

This article was downloaded by: [University of Arizona]

On: 18 January 2013, At: 10:18

Publisher: Taylor & Francis

Informa Ltd Registered in England and Wales Registered Number: 1072954 Registered office: Mortimer House, 37-41 Mortimer Street, London W1T 3JH, UK



Journal of Natural History

Publication details, including instructions for authors and subscription information:

<http://www.tandfonline.com/loi/tnah20>

Phylogenetic trends in the Scarabaeoidea (Coleoptera)

C.H. Scholtz^a

^a Department of Entomology, University of Pretoria, Pretoria, 0002, South Africa

Version of record first published: 24 Feb 2007.

To cite this article: C.H. Scholtz (1990): Phylogenetic trends in the Scarabaeoidea (Coleoptera), *Journal of Natural History*, 24:4, 1027-1066

To link to this article: <http://dx.doi.org/10.1080/00222939000770631>

PLEASE SCROLL DOWN FOR ARTICLE

Full terms and conditions of use: <http://www.tandfonline.com/page/terms-and-conditions>

This article may be used for research, teaching, and private study purposes. Any substantial or systematic reproduction, redistribution, reselling, loan, sub-licensing, systematic supply, or distribution in any form to anyone is expressly forbidden.

The publisher does not give any warranty express or implied or make any representation that the contents will be complete or accurate or up to date. The accuracy of any instructions, formulae, and drug doses should be independently verified with primary sources. The publisher shall not be liable for any loss, actions, claims, proceedings, demand, or costs or damages whatsoever or howsoever caused arising directly or indirectly in connection with or arising out of the use of this material.

Phylogenetic trends in the Scarabaeoidea (Coleoptera)

C. H. SCHOLTZ

Department of Entomology, University of Pretoria, Pretoria 0002, South Africa

(Accepted 7 October 1989)

Phylogenetic trends of the states of 24 adult and 14 larval characters of the major groups of Scarabaeoidea are discussed on the basis of outgroup and ingroup comparison. Evolutionary trends within the major groups are also discussed. The following (i) adult and (ii) larval characters are discussed: (i) antennal segments, antennal sensilla, ocular canthus, ommatidium structure, epipharynx, mandibles, maxillae, labium, tentorium, trochantin, coxal cavities, mesothoracic spiracles, wing venation, metendosternite, empodium, abdominal sternites, abdominal spiracles, male genitalia, female genitalia, ovarioles, karyotype, central nervous system, spermatozoan number and malpighian tubules; (ii) antennae, fronto-clypeal suture, lateral ocelli (stemmata), labial palpi, maxillae, maxillary palpi, maxillary/mandibular stridulatory areas, labrum, epipharyngeal tormae, legs, stridulatory apparatus, spiracles, abdominal apex and central nervous system.

KEYWORDS: Coleoptera, Scarabaeoidea, Dascilloidea, phylogeny, evolution.

Introduction

Despite several detailed comparative studies on various morphological structures of many groups of Scarabaeoidea over the past 20 years (Ritcher 1966, 1969a, 1969b, 1969c; Ritcher and Baker 1974; Iablokoff-Khnzorian 1977; Yadav and Pillai 1979; Howden 1982; Caveney 1986; d'Hotman and Scholtz, in press, as well as many general works in which scarabaeoids featured (Crowson 1955, 1981; Smith and Virkki 1978; Lawrence 1982, and in press; Lawrence and Newton 1982), and various detailed, broad phylogenetic studies of specific scarabaeoid groups (Scholtz 1986; Scholtz *et al.* 1987; Scholtz *et al.* 1988), a comprehensive review of the available literature has not been attempted. Consequently, because of the availability of information on various structures and taxonomic groups in the Scarabaeoidea and because of sustained interest in the superfamily, it was felt that it was appropriate to review the available published and unpublished information. Since the main purpose of this study was to review the data figures are only provided for structures that are not commonly encountered by systematists or where different interpretations of structures are possible. The data form the basis of a set which will eventually be analysed to determine possible relationships between the major scarabaeoid groups.

Definition of Scarabaeoidea

Adult scarabaeoids are distinguished by: a highly modified, burrowing prothorax,

with large coxae (almost always with concealed trochantins and closed cavities) and usually dentate tibiae with only one spur; hind wings with reduced venation and strong intrinsic spring mechanism for folding; a lamellate antennal club; no hind coxal plates; the second abdominal sternite represented by a lateral portion only; the eighth tergite forming a true pygidium and not concealed by the seventh; and four malpighian tubules (Lawrence and Britton, in press).

Larvae are grub-like and usually C-shaped, with well-developed antennae and legs, no urogomphi, and usually, cribriform spiracles.

Major trends in the group include the reduction in the adults of the eighth pair of abdominal spiracles, movement of the spiracles dorsally or ventrally, reduction in the number of antennal segments, reduction of the aedeagus from a trilobe to a bilobe, reduction in males of the genital segment from a genital capsule to a spiculum gastrale. In larvae there is loss of the spiracular closing apparatus, increase in antennal segments from 3 to 4, and fusion of the maxillary galea and lacinia to form a mala.

Origin of the Scarabaeoidea

Crowson (1955), following Böving and Craighead (1931), proposed the Dascilloidea as the sister group of the Scarabaeoidea, based mainly on larval characters. Dascillid larvae are similar to those of many Scarabaeoidea in that they are large, grub-like forms with a large head, long antennae, cribriform spiracles, similarly robust mandibles with well developed mola and accessory ventral process, separate galea and lacinia, and complex epipharynx and hypopharynx (Lawrence, in press). Ritcher's (1969b) reference to the supposedly homologous intersegmentalia associated with mesothoracic spiracles in adult Dascillidae and Scarabaeoidea, similarity in exocone ommatidium structure is dascilloids and Passalidae (Caveney 1986), similarity in trilobe male genitalia with a well defined genital capsule in some dascilloids and various primitive scarabaeoids (Glaresidae) (d'Hotman and Scholtz, in press), mouthparts (Nel and Scholtz, in preparation), as well as open procoxal cavities which are similar in *Dascillus* and Pleocomidae, lend support to this hypothesis. However, Lawrence and Newton (1982) and Lawrence and Britton (in press) reject this hypothesis claiming similarities between dascillid and scarabaeoid larvae are either plesiomorphic or associated with soil-dwelling habits, and that adult dascilloids share many more important features (such as the complex prothoracic interlocking device) with elateriform taxa such as Callirhipidae and Ptilodactylidae, than with scarabaeoids. However, they do not propose a more likely outgroup. An important, close similarity between Dascilloidea and *Pleocomia* which appears not to have been considered previously is that of the longitudinal division of the median lobe of the aedeagus (d'Hotman and Scholtz, in press). Consequently, it appears that the evidence presented for relationship between Dascilloidea and Scarabaeoidea is undoubtedly as strong as that presented against such relationship and that there seems to be little reason to deny the possibility that the Dascilloidea is the most likely outgroup of the Scarabaeoidea.

Dascillid larvae differ from most scarabaeoids in having: distinct tergal plates; labrum and clypeus at least partially fused together and to the frons; a very short epicranial stem; an articulated process beneath the mandibular retinaculum; heavily sclerotized, comb-like structures on the epipharynx and hypopharynx; a strongly bilobed ligula; a reduced anal segment without anal pads; and (with some exception), urogomphi on tergum 9 (Lawrence, in press).

Ancestral mode of life

Crowson (1981) proposed that ancestral scarabaeoids were small, convex beetles adapted for burrowing in soil [possibly something like modern-day Glaresidae, Ochodaeidae or Bolboceratinae] where they probably fed on subterranean fungi. Larvae, which are thought to have fed on fungi too, have evolved numerous adaptations for soil-living. Adaptations to various other food sources in and on the ground led to extensive radiation of the various groups. Some of the major shifts that have taken place in larvae are toward: living and feeding in rotting wood (Passalidae, Lucanidae); feeding on animal remains (Trogidae); feeding on arboreal fungi, or associated with social insects (Ceratocanthidae); feeding on living plant roots (Pleocomidae, some derived groups), humus (many derived groups) and herbivore dung (Scarabaeinae, Aphodiinae, some Geotrupidae). In many cases adults feed in similar situations on similar sources of food to those of the larvae. The most significant changes away from this situation are found in groups in which adults do not feed (Pleocomidae, Diphylostomatidae) or in the derived groups in which adults have turned to feeding on foliage and fruit (Melolonthinae, Rutelinae, Cetoniinae), or to carnivory (Cetoniinae).

The above hypothesis is consistent with the evolutionary trends in most characters.

Fossil record

The fossil record contributes little to understanding scarabaeoid phylogeny. Iablokoff-Khnzorian (1977) and Crowson (1981) reviewed what is known.

The oldest probable scarabaeoid, *Aphodiites*, is known from the Lower Lias (Lower Jurassic) of Switzerland. It is small (5 mm long), Aphodiine-like, with striated elytra and large prothorax with supposed notal marks indicating the characteristic scarabaeoid features of dorsal articulations of the coxae. Larger scarabaeoid-like fossils such as *Opiselleipon* (15 mm) are known from Upper Lias beds in Saxony and *Geotrupoides* (35 mm) from Upper Jurassic beds.

Fossils resembling modern Geotrupidae and Hybosoridae (based primarily on the presence of four main anal wing veins) have been recorded from Lower Cretaceous deposits in China (e.g. *Protoscarabaeus*). An unusual scarabaeoid with features similar to some termitophilous Aphodiinae but otherwise unlike any modern scarabaeoid, is known from Lower Cretaceous amber of Lebanon (Crowson 1981).

No fossil scarabaeoids are known from the Upper Cretaceous.

It is evident from the fossil record that the main divisions of modern Scarabaeoidea were distinct from the beginning of the Tertiary. About 80 species, some of which represent extant genera, are known from North America and Europe. Fossil dung balls such as those made by modern Scarabaeinae are known from Lower Oligocene beds of Chile, and forms similar to modern Aphodiinae from Lower Eocene London Clay. Baltic amber has yielded a lucanid, *Palaeognathus*, and an *Aphodius*, and Dominican amber (25–40 my, Poinar personal communication), Ceratocanthidae typical of more specialized forms with rolled body form and broad, flat posterior tibiae closely applied to the body (personal observation).

The oldest recorded higher scarabaeoid, *Eophyllocerus*, (assigned to Melolonthinae) is from Eocene coal deposits of Germany.

Families of Scarabaeoidea

Eleven families of 'primitive' Scarabaeoidea, based mainly on Crowson (1981),

Lawrence and Newton (1982) and Lawrence and Britton (in press), and the Scarabaeidae (higher Scarabaeoidea), are recognized (see Appendix). The primitive families are Passalidae (*sensu* Reyes-Castillo 1970). Lucanidae (*sensu* Holloway 1960; Howden and Lawrence 1974; Ratcliffe 1984), Glaresidae (*sensu* Scholtz *et al.* 1987), Diphylostomatidae (*sensu* Holloway 1972), Pleocomidae (*sensu* Lawrence 1982), Geotrupidae (*sensu* Zunino 1984; but see Howden 1982), Trogidae (*sensu* Scholtz 1986), Ochodaeidae (*sensu* Scholtz *et al.* 1988), Hybosoridae (see Paulian 1940), Ceratocanthidae and Glaphyridae (see Machatschke 1959). Scarabaeinae (see Halffter and Edmonds 1982), Aphodiinae (including Aegialiinae—*sensu* Jerath 1960), Melolonthinae (see Arnett 1968), Rutelinae (see Arnett 1968), Dynastinae (see Endrödi 1985) and Cetoniinae (see Krikken 1984) (including Cremastocheilini, Trichiini and Valgini, although there is some evidence to suggest that the latter two should be treated as separate subfamilies), are treated as subfamilies of the Scarabaeidae, and little-studied groups such as Aclopininae, Oncerinae, Chasmoderinae, Orphninae, Phaenomerinae and Aulonocneminae (but see Cambefort 1987) are treated as groups of uncertain phylogenetic status.

Characters of phylogenetic significance

ADULTS

Antennae

Antennae vary between 11- and 7-segmented, with a strongly asymmetrical 3- to 7-segmented, usually lamellate club. The antennae may be geniculate (Lucanidae) or not, and the lamellae may be capable of close apposition (most groups) or not (Lucanidae, Passalidae). The geniculate antennae and the lamellae which are not capable of close apposition are found in those groups which have evolved outside of the soil habitat and no longer require the antennae to be closely protected for burrowing.

Eleven-segmented antennae occur in Pleocomidae, Geotrupidae (excluding Taurocerastinae), some Glaphyridae (*Glaphyrus*—although there is some doubt about the interpretation of the number in this group since the last segment is liable to be partially divided to accommodate a special organ—Crowson *in litt.*) and some Melolonthinae (e.g. *Rhizotrogus*, where there is also often asymmetry in antennae—Iablokoff-Khinzorian, 1977; and males of *Phalangosoma*). The club is 3-segmented in Geotrupidae, 4- to 7-segmented in Pleocomidae and 3- to 7-segmented in Melolonthinae.

Antennae are 10-segmented with 3 or 7 club segments (Lucanidae), 3 to 6 club segments (Passalidae), or 3 club segments (Diphylostomatidae, Trogidae, Glaresidae, Taurocerastinae, Hybosoridae, and some Ochodaeidae and Ceratocanthidae), and 9-segmented with 3 club segments in some Ochodaeidae and Ceratocanthidae. Total number of antennal and club segments varies greatly in Scarabaeidae, with from 7 to 10 antennal and 3 to 7 club segments present.

Some groups with a 3-segmented club may have a circular and concave proximal segment into which the penultimate (some Geotrupidae and Glaresidae) or penultimate and terminal (Hybosoridae) segments fit.

Eleven antennal segments is regarded as the ancestral number and any reductions are regarded to be specializations. It is difficult to avoid concluding, however, that in at least some cases (notably the Melolonthinae) secondary division of segments may

have led to an increase in number. If this is so, a similar increase in number may have occurred in other groups.

Antennal sensilla

In a detailed study of sensilla on the antennae of various Scarabaeoidea, Meinecke (1975) and unpublished (according to H. Paulus, personal communication) arranged 44 sensilla types, which have multiple pore openings and are presumed to have an olfactory function, into a complex arbitrary system of *types*, *series* and *groups*.

He identified three major *groups*; the first two represent pore-plate sensilla and the third, trichoid or basiconic sensilla. The more specialized pore-plate sensilla tended to be concentrated on the apposable surfaces of the antennal club whereas the trichoid types tended to occur on the outer surfaces.

All Lucanidae, Trogidae (only the genus *Trox*), Scarabaeinae, Aphodiinae and Geotrupinae studied by Meinecke had the least specialized Group III sensilla, all Bolboceratinae, Ochodaeidae (genus *Ochodaeus*) and Melolonthinae (including Hopliini, placed by Meinecke, based on Balthasar (1963), in the Rutelinae), had intermediate Group II sensilla, and all Rutelinae, Dynastinae and Cetoniinae, the most specialized Group I. Although all Rutelinae studied had Group I sensilla, they were of a type quite distinct from others in Group I.

An unusual type of trichoid sensillum with numerous pores but with the dendrite of its neuron entirely encased in a dendritic sheath, was found in all groups studied except Lucanidae, *Bolbelasmus* (Bolboceratinae) and *Onthophagus* (Scarabaeinae).

Eye—canthus

An ocular (genal) canthus is present in most scarabaeoids. It is absent in some (primitive, Holloway 1969) Lucanidae, all *Diphyllostoma*, Trogidae, Ochodaeidae and a few Hybosoridae. Its absence (Holloway, Lucanidae), its absence or the presence of a small canthus (Howden and Gill 1988—various groups) was considered the plesiomorphic condition, whereas Scholtz (1986, Trogidae) and Scholtz *et al.*, (1988, Ochodaeidae) treated its absence as derived. Since the absence of a canthus occurs in groups with derived ommatidium structure (exocone or acone) as well as with the primitive condition (eucone), it seems likely that the presence/absence of a canthus may have been acquired/retained polyphyletically (based on Caveney 1986, see below), Furthermore, there is considerable variation in the origin of the canthus—in some groups it intrudes dorsally into the eye, in others ventrally.

Eye—ommatidium structure

The scarabaeoid ommatidium shows the greatest structural and functional diversity among the Polyphaga (Caveney 1986). Four different lens systems, eucone, acone, exocone and duocone are present.

The, probably ancestral, system with eucone ommatidia is widespread in the superfamily, occurring in all Glaresidae, Ceratocanthidae, Hybosoridae, Ochodaeidae, Glaphyridae and Scarabaeidae, in some Lucanidae, some Trogidae and some Geotrupidae. An acone system is restricted to Diphyllostomatidae and some Lucanidae. A simple exocone system is known only in the Passalidae, some Pleocomidae and Trogidae and most Bolboceratinae (Geotrupidae). The unique system in which an exocone and crystalline cone occur in the same ommatidium (duocone) is known only in some Pleocomidae and Trogidae.

Caveney (1986) hypothesized that the exocone system found in the Passalidae is the ancestral condition. This premise was based on Howden's (1982) analysis of numerous adult and larval characters on which he concluded that the Passalidae is the most primitive scarabaeoid family. In spite of Howden's analysis there is little convincing evidence to support the hypothesis that the Passalidae are the most primitive scarabaeoids. Caveney (personal communication) has subsequently reassessed the data on ommatidium structure and is of the opinion that the eucone system is most likely to be ancestral (as it is in most Polyphaga). Scholtz *et al.* (1987) briefly discussed this possible alternative.

Supposing the eucone to be ancestral in the Scarabaeoidea, the acone and exocone (possibly by way of a duocone intermediate state) would probably be independently derived (Caveney 1986) from a eucone such as is present in the Glaresidae (Scholtz *et al.* 1987).

Mouthparts

General mouthpart structure varies less in the primitive groups than it does in the derived groups and it is consequently easier to determine trends in the former groups than it is in the latter (Nel and de Villiers 1988; Nel and Scholtz, in preparation).

Mouthparts—epipharynx

A primitive intermandibular projection, which is a median extension of the clypeus, or fused clypeus and frons and lies between the mandibular bases, is present in Lucanidae, Diphylostomatidae and Pleocomidae (Fig. 1).

A primitive, true epipharynx (Fig. 2), which may be symmetrical or asymmetrical and which possesses single tormae, lateral combs present as setal patches, and a variable apical margin is present in most of the remaining scarabaeoid groups with the exception of the Scarabaeinae.

A derived epipharynx (Fig. 3) is one which is membranous and usually has double lateral tormal processes, and lateral combs of which the setae are arranged in 1–2 definite rows. This type occurs only in the Scarabaeinae.

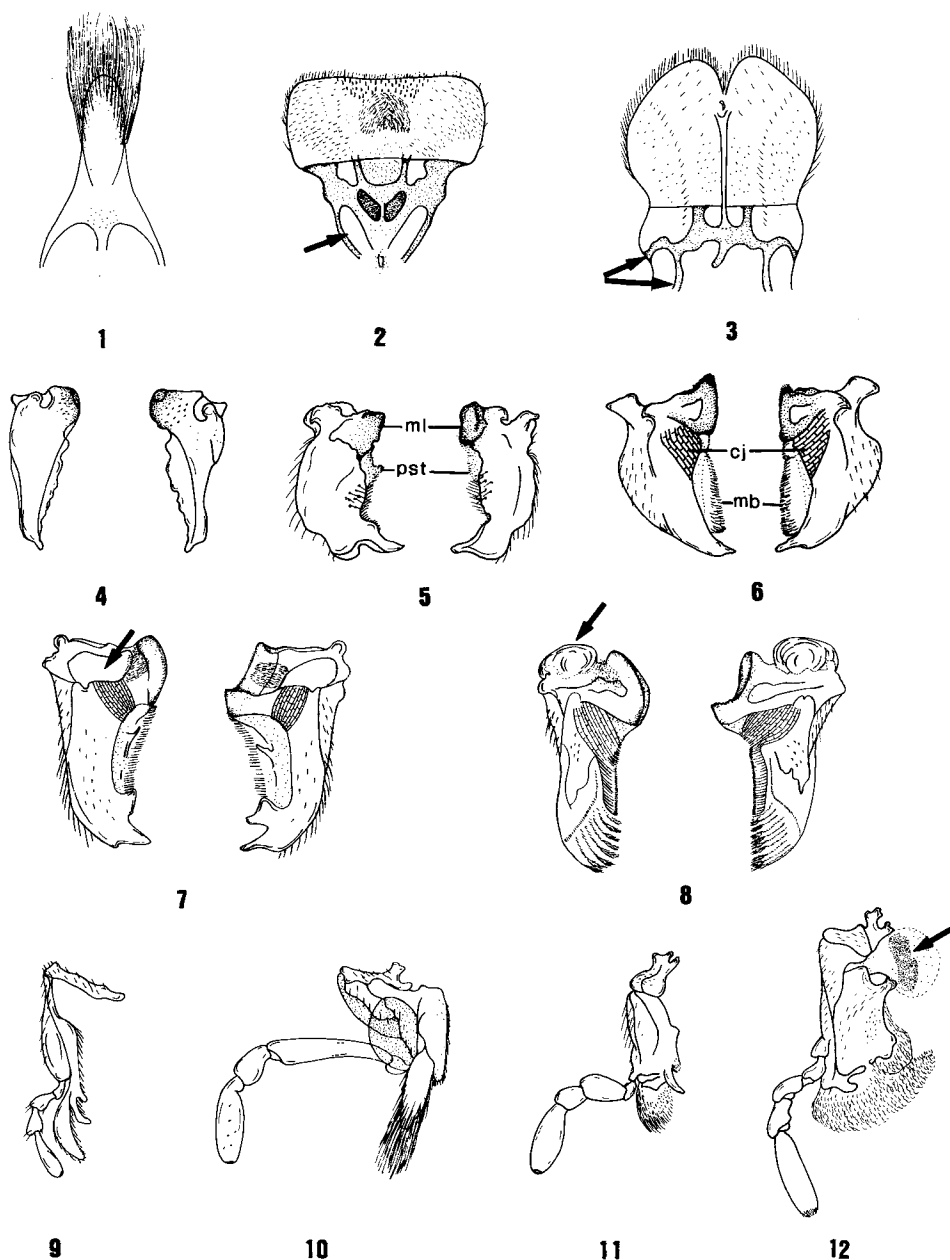
Mouthparts—mandibles

These may be developed, reduced or sexually dimorphic. Three basic types are found in the Scarabaeoidea.

Primitively the mandible has a sclerotized basalis, and apicalis which usually ends in a single tooth, and is without a prostheca and true molar area (Fig. 4). This type is found in Lucanidae, Passalidae and, in greatly reduced form, in Diphylostomatidae and Pleocomidae.

A more derived type has a definite molar lobe and prostheca (Fig. 5). This type may be divided further into: (i) one with a simple but distinct molar lobe and prostheca as in Glaresidae, Ochodaeidae, Bolboceratinae and Hybosoridae; (ii) one with a mesal brush (or developed prostheca), a conjunctive, and a well developed/ridged molar lobe (rest of Geotrupidae, Fig. 6), and occasionally, a mycangium (Fig. 7) (all Ceratocanthidae and some derived genera in various higher groups); (iii) one in which the molar surfaces are well developed, usually coarsely ridged and mostly asymmetrical (Rutelinae, Melolonthinae, Trichiinae).

The most derived type (Fig. 8) is found in the Scarabaeinae. The basalis is strongly sclerotized and is characterized by a receptaculum and asymmetrical molar lobes. The stiff membranous distal portion is the apicalis and consists of a lateral



FIGS 1–12. Scarabaeid mouthparts illustrating different states of various characters (not to scale). (1) The intermandibular projection of *Lamprima* ♂ (Lucanidae); (2) The primitive, true epipharynx of *Anoplotrupes* with single torma arrowed (Geotrupidae: Geotrupinae); (3) The derived epipharynx of *Heteronitis* with double tormae arrowed (Scarabaeidae: Scarabaeinae); (4) The primitive mandibles of *Prosopocoelus* ♂ (Lucanidae); (5) Mandibles of *Bolboceratex* (Geotrupidae: Bolboceratinae) illustrating the molar lobe (ml) and prostheca (pst); (6) Mandibles of *Anoplotrupes* illustrating mesal brush (mb) and conjunctive (cj); (7) Mandibles of *Acanthocerodes* (Ceratocanthidae) with possible mycangium illustrated; (8) Mandibles of *Heteronitis* with receptaculum arrowed; (9)–(12) Maxillae illustrating increasing complexity of galea, variable dentation on lacinia and the presence of maxacorial sclerites (arrowed); (9) *Didimus* (Passalidae); (10) *Lucanus* (Lucanidae); (11) *Namibiotalpa* (Ochodaeidae: Chaetocanthinae) (12) *Liatongus* (Scarabaeidae: Scarabaeinae).

sclerite, a comblike prostheca and a distinct conjunctive. Setae on the apicalis may be arranged into tufts, the so-called combs.

Mouthparts—maxillae

Maxillary structure is fairly uniform within most groups but varies considerably between them. Most variation is found: in the number of palp joints (4-jointed is plesiomorphic (–), fewer or more than 4, apomorphic (+)); whether the lacinia is present (–) or absent (+), and whether it has 2 or more teeth (–) or a single one (+): whether the galea is bilobed (–) or monolobed (+), dentate (–) or not (+), of normal size (–) or greatly enlarged (+), and whether its brush consists of long rigid setae or fine setae; whether articulatory and maxacorial sclerites are absent (–) or present (+) (see Figs 9–12).

Mouthparts—labium

The following trends in labial characters are apparent: reduction in palp joints from 4 (–) to fewer (+); ‘normal’ bilobed (–) to enlarged monolobed (+) mentum; prementum separate from mentum (–) to fused to mentum (+); mentum and submentum without extensions (–) to ones with extensions (+); ligula bilobed (–) to mono-, tri- or quadrilobed (+). Although the latter is contrary to what would normally be expected (since the primitive ligula consists of bilobed glossae and paraglossae, thus four lobes) there can be little doubt that the 4-lobed ligula (and the others) is derived secondarily from a bilobed one (see Figs 13, 14, 15).

Tentorium

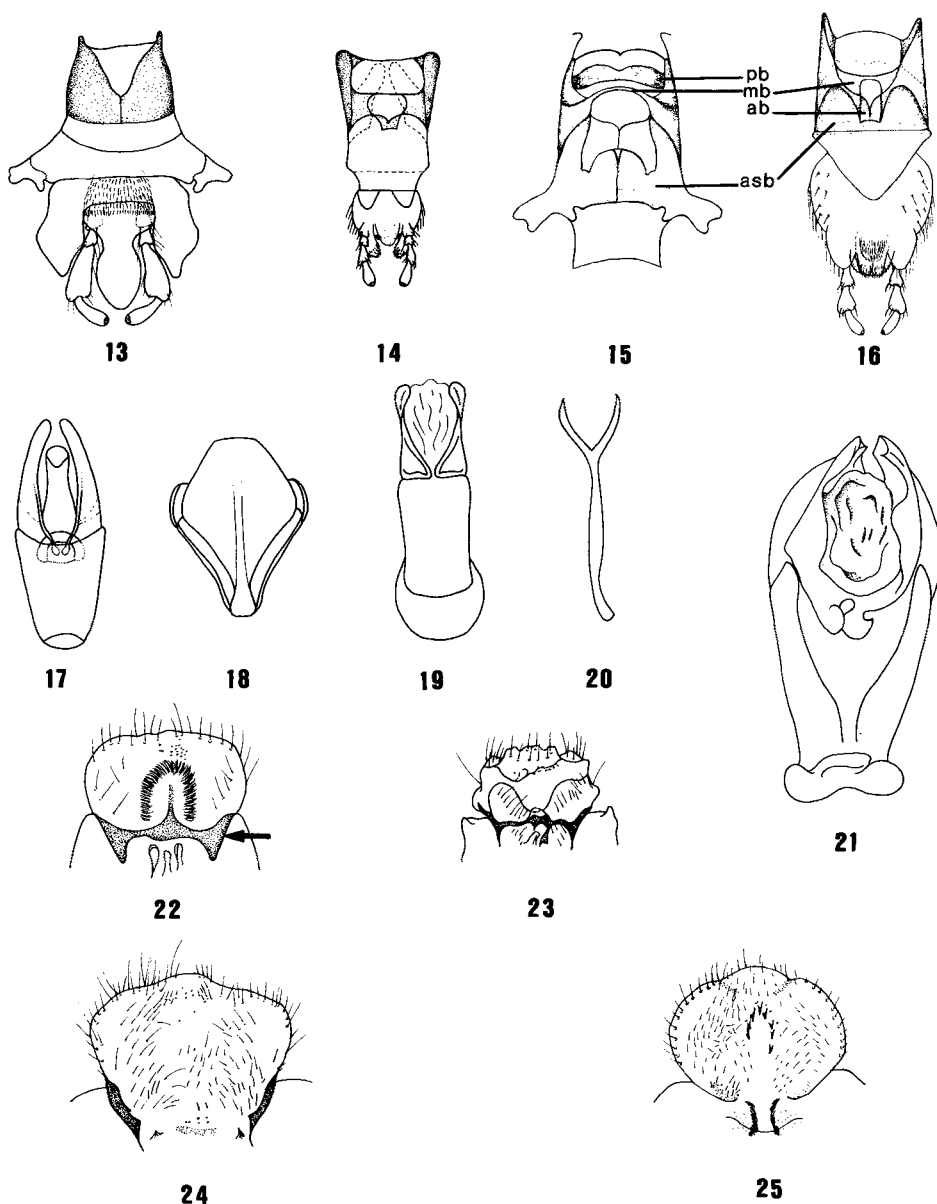
Two distinct types of tentoria are found in the Scarabaeoidea: a primitive, ‘invaginated tentorium’ (Fig. 13), with invaginations in the anterior or posterior margins, is found only in the Lucanidae; and a derived, foraminated tentorium. The latter can be subdivided into a less derived single-foramen-type (Fig. 14) and a more derived two-foramen-type (Fig. 15). The single-foramen-type has only an anterior foramen and a median tentorial bridge, whereas the two-foramen-type has two foramina in the tentorial bridge, a large posterior one, and a smaller anterior one. The single-foramen-type is most commonly encountered in the primitive Scarabaeoidea such as some Trogidae, Ochodaeidae, Hybosoridae and Geotrupidae, as well as in highly derived groups such as Cetoniinae, some Melolonthinae, Rutelinae and Dynastinae, and in some cases it may also have secondary bridges (Fig. 16). The two-foramen-type tentorium may also have secondarily derived additional tentorial arms arising from the posterior tentorial pits such as is found in some Pleocomidae, Ochodaeidae and most Melolonthinae. The most derived two-foramen-type tentorium is found in some Scarabaeinae (Fig. 15). In this type an anterior bridge bears two short arms pointing anteriorly and their bases may be fused to form an anterior secondary bridge.

Trochantin

Protrochantin is exposed only in the Diphylostomatidae. This is a primitive character in Coleoptera.

Coxae

Procoxal cavities are closed by the meeting of the proepimeron and the prosternal process in all Scarabaeoidea with the exception of Pleocomidae (Ritcher 1969c,



Figs 13–25. Morphological structures of various Scarabaeoidea illustrating different character states (not to scale). (13) Invaginated tentorium and monolobed ligula of *Prosopocoelus* ♂ (Lucanidae); (14) Single-foramen-type of tentorium and 4-lobed (two greatly reduced) ligula of *Ochodaeus congoensis* (Ochodaecidae); (15) Schematic two-foramen-type of tentorium illustrating anterior secondary bridge (asb), median bridge (mb) and posterior bridge (pb); (16) single-foramen-type of tentorium with anterior bridge (ab), anterior secondary bridge (asb) and median bridge (mb) as in *Anoplotrupes* (Geotrupidae: Geotrupinae); (17) Simple trilobed aedeagus of *Glaresis* (Glaresidae); (18) Genital capsule of *Glaresis*; (19) Bilobed aedeagus of *Drepanopodus* (Scarabaeidae: Scarabaeinae); (20) Spiculum gastrale of *Diphucephala* (Scarabaeidae: Melolonthinae); (21) Geotrupine-type of aedeagus of *Trypocopris* (Geotrupidae: Geotrupinae); (22)–(25) Larval epipharynxes illustrating symmetry and fusion of tormae (arrowed) (after Ritcher, 1966); (22) Symmetrical and fused—*Sinodendron* (Lucanidae); (23) Asymmetrical and fused—*Hybosorus* (Hybosoridae); (24) Symmetrical, not fused—*Odontotaenius* (Passalidae); (25) Greatly reduced—*Pleocomma* (Pleocomidae).

Hlavac 1975). Mesocoxal cavities are open laterally in Ceratocanthidae, Hybosoridae, Scarabaeidae and Lucanidae and closed by the meeting of the meso- and metasterna in Trogidae and Passalidae (Lawrence and Britton, in press). Open cavities are regarded as the primitive condition.

Mesothoracic spiracles

Ritcher (1969b) drew certain conclusions about evolutionary trends in the structure of mesothoracic spiracles and adjacent sclerites among numerous groups of scarabaeoids, but spiracle structure less clearly indicated interpretable trends than did the associated scleritic intersegmentalia. The trends in the evolutionary development of the mesothoracic spiracles are towards a porous or solid filter apparatus from separate atrial spines and towards a reduction in the size of the spiracular opening. Those in the intersegmentalia are towards a reduction in number, from several sclerites on each side to a median, setiferous sclerite.

Ritcher (1969b) treated the spiracles and intersegmentalia as belonging in three classes, generalized, intermediate and specialized, based on their complexity (spiracles) or state of reduction (intersegmentalia). All Passalidae, Lucanidae, Glaresidae, Pleocomidae, Diphyllostomatidae, Trogidae, Bolboceratinae, *Oncerus*, *Acoma*, *Podolasia* and Ceratocanthidae have the generalized condition, Glaphyridae and Ochodaeidae have something between the generalized and the intermediate condition found in Geotrupidae (other than Bolboceratinae), *Allidostoma*, Hybosoridae, Aphodiinae, Orphninae, *Chnaunanthus*, Melolonthinae and Rutelinae. Scarabaeinae, Cetoniinae and Dynastinae have the specialized condition. The trend in the intersegmentalia does not correlate precisely with that in the spiracles. The generalized condition is found in the Passalidae, most Lucanidae, Diphyllostomatidae, Pleocomidae, Glaresidae, most Trogidae and Geotrupidae. The intermediate state occurs in Glaphyridae, Ochodaeidae and Aphodiinae and the specialized in *Acoma*, *Oncerus*, *Podolasia*, *Allidostoma*, Ceratocanthidae, Hybosoridae, Orphninae, Scarabaeinae, *Chnaunanthus*, Melolonthinae, Dynastinae, Rutelinae and Cetoniinae.

Wing venation

The characters of most phylogenetic significance in the venation of Scarabaeoidea wings are the presence or absence of an M–Cu loop and the presence, of one or two, or the absence of, apical detached veins between the cubitus and first complete anal vein (Crowson 1955).

An M–Cu loop is absent in Passalidae and greatly reduced to absent in Ceratocanthidae. It is present in most other groups. Two apical detached veins are present in Lucanidae, some Trogidae and Hybosoridae, Geotrupidae, Pleocomidae and Ochodaeidae; one is present in Passalidae, some Trogidae and Hybosoridae, Diphyllostomatidae, Glaphyridae, Ceratocanthidae and most Scarabaeidae. They are absent in Glaresidae.

Metendosternite

Crowson (1938) and Iablokoff-Khznorian (1977) discussed various types of metendosternites but the structure is too variable in the Scarabaeoidea to determine evolutionary trends.

Empodium

A distinct empodium is present in many scarabaeoid groups. It usually takes the

form of an elongate lobe or plate bearing two setae. It is present in all primitive groups except Trogidae, Glaresidae, Ceratocanthidae and Hybosoridae, and in most Scarabaeinae, Melolonthinae, Rutelinae, Dynastinae and in some Cetoniinae. Loss of the empodium is probably the derived state but it is quite likely to have been lost independently in various lineages.

Abdominal sternites

Five abdominal ventrites (sternites 3–7) are readily visible in the Lucanidae (except males of *Platycerus* in which 3–8 are visible, H. Paulus, personal communication), Trogidae, Glaresidae and Passalidae (although the second is actually present in the form of small lateral sclerites in Passalidae). Six (sternites 3–8) are visible in the rest of the Scarabaeoidea except Diphylostomatidae in which seven (sternites 2–8) are visible. It is not clear whether the presence of five is homologous in the Lucanidae, Trogidae and Glaresidae or whether only five are visible as a possible result of connation of distal ventrites. Intuitively, the smaller number of visible ventrites would appear to be the derived condition but the groups with five are primitive in many other phylogenetically important characters so the possibility of reversals or non-homologous reductions cannot be ruled out.

Abdominal spiracles

The abdominal spiracles of adult Scarabaeoidea exhibit five main evolutionary trends (Ritcher 1969a): (a) a reduction in number of functional spiracles; (b) reduction in size of posterior pairs (2–8) of spiracles or their openings; (c) reduction in size of first abdominal spiracle; (d) change in structure of the filter apparatus from simple spinules to lips or solid walls; (e) migration of one or more posterior pairs of spiracles from the pleural membrane into the tergites or sternites, and associated with the latter, a trend toward fusion of the tergite and sternite of the seventh abdominal segment.

The plesiomorphic condition, in which all eight pairs are functional, is found in Lucanidae, Diphylostomatidae, Pleocomidae, some Trogidae, Glaresidae, Geotrupidae (excluding Bolboceratinae), Hybosoridae, Ceratocanthidae, Ochodaecidae and most Glaphyridae. Reduction to seven functional pairs has probably occurred independently several times and is found in Passalidae, some Trogidae, *Oncerus*, *Allidostoma* (although Ritcher 1969a reported eight functional pairs there are in fact only seven visible), Bolboceratinae, some Glaphyridae, *Chnaunanthus*, Aphodiinae, Orphninae, Scarabaeinae, most Melolonthinae, Dynastinae, Rutelinae and Cetoniinae. Further reduction, to five or six functional pairs, occurs in *Acoma* and *Gymnopyge*. When reduction in number has taken place vestiges of non-functional spiracles may still be found.

There are two distinct size trends in abdominal spiracles. The first is a general trend toward reduction in the size of the posterior (2–8) spiracles, and the second is a decrease in the relative size of the usually very large first spiracle. In some groups the spiracles become progressively smaller (Passalidae, many Lucanidae, some Trogidae, Glaresidae, Geotrupinae, Ochodaecidae, Aphodiinae and Glaphyridae), whereas in others there are several distinctly different sizes of spiracles (some Trogidae, *Allidostoma*, Hybosoridae, Ceratocanthidae, *Chnaunanthus*, Orphninae and Scarabaeinae). In the most specialized groups (some Melolonthinae, most Rutelinae, Dynastinae and Cetoniinae) the spiracle on the first abdominal segment is greatly

reduced in size and often barely larger than that on the second and successive segments.

The opening to the trachea is guarded by the filter apparatus in the spiracle. In its simplest form the filter apparatus consists of minute spinules projecting into the atrium from the atrial wall. In the Scarabaeoidea there is increasing complexity from: a system with simple atrial spines which are not in distinct rows (Glaresidae); a row or rows of separate trabeculae (many-branched spines) on one or both sides of the subatrial opening (some Lucanidae, Glaphyridae, *Oncerus*); opposing rows of separate trabeculae with some tips fused along the midline (Trogidae, *Chnaunanthus*); two separate lips composed of closely set trabeculae (some Lucanidae, Pleocomidae, Bolboceratinae, Geotrupinae, Lethrinae, Aphodiinae); solid lips fused except for a slitlike, subatrial opening (Passalidae, Taurocerastinae, Hybosoridae, Ceratocanthidae, Ochodaeidae, Orphninae); solid lips not fused, with a narrow slitlike opening (Melolonthinae, Dynastinae, Rutelinae, Cetoniinae).

In the least and most specialized taxa the filter apparatus is similar in all abdominal spiracles whereas in some intermediate groups (Geotrupidae, Hybosoridae, *Allidostoma*, Ceratocanthidae, Aphodiinae, Orphninae, Scarabaeinae and some Melolonthinae) the spiracle of the first segment differs from the others.

The plesiomorphic situation in which all the abdominal spiracles occur in the pleural membrane is found in the Passalidae, Lucanidae, Diphyllostomatidae, Pleocomidae, Trogidae, Glaresidae, some Geotrupidae, *Allidostoma*, Aphodiinae, Orphninae and Scarabaeinae. During the course of evolution there has been a trend for one or more pairs of posterior spiracles to migrate into the tergite or sternite. The latter situation is considered to be the most specialized. Groups with one or more pairs of spiracles in the tergite are found in most Glaphyridae, some Geotrupidae, the Ochodaeidae, Hybosoridae and Ceratocanthidae. The most derived situation, spiracles in the sternites, is found in most Melolonthinae, all Dynastinae, Rutelinae and Cetoniinae.

Male genitalia

Three types of aedeagi are encountered in the Scarabaeoidea (d'Hotman and Scholtz, in press). (a) In the trilobe-type (Fig. 17) the tegmen consists of a well sclerotized basal piece and paired parameres which surround the well developed, tubular median lobe. The genital segment is usually present as a genital capsule (Fig. 18). This type occurs in many of the primitive scarabaeoids. (b) A bilobe-type, in which the basal piece and parameres are well developed, a median lobe is absent and the genital segment is in the form of a U-/Y-shaped spiculum gastrale (Figs 19 and 20), is found in most Scarabaeidae as well as some Ceratocanthidae and Hybosoridae. (c) The geotrupine-type, as the name implies, occurs only in Geotrupinae (Fig. 21). The aedeagus is asymmetrical and the basal piece and parameres are well sclerotized. The basal piece is large in relation to the parameres and dominates the entire aedeagus. The parameres are small and form a complete ring which articulates with the interior wall of the basal piece. The median lobe is membranous and the small unarmed internal sac lies within the tegmen. A genital capsule is present.

The distinction between the trilobe and the bilobe lies in the discreteness of the median lobe/internal sac. In the trilobe the median lobe is usually sclerotized and easily distinguishable from the internal sac whereas in the bilobe the median lobe is membranous and indistinguishable from the internal sac. The genital capsule has

dorsal, lateral and ventral plates whereas the Y-/U-shaped sclerite of the spiculum gastrale is homologous with the dorsal plate of the genital capsule (Hieke 1966).

The evolutionary trends in male genitalia appear to be toward the simplification of a complex structure which was derived from an extremely simple form. Examples are the progression through a simple type such as that in Glaresidae through a complex one as in Trogidae to simple again as in Cetoniinae. Reversals are common, for example, the secondary loss of paramere extensions, temones and internal sac armature.

Female genitalia

Tanner (1927) and Holloway (1972) examined female genitalia of a few Scarabaeoidea. These studies indicated that the arrangement and form of sclerotized parts of segment 9 and of the genital hemisternites (coxites) are characteristic for various groups. In Lucanidae, Trogidae, Ochodaeidae and Glaphyridae the tergite, pleurite and sternite of segment 9 are distinguishable as sclerotized areas. Hemisternites (of segment 10?), with well developed styli, are also present. A similar situation is found in Pleocomidae (Lawrence and Newton 1982). The evolutionary trend is toward a progressive reduction of the sclerotized areas, the first stage of which is the loss of the hemisternites, their function having been taken over by the divided 9th sternite (valvifers) (Holloway 1972). Diphylostomatidae and Geotrupidae lack hemisternites. In Aphodiinae the 9th tergite (paraproct) is weakly sclerotized and in Hybosoridae and Ceratocanthidae it has become membranous along the midline, whereas in Scarabaeinae, Melolonthinae, Dynastinae, Rutelinae and Cetoniinae no trace of sclerotized parts of the 9th tergite are visible.

Ovarioles

Six ovarioles on each side is the most common number found in the Scarabaeoidea (Ritcher and Baker 1974). However, the number varies from about 25 ovarioles in each ovary as in some Pleocomidae to the greatly reduced situation in the Scarabaeinae in which there is only one ovary with a single ovariole. Besides Pleocomidae, in which ovariole number also varies within a species, no group has more than 12 per side. Some Lucanidae, and Rutelinae and several Cetoniinae have 12 per side. One species of Rutelinae has 9 per side. The greatest variation is to be found in the Aphodiinae where 7, 6, 5, 3 and 2 per side have been recorded. Six on each side have been recorded in some Lucanidae, Trogidae (*Trox*), Aphodiinae, Rutelinae and Cetoniinae and in Ochodaeidae, Geotrupidae, Glaphyridae, Ceratocanthidae and Melolonthinae. Glaresidae is the only family known to have 4 ovarioles per side. Some Trogidae (*Omorgus*) and some Aphodiinae have 3 per side and all Passalidae and some Aphodiinae have two per side.

Since ecological factors such as brood care obviously influence the number of progeny produced, ovariole number is probably of little use in phylogenetic deduction. Nevertheless, based on commonality, the 6-6 condition appears to be the ancestral one, with increases or decreases representing derived conditions. If this is so, there seems to be little reason to believe that the large number present in Pleocomidae is primitive, as suggested by Ritcher and Baker (1974).

Karyotype

Because of the marked preponderance of nine pairs of autosomes and an Xyp

sex-determining system ('modal system' of Yadav and Pillai 1979) in the Scarabaeoidea the ancestral system has been postulated to have had a $9+Xyp$ karyotype (Smith and Virkki 1978; Yadav and Pillai 1979) and that groups possessing different complements are derived forms. Five major changes have occurred in the evolution of scarabaeoid karyotypes: X-A fusion; A-A fusion; A fission; loss of the Y chromosome; and change from metacentry to acrocentry. However, interpretation of how this came about (Yadav and Pillai 1979), and of sex bivalents (Crowson 1981), is doubtful. Some authors (see Crowson 1981), have assumed that a small y, forming a 'parachute—p' figure in meiosis with a larger X, was a primitive feature which once lost could not be regained. Others have claimed that the addition of a pairing segment to the original y, leading to an Xy or XY bivalent, was a reversible process and that recent Xyp types are derived from Xy or XY ancestors. Loss of y results in XO, and the only sex bivalent which could develop from it is a neo-XY.

Chromosome numbers and sex determining systems differ greatly within the Scarabaeoidea with autosome numbers varying from 8–36, and with various sex determining systems. The greatest variation in autosome number is in the Lucanidae (8–18), Passalidae (16–36) and Scarabaeinae (10–20) although many of the latter have the modal number. In Lucanidae the modal number has only been found in Aesalinae. It has not been recorded in Passalidae. Most Trogidae, Pleocomidae, Bolbo-ceratinae (Geotrupidae; Geotrupinae have $2n=22$), Glaphyridae, Ceratocanthidae, Hybosoridae and Glaresidae have the modal number, as do most Aphodiinae, Melolonthinae, Rutelinae (except Rutelini with $2n=22$), Dynastinae and Cetoniinae.

Central nervous system

The abdominal ganglia all lie in the thorax and there is an evolutionary tendency towards fusion of ganglia, particularly those of the abdomen (Iabloukoff-Khinzorian 1977). Some Lucanidae have the three thoracic and six abdominal ganglia separate while others have 5 separate abdominal ganglia. In the Passalidae all the abdominal ganglia are fused to the last thoracic ganglion. In Glaphyridae the ganglia of the meso- and metathorax are fused but the six abdominal ganglia are separate. In Pleocomidae the meso- and metathoracic and the first abdominal ganglia are fused whereas 2–6 of the abdomen are separate. Geotrupinae have the ganglia of the meso- and metathorax only partially fused but all abdominal ganglia are fused to the latter. The condition in other primitive groups is unknown. All Scarabaeidae have all abdominal ganglia fused to that of the metathorax but whether those of the thorax are fused to each other varies. Scarabaeinae and Aphodiinae have the thoracic ganglia separate, some Melolonthini and Cetoniinae have the meso- and metathoracic ganglia fused while Sericini (Melolonthinae) have them all fused. Rutelinae have the suboesophageal ganglion in the prothorax whereas in *Rhizotrogus* (Melolonthinae) it is fused to the thoracic ganglia.

Spermatozoan number

Virkki (1969) drew phylogenetic conclusions based on the number of spermatozoa formed in each bundle (i.e. from a single definitive spermatogonium) in Coleoptera, including some Scarabaeoidea. He concluded that there is an irreversible stepwise reduction during evolution from a maximum of 512 (Pleocomidae) to 128 (Passalidae, some Aphodiinae e.g. *Aphodius*), with 256 being the commonest number (Glaphyridae, some Aphodiinae for example *Psammodyus*). Crowson (1981) expressed

doubts whether the evolution of this character would be as unidirectional as proposed.

Malpighian tubules

All scarabaeoids have four malpighian tubules but in some Lucanidae (*Lucanus*) the distal ends of the two pairs fuse to produce two looped tubules (Caveney 1986).

LARVAE

The following discussion is based largely on Ritcher (1966) and Costa *et al.* (1988).

Antennae

The ancestral condition in the scarabaeoidea is three segments (primitive Lucanidae, Geotrupidae, Pleocomidae, Trogidae). Three trends occur: towards a reduction in segment number, to two as in Passalidae; an increase to four segments (some Lucanidae and Hybosoridae, Ochodaeidae, Ceratocanthidae, Glaphyridae, Scarabaeidae), probably as a result of the subdivision of the scape (Crowson 1981); or there is secondary fusion of the 3rd and 4th segments (some Hybosoridae).

Fronto-clypeal suture

A distinct fronto-clypeal suture is present in most Scarabaeoids. It is absent or indistinct in some Trogidae, Ochodaeidae, and some Geotrupidae (Geotrupinae, Bolboceratinae). The fronto-clypeal suture is the external mark of an internal strengthening ridge between the dorsal articulations of the mandibles and is liable to be lost in some groups, but also possibly to be secondarily redeveloped in some (Crowson 1981).

Lateral ocelli (stemmata)

The only family in which all known species have ocelli is the Trogidae (unpublished). One lucanid genus, *Platycerus*, and one glaphyrid genus, *Glaphyris*, have lateral ocelli (Iablokoff-Khnzorian 1977) as do most Dynastinae (Ritcher 1966), several Cetoniinae (Crowson 1955; Ritcher 1966, personal observation) and some sericine Melolonthinae (Ritcher 1966). In the latter the ocelli are represented by little more than pigment spots whereas in the other groups well developed ocelli are present. Larvae with ocelli appear to frequent more superficial situations than do those without, so they are more likely to be brought into contact with light. Normally the presence of ocelli would be regarded as primitive because of the unlikelihood of so complex a structure being secondarily regained after a loss, but to assume this one would have to postulate an unlikely polyphyletic loss of ocelli by all the other groups of Scarabaeoidea (Crowson 1955).

Labial palpi

All scarabaeoids except some Ceratocanthidae have 2-segmented labial palpi. The ceratocanthid exceptions have them 1-segmented.

Maxilla

The maxillary galea and lacinia are distinctly separate in all primitive groups as well as in Scarabaeinae and Aphodiinae. There is a distinct transition by way of

partial fusion (fused proximally but free distally) between them in the Melolonthinae, to total fusion, to form a mala, in the Rutelinae, Dynastinae and Cetoniinae. The galea is 2-segmented in Trogidae and 1-segmented in all other groups.

Maxillary palpi

All scarabaeoids, with the exception of Passalidae and some New World Hybosoridae (Costa *et al.* 1988), have derived 4-segmented palpi. The Passalidae have them 2- (apparently 3-) segmented and the hybosorid exceptions have the ancestral 3-segmented condition.

Maxillary/mandibular stridulatory areas

A stridulatory area which consists of various structures such as ridges, and teeth, is present on the maxillary stipes of most scarabaeoids. It is absent in all Lucanidae (except *Platycerus*). When present, the stipital stridulatory area is brought in contact with the ventral stridulatory area on the mandible. The mandibular stridulatory area is absent in the Melolonthinae and some Cetoniinae.

Labrum

The anterior margin of the labrum is evenly rounded or evenly trilobed in most groups but in Hybosoridae it is truncately trilobed, in some Trogidae (*Omorgus*) it is distinctly bilobed, and in Ceratocanthidae it is serrate.

Epipharyngeal tormae

The tormae may be fused and more or less symmetrical (Lucanidae, Trogidae, Ochodaecidae), fused and distinctly asymmetrical (Hybosoridae, some Ceratocanthidae), not fused and symmetrical (Passalidae), mostly fused and slightly asymmetrical (Geotrupidae, Scarabaeinae, Aphodiinae), not fused and totally asymmetrical (some Ceratocanthidae, Glaphyridae, Melolonthinae, Rutelinae, Dynastinae, Cetoniinae), or greatly reduced (Pleocomidae) (see Figs 22–25).

Legs

All legs are fully developed (4 segments) in all groups except those with reduced metathoracic legs (Passalidae, some Geotrupinae, Tauroceratinae) and those in which all legs are equally reduced to three segments (some Geotrupinae, some Bolboceratinae, Lethrinae), or to two segments (Scarabaeinae).

Claws are well developed in most groups. They are reduced or absent in Geotrupidae (well developed in some Boboceratinae) and Scarabaeinae.

Stridulatory apparatus

A stridulatory apparatus is present on the legs of most members of the primitive families. It is absent in all Trogidae, Ochodaecidae, Glaphyridae, Scarabaeidae and some Geotrupidae (Lethrinae, some Geotrupinae and Bolboceratinae). In groups with well developed legs the plectrum of the stridulatory apparatus is usually situated on the metatrochanter and the pars stridens on the mesocoxa. In those with reduced metathoracic legs the apex of the leg usually serves as the plectrum. In some Hybosoridae and Ceratocanthidae the plectrum is situated on the femur and tibiotarsus of the mesothoracic leg and the pars stridens on the procoxa.

Spiracles

Larval spiracles differ fundamentally in the presence or absence of a closing apparatus, the type of ecdysial process and the form of their spiracular plates (Hinton 1967). The spiracles of Lucanidae, Passalidae, Trogidae and Glaphyridae have a closing apparatus (a device lying between the atrium and the tracheal trunk and consisting of an apodeme and muscle capable of closing the air passage), whereas those of the Pleocomidae, Geotrupinae (other subfamilies unknown) and Scarabaeidae lack a closing apparatus. A closing apparatus is a primitive feature of the spiracles of pterygote insects (Hinton 1967). Most beetles are provided with a closing apparatus. Because its presence represents the primitive condition in beetles its presence in some highly derived groups such as Elateriformia and Dryopoidea (Crowson 1981) has led to the proposal that it is secondarily redeveloped in these groups. However, there is no evidence of a reversal in the Scarabaeoidea.

Two types of ecdysial processes occur in Scarabaeoidea. In Lucanidae, Passalidae, Trogidae, Glaphyridae, Pleocomidae and Geotrupidae the ecdysial process is of the unspecialized elateroid type in which the old spiracle and tracheae are pulled through the ecdysial tube at ecdysis, whereas in Scarabaeidae the ecdysial process is of the more specialized pseudopanorpid type in which the old spiracle and tracheae are pulled out through the atrium of the new spiracle.

Two types of spiracular plates, biforous and cribriform, are found in the Scarabaeoidea. Biforous spiracles are found in some Trogidae, Bolboceratinae and Taurocerastinae, whereas cribriform spiracles are found in all other scarabaeoids. Cribriform spiracles are more specialized than biforous spiracles (Hinton 1967). The biforous spiracle in Trogidae appears less specialized than that in Geotrupidae whereas the cribriform spiracle in Trogidae is more specialized than that in other scarabaeoids (Hinton 1967). There is little doubt that the cribriform spiracular plate of the other scarabaeoids has been independently evolved (Hinton 1967).

Abdominal apex

A type of larval abdomen which may have been ancestral in Coleoptera is characterized by having an unmodified, subterminal 9th segment and a terminal 10th segment, with distinct tergum and sternum bordering a transverse anal opening (Lawrence, in press). This type occurs in many Scarabaeoidea (Passalidae, Ceratocanthidae, some Bolboceratinae, Hybosoridae, Glaphyridae and most Scarabaeidae). The major changes which have taken place in the abdominal apex are toward a slightly Y-shaped anal opening without fleshy lobes (Bolboceratinae), through a distinctly Y-shaped or transverse anal slit (Lucanidae, Ochodaecidae), to a Y-shaped slit with fleshy lobes (Trogidae, some Aphodiinae and Melolonthinae), and finally to a slit surrounded by large irregular lobes (Geotrupinae and Taurocerastinae).

A unique adaptation in the Scarabaeoidea occurs in the Australian scarabaeine genus *Cephalodesmus*, in which the 10th sternum bears a striate longitudinal ridge which acts as a plectrum that rubs against a pars stridens on the gula (Monteith and Storey 1981).

Central nervous system

In the most generalized form there are three thoracic ganglia, joined by distinct connectives. The evolutionary trend is toward a shortening of the connectives and anterior movement of the caudal ganglia (Areekul 1957). In *Pleocoma*, *Ceruchus*

(Lucanidae), *Passalus*, and *Trox* the ganglia are joined by long connectives, and one ganglion is situated in each of the thoracic segments. In *Lichnanthe* (Glaphyridae) and *Dichelonyx* (Melolonthinae: Macroductylini) the connectives are shorter and the ganglia have moved into the first two thoracic segments. In *Polyphylla* (Melolonthini), *Pelidnota* (Rutelinae), *Xyloryctes* (Dynastinae) and *Osmoderma* (Cetoniinae) connectives are absent and the ganglia are fused to the suboesophageal ganglion (Areekul 1957).

The trend in the abdominal ganglia is also toward a shortening of the connectives, anterior movement of the ganglia and a reduction in the number of ganglia (from eight). In *Pleocoma*, *Ceruchus*, and *Passalus* eight ganglia are joined by long connectives and lie in the region between the third thoracic segment and the fifth abdominal segment. The condition in *Trox* is similar except that only six abdominal segments are distinct. The eight ganglia of *Lichnanthe* and *Dichelonyx* are joined by short connectives and they have moved anteriorly, with most lying in the thorax. In *Polyphylla* and the other genera which belong to the derived groups mentioned above, all the ganglia are fused together and lie in the first thoracic segment (Areekul 1957).

Evolution of the groups

The order in which the following families are treated is what I intuitively feel to be the evolutionary progression of the families from primitive to derived. However, since evolution is not linear this system is not ideal for representing relationship between the groups but is merely a crude approximation of lineage. (See Appendix.)

Passalidae

The Passalidae are a large widespread tropical family, divided into two subfamilies, Passalidae and Aulacocyclinae (Reyes-Castillo 1970).

Adults are characterized by: 10-segmented antennae, with 3- to 6-segmented club, the segments of which are not capable of close apposition; eye with a distinct canthus and exocone ommatidium structure; epipharynx with lightly sclerotized, partially bilobed apex and membranous proximal part, with lateral tormae; mandibles simple, with a movable tooth distad of the molar lobe; maxillae characterized by a slender horizontal cardo, and 4-jointed palpi: labium with separated submentum, and bilobed mentum and distinct prementum; tentorium a closed tentlike structure with a single foramen and secondary anterior bridge; mesocoxal cavities are closed; generalized thoracic spiracles and intersegmentalia; wings without M-Cu loop, with one apical detached vein; empodium present; 5 abdominal ventrites visible; abdominal spiracles situated in pleural membrane, 7 pairs functional; male genitalia an atypical trilobe with large armed/unarmed internal sac with/without terminal flagellum; genital segment a U-shaped spiculum gastrale; 2 ovarioles present per ovary; karyotype variable; abdominal ganglia fused to last thoracic ganglion; 128 sperm per bundle; 4 free malpighian tubules.

Larvae are characterized by: 2-segmented antennae; fronto-clypeal suture distinct; galea and lacinia separate; maxillary palpi 2- (or apparently 3-) segmented; maxillary and mandibular stridulatory areas present; epipharyngeal tormae symmetrical, not fused; pro- and mesothoracic legs well developed, 4-segmented with long claws; mesocoxa with pars stridens; metathoracic legs reduced to a stub; spiracles with closing apparatus, cribriform.

Adult mesocoxal cavities are closed, a characteristic found only in Passalidae and Trogidae (Lawrence and Britton, in press).

The uniqueness of the passalid aedeagus lies in the fact that the entire aedeagus has a spherical appearance and is unusually sclerotized in that it has undergone reduction in lateral sclerotization and the dorsal aspect is membranous. The basal piece and parameres are small compared to the greatly enlarged spherical median lobe which is not tubular as is typical of most scarabaeoids (d'Hotman and Scholtz, in press).

Karyotype varies greatly in the Proculini (Passalinae), with 8, 12, 13, 16 or 18 + neo-XY to 11, 12, 13, 15, 17 or 18 + Xy systems, whereas in Passalini only 12 + X has been recorded (Smith and Virkki 1978).

Passalid larvae are not typically C-shaped, being more elongate than most other scarabaeoids. They have several unique features. The 2-segmented antennae and 2-segmented maxillary palpi are unique and the metathoracic leg is reduced to a stub which functions as a stridulatory plectrum. A similar but less reduced situation is found in some Geotrupinae.

Passalids exhibit a form of sub-social behaviour in which adults tend and feed the larvae (Reyes-Castillo and Halffter 1984). They occur in small family groups of a few individuals in rotting hardwood logs. They feed on the wood.

Diphyllostomatidae

The Diphyllostomatidae is a monotypic family. *Diphyllostoma*, with three species, is endemic to the western USA. Males and females are dimorphic—males are smaller and long-winged and females are larger, with reduced wings, eyes and antennae.

Adults are characterized by: straight 10-segmented antennae with 3-segmented club; eye without a canthus, and with acome ommatidia; intermandibular projection present; mandibles reduced, without apical teeth, prosthema and distinct molar areas; maxillae greatly reduced, with 4-jointed palpi; ligula absent, labial palpi 4-jointed; single-foramen tentorium, with broad median bridge and anterior arms directed antero-distally; protrochantin exposed; generalized mesothoracic spiracles and intersegmentalia; wings with M–Cu loop and one apical detached vein; tarsal empodium present; abdomen with 7 ventrites (second exposed); abdominal spiracles situated in pleural membrane, all functional; male genitalia with an asymmetrical trilobe and everted armed internal sac; genital capsule asymmetrical; female genitalia reduced, without hemisternites.

Larvae are unknown.

The acome ommatidium structure in the diphyllostomatid eye is similar to that in some Lucanidae (Caveney 1986). The protrochantin is exposed, a feature found only in Diphyllostomatidae. The exposed second abdominal segment is unique (Holloway, 1972). The asymmetrical trilobe genitalia with permanently everted, armed internal sac and the asymmetrical genital capsule, are distinctive. The internal sac is continuous with the median lobe and the two are difficult to distinguish. Basally the internal sac is armed and terminally a flagellum is present (d'Hotman and Scholtz, in press).

Diphyllostoma was traditionally treated as a member of the Lucanidae but, based mainly on the presence of exposed protrochantin, exposed second abdominal segment, reduced female genitalia, differences in wing venation, male genitalia and leg structure, Holloway (1972) proposed the family Diphyllostomatidae to accommodate

the genus. This system is now generally accepted (Lawrence and Britton, in press; d'Hotman and Scholtz, in press) although Caveney (1986) has presented strong evidence based on the derived ommatidium structure shared with several Lucanidae, that the Diphylostomatidae is probably more closely related to Lucanidae than to the Geotrupidae, for example, as proposed by Holloway (1972).

Lucanidae

Lucanidae is a large widespread, variable though distinctive family which is divided into several subfamilies (Holloway 1960; Howden and Lawrence 1974; Ratcliffe 1984).

Adults are characterized by: 10-segmented, usually geniculate antennae with relatively thick lamellae in a 3- or 7-segmented club; the segments of which are not capable of close apposition; antennal sensilla generalized; eyes with/without a canthus, ommatidium structure eucone or acone; intermandibular projection present; mandibles sexually dimorphic (larger in males), with sclerotized basalis and apicalis, without distinct protheca and molar area; maxillae with lobed galea, and reduced lacinia, or one terminating in a single tooth (males), and 1–3 jointed palpi; labium with prementum on inner side of monolobed mentum, ligula mono- or bilobed and palpi 3- or 4-jointed; tentorium invaginated; generalized mesothoracic spiracles and intersegmentalia; wings with M–Cu loop and two apical detached veins; empodium large; 5 visible abdominal ventrites; abdominal spiracles situated in pleural membrane, eight pairs functional; male genitalia symmetrical/asymmetrical trilobe; armed/unarmed, internal/everted internal sac with/without terminal flagellum; genital capsule distinct; tergite, pleurite and sternite of female 9th abdominal segment visible as distinctive sclerotized areas and hemisternites with styli are present; six or 12 ovarioles present per ovary; karyotype variable; abdominal ganglia free (six) or with first fused to last thoracic ganglion; 4 free malpighian tubules or two pairs fused to form two loops.

Larvae are characterized by: 3- or 4-segmented antennae; fronto-clypeal suture distinct; lateral ocelli rarely present (*Platycerus*); galea and lacinia distinctly separate; maxillary palpi 4-segmented; maxillary and mandibular stridulatory areas usually absent; epipharyngeal tormae symmetrically fused; legs are well developed, 4-segmented, with prominent claws; mesocoxa with pars stridens and metatrochanter with plectrum; spiracles with closing apparatus, cribriform; vertical anal opening with longitudinal oval pad on either side.

The lucanid eye may be entire or divided by a canthus and ommatidium structure may be eucone or acone (Caveney 1986). Some derived groups (Lucaninae; Lucanini—*Lucanus*; Dorcini—*Dorcus*) have eucone ommatidia and eyes partially or completely divided by a canthus, while others (Lucaninae—*Lissotes*) have acone ommatidia. In some groups considered to be primitive, the eye lacks a canthus and frequently the crystalline cone is absent (acone); in other primitive groups (*Aesalinae*—*Aesalus*) the eye has a partial canthus and eucone ommatidia.

The evolutionary trend in the male genitalia of the Lucanidae is toward a general reduction in sclerotization of the median lobe, with the tegmen playing an increasingly large role as the intromittent organ (d'Hotman and Scholtz, in press). An exception to the general pattern in Lucanidae is found in *Aesalinae* in which the primitive aedeagus resembles the articulate-type found in Adephega (d'Hotman and Scholtz, in press) because its reduced basal piece and parameres are fused together

and its median lobe is greatly enlarged. However, the aedeagus is symmetrical and the tegmen does not articulate to the median lobe by means of true condyles, so it is not considered a true articulate type. The derived condition in the Lucanidae is found in Lucaninae in which the aedeagus is asymmetrical and the internal sac, which is longer than the aedeagus, is permanently everted. Furthermore, the presence of additional anchoring or supporting sclerites attached to the aedeagus is considered derived.

Six or 12 ovarioles per ovary are present in the Lucanidae. Six are known from some Platycerini (Lucaninae) and Aesalinae and 12 from Lucanini and Sinodendriini (Syndesinae) (Ritcher and Baker 1974).

Karyotype varies considerably in Lucanidae, from 4+neoXY (Lucaninae: Dorcini), 8+Xyp (Syndesinae: Sinodendrinae), 9+Xyp (Aesalinae-modal number) to 12+Xyr (Lucaninae e.g. *Lucanus*) (Smith and Virkki 1978; Yadav and Pillai 1979).

Some Lucanidae (*Lucanus*, *Dorcus*, *Platycerus*) have the three thoracic and six abdominal ganglia separate while others (*Sinodendron*) have the first abdominal ganglion fused to that of the metathorax, leaving the rest of the abdominal ganglia separate.

The Lucanidae is the only scarabaeoid family with members (e.g. *Lucanus*) in which there is fusion in the distal ends of two pairs of malpighian tubules to form two looped tubules (Caveney 1986).

Larval antennae may be distinctly 3-segmented (e.g. *Ceruchus*), 4-segmented (e.g. *Lucanus*) or apparently 4-segmented (e.g. *Sinodendron*), with the first segment very short and partly fused to the base of the second, or alternatively, the basal segment may be incompletely divided into the basal and second segments (personal observation).

Larvae are usually found in rotting wood, often with the adults. Otherwise adults may occasionally visit flowers.

Glaresidae

This is a small, virtually cosmopolitan (it is absent in Australia) monotypic family.

Adults are characterized by: 10-segmented antennae with 3-segmented club; eye with a canthus, and with eucone ommatidia; epipharynx with single tormae and lateral combs not in rows; mandibles toothed, with a prostheca and distinct molar area; maxilla with lobed galea and lacinia terminating in two teeth, palpi 4-jointed; labium consists of fused mentum and prementum, and a triangular, partly bilobed ligula; tentorium with single foramen and small anterior and median bridges; 5 visible abdominal ventrites; generalized mesothoracic spiracles and intersegmentalia; wings with M-Cu loop, without apical detached veins; tarsal empodium absent; abdominal spiracles situated in pleural membrane, all functional; male genitalia a simple symmetrical trilobe; genital capsule distinct; four ovarioles present per ovary; karyotype 9+Xyp.

Larvae are unknown.

Glaresidae have a suite of characters which are in the generalized state for the Scarabaeoidea and with the possible exception of a four-ovarioles per ovary system (Ritcher and Baker 1974), have no demonstrable characters which could be interpreted as unique. Based on the non-chiasmate Xyp sex chromosome, Smith and Virkki (1978) concluded that *Glaresis* is the most primitive living scarabaeoid genus.

Glaresis was traditionally placed in the Trogidae based on a few generalized characters in common with some members of the Trogidae [and several other groups] (see Scholtz 1986). Scholtz *et al.* (1987) could find no demonstrable apomorphies

which *Glaresis* shares with any other scarabaeoid and consequently proposed the family Glaresidae to accommodate the genus. This system is gaining acceptance (Lawrence and Britton, in press).

Trogidae

The Trogidae is a small distinctive cosmopolitan family which consists of three genera, *Trox*, *Omorgus* and *Polynoncus* (Scholtz 1986).

Adults are characterized by: 10-segmented antennae with a 3-segmented club; eyes without a canthus; ommatidium structure variable; epipharynx symmetrical or asymmetrical, with lateral tormae; mandibles with definite mandible brush and prostheca; maxilla with lobed galea and tridentate lacinia, palpi 4-jointed; labium usually consists of a fused mentum and prementum, and a triangular, partly bilobed ligula; tentorium with single foramen and small anterior and median bridges; mesocoxae closed; generalized mesothoracic spiracles and intersegmentalia; wings with M-Cu loop and one or two apical detached veins; empodium absent; 5 visible abdominal ventrites; abdominal spiracles situated in pleural membrane, 7 or 8 pairs functional; male genitalia usually symmetrical, trilobe, internal sac usually unarmed; with U-shaped spiculum gastrale; tergite, pleurite and sternite of female 9th abdominal segment visible as distinct sclerotized areas and hemisternites with styli are present; 6 or 3 ovarioles present per ovary; karyotype 9 + Xyp.

Larvae are characterized by: 3-segmented antennae; presence of lateral ocelli; fronto-clypeal suture distinct or faint; galea and lacinia distinctly separate; maxillary palpi 4-segmented; maxillary and mandibular stridulatory areas present; epipharyngeal tormae fused, symmetrical; legs well developed, 4-segmented, with prominent claw, without stridulatory apparatus; spiracles with closing apparatus, biforous or cribriform.

Three of the four scarabaeoid ommatidium types occur in the Trogidae; eucone in *Trox* and *Polynoncus*, exocone in some *Omorgus* and duocone in some other *Omorgus* (Caveney 1986).

Mesocoxae are closed in Trogidae, a characteristic otherwise found only in Passalidae.

Wings of *Trox* and *Polynoncus* have two apical detached veins and *Omorgus*, one.

All trogids have the abdominal spiracles situated in a pleural membrane but *Omorgus* has the ancestral condition with eight functional pairs while *Trox* has the derived, seven pairs, with a vestigial eighth pair.

The aedeagus is strongly sclerotized and forms a distinct, usually symmetrical trilobe. Exceptions are mainly restricted to the genus *Polynoncus* in which the median lobe is usually, and the parameres sometimes, asymmetrical. The median lobe varies from a simple, symmetrical lobe (some *Trox*, most *Omorgus*) to a highly complex, often asymmetrical system of hooks, spines and knobs (some *Trox*, *Polynoncus*). The internal sac is usually unarmed but may be setose or heavily pigmented in areas. The genital segment is usually a strong, U-shaped spiculum gastrale which represents a deviation from the evolutionary trend where a trilobe is mostly associated with a genital capsule. However, the primitive Holarctic subgenus *Trox s. str.* has a distinct genital capsule (unpublished).

The generalized ovariole number of six per ovary is found in *Trox* and three per ovary is found in *Omorgus*.

The karyotype in all Trogidae is 9 + Xyp but the position of the centromere differs

between *Trox* and *Omorgus*. Autosomes are metacentric in *Trox* and acrocentric in *Omorgus*. An unconfirmed record (Virkki, 1967) of a *Polynoncus* species [recorded as *Trox*] (*P. aricensis*) indicates that this genus has most autosomes metacentric but at least one pair acrocentric. Virkki (1967) concluded that because scarabaeoid chromosomes are typically metacentric, an acrocentric karyotype, which allegedly results from a complete set of pericentric inversions, must be the derived one and that the karyotype found in *Polynoncus* is intermediate.

Trogidae is the only scarabaeoid family in which all known larvae have well developed lateral ocelli. The fronto-clypeal suture is distinct in *Omorgus* and faint in *Trox*. Spiracles are biforous in *Trox* and cribriform in *Omorgus*.

Adults are characterized by: 11-segmented antennae with a 4 to 7-segmented club; natural sources thereof. They are among the last insects that visit carcasses but also feed readily on old skins, feathers and various other animal remains. Adults stridulate audibly but larvae do not.

Pleocomidae

Pleocomidae is a monotypical family, restricted to the western USA. Males are winged and females flightless.

Adults are characterized by: 11-segmented antennae with a 4 to 7-segmented club; eyes with partial canthus, ommatidium structure exo- or duocone; intermandibular projection present; mandibles reduced, without apical teeth, prostheca and molar area; maxillae reduced, with 4-jointed palpi; ligula absent and labial palpi 4-jointed; tentorium with single foramen and median bridge with arms directed antero-distally; procoxae open; generalized mesothoracic spiracles and intersegmentalia; wings with M-Cu loop and two apical detached veins; empodium distinct; abdominal spiracles situated in pleural membrane, 8 pairs functional; male genitalia a symmetrical trilobe, internal sac unarmed, well developed genital capsule present; ovipositor with styli; 14–25 ovarioles per ovary; karyotype 9 + Xyp; 512 sperm/bundle.

Larvae are characterized by: 3-segmented antennae; fronto-clypeal suture distinct; galea and lacinia distinctly separate; maxillary palps 4-segmented; maxillary and mandibular stridulatory areas present; epipharyngeal tormae greatly reduced; legs well developed, 4-segmented, with strong claws, stridulatory apparatus present on meso- and metathoracic legs; spiracles without closing apparatus, cribriform.

The 11-segmented antennae in *Pleocoma* are generally regarded as being of the ancestral type but the highly modified 4–7 segmented club is obviously specialized and is similar to that found in some Melolonthinae.

Ommatidium structure in *Pleocoma* is quite variable, some species (for example *P. behrensi* having exocome and others (*P. australis*) duocone ommatidia.

Pleocomidae is the only scarabaeoid family in which the procoxae are open.

The aedeagus is a symmetrical trilobe with complex median lobe and small, unarmed, setose internal sac. The genital segment is a well developed capsule.

The large and highly variable number (14–25) of ovarioles per ovary is unique in the Scarabaeoidea.

The highest number of sperm/bundle (512) found in Coleoptera, occurs in the Pleocomidae.

Adult *Pleocoma* do not feed. Larvae are long-lived (8–12 years) and moult several times (9 + instars). They feed on roots and are well adapted for burrowing (Ellertson and Ritcher 1959).

Pleocomidae have several unique, mainly primitive, features (open procoxae, large and highly variable number of ovarioles and long-lived larvae) but few that might be regarded as synapomorphic with other groups. *Pleocoma* has been placed in the Geotrupidae (Paulian 1941) based on symplesiomorphies, or related to the Geotrupidae (Howden 1982) on the basis of doubtful synapomorphies. Crowson (1981), Lawrence (1982), Lawrence and Newton (1982), Lawrence and Britton (in press) have accorded *Pleocoma* family rank—a system which has gained general acceptance.

Geotrupidae

This large widespread family comprises four distinct subfamilies; Geotrupinae, Lethrinae, Taurocerastinae and Bolboceratinae (including Athyreini).

Adults are characterized by: 11- or occasionally 10-segmented antennae with 3-segmented club; antennal sensilla generalized/intermediate; eyes partially or completely divided; ommatidium structure eucone/exocone; mouthparts vary greatly; mesothoracic spiracles generalized/intermediate, intersegmentalia generalized; M–Cu loop and two apical detached veins present; empodium present; abdominal spiracles variable; male genitalia variable; well-developed genital capsule present; female genitalia without styli; 6 ovarioles present per ovary; karyotype variable.

Larvae are characterized by: 3-segmented antennae; fronto-clypeal suture usually absent; galea and lacinia separate; 4-segmented maxillary palpi; maxillary and mandibular stridulatory areas present; epipharyngeal tormae fused/not, asymmetrical/symmetrical; legs very variable; stridulatory apparatus present/absent; spiracles cribriform/biforous.

Antennae are 11-segmented in Geotrupinae, Lethrinae and Bolboceratinae and 10-segmented in Taurocerastinae. Antennal sensilla are less specialized in Geotrupinae than in Bolboceratinae.

The geotrupid eye may be partially or completely divided by a canthus. Geotrupinae have it completely divided, Taurocerastinae partially and Bolboceratinae partially or completely. Ommatidium structure is eucone in all Geotrupinae and Taurocerastinae and in *Bolboceras* (Bolboceratinae). All other Bolboceratinae have exocone ommatidia.

The epipharynx varies from rounded with the apical margin mesally indented (Lethrinae, Bolboceratinae) or straight (Taurocerastinae, Geotrupinae, Athyreini); single lateral tormal processes are present in Lethrinae and Geotrupinae, and single or double in the other subfamilies; a median tormal process and lateral combs are present in some Bolboceratinae and Geotrupinae; setal arrangement proximally on the epipharynx is sexually dimorphic in Lethrinae.

Mandibles of the Bolboceratinae are usually asymmetrical and sclerotized with concave ginglymus and convex condyle, and prostheca and mesal tuft (except *Prototrupes*, in which the prostheca is extended to form a mesal brush). Molar surfaces are rounded and convex on right and concave on left mandible. The molar lobes are characterized by a mandible brush. In the Taurocerastinae and Geotrupinae the mandibles are as above except that they are apically bidentate and more elongate and that they possess a mesal brush and conjunctive. In the Lethrinae they are sexually dimorphic (larger in males), heavily sclerotized, with symmetrically ridged molar surfaces, and a mandible brush.

The maxilla in the Lethrinae is unique—the cardo projects horizontally, the stipes is separate, and the parastipes is fused to the bidentate lacinia. The galea is rec-

tangular and the galea and lacinia brushes consist of stiff sclerotized setae. The palpi are 4-jointed. In the Bolboceratinae the galea is a boot-shaped lobe bearing a long setal brush. The lacinia is armed and is followed distally by a small boot-shaped lobe with a fine brush. Palpi are 4-jointed. The maxilla in the Taurocerastinae and Geotrupinae is as in the previous case except that the galea and lacinia lobes are round and covered with fine, short setae.

The labium does not vary greatly between the subfamilies except that the palpi are 3-jointed in the Lethrinae and 4-jointed in the other families.

The tentorium of the Bolboceratinae and Geotrupinae is of the single-foramen-type. That of the Taurocerastinae is unique in that it consists of a single median foramen with two lateral foramina, a secondary posterior bridge, a median bridge and a secondary anterior bridge. The median bridge is extended antero-ventrally to meet the gular floor. The Lethrinae tentorium also differs from that of the other subfamilies in that it is of the two-foramen-type.

Mesothoracic spiracles are generalized in Bolboceratinae and more specialized in Geotrupinae and Taurocerastinae. The mesothoracic intersegmentalia are generalized in all Geotrupidae.

Eight functional abdominal spiracles are present in Geotrupinae, Taurocerastinae and Lethrinae and seven are present in Bolboceratinae. In the latter the first pair (*Bradycinctulus*) or first two pairs (*Blackburnium*) lie in the sternite and the rest lie in the pleural membrane. In the Geotrupinae and Lethrinae the first pair lies in the sternite, pairs 2–7 lie in the pleural membrane, and the last pair lies in the tergite (*Geotrupes*) or in the pleural membrane. In the Taurocerastinae pairs 1–7 lie in the pleural membrane and the 8th pair lies in the tergite.

The male genitalia of Taurocerastinae, Bolboceratinae and Lethrinae have a well defined tegmen but membranous median lobe whereas Geotrupinae genitalia are unique. The median lobe is absent and the parameres are fused into a single ring-shaped sclerite. Both median lobe and parameres are strongly sclerotized and highly asymmetrical. The internal sac in all geotrupids is inverted and small but may be armed/unarmed or setose. All geotrupids have a well developed genital capsule.

Karyotype varies consistently between Geotrupinae and Bolboceratinae—it is 9 + Xyp in the latter and $2n = 22$ (mainly with XY sex-determination) in Geotrupinae.

The central nervous system in Geotrupinae (the only recorded geotrupid system) has the ganglia of the meso- and metathorax partially fused and all abdominal ganglia fused to the latter.

A fronto-clypeal suture is absent in larvae of Geotrupinae and Bolboceratinae but is distinct in Taurocerastinae.

The epipharyngeal tormae are symmetrical or asymmetrical and are fused in all groups with the exception of few Bolboceratinae (*Eucanthus*).

Legs may be: well developed, 4-segmented (some Bolboceratinae, for example *Bolbocerosoma*); reduced to 3-segmented (some Bolboceratinae, for example *Eucanthus*, Geotrupinae, for example, *Ceratophyus* (Ritcher and Duff 1971), and Lethrinae; with the pro- and mesothoracic legs 3-segmented and the metathoracic leg greatly reduced in size and 2-segmented (several Geotrupinae, for example, *Geotrupes*, *Mycotrupes*, *Ceratophyus*, and Taurocerastinae (Howden and Peck 1987).

A stridulatory apparatus is present on the meso- and metathoracic legs of some Geotrupinae with well developed legs (*Ceratophyus*); some Bolboceratinae with all legs reduced (*Bolboceras*), and all Geotrupinae with reduced metathoracic legs (also Taurocerastinae). It is absent in some Geotrupinae (e.g. *Typhoeus*), Bolboceratinae

(*Eucanthus*, *Bolbocerosoma*, *Bolborhachium* (Howden 1985) and Lethrinae. Claws are absent in Geotrupinae, Tauroceratinae, Lethrinae and some Bolboceratinae (present in *Eucanthus* and *Bolbocerosoma*).

Spiracles are biforous in Bolboceratinae and Taurocerastinae and cribriform in Geotrupinae and Lethrinae.

All geotrupids provision brood burrows with food for the larvae. The food is variable in Geotrupinae but may include herbivore dung or vegetable matter. Bolboceratinae use humus, Lethrinae cut green plant matter and Taurocerastinae use herbivore dung.

There are two distinct lineages within the Geotrupidae as presently constituted, the Bolboceratinae (including Athyreini) forming one, and the Geotrupinae, Taurocerastinae and Lethrinae the other. There is little evidence for the traditional view that the Geotrupidae constitutes a monophyletic assemblage. On the contrary, the evidence suggests a polyphyletic origin for the currently recognized family, and it may be desirable to elevate the Bolboceratinae to family status.

Glaphyridae

This small family comprises two subfamilies, Lichniinae and Glaphyrinae (see Machatsche 1959). The former is restricted to South America and the latter is widespread in the Holarctic Region.

Adults are characterized by: 9-, 10- or possibly 11-segmented antennae (but see page 4), with 3-segmented club; eyes divided, ommatidium structure eucone; epipharynx simple, with median toral process; mandibles sclerotized, with a mandible and mesal brush; a membranous prostheca may be present or absent; maxillary palpi 4- or 5-jointed; labial palpi 4-jointed, ligula bilobed; tentorium with median bridge, single foramen and anterior arms that extend anteriorly and unite; mesothoracic spiracles slightly specialized, intersegmentalia intermediate; wings with M-Cu loop and one apical detached vein; empodium present; abdominal spiracles variable; male genitalia a strongly arched trilobe with variable internal sac; genital segment a well sclerotized capsule; 6 ovarioles present per ovary; karyotype $9 + Xyp$; central nervous system with some fusion of ganglia.

Larvae are characterized by: 4-segmented antennae, ocelli present/absent; fronto-clypeal suture present, galea and lacinia separate, 4-segmented maxillary palpi; maxillary and mandibular stridulatory areas present; epipharyngeal tormae not fused, asymmetrical; legs well developed, 4-segmented with claws, without stridulatory apparatus; spiracles with closing apparatus, cribriform.

Lichniinae have 9- or 10-segmented antennae and Glaphyrinae usually have them 10-segmented (*Glaphyrus*, possibly 11-segmented).

A membranous prostheca is present in *Lichnanthe*, but is absent in *Amphicoma*, and maxillary palpi are 5-jointed in the former and 4-jointed in the latter.

Glaphyrid mesothoracic spiracles are of a slightly more complex type than the most generalized type.

Most glaphyrids have eight pairs of functional abdominal spiracles but their position varies. In Glaphyrinae pairs on segments 1-6 or 1-7 lie in the pleural membrane and pairs 7 and 8 or 8 lie in the tergites. In Lichniinae, *Lichnia* has 8 pairs of spiracles in the pleural membrane and *Cratoscelis* has pairs 1-6 in the pleural membrane and the 7th pair in the tergite.

The unusually well sclerotized, strongly arched basal piece, which is large in relation to the parameres, is diagnostic of the family (d'Hotman and Scholtz, in

preparation). The internal sac in *Amphicoma* is large and armed with a large lateral spine and well sclerotized apical flagellum-like setae (reminiscent of some Lucanidae), whereas in *Lichnanthe* it is small and punctose, without armature. The genital capsule is well sclerotized but reduction in the dorsal plate is apparent in *Amphicoma*.

The central nervous system in *Glaphyrus* has the ganglia of the meso- and metathorax fused and those of the abdomen separate.

Lateral ocelli are present in *Glaphyrus* larvae but absent in other species. Adults are floricolous and larvae are free-living in sandy areas where they feed on humus.

It has long been recognized that this group is distinct. Machatschke (1959) proposed a superfamily for the group but Hinton (1967), on the basis of the unusual larval spiracles, proposed that they more realistically be accorded family status. The latter status is now generally accepted (Crowson 1981, Caveney 1986, Lawrence and Britton, in press).

Ochodaeidae

The Ochodaeidae is a small virtually cosmopolitan family divided into two subfamilies (Ochodaeinae and Chaetocanthinae) (Scholtz *et al.* 1988).

Adults are characterized by: 9- or 10-segmented antennae with a 3-segmented club; eyes not divided; ommatidium structure eucone; mouthparts variable; mesotibial spur pectinate/crenulate; mesothoracic spiracles and intersegmentalia of intermediate structure; wings with M–Cu loop and two apical detached veins; empodium absent; abdominal spiracles all functional; 1–6 in pleural membrane, 7 and 8 in tergite; male genitalia with tegmen lightly sclerotized, median lobe membranous, continuous with long armed/unarmed internal sac; well-developed genital capsule present; tergite, pleurite and sternite of female 9th abdominal segment visible as distinct sclerites, hemisternites with styli present; 6 ovarioles present per ovary.

Larvae are characterized by: 4-segmented antennae; fronto-clypeal suture absent; galea and lacinia distinctly separate; maxillary palpi 4-segmented; maxillary and mandibular stridulatory areas present; epipharyngeal tormae fused, symmetrical; legs well developed, 4-segmented with strong claws, but without stridulatory apparatus; spiracles cribriform.

The epipharynx varies greatly between genera—the apex may be rounded, square, indented or bilobed, with a fringe of sparse or dense fine or stiff setae. Lateral combs are present (most primitive genera) or absent (derived genera). Tormae are single (e.g. *Codocera*), double (some *Ochodaeus*) or reduced (*Chaetocanthus*, *Pseudochodaeus*).

Mandibles are sclerotized, apically pointed, and usually have teeth on the median margin (except *Namibiotalpa*). A prostheca is present in all genera except *Namibiotalpa*.

The maxillae have the cardo projecting slightly upwards. The basistipes is always separated from the parastipes, but is sometimes fused to the lateral stipes (*Codocera*, some *Ochodaeus*). The lacinia is armed with one tooth in all genera except *Codocera* (two teeth). The galea is monolobed in *Codocera* and bilobed in *Namibiotalpa*. Palpi are usually 4-jointed, but are 5-jointed in *Namibiotalpa*, *Codocera* and some *Ochodaeus* (*O. congoensis*).

Labial palpi are usually 4-jointed, but are 3-jointed in some *Ochodaeus* and in *Odontochodaeus*. The ligula is usually bilobed, but is quadrilobed in *Codocera*, *Odontochodaeus* and some *Ochodaeus*. A unique feature of the labium of certain genera is the presence of extensions of the mentum (e.g. *Enodognathus*) or of the

submentum (*Odontochodaeus*). These structures occur nowhere else in the Scarabaeoidea.

A simple single-foramen-type tentorium is present in several genera. In *Pseudochodaeus* it has a single median foramen, but with four lateral foramina, a median bridge and a secondary anterior bridge with anterior tentorial arm rudiments. It is of the two-foramen-type in *Enodognathus*. The *Odontochodaeus* tentorium is unique in the Scarabaeoidea—it consists of three anterior foramina, with two pairs of anterior arms reaching the gular-fimbria.

Ten antennal segments occur in most groups, but antennae are 9-segmented in Chaetocanthini (Chaetocanthinae). The absence of an ocular canthus, the presence of two pairs of abdominal spiracles in the tergites, and the absence of stridulatory organs on the legs of larvae distinguish the Ochodaecidae from its relatives, and the presence of a unique pectinate/crenulate mesotibial spur establishes the monophyly of the group (Scholtz *et al.* 1988).

Hybosoridae

This is a large variable cosmopolitan family which is best represented in the tropics.

Adults are characterized by: 10-segmented antennae with a 3-segmented cupuliform club; eyes usually divided; ommatidium structure eucone; mouthparts variable; mesothoracic spiracles intermediate, intersegmentalia specialized; empodium absent; abdominal spiracles all functional, last pair in tergite; male genitalia very variable, symmetrical/asymmetrical; genital capsule present; female genitalia with 9th tergite membranous along midline; without styli; karyotype 9 + Xyp.

Larvae are characterized by: 3- or 4- segmented antennae; fronto-clypeal suture distinct; galea and lacinia separate; labrum truncately trilobed; maxillary palpi 3- or 4-segmented; maxillary and mandibular stridulatory areas present, epipharyngeal tormae asymmetrical, fused; legs well developed, 4-segmented, with distinct claws; stridulatory apparatus on pro- and mesothoracic legs, or absent; spiracles cribriform.

The eye is usually divided by a distinct canthus but this may be reduced in some genera (*Anaides*) or virtually absent (*Cryptogenius*).

The epipharynx apical margin varies from round (*Brenskea*), medially indented (*Phaeochrous*) to serrate (*Hybosorus*), with a fringe that varies from sparse fine setae (e.g. *Phaeocroops*), dense fine setae (*Liparochrus*) to sparse rigid setae (*Cryptogenius*); lateral combs may be present (*Cryptogenius*) or absent (*Anaides*); tormae may be double (*Brenskea*), single (*Hybosorus*) or absent (*Anaides*); a median brush is rarely present (*Metachaetodus discus*).

Mandibles consist of a sclerotized basalis and apicalis and are usually apically sharply pointed. The prostheca varies from small (*Hybosorus*), a row of setae (*Phaeocridius*) to a setose membrane (*Anaides*). A distinct mesal tuft is also present in *Hybosorus*.

The maxilla has the cardo projecting horizontally. The lateral stipes is reduced and separated from the median stipes which, in turn, is fused to the fused para- and ventrostipes. The galea consists of setose lobes. Palpi are usually 4-jointed but they are 3-jointed in *Chaetodus*. *Anaides* maxillae are characterized by a maxacorial sclerite, known otherwise only from the Scarabaeinae.

The labium always has the mentum and prementum fused, the ligula is usually bilobed (quadrilobed in *Phaeocroops*, absent in *Apolonychus*). Palpi are usually 4-jointed (3-jointed in *Anaides*).

The tentorium is usually of the single-foramen-type, with various levels of complexity of structure of additional (to the median) bridges.

Male genitalia vary greatly but all have an armed internal sac and a genital capsule, although the latter may be greatly reduced. The most significant differences within the family are between Old and New World genera—those of the New World have symmetrical genitalia whereas the ones in the Old World have asymmetrical genitalia.

Larval antennae are 4-segmented (*Cryptogenius* and *Chaetodus*—Costa *et al.* 1988), or apparently 3-segmented but with the line of secondary fusion of the third and fourth segment visible (*Hybosorus* and *Phaeochrous*—Ritcher 1966). The latter state is obviously derived from the 4-segmented situation and is also found in related groups (Ceratocanthidae). Consequently, it is quite clearly a reversal to the ancestral 3-segmented condition found in more primitive groups.

Maxillary palpi are 3-segmented in some New World genera (*Chaetodus*, *Cryptogenius*—Costa *et al.* 1988) and 4-segmented in Old World genera (*Hybosorus*, *Phaeochrous*—Ritcher 1966).

A stridulatory apparatus is usually present on the pro- and mesothoracic legs, but is absent in *Cryptogenius* (Costa *et al.* 1988).

Larvae have been found in decomposing plant material and adults feed readily on decomposing flesh in the early stages of decay.

Distinct, probably phylogenetically important, characters support the division of this family into an Old and a New World lineage. The major differences are in the male genitalia and mouthparts, and segmentation of the larval antennae and maxillary palpi.

Ceratocanthidae

Ceratocanthidae is a large cosmopolitan family of mainly small beetles which are capable of 'rolling up' into a ball. The family is best represented in the tropics.

Adults are characterized by: 9- or 10-segmented antennae with 3-segmented club; eyes divided; ommatidium structure eucone; mouthparts variable; mesothoracic spiracles generalized, intersegmentalia specialized; M–Cu loop reduced or absent; one apical detached vein present; empodium absent; abdominal spiracles all functional; last pair in tergite; male genitalia very variable; genital capsule well developed to reduced, symmetrical/asymmetrical; female genitalia with 9th tergite membranous along midline, without styli.

Larvae are characterized by: 4-segmented antennae; distinct fronto-clypeal suture; serrate labrum; 2-, or occasionally 1-segmented labial palpi; separate galea and lacinia; 4-segmented maxillary palpi; maxillary and mandibular stridulatory areas present; epipharyngeal tormae fused/not, asymmetrical; legs well developed, 4-segmented, with distinct claws; spiracles cribriform; stridulatory apparatus on pro-, meso-, and metathoracic legs or on meso- and metathoracic legs.

The epipharynx is apically sclerotized and proximally membranous. Lateral tormae are single in *Cloeotus* and double in *Pterorthocetes*. A median tormal process is always present.

Mandibles are characterized by a sclerotized basalis and pointed apicalis which has a well developed mesal brush. In *Pterorthocetes* the mesal brush is modified into a distal and mesal comb (prostheca) similar to that found in some Scarabaeinae. A distinct cavity (a mycangium?) is present posterior of the molar lobes.

The maxillary galea is characteristically large, with a dorsal and ventral articulatory sclerite in *Acanthocerodes*, or proximally sclerotized in *Ceratocanthus*. Palpi are usually 4-jointed but are 3-jointed in *Pterorthochaetes*.

The labium varies little. With one exception (*Pterorthochaetes*), the submentum is fused to the gula, but is separated from the mentum. Palpi are 4-jointed and the ligula is bilobed.

The tentorium is usually of the single-foramen-type. An exception is *Ceratocanthus* where it is characterized by a median as well as two lateral foramina.

Male genitalia vary considerably. The basal piece is usually asymmetrical, unevenly sclerotized and sometimes has ventral and lateral apophyses present. The parameres are usually very small relative to the basal piece, and symmetrical, and the median lobe is greatly reduced. The internal sac is large and armed in less specialized groups (*Ceratocanthus*), with reduced or no armature in specialized groups (*Philharmostes*). Temones are usually present (exception *Pterorthochaetes*). The genital capsule varies from well developed to reduced, and from symmetrical to asymmetrical.

This is the only scarabaeoid family with larvae which have 1-segmented labial palps (the Australian genera *Pterorthochaetes*, *Cyphopisthes*, Lawrence and Britton, in press). The general situation is 2-segmented palps.

Larval stridulatory pegs occur on the pro-, meso- and metathoracic legs in *Germarostes* but are most prominent on the pro- and mesothoracic legs (Costa *et al.* 1988). In *Cloetotus* the stridulatory apparatus is restricted to the meso- and metathoracic legs (Ritcher 1966). This family clearly illustrates the movement of the stridulatory mechanism from the more general meso-/meta situation to the pro-/meso- situation such as is found in the related Hybosoridae.

Adults and larvae have been found in rotten wood and beneath bark as well as in association with ants and termites. Adult mouthpart structure supports the view that they are fungus-feeders (Nel and Scholtz, in preparation).

Scarabaeidae

A very large diverse, cosmopolitan family consisting of several well-defined subfamilies and several groups of uncertain status.

Aphodiinae

A large cosmopolitan subfamily which consists of several tribes. Adults are characterized by: 9-segmented antennae with 3-segmented club; antennal sensilla generalized; eye divided; ommatidium structure eucone; mesothoracic spiracles of intermediate complexity; intersegmentalia reduced; wings with M-Cu loop and one apical detached vein; empodium present; abdominal spiracles in pleural membrane, 7 pairs functional; male genitalia a bilobe with unarmed or lightly armed internal sac; genital segment intermediate between a genital capsule and a spiculum gastrale; ovariole number variable; karyotype usually 9+Xy or 9+Xyp; central nervous system with meso- and metathoracic ganglia separate and abdominal ganglia fused to the latter; 128/256 sperm/bundle.

Larvae are characterized by: 4-segmented antennae; fronto-clypeal suture present; galea and lacinia separate; 4-segmented maxillary palpi; maxilla and mandibular stridulatory area usually present; epipharyngeal tormae fused, slightly asymmetrical; legs well developed, 4-segmented with claws but without stridulatory apparatus; spiracles cribriform.

The greatest variation in ovariole number in the Scarabaeoidea is found in the Aphodiinae. Numbers vary between 7–2 per side. The greatest variation is found in *Aphodius* (Aphodiini) where there are 7, 6 or 5 ovarioles per side. Three per side are found in Aegialiini (*Aegialia*), Eupariini and some Psammodiini (*Psammodius*) and two per side in some Psammodiini (*Trichiorhyssemus*, *Pleurophorus*).

Karyotype is usually $9+Xy$ or $9+Xyp$ but $10+Xyp$ is known in *Aphodius moestrus*.

The maxillary and corresponding mandibular stridulatory areas are usually present in larvae but are absent in some Psammodiini (*Psammodius*, *Pleurophorus*) and Eupariini (*Saprosites*).

Number of sperm/bundle may be 128 (*Aphodius*) or 256, the modal number (*Psammodius*).

Scarabaeinae

A large cosmopolitan subfamily of dung beetles, represented by six tribes (Halffter and Edmonds, 1982).

Adults are characterized by: 8- to 9-segmented antennae with 3-segmented club; antennal sensilla generalized, eye divided, ommatidium structure eucone; mouthparts variable; mesothoracic spiracles specialized, intersegmentalia greatly reduced; wings with M–Cu loop and one apical detached vein; empodium usually present (except Scarabaeini); abdominal spiracles in pleural membrane, 7 pairs functional; male genitalia a bilobe with a large, well sclerotized basal piece, large internal sac well armed with plates, spines and stiff setae, and strongly sclerotized, fused, spoon-shaped temones; genital segment intermediate between a greatly reduced genital capsule and a spiculum gastrale; one ovary with a single ovariole present, karyotype highly variable; meso- and metathoracic ganglia separate and abdominal ganglion fused to the latter.

The hump-backed larvae are characterized by: 4-segmented antennae; fronto-clypeal suture present; galea and lacinia separate; 4-segmented maxillary palpi; maxillary and mandibular stridulatory areas present; epipharyngeal tormae fused, slightly asymmetrical; legs reduced, 2-segmented, without claws and stridulatory apparatus; spiracles cribriform.

The mandibles are elongate, with the apicalis dorso-ventrally flattened. The molar lobes are symmetrical, the left concave and the right convex.

Maxillae. The galea and lacinia consist of soft, flexible, densely setose lobes, with fine setal brushes.

The epipharynx is membranous, with single or double tormae, and with or without a median brush.

The labium is variable, but usually with a partly fused mentum and prementum, the latter often membranous. Palps are 3- or 4-jointed.

The tentorium usually consists of a median bridge followed proximally by another.

Unlike all other scarabaeids, the scarabaeine basal piece is well sclerotized dorsally and ventrally and a large ventral expansion is always present. The temones are unique—they are fused medially and extend laterally to form a broad, spoon-shaped structure on which the internal sac rests. The genital segment is also unique as it is intermediate between a greatly reduced genital capsule and a spiculum gastrale (d'Hotman and Scholtz, in preparation).

The karyotype in the Scarabaeinae is highly variable, from $5+neoXY$

(*Phanaeus*—Coprini), 6+Xyp (*Copris lugubris*—Coprini), 8+Xyp (*Canthon*, *Canthochilum*—Scarabaeini), 9+Xyp (the modal number, numerous examples, *Scarabaeus*—Scarabaeinini, *Onthophagus*—Onthophagini) and 10+X ($2n=21$, *Copris fricator*).

Most adults and larvae are dung feeders. Adults provision brood chambers and in many instances remain with, and care for the brood (Halffter and Matthews 1966; Halffter and Edmonds 1982).

Melolonthinae

A very large diverse cosmopolitan subfamily with numerous ill-defined tribes and groups of uncertain status.

Adults are characterized by: 9-, 10- or rarely, 11-segmented antennae with 3- to 7-segmented club; antennal sensilla intermediate; eye divided; ommatidium structure eucone; mesothoracic spiracles of intermediate complexity, intersegmentalia greatly reduced; wings with M–Cu loop and one apical detached vein; empodium present; abdominal spiracles very variable; male genitalia very variable; genital segment a Y-/U-shaped spiculum gastrale; 6 ovarioles present per ovary; karyotype usually 9+Xyp; fusion of ganglia variable.

Larvae are characterized by: 4-segmented antennae; fronto-clypeal suture present; ocelli present/absent; galea and lacinia fused proximally, free distally; 4-segmented maxillary palpi; maxillary stridulatory area present, absent on mandible; epipharyngeal tormae not fused, asymmetrical; legs well developed, 4-segmented, usually without claws (present in Macroductylini), without stridulatory apparatus; spiracles cribriform.

Adult antennae are usually 9- or 10-segmented with a 3- to 7-segmented club, but 11-segmented antennae are found in males of *Phalangosoma*. Asymmetry in the antennae, with 10 and 11 segments on the same beetle, has been found in *Rhizotrogus bellieri* (Iablokoff-Khuzorian 1977).

Melolonthines usually have 7 pairs of functional abdominal spiracles (with a distinct vestigial 8th pair) but may be reduced to 5 or 6 pairs as in *Gymnopyge*; pairs 1 and 2, 1–4, 1–5 or 1–6 may be in the pleural membrane with the rest in the sternites, or with the pair on the 7th segment on the line of fusion between the sternite and tergite, or in the tergite (*Hoplia*).

The karyotype is usually 9+X ($2n=19$, *Aserica*) or 10+X ($2n=21$, *Apogonia*).

In all melolonthines the abdominal ganglia are fused to the metathoracic ganglion but some have the meso- and metathoracic ganglia fused (Melolonthini) while others have them separate (Sericini). In *Phyllophaga* (Melolonthini) the suboesophageal ganglion is fused to the thoracic ganglia.

Larvae usually have no sign of lateral ocelli but most Sericini and Macroductylini have distinct pigment spots.

Adults may be non-feeding, or feed on foliage or flowers. Larvae usually feed on roots, but also on humus, or rarely, on dung (Scholtz 1988).

Rutelinae

A large diverse cosmopolitan subfamily with several tribes.

Adults are characterized by: 9- or 10-segmented antennae with 3-segmented club; antennal sensilla specialized; eye divided, ommatidium structure eucone; mesothoracic spiracles of intermediate complexity; intersegmentalia greatly reduced; wings with M–Cu loop and one apical detached vein; empodium present; abdominal

spiracles vary in position, 7 pairs functional; male genitalia variable but usually with ventrally or dorsally fused parameres and strongly sclerotized dorsal basal piece plate; genital capsule a spiculum gastrale with setose median plate; ovariole number variable; karyotype usually $9 + Xyp$; suboesophageal ganglion lies in prothorax.

Larvae are characterized by: 4-segmented antennae; fronto-clypeal suture distinct; mala present, 4-segmented maxillary palpi; maxillary and mandibular stridulatory areas present; epipharyngeal tormae not fused, asymmetrical; legs well developed, 4-segmented, with claws but without stridulatory apparatus; spiracles cribriform.

Abdominal spiracles lie in the pleural membrane (pairs 1–4) in the sternites (pairs 5 and 6) and the 7th pair usually lies on the line of fusion between the sternite and tergite.

Ovariole number varies in the Rutelinae. Some Rutelini (*Cotalpa*, *Paracotalpa granicollis*) have 12 ovarioles per side, another, *P. deserta* has 9, whereas Anomalini and most Rutelini have 6 per side.

The karyotype in groups other than the Rutelini and some Adorrhinyptini (*Adorrhinyptia*) (in which it is $10 + Xyp$) is usually $9 + Xyp$. In some Anomalini (*Anomala* and *Popillia*) it is $8 + Xy$.

Adults are usually foliage feeders and larvae usually feed on roots of growing plants or decaying plant matter such as wood.

Dynastinae

A large, diverse cosmopolitan subfamily with several tribes.

Adults are characterized by: 9- or 10-segmented antennae with 3-segmented club; antennal sensilla specialized; eye divided, ommatidium structure eucone; mesothoracic spiracles specialized; intersegmentalia greatly reduced; wings with M–Cu loop and one apical detached vein; empodium present; abdominal spiracles vary in position, 7 pairs functional; male genitalia with dorsally membranous basal piece and apically fused temones which extend dorsally to encircle the base of the internal sac; genital segment a Y-shaped spiculum gastrale; 6 ovarioles present per ovary; karyotype variable.

Larvae are characterized by: 4-segmented antennae; fronto-clypeal suture distinct; lateral ocelli usually present; mala present; 4-segmented maxillary palpi; maxillary and mandibular stridulatory area well developed; epipharyngeal tormae not fused, asymmetrical; legs well developed, 4-segmented with claws but without a stridulatory apparatus; spiracles cribriform.

Dynastine abdominal spiracles vary in position. Pairs 1 and 2, 1–3 or 1–4 lie in the pleural membrane, 3–6, 4–6, or 5 and 6 lie in the sternites and the 7th pair usually lies in the line of the tergite and sternite.

The karyotype in the Dynastinae is usually $9 + Xyp$ but may vary considerably. In *Oryctes* (Oryctini) it is $5 + Xy$, in *Orizabus* (Oryctini) it is $8 + Xyp$ and in some *Pentodon* (Pentodontini) it is $9 + X$ ($2n = 19$).

Adults of many species are non-feeding but others feed on below-ground plant parts. Larvae feed on plant roots or rotting vegetable matter.

Cetoniinae

This large and diverse cosmopolitan subfamily consists of several quite distinctive tribes.

Adults are characterized by: 10-segmented antennae with 3-segmented club;

antennal sensilla specialized; eye divided, ommatidium structure eucone; mesothoracic spiracles specialized, intersegmentalia greatly reduced; wings with M–Cu loop and one apical detached vein; empodium present; abdominal spiracles vary in position, 7 pairs functional; male genitalia very variable; genital segment a Y-/U-shaped spiculum gastrale; number of ovarioles varies; karyotype 9 + Xy or Xyp; thoracic and abdominal ganglia fused.

Larvae are characterized by: 4-segmented antennae; fronto-clypeal suture distinct; lateral ocelli often present; mala present; 4-segmented maxillary palpi; maxillary and mandibular stridulatory areas usually well developed (absent in some Valgini); epipharyngeal tormae not fused, asymmetrical; legs well developed, 4-segmented, with claws but without stridulatory apparatus; spiracles cribriform.

Most cetoniines have the abdominal spiracles with pairs 1–3 in the pleural membrane, 4–6 in the sternites and pair 7 in the area of fusion of the tergite and sternite (no sign of fusion remains). However, some Trichiini (e.g. *Osmoderma*) have pairs 1 and 2 in the pleural membrane and 3–6 in the sternites, while others (*Trichiotinus*, *Trigonopeltastes*), have 1–5 in the membrane and 6 and 7 in the sternites.

Ovariole number varies between 12 (Gymnetini, Cetoniini and some Trichiini, for example *Osmoderma*) and 6 per side (Cremastocheilini, Valgini and some Trichiini, for example *Trichiotinus*).

Larvae of several genera of Cetoniinae have lateral ocelli. They are present in Gymnetini (*Cotinus*), Cetoniini (*Gnorimella*, *Cetonia*), Trichiini (*Trichiotinus*, *Trigonopeltastes*, *Osmoderma*) and Cremastocheilini (*Spilophorus lugubris*).

Adults may be flower or foliage feeders (most), predatory in the nests of social Hymenoptera (Cremastocheilini) or associated with termites (Valgini). Larvae almost exclusively feed on decomposing vegetable debris although some groups only occur in specific locations such as in ant (Cremastocheilini), bird (Cremastocheilini) or termite (Valgini) nests.

Acknowledgements

The bulk of this project was undertaken in the Department of Entomology at the University of California, Berkeley. I am very grateful to John T. Doyen for hosting me there and for many hours of stimulating discussion on phylogenetics of beetles. Furthermore, I am grateful to several people who have contributed information and opinions to my scarabaeoid studies over the years—I am especially grateful to: Roy Crowson, Glasgow University; Henry Howden, Carleton University, Ottawa; Stan Caveney, University of Western Ontario, London, Canada; and John Lawrence, CSIRO, Canberra. George Poinar, UC, Berkeley, allowed me to study his fossil Ceratocanthidae.

Shortly before this paper went to press I had the opportunity to discuss some of its contents with several colleagues at the recent International Congress of Coleopterology held in Barcelona. I wish to thank Roy Crowson who remains a source of inspiration, Hannes Paulus, Institute for Biology, Freiburg, Eduard Petitpierre, Universitat de les Illes Balears, Palma de Mallorca, and J. S. Yadav, Kurukshetra University.

This project was funded in part by the University of Pretoria, and by the Foundation for Research Development, Pretoria.

References

- AREEKULL, S., 1957. The comparative internal larval anatomy of several genera of Scarabaeidae (Coleoptera). *Annals of the Entomological Society of America* **50**, 562–577.
- ARNETT, R. H., 1968. *The beetles of the United States*. Ann Arbor (The American Entomological Institute).
- BALTHASAR, V., 1963. Monographie der Scarabaeidae und Aphodiidae der palaearktischen und orientalischen Region (Coleoptera Lamellicornia). *Tschechoslowak Akademie der Wissenschaften* (1963–4).
- BÖVING, A. G. and CRAIGHEAD, F. C., 1931. *An illustrated synopsis of the principal larval forms of the Coleoptera*. New York (Brooklyn Entomological Society).
- CAMBEFORT, Y., 1987. Insectes coléoptères Aulonocnemidae. *Faune de Madagascar* **69**, 3–86.
- CAVENEY, S., 1986. The phylogenetic significance of ommatidium structure in the compound eyes of polyphagan beetles. *Canadian Journal of Zoology* **64** (9), 1787–1819.
- COSTA, C., VANIN, S. A. and CASARI-CHEN, S. A., 1988. *Larvas de Coleoptera do Brasil*. São Paulo (Museu de Zoologia, Universidade de São Paulo).
- CROWSON, R. A., 1938. The met-endosternite in Coleoptera: a comparative study. *Transactions of the Royal Entomological Society, London* **87**, 397–416.
- CROWSON, R. A., 1955. *The natural classification of the families of Coleoptera*. Hampton (Classey).
- CROWSON, R. A., 1981. *The biology of the Coleoptera*. London (Academic Press).
- D'HOTMAN, DANIELLE and SCHOLTZ, C. H., in press. Phylogenetic significance of the structure of the external male genitalia in Scarabaeoidea. *Entomology Memoirs*.
- ELLERTSON, F. E. and RITCHER, P. O., 1959. Biology of rain beetles, *Pleocomma* spp., associated with fruit trees in Wasco and Hood River Counties. *Oregon Agricultural Experiment Station Bulletin* **44**, 1–42.
- ENDRÖDI, S., 1985. *The Dynastinae of the World*. Budapest (Dr W. Junk Publishers).
- HALFFTER, G. and EDMONDS, W. D., 1982. *The nesting behavior of dung beetles (Scarabaeinae)*. Instituto de Ecologia, Mexico.
- HALFFTER, G. and MATTHEWS, E. G., 1966. *The natural history of dung beetles of the subfamily Scarabaeinae (Coleoptera, Scarabaeidae)*. Folia Entomologica Mexicana, Mexico.
- HIEKE, F., 1966. Vergleichende funktionelle Anatomie der Abdominalmuskulatur einiger männlicher Coleopteren unter besondere Berücksichtigung des genitoanal Complexes. *Deutsche Entomologische Zeitschrift* **13** (1/3), 1–165.
- HINTON, H. E., 1967. Structure and ecdysial process of the larval spiracles of the Scarabaeoidea, with special reference to those of *Lepidoderma*. *Australian Journal of Zoology* **15**, 947–953.
- HLAVAC, T. F., 1975. The prothorax of Coleoptera (except Bostrichiformia-Cucujiformia). *Bulletin of the Museum of Comparative Zoology* **147** (4), 137–183.
- HOLLOWAY, B. A., 1960. Taxonomy and phylogeny in the Lucanidae (Insecta: Coleoptera). *Records of the Dominion Museum* **3** (4), 321–365.
- HOLLOWAY, B. A., 1969. Further studies on generic relationships in Lucanidae (Insecta: Coleoptera) with special reference to the ocular canthus. *New Zealand Journal of Science* **12**, 958–977.
- HOLLOWAY, B. A., 1972. The systematic position of the genus *Diphyllostoma* Fall (Coleoptera: Scarabaeoidea). *New Zealand Journal of Science* **15**, 31–38.
- HOWDEN, H. F., 1982. Larval and adult characters of *Frickius* Germain, its relationship to the Geotrupini, and a phylogeny of some major taxa in the Scarabaeoidea (Insecta: Coleoptera). *Canadian Journal of Zoology* **60** (11), 2713–2724.
- HOWDEN, H. F., 1985. A revision of the Australian beetle genera *Bolboleaus* Howden & Cooper, *Blackbolbus* Howden & Cooper, and *Bolborhachium* Boucomont (Scarabaeidae: Geotrupinae). *Australian Journal of Zoology Supplementary Series* **111**, 1–179.
- HOWDEN, H. F., and GILL, B. D., 1988. *Xenocanthus*, a new genus of inquiline Scarabaeidae from southeastern Venezuela (Coleoptera). *Canadian Journal of Zoology* **66**, 2071–2076.
- HOWDEN, H. F., and LAWRENCE, J. F., 1974. The New World Aesalinae, with notes on the North American lucanid subfamilies (Coleoptera, Lucanidae). *Canadian Journal of Zoology*, **52** (12), 1505–1510.

- HOWDEN, H. F., and PECK, S., 1986. Adult habits, larval morphology and phylogenetic placement of *Taurocerastes patagonicus* Philippi (Scarabaeidae: Geotrupinae). *Canadian Journal of Zoology* **65**, 329–332.
- IABLOKOFF-KHNZORIAN, S. M., 1977. Über die Phylogenie der Lamellicornia. *Entomologische Abhandlungen der Staatlichen Museum für Tierkunde in Dresden* **41** (5), 135–199.
- JERATH, M. L., 1960. Notes on larvae of nine genera of Aphodiinae in the United States (Coleoptera: Scarabaeidae). *Proceedings of the United States National Museum* **III** (3425), 43–94.
- KRIKKE, J., 1984. A new key to the suprageneric taxa in the beetle family Cetoniidae, with annotated lists of the known genera. *Zoologische Verhandlungen* **210**, 3–75.
- LAWRENCE, J. F., 1982. *Coleoptera*. In: Parker, S. P. (Ed.) *Synopsis and classification of living organisms*. New York (McGrawhill).
- LAWRENCE, J. F., in press. *Coleoptera*. In: Stehr, F. W. (Ed.) *Immature Insects*. Dubuque (Kendall-Hunt).
- LAWRENCE, J. F., and BRITTON, E. B., in press. *Coleoptera*. In: *Insects of Australia*. CSIRO, Canberra.
- LAWRENCE, J. F., and NEWTON, A. F., 1982. Evolution and classification of beetles. *Annual Review of Ecology and Systematics* **13**, 261–290.
- LUNINO, M., 1984. Sistematica generica dei Geotrupinae (Coleoptera, Scarabaeoidea: Geotrupidae), filogenesi della sottofamiglia e considerazioni biogeografiche. *Bollettino del Museo Regionale di Scienze Naturali-Torino* **2**(1), 9–162.
- MACHATSCHKE, J. W., 1959. Untersuchungen über die verwantschaftlichen Beziehungen der Gattungen der bisherigen Glaphyrinae (Coleoptera: Lamellicornia). *Beitrage zur Entomologie* **9**(5/6), 528–45.
- MEINECKE, C. C., 1975. Reichensensillen und Systematik der Lamellicornia (Insecta, Coleoptera). *Zoomorphologie* **82**, 1–42.
- MONTEITH, G. B. and STORY, R. I., 1981. The biology of *Cephalodesmius*, a genus of dung beetles which synthesizes dung from plant material (Coleoptera: Scarabaeidae: Scarabaeinae). *Memoirs of the Queensland Museum* **20** (2), 253–277.
- NEL, ANNETTE and DE VILLIERS, W. M., 1988. Mouthpart structure in adult scarab beetles (Coleoptera: Scarabaeoidea). *Entomologia Generalis* **13** (1/2) 95–114.
- PAULIAN, R., 1940. Le caractères larvaires des Geotrupidae et leur importance pour la position systématique du groupe. *Bulletin de las Société Zoologique de France* **64**, 351–360.
- PAULIAN, R., 1941. La position systématique du genre *Pleocoma* Le Conte (Col. Scarabaeidae). *Revue Francaise de Entomologie* **8**, 151–155.
- RATCLIFFE, B. C., 1984. A review of the Penichrolucaninae with analyses of phylogeny and biogeography, and a description of a second New World species from the Amazon Basin (Coleoptera: Lucanidae). *Quaestiones Entomologicae* **20**, 60–87.
- REYES-CASTILLO, P., 1970. Coleoptera Passalidae: Morfologia y division en grandes grupos generos americanos. *Folia Entomologica Mexicana* **20–22**, 1–236.
- REYES-CASTILLO, P. and HALFFTER, G., 1984. La estructura social de los Passalidae (Coleoptera: Lamellicornia). *Folia Entomologica Mexicana* **61**, 49–72.
- RITCHER, P. O., 1966. *White grubs and their allies. A study of North American scarabaeoid larvae*. Studies in Entomology No. 4. Corvallis (Oregon State University Press).
- RITCHER, P. O., 1969a. Spiracles of adult Scarabaeoidea (Coleoptera) and their phylogenetic significance. I. The abdominal spiracles. *Annals of the Entomological Society of America* **62** (4), 869–880.
- RITCHER, P. O., 1969b. Spiracles of adult Scarabaeoidea (Coleoptera) and their phylogenetic significance. II. Thoracic spiracles and adjacent sclerites. *Annals of the Entomological Society of America* **62** (6), 1388–1398.
- RITCHER, P. O., 1969c. Morphology of the posterior procoxal bridges in Scarabaeoidea (Coleoptera). *The Coleopterists Bulletin* **23** (4), 89–92.
- RITCHER, P. O. and BAKER, C. W., 1974. Ovariole numbers in Scarabaeoidea (Coleoptera: Lucanidae, Passalidae, Scarabaeidae). *Proceedings of the Entomological Society of Washington* **76**, 480–494.
- RITCHER, P. O. and DUFF, R., 1971. A description of the larva of *Ceratophyus gopherinus* Cartwright with a revised key to the larvae of North American Geotrupini and notes on the biology (Coleoptera: Scarabaeidae). *The Pan-Pacific Entomologist* **47** (2), 158–163.
- SCHOLTZ, C. H., 1986. Phylogeny and systematics of the Trogidae (Coleoptera: Scarabaeoidea). *Systematic Entomology* **11**, 355–363.

- SCHOLTZ, C. H., 1988. Biology of *Sparrmannia flava* Arrow (Scarabaeidae: Melolonthinae). *The Coleopterists Bulletin* **42**(1), 57–62.
- SCHOLTZ, C. H., D'HOTMAN, D. and NEL, A., 1987. Glaresidae, a new family of Scarabaeoidea (Coleoptera) to accommodate the genus *Glaresis* Erichson. *Systematic Entomology* **12** (3), 343–354.
- SCHOLTZ, C. H., D'HOTMAN, D., EVANS, A. V. and NEL, A., 1988. Phylogeny and systematics of the Ochodaeidae (Coleoptera: Scarabaeoidea). *Journal of the Entomological Society of Southern Africa* **51** (2), 207–240.
- SMITH, S. G. and VIRKKI, N., 1978. *Animal cytogenetics* Vol. 3. Insecta 5. Berlin (Gebrüder Borntraeger).
- TANNER, V. M., 1927. The female genitalia of Coleoptera. *Transactions of the American Entomological Society* **53**, 3–50.
- VIRKKI, N., 1967. Chromosome relationships in some North American scarabaeoid beetles, with special reference to *Pleocoma* and *Trox*. *Canadian Journal of Genetics and Cytology* **9**, 107–125.
- VIRKKI, N., 1969. Sperm bundles and phylogenesis. *Zeitschrift für Zellphysiologie* **101**, 13–27.
- YADAV, J. S., and PILLAI, R. K., 1979. Evolution of karyotypes and phylogenetic relationships in Scarabaeidae (Coleoptera). *Zoologischer Anzeiger* **202** (1/2), 105–118.

Appendix

Families of the Scarabaeoidea, with the classification adopted in this work, arranged in proposed, hypothetical evolutionary sequence. Supposedly related taxa are grouped together. The system followed here is based mainly on the authors listed below but changes have been made to the status of some taxa in some groups, while in others taxa have been added or deleted according to my interpretation of the literature or experience in the groups. Groups marked with an * are probably deserving of higher status.

Passalidae (Reyes-Castillo 1970)

Aulococyclinae

Passalinae

Passalini

Proculini

Diphyllostomatidae (Holloway 1972)**Lucanidae (Holloway 1960; Howden and Lawrence 1974; Ratcliffe 1984)**

Aesalinae

Lampriminae

Lucaninae

Platycerini

Dorcini

Lucanini

Figulini

Chiasognathini

Cladognathini

Chalcodini

Nicaginae

Penichrolucaninae

Syndesinae

Sinodendrini

Ceruchini

Glaresidae (Scholtz *et al.* 1987)**Trogidae (Scholtz 1986)****Pleocomidae (Lawrence 1982)****Geotrupidae (Howden 1982; Zunino 1984)**

Bolboceratinae*

Bolboceratini

Athyreini

Geotrupinae

Taurocerastinae

Lethrinae

Glaphyridae (Machatschke 1959)

- Glaphyrinae
- Lichniinae

Ochodaeidae (Scholtz *et al.* 1987)

- Ochodaeinae
 - Ochodaeini
 - Enodognathini
- Chaetocanthinae
 - Chaetocanthini
 - Pseudochodaeini
 - Synochodaeini

Hybosoridae

Ceratocanthidae

Scarabaeidae

- Aphodiinae
 - Aegialiini
 - Aphodiini
 - Eupariini
 - Psammodiini
- Scarabaeinae (Halffter and Edmonds 1982)
 - Onthophagini
 - Onitini
 - Oniticellini
 - Coprini
 - Eurysternini
 - Scarabaeini
- Melolonthinae (Arnett 1968)
 - Melolonthini
 - Sericini
 - Pachydemini
 - Macroductylini
 - Hopliini*
 - Camertini
 - Diphucephalini
- Rutelinae (Arnett 1968)
 - Anomalini
 - Rutelini
 - Anoplognathini
 - Adoretini
 - Adorrhinyptini
- Dynastinae (Endrödi 1985)
 - Cyclocephalini
 - Oryctoderini
 - Agaocephalini

Dynastini
Phileurini
Hexodontini
Pentodontini
Cetoniinae (Krikken 1984)
Trichiini*
Valgini*
Cremastocheilini
Xiphoscelidini
Stenotarsiini
Schizorhinini
Goliathini
Cetoniini
Gymnetini
Diplognathini
Phaedimini
Taenioderini

Groups of uncertain phylogenetic status

Aclopinæ
Oncerinae
Chasmopterinae
Orphninae
Phaenomerinae
Aulonocneminae