

A new genus and species and a revised phylogeny of Stereomerini (Coleoptera, Scarabaeidae, Aphodiinae), with notes on assumedly termitophilic aphodiines

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Abstract

A new genus and species of Stereomerini, *Cheleion malayanum* **gen. n.** and **sp. n.**, are described based on a single specimen from the Malacca peninsula in Malaysia. It is the first stereomerine found on the mainland of the Asian continent. A key to genera of Stereomerini and a phylogenetic estimate of the stereomerines using 24 species representing 7 tribes of Aphodiinae based on 53 morphological characters. The phylogenetic analysis places the new species within the tribe Stereomerini as a sister to the monophyletic group including *Adebrattia*, *Austaloxenella*, *Bruneixenus*, *Pseudostereomera* and *Stereomera*. A survey is given of the various taxa of Aphodiinae that are termite and/or ant inquiline, or have been presumed to be so based on morphology, and their phylogeny is discussed.

Keywords

termite association, Aphodiinae tribes, synanthran morphology

Introduction

The aphodiine tribe Stereomerini was erected by Howden and Storey in 1992 for four genera of minute, rare and supposedly termite-associated aphodiines *Stereomera* Arrow, *Termitaxis* Krikken, *Australoxenella* Howden and Storey, and *Bruneixenus* Howden and Storey (Howden and Storey 1992). In 1995 Bordat and Howden excluded *Termitaxis* from the tribe and described 3 new genera and species: *Adebrattia depressa* Bordat and Howden, *Danielssonina minuta* Bordat and Howden and *Pseudostereomera mirabilis* Bordat and Howden (Bordat and Howden 1995). Since then one new genus (*Daintreeola* Howden and Storey) and 11 new species of the genera *Daintreeola*, *Bruneixenus* and *Australoxenella* have been described (Storey and Howden 1996; Howden and Storey 2000). The number of genera of Stereomerini is presently 7 and the number of species 18, all from insular south east Asia and Australia.

Synapomorphies for the Stereomerini include a grooved head as well as a particular pattern of carinae and grooves on the pronotum with three pronotal carinae concentrated in median third and one transverse groove, plus convex body shape, wide epipleura and reduced eyes. Characters that may be either apomorphic or plesiomorphic are a more or less lanceolate posterior prosternal process, clypeus without dentation and flattened tibiae (Forshage 2002).

In the collections of the Swedish Museum of Natural History (NHRS) we found a remarkable specimen clearly belonging to Stereomerini but representing a new undescribed taxon, the first one from a locality on the Eurasian continent (the Malaysian Peninsula). As it has not been possible to accommodate the new taxon in one of the existing genera we felt impelled to describe a new genus as well. In order to test this, we performed a phylogenetic analysis of all the genera of Stereomerini. As the relationships between various aberrant tribes within the Aphodiinae, and between those tribes and the poorly delineated Eupariini, we included a wealth of other genera in the analysis.

Methods

Images of the new species were obtained with a digital Olympus DP70 camera mounted on an Olympus SZX12 stereo microscope using the imaging software AnalySIS 5.0 to montage section images with different focus. Micrographs were taken with a Zeiss Supra35VP scanning electron microscope on low vacuum. The low vacuum scanning electron microscopy does not require the specimen to be prepared in the traditional manner including critical point drying and gold-coating and is thus particularly suitable for type material. Character coding of the new taxon and other taxa at hand were done from a combination of stacked digital images and direct observation in stereo microscope. Taxa not at hand were coded from scorings and images found in literature. These include *Australoxenella humptydooensis* Howden and Storey, *Bruneixenus squamosus* Howden and Storey, *Cartwrightia intertribalis* Islas, *Ascharhyparus peregrinus* (Hinton), *Termitodiellus es-*

akii Nomura and *Stereomera pusilla* Arrow and *Termitaxis holmgreni* Krikken coded from Howden and Storey (1992), *Daintreeola grovei* Howden and Storey coded from Howden and Storey (2000) and *Termitoderus ultimus* Krikken coded from Krikken (2008a).

Our images of the following taxa are deposited on Morphbank (<http://www.morphbank.net>); the new taxon (*Cheleion malayanum* n.sp.) (image numbers 480710–480723) and of the types of the rare *Danielssonina minuta* (image numbers 497197–497199), *Pseudostereomera mirabilis* (image numbers 497204–497207) and *Adebrattia depressa* (image numbers 497200–497203) (all Bordat and Howden 1995)

Character selection

Several of the characters have been used in previous phylogenetic analyses (Howden and Storey 1992; Bordat and Howden 1995, Forshage 2002). In an attempt to further define the tribe Stereomerini based on morphological characters, we have added several characters (see Table 2) on the head (characters 4, 5, 10, 11), pronotum (characters 15, 18, 20, 22, 23, 24), legs (characters 34, 35), wings (characters 37, 38, 39, 44, 45), abdomen (characters 46, 53). We did not want to dissect the single type specimen of the new taxon so we have not been able to compare mouthparts and genitalia which are potential valuable sources of additional characters.

Taxon selection

For the phylogenetic analysis we included representatives from all genera of the tribe Stereomerini, as this was our primary group of interest. In addition we wanted to include representatives of the tribes believed to be closely related to the Stereomerini based on morphology as well as some taxa of unclear taxonomic status and phylogenetic position. In addition to the 8 Stereomerini species, we thus coded 5 species of Rhyparini (*Aschna rhyparus peregrinus*, *Termitodiellus esakii*, *Rhyparus suturalis* Schmidt, *Cartwrightia intertribalis* and *Sybacodes simplicicollis* Fairmaire), 1 species of Termitoderini (*Termitoderus ultimus* Krikken), 1 species of Termitotrogini (*Termitotrox consobrinus* Reichensperger), 2 species of Corythoderini (*Corythoderus loripes* Klug and *Neochaetopisthes heimi* Wasmann) as well as *Termitaxis holmgreni* (incertae sedis). As these aberrant taxa are of uncertain relationships with Eupariini – possibly differently to different parts of Eupariini – we wanted to include a fair representation of the diversity of that tribe. Thus we included a representative of an aberrant genus, morphologically similar to some of the truly or assumedly termitophilous tribes (*Notocaulus sculpturatus* Boheman), plus the largest genera of the tribe (*Ataenius scabrelloides* Petrovitz and *Saprosites laeviceps* Harold), as well as the type genus of the tribe (*Euparia castanea* LePeletier and Serville). As outgroup taxa we chose Aphodiini, since they are the major group of Aphodiinae that we expect to be safely outside the group of interest here; we included one more or less typical and one aberrant representative of Aphodiini (*Aphodius elegans* Allibert and *Sybx impressicollis* Boheman).

A note on the type specimen of *Termitotrox*

The type specimen of the type species of the type genus of Termitotrogini, *Termitotrox consobrinus* Reichensperger 1915, was long considered lost (Paulian 1985), but was recently rediscovered by author MF in a cabinet at the Lund museum, where it was left forgotten many years ago by B-O Landin who was acting as a courier between the Gothenburg museum where it was originally deposited and professor Balthasar in Prague who had borrowed it. The specimen is now again available at the Natural History Museum in Gothenburg.

Phylogenetic estimate

Fifty three morphological characters (Table 2) were coded for 24 species from 7 tribes of Aphodiinae (Table 3). Fourteen of the species were coded from specimens, whereas 10 were coded from literature. Character 10 is ordered, while all other multistate characters are unordered. Uniform weights were applied. The phylogenetic analyses were performed in Paup* Portable version 4.0b10 for Unix (Swofford 2002). Character evolution was explored using MacClade 4.08 (Maddison and Maddison 2005). Heuristic searches produced three equally parsimonious trees with 195 steps. Ensemble consistency index is 0.345 and retention index is 0.589.

Results

An identification key for the genera of Stereomerini is given in Table 1.

Table 1. Identification key to the genera of Stereomerini

1.	Elytra modified laterally or posteriorly	2
–	Elytra flattened or evenly convex.....	5
2.	Margin of clypeus with pronounced inflexion, triangular at apex; pronotum with conspicuous depressions laterally; deep lateral longitudinal furrow on each elytron	<i>Danielsonia</i> Bordat & Howden
–	Margin of clypeus weakly inflexed; pronotum not laterally depressed; elytra conspicuously declivous posteriorly, deep elytral furrow missing	3
3.	Elytra with strong transversal ridges.....	<i>Stereomera</i> Arrow
–	Elytra without strong transversal ridges.....	4
4.	Elytral costae strongly twisted	<i>Pseudostereomera</i> Bordat & Howden
–	Elytral costae subparallel, posterior elytral corners protruding.....	<i>Bruneixenus</i> Howden & Storey
5.	Each elytron with pronounced and widely separated longitudinal costae; transverse striation missing or inconspicuous; elytral epipleura wide	6
–	Each elytron lacking or with inconspicuous longitudinal costae; strong transverse striation on each elytron; elytral epipleura narrow	7

6. Posterior prosternal process lanceolate; body covered by appressed circular scales giving surface a granular appearance ***Australoxenella* Howden & Storey**
- Posterior prosternal process hastate; body covered with large punctures/tubercles giving surface a rough appearance..... ***Cheleion* gen. n.**
7. Body flattened; longitudinal elytral striae very weak, transverse striations profound; apical segment of maxillary palp securiform.....
- ***Adebrattia* Bordat & Howden**
- Body convex; longitudinal elytral striae pronounced with transverse striations only on the lateral elytron; apical segment of maxillary palp cylindrical
- ***Daintreeola* Howden & Storey**

Table 2. List of characters used in data matrix for phylogenetic analysis

General	
1	Entire dorsum with longitudinal costae: absent (0) or present (1)
2	Body shape cylindrical (0), flattened (1) or strongly convex (2) (unordered)
Head	
3	Head forward-pointing (0) or strongly retractable (1)
4	Antenna shorter than (0) or longer than (1) length of head
5	Maxillary palpi oval (0) or securiform (1)
6	Eyes with distinct dorsal portion (0), reduced (lacking dorsal portion) (1), or absent (2) (unordered)
7	Head posteriorly margined (1) or not (0)
8	Head wide (1) or not wide (0)
9	Anterior edge of clypeus inflexed (0), straight or slightly rounded (1) or pointed (2) (unordered)
10	Reflexed apical portion of clypeus absent (0), perpendicular (1), fully inflexed (2) (ordered 0-1-2)
11	Head grooves absent (0), present, parallel (1) or present, radial (2) (unordered)
Pronotum	
12	Prosternal process inconspicuous (0) flattened (1) or raised (2) (unordered)
13	Prosternal process inconspicuous (0) lanceolate (1) or hastate (2) (unordered)
14	Scutellum minute (0) or absent (1)
15	Pronotal anterior lateral angles evenly convex (0) or conspicuously depressed (1)
16	Pronotal sides concave (0), parallel (1) or convex (2)
17	Pronotal transverse furrow absent (0), basal (1), medial (2) or frontal (3) (unordered)
18	Pronotal transverse furrow absent (0), shallow (1), or deep (2) (unordered)
19	Pronotal posterior lateral angles protruding (1) or not protruding (0)
20	Pronotal basal medial lobe protruding (1) or basal border evenly convex (0)
21	Pronotum with (1) or without (0) broad lateral depressions
22	Bulbous posterior submedian lobes on pronotum absent (0) or present (1)
23	Pronotum anteriorly tapering (1) or of equal width (0)
24	Anterior median pronotal knob absent (0), present (1)
Legs	
25	Denticulation of fore tibiae normal (three distinct teeth) (0) or reduced (1)
26	Mid and hind tibial apical spurs pronounced (0) or reduced (1)
27	Mid and hind tibial apical spurs adjacent (0) or separated (1)

28	Transverse tibial ridges on mid and hindleg absent (0) or present (1)
29	Longitudinal tibial ridges on mid and hindleg absent (0) or present (1)
30	Legs of normal length (0) or very short (1)
31	Row of sulci on hind femora absent (0) or present (1)
32	Tarsomere count 555 (0) or 544(1)
33	Tibiae straight (0) or distinctly curved (1)
34	Midlegs not longer than other legs (0) or distinctly longer than others (1)
35	Midcoxae adjacent (0), widely separated (1)
Wings	
36	Elytral base margined (1) or not (0)
37	General orientation of longitudinal structures in posterior part of elytra roundly converging (0) or diverging (1)
38	Deep longitudinal elytral fold absent (0), present, straight (1) or present, twisted in posterior half (2) (ordered) (unordered)
39	Elytra with flat or weakly convex interstices between longitudinal rows of sulci (0), conspicuously elevated, cariniform interstices between rows of sulci (1), or costae apparently not corresponding to the rows of sulci (2) (unordered)
40	Elytra posteriorly evenly convex (0), flattened (1), bulbous (2), or abruptly declivous (3)
41	Elytral transverse ridges absent (0) or present (1) (unordered)
42	Epipleura inconspicuous (0) broadly inflexed (1)
43	Alae present (0) or absent (1)
44	Flaplike elytral apex absent (0) or present (1)
45	Hindleg emargination at elytra absent (0) or present (1)
Abdomen	
46	Pygidium covered by elytra (0) or free (1)
47	Transverse pygidial furrow absent (0) or present (1)
48	Ventrites mobile (0) or fused (1)
49	Punctures on ventrites scattered (0), arranged in rows (1) or arranged in dense rows (“fluting”) (2) (unordered)
50	Trichomes absent (0) or present (1)
51	Pygidium reflexed (1) or perpendicular (0)
52	Physogastry absent (0) or present (1)
53	Emargination of pygidial border absent (0) or present (1)

***Cheleion* gen. n.**

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Type species. *Cheleion malayanum* sp. n., here designated.

Etymology. Genus name after the ancient Greek name for shell; gender is neuter.

Diagnostic characters. The body shape of the imago is strongly convex and the elytra are not conspicuously modified posteriorly. Large tubercles on the entire body surface give a rough appearance. Longitudinal grooves on the pronotum converge into a median transverse groove giving it an hourglass pattern. The posterior prosternal process is hastate.

Table 3. Data matrix based on characters in Table 1

		Characters					
Species		1–10	11–20	21–30	31–40	41–50	50–53
1	<i>Aphodius elegans</i>	0210?11010	0000010000	0000000100	0000000000	000000?000	00?
2	<i>Euparia castanea</i>	0210010100	0000110011	0000001010	0010110000	0000001120	00?
3	<i>Ataenius scabrelloides</i>	0110011100	0000010000	0000000010	0000110000	000000?110	001
4	<i>Saprosites laeviceps</i>	0010000100	0000010000	0000000100	0010100000	0000011120	100
5	<i>Adebrattia depressa</i>	1111111112	1210011201	0011111011	1100001001	1100011111	101
6	<i>Australoxenella humptydooensis</i>	111?11011?	1210012201	000111?001	?100011011	0100111110	100
7	<i>Bruneixenus squamosus</i>	110?11011?	2210012211	0001110001	?10001?011	0101111110	101
8	<i>Cartwrightia intertribalis</i>	110?1011??	?000112100	000?10??10	?000?1???2	0000?????1	00?
9	<i>Corythoderus loripes</i>	1011110120	0000100011	0000110001	0011010020	0000110101	000
10	<i>Danielssonina minuta</i>	1211111111	12?1022100	1001111011	0200010020	1100111110	001
11	<i>Daintreeola grovei</i>	121?01110?	1211022200	000111?000	?100010010	100001?100	00?
12	<i>Neochaetopisthes beimi</i>	1011100120	0000000011	0000100000	0000010012	0000010001	000
13	<i>Notocaulus sculpturatus</i>	1210100110	2000110010	1000100010	0010110010	0000011110	00?
14	<i>Cheleion malayanum</i>	1211111111	2220012200	1101110001	1100001010	0100111110	001
15	<i>Pseudostereomera mirabilis</i>	1111111110	2220012211	0010111011	010001?223	0100111111	101
16	<i>Rhyparus suturalis</i>	1110110111	12211?2100	0000110010	0000010012	0001010011	101
17	<i>Stereomera pusilla</i>	111??1001?	2211012211	00111100?1	?100010013	11001?????	10?
18	<i>Sybacodes simplicicollis</i>	1210110111	0221020000	0000111010	0000000010	0000010011	101
19	<i>Sybox impressicollis</i>	0100011000	0000110000	0000000100	0000000000	000000?001	00?
20	<i>Termitoderus ultimus</i>	1211?0011?	0??0121111	1001100000	?000011010	00000100?0	?10
21	<i>Termitodiellus esakii</i>	111??111??	1?21022100	100001???1	?000011012	00010????1	01?
22	<i>Aschnarhyparus peregrinus</i>	111??111??	??211?2210	1000010??1	0000011012	100100?0?1	01?
23	<i>Termitaxis holmgreni</i>	1010?21111	0211020010	0000110001	?000011020	1110???0?1	11?
24	<i>Termitotrox consobrinus</i>	101??2?11?	0?01102200	1101110000	0001111110	101011?0?0	00?

Immature stages unknown.

Description. *Dorsal surface.* Head very wide, subrectangular dorsally, clypeus apically pointed and reflexed under head, frons slightly bulbous with 5 divergent furrows; posterior transverse furrow running across the head from the posterolateral side of the one eye across to the posterolateral side of the other eye. Antennae long, length equivalent to width of head; amber-color, with long setae. Maxillary palpi length equivalent to length of head, amber-color, with securiform apical segment. Labial palpi with long setae on apices. Eyes have no distinct dorsal part and mouthparts are retracted.

Pronotum large and transverse, sides evenly curved, anterior edge bisinuate, posterior edge with a broad median protrusion. Disc of pronotum medially with 5 furrows, converging towards the middle in an hourglass pattern, midfurrow shallower than lateral furrows. Anteromedial disc with distinctly raised tubercle, posteromedial disc and posterolateral sides with slightly lower tubercles. Lateral of the furrows are large elliptical depressions, delineated by furrows.

Hindbody narrower than pronotum, elytra only slightly longer than pronotum plus head.

Elytra posteriorly tapering, apically rounded, evenly, not abruptly (declivous) posteriorly. Each elytron with 6 longitudinal ridges before the lateral edge, elytral interstices alternating in height, elevated but discontinuous, consisting of series of longitudinal setae-bearing tubercles. Even interstices lower, rugose. Epipleura broadly inflexed, posterior two thirds of lateral edge slightly recurved to allow free movement of hindlegs.

Pygidium exposed, strongly punctured proximally, less strongly apically. Small emargination on proximal pygidial border.

Ventral surface. Prosternal process strongly elevated and apex expanded, transversely split anterior to procoxae, hastate posterior to procoxae. Mesosternum narrow with alutaceous and punctured surface. Metasternum triangular widest in front and tapering posteriorly, groove along midline, surface nitid and punctured. Abdomen with 5 segments visible ventrally.

Ventrites apparently fused.

Legs short with broad femora and tibiae, tarsi 4-segmented and short. Fore tibiae moderately wide, with finely serrated outer edge and one strong apical lateral tooth, tarsus inserted well before apex. Mid and hind tibiae broad with finely serrated outer edge and concave apex; each with at least two inconspicuous tibial spurs.

***Cheleion malayanum* sp. n.**

urn:lsid:zoobank.org:act:D8732C0E-4747-4276-8F27-2354509159F3

Material. Holotype: Malaysia, Pahang, Bukit Frazer, 1200 m, 7-9/4 – 1992, Malaise-trap in jungle, Heikki Hippa leg. Swedish Museum of Natural History (NHRS).

Etymology. The first specimen of the species was collected in Malaysia.

Diagnostic characters. Structures such as the hastate posterior prosternal process, pattern on the pronotum with a strong anteromedial knob as well as bulbous areas

medially and laterally on each side at the posterior end of the pronotum, the very long antennae and the strongly tuberculate and rugose surface of the body will easily separate this species from other known Stereomerini.

Description. Length 1.8 mm, width at broadest point 0.9 mm. Chestnut brown, whole body rather densely covered with strong puncture; strongly convex. Morphology as in generic description and as in Figures 1–6.

Phylogenetic estimate

The three resulting most parsimonious trees (Figure 7A–C) differ only in the internal relationships within the Stereomerini genera *Australoxenella*, *Bruneixenus*, *Pseudostereomera*, *Stereomera* and *Adebrattia* (as shown in the consensus tree, Figure 7D). The rest of the Stereomerini species, namely the new taxon, *Danielssonia* and *Daintreeola* appear in the same positions in all three trees (Figure 7A–C). None of the three configurations corresponds very well with Bordat and Howden's (1995) cladogram (we do not compare with Storey and Howden as they only included three representatives of

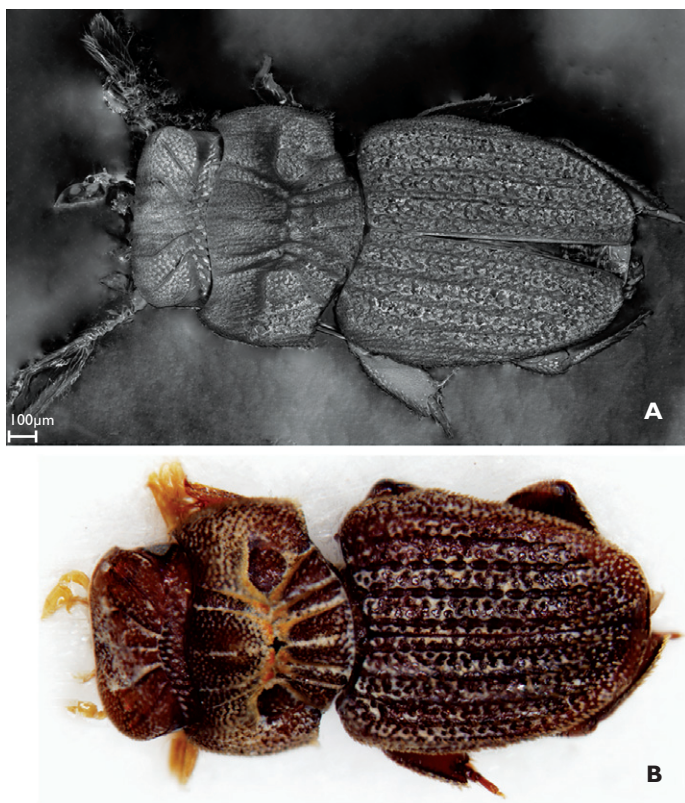


Figure 1. Dorsal view of *Cheleion malayanum* sp. n. **A** scanning electron micrograph **B** stereo microscope image.



Figure 2. Lateral view of *Cheleion malayanum* sp. n. **A** scanning electron micrograph **B** stereo microscope image.

Stereomerini in their 1992 analysis) in which the sister species *Adebrattia-Bruneixenus* forms a sister group to *Danielsonia-Australoxenella*-(*Stereomera-Pseudostereomera*). One reason for this may be that neither the new taxon nor *Daintreeola* were included in the Bordat and Howden (1995) analysis. Our results rather points to a close relationship between *Adebrattia* and *Pseudostereomera* and between *Australoxenella* and *Bruneixenus*. *Stereomera* was placed as a sister group to the *Adebrattia-Pseudostereomera* in 2 of the 3 trees and as sister group to *Australoxenella-Bruneixenus* in the third tree.

Concerning the relationships outside Stereomerini, our results point to a close relationship between Stereomerini and the genus *Termitaxis*, that was formerly included in Stereomerini but is now considered *incertae sedis* (Bordat and Howden 1995), and the Termitotrogini (*Termitotrox*). Corythoderini appears monophyletic, as does a core of Rhyparini (if excluding *Sybacodes*, the position of which has been ambiguous, and *Cartwrightia*, previously classified in Eupariini and recently transferred to Rhyparini). All representatives of the aberrant tribes form a monophyletic group together, while the more typical Eupariini genera form a grade basal to this group.

Discussion

History of classification of inquiline Aphodiinae

There are several taxa in Aphodiinae which have inquiline or inquiline-like morphologies (listed in Table 4). They are usually small, have integumental bulbs and ridges, particularly longitudinal dorsal ridges; sometimes contracted body shapes; short, broad

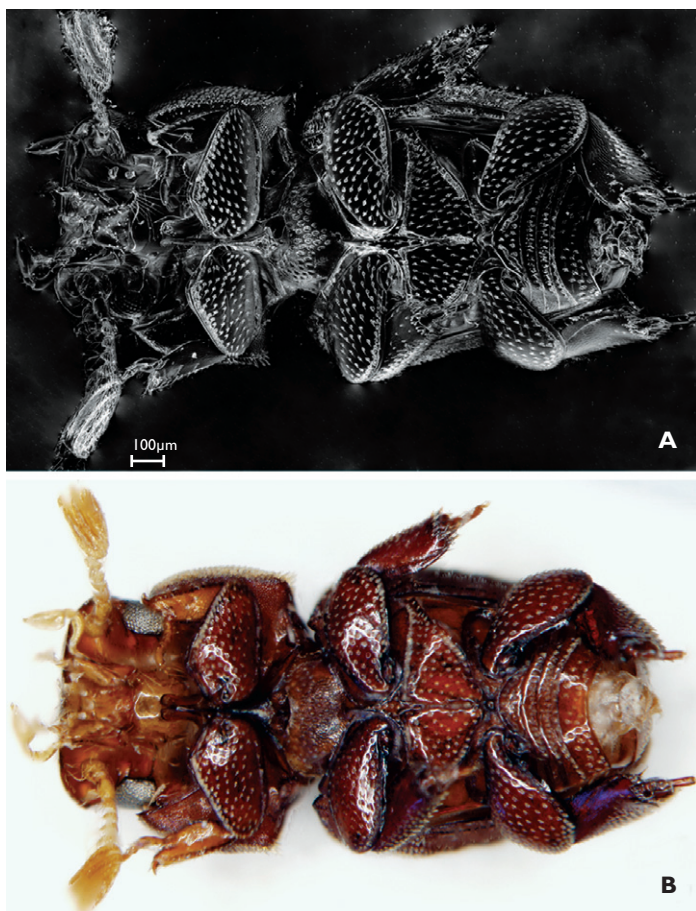


Figure 3. Ventral view of *Cheleion malayanum* sp. n. **A** scanning electron micrograph **B** stereo microscope image.

extremities, sometimes less so; and occasionally hair tufts or inflated abdomen. Their classification has included some moments of confusion.

In the first tribal division of Aphodiinae (Schmidt 1910), all the termitophilic or termitophile-like species were classified as Rhyparini and Corythoderini (only later were *Termitotrox* considered to be part of or closely related to Aphodiinae).

Termitoderini was added explicitly as a probable sister group to Corythoderini (Tangelder and Krikken 1982), and Stereomerini in a similar way as the sister group to Rhyparini (Howden and Storey 1992). The boundaries between all these tribes have been somewhat confused due to the uncertain status of some genera, and to the citing of all recent or problematic taxa as Termitoderini in Dellacasa's catalogue (Dellacasa 1987–88).

Termitoderini was erected as monotypic, but Dellacasa listed six genera there (including several from Rhyparini), which may have been a mere mistake, or a conscious reclassification with no arguments presented in the series of corrigenda to the cata-

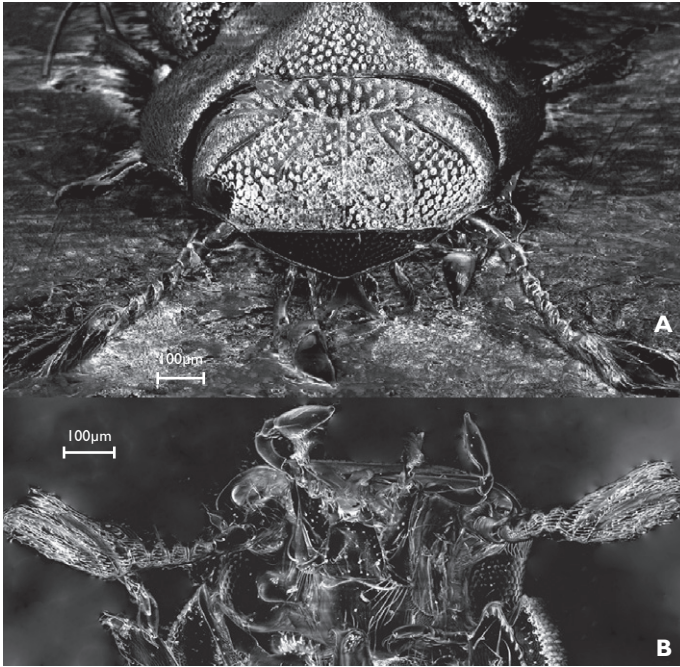


Figure 4. Head of *Cheleion malayanum* sp. n. **A** frontal view, scanning electron micrograph **B** ventral view, scanning electron micrograph.

logue. The genera that actually belonged to Ceratocanthidae were deleted (“dropped”) but no further information given on the others (Dellacasa 1991).

If disconsidering Dellacasa’s classification, it becomes rather straightforward: *Termitaxis* was described in Rhyparini (Krikken 1970) but removed to become *incertae sedis* (Howden and Bordat 1995), *Cartwrightia* was classified as Eupariini, but transferred to Rhyparini (Galante et al. 2003; Stebnicka 2009), *Sybacodes* were always considered Rhyparini but it has been questioned (Howden and Bordat 1995), *Notocaulus* were classified as Rhyparini, but transferred to Eupariini (Krikken and Huijbregts 1987; Howden and Storey 1992).

A number of more or less aberrant genera have been added to the Rhyparini in recent years (Howden 1995, 2003; Howden and Storey 2000; Makhan 2006; Pittino 2006), with Skelley (2007) making an effort to straighten up the classification and listing several papers describing new species or otherwise forwarding knowledge which are not listed here. Krikken (2008a, b) recently reconsidered and described new species in Termitoderini and Termitotrogini.

In addition to these, a number of ant inquilines have always been present in the Eupariini, including the type genus *Euparia*, and two species which are termite inquilines. At one point, Stebnicka erected the tribe Lomanoxiini for the most aberrant Neotropical ant inquilines (Stebnicka 1999), but that was synonymized into Eupariini (Skelley and Howden 2003). All these Neotropical forms were recently reviewed and pictured in Stebnicka (2009).

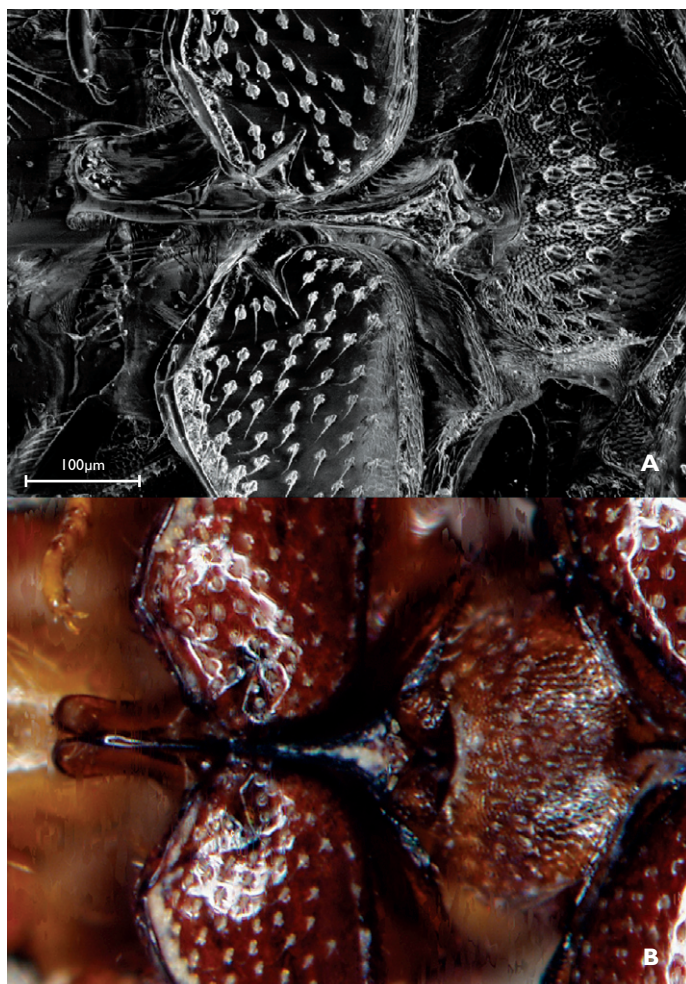


Figure 5. Posterior prosternal process of *Cheleion malayanum* sp. n. **A** scanning electron micrograph **B** stereo microscope image.

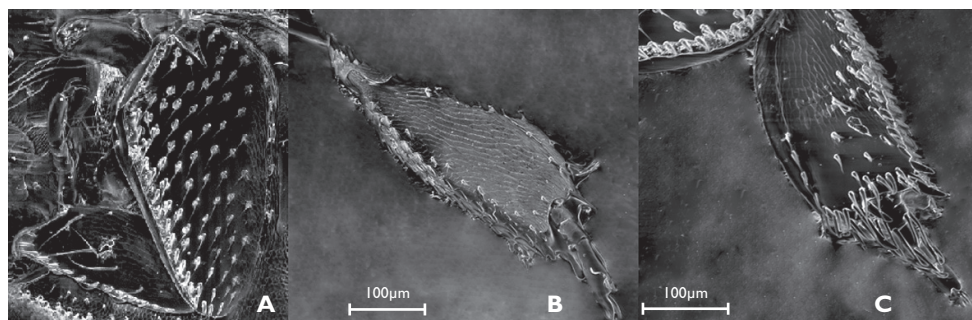


Figure 6. Legs of *Cheleion malayanum* sp. n. **A** scanning electron micrograph of foreleg **B** scanning electron micrograph of midleg showing un conspicuous tibial spurs **C** scanning electron micrograph of hindleg.

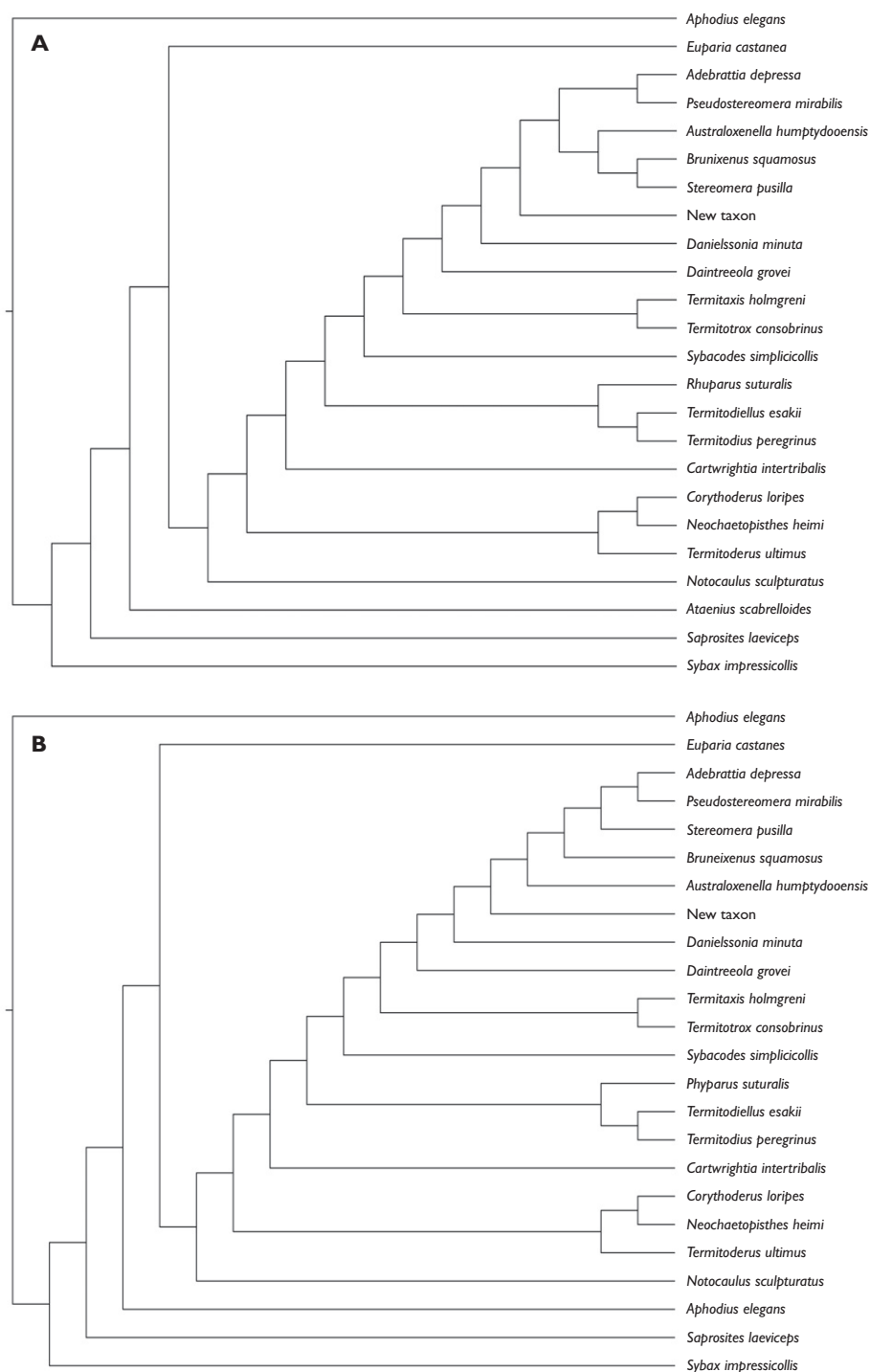
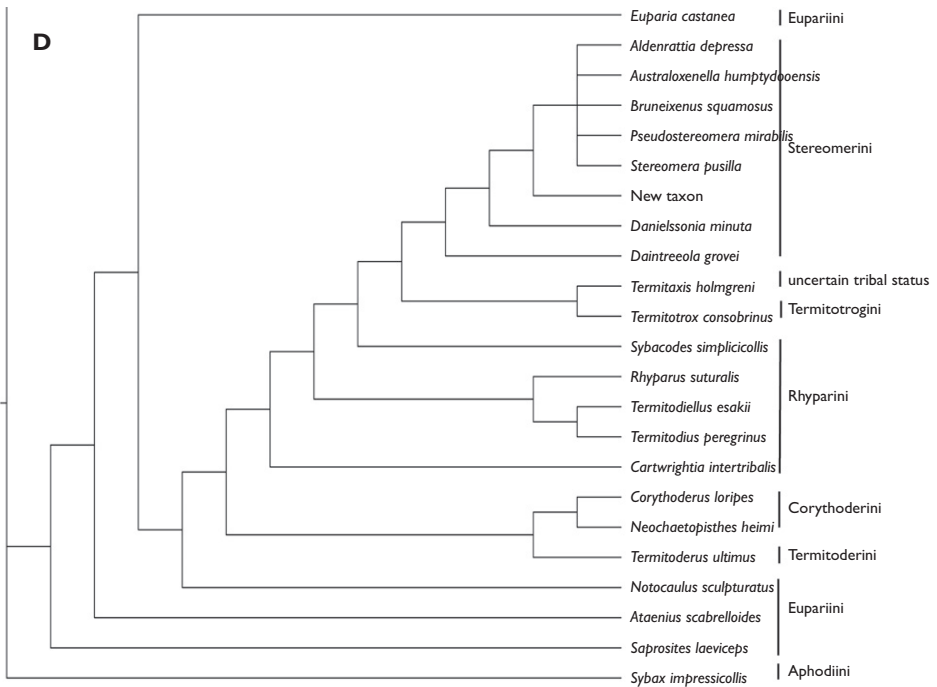
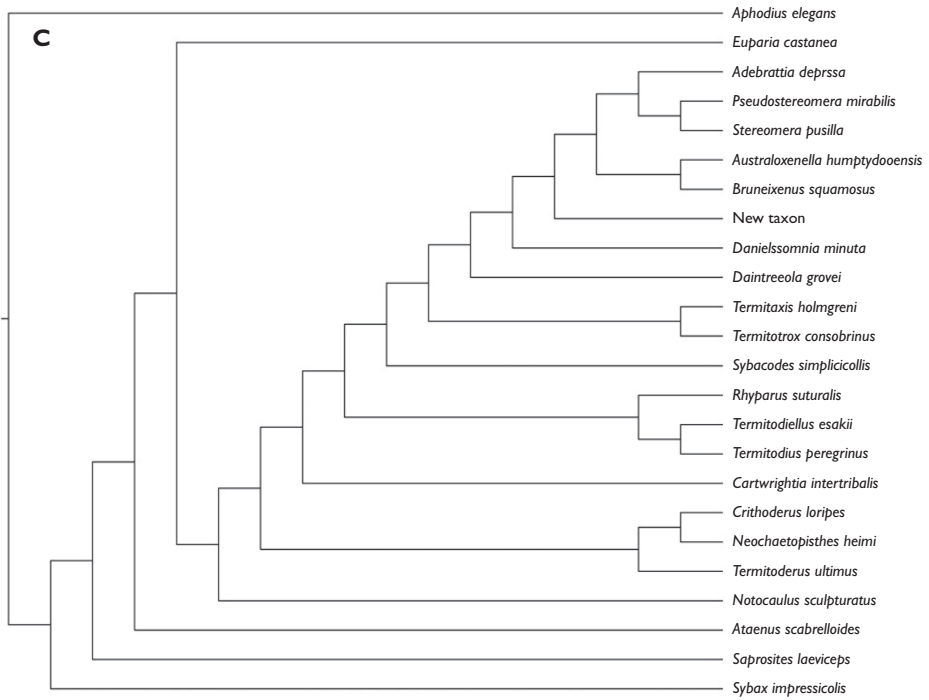


Figure 7. Resulting trees from phylogenetic analysis of morphological data of representatives of **A–C** The 3 most parsimonious trees **D** the strict consensus tree.



Stereomerini, Rhyparini, Corythoderini, Termitoderini, Termitotrogini, Aphodiini and Eupariini.

Table 4. Inquilines and suspected inquilines of Aphodiinae

Taxa	Habitat	Distribution	Species	Trichomes	Morphology type	Classification
Stereomerini	unknown; forest litter	South East Asian + Australian	19	trichomes	strongly synechthran	Stereomerini
Termitotrogini	termite inquilines	Afrotropical + Indian	10	not trichomes	strongly synechthran	Termitotrogini
<i>Rhyparus</i>	unknown; forest litter	Pantropical	56	trichomes	intermediate type	Rhyparini
<i>Termitodius</i> & <i>Termitodiellus</i> (+ <i>Aschnarhyparus</i>)	termite inquilines	Pantropical except Africa	10	trichomes	intermediate type	Rhyparini
Recent odd genera in Rhyparini (<i>Hadorhyparus</i> Howden, <i>Leptorhyparus</i> Howden, <i>Lioglyptoxenus</i> Pittino, <i>Microtermitodius</i> Pittino, <i>Monteithaeolus</i> Howden and Storey, <i>Nanotermitodius</i> Howden)	termite inquilines	Pantropical except Africa	6	trichomes	often intermediate	Rhyparini
Corythoderini	termite inquilines	Afrotropical + Indian	35	trichomes	symphilic type	Corythoderini
<i>Termitoderus</i>	termite inquilines	Afrotropical	4	not trichomes	symphilic type	Termitoderini
<i>Termitaxis</i>	termite inquilines	Neotropical	1	trichomes	symphilic type	incertae sedis
<i>Cartwrightia</i>	ant inquilines	Neotropical	3	trichomes	intermediate type	Rhyparini (recently Eupariini)

Taxa	Habitat	Distribution	Species	Trichomes	Morphology type	Classification
<i>Sylbacodes</i>	unknown	Oriental	3	?trichomes	weakly synechthran	Rhyparini?
<i>Notocaulus</i>	mostly dung	Afrotropical	13	not trichomes	weakly synechthran	Eupariini (recently Rhyparini)
<i>Sylax</i>	unknown	Afrotropical	3	?trichomes	weakly synechthran	Aphodiini
<i>Euparotrix</i> Stebnicka and Howden	unknown	Australian	1	trichomes	more or less conventional aphodiine	Eupariini
<i>Napoa</i> Ross and <i>Batesiana</i> Chalumeau	termite inquilines	Neotropical	2	not trichomes	more or less conventional aphodiines	Eupariini
<i>Euparia</i> and relatives (<i>Iarupea</i> Martinez, <i>Arupaia</i> Stebnicka, <i>Selviria</i> Stebnicka, <i>Flechtmanniella</i> Stebnicka, <i>Myrmecaphodius</i> Martinez, <i>Martineziana</i> Chalumeau & Ozdikmen, <i>Lomanoxoides</i> Stebnicka, <i>Paraplesiataenius</i> Chalumeau, <i>Bruchaphodius</i> Martinez)	mostly ant inquilines	Neotropical	>30	not trichomes	conventional aphodiines	Eupariini
<i>Lomanoxia</i> Martinez and relatives (<i>Euparixia</i> Brown & <i>Euparixoides</i> Hinton)	ant inquilines	Neotropical	22	not trichomes	more or less conventional aphodiines	Eupariini (briefly Lomanoxiini)

The classification, and above all the relationships between the inquiline tribes, remains unsure because of the more or less far-reaching morphological specializations, including both obvious strongly derived specializations in habitus and integument, as well as reductions in characters traditionally used for distinguishing aphodiine tribes. Many of these specializations often overlap between the inquiline tribes, thus obscuring relationships between each other and between them and the large aphodiine tribe Eupariini, which is speciose in the tropics and characterized mainly by plesiomorphies visavis most other tribes of Aphodiinae.

Often, the appearance of tibial ridges and position of tibial apical spurs are used as diagnostic characters between Eupariini and Aphodiini. These characters are often useless in inquiline-type aphodiines with highly modified, short tibiae and reduced spurs. The abdominal characters traditionally used (fusing of sternites, pygidial furrow, etc.) often unite several but not all inquiline-type taxa with most Eupariini. Perhaps the dissection-requiring mouthparts and aedeagus, which both have provided characters considered important for aphodiine classification (Dellacasa et al. 2001 and elsewhere), but were not studied here, may provide useful information in this respect.

Status of knowledge of biology of alleged inquilines

Strangely enough, it is only some of these inquiline-looking taxa that are actually found in association with social insects. Actually associated with termites are Termitotrogini, Corythoderini, Termitoderini, several small genera in Rhyparini (*Termitodius*, *Termitodiellus*, et al.), plus *incertae sedis* *Termitaxis*. One genus of similar morphology (*Cartwrightia*) and many more genera with more normal appearances are actually associated with ants. In several of the inquiline-type taxa, inquiline lifestyles have never been demonstrated; Stereomerini, a major part of Rhyparini (including *Rhyparus*), plus *Notocaulus* and *Sybacodes* (and *Sybox*). Instead, these are often found in forest litter, *Notocaulus* and *Sybacodes* also in dung. Of course, sifting forest litter and various trapping methods (light traps, Malaise traps, flight intercept traps) are far more common collecting methods than actually breaking into termite mounds. Thus, these taxa might be inquilines not yet encountered in their true habitat, or they may not live with social insects.

Typologies of social insect inquilines are from Wasmann (1894, 1903, 1918), who also studied many of these aphodiines, like Kolbe (1909). Balthasar (1963) summarized the knowledge. Later, Wilson (1971) and Kistner (1979, 1982) provided general discussion of inquiline types.

The basic division is between symphilic inquilines (those actually cared for by the hosts), and inquilines which are synoeketes (ignored by the hosts) or synechthrans (treated with hostility by the hosts). Morphologically, a symphilic lifestyle is often indicated by particular phenomena as possession of specialized tufts of glandular setae (trichomes) or enlarged abdomen (physogastry). Often, symphilic organisms display some kind of general morphological mimicking of their hosts. Synechthrans on the other hand are usually characterized with a “defensive” morphology, often very compact

body (sometimes referred to as “limuloid” body shape, after horseshoe crabs (*Limulus*)), with reinforcing ridges and the capacity to withdraw protruding appendages into folds or grooves.

Among the aphodiines, Corythoderini, Termitoderini and *Termitaxis* clearly correspond to the “symphilic” type (and are indeed found with termites). The clearest examples corresponding to the “synechthran” type are presented by Termitotrogini and Stereomerini (the one found with termites, the other not recognized). The Rhyparini are probably best considered synechthran in general morphology, but less so than Termitotrogini and Stereomerini, and also have symphilic-type trichomes. The typical Rhyparini are not found with termites, and could be described as weakly synechthran in morphology. Within Rhyparini, only the more or less aberrant taxa are actually found among termites, often being intermediate between the weaker synechthran-type and symphilic-type morphologies.

The rationale for classification of inquiline tribes

It is unsatisfactory that this cluster of characters is regarded as an indication of a particular lifestyle in so many taxa where that lifestyle has not been observed. Some of them are commonly collected under circumstances giving no support whatsoever for that assumption. In aphodiine classification, various selections from this cluster are utilized to diagnose several aberrant tribes, while still being assumed to be intimately connected with a particular lifestyle and therefore largely homoplastic, and so not necessarily indicating a relationship between these different tribes while still keeping them together one by one. This is a problematic line of reasoning. A Darwinist framework still rests on interpreting similarities as the result of shared ancestry *unless* in conflict with other similarities. In this data set, the number of characters is small and the taxon sampling, particularly in various groups of possibly related Eupariini, is limited. For this reason, our results are uncertain and do not form the basis for any confidence in suggesting a revised tribal classification. Indeed the consistency is relatively low, but not extremely low, and there is a small number of most parsimonious trees, indicating that there is a fairly strong signal in the data. The Stereomerini, the core Rhyparini (excluding *Sybacodes* and *Cartwrightia*), and the Corythoderini, are all retained as monophyletic groups without conflict. All the representatives of aberrant taxa form a monophyletic group together.

Again, this is not a strong test, but the possibility that their similarities are to a significant extent due to shared ancestry rather than just shared lifestyle must be considered, especially since this particular lifestyle has in fact not been observed in so many of them. The aberrant or termitophilous tribes have been suggested to possibly be related to each other in a few works (Nikolajev 1993; Forshage 2002). Nikolajev suggests they could be related to each other and to Aulonocnemini. The phylogenetic status of Aulonocnemini is not well investigated, and it too might prove to be near or in Eupariini.

The few representatives of Eupariini included, on the other hand, admittedly covering very little of the diversity of the group but nevertheless representing its three most principal genera, did not form a clade together, but instead a grade basal to a single clade of all the “termitophilic” tribes. Eupariini is historically delineated in contrast with Aphodiini, and most of its diagnostic characters are defined in that contrast. As the phylogeny of Aphodiinae remains uncertain, the polarity of most of these characters is not known. Regardless of whether the character states found in Eupariini are plesiomorphic or apomorphic visavis Aphodiini, they are either shared with or clearly plesiomorphic visavis Psammodiini and most minor tribes. In fact it seems impossible to circumscribe Eupariini as a monophyletic group. Eupariini may perhaps be a paraphyletic grade of basal groups of Aphodiini, or it may be a huge possibly monophyletic complex, but in both cases very possibly with Psammodiini and several smaller tribes intermixed.

A more robust phylogenetic analysis including a wealth of eupariine taxa, several of the minor tribes, and many more characters than used here, will highlight the difficulties of keeping Eupariini in its present form, and suggest a revised tribal classification. Whether this will result in the synonymy of several tribes into a solid Eupariini *sensu lato*, or identify monophyletic lineages that will allow for even further splitting into more tribes, will be up to the judgment of that revisor.

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