

A new blind *Lamyctes* (Chilopoda: Lithobiomorpha) from Tasmania with an analysis of molecular sequence data for the *Lamyctes-Henicops* Group

GREGORY D. EDGECOMBE¹ & GONZALO GIRIBET²

¹Australian Museum, 6 College Street, Sydney, NSW 2010, Australia; greged@austmus.gov.au

²Department of Organismic and Evolutionary Biology, Harvard University, 16 Divinity Avenue, Cambridge, MA 02138, USA; ggiribet@oeb.harvard.edu

Abstract

The cosmopolitan, parthenogenetic centipede *Lamyctes coeculus* (Brölemann, 1889), type species of *Lamyctinus* Silvestri, 1909, occurs in New South Wales and Lord Howe Island, Australia, the former genetically identical to specimens from Tucumán, Argentina. Parsimony analysis of complete sequences of 18S rRNA and fragments of 28S rRNA, 16S rRNA, and cytochrome *c* oxidase subunit I for the *Lamyctes-Henicops* group suggests that loss of ocelli in *Lamyctes coeculus* has an independent origin from blindness in *Lamyctes hellyeri* n. sp. from northern Tasmania. *Lamyctinus* is nested within *Lamyctes* Meinert, 1868, its senior synonym. *Lamyctes hellyeri* is known exclusively from females in gardens, and is probably introduced to Tasmania.

Key words: Chilopoda, Lithobiomorpha, Henicopidae, *Lamyctes*, *Lamyctinus*, *Lamyctes hellyeri*, taxonomy, molecular data

Introduction

Lamyctinus Silvestri, 1909, was proposed as a monotypic genus in the lithobiomorph family Henicopidae. Its type species, *Lithobius coeculus* Brölemann, 1889, is noteworthy for having a widespread, probably largely synanthropic distribution, being parthenogenetic in most occurrences (Enghoff 1975). The species has been recorded from European greenhouses (the types being from a greenhouse in Italy), Mexico (Silvestri 1909; Chamberlin 1943), Illinois, USA (Auerbach 1952), Venezuela (Turk 1955), Cuba and Tanzania (Enghoff 1975), Palestine (Negrea & Matic 1996), the Canary Islands (Eason & Enghoff 1992), and Hawaii (Zapparoli & Shelley 2000). *Lamyctinus coeculus* was reported from Sydney, Australia, by Silvestri (1909) but no additional Australian records have since been pub-

lished. Males are unknown or very rare in all occurrences except possibly from Cuba (Enghoff 1975).

Morphologically, *Lamyctinus* is distinguished from *Lamyctes* Meinert, 1868, by one conspicuous character, the absence of ocelli. Some workers considered this distinction to be insignificant at the generic level (Brölemann 1930; Enghoff 1975). However, larval characters of *L. coeculus* are peculiar within Lithobiomorpha (Andersson 1979). The species hatches with only six pairs of legs and two limb-buds [versus seven leg pairs and one pair of limb buds in *Lamyctes fulvicornis* (= *L. emarginatus*) and many Lithobiidae] and is unique in having eight antennal articles in larval stage L0 (versus seven in *L. fulvicornis* and many Lithobiidae) (Andersson 1979). These differences have been cited as criteria for retaining *Lamyctinus* (Eason 1982; Edgecombe et al. 2002), although it remains to be seen how these characters vary in other species of *Lamyctes*.

Here the occurrence of *Lamyctes coeculus* in Australia is reviewed. Morphologically and genetically identical specimens from Tucumán Province, Argentina, confirm the occurrence of *L. coeculus* in southern South America. Molecular sequence data from a new blind species of the *Lamyctes-Henicops* group from northern Tasmania are used to determine whether the loss of ocelli in this group has a single origin and to explore the status of *Lamyctinus*. The molecular data include four genes (two nuclear ribosomal genes, one mitochondrial ribosomal gene, and one mitochondrial protein coding gene). The markers utilised are 18S rRNA, the D3 region of 28S rRNA, a fragment of 16S rRNA, and a fragment of cytochrome *c* oxidase subunit I, as in previous analyses of hemicopid phylogeny (Edgecombe et al. 2002).

Taxonomy

The following abbreviations are used for repositories of specimens described herein: AM, Australian Museum, Sydney; ANIC, Australian National Insect Collection, Canberra; CAS, California Academy of Sciences, San Francisco; MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, MA; QM, Queensland Museum, Brisbane; QVMAG, Queen Victoria Museum and Art Gallery, Launceston.

Lamyctes Meinert, 1868

= *Lamyctinus* Silvestri, 1909
= *Metalamyctes* Verhoeff, 1941

Type species: *Lamyctes fulvicornis* Meinert, 1868 [= *L. emarginatus* (Newport, 1844)].

Assigned species: *Lamyctes adisi* Zaleskaja, 1994; *Henicops africanus* Porat, 1871 (= *H. insignis* Pocock, 1891); *L. albipes* Pocock, 1894 (= ?*L. mauriesi* Demange, 1981); *L. anderis* Chamberlin, 1955; *L. andinus* Kraus, 1954 (= *L. neglectus* Chamberlin, 1955; *L.*

rectus Chamberlin, 1955; ?*L. subtropicalis* Chamberlin, 1955); *L. baeckstroemi* Verhoeff, 1923; *L. caducens* Chamberlin, 1938; *L. cairensis* Chamberlin, 1921; *L. calbucensis* Verhoeff, 1939; *L. castaneus* Attems, 1909; *L. cerronus* Chamberlin, 1957; *Lithobius coeculus* Brölemann, 1889; *Lamyctes cuzcotes* Chamberlin, 1944 (= *L. alancayanus* Chamberlin, 1955); *L. diffusus* Chamberlin & Mulaik, 1940; *Henicops emarginatus* Newport, 1844 (= *Lamyctes chathamensis* Archey, 1917; *L. fulvicornis* Meinert, 1868; *L. fulvicornis* var. *hawaiiensis* Silvestri, 1904; *L. kermadecensis* Archey, 1917; ?*L. munianus* Chamberlin, 1920; *L. neozelanicus* Archey, 1917; ?*L. navaianus* Chamberlin, 1920; *L. tasmanianus* Chamberlin, 1920; *L. zelandicus* Chamberlin, 1920); *L. gracilipes* Takakuwa, 1940; *L. guamus* Chamberlin, 1946; *L. guamus koshiyamai* Shinohara, 1957; *L. hellyeri* n. sp.; *Henicops inermipes* Silvestri, 1897; *L. insulanus* Verhoeff, 1941; *L. leon* Chamberlin, 1944; *L. leleupi* Matic and Darabantu, 1977; *L. liani* Larwood, 1946; *L. medius* Chamberlin, 1951; *L. microporus* Attems, 1909; *L. neglectus* Lawrence, 1955a (homonym of *L. neglectus* Chamberlin, 1955); *L. neotropicus* Turk, 1955; *L. nesiotes* Chamberlin, 1952; *L. omissus* Kraus, 1957; *L. orthodox* Chamberlin, 1951; *L. oticus* Archey, 1921; *L. pachypes* Takakuwa, 1941; *L. pacificus* Silvestri, 1905 [subspecies of *L. inermipes* (Silvestri, 1987) *vide* Demange and Silva, 1976]; *L. pinampus* Chamberlin, 1910; *L. pius* Chamberlin, 1911; *L. remotior* Chamberlin, 1955; *L. robustus* Lawrence, 1955b; *L. setigerus* Lawrence, 1955b; *L. taulisensis* Kraus, 1954 (= *L. brattstroemi* Chamberlin, 1955); *L. tivius* Chamberlin, 1911; *L. tolucanus* Chamberlin, 1943; *L. transversus* Chamberlin, 1962; *Henicops tristani* Pocock, 1893.

Discussion: The phylogenetic analysis discussed below concludes that the absence of ocelli in *Lamyctes hellyeri* n. sp. has an independent origin from blindness in *L. coeculus*. Accordingly, these two species should not be united as a taxon defined by the absence of ocelli, as would be consistent with the *Lamyctinus* concept. Furthermore, the type species of *Lamyctinus*, *L. coeculus*, is nested within the cladistic structure of *Lamyctes*, rather than being its sister group. Recognising *Lamyctinus* as a separate genus (based on blindness and larval autapomorphies) renders *Lamyctes* paraphyletic. As such, we follow Brölemann (1930) and many subsequent workers in placing *Lamyctinus* in synonymy with *Lamyctes*.

Metalamyctes Verhoeff, 1941, defined by a bipartite first genital sternite in the male, may prove to be useful for a southern African/South Atlantic island clade that, in addition to the type (*Henicops africanus* Porat, 1871) also includes *Lamyctes baeckstroemi*, *L. castaneus*, *L. microporus*, *L. neglectus*, *L. robustus* and *L. tristani*. Several other African species with strong projections on tergites 9, 11 and 13 were recognised by Chamberlin (1951) as forming the subgenera *Lamyctes* (*Eumyctes*) and *L. (Neomyctes)*. *Henicops sinuatus* Porat, 1893, the type species of *Eumyctes*, is more closely related to *Lamyctopristus* Attems, 1928, than to *Lamyctes* (Edgecombe submitted), and we infer that other species referred to *Eumyctes* and *Neomyctes* by Chamberlin (1951) are likewise not members of *Lamyctes*. These species include the following: *Lamyctes denticulatus* Attems, 1907; *L. ergus* Chamberlin, 1951; and *L. numidicus* (Latzel, 1886).

***Lamyctes coeculus* (Brölemann, 1889)**

Figs. 1-4

- Lithobius coeculus* Brölemann, 1889: 273.
Lamyctinus coeculus: Silvestri, 1909: 39, fig. 1.
Lamyctes coeculus: Brölemann, 1930: 336, figs. 463-465.
Lamyctinus coeculus: Chamberlin, 1943: 25.
Lamyctinus coeculus: Auerbach, 1952: 413.
Lamyctes coeculus: Lehtinen, 1960: 105.
Lamyctes coeculus: Enghoff, 1975: 45-46.
Lamyctes coeculus: Negrea & Matic, 1996: 226, figs. 1-3.
Lamyctes coeculus: Zapparoli & Shelley, 2000: 37 (with Hawaiian records).
Lamyctinus coeculus: Edgecombe et al., 2002, figs. 1J, 3K, 6D.
Lamyctinus coeculus: Edgecombe, 2003, fig. 38E.

Material examined: **Australia** (New South Wales): AM KS 81367, 10 females, Victoria Park, near Alstonville, 28°54'S 153°25'E, G.D. Edgecombe & Z. Johanson, 18 June 2001, rainforest, soil; AM KS57961, 12 females, 13.4 km N Colo Heights work depot, Mellong Range, 33°16'S 150°41'E, G.D. Edgecombe, G. Giribet & Z. Johanson, 14 March 2000, eucalypt forest, soil; AM KS 81368, 2 females, Sydney, garden at Australian Museum, G.D. Edgecombe, 27 October 2001; ANIC (ex. Berlesate 850), 1 female, Castle Flat, Clyde R., 32°21'S 150°13'E, L. Hill, 5 September 1982, floodplain, under *Acacia*; ANIC (ex. Berlesate 833), 7 females, 4.5 km WNW Pigeon House Mt, 35°21'S 150°13'E, L. Hill, 16 May 1982. Lord Howe Island: AM KS 81369, 3 females, SE aspect of Transit Hill near summit, 31°32'13"S 159°04'13"E, Australian Museum, 24 November 2000, closed rainforest.

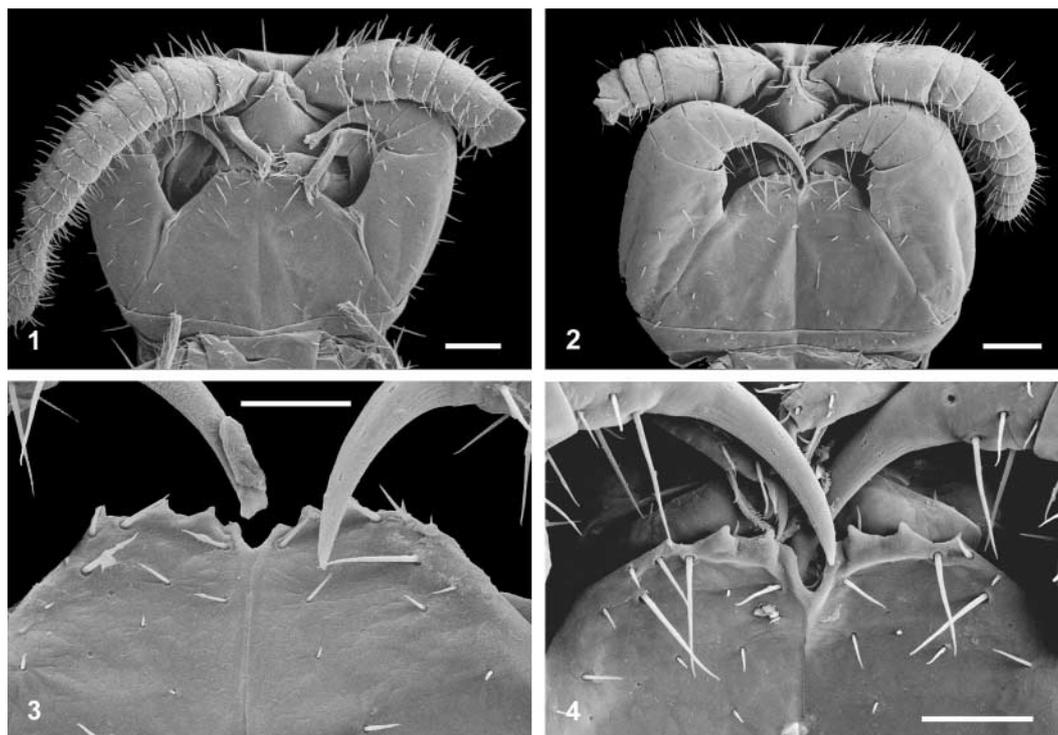
Argentina (Tucumán Province): MCZ DNA100472, 3 females, Horco Molle, Cerro San Javier, San Miguel de Tucumán, C. Mattoni, 16 September 2001.

Democratic Republic of Congo: CAS, 3 females, S slope of Mt Kahuzi, 1900 m, E.S. Ross & R.E. Leech, 5 September 1957.

Discussion: Previous morphological descriptions based on material from Italy (Brölemann 1889), Mexico (Silvestri 1909) and Palestine (Negrea & Matic 1996) apply to specimens from Australia, Argentina and the Democratic Republic of Congo. Particularly distinctive characters are the complete absence of ocelli, 24 antennal articles with the series of articles distal to article 4 being of similar size and shape (Figs. 1, 2) (versus shortened articles in pairs alternating with groups of longer articles in other species of *Lamyctes*), the dental margin of the maxilliped having two true teeth, a median swelling, and a conical, seta-like pseudopododont (Figs. 3, 4), and distal spinose projections on the tibiae confined to legs 1-11.

Molecular sequence data for the nuclear ribosomal genes 18S and 28S rRNA and the mitochondrial genes cytochrome *c* oxidase subunit I and 16S rRNA for a New South Wales specimen of *Lamyctes coeculus* were analysed by Edgecombe et al. (2002) (Gen-

Bank accession numbers AF334275, AF334296, AF334315, and AF334339). Sequences for the same four markers for a specimen from Horco Molle in Cerro San Javier, Tucumán Province, Argentina, are identical (GenBank AY213735, AY213745, AY214427, and AY214374). This identity contrasts with variability in these four markers displayed by other geographically widespread centipede species. DNA sequences for three populations of *Henicops maculatus* from New South Wales, Tasmania, and New Zealand (Edgecombe et al. 2002) show that, for the most conserved marker, 18S rRNA, the three populations have considerable variation, including length variation ranging from 2162 to 2272. All variation is obviously concentrated in some of the hypervariable regions found in the heni-copid species. Some variation is also found among three Queensland populations of *Paralamyctes monteithi* examined, although an insertion/deletion (hereafter indel) of only one bp occurs among these populations in the 18S rRNA. Intraspecific variation within the mitochondrial markers, however, is fairly high in both *H. maculatus* and *P. monteithi*. Considerable variation is also found between populations of the scutigermorph *Scutigera coleoptrata* from Barcelona, Spain, and New York, USA (GenBank accession numbers AF173238 and AF000772). These patterns lead us to regard the distribution of *Lamyctes coeculus* as synanthropic, as opposed to geographic variation in native species for *Henicops maculatus* and *Paralamyctes monteithi*.



FIGURES 1-4. *Lamyctes coeculus* (Brölemann). 1, 3, AM KS57961, female, Mellong Range, NSW, Australia. 2, 4, MCZ DNA100472, female, Cerro San Javier, Tucumán, Argentina. 1-2, ventral view of head, scales 100 μm ; 3-4, dental margin of maxillipede coxosternite, scales 50 μm .

The specimens from Argentina match the illustrations of the maxillipede dental margin and description of *Lamyctes inermipes pusillus* Demange & Silva, 1976, which was described from Tucumán. The distinctive features of this subspecies relative to three others include a body length of 4-5 mm, a small number of antennal articles (usually 24), and maxillipede dentition with two strong teeth and a pseudopododont developed as a stout, conical seta. Each of these characters corresponds to *Lamyctes coeculus* (e.g., the maxillipede details in Figs. 16-20 of Demange & Silva, 1976, are precisely as in Fig. 4 here). We suspect that *L. inermipes pusillus* may be a junior synonym of *Lamyctes coeculus* but refrain from making a formal synonymy without examining the material.

***Lamyctes hellyeri* n. sp.**

Figs. 5-37

Diagnosis: *Lamyctes* with body length up to 8.2 mm; tergites yellow or pale orange; ocellus lacking; 29-33 (most commonly 31) antennal articles, with a few groups of shortened articles in pairs; dental margin of maxillipede coxosternite with 2+2 teeth and stout, spine-like pseudopododont; two or three coxal pores on each of legs 12-15; sternites of segments 13-15 fringed with setae along posterior margin, setae most numerous on sternite 14; small distal spinose projection on tibia of leg 12; leg 15 basitarsus 9-10 times longer than wide, distitarsus 11-12 times longer than wide.

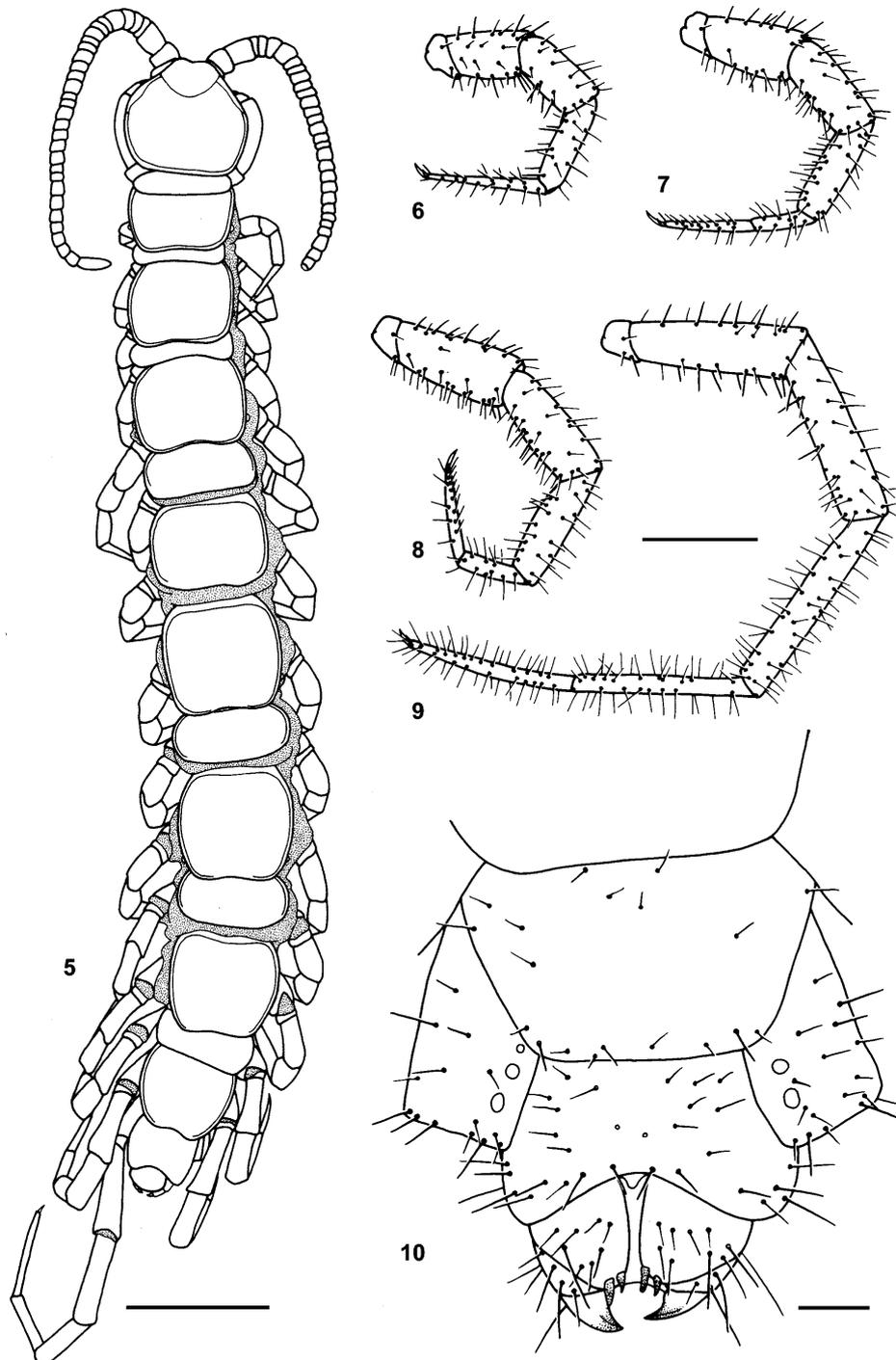
Holotype: QVMAG 23:25044 (Figs. 5, 10), female, Penguin, Tasmania, 41°07'04"S 146°04'40"E, R. Mesibov, 7 August 2001, garden soil.

Paratypes: Females: QVMAG 23:25045 (Figs. 6-9); 23:23046 (Figs. 11, 14-31); 23:23047 (Figs. 12-13, 32-33); 23:23048 (Figs. 34-37), 23:23049, seven unfigured specimens; MCZ DNA100639; all from type locality.

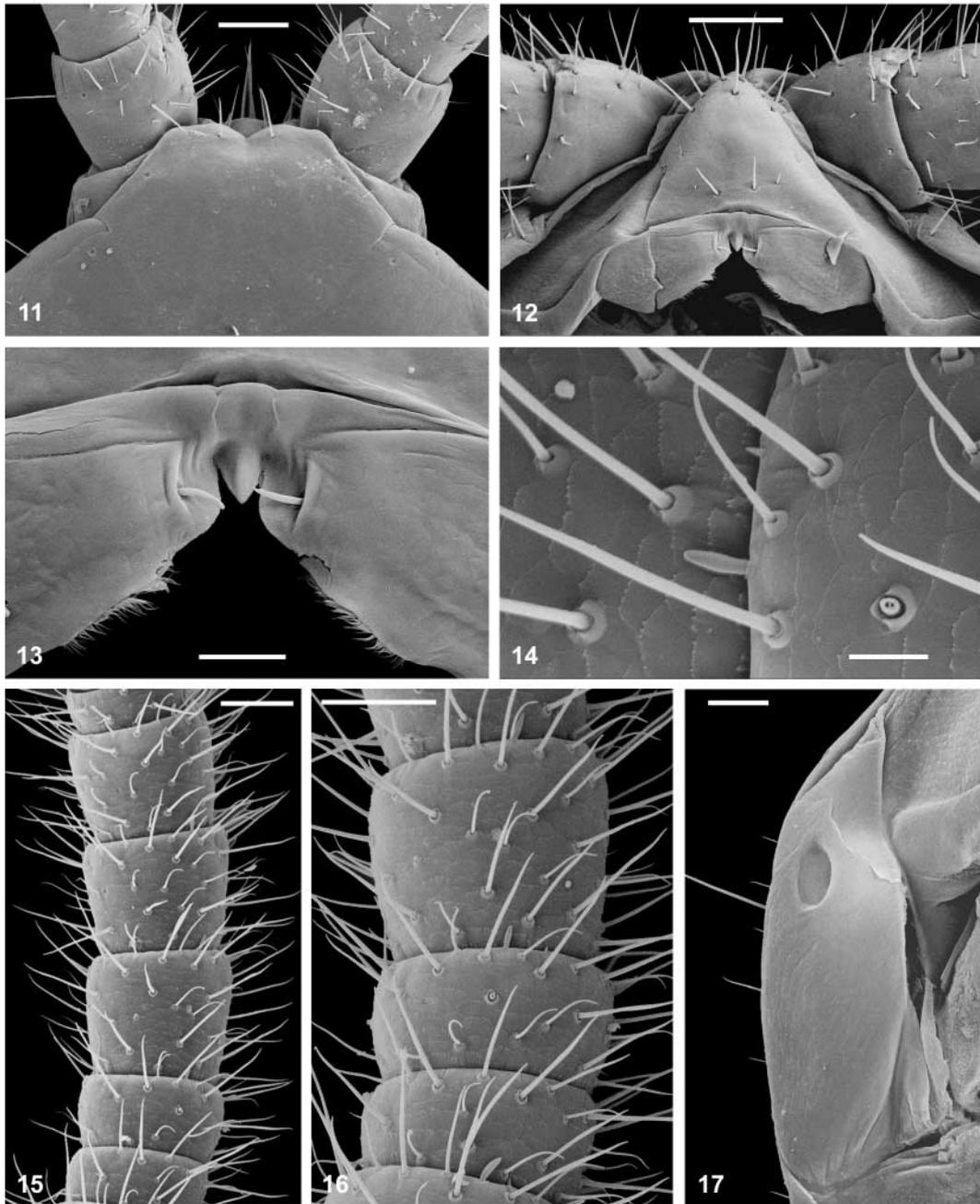
Etymology: For Henry Hellyer, Van Diemens Land Company surveyor and naturalist, who explored the interior of NW Tasmania in the 1820s, noting "young centipedes white as snow" in his journal.

Description: Length of body (head shield to telson) up to 8.2 mm. Leg 15 50% length of body. Colour in ethanol: head shield and maxillipede pale orange; tergites and sternites rather uniformly yellow except for pale orange segments 14-15 or all tergites pale orange with those of segments 14-15 darker; antenna yellow; legs pale yellow except for deeper yellow tarsi.

Head shield with length more than 90% its width, slightly wider than widest tergite (TT7-8). Frontal margin with strong median notch (Fig. 11), lacking median furrow. Region distal to antennocellar suture desclerotised, with no trace of ocellus (Fig. 11). Border of equal width posteromedially and posterolaterally; border continuous with desclerotised ("ocellar") region. Posterior margin of head shield weakly concave. Tömösváry organ moderately large, ovate, positioned slightly closer to midwidth of cephalic pleurite than to lateral margin (Fig. 17).



FIGURES 5-10. *Lamyctes hellyeri* n. sp. 5, 10, QVMAG 23:23044, holotype female. 5, dorsal habitus, scale 1 mm; 10, ventral view of posterior segments and gonopods, scale 100 μ m. 6-9, QVMAG 23:23045, female, scale 0.5 mm. 6, leg 12; 7, leg 13; 8, leg 14; 9, leg 15.



FIGURES 11-17. *Lamyctes hellyeri* n. sp. 11, 14-17, QVMAG 23:23046, female. 11, anterior part of head shield and basal part of antennae, scale 100 μ m; 14, sensilla on dorsal side of antenna, scale 10 μ m; 15-16, antennal articles, dorsal side, scales 50 μ m; 17, cephalic pleurite with Tömösváry organ, scale 50 μ m. 12-13, QVMAG 23:23047, female. 12, ventral view of clypeus and labrum, scale 100 μ m; 13, labral midpiece and inner parts of sidepieces, scale 30 μ m.

Antenna 33-39% length of body, 3.2-3.3 times length of head shield; basal two articles much larger than others; shortened articles in pairs include articles 3-4, 7-8, usually 10-11; articles in distal part of antenna submoniliform, mostly of about equal length and width; terminal article typically about 2.5 times length of penultimate article. Trichoid sensilla arranged in two to four imprecisely aligned whorls per article; most sensilla slanted anteriorly (Fig. 15); several shorter, more slender, curved sensilla on each article (Fig. 16); single digitiform thin-walled basiconic sensillum and single minute, conical thick-walled basiconic sensillum on anterior edge of articles on dorsal side of antenna (Fig. 14).

Clypeus with five or seven setae at apex, unpaired median seta and two or three pairs along clypeal margin; transverse band of four setae in front of labrum includes long inner pair and short outer pair (Fig. 12). Transverse seta projects from pit in sidepiece towards midpiece (Fig. 13). Labral margin weakly concave where fringe of branching bristles projects a short distance beyond margin (Fig. 13).

Maxillipede coxosternite subtrapezoidal (Fig. 18), length (measured from anterior-most projection of teeth) about 80% width; anterolateral margins converging at 60-70°. Dental margin narrow, about 37% maximum width of coxosternite, gently curved, with 2+2 large teeth; stout, spine-like pseudopododont just inside anterolateral corner of dental margin, separated from outer tooth by a greater distance than that separating the two teeth from each other (Fig. 20); median notch with rounded apex, angle about 65° (Fig. 19); rim along median notch forms small shoulder against base of inner tooth; setae of varied length on coxosternite, most concentrated on anterior part. Tarsal and pretarsal parts of tarsungulum about equal in length. Setae of similar density on inner, outer and ventral surfaces of tarsal part of tarsungulum, tibia and femur.

Mandible with four paired teeth (Fig. 26). Five aciculae, each with 10-13 weakly pointed pinnules on both anterior and posterior margins (Fig. 28). Fringe of branching bristles skirts aciculae; ventral bristles with fairly narrow bases, with even, dense branchings along entire length of each bristle (Figs 27, 29); bristle bases flattening slightly more dorsally on fringe, with abrupt transition to rows of flat, multifurcating, scale-like bristles against second tooth; scale-like bristles arranged two- or three-deep (Fig. 30), composed of up to 26 slender branches in a single row; fringe narrowing dorsally. Grooved ridges bearing row of angular accessory denticles well developed on teeth (Fig. 27); one or two rows of angular accessory denticles beside grooved ridge grade into wide band of flattened, multifurcating scales near fringe of scale-like bristles (Fig. 30). Furry pad composed of long, simple and multifurcating bristles, strongly differentiated from scale-like accessory denticles on dorsalmost tooth.

First maxilla with coxal parts of coxosternum meeting along most of their length medially, separated posteriorly by small, wedge-shaped sternite. Coxal process triangular, with cluster of about four simple setae at tip, one seta just posterior to this cluster along inner margin (Fig. 23). Distal article of telopod with two rows of about seven plumose setae along inner margin (Fig. 23), branching along more than half of length on distal part

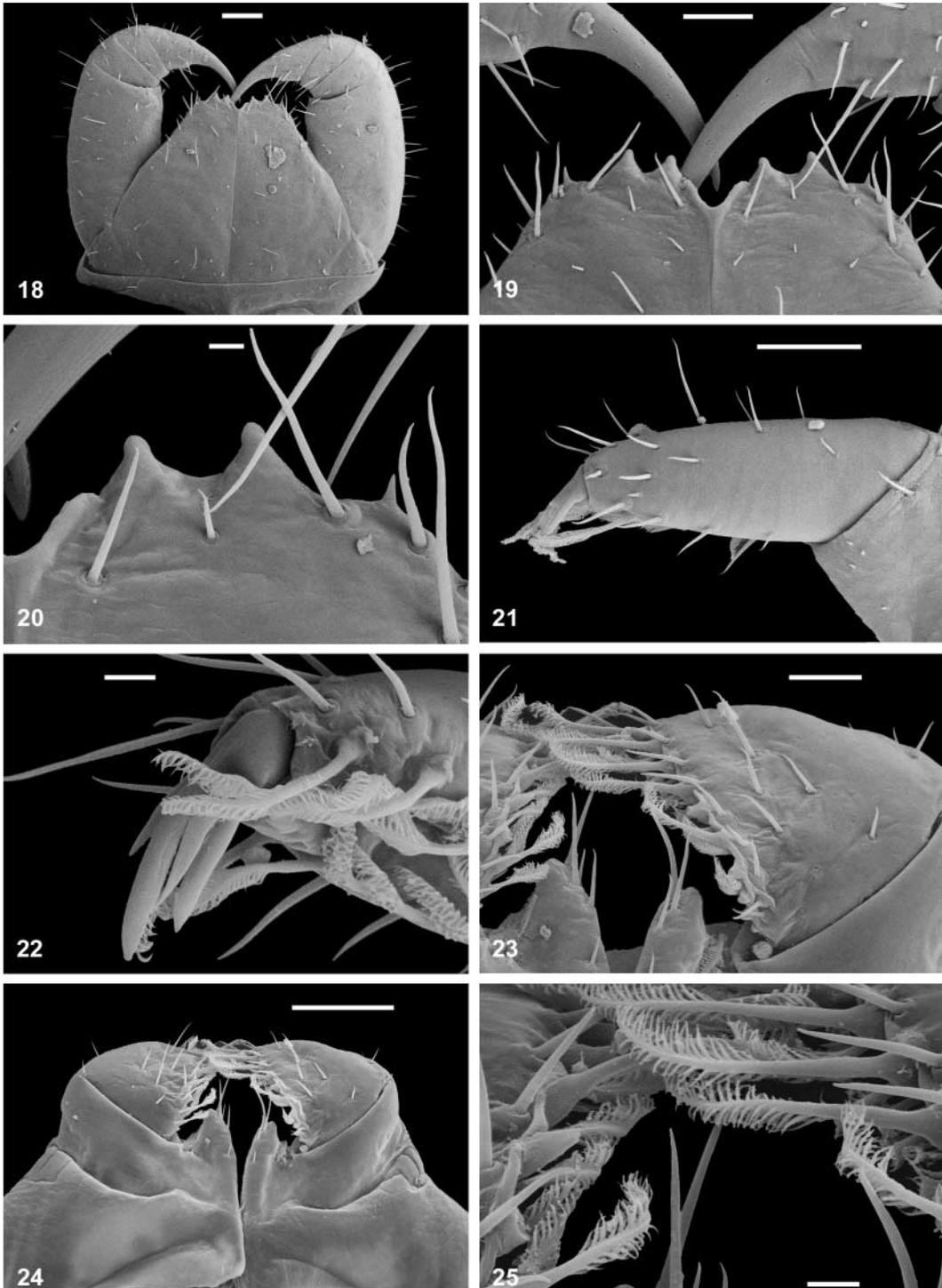
of setae; row of about ten shorter simple setae near bases of ventral row of plumose setae (Fig. 25); ventral surface of distal article with several simple setae, mostly on inner part, a few shorter setae near lateral margin.

Second maxillary sternite fused to coxa, margins distinct. Band of about six short setae across anterior part of coxa. Joint between trochanter and prefemur defined as a notch along inner margin of telopod. Inner face of tarsus with about ten plumose setae, densely branching along their distal halves (Fig. 22); outer face scattered with simple setae, more numerous on distal half (Fig. 21). Pretarsal claw composed of four digits of varied length and thickness (Fig. 22).

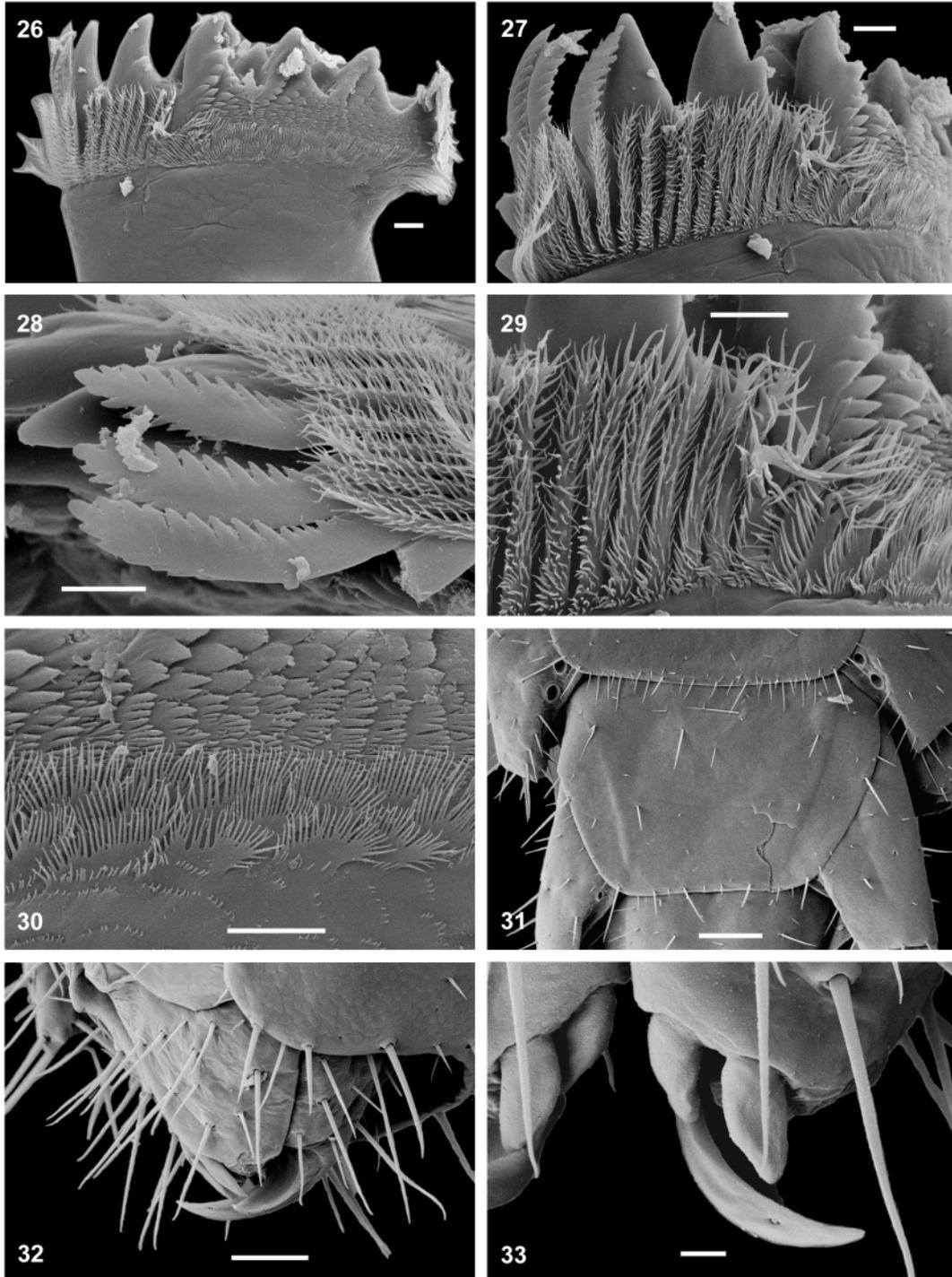
Tergites smooth; all posterior angles rounded, without projections (Fig. 5). All long tergites with concave posterior margins, with gradual increase in concavity posteriorly (margin of T1 gently concave; T14 moderately concave); posterior margins of short tergites subtransverse, with broadly rounded posterior angles. TT1, 3 and 5 bordered posteriorly; other long tergites bordered laterally only or with short extent of border posterolaterally; short tergites bordered laterally from T6. Tergite of intermediate segment with markedly concave posterior margin (in female). Tergite of first genital segment lightly sclerotised; telson tergite well sclerotised. Tergites with a few setae along margin and a pair anteromedially; several setae scattered on tergite of first genital segment.

Most sternites with few setae, near anterolateral and posterolateral corners, two or a few anteromedially; sternites 13-15 fringed with short setae along posterior margin, most abundant on sternite 14 (Fig. 31).

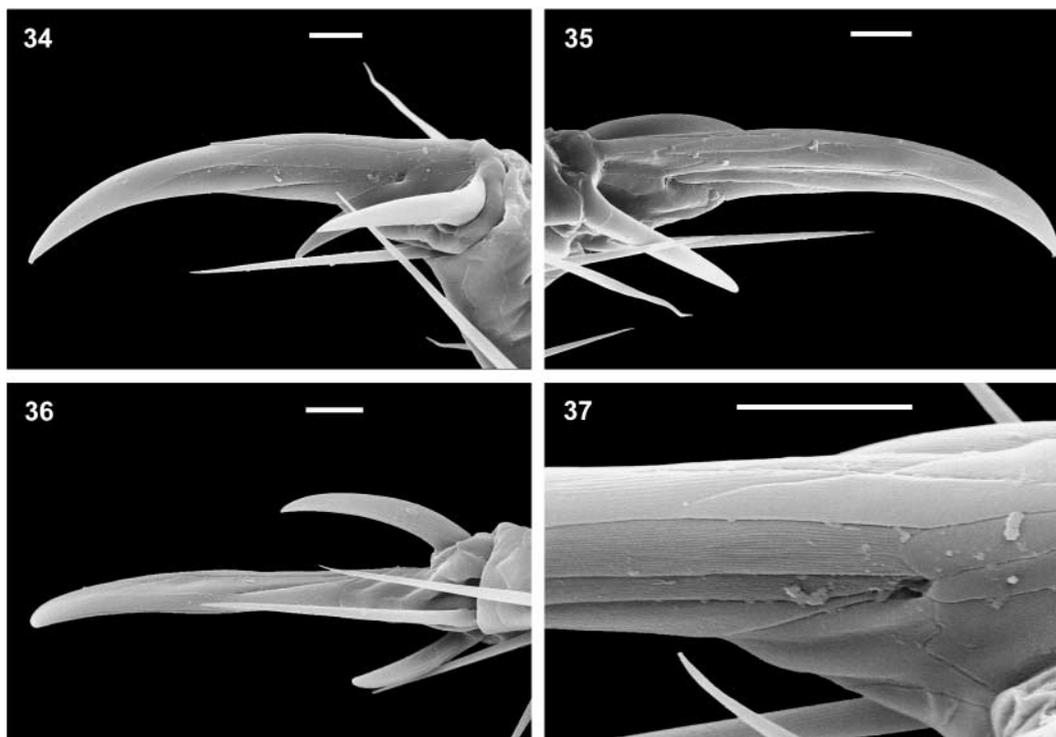
Strong distal spinose projection on tibiae of legs 1-11; small, blunt projection on leg 12 (Fig. 6); projections lacking on legs 13-15. Legs 12-15 with length ratios 1: 1.2 : 1.4 : 2.2. Leg 15 distitarsus about 90% length of basitarsus (Fig. 9); basitarsus about 85% length of tibia; tibia 6-6.5 times longer than wide, basitarsus 9-10 times, distitarsus 11-12 times. Basitarsus about 72% and 80% length of distitarsus on legs 13 (Fig. 7) and 14 (Fig. 8), respectively. Setae on prefemur and femur of leg 15 strongly pigmented, those on tibia and tarsus slender, radiating normal to surface of leg; tibial setae on legs 1-14 similar to those of prefemur and femur, tarsal setae shorter, denser, more slender than those on more proximal segments in legs 1-13, sloping distally, e.g., on distitarsus of legs 13 and 14. Anterior and posterior accessory claws on all legs, about 40% length of main claw, gently divergent (Fig. 36); accessory claws with closely-spaced linear ridges on their surface. Main claw curved along distal half, subdivided by sutures into numerous elongate scutes (Figs. 34-35); single large pore with a small pore (gland?) opening on both lateral sides of main claw at intersection of several scutes at about midlength of the accessory claws (Fig. 37); scutes proximal to pore nearly smooth, those distal to pore ornamented with fine linear ridges and grooves (Fig. 37). Elongate, slender spine (sensory spur of Eason 1964, fig. 486) originating beneath base of posterior accessory claw, extending more than half length of main claw, with a short spine emanating from its base, running parallel to long spine along its upper margin.



FIGURES 18-25. *Lamyctes hellyeri* n. sp. QVMAG 23:23046, female. 18, ventral view of maxillipede, scale 100 μ m; 19-20, dental margin of maxillipede coxosternite, scales 50 μ m, 10 μ m; 21, tarsus and claw of second maxilla, scale 50 μ m; 22, distal part of tarsus and claw of second maxilla, scale 10 μ m; 23, coxal projections and telopods of first maxillae, scale 50 μ m; 24, first maxillae, scale 100 μ m; 25, plumose setae on inner margins of telopods of first maxillae, scale 10 μ m.



FIGURES 26-33. *Lamyctes hellyeri* n. sp. 26-31, QVMAG 23:23046, female. 26-27, gnathal edge of mandible and detail of ventral part, scales 10 μ m; 28, aciculae, scale 10 μ m; 29, 30, fringe of branching bristles, on successively more dorsal part of mandible, scales 10 μ m; 31, sternite of segment 15 and posterior margin of sternite 14, scale 100 μ m. 32-33, QVMAG 23:23047, female, gonopod and detail of spurs and claw, scales 50 μ m, 10 μ m.



FIGURES 34-37. *Lamyctes hellyeri* n. sp. QVMAG 23:23048, female, pretarsus of leg 14, scales 10 μ m. 34-36, anterior, posterior, and ventral views; 37, detail of lateral pore and ornament on scutes of main claw.

Coxal pores all round, inner pores smaller; minimum of 2,2,2,2/2,2,2,2 in smaller specimens, maximum in largest specimen (holotype) 3,3,3,2/3,4,4,3; all other specimens with combination of two and three pores on each of legs 12-15.

Sternite of segment 15 in female with transverse posteromedian margin. Sternite of first genital segment with concave posteromedian margin; setae more abundant laterally than medially. Basal article of gonopod bearing eight to 11 setae; second article with four or five setae; third article with one or two setae (Figs. 10, 32); several long setae on first two articles. Two spurs on basal article, asymmetrical with straighter outer side, markedly tapering in distal half, with rounded tip (Fig. 33). Claw simple (Fig. 33).

Discussion: *Lamyctes coeculus* is the only other blind species in the *Lamyctes-Heniccops* group. *Lamyctes hellyeri* and *L. coeculus* are most easily distinguished by the former's larger size, greater number of antennal articles, and more marked alternation in length of the antennal articles, as in the other members of *Lamyctes*. Throughout its range, *L. coeculus* has 24 articles in mature specimens, whereas *L. hellyeri* has 29-33. A small distal spinose projection is present on the tibia of leg 12 in *L. hellyeri* (Fig. 6) but is absent in *L. coeculus*. The fringe of setae on the posterior sternites of *L. hellyeri* (Fig. 31) is lacking in *L. coeculus*. Coxal pore counts are usually lower in *L. coeculus* (1,2,2,2 *vide* Bröle-

mann 1889; 1,2,2,2 or occasionally 1,3,3,2 *vide* Silvestri 1909; 1,2,2,2 or 2,2,2,2, *vide* Negrea & Matic 1996).

Given the association between parthenogenesis and synanthropic dispersal in *Lamyctes coeculus*, it is plausible and even likely that the apparently parthenogenetic *L. hellyeri* is not a Tasmanian native. The species seems to be common in some gardens of exotic plants in the town of Penguin, but has not been collected in natural habitats (R. Mesibov, pers. comm.). Whether native or not, *L. hellyeri* does not conform to any previously described species of *Lamyctes*. The most likely suspects for a conspecific in the existing literature would be among the many species named by R. V. Chamberlin from many parts of the world. It seems unlikely that *L. hellyeri* is hidden among the often poorly described Chamberlin species because throughout his career Chamberlin (e.g., Chamberlin 1920, 1930, 1943; Chamberlin & Wang 1952) recognised *Lamyctinus* as a distinct genus. Thus, any species without ocelli (the presence of which Chamberlin sometimes did not record in his usually brief *Lamyctes* species descriptions) would presumably have been assigned to *Lamyctinus* rather than *Lamyctes*. The combination of presence/absence of ocelli, antennal segmentation, maxillipede dentition, distal spinose projections on the tibiae, and proportions of leg 15 distinguish *L. hellyeri* from all congeners listed above.

TABLE 1. Taxon sampling used in phylogenetic analyses, molecular partitions, and GenBank accession codes. 18S (complete 18S rRNA); 28S (D3 region of 28S rRNA); 16S (500 bp fragment of 16S rRNA); COI (750 bp fragment of cytochrome *c* oxidase I). Geographic abbreviations as follows: NSW (New South Wales), NZ (New Zealand), SEQLD (southeastern Queensland), TAS (Tasmania), TUC (Tucumán, Argentina). Vouchers in Australian Museum (prefix AM KS) and Museum of Comparative Zoology Harvard University (prefix DNA).

Species	CAT Number	18S	28S	16S	COI
<i>Henicops maculatus</i> NSW	AM KS57962	AF173245	AF173275	AF334340	AF334316
<i>Henicops maculatus</i> TAS	AM KS 57963	AF334276	AF334297	AF334341	AF334317
<i>Henicops maculatus</i> NZ	AM KS 57964	AF334277	AF334298	AF334342	AF334318
<i>Henicops dentatus</i>	DNA100378	AY213724-5	AY213742	AY214370	AY214424
<i>Henicops</i> sp. SEQLD	AM KS 57965		AF334299	AF334343	AF334319
' <i>Lamyctes</i> ' <i>brevilabiatu</i> s	DNA100381	AY213734	AY213744	AY214372	AY214426
<i>Lamyctes inermipes</i>	DNA100478	AY213726	AY213743	AY214371	AY214425
<i>Lamyctes africanus</i>	DNA100287	AF334274	AF334295	AY214373	AF334314
<i>Lamyctes emarginatus</i>	AM KS 57960	AF173244		AF334338	
<i>Lamyctes coeculus</i> NSW	DNA100288	AF334275	AF334296	AF334339	AF334315
<i>Lamyctes coeculus</i> TUC	DNA100472	AY213735	AY213745	AY214374	AY214427
<i>Lamyctes hellyeri</i> n. sp	DNA100639	AY213736	AY213746	AY214375	AY214428

Phylogenetic analysis: Methods

A clade that unites *Lamyctes/Lamyctinus* with *Henicops* Newport, 1844, is one of the best corroborated groups in the Henicopidae, being supported by morphological data (Edgecombe 2003), as well as molecular and total evidence analyses for a wide range of analytical conditions and molecular loci (Edgecombe et al. 2002; Edgecombe & Giribet 2003). They also share the presence of a large insertion in the 18S rRNA locus, accompanied by a few other small insertions. Morphological data suggest that *Lamyctopristus* Attems, 1928, and *Analamyctes* Chamberlin, 1955, are also members (Edgecombe 2003). The relationships of blind members of the group are appraised in the following section based on sequence data from the 18S and 28S nuclear ribosomal cistrons and mitochondrial 16S rRNA and cytochrome *c* oxidase subunit I.

The taxonomic sample (Table 1) includes data for *Lamyctes emarginatus* (Newport, 1844), *L. africanus* (Porat, 1871), *L. coeculus* (Brölemann, 1889), *Henicops maculatus* Newport, 1844, and *Henicops* n. sp. QLD used in a previous study (Edgecombe et al. 2002). Newly added taxa are '*Lamyctes*' *brevilabiatus* Ribaut, 1923, *L. hellyeri* n. sp., *L. inermipes* (Silvestri, 1897), and *Henicops dentatus* Pocock, 1901. The cladograms are rooted between *Henicops* and *Lamyctes/Lamyctinus*, both being resolved as monophyletic in previous morphological (Edgecombe 2003) and molecular (Edgecombe et al. 2002) analyses.

Procedures for DNA isolation, amplification, sequencing and editing are as detailed by Edgecombe et al. (2002: 33-34). That study should be consulted for specific details on both laboratory methods and analytical justification.

Molecular data were analysed using direct optimisation under parsimony (Wheeler 1996) in the computer program POY, version 3.0.5 (Wheeler et al. 2002). Direct optimisation was executed in parallel on a Linux cluster of 28 nodes at 1 GHz each at Harvard University (darwin.oeb.harvard.edu). Each analysis consisted of 100 random addition replicates with spr and tbr branch swapping followed by tree fusing, each replicate executed in a node.

As in previous studies (Edgecombe et al. 1999, 2002), the data are subjected to a sensitivity analysis under multiple optimisation parameter sets. The combined analysis tree for the parameter set that minimises overall incongruence among all partitions serves as the optimal working hypothesis. The Incongruence Length Difference (ILD) (Mickey & Farris 1981) is used as a measure of congruence between the four molecular partitions (18S rRNA, 28S rRNA, 16S rRNA, and COI).

Analyses were performed for 15 parameter sets varying the gap:change ratio and the transversion:transition ratio for each of the four separate molecular partitions as well as for combination of the four genes. Gap/change ratio values of 1, 2, and 4 were explored ("change" refers to the highest value for a base transformation, i.e., the transversions), as well as transversion/transition ratios of 1 (equal weights), 2 (transversions receive twice as much weight as transitions), 4, 8, and infinity (transversion parsimony). In addition to pre-

senting the shortest cladograms for each molecular partition based on the parameter set that minimises overall incongruence, we present the strict consensus of all cladograms obtained under all the explored analytical parameters as a more severe test of clade stability. For each molecular partition as well as for combined analysis of all four markers, parsimony jackknife values (Farris et al. 1996; Farris 1997) are calculated as a measure of node support, for the parameter set that minimizes overall incongruence (optimal parameter set).

TABLE 2. Tree lengths for the individual data sets (18S: 18S rRNA; 28S: 28S rRNA; 16S: 16S rRNA; COI: cytochrome *c* oxidase I) and combined data sets (MOL: molecular [18S + 28S + 16S COI]) at different parameter set values, and ILD values for the combined analyses of all data (ILD), at parameter (PAR) sets 110 to 481. Numbers in italics reflect the minimum incongruence among data sets as measured by ILD. PAR indicates ratio between gap-cost : transversion cost: transition cost (e.g., 121 indicates a gap: transversion ratio of 1, and a transversion: transition ratio of 2, or gap cost = 2, transversion cost = 2, transition cost = 1).

PAR	18S	28S	16S	COI	MOL	ILD
110	178	25	189	269	681	0.02937
111	377	62	422	617	1500	0.01467
<i>121</i>	<i>562</i>	<i>98</i>	<i>616</i>	<i>901</i>	<i>2198</i>	<i>0.00955</i>
141	922	160	996	1447	3579	0.01509
181	1642	284	1756	2534	6327	0.01754
210	214	33	215	269	756	0.03307
211	422	79	449	617	1588	0.01322
221	638	130	668	901	2365	0.01184
241	1077	220	1100	1447	3904	0.01537
281	1949	400	1963	2534	6976	0.01864
410	273	49	252	269	873	0.03436
411	486	105	486	617	1723	0.01683
421	765	184	741	901	2634	0.01632
441	1327	329	1248	1447	4439	0.01982
481	2451	621	2260	2534	8039	0.02152

Results and Discussion

Table 2 summarises cladogram lengths for each separate molecular partition and combined analysis of the four genes for the 15 explored parameter sets, with ILD values. For combined analysis, the most congruent parameter set, as measured by the ILD, is 121 (transition cost = 1; transversion cost = 2; indel cost = 2).

For the combined data, all 15 parameter sets are compatible with the monophyly of *Henicops* and *Lamyctes* (including *Lamyctinus*) except for the placement of '*Lamyctes*' *brevilabiatus* (Fig. 38). This New Caledonian species was originally assigned to *Lamyctes* (Ribaut 1923), having indistinctly jointed tarsi on legs 1-12 (a faint desclerotised band indicates the limits of two tarsomeres) and unprojected tergites, but all combined molecular analyses identify it as a member of the Australasian *Henicops* and, specifically, as most closely related to the Western Australian *Henicops dentatus*. This grouping has a high jackknife frequency for the combined molecular data (98%) and is independently retrieved under parameter set 121 for 18S rRNA, 16S rRNA, and COI (Fig. 38). The apparent incongruence between this result and previous morphological classification of '*L.*' *brevilabiatus* is reconciled by several characters. Notably, Ribaut (1923: 22) described a group of lacinate setae on the coxal process of the first maxilla in this species, an apomorphic character otherwise diagnostic of *Henicops* (Edgecombe et al. 2002, fig. 8H; Edgecombe 2003: character 31, state 2). The dental margin of the maxillipede coxosternite is fairly wide in '*L.*' *brevilabiatus*, as in *Henicops*; the pretarsus resembles *Henicops* rather than *Lamyctes* in having a minute spine beneath the posterior accessory claw, and the first genital sternite of the male is divided into two sclerites by a desclerotised median longitudinal band (pers. obs., AM KS 82580, KS 82626, QM S60636, S60651).

Within *Lamyctes/Lamyctinus*, supraspecific groupings are unstable for the combined analysis, but none of the 15 explored parameters resolves the two blind species, *L. coeculus* and *L. hellyeri*, as sister taxa. This finding contradicts the classification of blind species together as *Lamyctinus*. For the parameter set that minimises incongruence, the type species of *Lamyctinus*, *L. coeculus*, is nested within *Lamyctes*. The alternative resolutions of *L. hellyeri* are either as sister to *Lamyctes africanus* + *L. emarginatus* (selected by the minimal ILD parameters) or as sister to *L. africanus* alone. Because a blind grouping is either paraphyletic or polyphyletic and is, phylogenetically, a part of *Lamyctes*, a separate taxon *Lamyctinus* is rejected.

The only analysis that supports a blind clade for the parameter set that minimises incongruence between partitions is for 18S rRNA (Fig. 38). The grouping of *L. hellyeri* and *L. coeculus* is, however, supported in less than 50% of jackknife replicates for that parameter set and is slightly sensitive to parameter variation. The 18S rRNA dataset finds monophyly of *L. coeculus* + *L. hellyeri* under 13 parameter sets, and it is contradicted by three parameter sets (one of them is ambiguous in the resolution of the group). Some 28S rRNA analyses find monophyly of *L. coeculus* + *L. hellyeri*, and even though the optimal parameter set does not recover the group, the jackknife frequency for that grouping is 52%. However, the 28S parameter sets that find monophyly of '*Lamyctinus*', always resolve it as part of *Lamyctes*. While monophyly of '*Lamyctinus*' is not unambiguously contradicted by the nuclear ribosomal markers (as opposed to the mitochondrial genes), most data indicate that retaining the taxon *Lamyctinus* would render *Lamyctes* paraphyletic. The fact that the conflict between nuclear and mitochondrial markers is resolved

towards the latter set may be related to the amount of information contributing to the final data set (i.e., tree length of 18S is 562 steps, 28S is 98 steps; 16S is 616 steps, COI is 901 steps).

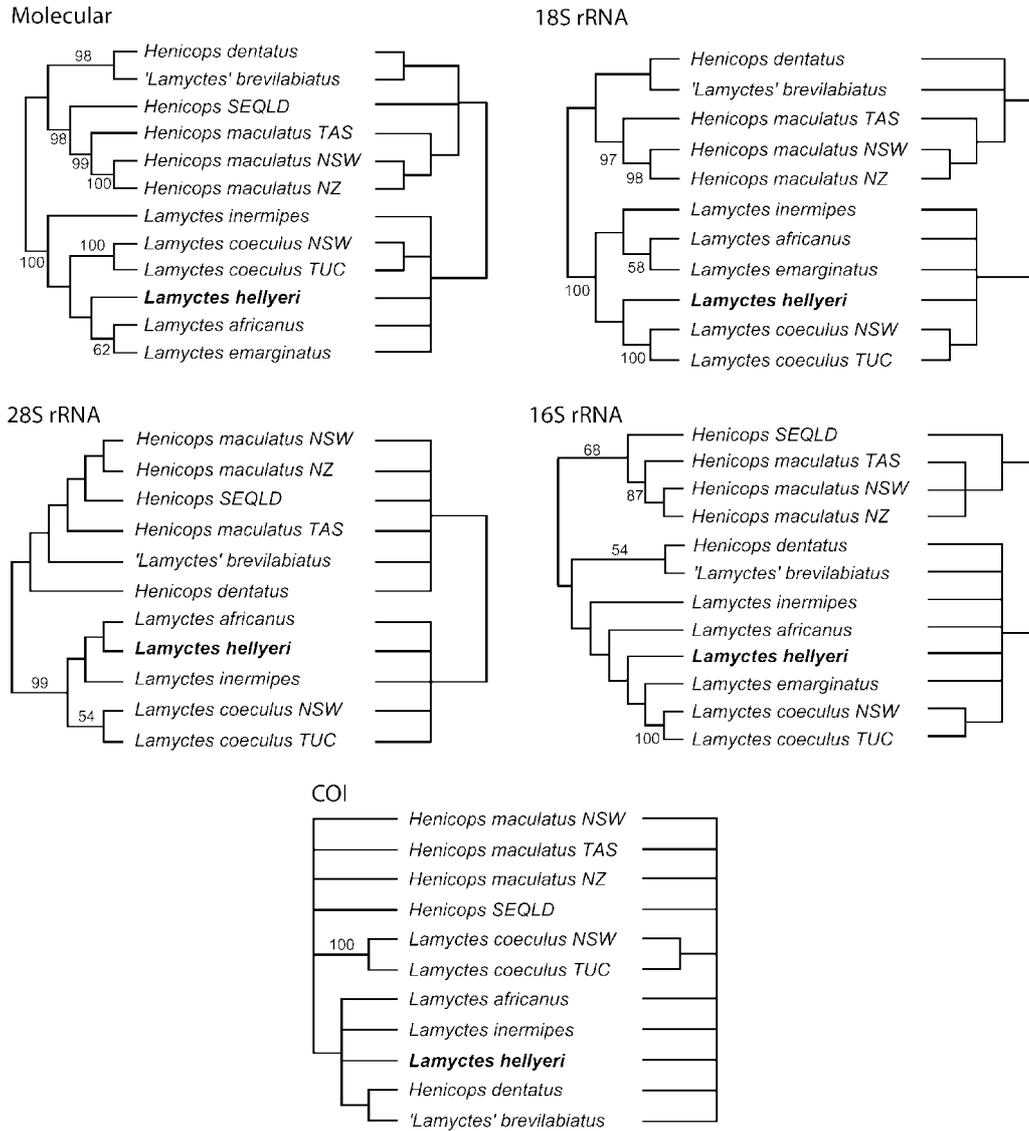


FIGURE 38. Cladograms based on molecular sequence data. Cladograms at left are shortest based on parameter set (121) that minimises incongruence between genes; cladograms at right are strict consensus of all 15 explored parameter sets. Numbers at nodes are parsimony jackknife frequencies. From left to right, top to bottom: cladograms based on combined molecular data (2198 steps); cladograms based on 18S rRNA (562 steps); cladograms based on 28S rRNA (98 steps); cladograms based on 16S rRNA (616 steps); cladograms based on COI (901 steps).

The other molecular markers (Fig. 38), analysed in isolation, resemble the combined analysis in that *L. coeculus* and *L. hellyeri* have separate sister taxa within *Lamyctes* for parameter set 121. However, the precise patterns of species interrelationships vary between the different markers and for every gene none of the supraspecific groupings within *Lamyctes* withstands all explored parameters.

As mentioned above, the two specimens of *L. coeculus* have identical sequence data for all examined molecular markers, but this was not due to contamination since the specimens were sequenced in different laboratories about three years apart. Their identical sequences are resolved as forming a clade in all analyses and all parameter sets analysed. This is also reflected in the jackknife analyses, having a support value of 100, with the exception of the 28S rRNA analysis, in which the node receives a low support value (54%). This is due to the fact that the regions analysed show little variation within the other species of *Lamyctes* and therefore few synapomorphies support the clade. However, no character contradicts it, hence its high stability.

In conclusion, the data analysed here suggest that blindness originated twice in centipedes of the genus *Lamyctes*, and that retention of the genus *Lamyctinus* cannot be justified because it renders *Lamyctes* paraphyletic.

Acknowledgements

Robert Mesibov brought *Lamyctes hellyeri* and Henry Hellyer to our attention. Suzanne Bullock, Sue Lindsay and Yongyi Zhen provided their skills at illustrations, SEM, and plate assembly, respectively. Collecting in Argentina was assisted by Adriana Chalup and Fernando Navarro. Labwork was assisted by Jared Feinman.

References

- Andersson, G. (1979) On the use of larval characters in the classification of lithobiomorph centipedes (Chilopoda, Lithobiomorpha). In: Camatini, M. (Ed) *Myriapod Biology*. Academic Press, London, pp. 73-81.
- Archev, G. (1917) The Lithobiomorpha of New Zealand. *Transactions and Proceedings of the New Zealand Institute*, 49, 303-318.
- Archev, G. (1921) Notes on New Zealand Chilopoda. *Transactions and Proceedings of the New Zealand Institute*, 53, 181-195.
- Attems, C. (1907) Die Myriopoden der deutschen Südpolar-Expedition 1901-1903. In: "*Deutsche Südpolar-Expedition 1901-1903*", 9. Zoologie. Georg Reimer, Berlin, pp. 415-433.
- Attems, C. (1909) Myriapoda. In: Schultze, L. (Ed) *Zoologische und anthropologische Ergebnisse einer Forschungsreise im westlichen und zentralen Südafrika ausgeführt in den Jahren 1903-1905. Denkschriften der Medizinisch-naturwissenschaftlichen Gesellschaft zu Jena*, 14. Gustav Fischer, Jena, pp. 1-52.
- Attems, C. (1928) The Myriapoda of South Africa. *Annals of the South African Museum*, 26, 1-431.

- Auerbach, S.I. (1952) Taxonomic notes on an exotic centipede taken from Illinois. *Annals of the Entomological Society of America*, 45, 413-414.
- Brölemann, H. (1889) Contributions à la faune myriapodologique méditerranéenne. *Annales de la Société Linnéenne de Lyon*, 35, 273-284.
- Brölemann, H. (1930) *Éléments d'une faune des Myriapodes de France. Chilopodes. Faune de France*, 25. P. Lechevalier, Paris, 405 pp.
- Chamberlin, R.V. (1910) The Chilopoda of California I. *Pomona College Journal of Entomology*, 2, 363-374.
- Chamberlin, R.V. (1911) The Lithobiomorpha of the southeastern states. *Annals of the Entomological Society of America*, 4, 32-48.
- 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*, 7, 50-87.
- Chamberlin, R.V. (1930) On some chilopods immigrant at Hawaii. *Pan-Pacific Entomologist*, 7, 65-69.
- Chamberlin, R.V. (1938) On eighteen new lithobiomorphous chilopods. *Annals and Magazine of Natural History*, Series 11, 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. (1946) A new millipede and two new centipeds 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*. Companhia de Diamantes de Angola, Servicos Culturais, Lisboa (97-111).
- 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. C.W.K. Gleerup, Lund, 61 pp.
- 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, 1-16.
- Chamberlin, R.V. & Mulaik, S. (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. & Wang, Y.M. (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) Scolopendromorphes et Lithobiomorphes (Myriapoda, Chilopoda) de la Guadeloupe et dépendences. *Bulletin du Muséum national d'Histoire naturelle, Paris*, 4e série, 3, 825-839.
- Demange, J.-M. & Silva G., F. (1976) Contribution à la connaissance de *Lamyctes inermipes* et *L. inermipes pacificus* Silv. par l'examen des spécimens types de la collection de F. Silvestri. *Bollettino del Laboratorio di Entomologia Agraria "Filippo Silvestri", Portici*, 33, 44-52.
- Eason, E.H. (1964) *Centipedes of the British Isles*. Frederick Warne & Co., London, 294 pp.

- Eason, E.H. (1982) A review of the north-west European species of Lithobiomorpha with a revised key to their identification. *Zoological Journal of the Linnean Society*, 74, 9-33.
- Eason, E.H. & Enghoff, H. (1992) The lithobiomorph centipedes of the Canary Islands. *Entomologica Scandinavica*, 23, 1-9.
- Edgecombe, G.D. (2003) The henicopid centipede *Haasiella* (Chilopoda: Lithobiomorpha): new species from Australia, with a morphology-based phylogeny of Henicopidae. *Journal of Natural History*, 37 (in press).
- Edgecombe, G.D. (Submitted) A new genus of henicopid centipede (Chilopoda, Lithobiomorpha) from New Caledonia. *Memoirs of the Queensland Museum*.
- Edgecombe, G.D. & Giribet, G. (2003) Relationships of Henicopidae (Chilopoda: Lithobiomorpha): New molecular data, classification and biogeography. *African Invertebrates*.
- Edgecombe, G.D., Giribet, G. & Wheeler, W.C. (1999) Filogenia de Chilopoda: combinando secuencias de los genes ribosómicos 18S y 28S y morfología. In: Melic, A., de Haro, J.J., Méndez, M. & Ribera, I. (Eds) *Evolución y Filogenia de Arthropoda*. *Boletín de la Sociedad Entomológica Aragonesa*, 26, 293-331.
- Edgecombe, G.D., Giribet, G. & Wheeler, W.C. (2002) Phylogeny of Henicopidae (Chilopoda: Lithobiomorpha): a combined analysis of morphology and five molecular loci. *Systematic Entomology*, 27, 31-64.
- Enghoff, H. (1975) Notes on *Lamyctes coeculus* (Brölemann), a cosmopolitan, parthenogenetic centipede (Chilopoda: Henicopidae). *Entomologica Scandinavica*, 6, 45-46.
- Farris, J. S. (1997) The future of phylogeny reconstruction. *Zoologica Scripta*, 26, 303-311.
- Farris, J.S., Albert, V.A., Källersjö, M., Lipscomb, D. & Kluge, A.G. (1996) Parsimony jackknifing outperforms neighbor-joining. *Cladistics*, 12, 99-124.
- 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. *Bombay Natural History Society*, 46, 133-139.
- Latzel, R. (1886) Les Myriapodes de la Normandie (2^e 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: Hanström, B., Brinck, P. & Rudebeck, G. (Eds) *South African animal life, II. Results of the Lund University expedition in 1950-1951*. Almqvist & Wiksell, Stockholm, pp. 4-56.
- Lehtinen, P.T. (1960) First records of *Geophilus carpophagus* Leach and *Lamyctes coeculus* Brol. (Chilopoda) from Finland. *Archivum Societatis zoologicae botanicae fennicae 'Vanamo'*, 15, 103-105.
- Matic, Z. & Darabantu, C. (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.
- Meinert, F. (1868) Danmarks Scolopender og Lithobier. *Naturhistorisk Tidsskrift*, 5, 241-268.
- Mickevich, M.F. & Farris, J.S. (1981) The implications of congruence in *Menidia*. *Systematic Zoology*, 27, 143-158.
- Negrea, S. & Matic, Z. (1996) Contribution à la connaissance des lithobiomorphes (Chilopoda) de la région palestinienne. In: Geoffroy, J.-J., Maurières, J.-P. & Nguyen Duy-Jacquemin, M. (Eds)

- Acta Myriapodologica. Mémoires du Muséum national d'Histoire naturelle, Paris*, 169, 225-233.
- 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*, 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*, 11, 121-142.
- Pocock, R.I. (1894) Chilopoda, Symphyla and Diplopoda from the Malay Archipelago. In: Weber, M. (Ed) *Zoologische Ergebnisse einer Reise in niederländisch Ost-Indien*, 3. Brill, Leiden, pp. 307-400.
- Porat, C.O. von. (1871) Myriopoda Africae australis, in Museo Regio Holmiensi asservata, recensuit. *Öfversigt af Kungliga Vetenskaps-akademiens Förhandlingar*, 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: Sarasin, F. & Roux, J. (Eds) *Nova Caledonia. Recherches scientifique en Nouvelle-Calédonie et aux Iles Loyalty. A. Zoology* 3(1). C.W. Kriedel's Verlag, Berlin, 79 pp.
- 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.
- 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. (1904) Myriopoda. *Fauna Hawaiiensis*, 3, 323-338.
- Silvestri, F. (1905) Myriopoda. *Fauna chilensis. Zoologische Jahrbücher, Abteilung für Systematik, Supplement*, 6, 715-772.
- Silvestri, F. (1909) Contribuzioni alla conoscenza dei Chilopodi. III. Descrizione di alcuni generi e specie di Henicopidae. *Bollettino del Laboratorio di Zoologia generale e agraria, Portici*, 4, 38-50.
- 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. (1923) Über Myriapoden von Juan Fernandez und der Osterinsel. In: Skottsberg, C. (Ed) *The Natural History of Juan Fernandez and Easter Island*, 3, 403-418.
- Verhoeff, K.W. (1939) Von Dr. G. H. Schwabe in Chile gesammelte Isopoda terrestria, Diplopoda und Chilopoda. *Archiv für Naturgeschichte, Zeitschrift für systematische Zoologie*, 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.
- Wheeler, W.C. (1996) Optimization alignment: the end of multiple sequence alignment in phylogenetics? *Cladistics*, 12, 1-9.
- Wheeler, W.C., Gladstein, D.S. & Delaet, J. (2002) POY: the Optimization of Alignment Charac-

- ters, version 3.0. Program and documentation available at [ftp.amnh.org/pub/molecular](ftp://amnh.org/pub/molecular). American Museum of Natural History, New York.
- Zaleskaja, N.T. (1994) The centipede genus *Lamyctes* MEINERT, 1868, in the environs of Manaus, Central Amazonia, Brazil (Chilopoda, Lithobiomorpha, Henicopidae). *Amazoniana*, 13, 59-63.
- Zapparoli, M. & Shelley, R.M. (2000) The centipede order Lithobiomorpha in the Hawaiian Islands (Chilopoda). I. The epigeal fauna. Records of the Hawaii Biological Survey for 1999. *Bishop Museum Occasional Papers*, 63, 35-49.