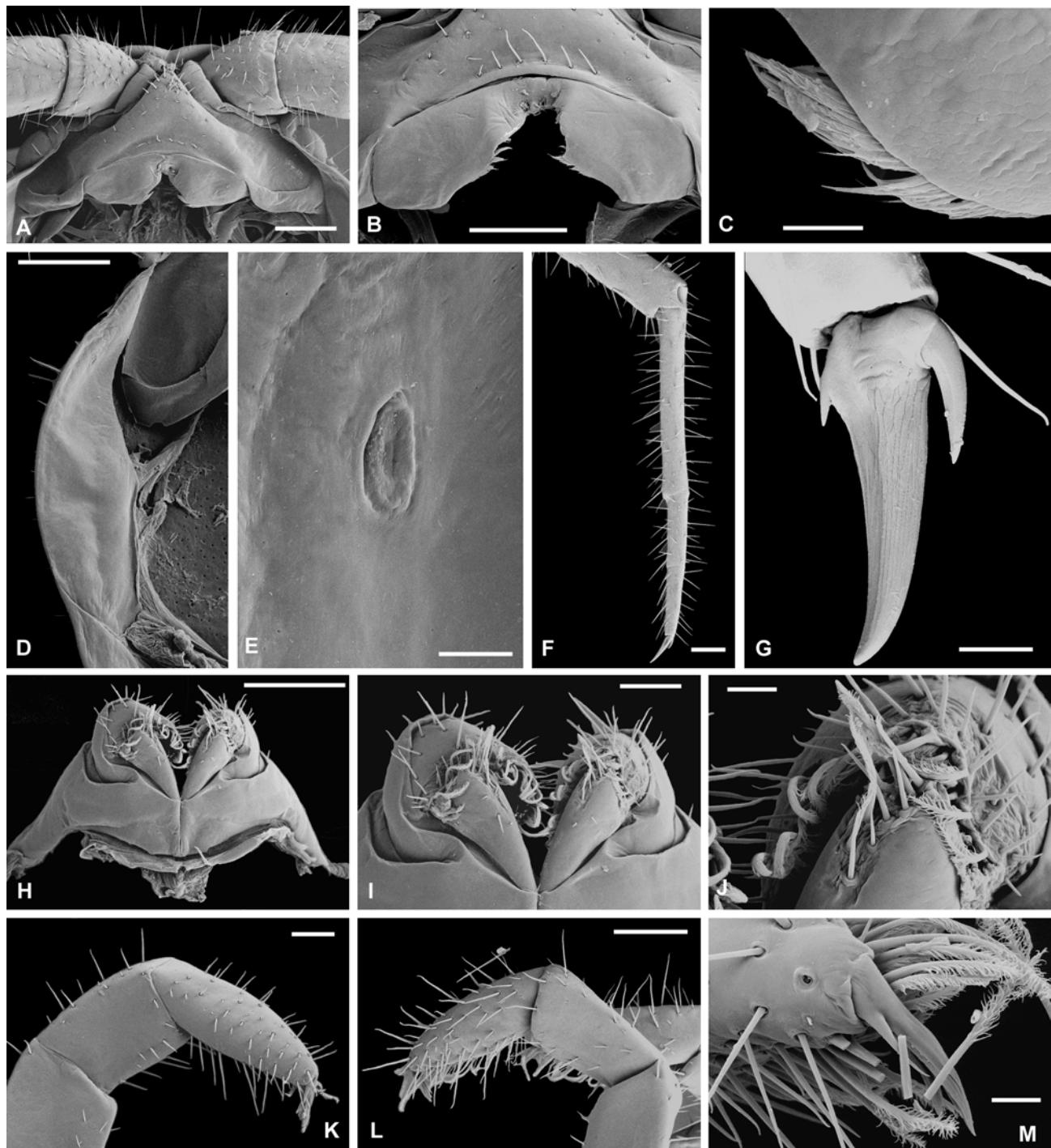


Fig. 15. *Henicops milledgei* n.sp. (A,C,H–K) ♀ AM KS83633, Grampians NP, VIC: (A) ventral view of head, scale 300 µm; (C) labral margin, scale 30 µm; (H) first maxillae, scale 300 µm; (I) coxal processes and telopodites of first maxillae, scale 100 µm; (J) setae on coxal process of first maxilla, scale 30 µm; (K) distal part of telopodite of second maxilla, scale 100 µm. (B,D,E,G,L,M) ♂ MV NOH-1779, Cement Creek Reserve, Central Highlands, VIC: (B) clypeus and labrum, scale 300 µm; (D) cephalic pleurite, scale 300 µm; (E) Tömösváry organ, scale 30 µm; (G) ventral view of pretarsus of leg 15, scale 100 µm; (L) distal part of telopodite of second maxilla, scale 200 µm; (M) tarsus and claw of second maxilla, scale 30 µm. (F) ♀ MV NOH-1059, Otway Range, VIC. Tibia, tarsus and pretarsus of leg 13, scale 300 µm.

Tergites wrinkled, faintly so anteriorly but considerably so in posterior half of trunk. T1 trapeziform, about as wide as head shield (Fig. 12A), about 80% width of widest tergite (T8), posterior angles rounded and posterior margin gently concave; lateral borders subparallel in TT3 and 5, posterior angles rounded, posterior margins gently concave; TT1, 3 and 5 bordered posteriorly; border of T7 incomplete

posteriorly; posterior margin of T7 evenly concave, posterior angle blunt; posterior margins of TT8 moderately, fairly evenly concave, posterior angles obtuse, blunt; posterior margins of TT6, 11 and 13 all evenly concave, increasingly so more posteriorly; T9 variably with nearly transverse median sector; posterior angle of T6 rounded, TT9, 11 and 13 with triangular projections; posterior margin of T14

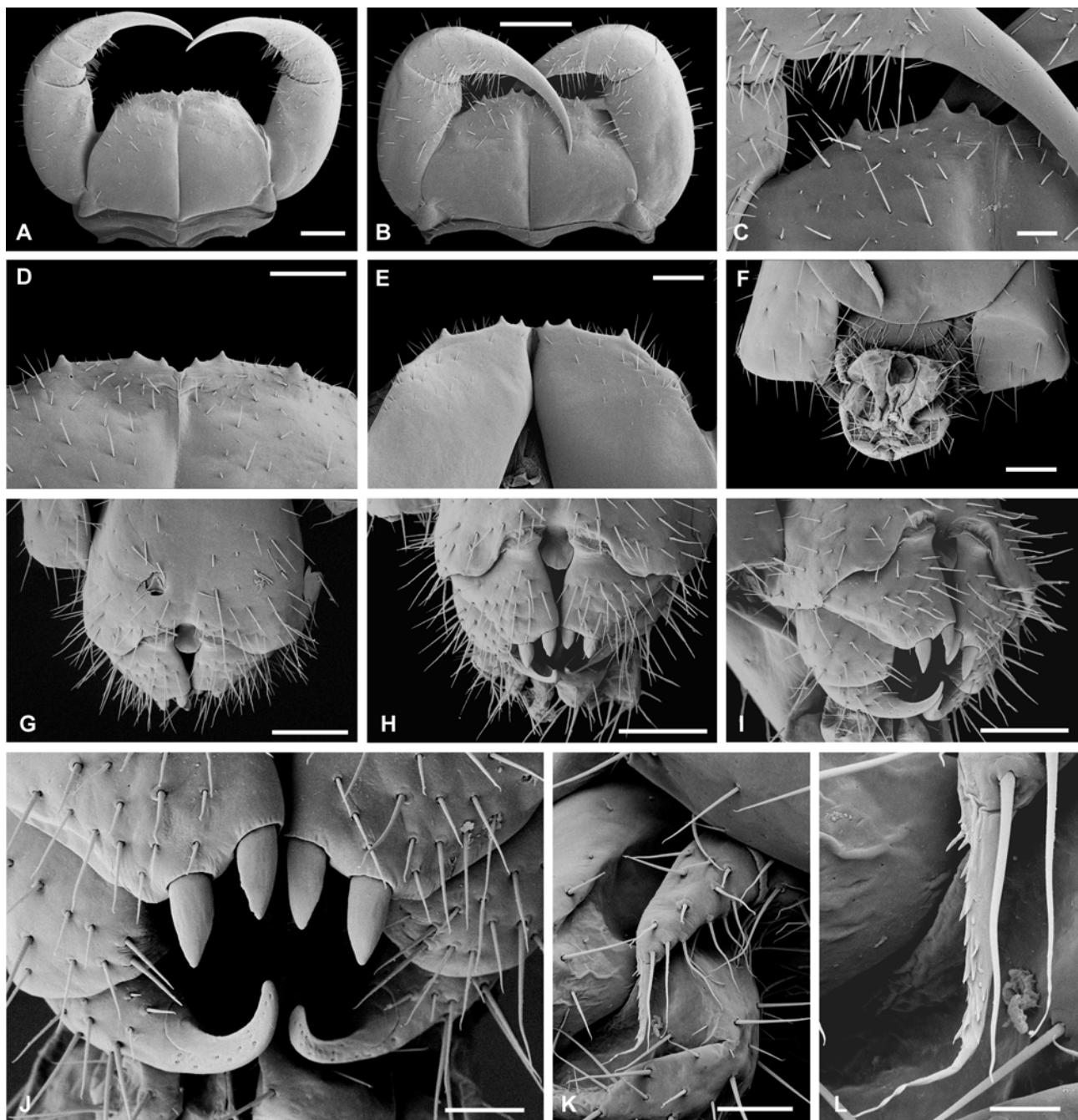


Fig. 16. *Henicops milledgei* n.sp. (A,D–F,K,L) ♂ MV NOH-1779, Cement Creek Reserve, Central Highlands, VIC: (A) ventral view of maxillipede, scale 500 µm; (D) ventral view of dental margin of maxillipede coxosternum, scale 300 µm; (E) dorsal view of dental margin of maxillipede coxosternum, scale 300 µm; (F) ventral view of terminal segments and gonopods, scale 300 µm; (K) distal end of gonopod, scale 100 µm; (L) terminal process of gonopod, scale 30 µm. (B,C) ♀ AM KS83633, Grampians NP: (B) ventral view of maxillipede, scale 500 µm; (C) setation of telopodite and dental margin of maxillipede, scale 100 µm. (G–J) ♀ MV NOH-1059, Otway Range, VIC: (G) ventral view of sternite of first genital segment and gonopods, scale 300 µm; (H,I) ventral and ventrolateral views of sternite of first genital segment and gonopods, scales 300 µm; (J) gonopods, scale 100 µm.

moderately concave, with obtuse posterior angles; tergite of intermediate segment with weakly concave posterior margin in female, moderately concave margin in male. Tergal surface and margins scattered with short setae, in some specimens relatively numerous, e.g., posterior margins of TT3 and 4 fringed by about 20 setae. Longitudinal median furrow confined to anterior part of sternites, not more than one-third length of sternite.

Legs: Distal spinose projections on tibiae strong, pointed on legs 1–14. Setae relatively uniformly distributed along

length of legs, with similar setal density on inner and outer faces of all podomeres; legs 14 and 15 (Fig. 13C,D) with similar setal density as 1–13 (Fig. 13A,B). Three tarsomeres in legs 1–12 (Fig. 13A), with divided basitarsus; tarsal articulations discontinuous on dorsal side of leg in anterior part of trunk; three pairs of consistently strong, pigmented, divergent setae on tarsi of legs 1–12, one just proximal to each articulation between tarsomeres, one near midlength of distal tarsomere. Basitarsus-distitarsus joint with a condyle in legs 13–15 only, basitarsus undivided in these

three legs; three tarsomeres in leg 13 (Figs. 13B, 15F); four tarsomeres in leg 14 (Fig. 13C), distitarsus about 65% length of basitarsus, three tarsomeres comprise about 45–55, 15–25 and 25–35% (proximal to distal) length of distitarsus; five tarsomeres in leg 15, the proximal distitarsal podomere about 50–55% length of distitarsus, second and third shorter than fourth (Fig. 13D). Distitarsus 70–85% length of basitarsus in leg 15; basitarsus 10–12 times longer than broad. Pretarsus with anterior and posterior accessory claws on all legs, about 30% length of main claw, inserted on dorsolateral side of main claw, with gentle dorsoventral curvature (Fig. 14K). Main claw gently curved, divided into many elongate, scales along most of its length, with short, polygonal scales ventrolaterally in region beneath proximal part of accessory claws, a few pores between these scales (Fig. 14L), pore openings in the middle of small polygons; scales weakly defined proximally beneath bases of accessory claws and on proximoventral surface of main claw, well defined dorsoproximally. Posteroventral spine ('sensory spur' of Eason, 1964: fig. 486) present on legs 1–14 (Fig. 14L), absent on leg 15 (Fig. 15G), about 15% length of main claw, directed distally, bearing slender subsidiary spine that parallels it on its dorsoproximal half (Fig. 14L); accessory claws and posteroventral spine with surface ornament of linear grooves and ridges.

Coxal pores round, transversely ovate, or elliptical, typically with round distal pores and elliptical proximal pores (Fig. 12B); overwhelmingly 6,5,5,5/6,5,5,5 in large females (width head shield >1.75 mm), 5,4,4,4/5,4,4,4 in large males; maximum in males 5,5,5,5/5,5,5,5. Coxal pore field set in shallow groove. Anal pores large in both sexes.

Female (Fig. 12B): Sternite of segment 15 transverse or convex posteromedially, with about a dozen setae along posterolateral and posteromedial margins. Tergites of first genital segment and telson usually well sclerotized; sternite of first genital segment large, posterior margin concave, with median bulge, between condyles of gonopods, surface scattered with setae, longest and densest posterolaterally (Fig. 16G). First article of gonopod bearing two moderately large, bullet-shaped spurs, inner spur slightly smaller (Fig. 16G–J); spurs gently curved such that tip points up (Fig. 16I); first article usually bearing more than 30 setae in large specimens (up to 38), second article with 12–20 moderately long setae; third article with three to eight setae. Claw large, undivided, numerous pores with sensilla coeloconica on dorsodistal surface of claw (Fig. 16J).

Male (Fig. 12C): Sternite of segment 15 with subtransverse (Fig. 12C) to moderately convex (Fig. 16F) posteromedial margin. Sternite of first genital segment small, divided, with transverse posterior margin, bearing about 20 moderate to long setae on each half with slight to moderate concentration near posterior margin. Gonopod of three articles and tapering, seta-like terminal process (Fig.

16K,L), with many short spine-like projections along its inner margin; articles of gonopod each typically bear 10–12 setae; many setae on gonopod and first genital sternite curved, at least distally.

Larval stadia: Stadium LII with 8 pairs of legs and two pairs of limb-buds; 14 antennal articles, all elongate; 3+3 teeth on dental margin of maxillipede coxosternum, outer tooth more distant than inner pair; tarsi unjointed. Stadium LIII with 10 pairs of legs and two pairs of limb-buds; 25 antennal articles; maxillipede dentition as in stadium LII; single tarsal articulation faintly defined on many legs.

**Discussion.** All specimens of *Henicops milledgei* share a large space between the outer and middle tooth of the maxillipede coxosternum (more than twice the distance between the inner and middle tooth), exceeded only by *H. brevilabiatus*. No notable geographic variation has been detected between populations of *H. milledgei* from different regions of *Nothofagus* forest in Victoria.

Segmentation of the larval antenna of *Henicops milledgei* and *H. tropicanus* presents a character that may be autapomorphic for *Henicops* or a group within the genus. Larval stadium LIII in both species has a uniquely high number of antennal articles (25), a count retained in larval stadium LIV in *H. tropicanus* at least. In comparison, *Lamyctes emarginatus* (=*fulvicornis*) and *L. coeculus* have only 14 articles in stadium LIII, and Lithobiidae have 14–17 articles in this stadium (Andersson, 1979: table III). Of Lithobiomorpha for which larval ontogeny has been described, only *Cermatobius longitarsis* approaches *Henicops* in having 20–24 articles in stadium LIII (Murakami, 1960; Andersson, 1979).

### Synoptic classification of Henicopidae

Synoptic classifications of Henicopidae were most recently published by Attems (1914, 1928). These predate the description of many species, particularly by R.V. Chamberlin, and changes to generic classification. The following list encapsulates the current classification of henicopid species, together with distributional data.

Type species are indicated by an asterisk. Junior subjective synonyms are indicated following the senior synonym. Many of the named species of *Lamyctes* may, upon restudy, fall into synonymy, but published names that have not been synonymized in published work are listed as valid. Literature sources for synonymies are indicated.

Division of Henicopini into two clades (Edgecombe & Giribet, 2003b) is accommodated by a *Lamyctes-Henicops* Group and *Paralamyctes*.

### Family Henicopidae Pocock, 1901b

(= Cermatobiidae by ICZN Opinion 1228)  
 Subfamily Henicopinae Pocock, 1901b  
 Tribe Henicopini Pocock, 1901b

#### *Lamyctes-Henicops* Group

*Analamyctes* Chamberlin, 1955

\**Analamyctes tucumanus* Chamberlin, 1955 (Argentina: Tucumán)  
*Paralamyctes andinus* Silvestri, 1903 (Argentina: Mendoza)

*Easonobius* Edgecombe, 2003a

\**Easonobius tridentatus* Edgecombe, 2003a (New Caledonia)  
*Paralamyctes humilis* Ribaut, 1923 (New Caledonia)

*Henicops* Newport, 1844

\**Henicops maculatus* Newport, 1844 (Australia: Tasmania, Victoria, New South Wales, Australian Capital Territory; New Zealand) (=*Henicops impressus* Hutton, 1877 *fide* Archey, 1937) (New Zealand)

*Lamyctes brevilabiatus* Ribaut, 1923 (New Caledonia)

*Henicops dentatus* Pocock, 1901a (=*Henicops oligotarsus* Attems, 1911; n.syn.) (Australia: Western Australia)

*Henicops milledgei* n.sp. (Australia: Victoria)

*Henicops tropicanus* n.sp. (Australia: Queensland)

*Lamyctes* Meinert, 1868 (=*Lamyctinus* Silvestri, 1909a; *Metalamyctes* Verhoeff, 1941)

*Lamyctes* (*Lamyctes*) Meinert, 1868

\**Lamyctes fulvicornis* Meinert, 1868 (junior subjective synonym of *Henicops emarginatus* Newport, 1844 *fide* Eason, 1996)

*Lamyctes adisi* Zalesskaja, 1994 (Brazil: central Amazonas)

*Lamyctes albipes* Pocock, 1894 (Java) (=?*L. mauriesi* Demange, 1981 *fide* Eason & Enghoff, 1992) (Guadeloupe, Canary Islands, Seychelles)

*Lamyctes andericus* Chamberlin, 1955 (Peru; Bolivia)

*Lamyctes andinus* Kraus, 1954 (Peru) (=*L. neglectus* Chamberlin, 1955; *L. rectus* Chamberlin, 1955; ?*L. subtropicalis* Chamberlin, 1955; synonyms *fide* Kraus, 1957) (Chile; Peru)

*Lamyctes caducens* Chamberlin, 1938 (USA: New Mexico)

*Lamyctes cairensis* Chamberlin, 1921 (Egypt)

*Lamyctes calbucensis* Verhoeff, 1939 (Chile)

*Lamyctes cerronus* Chamberlin, 1957 (Peru)

*Lithobioides coeculus* Brölemann, 1889 (Italy and other European greenhouse records; Canary Islands; Australia: New South Wales, Lord Howe Island; Argentina (Tucumán); Venezuela; Cuba; Mexico; USA: Hawaii, Illinois; Israel; Tanzania; Democratic Republic of Congo) (type species of *Lamyctinus* Silvestri, 1909a)

*Lamyctes cuzcotes* Chamberlin, 1944 (Peru) (=*L. alancayanus* Chamberlin, 1955 *fide* Kraus, 1957)

*Lamyctes diffusus* Chamberlin & Mulaik, 1940 (USA: Texas)

*Henicops emarginatus* Newport, 1844 (=*Lamyctes chathamensis* Archey, 1917; *L. kermadecensis* Archey, 1917; ?*L. munianus* Chamberlin, 1920; ?*L. navaianus* Chamberlin, 1920; *L. neozelanicus* Archey, 1917; *L. tasmanianus* Chamberlin, 1920; *L. zelandicus* Chamberlin, 1920; synonyms *fide* Archey, 1937) (Chatham Islands; New Zealand; Fiji; Kermadec Islands; Tasmania) (=*L. fulvicornis* Meinert, 1868 *fide* Eason, 1996) (widespread in Europe and USA; Greenland; Iceland; Kurile Islands; eastern Africa: Ethiopia, Kenya, Somalia, Tanzania; Brazil: central Amazonas; Canary and Azore Islands; New Caledonia; Australia: Western Australia, South Australia, Victoria, New South Wales) (=*L. fulvicornis* var. *hawaiiensis* Silvestri, 1904 *fide* Zapparoli & Shelley, 2000) (Hawaii)

*Lamyctes gracilipes* Takakuwa, 1940 (Ôagari, Ryukyu Islands)

*Lamyctes guamus* Chamberlin, 1946 (Guam; Torijima Island)

*Lamyctes guamus koshiyamai* Shinohara, 1957 (Japan)

*Lamyctes hellyeri* Edgecombe & Giribet, 2003a (Australia: Tasmania, probably introduced)

*Henicops inermipes* Silvestri, 1897 (Argentina: Salta)

*Lamyctes insulanus* Verhoeff, 1941 (Fernando Po)

*Lamyctes leon* Chamberlin, 1944 (Mexico)

*Lamyctes leleupi* Matic & Darabantu, 1977 (Saint Helena)

*Lamyctes liani* Larwood, 1946 (India)

*Lamyctes medioides* Chamberlin, 1951 (Angola; Democratic Republic of Congo; Gabon)

*Lamyctes neotropicus* Turk, 1955 (Peru)

*Lamyctes nesiotes* Chamberlin, 1952 (Bahamas)

- Lamyctes omissus* Kraus, 1957 (Peru)  
*Lamyctes orthodox* Chamberlin, 1951 (Angola; Gabon)  
*Lamyctes oticus* Archey, 1921 (New Zealand)  
*Lamyctes pachypes* Takakuwa, 1941 (Japan; far eastern Russia)  
*Lamyctes pacificus* Silvestri, 1905 (Chile) [subspecies of *L. inermipes* (Silvestri) *fide* Demange & Silva, 1976]  
*Lamyctes pinampus* Chamberlin, 1910 (USA: Nevada, California)  
*Lamyctes pius* Chamberlin, 1911a (USA: North Carolina, Georgia, New Jersey, Pennsylvania)  
*Lamyctes remotior* Chamberlin, 1955 (Bolivia)  
*Lamyctes taulisensis* Kraus, 1954 (Peru) (=*L. brattstroemi* Chamberlin, 1955 *fide* Kraus, 1957) (Chile)  
*Lamyctes tivius* Chamberlin, 1911a (USA: Mississippi, Louisiana, Alabama)  
*Lamyctes toluccanus* Chamberlin, 1943 (Mexico)  
*Lamyctes transversus* Chamberlin, 1962 (Chile)  
*Lamyctes (Metalamyctes)* Verhoeff, 1941  
\**Henicops africanus* Porat, 1871 (South Africa: widespread; Cameroon; Gabon; Democratic Republic of Congo; Madagascar; Juan Fernandez; Madagascar; Hawaii; Western Australia) (=*H. insignis* Pocock, 1891 *fide* Attems, 1928)  
*Lamyctes baekstroemi* Verhoeff, 1923 (erected as subspecies of *L. insignis* (Pocock)) (Juan Fernandez)  
*Lamyctes castaneus* Attems, 1909 (South Africa: Western Cape, Eastern Cape, KwaZulu-Natal, Northern Province; Lesotho; Zimbabwe)  
*Lamyctes microporus* Attems, 1909 (South Africa: Northern Cape)  
*Lamyctes neglectus* Lawrence, 1955a (South Africa: KwaZulu-Natal); homonym of *L. neglectus* Chamberlin, 1955  
*Lamyctes robustus* Lawrence, 1955b (South Africa: Eastern Cape; Lesotho; Namibia; Zimbabwe)  
*Henicops tristani* Pocock, 1893 (Tristan d'Acunha; Madagascar)  
*Lamyctopristus* Attems, 1928  
*Lamyctopristus (Lamyctopristus)* Attems, 1928  
\**Lamyctopristus validus* Attems, 1928 (South Africa: Western Cape) (=*Lamyctopristus granulosus* Lawrence, 1955b) (South Africa: Western Cape)  
*Lamyctopristus (Eumyctes)* Chamberlin, 1951 (=*Neomyctes* Chamberlin, 1951)  
\**Henicops sinuatus* Porat, 1893 (South Africa: Western Cape, Northern Cape)  
*Lamyctes denticulatus* Attems, 1907 (South Africa: Western Cape; Democratic Republic of Congo)  
*Lamyctes ergus* Chamberlin, 1951 (type of *Neomyctes* Chamberlin, 1951) (Angola)  
*Lamyctes numidicus* Latzel, 1886 (Algeria; Gabon)  
?*Lamyctes setigerus* Lawrence, 1955b (South Africa: KwaZulu-Natal, Northern Province; Zambia)  
*Pleotarsobius* Attems, 1909  
\**Lamyctes heterotarsus* Silvestri, 1904 (Hawaii)

### **Paralamyctes Group**

- Paralamyctes* Pocock, 1901b (=*Haasiella* Pocock, 1901b; *Triplobius* Silvestri, 1917)  
*Paralamyctes (Paralamyctes)* Pocock, 1901b (=*Triplobius* Silvestri, 1917)  
\**Paralamyctes spenceri* Pocock, 1901b (South Africa: Western Cape, KwaZulu-Natal, Northern Province; Swaziland; Madagascar)  
*Paralamyctes asperulus* Silvestri, 1903 (South Africa: Western Cape, Eastern Cape) (=*P. tabulinus* Attems, 1928 *fide* Edgecombe, 2003b)  
*Lamyctes bipartitus* Lawrence, 1960 (Madagascar)  
*Paralamyctes harrisi* Archey, 1922 (New Zealand)  
*Paralamyctes levigatus* Attems, 1928 (South Africa: Western Cape)  
*Paralamyctes (Paralamyctes) monteithi* Edgecombe, 2001 (Australia: Queensland)  
*Paralamyctes (Paralamyctes) neverneverensis* Edgecombe, 2001 (Australia: New South Wales)  
*Triplobius newtoni* Silvestri, 1917 (India)  
*Paralamyctes (Paralamyctes) prendinii* Edgecombe, 2003b (South Africa: Western Cape)  
*Paralamyctes quadridens* Lawrence, 1960 (Madagascar)  
*Paralamyctes tridens* Lawrence, 1960 (Madagascar)  
*Paralamyctes weberi* Silvestri, 1903 (South Africa: Western Cape)  
*Paralamyctes (Haasiella)* Pocock, 1901b (=*Wailamyctes* Archey, 1917)  
\**Henicops insularis* Haase, 1887 (New Zealand: Auckland Islands) (=*Wailamyctes munroi* Archey, 1923 *fide* Johns, 1964) (New Zealand: Auckland Islands)  
*Paralamyctes (Haasiella) cammooensis* Edgecombe, 2004a (Australia: Queensland, New South Wales)  
*Paralamyctes (Haasiella) ginini* Edgecombe, 2004a (Australia: New South Wales, Australian Capital Territory)  
*Wailamyctes halli* Archey, 1917 (New Zealand)  
*Paralamyctes (Haasiella) subicolor* Edgecombe, 2004a (Australia: Tasmania)

- Wailamyctes trailli* Archey, 1917 (New Zealand)  
*Paralamyctes (Nothofagobius)* Edgecombe, 2001  
 \**Paralamyctes (Nothofagobius) cassisi* Edgecombe, 2001 (Australia: New South Wales)  
*Paralamyctes (Nothofagobius) mesibovi* Edgecombe, 2001 (Australia: Tasmania)  
*Paralamyctes (Thingathinga)* Edgecombe, 2001  
 \**Paralamyctes (Thingathinga) grayi* Edgecombe, 2001 (Australia: New South Wales)  
*Paralamyctes (Thingathinga) hornerae* Edgecombe, 2001 (Australia: New South Wales)  
*Paralamyctes validus* Archey, 1917 (=*P. dubius* Archey, 1917 *fide* Archey, 1921, 1937) (New Zealand)  
*Paralamyctes* subgen. undet.  
*Henicops chilensis* Gervais in Walckenaer & Gervais, 1847 (Chile; Argentina: Neuquén, Rio Negro)  
*Paralamyctes wellingtonensis* Edgecombe, 2003c (Chile)

#### Tribe Zygethobiini Attems, 1914

- Buethobius* Chamberlin, 1911a  
 \**Buethobius oabitus* Chamberlin, 1911a (USA: Mississippi)  
*Buethobius arizonicus* Chamberlin, 1945a (USA: Arizona)  
*Buethobius conjugans* Chamberlin, 1911b (USA: California)  
*Buethobius heustoni* Williams & Hefner, 1928 (USA: Ohio)  
*Buethobius translucens* Williams & Hefner, 1928 (USA: Ohio)  
*Cermatobius* Haase, 1885 (=*Esastigmatobius* Silvestri, 1909a *fide* Würmli, 1977)  
 \**Cermatobius martensi* Haase, 1885 (Indonesia: Adenara)  
*Esastigmatobius japonicus* Silvestri, 1909a (Japan) (type species of *Esastigmatobius* Silvestri, 1909a)  
*Esastigmatobius curticornis* Chamberlin & Wang, 1952 (Japan)  
*Esastigmatobius kirgisicus* Zalesskaja, 1972 (Kirghizia)  
*Esastigmatobius longicornis* Takakuwa, 1939 (Japan; Taiwan)  
*Esastigmatobius longitarsis* Verhoeff, 1934b (Japan; Taiwan)  
*Hedinobius* Verhoeff, 1934a  
 \**Hedinobius hummelii* Verhoeff, 1934a (western China)  
*Yobius* Chamberlin, 1945b  
 \**Yobius haywardi* Chamberlin, 1945b (USA: Utah)  
*Zygethobius* Chamberlin, 1903 (=*Zantethobius* Chamberlin, 1911a)  
 \**Henicops dolichopus* Chamberlin, 1902 (USA: Utah, California)  
*Zygethobius columbiensis* Chamberlin, 1912 (Canada: British Columbia)  
*Zygethobius ecologus* Chamberlin, 1938 (USA: Oregon)  
*Zygethobius (Zantethobius) pontis* Chamberlin, 1911a (USA: Virginia, Tennessee) (type of  
*Zantethobius* Chamberlin, 1911a)  
*Zygethobius sokariensis* Chamberlin, 1911b (USA: California)

#### Henicopinae of uncertain affinity

- Remylamyctes* Attems, 1951  
 \**Remylamyctes straminea* Attems, 1951 (Madagascar)

#### Subfamily Anopsobiinae Verhoeff, 1907

- Anopsobius* Silvestri, 1899 (=*Promethon* Chamberlin, 1962; =*Tasmanobius* Chamberlin, 1920)  
 \**Anopsobius productus* Silvestri, 1899 (Chile)  
*Anopsobius actius* Chamberlin, 1962 (Chile)  
*Anopsobius (Promethon) diversus* Chamberlin, 1962 (Chile)  
*Dichelobius giribeti* Edgecombe, 2004b (Australia: New South Wales, Australian Capital Territory,  
 Victoria, Lord Howe Island)  
*Anopsobius macfaydeni* Eason, 1993 (Falkland Islands)  
*Anopsobius neozelanicus* Silvestri, 1909a (New Zealand)  
*Anopsobius patagonicus* Silvestri, 1909a (Argentina: Santa Cruz)  
*Anopsobius patagonicus calcaratus* Attems, 1928 (South Africa: Western Cape; possibly introduced  
*fide* Lawrence, 1984)  
*Tasmanobius relictus* Chamberlin, 1920 (Australia: Tasmania)  
*Dichelobius schwabei* Verhoeff, 1939 (Chile)  
*Anopsobius wrighti* Edgecombe, 2003d (Australia: New South Wales)  
*Anopsobiella* Attems, 1938  
 \**Anopsobius (Anopsobiella) dawydoffi* Attems, 1938 (Vietnam)  
*Catanopsobius* Silvestri, 1909b  
 \**Catanopsobius chilensis* Silvestri, 1909b (Chile)

- Dichelobius* Attems, 1911  
 \**Dichelobius flavens* Attems, 1911 (Australia: Western Australia)  
*Dichelobius bicuspis* Ribaut, 1923 (New Caledonia)  
*Ghilaroviella Zalesskaja*, 1975  
 \**Ghilaroviella valiachmedovi* Zalesskaja, 1975 (Tajikistan)  
*Rhodobius Silvestri*, 1933  
 \**Rhodobius lagoi* Silvestri, 1933 (Rhodes)  
*Shikokuobius* Shinohara, 1982  
 \**Anopsobius japonicus* Murakami, 1967 (Japan)

ACKNOWLEDGMENTS. For hosting collection studies and arranging loans, we thank M. Colloff (Australian National Insect Collection), M. Harvey and J. Waldock (Western Australian Museum), P. Lawless, G.B. Monteith and R. Raven (Queensland Museum), and K. Walker (Museum Victoria). Additional loans were facilitated by J. Beccaloni (Natural History Museum), H. Dastych (Universität Hamburg), C. Griswold (California Academy of Sciences), and V. Stagl (Naturhistorisches Museum Wien). We thank Suzanne Bullock, Sue Lindsay, and Yongyi Zhen for their expert work on illustrations. R. Mesibov and W.A. Shear kindly provided comments on the manuscript.

## References

- Andersson, G., 1978. An investigation of the post-embryonic development of the Lithobiidae—some introductory aspects. *Abhandlungen und Verhandlungen des Naturwissenschaftlichen Vereins in Hamburg* 22/22: 63–71.
- Andersson, G., 1979. On the use of larval characters in the classification of lithobiomorph centipedes (Chilopoda, Lithobiomorpha). In *Myriapod Biology*, ed. M. Camatini, pp. 73–81. London: Academic Press.
- Andersson, G., 1984. Post-embryonic development of *Lamycetes 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., 1921. Notes on New Zealand Chilopoda. *Transactions and Proceedings of the New Zealand Institute* 53: 181–195.
- 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., 1907. Die Myriopoden der deutschen Südpolar-Expedition 1901–1903. *Deutsche Südpolar-Expedition 1901–1903* 9. Zoologie, pp. 415–433. Berlin: Georg Reimer.
- Attems, C., 1909. Myriapoda. In *Zoologische und anthropologische Ergebnisse einer Forschungsreise im westlichen und zentralen Südafrika ausgeführt in den Jahren 1903–1905*, ed. L. Schultze. *Denkschriften der Medizinisch-naturwissenschaftlichen Gesellschaft zu Jena* 14: 1–52. Jena: Gustav Fischer.
- Attems, C., 1911. Myriapoda exkl. Scolopendridae. *Die Fauna Südwest-Australiens. Ergebnisse der Hamburger südwest-australischen Forschungsreise 1905* 3: 147–204. Jena: Gustav Fischer.
- Attems, C., 1914. Die indo-australischen Myriapoden. *Archiv für Naturgeschichte, Abteilung A* 4: 1–398.
- Attems, C., 1928. The Myriapoda of South Africa. *Annals of the South African Museum* 26: 1–431.
- Attems, C., 1938. Die von Dr. C. Dawydoff in Französisch Indochina gesammelten Myriopoden. *Mémoires du Muséum national d'Histoire naturelle, Paris* 6(2): 187–353.
- Attems, C., 1951. Myriapodes d'Afrique, de Madagascar et de la Réunion. *Mémoires de l'Institut scientifique de Madagascar, Série A*, 5(1): 173–186.
- Borucki, H., 1996. Evolution und Phylogenetisches System der Chilopoda (Mandibulata, Tracheata). *Verhandlungen des Naturwissenschaftlichen Vereins in Hamburg* 35: 95–226.
- Brölemann, H., 1889. Contributions à la faune myriapodologique méditerranéenne. *Annales de la Société Linnéenne de Lyon* 35: 273–284.
- Chamberlin, R.V., 1902. *Henicops dolichopus*, a new chilopod from Utah. *Proceedings of the United States National Museum* 24: 797–800.
- Chamberlin, R.V., 1903. *Henicops*. *Entomological News* 14: 335.
- Chamberlin, R.V., 1910. The Chilopoda of California I. *Pomona College Journal of Entomology* 2: 363–374.
- Chamberlin, R.V., 1911a. The Lithobiomorpha of the southeastern states. *Annals of the Entomological Society of America* 4: 32–48.
- Chamberlin, R.V., 1911b. Some Lithobiomorpha from the region of San Francisco Bay. *The Canadian Entomologist* 63: 378–385.
- Chamberlin, R.V., 1912. The Henicopidae of America north of Mexico. *Bulletin of the Museum of Comparative Zoology at Harvard College* 57: 1–36.
- Chamberlin, R.V., 1920. The Myriopoda of the Australian region. *Bulletin of the Museum of Comparative Zoology at Harvard College* 64: 1–269.
- Chamberlin, R.V., 1921. New Chilopoda and Diplopoda from the East Indian Region. *Annals and Magazine of Natural History, Series* 9(7): 50–87.
- Chamberlin, R.V., 1938. On eighteen new lithobiomorphous chilopods. *Annals and Magazine of Natural History, Series* 11(2): 625–635.
- Chamberlin, R.V., 1943. On Mexican centipeds. *Bulletin of the University of Utah, Biological Series* 33: 1–55.
- Chamberlin, R.V., 1944. Chilopods in the collections of the Field Museum of Natural History. *Field Museum of Natural History, Zoological Series* 28: 175–216.
- Chamberlin, R.V., 1945a. Notes on a small collection of chilopods from Arizona and adjacent parts. *Pomona College Journal of Entomology and Zoology* 17: 53–54.
- Chamberlin, R.V., 1945b. A new henicopid centipede from Utah. *Entomological News* 56: 153–154.
- Chamberlin, R.V., 1946. A new milliped and two new centipedes from Guam. *Proceedings of the Biological Society of Washington* 59: 161–163.
- Chamberlin, R.V., 1951. On Chilopoda collected in North-East Angola by Dr. A. de Barros Machado. *Museo do Dundo, Subsídios para o Estudo da Biologia na Lunda*, pp. 97–111. Lisboa: Companhia de Diamantes de Angola, Servicos Culturais.
- Chamberlin, R.V., 1952. The centipeds (Chilopoda) of South Bimini, Bahama Islands, British West Indies. *American Museum Novitates* 1576: 1–8.
- 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: 1–61.

- Chamberlin, R.V., 1957. A new henicopid chilopod from Peru. *Entomological News* 68: 126–127.
- Chamberlin, R.V., 1962. Chilopods secured by the Royal Society Expedition to southern Chile in 1958–59. *University of Utah Biological Series* 12: 1–23.
- Chamberlin, R.V., & S. Mulaik, 1940. On a collection of centipeds from Texas, New Mexico and Arizona (Chilopoda). *Entomological News* 51: 107–110, 125–128, 156–158.
- Chamberlin, R.V., & Y.M. Wang, 1952. Some records and descriptions of chilopods from Japan and other Oriental areas. *Proceedings of the Biological Society of Washington* 65: 177–187.
- Demange, J.-M., 1981. Scolopendromorphs et Lithobiomorphes (Myriapoda, Chilopoda) de la Guadeloupe et dépendances. *Bulletin du Muséum national d'Histoire naturelle* 3: 825–839.
- Demange, J.-M., & G.F. Silva, 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. *Bollettino del Laboratorio di Entomologia Agraria «Filippo Silvestri», Portici* 33: 44–52.
- Eason, E.H., 1964. *Centipedes of the British Isles*. London: Frederick Warne & Co.
- Eason, E.H., 1993. A new species of *Anopsobius* from the Falkland Islands, with commentary on the geographical distribution of the genus (Chilopoda: Lithobiomorpha). *Myriapodologica* 2: 83–89.
- Eason, E.H., 1996. Lithobiomorpha from Sakhalin Island, Kamchatka Peninsula and the Kurile Islands (Chilopoda). *Arthropoda Selecta* 5: 117–123.
- Eason, E.H., & H. Enghoff, 1992. The lithobiomorph centipedes in the Canary Islands (Chilopoda). *Entomologica scandinavica* 23: 1–9.
- Edgecombe, G.D., 2001. Revision of *Paralamyctes* (Chilopoda: Lithobiomorpha: Henicopidae), with six new species from eastern Australia. *Records of the Australian Museum* 53(2): 201–241. [http://www.amonline.net.au/pdf/publications/1328\\_complete.pdf](http://www.amonline.net.au/pdf/publications/1328_complete.pdf)
- Edgecombe, G.D., 2003a. A new genus of henicopid centipede (Chilopoda, Lithobiomorpha) from New Caledonia. *Memoirs of the Queensland Museum* 49: 269–284.
- Edgecombe, G.D., 2003b. *Paralamyctes* (Chilopoda: Lithobiomorpha: Henicopidae) from the Cape region, South Africa, with a new species from Table Mountain. *African Entomology* 11: 97–115.
- Edgecombe, G.D., 2003c. A new species of *Paralamyctes* (Chilopoda: Lithobiomorpha: Henicopidae) from southern Chile. *Zootaxa* 193: 1–12. <http://www.mapress.com/zootaxa/2003/zt00193.pdf>
- Edgecombe, G.D., 2003d. A new species of the Gondwanan centipede *Anopsobius* (Chilopoda: Lithobiomorpha) from New South Wales, Australia. *Zootaxa* 204: 1–15. <http://www.mapress.com/zootaxa/2003/zt00204.pdf>
- Edgecombe, G.D., 2004a. The henicopid centipede *Haasiella* (Chilopoda: Lithobiomorpha): new species from Australia, with a morphology-based phylogeny of Henicopidae. *Journal of Natural History* 38: 37–76.
- Edgecombe, G.D., 2004b. A new species of the henicopid centipede *Dichelobius* (Chilopoda: Lithobiomorpha) from southeastern Australia and Lord Howe Island. *Proceedings of the Linnean Society of New South Wales* 125: 189–203.
- Edgecombe, G.D., & G. Giribet, 2003a. A new blind *Lamyctes* (Chilopoda: Lithobiomorpha) from Tasmania with an analysis of molecular sequence data for the Lamyctes-Henicops Group. *Zootaxa* 152: 1–23. <http://www.mapress.com/zootaxa/2003/zt00152.pdf>
- Edgecombe, G.D., & G. Giribet, 2003b. Relationships of Henicopidae (Chilopoda: Lithobiomorpha): new molecular data, classification and biogeography. In *Proceedings of the 12th International Congress of Myriapodology*, ed. M. Hamer. *African Invertebrates* 44: 13–38.
- Edgecombe, G.D., G. Giribet & W.C. Wheeler, 2002. Phylogeny of Henicopidae (Chilopoda: Lithobiomorpha): a combined analysis of morphology and five molecular loci. *Systematic Entomology* 27: 31–64.
- Edgecombe, G.D., & L. Hollington, 2002. Morphology and distribution of *Australobius scabrior* (Chilopoda: Lithobiomorpha: Lithobiidae). *Memoirs of the Queensland Museum* 48: 103–118.
- Haase, E., 1885. Zur Morphologie der Chilopoden. *Zoologischer Anzeiger* 210: 1–4.
- Haase, E., 1887. Die indisch-australischen Myriapoden. I. Chilopoden. *Abhandlungen und Berichte des Königlichen Zoologischen Anthropologisch-Ethnographischen Museums zu Dresden* 5: 1–118.
- Hutton, F.W., 1877. Descriptions of New Species of New Zealand Myriapoda. *Annals and Magazine of Natural History*, Series 4(20): 114–117.
- 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, 1. *Senckenbergiana* 34: 311–323.
- Kraus, O., 1957. Myriapoden aus Peru, VI: Chilopoden. *Senckenbergiana biologica* 38: 359–404.
- Larwood, H.J.C., 1946. Some new Indian Lithobiidae. *Journal of the Bombay Natural History Society* 46: 133–139.
- Latreille, P.A., 1817. *Les Myriapodes*. In *Le Régne Animal*. 3, ed. G.L.C.F.D. Cuvier. Paris: Deterville.
- Latzel, R., 1886. Les Myriapodes de la Normandie (2<sup>e</sup> liste) suivie de diagnoses d'espèces et de variétés nouvelles (de France, Algérie et Tunisie). *Bulletin de la Société des Amis des Sciences naturelles, Rouen* 71: 165–177.
- Lawrence, R.F., 1955a. A revision of the centipedes (Chilopoda) of Natal and Zululand. *Annals of the Natal Museum* 13: 121–174.
- Lawrence, R.F., 1955b. Chilopoda. In *South African Animal Life: Results of the Lund University Expedition in 1950–1951*, 2, ed. B. Hanström, P. Brinck & G. Rudebeck, pp. 4–56. Stockholm: Almqvist & Wiksell.
- Lawrence, R.F., 1960. Myriapodes: Chilopodes. *Faune de Madagascar* 12: 1–122. *Publications de l'Institut de Recherche Scientifique, Tananarive-Tsimbazaza*.
- Lawrence, R.F., 1984. *The Centipedes and Millipedes of Southern Africa: A Guide*. Cape Town, Rotterdam: A.A. Balkema.
- Matic, Z., & C. Darabantu, 1977. Chilopoda. In: *La Faune Terrestre de l'Île de Sainte-Hélène: Quatrième Partie. Musée Royal de l'Afrique Centrale, Annales, Sciences zoologiques* 220: 345–359.
- Meiner, F., 1868. Danmarks Scolopender og Lithobier. *Naturhistorisk Tidskrift* 5: 241–268.
- Mesibov, R., 1986. *A Guide to Tasmanian Centipedes*. Zeehan: published by the author.
- Michaelsen, W., & R. Hartmeyer, 1907. Reisebericht. *Die Fauna Südwest-Australiens. Ergebnisse der Hamburger südwestaustralischen Forschungsreise 1905* 1: 1–116. Jena: Gustav Fischer.
- Murakami, Y., 1960. Postembryonic development of the common Myriapoda of Japan IX. Anamorphic stadia of *Esastigmatobius longitarsis* Verhoeff (Chilopoda: Henicopidae). *Zoological Magazine* 70: 430–434.
- Murakami, Y., 1967. Postembryonic development of the common Myriapoda of Japan XXIV. A new species of the Family Henicopidae. *Zoological Magazine* 76: 7–12.
- Newport, G., 1844. A list of the species of Myriapoda, order Chilopoda, contained in the cabinets of the British Museum, with a synoptic description of forty-seven species. *Annals and Magazine of Natural History* 13: 94–101.

- Pocock, R.I., 1891. Descriptions of some new species of Chilopoda. *Annals and Magazine of Natural History*, Series 6(8), 152–164.
- Pocock, R.I., 1893. Report upon the Myriopoda of the "Challenger" Expedition, with Remarks upon the Fauna of Bermuda. *Annals and Magazine of Natural History*, Series 6(11): 121–142.
- Pocock, R.I., 1894. Chilopoda, Symphyla and Diplopoda from the Malay Archipelago. In *Zoologisches Ergebnisse einer Reise in niederländisch Ost-Indien* 3, ed. M. Weber, pp. 307–400. Leiden: Brill.
- Pocock, R.I., 1901a. The Chilopoda or centipedes of the Australian Continent. *Annals and Magazine of Natural History*, Series 7(8): 451–463.
- Pocock, R.I., 1901b. Some new genera and species of Lithobiomorphous Chilopoda. *Annals and Magazine of Natural History*, Series 7(8): 448–451.
- Pocock, R.I., 1902. A new and annectant type of chilopod. *Quarterly Journal of Microscopical Science* 45: 417–448.
- Porat, C.O. von., 1871. Myriopoda Africæ australis, in Museo Regio Holmiensi asservata, recensuit. *Öfversigt af Kungliga Vetenskaps-akademiens Förfärlingar* 9: 1135–1167.
- Porat, C.O. von., 1893. Myriapoder från Vest-och Syd-Afrika. *Bihang till Svenska Vetenskaps-akademiens Handlingar* 18: 1–15.
- Ribaut, H., 1923. Chilopodes de la Nouvelle-Calédonie et des Iles Loyalty. In *Nova Caledonia. Recherches scientifique en Nouvelle-Calédonie et aux Iles Loyalty*. A. Zoology 3(1), ed. F. Sarasin & J. Roux, pp. 1–79. Berlin, Weisbaden: C.W. Kreidels Verlag.
- Shinohara, K., 1957. Taxonomical and morphological study of Myriapoda 2. *Lamyctes* species found in Japan and its vicinity (Henicopidae, Chilopoda). *Zoological Magazine* 66: 27–30.
- Shinohara, K., 1982. A new genus of centipede of the Subfamily Anopsobiinae (Henicopidae, Chilopoda). *Proceedings of the Japanese Society of Systematic Zoology* 24: 41–46.
- Silvestri, F., 1897. Viaggio del Dott. Alfredo Borelli nel Chaco boliviano e nella Repubblica Argentina, IV. Chilopodi e Diplopodi. *Bollettino del Musei di Zoologia ed Anatomia comparata della R. Università di Torino* 12: 1–11.
- Silvestri, F., 1899. Contribución al estudio de los quilópodos chilenos. *Revista chilena de História natural* 3: 141–152.
- Silvestri, F., 1903. Contribuzione alla conoscenza dei Chilopodi. II. Nuove specie di *Paralamyctes*. *Redia* 1: 256–257.
- Silvestri, F., 1904. Myriopoda. *Fauna Hawaïensis* 3: 323–338.
- Silvestri, F., 1905. Myriopoda. *Fauna chilensis*. *Zoologische Jahrbücher, Abteilung für Systematik, Ökologie und Geographie der Tiere, Supplement* 6: 715–772.
- Silvestri, F., 1909a. Contribuzioni alla conoscenza dei Chilopoda, III. Descrizione di alcuni generi e specie di Henicopidae. *Bollettino del Laboratorio di Zoologia Generale e Agraria, Portici* 4: 38–50.
- Silvestri, F., 1909b. Descrizioni preliminari di varii Arthropodi, specialmente d'America. V. Nuovi generi di Henicopidae (Chilopoda). *Rendiconti della R. Accademia dei Lincei* 18: 270–271.
- Silvestri, F., 1917. On some Lithobioidea (Chilopoda) from India. *Records of the Indian Museum, Calcutta* 13: 307–314.
- Silvestri, F., 1933. Nuovi contributi alla conoscenza della fauna delle isole italiane dell'Ageo. I. Descrizione di un nuovo genere di Chilopodo Henicopino. *Bollettino del Laboratorio di Zoologia generale e agraria, Portici* 27: 58–60.
- Takakuwa, Y., 1939. Dei *Esastigmatobius*-Arten aus Japan. *Zoological Magazine* 51: 581–585.
- Takakuwa, Y., 1940. Eine neue *Lamyctes*-Art (Chilopoda) aus Japan. *Transactions of the Natural History Society of Formosa* 30: 197–198.
- Takakuwa, Y., 1941. Eine neue leuchtende *Spirobolellus*-Art (Diplopoda) und eine neue *Lamyctes*-Art (Chilopoda). *Transactions of the Natural History Society of Formosa* 31: 84–86.
- Turk, F.A., 1955. The chilopods of Peru with descriptions of new species and some zoogeographical notes on the Peruvian chilopod fauna. *Proceedings of the Zoological Society of London* 125: 469–504.
- Verhoeff, K.W., 1907. Chilopoda. Systematik. In *H.G. Bronn's Klassen und Ordnungen des Tier-Reichs* 5(2): 217–264. Leipzig: C.F. Winter'sche Verlagshandlung.
- Verhoeff, K.W., 1923. Über Myriapoden von Juan Fernandez und der Osterinsel. In *The Natural History of Juan Fernandez and Easter Island* 3: 403–418, ed. C. Skottsberg. Uppsala: Almqvist & Wiksell.
- Verhoeff, K.W., 1934a. Schwedisch-chinesische wissenschaftliche Expedition nach den nordwestlichen Provinzen Chinas. *Arkiv för Zoologi* 26A(10): 1–41.
- Verhoeff, K.W., 1934b. Beiträge zur Systematik und Geographie der Chilopoden. *Zoologische Jahrbücher, Abteilung für Systematik, Ökologie und Geographie der Tiere* 66: 1–112.
- Verhoeff, K.W., 1939. Von Dr. G.H. Schwabe in Chile gesammelte Isopoda terrestria, Diplopoda und Chilopoda. *Archiv für Naturgeschichte, Zeitschrift für Wissenschaftliche Zoologie Abteilung B*, 8: 301–324.
- Verhoeff, K.W., 1941. 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.
- Walckenaer, M. LeB., & M.P. Gervais, 1847. *Histoire naturelle des Insectes. Aptères*, 4. Paris: Librairie Encyclopédique de Roret.
- Williams, S.R., & R.A. Hefner, 1928. The millipedes and centipedes of Ohio. *Ohio Biological Survey Bulletin* 18: 91–147.
- Würmli, M., 1977. Wiederbeschreibung und Identität von *Cermatobius martensii*, des vermeintlichen Bindegliedes zwischen Scutigeromorpha und Lithobiomorpha (Chilopoda: Cermatobiidae). *Entomologica Germanica* 3: 361–366.
- Zalesskaja, N.T., 1972. A new species of the genus *Esastigmatobius* (Lithobiomorpha, Henicopidae). *Zoologicheskii Zhurnal* 51: 608–611.
- Zalesskaja, N.T., 1975. New genera and species of Chilopoda (Lithobiomorpha) from central Asia and Far East. *Zoologicheskii Zhurnal* 54: 1316–1325.
- Zalesskaja, N.T., 1994. The centipede genus *Lamyctes* MEINERT, 1868, in the environs of Manaus, Central Amazonia, Brazil (Chilopoda, Lithobiomorpha, Henicopidae). *Amazoniana* 8: 59–64.
- Zapparoli, M., & R.M. Shelley, 2000. The centipede order Lithobiomorpha in the Hawaiian Islands (Chilopoda). I. The epigean fauna. Records of the Hawaii Biological Survey for 1999. *Bishop Museum Occasional Papers* 63: 35–49.

Manuscript received 26 March 2003, revised 24 June 2003 and accepted 25 June 2003.

Associate Editor: M.S. Moulds.