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Phylogeny of the Scarabaeini (Coleoptera: Scarabaeidae)

by

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…….. To Rachel, with love.

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Summary

Phylogeny of the Scarabaeini
(Coleoptera: Scarabaeidae)

The Scarabaeini comprises some 146 species of ball-rolling dung beetles belonging to the genera *Pachylomerus* and *Scarabaeus*, and *Scarabaeus* subgenera, *Kheper*, *Pachysoma*, *Scarabaeolus*, *Scarabaeus* and *Sceliages*. Their distribution extends throughout the Afrotropical region (including Madagascar) and southern latitudes of the Palaearctic. In this study, 244 morphological characters, including 154 multistate, and 3 biological characters were identified using 28 morphologically diverse members of the tribe. These taxa were polarized against 4 members from related tribes. Molecular sequence data from mitochondrial Cytochrome Oxidase subunit I (1197 bp) and 16S ribosomal RNA (461bp) genes of 25 of these taxa were also obtained in an attempt to further resolve broad phylogenetic relationships inferred from morphology-based hypotheses of tribal evolution.

All data sets were subjected to a battery of weighted and unweighted simultaneous analyses to help recover the most accurate representations of phylogeny. Results show poorly resolved trees with many of the intermediate and basal nodes forming the backbone of each topology collapsed following bootstrap analysis. In concordance with many insect studies involving mitochondrial DNA, many sites exhibited strong A+T nucleotide bias and high interlineage divergences evolving heterogeneously in both genes with transition: transversion ratios reaching saturation. Homoplasious morphological characters appeared to carry more weight than the molecular data leading to an over proportional impact on the latter in combined analyses. Despite a lack topological congruence, phylogenetic signal was present, however, in a number of well-supported relationships that were congruent between the molecular and morphological data.

Molecular evidence indicates the Scarabaeini have origins dating back to at least the mid-upper Miocene (8-18 Million years ago). During this time its members underwent a rapid phase of radiation followed by long periods of divergence. Flightlessness evolved in several lineages along with the polyphyletic evolution of behavioural adaptations associated with food specialization and relocation including pushing, dragging and carrying, or combinations of these techniques. Members of the *Scarabaeus* subgenus *Sceliages* Westwood have evolved extreme necrophagous behaviour of feeding and breeding exclusively on millipedes. Whilst necrophagy is an opportunist strategy utilised by many scarabaeines, only *S. (Sceliages)* beetles have become obligate specialists. Adaptations reported in this study include a positive chemotaxic response to the quinone-based allomones secreted by distressed or injured millipedes. These beetles do not construct food balls and roll them backwards in typical Scarabaeini fashion. Rather, whole or portions of millipedes are pushed away from potential competitors, buried and subsequently dismembered to access the internal tissues for food and reproduction. Phylogenetically, all analyses strongly supported the monophyly of *Sceliages* taxa within *Scarabaeus* S. L. , thereby providing justification of the proposed subgeneric classification of its members. Congruent trends recovered from simultaneous analyses of the morphological and molecular data thus provided a means to review the systematics of the tribe.

General Introduction

Rationale for investigating the mechanisms of evolution of the Scarabaeini (Scarabaeidae: Scarabaeinae)

The Scarabaeini comprise a behaviourally advanced guild of ball-rollers including *Scarabaeus sacer* L., the first described beetle (Linnaeus, 1758: 345). The rolling of prefabricated spherical balls of food by these beetles was idolised in ancient Egyptian society via the solar deity Khepera, half human and half sacred scarab, who controlled the sun's daily azimuth across the sky (Fig.1).

Fig. 1. Depiction of the ancient Egyptian solar deity, Khepera.

Systematics

The tribe includes approximately 146 species belonging to the genera *Drepanopodus* (Péringuey) *Kheper* Janssens, *Pachylomerus* Bertoloni, *Scarabaeus* L. and *Sceliages* Westwood, and the *Scarabaeus* subgenera *Pachysoma* M'Leay, *Scarabaeolus* Balthasar and *Scarabaeus sensu stricto* (*s. str.*). Their distribution spans the Afrotropical region (including Madagascar) and southern latitudes of the Palaearctic from SE Asia to the Iberian Peninsula. 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 and 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 and Matthews, 1966; Ferriera, 1972; Matthews, 1972, 1974; Halffter and Edmonds, 1979, 1982; Halffter and Halffter, 1989). The taxonomic definition of the Scarabaeini was attributed largely to the monophyletic evolution of horizontal relocation ("rolling") of food and often complex nesting behaviours (Halffter and Halffter, 1989). Using Balthasar's (1963) classification, Hanski and Cambefort (1991) promoted the subtribes to tribes (excl. Alloscelina) using morphological distinctions rather than the behavioural correlates shared by the guild. Hanski and Cambefort (1991) also bolstered the number of genera in the tribe to 11 by recognising several genera that are synonyms of the genus *Scarabaeus*. A recent study by Philips *et al.* (submitted) provides evidence to suggest the "rolling" behaviour of these tribes did not evolve monophyletically but two or more times from ancestral "tunnelers".

Evolution

The Scarabaeini are likely to have evolved around the same time as other Scarabaeines during the Cenozoic, stemming from ancestral lineages thought to date back into 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 scarabaeoids was thought to coincide with the radiation of both angiosperms (Eocene: ca.50 Mya) and mammalian herbivores, particularly artiodactyiforms (lower Oligocene: 35 Mya), with a shift from saprophagy and mycetophagy to coprophagy by adults and larvae (Cambefort, 1991b; Scholtz and Chown 1995. In contrast, see; Chin and Gill, 1996). Fossil dung balls similar to those constructed by modern Scarabaeinae were recovered

from lower Oligocene deposits from Chile (Halffter 1959, quoted by Scholtz and Chown, 1995). Clay covered brood balls and nests recovered more recently from the Chadian Pliocene Australopithecine levels (Duringer *et al.*, 2000) suggests brood ball construction and nesting behaviour seen in modern dung beetles was well established at least 3-3.5 Mya.

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, quoted by Cambefort, 1991b) when grasslands developed and expanded giving rise to open habitats exploited by many of the radiating artiodactyls and cojointly, coprophagous beetles (Cambefort, 1991b). Modern dung beetles, especially the Scarabaeinae are, at present, more abundant in open habitats than in forests (Halffter and Matthews, 1966; Cambefort and Walter, 1991).

Feeding Specialisation

Whilst the majority of the Scarabaeini consequently specialised in the utilisation of specific food types (e.g. ruminant/non-ruminant dung), resources tend to be patchy and ephemeral. Many of its members therefore become opportunists in exploiting many types of resources including carrion. Equal numbers of *Pachylomerus femoralis* Kirby, for example, were caught in traps baited with carrion, fermenting fruit or several types of dung (Endrödy-Younga, 1982; Doube, 1991). Furthermore, the subgenus *Scarabaeus* (*Scarabaeolus* Balthasar) contains species utilising dung and/or carrion. A courting pair of *S.* (*Scarabaeolus*) *xavieri* Ferreira have been 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 and Scholtz, 1986).

In contrast, few species in the tribe have become truly specialist feeders deviating from the archetypal feeding strategies of the majority of the tribe and adopting "aberrant" feeding behaviours. Moreover, the Scarabaeini contain species that are non-rollers (see Halffter and Halffter, 1989) and others that don't roll food backwards but push, drag and carry it forwards. Flightless *Scarabaeus* (*Pachysoma* M'Leay) utilise dry dung pellets and/or detritus that are dragged into pre-prepared burrows in sandy soil and buried in moist sand for rehydration in feeding and nesting galleries (Holm and Scholtz, 1979; Scholtz, 1989). Whilst unique in the Scarabaeini, convergence in this feeding behaviour is reported in the geotrupine, *Geotrupes* (*Thorectes*) *sericeus* Jekel (Klemperer and Lumaret, 1985), by most of the 18 species of southern neotropical Eucraniini (Zunino, 1983; Zunino *et al.*,1989), and by several Western Australian canthonines and onthophagines such as *Coproecus* Reiche, *Mentophilus* Castelnau, *Tesserodon* Hope, *Onthophagus* Latrielle (Matthews, 1974).

Some of the most specialised members of this tribe belong to the genus *Sceliages*, which exclusively utilise millipedes (Diplopoda) for food and reproduction. Millipede necrophagy has long been known in the Scarabaeinae (Halffter and Matthews, 1966: 25-34). Facultative opportunistic use of millipede carcasses by *Scarabaeus* (*Neateuchus* (syn.)) *proboscideus* Guérin, *S. satyrus* (Boheman), and *S.* (*Scarabaeolus*) *flavicornis* (Boheman), has been observed (Forgie and Scholtz, unpubl.). Necrophagy of millipedes has also been recorded in several species in two other tribes. In the Onthophagini, several species of *Onthophagus* Latreille, including *O. bicavifrons* d'Orbigny, and *O. latigibber* d'Orbigny, were attracted to fresh millipede carcasses (Krell *et al.*, 1997, 1998: Krell, 1999). Neotropical canthonines, *Canthon cyanellus cyanellus* Le Conte, and *C. morsei* Howden, utilize both live injured and dead diplopods (Villalobos *et al.*, 1998), whilst *Deltochilum kolbei* Paulian, (Halffter and Matthews,

1966) and *D. valgum acropyge* Bates, (Cano, 1998) are known to actively prey on live millipedes.

Various quinone-based defensive allomones are secreted particularly in spirobolid and spirostreptid millipedes to repel attack by predators (Krell *et al.*, 1998). Two species of the orders Spirostreptida and Julida were found to use quinonous defensive secretions as pheromones (Haacker, 1974), and is likely to be a secondary function for many species of millipedes using these secretions. Necrophagous onthophagine scarabaeids are reported to be attracted to millipede secretions used as repellents (Krell *et al.*, 1997, 1998; Krell, 1999) and are also likely to be attracted to the quinonous secretions used as pheromones by millipedes during copulation (Kon *et al.*, 1998). Positive chemotaxis to the defensive secretions of millipedes by *Sceliages* has not been tested prior to this study. Live, injured and freshly dead millipedes all attract *Sceliages* suggesting quinone-based secretions play a role in attracting these beetles (Krell, 1999; Forgie *et al.*, 2002).

With the description of the new species there are now seven in the genus *Sceliages*, all restricted to southern Africa. Members of the genus are rarely encountered in the wild and are likely to be mistaken for *Scarabaeus* L. Furthermore, specimens of *Sceliages* are rare in collections and often misidentified or unidentified. The biology of *Sceliages* has, to date, not been studied. Zur Strassen's (1965) revision of the genus was based on relatively few specimens held in several museums in Europe and southern Africa and left many open questions including the locality of several of the species types. Thus, the rationale to case study this genus which is perhaps the least known yet one of the most specialized of the Scarabaeini is realized.

Very few phylogenetic studies have centred exclusively on the Scarabaeini. Mostert and Scholtz (1986) considered the flightless Neotropical Eucraniini as the tribe closest to the ancestral stock that gave rise to the Scarabaeini. Although species included in the Eucraniini possess more plesiomorphic characters than those in the Scarabaeini, both tribes share a number of synapomorphies. Mostert and Scholtz (1986) also used members of the Gymnopleurini, considered the next closest tribe to the in-group, to test the relative apomorphies of characters in the Eucraniini that were effected by changes associated with flightlessness. The close association between the Eucraniini and the Scarabaeini was believed to be based on convergence of distinct apomorphic characters (Zunino *et al.*, 1989). We test the hypothesis that the close relationship between the Eucraniini and the Scarabaeini is the result of morphological convergence and is not due to common ancestry.

Barbero *et al.* (1998) examined interspecific relationships between 32 species of *Scarabaeus* distributed throughout the whole geographic range of the genus. Three distinct clades corresponding to subgenera *Scarabaeus*, *Scarabaeolus* and *Ateuchetus* Bedel, were identified. The later, with the exception of S. *catenatus* (Gerstaecker) and *S. savignyi* M'Leay, being restricted to the western Palaearctic. Most recently, Harrison and Philips (2003) investigated the evolution of flightless *Scarabaeus* (*Pachysoma*) restricted to western coastal regions of Southern Africa. Their phylogenetic analysis showed a clear basal dichotomy in the tribe's evolution between members of the scarabaeini that retained flight and those who lost it. Members of the subgenus *Pachysoma* were depicted as the most evolved of the flightless clade sharing with other flightless lineages a complex of convergent morphological characters associated with existence in arid desert environments.

To date, only morphological character sets have been used in phylogenetic studies to infer inter- and/or intra-generic relationships among members of the Scarabaeini (Mostert and Scholtz, 1986; Barbero *et al.,* 1998; Harrison and Philips, 2003). These studies were based on relatively small amounts of data that may have generated inaccurate or biased phylogenetic reconstructions (see Hillis, 1998; Grandcolas *et al.*, 2001). A recent study of Scarabaeinae (Philips *et al.*, 2004) was based on large morphological data sets comprising more than 200 characters in an attempt to improve phylogenetic signal and generate more robust hypotheses. Both studies support congruence in the polyphyletic evolution of ball-rolling and feeding behaviours deviating from coprophagy. However, a high degree of character homoplasy is reported in the scarabaeines, likely the product of nonheritable information brought about by environmental influences (Hillis, 1987).

Molecules and Morphology

The advent of Polymerase Chain Reaction (PCR; Saiki *et al.,* 1988) marked a proliferation in the use of sequenced regions within mitochondrial DNA (see Simon *et al.*, 1994), and more recently, nuclear ribosomal DNA in insect molecular systematics (see Caterino, Cho and Sperling, 2000). Within the former of these classes, the Cytochrome Oxidase subunit I (COI) and COII markers have historically proven useful in providing sufficient phylogenetic signal in estimating relationships corresponding to interspecific levels of recent divergence within Coleoptera (e.g. Emerson and Wallis, 1995; Langor and Sperling, 1997; Kobayashi *et al.*, 1998; Cognato and Sperling, 2000) including within the Scarabaeinae (Villalba *et al.*, 2002). In contrast, the highly conserved 3' region of the large ribosomal subunit (16S) of mitochondrial DNA has proven more effective at addressing deep levels of divergence evident among distantly related taxa (DeSalle, 1992; Derr *et al.*, 1992) Similarly, 18S nuclear ribosomal RNA has also been useful for resolving basal relationships in higher level phylogenetic studies (Chalwatzis *et al.*, 1996; Caterino *et al.*,

2002). Given that different genes evolve at different rates and the same gene may have different rates of evolution in different lineages (Lunt *et al.*, 1996), the quest to obtain suitable levels of variability has become increasingly important in attempting to resolve close, intermediate and deep levels of divergence where possible in any phylogenetic study.

Thus, the value of a total evidence approach to utilising multiple data sets and analysing them separately (Bull *et al.*, 1993; Miyamoto and Fitch, 1995), or combined (Kluge, 1998) and analysed simultaneously (Nixon and Carpenter, 1996; Baker and DeSalle, 1997) has become apparent. Indeed, multiple data sets are integral in many phylogenetic studies using molecular markers (Vogler and DeSalle, 1993; Funk *et al.*, 1995; Vogler and Welsh, 1997; Funk, 1999; Mardulyn and Whitfield, 1999; Durando, *et al.*, 2000) and morphology (Lafay *et al.*, 1995; Whiting *et al.*, 1997; Silvain and Delobel, 1998; Joy and Conn, 2001; Wieblen, 2001; Wiegmann *et al.*, 2002).

Thesis Format

Each of the three chapters are compiled as individual papers for publication. Each chapter contains its own reference list and appendices. Both the general introduction and conclusion are tailored from the introduction and conclusions of the respective chapters to pull together the autonomy of chapters written as papers. The first chapter is published in *Invertebrate Systematics* (formerly *Invertebrate Taxonomy*) appearing in the December 2002 issue (Vol. 16(6)). It comprises a revision and phylogeny of the genus *Sceliages* Westwood. A new species is described from the semi-arid western parts of Southern Africa (habitus illustration appears on the cover of *Invertebrate Systematics*, 16(6)) and neotypes are assigned to 2 species following a detailed search for missing types. Moreover, the authors provide for first time a larval

description of one species and give details of the remarkable biology of members of the genus feeding on Diplopoda.

The second chapter is accepted and in press at *Systematic Entomology* at time of binding. It forms the principal phylogenetic analysis for the tribe based in a suite of 246 adult morphological and behavioural characters. Several hypotheses are rigidly tested and discussed in relation to the evolution of flightlessness, ball-rolling, and feeding specialization. A new classification proposes the maintainance of only 2 genera, *Scarabaeus* and *Pachylomerus* and 3 sub-genera i.e. *Scarabaeus* S. Str., *Scarabaeolus* and *Pachysoma*. Of the remaining genera, *Kheper* and *Sceliages* are demoted to sub-genera and *Drepanopodus* is synonymised with *Scarabaeus*.

The third chapter is submitted to *Molecular Phylogenetics and Evolution* in February, 2004. This chapter introduces a molecular component to the tribal phylogeny by sequencing portions the COI and 16S rRNA mitochondrial genes as likely candidates for simultaneous analyses with and without morphological data to resolve as many of the relationships as possible between the close and not so closely related exemplars of the Scarabaeini. In doing so, the authors associated with this paper hope to compare the molecular evolution and phylogenetic utility of these two genes and assess the level of congruence these analyses hold with the morphology-based hypotheses presented in chapter two, and the relatedness between the Scarabaeini and the morphologically similar eucraniines. The molecular phylogenies are then used to assess the proposed tribal classification presented in the second chapter.

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Chapter 1

Revision of *Sceliages* Westwood, a millipede-eating genus of southern African dung beetles (Coleoptera: Scarabaeidae).

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Running title: Millipede-eating *Sceliages* (Scarabaeidae) from Africa

Key words: Biology, dung beetle, larval description, new species, phylogeny, revision.

Abstract

The genus *Sceliages* Westwood (Scarabaeinae: Scarabaeini) from southern Africa is revised. Seven species are recognised: *Sc. granulatus* sp. nov. (Botswana, South Africa), *Sc. augias* Gillet (Angola, Democr.Republ.Congo, Zambia), *Sc. adamastor* (Le Peletier de Saint-Fargeau and Serville) (South Africa), *Sc. brittoni* Zur Strassen (South Africa), *Sc. difficilis* Zur Strassen (South Africa, Zimbabwe), *Sc. gagates* Shipp (South Africa, Moçambique), and *Sc. hippias* Westwood (South Africa). The new species is described and the others are re-described. Neotypes are assigned to *Sc. adamastor* and *Sc. difficilis*. A key to the species is provided. A phylogenetic analysis of the genus is presented. Male genitalia and other diagnostic characters are illustrated. Distribution maps of all species are also provided. Mature larvae of *Sc. hippias* are described, the first for the genus. They can be distinguished from other Scarabaeinae larvae by a markedly reduced torma on the epipharynx, and complete absence of hypopharyngeal sclerites (oncyli). Millipede relocation and burial behaviour of the adults of *Sc. hippias* and *Sc. adamastor* are described. We also provide descriptions of the brood chamber and brood balls of *Sc. hippias*.

Introduction

The tribe Scarabaeini contains the genera, *Scarabaeus* Linnaeus, *Sceliages* Westwood, *Drepanopodus* Janssens, *Kheper*, *Pachylomerus* Kirby and the subgenus *Scarabaeolus* Balthasar comprising 146 species. Many of the species exhibit distinct morphological and biological variability and possess either facultative or obligate feeding strategies including necrophagy. Some of the most specialised members of this tribe belong to the genus *Sceliages*, which exclusively utilise millipedes (Diplopoda) for food and reproduction. Millipede necrophagy has long been known in the Scarabaeinae (Halffter and Matthews, 1966: 25-34). Facultative opportunistic use of millipede carcasses by *Scarabaeus* (*Neateuchus* (syn.)) *proboscideus* Guérin, *S. satyrus* (Boheman), and *S.* (*Scarabaeolus*) *flavicornis* (Boheman), has been observed by some of us (Forgie and Scholtz, unpubl.). Necrophagy of millipedes has also been recorded in several species in two other tribes. In the Onthophagini, several species of *Onthophagus* Latreille, including *O. bicavifrons* d'Orbigny, and *O. latigibber* d'Orbigny, were attracted to fresh millipede carcasses (Krell *et al.*, 1997, 1999). Neotropical canthonines, *Canthon cyanellus cyanellus* Le Conte, and *C. morsei* Howden, utilize both live injured and dead diplopods (Villalobos *et al.*, 1998), whilst *Deltochilum kolbei* Paulian, (Halffter and Matthews, 1966) and *D. valgum acropyge* Bates, (Cano, 1998) are known to actively prey on live millipedes.

In southern Africa, many animals prey on millipedes (see Lawrence, 1987: 82, 89-90). For example, adult and nymphal reduviid bugs (Hemiptera: Reduviidae), for example *Ectricodia crux* (Thunberg), *Cleptria cinctiventris* Stål, and nymphs of the genus *Glymmatophora* Stål, frequently specialise in preying on *Doratogonus* Attems, spirostreptids, but never prey on species of the genus *Centrobolus* Cook (Lawrence, 1987). Various quinone-based defensive allomones are secreted particularly in spirobolid and spirostreptid millipedes to repel attack by predators (Krell *et al.*, 1998). Two species of the orders Spirostreptida and Julida were found to

use quinonous defensive secretions as pheromones (Haacker, 1974), and is likely to be a secondary function for many species of millipedes using these secretions. Necrophagous onthophagine scarabaeids are reported to be attracted to millipede secretions used as repellents (Krell *et al.*, 1997, 1998; Krell, 1999) and likely to the quinonous secretions used as pheromones by millipedes during copulation (Kon *et al.*, 1998). Positive chemotaxis to the defensive secretions of millipedes by *Sceliages* has not been tested prior to this study. Live, injured and freshly dead millipedes all attract *Sceliages* suggesting quinone-based secretions play a role in attracting these beetles (Krell, 1999). *Sceliages* have also been collected by Endrödy-Younga in traps containing meat/carrion, horse dung and fruit, and observed rolling antelope dung pellets (Mostert and Scholtz, 1986:10). The observation recorded by Mostert and Scholtz (1986) is best described as aberrant behaviour for the genus or more likely the product of mis-identification of the beetle responsible. Likewise, records of *Sceliages* trapped in long-term ground traps baited with various ingredients by Endrödy-Younga are possibly misleading. For example, *Sc. brittoni* in this case, may have become trapped inadvertently after being attracted to millipedes that might have stumbled into the traps.

With the description of the new species there are now seven in the genus *Sceliages*, all restricted to southern Africa. Members of the genus are rarely encountered in the wild and are likely to be mistaken for *Scarabaeus* L. Furthermore, specimens of *Sceliages* are rare in collections and often misidentified or unidentified. The biology of *Sceliages* has, to date, not been studied. Zur Strassen's (1965) revision of the genus is the precedent for this study. It was based on relatively few specimens held in several museums in Europe and southern Africa. In his introduction, zur Strassen mentioned that encounters of generic misidentifications of a number of specimens in museum collections were because the genus *Sceliages* was not well known and the descriptions of the oldest species are very deficient. To worsen the situation, zur Strassen (1965) stated that later authors had described known species as new because they were unaware of the already

described species. It is not surprising to learn that the holotypes of *Sc. adamastor* and *Sc. gagates* are unattainable and, in accordance with zur Strassen (1965), should be considered as non-existing. As a result, we have assigned a neotype for each of these species.

In this paper we report the results of our review, present a phylogenetic analysis of the genus and describe a new species from the semi-arid western parts of the region. Moreover, we provide for first time a larval description of one species and give details of the remarkable biology of members of the genus feeding on Diplopoda.

Materials and methods

Adult material examined

The institutions to which the species belong are abbreviated as follows:

BMNH The Natural History Museum. Department of Entomology. Cromwell Road, London SW7 5BD, England. (M. Kerley)

DMSA Durban Museum. P.O. Box 4085, Durban 4000, South Africa. (T. Crouch)

HECO Oxford University Museum of Natural History. Hope Entomological Collections. The University Museum, Parks Road, Oxford OX1 3PW, England. (D. Mann)

ISNB Institut Royal des Sciences Naturelles de Belgique, Département d'Entomologie, Rue Vautier 29, B-1000 Bruxelles, Belgum. (D. Drugmand)

SAMC South African Museum. P.O.Box 61, Cape Town 8000, South Africa. (M. Cochrane)

SANC The National Collection of Insects. Plant Protection Research Institute. Private Bag X134, Pretoria 0001, South Africa. (R. Stals)

TMSA Museum of Natural History (Transvaal Museum). Northern Flagship Institution. P.O. Box 413, Pretoria 0001, South Africa. (J. du G. Harrison)

UPSA Department of Zoology and Entomology, University of Pretoria, Pretoria 0002, South Africa.

Larval material examined

Five mature larvae originated form brood balls collected together with females. Two larvae with one female were collected on December 17, 2000, at the Rustenburg Nature Reserve (25°40'S 27°12'E), NW Province, Republic of South Africa by S. Forgie and V. Grebennikov. Three more larvae with one female collected on January 12, 2001, the same locality and the same collectors. Voucher larvae and females are deposited in UPSA and BMNH.

Material examined

Latitude and longitude coordinates *in bold* are utilized for the distribution maps of each species. Locality information in parenthesis represents the current recognised localities, and also information not listed on the specimen collection data labels. A question mark in parenthesis immediately precedes a locality data item that could not be interpreted. Inverted commas surround exact wording taken from specimen collection data labels. Some latitude and longitude coordinates were obtained from "material examined" by zur Strassen (1965) for *Sceliages augias* Gillet, and are included in the distribution map (Fig. 81) for this species.

Distribution maps

Map coordinates were obtained either directly from specimen collection data labels or by submitting specimen localities into GeoName™ digital gazetteer (GDE Systems, Inc.™[1]) software. These coordinates were converted to decimal degrees and plotted as distribution maps using ArcView® GIS software (Environmental Systems Research Institute, Inc. ™, 380 New York, Redlands CA 92373-8100, USA).

Male genitalia

Aedeagi were removed from 21 specimens (*Sc. granulatus*: 1 Holotype SANC, 4 Paratypes SANC, 1 Paratype UPSA; *Sc. hippias*: 1 TMSA, 1 SANC; *Sc. augias*: 1 BMNH; *Sc. adamastor*: 1 TMSA; *Sc. brittoni*: 1 SANC, 1 TMSA; *Sc. difficilis*: 3 SANC, 1 UPSA, 3 TMSA; *Sc. gagates*: 2 SANC), and soaked in warm 10% KOH for ca.15 minutes. The internal sacs were extracted, stretched out and allowed to soak in warm 10% KOH for a further 5 minutes. Sacs were soaked successively in dH_2O, 70% EtOH, dH_2O prior to their preservation in glycerine. Virgular sclerites (Matthews, 1974) were dissected from the internal sacs and placed in drops of glycerine on glass slides for examination under a stereomicroscope.

Mature larvae

Sceliages larvae and females were preserved in Bouin's liquid for a week and then transferred into 70% ethanol. Two larvae were disarticulated as follows: head, left legs, mandibles, and the labio-maxillar complex, were separated and cleaned in a hot water solution of KOH. Separated parts were transferred into glycerol and studied under dissecting and compound microscopes. Morphological drawings were done using camera-lucida. The morphological terms utilized in this description are those explained by Böving (1936), Ritcher (1966) and Lawrence (1991).

[1] The distributors of GeoName™ have created a website with the same data and functionality as the software: http://gnpswww.nima.mil/geonames/GNS/index.jsp

Exception is made for terms applicable to the secondary thoracic and abdominal subdivisions; instead of "prescutum", "scutum" and "scutellum", we use "dorsal lobes" as explained in Baker (1968: 13). For comparative purposes, one larva of each of the following Scarabaeinae genera was studied as described in the "Materials and methods" section: *Circellium bacchus* Fabricius; *Heliocopris andersoni* Bates; *Kheper nigroaeneus* (Boheman); *Scarabaeus galenus* (Westwood); *Scarabaeus* (*Pachysoma*) *gariepinus* (Ferreira); *S.* (*Pachysoma*) *striatus* (Castelnau); *Synapsis tmolus* (Fischer); and, *Tragiscus dimidiatus* Klug.

Biology and nidification

Field study of *Sceliages hippias* was carried out at the Rustenberg Nature Reserve and observations *Sc. adamastor* at the De Hoop Nature Reserve (34°25'S 20°24'E), Western Cape Province, South Africa.

Trapping

Beetles were attracted to a series of pitfall traps baited with freshly killed millipedes unless otherwise stated. Traps were placed into the field before 0:900 and left for no longer than an hour to minimise stress of captured beetles.

Fig. 1. *Sceliages granulatus* sp. nov., habitus.

(Cover: *Invert. Syst.* 16(6), 2002)

Genus *Sceliages* Westwood

Sceliages Westwood 1837: 12. – Lacordaire 1856: 66; Shipp 1895: 37; Péringuey 1901: 16, 22, 62, 63; Gillet 1911a: 16; Ferreira 1961: 63; Ferreira 1967: 59-63; Ferreira 1972: 74-78; Zur Strassen 1965: 220; Halffter and Edmonds 1982: 138; Scholtz and Holm 1985: 220; Mostert and Scholtz 1986: 1, 8, 10, 11, 16, 22, 23; Hanski and Cambefort 1991: 167, 472; Krell 1999: 287.

Parascarabaeus Balthasar 1961: 174. – Ferreira 1972: 76; Mostert and Scholtz 1986: 10.

Type species of *Sceliages*: *Sceliages iopas* Westwood 1837(= *S. adamastor* (Le Peletier de Saint-Fargeau and Serville 1828)) [by monotypy].

Type species of *Parascarabaeus*: *Parascarabaeus tonkineus* Balthasar 1961 [by original designation].

Diagnosis

Unique morphological characters diagnosing the genus *Sceliages* are: shape and arrangement of the four up-turned clypeal teeth (two frontal medial teeth narrow and protrude further than lateral teeth. Rounded suture separates frontal medial teeth from each other; lateral teeth broad, angulate, skewed, and separated from frontal medial teeth by a sharply angled suture). Apex of mesotibia with two markedly developed spurs. Basal tarsomeres are distally flared appearing triangulate. Unique behaviour within Scarabaeini: utilisation of millipedes for feeding and breeding.

Re-description of adults

Body shape: body mostly hunched, reminiscent of species of the *Scarabaeus (Scarabaeolus) ebenus* (Klug), group (Zur Strassen, 1965).

Head (Fig. 2): clypeal margin with four up-turned teeth. Two frontal medial teeth narrow and protrude further than lateral teeth. Rounded suture separates frontal medial teeth from each other; lateral teeth broad, angulate, skewed, and separated from frontal medial teeth by sharply angled suture. Genal epistomae more pronounced than lateral teeth of clypeus. Anterior lateral corner of gena tooth-like and separated from clypeus by sharply angled suture. Posterior margin of gena obtusely rounded. Geno-clypeal suture laterally present with obvious groove at its basal terminus. Surface texture of genae and clypeus shagreened and rugose with dense often deep punctations. Punctations become simplified and less dense on frons and vertex.

Antennae: antennal furcle consists of three segments; first segment bowl shaped, second segment much smaller, less bowl shaped and fits into first segment. Third segment sits on top of second segment.

Pronotum: surface smooth with fine shagreen texture and covered with minute, regularly spaced punctations.

Sternites: surface of mesobasisternum shagreened with complex punctuation of varying density and size. Margins of punctations smooth. Distal halves of metasternum and adjacent metepisternites with simple sparse punctation. Mesosternal process markedly broad and pronounced. Markedly developed facet present between each inner margin of mesocoxal cavity

and lateral carinae of mesosternellum. Width of mesosternellum between closest point separating mesocoxae greater than width of mesocoxal cavity.

Legs: apical (fourth) denticle of protibia, sickle-shaped (Figs 16-19). Antero-ventral margin of profemora adjacent to protrochanter ridged in all species and armed with at least one spur-like projection in most species (Figs 3-5). Spur present in males and females and bluntened in aged specimens. Antero-ventral margin of protrochanter well defined and ridged in most species (Figs 3-5). Meso- and metatibia truncated distally (Figs 16-24). Two markedly developed mesotibial spurs present, outer spur larger than inner spur (Figs 16-19). Outer spur curved, spatulate and pointed. Inner spur evenly tapered to point. In males, dorsal truncation of distal portion of metatibia exaggerated, short and acutely fading towards medial region of tibia (Figs 14, 21, 23). Three clumps of setae present at base of metatibial truncation (Fig. 14): First clump forms row closest to truncation comprising dense row of short, equal length setae, aligned to angle of truncation across dorsal surface of metatibia; second clump of setae longer than first clump and positioned along metatibial margin in row transecting terminus of first clump of setae. Third clump consisting of short setae positioned basally from first clump along the outer dorsal margin of metatibia. In females, metatibia broad, rectilinear, without truncation and dorsal surface lacking clumps of setae (Fig. 15). Both sexes possess uniform row of setae running uninterrupted medially along length of inner metatibial surface (Fig. 20). Setae often arise from medial longitudinal carina or margin that defines the setal row. Basal tarsomeres flared distally appearing triangular in dorsal and ventral perspectives.

Male Genitalia (Figs 6-13): ventral structure, or handle, of virgular sclerite completely fused with primary sclerotised circular ring. Apical region of handle upturned with varying degree and twisted so that apex is approximately perpendicular to plane of basal region.

Comments

Ateuchus adamastor was first described by Le Peletier de Saint-Fargeau and Serville in 1828. In 1837, Westwood described the genus *Sceliages* (based on the species *Sc. iopas*) to differentiate species of *Scarabaeus*, including those of the genus *Ateuchus* Weber, that possess several "structural peculiarities" including 2 mesotibial spurs. Both Westwood (1837) and Lacordaire (1856) thought *A. adamastor* should belong to the genus *Sceliages* presumably without realising *A. adamastor* was conspecific with *Sc. iopas*. Synonymy of both species under the new combination *Sceliages adamastor* (Le Peletier de Saint-Fargeau and Serville 1828) was formalised by Shipp (1895). The genus *Ateuchus* was described by Weber in 1801 without the designation of a type- species and in 1901, Péringuey designated it a synonym of *Scarabaeus*. Currently, *Ateuchus* only appears as a new world genus within the tribe Coprini (Halffter and Edmonds, 1982).

As far as we are aware, Ferreira (1972: 76) is the first author to cite *Parascarabaeus* Balthasar as a synonym of *Sceliages*. However, Mostert and Scholtz (1986: 10-11) later proposed that the type species of *Parascarabaeus tonkineus* is likely to be a mislabelled specimen of *Sceliages* since all other specimens of *Sceliages* have been collected only in the southern half of the African continent. Nonetheless, its status remains as the only full generic synonym of *Sceliages* to date (Mostert and Scholtz, 1986).

Regarding the morphological differentiation of the genus, a second medial/inner mesotibial spur is also present in *Scarabaeus* subgenus *Scarabaeolus* Balthasar however differing from *Sceliages* in being vestigial and difficult to locate (e.g. Zur Strassen, 1967:130).

Key to the species of the genus *Sceliages* Westwood

1. Protibia slightly and evenly increasing in width distally; with slight to no inward angulation on medial facet at level of second external denticle (angulation less apparent in females) (Figs 25-32, 42-45).....2

Protibia abruptly increasing in width distally at level between second and third external denticle; with markedly developed inward angulation of medial facet at level from third external denticle to between third and halfway to second external denticle (angulation less apparent in females) (Figs 33-41).....5

2(1). Elytra surface complex, obvious corrugation or granulation; course shagreen texture; waxy indumentum present; general matt appearance; striae well defined, bordered with micro carinae.....3

Elytra surface plain, without obvious surface protuberances; fine shagreen texture, waxy indumentum usually absent, general glossy appearance; striae fine, narrow and grooved.....4

3(2). Elytra surface covered in dense, raised granulations.....***granulatus*** sp. nov.

Elytra surface longitudinally corrugated; tops of corrugations smooth, glossy providing a striped or ribbed appearance.....***augias*** Gillet

4(3). Antennae yellow-orange; posterior facet of mesofemora armed with single row of long setae closely paralleling ventral margin (Fig. 47); medial facet of mesotibia straight (Fig. 18)..... .....***hippias*** Westwood

Antennae brown-black; posterior facet of mesofemora armed with two to three rows of setae (Figs 54, 55); first row closely paralleling ventral margin; second and third row (if present) with

setation reduced in number from a few to several setae; medial facet of mesotibia slightly curved inwards.....***gagates*** Shipp

5(1). Obtuse inward angulation of medial facet of protibia from third external denticle (Figs 33-36); protibial width (in dorsal perspective) broadens abruptly in apical quarter; elytra surface glossy; striae on elytra fine, narrow grooved.....6

Slight inward angulation of medial facet of protibia from between third and half way to second external denticle (Figs 37-41); protibial width (in dorsal perspective) slightly increased in apical quarter; elytra surface matt with thin waxy indumentum; striae on elytra well defined often bordered with micro carinae (more apparent in teneral adults).....***difficilis*** Zur Strassen

6(5). setation red; mesotibia slightly bowed (Fig. 16); outer mesotibial spur elongate to approximately 1/2 length of mesotibia (Fig. 16); medial facet of metatibia (in dorsal perspective) relatively straight (Fig. 23).....***brittoni*** Zur Strassen

setation black; mesotibia obtusely bowed (Fig. 17); outer mesotibial spur 1/5 to 1/4 length of mesotibia (Fig. 17); entire metatibia bowed inwards (Figs 21, 22).....***adamastor*** (Le Peletier de Saint-Fargeau and Serville)

Sceliages adamastor (Le Peletier de Saint-Fargeau and Serville 1828)

(Figs 11, 17, 21, 22, 35, 36, 50, 51, 83)

Ateuchus adamastor Le Peletier de Saint-Fargeau and Serville 1828: 351. – Westwood 1837: 12; Lacordaire 1856: 66; Shipp 1895: 38.**Comb. nov.**

Sceliages adamastor (Le Peletier de Saint-Fargeau and Serville 1828). – Shipp 1895: 38; Péringuey 1901: 63; Felsche 1910: 339; Gillet 1911a: 16; Ferreira 1961: 63; Ferreira 1967: 60; Ferreira 1972: 77; Zur Strassen 1965: 220, 228, 229, 231; Halffter and Edmonds 1982: 138; Scholtz and Holm 1985: 220; Krell 1999: 288.

Sceliages iopas Westwood 1837: 12. – Lacordaire 1856: 66; Shipp 1895: 38. **Syn.**

Sceliages jopas [Sic!] Westwood 1837 – Zur Strassen 1965: 220, 228-230; Ferreira 1972: 77

Sceliages joppas [Sic!] Westwood 1837 – Ferreira 1972: 76

Sceliages curvipes Gillet 1911b: 310. – Gillet 1911a: 16; Zur Strassen 1965: 228. **Syn.**

Material Examined

Type specimens. See comments.

Sceliages adamastor. Neotype: ♂, labelled "SOUTH AFRICA, WC, De Hoop Nature Res., 34°25'S 20°24'E; 2 xi 2000, millipede baited p/f trap, S.A. Forgie", in SANC.

Sceliages iopas. Holotype: ♀, labelled "South Africa; *Sceliages iopas* Westwood 1837. Type coll.428" in HECO. Paratype: 1♂, labelled "South Africa; *Sceliages iopas* Westwood 1837. Type coll.428" in HECO.

Sceliages curvipes. Holotype: ♂, labelled "South Africa; *Sceliages curvipes* Gillet 1911" in BMNH.

Non-type specimens. 17 ♂ and 4 ♀. **SOUTH AFRICA**: **Western Cape Province**: De Hoop Nature Reserve (**34°25'S 20°24'E**). 13 x. 1984, J.H. Giliomee (1♂ UPSA). De Hoop Nature Reserve, nr. Koppie Alleen, **34°28'S 20°28'E,** 40 m alt. Strandveld; 3–7 x.1994, S. van Noort (2♂ SAMC). De Hoop Nature Reserve, (Cape Agulhas, 60 Km NE) 34°25'S 20°24'E, millipede trap nr.sand dunes,10h30 for ca.1h; 2 November 2000, S.A. Forgie (2♂,2♀ BMNH; 1♂,1♀ SANC; 1♂,1♀ UPSA). Klippe Rugt Farm, **34°42'S 20°12'E**, vegetated dunes, night; 27 x. 1983, Endrödy-Younga, E-Y 2026 (1♂ TMSA). **Northern Cape**: Klipvlei, Garies, Namaqualand (**30°25'S 17°54'E**); November 1931, museum staff (2♂ SAMC). Victoria West, "Cape-Karoo", **31°24'S 23°07'E**, ground traps, 94 days, baited with meat; 18 ix.r 1983, Penrith, E-Y 2012 (4♂ TMSA). **Eastern Cape**: Papiesfontein, Gamtoos (River) Mouth (**33°57'S 25°04'E**); January 1960, "S.A.M." (3♂ SAMC). (?)**Orange Free State** (Free State): Modder River, Brandfort; November 1939, museum staff (1♂ SAMC).

Diagnosis

Sc. adamastor possess obtusely curved inward angulation of the mesotibiae. Presence of an obvious inward curvature of the metatibia is apparent in both males and females. The length of the outer mesotibial spur relative to the length of the mesotibia is markedly reduced. Setation generally black.

Re-description

Length 12 -22 mm.

Head: surface smooth to slightly rugose on genal epistomae. Genae and clypeus densely covered with large punctations. Geno-clypeal suture well defined.

Sternites: surface of mesobasisternum coarsely shagreened with markedly-spaced, shallow, feebly developed crescent-shaped punctations. Dorsal margins of punctations smooth. Setation generally absent.

Legs: medial (inner) facet of protibia abruptly angled inwards from third (penultimate distal) external denticle (Figs 35, 36). Protibial width (in dorsal perspective) in distal quarter broadens markedly to apex. Mesotibia obtusely curved inwards, more rounded than rectilinear and truncate in apical third (Fig. 17). Inner mesotibial spur less than 1/2 length and thickness of outer mesotibial spur. Inner spur offset from outer spur by 15 to 20 degrees. Outer mesotibial spur 1/5 to 1/4 length of mesotibia (Fig. 17). Mesotarsi approximately half length of mesotibia. Mesofemora armed with many rows of dense long black setae on posterior facet (Fig. 51). Metatibia evenly curved inwards (Figs 21, 22).

Male genitalia (Fig. 11): handle of virgular sclerite broad in width, steep semi-circular concavity along dorso-basal margin; evenly concave along entire ventral margin. Dorsal margin notched at terminus of union with circular sclerite prior to obvious swelling to terminus of apical region of handle. Secondary sclerotisation of handle reduced between dorsal and ventral corners of apex, forming slight saddle.

Comments

Horn *et al.* (1990) provide no information regarding the Coleoptera collections of Le Peletier or Audinet-Serville. It therefore seems to be improbable that their locations including the type(s) of

Ateuchus (=*Sceliages*) *adamastor* will ever be found. Moreover, Yves Cambefort (pers. comm.) of the Paris Museum of Natural History, home to portions of Le Peletier's collections, states the types described by both Le Peletier and Audinet-Serville are apparently unknown and are likely to be lost. In accordance with zur Strassen (1965) and those who have helped us in attempting to locate the type(s), *Sc. adamastor* type(s) are considered as missing or non-existent. We have therefore assigned a neotype for this species.

Re-description and identification of this species was therefore based on the descriptions of *Ateuchus adamastor* by Le Peletier de Saint-Fargeau and Serville, examination of the conspecific types of *Sceliages iopas* and *Sc. curvipes*, the description of *Sc. iopas* by Westwood, description of *Sc. adamastor* by zur Strassen (1965) and identified non-type material.

It is worth noting the species labels of the 2 type specimens of *Sceliages iopas* held at the Hope Entomological Collections, University of Oxford, are hand written in a manner likely to be misinterpreted as *Sc. jopas*. The locality data of the Free State specimen is not considered accurate and is not included in the distribution map (Fig. 83). We also examined 12 specimens from the ISNB. Of these, 2 are mis-identified specimens of *Sc. gagates* and 2 of *Sc. difficilis*. The remaining 8 specimens of *Sc. adamastor* contain minimal to no original collection data to be of any use in distribution maps.

The body size of *Sc. adamastor* is approximately as large as *Sc. brittoni* and smaller adult specimens may also be confused initially with large specimens of *Sc. difficilis*. The posterior surface of the mesofemora of *Sc. adamastor* specimens from De Hoop is armed with a single row of long black setae closely paralleling the ventral margin and a second less dense, incomplete row inset from the posterior margin (Fig. 50). All other specimens of this species are

heavily setose (Fig. 51). The mesotibia of males is only slightly more obtusely bowed and the inner facet of the protibia more abruptly angled inwards than in females.

Geographical Distribution.

Sc. adamastor is known only from South Africa (Fig. 83).

Sceliages augias Gillet 1908

(Figs 4, 9, 31, 32, 48, 49, 81)

Sceliages augias Gillet 1908: 64. – Felsche 1910: 339; Gillet 1911a: 16; Ferreira 1961: 64; Ferreira 1972: 67, 68; Zur Strassen 1965: 220; Mostert and Scholtz 1986: 10.

Sceliages sulcipennis Felsche 1910: 339. – Gillet 1911a: 16. **Syn.**

Scarabaeus delaunay-larivierei Paulian 1934: 58. – Ferreira 1961: 64. [?]**Syn.**

Parascarabaeus tonkineus Balthasar 1961: 174 [Mislabelled specimen, Mostert and Scholtz 1986].

Material Examined

Type specimens.

Sceliages augias. Holotype: ♀, labelled "Angola, Benguela; F.C. Wallman Leg." in Institut Royal des Sciences Naturelles de Belgique (ISNB), Brussels; 10.640.

Non-type specimens. 7♂, 2♀. **ANGOLA:** Casonda (**7°23'S 20°54'E**) (1♂ TMSA). **DEMOCRATIC REPUBLIC OF CONGO**: Mukana (Mukama [sic]), 1810m; 29 xi. 1948, Mis.G.F. de Wittex 2033a (1♂ ISNB). **ZAMBIA**: "Rhodesie du Nord", Abercorn (Mbala) (**8°50'S 31°23'E**), 1600 m; 12 iv.1943, H.J. Brédo (1♂ ISNB). Algoa (Kabwe), Broken Hill, 180 Km E (**14°26'S 30°18'E**); January 1913, Ll. Lloyd (1♂ BMNH). Mpika, Muchinga Mountains (**11°42'S 27°10'E**), 1500 m; January 1908, S.H. Neave (1♂ ISNB). "Rhodesie du Nord", Mweru-Wantipa; H.J. Brédo (1♂ ISNB). Serenje (**13°10'S 30°47'E**), 1500m; December 1912, Ll. Lloyd (1♀ BMNH). Serenje District, 1350 m, 28 xii. 1907, Neave (1♂ BMNH). **TANZANIA**: Mpwapwa (6°21'S 36°29'E); no collection Data; "Nevinson Coll. 1918–14" (1♀ BMNH).

Diagnosis

Sc. augias is easily differentiated from the other species of *Sceliages* by the appearance of its elytra: pronounced longitudinal ridges/corrugations filled with a matt grey indumentum and the tops shiny black providing a striped appearance.

Re-description

Length. 10-18 mm.

Head: surface rugosely punctated on genae and clypeus. Distal halves of geno-clypeal sutures obscured by rugose surface. Frons and vertex with less dense and smaller punctations.

Pronotum: obtusely rounded with curvature in the posterior third of lateral margins. Thickness and angulation of lateral margins unvaried.

Elytra: pronounced longitudinal carina or corrugations positioned medially on surface between each stria. Surface texture coarsely shagreened. Surfaces between carinae covered with indumentum and appearing matt grey. Carinae shiny black without waxy indumentum. Elytra appearing striped or ribbed.

Sternites: surface of mesobasisternum coarsely shagreened with well spaced, crescent-shaped, facetted punctations. Punctations raised forming protrusions or turbercle-like structures. Dorsal margins of protrusions smooth. Protrusions each armed with single long seta.

Legs: spur-like projection markedly pronounced on anterior ventral ridges of both profemora and protrochanter (Fig. 4). Inner face of protibia slightly angled inwards from second external protibial denticle (Figs 31, 32). Mesofemora armed with few (Fig. 49) to many (Fig. 48) rows of long setae on the posterior facet. Inner mesotibial spur 2/3 length of outer spur and 1/2 its thickness; angle is offset from outer spur by 30 degrees. Mesotarsus between 1/2 and 2/3 length of mesotibia.

Male genitalia (Fig. 9): handle of virgular sclerite broad in width, steeply concave along dorsal margin of basal region and evenly concave along ventral margin. Dorsal margin notched immediately after distal terminus of union with circular sclerite. Dorsal margin angles abruptly upwards to apex of handle. Apical region tapers to its widest thickness at apex. Apex angulate and width nearly as broad as length of dorsal margin from apex to notch. Secondary sclerotisation of handle reduced in ventral corner of apical region and dorsal corner of basal region. Handle has small baso-ventral extension also with reduction in secondary sclerotisation.

Comments

We are not aware who formally synonymised *Scarabaeus delaunay-lariviereiwith* with *Sc. augias*; we follow Ferreira (1961: 64) who is the first author known to us to use this synonymy.

Intra-specific variation in the degree of setation or pubescence on the mesofemoral posterior surface is apparent among specimens of *Sc. augias*. Specimens from coastal Casonda, Angola possess dense setation similar to that of *Sc. brittoni* (Fig. 48) compared to inland specimens (eg. Fig. 49).

Geographical Distribution.

We saw specimens of *Sc. augias* from the Dominican Republic of Congo, Angola, Zambia and single specimen labelled "Mpwapwa" with no other collection information provided. The only locality fitting this name occurs in far eastern Tanzania. If this locality is correct the distribution of the species is extended all the way across central Africa. Its distribution point however has not been included in Figure 81. Further material examined are cited by zur Strassen (1965: 221): CONGO: Kankunda, Upemba National Park (**8°36'S 26°26'E**), 1300 m; 24-28 November 1947, G.F. de Witte; (1♂ Musée Royal de l'Afrique Central, Tervuren (MACT)). ZAMBIA: Mpika, Muchinga Mountains, 1500 m; January 1908, S.H. Neave; (1♂ MACT). The former of these two records is incorporated in Figure 81.

Sceliages brittoni Zur Strassen 1965

(Figs 5, 10, 16, 23, 33, 34, 48, 83)

Sceliages brittoni Zur Strassen 1965: 230. – Ferreira 1972: 77

Material Examined

Type specimens.

Sceliages brittoni. Holotype: ♂, labelled "South Africa: SW Cape (Western Cape Province); Leipoldtville, Eland's Bay (**32°13'S 18°29'E**); October 1947, museum exped." In SAMC. Paratypes: 1♀, labelled "South Africa: SW Cape (Western Cape Province); Darling (**33°23'S 18°23'E**); October 1906, L. Péringuey" in SAMC. 1♀, labelled "Eland's Bay; October 1947, museum exped." In SAMC. 1♀, labelled "Saldanha Bay (**33°03'S 18°00'E**); September 1960 "S.A.M."" in SAMC.

Non-type specimens. 23♂, 7♀. **SOUTH AFRICA. Western Cape Prov.:** Namaqualand Kommandokraal farm, **31°30'S 18°13'E**, on sandy ground; 23 ix. 1994, Endrödy and Bellamy, E-Y 3033 (1♂ TMSA). Langebaan, Geelbek, 12 Km SE (**33°06'S 18°02'E**), col. in sand and shrubland; 1–29 x. 1979, Davis and Payton (3♂, 2♀ SANC). Langebaan, Geelbek, 12 Km SE, 29 x. 1979, A.L.V. Davis (1♂ SANC). Nortier farm, **32°02'S 18°20'E**, ground traps, meat bait; 25 viii. 1981, Endrödy-Younga, E-Y 1845 (1♂ TMSA). Seweputs coast, **31°39'S 18°17'E**, ground traps, 64 days, banana bait 23 viii. 1981, Endrödy-Younga, E-Y 1836 (1♂ TMSA). **Northern Cape Prov.**: Hondeklipbaai, **30°19'S 17°16'E**; September 1974, E.K. Hartwig (1♀ SANC). Hondeklipbaai, 12km E, **30°21'S 17°25'E**, ground traps, 58 days, millipede bait; 30 viii. 1977, Endrödy-Younga, E-Y 1359 (11♂,4♀ TMSA). Kotzesrus, **30°57'S 17°50'E**, white dunes, day, ground traps, 62 days, meat bait; 23 viii. 1979, Endrödy-Younga, E-Y 1581/4 (2♂ TMSA). Quaggafontein, **30°13'S 17°33'E**, ground traps, 60 days, millipede bait; 29 viii. 1977, Endrödy-Younga, E-Y 1356b (1♂ TMSA). Vlakte farm, Gemsbok, **30°30'S 17°29'E**, ground traps, 56 days, meat bait; 1 xi. 1977, Endrödy-Younga, E-Y 1366 (1♂ TMSA). Vl akte farm, Gemsbok, 30°30'S 17°29'E, singled, dunes, day; 30 viii. 1977, Endrödy-Younga, E-Y 1361 (1♂ TMSA).

Diagnosis

Sc. brittoni is easily diagnosed with the following morphological characters: red setation; markedly elongate outer mesotibial spur relative to the length of the mesotibia; and a large body size. The distribution of *Sc. brittoni* is restricted to the west coastal regions of South Africa.

Re-description

Length 17-25 mm.

Sternites: surface of mesobasisternum texture coarsely shagreened. Punctations crescent-shaped and facetted. Punctations raised forming protrusion or turbercle-like structures; dense but generally unlinked radiating anterior-laterally from centre of mesosternal process. Setation generally absent.

Legs: medial (inner) facet of protibia abruptly angled inwards from third external denticle (Figs 33, 34). Protibial width (in dorsal perspective) in distal quarter broadens abruptly to apex. Profemoral spur-like projection pronounced with reduced tooth-like serrations on remainder of anterior ventral ridge of both profemora and protrochanter (Fig. 5). Spur-like projection may be present but reduced on anterior ventral ridge of protrochanter. Mesofemora armed with many rows of dense, obvious long red/brown setae on the posterior facet (Fig. 48). Outer mesotibial spur markedly elongate; approximately half length of mesotibia (Fig. 16). Inner mesotibial spur less than 1/3 length and width of outer spur; offset from outer spur by 30 to 45 degrees. Mesotarsus approximately 1/3 length of mesotibia. Minimal to no inward curvature of metatibia (Fig. 23).

Male genitalia (Fig. 10): handle of virgular sclerite narrow and relatively constant thickness through its length; widening slightly at each end. Handle evenly concave along majority of dorsal margin to an abrupt outward angulation near terminus of apical region; ventral margin slightly concave to angulate. Dorsal margin unnotched at terminus of union with circular sclerite. Secondary sclerotisation of handle reduced between dorsal and ventral corners of apex forming an obvious saddle. Dorsal and ventral corners of apical region of handle appear as protruding points. Baso-ventral corner forms a slight protruding extension with reduction in secondary sclerotisation from its apex to baso-dorsal union with circular sclerite.

Comments

The majority of the external morphological features of *Sc. brittoni* closely resemble those of *Sc. adamastor*.

Biological observations

A single *Sc. brittoni* in Namaqualand, South Africa, was observed displacing reduviid nymphs (species unknown) attacking a large harpagophorid millipede, *Zinophora* sp (Diplopoda: Spirostreptida). *Sc. brittoni* then relocated the millipede whilst it was still alive (J. Colville, personal communication).

Geographical distribution

Sc. brittoni is known from South Africa only (Fig. 83).

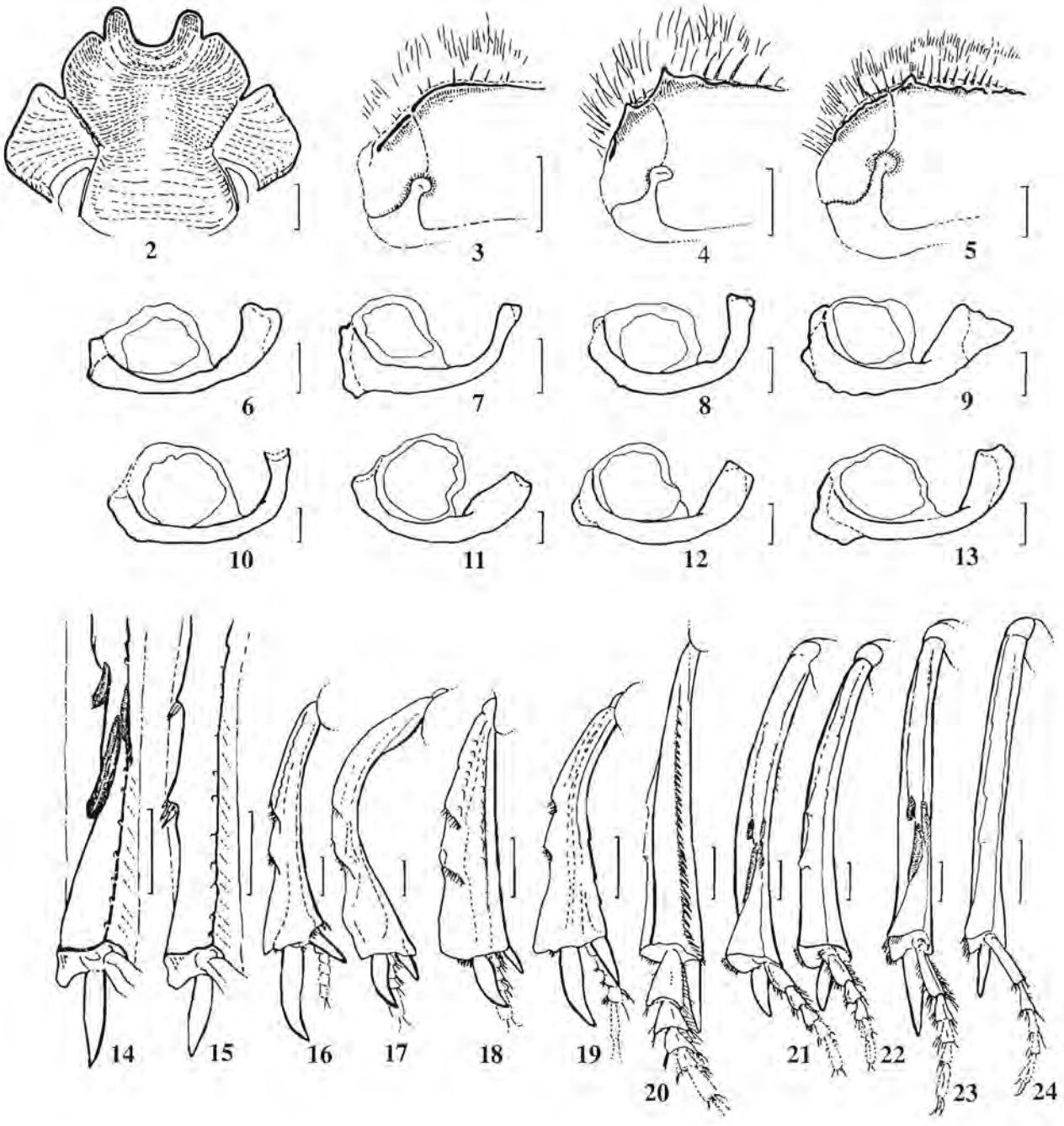
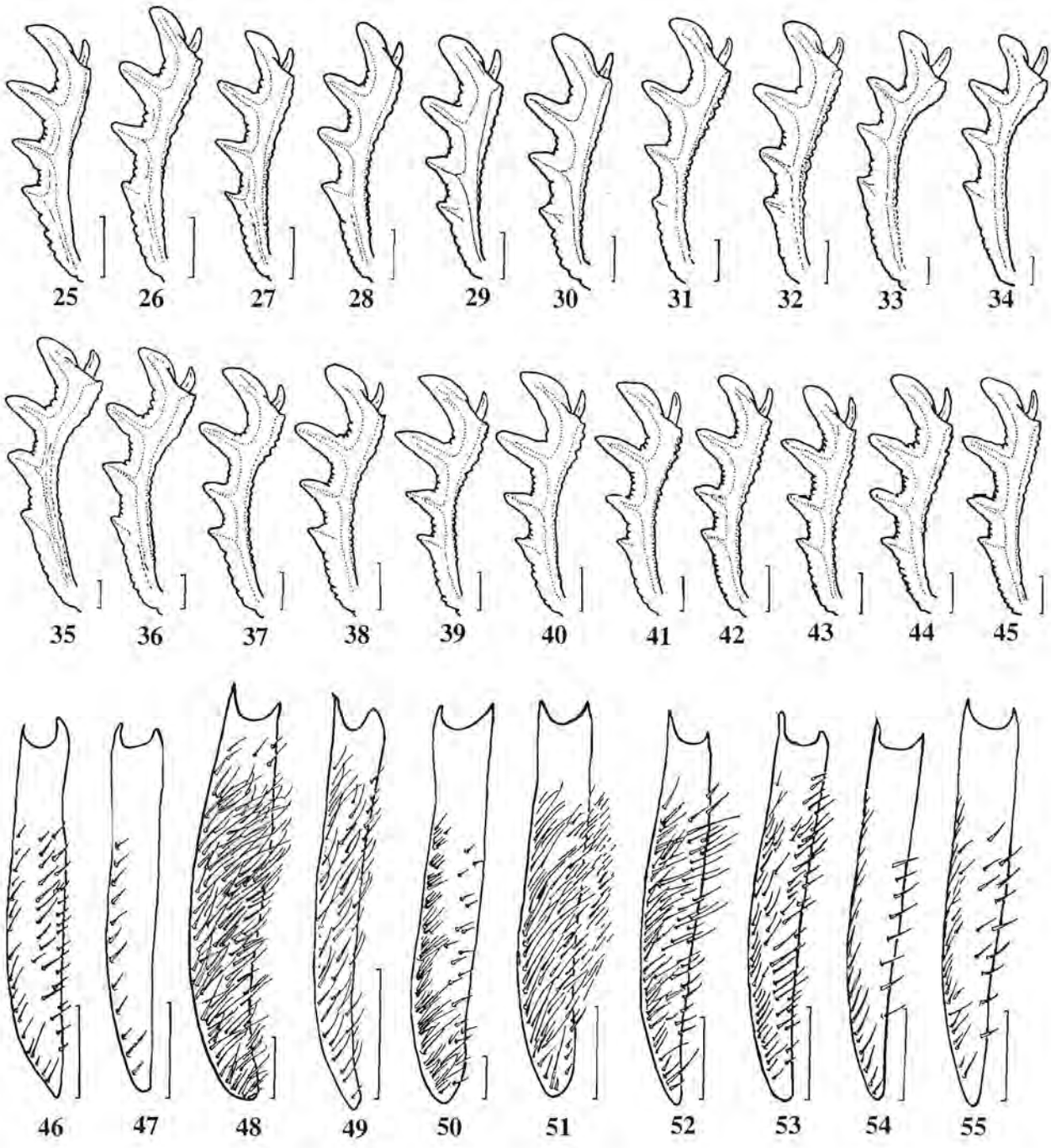


Fig. 2. Head plates of *Sceliages*, contour. **Figs 3-5.** Profemora and protrochanter development of basal region of anterior-ventral margin (ventral perspective). Scales = 1 mm. Fig 3– *Sc. hippias*; Fig. 4– *Sc. augias*; Fig. 5– *Sc. brittoni*. **Figs 6-13.** Male genitalia of *Sceliages*; virgular and circular sclerites of the internal sac, contour. Scales = 0.2 mm. Fig. 6– *Sc. granulatus* (Sekoma, Botswana); Fig. 7– *Sc. granulatus* (Kimberley, RSA); Fig. 8– *Sc. hippias*; Fig. 9– *Sc. augias*; Fig. 10– *Sc. brittoni*; Fig. 11– *Sc. adamastor*; Fig. 12– *Sc. difficilis*; Fig. 13– *Sc. Gagates*. **Figs 14-15.** Metatibia of *Sceliages*; sexual variation of distal apices (dorsal perspective), contours. Scales = 1 mm. Fig. 14– *Sc. hippias*, ♂; Fig. 15– *Sc. hippias*, ♀. **Figs 16-19.** Mesotibia and mesotibial spurs of *Sceliages* (dorsal perspective), contours. Scales = 1 mm. Fig. 16 – *Sc. brittoni*; Fig. 17– *Sc. adamastor*; Fig. 18– *Sc. hippias*; Fig. 19– *Sc. difficilis*. **Fig. 20.** Metatibia of *Sceliages gagates*; medial facet with medio-longitudinal setation/carina (dorso-lateral perspective), contour. Scale = 1 mm. **Figs 21-24.** Metatibia of *Sceliages*; inward curvation (dorsal perspective), contours. Scales = 1 mm. Fig. 21– *Sc. adamastor*, ♂; Fig. 22– *Sc. adamastor*, ♀; Fig. 23– *Sc. brittoni* ♂; Fig. 24– *Sc. granulatus* ♀.



Figs 25-45. Protibiae of *Sceliages* (dorsal perspective), contours. Scales = 1 mm. Fig. 25 – *Sc. granulatus*, ♂ (Kimberley, RSA); Fig.26– *Sc. granulatus*, ♀ (Kimberley, RSA); Fig. 27– *Sc. granulatus*, ♀ (Kang, Botswana); Fig. 28– *Sc. granulatus*, ♂ (Kang, Botswana); Fig. 29– *Sc. hippias*, ♂; Fig. 30– *Sc. hippias*, ♀; Fig. 31– *Sc. augias*, ♂; Fig. 32– *Sc. augias*, ♀; Fig. 33– *Sc. brittoni*, ♂; Fig. 34– *Sc. brittoni*, ♀; Fig. 35– *Sc. adamastor*, ♂; Fig. 36– *Sc. adamastor*, ♀; Fig. 37– *Sc. difficilis*, ♂ (Rhenosterpoort farm, RSA); Fig. 38– *Sc. difficilis*, ♀ (Rhenosterpoort farm, RSA); Fig. 39– *Sc. difficilis*, ♂ (Umtali, Zimbab.); Fig. 40– *Sc. difficilis*, ♀ (Umtali, Zimbab.); Fig. 41– *Sc. difficilis*, ♀ (Holotype, BMNH); Fig. 42– *Sc. gagates*, ♂ (Muzi Area, RSA); Fig. 43– *Sc. gagates*, ♀ (Muzi Area, RSA); Fig. 44– *Sc. gagates*, ♂ (Delagoa B., Moçamb.); Fig. 45– *Sc. gagates*, ♀ (Delagoa B., Moçamb.). **Figs 46-55**. Mesofemora of *Sceliages*; setation/pubescence on posterior facet. Left margins are dorsal, (lateral perspective). Scales = 1 mm. Fig. 46– *Sc. granulatus*; Fig. 47– *Sc. hippias*; Fig. 48– *Sc. brittoni* and *Sc. augias* (Casonda, Angola); Fig. 49– *Sc. augias* (Mpwapura); Fig. 50– *Sc. adamastor* (De Hoop Nat. Res., RSA); Fig. 51– *Sc. adamastor*; Fig. 52– *Sc. difficilis* (Badplaas, RSA); Fig. 53– *Sc. difficilis* (Boekenhoutskloof, RSA); Fig. 54– *Sc. gagates* (Muzi Area, RSA); Fig. 55– *Sc. gagates* (Muzi Area, RSA).

Sceliages difficilis Zur Strassen 1965

(Figs 12, 19, 37-41, 52, 53, 82)

Sceliages difficilis Zur Strassen 1965: 224. – Ferreira 1972: 77.

Material Examined

Type specimens.

Sceliages difficilis. Holotype: ♀, labelled "South Africa: Eastern Cape Province; Grahams town; ex. coll. Fry 1905 – 100", in BMNH.

Paratypes: 1 ♂ and 1 ♀, labelled "South Africa: Natal (Kwazulu-Natal); Krantzkop (Kranskop) (**28°58'S 30°51'E**); November 1917, K.H. Barnard", in SAMC. 1 ♂, labelled "Natal (Kwazulu-Natal); pt; "58.13"", in BMNH. 1 ♂, labelled "Natal (Kwazulu-Natal); ex. coll. Pascoe", in BMNH. 1 ♂, labelled "Natal (Kwazulu-Natal), Durban; A.E.Miller", in SAMC. 1 ♂, labelled "Zimbabwe: Salisbury(Harare), Mashunaland (**17°50'S 31°03'E**); 1893, G.A. Marshall", in SAMC. 1 ♂, labelled "Inyanyadzi River (Nyanyadzi), Gazaland (**19°45'S 32°25'E**); November 1901, G.A.K. Marshall", in BMNH. 1 ♂, labelled "Africa, austr.; Coll. J.J.Gillet", in ISNB

Non-type specimens. 28♂, 18♀. **SOUTH AFRICA. Gauteng.** Boekenhoutskloof, Pretoria, 30 Km NE (**25°31'S 28°25'E**), ex. Millipede (trap), 10.00 hours; 10 xi. 1976, P.D. Stickler (5♂,1♀ SANC). Same locality, 20 i. and 24 ii. 1977; G. Bernon (1♂,2♀ SANC). Johannesburg (**26°12'S 28°05'E**), January 1939, W.G.Kobrow (1♂,1♀ TMSA). Rhenosterpoort Farm, **25°43'S 28°56'E**, horse dung; 27 xii. 1975, L.Schulze E-Y 999 (1♂,1♀ TMSA). Same locality; 5 xi. 1978, L.Schulze (1♂,1♀ TMSA). Valhalla, Pretoria (**25°49'S 28°08'E**); 1 xi. 1963, (?)Zeiler (1♀

TMSA). Mpumalanga; Groenvaly farm, nr. Badplaas, 50 Km N (**25°50'S 30°45'E**), pitfall trap, millipede baited; 20 x. 1995, S.H.Ford (3♂,1♀ UPSA). Lydenburg District, Kopies Kraal, **25°06'S 30°12'E**, singled on ground; 6 xii. 1996, Endrödy-Younga, E-Y 3253 (2♂ TMSA). **Northern Province**. Motlakeng, Blouberg (**23°05'S 29°01'E**), 1600–1900 m; 6–15 i. 1955, Transvaal Mus. Exped. (1♀ TMSA). Nylsvley Nature Reserve, **24°39'S 28°42'E**; 24 xi. 1998, R. Kutranov (1♂ UPSA). Nylsvley, Smith Farm, 24°40'S 28°42'E, cattle dung, 5 days; 17 ix. 1975, Endrödy-Younga, E-Y 920 (1♂ TMSA). Pietersburg (**23°50'S 29°20'E**); 7 xii. 1961, A.Spies (1♂ TMSA). Sand River, Thabazimbi **24°32'S 27°39'E**; 31 iii. - 3 iv. 1986 (1♀ UPSA). Iron Crown, 2km W, Wolkberge, Haenertsberg Distr.(**24°00'S 29°57'E**), 2230 m; March 1970, O. and L. Prozesky (1♀ TMSA). **Kwazulu-Natal**. "ZuluLand"; 1894, Capel (ex. Nevinson coll. 1918 –14) (1♂ BMNH; *Sceliages iopas* W.). "Natal"; (ex. Nevinson coll. 1918 –14) (1♂ BMNH). (Free State); Glen; 28 xi. 1914. (1♀ SANC). **ZIMBABWE**. Harare, Mashunaland[sic], in dung; November 1898, G.A.K. Marshall (1♂ BMNH). Peak Mine, Selukwe (Shurugwi) (**19°40'S 30°00'E**); November 1920, C. Rawstone (1♀ SAMC). Chipinga (Chipinge) (**20°12'S 32°37'E**); 29 i. 1982, C.R.Owen (1♂ TMSA). Upper Búzi R. (**19°51'S 32°48'E**); December 1901, G.A.K. Marshall (1♀ BMNH;1908-212). Upper Búzi River, Gazaland (Melsetter Distr); December 1901, G.A.K. Marshall (1♂ BMNH;1931-138). Mt. Chirinda., "Gaza Ld." (**19°14'S 32°14'E**); 1-3 i. 1907, D.Odendaal (1♀ BMNH). Mt. Chirinda, Gazaland; December 1901, G.A.K. Marshall (1♂ BMNH; 1931-138). Chirinda Forest; December 1952, V.Son (1♀ TMSA). Umtali (Mutare) (**18°58'S 32°40'E**); 1902, A.Bodong (1♂ SAMC; specimen v.poor cond.). Umtali (Mutare), Mashonaland; December 1900, G.A.K.Marshall (3♂,1♀ BMNH;1904-206). "Rhodesie", Plumtree, Rhodesia; 22 xii.1905 (1♂ ISNB; *Sc. adamastor* 10.640). "Rhodesie", Salisbury (Harare), Mashonaland; November 1905, G.A.K. Marshall (1♀ ISNB; *Sc. adamastor*).

Diagnosis

Sc. difficilis can be diagnosed using the angulation of the protibiae (the medial facet of the protibia is slightly angled inwards from between the third external denticle to half-way to the second external denticle. Protibial width is even from the base to parallel with the third external denticle where the width broadens slightly to the apex), and the protruding extension of the baso-ventral corner of the virgular sclerite handle.

Re-description

Length 10-18 mm.

Pronotum: lateral margins evenly rounded. Thickness of lateral margin narrow and even.

Elytra: surface smooth with flat to slightly raised, minute granulations (more apparent in teneral adults). Stria markedly developed (more apparent in teneral adults) comprising a longitudinal pair of micro-carina. Minimal to no longitudinal groove bordered by micro-carinae.

Sternites: surface of mesobasisternum coarsely shagreened, large crescent-shaped punctations, densely arranged and often linked, radiating anterior-laterally from centre of mesosternal process. Punctations generally armed with single very short brown/black setae.

Legs: medial facet of protibia slightly angled inwards from between third external denticle to half-way to second external denticle (Figs 37-41). Even protibial width from base to parallel with third external denticle where width broadens slightly to apex. Protibial angulation and start of angulation more subtle in females (Figs 38, 40, 41). Mesofemora armed with three (Fig. 53) to four (Fig. 52) rows of long thick black/brown setae on posterior facet. Most rows approximately

equal in length. Second row from ventral marginal row often reduced setation. Mesotibia slightly curved inwards (Fig. 19). Outer mesotibial spur 1/3 length of mesotibia. Inner spur 2/3 length and 1/3 width of outer spur. Inner mesotibial spur offset from the outer spur by 10 to 20 degrees. Mesotarsus 2/3 length of mesotibia.

Male genitalia (Fig. 12): handle of virgular sclerite of relatively constant thickness through most its length, widening slightly at each end. Handle evenly concave along majority of dorsal and ventral margin. Dorsal margin unnotched at terminus of union with circular sclerite. Apical margin of handle rectangular. Basal margin between dorsal and ventral corners slightly concave. Secondary sclerotisation of handle reduced in apical ventral corner and apical dorsal corner. Baso-ventral corner forms protruding extension with reduction in secondary sclerotisation.

Comments

The etymology of the species name *difficilis* could be based on the difficulty to accurately diagnose this species. *Sc. difficilis* closely resembles *Sc. gagates* and *Sc. adamastor*. Geographic distribution (*Sc. gagates* is restricted to the eastern coastal regions), differences in width curvature/angulation of the protibiae, and pronotum lateral margins (more evenly rounded in *Sc. difficilis* and more obtusely rounded/flared in *Sc. gagates*), are the principal external characters in separating the two species. Some specimens of *Sc. difficilis* have been mis-identified as *Sc. adamastor*. This may be due to the curvature of mesotibia reminiscent of this strong diagnostic feature in *Sc. adamastor* (Fig. 17). Note, however, on *Sc. adamastor*, the outer mesotibial spur is markedly shorter than the length of mesotibia (Fig. 17) compared to *Sc. difficilis* (Fig. 19), and the mesotarsi of *Sc. difficilis* are 2/3 the length of the mesotibiae (c.f. mesotarsi of *Sc. adamastor* are 1/2 the length of the mesotibiae).

Geographical Distribution

Sc. difficilis is known from South Africa and Zimbabwe (Fig. 82).

Sceliages gagates Shipp 1895

(Figs 13, 20, 42-45, 54, 55, 82)

Sceliages gagates Shipp 1895: 38. – Gillet 1911a: 16; Ferreira 1961: 64; Ferreira 1967: 60; Ferreira 1972: 78; Zur Strassen 1965: 226-229.

Material Examined

Type specimens. See comments.

Sceliages gagates. Neotype: ♂, Labelled "SORDWANA BAY, Natal (3 Km from camp); 15 x 1978, Bornemissza and Aschenborn", in SANC; Database No: COLS 00045.

Sceliages gagates. ?type: Labelled "Limpopo" in BMNH.

Non-type specimens. 25♂, 13♀. **SOUTH AFRICA. Kwazulu-Natal**. Kozi Bay, SE 27 32 Bb (**26°52'S 32°50'E**); 8 x. 1990, T. Beyers, U.P (1♂ UPSA). Muzi, Tongaland (Ingwavuma Distr.) **26°52'S 32°29'E**; 4 xi. 1980, H.H. Aschenborn (2♂,1♀ SANC). Muzi Area (Ubombo Distr.)"N.Natal"(**27°29'S 32°23'E**); December 1980, E. Klingenhofer (5♂,2♀ SANC). Sodwana Bay, 3 Km from camp (**27°32'S 32°41'E**); 15 x. 1978, Bornemissza and Aschenborn, ex. coll.

CSIRO (2♂ SANC). St Lucia Estuary (**28°21'S 32°29'E**); 23 x. 1966, L.Louw (1♂,1♀ SANC). Tembe Elephant Pk., "N. Kwazulu Natal" **26°51'S 32°24'E**; 2 xii. 1998, P. le Roux (1♀ UPSA). **North West Province**. (?)Sand River Mountain, 24°32'S 27°39'E; 18-19 xii. 1985, C.L. Bellamy and D. d'Hotman (1♀ UPSA). **MOÇAMBIQUE**. Delagoa Bay (Maputo, Baía de) (**25°48'S 32°51'E**); ex. Nevinson coll. 1918-14 (5♂,6♀ BMNH; 1♂ collected 1895). "Delagoa"; ec. Pascoe coll. 93-60 (1♂ BMNH). Delagoa; No Coll. Data (2♂ ISNB). Delagoa; H.Junod (1♂ ISNB). "Dela. B., Mozamb."(Maputo, Baía de); ex. Fry coll. 1905-100 (1♂ BMNH). Inhambane (**23°52'S 35°23'E**); 7 xii. 1912, K.H. Barnard (1♀ SAMC). Lourenço Marques (Maputo); 1911, J.B. Paulus (2♂ SAMC). Nyaka, "P E. Afr."(**30°9'S 29°46'E**); February 1924, R.F. Lawrence (1♂ SAMC).

Diagnosis

Diagnostic morphological characters of *Sc. gagates* are: the lateral margins of the pronotum (obtusely rounded; thickness of lateral margins flared medially and narrow posteriorly; dorsal edge of margin upturned slightly); and the differences in protibia angulation (medial facet of protibia slightly angled inwards from second protibial denticle; even and slight increase of protibial width from base to apex) compared primarily to *Sc. difficilis*. The distribution of *Sc. gagates* is restricted to the coastal regions of north-eastern South Africa and Moçambique and is regarded as a key diagnostic character for the species.

Re-description

Length 10-18 mm.

Pronotum: lateral margins obtusely rounded. Thickness of lateral margins flared medially and narrow posteriorly. Dorsal edge of margin upturned slightly.

Comments

Type specimens were unable to be located for this revision nor their existence confirmed thereof (Horn *et al.*, 1990). Only a few types from the original Shipp collection were retained by the Hope Entomological Collections, Oxford University Museum of Natural History. Some of the collection was purchased by P.M. Bright however contains no scarabaeines (Darren Mann, pers. comm.). The location of the location of most of Shipp's types remains a mystery. According to zur Strassen (1965), a [Holo]type of *Sc. gagates* with the locality "limpopo" was apparently lodged with the BMNH. All specimens of *Sceliages* were loaned from the BMNH for this revision of which no types of *Sc. gagates* were present. Zur Strassen (1965) was met with the same fate and also questioned the existence of types, more especially, the supposed type specimen. Zur Strassen (1965) also argued that the original description by Shipp was inaccurate and could easily have been based on a specimen of *Sc. hippias* lacking its yellow apical antennomeres, or *Sc. difficilis*, an undescribed species in 1895.

With an absence of types, our description of this species was initially based on the original description by Shipp (1895) and, in accordance with zur Strassen (1965), found Shipp's description more akin to that of *Sc. difficilis*. We therefore relied on the description and key by zur Strassen (1965) and examination of as many specimens we could obtain. We noticed an obvious lack of zur Strassen's knowledge of the geographic localities of the specimens he examined and subsequently identified either as *Sc. gagates* or *Sc. difficilis* which made their differentiation rather ambiguous. This lead us to re-describe the species based on lowland coastal specimens of *Sc. gagates* or mis-labelled *Sc. difficilis* which possess uniformity in the morphological characters we regard as descriptive for *Sc. gagates*.

Based on the current re-description of *Sc. gagates* the [Holo]type with the locality "limpopo" is likely to be correct *only* if the specimen was collected in the eastern lowland coastal region of Moçambique through which the Limpopo(River) flows. However, its location, or that of any other type for this species, remains a mystery. General agreement by those who have helped us try to locate missing types is that they should be treated as non-existant and neotypes be assigned. This we have done.

Subtle intra-specific variations or external wear on diagnostic characters of both *Sc. gagates* and *Sc. difficilis* can easily lead to misidentification for either species. There are relatively few consistently sound diagnostic characters that could be described to separate the two species. "Ambiguous" male specimens of *Sc. gagates* that could be misidentified as *Sc. difficilis*, do however show reasonably consistent similarities in their virgular sclerites.

Geographical Distribution

Sc. gagates is known from the lowland coastal regions of north-eastern South Africa and southern Moçambique (Fig. 82).

Sceliages granulatus, sp. nov.

(Figs 1, 6, 7, 24, 25-28, 46, 80)

Material Examined

Type specimens. See comments

Holotype: ♂, labelled "Botswana: Kang, 35 Km SE, millipede-baited pitfall trap; 23 January 1978, A.L.V. Davis" (**23°46'S 22°51'E**), in SANC.

Paratypes: 3♂,1♀, same data as holotype, in SANC; 1♂, 2♀ labelled "Botswana: Sekoma, 26 Km E, millipede-baited pitfall trap, 24-25 January 1978, A.L.V. Davis" (**24°24'S 23°53'E**), 1♂ in UPSA, 2♀ in SANC.

Non-type specimens. 3♂, 2♀. SOUTH AFRICA: 1♂ labelled 'Northern Cape Province; Olifantshoek, 45 Km SW, 28 February 1973, Bornemissza and Temby' (27°56'S 22°44'E) in SANC; 1♀ labelled 'Vryburg' (26°57'S 24°44'E) in SAMC; 2♂, 1♀ labelled 'South Africa: "Cape Province", Kimberley 28°44'S 24°46'E, October - November, 1980, S. Erasmus', in SANC

Diagnosis

Sc. granulatus shares a similar overall appearance with small teneral adults of *Sc. difficilis* except for the following differences present in *Sc. granulatus*: an obvious indumentum covering the elytra. Granulations on elytra more obvious and pronounced. Striae on the elytra are more pronounced. Pronotum lateral margins are obtusely rounded (similar to *Sc. gagates*).

Description

Length 11-13 mm.

Head: surface rugose, densely punctated on genae and clypeus. Punctations on marginal regions of clypeus and gena form prolonged ripple-like ridges. Geno-clypeal suture obscured along apical half by punctations and roughness of surface near geno-clypeal margins. Antennae armed with dense array of pale minute sensilla on apical margins and dorsal surfaces on antennal club antennomeres.

Pronotum: surface coarsely shagreened, covered in minute punctations and fine, flat granulations. Lateral margins of pronotum obtusely rounded. Width of pronotal lateral margins constant in posterior half. Angulation of lateral margin without variation posteriorly and minimal to none medially. Entire dorsal lateral margin well defined.

Elytra: surface coarsely shagreened, covered in well developed granulations. Stria bordered with 2 evenly spaced carinae; granulation absent in strips running parallel with outer margins of each carina. Elytra covered with thin layer of indumentum providing dull matt appearance.

Sternites: surface of mesobasisternum finely shagreened, covered with large punctations often linked in ripple like chains of four or more. Punctations crescent-shaped and slightly facetted. Facets between inner margins of mesocoxal cavities and lateral carinae of mesosternellum undermined posteriorly and straightened to vertical at deepest point. Each facet outwardly curved twisting to horizontal anteriorly. Carina curved at union with mesobasisternal-mesepisternal suture.

Legs: medial (inner) facet of protibia poorly curved inwards. Females; curvature is even (Figs 26, 27). Males; curvature subtly more apparent from second external protibial denticle (Figs 25, 28). Medial facet of protibia twisted by 45 degrees from vertical in proximal half to horizontal position in distal half. Males; medial carina of keel of first (most basal) protibial denticle reaches dorsal longitudinal carina. Antero-ventral margin of profemora adjacent to protrochanter armed with one spur-like projection. Posterior facet of mesofemora armed with three rows of setae running parallel to dorsal and ventral margins (Fig. 46). Rows of variable length. Setae of variable density. Vagrant setae located sparsely between rows. Mesotibiae poorly curved inwards. Outer mesotibial spur approximately 1/3 length of mesotibia. Inner mesotibial spur more than 2/3length of outer spur. Inner mesotibial spur offset from outer spur by 15 degrees. Mesotarsus approximately 2/3 length of mesotibia. Metatibia (in dorsal perspective) without inward curvature (Fig. 24).

Male genitalia (Figs 6, 7): handle of virgular sclerite broadly concave along medial region; dorsal margins steeply curved upwards at both ends. Apical region tapers to its widest at apex. Apex rounded at dorsal corner; angled at ventral corner. Secondary sclerotisation reduced transversely in ventral corner of apex of handle. Basal region of handle has reduction of secondary sclerotisation at dorsal corner. Baso-ventral corner of handle has pronounced rectangulate extension.

Comments

The virgular sclerite of *Sc. granulatus* from Kimberley (Fig. 7) differs slightly from the Botswana specimens (Fig. 6) in possessing a slightly thinner, less tapered apical region without angulation at the apex. Generally, virgular sclerites show little to no intraspecific variation and are therefore regarded as species specific and highly conserved. Only two male specimens have

been collected from Kimberley that prevents testing whether or not these differences are consistent. Whilst no external differences are apparent between the South African and Botswana specimens, the former have not been included in the type series.

Geographical Distribution

Sc. granulatus is known from semi-arid regions of southern Botswana and the northern part of central South Africa (Fig. 80) in areas considered to represent Kalahari sands.

Specific epithet

Species name is derived from the small but pronounced granulations on the elytra.

Sceliages hippias Westwood 1844

(Figs 3, 8, 14, 15, 18, 29, 30, 47, 56-79, 80)

Sceliages hippias Westwood 1844: 100. – Shipp 1895: 39; Péringuey 1901: 64; Gillet 1911a: 16; Ferreira 1961: 65; Ferreira 1972: 78; Zur Strassen 1965: 221, 222, 224, 226-228.

Ateuchus microcephalus Boheman 1857: 176. – Shipp 1895: 38. **Syn.**

Material Examined

Type specimens. See comments.

Sceliages hippias. Holotype: 1♂, labelled "?type" "Int. S. Afr." in BMNH; 54-76.

Ateuchus microcephalus. Paratype: 1♀, labelled "Caffraria" in The Natural History Museum of Stockholm.

Non-type specimens. 30♂, 23♀. **SOUTH AFRICA**. "Cap"; No Data, Coll. J.J.Gillet (1♂ ISNB). **Mpumalanga**. Watervalriverpass, **24°54'S 30°21'E**, on ground and bush; 28 xi. 1986, Endrödy-Younga, E-Y 2326 (1♀ TMSA). Lydenburg, Waterval Pass, 11Km NE; 15 xi. 1972, A. Strydom (1♂ TMSA). Lydenberg District (1♂,1♀ SAMC). Schmoemansville (**25°01'S 30°31'E**); December 1932, G. Kobrow (1♀ TMSA). **Kwazulu-Natal**. "Burn" (1♂ SAMC). Tugela Ferry (**28°44'S 30°27'E**); 14 xi. 1971, C.H. Draper (1♀ TMSA). Weenen (**28°51'S 30°04'E**); November 1926, H.P. Thomasset (2♂ BMNH). Tugela River, Weenen; November 1996 (1♂, 1♀ DMSA). **Northern Province**. Blouberg (**23°05'S 29°01E**), 1910m-2138 m; 10 i. 1955, Transvaal Museum Exped. (1♂ TMSA). Blouberg, 23°05'S 29°01E, 1480 m; 4–7 xii. 1990, Chown, Steekamp and M^{c}Geoch (1♂ SANC). Nylstroom **24°40'S 28°15'E**; 22 iii. 1997, D.G. van Eeden (1♀ UPSA). Nylsvlei, Smith Farm **24°40'S 28°42'E**, cattle dung, 5 days; 17 ix. 1975, Endrödy-Younga, E-Y 920 (1♂ TMSA). Pietersburg, **24°14'**40"**S 29°15'**30"**E**; 22 x. 1989, R.C. Lutchman (1♀UPSA). Same locality, 18 ii. 1989, L. Dekker (1♂ UPSA). Same locality, 17 ii.1989, R. Jansen (1♀ UPSA). Rhenosterpoort Farm, (?)25°43'S 28°56'E (**24°45'S 28°23'E**), horse dung; 27 xii. 1975, L. Schulze, E-Y 999 (1♀ TMSA). Same locality, 15 ii. 1980, L. Schulze (1♀ TMSA). Vic. Mmafete **24°11'S 30°06'E**; 28 xi. 1985, A.V.Evans and C.L. Bellamy (1♂ UPSA). Warmbad, SE 24,28 cb (**24°50'S 28°20'E**); April 1979, P. Koelance (1♂ UPSA). **North West Province**. Rustenberg Nature Reserve **25°40'S 27°12'E**; 17-20 iii. 1980, C. G. E. Moolman (1♀ SANC). Rustenberg Nature Reserve 25°40'S 27°12'E; 17 xii 2000, millipede baited p/f trap (1hr @ 0900h), S. A. Forgie (1♂,1♀ SANC; 1♂, 8♀ UPSA). Tonguani Gorge, Pretoria, 81 Km W (**25°50'S 27°30'E**); 2 xii. 1972, Bornemissza and Insley, ex. coll. CSIRO (1♂ SANC). Retiefskloof, Rustenberg, 15 Km SE (**25°49'S 27°16'E**); 25 –26 x. 1975, I.D. Temby,

ex. coll. CSIRO (1♀ SANC). Thambazimbi, 30 Km W, SE 24 27 da (**24°35'S 27°20'E**); 26 v. 1979, E. Holm;(1♂ UPSA). **Gauteng.** Johannesburg (**26°12'S 28°05'E**); February 1932, G. Kobrow (1♂ TMSA). Same locality; December 1905, G. Kobrow (2♂ TMSA). Same locality, "Ross." (1♂ SAMC). Kameeldrift, Pretoria, 24 Km NE (**25°39'S 28°21'E**); 29 i. 1975, H.H. Aschenborn, ex. coll. CSIRO (1♂ SANC). nr. Johannesburg A.J. Chomley; (1♂ BMNH; 1906–29). Roodeplaat Farm, Pretoria, 20 Km NE (**25°34'S 28°22'E**); 15 xii. 1984, A.L.V. Davis (1♀ SANC). Hennopsriver, Pretoria, 32 Km W (**25°50'S 27°58'E**); 22 xii. 1971, H.P. Insley, ex. coll. CSIRO (1♂ SANC). Pretoria, 25°45'S 28°12'E; "Collected at dying millipede, 11h00 after rain. Later breaking millipede up into pieces, burrowing those"; October 1982, R. Oberprieler (1♂ SANC). Same locality; 10 ii. 1936, E.C.G. Bedford (1♂ SANC). Same locality; November 1972, R. Strydom (1♀ UPSA). Same locality, 25°47'S 28°20'E; 11 xii. 1998, A. Shongwe (1♂ UPSA). Pretoria District (1♂ SANC). Pretoria (1♂ SAMC). Swartkops, nr. Jhb (**26°05'S 27°45'E**); 10 xii. 1967, M.I.Russell (1♂ BMNH). Welgedacht, Pretoria, 50 Km N (**25°20'S 28°20'E**); 22 x. 1977, J. Boomker (1♂ UPSA).

Diagnosis

Sc. hippias is easily identifiable with the yellow/orange colour of the antennomeres, especially in live specimens. Should this character be ambiguous or missing in dead pinned specimens, then correct diagnosis of the species is assured with the unique setation on the posterior facet of the mesofemora, and mesotibiae are relatively short, evenly tapering to the distal apex, and without any curvature.

Re-description

Length 12-16 mm.

Head: surface of frons and vertex smooth with smaller, fewer punctations than in geno-clypeal region. Geno-clypeal suture is obscured by dense punctations and rough surface along its apical half. Antennal club yellow-orange.

Pronotum: lateral margins of pronotum obtusely rounded. Angulation of lateral margins of pronotum unvaried. Lateral margins of even width in posterior half.

Elytra: surface smooth, finely punctated and without waxy indumentum. Striae faint, lineal grooves infrequently bordered by minute carinae, and interrupted by punctations.

Sternites: surface of mesobasisternum smooth with large, evenly spaced, scalloped punctations radiating in vague linear fashion, antero-laterally from centre of mesosternal process. Mesosternum loosely covered in minute punctations, most armed with a single minute pale seta.

Legs: medial facet of protibia angled slightly, if at all, inwards from second protibial denticle (Figs 29, 30). Protibia width increasing evenly and slightly from base to apex. Antero-ventral margin of profemora adjacent to trochanter an obvious ridge, rounded, without serration; spur-like projection absent (Fig. 3). Mesofemora armed with single row of setae closely paralleling ventral margin in basal half of posterior facet (Fig. 47). Inner facet of mesotibia straight (Fig. 18). Outer mesotibial spur approximately 1/4 length of mesotibia. Inner mesotibial spur equal in length to outer spur and 1/2 its thickness. Angle of inner mesotibial spur is generally offset from outer spur by 10 degrees. Mesotarsus approximately 2/3 length of mesotibia.

Male genitalia (Fig. 8): handle of virgular sclerite thin in width, unevenly concave along baso-dorsal and ventral margins, and of relatively constant thickness. Dorsal margin angle down or notched at distal terminus of union with circular sclerite. Apical region of handle abruptly curved upward giving handle an overall sickle-shape appearance. Apical region is slightly

thicker than basal region and rectilinear at its apex. Both dorsal and ventral corners of apex have approximately equal reduction in secondary sclerotisation.

Comments

Much of the Westwood collection, including many of the types, was housed in the Zoological Society of London's collection, which was later incorporated into the main series collections of the BMNH before 1900. According to D. Mann (pers. comm.), the Westwood Type of *Sc. hippias,* if extant, would have been in the series we received from the BMNH for this revision. D. Mann warned the specimen (if present) may not be labelled as a Westwood species, as the labelling of that period was scant to say the least. We examined a specimen labelled "?type" and "Int. S. Afr." from the BMNH series with an accession number, 54-76. The type label may well have been added by zur Strassen during his revision of the genus in which he states this specimen, along with the female *Ateuchus microcephalus* paratype labelled "Caffraria" in The Natural History Museum of Stockholm, are dubious. Zur Strassen (1965) concluded in his discussion of *Sc. hippias* it is likely the holotype and paratype(s) are lost and should be regarded as non-existent. However, further examination of the BMNH "?type" specimen labels and cross referencing of its museum accession number with the accessions registrar in the entomology library of the BMNH reveals this specimen to be the actual holotype for *Sceliages hippias.* The specimen in question has subsequently been correctly labelled as the holotype by D. Mann and remains housed in the BMNH.

Re-description and identification of this species was therefore based on the descriptions by Westwood (1844) and zur Strassen (1965), identified material and diagnostic key of the genus by zur Strassen (1965).

NB: If some or all of the setae on the posterior facet of the mesofemora are absent then the setal sockets should be evident enough to identify this species.

Geographical Distribution

Sc. hippias is known only from the north-eastern corner of South Africa (Fig. 80).

Description of mature larvae of *Sceliages hippias*

Diagnosis

The appearance of mature *Sc. hippias* larvae is typical of those of the subfamily Scarabaeinae (Edmonds and Halffter 1978). They differ, however, from other larvae of the subfamily in possessing the following unique (*) or rarely found characters: (1*) tormae and epitormae are markedly reduced, close to absent; (2) dorsal surface of the stipes is without an irregular row of conical (="stridulatory") teeth along the basal margin; (3*) hypopharyngeal area is without two dissimilar sclerites (oncyli); (4) antennae with three segments; (5) venter of the last abdominal segment lacks any rows or patches of short setae; (6) raster absent.

Description

Body-shape typical for Scarabaeinae larvae: whitish body strongly bent at about middle with markedly developed secondary dorsal folds. Head capsule (Figs 58-61): width ca.3.0 mm. Each hypostomal ridge is subdivided into two short sub-elements. Epipharynx (Fig. 57): tormae markedly reduced and close to be absent. Antenna (Figs 71, 72): consists of three segments; basal segment with 5 pores and no setae; middle segment with flat sensorium, 2 pores and 4

setae; distal segment with 3 apical conical sensillae and 9 pores on ventral surface. Mandible (Figs 62-67): nearly symmetrical; scissorial part on right mandible markedly shorter than that on left one; each mandible with three groups of short setae in molar part and with one long seta in proximal third of lateral surface. Maxilla (Fig. 69): dorsal surface of stipes without irregular row of conical teeth along basal margin. Labium and hypopharynx (Fig. 69): hypopharyngeal bracon as on Fig. 69; hypopharynx without oncyli. Thorax (Figs 77): pro- and metathorax not subdivided by folds; mesothorax weakly subdivided dorsally. Tergum of prothorax with anterior process on each side. Mesothoracic spiracles not found. Legs (Figs 73-76): two-segmented, with weak additional dorsal fold between presumably trochanter and femur. Abdomen (Fig. 56): segments 1- 5 subdivided dorsally in 3 dorsal lobes; segment 6 subdivided in 2 dorsal lobes; segments 7 -10 not subdivided. Anal opening transverse (Fig. 79). Raster absent.

Remarks and discussion

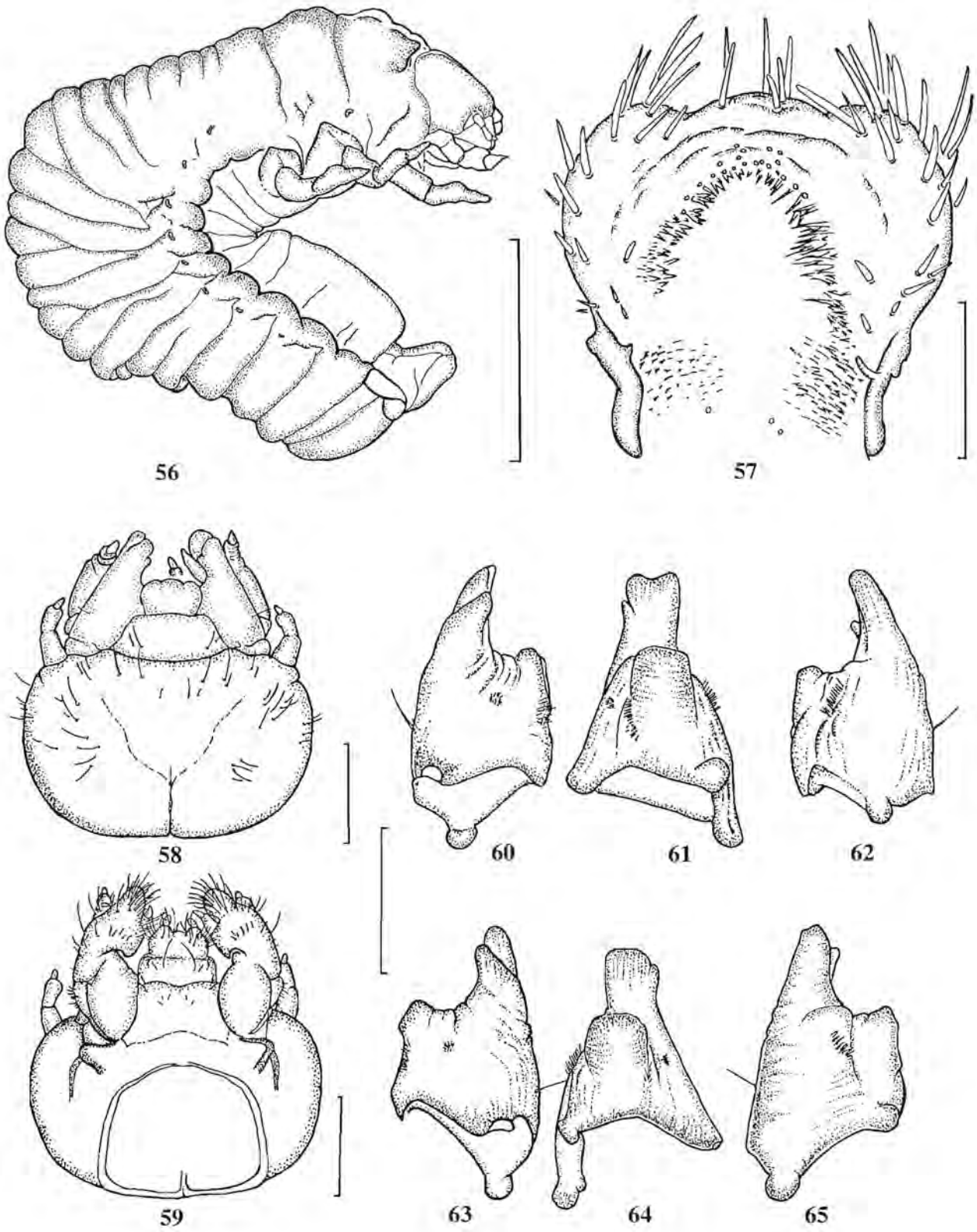
Sceliages hippias larvae resemble those of dung-feeding Scarabaeinae groups. They share a number of morphological characters outlined by Edmonds and Halffter (1978; with a few exceptions, see description). In the current paper we outline some of the major characters of *Sc. hippias* larvae and compare them to the larvae of other taxa of the Scarabaeinae. Putative phylogenetic trends are discussed below.

1. Tormae and their associated sclerites (epitorma, dexiotorma, laeotorma, pternotorma) are markedly reduced or absent. These structures are normally present throughout larvae of the Scarabaeoidea (Ritcher, 1966; Edmonds and Halffter, 1978). In some cases tormae are not united mesally or are somewhat reduced (Ritcher, 1966, Schuster and Reyes-Castillo, 1981). As far as we are aware, the degree of reduction of the tormae in larval *Sc. hippias* is the most extreme within the subfamily.

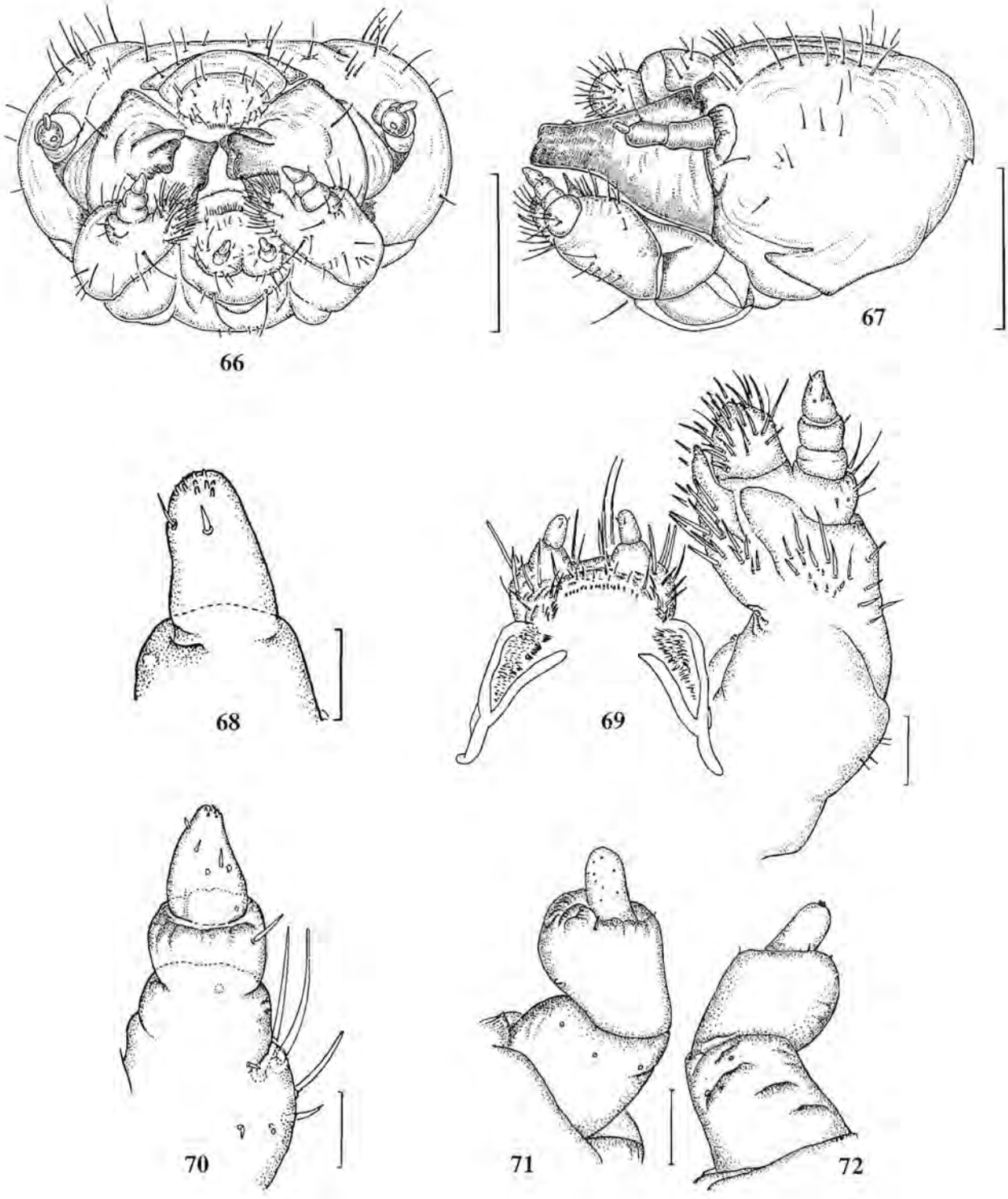
2. The dorsal surface of the stipes is without an irregular row of conical teeth along the basal margin. These teeth are present throughout Scarabaeinae (except *Sisyphus*, see: Edmonds and Halffter, 1978) and many other groups in the Scarabaeoidea. We are not aware of a study demonstrating homology in these structures between the different lineages of the Scarabaeoidea. Occasionally these teeth are referred to as stridulatory teeth (Ritcher, 1966: 26). This assumption has been doubted by Edmonds and Halffter (1978: 313). Moreover, Hirschberger and Rohrseitz (1995) were not able to detect any sound pattern from *Aphodius* larvae possessing these teeth (Hirschberger, personal communication).

3. The hypopharyngeal area is without oncyli. Hypopharyngeal sclerotisation is present in all known larvae of the subfamilies Scarabaeinae and Aphodiinae. Hypopharyngeal sclerotisation is also present in the larvae of the families Geoptrupidae and Lucanidae. As with the presence of "stridulatory" teeth on the stipes, no proof has been found to demonstrate the homology of these structures in the different groups of the Scarabaeoidea. The absence of these sclerites in *Sc. hippias* larvae appears to be unique within the subfamily.

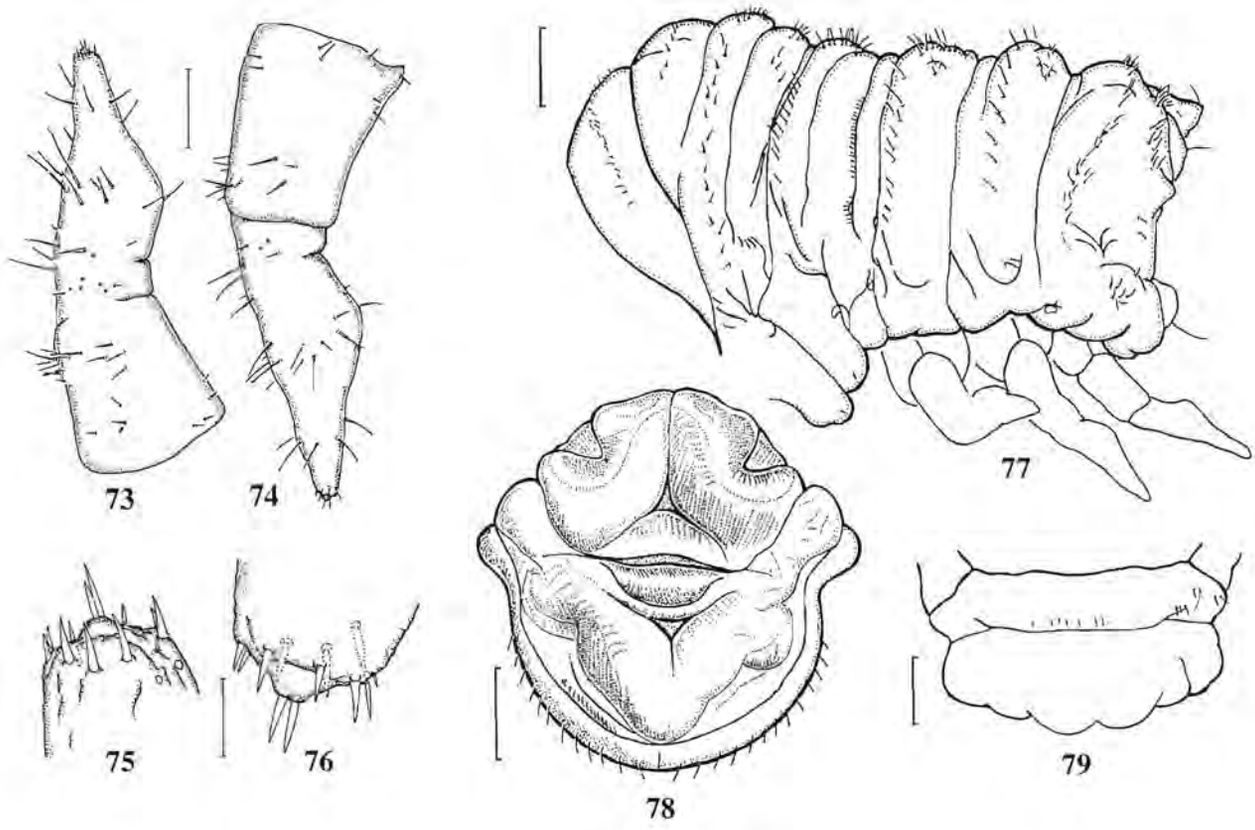
4. The antennae of *Sc. hippias* larvae consist of three antennomeres. In contrast, all other described larvae within the Scarabaeinae possess four antennomeres, even when the subdivision between the two basal segments is poorly distinguished. In *Sc. hippias* this subdivision is absent and, consequently, the two basal antennomeres are fused to form a single one. A three-segmented antenna is a character often utilised to separate Geotrupidae larvae from those of Scarabaeinae possessing four-segmented antennae. Three-segmented antennae have also been found in one unidentified *Scarabaeus* larva from South Africa (Grebennikov and Scholtz, unpubl.).



Figs 56-57. Mature larva of *Sceliages hippias*. Fig. 56– habitus, lateral view, scale = 5 mm; Fig. 57– epipharynx, scale = 0.2 mm. **Figs 58-65**. Mature larva of *Sceliages hippias*, details. Scales = 1 mm. Figs. 58-59– head, dorsal (Fig. 58) and ventral (Fig. 59); Figs. 60-62– left mandible, dorsal (Fig. 60), mesal (Fig. 61) and ventral (Fig. 62); Figs. 63-65– right mandible, dorsal (Fig. 63), mesal (Fig. 64) and ventral (Fig. 65).



Figs 66-67. Mature larva of *Sceliages hippias*, head frontal (Fig. 66) and lateral (Fig. 67), scales = 1 mm. **Figs 68-72**. Mature larva of *Sceliages*, details. Fig. 68– right apical labial palpomere, dorsal, scale = 0.01 mm; Fig. 69– labium, hypopharynx, and right maxilla, dorsal, scale = 0.25 mm; Fig. 70– right maxillary palp, dorsal, scale = 0.1 mm; Figs. 71-72– left antenna, ventral (Fig. 71) and dorsal (Fig. 72), scale = 0.1 mm.



Figs 73-76. Mature larva of *Sceliages hippias*, details. Scales = 0.4 mm. Figs. 73-74– left leg, anterior (Fig. 73) and posterior (Fig. 74) views; Figs. 75–76– apex of left leg, anterior (Fig. 75) and posterior (Fig. 76) views. **Figs 77-79**. Mature larva of *Sceliages hippias*, details. Scales = 1mm. Fig. 77– thorax and two first abdominal segments, lateral; Fig. 78– venter of last abdominal segment; Fig. 79– anal opening and anal lobes.

5. The raster is absent from the ventral surface of the last abdominal segment of *Sc. hippias*. This structure is often inconspicuous, but still present in larvae of the Scarabaeinae (except larvae of the genus *Sisyphus*, Edmonds and Halffter, 1978). We failed to see any setation on the median part of the tenth ventrite, even under high magnification.

Biology and nidification

Millipedes

Three relatively abundant species of millipedes from the order Spirostreptida are utilized by *Sc. hippias* at the Rustenberg Nature Reserve. Two species belong to the family Spirostreptidae: *Doratogonus rugifrons* (Attems 1922), and *D. levigatus* (Attems 1928). The former is a large black species approximately 12-14 cm long and 4-11 mm wide. The latter species is approximately 8-11 cm long and 5-7 mm wide. The third large orange-brown banded species, *Zinophora robusta* (Attems 1928), with similar dimensions to *D. levigatus*, belongs to the family Harpagophoridae.

Attraction to millipedes

It was important to confirm whether attraction to millipedes by *Sceliages* beetles is primarily due to a positive chemotaxic response to the quinone-based secretions produced by the millipedes (Krell *et al.*, 1998). To provisionally test this, healthy, uninjured *Z. robusta* and *D. rugrifrons* millipedes were wrapped in pieces of tissue paper and agitated to collect their quinone-based secretions (after Krell *et al.*, 1997). These pieces of tissue (including a control piece of tissue paper not containing secretions) were then suspended above 3 pitfall traps and left for approximately 1/2 an hour at 10:00h. Only the 'quinone' traps collected several adult *Sceliages*. A healthy, uninjured millipede suspended above a pitfall trap also attracted 4 adult *Sceliages* within 1/2 an hour. Other species of beetles known to utilise millipede carcasses in the research area were not attracted to the traps.

Millipede relocation

We tested the assumption that *Sceliages* make balls from the internal tissues of a freshly crushed millipede and roll the ball backwards using its forelegs for locomotion. We crushed several millipedes and left them for observation. Beetles, instead of making a ball, utilized the freshest and most intact portion of the millipede which was relocated using their head and forelegs. Whole millipede corpses and injured millipedes were relocated in the same way up to a distance of 5m.

Burial

Laboratory trials were set-up using 6 pairs of *Sc. adamastor* to observe male-female co-operation in millipede burial. Fighting took place when a single millipede corpse was introduced to each pair. When a second millipede corpse was added to each pair, relocation and burial were carried out individually. Similarly, no male-female cooperation of *Sc. hippias* was observed in the field.

In Rustenberg Nature Reserve, 6 female *Sc. hippias* were each given a whole millipede carcass to observe burial behaviour and to obtain larvae. Locations of each burial site were tagged and recorded with GPS. Two burial techniques were observed: *Sc. hippias* excavates directly in front of the millipede corpse and draws it into the tunnel as it is excavated. Initially, this is carried out by undermining the millipede either directly underneath or at an angle at one end of the millipede. Tunnels constructed by *Sc. hippias* are relatively straight and excavated at a 30° angle. A female *Scelaiges adamastor* was observed at the De Hoop Nature reserve excavating a tunnel wide enough for both beetle and millipede to fit. Once the tunnel was started the beetle aligned the millipede lengthways at its entrance and pushed the millipede in gradually from behind making directional and postural adjustments of the corpse using its head.

Six burial sites were excavated one month later. Four sites contained vacant burrows and/or chambers containing the empty, disarticulated segments of the millipedes presented to the beetles a month earlier. Two sites contained brood chambers with balls and an accompanying adult female. Each brood ball contained a third-instar larva. Chambers were found at a depth of 7 to 14cm beneath the surface. The tunnel leading to each chamber, and the entrance side of the chambers themselves, were filled with empty, separated millipede exo-skeletal body segments.

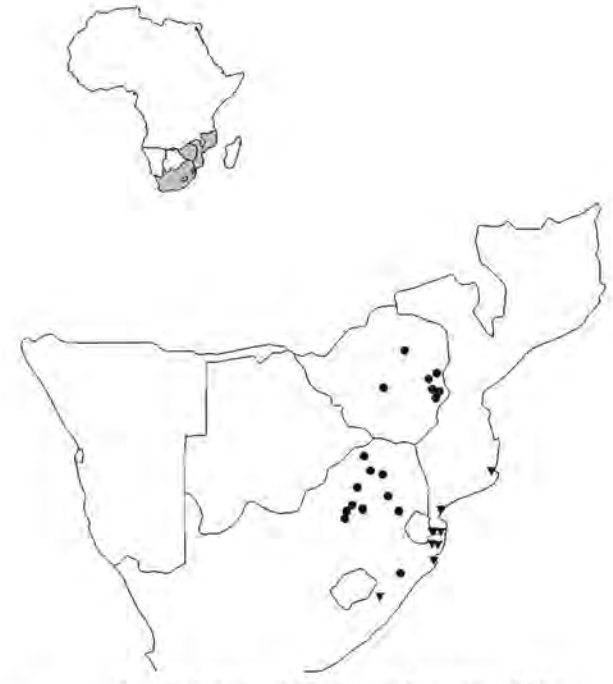
Brood balls

Millipedes of different sizes were measured to see how many balls a reproducing female *Sc. hippias* could make from them. Beetles presented with millipedes up to 7 mm in diameter produced a single brood ball. Millipedes around 11mm in diameter yielded two brood balls. Three millipedes between 7-8 mm in diameter were presented to a single female to test whether she could utilise the entire resource and produce more than the standard 1 or 2 brood balls from a single millipede. Four weeks later, the same female was recovered brooding three balls; two containing third-instar larvae; and a third with a second-instar larva. Brood balls are pear-shaped. The ball is encapsulated by a compact protective layer of soil up to 3.5 mm thick. Soil is also used to make an egg chamber on the side of the ball. The larval food ball of *Sc. hippias* is approximately 12 mm in diameter and constructed from the internal tissues, intestinal dung, and remnant chitinous pieces of the millipede.

Addition of a compacted soil substrate occurs within the brood chamber and is thought to prevent desiccation and protection against pathogens (Halffter and Matthews, 1966). Parental brooding by female *Sceliages* occurs in conjunction with the soil-encrusted balls, a behaviour different to that described for the majority of the Scarabaeini that were thought not to brood or encrust balls with soil (Halffter and Edmonds, 1982: 40).

80 ▲ *Sceliages granulatus* sp. nov.
⬟ *Sceliages hippias* Westwood 1844

81 ✱ *Sceliages augias* Gillet 1908



82 ● *Sceliages difficilis* zur Strassen 1965
▼ *Sceliages gagates* Shipp 1895

83 ■ *Sceliages brittoni* Zur Strassen 1965
✚ *Sceliages adamastor* (Le Peletier de Saint-Fargeau & Serville 1828)

Figs 80-83. Distribution maps of *Sceliages* Westwood species in southern Africa.

Methods and materials

Taxa

A cladistic analysis was performed including all seven species of *Sceliages*. Ingroup taxa character states were polarised against 2 species of *Scarabaeus*; *S. zambesianus* Péringuey and *S. rusticus* (Boheman). Outgroup selection was based on a combined morphological and molecular phylogenetic analysis of the tribe by Forgie, Bloomer and Scholtz (unpubl.), taking into consideration arguments by Nixon and Carpenter (1993). Twenty-seven characters (including 3 multi-state) were coded from the sclerotised external structures of teneral adults. The aedeagus and virgular sclerite of the internal sac were also utilised (see "Male genitalia" section for preparation). Larval characters were not used due to a lack of material. Morphological characters and their states were described using the terminology of Doyen (1966) and Lawrence and Britton (1991).

Phylogenetic Analysis

A character matrix was compiled in Dada version 1.2.7 (Nixon, 1998). *Sceliages hippias* has several interesting character states (i.e. character 0/state 1,16/0, 19/0 and 21/0) which it shares with at least one of the outgroup taxa. These states are either pleisiomorphic or were convergently evolved. Symplesiomorphies are also present in *Sc. adamastor* (26/0), and *Sc. brittoni* (24/0). Autapomorphic character states, whilst informative in describing the uniqueness of each species, are uninformative in the analyses and bias the consistency and retention indices by having zero homoplasy. Autapomorphic character states were therefore avoided during

coding and their absence confirmed using the mop-up option in Dada. Character states unique to *Sceliages* are informative in differentiating the genus from other genera within the Scarabaeini but are generally uninformative in a species-level phylogenetic study such as this and were therefore not coded.

All characters were spawned in Nona (Goloboff, 1993) with 1000 repititions to ensure all the shortest cladograms were found utilising branch and bound search options with randomised taxon order in each run. A single tree found in Nona was submitted to Hennig86 version 1.5 (Farris, 1988) and subjected to successive approximations weighting, hennig tree construction and branch breaker options (xs w; mh*; and bb*; commands respectively). Bremer support (decay index) was calculated with Nona up to a value of 5, i.e. searching for trees up to 5 steps longer in the tree(s) submitted for calculation. Trees were also calculated in Parsimony and Implied Weights (PIWE) version 2.6 (Goloboff, 1993, 1997). Five levels of concavity (0, 1, 2, 3 [default], 4, 5) where applied to the characters using rs0; hold1000; hold/100; mult*100 commands. High repetitions run in Nona ensured the best PIWE trees were generated. All DOS-based analysis programmes were run through WinClada (BETA), Version 0.9.9 (Nixon, 1999a).

Consistency (CI) and retention indices (R.I.) (see Farris, 1989), are indicated for each character in the 'morphological characters and their states' provided in Appendix 1. A table of character states of the taxa is provided in Table 1.

Results and Discussion

Unweighted vs weighted trees

A single most parsimonious tree generated with unweighted data had a length of 58 steps and consistency and retention indices of 0.51 and 0.57 respectively (Fig. 84). Weighting of data was applied two ways; successively in Hennig86 (Farris, 1988), and in PIWE (Goloboff, 1997), with the latter assigned 5 levels of weight (1-5) towards character homoplasy (see Goloboff, 1993). Both methods generated single trees with identical ingroup toplogies. In addition, there were no differences in the ingroup topologies between weighted and unweighted analyses. *Scarabaeus rusticus* always appears as sister to the *Sceliages s. str.* clade in all trees except the successive approximations weighting tree in which a basal trichotomy occurs.

Tree support

While the data is obviously very stable, low overall Bremer support in the tree topology is likely to result from a low number of characters and the relatively high consistency and retention indices (CI = 0.51, RI = 0.57) generated (Fig. 84). One of the highest decay values in the tree topology supports the genus thereby indicating its monophyly. Very high decay index and bootstrap values support the monophyly of *Sceliages* in morphological and molecular phylogenetic studies of the Scarabaeini (Forgie, Bloomer and Scholtz, unpubl.). The apical *Sc. brittoni* and *Sc. adamastor* clade also shares the greater support than the remaining nodes of the tree. This close relationship is also well supported in both phylogenetic studies by Forgie *et al.* (submitted) and Forgie, Bloomer and Scholtz (unpubl.). Four characters (i.e. 0, 15, 24, 26) had retention indices of zero suggesting their states were uninformative and therefore unable to support the branch topology of the species in the genus. Their deactivation did not significantly

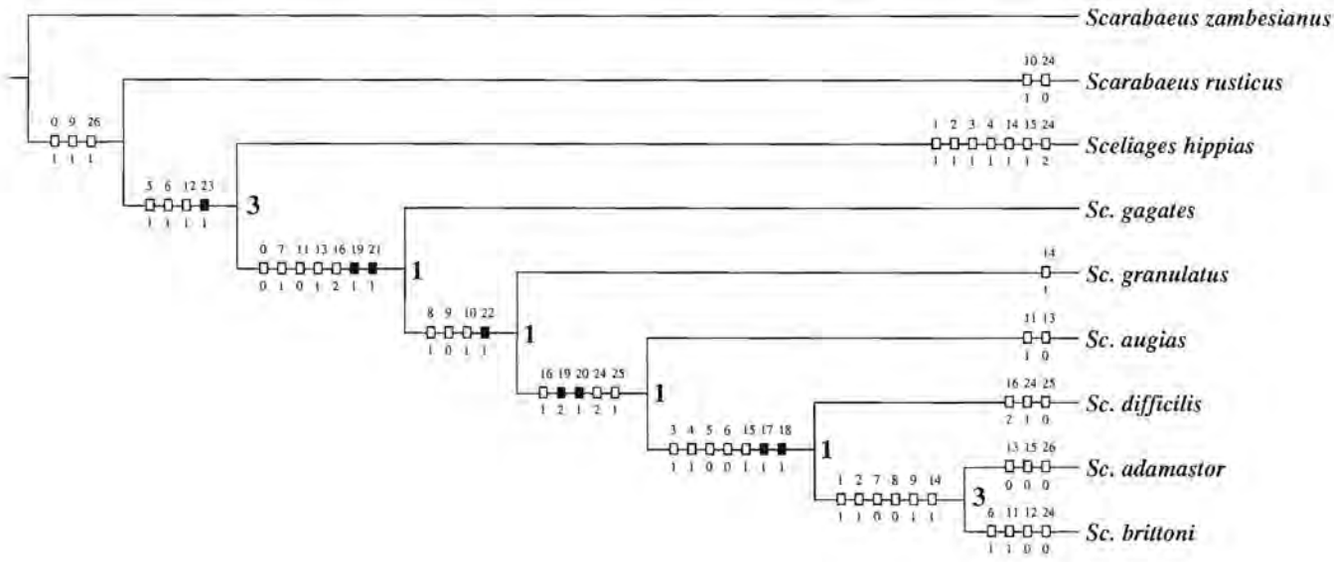


Fig. 84. Hypothesised relationships among species of *Sceliages* Westwood (Coleoptera: Scarabaeidae) represented by single Nona tree (CI = 0.51, RI = 0.57, length = 58 steps). Black hash marks indicate non-homoplasious changes (synapomorphies or autapomorphies), white hash marks indicate homoplasies. Numbers above hashmarks represent characters, numbers below hash marks represent character states (Nixon, 1999b). Bremer support indices (in bold) are provided next to each ingroup node.

Setation on the posterior surface of the mesofemora evolved from a plesiomorphic condition of one row (19/0) to two rows with a medial and sparsely pubescent third row present or not (19/1), to 3 or more uneven rows of setae (19/2) as a synapomorphy for *Sc. augias* (Casonda, Angola exemplar), *Sc. difficilis*, *Sc. adamastor* and *Sc. brittoni*. Such a condition, although variable in development both intra-and inter-specifically, evolved after the shift to millipede necrophagy since the plesiomorphic condition persists in *Sc. hippias*, the most ancestral member of the genus. The function of increased pubescence is unclear when sparsely pubescent species such as *Sc. hippias* are as successful in millipede necrophagy as species like *Sc. brittoni* that have dense pubescence on the posterior surface of the mesofemora.

A waxy indumentum on the surface of the elytra (7/1) is synapomorphic for the clade excluding *Sc. hippias, Sc. adamastor* and *Sc. brittoni*. The latter two species exhibit an evolutionary reversal back to the ancestral condition where a waxy indumentum is lacking (7/0). The semi-arid species, *Sc. granulatus*, exhibits the highest degree of wax indumentation in the genus and

Distribution

The ancestral lineage of *Sceliages* was distributed centrally within the geographical range of the genus from which subsequent lineages dispersed, morphologically adapting to the habitats they are currently distributed in (Figs 80-83). The sister relationship of *Sc. adamastor* + *Sc. brittoni* is reflected in their sympatric distributions (Fig. 83). Both species are adapted to similar habitats and exhibit the most congruency in derived morphological character states in the genus. The phylogenetic derivation of the common ancestor of *Sc. adamastor* and *Sc. brittoni* from that leading to *Sc. difficilis* is biogeographically feasible with a break between a north-eastern extension of the ancestral populations of the common ancestor of these species. The topological positioning of the remaining members of the genus as successive sisters to one another suggests their radiation from the ancestral lineage leading to *Sc. hippias* occurred on several independent occasions.

Conclusions

The majority of external morphological characters of *Sceliages* are shared with the genus *Scarabaeus*, however, a few synapomorphic character states are unique to *Sceliages* (see "Diagnosis" of the genus). The presence of a second mesotibial spur in this phylogenetic study appears as the single unique character state, yet it is present in other members of the Scarabaeini including *Scarabaeus s. str.* The degree of development of the second spur in *Sceliages* is unique however. Moreover, whilst necrophagy in the Scarabaeini is not unique to *Sceliages*, the apparent obligate utilisation of millipedes is and further strengthens the monophyly of the genus. Mostert and Scholtz (1986) likened *Sceliages* as the genus closest to the hypothetical common ancestor of the genera of the Scarabaeini, having undergone the least morphological evolution. In

contrast, a current phylogenetic analysis of the Scarabaeini by Forgie *et al.* (submitted) suggests the genus *Sceliages* is among the more derived members of the tribe. Evidence from both studies support the monophyly of the genus.

In this paper we were able to describe some behavioural characteristics of the adult beetles provisioning nests with millipedes for nidification. Many questions, however, remain unanswered: We know quinonous secretions of millipedes are responsible for attracting *Sceliages*, however, this was tested by stimulating a defensive reaction by millipedes. In a natural situation, are *Sceliages* beetles attracted to these secretions produced as allomones in response to the millipede being threatened or injured, and/or to these secretions being used as pheromones during millipede mate attraction and copulation? Do *Sceliages* beetles kill uninjured millipedes they may have been attracted to, or, must they rely solely on the demise of injured millipedes? Is *Sceliages* truly an obligate necrophage or are other food types also utilized? Are millipedes utilized for maturation feeding or nuptial courtship? Exactly how is the millipede disarticulated? A leverage action using the clypeal teeth and protibial external denticles is inferred (Villalobos *et al.*, 1998) but has not been witnessed. We hope that these questions will stimulate further study on the biology of *Sceliages*.

Acknowledgments

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museum curators responsible for issuing loan material; Richard Newberry (North West Parks and Tourism Board) and Magda Goosen (Rustenberg Nature Reserve) for permitting research of *Sc. hippias* in the Rustenberg Nature Reserve; Andre Olwage for the habitus illustration of *Sc. granulatus* and Pam Prowse for inking the illustrations. This research was funded by National Research Foundation of South Africa and the University of Pretoria.

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Appendix 1. Phylogeny of the genus *Sceliages* Westwood: List of characters and their states.

0. *Apical antennomeres*: (0) brown to black; (1) yellow to orange. CI 0.50, RI 0.00
1. *Medio-longitudinal hump-like process on clypeus*: (0) extending anteriorly; (1) absent anteriorly (clypeus ca. flat). CI 0.50, RI 0.50
2. *Geno-clypeal sutures*: (0) curved medially; (1) ca. straight. CI 0.50, RI 0.50
3. *Punctations on dorsum of head plates*: (0) uneven and irregular; (1) even and regular. CI 0.50, RI 0.66
4. *Head plate dorsal surface*: (0) rugosissimus; (1) rugulosus. CI 0.50, RI 0.66
5. *Lateral margins of pronotum*: (0) evenly rounded; (1) obtusely rounded. CI 0.50, RI 0.66
6. *'Epipleura' of the lateral margins of pronotum*: (0) even thickness throughout; (1) not so. CI 0.33, RI 0.33
7. Indumentum *on surface of elytra*: (0) absent (appearing glossy); (1) present. CI 0.50, RI 0.66
8. *Elytra surface*: (0) smooth (without raised granulation or corrugation); (1) complex (with raised granulation or corrugation). CI 0.50, RI 0.50
9. *Striae on elytra*: (0) markedly defined with bordering microcarinae; (1) not so. CI 0.33, RI 0.33
10. *Mesobasisternum punctation*: (0) facet of puncture forming a raised turbercle-like protrusion (punctation usually crescent-shaped and may be vestigial); (1) not so. CI 0.50, RI 0.50
11. *Mesobasisternum surface* (*due to size, density and arrangement of punctations*): (0) rugose; (1) not so. CI 0.33, RI 0.33
12. *Width between sclerotised medial margins of aedeagus paramere* (*anterior frontal view*): (0) uneven, widening in apical half; (1) relatively even through length. CI 0.50, RI 0.50
13. *Dorsal margin at distal terminus of union between handle of virgular sclerite and circular sclerite*: (0) downward turned (slight to markedly), discontinuous with remainder of dorsal margin; (1) not downward turned, forming a continuous uninterrupted curve with remainder of dorsal margin. CI 0.33, RI 0.33
14. *Baso-ventral corner of handle of virgular sclerite*: (0) forming a protruding extension (slight to markedly); (1) no protrusion. CI 0.33, RI 0.33
15. *Thickness of handle of virgular sclerite*: (0) uneven, thickest at basal and/or apical termini; (1) even throughout. CI 0.30, RI 0.00

16. *Anterior-ventral margin of profemora adjacent to protrochanter*: (0) uniform and unmodified; (1) armed with markedly developed spur; (2) armed with a vestigial spur. CI 0.66, RI 0.75
17. *Width of protibia*: (0) progressive increase in width from thinnest proximally to thickest distally; (1) abrupt increase in width distally between second and third external denticle. CI 1.00, RI 1.00
18. *Inward angulation of medial facet of protibia*: (0) between or at external denticles 1 and 2; (1) between external denticles 2 and 3 or at external denticle 3. CI 1.00, RI 1.00
19. *Setae on posterior surface of mesofemora*: (0) forming a single evenly spaced row of setae paralleling ventral margin; (1) forming two even rows of individually positioned setae (not clustered) parallel to dorsal and ventral margins with a medial third row containing fewer setae present or not; (2) three or more uneven rows of even or unevenly spaced setae. CI 1.00, RI 1.00
20. *Setation on posterior surface of mesofemora*: (0) sparse; (1) dense. CI 1.00, RI 1.00
21. *Shape of mesotibia*: (0) uncurved; (1) curved inwards. CI 1.00, RI 1.00
22. *Tapering/truncation through length of mesotibia*: (0) even; (1) uneven, truncation in apical half or third. CI 1.00, RI 1.00
23. *Number of mesotibial spurs*: (0) one; (1) two. CI 1.00, RI 1.00
24. *Length of major (or outer) mesotibial spur*: (0) ca. ½ length of mesotibia; (1) ca. ⅓ length of mesotibia; (2) much less than ⅓ length of mesotibia. CI 0.40, RI 0.00
25. *Length of mesotarsi*: (0) ca. ⅔ length of mesotibia; (1) less than ⅔ length of mesotibia. CI 0.50, RI 0.50
26. *Curvature of metatibia*: (0) markedly bowed inwards; (1) ca. straight. CI 0.50, RI 0.00

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).

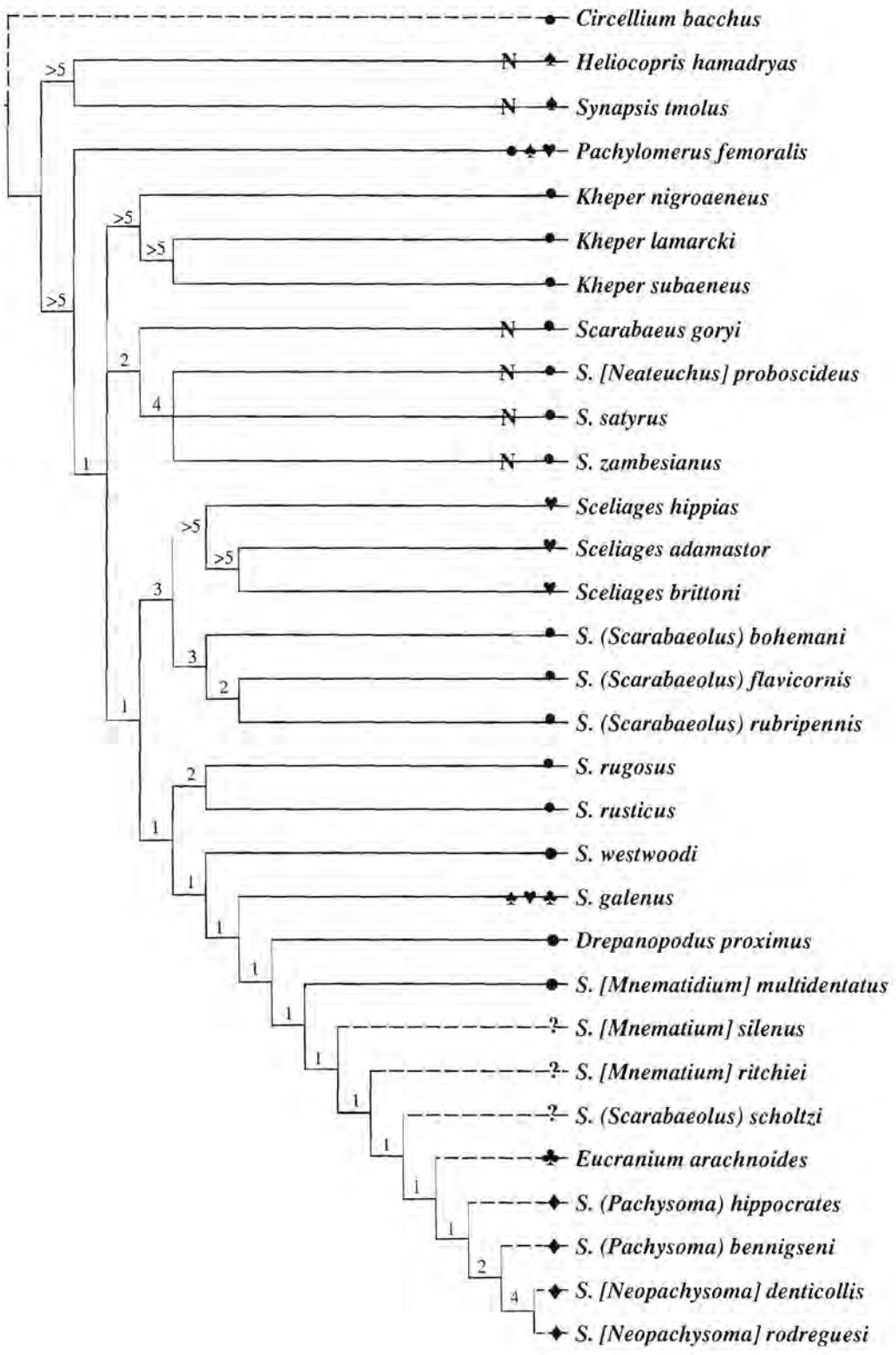

Fig. 1. Phylogeny of the Scarabaeini (Coleoptera: Scarabaeidae). Total Characters data set. NONA, unweighted, consensus of 3 trees (CI = 0.25, RI = 0.50, length = 1835). Branch supports (Bremer decay indices) provided above nodes. Flightless taxa (dashed branch). Nocturnal taxa (**N**). Modes of food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

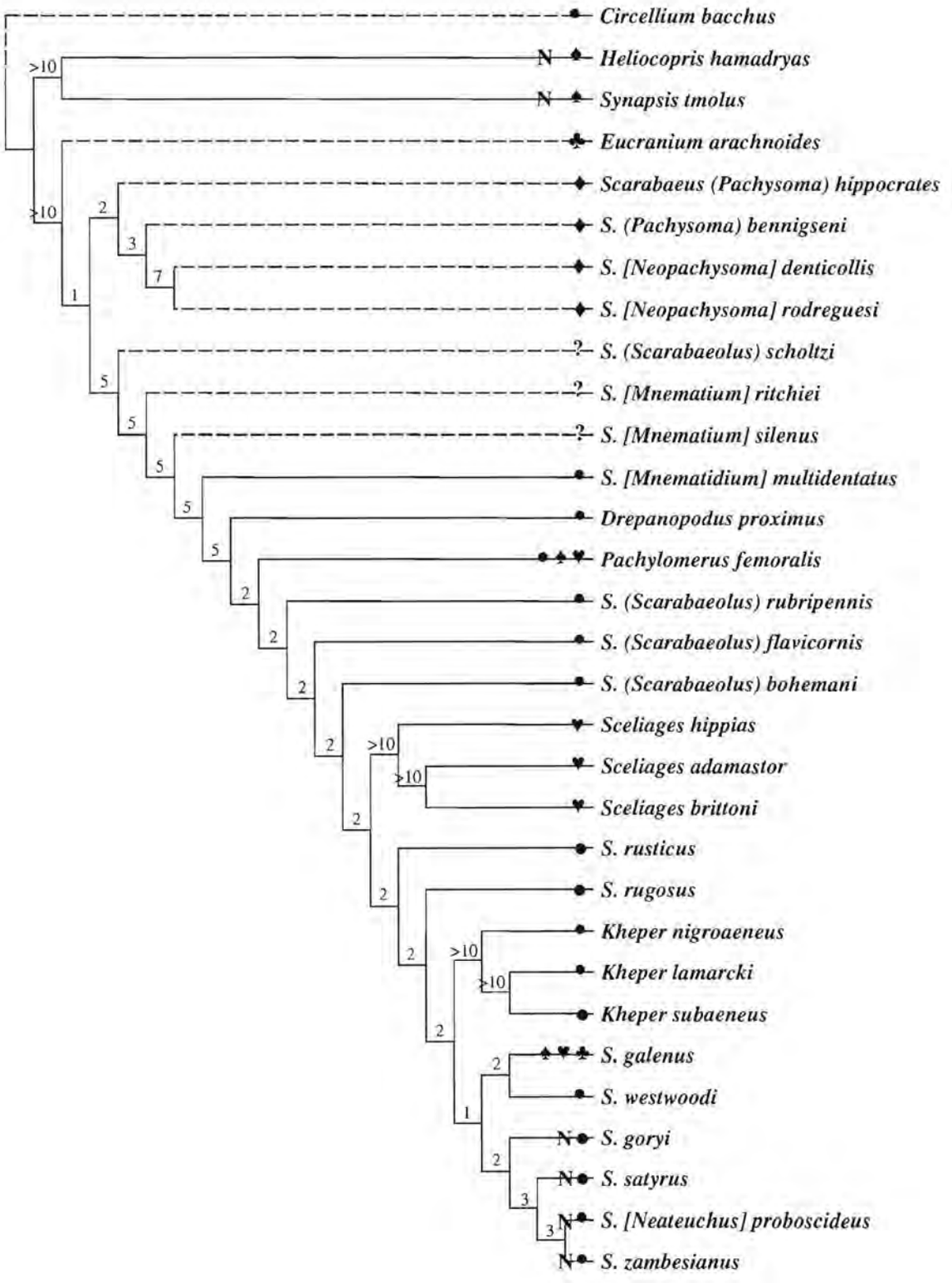

Fig. 2. Phylogeny of the Scarabaeini (Coleoptera: Scarabaeidae). Flight and flightlessness characters deactivated. NONA, unweighted, single tree (CI = 0.24, RI = 0.50, length = 1665). Branch supports (Bremer decay indices) provided above nodes. Flightless taxa (dashed branch). Nocturnal taxa (N). Modes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

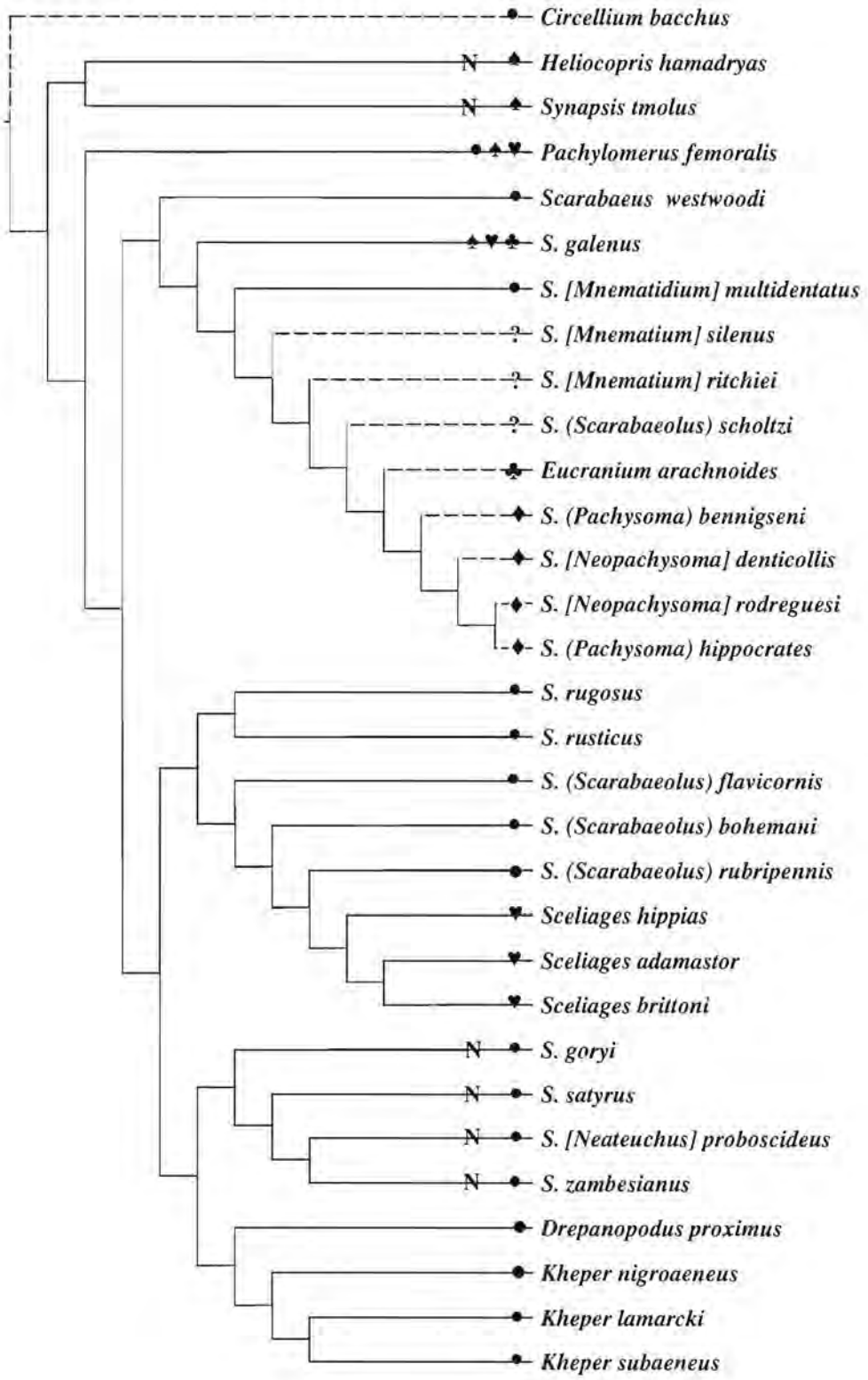

Fig. 3. Phylogeny of the Scarabaeini (Coleoptera: Scarabaeidae). Flight and flightlessness characters deactivated. PIWE (Parsimonious Implied Weights), single tree (CI = 0.24, RI = 0.48, fit = 662.8, length = 1702), CO = 2; Strong weighting against homoplasy. Flightless taxa (dashed branch). Nocturnal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

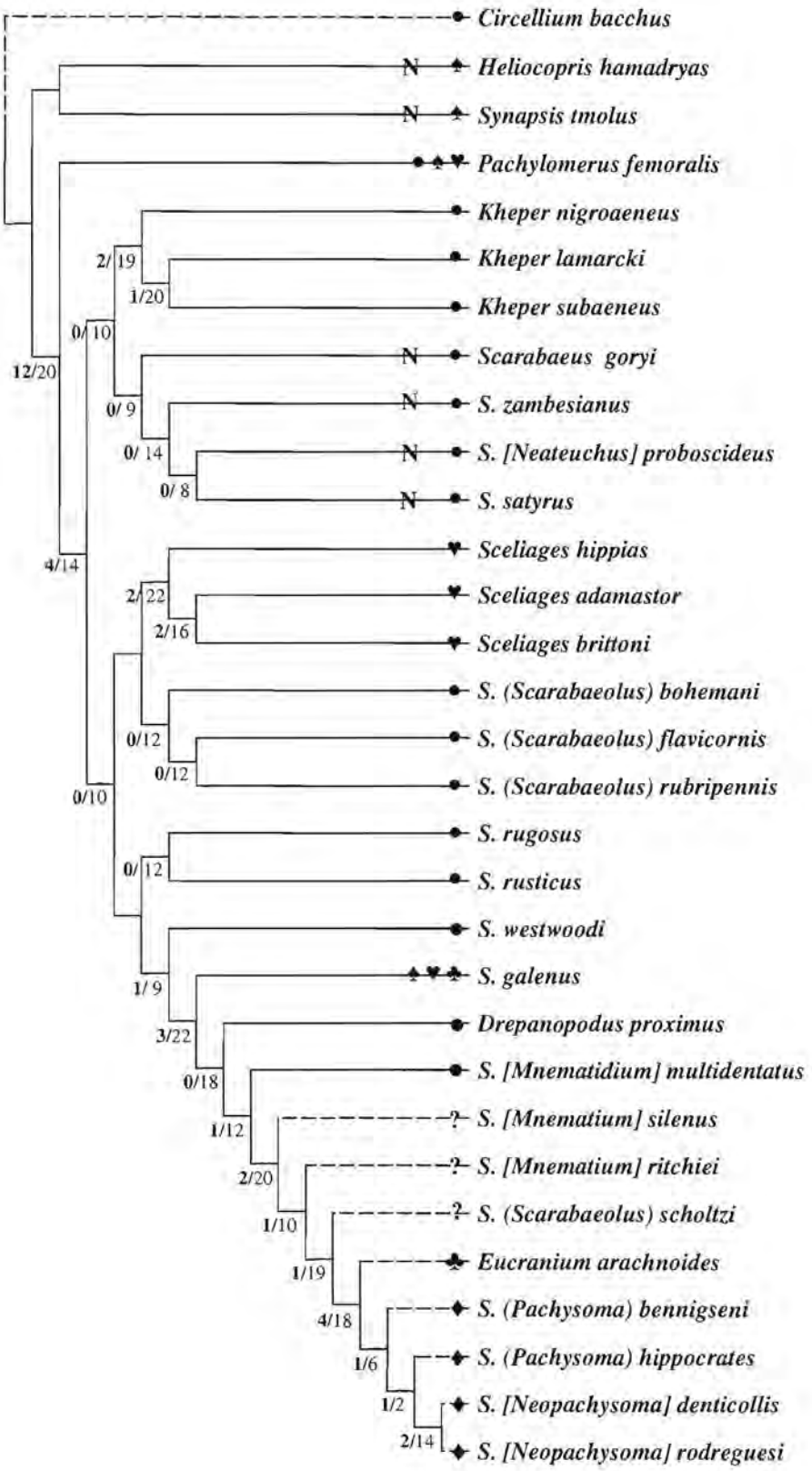

Fig. 4. Phylogeny of the Scarabaeini (Coleoptera: Scarabaeidae). Flight and flightlessness characters deactivated. PIWE (Parsimonious Implied Weights), single tree (CI = 0.24, RI = 0.49, fit = 973.3, length = 1673), CO = 4; slight weighting against character homoplasy. Unique synapomorphies (Bold)/homoplasious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

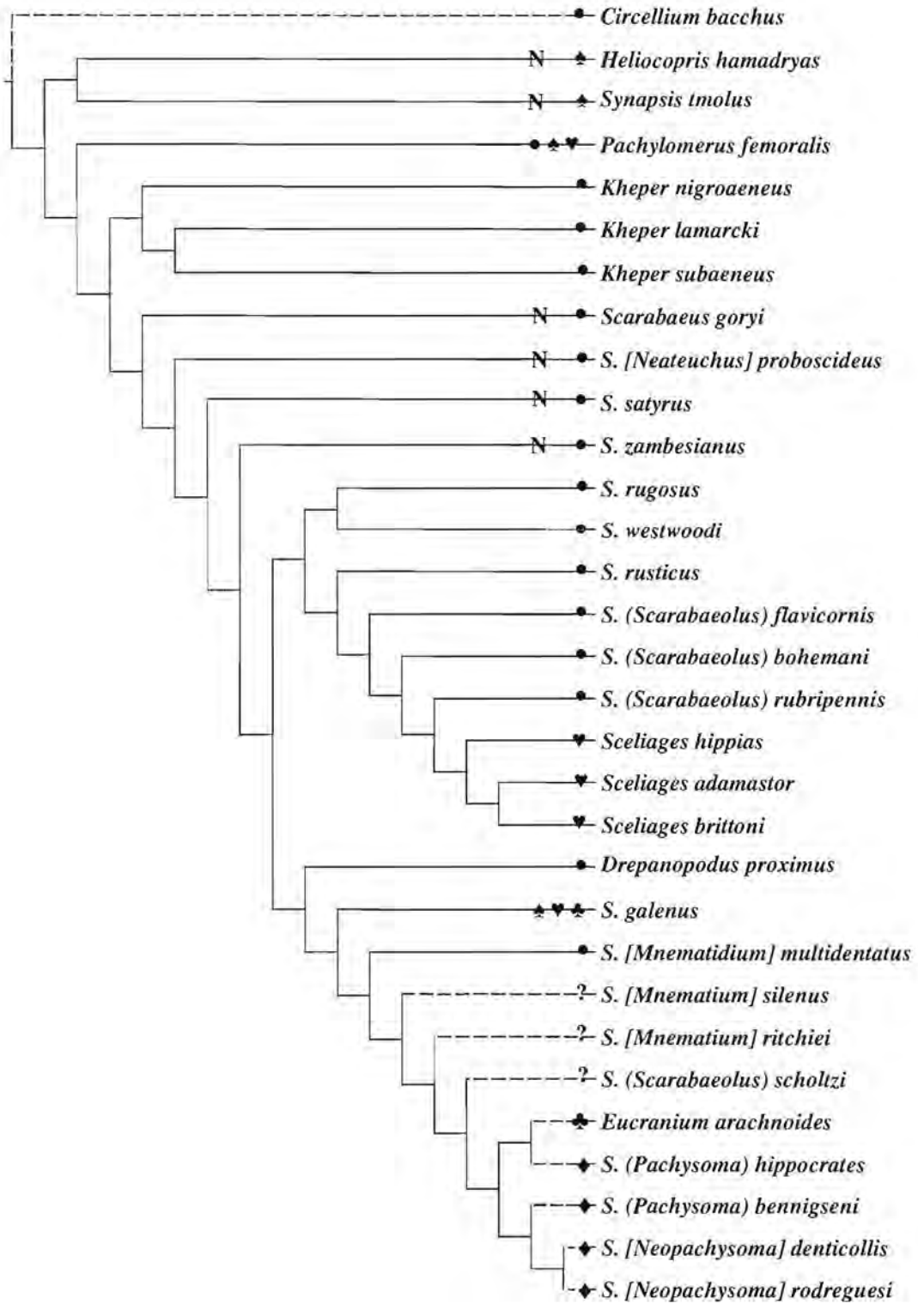

Fig. 5. Phylogeny of the Scarabaeini (Coleoptera: Scarabaeidae). Flight and flightlessness characters deactivated. PIWE (Parsimonious Implied Weights), single tree (CI = 0.24, RI = 0.49, fit = 1081.5, length = 1684 steps), CO = 5; minimal weighting against character homoplasy. Flightless taxa (dashed 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.

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.

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.

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 postocciputal 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) scutelium > 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).

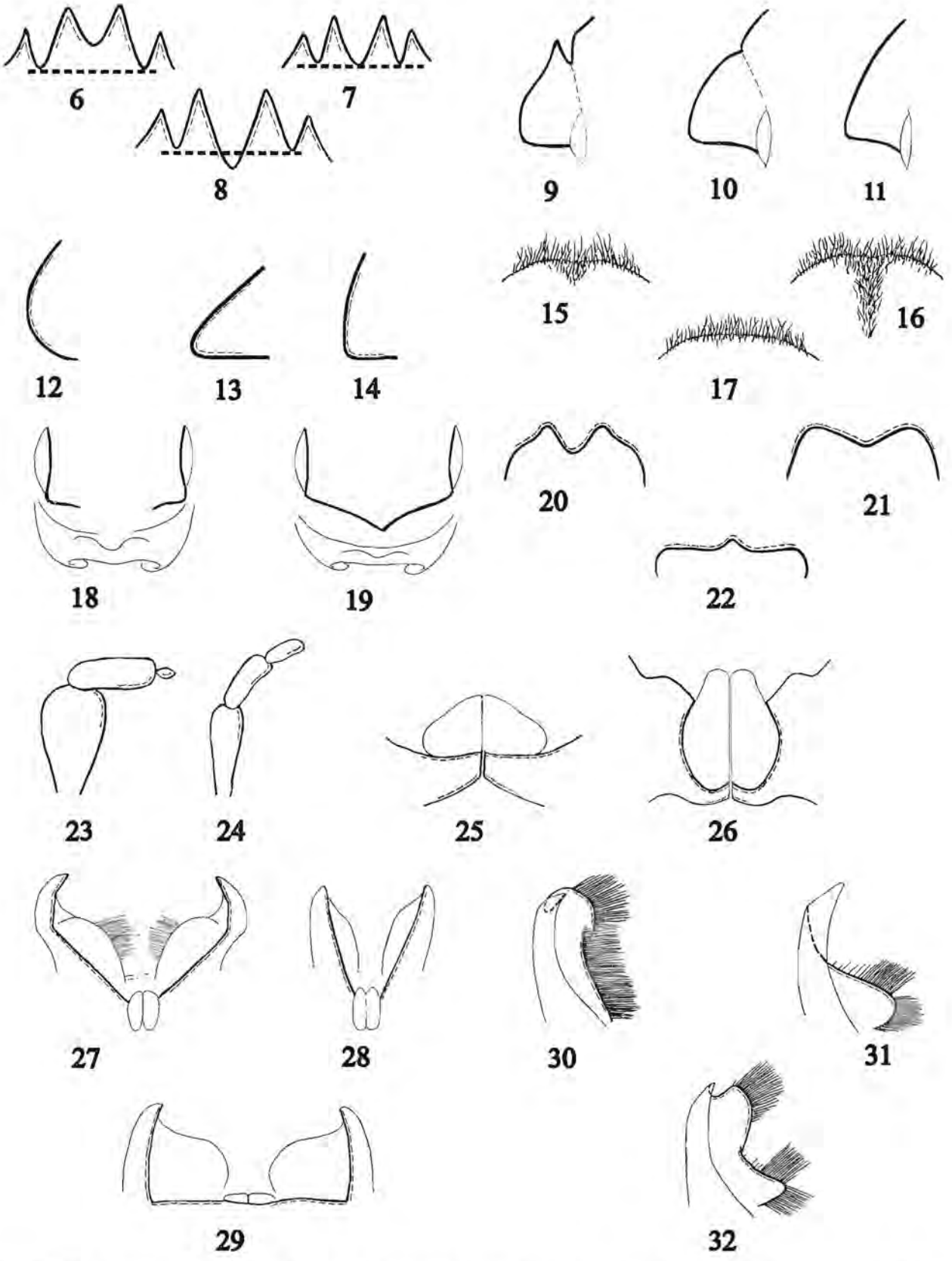
233. *Dorsal anterior margin*: (0) emarginate medially (Figs 145,147); (1) even, unmodified (Fig. 146).
234. *Anterior medial invagination*: (0) markedly developed, distinct (Figs 145,147); (1) slightly developed, indistinct (Fig. 146); (2) absent.
235. *Anterior medial invagination*: (0) completely 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

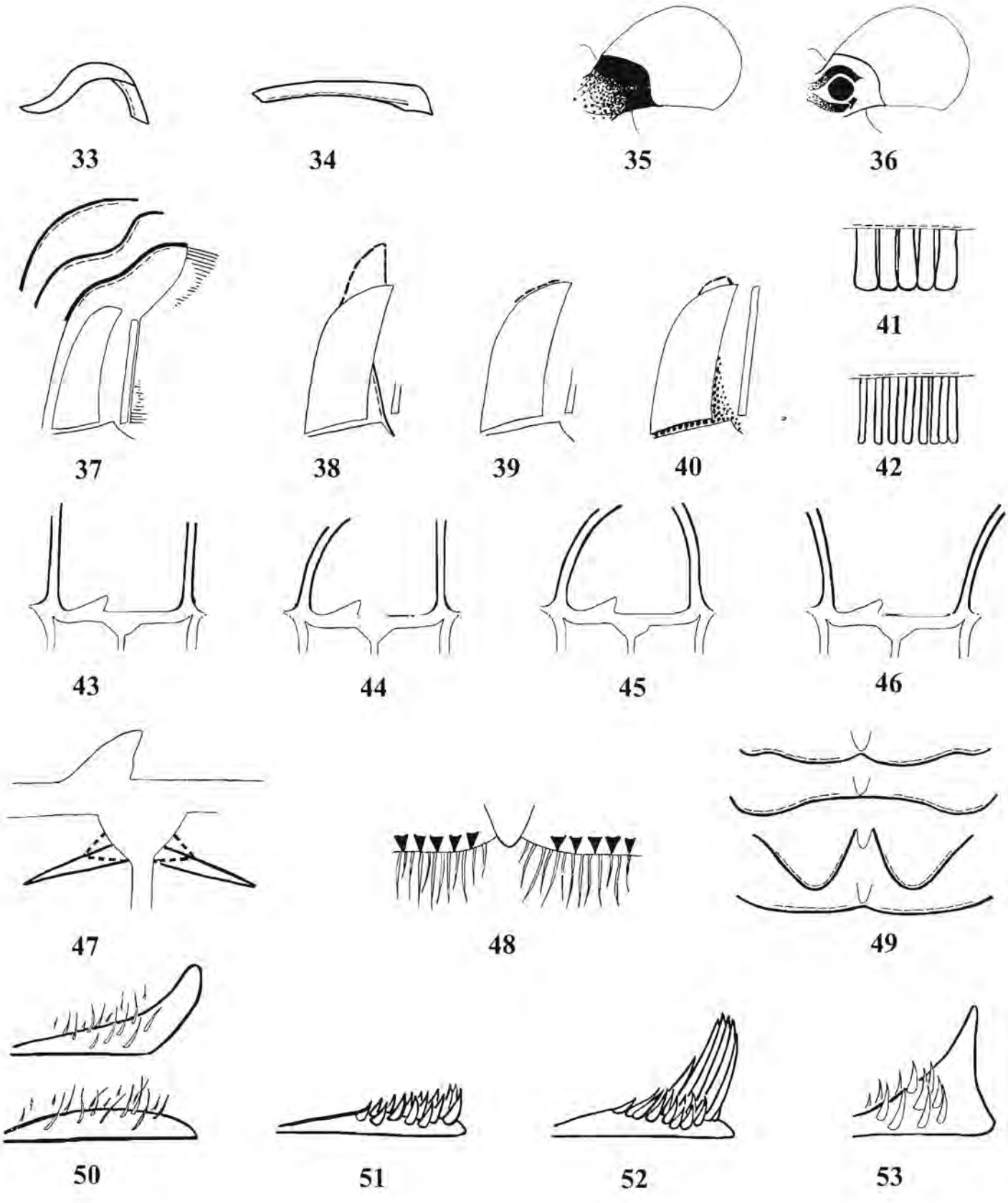
239. *Position of paramere relative to basal piece (lateral view)*: (0) obliquely angled; (1) acutely angled; (2) slightly angled to straight.
240. *Paramere shape (lateral view)*: (0) distinctly tapering to a point with evenly rounded on dorsum of posterior apical margin; (1) tapering to a point, markedly 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).



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).

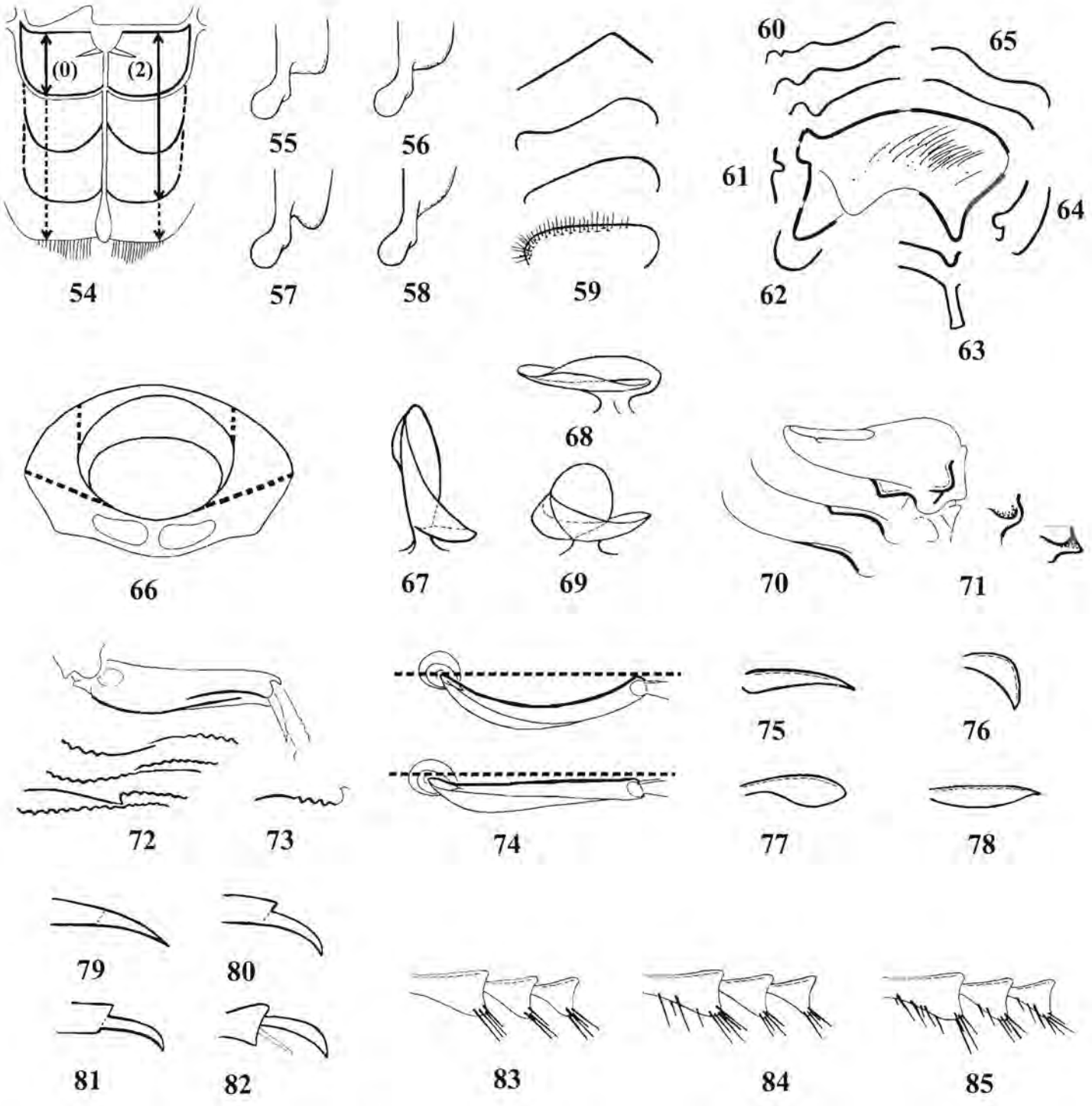
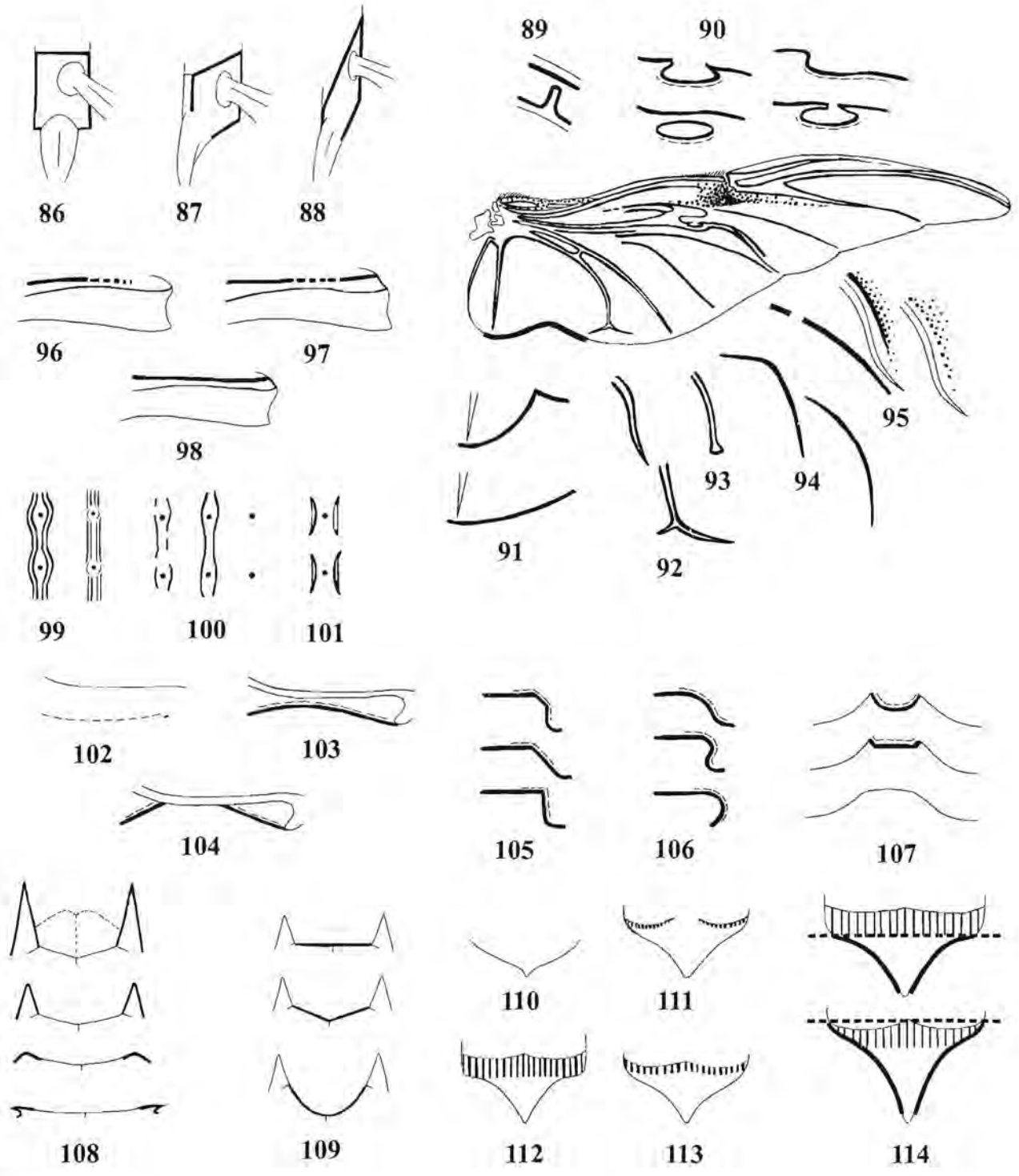
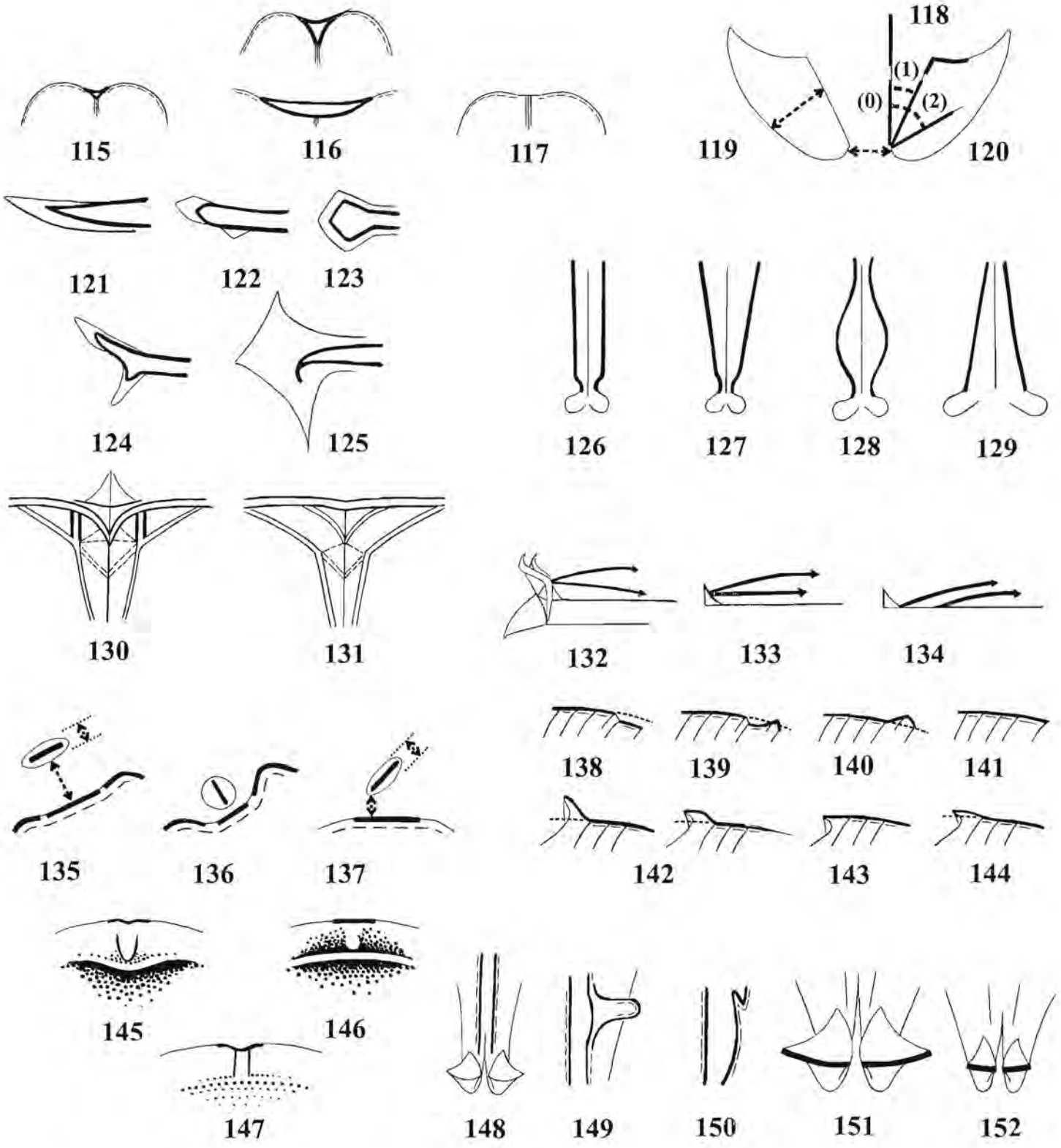


Fig. 54. Epipharynx Character 62(top to bottom; 0,2,1). **Figs 55–58**. Antennae Characters. Fig. 55- Chars 24(0), 25(0); Fig. 56- Chars 24(1), 25(0); Fig 57- Char. 25(1); Fig 58- Char. 25(2). **Figs 59–65**. Neck Sclerite Characters. Fig. 59- Char. 72(outwards; 0,1,2,2); Fig. 60- Char. 74(outwards; 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	1111111111222222222233333333334444444445 01234567890123456789012345678901234567890123456789
Circellium bacchus	00130311212001100200001112201000000010210021?010110
Heliocopris hamadryas	23-2-01--02000010002-012120010020000101000000110110
Synapsis tmolus	00120310201201210202-010121010010100012100000110111
Eucranium arachnoides	11110131012012210010011012101002000010021020110100
Drepanopodus proximus	11020201110202221012100000002001201000121021011110
Kheper lamarcki	12000201000212200201110000010102111010200111111110
Kheper nigroaeneus	12000201000211200202110002110201111010200111011110
Kheper subaeneus	1200020100021120020?110000110202111010100112111110
S. [Mnematidium] multidentatus	12020223101112200010200011002002210010101001?011100
S. [Mnematium] ritchiei	11010122110201201100201000111002201010211000?000000
S. [Mnematium] silenus	11020123010111121110210??111002201000121002111010
S. [Neateuchus] proboscideus	12020130000101222112112011002202200010020121011011
S. [Neopachysoma] denticollis	11110320111110022100112212001000001010010021110110
S. [Neopachysoma] rodreguesi	02110120211010022100011212001000001000021020?001100
S. (Pachysoma) bennigseni	11111221111110012100112202001000000011001020110100
S. (Pachysoma) hippocrates	00110320201101210210011202001000000000021020?001000
Pachylomerus femoralis	12021111110002120100110012010101010010210100?010110
S. (Scarabaeolus) bohemani	11031200010101221001201210012101111101120111110011O
S. (Scarabaeolus) flavicornis	11031200010001212101101112012101111010210111011O111
S. (Scarabaeolus) rubripennis	11121200110102022111101010012101111110210111110011
S. (Scarabaeolus) scholtzi	11122131111100012210201O??111011001101100121100100
Scarabaeus galenus	01120133200201100211210012202000100010201022111011O
Scarabaeus goryi	12030101000101020000110011002201111000120112011011O
Scarabaeus rugosus	12020222010201221000110000112111111010201112111110O
Scarabaeus rusticus	12030222000201221010200110112101211010200112111110O
Scarabaeus satyrus	11020102000102021012112010102201111010201112011111O
Scarabaeus westwoodi	12000230000201120001210010102102111010210111011011?
Scarabaeus zambesianus	12000121000101122112112011002201111010?001220110101
Sceliages adamastor	01132100200000222100100112110211201112001111100111
Sceliages brittoni	01132100200000222100101112010211211112001111100111
Sceliages hippias	0113210020100002210010117001021120110112011111001111

Taxa/Character	1 55555555566666666667777777777888888888899999999990 12345678901234567890123456789012345678901234567890
Circellium bacchus	00011013010000101110122003000011311000102020110110
Heliocopris hamadryas	10000102200112100102020212020011201002130221110111
Synapsis tmolus	10000111001111100111022103000001201002131021110110
Eucranium arachnoides	32210012202012202020l?001100101131210011102101211O
Drepanopodus proximus	01000001111200203222011112011220111012011110011001
Kheper lamarcki	00001000111211100102201100011101011022011120101110
Kheper nigroaeneus	01001002010011103102202100111211111022110220111120
Kheper subaeneus	00001002100211100102202100111101011022111110111110
S. [Mnematidium] multidentatus	320000011?2101310021011002011101011112011110112000
S. [Mnematium] ritchiei	02100111002201313020011010011010112132011210012102
S. [Mnematium] silenus	02000111110101303021011003111100311112011210112100
S. [Neateuchus] proboscideus	10001012110101101112100113121220211030110100111100

Appendix 3 *continued.*

Taxa/Character	1 5555555556666666666777777777888888888999999999990 1234567890123456789012345678901234567890123456789012345678901234567890
S. [Neopachysoma] denticollis	12212003002012002020100302012110312152022020012001
S. [Neopachysoma] rodreguesi	12212003102012002020101311012000310152022020012001
S. (Pachysoma) bennigseni	12211003102212002020101311101111312131022020012102
S. (Pachysoma) hippocrates	12212001102012102020111311101011312152002120012112
Pachylomerus femoralis	31000002011101101222001102001001211021010200000121
S. (Scarabaeolus) bohemani	01002101?011011011111011000210201110500 10?21111102
S. (Scarabaeolus) flavicornis	01002111101101101112001100121210111012010121111122
S. (Scarabaeolus) rubripennis	01100101100101101112112002111220111050010220001101
S. (Scarabaeolus) scholtzi	01002103011202303112000303121010112112?11010012021
Scarabaeus galenus	11000001111211303022 1?11131111010110321102111 2001
Scarabaeus goryi	00000100011111201110002110011121211011110111111110
Scarabaeus rugosus	00000001001211003102201110111020111042000220111122
Scarabaeus rusticus	01000111000101101112212200121020111010110110111101
Scarabaeus satyrus	00001101011201203111000310221221111031110211011122
Scarabaeus westwoodi	?00000100010110311200001200110011103210021111 2120
Scarabaeus zambesianus	11000002111201103112001310011121111030010120111120
Sceliages adamastor	00111112202200101112101202011021011010110221103020
Sceliages brittoni	00111112202 2?0101102101202011020011010110221103021
Sceliages hippias	00112112202000103102101200020021011010110221113010

Taxa/Character	11111111111111111111111111111111111111111111111111111 00000000011111111112222222222333333333344444444444445 12345678901234567890123456789012345678901234567890123456789012345678901234567890
Circellium bacchus	10021112102013121111301132000031001102100201 1----0
Heliocopris hamadryas	10021112012203021211301032010211001100200201 01-101
Synapsis tmolus	10021112012203021101001032010201000112200201 01-101
Eucranium arachnoides	11001112112203100111002132011030 2-00201112101----0
Drepanopodus proximus	10001100110112122030120-000102311111210210100 01201
Kheper lamarcki	30210011102222211121220-101110321111100201010 00121
Kheper nigroaeneus	10211000102222311121220-101210321111000202010 01121
Kheper subaeneus	30210011102222211121220-101110321011000202010 01021
S. [Mnematidium] multidentatus	00001000110120100010121-201100310010102 2?2101-121
S. [Mnematium] ritchiei	01001100110121232121220-201102310001112201021----1
S. [Mnematium] silenus	01001100110121232011211-200202310000122200001----1
S. [Neateuchus] proboscideus	10001000112112100031221-200102310100110210120 00111
S. [Neopachysoma] denticollis	02101100112121200320322-301101300100201212101----0
S. [Neopachysoma] rodreguesi	02101100112121200320322-300113100110222212101----0
S. (Pachysoma) bennigseni	00001112110021300020122-301101300100201210101----0
S. (Pachysoma) hippocrates	12101102110011211020122-310113100111202110101----0
Pachylomerus femoralis	20000111110010100220120-211202010101222100000 00121
S. (Scarabaeolus) bohemani	10001001100011113031111021100331001111210201 01-121
S. (Scarabaeolus) flavicornis	10001112100011133031111021020231001122210102 01-111
S. (Scarabaeolus) rubripennis	10001101100011133031111020120331001111221112 01-121
S. (Scarabaeolus) scholtzi	03001101110021232031 11?020020222000120210?0?1----0
Scarabaeus galenus	10011000110020132110121-211003120011001111120 01121
Scarabaeus goryi	10000011111022211111120-201212110100010202010 01111
Scarabaeus rugosus	10011000100011122011121-201203210011121111020 00221
Scarabaeus rusticus	13001000100011111111121-201003310010121101020 01221

Appendix 3 *continued.*

Taxa/Character	1111111111111111111111111111111111111111111111111111111111 0000000001111111111222222222233333333334444444444445 1234567890123456789012345678901234567890123456789012345678901234567890
Scarabaeus satyrus	10001012100012132011221-20120231010011020102000111
Scarabaeus westwoodi	03011000100220111031120-21100332001020110101001221
Scarabaeus zambesianus	10001112110012232131121-20120211011112020102000111
Sceliages adamastor	10011101110011123121403222010330001022210201000021
Sceliages brittoni	10011101110011123120413222010330001122210201000021
Sceliages hippias	10001102110011112111103021020131001120210201001121

Taxa/Character	1111111111111111111111111111111111111111111111111111111112 5555555556666666666777777777888888888899999999990 1234567890123456789012345678901234567890123456789012345678901234567890
Circellium bacchus	------5----021111022011120012311011010010111010201
Heliocopris hamadryas	1102225013202001100211002010214100000001001000010--
Synapsis tmolus	1112125013002101202113100010214100000000010000101
Eucranium arachnoides	------5----33-11101110-0-00123--11101?0111201120--
Drepanopodus proximus	2001101011102022002023010120223100020102101010120 0
Kheper lamarcki	3111100013112000122023010120002201020000101010120 1
Kheper nigroaeneus	0111210013102010022012110110111 20?0100000000101101
Kheper subaeneus	3111203012112000122013012120003200020102101010110 1
S. [Mnematidium] multidentatus	2010101000211022112013012130123000020001001021220 0
S. [Mnematium] ritchiei	------51---2211111101211113122221110110000112121 10
S. [Mnematium] silenus	------51---2011102013111031213211101101001121211 0
S. [Neateuchus] proboscideus	1100115113012002010022111110101001020002000020121 0
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	2010002102102000002022111130011101010100000100211
S. (Scarabaeolus) flavicornis	2010112100002022002022111130112107010200001012 10
S. (Scarabaeolus) rubripennis	2012112102102020002012111120110101011101001010121 0
S. (Scarabaeolus) scholtzi	------5----22111010020110112 3--1110111-10211020--
Scarabaeus galenus	1100112013200000110003010120100000010000000020110 0
Scarabaeus goryi	0010215111212000000003000110113200020000000010110 0
Scarabaeus rugosus	2110111010200002031022111120011200010100000020020 0
Scarabaeus rusticus	2110114011201000001022111130013007010200001002 01
Scarabaeus satyrus	1010111011212010000022111130014000011101001010110 1
Scarabaeus westwoodi	2100201101200000112022010130103001010102000021120 1
Scarabaeus zambesianus	2100201101200000112022010130103001010102000021120 1
Sceliages adamastor	2100111000202010012012110130123100010101000010 00--
Sceliages brittoni	2100111011102010012012100130123000010100000010020 1
Sceliages hippias	2110111000102000012012110110103201010101000010 00--

Appendix 3 *continued.*

Taxa/Character	22222**2**22222222222222222222222222222222222222
	00000**0**0001111111112222222222333333333344444444
	12345**6**78901234567890123456789012345678901234567
Circellium bacchus	0-211**0**2310-322---2000011010110100010021110000**1**
Heliocopris hamadryas	0-200**0**2222010020200001220130021002022100011**0**0
Synapsis tmolus	??201**2**0220-3?00102000110210201200020020000110**0**
Eucranium arachnoides	10211**0**23212?2012220122203011210010100200001**0**02
Drepanopodus proximus	22000**2**0322001011020101102011102111000010000001
Kheper lamarcki	21011**2**0100101011001112200012100011002111000001
Kheper nigroaeneus	21000**2**0100100001021102100010000001000011110021
Kheper subaeneus	21011**2**0100000001?1102000013100001202101000011
S. [Mnematidium] multidentatus	22000**2**0322210000011010000001212011102210111?0?
S. [Mnematium] ritchiei	22001**1**1002011011020110012001012111001200111?0?
S. [Mnematium] silenus	22001**1**132011201?2111000021012120112002101111?0?
S. [Neateuchus] proboscideus	20100**2**0301000013001000122113001011002101111101
S. [Neopachysoma] denticollis	10211**1**1420000111?002100001110112--11110120002
S. [Neopachysoma] rodreguesi	11211**1**24?1001111210010010011101 02--12110120002
S. (Pachysoma) bennigseni	10211**1**0422201011210021010000101011112101121002
S. (Pachysoma) hippocrates	11211**1**14100022---1001000000310100010200012100**2**
Pachylomerus femoralis	22011**0**0122210000011101100113111010202011000**0**?
S. (Scarabaeolus) bohemani	21000**2**0100100011011 0?2212013011101200020121021
S. (Scarabaeolus) flavicornis	22100**2**0312000000011011112012011?1?000020111001
S. (Scarabaeolus) rubripennis	21000**0**0022020000010122202013002111200020001001
S. (Scarabaeolus) scholtzi	101?1**1**2412002112210010112012101011201??????0?
Scarabaeus galenus	21101**2**0202210000001100112112211?11110000111022
Scarabaeus goryi	21100**2**0320100013001000100110110 12--02101110101
Scarabaeus rugosus	11000**2**0322121000101111010012010101011011110001
Scarabaeus rusticus	11000**0**0310000011001111112101000011003020111011
Scarabaeus satyrus	21100**2**0320000012001??0202003100010100101101101
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).

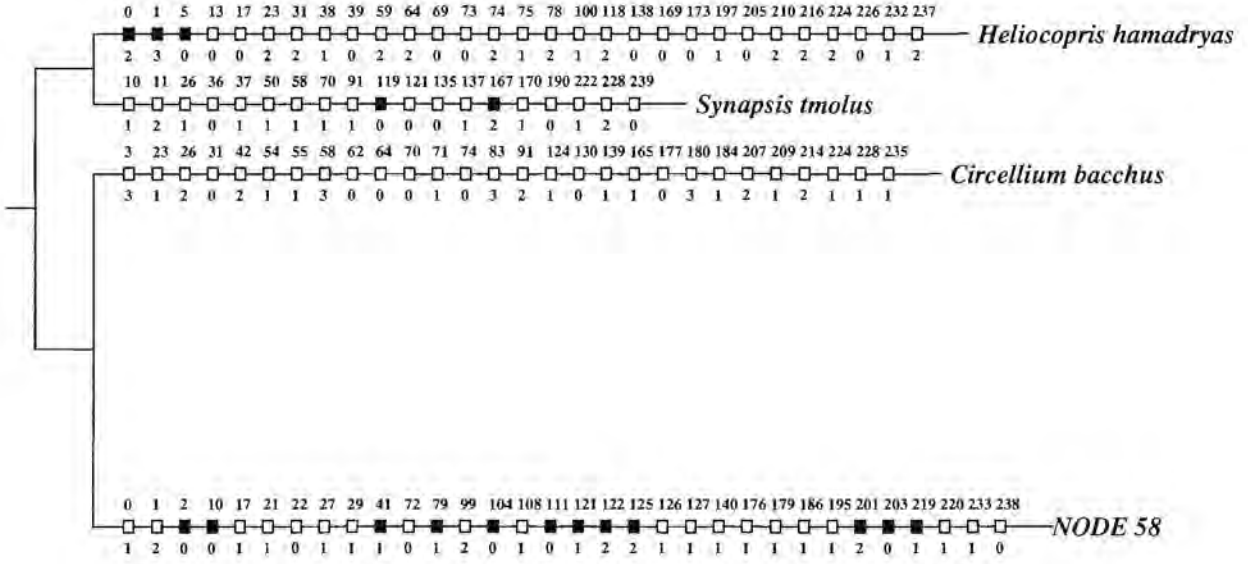


Fig. 153.01. Basal nodes (Rerouted).

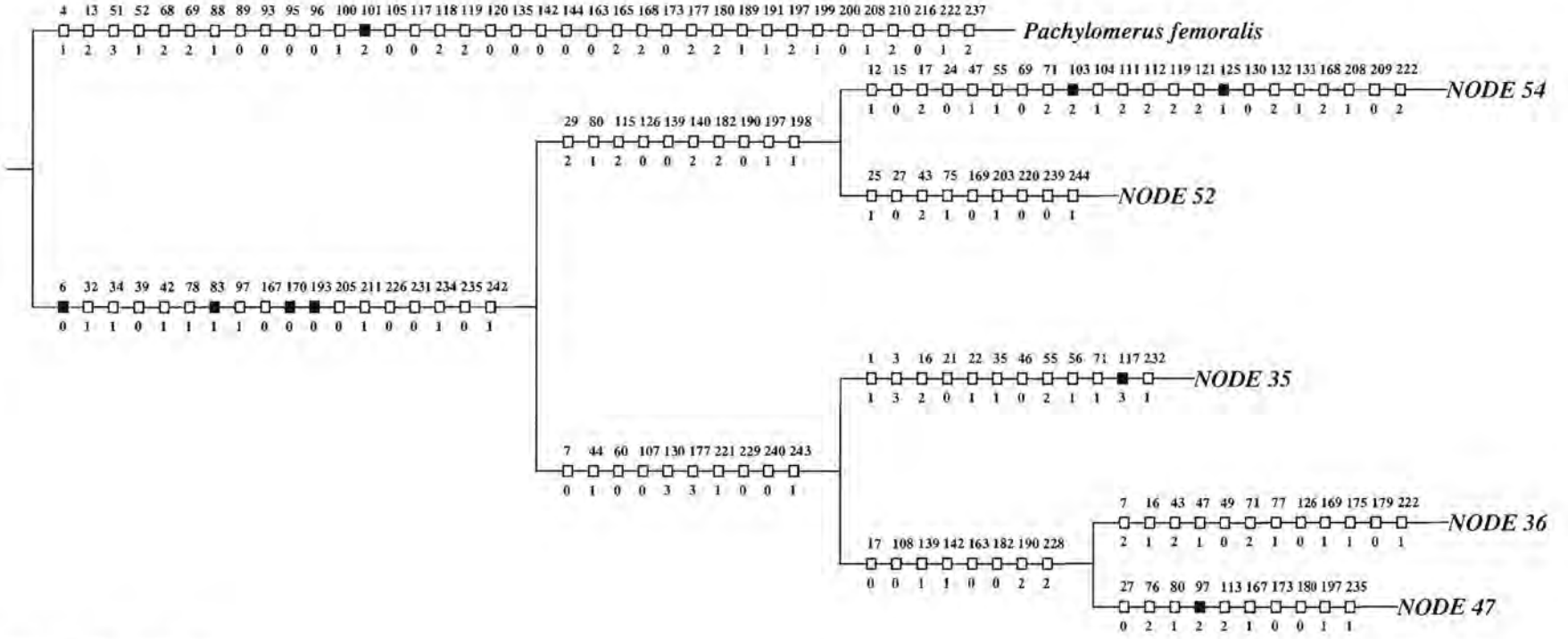


Fig. 153.02. Node 58

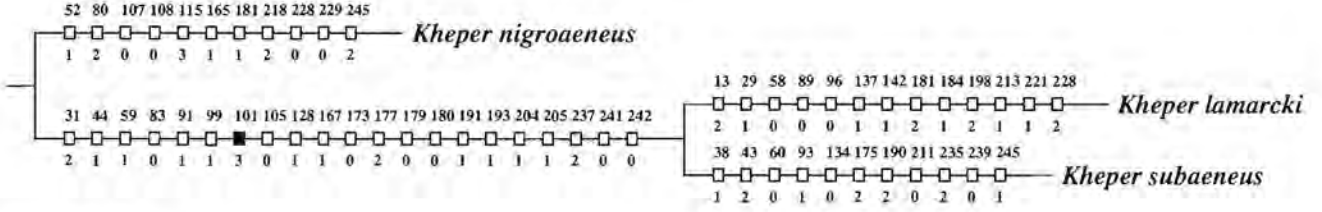


Fig. 153.03. Node 54.

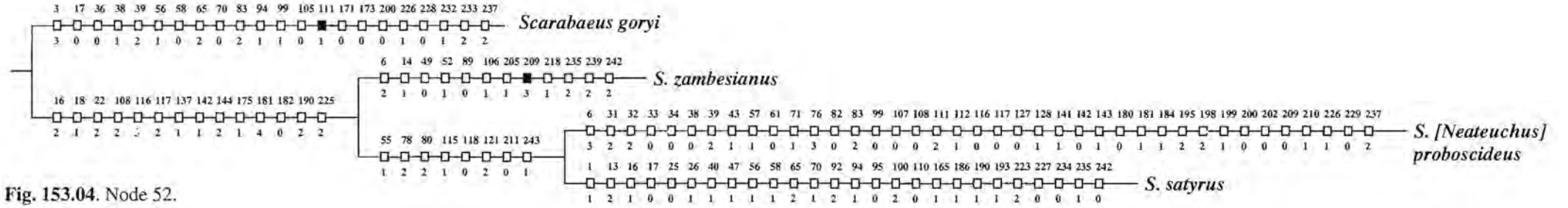


Fig. 153.04. Node 52.

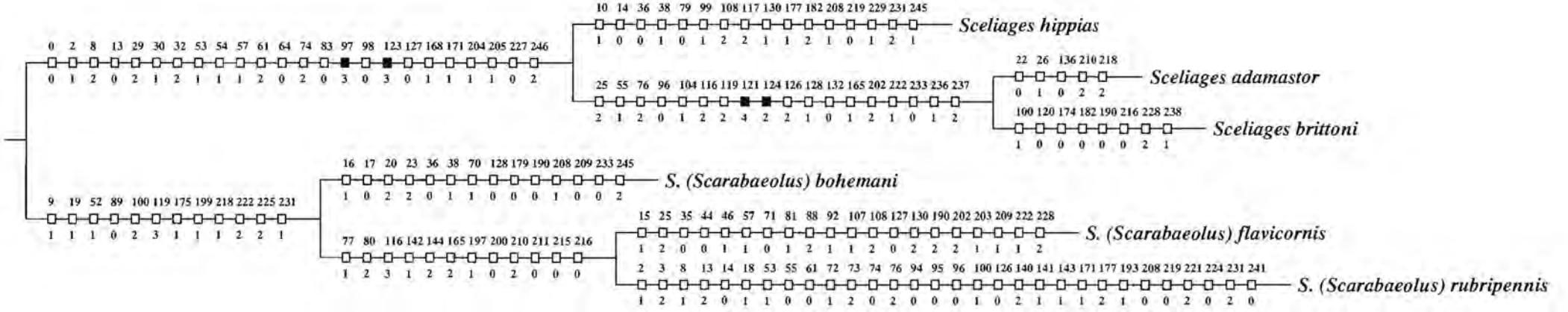


Fig. 153.05. Node 35.

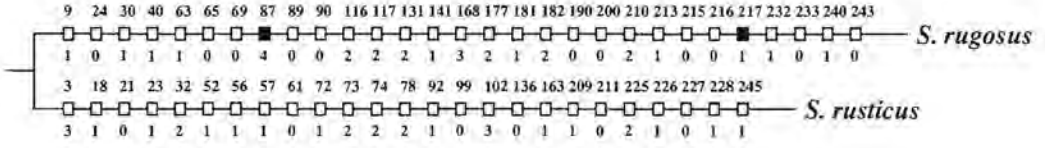


Fig. 153.06. Node 36.

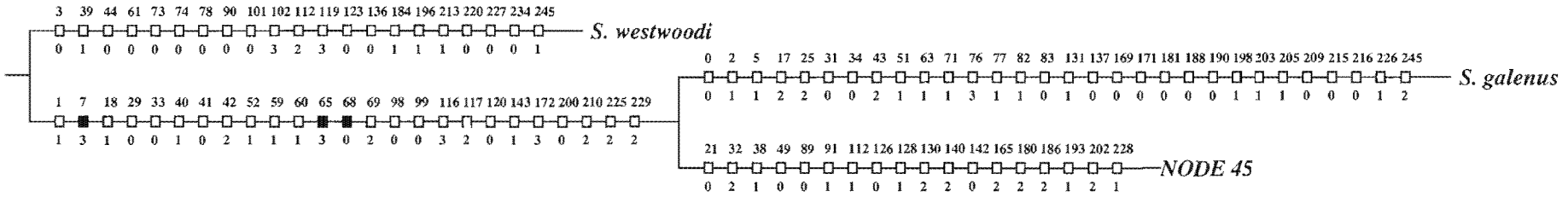


Fig. 153.07. Node 47.

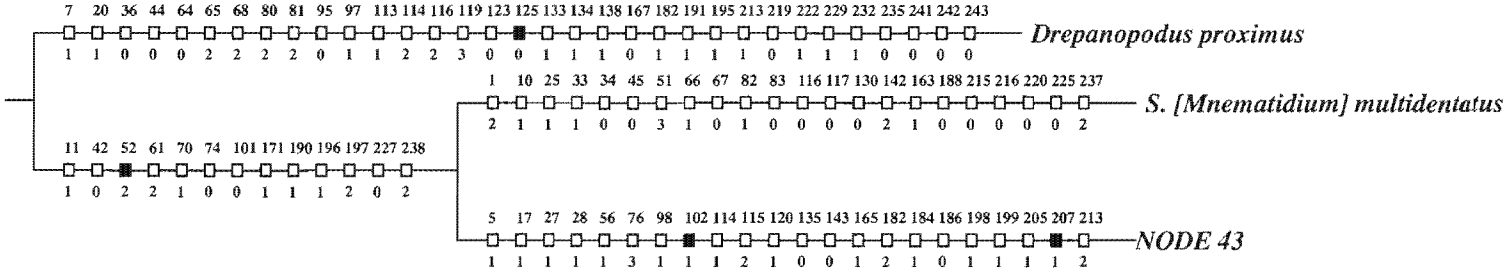


Fig. 153.08. Node 45.

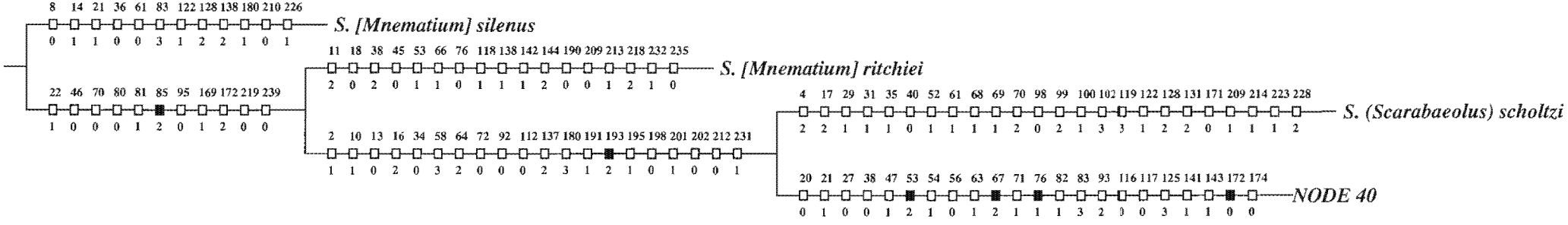


Fig. 153.09. Node 43.

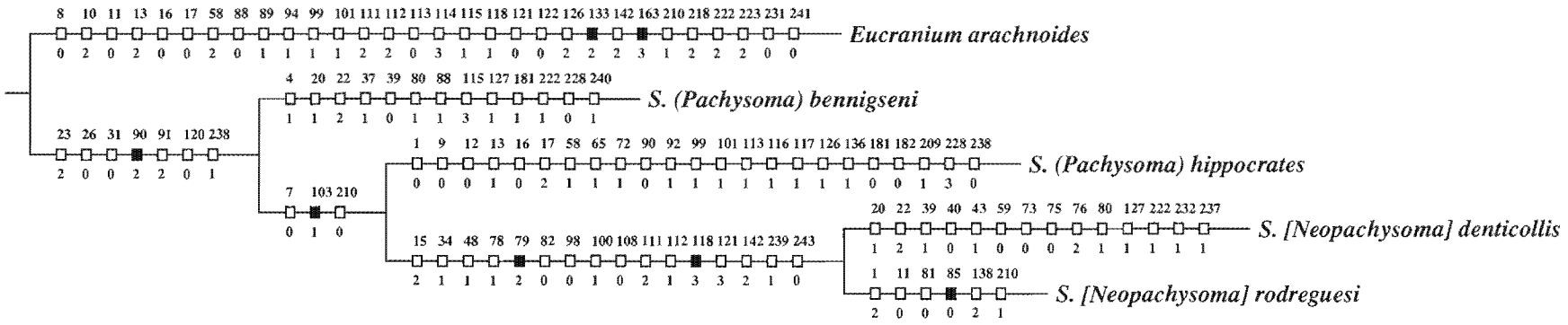


Fig. 153.10. Node 40.

Molecular Phylogenetics and Evolution (2004), submitted

Chapter 3

Phylogenetic Patterns in Multiple Data Sets used for Inferring Relationships among Genera of ball-rolling Scarabaeini (Coleoptera: Scarabaeidae).

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Running title: Phylogeny of the Scarabaeini

Key words: Combined Analysis, Dung beetle, Evolution, CO1, 16S, Morphology, Phylogeny

Abstract

The Scarabaeini is an old world tribe of ball-rolling dung beetles that have origins dating back to at least the mid-upper Miocene (8-18 Million years ago). The oldest classified 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, *Khepera*, who controlled the Sun's daily path across the sky. Yet, despite the notoriety of its members in societies old and new, the tribe has received little to no attention in morphological or molecular phylogenetics. We obtained sequence data from the mitochondrial Cytochrome Oxidase subunit I (1197 bp) and 16S ribosomal RNA (461bp) genes for 25 species of the Scarabaeini in an attempt to further resolve broad phylogenetic relationships inferred from morphology-based hypotheses of the tribe's evolution. Sequence data from both markers along with 216 morphological and 3 biological characters were analysed separately then combined and analysed simultaneously. Results show poorly resolved trees with many of the intermediate and basal nodes forming the backbone of each topology collapsed by low bootstrap values. In concordance with many insect studies involving mitochondrial DNA, many sites in both genes exhibited strong A+T nucleotide bias and high interlineage divergences with transition: transversion ratios reaching saturation. Morphological characters therefore appeared to carry more weight than the molecular data in combined analyses thus increasing their influence on tree reconstructions. Despite extensive topological incongruence, phylogenetic signal was present, however, in a number of well-supported relationships that were congruent between the molecular and morphological data. We investigated conflict and congruence in the data to evaluate if the combined analysis can be considered the most accurate estimate of the tribe's phylogeny.

Introduction

The Scarabaeini comprise a behaviourally advanced guild of Old World beetles within the Scarabaeinae best known for rolling balls of dung. The tribe includes approximately 146 species belonging to the genera *Scarabaeus* L., and *Pachylomerus* Bertoloni, *Kheper* Janssens, *Sceliages* Westwood and the *Scarabaeus* subgenera *Scarabaeus* S. Str., *Scarabaeolus* Balthasar and *Pachysoma* M'Leay. The tribe's origins are thought to date back to the Cenozoic stemming from ancestral lineages that may have appeared in the lower Jurassic ca.180-200 Mya (Million years ago) (Crowson, 1981; Cambefort, 1991a; Scholtz and Chown, 1995). Diversification of these scarabaeoids was thought to coincide with the radiation of both angiosperms (Eocene: ca.50 Mya) and, particularly artiodactyls (lower Oligocene: ca.35 Mya), with a shift from saprophagy and mycetophagy to coprophagy by adults and larvae (Cambefort, 1991b; Scholtz and Chown, 1995. But see Chin and Gill, 1996). While the majority of the Scarabaeini consequently evolved as dung specialists, many of its members also became opportunists in exploiting many types of dung or carrion and some even becoming obligate necrophages. Moreover, the Scarabaeini contain species that are non-rollers (see Halffter and Halffter, 1989) and others that don't roll food backwards but push, drag and carry it forwards.

To date, only morphological character sets have been used in phylogenetic studies to infer inter- and/or intra-generic relationships among members of the Scarabaeini (Mostert and Scholtz, 1986; Barbero *et al.*,1998; Harrison and Philips, 2003). These studies were based on relatively small amounts of data that may have generated inaccurate or biased phylogenetic reconstructions (see Hillis, 1998; Grandcolas *et al.*, 2001). Recent studies of the Scarabaeini (Forgie *et al.*, in press) and the Scarabaeinae (Pretorius *et al.*, 2001; Philips *et al.*, 2004.) were based on large morphological data sets comprising more than 200 characters in an attempt to improve phylogenetic signal and generate more robust hypotheses. Both studies support congruence in the polyphyletic evolution of ball-rolling and feeding behaviours deviating from coprophagy.

However, a high degree of character homoplasy was reported among the scarabaeines (Pretorius *et al.*, 2001; Philips *et al.*, 2004), likely the product of convergent evolution brought about by similar environmental influences (Hillis, 1987).

The advent of Polymerase Chain Reaction (PCR; Saiki *et al.*, 1988) marked a proliferation in the use of sequenced regions within mitochondrial DNA (see, Simon *et al.*, 1994), and more recently, nuclear ribosomal DNA in insect molecular systematics (see, Caterino, Cho and Sperling, 2000). Within the former of these classes, the COI and COII markers have historically proven useful in providing sufficient phylogenetic signal in estimating relationships corresponding to interspecific levels of recent divergence within Coleoptera (e.g. Emerson and Wallis, 1995; Langor and Sperling, 1997; Kobayashi *et al.*, 1998; Cognato and Sperling, 2000) including within the Scarabaeinae (Villalba *et al.*, 2002). In contrast, the highly conserved 3' region of the large ribosomal subunit (16S) of mitochondrial DNA has proven more effective at addressing deep levels of divergence evident among distantly related taxa (DeSalle, 1992; Derr *et al.*, 1992). Similarly, 18S nuclear ribosomal RNA has also been useful for resolving basal relationships in higher level phylogenetic studies (Chalwatzis *et al.*, 1996; Caterino *et al.*, 2002). Given that different genes evolve at different rates and the same gene may have different rates of evolution in different lineages (Lunt *et al.*, 1996), the quest to obtain suitable levels of variability has become increasingly important in attempting to resolve close, intermediate and deep levels of divergence where possible in any phylogenetic study.

Thus, the value of a total evidence approach to utilising multiple data sets and analysing them separately (Bull *et. al.* 1993; Miyamoto and Fitch, 1995), or combined (Kluge, 1998) and analysed simultaneously (Nixon and Carpenter, 1996; Baker and DeSalle, 1997) has become apparent. Indeed, multiple data sets are integral in many phylogenetic studies using molecular markers (Vogler and DeSalle, 1993; Funk *et al.*, 1995; Vogler and Welsh, 1997; Funk, 1999; Mardulyn and Whitfield, 1999; Durando, *et al.*, 2000) and morphology (Lafay *et al.*, 1995;

Whiting *et al.*, 1997; Silvain and Delobel, 1998; Joy and Conn, 2001; Wieblen, 2001; Wiegmann *et al.*, 2002).

An examination of the evolution of flightlessness in the Scarabaeini has been made possible by the inclusion of morphological characters from old and rare brachypterous specimens curated in museums (Harrison and Philips, 2003; Forgie *et al.*, in press). While this current study attempted to obtain amplifiable DNA from these museum specimens for comparative analyses, a major limitation of molecular phylogenetics is realised with the difficulties not only in obtaining uncontaminated DNA of sufficient molecular-weight to amplify but in achieving repeatability (for overview, see Wayne *et al.*, 1999). However, with the development of improved DNA extraction methods and materials, limited success is achievable in the amplification and study of short mitochondrial DNA sequences from museum pinned beetles (Cognato and Sperling, 2000).

For this study, we chose portions of the COI and 16S rRNA mitochondrial genes as likely candidates for simultaneous analyses with and without morphological data to resolve as many of the relationships as possible between the close and more distantly related exemplars of the Scarabaeini. In doing so, we aimed to compare the molecular evolution and phylogenetic utility of these two genes and assess the level of congruence these analyses held with the morphology-based hypotheses of Scarabaeini phylogenetics by Forgie *et al.* (in press). This would then provide for a better understanding of the evolution of ball-rolling, flightlessness, feeding specialisation and relatedness between the Scarabaeini and the morphologically similar eucraniines (see Philips *et al.*, 2002). We then used this combined set of analyses to assess the current classification of the tribe (Forgie *et al.*, in press) in which *Kheper* and *Sceliages* are assigned as subgenera of *Scarabaeus* and *Drepanopodus* lineages synonymised with *Scarabaeus s. str.*

Materials and methods

Taxa

The 27 ingroup taxa used in this study are a majority representation of the exemplars selected by Forgie *et al.* (in press) to represent the most morphologically and behaviourally discordant members in the Scarabaeini (Table 1). Some of these taxa were historically classified into genera (retained in square brackets) that have since become synonyms of *Scarabaeus* (e.g. *Scarabaeus [Neateuchus] proboscideus*). Selectionof the three outgroup species *Heliocopris hamadryas* (Coprini), *Circellium bacchus* (Canthonini), and *Eucranium arachnoides* (Eucraniini) were based on their topological positioning relative to the Scarabaeini inferred in the phylogenetic study of the Scarabaeinae by Philips *et al.* (2004). Moreover, outgroup selection criteria discussed by Nixon and Carpenter (1993) were taken into account. A second eucraniine *Anomiopsoides heteroclytus* was utilised for COI and 16S rRNA sequencing to improve phylogenetic signal of the Eucraniini in an effort to qualify recent tribal analyses based on molecular data supporting convergence as the most likely cause of similar morphology between the eucraniines and scarabaeines (Ocampo, unpubl.).

Morphology

We compared the phylogenetic utility and levels of congruence of the DNA data with a set of morphological characters described in detail by Forgie *et al.* (in press). Two hundred and sixteen adult morphological and three biological characters were utilised for this study. Twenty-eight characters from the original data set directly associated with flight and flightlessness were excluded from this study due to their obvious lack of character independence and potential convergent nature.

DNA preservation and extraction

Apart from the pinned museum specimens listed in Table 1, all other specimens were freshly collected in the field. Larger beetles were either split in half or injected with 96-100% ethanol immediately prior to preservation in order to accelerate the infusion of preservative throughout the body. All material was stored at -20°C and ethanol changed at least twice for each specimen shortly after the initial steps of preservation. One of two methods was used in the extraction of mitochondrial DNA from prothoracic or profemoral muscle of ethanol specimens and tarsi from pinned beetles. Tissue was rinsed in insect Ringer's solution (10xStock pH7.4: 58 mol/g NaCl at 1280mM; 147 mol/g $CaCl_2$ + $2H_2O$ at 15mM; 74.6 mol/g KCl at 50mM), dried, frozen with liquid nitrogen then ground separately in 1.5ml microfuge tubes prior to the extraction of DNA. The first method was based on Chelex DNA preparation protocols of Walsh *et al.* (1991) and Belshaw *et al.* (1999). Approximately 1mg of tissue was added to 100 µl stirred 5% solution of Chelex100® (1-800-4BIORAD, Cat.# 143-2832) and heated to 95-100°C for 15min. Without being removed from the microtubes, homogenised samples were stored at -20°C until required for short term use as templates in polymerase chain reaction (PCR). When required, samples were thawed, vortexed thoroughly and spun down in a centrifuge 14 000 rpm for 3 minutes to separate the Chelex beads from the supernatant. Alternatively, a DNeasy Tissue Kit (Qiagen Inc., Santa Clara, CA) was used for the extraction and long term storage of DNA from pinned and ethanol specimens. The manufacturer's protocol was followed, except for the DNA elution, which consisted of one elution in 150 µl of sterile ddH_2O. For DNA from pinned specimens, this step was increased to two 200 µl elutions of pure water incubated at R/T for 5 min. Both eluates of each specimen were then combined and spun in an evaporator to increase concentration of the overall DNA yield.

Table1. Representative ingroup and outgroup (in bold) taxa used in this study.

Taxa	Collection Locality	DNA Preserv[n] method	CO1 analysis (Genbank accession number)	16S analysis (Genbank accession number)	Morph[y] analysis	Combined analysis
***Circellium bacchus* Fabr.**	E Cape, SA	EtOH	AF499750	AF499690	✓	✓
***Heliocopris hamadryas* (Fabr.)**	NW Prov., SA	EtOH	AF499751	AF499691	✓	✓
***Eucranium arachnoides* Brullè**	Mendoza, Arg.	EtOH	AF499752	AF499692	✓	✓
***Anomiopsoides heteroclytus* (Blanchard)**	La Rioja, Arg.	EtOH	AF499753	AF499693		
S. [Drepanopodus] proximus (Péringuey)	Namib Des., Nam.	EtOH	AF499754	AF499694	✓	✓
S. (Kheper) lamarcki (M'Leay)	Gauteng, SA	EtOH			✓	
S. (Kheper) nigroaeneus (Boheman)	Gauteng, SA	EtOH	AF499755	AF499695	✓	✓
S. (Kheper) subaeneus (Harold)	N Prov., SA	EtOH	AF499756	AF499696	✓	✓
S. [Mnematidium] multidentatus (Klug)	Palestine	Pinned			✓	
S. [Mnematium] ritchiei M'Leay	Tripoli, Libya	Pinned			✓	
S. [Mnematium] silenus Gray	Sanai Pen., Egypt	Pinned			✓	
S. [Neateuchus] proboscideus (Guérin)	Namaqualand, SA	EtOH	AF499757	AF499697	✓	✓
S. [Neopachysoma] denticollis (Péringuey)	Namib Des., Nam.	EtOH			✓	
S. [Neopachysoma] rodriguesi Ferreira	Namib Des., Nam.	EtOH	Sole *et al.* Unpubl. Seq.		✓	
S. (Pachysoma) bennigseni Felsche	Namib Des., Nam.	EtOH	AF499758	AF499698	✓	✓
S. (Pachysoma) hippocrates M'Leay	Namaqualand, SA	EtOH	AF499759	AF499699	✓	✓
Pachylomerus femoralis Kirby	Gauteng, SA	EtOH	AF499760	AF499700	✓	✓
S. (Scarabaeolus) bohemani Harold	Gauteng, SA	EtOH	AF499761	AF499701	✓	✓
S. (Scarabaeolus) flavicornis (Boheman)	NW Prov., SA	EtOH	AF499762	AF499702	✓	✓
S. (Scarabaeolus) rubripennis (Boheman)	Namib Des., Nam.	EtOH	AF499763	AF499703	✓	✓
S. (Scarabaeolus) scholtzi Mostert & Holm	Chalbi Des. Som.	Pinned			✓	
S. galenus (Westwood)	Kruger NP, SA	EtOH	AF499764	AF499704	✓	✓
S. goryi Castelnau	Kruger NP, SA	EtOH	AF499765	AF499705	✓	✓
S. rugosus (Hausman)	W Cape, SA	EtOH	AF499766	AF499706	✓	✓
S. rusticus (Boheman)	NW Prov., SA	EtOH	AF499767	AF499707	✓	✓
S. satyrus (Boheman)	N Cape, SA	EtOH	AF499768	AF499708	✓	✓
S. westwoodi Harold	Sani Pass, Lesotho	EtOH	AF499769	AF499709	✓	✓
S. zambesianus Péringuey	N Prov., SA	EtOH	AF499770	AF499710	✓	✓
S. (Sceliages) adamastor (Serville)	W Cape, SA	EtOH	AF499771	AF499711	✓	✓
S. (Sceliages) brittoni zur Strassen	Namaqualand, SA	EtOH	AF499772	AF499712	✓	✓
S. (Sceliages) hippias Westwood	NW Prov., SA	EtOH	AF499773	AF499713	✓	✓

NOTE. Key to abbreviations: Desert (Des); Province (Prov.); National Park (NP); Argentina (Arg.); Namibia (Nam.); Somalia (Som.); South Africa (SA). In the taxa column, *S.* is an abbreviation for the genus *Scarabaeus.*

PCR amplification and DNA Sequencing

Primer sequences used for amplification of DNA fragments were obtained from Simon *et al.* (1994). Initial COI sequences comprising 1296 nucleotide bases were obtained by amplifying C1-J-1718 (5' GGAGGATTTGGAAATTGATTAGTTCC 3') in conjunction with the tRNA-Leucine (UUR) primer TL2-N-3014 (5' TCCAATGCACTAATCTGCCATATTA 3'). Over-lapping sequences were generated with C1-J-1718 in combination with C1-N-2329 (5' ACTGTAAATATATGATGAGCTCA 3' with the A in position 12 from the 5' end substituted

with a G for improved primer specificity) and C1-J-2183 (5' CAACATTTATT TTGATTTTTTGG 3') with TL2-N-3014 to yield the 1197 bp segments used in the analyses. The Lunt *et al.*, (1996) primer UEA7 (5' TACAGTTGGAATA GACGTTGATAC 3') was tested in conjunction with TL2-N-3014 for shorter length COI sequences of pinned museum specimens. For 16S rRNA, we obtained 450 bp fragments using the 16Sb2 primer (5' TTTAATCCA ACATCGAGG 3') in conjunction with LR-N-13398 (5' CGCCTGTTTAACAAAAACAT 3') after Vogler *et al.* (1993). PCR reactions contained 2.5 mM of each dNTP ,10x Reaction Buffer, 25 mM $MgCl_2$, 25 pmol of each primer and 1.5 units Super-Therm™ *Taq* (Hoffman-la-Roche, Cat# JMR-801) gave approximately 70-110ng of DNA template. PCR cycle conditions for COI were 2 min at 94°C initial denaturing, 30 sec at 94°C, 30 sec at 48°C and 1min at 72°C for 35 cycles and a final extension of 72°C for10 min. For museum specimens the COI cycle conditions were altered by increasing the annealing temperature to 52°C and the number of cycles to 40. Cycle conditions for 16S were 2 min at 94°C initial denaturing, 20 sec at 94°C, 20 sec at 52°C and 1min at 72°C for 35 cycles and a final extension of 72°C for10 min.

PCR products were visualised by electrophoresis through agarose gels (1xTAE), then cut from the gels and the DNA recovered and purified with a High Pure PCR Purification Kit (Roche Diagnostics Corp.; Cat#1732676) following the manufacturer's protocol. Approximate concentration of the purified product was determined by comparing the intensity of the products to known concentration pGEM vector in agarose gels (1xTAE). Purified PCR fragments were sequenced using the same primers at 3.2 pmol, 2 ul BigDye™ terminator reaction mix (PE Applied Biosystems, Foster City, CA.), 200ng template and the BigDye cycle sequencing conditions provided by the GeneAmp™ PCR system 9700 (PE Applied Biosystems), Cycle sequencing products were precipitated following their addition to 1.5 ml centrifuge tubes containing 3M NaOAc (2 µl), absolute EtOH (50 µl) and ddH_2O (10 µl), then pelleted, dried and sequenced using an ABI 377 automated sequencer. Automated DNA sequences for each species were inspected and corrected using Sequence Navigator® software (PE Applied Biosystems)

with largely overlapping reads from both heavy and light strands. All complete sequences were submitted to GenBank (Table 1). We failed to obtain sufficient repeatable fragments of both the COI and 16S genes for the pinned specimens and they were therefore not used in the phylogenetic analyses of molecular and combined data sets. These species, however, were included in the morphological tree (Fig. 1A) of Forgie, Philips and Scholtz (unpubl.) and served to provide us with an estimate of their relatedness to other members of the tribe and their topological placement in the trees generated in this study.

Alignment and Phylogenetic Analysis

Alignment of COI and 16S rRNA sequences was done using the default parameters of Clustal X (Gibson *et al.*, 1994) taking the theoretical considerations of Gatesy *et al.* (1993) into account. Any ambiguous base(s) appearing in the aligned sequences were checked against several specimens showing nucleotide congruency in the same codon position(s) as viewed in Sequence Navigator. Gaps were coded as missing characters.

In order to gain the best estimates of phylogeny, simultaneous analyses of the data sets individually and in combination (i.e. Morphology + CO1, Morph. + 16S, CO1 + 16S, Morph. + CO1 + 16S) were carried out (Nixon and Carpenter, 1996). All analyses were performed using PAUP* 4.0b10 (Swofford, 1999). Both the eucraniines, *Eucranium arachnoides* and *Anomiopsoides heteroclytus*, were included in theoutgroup to ascertain their relationship to *Scarabaeus* subgenus *Pachysoma sensu lato* (S. L. : incl. *Neopachysoma* [Syn.]) lineages. Unweighted parsimony analyses were based on heuristic and branch-and-bound search options with 100 random additions of sequences and tree-bisection-reconnection (TBR) swapping unless otherwise stated. Neighbour-Joining analyses (NJ; Saitou and Nei, 1987) of the molecular data sets used a randomised input order for the taxa (see Farris, 1995) and employed distances corrected with HKY85 (Hasegawa *et al.*, 1995) which adjusts for variance in transition:

transversion ratios and unequal nucleotide frequencies. COI and 16S rRNA gene fragments operate under discordant molecular constraints (Matthee and Robinson, 1997), evolve at different rates (Lunt *et al.*, 1996) and may accumulate some degree of saturation of substitutions among the nucleotide sites (Mardulyn and Whitfield, 1999). We therefore conducted the following analyses in an attempt to improve the overall phylogenetic signal of the sequence data.

Weighted parsimony analyses

Character reweighting of conserved first and second codon changes against variable third-position changes in the COI sequences was carried out on the basis of the frequency of change for each position within a codon for all taxa using PAUP* (characters were weighted according to the inverse of their variability). Substitution weighting of transversions (TV) relative to transitions (TI) for both COI and 16S rRNA was performed based on the frequencies of the two substitution types calculated using the 'State Changes and Stasis' option counting 100 "equiprobable" random parsimony trees with MacClade's version 3.08 chart menu (Maddison and Maddison, 1992). Since this is likely to underestimate the ratios between more closely related taxa, less conserved ratios were also examined in maximum-likelihood and parsimony analysis. Saturation/homoplasy of molecular data usually occurs as sequence divergence among taxa increases. Its prevalence in the sequence data is measurable by comparing consistency and retention indices (CI and RI respectively) resulting from unweighted parsimony analyses with and without the removal of transitions (see Matthee and Davis, 2001). Transitions were also used to assess levels of saturation/homoplasy among weighted analyses since their removal may not fundamentally increase general levels of resolution or congruence (Vidal and Lecointre, 1998; Broughton *et al.*, 2000). We opted for this method rather than using regression analysis to determine the slope of saturation plots to estimate rates of nucleotide variance in genes (Simon *et al.*, 1996).

Maximum likelihood analyses

Maximum likelihood analyses (ML, Felsenstein, 1981), were conducted on both molecular data sets using the heuristic search option with the as-is addition sequence. We employed the HKY85 + Invariant (I) + Gamma (G) distribution model for the ML analyses which takes into account unequal substitution rates, site rate heterogeneity allowing for a proportion of invariant sites, simultaneously estimating these three variables from the sequence data when the tree(s) are calculated (Gu *et al.*, 1995). A maximum of 100 bootstrap replications were performed due to computational time constraints.

Combined data parsimony analysis

A partition homogeneity test with 1000 iterations and no branch swapping was performed on the combined data to identify possible conflicting phylogenetic signals (Liu and Miyamoto, 1999). Weighting of characters is possible in combined data sets but is prone to subjectivity (Hillis, 1987). We have therefore chosen not to apply weighting in the combined data.

Statistical support

Statistical support for each clade node in all analyses was estimated by bootstrapping (Felsenstein, 1985) with heuristic search, with 1000 iterations, as-is addition sequence and TBR branch swapping. It is worth noting that bootstrapping values should not be strictly interpreted as confidence limits on monophyly (Kluge and Wolf, 1993; Lee, 2000). Rather, they should provide an indication only for the degree of support of a particular clade node, as the values are usually very conservative estimates of the probability that a particular clade is a true historical group (Hillis and Bull, 1993; See also argument on tree robustness and clade significance by Lee, 2000).

Results and discussion

Pinned specimens

All pinned specimens (Table 1) yielded small amounts of DNA which gave limited success being amplified with CO1 primer pairs UEA7 and TL2-N-3014, in addition to C1-J- 1718 and C1-N-2191. Only small portions of sequence were obtained from *Scarabaeus (Scarabaeolus) scholtzi*, and *S. [Mnenatium] ritchiei*. A GenBank BLAST search on the sequences we generated confirmed we had amplified beetle DNA and not contaminant DNA. These sequence fragments possessed varying degrees of background noise and with minimal to no overlapping of complementary sequences, problematic bases were unresolved. Moreover, we were unable to obtain repeatability and with a lack of material to sample decided not to continue. Two suggestions as to why we were unsuccessful came to light, (a) the fragments we were trying to amplify were too long, and (b) the DNA was too old and/or degraded. Similar-sized fragments (~ 400-550 bp) of COI were sequenced successfully from recently pinned specimens (<30 years old) of the genus *Ips* (Coleoptera: Scolytidae) by Cognato and Sperling (2000). By contrast, the rare pinned material used in our study lacked any reliable collection data or dates. Moreover, the method of preservation is unknown and therefore unreliable (Prost *et al.*, 1993). The degradation of the DNA of old pinned specimens, are invariably the product of bacterial activity and the oxidative processes associated with time (Pääbo, 1989). Nonetheless, dry tissues up to 14, 000 years old has been shown to yield short mitochondrial DNA fragments (~100-200 bp) of sufficient concentration for sequencing (e.g. Pääbo, 1989; Roy *et al.*, 1994).

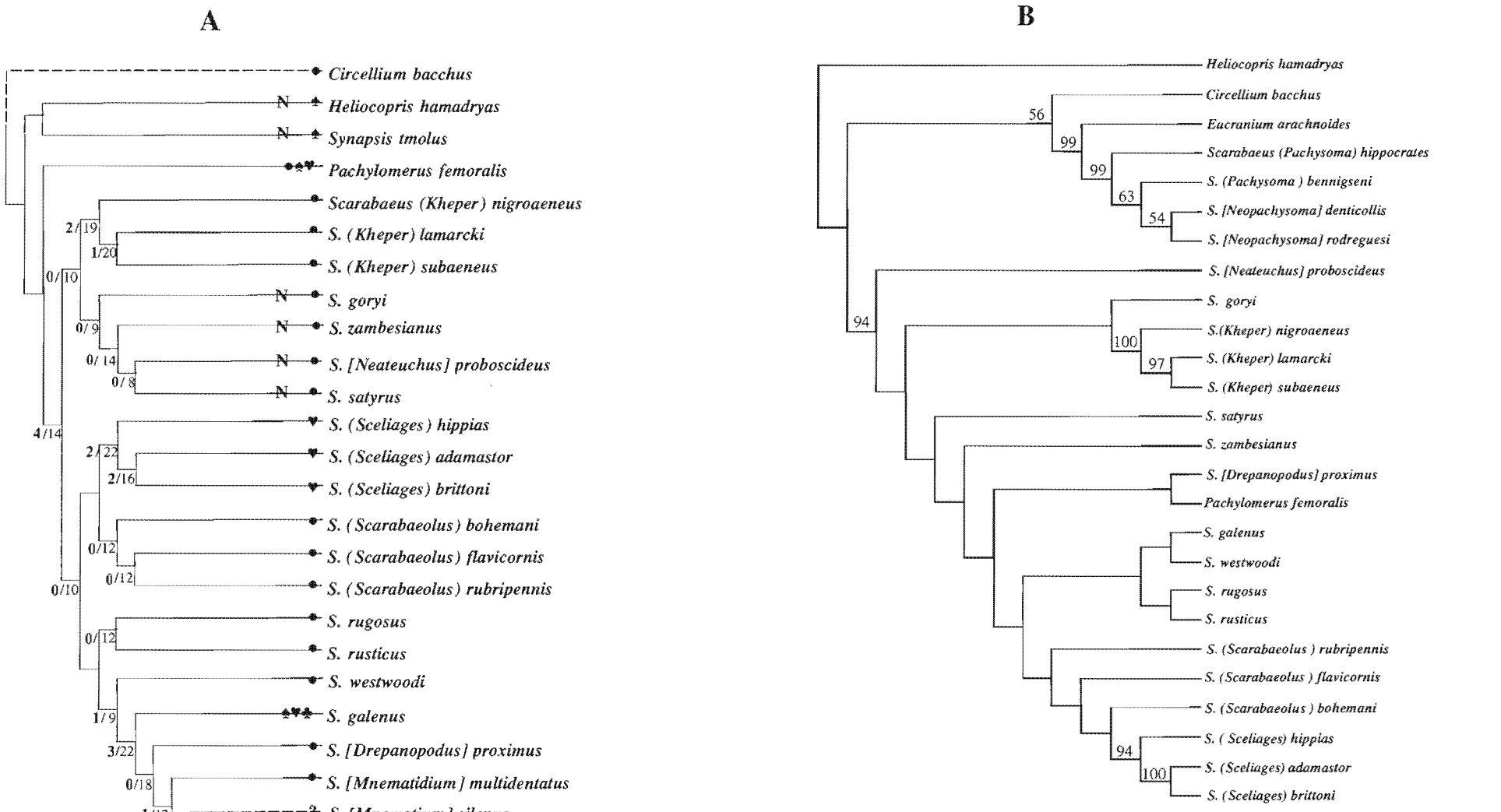

Fig. 1. Morphological Trees based on 216 morphological and 3 biological characters of the Scarabaeini (Coleoptera Scarabaeidae). (**A**) Single PIWE (Goloboff 1997) tree (CI=0.24, RI=0.49, Length =1673) from Forgie *et al.* (in press) following less strong weighting against homoplasious characters with concavity index = 4. Unique synapomorphies (Bold)/homoplasious synapomorphies provided below nodes. Flightless taxa (dashed branches). Nocturnal taxa (N). Modes of food relocation: 'rolling" ●; Tunnelling, ♠; Pushing, ♥; Dragging, ♦; Carrying, ♣; Unknown, ?. (**B**) Single MP tree recovered by heuristic search (CI=0.29, RI=0.51, Length =1336). All characters are unweighted. Bootstrap values above 50% support are given at nodes.

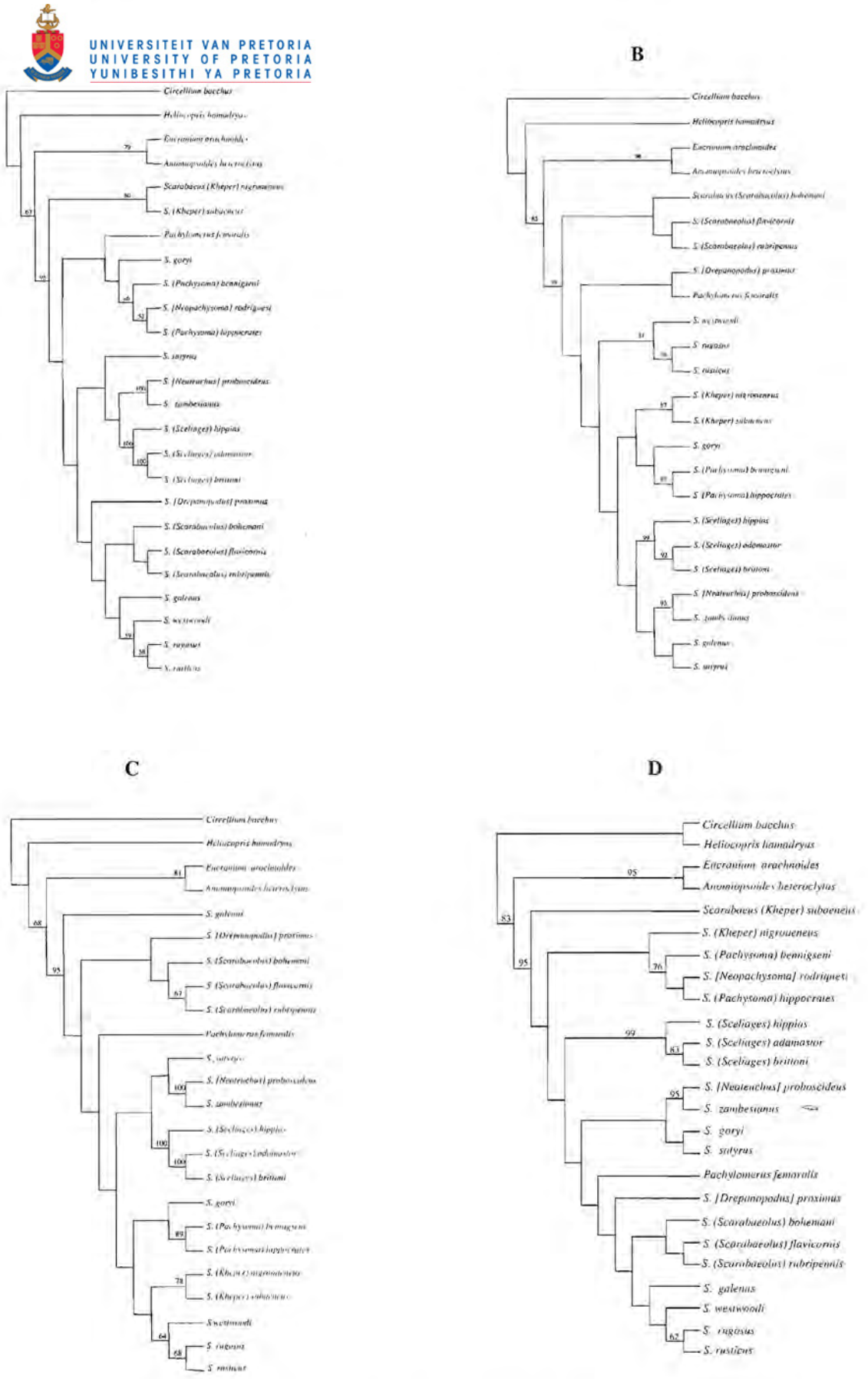

Fig. 2. Analysis of the Scarabaeini based on 1198 nucleotide sequences of the CO1gene of mitochondrial DNA. Single MP tree (A) recovered from heuristic search of unordered, unweighted parsimoniously informative characters. ML analysis with, branch swapping, TBR and 1000 iterations; recovery of single heuristic tree (B). Weighted MP analyses based on heuristic searches following reweighting codon positions 1-3 with a 3:10: 1 ratio respectively (C), and TI:TV = 1.3 weighting scheme (D). Bootstrap values above 50% support are given at nodes on all trees.

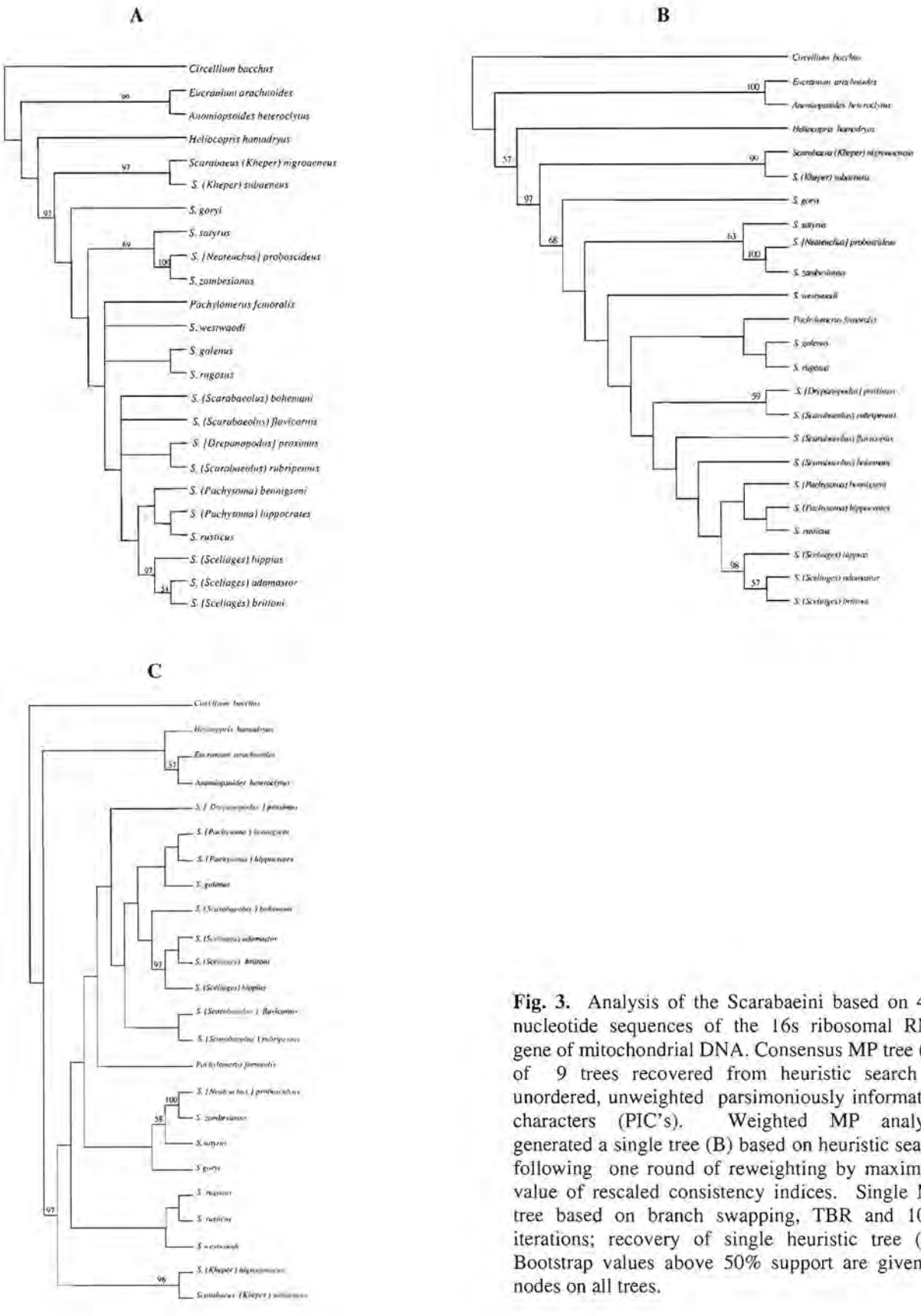

Fig. 3. Analysis of the Scarabaeini based on 461 nucleotide sequences of the 16s ribosomal RNA gene of mitochondrial DNA. Consensus MP tree (A) of 9 trees recovered from heuristic search of unordered, unweighted parsimoniously informative characters (PIC's). Weighted MP analysis generated a single tree (B) based on heuristic search following one round of reweighting by maximum value of rescaled consistency indices. Single ML tree based on branch swapping, TBR and 1000 iterations; recovery of single heuristic tree (C). Bootstrap values above 50% support are given at nodes on all trees.

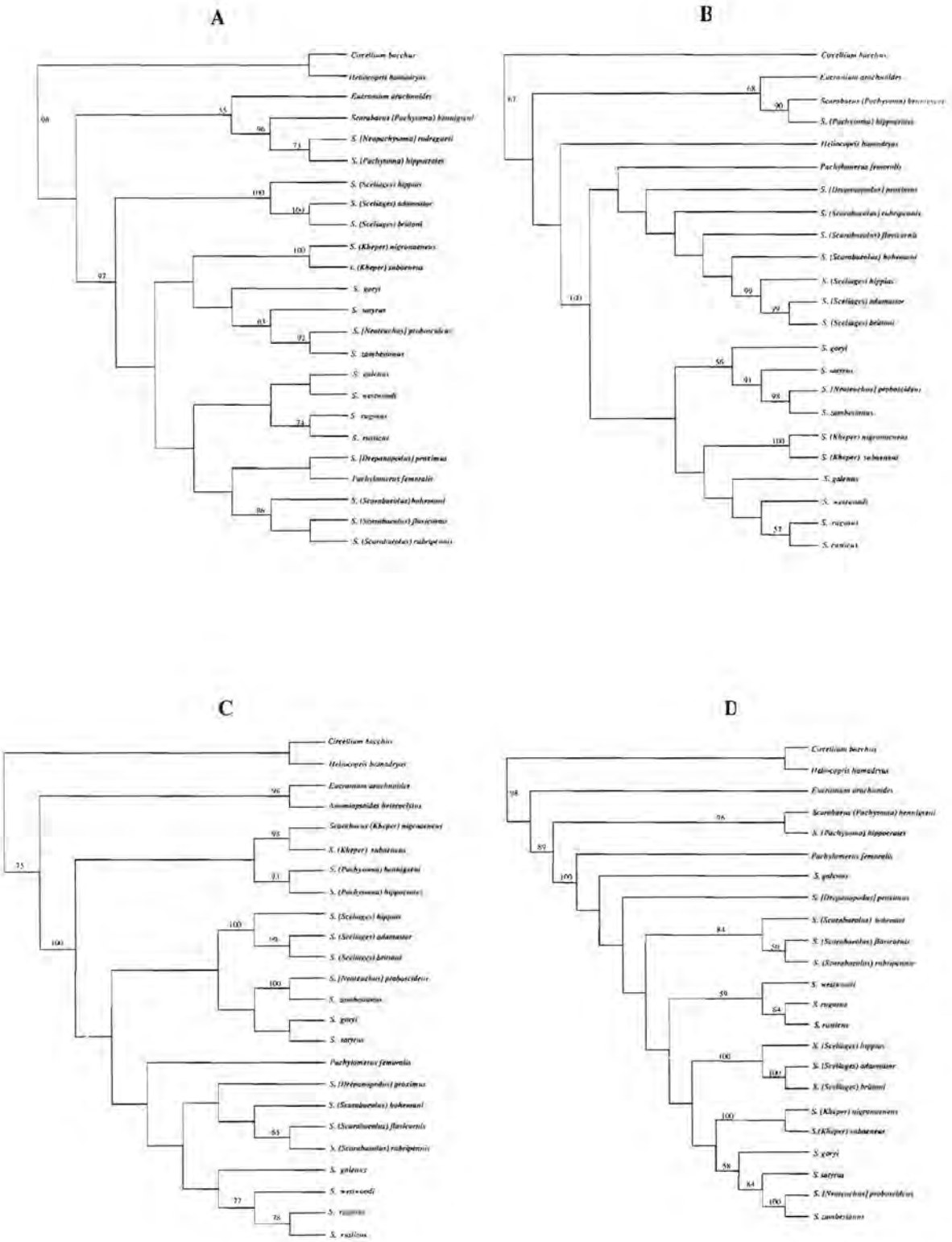

Fig. 4. Combined MP analyses of the Scarabaeini (Coleoptera: Scarabaeidae). Morphological + CO1 mtDNA (A), Morphological + 16S rRNA mtDNA (B), CO1+ 16S rRNA mtDNA (C), and all three data sets combined (D) recovered single tree topologies following Heuristic searches in each analysis. Bias in trees A, B and D towards a morphological topology (Fig. 1A) may be due to more weight being applied to morphological characters than molecular characters or more morphological than molecular characters supporting nodes that are topologically similar to those of the morphological trees. Bootstrap values above 50% support are given at nodes on all trees.

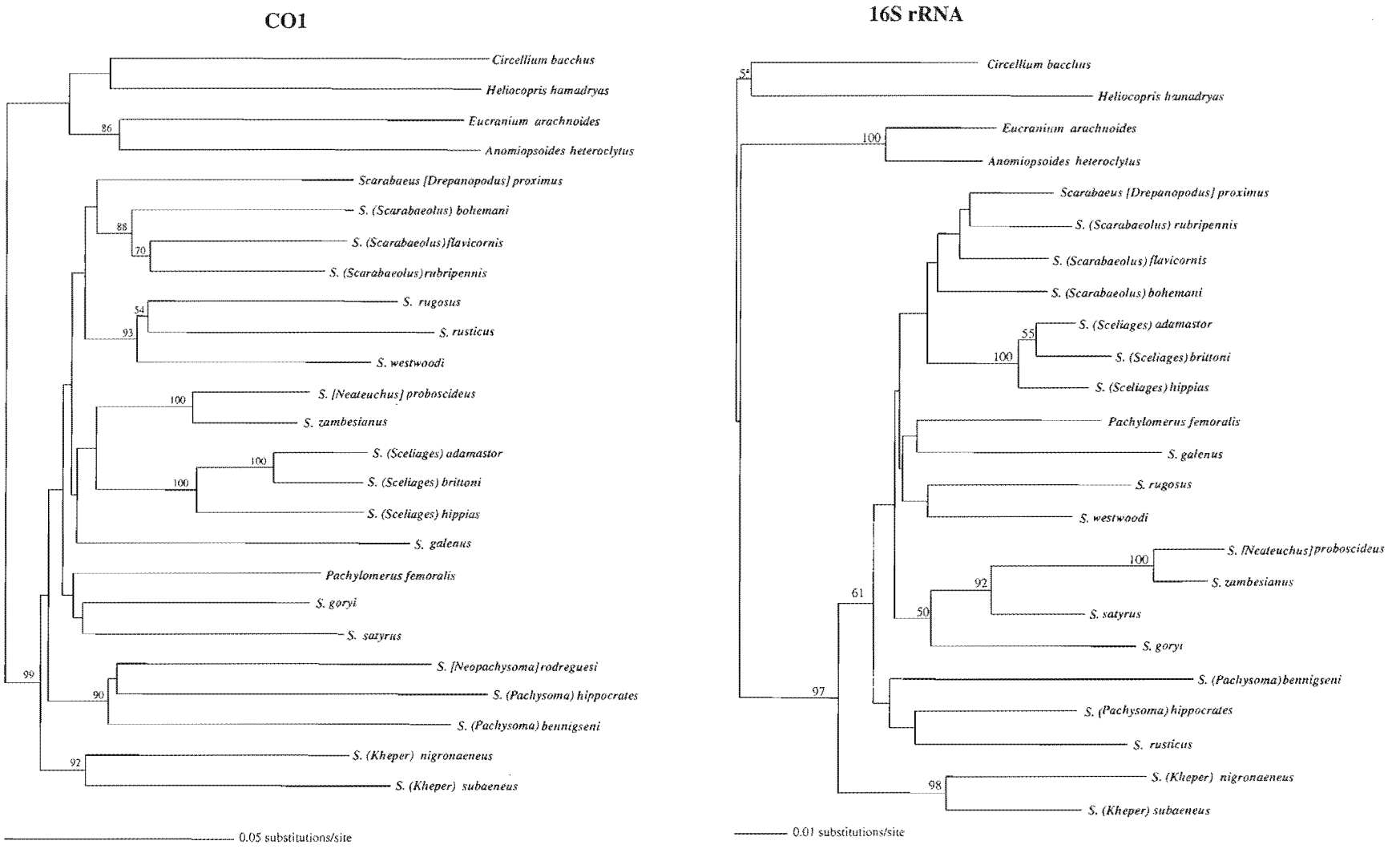

Fig. 5. Phylograms of Scarabaeini COI and 16S rRNA mitochomdrial genes based on Neighbour Joining analysis. Bootstrap values above 50% support are given at nodes. Arrows indicates node from which rapid divergence of the majority of lineages occurs. CO1 NJ trees shows predictably longer branches with greater accumulation of character changes over time than the 16S sequence data for the same taxa.

Morphological Analysis and Characteristics

Unweighted parsimony analysis of 219 characters in the morphological data set with 3 uninformative characters removed, generated a single tree 1336 steps in length (Fig. 1B; CI= 0.29, RI= 0.51). The majority of the relationships were unresolved. An over abundance of character homoplasy is evident in the morphological data (Fig. 1A). Even under the most stringent weighting (concavity indices 1 and 2) against homoplasious characters using PIWE (Parsimony Implied Weights; Goloboff, 1997), complete resolution of the resulting topologies (results not shown) was not achieved by Forgie, Philips and Scholtz (unpubl.).

COI mt DNA Analysis and Characteristics

A 1197 bp region of the mtDNA COI gene from 23 ingroup taxa and 2 outgroup taxa (*C. bacchus* and *H. hamadryas*) contained 480 variable characters (Appendix 1a) including 378 that were phylogenetically informative. The majority of phylogenetic information occurred at the 3rd codon position accounting for the vast majority (71%) of the variability followed by 1st and highly conserved 2nd codon positions (22% and 7% respectively), as seen for example in recent insect studies using COI (e.g. Emerson and Wallis, 1995; Langor and Sperling, 1997; Funk, 1999; Mardulyn and Whitfield, 1999; Cognato and Sperling, 2000, Villalba *et al.*, 2002). Mean base composition across all lineages showed an excess of A (31.7%) and T (39.6%) over C (14.8%) and G (13.9%) in our COI data corresponding to a similar A+T bias occurring at the 3rd codon position recorded in several of the studies cited above including Liu and Beckenbach, (1992) and Juan *et al.* (1995).

Unweighted parsimony analysis generated a single tree (CI = 0.30, RI = 0.34) with a length of 1917 steps (Fig. 2A). Reweighting 1st, 2nd and 3rd codon positions according to site variability also resulted in a single tree (CI = 0.34, RI = 0.37, length = 2904) sharing several topological

congruencies (Fig. 2C). A transversion weighting scheme (TI/TV= 1.3) generated a single tree (Fig 2D; CI = 0.34, RI= 0.35, length =2244.8). Maximum Likelihood analysis with an empirical estimated proportion of invariant sites of 0.49 is shown in Fig. 2 B (Log L score = -9567.485, gamma = 0.628). Although COI sequences yielded many parsimoniously informative characters (Appendix 2), they appear to be plagued by homoplasy due to saturation of the 3rd codon positions (but see Funk, 1999). As a result, approximately half of the tribal relationships depicted in figure 2 were unresolved at a variety of hierarchical levels. Interestingly, COI provided strong support for the deepest nodes that clearly differentiate the Scarabaeini from the outgroup lineages including the two eucraniines (*A. heteroclytus* and *E. arachnoides*).

16S rRNA mt DNA Analysis and Characteristics

Maximum Parsimony and Likelihood analyses were carried out using 461 bp sequences (including alignment gaps) of the 16S ribosomal RNA gene of mtDNA obtained from 22 ingroup taxa and 2 outgroup taxa. One hundred and forty-six characters were variable (Appendix 1b) with 107 of these being parsimony informative. While our analysis did not ascertain whether the majority of character variability occurred in stems or loops, studies by Funk *et al.*, (1995), Matthee and Robinson (1997) and Funk (1999), among others, report general consensus in site variability, A+T bias and indeed saturation being more prevalent in loops than in stems. Our data showed predictably high A+T richness (76%) compared to C (15%) and G (9%) nucleotide frequencies in the variable informative characters. The strict consensus tree (CI = 0.43, RI = 0.50) of nine most parsimonious trees recovered following an unweighted heuristic search is shown in Fig. 3A. This consensus tree contains two sets of tetratomies resulting from the collapse of several poorly supported nodes located medially in the topology. One round of consistency index-based reweighting of the parsimony informative sites (based on the individual character CI's in the nine trees) assigned 15 characters with a weight of 1 and 92 characters with weights less than 1. A single tree (Fig. 3B; CI = 0.52, RI = 0.57, Length = 157) was recovered

some 211 steps shorter than the consensus tree. A Maximum Likelihood analysis based on an empirically estimated proportion of invariant sites at 0.6 is shown in Fig. 3C (Log L score = -2574.429, gamma = 1.628).

Distance Analysis

The presence of many short branches stemming from the more basal nodes in the trees of both COI and 16S NJ trees (Fig. 6) suggests a short time period of rapid radiation of a majority of the ingroup taxa. Virtually all lineages in both COI and 16S NJ trees exhibit long branches following on from the short burst of rapid speciation. In the COI tree however, these branches are predictably longer with an accumulation of more character changes over time than in the 16S tree given the faster evolution rate in COI. Despite the difficulties in achieving good resolution of [ancient] rapid radiations, bootstrap support was given to more relationships recovered by the neighbour joining method in both molecular data sets thereby providing perhaps the most robust hypotheses of tribal evolution.

Sequence Divergence

Pairwise sequence divergences exhibited up to 19.1% divergence recorded between flight capable *S. rugosus* and flightless *S. (Pachysoma) hippocrates* within the Scarabaeini and up to 22.7% between ingroup and outgroup lineages in the COI data (Table 2). These values fall within the range of divergences reported in several insect COI studies (reviewed by Funk, 1999; Mardulyn and Whitfield, 1999, Cognato and Sperling, 2000). Maximum sequence divergences for 16S within ingroup taxa were up to 14.4% recorded between *S. rusticus* and *S. (Kheper) nigroaeneus*, and similarly up to 14.8% scarabaeine divergence from outgroup taxa (Table 3).

TABLE 2. CO1 mtDNA uncorrected sequence divergence values (%) between members of the Scarabaeini (Coleoptera: Scarabaeidae) used in this study. Square brackets denote genera synonymised with *Scarabaeus* (*S.*) and parentheses denote subgenera of *Scarabaeus* recognised by Forgie *et al.* (in press). Outgroup taxa are highlighted in bold.

		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
1	***Circellium bacchus***	-																								
2	***Heliocopris hamadryas***	16.28	-																							
3	***Eucranium arachnoides***	17.93	18.22	-																						
4	***Anomiopsoides heteroclytus***	17.25	17.79	15.30	-																					
5	*S. [Drepanopodus] proximus*	17.46	17.47	16.41	17.29	-																				
6	*S. (Kheper) nigronaeneus*	18.75	18.33	16.28	18.04	13.73	-																			
7	*S. (Kheper) subaeneus*	20.19	17.89	16.85	19.22	14.42	12.41	-																		
8	*S. [Neateuchus] proboscideus*	15.57	16.61	17.37	16.33	11.12	12.90	13.30	-																	
9	*S. [Neopachysoma] rodriguesi*	20.33	19.88	20.31	19.64	15.58	15.57	16.94	14.12	-																
10	*S. (Pachysoma) bennigseni*	19.79	18.65	17.61	19.80	14.69	16.55	16.88	15.34	14.71	-															
11	*S. (Pachysoma) hippocrates*	21.60	22.60	19.39	21.24	17.34	15.58	16.65	15.38	14.92	15.45	-														
12	*Pachylomerus femoralis*	17.46	16.73	16.51	17.25	11.81	12.69	14.62	11.01	14.76	14.47	14.99	-													
13	*S. (Scarabaeolus) bohemani*	17.78	15.26	18.33	17.90	10.84	14.33	14.73	11.60	13.60	14.88	16.00	10.93	-												
14	*S. (Scarabaeolus) flavicornis*	17.03	17.13	17.29	17.16	11.32	13.92	14.63	11.03	14.74	15.10	15.90	11.83	9.58	-											
15	*S. (Scaerabaeolus) rubripennis*	17.58	17.24	17.46	16.84	10.94	13.91	14.32	10.44	13.84	14.76	16.10	11.31	8.89	8.08	-										
16	*S. galenus*	18.77	19.01	17.64	18.60	13.88	14.45	16.10	11.81	15.89	16.58	16.54	13.54	13.51	13.94	12.81	-									
17	*S. goryi*	18.74	16.82	16.73	18.11	12.30	11.70	13.91	10.63	15.03	12.72	14.64	10.72	11.53	11.33	10.91	13.73	-								
18	*S. rugosus*	18.86	18.66	19.87	19.66	12.72	13.81	14.44	13.31	15.27	17.56	16.43	13.21	12.91	12.83	11.71	14.67	12.60	-							
19	*S. rusticus*	19.41	18.84	18.91	19.10	14.37	14.96	15.56	13.82	16.29	17.23	19.06	14.74	13.72	12.42	12.01	14.22	13.01	11.64	-						
20	*S. satyrus*	18.67	18.47	18.03	17.83	12.12	13.10	14.75	10.74	14.36	15.38	16.75	11.11	13.12	12.34	11.91	13.53	10.62	12.91	14.63	-					
21	*S. westwoodi*	19.76	19.11	19.70	19.59	12.23	13.32	13.72	12.11	15.60	16.42	17.64	11.62	11.44	11.04	11.63	13.64	11.22	10.60	11.73	13.94	-				
22	*S. zambesianus*	16.31	17.68	16.09	15.80	10.82	12.70	13.61	4.86	13.82	15.51	14.94	10.82	11.89	9.85	9.66	11.81	10.23	12.61	13.71	10.05	11.80	-			
23	*S. (Sceliages) adamastor*	17.06	18.54	17.15	17.80	12.42	14.53	14.43	10.34	15.14	16.38	16.54	12.41	13.81	13.13	11.91	14.11	11.61	12.12	14.44	12.11	13.05	10.24	-		
24	*S. (Sceliages) brittoni*	16.94	18.35	17.60	18.04	12.45	14.35	14.76	10.15	15.48	15.98	16.15	11.72	13.23	12.64	11.73	14.02	11.83	12.24	14.44	12.01	12.45	9.86	4.00	-	
25	*S. (Sceliages) hippias*	17.16	19.00	17.61	17.82	11.83	14.31	14.13	10.44	15.27	16.21	16.89	12.03	12.91	12.94	11.12	13.81	11.93	12.14	13.74	12.24	13.27	10.73	7.01	7.59	-

TABLE 3. 16S rRNA mtDNA uncorrected sequence divergence values (%) between members of the Scarabaeini (Coleoptera: Scarabaeidae) used in this study. Square brackets denote genera synonymised with *Scarabaeus* and parentheses denote subgenera of *Scarabaeus* recognised by Forgie *et al.* (in press). Outgroup taxa higlighted in bold

		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
1	***Circellium bacchus***	-																							
2	***Heliocopris hamadryas***	11.86	-																						
3	***Eucranium arachnoides***	11.48	12.68	-																					
4	***Anomiopsoides heteroclytus***	10.42	12.13	3.47	-																				
5	*Scarabaeus [Drepanopodus] proximus*	9.83	12.39	12.42	10.78	-																			
6	*S. (Kheper) nigronaeneus*	13.26	13.73	10.79	10.78	12.40	-																		
7	*S. (Kheper) subaeneus*	10.17	10.80	9.95	9.93	7.94	7.45	-																	
8	*S. [Neateuchus] proboscideus*	11.43	14.28	14.30	13.20	7.10	13.41	10.41	-																
9	*S. (Pachysoma) bennigseni*	14.72	15.47	12.32	12.36	8.18	12.69	9.41	13.68	-															
10	*S. (Pachysoma) hippocrates*	10.95	10.75	9.69	10.28	7.92	10.26	9.67	12.05	8.38	-														
11	*Pachylomerus femoralis*	12.77	13.38	10.42	9.89	6.51	11.79	8.54	11.37	9.39	7.12	-													
12	*S. (Scarabaeolus) bohemani*	12.48	13.80	12.75	11.65	4.97	11.88	9.21	10.07	7.94	5.90	7.03	-												
13	*S. (Scarabaeolus) flavicornis*	10.84	11.88	10.57	9.49	3.52	11.11	7.16	8.95	6.42	5.65	5.28	3.25	-											
14	*S. (Scaerabaeolus) rubripennis*	10.72	12.68	13.30	12.20	3.99	13.86	9.76	8.42	8.46	8.19	7.86	4.73	3.73	-										
15	*S. galenus*	12.85	14.33	13.60	13.34	7.71	13.27	9.00	12.39	10.08	10.56	7.79	8.47	7.47	8.49	-									
16	*S. goryi*	12.26	13.21	13.48	13.51	7.19	11.61	8.43	8.14	11.34	9.46	7.74	8.00	6.94	8.52	8.69	-								
17	*S. rugosus*	14.81	13.52	13.75	14.37	8.42	14.30	8.98	12.88	9.72	8.67	7.28	6.94	7.72	9.80	7.93	8.47	-							
18	*S. rusticus*	12.52	11.88	14.58	15.20	7.20	14.36	12.67	11.78	11.86	7.39	10.16	6.40	8.20	8.67	11.64	10.00	7.47	-						
19	*S. satyrus*	11.09	11.30	11.20	10.15	7.39	9.72	8.37	7.58	11.23	8.90	6.75	7.68	5.67	8.18	9.76	6.40	9.98	10.51	-					
20	*S. westwoodi*	11.96	12.09	10.77	10.77	6.40	10.49	9.75	9.17	10.01	7.95	6.04	5.24	5.49	6.53	9.77	7.21	8.42	7.98	4.21	-				
21	*S. zambesianus*	10.99	12.44	11.57	10.54	7.46	12.43	9.23	2.29	11.86	9.46	8.82	9.28	7.73	9.81	10.81	7.39	11.36	11.57	5.41	8.48	-			
22	*S. (Sceliages) adamastor*	12.63	13.20	11.61	10.51	5.17	11.83	7.43	9.18	7.68	6.39	6.79	4.46	3.02	4.95	6.91	7.69	8.41	9.00	5.16	6.15	6.94	-		
23	*S. (Sceliages) brittoni*	12.39	12.37	10.75	10.20	4.95	11.58	7.62	8.89	7.37	6.61	6.54	4.20	2.76	4.68	6.95	7.93	8.71	8.68	5.64	5.95	7.19	1.15	-	
24	*S. (Sceliages) hippias*	12.38	12.09	11.82	11.03	5.43	12.12	8.38	8.90	7.87	5.63	7.05	4.69	3.24	5.17	7.20	6.90	8.46	8.68	4.92	5.94	6.69	1.60	2.77	-

Mean sequence divergences between ingroup taxa with relationships supported by bootstrap analysis particularly in NJ and ML trees ranged from 4.0-15.3% in COI and 1.2-7.5% in 16S data. This, in conjunction with high A-T richness and multiple substitutions in the most variable sites of the molecular data, suggests saturation of substitutions occurs in taxa with sequence divergence values above the mean range of each data set (i.e. above 15.3% in COI and 7.5% in 16S). Mean divergences within the ingroup subgenera varied between 6.2 % (COI):1.9% (16S) (*Sceliages*), 8.9%:3.9% (*Scarabaeolus*), 12.4%:7.5% (*Kheper*) and 15%:8.4% (*Pachysoma*) S. L. Among the closely related taxa within each subgenus, the overall divergence was relatively low, homoplasy was therefore low, hence, the noise:signal ratio was in favour of truly homologous base substitutions. Highest divergence values occurred between ingroup and outgroup taxa yet the basal node differentiating the scarabaeines from the outgroup taxa in both trees received strong bootstrap support. Resolution, at least in the COI data, was likely to be gained from the highly conserved sites as reported by Mardulyn and Whitfield (1999).

Several studies have provided molecular clock calibrations for insect mt DNA ranging from approximately 0.98-2.3% divergence per million years to estimate phylogenetic time frames (DeSalle *et al.*, 1987 (2.0%); Brower, 1994 (2.3%); Prüser and Mossakowski, 1998 (0.98-2.3%)). Based on this range, our data suggests the Scarabaeini appeared around 8-19 Mya. The current school of thought suggests the Scarabaeini may have evolved around the same time as other Scarabaeines during the Eocene epoch (37-54 Mya) of the Cenozoic (Crowson 1981; Cambefort 1991a; Scholtz and Chown 1995). Our molecular data suggest this tribe is more recently derived than previously speculated. Clay covered brood balls and nests recovered from the Chadian Pliocene Australopithecine levels (Duringer *et al.*, 2000) suggest brood ball construction and nesting behaviour practiced by many of the Scarabaeini were well established at least 3-3.5 million years ago. According to our estimates, this advanced level of reproductive behaviour had at least 4 million years to evolve in the tribe.

Combined Data Analysis and Characteristics

A partition homogeneity test of the three data sets supported their combinability (P = 0.001). Analysis of each combination recovered a single most parsimonious tree (Fig. 4). Analysis of the molecular data sets either simultaneously (Figs 4A; CI = 0.30, RI = 0.39, length = 3.173 and 4B; CI = 0.33, RI = 0.45, length = 1.680) or together (Fig 4D; CI = 0.30, RI = 0.39, length = 3.413) with the morphological data yielded topologies reflecting an over proportional impact by the latter (but see Hillis, 1987). This may stem from a greater weight given to individual homoplasious morphological characters than saturated molecular characters supporting nodes at a number of hierarchical levels. The majority of topologies recovered from separate COI and 16S analyses were largely conflicting and poorly supported apart from relationships between closely related taxa (see discussions below). The tree recovered from the combined molecular data (Fig. 4C; CI= 0.33, RI= 0.37, length = 2,200) bears little to no improvement in topological robustness and prompts us to question their effectiveness in further resolving morphologically based Scarabaeini phylogeny. Given that our molecular data sets markedly differ in rates of evolutionary change (see Brown *et al.*, 1982; DeSalle *et al.*, 1987; Knight and Mindell, 1993), the pooling of these heterogeneous data may yield incorrect topologies (Bull *et al.*, 1993) that are poorly supported (Brower and DeSalle, 1994), thus, providing us with less confident estimations of relationships. Nonetheless, inclusion of the molecular with morphological data recovered a single "total evidence" tree (Fig.4D; 683 PIC's) that contained some groupings compatible with certain elements of the preferred weighted morphological tree by Forgie, Philips and Scholtz (Fig. 1A, unpubl.).

Saturation

The mean empirical Scarabaeini TI:TV scores calculated in PAUP for all COI and 16s rRNA characters were 1.29 and 1.00 respectively. In contrast, the overall transversions exceeded

transitions in ratios of 0.64 and 0.72 for all COI and 16S rRNA characters respectively when analysed in MacClade. Similarly, by comparing the CI and RI values, with and without the removal of transitions and/or uninformative characters, it is evident a high degree of homoplasy is present in most of the unweighted data, particularly COI. The same holds true even following weighting against presumably highly homoplasious nucleotides most prevalent at third codon positions in the molecular data. This site tends to become saturated quickly due to a higher frequency of silent substitutions than replacement substitutions in genes, particularly in genes subject to strong selection (Swofford *et al.*, 1996). Equally, saturation is problematic when inferring relationships among taxa that have been diverged for a long time (Brower and DeSalle, 1994; Källersjö *et al.*, 1999). Brown *et al.* (1982) estimated 10-30 million years for saturation of silent sites in parts of two protein genes (URF 4 and 5 after Anderson *et al.*, 1981) and three transfer RNAs (i.e. His, Ser, Leu) of hominoid primate mtDNA. Whilst third codon positions are therefore thought to be less informative indicators in phylogenetic studies than more slowly evolving first and second codon positions, Källersjö *et al.* (1999) have shown the contrary: third positions, although highly homoplasious, contain most of the phylogenetic signal in their data. Weighting schemes aimed to reduce or eliminate highly variable [homoplasious] positions from nucleotide sequences tend to decrease phylogenetic signal rather than noise (Philippe *et al.*, 1996) and therefore does not fundamentally increase general congruence (Vidal and Lecointre, 1998). Indeed, weighting of our data had no significant effect in improving congruency or resolution of many of the mid to deep-level nodes in tribal phylogeny as 16S and the third codon positions of COI gene appear to be too saturated. For similar problems encountered with COI and 16S data Mardulyn and Whitfield (1999: 290-1) suggest the level of divergence of the generic relationships examined are located in a window in which rapidly evolving sites are too saturated and highly conserved sites are not variable enough to provide sufficient phylogenetic signal.

Despite the lack of topological congruence, all trees support the following behavioural inferences: Feeding specialisation in terms of shifts from coprophagy (*Kheper, Pachylomerus, Scarabaeus, Scarabaeolus*) to necrophagy (*Sceliages, Scarabaeolus, Scarabaeus* (In part)) and saprophagy (*Pachysoma* S. L. (In part)) is polyphyletic in Scarabaeini evolution. The same inference can be made for food relocation behaviour when "ball-rolling" is defined in terms of mode and direction i.e., rolling backwards (*Scarabaeus, Kheper, Pachylomerus*) pushing forwards (*Pachylomerus, Sceliages, S. galenus*), dragging forwards (*Pachysoma*) S. L. or carrying forwards (*S. galenus*) (refer to Fig. 1A). Both *Pachylomerus femoralis* and *S. galenus* practice tunnelling behaviour in addition to "ball-rolling". Their disparate placement within all topologies suggests a polyphyletic reversal back to an ancestral tunnelling behaviour (Philips, Pretorius and Scholtz, unpubl.).

The general pattern emerging from all analyses indicates significant disagreement in the hypotheses generated. For instance, *S. (Sceliages)* taxa have a medially derived placement within the ingroup in virtually all trees recovered. The exception lies with the 16S MP trees (Figs 3A, B) where its representatives become the most highly derived clade within the tribe. Moreover, conflicting inferences are made as to the clade's relatedness with other lineages between the different data sets. *S. (Sceliages)* is closely related to the noturnal taxa *S. satyrus, S. proboscideus, and S. zambesianus* in all COI trees recovered, *S. (Pachysoma)* S. L. in 16S MP trees and members of *S. (Scarabaeolus)* in the morphology and 16S MP trees. The majority of trees reconstructed place the *Kheper* lineages most basal in the ingroup as sister to the remaining members of *Scarabaeus* S. L. This inference has strong bootstrap support only from distance analyses of both genes (Fig. 6). In contrast, the morphology and reweighted COI MP and COI ML trees place *Kheper* taxa among the more derived lineages of the Scarabaeini. Flightlessness in the ingroup is limited to *S. (Pachysoma)* S. L. in the molecular data and is subject to the

highest degree of conflict in terms of topological placement and relationship with fully winged taxa. In the morphological data where flightless lineages are well represented, there is virtually complete reversal in ingroup polarity from a paraphyletic flightless origin of scarabaeine evolution (results not shown) to the loss of flight becoming a derived condition that has evolved monophyletically (Fig. 1A). Flightlessness is generally accepted as a derived condition from a macropterous ancestry (Darlington, 1936; Goldschmidt, 1940; Southwood, 1962; den Boer *et al.*, 1980; Harrison, 1980; Kavanaugh, 1985; Roff 1986, 1990. Cited by Emerson and Wallis, 1995. See also Scholtz, 2000) and is derived in the morphological trees recovered from a majority of weighted schemes conducted by Forgie *et al.*, (in press).

All analyses were characterised by low consistency and retention indices and a low degree of resolution. Bootstrap analysis collapsed the majority of the nodes in all trees recovered apart from the basal node differentiating the Scarabaeine clade from the outgroup taxa and those on the apical branches exhibiting strongly supported relationships among closely related taxa. These include the two nocturnal species *S. satyrus* + (*S. proboscideus* + *S. zambesianus*), *S. rugosus* + *S. rusticus* and *Scarabaeus* subgenera *Sceliages* and *Kheper*. *Scarabaeus (Pachysoma)* S. L. taxa were only moderately supported as a monophyletic clade following bootstrapping in the COI data but gained strong support in the COI NJ tree (Fig. 6). In contrast, members of *S. (Scarabaeolus)* (with the exception of *S. (S.) scholtzi*) were well supported by bootstrap analysis as a monophyletic clade only in the COI NJ tree (Fig. 6) and Combined MP trees (Figs 4A, D).

The conflicting topologies and poor resolution in the separate analyses are problematic in establishing to what degree the data are able to support both phylogenetic signal and hypotheses of intra-tribal relationships that emerge when the data are combined (Vogler and Welsh, 1997; Durando *et al.*, 2000). Moreover, it becomes difficult to consider whether or not the combined analysis is the best phylogenetic estimate for the tribe (Vogler and Welsh, 1997). We suspect not. Although the "total evidence" tree shares several elements in common with the preferred

weighted morphological tree by Forgie *et al.* (Fig. 1A, in press), heterogeneity among data sets as mentioned is apparent even though none of the strongly divergent topologies are well supported. There are many arguments for and against combined analysis of multiple data sets in phylogenetic inference (see review by Nixon and Carpenter, 1996). In essence, combination of different data sets providing phylogenetic signals at different but complementary hierarchical levels results in improved overall resolution. Where our combined data falls short of this notion, it does provide us with useful phylogenetic information when analysed separately for two reasons: (1) heterogeneity can be circumvented when looking separately at areas of congruence and conflict of trees (Nixon and Carpenter, 1996); (2) the independence of separate analyses increases the significance of corroboration (Miyamoto and Fitch, 1995).

Comparison with Forgie, Philips and Scholtz (in press) classification of the Scarabaeini

The proposed classification of the Scarabaeini by Forgie *et al.*, (in press) is based on comprehensive morphological phylogenetic evidence. Genera forming monophyletic clades within *Scarabaeus* S. L. lineages that remained well supported after subjection to even the most stringent weighting schemes against character homoplasy (PIWE concavity indices 1 and 2) were given subgeneric status (i.e. *Kheper* and *Sceliages*). The genus *Pachylomerus* was maintained as it appeared basal to *Scarabaeus* S. L. in the majority of trees recovered, while the only remaining genus, *Drepanopodus*, was synonymised with *Scarabaeus* due to its derived placement within *Scarabaeus* S. L. and lack of both statistical support and distinct apomorphic characters. The two existing subgenera, *Pachysoma* S. L. and *Scarabaeolus* (excluding *S. (S.) scholtzi*) were adequately supported as derived lineages within *Scarabaeus* S. L. to warrant their taxonomic maintenance. With the exception of *Pachylomerus*, phylogenetic signal in our molecular data is apparent in several congruently supported clades representing the principal genera and subgenera of the Scarabaeini according to Forgie *et al.*, (in press). The placement of

Pachylomerus within the molecular framework of *Scarabaeus* S. L. lineages however is discordant with the proposed classification. It is worth noting that NJ analysis of both molecular data sets suggest *Kheper* lineages are sister to those of *Scarabaeus* S. L. . Pairwise sequence divergences between *Kheper* and *Scarabaeus* lineages are moderate to high in COI (11.7-16.9%) and 16S (7.5-14.4%), but not more so than divergences between *Scarabaeus* lineages. Unfortunately, there is insufficient weight from either the COI or 16S data alone to argue against the proposed classification of either *Kheper* or *Pachylomerus*. However, further investigation with more conserved genes is likely to clarify any ambiguity.

Eucraniinii vs Scarabaeini

The putative close association between the Neotropical Eucraniini and the Scarabaeini was believed to be based on morphological convergence of characters (Zunino *et al.*, 1989; Philips *et al.*, 2002) likely to be associated with existence in arid environments where all flightless lineages of these tribes occur. The molecular component of this study was able to test the hypothesis that the close relationship between the Eucraniini and the Scarabaeini is the result of morphological convergence and is not due to common ancestry. Both molecular data sets infer an obvious genetic dissimilarity between the eucraniines and the morphologically congruent scarabaeines particularly members of the subgenus *Scarabaeus* (*Pachysoma*) MacLeay with 19.6% and 11.2% mean sequence divergences between the *E. arachnoides* + *A. heteroclytus* and *S. (Pachysoma)* S. L. lineages for the COI and 16S data respectively. These values are above the saturation thresholds indicated for each but are no more divergent than the comparisons scored between each eucraniine and the remaining scarabaeine lineages. While the eucraniines and *S. (Pachysoma)* S. L. lineages are morphologically very similar, their genes are not. All molecular topologies recovered from MP, ML and NJ analyses do not support a close relationship between them with the MP and ML COI trees (apart from the TI:TV=1.3 reweighting tree; Fig. 2D) inferring the least measure of relatedness. Our molecular data

therefore concur with Philips *et al.*(2002) morphological and Ocampo's (unpubl.) molecular findings supporting a convergence hypothesis in the evolution of eucraniines and *S. (Pachysoma)* S. L. lineages rather than one of parallel evolution, stemming from a common "Gondwanan" ancestor. For us to accept the latter hypothesis, there would have to be a high degree genetic similarity between them and a tribal evolution far preceding the earliest estimates of African-South American separation of West Gondwanaland around 120-150 Mya (Thayer, 1985).

Conclusions

It is obvious the limitations of this study result from conflicting signals and poor resolution between the morphological and molecular data sets making it difficult to estimate the true phylogeny of the tribe when these data are combined. Resolution is achieved in all analyses between the closely related taxa providing good support for Scarabaeini systematics and several phylogenetic inferences. Of these, the NJ trees provided the hypotheses most strongly supported by bootstrap analysis. Nonetheless, COI and 16S genes have not contributed to fully resolving tribal relationships other than those between closely related lineages and this is likely due to the ancient rapid radiation of the group. Sampling of rare North and North East African flightless taxa is necessary to gain molecular perspective on the levels of divergence between these lineages and those of South Western Africa and whether or not there is molecular support for the monophyly of flightlessness.

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Appendix 1a. Variable character matrix for Cytochrome Oxidase subunit I (COI). Question marks (?) denote unknown nucleotides. Names of taxa starting with '*S*' belong o the genus *Scarabaeus* L. Moreover, subgenera and synonyms of *Scarabaeus* are denoted by parentheses and square brackets respectively. Outgroup taxa are highlighted in bold.

Taxon/Node	1111111111111111111111111111111111 1122223333344444456666677777888999900001111122222233334444555666667778 9582457036790235691123461257814734692568124780367892568145806902568145 70
Circellium bacchus	TATCTCCCTTTATATTTTAATAATATGCTATAAGTTCATATGTTCTCTAGAAATATTCGATATATCAAAATA
Heliocopris hamadryas	TATCTTAAAATAAACTTTAATAGAGAACCTAATGTCCACATGTTGACTATAACTATTTGTTCTATTATAATT
Eucranium arachnoides	TATCTCAATTCAATCTTTAATAGAGTACTTATAGTCCATATGTTATCTGGTTTTAATTATCACTTTATAGTC
Anomiopsoides heteroclytus	CATCTCAAATTAATTATTAATAGAGCACAATGTGTCATTAAGTTATTTGGTTAGATTCGATCCCTCATAACA
S. [Drepanopodus] proximus	TATTATATATATAATTTTAATAGTGATCTTTTTGTTAACTCATTATCTACAATTATCTGATTTATCTTAATC
S. (Kheper) nigroaeneus	TATTATACTAATAATTTTATTAGAGAGCATAAAGATTTTATATTATTTACTATTAATTGTTCCTTTACAACC
S. (Kheper) subaeneus	TATCTTATTAATATTTTTATTAGAGATCAAAATGCTCACTCATTATTTACATATAACTGTTTCTTTATTATT
S. [Neateuchus] proboscideus	TATCATAATAATAATTTTAATAGTGAACAATTAGTTAATATATTATATACTAATATTTGTTATATTAAAATA
S. [Neopachysoma] rodriguesi	TATTATATTCATATTTTTAATAGAGAACTATGTGTCTTTAAATTATCTACTTATTTTTAATCTATTAGAATC
S. (Pachysoma) bennigseni	TATCATACTTATATTTTTAATAGAGTCCCATTTGGCCTCAAATTACCTACAGATTTTTGTTGCTTCATAATA
S. (Pachysoma) hippocrates	TACTATACCCCTATTTTTAGCTGAACGTTTTTTACCTTTATATTATTTACCGATTTTTGTTCTATCACAATA
Pachylomerus femoralis	TATTATAAATATAATTTTAATAGAGAACTTATTGTTAATAAAATGTTTACAATTATTTGTTACTTCAAAACT
S. (Scarabaeolus) bohemani	TATTATATAAATAATTTTAATAGAGATCAAAATGTCTTCTTAACATCCACATCTATTTGTTACACCAGAATT
S. (Scarabaeolus) flavicornis	TATTACATAAATAATTTCAATAGAGAGCCATTAGACATCTAAACATCTACTGATACTTGTCTCTTCAAAATT
S. (Scarabaeolus) rubripennis	TATTATATAAATAATTCTAATAGAGAGCCATAAGTCCACTAAATATCTACTAATATTTGTTTCTTTAAAATT
S. galenus	CATCTTACCAATATTTTTAATAGAGGGCAATATGTTATTAAATTATATACAGTTAATTGTTTTATTAGAATT
S. goryi	TATTATATTAATAATTTTAATAGAGAGCAAATAGTTAATAAAATGAATACAATTATTTGATACTTTATAATC
S. rugosus	TATTACATAAATAATTTTATTAGTGATCTTTTTGATACCTAATTGTTTACAATTAATTGATTCTTTAATATA
S. rusticus	TTTTATACATATAATTTCATTAATGGGCAATTAGATATCTAAATGTTTACGATTAATTGTTGCTTTATAATT
S. satyrus	TACTATAATTATAATTTTAATAGAGAGCTTTATGATAATAAAATGTCTACATATATTTGATTCTTCTTTACC
S. westwoodi	TATTACACATATAATTTCATTAGTGATCAAATTGATTCCTAACTATCTACAATTAATTGTTTCTTTAATATT
S. zambesianus	TATTATAATAATAATCTTAATAGTGAGCGATTAGACAATATATTATCTACTAATATTTGTTACATTAAAATA
S. (Sceliages) adamastor	TATTATATATATAATTTTGATAGTGATCTATTTGTTAATAAATTATTTACTAATAACTGATACTTTATTATT
S. (Sceliages) brittoni	TATTATATATATAA?TTTAATAGTGATCTATTTGTTAATAAATTATCTACTAATAATTGATACTTTATTATT
S. (Sceliages) hippias	CATTATAATTATAATTTTAATAGTGATCTACTTGTTAATAAATTATTTACAAATATTTGATACTTTGTTATT

COI variable characters (continued):

Taxon/Node	1111111122222222222222222222222222222222222222222233333333333333333333 8888999900011111233333444455556666677777888889999990000001111222333344 3679256814803469913478013925891456703678902589124578013679256814703679 02
Circellium bacchus	ATCTCTATTTTTTGTTGTCAAAATATAACCTTGCTAATTCTATATTACTCCCTTATCTTTCTTGATAACTCT
Heliocopris hamadryas	ATTAGTGATTAATGCTATCAAAAAATAATCTTGCTATAGCTTAAATATACTCTATTCACATATGATTACTTA
Eucranium arachnoides	TTCTTTGATTAAAGATTACTAGAATTTAATATGTTAAAGTTTAATGATACACATAATAATTAAAACAACATA
Anomiopsoides heteroclytus	TTCTTAGATTATAGATTTCAAATAATAACTATGTTAAAGTATAACGATATACTTAATAATCTATATAATATA
S. [Drepanopodus] proximus	TTTAGTATTTATAATTTACTAAAAATTATTATGCTATAGGTATATTATACTCATATTAATCAAATTTACATA
S. (Kheper) nigroaeneus	ATCTCTATTTATTATTTTCTAAAATTAAATATGCTATAGGAATATTATATATACTTTATTTAAGTTAACATA
S. (Kheper) subaeneus	TTCTGTATTTATTATCTACTAAAATTAATTATGCTATAGGAATATTATATATACTATATATATATTAACATA
S. [Neateuchus] proboscideus	ATTAAAATTTATTATTTTCTTAAATTAATTATGCTAATGGTATTTTATATATACTTTAACTATTATTATATA
S. [Neopachysoma] rodriguesi	ATTAACATTTATCATTTACAAAAATTTATTATGCTGAAGGGATTCCTCTCTTACCCTACATATCATAACATA
S. (Pachysoma) bennigseni	A?TATTATTTAAAATTTACCAAAATCTGTTATGCGATAGGTATAATATATACTTACC?ATTA?CATTATATA
S. (Pachysoma) hippocrates	ATTAGTATCTAAAATCTATTAAAATTTATTATGCTGAAGGAATTACATATATATAATAAATATGTTAATATA
Pachylomerus femoralis	ATTAATATTTATAACTTTCTTAAATTAATTACACTATAGGAATATTATATACATAATATATATTATTACGTA
S. (Scarabaeolus) bohemani	ATTAGCATTTATTATTTACTAAAAATAACTATGCTGAAGGAATATCACACTCTTAATAATTATTTTTACTCA
S. (Scarabaeolus) flavicornis	ATCAGTATTCAATATTTACCAAAAATTATTATGCTATAGGTATATTATACTTATAATAAACAAATTAACTTA
S. (Scarabaeolus) rubripennis	ATTAGTATTTATTATTTACTAAAAATTATTATGCCGACGGAATACCATACCCATAATATATAATTTAACTTA
S. galenus	ATTAATATTTATAATTTACAAAAATTTATTATGCTAATGGAATTACATACTCTCTTTGATTAAATTAACACA
S. goryi	ACTAGTATCTAAAATTTACTAAAATTAATTATGCTATAGGTACATTATATATACTATAATTATGTTTATATA
S. rugosus	ATTAAAATCTATTATTTACTAAAAATTAATACCCTATAGGAATTTCTTACTCAGTTTATATATATTAACTTA
S. rusticus	ATTATTATTTATTATTTACTAAAAATTATTATGCTATTGGAACACCTTACACACTATAATTAAGTTAACTTA
S. satyrus	ATCAATATTTATTATTTTCAAAAATCGAATATGCTATTGGAATTTTATATATACTTTAAATAAAATAATGTA
S. westwoodi	ACCAGTATTTATTATTTACTAAAAATTATTATGCTATAGGAATATTATACATACTTTAATTATTTTAACTTA
S. zambesianus	ATTAATATTTATTATTTTCTTAAATTAATTATGCTAAAGGAATTTTATACTTACTTTAAATAAAATAATATA
S. (Sceliages) adamastor	ATCAATATTTAATATTTACTAAAAATTATTATACAATTGGAACTTCACTCATACTTCTACTATTCTTATACT
S. (Sceliages) brittoni	ATTAATATTTAATATTTACTAAAAATTATTATGCAACTGGAATTTCACTCATACTTCTACTATTTTTATGCT
S. (Sceliages) hippias	ATTAATATTTATTATTTACTAAAAATTATTATGCAATTGGAATTCTACTTATACTACTATCATATTTGCACT

COI variable characters (continued):

Taxon/Node	333333333333333333334444444444444444444444444445555555555555555555555555 445555666777788889999000011112223344455566677888000001111222334444555556 581457369258901470369025812473692514846925847039014790369238470379256894
Circellium bacchus	CTTTTAATCTTTATAATGTTTTATATTATTTATTATTTAAATATTTTTGAAAAAATTTTGTCAAGATATATA
Heliocopris hamadryas	TTTTATTTTTTTATTAAGTTTCTTATTATTTCTTTTTTATATTCTTTTGAAGAATTAATATTTAGTTTTACC
Eucranium arachnoides	TTATTATATTCTGTATTTTTTTACATTACTTCTTTTTCAATTTTTTTGACAAAAATTTTTTTTAGTTTTATT
Anomiopsoides heteroclytus	ATACTACCCTCAACTAGATATTACATTATCTATATTTTATGTATTTTAGAAGGAATTATATTAAGACTCATT
S. [Drepanopodus] proximus	ATACTAAACTTAATAAAATATTATATTATTTTTATCTTATATTTATTAGAAAAATTAACATTTAAATATATA
S. (Kheper) nigroaeneus	ATATCTCTTTTTATAAATCATTATATTATTTACTTTCTAATTTTATTAGAAAAATTTTTTTTTAAATTTATA
S. (Kheper) subaeneus	ATATCTTCTTTAATAAATTATTATATTATTTTTTTTTTATTCGTATTGGAAAAATTTATATTTAATTTTATA
S. [Neateuchus] proboscideus	TTATTATTTTTAATAAAATATCACACTATTTATTTTTTATGTATCTTAGAAAAATTTACATTTAAATCTATA
S. [Neopachysoma] rodriguesi	ATATTAATTTCAATAAGATTTCTTATCTTTTTCTTTCCTAATGTCTTCGAAAAACTATTCCTAAATCGCTCA
S. (Pachysoma) bennigseni	ATATTAACTTTTATACGATATTATATTATTTCCATTCCCTATGTTTCGGTAAAATTATTGTTTAATTTTATA
S. (Pachysoma) hippocrates	ACACTAATTTCTATAAGACTTTATGTTATTTTTTTTTCTCTTATTCTCATAAAATTATTTTTTAATTGTATA
Pachylomerus femoralis	ATATTAACTTCTATAAATTATCTTATTATTTTTTTTTCTTGTATTTTAGAAAAATTATTATTCAAATGTATA
S. (Scarabaeolus) bohemani	ATATTAATTTTAATAATTTTTCATATTATCTTTATTTCCTATTCATTAGAAAAATTAACATTTAAATATATT
S. (Scarabaeolus) flavicornis	TTACTATATTTAATAATCTATCATATTATTTTCATTTTATATACTTTAGAAAAATTCATATTTAAATCCATA
S. (Scarabaeolus) rubripennis	TTATTAAATTCAATAAAACATTATATTATCTTCAATTTATATGTATTAGAAAAATTAATATTTAAATTTATA
S. galenus	TTATTAAATCCTATAAGTTATCTTACTATTTTTTTTCCTAATTTCTTAGAAAAATCTTTTTTTAAATATATA
S. goryi	ATATTATCTTCAATAAGTCATTATATTATTTACATTCCTAATTTTTTTGAAAAATTAATTTTTAATTTTATA
S. rugosus	ATATTAATCTTTATAATATTTTATATTATCTTCAATTTAAATTCTTTGGAAAAATTAATATTAAAATATACA
S. rusticus	ATTTTAAATTTTATACTTTTTCATATTATTTTTATTCTATATATATTTGGAAAGTTAATATTTAAATATACA
S. satyrus	ATATTATCTTCAATAAGATTTTATATTATTCACTTTTCTTATTTTTTAGAAAAATCAATTCTAAAATTTATA
S. westwoodi	ATATTATCTTCTATAAATTATCATATTATTTTTTATTCTATGTTTTTTAGAAAAACTAACATTTGAATACATA
S. zambesianus	ATACTATATTCAATAAAATATTATATTATTTATTTTTTATATATTTTAGAAAAACTTATATTAAATTATATA
S. (Sceliages) adamastor	TTATTATATTCTATAAAATACTATATTATTTACATTTTATTTTTTTTAGAAAAATTTATATTAAAATTTATA
S. (Sceliages) brittoni	TTATTATATTCTATAAAATACCATATTATTTATATTTTATCTTTTTTAGAGAAATTTATATTAAAATTTATA
S. (Sceliages) hippias	TTACTATATTTAATATAATTTTATATCATTTATATTTTATATTTCTTAGAAAAATTTATATTTAAATTTATA

COI variable characters (continued):

Taxon/Node	555555555556666666666666666666666666666666677777777777777777777777777777 677778899990000112223333445555667788889999900000111222222333344455555666 723692514570369581470369251247035812470136901268147013469356814701369025
Circellium bacchus	TTGGTTTTTGTAATTCATTTTTTTATAGTATATAATATTCTTTATTTATTCCGCTATGATATTATCATTGTG
Heliocopris hamadryas	TTTACTTCAGATATACACTTTAATATAGTTAATAATAACCATCACATATTCCTATATGTAAATATTACAATG
Eucranium arachnoides	TTAATCTTTATAATTTATTTATATATAGAAATCAGTATACTTCTCTCTCTTTTATATGTTAATATTATAGCT
Anomiopsoides heteroclytus	TTTAACTTAATAACTTATTTAATAATTGATAACTATAAATATTACTTATCTATATATGATAATACTATAGTT
S. [Drepanopodus] proximus	TTAACTTTAGAAATTAATTCTATAATTGAAATTAATATATTTTGCTCTTTAATATATGTTATTATCATAGAG
S. (Kheper) nigroaeneus	TGTAATTTAGAAATTTATTCTTAAATTGGCATTAACACATTTAACTATTTATTATATGTTAGTATTATTGTC
S. (Kheper) subaeneus	TTTAATTTAGTAATTAATCTAAAAATTGTAATTTATATTTTTAACTATTTATTATATAATAATTCTATTAAT
S. [Neateuchus] proboscideus	TTAAATTTAGTAATTAAATTAATAATTGTTAATAATAATTTTTTCTCTTTAATATATGAAAATTCCATAGTA
S. [Neopachysoma] rodriguesi	TTAAATTTAGAAATTTATTTCATTATCATTAATTATATTTCTATCTCTTTTATTAATTTTAGTATTATAGTG
S. (Pachysoma) bennigseni	TTAGTCTTAGAAATATGATTTATAATTGTAAATGATATCTCTCTCCTACTCATATATGTTAATATTACTGAG
S. (Pachysoma) hippocrates	TGTATTTTAGAAATATTCTTTAAAATTATCAACTGTACTTTCAACTCTTTAATATATTCCTTCTCTATTGAA
Pachylomerus femoralis	TTAATTTTAGATATTATTTCTAATATCGTTTATAATATCTTTAACACTTTATTATATGTTATTATTATAGAA
S. (Scarabaeolus) bohemani	TTAATTTTAGATATGAATTTTTATATTGTTAATAATAAATCTATCTCTTTATTTTATGTAAATATTATTGTG
S. (Scarabaeolus) flavicornis	TTAAATTTAGTTATAAGTTTTTTAATTGTTTATAATACTTTTATCTCTTTATTTTATGTAAATATTATAGTC
S. (Scarabaeolus) rubripennis	TTAAATTTAGTAATTAAATTTACAATTGATTACTATGATTTTATCTCTTCATTTTATGTAAATATTATAGTG
S. galenus	TTTATTTTTGGTGTTATTTTTAGAATAGACTTTAATATATTTATCTTATCATTATATGACAATACTATAATG
S. goryi	TTAACTTTAGATATATAATTTTAAATTGATAATAATAATTTTAACTTACTACTATATGTAAATATTGTTGAT
S. rugosus	TTAAATTTAGAAATTAAATTTAAAATTATTATTGATAATTTTAACTTATTATTTTTGTGATAGTTTTATAGAA
S. rusticus	CTAAATTTAGTAATTATACTCAATATTATTAATAATATTCATAACTCTTCAATATACTATAATATTATAGTT
S. satyrus	TTAAATCTAGATATTAAATCCTAAGTTGTAAATAATATATTTATCTCTTTCATATATGTAAATACTACAGTC
S. westwoodi	TTAAATTTTGATATTAATCTTAAAATTATTAATCACATATCTCTCTCTTCACTTTATTATAATATTATAGAA
S. zambesianus	TTAAATTTAGTAATTAAATTAATAATTGATAATAATAATTTTTTCTCTCTATTATATGAAAATTCTATAGTA
S. (Sceliages) adamastor	TTAAACTCTGAAATTAAATTTAATATTGATATTAATAATTCTAACTCTTTTTTACATGACATTACTATAGAT
S. (Sceliages) brittoni	CTTAATTTAGAAATTAAACTTAATATTGATATTAATAATTTTGACTCCTTCTTATATGTAATTACTATAGAA
S. (Sceliages) hippias	TTAAATTTAGGAACTATATTAAATACTGTTATTAATAATTTCAACTCTTCTTTACATGTTATTATTATAGAC

COI variable characters (continued):

Taxon/Node	77777777777777788888888888888888888888888888888899999999999999999999999 66777788888999900001111222333444455556677788999990000111122233333455556 89147801349258914580136258147036923584703658123472367258923401236904567O
Circellium bacchus	TTATAGAGATCTAAGTTAGTCTTTTTAATCTTTATAATTATTTATATTTTCCTTTATACATTCTATTTATTT
Heliocopris hamadryas	ATATCGAATTATTTATTAGTTATACTAATTTTTTTAAGTATTTACACATTCTTTATTGTATAGAATTTTTAT
Eucranium arachnoides	ATGATGAGTTTTAAATTGGATATTTTTTCTTTTATAAGAATATATGTCTTTTTTTTATATATTCTATTTTTAT
Anomiopsoides heteroclytus	ATATGGAATTATAAACTAGTTATTCCAATTTTTATATATATACACATTTTCATCAATACTTACTATTTCTAT
S. [Drepanopodus] proximus	CTAAGGAGTCTTAAATTAGTTATTTTATCCCTTTTAAGTATTAATGTTCTTTTTAGTATATGCTATTTTTAT
S. (Kheper) nigroaeneus	ATATGGAATTTTAAATTAGATATTTTATTTTTTTCTTATATAAATGTCTTTTTTTTACACTTTTAATCTTTAA
S. (Kheper) subaeneus	TTAAAGTGATATATATTAGATATTCTTTTTTTTTATAAAATTAATTACACTTTTTAATACATTCTATTTTTAT
S. [Neateuchus] proboscideus	TTAAAGTGATTCTAATTAGTCTTTTTTTACCTCTTCTAATATTTATGTTTTTTTTTAATACATTCAATTTTTAT
S. [Neopachysoma] rodriguesi	ATAATGTGATTTCTATTAATCATTCTATATTTTTCTAATATTAGTATTCATATTAATACTTTCTATTTTTAT
S. (Pachysoma) bennigseni	ATACAGCGATTTTAATTAG?CCTTTTATATTTTACCA?AATAATCGTATTCTTTTTATATATTCTATTTTGAT
S. (Pachysoma) hippocrates	ATATTGTGATTTCAGTCAGACTTTTCAACTTTTATAAGTATAAATGTACTTTTTTAATACATTCTACTTTTAT
Pachylomerus femoralis	ATATTGAGATTTATATTAGACTTTTTTAATTCTTTCTTGAATCTATGTATTCATTTATACTTACTATTTTTAT
S. (Scarabaeolus) bohemani	ATAATGAGACTTTTATCAGTCTTACTAACTTTTACCACTATTAATGTATTTTTTTAATACATACTATTTTTAT
S. (Scarabaeolus) flavicornis	ATAATGAGATTTAAGTTAGACTTACTAAATTTTACTAATATTAATGTTCTCATTAACACATGCTATTTTTAT
S. (Scarabaeolus) rubripennis	ATAAAGAGATTTAAATTAGTCTTCTTAAATTTTACTAGAACTTATGTTTTTTTTTAATACTTTCTATTTTTAT
S. galenus	GCATAGTAACATAAATCAATCACTTTTTATTTTTCTTAAATATATGTTTTTTTTTAACACATACTACTTTTAT
S. goryi	ATAAAGTGATTTAAACTAGTCTTATCAAATTTTTCTAGAATAATTGTATTTACTTTTACATCCAATTTTTAT
S. rugosus	ATATAATGTTATAAATTAGTTATTTTTATTTTTTACCAAAATTAATGTATTTATTAATATATACTACTCTTAT
S. rusticus	ACAAAGTACTCTTAATTAGTTATACTTAATTCTACTAAAATAATTATTTTCTCTAACACTTACTATTTCTAT
S. satyrus	TTATAGAGATTTAAATTAGATATTTTTAATTCTTCTAGTATTAATGTATTTTCTAATACATTCTGTTTTTAT
S. westwoodi	ATATAATACCACAAATCAATCTTATTTATTCTCTCTAAAATTAACGTTCTTATTTTTACATCATACTTTTAT
S. zambesianus	TCAAGGTGACTTAAATCAGTCTTTTTTACTCTTTCTAATATTCATGTTTTCTTTAATACATTCAATTTTTAT
S. (Sceliages) adamastor	CTAATGTATTTTAAATTAGTCCTTTTAACTTCTATAATAATTTATGTATTTATTAATACATTCTATTTTTAT
S. (Sceliages) brittoni	ATAATGTATTTTAAATTAGCCTTTTTAACTTCTATAATAATCAATGTGTTCATTAATACATTCTATTTTTAT
S. (Sceliages) hippias	ATAAAGTATTTTAAATTAGTCTTCTTAACTTTTATAATAACTTATGTATTTATTAATACACTCTATTTTTAT

COI variable characters (continued):

Taxon/Node	1111111111111111111111111111111111111111111111111111111111 9999999999990000000000000000000000000000000000000000111111111111111 6677778889999000001111122223334445555566666777888899999000001111122222 6925891470369235891345703692581470345925689147036792568901478013671245
Circellium bacchus	TTAATAACCCCACTTAATAGTGCATAATTTCACCTACAATATATAATAATATCTAGTAATTTTATTTTTTTA
Heliocopris hamadryas	TTTATAACTCCATTTATTAGAGTAACTTATTATCTACTGTATACTATAATATATAGTAATATTATGTTTTTA
Eucranium arachnoides	TTAATGAATTCATCTAATAGTGAGAAATATCTTATATAATGTATAACAAAATCTAATTTTTTTATCTTTTTA
Anomiopsoides heteroclytus	TTAATAAACCTATTTAATAGAGTAAATTATCATTTATAATATATAATATAGCATAGTTATTCTACTTTTTTA
S. [Drepanopodus] proximus	TTAATAACTCTATCCATTAGAGTGATATATTTTTTCTAATAAGAATTACTATCTAATTATTTGACCTTTTTG
S. (Kheper) nigroaeneus	TTTACAATTCGATTCAATAGTGAATTATACCTTACTTTATAAGATTTAATATATAACTATTTAATTTTTTTA
S. (Kheper) subaeneus	TTATTAACTCCATCCTTTATAGAATAATATCTTATTTAATAAGATACAATATATAATTATTTAATTTTTTCA
S. [Neateuchus] proboscideus	TTAATAATTCTATCTATTAGAGTATAATTTTATATTTAATAAGATATAATACTTAATTATTTTATTTTTTTA
S. [Neopachysoma] rodriguesi	TTATTAACTCCATTCTTCTGAGAATCTTTCTTTATTTAATAAAACTTCATATATAATTATTTTACTGATTTA
S. (Pachysoma) bennigseni	CTATTAACTCTGTTCTCCTGAGAGATTTATCACATTTAATAAGACTTTACATTTAATTTTTTTATCGATTTG
S. (Pachysoma) hippocrates	TAATTAATTTAATTCAATAGAGAATCATTTCCTACTTAATAATATACAATATTCCATTACTATATTGATTCA
Pachylomerus femoralis	TTATTAACTCTATCCAATAGAGCATATTTTCTTTTTTAATAAGAAATAATACATAATTTTTTCTTTTTTTCA
S. (Scarabaeolus) bohemani	TCTTTAACTCTATTTATTAGAGTAAATTATTTTTTTTAATAAGAAATGCTATATAATTATTTGATTTTTTCA
S. (Scarabaeolus) flavicornis	TTATTAATTCCATTTAATAGAATATAATATTATATTTAATAAGAAATACTATACAGTTATTTTATTTTTTTA
S. (Scarabaeolus) rubripennis	TTATTAACTTTATTTATTAGAGTAATATATTATATTTAATAAGAAATGCTACATAATTATTTACTTTTTTTA
S. galenus	TTAACAAATTTATCTATTAGAGTAAAACTTTATCTTTAATAAGATATACCATTCAATTATTTGATTTTTTTA
S. goryi	TTATTAAATCAATTCAATAGAGAAAAACATTTTATTTAATAAGAAATAATATATAATTATTCAATTTTTTTA
S. rugosus	TTATCTAATTTACTTATTAGAGAATAACACTTTACTTAATAATATATAATATATGATTATTCATCTTTCATA
S. rusticus	TTAATTAATTAATTTATTAGTGAAAAACATTTTATTTAATAACCATTGATATCCAATTATTTATCTTTTTTA
S. satyrus	TTATTAAACTTATTCTTTAGAGTATAATTCTTTTTTTTAATAAGAAATGTCATATAATTATTCCACTTTTTTA
S. westwoodi	CTATTAGCTCTATTCATTAGAGAATAATATTTTACTTAATAAGAAATTATATATAATTACTTATTTTTTTTA
S. zambesianus	TTAATAAATTTATCTAATAGAGTATAATTTTATATTTAATAAGACATAATATATAATTTTTTCATTTTTTTA
S. (Sceliages) adamastor	TTATTAATCTAATCCAATAGCGTATAACTTTATCTCTAATAAGATATAATATATAATTTTTTGACTTTTTTA
S. (Sceliages) brittoni	CTATCAATCTAACCCAACAGTGTATAATTTTATTTCTAATAAGATATAACATATAATTTTTTAACTTTTTTA
S. (Sceliages) hippias	TTACCAACTTTATCTATTAGAGAATAACTCCATTTTTAACAAGAAATAACATATAATTTTTTGATTTTTTTA

COI variable characters (continued):

Taxon/Node	1111111111111111111111111111111111111111111111111 1111111111111111111111111111111111111111111111111 3344444444455566666667777777778888888889999999 4701234678926812345780123456789012456789013456 7
Circellium bacchus	TATATTTTTTAAGTTAGAACTAAGAATATCAACACCCTTGAAGAATA
Heliocopris hamadryas	AATATTTTATGATTTGGAATTAAGACTGCCAACTCTTTAGAAGATAT
Eucranium arachnoides	TACATTTAATAATATGGAATTAAATATAAATTCTCTCTTGAAGATTT
Anomiopsoides heteroclytus	TATGTATTATAATATGGAATTAAGAATAAACTCACTATTGAAGATTA
S. [Drepanopodus] proximus	TATATTGTATAATATGCCCTCAAGAACATCATCACAATTGAAGGTTC
S. (Kheper) nigroaeneus	AATACTTTATAATATATCCTTAAGAACAAACTCACTATTGAGGATTT
S. (Kheper) subaeneus	AATATTTAATAATATAGACTTAGAACAATTCATCATTGATGATCAAT
S. [Neateuchus] proboscideus	TATATTGTATAATATACACTTAAGAACTTCATCACAATTGAAGATTT
S. [Neopachysoma] rodriguesi	AATTCCTTATATTTTATCCATAAGAACATCTTCACTATTGAAGATTT
S. (Pachysoma) bennigseni	ATTACCTAACAATACATATTTAAGAACGTCATCACAATTGAAGATTT
S. (Pachysoma) hippocrates	ATTACCTAATAATATACAAACAAGAACATCGTCACTATTGAAGATTT
Pachylomerus femoralis	TTTATTGTATAATATGCACTTAAGAACATCTTCACAATTGAAGATTT
S. (Scarabaeolus) bohemani	CATATTTTATAATATACTCTTAAGAACATCATCACAATTGAAGATTT
S. (Scarabaeolus) flavicornis	TATATTTAATAATTTGCACTTAAGAACATCATCACAATTGAAGATTC
S. (Scarabaeolus) rubripennis	TTTATTTTATAATTTGCTCATAAGAACATCATCTCAATTGAAGATTC
S. galenus	TATACAGAATAATATGCACCTAAGAACATCATCTCAATTGAAGATTT
S. goryi	TATATTGTATAATATACACATAAGAACTTCATCACAATTGAAGATTC
S. rugosus	AATATTTTATAATTTACACACTAGAACATCATCACAATTGAAGATTT
S. rusticus	AACATTTTATAATTTGTACTCTAGAACTTCATCACAATTGAAGAATA
S. satyrus	TATATTGTATAATTTGCACTCAAGAACTTCAACTCAATTGAAGATTT
S. westwoodi	TATATTTTATAATATACACATAAGAACATCATCACAATTGAAGATTA
S. zambesianus	TATATTGTATAATATACACTTAAGAACTTCTTCACAATTGAAGATTC
S. (Sceliages) adamastor	TATATCTTATAATTTATACATAAGAACCTCTACACAATTGAAGATTT
S. (Sceliages) brittoni	TATATCTTATAATATACACATAAGAACATCTACACAATTGAAGATTT
S. (Sceliages) hippias	TATATTTTATAATTTATACACAAGAACATCCTCACAATTGAAGATTT

Appendix 1b. Variable character matrices for 16S ribosomal RNA (16S). Dashes (-) represent gaps/deletions. Names of taxa starting with '*S*' belong o the genus *Scarabaeus* L. Moreover, subgenera and synonyms of *Scarabaeus* are denoted by parentheses and square brackets respectively. Outgroup taxa are highlighted in bold.

	1111111111111111111111111111111111111111111111111112222
	1112223337788888899990000111111122333334444455566666677777777888889999990000
Taxon/Node	6901413905909023456045824792345679010345735679078456789234567890348901235901 23
Circellium bacchus	ATTTTAGAAATATA-ATTAACTCTCCATTATAA-TTGCATCTTAATGCCCTAATTTATATAACTATTTAAGATTCAAC
Heliocopris hamadryas	ATTTTAACAAAATAATATAACTCTACATTATTA-AAGCATCTTAACGTCTTGAATTTTAAAAATATTAATAATATAAC
Eucranium arachnoides	ATTTAAACAATATA-ACTAACTATTCATTATTA-TTATATTTTGATGCCTAATTTAATATATTTATTTAAAATTTAAC
Anomoipsodes heteroclytus	ATTTTAA-AATATA-ATTAACTATTCATTATTA-TTACATTTTAATGCCTAATTTAATATATTCATCTAAAATTTAAC
S. [Drepanopodus] proximus	CTTTTTAAAAAATA-ATAAATTCTTCATTTTAA-TAGAATTTTAGTGCTTTTATATAAATACCTATCTTAAAATAAAC
S. (Kheper) nigronaeneus	ATCTTAAAAAAATAAATTAACTATATATTTTAA-TAGCATACCAGTGCTTTATAATAAATATTTATTATATAATAAAT
S. (Kheper) subaeneus	ATTTTTAAAAAATA-ATTAACTCTTCAATTGAAATAGTATATTAGTGCTTTAATTTAAATATTTATTTTATAATAAAT
S. [Neateuchus] proboscideus	GCTTTTAAAGTAAAAATATACTCTTCATATTATATAGATTTTTAGTGCCTAAATATATATATCTATCTATAACTAACC
S. (Pachysoma) bennigseni	ATTTTTAAAAAATA-ATTAATTTATCTTTATAA-TAGTATATTAATATCTATACCTATATGCTTTTTTAATGAAAAAT
S. (Pachysoma) hippocrates	ATTTTTAAAAAAAAAAATAATTTTATATTTTAA-TAGCATATCGATGTCTTTCTATAAATATTTTTTTAAAATTAAAT
Pachylomerus femoralis	ATTTTTAAAAAACA-AATGACTCTTCAGTTTAATTAGTATCTTAGTGCCTGTCTATAAATACTTACCTAAAATTACAC
S. (Scarabaeolus) bohemani	ATTTTTAAAATGTA-AATAATTTTCTATTTTAA-TAGACTTTCAGTGCTTTTATATATAAACTTATCTAAAAATAAAC
S. (Scarabaeolus) flavicornis	ATTTTTAAAAAATA-ATTAATTTTTCATTTTAA-TAGAATTTTAGTGCTTTTATATAAATACTTATCTAAAAATAAAC
S. (Scarabaeolus) rubripennis	ATTTTTAAAAAATA-AATAATCTTTCATTTTAA-TAGATATTTAGTGCTTTTATATAAATACCTATCTAGAAAAAAAC
S. galenus	ATTTTTAAAAAATA-AAAAAAAATTCAGTTTAA-TAGTATATTAGTACTCTTATATAAATAATAAATAATAAATAAAC
S. goryi	GTTTTTAAGAAATT-AATAACTCTTCAGTTTAA-TAGATTATTAGTGCCTGTATATTTATATTCAATAAAAAATAAAC
S. rugosus	ATTTTAAAAAAAATAAAAAACTCTATAGTTTAA-TAGTATTTCAGTGCTTGTATATATAAGTTTAATTAAAAATAAGC
S. rusticus	ATTTTAAAAAATTA-TATAATTCTATATTTTAA-TAGAATATCAATGTCTGTATACTTTAACCTAGTAAAAAGTAAAT
S. satyrus	ATTTTTAAAATATA-AATAACTCTTCATTTTTA-TAGAATTTTAGTGCCTATATATATATATTCATCTTTAAATAAAC
S. westwoodi	ATTTTTAAAAAATATAATACCTCTACATTTTTA-TAGACTTTTAGTGCTTGTATACATATATTTATCTAAAAAAAAAC
S. zambesianus	GCTTTTAAAGTAAA-ATATACTCTTCATATTAT-TAGAATTTTAATGCCTAAATATATATATTCATCTTTAATTAAAC
S. (Sceliages) adamastor	ATTTTTAAAATATAAAATAATTTTTCATTTTAA-TAGAATTTTAGTGCTTTTATACTTATATTCATCTATAAATAAAC
S. (Sceliages) brittoni	ATTCTTAAAATATAAAATAATTTTTCATTTTAA-TAGAATATTAGTGCTTTTATACTTATATTTATCTATAAATAAAC
S. (Sceliages) hippias	ATTTTAAAAAAATAAAATAATTTTTCATTTTAA-TAGAATATTAGTGCTTTTATATTTATATTCATCTATAAATAAAC

16S variable characters (continued):

Taxon/Node	22222222222222222222222222222233333333333333333333333344444444444444 00000111111111222223566677889990001112222233344556899911111233444555 45678012356789023483901246040892897890234901519476526901237425289089
Circellium bacchus	GATCAATTAATAAACGAAACGATTTTTAGTTATTTCCTCTCCAAATCTGTGGCAAAT-AACGAAATAC
Heliocopris hamadryas	TCTCTATTCTAAAATAAAACGAATCTTAATTATTTTTTTTCCCGTACTATGGCATAT-AACAATAACC
Eucranium arachnoides	TTTCAAAAAATCAAATTAACGTTTTTTAATTATTTCTTTTCGAGTACTATGGCAAACATACGAAATAC
Anomoipsodes heteroclytus	TTTCGAATAATTAAAGTAATGTTTTTTGATTATTTCTTTTCTCGTACTATGACAAGCATATGAAATAC
S. [Drepanopodus] proximus	TTTCAAATATTATATAAAATTATTTTTAATTATTTCTTCCCCAATATTATGGCGAATGTATGTAATAC
S. (Kheper) nigronaeneus	ATCCAAATATTAATATAAATAATATTTAATTATTTATTTCTCAATTTTAGGACAAAA-TACGATATCC
S. (Kheper) subaeneus	TTCTAATTATTAAATTAAATATATTTTAATAATTTATTTCTCAATTTTAGGACAATT-AATGATATCC
S. [Neateuchus] proboscideus	TTTCAAATAATATAGGGAATAATCTTTAAATATCTATTCCCCAATATTATGGCGAGTATTCGTAATCC
S. (Pachysoma) bennigseni	TTTTAAACAATACTTATTATAGTTTTTAATATTTTTTTTCCCAATATTATGACGAATATGTGTAATAC
S. (Pachysoma) hippocrates	TTTTAAATAATATATATAATAATTTTTAAAAATTTCTTCCCCAATATTATGACATATATACGAAATAC
Pachylomerus femoralis	TTTTAAATACTATATAAAATAGTTTTTAATTATTTCTTCCCCAATATTATAGTGAA---ATGTGATAC
S. (Scarabaeolus) bohemani	TTTTAAATAATATATAAAATAATTTTTAATTATTTTTCCCCCAATATTATGACGAATATATGTACTAC
S. (Scarabaeolus) flavicornis	TTTCAAATAAAATATAAAATAATTTTTAATTATTCTTTCTCCAACATTATGACGAATATATGTTATAC
S. (Scarabaeolus) rubripennis	TTTCAAATATTATATAAAATAATTTTTAATTATTTCCCCTCCAATATTATGACGAATATATGTAATAC
S. galenus	ATATAATTATTATATAAATTATTTTATTATTATTTCTCCCCCAAAATTATGACGAATATATGTAATAC
S. goryi	TCCCAAATAAAAAATAAAATAATTTTTAGTTATTTCTTCCCCAATGTTATGGCGAAT-TACGTAAGCG
S. rugosus	TTTTATACTATATATAAAATATATTTTAATAATTTCTCCCCCAATATTATGACGATTATATGAAATAC
S. rusticus	TTTTAGATTAAATATAAAATAATTTTTAATTATTTCTCCCCCAATATTATGGCGTAT-TACGAACTAC
S. satyrus	TTTCAAATAATATACGAAATAATTTTTAGTGATTTCTTCCCCAATATTATGGCGAGAATACGTTATCC
S. westwoodi	TTTTAAATAATATATAAAATAATCTTTAATTATTTCTCCCCCAATATTATGACGATA-TACGAAATAC
S. zambesianus	TTTCAAATAATATAGGGAATAATTTTTAAATATCTATTCCCCAATATTATGGCGAGTATCCGTAATCC
S. (Sceliages) adamastor	TTTTAAATAAAATATTAAATAATTTATAATAACTTTTTTCCTCAATATTATGACGAAT-TATGTAATAC
S. (Sceliages) brittoni	TTTTAAATAAAATATTAAATAATTTACAATTACTTTTTTTCCCAATATCATGACGATT-AATGTAATAC
S. (Sceliages) hippias	TTTTAAATAAATTATAAAATAACTTATAATAACTTTTTTCCTCAATATTATGACGAAT-AACGTAATAC

General Conclusions

Due to the size of the morphological character set and the robustness of the analyses, we do not expect any significant changes in overall tree topologies with the inclusion of additional morphological data or taxa.

High levels of homoplasy in the morphological data prevented the complete resolution of all intermediate and deep level nodes supporting relationships between less closely related lineages. It was predicted the inclusion of molecular data of the same taxa would further resolve these relationships. However, it became obvious the limitations of this study resulted from poor resolution achieved by the COI and 16S genes and conflicting signals and between the molecular and the morphological data sets. Whilst Resolution was achieved in all analyses between the closely related taxa providing good support for Scarabaeini systematics and several phylogenetic inferences, estimations of the true phylogeny of the tribe became difficult when all morphological and molecular characters were combined and analysed simultaneously.

In the first chapter we were able to describe some behavioural characteristics of the adult *Sceliages* beetles provisioning nests with millipedes for nidification. Many questions, however, remain unanswered: We know quinonous secretions of millipedes are responsible for attracting *Sceliages*, however, this was tested by stimulating a defensive reaction by millipedes. In a natural situation, are *Sceliages* beetles attracted to these secretions produced as allomones in response to the millipede being threatened or injured, and/or to these secretions being used as pheromones during millipede mate attraction and copulation? Do *Sceliages* beetles kill uninjured millipedes they may have been attracted to, or, must they rely solely on the demise of injured millipedes? Is *Sceliages* truly an obligate necrophage or are other food types also utilized? Are millipedes utilized for maturation feeding or nuptial courtship? Exactly how is the millipede

disarticulated? A leverage action using the clypeal teeth and protibial external denticles is inferred (Villalobos *et al.*, 1998) but has not been witnessed. We hope that these questions will stimulate further study on the biology of *Sceliages*.

Further attention needs to be directed towards the biology of the flightless Scarabaeini, *Mnematium ritchiei*, *M. silenus* and *Neomnematium sevoistra*. Sampling of these flightless taxa is necessary to gain molecular perspective on the levels of divergence between these lineages and those of South Western Africa, and whether or not there is molecular support for the monophyly of flightlessness.

Additionally, it would be interesting to further test relationships between the "ball-rolling" Scarabaeini that never or rarely horizontally relocate food resources (Halffter and Halffter, 1989) and those that do so exclusively. Both *Pachylomerus femoralis* and *Scarabaeus galenus* represent links between rolling and tunnelling by exploiting both behavioural strategies whilst equipped with true telecoprid morphologies