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STATE OF KNOWLEDGE OF DUNG BEETLE PHYLOGENY
- a review of phylogenetic hypotheses regarding Aphodiinae (Coleoptera; Scarabaeidae)

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Abstract:

As a preparation for proper phylogenetic analysis of groups within the coprophagous clade of Scarabaeidae, an overview is presented of all the proposed suprageneric taxa in Aphodiinae. The current knowledge of the affiliations of each group is discussed based on available information on their morphology, biology, biogeography and paleontology, as well as their classification history. With this as a background an attempt is made to estimate the validity of each taxon from a cladistic perspective, suggest possibilities and point out the most important questions for further research in clarifying the phylogeny of the group.

The introductory part A) is not a scientific paper but an introduction into the subject intended for the seminar along with a polemic against a fraction of the presently most active workers in the field: Dellacasa, Bordat and Dellacasa.

The main part B) is the discussion of all proposed suprageneric taxa in the subfamily from a cladistic viewpoint. The current classification is found to be quite messy and unfortunately a large part of the many recent attempts to revise higher-level classification within the group do not seem to be improvements from a phylogenetic viewpoint.

Most recently proposed tribes (as well as Aulonocemini and Termitotrogini, sometimes regarded as distinct subfamilies) seem to be nested within larger tribes; the synonymisation of Didactyliini and Proctophanini does not seem appropriate, nor does the subtribal division of Psammodiini (though if it is kept the name Pleurophorina Mulsant, 1842 will have to replace Rhyssemina Pittino & Mariani, 1986) and the two large tribes Eupariini and Psammodiini will become monophyletic only if they are merged; while Aegialiini (often regarded as a distinct subfamily) seems paraphyletic. The classification of the termitophilous groups remains a major issue to be solved, as does the subdivision of Eupariini-Psammodiini and the question of genera/subgenera within the reliably monophyletic Aphodiini.

In addition to this C) a phylogenetic analysis is carried out from an outer morphological character set with 40 characters and 44 exemplar taxa. The consensus tree of the few shortest trees attained has a high degree of resolution, but since the character distribution is very homoplastic the result is very poorly supported, and could best serve as a working hypothesis, giving some support for some of the traditional groups and some of the results in the cladistic reinterpretation but not for others.

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STATE OF KNOWLEDGE OF DUNG BEETLE PHYLOGENY

1a. Introduction

The taxonomy of the Scarabaeidae subfamily Aphodiinae is quite messy. This is largely because of its species-richness and the lack of general phylogenetic studies. Most workers active in the field only describe new species, subgenera and genera and very few have been interested in investigating how they are related and thus grouping them naturally.

Specifically, the problems might be regarded as pertaining to four major categories.

1. The lack of knowledge regarding the monophyly and basic relationships of the major subgroups, which leads workers to erect new tribes for various deviant genera. This is especially difficult since most of the traditionally relationship-informative characters are evidently more or less homoplastic within the subfamily, and since the polarity of these characters isn't ascertained.

2. An old continuing controversy regarding whether to include a few presumably basal groups or not.

3. The difficulties in studying the relationships of the most aberrative genera (almost always termite inquilines) which are deviant enough to have retained very few of the characters usually utilised for classification.

4. The difficulty to define and overview some large genera, especially *Aphodius*, but also *Aegialia*, *Ataenius*, *Psammodius*, *Rhyssemus* etc, resulting in conflicting views on which supraspecific taxa should be regarded as genera or subgenera, and which species should be included or excluded.

The aim of this study is to state the problems clearly and point out possibilities of alternative solutions, thereby hopingly contributing to their solution by future empirical studies.

1b. Method

In the following the validity of each proposed suprageneric taxon within the group is discussed from a cladistic viewpoint. Proposed hypotheses of phylogeny are critically reviewed, and the primary concern is whether the diagnostic characters proposed in literature are plesiomorphic or apomorphic and thus whether they support the group's monophyly or not. The nomenclatoral history of each group is also sketched, and the age and biogeographical history is touched upon, from the background of both the paleontological evidence (mostly according to Krell's (2000) extremely useful presentation of the fossil record) and the geographical distribution of the taxon (collected from scattered information in regional faunas, old catalogues, various articles, label data in collections and type localities as stated in Dellacasa (1987)), whether it fits any common biogeographical pattern and whether it implies any hypothesis of sister group relationships and age, either directly from the fossils, or somewhat more indirect through the prevailing hypotheses of paleogeography, or through supposed sister group relations with taxa dated using afore-mentioned methods. Finally the different possibilities of phylogeny are pointed out.

Tab 1. History of classification of subgroups of Aphodiinae.

Schmidt (1910a, b, 1922):

- Aegialiinae
- Aphodiinae
    - Aphodiina
    - Corythoderina
    - Eupariina
    - Psammobiina
    - Rhyparina
- Chironinae

(Aegialiinae and Chironinae not mentioned in 1910a, b, 1922, but treated in other works (1912, 1913))

Janssens (1949):

- Aegialiinae
- Aphodiinae
    - Aphodiini
    - Corythoderini
    - Eupariini
    - Psammobiini
    - Rhyparini
    - Termitotrogini
- Aulonocneminae
- Chironinae

Balthasar (1963. 1964):

- Aegialidae
    - Aegialinae
    - Chironinae
- Aphodiidae
    - Aphodiini
    - Corythoderini
    - Demarziellini
    - Eupariini
    - Psammobiini
    - Rhyparini
    - Thinorycterini
- Aulonocnemidae

(Termitotrogini considered of doubtful status within Coprinae (= Scarabaeinae))

Iablokoff-Khnzorian (1977):

- Aegialitinae
    - Aegialitini
    - Chironini
    - Eremazini
- Aphodiinae
    - Aphodiini
    - Corythoderini
    - Demarziellini
    - Eupariini
    - Psammodiini
    - Rhyparini
    - Thinorycterini

(Aulonocnemini considered part of Eupariini. Psammodiini and Thinorycterini not mentioned, but author accepts Balthasars system except for regarding specifically mentioned issues)

Rakovic (1987):

- Aegialiinae
- Aphodiinae
    - Aphodiini
    - Corythoderini
    - Eupariini
    - Odochilini
    - Psammodiini
    - Rhyparini
    - Termitoderini
    - Thinorycterini

(Termitotrogini, Aulonocnemini and Chironini not mentioned, probably not considered closely related to Aphodiinae)

Dellacasa (1987):

- Aegialiidae
    - Aegialiini
    - Eremazini
- Aphodiidae
    - Aphodiinae
        - Aphodiini
        - Didactyliini
    - Corythoderinae
    - Eupariinae
    - Odochilinae
    - Psammodiinae
        - Psammodiini
        - Rhyssemini
    - Rhyparinae
    - Termitoderinae
    - Thinorycterinae
- Aulonocnemidae
- Termitotrogidae

(Chironini not considered)

Scholtz (1990):

- Aphodiinae
    - Aegialiini
    - Aphodiini
    - Eupariini
    - Psammodiini

(Aulonocneminae listed among ”groups of uncertain phylogenetic status”. Chironini not mentioned at all for unclear reasons. Small tribes (including Termitotrogini) not mentioned, implying authors probable view of their being part of major tribes.

Lawrence & Newton (1995)

- Aphodiinae
    - (including Aegialiinae, Aulonocneminae, Chironinae, Silluviinae, Termitotroginae)

(The authors do not consider tribal levels, only state that all of these proposed subfamilies belong within Aphodiinae, but not whether as tribes or as synonyms)

compilation/compromise (2002):

- Aphodiinae
    - Aegialiini
        - Aegialiina
        - Eremazina
    - Aphodiini
    - Aulonocnemini
    - ?Chironini
    - Corythoderini
    - Didactyliini
    - Eupariini
    - Lomanoxiini
    - Odochilini
    - Odontolochini
    - Proctophanini
    - Psammodiini
        - Phycocina
        - Psammodiina
        - Rhyssemina
    - Rhyparini
    - Stereomerini
    - Termitoderini
    - Termitotrogini

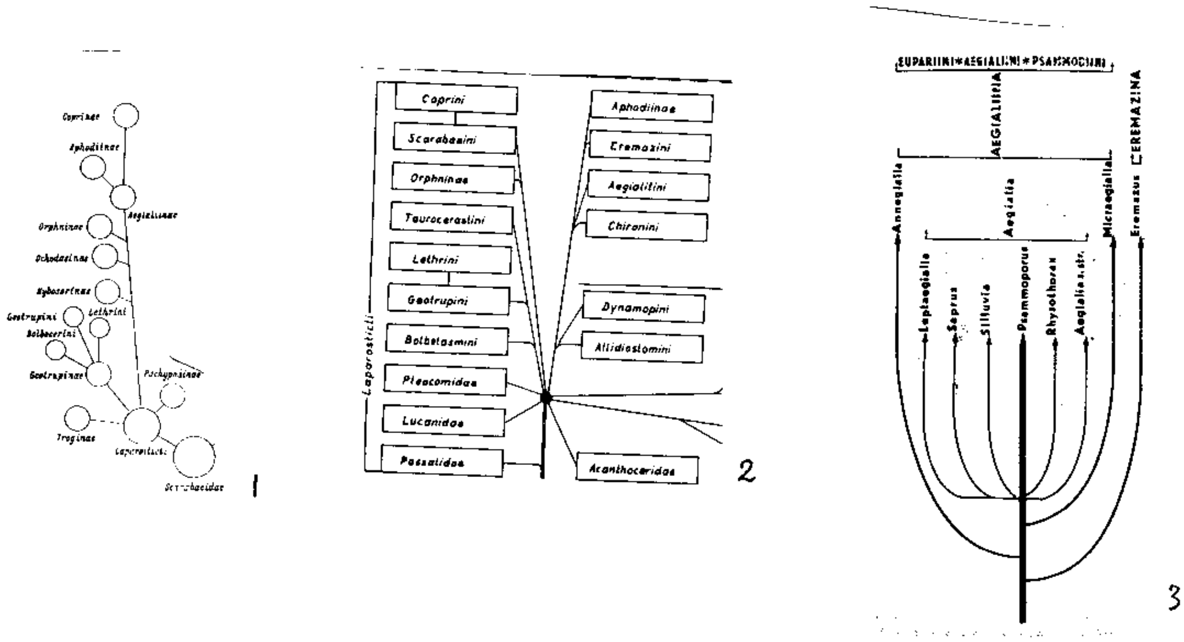
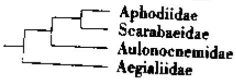
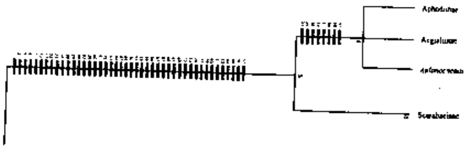


Fig 1.1-3. Non-cladistic attempts at reconstructing phylogeny of Aphodiinae.
1.1 Excerpt from Medvedev's figure representing the phylogeny of Scarabaeoidea (1976). NB Coprinae = Scarabaeinae. **1.2** Excerpt from Iablokoff-Khnzorian's "Schema" representing the phylogeny of Scarabaeoidea (1977). Note that in this hypothesis Scarabaeinae is not considered very close to Aphodiinae. **1.3** Stebnicka's reconstruction of the phylogeny of Aegialiini (1977), appearently suggesting Aegialiini to be part of a group also comprising Eupariini and Psammodiini.

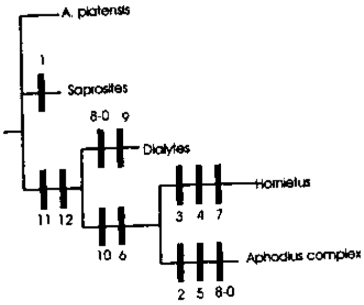
Fig 2.1-5. Attempts in cladistic terms at reconstructing phylogeny.



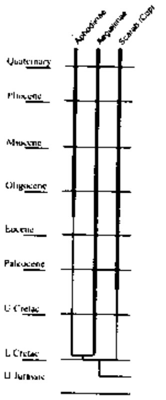
2.1. Cambefort's hypothesis (1987). In Dellacasa (1987) Termitotrogini (as Termitotrogidae) is added as a sister group to Aphodiidae (= Aphodiinae)



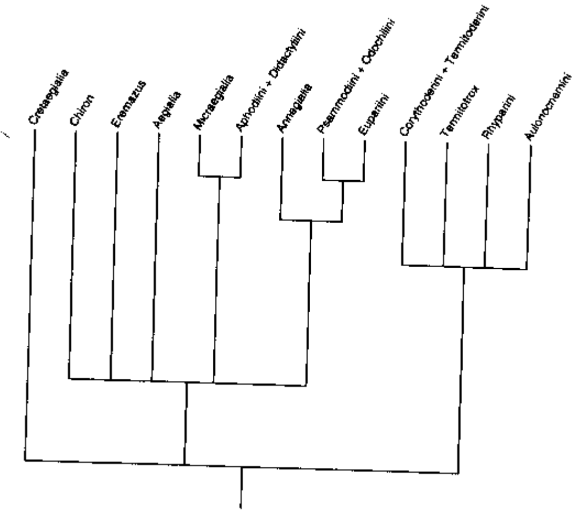
2.2. Excerpt from consensus tree in Browne's and Scholtz' analysis of the phylogeny of Scarabaeidae (1988). Bars represent synapomorphies in wing base and wing articulation.



2.4. Stebnicka's analysis of the relation of some aphodiinae taxa (2000). *A platensis* is *Ataenius platensis*, and *Dialytes* and *Hornietus* are genera within Aphodiini, but what is meant by "Aphodius complex" is not demarcated.



2.3. Excerpt from Krell's figure dating Browne's & Scholtz'phylogeny with the fossil record (2000).



2.5 An attempt by the present author to construct a tree according to Nikolajev's hypothesis (1993). The tree may however not fully coincide with that author's intentions.

Thus it is constituted as a literature study, even though proposed characters had to be controlled, and ideas of possible relationships stimulated, by studying specimens. Most, but not all of the discussed taxa, were to be found in NRM (Naturhistoriska Riksmuseet, Stockholm) and LZM (Lunds Universitets Zoologiska Museum) while common taxa also could be studied in the authors collection and in UUZM (Uppsala Universitets Zoologiska Museum, Evolutionsmuséet). Some of the rarer taxa were obtained from the Zoological Institute of St Petersburg or from Landins loans from various sources in LZM, though others were not possible to find at all for the present author.

1c. Present state of Aphodiine classification

The current classification of Aphodiinae is basically the system of Schmidt (1910a) with several recent splittings of the last 25 years (tab 1).

As in Schmidt's system, there are three major tribes: Aphodiini, Eupariini and Psammodiini.

There are also three groups of presumedly ”primitive” problematica, that some authors include and some do not. Of these Aegialiini have always been placed either within or very close to Aphodiinae, Chironini are usually left out and rarely treated at all, and Aulonocnemini was transferred to a position within or very close to Aphodiinae from within Scarabaeinae.

Then there are a number of tribes of highly aberrant termite inquiline tribes; of these, the traditional Schmidtian are Rhyparini and Corythoderini, while Termitotrogini was transferred within Aphodiinae more recently, and Termitoderini and Stereomerini were erected as new tribes recently.

Then there are a number of smaller tribes recently erected for aberrant animals from the three major tribes; from Psammodiini the Odochilini were separated, from Eupariini the Odontolochini and Lomanoxiini, and from Aphodiini the two parallell tribes Didactyliini and Proctophanini, which are used by different workers, partly being diagnosed by the same characters and partly comprising the same genera. To the recent splittings also belong the subdivision of Psammodiini into subtribes, namely Psammodiina, Phycocina and Rhyssemina. The two small tribes Demarziellini and Thinorycterini have been removed from Aphodiinae.

Just like in the whole Scarabaeoidea, the major dividing question between different authors is between lumpers and splitters, and thus most contemporary South and East European workers regard Aphodiinae as a family, while North American, South African and North European workers prefer to keep it a subfamily like in the present work. This is however a question of minor scientific interest and will not be discussed at length here.

The three systematic issues that divide the workers within this group are:

1) whether Aegialiini, Chironini, Aulonocnemini and Termitotrogini are part of Aphodiinae or groups of their own in the close vicinity,

2) if both Didactyliini and Proctophanini are valid or not, and what genera should be placed in which tribe, and

3) which subgroups of the enormous genus *Aphodius* should be regarded as subgenera or proper genera. The same question also exists regarding the minor genus *Aegialia*.

There are several more critical issues than these, but these aren't usually debated.

1d. Published hypotheses on Aphodiine phylogeny

The three authors that have discussed the phylogeny of Aphodiinae in the most explicit terms are Cambefort, Stebnicka and Nikolajev.

Cambefort discussed the relation between Aphodiinae, Scarabaeinae, Termitotrogini, Aegialiini and Aulonocnemini in his monograph on the latter (1987) and proposed a phylogeny deduced from his general ideas put in cladistic terms (thus no proper analysis) (fig 2.1). This hypothesis was referred (without stating the source) in Dellacasa's catalogue (1987). Later (1991 a, b) Cambefort provided a more extensive discussion on evolution and biogeographical history of the coprophagous Scarabaeids.

Stebnicka published her ideas on the phylogeny of the Aphodiine tribes early (1977), along with a figure somewhat resembling a cladogram but without an analysis (fig 1.3). Recently, she performed a real cladistic analysis with few taxa and few characters in order to place a new genus (2000), but the resulting cladogram implies a hypothesis involving more taxa (fig 2.4). In several other works the same author delivers scattered remarks about the phylogeny of Aphodiine groups.

Nikolajev discussed the phylogeny of the group when he described a pair of fossil species (1993). Even though no actual phylogenetic analysis is performed, Nikolajev's arguments are cladistically based and would have made up the most detailed published hypothesis on the subject if a few ambiguities in the text had been solved by drawing a tree figure (fig 2.5).

Apart from this, the small tribes Termitoderini and Stereomerini have been cladistically analysed (Howden & Storey 1992, Bordat & Howden 1995), and Corythoderini phylogenetically discussed though not really analysed (Tangelder & Krikken 1982). Some discussions of the evolution of Scarabaeoidea has contained well-developed specific ideas on the Aphodiinae (i e Scholtz & Chown 1996) and other studies in the phylogeny of Scarabaeoidea have at least contained a discussion of those group that the authors in question regarded as subfamilies (Medvedev 1976 (fig 1.1), Iablokoff-Khnzorian 1977 (fig 1.2), Scholtz 1990, Scholtz & Brown 1998 (fig 2.2)).

1e. Basis for present classification

Since there has been very little of phylogenetic analyses in the group, the basis for the present classification is more or less a pre-Hennigian typological perspective. The groups are kept together by shared characters that may be synapomorphic or symplesiomorphic, and new suprageneric taxa are erected on the basis of unusual combinations of characters (”transition forms”) or unusual unique characters (”different enough”).

As in all organisms, thus founded groups may represent natural groups, but often they do not. Suprageneric taxa erected as ”transition forms” often belong in either of the groups it is thought to be intermediate between, and/or are paraphyletic. The autapomorphous animals that make suprageneric taxa of their own are often highly derived close relatives of other less derived animals and thus belong within larger groups. In order to obtain a natural classification then, the transition forms and different enough taxa, if they turn out to be ingroups within larger groups, must be transferred to these groups, and some of the larger groups will, if they turn out to be paraphyletic, have to be either split into monophyletic subgroups or lumped together with the monophyletic group/groups that their clade includes.

2: Monophyly of Aphodiinae

2a. Nomenclatoral history

In the oldest days of classification, the aphodiines were like all Scarabaeoids part of Linnaeus' genus *Scarabaeus*(Linnaeus 1758). During the second half of the 18th century different workers erected new genera, thus splitting up the linnaean groups, but still rather carefully, with still no need for suprageneric taxa like families, subfamilies and tribes. Illiger (1798) proposed *Aphodius.* The latter became widely accepted only when Fabricius picked it up in his authoritative *Systema eleutheratorum* (1801), and included all known aphodiines.

When suprageneric classifications were sketched upon during the 19th century, for the aphodiines the names were always derived from *Aphodius*, causing no nomenclatoral problems in that respect. Even though the suffixes varied with each author until recently this family-level group taxon has always been recognisable by a name derived from *Aphodius* ever since Leach's Aphodida (1815).

2b. Monophyly of coprophag clade

To analyse the phylogeny of Aphodiinae, the first thing to do is to establish its monophyly. In order to do that it's not entirely sufficient only to identify some more or less unique synapomorphies, but it's also desirable to identify its sister group, and then also to establish the monophyly of that group and of the common ”mother-group”.

Even though the monophyly of Aphodiinae may be problematic because of the presumedly basal groups that are sometimes included and sometimes not, it is generally assumed that the sister group of Aphodiinae is Scarabaeinae and that they form a coprophag clade, which represent one of the main branches of Scarabaeoidea and probably has a sister-group relation to the pleurostict scarabs (Melolonthinae, Rutelinae, Dynastinae, Cetoniinae and smaller groups).

The coprophag clade is not used as a formal taxon. They form the core of the paraphyletic group Laparosticti (suggested by Erichson 1847) which was widely in use for more than a century, and often even today for practical reasons. This paraphyletic group has sometimes been called Coprophaga or similar (Latreille 1802, Kolbe 1905, and others). A name uniting Aphodiinae and Scarabaeinae but excluding the other Laparostict group like Trogids, Geotrupids and Hybosorids is much harder to find in the litterature; the only example found during this study is the Coprophages of Reiche, 1842.

Most of the traditional diagnostic characters though are plesiomorphic in relation to the Pleurosticti (and shared with the other laparostict groups: tomentose antennal club, laparostict spiracles) or not present in basal taxa (coprophagy, highly derived membranous mandibles and epipharynx, widened clypeus covering mouthparts) but there are other specialisations that unite this group. In Brownes &

Scholtz’ phylogenetic analysis the monophyly of this clade (called the ”aphodiine line”) was well supported with 44 derived states of hindwing articulation and wing base (Browne & Scholtz 1998). In passing, Browne & Scholtz (1998) and others have suggested specialisations in legs and mouthparts as synapomorphies of the clade, but the present author has not been able to detect which characters they are referring to.

2c. Monophyly of Aphodiinae visavis Scarabaeinae; the status of Aegialiini and Aulonocnemini

The traditional diagnostic characters to distinguish Aphodiinae from Scarabaeinae are almost invariably both plesiomorphic for Aphodiinae visavis Scarabaeinae and variable within Aphodiinae (two hind tibial spurs, pygidium covered, middle coxae oblique and narrowly separated, scutellum present, free-living larvae, small size). Fortunately there are other character suites described. In litterature, several apomorphies for Aphodiinae are stated: 4 derived states of hindwing veins evident from the illustrations in Balthasar’s study (1942), 8 derived states of hindwing articulation and wing base (Browne & Scholtz 1998), abdominal spiracles progressively smaller (Ritcher 1969). Furthermore there are derived states of male genitalia: temones articulated to internal sac, partly unsclerotised basal piece, symmetrical and dorsomedially membranous parameres, genital segment intermediate between genital capsule and U-shaped spiculum gastrale (d’Hotman & Scholtz 1990) (of these, only the first is more or less a unique synapomorphy; most are either symplesiomorphic visavis the pleurosticti, apomorphies spread in other groups too, and/or lacking in some or all Aegialiini). In passing, Browne & Scholtz (1998) and others have suggested specialisations in chromosomes and mouthparts as synapomorphies of the clade, but the present author has not been able to detect which characters they are referring to.

For Scarabaeinae, the traditional diagnostic characters implied above are synapomorphic though sometimes variable within the group (only one hind tibial spur, elytra truncated leaving pygidium free, scutellum strongly reduced or absent, burying of brood balls for the offspring, larger size). But there are no problems finding more synapomorphies: only one pair of ovarioles (Ritcher & Baker 1974), 12 derived states of hindwing articulation (Browne & Scholtz 1998), mouthparts highly derived: mandibles uniquely specialised with receptaculum and asymmetrical molar lobes, membranous epipharynx with double lateral tormae and definite rows of setae (Scholtz 1990, Nel & Scholtz 1990), male genitals with well armed internal sac and temones medially fused to form spoon-shaped structure (Scholtz 1990, d’Hotman & Scholtz 1990), reduced thoracical intersegmentalia, complex thoracical spiracles, differentiation among abdominal spiracles (Ritcher 1969), larvae humpbacked, with legs with only two segments and no claws (Scholtz 1990).

Some authors strongly stress the problematic status of Aegialiini and Aulonocnemini, and thus the possible paraphyly of Aphodiinae (Stebnicka 1985; Matthews & Stebnicka 1986; Cambefort 1987; 1992; Dellacasa 1987). To cope with this situation several authors are eager to have both groups as separate subfamilies, not noticing that this actually doesn’t solve the problem: they still state only plesiomorphies for all groups.

However, the hindwing articulation and wing base characters studied by Browne & Scholtz (1998) are all shared between Aegialiines, Aulonocnemines and proper Aphodiines (actually, they found no characters to divide these three taxa). The same is true regarding the wing veins illustrated in Balthasar (1942), and according to Browne & Scholtz also mouthparts and male genitalia are in favor of inclusion. Thus it shouldn't be a question of debate whether to include them or not, and the problems with their primitive character states is more a problem of phylogeny within Aphodiinae, that we will return to further on.

2d. Chironini and Termitotrogini

Chironini seems to have been rarely treated at all (no systematic treatment between Arrow 1936 and Huchet 2000). The authorship of the taxon belongs to Harold, 1867 (which is overlooked by Huchet (2000)). It contains beetles with general Aphodiine characteristics, but sharing the presumedly primitive exposed labrum and sclerotised mandibles with Aegialiini and Aulonocnemini, and showing a peculiar autapomorphy in its strongly developed waist and cylindrical body shape (plus some wing characters (Iablokoff-Khnzorian 1977) and peculiar genitals (Huchet 2000)). In the 19th century *Chiron* was considered to belong in Lucanidae (Westwood 1840) and then as close to Hybosoridae and Geotrupidae (Arrow 1909), but treated as very close to Aegialiini in Schmidt (1912, 1913), and as part of Aegialiini by Reitter (1892), Balthasar (1964) and Iablokoff-Khnzorian (1977). However, it has never been treated by the present authority on Aegialiini, Stebnicka, and was not included in Dellacasas catalogue (1987). Neither has the group been mentioned in the works of Scholtz and co-workers (i e Scholtz 1990; Browne & Scholtz 1998). Nikolajev (1993) retains the group within Aphodiinae and suggest it to be the sister group of Aphodiini + Eupariini + Psammodiini (however this is not unambiguously stated). Huchet (2000) disregards all previous authors suggestions of the groups relationships and keeps it as a proper family without discussing its place in phylogeny. However, it shares general morphology of tibial spurs, mouth parts and pronotum outline (usually considered important characters) with Aegialiini, and seems not to show synapomorphies with other scarab groups – and ought, according to the present author's judgement, to be treated in accordance with Schmidt, as very close to Aegialiini – while waiting for the on-going research of Huchet to produce any positive results concerning its placement.

Termitotrogini is even more poorly investigated as Chironini, and since it consists of highly autapomorphous termite inquilines it is hard to say something about its relationships without a thorough investigation. It is usually considered a part of the Aphodiine complex, and will be treated among the inquiline tribes here.

2d. Paleontology and biogeography

The oldest fossils within the coprophag clade are Aegialiini from the lower Cretaceous (Scarabaeinae fossils are of younger age, upper Cretaceous) (Nikolajev 1993, Krell 2000). From lower Cretaceous there are also fossils of their sister group Pleurosticti. The implications for age and historical biogeography by the Aegialiine fossil are all dependent on its assumed place in the phylogeny, and thus will be returned to later.

Scholtz & Chown (1995) have proposed the most elaborated hypothesis of Scarabaeid evolution so far, and in their view Scarabaeinae and Aphodiinae diverged (originated) in the Tertiary following the radiation of the mammal order Artiodactyla, the presently most important grazers. They were not conscious of the earlier fossils both of Aegialiini and of the sister group of the coprophages, Pleurosticti. But apart from that it does not seem motivated to assume that Scarabaeinae and Aphodiinae only originated with the abundant availability of mammalian dung, since in both subfamilies there are saprophagous lineages considered to be older than coprophagous ones (in Scarabaeinae only a few Canthonini and Ateuchini, but in Aphodiinae most tribes – cf Cambefort 1991a,b). Furthermore there is no reason to assume apriori that the time of origin (=divergence from sister group) is identical with the time of radiation (=morphological differentiation, more or less abundant speciation and dispersal); actually the phylogenetic hypothesis utilised by Scholtz & Chown also contains a remarkable example of such a ”delayed radiation” in that they assume that Scarabaeidae diverged from all other Scarabaeoidea in the Jurassic but didn’t produce any extant (or fossil-producing) off-shoots until after the Cretaceous mass extinctions, which is 100 MYR later. Krells (2000) hypothesis of a dated phylogeny based on fossil record dates the Aphodiinae-Scarabaeinae-split in the boundary between Jurassic and Cretaceous.

Aphodiinae and Scarabaeinae are cosmopolitan groups, but Scarabaeinae is restricted by cold; few species occur in cold temperate areas and none go far north. The greatest scarabaeine diversity is to be found on Gondwana continents. Most of the genera of supposedly basal subgroups occur in tropical South America, with related genera above all in the Australian region and Madagascar. In continental Africa and tropical Asia these basal taxa are fewer, commonly supposed to have been out-competed by the more species-rich and assumedly more derived groups. It is in Africa that these supposedly derived groups have their center, giving this region by far the largest total number of scarabaeine species. In the Holarctic region such derived taxa dominate strongly, and only a few representatives are present of the basal groups, apparently recently dispersed. All this, above all the close relationships of the Neotropical and Australian faunas indicate that the group was there before the split of Gondwana, thus upper Jurassic.

All of this seem to indicate that the two sister groups date back to upper Jurassic, but the historical biogeography of Aphodiinae will be discussed later after the establishment of probable basal subgroups.

3. Monophyly and relationships of the main tribes

3a. Aphodiini

Aphodiini is an old grouping, the name dating its authorship back to Leach, 1815 (as ”Aphodida”, including the whole Aphodiinae), but the concept of an Aphodiine *tribe* is the work of Schmidt (1910a). Recently is has been extensively and globally treated by Dellacasa et al (2001) who, together or individually, have offered several studies on particular subgroups too. Other workers, including Stebnicka, Kral and others have made thorough revisions of included subgenera or of regional faunas.

After Psammodiini and Eupariini had been split off by Schmidt, Aphodiini was generally thought to be well characterised by the two transverse carinae on the middle and hind tibiae (fig 5.2). A few included taxa had these very poorly developed, but they were recently found to lack the second important characteristic of Aphodiini, the tibial apical spurs widely separated, and were split off as Didactyliini (Pittino 1984). A number of genera, lacking the separated tibial spurs but with the tibial carinae well developed, went along in Didactyliini (for authors following Dellacasa) or formed Proctophanini (for authors following Stebnicka). Thus the separated tibial spurs became the major synapomorphy instead of the carinae. However, this is shared with the core of Aegialiini (and *Chiron*). Other characters that characterise most Aphodiini is their forward-oriented head with clearly visible eyes, and their more or less elongate body shape with more or less elongate legs and tarsi. These latter characters are variable and all seem like rather simple adaptations to a more mobile life in the open, away from only digging, and can therefore not be considered strong as synapomorphies. Mouth parts are highly specialised with a number of apomorphies in the epipharynx, none of which are shared by all Aphodiini or unique, but showing (like in those tribes) a varying degree of adaptation towards ”soft saprophagy” (Stebnicka & Howden 1996) (fig 4.1). Wings do not seem to contribute with any unique synapomorphy either, but genitalia do: increased number of testicular follicles in males (6-7) and ovarioles in females (5-11), similar glandular reservoirs and presence of preputial ventral gland (both in males) (Martínez et al 2001); phallobase of male aedeagus with dorsal hump or arcuately rounded (Stebnicka 2001).

The monophyly of Aphodiini thus seems probable but not very well supported. Some authors prefer to view Aphodiini as ”primitive” versus Eupariini and Psammodiini (Howden & Storey 1992, Browne & Scholtz 1998; also implied in Nikolajev 1993). Their closest relatives may be Aegialiini or Didactyliini-Proctophanini, a question we will inquire into further on.

3b. Biogeography of coprophages

Aphodiini are very numerous and truly cosmopolitan, *Aphodius* being more widespread than any other scarabaeoid genus. Several subgenera and even a number of species are more r less cosmopolitan. Overall diversity seems everywhere larger in temperate areas, and the largest number of species are found in the Palearctic. Of all suprageneric taxa (genera/subgenera) about half of the number are predominantly Palearctic taxa, showing either a Mediterranean or a Central Asian overweight. The Afrotropical region has many taxa too, the Nearctic somewhat fewer. Even fewer belong to the Neotropical, Oriental and Australian regions. The Oriental fauna has very few endemic subgroups and seems to consist of spill-overs from Afrotropic and East Palearctic groups. The Australian and Neotropic faunas though show a great degree of endemism and also some affinity with each other. Gondwana part long isolated (like Madagascar and New Zealand) have a poor fauna, and isolated volcanic islands usually only have one or two widespread species.

Beside the largest diversity of Aphodiini in Central Asia and the Mediterranean,a remarkable diversity is to be found in South and East Africa. Thus the group has four different centres, of which either may represent some kind of place of origin and the other three secondary radiation centers. Whatever the time of origin and distribution in its earliest days, it seems safe to conclude that the major diversification occured in close connection with the radiation of large grazing artiodactyl herds in the Tertiary creating large grassland habitats (more or less adhering to the scenario assumed by Scholtz & Chowne (1995) but restricting it to concern Aphodiini), which took place above all in Africa, North America and Eurasia. Meanwhile, South America, India, South East Asia and Australia were all more or less isolated with mostly other groups of grazing animals and often much more wooded. The biology of Aphodiini in most parts of the world is insufficiently known. While the majority of Western Palearctic species mainly live in/on herbivore dung (and as it seems most Eastern Palearctic, Oriental and Afrotropical too), there are several subgroups (in South America and Australia perhaps the majority of taxa) that are saprophagous, and others (in North America at least half the number of species) that live in rodent nests. Others are psammophilous and might be more or less ”hard saprophages”, and at least one recently erected genus supposed to be basal within Aphodiini are stated to be subcorticeous (Stebnicka 2000), a biology that has been suggested for the common ancestor of Aphodiinae and Scarabaeinae (Cambefort 1991a).

The group seems most likely to have a western –central old-world origin, a basic adaptation to temperate climates, a strong dispersal ability and therefore a succesful radiation, along with lesser competitivity visavis Scarabaeinae in dung communities in warm areas. The distribution to a large extent fits the present distribution of continents best, supporting that most speciation and dispersal has taken place rather recently.

Fossils of *Aphodius* are found from Eocene (Europe), Oligocene (USA & Europe), Miocene (Europe), Pleistocene (USA & Europe), and *Oxyomus* from Oligocene (USA), supporting a long presence in the Holarctic.

3c. Psammodiini

Psammodiini was proposed by Mulsant (1842), but his concept of ”les Psammodiaires” comprised only the present Psammodiina. Before that, several authors had a concept of a genus comprised by all psammophilous aphodiines (Gyllenhal (1808) under the name *Psammodius*, Billberg (1820) as *Aegialea* (sic)). The present concept of the group was introduced by Schmidt (1910a). Recent work in the group (by Rakovic, Gordon, Cartwright, Pittino, Mariani and Kral) has changed its taxonomy with a brand new subdivision into subtribes, and the splitting of a few large genera into several smaller. Stebnicka & Howden (1996) claim that Psammodiini are most closely related to Eupariini, but not whether as true sister groups or not. Browne & Scholtz (1998) hint at a sistergroup relation in saying that Psammodiini and Eupariini are derived and similar. Landin (1960) stresses the similarities between Psammodiini and Aegialiini but says nothing clearly about the consequences for the phylogeny, and the similarities he stresses are either plesiomorphic or homoplastic due to shared psammophilous biology. There has in fact been some doubt as to whether Psammodiini and Eupariini are readily distinguishable. Cartwright (1955) noted in passing that they would best make one tribe, and Nikolajev (1993) said they possibly form a ”single phyletic line” – not being distinguishable from each other in his character matrix, but no one has yet gone as far as synonymising them. Stebnicka (2001) recognises the difficulties in keeping the groups apart, noting that both external morphology and male genital characters overlap, but states that epipharyngeal structures ”are usually sufficient for tribal placement” without specifying these characters.

From Schmidt on, the concept of the Psammodiini (then as Psammobiina) has seemed clear and distinct, comprising beetles characterised by shortened and often flattened tarsi with often conical joints, flattened tibiae, retracted head with concealed eyes and rugose sculpture, often sculptured elytral interstices, as well as generally very small size and psammophilous biology (though the biology of most species remains unknown, specimens being collected mostly at light). The epipharynx is homogenously plesiomorphic (Pittino & Mariani 1986); adapted to ”hard saprophagy” (Stebnicka & Howden 1996), neither showing variation nor any apomorphic states visavis other Aphodiinae. The strongest indication of the groups monophyly lies in the peculiar pattern of ridges and grooves on the pronotum, which often is more or less reduced but almost always with a recognizable groundplan. However, Rakovic & Kral (1997) recently suggested that this structure have been acquired twice independently, the authors not recognising that this removes the support for the monophyly of Psammodiini.

In fact all Psammodiines share some of the general characteristics of Eupariines, and some genera share all (including fluted abdominal segments etc). The reduced pronotal pattern of some Psammodiini (considered vestigial) is practically indistinguishable from the supposedly plesiomorphic pronotal structure of Eupariini. Thus, it seems more likely that Psammodiini is either a paraphyletic stem group of Eupariini, or nested within Eupariini.

No psammodiine fossils have been found. Distribution of the group is cosmopolitan, excepting cold areas. The greatest species numbers seem to be found in the Afrotropical region, but several individual genera are quite widespread or show strangely disjunct distributions like African-Australian, African-Nearctic, Madagassic-Japanese, Nearctic-Australian etc.

3d. The subtribes of Psammodiini

Pittino & Mariani (1986) split Psammodiini into two subtribes, Psammodiina and Rhyssemina, and even more recently Rakovic & Kral (1997) suggested a third subtribe, that they called Phycochina but which ought to be Phycocina since the original spelling of the type genus is *Phycocus* (Stebnicka 2001).

Psammodiina have very broad hind femurs, and hind tarsi joints short, flattened and dilatate. This seems to make good synapomorphies. The group is cosmopolitan but not very species-rich. Most genera belong to the Palearctic region (especially the Mediterranean, surprisingly few in Central Asia, some in Eastern Asia), but several are Afrotropic, and a few Nearctic, Neotropic and Oriental; only very few species are Australian.

Rhyssemina have less derived tarsi, and the fore femurs are broader than the hind ones, the latter character superficially appearing to be a synapomorphy for the group (Pittino & Mariani 1986) but actually shared with Eupariini and several other Aphodiinae and thus plesiomorphic. Rhyssemina is best regarded as a paraphyletic stem group within Psammodiini and not a good group.

If the group is maintained as a classificatory unit in spite of these problems, it ought to be called Pleurophorina. Mulsants name ”les Pleurophorates”, which with a modern suffix would be Pleurophorina, was proposed back in 1842 for a group uniting *Pleurophorus* and *Rhyssemus* (both within the suggested

Rhyssemina) with a few Aphodiini. Since the name hasn't been used afterwards, it might seem that reversal of precedence by prevailing usage (article 23.9, ICZN 1999) would make it unavailable, but to gain this precedence the junior name will also have to be wide-spread in accordance with article 23.9.2, ("used for a particular taxon, as its presumed valid name, in at least 25 works, published by at least 10 authors in the immediately preceding 50 years and encompassing a span of not less than 10 years") which it's not. Thus the senior name in this case, in spite of its forgotten state, should gain priority over Pittino's & Mariani's name. Thus the group should be named Pleurophorina Mulsant, 1842 (Rhyssemina Pittino & Mariani, 1986) **n. syn.**

Rakovic and others have worked a lot with this group too, creating a number of genera, but the large genus of *Rhyssemus* remains largely unrevised and somewhat heterogenous. The group is cosmopolitan and rather evenly destributed around the globe, though it seems that most taxa are Afrotropical, and a surprisingly large number are from the Pacific islands, Madagascar, and other oceanic islands. Since a large part of these never belonged to a continent but are of more recent volcanic origin, we can draw the conclusion that rhyssemines are capable of long distance dispersal with water, and of extensive speciation among thus isolated populations.

Phycocina comprises a single peculiar species in New Zealand, characterised by autapomorphies such as a reduction in antennal segments to 8, narrow tibial apical spurs and very shortened tarsi. It also shares the characteristics of Psammodina, and evidently is best regarded as an ingroup there.

So, if Phycocina is an ingroup within Psammodiina, and Pleurophorina/ Rhyssemina is most probably paraphyletic, then the whole subtribal division of Psammodiini falls.

3e. Eupariini

Eupariini was not sharply defined when Schmidt (1910a) established the name in his division of Aphodiinae in tribes (as "Eupariina") (NB. actually a junior synonym of Ataeniini Harold, 1867 (as Ataenidae); however that name shall not gain priority, because of "reversal of precedence by prevaling usage" article 23.9 in the Code (ICZN 1999)). Analysis and splitting of the few original genera have been conducted by Cartwright, Martínez, and more recently by Chalumeau, Stebnicka & Howden. Stebnicka has also transferred some aberrant genera to their own new tribes, Lomanoxiini (Stebnicka 1999a) and Odontolochini (Stebnicka & Howden, 1996).

Eupariini is characterised by some plesiomorphic characters (tibial apical spurs close together, lack of tibial transverse carinae, free pygidium), a number of characters that may be plesiomorphic or apomorphic, but not shared by all Eupariini, though often with some or all Psammodiini (wide head, strongly developed tibal apical spurs, curved tibiae, tibial longitudinal ridges, abdominal segments with fluting, grooved femora), and also a number of characters that seem apomorphic, but are shared with some or all Psammodiini (retracted head with concealed eyes, fused abdominal segments, pygidial transversal ridge, lateral parts of pronotum flattened at least in front, bordered basal margin of elytra). The lack of transverse carinae seems like a plesiomorphy, but is regarded by Howden & Storey (1992) as an apomorphy, a secondary loss. The location of the clypeo-labral suture, across or below the

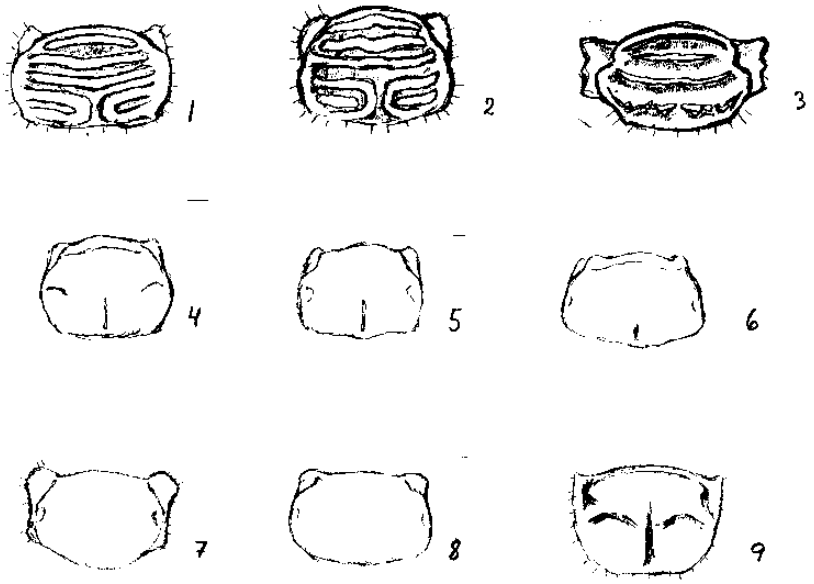


Fig 3.1-9. Outline and structure of pronotum of psammodiine and related taxa. 1.1. Full psammodiine structure in *Psammodius*. **1.2.** Full psammodiine structure in *Rhyssemus*. **1.3.** Non-psammodiine structure in *Odochilus* (Odochilini). **1.4** Vestigial psammodiine structure in *Diastictus*. **1.5** Vestigial psammodiine structure in *Pleurophorus*. **1.6** Vestigial psammodiine structure in *Platytomus*. **1.7** Non-psammodiine structure in *Euparia* (Eupariini). **1.8.** Non-psammodiine structure in *Ataenius* (Eupariini). **1.9** Structure in *Annegialia* (recently moved from Aegialiini to Eupariini). (Originals, partly redrawn from various sources.)

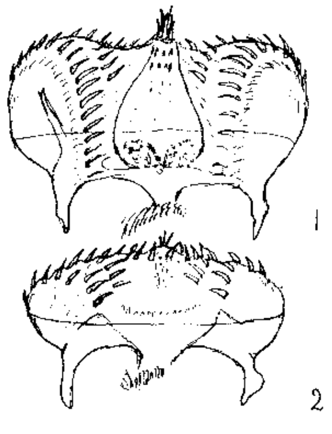


Fig 4.1-2. Epipharynxes in Aphodiinae. 4.1 Schematic epipharynx adapted to "soft saprophagy". **4.2** Schematic epipharynx adapted to "hard saprophagy". (Modified from Stebnicka & Howden 1995)

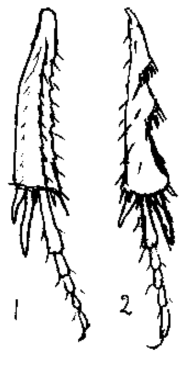


Fig 5.1-2. Tibiae in Aphodiinae. 5.1 Typical tibia in Eupariini with longitudinal ridges and narrowly separated apical spurs. **5.2** Typical tibia in Aphodiini with transversal ridges and widely separated apical spurs. (orig)

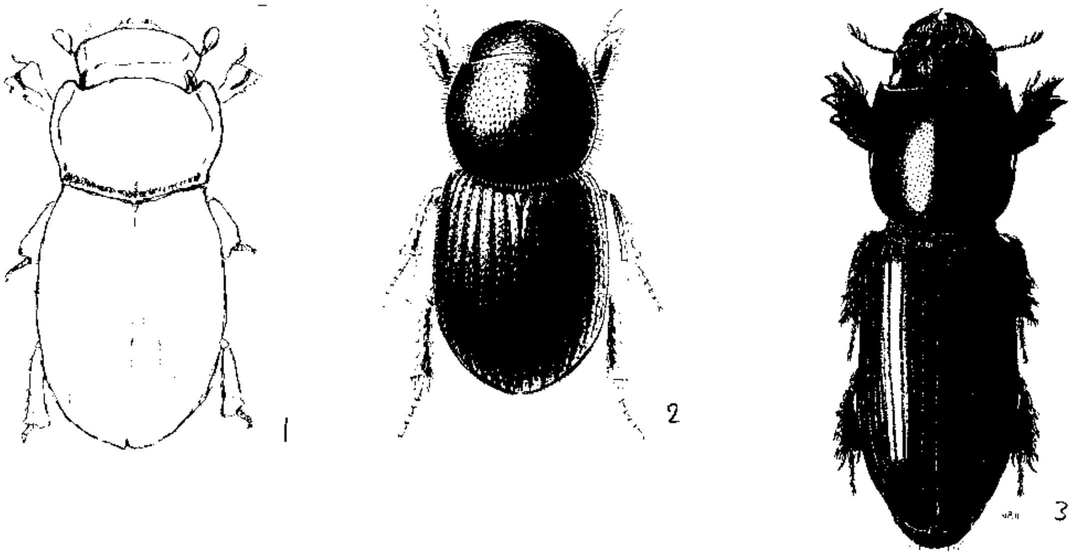


Fig 6.1-3. Representatives of supposedly basal taxa in Aphodiinae. 1.1 *Aulonocnemis* (redrawn from Cambefort 1987), **1.2** *Micraegialia* (Aegialiini) (Gordon & Cartwright 1977), **1.3** *Chiron* (or *Theotimius* of author) (Chironini) (Huchet 2000).

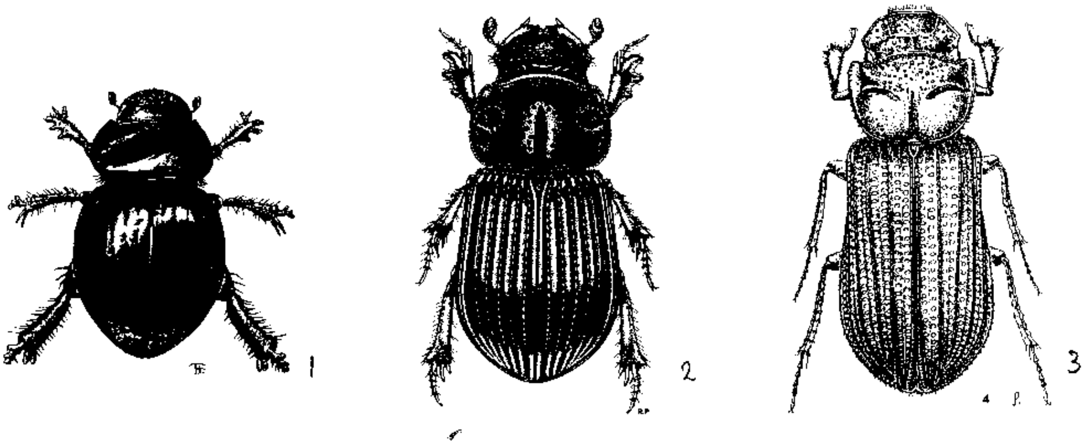


Fig 7.1-3. Representatives of Psammodiini plus *Annegialia*. 1.1 *Phycocus* (Stebnicka 2001) **1.2** *Diastictus* (Pittino & Mariani 1986), 1.3 *Annegialia* (Howden 1971).

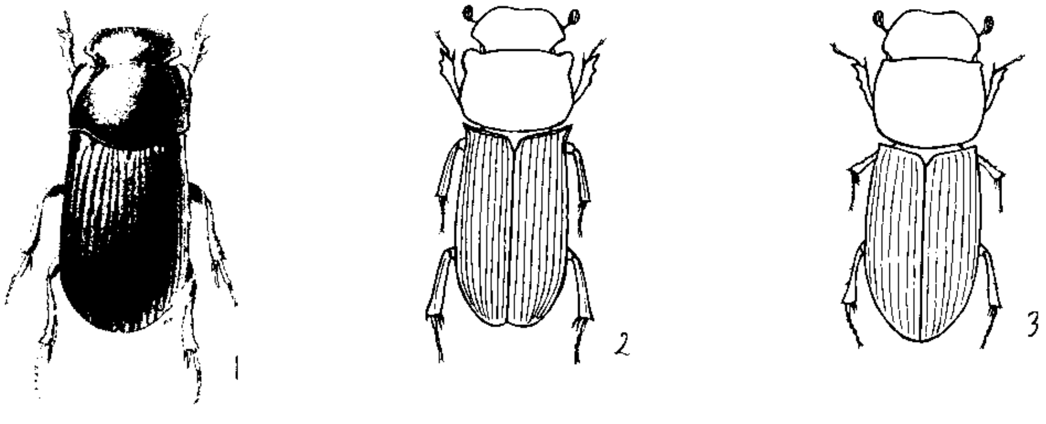


Fig 8.1-3 Representatives of the main types of Eupariini. 1.1 *Euparia* (Chalumeau & Howden 1984), **1.2** *Ataenius*, **1.3** *Saprosites* (both Dellacasa et al 2001).

sensilla band at suspensorium labrale, is suggested by Stebnicka & Howden (1996) as a synapomorphy, but it might be plesiomorphic visavis the more distal location in Aphodiini, Psammodiini and others.

The limits of Eupariini have been debated too, highly derived taxa lifted out now and then, and sometimes also put back. Actually, no unique synapomorphies support the group. But as noted above Eupariini + Psammodiini seems to make a good group.

Even though *Ataenius* and *Saprosites* are more or less cosmopolitan genera, most species are Neotropic, whereas the remaining ones are usually either Australian or Nearctic (fewer Oriental and African, where competition with younger groups probably has been severe). This pattern shows among Eupariini on the whole, and conforms to an old Gondwanan pattern, but since it does not share other characteristics of such patterns (such as rich and distinct species groups in long isolated old Gondwana parts like Madagascar, New Zealand and New Caledonia), the age might not be as old as that pattern indicates.

Fossils are present of *Ataenius* from Eocene (Baltic amber) and Oligocene (USA), and of *Saprosites* from Eocene (England & Baltic) (Krell 2000), thus indicating that these genera have been widespread for a long time.

Different authors do not agree on the degree of coprophagy within Eupariini. Since most specimens generally are taken on light, the habitat and food resources for both larvae and adults are poorly known. Specimens of at least *Ataenius* (and related) and *Notocaulus* are regularly found in dung, and some authors believe coprophagy to be important within Eupariini while others disagree. Another association which has not yet been sufficiently investigated is with ants; while a few species are demonstratedly inquilines in nests of leaf-cutting ants, *Atta* and *Acromyrmex*, a large number of species have been presumed to be either myrmecophilous or termitophilous, because of their relatedness to myrmecophilous taxa or only by odd dorsal sculpturing. Even though ants were present already in the upper Cretaceous (Crowson 1981) the lineage of leaf-cutting ants was not, and to develop their leaf-cutting habits which typically produces the rich inquiline habitats, there will have to be rich angiosperm foliage. Cambefort (1991a) suggests that the primary food-source and habitat for the earliest Aphodiinae (and Scarabaeinae), for which they developed their ”soft-saprophagy” mouthparts, is the fluid nutrient-rich humus under bark and in leaf bases of tropical trees and other plants. But today only a few genera (*Saprosites* and related) are collected in such habitats and not exclusively.

4. Monophyly and relationships of Aegialiini and Aulonocnemini

4a. Aegialiini

Aegialiini was first given suprageneric rank by Laporte de Castelnau (1840) (not Lacordaire, 1856 as some authors cite) but the name did not come into general use since after Reitter (1909). The first modern analysis of the group was conducted by Stebnicka (1977) who split it into two subtribes, Aegialiina and

Eremazina, but included in Aegialiina, even in type genus *Aegialia*, the species of a subfamily proposed by Landin (1949) as Silluviinae, and excluded (without mentioning the fact) Chironini.

Stebnicka (1977) admitted that the characters diagnosing the group generally are plesiomorphic (”primitive”) in the Aphodiinae. She stated though that the group is ”linked to Psammodiini and Eupariini” at the same time. Judging from her tree figure this might imply a sistergroup relationship with either or both of these taxa, but the figure isn’t in cladistic terms and it doesn’t rule out the possibility of a sistergroup relationship with all other Aphodiinae (fig 1.3). Later (1985) she claimed that the Aegialiini were close to Aulonocnemini. Tangelder & Krikken (1982) found the Aegialiini seemingly paraphyletic (”a complex of paraphyletic lineages sprouting from the extreme base of the ’evolutionary tree’ constituted by the remaining Aphodiinae”), citing Stebnicka’s discussion as an indication of this. Cambefort’s hypothesis (Cambefort 1987, Dellacasa 1987) considers only a few characters and guesses – primarily only because of the mouthparts - that Aegialiini is basal within the whole Coprophaga clade and thus the sister group of Aulonocnemini + Scarabaeinae + Aphodiinae + Termitotrogini.

The traditional diagnostic characters only concern the external mouthparts; truncated clypeus and thus partly exposed mandibles and labrum, plus sclerotised mandibles. This is generally considered plesiomorphic, and it does not even represent a unique plesiomorphy, since the same state is found in Aulonocnemini and Chironini. Furthermore, *Annegialia* was recently transferred away from Aegialiini in spite of its mouthparts being of the aegialiine type, since other characters, especially tibial, indicated that it belongs in the Eupariini. The diagnosis of Aegialiini in Stebnicka & Howden (1996) consists of a long list of varying or apparently plesiomorphic characters. Nikolajev (1993) hints at the paraphyly of Aegialiini, citing no synapomorphies to keep the group united, and placing the genus *Micraegialia* as a sister group to Aphodiini (fig 2.5).

But if the character polarity is addressed, the view changes somewhat. Since the sister group of Aphodiinae, Scarabaeinae, possess a wide clypeus covering membranous mouthparts, the exposed mouthparts might well be an apomorphy, a secondary reduction of the clypeus and resclerotisation of mandibles, which in fact are closely interrelated traits resulting from an adaption to ”hard saprophagy”. This might be taken as an indication of the monophyly of Aegialiini, but since the Aegialiini show very different degrees of similiarities with other Aphodiinae, it may also be an independently reached state and Aegialiini thus becoming not paraphyletic but polyphyletic.

Especially disturbing is the fact that while *Annegialia* was moved, primarily because of its Eupariine legs, another Aegialiine genus, *Saprus*, show similar Eupariine legs (tibial spurs narrowly separated, longitudinal ridges) but was not moved in the revision of Stebnicka & Howden (1995), in spite of their acknowledging the similarity and of Cassis & Weir having suggested the possibility in print (1992). *Saprus*, occuring in Australia, are geographically isolated from the other, almost exclusively holarctic, true Aegialiines. Stebnicka & Howden point to the similaritites between *Saprus* and *Leptaegialia* (seemingly not accepting the priority of *Caelius* Lewis, 1895 over *Leptaegialia* Brown, 1931 even though Stebnicka synonymised them herself (1986)), which are striking, and in fact *Leptaegialia/Caelius* have tibial characters intermediate between true Aegialiini on one hand and *Annegialia*, *Saprus* and all Eupariini on the other. Another interesting point is that there is, in Landin’s collection in Lund, a specimen of a typical Psammodiine (similar to *Afrodiastictus* or *Bordatius*) with typical aegialiine-type mouthparts, further indicating either that this trait has originated several times, or that Aegialiini on the whole is part of the Eupariini-Psammodiini complex.

Eremazina was established by Stebnicka (1977) for a genus of heat-adopted Aegialiini with several autapomorphies (smooth elytra without striae, increased number of fore tibia teeth, apically widened tarsal segments) plus narrowly separated tibial spurs (like *Annegialia*, *Saprus* and Eupariini). Even though Eremazina is an evidently monophyletic group, the resulting Aegialiina is not, and the division is not satisfactory.

In Aegialiini there is also a controversy about whether most groups of species should be regarded as subgenera of *Aegialia* or proper genera. In many cases such controversies are more of a practical and aesthetical nature, but in this case the possible paraphyly or even polyphyly of the group provides an argument for splitting the rather large and heterogenous *Aegialia* into its subgroups.

Aegialiini contains the oldest of all fossils of Coprophaga; two species placed in an extinct genus, *Cretaegialia,* from lower Cretaceous in Russia (Nikolajev 1993). A fossil placed in the extant genus *Aegialia* (which however as we've seen may be paraphyletic) was found in USA from Eocene.

The distribution of Aegialiini is almost cosmopolitan but fragmented. Most genera (or subgenera) have a cold-temperate Holarctic distribution (most species in coastal areas of North America, fewer in inland North America, in Europe and East Asia and one single species in South America), while *Eremazus* live within the warm parts of the western and central Palearctic, *Silluvia* in the Himalaya, *Chiron* mostly in continental Africa but also Madagascar and warm-temperate and tropical parts of Asia, *Saprus* in southern Australia. *Saprus* remains far from any other species regardless of whether *Eremazus* and *Chiron* are included or not. Hypotheses on the biogeographic history of the group have to await any evidence for the monophyly of the group to become really meaningful.

4b. Aulonocnemini

Aulonocnemini bears its authorship from Janssens (1946) in his revision of Scarabaeinae, as a subfamily (Aulonocneminae) for a genus in Ateuchini (=Dichotomiini/ Pinotini) showing the - for Scarabaeinae - unique plesiomorphy of having partly exposed mouthparts. Subsequent authors concluded that it might not be part of Scarabaeinae at all, but a distinct, ”primitive” group. Later investigations have suggested the Aulonocnemini to be close to Aegialiini, based on characters in larvae (Paulian & Lumaret 1974), wings (Balthasar 1943), mouthparts and feeding habits (Stebnicka 1985, Cambefort 1987, Nel & Scholtz 1990) and male genitalia (d'Hotman & Scholtz 1990). However, most if not all of these similarities are likely to be plesiomorphic within the Aphodiinae, and therefore do not provide any evidence of close relationship. Thus it's still possible to arrive at different conclusions, such as keeping it a separate subfamily forming a ”missing link” between Aphodiinae and Scarabaeinae (Stebnicka 1985) or even basal to the dichotomy of Aphodiinae and Scarabaeinae (Cambefort 1987, Dellacasa 1987).

Browne & Scholtz (1998) however found no differences in wing characters between Aulonocnemini and the bulk of Aphodiinae. They discarded most arguments for its supposed primitivity or affinity with Aegialiini, and guessed that it might be an ingroup in Eupariini (the same idea had been suggested in passing by Iablokoff-Khnzorian (1977)). However, they still did not formally propose any classificatory change, but cited the subfamily name Aulonocneminae in quotation marks as to indicate the doubts concerning its position.

Actually the similarities with Eupariini are not only in characters assumed to be plesiomorphic (narrowly separated tibial spurs on middle legs, fused abdominal segments, free pygidium, denticulate shoulder), but also in some apomorphic ones shared with only parts of Eupariini (thick and broad mesosternal apophyse, fluting along abdominal segments, flattened frontal pronotal angles) suggesting the Aulonocnemini to be either part of, or very close to, the *Saprosites* complex within Eupariini. Nikolajev (1993) though suggests that Aulonocnemini may make up one group with all the termitophilous tribes, without stating anything to support it.

The reason why these beetles used to be in Scarabaeinae is a clear indication of the monophyly of the group; hind tibial spurs reduced to one, and rather widely separated middle coxae, giving some superficial resemblance to scarabaeines. Other unique apomorphies are the groves in the mesosternum and the tarsal groves in the front tibiae.

In his monograph of the group, Cambefort (1987) actually claims to have performed a phylogenetic analysis (the process is however not specified), and he offers one tree (”dendrogramme”) of the relation of the four genera, and one of the relation of the species in the large genus *Aulonocnemis*. His result is that *Aulonocnemis* does not form a monophyletic group, but the three other genera together do. In his analysis he is able to define several specific species-groups within *Aulonocnemis*, of which most or all seem possible to define by synapomorphies. Unfortunately he does not suggest the necessary nomenclatory changes resulting from his analysis, i e, either to lump all species and make the names of the three other genera junior synonyms of *Aulonocnemis* (and find three replacement names for species with names occurring in both *Aulonocnemis* and *Ankarotrotrox*), or to situate the clade of the other three genera in the tree of *Aulonocnemis* and suggest new generic names for the species-groups that are basal in relation to this clade.

Distribution is limited to warm areas around the indian ocean, namely Madagascar (most species), India, China, eastern and southern Africa and islands in the Indian Ocean. Its presence on oceanic islands indicates a capability of long distance dispersal and makes it probable that Madagascar is an ancestral area of the taxon, from which one stock spread to Asia (genus *Palnia*), and various stragglers reached the African mainland and different islands. This indicates a rather young age of the group and thus may support the idea of it belonging inside Eupariini.

5. The relationships of the termite inquiline tribes

5a. Rhyparini and Stereomerini

Schmidt (1910a) proposed Rhyparini (as Rhyparina) as a tribe for presumedly termitophilous Aphodiines with longitudinal ridges on the pronotum. Howden & Storey (1992) split off Stereomerini as a distinct tribe, but instead included a few other genera from Eupariini and Termitoderini in Rhyparini, and then Bordat & Howden (1995) further refined the delimitations between the tribes.

The resulting Rhyparini was phylogenetically analysed by Howden & Storey (1992), and found to be the sister group of Stereomerini. Characterised by apomorphic features as the six longitudinal carinae on pronotum, head with carinae, laterally lobed pronotum, and the hastate posterior prosternal process with lateral projections over the mesofemoral apex acting as a locking device. Several synapomorphies with Stereomerini are cited to support their sister group relation (termitophilous biology, strongly retracted head and hidden eyes, raised posterior prosternal process, lateral carinae on pronotum and elytra, minute or absent scutellum, reduced teething on protibia and reduced tibial apical spurs), though actually most if not all of these are present in other termitophilous taxa too, and are obvious adaptations for inquiline biology which might be subject to homoplasy.

Rhyparini shows a pantropical distribution. Their occurence on isolated islands like Mauritius and Fiji indicates that they are capable of long-distance dispersal. Howden & Storey (1992) speculated that their age is Cretaceous, although they did not present any evidence to support this.

Stereomerini has a number of clear synapomorphies too: three pronotal carinae concentrated in median third, longitudinal grooves on head, convex body shape, reduced eyes, and wide epipleura. Some characters of Stereomerini are not evident whether apomorphic or plesiomorphic; lanceolate prosternal process, clypeus not dentate, flattened metatibiae. A few good apomorphies are not shared by all Stereomerini like reduced number of tarsomeres, and long segments in the antennal club.

Stereomerini are present in South America, South East Asia and Australia, thus Gondwanan, but the distribution of the group is probably conditioned foremost by the presence of the termite hosts. Age is suggested to be early-middle Tertiary (Howden & Storey, 1992), though without supporting evidence, without acknowledging that it must be as old as its sister group, and with the confusing addition that the included taxa ”may be relicts of a Gondwanian group”.

No one seems to have studied Rhyparines and Stereomerines for characters that would unite them with any aphodiine relatives. Nikolajev (1993) suggests in passing that all the inquiline tribes may make up a group with Aulonocnemini. Tangelder & Krikken (1982) argue that they are very old and not closely related to any other Aphodiines, without suggesting any relationships explicitly. Perhaps a thorough study would show that they are nested within the widespread tropical, highly diverse and rather morphologically plastic, sometimes inquiline, Eupariini. Actually two genera (*Notocaulus* and *Cartwrightia*) have more or less recently been moved from Rhyparini to Eupariini, showing most rhyparine characteristics except for the prosternal apophyse and the reduced tibial spurs. Of course this may be a convergence, as assumed in moving them, but it would be more parsimonous to view them as a transition series. Another possibility is that Rhyparini and Stereomerini are not sister groups, in which case what is said about relations with Eupariini concerns primarily Rhyparini.

5b. Corythoderini and Termitoderini

Corythoderini was proposed by Schmidt (1910a) (as Corythoderina) for termitophilous Aphodiinae without longitudinal dorsal ridges. Tangelder & Krikken (1982) erected Termitoderini from it. Dellacasa (1987) in his catalogue included a number of ”unplaced” termotophilous genera in Termitoderini, but they actually belonged in either Rhyparini or in Ceratocanthidae. Tangelder & Krikken (1982) call

Corythoderini and Termitoderini ”cladistic twins” by which they probably mean sister groups. The relationship of the genera within Corythoderini is investigated by Tangelder & Krikken, who do not perform a phylogenetic analysis, and leave many questions unsolved.

Corythoderini have a number of synapomorphies; very long legs, downward-bent pygidium, somewhat pointed clypeus, distinct pronotal pattern with median sulcus, paramedian protrusions, lateral sulci and lateral lobes. Shared with Termitoderini are the reduced mouth parts, pronotal trichomes and the general outline of the pronotal pattern. The tribe has an African-Oriental distribution, following the distribution of their hosts, *Odontotermes* termites.

Termitoderini are very rarely studied. The single included species is characterised by the synapomorphies of a particular pronotal pattern with diagonal groves from hind corners, plus physogastry, loss of alae and flaplike elytral apex. It has a neotropical distribution. The distribution and the termite host are different from most other termitophilous aphodiines, and the taxon might actually belong anywhere.

Corythoderini and Termitoderini could make good sister groups like Tangelder & Krikken (1982) suggested. But no one seems to have studied them for characters that would unite them with any aphodiine relatives. Such study might perhaps show that either or both could be nested within either a larger termitophilous group or even in the widespread tropical, highly diverse and rather morphologically plastic, sometimes inquiline, Eupariini. Tangelder & Krikken (1982) however argue that they are very old and not closely related to any other Aphodiines. Actually, the same termitophily adaptations are for these authors an indication of relationship between Corythoderini and Termitoderini on one hand, but an indication of parallelism between this group and Rhyparini (and Termitotrogini, and for that matter also other termitophilous scarabs now considered to be Ceratocanthids) on the other.

5c. Termitotrogini

Termitotrogini was erected by Wasmann (1918) (as a tribe within Scarabaeinae) for one of the most highly derived inquiline scarabs. Around the same time Arrow (1920) erected the subfamily Aphodiocoprinae for a very similar genus, the name subsequently becoming a junior synonym. Termitotrogini are rather highly autapomorphous termite guests with few relationship-informative characters retained. Most authors therefore conclude that the group is very old and not closely related to any living groups, while in fact its high specialisation on the contrary might be a product of a rapid evolution, so that the group might be an in-group in any existing larger group. Cambefort’s guess (1987) has Termitotrogini (as a distinct family) as a sister group to Aphodiinae (excluding Aegialiini and Aulanocnemini), while Nikolajev (1993) suggests that it makes a group with the other inquiline genera plus Aulonocnemini.

These animals are very rarely studied. In fact only the widely separated middle coxae make them different from all other Aphodiinae. The lobed pronotal base are shared by all the other termitophilous tribes (and some Aulonocnemini). The *Odontotermes* inquiline biology, the Africa-Oriental distribution connected with their hosts, the divergent arrangement of costae and sulci on the elytra, and the somewhat pointed clypeus is shared with Corythoderini (with most of Corythoderini it also shares symplesiomorphically retained tibial apical spurs). The strong ridges over elytra and pronotum are shared with Rhyparini and some Stereomerini, the general shape of legs including stout curved tibiae and short tarsi are shared with Stereomerini, and the globous body shape and the wide and totally retracted head are shared with some Stereomerini like *Termitaxis*.

Morphology thus suggests that Termitotrogini very well might be nested within either Corythoderini or Stereomerini, or at least closely related to one of them, and its isolated status is not supported.

5d. Historical biogeography of inquilines

Since most apomorphies for these groups are widespread adaptations for inquiline life, it seems likely that these have evolved in the presence of the host and not as pre-adaptations. Then the origin of these groups are conditioned by the origin and dispersal of the termites.

Odontotermes, which is by far the most common host among the known cases, is stated to have evolved during early Tertiary in Africa, reached first India and then Southeast Asia through land connections after the Indian subcontinent collided with the Eurasian continent, in the Miocene (Emerson 1955, Krishna 1970). Of the beetles specialised on these termites, some genera are African, while some are Indian. Being an *Odontotermes* inquiline restricted to India seems to suggest a rather young age, if a host shift isn’t assumed.

Within Corythoderini this perhaps suggests a scenario of co-evolution with hosts in Africa, the Indian genera representing one or a few ingroups. But the suggested sister group relation with the Neotropic Termitoderini would fit better with presuming an older age of the group. Either they represent a relict distribution of a widespread gondwanan inquiline lineage, or the phylogenetic hypothesis is incorrect – Termitoderini might perhaps instead belong to the widespread Stereomerini. If that is the more likely alternative, then the sister group of Corythoderini must be sought elsewhere, either within Stereomerini too, or within Eupariini. If more detailed information on the hosts were available, the phylogeny of the hosts would provide interesting suggestions for the phylogeny of the beetles.

The same young age is therefore suggested for Termitotrogini, with a distribution resembling that of Corythoderini. Since that group shares some characteristics with Stereomerini, it might very well be an ingroup there.

The widespread distribution of Rhyparini and Stereomerini suggests either an older age of origin, or very good dispersal capabilities. That the species are known to be capable flyers, and Rhyparini are found on remote volcanic islands, seems to speak for the latter possibility. On the other hand, the fragmented distribution and rarity of Stereomerini suggests a relict pattern rather than one of recent dispersal. Perhaps this could be seen as another point in favor of disbelieving the sister group relation of Rhyparini and Stereomerini. Then the Stereomerini might be an old (Cretaceous) Gondwanan group, some african stock of which may have co-evolved with *Odontotermes* to form Termitotrogini and possibly Corythoderini, while another stock evolved in the neotropic to form Termitoderini; while Rhyparini – most of which actually never have been proved to really live with termites – might belong to the Eupariini.

6. Monophyly of other small tribes

6a.The splitting of Aphodiini and the controversy over Didactyliini/ Proctophanini

Pittino (1984), in a revision of the aphodiine fauna of Saudi Arabia, split Aphodiini into two subtribes, Aphodiina and Didactyliina, the latter for Aphodiines with the best characteric of the tribe, the two tibial carinae, poorly developed, and having the plesiomorphic state of tibial apical spurs closely together. In his view, the new taxon had an ”intermediate position between tribes Aphodiini and Eupariini”. Since he treated only a regional fauna, the boundaries of the new taxon weren’t clear. In Dellacasa’s catalogue (1987) a number of genera from the world were ascribed to this taxon (as Didactyliini), sharing the plesiomorphic tibial spur arrangement but often having well-developed carinae.

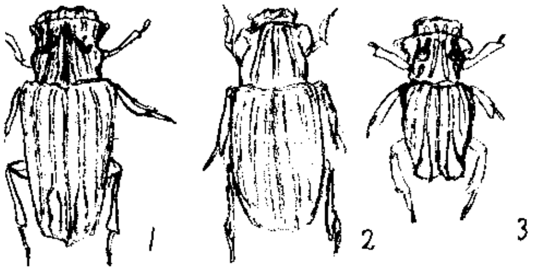
When Stebnicka & Howden (1995) revised the australian Aphodiini, they erected a new tribe, Proctophanini, for those genera sharing well-developed carinae and plesiomorphic spur arrangement, without any mention of fact that the new taxon large coincided with Pittino’s. The new group was ”representing a transitional link between the Aphodiini and the Eupariini” just like Pittino’s. Stebnicka & Howden didn’t treat the world fauna but said that several Afrotropical taxa fitted nicely in their new group along with the Australian ones. Recently Dellacasa et al (2001) synonymised Proctophanini under Didactyliini

However, it seems evident that the Didactyliini *sensu lato* of these authors isn’t a very good group. The only shared character is the plesiomorphic tibial spur arrangement, and the lack of well-developed other Eupariine characters. The Didactyliini *sensu stricto*, not including forms with well-developed tibial carinae, share a similar habitus and are united by the rudimentary carinae. Their epipharynxes seem largely plesiomorphic. This does not settle wether it is a reduction of the carinae or an intermediate stage in a transformation series, and thus not whether the group is actually monophyletic. The distribution is mostly Afrotropical and Neotropical, extending into Palearctic and Nearctic areas.

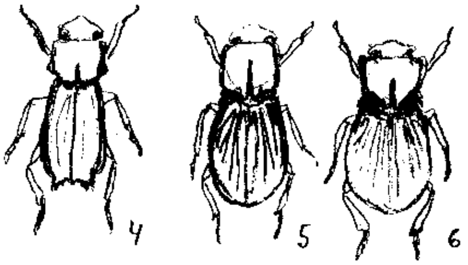
The Proctophanini of Stebnicka & Howden is not clearly delimited, but if the characteristics in the original description are followed, it will have to be extended with a number of genera from the Didactyliini of Dellacasaet al (2001) (namely all genera from couplet 4 onwards in the identification key on pp 59f). These genera share the plesiomorphic tibial spur arrangement, and have the well-developed tibial carinae as a synapomorphy with Aphodiinae. Most of the included taxa are South African, a few Australian (plus one widespread species occuring also in America, and the odd Saudi Arabian genus *Pseudomothon* which might perhaps belong elsewhere, perhaps among the mendidiform Aphodiini, or even the Hybosoridae). Their habituses fall into two categories, resembling either Didactyliini sensu stricto or general Aphodiini. They all (again, except *Pseudomothon*) have similar epipharynxes (with dense chaetopariae mostly in two even rows, well-developed coryphal spiculae etc). Several, but not all, have double elytral striae and more or less cariniform insterstices.

The monophyly of Proctophanini is probable, and if it can be ascertained it will probably turn out to be the sister group of Aphodiini, or perhaps of Aphodiini + core Aegialiini (sharing the apomorphic tibial spur arrangement). The Didactyliini sensu stricto, if monophyletic, might be either

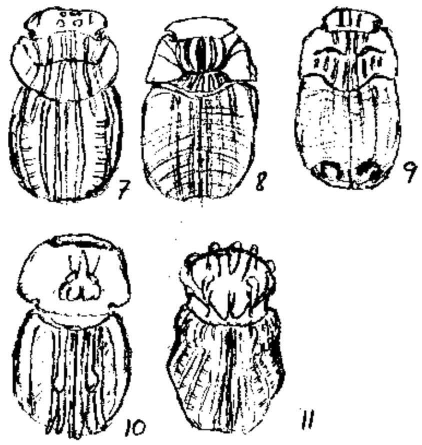
Fig 9.1-11. Representatives of termitophilous taxa and similar. (Redrawn from various sources)



9.1 *Rhyparus* (Rhyparini), **9.2** *Notocaulus* (Euparini), **9.3** *Termitodius* (Rhyparini).



9.4 *Chaetopisthes*, **9.5** *Termitopisthes*, **9.6** *Corythoderus* (all Corythoderini).



9.7 *Danielssonia*, **9.8** *Adebrattia*, **9.9** *Stereomera*, **9.10** *Termitaxis* (all Stereomerini), **9.11** *Termitotrox* (Termitotrogini).

Fig 10. Studies of type specimen of *Termitotrox consobrinus* Reichensperger. 10.1 dorsal aspect, **10.2** lateral aspect, **10.3** pattern of pronotal ridges, **10.4** pattern of elytral ridges, **10.5** frontal aspect, **10.6** ventral aspect, **10.7** fore leg (dorsal aspect), **10.8** middle leg (ventral aspect), **10.9** hind leg (ventral aspect). (orig)

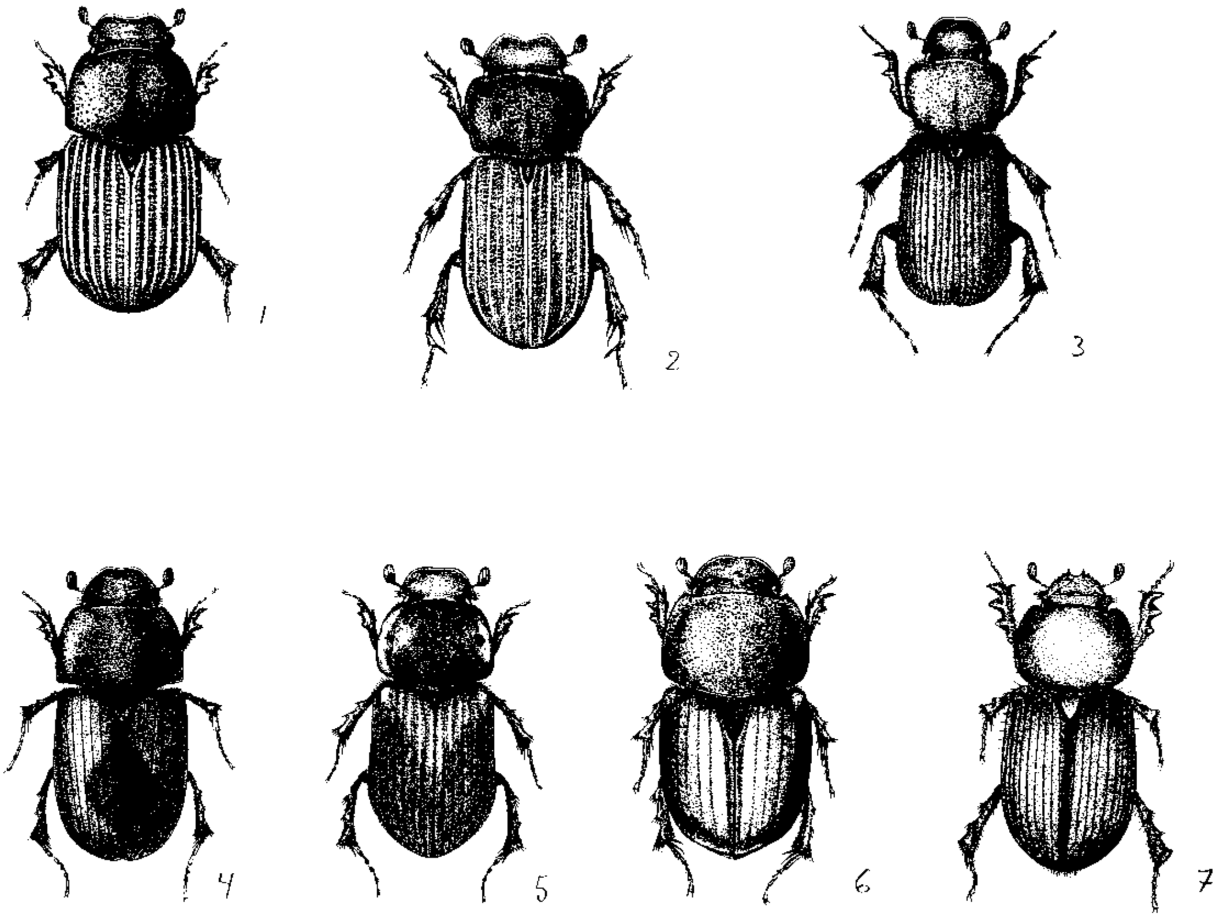


Fig 11.1-7 Representatives of Proctophanini, Didactyliini and Aphodiini. 11.1 *Proctophanes* (Proctophanini), **11.2** *Drepanocanthus* (ascribed to Didactyliini but belonging in Proctophanini). **11.3** *Didactylia* (Didactyliini). **11.4** *Aphodius* (subgenus *Biralus*) (Aphodiini), **11.5** *Aphodius* (subgenus *Melinopterus*) (Aphodiini), **11.6** *Aphodius* (subgenus *Colobopterus*) (Aphodiini), **11.7** *Apsteiniella* (Aphodiini). (Dellacasa et al 2001)

the sister group of Proctophanini + Aphodiini (or Proctophanini + Aphodiini + core Aegialiini), or a branch of reduced Proctophanini, or a branch of specialised Eupariini.

6b. Small tribes derived from Psammodiini and Eupariini: Odochilini, Odontolochini, Lomanoxiini

Rakovic (1984) erected the tribe Odochilini for a genus of peculiar South east Asian Psammodiini. He studied the pronotal structure and did not find that the structure in this genus was derivable from the Psammodiini groundplan, and thus found that the ridging/furrowing in the two groups must have evolved independently. He also noticed other differences, like the Odochilini having a forward-oriented, only moderately convex head, and three apical spurs on hind tibiae, and living in rain forest litter. Actually, there is really no way to be sure that a structure of four transverse furrows is not derivable from a structure of five furrows. Since Odochilini shares most characters with Eupariini and a few with Psammodiini, and these two tribes actually share most characteristics and one is probably a paraphyletic stem group of the other, Odochilini may be a form in a transition series in either direction, or a derived group nested within either.

The tribe Odontolochini, erected by Stebnicka & Howden (1996), consists of a few genera (in sum pantropical) separated from Eupariini, and is characterised as a close relative of Eupariini. Actually it is said to be closely related to Odochilini and some specified Eupariini genera at the same time. In cladistic terms this implies that both Odochilini and Odontolochini would be Eupariini ingroups. Diagnostic characters for Odontolochini: sides of pronotum denticled, clypeus with broad inflexed edge, are minor autapomorphies. The group shares all important characters with Eupariini and evidently ought to have stayed there.

Lomanoxiini was recently erected by Stebnicka (1999) for a genus of myrmecophilous Eupariini from South America. She states that the genus is closely related to other myrmecophilous eupariine genera but different enough because of the structure of the middle coxae. This of course implies that the group is deeply nested within Eupariini and thus not a good group.

6c. Small tribes transferred away from Aphodiinae: Demarziellini and Thinorycterini

For reasons of completeness, there should perhaps be a mention here of the tribal name Demarziellini that Balthasar (1961) erected for a genus of peculiar Australian aphodiines showing all characteristics of Scarabaeinae. Twenty years later it was found that they actually were Scarabaeines and that several species were described in both subfamilies (Matthews & Stebnicka 1986).

Until recently there was also an Aphodiine tribe called Thinorycterini, described by Semenov Tian-Sjanskij and Reichardt (1925) for a small genus of peculiar flightless saprophagous beetles from warm temperate areas of west and central Asia. As such it is included in Dellacasa’s catalogue (1987) and other overviews, but very rarely studied. Recently Nikolajev transferred the tribe into another scarab family, Hybosoridae (= Hybosorinae in his view) (Nikolajev 1993, 1999).

7. Some suggestions as how to proceed in order to reclassify the major tribes

7a. Aphodiini after the recent assault

Dellacasa et al in their recent monograph (2001) examined type specimens of all type species of all supraspecific taxa within the Aphodiini. However they strangely refrained from any discussion of the relationships of the taxa, and arranged them in a completely flat system where all species groups formed genera of their own. These genera were simply listed in alphabetical order. In doing this, they point out the total arbitrariness in distinguishing *Aphodius* subgenera from other Aphodiini genera in traditional classification.

From their careful morphological analysis it is probably possible to identify a number of groupings, which above all may serve a practical purpose for workers facing this big mess, but also possibly represent monophyletic lineages, of which we of course do not know the interrelationships.

Anyway it is of utter importance for aphodiine workers today to recreate a classification that in some way reflects a reasonable hypothesis of aphodiine phylogeny. That is done from two directions, one downwards perspective including trying to find delimitations for a reformed *Aphodius* s lat, one upwards (more important in the long run), revising the subgenera one after another, finding their synapomorphies and affinities with other subgenera. The process must probably include the sinking in rank – at least provisionally until *Aphodius* is more satisfyingly delimited - of several or most traditional genera to *Aphodius* subgenera and thus finding replacement names for specific names present elsewhere in *Aphodius* s lat.

One group that appears as a natural and more or less well-defined group is the ”mendidiform” (or ”pseudopsammodoid”) taxa. All seem to be psammophilous-xerophilous and saprophagous, offering a superficial resemblance to Psammodiines. Many characteristics of the group are commonly associated with psammophilous habits; small size, very convex body, reddish colour, deflexed and granulate-rugose head, strikingly short legs and tarsi, tibiae strongly widened towards apex. Other characters, less common elsewhere, and thus more strongly pointing to the monophyly of the group, is the distinctly dentate (most often multidentate) clypeus, and the long setae of the tarsal joints. Most have a border of setae around the head and pronotum, very short apical tibial spinulae, and a subgroup have setiform claws. The group consists of 10 supraspecific taxa (of which *Apsteiniella*, *Cnemargulus*, *Cnemisus*, *Mothon*, *Sugrames* and *Xeropsamobeus* are usually given generic rank, but not *Mendidius*, *Mendidaphodius*, *Nialosternus* and *Sitiphus*). (This group might at least in part coincide with Harolds proposed Pseudaphodiidae (1867), but the name remains a nomen nudum since he didn’t designate a type genus and the name isn’t derivable from any genus – actually the only character on which the group was based was the extremely short apical tibial spinulae.) All (except for two Nearctic genera) have a total or core distribution in the Central (or West) Asian deserts and steppes. It is interesting to note that Psammodiini have remarkably few species in that area, but more species in the Mediterranean and East Asia, thus suggesting that the presumedly younger mendidiforms have speciated and offered the Psammodiines hard competition in Central Asia though not having been able to spread well. They seem rather close to the Nearctic-East Palearctic species placed in subgenera like *Tetraclipeoides*, *Cinacanthus, Stenotothorax* and *Coelotrachelus*.

Another acceptable group consists of the taxa sharing a large scutellum, that is the genus *Colobopterus* of Endrödi and Landin. A few taxa might be problematic whether to include or not, but the group is homogenous in habitus, coprophagous habits, and in having a large scutellum. Most but not all taxa share important epipharyngeal characters like strongly protruding corypha and/or jagged anterior margin. This group is almost cosmopolitan, but most of the 18 subgenera (genera with Dellacasa et al) are either Afrotropical or Palearctic, only a well-defined subgroup of two subgenera are American (along with some widespread species presumably of Palearctic origin), and the Oriental species are in most cases probably of either Palearctic or Afrotropical origin. Of these only *Macroretrus* are usually considered a genus and not a subgenus of either *Aphodius* or *Colobopterus*. Still, similarities with Palearctic *Aphodius* s str on one hand, and with the Afrotropical *Exaphodius* groups (genus *Exaphodius* and *Aphodius* subgenera *Craterocyphus* and *Hemicyclium*) on the other, makes the placement of this lineage still unclear.

Apart from these two groups no higher groupings are really obvious. The rest of the genera and subgenera makes a very big set, with no evident unique synapomorphies regardless of whether the traditional proper genera of *Sybax*, *Heptaulacus, Oxyomus, Lorditomaeus* and others are included or excluded. The characters usually thought to provide most phylogenetic information (pronotal base bordered or not, scutellum triangular or pentagonal, elytral interstices cariniform or not, tibial apical spinules long and unequal or short and equal, elytral striae united at apex or not, frontal suture with tubercles or not, genae protruding before eyes or not, length of tarsi and especially first hind tarsal joint) are combined in almost every possible way within the group, and often differ between evidently close taxa; thus proving most characters to be homoplastic.

7b. Eupariini/Psammodiini

Eupariini would best be lumped with Psammodiini, and with several of the small tribes (Odochilini, Odontolochini, Lomanoxiini – if with any or all of Rhyparini, Stereomerini, Corythoderini, Termitoderini, Termitotrogini too remains to be investigated). In such a large and diverse group a subdivision will be needed. It must be noted that the oldest available name for this grouping is Mulsants ”Psammodaires”, making Psammodiini the valid name of the group. Even if Eupariini is not lumped together with Psammodiini it will be necessary to subdivide in order to create monophyletic groups inside the most probably not monophyletic Eupariini.

The subdivision may possibly take its starting point in considering the former three large main genera of the tribe: *Euparia*, *Ataenius* and *Saprosites*.

The fact that a large part of former *Euparia* probably forms a monophyletic group was noted in passing by Howden & Storey (1992), and most of the former *Euparia* or *Euparia*-like genera may eventually prove to belong to this lineage. It would probably include Lomanoxiini and Odontolochini, and might consist of around 20 genera, with a distinct Neotropical overweight, several Nearctic, Oriental and Australian taxa and remarkably few Afrotropical and Palearctic. *Annegialia*, described in Aegialiini and moved to Eupariini, belongs here, and Howden & Storey suggest that more aegialiines may possibly do so too (however Nikolajev (1993) believed *Annegialias* exposed mouthparts to be plesiomorphic and suggested that it makes the sister group of Eupariini + Psammodiini). Here we also find the presumedly termitophilous genera moved from Rhyparini, which are similar to Rhyparines in most respects except for some plesiomorphies, suggesting that Rhyparini (+ Stereomerini, and possibly Termitotrogini) may make an ingroup within Eupariini. Morphologically they are characterised by laterally flattened pronotum and strongly dilatated and curved tibiae. Ecologically a great number are stated to be ant (and termite) inquilines, though the habits of most species are very insufficiently known.

The forms resembling *Ataenius* make a group of around 15 genera, being cosmopolitan but sharing the general geographical pattern of the *Euparia*-group; Neotropical dominance, several Nearctic and Australian taxa but fewer Oriental, few Afrotropic, very few Palearctic. They have a subcylindrical body and an excavate mesosternum, more or less capable of ”rolling up”, flattened hind tibiae, and seem to be rather broad saprophages - the extent to which they are coprophagous has been debated, and the habits of most species are poorly known.

The forms resembling *Saprosites* finally, make a group of less than 10 genera. Like the former they are predominantly Neotropic, with a substantial number of species being Oriental, a few Australian, and very few Palearctic; but in contrast there is a larger number of Afrotropical species and very few Nearctic. Here might belong some aegialiine genera (which would strengthen its representation in the Nearctic and Palearctic) and the Aulonocnemini (which would substantially strengthen its representation in the Afrotropical region). Actually Dellacasaet al (2001) in a footnote state that *Saprosites* might perhaps belong to the Didactyliini, a classification for which no supporting synapomorphies are stated nor easy to find. They share a cylindrical or flattened body shape, a very broad head, and a very strong, unevenly surfaced, flatly protruding mesosternum making the mesocoxae widely separated. The flat body shape is apparently an adaptation to living under bark, where specimens are sometimes collected and many other flattened saprophages occur, but the habits of most species are insufficiently known.

If the pronotal pattern of the most Eupariine-like forms of Psammodiini (i e *Pleurophorus, Platytomus* etc) is vestigial, then Psammodiini becomes the paraphyletic stem group of a possibly monophyletic Eupariini within it. We then would have to find the monophyletic subgroups of Psammodiini (present Psammodiina including Phycocina being one, present Odochilini probably being one, but a few new having to be erected for the other genera, where probably both Mariano’s & Pittino’s name Rhyssemina and Mulsant’s Pleurophorina would come to use). If on the other hand the pronotal pattern is considered the first step in a transition series terminating in the full psammodiine structure, then the Eupariini is the paraphyletic stem group of Psammodiini, and the simplest provisional classification would be four subtribes: Eupariina, Ataeniina, Saprositina and Psammodiina.

8. Summary

A cladistic perspective thus has some immediate implications for the classification of Aphodiinae (tab 3). First of all, it places Aegialiini and Aulonocnemini (and provisionally Chironini) inside Aphodiinae. It shows Eupariini or Psammodiini or both to be likely to be paraphyletic, and suggests the necessity of merging them. Aegialiini seems paraphyletic too. It invalidates the subtribal subdivision of Psammodiini, and the synonymisation of Proctophanini under Didactyliini, as well as the erection of Lomanoxiini, and strongly questions the validity of the separate status of Odochilini, Odontolochini and Aulonocnemini. The four latter-mentioned taxa might best be transferred into Eupariini (or Psammodiini including Eupariini), along with some taxa of Aegialiini, and possibly some or all termitophilous tribes. The cladistic perspective also invalidates the traditional classification of genera and *Aphodius* subgenera within Aphodiini, but since the erection of a natural classification of Aphodiini requires a vast and time-consuming amount of work and discussion among researchers, the question of an interim classification is perhaps above all a pragmatic, aesthetic and research-strategic question – how do we best offer overview and facilitate the selection of relevant study objects without creating or maintaining mere illusions of knowledge.

A HYPOTHESIS OF APHODIINE PHYLOGENY AND BIOGEOGRAPHICAL HISTORY

Introduction

In order to perform a first test of the suggestions reached in the phylogenetic discussion of proposed suprageneric taxa within Aphodiinae, a preliminary phylogenetic analysis has been performed with a selection of species representing a diversity as wide as possible within Aphodiinae. Characters were coded from stereo microscope observation of specimens in the authors collection or borrowed from NRM, ZML, UUZM (with a few exceptions coded from descriptions in literature: *Annegialia* (coded from Howden 1971), *Saprus* (coded from Stebnicka & Howden 1996)).

Character matrix

Characters

Multistate characters are ordered.

HEAD

1. Clypeus length	0-long (covering mouthparts), 1-shortened (exposing mouthparts)
2. Mandibles sclerotisation	0-soft, 1-hard
3. Protrusion of genae	0-not protruding before eyes, 1-protruding, 2-strongly protruding
4. Orientation of head	0- forwardoriented, 1-downwardoriented, 2-backwardbent ventrally
5. Canthus	0-present, 1-absent (frontal border of eye uninterruptedly curved)
6. Tubercles on clypeofrontal suture	0-absent (suture smooth or groove-like), 1-present
7. Texture of head	0-punctate, 1-granulate

PRONOTUM & SCUTELLUM

8. Pronotal lateral fovea	0-present, 1-absent
9. Pronotal median sulcus	0-present, 1-absent
10. Pronotal transversal grooves	0-absent, 1-present
11. Pronotal longitudinal costae	0-absent, 1-present
12. Length of scutellum	0-short (less than 1/6 of elytra) 1-long
13. Shape of scutellum	0- triangular (sides straightly convergent or evenly rounded),

	1-subpentagonal (basally convergent at distinctly less steep angle than apically) , 2-pentagonal (paralell or divergent basally)
14. Bordering of pronotal base	0-present, 1-absent
15. Lobes of pronotal base	0-absent, 1-present
16. Flattening of pronotal sides	0-absent, 1-present

ELYTRA & PYGIDIUM

17. Truncation of elytra	0- not truncate (covering pygidium) 1-truncate (exposing pygidium)
18. Humeral denticle	0-absent, 1-present
19. Elytral longitudinal costae	0-absent, 1-present
20. Bordering of elytral base	0-absent, 1-present
21. Transversal pygidial sulcus	0-absent, 1-present

LEGS

(all leg characters concern middle and hind legs if not otherwise stated)

22. Tibial longitudinal carinae	0-absent, 1-present
23. Tibial apical spinulae	0- uneven & long, 1-even & short
24. Tibial transversal carinae	0-absent, 1-poorly developed, 2-strongly developed
25. Number of tibial apical spurs	0-two , 1-one, 2-none
26. Length of legs	0-short, 1-notably long
27. Femoral sulcus	0-absent, 1-present
28. Shape of tibial distal edge	0-largely even, 1-crenate
29. Placement of middle tibial apical spurs	0-narrowly separated, 1-widely separated
30. Placement of hind tibial apical spurs	0-narrowly separated, 1-widely separated

VENTRAL ASPECT

31. Prosternal apophyse	0-absent, 1-projecting backwards between fore coxae
32. Sternites	0- movable, 1-fused
33. Longitudinal carinae of sternites (”fluting”)	0-absent, 1-present
34. Mesosternal appophyse	0-absent, 1-projecting forwards between middle coxae, 2-strongly developed

GENERAL & ADDITIONAL

35. Dorsal side setae	0- sparse, 1-rich
36. Middle coxae	0- broadly separate, 1-narrowly separate

37. Trichomes	0-absent, 1-present
38. General body outline	0-more or less oval (or elongate), 1- round
39. General body shape	0- convex (or flattened), 1- cylindrical
40. Colour	0- dark (or light due to poor sclerotisation), 1-light pigmentation

Taxa

The selection of exemplar taxa contains:

10 taxa representing as wide diversity as possible within Aphodiini; 4 of which are generally considered genera (*Lorditomaeus*, *Heptaulacus*, *Macroretrus* and *Sybax*) and 6 subgenera of *Aphodius* (*Aphodius* s str, *Mendidius*, *Teuchestes*, *Colobopterus*, *Melinopterus* and *Acrossus*).

As many different genera/subgenera within Aegialiini as possible, which turned out 8 taxa: only *Eremazus* usually considered genus, 4 usually considered subgenera within *Aegialia* (*Aegialia* s str, *Psammoporus*, *Silluvia*, *Saprus*), while *Caelius* and *Leptaegialia* are usually considered parts of the same subgenus *Caelius*; and the eighth is an undescribed taxon represented by an odd specimen from South Africa in Landin's collection in Lund mentioned in the previous section ("Aegialiin X").

One representative each of Didactyliini s str (*Didactylia*), Proctophanini (*Proctophanes*) and of genera ascribed to Didactyliini though belonging in Proctophanini (*Drepanocanthus*).

One representative each of Chironini (*Chiron*) and Aulonocnemini (*Aulonocnemis*).

Major genera of Eupariini, 4 taxa (*Euparia*, *Airapus*, *Ataenius*, *Saprosites*) plus 2 taxa recently transferred to Eupariini from other tribes (*Notocaulus*, *Annegialia*). More would have been desirable but were difficult to obtain correctly identified specimens (or detailed enough descriptions) of.

A selection of Psammodiini, 4 taxa (*Psammodius*, *Rhyssemus*, *Diastictus*, *Pleurophorus*) representing most of the range of variation but unfortunately not including *Phycocus*, base for a separate subtribe, of which the author wasn't able to obtain neither specimens nor detailed enough descriptions.

One representative each of small tribes recently erected out of Eupariini and Psammodiini: Odontolochini (*Odontolochus*), Odochilini (*Odochilus*), Lomanoxiini (*Lomanoxia*).

As wide diversity as could be obtained within inquiline tribes, which turned out to be only 5 taxa, of which two Rhyparini (*Rhyparus*, *Termitodius*), two Corythoderini (*Corythoderus*, *Termitopisthes*) and one Termitotrogini (*Termitotrox*); unfortunately neither Stereomerini nor Termitoderini.

As outgroup functioned three taxa from Scarabaeinae which were readily at hand (*Scarabaeus*, *Copris*, *Onthophagus*), unfortunately not representing supposedly basal, plesiomorphic lineages therein, but hopingly representing a wide enough selection of the subfamily to "neutralise" apomorphies and set the character polarity right.

Matrix

tab 2

Aphodiinaematris 1		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40
1	Sca: Scarabaeus	0	0	2	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	1	1	1	0	0	0	0	1	0	1	0	0	0	0	0	0
2	Sca: Copris	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	1	1	0	1	0	0	0	0	1	0	1	0	0	0	0	0	0
3	Sca: Onthophagus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	1	0	1	1	0	0	0	1	0	1	0	0	0	0	0	0
4	Aul: Aulonocnemis	1	1	0	1	0	0	0	0	1	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	1	1	2	1	0	0	0	0	0
5	Aeg: Aegialia	1	1	0	0	0	0	1	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	2	0	0	1	1	1	1	0	1	0	0	0	1	0	1	0	0
6	Aeg: Psammoporus	1	1	0	0	0	0	0	0	1	0	0	0	0	0	0	1	1	1	0	0	0	0	0	2	0	0	1	1	1	1	0	1	0	0	0	1	0	0	0	0
7	Aeg: Caelius	1	1	0	0	1	0	0	0	0	1	0	0	1	0	0	0	0	1	0	?	0	0	0	?	0	0	?	1	?	?	0	1	0	0	0	1	0	0	1	1
8	Aeg: Leptaegialia	1	1	0	0	0	0	1	0	1	0	0	0	1	0	0	0	0	1	0	0	0	0	0	1	0	0	0	1	0	1	0	1	0	0	0	1	0	0	0	0
9	Aeg: Saprus	1	1	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	1	0	1	0	0	0	?	0	0	0	1	0	0	0	1	1	0	0	1	0	0	0	0
10	Aeg: Silluvia	1	1	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	1	0	1	0	1	0	0	0	1	0	0	0	0
11	Aeg: Eremazus	1	1	0	0	1	0	0	1	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	1	0	0	0	?	0	0	0	1	0	0	0	0
12	Chi: Chiron	1	1	0	0	0	0	0	1	1	0	0	0	1	1	0	0	0	0	0	0	0	0	0	2	0	0	0	1	0	1	0	0	0	0	0	1	0	0	2	0
13	Rhy: Termitodius	0	0	2	1	0	0	0	0	0	0	1	0	0	0	0	1	0	0	1	1	0	1	0	0	2	0	0	0	0	0	1	0	0	0	0	1	1	0	1	0
14	Cor: Termitopisthe	0	0	2	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	2	1	0	0	0	0	0	1	0	0	1	1	1	0	0	0
15	Trr: Termitotrox	0	0	2	2	0	0	0	0	0	0	1	0	0	0	1	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	1	0	0
16	Rhy: Rhyparus	0	0	2	1	0	0	0	0	1	0	1	0	0	0	0	1	0	0	1	1	0	1	0	0	2	0	0	0	0	0	1	0	0	0	0	1	1	0	1	0
17	Odc: Odochilus	0	0	2	1	0	0	0	0	1	1	0	0	2	0	0	1	0	1	1	1	1	1	0	0	0	0	1	1	0	0	0	1	0	0	0	1	0	0	0	0
18	Psa: Psammodius	0	0	1	1	1	0	1	0	0	1	0	0	0	0	0	1	0	0	0	1	1	1	0	0	0	0	1	1	0	0	0	1	0	0	0	1	0	0	0	0
19	Psa: Rhyssemus	0	0	1	1	1	0	1	0	0	1	0	0	0	0	0	1	0	1	0	1	1	1	0	0	0	0	1	1	0	0	0	1	0	0	0	1	0	0	1	0
20	Odl: Odontolochus	0	0	1	1	0	0	0	0	1	0	0	0	0	1	0	1	0	0	1	1	1	1	0	0	0	0	1	1	0	0	0	1	1	1	0	1	0	0	1	0
21	Lom: Lomanoxia	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	1	0	1	0	1	1	1	0	0	0	0	1	1	0	0	0	1	1	0	0	1	0	0	1	0
22	Eup: Notocaulus	0	0	0	1	1	0	0	0	1	0	1	0	0	1	0	1	0	0	1	1	0	0	0	1	0	0	?	0	0	1	0	1	?	?	0	1	0	0	1	0
23	Eup: Euparia	0	0	1	1	1	0	0	1	1	0	0	0	0	1	0	1	0	0	0	1	1	1	0	0	0	0	0	1	0	0	0	1	0	1	1	1	0	0	0	0
24	Eup: Ataenius	0	0	1	1	1	0	0	0	1	0	0	0	1	0	0	0	0	1	0	1	1	1	0	0	0	0	1	1	0	0	0	1	1	0	0	1	0	0	1	0
25	Eup: Saprosites	0	0	1	1	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	1	1	1	2	0	1	0	0	1	0
26	Aph: Mendidius	0	0	1	1	1	0	1	1	1	0	0	0	0	0	0	0	1	0	0	0	0	0	1	2	0	0	1	0	1	1	0	0	0	0	0	1	0	0	0	0
27	Aph: Sybax	0	0	1	1	0	0	0	0	0	0	1	0	1	0	0	1	1	1	1	0	0	0	0	1	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	1
28	Aph: Heptaulacus	0	0	1	0	0	0	0	1	1	0	0	0	1	1	0	0	1	0	1	0	0	0	0	2	0	1	0	0	1	1	0	0	0	1	1	1	0	0	0	1
29	Aph: Colobopterus	0	0	0	0	0	1	0	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	1	1	0	0	0	1	0	1	0	0	0	0
30	Aph: Teuchestes	0	0	1	0	0	1	0	1	1	0	0	1	1	0	0	0	1	0	0	0	0	0	1	2	0	0	0	0	1	1	0	0	0	1	0	1	0	0	2	0
31	Aph: Aphodius	0	0	1	0	0	1	0	1	1	0	0	0	0	0	0	0	1	0	0	0	0	0	1	2	0	0	0	0	1	1	0	0	0	1	0	1	0	0	0	0
32	Aph: Melinopterus	0	0	2	0	0	1	0	1	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	2	0	1	0	0	1	1	0	0	0	1	1	1	0	0	0	1
33	Did: Didactylia	0	0	2	0	0	0	0	1	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	1	0	0	0	1	0	0	0	1
34	Did: Drepanocanthu	0	0	1	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	1	0	1	0	1	0	0	1	0
35	Aph: Lorditomaeus	0	0	1	0	0	0	0	1	1	0	0	0	0	1	0	0	1	0	0	0	0	0	0	2	0	1	0	0	1	1	0	0	0	0	1	1	0	0	0	1
36	Aph: Acrossus	0	0	2	0	0	0	0	1	1	0	0	0	0	1	0	0	1	0	0	0	0	0	0	2	0	1	0	0	1	1	0	0	0	1	0	1	0	0	0	0
37	Aph: Macroretrus	0	0	0	0	0	0	0	1	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	1	0	0	1	1	0	0	0	1	0	1	0	0	0	0
38	Psa: Pleurophorus	0	0	0	1	1	0	1	0	0	1	0	0	0	0	0	1	0	1	0	1	1	1	0	0	0	0	1	1	0	0	0	1	1	0	0	1	0	0	2	0
39	Aegialiin X	1	1	0	0	0	0	0	0	0	1	0	0	0	1	0	1	1	0	1	0	0	0	0	0	0	0	?	1	0	0	0	?	?	?	1	1	0	0	0	0
40	Eup: Airapus	0	0	1	1	1	0	0	0	1	0	0	0	0	0	0	1	0	1	0	1	1	1	0	0	0	0	1	1	0	0	1	1	1	1	0	0	0	0	0	0
41	Eup: Annegialia	1	1	0	1	1	0	1	0	0	1	0	0	0	0	0	0	1	0	1	1	1	1	0	0	0	0	?	1	0	0	0	1	1	0	0	1	0	0	0	0
42	Pro: Proctophanes	0	0	1	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	2	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0
43	Psa: Diastictus	0	0	1	1	1	0	1	0	0	0	0	0	0	0	0	1	0	0	0	1	1	1	0	0	0	0	0	1	0	0	0	1	0	0	0	1	0	0	0	0
44	Cor: Corythoderus	0	0	2	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	1	1	0	0	0

Tab 2. Character matrix in phylogenetic analysis of 41 aphodiine taxa utilising a set of 40 morphological characters.

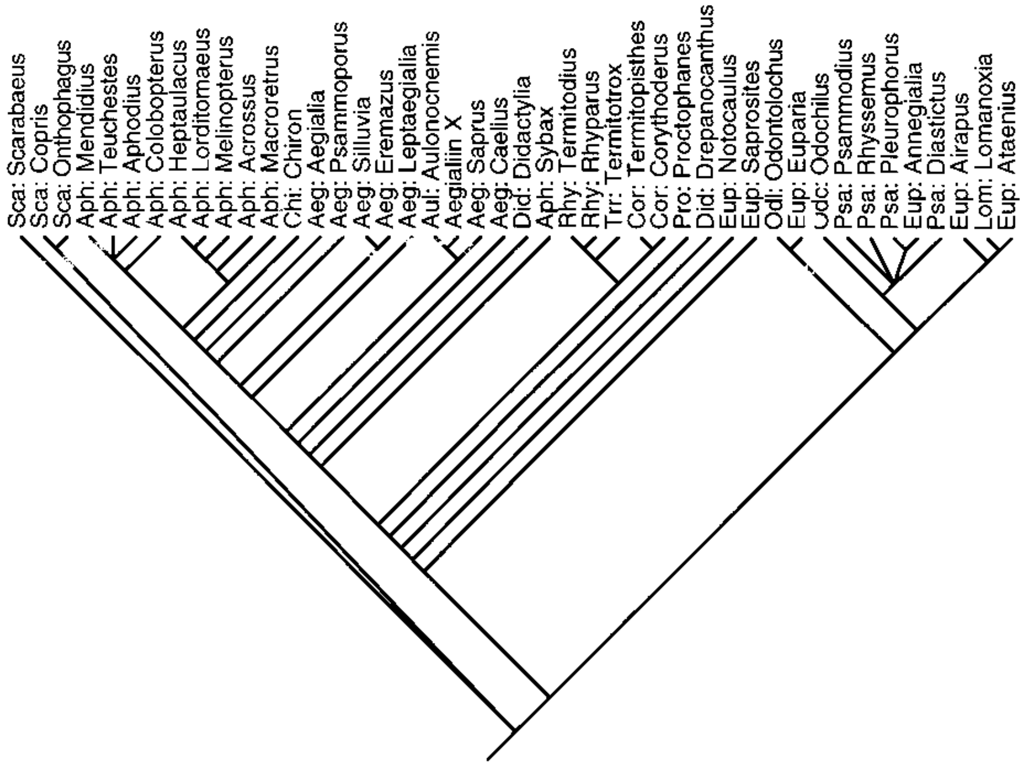


Fig 12. Consensus tree of 15 shortest trees in phylogenetic analysis of Aphodiinae.

Tab 3. Fate of taxonomic groups in the present review and analysis

Taxa	Consideration in present review	Fate in present phylogenetic analysis
Aphodiinae	Monophyletic	No problems in being treated as monophyletic
Aegialiini	Paraphyletic, polyphyletic or monophyletic	Paraphyletic, forming ”grade” at base of Aphodiini
Aegialiina	Paraphyletic or polyphyletic	Paraphyletic, forming ”grade” at base of Aphodiini
Eremazina	Monophyletic but closely related to other Aegialiini	Nested within Aegialiina ”grade”
Aphodiini	Monophyletic	Monophyletic (if *Sybax* is excluded)
Aulonocnemini	Monophyletic but probably nested within Eupariini	Nested within Aegialiini ”grade”
?Chironini	Monophyletic, possibly part of Aegialiini complex (or outside Aphodiinae)	Sister group to Aphodiini at the ”upper end” of Aegialiini ”grade”
Corythoderini	Monophyletic but closely related to other inquiline tribes and possibly Eupariini	Monophyletic but closely related to other inquiline tribes
Didactyliini	Monophyletic or paraphyletic	Sister group to Aphodiini + Aegialiine ”grade” (if appropriately delimited)
Eupariini	Paraphyletic, probably basal lineages of Eupariini-Psammodiini complex	Paraphyletic, a large number of basal lineages of Aphodiinae on the whole
Lomanoxiini	Monophyletic but nested within Eupariini	Closely related to other Eupariini taxa
Odochilini	Monophyletic but nested within Psammodiini	Sister group of Psammodiini
Odontochilini	Monophyletic but nested within Eupariini	Closely related to other Eupariini taxa
Proctophanini	Monophyletic (if appropriately delimited)	Paraphyletic (if appropriately delimited) at the base of the whole non-Eupariini-Psammodiini part of tree
Psammodiini	Monophyletic (or paraphyletic) part of Eupariini-Psammodiini complex	Monophyletic (if *Annegialia* is included) part of Eupariini-Psammodiini complex
Phycocina	Monophyletic but nested within Psammodiina	(not included in analysis)
Psammodiina	Monophyletic	(not resolved)
Rhyssemina	Paraphyletic, probably basal lineages of Psammodiini	(not resolved)
Rhyparini	Monophyletic but closely related to other inquiline tribes and Eupariini	Monophyletic but closely related to other inquiline tribes
Stereomerini	Monophyletic but closely related to other inquiline tribes and possibly Eupariini	(not included)
Termitoderini	Monophyletic but closely related to other inquiline tribes and possibly Eupariini	(not included)
Termitotrogini	Monophyletic but closely related to other inquiline tribes and possibly Eupariini	Closely related to other inquiline tribes

Results

The analysis

In a PAUP version 4.0b10 run performing a heuristic search (TBR) with 25 random addition sequence replicates, a set of 15 shortest trees with treelength=190 was obtained. The consensus tree obtained from the 15 equally shortest trees shows a great degree of resolution and contains only 3 polytomies in the ingroup. The weakness of the tree and the high degree of homoplasy is shown by the low consistency (CI=0,25, RI=0,65) and the fact that no single character is distributed as a unique synapomorphy. Actually, several searches had to be aborted since the computer ran out of memory while saving the apparently inexhaustible numbers of trees with tree-length=191, only one step longer than the shortest tree. For that reason it was not considered meaningful to subject the data to a bootstrap analysis.

Tree description

In the consensus tree obtained (fig 12), Aphodiinae is divided in two major branches, one containing the larger part of the Eupariini-Psammodiini-complex, and the other containing Aphodiini and several minor tribes.

In the Aphodiini branch the first off-shoots are successively two Eupariini genera and two Proctophanini genera (neither grouping together). The next division is between the termite inquilines (forming one group) and the rest. Further up the Aphodiini branch comes successively Aphodiini genus *Sybax* (a remarkably isolated position), Didactyliini and then a long series of branches with various taxa from Aegialiini (including Aulonocnemini and the mysterious psammodiine-aegialiine together making a group with *Saprus*). Uppermost in this ”grade” we have Chironini, thus making the sister-group of Aphodiini. The Aphodiini taxa traditionally considered proper genera are, as suspected, intermixed with the ones considered subgenera, genus *Heptaulacus* for example coupling with subgenus *Melinopterus*.

The Eupariini-Psammodiini branch consists of three groups. One group uniting *Euparia* with Odontolochini forms the sister-group of the others. *Ataenius* grouping with Lomanoxiini and the *Euparia*-like eupariine genus *Airapus* forms the sister group of a clade divided into Odochilini and Psammodiini, the latter also including *Annegialia* but with no resolution.

Fate of taxonomic groups in the analysis

Only two of the Aphodiinae tribes with more than one representative in the analysis turned out entirely monophyletic, the homogenous inquiline tribes Rhyparini and Corythoderini. Tribes with only one representative (the monophyly of which was thus not tested) were Chironini, Aulonocnemini, Didactyliini s str, Odontolochini, Odochilini, Lomanoxiini. But the major tribe Aphodiini, which the selection of taxa renders polyphyletic, will easily become monophyletic if *Sybax* is excluded. As expected, genus *Aphodius* shows to be polyphyletic and will have to include several other Aphodiini genera to become monophyletic.

Proctophanini turns out paraphyletic, and a Didactyliini s lat which includes it is polyphyletic.

Psammodiini turns out paraphyletic, but will easily become monophyletic if *Annegialia* is included. But there is no resolution within this clade.

Eupariini turns out to be the severely paraphyletic-polyphyletic basal group of the whole Aphodiinae. Actually the six included Eupariini genera made no single pair. *Euparia* paired with *Odontolochus*, presently considered a separate tribe. *Annegialia* appeared, as we´ve seen, nested within Psammodiini. *Ataenius* and *Airapus* grouped with *Lomanoxia*, presently considered a distinct tribe. *Notocaulus* and *Saprosites* stayed separate. Of the informal groups based the three main genera only the *Euparia*-group contained more than one taxon in the analysis and was thus tested; it did not keep together at all. Thus in order to make monophyletic groups, Eupariini (at least the representatives included here) would have to make four groups, and *Lomanoxia* and *Odontolochus* would have to be included in these.

Aegialiini turns out a paraphyletic grade at the base of Chironini+Aphodiini, including Aulonocnemini.

Discussion

General unrelialibility and lines to proceed

Since several steps in the analysis were carried out in a suboptimal way and the resulting tree is weakly supported, it would be premature to launch any taxonomic changes, moving of genera and nomenclatoral acts based upon it alone. Several stages in this process have not been thorough enough to make it a proper and reliable phylogenetic analysis, and thus the result should best be regarded as a working hypothesis.

The selection of exemplar taxa in this analysis seems relevant in order to represent the width of Aphodiinae (and has actually been changed several times during the process); however, in a future analysis it may not be necessary to include several taxa from the reliably monophyletic Aphodiini, or all stages in the Aegialiini ”grade”. Instead it would be more interesting to include more genera of Eupariini, and if possible also *Stereomera*, *Termitaxis* and *Termitoderus,* to solve the relationships of the termitophiles. In a future analysis it may also be desirable to include *Phycocus* to ascertain its status as a Psammodiina ingroup, and perhaps also some aberrant genera such as *Oxycorythus* and *Pseudomothon* to find whether they’re closely related to any aphodiine at all. In a future analysis the characters ought to be coded from SEM pictures and have the character states illustrated, in order to facilitate direct comparison, counter-checking and a more objective scoring of character states. The character set, though having been changed during the process too, is not optimal; the traditionally used characters emphasizing the isolated position of the inquiline taxa, ought to be complemented by finding character suites that are more readily available for actual comparison between all the included taxa. The mouth parts and genitals may, as many contemporary workers claim, offer such character suites. There are also more characters to be found in the shape and orientation of the middle coxae and mesosternum.

Comparison with cladistic discussion

In spite of its limited reliability the analysis does give some additional support to several ideas proposed in the taxonomical overview section. That is:

1) the polyphyly-paraphyly of Eupariini and the belonging of Odochilini, Odontolochini, Lomanoxiini and Psammodiini inside this complex,
2) the belonging of Aegialiini, Chironini, Aulonocnemini and Termitotrogini safely within Aphodiinae,
3) the interrelatedness of the inquiline tribes, and
4) the paraphyly of Aegialiini.

On the other hand, it shows nothing to support several other ideas put forth there, such as:

1) The belonging of Aulonocnemini, one or more Aegialiini genera (*Saprus* etc), and one or more inquiline tribes within the Eupariini complex. In the analysis, *Saprus*, *Caelius*, *Leptaegialia* and Aulonocnemini all appear as parts of the Aegialiini ”grade”.
2) The monophyly of the Eupariini complex (that is Eupariini+Psammodiini+at least some small tribes). In the analysis, Eupariini appears as a paraphyletic stem group of Aphodiinae on the whole, with some genera appearing closer to the Aphodiini and other tribes than to other Eupariini + Psammodiini.
3) Monophyly of Aphodiini + Proctophanini. On the contrary, in the analysis Proctophanini not only turns out paraphyletic but are also to be find further down in the tree topology, the sister group of Aphodiini being Chironini.
4) The usefulness of Eupariini subgroups based on the older, traditionally large genera. As already noted, only the *Euparia*-group was tested, and the representatives thereof did not make a group. Two of them instead grouped with *Ataenius*, while *Notocaulus* (if that taxon should be counted within this informal group) was among the scattered taxa basal in the Aphodiini branch. There it appeared alongside *Saprosites* and Proctophanini (but grouping with neither) – making the idea of *Saprosites* being part of Didactyliini sensu lato(Dellacasa et al 2001) appear less far-fetched (but of course that Didactyliini is not at all a monophyletic group).

D. FORMALITIES

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2. Litterature

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3. Specimens studied

Eupariini/ Ataenius-group:	Ataenius picinus Har., Brazil & New Caledonia, NRM coll mond
Eupariini/ Ataenius-group:	Ataenius acutulus Schm., Sumatra, NRM coll Schmidt
Eupariini/ Ataenius-group:	Ataenius abditus Hald., Mexico, LZM coll mond
Eupariini/ Saprosites-group:	Saprosites mendax Blackb., Australia, NRM coll mond
Eupariini/ Euparia-group:	Arupaia friedenreichi Har., NRM coll Schmidt
Eupariini/ Euparia-group:	Bruchaphodius bruchi Schm., NRM coll Schmidt
Eupariini/ Euparia-group:	Euparia castanea Lep. & Serv., USA, NRM coll Schmidt & LZM coll mond
Eupariini/ Euparia-group:	Lomanoxoides bitubericollis Schm., NRM coll Schmidt
Eupariini/ Euparia-group:	Notocaulus abessinicus Mach., Uganda, coll Snäll
Lomanoxiini:	Lomanoxia costulata Har., Argentina, NRM coll Schmidt
Odontolochini:	Odontolochus gestroi Clouët, NRM coll Schmidt
Odontolochini:	Odontolochus oberthuri Clouët, NRM coll Schmidt
Odochilini:	Odochilus haroldi Rak., Borneo, LZM coll mond
Odochilini:	Odochilus balthasari Rak., Borneo, NRM unsorted
Psammodiini/ Psammodiina:	Diastictus vulneratus Sturm, Sweden, coll MF
Psammodiini/ Psammodiina:	Psammodius asper F., Sweden, coll MF
Psammodiini/ Psammodiina:	Tesarius sulcipennis Lea, New Zealand, NRM unsorted
Psammodiini/ Rhyssemina:	Platytomus tibialis F., Tunisia, coll MF
Psammodiini/ Rhyssemina:	Pleurophorus caesus Cr., Greece, coll MF
Psammodiini/ Rhyssemina:	Rhyssemus germanus L., coll MF
Corythoderini:	Corythoderus loripes Kl., NRM coll Schmidt
Corythoderini:	Termitopisthes wasmanni Schm., syntypus, NRM coll Schmidt
Rhyparini:	Rhyparus suturalis Schm., Cameroun, NRM coll Schmidt
Rhyparini:	Termitodius chaki Mart., Mexico, LZM coll mond
Termitotrogini:	Termitotrox consobrinus Rchspg., South Africa, holotypus, GNM
Didactyliini/Proctophanini:	Australaphodius frenchi Blackb., South Africa, NRM coll mond & Schmidt
Didactyliini/Proctophanini:	Harmogaster exarata Har., South Africa, NRM coll mond
Didactyliini/Proctophanini:	Drepanocanthus lineatus Wied., South Africa, NRM coll mond & Schmidt

Didactyliini/Proctophanini:	Didactylia infuscatopennis Schm., Brazil, NRM coll mond
Didactyliini/Proctophanini:	Didactylia varia Schm., Congo, syntypus, NRM coll Schmidt
Didactyliini/Proctophanini:	Didactylia pura Schm., Ethiopia, coll Snäll
Didactyliini/Proctophanini:	Proctophanes sculptus Hope, Australia, NRM coll mond
Didactyliini/Proctophanini:	Coptochirus vulgatus Har., South Africa, NRM
Aphodiini:	Aphodius (Ammoecius) brevis Er., Sweden, coll MF
Aphodiini:	Aphodius (Aphodius) fimetarius L., Sweden, coll MF
Aphodiini:	Aphodius (Agrilinus) ater DeG., Sweden, coll MF
Aphodiini:	Aphodius (Acrossus) depressus, Sweden, coll MF
Aphodiini:	Aphodius (Amidorus) obscurus F., NRM coll mond & Schmidt
Aphodiini:	Aphodius (Anomius) castaneus Ill., NRM coll Schmidt
Aphodiini:	Aphodius (Pseudagolius) coloradensis Horn, Mexico, NRM coll mond
Aphodiini:	Aphodius (Mendidius) fimbriolatus Mann., paratypus, NRM coll mond
Aphodiini:	Aphodius (Mendidius) incommunis Fall, USA, LZM coll mond
Aphodiini:	Aphodius (Parammoecius) corvinus Er., NRM coll mond & Schmidt
Aphodiini:	Aphodius (Pharaphodius) marginellus F., NRM
Aphodiini:	Aphodius (Stenotothorax) nevadensis Horn, NRM
Aphodiini:	Aphodius (Paradidactylia) biseriatus Schm., NRM coll Schmidt
Aphodiini:	Aphodius (Colobopterus) erraticus L., Sweden, coll MF
Aphodiini:	Aphodius (Teuchestes) fossor L., Sweden, coll MF
Aphodiini:	Aphodius (Calamosternus) granarius L., Sweden, coll MF
Aphodiini:	Aphodius (Koshantschikovius) stercorosus Melsh., USA, NRM coll mond
Aphodiini:	Aphodius (Esymus) merdarius F., Sweden, coll MF
Aphodiini:	Aphodius (Euorodalus) coenosus panz., Sweden, coll MF
Aphodiini:	Aphodius (Pleuraphodius) sp, Kenya, coll Snäll
Aphodiini:	Aphodius (Trichonotulus) scrofa F., Sweden, coll MF
Aphodiini:	Aphodius (Plagiogonus) arenarius Ol., Sweden, coll MF
Aphodiini:	Aphodius (Sigorus) porcus F., Sweden, coll MF
Aphodiini:	Aphodius (Limarus) zenkeri Germ., Sweden, coll MF
Aphodiini:	Aphodius (Nimbus) contaminatus, Hbst. Sweden, coll MF
Aphodiini:	Aphodius (Bodilus) lugens Cr., Sardinia, coll MF
Aphodiini:	Aphodius (Melinopterus) prodromus Brahm, Sweden, coll MF
Aphodiini:	Aphodius (Chilothorax) conspurcatus L., Sweden, coll MF
Aphodiini:	Aphodius (Liothorax) plagiatus L., Sweden, UUZM
Aphodiini:	Aphodius (Paradidactylia) flavescens Balth., Gambia, LZM coll mond
Aphodiini:	Aphodius (Paradidactylia) haafi Petr., Sri lanka, LZM coll mond
Aphodiini:	Simogonius beccari Har., Uganda, coll Snäll
Aphodiini:	Lorditomaeus infuscatus Schm., Guinea, NRM coll mond
Aphodiini:	Macroretrus singularis Pér., East Africa, NRM coll mond
Aphodiini:	Sybax distortus Schm., holotypus, NRM coll Schmidt and LZM coll mond
Aphodiini:	Sybax impressicollis Boh., holotypus, NRM coll mond and coll Schmidt
Aphodiini:	Sybax sulcicollis Boh., holotypus, NRM coll mond and coll Schmidt
Aphodiini:	Heptaulacus (Heptaulacus) testudinarius F., UUZM
Aphodiini:	Heptaulacus (Euheptaulacus) sus, Hbst. Sweden, coll MF
Aphodiini:	Oxyomus silvestris Scop., Sweden, UUZM
Aulonocnemini:	Aulonocnemis laevis Shaufuss, Madagascar, NRM coll mond
Aulonocnemini:	Aulonocnemis crassecostata Fairm., NRM unsorted
Aulonocnemini:	Aulonocnemis opatrina Kl., Madagascar, NRM unsorted
Aegialiini/ Eremazina:	Eremazus cribratus Sem., NRM coll mond & LZM coll mond
Aegialiini/ Aegialiina:	Aegialia (Aegialia) arenaria F., Sweden, coll MF
Aegialiini/ Aegialiina:	Aegialia (Aegialia) argentina Mart., Per. & Vulc., Argentina, NRM unsorted
Aegialiini/ Aegialiina:	Aegialia (Rhysothorax) rufa F., NRM coll mond
Aegialiini/ Aegialiina:	Aegialia (Psammoporus) sabuleti Panz., Sweden, coll MF
Aegialiini/ Aegialiina:	Caelius (Leptaegialia) humeralis Brown, USA, LZM coll mond
Aegialiini/ Aegialiina:	Caelius (Caelius) denticollis Lewis, Japan, LZM coll Landin
Chironini:	Chiron cylindrus F., South Africa, NRM coll mond and unsorted
Chironini:	Chiron grandis Gory, NRM coll mond and unsorted
?	indet Psammodiini-Aegialiini, South Africa, LZM coll Landin