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Phylogeny and classification of Corylophidae (Coleoptera: Cucujoidea) with descriptions of new genera and larvae

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Abstract. Phylogenetic relationships within the family Corylophidae were investigated. Twenty ingroup taxa and six outgroups were included in a cladistic analysis, based on 48 characters derived from adult and larval morphology. Phylogenetic analysis confirms that Corylophidae are monophyletic within the superfamily Cucujoidea and may be subdivided into two subfamilies: the Australian Periptycinae and the cosmopolitan Corylophinae containing 10 tribes: Foadiini **trib.n.**, Cleidostethini, Aenigmaticini, Parmulini, Sericoderini, Peltinodini, Orthoperini, Corylophini, Teplinini and Rypobiini. All currently recognized family-group taxa are thoroughly diagnosed, and keys to their identification based on adults and larvae are provided. Two new genera and three species are described: *Weirus* **gen.n.**, containing only *W. tozer* **sp.n.** (Australia: Queensland), and *Stanus* **gen.n.**, with the two species *S. bowesteadi* **sp.n.** (New Zealand) and *S. tasmanicus* **sp.n.** (Tasmania). The larvae of *Pakalukodes bimaculatus* Ślipiński *et al.* from Queensland and of *Stanus bowesteadi* **sp.n.** from New Zealand are described and illustrated for the first time.

Introduction

The classification of Corylophidae remained static until relatively recently, with the family-group concepts of Paulian (1950), based largely on those of Matthews (1899) and Casey (1900), being used subsequently by Lawrence & Newton (1995) and Pakaluk *et al.* (1995). The first indications that change might be warranted were in a series of papers by Pakaluk (1985a–c) and Pakaluk & Lawrence (1986) dealing with the atypical, elongate and flattened corylophids sometimes included in the tribe Aenigmaticini, here often referred to as 'latridiid-like' taxa. These authors suggested that aenigmaticines formed a single lineage or a polytomic assemblage sister to the remaining corylophid taxa. In a major revision of Palaearctic Corylophidae, Bowestead (1999) elevated the tribes Rypobiini and Orthoperini to subfamily rank and restricted the latter group to *Orthoperus* Stephens; however, the aenigmaticine group was not treated in this work. Bowestead also synonymized a number of genera used by Paulian (1950), and included in Peltinodinae the single, widely distributed genus *Holopsis* Broun (a senior synonym of both *Peltinodes* Paulian and *Corylophodes* Matthews). Two more important emendations were made in the familial limits subsequent to Bowestead's work: first, the genus *Periptyctus* Blackburn, doubtfully included by Strohecker (1953) in the endomychid subfamily Stenotarsinae, was transferred to Corylophidae and placed with a new genus *Pakalukodes* Ślipiński *et al.* in a new subfamily Peripytctinae (Ślipiński *et al.*, 2001; Tomaszewska & Ślipiński, 2002); and second, the highly modified bee commensal, *Cleidostethus meliponae* Arrow, was transferred from Coccinellidae to Corylophidae and placed in a new tribe of Corylophinae (Bowestead *et al.*, 2001). The present paper was stimulated by the discoveries of a new aenigmaticine genus group from New Zealand and Tasmania and of another new genus of Periptyctinae from Australia. These discoveries also provided the opportunity to use available adult and larval characters in a cladistic analysis of exemplars from all major Corylophidae lineages.

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Materials and methods

Studied material is deposited in the Australian National Insect Collection, Canberra, Australia (ANIC); the Museum and Institute of Zoology, PAS, Warszawa, Poland (MIZ); the New Zealand Arthropod Collection (NZAC); and the Queensland Museum, Brisbane, Australia (QM).

Measurements were made using a filar micrometer as follows: body length, from apical margin of clypeus to apex of elytra; width, across both elytra (at widest part); pronotal length, from the middle of anterior margin to margin of basal foramen; pronotal width, across widest part; elytral length along suture, including scutellum.

Drawings were made using a camera lucida attached to an Olympus (SZH 10) dissecting microscope. Photographic images were produced using various digital cameras at CSIRO Entomology and enhanced using AUTO MONTAGE® software.

Cladistic analyses were performed using NONA version 2 (Goloboff, 1993) via WINCLADA (Nixon, 1999) which was subsequently used to construct the trees and analyse the distribution of characters on individual trees. A total of 48 characters were scored for 18 ingroup and 6 outgroup taxa. *Hapalips* (Erotylidae) was utilized as a distant outgroup, owing to its placement outside the Cerylonid Series (Leschen *et al*., 2005) and the remaining taxa chosen as related outgroups within the Cerylonid Series to which Corylophidae belongs (Ślipiński & Pakaluk, 1991). All characters were treated as unordered.

Parsimony analyses were performed via Ratchet (500 iterations, five trees held, six characters sampled; ambiguity set to polytomy). The resulting cladograms with unsupported nodes were collapsed in WINCLADA and only 'best trees' were further investigated. Bremer support values were calculated by nona for 10 000 suboptimal trees that were up to six steps longer.

Taxa

Exemplar taxa for phylogenetic analyses were selected from available material with emphasis on taxa containing adults and larvae of the same species that were available for coding. A considerable effort was made to include multiple species representing each recognized family-group taxon according to the classification of Bowestead (1999); taxa not treated therein are listed as 'incertae sedis'. Of the included taxa, at least one specimen was examined as a full-body dissection as a glycerine slide mount. 'A' denotes dissected adult and 'L' denotes dissected larva.

Ingroup Taxa.

Peltinodinae. *Holopsis* Broun: unnamed species from New Zealand (A, L), Chile (A, L), Australia (A, L) and U.S.A. (A). Larva: Böving & Craighead (1931); Lawrence (1991).

Corylophinae. Parmulini. *Clypastraea* Haldeman: unnamed species from North America (A) and Australia (A, L). *Athrolips* Wollaston: unnamed species from Europe (A), U.S.A. (A) and Australia (A, L). Larva: Böving & Craighead (1931); Peyerimhoff (1919, 1921); Costa *et al*. (1988).

Sericoderini. *Sericoderus* Stephens: unnamed species from Europe (A), U.S.A. (A, L), Panama (A, L) and Australia (A, L). *Aposericoderus* Paulian: unnamed species from Indonesia (A). Larva: Peyerimhoff (1921); Hinton (1941).

Corylophini. *Corylophus* Stephens: *C. cassidioides* (Marsham) from Germany (A). Larva unknown.

Teplinini. *Teplinus* Pakaluk *et al*: *T. velatus* (Mulsant & Rey) from Spain (A). Larva unknown.

Orthoperinae. Orthoperini. *Orthoperus* Stephens: unnamed species from England (A, L) and Australia (A, L). Larva: Chandler (1983); Costa *et al*. (1988).

Rypobiinae. Gloeosomatini. *Gloeosoma* Wollaston: unnamed species from U.S.A. (A) and Australia (A, L).

Rypobiini. *Rypobius* LeConte: unnamed species from Australia (A, L). Larva: Böving & Craighead (1931); Lawrence (1991).

Corylophidae incertae sedis. *Aenigmaticum* Matthews: unnamed species from U.S.A. (A). Larva: unknown.

Cleidostethus meliponae (A, L), Zaire (A). Larva: unknown.

Foadia maculata Pakaluk: (A, L), U.S.A., Florida. Larva: Pakaluk (1985a).

Hyplathrinus Reitter: unnamed species, Brazil (A). Larva: unknown.

Ectinocephalus Matthews: unnamed species, Mexico (A, L).

Pakalukodes Ślipiński *et al.*: *P. bimaculatus* Ślipiński *et al*., Australia: Queensland (A, L).

Periptyctus Blackburn: *P. kosciuszko* Ślipiński & Tomaszewska, Australia (A, L). Larva: McHugh & Pakaluk (1997).

Priamima rubicunda (MacLeay), Australia (A). Larva: unknown.

Stanus gen.n.: *S. bowesteadi* sp.n., New Zealand (A, L).

Weirus gen.n.*: W. tozer* sp.n., Australia (A). Larva unknown.

Outgroup Taxa. Erotylidae: Hapalipini. *Hapalips prolixus* Sharp, New Zealand (A, L).

Coccinellidae: Sticholotidini. *Sticholotis* sp., Christmas Island (A, L).

Coccinellidae: Microweiseini. *Coccidophilus* sp., Brazil (A, L).

Discolomatidae. *Aphanocephalus* sp., Australia, Queensland (A, L); *Notiophygus* sp., South Africa (A, L).

Endomychidae: Anamorphinae. *Bystus decorator* Leschen & Carlton, Peru (A, L).

Characters

Discrete characters were selected from adults and larvae of all taxa. Initial selection of adult characters followed

Bowestead (1999), expanded subsequently (in this paper) for adult and larval characters to account for observed diversity. Morphological terminology follows Lawrence (1991) for larvae and Lawrence & Britton (1994) for adults, with changes proposed by Lawrence (1999) for the pterothorax and by Kukalová-Peck & Lawrence (2004) for the hind wing.

Adult.

0. Anterior edge of pronotum: (0) distinctly arcuate anteriorly and produced over head; (1) truncate and at same level as anterior angles, which are not distinct; (2) distinctly emarginate exposing head and with prominent anterior angles.

Most Corylophidae have a prominent, hood-like pronotum covering the head from above. Head is partially exposed in *Orthoperus*, and largely visible in the latridiid-like genera (*Aenigmaticum*, *Conodes*, *Ectinocephalus*, *Hyplathrinus*, *Priamima*, *Foadia*) and Periptycinae (Ślipiński *et al*., 2001). Head typically exposed in out-group taxa, although in some Coccinellidae (e.g. *Cassiculus* Pascoe, *Cranophorus* Mulsant, *Oryssomus* Mulsant) and Discolomatidae (*Cassidoloma* Kolbe) it is dorsally covered by pronotum.

1. Anterior tentorial arms: (0) complete; (1) reduced, visible at base only or apparently absent.

The corylophid head usually lacks distinct gular sutures. In some genera, the sutures may be reduced but are separate and traceable at the base of head capsule. Taxa with traces of gular sutures (Periptyctinae, *Holopsis* and latridiid-like taxa excluding *Aenigmaticum* and *Stanus*) have complete tentorial arms. Well-developed tentorial arms are present in all examined Discolomatidae, Coccinellidae, *Bystus* and *Hapalips*.

2. Frontoclypeal suture: (0) present; (1) absent.

The frontoclypeal suture is present in *Bystus* and Discolomatidae, and absent in Corylophidae and Coccinellidae.

3. Maxillary galea: (0) well developed; (1) absent.

In Corylophidae the galea is absent. Both maxillary lobes are developed in all outgroup taxa, although the galea is relatively small in *Sticholotis* and *Coccidophilus*.

4. Terminal labial palpomere: (0) approximately as long as preceding segment; (1) distinctly longer than preceding segment; (2) distinctly shorter than preceding segment.
5. Antennal pedicel: (0) shorter than or subequal to scape; (1) distinctly longer than scape.

Periptycinae are unique among the examined taxa in having a pedicel longer than the scape; the common condition is for both segments to be subequal or the scape longer.

6. Antennal club segments: (0) flattened in cross-section; (1) oval or circular in cross-section.

The antennal club of Periptycinae is distinctly flattened as compared with the remaining Corylophidae, and variable in the outgroup taxa.

7. Antennal club: (0) without membranous sensory vesicles; (1) with membranous vesicles on at least two basal segments; (2) with Y-shaped vesicles on first two segments.

The sensory vesicles on the club segments of Corylophidae provide strong apomorphies for the family. The smaller sensory areas on the club segments of *Teplinus* and *Cleidosthetus* as well as the Y-shaped sensilla in Periptycinae are treated here as homologous to the larger membranous vesicles in the remaining Corylophidae.

8. Gula: (0) simple; (1) with median endocarina.

A median endocarina is unique amongst Rypobiinae and appears to be formed by the medially fused gular sutures invaginated internally to form an endocarina.

9. Posterior gular region: (0) evenly sclerotized to basal foramen; (1) lightly sclerotized or membranous immediately posterior to abbreviated submentum. This feature is unique amongst the corylophid genera *Pakalukodes* and *Weirus*.
10. Mandible: (0) well developed and triangular with mola usually in contact with opposing mandible; (1) endognathous and variously reduced.

Endognathous, stylet-like articulated mandibles historically have been used to define Rypobiinae (Matthews, 1899; Paulian, 1950). There is considerable variation in shape and development of the corylophid mandibles, ranging from a broad-based, triangular mandible with asperate mola (e.g. *Holopsis* or *Orthoperus*) to a narrower form with molar region reduced.

11. Mentum: (0) large and quadrate or trapezoidal (submentum broad, not prominent); (1) reduced and fused with prementum (submentum elongate); (2) triangular and pointed posteriorly (submentum not prominent).

The first state is in most ingroup and outgroup taxa. A strongly reduced, transverse mentum that is fused to the prementum occurs in Sericoderini and is associated with a narrow and prominent submentum as well as with an elongate basal labial palpomere. In Rypobiini, the mentum forms a triangle and is associated with strongly retracted and modified mouthparts. A somewhat similar condition occurs in *Coccidophilus* (Coccinellidae: Microweiseini).

12. Medial region of prosternum, as measured from anterior margin of prosternum to midline between procoxae along prosternal process: (0) at least 2.0× as long as longitudinal diameter of coxa; (1) 1.1–1.6× as long as longitudinal diameter of coxa; (2) shorter than longitudinal diameter of coxa.

Taxa with elongate, flattened bodies and exposed head have a long prosternum; in some cases (i.e. *Periptyctus*) a chin piece is formed that conceals the head ventrally. Within Corylophidae, the more globose forms with transverse procoxae typically possess a shorter prosternum.

13. Prosternal carinae: (0) absent; (1) present at least at base.

Among the taxa examined, Periptycinae is the only exemplar with a variously developed prosternal carinae. Prosternal carinae are also present in many Coccinellidae, but they are not likely to be homologous, as they are much closer together as compared with the lateral carinae in Periptycinae.

14. Postcoxal hypomeral projections: (0) fused at midline; (1) abutting apex of prosternal process; (2) not reaching midline or prosternal process (procoxal cavities open).

Holopsis is the only known Corylophidae with narrowly open procoxal cavities. Taxa with more prominent projecting procoxae have the postcoxal projections narrow and fused. In taxa with rounded and not projecting procoxae the prosternal process expands beyond the procoxae and meets broader and separate postcoxal projections.

15. Postcoxal hypomeral projection immediately laterad of its junction with prosternal process: (0) less than 0.3× as wide as longitudinal diameter of procoxal cavity; (1) 0.5 or more times as wide as longitudinal diameter of procoxal cavity.

Taxa with open procoxal cavities or solidly fused postcoxal projections are coded as inapplicable for this character.

16. External portion of procoxa: (0) circular or oval in outline, not or only slightly projecting; (1) distinctly transverse and strongly projecting.

The transverse and projecting procoxae have been observed only in *Gloeosoma*, *Holopsis*, *Orthoperus* and *Teplinus*.

17. Procoxal cavity: (0) with lateral slits; (1) without slits.

Distinct lateral slits are present only in *Periptyctus*, *Weirus* and *Pakalukodes*.

18. Posterior angles of pronotum: (0) not strongly projecting posteriorly; (1) strongly projecting posteriorly and embracing elytral humeri.

Character state 1only occurs in *Sericoderus* and *Apossericoderus*.

19. Mesoventrite: (0) with cavity for reception of prosternal process; (1) with median carina and lateral procoxal rests; (2) flat, without cavity or distinct procoxal rests.

A cavity at the anterior end of the mesoventrite occurs in *Corylophus* and other Corylophini, as well as in *Periptyctus* and *Coccidophilus* (absent in *Pakalukodes* and *Weirus*). A similar, but much deeper, cavity occurs in *Cleidostethus*.

20. Mesocoxal cavity: (0) circular in outline: (1) strongly transverse.

Circular or slightly oval mesocoxal cavities occur in most Corylophidae as well as in all outgroup taxa. The cavities are distinctly transverse in *Orthoperus* and *Teplinus*.

21. External mesocoxal cavity: (0) closed by meso- and metaventrites: (1) open with mesepimeron touching coxa.

Although Matthews (1899) asserted that the mesocoxal cavities were open in many genera (e.g. *Ectinocephalus*, *Teplinus*, *Orthoperus*) others have observed closed mesocoxal cavities in *Ectinocephalus* (Pakaluk & Lawrence, 1986) and *Orthoperus* (Bowestead, 1999). We confirm that the mesocoxal cavities are closed in all Corylophidae examined except *Teplinus* and *Cleidostethus* (as stated by Bowestead *et al*., 2001).

22. Metaventral postcoxal lines: (0) present: (1) absent.

Postcoxal lines (femoral lines) on the metaventrite are widely distributed in Cucujoidea (e.g. Cerylonidae, Coccinellidae) but are generally absent in Corylophidae with the exception of *Holopsis* and *Orthoperus*.

23. Medial fleck on hind wing: (0) present; (1) absent.

The medial fleck (sensu Kukalová-Peck & Lawrence, 1993; subcubital fleck of Crowson, 1955) occurs in *Periptyctus*, *Pakalukodes*, *Holopsis*, and *Hapalips*.

24. Mesotrochanter: (0) strongly oblique; (1) elongate and less oblique.

In all examined Corylophidae the trochanter is strongly heteromeroid and the femoral apex touches the coxa. This mesocoxa/trochanter condition is a potential synapomorphy for Corylophidae and is in sharp contrast to the condition in Coccinellidae, in which the longer and less heteromeroid trochanter is concave dorsally and receives the tibial apex in repose.

25. Visible portion of metacoxae: (0) circular; (1) transverse.

The externally concealed hind coxal extension is found only in Discolomatidae and is a potential apomorphy for the family.

26. Abdominal postcoxal lines: (0) absent or rudimentary; (1) strongly arcuate externally; (2) straight or oblique.

Postcoxal lines on ventrite 1, like those on the metaventrite, occur among many Cucujoidea. They are generally absent from Corylophidae except for *Holopsis* and some of the latridiid-like taxa. The lines are arcuate in *Holopsis* and Coccinellidae, whereas they are straight or slightly oblique in *Foadia*, *Hyplathrinus*, *Ectinocephalus and Priamima*.

27. Number of visible abdominal ventrites: (0) five; (1) six.
28. Abdominal ventrites 1 and 2: (0) articulated; (1) fused.

Corylophidae typically have six freely articulated ventrites, but only five occur in *Periptyctus*, *Weirus* and *Cleidostethus*. The reduced condition in *Cleidostethus* is to the result of a complete fusion of the two basal segments without trace of division. In Coccinellidae there is always a suture visible between fused segments.

29. Number of functional abdominal spiracles: (0) five; (1) seven.

Seven pairs of functional abdominal spiracles are shared by most Corylophidae and *Hapalips*; however, only five

pairs occur in *Cleidostethus*, *Orthoperus* and all Coccinellidae, Discolomatidae and Endomychidae.

30. Pygidium: (0) with median groove; (1) without median groove.

The medially grooved pygidium is present only in Discolomatidae, and may represent a potential apomorphy for the family.

31. Tarsal formula: (0) 5-5-5; (1) 4-4-4; (2) 3-3-3.

All Corylophidae have 4-segmented tarsi with the two basal tarsomeres lobed and tarsomere III minute. In Coccinellidae 3-segmented tarsi are the typical condition.

32. Number of spurs on mesotibia: (0) two; (1) one; (2) none.
33. Tegmen: (0) 'corylophid type' with ventral phallobase and articulated parameral plate; (1) 'coccinellid type' with phallobases bearing median strut, large articulated parameres and penis guide; (2) 'discolomatid type' with a single fused phallobase and parameres; (3) 'erotylid type' with phallobase bearing median strut and small articulated parameres.
34. Penis: (0) sclerotized simple rod without basal struts or endophallic sclerites; (1) broad and stout without basal struts but possessing complex endophalic sclerites; (2) with paired basal struts and endophallic flagellum.

The slender, curved penis (or sipho) with enlarged base and no endophallic sclerites is characteristic of Coccinellidae. The Corylophid penis (Bowestead, 1999) is short, stout and curved with endophalic sclerites.

Larva.

35. Number of stemmata on each side of head: (0) one; (1) two; (2) three; (4) five; (5) none.

All corylophid larvae except *Pakalukodes* have two stemmata; Coccinellidae and Discolomatidae typically possess three, whereas the number in Endomychidae is variable.

36. Frontal arms: (0) present; (1) absent.

All corylophid larvae possess V- or U-shaped frontal arms clearly joined at bases. A similar condition occurs in *Sticholotis* (Coccinellidae).

37. Antenna: (0) 3-segmented; (1) 2-segmented.

In Corylophidae, Coccinellidae and Discolomatidae the antennae are 3-segmented, but reduction (some Coccinellidae, i.e. *Chilocorus* Leach) or fusion (as in some Corylophidae, i.e. *Rypobius*) of segments is frequent.

38. Antennomere II: (0) at most 2× as long as wide; (1) more than 4× as long as wide.

An elongate second antennomere is found in *Holopsis*, *Gloeosoma*, *Periptyctus* and *Pakalukodes*, as well as in larvae of Discolomatidae and *Bystus* (Endomychidae).

39. Labrum: (0) free: (1) fused to clypeus.
40. Mandible: (0) not endognathous; (1) endognathous but with rudimentary mola; (2) endognathous and styliform.

Rypobiinae larvae possess endognathous falcate mandibles. This condition is similar to that of some Cerylonidae (e.g. *Cerylon*). *Holopsis* and Periptycinae have endognathous mandibles but the mola and sometimes prostheca are visible.

41. Antennal socket separated from mandibular articulation by: (0) narrow strip of cuticle equal to or less than diameter of antennal socket; (1) area that is longer than diameter of antennal socket.

This character illustrates a difference between Coccinellidae and Corylophidae. Coccinellidae larvae possess an antennal insertion close to the mandibular articulation, whereas Corylophidae (and *Bystus*) possess an antennal socket located far from the mandibular articulation.

42. Maxillary cardo: (0) distinctly separate from stipes; (1) fused to stipes.
43. Maxillary articulating area; (0) absent; (1) present.

Larvae of Coccinellidae and Corylophidae have the cardo fused to the stipes without a maxillary articulation area.

44. Labial palpi: (0) 3-segmented; (1) 2-segmented; (2) 1-segmented.
45. Abdominal glandular openings: (0) absent; (1) present on segments I to VI or VII; (2) present on segments I and VIII; (3) present on segments IV to VIII.

Larvae of some Coccinellidae possess eight pairs of glandular openings on abdominal segments or on the metathorax and abdomen, whereas in Corylophidae there is variation in their placement. In *Orthoperus*, *Arthrolips*, *Clypastraea* and *Stanus* they occur on segments I to VII. In *Sericoderus*, *Holopsis* and Rypobiini they occur only on segments I and VIII. There has been much confusion concerning the identity of a larva identified as *Molamba* (= *Clypastraea*) in Böving & Craighead (1931), as observed by Lawrence (1991). There is little doubt that the figured larva belongs in Rypobiinae because of the disc-like body, presence of glandular openings on abdominal segments I and VIII, distinctive mandibles, and 2-segmented antennae. Larvae associated with two or three species of *Clypastraea* have a narrow body, 3-segmented antenna and glandular openings on abdominal segments I to VII. Glandular openings are absent in larvae of *Foadia*, *Ectinocephalus* and Periptycinae as well as in the outgroup taxa (except *Notiophygus* – Discolomatidae).

46. Glandular opening on abdominal segment I: (0) absent; (1) located at body surface; (2) located at apex of short tube.
47. Tergite IX: (0) with sclerotized asperities; (1) may appear darker in coloration but sclerotized asperities absent.

Results and discussion

Phylogenetic analysis

The Ratchet analysis of the data matrix (Table 1) resulted in 33 most parsimonious trees (L, 121; CI, 56; RI, 73) with a highly stable main topology but several alternative associations for some terminal taxa among the 'higher Corylophidae', in particular for those taxa with missing larval data (e.g. *Corylophus* or *Teplinus*). The Nelsen (Fig. 1 B) and majority-rule (Fig. 1C) consensus trees were largely congruent, with the latter better resolved. To test the stability of the configuration, a separate analysis of the adult matrix was performed using the same analytic procedure, resulting in four most parsimonious, highly resolved trees (L, 83; CI, 57; RI, 77) that were consistent with trees generated from the full matrix. The Nelsen (Fig. 1A) consensus tree was two steps longer than the original trees and identical to the majority consensus tree.

The discussion below uses a majority-rule consensus tree (L, 124; CI 54; RI, 72) derived from the 33 most parsimonious trees of the full data matrix (Fig. 1C, D). Characters and character states on the trees were optimized using unambiguous character changes in WinClada.

Phylogenetic assessment of major Corylophidae groups

Corylophidae. The monophyly of Corylophidae (including Periptycinae and *Cleidostethus*) is well supported by two adult and two larval synapomorphies. The absence of a galea (3, 1) and the presence of a short and strongly oblique mesotrochanter (24, 0) are unique to Corylophidae in the examined data set. Larval synapomorphies include one or two stemmata (35, 0 or 1) and the antennal insertion broadly separated from the mandibular articulation (41, 1) that is independently derived in *Bystus* (Endomychidae).

Periptycinae. This endemic Australian group (Ślipiński *et al*., 2001) is monophyletic and probably sister to the remaining Corylophidae. Their large size, long and not distinctly geniculate antenna with pedicel longer than scape (5, 1) and flattened club (6, 0) in addition to prosternal carinae (13, 1) and procoxae bearing distinct slits (17, 0) support monophyly of the group.

Aenigmaticini and Foadiini **trib.n.** The elongate, latridiid-like taxa or 'lower Corylophidae' of Pakaluk (1985a–c) form two distinct clades on all our trees and are always separated by a *Cleidostethus* clade. The '*Aenigmaticum* clade' clusters with remaining Corylophidae based on the absence of a tentorium (1, 1) (reversal in *Holopsis*), a shorter prosternum anterior to procoxae (12, 1) and a single tibial spur (32, 1), whereas taxa related to *Foadia* form a monophyletic group based on 2-segmented larval palps (44, 1) and straight postcoxal lines (26, 2) on first visible abdominal segment. This division also is supported by larvae bearing 8 pairs of glands in the '*Aenigmaticum* clade' versus none in the '*Foadia* clade'. Thus, we recognize the following formal division of two tribes: Aenigmaticini and Foadiini.

Table 1. Data matrix used in the cladistic analysis.

Taxa	0 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25 26 27 28 29 30 31 32 33 34 35 36 37 38 39 40 41 42 43 44 45 46 47
Hapalips	2 1 2 1 2 1 2 1 1 1 1 1 1 1 2 2 1 2 1 3 1 2 2 1 2 2 1 1 1 2 2 1 1 4 3 4 1 1 1 1 1 1 1 2 2 1 1 2
Holopsis	1 1 2 2 3 1 2 2 1 1 1 1 3 1 3 - 2 2 1 2 1 1 1 1 1 2 2 2 1 2 2 2 2 1 2 1 1 1 2 2 2 2 2 1 2 3 1 2
Clypeastrea	1 2 2 2 1 1 2 2 1 1 1 1 3 1 2 1 1 2 1 3 1 1 2 2 1 2 1 2 1 2 2 2 2 1 2 2 2 1 1 1 1 1 2 2 1 2 2 1 1
Athrolips	1 2 2 2 1 1 2 2 1 1 1 1 3 1 2 1 1 2 1 3 1 1 2 2 1 2 1 2 1 2 2 2 2 1 2 2 1 1 1 1 1 2 2 1 2 2 1 1
Sericoderes	1 2 2 2 3 1 2 2 1 1 1 2 3 1 2 1 1 2 2 3 1 1 2 2 1 2 1 2 1 2 2 2 2 1 2 2 1 2 2 1 1 2 2 1 2 3 1 2
Aposericoderus	1 2 2 2 3 1 2 2 1 1 1 2 3 1 2 1 1 2 2 3 1 1 2 2 1 2 1 2 1 2 2 2 2 1 2 ? ? ? ? ? ? ? ? ? ? ? ? ?
Corylophus	1 2 2 2 1 1 2 2 1 1 1 2 3 1 1 - 2 2 1 1 1 1 2 2 1 2 1 2 1 2 2 2 2 1 2 ? ? ? ? ? ? ? ? ? ? ? ? ?
Teplinus	1 2 2 2 1 1 2 2 1 1 1 2 2 3 1 1 - 2 2 1 2 2 2 2 2 2 1 2 1 2 1 2 2 2 2 1 2 ? ? ? ? ? ? ? ? ? ? ? ? ?
Orthoperus	3 2 2 2 2 1 2 2 1 1 1 1 3 1 1 - 2 2 1 2 2 1 1 2 1 2 1 2 1 1 2 2 2 1 2 2 1 1 1 1 1 2 2 2 3 2 1 2
Gloeosoma	1 2 2 2 2 1 2 2 2 1 2 3 3 1 1 - 2 2 1 2 1 1 2 2 1 2 1 2 1 2 2 2 2 1 2 2 2 2 2 2 3 2 2 1 2 3 1 2
Rypobius	1 2 2 2 2 1 2 2 2 1 2 3 3 1 1 - 2 2 1 2 1 1 2 2 1 2 1 2 1 2 2 2 2 1 2 2 1 2 2 2 3 2 2 1 2 3 1 2
Foadia	3 1 2 2 3 1 2 2 1 1 1 1 1 1 2 2 1 2 1 3 1 1 2 2 1 2 3 2 1 2 2 2 3 1 2 2 1 1 1 ? 1 2 2 1 2 1 1 2
Priamima	3 1 2 2 3 1 2 2 1 1 1 1 1 1 2 2 1 2 1 3 1 1 2 2 1 2 3 2 1 2 2 2 3 1 2 ? ? ? ? ? ? ? ? ? ? ? ? ?
Hyplathrinus	3 1 2 2 3 1 2 2 1 1 1 1 1 1 2 2 1 2 1 3 1 1 2 2 1 2 3 2 1 2 2 2 3 1 2 ? ? ? ? ? ? ? ? ? ? ? ? ?
Ectinocephalus	3 1 2 2 3 1 2 2 1 1 1 1 1 1 2 2 1 2 1 3 1 1 2 2 1 2 3 2 1 2 2 2 3 1 2 ? ? ? ? ? ? ? ? ? ? ? ? ?
Aenigmaticum	2 2 2 2 1 1 2 2 1 1 1 1 2 1 2 2 1 2 1 3 1 1 2 2 1 2 1 2 1 2 2 2 2 1 2 ? ? ? ? ? ? ? ? ? ? ? ? ?
Stanus	2 2 2 2 1 1 2 2 1 1 1 1 2 1 2 2 1 2 1 3 1 1 2 2 1 2 1 2 1 2 2 2 2 1 2 2 1 1 1 1 1 2 2 1 2 2 2 2
Cleidostethus	1 2 2 2 2 1 2 2 1 1 1 1 2 1 2 2 1 2 1 1 1 2 2 ? 1 2 1 2 2 1 2 2 3 1 2 ? ? ? ? ? ? ? ? ? ? ? ? ?
Periptyctus	3 1 2 2 1 2 1 3 1 1 1 1 2 2 1 1 1 2 1 3 1 1 1 1 1 1 2 2 2 3 1 2 2 1 1 2 2 2 2 2 1 2 1 1 2
Pakalukodes	3 1 2 2 1 2 1 3 1 2 1 1 1 2 2 2 1 1 1 3 1 1 2 1 1 2 1 2 1 2 2 2 3 1 2 1 1 1 2 2 2 2 2 1 2 1 1 2
Weirus	3 1 2 2 1 2 1 3 1 2 1 1 1 2 2 2 1 1 1 3 1 1 2 ? 1 2 1 1 1 2 2 2 3 1 2 ? ? ? ? ? ? ? ? ? ? ? ? ?
Sticholotis	3 1 2 1 3 1 2 1 1 1 1 1 2 1 3 - 1 2 1 1 1 2 1 2 2 2 2 1 2 1 2 2 3 2 1 3 1 1 1 1 1 1 2 1 2 2 2 2
Coccidophilus	3 1 2 1 1 1 1 1 1 1 1 3 3 1 3 - 1 2 1 1 1 2 1 2 2 2 2 2 2 1 2 2 3 2 1 3 1 1 1 1 1 1 2 1 2 1 1 2
Bystus	3 1 1 1 2 1 2 1 1 1 1 1 3 1 3 - 1 2 1 3 1 1 2 2 2 2 1 1 1 1 2 2 3 1 2 5 2 1 2 1 1 2 2 2 2 1 1 2
Aphanocephalus	3 1 1 1 1 1 1 1 1 1 1 1 1 1 2 2 1 2 1 3 1 1 2 2 2 1 1 1 1 1 1 3 3 3 2 3 1 2 2 1 1 1 1 2 1 1 1 2
Notiophygus	3 1 1 1 1 1 1 1 1 1 1 1 1 1 2 2 1 2 1 3 1 1 2 ? 2 1 1 1 1 1 1 3 3 3 2 3 1 2 2 1 1 1 1 2 1 4 1 2

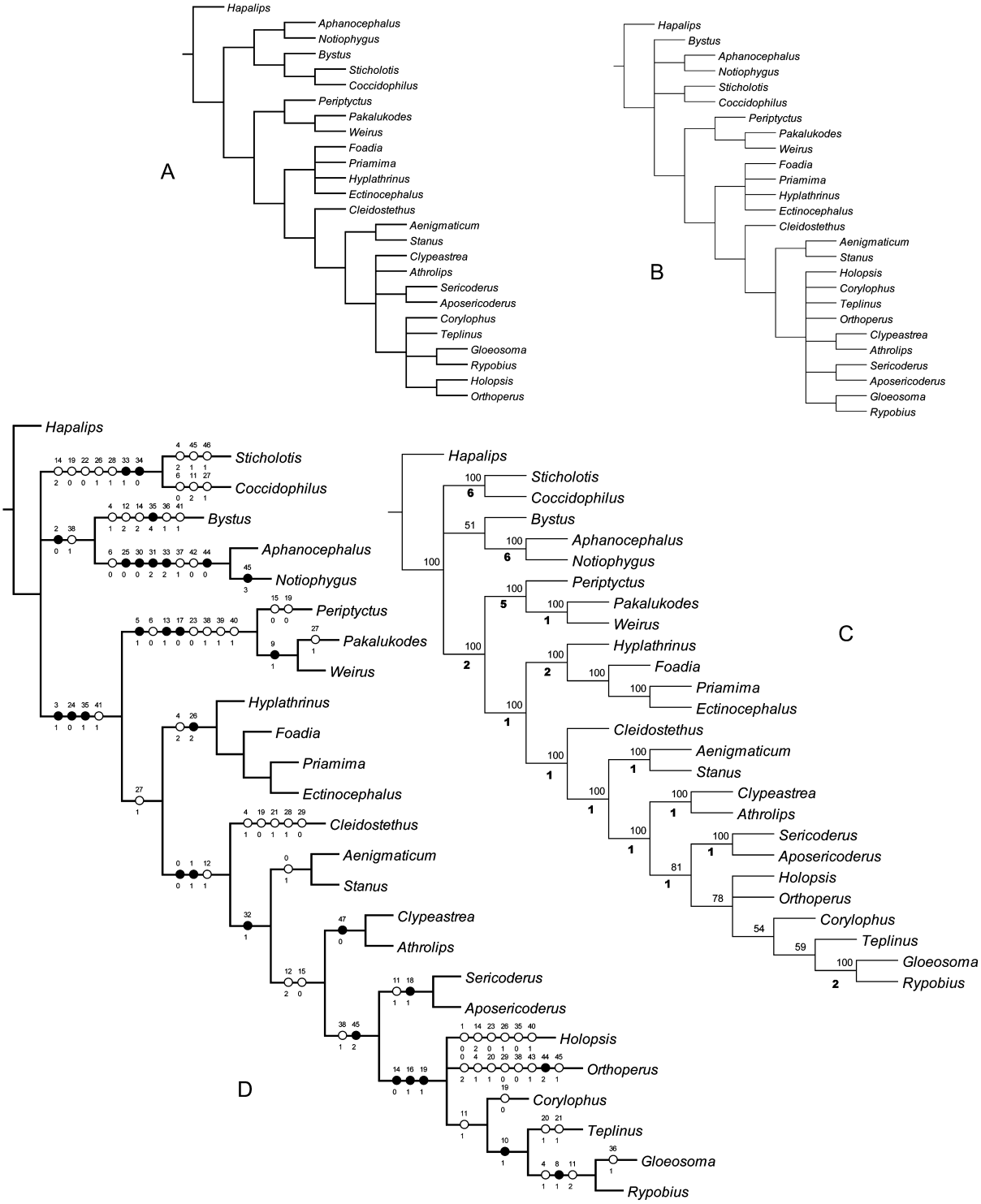

Fig. 1. Phylogenetic reconstructions of Corylophidae: (A) Nelsen consensus tree of four MPTs (most parsimonious trees) based on adult characters; (B) Nelsen consensus tree of 33 MPTs based on adult and larval characters; (C) majority-rule (>50%) consensus tree of 33 MPTs based on adult and larval characters with the frequencies with which nodes were retrieved indicated above the branches and Bremer support values indicated below branches; (D) same tree as (C) with characters mapped on branches using unambiguous character changes in WinClada – solid circles indicate non-homoplasious changes, open circles indicate homoplasious changes; the numbers above circles gives the character number, the numbers below give the character state.

Position of Holopsis (Peltinodinae). Our analyses do not support the hypotheses by Paulian (1950) or Bowestead (1999) concerning the sister-group relationship between *Holopsis* and the remaining Corylophidae. Paulian's findings on the position of *Holopsis* (=*Peltinodes* Paulian, *Corylophodes* Casey) were rather ill-founded and speculative. Bowestead, however, correctly observed that open procoxal cavities, distinct metaventral and abdominal postcoxal lines and wing with medial fleck are present only in *Holopsis*. Based on the distribution of these characters in other cucujoids, Bowestead concluded *Holopsis* to be 'primitive' and sufficient to warrant the separate subfamily Peltinodinae. In our phylogenetic reconstructions, *Holopsis* is contained within a terminal group and often clusters with *Orthoperus*. When forced to assume the sister-group position suggested by Bowestead (1999), the tree is four to five steps longer than the most parsimonious.

Position of Cleidostethus. It is difficult to assess the relationships of *Cleidostethus*, partly owing to the profound morphological changes resulting from its inquilinous habitats in bee nests. A reduced tentorium (1, 1) and distinct membranous vesicles (7, 1) are shared with the main group of Corylophidae (Corylophinae below), and the taxon is tentatively placed in its own tribe pending further analyses with a more robust in-group dataset.

Status of 'higher' Corylophidae. There is little support for resolution of relationships among taxa in this group, which is characterized by a relatively short anterior part of the prosternum (12, 2) and open or very narrowly closed procoxal cavities (15, 0), and it appears that each taxon or pair of taxa represents an independent lineage, traditionally treated as a separate tribe. This tradition is followed here and the composition of these groups is discussed under their appropriate headings in the classification section.

Classification

The following classification is consistent with the above phylogenetic hypotheses.

Family Corylophidae LeConte, 1852

Subfamily Periptycinae Ślipiński *et al.*, 2001

Genera: *Pakalukodes* Ślipiński *et al.*, 2001; *Periptyctus* Blackburn, 1895; *Weirus* **gen.n.**

Subfamily Corylophinae LeConte, 1852

Tribe Foadiini **trib.nov.**

Genera: *Ectinocephalus* Matthews, 1888; *Foadia* Pakaluk, 1985; *Hyplathrinus* Reitter, 1878; *Priamima* Pakaluk & Lawrence, 1986

Tribe Cleidostethini Bowestead *et al.*, 2001

Genus: *Cleidostethus* Arrow, 1929

Tribe Aenigmaticini Casey, 1900

Genera: *Aenigmaticum* Matthews, 1888; *Stanus* **gen.n.**

Tribe Orthoperini Jacquelin du Val, 1857

Genus: *Orthoperus* Stephens, 1829

Tribe Parmulini Poey, 1854

Genera: *Arthrolips* Wollaston, 1854; *Clypastraea* Haldeman, 1842; *Lepesmella* Paulian, 1950; *Sicardianus* Paulian, 1950; *Villiersium* Paulian, 1950

Tribe Peltinodini Paulian, 1950

Genus: *Holopsis* Broun, 1883

Tribe Sericoderini Matthews, 1888

Genera: *Aposericoderus* Paulian, 1950; *Sericoderus* Stephens, 1829

Tribe Corylophini LeConte, 1852

Genera: *Corylophus* Stephens, 1833; *Homogrypinus* Reitter, 1908, *Microstagetus* Wollaston, 1861

Tribe Teplinini Pakaluk *et al.*, 1994

Genus: *Teplinus* Pakaluk *et al.*, 1994

Tribe Rypobiini Paulian, 1950

Genera: *Catoptyx* Matthews, 1887; *Gloeosoma* Wollaston, 1854; *Hoplicnema* Matthews 1899; *Rypobius* LeConte, 1852

Keys to subfamilies and tribes of Corylophidae

Adults

1. Large-bodied (length 1.6–3.8 mm), anterior margin of pronotum deeply emarginate, exposing head (Fig. 2); antenna not geniculate with pedicel longer than scape; antennal club segments flattened in cross-section; antennal sensilla short, hardly visible and Y-shaped (Fig. 3H, I); prosternum elongate anterior to coxae with median part prominent and forming chin piece; hindwing with medial fleck present (Australia).....Periptycinae
– Smaller-bodied (length <1.5 mm); anterior margin of pronotum emarginate and anteriorly exposing head or not emarginate and covering head; antennae geniculate; antennal club segments oval in cross-section with large, variously shaped, membranous vesicles, prosternum shorter, may or may not form chin-piece; hindwing without medial fleck (Global).....2
2. Body elongate, latridiid-like; anterior margin of pronotum straight or emarginate, exposing head (Fig. 7A–C, E–G); anterior part of prosternum ≥1.5× as long as procoxa; postcoxal projections broad and firmly fused to expanded prosternal process 3
– Body oval or almost circular, anterior margin of pronotum may or may not be emarginate, with head exposed or concealed; anterior part of prosternum reduced to narrow sclerite <1.5× as long as procoxa; postcoxal projections, if present, narrow and not fused to expanded prosternal process.....4
3. First abdominal ventrite with postcoxal lines; anterior margin of pronotum emarginate medially.....Foadiini
– First abdominal ventrite without postcoxal lines; anterior margin of pronotum straight medially .....Aenigmaticini
4. Metaventrite with distinct postcoxal lines.....5
– Metaventrite without postcoxal lines.....6
5. Head exposed by medially emarginate pronotum; procoxal cavities externally closed; abdomen with five pairs

of spiracles; abdominal postcoxal lines reduced or absent; wing without medial fleck.....Orthoperini
– Head covered by anteriorly rounded pronotum; procoxal cavities narrowly open externally; abdomen with seven pairs of spiracles; abdominal postcoxal lines large and circular; wing with medial fleck present..... Peltinodini
6. Antenna short, 8-segmented; eyes absent; ventrites of pterothorax and abdominal ventrites 1–2 solidly fused (Fig. 7H, I); abdomen with five pairs of spiracles (Africa) .....Cleidostethini
– Antenna moderately long, 10- or 11-segmented; abdomen with seven pairs of spiracles; thoracic and abdominal ventrites articulated.....7
7. Prosternal process not carinate between coxae, expanded posterior to coxae and meeting postcoxal projections; postcoxal projections not fused to each other; procoxa oval and flat.....8
– Prosternal process raised or carinate between coxae, may or may not be expanded posterior to coxae, with narrow postcoxal projections; postcoxal projections always abutting; procoxae globular to conical and strongly projecting.....9
8. Posterior angles of pronotum acute and prominent; submentum narrow and prominent; mentum strongly reduced and transverse; basal labial palpomere elongate and distinctly longer than apical segment Sericoderini
– Posterior angles not distinctly prominent, mostly obtuse; submentum broad and short, mentum large, quadrate; basal labial palpomere short and about as long as terminal segment.....Parmulini
9. Mouthparts strongly modified; labrum triangularly prominent; endognathous mandible forming articulated blade bearing two apical hooks; gular region of head with median endocarina.....Rypobiini
– Mouthparts not modified, labrum arcuate anteriorly; mandible variable but never forming endognathous blade; gular region without endocarina.....10
10. Mesocoxal cavities transverse and externally open; mesoventrite without fossa.....Teplinini
– Mesocoxal cavities oval and externally closed; mesoventrite with median fossa receiving prosternal process .....Corylophini

Larvae

1. Abdominal segments without glandular openings.....2
– Abdominal segments with at least two glandular openings.....3
2. Length 2.5–4.0 mm; thorax wider than abdomen and $\geq$0.75$\times$ as long as abdomen; lateral tergal processes present on all thoracic segments and abdominal segments I–VIII; thorax and abdominal segment IX with elongate simple setae; antennomere two distinctly longer than wide; labrum fused with clypeus..... .....*Periptyctus*, *Pakalukodes* (Periptycinae)
– Length $\leq$1.8 mm; body narrow and almost parallel-sided (Fig. 7J); thorax not wider than abdomen, <0.45$\times$ as long as abdomen; antennomere 2 almost as long as wide; labrum free..... ..... *Foadia* (Foadiini)
3. Glandular openings present on abdominal segments I and VII only.....4
– Glandular openings present on segments I–VI or I–VII6
4. Body disc-like (Fig. 8A), evenly sclerotized dorsally; lateral margins of pronotum and abdomen with short fan-like scales; mouth parts strongly modified; mandible stylet-like and without mola or prostheca; antenna long and 2-segmented..... .....*Rypobius*, *Gloeosoma* (Rypobiini)
– Body variable in shape, lighty sclerotized, sometimes disc-like; numerous scale-like setae present along body margins in addition to a few longer, simple setae on the pronotum and abdominal segment IX; if antennae elongate then 3-segmented, if short then 2-segmented 5
5. Labrum and clypeus not fused; antenna shorter and 2-segmented; labial palp 2-segmented; body elongate and not appearing disc-like (Fig. 8D)..... .....*Sericoderus* (Sericoderini)
– Labrum and clypeus solidly fused; antenna elongate and 3-segmented; labial palp 1-segmented; body more disc-like (Fig. 8C).....*Holopsis* (Peltinodini)
6. Glandular openings present on abdominal segments I–VI; labial palp 1-segmented *Orthoperus* (Orthoperini)
– Glandular openings present on abdominal segments I–VII; labial palp 2-segmented.....7
7. Tergum IX well sclerotized (Fig. 8B) with short spines/asperities; antennomere 3 longer than sensorium; abdominal glandular openings usually on short tubes, the first tube often directed anteriorly..... .....*Clypastraea*, *Arthrolips* (Parmulini)
– Tergum IX dark but not well sclerotized and lacking asperities; antennomere 3 about as long as sensorium; abdominal glandular openings located on body surface.....*Stanus* (Aenigmaticini)

Review of subfamilies and tribes

Subfamily Periptycinae Ślipiński *et al.* (2001)

McHugh & Pakaluk (1997): 69, larva; Ślipiński *et al.* (2001): 311–317; Tomaszewska & Ślipiński (2002): 499–532.

Included genera. *Pakalukodes* Ślipiński *et al.*, 2001; *Periptyctus* Blackburn, 1895; *Weirus* gen.n.

Adult. Length 1.6–3.8 mm. Head partially withdrawn into prothorax but visible from above (Fig. 2). Tentorial arms complete and separate. Antenna 11-segmented, long and not geniculate in repose, resting in groove along raised prosternum; pedicel distinctly longer than scape; club segments flat, asymmetrical; Y-shaped sensilla on sides of first two club segments (Fig. 3H, I). Submentum not well defined; mentum distinct, quadrate; labial palps 2-segmented, basal palpomere short and about as long as apical segment. Mandible triangular, flat with reduced mola and

large complex prostheca. Anterior margin of pronotum deeply emarginate medially. Prosternum in front of coxae ≥2.5× as long as longitudinal coxal diameter; anterior portion expanded to form chin piece, concealing part of head from below. Notosternal suture visible anteriorly. Procoxae oval, flat, narrowly closed externally; procoxal cavities with narrow slits; prosternal process about as broad as coxal diameter, weakly expanded posteriorly, extending behind coxae and weakly overlapping mesoventrite. Mesocoxae oval, broadly separated; mesocoxal cavities laterally closed. Metaventral postcoxal lines absent. Elytral epipleura broad at base and almost complete apically. Wing with medial fleck. Abdomen with five or six ventrites and seven pairs of functional spiracles; ventrite 1 as long as 2–4 combined.

Larva (Periptyctus, Pakalukodes). Body with pronotum distinctly wider than abdomen (Fig. 6C), ≥0.75× as long as wide, covering most of head from above; prominent lateral tergal processes on all thoracic and most abdominal segments; thoracic and abdominal margins with long simple setae. Head prognathous; labrum and clypeus solidly fused to head capsule; one or two stemmata; frontal arms U-shaped and not clearly joined at base. Antenna 3-segmented, elongate, with second antennomere five to six times as long as wide. Mandibles endognathous, broad and flat with reduced mola and prostheca. Labial palps 2-segmented. Legs long and slender; claw slender with single simple seta. Glandular openings absent.

Discussion. Periptycinae are robust-bodied Corylophidae and externally appear more like Endomychidae than Corylophidae. The original diagnosis by Ślipiński *et al.* (2001) remains valid with an amendment to the nature of the antennal vesicles; here studied in detail with SEM imaging and observed to be Y-shaped processes on both sides of the flattened surfaces of antennomeres 9 and 10. In addition, the larva of *Pakalukodes bimaculatus* described below differs from *Periptyctus* by having the pronotum less prominent, only one stemma on each side of the head and the frontal arms clearly joined at base.

Key to Periptyctinae genera

1. Abdomen with six visible ventrites; pronotum without sublateral carina or groove.....*Pakalukodes* Ślipiński *et al.*
– Abdomen with five visible ventrites; pronotum with a weak to strong sublateral carina or groove.....2
2. Body circular in outline (1.12–1.17× as long as wide); pronotum narrowly and finely bordered; median part of prosternum in conjunction with intercoxal process forming a well-defined and raised parallel-sided structure (Fig. 3C).....*Weirus* **gen.n.**
– Body more elongate (1.27–2.00× as long as wide); pronotum with strong lateral carinae or grooves; median part of prosternum bordered by diverging anterior carinae or lines.....*Periptyctus* Blackburn

Weirus **gen.n.** (Figs 2B, 3, 4)

Type species. *Weirus tozer* **sp.n.**

Etymology. The generic name is dedicated to our colleague Tom Weir, who collected specimens of this beautiful beetle. Gender masculine.

Diagnosis. This genus is closely related to *Pakalukodes*, but can be separated from it by having the body almost circular in outline, the pronotum distinctly, moderately widely bordered, and the intercoxal process of mesoventrite 1 trapezoidal.

Description. Body (Fig. 2B) almost circular in outline, wingless, strongly convex, shiny, sparsely setose. Head visible dorsally, transverse with clypeal region slightly declined. Eyes coarsely faceted. Gular region well defined, translucent; gular sutures weakly apparent, short. Antennal insertions close to eyes. Antenna (Fig. 3E) long, 11-segmented with moderately loose 3-segmented club; pedicel longer than scape; antennomere 5 about 2× as long as either 4 or 6; antennomere 7 slightly longer than 6 or 8; club asymmetrical, weakly flattened, with very small Y-shaped sensilla at apex of antennomeres 9 and 10. Mouthparts somewhat modified. Mandibles, laciniae and ligula fitting

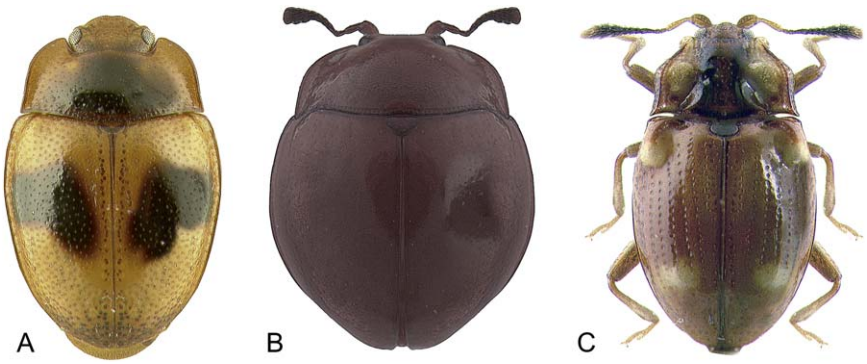

Fig. 2. Genera of Periptycinae: (A) *Pakalukodes bimaculatus*; (B) *Weirus tozer*; (C) *Periptyctus quadrinotatus*.

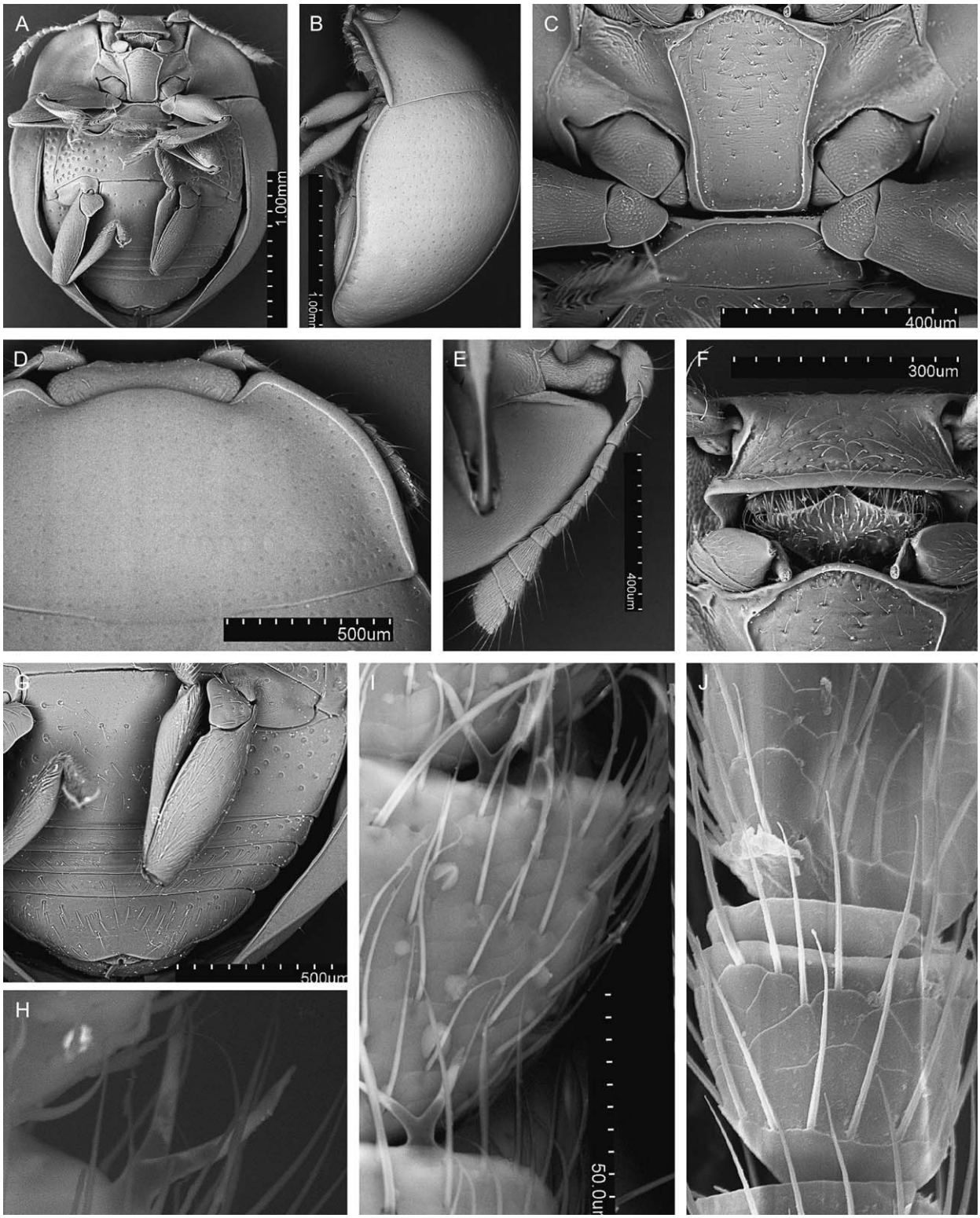

Fig. 3. (A–G) *Weirus tozer*, male: (A) ventral view; (B) lateral view; (C) prosternum; (D) pronotum; (E) antenna; (F) Clypeus and mouth parts; (G) abdomen; (H) *Periptyctus* sp., sensillum on antennomere 9; (I) *Pakalukodes bimaculatus*, sensilla on antennomeres 9, 10; (J) *Rypobius* sp., sensilla on antennomeres 9, 10.

tightly together to function as a single 'grinding' structure. Labrum (Fig. 3G) transverse, deeply emarginate medially, densely covered with long setae. Mandible (Fig. 3B) strongly flattened, with apex submembranous, rounded and setose; weakly developed; mola transversely ridged with a small setose area 'pseudoprostheca' present. Maxilla with 3-segmented club; palpomeres 1 and 2 transverse, terminal palpomere conical; lacinia moderately sclerotized, expanded apically, ridged and asperate along upper apical surface. Labium (Figs 2F, 3F) forms a three-dimensional structure; mentum weakly trapezoidal; ligula sclerotized, expanded apically and shallowly emarginate medially at apex; in dorsal view a middle, acute projection is visible; palps 2-segmented, inserted ventrolaterally.

Pronotum (Fig. 3D) convex with weak concavities along lateral margins, which are distinctly bordered; anterior margin deeply emarginate, bordered except for medial section; anterior angles weakly produced and somewhat acute, posterior angles right-angled; lateral margin gently rounded; basal margin not emarginate; disc without pits or grooves.

Prosternum forming medially a large, well-defined, prominent and bordered, parallel-sided prosternal process, which is arcuate anteriorly forming a short chin piece; prosternum in front of coxae concave to receive antennal pedicel in repose; prosternal process (Fig. 3C) about as broad as coxa, not extending much beyond front coxae, truncate at apex. Procoxal cavity externally and internally closed with shallow slit at the base of notosternal suture; procoxa weakly oval in outline, trochantin concealed.

Scutellum small, transverse, somewhat pentagonal in shape with pointed apex, very coarsely punctured. Mesoventrite (Fig. 3C) weakly ridged with intercoxal process strongly transverse, 1.6–1.7× as broad as coxal diameter, flat, apparently glabrous, trapezoidal in shape; extending to about mid length mesocoxae. Mesocoxa circular in outline, its cavity outwardly closed; trochantin hidden. Meso-metaventral junction straight. Elytra (Fig. 3A, B) covering entire abdomen; widest near anterior third, distinctly narrowing towards posterior third, thence abruptly rounded with blunt apices; strongly convex with punctures moderately dense, coarse and irregular (with only regular row along lateral margin and short row along suture); humeri flat; lateral margin distinct, with narrow bead that is incomplete apically; epipleuron wide at base but incomplete at very apex. Apex and both outer and inner sides of ventral surface of elytron covered with sharp spinulae. Metaventrite weakly convex, strongly transverse, slightly shorter than abdominal ventrite 1; very coarsely punctured, without postcoxal lines, with very short discrimen.

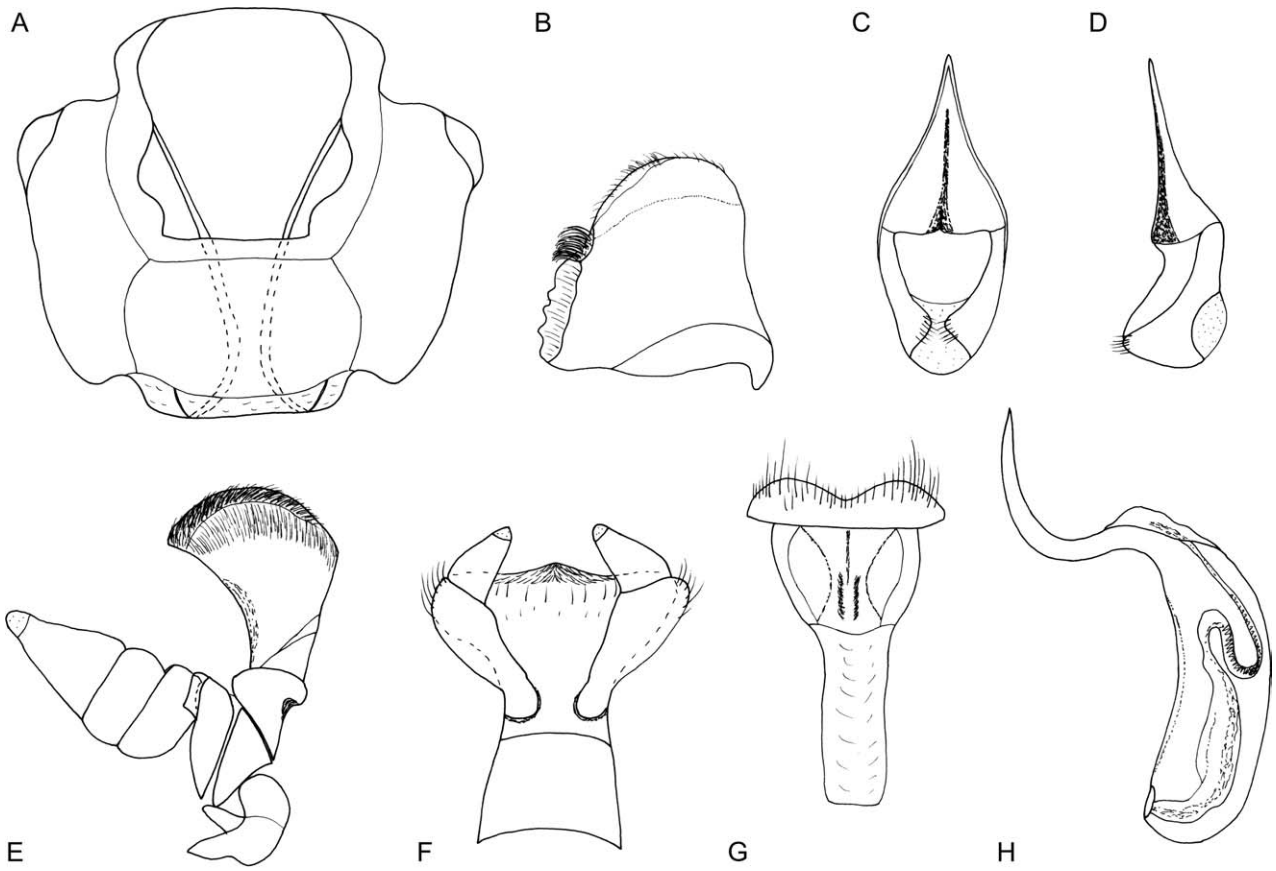

Fig. 4. *Weirus tozer*, male: (A) head, ventral; (B) mandible; (C) tegmen inner; (D) tegmen, lateral; (E) maxilla; (F) labium; (G) labrum; (H) penis.

Metacoxae transverse, widely separated. Metendosternite with rather short stalk and widely separated anterior arms. Legs comparatively long and rather slender; trochanterofemoral attachment heteromeroid (Fig. 3G). Femur subcylindrical with deep groove throughout to receive tibia; tibia widening towards tarsus, with short apical spinulae; tarsi 4-4-4 in both sexes; tarsomeres 1 and 2 weakly lobed and densely setose ventrally. Claws simple, empodium absent.

Abdomen with five freely articulated ventrites; intercoxal process of ventrite 1 broad and truncate, without femoral lines. Ventrite 1 only slightly shorter than ventrites 2–5 combined; ventrites 2–4 equal in length. Ventrite 5 in male shallowly excised medially at apex (Fig. 3G), in female rounded apically. Male abdominal segment VIII with sternite short and finely denticulated at apex; tergite with weak apical emargination. Aedeagus long and stout, strongly sclerotized along apical half and moderately sclerotized along basal half; resting on its side when retracted. Penis (Fig 4H) with long, strongly sclerotized branch, pointed at apex. Tegmen (Fig. 4C, D) with basal piece reduced to simple ring encircling penis; oval apertures and parameres absent; tegminal strut pointed apically with long median endocarina. Female sternite VIII pointed apically; ovipositor long, styli long and terminal with two apical setae; bursa copulatrix large without apical sclerites; spermathecal duct sclerotized at origin without infundibulum; spermatheca as in Fig. 8(I).

Discussion. *Weirus* is very similar and probably sister to *Pakalukodes*, sharing the peculiar gular region and the modified mouthparts with mandibles, laciniae and ligula fitting together and forming a 'grinding' structure; however, it shares with *Periptyctus* many features such as the gular sutures weakly indicated at base, the tegmen with a single, median carina and the abdomen with five ventrites. At least the modified mouthparts (as opposed to the normal chewing type mouthparts in *Periptyctus*) may serve as a potential synapomorphy for the two genera.

Weirus tozer sp.n.

Type material. Holotype ♂: 12°43 S 143°17E, 9 km ENE of Mt. Tozer QLD, 5–10.vii.1986 (*T. Weir*) Berlesate, ANIC 1061, open forest litter (ANIC); three paratypes, same data as holotype (two, ANIC; one, MIZ, dissected on slide).

Etymology. Named after Mount Tozer, near the type locality.

Description. Length 2.17–2.35 mm. Body 1.12–1.17× as long as wide; pronotum 0.50–0.55× as long as wide; elytra 0.88–0.90× as long as wide; 2.10–2.17× as long as pronotum, 1.16–1.28× as wide as pronotum. Dorsal surfaces black with at least clypeus and area around eyes, and lateral margins of pronotum orange-brown, and scutellum infuscated. Ventral surface with mouthparts and prothorax orange-brown, meso-and metathorax, elytral epipleura, and abdominal ventrites black (apex of terminal ventrite and apical part of epipleura infuscated). Pronotum with lateral edges smooth, with base almost as broad as base of elytra; punctures moderately coarse, a little denser than those on elytra, 1–2 diameters apart, interspaces smooth. Elytra with punctures slightly coarser than the pronotal ones, 1.5–2.5 diameters apart, some of them are setigerous. Aedeagus as in Fig. (4C, D, H).

Distribution. Australia (Queensland).

Pakalukodes bimaculatus Ślipiński *et al.* (2001) – mature larva (Fig. 6A–G)

Material examined. Queensland, Palmerston National Park, E Margin (17.37S, 145.46E), pyrethrum trees and logs, 9.xii.1995 (*Monteith*); 10 larvae associated with adults (QM, ANIC).

Diagnosis. This larva is similar to that of *Periptyctus* but may be distinguished by the less laterally expanded thorax (only slightly wider than the abdomen), the bilobed lateral tergal process on each side of the prothorax and mesothorax, and the presence of only one stemma on each side.

Description. Length 3.0–3.5 mm; body elongate oval, with thorax slightly wider than and about 0.80× as long as abdomen; head almost entirely covered by prothorax from above (Fig. 6C). Dorsal surfaces irregularly pitted, rough, with dense scale-like or stellate processes. Colour brown or yellowish brown, sometimes with darker irregular pattern. Vestiture of sparse, simple setae; dorsum with six setae on protergum, two on metatergum and six (four long and two shorter ones) on abdominal tergum IX, the long setae about as long as protergum; venter with pairs of moderately long admedian setae on each abdominal segment. Head (Fig. 6G) 0.6× as long as wide, prognathous and protracted; head capsule arcuate dorsally, deeply emarginated ventrally. Frontal arms U-shaped, joined at base and extending anteriorly to the level of antennal foramen; weak endocarine developed under arms, especially anteriorly; epicranial stem absent. Stemmata reduced to a single lens located immediately posterior to antennal insertion. Antenna (Fig. 6E) 0.8–0.9× as long as head width; antennomere length ratios 2:10:3; antennomere 3 swollen apically and bearing several sensilla; sensorium conical and about as long as antennomere 3; antennal insertion very distant from mandibular articulation. Frontoclypeal suture absent. Labrum fused to clypeus to form a well-sclerotized and dentate clypeolabrum (Fig. 6F). Mandibles symmetrical (Fig. 6A) not visible externally, covered by clypeolabrum, flat and endognathous; mandible triangular, unidentate apically with large complex prostheca and obsolete mola. Ventral mouthparts retracted with maxillary articulating area absent. Maxilla (Fig. 6B) with all basal components fused, sclerotized along inner and outer margins; mala large and flattened with truncate apex bearing inner apical spines and basal sclerotized angular structure; maxillary palp about as long as mala, 3-segmented;

palpomere length ratio 1:1:2. Gula, submentum and mentum form single membranous structure; prementum partially separated; labial palps broadly separated at base, 2-segmented with apical palpomere at least twice as long as basal one; ligula membranous and densely setose, slightly longer than labial palps. Hypopharyngeal sclerome well developed. Hypostomal rods and ventral epicranial lines absent. Prothoracic tergum about 2× as long as meso- or metatergum, arcuate anteriorly and weakly incised at middle, with broad, bilobed tergal process on each side; mesotergum with similar bilobed processes, metatergum and abdominal segments I–VIII each with undivided lateral process; tergum IX longer and emarginated medially; segment X circular and ventral. Legs slender and long; all coxae separated by slightly more than their transverse diameter; claw slender with single apically clavate seta (Fig. 6D). Spiracles annular located ventrally on mesothorax and abdominal segments I–VIII.

Subfamily Corylophinae LeConte, 1852

This subfamily is equivalent to the traditional Corylophidae (Bowestead, 1999; Bowestead & Leschen, 2002), and is defined here based on the presence of membranous vesicles on at least the two basal segments of the antennal club (#7,1). There is considerable variation in the number and form of these vesicles, and the potential exists that these may provide some useful characters for a more natural classification of the taxon. Other distinguishing characters among the adults are shorter antennae with an oval club in cross-section, prosternum short and not forming a chin piece, and procoxal cavities without lateral slits.

Tribe Foadiini trib.n.

Type genus. *Foadia* Pakaluk, 1985a. – Pakaluk, 1985a: 406, 1985b: 69, 1985c: 207; Pakaluk & Lawrence, 1986: 81.

Included genera. *Ectinocephalus* Matthews, 1888 (= *Conodes* Matthews, 1888), *Foadia* Pakaluk, 1985a, *Hyplathrinus* Reitter, 1878, *Priamima* Pakaluk & Lawrence, 1986.

Adult. Length 1.0–1.2 mm. Head exposed and well visible from above (Fig. 7C). Tentorial arms complete and joined posteromedially. Antenna 10- or 11-segmented, not apparently geniculate; pedicel subequal to scape; club segments oval in cross-section and weakly asymmetrical; small membranous sensilla on sides of first two club segments. Submentum broad, not well defined; mentum distinct, quadrate; labial palps 2-segmented, basal palpomere elongate and 2× as long as apical one. Mandible triangular with large tuberculate mola and prostheca. Anterior margin of pronotum distinctly emarginate anteriorly. Prosternum in front of coxa 2× as long as coxal longitudinal diameter; anterior portion straight; notosternal sutures distinct anteriorly. Procoxa circular, flat; procoxal cavities without slits, firmly closed externally; prosternal process 0.3–0.5 width of coxal diameter, narrowed between coxae and weakly expanded posteriorly, reaching distinctly behind coxae. Mesocoxae circular, broadly separated; mesocoxal cavities broadly closed laterally. Metaventral postcoxal lines absent. Wing without medial fleck. Abdomen with six ventrites and seven pairs of spiracles; ventrite 1 as long as 2–4 combined, with straight or slightly curved externally postcoxal lines.

Larva (Foadia). Body elongate (Fig. 7J), lightly sclerotized except for darker head, pronotum and abdominal tergum IX; pronotum longer than wide not covering head from above; thoracic and abdominal margins with short fan-shaped setae. Head prognathous; labrum and clypeus separated; two stemmata on each side; frontal arms U-shaped and not clearly joined at base. Antenna 3-segmented with antennomere 2 about as long as wide. Mandibles triangular, broad and tridentate apically, mola tuberculate, prostheca absent. Labial palps 2-segmented. Legs moderately long and slender; claw slender with single, simple seta. Gland openings absent.

Discussion. This group is recognized here to include the three New World genera *Foadia* Pakaluk, *Ectinocephalus* Matthews and *Hyplathrinus* Reitter, plus the Australian genus *Priamima* Pakaluk & Lawrence. These genera traditionally have been associated with *Orthoperus* (Orthoperini) or with *Aenigmaticum* (Aenigmaticini). The first placement was questioned by Pakaluk (1985c), who noted that *Orthoperus* belongs with the 'higher Corylophids' whereas the latridiid-like genera belong to the 'lower Corylophids', resulting in a paraphyletic Orthoperini (sensu Paulian, 1950). Pakaluk (1985a, c) also noted that *Aenigmaticum* differs from other 'lower Corylophids' by the lack of abdominal postcoxal lines, reduced subbasal pronotal impressions and long humeral striae on the elytra. Bowestead (1999) suggested a similar split based on the presence or absence of abdominal postcoxal lines.

Tribe Aenigmaticini Casey, 1900

Aenigmaticini Casey, 1900: 61. – Pakaluk, 1985a: 406, 1985b: 69, 1985c: 207; Pakaluk & Lawrence, 1986: 81; Bowestead & Leschen, 2002: 392.

Included genera. *Aenigmaticum* Matthews, 1888, *Stanus* **gen.n.**

Adult. Length 1.0–2.1 mm. Head partially exposed and visible from above (Fig. 7A). Tentorial arms strongly reduced, visible at base. Antenna 9- or 11-segmented, weakly geniculate; pedicel at most subequal to scape; club perfectly symmetrical and its segments oval in cross-section; small membranous sensilla present on at least the first two club segments. Submentum broad, not well defined; mentum distinct, quadrate; labial palps 2-segmented, basal palpomere short and as long as apical one. Mandible triangular with large tuberculate mola and prostheca. Anterior margin of pronotum straight. Prosternum in front

of coxae 1.0–1.2× as long as coxal longitudinal diameter; anterior portion straight or weakly arcuate; notosternal sutures defined anteriorly. Procoxae almost circular, flat; procoxal cavities without slits, firmly closed externally; prosternal process 0.3–0.5× as broad as coxal diameter, narrowed between coxae and expanded posteriorly, reaching distinctly behind coxae. Mesocoxae oval broadly separated; mesocoxal cavities laterally closed. Metaventral postcoxal lines absent. Wing without medial fleck. Abdomen with six ventrites and seven pairs of functional spiracles; ventrite 1 as long as 2–4 combined, without postcoxal lines.

Larva (Stanus). Body elongate (Fig. 6I, J), lightly sclerotized except for head, paired admedian thoracic sclerites and dark macula on abdominal tergum IX. Head visible from above. Thoracic and abdominal margins with simple and short scale-like setae. Head prognathous; labrum and clypeus separate; stemmata two; frontal arms U-shaped and not clearly joined at base. Antenna 3-segmented with antennomere 2 as long as wide. Mandibles broad tridentate apically with tuberculate mola, prostheca absent. Labial palps 2-segmented. Legs short; claw thickened at base with single spatulate seta. Gland openings larger than spiracles on surface of segments I to VII (last on VIII).

Discussion. This tribe, limited here to *Aenigmaticum* Matthews and *Stanus* **gen.n.** corresponds to the second group (without postcoxal lines) among the 'lower Corylophidae' mentioned by Bowestead (1999). The discovery of *Aenigmaticum* larva will test the present phylogenetic hypothesis, and it is assumed that it will have eight pairs of defensive glands similar to those described below for *Stanus*.

Stanus gen.n.

Type species. *Stanus bowesteadi* sp.n.

Etymology. Both genus and type species are named after Stanley Bowestead, a well-known corylophid researcher. Gender masculine.

Diagnosis. *Stanus* differs from *Aenigmaticum* by its 11-segmented antenna with segment VIII very small, the anterior prosternal margin weakly prominent medially and the mesoventral process with arcuate carina.

Adult description. Body (Fig. 7F) elongate, widest at middle of elytra, weakly convex and dorsally setose; elytra apically truncate exposing pygidium. Head well visible from above. Eyes coarsely faceted. Gular region long but without distinct gular sutures (Fig. 5C). Tentorium reduced to short sclerotized processes at the base of foramen directed posteriorly. Antenna (Fig. 5B) 11-segmented with distinct 3-segmented club; scape longer than pedicel; antennomere 7 distinctly larger than 6 or 8 and asymmetrical; club segments symmetrical, oval in cross-section, with very small eversible vesicles on antennomeres 9 and 10. Labrum transverse, emarginate medially. Mandible with three strong apical teeth, tuberculate mola and membranous prostheca. Maxilla with 3-segmented palp, palpomeres 1 and 2 transverse, terminal palpomere conical; lacinia sclerotized and dentate apically. Submentum narrow, weakly prominent. Labium (Fig. 5E) with subquadrate; ligula sclerotized, long and weakly expanded apically; labial palp 2-segmented with basal segment only slightly larger than apical one. Pronotum widest at base, anterior margin straight not bordered; lateral margins with narrow borders; disk evenly convex without subbasal pits or grooves. Prosternum in front of coxae about as long as longitudinal coxal diameter, medially arcuate and slightly prominent; prosternal process (Fig. 5G) 0.6–0.7× as broad as coxa, distinctly widened beyond front coxae, meeting separate postcoxal extensions, truncate at apex. Procoxal cavity externally and internally closed without slits; notosternal suture absent; procoxa weakly oval in outline, trochantin concealed. Mesoventrite (Fig. 5A) flat, without distinct coxal rests or foveae anteriorly but with complete transverse carina at about midlength of midcoxae; intercoxal process transverse, 1.2× as broad as coxal diameter, flat. Mesocoxa circular in outline, its cavity outwardly closed; trochantin hidden. Meso–metaventral junction straight. Elytra covering entire abdomen except for part of pygidium; flattened with sparse, irregular punctures; epipleuron very narrow, disappearing from the level of abdomen. Metaventrite weakly convex without postcoxal lines, without discrimen. Metacoxae transverse, broadly separated. Metendosternite with rather short stalk and widely separated anterior arms. Hind wing without medial fleck. Legs with trochanterofemoral attachment strongly heteromeroid; all tibiae with short but strong apical spur; tarsi 4-4-4 in both sexes; tarsomeres 1 and 2 weakly lobed and setose ventrally; claws simple, empodium absent. Abdomen with six freely articulated ventrites (Fig. 5 D); ventrite 1 as long as ventrites 2 and 3 combined; ventrite 6 long, arcuate and crenulated along external margin at apex. Intercoxal process of ventrite 1 very broad and truncate, without postcoxal lines. Penis (Fig. 8J, K) short, sclerotized with complex internal sack; tegmen with basal piece reduced to narrow ring encircling penis; oval apertures and parameres absent; tegminal strut pointed apically without median endocarina. Ovipositor with long triangular coxites and styli bearing two apical setae; bursa copulatrix large, membranous with sperm duct originating terminally in a short infundibulum; spermatheca simple (Fig. 8G).

Larval description. Length 2.0–2.2 mm. Body elongate, convex, lightly sclerotized except for head, paired admedian thoracic sclerites and dark macula on abdominal tergum IX; dorsal surfaces densely spinulose. Thoracic and abdominal margins with both sparse simple pointed setae and numerous short scale-like setae. The simple setae are distributed as follows: prothorax four setae anteriorly and four on each side; meso-, metathorax and abdominal segments I–VIII each with single lateral seta; segment IX with six setae along posterior margin. Head prognathous, 1.3× as wide as long, well visible from above. Labrum transverse, well separated from clypeus. Frontal arms U-shaped anteriorly reaching clypeus and not clearly joined at base. Stemmata 2 situated

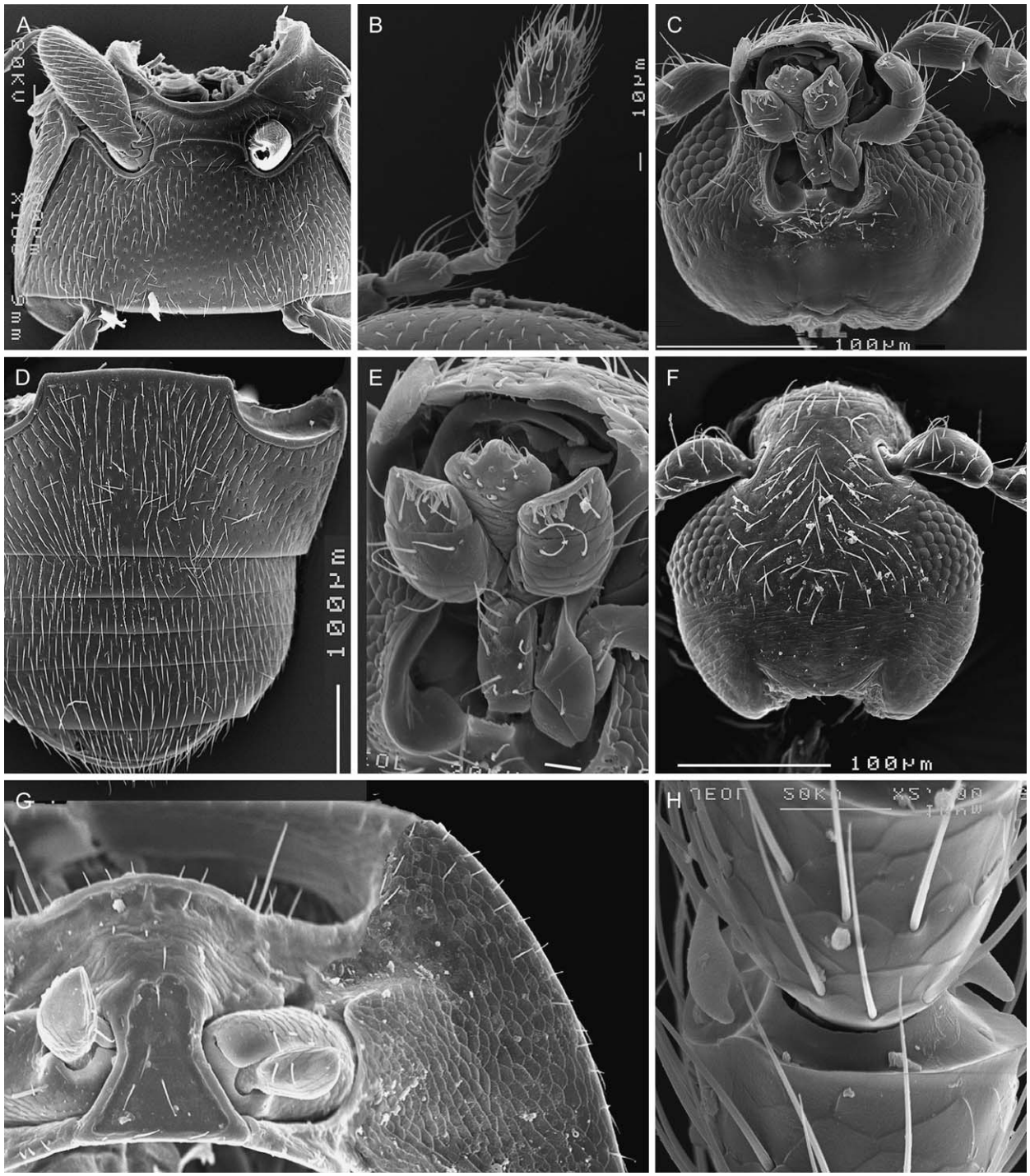

Fig. 5. *Stanus bowesteadi*: (A) meso-metathorax; (B) antenna; (C) head ventral; (D) abdomen; (E) labium; (F) head dorsal; (G) prothorax, ventral; (H) antennomere IX with sensory vesicles.

laterally below antennal foramen. Antenna 3-segmented, its length 0.3–0.35× head width; antennomere 2 about as long as wide; 3 slightly shorter than 2; sensory appendix located ventrally to segment III and about as long as that segment. Ventral mouth parts strongly protracted. Mandibles (Fig. 6H) broad tridentate apically with large tuberculate mola, prostheca absent. Maxillary cardo indistinct; mala short, blunt apically; maxillary palp 3-segmented, segments one and two very short, segment three longer than one to two. Labial palps 2-segmented with apical segment much longer than the basal

one. Legs short; claw thickened at base with single spatulate seta. Gland openings larger than spiracles, on surface of segments one to seven (last extending on segment eight).

Stanus bowesteadi sp.n.

Types. Holotype, NEW ZEALAND WD/OL, Haast Pass, 550 m, W of Summit, 24.i.1978, sifted litter and rotten wood 78/52 (*G. Kuschel*) (NZAC). – Paratypes. Picton, ix.1969 (*G. Kuschel*) (2, NZAC); WO: Onewhero, 19.iii.1984, 84/53, lichen (*A.K. Walker*) (4, NZAC; 2, ANIC; 1, MIZP); same locality, 8.iv,1985, Malaise trap north of *Beilschmiedia taruairi* forest (*R.A. Galbreath & S. Grant*) (1, NZAC); WD: Hunts Beach SF, ii.1984, Malaise trap in *Kahikatea* forest (*P.D. Gaze*) (1, NZAC); HB: Kaweka Ra, 965 m, Ngahere Basin, 20–27.xii.1983, window trap (*J.C. Watt*) (1, NZAC); NC: 8 km S Arthur's Pass (town) 670 m, 19–21.iii.1980, Berlese lichens, sooty mould & moss on *Nothofagus* (*A. Newton & M. Thayer*) (2, ANIC; 1, MIZP; several larvae in ANIC).

Diagnosis. The species differs from *S. tasmanicus* in having the pygidium exposed, the pronotum widest at base with the sides narrowing anteriorly, the lateral margins simple, the elytra distinctly bicoloured and the spermathecae of a different shape.

Description. Length 0.9–1.2 mm. Dorsum light brown to dark brown with elytra often bearing oblique or longitudinal yellowish markings (Fig. 7F); antennae and legs testaceous; upper surfaces shiny and covered by moderately dense adpressed setae. Antenna 11-segmented, as in Fig. 5 (B). Pronotum transverse, 0.6–0.7× as long as wide, widest near middle with lateral margins clearly beaded and more strongly arcuate anteriorly than posteriorly; anterior margin straight; anterior angles rounded and indistinct, posterior ones right-angled; base arcuate medially. Pronotal disc weakly convex, densely punctate, punctures about as large as eye facets and 1–1.5 diameters apart; interspaces shiny without visible microsculpture. Scutellum transverse, relatively large and arcuate posteriorly. Elytra 1.2–1.3× as long as wide and 2.4–2.6× longer than pronotum, oval in shape, widest near middle and truncate apically exposing 1–2 abdominal tergites; apico-sutural angle rounded; sutural stria visible in apical half of elytron; elytral surface densely punctate, punctures similar in size and distribution to the pronotal ones. Aedeagus as in Fig. 8(J, K); spermatheca as in Fig. 8(G).

Stanus tasmanicus sp.n.

Types. Holotype, AUSTRALIA, Tasmania: 9 km W by S Poatina, 20.i.1993 (*I.D. Naumann & J. Cardale*), ANIC Berl. 789, *Eucalyptus* litter (ANIC). Paratype: Waddamanna, 1.iii.1982 (*G. Bornemissza*) (1, ANIC).

Diagnosis. The species is easily separated from *S. bowesteadi* by having the pygidium covered by elytra, the pronotal sides distinctly narrowing towards base, the lateral margins crenulated and very different spermathecae.

Description. Length 1.3–1.5 mm. Dorsum brown with pronotum slightly lighter than head or elytra (Fig. 7G); antennae and legs testaceous; upper surfaces shiny and covered by short and sparse adpressed setae. Pronotum transverse, 0.75× as long as wide, widest near anterior third and more strongly narrowing posteriorly than anteriorly; lateral margins clearly beaded and weakly crenulated at edges; anterior angles blunt, posterior ones right-angled; base arcuate medially. Pronotal disc slightly convex, densely punctate, punctures about as large as eye facets and one or less diameters apart; interspaces shiny without visible microsculpture. Scutellum transverse, relatively large and arcuate posteriorly. Elytra 1.63× as long as wide and 2.17× as long as pronotum, elongate oval in shape, widest near middle and rounded apically completely covering abdominal tergites; sutural stria invisible; elytral surface densely punctate, punctures similar in size but slightly sparser than the pronotal ones. Aedeagus not examined; spermatheca as in Fig. 8(H).

Discussion. This species differs significantly from the type species by the pronotal and pygidial characters described above, and by the mesoventral process narrow and lacking the arcuate carina.

Tribe Cleidostethini Bowestead *et al.* (2001)

Included genus. *Cleidostethus* Arrow, 1929.

Adult. Length 1.6–1.8 mm. Head entirely withdrawn into prothorax and not visible from above (Fig. 7H, J). Eyes absent. Tentorial arms reduced and visible at base only. Antenna 8-segmented, short and not doubly geniculate in repose; pedicel distinctly shorter than scape; club segments oval in cross-section, asymmetrical; membranous sensilla on sides of first two club segments. Submentum broad; mentum distinct, longer than broad; labial palps 2-segmented, basal palpomere short slightly longer than the apical one. Mandible triangular, tridentate apically, with large but smooth mola and no prostheca. Anterior margin of pronotum arcuate medially. Prosternum about as long as coxal longitudinal diameter; anterior portion emarginate medially but covering most of deeply inserted head from below. Procoxae circular, flat; procoxal cavities without slits, closed externally; prosternal process broader than coxal diameter, distinctly expanded posteriorly with median projection reaching far behind coxae and received in mesoventral cavity. Mesocoxae oval, very broadly separated; mesocoxal cavities laterally open. Metaventral postcoxal lines absent. Sutures between meso- and metaventrite, metaventrite and first abdominal ventrite and first two abdominal ventrites completely obsolete. Elytral epipleura broad at base and complete

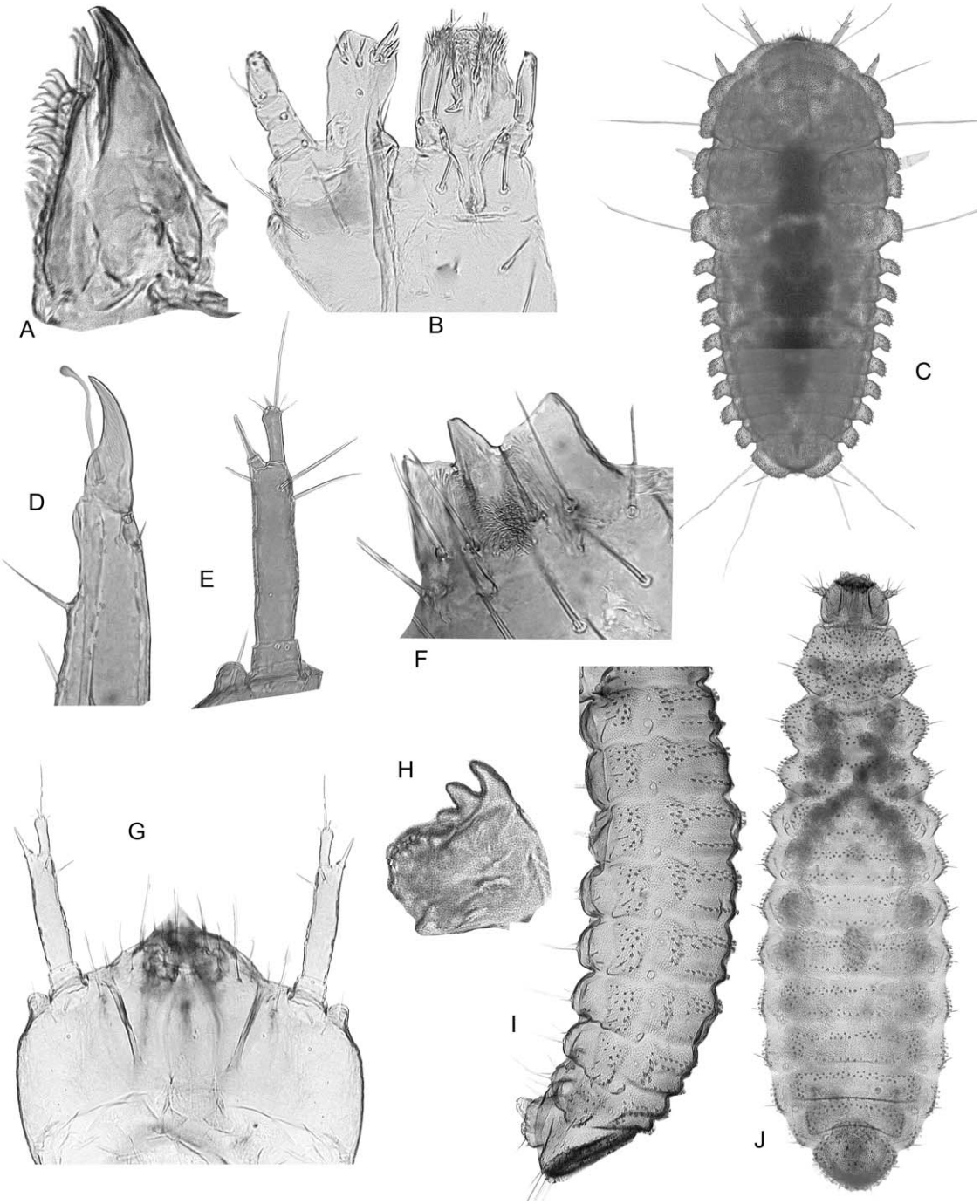

Fig. 6. Larvae. (A–G) *Pakalukodes bimaculatus*: (A) mandible; (B) labium and maxilla, ventral; (C) dorsal habitus; (D) tarsal claw; (E) left antenna, dorsal; (F) clypeolabral complex; (G) head dorsal. (H–J) *Stanus bowesteadi*: (H) mandible; (I) abdomen lateral; (J) dorsal habitus.

apically. Wings absent. Abdomen with six ventrites, first two completely fused, without postcoxal lines; five pairs of functional spiracles.

Larva. Unknown.

Discussion. This group consists of a single species *Cleidostethus meliponae* (Arrow, 1929, 1930) thoroughly redescribed and discussed by Bowestead *et al*. (2001). The genus is very difficult to place in the system because of strong modifications of the exoskeleton,

Fig. 7. (A) *Aenigmaticum californicum*; (B) *Priamima rubicunda*; (C) *Foadia maculata*; (D) *Clypastraea* sp.; (E) *Ectinocephalus* sp.; (F) *Stanus bowesteadi*; (G) *Stanus tasmanicus*; (H) *Cleidostethus meliponae*, dorsal; (I) same ventral; (J) *Foadia maculata*, larva, dorsal.

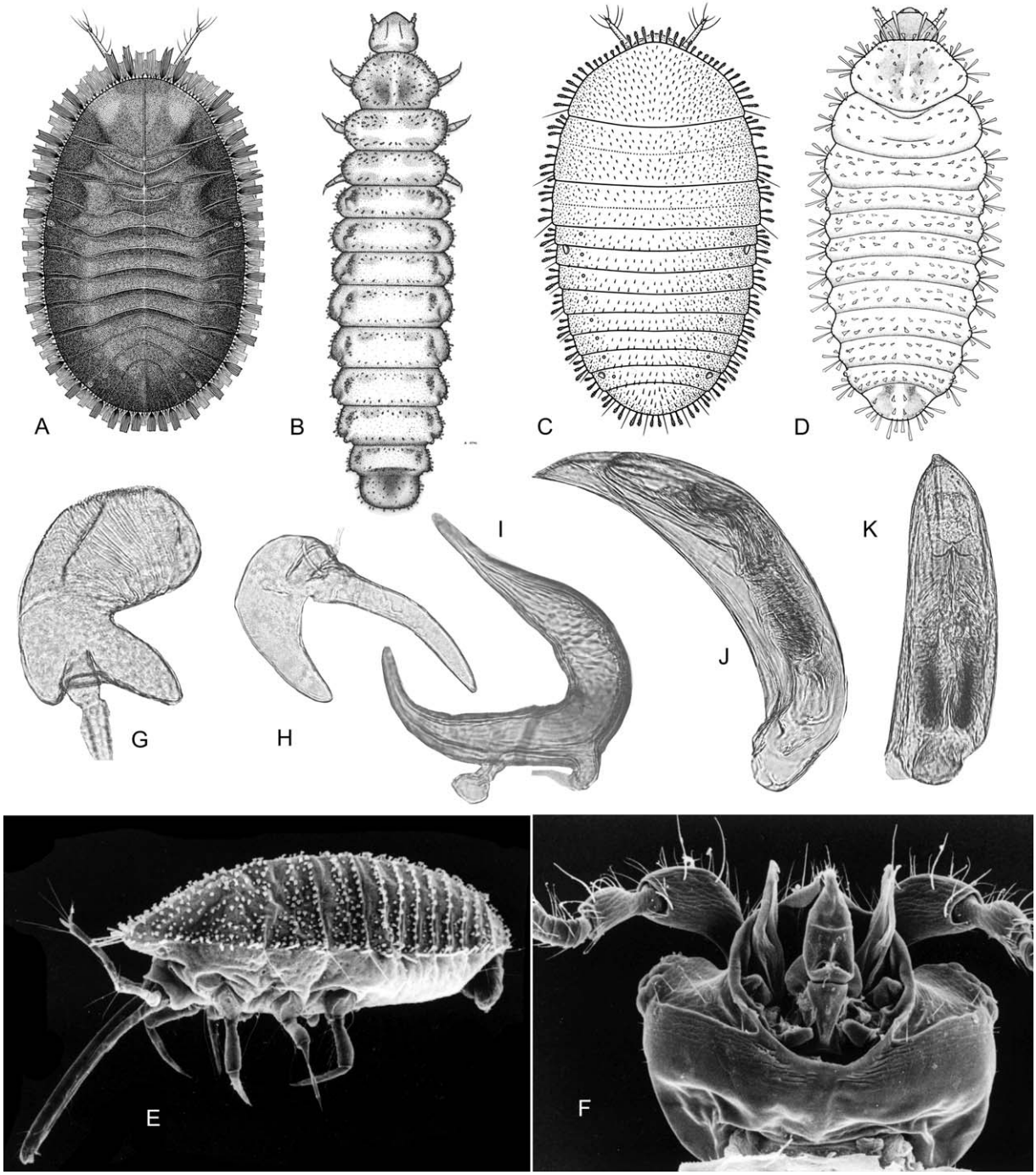

Fig. 8. (A–E) larvae: (A) *Rypobius* sp., dorsal habitus; (B) *Arhtrolips* sp., dorsal habitus; (C) *Holopsis* sp., dorsal habitus; (D) *Sericoderus* sp., dorsal habitus; (E) *Holopsis* sp., lateral; (F) *Rypobius* sp, head ventral with maxillae removed; (G), *Stanus tasmanicus*, spermatheca; (H) *Stanus bowesteadi*, spermatheca; (I) *Weirus tozer*, spermatheca; (J) *Stanus bowesteadi*, penis lateral; (K) *Stanus bowesteadi*, penis ventral view. (A–D) from Lawrence (1991); (E) from Lawrence (1989).

apparently adaptations to its life in the nests of the stingless bee *Melipona alinderi* Alfken (Bowestead *et al.*, 2001). Its position on the cladogram as sister-group to the 'higher Corylophidae' requires further investigation.

Tribe Othoperini Jacquelin du Val, 1857

Included genera. *Orthoperus* Stephens, 1829 (= *Pithophilus* Heer, 1841, *Microsphaera* Redtenbacher, 1845, *Eutrilia* Casey, 1900).

Adult. Length 0.6–1.3 mm. Head slightly withdrawn into prothorax but well visible from above. Tentorial arms reduced and visible at base only. Antenna 9-segmented, doubly geniculate in repose; pedicel and scape subequal in length; club segments oval in cross-section, asymmetrical; membranous sensilla on all club segments. Submentum broad; mentum distinct, subquadrate; labial palps 2-segmented, basal palpomere very short and hardly visible, apical one elongate. Mandible triangular, tridentate apically, with large tuberculate mola and short prostheca. Anterior margin of pronotum emarginate medially.

Prosternum in front of coxa reduced to a narrow strip medially forming a short and apically rounded process directed anteriorly. Procoxae strongly transverse, conical; procoxal cavities without slits, closed externally; prosternal process reduced to a narrow carina between projecting coxae meeting postcoxal projections that appear to be meeting each other. Mesocoxae transverse, very broadly separated; mesocoxal cavities laterally closed. Metaventral postcoxal lines arcuate, extending laterally onto metepisterna. Elytral epipleuron very narrow at base, incomplete apically. Wing without medial fleck. Abdomen with six ventrites and five pairs of functional spiracles; ventrite 1 as long as 2 and 3 combined, with postcoxal lines very close to coxal cavity.

Larva. Body elongate, lightly sclerotized except for head, paired admedian sclerites on prothorax and a weak macula on abdominal tergum IX. Pronotum transverse not covering head from above; thoracic and abdominal margins with sparse simple and various modified setae. Head prognathous; labrum and clypeus separated; two stemmata on each side; frontal arms U-shaped and not clearly joined at base. Antenna 3-segmented with antennomere 2 about as long as wide. Mandible triangular, broad and tridentate apically, mola tuberculate, prostheca absent. Labial palps 1-segmented. Legs moderately long and slender; claw slender with single, spatulate seta. Gland openings large, on segments I–VI.

Discussion. As delimited by Bowestead (1999) this tribe consists of the single cosmopolitan genus *Orthoperus*, characterized by a minute rather globose body, exposed head, distinct metavental postcoxal lines and only five pairs of functional spiracles.

Tribe Parmulini Poey, 1854

Included genera. *Arthrolips* Wollaston, 1854 (= *Lepadodes* Matthews, 1887, *Sacina* Broun, 1893, *Meioderus* Matthews, 1899, *Meizoderus* Matthews, 1899, *Sericoderistes* Reitter, 1913, *Alloparmulus* Paulian, 1950, *Pseudoparmulus* Paulian, 1950), *Clypastraea* Haldeman, 1842 (= *Aspidocha* Gistel, 1848, *Sacium* LeConte, 1852, *Parmulus* Gundlach, 1854, *Clypeastodes* Casey, 1900, *Molamba* Casey, 1900, *Sacinops* Paulian, 1950, *Aposacium* Paulian, 1950), *Lepesmella* Paulian, 1950, *Sicardianus* Paulian, 1950, *Villiersium* Paulian, 1950.

Adult. Length 0.9–2.3 mm. Head not visible from above, covered by large, anteriorly circular pronotum (Fig. 7D). Tentorial arms reduced and visible at base only. Antenna 10- or 11-segmented, doubly geniculate in repose; pedicel and scape subequal in length; club segments oval in cross-section, weakly asymmetrical; membranous sensilla on all club segments. Submentum short and broad; mentum large, quadrate or slightly longer than broad; labial palps 2-segmented, basal palpomere short, transverse as long as the apical one. Mandible triangular, multidentate apically, with tuberculate mola and reduced prostheca. Anterior margin of pronotum arcuate medially. Prosternum in front of coxa 0.1–0.5× as broad as coxal length, sometimes with median projection forming a chin piece. Procoxae oval, flat; procoxal cavities without slits, closed externally; prosternal process narrow between coxae, expanding posteriorly into a triangle meeting postcoxal projections. Mesocoxae transverse, broadly separated; mesocoxal cavities laterally closed. Metaventral postcoxal lines absent. Elytral epipleuron narrow at base and very incomplete apically. Wing without medial fleck. Abdomen with six ventrites and seven pairs of functional spiracles; ventrite 1 as long as 2 and 3 combined; postcoxal lines absent.

Larva (Clypastraea, Arthrolips). Body elongate (Fig. 8B), lightly sclerotized except for head, paired admedian sclerites on thoracic segments and dark macula on abdominal tergum IX. Pronotum weakly transverse not covering head from above; thoracic and abdominal margins with sparse simple setae only. Head prognathous; labrum and clypeus separated; stemmata two; frontal arms U-shaped and not clearly joined at base. Antenna 3-segmented with antennomere 2 about as long as wide. Mandibles triangular, broad and tridentate apically, mola tuberculate, prostheca absent. Labial palps 2-segmented. Legs moderately long and slender; claw slender with single, spatulate seta. Gland openings on short tubes on segments I–VII. Tergum IX with short spines on the sclerotized surface.

Discussion. This group, redefined by Bowestead (1999), includes two cosmopolitan genera, *Clypastraea* Haldeman and *Arthrolips* Wollaston, characterized by their oval and rather depressed body, large, anteriorly arcuate pronotum and prosternal area in front and between procoxae flat, forming normal, posteriorly expanding prosternal process, meeting separate postcoxal projections. Our analyses indicate that this group may not be monophyletic because these defining features are probably plesiomorphic, as are the eight pairs of larval gland openings shared with Aenigmaticini. The larval tergite IX bearing very short asperities, used here as distinguishing character, needs further investigation, as only few larvae were available for study.

Tribe Sericoderini Matthews, 1888

Included genera. *Aposericoderus* Paulian, 1950: 66, *Sericoderus* Stephens, 1829 (= *Gryphinus* Redtenbacher, 1849, *Anisomeristes* Matthews, 1886).

Adult. Length 0.9–2.3 mm. Head not visible from above, covered by anteriorly circular pronotum. Tentorial arms reduced and visible at base only. Antenna 10- or 11-segmented, doubly geniculate in repose; pedicel smaller than scape; club segments oval in cross-section, weakly asymmetrical; membranous sensilla on all club segments. Submentum very narrow and prominent; mentum small, hardly visible; labial palps 2-segmented, basal palpomere elongate, distinctly longer than transverse apical segment. Mandible narrowly triangular, flat and unidentate apically serrate subapically, with large prostheca and no mola. Anterior margin of pronotum arcuate medially. Prosternum in front of coxa reduced to a narrow stripe. Procoxae oval, flat; procoxal cavities without slits, closed externally; prosternal process narrow between coxae, expanding posteriorly into a small triangle above meeting postcoxal projections. Mesocoxae circular, moderately separated; mesocoxal cavities laterally closed. Metaventral postcoxal lines absent. Elytral epipleuron narrow at base and very incomplete apically. Wing without medial fleck. Abdomen with six ventrites and seven pairs of functional spiracles; ventrite 1 as long as 2 and 3 combined; postcoxal lines absent.

Larva (Sericoderus). Body elongate oval, lightly sclerotized except for head, paired admedian sclerites on pronotum and sometimes a darker tergum IX. Pronotum weakly transverse not covering head from above; thoracic and abdominal margins with variable fan-shaped setae and sparse longer, simple setae on thoracic segments. Head prognathous; labrum and clypeus separated; stemmata two; frontal arms U-shaped and not clearly joined at base. Antenna apparently 2-segmented with segments 2 and 3 fused; antennomere 2 about 4× as long as wide. Mandibles triangular, broad and tridentate apically, mola tuberculate, prostheca absent. Labial palps 2-segmented. Legs moderately long and slender; claw slender with single, clubbed seta. Gland openings on lateral surfaces of segments I and VII (the posterior one extends somewhat onto segment VIII and may be placed on a short projection).

Discussion. Two cosmopolitan genera, *Sericoderus* Stephens and *Aposericoderus* Paulian, share a characteristic habitus, broadest at pronotal base with its posterior angles prominent posteriorly over the elytral humeri. The anteriorly arcuate pronotum and relatively unmodified structure of prosternum are shared with Parmulini, but Sericoderini sharply differ from that tribe by a peculiar narrowly prominent submentum, strongly reduced mentum and basal segment of labial palps distinctly elongated. The *Sericoderus* larva has only two pairs of dorsal gland openings and apparently 2-segmented antennae.

Tribe Peltinodini Paulian, 1950

Included genera. *Holopsis* Broun, 1883 (= *Corylophodes* Matthews, 1885, *Bathona* Casey, 1900, *Peltinodes* Paulian, 1950).

Adult. Length 1.0–2.5 mm. Head not visible from above, covered by large, anteriorly circular pronotum. Tentorial arms complete and fused at base. Antenna 11-segmented, doubly geniculate in repose; pedicel smaller than scape; club segments oval in cross-section, weakly asymmetrical; membranous sensilla on all club segments. Submentum broad and not very prominent; mentum large, trapezoidal; labial palps 2-segmented, basal palpomere oval, distinctly longer than minute apical segment. Mandible plate-like, flat and obtuse apically, with distinct tuberculate mola prostheca represented by few setae. Prosternum in front of coxa reduced to a narrow strip. Procoxae transverse and conical; procoxal cavities without slits, narrowly open externally; prosternal process forming carina between coxae, weakly expanding behind but not meeting postcoxal projections. Mesocoxae oval, broadly separated; mesocoxal cavities laterally closed. Metaventral postcoxal lines complete. Elytral epipleuron narrow at base and very incomplete apically. Wing with medial fleck (sometimes brachypterous). Abdomen with six ventrites and seven pairs of functional spiracles; ventrite 1 as long as 2 and 3 combined; postcoxal lines arcuate and complete laterally.

Larva. Body broadly ovate, disc-like (Fig. 8C, E), lightly sclerotized except for irregular darker markings on thoracic and abdominal tergites. Pronotum strongly transverse usually covering most of head from above; thoracic and abdominal margins with narrow, modified somewhat scale-like setae and few longer, simple setae on thoracic segments only. Head prognathous and elongate (sometimes distinctly rostrate, Fig. 8E); labrum and clypeus fused; stemmata two; frontal arms U-shaped and not clearly joined at base. Antenna 3-segmented; antennomere 2 about 6–7× as long as wide; antennomere 3 minute, shorter than sensory appendage. Mandibles endognathous to various degree, triangular, multidentate apically, mola tuberculate, prostheca absent. Labial palps 1-segmented. Legs moderately long and slender; claw slender with simple, short seta. Gland openings on lateral surfaces of segments I and VII (extending somewhat onto segment VIII).

Discussion. Bowestead (1991) provided excellent illustrations of *Holopsis* and extensive discussion on characters and taxonomy of this unique genus. Adults show at least three unique and apparently plesiomorphic characters for Corylophidae (open procoxal cavities, complete postcoxal lines, and wing with medial fleck) but the larvae are highly derived (Lawrence, 1989, 1991; Morrill, 1903), with strongly modified mouthparts, 2-segmented antennae and two pairs of defensive glands.

Tribe Corylophini LeConte, 1852

Included genera. *Corylophus* Stephens, 1833 (= *Oligarthrum* Matthews, 1887, *Daubania* Scott, 1917), *Homogrypinus* Reitter, 1908, *Microstagetus* Wollaston, 1861.

Adult. Length 0.6–1.2 mm. Head not visible from above, covered by large, anteriorly circular pronotum. Tentorial

arms reduced and visible only at base. Antenna 11-segmented, doubly geniculate in repose; pedicel about as long as scape; club segments oval in cross-section, asymmetrical; membranous sensilla on all club segments. Submentum peculiar, forming a trapezoidal plate covering very narrowly separated maxillae from below; mentum transverse, pentagonal. Labial palps 2-segmented, basal palpomere oval, about as long as apical one. Mandible plate-like, triangular, elongate with inner edge serrate and covered by long fringe of setae. Prosternum in front of coxa reduced to a narrow strip. Procoxae oval, weakly conical; procoxal cavities without slits, closed externally; prosternal process forming carina between coxae, expanding into a triangular process posteriorly meeting postcoxal projections joined at middle. Mesoventrite with fossa receiving tip of prosternal process; mesocoxae oval, broadly separated; mesocoxal cavities laterally closed. Metaventral postcoxal lines absent. Elytral epipleuron narrow at base and very incomplete apically. Wing without medial fleck. Abdomen with seven ventrites and seven pairs of functional spiracles; ventrite 1 as long as 2 and 3 combined; postcoxal lines absent.

Larva. Unknown.

Discussion. Bowestead (1999) delimited this tribe to the primarily Palaearctic and Afrotropical genera *Corylophus* Stephens and *Microstagetus* Wollaston, with the main characters distinguishing this group being a mesoventral fossa, which receives the prosternal process. The validity of this taxon is difficult to assess as no larvae were described or available and we could examine only a single species of *Corylophus*. The very close insertion of maxillary cardines illustrated by Bowestead (1999) is reminiscent of the condition in Sericoderini with a narrow prominent submentum, but at least in *Corylophus* cardines are very close together, the cuticle between them is narrow, and the entire structure, transparent on cleared specimens, is concealed from below by a much broader 'submentum'.

Tribe Teplinini Pakaluk *et al.*, 1994

Included genera. *Teplinus* Pakaluk *et al*., 1994 (= *Peltinus* Mulsant & Rey, 1861, not Rafinesque, 1815).

Adult. Length 0.6–0.8 mm. Head not visible from above, covered by large, anteriorly circular pronotum. Tentorial arms reduced and visible only at base. Antenna 10-segmented, doubly geniculate in repose; pedicel shorter than scape; club segments oval in cross-section, asymmetrical; membranous sensilla not apparently visible. Submentum narrow, slightly prominent; mentum very small and quadrate. Labial palps 2-segmented, basal palpomere oval, slightly longer than apical segment. Mandible plate-like, triangular and mola and prostheca indistinct. Prosternum in front of coxa reduced to a narrow strip. Procoxae strongly transverse and conical; procoxal cavities without slits, closed externally; prosternal process forming narrow raised area between coxae and a projection anteriorly meeting fused postcoxal projections. Mesoventrite with weak median carina and transverse coxal rests; mesocoxae transverse, narrowly separated; mesocoxal cavities laterally open. Metaventral postcoxal lines absent. Elytral epipleuron narrow at base and very incomplete apically. Wing without medial fleck. Abdomen with six ventrites and seven pairs of functional spiracles; ventrite 1 as long as 2 and 3 combined; postcoxal lines absent.

Larva. Unknown.

Discussion. *Teplinus* Pakaluk *et al*. is widely distributed in the Mediterranean region and consists of a few very small globose species with strongly transverse coxae and laterally open mesocoxal cavities. The mesocoxal condition is unique in Corylophidae but paralleled to some extent in *Cleidostethus* owing to a major modification of the pterothorax bearing a strong hinge for the elytra (Bowestead *et al*., 2001).

Tribe Rypobiini Paulian, 1950

= Gloeosomatini Bowestead, 1999: 128, **syn.n.** – Pakaluk, 1987; Leschen & Bowestead, 2001

Included genera. *Catoptyx* Matthews, 1887; *Gloeosoma* Wollaston, 1854 (= *Moronillus* Jacquelin du Val, 1854, *Lewisium* Matthews, 1899, *Gronevus* Casey, 1900, *Sahlberginus* Bruce, 1948); *Rypobius* LeConte, 1852; *Hoplicnema* Matthews, 1899 (= *Matthewsiella* Hetschko, 1913).

Adult. Length 0.8–2.1 mm. Head not visible from above, covered by large, anteriorly circular pronotum. Tentorial arms reduced and visible only at base. Antenna 11- or 10-segmented, doubly geniculate in repose; pedicel subequal to scape; club segments oval in cross-section, asymmetrical; membranous sensilla on all segments. Mouth parts comparatively retracted; submentum indistinct; mentum triangular, elongate and pointing posteriorly (Fig. 8F). Labial palps 2-segmented, basal palpomere elongate and distinctly longer than apical segment. Mandible endognathous articulated apically forming narrow style with two apical hooks, mola and prostheca absent. Gular sutures fused to form median carina. Prosternum in front of coxa reduced to a narrow strip. Procoxae strongly transverse and conical; procoxal cavities without slits, closed externally; prosternal process forming narrow raised area between coxae and extending posteriorly meeting fused postcoxal projections. Mesoventrite with weak median carina and transverse coxal rests; mesocoxae transverse, narrowly separated; mesocoxal cavities laterally closed. Metaventral postcoxal lines absent. Elytral epipleuron narrow at base and very incomplete apically. Wing without medial fleck. Abdomen with six ventrites and seven pairs of functional spiracles; ventrite 1 as long as 2 and 3 combined; postcoxal lines absent.

Larva (Rypobius, Gloeosoma). Body broadly ovate (Fig. 8A), disc-like, lightly but rather evenly sclerotized dorsally. Pronotum strongly transverse, usually covering most of head from above; thoracic and abdominal margins with broad scale-like setae only. Head prognathous and transverse; labrum and clypeus fused; stemmata two; frontal arms U-shaped and not clearly joined at base. Antenna apparently 2-segmented with antennomeres 2 and 3 fused; antennomere 2 about 6–7× as long as wide; antennomere 3 minute, shorter than acute sensory appendage. Mandibles falcate, endognathous with apical hooks, mola and prostheca absent. Labial palps long, 1-segmented (apparently two fused segments); maxillary palp 2-segmented, mala blade-like. Legs moderately long and slender; claw short and curved with fan-like seta at its base. Gland openings on lateral surfaces of segments I and VII (extending somewhat on segment VIII).

Discussion. This clearly defined, monophyletic taxon is based primarily on modifications of adult and larval mouth parts bearing endognathous mandibles transformed into articulated blades bearing double hooks apically. The gular median endocarina, and triangular mentum are also unique in this group. The subdivision of Paulian's (1950) Rypobiinae into two tribes Gleosomatini and Rypobiini proposed by Bowestead (1999) is not justified, and the recognized taxa are rather grades than monophyletic clades.

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