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A review of the biology and systematics of Chlamydopsinae (Coleoptera: Histeridae)

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Abstract. The histerid subfamily Chlamydopsinae is a clade of obligate inquilines of social insects, mainly ants. They show a wide range of bizarre morphological characteristics, including highly varied trichomes, associated with this lifestyle. They occur throughout Australia and Indomalaysia, with a few species occurring as far from this centre of diversity as India and Japan. At present the subfamily contains 12 genera and 174 species, several of which are newly described herein (*Teretriopsis theryi*, gen. nov., sp. nov., *Papuopsis andersoni*, gen. nov., sp. nov. and *Quasimodopsis riedeli*, gen. nov. sp. nov.). This paper presents a phylogenetic analysis based on morphological characters of all of the main lineages of the family, provides a complete catalogue of the species, a key to all the genera, and proposes several new combinations. The phylogenetic analysis reveals two large clades, one (including the genera *Chlamydopsis* Westwood, *Eucurtia* Mjöberg, and *Ectatomphila* Lea) is largely restricted to the Australian continent, whereas the other, containing all other genera, is much more widespread, including many Australian species, but extending also through Indomalaysia into south-east Asia. The beetles are known to utilise many hosts, including ants in four different subfamilies (Myrmicinae, Ponerinae, Dolichoderinae, and Formicinae), as well as termites in the genus *Eutermes*. However, host records are not yet sufficiently comprehensive to exhibit any clear phylogenetic signal.

Introduction

The Histeridae is a moderate sized (*c.* 3800 species; Mazur 1997) family of predaceous beetles. The compact morphology typical of the family is thought to have aided the adoption, by many lineages, of inquiline habits. As many as one-third of the species live in close association with diverse organisms, most spectacularly with various social insects (Kovarik and Caterino 2000). At least a few members of most of the 11 histerid subfamilies have successfully adopted the latter lifestyle, but two subfamilies appear to have diversified entirely in association with social insects, the Hetaeriinae and Chlamydopsinae (Helava *et al.* 1985; Hölldobler and Wilson 1990; Ślipiński and Mazur 1999), exhibiting, in many cases, complex behavioural interactions with their hosts (Oke 1923; Rettenmeyer 1961; Akre 1968; Kistner 1982). The biology and classification of the Hetaeriinae was reviewed recently by Helava *et al.* (1985). However, no comprehensive works have yet treated the Chlamydopsinae. In the present paper we review the biology, taxonomy, and distribution of this subfamily. We also present a phylogenetic analysis of the major lineages, propose a revised classification, and redescribe the type species of some poorly known genera.

The Chlamydopsinae is one of the smaller histerid subfamilies. Mazur's (1997) catalogue listed 47 species. Dégallier (1998) removed the misplaced neotropical hetaeriine *Pelatestister* Reichensperger and its sole species. We have recently described numerous additional species (Caterino 2000; Caterino 2003; Dégallier and Caterino 2005a, 2005b), and many species undoubtedly remain to be collected and described. Most of the described diversity of Chlamydopsinae is found in Australia

(Mazur 1997), although species are known as far west as India, north to Japan, and east to Fiji (Caterino 2000; Dégallier 1984; Nishikawa 1995, 1996). It is likely that with sufficient collecting effort, chlamydopsines will eventually be found throughout south-east Asia. It nonetheless seems likely that Australia represents the original source of the subfamily. The phylogenetic analyses presented herein, in part, serve to test this idea.

The taxonomy of the Chlamydopsinae is also in need of phylogenetic assessment. The monophyly of the group has not been questioned and seems well established on the basis of antennal structure and the presence of elytral trichomes (Ślipiński and Mazur 1999; Caterino and Vogler 2002). However, the generic level taxonomy has been developed without regard to phylogenetic concerns and no attempts to discern relationship among supraspecific taxa have been made. Most chlamydopsine genera have been established for one or two distinctive species (an unfortunately widespread practice in studies of myrmecophiles) without regard for clear designation of generic level characters. Assignment of new species to existing taxa, therefore, remains a purely subjective exercise. It is our goal to examine the phylogenetic validity of the existing classification towards the development of one that is more cladistically meaningful.

Systematic history

The first Chlamydopsines were described by Westwood (1869) in the genus *Chlamydopsis* Westwood, only barely preceding the now synonymous *Byzenia* King (1869). Until the early 20th

century, the group's described diversity grew slowly but steadily through isolated species descriptions (Lewis 1885; Blackburn 1891; Blackburn 1900; Blackburn 1901). Lewis (1903) described the group's second genus, *Orectoscelis* Lewis, to accommodate a distinctive species from Queensland. Shortly thereafter, Arthur Lea became interested in the group and its diversity grew rapidly through his contributions (Lea 1910, 1912, 1914a, 1914b, 1918, 1919, 1925). In 1914, when the described species numbered 27, some important divisions became apparent and Lea (1914a) erected the genera *Pheidoliphila* Lea and *Ectatomiphila* Lea. Until around this time, the distribution of the Chlamydopsinae was considered to be restricted to the Australian continent. The description of *Chlamydopsis papuae* Lewis (Lewis 1913) from New Guinea provided the first indication that this was not the case. Aside from a few additional descriptions and interesting biological data provided by Oke (1923), the most significant subsequent developments in knowledge of Chlamydopsinae were the discoveries of species even further from the supposed centre of diversity, including species from India (Reichensperger 1924) Taiwan (Silvestri 1926), Fiji (Dégallier 1984), Japan (Sawada 1994), Indomalaysia (Caterino 2000; Dégallier and Caterino 2005a, 2005b), and New Caledonia (Caterino 2006). Caterino (2003) has recently reviewed the species of *Chlamydopsis*, providing descriptions of an additional 40 species, mostly from Australia, but also including an additional New Guinean species.

Biology

Reported host associations of Chlamydopsinae are summarised in Table 1. The overall host range is quite wide, including the termite genus *Eutermes* Heer as well as members of four different ant subfamilies. The most common hosts of species of *Chlamydopsis* appear to be Ponerinae, although hosts in the Dolichoderinae, Formicinae, and Myrmicinae have also been reported. Species of *Ectatomiphila* are only known from Ponerine hosts (apparently only *Rhytidoponera metallica* (Smith) [formerly *Ectatomma metallicum*]), whereas those of *Pheidoliphila* have only been reported from the nests of *Pheidole* Westwood (Myrmicinae). It is interesting that at least a few species seem to use hosts in more than one subfamily. This has obvious implications for their chemical defenses, perhaps indicating that some of these species' defenses are acquired from the environment rather than produced endogenously. It has been demonstrated that a myrmecophilous scarab beetle *Myrmecaphodius excavaticollis* (Blanchard), which has multiple hosts, may obtain chemical camouflage from its environment (van der Meer and Wojcik 1982; May 1983).

Behavioural observations on Chlamydopsinae, although few, have been quite revealing. The extremely elongate hairs of *Eucurtia comata* (Blackburn) apparently serve to disseminate substances attractive to their termite hosts (Mjöberg 1912). Oke (1923) described the interactions of several Chlamydopsinae with their ant hosts, as well as the consumption of ant larvae by at least one chlamydopsine (*Chlamydopsis striatipennis* Lea). McMillan (1950) described apparently characteristic phoresy in *Chlamydopsis loculosa* Lea (erroneously as *C. duboulayi* [sic] Westwood; McMillan 1954), with the beetle often mounting and riding on the thorax of its hosts (*Rhytidoponera convexa* vio-

lacea Forel). It is especially interesting to note that the unusually elongate legs of this beetle appear to function to grasp the host during phoresy, rather than serving as a locomotory specialisation of the beetle itself. These observations, although fragmentary, indicate that at least some Chlamydopsinae do enjoy the status of true symphiles (*sensu* Wasmann 1894) and are accepted as members of the colony by their hosts.

Materials and methods

Phylogenetic analysis

Taxa

Multiple representatives of all described supraspecific taxa were included in the phylogenetic analysis (see Table 2 for complete list). In groups exhibiting substantial diversity, we attempted to sample the morphological diversity evenly. Given the size of the subfamily, a global analysis including all species should eventually be feasible but for our present purposes, stabilising the taxonomy and looking at broad evolutionary patterns, a more restrictive sampling allowed sufficient resolution. The dataset includes representatives of two undescribed species from Fiji (hereafter, Fiji1, Fiji2). Their inclusion helped to determine their phylogenetic placement, but finding them apparently to belong with an existing genus (*Pheidoliphila*) we leave them to be described elsewhere.

Nearly all taxa were scored from direct examination of specimens, primary types in many cases. The data matrix (Table 2) contains many missing states. In the majority of cases this results from inadequate material for dissection, as many species are known only from primary types, which we have rarely risked to dissect. Thus many genitalic, as well as generally concealed mouthpart, states are unknown. This has also discouraged the use of some additional genitalic characters, which might prove useful with more complete material. In addition, many species are known only from one sex, leading to uncertainty not only in genitalic characters, but also in characters of dimorphism. Finally, in taxa scored from the literature, many features were not adequately described or illustrated to provide unambiguous state assignment.

An appropriate outgroup to Chlamydopsinae was difficult to choose. The specific placement of the subfamily among Histeridae has proven problematic (Ślipiński and Mazur 1999; Caterino and Vogler 2002). The Hetaerinae have long been considered the closest relatives of Chlamydopsinae, and Chlamydopsinae were once even considered a tribe of the former. But there are few characters that would support such a relationship outside of shared adaptations to myrmecophily. Wenzel (1944) considered their similarity entirely convergent, including the Chlamydopsinae in his Saprinomorphae. This assemblage, however, has been subsequently shown to be polyphyletic, thus opening the door once again to the Hetaerinae + Chlamydopsinae hypothesis. The characters identified by Ślipiński and Mazur (1999) as potential synapomorphies of the two subfamilies, loss of protibial spurs and loss of labral setae, are both highly homoplasious, and those authors admit that support for a sister group relationship between the two is weak. Ôhara (1994) has suggested a sister-group relationship between Chlamydopsinae and Onthophilinae, citing the complete ventral closure of the antennal cavities as evidence. In Ôhara's charac-

Table 2. Character state data for analysis of chlamydopsine relationships
Multiple states: a = 1/2; b = 1/3; c = 2/3.

Taxa	Characters				
	0000000001 1234567890	1111111112 1234567890	2222222223 1234567890	3333333334 1234567890	4444444 1234567
<i>Stictostix</i>	1122111111	1111111111	1111111111	1311121212	42111111
<i>Peplolyptus mulu</i>	11221?1111	1111223111	1111111111	1311121221	32211??
<i>Onthophilus</i>	11a1111111	1111111111	1111111111	1311121212	42131111
<i>Eucurtia comata</i>	11222?1111	112?111113	1112312232	3113121221	1?112??
<i>Ectatomphila opaca</i>	11222211??	2111111111	1?22212232	3112123?21	1?112??
<i>Quasimodopsis riedeli</i>	112222?2??	1131111121	1112222232	3112111111	1????12
<i>Chlamydopsis longipes</i>	12222211??	2211111121	11124122?2	2322122?21	1?212??
<i>C. striatipennis</i>	1122221111	2111111111	1112412252	2122121121	1121221
<i>C. dimorpha</i>	1122221111	2111111111	1122112232	3222111121	1221222
<i>C. convergens</i>	1322221111	2121111121	1112212222	3222121121	12212??
<i>C. inaequalis</i>	12222?11??	2111111111	1112512222	3222122421	1????11
<i>C. ectatommae</i>	1122221111	2112111123	1122112222	2222122121	1111122
<i>C. convexa</i>	1122221111	2121111113	1122212243	3122123121	1111121
<i>C. formicicola</i>	1122221111	2121111123	1112412243	3122121121	1111121
<i>C. inquilina</i>	11222111??	2121111113	1112412243	3122121421	112122?
<i>C. tuberculata</i>	11222?11??	2121111121	1112312232	3322121??1	1??????
<i>C. caledoniae</i>	1122221212	2111111112	1122312243	2212121111	1111111
<i>C. n. sp. [Japen Isl.]</i>	11222???11	2121111113	1112412222	3222122121	1?????22
<i>Chlamydonia sol</i>	1322221212	2211122111	1122232222	2312111321	12111?1
<i>Kanakopsis amieuensis</i>	11222?1212	1211111111	1122322232	33122112??	1??????
<i>Teretriopsis theryi</i>	21222?2222	1211111111	1222321111	131111122?	1??????
<i>Pheidoliphila sternalis</i>	21222222??	3211124111	2222222332	3314111?2?	3??????
<i>P. minuta</i>	11222222??	321112?111	2222322332	3314111221	32111??
<i>P. carbo</i>	11222222??	3211124111	1222223?2	3314111?2?	1??????
<i>P. granulosa</i>	11222222??	3211124111	222222332	3314111?21	1??????
<i>P. rugosa</i>	1122222222	3211124111	222222332	3314111221	b2111??
<i>P. wenzeli</i>	2122222222	3211124211	1222322332	33141112a1	a211121
<i>P. magna</i>	2122222222	3211125211	1222322332	3114111221	a211121
<i>P. secqi</i>	2422222222	3211124111	3222221111	1411212121	1311121
<i>P. storeyi</i>	21222?????	3211124111	422222332	3314212121	4??????
<i>P. dahlgreni</i>	21222?????	3211124111	122222332	331421212?	1??????
<i>P. micra</i>	21222?????	1211122111	122222332	331111122?	3??????
<i>P. unita</i>	2122222222	3211124211	122222332	2314111221	2?11121
<i>P. bifida</i>	2122222222	1211124211	122222312	3314111211	3??????
<i>Fiji1</i>	11222???22	1211123111	1222?31111	131121122?	1??????
<i>Fiji2</i>	21222???22	3211114111	3222221111	131122222?	3??????
<i>Orectoscelis humeralis</i>	21222222??	1211123111	1222222222	2312111221	1??????
<i>O. kovariki</i>	21222222??	1211122111	1222222222	2312111221	32111??
<i>O. punctatus</i>	21222222??	1211123111	1222222422	331211122?	3??????
<i>O. attenuatus</i>	21222???22	1211122111	1222222222	3312111221	1??????
<i>O. westwoodi</i>	21222222??	1211123111	1222222222	2312111221	1211111
<i>O. aurolepidus</i>	2122222222	3211124111	1222222432	3312111221	3??????
<i>O. dumogae</i>	21222222??	1211124111	122222332	3312111221	4??????
<i>O. obliquus</i>	21222222??	1211122111	122222332	3112111211	1??????
<i>Eucurtiopsis tishechkini</i>	21222222??	1211123111	1222322232	3?12111??1	1??????
<i>E. brendelli</i>	2122222222	1111111111	1222322232	3114111212	33111??
<i>E. hammondi</i>	2122222222	1211122111	1222222222	211211121?	2??????
<i>E. elongatus</i>	21222222??	1211122111	1222322222	3112111??2	1??????
<i>E. zecki</i>	21222222??	1211123111	1222322222	2112111211	3??????
<i>E. reichenspergeri</i>	21222222??	1211123111	1222222232	31121112??	3??????
<i>E. kanaari</i>	2122222222	1211122111	1222222232	231211121?	1?????21
<i>E. marinae</i>	2122222222	1211122111	1222322232	231312122?	a?????21
<i>E. adebratti</i>	21222222??	1211123111	1222322232	311?1112??	1??????
<i>E. chungi</i>	21222222??	1211123111	1222322222	211211121?	4??????
<i>E. carinatus</i>	21222222??	1211123111	1222322232	211211122?	c??????
<i>E. mazuri</i>	21222222??	1211123111	1222422232	31131112??	2??????
<i>E. mirabilis</i>	21222?22??	1211122111	1222222222	3?131?1?2?	b?111??
<i>Ceratohister leai</i>	?1222222??	1211111111	1222221111	1311111???	3??????
<i>C. cornutus</i>	21222222??	1211124111	1222221111	1311111221	3??????

character is otherwise the defining synapomorphy of Chlamydopsinae. A few other general similarities could be cited, although all are highly homoplasious at the subfamily/tribe level. These characters are also shared by a recently discovered species of *Peploglyptus* (Onthophilinae), from Malaysian Borneo (Caterino 2004). What is particularly intriguing about this as a possible outgroup is its possession of pronotal and prosternal trichomes, indicative of myrmecophily (the North American *Peploglyptus belfragei* LeConte has been collected with ants; Kovarik and Caterino 2000).

Characters

- (1) *Frons, outline*: 1, lateral margins rounded, without lateral marginal stria, outline distinctly interrupted at antennal insertions (Fig. 1A); 2, margins straight, usually parallel (sometimes slightly convergent) and with marginal stria, outline not markedly interrupted by antennal insertions (Fig. 1B).
- (2) *Frons, surface*: 1, more or less flat, without prominent tubercles (Fig. 2A); 2, with single, broad, transverse protuberance above labrum; 3, with multiple (usually six) protuberances (Fig. 2C); 4, with a single vertical tubercle in most of apical half (Fig. 2D).
- (3) *Antennal insertion*: 1, near the (dorsoventral) middle of the frons; 2, at the vertex near the top of the eye (Figs 1, 2). State 1 is found only among the outgroups, whereas state 2 is one of the primary defining characters of Chlamydopsinae.
- (4) *Antennal scape, at rest*: 1, separated from eye by vertical band of cuticle; 2, not separated from eye, inner edge of scape and eye in contact. As with the previous character this does not vary among Chlamydopsinae, and is informative only with respect to outgroups.
- (5) *Antennal scape*: 1, narrow, more or less cylindrical; 2, substantially widened, in apical half extending laterally to prosternal alae, concealing eye.
- (6) *Antennal club*: 1, identical in both sexes; 2, more elongate in male. Nearly all Chlamydopsinae exhibit this striking dimorphism (though it is unscored for many species for which only a single sex is known).
- (7) *Mentum*: 1, a flat, external sclerite, basally articulated and separate from prementum (Fig. 3A, B, D); 2, not present as a separate sclerite (Fig. 3C), either fused with submentum or with prementum (it is not clear which, though probably only one of these applies throughout). The very small oral cavity in many chlamydopsines has resulted in varying degrees of mouthpart reduction. A conspicuous loss in some taxa is that of a free, exposed mentum. It appears most likely that the mentum has become fused with the submentum, as this area projects anteriorly between bases of maxillae in these species. However, it is possible that this projection is composed entirely of submentum, and that the mentum has simply been lost, or internalised. In these, the labial palpi originate close together on a small, elongate conical prementum (Fig. 3C).
- (8) *Submentum*: 1, delimited posteriorly by sutures that diverge from median gular suture (Fig. 3A, B, D); 2, indistinguishably fused with head; gular suture ending freely or absent (Fig. 3C). This character is difficult to score for the New Caledonian *Chlamydonia* and *Kanakopsis*. In complete disarticulations of *Chlamydonia* it is clear that the median gular suture ends freely, not diverging around submentum, and from external observation, that of *Kanakopsis* appears similar. However, externally, faint depressions delimiting the submentum can be seen, and the region is texturally distinct from the surrounding gena. As this is basically fused, with the sutures not completely obsolete, we score it as state 2.
- (9) *Labial palpus*: 1, with three palpomeres (Fig. 3A, B, D); 2, with two palpomeres (Fig. 3C). The plesiomorphic labial palpus clearly comprises three palpomeres. This has been reduced to two in *Phediophilila* and related genera. A vestigial third (basalmost) palpomere is present in *Chlamydonia*.
- (10) *Maxillary palpus*: 1, with four palpomeres (Fig. 3A, B); 2, with three palpomeres (Fig. 3C, D). Prior to discovery of the New Caledonian *Chlamydonia*, this reduction in maxillary palpal segmentation had been found in exactly the same taxa as the reduction in labial palpal segmentation (the preceding character), and it was considered that as serial homologues they might not have been completely independent. However, *Chlamydonia* shows the characters to be evolving independently, showing loss of a maxillary palpomere, but with the basal labial palpomere present, though reduced. It is not certain if this is the case in *Kanakopsis*, as it has not been possible to fully disarticulate the mouthparts of the type.
- (11) *Medial portion of anterior pronotal margin*: 1, fine, flat (Fig. 2A); 2, distinctly elevated anteriorly exposed surface below margin (Fig. 2B). 3, neither of these, anterior pronotal margin obliterated by anterior projections of pronotal disk (Fig. 2C–F).
- (12) *Pronotum*: 1, pronotum margined laterally; 2, pronotum without lateral margin.
- (13) *Lateral pronotal disk*: 1, margins absent, or present and not elevated at sides; 2, elevated, the margins meeting the elevated anterior margins at obtuse angle; 3, lateral and anterolateral margins forming a single oblique carina from near anterior midpoint to posterolateral pronotal corners (Fig. 4C).
- (14) *Shallow groove extending from antennal cavity posteriorly to pronotum*: 1, absent; 2, present, leading to longitudinal submarginal groove (= supracoxal groove); 3, present and leading to dorsal pronotal pit. This character only varies among species of Chlamydopsis, and is included to provide some resolution there though their relationships have been examined in more detail elsewhere (Caterino 2003).
- (15) *Pronotal trichomes*: 1, absent; 2, present. Outside of Chlamydopsis pronotal trichomes are only seen in *Gomyopsis kuscheli* (Fig. 12A). It is unlikely that it is synapomorphic for all of these, but we include it nonetheless.
- (16) *Anterior marginal or near marginal processes of pronotal disk*: 1, absent; 2, present (e.g. Fig. 2C–F).
- (17) *Form of anterior marginal pronotal processes*: 1, without anterior pronotal processes; 2, two small separate projections at apical margin (Fig. 2C); 3, two small separate

- projections behind apical margin; 4, erect, basally united, apically bifid anterior marginal projection (Fig. 2D, F); 5, prominent, outwardly arcuate 'horns' (Fig. 2E).
- (18) *Connection between anterior pronotal processes*: 1, pronotal projections absent, or present and not connected by thin anterobasal 'shield'; 2, pronotal projections connected by translucent anterobasal shield (Fig. 2F).
- (19) *Single median pronotal tubercle*: 1, absent; 2, present (Figs 4C, 13D).
- (20) *Anterior marginal stria of prosternal lobe*: 1, finely impressed, a simple stria very close to margin; 2, deeply impressed, forming a marginal groove; 3, deeply impressed, and departing from the anterior margin at sides to meet a supraprofemoral carina. This character is only informative within Chlamydopsis, and has been discussed and illustrated in Caterino (2003).
- (21) *Prosternal keel*: 1, flat or simply convex (Fig. 5A); 2, longitudinally grooved (Fig. 5B); 3, unicarinate (though usually not over entire length) (Fig. 5C); 4, bicarinate (Fig. 5D).
- (22) *Prosternal/mesosternal junction*: 1, mesosternum projecting, prosternum emarginate (Fig. 5A); 2, prosternum posteriorly truncate to rounded, projecting over anterior margin of mesosternum (Fig. 5B–D).
- (23) *Sternal cavities for retraction of legs*: 1, poorly developed, not margined all the way around; 2, well developed, bordered by sternal carinae.

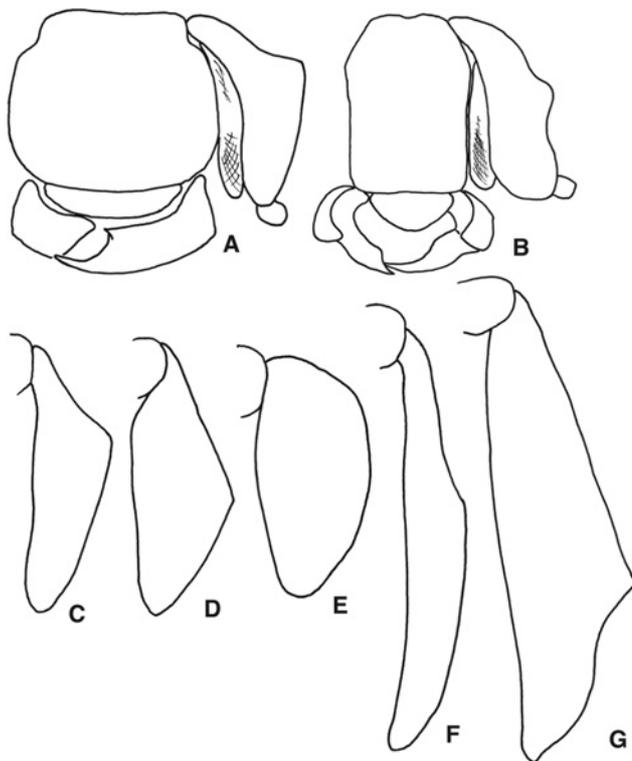


Fig. 1. A, Anterior view of head of *Chlamydopsis myrmecophila*; B, Anterior view of head of *Orectoscelis howdeni*. C–G, metatibia. C, *Chlamydopsis ectatommae*; D, *Chlamydopsis transversa*; E, *Pheidoliphila magna*; F, *Chlamydopsis striatipennis*; G, *Chlamydopsis inaequalis*.

- (24) *Meso- and metatibiae*: 1, without tarsal grooves; 2, with grooves for retraction of tarsi.
- (25) *Metatibial shape*: 1, short, slender, outer margin angulate (Fig. 1C); 2, short, broader, outer margin angulate (Fig. 1D); 3, short, outer margin broadly rounded (Fig. 1E); 4, elongate, slender (Fig. 1F); 5, elongate, broad (Fig. 1G).
- (26) *Scutellum*: 1, easily visible (Fig. 4A); 2, hidden beneath junction of anteromedial elytral corners (Fig. 4B, C); 3, visible within triangular opening between elytral bases, but receded, on a lower plane than elytra (Fig. 4D).
- (27) *Humeral elytral trichome*: 1, absent (Fig. 6A); 2, present (Fig. 6B–H). As discussed in Caterino (2003) morphology of the humeral trichome (or 'epaulette' of some former authors) is extremely varied, though difficult to parse into discrete characters. At the levels examined here, homologous states among different genera are particularly difficult to ascertain. The present arrangement represents a slight refinement of that presented in the previous paper. However, it is still far from satisfactory. Some states of most of these trichome characters are found only in Chlamydopsis. These are discussed and illustrated in greater detail by Caterino (2003).
- (28) *Position of humeral trichomes*: 1, absent; 2, posteriorly removed from humeri (Fig. 6B, E–H); 3, limited to humeri, oblique in orientation (Fig. 6C, D); 4, limited to humeri, an anteriorly inclined semicircle. State 4 is observed only a couple of species from northern Sulawesi, illustrated and described in Caterino (2000).
- (29) *Setal fringe of humeral trichome*: 1, trichome absent. 2, single continuous marginal fringe, usually encircling fairly simply arcuate trichome opening (e.g. *Orectoscelis humeralis*) (Fig. 6E, F, G); 3, with separate anterior marginal and posterior marginal setae, discontinuous at sides (Fig. 6C); 4, trichome setae with three distinct origins, a semicircular fringe along outer edge separated from bunches of setae arising from the inner anterior and posterior corners; 5, trichome setae arising from two origins, one in an elongate (usually sinuate) fringe along the inner edge of the dorsal 'roof' of the trichome, and one (more or less circular) hidden within the small mesal opening of the trichome, mostly hidden by the dorsal fringe; 6, with a single small setal origin on the mesal surface of incurved anterolateral trichome elevation. States 4–6 vary only among species of Chlamydopsis. (See Caterino (2003) for illustrations and further discussion.)
- (30) *Inner edges of anterior and posterior trichome elevations*: 1, trichome absent; 2, inner edges distant, the trichome cavity open mesally (Fig. 6G, H); 3, trichome nearly or fully closed by anterior and posterior elevations mesally. Most Chlamydopsinae possessing a trichome exhibit state 2, whereas state 3 is observed only in some species of Chlamydopsis. (See Caterino [2003] for illustrations and further discussion.)
- (31) *Outer edges of anterior and posterior trichome elevations*: 1, trichome absent; 2, meeting and closing trichome externally (an indentation may be visible but not continuous with trichome opening); 3, not closing trichome externally.

(32) *Anterior superficial groove of trichome*: 1, with anterior groove up the middle of the anterior elevation; 2, with anterior groove oblique, entering the trichome from scutellar corner; 3, without any visible groove on anterior elevation of trichome; 4, trichome absent, but with groove extending $\sim 3/4$ elytral length. In most Chlamydopsinae a

distinct fine groove extends from the anterolateral elytral corner to the trichome. It exhibits varied orientations. The groove indicated by state 4 is somewhat less certainly homologous. This is the condition seen in the strongly sculptured *Pheidoliphila secqi* lineage, which lack trichomes. In some *Ceratohister*, despite the trichome's

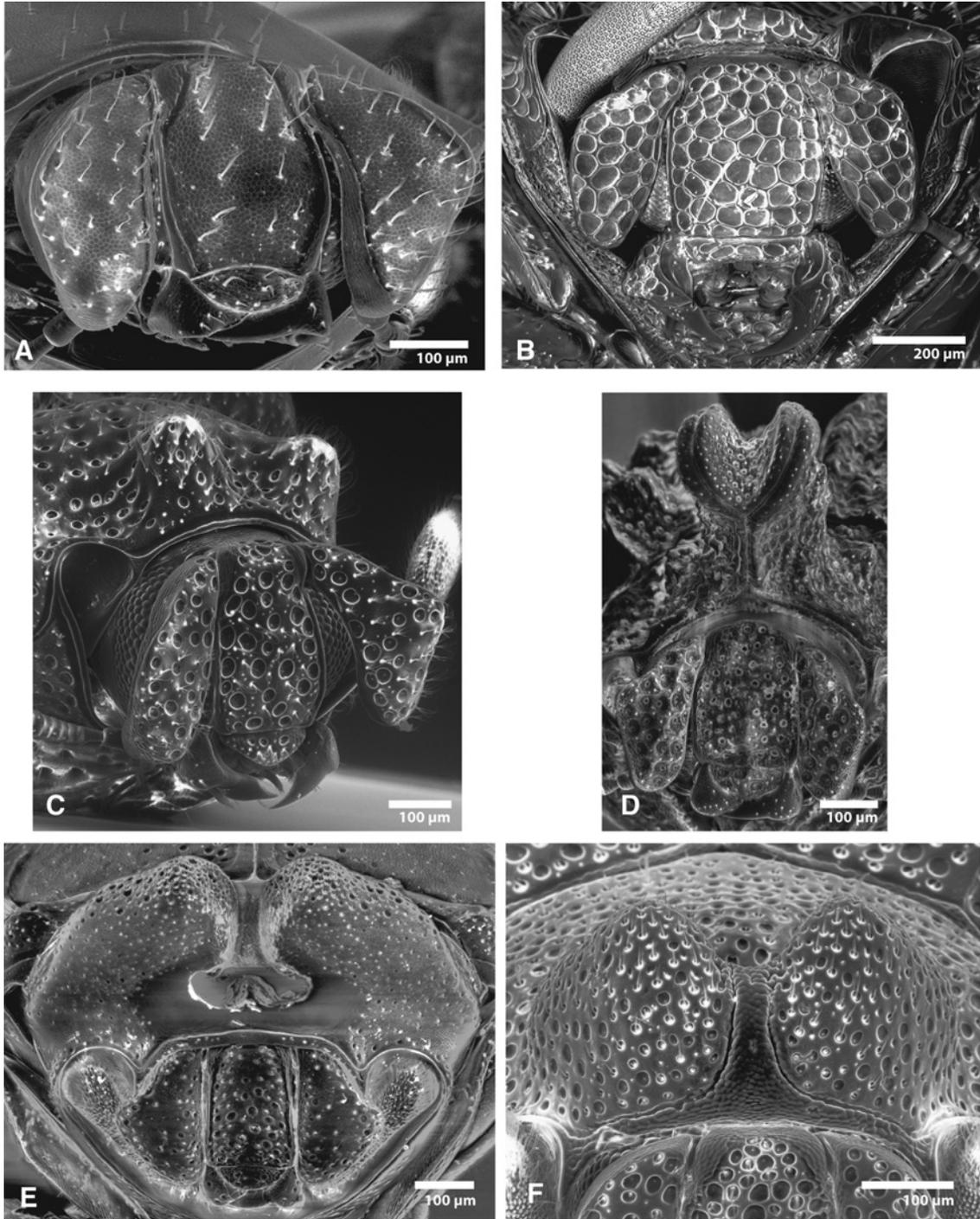


Fig. 2. Anterior view of head and pronotum: *A*, *Eucurtiopsis brendelli*; *B*, *Chlamydopsis striatipennis*; *C*, *Eucurtiopsis hammondi*; *D*, *Pheidoliphila secqi*; *E*, *Pheidoliphila ruginota*; *F*, *Ceratohister demotus*.

- absence, a probably homologous groove can be seen extending posterad from the anterior elytral margin.
- (33) *Elytral mediobasal area*: 1, lacking transverse tubercles or carinae; 2, with transverse elevations between the trichomes.
- (34) *Elytron, mediobasal depression*: 1, lacking, elytra convex throughout; 2, single confluent mediobasal depression between humeral trichomes, confined to basal half; 3, single confluent mediobasal depression extending beyond basal half; 4, separate anterolateral basal depressions confined to humeral corners, not confluent across elytral suture.
- (35) *Elytron, discal carinae*: 1, without longitudinal carinae; 2, with elevated longitudinal carinae.
- (36) *Elytron, marginal stria*: 1, continuous around all edges, including along elytral suture; 2, absent at least along suture.
- (37) *Elytron*: 1, without apical or lateral marginal carinae (distinct from marginal stria); 2, carinate apically but not laterally; 3, with carina running from trichome to and around the elytral apex.
- (38) *Lateral epipleural margin*: 1, With single stria paralleling elytral margin without exception; 2, with single stria departing from margin (in nearly all cases describing the upper arc of the femoral apex); 3, with two striae, one parallel to margin, one describing femoral arc; 4, marginal striae obsolete over metafemur.
- (39) *First visible abdominal segment (S3)*: 1, with anterior marginal stria which is continuous with metafemoral line; 2, anterior marginal stria obsolete, at least between metacoxae.
- (40) *Propygidium*: 1, without transverse carina in either sex (sexually monomorphic); 2, transversely carinate in female (sexually dimorphic).
- (41) *Body setae*: 1, simple; 2, branched (Fig. 7A); 3, scale-like (Fig. 7B); 4, absent. The setal vestiture of chlamydopsines is highly varied, from simple to variously modified types of setae. In some species simple setae are observed on some areas, whereas one or modified types are present elsewhere. Thus some taxa are scored as polymorphic.
- (42) *Female, proximal struts of 8th sternite*: 1, convergent near middle, subparallel to bases (Fig. 8A); 2, outwardly arcuate throughout length, meeting but not fused proximally (Fig. 8B); 3, outwardly arcuate, tips fused proximally (Fig. 8C).
- (43) *Female, gonocoxite length*: 1, coxite < half as long as valvifer (Fig. 8D, F); 2, coxite half or more as long as valvifer (Fig. 8E).
- (44) *Female, apex of gonocoxite*: 1, bidentate (Fig. 8D, E); 2, unidentate (Fig. 8F); 3, quadridentate. State 3 is only observed among the outgroups.
- (45) *Female, gonostyle*: 1, not projecting beyond apex of coxite (Fig. 8D, F); 2, enlarged, projecting beyond apex of coxite (Fig. 8E).
- (46) *Male, apices of 9th terga*: 1, not, or only weakly, convergent (Figs 8J, 13B); 2, convergent, sometimes fused (Fig. 8K). The two lateral halves of T9 converge apically in most species. In some they appear to cradle the aedeagus, functioning much as the spiculum gastrale, which is poorly developed in most Chlamydopsinae.

- (47) *Male, spiculum gastrale*: 1, basally emarginate, sometimes divided into two longitudinal halves throughout (Fig. 8G, H); 2, basally entire (Figs 8I, 13C).

Analysis

The data were analysed using parsimony in a β test version of PAUP* (PAUP 4.0b10; Swofford 2002). Initial analyses were carried out with all characters unweighted and unordered, but successive weighting according to rescaled character consistency indices was utilised to reduce an unwieldy number of equally parsimonious trees. Both searches applied tree bisection-reconnections (TBR) branch swapping to 500 randomly constructed stepwise addition starting trees, saving no more than 1000 trees for each iteration. Branch support was examined using decay indices (Bremer 1994), calculated by the program TreeRot (Sorenson 1999).

Conventions

For new species, some body measurements and proportions are provided. Following histerid conventions, total body length (L) is measured from the anterior margin of the pronotum to the posterior margin of the elytra, whereas width (W) is taken at the widest point, invariably near the elytral humeri. Measurements were made of the holotype where possible, are grouped at the beginning of each description, are given as mm, and are otherwise abbreviated as follows: E/PnL (ratio: elytral length/pronotal length); E/PnW (ratio: elytral width/pronotal width); Pn W/L (ratio: pronotum width/length); E L/W (ratio: elytra length/width); Pr/Py (ratio: propygidium length/pygidium length); sterna: pro, meso, meta (mm = lengths along midline); tibiae: pro, meso, meta (mm = straight line length from base to apex, ignoring curvature).

Some of the newly described species share type localities. New type localities are mapped in Fig. 15. Repositories are abbreviated as follows: BMNH: The Natural History Museum, London; DPIM: Department of Primary Industries, Mareeba, Queensland; CHSM: Slawomir Mazur Collection, Warsaw; QM: Queensland Museum, Brisbane; CMN: Canadian Museum of Nature, Ottawa; NHRS: Swedish Museum of Natural History, Stockholm. We designate one lectotype (of *Eucurtia paradoxa* Mjöberg) below, in order unambiguously to fix that name to the unique specimen in the NHRS collection.

Results

Initial, unweighted parsimony searches resulted in 19000 trees with a length of 213 steps ($CI = 0.361$; $RI = 0.747$). That is, 19 of the random addition replicates found the same shortest tree length, each saving 1000 trees from apparently separate 'islands'. Clearly additional equally parsimonious trees exist beyond those saved here, which might be expected to reduce the resolution of the consensus trees presented here somewhat. Decay analyses, however, indicate that additional trees represent rearrangements of already poorly supported branches, and that the strict consensus shown here may be an accurate overall representation of the signal in the data. This tree is shown in Fig. 9. The reweighted parsimony search resulted in over 100000 equally parsimonious trees, the strict consensus of which is shown in Fig. 10.

These trees are relatively consistent with regard to broad scale relationships. Both strongly support monophyly of Chlamydopsinae as a whole (unweighted decay index = 6), though outgroup relationships are not clearly resolved. The most significant observation is a basal split between two large groups of genera, with *Chlamydopsis*, *Ectatomphila*, and *Eucurtia* on one side of this divide, and all remaining genera on the other. The first of these lineages is supported by two transformations, one unique, the struts of the 9th sternite of the female convergent and subparallel in the basal half. It is also supported by the homoplasious elevation of the anterior pronotal margin. The first of these characters is quite promising, though its ambiguity in many unexamined taxa must be kept in mind.

Relationships within *Chlamydopsis* have been examined in detail in Caterino (2003). However, placements of the genera *Ectatomphila* and *Eucurtia* with respect to *Chlamydopsis* are worth further examination. Both of these taxa were included in the previous analysis of *Chlamydopsis* relationships, resolving outside of that genus. However, the character sampling in the present study is broader, and it has been possible to study *Eucurtia* in greater detail since the previous analysis, resulting

in resolution of some character state uncertainties. The present analyses concur with the previous, placing these genera outside of *Chlamydopsis*, with *Eucurtia* sister to *Ectatomphila* and *Chlamydopsis*. Although both of these genera are highly distinctive, *Chlamydopsis* itself contains a great diversity of forms (Caterino 2003), and we had considered it possible that these had been derived from within it. We would not reject this possibility completely yet, especially considering remaining ambiguities in some character states, but their status as distinct genera remains justified.

All other Chlamydopsinae form a sister clade to the *Chlamydopsis* lineage. This clade is supported by one decay step, and three character transformations. Synapomorphies include a complete circumlytral marginal stria, incomplete gular sutures, and a hidden scutellum. The first two of these characters undergo reversal on more distal branches in the clade, and must be regarded as relatively weak. The hidden scutellum is the most interesting of these characters, though of somewhat uncertain homology. In *Quasimodopsis riedeli*, it is unambiguously hidden, and is scored as such. But it represents a rather different configuration, with the pronotum projecting strongly

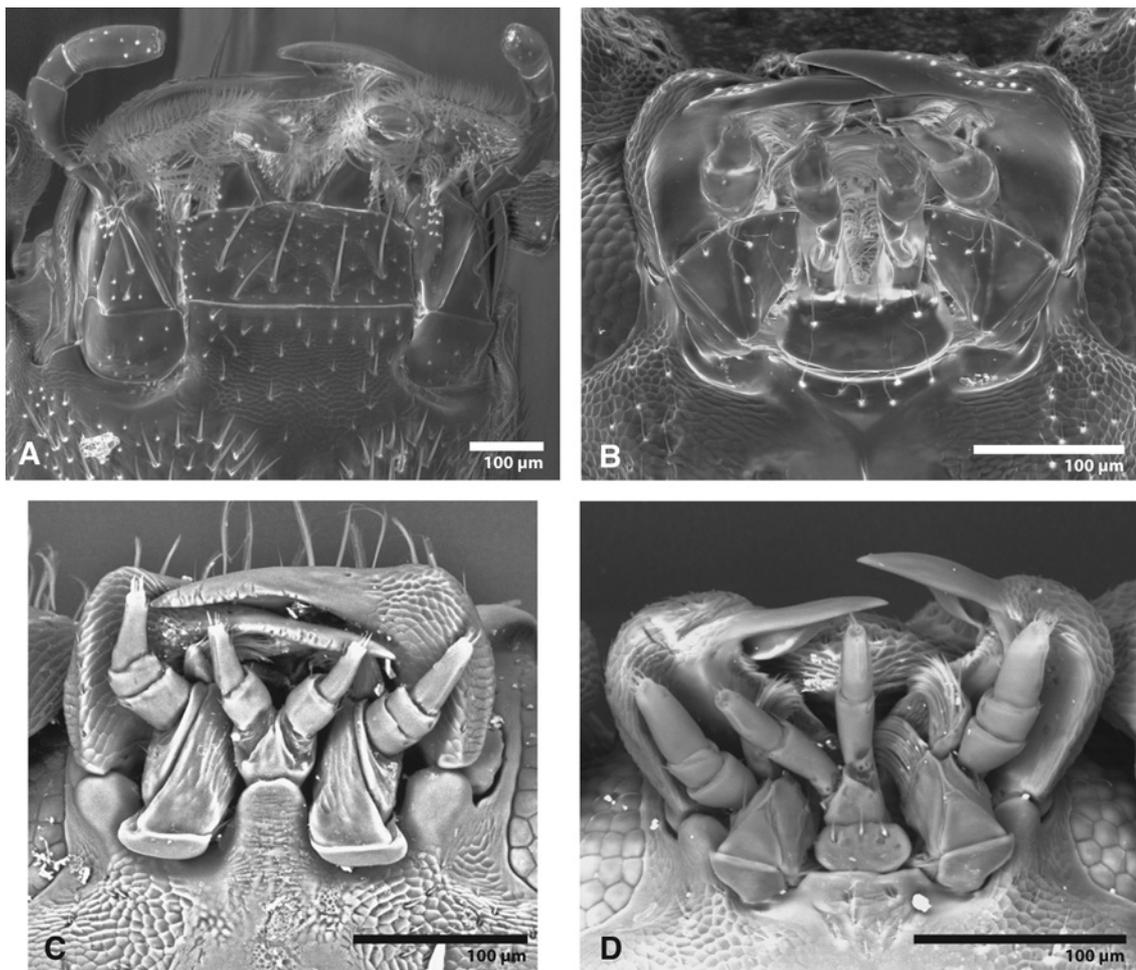


Fig. 3. Ventral view of head and mouthparts: A, *Onthophilus flohri*; B, *Chlamydopsis erupta*; C, *Eucurtiopsis brendelli*; D, *Chlamydonia sinuata*.

posterad between the elytral bases, than the *Orectoscelis* configuration, where the elytral bases meet at near right angles, behind a minimal posterior pronotal angle. Additional dissectable material will be necessary to determine exactly how distinct the *Quasimodopsis* configuration is. The New Caledonian *Kanakopsis* shares the *Orectoscelis*-like state, whereas in *Chlamydonia*, the scutellum exhibits what might be

considered a transitional conformation, being barely visible in the gap between the elytral bases, but reduced and receded. As the characters were not ordered in the analysis, this state is scored as an autapomorphy of the lineage. The complete circumelytral marginal stria, although of more certain homology, may properly be a synapomorphy of a larger group. It is not observed in any non-chlamydopsine outgroups, and has appar-

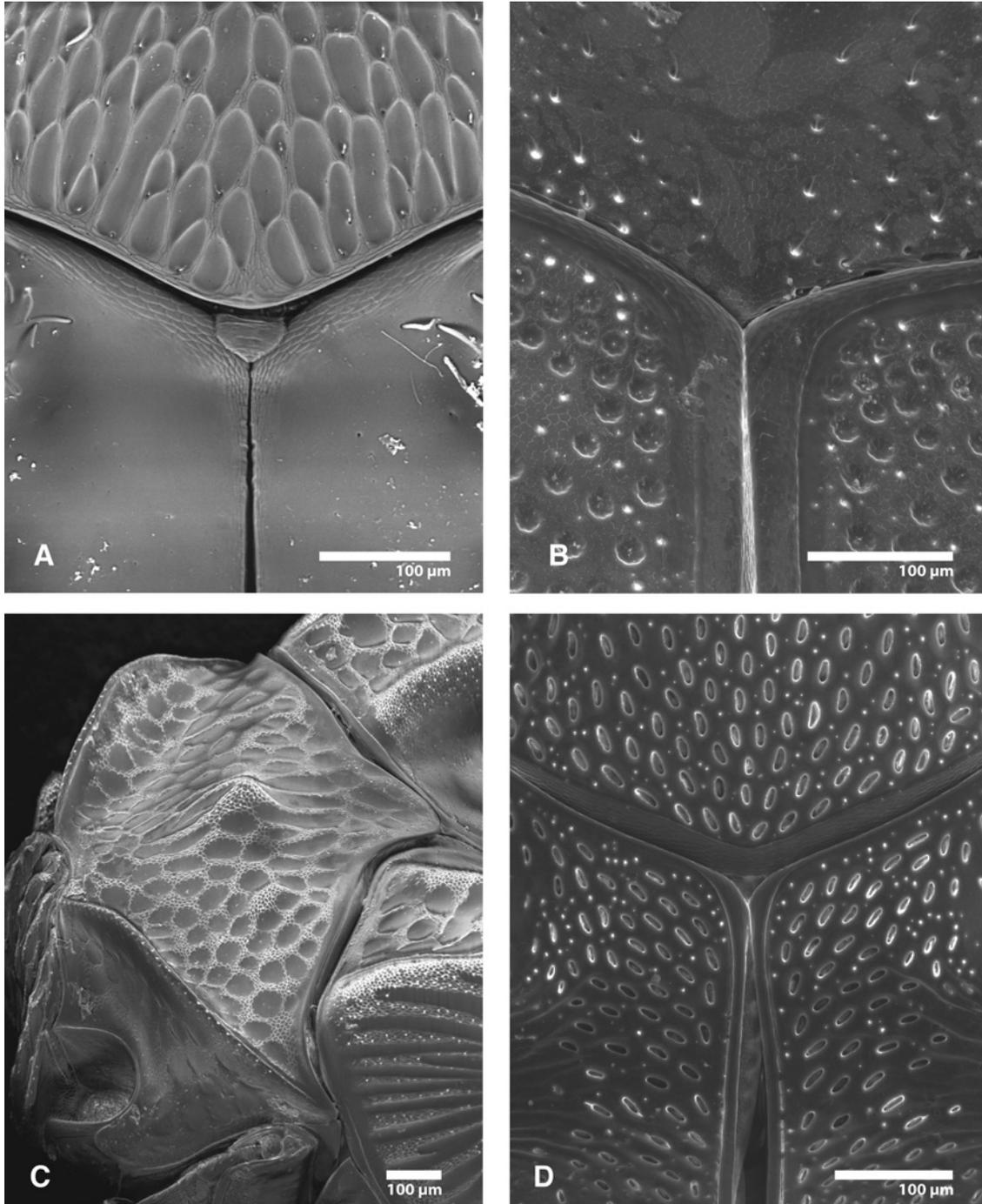


Fig. 4. A, pronotal-elytral junction of *Chlamydopsis caledoniae*; B, pronotal-elytral junction of *Pheidoliphila ruginota*; C, dorso-lateral view of prothorax of *Quasimodopsis riedeli*; D, pronotal-elytral junction of *Chlamydonia sinuata*.

ently arisen within the group. However, it is very nearly complete in many *Chlamydopsis*, typically interrupted only between the trichomes, thus it is not scored as complete in these, even though it is more nearly so than in any non-Chlamydopsinae.

Most of the genera in this clade, including *Eucurtiopsis*, *Ceratohister*, *Orectoscelis*, *Pheidoliphila*, and *Gomyopsis* (referred to hereafter as the ‘*Orectoscelis* lineage’) form a very distinctive group, discussed further below. The resolution of genera outside of this clade, however, is especially interesting. Both analyses place the newly described *Quasimodopsis riedeli* as sister to the rest of this group, with the New Caledonian *Kanakopsis* and *Chlamydonia* as independent branches at successively less inclusive levels. Although very distinctive, *Quasimodopsis* was initially considered an extremely aberrant *Chlamydopsis*, and had been identified as such by some previous determiners. Its prothorax in particular exhibits many *Chlamydopsis*-like characters, including elevated lateral margins, a very short prosternum, and a posteriorly emarginate prosternal keel. However, most of these represent sympleiomorphies, and the characters shared with the *Orectoscelis* lineage (especially the reduced gular sutures and hidden scutellum) offer a seemingly reliable resolution.

The two New Caledonian genera differ substantially from each other, and are resolved as independent lineages here (as in the more restricted analysis of Caterino 2006) subtending the *Orectoscelis* lineage. Decay support for a couple of these internal branches, though not high, is above average for this tree. Despite being supported by two decay steps, monophyly of these plus the *Orectoscelis* lineage is not supported by any unambiguous transformations. Some reconstructions show a reduction of maxillary palp segmentation and elongation of prosternum. The branch leading to *Chlamydonia* and the *Orectoscelis* lineage is supported by more unambiguous changes, though all of these still show some homoplasy. Most reliable would probably be the presence of a bifid pronotal process near the anterior pronotal margin. Other changes mapping to this branch are more superficial (body setae) or of less certain homology. *Kanakopsis* superficially appears more similar to members of the *Orectoscelis* lineage than *Chlamydonia*, with transversely incised trichomes like those of *Eucurtiopsis*. Its mouthparts, however, appear to be identical to those of *Chlamydonia*. In fact, it may be more closely related to *Chlamydonia* than indicated here. But it lacks the pronotal tubercles that here unite *Chlamydonia* with the *Orectoscelis* lineage. An important character state ambiguity also hinders definite placement, whether or not the scutellum is visible in *Kanakopsis*. It is not obviously visible in the unique type. However, to be absolutely certain it would be necessary to partially dissect the specimen to expose the mesonotum. In the present dataset the scutellum is scored as ‘hidden’. Changing this scoring to ‘visible’ yields a monophyletic *Chlamydonia* + *Kanakopsis* (as sister to the *Orectoscelis* lineage) as an equally parsimonious solution (results not shown). Resolution of numerous missing character states will be necessary before these relationships can be very confidently established.

Monophyly of the ‘*Orectoscelis* lineage’ has previously been suggested, though not specifically examined (Caterino 2003). Several unambiguous transformations map as synapomorphies of this lineage, including emargination of the anterior mesosternal margin, reduced palp segmentation, loss of free mentum and sub-

mentum, and narrowing of the frons; the clade has Bremer support of 1 step. Although its monophyly is not in question, this is a highly varied lineage. Many members (*Ceratohister*) have lost the humeral trichomes, pronotal processes range from absent to extremely prominent, and surface textures from completely smooth to deeply, densely punctatorugose. This tremendous morphological range makes internal relationships difficult to resolve, and none of the included genera, as heretofore conceived, is resolved as monophyletic. Several major clades appear in the unweighted consensus tree, but none with strong support. One of the better supported branches (decay index = 2) is that supported by the loss of humeral trichomes, which includes the genus *Ceratohister* and a few other species we have placed elsewhere. This loss has almost certainly occurred multiple times, these results notwithstanding. One clade, comprising mainly species of *Pheidoliphila*, is supported by the restriction of the trichomes to the extreme anterolateral corner of the elytra. Inclusion of *Orectoscelis aurolepidus*, which exhibits a different (and here autapomorphic) state, and *O. dumogae*, which is scored as for *Pheidoliphila*, disrupt what would otherwise be a nearly monophyletic *Pheidoliphila*. *Pheidoliphila secqi* lacks humeral trichomes, and does not resolve with other *Pheidoliphila* for that reason. Most representatives of *Eucurtiopsis* also resolve together, based on the dual, anterior and posterior, origins of the setae of the humeral trichome, but with the additional inclusions of *Papuopsis*, *Gomyopsis*, and a species of *Orectoscelis*. A couple of unquestioned species of *Eucurtiopsis* also fall outside this clade. In short, there is limited phylogenetic support for any of the genera currently recognised within the *Orectoscelis* lineage.

Revised classification and catalogue

Here we present a summary classification of the entire subfamily. This section includes the description of a few new monotypic genera, and reassignment of several species according to the phylogenetic analysis presented above. Diagnoses are provided for all genera, as are additional descriptive data of the type species of *Eucurtia* and *Pheidoliphila*, based on recently studied type specimens of their type species. We refer readers to Mazur (1997) for complete species level synonymy of species described before Caterino (2000). Brief indications of distributions are given following each name. Some geographic regions are abbreviated as follows: AUS, Australia; NT, Northern Territory, Australia; Qld, Queensland, Australia; NSW, New South Wales, Australia; ACT, Australian Capital Territory, Australia; Vic., Victoria, Australia; SA, South Australia, Australia; WA, Western Australia, Australia; Tas., Tasmania, Australia; IND, Indonesia; Sul., Sulawesi, Indonesia; WP, West Papua, Indonesia (formerly Irian Jaya); MAL, Malaysia; Sab., Sabah (Borneo), Malaysia; Sar., Sarawak (Borneo), Malaysia; PNG, Papua New Guinea.

Subfamily CHLAMYDOPSINAE Bickhardt

Genus *Chlamydopsis* Westwood

Byzenia King, 1869: 74. – Lea, 1914, (*syn.*) Type species. *Byzenia formicicola* King, 1869: 74.

Type species. *Chlamydopsis striatella* Westwood, 1869: 318. Designated by Lewis, 1903: 428.

Diagnosis

Species of *Chlamydopsis* are very diverse in morphology, and cannot be defined at present by any definite synapomorphies (Caterino 2003). The species currently contained in *Chlamydopsis* all share a visible scutellum and an upturned anterior pronotal margin, at least above the antennal cavities, if not along the entire margin. None are entirely flattened dorsally (like *Ectatomphila*) and none have the strikingly elongate trichome setae seen in *Eucurtia*.

Distribution

Various species of *Chlamydopsis* are known from throughout Australia. Two are reported from New Guinea, and two have been recently described from New Caledonia (Caterino 2006). It is difficult to determine the extent to which diversity patterns result from varied sampling effort, but the tropical parts of Queensland appear to harbour greater phylogenetic diversity than other areas. However, given the sampling that has been done in Queensland, it is also apparent that several species groups do not occur there.

Included species (See Caterino (2003) for species groups within *Chlamydopsis*)

1. *Chlamydopsis acutricha* Caterino, 2003; AUS: Qld
2. *C. agilis* Lea, 1914; AUS: NSW, SA
3. *C. antennata* Caterino, 2003; AUS: Qld
4. *C. australis* Caterino, 2003; AUS: SA
5. *C. baloghi* Caterino, 2006; New Caledonia
6. *C. bataviae* Caterino, 2003; AUS: Qld
7. *C. bifovaecollis* (Oke, 1923); AUS: Vic.
8. *C. burnetta* Caterino, 2003; AUS: Qld
9. *C. caledoniae* Caterino, 2006; New Caledonia
10. *C. carinicornis* Lea, 1919; AUS: Vic.
11. *C. carinota* Caterino, 2003; AUS: Qld
12. *C. cavicornis* Lea, 1912; AUS: NSW
13. *C. compressipes* Lea, 1919; AUS: Qld
14. *C. contorta* Caterino, 2003; AUS: Qld
15. *C. convergens* Caterino, 2003; AUS: Qld
16. *C. convexa* Caterino, 2003; AUS: SA
17. *C. coronis* Caterino, 2003; AUS: NSW, ACT
18. *C. crowcrofti* Caterino, 2003; AUS: SA
19. *C. degallieri* Caterino, 2003; AUS: SA, WA
20. *C. detecti* Lea, 1914; AUS: Qld
21. *C. dimorpha* Caterino, 2003; AUS: Qld
22. *C. dispersa* Caterino, 2003; AUS: NT, Qld
23. *C. ectatommata* Lea, 1912; AUS: NSW, ACT, Vic.
24. *C. epipleuralis* Lea, 1912; AUS: NSW, Vic., SA, WA
25. *C. erupta* Caterino, 2003; AUS: Qld
26. *C. formicicola* (King, 1869); AUS: NSW, Vic.
27. *C. inaequalis* Blackburn, 1891; AUS: ACT
28. *C. inquilina* Lewis, 1885; AUS: WA, NSW?
29. *C. jayawijaya* Caterino, 2003; IND: WP
30. *C. kununurra* Caterino, 2003; AUS: WA
31. *C. latipennis* Lea, 1912; AUS: SA
32. *C. latipes* Lea, 1919; AUS: WA
33. *C. lawrencei* Caterino, 2003; AUS: ACT
34. *C. leai* Oke, 1923; AUS: Vic.
35. *C. lepida* Caterino, 2003; AUS: SA
36. *C. loculosa* Lea, 1925; AUS: NSW, SA, WA
37. *C. longipes* Lea, 1910; AUS: Vic., SA
38. *C. lucifer* Caterino, 2003; AUS: NT, Qld
39. *C. macmillani* Caterino, 2003; AUS: WA
40. *C. mallee* Caterino, 2003; AUS: SA
41. *C. mareeba* Caterino, 2003; AUS: Qld
42. *C. matthewsi* Caterino, 2003; AUS: NSW
43. *C. monteithi* Caterino, 2003; AUS: Qld
44. *C. mormolyce* Lea, 1925; AUS: WA
45. *C. myrmecophila* Caterino, 2003; Qld
46. *C. nielseni* Caterino, 2003; AUS: SA
47. *C. nullarbor* Caterino, 2003; AUS: WA
48. *C. pallida* Lea, 1918; AUS: NSW
49. *C. papuae* Lewis, 1913; PNG: Central Province
50. *C. parallelus* Caterino, 2003; AUS: Qld
51. *C. pecki* Caterino, 2003; AUS: WA
52. *C. pilosipes* Caterino, 2003; AUS: Qld
53. *C. pluriseta* Caterino, 2003; AUS: Qld
54. *C. pygidialis* Blackburn, 1900; AUS: ACT, Vic.
55. *C. rana* Caterino, 2003; AUS: Qld
56. *C. reticulata* Lea, 1910; AUS: NSW, ACT, Vic., Tas.
57. *C. rotunda* Caterino, 2003; AUS: Qld
58. *C. sculptus* Oke, 1923; AUS: Vic., SA
59. *C. serricollis* Lea, 1914; AUS: NSW
60. *C. setifera* Caterino, 2003; AUS: Qld
61. *C. setipennis* Oke, 1923; AUS: Vic.
62. *C. storeyi* Caterino, 2003; AUS: WA
63. *C. striatella* Westwood, 1869; AUS: WA
64. *C. striatipennis* Lea, 1919; AUS: NSW, ACT, Vic.
65. *C. strigicollis* Oke, 1923; AUS: NSW, ACT, Vic.
66. *C. transversa* Caterino, 2003; AUS: Qld
67. *C. trichonota* Caterino, 2003; AUS: Qld
68. *C. tuberculata* Lea, 1912; AUS: Vic.
69. *C. variolosa* Lea, 1910; AUS: Qld
70. *C. weiri* Caterino, 2003; AUS: Qld
71. *C. zborowskii* Caterino, 2003; AUS: Qld

Genus *Eucurtia* Mjöberg

Type species. *Eucurtia paradoxa* Mjöberg, 1912: 122, by original designation.

Diagnosis

The lone valid species *Eucurtia comata* (Blackburn) is recognisable principally by its large size and by the dense, elongate tufts of setae arising from the anterior and posterior elevations of the elytral trichomes (Fig. 14A–B)

Eucurtia comata (Blackburn, 1901)

Chlamydopsis comata Blackburn, 1901: 129. Holotype, 'Australia, Blackburn Coll., B.M. 1910-236' [middle label with barely legible '6961, T' and a four or five letter word starting with 'W'] '*Chlamydopsis comata* Blackb.'; BMNH, examined by MSC 2005.

Eucurtia paradoxa Mjöberg, 1912: 122; Reichardt, 1941: 57, (*syn.*). Lectotype, hereby designated: 'Riksmuseets Entomologiska Afdelning, *Eucurtia paradoxa* Mjobj., Williamstown Syd-Australien,

Colleg. E. Mjoberg, Determ. E. Mjoberg' [all handwritten]; stored in ethanol, NHRS (Stockholm), examined by MSC 2005. This lectotype is designated to clarify the status of the unique specimen representing the original series.

Redescription

L: 3.08; W: 2.37; E/Pn L: 1.68; E/Pn W: 1.41; Pn W/L: 1.46; E L/W: 0.82; Pr/Py: 0.95; sterna: 0.62, 0.10, 1.03; tibiae: 0.90, 0.90, 0.10. Body dark rufescent brown, with elytra and legs slightly lighter, most of dorsum smooth and shining (with exceptions as below). Frons slightly wider than long, with sides broadly rounded, indented at antennal insertions, completely reticulopunctate, with raised areas alutaceous, bearing scattered setae, depressed areas smooth and shining; labrum short, arcuate, with transverse microsculpture and fine scattered setae; mandibles with left strongly overlapping right, with fine reticulate microsculpture and few setae near sides; antennal scape about half as broad as long, arcuate, widest at midpoint, somewhat abruptly narrowed to base; antennal funicle (of female)

collectively about half as long as scape; antennal club (of female) oval, slightly shorter than funicle, mostly glabrous in basal half, with transverse series of setae about one-third from base on anterior surface.

Pronotum with posterior margin arcuate, sides widest about one-third from base, subangulate, strongly narrowed to anterior margin, which is approximately equal in width to head; lateral margins elevated, bearing a continuous fringe of conspicuous setae; anterior margin not elevated above head, lacking setae; pronotal disk convex in middle, but strongly depressed at sides, especially at lateral angle; disk smooth and glabrous at middle, reticulostriate and with few setae in posterior corners; antennal cavities largely open above.

Scutellum visible. Elytra with pronounced humeral trichomes; anterior and posterior elevations completely divided by deep incision; anterior elevation with fine anteromedian groove extending from anterior margin to inner base of setal insertion, at apex bearing dense clump of very long setae. (In the *E. comata* type these extend posteriorly, nearly reaching elytral

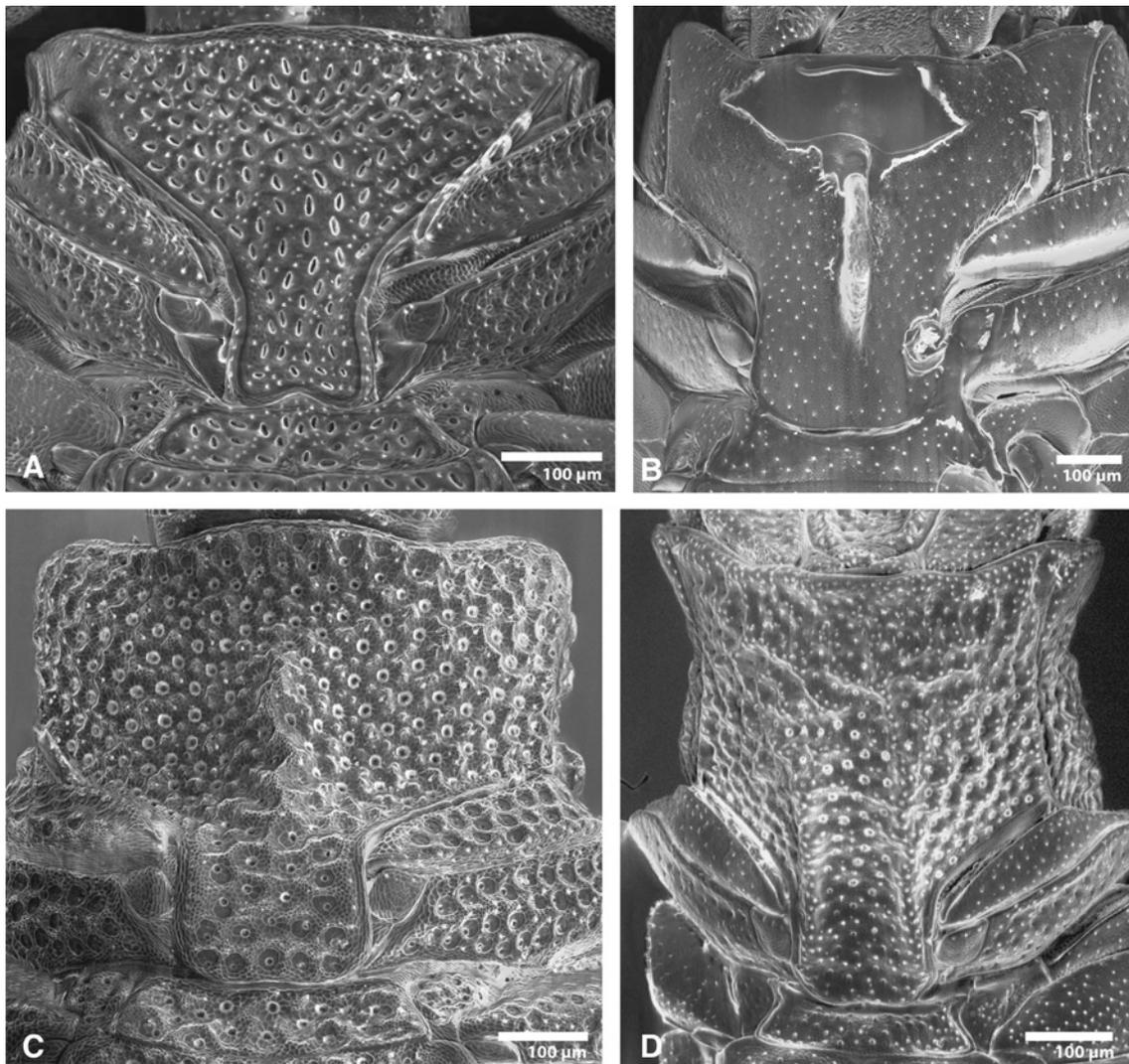


Fig. 5. Prosternum: A, *Chlamydonia sinuata*; B, *Pheidoliphila minuta*; C, *P. secqi*; D, *P. storeyi*.

apex. However, it is unclear what their orientation would be in life. In Mjöberg's type (*E. paradoxa*), preserved in ethanol, this anterior setal bundle extends to sides and curves anterad.) Posterior elevation with arcuate anterior inner edge bearing short fringe of setae, at apex with dense bundle of setae (as above, of uncertain orientation; in *E. comata* type these curve up and posterad, whereas in the type of *E. paradoxa* these extend anterodorsad); posterior elevation broadening posteriorly and descending gradually to elytral apex; elytral disk deeply depressed in anterior half between trichomes; with few setae at sides (at inner base of trichome), entirely smooth and shining;

elytral marginal stria present only along posterior and epipleural margins, departing slightly from margin above metothoracic leg; epipleuron densely reticulostriate, with strigae converging to trichome incision, bearing few conspicuous setae beneath incision.

Prosternum short, with anterior margin deeply grooved, the lower edge projecting slightly on either side of mandibles, the marginal groove departing from the margin at sides to meet supracoxal carina; prosternal leg depression margined by strongly raised carina; prosternal keel emarginate at base, with the posterior marginal stria obsolete; prosternal disk transversely

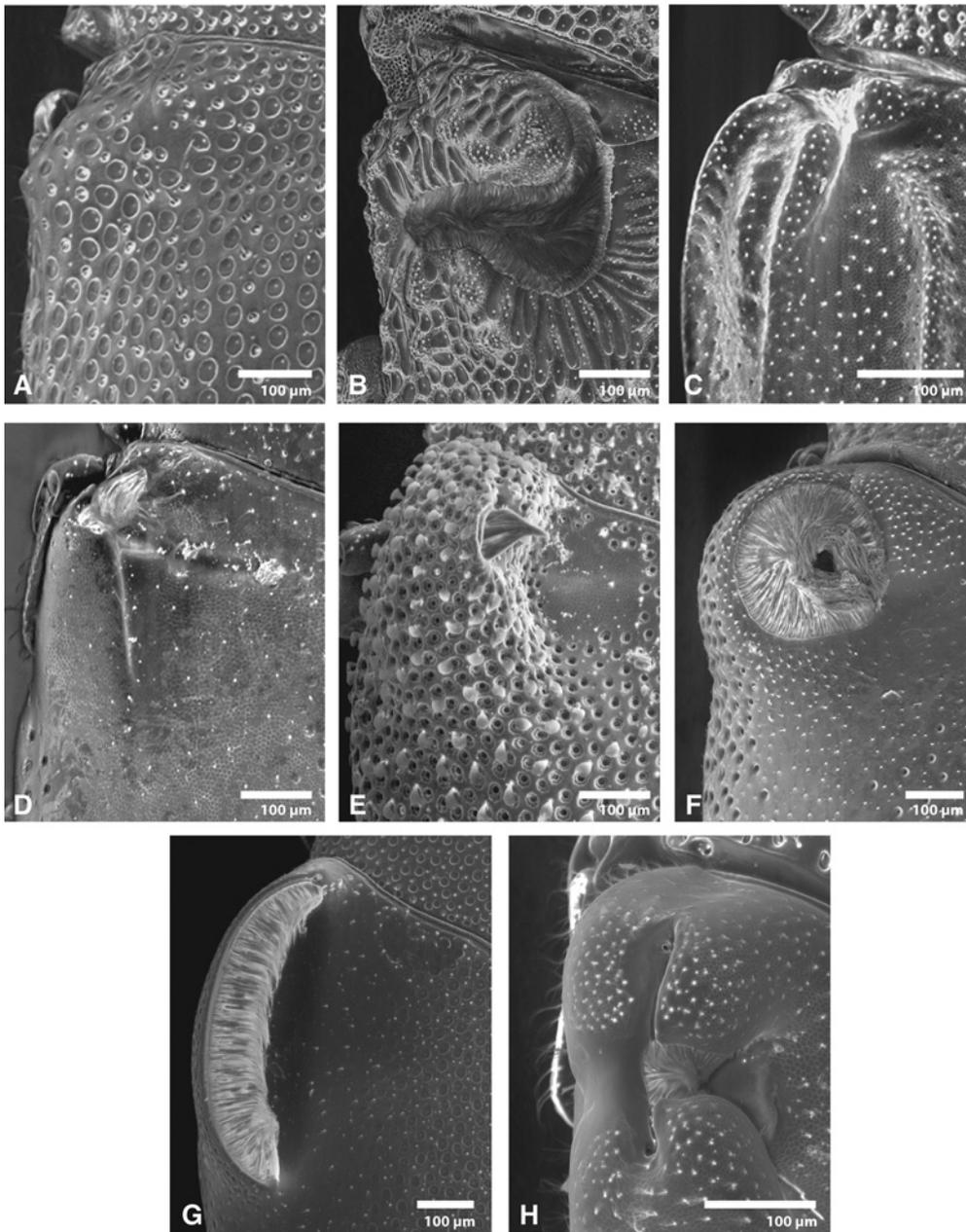


Fig. 6. Left elytron showing humeral trichomes: A, *Ceratothister demotus*; B, *Chlamydopsis erupta*; C, *Pheidoliphila secqi*; D, *P. ruginota*; E, *Orectoscelis kovariki*; F, *Orectoscelis okei*; G, *Orectoscelis ubirr*; H, *Eucurtiopsis hammondi*.

reticulopunctate along anterior margin, becoming impunctate, alutaceous, with very fine polygonal microsculpture, in posterior two-thirds; mesosternum very short, $\sim 8\times$ as wide as median length; weakly projecting at middle, anteriorly bordered by a raised carina, with a short carina from posteromedial corner of mesocoxa meeting it behind the prothorax; mesosternal disk convex behind the anterior margin, with dense alutaceous microsculpture in posterior half; mesepimeron prominent, projecting at anterior corner, forming a cradle for reception of apex of profemur; mesometasternal suture finely impressed, continuous at side with stria delimiting the mesothoracic leg depression; metathoracic disk impunctate, with uniform alutaceous microsculpture and few fine setae; 1st abdominal ventrite similar in texture to metasternum, with raised stria delimiting depression for reception of metathoracic leg.

Femora slender, with edges of meso- and metafemora only weakly arcuate, margined along anterior and posterior sides; protibia angulate about one-third from base, arcuate to narrow rounded apex; mesotibia with basal marginal angulation less pronounced; metatibia almost symmetrically rounded, widest near middle; tarsi slightly laterally compressed, tarsomeres 1 and 5 similar in length, $\sim 1.6\times$ length of tarsomeres 2–4; tarsal claws simple, divergent, weakly arcuate.

Propygidium shallowly but uniformly punctate, the punctures separated by about half their widths, the intervening spaces alutaceous; pygidium similarly textured but with punctures smaller, sparser, and becoming obsolete to apex.

Biology

Mjöberg's (1912) description of *E. paradoxa* included observations on its biology. The species was found in a colony of an unidentified species of 'Eutermes' (Isoptera). Unfortunately, this is no longer a valid name of any Australian termites, and the host is therefore uncertain. However, the observations are unique and valuable nonetheless. A fluid was observed to be secreted from the apices of the humeral trichome setae. This substance attracted the termites, which apparently consumed the secretion. Mjöberg asserted that these setae were themselves hollow and conducted the fluid. This seems unlikely, and if indeed some fluid is being produced it is more likely transported along the setae by capillary action from the base of the trichomes.

Remarks

Although highly distinctive, *Eucurtia* appears likely to be a divergent *Chlamydopsis*, sharing a few character states with members of the *ectatommae* group, in particular. As it is still only known from two specimens, both probably females, however, we maintain its generic status here, pending availability of additional material.

Distribution

South Australia.

Included species

1. *Eucurtia comata* (Blackburn, 1901); AUS: SA

Genus *Ectatommiphila* Lea

Type species. *Chlamydopsis glabra* Lea, 1910: 203. Designated by Mazur, 1984: 113.

Diagnosis

Ectatommiphila is easily recognised by its large size (c. 4 mm, and flat dorsum (Fig. 14C, D). Its small trichomes open as transverse slits which are not raised above the level of the elytra.

Biology

As the name implies, species of this genus have been collected in nests of what were once known as *Ectatomma metallica* (now *Rhytidoponera*).

Remarks

Lea (1914) regarded this genus as 'nearer the normal Histeridae than any of the others,' apparently suggesting it might be sister to much of the subfamily. Our data do not support this and instead suggest that its relatively inconspicuous trichomes result from reduction. It is possible that *Ectatommiphila* represents a highly divergent lineage of *Chlamydopsis*.

Distribution

This distinctive genus is apparently rather widespread in Australia. We have seen specimens of *E. opaca* from Western

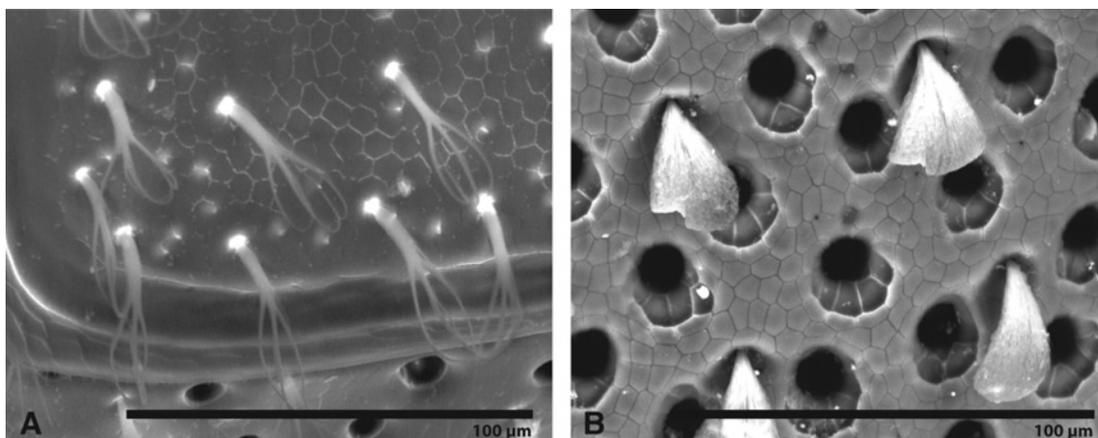


Fig. 7. Setae: A, *Eucurtiopsis hammondi*; B, *Orectoscelis kovariki*.

Australia, New South Wales, and Brisbane, Queensland, and Oke (1923) reported it from southern Victoria (Geelong) as well.

Included species

1. *Ectatomphila glabra* (Lea, 1910); AUS: NSW
2. *E. opaca* (Lea, 1912); AUS: Qld, NSW, Vic.

Genus *Orectoscelis* Lewis

Orectochilus Mjöberg, 1912: 121 (*lapsus calami*).

Type species. *Orectoscelis humeralis* Lewis, 1903: 427, by monotypy.

Diagnosis

Orectoscelis is herein restricted to those species with a completely hidden scutellum and circular, usually obliquely elevated humeral trichomes, fringed by a single continuous setal margin. Several species placed here by Caterino (2000) are removed to other genera, whereas a few others described therein are retained here with reservation.

Distribution

The combined distribution of the species included here ranges from northern Australia (both Queensland and Northern Territory) through New Guinea, north-west to Sulawesi

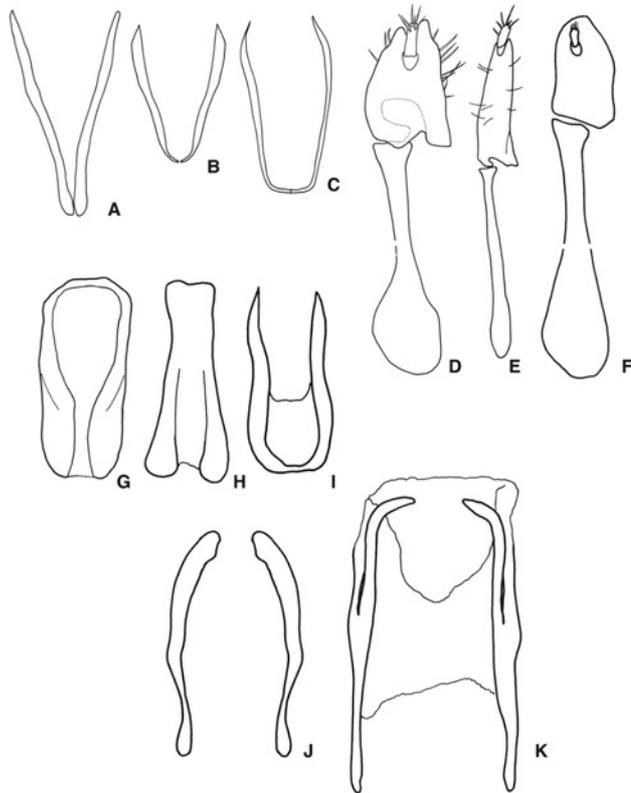


Fig. 8. Genitalia: A–C, struts of female 9th segment. A, *Chlamydopsis formicicola*; B, *Orectoscelis westwoodi*; C, *Pheidoliphila secqi*. D–F, ovipositor of female. D, *Chlamydonia sol.*; E, *Chlamydopsis rana*; F, *Chlamydopsis matthewsi*. G–I, male spiculum gastrale. G, *Chlamydopsis caledoniae*; H, *Chlamydopsis formicicola*; I, *Chlamydopsis*, sp. nov. [Japan Island]. J–K, male ninth tergite(s). J, *Orectoscelis westwoodi*; K, *Chlamydopsis formicicola*.

Included species

Orectoscelis duboulaii (Westwood) is still provisionally included in *Orectoscelis* (as originally suggested by Lewis 1903). Although the laterally open trichomes in Westwood's drawing appear more like those of *Eucurtiopsis*, no *Eucurtiopsis* are known to us from the Australian continent, and it may be a convergent development. Unfortunately, the type of *O. duboulaii* (which was said by Westwood to be in the du Boulay collection) cannot be located and no additional specimens are known. Therefore its placement cannot be determined satisfactorily at present.

1. *Orectoscelis attenuatus* Dégallier & Caterino, 2005a; PNG: Madang
2. *O. aurolepidus* Caterino, 2000*; IND: Sul.
3. *O. blackburni* Dégallier & Caterino, 2005a; AUS: Qld
4. *O. circularis* Caterino, 2000; IND: Sul.
5. *O. duboulaii* (Westwood, 1869); AUS: Vic.
6. *O. dumogae* Caterino, 2000*; IND: Sul.
7. *O. halmaherae* Dégallier & Caterino, 2005a; IND: Halmahera
8. *O. howdeni* Dégallier & Caterino, 2005a; PNG: East New Britain
9. *O. humeralis* Lewis, 1903; AUS: Qld
10. *O. kovariki* Dégallier & Caterino, 2005a; AUS: Qld
11. *O. marginicollis* Dégallier & Caterino, 2005a; AUS: Qld
12. *O. obliquus* Caterino, 2000*; IND: Sul.
13. *O. okei* Dégallier & Caterino, 2005a; AUS: Qld
14. *O. peninsularis* Dégallier & Caterino, 2005a; AUS: Qld
15. *O. punctatus* Caterino, 2000*; IND: Sul.
16. *O. shihoae* Nishikawa, 2002; Japan
17. *O. ubirr* Dégallier & Caterino, 2005a; AUS: NT
18. *O. westwoodi* Dégallier & Caterino, 2005a; AUS: Qld

* These four species are retained in *Orectoscelis* for the present, although they do not conform well to the taxon as redefined here. Clarification of their status will require additional material.

Genus *Ceratohister* Reichensperger

Type species. *Ceratohister pheidoliphilus* Reichensperger, 1924: 302, by original designation. Despite multiple searches in the Reichensperger and Wasmann collections (in Bonn, Germany and Maasricht, Holland, respectively), no type of *Ceratohister pheidoliphilus* can be found (Dégallier 1993; A. Tishechkin personal communication). However, the original description and accompanying photograph are sufficient to determine the most taxonomically significant character states.

Diagnosis

Ceratohister is here defined to include *Orectoscelis*-like species which have lost any indication of elytral trichomes, and which lack the elevated elytral carinae of the undescribed Fijian species and some Australian species of *Pheidoliphila* (e.g. *P. storeyi* Dégallier & Caterino, *P. dahlgreni* Dégallier & Caterino).

Remarks

The monophyly of this group is supported principally by the loss of a humeral elytra trichome. The species are otherwise rather varied, and the group's monophyly requires additional testing

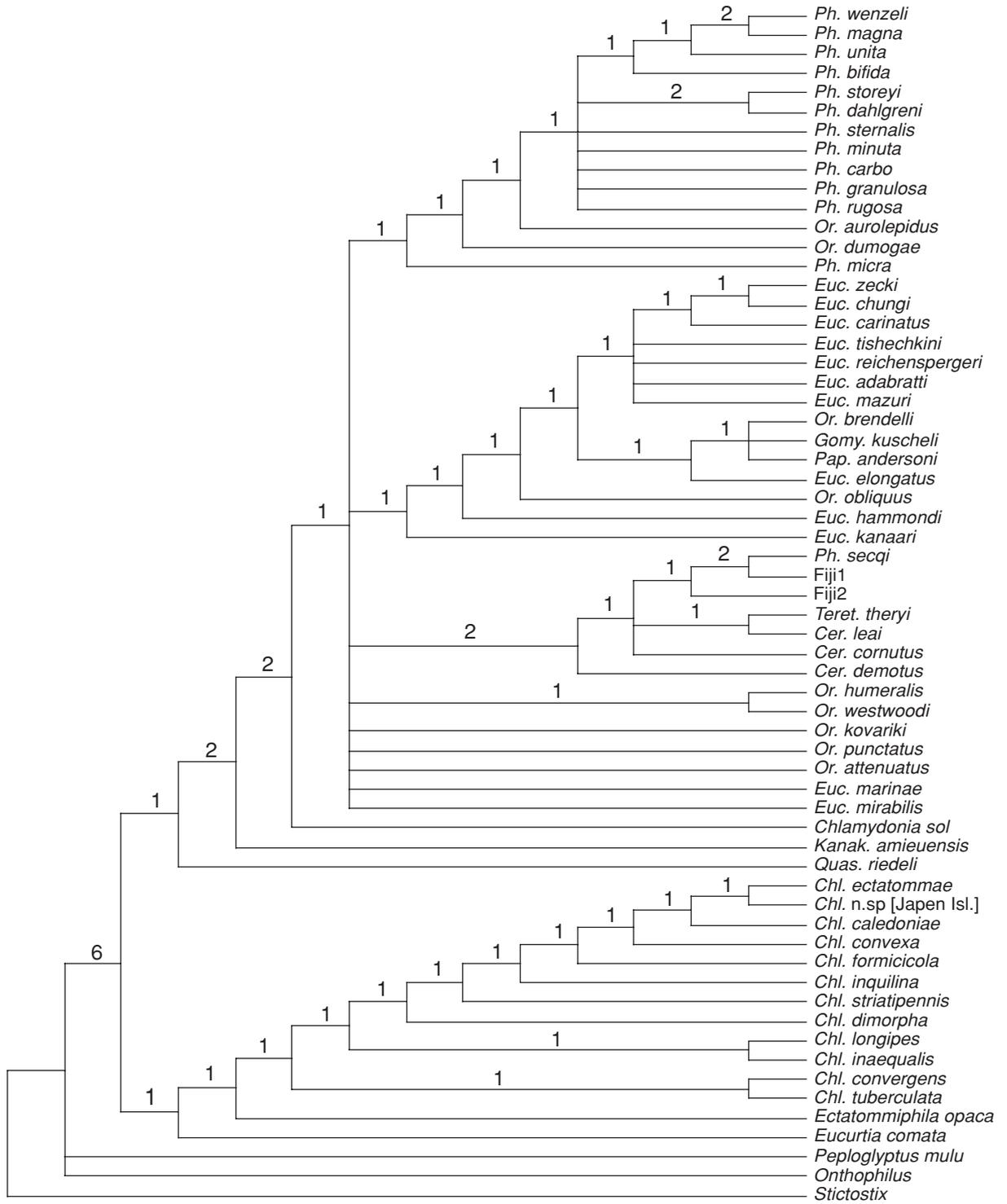


Fig. 9. Strict consensus of 19000 equally parsimonious trees resulting from unweighted analysis of character data. Numbers on branches indicate decay indices.

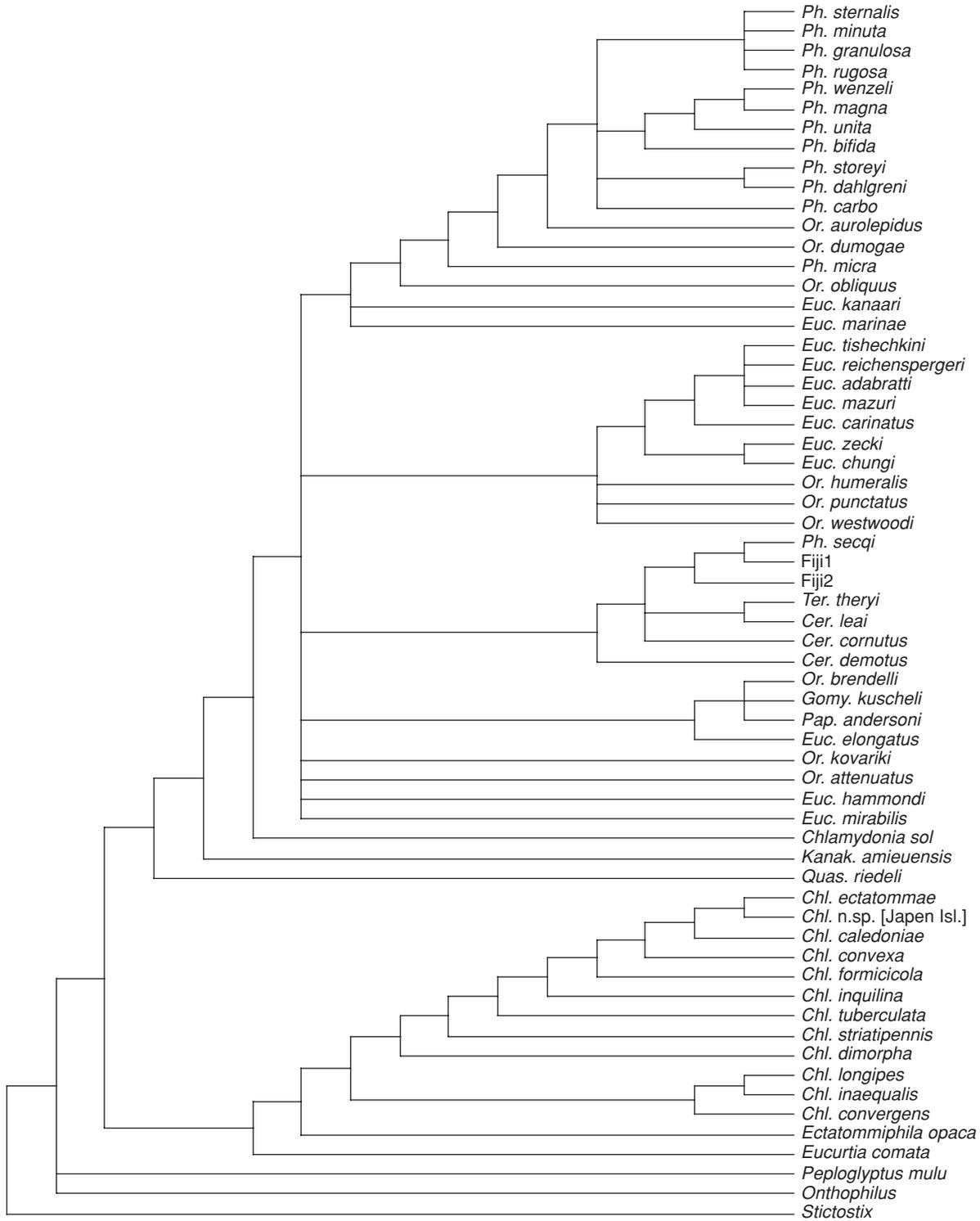


Fig. 10. Strict consensus of 107020 trees resulting from reweighted analysis of character data.

Distribution

The type of *Ceratothister*, *C. pheidoliphilus*, was described from India. The more recently described species in the group are all from the Indomalaysian islands, Borneo and Sulawesi.

Included species

1. *Ceratothister ankylonotum* Dégallier & Caterino, 2005a; MAL: Sabah (Borneo)
2. *C. cornutus* Dégallier & Caterino, 2005a; Brunei (Borneo)
3. *C. demotus* (Caterino, 2000) nov. comb.; IND: Sul.
4. *C. leai* Dégallier & Caterino, 2005a; MAL: Sarawak (Borneo)
5. *C. pheidoliphilus* Reichensperger, 1924; India

Genus *Pheidoliphila* Lea

Type species. *Pheidoliphila minuta* Lea. The type fixation of *Pheidoliphila* has not previously been properly cited. Bickhardt's (1916) citation of *Pheidoliphila minuta* Lea in this context was taken by Mazur (1984, 1997) to constitute a valid type designation. However, Bickhardt appears not to have seen Lea's actual publication (he cited the genus as '*in litt.*') and his designation is listed with a '(?)'. This ambiguity precludes Bickhardt's citation as a valid type fixation, and Mazur's (1984) unambiguous statement that *P. minuta* is the type of *Pheidoliphila* should instead be cited.

Diagnosis

Lea originally characterised this genus as follows: 'The species of this genus are all small. The prothorax is strongly raised in front, with the raised portions overhanging the head. The elytra are not depressed immediately behind the scutellar region, but there is a depression close to each shoulder; there is an oblique incision at each shoulder, but the shoulders themselves are not raised above the general level, although clothed internally. All the legs are fitted into grooves.' We have conceived of this group more broadly (Dégallier and Caterino 2005b), in particular including a few species that lack humeral trichomes (*P. secqi*, *P. penatii*, and *P. oharai*). All may still be characterised by the presence of some sort of bifid projection, usually prominent, extending dorsad, and often anterad of anterior pronotal margin. Where trichomes are present, they are small, oblique, and found in the extreme anterolateral corners of each elytron.

Pheidoliphila minuta Lea

Pheidoliphila minuta Lea, 1914: 214.

Material examined

Paratype. female, 'Co-type'/'Fern Tree Gully, with Pheidole, F. P. Spry'/'George Lewis Coll. B.M. 1926-369'/'*Pheidoliphila minuta* Lea, Co-type', BMNH.

Redescription

Body wholly covered by fine, superficial, evenly and rather widely spaced punctuation (punctures separated by 2–3× their diameters), each puncture bearing a fine, erect seta; setae of frons, antennal scapes, and bases of mandibles longer, curved

and flattened; on the basal 2/3 of the pronotum, punctures obscured by finely and densely chagrined surface. Frons hardly longer than wide, feebly concave, labrum bluntly triangular.

Pronotum 1.3 wider as long, its apex 0.8 and 0.6 as wide as the base and as the elytra, respectively. Scutellum not visible. Propygidium and pygidium 2 and 1.7× as wide as long, respectively.

Distance between the procoxae wide, 0.73 and 0.53× those separating the meso- and metacoxae, respectively; prosternal keel with a deep median longitudinal groove, whose sides are wide and convex; mesosternum with a rounded fovea mediat to its base; lateral metasternal stria semicircularly curved in front where it meets the metasternal-metepisternal suture; one curved post-metasternal stria is present on each side of the first abdominal sternite.

Biology

Though hosts are now known for only a few species, all records are with ants in the genus *Pheidole*. Oke (1923) reported *P. minuta* being carried around by its hosts, held in the ants' mandibles apparently by the humeral trichome.

Distribution

Pheidoliphila have been found throughout eastern Australia, as well as in Tasmania, and a single species placed here (*P. micra*) occurs in Papua New Guinea. Two apparent species of *Pheidoliphila*, recently found from Fiji, will be described in a subsequent paper.

Included species

1. *Pheidoliphila acutistria* Dégallier & Caterino, 2005b; AUS: Qld
2. *P. arriagadai* Dégallier & Caterino, 2005b; AUS: Qld
3. *P. bifida* Dégallier & Caterino, 2005b; AUS: Qld
4. *P. carbo* (Lea, 1910); AUS: Vic.
5. *P. dahlgreni* Dégallier & Caterino, 2005b; AUS: Qld
6. *P. finnigana* Dégallier & Caterino, 2005b; AUS: Qld
7. *P. granulata* (Lea, 1912); AUS: Vic.
8. *P. kapleri* Dégallier & Caterino, 2005b; AUS: Qld
9. *P. lackneri* Dégallier & Caterino, 2005b; AUS: Qld
10. *P. macmillani* Dégallier & Caterino, 2005b; AUS: NSW
12. *P. magna* Dégallier & Caterino, 2005b; AUS: Qld
12. *P. micra* Dégallier & Caterino, 2005b; PNG: Madang
13. *P. minuta* Lea, 1914; AUS: Vic.
14. *P. oharai* Dégallier & Caterino, 2005b; AUS: Qld
15. *P. penatii* Dégallier & Caterino, 2005b; AUS: Qld
16. *P. pseudocephala* (Lea, 1912); AUS: Tas.
17. *P. ruginota* Dégallier & Caterino, 2005b; AUS: Qld
18. *P. rugosa* Dégallier & Caterino, 2005b; AUS: NSW, Vic.
19. *P. secqi* Dégallier & Caterino, 2005b; AUS: Qld
20. *P. sternalis* (Blackburn, 1891); AUS: SA
21. *P. storeyi* Dégallier & Caterino, 2005b; AUS: Qld
22. *P. suturalis* Dégallier & Caterino 2005b; AUS: Qld
23. *P. unita* Dégallier & Caterino, 2005b; AUS: Qld
24. *P. verityi* Dégallier & Caterino, 2005b; AUS: Qld
25. *P. wenzeli* Dégallier & Caterino, 2005b; AUS: Qld
26. *P. yelamosi* Dégallier & Caterino, 2005b; AUS: Qld

Genus *Eucurtiopsis* Silvestri

Boreochlamydes Sawada, 1994: 357. Ôhara, 1994: 78 (*syn.*). Type species *Boreochlamydes ohtanii* Sawada, 1994: 359. By original designation.

Type species. *Eucurtiopsis mirabilis* Silvestri, 1926: 268, by original designation. Although we have not studied this type, and have not been able to determine where it is deposited, it is sufficiently well illustrated in the original description as to leave no doubt about its identity and relationships.

Diagnosis

Elytra broader than prothorax; trichome transversely incised; pronotum of most species with paired subapical dorsal processes; most species with branched setae on some part of the body.

Biology

Host associations have been reported for *E. mirabilis* ('cum formica'), and more usefully, for *E. ohtanii* (with *Pheidole fervida* Smith; Nishikawa, 1995).

Remarks

Although our analyses support a clade containing most *Eucurtiopsis* (and a few additional monotypic genera that may eventually be sunk), it may be troubling that the type species of

the genus (*E. mirabilis*) is not among them. This primarily results from numerous unscored characters for this species, as we have not been able to study type (or any other) material of this species. Original illustrations of the species leave no doubt, however, that it is closely related to other members of this clade, and it is very similar to *E. mazuri* in particular.

Distribution

The species of *Eucurtiopsis* represent a relatively northern radiation of Chlamydopsinae. Most of the known species have been described from Borneo and Sulawesi, but species have also been described from Taiwan and Japan, and as yet undescribed species are known from the Philippines (Tishechkin, personal communication).

Included species

1. *Eucurtiopsis adebratti* Dégallier & Caterino, 2005a; MAL: Sab.
2. *E. brendelli* (Caterino, 2000) nov. comb.; IND: Sul.
3. *E. carinatus* (Caterino, 2000) nov. comb.; IND: Sul.
4. *E. chungi* Dégallier & Caterino, 2005a; MAL: Sab.
5. *E. danielssoni* Dégallier & Caterino, 2005a; MAL: Sab.
6. *E. elongatus* (Caterino, 2000) nov. comb.; IND: Sul.
7. *E. gomyi* Dégallier & Caterino, 2005a; MAL: Sab.
8. *E. hammondi* (Caterino, 2000) nov. comb.; IND: Sul.

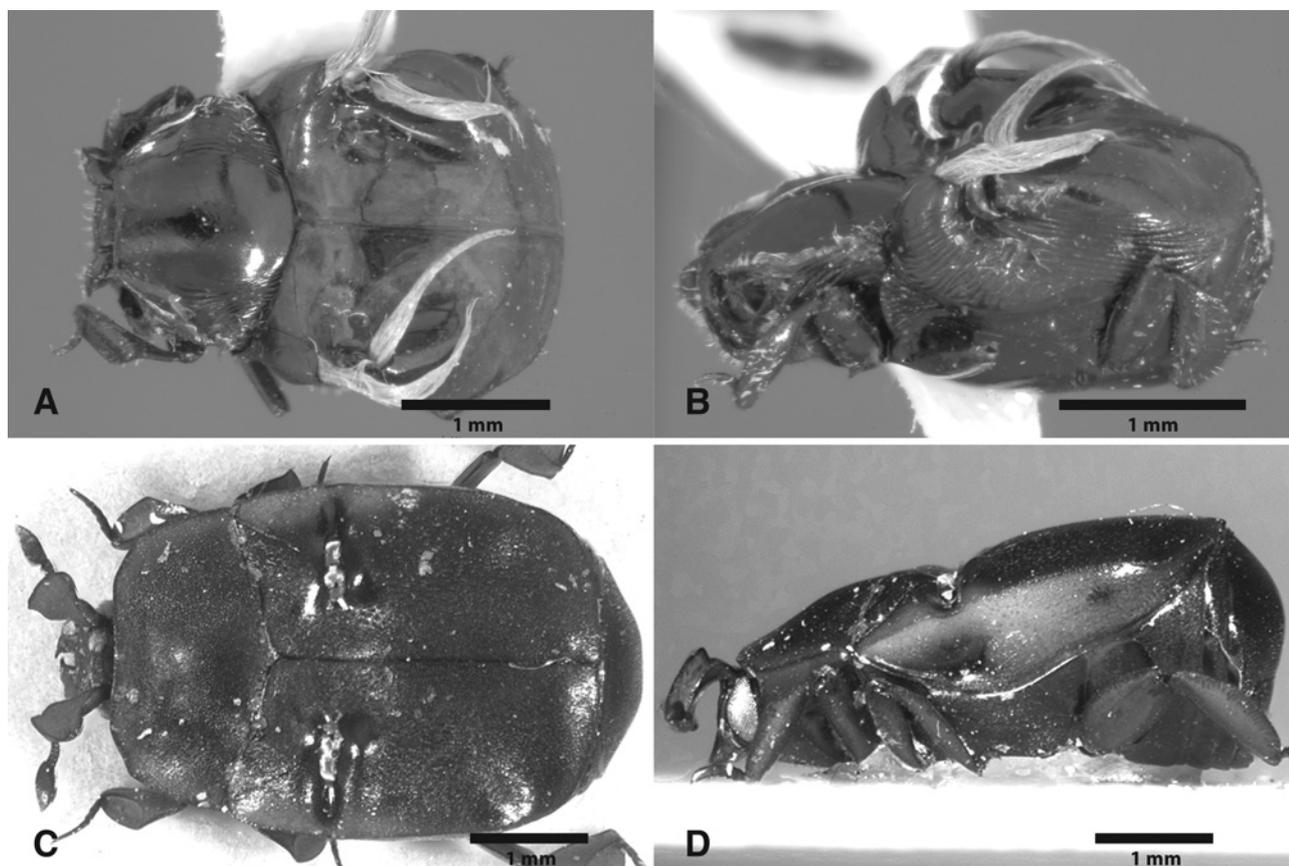


Fig. 11. Dorsal and lateral habitus photographs of holotype of *Eucurtia comata* (A, B) and nontype of *Ectatommiphila opaca* (C, D).

9. *E. hiranoi* Nishikawa, 1995: Japan
10. *E. kanaari* Dégallier & Caterino, 2005a; MAL: Sab.
11. *E. marinae* Dégallier & Caterino, 2005a; MAL: Sab.
12. *E. mazuri* Dégallier & Caterino, 2005a; MAL: Sar.
13. *E. mirabilis* Silvestri, 1926; Taiwan
14. *E. ohtanii* (Sawada, 1994): Japan
15. *E. tishechkini* Dégallier & Caterino, 2005a; Brunei
16. *E. reichenspergeri* Dégallier & Caterino, 2005a; MAL: Sab.
17. *E. viennai* Dégallier & Caterino, 2005a; MAL: Sab.
18. *E. zecki* Dégallier & Caterino, 2005a; MAL: Sab.

Genus ***Gomyopsis*** Dégallier

Type species. *Gomyopsis kuscheli* Dégallier, 1984: 57, by original designation.

Diagnosis

The pronotal trichomes (Fig. 12A–B) of *Gomyopsis* are unknown in the subfamily outside of *Chlamydopsis*. The sole species in this genus is similar in general body shape to *Eucurtiopsis brendelli*, from Sulawesi, with which it also shares a margined pronotum. It is not clear, however, if these features are indicative of a close relationships between the two.

Distribution

Fiji.

Included species

1. *Gomyopsis kuscheli* Dégallier, 1984; Fiji

Genus ***Teretriopsis*** Caterino & Dégallier, gen. nov.

Type species. *Teretriopsis theryi* Caterino & Dégallier, sp. nov.

Diagnosis

Because this genus is known from a single species, it is impossible to confidently determine characters by which it will consistently differ from other genera. It shares with *Ceratothister* the (apomorphic) lack of humeral trichomes, but differs from all known *Ceratothister* quite radically in body shape, mainly in its subcylindrical habitus. Its lack of pronotal processes also separates it from most *Ceratothister* (except for *C. leai*, which occurs in Sarawak, Bornean Malaysia).

Biology

The single species of this genus has been collected only by flight interception traps.

Etymology

The name references its similarity in body shape to the cylindrical abraeine histerid, *Teretrius*, with the ending *-opsis* as a generic suffix common to many Chlamydopsinae.

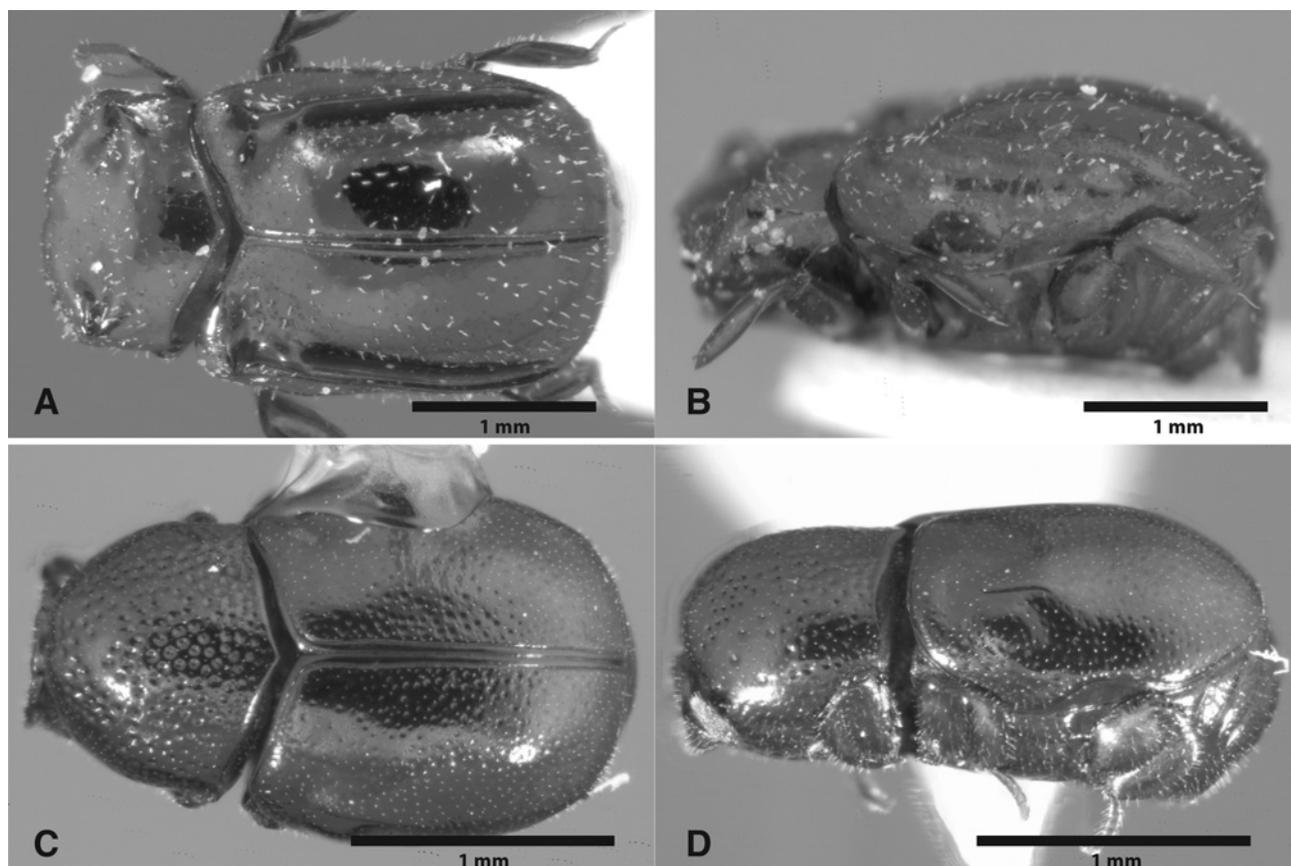


Fig. 12. Dorsal and lateral habitus photographs of holotype of *Gomyopsis kuscheli* (A, B) and paratype of *Teretriopsis theryi* (C, D).

Teretriopsis theryi* Caterino & Dégallier, sp. nov.*Material examined**

Holotype. male. '17.5 km ESE of Mareeba [17°1'28''S, 145°34'46''E] n. Qld 18.I – 3.II.1987 R. I. Storey MDPI FIT Sre 98' (QM, QMT 144000).

Paratypes. 3 ex.: '16.58.19S 145.25.57 [= 16°58'19''S, 145°25'57''E] Emerald Hill, Mareeba, Qld Storey & DeFaveri 15-31.i.1997 Flight Intercept Trap'; 1 ex.: '11 km WSW of Petford, n. QLD 15-29.XI.1992 P. Scammell Flight Int. Trap'; 1 ex. (only head & pronotum): '11 km WSW of Petford, n. QLD 19.III.1993 P. Scammell Flight Int. Trap' (DPIM, QM).

Description

L: 2.18; W: 1.42; E/Pn L: 1.41; E/Pn W: 1.31; Pn W/L: 1.21; E L/W: 0.89; Pr/Py: 1.42; sterna: 0.68, 0.06, 0.47; tibiae: 0.50, 0.47, 0.50. Body subcylindrical, narrowed in both dorsoventral and lateral dimensions anteriorly (Fig. 12C–D), rufescent, the prothorax slightly darker than the elytra, most surfaces with sparse, minute inconspicuous setae, appearing glabrous at low magnification; head hidden from above beneath weakly projecting pronotal margin; head small, frons subquadrate, with sides faintly outwardly arcuate, diverging slightly to antennal insertion; frontal disk with minute, shallow punctures separated by four to five times their widths, shining, though with extremely fine reticulate microsculpture; clypeolabral suture straight; labrum with apical margin rounded, punctures becoming denser towards apex; mandibles small, their outer surfaces minutely punctate; antennal scape subtriangular with acute lateral projection, surface more shallowly and sparsely punctate than frons; antennal funicle short, its total length $\sim 4/5$ as long as club; antennal club $\sim 2/3$ length of scape.

Prothorax strongly convex above, widest at base, sides weakly narrowed to middle, then forming a more or less uninterrupted anterior arc (though actual anterior margin is hidden from dorsal view); without lateral margin; occipital foramen small, only about (lower) half prothoracic height; pronotum curved downward anteriorly, becoming vertical for a short distance above head, this vertical portion very faintly protuberant on either side of shallowly depressed midline; middle of pronotal disk densely, though shallowly and somewhat irregularly covered with large punctures, most of these with a minute, but distinct inner puncture, possibly a gland opening, the large punctures becoming sparser towards front and sides. Prosternum with broad, weakly depressed median keel, slightly elevated at inner edges of procoxae; precoxal portion of prosternum about twice as long as coxal depression, broadly emarginate anteriorly beneath head, with fine marginal stria; disk of prosternum with large, shallow, close but irregularly spaced punctures, particularly in anteromedial two-thirds; procoxal depression with fine marginal stria ending behind coxa, not extending across rounded posterior apex of keel.

Scutellum hidden; elytra lacking humeral trichomes; humeri slightly inflated, and with a short, faint longitudinal stria, possibly representing a vestige of the trichome; elytra together approximately as long as their combined width, sides subparallel, though distinctly narrowed to pronotum and at apices; each elytron with continuous marginal stria around all edges, departing slightly from edge above the metafemur; elytral disk with sparse, small,

faint punctures, slightly more densely along sutural margin, and with minute setae, some not associated with these punctures. Mesosternum short, strongly transverse, broadly emarginate anteriorly for reception of prosternal keel, with few shallow punctures and fine, complete marginal stria; median length of metasternum $\sim 7\times$ as long as mesosternum, separated from it by fine, impressed suture; metasternal disk weakly convex, with fine median longitudinal suture weakly impressed anteriorly, more or less horizontal in median area, ascending at sides, with punctures smaller and sparser than those of prosternum; lateral depression for reception of mesothoracic leg well defined, delimited by elevated carina, extending from inner corner of mesocoxa laterad to elytral epipleuron; first abdominal ventrite about two-thirds length of metasternum along midline, disk with sparse, shallow punctures, becoming smaller and more widely scattered posteriorly; depression for reception of metathoracic leg delimited by carina extending from inner corner of metacoxa laterad to elytral epipleuron. Profemur parallel sided, convex on outer (posterior) surface; protibia broad, outer margin bluntly angulate one-third from base, narrowed to apex; inner half of protibia overlapped by profemur in repose, the overlapped portion delimited by a longitudinal carina; meso- and metafemora broader, flatter than profemur, their posterior margins weakly, and anterior margins strongly, arcuate; meso- and metatibiae with outer margins nearly evenly arcuate; all femora and tibiae smooth, with only fine punctures and minute setae; tarsi strongly laterally compressed; tarsal claws short, simple.

Propygidium vertical, nearly hidden from dorsal view; pygidium turned slightly under; propygidium about two-thirds as long as maximum width, with anterolateral and anterior margins forming an almost uninterrupted semicircle; disk with sparse, small, very shallow punctures and few minute setae, lacking marginal striae; pygidium small, with punctures finer and sparser than those of propygidium, minutely setose.

Male: dorsum of abdominal segment 8 lightly sclerotised, feebly convex, parallel-sided in its basal half, sides straight and convergent apically, base and apex deeply emarginate; venter of segment 8 bilobed at apex, bearing short and erect setae at apex and membranous area mesally; aedeagus with basal piece ~ 0.3 of total aedeagal length, cylindrical in shape, apical piece (parameres) laying at right angle with the basal piece, $4.5\times$ as long as wide at base, near parallel-sided from base to gonopore, dorsally and ventrally flat, thin but slightly thickened before apical curve, then divided in two convergent and shortly ventrally hooked rods, no setae visible.

Etymology

We name this species in honour of Thomas Théry, an up-and-coming specialist on Histeridae.

Genus *Papuopsis* Caterino & Dégallier, gen. nov.

Type species. *Papuopsis andersoni* Caterino & Dégallier sp. nov.

Diagnosis

Papuopsis is distinguished from other genera by its laterally margined pronotum and elytra (Fig. 13A–B), lack of pronotal tubercles, short prothorax, and broadly rounded prosternal keel which extends nearly to the metasternum.

Biology

The single species of this genus has been collected by sifting leaf litter in montane forest.

Etymology

The name of the genus derives from its country of origin, Papua New Guinea, in combination with the common chlamydopsine suffix *-opsis*.

Papuopsis andersoni Caterino & Dégallier, sp. nov.*Material examined*

Holotype. Male labelled 'PAPUA NEW GUINEA: Morobe, Wau (9 km N.N.W.), Mt. Kaindi, 2050m, 6.II.2000, 7°20'24"S 146°20'01"E, R.S. Anderson, montane forest litter, RSA 2000-035c'; CMN.

Description

L: 2.12; W: 1.68; E/Pn L: 2.24; E/Pn W: 1.46; Pn W/L: 1.76; E L/W: 0.87; Pr/Py: 1.25. Sterna: 0.59, 0.03, 0.56. Tibiae: 0.60, 0.60, 0.62; Body elongate oval, strongly and evenly convex dorsally, rufescent brown, smooth, shining, with conspicuous setae only on the trichomes and along the anterior pronotal margin.

Frons with sides weakly arcuate, margined, widest near labrum; frontal disk with pair of low, elongate tubercles extending slightly forward from base bearing series of ~5 setae, other-

wise flat, with irregularly spaced, sparse, shallow punctures and few interspersed setae; clypeolabral suture well impressed, faintly inwardly arcuate; labrum semicircular, flat, with few elongate setae and rather coarse reticulate microsculpture; mandibles square, with few setae on anterior and lateral surfaces; antennal scape with inner edge evenly arcuate, outer edge arcuate to midpoint, there abruptly widened to form rounded, blade-like lamella, apically narrowing to angulate apex; surface of scape convex in basal half, nearly flat along inner edge and in apical half, with very shallow, inconspicuous, broad punctures interspersed with dense polygonal microsculpture and rather dense, elongate setae, all of them 'bent' dorsolaterad at their apices; antennal club (of male) cylindrical, densely setose, approximately equal to scape in length.

Prothorax transverse, 1.9× as wide as median length, sides margined, faintly arcuate, narrowed from base to apex; apical pronotal margin sinuate (almost exactly '}'-shaped, with apices at inner edge of each antennal cavity); antennal cavities broadly open dorsally; pronotal margin with complete marginal stria continuous around all edges; pronotal disk evenly convex, impunctate, shining, with few fine setae along anterior and lateral margins. Prosternum wide, short, with complete anterior and posterior marginal striae; anterior prosternal margin very faintly sinuate; prosternal keel broadly rounded posteriorly, widened slightly behind procoxae, extending over anterior margin of mesosternum; prosternal disk smooth, impunctate, with scattered fine setae.

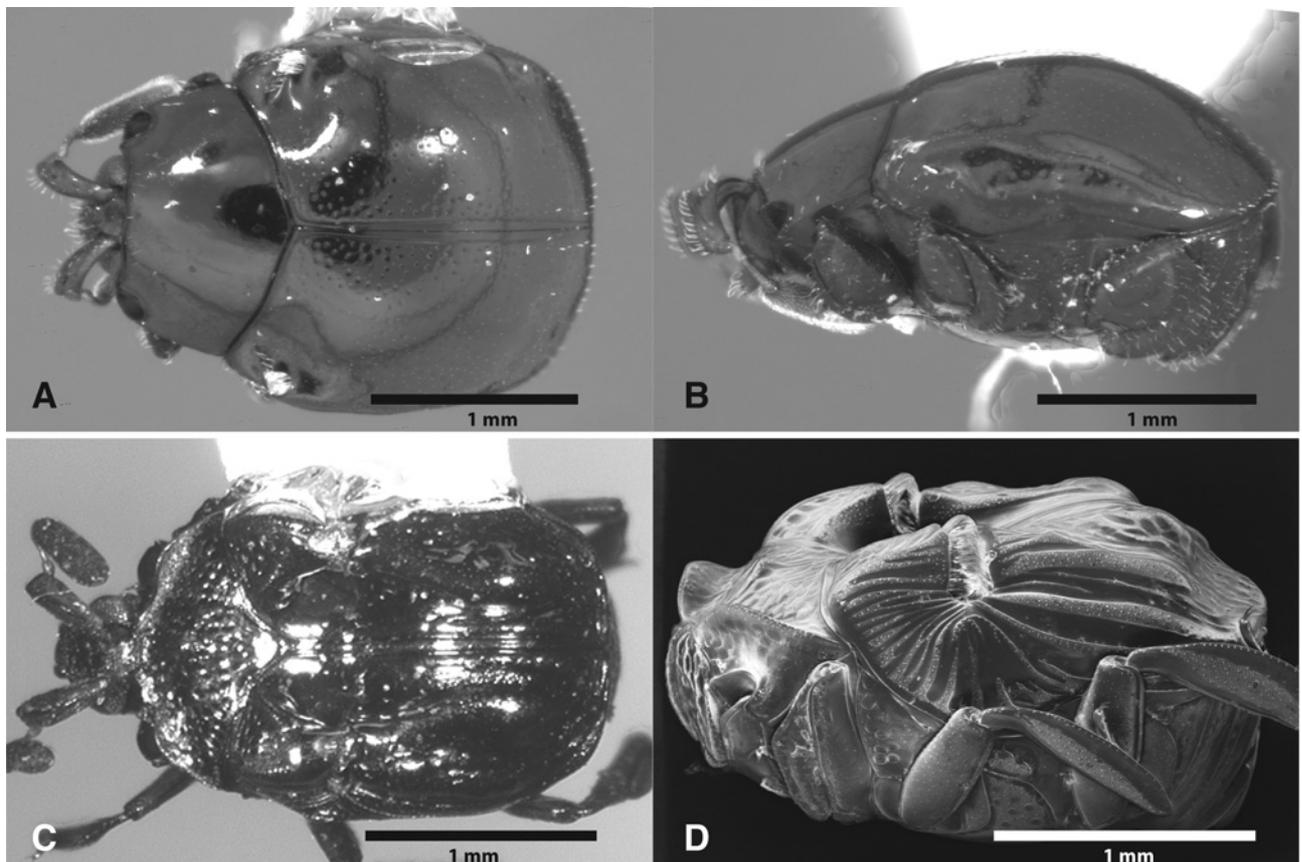


Fig. 13. Dorsal and lateral habitus photographs of holotype (*A, B* and *C* only) specimens of *Papuopsis andersoni* (*A, B*) and *Quasimodopsis riedeli* (*C, D*).

Scutellum hidden; elytra with sides weakly outwardly arcuate, widest just behind humeri; humeral trichomes small, barely evident in lateral view, consisting of a triangular humeral impression very close to corner, with oblique anterior carina lined with short fringe of posteriorly directed setae near lateral margin; anterior elevation of trichome with short superficial humeral groove near apex, extending anteriorly only about halfway to anterior elytral margin; dorsum of elytral disk evenly convex, finely and sparsely punctate, with fine, inconspicuous setae, and faint granulate microsculpture; dorsum separated from epipleuron by marginal stria, extending from just behind trichome to very near apical margin, curving inwardly at apex but ending freely; epipleuron similar in texture to dorsum; elytron with continuous marginal stria around all edges, diverging slightly from margin on epipleuron above apices of meso- and metafemora (in repose).

Middle of mesosternum largely hidden beneath prosternal keel, with complete, arcuate marginal stria nearly meeting mesometasternal suture, at sides with fine setiferous punctures; mesometasternal suture finely impressed at middle, more deeply so near mesocoxae, continuous with postmesocoxal stria, which extends laterally across metepisternum to epipleuron; median metasternal suture very finely impressed, nearly obsolete at anterior and posterior extremes; metasternal disk with few small punctures at centre, with only very fine setiferous punctures at sides; posterior marginal metasternal stria originating on posterior margin about halfway between midpoint and metacoxa, extending $\sim 30^\circ$ anterolaterally sinuately to metepisternum; first abdominal ventrite with postmetacoxal stria originating near metacoxa, extending posteriorly to near ventrite margin, curving laterally to epipleuron; disk of first abdominal ventrite smooth, with only sparse, fine setiferous punctures.

All femora broadly rounded, $\sim 2\times$ as long as maximum width, with both anterior and posterior margins strongly arcuate, flattened, finely margined anteriorly and posteriorly; all tibiae similarly flattened and broadly rounded, about half concealed (in repose) by femora, margined along outer edges; femora and

tibiae with outer surfaces smooth, bearing sparse, fine setiferous punctures; tarsi not examined.

Propygidium $\sim 2\times$ as wide as long, convex, maximally so in apical half; pygidium evenly weakly convex, slightly wider than long; pygidium and propygidium both smooth, with sparse, fine setiferous punctures, both with complete marginal striae.

Genitalia not examined.

Etymology

This species is named in honour of its collector, weevil specialist Dr Robert Anderson of the Canadian Museum of Nature.

Genus *Quasimodopsis* Caterino & Dégallier, gen. nov.

Type species. *Quasimodopsis riedeli* Caterino & Dégallier, sp. nov.

Diagnosis

This taxon is very distinctive and phylogenetically isolated among the Chlamydopsinae. It is best defined and diagnosed based on the form of the prothorax (Figs 4C, 13C–D), which is very different from that of any other member of the subfamily. Although in gross terms it shares the hidden scutellum with *Orectoscelis*, *Pheidoliphila*, and others, the manner in which the scutellum is concealed, by the posteriorly prolonged pronotal margin, is very different. The short prothorax, raised (oblique) anterior pronotal margin, and single median pronotal projection are also distinctive. The pronotal shape and hidden scutellum also immediately distinguish it from *Chlamydopsis*, *Eucurtia* or *Ectatomiphila*. The male genitalia of *Quasimodopsis* are highly distinctive, with the dorsal portion of the 8th abdominal segment (Fig. 14A) divided into two lightly sclerotised, apically incurving processes, much like the processes of segment 9 in *Chlamydopsis* (e. g., Fig. 8K).

Biology

The single species of this genus has been collected only by flight interception traps.

Etymology

The genus name refers to Victor Hugo's Quasimodo, owing to the humpbacked appearance of its type species.

Quasimodopsis riedeli Caterino & Dégallier, sp. nov.

Material examined

Holotype. Male labelled 'IRIAN JAYA, Jayapura Prov., leg. A. Riedel' / 'Sentani, 950m, Cyclops Mts. [2.57°S, 140.48°E], 3.X.1992'; BMNH.

Paratype. Undetermined sex, labelled '[Papua] New Guinea, Haus Copper, Wau, Mt. Missim [7.2°S, 146.8°E], 22.-24.IV.1965' / 'Coll. Dr J. Balogh et Dr J. J. Szent-Ivany'; CHSM.

Description

L: 1.96; W: 1.43; E/Pn L: 2.15; E/Pn W: 1.28; Pn W/L: 1.80; E L/W: 0.93; Pr/Py: 1.08. Sterna: 0.50, 0.09, 0.50. Tibiae: 0.75, 0.75, 0.75; body piceus to slightly rufescent, subquadrate; dorsum without conspicuous setae (except within elytral trichomes); most surfaces with fine, dense, polygonal (reticulate) microsculpture.

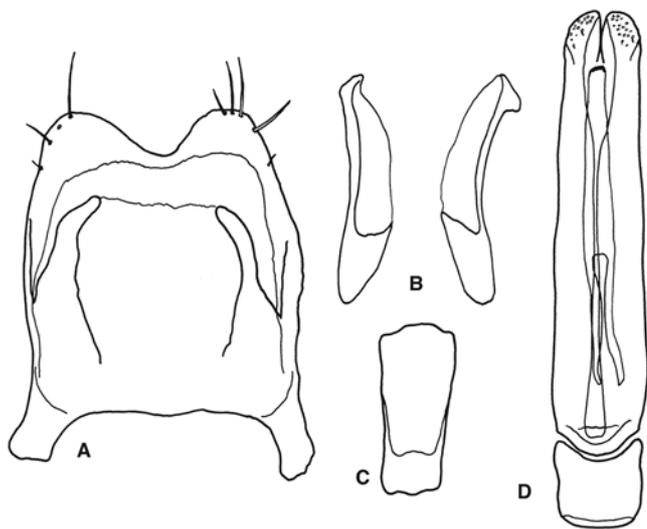


Fig. 14. Male genitalia of *Quasimodopsis riedeli*. A, segment 8; B, terga of segment 9; C, spiculum gastrale; D, aedeagus.

Head small; frons with coarse reticulate sculpturing, its sides weakly outwardly arcuate; clypeolabral suture evident, labrum semicircular, without setae; mandibles small, quadrate, coarsely textured laterally, smooth at apices; scape smooth, obtusely triangular (40–40–100), shallowly depressed along lateral margin; antennal funicle thin, very slightly thickened towards club, the junctions between funicular antennomeres visible as sutures but not conspicuous; club of male approximately equal in length to scape, uniformly tomentose.

Prothorax short, less than one-fourth of PE length, in dorsal view approximately diamond shaped, with prominent oblique lateral carinae, extending from posterolateral corners to near middle of anterior margin; antennal cavities exposed from above; narrow anterior margin (between oblique carinae) not elevated; posterior margin of pronotum acutely prolonged at middle, this posterior extension concealing scutellum; pronotal disk with a low acute dorsal projection at middle, entire disk with conspicuous large, shallow punctures (divots).

Prosternum short, portion anterior to protibial excavations much shorter than posterior portion; anterior margin striate but not deeply grooved, emarginate at middle; prosternal keel with similar sculpture to pronotum (large shallow punctures), keel narrowed posteriorly, distinctly emarginate at apex.

Elytra dominated by strongly elevated trichomes, deeply depressed between; anterior and posterior elevations of trichomes meeting at a deep, narrow, vertical incision, with setae lining this incision; anterior elevation approximately pyramidal, with the outer face convex and slightly arcuate; anterior face with large shallow punctures and a fine humeral groove parallel to and near the outer edge, this groove extending from the anterior elytral margin to the posterior apex of the anterior elevation of trichome, which is acutely emarginate where the groove meets the edge; posterior elevation of trichome not quite as strongly elevated as anterior portion, similar in width, but continued posteriorly by a blunt ridge, which extends obliquely to apical one-third of elytron, thence posteriorly to near apex, ending abruptly; elytral apices depressed, rugose; epipleurae strongly and deeply striate, with striae converging to lateral incision of trichome; elytral with fine marginal stria complete around all sides.

Mesosternum $\sim 4\times$ as wide as length along midline, bluntly projecting at middle, slightly swollen at middle, otherwise shallowly depressed behind complete, evenly arcuate marginal stria; mesometasternal suture complete, anterior margin of metasternum depressed as series of large, subcoalescent punctures behind; median metasternal suture finely indicated posteriorly, obsolete anteriorly; metasternal disk largely smooth, with few irregularly scattered large shallow punctures and intervening fine microsculpture; posterior margin of metasternum with unique transverse stria, close to margin at middle, diverging from it to sides, continuing in front of metacoxae, thence angled 45° anteriorly to metepisternum, faintly interrupted, then continued to epipleuron; visible abdominal ventrite one with continuous anterior marginal stria, very close to anterior suture, diverging posteriorly along inner edge of metacoxa nearly to posterior margin, then curving laterally to epipleuron; disk of ventrite one with only couple of large, but very shallow, inconspicuous punctures at sides.

Femora slender, nearly parallel sided, outer surfaces margined along anterior and posterior edges, surface with reticulate microsculpture distinct on profemur, less conspicuous on meso- and metafemora; tibiae slender, widest about one-third from base, protibia bluntly angulate, meso- and metatibiae more nearly rounded, outer surfaces strongly convex along longitudinal axis, lateral edges flattened, unmargined, inner edges margined, surfaces with reticulate microsculpture; tarsi slender, slightly laterally compressed, ratio of tarsomere lengths $\sim 1.5:1:1:1:2.1$, tarsomeres 1–4 with 2–3 conspicuous setae at ventral apices, tarsomere 5 with two finer setae along ventral midline; pretarsal claws small, evenly curved.

Propygidium $\sim 1.3\times$ as wide as length along midline, evenly, arcuately depressed along anterior and lateral margins, weakly convex medioposteriorly, with complete posterior marginal stria; propygidial disk with large, shallow, irregularly spaced punctures separated by about their widths, these slightly denser posteriorly; pygidium flat to weakly convex, with marginal stria along anterior and basal thirds of lateral margins, disk with shallow punctures smaller and sparser than those of propygidium, becoming obsolete in apical half.

Male: dorsum of abdominal segment 8 divided into two separated, lightly sclerotised, apically convergent, longitudinal processes, extending about two-thirds the length of the segment's venter; venter of segment 8 bilobed at apex, bearing 4–5 prominent setae at apex; lateral halves of segment 9 about two-thirds length of segment 8, broadly but lightly sclerotised at base, sclerotisation narrowed abruptly one-fourth from base, extending

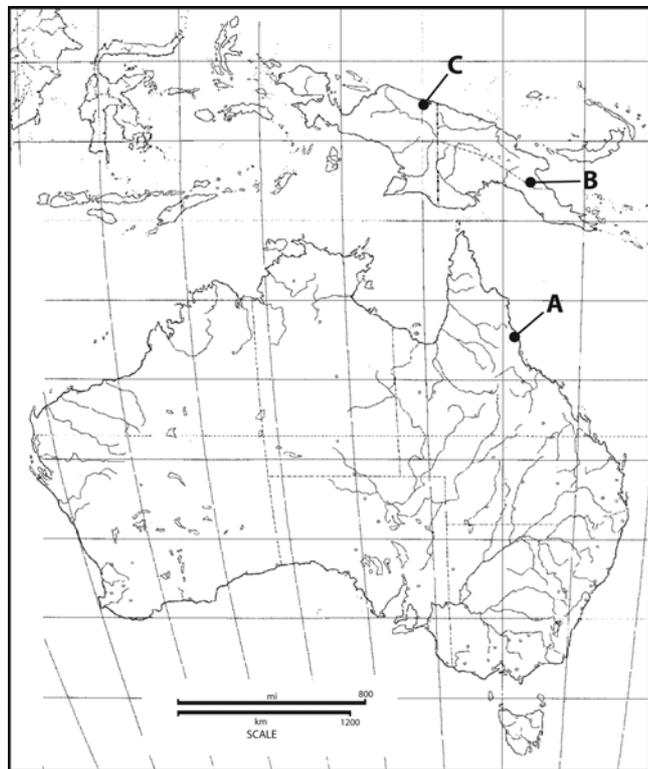


Fig. 15. Map of type localities of new species described in this paper. A, type locality of *Teretriopsis theryi*; B, type locality of *Papuiopsis andersoni*; C, type locality of *Quasimodopsis riedeli*.

along dorsal edge broadening slightly to form a blunt hook at apex; spiculum gastrale flat, subquadrate, sclerotised along basal and lateral edges; aedeagus with basal piece about one-sixth total aedeagal length, tegmen subcylindrical, narrowed very slightly to apex, desclerotised along dorsal midline to base, with setose area at apex; median lobe about four-fifths tegmenal length, with proximal apodemes separate in basal two-fifths; gonopore indistinct.

Etymology

We name this species in honour of the collector of the holotype specimen, Alexander Riedel.

Genus *Chlamydonia* Caterino

Type species. *Chlamydonia sol* Caterino, 2006: 36, by original designation.

Diagnosis

The species of *Chlamydonia* all possess frontal tubercles, in two parallel, longitudinal series, median and lateral paired protuberances at the anterior pronotal margin, epipleural marginal stria doubled above the metathoracic leg, and humeral trichomes that are more or less elongate in orientation. This newly described genus is characterised in greater detail by Caterino (2006).

Distribution

New Caledonia.

Included species

1. *Chlamydonia sol* Caterino, 2006; New Caledonia
2. *C. coutume* Caterino, 2006; New Caledonia
3. *C. gomyi* Caterino, 2006; New Caledonia
4. *C. tjibaoui* Caterino, 2006; New Caledonia
5. *C. foveata* Caterino, 2006; New Caledonia
6. *C. inflata* Caterino, 2006; New Caledonia
7. *C. densa* Caterino, 2006; New Caledonia
8. *C. stellata* Caterino, 2006; New Caledonia
9. *C. erectipilosa* Caterino, 2006; New Caledonia
10. *C. eucurtiopsoides* Caterino, 2006; New Caledonia
11. *C. punctinota* Caterino, 2006; New Caledonia
12. *C. fauveli* Caterino, 2006; New Caledonia
13. *C. terapoides* Caterino, 2006; New Caledonia
14. *C. sinuata* Caterino, 2006; New Caledonia
15. *C. dzumacensis* Caterino, 2006; New Caledonia
16. *C. volans* Caterino, 2006; New Caledonia
17. *C. angulata* Caterino, 2006; New Caledonia
18. *C. wenzeli* Caterino, 2006; New Caledonia

Genus *Kanakopsis* Caterino

Type species. *Kanakopsis amieuiensis* Caterino, 2006: 33, by original designation.

Diagnosis

This distinctive chlamydopsine resembles members of the *Orectoscelis* lineage. However, it is distinguished by the combination of a distinct prementum, 3-segmented labial palpi, lack of an accessory epipleural stria, and lack of any frontal or ante-

rior pronotal processes. It also apparently has a visible, though recessed, scutellum. This character requires additional confirmation (Caterino 2006).

Distribution

New Caledonia.

Included species

1. *Kanakopsis amieuiensis* Caterino, 2006; New Caledonia

Key to the genera of Chlamydopsinae

(Note: *Kanakopsis* keys out in two places given unconfirmed visibility of the scutellum.)

1. Scutellum visible (Fig. 4A, D) 2
Scutellum hidden, either by posterior margin of pronotum, or by junction of elytra (Fig. 4B, C) 6
2. Dorsum entirely flat, brown, lighter around edges (Fig. 11C–D); humeral trichome transverse; found only in Australia *Ectatommmiphila*
Dorsum varied, but never entirely flat; found in Australia and elsewhere 3
3. Scutellum recessed, on lower plane than elytra (Fig. 4D); found only in New Caledonia 4
Scutellum on same plane as elytra, distinct (Fig. 4A); found in New Caledonia and elsewhere 5
4. Frons and pronotum smooth, lacking protuberances; epipleuron lacking accessory stria; body impunctate *Kanakopsis*
Frons with longitudinal series of tubercles; pronotum with paired anterior median, and sometimes lateral projections; epipleuron with accessory stria in addition to marginal stria above metathoracic leg; body texture varied, but generally densely punctate at least on pronotum *Chlamydonia*
5. Pronotum without raised anterior margin; humeral trichome bearing elongate hairs, as long as the elytra (Fig. 11B) *Eucurtia*
Anterior margin of pronotum varied, raised in most, but trichome never with hairs as long as the body *Chlamydonia*
6. Pronotum with prominent, oblique lateral carinae from the posterolateral corners of the pronotum to near the middle of the anterior margin; prothorax short, less than one-fourth of body length (Fig. 13C–D) *Quasimodopsis*
Pronotum lacking oblique lateral carinae; prothorax longer, approximately one-third of entire body (pronotal+elytral) length 7
7. Pronotum with lateral trichomes; pronotum and elytra margined laterally (Fig. 12A); found in Fiji *Gomyopsis*
Pronotum without lateral trichomes; found in Fiji and elsewhere 8
8. Pronotum unmargined, strongly inflated, lacking any tubercles or processes; elytral humeral trichome conspicuous, forming a transverse incision; labial palpi 3-segmented, basalmost palpomere very short; found only in New Caledonia *Kanakopsis*

- Labial palpi 2-segmented; otherwise without above combination of characters; pronotum of most with small to large median or anterior marginal processes; widespread but not known from New Caledonia 9
9. Elytra without trichomes 10
Elytra with trichomes 12
10. Elytra longitudinally carinate. . . . *Pheidoliphila* (in part)
Elytra smooth or punctate, but lacking longitudinal carinae. 11
11. Body elongate, cylindrical, approximately circular in cross section, with prothorax equal in height, and nearly in width to mesothorax; prothorax strongly convex, lacking tubercles or other dorsal processes; head and occipital foramen small, approximately half pronotal height; known only from Australia.
. *Teretriopsis*
Body generally oval in cross section and/or prothorax distinctly narrower than mesothorax; pronotum of most with prominent median or dorsal processes; occipital foramen more than half pronotal height; not known from Australia *Ceratohister*
12. Pronotum and elytra margined; pronotum lacking median or anterior marginal processes; dorsum uniformly convex, profile uninterrupted between pronotum and elytral (Fig. 13A–B); found only in New Guinea
. *Papuopsis*
Pronotum rarely margined, and never in conjunction with elytra; pronotum almost always bearing median or anterior marginal processes; dorsal profile never continuously convex, always interrupted at pronotal-elytral junction; found in New Guinea and elsewhere 13
13. Elytral trichome forming small, oblique incision in extreme humeral corner (Fig. 6C–D); pronotum of most with prominent, bifid (rarely paired separate) anterior marginal processes
. *Pheidoliphila* (in part)
Elytral trichome usually located distinctly posterad of humeral corner (Fig. 6B, E–F, H), rarely forming a small, oblique incision; pronotal processes usually paired and separate, in some occurring posterad of anterior margin, rarely absent 14
14. Elytral trichome forming an elevated, arcuate opening, with continuous marginal setal fringe (Fig. 6F–G); trichome opening rarely descending lateral surface of epipleuron *Orectoscelis*
Elytral trichome comprising a transverse, rarely oblique, incision, with separate anterior and posterior setal fringes (Fig. 6H) *Eucurtiopsis*

Conclusions

Since the previous catalogue of the subfamily Chlamydopsinae by Mazur (1997), the numbers of valid genera and species have grown from nine to 12, and from 47 to 174, respectively. These increases may be attributed primarily to the use of flight interception traps (FIT) in appropriate areas. Sampling in tropical parts of Australia and the islands of south-eastern Asia has also tapped a previously unsuspected fauna. Although we are beginning to get a grasp of the diversity and phylogeny of the group, many challenges remain. Many taxa remain known from only

one or a few specimens, precluding thorough studies of their morphology or even sexual dimorphism. The scant knowledge we have of the life history of these beetles has grown little in the past 100 years, and we lack any host records for most of the species. The biogeographic history of these beetles is of great interest, as there appear to have been multiple colonisations of several island systems in the Indomalaysian region, and Chlamydopsinae are unusual in having apparently freely traversed Wallace's line (Caterino 2000).

Future studies on the Chlamydopsinae should thus concentrate on FIT sampling in new areas, while at the same time attempting to observe the ecology and behaviour of these discrete beetles. Hopefully one day it will be possible to synthesise phylogeny, behavioural data, and geography, to develop a full evolutionary picture of these bizarre histerids.

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