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Classification of basal Cucujoidea (Coleoptera : Polyphaga): cladistic analysis, keys and review of new families

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Abstract. Phylogenetic relationships among the basal Cucujoidea were reconstructed by a cladistic analysis of a data matrix consisting of 37 exemplar taxa and 99 adult and larval characters. Eight most parsimonious cladograms provided evidence for the polyphyly of Phloeostichidae, the paraphyly of Cucujoidea (with respect to the placement of Trogossitidae), and the monophyly of Protocucujidae + Sphindidae, Biphyllidae + Erotylidae, Cryptophagidae, Cucujidae + Silvanidae, Propalticidae + Laemophloeidae, and the Nitidulidae groups (Nitidulidae, Smicripidae, and Brachypteridae). The following families are elevated from subfamily to family status: Agapythidae (one genus), Phloeostichidae (four genera; the subfamilies Phloeostichinae and Hymaeinae are supressed), Priasilphidae (three genera), Tasmosalpingidae (one genus), and Myraboliidae (one genus). These families are described in detail and adult and larval keys to all families of Cucujoidea are provided. The genus *Bunyastichus*, gen. nov. (type species: *B. monteithi*, sp. nov.) is described in the family Phloeostichidae and the family Priasilphidae is revised with the following new taxa: *Chileosilpha*, gen. nov. (type species: *C. elguetai*, sp. nov.), *Priasilpha* (*P. angulata*, sp. nov., *P. aucklandica*, sp. nov., *P. bufonia*, sp. nov., *P. carinata*, sp. nov., *P. earlyi*, sp. nov., and *P. embersoni*, sp. nov.), *Priastichus* (*P. crowsoni*, sp. nov. and *P. megathorax*, sp. nov.).

Introduction

Of the six superfamilies in the series Cucujiformia, Cucujoidea is the most problematic because it seems to have been established only for convenience to contain a heterogenous group of families with a similar habitus (Figs 1–10). The superfamily presently consists of 32 families (Lawrence and Newton 1995), when Languriidae and Erotylidae are combined (Wegrzynowicz 2002; Leschen 2003) and Cyclaxyridae recognised at the family level (Lawrence *et al*. 1999*b*). Cucujoid workers recognise two informal groupings in the superfamily: the cerylonid series may be a monophyletic lineage within the superfamily consisting of eight families (Sen Gupta and Crowson 1973; Ślipiński 1990; Ślipiński and Pakaluk 1992): Bothrideridae, Cerylonidae, Discolomatidae, Coccinellidae, Endomychidae, Alexiidae, Corylophidae, and Latridiidae. The remaining members of Cucujoidea are considered part of the basal Cucujoidea (or lower Cucujoidea, Leschen 1996), a colloquial designation for what may be the more primitive members of the group (along with enigmatic families such as Helotidae and Passandridae). Among the basal cucujoids, the family Phloeostichidae, consisting of only a handful of genera, has been controversial with regard to its monophyletic status. In this paper we provide a cladistic analysis of the basal groups, mainly to place the Phloeostichidae subfamilies in broader phylogenetic context.

The family Phloeostichidae was proposed by Sen Gupta and Crowson (1969) for the European *Phloeostichus* Redtenbacher (Fig. 6, Cucujidae), the New Zealand *Agapytho* Broun (Fig. 4, Salpingidae), the Australian *Hymaea* Pascoe (Fig. 5), originally included in Tenebrionidae but made the type of the boganiid subfamily Hymaeinae by Sen Gupta and Crowson (1966), and the Chilean *Rhopalobrachium* Boheman (Fig. 8), which had been placed in Oedemeridae or Pythidae. Crowson (1973) added the subfamily Priasilphinae comprised of the New Zealand *Priasilpha* Broun (Fig. 1) placed by Broun (1893) and Grouvelle (1913) in Nitidulidae, and a newly described Tasmanian genus *Priastichus* Crowson (Fig. 2). In this same paper, Crowson (1973: 55) admitted that the phloeostichid subfamilies Phloeostichinae, Hymaeinae, Agapythinae and Priasilphinae 'would be better treated as independent families, with individual affinities to other clavicorn families'. Lawrence (1988) added two other genera to the family based in part on discussions with Crowson: *Tasmosalpingus* Lea (1919, Fig. 10) from Salpingidae and *Myrabolia* Reitter (1876, Fig. 9) from Silvanidae (Blackburn 1903). Lawrence and Britton (1991) proposed two additional subfamilies, Myraboliinae and Tasmosalpinginae, for their inclusion, and Lawrence (1995) added an Australian and Chilean species to the formerly monotypic *Rhopalobrachium*. In the past few years an additional two genera have been discovered which

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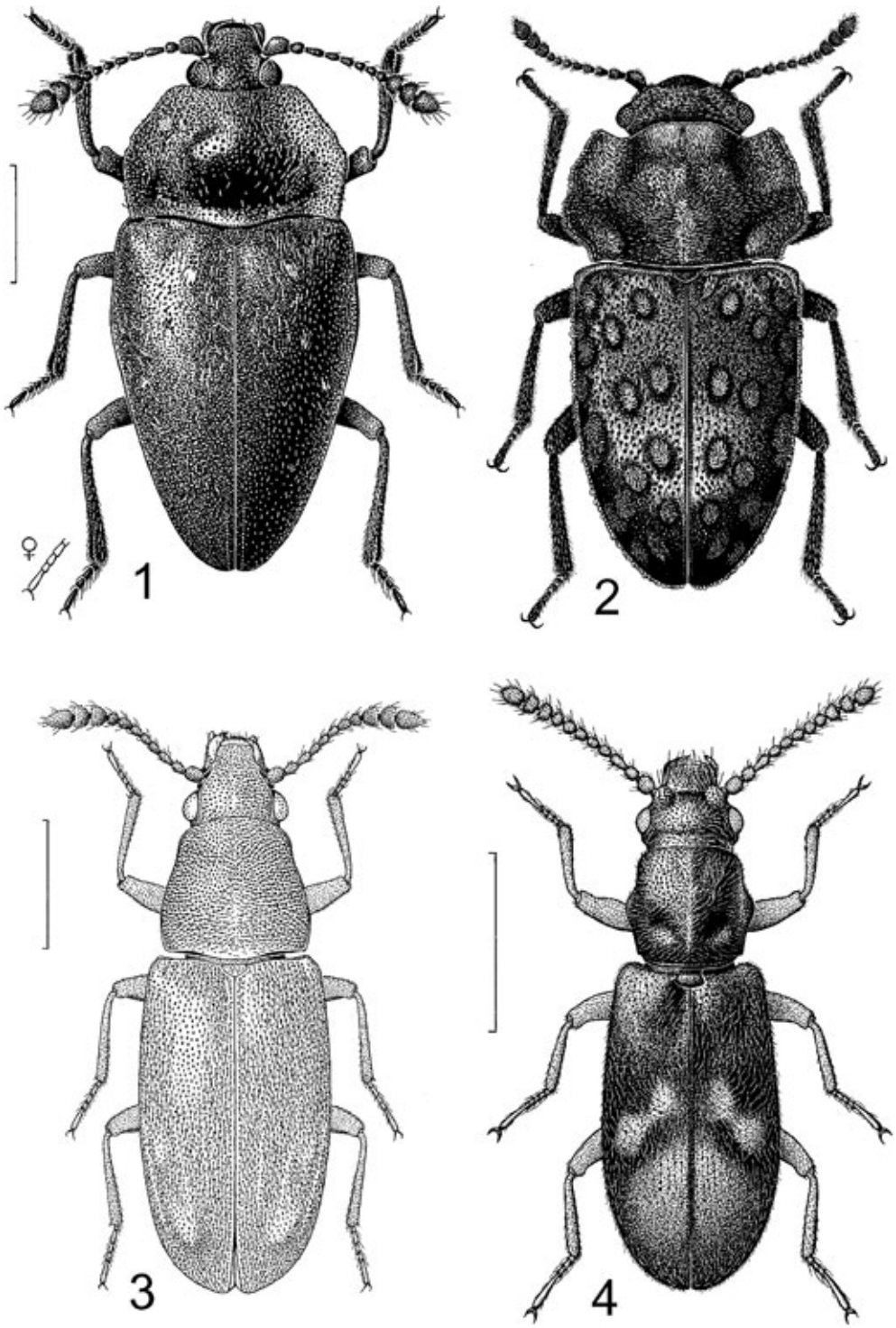
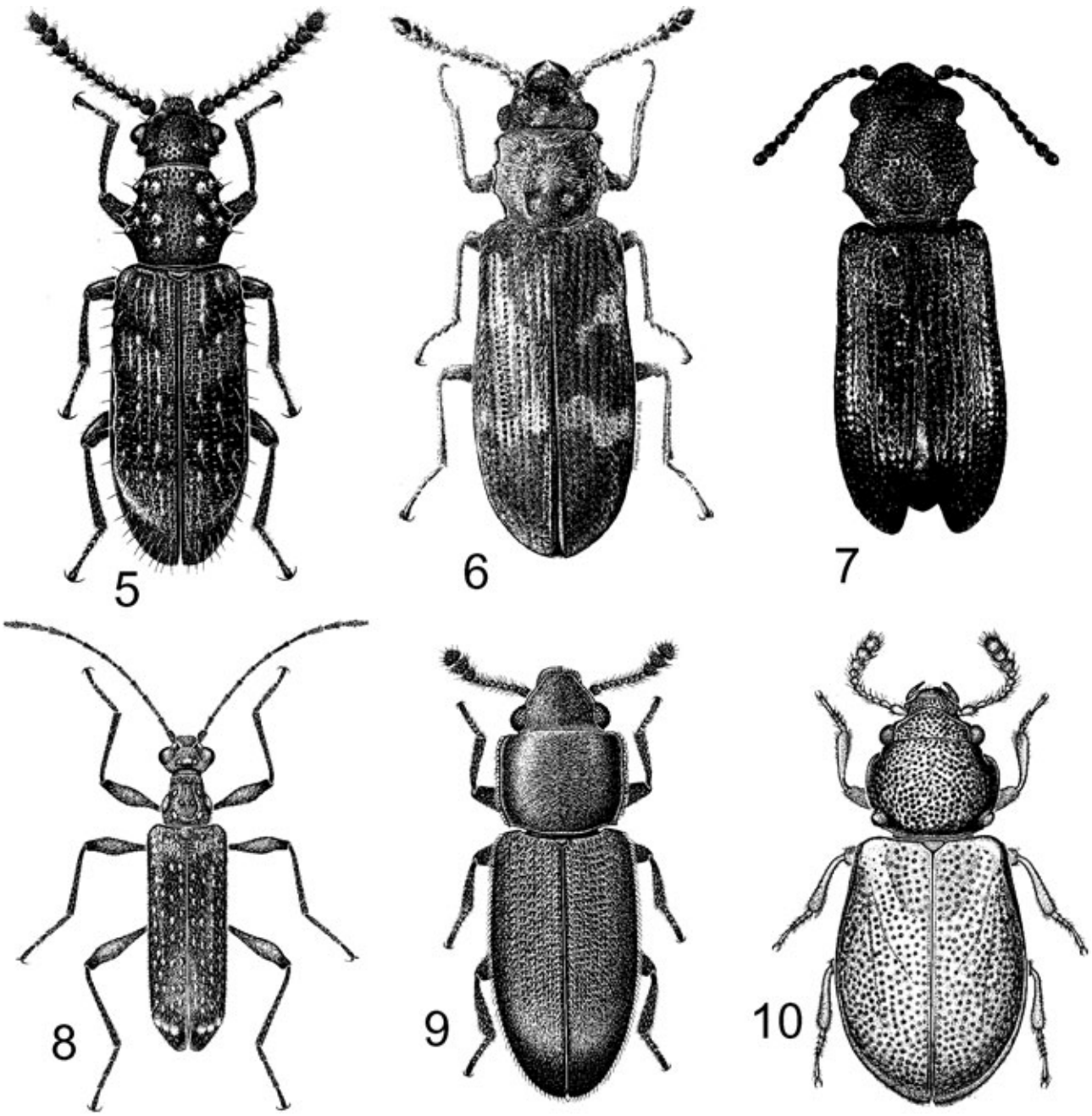


Figs 1–4. Dorsal views of adult Priasilphidae and Agapythidae: *1*, *Priasilpha obscura*; *2*, *Priastichus megathorax*, sp. nov. (length = 3.6 mm); *3*, *Chileosilpha elguetai*, sp. nov.; *4*, *Agapytho foveicollis*. Scale bars = 1 mm.

belong in this complex: one from Chile related to the Priasilphinae and one from Australia related to the Phloeostichinae and Hymaeinae; in addition several new species have been discovered in the genera *Priasilpha* and *Priastichus*. These are described in the present paper.

Although the family Phloeostichidae appears to be a taxon of convenience, consisting mainly of monogeneric Notogean subfamilies with a suite of basal cucujoid features, it is not at all clear which of these taxa should be elevated to family rank and which transferred to other known families. In order to shed some light on this problem we have examined 37 exemplar genera, including all eight currently included in Phloeostichidae, the two new genera described below, and members of all remaining families of basal Cucujoidea. Based on this analysis we revise the classification for Cucujoidea, review the families Priasilphidae, Phloeostichidae, Agapythidae, Tasmosalpingidae and Myraboliidae, and provide keys to adults and larvae of all cucujoid families.



Figs 5–10. Dorsal views of adult basal Cucujoidea. *5*, *Hymaea magna* (length = 4.5 mm); *6*, *Phloeostichus denticollis* (length = 5.0 mm); *7*, *Bunyastichus monteithi*, sp. nov. (length = 3.6 mm); *8*, *Rhopalobrachium penai* (length = 11.0 mm); *9*, *Myrabolia* sp. (length = 4.3 mm); *10*, *Tasmosalpingus* sp. (length = 1.8 mm).

Materials and methods

Terms and measurements

The terms *mesoventrite* and *metaventrite* used in keys, descriptions and character discussions were coined by Lawrence (1999) and Lawrence *et al*. (1999*b*) to replace the misapplied terms mesosternum and metasternum (see also Campau 1940; Ferris 1940; Beutel and Haas 2000). Wing vein terminology is from Kukalová-Peck and Lawrence (2004); specifically the *medial field* refers to the area of wing membrane between the medial bar (posterior wing strut or MP_{1+2}) and the anal fold, thus excluding AP_{3+4}; the number of free veins in this field is equivalent to Crowson's term 'anal veins in the main group'. The term *decumbent* is used for setae that are erect basally but strongly recurved at apex, and *recumbent* refers to setae that are strongly declined at base and more or less adpressed to the surface. The terms *proximal gonocoxite* and *distal gonocoxite* are those used by Burmeister (1976, 1980), whereas the terms *paraproct* (= hemitergite IX or laterotergite IX) and *proctiger* (tergite X) are taken from Tanner (1927). The terms *baculum* and *bacula* are used for the longitudinal supporting struts on each side of the proctiger and on the ventral or mesal edge of each paraproct and to the transverse or oblique strut at the base of the proximal gonocoxite. Measurements: PL, median length of pronotum; PW, greatest width of pronotum; EL, length of the elytra along suture; EW, combined greatest widths of elytra; BL, body length (excluding head) or PL + EL; GD, greatest depth (metaventrite to basal third of elytra).

Sources of material

Abbreviations for collections used in the text are as follows:

AA	Albert Allen Collection, Boise, Idaho (private)
ANIC	Australian National Insect Collection, CSIRO Entomology, Canberra
AMNZ	Auckland War Memorial Museum, Auckland (John Early, Stephen Thorpe)
CAS	California Academy of Sciences, San Francisco (Roberta Brett)
FMNH	Field Museum of Natural History, Chicago (Al Newton, Phil Parillo)
JNIC	John Nunn Insect Collection, Dunedin, New Zealand (private)
LUNZ	Lincoln University Insect Museum, Lincoln, New Zealand (John Marris)
MCZH	Museum of Comparative Zoology, Harvard University, Cambridge (Phil Perkins)
MHNS	Museo Nacional de Historia Natural, Santiago (Mario Elgueta)
MV	Museum of Victoria, Melbourne: (Ken Walker, Catriona McPhee)
NHML	The Natural History Museum, London (Max Barclay)
NMNH	National Museum of Natural History, Smithsonian Institution, Washington, D.C. (Steve Lingafelter)
NZAC	New Zealand Arthropod Collection, Auckland
QM	Queensland Museum, Brisbane (Geoff Monteith)
SAM	South Australian Museum, Adelaide (Eric Matthews)
TUPC	Teruhisa Ueno Personal Collection, Kyushu University, Japan (private)

New Zealand localities are arranged according to the two-letter area codes proposed by Crosby *et al*. (1998). For specimens of *Priasilpha*, longitude and latitude positions have been added in parentheses to the original label data.

Terminal taxa used in cladistic analysis

The phylogenetic analysis was prompted by the uncertain relationships of Phloeostichidae to other members of the basal Cucujoidea, though the phylogenetic problem relates to the larger question of monophyly of Cucujoidea and relationships of some cucujoid families to other superfamilies, namely Cleroidea. A more extensive study than the present one is necessary for ascertaining whether the basal Cucujoidea or cerylonid series are monophyletic; here we are concerned mainly with the controversial taxa of Phloeostichidae and the monophyletic status of its subfamilies, and members of the cerylonid series were not included. Instead of members of the cerylonid series, we decided to include more primitive cucujiform taxa representing Bostrichiformia (Derodontidae) and Cleroidae (Trogossitidae) to focus attention on the problems in the basal Cucujoidea (see below).

Cucujoidea is characterised by several features (e.g. presence of a cucujoid aedeagus and pygopod-like 10th abdominal segment of the larva). These and other characters aid in distinguishing the group from Tenebrionoidea (Lawrence and Britton 1991) but cannot count as synapomorphies because they occur in other superfamilies. Futhermore, the ring-like tegmen (Fig. 31) may be a plesiomorphic condition transformed to character states seen in cleroids, cucujoids, and tenebrionoids (Crowson 1955; Lawrence and Leschen 2003). Crowson (1955) listed several other characters, but admitted that none of the characters he provided were reliable estimates for the monophyly of the superfamily.

To resolve the relationships of basal cucujoids, we use an exemplar approach to taxon sampling (Yeates 1995) because such morphological studies of a subset of taxa can lead to more robust hypotheses about phylogenetic relationship (Bremer *et al*. 1999). This is also an important consideration in morphological studies where the ratio of the number of informative characters to terminal taxa may be quite low compared to molecular studies. In most cases we use a single species to represent genera as terminals (Wiens 1998), and selected 37 key taxa that are rather generalised and represent typical members of their families (Appendix 1). All genera of Phloeostichidae are represented and the family Passandridae is represented by two taxa: the larva of *Aulonosoma* is unknown to us and we used *Ancistria* to score larval characters. Though most of the species of *Priasilpha* are wingless, we coded the only winged species, *P. obscura* Broun, for adult and larval characters (this species is also a plesiomorphic member of the genus, R. A. B. Leschen and B. Michaux, personal communication). The scoring of larval characters was based mainly on specimens associated with adults in the same habitats, often confirmed by subsequent associations or by a process of elimination in limited faunas. Two genera representing Cryptophagidae were included in the analysis to test the monophyly of this family because of the differences between Atomariinae and Cryptophaginae, and especially of the similarities between the former subfamily and Hobartiidae (Leschen 1996). Though we coded characters based on the key taxa listed in Appendix 1, we confirmed the characters and their states in dissected and whole specimens of other taxa available in our collections to clarify the coding of ambiguous characters that were difficult to interpret. To root the trees, we chose two members of the cleroid family Trogossitidae because of the similarities of this family to other members of Cucujoidea (Lawrence and Newton 1995; Lawrence and Leschen 2003). As a more distant outgroup to root trees, we coded Derodontidae (*Derodontus*), a basal Polyphagan. Derodontidae was chosen as a distant outgroup because Caterino *et al*. (2002) in their DNA analysis showed that *Laricobius* (Derodontidae) and *Eucinetus* (Eucinetidae) are the two most basal polyphagan clades, whereas Lawrence (1999, 2001) noted that a membranous joint between the meso- and metathorax, a basal coleopteran feature by Beutel and Haas (2000), also occurs in Derodontidae, Eucinetoidea and some Staphylinoidea.

Characters

In total, 99 characters were coded and consisted of 66 adult and 33 larval characters (Table 1). Larvae of *Bunyastichus*, gen. nov. and

Table 1. Character state definitions

Adult characters

(*1*) *Postocular constriction:* (1) absent (Fig. 24); (2) present (Fig. 65).
This constriction of the head may be located immediately behind the eyes or well behind them and it may be abrupt or more gradual, so that the temples so formed vary in length and may be more or less rounded to sharply angulate. In some cases the constriction is clearly demarcated in ventral view but only slightly indicated from above.

(*2*) *Vertexal line:* (1) absent (Figs 24, 66); (2) present (Fig. 111).
This refers to a relatively sharp transverse line or carina extending across the dorsal part of the head behind the eyes and often abutting the anterior edge of the pronotum (Leschen 1996, 2003). Lawrence *et al*. (1999*b*) referred to this as a transverse occipital ridge.

(*3*) *Median occipital stridulatory file:* (1) absent (Figs 24, 66); (2) present.
This refers to a single, broad median file lying in front of the occipital foramen. This type of stridulatory file, which occurs in *Myrabolia* and *Tasmosalpingus*, and is probably not homologous to the paired files known in several Erotylidae (including *Pharaxonotha*, see Fig. 111) or in *Atomaria* among the Cryptophagidae.

(*4*) *Paired occipital incisions:* (1) absent (Fig. 66); (2) present (Fig. 24).
These paired incisions occur along the dorsal edge of the occipital foramen, thus defining a rounded lobe between them.

(*5*) *Frontoclypeal suture:* (1) present; (2) absent.
The frontoclypeal or epistomal suture is coded as present only when it is delimited by a clearly impressed line and indicated internally by an epistomal ridge. When the frontoclypeal region is crossed by a vague impression, it is coded as lacking the suture.

(*6*) *Antennal insertions:* (1) exposed from above (Fig. 24); (2) concealed by frontal ridge (Fig. 66).
The character states are not very clearly defined in many cucujoid taxa in which the insertions may be barely exposed or barely concealed. A taxon is coded as having concealed insertions when in a dissected specimen with the antenna removed, no portion of the antennal socket may be seen from directly above.

(*7*) *Subantennal groove:* (1) absent (Fig. 65); (2) not extending below or behind eye; (3) extending below or behind eye.
This groove lies between the eye and the mandibular and maxillary articulations, and houses the basal antennomere(s); it usually does not extend beyond the lower edge of the eye, but in some groups it may continue posteriorly behind the eye.

(*8*) *Genal projection:* (1) absent; (2) anterior, truncate or rounded; (3) anterior, acute (Fig. 25); (4) anterolateral.
That portion of the head capsule just laterad of the maxillary articulation may project anteriorly or anterolaterally and the shape is that as seen from above and not from a lateral perspective.

(*9*) *Anterior cervical sclerites:* (1) not contiguous with head capsule or placed in paired emarginations; (2) contiguous with head capsule and usually placed within paired emarginations on ventral edge of occipital foramen (Fig. 25); (3) apparently absent.
The anterior cervical sclerites occur in many basal cucujoids, although they may be quite small and lightly sclerotised. They are usually loosely attached to the head capsule and lie in the neck membrane; they may or may not be accompanied by a pair of posterior cervical sclerites (often remaining attached to the thorax in dissections). In several basal cucujoids, these anterior sclerites are more closely associated with the ventral portion of the head capsule, more or less abutting the cuticle and usually lying in emarginations on either side of the gula.

(*10*) *Apex of mandible:* (1) unidentate; (2) bidentate (Fig. 97); (3) tridentate.
This character may be difficult to code when the apical teeth are on the same plane and when smaller, subapical teeth are also present on the cutting edge of the mandible. If in a mandible with three more or less apical teeth, the middle tooth is longest and those on either side shorter or somewhat subapical, then the mandible is coded as tridentate (3). If, on the other hand, two adjacent teeth are more or less coplanar and of a similar size, whereas a third tooth is smaller and more subapical, then this is bidentate (2).

(*11*) *Dorsal surface of mandible:* (1) without tubercle fitting into lateral clypeal emargination (Fig. 98); (2) with tubercle fitting into lateral clypeal emargination (Fig. 112).
This tubercle or rounded ridge-like structure projects mesally and fits into an emargination at the base of the clypeus; it usually lies above and may partly overlap the mandibular cavity (see following character).

(*12*) *Dorsal surface of mandible:* (1) without cavity (Fig. 98); (2) with glabrous cavity; (3) with setose cavity.
The area mesad of the dorsal mandibular tubercle may be broadly concave, but this does not constitute a mandibular cavity, which is either deep and well defined (state 1) or densely lined with setae (state 2). The setose cavity is restricted to members of the families Sphindidae and Boganiidae, whereas a deep, glabrous one occurs in Hymaeinae and Silvanidae (reduced and lost in most Silvaninae).

(*13*) *Mandibular mola:* (1) present (Fig. 98); (2) absent.

(*14*) *Galea:* (1) at least 2.5× as wide as lacinia; (2) between 1× and 2.5× as wide as lacinia (Figs 68, 100); (3) distinctly narrower than lacinia; (4) absent.

(*15*) *Lacinial uncus:* (1) absent; (2) present (Figs 68, 111).
This structure, which is usually bidentate or occasionally tridentate, is located at the apicolateral angle of the lacinia and curves mesally; it may be difficult to distinguish from stout spines lying adjacent to it and below it.

(*16*) *Lateral pronotal carinae:* (1) complete (Figs 1, 2); (2) incomplete or absent (Figs 4, 8).

(*17*) *Sides of pronotum:* (1) without 4–6 sharp teeth (Figs 1, 2); (2) with 4–6 sharp teeth (Figs 6, 72).
The sharp teeth include those at the anterior and posterior angles. These teeth face laterally in most taxa but are curved posteriorly in *Derodontus*. Among those taxa coded as having state 0, *Cryptophagus* may have a single tooth in addition to the anterior callosity, but this varies in the genus. Other genera may have blunt lobe (*Rhopalobrachium*), or more numerous fine tubercles or serrations (several genera).

(*18*) *Anterior pronotal angles:* (1) absent or not produced forwards (Figs 3, 4); (2) produced forwards (Figs 1, 2).

(*19*) *Anterior portion of prosternum at midline:* (1) longer than prosternal process (Fig. 26); (2) as long as as prosternal process (Fig. 72); (3) shorter than prosternal process.

(*continued next page*)

Table 1. (continued)

(*20*) *Anteromesal corner of hypomeron*: (1) without tooth; (2) with tooth (Fig. 102).
The presence of a tooth occurs in the genera *Chileosilpha* and *Priasilpha*.
(*21*) *Apex of prosternal process:* (1) without lateral projections; (2) with lateral projections (Fig. 26, 72).
The presence of lateral processes are very widespread in basal Cucujoidea, and these may also form a closer of the procoxal cavity when joined with the postcoxal projections of the hypomeron, a character present in many higher Erotylidae.
(*22*) *Shortest distance between procoxal cavities:* (1) less than half as great as mid length of cavity (Fig. 72); (2) more than half as great but less than mid length of cavity; (3) more than mid length of cavity (Fig. 26).
(*23*) *Notosternal suture:* (1) complete (Fig. 72); (2) incomplete (Fig. 26).
(*24*) *Procoxa:* (1) without or with short, concealed lateral extension (Figs 26, 72); (2) with long, concealed lateral extension.
An internal coxal extension is said to be long if it is at least 0.75× the length of the exposed portion of the coxa.
(*25*) *Protrochantin:* (1) exposed (Figs 26, 72); (2) concealed.
The protrochantin can be concealed from ventral view in taxa with concealed lateral extensions of the procoxae (C24–2) or thos taxa having more or less rounded procoxal cavities (C26–3), but these three characters do not co-occur and they are treated separately in this study.
(*26*) *Procoxal cavity:* (1) strongly transverse (Fig. 26); (2) slightly transverse; (3) about as long as wide.
(*27*) *Procoxal cavities externally:* (1) open; (2) closed (Fig. 26).
(*28*) *Procoxal cavity:* (1) without lateral notch, only slightly or gradually narrowed laterally (Fig. 26); (2) with narrow lateral notch (less than 0.25× as wide as mid lenth of cavity).
(*29*) *Procoxal cavity:* (1) internally open (Fig. 26, 72); (2) internally closed.
(*30*) *Elytral punctation:* (1) not seriate or striate (Fig. 1); (2) seriate or striate (Fig. 6).
(*31*) *Scutellary striole:* (1) absent; (2) present.
(*32*) *Elytral sutural flange:* (1) not widened apically (Fig. 2); (1) widened apically (Fig. 3).
This character is sometimes referred to as a subapical gape (see Leschen 1996).
(*33*) *Epipleuron:* (1) complete to apex; (2) incomplete or absent.
The epipleural is variable in Cucujoidea, and in many taxa the structure may have the same width throughout its length, but in many taxa scored in this study the anterior portion is relatively wide usually up to a level of the posterior edge of the metaventrite.
(*34*) *Anteromesal corner of mesepisternum:* (1) without cuticular pocket; (2) with cuticular pocket (Fig. 113).
The cuticular pocket is quite variable in the groups that have them (Erotylidae and Cryptophagidae) and may be present as fairly deep fovea containing setae or a rather shallow impression (Leschen 2003).
(*35*) *Shortest distance between mesocoxal cavities:* (1) less than half as great as shortest diameter of cavity (Fig. 75); (2) more than half as great but less than shortest diameter of cavity; (3) more than shortest diameter of cavity.
(*36*) *Meso-metaventral junction:* (1) dicondylic; 1) monocondylic (Fig. 75); (3) simple.
The meso-metaventral articulation is variable in Cucujoidea. A monocondylic form has a single ball-like process arising from the metaventrite that fits into a corresponding fossa located on the posterior margin of the mesoventrite, whereas a dicondylic form is one that has two processes The simple or straight-line type lacks well developed anterior processes.
(*37*) *Mesocoxal cavities laterally:* (1) open (partly closed by mesepimeron) (Fig. 75); (2) closed (by meeting of mesoventrite and metaventrite).
Occasionally the mesoventrite and metaventrite do not quite meet, but the mesepimeron does not extend between them and is well removed from the coxa and trochantin; in this case the mesocoxal cavities are considered to be laterally closed.
(*38*) *Metaventral discrimen:* (1) present (Fig. 75); (2) absent.
This structure, often referred to a median or longitudinal suture, is the line of invagination of the metendosternite.
(*39*) *Metaventral transverse suture (katepisternal suture):* (1) present; (2) absent (Fig. 75).
This suture is said to be present whether or not it crosses the discrimen.
(*40*) *Metacoxae:* (1) contiguous or narrowly separated (Fig. 75); (2) widely separated.
Metacoxae coded as state (2) are separated by a distance at least a third as great as the metacoxal width (longest coxal diameter).
(*41*) *Metacoxae:* (1) extending laterally to meet elytral epipleura, ventrite one not in contact with metepimeron; (2) not extending laterally to meet elytral epipleura, ventrite one in contact with metepimeron (Fig. 75).
(*42*) *Metacoxal carina:* (1) present; (2) absent (Fig. 75).
The metacoxal carina extends from the coxotrochanteral joint laterally and forms an anterior abutment for the femur. In many basal polyphagans it extends to the lateral edge of the coxa and may be well developed, forming a distinct coxal plate concealing the femur in repose. In Cucujoidea, the carina is rarely weakly developed and usually absent.
(*43*) *Metendosternal laminae:* (1) well developed; (2) reduced; (3) absent. Reduced laminae (2) tend to be slender and not broad and plate-like.
(*44*) *Anterior tendons of metendosternite:* (1) narrowly separated; (2) widely separated.
(*45*) *Radial cell of hind wing:* (1) complete (closed basally, Fig. 63); (2) incomplete (open basally) or absent (Fig. 62).
(*46*) *Free veins in medial field of hind wing:* (1) five (Fig. 62); (2) four; (3) three or fewer.
The medial field lies between the posterior wing strut (medial bar, MP_{1+2}) and the anal fold. There is a maximum of five free veins in this field (MP_3, MP_4+CuA1, CuA_2, AA_3 and AA_4), but in most cucujiforms this number is reduced to four or fewer.
(*47*) *Tarsi in male:* (1) 5–5–5; (2) 5–5–4.
(*48*) *Mesotarsomere four:* (1) not or slightly reduced and not enclosed within lobe on tarsomere three; (2) highly reduced and partly or entirely enclosed within ventral lobe on tarsomere three (Fig. 73).
State 1 represents the condition known as pseudotetramerous in Chrysomeloidea and Curculionoidea; however the reduction of tarsomere 4 is usually not as great in cucujoids.
(*49*) *Apex of terminal tarsomere:* (1) without fringe of short setae; (2) with fringe of short setae (Fig. 105).
A fringe of modified setae is present on the terminal tarsomeres of *Priasilpha* and *Priastichus*.

(*continued next page*)

Table 1. (continued)

(*50*) *Empodium:* (1) projecting between pretarsal claws; (2) absent or not visible between pretarsal claws (Fig. 105).
In most cucujoids, the empodium is reduced and rarely extends beyond the bases of the pretarsal claws, although the empodial setae at its apex may be visible (Fig. 105). In taxa coded as having state 0, the body of the empodium is visible between the claws.
(*51*) *Number of basal ventrites connate:* (1) none; (2) two.
(*52*) *Ventrite 1:* (1) not much longer than 2 (Fig. 71); (2) much longer than 2.
(*53*) *Abdominal intercoxal process:* (1) acute or narrowly rounded (Fig. 71); (2) broadly rounded; angulate or truncate (Fig. 104).
(*54*) *Abdominal tergite VII:* (1) concealed from above; (2) exposed from above.
(*55*) *Functional spiracles on abdominal segment VII:* (1) present; (2) absent.
(*56*) *Tergite VIII in male:* (1) completely dorsal; (2) with sides curved ventrally; (3) with sides and apex curved ventrally to form genital capsule.
(*57*) *Anterior edge of sternite VIII in male:* (1) without median strut; (2) with median strut.
(*58*) *Apex of sternite IX in male:* (1) with mesal lobe (Fig. 35); (2) without mesal lobe.
(*59*) *Anterior edge of sternite IX in male:* (1) without spiculum gastrale; (2) with spiculum gastrale (Fig. 35).
(*60*) *Base of tegmen:* (1) broadly rounded; (2) narrowly rounded to acute (Fig. 55); (3) produced anteriorly forming strut.
(*61*) *Parameres:* (1) free from one another (Figs 28, 29); (2) fused into single piece.
(*62*) *Parameres:* (1) articulated to phallobase (Figs 28, 31); (2) fused to phallobase.
(*63*) *Penis:* (1) not divided into distinct basal and apical sections (Fig. 78); (2) divided into distinct basal and apical sections (Figs 29, 30).
The division into sections is a character present in only a few basal Cucujoidea, including all Priasilphinae and *Agapytho*.
(*64*) *Basal portion of penis:* (1) distinctly wider than apical portion (Fig. 36); (2) as wide as or narrower than apical portion (Fig. 81).
(*65*) *Base of penis:* (1) without median carina (Fig. 78); (2) with median carina (Fig. 41).
(*66*) *Anterior edge of penis:* (1) without struts (Figs 29, 78); (2) with paired struts; (3) with single strut.

Larval characters
(*67*) *Posterior edge of head capsule:* (1) not, or only slightly, emarginate (Fig. 87); (2) distinctly emarginate.
(*68*) *Bases of frontal arms:* (1) contiguous; (2) well separated (Figs 79, 87).
(*69*) *Median endocarina:* (1) absent (Fig. 87); (2) present.
(*70*) *Paired endocarinae:* (1) absent (Fig. 87); (2) present.
(*71*) *Stemmata:* (1) six; (2) five; (3) four or fewer.
(*72*) *Antennal length:* (1) less than 0.15× head width; (2) 0.15–0.5× head width; (3) more than 0.5× head width (Figs 80, 87).
(*73*) *Sensorium:* (1) shorter than apical antennomere (Figs 87, 80); (2) longer than apical antennomere.
(*74*) *Labrum:* (1) separated from head capsule by complete suture (Fig. 87); (2) partly or completely fused to head capsule (suture incomplete or absent).
(*75*) *Apex of mandible:* (1) unidentate; (2) bidentate; (3) tridentate (Fig. 106).
This character varies among specimens of Priasilphidae that may have lost teeth due to wear (Fig. 91, *Priastichus*) or where a subapical lobe may be present (compare Figs 84 and 106 for *Priasilpha*).
(*76*) *Accessory ventral process of mandible:* (1) absent; (2) present (Fig. 90).
This is the accessory ventral condyle of Böving and Craighead (1931) and it appears to be a plesiomorphic feature in basal Polyphaga and Myxophaga (Lawrence *et al*. 1999*a*).
(*77*) *Mesal surface of mandibular base:* (1) with asperate or tuberculate mola (Figs 106, 107); (2) with 1–3 hyaline processes; (3) simple.
(*78*) *Ventral mouthparts:* (1) strongly retracted (distance between mandibular and maxillary articulations greater than width of stipes, Figs 80, 88); (2) protracted or slightly retracted (distance between mandibular and maxillary articulations less than width of stipes).
(*79*) *Maxillary articulating area:* (1) well developed (Figs 80, 88); (2) highly reduced or absent.
(*80*) *Inner apical angle of mala or lacinia:* (1) rounded or truncate; (2) more or less acute (falciform) (Figs 82, 92).
The mala in the larva of *Myrabolia* is weakly falcate and this has been coded as acute.
(*81*) *Number of labial palpomeres:* (1) two (Figs 80, 88, 108); (2) one.
(*82*) *Labial palps:* (1) contiguous or separated by less than width of first palpomere; (2) separated by more than width of first palpomere (Figs 80, 88).
(*83*) *Ligula:* (1) absent; (2) present (Fig. 93).
(*84*) *Hypopharyngeal sclerome:* (1) absent; (2) present.
(*85*) *Hypostomal rods:* (1) subparallel; (2) diverging (Figs 80
(*86*) *Ventral epicranial ridges:* (1) absent (Figs 80, 88); (2) present.
(*87*) *Gula:* (1) wider than long (Figs 80, 88); (2) longer than wide.
(*88*) *Thoracic and most abdominal terga:* (1) without long lateral processes; (2) with long lateral processes (Figs 79, 109).
(*89*) *Mesocoxae separated by:* (1) less than two coxal diameters; (2) more than two coxal diameters.
(*90*) *Number of pretarsal setae:* (1) two (Fig. 94); (2) one.
(*91*) *Abdominal tergites:* (1) without rows of asperities (Fig. 79); (2) with curved rows of asperities.
(*92*) *Abdominal tergum IX:* (1) not forming articulated plate (Figs 85, 109); (2) forming articulated plate (Fig. 86).
(*93*) *Abdominal tergum IX:* (1) simple; (2) with paired urogomphi (Figs 86, 109).
(*94*) *Urogomphi:* (1) straight (Figs 79, 109; (2) curved upwards.
(*95*) *Urogomphi:* (1) subparallel (Fig. 79); (2) strongly diverging (Fig. 109).
(*96*) *Sternum IX:* (1) partly or entirely exposed (Fig. 85); (2) completely concealed or apparently absent.
(*97*) *Segment X and anal opening:* (1) posterior or terminal; (2) posteroventral; (3) ventral.
(*98*) *Spiracles:* (1) annular (Fig. 81); (2) annular–biforous.
(*99*) *Abdominal spiracles:* (1) not at ends of spiracular tubes; (2) at ends of short spiracular tubes on segments I–VIII; (3) at ends of long spiracular tubes on segments I–VIII (Fig. 79); (4) at end of spiracular tubes on segment VIII only.

Table 2. Data matrix used for generating cladograms for basal Cucujoidea
Character and state numbers correspond to those in Table 1 and in the text

Taxa	Characters									
	10	20	30	40	50	60	70	80	90	
Derodontus	1111211312	1112112131	2111112112	2121131111	1131211111	1111112211	1111122111	1211221112	1222321111	112211122
Thymalus	1111213212	1112111131	1211111111	–111221111	1122121111	1111111223	2112122121	2111212121	1111111112	112211221
Eronyxa	1112222112	1112111131	1111111111	–121131111	1231121111	1111111123	1112122121	3211212121	1111112122	112211321
Helota	2111223312	1112211211	2311232122	2121311112	2122121111	1121121223	2212121211	1212221111	1222221111	112121222
Amartus	1112122211	1113111111	1111111121	–121231112	2121231212	1122231221	1112131111	3211111221	2222211112	111??1121
Australaethina	1212223212	1114211131	2211112222	1121231112	2231231212	1122231223	2212131211	3211211121	2222311121	112211221
Smicrips	1111112313	1114211111	1211111121	–121231222	2231231112	1222231221	1112132211	3211211221	2112112122	112211221
Rhizophagus	1112223322	1113211111	2211112122	2121121121	2221232112	1212131221	2212121211	3211321112	1222221111	112211221
Ericmodes	2112122213	1112211121	2211112112	2121121111	2211112111	1111121223	2212121111	2221321112	1222211111	112221222
Protosphindus	2111113313	2312212121	2211112112	2111211111	2211111112	1111121212	2212121111	1211321111	1212211111	112211211
Paracucujus	1111111113	2313111131	1111111112	2121131111	2221121212	1111122122	1112121111	1311121112	1222111111	112111121
Chileosilpha	1112211322	1112111112	2321112111	–221211121	2221221112	2111111122	112121????	??????????	??????????	?????????
Priasilpha	1112211222	1112111212	1311111111	–221311122	2211112122	2121111122	1121211211	2311321112	1212211221	112121223
Priastichus	1112213222	1111111211	1311111111	–121331222	2222??2122	2121111122	1121211211	3311221112	1212211221	112111223
Hymaea	2112211422	2212112111	1111131212	2221121121	2211212112	1111111223	1112212211	1212321112	1222211121	212211321
Rhopalobrachium	2112211422	2212121111	1121121211	–221121121	2211212112	2111111221	1112112211	1212321112	1222211121	212211321
Bunyastichus	2112121423	2112112121	2111112112	2211121121	2211212212	1111111223	111211????	??????????	??????????	?????????
Phloeostichus	2112221422	1112112111	1111111112	2211131121	2211212112	1111111111	1111112211	1212321112	1222211121	112211321
Agapytho	2112221122	1112121111	2111121211	–221121121	2221212112	1111111221	2221112111	2211221112	1222211111	112221221
Cryptamorpha	2211121122	2212111111	1222232112	2121231121	2222211212	2111111211	1112111111	1311321112	1222211111	122112114
Ahasverus	2111221322	1111111111	1322232122	1111231122	2232231112	2121111222	1212111111	1311321112	1222211122	111??2111
Cucujus	2212221322	1112211111	1212121211	?111331121	1221112112	1111111123	1122211111	1311221212	1222211121	122222311
Passandridae	2112223131	1122211211	2312232112	1111131121	2211231112	1111111211	1112121211	2112113221	1211211122	111??1222
Myrabolia	1122212322	1112111111	2222231212	1211222121	2221222112	1211111121	1111122111	3211312212	1221211121	112211311
Tasmosalpingus	1121212323	1122211211	1211111121	?221231222	2222232112	1121211222	1212122212	2221312221	1221212112	111??13?1
Cyclaxyra	1112213123	1111211231	1211111121	?111331221	2222232112	1111211222	1212132112	2211312221	1221212121	111??1221
Lamingtonium	1112211223	1121211211	1211121212	1121231221	2221121112	1111111223	1112112112	1221312221	1111212121	112211224
Propalticus	2211211133	1111111211	1322221121	?121332122	2232231112	1121111221	1112132212	3111212221	1??121?121	121??1311
Laemophloeus	1211111313	1111111111	2312231121	?111331122	2232232112	1121111211	2112132212	2211312221	1221112122	222121311
Acylomus	1112221332	1111111231	1111231122	1121232121	2222231112	1111111221	2212111211	2221311221	1221212122	112222111
Hobartius	1112112212	2112111221	1211111111	?121121111	2221232112	1211111221	1112111111	2211221112	2222211111	112211222
Cavognatha	1112211113	1112121121	1211221211	?212331121	2221211112	1111111213	1112111211	1211312111	1211211111	112111221
Atomaria	1111111312	1112111111	1321221211	?222232122	2221231112	1221211211	2212211111	3211221112	1222211111	111??1111
Cryptophagus	1212211312	1112111211	1211231111	?222212122	2221232112	1221111222	2212111211	3211221112	2222211111	112211221
Pharaxonotha	1111221213	1112111111	1211231121	?112222121	2222121112	1111111111	1112121121	2211221112	1222221111	112211221
Xerasia	1112211112	1112111131	1111112221	?121131111	2222121211	1111112223	1212121111	1212211112	1222211112	111??1121
Anchorius	1212223212	1112111211	1111222122	2111222121	2212121112	1111112123	2212121111	1212221112	1222221112	111??1124

Chileosilpha, gen. nov. are not known and larval characters for these were coded as unknown (?). Also coded as unknown for certain characters are the following: *Propalticus* (82, 83, 87; these characters were not recorded from a single specimen residing in the BMNH), and *Tasmosalpingus* (98; body of presumed larva lost before coding this character). Other details about character coding are in Table 1.

Analytical methods

The data were initially coded and entered into DELTA (Dallwitz *et al*. 2000) and converted to NEXUS files for use in MacClade version 3 (Maddison and Maddison 1992) for character analysis and PAUP* version 4.0 (Swofford 2003) for tree construction. DELTA files were also converted to Hennig86 files for use with Hennig86 (Farris 1988), Winclada (Nixon 1999) and Nona (Goloboff 1999) for confirming characters and trees (the results are the same among the different programmes). The complete data matrix is provided in Table 2. The settings used in PAUP* for heuristic tree searches included random addition sequences (100 replicates) with steepest descent; character states were treated as unordered. The trees were rooted by default using the first taxon in the matrix (*Derodontus*) while executing the searching in PAUP* (see methods for rooting in Nixon and Carpenter 1993).

To date there is no completely satisfactory statistical method to determine confidence intervals for branches on a cladogram (see Sanderson 1995), though for parsimony analyses the co-occurrence of minimised character state changes on branches are acceptable as adequate and testable hypotheses for determining the relationships among taxa (Farris 1983). Bremer support (Bremer 1988), which measures the number of additional steps required to collapse a branch of a tree, was determined by Autodecay 4.0.2'ppc (Eriksson 2000; see also Eriksson and Wikström 1995). Bootstrap (Felsenstein 1985; Sanderson 1995) and jackknife analyses (Farris *et al*. 1996), which determine branch support by resampling a certain percentage of characters or taxa per replication, were done with 1000 replications to determine support for some of the major clades we refer to in this paper. Search settings in PAUP* for these analyses were the same as above, except simple searches were performed holding one tree at each step and swapping on best tree.

Accelerated transformation (ACCTRAN) of character states with ambiguous reconstructions was selected in PAUP* while executing tree searches. However, because different optimisations for ambiguous characters will indicate alternative ancestral reconstructions and character support for the clades we recognise below, characters were also optimised onto trees using standard DELTRAN (delayed transformation) optimisations (Maddison *et al*. 1984) and the alternative reconstructions were examined in MaClade. In the discussion below, character states that reverse or transform to other states are indicated by superscripts C^r and C^t, respectively.

The data matrix (in nexus format), tree files and bootstrap and jackknife trees are available as Accessory material on the *Invertebrate Systematics* website.

Results of the cladistic analysis

The analysis resulted in eight most parsimonious trees (tree length (*TL*) = 607, consistency index (*CI*) = 0.21; retention index (*RI*) = 0.45); and a strict consensus of these trees is shown in Fig. 11. We chose one of these trees randomly (tree 3) as a reference tree, and it is shown in Fig. 12 marked with the nodes we discuss in the text. The trees are consistent apart from the relationships among the basal clades and are indicated by lower values derived from a 50% majority rule consenus tree on the reference tree. Based on these eight trees it is clear that the family Phloeostichidae is not a monophyletic group and has the following relationships: *Agapytho* (Agapythinae) is part of a basal grade or is sister taxon to a monophyletic group Cryptophagidae; Priasilphinae is monophyletic (node C); Phloeostichinae and Hymaeinae (mainly with the relationship (*Hymaea* + *Rhopalobrachium*) (*Bunyastichus*, gen. nov. + *Phloeostichus*)) form a monophyletic group (node E); *Myrabolia* is sister taxon to the other groups contained in clade G; and *Tasmosalpingus* is placed as sister taxon to *Cyclaxyra* (node I). Other important results include the placement of trogossitids (*Thymalus* and *Eronyxa*) inside Cucujoidea in five trees (node L) and evidence for four monophyletic groups: *Anchorius* + *Pharaxonotha* (node A); Cryptophagidae (*Atomaria* + *Cryptophagus*, node B); Cucujidae + Silvanidae (node F); Propalticidae + Laemophloeidae (node H); the Nitidulidae group (*Smicrips*, *Amartus*, and *Australaethina*, but not *Rhizophagus*, node J); and *Ericmodes* + *Protosphindus* (node K).

The monophyletic groups above were also recovered in the jackknife and bootstrap trees, but most of the groupings are poorly supported by statistical measures due to the

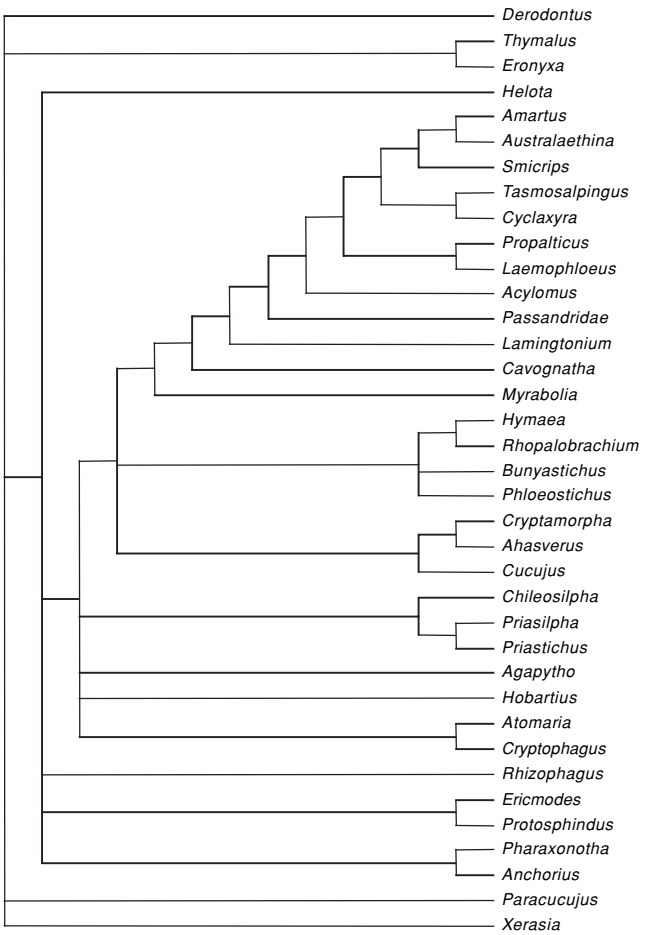


Fig. 11. Strict consensus tree of eight most parsimonious trees based on adult and larval data.

paucity of synapomorphies for each group. The lack of supportive characters, however, tends to be in the internal nodes and if a single taxon is deleted from the analysis (e.g. *Myrabolia* that has uncertain relationships), the phylogenetic arrangement changes significantly though the major lineages we discuss below hold. We believe that instability may be related in part to the poor signal in larval data (though there are fewer larval characters anyway). A 50% majority rule consensus tree based on adult characters is shown in Fig. 13 (204 trees, *TL* = 417, *CI* = 0.20, *RI* = 0.09). In this adult-based tree some of the major results are consistent with the combined analysis (nodes B, C, E, H, I, and K are present also in this tree), though the relationships differ. Compare these relationships to the 23 larval trees, shown as a 50% majority rule consensus tree in Fig. 14 (*TL* = 146, *CI* = 0.28, *RI* = 0.17). The larval data supports the inclusion of a monophyletic Trogossitidae in Cucujoidea and also nodes C, E, and F. They also support the sister relationship of Biphyllidae and Byturidae, which is not supported by adult characters or in the combined analysis (see below). Otherwise the larval characters, though being less in number, appear to support some spurious combinations of taxa (e.g. Passandridae + *Amartus*). More importantly, though, larval characters in combination with adult characters support many of the groups we recognise below, and should not be disregarded (e.g. the monophyly of Hymaeinae + Phloeostichinae and Priasilphinae are supported by three unambiguous larval characters).

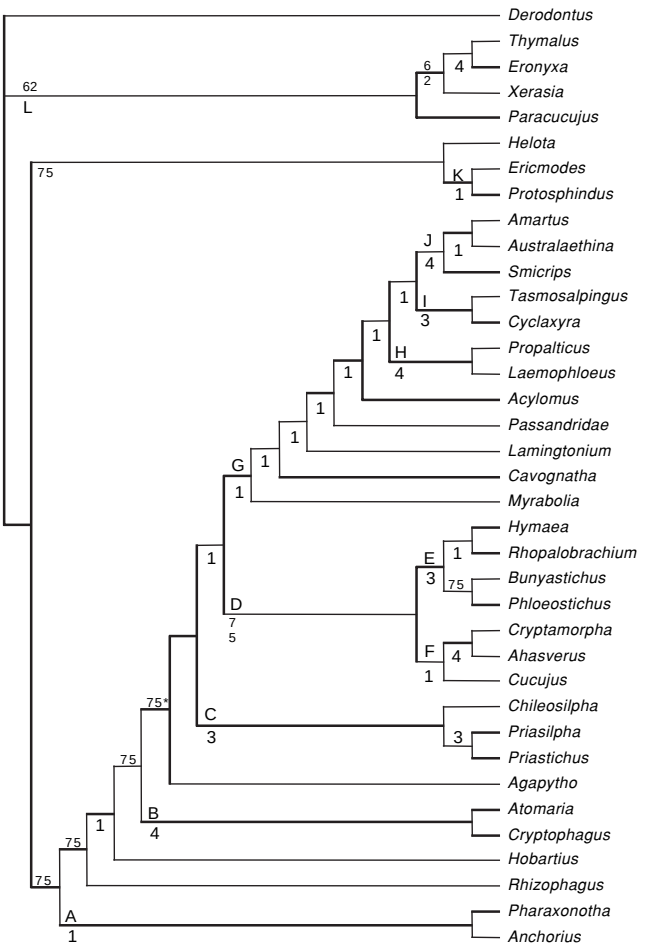


Fig. 12. Reference tree with marked nodes referred to in the text. All nodes are consistent among the original eight parsimonious trees, except those that are indicated by the values derived from a 50% majority consensus tree, that also includes a trichotomy (*) of *Agapytho*, Priasiliphidae and taxa included at nodes D and G. Bremer support is indicated at consistent nodes.

Major lineages and the subfamilies of Phloestichidae

There have been numerous hypotheses proposed concerning relationships among basal Cucujoidea, and these are to be found in the papers by Roy Crowson and Tapan Sen Gupta (see References) that are narrative and not based on Hennigian argumentation (see discussion in Leschen 2003). Their narrative descriptions may be confusing to readers because they are often inconsistent and many taxonomic conclusions for controversial taxa are based on similarities to rather generalised groups such as Cryptophagidae and

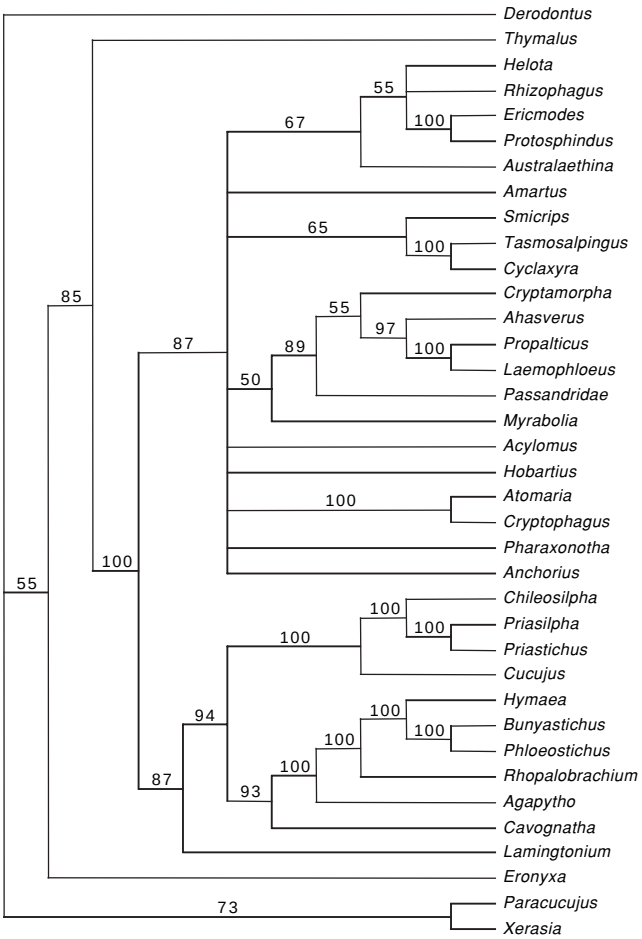


Fig. 13. 50% majority rule consensus tree of most 204 parsimonious trees derived from adult characters.

Cucujidae. In the following sections we limit reference to previous statements about relationships and refer to the tree shown in Fig. 12.

Subfamilies of Phloestichidae

Agapythinae

The genus *Agapytho* is placed in a basal grade of taxa (see Fig. 11) or as sister taxon to Cryptophagidae in two of the parsimonious trees based on three characters: 61–2 (parameres fused into a single piece), 62–2 (parameres fused to phallobase), 89–1 (larval mesocoxae separated by less than two coxal diameters, ACCTRAN). Sen Gupta and Crowson (1966) listed *Agapytho* as an enigmatic genus of Hobartiidae, though later included it in a monotypic subfamily of Phloeostichidae (Sen Gupta and Crowson 1969). Grouping *Agapytho* at the bases of Priasilphinae or Phloeostichinae + Hymaeinae in Fig. 12 results in a one-step increase in tree length and there are relatively low bootstrap (20) and jackknife (24) values for the inclusion of the genus at the base of Phloeostichinae + Hymaeinae. The genus *Agapytho* differs from these taxa in many characteristics (see description below) and is defined by 13 characters with unambiguous characters indicated by an asterisk (*): *1–2, *6–2, *8–1, *16–2, *21–2, *22–1, 22–1, 28–2, 35–1, 63–2, 64–1, *67–2, 71–2, *95–2.

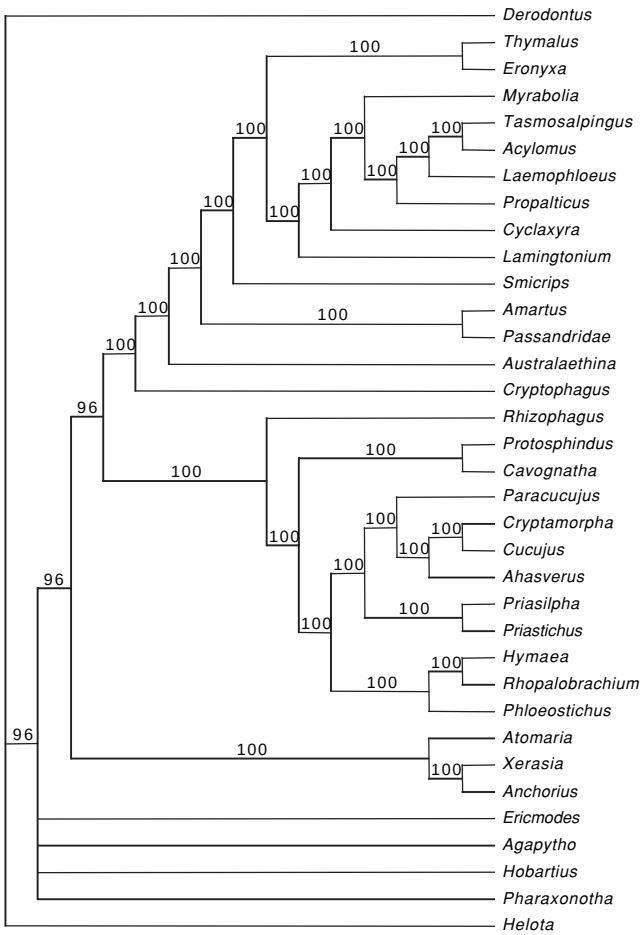


Fig. 14. 50% majority rule consensus tree of 23 most parsimonious trees derived from larval characters.

Priasilphinae

This subfamily is shown as a monophyletic group in all of the trees produced. It is rather isolated from other members of Phloeostichidae, and in jacknife and bootstrap trees it forms a sister taxon to Cucujidae. The monophyly of Priasilphinae is supported by the following synapomorphies (node C, Fig. 12): 20–2^{r} (anteromesal corner of hypomeron with tooth; reverses in *Priastichus*), 22–3 (shortest distance between procoxal cavities more than midlength of cavity), 26–1 (procoxal cavity strongly transverse), 28–1 (procoxal cavity without narrow lateral notch, ACCTRAN), 36–1^{t} (meso-metaventral junction simple; transforms to state 3 in *Priastichus*), 51–2 (two basal ventrites connate), 58–1 (apex of sternite IX in male with lobe), 60–2^{t} (base of tegmen narrowly rounded; transforms to state 3 in *Priasilpha*), 63–2 (penis divided into basal and apical portions, DELTRAN), 64–1 (basal portion of penis distinctly wider than apical portion, DELTRAN), 65–2 (base of penis with median carina), 72–3 (antennal length more than 0.5× head width in larva, ACCTRAN), 83–1 (larval ligula absent, ACCTRAN; coded as ? in *Chileosilpha*, gen. nov.), 88–2 (thoracic and most abdominal terga with long lateral processes, ACCTRAN; coded as ? in *Chileosilpha*, gen. nov.), 94–1 (urogomphi straight, ACCTRAN; coded as ? in *Chileosilpha*, gen. nov.), 99–3 (abdominal spiracles at ends of long spiracular tubes, ACCTRAN; coded as ? in *Chileosilpha*, gen. nov.).

There are two unique larval characters that support the monophyly of Priasilphinae (88–2, 99–3, see larval tree in Fig. 14) and the support for this group is rather robust (Bremer support (BS) = 3, Bootstrap support (BO) = 60, Jackknife (JS) = 72). Sen Gupta and Crowson (1969) thought at one time that *Priasilpha* was related to *Helota*; but based on our study Priasilphinae falls nowhere near to helotids.

Phloeostichinae + Hymaeinae

These two subfamilies consistently occur together in all of the trees produced, and were often grouped as sister taxon to the Cucujidae group at node D (Fig. 12). The relationships are fairly consistent with the combination of (*Hymaea* + *Rhopalobrachium*) and (*Bunyastichus*, gen. nov. + *Phloeostichus*) shown in most trees. This group is supported by the following synapomorphies (node E, Fig. 12): 8–4 (genal projection lateral), 11–2^{r} (dorsal surface of mandible with tubercle fitting into lateral clypeal emargination, ACCTRAN; reverses in *Phloeostichus*), 17–2^{r} (sides of pronotum with lateral teeth, ACCTRAN; reverses in *Rhopalobrachium*), 22–1 (shortest distance between procoxal cavities less than half as great as mid length of cavity),

35–1 (shortest distance between mesocoxal cavities less than half as great as shortest diameter of cavity), 43–1 (metendosternal laminae well developed), 67–2 (posterior edge of larval head capsule distinctly emarginate; coded as ? in *Bunyastichus*, gen. nov.), 68–2 (bases of frontal arms well separated in larval head capsule, DELTRAN; coded as ? in *Bunyastichus*, gen. nov.), 74–2 (labrum fused to head capsule, partly fused in *Rhopalobrachium*; coded as ? in *Bunyastichus*, gen. nov.).

There are no unique characters that support the monophyly of Phloeostichinae and Hymaeinae, though two characters supporting node D are not common in basal cucujoids (43–1, 74–2). The group is relatively well supported by statistical values (BS = 3, BO = 57, JS = 67).

Myraboliinae

The genus *Myrabolia* is placed at a consistent location among the trees at the base of node G (Fig. 12). The genus is not associated with other members of Phloeostichidae and has numerous characters that separate it from other families of Cucujoidea (see Description below) and is defined by the following 18 characters (unambiguous characters are indicated by an asterisk (*)): *3–2, *7–2, *21–2, *23–2, *24–2, *26–3, *37–2, 46–2, *52–2, *58–1, 64–1, *66–2, *67–2, 68–1, 71–3, 78–2, 97–3, *98–1.

Tasmosalpinginae

The genus *Tasmosalpingus* is placed consistently in all of the trees as sister taxon to *Cyclaxyra* (apart from the larval tree where it is placed as sister taxon to *Acylomus*) based on the following characters (node I, Fig. 12): 9–2 (anterior cervical sclerites contiguous with head capsule, DELTRAN (transformed from state 3) and ACCTRAN (transformed from state 1), 38 (metaventral discrimen absent, DELTRAN), 43–2 (metendosternal laminae reduced, ACCTRAN), 47–2 (tarsi in male 5–5-4), 60–2 (base of tegmen narrowly rounded), 62–2 (parameres fused to phallobase), 70–2 (paired endocarinae present in the ventral head capsule of larvae, DELTRAN), 93–1 (abdominal tergum IX simple in larva).

Tasmosalpingus is not closely related to other members of Phloeostichidae and has numerous characters that separate it from other groups of Cucujoidea (see Description below) and is defined by 9 characters (unambiguous characters indicated by an asterisk (*)): *3–2, 4–1, *13–2, *14–2, *32–2, *66–2, *73–2, *89–1, *97–3. The relationship of *Tasmosalpingus* to *Cyclaxyra* may be incorrect because there are no unique characters that support their sister relationship even though the statistical support is relatively high (BS = 3, BO = 58, JS = 62). It is also possible that *Cyclaxyra* may be more closely related to Lamingtoniidae (Lawrence and Leschen 2003) as shown in the larval tree (Fig. 14) where *Tasmosalpingus* is also grouped with *Acylomus*. Moving *Tasmosalpingus* to a position as sister taxon to *Acylomus* in the combined tree (Fig. 12) results in a tree that is an additional 13 steps.

Other basal Cucujoidea

Erotylidae + Biphyllidae

The genera *Pharaxonotha* and *Anchorius* are consistently grouped as sister taxa in the eight parsimonious trees based only on adult characters (Fig. 12, node A): 8–2 (genal projection anterior, truncate or rounded), 21–1 (apex of prosternal process without lateral projections, DELTRAN), 25–2 (protrochantin concealed), 29–2 (procoxal cavity internally closed, DELTRAN), 33–1 (epipleuron complete to apex), 35–2 (shortest distance between mesocoxal cavities more than half as great but less than shortest diameter of cavity), 37–2 (mesocoxal cavities laterally closed), 44–2 (anterior tendons of metendosternite widely separated), 58–1 (apex of sternite IX in male with mesal lobe).

In the past, Biphyllidae and Erotylidae were classified together in a very broad definition of the family (e.g. Ganglbauer 1899; Arrow 1929; Rymer-Roberts 1958) and the relationships between these two groups is relatively weakly supported in the combined analysis (BS = 1, BO = 23, JS = 24). These results may be suprising since Biphyllidae and Byturidae were thought to be sister taxa (Falcoz 1926; Lawrence and Newton 1995), a relationship supported in the larval trees (Fig. 14) by nine unambiguous characters (27–2, 44–2, 45–1, 46–2, 57–2, 60–3, 66–2, 74–2, and 90–2).

Cryptophagidae

The monophyly of Cryptophagidae (*Atomaria* and *Cryptophagus*) is clearly supported in this study based on the following characters (node B, Fig. 12): 25–2 (protrochantin concealed), 34–2 (anteromesal corner of mesepisternum with cavities), 35–2 (shortest distance between mesocoxal cavities more than half as great but less than shortest diameter of cavity, DELTRAN), 37–2 (mesocoxal cavities laterally closed by metaventrite), 40–2 (metacoxae widely separate), 53–2 (abdominal intercoxal process broadly rounded), 71–3 (four or fewer larval stemmata, DELTRAN).

There are no unique characters that support the monophyly of Cryptophagidae, though statistical values are relatively high (BS = 4, BO = 72, JS = 65).

Cucujidae and Silvanidae

The group *Cucujus* (*Ahasverus* + *Cryptomorpha*) is supported in the combined analysis based on the following characters (node F, Fig. 12): 2–2^{r} (vertexal line present, ACCTRAN, reverses in *Ahasverus*), 6–2 (antennal insertions concealed by frontal ridge, DELTRAN), 24–2 (procoxa with long, concealed lateral extension), 32–1 (elytral sutural flange not widened apically), 36–3 (meso-metaventral junction simple), 68–1 (bases of frontal arms contiguous in larva,

ACCTRAN), 72–3 (larval antennal length more than 0.5× head width), 92–2^{r} (larval abdominal tergum IX forming an articulated plate, ACCTRAN; reverses in *Ahasverus*), 96–2 (larval sternum IX completely concealed or apparently absent), 98–1 (larval spiracles annular).

The Cucujidae and Silvanidae are sometimes included together in a broadly defined Cucujidae (along with Passandridae and Laemophloeidae, e.g. Forbes 1926), though they have been treated separately (Böving and Craighead 1931; Lawrence and Newton 1995). The monophyly of the Cucujidae + Silvanidae is relatively poorly supported in the combined analysis (BS = 1) and it is also recovered with different relationships in the larval tree (Fig. 14).

Laemophloeidae and Propalticidae

Laemophloeus and *Propalticus* are consistently placed as sister taxa based on the following characters (node H, Fig. 12): 2–2 (vertexal line present), 4–1 (paired occipital incisions absent, DELTRAN), 22–3 (shortest distance between procoxal cavities, DELTRAN), 24–2 (procoxa with long concealed extensions), 35–3 (shortest distance between mesocoxal cavities more than shortest diameter of cavity), 43–3 (metendosternal laminae absent, DELTRAN), 70–2 (larval head capsule with paired endocarinae, DELTRAN), 92–2 (abdominal tergum IX forming an articulated plate), 94–1 (urogomphi straight, ACCTRAN; coded as unknown in *Propalticus*), 97 (larval segment X and anal opening ventral), 98–1 (larval spiracles annular, DELTRAN).

Though the larva of Propalticidae has not been formally described (the one described in Crowson and Sen Gupta (1969) was based on a misidentification), Lawrence and Newton (1995), R. A. Crowson (unpublished data), and Lawrence and Newton (1995) proposed that the families Propalticidae and Laemoploeidae are sister taxa. Support for the monophyly of this group is relatively robust (BS = 4, BO = 86, JS = 85), though it is not supported in the larval analysis (Fig. 14).

Nitidulidae group

The Nitidulidae families (Brachypteridae, Nitidulidae, and Smicripidae) are supported by the following synapomorphies (node J, Fig. 12): 5–1^{r} (frontoclypeal suture present, ACCTRAN; reverses in *Australaethina*), 9–1 (anterior cervical sclerite not contiguous with head capsule or placed in paired emarginations, DELTRAN), 14–4^{t} (galea absent; transforms to state 3 in *Amartus*), 18–1 (anterior pronotal angles absent or not produced forwards), 44–1 (anterior tendons of metendosternite narrowly separated), 54–2 (abdominal tergite VII exposed in dorsal view), 56–3 (tergite VIII in male with sides curved ventrally forming a genital capsule), 70–1 (paired endocarinae absent in the ventral head capsule of larvae, ACCTRAN), 71–3 (number of stemmata four or fewer), 75–2^{t} (apex of larval mandible bidentate; transforms to state 1 in *Amartus*), 77–1 (mesal surface of larval mandible with asperate or tuberculate mola), 81–2 (labial palpi 1-segmented in larva), 84–3^{t} (larval hypopharyngeal sclerome an irregular molar-like tooth; transforms to state 2 in *Australaethina*).

The Nitidulidae group is supported by one unique character (14–4) and two others found only in this group and Monotomidae (54–2, 56–3) and with relatively strong statistical support (BS = 4, BO = 58, JS = 67). Crowson (1955) (see also Sen Gupta 1988) included Monotomidae in the Nitidulidae group, though in later years (R. A. Crowson, unpublished data) he thought that the relationship to Monotomidae was erroneous, and this hypothesis is supported here. Moving Monotomidae to the base of the Nitidulidae group at node J (Fig. 12) increases the tree by 13 steps. Crowson also excluded the Nitidulidae group from Cucujoidea and was planning to erect it as a separate superfamily Nitiduloidea in an unpublished manuscript (Audisio 1993), but there is no evidence for this change in the classification.

Protocucujidae + Sphindidae

The close relationship between these two families (*Ericmodes* and *Protosphindus*) is well accepted (Sen Gupta and Crowson 1979; McHugh 1993; Ślipiński 1998) and is supported by the following characters (node K, Fig. 12): 5–1 (frontoclypeal suture present), 10–3 (apex of mandible tridentate), 19–2 (anterior portion of prosternum at midline as long as prosternal process), 29–1 (procoxal cavity internally open, ACCTRAN), 43–1 (metendosternal laminae well developed), 46–1 (5 free veins present in medial area), 75–3 (apex of larval mandible tridentate) and 86–1 (ventral epicranial ridges of larval head capsule absent). This group is not well supported by unique characters and statistical values are relatively low (BS = 1, BO = 48, JS = 46).

Changes in classification and future work

Several important changes in Cucujoidea classification are warranted based on the phylogenetic conclusions above. First and foremost are the changes in ranks for most of the subfamilies of Phloeostichidae to family: Agapythidae, Myraboliidae, Phloeostichidae, Priasilphidae, and Tasmosalpingidae. The subfamily names Hymaeinae (that previously included *Hymaea* and *Rhopalobrachium*) and Phloeostichinae (for *Phloeostichus*) are unnecessary, though these could be reinstated if the larva of *Bunyastichus*, gen. nov. is discovered and the evidence would add further support for a closer kinship of it to *Phloeostichus*.

The inclusion of Cleroidea within Cucujoidea is supported here and elsewhere (Beutel and Pollock 2000; Beutel and Ślipiński 2001) suggesting that the two superfamilies Cucujoidea and Cleroidea should be synonymised. These superfamilies are classified separately, despite the sharing of characters by basal cleroids and cucujoids (e.g. Crowson

1964; Lawrence and Newton 1995; Lawrence and Leschen 2003). Historically the members of these superfamilies were mixed. One group was referred to by one name (e.g. Clavicornia) with the others consisting of derived cleroids having soft bodies like Melyridae being placed in Malacodermata with unrelated cantharoids and other taxa (e.g. Lameere 1900; see review by Lawrence *et al*. 1995). Any action to synonymise the two superfamilies would be premature for several reasons and a more appropriate study should be designed to include additional taxa representing the major lineages of trogossitids (a heterogenous group) and the families of Cleroidea.

For this study we have concentrated efforts to place the former subfamilies of Phloeostichidae by scoring characters that are found in these subfamilies as well as many key characters used repeatedly by cucujoid workers. Others have not been used (e.g. presence of a sublateral lines present on the pronotum that would support the sister relationship between *Laemophloeus* and *Propalticus*) and the study of additional character systems is needed. Moreover, many questions about phylogenetic relationships remain, including the basal relationships of Cucujoidea, the monophyly of the basal families, and the relationships of the monogeneric families Agapythidae, Cyclaxyridae, Lamingtoniidae, Myraboliidae, and Tasmosalpingidae. Likewise, the phylogenetic position of Helotidae has always posed problems for cucujoid workers and it has been closely allied with Erotylidae, Cucujidae, Nitidulidae, Cleroidea, and other taxa (Crowson 1995; Kirejtshuk 2000): It has even been considered a member of its own superfamily (R. A. Crowson, unpublished data). Though we have been able to address the monophyletic status of Phloeostichidae (*sensu lato*), cucujoid workers will need to polarise characters based on multiple outgroups (e.g. Ślipiński 1998; Leschen 1996, 2003). If anything, the analytical results may help to guide future studies of cucujoids and other members of Cucujiformia.

Taxonomy

Family **PRIASILPHIDAE** Crowson

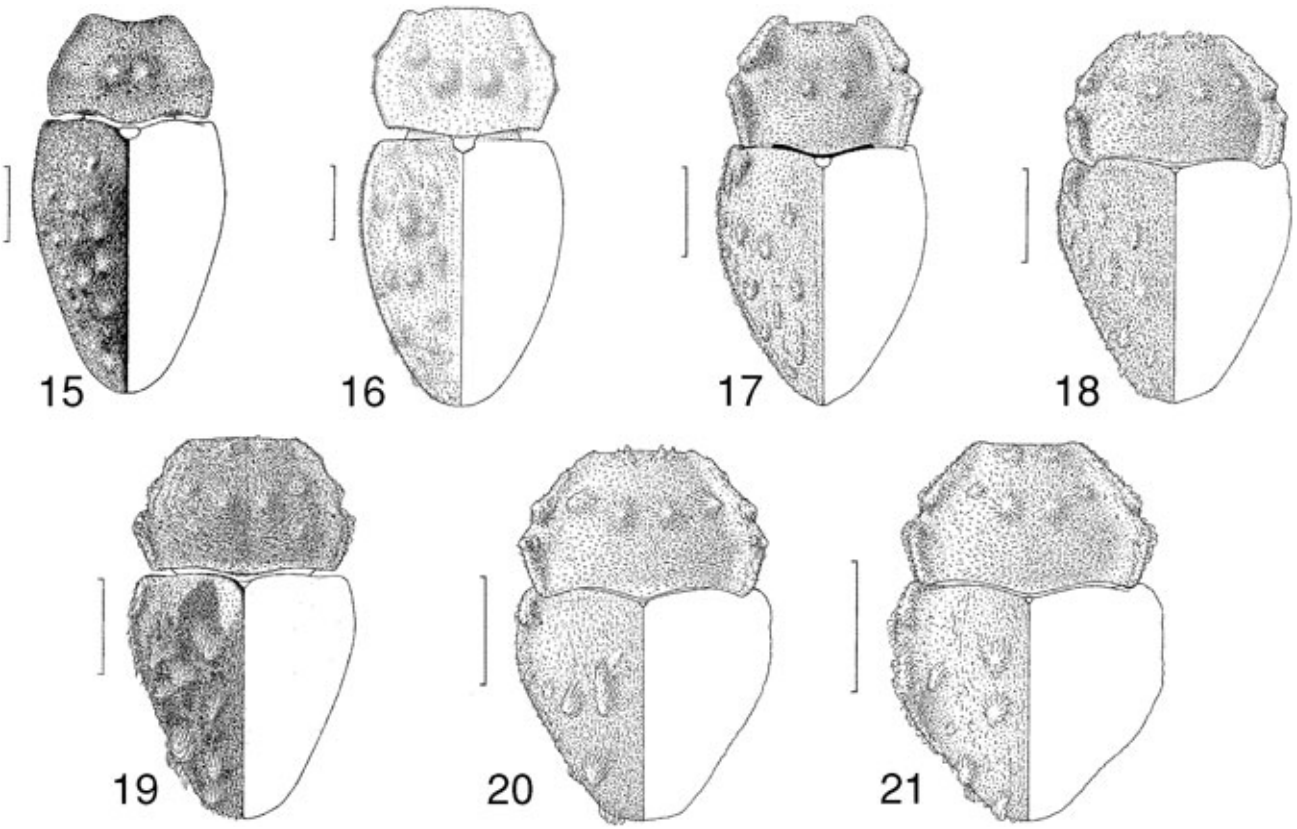
Priasilphinae Crowson, 1973: 56 (Phloeostichidae).

Adult diagnosis (Figs 1–3, 15–26, 29–63, 97–105, 110)

Head without postocular constriction, stridulatory file or frontoclypeal suture. Antennal insertions exposed and subantennal grooves absent (except in *Priastichus*); genae projecting forwards, rounded or acute. Anterior cervical sclerites contiguous with head capsule. Mandible without dorsal tubercle or cavity, with mola. Lacinia with uncus. Pronotum with complete, simple lateral carinae; prosternum long in front of coxae; prosternal process broad, not apically expanded. Procoxae transverse, with exposed trochantins, cavities internally open, externally narrowly open or narrowly closed. Elytral punctation not seriate; sutural flange apically widened in winged species. Mesocoxal cavities widely separated, laterally open; meso-metaventral junction dicondylic or simple (*Priastichus*). Metacoxae narrowly to widely separated. Hind wing with or without closed radial cell and with four or five free veins in medial field; wings absent in all *Priastichus* and most *Priasilpha*. Tarsi usually 5–5–4 in male (5–5–5 in *Chileosilpha*, gen. nov.); tarsomeres without ventral lobes. Abdomen with basal two ventrites connate. Sternite VIII in male without median strut; spiculum gastrale present. Tegmen anteriorly narrowly rounded, acute or produced forming strut; parameres separate and articulated. Penis distinctly divided into basal and apical sections, base with median carina, without anterior struts.

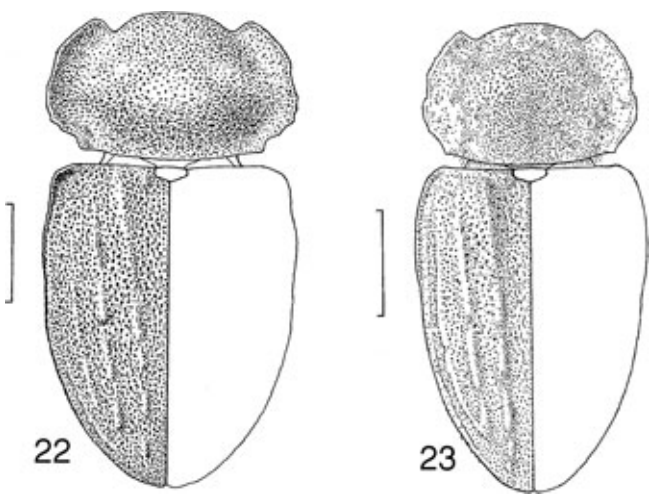
Adult description

Length ~3.3–5.5 mm. Body narrowly oblong to broadly ovate, slightly to moderately convex; dorsal surfaces smooth and even or with tubercles or carinae on elytra; derm more or less shiny, but often covered with exudate and debris; vestiture of fine, recumbent hairs or recurved or erect, stout bristles, evenly distributed or forming clusters dorsally. Head as long as wide or somewhat elongate, slightly flattened, not, or only slightly, declined, without postocular constriction, vertexal line or stridulatory file; posterior edge dorsally with pair of weak or strong incisions just above occipital foramen. Tentorial arms relatively close together, joined by moderately broad corporotentorial bridge. Frontoclypeal suture absent; clypeus extending well in front of antennal insertions, sides subparallel or slightly convergent, without lateral emarginations; apex truncate. Eyes moderately large, vertically oval and slightly emarginate to small and circular, prominent or not, moderately to coarsely facetted, without interfacetal setae. Antennae 11-segmented with distinct 3-segmented, pubescent club; scape slightly to distinctly elongate and asymmetrically inflated; insertions widely separated, exposed or barely concealed from above; subantennal grooves present or absent; genae produced forwards and narrowly rounded or acute. Gular sutures well separated; pregular region flat or slightly concave. Cervical sclerites present, sometimes enlarged. Labrum strongly transverse and slightly inclined. Mandible usually bidentate, occasionally unidentate or obliquely tridentate, with well developed, transversely ridged mola and extensive, setose prostheca; without dorsal tubercle or setose cavity. Maxilla with broad, setose galea and lacinia with setose inner edge and apical bifid uncus; terminal maxillary and labial palpomeres fusiform, narrowed apically with rounded apex. Mentum strongly transverse; ligula laterally expanded, apically emarginate, membranous and setose. Pronotum subquadrate to strongly transverse, broadest at middle or posterior third; sides not to strongly explanate and usually irregularly undulate, with distinct lateral carinae; anterior angles not to slightly produced forwards and angulate or broadly rounded; posterior angles



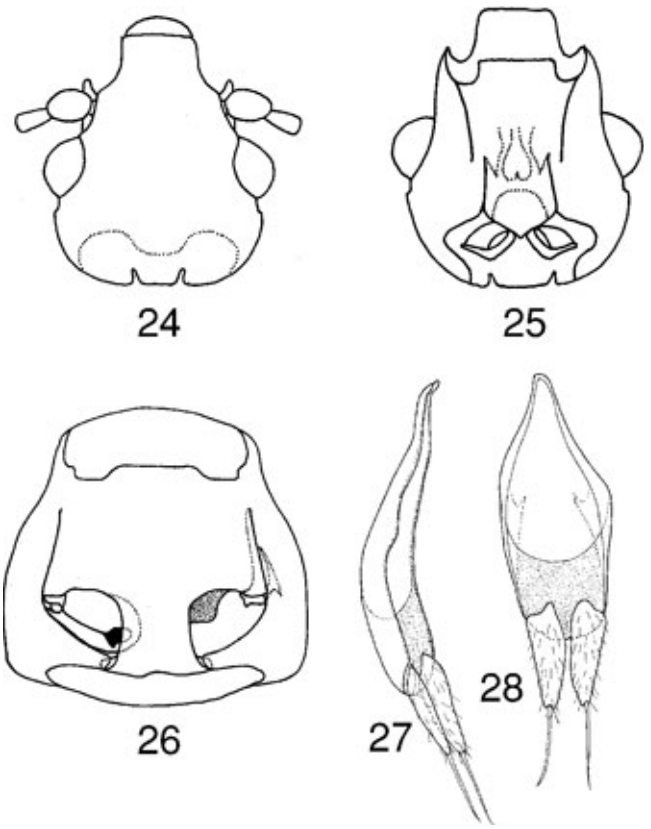
Figs 15–21. Dorsal views of adult *Priasilpha*: *15*, *P. obscura*; *16*, *P. aucklandica*, sp. nov.; *17*, *P. angulata*, sp. nov.; *18*, *P. carinata*, sp. nov.; *19*, *P. earlyi*; *20*, *P. embersoni*; *21*, *P. bufonia*, sp. nov. Scale bars = 1 mm.

more or less right or slightly produced to fit over elytral humeri; posterior edge straight to strongly bisinuate, not margined. Disc slightly, to strongly convex, usually somewhat uneven with large, shallow impressions. Hypomeron with anteroventral angle slightly, to strongly produced and not at same level as anterior edge of prosternum. Scutellum slightly, to strongly transverse, usually abruptly raised at base, rounded to broadly angulate posteriorly. Elytra oblong to somewhat ovate, complete, widest at middle or anterior third; sides subparallel or somewhat rounded, sometimes strongly narrowed posteriorly; apices broadly or narrowly rounded; humeral region rounded or angulate, sometimes with slight notch for posterior pronotal angles; base with carina extending from scutellum laterally, below humerus and posteriorly forming upper edge of epipleuron. Disc evenly convex, sometimes explanate laterally, with or without tubercles or longitudinal costae; punctation irregular; sutural flange widened apically, except in wingless forms. Epipleura narrow to moderately broad at base, narrowing posteriorly and not extending to apex. Prosternum well developed in front of coxae, at least as long as and usually longer than mid coxal length; anterior edge usually concave, sometimes with narrow notch at each end, rarely bisinuate, forming short, broad chin piece flanked by broad emarginations; prosternal process very broad, slightly curved behind coxae, with sides subparallel, slightly expanded at middle or rarely abruptly expanded at apex, which may be truncate or slightly emarginate. Notosternal suture almost always complete. Procoxae not projecting ventrally, without long internal extension. Procoxal cavities



Figs 22-23. Dorsal views of adult *Priastichus. 22*, *P. crowsoni*, sp. nov.; *23*, *P. tasmanicus*. Scale bars = 1 mm.

strongly transverse, without narrow lateral notch, internally open, externally narrowly open or closed; postcoxal projections of hypomera relatively long and acute or rarely interlocking with lateral projections of prosternal process; trochantins exposed. Mesoventrite simple or with paired longitudinal carinae, rarely defining a median shallow concavity; anterior edge with pair of strongly transverse, slightly, to strongly declined procoxal rests. Mesocoxal cavities slightly transverse, separated by a distance more than half as great as and sometimes greater than shortest diameter of cavity, open laterally (partly closed by mesepimeron), with exposed trochantins; meso-metaventral junction a simple straight line or with paired metaventral knobs. Metaventrite moderately convex to flattened, without post-coxal lines; discrimen usually absent, rarely long. Exposed portion of metepisternum long and narrow, slightly widened anteriorly. Metendosternite with moderately to very short, broad stalk, long arms, reduced laminae and anterior tendons arising close together or moderately to widely separated. Metacoxae transverse, narrowly to widely separated. Hind wing, if present, relatively long and narrow, more than 3× as long as wide; apical field more than half total wing length, containing long extensions of RA and RP; radial cell complete or incomplete basally, with short, broad sclerite near its apical end; r3, if present, almost longitudinal; crossvein r4 bisected by longitudinal sclerite; radio-medial loop forming acute angle; MP_{1+2} with long, slender apical extension; medial field with four or five free veins; medial fleck and wedge cell absent; anal notch distinct. Legs relatively long and slender; trochanterofemoral joint strongly oblique; femur slightly expanded near middle; tibia not or slightly expanded at apex, without carinae, teeth or spines, occasionally denticulate or spiculate, with or without subapical ctenidium; tibial spurs relatively small, paired. Tarsi 5–5–5 in female and 5–5–4 in male (rarely 5–5–5 in both sexes); tarsomeres simple, 1 shorter than 2, 1–4 together shorter than to almost twice as long as 5; terminal tarsomere usually with fringe of short setae at apex; claws simple; empodium relatively small and not projecting between claws. Abdomen with five ventrites, the first two of which are more or less connate; ventrite 1 not much longer than 2, without postcoxal lines; intercoxal process usually broadly rounded or truncate, rarely narrowly rounded; tergites I–VI lightly to moderately pigmented, VII and VIII more heavily pigmented; lateral wing-folding patches present on III or V to VII in winged forms, reduced in wingless forms. Abdominal spiracles: seven, first six located in pleural membrane, 7th on tergite. Sternite VIII in male without anterior median strut. Sternite IX in male deeply emarginate apically, with articulated median process, basally with anterior strut (spiculum gastrale). Aedeagus of inverted cucujiform type, with parameres ventral to penis; basal portion of tegmen attenuate anteriorly forming narrowly rounded to subacute plate, but not drawn out to form anterior strut, apical portion well developed, with short, broad to moderately elongate, articulated parameres. Penis divided into distinct basal (anterior) and apical (posterior) sections, the former broad, somewhat flattened, rounded or truncate basally, with or without median, basal carina; the latter narrower, slightly flattened to cylindrical or laterally compressed, parallel-sided or converging apically, with sclerotised endoskeleton and with apex emarginate or produced and acute; endophallus usually with one or more sclerites. Female sternite VIII with well developed spiculum ventrale. Ovipositor short to moderately long and broad, with paired longitudinal bacula on paraprocts and proctiger); proximal gonocoxite short and broad, with oblique, curved or sinuate transverse baculum; distal gonocoxite moderately to very elongate, narrowed apically, lightly to darkly pigmented; stylus moderately long and cylindrical, attached apically or subapically.



Figs 24–28. Characters of adults. *24*, *Chileosilpha elgueti*, sp. nov., dorsal view of head; *25*, same, ventral view of head; *26*, same, ventral view of prothorax; *27*, *Bunyastichus monteithi*, sp. nov., lateral view of tegmen; *28*, same, ventral view of tegmen.

Larval diagnosis (Figs 79–83, 87–94, 106–109)

Body oblong to moderately elongate, somewhat elliptical and narrowed posteriorly, flattened, with long lateral processes on all thoracic terga and abdominal terga I–VIII, in addition to well developed urogomphi on tergum IX; upper surfaces usually moderately well sclerotised, with or without

numerous setiferous tubercles forming straight or curved rows, which may meet up to form cells (setiferous tubercles more developed in late instars of *Priasilpha*). Head broad, not emarginate posteriorly; epicranial stem absent; frontal arms lyriform, well separated at base; endocarinae absent. Stemmata: six, on raised projections, upper three on single projection, lower three on individual projections. Antennae almost half as long as head length; antennomere 1 slightly longer than wide, 2 almost twice as long as 1; 3 very short, less than 0.2× as long as 2; sensorium almost as long as apical antennomere. Frontoclypeal suture absent; labrum free. Mandible tridentate (*Priasilpha*) or bidentate (*Priastichus*) (reduced and worn in some specimens), with accessory ventral process, well developed, tuberculate mola, and narrow-based, acute prostheca. Ventral mouthparts strongly retracted, with well developed maxillary articulating area; mala falciform; maxillary palps 3-segmented; labial palps 2-segmented, separated by more than width of basal palpomere; ligula short; hypopharyngeal sclerome a transverse bar. Hypostomal rods diverging; ventral epicranial ridges absent or weakly developed; gula wider than long. Prothorax on each side with two long, posteriorly curved, acute tergal processes bearing elongate setiferous tubercles (more developed in late instars of *Priasilpha*); meso- and metathorax each with one similar process on each side; abdominal tergum I on each side with a short, straight, lateral processes bearing a spiracle, terga II–VIII each with a pair of elongate, slender, posteriorly curved lateral spiracle-bearing processes; tergum IX with pair of moderately to very long urogomphi, approximate or separated at base and subparallel or strongly diverging, each with lateral elongate setiferous tubercles, urogomphi of *Priasilpha* with one (*P. earlyi* and *P. obscura*) or two (*P. angulata*, sp. nov., *P. bufonia*, sp. nov., and *P. carinata*, sp. nov.) long subapical setae that are much longer in first instars. Coxae moderately widely separated; pretarsal setae two. Sternum IX exposed, well developed; segment X distinct and sclerotised, at least ventrally, but not visible from above. Spiracles annular–biforous.

Constitution, geographical distribution and biological notes

As here redefined and expanded, Priasilphidae includes the single Chilean species *Chileosilpha elguetai*, sp. nov., three species of *Priastichus* from Tasmania and seven species of *Priasilpha* from New Zealand. Although no biological information is available for *Chileosilpha*, gen. nov., adults and larvae of *Priasilpha* and *Priastichus* species have been collected mainly in leaf litter, but also in decayed wood or among moss on rock or log surfaces. The species may be mycophagous and some members of *Priasilpha* may be feeding on sooty mould. Specimens of *Priasilpha* and *Priastichus* larvae and adults are often found covered by debris and exudate, which may be held in place by scale-like setae (Fig. 110) and accumulate in foveae (Fig. 103).

Key to genera of Priasilphidae

1. Body more elongate and narrow, BL/EW greater than 2.25 (Fig. 3); pronotum about as long as wide; prosternum produced anteriorly forming chin piece flanked by pair of broad emarginations (Fig. 26); procoxal cavities closed behind; tarsi 5–5–5 in both sexes; intercoxal process on ventrite 1 narrowly rounded; Chile. . . . . *Chileosilpha*, gen. nov.
   Body shorter and broader, BL/EW less than 2.25 (Figs 1, 2); pronotum less than 0.75× as long as wide; chin piece, if present, flanked by pair of narrow, deep notches (Fig. 102); procoxal cavities narrowly open behind; tarsi 5–5–4 in male; intercoxal process on ventrite 1 broadly rounded to truncate (Fig. 104). 2
2. Posterior edge of pronotum relatively straight and posterior angles not produced over elytra (Fig. 2); scutellum less than half as long as wide; elytral surfaces with tubercles and/or ridges (Figs 2, 22, 23); eyes more or less circular and strongly protruding; Tasmania. . . . . *Priastichus* Crowson
   Posterior edge of pronotum sinuate and posterior angles produced over elytra (weakly sinuate in *P. aucklandica*, sp. nov.) (Fig. 1); elytral surfaces usually smooth (tuberculate in *P. aucklandica*, sp. nov.) (Figs 15–21); eyes vertically oval and not strongly protruding; New Zealand . . . . . *Priasilpha* Broun

Genus ***Chileosilpha***, gen. nov.

(Figs 3, 24–26, 29–35, 62)

Type species: *Chileosilpha elguetai*, sp. nov.

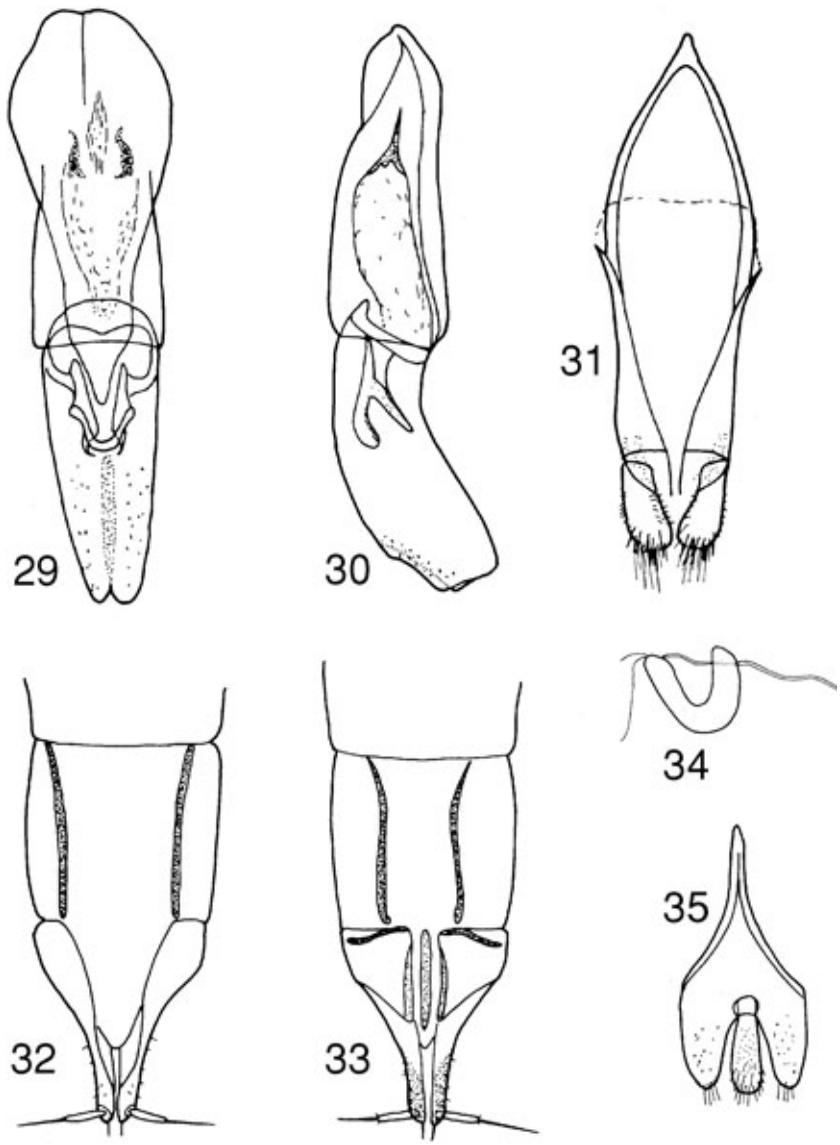
Diagnosis

Chileosilpha differs from both *Priasilpha* and *Priastichus* in the more elongate body, distinct prosternal chin piece flanked by broad emarginations, externally closed procoxal cavities, 5–5–5 tarsi in both sexes, and narrowly rounded intercoxal process on ventite 1.

Description

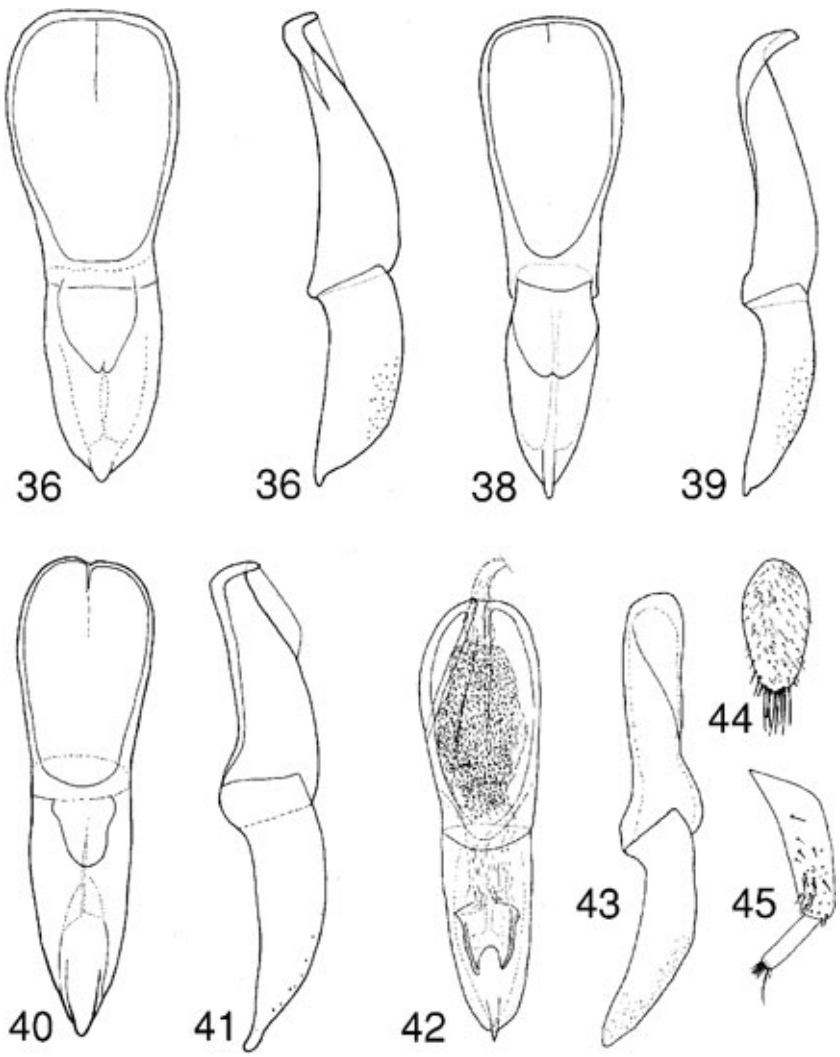
Length ~3.3–4.3 mm. Body oblong, somewhat narrowed anteriorly and moderately convex; ratio of body length to greatest body width 2.1–2.5. Upper surfaces clothed with moderately long, fine, decumbent hairs. Head longer than wide, posterior edge dorsally with a pair of deep incisions, representing lateral cuticular infoldings supporting occipital foramen on each side. Eyes strongly protuberant, entire. Antennae with scape only slightly longer than wide and slightly longer than pedicel that is shorter than antennomere 3. Antennal insertions exposed from above; subantennal groove absent; genae produced well beyond mandibular articulations and subacute as seen from above. Clypeal region with sides slightly convergent. Gula extending forwards to about middle of eye; pregular area broadly concave, with pair of obliquely longitudinal grooves extending to maxillary articulations. Posterior edge of head broadly excavate on each side of gular base, which extends posteriorly and is subacute at apex; each excavation containing an irregularly ovoid, thin and translucent anterior cervical sclerite, which is

connected to the gular base, the base of the tentorium and the lateral occipital infoldings. Tentorial bridge bearing a fine anterior median process. Mandible ~1.5× as long as wide, more or less abruptly curved mesally at apical 4th and obliquely tridentate. Apical maxillary and labial palpomeres elongate, about twice as long as wide, distinctly narrowed apically. Pronotum about as long as wide, widest posteriorly; sides distinctly sinuate; lateral carinae complete, barely visible for their entire lengths from above, simple, without marginal bead; anterior angles not produced forwards; posterior angles more or less right; posterior edge bisinuate, simple, without marginal bead; disc with weak, broadly transverse impression. Scutellum about half as long as wide, abruptly elevated basally, rounded laterally and obtusely angulate posteriorly. Elytra ~1.6× as long as wide and 2.2× as long as pronotum; surface even, except for distinct humerus and slight boss at apical fifth. Prosternum in front of coxae about twice as long as mid length of a coxal cavity, moderately convex; anterior edge produced forwards at middle to form chin piece, which is flanked by pair of broad emarginations. Notosternal sutures deeply impressed but incomplete anteriorly; anteromesal corner of hypomeron with short tooth. Prosternal process parallel-sided, but abruptly expanded laterally at apex, which is subtruncate. Procoxal cavities broadly closed externally by notal projections extending over and fitting into concavities in lateral



Figs 29–35. Characters of adult of *Chileosilpha elgueti*, sp. nov. *29*, dorsal view of penis; *30*, lateral view of penis; *31*, dorsal view of tegmen; *32*, dorsal view of ovipositor; *33*, ventral view of ovipositor; *34*, spermatheca; *35*, ventral view of male sternite IX.

expansions of prosternal process. Mesoventrite anteriorly with pair of narrow, strongly declined procoxal rests and posteriorly with a broad, shallow depression, flanked by longitudinal carinae. Mesocoxal cavities separated by distance equal to shortest diameter of a mesocoxal cavity. Mesometaventral junction complex, with pair of metaventral knobs fitting into paired mesoventral cavities. Metaventrite moderately long and convex; discrimen long but weakly indicated. Metacoxae narrowly separated. Metendosternite with anterior tendons arising close together. Hind wing with incomplete (basally open) radial cell and four free veins (MP_4+CuA_1, CuA_2, AA_3 and AA_4) in medial field. Legs simple, with weak subapical ctenidium. Tarsi 5–5–5 in both sexes; tarsomeres 1–4 together 1.5× as long as tarsomere 5. Abdomen with intercoxal process narrowly rounded. Tegmen with parameres broader apically than at base; anterior plate narrowed and subacute. Penis with basal section slightly depressed, broadly rounded anteriorly, with median carina; apical section laterally compressed and narrowed apically, notched at apex; endoskeleton relatively complex, including paired hooks and a semicircular sclerite; endophallus with a pair of longitudinal, complexly sinuate, darkly pigmented sclerites. Ovipositor about twice as long as wide; combined gonocoxites slightly longer than paraprocts, proximal gonocoxite subquadrate and apically oblique with sinuate transverse baculum, distal one slightly longer, distinctly narrowed apically, pigmented on apical half, with well developed stylus attached laterally just before apex.



Figs 36–45. Characters of adult new species of *Priasilpha*. *36*, *P. angulata*, sp. nov., ventral view of penis; *37*, same, lateral view; *38*, *P. bufonia*, sp. nov., ventral view of penis; *39*, same, lateral view; *40*, *P. carinata*, sp. nov., ventral view of penis; *41*, same, lateral view; *42*, *P. earlyi*, ventral view of penis; *43*, same, lateral view; *44*, same, detail of left paramere; *45*, same, distal portion of gonocoxite and stylus.

Chileosilpha elguetai, sp. nov.

(Figs 3, 24–26, 29–35, 62)

Material examined

Holotype. ♂ 'Chile, T. Ueno PN Puyehue Anticura, 17 Feb 2003.' (MNHS)

Paratypes. ♀, **Chile**. **Chiloe:** Chiloe I., ii.1990 (AA). ♂ (dissected, parts on card and in glycerine), **Chile. Llanquihue:** P[arque]. N[ational], Vicente Perez R[osales], C° [Cerro] Derrumbe [41°11′S, 72°15′ W], 8-v-1971, J. Solervicens / formacion Caigue-Tepa (ANIC).

Description

With the characters of the genus. TL = 4.8, 3.85 mm; BL/EW = 2.35, 2.33; PL/PW = 1.0, 0.96; EL/EW = 1.59, 1.6; EL/PL = 2.11, 2.18; GD/EW = 0.73, 0.76. Colour reddish-brown; anterior portion of head, palps and legs yellowish-brown. Dorsal surfaces smooth and shiny, clothed with moderately long, recumbent yellow hairs, those on elytra posteriorly directed, those on head and prothorax more or less laterally directed from midline; ventral surfaces clothed with short, recumbent hairs. Punctation of head and pronotum moderately fine and dense, which on elytra is fine but somewhat sparser; punctation moderately fine and dense on most surfaces, extremely fine and sparse on hypomera, coarse and dense on posterior portion of mesoventrite. Aedeagus as in Figs 29–31. Ovipositor as in Figs 32, 33.

Distribution

Valdivian region, Chile.

Remarks

The holotype specimen was collected in a forest where the dominant tree species were *Nothofagus dombeyi* (Fagaceae) and *Laurelia philippiana* (Atherospermataceae).

Genus ***Priasilpha*** Broun

(Figs 1, 15–21, 36–52, 63, 97–105, 110, 80, 83)

Priasilpha Broun, 1893: 1077. Type species, by monotypy, *P. obscura* Broun.

Diagnosis

Priasilpha species are always shorter and broader than *Chileosilpha elguetai*, and differ also in having either no chin piece or one that is shorter, broader and flanked by deep notches, and in having narrowly open procoxal cavities, a broader abdominal process and 5–5–4 tarsi in the male. The genus differs from *Priastichus* in having the prothorax distinctly wider posteriorly than anteriorly, with a bisinuate posterior edge and somewhat acute and produced posterior angles; in addition the eyes are vertically oval and not strongly projecting. In most *Priasilpha* the elytral surfaces are completely devoid of tubercles or ridges, which characterise species of *Priastichus*; however these do occur in *P. aucklandica*, sp. nov. (see below).

Description

Length ~3.4–5.8 mm. Body oblong to broadly ovate, slightly narrowed anteriorly, strongly so posteriorly, moderately to strongly convex; ratio of body length to greatest body width 1.3–2.04. Upper surfaces clothed with short to moderately long, stout, yellow setae, mainly recumbent but with a variable number of suberect setal clusters. Head as long as wide or slightly elongate; posterior edge dorsally with a pair of shallow emarginations. Eyes vertically oval and slightly emarginate. Antennae with scape distinctly longer than wide and distinctly longer than pedicel that is shorter than antennomere 3. Antennal insertions exposed from above; subantennal grooves absent; genae moderately produced forwards and rounded. Pregular area flat. Tentorial bridge without median process. Clypeal region with sides slightly convergent. Mandible slightly longer than wide, more or less abruptly curved mesally at apical 3rd and bidentate. Apical maxillary and labial palpomeres elongate, ~1.5× as long as wide, not, or only slightly, narrowed apically. Pronotum ~0.50–0.76× as long as wide, widest at or just behind middle, and wider at base than at apex; sides somewhat irregularly undulate, not explanate but often slightly raised; lateral carinae visible for their entire lengths from above, anterior angles not or slightly produced forwards and rounded; posterior angles slightly produced and subacute; disc sometimes with pair of weak elevations. Scutellum slightly more than half as long as wide, usually abruptly elevated basally, rounded or acutely angulate laterally and rounded to sharply angulate posteriorly. Elytra ~0.77–1.65× as long as wide and 1.37–3× as long as pronotum, widest at anterior third; sides slightly converging anteriorly, strongly so posteriorly; apices broadly to narrowly rounded; anterior edge with slight notch or depression on each side for receiving posterior pronotal angles; humerus sharply angulate, sometimes laterally produced; disc even or with irregular elevations; epipleura broad at base, strongly narrowed posteriorly. Prosternum in front of coxae ~1.3 to 1.8× as long as mid length of a coxal cavity, moderately convex; anterior edge concave, not produced forwards or slightly produced to form short, broad chin piece, with deep, narrow notch at each end between sternum and hypomeron; notosternal sutures complete; prosternal punctation finely spiculate, in contrast to coarsely punctate hypomeral punctation. Prosternal process shorter than wide, sides diverging apically or rounded (diverging and then converging); apex subtruncate or concave, without lateral expansions. Procoxal cavities narrowly open behind; notal projections acute, extending beyond middle of coxal cavities but not meeting prosternal process. Mesoventrite with pair of slightly oblique procoxal rests, with or without a pair of weak longitudinal carinae. Mesocoxal cavities separated

by distance at least 1.2× as great as shortest diameter of a mesocoxal cavity. Meso-metaventral junction forming a straight line. Metaventrite less than one-third to slightly more than half as long as wide; discrimen absent. Metacoxae widely separated. Metendosternite with stalk much shorter and anterior tendons more widely separated in wingless forms. Hind wing, if present, with complete (basally closed) radial cell and five free veins (MP3, MP_4+CuA_1, CuA_2, AA_3 and AA_4) in medial field. Legs simple; tibiae slightly expanded apically, with distinct subapical ctenidium. Tarsi 5–5–5 in female, 5–5–4 in male; tarsomeres 1–4 together longer than tarsomere 5. Abdomen with intercoxal process broadly rounded or truncate. Tegmen with parameres about twice as long as wide and narrower apically; anterior plate narrowly rounded. Penis with basal section depressed, broadly rounded anteriorly, with or without median carina; apical section narrowed apically, acute at apex; endoskeleton simple, trapezoidal; endophallus with pair of lightly pigmented, longitudinal sclerites. Ovipositor with proximal gonocoxites subquadrate or slightly transverse, distal ones 3× as long and much narrower, pigmented except at base, with apically attached styli.

Key to species of *Priasilpha* based on adults

1. Body elongate, length of elytra exceeding 2.5× length of pronotum (Fig. 15); apical sutural flanges of elytra present (Fig. 1); hind wings present; widely distributed . . . *P. obscura* Broun
   Body shortened or moderately elongate, length of elytra 2.0× or less length of pronotum (Figs 16–21); apical flanges of elytra absent; hind wing absent; distributions restricted. 2
2. Posterior edge of pronotum evenly convex; sides of pronotum without deep sulci; dorsal surface with tubercles (Fig. 16); Auckland Islands . . . . . *P. aucklandica*, sp. nov.
   Posterior edge of pronotum sinuate; sides of pronotum with deep furrows; dorsal surface without tubercles (Figs 17–21) . . . 3
3. Scutellum well developed and rounded; anterior edge of pronotum emarginate; anterior angles produced forwards (Fig. 17); Franz Joseph Glacier, Westland . . . . . *P. angulata*, sp. nov
   Scutellum poorly developed and triangular; anterior edge of pronotum not emarginate (Figs 18–21); anterior angles not produced forwards. 4
4. Elytra twice as long as pronotum; body elongate-oval (Figs 18, 19) 5
   Elytra 1.3–1.5× as long as pronotum; body rounded (Figs 20, 21) 6
5. Antennomere 3 as long as 4; asetose area present on central anterior portion of elytra (Fig. 19); Arthur's Pass, Westland . . . . . *P. earlyi*, sp. nov.
   Antennomere 3 longer than 4; asetose area on elytra absent (Fig. 18); north-west Nelson . . . . . *P. carinata*, sp. nov.
6. Elytra distinctly shorter than their combined widths; sides converging from middle to apex; humeral rim extending to middle (Fig. 21); penis with posterior carina but without anterior keel (Figs 38, 39); Marlborough . . . . *P. bufonia*, sp. nov.
   Elytra only slightly shorter than combined widths; sides converging before middle; humeral rim short, not extending to middle (Fig. 20); penis with anterior keel but without posterior carina (Figs 46, 47); Buller . . . . . *P. embersoni*, sp. nov.

Priasilpha angulata, sp. nov.

(Figs 17, 36, 37, 95)

Material examined

Holotype. ♂, 'Fox Glacier, Westland Natl Pk [43°27′S, 170°01′E] 16–17.xii 99, T. Ueno leg;' (NZAC).

Paratypes. **New Zealand: South Island. WD,** 10, Fox Glacier, Westland Natl Pk, [43°27′S, 170°01′E] 16–17.xii 99, T. Ueno (3 NZAC, 7 TUPC); 2, same locality, 12–15.xii 99, T. Ueno leg (TUPC); 3, Canavan Knob Walk, 43°23′S, 170°10′E, 13.ii.1999, R. Leschen, R. Hoare, slime flux, RL309 (NZAC); 1, Lake Ianthe [43°03′S, 170°37′E] 7.ii.1984, J. C. Watt, sifted litter and wood mould 84/22 (NZAC).

Associated larva. 1, Canavan Knob Walk, 43°23′S, 170°10′E, 13.ii.1999, R. Leschen, R. Hoare, slime flux, RL309 (NZAC).

Diagnosis

Body moderately elongate, elytra ~1.1× as long as wide and 1.8× as long as the pronotum. Dorsal surfaces lacking tubercles. Pronotum with lateral rims well developed; side with one notch; deep sublateral sulci present; anterior angles strongly produced forwards; two setal patches present at centre. Scutellum fully exposed. Humeral ridge of elytron short. Femur not bicolored. This is the only species in which the anterior edge of the pronotum is deeply emarginate and the anterior angles strongly produced forwards.

Description

Length 4.5–5.2 mm (mean = 4.76, n = 10). Body ~1.80× as long as wide (BL/EW = 1.73–2.06), and greatest depth ~0.56× as great as elytral width (GD/EW = 0.52–0.61). Colour dark reddish brown; mouthparts, legs, and clypeus dark red; dorsal surfaces lacking tubercles; vestiture of thick yellow setae; anterior portion of prosternum, all of the hypomeron, and epipleuron covered with microtubercles. Head coarsely and densely punctate posteriorly, more finely so anteriorly. Antennomeres 3 and 4 subequal in length. Eye coarsely facetted, greatest length five facets, greatest width 11 facets. Pronotum ~0.7× as long as wide (PL/PW = 0.64–74), widest at basal 1/3; sides broadly, irregularly sinuate, lateral notch present at middle; lateral rim well developed with deep sublateral sulcus; anterior margin deeply incised with anterior angles strongly produced forwards, with internal angles right; posterior angles slightly acute; posterior margin sinuate; disc uneven, glabrous areas present in anterior half (in some specimens) and associated with sublateral sulci; setal patches present at anterior margin (two, sometimes fused to form a single patch), centre (two), and either side of notch on lateral rim. Hypomeron lacking large ovate punctures; well developed ventrally directed tooth present above anterior hypomeral notch; shallow posterior fovea absent. Prosternum without chin piece; width of prosternal process equal to width of procoxal cavity; bead not present running parallel to notosternal suture; short transverse groove at either side of anterior margin absent.

Scutellum fully exposed; rounded and slightly transverse. Elytra ~1.1× as long as wide (EL/EW = 1.07–1.37) and ~1.8× as long as pronotum (EL/PL = 1.61–1.97); sides evenly rounded, widest at middle; humeral ridge present, extending a short distance, not to midline of elytron (1/6 length of elytron); 10 setal patches present, posterior patches linear; glabrous areas absent; width of epipleuron at level of metacoxa 1/2 that of metacoxa; apical sutural flanges absent. Hind wing absent. Width of mesoventral process greater than that of mesocoxa. Abdominal process of first ventrite broad and square, width greater than that of metacoxa. Abdominal ventrites on different planes. Femur not bicolored, uniformly red or reddish brown. Penis with anterior hyaline keel and lateral rim extending to anterior 1/3 in anterior portion; posteriorly carinate (carina short and rather broad), with dorsal edge evenly rounded and sinuate just before acute apex. Paramere 1.5× longer than wide with many apical setae.

Remarks

The species is restricted to an area known as the Westland beech gap, where *Nothophagus* species are completely absent, one of the major biogeographic mysteries in the South Island. Three adult specimens were collected with a larva feeding on slime flux oozing from a cut edge of a tree. Gut contents of a dissected specimen contained mainly unidentified matter and a few fungal hyphae. The name refers to the strongly angulate and produced anterior angles of the pronotum.

Distribution

South Island, Westland.

Priasilpha aucklandica, sp. nov.

(Fig. 16)

Material examined

Holotype. ♀, 'Fairchilds Garden, Adams Id, Auckland Is [50°35′S, 166°10′E] 20.i.66, litter 66/77, Ent. Div. D.S.I.R. N. Zealand' (NZAC).

Associated larvae. 2, same label data as Holotype, but 2.ii.66 (slide mounted, NZAC); 4, same except 2 Feb 1966, litter 66/95 (2 slide mounted, NZAC); 1, Fairchilds Garden, 20.i.66, fellfield, P. M. J. (NZAC).

Diagnosis

Body moderately elongate, elytra ~1.3× as long as wide and 2.0× as long as the pronotum. Dorsal surfaces tuberculate. Pronotum without lateral rims or deep sublateral sulci; side without notch; anterior angles produced forwards; four setal patches present at centre. Scutellum fully exposed. Humeral ridge of elytron absent. Femur unicolored. This species differs considerably from its congeners, most notably by the presence of dorsal tubercles and the shape of the pronotum.

Description

Length 5.8 mm. Body twice as long as wide (BL/EW = 2), and greatest depth ~0.6× as great as elytral width (GD/EW = 0.62). Colour of body light tan; ventrites and head dark tan; dorsal surfaces tuberculate; vestiture of thick setae; anterior portion of prosternum and lateral and anterior portion of hypomeron covered with microtubercles. Head coarsely and densely punctate. Antennomere 3 longer than 4. Eye coarsely facetted, greatest length eight facets, greatest width 12 facets. Pronotum ~0.8× as long as wide (PL/PW = 0.76), widest at middle; sides evenly rounded and slightly sinuate with carina explanate with lateral bead; lateral notch, rim and deep sublateral sulci absent; anterior margin shallowly incised with anterior angles produced forwards and rounded, interior angle oblique; posterior angles acute; posterior margin weakly sinuate and more or less convex; disc uneven, glabrous areas absent; setal patches on tubercles and present at centre (4), longer setae present on carina at basal and apical 1/3 and along anterior margin. Hypomeron lacking large ovate punctures absent; well developed ventrally directed tooth present above anterior hypomeral notch present; shallow posterior fovea absent. Prosternum without chin piece; width of prosternal process slightly less than width of procoxal cavity; bead present running parallel to notosternal suture; short transverse groove at either side of anterior margin absent. Scutellum fully exposed; angulate and transverse. Elytra ~1.3× as long as wide (EL/EW = 1.34) and ~2× as long as pronotum (EL/PL = 2.05); sides evenly rounded, widest at middle; humeral ridge absent; nine setal patches present on rounded tubercles, posterior and lateral tubercles shallower than those at centre; glabrous areas absent; width of epipleuron at level of metacoxa 1/2 that of metacoxa; apical sutural flanges absent. Hind wing absent. Width of mesoventral process narrower than that of mesocoxa. Abdominal process of first ventrite broad and square, width less than that of metacoxa. Abdominal ventrites on different planes. Femur unicolorous light tan.

Remarks

This species is known from one female adult specimen and five larvae, which were in alcohol up until the start of this study. All specimens were bleached, apparently due to improper storage in sunlight, and the larvae were very fragile and four were slide mounted for better preservation and future study. *Priasilpha aucklandica* is known only from Adams Island, the large and pristine southernmost island of the subantarctic Auckland Islands. The Auckland Island archipelago is the largest of all New Zealand's subantarctic islands, and is the only island group with a forest canopy (composed of *Metrosideros umbellata* or Southern Rata). Of the four slide mounted larvae, the gut of one was empty, otherwise they were filled with undetermined debris and the debris affixed to the body was undetermined, apart form

spores found on the body of one individual. The name is based on the type locality.

Distribution

Auckland Island, Adams Island.

Priasilpha bufonia, sp. nov.

(Figs 21, 38, 39, 95)

Material examined

Holotype. ♂, 'Mt Duppa, Nelson, 3500' [41°13S, 173°30E] 16–3–38, E. S. Gourlay, E. S. Gourlay Acc. 1970 Ent. Div' (NZAC).

Paratypes. **New Zealand: South Island. MB**, 3, Fell Pk, Richmond Ra, 1296 m, [41°27′S, 173°24′E] 13.iii.1969, A. C. Eyles, litter (NZAC). **NN**, 3, Third House, Dun Mt track, Nelson [41°19′S, 173°19′E], 14.ix.1971, G. W. Ramsay, litter (NZAC); 2, Dun Mt, Nelson [41°19′S, 173°22′E] 9.xi.1957, R. M. Bull Collection (NZAC).

Associated larvae. 1, **MB,** Fell Pk, Richmond Ra, 1296 m [41°27′S, 173°24′E], 13.iii.1969, A. C. Eyles, litter (NZAC); 9, **NN,** Third House, Dun Mt track, Nelson [41°19′S, 173°19′E], 14.ix.1971, G. W. Ramsay, litter (NZAC).

Diagnosis

Body round, elytra ~0.8× as long as wide and 1.5× as long as the pronotum. Dorsal surfaces lacking tubercles. Pronotum with lateral rims well developed; side with one notch; deep sublateral sulci present; anterior angles reduced; four setal patches present at centre. Scutellum reduced. Humeral ridge of elytron elongate. Femur not bicolored. This is the only species with an elongate humeral ridge that extends to the midlength of the elytron.

Description

Length 3.4–3.9 mm (mean = 3.63, *n* = 7). Body ~1.38× as long as wide (BL/EW = 1.30–1.43), and greatest depth ~0.54× as great as elytral width (GD/EW = 0.50–0.58). Colour of body dark reddish brown or brown; mouthparts, legs, and clypeus dark red to light brown; dorsal surfaces lacking tubercles; vestiture of thick yellow setae; anterior portion of prosternum, lateral and anterior portion of hypomeron, and epipleuron covered with microtubercles. Head coarsely and densely punctate. Antennomeres 3 and 4 subequal in length. Eye coarsely facetted, greatest length five facets, greatest width 12 facets. Pronotum ~0.6× as long as wide (PL/PW = 0.54–64), widest at basal 1/3; sides broadly, irregularly sinuate, lateral notch present at middle; lateral rim well developed with deep sublateral sulcus; anterior margin weakly incised with anterior angles weakly produced forwards; posterior angles rounded; posterior margin sinuate; disc uneven, glabrous areas not present; setal patches present at anterior margin (two fused to form a single patch), centre (four), and either side of notch on lateral rim. Hypomeron with posteromesal surface glabrous, large ovate punctures absent; poorly developed ventrally directed tooth present above anterior hypomeral notch; shallow posterior fovea absent. Prosternum without chin piece; width of prosternal process subequal to width of procoxal cavity; bead present running parallel to notosternal suture; short transverse groove at either side of anterior margin present. Scutellum partly exposed; triangular. Elytra ~0.8× as long as wide (EL/EW = 0.77–0.89) and ~1.5× as long as pronotum (EL/PL = 1.37–1.67); sides subparallel to middle and abruptly converging to apex; humeral ridge present, extending a long distance to midline of elytron (~1/2 length of elytron); five rounded setal patches present; glabrous areas present in basal 1/3 of some specimens; width of epipleuron at level of metacoxa slightly wider than that of metacoxa; apical sutural flanges absent. Hind wings absent. Width of mesoventral process greater than that of mesocoxa. Abdominal process of first ventrite broad and square, width greater than that of metacoxa. Abdominal ventrites on slightly different planes. Femur not bicolored, uniformly reddish or light brown. Penis without anterior hyaline keel and lateral rim extending to anterior third; posteriorly carinate (carina narrow), with dorsal edge evenly rounded and sinuate just before apex, apex acute. Paramere twice as long as wide with few apical setae.

Remarks

The species is restricted to Richmond Range in the Marlborough area at the northern end of the South Island. The gut of a single dissected specimen was filled with dark sooty mould fungal spores that are essentially long chains hyphae that fragment into spores (P. Johnston, personal communication). Scrapings of the surface debris of the same specimen also contained the same hyphae, which can be seen in some of the pinned specimens. A single early instar from the Richmond Range had a gut filled with undetermined material. The species name is taken from the Latin word *bufo* for toad and refers to the toad-like body form.

Distribution

South Island, Nelson and Marlborough regions.

Priasilpha carinata, sp. nov.

(Figs 18, 40, 41, 95)

Material examined

Holotype. ♂, 'Paradise Peak, 4500′ [40°55′S, 172°38′E] 6.11.38, E. S. Gourlay' (NZAC).

Paratypes. **New Zealand: South Island. NN**, 5, Mt Arthur (Salisbury), 3000′ [41°11′S, 172°44′E] 23.x.1943, E. S. Gourlay (4, NZAC; 1 slide mounted, ANIC); 1, Mt Arthur (G.), 4500′ [41°11′S, 172°44′E] 17.i.1943, E. S. Gourlay (NZAC); 1, Mt Arthur, Kahurangi Nat. Pk [41°11′S, 172°44′E] 25–28.xi.1999, T. Ueno (TUPC); 1, Bush behind Mytton Hut, Cobb Valley 4000′ [41°06′S, 172°35′E] 13.xii.1967, litter, S. Edridge (NZAC);

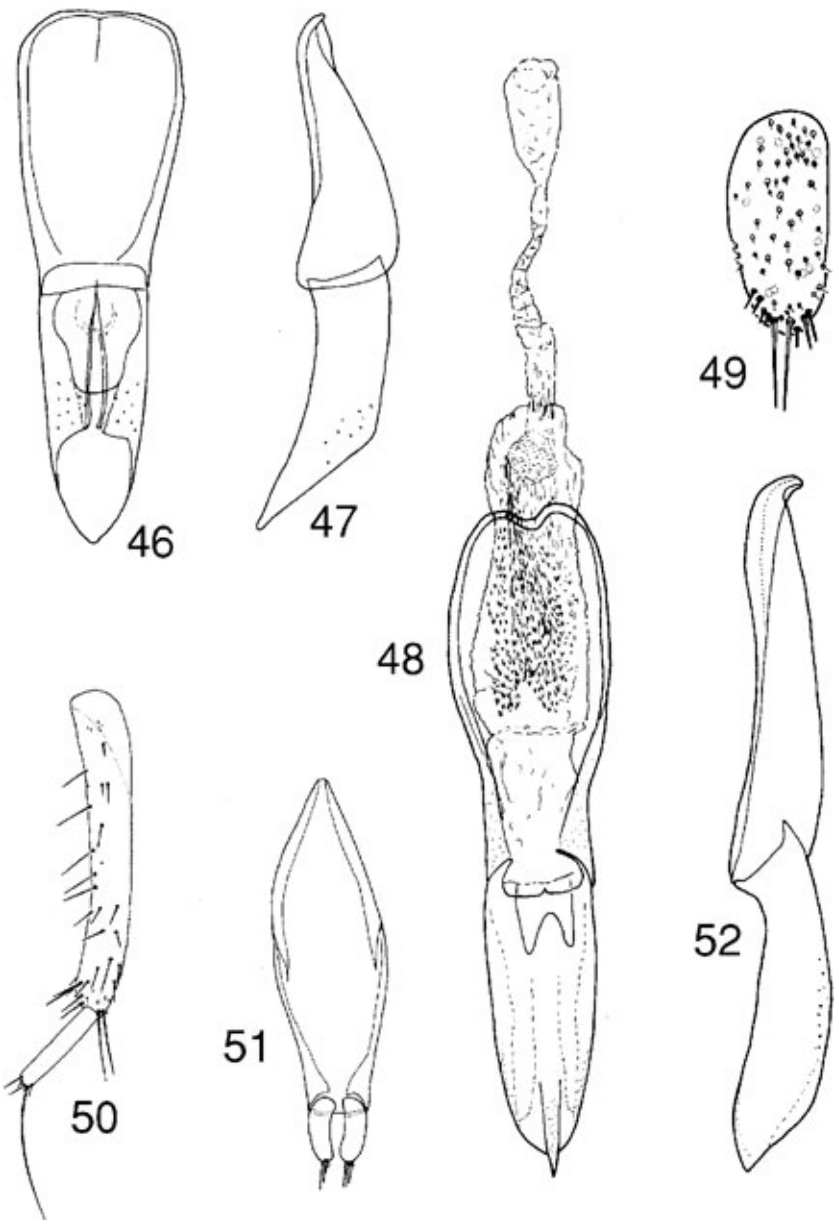
Associated larvae. **New Zealand: South Island. NN**, 2 (slide mounted), Mt Domett, 1000 m [41°04′S, 172°19′E] 1 Dec 1971, G. W. Ramsay, under *Nothofagus menziensii* litter 71/176 (NZAC).

Diagnosis

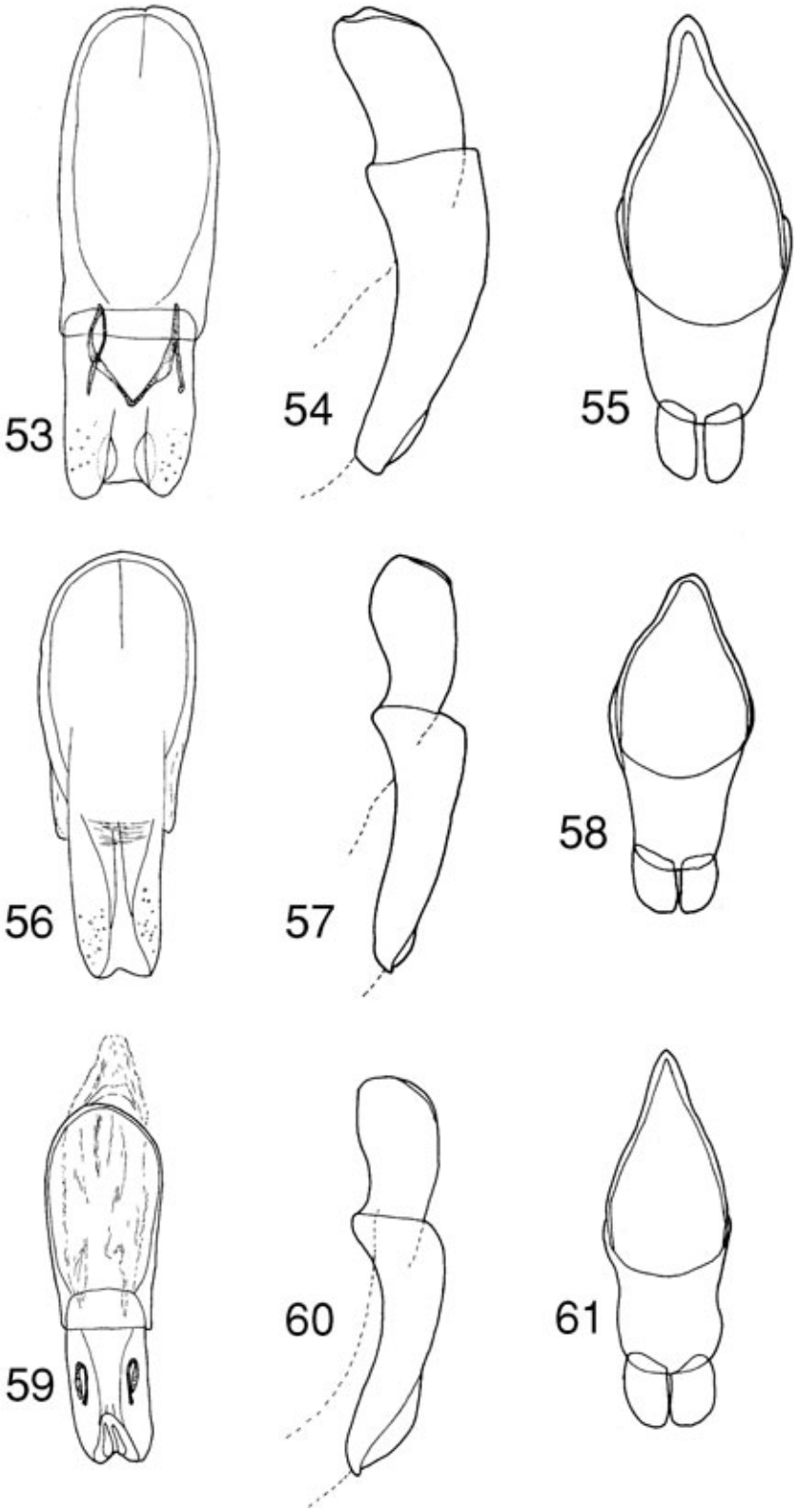
Body moderately elongate, elytra ~0.97× as long as wide and 1.6× as long as the pronotum. Dorsal surfaces lacking tubercles. Pronotum with lateral rims well developed; side with one notch; deep sublateral sulci present; anterior angles weakly produced forwards; four setal patches present at centre. Scutellum partially exposed. Humeral ridge of elytron short. Femur bicolored. The species can be recognised by the relatively poorly developed setal patches on the elytra, the longer third antennomere, and wide epipleuron that separates it from the similar species *P. earlyi*.

Description

Length 3.5–4.5 mm (mean = 3.92, n = 6). Body ~1.55× as long as wide (BL/EW = 1.48–1.60), and greatest depth ~0.57× as great as elytral width (GD/EW = 0.50–0.64). Colour of body dark reddish brown; anterior portion of head, mouthparts, legs, and clypeus dark red to light brown; dorsal surfaces lacking tubercles; vestiture of thick yellow

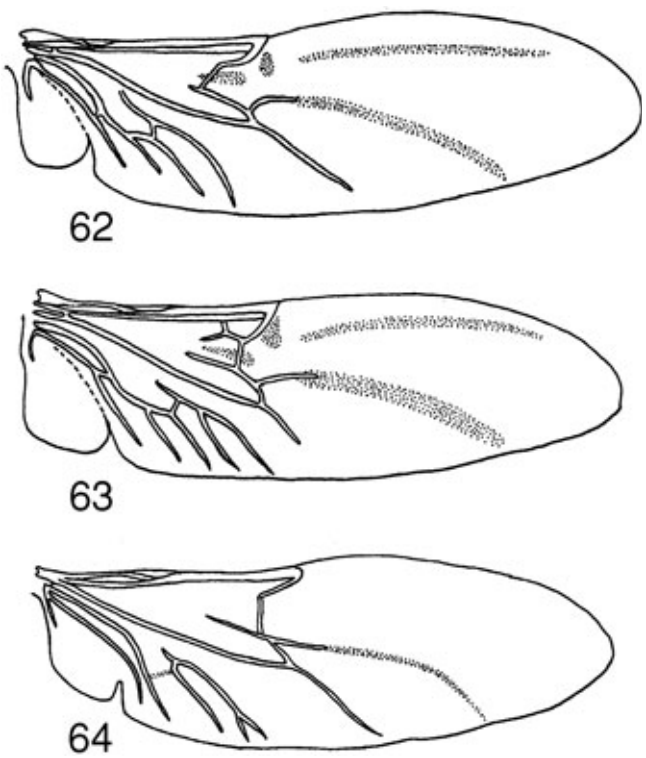


Figs 46–52. Characters of adult *Priasilpha*. *46*, *P. embersoni*, sp. nov., ventral view of penis; *47*, same, lateral view; *48*, *P. obscura*, ventral view of penis; *49*, same, detail of right paramere; *50*, gonocoxite and stylus; *51*, same, tegmen; *52*, lateral view of penis.



Figs 53–61. Terminalia of adult *Priastichus*. *53*, *P. crowsoni*, sp. nov., dorsal view of penis; *54*, same, lateral view of penis; *55*, same, dorsal view of tegmen; *56*, *P. megathorax*, sp. nov., dorsal view of penis; *57*, same, lateral view of penis; *58*, same, dorsal view of tegmen; *59*, *P. tasmanicus*, dorsal view of penis; *60*, same, lateral view of penis; *61*, same, dorsal view of tegmen.

setae; anterior portion of prosternum, lateral and anterior portion of hypomeron, and epipleuron covered with microtubercles. Head coarsely and densely punctate. Antennomere 3 longer than 4. Eye coarsely facetted, greatest length five facets, greatest width 12 facets. Pronotum ~0.6× as long as wide (PL/PW = 0.59–67); sides broadly, irregularly sinuate, lateral notch present at middle; lateral rim well developed with deep sublateral sulcus; anterior margin weakly incised with anterior angles slightly produced forwards; posterior angles slightly rounded; posterior margin sinuate; disc uneven, glabrous areas present in anterior half (in some specimens); setal patches present at anterior margin (two, weakly produced), centre (four, two central ones reduced in two specimens), and either side of notch on lateral rim. Hypomeron with posteromesal surface glabrous and large ovate punctures absent; ventrally directed tooth present above anterior hypomeral notch, well or poorly developed; shallow posterior fovea absent. Prosternum without chin piece; width of prosternal process slightly wider than width of procoxal cavity; bead present running parallel to notosternal suture; short transverse groove at either side of anterior margin absent. Scutellum partially exposed; triangular. Elytra ~0.97× as long as wide (EL/EW = 0.92–0.97) and ~1.6× as long as pronotum (EL/PL = 1.53–1.84); widest at basal 1/3, sides converging apically; humeral ridge present, extending a short distance, not to midline of elytron (1/6 length of elytron); 7–9 round setal patches present, posterior and lateral patches reduced and may be diffuse in some specimens; glabrous areas absent; width of epipleuron at level of metacoxa subequal to that of metacoxa; apical sutural flanges absent. Hind wing absent. Width of mesoventral process greater than that of mesocoxa. Abdominal process of first ventrite broad and square, width greater than that of metacoxa. Abdominal ventrites on slightly different planes. Femur bicolored, basal third dark. Penis with anterior hyaline keel and with lateral rim extending to base; posteriorly carinate (carina rather broad), with dorsal edge evenly narrowed and slightly sinuate just before apex, apex acute. Paramere 1.5× longer than wide with many apical setae.



Figs 62–64. Wings of basal Cucujoidea. *62*, *Chileosilpha elguetai*, sp. nov.; *63*, *Priasilpha obscura*; *64*, *Bunyastichus monteithi*, sp. nov.

Remarks

The species is restricted to the Nelson region of the South Island. The gut of one adult specimen contained fungal hyphae and unidentified matter. Two early instars from Mt Domett had little unrecognisable debris in their guts and on the outside of their bodies. The species name is based on the Latin word *carina* and refers to the hyaline keel on the anterior portion of the penis.

Distribution

South Island, Nelson region.

Priasilpha earlyi, sp. nov.

(Figs 19, 42, 43, 95)

Material examined

Holotype. ♂, 'Arthurs Pass Natl Pk, Kellys Ck [42°59′S, 171°35′E] 14.i.1983, J. W. Early, moss from stones on bush floor, LCNZ 83/3' (LUNZ).

Paratypes. **New Zealand: South Island. WD**, 2, same data as Holotype (LUNZ, NZAC).

Associated larvae. **New Zealand: South Island. WD**, 1 (slide mounted), Arthurs Pass Natl Pk, Kellys Ck [42°59′S, 171°35′E] 18.v.1970, C. S. Horning (NZAC).

Diagnosis

Body moderately elongate, elytra ~0.95× as long as wide and 1.6× as long as the pronotum. Dorsal surfaces lacking tubercles. Pronotum with lateral rims well developed; side lacking deep notch; deep sublateral sulci present; anterior angles weakly produced forwards; four setal patches present at centre (two additional ones present posteriorly). Scutellum partially exposed. Humeral ridge of elytron short. Femur bicolored. The species is most similar to *P. carinata* (see Comments of that species).

Description

Length 3.5–3.8 mm (mean = 3.65, *n* = 2). Body ~1.59× as long as wide (BL/EW = 1.58–1.61), and greatest depth ~0.63× as

great as elytral width (GD/EW = 0.62–0.65). Colour of body dark reddish brown; lateral portions of pronotum, posterior portion of head, mouthparts, legs, and clypeus dark to yellow brown; dorsal surfaces lacking tubercles; vestiture of thick yellow setae; anterior portion of prosternum, lateral and anterior portion of hypomeron, and epipleuron covered with microtubercles. Head finely punctate. Antennomeres 3 and 4 subequal. Eye coarsely facetted, greatest length five facets, greatest width 10 facets. Pronotum ~0.7× as long as wide (PL/PW = 0.66), widest at basal 1/3; sides irregularly sinuate with two weak lateral notches with the deeper present in basal 1/2; lateral rim well developed with deep sublateral sulcus; anterior margin weakly incised with anterior angles slightly produced forwards; posterior angles slightly produced and angulate; posterior margin weakly sinuate; disc uneven, glabrous areas absent; setal patches present at anterior margin (two), centre (four plus two weaker patches posteriorly), and either side of deeper notch on lateral rim. Hypomeron with posteromesal surface glabrous and large ovate punctures absent; ventrally directed tooth present above anterior hypomeral notch; shallow posterior fovea absent. Prosternum without chin piece; width of prosternal process slightly wider than width of procoxal cavity; bead present running parallel to notosternal suture; short transverse groove at either side of anterior margin absent. Scutellum partially exposed; triangular. Elytra ~0.95× as long as wide (EL/EW = 0.95–1.00) and ~1.6× as long as pronotum (EL/PL = 1.50–1.71), widest in basal 1/3, sides converging apically; humeral ridge present, extending a short distance (1/6 length of elytron); nine round setal patches present; glabrous area present at centre of basal 1/3; width of epipleuron at level of metacoxa narrower than that of metacoxa; apical sutural flanges absent. Hind wing absent. Width of mesoventral process greater than that of mesocoxa. Abdominal process of first ventrite broad and square, width subequal to that of metacoxa. Abdominal ventrites not on different planes. Femur bicolored, basal tip dark, as is the trochanter. Penis without anterior hyaline keel; posteriorly carinate (carina rather narrow), with dorsal edge evenly narrowed towards rounded apex. Paramere 1.5× longer than wide with many apical setae.

Remarks

The species is known only from Arthur's Pass in the South Island. The aedeagus of the dissected male appears to be deformed and when additional specimens are collected the structure of the anterior portion of the structure needs to be described. The gut of one adult specimen contained unidentified matter and one short strand of sooty mould (?) fungal hyphae. The species name is a patronym for John Early, collector of the species and in recognition for his contributions to New Zealand entomology.

Distribution

South Island, Westland near Arthur's Pass.

Priasilpha embersoni, sp. nov.

(Figs 20, 46, 47, 95)

Material examined

Holotype. ♂, 'Paparoa Range, Moonlight V track, 600 m [42°04′S, 171°34′E] 14.xi 1997, R. M. Emberson, ex litter from *Nothofagus fusca*/*Dacrydium* forest' (LUNZ).

Paratype. **New Zealand: South Island. BR**, 1, Fletchers Ck, 6 km SW of Rotokoku [41°59′S, 171°50′E] 25.i.1972, J. McBurney, litter 72/84, Beech Forest Utilisation Project (NZAC).

Diagnosis

Body oval, elytra ~0.6× as long as wide and 1.7× as long as the pronotum. Dorsal surfaces lacking tubercles. Pronotum with lateral rims well developed; side with one notch; deep sublateral sulci present; anterior angles weakly produced forwards; four setal patches present at centre. Scutellum partially exposed. Humeral ridge of elytron short. Femur bicolored. This species is most similar to *P. bufonia* (both being rather convex with an oval to round body outline), but can be distinguished from it by many characters, including the short humeral ridge and bicolored femur.

Description

Length 3.5 mm (n = 2). Body ~1.5× as long as wide (BL/EW = 1.52), and greatest depth 0.5× as great as elytral width (GD/EW = 0.52). Colour of body red to dark brown; anterior portion of head, mouthparts, legs, and clypeus dark red to light brown; ventral portions darker; dorsal surfaces lacking tubercles; vestiture of thick yellow setae; anterior portion of prosternum, lateral and anterior portion of hypomeron, and epipleuron covered with microtubercles. Head finely and densely punctate anteriorly and coarsely punctate at vertex. Antennomere 3 longer than 4. Eye coarsely facetted, greatest length five facets, greatest width 10 facets. Pronotum ~0.6× as long as wide (PL/PW = 0.59), widest at basal 1/3; sides broadly, irregularly sinuate, lateral notch present at middle; lateral rim well developed with deep sublateral sulcus; anterior margin weakly incised with anterior angles slightly produced forwards; posterior angles slightly rounded; posterior margin sinuate; disc uneven, two glabrous areas present in anterior half; setal patches present at anterior margin (two, weakly produced), centre (four), and either side of notch on lateral rim. Hypomeron with posteromesal surface glabrous and large ovate punctures absent; ventrally directed tooth present above anterior hypomeral notch, well or poorly developed; shallow posterior fovea absent. Prosternum without chin piece; width of prosternal process subequal to width of procoxal cavity; bead present running parallel to notosternal suture; short transverse groove at either side of anterior margin present. Scutellum partially exposed; triangular. Elytra ~0.96× as long as wide (EL/EW = 0.96) and ~1.7× as long as pronotum (EL/PL = 1.69), widest in basal 1/2; sides converg-

ing apically; humeral ridge present, extending a short distance (1/6 length of elytron); 4–6 round setal patches present, with central-most linear, posterior and lateral ones reduced and sometimes diffuse; glabrous areas present; width of epipleuron at level of metacoxa narrower than that of metacoxa; apical sutural flanges absent. Hind wing absent. Width of mesoventral process greater than that of mesocoxa. Abdominal process of first ventrite broad and square, width greater than that of metacoxa. Abdominal ventrites not on different plane. Femur bicolored, basal third dark. Penis with anterior hyaline keel and lateral rim extending to basal 1/3; posteriorly acarinate, with dorsal edge narrowed obliquely, apex acute. Paramere 3× longer than wide with few apical setae.

Remarks

The species is known only from the Buller area in the South Island. The gut of one adult specimen contained unidentified matter and unidentified fungal hyphae (not sooty mould). The species name is a patronym for Rowan Emberson, collector of the species and for his contributions to New Zealand zoology.

Distribution

South Island, Buller region.

Priasilpha obscura Broun

(Figs 1, 15, 48–52, 63, 80–83, 95, 97–110)

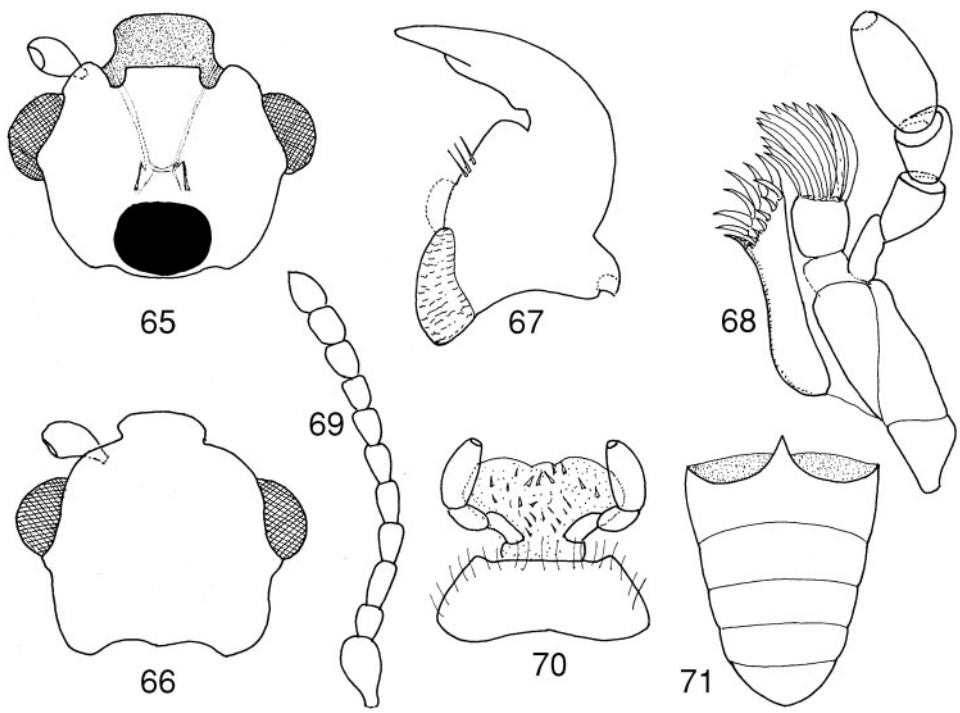
Priasilpha obscura Broun, 1893: 1078. Type locality: Mount Cook, New Zealand. Type with following labels: 1, Type [round label with red border]/1920./ Hermitage Mt Cook./New Zealand Broun Coll. Brit. Mus. 1922–482./Priasilpha obscura (NHML).

Diagnosis

Body elongate, elytra ~1.78× as long as wide and 2.6× as long as the pronotum. Dorsal surfaces lacking tubercles. Pronotum without lateral rims, sulci, and notches; anterior angles weakly produced; two setal patches present at centre (an additional two may be present). Scutellum fully exposed. Humeral ridge of elytron absent. Femur unicolored. This is the only winged species of the genus known, and associated with flight-capability are several easily recognisable characters that are useful for identification, such as the apically widened elytral sutural flange.

Redescription

Length 4.1–4.8 mm (mean = 4.43, n = 10). Body ~1.94× as long as wide (BL/EW = 1.75–2.04), and greatest depth ~0.64× as great as elytral width (GD/EW = 0.59–0.69). Colour of body dark or red brown to black; anterior portion of head, mouthparts, tibiae, and clypeus dark to light brown; dorsal surfaces lacking tubercles; vestiture of thick yellow setae; anterior portion of prosternum, lateral and anterior

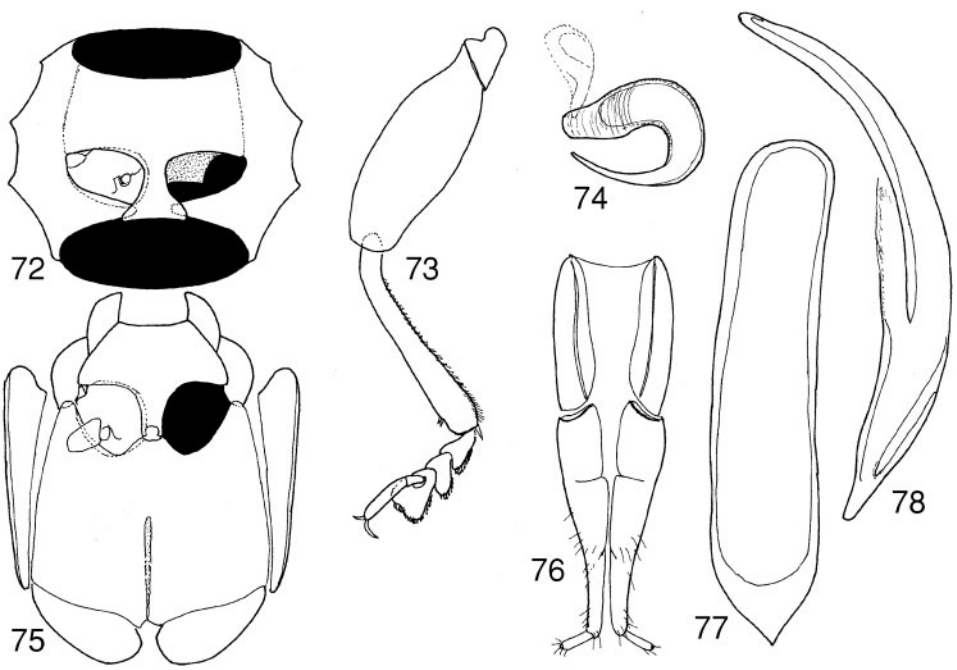


Figs 65–71. Adult characters of *Bunyastichus monteithi*, sp. nov. *65*, Ventral view of head; *66*, same, dorsal view; *67*, dorsal view of left mandible; *68*, ventral view of right maxilla; *69*, antenna; *70*, ventral view of labium; *71*, ventral view of abdomen.

portion of hypomeron, and epipleuron covered with microtubercles. Head finely punctate anteriorly, coarsely posteriorly. Antennomere 3 slightly longer than 4. Eye finely facetted, greatest length 10 facets, greatest width 13 facets. Pronotum ~0.6× as long as wide (PL/PW = 0.5–67), widest at basal 1/3; sides broadly, irregularly sinuate, lateral notch absent; lateral rim and deep sublateral sulcus absent; anterior margin weakly incised with weak anterior angles; posterior angles slightly angulate; posterior margin sinuate; disc uneven, glabrous areas absent; setal patches present at anterior margin at centre (four, two posterior ones absent in many specimens, and all four rarely absent). Hypomeron with posteromesal surface tuberculate and with large ovate punctures; anteriorly directed tooth present above anterior hypomeral notch; shallow posterior fovea present. Prosternum with weak chinpiece; width of prosternal process subequal to width of procoxal cavity; bead present running parallel to notosternal suture; short transverse groove at either side of anterior margin absent. Scutellum fully exposed; rounded and transverse. Elytra ~1.41× as long as wide (EL/EW = 1.25–1.65) and ~2.6× as long as pronotum (EL/PL = 2.38–3.00), widest at basal 1/3, sides converging apically; humeral ridge absent; up to 11 round setal patches present, may be reduced in number in many specimens and rarely completely absent; glabrous areas absent; width of epipleuron at level of metacoxa much narrower than that of metacoxa; apical sutural flanges present. Hind wing present. Width of mesoventral process narrower than that of mesocoxa. Abdominal process of first ventrite apically convex, width less than that of metacoxa. Abdominal ventrites on same plane. Femur unicolored. Penis without anterior hyaline keel and with lateral rim extending to base; posteriorly carinate (carina narrow), with dorsal edge evenly narrowed and tapering to pointed apex. Paramere 3× longer than wide with few apical setae.

Records

New Zealand. North Island: BP, 1, Whinray SR, 7 km N of Motu, 38°14′S, 177°33′E, 28.xi.1997, M-C. Lariviere & A. Larochelle, litter 97/14 (NZAC); 1, Mamaku Ra., Rotorua, 38°06′S, 176°05′E, 18.i.1972, G. W. Ramsay, litter (NZAC); 1, Opotiki, 38°00′S, 177°17′E, 7.xii.1912, T. Broun Collection (NZAC); 4, Upper Kaimai, 37°52′S, 175°56′E, 1.i.1931, A. E. Brookes (NZAC); 1, Upper Kaimai, 37°52′S, 175°56′E, 20.ii.1938, A. E. Brookes Collection (NZAC). **GB**, 58 (+ 14 larvae), Hikurangi Hut, 260 m, 38°17′S, 178°13′E, 4.v.1996, P. Poortman, L4459 (AMNZ); 2, Mt Maungapohatu, 762 m, 38°34′S, 177°58′E, 3.iii.1971, I. Townsend, litter (NZAC); 1 (+ 1 larva), Huiarau Ra., 914 m, 38°37′S, 177°60′E, 17.i.1972, G. W. Ramsay, litter 72/22. **RI**, 1, Mangaweka Apiti Scenic Res, 39°59′S, 175°52′E, xi.1999, G. M. Coombe, Pit trap 7.32, ha hinau, five-finger, mahoe, *Dicksonia fibrosa* forest remnant, NZMS 260 T22 593365 (AMNZ). **TK**, 2, Potaema Walk, Mt Egmont, 39°17′S, 174°04′E, 9 12 95, in leaf litter, J. T. Nunn (JNIC); 2 (+ 2 larvae), Mt Egmont, 914 m, 39°17′S, 174°04′E, 23.i.1972, litter, G. W. Ramsay, (NZAC); 8, Dawson Falls, 914 m, 39°20′S, 174°06′E, 23.i.1972, Litter 72/68, G. W. Ramsay (NZAC); 1, Wilkies Pools Track, Dawson Falls, 3200', 39°19′S, 174°06′E, 16.vi.1965, litter, J. I. Townsend (NZAC). **TO**, 1, 19 km E of Taumarunui, 701 m, 38°52′S, 175°32′E, 20.xi.1965, J. I. Townsend (NZAC); 1, Waituhi Sdl, 38°52′S, 175°32′E, 1.ix.1993, in leaf litter, J. T. Nunn (JNIC); 2, Raurimu, 39°07′S, 175°23′E, 25.xii.1940, C. E. Clark Collection (AMNZ). **WA**, 2, Waiohine Gorge, Rd end, 41°02′S, 175°24′E, 10.vi.1995, in leaf litter, J. T. Nunn (JNIC). **WN**, 2,



Figs 72–78. Adult characters of *Bunyastichus monteithi*, sp. nov. *72*, ventral view of prothorax; *73*, middle leg; *74*, spermatheca; *75*, ventral view of meso- and metaventrites; *76*; ventral view of ovipositor; *77*, ventral view of penis; *78*, lateral view of penis.

Akatarawa Rd Smt, 40°58′S, 175°06′E, 21.viii.1993, in decayed wood, J. T. Nunn (JNIC); same locality, 19.viii.1991, J. T. Nunn (NZAC); 6, Akatarawa Sdle, 600 m, 40°58′S, 175°06′E, 7.iii.1978, S. B. Peck, litter (NZAC); 1, same locality, 21.x.1990, ex leaf litter mostly *Weinmannia*, G. W. Gibb NZAC), 1, same locality, 17.i.1984, litter 5/84, H. P. McColl (NZAC); 1, Silverstream, 41°09′S, 175°01′E, 19.xi.1951, E. S. Gourlay (NZAC); 2 larvae, Haurangi, Aorangi Mts, Wellington, 670 m, 41°30′S, 175°20′E, 2.ix.1965, Litter 65/460, J. T. Townsend, (NZAC). **WO**, 1, Taumatatotara Te Anga, 38°15′S, 174°55′E, 31.x.1967, *B. tawa* & *Hedycarya*, B. M. May (NZAC). **South Island BR**, 2, Rotoiti, ~500–700 m, 41°48′S, 172° 49′E, 23–27.xii.1983, sedge tussock litter, P. M. Hammond (RALC); 1 larva, Mawhera SF, 42°27′S, 171°29′E, 10.xi.1971, Litter 71/143, J. S. Dugdale (NZAC); 3, Lake Rotoiti, nr. Paddys Hut, 900 m, 41°48′S, 172°49′E, 9.i.1993, beaten from dead *Nothofagus fusca* and *N. solandri cliffortioides* branches, J. W. M. Marris (LUNZ); 1, Upper Grey V, 370 m, 42°20′S, 171°43′E, 7.vi.1982, *Nothofagus fusca* litter, J. W. Early, LCNZ 82/14 (LUNZ); 4 larvae, Lake Rotoiti, Paddys Lookout, 2600 m, 41°48′S, 172°49′E, 12.x.1969, *Nothofagus fusca* litter, G. W. Ramsay (NZAC); 2, Lake Rotoiti, 2800′, 41°48′S, 172°49′E, 21.iii.1965, leaf litter, N. A. Walker (NZAC); 4, Maruia Springs, 2500′, 42°23′S, 172°20′E, 18.xi.1961, 61/3, G. Kuschel (NZAC); 2, Waipuna, Grey Valley, Nelson, 42°20′S, 171°43′E, 21.iv.1971, leaf litter, 71/97, J. S. Dugdale (NZAC), 2, Capleston, Inangahua V., 42°04′S, 171°55′E, 8–9.xi.1972, at light, J. S. Dugdale, Beech Forest Utilisation Project (NZAC); 2 + 58 larvae, Lake Rotoiti, 41°32′S, 172°51′E, 13.xi.1999, ex compost pile, RL467, R. Leschen & R. Hoare (NZAC); 5 larvae (3 slide mounted), Rahu Sdle, Reefton, 670 m, 42°19′S, 172°07′E, 1.vi.1965, moss, 65/334, J. I. Townsend (NZAC); 1, Rapahoe, 42°22′S, 171°15′E, 3.xi.1940, E. S. Gourlay (NZAC). **FD**, 1 larva, N. Te Anau, Southland, 45°15′S, 167°45′E, 19.ii.1965, litter, 65/47, N. A. Walker (NZAC); 2 larvae, Spey River, W. Manapouri, 180 m, 45°32′S, 167°13′E, 19.i.1970, mats, 70/61, A. C. Eyles (NZAC); 1, W. side of Mt Burns, Hunter Mts, 755 m, 45°45′S, 167°25′E, i.1979, J. I. Townsend, Manapouri Exp. (NZAC); 1, Wolfe Flat, Turret Ra, 600 m–680 m, 45°33′S, 167°18′E, i.1979, moss, J. McBurney, Manapouri Exp. (NZAC); 1, Mica Burn, 180 m–230 m, 45°31′S, 167°13′E, i.1979, beating, G. Kuschel, Manapouri Exp. (NZAC); 1, Sweep Flat, 1/2 way up to Wolfe Flat, 45°33′S, 167°18′E, i.1979, A. C. Eyles, Manapouri Exp. (NZAC); 25 + 5 larvae, Hollyford Tk, 44°42′S, 168°08′E, 22.i.1998, flood debris *Nothofagus*/coastal forest, RL109, R. Leschen & C. Carlton (NZAC); 1 larva, Waikaia River, Piano Flat, Southland, 45°33′S, 169°11′E, 16.x.1966, Black beech litter 66/370 (NZAC); 1, L. Hauroko, 46°00′S, 167°02′E, 19.ii.2003, rotting *Fomitopsis*, RL756, R. Leschen (NZAC). **MC**, 1, Sharplin Falls, Staveley, 43°39′S, 171°26′E, 25.x.1997, J. T. Nunn (JNIC); 1 larva, McLennans Bush, Canterbury, 43°34′S, 171°32′E, 28.vii.1966, litter, 66/223, A. D. Lowe (NZAC); 1, McLennans, 23.iv.1912, Broun Coll., 1922–482 (NHML); 1, Mt Hutt, 43°28′S, 171°32′E, 28.xii.1912, T. Broun Collection, A. E. Brookes Collection (NZAC); 1, Pudding Hill, 43°34′S, 171°32′E, 4.v.1912, Broun Coll., 1922–482 (NHML); 1, Puddg. (Pudding Hill), 43°34′S, 171°32′E, 4–5.xii.1920, A. E. Brookes Collection (NZAC); 1, Oakden, 43°18′S, 171°26′E, 23.ix.1913, T. Broun Collection. A. E. Brookes Collection (NZAC); 5, Wilberforce Riv., 1950', 43°14′S, 171°23′E, 15.i.1948, E. S. Gourlay (NZAC); 2, Moa, 43°05′S, 171°15′E, 20.x.1913, T. Broun Collection. A. E. Brookes Collection (NZAC). **MK**, 2, Sealy Range, Hooker Valley, Southern Alps, 43°43′S, 170°04′E, 10–15.iii.1953, A. E. Brookes Collection (NZAC). **NC**, 1 + 1 larva, 4.5 km S.E. Arthur's Pass, 725 m, 42°55′S, 171°33′E, 11.i.1998, *Nothofagus solandri* leaf litter/flood debris, RL046, R. Leschen & C. Carlton (NZAC). **NN,** 1, Abel Tasman Natl Pk, Bark Bay, 40°55′S, 173°03′E, 5.ii.1981, under bark Pinus, S. P. Worner, (LUNZ); 1, Mt Arthur, Salisbury Crossing, 3000′, 41°13′S, 174°21′E, 18.i.1943, E. S. Gourlay (NZAC); 9 + 1 larva, Oparara R., nr. Karamea, 13.iii.1939, A. E. Brookes Collection (NZAC); 1 larva, Oparara R., Karamea, 11.iii.1971, litter, 71/47, J. I. Townsend (NZAC). **OL**, 1, Mt Alfred, 44°45′S, 168°22′E, 1914, A. E. Brookes Collection (NZAC); 2, Routeburn, Otago, 44°44′S, 168°15′E, 22.iii.1943, E. Fairburn (NZAC); 4, Clippings, South Island (Bush, Kingston), 45°16′S, 168°40′E, 28.i.1914, T. Broun Collection. A. E. Brookes Collection (NZAC). **SC**, 1, Kelsey's Bush, Waimate, 700′, 44°41′S, 170°57′E, 20.i.1966, litter in forest, J. I. Townsend (NZAC). **SL**, 1, Purakaunui, nr Owaka, 46°31′S, 169°34′E, 31.xii.1995, J. T. Nunn (JNIC); 1, Cathedral Caves Rd, Catlins, 46°36′S, 169°22′E, 6.vi.1999, in forest floor litter, J. T. Nunn (JNIC); 3, Thomsons Bush, Invercargill, 46°22′S, 168°21′E, 30.vi.1997, in decayed wood, J. T. Nunn (JNIC, NZAC); 10, Wapati Beach, 38 km SW of Owaka, 46°39′S, 169°23′E, 15,19.i.1978, sifted litter and rotten wood, 78/33, 78/43, G. Kuschel (NZAC); 1, Owaka, Table Hill, 46°30′S, 169°40′E, 17.i.1978, sifted litter, rotten wood and ground plants 78/38, G. Kuschel (NZAC); 3, Mistake (probably Chaslands Mistake), 9.x.1913, T. Broun Collection, A. E. Brookes Collection (NZAC). **WD**, 2, L. Ianthe, lowland forest, 43°03′S, 170°37′E, 7.ii.1984, litter, P. M. Hammond (NZAC); 2, L. Ianthe Scenic Res, 43°03′S, 170°37′E, 29.x.1978, leaf litter, M. R. Butcher (LUNZ); 2, Westland Natl Pk, adj Canavans Knob, 140 m, 43°23′S, 170°10′E, 19.viii–12.ix.1982, malaise trap, A. B. Miller, (LUNZ); 6 + 3 larvae, Devils Punch Bowl Tr. Arthurs Pass, 2600′, 42°56′S, 171°35′E, 16.xi.1966, *Nothofagus* litter, 66/412, A.K. Walker (NZAC); 4, L. Ianthe, 43°03′S, 170°37′E, 18.i.1957, E. S. Gourlay (NZAC); 1, same locality, 7.ii.1984, fungus, 84/16, J. C. Watt & W. Pond (NZAC); 2, same locality, sifted litter and wood mould, 84/22, J. C. Watt (NZAC); 1, Franz Josef, 43°24′S, 170°11′E, 2.xi.1965, A. C. Eyles (NZAC); 1, Callery gorge, Franz Josef, 43°24′S, 170°11′E, 2.xi.1965, at night, A. C. Eyles (NZAC); 1, L. Mahinapua, Jum Michel Tk 42°47′S, 170°55′E, 12.ii.1999, berlesate leaf litter/fungusy logs, RL305, R. Leschen & R. Hoare (NZAC); 1, Cole's Flat (could be Cole Creek), 43°44′S, 169°11′E, 9.x.1938, E. S. Gourlay (NZAC). **Outlying Islands. CH**, 2, Chatham Is., 44°00′S, 176°30′, W, Broun, A. E. Brookes Collection (probably mislabelled).

Remarks

Priasilpha obscura is also very widespread in the South Island and known as far north as Lake Waikaramoana in the central North Island. A slide mounted adult specimen had sooty mould spores contained within the debris in its body, and some contained within the hypomeral fovea. A single larva collected from Arthur's Pass had a gut filled with undetermined material and a few fungal spores. A selection of four larvae from a series collected at Lake Rotoiti had guts that were filled with undetermined material and spores (mainly of sooty moulds) and debris affixed to their bodies was mostly unrecognisable material and sooty mould spores. This species was described by Broun (1893) who was 'indebted to Mr. H. Suter for a good series of this curious insect'. We could only locate one definitive specimen from the type locality, Mount Cook, although five additional specimens were also in the Broun collection (NHML).

Distribution

Widespread from the central portion of the North Island and most of the South Island .

Genus *Priastichus* Crowson

(Figs 2, 22, 23, 53–61, 79, 87–94)

Priastichus Crowson, 1973: 56. Type species, by original designation, *P. tasmanicus* Crowson.

Diagnosis

Priastichus species differ from *Chileosilpha elguetai* in lacking a chin piece and having narrowly open procoxal cavities, a broader abdominal intercoxal process and 5–5–4 tarsi in the male. The genus differs from *Priasilpha* in having the prothorax less narrowed anteriorly, with a straight posterior edge posterior angles more or less at right angles, abutting the elytral humeri, and the eyes more circular and more strongly projecting. The elytra are always armed with ridges or tubercles, lacking in almost all *Priasilpha* species. *Priastichus* superficially resemble some Ulodidae and Zopheridae that are similarly tuberculate and often covered in debris; however the latter groups are characterised by having 5–5–4 tarsi in both sexes and a tenebrionoid type of aedeagus.

Description

Length ~3.3–5.3 mm. Body oblong and moderately convex; ratio of body length to greatest body width 1.75 to 2.15, and ratio of greatest depth to body width 0.64–0.78. Upper surfaces shiny, punctate and clothed with short, recumbent and/or decumbent, yellow setae, sometimes forming clusters, but often obscured by exudate to which dirt and debris adhere; lower surfaces shiny and punctate or finely granulate and spiculate, clothed with short, recumbent setae. Head about as long as wide; posterior edge with pair of shallow emarginations. Eyes small, round, strongly protuberant. Frontal ridges on each side slightly elevated, barely concealing antennal insertions from above; subantennal grooves moderately well developed, extending below and behind eyes; genae slightly produced forwards, subacute to rounded. Pregular area flat or concave. Tentorial bridge without median process. Clypeal region with sides more or less parallel. Antennae with scape and pedicel subequal in length, the latter distinctly longer than antennomere 3. Pronotum strongly transverse, broadest at posterior third; sides distinctly explanate and slightly raised; anterior angles slightly produced forwards and rounded to sharply angulate; lateral carina variably undulate with finely crenulate edge; posterior angles abutting elytral humeri; posterior edge very weakly curved; disc usually evenly convex except for an anterior and posterior impression at base of explanate side, sometimes with additional weak elevations and impressions. Scutellum strongly transverse, with sides apically converging and apex broadly angulate. Elytra ~1.2–1.45× as long as wide and 1.8–2.4× as long as pronotum; sides weakly curved or subparallel, and apices broadly rounded; epipleuron extending to base of last ventrite, epipleural carina sometimes slightly explanate and elevated; disc moderately convex and bearing series of rounded or elongate tubercles, sometimes forming longitudinal ridges, broken in several places; punctation irregular; decumbent setae usually concentrated on tubercles or ridges; sutural flanges not apically widened. Prosternum in front of coxae about as long as mid length of a coxal cavity, moderately convex; not produced forwards to form chin piece; notosternal sutures complete; prosternal punctation moderately coarse, in contrast to very fine, spiculate hypomeral punctation. Prosternal process shorter than wide, sides subparallel or slightly rounded (diverging and then converging); apex truncate. Mesoventrite simple, with slightly declined procoxal rests; mesocoxal cavities separated by a distance equal to or slightly less than shortest diameter of a cavity; mesometaventral junction forming a straight line. Metaventrite short, about a third as long as wide, somewhat flattened. Metendosternite with anterior tendons widely separated on lateral arms. Hind wings absent. Legs with distinctly denticulate or spiculate surfaces; tibiae barely expanded apically, without subapical ctenidium. Abdomen with ventrites on different planes, intercoxal process on ventrite 1 broadly truncate. Tegmen with parameres short and broad, more or less parallel-sided and broadly rounded apically; anterior plate narrowly rounded to subacute. Penis with apical section distinctly shorter than basal one, slightly depressed and parallel-sided, broadly emarginate at apex, with paired, subapical, longitudinal sclerites; basal section depressed, with distinct, basal, median carina; endoskeleton consisting of pair of dorsoventrally oriented, forked processes, which may or may not meet at midline; endophallus with single, transverse, curved sclerite. Ovipositor with proximal gonocoxites subquadrate or slightly transverse, distal ones 2× as long and much narrower, pigmented except at base, with slightly subapically attached styli.

Key to species of *Priastichus*

1. Greatest width of prothorax distinctly greater than combined elytral widths (Fig. 2); sides of elytra subparallel or only slightly curved; most elytral prominences circular to oval and tuberculate; tegmen less than twice as long as wide (Fig. 58) . . . . . *P. megathorax*, sp. nov.
   Greatest width of prothorax less than combined elytral widths (Figs 22, 23); sides of elytra more strongly curved; most elytral prominences elongate and costate; tegmen more than twice as long as wide (Figs 55, 61). 2
2. Elytra shorter and broader, less than 1.33× as long as wide (Fig. 22); lateral edges of prothorax finely undulate forming variable number of weak lobes; base of tegmen subacute (Fig. 55); basal carina of penis shorter, only slightly elevated (Fig. 54); southern Tasmania. . . . . *P. crowsoni*, sp. nov.
   Elytra longer and narrower, more than 1.33× as long as wide (Fig. 23); lateral edges of prothorax even or more broadly undulate, with fewer weak lobes; base of tegmen narrowly rounded (Fig. 61); basal carina of penis longer, strongly elevated (Fig. 60); northern Tasmania . . . . . *P. tasmanicus* Crowson

Priastichus crowsoni, sp. nov.

(Figs 22, 23, 53–55, 87–94, 96)

Material examined

Holotype. ♂, '42.41 S, 146.37 E Mt. Field N. P. nr. Lake Fenton TAS, 1000m, 31 Jan. 1980, Lawrence & Weir, / Berlesate ANIC 667 litter, *Nothofagus gunni Arthrotaxis selaginoides*' (ANIC).

Paratypes. **Australia. Tasmania:** 2, no specific locality (MV); 1, Lake Dobson Road, 42°41′S, 146°37′E, 960 m, 25.ii.1980, L. Hill (ANIC); 1, Mt Wellington, 42°54′S, 147°14′E, Griffith Collection (SAM); 1, Mt Wellington, Summit, 42°54′S, 147°14′, E, H. H. Griffith, Lea 2743 (SAM).

Larval material. **Australia. Tasmania:** 3, Mt Field N. P., nr. Lake Fenton, 42.41′S, 146.37′E, 1000 m, 31.i.1980, Lawrence & Weir, ANIC Berl. 667, litter, *Nothofagus gunni*, *Arthrotaxis selaginoides* (ANIC); 4, Mt Field N. P., Wombat Moor, E. edge, 1060 m, 30.i–5.ii.1980, berlese leaf litter, A. Newton, M. Thayer (ANIC).

Diagnosis

Priastichus crowsoni is similar to *P. tasmanicus* and different from *P. megathorax* in having mainly elongate, ridge-like prominences on the elytra and in lacking the laterally expanded prothorax; it differs from *P. tasmanicus* in having shorter and broader elytra, more finely undulate lateral pronotal edges, a subacute tegminal base and shorter, less prominent basal penile carina.

Description

Length 4.2–5.3 mm. Body ~1.85× as long as wide (BL/EW = 1.91–2.09), and greatest depth ~0.66× as great as elytral width (GD/EW = 0.64–0.68). Colour dark reddish-brown above, usually lighter at sides of pronotum; under surfaces, antennae, palps and legs yellowish-brown to reddish brown. Dorsal vestiture of short recumbent or decumbent, stout, yellowish setae, those on elytral ridges usually decumbent; setae on ventral surfaces much shorter. Antennomere 3 subequal in length to 4; first club segment ~1.15× as long as wide. Pronotum ~0.63× as long as wide (PL/PW = 0.60–64); anterior angles produced, right but rounded at apex; sides diverging to posterior third, then abruptly converging, unevenly undulate forming variable number of weak lobes, with broad emargination at about middle and another before posterior angle, which is oblique. Elytra ~1.25× as long as wide (EL/EW = 1.19–1.32) and ~2.05× as long as pronotum (EL/PL = 1.94–2.15); sides weakly curved; humeri strongly developed and distinctly elevated; disc with combination of long and short ridges grading into tubercles; mesal sutural ridge broken into six short pieces and extending almost to apex; lateral ridge almost complete but very weak in places; second ridge with five short pieces, third one with four. Aedeagus as in Figs 53–55.

Distribution

South-eastern Tasmania.

Priastichus megathorax, sp. nov.

(Figs 2, 56–60, 79, 96)

Priastichus tasmanicus Lawrence & Britton, 1991: 650, figs 35.46J, 35.50B. – Lawrence & Britton, 1994: 124, figs 46J, 50B; Lawrence *et al*., 1999*a*, 1999*b*. Misidentification.

Material examined

Holotype. ♂, 'SW Tasmania, Lower Gordon R., 42.56 S 145.50 E 42.54 S, 145.54 E Howard …Hill / H.E.C. Survey, 12L.820, Feb. 1977, moss' (ANIC).

Paratypes. **Australia. Tasmania**: 1, Cradle Mountain Camp Ground, 41°35′S, 145°56′E, 880 m, Site 2, Tree 2, 14.xi.1989, pyrethrin knockdown, H. Mitchell (ANIC); 3, Lake St Clair, 42°06′S, 146.10′E, 750 m, 25–27.i.1980, ANIC Berl. 664, litter under tree ferns and *Nothofagus*, J. Lawrence, T. Weir (ANIC); 2, Lower Gordon River, 42°31′–32′ S, 145°45′–47′ E, H.E.C. Survey, 3L.60, i.1978, moss, Howard, Hill (ANIC); 6, Lower Gordon River, 42°31′–32′S, 145°45′–47′E, H.E.C. Survey, 3R.750, 19.i.1978, moss, litter, Howard, Hill (ANIC); 1, Lower Gordon River, 42°37′–38′S, 145°53′–56′E, H.E.C. Survey, 14L.2650, i.1978, moss, Howard, Hill (ANIC); 1, Lower Gordon River, 42°43′ S, 145°45′–50′E, H.E.C. Survey, 12L.1140, ii.1977, moss, Howard, Hill (ANIC); 1, Lower Gordon River, 42°43′S, 145°45′–145°50′E, H.E.C. Survey, 12L.4500, i.1977, moss, Howard, Hill (ANIC); 1, Lower Gordon River, 42°43′S 145°45′–50′, H.E.C. Survey, 2L.4350, i.1977, moss, Howard, Hill (ANIC); 1, Lower Gordon River, 42°54′–56′S, 145°50′–54′E, H.E.C. Survey, 12L.820, ii.1977, moss, Howard, Hill (ANIC); 1, Lower Gordon River, 42°48.5′S, 145°51′–54′E, H.E.C. Survey, 5R.2200, iii.1977, moss, Howard, Hill (ANIC); 1, Lower Gordon River, 42°31′–32′S, 145°45′–47′E, H.E.C. Survey, 3R.10, i.1978, litter, Howard, Hill (ANIC); 1, Lower Gordon River, 42°48.5′S, 145°51′–54′E, H.E.C. Survey, 5R.2480, iii.1977, moss, Howard, Hill (ANIC); 1, Mt Murchison, 41°50′ S, 145°37′E, 18.iv.1989, pyrethrin knockdown, P. Greenslade (ANIC); 1, Pelion Hut, 3 km S Mt Oakleigh, 41°50′ S, 146°03′E, 18–23.xi.1991, at night, I. D. Naumann (ANIC); 1, Strahan, 42°09′S, 145°19′ E, 26.xii.1953, C. Oke (MV).

Associated larvae. **Australia. Tasmania:** 2, Lake St Clair, 42°06′S, 146.10′E, 750 m, 25–27.i.1980, ANIC Berl. 664, litter under tree ferns and *Nothofagus*, J. Lawrence, T. Weir (ANIC); 1, Pelion Hut, 3 km S Mt Oakleigh, 41°50′S, 146°03′E, iv–v.1992, pyrethrin knockdown logs, P. Greenslade (ANIC).

Diagnosis

This species is easily distinguished from either *P. tasmanicus* or *P. crowsoni* by the expanded prothorax, which is wider than the combined elytra, and by the tuberculate nature of most elevations on the elytra (longitudinal ridges in the other two species). The tegmen is also shorter and broader in this species.

Description

Length 3.3–4.25 mm (mean = 3.63, *n* = 22). Body about twice as long as wide (BL/EW = 1.91–2.09), and greatest depth ~0.7× as great as elytral width (GD/EW = 0.66–0.76). Colour dark reddish-brown above, usually lighter at sides of pronotum; under surfaces, antennae, palps and legs yellowish-brown to reddish brown. Dorsal vestiture of short recumbent or decumbent, stout, yellowish setae, those on elytral tubercles usually decumbent; setae on ventral surfaces much

shorter. Antennomere 3 subequal in length to 4; first club segment ~1.25× as long as wide. Pronotum ~0.6× as long as wide (PL/PW = 0.55–0.65); anterior angles produced, right but rounded at apex; sides diverging to posterior third, then more abruptly converging, with few weak undulations and moderately deep emargination at about middle and another before posterior angle, which is more or less right. Elytra ~1.35× as long as wide (EL/EW = 1.25–1.44) and ~2.1× as long as pronotum (EL/PL = 1.82–2.45); sides subparallel anteriorly, converging apically; humeri weakly developed and slightly elevated; disc with slightly elongate tubercles and a few short ridges; in general tubercles more elevated than in other species, and lateral tubercles tend to be more elongate; sutural row contains five, second row four, third one three and lateral one four. Aedeagus as in Figs 56–58.

Distribution

Highlands of central and south-western Tasmania.

Priastichus tasmanicus Crowson

(Figs 23, 59–61, 96)

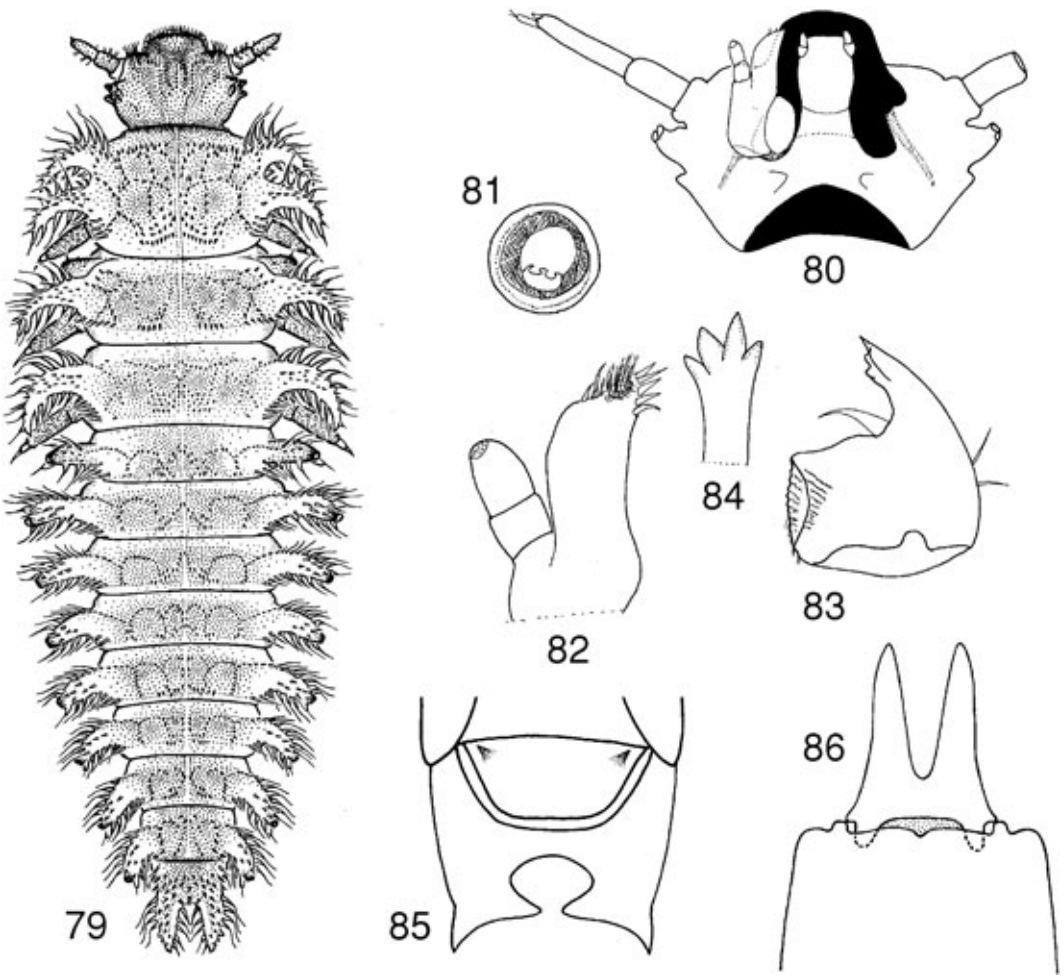
Priastichus tasmanicus Crowson, 1973: 57. Type locality: Highland of Burnie, Tasmania. Type in MCZH (?).

Records

Australia. Tasmania: 1, Ben Lomond, 41°34′S, 147°39′E, ~5000 ft, iii.1957, P. J. Darlington (paratype, female, MCZH?); 6, Cradle Mountain, 41°35′S, 145°56′E, J. W. Armstrong (ANIC); 1, Drys Bluff, 41°42′S, 146°49′E, top, 4.ix.1981, under bark, S. Fearn (ANIC); 1♀, Highland of Burnie, 41°04′S, 145°54′E, iii.1957, P. J. Darlington (holotype, female, MCZH?).

Diagnosis

Priastichus tasmanicus differs from *P. megathorax* in having the prothorax slightly narrower than the combined elytral widths and the elytral elevations weak and more or less elongate and ridge-like. It is similar to *P. crowsoni*, but differs from that species in having more elongate elytra and more broadly undulate lateral pronotal edges; in addition, the base



Figs 79–86. Larval features. *79*, *Priastichus megathorax*, sp. nov., dorsal habitus (length = 3.5 mm); *80*, *Priasilpha obscura*, ventral head capsule; *81*, same, abdominal spiracle; *82*, same, ventral view of maxilla; *83*, same, ventral view of mandible; *84*, same, inner view of incisor lobe of mandible; *85*, dorsal view of abdominal apex of *Rhinosimus* sp. (Salpingidae); *86*, ventral view of abdominal apex of larval *Litochrus* sp. (Phalacridae).

of the tegmen is narrowly rounded (rather than acute) and the penile carina is longer and more prominent.

Redescription

Length 4.1–4.9 mm (mean = 4.58; $n = 6$). Body about twice as long as wide (BL/EW = 1.95–2.11) and greatest depth ~0.72× elytral width (GD/EW = 0.68–0.75). Colour dark reddish-brown to black above, sometimes slightly lighter anteriorly; under surfaces, antennae, palps and legs yellowish-brown to reddish brown. Vestiture of short recumbent or decumbent, stout, yellowish setae, those on ventral surfaces much shorter than those above. Antennomere 3 distinctly longer than 4; first club segment ~0.8× as long as wide. Pronotum ~0.65× as long as wide (PL/PW = 0.62–0.71); anterior angles produced and sharply right-angled; sides broadly rounded and very weakly, unevenly undulate, each with broad, shallow emargination at about middle and another in front of posterior angle that is slightly obtuse; disc moderately convex and even, finely, moderately densely punctate, the punctures longitudinally or obliquely reniform. Elytra ~1.4× as long as wide (EL/EW = 1.36–1.43) and ~2.2× as long as pronotum (EL/PL = 2.07–2.31); sides weakly rounded; humeri strongly developed and distinctly elevated; disc with four weak longitudinal ridges, the first (sutural) and fourth extending almost to apex, the second extending to posterior fifth, the third to posterior fourth. Aedeagus as in Figs 59–61.

Remarks

Although Crowson (1973: 57) indicated that both female specimens (one dissected and slide mounted) were in the MCZH, these specimens cannot now be located. It is possible that they were never returned to that institution and are among Crowson's specimens maintained at the NHML.

Distribution

Northern Tasmania.

Family **PHLOEOSTICHIDAE** Reitter

(Figs 5–8, 27, 28, 66–78)

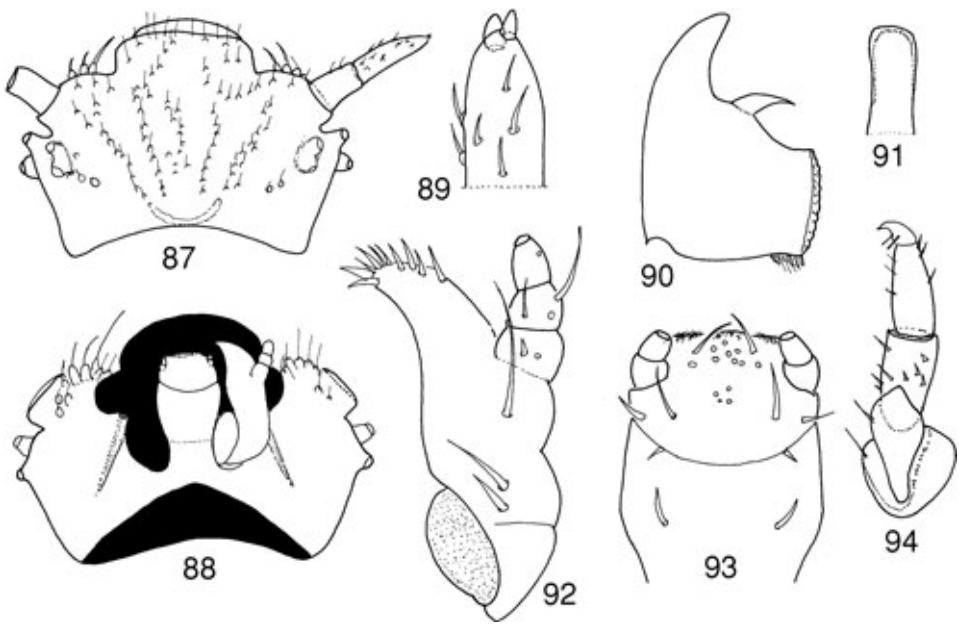
Phloeostichinae Reitter, 1911: 48 (Cucujidae). – Crowson 1955: 103 (Cucujidae).

Phloeostichidae Sen Gupta & Crowson, 1969: 578.

Hymaeinae Sen Gupta & Crowson, 1966: 77 (Boganiidae). – Sen Gupta & Crowson, 1969: 580 (Phloeostichidae); Crowson, 1973 (Phloeostichidae); Lawrence, 1995 (Phloeostichidae).

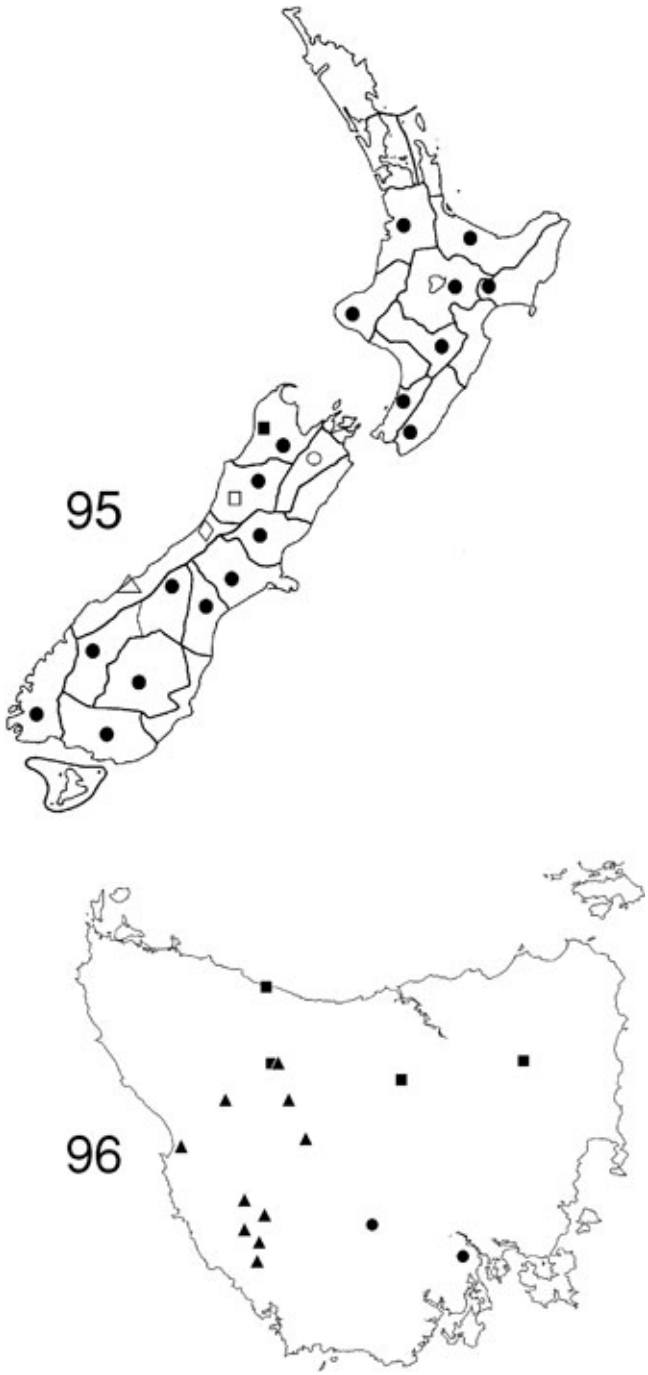
Adult diagnosis

Head with postocular constriction; without stridulatory file; frontoclypeal suture absent (except in *Bunyastichus*, gen. nov.). Antennal insertions exposed or concealed; subantennal grooves absent. Genae produced laterally. Anterior cervical sclerites contiguous with head capsule. Mandible bidentate (tridentate in *Bunyastichus*, gen. nov.), with dorsal tubercle (except in *Phloeostichus*), with dorsal glabrous cavity in *Hymaea* and *Rhopalobrachium*; mola present. Lacinia with uncus. Pronotum with lateral carinae bearing four to six sharp teeth (except in *Rhopalobrachium*). Prosternum long in front of coxae; procoxal cavities strongly transverse to almost as long as wide, with narrow lateral notch in *Hymaea*



Figs 87–94. Larval characters of *Priastichus crowsoni*, sp. nov. *87*, Dorsal view of head capsule; *88*, ventral view of head capsule; *89*, detail of left antenna; *90*, left mandible; *91*, inner view of incisor lobe of mandible; *92*, ventral view of maxilla; *93*, ventral view of submentum and labium; *94*, ventro-posterior view of leg.

and *Rhopalobrachium*, internally open, externally open (except in *Bunyastichus*, gen. nov.). Elytral punctation seriate with scutellary striole (except in *Rhopalobrachium*). Mesocoxal cavities narrowly separated, laterally open; meso-metaventral junction usually monocondylic (simple in *Bunyastichus*, gen. nov.). Metacoxae subcontiguous. Hind wing without closed radial cell; five free veins in medial field. Tarsi in male 5–5–4; penultimate tarsomere reduced and antepenultimate ventrally lobed in *Bunyastichus*, gen. nov. Ventrites usually free (first two connate in *Rhopalobrachium*). Sternite VIII in male without anterior strut; sternite IX in male with mesal lobe and spiculum gastrale (except in *Phloeostichus*). Tegmen broadly rounded anteriorly or with strut; parameres separate and articulated; penis not divided, without anterior struts, rarely with median carina.



Figs 95–96. Distribution maps. *95*, New Zealand *Priasilpha* spp. (white triangle, *P. angulata*, sp. nov.; white circle, *P. bufonia*, sp. nov.; black square, *P. carinata*, sp. nov.; white diamond, *P. earlyi*, sp. nov.; white square, *P. embersoni*, sp. nov.; black circle, *P. obscura*); 96, Tasmanian *Priastichus* spp. (black circle, *P. crowsoni*, sp. nov.; black triangle, *P. megathorax*, sp. nov.; black square, *P. tasmanicus*).

Adult description

Length ~2.4–15 mm. Body 2.35–4.0× as long as wide, narrowly oblong to elongate, usually parallel-sided, slightly to moderately convex; dorsal surfaces often with tubercles on pronotum and tubercles and/or carinae on elytra; derm more or less shiny; vestiture of fine, erect or recumbent hairs, evenly or unevenly distributed and sometimes very sparse. Head at least as long as wide (usually longer), not or only barely declined at base, but anterior portion usually bent ventrally, so that pregular region is concave and mouthparts anteroventrally oriented, postocular constriction usually present but often weak, temples well developed and abrupt or more gradual; posterior edge dorsally with pair of weak or strong incisions just above occipital foramen. Tentorial arms relatively close together, corporotentorial bridge short, narrow to moderately broad, without median process. Frontoclypeal suture indistinct or absent; clypeus extending well in front of antennal insertions, sides subparallel or with lateral emarginations; apex truncate. Eyes moderately large, prominent, moderately finely to coarsely facetted, without interfacetal setae. Antennae 11-segmented with weak 3-segmented club; exposed from above or concealed by frontal ridges; subantennal grooves absent; genae produced laterally. Gular sutures well separated; pregular region slightly concave to transversely grooved. Anterior cervical sclerites closely adpressed to head capsule, prominent or not. Labrum strongly transverse, often slightly declined. Mandible at least 1.5× as long as wide; outer edge strongly, more or less abruptly curved; dorsal surface usually with mesally directed tubercle, fitting into lateral clypeal notch, and glabrous cavity (with tubercle only in *Bunyastichus*, gen. nov. or with neither in *Phloeostichus*); apex usually bidentate (tridentate in *Bunyastichus*, gen. nov.), cutting edge sometimes with rounded or angulate projection; prostheca usually membranous and setose (reduced in *Bunyastichus*, gen. nov.); mola well developed and transversely ridged. Maxilla with galea slightly wider than to twice as wide as lacinia, which has bifid uncus; terminal maxillary palpomeres usually fusiform, occasionally expanded and truncate. Mentum slightly to strongly transverse, subtrapezoidal, with broad, shallow, apical emargination, with curved, transverse carina in *Phloeostichus*; terminal labial palpomeres cylindri-

cal to subulate, rarely expanded apically. Pronotum 0.75–1.55× as long as wide, usually longer than wide, base distinctly narrower than elytral bases (except in *Hymaea succinifera*), broadest at middle or posterior third; sides usually irregularly dentate or tuberculate; lateral carinae often absent, incomplete or vaguely defined (well developed in *Phloeostichus*); anterior angles not produced forwards; posterior angles rounded or obtuse; posterior edge straight, margined or not. Disc slightly to strongly convex, usually with tubercles and/or impressions. Scutellum usually broadly rounded or truncate posteriorly. Elytra 1.55–2.85× as long as wide and 1.7–4.35× as long as pronotum, parallel-sided, with well developed humeri and apically widened sutural flange (laterally curved with weakened humeri and no widened flange in *Hymaea succinifera*). Disc slightly convex or somewhat flattened, usually tuberculate and occasionally with short carinae; punctation usually seriate, with scutellary striole (puncture rows obscured or absent in *Rhopalobrachium*). Epipleura narrow and usually extending almost to apex. Prosternum well developed in front of coxae, distinctly longer than coxal cavity; prosternal process moderately broad, at least 0.25× as wide as mid length of coxal cavity, slightly curved behind coxae, with sides slightly to strongly expanded laterally at apex, which may be truncate or rounded. Notosternal suture complete to absent. Procoxae not projecting ventrally. Procoxal cavities strongly transverse to subcircular, with or without narrow lateral extension, internally open, externally widely open to narrowly closed; postcoxal projections of hypomera short and angulate, long and acute or rarely interlocking with lateral projections of prosternal process; trochantins exposed. Mesoventrite simple, slightly convex; with pair of weakly developed, slightly declined anterior procoxal rests. Mesocoxal cavities subovate, separated by 0.3 to more than 0.5× shortest diameter of cavity, open laterally (partly closed by mesepimera), with exposed trochantins; meso-metaventral junction usually with a single metaventral knob fitting into cavity at apex of mesoventral process (a straight line in *Phloeostichus*). Metaventrite usually slightly transverse to elongate and slightly to moderately convex, with well developed discrimen (strongly transverse without discrimen in *H. succinifera*). Exposed portion of metepisternum long and narrow, slightly widened anteriorly. Metendosternite with moderately long, broad stalk, long arms, broad or slender laminae and anterior tendons arising close together. Metacoxae strongly transverse and narrowly separated (widely separated in *H. succinifera*). Hind wing relatively long and narrow (absent in *H. succinifera*), apical field more than half total wing length, usually with long, vaguely indicated, extensions of RA and RP; with transverse sclerite just beyond radial cell in *Phloeostichus*; radial cell incomplete basally; cross-vein r3 longitudinal or absent, r4 complete, usually bisected by longitudinal sclerite; radio-medial loop forming acute angle; MP_{1+2} with short or long, slender apical extension; medial field with five free veins; medial fleck and wedge cell absent; anal notch distinct. Legs relatively long and slender; trochanterofemoral joint strongly oblique; femur weakly to strongly inflated near middle; tibia not or slightly expanded at apex, with or without apical ctenidium; mesotibia or pro- and mesotibiae sometimes with inner apical or subapical tooth in male; tibial spurs paired. Tarsi 5–5–5 in female and 5–5–4 in male; tarsomeres usually simple, with 1 longer than 2 and penultimate only slightly shorter than antepenultimate; tarsomeres 2 and 3 with ventral lobes and 4 highly reduced in *Bunyastichus*, gen. nov.; male protarsomeres 1–3 with densely pubescent ventral pads in *Rhopalobrachium*, pretarsal claws simple; empodium relatively small and usually not projecting between claws. Abdomen with five free ventrites (first three connate in *H. succinifera*), ventrite 1 not much longer than 2, without post-coxal lines; intercoxal process usually acute (truncate in *H. succinifera*); tergites I–VI lightly to moderately pigmented, VII and VIII more heavily pigmented. Abdominal spiracles: seven, first six located in pleural membrane, 7th on tergite. Sternite IX in male deeply emarginate apically, with articulated median process, basally with narrow plate or anterior strut (spiculum gastrale). Aedeagus of cucujiform type, inverted or not; basal portion of tegmen attenuate anteriorly forming narrowly rounded to subacute plate, occasionally drawn out to form anterior strut, apical portion well developed, with short, broad to moderately elongate, articulated parameres. Penis not subdivided; usually narrower and parallel-sided basally, without basal struts, broader apically and angulate to acute at apex; endophallus usually with a rod-like sclerite. Female sternite VIII with well developed spiculum ventrale. Ovipositor with gonocoxites subequal to or longer than paraprocts; proximal gonocoxite subquadrate or slightly longer than wide, distal one 2–3× as long and distinctly narrower or gradually narrowed apically, usually pigmented in apical half; styli well developed and apically attached; internal tract with spermatheca sclerotised, curved and narrowed at both ends, with attached accessory gland.

Larval diagnosis

Body elongate, parallel-sided and flattened, lightly pigmented, except for mandibles, urogomphi and sometimes part or all of tergum IX; vestiture of scattered setae. Head broad, as wide as or slightly wider than prothorax; epicranial stem absent; frontal arms lyriform, well separated at base; endocarinae absent. Stemmata: six on each side. Antennae moderately long, with antennomere 1 subquadrate or slightly longer than wide, 2 about twice as long as 1 and 3 ~0.75× as long as 2; sensorium very short, only ~0.2× as long as antennomere 3. Frontoclypeal suture absent; labrum fused to head capsule. Mandible tridentate with large tuberculate mola, accessory ventral process, and acute prostheca. Ventral mouthparts strongly retracted; maxillary articulating area well developed; mala with acute inner apical angle; palp

3-segmented. Labial palps 2-segmented, separated by more than width of first palpomere; ligula well developed, rounded or truncate. Hypopharyngeal sclerome a transverse bar. Hypostomal rods diverging; ventral epicranial ridges absent; gula wider than long. Legs widely separated; pretarsus with two setae. Abdominal terga and sterna I–VII each bearing a pair of curved rows of asperities in *Hymaea* and *Rhopalobrachium*. Tergum IX slightly shorter than VIII, moderately heavily pigmented with four small plates at anterior edge in *Hymaea*; with two small pigmented plates between urogomphi in *Rhopalobrachium*, and with small pit between urogomphi in *Phloeostichus*; urogomphi long, widely separated, subparallel or slightly inwardly curved, upturned at apex, occasionally with small tubercles near base. Sternum IX well developed, ventral. Spiracles annular–biforous, not at ends of spiracular tubes.

Constitution, geographical distribution and biological notes

As here constituted, the family Phloeostichidae contains four genera and eight species that may be distinguished using the key below. *Phloeostichus denticollis* is a rare species in central Europe (Vogt 1967) and has also been recorded from the Carpathian region and the Caucasus (Nikitsky 1991) and from the Sikhotealin Range in eastern Siberia (Krivolushkaya 1992). Larvae were described briefly by Weise (1897) from specimens collected in mossy bark of old maple trees (*Acer*), and larvae were collected by N. B. Nikitsky under the bark of *Acer*. The larval specimen used in the interactive key by Lawrence *et al*. (1999*a*) and the two larvae described as *P. denticollis* by Kolibáč (2003) are considered to be misidentified. *Rhopalobrachium* contains one Australian species and two more from Chile (Lawrence 1995), whereas *Hymaea* includes the wingless Tasmanian *H. succinifera* Pascoe, and two winged species from the east coast of mainland Australia. The larva of *Rhopalobrachium clavipes* Boheman was described by Sen Gupta and Crowson (1969) and Cekalovic (1976), and that of *H. magna* was described by Sen Gupta and Crowson (1966). Larvae of *Hymaea* and *Rhopalobrachium* are usually found under bark of decayed logs, but those of *Hymaea succinifera* have also been collected in the galleries of the ambrosia beetle *Platypus subgranosus* Schedl (Candy 1990). The hindgut of a dissected male specimen of *H. succinifera* was packed with very dark, elliptical fungal spores lacking an apiculus.

Key to genera and species of Phloeostichidae

1. Procoxal cavities externally closed (Fig. 72); frontoclypeal suture present; mandible with dorsal tubercle but no cavity (Fig. 67); tarsomeres 2 and 3 expanded ventrally forming setose lobes (Fig. 73); tarsomere 4, if present, highly reduced and not extending beyond apex of lobe on 3; North Queensland . . . . *Bunyastichus monteithi*, gen. nov., sp. nov.

   Procoxal cavities externally open; frontoclypeal suture absent; if mandible with dorsal tubercle, then cavity also present; tarsomeres 2 and 3 simple 2

2. Antennal insertions slightly concealed from above (Fig. 6); mandible with neither dorsal tubercle nor cavity; sides of pronotum with at least four sharp teeth; procoxal cavity without narrow lateral notch; surfaces of pronotum and elytra without tubercles or carinae; elytral epipleuron complete to apex; tarsomere 1 much shorter than 2; Europe. . . . . *Phloeostichus denticollis* Redtenbacher

   Antennal insertions exposed from above (Figs 5, 8); mandible with dorsal tubercle and cavity; sides of pronotum without or with fewer than four sharp teeth; procoxal cavity with narrow lateral notch; surfaces of pronotum and elytra more or less tuberculate or carinate; elytral epipleuron incomplete; tarsomere 1 not, or only slightly shorter than, 2; southern hemisphere 3

3. Total length greater than 5 mm; last three antennomeres distinctly elongate, at least 1.8× as long as wide; eyes relatively large, more than 0.35× as long as head width behind eyes, moderately prominent and hemispherical; sides of pronotum expanded to form elongate, rounded or truncate processes; elytral punctation not distinctly seriate, puncture rows indistinct or interrupted 4

   Total length less than 4.5 mm; last three antennomeres not, or only slightly, elongate; eyes smaller, less than 0.3× as long as head width behind eyes, very prominent and elliptical; temporal regions more abruptly narrowed posteriorly or reduced; sides of pronotum simple or with three sharp teeth on each side; elytral punctation distinctly seriate. 6

4. Total length less than 7 mm; pronotum without lateral processes; procoxal cavities very narrowly open behind; metaventrite and abdomen strongly convex; elytra sparsely clothed with erect hairs only, with well developed, sharp carinae and tubercles; Eastern Australia . . . . . *Rhopalobrachium crowsoni* Lawrence

   Total length greater than 9 mm (Fig. 8); pronotum with distinct lateral processes behind middle; procoxal cavities more broadly open behind; metaventrite and abdomen slightly convex; elytra with short, decumbent hairs (sometimes in scattered patches) in addition to scattered erect hairs and with low, rounded carinae or tubercles; southern South America. 5

5. Antennomere 2 more than 2.5× as long as wide and longer than 1; antennomere 3 ~5× as long as wide; elytra densely clothed with decumbent, yellow hairs and armed with numerous small tubercles; inner edge of fore and mid tibiae in male with subapical tooth; apical maxillary palpomere in male strongly inflated and obliquely truncate . . . . . *Rhopalobrachium penai* Lawrence

   Antennomere 2 less than 1.5× as long as wide and shorter than 1; antennomere 3 ~3.5× as long as wide; elytra subglabrous (with few patches of white decumbent hairs and scattered erect hairs only) and armed with a few vaguely defined tubercles and irregular costae; inner edge of fore and mid tibiae in male with apical tooth; apical maxillary palpomere in both sexes slightly expanded apically and with straight sides . . . . . *Rhopalobrachium clavipes* Boheman

6. Pronotum more than half as long as elytra, without lateral teeth; sides of elytracurved, humeri indistinct and sutural flanges not apically widened; metaventrite strongly transverse, without discrimen; metacoxae well separated; abdominal ventrites 1–3 connate; Tasmania . . . . . *Hymaea succinifera* Pascoe

Pronotum less than half as long as elytra, with distinct lateral teeth (Fig. 5); sides of elytra subparallel, humeri distinct and sutural flanges apically widened; metaventrite not strongly transverse, with distinct discrimen; metacoxae more or less contiguous; abdominal ventrites free; mainland Australia 7

7. Pronotum with 10 tubercles (Fig. 5); elytra dark brown to black with pair of transversely oblique yellowish maculae at anterior third; antennomeres 9 and 10 transverse; length more than 3.6 mm . . . . . *Hymaea magna* Sen Gupta & Crowson

Pronotum with two tubercles; elytra yellowish-brown with four pairs of dark maculae; antennomeres 9 and 10 longer than wide; length less than 3.6 mm. . . . *Hymaea parallela* Carter

Genus *Bunyastichus*, gen. nov.

(Figs 7, 27, 28, 64–78)

Type species: *B. monteithi*, sp. nov.

Diagnosis

This genus may be distinguished from all other Phloeostichidae by the externally closed procoxal cavities, mandible with a dorsal tubercle but no associated cavity, and distinctive tarsi with tarsomeres 2 and 3 expanded and setose and tarsomere 4 reduced. *Bunyastichus* superficially resembles some brontine Silvanidae, but differs from them in having 5–5–4 tarsi in the male, externally closed procoxal cavities, apically widened elytral sutural flange, and a dorsal mandibular tubercle.

Description

Length ~2.4–2.7 mm. Body elongate, more or less parallel-sided, and somewhat flattened. Upper surfaces clothed with suberect or slightly recurved, fine, hairs. Head slightly longer than wide, posterior edge dorsally with pair of deep incisions. Vertex with very weak transverse impression just behind eyes, extending ventrally on each side to meet maxillary articulations. Eyes strongly protuberant, subcircular. Antennae with scape only slightly longer than wide and slightly longer than pedicel that is shorter than antennomere 3. Frontoclypeal suture slightly impressed and slightly curved; clypeus slightly transverse, sides notched for reception of mandibular tubercles, apex subtruncate. Gula short, ending well behind eyes; pregular area flat, except for transverse groove at base of strongly transverse submentum. Corporotentorial bridge slender and arched, without median process. Mandible ~1.5× as long as wide, outer edge strongly and more or less evenly curved and apex obliquely tridentate; dorsal surface with mesally directed tubercle, broadly concave between tubercle and mola but without distinct cavity; mesal edge produced to form rounded lobe and prostheca reduced to short membrane and few setae between lobe and mola; molar surface transversely ridged. Apical maxillary and labial palpomeres elongate, subulate; mesal edge of lacinia with three adjacent, stout setae at apical third, having the appearance of a second uncus. Pronotum ~0.9× as long as wide, widest at middle; sides distinctly emarginate forming three sharp teeth, a smaller one at anterior angle and two larger ones at apical and basal third; lateral carinae complete but barely visible for their entire lengths from above, without marginal bead; anterior angles not produced forwards; posterior angles slightly obtuse; posterior edge straight, simple, without marginal bead; disc more or less evenly convex. Scutellum slightly transverse, weakly elevated basally, rounded laterally and obtusely angulate posteriorly. Elytra ~1.9× as long as wide and 2.7× as long as pronotum; humeri well developed; surface even, except for slight transverse impression at basal third; punctation seriate, with scutellary striole and 11 more or less complete puncture rows, epipleura narrow, ending before apex. Prosternum in front of coxae slightly longer than mid length of a coxal cavity, moderately convex; anterior edge simple; notosternal sutures complete. Prosternal process slightly narrowed to middle, then expanded to apex, which is subtruncate, ~0.25× as wide at middle as mid length of coxal cavity, distinctly arched. Procoxal cavities broadly closed externally by notal projections extending over and fitting into concavities in lateral expansions of prosternal process. Mesoventrite transverse and slightly convex, simple, with anterior pair of narrow, slightly declined procoxal rests. Mesocoxal cavities separated by ~0.3× shortest diameter of a mesocoxal cavity. Meso-metaventral junction complex, with single metaventral knob fitting into cavity at apex of mesoventral process. Metaventrite about two-thirds as long as wide, moderately convex; discrimen about half as long as mid length of ventrite. Exposed portion of mesepisternum ~4.5× as long as wide, tapering posteriorly to a point. Metacoxae narrowly separated, laterally extending almost to elytral epimera. Hind wing ~3.5× as long as wide; apical field more than half as long as total wing length, without sclerotisations but with two long, vaguely defined radial extensions; radial cell incomplete (basally open); cross-vein r3 absent, r4 complete and basal portion of RP short; medial field with five free veins; anal notch present. Legs simple; femora and tibiae subequal in length; tibial apices with well developed ctenidium and paired tibial spurs; mesotibial apex in with mesal tooth between tibial spurs; tarsi 5–5–5 in female, 5–5–4 in male; tarsomere 1 distinctly longer than 2; 2 and 3 with well developed ventral lobes; 4 highly reduced (absent in male); terminal tarsomere as long as 2 and 3 combined; pretarsal claws slightly enlarged basally; empodium not obvious. Abdomen with intercoxal process narrowly acute; ventrite 1 only slightly longer than 2; laterosternites sharply delimited; first six spiracles in pleural membrane, 7th at edge of tergite; tergite VIII in male enlarged and well sclerotised; sternite VIII much shorter and strongly tranverse; tergites IX and X membranous; spiculum gastrale well developed, slightly asymmetrical. Tegmen inverted, with parameres ventral to penis and anterior strut dorsal; parameres ~3.5× as long as wide, slightly narrowed and rounded apically with long ter-

minal seta and several shorter setae; anterior plate strongly narrowed forming short strut. Penis ~4.8× as long as wide, strongly curved, not divided into basal and apical sclerites; slightly expanded subapically and abruptly narrowed and angulate at apex; base broadly rounded, without struts; paired oblique internal sclerites between middle and apex. Ovipositor ~4.5× as long as wide and about as long as ventrites 3–5 combined; combined gonocoxites ~1.75× as long as paraprocts, proximal gonocoxite slightly longer than wide, lightly sclerotised, distal one ~2.7× as long, narrowed apically and slightly darker on apical half; styli well developed, apically attached; internal tract expanded apically to form bursa; spermatheca sclerotised, curved, narrowed at each end.

Bunyastichus monteithi, sp. nov.

(Figs 7, 27, 28, 64–78)

Material examined

Holotype. ♂, **'**QLD: 16°35′S, 145°16′E Upper Leichhardt Creek upper 28 May 2003, G. B. Monteith, Pyrethrum on Bunya Pine trunks 11311' (QM).

Paratypes. **Australia**. **Queensland:** 2 ♀, same data as holotype (QM, ANIC); 3 ♀, same locality, 18.xii.1997, G. B. Montieth, 11311 (QM, ANIC).

Description

With the characters of the genus. TL = 2.45–2.7 mm; BL/EW = 2.61–2.74; PL/PW = 0.85–0.92; EL/EW = 1.87–1.96; EL/PL = 2.42–2.53; GD/EW = 0.57–0.58. Colour yellowish-brown; elytra darker along suture. Dorsal surfaces smooth and shiny, clothed with moderately long, decumbent or suberect yellow hairs, ventral surfaces clothed with short, recumbent hairs. Punctation moderately coarse and dense. Aedeagus as in Figs 27, 28, 77, 78. Ovipositor as in Fig. 76.

Distribution

Known only from the type locality in northern Queensland.

Family **AGAPYTHIDAE** Sen Gupta & Crowson

(Fig. 4)

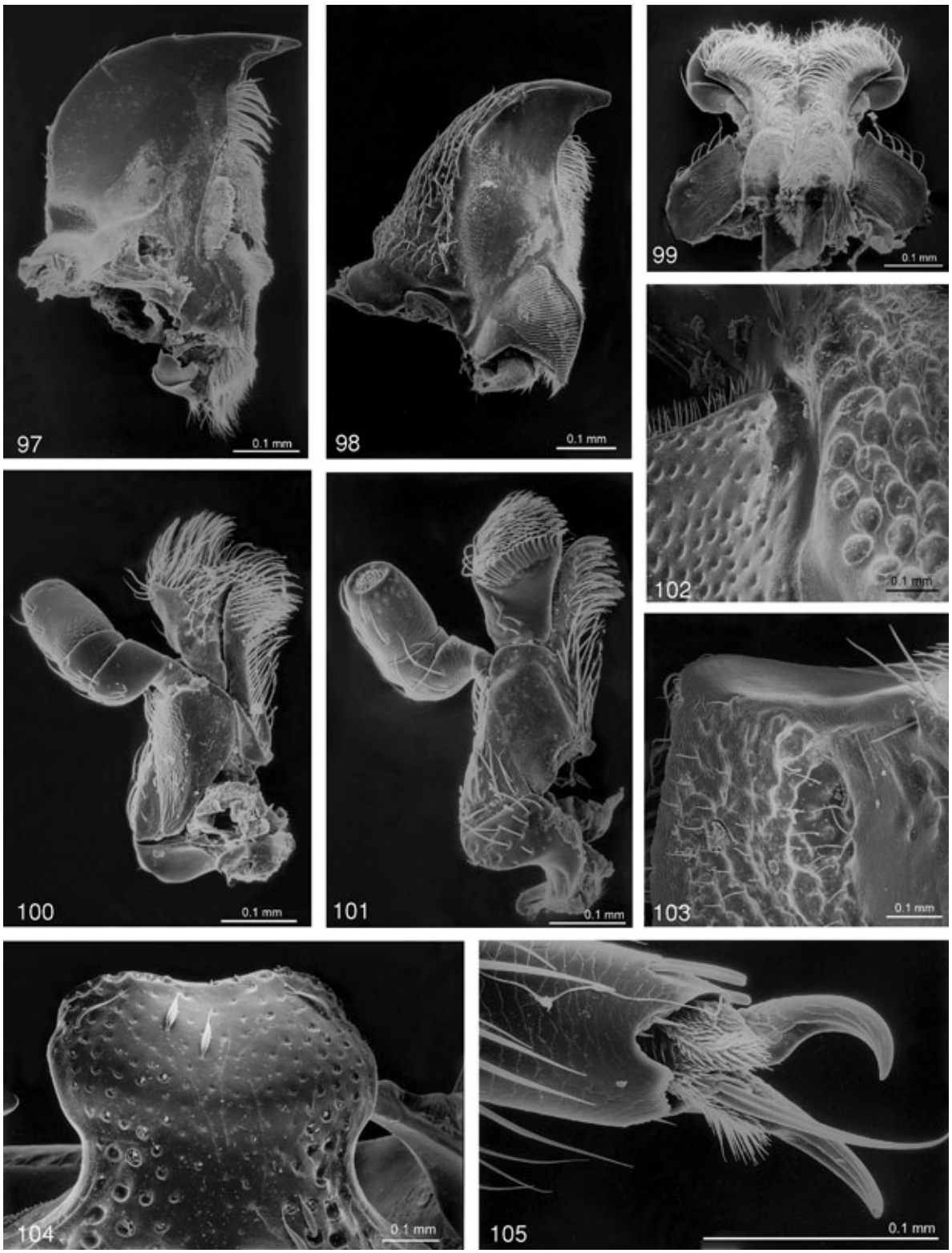
Agapythinae Sen Gupta & Crowson, 1969: 579 (Phloeostichidae).

Adult diagnosis

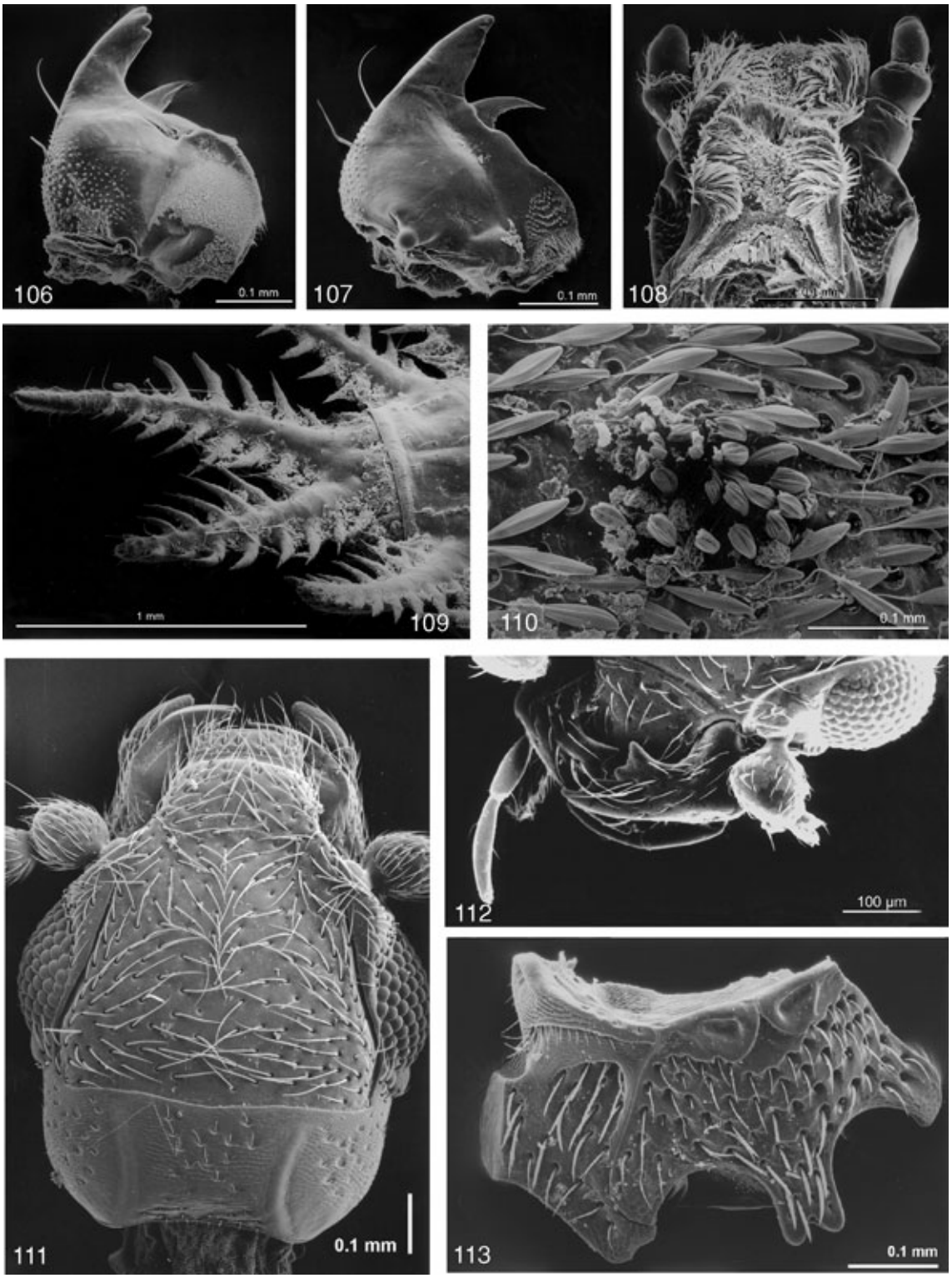
Head with postocular constriction, without stridulatory file. Antennal insertions concealed; subantennal grooves absent. Genae not projecting. Anterior cervical sclerites contiguous with head capsule. Mandible bidentate, without dorsal tubercle or cavity; mola present. Lacinia with uncus. Sides of pronotum simple, without lateral carinae. Prosternum long before coxae; prosternal process expanded laterally at apex; procoxal cavities slightly transverse, internally and externally open, without narrow lateral extensions; trochantin exposed. Elytral punctation neither seriate nor striate; sutural flange apically widened. Mesocoxal cavities narrowly separated, laterally open; meso-metaventral junction monocondylic. Metacoxae subcontiguous. Hind wing without closed radial cell; five free veins in median field. Male tarsi 5–5–4; tarsi simple. Ventrites free; intercoxal process acute. Sternite VIII in male without anterior strut; sternite IX in male with spiculum gastrale but no mesal lobe. Base of tegmen rounded; parameres fused into single piece and fused to phallobase. Penis divided into two sections, without anterior struts or carina.

Adult description

Length 2.3–3.0 mm. Body 2.5–2.7× as long as wide, more or less parallel-sided, moderately convex; dorsal surfaces relatively smooth and even, except for a pair of oblique impressions on pronotum and elytra; vestiture of fine, recumbent hairs. Head slightly longer than wide, not or only barely declined at base, but anterior portion slightly bent ventrally, so that pregular region is concave and mouthparts anteroventrally oriented, postocular constriction moderately well developed, temples about two-thirds as long as eyes; posterior edge dorsally with pair of incisions just above occipital foramen. Tentorial arms well separated, corporotentorial bridge long, slender and straight, without median process. Frontoclypeal suture absent; clypeus extending well in front of antennal insertions, sides without lateral emarginations; apex truncate. Eyes not very large, subcircular, prominent, moderately coarsely facetted, without interfacetal setae. Antennae 11-segmented with weak 3-segmented club; insertions concealed from above; subantennal grooves absent; genae not produced. Gular sutures well separated; pregular region slightly concave, with pair of curved, longitudinal grooves extending from maxillary articulations to near ends of gular sutures. Anterior cervical sclerites closely adpressed to head capsule, not prominent. Labrum strongly transverse and slightly declined. Mandible 1.5× as long as wide at base, abruptly bent mesally, without dorsal tubercle or cavity; apex bidentate, cutting edge simple or slightly angulate; mola well developed and transversely ridged; prostheca consisting of small apical tuft of setae and narrow membrane. Maxilla with galea about twice as wide as lacinia, which has bifid uncus; terminal maxillary palpomere ~2.5× as long as wide, widest near base. Mentum strongly transverse; apical labial palpomere ~1.5× as long as wide, slightly expanded and truncate apically. Pronotum 0.93–1× as long as wide, base distinctly narrower than elytral bases; sides more or less swollen at middle; lateral carinae incomplete, extending to anterior edge of lateral swelling; anterior and posteriorly angles absent; posterior edge straight, with distinct margin. Disc with moderately deep, oblique impression on either side of midline at posterior third. Scutellum strongly transverse,



Figs 97–105. Adult *Priasilpha obscura* features. *97*, mandible, ventral view; *98*, same, dorsal view; *99*, dorsal view of hypopharyngeal region; *100*, dorsal view of maxilla; *101*, same, ventral view; *102*, left anterolateral corner of prosternum; *103*, fovea located in left posterior area of hypomeron; *104*, intercoxal process on ventrite 1; *105*, apical region of tarsus, ventral view.



Figs 106–113. Adult and larval characters of basal Cucujoidea. *106*, larva of *Priasilpha obscura*, dorsal view of right mandible; *107*, same, ventral view of left mandible; *108*, same, dorsal view of hypopharyngeal area; *109*, same, urogomphi; *110*, adult of *Priasilpha obscura*, view of elytral setal patch; *111*, *Loberonotha olivascens* (Broun) (Erotylidae), dorsal view of adult head; *112*, *Athertonium parvum* Crowson (Boganiidae), anterior view of head; *113*, *Leucohimatium arundinaceus* (Forskål) (Erotylidae), mesoventrite.

apically widened and broadly angulate. Elytra 1.8–1.95× as long as wide and 2.5–2.7× as long as pronotum, with well developed humeri and apically widened sutural flange. Disc slightly convex, with weak, oblique impression at basal third; punctation moderately fine, dense and confused. Epipleura narrow and incomplete. Prosternum well developed in front of coxae, about twice as long as a coxal cavity; prosternal process moderately broad, slightly curved behind coxae, with sides strongly expanded laterally at apex, which is very slightly produced and rounded at midline. Notosternal suture incomplete. Procoxae not projecting ventrally. Procoxal cavities slightly transverse, with narrow lateral extension, internally open, externally narrowly open; postcoxal projections of hypomera relatively long and acute; trochantins exposed. Mesoventrite simple, slightly convex; with pair of weakly developed, slightly declined anterior procoxal rests. Mesocoxal cavities subovate, separated by ~0.5× shortest diameter of cavity, open laterally (partly closed by mesepimera), with exposed trochantins; meso-metaventral junction complex, with a single metaventral knob fitting into cavity at apex of mesoventral process. Metaventrite usually slightly transverse slightly convex, with well developed discrimen. Exposed portion of metepisternum long and narrow, slightly widened anteriorly. Metendosternite with moderately long, broad stalk, long arms, slender laminae and anterior tendons arising close together. Metacoxae strongly transverse and separated by ~0.37× longest coxal diameter. Hind wing relatively long and narrow; apical field more than half total wing length, without sclerotisations; radial cell incomplete basally; cross-vein r3 absent, r4 complete; radiomedial loop forming acute angle; MP_{1+2} with very short apical extension; medial field with five free veins; medial fleck and wedge cell absent; anal notch distinct. Legs relatively long and slender; trochanterofemoral joint strongly oblique; femur only weakly inflated near middle; tibia not or slightly expanded at apex; tibial spurs paired. Tarsi 5–5–5 in female and 5–5–4 in male; tarsomeres simple, with 1 longer than 2 and penultimate only slightly shorter than antepenultimate; pretarsal claws simple; empodium small and not projecting between claws. Abdomen with five free ventrites, ventrite 1 not much longer than 2, without post-coxal lines; intercoxal process acute; tergites I–VI lightly pigmented, VII and VIII more heavily pigmented. Abdominal spiracles: seven, first six located in pleural membrane, 7th on tergite. Sternite IX in male apically membranous, basally with anterior strut (spiculum gastrale). Aedeagus uninverted; tegmen narrowly rounded anteriorly; parameres more or less fused together and to tegmen. Penis subdivided into short basal section, broadly rounded anteriorly, without struts, and an apical section that is twice as long, and somewhat angulate at apex; endophallus usually with at least one sclerite. Female sternite VIII with well developed spiculum ventrale. Ovipositor ~1.6× as long as wide and almost as long as ventrites 3–5 combined; combined gonocoxites ~1.4× as long as paraprocts, proximal gonocoxite shorter and more transverse, distal one one long and narrow; styli well developed, apically attached; internal tract expanded apically to form bursa; spermatheca sclerotised, c-shaped, narrowed at the distal end.

Larval diagnosis

Body elongate, parallel-sided, slightly flattened, lightly pigmented, except for head, mandibles and tips of urogomphi; vestiture of scattered, long, fine setae. Head slightly flattened, slightly emarginate posteriorly; epicranial stem absent, frontal arms more or less contiguous at base, lyriform, extending to antennal insertions; median or paired endocarinae absent. Stemmata: five on each side. Antennae moderately long; 1st antennomere short and broad, 2nd 3× as long as 1st, 3rd about two-thirds as long as 2nd, and sensorium less than half as long as 3rd. Frontoclypeal suture absent; labrum free. Mandible bidentate, with accessory ventral process, mandibular base with distinct basal and acute prostheca. Ventral mouthparts strongly retracted; maxillary articulating area well developed; apex of mala falciform; maxillary palps 3-segmented; labial palps 2-segmented, separated by more than width of first palpomere; ligula present. Hypopharyngeal slcerome molar-like. Hypostomal rods moderately long and diverging; ventral epicranial ridges absent; gula wider than long. Thoracic and abdominal terga without lateral processes; mesocoxae separated by slightly more than two diameters; number of pretarsal sertae, two. Abdominal terga without rows of asperities; tergum IX not forming articulated plate, with moderately long urogomphi, approximate basally, diverging and upcurved, with dorsal and lateral tubercle at base of each. Sternum IX exposed, posteroventrally oriented. Spiracles annular–biforous, not at ends of tubes.

Constitution, geographic distribution and biological notes

This family contains the single species *Agapytho foveicollis* Broun, which is known from the South Island of New Zealand and has been associated with ‘fumagine’ or sooty mould (Ascomycetes: Dothideales) on the bark of *Nothofagus* and a dissected female specimen contained spores of sooty mould in its hindgut. The larva has been described by Sen Gupta and Crowson (1969).

Family **MYRABOLIIDAE** Lawrence & Britton

(Fig. 9)

Myraboliinae Lawrence & Britton, 1991: 650 (Phloeostichidae).

Adult diagnosis

Head without postocular constriction, with stridulatory file. Antennal insertions exposed; subantennal grooves present. Genae projecting anteriorly, acute. Anterior cervical sclerites contiguous with head capsule. Mandible bidentate, without

dorsal tubercle or cavity; mola present. Lacinia with uncus. Sides of pronotum with finely crenulate lateral carinae. Prosternum long before coxae; prosternal process expanded laterally at apex; procoxal cavities about as long as wide, internally and externally open, with narrow lateral extensions; trochantin concealed. Elytral punctation seriate; sutural flange apically widened. Mesocoxal cavities moderately widely separated, laterally open; meso-metaventral junction monocondylic. Metacoxae subcontiguous. Hind wing without closed radial cell; four free veins in median field. Male tarsi 5–5–4; tarsi simple. Ventrites free; intercoxal process acute; ventrite 1 much longer than 2. Sternite VIII in male without anterior strut; sternite IX in male with spiculum gastrale and mesal lobe. Base of tegmen broadly truncate; parameres separate and free. Penis not divided into two sections, with anterior struts and no carina. *Myrabolia* adults resemble some silvanine Silvanidae, but may be distinguished from them by the male 5–5–4 tarsi, externally open procoxal cavities with narrow, slit-like lateral extensions, median occipital stridulatory file, apically widened elytral sutural flanges and elongate first ventrite with paired depressions in the male.

Adult description

Length 1.7–3.5 mm. Body 2.35–2.8× as long as wide, parallel-sided and strongly flattened; vestiture of fine, decumbent hairs, which are distinctly seriate on elytra. Head slightly longer than wide, neither declined at base nor bent ventrally, so that mouthparts anteriorly oriented; postocular constriction absent; posterior edge dorsally with pair of incisions just above occipital foramen; vertex with broad median stridulatory file. Tentorial arms well separated, corporotentorial bridge moderately long and narrow, slightly arched, without median process. Frontoclypeal suture absent; clypeus extending in front of antennal insertions, sides converging anteriorly; apex truncate. Eyes moderately large, transversely oval, moderately coarsely facetted, with short interfacetal setae. Antennae 11-segmented with weak 3-segmented club; insertions exposed from above; subantennal grooves well developed but not extending behind eyes; genae produced anteriorly and more or less acute. Gular sutures short and well separated; pregular region simple and flattened. Anterior cervical sclerites closely adpressed to head capsule. Labrum strongly transverse. Mandible slightly longer than wide; outer edge evenly curved; dorsal surface without tubercle or cavity; apex bidentate; cutting edge with or without small tooth; prostheca consisting of an apical dense brush of setae, a narrow setose membrane and another setal brush next to mola, which is well developed and transversely ridged and bears a basally projecting, setose lobe that is larger than the mola. Maxilla with galea about twice as wide as lacinia, which has bifid uncus; terminal maxillary palpomere about twice as long as wide, widest at about middle and truncate apically. Mentum strongly transverse; terminal labial palpomere ~1.5× as long as wide and truncate apically. Pronotum 0.72–0.93× as long as wide, not, or only slightly, narrower at base than combined elytral bases; anterior angles more or less rounded, not produced forwards; sides subparallel with complete lateral carinae that are margined and finely crenulate; posterior angles right; posterior edge bisinuate forming weak, broad mesal lobe with distinct bead. Disc very slightly convex and flattened at middle. Scutellum strongly transverse and broadly angulate apically. Elytra 1.68–1.93× as long as wide and 2.25–2.47× as long as pronotum, parallel-sided, with weak humeri and apically widened sutural flange. Disc somewhat flattened, simple; punctation distinctly seriate, with 10 rows of larger punctures separated by rows of smaller punctures, without scutellary striole. Epipleuron relatively narrow and complete to apex. Prosternum well developed in front of coxae, more than twice as long as a coxal cavity, anterior edge on each side with narrow incision between it and hypomeron; prosternal process about as wide as mid length of coxal cavity, flat, with sides expanded at apex, which is truncate. Notosternal suture incomplete anteriorly. Procoxae not projecting ventrally. Procoxal cavities about as long as wide, with narrow lateral extension, internally open, externally narrowly open; postcoxal projections of hypomera relatively long and acute; trochantins exposed. Mesoventrite simple, more or less flattened; with pair of weakly developed, slightly declined anterior procoxal rests. Mesocoxal cavities globular, separated by a distance about equal to shortest diameter of cavity, closed laterally by meeting of ventrites, trochantins concealed; meso-metaventral junction complex, with a single metaventral knob fitting into cavity at apex of mesoventral process. Metaventrite moderately long and flattened, with well developed discrimen. Exposed portion of metepisternum long and narrow, slightly widened anteriorly. Metendosternite with short, broad stalk, long arms, slender laminae and anterior tendons arising close together. Metacoxae strongly transverse and narrowly separated. Hind wing relatively long and narrow, apical field about half total wing length, without veins or sclerotisations; radial cell incomplete basally; cross-veins r3 and r4 absent; radiomedial loop forming acute angle; MP_{1+2} with short apical extension; medial field with four free veins; medial fleck and wedge cell absent; anal notch distinct. Legs relatively long and slender; trochanterofemoral joint strongly oblique; femur weakly inflated near middle; tibia not expanded at apex, without apical ctenidium; tibial spurs paired. Tarsi 5–5–5 in female and 5–5–4 in male; tarsomeres simple, with 1 subequal to or slightly shorter than 2 and penultimate only slightly shorter than antepenultimate; pretarsal claws simple; empodium relatively small and not projecting between claws. Abdomen with five free ventrites, ventrite 1 more than twice as long as 2, without post-coxal lines, with paired, setose impressions in male; intercoxal process acute;

tergites I–VI lightly pigmented, VII slightly more heavily pigmented. Abdominal spiracles: seven, first six located in pleural membrane, 7th on tergite. Sternite IX in male with articulated mesal lobe apically, basally with short anterior strut (spiculum gastrale). Aedeagus not inverted, with the parameres dorsal to the penis; basal portion of tegmen broadly truncate anteriorly, narrowed posteriorly, with short, narrow, articulated parameres. Penis not subdivided; widest at base, with short anterior struts, narrowed to acute at apex; endophallus with rod-like sclerites. Female sternite VIII with well developed spiculum ventrale. Ovipositor with combined gonocoxites slightly longer than paraprocts; proximal gonocoxites slightly longer than wide, distal ones ~1.5× as long and much narrower, pigmented on apical half; styli long and apically attached; spermatheca long, slender, curved, rounded at one end, acute at the other.

Larval diagnosis

Body flat, parallel-sided, white, with head and posteromesal portion of tergum IX yellow, mandibles, mouth frame and urogomphi brown; vestiture of scattered fine setae. Head short, broad, flattened, deeply emarginate posteriorly; epicranial stem absent; frontal arms contiguous at base, lyriform; endocarinae absent. Stemmata: two on each side. Antennae moderately long with antennomere 1 short, 2 and 3 subequal and elongate, and sensorium long but shorter than 3. Frontoclypeal suture absent; labrum free. Mandible tridentate, without accessory ventral process; mesal surface at base with three blunt, hyaline processes and an additional acute process distad of these. Ventral mouthparts somewhat retracted, with well developed articulating area; weakly falcate; maxillary palps 3-segmented. Labial palps 2-segmented, separated by more than width of first palpomere; ligula short; hypopharyngeal sclerome absent. Hypostomal rods moderately long and diverging; ventral epicranial ridges absent; gula wider than long. Legs widely separated; pretarsi with two setae. Thoracic and abdominal terga without lateral processes or dorsal asperities. Tergum IX with short, upturned, approximate and more or less parallel urogomphi. Sternum IX exposed, ventral; segment X more or less circular. Spiracles annular, not at ends of tubes.

Constitution, geographic distribution and biological notes

This family contains the single genus *Myrabolia* Reitter containing seven or eight described species occurring in the south-eastern part of Australia. Adults and also a putative larva have been collected under bark of living *Eucalyptus*.

Family **TASMOSALPINGIDAE** Lawrence & Britton

(Fig. 10)

Tasmosalpinginae Lawrence & Britton, 1991: 651 (Phloeostichidae). – Lawrence & Britton, 1994; Lawrence & Newton, 1995.

Adult diagnosis

Head without postocular constriction, with stridulatory file. Antennal insertions exposed; subantennal grooves present. Genae anteriorly projecting, acute. Anterior cervical sclerites contiguous with head capsule. Mandible tridentate, without dorsal tubercle, dorsal cavity or mola. Lacinia without uncus. Sides of pronotum simple, with distinct lateral carinae. Prosternum moderately long before coxae; prosternal process not apically expanded; procoxal cavities strongly transverse, internally closed and externally open, without narrow lateral extensions. Elytral punctation neither seriate nor striate; sutural flange apically widened. Mesocoxal cavities moderately separated, laterally open; meso-metaventral junction simple. Metacoxae widely separated. Hind wing without closed radial cell; one free vein in medial field. Male tarsi 5–5–4; tarsi simple. Ventrites free; intercoxal process broadly rounded. Sternite VIII in male without anterior strut; sternite IX in male with spiculum gastrale but no mesal lobe. Base of tegmen broadly angulate; parameres separate but fused to phallobase. Penis not divided into two sections, with anterior struts and no carina.

Adult description

Length ~1.2–2.2 mm. Body 1.95–2.05× as long as wide, broadest at posterior third of elytra, narrowest between prothorax and elytra; vestiture of fine, recumbent hairs, much shorter on elytra than on pronotum. Head slightly longer than wide, not or only barely declined at base, but anterior portion somewhat bent ventrally, so that pregular region is concave and mouthparts anteroventrally oriented, postocular constriction absent; posterior edge dorsally with pair of incisions just above occipital foramen. Tentorial arms well separated, corporotentorial bridge very narrow, straight, without median process. Frontoclypeal suture absent; clypeus extending well in front of antennal insertions, sides not clearly demarcated from genae, which lie on about the same level, and forming with genae a short, broad, flattened, truncate muzzle to which the mouthparts are attached. Eyes small, round, prominent and moderately finely facetted, without interfacetal setae. Antennae 11-segmented with weak 3-segmented club; insertions broadly exposed from above; subantennal grooves absent; genae produced anteriorly and subacute. Gular sutures short, well separated; pregular region slightly concave, in male with curved transverse groove delimiting an anterior area in the centre of which is a patch of glandular hairs. Anterior cervical sclerites closely adpressed to head capsule, located in slight emarginations, not prominent. Labrum strongly transverse. Mandible slightly longer than wide, flattened; outer edge slightly, evenly curved; dorsal surface with neither tubercle nor cavity; cutting edge with single subapical tooth; prostheca consisting of row of setae only; mola absent; base of mesal edge with short, slender, setose membranous lobe. Maxilla with galea only slightly

wider than lacinia, which lacks an uncus; terminal maxillary palpomere about twice as long as wide, widest at base, strongly narrowed and narrowly rounded at apex. Mentum slightly transverse with rounded anterior angles; terminal palpomere narrowly rounded at apex. Pronotum 0.78–0.85× as long as wide, base distinctly narrower than combined elytral bases, broadest at about middle; sides straight or very slightly curved; lateral carinae complete anteriorly and visible from above, their edges weakly crenulate, but interrupted posteriorly by pair of large, deep, laterally opening setose cavities; anterior angles produced forwards and rounded but partly obscured from above by anterior edge of pronotal disc; posterior angles slightly obtuse; posterior edge slightly curved, unmargined. Disc moderately convex and simple. Scutellum strongly transverse, broadly rounded posteriorly. Elytra 1.34–1.40× as long as wide and 2.05–2.2× as long as pronotum; sides moderately rounded, strongly convergent posteriorly, with weak humeri and apically widened sutural flange. Disc slightly convex; punctation not distinctly seriate. Epipleura narrow and extending at about middle. Prosternum well developed in front of coxae, slightly longer than coxal cavity; prosternal process almost as wide as mid length of coxal cavity, flat, with sides slightly expanded towards apex, which is emarginate. Notosternal suture complete. Procoxae not projecting ventrally. Procoxal cavities strongly transverse, without narrow lateral extensions, internally closed, externally broadly open, postcoxal projections of hypomera short and acute; trochantins exposed. Mesoventrite strongly transverse, slightly convex; with pair of weakly developed, slightly declined anterior procoxal rests. Mesocoxal cavities separated by a distance almost as great as shortest diameter of cavity, open laterally (partly closed by mesepimera); mesometaventral junction a straight line. Metaventrite strongly transverse and slightly convex, without discrimen. Exposed portion of metepisternum long and narrow, barely widened anteriorly. Metendosternite with short, broad stalk, long arms, slender laminae and anterior tendons well separated. Metacoxae strongly transverse and widely separated. Hind wing short and broad, about twice as long as wide, widest at apical third; apical field very short and without sclerotisation; radial cell; cross-veins r3 and r4, and radio-medial loop absent; medial field with a single free vein; medial fleck, wedge cell and anal notch absent. Legs relatively slender; trochanterofemoral joint oblique; femur weakly inflated; tibia not or slightly expanded at apex, without apical ctenidium; tibial spurs paired. Tarsi 5–5–5 in female and 5–5–4 in male; tarsomeres simple, with 1 longer than 2 and penultimate only slightly shorter than antepenultimate; empodium relatively small and often not projecting between claws. Abdomen with five free ventrites, ventrite 1 not much longer than 2, without post-coxal lines; intercoxal process broadly rounded; tergites I–VI lightly to moderately pigmented, VII more heavily pigmented. Abdominal spiracles well developed on segments I–V, reduced and non-functional on VI, located in pleural membrane; absent on VII. Sternite IX in male membranous apically, without articulated median process, basally with anterior strut (spiculum gastrale). Aedeagus with basal portion of tegmen broadly angulate anteriorly, apical portion well developed, with short, broad parameres, which are separate from one another but not basally articulated. Penis not subdivided; narrow and parallel-sided basally, with short basal struts, broader apically and angulate or acute at apex; endophallus usually with long, rod-like sclerite. Female sternite VIII with well developed spiculum ventrale. Ovipositor with combined gonocoxites subequal to paraprocts; proximal gonocoxite slightly longer than wide, distal one ~1.33× as long and much narrower, pigmented on apical half; styli well developed and apically attached; internal tract with strongly curved, slender, sclerotised spermatheca.

Larval diagnosis

Body flat, parallel-sided, white with yellow head and vestiture if long, fine setae. Head flattened, deeply emarginate posteriorly, with pair of short incisions above occipital foramen; frontal arms separated at base, lyriform and joined anteriorly by transverse line; paired endocarinae relatively narrowly separated. Stemmata: five with cluster of three and two behind them. Antennae relatively long, with antennomere 2 about twice as long as 1 and 3 slightly shorter than 1, with sensorium longer than 3. Frontoclypeal suture absent; labrum free. Mandible tridentate, without accessory ventral process; base with three hyaline processes. Ventral mouthparts protracted or only slightly retracted, mala blunt; maxillary articulating area absent; maxillary palps 3-segmented; labial palps 2-segmented, separated by more than width of first palpomere; ligula short; hypopharyngeal sclerome absent. Gula longer than wide. Hypostomal rods diverging; ventral epicranial ridges absent. Prothorax with ventral, longitudinal median endocarina; legs moderately widely separated; pretarsus with single seta. Tergum IX simple; segment X more or less ventrally oriented, not visible from above. Spiracles annular, not at ends of tubes.

Constitution, geographical distribution and biological notes

The single genus *Tasmosalpingus* Lea includes two described species (*T. promiscuus* Lea and *T. quadrispilotus* Lea) from Tasmania but is also known from Victoria. Adults have been collected in Malaise traps, and a putative larva was collected by pyrethrum fogging the ark of *Phyllocladus asplenifolius* (Labilladière) Hooker (Podocarpaceae). The hindgut of a dissected male was packed with fungal hyphae and possibly spores of a hyphomycete.

Key to families of Cucujoidea

The following keys include all families of Cucujoidea (*sensu stricto*, excluding Tenebrionoidea) plus some other groups that have been or may be confused with cucujoids (i.e.

Jacobsoniidae, basal or atypical Cleroidea, Tenebrionoidea with four or fewer mesotarsomeres). All non-cucujoid families have the superfamily in brackets. All other taxa that are likely to be confused with cucujoids have either a trilobate, staphylinoid or bostrichoid type of aedeagus and often have functional 8th spiracles and distinctly excavate metacoxae. Strepsiptera have been added to the larval key because of their likely confusion with some modified Cucujoidea.

Adults (larvae on p. 66)

1. Metacoxae extending laterally to meet edges of elytral epipleura; metepimeron not meeting anterior angles of ventrite 1; tarsomeres never lobed; wings never with medial fleck; procoxae nearly always transverse with broadly exposed trochantins, or if not, then tarsi 4-segmented and antennae 8-segmented with 1-segmented club; empodium usually well developed . CLEROIDEA (part)
   Metacoxae not meeting edges of elytral epipleura; metepimeron meeting anterior angle of ventrite 1; if procoxae transverse with broadly exposed trochantins, then other characters different; empodium usually absent or concealed 2

2(1). Metaventrite at least as long as prothorax and mesoventrite combined; tarsi not lobed, apical tarsomere longer than previous ones combined; lateral pronotal carinae obsolete; trochanters elongate; wings without medial fleck; abdominal segment VIII with functional spiracles . . . . . Jacobsoniidae (DERODONTOIDEA)
   Metaventrite very rarely as long as prothorax and mesoventrite combined; segment VIII without functional spiracles 3

3(2). Metaventrite with complete transverse suture; tarsi 5–5–5, without lobed segments, tarsomere 5 longer than previous ones combined; procoxae globular, their cavities externally closed behind; mesocoxal cavities laterally open; metacoxae slightly transverse, widely separated and weakly excavate. . . . . Helotidae
   Transverse suture of metaventrite incomplete or absent; with other characters different. 4

4(3). Aedeagus with tegmen incomplete, not forming ring around penis; tarsi 4–4–4 (or 3–4–4 in male), very rarely with lobed segments; antennal insertions often concealed; basal 2–4 ventrites often connate . . . . . TENEBRIONOIDEA (part)
   Aedeagus with tegmen forming ring around penis; if tarsi 4–4–4, then antennal insertions rarely concealed; all ventrites usually free 5

5(4). Tarsi 5–5–5, without lobed segments; form convex and rounded dorsally, flattened ventrally; procoxae strongly transverse, with exposed trochantins, their cavities internally closed; protibiae outwardly keeled and crenulate. . . . . Trogossitidae: Rentoniinae (CLEROIDEA)
   If tarsi so formed, then other characters different 6

6(5). Tarsi 5–5–5 at least in female; wings often with five free veins in medial field (between MP_{1+2} and anal fold); elytra often with scutellary striole; protrochantins often exposed 7
   Tarsi 4–4–4 or 3–3–3; wings rarely with five free veins in medial field; elytra very rarely with scutellary striole; protrochantins rarely exposed 39

7(6). Mesocoxal cavities laterally open (not closed by meeting of mesoventrite and metaventrite) 8
   Mesocoxal cavities laterally closed by meeting of mesoventrite and metaventrite; protrochantins very rarely exposed 32

8(7). Procoxae transverse with broadly exposed trochantins; galea very slender or absent; outer edge of protibia usually with spines or denticles; head usually with subocular antennal grooves; elytra often truncate, exposing abdominal apex (pygidium), never with scutellary striole. 9
   If procoxae transverse with exposed trochantins, then galea broad and setose and outer edge of protibial apex neither spinose nor dentate 13

9(8). Antennae 9- or 10-segmented with 1- or apparently 2-segmented club; elytra truncate, exposing at least one tergite. 10
   Antennae almost always 11-segmented; if rarely 10-segmented, then antennal club 3-segmented; elytra variable 12

10(9). Antennal club consisting of single segment that is basally glabrous and apically clothed with rings of pubescence; galea present, with few apical setae; tibial apex expanded and dentate; male tarsi 5–5–4; 7th abdominal spiracles distinct; temperate parts of northern hemisphere . . . . . Monotomidae (Rhizophaginae)
   Antennal club consisting of single, entirely pubescent segment preceded by strongly transverse, glabrous, cupule-like segment; galea absent; tibial apex narrow and simple; tarsi 5–5–5 in both sexes; 7th abdominal spiracles not distinct 11

11(10). Antennae 10-segmented; cupule relatively broad, so that club appears 2-segmented; elytra exposing pygidium only; south-east Asia . . . . . Nitidulidae (*Calonecrus*)
   Antennae 9-segmented; cupule very slender; elytra exposing three abdominal tergites; tropical Africa . . . . . Nitidulidae (*Maynipeplus*)

12(11). Galea present; antennal club weak; subocular antennal grooves weak or absent; frontoclypeal suture distinct; elytra truncate, exposing last two abdominal tergites; outer edge of protibia not dentate, with few or no spines . . . . . Kateretidae
   Galea absent; antennal club usually strong; if elytra exposing last two abdominal tergites, then subocular grooves strong. . . . . Nitidulidae

13(8). Ventrite 1 always with femoral lines; pronotum almost always with sublateral carinae; procoxal cavities transverse, closed behind, trochantins partly concealed; pregular region with pair of deep, laterally-opening pockets; outer edge of protibia dentate or spinose; wings with closed radial cell and four free veins in medial field, the anterior one running into medial fleck . . . . . Biphyllidae (major part)
   Ventrite 1 rarely with femoral lines, and if so then pronotum without sublateral carinae; pregular region never with laterally-opening pockets; outer edge of protibia rarely spinose or dentate 14

14(13). Pronotum with sublateral carinae; elytra usually with three raised, longitudinal ridges; procoxal cavities small, rounded; tarsi never with lobed segments; antennal club weak or absent . . . . . Laemophloeidae (major part)
   Pronotum rarely with sublateral carinae; if present, then, tarsi and antennae of a different type 15

15(14). Antennae 10-segmented with 1- or 2-segmented club; elytra truncate, exposing pygidium; galea slender, with few apical setae; procoxal cavities closed behind, trochantins concealed; tarsomere 1 often very small, so that tarsi

appear to be 4–4–4 or 4–4–3 (male) . . . . . Monotomidae (Monotominae part)

If antennae 10-segmented, then elytra completely concealing abdominal apex; galea broader with multisetose apex 16

16(15). Antennae 10-segmented with 1-segmented club; outer edge of protibia with stout spines; tarsi 5–5–5 in both sexes, without lobed segments; segment 1 shortest; mandible without mola; procoxae transverse, their cavities closed behind, with narrow lateral extensions; wingless species with short metaventrite and metepisterna widened posteriorly; Australia, New Zealand, New Hebrides, New Caledonia. . . . . Phycosecidae (CLEROIDEA)

Antennae not so formed; outer edge of protibia rarely spinose; mandible rarely without mola; without other characters in combination 17

17(16). Tarsomeres 2 and 3 each with membranous ventral lobe, which extends well beyond apex of tarsomere; procoxae transverse, their cavities internally and externally closed, with narrow lateral extensions partly exposing trochantins; wings with closed radial cell and four free veins in medial field (between MP_{1+2} and anal fold), the anterior one running into medial fleck . . . . . Byturidae

Tarsomeres 2 and 3 without membranous ventral lobes; wings never with vein running into medial fleck 18

18(17). Procoxal cavities rounded, trochantins completely concealed; sutural flanges of elytra not at all widened apically; tarsi 5–5–5 in both sexes; antennal club indistinct or procoxal cavities closed behind; wings without closed radial cell or medial fleck. . . . . Silvanidae (major part)

Procoxal cavities with lateral extensions at least partly exposing trochantins; without other characters in combination. 19

19(18). Mandible with dorsal tubercle and associated setose cavity; frontoclypeal suture deeply impressed; clypeus subquadrate or slightly elongate with sides emarginate basally; sutural flanges of elytra not widened apically; aedeagus without articulated parameres 20

If mandible with dorsal tubercle, then associated cavity glabrous or absent; if clypeus subquadrate with basolateral emarginations, then elytra with sutural flanges widened apically and/or aedeagus with articulated parameres 21

20(19). Frontoclypeal suture distinctly arcuate; antennal club strong, as long as previous five or six antennomeres combined, and more or less uniformly, densely clothed with setiferous punctures and sensilla, creating a matt appearance; procoxal cavities externally closed or antennae 10-segmented; tarsomeres all simple; male tarsi 5–5–4 . . . . . Sphindidae

Frontoclypeal suture not, or only slightly, arcuate; antennae 11-segmented; antennal club weak or apparently absent, its segments sparsely setose and shiny basally with sensilla concentrated at or near apex; procoxal cavities externally open; tarsomere 3 distinctly lobed below, 4 reduced and simple; tarsi 5–5–5 in both sexes; Australia and southern Africa . . . . . Boganiidae

21(19). Tarsomeres 1–3 expanded and lobed below, 4 reduced and simple; mandible without dorsal tubercle or cavity; antennal insertions concealed; procoxal cavities externally closed; elytral sutural flanges not widened apically; body elongate and parallel-sided, usually somewhat flattened; hind wing with closed radial cell and five free veins in medial field; aedeagus without articulated parameres; Chile and Australia . . . . . Protocucujidae

If tarsi with expanded basal tarsomeres and reduced tarsomere 4, then mandible with dorsal tubercle and antennal insertions exposed; elytral sutural flanges usually widened apically; if parameres not articulated, then without closed radial cell and with a single vein in medial field 22

22(21). Mandible with distinct dorsal tubercle that fits into basolateral emargination of clypeus; Chile and Australia . . . 23

Mandible without dorsal tubercle or clypeal emargination. 24

23(22). Mandible with glabrous dorsal cavity or with mesal edge produced forming rounded lobe; antennal club very weak; prothorax subquadrate to elongate, without or with weak lateral carinae but often with lateral tubercles or teeth; procoxal cavities narrowly open or narrowly closed externally; elytral sutural flanges apically widened (except in wingless species); wings, if present, with at least three free veins in medial field . . . . . Phloeostichidae (*Hymaea*, *Rhopalobrachium*, ... *Bunyastichus*)

Mandible with neither dorsal cavity nor rounded lobe on mesal edge; antennal club well developed; prothorax distinctly transverse, with complete crenulate or denticulate lateral carinae; procoxal cavities broadly open externally; elytral sutural flanges not apically widened; wings with only one free vein in medial field. . . . . Hobartiidae

24(22). Body broadly ovate, convex and glabrous; elytral sutural flanges not widened apically; epipleuron broad at base with elongate, deep cavity (often filled with solid exudate); subantennal grooves long, deep and parallel, extending well behind eyes; New Zealand . . . . . Cyclaxyridae

Body oblong to elongate; epipleuron without deep cavity; subantennal grooves usually absent or, if present, not extending behind eyes 25

25(24). Procoxal cavities externally broadly open 26

Procoxal cavities externally narrowly open or closed; southern hemisphere 29

26(25). Procoxal cavities internally closed; occiput with broad, median stridulatory file; pronotal disc with pair of posterolateral setose cavities; aedeagus with parameres less than twice as long as wide at base and not distinctly articulated; Tasmania and Victoria . . . Tasmosalpingidae

Procoxal cavities internally open; occiput without stridulatory file; pronotal disc without setose cavities; aedeagus with parameres at least twice as long as wide and distinctly articulated. 27

27(26). Tarsomere 1 much shorter than 2; labrum externally apparent; elytral sutural flange widened apically; elytral punctures seriate, with scutellary striole; central and southern Europe and Russia and Russian Far East . . . . . Phloeostichidae (*Phloeostichus*)

Tarsomere 1 at least as long as 2; labrum not externally apparent, either completely concealed beneath clypeus or with a very narrow anterior strip exposed; elytral sutural flange not widened apically; if elytral punctation seriate, scutellary striole absent. 28

28(27). Body not strongly flattened; head with oblique, raised frontal carinae; antennal club well marked; elytral punctures seriate; tarsi 5–5–5 in both sexes; mesometaventral junction between mesocoxae with single, broad, internal metaventral knob; Australia . . . . . Lamingtoniidae

Body strongly flattened; head without frontal carinae; antennal club weak or absent; elytral punctures confused; male

tarsi 5–5–4; mesometaventral junction between mesocoxae without internal knob . . . . . Cucujidae

29(26). Procoxal cavities with very narrow lateral slits, trochantins largely concealed; mandible with one or two laterally-opening internal vesicles; frons usually with a pair of deep pits, often joined by arcuate groove; procoxal cavities narrowly open; male tarsi 5–5–5; Australia, New Zealand, Brazil and Chile . . . . . Cavognathidae

If procoxal cavities with narrow lateral slits, then ventrite 1 as long as next two combined; mandible without laterally-opening vesicles; frons without deep pits or groove; male tarsi almost always 5–5–4, if 5–5–5, then procoxal cavities externally closed 29

30(29). Occiput with stridulatory file; procoxal cavities with narrow lateral slits, largely concealing trochantins; ventrite 1 at least as long as next two ventrites combined; body elongate, parallel-sided and flattened; elytral punctation distinctly seriate; parameres long and narrow; penis not divided into basal and apical sections; Australia. . . . . Myraboliidae

Occiput without stridulatory files; if protrochantins largely concealed, then then body not flattened and elytral punctation not seriate; ventrite 1 never as long as next two combined; parameres shorter and broader; penis divided into distinct basal and apical sections 31

31(30). Protrochantins fully exposed; prosternal process wider than shortest diameter of a procoxal cavity; head without postocular constriction; Australia, New Zealand and Chile. . . . . Priasilphidae

Protrochantins partly concealed; prosternal process much narrower than shortest diameter of a procoxal cavity; head with weak postocular constriction; New Zealand. . . . . Agapythidae

32(7). Elytral punctation confused, sutural flanges apically widened (except in apterous species); epipleura oblique, obsolete posteriorly; trochanters more or less elongate; ventrite 1 much longer than 2; wings never with closed radial cell or medial fleck. . . . . Cryptophagidae (major part)

Elytral sutural flanges rarely apically widened, if so then with distinct striae; if ventrite 1 much longer than 2, then other characters different. 33

33(32). Elytra truncate, exposing pygidium, which is slotted along midline; head sharply constricted behind eyes; antennae 10-segmented with 1-segmented club; galea very slender with few apical setae; procoxal cavities broadly closed behind; New Zealand. . . . . Monotomidae (*Lenax*)

Elytra not truncate, fully concealing abdomen from above; head not or weakly constricted behind eyes; galea never very slender, multisetose at apex; antennae usually 11-segmented with 3-segmented club 34

34(33). Mandible with dorsal tubercle and setose cavity; head with strongly arcuate frontoclypeal suture; male tarsi 5–5–4; antennae 10-segmented; procoxal cavities closed behind; eastern hemisphere . . . . . Sphindidae (*Aspidiphorus*)

Mandible without dorsal tubercle or cavity; frontoclypeal suture straight or absent; if male tarsi 5–5–4, then procoxal cavities open behind; antennae usually 11-segmented 35

35(34). Maxillae largely concealed by expansions of head capsule; gular sutures confluent; labrum not evident; antennae thick, with club weak or absent; sutural flanges of elytra apically widened; wings with four or five free veins in medial field (between MP_{1+2} and anal fold), medial fleck absent; radial cell often closed; male tarsi 5–5–5; form elongate, parallel-sided, usually glabrous above . . . . . Passandridae

Maxillae exposed; gular sutures not confluent; labrum usually evident; antennae usually thinner with distinct club; sutural flanges not widened apically; if wings with more than three free veins in medial field, then medial fleck present or male tarsi 5–5–4 36

36(35). Pronotum with sublateral carinae; each elytron with three raised, longitudinal ridges; male tarsi 5–5–4, without lobed tarsomeres, claws simple; antennae 11-segmented with loose, 3-segmented club; wings without closed radial cell, with 1 free vein in medial field (between MP_{1+2} and anal fold); New World and Africa . . . . . Laemophloeidae (*Lathropus* and *Carinophloeus*)

Pronotum without sublateral carinae; if male tarsi 5–5–4, then some tarsomeres lobed below or tarsal claws toothed; without other characters in combination 37

37(36). Procoxae widely separated, their cavities small and rounded, externally and internally open behind; form broadly ovate, strongly flattened; prothorax very large; elytra with raised longitudinal ridges; antennae slender, club segments elongate; male tarsi 5–5–5, without lobed tarsomeres . . . . . Propalticidae

If procoxae widely separated, then their cavities externally closed behind; if form broadly ovate, then not at all flattened; prothorax not so large; antennae thicker, club segments not elongate. 38

38(37). Form highly convex and usually glabrous above, flattened below; procoxal cavities externally open, internally closed; claws basally toothed; wings never with closed radial cell or medial fleck; mesometaventral junction between mesocoxae without internal knob; lacinia very narrow, with few apical setae; without occipital stridulatory file . . . . . Phalacridae

Form less convex dorsally, less flattened ventrally; claws rarely toothed; wings often with closed radial cell or medial fleck; lacinia broader, apically plurisetose; occiput usually with stridulatory file . . . . . Erotylidae

39(6). Tegmen not completely surrounding penis; medial fleck, if present, not bisected by vein; elytra often with scutellary striole; two or more basal ventrites often connate. . . . . TENEBRIONOIDEA

Tegmen either completely surrounding penis or rarely absent; medial fleck, if present, bisected by vein; elytra without scutellary striole; basal ventrites rarely connate 40

40(39). Procoxae with fully exposed trochantins; mesocoxal cavities not closed laterally by meeting of ventrites; galea absent; tarsi 4–4–4; elytra exposing pygidium from above or tarsomere 3 lobed beneath. 41

Protrochantins concealed; mesocoxal cavities often closed laterally by meeting of ventrites; galea present; if tarsi 4–4–4 and elytra exposing pygidium, then mesocoxal cavities closed outwardly by meeting of ventrites. . . . 42

41(40). Procoxal cavities externally closed behind; elytra truncate, not concealing pygidium from above; head without subocular grooves; tarsomeres not lobed below; form elongate, parallel-sided, flattened . . . . . Smicripidae

Procoxal cavities externally open behind; elytra not truncate, at least partly concealing pygidium from above; head with subocular antennal grooves; tarsomeres 2 and 3 lobed below; form rounded, very convex . . . . . Nitidulidae (Cybocephalinae)

42(40). Elytral sutural flanges apically widened; frontoclypeal suture present; ventrite 1 as long as 2 and 3 combined;

trochanters elongate; Afrotropical and eastern Palaearctic regions . . . . . Cryptophagidae (*Cryptafricus* and *Atomaroides*)

Elytral sutural flanges not apically widened; without other characters in combination 43

43(42). Elytra truncate exposing pygidium from above; antennae 10-segmented with 1- or 2-segmented club; male tarsi apparently 4–4–3; galea very slender with few apical setae . . . . . Monotomidae (Monotominae part)

Elytra rarely exposing pygidium, or if so then antennae different; tarsi 4–4–4 or 3–3–3 in both sexes; galea well developed. 44

44(43). Procoxal cavities broadly closed behind externally; mesocoxal cavities laterally open (not closed laterally by meeting of ventrites); pregular region with paired, laterally-opening pockets; tarsomere 2 with setose ventral lobe; body elongate and somewhat flattened; Australia . . . . . Biphyllidae (part)

If procoxal cavities closed behind, then mesocoxal cavities nearly always closed laterally by ventrites; pregular region without paired pockets 45

45(44). Form usually elongate and cylindrical, if somewhat flattened, then trochanterofemoral joint strongly oblique and trochanter sometimes partly concealed by base of femur; protibiae markedly widened and angulate at outer apex; tarsi 4–4–4, without lobed tarsomeres; antennal club usually 1-segmented; elytra with striae or rows of punctures . . . . . Bothrideridae (part)

Form never elongate and cylindrical; trochanters never strongly oblique or concealed; protibiae rarely apically widened and angled. 46

46(45). Antennae 8-segmented with 1-segmented club; antennal insertions concealed beneath sides of frons; empodium well developed, bisetose; meso- and metacoxae very narrowly separated; apterous species with very short metaventrite lacking femoral lines . . . . . Trogossitidae (*Colydiopeltis* and *Parapeltis*) . . . . . (CLEROIDEA)

Antennae, if 8-segmented and with 1-segmented club, not inserted under sides of frons; without other characters in combination. 47

47(46). Tarsi 4–4–4 48

Tarsi 3–3–3 62

48(47). Body elongate and strongly flattened; head abruptly narrowed behind eyes forming distinct temples; antennae long and filiform with scape more than 3× as long as pedicel; sides of pronotum dentate . . . . . *Uleiota* (part) Silvanidae

If body elongate and flattened, then antennae different; without other characters in combination 49

49(48). Mesocoxal cavities closed laterally by meeting of ventrites. 50

Mesocoxal cavities not closed laterally by ventrites 57

50(49). Procoxal cavities externally and internally closed 51

Procoxal cavities, if closed externally, open internally . . . 52

51(50). Head moderately large and exposed from above, more than half as wide as pronotal base; body moderately convex; antennae shorter than head width; maxilla with distinct galea and lacinia; abdomen with five pairs of spiracles; Central and South America . . . . . Endomychidae (*Acritosoma*)

Head very small and usually concealed from above, less than half as wide as pronotal base; if head exposed from above, then body strongly flattened; antennae longer than head width; maxilla with single lobe; abdomen with seven pairs of spiracles . . . . . Corylophidae (part)

52(50). Apical edge of last abdominal ventrite inflexed and lined with dorsoventrally oriented grooves, so that it appears crenulate in ventral view; spiracles on first five abdominal segments. . . . . Cerylonidae (part)

Apical edge of last abdominal ventrite smooth; spiracles on first five or seven abdominal segments. 53

53(52). Frontoclypeal suture absent; maxillary and labial palps aciculate; mesal portions of metacoxae concealed by expanded intercoxal process of ventrite 1; Nepal, India and Thailand . . . . . Cerylonidae (Loebliorylinae)

Frontoclypeal suture present; maxillary and labial palps subulate 54

54(53). Body distinctly elongate and usually subcylindrical; protibia expanded apically and spinose along outer edge; antennal club 2–3 –segmented; tarsomeres always simple . . . . . Bothrideridae (Teredinae)

If body elongate and protibia somewhat expanded, then antennal club 1-segmented 55

55(54). Procoxal cavities externally closed and internally open; tarsomere 2 never lobed below; spiracles on first seven abdominal segments . . . . . Cerylonidae (Euxestinae)

Procoxal cavities externally open and internally closed; tarsomere 2 usually more or less lobed below. 56

56(55). Frontoclypeal suture present; maxilla with distinct galea and lacinia; metaventrite often with postcoxal pits; spiracles on first five abdominal segments; head larger and not concealed by pronotum . . . . Endomychidae (major part)

Frontoclypeal suture absent; maxilla with single lobe; metaventrite never with postcoxal pits; spiracles on first seven abdominal segments; head very small and more or less concealed by pronotum . . . . . Corylophidae (Peltinodinae)

57(49). Mesoventrite, metaventrite and abdomen completely fused, without sutures or lines separating them; body flattened and disc-like; antennae 8-segmented with 4-segmented club; scutellum not visible; abdominal spiracles: five; eastern Africa. . . . . Corylophidae (Cleidostethini)

Mesoventrite, metaventrite and abdomen distinctly separated; without other characters in combination 58

58(57). Head without frontoclypeal suture; metaventrite and abdominal ventrite 1 almost always with curved femoral lines 59

Head with frontoclypeal suture; femoral lines rarely present 60

59(58). Antennae relatively short, usually not, or only slightly, longer than head width; antennal club weak, compact, shorter than preceding antennomeres combined, without vesicles; ventrites 1 and 2 more or less connate; tegmen with median posterior projection (basal lobe) lying between parameres and with articulated anterior strut (trabes); penis (sipho) slender and curved, with enlarged base and no endophallic armature . . . . . Coccinellidae

Antennae much longer than head width; antennal club strong, loosely-organised and longer than preceding antennomeres combined, with vesicles; all ventrites free; tegmen reduced, without median projection or articulated strut; penis broader with complex endophallic armature Corylophidae (minor part)

60(58). Tarsomeres simple, not lobed below; body elongate to subcylindrical; antenna 11-segmented with compact 2-segmented club; procoxal cavities externally and internally open . . . . . Bothrideridae (Xylariophilinae)

Tarsomere 2 at least slightly lobed below; if simple then antenna 10-segmented with 3-segmented club; body broadly oval, never subcylindrical 61

61 (60). Procoxal cavities externally and internally open; spiracles on first seven abdominal segments; antennae 10-segmented with 3-segmented club; tarsomere 2 not, or only slightly, lobed below; apical maxillary palpomere inflated and securiform; Southern Europe, North Africa and Asia Minor . . . . . Alexiidae

Procoxal cavities externally open and internally closed behind; spiracles on first five abdominal segments only; apical maxillary palpomere subulate . . . . . Endomychidae (part)

62(47). Metacoxae externally very small; metaventrite broadly meeting ventrite 1 laterally; gland openings along lateral edges of prothorax and elytra; antennae 9- or 10-segmented with 1-segmented club . . . . . Discolomatidae

Metacoxae larger; metaventrite not meeting ventrite 1 laterally; lateral edges of prothorax and elytra without gland openings 63

63(62). Apical edge of terminal abdominal ventrite inflexed and lined with dorsoventrally oriented grooves, so that it appears crenulate in ventral view; tarsomeres simple, not lobed below . . . . . Cerylonidae (minor part)

Apical edge of terminal abdominal ventrite smooth, if it appears as crenulate then tarsomere 2 distinctly lobed below 64

64(63). Procoxal cavities externally and internally closed; labrum laterally expanded beyond anterior angles of clypeus; lacinia vestigial; elytral punctures in rows; spiracles on first seven abdominal segments. . . . . Latridiidae (major part)

Procoxal cavities externally open 65

65(64). Procoxal cavities internally open; spiracles on first seven abdominal segments; wings absent; eyes reduced or absent. 66

Procoxal cavities internally closed; spiracles on first five abdominal segments; wings and eyes almost always well developed. 67

66(65). Protibia widened and spinose at outer apical angle; labrum not laterally expanded; Europe, North Africa and Asia Minor, widely introduced elsewhere . . . . . Bothrideridae (Anommatinae)

Protibia neither widened nor spinose at outer apex; labrum laterally expanded; Western North America . . . . . Latridiidae (*Akalyptoischion*)

67(65). Frontoclypeal suture absent; ventrites 1 and 2 connate; femoral lines present on metaventrite and abdominal ventrite 1; tegmen with median posterior projection (basal lobe) lying between parameres and with articulated anterior strut (trabes); penis (sipho) slender and curved, with enlarged base . . . . . Coccinellidae (part)

Frontoclypeal suture present; ventrites freely articulated; femoral lines rarely present; aedeagus of a different type . . . . . Endomychidae (part)

Larvae

1. Larva of triungulin type, with dorsum evenly sclerotised and bearing posteriorly-projecting spines; urogomphi absent; maxillary articulating area absent; mandible without mola; labrum usually fused to clypeus 2

Larva not of triungulin type; dorsum without strong, posteriorly-projecting spines; without other characters in combination. 6

2(1). Maxillary palps absent; abdominal segment VIII without distinct spiracles; antenna with short single segment and long terminal bristle; stemmata: 3–5. . . . . Order STREPSIPTERA

Maxillary palps distinct; abdominal segment VIII with distinct spiracles; antenna 2- or 3-segmented; stemmata variable 3

3(2). Stemmata: five or six on each side 4

Stemmata: one or two on each side. 5

4(3). Abdominal spiracles annular–biforous; ventral mouthparts slightly retracted, distance between mandibular and maxillary articulations less than width of stipes; pretarsus without adhesive organ . . . . . Passandridae (part)

Abdominal spiracles annular; ventral mouthparts strongly retracted distance between mandibular and maxillary articulations greater than width of stipes; pretarsus with adhesive organ . . Rhipiphoridae (TENEBRIONOIDEA)

5(3). Pretarsus bisetose; head with distinct coronal suture (epicranial stem); maxillary palp 3-segmented; antenna with sensorium short, attached to apex of antennomere 2 . . . . . Meloidae (TENEBRIONOIDEA)

Pretarsus unisetose; head without coronal suture; maxillary palps 2-segmented; antenna with sensorium long, attached near base of antennomere 2. . . . . Bothrideridae (part)

6(1). Larva ectoparasitic, unpigmented, fleshy; broader at middle and narrowed at either end; legs short or absent; stemmata absent; mandible without mola; maxillary articulating area obsolete; spiracles annular. 7

Larva not ectoparasitic, usually with at least head capsule pigmented; stemmata usually present; legs always well developed; without other characters in combination. . . 8

7(6). Ventral mouthparts slightly retracted, distance between mandibular and maxillary articulations less than width of stipes; hypostomal rods distinct, strongly divergent; legs distinct . . . . . Passandridae (part)

Ventral mouthparts strongly retracted, distance between mandibular and maxillary articulations less than width of stipes; hypostomal rods indistinct; legs sometimes absent . . . . . Bothrideridae (part)

8(6). Maxillary mala deeply cleft so that partially fused galea and lacinia are still evident; dorsal surfaces granulate and usually with setiferous tubercles; mandible with accessory ventral process, well developed, asperate mola extending onto ventral surface and acute hyaline prostheca; stemmata: six; ventral epicranial ridges usually present. 9

Maxillary mala undivided or cleft only at apex, separate galea and lacinia not evident 10

9(8). Labrum partly fused to head capsule; hypostomal rods present; segment X ventral, membranous; spiracles not borne on tubes . . . . . Helotidae

Labrum free; hypostomal rods absent; abdominal segment X terminal, usually with sclerotised tergum; spiracles borne on short tubes. . . . Derodontidae (DERODONTOIDEA)

10(8). Frontal arms more or less V-shaped, sometimes slightly curved or sinuate but rarely lyriform; usually with either long epicranial stem or long median endocarina; paired endocarinae rarely present and then combined with retracted ventral mouthparts; mandibular mola absent, mandibular base simple or with one or more hyaline processes; ventral mouthparts often protracted; maxillary mala often with pedunculate seta; pretarsus always unisetose; tergum IX not forming articulated plate; body

always elongate and more or less parallel-sided . . . . . (CLEROIDEA)

Frontal arms usually lyriform with epicranial stem short or absent; base of mandible rarely with one or more hyaline processes instead of a mola; paired endocarinae usually associated with protracted ventral mouthparts in combination with two pretarsal setae, lyriform frontal arms, rings of abdominal asperities or an articulated 9th tergum; pedunculate malar setae sometimes present in taxa with retracted ventral mouthparts, an oblong or posteriorly tapered body and an expanded or flattened pretarsal seta 11

11(10). Ventral mouthparts protracted or slightly retracted, distance between mandibular and maxillary articulations less than width of stipes; maxillary articulating area highly reduced or absent; labial palps 2-segmented; mandible often without mola, or with mola but no prostheca; maxillary mala obtuse; base of epicranium often deeply emarginate and with median or paired endocarinae; coxae widely separated; abdominal segment X small, transverse, not forming typical pygopod 12

If ventral mouthparts protracted or slightly retracted, then labial palps 1-segmented and/or maxillary articulating area well developed 17

12(11). Urogomphi absent; abdomen without pigmented terga; mesal surface of mandibular base with cluster of hyaline processes 13

Urogomphi present; abdomen usually with tergum IX or terga VIII and IX pigmented; mesal surface of mandibular base varying 15

13(12). Antenna very short, antennomeres 1 and 2 transverse, 3 much longer and narrow; paired endocarinae parallel; tergum IX unusually short, with pair of articulations at base; spiracles annular . . . . . Propalticidae

Antenna longer, with antennomere 2 distinctly longer than either 1 or 3; tergum IX not unusually short or articulated; spiracles annular–biforous 14

14(13). Posterior edge of head capsule gradually emarginate; paired endocarinae contiguous at base and anteriorly divergent; sensorium subequal in length to antennomere 3; pretarsus bisetose . . . . . Cyclaxyridae

Posterior edge of head capsule abruptly emarginate; paired endocarinae distant at base, parallel, and interrupted anteriorly; sensorium longer than antennomere 3; pretarsus unisetose . . . . . Tasmosalpingidae

15(12). Hypostomal rods parallel, very long, almost reaching posterior edge of head capsule; cardo indistinct; tergum IX forming articulated plate; sternum IX and segment X reduced, membranous and partly enclosed within emargination of sternum VIII; pretarsus unisetose; abdominal spiracles annular . . . . . Laemophloeidae

Hypostomal rods divergent, usually shorter; cardo usually distinct; spiracles annular–biforous 16

16(15). Abdominal spiracle 8 located on long, posteriorly-projecting, acute process; sternum IX and segment X exposed; head without median endocarina, with paired endocarinae; pretarsus bisetose . . . . . Lamingtoniidae

Abdominal spiracle 8 not located on posterorly-projecting process; sternum IX and segment X more or less concealed beneath posteriorly projecting lobe on sternum VIII; head often with median endocarina; pretarsus unisetose . . . . . Phalacridae

17(11). Ventral mouthparts strongly retracted, maxillary articulating area strongly reduced or absent; hypostomal ridges gradually curved mesally and hypostomal cavity narrowly rounded posteriorly; cardines longitudinally oriented; prostheca almost always complex, consisting of several to many processes (rarely simple and broadly angulate or absent); maxillary mala almost always broadly rounded apically, with subapical bidentate or unidentate process on mesal edge (rarely truncate, without mesal process); labial palps 1-segmented; stemmata: four or fewer; urogomphi almost always present, sometimes accompanied by pregomphi (if urogonmphi absent, then segments VIII and IX with lateral spiniform processes); if hypostomal rods present, then pretarsus with spatulate seta. . . . . Nitidulidae

If ventral mouthparts strongly retracted, then maxillary articulating area usually distinct, hypostomal ridges abruptly curved mesally, so that hypostomal cavity more truncate posteriorly and cardines more or less transversely oriented; without other characters in combination . . . 18

18(17). Ventral mouthparts strongly protracted; cardo not distinct; hypostomal rods long and subparallel; prostheca absent; maxillary mala wider than long, obtuse, simple; labial palps 1-segmented; with single stemma on each side; body elongate, parallel-sided and flattened; pretarsus unisetose; tergum IX well sclerotised with urogomphi; spiracles annular–biforous . . . . . Smicripidae

Without above characters in combination 19

19(18). Mandible with reduced mola, not extending onto dorsal or ventral surfaces, and without prostheca or ventral accessory process; ventral mouthparts slightly retracted; maxilla with transverse stipes and simple, plapiform mala articulated at base; labial palps 1-segmented; hypostomal rods divergent; pretarsus unisetose; urogomphi absent; segment X terminal with short pygopods . . . . . Kateretidae

If mandibular mola reduced and restricted to mesal surface, then prostheca present; if mala articulated at base, then labial palps 2-segmented; without other characters in combination 20

20(19). Abdominal segment X more or less transverse, forming bilabiate structure; stemma not more than 5; mandible never with prostheca; molae usually asymmetrical; maxillary mala never falcate (but sometimes acute at inner apex), occasionally cleft; head often with coronal suture (epicranial stem); pretarsus rarely unisetose . . . . . (TENEBRIONOIDEA)

Abdominal segment X usually cylindrical; stemmata: often six; prostheca usually present; maxillary mala often acute at apex; mandibles usually symmetrical; head rarely with coronal suture; pretarsus often unisetose 21

21(20). Tergum IX reduced and sternum IX highly reduced and concealed or apparently absent; segment X forming elongate, cylindrical, pygopod-like structure; spiracles annular; maxillary mala acute at apex; antennomere 2 at least twice as long as 1; urogomphi long, slender and straight or absent; pretarsus bisetose . . . . . Silvanidae

Tergum IX well developed; sternum IX exposed; segment X short and cylindrical or reduced; if spiracles annular, then maxillary mala blunt, urogomphi variable 22

22(21). Body of tergum IX much shorter than tergum VIII, forming heavily sclerotised, articulated plate with forked posterior projection or pair of urogomphi; sternum IX very short, slightly to strongly retracted into apex of sternum VIII; segment X scarcely projecting; head wider than prothorax, with sides more or less straight and subparallel or

converging anteriorly; antennomeres 2 and 3 elongate and usually subequal; sensorium less than 0.2× as long as antennomere 3; body flattened; abdominal segments without rows of asperities and urogomphi, if present, without cavity between them. . . . . Cucujidae

Body of tergum IX not, or only slightly, shorter than tergum VIII, not forming articulated plate; of urogomphi; sternum IX not retracted into apex of sternum VIII; segment X sometimes projecting; if head wider than prothorax, sides more rounded and cavity present between urogomphi or abdominal segments with curved rows of tergal and sternal asperities; sensorium more than 0.2× as long as antennomere 3. 23

23(22). Ventral mouthparts slightly retracted; mesal surface of mandibular base with brush of hairs and fixed, hyaline process, mola absent; maxillary mala falcate; endocarinae absent; hypostomal rods long and divergent; pretarsus bisetose; urogomphi short and upturned spiracles annular; body parallel-sided, flat and lightly sclerotised except for head and urogomphi . . . . . Myraboliidae

Ventral mouthparts strongly retracted; without other characters in combination. 24

24(23). Maxillary mala long, falcate, articulated at base, without setae; mandible with broad-based hyaline prostheca; mandibular mola not extending onto dorsal or ventral surfaces; urogomphi very short and blunt; segment X with pair of long, cylindrical pygopods. . . . . Boganiidae

Maxillary mala shorter, setiferous, not basally articulated; abdominal segment X without paired pygopods; without other characters in combination 25

25(24). Prostheca with narrow base; maxillary mala blunt; mandibular mola well developed with accessory ventral process; spiracles annular or annular-multiforous; terga without setiferous tubercles; dorsal setae simple; urogomphi small and simple or absent . . . . . Sphindidae

If prostheca with narrow base, then maxillary mala more or less acute at apex or spiracles annular–biforous; without other characters in combination 26

26(25). Pretarsus unisetose; prostheca, if present, consisting of numerous comb-hairs or two or more acute, hyaline processes; if prostheca absent, then base of mola with strongly projecting, membranous, setose lobe; stemmata: six; mala falciform or somewhat truncate with acute inner angle. 27

If pretarsus unisetose, then mola absent or prostheca consisting of single hyaline process; if mola is present without prostheca, then there is no membranous, setose projection at its base 28

27(26). Mandible without accessory ventral process; prostheca either absent or consisting of a few simple hyaline processes; pigment and sculpture on dorsal surfaces more or less uneven; 8th spiracles lateral . . . . . Byturidae

Mandible with accessory ventral process; prostheca consisting of numerous comb-hairs; dorsal surfaces more or less evenly pigmented and sculptured; 8th spiracles dorsal near edge of tergum . . . . . Biphyllidae

28(26). Mola, if present, accompanied by prostheca with narrow base and acute apex; if mola absent, mesal surface of mandibular base with two hyaline lobes, one acute and one fimbriate; maxillary mala more or less acute at inner apex; pretarsus bisetose; spiracles usually annular–biforous 29

Mola, if present, almost always accompanied by prostheca with broad base and broadly angulate apex (prostheca rarely absent); if mola absent, mesal surface of mandibular base either simple or with membranous lobe; maxillary mala often blunt at inner apex; urogomphi often absent; spiracles often annular 36

29(28). Head with distinct ventral epicranial ridges; stemmata: none or two; mandible with well developed mola and narrowly acute or occasionally bidentate prostheca; cutting edge often serrate cutting edge; labial palps usually 1-segmented; abdominal terga usually granulate or with setiferous tubercles, sometimes forming transverse rows; urogomphi usually broad and blunt or divided, rarely absent . . . . . Monotomidae

Ventral epicranial ridges absent; stemmata: usually more than two, or if not, then mola replaced by an acute and fimbriate hyaline process and urogomphi simple and upturned. 30

30(29). Labial palps 1-segmented; dorsal surfaces with setose tubercles; stemmata: five; prostheca small and acute; maxillary mala falcate or obtuse with acute inner angle; urogomphi simple and upturned; spiracles annular–biforous, borne on distinct spiracular tubes . . . . . Hobartiidae

If labial palps 1-segmented, dorsal surfaces without setose tubercles and prostheca different; without other characters in combination 31

31(30). Mandibular mola absent; mesal surface of mandibular base with an acute hyaline process adjacent to a membranous, apically fimbriate lobe; accessory ventral process absent; maxillary mala obliquely truncate but with one or more spines at inner apical angle; urogomphi short, posteriorly directed, not upturned; head and major portions of all terga (including X) with relatively smooth, more or less evenly pigmented surface; pretarsus bisetose . . . . . Cavognathidae

Mandible with well developed, asperate mola; maxillary mala acute at apex; urogomphi, if present, longer and upturned or complex 32

32(31). Labial palps 1-segmented or spiracles annular; mandible with well developed mola and usually with serrate cutting edge; prostheca often bifid, its proximal edge sometimes fimbriate; dorsal surfaces relatively lightly pigmented and smooth or finely granulate, without setiferous tubercles; urogomphi simple and upturned or absent. . . . . Cryptophagidae

Labial palps 2-segmented; spiracles annular–biforous; mola well developed and asperate; prostheca simple and acute; dorsal surfaces often with setiferous tubercles or rows of asperities; urogomphi often complex 33

33(32). Pretarsus strongly toothed at base; abdominal spiracles annular–biforous, borne on spiracular tubes; trunk terga uniformly sclerotised and pigmented, with anterior transverse carinae and setiferous tubercles, without lateral outgrowths; urogomphi long, with lateral spines and pregomphi; stemmata: six . . . . . Protocucujidae

Pretarsus not markedly toothed at base; if trunk terga sclerotised and pigmented, then they have lateral outgrowths; stemmata variable 34

34(33). Thoracic and abdominal terga with long lateral outgrowths, those on abdominal terga I–VIII with spiracles at their ends; urogomphi moderately to very long, posteriorly-projecting and slightly to strongly divergent; antennomere 2 ~2× as long as 1 and more than 5× as long as 3; stemmata on each side located on one or more projecting tubercles . . . . . Priasilphidae

Trunk terga without lateral outgrowths; antennomere 2 not much longer than 3; stemmata not located on projecting tubercles 35

35(34). Spiracles large, with accessory chambers much longer than peritreme diameter; labrum freely articulated; urogomphi approximate at base, upturned and divergent, with lateral spines; body only slightly flattened; abdominal terga and sterna without paired patches of asperities . . . . . Agapythidae

Spiracles smaller, with accessory chambers subequal in length to peritreme diameter; labrum fused to clypeus; urogomphi distant at base, posteriorly directed and upturned at apex only, without lateral spines; body markedly flattened; urogomphi with small cavity between them (*Phloeostichus*) or abdominal terga and sterna I–VII each with paired curved rows of asperities (*Hymaea* and *Rhopalobrachium*) . . . . . Phloeostichidae

36(28). Pretarsus bisetose; maxillary mala acute at inner apex; mandible with well developed mola; prostheca broad-based, sometimes membranous; antenna with sensorium much shorter than antennomere 3; spiracles annular–biforous 37

Pretarsus unisetose; without other characters in combination 40

37(36). Head with long epicranial stem (coronal suture); stemmata: two or fewer; maxillary mala falcate; body more or less cylindrical; dorsal surfaces lightly pigmented and even, without granulations or setiferous tubercles; urogomphi simple and upturned. . . . . Erotylidae (Languriini)

If epicranial stem long; stemmata: five or six and maxillary mala truncate; upper surfaces heavily pigmented and/or with granulations or setiferous tubercles; urogomphi usually complex, with accessory processes or pregomphal tubercles 38

38(37). Epicranial stem absent; median endocarina present between frontal arms; maxillary mala falcate; dorsal surfaces at least slightly granulate, without lateral projections; setiferous tubercles present only on tergum IX; urogomphi relatively simple and upturned, with one or more pairs of pregomphal tubercles . . . . Erotylidae (Pharaxonothinae)

Median endocarina, if present, combined with long epicranial stem and truncate maxillary mala 39

39(38). Thoracic and abdominal terga with processes extending over spiracles or body distinctly tapered posteriorly; vestiture often including expanded or frayed setae; tergum IX without pregomphal processes; urogomphi short and posteriorly-directed, sometimes with lateral setiferous processes; mala falcate; mandibular mola always present and prostheca apically acute . . . . . Erotylidae (Cryptophilinae)

Lateral tergal processes absent; urogomphi usually strongly upturned or very long, rarely absent and replaced by median spine; upper surfaces granulate, tuberculate, with patches of asperities or bearing complex processes; mala usually more or less truncate, with stout apical teeth or spines; mandibular mola sometimes absent and prostheca broad and membranous . . . . . Erotylidae (major part)

40(36). Mandible and maxilla stylet-like, either entognathous or enclosed within tubular piercing beak; head strongly hypognathous, often concealed from above; dorsal surfaces somewhat flattened, usually granulate or with setose tubercles and often with modified setae; urogomphi absent . . . . . Cerylonidae (Ceryloninae)

Mandible of normal chewing type, usually with basal asperate mola; urogomphi variable 41

41(40). Mandibular mola absent or reduced to a tooth-like process; prostheca absent; tibiotarsus almost always bearing spatulate, adhesive setae at apex; pretarsus usually wide at base and abruptly narrowing apically; maxillary articulating area obsolete; frontal sutures visible, usually lyriform; stemmata: three; terga usually pigmented and tuberculate; vestiture often complex; urogomphi rarely present . . . . . Coccinellidae

Mandible with well developed, asperate mola; tibiotarsus without adhesive setae apically; pretarsus gradually narrowing apically; without other characters in combination 42

42(41). Urogomphi short and complex or acute and upturned . . . 43

Urogomphi absent or long and divergent 46

43(42). Stemmata absent; lateral edges of terga VI–IX more strongly produced posteriorly than those of anterior terga; abdominal spiracles annular, not placed on tubes . . . . . Bothrideridae (Anommatinae)

Stemmata: five or six; terga equally projecting; spiracles annular–biforous and placed at ends of spiracular tubes. 44

44(43). Stemmata: five; urogomphi short, simple and upturned. . . . . Alexiidae

Stemmata: six; urogomphi simple or complex 45

45(44). Urogomphi complex; tergum IX with median boss between and in front of urogomphi; sensorium longer than antennomere 3; spiracular chambers much longer than peritreme and extending out onto surface of long spiracular tube . . . . . Bothrideridae (Xylariophilinae)

Urogomphi simple; tergum IX with paired setiferous processes in front of urogomphi; sensorium shorter than antennomere 3; spiracular chambers not much longer than peritreme, spiracular tubes shorter . . . . . Bothrideridae (Teredinae)

46(42). Urogomphi long and divergent; terga often with lateral processes; stemmata: none or two; spiracles placed on short processes. . . . . Cerylonidae (Euxestinae)

Urogomphi absent or inconspicuous; terga usually without processes; spiracles not on tubes. 47

47(46). Antenna 2-segmented with sensorium at apex . . . . . Discolomatidae

Antenna 3-segmented with sensorium situated laterally on apex of antennomere 2 48

48(47). Mandible with apical part and prostheca absent; maxillary articulating area distinct; stemmata absent; dorsal setae simple and acute. . . . . Endomychidae (Anamorphinae)

Mandible complete, with prostheca, or stemmata present; at least some dorsal setae modified or maxillary articulating area obsolete 49

49(48). Maxillary articulating area obsolete 50

Maxillary articulating area present 51

50(49). Stemmata: usually two; abdomen almost always with glandular openings on segments I–VII or on I and VIII; form often more or less onisciform; pretarsal seta long and spatulate; labial palps usually 2-segmented; mandible entirely sclerotised. . . . . Corylophidae

Stemmata: four or five; abdomen without glandular openings; form not onisciform; pretarsal seta short and simple; labial palps usually 1-segmented; mandible often partly membranous . . . . . Latridiidae

51(49). Body onisciform; head with long median endocarina . . . . . Cerylonidae (Mumidiinae)

Body shape not or less strongly onisciform; endocarina absent. . . . . Endomychidae (part)

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Appendix 1. Terminal taxa

A list of taxa examined for the cladistic analysis follows. Supplemental references that include descriptions of larvae or adults are included for some entries

Acylomus Sharp, 1888 (Phalacridae: Phalacrinae). Based on adults and larvae of *A. ergoti* Casey, and larval description of *A. pugetanus* Casey by Steiner and Singh (1987).

Agapytho Broun, 1921 (Phloeostichidae: Agapythinae). Based on adults and larvae of *A. foveicollis* Broun.

Ahasverus Gozis, 1881 (Silvanidae: Silvaninae). Based on adults and larvae of *A. advena* (Waltl).

Amartus LeConte, 1861 (Kateretidae). Based on adults of *A. rufipes* LeConte and larvae of *Amartus* sp.

Anchorius Casey, 1900 (Biphyllidae). Based on adults and larvae of *A. lineatus* Casey and published material in Goodrich and Springer (1992).

Atomaria Stephens, 1829 (Cryptophagidae: Atomariinae). Based on adults and larvae of *Atomaria lewisi* Reitter. (Leschen 1996)

Aulonosoma Motschulsky, 1858 and *Ancistria* Erichson, 1845 (Passandridae). Based on adults of *Aulonosoma tenebriodes* Motschulsky and a first instar larva of *Ancistria* sp. from New Guinea.

Australaethina Kirejtshuk & Lawrence, 1990 (Nitidulidae: Nitidulinae). Based on adults and larvae of *Australaethina froggatti* (Kirejtshuk & Lawrence).

Bunyastichus, gen. nov. Based on adults of *B. monteithi*, sp. nov.

Cavognatha Crowson, 1964 (Cavognathidae). Based on adults and larvae of *C. pullivora* Crowson.

Chileosilpha, gen. nov. Based on adults of *C. alleni*, sp. nov.

Cryptamorpha Wollaston, 1854 (Silvanidae: Brontindae). Based on adults and larvae of *C. desjardinsi* (Guérin-Méneville).

Cryptophagus Herbst, 1972 (Cryptophagidae: Cryptophaginae). Based on adults of *C. cellaris* (Scopoli) and larvae of *C. lycoperdi* Herbst. (Leschen 1996).

Cucujus Fabricius, 1775 (Cucujidae). Based on adults and larvae of *Cucujus clavipes* Fabricius.

Cyclaxyra Broun, 1893 (Cyclaxyridae). Based on adults and larvae of a *Cyclaxyra* assumed to be *C. politula* Broun.

Derodontus LeConte, 1861 (Derodontidae). Based on adults and larvae of *D. maculatus* (Melsheimer), and published larval descriptions and illustrations in Böving and Craighead (1931) and Lawrence and Hlavac (1979).

Ericmodes Reitter, 1878 (Protocucujidae). Based on adults of *E. sylvaticus* (R. Philippi, larvae of *Ericmodes* species from Chile and Australia, and published material in Ślipiński (1998).

Eronyxa Reitter, 1876 (Trogossitidae: Lophocaterinae). Based on adults and larvae of *E. pallida* (Motschulsky) and larval description and illustrations of *E. expansa* Van Dyke in Tait *et al*. (1990).

Helota Macleay, 1825 (Helotidae). Based on adults of *Helota* sp. from West Sumatra and larval descriptions and illustrations in Rymer Roberts (1958) and Hayashi (1986).

Hobartius Sen Gupta & Crowson, 1966 (Hobartiidae). Based on adults and larvae of *H. eucalypti* (Blackburn) (Tomaszewska and Ślipiński 1995).

Hymaea Pascoe, 1869 (Phloeostichidae: Hymaeinae). Based on adults of *H. magna* Sen Gupta & Crowson and larvae of *H. succinifera* Pascoe.

Laemophloeus Dejean, 1835 (Laemophloeidae). Based on adults and larvae of *L. biguttatus* (Say).

Lamingtonium Sen Gupta & Crowson, 1969 (Lamingtoniidae). Based on adults and larvae of *L. thayerae* Lawrence & Leschen (Lawrence and Leschen 2003).

Myrabolia Reitter, 1876 (Phloeostichidae: Myraboliinae). Based on adults of various species and a tentatively identified *Myrabolia* larva from the Brindabella Range, ACT.

Paracucujus Sen Gupta & Crowson, 1966 (Boganiidae: Paracucujinae). Based on adults and larvae of *P. rostratus* Sen Gupta & Crowson.

Pharaxonotha Reitter, 1875 (Erotylidae: Pharaxonothinae). Based on adults and larvae of *P. floridana* (Casey) (Leschen 2003).

Phloeostichus Redtenbacher, 1842 (Phloeostichidae: Phloeostichinae). Based on adults of *P. denticollis* Redtenbacher, and a presumed larva from Guzeripl, Adygeya Autonomous Region (north-western Caucasus), Russia.

Priasilpha Broun, 1893 (Phloeostichidae: Priasilphinae). Based on adults and larvae of *P. obscura* Broun.

Priastichus Crowson, 1973 (Phloeostichidae: Priasilphinae). Based on adults and larvae of *P. megathorax*, sp. nov.

Propalticus Sharp, 1879 (Propalticidae). Based on adults of *P. doddi* John and notes on a presumed larva of a *Propalticus* sp. collected in Lamington National Park, Queensland, under bark of dead *Casuarina*, by R. A. Crowson and preserved on a slide in Crowson's collection.

Protosphindus Sen Gupta & Crowson, 1979 (Sphindidae: Protosphindinae). Based on adults and larvae of *P. chilensis* Sen Gupta & Crowson and published material in Burakowski and Ślipiński (1987).

Rhizophagus Herbst, 1793 (Monotomidae: Rhizophaginae). Based on adults of *Rhizophagus* sp. from New York and larvae of *Rhizophagus* sp. from Mt Rainier National Park, Washington.

Rhopalobrachium Boheman, 1858 (Phloeostichidae: Hymaeinae). Based on adults and larvae of *R. clavipes* Boheman.

Smicrips LeConte, 1878 (Smicripidae). Based on adults and larvae of *Smicrips* spp. (from Panama and Arizona).

Tasmosalpingus Lea, 1918 (Phloeostichidae: Tasmosalpinginae). Based on adults of *T. quadrispilotus* Lea and tentatively identified larvae of this species from Bruny Island, Tasmania.

Thymalus Latreille, 1802 (Trogossitidae: Peltinae). Based on adults and larvae of *T. marginicollis* Chevrolat.

Xerasia Lewis, 1895 (Byturidae: Byturinae). Based on adults and larvae of *X. grisescens* (Jayne).