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Chapter 2

Evolution of the Scarabaeini (Scarabaeidae: Scarabaeinae)

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Abstract

A phylogenetic analysis of the Scarabaeini, based on 244 morphological characters, including 154 multistate, and 3 biological characters, is given. Tree topologies generated from unweighted data and some weighted algorithms are similar and support only two genera in the tribe; Scarabaeus L. and Pachylomerus Bertoloni. The basal clade is Pachylomerus and sister to Scarabaeus. Kheper Kirby stat. nov., Pachysoma MacLeay, Scarabaeolus Balthasar and Sceliages Westwood stat. nov are the only supported subgenera. The genus Drepanopodus Janssens syn. nov. is synonymised with Scarabaeus and six additional names, Madateuchus Paulian, Mnematidium Ritsema, Mnematium M'Leay, Neateuchus Gillet, Neomnematium Janssens and Neopachysoma Ferreira remain synonyms. A monophyletic origin of flightlessness is generally supported with the subgenus Pachysoma the most derived group in this clade. Rolling dung balls backwards is the ancestral behaviour and predominant mode of food relocation in Scarabaeini although tunnelling, forward pushing, and carrying are also utilised by some lineages. Pushing food has evolved independently in Sceliages species and S. galenus (Westwood) and a novel mode of forward food relocation evolved in the subgenus Pachysoma. Feeding on wet dung is the plesiomorphic condition and maintained by the majority of species in the tribe. The most unusual feeding behaviours in the tribe are represented by the obligate millipede-feeding species of Sceliages and the dry dung pellets and/or detritus used by members of the subgenus Pachysoma.

Introduction

The Scarabaeini comprise some 146 species of ball-rolling dung beetles are currently classified into five genera and three subgenera. Their distribution extends throughout the Afrotropical region (including Madagascar) and southern latitudes of the Palaearctic extending into the Orient. The oldest described and most revered of these beetles is the sacred scarab *Scarabaeus sacer* Linneaus,1758 once worshiped by ancient Egyptian society in the form of the solar deity, Khepri, who controlled the sun's daily path across the sky (see Vernus, 1998).

The Scarabaeini may have evolved around the same time as other scarabaeines during the Cenozoic, stemming from ancestral scarabaeoid lineages dating back to the lower Cretaceous ca. 98-144 mybp (Krell, 2000) or possibly even the lower Jurassic ca. 180-200 mybp (Scholtz & Chown, 1995; Cambefort, 1991a; Crowson, 1981. However, Krell, 2000, reports there are currently no reliable records of fossil Scarabaeoidea existing before the Lower Cretaceous). Diversification of these scarabaeines was thought to coincide with the radiation of both angiosperms (Eocene: ca. 50 mybp) and mammalian herbivores, particularly artiodactyiforms (lower Oligocene: ca. 35 mybp), with a shift from saprophagy and mycetophagy to coprophagy by adults and larvae (Scholtz & Chown, 1995; Cambefort, 1991b. In contrast see Chin & Gill, 1996). Fossil dung balls similar to those constructed by modern Scarabaeinae were recovered from lower Oligocene deposits from Chile (Halffter, 1959) and several Uruguayan ichnofossils from the Upper Cretaceous (see Krell, 2000) suggests brood ball construction and nesting behaviour seen in modern dung beetles was established at least 65 million years ago.

The evolution of habitat use by ancestral scarabaeoids was largely influenced by climatic changes taking place during the Cenozoic. Records of grass pollen grains first appeared around the Middle Eocene (Van der Hammen, 1983), when grasslands developed and expanded giving rise to open habitats exploited by many of the radiating artiodactyls and conjointly, coprophagous beetles (Cambefort, 1991b). Modern dung beetles, especially the Scarabaeinae are, at present, more abundant in open habitats than in forests (Halffter & Matthews, 1966; Cambefort & Walter, 1991).

The majority of the species of Scarabaeini are adapted to open habitats and feed on resources that are usually patchy and ephemeral. True food specialisation is uncommon in the tribe, but does occur. All species of the genus *Sceliages*, for example, are obligate necrophages specialising on millipedes for both larval and adult feeding (Bernon, 1981; Mostert & Scholtz, 1986; Forgie *et al.*, 2002). Some flightless *Scarabaeus (Pachysoma)* utilise dry dung pellets and/or detritus that are transported into pre-prepared burrows in sandy soil and buried in moist sand for rehydration in feeding and nesting galleries (Holm & Scholtz, 1979; Scholtz, 1989).

In contrast to feeding specialisation, the Scarabaeini also contain generalist or opportunist feeders. *Pachylomerus femoralis* Kirby was caught in equal numbers in traps baited with carrion, fermenting fruit or several types of dung (Endrödy-Younga, 1982; Doube, 1991). Furthermore, the subgenus *Scarabaeus* (*Scarabaeolus*) contains species utilising dung and/or carrion. A courting pair of *S.* (*Scarabaeolus*) *xavieri* Ferreira .were observed rolling a carcass of their larger cousin, *P. femoralis* (Forgie, pers. observ.). While dung is likely the preferred diet of the majority of the Scarabaeini, some degree of opportunism is displayed in desert dwelling species. *S.* (*Scarabaeolus*) *rubripennis* (Boheman) has been observed rolling pieces of millipede along in the same manner it moves balls of dung (Mostert & Scholtz, 1986). *S.* (*Pachysoma*) *denticollis* (Péringuey) drags all manner of dung and leaf detritus into its burrows for use as food (Holm & Scholtz, 1979).

Historically, the name Scarabaeini is relatively recent (Péringuey, 1901). However, the tribe was more or less defined by Reiche (1842) when he morphologically differentiated Ateuchides (Scarabaeini) from Coprides (Mostert & Scholtz, 1986). Janssens' (1949) division of the

Scarabaeini into the subtribes Eucraniina, Alloscelina, Gymnopleurina, Canthonina, Sisyphina and Scarabaeina, formed the basis for all major subsequent works involving scarabaeine taxonomy (Balthasar, 1963; Halffter & Matthews, 1966; Ferreira, 1972; Matthews, 1972, 1974; Halffter & Edmonds,1979, 1982; Halffter & Halffter, 1989). This taxonomic definition of the Scarabaeini was attributed largely to the supposedly monophyletic evolution of horizontal relocation ("rolling") of food and often complex nesting behaviours (Halffter & Halffter, 1989). Using Balthasar's (1963) classification, Hanski & Cambefort (1991) elevated the subtribes to tribes (excl. Alloscelina) using morphological distinctions rather than the behavioural correlates shared by the guild. Hanski & Cambefort (1991) also bolstered the number of genera in the tribe to 11 by recognising several genera that were previously synonymised with the genus *Scarabaeus* L.

Recently a number of phylogenetic studies incorporating members of the Scarabaeini have been conducted using morphological data (Barbero *et al.,* 1998; Philips *et al.*, 2002; Harrison & Philips, 2003; Philips *et al.*, 2004b) and/or molecular data (Inward, 2002; Villalba *et al.*, 2002; Forgie, Bloomer & Scholtz, unpubl.; F.C. Ocampo, unpubl.). This study focuses exclusively on the Scarabaeini and is based on a broad morphological data set using taxa representing primarily adult morphological characters, and behavioural differences exhibited in the tribe. Here, we propose a new classification and discuss the evolution of flightlessness, dung manipulation, and feeding specialisation for this tribe.

Materials and methods

Taxa

A cladistic analysis of 27 species of the Scarabaeini, and *Circellium bacchus* (Fabr.) (Canthonini), *Eucranium arachnoides* Brullé (Eucraniini), *Heliocopris hamadryas* (Fabr.) (Dichitomiini) and *Synapsis tmolus* (Fischer) (Coprini) as outgroup taxa (see Appendix 1) was performed using morphological and biological characters of adults. Ingroup exemplars are used from *Drepanopodus* Janssens, *Kheper* Janssens, *Pachylomerus* Bertoloni, *Sceliages* Westwood and *Scarabaeus* L., including the *Scarabaeus* subgenera *Scarabaeus* S. Str., *Scarabaeolus* Balthasar and *Pachysoma* MacLeay. Synonyms of *Scarabaeus* used in this study appear in square brackets and include *Mnematidium* Ritsema (synonymised by Mostert & Scholtz, 1986), *Mnematium* MacLeay (synonymised by Holm & Scholtz, 1979) *Neateuchus* Gillet (synonymised by Mostert & Scholtz, 1986) and *Neopachysoma* Ferreira (synonymised with *Pachysoma* by Holm & Scholtz, 1979). No representatives from the Madagascan synonyms of *Scarabaeus*, *Neomnematium* Janssens (synonymised by Mostert & Holm, 1982) and *Madateuchus* Paulian (synonymised by Mostert & Scholtz, 1986) were used due to the unavailability of material during the course of this study. Similarly, *Scarabaeus [Mnematium] cancer* (Arrow), the largest flightless member of the tribe was not used due to its extreme rarity in collections. Phylogenetic inference of this species in relation to *S. (Pachysoma)* and other flightless Scarabaeini has however been covered by Harrison and Philips (2003).

The genus *Drepanopodus* contains the two species *D. proximus* (Péringuey) and *D. costatus* (Wiedeman). *Drepanopodus proximus* shares virtually identical morphologies with *D. costatus* apart from a slightly larger body size, less pronounced striae along the elytra and a presence of morphs exhibiting orange and/or black bicoloration of the elytra (see Holm & Kirsten, 1979). Moreover, the genus *Pachylomerus* contains two morphologically similar species, *P. femoralis* (Kirby) and *P. opacus* (Lansberge). The only differences that we diagnose the latter from *P.*

femoralis include their smaller body size and slightly more obtuse angulation of the lateral margins of the pronotum. Both species of *Pachylomerus* have large, potentially overlapping distributions (Tribe, 1976) and similar abbarent nesting behaviours (Walter, 1980; Tribe, 1976). We therefore base the systematics and phylogenetic inferences of both these genera on *D. proximus* and *P. femoralis* alone.

Outgroup representatives were chosen according to a recent phylogenetic study of the Scarabaeinae by Philips *et al.* (2004b) and taking into account outgroup selection criteria discussed by Nixon and Carpenter (1993). In this study, the above-mentioned tribes appear as the most recent ancestors with the Eucraniini as sister to the Scarabaeini. *Synapsis tmolus* exhibits a number of morphological features (Philips *et al.*, 2004b) and behavioural characteristics (Siyazov, 1913) in common with both the Dichitomiini and the Scarabaeini. *Heliocopris hamadryas* is the most basal macropterous exemplar of the outgroup and was also used by Philips *et al.* (2004b). *Circellium bacchus* is a large brachypterous canthonine possessing many plesiomorphic characters shared by the Scarabaeini (see Appendix 4; Fig. 153.01). This species was described by monotypy by Fabricius in 1781 as a species of *Scarabaeus* and included as a monotypic genus in the Scarabaeini by Janssens (1938) and Ferreira (1972).

Authors of each taxon used in this study are listed in Appendix 1 and are omitted from the main body of the text. Moreover, in the 'Results and discussion' section, the genus *Scarabaeus* S. L. incorporates species in the subgenera *Pachysoma, Scarabaeolus* and *Scarabaeus* which includes species formerly placed in *Mnematidium*, *Mnematium*, and *Neateuchus*. Similarly, the subgenus *Pachysoma* S. L. incorporates *Neopachysoma*. Likewise, discussion of *S.* (*Scarabaeolus*) S. L. incorporates *S.* (*Mnematium*) *silenus* and *S.* (*Scarabaeolus*) *scholtzi*. Both species were assigned to this subgenus by Mostert & Holm (1982) because of their possession of a vestigial second mesotibial spur. *Scarabaeus* (*Scarabaeolus*) S. Str. excludes these two species since they share no other synapomorphies.

Preparation of taxa

Preparation of the material was based on the protocol outlined by Philips (2000) and Pretorius *et al.* (2001). Pinned specimens and those preserved in alcohol were rehydrated in hot water for at least 30 minutes before being immersed in lactic acid and warmed for one to three hours to facilitate maceration of tissues. Complex parts requiring further clearing of tissue were placed in a warmed solution of 10% KOH for several minutes then rinsed in water and 70% EtOH.

Characters

We designed 244 characters specifically for the Scarabaeini, including 154 multistate characters (see Appendix 2 for characters and states & Appendix 3 for their data matrix), from the sclerotised internal and external structures with no or minimal morphological degradation from wear and tear. Characters and their states were described using the terminology of Doyen (1966), Lawrence and Britton (1991). Functional understanding and descriptive terminology of the metendosternite was obtained from Pretorius *et al.* (2001) and Crowson (1938, 1944).

As many characters as possible were found to hypothesise unbiased relationships within the tribe (see Grandcolas *et al.*, 2001) including many beyond the traditional ones previously used. We hope that by using a large data set, during the analysis the homoplastic character set will cancel each other out through their random signal (noise) enabling the set based on common ancestry to produce the "real" (or "true") tree. Three biological/behavioural characters were also included as there is no reason to exclude them as evidence. These types of characters are as heritable as any other and can define monophyletic groups as well as morphological or molecular data (see Michener, 1953, Wenzel 1992, 1993; Schuh, 2000). Soil preference (char. 245) of the taxa was coded with a majority rules (80-100%) collection occurrence on either sand or clay soil types using data by Davis (1996, 1997). Taxa occurring equally on both soil types were coded as generalists. The remaining two characters coded the principal activity periods of the taxa (char. 244) and their modes of food relocation (char. 246). In the Results and discussion, the number of any character is separated from its accompanying state(s) by a forward slash and appears within parentheses e.g. (150/1).

Analyses

The character matrix was compiled in Dada, Version 1.2.7 (Nixon, 1998). The Mop-up option in Dada found no uninformative autapomorphic characters. Characters in both the total data set and the restricted data set were then spawned in Nona (Goloboff, 1993a) with 1000 repetitions to ensure all the shortest trees were found utilising branch and bound search options with randomised taxon order in each run. No further analyses were carried out with the total characters data set. Trees recovered from this data provide a set of hypotheses for comparative purposes with those inferred from analyses of the restricted data set.

Nona trees from the restricted data set were subjected to successive approximations weighting (Farris, 1988) using Hennig 86 version 1.5 (using xs w; mh* and bb* command string). Trees were also calculated using Parsimony and Implied Weights (PIWE) version 2.6 (Goloboff, 1997; 1993b). Up to 5 levels (1-5; 3 = default) of concavity (CO) were applied to the characters (using rs0; hold1000; hold/100; mult*100; command string). High repetitions run in Nona ensured the best PIWE trees were generated. Bremer support (decay index) was calculated with Nona up to a value of 10, i.e. searching for trees up to 10 steps longer in the tree(s) submitted for calculation. Support is based on trees found with unweighted data.

Character state distributions were examined with Clados version 1.8.1 (Nixon, 1993). All software programmes were run in conjunction with WinClada (BETA), Version 0.9.9 (Nixon, 1999). Character polarizations by rooting trees between their ingroups and outgroups (Nixon &

Carpenter, 1993) was not required. Three out of the four outgroup taxa were the most basally positioned in all trees generated. The exception is the eucraniine, *Eucranium arachnoides* whose unorthodox positioning in all but two trees examined is discussed.

Deactivated Characters

Twenty-eight characters directly associated with flight and flightlessness were deactivated in the total characters data set after the initial Nona analysis of the total characters data set. We did so to reduce any bias they may have on phylogenetic relationships among flightless taxa and among these taxa and the remaining tribal members. All subsequent analyses of the 'restricted data set' could therefore likely to provide more accurate representations of tribal evolution. Hence, all wing characters (i.e. Characters, 145-161) and characters with states exclusively shared by flightless Scarabaeini (i.e. Pronotum, 86; (Wings, 145,150); Elytra, 162, 164, 166; Mesonotum, 178, 183; Metanotum, 185, 187, 192, 194; Metendosternite, 206) were deactivated.

Results and discussion

Total Data Nona Trees

Three trees based on the unweighted total data each have a length of 1805 steps, and consistency (C.I.) and retention index (R.I.) values of 0.25 and 0.50 respectively (consensus Fig. 1). *Pachylomerus femoralis* appears the most basal member of the Scarabaeini. The flightless Scarabaeini are monophyletic and contain the most derived members within the tribe with *S.* (*Pachysoma*) S. L. representing the most highly evolved of these lineages. Several other clades are monophyletic including *Kheper*, *S.* (*Pachysoma*) S. L., *S.* (*Scarabaeolus*) S. Str., *S. rugosus*

+ *S. rusticus*, *Sceliages*, and the outgroup taxa *Heliocopris hamadryas* + *Synapsis tmolus*. The topologies of these trees are incongruent in two ways: The genus *Kheper* is placed as sister to the tribe in the first of the 3 trees. The topologies in the other two unweighted trees place the genus *Kheper* within *Scarabaeus* S. L. as sister to the nocturnal monophyletic clade forming the most basal clades within *Scarabaeus* S. L. Also, alternative relationships among *S. satyrus*, *S. [Neateuchus] proboscideus* and *S. zambesianus* resulted in these nodes collapsed by strict consensus, although *S. goryi* remained the most basal nocturnal representative in all trees.

Restricted Data Nona and Hennig86 Trees

A single tree was recovered from the unweighted data following the deactivation of 28 characters associated with flight and flightlessness (Fig. 2: C.I. = 0.24, R.I. = 0.50, length = 1665). Successive approximations weighting of this tree also generated a single tree (C.I. = 0.33, R.I. = 0.67, length = 1016) by the third run. The topologies of both trees are very similar with the exception of a few slight incongruencies appearing in the more apical nodes of the weighted tree; the *Sceliages* taxa become the derived members of a larger clade in which S. (*Scarabaeolus*) *flavicornis* and *S.* (*Scarabaeolus*) *bohemani* are basal. *Scarabaeus rusticus* + *S. rugosus* form a clade with *S. galenus* + *S. westwoodi* and the *Kheper* clade is sister to the nocturnal clade positioned as *S. goryi*, (*S. satyrus*, (*S. [Neateuchus] proboscideus* + *S. zambesianus*)).

The placement of *Eucranium arachnoides* outside the Scarabaeini as seen in both topologies may be the most likely hypothesis (Fig. 2). In contrast, the evolutionary scenerio in which macropterous evolved from a brachypterous condition is unlikely. The most basal dichotomy of the Scarabaeini separates the monophyletic clade of flightless *S.* (*Pachysoma*) S. L. from other basal flightless species and the more derived flighted species of *Scarabaeus*. Flightlessness is therefore portrayed paraphyletically in both topologies either including or excluding *Eucranium*. *Scarabaeus [Mnematidium] multidentatus* bridges the evolutionary transition from flightlessness to flight as the most basal Scarabaeini with fully developed wings. Two or more origins of the loss of flight are probable considering its occurrence independently thousands of times in the Coleoptera (Kavanaugh, 1985; Wagner & Liebherr, 1992). However, brachyptery is generally accepted as a derived condition from a macropterous ancestor (e.g. Darlington, 1936; Goldschmidt, 1940; Southwood, 1962; Den Boer *et al.,* 1980; Harrison, 1980; Kavanaugh, 1985; Roff, 1990; Emerson & Wallis, 1995. See also Scholtz, 2000.). It therefore seems less likely the stem species of the oldest clades in the tribe are flightless. Moreover, to regain adaptations needed for flight is also unlikely (Liebherr, 1988; Andersen, 1993. In contrast see Whiting, 2003). Therefore, except for the placement of *Eucranium* in the outgroup, we consider this topology showing flightless species to be basal, as poorly supported.

Restricted Data PIWE Trees

Parsimony analysis under implied weights (PIWE) estimates character weights during a search for trees that have maximum total fit, where fit is a concave function of homoplasy. Total fit increases as concavity decreases along with decreasing strength of weighting towards characters with homoplasy. Characters supporting a tree topology that are more homoplastic are less influential when compared with a tree of equal length whose topology is supported by characters with less homoplasy (see Goloboff, 1993b). Trees calculated with lower CO values have the strongest weighting (= reliability) against homoplastic characters. The antithesis applies to the higher CO values.

Trees found with concavity of 1 produced 2 topologies with a fit of 424.8 and lengths of 1701 and 1703 steps. Trees calculated at CO = 2 resulted in a single topology (Fig. 3) with a fit of 662.8 and a length of 1703 steps. Weighting with the default concavity value of 3 produced 2 trees with a fit of 837.3 and lengths of 1698 and 1700 steps. PIWE trees with the strongest weighting (CO = 1, 2) share similar topologies inferring a single origin of flightlessness. All

PIWE trees examined depict the loss of flight as a derived adaptation, but those with the strongest weighting separate macropterous *S. westwoodi*, *S. galenus* and *S. [Mnematidium] multidentatus* from the rest of the scarabaeines capable of flight by placing them as basal lineages in the flightless clade. Incongruence between these trees occurs with the placement of *S. westwoodi* either basal to *S. galenus* and *S. [Mnematidium] multidentatus*, or as sister to the remaining clades (i.e. one CO = 1 tree, both CO = 3 trees). Strict consensus of the CO = 1 trees collapsed the node supporting the placement of *S. westwoodi* forming a basal trichotomy in the tribe. Further incongruence with the topology of the CO = 2 tree is the placement of *E. arachnoides* within the *S.* (*Pachysoma*) S. L. clade in both CO =1 trees and 1 of the CO = 3 trees.

In contrast, the individual trees calculated at a concavity levels of 4 (Fig. 4) and 5 (Fig. 5) had fits of 973.3, and 1081.5 and lengths of 1673 and 1684 steps respectively. Hence, trees produced with concavities of 4 and 5 have predictably higher fits but are shorter than the trees recovered from the lower CO values. In terms of maximising explanatory power and the robustness of hypotheses testing tribal phylogeny, the tree of minimum length is preferred (Kluge, 1997). In this instance, the shortest length tree calculated with CO = 4 (Fig. 4) shares a topology virtually congruent with that of the 3 trees calculated using the total characters data set (Fig. 1) and is up to 132 steps shorter. The only incongruencies between the CO = 4 tree and the 3 total characters data trees lie in the placement of *S.* (*Pachysoma*) *bennigseni* or *S. (Pachysoma) hippocrates* as the most basal member of the *S.* (*Pachysoma*) S. L. clade, and *S. zambesianus* or *S. satyrus* as the most derived member of the nocturnal clade. Moreover, 1 of the 3 total characters data trees does not support the basal placement of the genus *Kheper* within *Scarabaeus* S. L. as sister to the nocturnal clade. From an evolutionary perspective, congruence in these topologies further corroborates as close as possible the true phylogenetic inference.

The tree calculated at a concavity of 5 (Fig. 5) is the only hypothesis of the tribe's evolution without the flight and flightlessness characters where *Kheper* does not appear within *Scarabaeus* S. L. Rather, the *Kheper* clade is portrayed as the sister clade to *Scarabaeus* S. L. In turn, both *Scarabaeus* S. L. and *Kheper* are sisters to *Pachylomerus*. The nocturnal clade is not monophyletic but instead appears as a basal paraphyletic clade of *Scarabaeus* S. L. *Scarabaeus rugosus* is placed as sister of *S. westwoodi* and the subgenus *Scarabaeolus* S. Str. appears paraphyletic (see Figs 2, 3).

Regardless of which tree is examined, the same patterns are illustrated: The monophyly of flightlessness as a derived adaptation. The obligate millipede feeding genus *Sceliages* are closely related to *S.* (*Scarabaeolus)* S. Str. either as a sister clade or a derived monophyletic clade. Feeding strategies not involving the direct utilisation of wet dung but rather carrion or dry dung and detritus evolved on several independant occasions. The same holds true for shifts in the mode of food relocation from rolling in a backwards direction. *Pachylomerus* is the sister genus to *Scarabaeus* S. L. Members of *Pachylomerus* not only engage in telecoprine food relocation by rolling backwards or pushing forwards but also tunnelling in true paracoprine fashion. Finally, taxa that have evolved adaptations required for nocturnal activity have done so monophyletically (Figs 1-4) or paraphyletically (Fig. 5).

Tree Support

The Bremer calculations on the complete and restricted unweighted data sets indicate very strong support for the monophyly of *Kheper*, *Sceliages* and the entire tribe including the eucraniine, *E. arachnoides* (Figs 1, 2). A strong decay value of 5 supports each node of the flightless lineages *S.* (*Scarabaeolus*) *scholtzi*, *S. [Mnematium] ritchei*, *S. [Mnematium] silenus*, their sister *S. [Mnematidium] multidentatus* and their relationship with *S.* (*Pachysoma*) S. L. following the deactivation of characters associated with flight and flightlessness (Fig. 2).

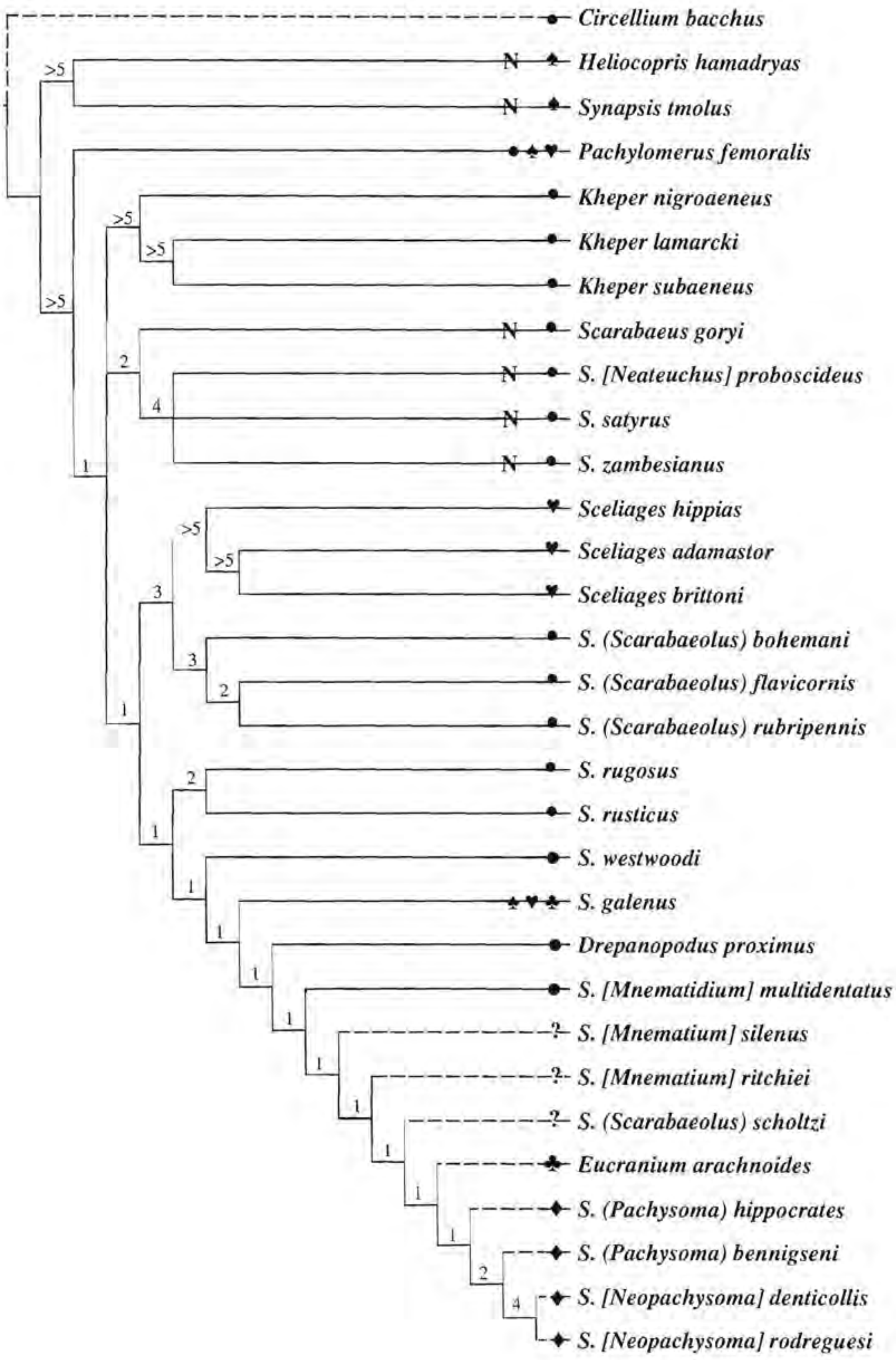

Fig. 1. Phylogeny of the Scarabaeini (Coleoptera: Scarabaeidae). Total Characters data set. NONA, unweighted, consensus of 3 trees (CI = 0.25, RI = 0.50, length = 1835). Branch supports (Bremer decay indices) provided above nodes. Flightless taxa (dashed branch). Nocturnal taxa (N). Modes of food relocation: "Rolling", ●; Tunnelling, ♠; Pushing, ♥; Dragging, ♦; Carrying, ♣; Unknown, ?.

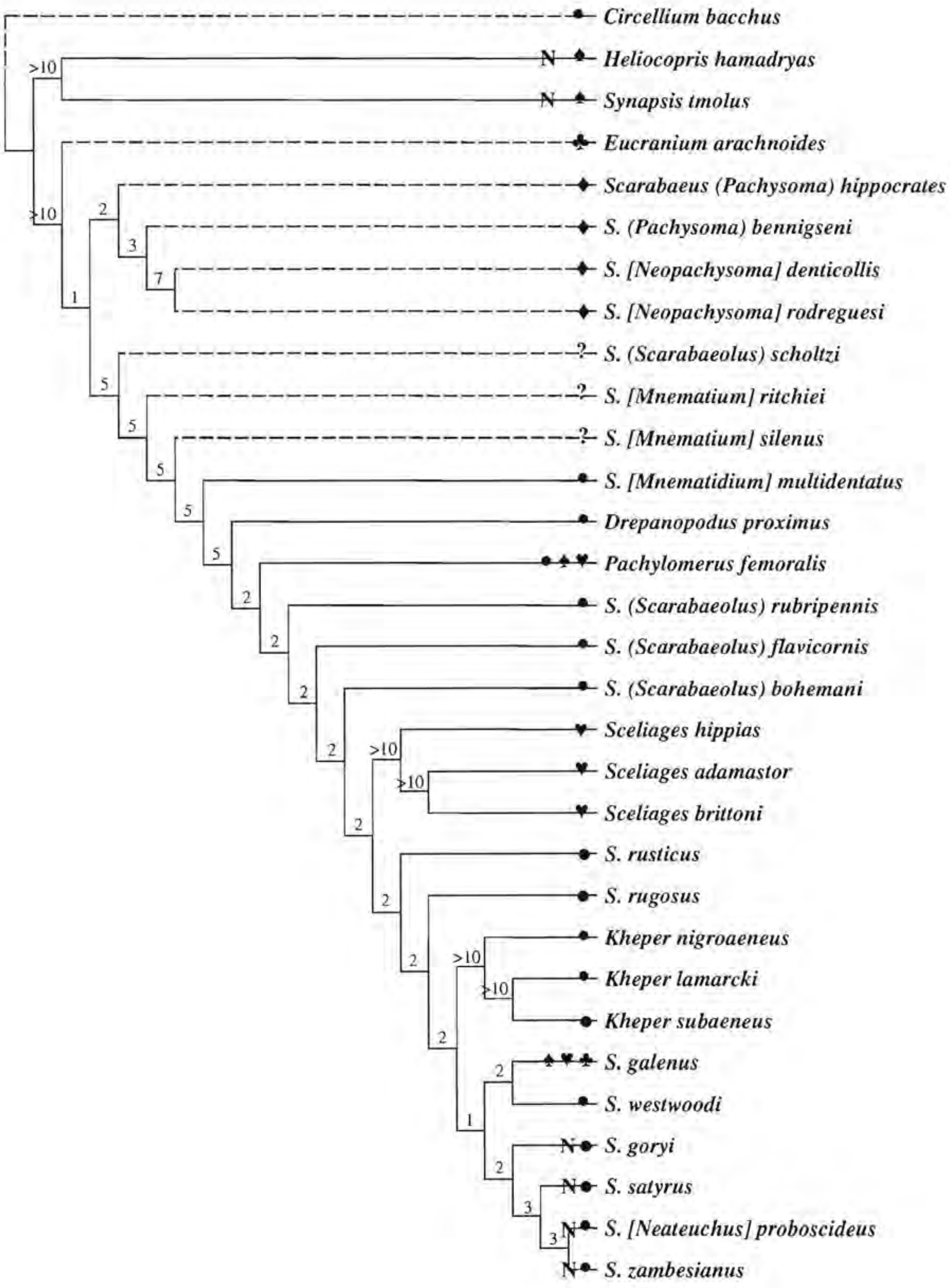

Fig. 2. Phylogeny of the Scarabaeini (Coleoptera: Scarabaeidae). Flight and flightlessness characters deactivated. NONA, unweighted, single tree (CI = 0.24, RI = 0.50, length = 1665). Branch supports (Bremer decay indices) provided above nodes. Flightless taxa (dashed branch). Nocturnal taxa (N). Modes of food relocation: Rolling, ●; Tunnelling, ♠; Pushing, ♥; Dragging, ♦; Carrying, ♣; Unknown,?.

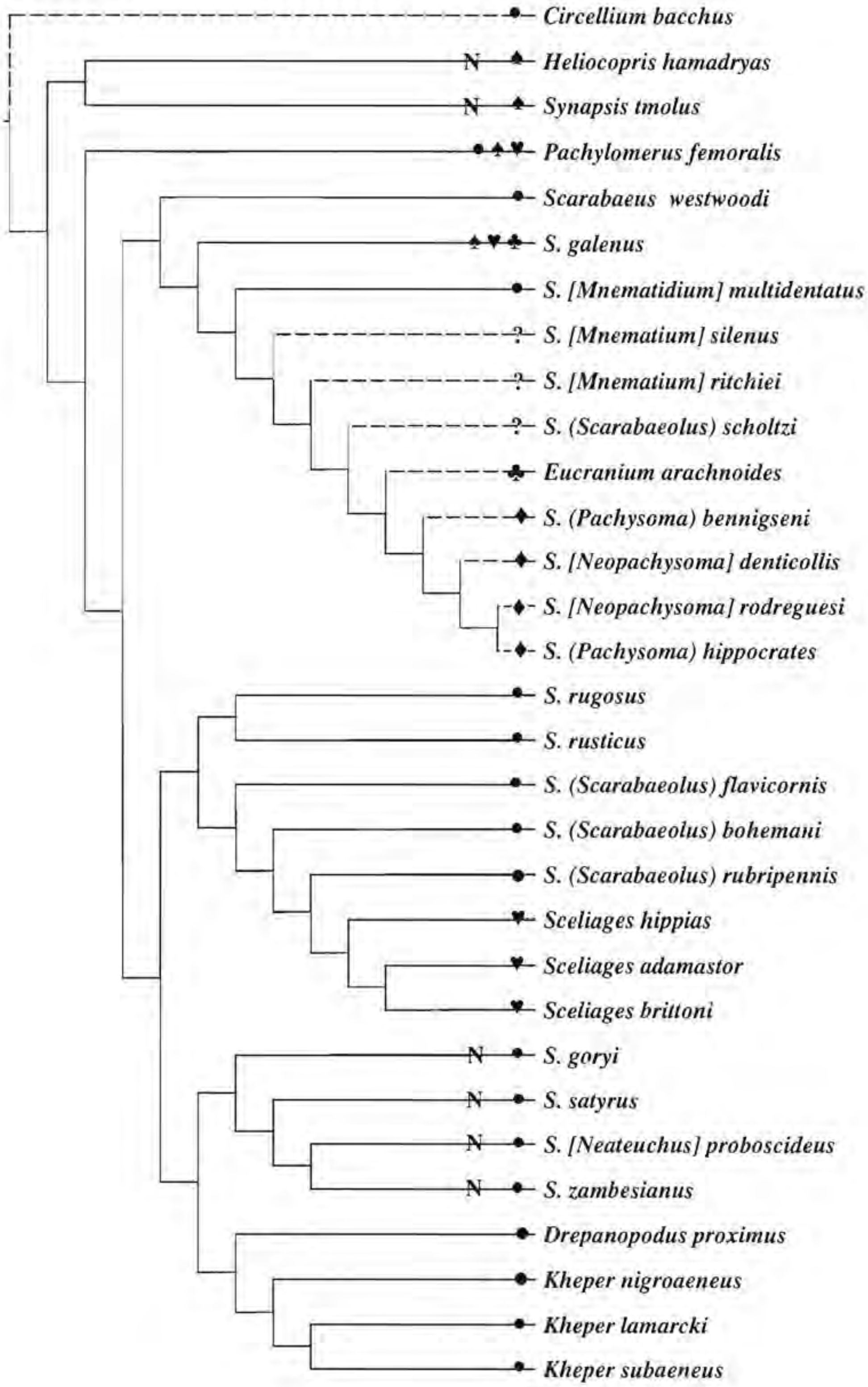

Fig. 3. Phylogeny of the Scarabaeini (Coleoptera: Scarabaeidae). Flight and flightlessness characters deactivated. PIWE (Parsimonious Implied Weights), single tree (CI = 0.24, RI = 0.48, fit = 662.8, length = 1702), CO = 2; Strong weighting against homoplasy. Flightless taxa (dashed branch). Nocturnal taxa (N). Modes of food relocation: "Rolling", •; Tunnelling, ♠; Pushing, ♥; Dragging, ♦; Carrying, ♣; Unknown, ?.

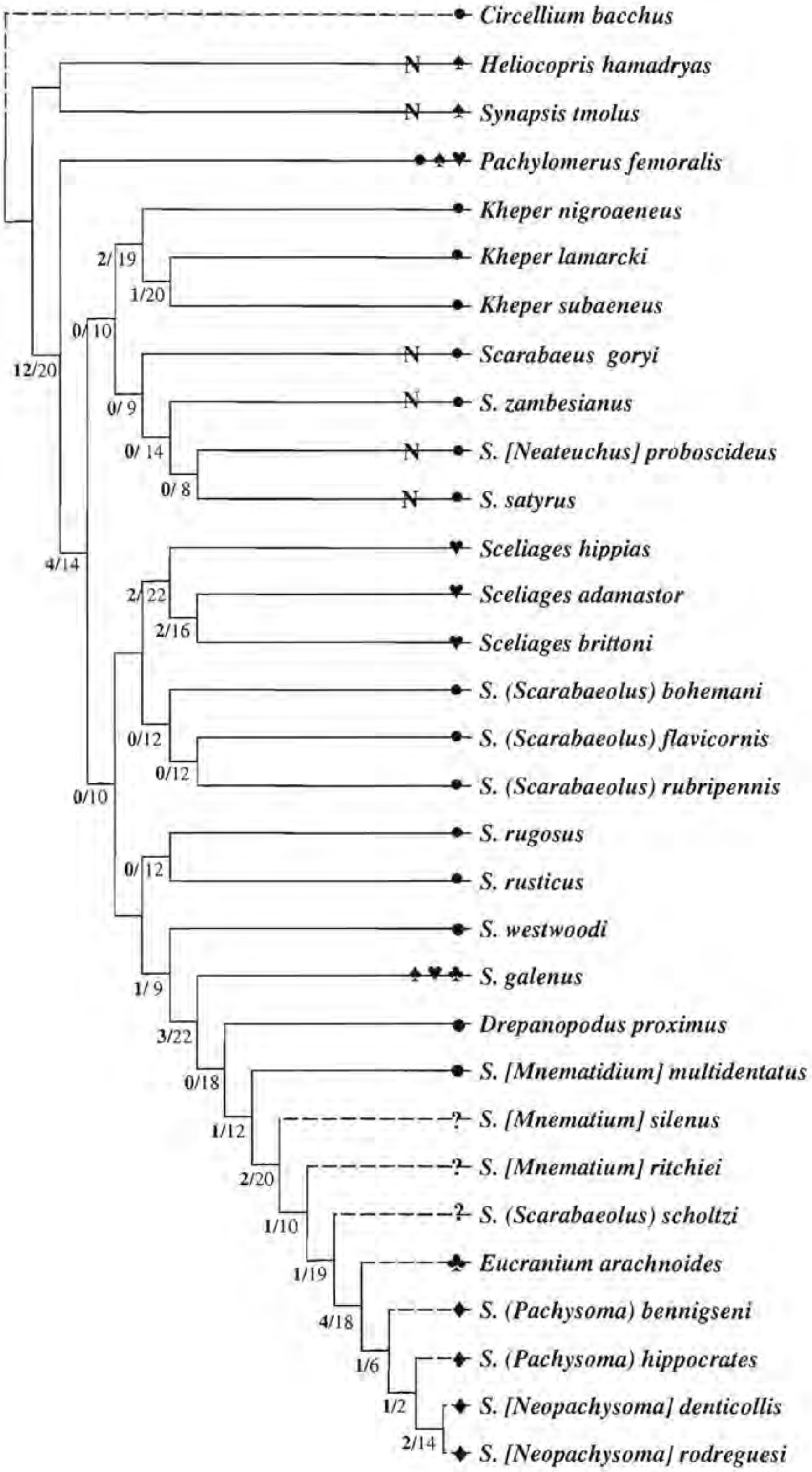

Fig. 4. Phylogeny of the Scarabaeini (Coleoptera: Scarabaeidae). Flight and flightlessness characters deactivated. PIWE (Parsimonious Implied Weights), single tree (CI = 0.24, RI = 0.49, fit = 973.3, length = 1673), CO = 4; slight weighting against character homoplasy. Unique synapomorphies (Bold)/homoplasious synapomorphies provided below nodes. Flightless taxa (dashed branch). Nocturnal taxa (N). Modes of food relocation: "Rolling", ●; Tunnelling, ♠; Pushing, ♥; Dragging, ♦; Carrying, ♣; Unknown, ?.

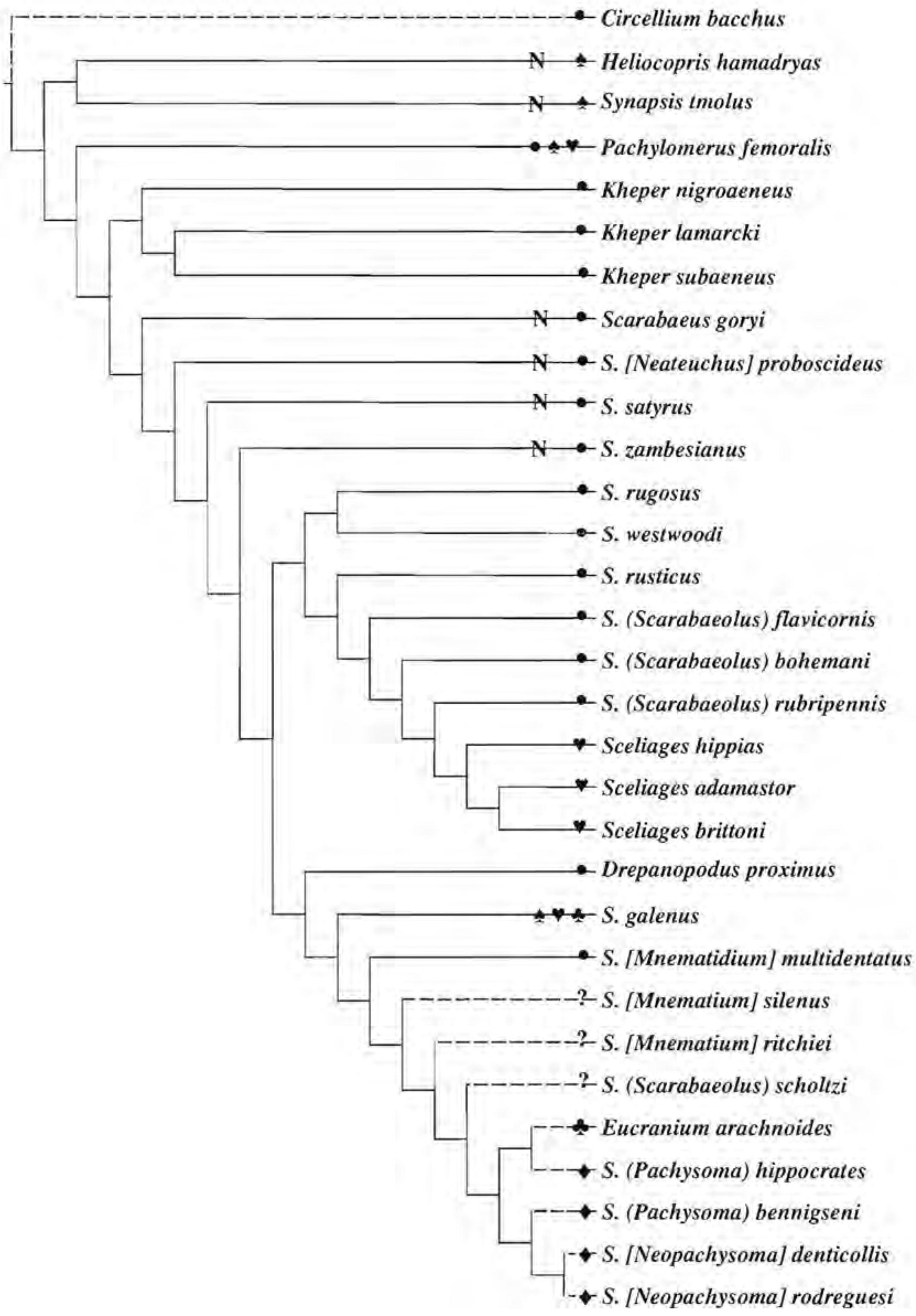

Fig. 5. Phylogeny of the Scarabaeini (Coleoptera: Scarabaeidae). Flight and flightlessness characters deactivated. PIWE (Parsimonious Implied Weights), single tree (CI = 0.24, RI = 0.49, fit = 1081.5, length = 1684 steps), CO = 5; minimal weighting against character homoplasy. Flightless taxa (dashed branch). Nocturnal taxa (N). Modes of food relocation: "Rolling", ●; Tunnelling, ♠; Pushing, ♥; Dragging, ♦; Carrying, ♣; Unknown, ?.

Bremer calculations on this data set indicate poor support among the remaining relationships within the tribe. Surprisingly, this includes support for the monophyly of the *S.* (*Pachysoma*) S. L. clade and branch support within, with the exception of the node whose character states distinguish the 2 *S. [Neopachysoma]* species (branch support = 7). Much weaker branch support is evident in the trees generated from the total data set (Fig. 1) suggesting the 28 characters associated with flight and flightlessness may have contributed significantly to conflicting and noisy data. Bremer support values tend to reflect the number of synapomorphies and/or homoplasious character states at each node. A high degree of homoplasy is evident in the data. However, based on the retention indices (R.I. = 0.49-0.50), many of the homoplasious characters appear quite informative. Philips *et al.* (2004b) also report a high incidence of convergent homoplasious characters occurring in the Scarabaeinae citing noisy data or rapid evolution as suggested causes. Källersjö *et al.* (1999) demonstrate that rapidly evolving, highly homoplastic characters are more informative than previously thought (e.g. Swofford *et al.*, 1996), and can be reliable as indicators that improve phylogenetic structure.

Trends among trees

All of the trees we examined (excluding consensus trees) portray 4 general topologies representing tribal evolution. Based on both shortness of tree length and character fit, we consider the most likely topology is that of the single PIWE tree calculated at CO = 4 (Fig. 4). The topological robustness of the trees calculated at the lowest concavity levels (i.e. CO = 1, 2 and 3) also provides a plausible hypothesis (Fig. 3). However, weighting at this extreme level against homoplastic characters that may be phylogenetically informative (e.g. Källersjöv *et al.*, 1999) is deemed unacceptable in terms of obtaining truly parsimonious cladograms by some (e.g. Kluge, 1997). While the remaining topologies resulting from analyses with the restricted data set are considered less likely to convey believable phylogenetic inferences of Scarabaeini evolution, they are not ruled out. What is most important is the homogeneity of trends across virtually all trees examined in providing strong evidence to support tribal systematics and our interpretation of the evolution of flightlessness, food relocation, and feeding specialisation in the Scarabaeini.

Scarabaeini Systematics

Systematics of the tribe are based on the apomorphies seen in the topology of figure 4 which represents the most supported and therefore preferred tribal phylogeny as previously discussed. The placement of all the characters and states on this tree are found in Appendix 4 (Figs 153.01-10) and their descriptions are found in Appendix 2. A proposed classification (Table 1) of the tribe is based on the concordance of these clades in the majority of the trees examined.

Scarabaeini Péringuey, 1901

The monophyly of the Scarabaeini is supported in this study by 32 synapomorphic character states with 12 of them that are unique to the tribe (Fig. 153.01). Two are head characters (2/0, 10/0), 1 of the mouthparts (41/1), 1 pronotum (79/1), 5 leg (104/0,111/0,121/1,122/2,125/2), 2 meso-metasternite (201/2, 203/0) and 1 abdominal spiracular character (219/1). While the presence of 4 clypeal teeth (0/1) is not a unique synapomorphy for the Scarabaeini, this character proves more diagnostic for the tribe when described in conjunction with the presence of a third pair of dentations on the genae formed by a distinct (10/0) notch-like emargination dividing the epistoma of each gena and the clypeus. Mostert & Scholtz (1986: 6) also described many synapomorphs that define the tribe including the presence of 3 pairs of forward projecting dentations on the head. The remaining character states are homoplastic but still contribute to a very robust node with strong Bremer supports in both unweighted analyses (Figs 1, 2). None of the homoplastic character states supporting the basal node defining the Scarabaeini are apomorphies of *E. arachnoides*.

Pachylomerus Bertoloni, 1849

Definitive support for the monophyly of genus is indicated by 36 apomorphic character states including an absence of a definitive anterior ventral carina located distally on the profemora (101/2) which is unique to the genus (Fig. 153.02). Support for the basal placement of *P. femoralis* in a phylogenetic study of the flightless Scarabaeini by Harrison & Philips (2003) is based on the four controverted characters as follows: a small distinct projection on the anterior edge of the pronotum; coarse serrations on the lateral edge between the external protibial denticles; a single, well-developed mesotibial spur; and partial basal sclerotisation of the inner ligular lobes armed with tufted setation on the apices.

Table 1. Proposed classification of the Scarabaeini (Coleoptera: Scarabaeidae). 1, described as subgenus by Balthasar (1965); 2, synonymised by Holm and Scholtz (1979); 3, synonymised by Mostert and Holm (1982); 4, synonymised by Mostert and Scholtz (1986); 5, subgeneric status proposed by Harrison *et al.* (2002).

Current recognised genera of the Scarabaeini	Genera to be maintained	Proposed/maintained subgenera of *Scarabaeus* sensu lato	Proposed/maintained synonymy with *Scarabaeus* sensu stricto
Drepanopodus	*Scarabaeus* S. L.	*Kheper* **stat. nov.**	*Drepanopodus* **syn. nov.**
Kheper	*Pachylomerus*	*Sceliages* **stat. nov.**	
Pachylomerus			*Madateuchus*[4]
Sceliages		*Scarabaeus*	*Mnematidium*[4]
Scarabaeus		*Scarabaeolus*[1]	*Mnematium*[2]
		Pachysoma[5]	*Neateuchus*[4]
			Neomnematium[3]

Mostert & Scholtz (1986) list several apomorphies to justify the validity of the genus *Pachylomerus* including sexual dimorphism, reduced tarsal claws, a broad sculptured pronotum and a highly evolved aedaegus. They also recognise four plesiomorphic states of the tribe retained by the genus; an ovate and slightly concave basal lamella of the antennal club, externally serrated protibia, two tarsal claws and closely set elytral carina. Moreover, Mostert & Scholtz (1986) indicate a number of derived characters *Pachylomerus* shares with the genus

Kheper thereby suggesting they are reasonably close phylogenetically and morphologically and are the more highly evolved lineages of the tribe. All but one tree (not shown) in our study supports *Pachylomerus* as sister to all other taxa in the tribe. As recognition of the former does not violate monophyly of the latter, *Pachylomerus* is maintained/recognised as a genus.

Kheper Janssens, 1940

Only 2 out of 20 characters supporting the *Kheper* clade are unique (Figs 153.02-03). The distal apex of the mesotibia is armed with a spur that is completely fused, becoming a tibial extension (103/2) which is flush with the ventral margins of the mesotibia (125/1). The creation of the genus by Janssens (1940) was based largely on the presence of one tarsal claw, an apomorphic state also shared by the genus, *Drepanopodus*. The separation of *Kheper* from *Drepanopodus* and *Scarabaeus* S. L. survived 2 demotions to subgenera by Balthasar (1963) and Halffter & Matthews (1966). Mostert & Scholtz (1986) highlighted several autapomorphies supporting the phylogenetic distinction of *Kheper* from *Scarabaeus* S. L. and therefore its validity as a genus. These characters included: no serrations between or proximal to the external protibial denticles, of which the most proximal of the 4 is reduced; a single fixed tarsal claw; inflected meso- and metatibial spurs; and laterally expanded apical hooks of the aedaegus parameres. Our character states 111/2 and 112/2, in combination, support the lack of serrations along the entire length of the external protibial margin as an autapomorphy for the genus. Both *S. [Neopachysoma]* spp and *S. [Neateuchus] proboscideus* lack serrations between the external protibial denticles but are armed with serrations proximal to the dentation. *Scarabaeus westwoodi* lacks setation proximal to the dentation but is armed with hairs between the denticles. Acording to our study, the remaining characters listed by Mostert & Scholtz (1986) are not exclusive to the genus *Kheper*. Both studies by Mostert & Scholtz (1986) and Harrison & Philips (2003) depict *Kheper* as a highly derived lineage of *Scarabaeus* S. L. closely related to *Pachylomerus* and *Scarabaeus sacer* L. respectively. Our results suggest the genus is also a derived lineage of Scarabaeus S. L., strongly characterised by autapomorphies and strong bremer support values in both unweighted analyses (Figs 1, 2). Moreover, *Kheper*'s apical positioning within *Scarabaeus* S. L. is congruent in virtually every tree generated by this study. In total, the evidence presented herein supports the monophyly of *Kheper* but as a subgenus (**stat. nov.**).

Sceliages Westwood, 1837

Sceliages lineages are medially placed within *Scarabaeus* S. L. in all of the trees recovered. Mostert & Scholtz (1986) suggest this genus has undergone the least morphological evolution in the tribe possessing an array of plesiomorphic character states including the large second mesotibial spur regarded as the principal diagnostic character. All trees generated in our phylogeny clearly depict *Sceliages* as monophyletic with very strong Bremer support. Out of 24 synapomorphies supporting the clade, only evenly tapered (slight bulge on ventral surface) femora (97/3), and spatulate, relatively straight, pointed major (outer) tibial spur (123/3) are unshared by the remaining members of the tribe (Fig. 153.05). In addition to the strong nodal support for the clade, members of the genus display behavioural monophyletic support in being obligate necrophages that exclusively utilise millipedes for feeding and reproduction (Forgie *et al.*, 2002). Mostert & Scholtz (1986:22) maintained the genus on the grounds it can be cladistically distinguished from *Scarabaeus* S. L. by retaining plesiomorphies not found in even the most plesiomorphic species of *Scarabaeus* S. L. (e.g. *S. (Scarabaeolus) rubripennis*). We support Mostert & Scholtz (1986) in terms of the monophyly of the clade but not as the most ancestral lineage. Its medial position in all trees recovered indicates that *Sceliages* is a derived *Scarabaeus* S. L. with distinct morphological and behavioural apomorphs. Therefore, *Sceliages* is considered a subgenus (**stat. nov.**).

Scarabaeus (*Scarabaeolus* Balthasar, 1965*)*

Scarabaeolus was described as a subgenus by Balthasar (1965). Since then, its status has been doubtful, as the group is largely based on the presence of a second (vestigial) mesotibial spur (Mostert & Scholtz, 1986:16). Both *S. [Mnematium] silenus and S.* (*Scarabaeolus*) *scholtzi* are morphologically convergent with *S. [Mnematium] ritchiei and S. [Mnematium] cancer,* two species that lack a second mesotibial spur. The development and/or subsequent loss of such a small, non-functional spur must have occurred more than once (Mostert & Holm, 1982). Our study is concordant with Mostert & Holm (1982), and indeed supports the polyphyly of *S. (Scarabaeolus)* S. L. Ultimately, we find no reason to affiliate *S.* (*Scarabaeolus*) *scholtzi* or *S. [Mnematium] silenus* with the subgenus *Scarabaeolus* and propose their inclusion in the subgenus *Scarabaeus.*

Species belonging to *S.* (*Scarabaeolus*), in the strict sense, (e.g. *rubripennis, flavicornis* and *bohemani*) are supported by monophyly with only 12 homoplastic synapomorphies (Figs 1, 4) and are, at most, paraphyletic (Figs 2, 3, 5) in the less preferred hypotheses. Their recognition is also supported by a small body size in comparison to the majority of the Scarabaeini (Mostert & Scholtz, 1986). Furthermore, members of *S.* (*Scarabaeolus*) S. Str. are confined to the southern half of the Afrotropics with relatively few species occurring outside the region (Endrödy-Younga, 1978). The second mesotibial spur, in conjunction with other evidence we have discussed differentiating *S.* (*Scarabaeolus*) S. Str., is sufficient reason not to synonymise it with *Scarabaeus* S. Str. and we therefore maintain its subgeneric status.

Fully-winged *Scarabaeus* S. Str. (incl. *Drepanopodus* Janssens, 1940)

Mnematidium, Neateuchus and *Madateuchus,* were synonymised with *Scarabaeus* S. Str. by Mostert & Scholtz (1986) due to either an insufficient number or complete lack of unique characters to warrant generic status. We support this synonymy having found no phylogenetic evidence to the contrary.

The creation of the genus *Drepanopodus* by Janssens (1940) was based on the single tarsal claw condition (133/1) shared by *Kheper* species, and a very high tarsal insertion point on the mesotibia, a unique apomorphy present in the genus. In our study, a complete fusion of the mesotibial spur with the mesotibia with their margins flush (125/0) represents the only non-homoplasious character state out of 33 apomorphies that support the genus (Fig. 153.08). *Drepanopodus* is positioned medially amongst members of *Scarabaeus* S. L. in the majority of the trees recovered and forms a sister clade with several different lineages when all cladograms are examined. This may be due to the large number of convergent characters the genus shares and hence very weak bremer support dispite the presence of a single autapomorphy (= unique syn- since this state is shared by *D. costatus*). As it stands, the recognition of the genus *Drepanopodus* makes *Scarabaeus* S. L. paraphyletic. Based on our phylogenetic evidence and poor statistical support of the apomorphies differentiating the uniqueness of the genus, we see little reason to retain it. We therefore suggest *Drepanopodus* be considered a synonym of *Scarabaeus* (**syn. nov.**)

Flightless *Scarabaeus* S. Str.

There are 22 homoplasious synapomorphies at node 43 which support the flightless *Scarabaeus* S. Str. (including derived *S. (Pachysoma)* S. L. lineages; Fig. 153.08). Two non-homoplasious traits supporting this paraphyletic clade are: the dorsal carina of the profemora (leading basally from the tibia/femora articulation) is indistinct and almost joined medially, forming a single carina with the dorso-anterior carina (102/1); and the medial portion of the anterior laminae of the metendosternite bearing a slightly triangular-shaped projection (207/1). *Mnematium cancer* and *Neomnematium sevoistra* (Alluaud) were synonymised with *Scarabaeus* S. Str. by Mostert

& Holm (1982), and although not examined in this study, are unlikely to effect the topological placement of the flightless *Scarabaeus* S. Str. Their classification as synonyms of *Scarabaeus* is therefore uncontested.

Scarabaeus (*Pachysoma* MacLeay, 1821)

The node supporting *S. (Pachysoma)* S. L. shares 22 synapomorphic characters with the remaining members of the tribe including morphologically congruent and no doubt convergent *E. arachnoides*. Four character states present in the mandibles (53/2), epipharynx (67/2), neck sclerites (76/1) and mesonotum (172/0) are unique to the clade (Fig. 153.09). Members of *S.* (*Pachysoma*) S. L. clade are differentiated from the *E. arachnoides* by 7 homoplasious apomorphies (Fig. 153.10) and is the only clade in the phylogeny whose members possess a single lateral plate on each prothoracic apodeme (90/2). In contrast to a paraphyletic origin of *S.* (*Pachysoma*) S. L. suspected by Holm & Scholtz (1979), all trees generated in this study clearly support the clade as monophyletically derived from ancestral *Scarabaeus* S. L. lineages. Harrison & Philips (2003) report a similar likely origin of the subgenus. The unique biology and foraging behaviour discussed by Scholtz (1989) provide further support for the uniqueness these scarabaeines. Within the subgenus, species of synonymised *Neopachysoma* (e.g. *S. denticollis* and *S. rodriguesi*) form a monophyletic sub-clade and are consistently derived from *S. (Pachysoma)* S. Str. lineages in all trees examined. Sixteen apomorphies, including 2 that are unique to *Neopachysoma* also receive strong decay support (Figs 1, 2, 153.10). Recognition of *Neopachysoma* as a genus would therefore make *S.* (*Pachsoma*) S. Str. paraphyletic. We therefore retain the synonymy but note that it is a distinct lineage within the subgenus *Pachysoma* S. L. In concordance with the review of the subgenus by Harrison *et al.* (2002), we support the recognition of *Pachysoma* S. L. as a subgenus of *Scarabaeus* S. L.

Flightlessness in the Scarabaeini

Predominantly, flightlessness in the Scarabaeini is derived from fully winged members of the tribe that are capable of flight. Its evolution is likely to evolve as a consequence of habitat permanence or environmental heterogeneity (Roff, 1990). Adaptations (mutations) favouring flightlessness are considered very rare, yet in relatively persistent habitats such as deserts, a high frequency of beetle species, particularly tenebrionids (Koch, 1962a,b) and a number of scarabaeines (Mostert & Holm, 1982; Harrison & Philips, 2003; Harrison, Scholtz & Chown, 2003), have secondarily become flightless (Roff, 1990). Morphological and physiological adaptations associated with a loss of flight have been well studied (for detailed overviews, see Harrison & Philips, 2003; Scholtz, 2000; Roff, 1990). The degree of wing reduction is one such example; *Scarabaeus [Mnematium] silenus* and *S. [Mnematium] ritchiei* retain the MP vein (150/1) supporting more allbeit vestigial wing membranes than those present in both *S.* (*Pachysoma*) S. L. and *S.* (*Scarabaeolus*) *scholtzi*. The latter species have completely lost the MP vein (150/0) and particularly with all species of *S.* (*Pachysoma*) S. L., possess extremely reduced minute structures that barely resemble wings. This is reflected in the majority of the topologies we recovered, in which *S. [Mnematium]* spp. retain a less evolved, ancestral character state (i.e. MP vein present). The monophyly of flightlessness in this study implicates wing reduction as a factor promoting speciation within the Scarabaeini. Studies of flightless genera of tenebrionids and carabids (Mayr, 1963) and borborid dipterans (Hackman, 1964) further suggest flightlessness may influence speciation. Indeed, flight loss may be a factor implicated in the speciation of *S. (Pachysoma)* S. L. in the Namib Desert and the Southwest Africa (Harrison & Philips, 2003). However, the disjunct geographical distributions of the Scarabaeini that have lost flight may not reasonably support the inference of the clade's monophyletic evolution (Sensu Harrison & Phillips 2003). Rather, we explain the monophyly of the flightless lineages in this instance as the result of character convergence.

A consistent link between the fully winged and brachypterous lineages is represented by the North African *S. [Mnematidium] multidentatus*. This fully winged species, whose biology is apparently similar in all respects to that of true *Scarabaeus* species (Balthasar, 1963), shares a number of morphological similarities with species in the flightless clade, particularly with other *S. [Mnematium]* spp. These include derived characters associated with walking such as the circular, marginal circumference of the procoxal cavity (86/1) and closely set mesocoxae (197/2)) present in all flightless Scarabaeini. Two hypotheses for the evolution of *S. [Mnematidium] multidentatus* are presented. Firstly, this species may posses a flightless polymorphic condition resulting from reduced wing muscles as suspected in the North American Geotrupidae genus, *Peltotrupes* (Olsen *et al.*, 1954; Howden, 1955). Secondly, *S. [Mnematidium] multidentatus* may resort to a flightless phase at some point in adult life enabling greater reproductive potential. Newly emerged adult females may be capable of flight but lose it permanently upon location of a mate and/or food resource by histolysing flight musculature. Indeed, Roff (1990) and Scholtz (2000) report that many insects histolyse their wing muscles which allows for increased egg production. For instance, fully winged females of the dynastine *Oryctes rhinoceros* L. and the lucanid *Lucanus cervus* L. "trade-in" flight in favour of reproduction by autolysing thoracic muscles in autumn and replacing them with fat-body cells (Smith, 1964). Moreover, Scholtz and Caveney (1992) report wing muscle histolysis in the southern African desert trogid, *Omorgus asperulatus* (Harold) during the utilisation of a large mammal carcase for reproduction.

Eucraniini sister to Scarabaeini?

The Eucraniini are restricted to xeric, sandy areas of Argentina. The tribe contains 18 flightless species in the genera, *Eucranium* Brullé, *Glyphoderus* Westwood and *Anomiopsoides* Blackwelder, and a single flighted species in the genus *Ennearabdus* Van Lansberge (Zunino *et* *al.*, 1989; Hanski & Cambefort, 1991). A close relationship between this tribe and the Scarabaeini was proposed in earlier taxonomic work based on morphological and behavioural evidence (Halffter & Matthews, 1966; Mostert & Scholtz, 1986; Philips *et al.*, 2004a). Both tribes share a number of potential synapomorphies including an oblique orientation of the mesocoxae, absence of protarsi and four large external protibial dentations on elongate, slender protibiae (Mostert & Scholtz, 1986). Zunino *et al.* (1989) believe these similarities are based on convergence, and in contrast to the inferences made by Mostert & Scholtz (1986), various authors closely associate the Eucraniini with the Phanaeini (Zunino, 1983; Philips *et al.*, 2002; Philips *et al.*, 2004a) or the Onitini (Zunino, 1985; Luzzatto, 1994). In this study, a close Eucraniini + Scarabaeini relationship is reflected by the placement of *E. arachnoides* as sister to *S.* (*Pachysoma*) S. L. in virtually all weighted and unweighted analyses.These cladograms could be evidence for a close relationship between these two tribes. In this case, the common ancestor was divided into two lineages after the African-South American separation of West Gondwanaland (Powell *et al.*, 1981) around 90 mybp (Rosen, 1978) to 120-150 mybp (Thayer, 1985). While fossil records indicate ancient Scarabaeoids had already been in existence for at least 30 to 110 million years (Krell, 2000), this far predates estimated radiations of 'true' or modern sarabaeines (see: Scholtz and Chown, 1995; Cambefort 1991b; Crawson, 1981). Molecular sequence data of the Cytochrome Oxidase 1 and 16s rRNA genes indicate the Scarabaeini are relatively young, having radiated between 8-16mybp (Forgie, Bloomer & Scholtz, unpubl.). Moreover, none of the molecular topologies recovered supported a close relationship between the Scarabaeini and the Eucraniini with both gene regions exhibiting significantly divergent sequences between them. The close association between the Eucraniini and the Scarabaeini is therefore believed to be based on the morphological convergence of characters (Sensu Zunino *et al.* 1989; Philips *et al.*, 2002; Philips *et al.*, 2004b) likely to be associated with their existence in arid environments.

Food relocation in the Scarabaeini

Rolling balls of dung for feeding and breeding appears to have evolved independently in the Scarabaeinae on several occasions based on morphological evidence (Philips *et al.*, 2004b) and occurs not only in the Scarabaeini but also in the Canthonini, Gymnopleurini, and the Sisyphini. The evolution of ball-rolling may be a behavioural adaptation brought about by individuals competing for an ephemeral and patchy resource (for detailed overview, see Hanski & Cambefort, 1991). While the majority of the "true" rollers manipulate a portion of dung from a larger food mass into a spherical ball before rolling, many scarabaeines and canthonines exhibit behaviours relocating sub-spherical food items or have lost horizontal relocation behaviour completely (Halffter & Halffter, 1989). For example, all species of *S.* (*Pachysoma*) S. L. relocate dung or detritus by dragging the resource secured between the hind legs as the beetles move forward (Scholtz, 1989). Dragging dung in a similar manner is also known in *Canthon obliquus* Horn (Canthonini) (Halffter & Halffter, 1989). Injured millipedes, or portions of millipedes, are pushed forwards in a "bull-dozer" action by species of *Sceliages* when relocated (Forgie *et al.*, 2002).

Cambefort (1991a) suggests ball-rolling may have evolved in beetles that started to transport pieces of food with behaviours similar to those adopted by the saprophage *Cephalodesmius armiger* (Canthonini) (see Monteith & Storey, 1981, for behavioral details). Tribe (1976:152) suggests the same evolutionary progression for the mycetophagous *Coptorhina* Hope (Dichotimiini) which utilises detached portions of mushrooms. Alternatively, and perhaps more likely, ball-rolling may have evolved in coprophagous tunnelling species exploiting naturally spherical or sub-spherical dung balls similar to the behaviour used by the derived *S. galenus* (Halffter & Halffter, 1989) and *Pachylomerus femoralis*, the most basal member of the Scarabaeini in the majority of the trees generated in our study (e.g. Fig.1). Members of the latter provision tunnels excavated next to the resource patch and relocate food horizontally where sub-spherical portions of food are predominantly pushed forwards (Tribe, 1976:148). "True" rolling behaviour, by relocating spherical balls of dung carved out of a dung pad backwards, is also common in this species (Tribe, 1976; pers. observ.).

Specialisation in rolling a ball of dung backwards has become the predominant evolutionary mode of food relocation in the Scarabaeini. However, an evolutionary reversal to pushing and/or carrying and tunnelling occurred at least twice in the tribe. Firstly, *Scarabaeus galenus* provisions burrows excavated at or near a resource patch by pushing or carrying wet dung pellets forwards (pers observ.). Halffter & Halffter (1989:20) also report this species carrying portions of dung in its hind legs and moving backwards. In either case, 'true' rolling behaviour has been lost in favour of carrying and provisioning burrows in a manner similar to tunnelling behaviour utilised by paracoprid beetles. Secondly, species of *Sceliages* push whole or fragmented millipedes forward. *Sceliages adamastor* relocates the food and then excavates a tunnel deep enough to push the millipede inside before continuing the burial. *Sc. hippias* is similar but prefers to directly undermine one end of the millipede to "sink" it beneath the soil (Forgie *et al.*, 2002). Additionally, ball-rolling behavior has also been lost in the dry habitat dwelling *S.* (*Pachysoma*) S. L. which holds food by its hind legs and drags it forwards.

Unfortunately, little to no published work has been done regarding the behaviour of the flightless species of *Scarabaeus* S. Str. As they share a common ancestor with *S.* (*Pachysoma*) S. L. in most topologies and are found in similar xeric habitats, we can infer that their food relocation behaviour may be similar. They might even have behaviours similar to that found in the Argentinian eucraniines.

Feeding specialisation in the Scarabaeini

It is difficult to accurately describe feeding specialisation in the Scarabaeini when many of the species have been known to feed on different types of food resources opportunistically. One example is *P. femoralis* which use carrion, fermenting fruit and several types of dung (Endrödy-Younga, 1982; Doube, 1991). However, the specialisation in the exploitation of either wet or dry food by the Scarabaeini is clearly defined. We can infer from this phylogenetic study that the exploitation of wet dung is a plesiomorphic condition that is maintained in the majority of the Scarabaeini. *Sceliages* and *S.* (*Pachysoma*) S. L. contain the only known species in the tribe that display truly specialized feeding in terms of behavioural shifts away from this ancestral condition. The former exclusively utilise the soft internal contents of disarticulated millipedes. This resource is used by adult beetles for feeding and constructing brood balls which are later encapsulated by soil and brooded by the females (Forgie *et al.*, 2002). Secondly, members of the *S.* (*Pachysoma*) S. L. clade use dry dung pellets and/or detritus (Scholtz, 1989; Holm & Scholtz, 1979). While unique in the Scarabaeini, these specialised feeding behaviours are also practiced by other members of the Scarabaeinae. Rehydration of dry dung pellets is also practiced by the geotrupine, *Geotrupes* (*Thorectes*) *sericeus* Jekel (Klemperer & Lumaret, 1985), most of the 18 species of southern neotropical Eucraniini (Zunino *et al.*, 1989,1993), and by several Western Australian canthonines and onthophagines such as *Coproecus* Reiche, *Mentophilus* Castelnau, *Tesserodon* Hope, *Onthophagus* Latrielle (Matthews, 1974). Moreover, several species from the genera *Onthophagus* Latreille (Krell, 1999; Krell, *et al.*, 1997), *Canthon* Hoffmannsegg (Villalobos *et al.*, 1998) and *Deltochilum* Eschscholtz (Cano, 1998; Halffter & Matthews, 1966) are necrophagous on millipedes.

All scarabaeines have membranous filtering mouthparts that vary subtly in form and function, enabling the use of liquid components of various ruminant or non-ruminant animal dung types (Halffter & Edmonds, 1982; Nel & Scholtz, 1990; Cambefort, 1991b). Harrison & Philips (2003) is known of their biologies and relatively few are available for molecular or morphological-based study.

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Appendix 1. All taxa included in this phylogenetic study of the Scarabaeini. Taxa in bold represent outgroup representatives. Subgenera and synonyms of the genus *Scarabaeus* L. (*S.*) are surrounded by parentheses and square brackets respectively. Flightlessness (Fl) taxa are brachypterous (b). Wings of all other taxa are macopterous. Activity period (A) is generally diurnal or suspected as diurnal (?d), or nocturnal (n). Soil preference (Sp) of the taxa is sand (s), clay (c), or generalist (g) where both are equally preferred. Food relocation technique is denoted by 'Fr'. Distributional zones are Afrotropical (At), Neotropical (Nt), or Palaearctic (Pa).

Taxa	Tribe	A	Sp	Fl	Food preference	Fr	Distribution
Circellium bacchus **Fabr.**	Canthonini		s	b	wet dung	ball roller	At (South Africa)
Heliocopris hamadryas (Fabr.)	Coprini	n	s		wet dung	tunneller	At (southern Africa)
Synapsis tmolus (Fischer)	Coprini	n	s		wet dung	tunneller	Pa (middle Asia)
Eucranium arachnoides Brullè	Eucraniini		s	b	dry dung pellets	carrier	Nt (NW Argentina)
Drepanopodus proximus Jannsens	Scarabaeini		s		wet dung	ball roller	At (South Africa)
Kheper lamarcki (M'Leay)	Scarabaeini		s		wet dung	ball roller	At (southern + Central Africa
Kheper nigroaeneus (Boheman)	Scarabaeini		g		wet dung	ball roller	At (southern Africa)
Kheper subaeneus (Harold)	Scarabaeini		c		wet dung	ball roller	At (southern + East Africa)
S. [Mnematidium] multidentatus (Klug)	Scarabaeini	?d	s	?	wet dung	ball roller	Pa (northern Sahara Desert)
S. [Mnematium] ritchiei M'Leay	Scarabaeini	?d	s	b	unknown	unknown	Pa (northern Sahara Desert)
S. [Mnematium] silenus Gray	Scarabaeini	?d	s	b	unknown	unknown	Pa (Sinai Pen., Arabia, Iraq)
S. [Neateuchus] proboscideus (Guérin)	Scarabaeini	n	s		wet dung	ball roller	At (W South Africa, Kalahari
S. [Neopachysoma] denticollis (Péringuey)	Scarabaeini		s	b	dry dung pellets/detritus	dragger	At (Namib Desert)
S. [Neopachysoma] rodriguesi Ferreira	Scarabaeini		s	b	dry dung pellets	dragger	At (Namib Desert)
S. (Pachysoma) bennigseni Felsche	Scarabaeini		s	b	dry dung pellets/detritus	dragger	At (Namib Desert)
S. (Pachysoma) hippocrates M'Leay	Scarabaeini		s	b	dry detritus/dung pellets	dragger	At (W South Africa)
Pachylomerus femoralis Kirby	Scarabaeini		s		wet dung	roller/tunneller/pusher	At (southern + Central Africa
S. (Scarabaeolus) bohemani Harold	Scarabaeini		g		wet dung/carrion	ball roller	At (southern Africa)
S. (Scarabaeolus) flavicornis (Boheman)	Scarabaeini		s		wet dung/carrion	ball roller	At (Kalahari)
S. (Scarabaeolus) rubripennis (Boheman)	Scarabaeini		s		wet dung/carrion	ball roller	At (Namib Desert)
S. (Scarabaeolus) scholtzi Mostert & Holm	Scarabaeini	?d	s	b	unknown	unknown	Pa (coastal Somalia)
S. galenus (Westwood)	Scarabaeini		g		wet dung pellets	carrier/tunneller/pusher	At (southern Africa)
S. goryi Castelnau	Scarabaeini	n	s		wet dung	ball roller	At (South Africa)
S. rugosus (Hausman)	Scarabaeini		s		wet dung	ball roller	At (SW South Africa)
S. rusticus (Boheman)	Scarabaeini		c		wet dung	ball roller	At (South Africa)
S. satyrus (Boheman)	Scarabaeini	n	s		wet dung	ball roller	At (South Africa, Namibia)
S. westwoodi Harold	Scarabaeini		c		wet dung	ball roller	At (southern + East Africa)
S. zambesianus Péringuey	Scarabaeini	n	s		wet dung	ball roller	At (southern Africa)
Sceliages adamastor (Serville)	Scarabaeini		s		millipedes	pusher	At (SW South Africa)
Sceliages brittoni zur Strassen	Scarabaeini		s		millipedes	pusher	At (W South Africa)
Sceliages hippias Westwood	Scarabaeini		c		millipedes	pusher	At (N South Africa)

Appendix 2. Morphological characters and their states with reference to anatomical drawings (Figures 6-152).

Head plates

0. *Clypeal teeth*: (0) two; (1) four; (2) none.
1. *Shape of medial teeth of clypeus*: (0) blunt and rounded; (1) narrow triangular shape (tooth width ≤ 2/3 length); (2) wide triangular shape (tooth width ≡ length); (3) teeth absent.
2. *Position of medial clypeal teeth* (*cf. lateral clypeus teeth/anterior margin of clypeus*): (0) not projecting anterior of marginal curvature of clypeus; (1) markedly projecting anterior of marginal curvature of clypeus.
3. *Clypeal curvature (at plane) between distal edges of geno-clypeal suture (in dorso-frontal view)*: (0) flat; (1) slightly convex; (2) convection forming projection, carina, etc; (3) concave.
4. *Emargination between medial clypeal teeth relative to lateral emarginations between medial and lateral clypeal teeth:* (0) anteriorly positioned to a line drawn between base of both lateral emarginations (Fig. 6); (1) even with line (Fig. 7); (2) posteriorly positioned to line (Fig. 8).
5. *Shape between medial clypeus teeth*: (0) no emargination; (1) emargination U-shaped; (2) emargination V-shaped; (3) emargination a slight notch.
6. *Ventral transverse margin of clypeus with*: (0) no protuberances; (1) carina present; (2) carina present with one or more tooth-like projections; (3) carina absent. One or more tooth-like projections present
7. *Ventral surface of clypeal teeth:* (0) no protuberances; (1) simple longitudinal carinae present; (2) each longitudinal carina forming a tooth-like projection distad; (3) longitudinal carinae absent. Tooth-like projection distad.
8. *Lateral margins of clypeal epistoma*: (0) forming an obvious tooth-like projection; (1) plate-like with anterior-lateral angle forming reduced tooth-like projection; (2) rectangular plate without projection.
9. *Geno-clypeal suture*: (0) markedly defined; (1) not so.
10. *Anterio-lateral margin of genal epistoma*: (0) distinct from clypeus forming an obvious notch-like emargination (Fig. 9); (1) forming a slight notch-like emargination(Fig. 10); (2) completely indistinct forming approximately a continual margin with clypeus (Fig. 11).

11. *Posterior facet of gena epistoma*: (0) approximately parallel between dorsal and ventral edges; (1) slight angle between dorsal and ventral edges becoming obsolete at lateral margin; (2) obtuse angle between dorsal and ventral edges becoming obsolete at lateral margin.
12. *Lateral edge of gena*: (0) smooth; (1) serrated.
13. *Posterio-lateral corner of gena*: (0) rounded (Fig. 12); (1) angled (45° to 80°) (Fig. 13); (2) approximately 90° (Fig. 14).
14. *Lateral development of gena epistoma*: (0) width <½ distance between eyes; (1) width >½ distance between eyes; (2) width approximately = ½ distance between eyes.
15. *Eye canthus position*: (0) ½ of eye above canthus; (1) ⅓ eye above; (2) ⅜ eye above.
16. *Gula median longitudinal groove*: (0) absent; (1) present in anterior ½; (2) present ≥ ¾ length of gula.
17. *Gula setation* anterior transverse band of setae: (0) forming a slight triangulation deflexed posteriorly (Fig. 15); (1) forming a pronounced or drawn-out triangulation deflexed posteriorly (Fig. 16); (2) without triangulation (Fig. 17).
18. *Gula posterior margin emargination*: (0) very slight to absent; (1) markedly developed.
19. *Frons* protruberance: (0) lacking; (1) as a medio-longitudinal carina (may be slight); (2) as a horn or bump-like projection.
20. *Supra orbital crest above each eye*: (0) not forming carinae posterior to eyes; (1) forming short carinae projecting posterio-medially (Fig. 18); (2) forming long carinae joining posterio-medially to form a single ridge (Fig. 19).
21. *Posterior transverse groove*: (0) complete; (1) not so
22. *Dorsal postoccipital margin*: (0) pronounced medio-ventral deflection forming a "M" (Fig. 20); (1) slight medio-ventral deflection forming a "m" (Fig. 21); (2) no medio-ventral deflection, rather, a medial notch-like emargination forming a "w". (Fig. 22).
23. *Junction of geno-clypeus suture and frons*: (0) forming a transverse carinae; (1) forming a transverse suture; (2) transverse carina or suture absent.

Antennae

24. *Posterior basal facet of scape leading to articulatory process*: (0) angulate (Fig. 55); (1) rounded (Fig. 56).
25. *Angulation of basal facet relative to articulatory process*: (0) 90° (Figs 55, 56); (1) <90° (Fig. 57); (2) >90° (Fig. 58).
26. *Third antennomere compared to fourth antennomere*: (0) longer; (1) equal; (2) shorter.
27. *Forth antennomere compared to fifth antennomere*: (0) longer; (1) equal.

28. *Seventh antennomere (basal lamella of club)*: (0) cup-shaped, rounded; (1) slightly leaf-shaped, relatively elongate, flattened; (2) Intermediate form: oval leaf-shaped, slightly rounded.

Mouth parts

Labium

29. *Mentum anterior margin*: (0) slightly emarginate; (1) markedly emarginate; (2) straight.
30. *Mentum surface*: (0) flat and simple; (1) contoured with mounds and depressions; (2) convex and simple.
31. *Mentum pubescence/setation*: (0) mainly restricted to anterior region (projecting forwards); (1) mainly unrestricted, covering most of ventral surface; (2) mainly restricted to anterior and lateral regions (absent medially).
32. *Labial palps (basal palpomere)*: (0) fat in width from base to apex (Fig. 23); (1) thin in width from base to apex (Fig. 24).
33. *Labial palps (middle palpomere)*: (0) positioned perpendicularly on lateral edge of (to) basal palpomere and directed inwards (Fig. 23); (1) not so (Fig. 24).
34. *Labial palps (apical palpomere)*: (0) markedly reduced in size compared to middle and basal palpomeres and appearing as a small "nipple;" (1) slightly reduced in size compared to with middle and basal palpomeres.
35. *Labial palps*: (0) markedly developed and much larger in size to dorsal paraglossal processes; (1) reduced and similar in size to dorsal paraglossal processes.
36. *Baso-medial paraglossal torma*: (0) slight to no interruption by glossa (Fig. 25); (1) forms a deep cradle-like emargination to house the glossa (Fig. 26).
37. *Glossa (dorsal view)*: (0) markedly developed anterior protrusion; (1) not so.
38. *Posterior margin of baso-medial paraglossal torma*: (0) very slight to no emargination; (1) markedly pronounced emargination; (2) intermediate emargination.
39. *Dorsal paraglossal processes with anterior medial margins*: (0) oblique basally and angulate apically (Fig. 27); (1) oblique and straight (Fig. 28); (2) basally perpendicular to glossa and approximately right-angled apically (Fig. 29).
40. *Dorsal paraglossal process*: (0) markedly developed, elongate; (1) not so
41. *Ventral paraglossal process*: (0) markedly pronounced lobes (sclerotised or not so); (1) reduced and primarily serving as rigid spine for ventral paraglossal process and basal comb setae.
42. *Setal arrangement on medial margin of ventral paraglossal process*: (0) comb-like setae forming a continuous band along entire margin (Fig. 30); (1) one to two comb-like

43. clusters located medially and/or basally (adjacent to dorsal surface of mentum) (Fig. 31); (2) three comb-like clusters: one apical, one medial, one basal (Fig. 32)

44. *Apicies of labial apodemes*: (0) circular; (1) elongate, ecliptical; (2) ovoid (intermediate form).

Maxillae

45. *Anterior articulatory sclerite of basigalea*: (0) markedly hook-shaped (Fig. 33); (1) relatively straight (Fig. 34).

46. *Basigalea*: (0) heavily melanisation of articulatory sclerites and cuticle (Fig. 35); (1) not so, heavy melanisation only on articulatory sclerites (Fig. 36).

47. *Galea*: (0) reduced in size compared with stipes; (1) markedly developed in size compared with stipes.

48. *Apex of lacina inner strut*: (0) pointed; (1) rounded or clubbed.

49. *Basistipes*: (0) stout, broadened laterally and convex along outer lateral margin; (1) slender, relatively straight.

50. *Mediostipes*: (0) robust, broadened laterally; (1) not so.

Mandibles

51. *Stem of abductor apodeme*: (0) short, stout; (1) elongate, slender.

52. *Apex of abductor apodeme* (0) fan-shaped, simple (without transverse facets); (1) trumpet-shaped, complex (with/without medio-longitudinal facet)

53. *Lateral margin of apicalis membrane distad from sclerotised incisoral lobe* (Fig. 37): (0) uniformly curved to its apex; (1) curvature to apex slightly sinuate; (2) curvature to apex markedly indented with increased membrane width.

54. *Medial prosthecal "rod"*: (0) markedly developed and with melanisation; (1) developed with minimal to no melanisation (Fig. 40); (2) reduced/absent.

55. *Membrane between incisoral lobe and post-median process*: (0) with markedly defined medial margin (Fig. 38); (1) undefined or lacking medial margin (Figs 39, 40).

56. *Degree of development of melanised apicalis membrane at apex of incisoral lobe*: (0) markly developed, extending close to apical margin of mandible (Fig. 38); (1) minimal to absent development (Fig. 39); (2) intermediate (Fig. 40).

57. *Setal comb on ventrad of left (concave) molar*: (0) coarse, robust (Fig. 41); (1) not so (Fig. 42).

58. *Setae on comb on ventrad of left (concave) molar*: (0) closely set/tightly clustered together (Fig. 41); (1) not so (Fig. 42).

Epipharynx

59. *Arms of posterior lateral tormal process (ignoring development of outer apodeme)*: (0) approximately parallel (Fig. 43); (1) one arm converging apically (Fig. 44); (2) both arms converging apically (Fig. 45); (3) both arms diverging apically (Fig. 46).

60. *Outer apodeme/extension on each arm of posterior- lateral tormal process*: (0) markedly developed; (1) vestigial; (2) absent.

61. *Inner margins of anterior transverse tormal process and lateral tormal processes* (0) "D" shaped; (1) "B" shaped.

62. *Union with median process and posterior transverse tormal process* (Fig. 47): (0) with markedly developed, obliquely extended hooks; (1) with reduced/vestigial hooks; (2) hooks absent.

63. *Length of median ventral process between posterior and anterior transverse tormal processes*: (0) <¼ length between anterior transverse tormal process & anterior apex of median process (Fig. 54); (1) > length between anterior transverse tormal process & anterior apex of median process; (2) ½-⅔ length between anterior transverse tormal process & anterior apex of median process (Fig. 54).

64. *Anterior labral bristles*: (0) restricted to lateral margins; (1) present across majority of anterior margin (absent at median point); (2) absent.

65. *Outer lateral comb*: (0) arranged in straight to slightly curved line to anterior lateral margin; (1) uniform and markedly curved to anterior lateral margin; (2) roughly sinusoidal in curvature.

66. *Anterior labral setae*: (0) absent; (1) present with uneven distribution over width of apical margin; (2) present with dense medially, sparse to absent laterally; (3) present with uniform distribution laterally, absent medially (inner most lateral seta reduced on each side).

67. *Sclerotised transverse row of tooth-like protrusions on anterior margin of epipharynx*: (0) absent; (1) present (Fig. 48).

68. *Anterior margin of epipharynx* (Fig. 49): (0) straight to slightly emarginate laterally and medially; (1) broad shallow emargination medially; (2) broad deep emargination medially; (3) narrow shallow emargination medially.

69. *Anterior sclerotisation medially* (Fig. 50): (0) forming an obvious spike-like protrusion; (1) not so.

70. *Anterior medial sclerotisation*: (0) armed with short bristles clumped together to form a subtle protrusion (Fig. 51); (1) armed with long bristles clumped together to form an

obvious protrusion (short bristles usually present at base of protruding long bristles) (Fig. 52); (2) neither long or short bristles forming protrusion (short bristles may be present at base and/or apex of Sclerotised protrusion) (Fig. 53).

71. *Anterior medial sclerotisation (excluding setae and anterior labral bristles)*: (0) extending beyond anterior margin of epipharynx; (1) approximately at level with anterior margin of epipharynx; (2) set back, posterior to anterior margin of epipharynx.

Neck sclerites

Dorsal sclerites (located dorso-medially in cervical region adjacent to postoccipital margin)

72. *Setal arrangement*: (0) uneven, dense setal distribution covering entire length of sclerite and continuing around lateral apices; (1) moderately even, less dense setal distribution but not covering entire length of sclerite; (2) even rows of setae only on dorsum of sclerite similar to a row of "eyelashes".

73. *Shape of dorsum from lateral perspective* (Fig. 59): (0) evenly convex; (1) unevenly convex (egg-shaped); (2) irregularly shaped.

Ventral sclerites (located dorsally in cervical region)

74. *Outer anterior margin leading to medial "bump" (dorsal view)* (Fig. 65): (0) convex; (1) marked concavity; (2) slight concavity.

75. *Inner anterior margin* (Fig. 60): (0) convex with notch or groove-like emargination (marked or slight) on leeward side of inner anterior apodeme/flange; (1) concavity on leeward side of inner anterior apodeme/flange interrupted by a "bump" (bump may be markedly developed or a faint sclerotisation); (2) as with (1) but with a faint notch immediately leeward of inner anterior appodeme/flange; (3) long shallow concavity without modifications.

76. *Inner anterior apodeme/flange* (Fig. 61): (0) separated from posterior ventral apodeme/flange with a notch-like emargination; (1) separated from posterior ventral apodeme/flange with an obvious groove-like emargination.

77. *Shape of posterior ventral apodeme/flange* (Fig. 62): (0) straight tapered (apex pointed or blunt); (1) circular rounded; (2) outer facet convex, inner facet straight; (3) irregular shaped facet(s) and apex usually rectangulate.

78. *Margin between posterior lateral apodeme/flange and outer anterior apodeme/flange* (Fig. 64): (0) notched; (1) grooved; (2) unmodified, uniform.

79. *Posterior lateral apodeme/flange* (Fig. 63): (0) markedly projected, tooth-like; (1) projected with inner margin of apodeme sustained and drawn-out to posterior ventral apodeme/flange; (2) reduced (in proportion to posterior ventral apodeme/flange).

Prothorax (excluding legs)

80. *Pronotum lateral edges*: (0) smooth; (1) serrated; (2) armed with spike-like teeth.
81. *Pronotum dorsal-posterior edge*: (0) smooth; (1) serrated; (2) serrated only on lateral margins of posterior edge, fading medially.
82. *Pronotum. Corners where anterior margin meets lateral margins*: (0) form obvious spikes projecting anteriorly; (1) forms an angulate corner (sharp or not so) without projection; (2) forms a spike (obvious or not) projecting laterally.
83. *Corners of pronotum where posterior margin meets lateral margins*: (0) pronounced, obvious with projecting "flared edge"; (1) not so.
84. *Shape of pronotum posterior margin*: (0) rounded; (1) rounded with V-shaped projection medially; (2) V-shaped; (3) straight laterally with slight to obvious concave emargination medially.
85. *Dorso-anterior region of pronotum*: (0) with obvious carina running transversely; (1) uniform without any carina.
86. *Posterior tergo-sternal suture (or carina) running in a dorso-lateral angle from the sternal portion of the posterior prothoracic foramen* (Fig. 66): (0) absent; (1) angled wide and low providing a large facetted plane surrounding the posterior prothoracic foramen; (2) angled narrow and high providing a small large facetted plane surrounding the posterior prothoracic foramen.
87. *Shape of external circumference of procoxal cavity*: (0) markedly ecliptical; (1) semi-circular (more circular than ecliptical).
88. *Surface texture of pronotum*: (0) smooth with large or small punctations; (1) granulose fine/smooth. Minimal to no punctations and/or terbercles; (2) granulose medium/large grain. Abundant punctations and/or terbercles; (3) shagreened coarse or fine; (4) rugose; (5) smooth with punctations and/or turbercles. Fine granulation confined to lateral regions of pronotum.
89. *Contouring on pronotum surface*: (0) punctations only; (1) terbercles only; (2) both terbercles and punctations.
90. *Setation on pronotum surface*: (0) present; (1) absent.

91. *Lateral plates of prothoracic apodemes* (0) relatively even in size; (1) outer plate larger than inner plate; (2) one of the two lateral plates absent; (3) inner plate larger than outer plate.

92. *Angulation of outer lateral plates relative to central chitinous supports of the prothoracic apodemes (when viewed through posterior prothoracic foraman)*: (0) greater than 45° (Fig. 67); (1) slightly angled above horizontal (Fig. 68); (2) horizontal (Fig. 69).

Forelegs

93. *Edge of coxal depression (dorso- lateral view)* (Fig. 70): (0) forming an abrupt ridge or carina much like an "Adam's apple"; (1) forming a very slight ridge or carina; (2) intermediate form between (1) and (2).

94. *Baso-lateral "ankle"* of coxa (Fig. 71): (0) possessing an obvious spike-like protrusion; (1) possessing a knobbed, rounded protrusion; (2) lacking any protrusion.

95. *Trochanter*: (0) with a distinct "heel-like" carina or ridge which may/may not be serrated or forming a spike-like protrusion; (1) not so.

96. *Trochanter*: (0) posterior facet possessing serrations or one to several spike-like protrusions; (1) not so.

97. *Baso-anterior ventral corner of the femora*: (0) possessing a spike-like protrusion; (1) not so.

98. *Shape of femora*: (0) fat and laterally enlarged; (1) enlarged basally, not so distally (much like a chicken drum-stick); (2) approximately parallel-sided and even thickness through length of femora; (3) evenly tapered (slight bulge on ventral surface).

99. *Dorso-posterior edge of femora*: (0) serrated/toothed; (1) smooth.

100. *Dorsal carina of femora leading basally from tibia/femora articulation* (Fig. 73): (0) markedly toothed; (1) smooth; (2) finely serrated (often giving rise to setae).

101. *Dorso-anterior edge/carina running distally from the "heel" terminating medio-ventrally on anterior facet beneath* 99 (Fig. 72): (0) smooth; (1) toothed or serrated through majority of its length; (2) toothed or serrated basally, fading to smooth distally.

102. *Distal anterior ventral edge or carina of femora*: (0) toothed or serrated; (1) smooth; (2) absent or merging medially with 100; (3) smooth with single tooth.

103. *Relationship between* 99 *and* 100 (Fig. 72): (0) distinct and separate; (1) indistinct, virtually joined medially forming a single edge or carina; (2) converge medially then separate as distinct carinae along majority of femora; (3) converge medially with 99 terminating at this convergence.

104. *Distal apex of tibia*: (0) with simple spur, unfused with tibia; (1) bifurcated or lobed spur, unfused with tibia; (2) with simple spur, completely fused becoming a tibial extension.

105. *Forth external denticle (tooth) of tibia*: (0) present; (1) markedly reduced (posterior edge of tooth indistinct from lateral edge of tibia); (2) absent.

106. *Single tooth within basal half of dorso-medial edge of tibia*: (0) present; (1) absent.

107. *Dorsal facet (adjacent to external denticles)*: (0) possessing at least one tooth-like protrusion; (1) not so.

108. *Dorso-medial edge of tibia*: (0) coarsely serrated; (1) smooth.

109. *Dorso-medial apex of tibia (adjacent to first external denticle)*: (0) forms a protrusion (pointed or not) orientated in a "thumbs-up" position; (1) forms a sharp, non-obtrusive point or spur; (2) forms a featureless, non-protruding corner.

110. *Tarsi*: (0) present; (1) absent.

111. *Single medial carina (keel) on ventral facets of first two external denticles*: (0) present; (1) absent.

112. *Serrations on lateral edge between external denticles*: (0) present between denticles 1-4; (1) present between denticles 2-4; (2) absent.

113. *Lateral edge basal to forth external denticle*: (0) serrated (similar in stature to serration between denticles); (1) toothed (similar in stature to external denticles); (2) smooth.

Midlegs

114. *Length of coxa*: (0) approximately equal to length of mesofemora; (1) approximately ⅔ length of femora; (2) approximately ½ length of femora.

115. *Shape of coxa*: (0) rectilinear and relatively even in width longitudinally; (1) ecliptical (widest medially); (2) slightly tapered (widest distally); (3) markedly tapered (widest distally).

116. *Length of coxal foramen*: (0) 20-30% of coxal length; (1) 30-40%; (2) 40-50%: (2) >50%.

117. *Anterior margin of mesofemora*: (0) straight for most its length; (1) markedly sinusoidal; (2) evenly convex; (3) slightly sinusoidal.

118. *Posterior margin of mesofemora*: (0) straight for most its length; (1) markedly convex; (2) slightly convex; (3) sinusoidal.

119. *Curvature of femora (lateral view)*: (0) strong deflection dorsally; (1) weak deflection dorsally (Fig. 74); (2) without curvature; (3) very strong deflection dorsally (obtusely bowed) (Fig. 74).

120. *Width of posterior facet of femora*: (0) relatively even width; (1) tapering to a distal width approximately ⅔ greater than basal width; (2) tapering to a distal width approximately ½ greater than basal width.

121. *Posterior ventral margin of femora*: (0) serrated or toothed; (1) smooth.

122. *Setation on posterior facet of femora*: (0) restricted to dorsal margin; (1) restricted to ventral margin; (2) restricted medially; (3) setation absent; (4) unrestricted, forming pubescence.

123. *Apex of mesotibia*: (0) 2 spurs approximately equal in size; (1) 2 spurs, 1 markedly reduced; (2) 1 spur only.

124. *Shape of major (outer) tibial spur*: (0) slightly sickle-shaped, pointed (Fig. 75); (1) obtusely sickle-shaped (dorsal margin angulate, ventral margin evenly curved), pointed (Fig. 76); (2) spatulate, bent, blunt/rounded (Fig. 77); (3) spatulate, relatively straight, pointed (Fig. 78).

125. *Shape of minor (inner) tibial spur (if present)*: (0) straight tapering to a point; (1) bent, sickle-shaped; (2) bent, spatulate.

126. *Major tibial spur*: (0) completely fused with mesotibia, dorsal and ventral margins of spur and mesotibia flush (Fig. 79); (1) completely fused with mesotibia, ventral margins of spur and mesotibia flush (Fig. 80); (2) fused with mesotibia, no margins of spur flush with margins of mesotibia (Fig. 81); (3) socketed into mesotibia, no margins of spur flush with margins of mesotibia (Fig. 82).

127. *Expansion of tibia towards distal apex*: (0) absent to slight (only at apex); (1) moderately expanded; (2) greatly expanded (approximately ½ of length).

128. *Curvature of mesotibia* (0) bent; (1) straight.

129. *Size of tarsomeres*: (0) 1st tarsomere shorter than 5th; (1) 1st tarsomere longer than 5th; (2) 1st tarsomere equal in length to 5th.

130. *"Comb" setae on ventral margin of 1st tarsomere*: (0) present; (1) absent.

131. *Setation on ventral margins of tarsomeres 2-4*: (0) restricted apically on 2, 3 and 4 (Fig. 83); (1) restricted apically on 3 and 4 only (Fig. 84); (2) not restricted apically on 2, 3 and 4 (Fig. 85).

132. *Setation on dorsal margins of tarsomeres 2-4*: (0) sub-apical on 2, 3, 4: (1) sub-apical on 2, 3; (2) sub-apical on 2; (3) restricted apically on 2, 3, 4.

133. *Setation on tarsomeres 1-4*: (0) dense; (1) intermediate condition between dense and sparse; (2) sparse.

134. *Tarsal apex*: (0) with 2 claws; (1) with 1 claw; (2) without claws.

135. *Tarsal claws*: (0) fully developed; (1) markedly reduced.

Hindlegs

136. *Dorsal anterior margin of femora (excluding curvature of apex)*: (0) straight; (1) curved.

137. *Dorsal posterior margin of femora*: (0) straight; (1) curved.

138. *Deflection (concavity) of dorsal facet of femora (from a line drawn between base and apex of femora)*: (0) absent; (1) present, weak; (2) present, strong.

139. *Curvature of tibia*: (0) straight; (1) curved in distal half; (2) evenly curved through length.

140. *Width of tibia*: (0) even, uniform from base to apex; (1) as with (0) but flared at apex, (2) evenly tapering to its widest at apex.

141. *Angle of posterior facet of tibia*: (0) perpendicular to lateral (outer) and medial (inner) facets (Fig. 86); (1) approximately 45° to lateral and medial facets (Fig. 87); (2) acutely sheered between lateral and medial facets (Fig. 88).

142. *Length of setae on tibia*: (0) majority less than or approximately equal to width of tibia; (1) majority at least twice the width of the tibia.

143. *Density of setae on tibia*: (0) densely arranged without spaces between setae; (1) evenly spaced with a gap of at least the width of 1 seta between them; (2) sparse with rows often broken, clumped and short.

144. *Length of setae on tarsi*: (0) short; (1) long.

145. *Setation on tarsomeres*: (0) densely arranged on distal apices of each tarsomere and/or base of each tarsomere; (1) sparse-reduced to a few setae restricted to distal apices of each tarsomere; (2) well spaced basally and apically on each tarsomere (not dense or sparse).

Wings

146. *Development of wings*: (0) macopterous; (1) brachypterous.

147. *Distal terminus of AA vein* (Fig. 92): (0) forked; (1) not so.

148. *Fork of AA vein* (Fig. 92): (0) approximately even in length; (1) uneven in length (one branch reduced, vestigial or absent).

149. *Distal terminus of CuA + AA vein*: (0) forked; (1) pointed (Fig. 93); (2) clubbed (Fig. 93).

150. *Jugal vein*: (0) long, distally converging and/or forming a closed cell with AP vein; (1) short, diverging from AP vein; (2) long, diverging from AP vein.

151. *MP vein*: (0) absent; (1) present.

152. *Basal "notch" of MP-C vein* (Fig. 90): (0) notch fully enclosed by MP-C vein thus forming a cell; (1) MP-C vein enclosing ½ or more of the notch; (2) MP-C vein enclosing < ½ the length of the notch; (3) notch appears vestigial or absent.

153. *Proximal vein of "Z" vein process (medial region of MP-C vein)* (Fig. 95): (0) broken; (1) unbroken/continuous.

154. *Distal vein of "Z" vein process (distal region of MP-C vein)* (Fig. 95): (0) "Z" vein process with secondary melanisation present; (1) distal vein of "Z" vein process without secondary melanisation.

155. *MP-A vein* (Fig. 94): (0) with basal angulation; (1) obtusely curved along basal ½ of vein; (2) even bow-like arc through length of vein.

156. *MP-A vein distal terminus in anal region of wing*: (0) reaching posterior margin; (1) almost reaching posterior margin (Fig. 94); (2) terminating well before posterior margin.

157. *Posterior margin of wing in anal region* (Fig. 91): (0) with shallow notch-like emargination; (1) with deep, pronounced notch-like emargination; (2) without emargination.

158. *Secondary dark melanisation of wing membrane*: (0) occurring throughout the majority of wing; (1) occurring from approximately AA vein distally; (2) occurring from approximately RP vein distally; (3) occurring within anterior proximal region of wing; (4) occurring distally from anterior proximal region of wing; (5) wing membrane without secondary dark melanisation.

159. *Wing membrane between R vein and MP vein*: (0) melanised (primary or secondary); (1) transparent, without melanisation.

160. *Cu-A and AA cell* (Fig. 89): (0) open; (1) closed (including closure from melanisation or sclerotisation extending from un-joined bridging vein between AA and Cu-A veins).

161. *Proximal angle between AA and bridging vein to Cu-A vein*: (0) 90°; (1) < 90°; (2) > 90°; (3) curved.

162. *RP and RA veins on anterior distal margin of wing*: (0) converge apically; (1) diverge apically; (2) run parallel apically.

Elytra

163. *Humeral or "shoulder" angle*: (0) sharp angulate; (1) curved angulate; (2) rounded with a carinal margin extending towards medial margin of elytra; (3) markedly rounded (carinal margin absent).

164. *Lateral margins of elytra*: (0) with double pseudoepipleura-medial(inner) pseudoepipleurite is present posteriorly but disappears anteriorly (Fig. 96); (1) with

double pseudoepipleura- medial pseudoepipleurite is broken/punctated medially (Fig. 97); (2) with double pseudoepipleura- medial pseudoepipleurite is continuous/unbroken (Fig. 98); (3) lacking pseudoepipleura.

165. *Width of lateral (outer) pseudoepipleurite*: (0) approximately even through its length; (1) markedly wider anteriorly than posterior.

166. *Curvature of elytra along lateral longitudinal margin (lateral view with all 3 corners of elytra in plane)*: (0) slightly convex; (1) markedly convex; (2) evenly flat.

167. *Curvature of elytra along medial longitudinal margin (lateral view with all 3 corners of elytra in plane)*: (0) unevenly convex, wave-like curvature in posterior third of elytra; (1) even, markedly convex curvature; (2) even, slightly convex curvature.

168. *Striae*: (0) comprising facetted grooves with obvious carinae (Fig. 99); (1) grooves bordered by slight to no faceting and/or carinae (Fig. 100); (2) grooves bordered by unlinked palisade-like carinae (Fig. 101).

169. *Elytra surface texture/patterning (NB: Punctations or tubercles may/may not be abundant or setose)*: (0) smooth with small or large punctations; (1) finely shagreened with/without punctations; (2) coarsely shagreened with/without punctations; (3) rugose with/without turbercles and/or punctations; (4) smooth with turbercles.

Mesonotum

170. *Phragmal arm (dorsal view)* (Fig. 108): (0) markedly developed (less than to equal length of scutum); (1) reduced to vestigial (minimal to no projection); (2) developed (½ length of scutum).

171. *Union between each phragmal arm and scutum*: (0) defined by a groove/suture; (1) undefined; (2) defined by a carina (At union; phragmal arms projecting anterior-ventrally or offset from horizontal plane of scutum dorsal surface).

172. *Anterior transverse margin of scutum (excluding anterior medial margins of phragmal arms)* (Fig. 109): (0) approximately straight; (1) emarginate, curved; (2) emarginate, angulate at anterior terminus of longitudinal mesothoracic suture.

173. *Region posterior to transverse ridge/carina separating scutum from scutellum*: (0) no facet or decavity (transverse ridge/carina absent- scutum and scutellum merged as one) (Fig. 110); (1) slightly facetted with weak decavity (carina often absent medially) (Fig. 111); (2) markedly facetted with strong decavity (Fig. 112); (3) intermediate condition (transverse ridge/carina unbroken medially) (Fig. 113).

174. *Terminus of lateral margins of scutellum in relation to scutum/scutellum decavity* (Fig. 114): (0) anterior of decavity; (1) posterior of decavity.

175. *Lateral corners at union with posterior transverse ridge/carina and scutellum*: (0) rounded; (1) angulate (approximately 90°).

176. *Posterior transverse ridge/carina*: (0) carina complete/unbroken with its emargination evenly rounded into 2 lobes divided by longitudinal mesothoracic suture (1) carina complete/unbroken with its emargination angled at longitudinal mesothoracic suture; (2) carina incomplete forming 2 separate lobes with emargination restricted to anterior medial region of each lobe unjoined at longitudinal mesothoracic suture.

177. *Scutellum apex*: (0) projecting upwards; (1) not so.

178. *Length of scutellum (measured from apical tip of scutellum to transverse line drawn along most posterior point of transverse ridge/carina, compared with length of scutum measured from this line to anterior terminus of longitudinal mesothoracic suture)*: (0) scutellum < ½ length of scutum; (1) scutellum between ½ and ¾ length of scutum; (2) scutellum > length of scutum; (3) scutellum length equal to scutum length.

179. *Prescutum*: (0) markedly developed; (1) reduced.

180. *Prescutum*: (0) directed anteriorly beyond apicies of phragmal arms; (1) approximately equal to apicies of phragmal arms; (2) sub-equal to apicies of phragmal arms.

181. *Lateral margins of prescutum (anterior-ventral view)*: (0) approximately straight; (1) markedly tapering; (2) evenly rounded; (3) vestigial or absent.

182. *Emargination of anterior ventral margin of prescutum*: (0) shallow, narrow; (1) shallow, broad; (2) deep, broad; (3) convex/round, with minimal to no emargination; (4) deep, narrow.

183. *Anterior ventral margin of prescutum at union with longitudinal mesothoracic process (ventral view)*: (0) slightly decurved posteriorly (Fig. 115); (1) markedly decurved posteriorly (Fig. 116): (2) not decurved (Fig. 117).

184. *Scutellar process (ventral view)*: (0) markedly developed; (1) reduced to absent.

185. *Lateral process (axillary chord; ventral view)*: (0) markedly developed; (1) reduced to absent.

Metanotum

186. *Prescutum*: (0) developed; (1) reduced.

187. *Prescutal membrane between dorso-lateral margins of prescutum and ventro-lateral margins of scutum*: (0) undivided, approximately even width through its length (Fig. 102); (1) undivided, constricted (Fig. 103); (2) divided (Fig. 104).

188. *Scutum*: (0) developed; (1) reduced to vestigial.

189. *Anterior margin of scutum leading to apex of lateral notch*: (0) angulate (Fig. 105); (1) curved (Fig. 106).

190. *Medial emargination of anterior margin* (Fig. 107): (0) interrupted by a ventral extension of median groove/scutellum anterior apical extension; (1) uninterrupted (extension absent).

191. *Apex of median groove/scutellum anterior apical extension*: (0) without emargination, rounded; (1) emarginate- notched; (2) emarginate- shallow grooved.

192. *Alar ridges of scutum*: (0) markedly defined, persisting beyond scutellar/scutum medial most union; (1) not so.

193. *Scutellum*: (0) present; (1) absent.

194. *Setation on dorso-posterior apex of median groove and alar ridges*: (0) present, long; (1) present, short; (2) absent.

195. *Postphragma (mediophragma and laterophragmites)*: (0) all of post phragma pesent and markedly developed; (1) mediophragma absent, laterophragmites reduced/vestigial.

Meso- and Metasternites

196. *Posterior ½ of medial margin of mesocoxal formen/cavity* (Fig. 120): (0) approximately parallel; (1) slightly oblique (< 30°); (2) markedly oblique (> 30°).

197. *Anterior ½ of medial margin of mesocoxal formen/cavity* (Fig. 118): (0) differentiated from posterior ½ by an obvious point of changed angulation in lateral direction; (1) not so.

198. *Width of mesosternellum between closest point of the posterior median margins of mesocoxal foramen compared to width of mesocoxal formen (measured from middle of posterior ½ of mesocoxal formen)*: (0) greater than width of mesocoxal forman; (1) greater than to equal ½ width of mesocoxal forman (Fig. 119); (2) less than to egual ½ width of mesocoxal forman.

199. *Longitudinal invagination of mesosternellum and metabasisternum*: (0) absent; (1) short. Restricted between posterior median margins of mesocoxal foramen and mesosternellum; (2) long. Extending through both sternites.

200. *Shape of longitudinal invagination*: (0) depression; (1) suture.

201. *Condition of longitudinal invagination (depression or suture)*: (0) markedly developed, distinct; (1) not so.

202. *Anterior medial margin of mesobasisternum*: (0) not projecting anteriorly; (1) forming a slight projection directed anteriorly; (2) forming an obvious projection directed anteriorly.

203. *Projection of mesobasisternum*: (0) slightly emarginated; (1) markedly emarginated; (2) emargination absent.

204. *Anterior region of mesosternellum*: (0) forming a distinct, apexed ridge/carina or lump; (1) forming a slight, rounded ridge/carina or lump; (2) anterior region of mesosternellum plain, unmodified.

205. *Predominance of setae on mesobasisternum and anterior region of mesosternellum (around protuberance)*: (0) developed; (1) reduced to vestigial.

206. *Setation on mesobasisternum and anterior region of mesosternellum*: (0) dense; (1) evenly distributed to sparse.

Metendosternite

207. *Shape of lateral support of furca (dorsal view)*: (0) straight to very slight concavity with minimal to no posterior deflection at distal apices; (1) even concavity with no posterior deflection at distal apices; (2) even concavity restricted medially with handle-bar like posterior deflection at distal apices.

208. *Shape of medial portion of anterior lamini (dorsal view)*: (0) markedly triangulate (beak-like) with medial apex of triangulation projecting anterior ventrally; (1) slightly triangulate, slightly projecting; (2) vestigial to no triangulation, without anterior ventral projection.

209. *Apical tips of furca*: (0) simple, pointed with no projecting membranous lobe-like apodemes (Fig. 121); (1) simple, not pointed with 2 separate apodemes.One extending laterally from each apex of furca and a vestigial apodeme present on posterior margin of furca immediately prior to each apex (Fig. 122); (2) enlarged angulate/clubbed, enveloped by a single membranous apodeme (Fig. 123); (3) bifurcated (markedly or not), each accompanied by a membranous apodeme (Fig. 124); (4) complex, radiating into a hyper-extended membranous apodeme extending anteriorly and/or posteriorly in a horizontal plane (Fig. 125).

210. *Shape of lateral margins of stork (dorsal view)*: (0) approximately straight-sided and parallel (may be slight crimping immediately prior to basal process) (Fig. 126): (1) straight-sided and uniformly tapered to its narrowest point basally (may be slight 'crimping' immediately prior to basal process) (Fig. 127); (2) curved with swelling in

medial region of stalk (Fig. 128); (3) straight-sided and uniformly tapered to its widest point basally (Fig. 129).

211. *Extension of lateral margins of stalk anterior to union between stalk and posterior lamini of furca*: (0) present as a rigid structural extension located dorsally (Fig. 130); (1) present as a rigid structural extension located ventrally; (2) vestigial to absent (Fig. 131).

212. *Dorsal longitudinal ridge (lateral view)*: (0) arising from top of medial point of lateral support of furca (Fig. 132); (1) arising approximately half-way between top and bottom of medial point of lateral support of furca (Fig. 133); (2) arising from bottom of medial point of lateral support of furca or from the stalk (Fig. 134).

213. *Shape of dorsal longitudinal ridge (lateral view)*: (0) approximately convex through its length; (1) approximately flat, even through most its length but tapering away at posterior end; (2) evenly tapered from highest anteriorly, dying away posteriorly (may/may not run length of stalk); (3) absent.

214. *Shape of ventral longitudinal ridge (lateral view)*: (0) straight through entire length (Fig. 132); (1) straight anteriorly, curved posteriorly; (2) convex through entire length.

215. *Frontal region of the ventral longitudinal ridge anterior of its union with posterior lamini of furca (lateral view)*: (0) projecting anteriorly; (1) not projecting, vertically aligned; (2) absent.

216. *Angulation of anterior margin of ventral longitudinal ridge at union with posterior lamini of furca*: (0) angled ventrally so that anterior apex of ventral longitudinal ridge lower than margin posterior to union (Fig. 132): (1) without angulation, in approximately equal plane with ventral margin posterior of union.

217. *Shape of apical region of ventral longitudinal ridge anterior of its union with posterior lateral lamini of furca (lateral view)*: (0) angulate with convex ventral margin; (1) angulate with straight ventral margin; (2) rounded, without angulate apex; (3) beak like with straight ventral margin (Fig. 132).

218. *Angulation of ventral most portion of posterior lateral lamini taken from a vertical line passing through ventral most point of its union with ventral longitudinal ridge (lateral view)*: (0) angled anteriorly; (1) angled approximately vertical; (2) angled posteriorly.

Abdomen

219. *Size of spiracle #1 compared with spiracle #2*: (0) slightly larger (1.1-1.2x); (1) equally sized; (2) markedly larger (1.5-2.0x).

220. *Shape of spiracle #2*: (0) circular (Fig. 136); (1) ecliptical/sausage-shaped (Fig. 135).

221. *Orientation of spiracle #2 (using aperture or slit of spiracle)*: (0) approximately parallel to dorso-medial margin of adjacent latero-tergite (Fig. 135); (1) oblique-perpendicular to dorso-medial margin of adjacent latero-tergite (Figs 136,137).

222. *Position of spiracle #2 relative to dorso-medial margin of adjacent laterotergite*: (0) distance from margin less than to equal ½ spiracular width (Fig. 136); (1) distance from margin = spiracular width (Fig. 137); (2) distance from margin > spiracular width (Fig. 135).

223. *Dorso-medial margin of laterotergite adjacent to spiracle #2*: (0) markedly emarginate (Fig. 136); (1) slightly emarginate (Fig. 135); (2) without emargination (Fig. 137).

224. *Apex of intercoxal process of third ventrite (lateral view)*: (0) markedly projecting ventrally below ventrites 4-7 (Fig. 142); (1) in plane with ventrites 4-7 (Fig. 143); (2) slightly projecting ventrally below ventrites 4-7 (Fig. 144).

225. *Surface of third ventrite adjoining its intercoxal process*: (0) Raised/swollen along margin (epipleural zone) only; (1) raised/swollen on margin and surface to ventrite #4; (2) even, not raised/swollen.

226. *Ventrite #8 medially*: (0) longest, ventrites 4-8 slightly shortened or not so; (1) longest, ventrites 4-7 markedly shortened; (2) ventrites 4-8 equal (shortened or not so); (3) markedly shortened.

227. *Lateral line of at least anterior half of ventrite #8 in relation to lateral line of ventrites 4-7 (lateral view)*: (0) offset below lateral line of ventrites 4-7 (NB: if lateral line of each of ventrites 4-8 are consecutively offset below each other then character state is 1) (Figs 138,139); (1) not so (Figs 140,141).

228. *Posterior apex of ventrite #8 in relation to lateral line extending through ventrites 4-7 (lateral view)*: (0) projecting ventrally to or beyond lateral line (Figs 139,140); (1) not so (Figs 139,142).

Pygidium

229. *Length to width ratio*: (0) 0.5-0.55; (1) 0.56-0.60; (2) 0.61-0.65, (3) 0.66-0.70.

230. *Transverse ridge, medially*: (0) angulate; (1) curved; (2) straight.

231. *Transverse ridge, laterally*: (0) decurved from medial portion of transverse ridge (Fig. 145); (1) unvaried from medial portion of transverse ridge (Figs 146,147).

232. *Development of transverse ridge*: (0) markedly developed, pronounced ventral facet (Fig. 145); (1) markedly developed, pronounced ventral and dorsal facet (Fig. 146); (2) reduced, weak ventral facet (Fig. 147).

233. *Dorsal anterior margin*: (0) emarginate medially (Figs 145,147); (1) even, unmodified (Fig. 146).

234. *Anterior medial invagination*: (0) markedly developed, distinct (Figs 145,147); (1) slightly developed, indistinct (Fig. 146); (2) absent.

235. *Anterior medial invagination*: (0) completely divides facet between dorsal anterior margin and transverse ridge (Fig. 147); (1) partially divides facet (Figs 145,146).

236. *Anterior medial invagination*: (0) scalloped/notched (Figs 145,146); (1) parallel sided (Fig. 147); (2) sub-parallel sided.

237. *Pygidium surface*: (0) even; (1) rippled.

238. *Pygidium surface*: (0) punctated: (1) with protuberances (e.g. granulations); (2) both punctations and protuberances present; (2) without punctations or protuberances, featureless.

Aedaegus

239. *Position of paramere relative to basal piece (lateral view)*: (0) obliquely angled; (1) acutely angled; (2) slightly angled to straight.

240. *Paramere shape (lateral view)*: (0) distinctly tapering to a point with evenly rounded on dorsum of posterior apical margin; (1) tapering to a point, markedly truncate and angulate on dorsum of posterior apical margin; (2) blunt, no point (acute angle on dorsum of posterior apical margin may be present).

241. *Paramere apical hooks*: (0) reduced, simple; (1) markedly developed, complex.

242. *Paramere symmetry (anterior frontal view)*: (0) symmetrical; (1) asymmetrical.

243. *Baso-medial region of paramere (anterior frontal view)*: (0) simple, unmodified (Fig. 148); (1) one side with laterally protruding hook (markedly developed or not so) (Fig. 149); (2) one side with modified anterior medial margin protruding baso-ventrally (hook-like) with posterior ridge (Fig. 150).

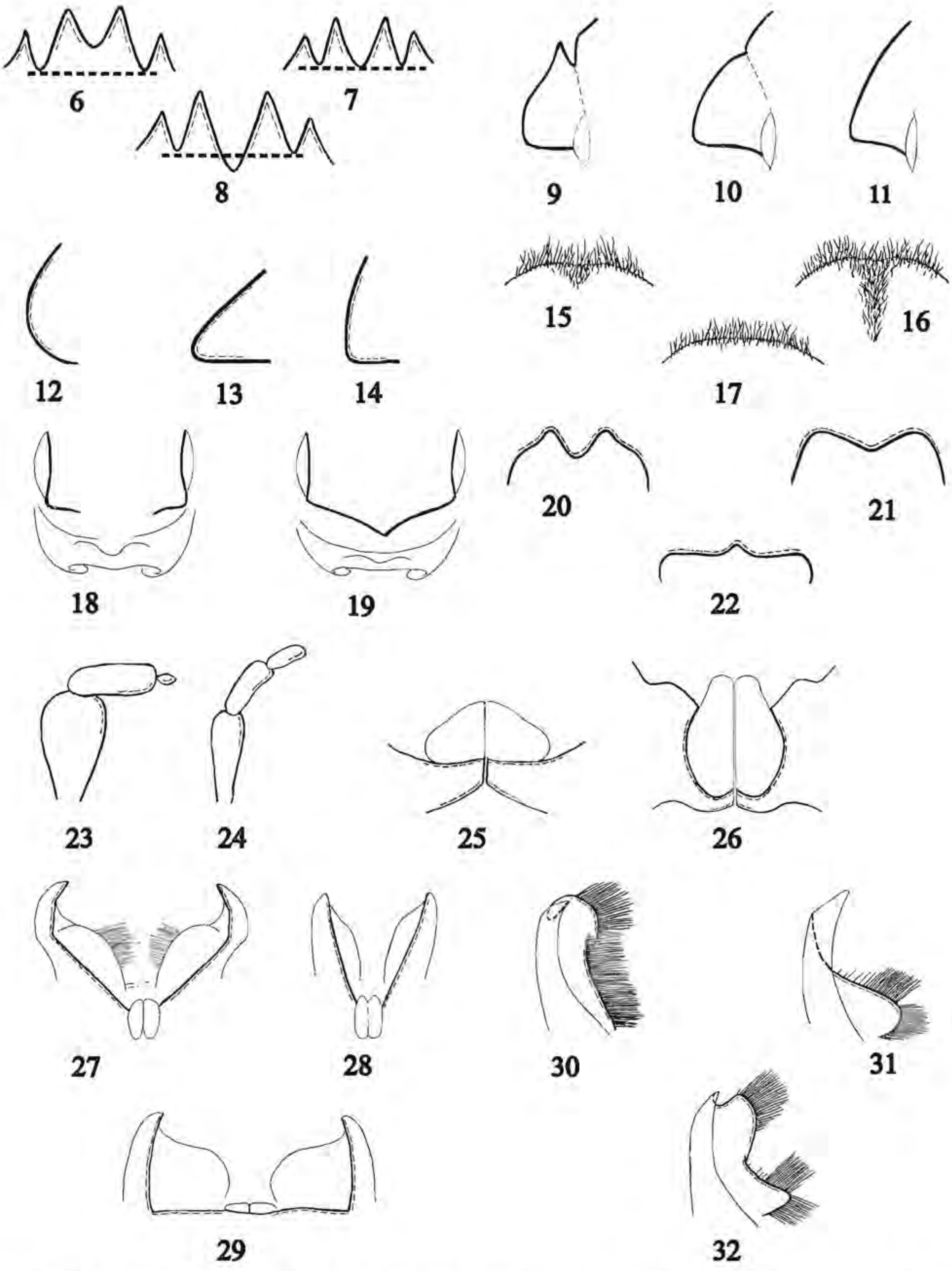
244. *Lateral expansion of paramere apical hooks (anterior frontal view)*: (0) markedly developed, obvious (Fig. 151); (1) markedly reduced to absent (Fig. 152).

Biological Characters

245. *Principal activity period*: (0) diurnal; (1) nocturnal.

246. *Soil type preference*: (0) sand; (1) clay; (2) generalist (i.e. will utilise both soil types).

247. *Mode of food relocation*: (0) tunneller; (1) roller; (2) modified (e.g. pusher, carrier, dragger).



Figs 6–152. Anatomical drawings of select characters and states (in parentheses) described in Appendix 2 of the Phylogeny of the Scarabaeini (Coleoptera: Scarabaeidae). **Figs 6–22**. Head plate characters. Fig. 6- Character 4(0); Fig. 7- Char. 4(1); Fig. 8- Char. 4(2); Fig. 9- Char. 10(0); Fig. 10- Char. 10(1); Fig. 11- Char. 10(2); Fig. 12- Char. 13(0); Fig. 13- Char. 13(1); Fig. 14- Char. 13(2); Fig. 15- Char. 17(0); Fig. 16- Char. 17(1); Fig. 17- Char. 17(2); Fig. 18- Char. 20(1); Fig. 19- Char. 20(2); Fig. 20- Char. 22(0); Fig. 21- Char. 22(1); Fig. 22- Char. 22(2). **Figs 23–32**. Labium Characters. Fig. 23- Chars 32(0), 33(0); Fig. 24- Chars 32(1), 33(1); Fig. 25- Char. 36(0); Fig. 26- Char. 36(1); Fig. 27- Char. 39(0); Fig. 28- Char. 39(1); Fig. 29- Char. 39(2); Fig. 30- Char. 42(0); Fig. 31- Char. 42(1); Fig. 32- Char. 42(2).

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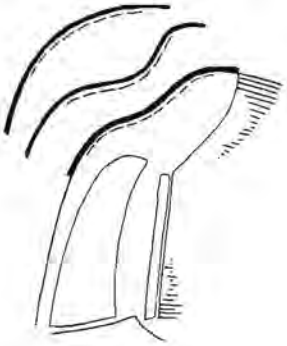

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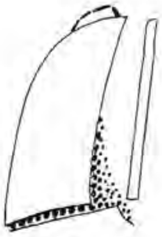

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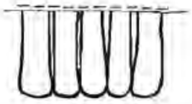

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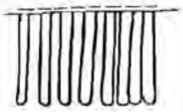

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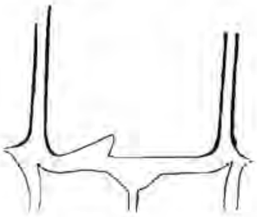

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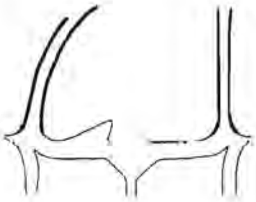

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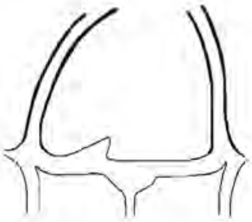

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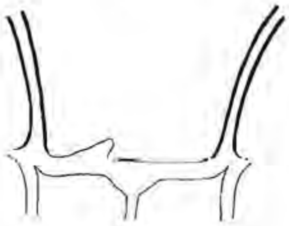

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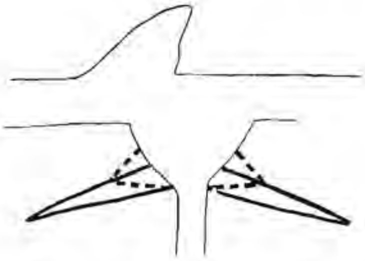

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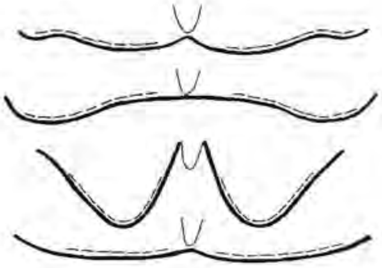

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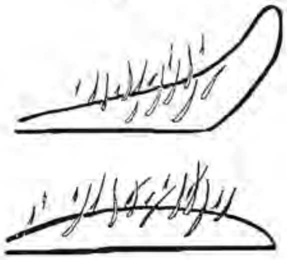

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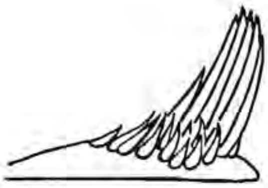

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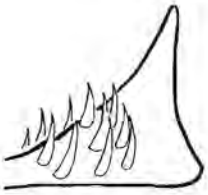

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Figs 33–36. Maxillae Characters. Fig. 33- Char. 44(0); Fig. 34- Char. 44(1); Fig. 35- Char. 45(0); Fig. 36- Char. 45(1). **Figs 37–42**. Mandible Characters. Fig. 37- Char. 52(outwards from illustration;1,2,0); Fig. 38- Chars 54(0), 55(0); Fig. 39- Chars 54(1), 55(1); Fig. 40- Chars 53(1), 54(1), 55(2); Fig. 41- Chars 56(0), 57(0); Fig. 42- Chars 56(1), 57(1). **Figs 43–53**. Epipharynx Characters. Fig. 43- Char. 58(0); Fig. 44- Char. 58(1); Fig. 45- Char. 58(2); Fig. 46- Char. 58(3); Fig. 47- Char. 61(markedly developed to absent; 0,1,2); Fig. 48- Char. 66(1); Fig. 49- Char. 67(top to bottom; 0,1,2,3); Fig. 50- Char. 68(top,0; bottom,1); Fig. 51- Char. 69(0); Fig. 52- Char. 69(1); Fig. 53- Char. 69(2).

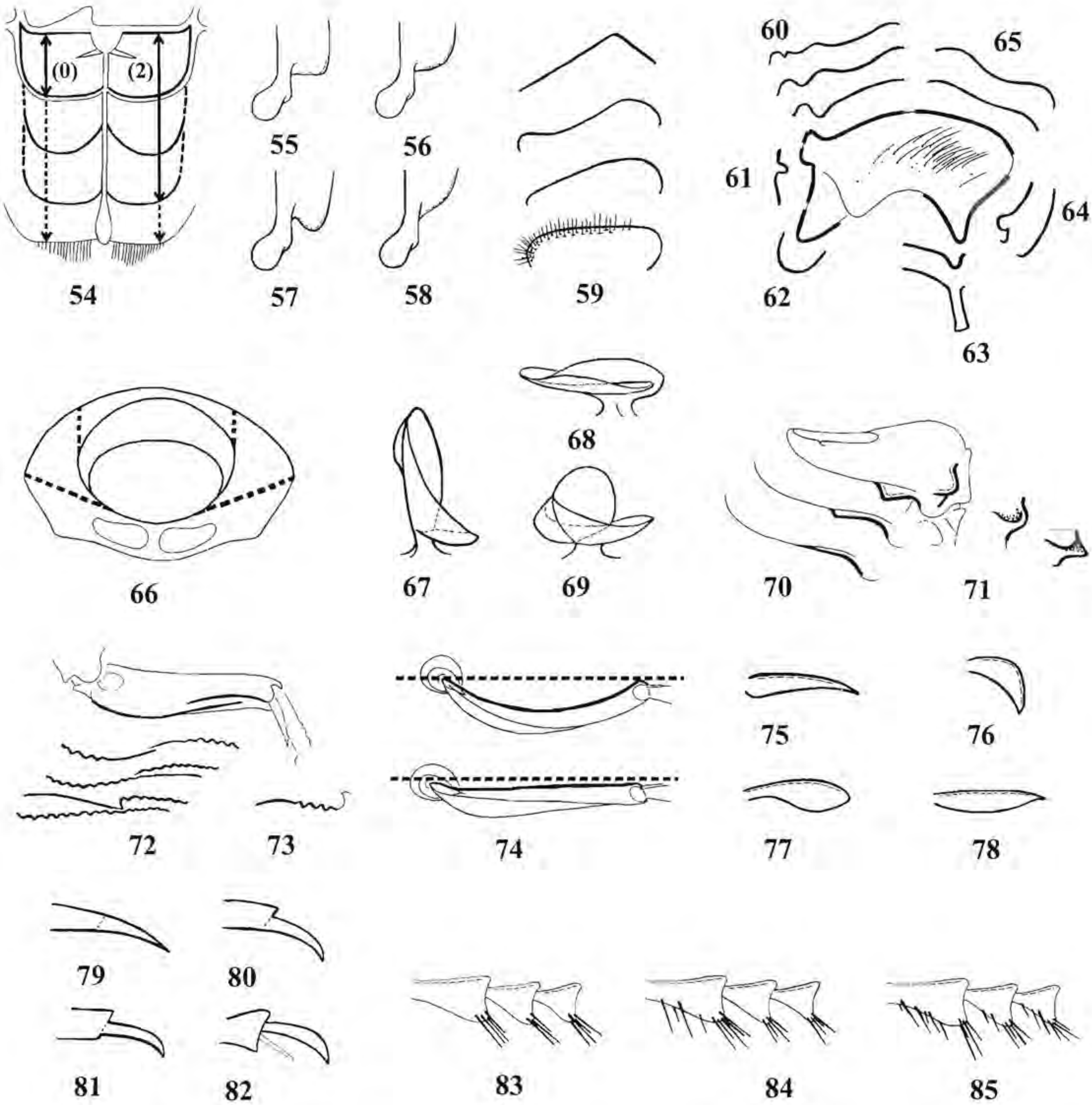
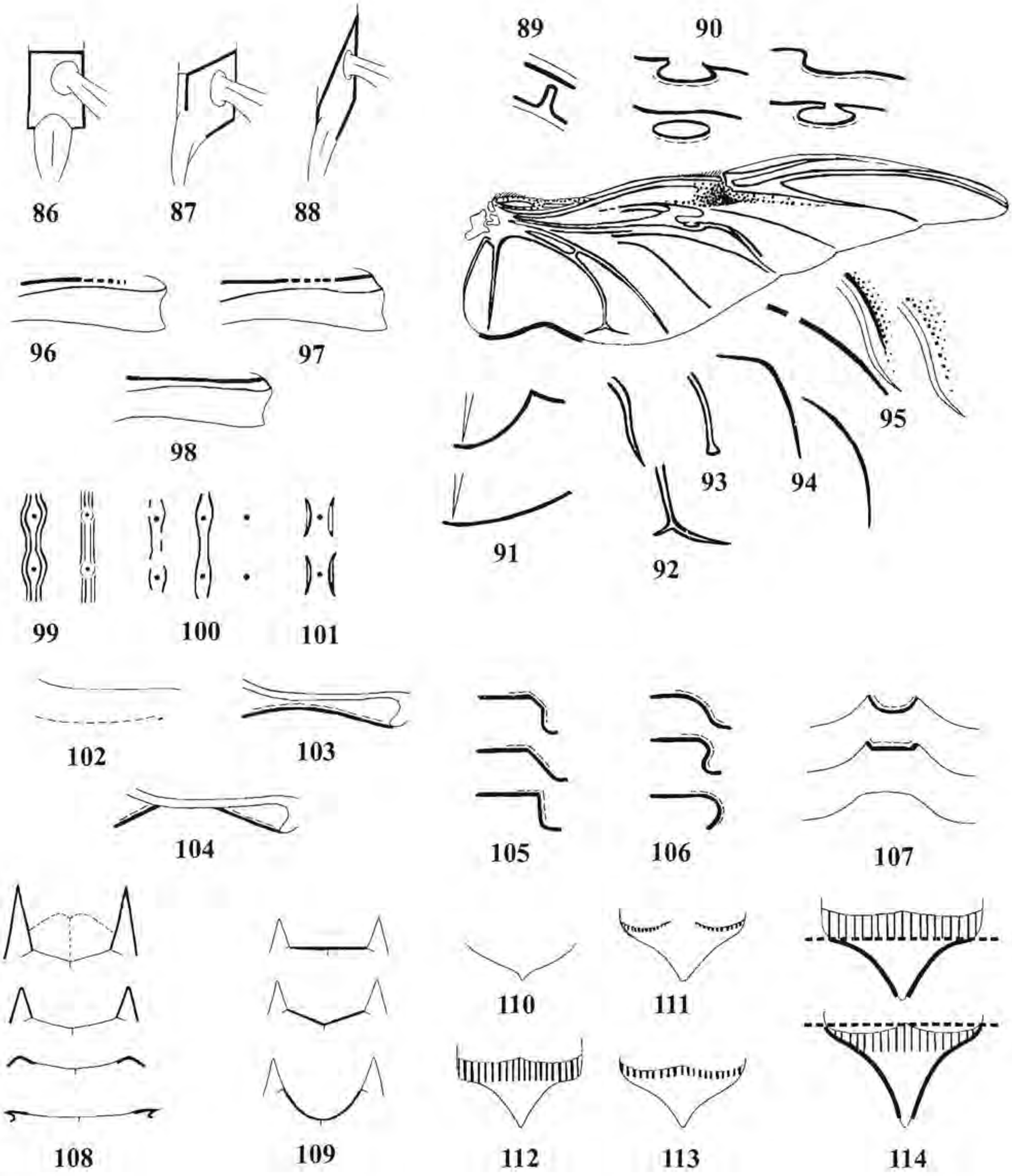
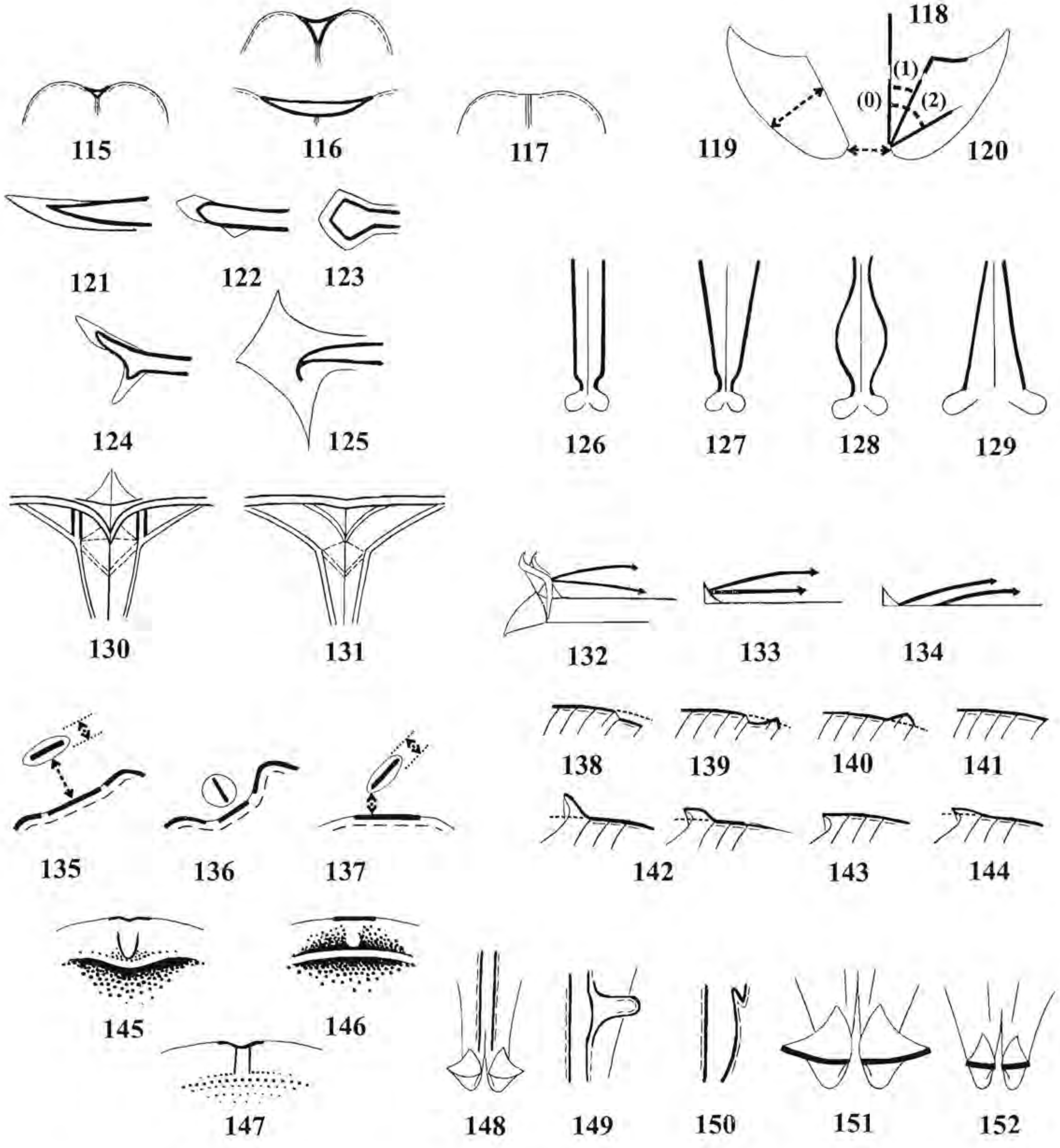


Fig. 54. Epipharynx Character 62(top to bottom; 0,2,1). **Figs 55–58**. Antennae Characters. Fig. 55- Chars 24(0), 25(0); Fig. 56- Chars 24(1), 25(0); Fig 57- Char. 25(1); Fig 58- Char. 25(2). **Figs 59–65**. Neck Sclerite Characters. Fig. 59- Char. 72(outwards; 0,1,2,2); Fig. 60- Char. 74(outwards; 3,0,1,2); Fig. 61- Char. 75(inner,1; outer,0). Fig. 62- Char. 76(inner,0; outer,1); Fig. 63- Char. 78(outwards; 1,2,0); Fig. 64- Char. 77(outwards; 1,0,2); Fig. 65- Char. 73(outwards; 0,2,1). **Figs. 66–69**. Prothorax Characters. Fig. 66- Char. 85(oblique broken lines, 1; vertical broken lines, 2; without broken lines, 0); Fig. 67- Char. 91(0); Fig. 68- Char. 91(2); Fig. 69- Char. 91(1). **Figs 70–73**. Foreleg Characters. Fig. 70- Char. 92(outwards, 0,2,1); Fig. 71- Char. 93(outwards; 2,1,0); Fig. 72- Chars 100(outwards; 0,2,2,1), 102(outwards; 0,1,3,2); Fig. 73- Char. 99(inner,1; outer,0). **Figs 74–85**. Midleg Characters. Fig. 74- Char. 118(top,3; bottom,1); Fig 75- Char. 123(0); Fig 76- Char. 123(1); Fig. 77- Char. 123(2); Fig. 78- Char. 123(3); Fig. 79 Char. 125(0); Fig. 80- Char. 125(1); Fig. 81- Char. 125(2); Fig. 82- Char. 125(3); Fig. 83- Char. 128(0); Fig. 84- Char. 128(1); Fig. 85- Char. 128(2).



Figs 86–88. Hindleg Characters. Fig. 86- Char. 140(0); Fig. 87- Char. 140(1); Fig. 88- Char. 140(2). **Figs 89–95**. Wing Characters. Fig. 89- Char. 159(0; on wing habitus,1); Fig. 90- Char. 151(inner left,0; inner right,1; outer left,2; outer right,3); Fig. 91- Char. 156(outwards from wing habitus; 0,1,2); Fig. 92- Chars 146(middle,1; outer,0), 147(on wing habitus,0; outer,1); Fig. 93- Char. 148(on wing habitus,1; outer,2); Fig. 94- Chars 154(outwards from wing habitus, 0,1,2), 155(on wing habitus,1); Fig. 95- Chars Char. 152(0; on wing habitus,1), 153(inner,0; outer,1). **Figs 96–101**. Elytra Characters. Fig. 96- Char. 163(0); Fig. 97- Char. 163(1); Fig. 98- Char. 163(2); Fig. 99- Char. 167(0,0); Fig. 100- Char. 167(1,1,1); Fig. 101- Char. 167(2). **Figs 102–107**. Metanotum Characters. Fig. 102- Char. 186(0); Fig. 103- Char. 186(1); Fig. 104- Char. 186(2); Fig. 105- Char. 188(0,0,0); Fig. 106- Char. 188(1,1,1); Fig. 107- Char. 189(top to bottom; 0,0,1). **Figs 108–114**. Mesonotum Characters. Fig. 108- Char. 169(top to bottom; 0,2,1,1); Fig. 109- Char. 171(top to bottom; 0,2,1); Fig. 110- Char. 172(0); Fig. 111- Char. 172(1); Fig. 112- Char. 172(2); Fig. 113- Char. 172(3); Fig. 114- Char. 173(top,1; bottom,0).



Figs 115–117. Mesonotum Characters. Fig. 115- Char. 182(0); Fig. 116- Char. 182(1,1); Fig. 117- Char. 182(2). **Figs 118–120**. Mesosternum Characters. Fig. 118- Char. 196(inner,0; outer,1); Fig. 119- Char. 197(1); Fig. 120- Char. 195(outwards from centre; 0,1,2). **Figs 121–134**. Metendosternite Characters. Fig. 121- Char. 208(0); Fig. 122- Char. 208(1); Fig. 123- Char. 208(2); Fig. 124- Char. 208(3); Fig. 125- Char. 208(4); Fig. 126- Char. 209(0); Fig. 127- Char. 209(1); Fig. 128- Char. 209(2); Fig. 129- Char. 209(3); Fig. 130- Char. 210(0); Fig. 131- Char. 210(2); Fig. 132- Chars 211(0,0), 213(0), 215(0), 216(3); Fig. 133- Char. 211(1,1); Fig. 134- Char. 211(2,2). **Figs. 135–144**. Abdomen Characters. Fig. 135- Chars 219(1), 220(0), 221(2), 222(1); Fig. 136- Chars 219(0), 220(1), 221(0), 222(0); Fig. 137- Chars 220(1), 221(1), 222(2); Fig. 138- Chars 226(0), 227(1); Fig. 139- Chars 226(0), 227(0); Fig. 140- Chars 226(1), 227(0); Fig. 141- Chars 226(1), 227(1); Fig. 142- Char. 223(0,0); Fig. 143- Char. 223(1); Fig. 144- Char. 223(2). **Figs 145–147**. Pygidium Characters. Fig. 145- Chars 230(0), 231(0), 232(0), 233(0), 234(1), 235(0); Fig. 146- Chars 230(1), 231(1), 232(1), 233(1), 234(1), 235(0); Fig. 147- Chars 230(1),

231(2), 232(0), 233(0), 234(0), 235(1). **Figs 148–152**. Aedaegus Characters. Fig. 148- Char. 242(0); Fig. 149- Char. 242(1); Fig. 150- Char. 242(2); Fig. 151- Char. 243(0); Fig. 152- Char. 243(1).

Appendix 3. Data matrix. Deactivated flight and flightlessness characters/states are indicated in bold. Characters not applicable to taxa are indicated by a dash (-) and a question mark (?) denotes ambiguity of the state or missing data. Subgenera and synonyms of the genus *Scarabaeus* L. (*S.*) are surrounded by parentheses and square brackets respectively.

Taxa/Character	1111111111222222222233333333334444444444 5 012345678901234567890123456789012345678901234567890
Circellium bacchus	00130311212001100200001112201000000010210021?010110
Heliocopris hamadryas	23-2-01--02000010002-012120010020000101000000110110
Synapsis tmolus	00120310201201210202-010121010010100012100000110111
Eucranium arachnoides	111101310120122100100110121010020000100210201101000
Drepanopodus proximus	110202011102022210121000000020012010001210210111100
Kheper lamarcki	120002010002122002011100000101021110102001111111110
Kheper nigroaeneus	120002010002112002021100021102011110102001110111110
Kheper subaeneus	1200020100021120020?1100001102021110101001121111110
S. [Mnematidium] multidentatus	12020223101112200010200011002002210010101001?011100
S. [Mnematium] ritchiei	11010122110201201100201000111002201010211000?000000
S. [Mnematium] silenus	110201230101111211102100??1110022010001210021110100
S. [Neateuchus] proboscideus	120201300001012221121120110022022000100201210110111
S. [Neopachysoma] denticollis	111103201111100221001122120010000010100100211101100
S. [Neopachysoma] rodreguesi	02110120211010022100011212001000001000021020?001100
S. (Pachysoma) bennigseni	111112211111100121001122020010000000110010201101000
S. (Pachysoma) hippocrates	00110320201101210210011202001000000000021020?001000
Pachylomerus femoralis	12021111110002120100110012011010110010210100?010110
S. (Scarabaeolus) bohemani	110312000101012210012012100121011111011201111100110
S. (Scarabaeolus) flavicornis	110312000100012121011011120121011110102101110110111
S. (Scarabaeolus) rubripennis	111212001101020221111010100121011111102101111100111
S. (Scarabaeolus) scholtzi	111221311111000122102010??1111011001101100121100100
Scarabaeus galenus	011201332002011002112100122020001000102010221110110
Scarabaeus goryi	120301010001010200001100110022011110001201120110110
Scarabaeus rugosus	120202220102012210001100001121111110102011121111100
Scarabaeus rusticus	120302220002012210102001101121012110102001121111100
Scarabaeus satyrus	110201020001020210121120101022011110102011120111110
Scarabaeus westwoodi	12000230000201120001210010102102111010210111011011?
Scarabaeus zambesianus	12000121000101122112112011002201111010?001220110101
Sceliages adamastor	011321002000002221001001121102112011112001111100111
Sceliages brittoni	011321002000002221001011120102112111112001111100111
Sceliages hippias	011321002010000221001011?00102112011011201111100111

Taxa/Character	1 55555555566666666667777777777888888**8**888999999999990 12345678901234567890123456789012345**6**78901234567890
Circellium bacchus	00011013010000101110122003000011311**0**00102020110110
Heliocopris hamadryas	10000102200112100102020212020011201**0**02130221110111
Synapsis tmolus	10000111001111100111022103000001201**0**02131021110110
Eucranium arachnoides	322100122020122020201?0011001011312**1**00111021012110
Drepanopodus proximus	01000001111200203222011112011220111**0**12011110011001
Kheper lamarcki	00001000111211100102201100011101011**0**22011120101110
Kheper nigroaeneus	01001002010011103102202100111211111**0**22110220111120
Kheper subaeneus	00001002100211100102202100111010110**0**22111110111110
S. [Mnematidium] multidentatus	320000011?2101310021011002011101011**1**12011110112000
S. [Mnematium] ritchiei	02100111002201313020011010011010112**1**32011210012102
S. [Mnematium] silenus	02000111110101303021011003111003111**1**12011210112100
S. [Neateuchus] proboscideus	10001012110101101112100113121220211**0**30110100111100

Appendix 3 *continued.*

Taxa/Character	1
	55555555556666666666777777777788888**8**88889999999990
	12345678901234567890123456789012345**6**78901234567890
S. [Neopachysoma] denticollis	12212003002012002020100302012110312**1**52022020012001
S. [Neopachysoma] rodreguesi	12212003102012002020101311012000310**1**52022020012001
S. (Pachysoma) bennigseni	12211003102212002020101311101111312**1**31022020012102
S. (Pachysoma) hippocrates	12212001102012102020111311101011312**1**52002120012112
Pachylomerus femoralis	31000002011101101222001102001001211**0**21010200000121
S. (Scarabaeolus) bohemani	01002101?01101101111101100021020111**0**50010?21111102
S. (Scarabaeolus) flavicornis	01002111101101101112001100121210111**0**12010121111122
S. (Scarabaeolus) rubripennis	01100101100101101112112002111220111**0**50010220001101
S. (Scarabaeolus) scholtzi	01002103011202303112000303121010112**1**12?11010012021
Scarabaeus galenus	110000011112113030221?1113111101011**0**32110211112001
Scarabaeus goryi	00000100011111201110002110011121211**0**11110111111110
Scarabaeus rugosus	00000001001211003102201110111020111**0**42000220111122
Scarabaeus rusticus	01000111000101101112212200121020111**0**10110110111101
Scarabaeus satyrus	00001101011201203111000310221221111**0**31110211011122
Scarabaeus westwoodi	?0000001000101103112000012001100111**0**32100211112120
Scarabaeus zambesianus	11000002111201103112001310011121111**0**30010120111120
Sceliages adamastor	00111112202200101112101202011021011**0**10110221103020
Sceliages brittoni	001111122022?0101102101202011020011**0**10110221103021
Sceliages hippias	00112112202000103102101200020021011**0**10110221113010

Taxa/Character	11111111111111111111111111111111111111111111**111111**
	00000000011111111112222222222333333333344444**444445**
	12345678901234567890123456789012345678901234**567890**
Circellium bacchus	10021112102013121111301132000031001102100201**1----0**
Heliocopris hamadryas	10021112012203021211301032010211001100200201**01-101**
Synapsis tmolus	10021112012203021101001032010201000112200201**01-101**
Eucranium arachnoides	1100111211220310011100213201103 02-0020111210**1----0**
Drepanopodus proximus	10001100110112122030120-000102311111210210 10**001201**
Kheper lamarcki	30210011102222211121220-10111032111110020101**000121**
Kheper nigroaeneus	10211000102222311121220-10121032111100020201**001121**
Kheper subaeneus	30210011102222211121220-10111032101100020201**001021**
S. [Mnematidium] multidentatus	00001000110120100010121-2011003100101022?210**01-121**
S. [Mnematium] ritchiei	01001100110121232121220-20110231000111220102**1----1**
S. [Mnematium] silenus	01001100110121232011211-20020231000012220000**1----1**
S. [Neateuchus] proboscideus	10001000112112100031221-20010231010011021012**000111**
S. [Neopachysoma] denticollis	02101100112121200320322-30110130010020121210**1----0**
S. [Neopachysoma] rodreguesi	02101100112121200320322-30011310011022221210**1----0**
S. (Pachysoma) bennigseni	00001112110021300020122-30110130010020121010**1----0**
S. (Pachysoma) hippocrates	12101102110011211020122-31011310011120211010**1----0**
Pachylomerus femoralis	20000111110010100220120-21120201010122210000**000121**
S. (Scarabaeolus) bohemani	10001001100011113031111021100331001111210201**01-121**
S. (Scarabaeolus) flavicornis	10001112100011133031111021020231001122210102**01-111**
S. (Scarabaeolus) rubripennis	10001101100011133031111020120331001111221112**01-121**
S. (Scarabaeolus) scholtzi	030011011100212320311 11?02002022200012021 0?0?**1----0**
Scarabaeus galenus	10011000110020132110121-21100312001100111112**001121**
Scarabaeus goryi	10000011111022211111120-20121211010001020201**001111**
Scarabaeus rugosus	10011000100011122011121-20120321001112111102**000221**
Scarabaeus rusticus	13001000100011111111121-20100331001012110102**001221**

Appendix 3 *continued.*

Taxa/Character	11111111111111111111111111111111111111111111111111 00000000011111111112222222222333333333344444444445 12345678901234567890123456789012345678901234567890
Scarabaeus satyrus	10001012100012132011221-20120231010011020102000111
Scarabaeus westwoodi	03011000100220111031120-21100332001020110101001221
Scarabaeus zambesianus	10001112110012232131121-20120211011112020102000111
Sceliages adamastor	10011101110011123121403222010330001022210201000021
Sceliages brittoni	10011101110011123120413222010330001122210201000021
Sceliages hippias	10001102110011112111103021020131001120210201001121

Taxa/Character	11111111111111111111111111111111111111111111111112 55555555566666666667777777777888888888899999999990 12345678901234567890123456789012345678901234567890
Circellium bacchus	------5----021111022011120012311011010010111010201
Heliocopris hamadryas	110222501320200110021100201021410000000100100010--
Synapsis tmolus	11121250130021012021131000102141000000000010000101
Eucranium arachnoides	------5----33-11101110-0-00123--11101?0111201120--
Drepanopodus proximus	20011010111020220020230101202231000201021010101200
Kheper lamarcki	31111000131120001220230101200022010200001010101201
Kheper nigroaeneus	011121001310201002201211011011120?0100000000101101
Kheper subaeneus	31112030121120001220130121200032000201021010101101
S. [Mnematidium] multidentatus	20101010002110221120130121301230000200010010212200
S. [Mnematium] ritchiei	------51---2211111101211113122221110110000011212110
S. [Mnematium] silenus	------51---2011110201311103121321110110100011212110
S. [Neateuchus] proboscideus	11001151130120020100221111101010010200020000201210
S. [Neopachysoma] denticollis	------2----32111141010-0-00123221110111-11211020--
S. [Neopachysoma] rodreguesi	------2----32111141110-0-10113321110111-11211020--
S. (*Pachysoma*) *bennigseni*	------2----32110131010-0-00123121110111-11211020--
S. (*Pachysoma*) *hippocrates*	------2----22111141110-0-10113001110011-11211020--
Pachylomerus femoralis	0102020013010022122223010120123?0001011-1010112210
S. (*Scarabaeolus*) *bohemani*	20100021021020000020221111300111010101000000100211
S. (*Scarabaeolus*) *flavicornis*	201011210000202200202211113011210?0101020000101210
S. (*Scarabaeolus*) *rubripennis*	20121121021020200020121111201101010111010010101210
S. (*Scarabaeolus*) *scholtzi*	------5----2211110100201101123--1110111-10211020--
Scarabaeus galenus	11001120132000001100030101201000000100000000201100
Scarabaeus goryi	00102151112120000000003001101132000200000000101100
Scarabaeus rugosus	21101110102000020310221111200112000101000000200200
Scarabaeus rusticus	211011401120100000102211113001300?0101020000100201
Scarabaeus satyrus	10101110112120100000221111300140000111010010101101
Scarabaeus westwoodi	21002011012000001120220101301030010101020000211201
Scarabaeus zambesianus	21002011012000001120220101301030010101020000211201
Sceliages adamastor	21001110002020100120121101301231000101010000 1000--
Sceliages brittoni	21001110111020100120121001301230000101000000100201
Sceliages hippias	211011100010200001201211011010320101010100001000--

Appendix 3 *continued.*

Taxa/Character	22222**2**2222222222222222222222222222222222222222 00000**0**000111111111122222222223333333333 4444444 12345**6**7890123456789012345678901234567890123456
Circellium bacchus	0-211**0**2310-322---20000110101101000100211100001
Heliocopris hamadryas	0-200**0**0222201002020000122013002100202210001100
Synapsis tmolus	??201**2**0220-3?001020001102102012000200200001100
Eucranium arachnoides	10211**0**23212?2012220122203011210010100200001002
Drepanopodus proximus	22000**2**0322001011020101102011102111000010000001
Kheper lamarcki	21011**2**0100101011001112200012100011002111000001
Kheper nigroaeneus	21000**2**0100100001021102100010000001000011110021
Kheper subaeneus	21011**2**01000000010?1102000013100001202101000011
S. [Mnematidium] multidentatus	22000**2**0322210000011010000001212011102210111?0?
S. [Mnematium] ritchiei	22001**1**100201101102011001200101211100120 0111?0?
S. [Mnematium] silenus	22001**1**132011201?21110000210121201120 0210111?0?
S. [Neateuchus] proboscideus	20100**2**0301000013001000122113001011002101111101
S. [Neopachysoma] denticollis	10211**1**14200001112?002100001110112--11110120002
S. [Neopachysoma] rodreguesi	11211**1**24?100111121001001001110102--12110120002
S. (Pachysoma) bennigseni	10211**1**0422201011210021010000101011112101121002
S. (Pachysoma) hippocrates	11211**1**14100022---10010000003101000102000121002
Pachylomerus femoralis	22011**0**01222100000111011001131110102020110000 0?
S. (Scarabaeolus) bohemani	21000**2**01001000110110?221201301110120002012 1021
S. (Scarabaeolus) flavicornis	22100**2**0312000000011011112012011?1?000020111001
S. (Scarabaeolus) rubripennis	21000**0**0022020000010122202013002111200020001001
S. (Scarabaeolus) scholtzi	101?1**1**24120021122100101120121010112 01???????0?
Scarabaeus galenus	21101**2**0202210000001100112112211?11110000111022
Scarabaeus goryi	21100**2**03201000130010001001101101 2--02101110101
Scarabaeus rugosus	11000**2**0322121000101111010012010101011011110001
Scarabaeus rusticus	11000**0**0310000011001111112101000011003020111011
Scarabaeus satyrus	21100**2**0320000012001??020200310001010 0101101101
Scarabaeus westwoodi	11000**0**0220121011001010000002000010111020111011
Scarabaeus zambesianus	21101**0**0330100002011000122013101011200021120101
Sceliages adamastor	12011**2**0322120011021111010003000101012000121002
Sceliages brittoni	12011**2**0320120010001111010002000101012100121002
Sceliages hippias	11011**2**0120120011000110010003112111000000121012

Appendix 4. **Figs 153.01 – 153.10**. Subtrees of the single PIWE Tree calculated at CO = 4 in the Evolution of the Scarabaeini (Scarabaeidae: Scarabaeinae). Characters and states on nodes/branches; Black hash marks indicate non-homoplasious changes (synapomorphies or autapomorphies), White hash marks indicate homoplasies., Numbers above hashmarks represent characters, numbers below hash marks represent character states (Nixon, 1999).

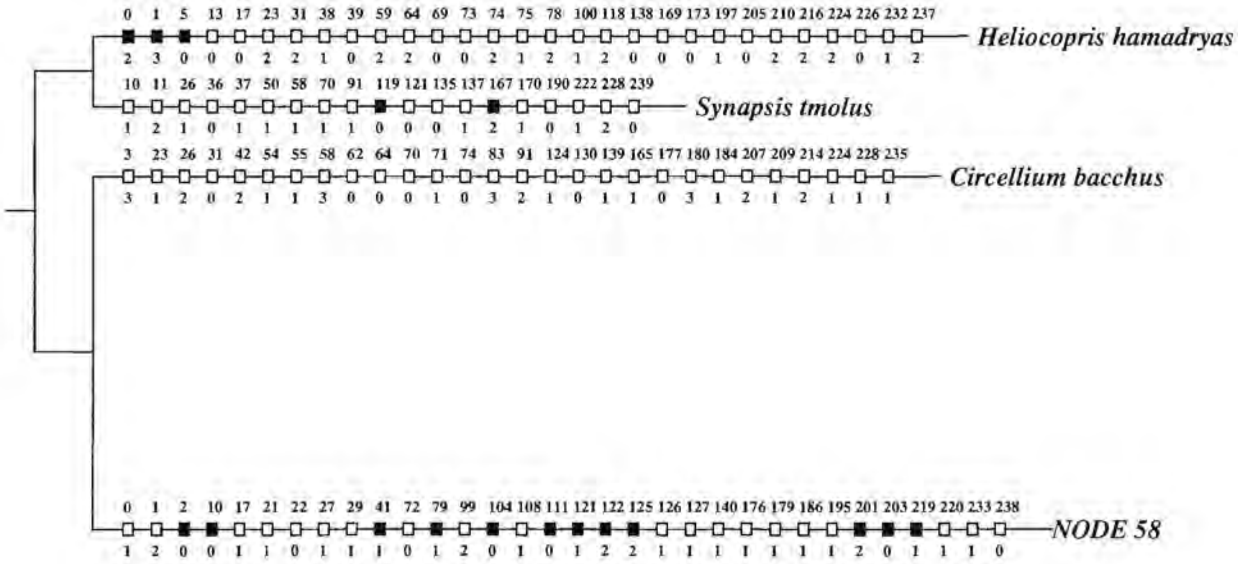


Fig. 153.01. Basal nodes (Rerouted).

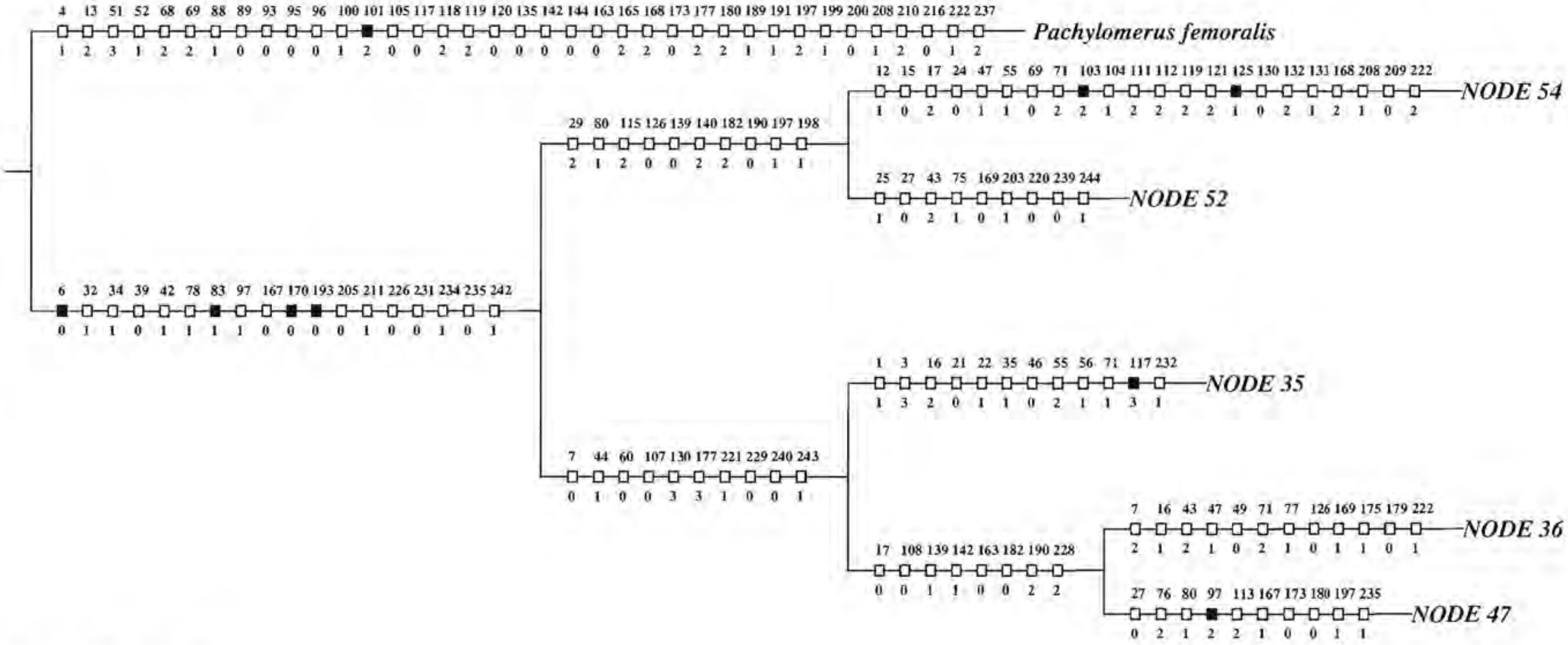


Fig. 153.02. Node 58

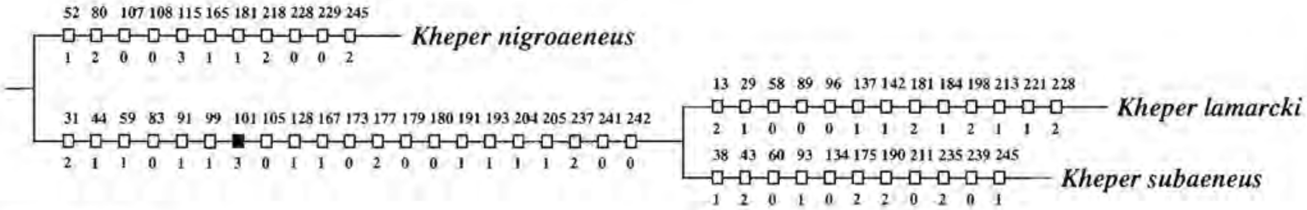


Fig. 153.03. Node 54.

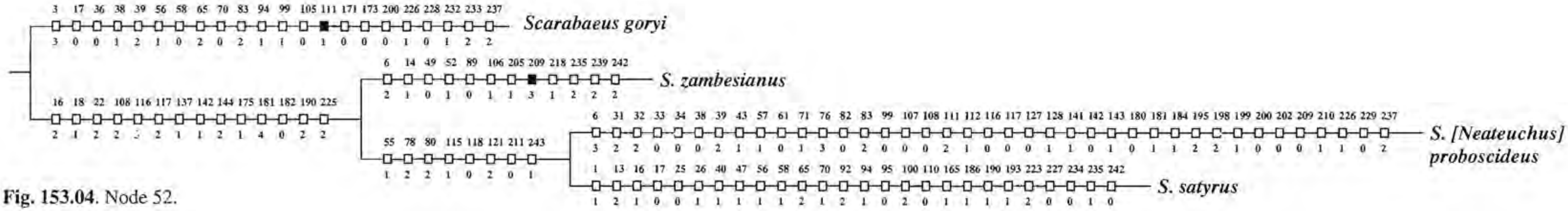


Fig. 153.04. Node 52.

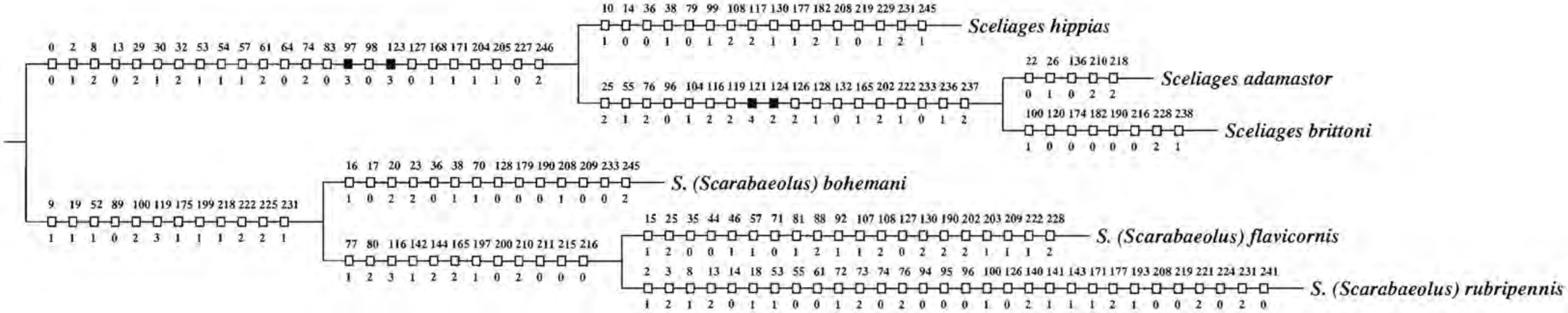


Fig. 153.05. Node 35.

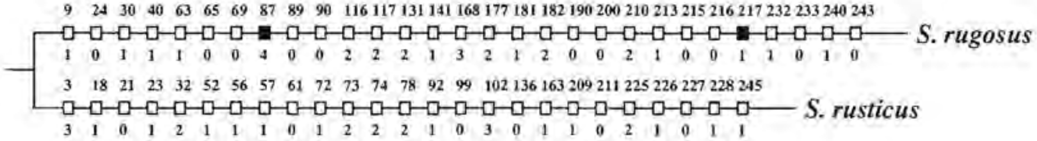


Fig. 153.06. Node 36.

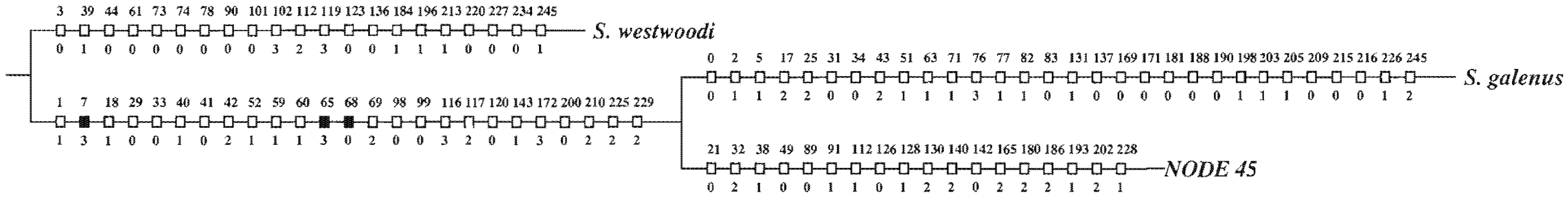


Fig. 153.07. Node 47.

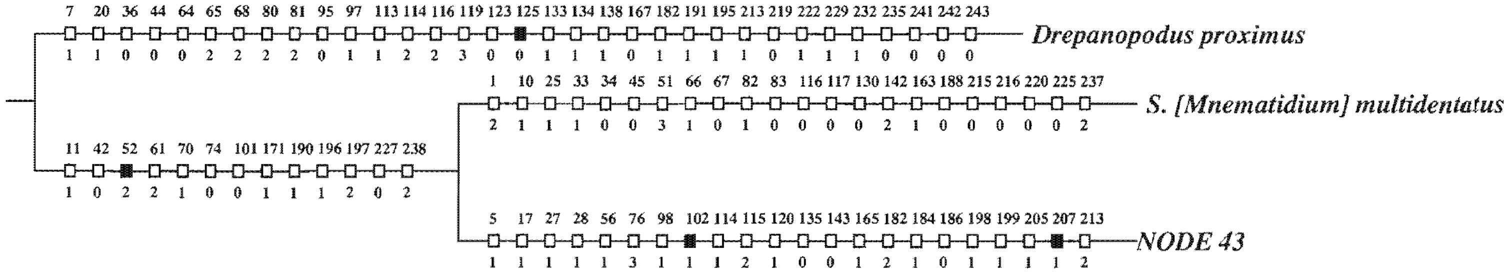


Fig. 153.08. Node 45.

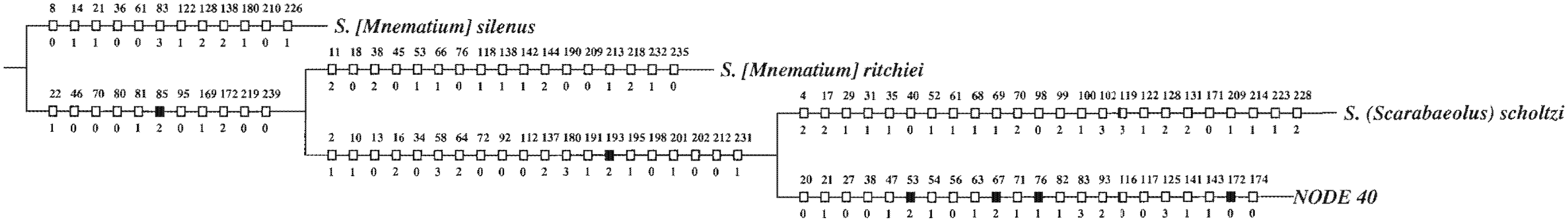


Fig. 153.09. Node 43.

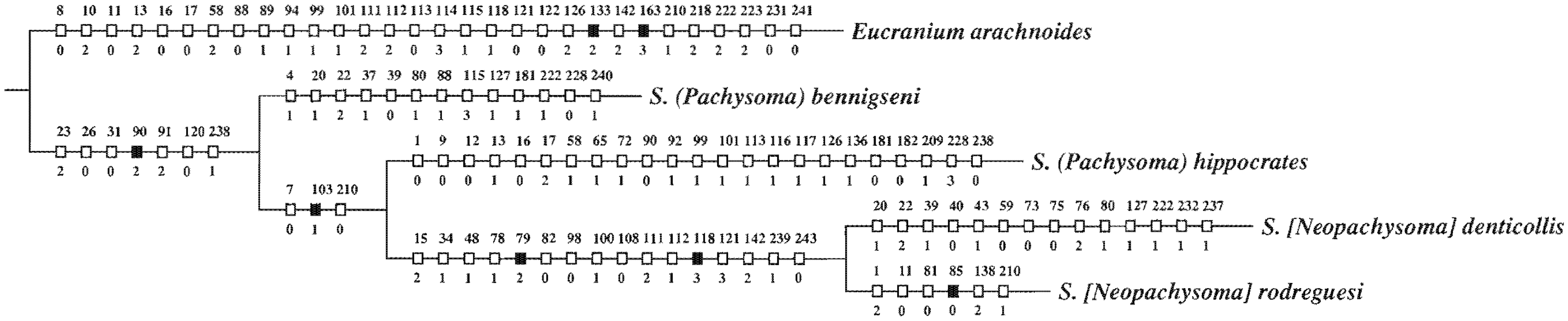


Fig. 153.10. Node 40.