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Morphology and relationships of a new species of *Henicops* (Chilopoda: Lithobiomorpha) from New South Wales and Queensland, Australia

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Abstract

The henicopid centipede *Henicops* Newport, 1845, is common and widespread in wet forests in Australia and New Zealand. A new species of *Henicops*, *H. washpoolensis*, is widely distributed in northern New South Wales and southern Queensland, ranging into the wet tropics of north Queensland. Parsimony analysis of morphological characters identifies the monophyly of an Australasian group within *Henicops* relative to more distantly allied species from Lord Howe Island and New Caledonia. The most parsimonious cladograms unite the three species from southeastern Australia and New Zealand to the exclusion of congeners from Western Australia and north Queensland or unite all Australasian species to the exclusion of *H. washpoolensis*.

Key words: Chilopoda, Lithobiomorpha, Henicopidae, *Henicops*, *Henicops washpoolensis*, Australia

Introduction

The lithobiomorph centipede *Henicops* Newport, 1845, has a widespread distribution in Australia and New Zealand. A review of the genus (Hollington & Edgecombe 2004) recognized four Australian species, one endemic to the southwest of Western Australia (*H. dentatus* Pocock, 1901), another in Tasmania, Victoria, southern New South Wales, and New Zealand (*H. maculatus* Newport, 1845), and new species endemic to Victoria (*H. milledgei* Hollington & Edgecombe, 2004) and north Queensland (*H. tropicanus* Hollington & Edgecombe, 2004). A species from each of Lord Howe Island (*H. howensis* Edgecombe, 2004) and New Caledonia [*H. brevilabiatus* (Ribaut, 1923)] are the only non-Australasian members of *Henicops*.

Rainforest and wet sclerophyll forest in New South Wales and Queensland (Fig. 1) provide a new species, *Henicops washpoolensis*, described herein. This new species is

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among the most common centipedes in eastern Australia but has not been recognised in previous studies, an indication of the rudimentary knowledge of parts of the Australian centipede fauna. The present study aims to document the morphology and distribution of *H. washpoolensis* and assess its phylogenetic relationships based on morphological characters.

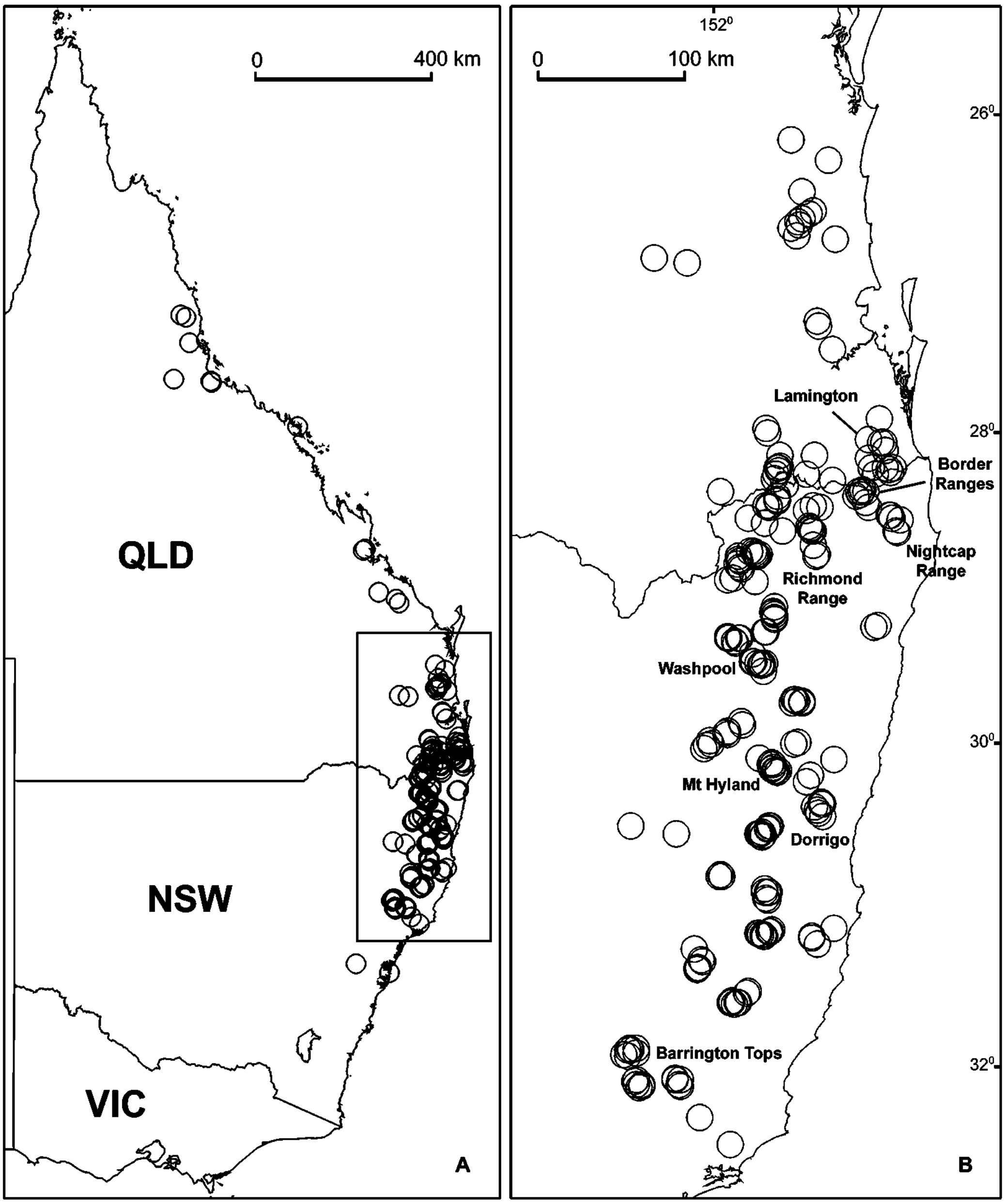


FIGURE 1. Distribution of *Henicops washpoolensis* n. sp. in New South Wales and Queensland. Geographic regions cited in text discussion are indicated in the inset (B).

Type and figured specimens are in the collections of the Australian Museum (prefixed AM KS). Electron microscopy used a LEO 435VP with a Robinson backscatter collector.

Taxonomy

Order LITHOBIOMORPHA Pocock, 1902
Family HENICOPIDAE Pocock, 1901
Subfamily HENICOPINAE Pocock, 1901
Tribe HENICOPINI Pocock, 1901
***Lamyctes-Henicops* group *sensu* Edgecombe & Giribet, 2003**

Henicops Newport, 1845

Type species: *Henicops maculatus* Newport, 1845; by original designation.

Diagnosis: Member of *Lamyctes-Henicops* group with 26–51 antennal articles; dental margin of maxillipede coxosternum with 3+3 or 4+4 teeth (exceptionally up to 6+6), lacking pseudoporodont; 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; 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.

Discussion: The diagnosis of *Henicops* above accounts for two characters of *H. washpoolensis* that differ from previously described species and had been cited in early generic diagnoses (Pocock 1901; Attems 1928; Archey 1937). These characters are the presence of more than 3+3 teeth on the maxillipede dental margin, and the bipartite (rather than tripartite) tarsi on legs 1–12 (also bipartite in *H. howensis* Edgecombe, 2004). Some specimens of *H. washpoolensis* share the 3+3 dentition with other *Henicops*, and the subdivision of the basitarsus of legs 1–12 is marked by the position of thickened setae, though not by an articulation. The phylogenetic analysis discussed below indicates that *H. washpoolensis* is either nested within *Henicops* as conventionally delimited (e.g., Attems 1911, 1914, 1928; Archey 1917, 1937) or is sister group to that clade, and the diagnosis is accordingly modified.

Henicops washpoolensis n. sp.

Figs. 2–48

Henicops sp., QLD Edgecombe et al., 2002 — Syst. Entomol. 27: 61
Henicops SE QLD Edgecombe & Giribet, 2003 — Afr. Inverts. 44: figs. 1–3.
Henicops sp. SE QLD Edgecombe & Giribet 2003 — Zootaxa 152: table 1, fig. 38.
Henicops n. sp. Edgecombe, 2004 — Insect. Syst. Evol. 35: fig. 1.1, 1.6

Diagnosis: *Henicops* with 33–51 (usually 38–45) antennal articles; posterior part of ocellus set inward of lateral margin of head shield; Tömösváry organ small, shallow, positioned inward of margin of cephalic pleurite; three or four teeth on each dental margin of maxillipede coxosternum, rarely five or exceptionally six; T7 with rounded, concave margin; two tarsomeres in legs 1–12, three tarsomeres in legs 13 and 14, distitarsus divided; leg 15 with three or four tarsomeres, basitarsus undivided, distitarsus with two or three tarsomeres; female gonopod with two relatively large, elongate, bullet-shaped spurs.

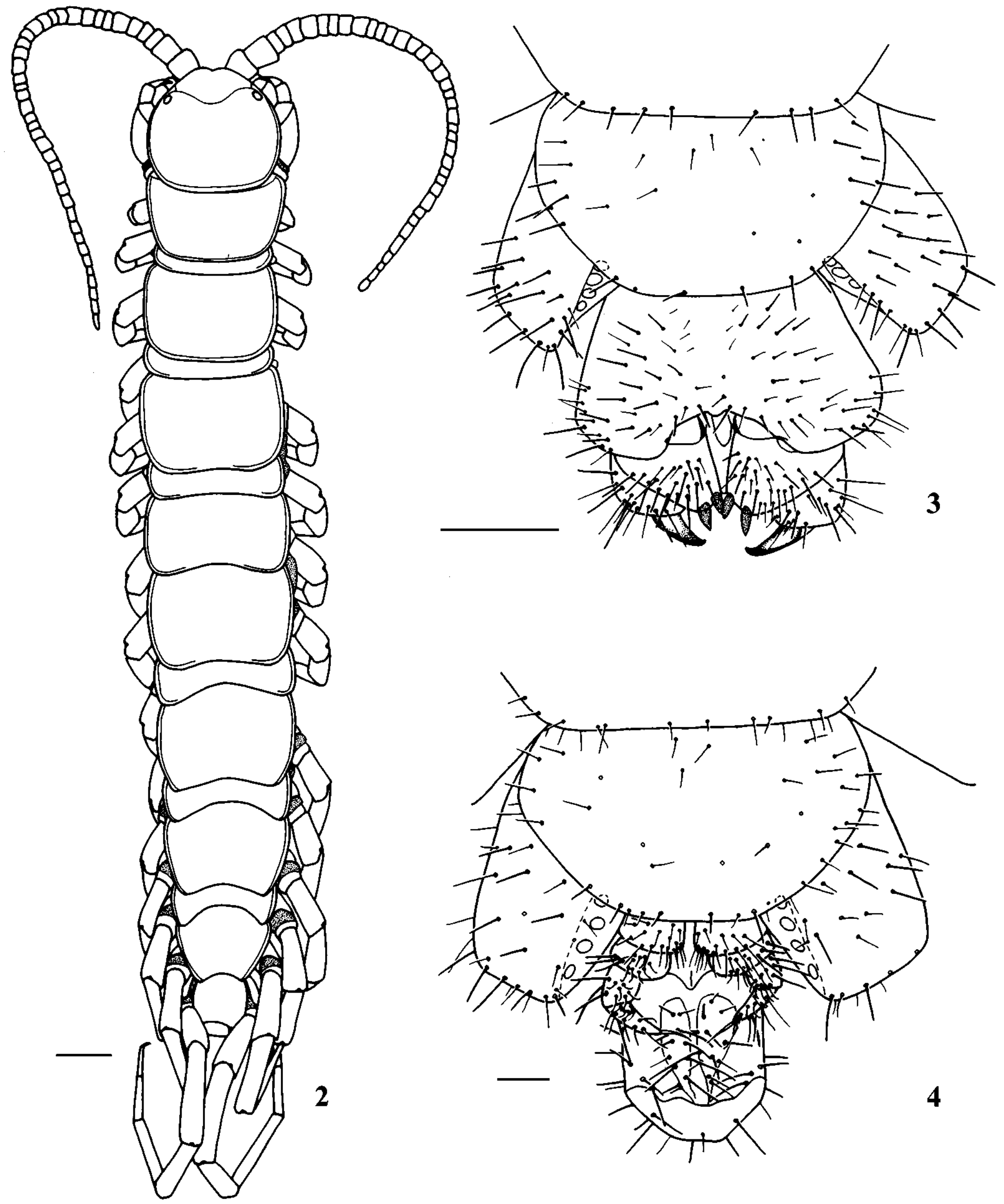
Holotype: Australian Museum [AM] KS 85696 (ex. AM KS 35225), male (Fig. 2), Washpool State Forest (now Washpool National Park), 29º28'29"S 152º20'53"E, track off Cedar Trail, 950 m, M. Gray and P. Croft, 22.ii.1992, pitfall. Length of head 2.3 mm; length of body 18.0 mm.

Paratypes: All Washpool NP. AM KS 35225, 1 female, 2 males, from type collection. AM, M. Gray and P. Croft, 22.ii.–19.iii.1992. From type locality: KS 35224, 2 males; KS 35226, 1 female; KS 35227, 1 male; KS 35228, 2 females, 1 male; KS 35229, 1 female, 1 male; KS 35230, 2 females; KS 35231, 4 males; KS 35232, 1 female, 3 males. Other sites off Cedar Trail: KS 35206, 1 female, 1 male; KS 35207, 1 female, 1 male; KS 35208, 2 males; KS 35209, 1 female; KS 35210, 3 females, 2 males; KS 35211, 1 female, 2 males (Fig. 4); KS 35212, 2 males; KS 35213, 2 females; KS 35214, 1 female; KS 35220, 3 females (Fig. 3); KS 35221, 1 female (Figs. 5–8, 33–36); KS 35222, 1 male; KS 35223, 1 female, KS 9359, 2 males, 2.3 km from Coombadjah along Moogem Rd, C. Horseman, 12.ii.1982; KS 85697, 1 male (Figs. 11–16, 19–32), Coombadjah Creek, C. Horseman, 12.ii.1982. M. Gray and G. Cassis, 4.ii.–9.iv.1993: KS 86367, 6 females, 18 males, NW Fire Trail, 29º27'30"S 152º16'52"E, 950 m; KS 86368, 8 females, 6 males, track off Cedar Trail, 29º28'42"S 152º20'23"E, 950 m; KS 86369, 3 females, 5 males, Cedar Creek, Cedar Trail, 29º28'29"S 152º20'53"E, 920 m; KS 86370, 8 males, 5 females, Washpool Forest Way, 29º24'48"S 152º17'01"E, 860 m; KS 86371, 3 females, 4 males, upper reaches of Eagle Hawk Ck, 29º24'31"S 152º16'53"E, 980 m; KS 86372, 1 female, 5 males, NW Fire Trail, 29º27'36"S 152º17'25"E, 950 m. KS 85698, 1 male (Figs. 9, 17, 40), Washpool NP, Washpool Walk, G. Edgecombe and Y. Y. Zhen, 26.ii.2002.

Other material: The Australian Museum and Queensland Museum have approximately 2000 registered specimens from some 300 localities (Fig. 1). A spreadsheet including those records, with geographical coordinates, elevation, collectors and collection dates, numbers of specimens and registrations, is available at the Zootaxa website (http://www.mapress.com/2005f/zt00961.xls) and is deposited in hardcopy in the Archives of the Australian Museum.

Etymology: For Washpool National Park, the type locality.

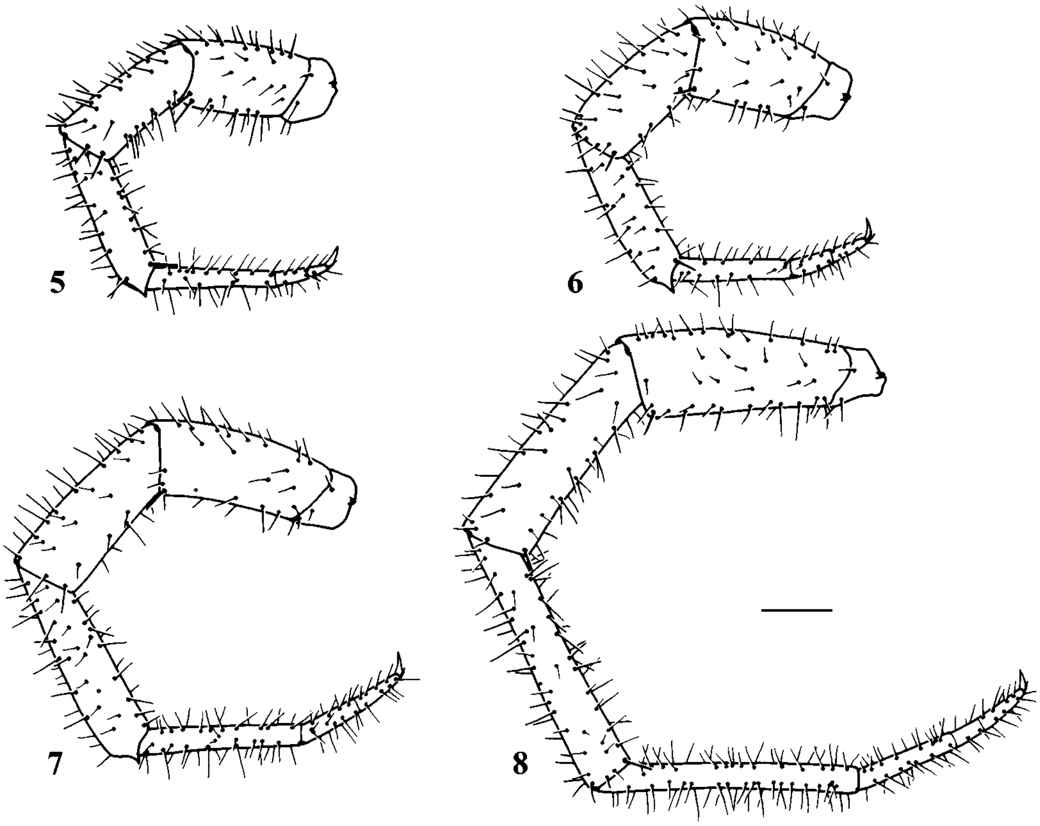
Distribution: New South Wales and Queensland: southern distribution to Narrabeen, Sydney (33º43'), northern distribution to Mt Fisher (17º32') near Ravenshoe, Queensland. Most records in southeastern Queensland and northeastern New South Wales (Fig. 1); wet sclerophyll forest and rainforest; elevation range 10–1450 m.



FIGURES 2–4. *Henicops washpoolensis* n. sp. 2, holotype AM KS 85696, male, scale 1 mm; 3, AM KS 35220, female, posterior segments and gonopods, scale 500 µm; 4, AM KS 35211, male, posterior segments and gonopods, scale 200 µm.

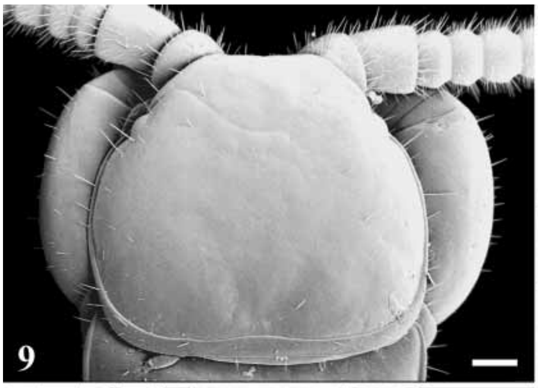
Description: Length (anterior margin of head shield to posterior end of telson) up to 32 mm; width of head shield up to 3.9 mm.

Colour based on specimens in absolute ethanol: antenna deep orange with dark spots scattered over most articles; head shield orange with chestnut mottled network; tergites pale orange with brown mottling concentrated in longitudinal median band and near margins, and dark spots concentrated on margins; maxillipedes orange; sternites pale orange to yellow with purple mottling, darker mottling concentrated on posterior sternites and first genital sternite; prefemur to tibia yellow to pale orange with a large patch of purple mottling on anterior and posterior sides; tarsi deeper orange; genital sternite and gonopods orange. Head and posterior tergites typically chestnut in preserved specimens; most of trunk tergites light brown.



FIGURES 5–8. *Henicops washpoolensis* n. sp. AM KS 35221, female. 5, leg 12; 6, leg 13; 7, leg 14; 8, leg 15. Scale for all 500 µm.

FIGURES 9–16. *Henicops washpoolensis* n. sp. Washpool NP except 10, Richmond Range NP. 9, AM KS 85698, male, dorsal view of head, scale 300 µm. 10, AM KS 85699, female, anterior part of head shield, scale 100 µm. 11–16, AM KS 85697, male. 11, labrum and clypeus, scale 100 µm; 12, bristles on labral sidepiece, scale 5 µm; 13, proximal part of antenna, scale 100 µm; 14, articles from midlength of antenna, scale 50 µm; 15, 16, cephalic pleurite and Tömösváry organ, scales 100 µm, 50 µm.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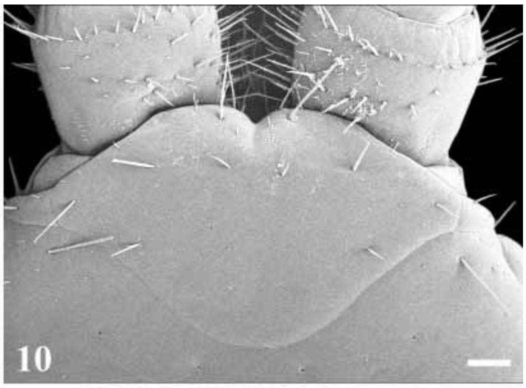
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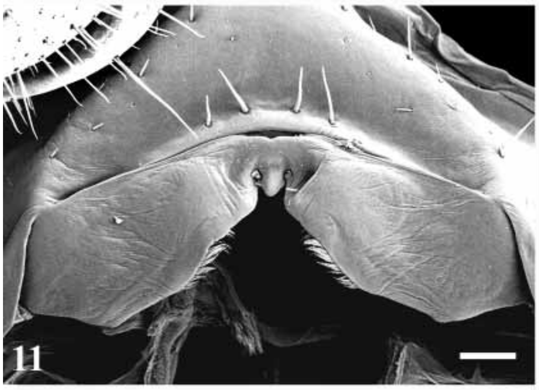
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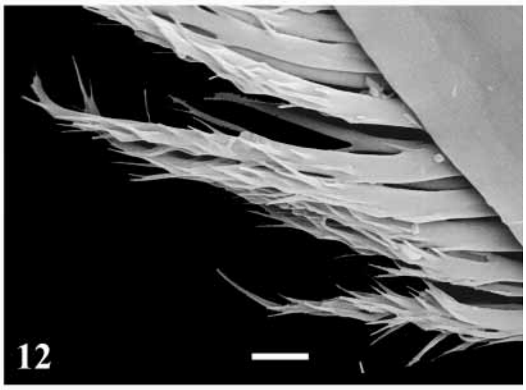
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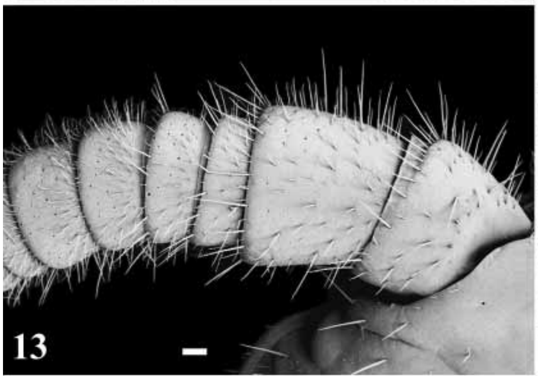
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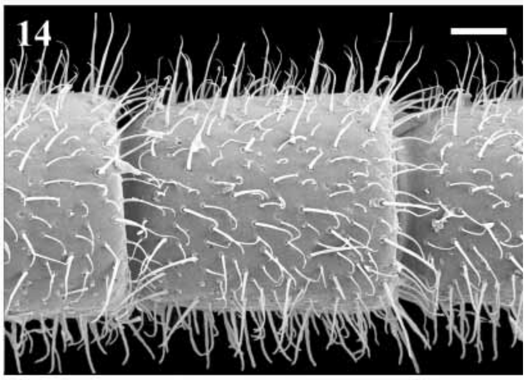
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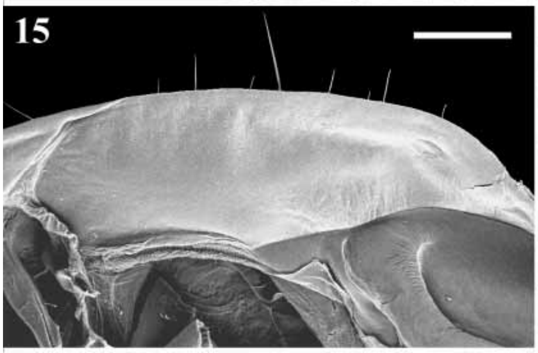
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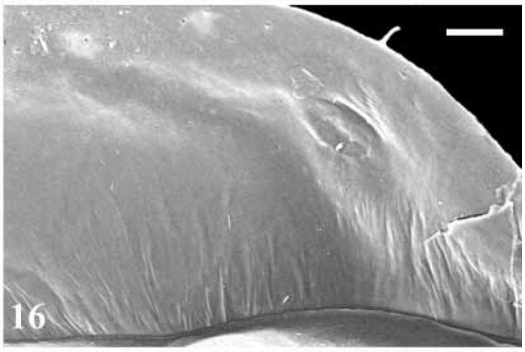
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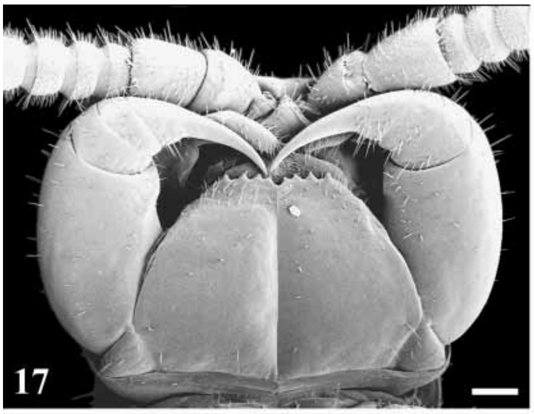
Head shield smooth. Frontal margin with strong anterior notch, weak median furrow confined to area just behind anterior notch (Fig. 10); posterior margin of head shield transverse or faintly concave; border variably slightly wider posteromedially than posterolaterally (Fig. 9). Antenna usually extends back to tergite 5 or 6; 33–51 antennal articles in specimens with head greater than 1.75 mm wide, majority of specimens with 38–45; basal two articles much larger than succeeding two (Fig. 13); markedly uneven change in the length of articles in proximal part of antenna, with short paired articles interspersed between longer articles, gradually elongating along antenna; trichoid sensilla increasing in density between articles 3 and 6, then about evenly dense along rest of antenna (Figs. 14, 45); one or two club-shaped thin-walled basiconic sensilla (Fig. 47) and groups of two (Fig. 48) to four conical thick-walled sensilla at anterior end of articles on dorsal side of antenna; cluster of slender, tapering sensilla brachyconica at tip of terminal antennal article (Fig. 46). Posterior part of ocellus set inward of lateral margin of head; ocellus domed, usually translucent, sometimes whitish to dark purple. Tömösváry organ small, shallow, its outer edge positioned well inward of lateral margin of cephalic pleurite (Figs. 15, 16). Labral margin with rounded shoulder beside midpiece, with a gradual break in curvature where fringe of branching bristles overhangs margin (Fig. 11); bristles with many short, spine-like projections along most of their length, sparse or lacking proximally (Fig. 12).

Maxillipede coxosternum trapezoidal (Figs. 17, 18, 41), dental margin broad, each half weakly convex (Figs. 19, 20); median notch shallow; teeth moderately large, triangular projections, usually 3+3 (Figs. 41–43) or 4+4 (Figs. 17–20) in large specimens, sometimes 5+5 in New South Wales samples, rarely 4+5/5+4, 5+6/6+5, very exceptionally 6+6; immature specimens typically 3+3; in 4+4 arrangement, outer pair distinctly more distant from each other than are inner pair (Fig. 20), as much as 1.8 times distance between inner pair. Coxosternum bearing moderate number of mostly short and moderately long setae, mostly in anterior half, especially concentrated behind dental margin and anterolaterally (Fig. 18). Tarsungulum with long, slender pretarsal part, about twice length of tarsal part (Fig. 21). Setae longer and slightly more densely clustered on inner side of tarsal part of tarsungulum than on outer side (Fig. 19). Duct of poison gland gradually widening distally, extending into tibia.

FIGURES 17–24. *Henicops washpoolensis* n. sp. Washpool NP except 18, Richmond Range NP. 17, AM KS 85698, male, ventral view of head, scale 300 µm. 18, AM KS 85699, female, ventral view of maxillipedes, scale 100 µm. 19–24, AM KS 85697, male. 19, 20, dental margin of maxillipede coxosternum, scales 100 µm, 50 µm; 21, dorsal view of maxillipede tarsungulum, scale 100 µm; 22, second maxillary coxosternum, scale 50 µm; 23, 24, tarsus and claw of second maxilla, scales 50 µm, 20 µm.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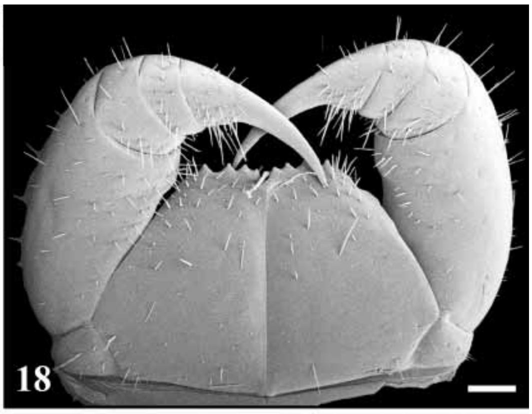
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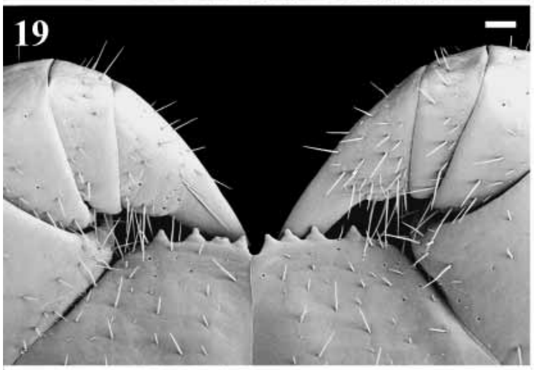
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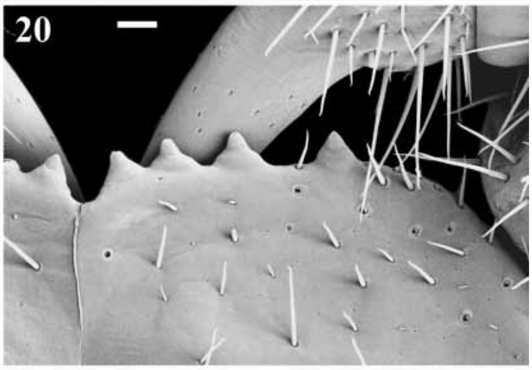
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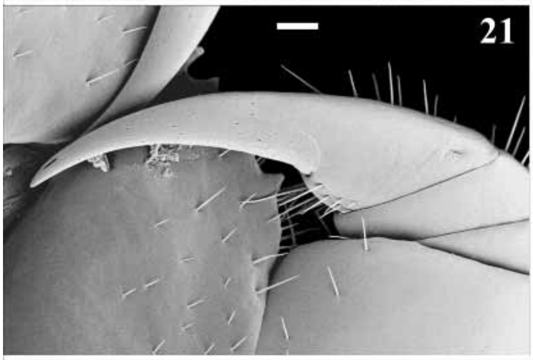
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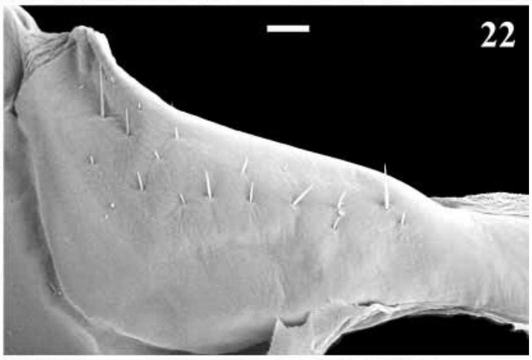
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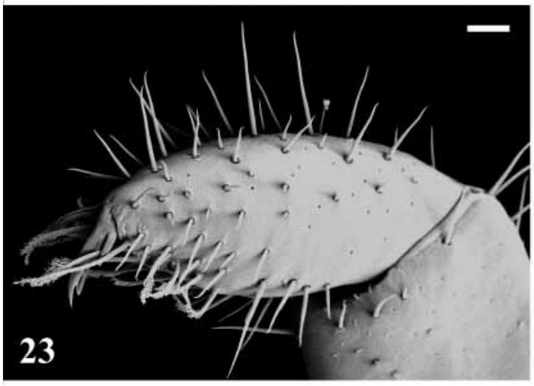
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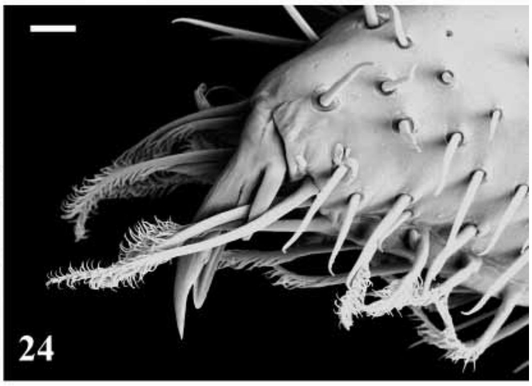
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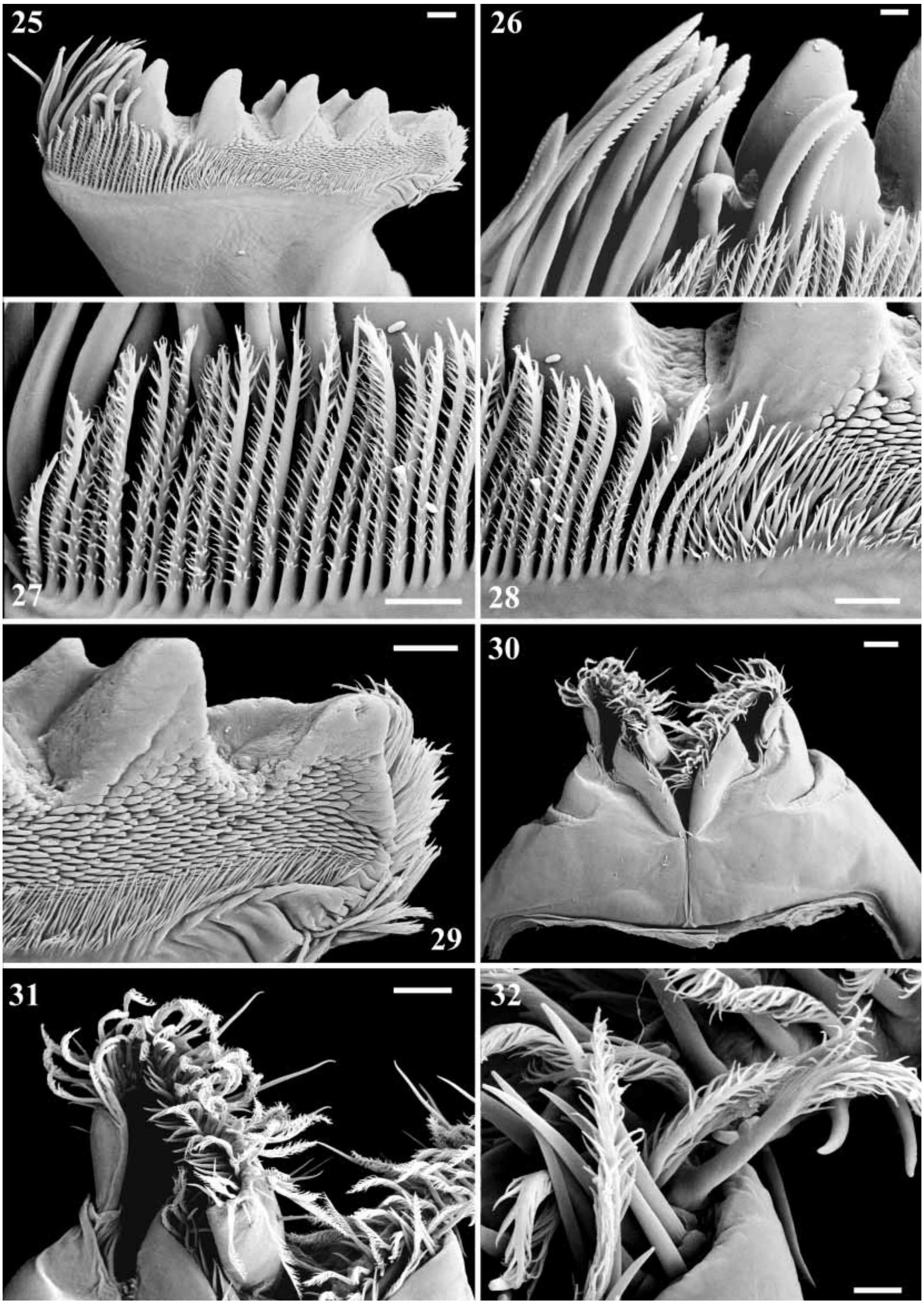


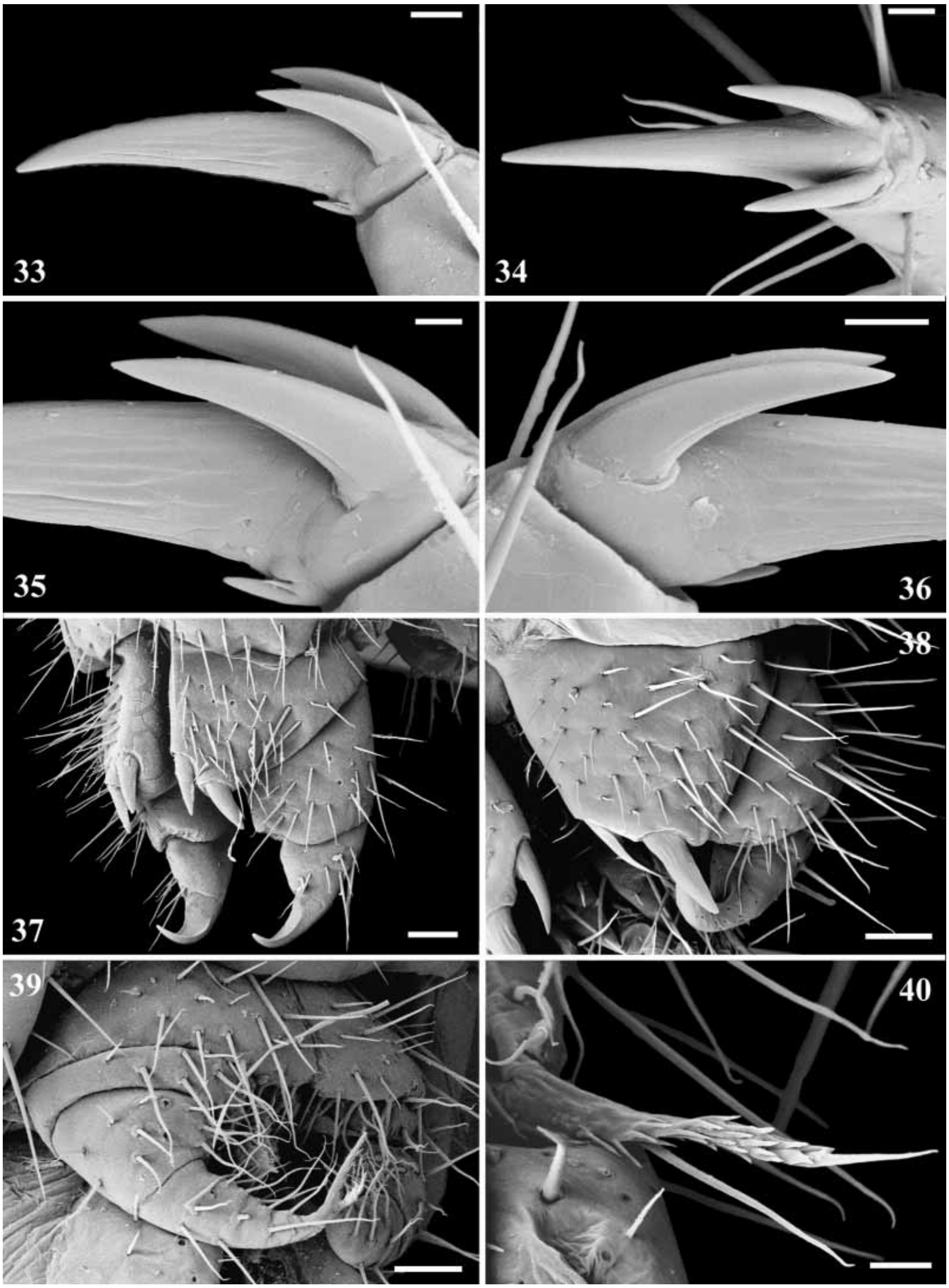
FIGURES 25–32. *Henicops washpoolensis* n. sp. AM KS 85697, male, Washpool NP. 25–29, mandible. 25, gnathal edge, scale 30 µm; 26, aciculae, scale 10 µm; 27, 28, fringe of branching bristles, scales 10 µm; 29, dorsal teeth and furry pad, scale 10 µm. 30–32, first maxillae. 30, scale 50 µm; 31, coxal processes and telopodite, scale 50 µm; 32, apical setae on coxal process, scale 10 µm.

Four paired teeth on right mandible, left mandible with smaller flattened fifth tooth adjacent to furry pad (Fig. 29). 14–20 aciculae arranged as inner and outer rows (Fig. 26); some aciculae with pronounced serrations on both margins, along distal half to quarter of both sides of each acicula, others with simple margin along most of length except for near distal tip. Fringe of plumose bristles skirts aciculae, with abrupt transition to shorter row of scale-like bristles adjacent to midpoint of second tooth (Fig. 28); row of scale-like bristles evenly narrowing dorsally to very narrow fringe near furry pad (Fig. 29); plumose bristles narrow-based, basal part (not more than 20% of total length) lacking spines (Fig. 27); remainder of bristle with short, slender spines over all surfaces, spines gradually lengthening distally; bristles with a few strong spines distally. Accessory denticle field with pronounced groove between rows of denticles or at margin of denticle field (Figs. 25, 29); largest accessory denticles flattened conical, grading into small, slender, pointed denticles near fringe of scale-like bristles; slender, elongate accessory denticles do not intergrade with furry pad, separated by a narrow band of unsculpted cuticle; furry pad with many elongate, simple bristles, some bifid or pauciramous bristles (Fig. 29).

First maxilla with minute, wedge shaped sternite (Fig. 30). Apex of coxal process with a few (3–5) plumose setae and up to 14 simple setae (Fig. 32); distal article of telopodite with two rows of up to 18 long, plumose setae along inner margin, of similar structure to plumose setae on coxal process; branches developed along distal half of these setae (Figs. 31, 44). Band of short, simple setae on membranous strip alongside inner margin; main, more sclerotised field of distal article of telopodite usually with numerous evenly scattered setae (Fig. 44).

Second maxillary sternite small, fused with coxae. Up to 20 short setae scattered across anterior part of coxa (Fig. 22). Tarsus bearing numerous simple setae on outer surface (Fig. 23), dense cluster of plumose setae on membranous patch on inner surface (Fig. 24), up to 40 plumose setae in exceptionally large specimens; branches on plumose setae mostly confined to distal half. Claw small, composed of five digits, median and outer pair long, thick, with shorter, needle-like digit between median and each outer digit (Fig. 24).

Tergites weakly wrinkled. T1 trapeziform, varying from slightly narrower than head shield to slightly wider (Fig. 2), about 70% width of widest tergite (T8), posterior angles rounded, posterior margin transverse or (usually) faintly concave; lateral borders subparallel in TT3 and 5, posterior angles rounded; posterior border transverse or (usually) gently concave in T3, gently concave in T5; TT1, 3 and (variably) 5 bordered posteriorly; border of T7 incomplete posteriorly; posterior margin of T7 moderately and rather evenly concave; posterior margin of T8 slightly less concave than T7; posterior angles of TT7 and 8 blunt; posterior margins of TT10 and 12 moderately concave, posterior angles with obtuse, blunt corners; T9 with short projections; TT11 and 13 with moderately long projections; posterior margin of T14 strongly concave. Lateral margins of anterior tergites with a few moderately large setae, posterior margins with fringe of minute, slender setae; posterior tergites with more numerous moderate sized setae on lateral and posterior margins and scattered on surface.



FIGURES 33–40. *Henicops washpoolensis* n. sp. 33–36, AM KS 35221, female, Washpool NP. 33, 34, pretarsus of leg 14, posterior and dorsal views, scales 20 µm; 35, 36, proximal part of pretarsus of leg 14, posterior and anterior views, scales 10 µm. 37, AM KS 85699, female, Richmond Range NP, ventrolateral view of gonopods, scale 100 µm. 38, AM KS 89347, female, Border Ranges NP, gonopods, scale 100 µm. 39, AM KS 89633, male, Mt Hyland Nature Reserve, gonopods, scale 100 µm. 40, AM KS 85698, male, Washpool NP, terminal filament on gonopod, scale 20 µm.

Strong, pointed distal projections with sclerotised tips on tibiae of legs 1–14. Prefemur and femur with scattered moderate-sized setae; a few thickened setae encircling distal margin of femur; most setae on tibia of similar length to those on prefemur and femur but slightly more slender; three or four irregularly paired thicker, more pigmented setae on ventral face of tibia of legs 1–13; tarsus with combination of scattered slender setae, of fairly even length, and irregularly paired, thicker, pigmented setae at intervals along ventral face, two or three pairs on basitarsus, one or two on distitarsus. Setae on legs 14 and 15 more slender than on preceding legs, fine radiating setae on tarsus of leg 15. Two tarsomeres in legs 1–12, articulation between them strong on all legs, with small condyle dorsally; three tarsomeres in legs 13 (Fig. 6) and 14 (Fig. 7), basitarsus undivided, distitarsus with two parts; distitarsus of leg 14 occasionally with weak indication of an additional articulation on ventral half of distal tarsomere; leg 15 with three or four tarsomeres, basitarsus undivided, distitarsus in two or three parts (Fig. 8), the latter involving a weaker distal articulation; distitarsus about 70% length of basitarsus on leg 15; leg 15 basitarsus approximately 12 times longer than maximum width. Pretarsus with anterior and posterior accessory claws on all legs, about 40% length of main claw (Fig. 34), inserted on dorsolateral side of main claw, with gentle dorsoventral curvature (Figs. 33, 35, 36). 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 (e.g., two) pores between some of these scales (Fig. 35), few pores on dorsal side of claw; scales indistinct proximally beneath bases of accessory claws, well defined dorsoproximally. Posteroventral spine present on all legs, about 10% length of main claw, directed distally, bearing slender subsidiary spine that parallels it on its dorsoproximal half (Fig. 35).

Sternal margins with numerous mostly moderately long setae; two pairs of setae across anteromedial part of sternites; setae slightly more numerous on posterior sternites.

Coxal pores round or transversely ovate, overwhelmingly 4,4,4,4/4,4,4,4 in large males and 5,5,5,5/5,5,5,5 in large females, males (width head shield >1.75 mm) maximum 4,5,5,5/4,5,5,5, minimum 2,3,3,3/2,3,3,3; females (width head shield >1.75 mm) maximum 6,5,5,5/6,5,5,5, minimum 3,3,3,3/3,3,3,3. Coxal pore field delimited from anteroventral face of coxa by rounded edge in most specimens, or with variably developed fold, when present, distal coxal pores may be partly concealed in ventral view by fold. Anal pores large in both sexes.

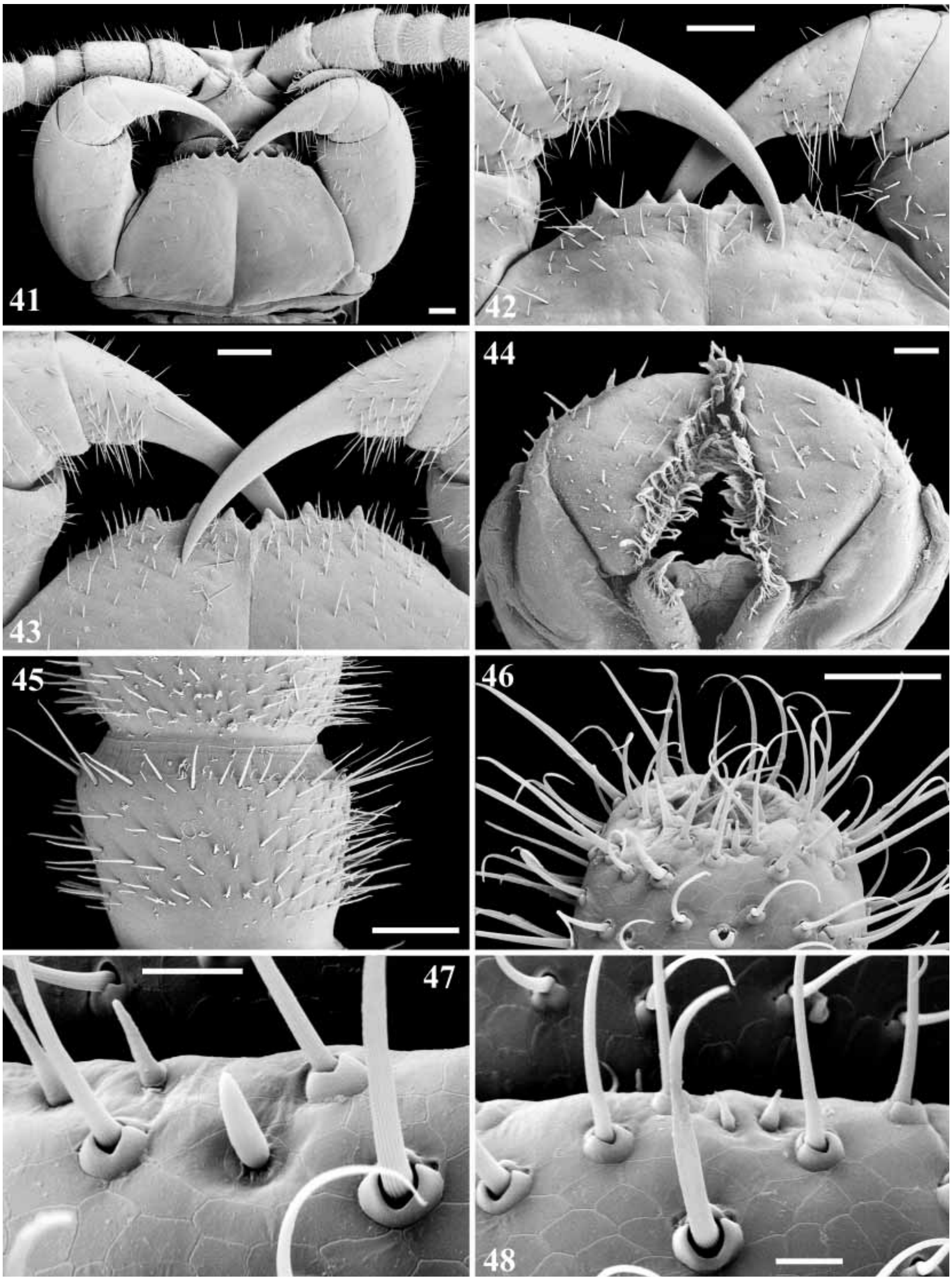
Female with sternite of segment 15 transverse or convex posteromedially. Tergites of first genital segment and telson usually well sclerotised. Sternite of first genital segment evenly scattered with a combination of up to 70 short and moderately long setae (Fig. 3). First article of gonopod bearing two elongate, bullet-shaped spurs of equal size; spurs gently curved (Fig. 38); generally 20–40 moderate to long setae on first article of gonopod (Figs. 37, 38), 15–20 on second, up to 30 in exceptionally large specimens; third article with up to 15 setae in very large specimens. Claw undivided, with numerous sensilla coeloconica on its dorsodistal surface.

Male with sternite of segment 15 rounded posteriorly/posterolaterally. Sternite of first genital segment small, divided, bearing about 15 long, evenly scattered setae on each half, including fringe of about 8 setae along each half of posterior margin (Figs. 4, 39). Gonopod of three articles and tapering terminal process; setae mostly moderately long, generally 10–12 on first article, 8–12 on second (Fig. 39), up to 13 on third; terminal process with about 20 short, slender spines densely grouped along much of its length (Fig. 40).

Discussion: *Henicops washpoolensis* is easily distinguished from all previously named mainland Australian species by the presence of only two tarsomeres on legs 1–12 (versus three in the other species, with the basitarsus divided). The ocellus is situated relatively inward on the head shield (versus more strongly bulging over the lateral margin of the head shield in other species). Most specimens through most of the species' range in New South Wales have more than three teeth on the dental margin of the maxillipede coxosternum (versus fixed at three in other species), and most specimens have a greater number of articles in the antenna than do most other *Henicops*. The female gonopod spurs are more elongate (Figs. 3, 37, 38) than in several other species, such as *H. dentatus* and *H. milledgei*. The weakly recessed Tömösváry organ and simple, concave margin of tergite 7 allow for further distinction from *H. dentatus* and *H. tropicanus*.

Specimens from southeastern Queensland and the Border Ranges and Nightcap Range in northernmost New South Wales nearly invariably have 3+3 teeth on the maxillipede coxosternum, 4+4 being exceptional (see Fig. 1 for geographic locations cited in the following discussion). Samples from the Richmond Range and the type area (Washpool National Park) have a higher frequency of moderate sized and large (adult) specimens with 3+3 teeth than is observed farther south in the species' range (e.g., Dorrigo, Barrington Tops, Mt Wilson), where the count of 4+4 is more constant. In the more southerly samples, 4+4 teeth are present in specimens smaller than the smallest of those with 4+4 teeth in the Washpool or Richmond Range samples, and the frequency of specimens with five teeth on one or both dental margins increases to the south.

Antennal segmentation also exhibits geographic variation. Most large specimens from northern New South Wales and southernmost Queensland (e.g., Lamington National Park) have more than 40 antennal articles. A population from the southern end of the distribution, Mt Wilson in the Blue Mountains, New South Wales, has only 34–37 articles, and with only rare exceptions specimens from north of 27ºS in Queensland likewise have relatively few (35–39) articles. Exceptionally specimens from the wet tropics (north Queensland) have antennal segmentation and maxillipede dentition more typical of samples from northern New South Wales (e.g., QMS 39916 from Mt Fisher has 45 antennal articles and 4+4 coxosternal teeth). Specimens from the northern part of the distribution in Queensland (Rockhampton region to the wet tropics) have fewer coxal pores than do samples from other parts of the species' range (only 2,3,3,3/2,3,3,3 or 3,3,3,3/3,3,3,3 in males versus a typical 4,4,4,4/4,4,4,4 farther south).



FIGURES 41–48. *Henicops washpoolensis* n. sp. 41, 42, 46–48, AM KS 89347, Border Ranges NP. 41, 46–48, male. 41, ventral view of head, scale 200 µm; 46, sensilla at tip of antenna, scale 15 µm; 47, 48, basiconic sensilla at anterior edge of antennal article, scales 10 µm; 42, female, maxillipedes, scale 200 µm. 43, 44, AM KS 89343, male, Barrington Tops. 43, maxillipedes, scale 200 µm; 44, coxal processes and telopodites of first maxillae, scale 50 µm. 45, AM KS 89632, female, Mt Hyland Nature Reserve, third antennal article, scale 100 µm.

The maximum number of coxal pores differs between females and males in that females have an anteroposterior polarity of an anterior increase (maximum 6,5,5,5/6,5,5,5) whereas males increase posteriorly (maximum 4,5,5,5/4,5,5,5). However, some specimens exhibit the opposite trends, with females increasing posteriorly (4,5,5,5/4,5,5,5) and males increasing anteriorly (5,4,4,4/5,4,4,4).

Several samples throughout the geographic range of the species in New South Wales include a few particularly large individuals (length up to 32 mm) that consistently have 3+3 teeth on the maxillipede coxosternum (Fig. 43). This is the case even where other co-occurring individuals of more typical size, up to about 25 mm in body length, have 4+4 teeth (e.g., at Mt Hyland, Dorrigo and the Barrington Tops). Other than size, no other morphological characters permit the anomalously large individuals to be distinguished from *H. washpoolensis*. A 435 bp fragment of mitochondrial 16S rRNA for one of the large individuals from Mt Hyland with 3+3 teeth is identical to that of specimens of *H. washpoolensis* from Washpool National Park with 4+4 teeth, and these sequences differ at several positions from other populations in New South Wales, e.g., Dorrigo, Nightcap Range, Border Ranges (work in preparation). Accordingly we have retained the large specimens in *H. washpoolensis*.

Phylogenetic analysis

Henicops washpoolensis was scored for the 41 morphological characters used by Edgecombe (2004, Table 1 and Appendix therein) for an analysis of *Henicops* in the context of the Henicopinae. One additional character was added to code for the absence of ocelli (character 42: absent in *Lamyctes coeculus*, *L. hellyeri*, and *Paralamyctes* (*Haasiella*) *trailli*; present in all other species). The taxonomic sample used in the earlier analysis is augmented with three species, *Henicops washpoolensis*, *Lamyctes hellyeri* Edgecombe & Giribet, 2003, and *L. inermipes* (Silvestri, 1897), the codings for which are shown in Table 1. As described previously (Edgecombe 2004), cladograms are rooted between Zygethobiini (*Zygethobius* and *Cermatobius*) and Henicopini (*Paralamyctes* and the *Lamyctes-Henicops* group). Multistate characters are unordered. One multistate character was coded and analysed as polymorphic (mstaxa=polymorph).

TABLE 1. Codings for three species added to morphological character data of Edgecombe (2004, Appendix and Table 1 therein). 'A' indicates polymorphism (states 0 + 1). New character 42 is discussed in the text.

Lamyctes hellyeri	-100000001 0000100100 0010000110 00--0001?0 01
Lamyctes inermipes	0100000001 0000100100 0010000210 00--000100 00
Henicops washpoolensis	0101000100 1000000110 0000010300 010A000010 00

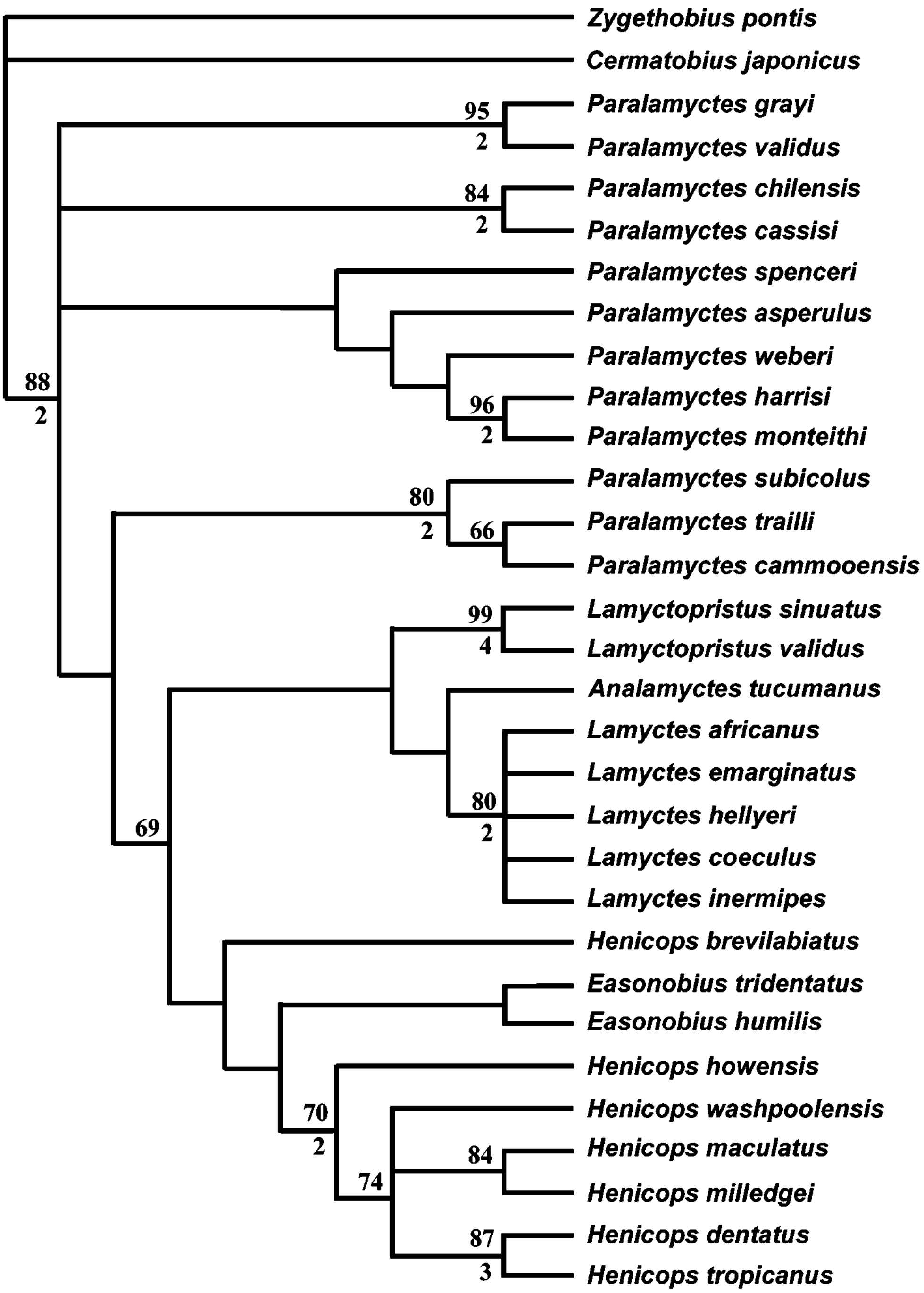


FIGURE 49. Strict consensus of 44 shortest cladograms for *Henicops* and other Henicopinae based on 42 morphological characters (Edgecombe 2004: Table 1, supplemented with Table 1 herein) with equal character weights. Numbers above nodes are jackknife frequencies above 50%. Numbers below nodes are Bremer support values greater than 1.

Parsimony analysis used PAUP* 4.0b10 (Swofford 2002). A heuristic search used 1000 random stepwise addition sequences, saving 5 trees per replicate, then swapping on those trees with TBR (Tree Bisection Reconnection) branch swapping. Support for nodes was evaluated by parsimony jackknifing, with 1000 jackknife replicates using the same heuristic search procedure as described above, each with 37% character deletion and 'jac' resampling. Bremer support was computed by the 'enforce converse constraints' command in PAUP*, using MacClade version 4.0 (Maddison and Maddison 2000) to generate the PAUP* command file with converse constraints. Stability of clades to alternative measures of character fit was explored by reanalyzing the data with implied weights during tree search (Goloboff 1993), exploring a range of concavity parameters for character fit (k=1, 2, 3, 4, 5 and 6). Each analysis used a heuristic search with 1000 random stepwise addition sequences, saving 5 trees per replicate.

Analysis of the morphological data with the commands described above retrieves 44 shortest cladograms for equal weights (Length=105; Consistency Index=0.52; Retention Index=0.75; Rescaled Consistency Index=0.39), the strict consensus of which is shown in Fig. 49. In half the shortest cladograms, *Henicops washpoolensis* is resolved as sister to a southeastern Australian/New Zealand clade composed of *H. maculatus* and *H. milledgei*, whereas in the remaining cladograms those latter species are more closely related to a clade composed of *H. dentatus* and *H. tropicanus* than to *H. washpoolensis*. The five *Henicops* species in Australia and New Zealand are a monophyletic group, with *H. howensis* from Lord Howe Island their sister. Under equal weights, the two New Caledonian species that comprise the genus *Easonobius* Edgecombe, 2003, are more closely related to *Henicops* than is the New Caledonian species *H. brevilabiatus* (Ribaut, 1923), although an alternative resolution for the latter species is discussed below.

The traditional delimitation of *Henicops* (Attems 1911, 1914, 1928; Archey 1917, 1937; Chamberlin 1920) is the most inclusive clade that includes *H. maculatus* and *H. dentatus*. That grouping is defined in one resolution by two unambiguous, unreversed autapomorphies, a relatively wide and straight dental margin of the maxillipede coxosternum, and mandibular aciculae arranged as an inner and an outer row (Fig. 26). Two additional characters support the same group under Accelerated Transformation: a tripartite tarsus on legs 1–12, and a tripartite distitarsus on leg 15. In the other equally parsimonious resolution, the traditional grouping of *Henicops* is defined by the tripartite tarsus on legs 1–12 alone, and the other characters listed above define a broader grouping that unites *H. maculatus*, *H. milledgei*, *H. dentatus* and *H. tropicanus* with *H. washpoolensis*. In the topology in which *H. washpoolensis* groups with *H. maculatus* and *H. milledgei*, those three species are united by a weakly recessed Tömösváry organ situated near midwidth of the cephalic pleurite (Figs. 15, 16) rather than near the margin of the pleurite.

Of the two equally parsimonious placements for *Henicops washpoolensis* based on morphology, molecular data favour a closer relationship between *H. washpoolensis* and *H. maculatus* than either shares with *H. dentatus*. Combined analysis of 18S rRNA, 28S rRNA, 16S rRNA and COI sequences (Edgecombe & Giribet 2003a, b) retrieved a grouping of *H. washpoolensis* ("*Henicops* SE QLD" in those studies) and *H. maculatus* to the exclusion of *H. dentatus* in 98% of jackknife replicates for the optimal analytical parameters.

In all 44 minimal length cladograms based on morphology under equal weights, two unambiguous, unreversed characters unite the five Australasian species of *Henicops* with *H. howensis*: leg 14 has a strong distal spinose projection on the tibia, and legs 14 and 15 have divided distitarsi. That node receives a moderate jackknife value (70%) and Bremer support of 2, with higher jackknife values for the node uniting the five Australasian species (74%) and the sister species pairs *H. maculatus* + *H. milledgei* (84%) and *H. dentatus* + *H. tropicanus* (87%).

Analyses using implied weights with k=1, 2, 3 and 4 each retrieve 837 or 838 cladograms with optimal fit. The strict consensus is identical to that figured by Edgecombe (2004, fig. 2) except that the two additional *Lamyctes* species are nested within that genus, and *Henicops washpoolensis* has the same (unresolved) relationships as in Fig. 49. Analyses with k=5 and 6 retrieve 20 optimal cladograms that are a subset of those found using equal weights. Implied weights for k=1–4 favour *Henicops brevilabiatus*, rather than *Easonobius*, being sister group of *Henicops howensis* and Australasian *Henicops*. This hypothesis is supported by the division of the first genital sternite of the male into two sclerites, an apomorphic character otherwise only observed in a subgroup of *Lamyctes*. The rival characters that unite *Easonobius* and *Henicops* (exclusive of *H. brevilabiatus*) under equal weights exhibit considerable homoplasy, and are optimised as reversals at that node (a short pretarsal section of the maxillipede tarsungulum; divided tarsi). In light of the resolution favoured by implied weights (Edgecombe 2004, fig. 2) and strong molecular support for a relationship between *H. brevilabiatus* and *Henicops* (Edgecombe & Giribet 2003a, b), the species is assigned to *Henicops*.

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