

## CHAPTER 1

### GENERAL INTRODUCTION

The genus *Pachysoma* MacLeay, 1821 is a member of the large (4940 species) and variable (234 genera) subfamily of Scarabaeidae, the Scarabaeinae (Hanski and Cambefort 1991). Scarabaeines, or dung beetles, feed mostly on dung although they also feed on carrion, humus and fungi (Scholtz and Chown 1995). The subfamily Scarabaeinae is divided into 12 tribes that show a basic behavioural dichotomy, i.e. those that bury the dung in preformed burrows at the food source (Coprini, Oniticellini, Onitini, Onthophagini, Dichotomiini and Phanaeini), and those that remove dung (usually as balls) and bury it some distance from the dung source (Scarabaeini, Canthonini, Gymnopleurini, Sisyphini, Eucraniini and some Eurysternini), (Hanski and Cambefort 1991). The tribe Scarabaeini, which is of concern here, following Mostert and Scholtz's (1986) system is currently represented by five genera, i.e. *Scarabaeus* Linnaeus, 1758 (which includes *Pachysoma* MacLeay, 1821; *Neopachysoma* Ferreira, 1953; *Mnematum* MacLeay, 1821; and *Neomnematum* Janssens, 1938); *Kheper* Janssens, 1940; *Sceliages* Westwood, 1837; *Drepanopodus* Janssens, 1940 and *Pachylomerus* Bertoloni, 1849. However, Endrödy-Younga (1989) and Scholtz (1989) retain *Pachysoma* at the subgeneric and generic levels, respectively. The tribe has an Old World distribution, occurring throughout Africa, Asia, the Middle East and southern Europe, and is found in moist savanna through drier regions to very hot, dry deserts (Scholtz 1989).

#### Conservation rationale for the study

The 13 species of *Pachysoma* examined here are endemic to the arid, sandy coastal area of southwestern Africa from Cape Town (3356'S 1828'E) to Walvis Bay (2258'S 1430'E), (Holm and Scholtz 1979). They are all flightless, collect dry dung or detritus for food and can survive in an arid environment (Scholtz 1989). Within this range *Pachysoma* species have discontinuous distributions owing to their low vagility (they are all flightless), specificity to particular sandy habitats, and historical factors. Thus, *Pachysoma* species distributions consist of small isolated populations, and many of these populations are potentially threatened by habitat disturbance.

Habitat destruction and/or deterioration (direct or indirect) is arguably the greatest threat to insect diversity (Collins and Thomas 1991, Gaston *et al.* 1993, Pyle *et al.* 1981, Samways 1994). This is especially true for species that have specific habitat requirements and restricted distributions. For example, the flightless lucanid genus *Colophon* Gray only has species endemic to peaks in the Cape Mountain Biome (Endrödy-Younga 1988). *Colophon* species are probably threatened by insect collecting for resale purposes. The flightless canthonine *Circellium bacchus* (Fabricius), whose historical range has diminished due to habitat

modification and loss of a persistent dung source, is of conservation concern (Coles 1994, Chown *et al.* 1995, Tukker 1999).

*Pachysoma* species occur in the Succulent Karoo, Fynbos and Desert Biomes (Holm and Scholtz 1979, Rutherford and Westfall 1994). These biomes contain vegetation types of conservation priority (Hilton-Taylor and Le Roux 1989). Potential threats to the conservation of *Pachysoma* specifically include the following: removal of the natural vegetation for large scale wheat farming, south western Cape; commercial development on the West Coast for holiday and recreational purposes, e.g. Lambert's Bay and Strandfontein; industrial development and its supporting infrastructure, e.g. possible harbour at Port Nolloth; mining for diamonds and other minerals, e.g. Namaquasands, Alexkor, DeBeers mines (but see Mackenzie and Molyneux (1996) for positive effects of mining companies owning large sections of unmined and pristine land, large portions (55 km of coastline) of which are already earmarked for a National Park); exotic plant invaders modifying dune systems, e.g. Port Jackson (*Acacia saligna*) and Rooikrans (*Acacia cyclops*); and potentially the collecting and sale of *Pachysoma* for commercial gain (especially in species with narrow distributions). Due to the above factors, precise knowledge of their taxonomy, distribution and habitat requirements is essential to initiate conservation plans.

This project was initiated out of concern for the future conservation of *Pachysoma* species. The initial scope was refined by circumstances and time. Thus, no conservation plans are included here. Nevertheless, the updated taxonomy, precise distribution data and a better understanding of *Pachysoma*'s habitat preference provides the foundation for future conservation efforts.

### **Adaptations of *Pachysoma* to the Desert Biome**

Deserts are thought to pose considerable constraints to the survival and reproduction of animals and plants. Morphological, behavioural and physiological adaptations permit desert animals to survive the severity of an arid climate and to reduce water loss (Scholtz and Caveney 1988, Cloudsley-Thompson 1991, Costa 1995, Sømme 1995). *Pachysoma* species have a variety of morphological adaptations to deal with their arid environment. All *Pachysoma* have fused elytra due to the loss of flight, and the resulting subelytral cavity is thought to reduce water loss in flightless desert trogids, tenebrionids and other scarabs via spiracular transpiration, because the spiracles open into a sealed cavity (see Scholtz 1981, Draney 1993, Chown *et al.* 1998). *P. garipepinum*, *P. striatum* and *P. endroedyi* all have a waxy layer of indument around the periphery of the elytra. Desert tenebrionids produce wax blooms that function to reduce water loss (McClain and Gerneke 1990). *P. rodriguesi* and *P. hippocrates* are the largest diurnal scarab species in their biomes. The large body size of *Pachysoma* potentially enables them to store more water and body fat than the smaller sympatric flying dung scarabs. Klok (1994) compared the desiccation resistance of dung beetles from mesic and arid

environments and discovered that *P. garipeinum* and *P. striatum* both have high resistance to desiccation. The principal mechanism accounting for this desiccation resistance is a reduced rate of water loss, while other factors that contributed are large body size and their behavioural ecology (Klok 1994). These two *Pachysoma* species also have excellent haemolymph osmoregulatory capabilities (Klok 1994), that is, the process by which an organism maintains control over its internal osmotic pressure despite variations in the environment. *Pachysoma* beetles are thus well-adapted to their arid environment.

### **Taxonomic history of *Pachysoma* and other flightless Scarabaeini**

The 17 flightless species of Scarabaeini were described in five genera; three in *Scarabaeus* and in *Mnematium*, eight in *Pachysoma* and one species each in *Neomnematium* and *Neopachysoma*. Most recently, *Scarabaeus (Scarabaeolus) scholtzi*, was described (Mostert and Holm 1982).

As early as 1919 Arrow noted the dilemma of some morphological systematists when deciding the taxonomic placement of the flightless Scarabaeini. He commented that 'I refrain from establishing a new genus for this species [*Mnematium cancer*] in view of the unsatisfactory character of several of those at present recognised in the group'. Ferreira (1953) however, established the subtribe Pachysomina for the flightless dung beetles on the southwestern coast of southern Africa and the other flightless scarabs from Libya (*Mnematium ritchiei* MacLeay), Egypt, Iraq and Iran (*Mnematium silenus* Gray), Madagascar (*Neomnematium sevoistra* (Alluaud)) and Angola (*Mnematium cancer* Arrow).

In their evaluation of the subtribe Pachysomina, Holm and Scholtz (1979) argued that the characters defining Pachysomina all relate to aptery either directly (aptery or absence of humeral calli) or indirectly (contiguous mesocoxae, and short mesostema). They concluded that the subtribe Pachysomina, as defined, lacks any demonstrable synapomorphic characters and therefore has no phylogenetic justification. The Pachysomina genera *Mnematium* and *Neopachysoma* were based on the shape of the genae, the length of the third segment of the maxillary palps, and additional characters of the maxillary palp, protibia, mesotibia and mesofemur that Holm and Scholtz (1979) interpreted to show no meaningful difference between *Pachysoma*, *Mnematium* and *Neopachysoma*. Thus, Holm and Scholtz (1979) synonymised *Mnematium* and *Neopachysoma* with *Pachysoma*.

Subsequently, based on new findings, Mostert and Holm (1982) synonymised *Pachysoma* and *Neomnematium* Janssens, 1938 with the widespread and variable genus *Scarabaeus sensu stricto*, because, except for morphological characters associated with aptery, these genera did not differ significantly from *Scarabaeus sensu lato*. These findings included the following: (1) two species of flightless Scarabaeini, i.e. *Scarabaeus (Scarabaeolus) scholtzi* and *Mnematium silenus*, that both have a vestigial second mesotibial spur that places them in the subgenus *S. (Scarabaeolus) (sequens* Balthasar 1965; Mostert and Scholtz 1986) rather

than the subgenus *S. (Scarabaeus)*; (2) *Pachysoma gariepinum* was observed by Mostert and Holm (1982) making and rolling a dung ball. These findings suggest a polyphyletic origin of the flightless Scarabaeini, and question the validity of using the unique foraging behaviour of *Pachysoma* as a behavioural synapomorphy. Thus, as no synapomorphic characters were discovered by Mostert and Holm (1982) to justify these genera phylogenetically, they synonymised *Pachysoma* and *Neomnematium* with *Scarabaeus*.

Since the synonymy of all the genera containing flightless Scarabaeini with *Scarabaeus*, there has been little adherence to the proposed new system. Scholtz (1989) stated that 'In spite of it being strictly taxonomically incorrect, I have chosen to treat *Pachysoma* as valid because of its distinctiveness and its unique feeding behaviour...'. While in a paper entitled 'The evolution of alternative life styles in Coleoptera' Endrödy-Younga (1989) treated *Pachysoma* and *Neopachysoma* as subgenera although these names have never been published as such. Zunino (1991) followed Scholtz's (1989) use of *Pachysoma* when discussing food relocation behaviour in Coleoptera. In a study of the cost of transport and ventilatory patterns in three flightless beetles, Lighton (1985) uses *Pachysoma hippocrates* but incorrectly refers to it a ball roller. Klok (1994) needed to use *Pachysoma* to differentiate it from the flying *Scarabaeus* in a study of the desiccation resistance of dung beetles. Most recently Chown *et al.* (1998) included *Pachysoma* in a morphological study of the Scarabaeini and Canthonini. There is thus an obvious need to maintain the name *Pachysoma* at either generic or subgeneric level for practical diagnostic purposes. However, such a decision will only be readily accepted (if ever a consensus is possible) if it well supported by a phylogenetic study, as is undertaken here.

## Phylogeny

Although Holm and Scholtz (1979) drew up a table of morphological characters for the flightless Scarabaeini, they had difficulty in interpreting these characters and did not draw a cladogram or dendrogram. Mostert and Holm (1982) listed four groups of species based on overall similarity and apparent synapomorphies, but went no further. Davis (1990) plotted a dendrogram based on Holm and Scholtz's (1979) table of morphological characters (see chapter 2 for details under species groups). Justification to analyse phylogenetically the flightless Scarabaeini is thus evident, especially because no study has used cladistic methods to examine this group of morphologically similar, but phylogenetically puzzling species.

Cladistics offer a rigorous method of hypothesising relationships between the flightless Scarabaeini. Cladistics is a taxonomic theory by which organisms are ordered and ranked exclusively based on shared descent from a single ancestral species, (i.e. based on the most recent branching point of the inferred phylogeny) and in which taxa are delimited by holophyly (Mayr and Ashlock 1991). Thus, a cladogram should help to understand the possible evolution of the flightless Scarabaeini. A cladistic analysis might also provide the evidence to take a

decision on the current generic classification of the flightless Scarabaeini, either maintaining synonymy with *Scarabaeus*, or reinstating *Pachysoma* to generic or subgeneric level.

## Biology of *Pachysoma*

An especially intriguing set of adaptations ascribed to *Pachysoma* is their foraging and feeding behaviour. Typical food relocation behaviour of *Pachysoma* is as follows: random searching for dry dung pellets or plant matter (detritus); burrow construction nearby after food location; no ball formation but rather the food is held in the hind legs and dragged forward; food storage in the preconstructed holding chamber; repetition of foraging to provision the chamber; elaboration of the nest below the soil moisture line, before moving the food from the holding-chamber to the feeding/nesting chamber (Scholtz 1989). This differs markedly from the typical ball rolling behaviour of the flying Scarabaeini, i.e. *Scarabaeus*, *Kheper* (Edwards and Aschenborn 1988, Halffter and Edmonds 1982, Sato and Imamori 1987), *Sceliages*, and *Drepanopodus* (Mostert and Scholtz 1986).

Additional information on the evolution of the foraging, feeding and breeding behaviour of *Pachysoma* is of interest for three main reasons. First, to determine whether their foraging biology is unique in the Scarabaeinae. Second, because they do not make and roll a dung ball like all other Scarabaeini, the question of how they construct a brood-pear from dry pelleted dung is raised. Third, their biology has previously been used as a behavioural synapomorphy for *Pachysoma* as a genus (Holm and Scholtz 1979, Scholtz 1989), and is thus of considerable taxonomic interest.

## Taxonomy

*Pachysoma* species are relatively rare in collections (based on available museum material and in comparison to other dung scarabs). This is due to their restricted, patchy distribution in isolated places, seasonal activity tied to very unpredictable rainfall, and a disinterest by *Pachysoma* for fresh dung or carrion, which are often used as baits for short-term, dung beetle pitfall trapping. Furthermore, many of the available specimens have no habitat data, or it is very general or inaccurate. To collect *Pachysoma* specimens with accurate distribution data, and investigate threats to the conservation of *Pachysoma*, six months were spent in the field collecting and studying the South African *Pachysoma* species. This was deemed essential for improving taxonomic resolution within the group.

## The thesis

The above questions are investigated in chapters two and three of this thesis, written and formatted as two independent papers for '*Journal of Natural History*'.

Chapter two, 'Phylogeny of *Pachysoma* MacLeay and related flightless Scarabaeini (Scarabaeidae: Scarabaeinae)', is a cladistic study of the phylogenetic relationship among species attributed to *Pachysoma* (including *Neopachysoma*) and representatives of the other flightless Scarabaeini genera (viz. *Mnematium* and *Neomnematium*). Available biological information is discussed in view of the unique feeding preference and foraging behaviour of *Pachysoma*. An evolutionary history of *Pachysoma* is proposed based on the phylogenetic analysis, biology, wing status and substrate preference.

Its main aims are therefore to:

- 1) Provide cladistic evidence to support the taxonomic placement of *Pachysoma*.
- 2) Hypothesise the phylogenetic relationship between species attributed to *Pachysoma*.
- 3) Examine the phylogenetic relationship between the southern African flightless Scarabaeini and those from North Africa, the Middle East, Somalia and Madagascar.
- 4) Estimate the main conditions or factors that led to the evolution and proliferation of *Pachysoma*.
- 5) Examine the phylogenetic relationship between the Scarabaeini genera.

Chapter 3, 'Systematics of the endemic southwest African dung beetle subgenus *Scarabaeus* (*Pachysoma*) MacLeay, with notes on the other flightless Scarabaeini (Scarabaeidae: Scarabaeinae)', was initiated by the discovery of two new species of *Pachysoma*. As the study progressed, I realized that an update on the last revision, published 20 years ago, was appropriate. Standard taxonomic practices are applied to a small group of species.

Its main aims are therefore to:

- 1) Describe the two new species of *Pachysoma*.
- 2) Update and refine the distribution of all species of *Pachysoma*.
- 3) Reinvestigate previously proposed clines.
- 4) Reevaluate synonyms from areas where previously no specimens were available for study.
- 5) Clarify the status of primary and secondary types where new information and previously mislaid specimens permit.
- 6) Update biological and ecological knowledge where possible.
- 7) Include comments on the other flightless Scarabaeini for the sake of completeness.

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## Phylogeny of *Pachysoma* MacLeay and related flightless Scarabaeini (Scarabaeidae: Scarabaeinae)\*

The phylogenetic validity of *Pachysoma* MacLeay, 1821, is assessed. Cladistic analysis of 64 adult characters from 37 taxa comprising all Scarabaeini genera (except the monotypic *Madateuchus* Paulian, 1953) and two outgroup Canthonini genera, resulted in some currently recognised genera (i.e. *Sceliages* Westwood, 1837; *Kheper* Janssens, 1940; and *Drepanopodus* Janssens, 1940) being recognised as paraphyletic. *Pachysoma* comprises a monophyletic clade of highly derived *Scarabaeus* Linnaeus, 1758. To further nomenclatural stability within the Scarabaeini, *Pachysoma* should best be considered a subgenus of an expanded genus *Scarabaeus*. *Neopachysoma* Ferreira, 1953; *Mnematum* MacLeay, 1821 and *Neomnematum* Janssens, 1938 are maintained as synonyms of *Scarabaeus s.l.* The unique biology of *Pachysoma* is interpreted as an adaptation to arid conditions, and is presumably derived from ball rolling and wet dung feeding. Aridification of the Namib Desert is postulated to have initiated the evolution of *Pachysoma* from a *Scarabaeus*-like ancestor, while dune movement accounts for their current distribution. The evolutionary history of *Pachysoma* is discussed based on the phylogenetic analysis, and distributional and biological information.

KEYWORDS: Phylogeny, *Pachysoma*, *Scarabaeus*, *Kheper*, *Sceliages*, *Drepanopodus*, *Pachylomerus*, biology, psammophily, aptery.

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### Introduction

The genus *Pachysoma* MacLeay, 1821 is considered a synonym of the large and variable genus *Scarabaeus* Linnaeus, 1758 (Mostert and Holm 1982). However, *Pachysoma* species share a variety of features that are absent in *Scarabaeus sensu stricto*. These include: unique foraging and feeding biology (Scholtz 1989), a high degree of morphological similarity due to common ancestry or flightlessness, and a restricted southwestern African distribution. The synonymy of *Pachysoma* with *Scarabaeus* (Mostert and Holm 1982) has been questioned by various authors, e.g. Scholtz (1989) and Endrödy-Younga (1989). Since no phylogenetic study has examined the relationship between *Pachysoma* and the other Scarabaeini genera, the validity of *Pachysoma* as a genus is investigated here.

MacLeay (1821) described the genera *Pachysoma* and *Mnematium* for flightless species of Scarabaeini from the southwestern Cape and Libya respectively. Subsequently, most flightless species of Scarabaeini were placed within *Pachysoma* or *Mnematium*. The only known flightless species of Scarabaeini from Madagascar was described as *Scarabaeus sevoistra* Alluaud, 1902. It was moved to *Neateuchus* by Gillet (1911) and then the genus *Neomnematium* was created by Janssens (1938) for it. Ferreira (1953) created *Neopachysoma* to differentiate between the central Namib species of *Pachysoma* from those of the southwestern Cape, and unified all the genera containing flightless species of Scarabaeini within the subtribe Pachysomina (tribe Scarabaeini).

The subtribe Pachysomina was defined by the following characters: (1) apterous; (2) absence of humeral calli; (3) semi-contiguous mesocoxae; (4) short mesostema. Holm and Scholtz (1979) evaluated these characters and concluded that they were either due to convergence or were too variable and inconsistent for a clear division between the subtribes Scarabaeina and Pachysomina. They found no support for the separation of *Neopachysoma* and *Mnematium* and consequently synonymised them with *Pachysoma*. However, although *Pachysoma* was suspected to be paraphyletic or polyphyletic in origin, they tentatively maintained *Pachysoma* as a genus due to its unique foraging and feeding biology.

The unique foraging behaviour of *Pachysoma* species was first documented by Holm and Scholtz (1979). Scholtz (1989) provided the first detailed study on foraging and nest construction of a *Pachysoma* species, that of *P. striatum*. Typically, food selection and foraging behavior in *Pachysoma* are as follows: (1) random searching for dry dung pellets or plant detritus; (2) excavation of a holding-chamber nearby, after food location; (3) no ball construction but instead the food is held by the hind legs and dragged forward to the preconstructed holding-chamber; (4) repetition of foraging to provision the same holding-chamber; (5) enlargement of the nest by excavation of a second chamber below the moisture line in the soil, before the food is moved from the holding-chamber to the feeding or nesting-chamber; (6) finally the closure of the nest tunnel and entrance with sand. This foraging strategy differs significantly from the flying members of the tribe Scarabaeini, i.e. *Scarabaeus*, *Kheper* (see Halffter and Edmonds 1982, Edwards and Aschenborn 1988, Sato and Imamori 1986a,b, 1987, 1988), *Sceliages* and *Drepanopodus* (Tribe 1976, Mostert and Scholtz 1986), which all collect fresh dung (or millipedes in the case of *Sceliages*) and form a ball that is relocated and buried. The foraging strategies and food selection differ between *Pachysoma* and the other flying Scarabaeini in the following respects: (1) *Pachysoma* collects only dry, not wet food; (2) *Pachysoma* digs a holding-chamber before and not after food relocation begins; (3) *Pachysoma* does not construct a dung ball, and makes many foraging trips to provision the nest; (4) *Pachysoma* only drags the food forward rather than pushing it backwards. The foraging behaviour of *Mnematium* species is unknown, although Arrow (1919) and Balthasar (1963) assume that they are ball rollers.

New discoveries by Mostert and Holm (1982) enabled them to reevaluate *Pachysoma* and to examine *Neomnematium* excluded from the study by Holm and Scholtz (1979). They described a new flightless species *Scarabaeus (Scarabaeolus) scholtzi* from the Somali-Chalbi Desert (Costa 1995) that matches *Pachysoma* in all aspects of its morphology, but they claimed it belongs to the subgenus *Scarabaeolus (secundum, i.e. 'according to' Balthasar 1965, and Mostert and Scholtz 1986)*. Further investigation by Mostert and Holm (1982) revealed two mesotibial spurs (i.e. one vestigial and one large) in *Mnematium silenus*, placing it also within the subgenus *Scarabaeolus*. Only two of the 18 species of flightless Scarabaeini share this subgeneric characteristic, which suggests a polyphyletic origin of the north and east African flightless Scarabaeini. Mostert and Holm (1982) also questioned the behavioural uniqueness of *Pachysoma* as a potential synapomorphy for the genus after *Pachysoma garipepinum* was observed in the field making and rolling a dung ball. Based on the above evidence they synonymised *Pachysoma* and *Neomnematium* with *Scarabaeus, s.l.* However, no phylogenetic analysis was undertaken to support the synonymy of *Pachysoma* with *Scarabaeus*.

In this study the phylogenetic validity of *Pachysoma* as genus is evaluated for the first time using cladistic methods. The phylogenetic relationships among all the flightless (i.e. *Pachysoma, Neopachysoma, Mnematium* and *Neomnematium*) and flying genera (i.e. *Scarabaeus, Kheper, Drepanopodus, Sceliages* and *Pachylomerus*) of the tribe Scarabaeini, are also examined. All available biological information pertinent to understanding the possible origin of *Pachysoma*'s unique food-selection and foraging behaviour is examined. Evolutionary trends relating to flightlessness, food preference, food relocation, dominant substrate, mesocoxal distance, and larval development within the Scarabaeini, are discussed. Hypotheses are proposed for the evolution of alternative life history strategies in the *Pachysoma* clade, and their dispersal in the Namib Desert.

## Materials and Methods

### Taxa

The subfamily classification of Scholtz and Chown (1995), and tribal level classification of Hanski and Cambefort (1991), is followed here for the Scarabaeidae. This study is based on all species in the genera *Pachysoma, Neopachysoma, Mnematium* and *Neomnematium* within the tribe Scarabaeini (table 1). The tribe currently includes the following five genera: *Scarabaeus* (90+ species); *Kheper* (21 species); *Sceliages* (six species); *Drepanopodus* (two species); and *Pachylomerus* (two species) (*sequens* i.e. following zur Strassen 1967; Janssens 1940; zur Strassen 1965; Mostert and Scholtz 1986, respectively). All these genera and most of their species were available for study in the extensive dung beetle collections of the Transvaal Museum, Pretoria and the 'CSIRO Dung Beetle Research Unit' Collection, now housed at the National Collection of Insects, Pretoria. Species not housed in the above collections were borrowed from the museums listed in the acknowledgments.

*Scarabaeus sensu stricto* (s.s.); *sensu lato* (s.l.); and *sensu amplificato* (s.a.) as used in this study are defined as follows. *Scarabaeus* s.s. includes only the flying members of the genus which can be unequivocally placed in *Scarabaeus* (*sequens* zur Strassen 1967). *Scarabaeus* s.l. also includes the flightless members of *Scarabaeus* (i.e. *Pachysoma*, *Neopachysoma*, *Mnematium* and *Neomnematium sequens* Mostert and Holm (1982)) and other flying genera considered by Mostert and Scholtz (1986) to be synonymous with *Scarabaeus* (i.e. *Mnematidium*, *Neateuchus* and *Madateuchus*). *Scarabaeus* s.a. includes the above and the genera *Kheper*, *Sceliages*, and *Drepanopodus*. *Pachysoma sensu stricto* (s.s.) excludes species included by Ferreira (1953) in *Neopachysoma*, while *Pachysoma sensu lato* (s.l.) includes these species.

To examine the phylogenetic relationships among *Pachysoma*, *Neopachysoma*, *Mnematium* and *Neomnematium*, and the other genera within the tribe Scarabaeini, a representative species from all recognized and synonymised Scarabaeini genera (*sequens* Mostert and Scholtz 1986) was included in the analysis. The following guidelines were used to choose species: (1) species previously placed within their own genera, which by definition represent the morphological diversity within the tribe; (2) type-species of the Scarabaeini genera; (3) southwestern African coastal endemics, before eurytopic species; (4) and species with known biologies from literature or field experience. Thus, under criterion one and two the type species for the following genera were included: *Scarabaeus* Linnaeus, 1758; *Mnematium* MacLeay, 1821; *Pachysoma* MacLeay, 1821; *Sebasteos* Westwood, 1847; *Pachylomerus* Bertoloni, 1849; *Octodon* Lansberge, 1874; *Mnematidium* Ritsema, 1889; *Neoctodon* Bedel, 1892; *Parateuchus* Shipp, 1895; *Irrorhotides* Shipp, 1896; *Neateuchus* Gillet, 1911; *Neomnematium* Janssens, 1938; and *Neopachysoma* Ferreira, 1953. The only Scarabaeini genus not included due to lack of material, is *Madateuchus viettei* Paulian, 1953 a rare Madagascan monotypic genus considered a synonym of *Scarabaeus* (see Mostert and Scholtz 1986).

Twelve species of winged *Scarabaeus* were chosen to represent the morphological and biological diversity within *Scarabaeus* s.s. (table 1). These species include the following: *Scarabaeus sacer* Linnaeus, 1758 (type-species of *Scarabaeus*); *Scarabaeus galenus* (formerly in the genus *Sebasteos* Westwood, 1847); *Scarabaeus multidentatus* (formerly *Octodon* Lansberge, 1874; *Mnematidium* Ritsema, 1889; and *Neoctodon* Bedel, 1892); *Scarabaeus proboscideus* (formerly *Neateuchus* Gillet, 1911; and a species with two foraging strategies); *Scarabaeus rugosus* (coastal Namaqualand endemic; two foraging strategies); *Scarabaeus catenatus* (two foraging strategies); *Scarabaeus caffer* (two foraging strategies); *Scarabaeus westwoodi* (unusual head morphology, otherwise a typical telecoprid); *Scarabaeus rusticus* (typical telecoprid); *Scarabaeus* (*Scarabaeolus*) *intricatus* (coastal Namaqualand endemic; typical telecoprid); *Scarabaeus* (*Scarabaeolus*) *rubripennis* (coastal Namib Desert endemic; typical telecoprid); and *Scarabaeus* (*Scarabaeolus*) *palemo* (formerly *Parateuchus* Shipp, 1895) (see table 1).

Representative species of the other Scarabaeini genera were included. These are: *Sceliages brittoni*; *Drepanopodus proximus*; *Kheper bonellii*; *Kheper lamarcki* and *Pachylomerus femoralis* (see table 1). *Sceliages brittoni* is the largest species in the genus and endemic to the coastal sands on the southwestern African coast. The two species of *Drepanopodus* both inhabit arid areas, i.e. the Kalahari and Namib Deserts. The coastal *Drepanopodus proximus* was chosen. *Kheper bonellii* is a coastal endemic in southwestern Africa, while *Kheper lamarcki* and *Pachylomerus femoralis* have a wider southern African distribution. To differentiate between *Pachysoma* [P.] and *Pachylomerus* [Pa.], and between *Scarabaeus* [S.], *Scarabaeolus* [Sc.] and *Sceliages* [Sce.], the bracketed abbreviations are used. Voucher specimens of all the species in table 1, except *Mnematum cancer* which has been returned to the BMNH, have been deposited in the TMSA collection.

### Outgroups

In a phylogenetic study of the subfamily Scarabaeinae, Philips and Scholtz (pers. comm.) found *Circellium bacchus* (tribe Canthonini) to be the sister taxon to the Scarabaeini. Thus, character polarity for wingless species is based on this monotypic, flightless, telecoprid species. However, since the tribal placement of *C. bacchus* has varied between the Scarabaeini (Janssens 1938, Ferreira 1969) and the Canthonini (Cambefort 1978, Mostert and Scholtz 1986, Scholtz and Howden 1987), *Anachalcos convexus* (tribe Canthonini) was also included as an outgroup that would assist in polarizing winged species. Additionally, in Doube's (1990) functional classification of dung beetle assemblages, *A. convexus* is included in FGI with the larger (>400 mg dry weight) species of *Scarabaeus*, *Kheper* and *Pachylomerus*.

### Morphological analysis and character set

The chosen taxa (listed in table 1) were all examined macro- and microscopically using Zeiss® dissecting and compound microscopes. Mouthpart terminology follows Nel and Scholtz (1990) while that of Lawrence and Britton (1991) is used for gross morphology. To dissect out male genitalia, beetles were placed in boiled distilled water (90-99 °C) for a few minutes to soften the tissue before carefully removing the aedeagus with fine forceps. Genitalia were then fixed onto cardboard points with water soluble glue ('Otto Ring's fluessiger Leim Syndetikon', available from Bioform in Germany).

Mouthparts were dissected out by softening the whole beetle as described above. To remove the whole head it was gently twisted to both sides, before pulling forward. The head was placed in lactic acid and left for 24 hours to soften. Larger heads were heated in lactic acid on a hot plate for 12 hours. The mouthparts were then removed as follows: (1) holding the head with fine forceps, the mandibles were prised downwards and forward with a blunt probe; (2) using a micro-scalpel-blade, the labium was separated from the mentum and then teased forward and out with

**Table 1.** Taxa included in the phylogenetic analysis. Their distribution or origin and wing status are included. The generic placement as used by Ferreira (1953) is used to differentiate the flightless taxa, i.e. *Pachysoma*, *Neopachysoma*, *Mnematum* and *Neomnematum* from the flying taxa. However, see *Taxa* for previous generic placement of the flying *Scarabaeus* species.

Tribe Scarabaeini: Ingroup	Distribution and Origin	Wing Status
<i>Neopachysoma rodriguesi</i> Ferreira, 1953	Namib Desert, Namibia	Apterous
<i>Neopachysoma rotundigenum</i> (Felsche), 1907	Namib Desert; Namibia	Apterous
<i>Neopachysoma denticolle</i> (Péringuey), 1888	Namib Desert, Namibia	Apterous
<i>Pachysoma fitzsimonsi</i> Ferreira, 1953	Namib Desert, Namibia	Apterous
<i>Pachysoma vaeiflorae</i> Ferreira, 1953	Namib Desert, Namibia	Apterous
<i>Pachysoma schinzi</i> Fairmaire, 1888	Namib Desert, Namibia	Apterous
<i>Pachysoma bennigseni</i> Felsche, 1907	Namib Desert, Namibia to South Africa	Apterous
<i>Pachysoma ganepinum</i> Ferreira, 1953	Namib Desert, Namibia to South Africa	Apterous
<i>Pachysoma striatum</i> Castelnau, 1840	Namaqualand, South Africa	Apterous
<i>Pachysoma endroedyi</i> sp.n.	Coastal South Western Cape	Apterous
<i>Pachysoma glentoni</i> sp.n.	Coastal South Western Cape	Apterous
<i>Pachysoma hippocrates</i> MacLeay, 1821	Coastal South Western Cape	Apterous
<i>Pachysoma aesculapius</i> (Olivier), 1789	Coastal South Western Cape	Apterous
<i>Mnematum cancer</i> Arrow, 1919	Angola	Apterous
<i>Mnematum silenus</i> Gray, 1832	Sinai Peninsula, Iran, Iraq	Apterous
<i>Mnematum ritchiei</i> MacLeay, 1821	Libya	Apterous
<i>Neomnematum sevoistra</i> (Alluaud), 1902	Madagascar	Apterous
<i>S. (Scarabaeolus) scholtzi</i> Mostert & Holm, 1982	Coastal Somalia	Apterous
<i>S. (Scarabaeolus) intricatus</i> (Fabricius), 1801	Coastal South Western Cape	Macropterous
<i>S. (Scarabaeolus) rubripennis</i> (Boheman), 1860	Namib Desert	Macropterous
<i>Scarabaeus multidentatus</i> (Klug), 1845	Egypt, Northern Sahara Desert	Macropterous
<i>Scarabaeus sacer</i> Linnaeus, 1758	North Africa to Central Asia	Macropterous
<i>Scarabaeus palemo</i> Olivier, 1789	West Africa	Macropterous
<i>Scarabaeus galenus</i> (Westwood), 1844	Southern Africa	Macropterous
<i>Scarabaeus proboscideus</i> (Guérin), 1844	Kalahari to coastal South Western Cape	Macropterous
<i>Scarabaeus caffer</i> (Boheman), 1857	Eastern African Highlands	Macropterous
<i>Scarabaeus catenatus</i> (Gerstaecker), 1871	East Africa	Macropterous
<i>Scarabaeus westwoodi</i> Harold, 1869	Kwazulu-Natal, Drakensberg	Macropterous
<i>Scarabaeus rusticus</i> (Boheman), 1857	Northern South Africa	Macropterous
<i>Scarabaeus rugosus</i> (Hausmann), 1807	Coastal South Western Cape	Macropterous
<i>Drepanopodus proximus</i> (Péringuey), 1900	Coastal Namaqualand	Macropterous
<i>Sceliages brittoni</i> Zur Strassen, 1965	Coastal South Western Cape	Macropterous
<i>Kheper bonellii</i> (MacLeay), 1821	Coastal South Western Cape	Macropterous
<i>Kheper jamarcki</i> (MacLeay), 1821	Southern African to Mega Kalahari	Macropterous
<i>Pachylomerus femoralis</i> (Kirby), 1828	Southern African to Mega Kalahari	Macropterous
<b>Tribe Canthonini: Outgroups</b>		
<i>Circellium bacchus</i> (Fabricius), 1781	Coastal Southern Cape	Apterous
<i>Anachalcus convexus</i> (Boheman), 1857	Africa, South of the Sahara	Macropterous



fine forceps; (3) the mandibles were then pushed inwards and backwards to disarticulate them from the head; (4) a micro-scalpel-blade was slid underneath the anterior edge of the epipharynx, before slicing the tissue holding it to the head; (5) the whole epipharynx (with the mandibles still attached) was then pulled forward and out. After rinsing the mouthparts in 90% ethanol, they were placed in glycerine on microscope slides for examination; (6) after examination the mouthparts were placed in micro-vials filled with glycerine on the same pin as the voucher specimen.

Looking especially for characters that would differentiate *Pachysoma* from *Mnematum* and *Scarabaeus*, more than 90 potential characters were selected and scored against the 37 taxa. However, many were discarded because they were difficult or impossible to code consistently and objectively. The following characters, traditionally used to define the Scarabaeini genera, were also included: (1) the number and size of tarsal claws and mesotibial spurs; (2) the number and form of protibial teeth; (3) the profemoral morphology; (4) position of the mesotarsal insertion point on the mesotibia; (5) serrations between and below the protibial teeth; (6) and the shape of the tarsal segments. Characters one to five were useful, but some generic inconsistencies were discovered (e.g. *S. sevoistra* and *S. proboscideus* lack serrations between their protibial teeth, while *S. caffer* has only three protibial teeth like *Kheper*). Character six, as used to define *Sceliages*, varied too much to be reliable (especially when compared with *Neopachysoma* species) and was thus excluded. The final character set included 63 characters, comprising 39 external and 25 internal morphological characters (table 2).

The outgroup method (Watrous and Wheeler 1981, Nixon and Carpenter 1993) was used when deciding the plesiomorphic or apomorphic nature of a character state. The characters used and the resulting data matrix are tabulated in tables 2 and 3 respectively.

### *Phylogenetic analysis*

The data matrix of 37 taxa and 64 characters (16 bipolar; 48 multistate) were entered into the program Dada (Nixon 1998). The data were analysed as non additive (unordered) in the programs Nona and Hennig86. Unordered analyses of the matrix make no assumptions about the character state polarity, (i.e. from plesiomorphic to apomorphic). Trees were calculated using Nona and the following series of commands (rs=zero, i.e. randomized entry of taxa for each calculation; mult\* 50 search, i.e. searches 50 times for the shortest tree; ksv\*, i.e. the tree saving function; best, i.e. to remove trees that rely on arbitrary resolution or pseudotrees), (Goloboff 1993). Hennig86 was used to successively approximate the weight of characters, i.e. those with low homoplasy are given lower weights, with the xs\_w, mhennig\*; bb\* commands (note that mhennig\* constructs several trees, each by a single pass but adding the taxa in a different sequence each time and then applies branch-swapping to each of the trees, retaining just one tree for each initial one (Lipscomb 1994); and bb\* applies branch-swapping to each tree. The strict consensus tree (with the nelsen command) was produced from all the most parsimonious trees discovered (Farris 1988). The



resulting trees and their character states were investigated using the program Clados (Nixon 1993). Node support for the final tree was calculated using 'Phylogenetic Analysis for Sankovian Transformations' or PhAST (Goloboff 1996) and the following settings (hold = 200, i.e. retain 200 trees in memory; branch support = 5, i.e. search for branch support between 0 and >5). PhAST calculates the number of extra steps needed to collapse a branch node. Thus, the higher the decay indexes the greater the support for the respective nodes.

**Table 2.** Description of characters used in the phylogenetic analysis. The consistency index (C.I.) and retention index (R.I.) for each character are included. 0 primitive; 1-5 derived (in sequence); ? unknown character state; - not applicable character state. Refer to appendix 1 for the character matrix.

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**Head:**

0. Surface of the ventral clypeal-teeth: unmodified (0); two teeth each raised into a ridge (1); four teeth each raised into a ridge (2); teeth raised into a small spine (3); teeth raised into a large spine (4). C.I. 0.40, R.I. 0.45.

1. Medial, ventral clypeal-spine: absent (0); small (1); large (2). C.I. 0.22, R.I. 0.65.

2. Clypeal 'scraper': absent (0); ridge only (1); low ridge with a small medial tooth (2); medially incised ridge with or without a medial tooth (3); ridge with an irregular edge (4). C.I. 0.57, R.I. 0.80.

3. Anterior margin between medial clypeal-teeth: 'U' shaped (0); 'V' shaped (1); 'W' shaped (2); convex to straight (3); broad "V" (4). C.I. 0.50, R.I. 0.50.

4. Size of four clypeal-teeth: equal (0); unequal (1); not applicable (-). C.I. 0.20, R.I. 0.69.

5. Outer clypeal-tooth: prominent (0); reduced (1); absent (2). C.I. 0.25, R.I. 0.57.

6. Total number of clypeal-teeth: four (0); two (1); not applicable (-). C.I. 0.25, R.I. 0.50.

7. Genal edge: serrated or irregular (0); unserrated or smooth (1). C.I. 0.16, R.I. 0.61.

8. Genal anterior apex: blunt (0); pointed (1); semi-contiguous with the clypeus (2) contiguous with the clypeus (3). C.I. 0.27, R.I. 0.60.

**Thorax:**

9. Edge of **anterior** pronotal margin: unserrated (0); slightly serrate (1); serrate (2); serrations produced into spike-like-projections (3). C.I. 0.42, R.I. 0.63.

10. Edge of **posterior** pronotal margin: unserrated (0); slightly serrate (1); serrate (2); serrations produced into spike-like-projections (3). C.I. 0.42, R.I. 0.71.

11. Distinct projection on the **anterior** edge of pronotum: absent (0); present, small (1); present, large (2). C.I. 0.25, R.I. 0.62.

**Forelegs:**

12. Fourth protibial tooth: distinct, i.e. equal in size to the 3rd protibial tooth (0); reduced, i.e. half or less the size of the 3rd protibial tooth (1); absent (2). C.I. 0.20, R.I. 0.50.

13. Protibial spur in males: straight (0); strongly curved (1); bifurcate (2); broad and curved downwards (3). C.I. 0.30, R.I. 0.50.
14. Sexual dimorphism of protibia: absent (0); slight (1); marked (2). C.I. 0.13, R.I. 0.35.
15. Distal morphology of protibia: unmodified (0); expanded (1); a distinct protuberance (2). C.I. 0.40, R.I. 0.72.
16. Setae between the protibial teeth: absent (0); sparse (1); dense (2). C.I. 0.33, R.I. 0.20.
17. Serrations between protibial teeth: present (0); absent (1); very slight (2); intermediate, i.e., present and absent (3). C.I. 0.30, R.I. 0.36
18. Serrations below outer protibial teeth: serrate (0); slightly serrate (1); coarsely serrate (2); unserrated (3). C.I. 0.21, R.I. 0.47.
19. Setae below outer protibial teeth: absent (0); sparse (1); dense (2); very dense (3). C.I. 0.33, R.I. 0.68.
20. Inner edge of protibia: serrate (0); slightly serrate (1); unserrated (2). C.I. 0.22, R.I. 0.53.
21. Profemur: unmodified (0); enlarged (1); spined (2); enlarged and spined (3); greatly enlarged and spined (4). C.I. 0.40, R.I. 0.57.

#### **Middle legs:**

22. Mesotarsal spur tip: pointed (0); round (1). C.I. 0.25, R.I. 0.40.
23. Mesotarsal spur: discontinuous from the tibia (0); continuous with the tibia (1). C.I. 0.50, R.I. 0.66.
24. Number and size of mesotarsal spurs: two, well developed (0); two, second spur very reduced (1); one, well developed (2). C.I. 0.40, R.I. 0.25.
25. Mesospur shape: straight (0); slightly sickle-shaped (1); strongly sickle-shaped (2); spatulate (3); strongly spatulate (4). C.I. 0.36, R.I. 0.65.
26. Number of mesotarsal claws: two (0); one (1). C.I. 0.50, R.I. 0.50.
27. Size of mesotarsal claws: two, equally developed (0); two, one reduced (1); two, both reduced (2); one, developed (3); one, reduced (4). C.I. 0.66, R.I. 0.75.

#### **Hind legs:**

28. Metatarsal spur: straight (0); straight but elbowed (1); slightly sickle-shaped (2); strongly sickle-shaped (3); spatulate (4); strongly spatulate (5). C.I. 0.45, R.I. 0.66.
29. Metatibial insertion: apical (0); subapical (1); distal (2). C.I. 0.22, R.I. 0.46.

#### **Elytra:**

30. Humeral callus on elytra: present (0); absent (1). C.I. 0.25, R.I. 0.82.
31. Elytral striae: absent (0); present, shallow (1); present, deep (2). C.I. 0.25, R.I. 0.33.
32. Sub-elytral ridge: absent (0); present but indistinct (1); present and distinct (2). C.I. 0.33, R.I. 0.63.
33. Indument: absent (0); present (1). C.I. 0.50, R.I. 0.50.

**Abdomen:**

- 34.** Mesosternal ridge: very prominent (0); prominent (1); reduced (2); absent (3). C.I. 0.50, R.I. 0.83.
- 35.** Development of setae on mesosternum: well developed (0); reduced (1); absent (2). C.I. 0.33, R.I. 0.78.
- 36.** Area between mesocoxae: oblique and separate (0); semi-contiguous (1); practically contiguous (2); contiguous (3); parallel and separate (4). C.I. 0.50, R.I. 0.76.
- 37.** Mesocoxal incision and/or depression: absent (0); slight longitudinal depression (1); distinct longitudinal depression (2); slight hollow (3); deep hollow (4); broad, shallow hollow, with two small rises (5). C.I. 0.83, R.I. 0.94.
- 38.** Abdominal sternites: all setose (0); some setose (1); none setose (2). C.I. 0.13, R.I. 0.35.

**Aedeagi:**

- 39.** Aedeagus: simple, i.e. paramere points unmodified, no complex hook (0); complex, i.e. paramere points modified, complex hook present (1). C.I. 0.25, R.I. 0.72.
- 40.** Aedeagus: symmetrical (0); asymmetrical (1). C.I. 0.20, R.I. 0.20.

## Aedeagi in anterior view

- 41.** Paramere points: expanded laterally (0); not expanded laterally (1); expanded posteriorly (2). C.I. 0.25, R.I. 0.25.
- 42.** Number of hooks on the aedeagi: none (0); one (1); two (2); three (3); four (4). C.I. 0.33, R.I. 0.50.

## Aedeagi in transverse view

- 43.** Paramere apex: blunt (0); pointed (1); hooked (2). C.I. 0.15, R.I. 0.42.

**Mouthparts:**

## Epipharynx

- 44.** Shape of the apical fringe: slightly concave (0); slightly convex (1); straight (2); strongly bilobed (deeply emarginate) (3); trilobed (4). C.I. 0.40, R.I. 0.68.
- 45.** Shape of the median brush: flat (0); raised into a distinct protuberance (1). C.I. 0.50, R.I. 0.80.
- 46.** Setal structure of the median brush: a small clump of short setae (0); a large clump of short setae (1); a distinct protuberance of setae (2); setal protuberance partially sclerotized (3); the protuberance completely sclerotized (4). C.I. 0.57, R.I. 0.82.
- 47.** A sclerotized protuberance on the anterior margin of the Epipharynx: absent (0); present (1). C.I. 0.50, R.I. 0.93.
- 48.** Anterior membranous lobes: setose (0); hardly setose (1). C.I. 1.00, R.I. 1.00.
- 49.** Large outer lateral combs of setae: two rows fused (0); two rows separate (1); one row (2). C.I. 1.00, R.I. 1.00.
- 50.** Spaces in the anterior median process: large 'D' or 'B' shaped (0); reduced 'tear shaped' (1); other (2). C.I. 1.00, R.I. 1.00.

51. Sclerotized protuberance, protruding over the apical fringe: absent (0); present, horizontally (1); present, vertically (2). C.I. 0.66, R.I. 0.93.

52. Lateral tormal process: well sclerotized, long and thin, nearly touching posterior median process (0); partially sclerotized, short and wide, half the width to the posterior median process (1); other (2). C.I. 1.00, R.I. 1.00.

#### Labium (dorsal)

53. Development of the inner ligular lobe: undeveloped, i.e. small number of unclustered setae (0); developed into a dense clump of thin setae (1); base partially sclerotized with a short tuft of setae on the end (2); well developed and highly sclerotized with a short tuft of setae on the end (3). C.I. 0.42, R.I. 0.80.

54. Setae on the last segment of the labial palps: present (0); absent (1). C.I. 0.50, R.I. 0.92.

#### Maxilla

55. Tentorial apodemes/sclerites: parallel (0); divergent (1). C.I. 0.50, R.I. 0.93.

56. Shape of the anterior edge of the mentum: convex (0); slightly concave (1); deeply concave (2). C.I. 0.50, R.I. 0.88.

57. Distribution of setae on the mentum: uniform (0); concentrated anteriorly (1); two ridges of setae (2). C.I. 0.40, R.I. 0.70.

58. Galea: well developed (0); partially reduced (1); very reduced (2). C.I. 0.66, R.I. 0.93.

59. Galeal morphology: short brush, galea setose (0); long brush, galea unsetose (1). C.I. 1.00, R.I. 1.00.

60. Ventral articulatory sclerite of the galea: unmodified 'V' shaped apodemes (0); highly sclerotized disc, notched anteriorly (1). C.I. 1.00, R.I. 1.00.

#### Mandibles

61. Sculpture on mola surface: smooth (0); finely serrated (1); coarsely serrated (2). C.I. 1.00, R.I. 1.00.

62. Mola apodeme: long, unsclerotized, fan shaped (0); short, sclerotized, trumpet shaped (1); short, sclerotized, fan shaped (2). C.I. 0.66, R.I. 0.93.

63. Shape of apicalis membrane of the mandibles: outer edge continuous (0); outer edge discontinuous (1). C.I. 0.50, R.I. 0.92.

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## Results and Discussion

### *Analysis*

The analysis produced 12 trees, with a length of 400-steps, consistency index (C.I.)=0.36, retention index (R.I.)=0.70. The single successive approximation weighting procedure (Farris 1969) in Hennig86 using the 'xs\_w; mh\*; bb\*;' commands, resulted in a single tree of 823-steps, with C.I.=0.52 and R.I.=0.85 (figure 1). The Nelsons' consensus tree, obtained from the 12 trees in Hennig86 using the 'nelsen;' command was longer, with 415-steps, with C.I.=0.34 and R.I.=0.68.

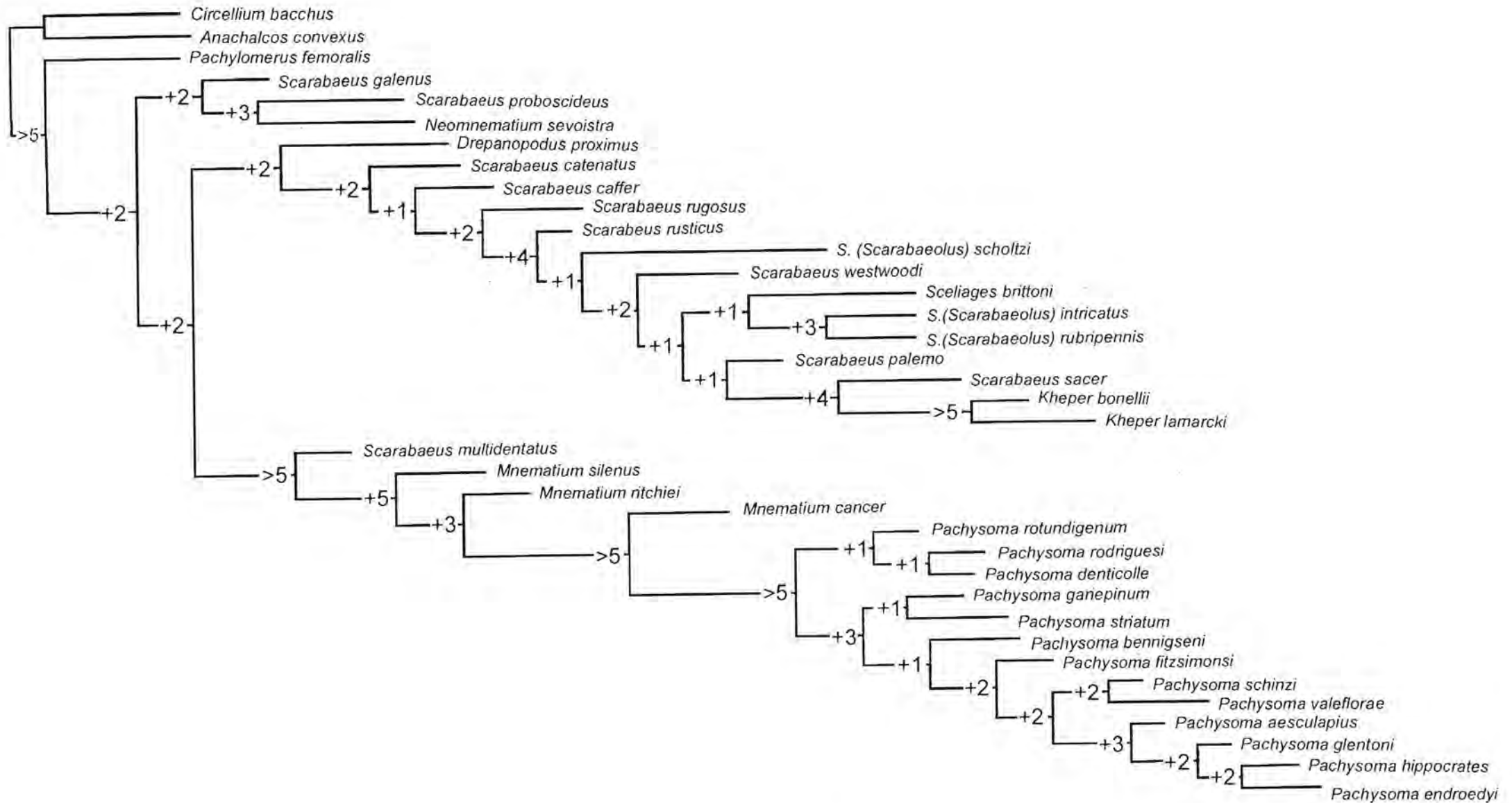


FIGURE 1. Cladogram depicting the relationship between the flightless Scarabaeini (i.e. *Pachysoma*, *Neopachysoma*, *Mnematium* and *Neomnematium*) and representative taxa of the flying Scarabaeini genera (i.e. *Scarabaeus*, *Kheper*, *Pachylomerus*, *Sceliages* and *Drepanopodus*) with *Circellium* and *Anachalcos* (tribe Canthonini) as outgroup taxa. The 823-step cladogram (C.I. = 0.52, R.I. = 0.85) was obtained after successive weighting of the 37 taxa and 64 characters. Decay Indices, i.e. the number of extra steps needed to collapse a node, are included at each node.

However, this tree lacks the resolution of clades (due to polytomies) when compared with the weighted tree (figure 1), and is not included here. Rooting the tree with *Circellium* and *Anachalcos* (tribe Canthonini) gives a polyphyletic origin of some current Scarabaeini genera (figure 1), e.g. *Drepanopodus*, *Sceliages* and *Kheper*, but rooting the tree with a Scarabaeini outgroup, e.g. *Sceliages* or *Kheper*, places *Pachylomerus* within the mixed *Scarabaeus* clade.

To facilitate the presentation of results, character state numbers are listed before the character description while table 2 contains the full character description and accompanying C.I. and R.I. values.

## Clades

### *Pachysoma sensu lato*

All flightless Scarabaeini included within *Pachysoma s.l.*, form a single monophyletic clade, which is supported by the following five uncontroverted (i.e. C.I.=1.00) synapomorphies: (48) anterior lobes of the epipharynx slightly setose; (49) lateral combs of setae on the epipharynx composed of two fused rows; (50) anterior median process of the epipharynx tear shaped; (60) ventral articulatory sclerite of the galea composed of a highly sclerotized disc, which is notched anteriorly; (61) coarsely serrated mola surfaces. Controverted character states, supporting the *Pachysoma* clade include: (2) 'clypeal scraper' composed of a medially incised ridge with or without a medial tooth; (53) inner ligular lobes, well developed and highly sclerotized with a short tuft of setae on the apex.

Mouthpart characters, especially the epipharynx, provide the main support for the *Pachysoma* clade. The ability of *Pachysoma* species to feed on dry dung and detritus, differentiates them markedly from all other Scarabaeini and even most Scarabaeinae (see Matthews 1974, Halffter and Halffter 1989, Zunino *et al.* 1989 for some exceptions). Thus, it is not surprising that the mouthparts provide synapomorphies for differentiating *Pachysoma* from all other Scarabaeini.

Additional controverted support for the *Pachysoma* clade comes from varying states of these characters: (5) form of outer clypeal teeth; (9) serrations on anterior pronotal margin; (28) shape of metatarsal spur; (32) sub-elytral ridge; (37) mesocoxal incision; (44) apical fringe of epipharynx; (51) sclerotized protuberance on epipharynx; (62) mandibular mola apodeme.

### *Neopachysoma sensu stricto*

The *Pachysoma s.l.* clade is further divided into two monophyletic clades, which represent *Neopachysoma s.s.*, i.e. (*P. rotundigenum*, *P. rodriguessi* and *P. denticolle*) and *Pachysoma s.s.* (*sequens* Ferreira 1953). *Neopachysoma s.s.* is supported by the following controverted characters: (8) genal apex semi-contiguous with clypeus; (13) bifurcate protibial spurs in males; (14) marked sexual dimorphism of protibia; (22) rounded apexes of mesotarsal spurs; (27) two reduced mesotarsal claws. Ferreira (1953) used the first three characters to define *Neopachysoma*. The

rounded mesotarsal spur tip relates to ultrapsammophily and the deep sand on which *Neopachysoma* species occur. This adaptation is also found in other soft sand species, e.g. *P. bennigseni*, *P. valeflorae* and *P. hippocrates*. The extensive reduction of the mesotarsal claws to a nonfunctional state, with the accompanying enlargement of the mesotarsal setae to form 'tarsal sand shoes' is undoubtedly an adaptation to soft desert sand (see Koch 1961, 1962, 1969, Lawrence 1969, Newlands 1972, and Henschel 1997 for similar adaptations in other groups). Thus, not surprisingly it recurs to a lesser degree in *P. fitzsimonsi*, *P. schinzi*, *P. valeflorae*, *P. aesculapius* and *P. glentoni*. Ferreira (1953) distinguished *Neopachysoma* from *Pachysoma* based on the following characters: (1) shape of genae; (2) lengths of the third and fourth segments of the maxillary palp; (3) subapical projection on inside of the protibia; (4) convexity of the mesofemur; (5) sinuosity on the outside of the mesotibia; (6) and height of insertion of the tarsus on the metafemur. Holm and Scholtz (1979) discussed these characters and concluded that there is too much gradation within *Neopachysoma* and recurrence of these characters in *Pachysoma* and *Scarabaeus* to warrant generic status. The character support here (decay index =1) for resurrecting *Neopachysoma* to generic or subgeneric level is weak and thus the synonymy of *Neopachysoma* with *Pachysoma* (*sequens* Holm and Scholtz 1979) is followed. *Neopachysoma* can, however, be regarded as a distinct species group.

#### *Pachysoma sensu stricto*

The *Pachysoma* subclade is supported by six controverted characters that include: (8) form of anterior genal apices; (11) absence of distinct projection on anterior edge of pronotum; (17) form of serration between protibial teeth; (18) form of serration below outer protibial teeth; (21) unmodified profemora; (43) shape of paramere apex. Characters 11 and 21 are uncontroverted character states within *Pachysoma*, but not within *Scarabaeus*. Thus, support for the *Pachysoma* subclade is weak.

To summarise, all species of *Pachysoma* are supported by five uncontroverted synapomorphies, two uncontroverted character states and eight controverted characters. However, any support for recognising *Neopachysoma* and *Pachysoma* at the generic level is weak.

Previous authors (Holm and Scholtz 1979, Mostert and Holm 1982) viewed *P. schinzi* (including *P. valeflorae*) as a separate evolutionary lineage, probably due to the unusual clypeal horns in the males and a very restricted distribution in the middle of the *Pachysoma s.l.* range (refer to chapter 3 for details). Their position as sister taxa to the southwest Cape clade, i.e. (*P. aesculapius*, *P. glentoni*, *P. hippocrates* and *P. endroedyi*) is of geographic interest, because there is a considerable gap in the distribution between Aus (26 41'S 16 16'E) in Namibia and Port Nolloth (29 17'S 16 51'E) in South Africa (see figures 4 and 9 in chapter 3). Controverted support for their placement as sister to the southwest Cape clade comes from the following three characters: (10) edge of posterior pronotal margins slightly serrate; (17) form of serrations between protibial teeth,

generally lacking; (38) all abdominal sternites setose. These are subtle characters that can easily be overlooked, but disregarding the unusual head morphology of *P. schinzi* and *P. vaefflorae*, their morphology matches the *P. aesculapius* species group better than any other *Pachysoma* group.

#### *Mnematium cancer*

*Mnematium cancer* was described by Arrow (1919) who refrained from placing it within its own genus, because of the unsatisfactory distinction between certain of the flightless genera in the Scarabaeini at that time. Holm and Scholtz (1979) suggested that if any flightless Scarabaeini warranted a separate genus it would be *M. cancer*. In contrast Mostert and Holm (1982) referred to *M. cancer* as *incertae sedis*, and moved it from *Mnematium* to *Scarabaeus*.

*M. cancer* is enigmatic because it shares three distinctive characters with *Pachylomerus femoralis*, namely large spined profemora, two short tarsal claws and large body size. However, there are also some important differences: (1) *M. cancer* has an asymmetrical *Scarabaeus*-like aedeagus that is ventrally extended, while the aedeagus of *Pachylomerus* is symmetrical and not ventrally extended; (2) the shape of the head and form of the clypeal teeth are quite different between *Pachylomerus* and *M. cancer*. Support for the placement of *M. cancer* as the morphological ancestor of *Pachysoma* is due to the following, 10 controverted and one uncontroverted character states, and two uncontroverted synapomorphies: (0) surface of ventral clypeal teeth unmodified; (4) size and form of four clypeal teeth; (17) form of serrations between protibial teeth; (19) setae dense below outer protibial teeth; (25) mesospur shape spatulate to strongly spatulate; (34) mesosternal ridge absent; (35) absence of setae on mesosternum; (42) number of hooks on aedeagi; (52) well sclerotized long and thin lateral tormal process, which nearly touches posterior median process; (54) absence of setae on last segment of labial palps; (56) shape of anterior edge of mentum deeply concave; (58) very reduced galea; (59) long galeal brush with galeal face unsetose. Lacking biological information for *M. cancer*, it is interesting that the two uncontroverted characters (52 and 59) undoubtedly reflect mouthparts evolved to deal with dry, coarse food as seen in *Pachysoma*. The mouthparts of *Pa. femoralis* on the other hand reflect their specialization towards feeding on wet dung.

#### *Mnematium sensu lato*

No controverted synapomorphies support the *Mnematidium*, *Mnematium* and *Pachysoma* clade, (i.e. *S. multidentatus*, *M. silenus*, *M. nitchei*, *M. cancer* and *Pachysoma* s.l.). Support for this clade comes from characters: (7) serrations on genal edge; (9) serrations on edge of anterior pronotal margins; (19) setae below outer protibial teeth; (29) position of metatibial insertion; (46) setal structure of median brush on epipharynx; (51) sclerotized tooth, protruding over apical fringe of epipharynx; (58) form of galea.



### The *Drepanopodus*, *Scarabaeus*, *Sceliages*, *Scarabaeolus* and *Kheper* clade

The clade composed of *D. proximus*, *S. catenatus*, *S. caffer*, *S. rugosus*, *S. rusticus*, *S. (Sc.) scholtzi*, *S. westwoodi*, *Sc. brittoni*, *S. (Sc.) intricatus*, *S. (Sc.) rubripennis*, *S. (Sc.) palemo*, *S. sacer*, *K. bonellii* and *K. lamarcki* is supported by six controverted characters: (10) form of serrations on edge of posterior pronotal margin; (25) mesospur shape; (32) absence of sub-elytral ridge; (34) size of a mesosternal ridge; (36) mesocoxal distance; (44) shape of apical fringe of epipharynx. The placement of *S. (Scarabaeolus) scholtzi* in the above clade is additionally supported by two characters: (0) surface of ventral clypeal teeth; (28) metatarsal spur shape.

The genus *Sceliages* is placed with *S. (Scarabaeolus)* and specifically supported by three controverted characters: (8) blunt genal anterior apexes; (15) distal morphology of protibia; (20) form of serration on inner edge of protibia.

The two *Kheper* species have 12 controverted characters supporting their position as highly derived *Scarabaeus*. These characters include: (3) 'V' shaped margin between two medial clypeal teeth; (7) genal edge serrated or irregular; (9) edge of anterior pronotal margins serrate; (13) protibial spurs in males straight; (17) absence of serrations between protibial teeth; (18) absence of serrations below protibial teeth; (25) mesospur strongly sickle-shaped; (26) one mesotarsal claw; (27) one reduced mesotarsal claw; (42) four hooks on parameres; (44) apical fringe of epipharynx straight; (46) median brush on epipharynx composed of large clump of short setae.

The clade composed of *S. galenus*, *S. proboscideus*, and *N. sevoistra* is supported by three controverted characters: (8) blunt genal anterior apexes; (18) form of serration below outer protibial teeth; (62) mola apodemes, short, sclerotized and trumpet shaped. These species (two flighted, one flightless) were previously each placed in their own genera, i.e. *Sebasteos*, *Neateuchus* and *Neomnematum*. This clade thus represents a group of morphological outliers which do not conform to typical *Scarabaeus* structure.

Support for the basal placement of *Pa. femoralis* in the tree comes from three controverted characters: (11) small distinct projection on anterior edge of pronotum; (18) coarsely serrate below outer edges of protibial teeth; (24) one well-developed mesotarsal spur; (53) inner ligular lobes, base partially sclerotized with short tuft of setae on apex. But recall rooting the tree with a *Scarabaeini* outgroup, e.g. *Sceliages* or *Kheper*, places *Pa. femoralis* within the mixed *Scarabaeus* clade.

### Species groups

Holm and Scholtz (1979) coded 28 characters for 10 *Pachysoma* and three *Mnematum* species. They had difficulty in interpreting these characters and compiled their results in a table but did not construct a tree. They concluded that, 'we therefore fail to see phylogenetic discreet groupings of species in *Pachysoma* but rather suggest a number of evolutionary trends which may

but need not have a phylogenetic basis. The best expressed is that which starts in *P. rodriguesi* and *P. denticolle*, while *P. hippocrates*, *P. schinzi*, *P. ritchiei* and *P. cancer* all constitute terminal forms of different trends. All the geographic forms (except *P. schinzi*) are also geographically terminal or isolated'.

Mostert and Holm (1982) listed four groups of species based on 'overall similarity and apparent synapomorphies such as protibial and aedeagal form'. These include Mostert and Holm's (1982);

- i) *aesculapius* group: *P. aesculapius* and *P. hippocrates*.
- ii) *schinzi* group: *P. schinzi* and *P. fitzsimonsi*.
- iii) *striatum* group: *P. striatum*, *P. bennigseni* and *P. gariepinum*.
- iv) *denticolle* group: *P. denticolle*, *P. rotundigenum* and *P. rodriguesi*.

Davis (1990) plotted a phenogram using Holm and Scholtz's (1979) table of morphological characters and found three species groups (*M. cancer* and *M. ritchiei* was excluded from the study that focussed on southwest Cape taxa only).

- i) *P. aesculapius*, *P. hippocrates* and *P. schinzi*.
- ii) *P. bennigseni*, *P. gariepinum*, *P. fitzsimonsi* and *P. striatum*.
- iii) *P. rodriguesi*, *P. rotundigenum* and *P. denticolle*.

Based on this study (figure 1) the following species groups within the flightless Scarabaeini were recognised:

- i) *P. rodriguesi*, *P. rotundigenum* and *P. denticolle* (previously placed in *Neopachysoma*).
- ii) *P. striatum*, *P. gariepinum*, *P. bennigseni* and *P. fitzsimonsi*.
- iii) *P. schinzi*, *P. valeflorae*, *P. aesculapius*, *P. glentoni*, *P. endroedyi* and *P. hippocrates*.
- iv) *S. multidentatus* (winged), *M. silenus* and *M. ritchiei*.
- v) *M. cancer*.
- vi) *S. (Scarabaeolus) scholtzi*.
- vii) *N. sevoistra*

## Evolutionary trends within the Tribe Scarabaeini

### i) Food preference

Adult dung beetles extract the microbial moisture-rich component from dung while their larvae feed on the dung itself (Halffter and Matthews 1966, Halffter and Edmonds 1982, Hata and Edmonds 1983). The Scarabaeini genera use a range of food types. Here, reference will be made only to the state in which the food is collected because in certain taxa the nature of the food consumed is unknown. For example, although *Pachysoma* collect dried dung pellets, these are rehydrated before feeding commences and fungus might be the true food source.

Freshly voided herbivore dung is the preferred food source for most Scarabaeini. This is due to its pliability, high nutritional value and moisture content (Edwards 1991, Al-Houty and Al-Musalam 1997). However, certain Scarabaeini lineages have evolved specifically to be able to feed on dry dung, detritus, dead millipedes and carrion. This undoubtedly led to the diversification of the Scarabaeini into previously under-utilized feeding niches. *Pachysoma* species predominately collect dry dung pellets and detritus, but fallen moist flower petals are also collected (Harrison unpubl.). *Sceliages* species are very rarely seen at dung, but are readily attracted to dead millipedes (Mostert and Scholtz 1986). According to Bernon (1981) *Sceliages* are able to make a brood ball out of millipede in the same way as dung is used by dung breeders. The smaller *Scarabaeus* (*Scarabaeolus*) species (length 11.8 mm; width 6.70 mm from Tribe 1976), which have an arid distribution (Tribe 1976), collect both wet dung and carrion. The larger *Scarabaeus* (*Scarabaeus*) species (length 20.90 mm; width 13.30 mm from Tribe 1976), are inclined to wetter areas (Tribe 1976) and collect predominately wet dung, but might also take carrion. *Kheper* and *Drepanopodus* are only known to collect wet dung, while *Pachylomerus* appear to have a wider dung preference, but also include carrion (Endrödy-Younga 1982b) and fruit in their mixed diet (Tribe 1976, Burger and Petersen 1991).

The morphological adaptations for wet and dry dung feeding as observed in the dissected mouthparts, vary markedly. This is apparent in the cladogram (figure 1) where the two main lineages represent the extremes of divergence in feeding specialization within the Scarabaeini. *Pachysoma s.l.* represents a clade of highly derived dry dung and detritus feeders, while the *Scarabaeus s.a.* clade only includes wet feeders (dung, carrion, millipedes). The *Scarabaeus s.a.* clade can be subdivided into highly specialized wet dung feeders at the apex, i.e. *Kheper*, followed by wet dung and carrion feeders [*S. (Scarabaeolus)*], wet millipede [*Sceliages*], and generalized wet dung feeders (usually with more than one foraging strategy), i.e. [*S. (Scarabaeus)*] basally. The mouthpart morphology of the arid adapted *Drepanopodus proximus* suggests the ability to deal with coarser (or perhaps drier) dung.

Within *Pachysoma*, *P. striatum* and *P. gariepinum* feed predominately on dry dung pellets, while *P. endroedyi*, *P. glentoni*, and *P. hippocrates* prefer detritus (although dry pellets are possibly used for breeding). Within the Cape clade, the most basal *P. aesculapius* prefers pellets to detritus, as shown by field observations and morphological adaptation (absence of an enlarged setal cage and long metatarsal claws that facilitate the collection of detritus), (chapter 2 includes nest content results under biology). Unfortunately no records of *Mnematium* feeding preference are available, but their mouthpart morphology when compared with *Pachysoma* suggests two possibilities, either dry dung feeding or wet and dry dung feeding. Two important controverted mouthpart characters (46, 58) shared by both *Mnematium* and *Pachysoma* support this hypothesis.

*Kheper* species have only been recorded feeding on wet dung, which they very efficiently make into a ball and roll (Edwards 1988b, Edwards and Aschenborn 1988, Sato and Imamori

1986a,b, 1987, 1988). Their apical placement indicates that they are the most derived lineage within the *Scarabaeus s.a.* clade. Controverted mouthpart characters supporting their morphological specialization for wet dung include: (44) broad, straight epipharyngeal apical fringe; (46) and an epipharyngeal median brush composed of large clump of short setae. Thus, definite food preferences are expressed by clades in the cladogram (figure 1).

## ii) Food relocation

The dominant food-relocation-behaviour is correlated with the food preference. Dung beetles have been divided, on the basis of their behaviour, into four groups. These are adequately described elsewhere (Halffter and Mathews 1966, Bornemissza 1969, Hammond 1976, Klemperer 1983), but include (1) paracoprids or tunnellers; (2) telecoprids or rollers; (3) endocoprids or dwellers; (4) kleptocoprids or parasites. To prevent confusion (e.g. Sato (1997) uses tunneller and roller for a telecoprid) with these standard and widely used terms, I define aberrant modes of the telecoprid behaviour. Five main foraging strategies used to relocate food have been observed in the Scarabaeini, these include the following: (1) 'ball rolling and burying', which is the most common and typical strategy. After construction of a dung ball from wet dung, it is rolled backwards using the hind legs, while the beetle pushes in a head-down-position with the front legs (examples include, all *Kheper*, most *Scarabaeus*, *S. (Scarabaeolus)*, *Drepanopodus* and *Sceliages*; (2) 'burrowing and carrying backward', a strategy probably derived from true ball rolling. It involves no dung ball construction, but the beetle moves to and from accumulations of wet dung pellets (e.g. Impala, *Aepyros melampus*, middens), collects a single pellet which is held above the ground with the hind legs, while the beetle walks backward towards its preconstructed burrow (examples include *S. galenus* see Tribe 1976, Edwards pers. comm. in Halffter and Halffter 1989, Doube 1990, Ybarrondo and Heinrich 1996); (3) 'ball rolling and burying' or 'burrowing and fragment rolling', *S. catenatus* use two relocating strategy's one above or burrowing and fragment rolling (Sato's 1997 tunnel-digging-burial sequences), which involve the digging of a tunnel (0-1m from the dung pad), followed by several trips to and from the dung source to provision the tunnel. No dung ball is made but the wet dung fragments are rolled backwards (Sato 1997, 1998); (4) 'pad covering while burrowing' or rarely 'fragment rolling and burying', *Pachylomerus femoralis* digs a sloping burrow near a dung pad, the excavated soil is bulldozed over the dung pad (which presumably reduces dung odour to competitors, especially *Kheper lamarcki* and hampers ball construction by other telecoprids). Once the burrow is excavated *Pa. femoralis* then cuts fragments of dung which are moved into the burrow (see Tribe 1976, Bernon 1981); (5) 'burrowing and dragging forward' the *Pachysoma* dry pellet and detritus dragging behaviour (see introduction for details).

Nine of the thirteen species of *Pachysoma* have been observed only dragging food forward. The monophyly of the group and morphology of the remaining four species strongly suggests the same strategy. Morphological evidence (see results *Mnematium s.l.*) suggests that *Mnematium*

species could exhibit the same behaviour. The apically positioned species of *Kheper*, *Sceliages* and *Scarabaeus* (*Scarabaeolus*) have only one foraging strategy (figure 1). *Kheper* species appear to be especially efficient ball makers and rollers (Edwards 1988b, Edwards and Aschenborn 1988, Sato and Imamori 1986a,b, 1987, 1988). *Kheper* species are regarded to display preemptive resource competition of cattle pads in southern Africa (Hanski 1991). Doube (1991) regards *Kheper nigroaeneus* (Boheman) as a top competitor, which is able to use a wide variety of wet dung types. While *Kheper nigroaeneus* has the highest degree of parental investment possible in insects (Edwards 1988a,b, Edwards and Aschenborn 1988, 1989), and well developed pheromone release in both sexes (Tribe 1975, 1976). Pairs of *Kheper platynotus* (Bates) construct such large brood balls, that single individuals have difficulty in rolling them (Sato and Imamori 1987). Thus not surprisingly, *Kheper* is the most derived within the *Scarabaeus* clade, and the character states supporting their apical placement can be interpreted to relate to morphological specialization for ball construction and especially ball rolling (recall there are no records of *Kheper* species not rolling dung balls). For example: (23) fusion of tibia and tarsal spur into a strong calliper-like structure; (24) reduction in number of tarsal claws from two to one (possibly due to the efficiency of character 23); (25) well-developed sickle-shaped mesotatarsal spurs; (27) and small size of mesotarsal claws. The basal placement of *Drepanopodus*, another derived 'super-roller', is possibly due to its arid-adaptions which place it closer to *Pachysoma*, as shown by mouthpart characters that suggest wet to partially dry dung feeding.

*Pa. femoralis* appears to be a generalized feeder (Endrödy-Younga 1982b, Doube 1991), being caught in almost equal numbers in baited (cattle dung, human dung, carrion and fermenting fruit) pitfalls traps. They also have a broad flight activity period (Doube 1991), and pad covering while burying rather than rolling behaviour (Tribe 1976, Bernon 1981). The nocturnal *S. proboscideus* uses both ball and fragment rolling (Harrison unpubl.), while *S. galenus* appears to only use backward carrying (Halffter and Halffter 1989).

To summarize, the *Pachysoma* lineage represents a highly derived clade of draggers, while *Kheper* represents derived 'super-telecoprids'. Basal taxa in the tree exhibit more than one foraging strategy. Thus, within the Scarabaeini a clear morphological and behavioural transformation series from 'super-telecoprid' to 'multi-strategy' to 'super-dragger' exists. These functional groups have previously been afforded generic or sub-generic status.

### iii) Flightlessness

Aptery has evolved independently at least three times within the Scarabaeini (figure 1). The flightless *Neomnematium sevoistra* from Madagascar occurs basally within a clade that includes three species in three genera. The Somali flightless *S. (Sc.) scholtzi* is centrally placed within the *Scarabaeus s.a.* clade. While the flightless *Mnematium* and *Pachysoma* clade includes a flying exception, *Mnematidium multidentatus*, an arid adapted north African coastal species.

Geographically, the two most speciose flightless groups form one large clade, divided apically into the southwestern African *Pachysoma* group, with the north African *Mnematium* as their basal morphological ancestors. *N. sevoistra* and *S. (Sc.) scholtzi* in contrast, each represent single flightless species disjunct from each other and the main flightless clade (figure 1). This confirms the hypothesis (Holm and Scholtz 1979, Mostert and Holm 1982) that the flightless Scarabaeini are polyphyletic.

#### iv) Soil type (especially sand)

Soil type is known to have a marked effect on the distribution of dung beetles (Nealis 1976, Doube 1983, Davis *et al.* 1988) with even congeneric species having marked substrate preferences (see Osberg and Hanrahan 1992, Osberg *et al.* 1993, 1994) for example in two *Allogymnopleurus* Janssens, a gymnopleurine genus of telecoprids. Large telecoprids are often associated with deep sandy soils, for example *Scarabaeus goryi* Castelnau, *Scarabaeus zambesianus* Péringuey, *Kheper lamarcki* (MacLeay) and *Pachylomerus femoralis* (Kirby). Doube (1991) found that *Pa. femoralis* was more than five hundred times more abundant in deep sand than in clay or loam soil. While other closely related species, e.g. *Kheper nigroaeneus* (Boheman) were found in almost equal numbers on sand, duplex, loam and clay soils (appendix B8 in Hanski and Cambefort 1991).

All *Pachysoma* collected for this study (see chapter 3) were found on sand of varying coarseness. All other Scarabaeini species with aberrant relocation strategies, e.g. *S. galenus*, *S. proboscideus*, *S. rugosus*, *S. catenatus* and *Pa. femoralis* have a preference for sandy soil. Sato (1997) first noted that the evolution of tunnel-digging-burial (TDB) in *S. galenus*, *S. catenatus* and *Pa. femoralis* (and *S. proboscideus*, *S. rugosus*) among rollers relates to soil type, and suggests that TDB may be an adaptation to the construction of a nest-chamber in sandy soil.

#### iv) Mesocoxal distance

*Pachylomerus femoralis* illustrates that large generally non-rolling Scarabaeini have smaller mesocoxal distances relative to body size than large super-rollers, e.g. *Kheper lamarcki* (Harrison unpubl.). All *Pachysoma* have contiguous mesocoxae, while *Mnematium* species have semi to completely contiguous mesocoxae, thus although the reduction in mesocoxal distance is correlated with aptery (but the flightless Canthonini are an exception), it secondarily appears to be correlated with foraging strategy, i.e. *Kheper* species have the largest mesocoxal distance relative to body size while large *Scarabaeus* which employ other relocation strategies (e.g. *Scarabaeus proboscideus*) has a surprisingly small mesocoxal distance. *Scarabaeus catenatus* has both reduced mesocoxal distance and enlarged profemora (two characteristics shared by the fragment relocating *Pa. femoralis*). The flightless canthonines, *Circellium* (telecoprid), *Gyronotus* Lansberge (relocation unknown), *Canthodimorpha* Davis, Scholtz & Harrison (relocation unknown) have very large

mesocoxal distance (see Chown *et al.* 1998, Davis *et al.* 1999), which possibly is a result of their relocation strategy, i.e. ball making and rolling rather than dragging or fragment rolling.

#### v) Larvae

Currently the only larval Scarabaeini described are from the genera *Scarabaeus* and *Kheper* (see Ronchetti 1949, Medvedev and Medvedev 1958, Oberholzer 1959, Paulian and Lumaret 1975, Edmonds and Halffter 1978, Palestirini and Barbero 1992). Larval evidence to possibly support placing *Kheper* as a subgenus of *Scarabaeus* comes from the comparative study by Palestirini and Barbero (1992) who described the larva of *Kheper aeratus* (Gerstaecker) and compared it to the suite of larval characters defining *Scarabaeus* selected by Edmonds and Halffter (1978) from all available literature. Palestirini and Barbero (1992) concluded that 'this combination of characters seems to place the *Kheper* larva very near to that of the genus *Scarabaeus*...the genus *Kheper* seems to represent a derived phyletic line (i.e. subclade or subgenus of *Scarabaeus*) in comparison with that represented by the similar genus *Scarabaeus*' (parentheses mine).

#### Classification

There are three main schools of macro taxonomy, i.e. phenetics, cladistics and evolutionary classification (Mayr and Ashlock 1991). This study is based on the cladistic approach, which strictly applied recognizes only monophyletic groups at taxonomic level. However, there are a variety of problems when transforming a cladogram into a classification (see Mayr and Ashlock 1991); hence a conservative cladistic classification is used.

Although, *Pachysoma s.l.* forms a distinct clade in figure 1, the synapomorphies supporting their monophyly are all from mouthpart characters which are correlated with their feeding biology. Although it is possible that their apparent monophyly is merely the result of convergence in feeding biology, support is based upon five uncontroverted character states (and an additional eight controverted states), very strong morphological support for common ancestry. Recall that, Holm and Scholtz (1979) and Chown *et al.* (1998) have previously thought that *Pachysoma* may be paraphyletic or polyphyletic. An examination of the mouthparts of the unrelated Eucraniini, which also feed on dry dung (Zunino *et al.* 1989) reveals similar, but not identical, mouthpart structure to that of *Pachysoma s.l.*

Thus, there are three possible classifications to choose from: (1) *Pachysoma s.l.* as synonymous with *Scarabaeus s.l.*, due to their origin from within *Scarabaeus s.l.*; (2) *Pachysoma s.l.* as genus due to their monophyletic origin; (3) *Pachysoma s.l.* as subgenus to prevent a paraphyletic *Scarabaeus s.l.* The third more conservative approach is used as discussed below.

## i) Generic and subgeneric criteria

A genus is by definition, a category for a taxon that includes one or more species, presumably of common phylogenetic origin, which is separated from related genera by a decided gap (Mayr and Ashlock 1991). Holm and Schoeman (1999) discuss criteria and considerations for erecting genera and subgenera. Their system is followed in this paper. They define genera as groups of species sharing the following characteristics: (1) 'a genus should constitute a monophyletic group'; (2) 'a genus should be defined by at least one, but preferably more, recognizable and unique apomorphic characters'; (3) 'overall similarity between members of a genus should be greater than between genera of any given group'; (4) 'phylogenetic and/or phenotypic distances between genera should be approximately of the same magnitude in different taxonomic groups. An objective measure of distance is obviously impossible, but there is a traditional agreement on approximate limits for the genus'.

They consider subgenera to be ideal for species-groupings, which enables one to identify related species without affecting stability of genera or species names. Holm and Schoeman (1999) suggest the use of subgenera in the following cases: (1) 'mosaic evolution, i.e. disjunct distribution of apparently homologous character states'; (2) 'diagnostic character states consistent but grading, weak, or difficult to identify'; (3) paraphyletic groups, i.e. clearly defined specialized groups that split from (within) an unspecialized group that is then defined by plesiomorphic (or apomorphic) features only (parentheses mine).

Furthermore, names need to satisfy at least three requirements: (1) ideally they should be consistent with the phylogeny of the group, but not contradict it; (2) they should serve as a practical system for identification purposes; (3) nomenclatural stability should be maintained where possible (Holm and Schoeman 1999).

The generic subdivisions of the tribe Scarabaeini are traditionally based on characteristics of the protibia and tarsal claw and spur of the meso and metatibia (Mostert and Scholtz 1986). For example, *Kheper* is defined by three unserrated protibial teeth and one tarsal claw, while *Scarabaeus* has four serrated protibial teeth and two tarsal claws. Within the current generic classification of the tribe Scarabaeini (Mostert and Scholtz 1986) *Pachysoma*, *Neopachysoma*, *Mnematium*, and *Neomnematium* all share four serrated protibial teeth and two tarsal claws with *Scarabaeus*, and are considered synonyms of *Scarabaeus* (*secundum* Mostert and Holm 1982). However, in the phylogenetic analysis *Kheper*, *Sceliages*, and *Drepanopodus* (figure 1) come out within *Scarabaeus*, which makes *Scarabaeus* paraphyletic if these genera are maintained.

## ii) Classification of *Kheper*, *Drepanopodus*, *Sceliages* and *Pachylomerus*

It is beyond the intended scope of this study to alter the status of these genera. However, retaining *Kheper*, *Sceliages* and *Drepanopodus* as genera makes *Scarabaeus* paraphyletic. *Scarabaeus s.a.* appears to represent a diverse group of species that have radiated to deal with



a variety of food sources (see feeding under evolutionary trends in the Scarabaeini above). I suggest future workers on the Scarabaeini should investigate considering *Scarabaeus* as a monophyletic genus, with *Pachysoma*, *Kheper*, *Sceliages*, *Drepanopodus* and possibly even *Pachylomerus* as subgenera of *Scarabaeus s.a.* This system has been suggested in part by previous workers (Bedel 1892, Shipp 1895a,b, Péringuey 1902, Balthasar 1963, Halffter and Mathews 1966) and is possibly a better reflection of the phylogenetic relationships within *Scarabaeus s.a.*

For example, Bedel (1892) is the first author to divide *Scarabaeus* into four subgenera (i.e. *Scarabaeus*; '*Ateuchetus*'; '*Neoctodon*'; and '*Mnematium*'), synonyms in quotes, my additions in square brackets. Shipp (1895a,b) divides *Scarabaeus* [*Ateuchus*] into six subgenera (i.e. '*Sebasteos*', '*Ateuchus*', '*Helioantharus*', '*Actinophorus*', '*Ateuchetus*', and '*Mnematidium*') while he described '*Parateuchus*' as a new genus for *Scarabaeus palemo*. Péringuey (1902) viewed *Scarabaeus*, *Pachysoma* and *Sceliages* as valid genera, but divided *Scarabaeus* into three subgenera, i.e. *Scarabaeus* (which included species now attributed to *Kheper*, *S. (Scarabaeolus)* and *Drepanopodus*), *Pachylomerus* and '*Sebasteos*'. Péringuey (1902) regarded '*Mnematium*' as synonymous with *Scarabaeus*. In contrast Balthasar (1963) regarded '*Mnematium*' as a valid genus, but placed *Kheper* as a subgenus of *Scarabaeus*. Finally, Halffter and Mathews (1966) divided *Scarabaeus* into three subgenera, i.e. *Scarabaeus*, *Scarabaeolus*, and *Kheper*.

### iii) Classification of *Pachysoma* and the other flightless Scarabaeini

Apically situated in the cladogram, *Pachysoma* represents a monophyletic clade of derived *Scarabaeus*, supported by five synapomorphies based on mouthparts and feeding. This makes *Pachysoma s.l.*, a readily identifiable and distinct group of Scarabaeini. According to the generic criteria of Holm and Schoeman (1999) *Pachysoma* deserves generic status, but support for the whole *Mnematium / Pachysoma* clade is weak (no synapomorphies). This poses a problem, as there is no phylogenetic support for including the *Mnematium* species within *Pachysoma*, which would provide grounds for generic status of the *Mnematium / Pachysoma* clade. Additionally, the recognition of *Pachysoma* as a genus makes *Scarabaeus s.l.* paraphyletic. Therefore, from a cladistic viewpoint there is no justification to elevate *Pachysoma s.l.* to generic status.

Although *Pachysoma* share characters relating to wing loss and arid adaptation with the other flightless Scarabaeini, their mouthpart morphology and geographic distribution separates them clearly from these taxa. Consequently, as shown in the cladogram (figure 1), *Pachysoma* represents a distinct clade of *Scarabaeus*, which deserves at least subgeneric status. For example, *Pachysoma* is as distinct from *Scarabaeus* as *Drepanopodus* is from *Kheper*. From an identification viewpoint, *Pachysoma* as subgenus would be a very useful taxonomic category for separating and identifying *Scarabaeus s.a.* I thus propose that *Pachysoma* be considered a subgenus of *Scarabaeus*. This decision satisfies the cladistic criterion that genera should strictly represent

monophyletic units (*Scarabaeus* in this case), while subgenera according to Holm and Schoeman (1999) and Endrödy-Younga (pers. comm.) need not. It also fulfils the practical requirements of nomenclatural stability and simplifies the identification of large groups of species. The phylogenetic relationship between *Scarabaeus* and *Pachysoma* is additionally highlighted in the classification. Furthermore, it provides a practical and useful nomenclatural system for future ecological, physiological, behavioural and biological studies. See studies by Lighton (1985), Endrödy-Younga (1989), Scholtz (1989), Klok (1994) and Chown *et al.* (1998), where even though *Pachysoma* was synonymised with *Scarabaeus* (Mostert and Holm 1982) the name (or category) is needed to differentiate them for practical purposes.

Elevating *Pachysoma* to subgeneric level necessitates discussion on the status of *Mnematium* and *Neomnematium*. To elevate *Mnematium* to subgeneric level poses the following problems: *Mnematium silenus* and *S. (Scarabaeolus) scholtzi* (regarded as *Mnematium scholtzi* by Carpaneto and Piattella (1988)) are already considered to belong to the subgenus *Scarabaeolus* (*sequens* Mostert and Holm 1982). Without a detailed phylogenetic analysis (and taxonomic survey or revision) of the relationship between *Scarabaeolus* and *Scarabaeus* I refrain from making any changes to the current classification of these species. I believe, however, that there is sufficient evidence (see figure 1) to regard *S. (Scarabaeolus) scholtzi* and *Neomnematium sevoistra* as examples of isolated flightless taxa within *Scarabaeus s.a.* That can be expected because aptery does not imply monophyly (for example there are flightless species in all three monophyletic genera of Trogidae (see Scholtz 1981, 1986)). However, disregarding the presence of vestigial mesotibial spur in *M. silenus* there appears to be a closer phylogenetic relationship between *S. multidentatus*, *M. silenus*, *M. ritchiei* and *M. cancer* (which is especially marked if one examines clypeal and protibial shape), than between *M. silenus* and *S. (Sc.) scholtzi* (as seen in figure 1).

The subgenus *Scarabaeus (Pachysoma)* MacLeay is redefined in chapter 3 using the only known characters, other than aptery, which unequivocally unify them, i.e. mouthpart characters. Due to the above mentioned reasons, *Mnematium* and *Neomnematium* can only be considered synonymous with *Scarabaeus s.l.*

### **Dry dung feeding and dragging as a behavioural synapomorphy for *Pachysoma***

To evaluate the unique foraging and feeding biology of *Pachysoma* as a behavioural synapomorphy for the genus a literature review was undertaken both within the tribe Scarabaeini (discussed under evolutionary trends in the Scarabaeini above) and within the subfamily Scarabaeinae and family Geotrupidae (discussed below). Only examples of aberrant relocation and or feeding biology deemed relevant to understanding the origin of the unique biology in *Pachysoma* are included here.

A notable exception to the typical ball rolling behaviour of telecoprids is found in the South American Eucraniini that occur in arid, sandy regions of the southern Neotropics (Halffter and

Matthews 1966, Zunino *et al.* 1989). The Eucraniini include about 19 species in four genera (Hanski and Cambefort 1991), most species are flightless and morphologically classified as rollers. Zunino *et al.* (1989), studied the foraging behaviour of *Anomiopsoides heteroclytum* (Blanchard), *A. xerophilum* Martinez and *Glyphoderus centralis* Burmeister which is summarized as follows: (1) with protibia held outwards the beetle run on the hind four legs in search for dry rodent pellets; (2) a burrow is always excavated before relocating the food item (it is not recorded if this happens before or after foraging commences, but as in *Pachysoma* it probably occurs after the food is found); (3) the food item is carried in forelegs (held under the head and between the protibia) while walking forward on the hind legs to the preformed burrow; (4) at the burrow entrance, the pellet is dropped, the beetle faces the nest backwards, and drags the pellet into the burrow using its protibia; (5) the nest consists of a *holding-chamber* leading to a deeper feeding or nesting-chamber (Zunino *et al.* 1989).

Mostert and Scholtz (1986) included the subtribe Eucranina in the Scarabaeini. Zunino *et al.* (1989) place eucranines near the Ennearabdina (with an ancient link to the Onitini (paracoprids)). The monospecific *Ennearabdus* Van Lansberge, is included in the subtribe Ennearabdina of the Eucraniini by Zunino *et al.* (1993). *Ennearabdus lobocephalus* (Harold) is the only known species of eucranine that collects wet dung which is manipulated as a paracoprid Zunino *et al.* (1993) and of interest it is flighted.

The eucranine strategy, as exemplified by representatives of *Anomiopsoides* and *Glyphoderus* but not *Ennearabdus*, only differs from *Pachysoma* in that the food is relocated using the anterior rather than posterior legs. This suggests that *Pachysoma* and some Eucraniini (excluding *Ennearabdus*) have evolved a relocation strategy and diet which enables them to exploit dispersed dry dung in a desert environment where the sandy substrate has rehydrating potential. This apparent convergence in strategies is best explained by adaptation to similar environmental pressures, rather than by close evolutionary links.

Flightless canthonines also feed on dry dung and 'of particular interest is the ability of several Western Australian species of the genera *Coproecus*, *Mentophilus*, and *Tesserodon* (as well as *Onthophagus*) to use old, dried faecal pellets as a source of food (but only during the wet season). These dried pellets are buried, often in groups, to the depth of the moisture line in the soil, the beetle then sinking a feeding shaft down from the from the pellet storage chamber in some cases...It can be assumed that the moisture seeping into the pellets revives bacterial and fungal activity, and that the beetles then feed on these microorganisms. Apparently worthless dried pellets can thus be reactivated and their food value restored in this manner, and all of the Scarabaeinae occurring from the Murchison River to the North West Cape appear to be able to adopt this strategy' (Matthews 1974). Both *Coproecus* Reiche and *Mentophilus* Castelnau are entirely flightless genera, while *Tesserodon* Hope (like *Scarabaeus*) contains flightless and flying species (Matthews 1974). The use of dry dung as reported above, excluding its relocation, is practically identical to that

documented by Scholtz (1989) for *Pachysoma striatum*. Additionally, this strategy is only employed during the wet season, enabling rehydration in sand, two separate chambers are used, pellets collected 'often in groups' implies more than one foraging trip, and they inhabit the arid western coast of Australia. However, unlike *Pachysoma* that drag forward *Coproecus* and *Mentophilus* roll their pellets backwards (Matthews 1974).

An especially relevant example, is that of *Canthon obliquus* Horn which is able to climb vertically while dragging an unmanipulated fragment of dung in its hind tarsi (Halffter and Halffter 1989). This species has reduced wings and is endemic to canyons in tropical sub-deciduous oak forest on the southern tip of the Baja Californian Peninsula. Halffter and Halffter (1989) maintained pairs of *C. obliquus* in the lab, supplied with fresh cow dung, but 'the *C. obliquus* used the dung that was several days old, which had lost humidity...' rather than fresh wet dung and rolling was never observed. The only relocation behaviour of *C. obliquus* as observed in the field follows. 'While the insect moved forward with the middle and anterior legs, a small fragment of dung was taken by the tarsi of the posterior ones. The fragment was not being rolled as it did not touch the ground. It was small in relation to the insect's body, it had been separated from a cow pad using the clypeus and the anterior legs. Of all the forms of relocation known (they were unaware of *Pachysoma*), the only one that is comparable is the behaviour of *Scarabaeus galenus*...' (Halffter and Halffter 1989). 'I have observed in Mkuzi Game Reserve (South Africa) on many occasions the behaviour of *Scarabaeus galenus*. This species carries a piece of dung in its hind legs, lifted off the ground, while walking backwards to its burrow' (Edwards' pers. comm. in Halffter and Halffter 1989). Additionally, *C. obliquus* excavate 'resting galleries' independently coined here as the holding-chamber for *Pachysoma*. Scholtz (1989) illustrates the holding-chamber as used by *Pachysoma striatum* to store collected food before construction of the feeding or breeding-chamber. Several other species in genera close to *Canthon* (i.e. *Boreocanthon*, *Melanocanthon*, *Glaphyrocantion* and *Pseudocanthon*) also include pelleted dung in their diet (Gordon and Cartwright 1974).

*Geotrupes (Thorectes) sericeus* (Geotrupidae) is restricted to coastal dunes in western France and shares with *Pachysoma* various parallels in its habitat preference and biology (see chapter 3 for larval parallels with *S. (P.) striatus*). Of importance *G. (T.) sericeus* constructs its nest chamber first, drag dry pellets (direction not specified in study), occurs on sand, and is flightless (Klemperer and Lumaret 1985). This behavioural convergence in such divergent scarabaeoid lineages (see total evidence phylogram in Browne and Scholtz 1999) can only be explained by adaptation to deep sand, dry food and possibly even aptery.

## Synthesis

Scholtz (1989) aptly titled his paper 'Unique foraging behaviour in *Pachysoma*...an adaptation to arid conditions?' Independently, Zunino *et al.* (1989) used 'Food relocation behaviour...and the constraints of xeric environments' for the Eucraniini. I believe both these taxa

and others have adapted their food preference, foraging behaviour, and subsequently and inadvertently their wing status in response to aridification in a sandy biotope. The evidence as presented above also suggests that a substrate of water retaining sand plays a vital role in the evolution of alternative life histories in arid areas. Although, it becomes a chicken and egg scenario, if one finds an apterous scarab on sand, its foraging and feeding biology most probably differ from its closest flying relatives. This hypothesis is testable and already has predictive value.

The evolution of aptery in insects has been reviewed by Roff (1986, 1990), Wagner and Liebherr (1992), while Scholtz (in press) specifically reviewed aptery in the Scarabaeoidea. Ecologically the development of flightlessness is attributed mainly to habitat stability (see Roff 1994a,b, Scholtz, in press) but additional factors, e.g. ecophysiology, play a vital role in the process (see Draney 1993, Chown *et al.* 1998). However, I know of no reference suggesting an association between sandy environments with an abundance of detritus and the reoccurrence of aptery. The Desert Biome has long been regarded as having a high incidence of aptery (Koch 1962a,b Scholtz 1981, in press, Draney 1993), and sand is usually synonymous with the Desert Biome. To test this hypothesis flightless scarabs (or insects in general) should be sought in non-sandy arid areas (e.g. rock and gravel desert). The hypothesis predicts that few, if any, will be found. Seely (1978) proposed a variety and not one single factor accounting for the high endemism and species richness of flightless (98% of species) tenebrionids in the Namib Desert, which are mostly detritus feeders living on sand (Koch 1962a,b). Thus a combination of the following factors is proposed to facilitate the evolution of aptery in Coleoptera in arid areas: (1) a substrate of aeolian sand with water retaining potential; (2) unpredictable and limited rainfall, selecting for water conservation ability (either behaviourally, morphologically or ecophysiological); (3) coastal fog as a limited but reliable source of water; (4) situated in the coastal zone which is cooled by the sea and incoming fog in contrast to higher temperatures inland; (5) an abundance of wind accumulated detritus, which rehydrates once buried in moist sand; (6) strong selection pressure to increase mobility over and into fine sand (i.e. psammophilous adaptation), in order to reduce transport costs, escape midday temperature extremes and predation; (7) harsh but stable environment i.e. habitat stability.

Is the foraging biology of *Pachysoma* unique? Within the Scarabaeini no species other than *Pachysoma* are known to relocate food forwards and collect dry food (but recall that the biology of *Mnematium* and *Neomnematium* is currently unknown). While the possibility does exist that *Mnematium* species at least share a similar diet (based on mouthpart evidence). *Scarabaeus galenus* and *Scarabaeus catenatus* have the closest and a seemingly intermediate foraging strategy between dragging and rolling. Based on the examples above, aberrant foraging and feeding behaviours reoccurs in telecoprids. This illustrates the behavioural and biological plasticity within the Scarabaeinae, a factor which probably accounts for the diversity, success and variety of life styles in dung beetles. Thus, the biology of *Pachysoma*, is merely the end point of a highly derived lineage adapted to an arid, sandy biotope. The occurrence of *Pachysoma*-like behaviour

in other flightless taxa, (e.g. Eucraniini, Australian desert canthonines and *Canthon obliquus*), is undoubtedly convergence due to arid adaptation.

### **Hypothesised evolution of *Pachysoma***

The evolution of *Pachysoma* was probably initiated by climatic change from semiarid to very arid conditions as documented by Rogon (1996) for Africa. Aridification placed high selection pressure on the resident stock of xeric-adapted, but flying wet-dung-feeders (FWDF). The ancestor of *Pachysoma* possibly already exhibited the following behavioural and morphological attributes enabling them to adapt to their changing environment. First, both rolling and carrying foraging strategies for wet dung. Second, a degree of psammophilous adaptation, possibly associated with sandy river courses and river mouths (as suggested by Endrödy-Younga 1982a for tenebrionids), which act as corridors for dung producing herbivores dependent on water. Aridification results in dung desiccating faster (Anderson and Coe 1974) and decreasing in amounts as herbivores migrate to more favourable environments. Arid adapted herbivores would be forced to produce drier pelleted dung to reduce water loss in their faeces (Wilson 1989). Thus, FWDF either has to forage for wet dung more efficiently (i.e. reduce energy and water loss); migrate away from the arid area; alter their foraging and feeding habits; or face extinction. Evidence, based on the extant scarab fauna of the Namib Desert suggest three main solutions to deal with the arid environment: (1) increased efficiency as a diurnal FWDF, i.e. fly less, forage faster, reduce body size and feed on both dung and carrion. Examples of this strategy include *S. (Scarabaeolus) rubripennis*, *S. (Scarabaeolus) intricatus* and *Drepanopodus proximus*; (2) the *Pachysoma* strategy, i.e. feed on dry dung and detritus, reduce energy costs and save water by not flying (Klok 1994); (3) temporal activities shift from diurnal to crepuscular or nocturnal, which reduces water loss and competition with diurnal species, e.g. *S. proboscideus* and *S. canaliculatus*.

An additional consequence of aridification, is an increase in accumulated sand, which requires adaptation in animals who 'choose' to inhabit it. Morphological changes are required to ease transport over and into sand, which includes increasing the surface area of the legs. Morphological adaptations in psammophilous dung scarabs include the following: (1) an increase in the setal length on all structures used to walk on and dig into sand, while a decrease or absence of setae from other areas; (2) the protibia becomes wider, mesotarsal claws decrease in length, while metatarsal claws increase in length; (3) rounded tarsal spurs become flat and spatulate. For FWDF, there is a trade off between being terrestrially efficient (psammophilous) and reducing wind resistance during flight, while being able to manipulate wet-dung efficiently, without clogging long setae. Thus, FWDF's are constrained from at least two directions not to overly elaborate their tarsal setae; (1) they increase resistance and thus energy expenditure in flight; (2) the setae become matted and thus nonfunctional when dealing with sticky-wet-dung. Evidence for this is apparent in *Pachysoma*, which have greatly elaborate tarsal brushes, which immediately mat on contact with

wet dung, while flying psammophilous species have functional, but smaller setal brushes. Thus, to radiate into soft sand demands enlarged setae, but these setae potentially influence flight and foraging efficiency.

Dry dung and detritus present an ideal solution to this problem. In the aridifying environment dry dung was most probably an unutilized resource, which it seemingly remains to this day (personal observation). The combination of low (or no) competition for dry dung, the rehydrating potential of wet sand (see Klemperer and Lumaret 1985, Scholtz 1989), the morphological constraints of occupying a sandy niche while maintaining flight and wet-dung feeding all provided sufficient selection pressure for a multi-foraging, psammophilous species to change from feeding on wet to dry dung. The ability to feed on plant detritus is probably a secondary adaptation (more derived) following dry dung feeding. The terminal placement of the detritus feeders (southwest Cape Clade) in figure 1 supports this hypothesis.

The uniqueness (Seely 1978) and stability of the Namib environment, abundance of dry dung, success of dry-dung-feeding (DDF) on a sandy substrate, enabled DDF to lose their ability to fly, as the DDF perfected their new diet they lost the need to compete with the FWDF and to fly. The physiological advantages of reducing water and energy loss in an arid environment (see Cloudsley-Thompson 1991, Klok 1994, Somme 1995, Chown *et al.* 1998) by not flying would additionally facilitate this change, and allow for a sub-elytral cavity to develop (Draney 1993).

Certain extant *Scarabaeus* species have all the necessary criteria to speciate into *Pachysoma* under the appropriate selection pressure, e.g. *S. galenus* and *S. catenatus* (see Halffter and Halffter 1989, Sato 1997, 1998). *Mnematium* species appear less derived than *Pachysoma*, and although they are the morphological ancestors of *Pachysoma*, I suspect they evolved aptery after *Pachysoma* during another aridification event (Rogon 1996). The mouthparts of *Mnematium* spp. suggest a drier diet than the FWDF, but unlike the highly modified mouthparts of *Pachysoma*. Other, flying desert species, e.g. *S. multidentatus* and *D. proximus* also share with *Mnematium* spp. slightly modified mouthparts. Surprisingly, the mouthparts of the flightless *S. (Scarabaeolus) scholtzi* and *N. sevoistra* are closer to FWDF than to DDF. The absence of this very successful adaptation in these species, possibly contributes towards the low species richness of flightless Scarabaeini in the Somali-Chalbi Desert, and semiarid southwest of Madagascar. To conclude, I propose that the evolution of dry dung and detritus feeding in a *Scarabaeus*-like ancestor of *Pachysoma*, led to the radiation of *Pachysoma* on the coastal sands of southwestern Africa.

### **Hypothesized dispersal of *Pachysoma* in the Namib Desert**

Koch (1962a), suggested that the sands of the Namib Desert are of considerable age due to the high diversity of tenebrionid species specialized to the ultra psammophilous conditions on the Namib dunes. That is, when compared with all other deserts supporting a tenebrionid fauna.

Consequently he proposed that a considerable time was needed for this proliferation of specialized beetles to have evolved, and thus the Namib was probably the oldest desert in the world. Endrödy-Younga (1978), pointed out that this diversity is only high at the species and generic levels on the Namib sands, but not at higher phylogenetic categories. Endemic tribes and subfamilies of Coleoptera are only found on the stone and gravel plains of the Namib, which is a much older environment than the dunes themselves (Endrödy-Younga 1978). All *Pachysoma* species share a variety of adaptations to their arid, sandy environment. The development of ultra psammophilous and psammophilous adaptations is especially marked in certain species, e.g. *S. (P.) rodriguesi* from the central Namib, and *S. (P.) hippocrates* from the southwestern Cape.

The geographic range of *S. (Pachysoma)* species is restricted to the Namib sands, and the coastal sands of the southwestern Cape (see figure 1 in chapter 3). Ignoring the outlier localities (open circles) leaves a very restricted distribution for *S. (Pachysoma)* when compared with the possible array of sandy habitats on the subcontinent. For example, no *S. (Pachysoma)* occur in the adjacent sandy Kalahari Desert.

Seely (1978) proposed that a combination of simultaneously occurring environmental factors in the Namib desert, account for its diverse beetle fauna. No other desert shares this combination of environmental factors, which include the following: (1) a cool coastal climate in the dune area; (2) extensive dune masses; (3) and a diverse, arid-adapted beetle fauna over the western half of southern Africa, including the Namib during the quaternary (Seely 1978). Of all the arid areas in the world the Namib Desert has the highest species diversity of flightless Scarabaeini (i.e. 13 species), more than the total (five species) known from all other arid areas.

Endrödy-Younga (1978) proposes that the Namib dune environment evolved in the following way: (1) a coastal fauna was preserved when the continent shifted northwards during the first half of the Tertiary. Preadapted taxa with xerophilous and psammophilous tendencies could adapt best to the changing conditions; (2) pocket development could have begun at an early stage in sand accumulations at the mouths of active rivers, initiating the isolated differentiation and sand adaptation; (3) expansion of the dune area northwards, during which established congeneric species either meet or interconnecting dunes are kept isolated.

The hypotheses of Endrödy-Younga (1978) and Seely (1978) are supported by the highest species' diversity of flightless Scarabaeina in the Namib, and the present distribution and habitat preference of *S. (Pachysoma)* species in the Namib respectively (see figures 1, 3-13 in chapter 3). No *S. (Pachysoma)* species are restricted to the older stone and gravel plains, while all *S. (Pachysoma)* were collected on a sandy substrate. The association of *S. (Pachysoma)* species with sand bodies originating from the coastlines rivers, supports Endrödy-Younga's second phase in the evolution of the Namib fauna. Of specific interest are restricted species, e.g. *S. (P.) endroedyi*, that only occur in the small dune fields north of the Olifants River and *S. (P.) glentoni* that has only been collected from the banks of the Olifants River and its tributary the Groot-sandleegte River. The



expression of black elytra is only found in the most northerly, (Walvis Bay 22 58'S 14 30'E) and southerly populations, (Lüderitz 26 35'S 15 10'E) of *S. (P.) denticollis*, which could possibly be a result of the history of dune expansion across the Namib plains. The geographic analysis of *S. (Pachysoma)* thus provides valuable insights into their diversification. From their current distribution they undoubtedly evolved and speciated under the specific conditions in the Namib desert. Especially as no ecological equivalents to *S. (Pachysoma)* are present in the sandy Kalahari Desert, as found in the Tenebrionidae (Holm 1984).

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**Appendix 1.** Character states of the taxa used in the phylogenetic analysis. 0 primitive; 1-5 derived (in sequence); ? unknown character state; - not applicable character state. All characters are listed in table 2.

Taxa	Characters	0					1					2					3				
		0	1	2	3	4	0	1	2	3	4	0	1	2	3	4	0	1	2	3	4
<i>Pachysoma rodriguesi</i>		0	1	2	3	4	0	1	2	3	4	0	1	2	3	4	0	1	2	3	4
<i>Pachysoma rotundigenum</i>		0	1	2	3	4	0	1	2	3	4	0	1	2	3	4	0	1	2	3	4
<i>Pachysoma denticolle</i>		0	1	2	3	4	0	1	2	3	4	0	1	2	3	4	0	1	2	3	4
<i>Pachysoma bennigseni</i>		0	1	2	3	4	0	1	2	3	4	0	1	2	3	4	0	1	2	3	4
<i>Pachysoma gariepinum</i>		0	1	2	3	4	0	1	2	3	4	0	1	2	3	4	0	1	2	3	4
<i>Pachysoma striatum</i>		0	1	2	3	4	0	1	2	3	4	0	1	2	3	4	0	1	2	3	4
<i>Pachysoma fitzsimonsi</i>		0	1	2	3	4	0	1	2	3	4	0	1	2	3	4	0	1	2	3	4
<i>Pachysoma schinzi</i>		0	1	2	3	4	0	1	2	3	4	0	1	2	3	4	0	1	2	3	4
<i>Pachysoma valeflorae</i>		0	1	2	3	4	0	1	2	3	4	0	1	2	3	4	0	1	2	3	4
<i>Pachysoma hippocrates</i>		0	1	2	3	4	0	1	2	3	4	0	1	2	3	4	0	1	2	3	4
<i>Pachysoma endroedyi</i>		0	1	2	3	4	0	1	2	3	4	0	1	2	3	4	0	1	2	3	4
<i>Pachysoma glentoni</i>		0	1	2	3	4	0	1	2	3	4	0	1	2	3	4	0	1	2	3	4
<i>Pachysoma aesculapius</i>		0	1	2	3	4	0	1	2	3	4	0	1	2	3	4	0	1	2	3	4
<i>Mnematum silenus</i>		0	1	2	3	4	0	1	2	3	4	0	1	2	3	4	0	1	2	3	4
<i>Mnematum cancer</i>		0	1	2	3	4	0	1	2	3	4	0	1	2	3	4	0	1	2	3	4
<i>Mnematum ritchiei</i>		0	1	2	3	4	0	1	2	3	4	0	1	2	3	4	0	1	2	3	4
<i>Neomnematum sevoistra</i>		0	1	2	3	4	0	1	2	3	4	0	1	2	3	4	0	1	2	3	4
<i>S. (Scarabaeolus) scholtzi</i>		0	1	2	3	4	0	1	2	3	4	0	1	2	3	4	0	1	2	3	4
<i>S. (Scarabaeolus) intricatus</i>		0	1	2	3	4	0	1	2	3	4	0	1	2	3	4	0	1	2	3	4
<i>S. (Scarabaeolus) rubripennis</i>		0	1	2	3	4	0	1	2	3	4	0	1	2	3	4	0	1	2	3	4
<i>Scarabaeus rugosus</i>		0	1	2	3	4	0	1	2	3	4	0	1	2	3	4	0	1	2	3	4
<i>Scarabaeus sacer</i>		0	1	2	3	4	0	1	2	3	4	0	1	2	3	4	0	1	2	3	4
<i>Scarabaeus galenus</i>		0	1	2	3	4	0	1	2	3	4	0	1	2	3	4	0	1	2	3	4
<i>Scarabaeus catenatus</i>		0	1	2	3	4	0	1	2	3	4	0	1	2	3	4	0	1	2	3	4
<i>Scarabaeus westwoodi</i>		0	1	2	3	4	0	1	2	3	4	0	1	2	3	4	0	1	2	3	4
<i>Scarabaeus caffer</i>		0	1	2	3	4	0	1	2	3	4	0	1	2	3	4	0	1	2	3	4
<i>Scarabaeus multidentatus</i>		0	1	2	3	4	0	1	2	3	4	0	1	2	3	4	0	1	2	3	4
<i>Scarabaeus palemo</i>		0	1	2	3	4	0	1	2	3	4	0	1	2	3	4	0	1	2	3	4
<i>Scarabaeus proboscideus</i>		0	1	2	3	4	0	1	2	3	4	0	1	2	3	4	0	1	2	3	4
<i>Scarabaeus rusticus</i>		0	1	2	3	4	0	1	2	3	4	0	1	2	3	4	0	1	2	3	4
<i>Pachylomerus femoralis</i>		0	1	2	3	4	0	1	2	3	4	0	1	2	3	4	0	1	2	3	4
<i>Sceliages brittoni</i>		0	1	2	3	4	0	1	2	3	4	0	1	2	3	4	0	1	2	3	4
<i>Kheper bonellii</i>		0	1	2	3	4	0	1	2	3	4	0	1	2	3	4	0	1	2	3	4
<i>Kheper lamarcki</i>		0	1	2	3	4	0	1	2	3	4	0	1	2	3	4	0	1	2	3	4
<i>Drepanopodus proximus</i>		0	1	2	3	4	0	1	2	3	4	0	1	2	3	4	0	1	2	3	4
<b>Outgroups</b>																					
<i>Circellium bacchus</i>		0	1	2	3	4	0	1	2	3	4	0	1	2	3	4	0	1	2	3	4
<i>Anachalcos convexus</i>		0	1	2	3	4	0	1	2	3	4	0	1	2	3	4	0	1	2	3	4

**Appendix 1 (continued).** Character states of the taxa used in the phylogenetic analysis. 0 primitive; 1-5 derived (in sequence); ? unknown character state; - not applicable character state. All characters are listed in table 2.

Taxa	Characters	3					4					5					6		
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
<i>Pachysoma rodriguesi</i>		2	0	0	3	2	3	1	4	1	1	1	1	1	1	1	1	1	
<i>Pachysoma rotundigenum</i>		0	0	0	3	2	3	1	4	1	1	1	1	1	1	1	1	1	
<i>Pachysoma denticolle</i>		2	0	0	3	2	3	1	4	1	1	1	1	1	1	1	1	1	
<i>Pachysoma bennigseni</i>		2	0	0	3	2	3	1	4	1	1	1	1	1	1	1	1	1	
<i>Pachysoma gariepinum</i>		1	0	1	3	2	3	1	4	1	1	1	1	1	1	1	1	1	
<i>Pachysoma striatum</i>		1	0	1	3	2	3	1	4	1	1	1	1	1	1	1	1	1	
<i>Pachysoma fitzsimonsi</i>		1	1	0	3	2	3	1	4	1	1	1	1	1	1	1	1	1	
<i>Pachysoma schinzi</i>		0	0	0	3	2	3	1	4	1	1	1	1	1	1	1	1	1	
<i>Pachysoma valeflorae</i>		0	0	0	3	2	3	1	4	1	1	1	1	1	1	1	1	1	
<i>Pachysoma hippocrates</i>		0	2	0	3	2	3	1	4	1	1	1	1	1	1	1	1	1	
<i>Pachysoma endroedyi</i>		0	2	1	3	2	3	1	4	1	1	1	1	1	1	1	1	1	
<i>Pachysoma glentoni</i>		0	2	0	3	2	3	1	4	1	1	1	1	1	1	1	1	1	
<i>Pachysoma aesculapius</i>		0	2	0	3	2	3	1	4	1	1	1	1	1	1	1	1	1	
<i>Mnematium silenus</i>		0	1	0	1	0	2	2	0	0	1	4	1	0	0	0	2	0	
<i>Mnematium cancer</i>		0	1	0	3	2	3	2	2	1	1	3	1	0	0	0	2	1	
<i>Mnematium nitchei</i>		0	1	0	1	1	3	2	1	1	1	4	1	0	0	0	2	1	
<i>Neomnematium sevoistra</i>		0	1	0	2	1	2	2	1	1	1	2	0	0	0	0	0	1	
<i>S. (Scarabaeolus) scholtzi</i>		0	0	0	1	2	3	0	2	0	0	1	2	0	0	0	0	0	
<i>S. (Scarabaeolus) intricatus</i>		0	0	0	1	0	0	0	0	2	0	0	0	0	0	0	0	0	
<i>S. (Scarabaeolus) rubripennis</i>		2	0	0	1	0	0	1	0	0	0	2	0	0	0	0	0	0	
<i>Scarabaeus rugosus</i>		0	0	0	1	0	2	1	2	0	0	0	0	0	0	0	0	0	
<i>Scarabaeus sacer</i>		0	0	0	2	0	1	3	1	1	1	2	0	0	0	0	0	0	
<i>Scarabaeus galenus</i>		0	1	0	2	0	1	2	1	1	3	0	0	0	0	0	0	1	
<i>Scarabaeus catenatus</i>		0	0	0	0	0	4	0	0	1	0	2	1	2	0	0	0	0	
<i>Scarabaeus westwoodi</i>		0	0	0	1	0	0	1	0	2	1	2	0	0	0	0	0	0	
<i>Scarabaeus caffer</i>		0	0	0	1	0	1	2	1	2	0	0	0	0	0	0	0	0	
<i>Scarabaeus multidentatus</i>		0	1	0	2	0	1	2	0	0	1	1	4	0	0	0	0	0	
<i>Scarabaeus palemo</i>		1	0	0	1	0	0	3	1	0	1	0	0	2	0	0	0	0	
<i>Scarabaeus proboscideus</i>		0	0	0	2	0	1	2	0	1	2	0	0	0	0	0	0	1	
<i>Scarabaeus rusticus</i>		0	0	0	1	0	0	1	0	0	1	2	0	0	0	0	0	0	
<i>Pachylomerus femoralis</i>		0	1	0	2	1	1	2	2	1	0	0	1	3	0	0	0	0	
<i>Sceliages brittoni</i>		0	0	0	1	2	0	1	2	0	1	2	0	1	0	0	0	0	
<i>Kheper bonellii</i>		0	0	0	1	0	0	3	1	1	1	4	0	2	0	1	0	0	
<i>Kheper lamarcki</i>		0	0	0	1	0	0	3	0	1	0	1	2	0	1	0	0	0	
<i>Drepanopodus proximus</i>		2	0	0	1	0	0	2	1	0	0	1	3	0	0	0	0	0	
<b>Outgroups</b>																			
<i>Circellium bacchus</i>		1	1	0	3	1	4	5	0	1	1	0	1	3	1	0	2	0	
<i>Anachalcus convexus</i>		1	0	0	3	1	4	5	2	1	2	0	3	1	1	0	2	0	

## Revision of the endemic southwest African dung beetle subgenus *Scarabaeus* (*Pachysoma*) MacLeay, including notes on other flightless Scarabaeini (Scarabaeidae: Scarabaeinae)

The subgenus *Scarabaeus* (*Pachysoma*) MacLeay, 1821 is revised. All thirteen species of the subgenus are endemic to the west coast of southern Africa. A key to all *S.* (*Pachysoma*) species is provided, and their distributions are mapped. Two new species *Scarabaeus* (*Pachysoma*) *endroedyi* and *Scarabaeus* (*Pachysoma*) *glentoni* from the southwestern Cape are described. The subspecies *S.* (*P.*) *denticollis penrithae* (Zunino) is synonymised with *S.* (*P.*) *denticollis denticollis* (Péringuey). The synonymy of *S.* (*P.*) *hessei* (Ferreira) with *S.* (*P.*) *hippocrates* (MacLeay) is confirmed. *S.* (*P.*) *valeflorae* (Ferreira) previously considered a synonym of *S.* (*P.*) *schinzi* (Fairmaire) is reinstated as a valid species. The missing type series of *Pachysoma hessei* Ferreira is traced. A lectotype is designated for *Scarabaeus aesculapius* Olivier, three paralectotypes are designated for *Pachysoma marginatus* Péringuey and one paralectotype for *Pachysoma denticolle* Péringuey. Notes on the type series, distribution records, morphological variation and known biology, are provided for all flightless Scarabaeini. A checklist of all valid species and their synonyms of *Pachysoma*, *Neopachysoma*, *Mnematium* and *Neomnematium* is included.

KEYWORDS: Coleoptera, Scarabaeini, Afrotropical, systematic revision, *Scarabaeus* (*Pachysoma*), biology, distribution.

\*Formatted for submission to 'Journal of Natural History' as J. du G. HARRISON, C.H. SCHOLTZ and S.L. CHOWN, currently in the singular person for thesis purposes.

### Introduction

The genus *Pachysoma* MacLeay, 1821 was last revised by Holm and Scholtz (1979). In a study that focussed on all the flightless Scarabaeini Mostert and Holm (1982) synonymised *Pachysoma* with *Scarabaeus* Linnaeus, 1758 and raised *Neopachysoma penrithae* Zunino to a subspecies of *Scarabaeus denticollis* (Péringuey). The only subsequent papers on *Pachysoma* include the first detailed study of the foraging and burrow construction of *Pachysoma striatum* Castelnau by Scholtz (1989) and the unofficial use by Endrödy-Younga (1989) of *Pachysoma* and *Neopachysoma* Ferreira, 1953 as subgenera.

The genera *Pachysoma* and *Neopachysoma* (*sensu* Ferreira 1966) are treated here as a single subgenus of *Scarabaeus*, viz. *Scarabaeus* (*Pachysoma*) (refer to chapter 2 for rationale). Holm and Scholtz (1979) included the species of *Mnematium* MacLeay, 1821 within *Pachysoma*. Their system is not followed here, because *Mnematium*, *Neomnematium*