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A re-evaluation of the genera of New Zealand aesaline stag beetles (Coleoptera: Lucanidae)

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The purpose of the study is to reassess the taxonomic placement of the New Zealand aesalines currently assigned to the genus *Ceratognathus* Westwood This is done by comparison with two Australian species of *Ceratognathus*, including the type species, *C niger* Westwood, using elytral surface structures, the fore legs, and genitalia The New Zealand species are transferred from *Ceratognathus* to *Mitophyllus* Parry a reinstated genus, and *Holloceratognathus* Nikolaev which is given generic status *Mitophyllus* contains *Ceratognathus alboguttatus* Bates, *C dispar* Sharp *C foveolatus* Broun, *C gibbosus* Broun, *Mitophyllus insignis* Broun, *M irroratus* Parry, *C macrocerus* Broun, *M parrianus* Westwood, and *M reflexus* Broun *Holloceratognathus*, previously a subgenus of *Ceratognathus* has as a synonym *Ceratognathus* subgenus *Neoceratognathus* Nikolaev It contains *Mitophyllus cylindricus* Broun, *Ceratognathus helotoides* Thomson, and *C passaliformis* Holloway The paper contains illustrations of the heads, legs, and male and female genitalia of *Ceratognathus*, *Mitophyllus*, and *Holloceratognathus* The female genitalia of *Aesalus scarabaeoides* (Panzer) and *A asiaticus* Lewis are also illustrated to highlight the diversity and taxonomic importance of these structures in the Aesalinae

Keywords Coleoptera Lucanidae stag beetles Aesalinae *Aesalus* *Ceratognathus* *Holloceratognathus* *Mitophyllus* morphology taxonomy New Zealand Australia

INTRODUCTION

Proposed by MacLeay (1819) initially as a family within Thalerophaga the Aesalinae with fewer than 50 described species is one of the smaller subfamilies of Lucanidae The two major lucanid catalogues of this century placed six or eight genera in this subfamily (Roon 1910, Benesh 1960) but subsequent morphological studies reduced the aesaline genera to *Aesalus* Fabricius, from Europe, Asia, and Central America, *Ceratognathus* Westwood, from Australia, Tasmania, and New Zealand (and since reported by Martinez (1976) from Chile), and *Nicagus* LeConte from North America and Asia (Holloway 1960, 1968, 1969, 1972)

In 1974 Howden & Lawrence erected *Lucanobium* to accommodate a Venezuelan aesaline closely resembling some species of *Aesalus* Adults of *Lucanobium* and *Aesalus* are distinctive in having the prosternal process expanded anteriorly and the first abdominal ventrite fused to the second ventrite In *Ceratognathus* and *Nicagus* the prosternal process is not expanded anteriorly and all the abdominal ventrites are free Howden & Lawrence (1974) considered these features to have subfamily significance, limiting the Aesalinae to include only *Aesalus* and *Lucanobium* and erecting a new subfamily, Nicaginae, for *Nicagus* and *Ceratognathus* Their classification has been followed by Scholtz (1990) and Lawrence & Newton (1995) but the broader concept of Aesalinae (Holloway 1968) has continued to be used by other authors (D'Hotman & Scholtz 1990, Nel & Scholtz 1990, Holloway 1997) In this paper I am continuing to treat *Nicagus* and *Ceratognathus* as aesalines

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With at least 12 described species (Holloway 1961, 1962) and several that are undescribed, New Zealand has a relatively rich aesaline fauna. Parry (1843) erected *Mitophyllus*, an endemic genus, for *M. irroratus* Parry, the first aesaline to be described from New Zealand. The genus was considered by Burmeister (1847) and Lacordaire (1856) to be a synonym of the Australian *Ceratognathus* Westwood but new species continued to be assigned to it and *Mitophyllus* appeared as a valid genus in the first edition of the Catalogus Coleopterorum (Roon 1910). However, in the second edition of the catalogue (Benesh 1960) it was reduced to a synonym of *Ceratognathus* which has since been the only generic name applied to Australasian aesalines.

Although in general appearance the New Zealand aesalines seem not to be out of place in *Ceratognathus*, their female genitalia differ in several respects from those of the Australian type species and, furthermore, two distinct forms of female genitalia can be recognised within the New Zealand group itself (Holloway 1961, 1962). The recent discovery that these genitalic differences are mirrored by equivalent differences in the elytral ultrastructure (Holloway 1997) suggested that the generic status of the Australasian aesalines needed investigation. Consequently I made a comparative study of a range of structures in all of the New Zealand aesalines, in two species of *Ceratognathus* from Australia (*C. niger* Westwood, the type species of *Ceratognathus*, and *C. westwoodi* Thomson), and in several species of *Aesalus* and *Nicagus*, giving special attention to the male and female genitalia which in Lucanidae contain some of the most distinctive generic characters. This distinctiveness is particularly apparent in the female genitalia where the shape and configuration of the various sclerotised internal structures (bursa copulatrix, spermatheca, accessory gland, and associated structures) produce easily recognisable generic patterns on which relatively minor specific differences (the size of some structures and the length and insertion positions of some ducts) are "superimposed". Illustrations of the female genitalia of the two representative Australian aesalines and of two species of the Northern Hemisphere genus *Aesalus* are presented in this paper. The *Aesalus* illustrations have been included because they provide an outstanding example of a generic pattern and specific differences and they also feature an accessory gland, a structure that is not present in the genitalia of the Australasian aesalines, nor in *Nicagus*.

The results of the study provide the evidence for removing the New Zealand aesalines from *Ceratognathus* and assigning them to two endemic genera. The need for this work has been highlighted recently by the publication of two papers dealing with the morphology and phylogeny of *Ceratognathus* (D'Hotman & Scholtz 1990; Nikolaev 1998). In both, the authors did not examine the type species of *Ceratognathus* nor any other Australian species, but instead based their conclusions about the genus solely on New Zealand aesalines. Furthermore, without examining any *Ceratognathus* specimens at all, Nikolaev assigned the New Zealand species to three subgenera of *Ceratognathus*, working only from illustrations contained in my papers of 1961, 1962, and 1963. Other Australian aesalines need to be studied in detail before *Ceratognathus* can be conclusively defined; the present paper should provide the basis for that work.

MATERIALS, METHODS, AND CONVENTIONS

New Zealand aesalines and some exotic species were borrowed from the New Zealand Arthropod Collection (NZAC) at Landcare Research New Zealand Limited, Auckland. Additional exotic material was sent either on loan or as a gift by the overseas sources named in the acknowledgments. Some of the material of *Aesalus asiaticus*, *A. imanishii*, and *Nicagus japonicus* that I received as a gift has been deposited in the NZAC. Repositories and label data of figured specimens are listed in the appendix.

The genitalia were dissected from whole abdomens macerated in warm 10% potassium hydroxide. They were examined and drawn in a dish of ethanol, and stored in glycerine in

minivials placed below the pinned specimens A drawing tube was used to prepare the illustrations

The names applied to the various parts of the male and female genitalia agree with those proposed by Lindroth (1957) and used by me in previous papers The only change relates to the structure I referred to in the past as an accessory gland in the female genitalia of the New Zealand aesalines (Holloway 1961, 1962) Having now seen the accessory gland in *Aesalus* (see Fig 37, 38) I consider the so called accessory gland in the New Zealand Aesalinae to be a lobe of the bursa copulatrix

SYSTEMATICS

Subfamily **AESALINAE** MacLeay, 1819

RECOGNITION CHARACTERS Small to medium-sized, convex, non metallic, brown or black lucanids (length including mandibles approximately 4–19 mm) Maxillae lacking hooks and hooklets in both sexes Eyes entire (not divided by a canthus) Antennae (Fig 7–9) not geniculate, the pedicel inserted on the truncate end of the scape (not on the dorsal surface of the scape), scape with a variably developed, dorsal or posterodorsal, longitudinal groove that has an associated row or group of erect setae or scales, antennal club three-segmented Legs rather slender, not fossorial Elytra punctate, the punctures relatively deep and with sharply defined margins, elytral vestiture mostly squamose, the scales with variably interconnected longitudinal ribs on their dorsal surface Hindwings fully developed Male terminalia lacking struts at the base of the penis, internal sac eversible, parameres narrowing apically and not lamellate Female terminalia with the hemisternites and other components of the ninth segment rather weakly sclerotised, styli very narrow, with minute setae at the apex, spermatheca variably curved, annulate on at least the proximal half of its length

KEY TO THE NEW ZEALAND GENERA OF AESALINAE

Dorsal edge of front tibia with a large apical spine, a large spine slightly beyond the middle, and numerous small, equal sized spines elsewhere, elytral pits with a structurally raised, sculptured floor *Mitophyllus*

Dorsal edge of front tibia with a large apical spine, a large spine slightly beyond the middle, and numerous variably-sized, smaller spines elsewhere, elytral pits with a concave floor which may be artificially raised by the presence of varying amounts of a smooth, glassy exudate *Holloceratognathus*

Genus ***Mitophyllus*** Parry reinstated

Mitophyllus Parry, 1843 362, 1845 55 Burmeister 1847 324 (as synonym of *Ceratognathus* Westwood) Type species *Mitophyllus irroratus* Parry, by original designation

Ptilophyllum Guerin-Meneville, 1845 439, 1846 xcvii Lacordaire 1856 41 (as synonym of *Ceratognathus* Westwood) Type species *Ptilophyllum godeyi* Guerin-Meneville, by original designation

There has been confusion about the publication dates of *Mitophyllus* and *Ptilophyllum* Parry's paper describing *Mitophyllus* was read before the Entomological Society of London on 3 October 1842 but was not published in the Society's *Transactions* until 1845 when it appeared in volume 4, part 1, pages 55–56, plate 1, figure 4 The first published description of *Mitophyllus* and its type species appears in an abbreviated form and without figures in the *Annals & Magazine of natural history* volume 12, number 78 (November 1843) in an account of the proceedings of the entomological society meeting of 3 October 1842

The description of *Ptilophyllum* Guerin-Meneville was published in the *Revue zoologique volume 8* in November 1845 in a report of the meeting of 8 October 1845 of the Société Entomologique de France *Ptilophyllum godeyi* was named as the type species but was not described at that time A description of *P godeyi* was provided by Guerin Méneville in the

Bulletin de la Société entomologique de France for 1845, contained in the *Annales de la Société entomologique de France* series 2, volume 3, for 1845, but apparently not published until 1846.

DESCRIPTION

GENERAL HABITUS Small to moderately large aesalines (length including mandibles 6–18 mm) with black or brown, dull or glossy integument and sexually dimorphic mandibles, antennae, and eyes. Integumental pits (punctures) of the dorsal and ventral surfaces small to very large, sparse to dense, with well defined margins, polygonally sculptured walls and floor (sculpturing visible at high magnifications), the floor raised and separated from the walls by a groove. Vestiture of the dorsal surface consisting of variably-sized, fully expanded, white, yellowish, brown or black, ribbed, blunt-tipped, oval scales and microscopic setae; vestiture of the ventral surface consisting of scales similar to those on the dorsal surface and long, thickened setae. Elytral surface not uniformly striated, instead smooth or with depressed areas, or indistinctly ribbed; vestiture sometimes arranged in longitudinal tracts. Legs slender; dorsal edge of the front tibia with two large spines and numerous small, similar-sized spines; middle and hind tibiae not very spiny.

HEAD (Fig. 1, 4; for illustrations of the entire head of *Mitophyllus* species see Holloway 1961, fig. 68–70, 74, 75, 80, 81, 83–86, 88, 90–96). Anterior margin varying from shallowly indented to strongly protruding, with or without a rim, tuberculate on the midline in some species. Preocular margin short, not laminate. Mandibles punctate, setose, sometimes also with scales; in males moderately long, either laterally curved and approximately the same width throughout their length or somewhat triangular, sometimes with erect cusps; in females short, elongate-triangular, both mandibles with an apical tooth and a subapical dorsal tooth, the left mandible with a subapical ventral tooth, the right mandible lacking this tooth. Maxilla with an elongate galea and a minute lacinia (Holloway 1960, fig. 93; 1961, fig. 15). Mentum small, approximately semicircular, setose, not covering the base of the first segment of the labial palp (Holloway 1960, fig. 94; 1961, fig. 19); ligula small, notched apically. Intermandibular projection short, extremely short in some species, wider than long, descending vertically or anteroventically or receding. Labral suture present; labrum short, wider than long, setose, directed anteroventrally or anterodorsally, its apex concave to convex. Frons with a distinctly demarcated, elongate, depressed or slightly raised, triangular area extending to the level of the posterior margin of the eyes; not tuberculate. Antenna (Fig. 7) with its club segments stout or slender, their vestiture consisting of dense, short or long setae either uniformly distributed over the surface or absent from the base or medial surface, the segments stouter and vestiture shorter in females. Supra antennal brow variably developed. Eyes protruding, small to very large, usually much larger in males; in dorsal aspect broadest near the middle and with a uniformly convex outer margin. Postocular margins very short to long, often much longer in females, slightly concave to slightly convex, neither lobed nor tuberculate, sometimes convergent posteriorly.

THORAX Pronotum wider than long; front angles acute to obtuse, blunt or sharp; disc smooth or uneven, often depressed on part of the midline, with or without a pair of tubercles; sides of disc descending gradually to the lateral margin which is convex, serrated, and has a horizontal brim; hind angles obtuse or right angled, blunt or sharp. Scutellum triangular or semicircular, its length greater or less than its width. Elytra parallel-sided; surface smooth or with a few broad ribs, or with depressed oval areas; no more than two striae visible on each elytron and these if present are barely discernible; humeral and sutural margins either low or conspicuously arched; outer margin with a low, punctate rim containing scales or setae; brim narrow; pits (punctures) small to large, polygonally sculptured on both the floor and walls (Holloway 1997, fig. 64, 65), the floor raised, flat-topped, and separated from the walls by a

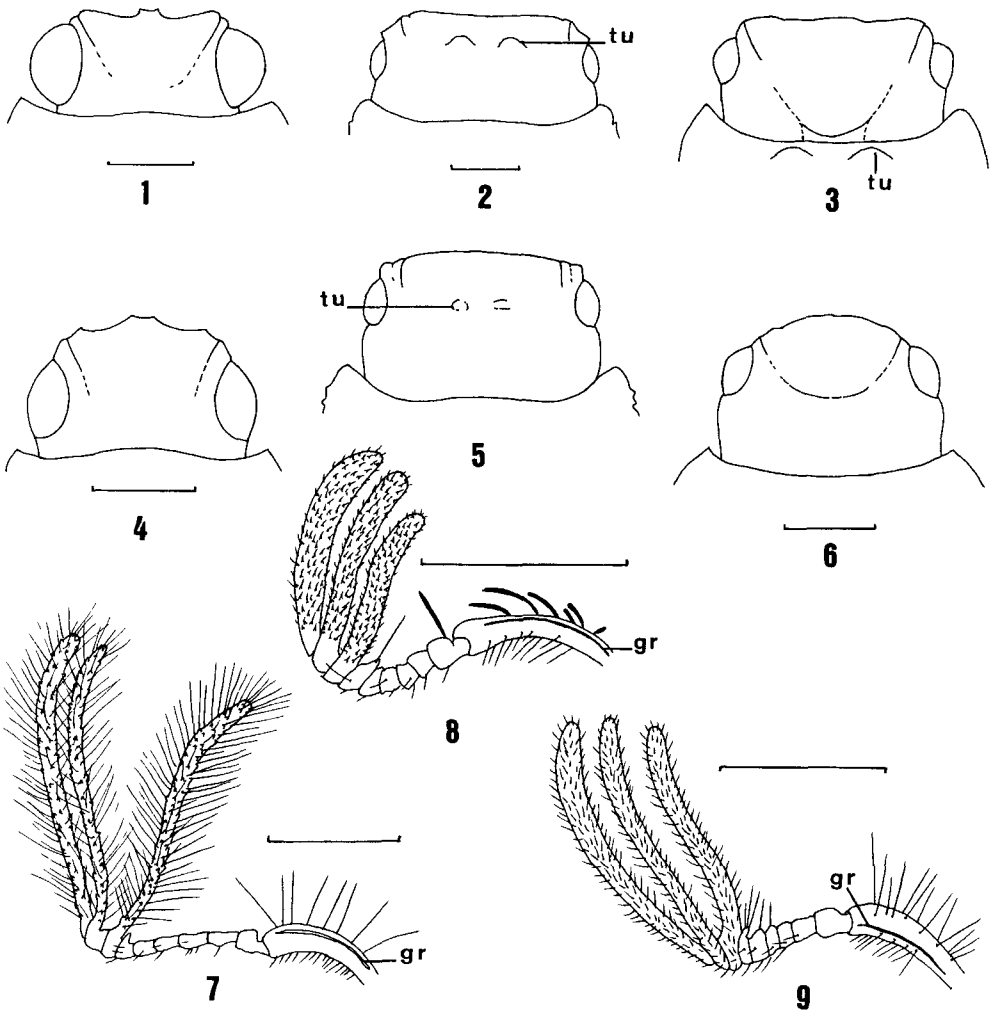

Fig. 1–9 External morphology of aesalines (1–3, heads of males; 4–6, heads of females; 7–9, left antennae of males). **1, 4, 7,** *Mitophyllus irroratus*; **2, 5, 8,** *Ceratognathus niger*; **3, 6, 9,** *Holloceratognathus helotoides*. All scales 1.0 mm; fig. 3, 6 same scale; fig. 4, 5 same scale. Abbreviations: gr, groove, tu, tubercle.

conspicuous groove; each pit with either a large appressed or standing scale or a minute, erect seta, both types of vestiture arising anteriorly in the floor, the scales oval, rather blunt-tipped, with very dense, interconnected, irregular, longitudinal ribs on their dorsal surface (Holloway 1997, fig. 32, 66, 67), the setae with divided tips; integument adjacent to the pits extremely finely reticulate (Holloway 1997, fig. 65). Hindwings fully developed (Holloway 1963, fig. 16). Prosternal process very narrow, concealed by the procoxae (Holloway 1960, fig. 5; 1961, fig. 9). Mesosternal process narrow, smooth or tuberculate. Legs long and slender; procoxal process well developed (Holloway 1960, fig. 5; 1961, fig. 9); femora with numerous setae or scales, the front femur about three times longer than wide, its silky setiferous patch large, reaching to about the middle of the segment but the associated punctures dense only on the upper part of the patch; tibial vestiture consisting of standing scales and setae, most with

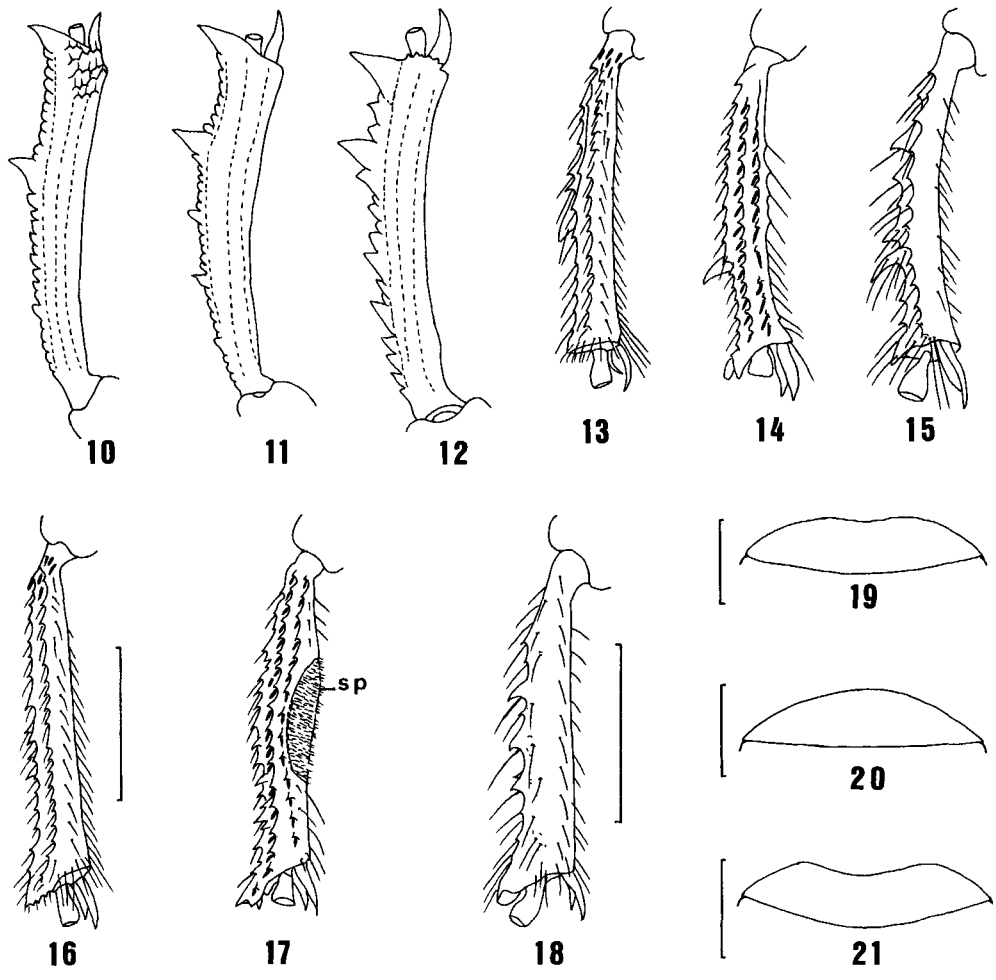

Fig. 10–21 External morphology of male aesalines (10–12, left front tibiae; 13–15, left middle tibiae; 16–18, left hind tibiae; 19–21, fifth abdominal ventrites). **10, 13, 16, 19,** *Mitophyllus irroratus*; **11, 14, 17, 20,** *Ceratognathus niger*; **12, 15, 18, 21,** *Holloceratognathus helotoides*. All scales 1.0 mm; fig. 10, 13, 16 same scale; fig. 11, 12, 14, 15, 17, 18 same scale. Abbreviation: sp, setiferous patch.

their bases concealed by an overhanging spinule; front tibia (Fig. 10) narrow, straight or slightly arched, its dorsal edge with a large apical spine, a similar spine beyond the middle, and numerous small, similar-sized spines elsewhere; middle and hind tibiae (Fig. 13, 16) gradually expanding from base to apex and lacking setiferous sex patches, the vestiture mostly aligned in seven longitudinal rows or grooves that are evenly distributed around the segment which appears approximately circular in cross-section; dorsal surface with or without a dorsal spine beyond the middle of the segment in addition to the spinules; ventral surface of the first to fourth tarsomeres with short or long setae which are either numerous and cover most of the surface or sparse and apical; arolium with a bristle on either side of its apex.

ABDOMEN Lateral margins of ventrites flanged; distal margin of fifth ventrite sexually dimorphic, truncate, angulate, or emarginate in males (Fig. 19), truncate to strongly convex in females.

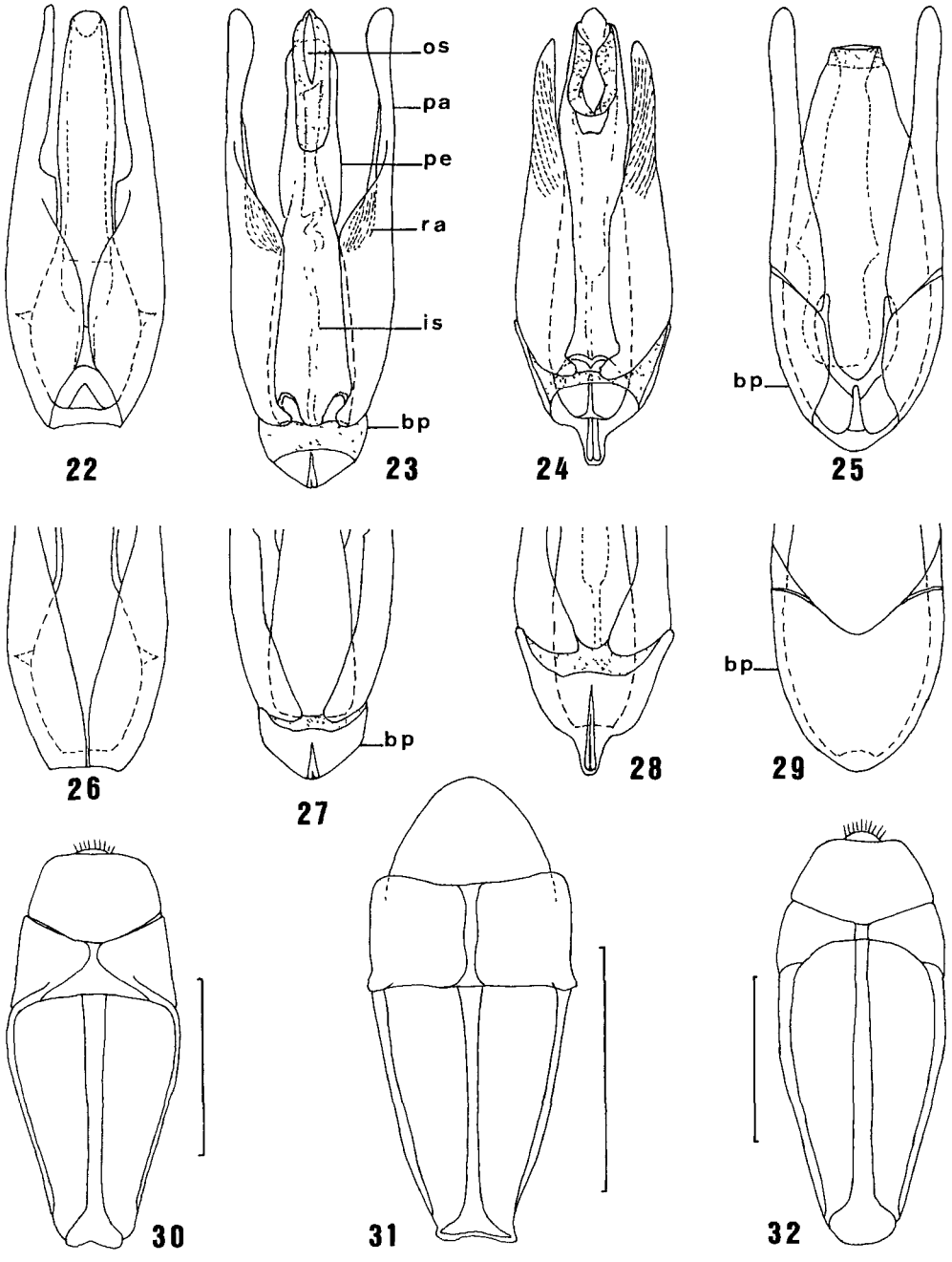

Fig. 22–32 Male terminalia of aesalines (22–25, aedeagus, dorsal aspect; 26–29, proximal half of aedeagus, ventral aspect; 30–32, ninth abdominal segment, dorsal aspect). **22, 26, 30,** *Mitophyllus irroratus*; **23, 27, 31,** *Ceratognathus niger;* **24, 28,** *C. westwoodi*; **25, 29, 32,** *Holloceratognathus helotoides*. All scales 1.0 mm; fig. 22, 26, 30 same scale; fig. 23, 27, 31 same scale; fig. 24, 25, 28, 29, 32 same scale Abbreviations: bp, basal piece; is, internal sac; os, ostium: p, penis; pa, paramere; ra, ridged area on medial surface of paramere. Stipple indicates membrane

Male terminalia. Ninth abdominal segment rather slender, symmetrical (Fig. 30) or asymmetrical (Holloway 1961, fig. 199, 202, 203); distal margin of sternite entire and setose. Tegmen (basal piece + parameres) symmetrical (Fig. 22) or asymmetrical (Holloway 1961, fig. 177, 187), the parameres separated from the basal piece by a narrow, rigid membranous strip (Holloway 1961, fig. 173, 177), or partially continuous with the basal piece (Holloway 1961, fig. 165) or completely continuous with it (Fig. 22). Basal piece or basal piece region short, broad, somewhat cylindrical, surrounding less than half the length of the penis, divided longitudinally at or near the midline both dorsally and ventrally, the dorsomedial edges either touching over all or part of their length (Holloway 1961, fig. 165, 187) or narrowly separated from each other (Fig. 22), the ventromedial edges narrowly separated from each other (Fig. 26). Parameres much longer than the basal piece, symmetrical (Fig. 22) or asymmetrical (Holloway 1961, fig. 177, 187), somewhat conical, tapering, the tip rounded, pointed, or slightly expanded; medial surface smooth, not ribbed. Penis symmetrical or asymmetrical, cylindrical, narrow or moderately broad, long, its apex approximately in line with the tips of the parameres; ostium dorsal (Holloway 1961, fig. 187) or ventral (Fig. 22) or terminal (Holloway 1961, fig. 175); internal sac longer or shorter than the penis, clothed with colourless spinules and minute setae (Holloway 1961, fig. 163, 164).

Female terminalia (Fig. 33; Holloway 1961, fig. 207–212, 214, 215). Accessory gland absent. Bursal duct short or long, narrow or broad. Bursa copulatrix bilobed, one of the lobes always large, the other very small to large. Spermathecal duct very short to moderately long, arising in various positions on the smaller lobe of the bursa copulatrix and always widely separated from the base of the median oviduct. Spermatheca small to rather large. Spermathecal gland long and slender, not strongly demarcated from its duct which is of variable length, the combined length of the duct and gland much greater than the length of the spermatheca.

REMARKS The most easily seen diagnostic feature of *Mitophyllus* adults is the row of close-set, equal-sized, small spines on the dorsal edge of the front tibia, in addition to the two large spines on this segment. In *Ceratognathus* there are two or three larger spines among the small spines on the proximal half of the front tibia, while in *Holloceratognathus* all the spines in this row vary greatly in size. The elytral ultrastructure of *Mitophyllus* provides distinctive features in the sculpturing of the scales (with numerous crossbars connecting the close-set longitudinal ribs), the form of the pits (with polygonal sculpturing on the walls and raised floor) and the sculpturing of the integument adjacent to the pits (finely reticulate). *Ceratognathus* also has the elytral integument finely reticulate and pits with a raised floor but the floor has crumpled sculpturing and the pit walls are vertically ribbed. The pits in *Holloceratognathus* are concave and have polygonal sculpturing similar to that on the adjacent integument. The different features of the pit floor can usually be seen with a stereomicroscope. *Mitophyllus* males, like those of *Holloceratognathus*, have neither the hind tibial setiferous patch nor the tuberculate frons present in males of *Ceratognathus*.

The male genitalia of *Mitophyllus* are extremely variable. They may be symmetrical or asymmetrical, have simple or ornate parameres (but never with the longitudinal ribbing that is present on the medial surface of the parameres in *Ceratognathus)*, and have a basal piece that is separated by a rigid membrane from the parameres or is partially or completely fused to the parameres. The distinctive genitalic feature is the longitudinal suture on or near the midline on the ventral surface of the basal piece (or basal piece region in species that have the parameres and basal piece conjoined). The ventral surface of the basal piece is undivided in both *Ceratognathus* and *Holloceratognathus*. Confirming generic characters in the female genitalia involve the bursa copulatrix and spermathecal structures. *Mitophyllus* and *Ceratognathus* both have a bilobed bursa copulatrix with the spermathecal duct inserting on the smaller lobe of this structure in contrast to the saccate bursa copulatrix of *Holloceratognathus*. The combined length of the spermathecal gland and spermathecal gland

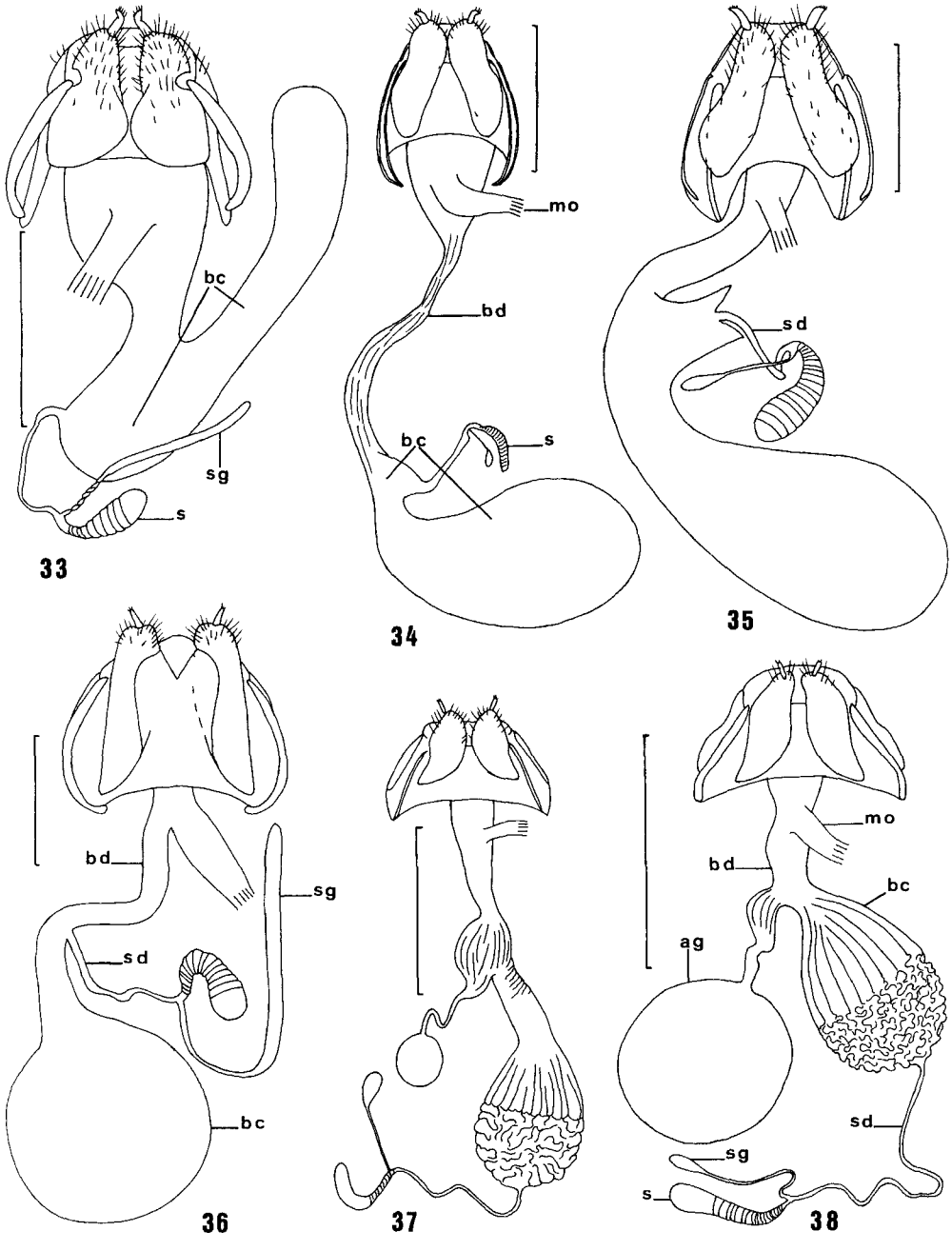

Fig. 33–38 Female terminalia of aesalines, ventral aspect **33,** *Mitophyllus irroratus*, **34,** *Ceratognathus niger* **35,** *C westwoodi*, **36,** *Holloceratognathus helotoides*, **37,** *Aesalus asiaticus*, **38,** *A scarabaeoides* All scales 1 0 mm Abbreviations ag, accessory gland, bc, bursa copulatrix, bd, bursal duct, mo, median oviduct, s, spermatheca, sd, spermathecal duct, sg, spermathecal gland

duct is much greater than the spermathecal length in *Mitophyllus* but about equal to it in *Ceratognathus*.

There is a summary of major character states in the three Australasian genera at the end of this paper.

The species belonging in *Mitophyllus* are *Ceratognathus alboguttatus* Bates, 1867, *C. dispar* Sharp, 1882, *C. foveolatus* Broun, 1880, *C. gibbosus* Broun, 1886, *M. insignis* Broun, 1923, *M. irroratus* Parry, 1843, *C. macrocerus* Broun, 1886, *M. parrianus* Westwood, 1863, and *M. reflexus* Broun, 1909. Of these seven species Nikolaev (1998) assigned *dispar*, *gibbosus*, *irroratus*, and *macrocerus* to *Ceratognathus* subgenus *Ceratognathus* and the remainder to *Ceratognathus* subgenus *Holloceratognathus*. The diagnostic characters he gave for the subgenus *Ceratognathus* are the absence of a discrete basal piece in the male genitalia (that is there is no suture between the basal piece and the parameres) and the "reduction of the labrum in the majority of males". No other characters are mentioned. As can be seen from the illustrations of male genitalia included in the present paper, *C. niger* (the type species of *Ceratognathus*) and *C. westwoodi* both have the parameres separated from the basal piece by a conspicuous suture. Martinez (1976) considered the neotropical *Ceratognathus penai* Martinez, known only from males, to be close to *M. insignis* Broun but his description of *penai* lacks the morphological details that are required to confirm this relationship.

Genus ***Holloceratognathus*** Nikolaev new status

Holloceratognathus Nikolaev, 1998: 55 (as subgenus of *Ceratognathus* Westwood). Type species *Ceratognathus helotoides* Thomson, by original designation.

Neoceratognathus Nikolaev, 1998: 56 (as subgenus of *Ceratognathus* Westwood). Type species *Ceratognathus passaliformis* Holloway, by original designation and monotypy. New synonymy.

DESCRIPTION

GENERAL HABITUS Small to moderately large aesalines (length including mandibles 6–15 mm) with black or brown, glossy integument; sexual dimorphism always apparent in the mandibles, sometimes apparent in the antennae and eyes. Integumental pits (punctures) of the dorsal and ventral surfaces numerous, minute to large, with well defined margins and a polygonally sculptured surface (sculpturing visible only at very high magnifications), the floor structurally concave but appearing to be convex in pits that are partially or completely filled with exudate. Vestiture of the dorsal surface consisting of minute to large, fully expanded, cream, yellow, or brown, ribbed, pointed, elongate-oval or linear scales and microscopic setae; vestiture of the ventral surface consisting of pale linear scales and thickened setae. Elytral surface finely striated. Legs slender; dorsal edge of the front tibia with two large spines and numerous smaller spines of varying sizes; dorsal surface of the middle and hind tibiae very spiny.

HEAD (Fig. 3, 6; for illustrations of the entire head see Holloway 1961, fig. 65, 66, 90; 1962, fig. 1). Anterior margin varying from concave to convex, with or without a rim, not tuberculate. Preocular margin short, not laminate. Mandibles punctate, setose; in males rather short, laterally curved, and approximately the same width throughout their length, sometimes with an erect cusp; in females short, elongate-triangular, both mandibles with an apical tooth, a subapical dorsal tooth, and a subapical ventral tooth which is large on the left mandible and very small on the right mandible. Maxilla with a short, broad galea and a minute lacinia. Mentum small, approximately semicircular, setose, not covering the base of the first segment of the labial palp; ligula small, its apex convex. Intermandibular projection short, often extremely short, wider than long, descending anteroventrally or receding. Labral suture present; labrum short, wider than long, setose, directed anteroventrally or horizontally, its

apex truncate or slightly convex Frons concave or flattened, not with a conspicuous triangular outline between the eyes, not tuberculate Antenna (Fig 9) with its club segments stout or slender and with dense, rather short, uniformly distributed setae, the segments either stout and almost identical in both sexes or, if sexually dimorphic, slender in both sexes but considerably longer in males Supra antennal brow short, only slightly arched Eyes weakly protruding, small to moderately large, in dorsal aspect unevenly convex Postocular margins moderately long, slightly concave to slightly convex, neither lobed nor tuberculate, sometimes convergent posteriorly

THORAX Pronotum wider than long, front angles acute to obtuse, blunt or sharp, disc smooth or uneven, sometimes depressed on the midline anteriorly, with or without a pair of tubercles, sides of disc descending vertically to the lateral margin which is serrated and almost straight, brim very broad (*passaliformis*) or absent, hind angles obtuse, blunt or sharp Scutellum triangular or semicircular, its length greater or less than its width Elytra parallel sided, surface almost smooth or with four broad, raised interstriae on each elytron, at least five punctate striae visible at low magnifications on each elytron, humeral angles and sutural margins low, outer margin with a low, punctate rim containing scales or setae, brim either strongly developed on the distal third of each elytron (*passaliformis*) or entirely absent, pits (punctures) minute to large, polygonally sculptured on both the floor and walls (Holloway 1997, fig 68, 70), the floor concave but often covered with a mound of hard, glossy, exudate which meets the pit wall at an acute angle (exudate is not separated from the wall by a conspicuous groove), each pit with either a large, curved scale or a minute, erect seta, both set slightly off centre in the floor, the scales elongate oval or linear, sharply pointed, with either a single rib (*passaliformis*) or several interconnected longitudinal ribs on their dorsal surface (Holloway 1997, fig 31, 68, 70), the setae with divided or undivided tips and often obscured by exudate, integument adjacent to the pits polygonally sculptured (Holloway 1997, fig 68, 70) Hindwings fully developed or, in *passaliformis*, with the anal area very slightly reduced (Holloway 1963, fig 17) Prosternal process very narrow, concealed by the procoxae Mesosternal process narrow, smooth Legs moderately long and slender, procoxal process well developed, femora with numerous narrow scales, the front femur about two times longer than wide, its silky setiferous patch large or small, reaching almost three-quarters or barely one quarter the distance along the femur, the associated punctures present on only the upper part of the patch, tibial vestiture composed of standing setae or very narrow scales, some with their bases concealed by an overhanging spine or spinule, front tibia narrow (Fig 12) or, in *passaliformis*, rather broad (Holloway 1962, fig 1), straight or slightly arched, its dorsal edge with a large apical spine, a large spine beyond the middle, and numerous variably-sized but smaller spines elsewhere (the size variation of these is slight in *passaliformis*). middle and hind tibiae (Fig 15, 18) gradually expanding from base to apex and lacking setiferous patches, the vestiture mostly aligned in seven longitudinal grooves that are evenly distributed on all the surfaces except the posteromedial one which is flattened and almost bare, dorsal surface of the middle and hind tibiae with about three longitudinal rows of variably-sized spines (in *passaliformis* the dorsal surface is very narrow and all the spines are small), ventral surface of the first to fourth tarsomeres with short or long setae which are either sparse and apical or numerous and cover most of the surface, arolium with a bristle on either side of the apex

ABDOMEN Lateral margins of the ventrites with or without a flange, distal margin of the fifth ventrite sexually dimorphic, emarginate (Fig 21) or angulate (Holloway 1962, fig 2) in males, truncate or slightly convex in females

Male terminalia Ninth abdominal segment moderately slender, symmetrical (Fig 32, Holloway 1961, fig 200, 1962, fig 4), distal margin of the sternite entire and setose Tegmen (basal piece + parameres) symmetrical (Fig 23, Holloway 1962, fig 3) or very slightly

asymmetrical (Holloway 1961, fig. 183), the parameres separated from the basal piece by a very narrow, rigid, membranous strip. Basal piece short, broad, somewhat cylindrical, surrounding less than half the length of the penis, divided longitudinally at or near the midline on the dorsal surface, the dorsomedial edges either touching over part of their length (Holloway 1961, fig. 183) or widely separated from each other (Fig. 25; Holloway 1962, fig. 3); ventral surface of the basal piece undivided (Fig. 29). Parameres longer than the basal piece, symmetrical or asymmetrical, conical, tapering, the tip rounded or pointed; medial surface smooth, not ribbed. Penis symmetrical or very slightly asymmetrical, cylindrical, broad, moderately long, its apex not reaching as far as the tips of the parameres; ostium terminal; internal sac broad, about as long as the penis, clothed with colourless and brown spinules of varying sizes.

Female terminalia (Fig. 36; Holloway 1961, fig. 204, 213; 1962, fig. 5). Accessory gland absent. Bursal duct short or moderately long, relatively broad. Bursa copulatrix saccate. Spermathecal duct long, arising on the proximal half of the bursa copulatrix, its insertion point widely separated from the base of the median oviduct. Spermatheca rather large. Spermathecal gland very long and slender, conspicuously demarcated from its duct which is of variable length, the combined length of the duct and gland very much greater than the length of the spermatheca.

REMARKS Males and females of *Holloceratognathus* are distinguished externally from those of both *Mitophyllus* and *Ceratognathus* by the variably-sized smaller spines on the dorsal edge of their front tibiae, the spiny dorsal surface and flattened, almost naked posteromedial surface of the middle and hind tibiae, and the structurally concave surface of the elytral pits. They are further separable from *Mitophyllus* adults by their completely or partially striate (either lined or furrowed) elytra and their elytral scales which have a small number of longitudinal ribs with very few anastomoses. The absence of both a hind tibial setiferous patch and frontal tubercles immediately distinguishes *Holloceratognathus* males from those of *Ceratognathus*.

Distinctive genitalic features of *Holloceratognathus* compared with *Mitophyllus* are, in males, a ventrally undivided basal piece and, in females, a saccate (single-lobed) bursa copulatrix, and a spermathecal duct that inserts on the proximal half of the bursa copulatrix. In *Ceratognathus* the basal piece is also undivided ventrally but is distinctive in being membranous dorsally. Genitalic configurations similar to those in *Holloceratognathus* are present in both sexes of the Northern Hemisphere aesalines *Nicagus obscurus* LeConte and *N. japonicus* Nagel (see Holloway 1969 for the morphology of *N. obscurus* and Tabana & Okuda 1992 for the male genitalia of *N. japonicus*). These two *Nicagus* species also have in common with *Holloceratognathus* elytral pits that are concave and may contain a smooth, glassy exudate.

The species belonging in *Holloceratognathus* are *Mitophyllus cylindricus* Broun, 1895, *Ceratognathus helotoides* Thomson, 1862, and *C. passaliformis* Holloway, 1962.

Nikolaev (1998) assigned *M. cylindricus* Broun, *C. helotoides* Thomson, *Ceratognathus alboguttatus* Bates, *C. foveolatus* Broun, *Mitophyllus insignis* Broun, *M. parrianus* Westwood and *M. reflexus* Broun to *Ceratognathus* subgenus *Holloceratognathus*, but the latter five species belong in *Mitophyllus*. He used the presence of a suture between the basal piece and parameres of the male genitalia as a defining character for *Holloceratognathus* but this suture also features in *Ceratognathus* and in some species of *Mitophyllus*. Nikolaev did not look further into the structure of the male genitalia nor did he take into consideration the female genitalia and external morphology of both sexes. The subgenus *Neoceratognathus* which he erected for *passaliformis*, and which I am placing in synonymy, is based on several unique features of this species, such as the broader, supposedly longer basal piece of the male genitalia, and the modified scales and hindwing. Although *passaliformis* has these and

several other "atypical" generic features its antennae, mouthparts, elytral pits, elytral sculpturing, and male and female genitalia are like those of the other two species of *Holloceratognathus*. *H. passaliformis* is a very small aesaline which has only ever been found in nests of the endemic ant *Prolasius advena* (Fr. Smith) (Holloway 1962, Grehan 1980) and it seems likely that the flattened body, greatly reduced elytral scales, slightly reduced hindwings, paddle-like legs with few spines, exceptionally broad pronotal flange, and wide elytral brim are modifications associated with its inquiline, subterranean life style. Interestingly, however, some of these modifications have arisen independently in a few "free living" aesalines, paddle-shaped legs, for example, have evolved in *Aesalus scarabaeoides* (Panzer) but not in other species of *Aesalus*, and a very broad pronotal flange is present in males of *Mitophyllus reflexus* Broun and *M. gibbosus* (Broun) but not in males of other species nor in any females of *Mitophyllus*.

As has been noted above, adults of *Holloceratognathus* are morphologically very similar to those of *Nicagus*.

Distribution of some adult character states in *Ceratognathus* (based on *C. niger* Westwood (the type species) and *C. westwoodi* Thomson), *Holloceratognathus*, and *Mitophyllus*

HEAD

01 1 Maxilla with an elongate, narrow galea. *Ceratognathus*, *Mitophyllus*
01 2 Maxilla with a short, broad galea. *Holloceratognathus*
02 1 Right mandible of female with a subapical ventral tooth. *Ceratognathus*, *Holloceratognathus*
02 2 Right mandible of female lacking a subapical ventral tooth. *Mitophyllus*
03 1 Frons in male with a pair of variably developed tubercles (Fig. 2), these tubercles rudimentary in the female (Fig. 5). *Ceratognathus*
03 2 Frons lacking tubercles in both sexes (Fig. 1, 3, 4, 6). *Holloceratognathus*, *Mitophyllus*

THORAX

04 1 Dorsal edge of front tibia with a large apical spine, a large postmedial spine, and numerous small, equal-sized spines elsewhere (Fig. 10). *Mitophyllus*
04 2 Dorsal edge of front tibia with a large apical spine, a large postmedial spine, 2 or 3 smaller, widely separated spines on the proximal half of the segment, and numerous much smaller, equal-sized spines elsewhere (Fig. 11). *Ceratognathus*
04 3 Dorsal edge of front tibia with a large apical spine, a large postmedial spine, and numerous variably-sized, smaller spines elsewhere (Fig. 12). *Holloceratognathus*
05 1 Middle and hind tibiae more or less circular in cross-section, and with evenly distributed longitudinal rows of setae or scales (Fig. 13, 14, 16, 17). *Ceratognathus*, *Mitophyllus*
05 2 Middle and hind tibiae somewhat rectangular in cross-section, and with longitudinal rows of setae or scales absent on much of the posteromedial surface (Fig. 15, 18). *Holloceratognathus*
06 1 Dorsal surface of middle and hind tibiae with fine spines only (a single large spine is sometimes present) (Fig. 13, 14, 16, 17). *Ceratognathus*, *Mitophyllus*
06 2 Dorsal surface of middle and hind tibiae with many coarse spines (Fig. 15, 18). *Holloceratognathus*
07 1 Hind tibia of male with a setiferous patch on the ventral surface (Fig. 17). *Ceratognathus*
07 2 Hind tibia of male lacking a setiferous patch (Fig. 16, 18). *Holloceratognathus*, *Mitophyllus*
08 1 Elytral scales broadly oval, rather blunt-tipped, their dorsal surface with numerous

longitudinal ribs connected by short, closely spaced cross-bars (Holloway 1997, fig. 32, 64, 66): *Mitophyllus*.

08.2 Elytral scales elongate oval, sharp-tipped, their dorsal surface with a relatively small number of longitudinal, slightly anastomosing ribs (Holloway 1997, fig. 30, 31, 69, 71): *Ceratognathus*, *Holloceratognathus*.

09.1 Elytral pits with a structurally raised, sculptured floor (Holloway 1997, fig. 64, 65, 71): *Ceratognathus*, *Mitophyllus*.

09.2 Elytral pits with a concave floor which may be artificially raised by varying amounts of a smooth, glassy exudate (Holloway, 1997, fig. 68, 70): *Holloceratognathus*.

10.1 Walls and floor of elytral pits with crumpled, somewhat reticulate sculpturing, stretched out on the walls (Holloway 1997, fig. 74): *Ceratognathus*.

10.2 Walls and floor of elytral pits polygonally sculptured (Holloway 1997, fig. 64, 68, 70): *Holloceratognathus*, *Mitophyllus*.

11.1 Integument adjacent to elytral pits very finely reticulate (Holloway 1997, fig. 65, 73): *Ceratognathus, Mitophyllus*.

11.2 Integument adjacent to elytral pits polygonally sculptured (Holloway 1997, fig. 68, 70): *Holloceratognathus*.

ABDOMEN

12.1 Apex of fifth ventrite of male convex (Fig. 20): *Ceratognathus*.

12.2 Apex of fifth ventrite of male truncate, angulate, or emarginate (Fig. 19, 21): *Holloceratognathus*, *Mitophyllus*.

Male terminalia

13.1 Paired plates on dorsal surface of ninth abdominal segment in males rectangular (Fig. 31): *Ceratognathus*.

13.2 Paired plates on dorsal surface of ninth abdominal segments in males triangular (Fig. 30, 32): *Holloceratognathus*, *Mitophyllus*.

14.1 Basal piece entirely membranous dorsally (Fig. 23, 24): *Ceratognathus*.

14.2 Basal piece sclerotised dorsally except for a membranous strip of varying width on the midline (Fig. 22, 25, 26, 29): *Holloceratognathus*, *Mitophyllus*.

15.1 Basal piece undivided on the ventral surface (Fig. 27–29): *Ceratognathus*, *Holloceratognathus*.

15.2 Basal piece (or basal piece region if basal piece is fused to parameres) divided on or near the ventral midline (Fig. 26): *Mitophyllus*.

16.1 Parameres separated from basal piece by a rather wide, flexible membrane (Fig. 27, 28): *Ceratognathus*.

16.2 Parameres either continuous with basal piece or separated from it by a narrow, rigid membrane (Fig. 22, 25; Holloway 1961, fig. 173, 177): *Holloceratognathus*, *Mitophyllus*.

17.1 Parameres with a variably-sized patch of longitudinal ribbing on the medial surface (Fig. 23, 24): *Ceratognathus*.

17.2 Parameres not ribbed on the medial surface (Fig. 22, 25): *Holloceratognathus*, *Mitophyllus*.

Female terminalia

18.1 Bursa copulatrix consisting of a single sac (Fig. 36): *Holloceratognathus*.

18.2 Bursa copulatrix bilobed, one of the lobes very small (Fig. 33–35): *Ceratognathus*, *Mitophyllus*.

19.1 Combined length of spermathecal gland and its duct much greater than the length of the spermatheca (Fig. 33, 36): *Holloceratognathus*, *Mitophyllus*.

19.2 Combined length of spermathecal gland and its duct about equal to the length of the spermatheca (Fig. 34, 35): *Ceratognathus*.

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APPENDIX

LABEL DATA AND REPOSITORIES OF FIGURED SPECIMENS.

Collection abbreviations: ANIC, Australian National Insect Collection, CSIRO, Canberra; NZAC, New Zealand Arthropod Collection, Landcare Research New Zealand Limited, Auckland.

Aesalus asiaticus, female. JAPAN, Mt Syakagadake, 1600 m, Nara Prefecture, 18 October 1987, N. Okuda. (NZAC); Fig. 37.

Aesalus scarabaeoides, female. N. ITALY, Carnia, 1000 m, May 1968, Gobbi, M. Ciaurlec (Luca Bartolozzi Private Collection, Florence); Fig. 38.

Ceratognathus niger, male. [AUSTRALIA], Kangaroo Island (NZAC); Fig. 2, 23, 27, 31.

C. niger, male. TASMANIA, Freycinet Peninsula, 9 January 1978 (NZAC); Fig. 8, 11, 14, 17.

C. niger, male. [AUSTRALIA], Higgins, ACT, January 1984, in rotten wood, J. Wiggins (ANIC); Fig. 20.

C. niger, female. (TASMANIA), Launceston, 126, Littler Collection (NZAC); Fig. 5, 34.

Ceratognathus westwoodi, male. (TASMANIA), Bermuda Road, SW Huonville, 4 February 1989, R. Bell (ANIC); Fig. 24, 28.

C. westwoodi, female. [AUSTRALIA], Arve Loop, in *Atherosperma moschatum*, coll. 3 September 1981, em. 6 November 1981, R. Bashford, Sp. K (ANIC); Fig. 35.

Holloceratognathus helotoides, male. [NEW ZEALAND], Mackays Bluff, 2000 feet, Nelson, 8 November 1944, E.S. Gourlay (NZAC); Fig. 3, 9, 12, 15, 18, 25, 29, 32.

H. helotoides, male and female. [NEW ZEALAND], Head of Lake Rotoiti, Nelson, 11 October 1964, ex rotten log, Travers River, A.K. Walker (NZAC); Fig. 6, 21, 36.

Mitophyllus irroratus, male. [NEW ZEALAND], Westport, 20 January 1935, E.S. Gourlay (NZAC); Fig. 1, 7, 10, 13, 16, 22, 26, 30.

M. irroratus, male. [NEW ZEALAND], Pureora S.F., TO, 13 February 1984, R.C. Craw (NZAC); Fig. 19.

M. irroratus, female. [NEW ZEALAND], New Brighton, Christchurch, 20 January 1948, E.S. Gourlay (NZAC); Fig. 4, 33.