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Systematics of the endemic south-west African dung beetle genus *Pachysoma* MacLeay (Scarabaeidae: Scarabaeinae)

by

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for the degree of

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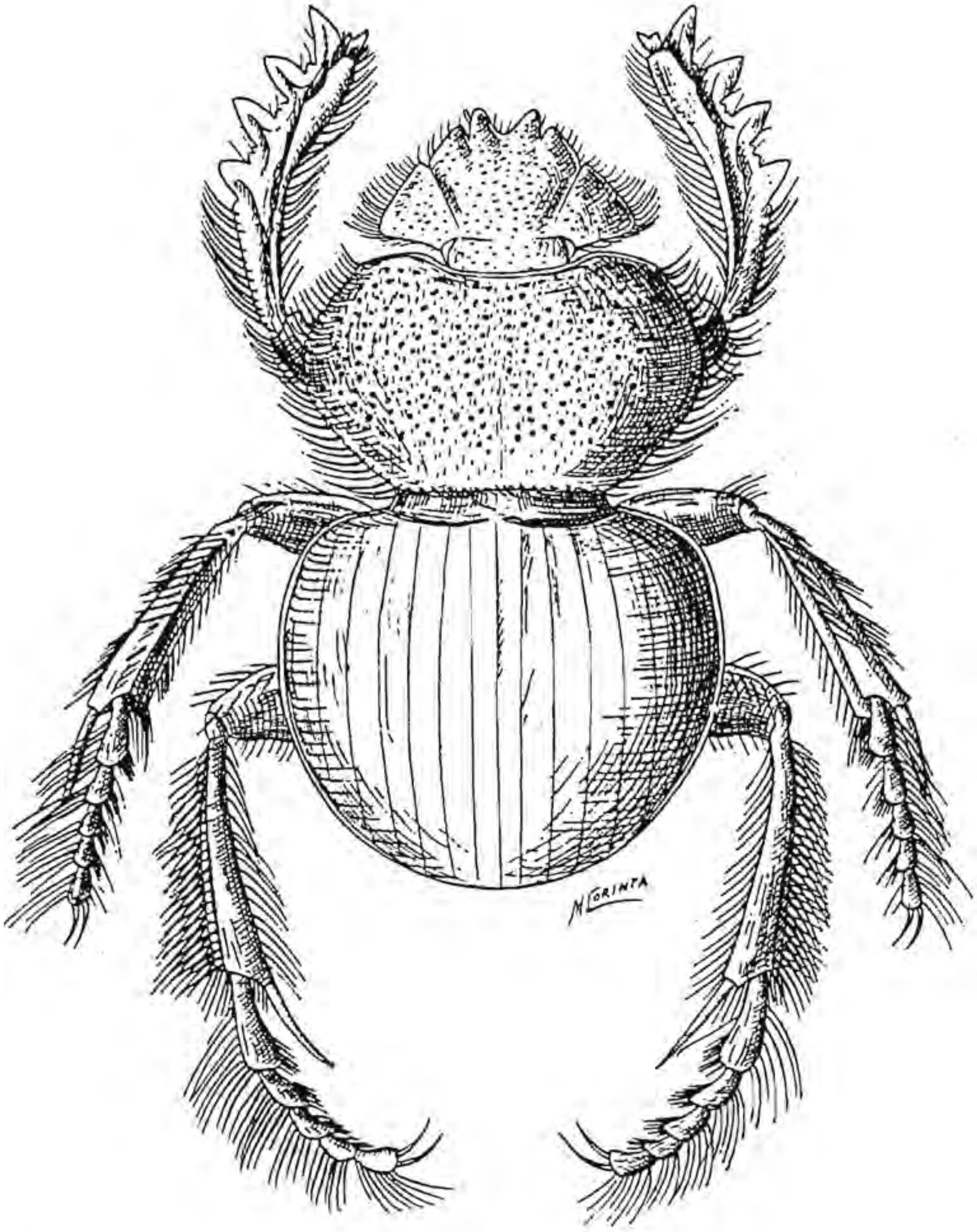

Scarabaeus (Pachysoma) hippocrates (MacLeay, 1821)

Drawn by: Dr Maria Corinta Ferreira

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I humbly dedicate this thesis to:

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Ron and Margaret Harrison, Pete, Amanda, Timothy, and Philip Harrison,
Chris and Cath Watkins, Cyril and Jeanette Friend, Edwin and Lillian Harrison,
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Research Unit, Foundation for Research Development, Mazda Wildlife Fund, Honda,
Scarabiology 1996, The South African Defence Force, Namaqualand, sand, wind and sea,
Series IIa Land~Rover, a snapped half-shaft, one spade and trowel, the Honda ATV,
telecoprids, the tribe Scarabaeini, and the unfriendly farmer.

Who all wittingly or unwittingly made a contribution.

'From James, a servant of God and of the Lord Jesus Christ, To the twelve tribes scattered among the nations: Greetings' James 1:1.

Content **Page**

Systematics of the endemi eetle genus *Pachysoma* MacLeay (Scarabaeidae: Scarabaeinae)

by

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ABSTRACT

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; *Mnematium* MacLeay, 1821 and *Neomnematium* 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.

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 [illegible] *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 FOR THESIS RETRIEVAL: Insects, Coleoptera, Scarabaeidae, Scarabaeinae, Scarabaeini, Afrotropical, *Pachysoma, Neopachysoma, Mnematium, Neomenmatium, Scarabaeus, Kheper, Sceliages, Drepanopodus, Pachylomerus*, cladistic, phylogeny, endemic, dung beetles, flightless, food preference, dry dung, detritus, psammophily, relocation strategy, systematic revision, biology, distribution.

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; *Mnematium* MacLeay, 1821; and *Neomnematium* 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. gariepinum*, *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. gariepinum* 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 vestigeal 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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CHAPTER 2

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; *Mnematium* MacLeay, 1821 and *Neomnematium* 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 gariepinum* 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 *Mnematium 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) 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*, *Mnematium* and *Neomnematium* from the flying taxa. However, see *Taxa* for previous generic placement of the flying *Scarabaeus* species.

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

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 unclusttered 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. 66, R.I. 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.

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.

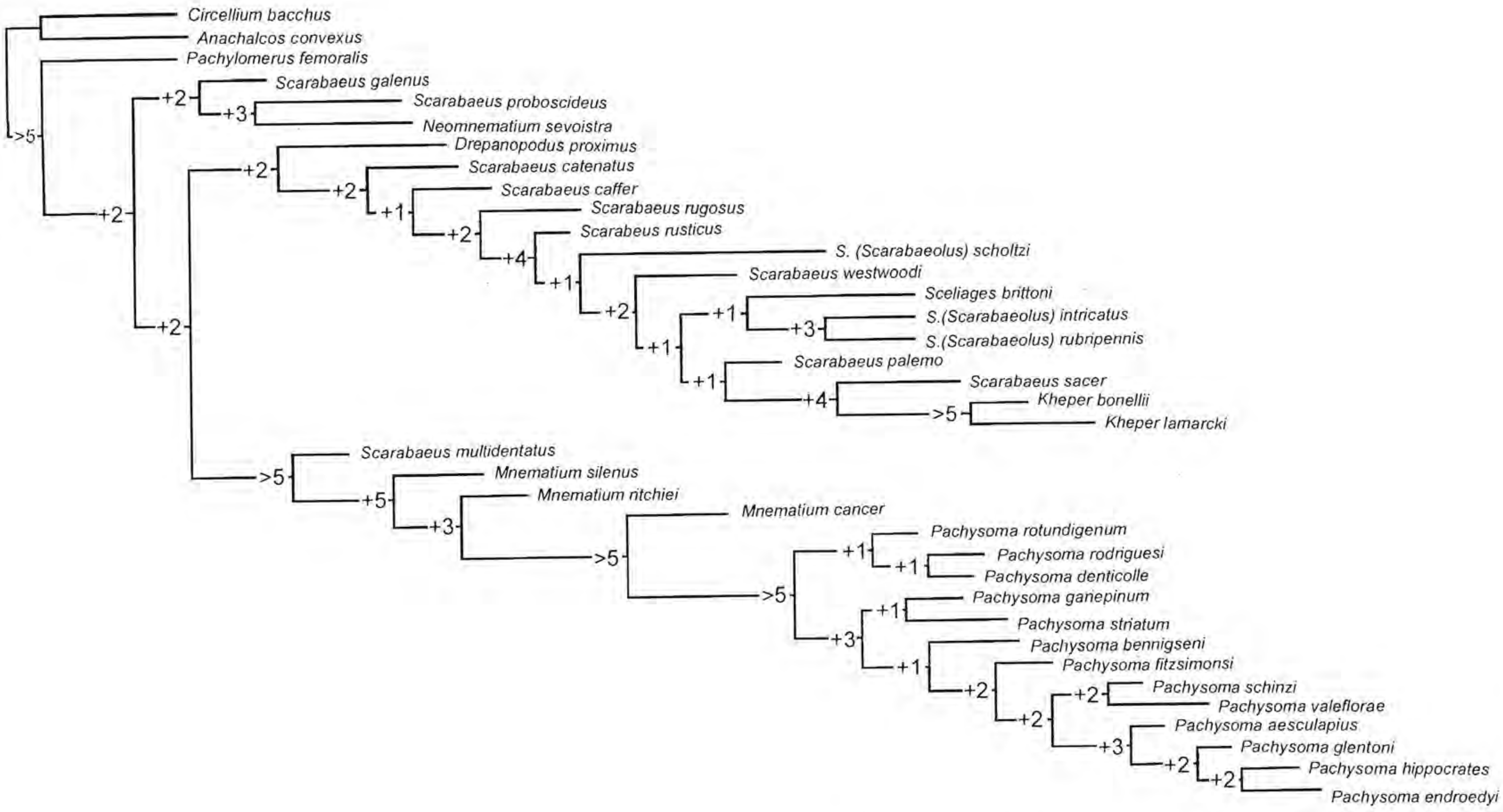

FIGURE 1. Cladogram depicting the relationship between the flightless Scarabaeini (i.e. *Pachysoma*, *Neopachysoma*, *Mnematium* and *Neomnematium*) and representative taxa of the flying Scarabaeini genera (i.e. *Scarabaeus*, *Kheper*, *Pachylomerus*, *Sceliages* and *Drepanopodus*) with *Circellium* 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. rodriguesi* 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 apexes; (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. valeflorae*, 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. ritchiei, 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, Sce. 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 *Neomnematium*. 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 *Mnematium* 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 form 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 unpbl.). *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, *Aepyceros 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 unpbl.), 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 Somalian 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 specious 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 unpbl.). All *Pachysoma* have contiguous mesocoxae, while *Mnematium* species have semi to completely contiguous mesocoxae, thus although the reduction is 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, Palestrini and Barbero 1992). Larval evidence to possibly support placing *Kheper* as a subgenus of *Scarabaeus* comes from the comparative study by Palestrini 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. Palestrini 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'*, *'Heliocantharus'*, *'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 synapomorpy 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, Glaphyrocanthon* 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 endemicity 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 ecophysiologically); (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 adaptions 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 Grootsandleegte 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 01234567890	2 1234567890	3 1234567890
Pachysoma rodriguesi	01301100233	1022211230	3102401511
Pachysoma rotundigenum	01301100233	1022211030	2102301011
Pachysoma denticolle	01301100233	1022212230	3102301011
Pachysoma bennigseni	01301100233	0011012032	0102300011
Pachysoma gariepinum	02301100333	0001212031	0002300011
Pachysoma striatum	0130-211333	0002210030	0002300001
Pachysoma fitzsimonsi	02301100313	0001012032	0002301001
Pachysoma schinzi	01321000111	0101020032	0002301001
Pachysoma valeflorae	01331000111	0101021332	0102301001
Pachysoma hippocrates	0131-211311	0122010130	0102400101
Pachysoma endroedyi	0031-211311	0021010032	0002300111
Pachysoma glentoni	0131-211311	0022010130	0002301101
Pachysoma aesculapius	0131-211311	0100010032	0002301101
Mnematium silenus	22000000133	1001210220	2001100211
Mnematium cancer	01401000122	100?2?1230	4002300401
Mnematium ritchiei	11000001121	0001210220	2002100211
Neomnematium sevoistra	00100001010	0102211320	0002200301
S. (Scarabaeolus) scholtzi	01001101311	0102200000	0001000001
S. (Scarabaeolus) intricatus	00010001011	1010010121	2001200000
S. (Scarabaeolus) rubripennis	00000001011	1011110111	2002100200
Scarabaeus rugosus	11001001011	1110210010	0002200200
Scarabaeus sacer	10000001112	1012210012	0012100310
Scarabaeus galenus	42001101010	2102210110	2002100200
Scarabaeus catenatus	12000001011	1100210111	3002200200
Scarabaeus westwoodi	40010001111	1110210310	0002100000
Scarabaeus caffer	12200001111	1201210110	3002200200
Scarabaeus multidentatus	32200000120	1000210220	2002100210
Scarabaeus palemo	00000001111	1101010110	0002100000
Scarabaeus proboscideus	32001001010	1010221120	2002100210
Scarabaeus rusticus	11000001111	111?210110	0002200300
Pachylomerus femoralis	10101000132	1000200201	4002102200
Sceliages brittoni	0000-211011	1110100101	0000300010
Kheper bonellii	00010000021	0100211312	0012213310
Kheper lamarcki	20010000121	1101201302	2012213310
Drepanopodus proximus	10000001111	0011210230	2012214320
Outgroups			
Circellium bacchus	**1041-211310**	**0230011002**	**1000100201**
Anachalcos convexus	**-004-2-1300**	**0200215002**	**1000000000**

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	
	1234567890	1234567890	1234567890	123
Pachysoma rodriguesi	2003230111	0323141111	1131121211	111
Pachysoma rotundigenum	0003230111	1313141111	1131121211	111
Pachysoma denticolle	2003230111	0323141111	1131121211	111
Pachysoma bennigseni	2003230111	0223141111	1131120211	111
Pachysoma gariepinum	1013230011	0323141111	1131121211	111
Pachysoma striatum	1013230011	0323141111	1131121211	111
Pachysoma fitzsimonsi	1103230011	0223141111	1131121211	111
Pachysoma schinzi	0003230211	0223141111	1131121311	111
Pachysoma valeflorae	0003230211	0113141111	1131121211	110
Pachysoma hippocrates	0203230211	0113141111	1131121211	111
Pachysoma endroedyi	0213230211	0103141111	1131121211	111
Pachysoma glentoni	0203230211	0113141111	1131121211	111
Pachysoma aesculapius	0203230211	0223141111	1131121211	111
Mnematium silenus	0101022001	0100141000	2020111100	201
Mnematium cancer	0103232211	1314131000	2121121210	201
Mnematium ritchiei	0101132111	0111141000	2020111100	201
Neomnematium sevoistra	0102122111	0111120000	002?011000	010
S. (Scarabaeolus) scholtzi	0001230200	0110120000	0020010100	000
S. (Scarabaeolus) intricatus	0001001100	0000020000	0010010000	000
S. (Scarabaeolus) rubripennis	2001001000	1000020000	0010010000	000
Scarabaeus rugosus	0001002111	1302120000	0010010000	000
Scarabaeus sacer	0002013111	1320120000	0010000000	000
Scarabaeus galenus	0102012111	0101130000	0010011000	010
Scarabaeus catenatus	0000004001	0102120000	0010011000	000
Scarabaeus westwoodi	0001001001	0102120000	0010011000	000
Scarabaeus caffer	0001012101	0102120000	0010010000	000
Scarabaeus multidentatus	0102012001	0101140000	2020?11100	000
Scarabaeus palemo	1001003101	0100020000	0010010000	000
Scarabaeus proboscideus	0002012011	1322120000	0000001000	010
Scarabaeus rusticus	0001000101	0100120000	0010010000	000
Pachylomerus femoralis	0102112210	1400130000	0020011000	000
Sceliages brittoni	0001201201	0110000000	0000010000	000
Kheper bonellii	0001003111	1402010000	0010000000	000
Kheper lamarcki	0001003010	1412010000	0010001000	000
Drepanopodus proximus	2001002100	0002130000	0020111000	000
Outgroups				
Circellium bacchus	**1103145011**	**0110131022**	**1210012000**	**0?0**
Anachalcos convexus	**1003145211**	**2203110022**	**0211021000**	**020**

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.

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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*

CHAPTER 3

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

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Janssens, 1938 and *Mnematidium* Ritsema, 1889 are included within *Scarabaeus sensu lato* (see chapter 2). All subsequent use of *Pachysoma* herein is at the subgeneric level.

S. *(Pachysoma)* currently comprises thirteen species endemic to the sandy coastline from Cape Town (33°56'S 18°28'E) in South Africa to Walvis Bay (22°58'S 14°30'E) in Namibia (figure 1). The northerly distribution of S. *(Pachysoma)* is abruptly halted at the Kuiseb River (23°03'S 14°27'E), which marks the end of the sandy central Namib dune sea. While the southern and easterly limits of S. *(Pachysoma)* are defined by the Cape Fold Mountains and escarpments rising from the coastline (see Kruger 1983) as topographical and climatic barriers preventing the southerly and easterly expansion of S. *(Pachysoma)* species. Holm and Scholtz (1979) were the first authors to record the unique foraging behaviour in *Pachysoma*. Unlike typical ball rolling S. *(Scarabaeus)*, S. *(Pachysoma)* do not make dung balls but collect dry dung pellets and detritus, which they drag forward to preconstructed burrows (refer to chapter 2 for details on their biology).

Holm and Scholtz (1979) examined 664 specimens of S. *(Pachysoma)*. Substantial new material (totalling 2629 specimens) and two new species enable S. *(Pachysoma)* to be reexamined. The study by Holm and Scholtz (1979) was based mainly on new material from Namibia. Very little new material (since Ferreira 1953a,b, 1966) of the South African species was available for them to study. This imbalance is rectified by a combination of subsequent collecting efforts from various institutions (see Endrödy-Younga 1996), and access to previously unavailable material. The new material (i.e. not examined by Holm and Scholtz (1979)) was obtained from the following sources: (1) the systematic coastal survey (1973-1989), by the late Sebastian Endrödy-Younga, from the Kunene River (17°16'S 11°48'E Angola's southern border) to Cape Town (Endrödy-Younga 1996); (2) collecting trips to Namibia between 1977-1981, led by Erik Holm (formerly Head of the Department of Entomology, Pretoria University); (3) pitfall trapping by Eugene Marais and Ashley Kirk-Spriggs of the State Museum of Namibia; (4) donation of the Desert Ecological Research Unit of Namibia (DERU) collection to the State Museum of Namibia; (5) access to the remains of Ferreira's collection in the National Museum in Bloemfontein; (6) reorganisation of the South African Museum collection (Cochrane 1995); (7) while most recently, collecting done specifically by JDUGH for the purposes of this study.

From June 1996 to January 1997, the South African West coast from Alexander Bay (28°40'S 16°30'E) to Cape Town (33°56'S 18°28'E) was specifically surveyed for S. *(Pachysoma)* species. Before fieldwork commenced all the available locality data (from museum material and publications) was mapped onto 1:250 000 Topo-cadastral maps. Collecting efforts were thus focussed on gaps in distributions, range extensions, and unlikely locality records. Specific efforts were made to expand upon known distributions and investigate the continuity of previously suspected clines. Thus all material collected since the last revision, (1979-1997) including most material used for the last revision is examined (a total of 2629 specimens).

In this study two new species of S. *(Pachysoma)* are described and all species are revised. Existing species are not redescribed as this has been adequately done elsewhere (Ferreira 1953a, 1966). Observations on biology are recorded for all the South African species, some for the first time. The habitat preference of *S. (Pachysoma)* species is included, based on known distributions and confirmed by field work. Distribution maps and a revised key are provided for all *S. (Pachysoma)* species. The accuracy (use of a Global Positioning System in degrees°, minutes" and seconds') and number of unique localities (563) for *S. (Pachysoma)* are substantially increased. This provides a valuable database for conservation planners to use when making recommendations to insure the future conservation of these endemic species.

Material and Methods

Material examined is in the following depositories and acronyms unless marked by an asterisk follow Arnett *et al.* (1999):

AMGS	Albany Museum, Grahamstown, South Africa.
BMNH	The Natural History Museum, London, United Kingdom.
BMSA	National Museum Bloemfontein, Bloemfontein, South Africa.
COCS*	Mr C.R. Owen Collection, Somerset West, South Africa.
CPMM	Dr Alvaro de Castro Provincial Museum, Lourenço Marques, Mozambique.
DMSA	Durban Natural Science Museum, Durban, South Africa.
MIZT	Università di Torino, Torino (M.Zunino Collection), Italy.
MNHN	Muséum National d'Histoire Naturelle, Paris, France.
MMKZ	Alexander McGregor Memorial Museum, Kimberly, South Africa.
NHMB	Naturhistorisches Museum, Basel, Switzerland.
NHRS	Naturhistoriska Riksmuseet, Stockholm, Sweden.
SAMC	South African Museum, Cape Town, South Africa.
SANC	South African National Collection of Insects, Pretoria, South Africa.
SMTD	Staatliches Museum für Tierkunde, Dresden, Germany.
SMWN	National Museum of Namibia, Windhoek, Namibia.
TMSA	Transvaal Museum, Pretoria, South Africa.
UPSA	University of Pretoria Collection, Pretoria, South Africa.
USSA*	University of Stellenbosch Collection, Stellenbosch, South Africa.
UZIU	Uppsala University, Uppsala, Sweden.
ZMHB	Museum für Naturkunde der Humboldt-Universität, Berlin, Germany.

Selected material was borrowed from the BMNH and only material not determined by Holm and Scholtz (1979) was lent by the SMWN. The MMKZ is currently housed and curated by the BMSA (who code it as AMMM). Most of the material examined were dry pinned specimens. However, fragments of dead specimens were collected and often represent the only evidence that a *S. (Pachysoma)* species occurs at a particular locality. These pieces were pinned and labelled and are referred to in the material examined as (p.). The numbers (#) of specimens examined is summarized as follows: (Σ#) total number of specimens; [#] specimens studied by Holm and Scholtz (1979); (#♀ #♂) females and males; (#uns.) unsexed individuals; (#diss.) male genitalia dissected/examined; (#eth.) specimens preserved in ethanol; (#p.) pieces/fragments. Specimens were sexed using the following external characteristics: prensence (♂) or absence (♀) of pheromone glands on the lateral abdominal sternites; dimorphic protibia or protibial spurs; and width of the last abdominal sternite at the apex of the pygidium (narrow♂; broad♀).

Label data. All information on type material is cited verbatim (for the first time) using a comma to separate lines on the same label and a forward slash (/) to separate consecutive labels on the same pin. Additional information when included is placed in parentheses ( ). Data on the reverse of labels, which is easily overlooked, is shown by a double forward slash (//). The following terminology is used when referring to the lettering on type labels: written (handwritten); printed (letters not embossed into the paper); typed (letters embossed into the paper). Unless otherwise specified, black ink was used to write, type or print labels. Where reference is made to an author's handwriting, it was confirmed by comparison with handwriting known to belong to the author. Locality data for nontype specimens are amended for clarity only where necessary and listed alphabetically according to country. Where material collected by JDUGH includes many localities, these are listed sequentially. Localities outside the apparent distribution range of a species are included at the end of material examined as potentially incorrectly labelled or vague locality records.

Types. Ferreira (1953a,b) and Péringuey (1888) described six and two species of *Pachysoma,* respectively, although two of Ferreira's species are viewed as synonyms. Confusion surrounding valid Péringuey and Ferreira types, necessitated checking all labelled 'type' material against that listed or referred to in the original description. This was necessary because the types of Péringuey and Ferreira species were not always labelled as such. Furthermore, a duplicate series of specimens collected at the same locality by the same collector often exists for Ferreira types (e.g. *P. gariepinum* and *P. granulatum*). To prevent future confusion I have checked all 'labelled Ferreira types' against those listed by her, and made amendments where necessary. New labels for unlabelled but traced paratypes (only *P. gariepinum*) are printed onto yellow card, using the spelling and date of Ferreira's type labels. Institutions from which type material was not seen, but where Holm and Scholtz (1979) verified the type to be housed are included in brackets [ ]. Braces { } are used for types not examined, but to show where the original author deposited the specimen/s. Types deposited by Holm and Scholtz (1979) in the UPSA collection have been moved to collections as listed under type material. Labels for primary and secondary types of new species described herein are laser printed in black ink onto red (Holotype ♂) and yellow (Allotype ♀ and paratypes) card using the following format: HOLOTYPE ♂, SCARABAEUS (PACHYSOMA) endroedyi, HarrisonScholtzChown, Manuscript date 2000.

Distribution maps. Grid references in degrees and minutes are given for all localities. Where the grid reference was excluded from the original label, it was traced using Leistner and Morris (1976), Skead (1973) or calculated from 1:250 000 and 1:500 000 Topo-cadastral maps for South Africa and Namibia respectively. Grid references for flightless Scarabaeini occurring in Madagascar, Somalia, Libya, Angola, and Syria were obtained from the 'National Imagery and Mapping Agency (NIMA) GEOnet Names Server' (Rohrer 1999). Using all available locality data maps were drawn with 'MAPPIT' Geographical Mapping System, Version 2.0 (Arnold *et al.* 1996). Locality records well outside the established distribution range are mapped as labelled open circles, for example ○ Sneeukop. Grid references are only repeated in the text where necessary, as the grid reference for the majority of localities mentioned are included in the material examined for the respective species under discussion.

Morphology. Terminology used follows Lawrence and Britton (1991), and Torre-Bueno (1989). Using external morphology specimens were sorted into morphospecies, after which microscopic examination separated species. Male genitalia were examined when necessary and proved a reliable and robust method for distinguishing species. Genitalia were especially useful in the *hippocrates* species complex.

Certain morphological attributes of *S. (Pachysoma)* species can potentially mislead accurate species identification. These pitfalls include the following: (1) variable expression of elytral and pronotal waxy indument. These species *S. (P.) striatus*, *S. (P.) gariepinus*, *S. (P.) endroedyi*, the Olifants to Groen River *S. (P.) hippocrates*, and northern populations of *S. (P.) aesculapius* all exhibit indument to varying degrees. The indument absorbs the colour of the substrate and varies due to abrasion and age of the specimen. For example, *S. (P.) gariepinus* from near the Buffels River (29°55'S 17°40'E) are easily identified by their red indument, while the same species from Hohenfels (28°30'S 16°37'E) have grey to white indument; (2) well preserved dead specimens/s, that have been finely abraded by sand and wind-action, are very glossy in appearance with altered or obliterated micro-sculpture and subsequently can be misleading. However, unabraded specimens are usually available from the same locality for comparison, and the protibial and clypeal wear reveals their age; (3) colouration from the sand type of micro-sculpture, pronounced elytral rim and elytral intervals. Care should be taken to focus on the actual micro-sculpture rather than the apparent colour or highlights. This is especially true of the northern population of *S. (P.) aesculapius* that have their elytral intervals highlighted (by the white clay from their substrate) to such an extent that they appear to represent another species; (4) very small individuals are also confusing, especially when associated with malformation or when only one sex is present. The adult size of dung scarabs (within species limits) is dependant on the food resource (provisioned by the adults) and environmental factors during their development (Davidson and Roberts 1968, Davidson *et al.* 1972). Very small individuals and malformed specimens are probably the result of insufficient food or adverse growth conditions or both. For example, very small females of *S. (P.) striatus* from Rooidam (31°04'S 17°48'E) and Dembergdraai (30°47'S 17°43'E) were previously thought to represent a new species (Endrödy-Younga pers. comm.).

Dissection and examination of male genitalia. The male genitalia of Coleoptera are generally diagnostic for species identification (D'Hotman and Scholtz 1990a), and can be especially useful in species where the external morphology hardly differs (e.g. *S. (P.)*

hippocrates and *S. (P.) glentoni*). D'Hotman and Scholtz (1990b) observed that the genitalia of the Scarabaeinae genera are similar, but they vary considerably in structural detail, enabling their use for species identification. Male genitalia were examined from the northern, central and southern extreme of a species' distribution and from any geographic outliers. However, the preparation technique used and orientation of the male aedeagi can lead to misinterpretation of the structure and form of the genitalia. To facilitate reliable comparison of genitalia the following procedure was used: (1) specimens' labels were removed and placed in a unit tray before the beetle was relaxed in boiled distilled water (*ca.* 90 °c). Due to the tight seal of the pygidium, the beetle was usually removed after about three minutes and the pygidium prised open then replaced to enable the internal tissue to soften; (2) genitalia were removed with forceps, rinsed in warm water, and without removing the internal sac the base of the aedeagus was oriented dorsally onto a pointed mounting card and glued with water soluble glue ('Otto Rings Fluessiger Leim Syndetikon™', available from Bioform in Germany); (3) the specimen and aedeagus were then both labelled with the species acronym and a number, e.g. hipp1; (4) where necessary genitalia previously dissected and mounted on their sides, were softened and remounted to simplify comparison. After it was discovered that extended exposure (> 3 min) to hot water results in the anterior apex of the parameres swelling and altering the appearance of the genitalia, long exposure to hot water was avoided; (5) genitalia were aligned sequentially on a balsa strip, according to their geographic position (i.e. from south to north), which enabled microscopic comparison across a geographic range. In this way the presence of clines versus abrupt and distinct changes in aedeagal morphology were discernable; (6) on completion of the comparison, each aedeagus was placed on the pin underneath its respective specimen.

Measurements. Were made using a Mitutoyo™ calliper (No. 505-646) to two decimal places in millimetres. Body length equals the distance between the medial incision on the clypeus to the furthest point of the abdomen; body width equals the maximum distance across the thorax.

Illustrations. Drawings were done by Erik Holm (formerly UPSA), and previously published in Holm and Scholtz (1979) and Mostert and Holm (1982). Additional drawings (figures 20-21; 26a,b; 37-39a,b; 43-44a,b; 54-56; 58-60a,b,c; 64-65a,b,c) were drawn by JDUGH using a *camera lucida* (Wild™ Typ. 308700), on a dissecting microscope (Wild™ M38). The drawings are not shown to scale.

Systematics

Subgenus *Scarabaeus (Pachysoma)* MacLeay

Pachysoma MacLeay, 1821: 507. Type species *Pachysoma hippocrates* MacLeay, by original designation.

Irrorhotides Shipp, 1896: 116. Type species *Irrorhotides fryi* Shipp, by monotypy.

Neopachysoma Ferreira, 1953a: 37. Type species *Pachysoma denticolle* Péringuey, by original designation.

Diagnosis

Clypeus: 'Clypeal scraper' composed of medially incised ridge with or without medial tooth.

Mouthparts: Epipharynx; Anterior lobes slightly setose; lateral setal combs formed by two fused rows of setae; anterior median process tear shaped. *Maxilla*; ventral articulatory sclerite of galea composed of highly sclerotized disc, which is notched anteriorly. *Mandibles;* Coarsely serrated mola surfaces. *Labium;* Inner ligular lobes, well developed and highly sclerotized with short tuft of setae on apex.

Comments. Holm and Scholtz (1979) provide a thorough discussion on *Pachysoma*, and only a few general remarks will be made here. I believe *Scarabaeus (Pachysoma)* MacLeay represents a derived branch of *Scarabaeus* (see Harrison *et al.* 200x), which probably evolved as a response to aridification. This is contrary to their primitive or ancient origin as suspected by Balthasar (1963). They have a restricted coastal distribution to southwestern African coastal sands from Cape Town (33°56'S 18°28'E) in South Africa to Walvis Bay (22°58'S 14°30'E) in Namibia. All species are flightless and feed on dry dung or detritus, which they drag forward to their burrows. Their preferred habitat includes a variety of sandy habitats, as shown by their psammophilous adaptations, (i.e. elongated body setae and spatulate mesotarsal spurs).

Key* to the species of *Scarabaeus (Pachysoma)* MacLeay

1 Sub-elytral ridge present 9
_ Base of elytra rounded, without a ridge on base 2

2(1) Distance between medial clypeal teeth at least one-third width of clypeus in front; male with clypeal teeth strongly produced into hornlike structures (figures 25, 26) 3
_ Distance between medial clypeal teeth at least one-quarter of width of clypeus in front 4

3(2) Distance between second and third protibial teeth notably greater than between others; serrations between protibial teeth (figure 43) . . . . ***schinzi*** (Fairmaire)
_ No serrations between or proximal to protibial teeth (figure 44) . . . . ***valeflorae*** (Ferreira)

4(2) Frons with prominent tubercle between eyes (figure 29); specimens large, shiny, reddish brown to black; with median and two lateral longitudinal depressions on pronotal disc . . . . ***rodriguesi*** (Ferreira)
_ Frons without tubercle 5

5(4) Outer margin of genae smooth (figure 22); posterior, lateral pronotal edges hooked; males with protibia (figure 40) and metatibia strongly modified . . . . **striatus** (Castelnau)

– Outer margin of genae serrated or irregular (e.g. figure 23) 6

6(5) Pronotum with median and two oblique lateral depressions on disc 7

– Pronotal disc evenly rounded 8

7(6) Protibia with denticulate projection on inside, opposite sub-apical outside serration; specimens mostly with orange to black on elytra; protibia with two long rows of spines on inside, males with protibial spur bifurcate (figure 48) . . . . **denticollis** (Péringuey)

– Protibia without internal projections opposite sub-apical outside serration (figure 42); elytra markedly flat and deeply striate . . . . **bennigseni** (Felsche)

8(6) Elytra smooth, shiny; protibia with sub-apical projection on inside (figure 46) . . . . **rotundigenus** (Felsche)

– Elytra striate; pronotum and elytra greyish black with band of indument around outer margin; protibia not dimorphic, spur simple (figure 41) . . . . **gariepinus** (Ferreira)

9(1) Metatarsal claws equal in length or longer than last tarsal segment 10

– Metatarsal claws shorter than last tarsal segment 11

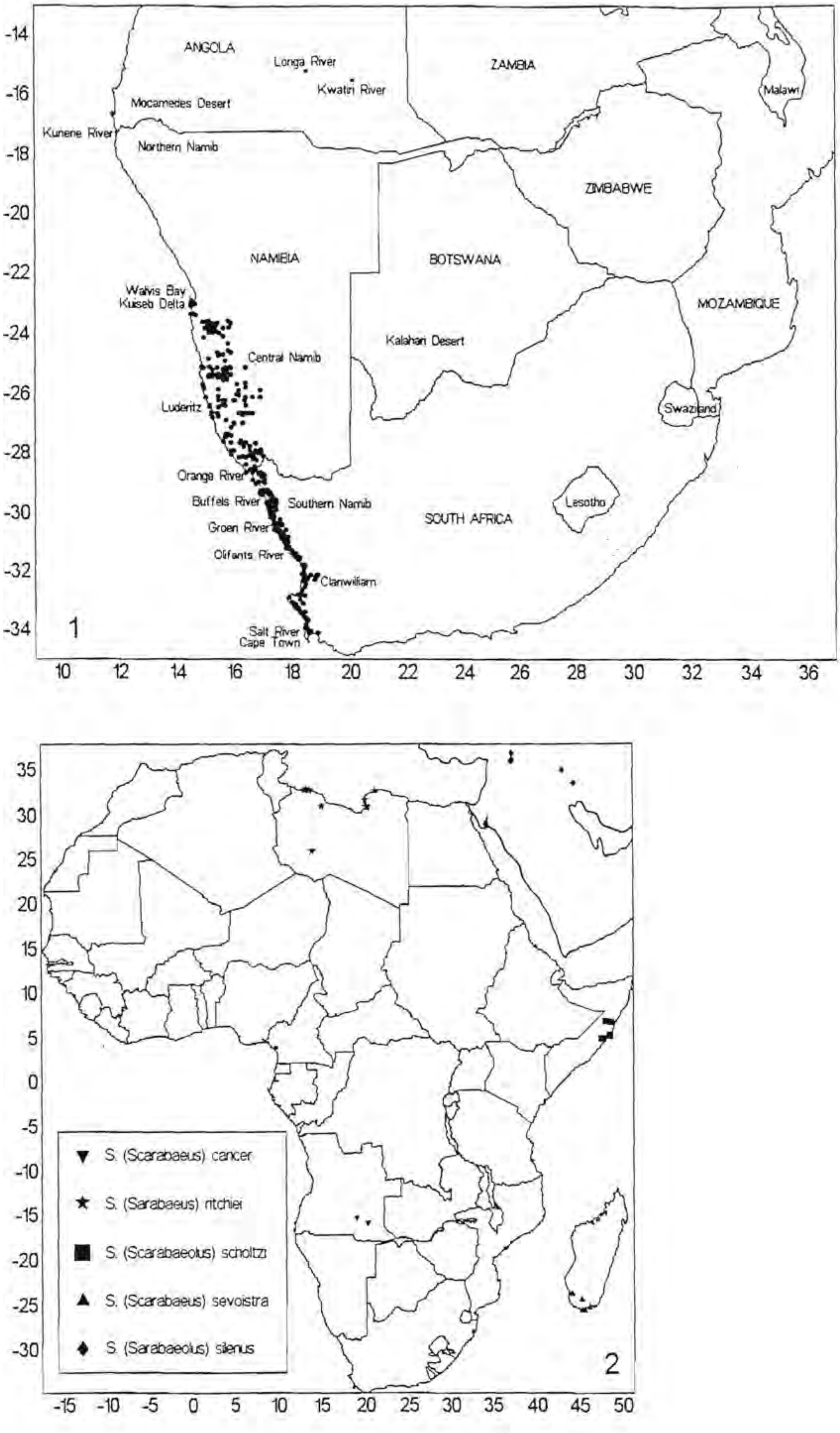
10(9) Protibial spurs bifurcate (figure 37); mesotarsal spurs spatulate, with basal extension (figure 54) . . . . **hippocrates** (MacLeay)

– Mesotarsal spur spatulate but not expanded (figure 55); parameres asymmetrical, short, surface irregular (figure 59); restricted distribution from north of Lambert's Bay (32°05'S 18°18'E) to just south of the Olifants River (*ca.* 31°45'S 18°14'E) . . . . **glentoni** sp. n.

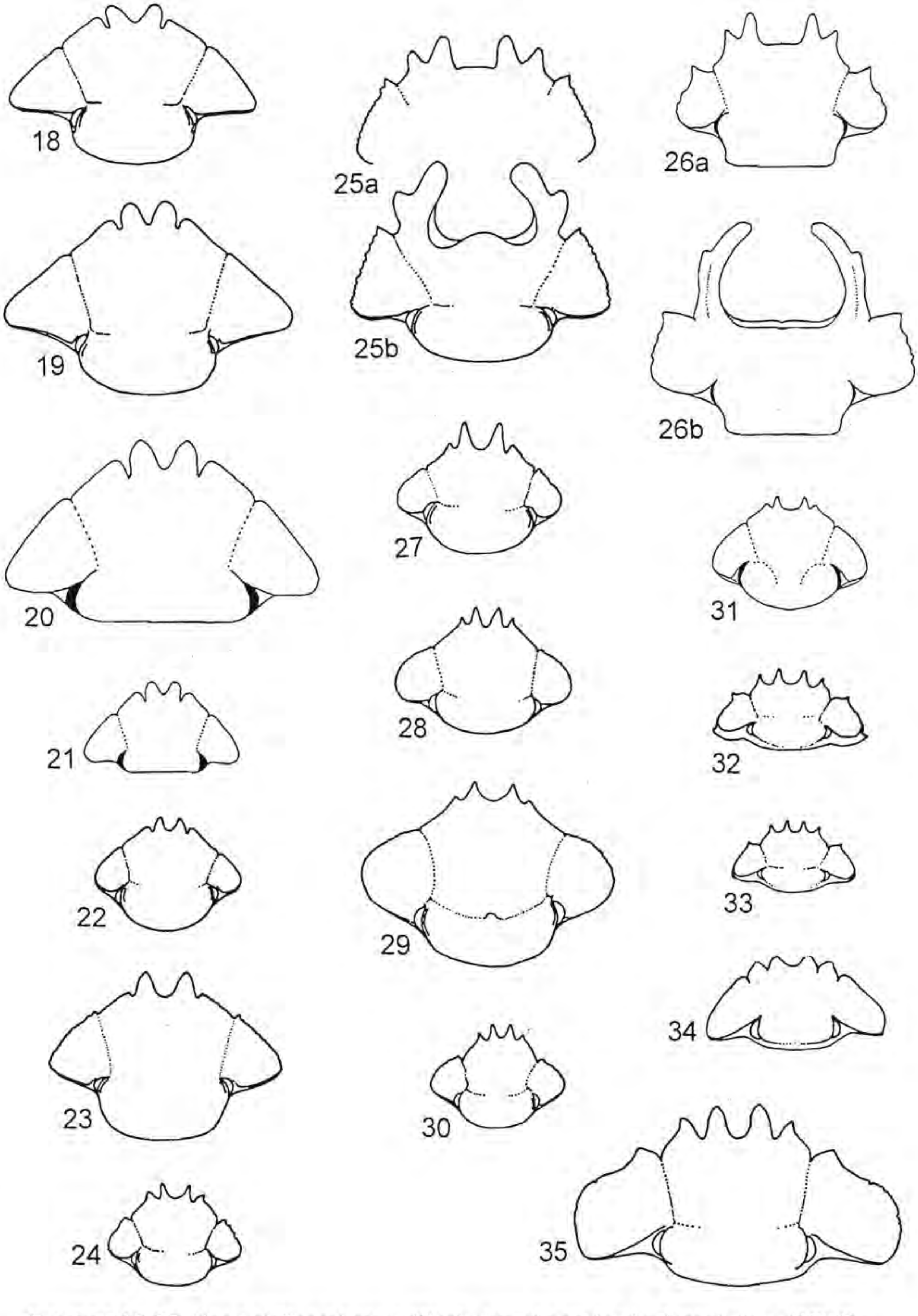
11(9) Band of indument around base of elytra; protibial spurs bifurcate (figure 39); mesospur parallel sided (figure 56); metatarsal claws shorter than last tarsal segment . . . . **endroedyi** sp. n.

– Metafemur with two dense, semicircular combs of bristles on the underside . . . . **fitzsimonsi** (Ferreira)

12 Genae straight in front, without any points, and hardly separated from clypeus by an incision (figure 18); distribution south of the Olifants River (31°42'S 18°12'E) to Cape Town (33°55'S 18°25'E) . . . . **aesculapius** Olivier



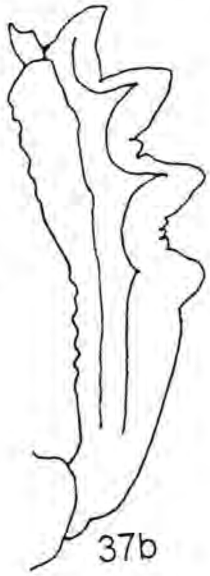
FIGURES 1-2. (1) Distribution of *Scarabaeus (Pachysoma)* ● in southern Africa, occurring from Cape Town (33°56'S 18°28'E) to Walvis Bay (22°58'S 14°30'E). The only known localities in Angola for the flightless *Scarabaeus cancer* ■ (formerly *Mnematium*), are included. (2) Distribution map of other flightless *Scarabaeus* species (formerly *Mnematium* and *Neomnematium*).



FIGURES 18-35. Head of *Scarabaeus (Pachysoma)* species in dorsal view. (18) *S. (P.) aesculapius;* (19) *S. (P.) hippocrates;* (20) *S. (P.) glentoni;* (21) *S. (P.) endroedyi;* (22) *S. (P.) striatus;* (23) *S. (P.) gariepinus;* (24) *S. (P.) bennigseni;* (25) *S. (P.) schinzi;* (a) female, (b) male; (26) *S. (P.) valeflorae;* (a) female, (b) male; (27) *S. (P.) fitzsimonsi;* (28) *S. (P.) rotundigenus;* (29) *S. (P.) rodriguesi;* (30) *S. (P.) denticollis.* Head of flightless *Scarabaeus (Scarabaeolus)* species in dorsal view. (31) *S. (Scarabaeolus) scholtzi;* (32) *S. (Scarabaeolus) silenus.* Head of flightless *Scarabaeus (Scarabaeus)* species in dorsal view. (33) *S. (Scarabaeus) ritchiei* (34) *S. (Scarabaeus) sevoistra;* (3 *us) cancer.*


36


37a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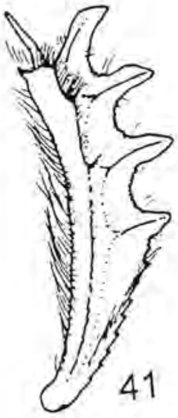
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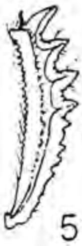
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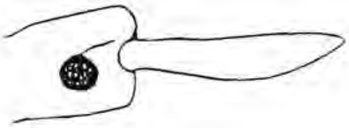
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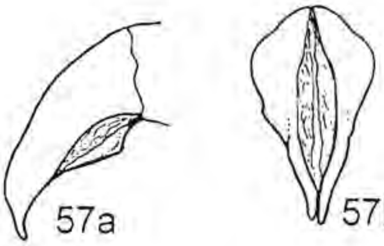
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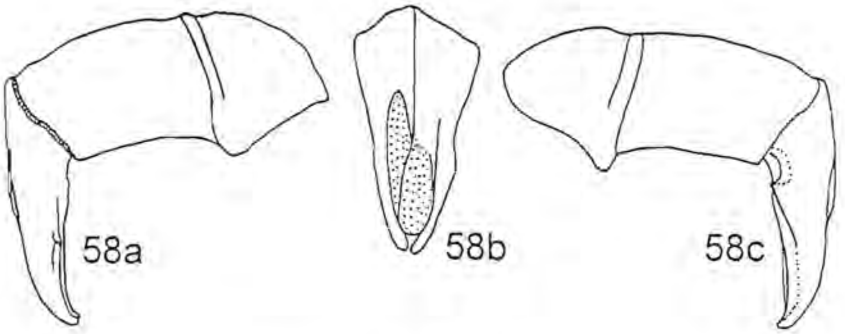
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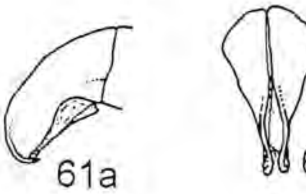
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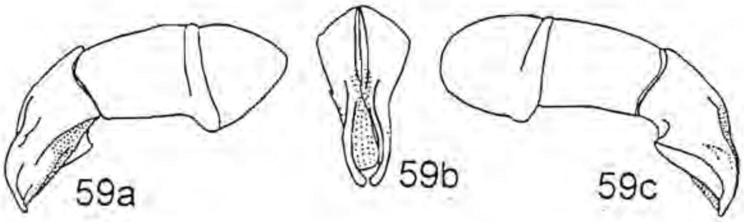
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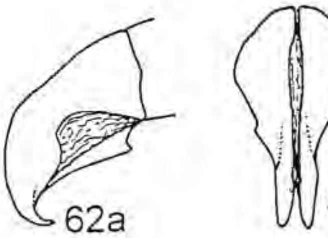
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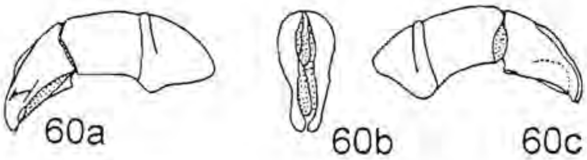
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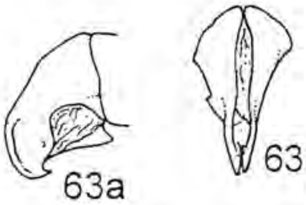
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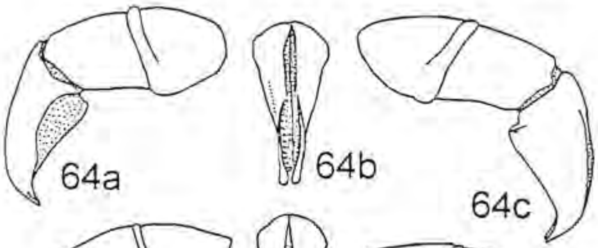
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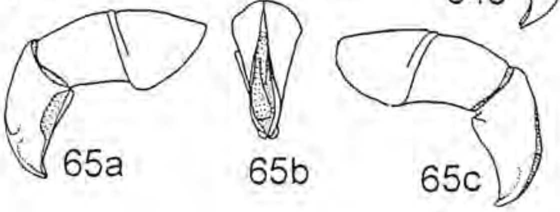
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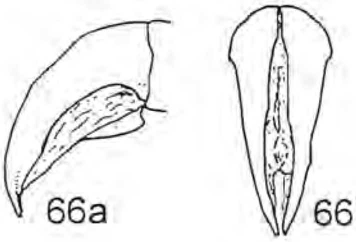
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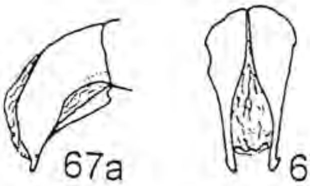
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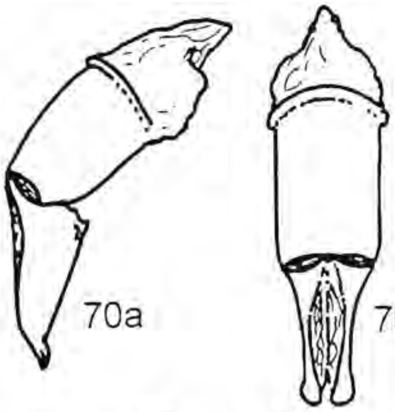
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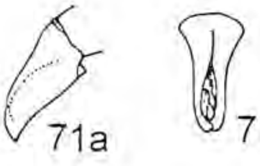
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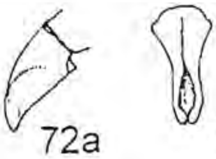
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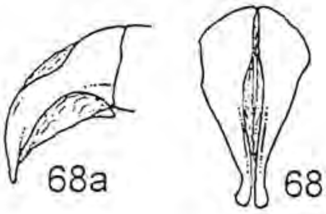
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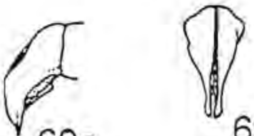
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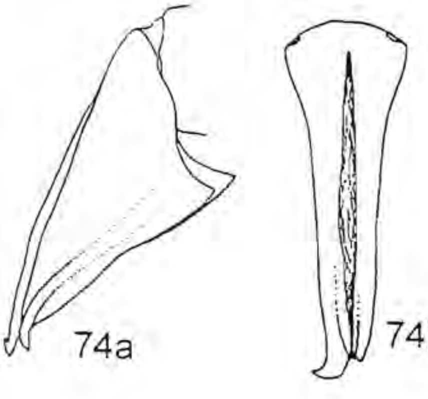

74a 74b


73a 73b

Key* modified from Holm and Scholtz (1979).

Scarabaeus (Pachysoma) aesculapius Olivier, 1789
(Figures 3, 18, 36, 57)

Scarabaeus aesculapius Olivier, 1789: 154; Olivier, 1790: 172; Hausmann 1807: 252; Mostert and Holm, 1982: 275. Lectotype designated here: No locality, (1♂ BMNH).

Pachysoma aesculapius (Olivier): MacLeay, 1821: 507; MacLeay, 1833: 55; Castelnau, 1840: 68; Reiche 1841: 212; Reiche, 1842: 89; Péringuey 1902: 77; Felsche 1907: 273; Gillet 1911a: 6; Ferreira 1953a: 15; Ferreira 1961: 22; Ferreira 1966: 57; Ferreira 1969: 20; Holm and Scholtz, 1979: 229.

Ateuchus barbatus Thunberg, 1818: 409; Gillet 1911a: 6; Ferreira 1953a: 15; Ferreira 1961: 22. [Holotype]: No locality: [1 UPSS].

Pachysoma validum Boheman, 1857: 180; Péringuey, 1902: 78; Felsche 1907: 273: Gillet: 1911a: 6; Ferreira 1961: 22. [Lectotype]: Caffraria, Walberg: [1 NHRS].

Diagnosis. Clypeus bidentate, genal and clypeal edges unserrated and continuous (figure 18); protibia not sexually dimorphic, with simple protibial spurs (figure 36); well-developed sub-elytral ridge, slight elytral indument present in northern populations; metatarsal claws shorter than last tarsal segment; size range in populations increases from small in south to larger in north.

Distribution, Habitat and Conservation. Historically distributed from Cape Town (33°56'S 18°28'E) to the mouth of the Olifants River (34°05'S 18°33'E), (figure 3). Locality records and fieldwork suggest that the Olifants River might be a barrier to the northward extension of *S. (P.) aescualpius* distribution. The southern populations (Somerset West; Cape Flats; Salt River; material only dated between 1882 and 1886) are possibly now extinct, as the most recent collection of *S. (P.) aesculapius* in the south is from the Modder River (33°28'S 18°20'E) in 1987. Currently, the coastal section of the Modder River Farm (or Modderrivier) is run as a private nature reserve (Davis pers. comm.).

S. (P.) aesculapius appear to prefer firm sand on coastal hummocks, river banks and vegetated dunes. The short tarsal claws, hardly spatulate mesospurs and shorter tibial brushes than *S. (P.) hippocrates* support this field observation.

The West Coast National Park (WCNP) is the closest conservation area for *S. (P.) aesculapius*. A single record of *S. (P.) aesculapius* in the WCNP labelled ([Hopefield crossed out] Saldanha) and dated 1960, is in the SAMC. Although this locality is possible, it remains unconfirmed by all subsequent collecting. I suspect the use of a generalized label (same label format is used for five *S. (P.) hippocrates*) referring to the Hopefield District rather than Saldanha Bay itself. Three days were spent by JDUGH during December 1996 in a variety of habitats in the WCNP looking specifically for *S. (P.) aesculapius*. No sign of this species was found, but adults and many fragments of *S. (P.) hippocrates* were collected. However as *S. (P.)*

aesculapius may be more cryptic in habits than *S. (P.) hippocrates*, one cannot exclude the possibility that *S. (P.) aesculapius* does occur in the WCNP, but currently it seems unlikely. As most of the historical distribution range of *S. (P.) aesculapius* is within modified or developing coastline, and since *S. (P.) aesculapius* might not be in the WCNP it must be regarded as the most threatened South African *S. (Pachysoma)* species.

Comments on locality data. All the specimens labelled Salt River have been ascribed to Salt River in Cape Town, and not to Salt River near Vredendal (as done by Holm and Scholtz 1979) for the following reasons. These specimens match in all aspects of morphology, (i.e. genitalia, pronotal microsculpture and body size) to the southern population (i.e. specimens labelled Cape Town). They were all collected during 1882 when Salt River in Cape Town was probably still a suitable locality for this species. No collectors have recorded *S. (P.) aesculapius* north of the Olifants River (which might be a barrier to the northern extension of the range of *S. (P.) aesculapius*). Salt River (Vredendal) is north of this suspected boundary.

The single female labelled Bontebok National Park (BNP) Swellendam, matches *S. (P.) aesculapius* in morphology from Leipoldtville. Additionally, this record is undoubtedly incorrect as the Cape fold mountains (Kruger 1983) act as a barrier to the eastward movement of *S. (Pachysoma)* species. According to Irish (pers. comm.) currently at the BMSA, the catalogue number (NMBH26926) for this specimen falls directly between long series of material from the BNP and other southern Cape localities from a single field trip. Thus retrospectively, there is no way of determining where the specimen actually came from. During February 1998 the BNP was visited by JDUGH and no habitat remotely suitable for *S. (P.) aesculapius* was found.

A single male collected by Koch and labelled Strandfontein (close to where *S. (P.) aesculapius* were collected by JDUGH for this study), conforms to all aspects of morphology to *S. (P.) aesculapius* from the southern population. Koch (1952) lists the areas visited during the expedition on which this specimen was collected. They travelled from Cape Town to Strandfontein. I suspect that this specimen comes from the southern population, as it does not conform with *S. (P.) aesculapius* specimens collected near Strandfontein. The *S. (P.) aesculapius* from Zambia, Monze (16°16'S 27°29'E) are clearly incorrectly labelled.

Morphological variation. The smallest specimens of *S. (P.) aesculapius* collected are all from the south (Cape Town, Cape Flats, Somerset West and Salt River). These populations share similar genitalia when viewed anteriorly, i.e. very narrow and straight parameres, and only 70% of the thorax is distinctly punctate. The type series of *Scarabaeus aesculapius* (length 21-24 mm; width 15-17 mm) is probably based on the southern population and distributed according to Boheman (1857) in all of Caffraria (i.e. 'Caffraria tota'). Moving northwards from the Modder River to Strandfontein the parameres in anterior view are stouter with a distinct widening before the two paramere points meet, with 90% of the pronotal disc deeply and irregularly punctate. Populations in the north (from Leipoldtville inland) are characterised by having slight elytral indument and consequently very distinct elytral interstriae with single setose granules, interspersed by a smooth ridge (there are five ridges per elytron). This population probably represents individuals described as *Pachysoma validum* (length 27mm; width 19mm) occurring in the 'Caffraria interiore' (Boheman 1857). Holm and Scholtz (1979) examined the holotype of *Ateuchus barbatus* Thunberg and matched it to a female of *S. (P.) aesculapius* from Dwarskersbos. Curiously however, the original description of *A.barbatus* records the clypeus as quadridentate (Thunberg 1818), while the clypeus of *S. (P.) aesculapius* is definitely bidentate.

Although specimens from the opposite ends of the *S. (P.) aesculapius* distribution share characteristics unique to them, the material examined suggests a cline in morphology rather than a clear division into two separate species or subspecies. For example, of the six *S. (P.) aesculapius* from Grootdrift the indument and elytral soil staining is marked in one male, but variable to absent in all other specimens.

Biology. All seven burrows of *S. (P.) aesculapius* excavated by JDUGH contained only dry dung pellets. *S. (P.) aesculapius* occurs sympatrically with *S. (P.) hippocrates* and *S. (P.) glentoni*, which both prefer detritus rather than dry dung pellets. This suggests that these species coexist by having different dietary preferences.

Péringuey (1900) mentions that *S. (P.) hippocrates*, *S. (P.) aesculapius*, *S. (P.) striatus*, and *S. (P.) denticollis* are diurnal. Holm and Scholtz (1979) questioned Péringuey's claim as they did not find any *S. (P.) aesculapius* active during the day other than by excavating their burrows. During December 1996 most *S. (P.) aesculapius* collected were from burrow excavation, but individuals were also seen to be active for a short period in the early morning (*ca.* 7:00-9:00 am), and late afternoon (*ca.* 16:00-18:00 pm). The larvae are unknown.

Comments. Similar to *S. (P.) hippocrates*, but smaller, *S. (P.) aesculapius* has a dull cuticle, and well-preserved specimens from the north of their range have slight indument that highlights their elytral intervals.

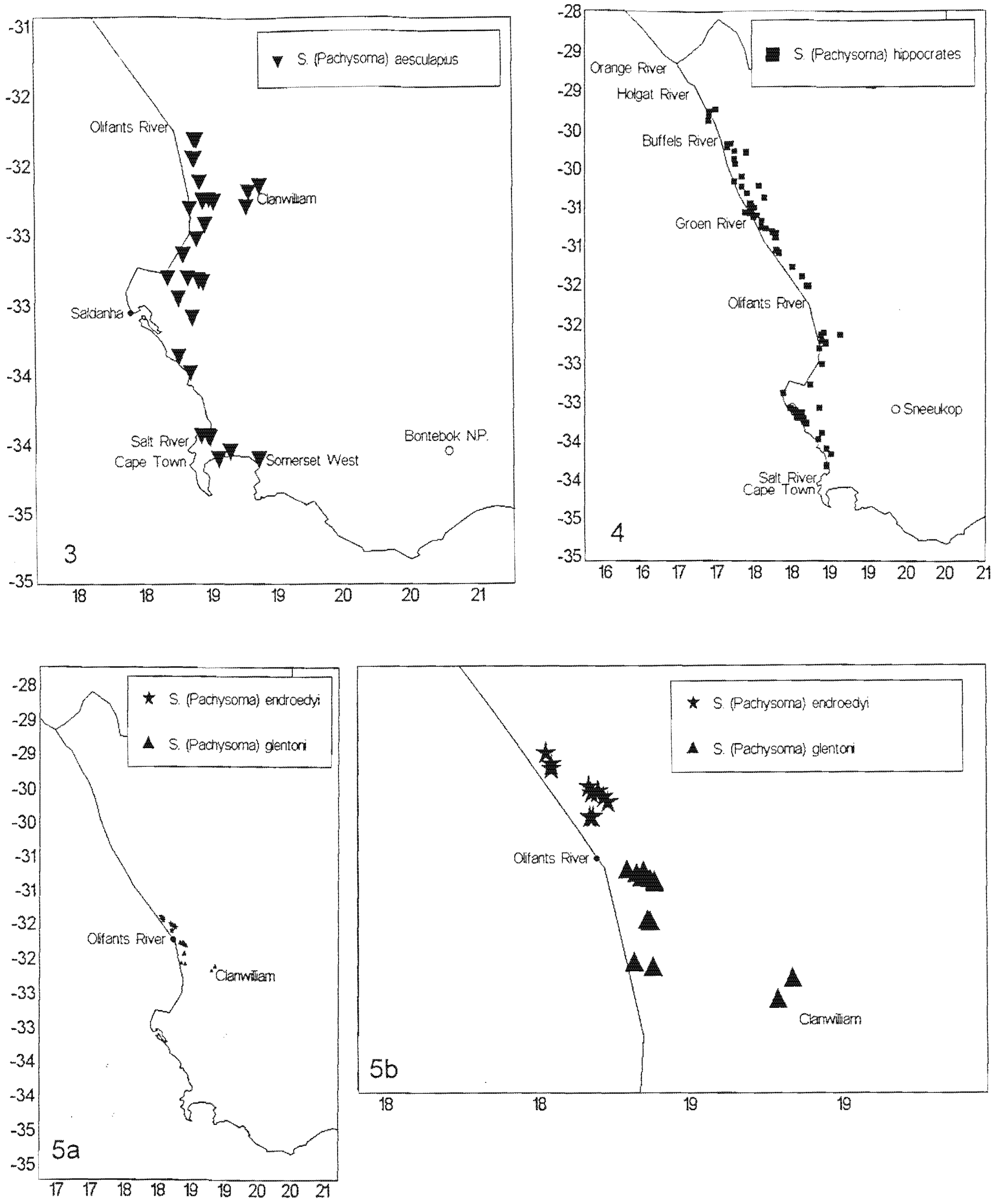
Types. Holm and Scholtz (1979) could not trace the type of *Scarabaeus aesculapius* Olivier, 1789. An old repined specimen of *S. (P.) aesculapius* labelled in the exact manner as MacLeay's holotype of *Pachysoma hippocrates*, was found in the BMNH collection (refer to type material below for label data). MacLeay described the genus *Pachysoma* in 1821 and included two species in the genus, i.e. *P. hippocrates* and *P. aesculapius*. The possibility exists that MacLeay had borrowed a specimen or specimens from Olivier, which MacLeay then labelled as his type or compared with *P. aesculapius* material in the BMNH, before labelling it as his type. As Olivier's types are considered lost, this specimen either came from the Olivier series or was at least compared to Oliviers' type of *S. aesculapius*. Thus it is designated as the lectotype of *Scarabaeus aesculapius* Olivier, 1789. This specimen agrees in microsculpture and genital structure, with *S. (P.) aesculapius* from near the Modder River (33°28'S 18°20'E).

Péringuey (1902) could find no differences between *P. aesculapius* from Somerset West and one of Boheman's 'co-type' of *P. validum*. Of the two paralectotypes of *S. (P.) validum* examined, both southern (1♂ BMNH) and northern (1♀ TMSA) populations of *S. (P.) aesculapius* may be represented (see morphological variation above). Which would explain why Péringuey (1902) found no differences.

From the Boheman series of *Pachysoma validum*, Holm and Scholtz (1979) designated a male lectotype (1♂ NHRS) and three paralectotypes (2x NHRS), (1♂ BMNH). An additional female paralectotype (see type material for label data) is however in the TMSA collection.

Type material examined (Σ3 spec. [5], 1♀ 2♂, 2♂ diss.). **SOUTH AFRICA**: LECTOTYPE ♂, *Scarabaeus aesculapius* Olivier, designated here: 1751 (typed) / M'Leay's Type / (refer to type discussion above, white paper disk, with a red border with type printed, M'Leay's written above type in the same hand writing as the holotype label of *Pachysoma hippocrates*) / *Pachysoma aesculapius* [M'Leay's type] Oliv. (written on white paper, same writing as before, brackets [ ] on original label), (1♂ BMNH); PARALECTOTYPES 2 of [3]: *Pachysoma validum* Boheman, designated by Holm and Scholtz (1979): Caffraria, J.Wahlb, Type, ♀ (four labels stuck onto one card [probably by Endrödy-Younga]) / Typus (typed in black on red card) / 378 77 (red paper, 378 printed, 77 written) / *validum* Bhm (written on white paper) / Paralectotypus, *Pachysoma validum* Boheman, Holm & Scholtz, (this paralectotype is not recorded by Holm and Scholtz (1979) as being in the TMSA collection), (1♀ TMSA); Caffraria. / J.Wahlb / C.Bon Spei / Fry Coll. 1905-100. / Paralectotype (typed on white circle with a light blue border) / *P.validum* paralectotype Holm & Scholtz 1978, (1♂ BMNH).

Additional material examined (Σ173 specs. [42], 61♀ 107♂, 28♂ diss., 5uns., 2eth., 7p.). **SOUTH AFRICA**: Western Cape; **Brackfontein Farm** 32.56S 18.15E, 23. viii.1983, E-Y:1968, sandy ground & grid, leg. Endrödy & Penrith, (1♀ TMSA); **C.(ape) Flats**, (34.02S 18.38E), xii.(18)85, (1♀ SAMC); **Cape, Cape Town**, (33.56S 18.28E), 1882, // Pres. Lightfoot // (1♀ SAMC); Cape T.(own), (33.56S 18.28E), xii. (18)85, (1♂ SANC); C.(ape) T.(own), (33.56S 18.28E), x.(18)86, (1♂ SANC); Cape Town, 65 km N, 33.21S 18.15E, 30.viii.1983, E-Y:1999B, ground traps 63 days, Endrödy, Penrith, groundtraps with meat bait (1♂ TMSA); **Clanwilliam**, (32.07.05S 18.52.05E), 29.ix.(19)27, A.Engelbrecht, NMBH3679, (1♂ BMSA); Cape Col., Clanwilliam, (32.07.05S 18.52.05E), (1♀ SAMC); Clanwilliam, near **Lambert's Bay**, Suurfontein C 527, 32°05'29S 18°24'41E, 17-19.xii.1996, J.duG.Harrison, site 206, dunes, white sand, dune periphery, (1♀ TMSA); Clanwilliam, near **Leipoldtville**, 32°14'S 18°31'E, 19.xii.1996, J.duG.Harrison, site 207, Langvleirivier bank, soft white sand, (1♀ 1♂ SANC), (1♀ 1♂eth. TMSA); Clanwilliam, 11.7km W, (*ca.*32.10S 18.47E), near **Ysterfontein**, 5.viii.1997, C.R.Owen, (2♀ COCS); E Doubleday, (not traced), Cape, Ent. Club. 44-12, (1x BMNH); 10km N, **Dwarskersbos**, (32.37S 18.17E), 20.xii.1977, E.Holm, (1♀ 3♂ TMSA), (3♂ SANC), *idem*, but Comp(ared) to type, Paralectotype, *Ateuchus barbatus* Thunberg, (HT: UPS), Holm & Scholtz 1978, (1♀ TMSA); **Grootdrif Farm**, 32.24S 18.27E, 29.viii.1981,E-Y:1860, day, sandy hill, Endrödy-Younga, (3♀ 3♂ TMSA); **Hopefield**, (33.04S 18.21E), Saldanha Bay crossed out, // ix. (19)60 //, (2♀ SAMC); **Jakkalsvlei**, (*ca.* 32.16S 18.46E at Jakkalsvlei), R364 to Jakkalsvlei, South 11.3km, 5.viii.1997, C.R.Owen, (1♀ 2♂ COCS); **Klein Klipheuwel**, 32.14S 18.26E, 26.viii.1981, E-Y:1851B, groundtraps 63 days, Endrödy-Younga, hand-collected around traps at setting, (1♀ TMSA); **Leipoldtville**, (32.13S 18.29E), **Eland's Bay**, (32.17S 18.20E), //



FIGURES 3-5. Distribution of *Scarabaeus (Pachysoma)* species in South Africa. Questioned locality records or range extensions are shown by an open circle. (3) *S. (P.) aesculapius*; (4) *S. (P.) hippocrates*; (5a) *S. (P.) endroedyi* and *S. (P.) glentoni* mapped at large scale to compare with *S. (P.) hippocrates*; (5b) *S. (P.) endroedyi* and *S. (P.) glentoni* mapped at small scale.

xi.1948, Mus. Exp. //, (1♀ 4♂ SAMC), *idem*, but NMBH3678, (1♂ BMSA); Leipoldtville, (32.13S 18.29E), x.1991, C.R.Owen, (1♂ COCS); **Modder River 721**, 33.28S 18.20E, 28-29.viii.1987, (1♀ 6♂ SANC), 7-8.ix.1987, (2♀ 6♂ BMNH), 17-18.ix.1987, (5♀ 4♂ UPSA), 20-21.x.1987, (3♀ 12♂ TMSA), 29-30.x.1987, (2♀ 2♂ BMSA), 10-11.xi.1987, (5♀ 8♂ SMWN), 21-22.xi.1987, (2♀ 7♂ SAMC), 28-29.xi.1987, (1♀ 4♂ UPSA), 12-14.xii.1987, (2♀ 2♂ ZMHB), (1♀ 1♂ UPSA), A.L.V. Davis, Ex. cattle dung baited pitfall, Fynbos thicket, sand; **Piketberg**, 52km NW, 32.48S 18.24S, 27.iv.1976, 60m, Davis & Aschenborn, (1♀ 1♂ SANC); Piketberg, (32.53S 18.45E), 30.x.1942, NMBH03680, (1♀ BMSA); Piketberg D., Bottel Fontein 11, near Brakkuil, 32°30'S 18°23'E, 19-20.xii.1996, J.duG.Harrison, site 208, vegt. sand rises, soft white sand, (1♀ 1♂ TMSA), (2p SANC); Piketberg D., **Rocherpan N.R., Bookram 30**, 32°37'S 18°17'E, 20-21.xii.1996, J.duG.Harrison, site 209, behind 1° dunes, white sand plain, (1♂ TMSA); **Salt River Flats**, (Cape Town, *ca.* 33.56S 18.59E), (and not 31.15S 17.52E), 3.x.(18)82, (1♀ SAMC); **Salt River**, (Cape Town, *ca.* 33.55S 18.28E), x.1882, (1♀ SANC), (1♀ 1♂ SAMC); Salt River, (Cape Town, *ca.* 33.55S 18.28E), xi.1882, (1♂ SAMC); **Strandfontein**, NAT. **Olifants R. Mouth**, (34.05S 18.33E), xi.1949, C.Koch, (1♂ TMSA); **Vredendal D.**, nr. **Strandfontein**, Byneslaagte 274, Onderputs, 31°47'29S 18°22'59E, 14.xii.1996, J.duG.Harrison, site 202, Grootsandleegte R., Y. firm sand plain, (1♀ 1♂ SANC); nr. Strandfontein, Byneslaagte 274, Onderputs, 31°47'01S 18°22'11E, 14-15.xii.1996, J.duG.Harrison, site 203, Grootsandleegte R., Y. firm sand plain, (2♀ 6♂ SAMC); **Fonteintjie** 466, near Witwater, 31°54'58S 18°21'37E, 15.xii.1996, J.duG.Harrison, site 204a, sand rise, yellow sand, (2♀ 4♂ TMSA), (5p SANC); **Somerset West**, (34.05S 18.51E), 27.iii.(18)83, (1♀ SANC); **Velddrift**, 32.47S 18.10E, 17.x.1971, Bornemissza & Kirk (1♂ SANC); Velddrif,14km E, 32.47S 18.19E, 10.x.1973, I.D. Temby, DRU1256, (1♀ SANC); Velddrift, 24km E, 32.49S 18.26S, 10.x.1973, I.D. Temby, DRU1255, (1♂ SANC); No locality data: (2 SANC), (2 SAMC); No locality data but Ex. Coll. Dr.H.Brauns, (small specimens probably from near Cape Town), (3♂ TMSA).

Specimens from the following localities may be incorrectly labelled because they are outside the species' established range: SOUTH AFRICA: Swellendam, **Bontebok National Park**, 34.04S 20.27E, 27-31.x.1987, Entomol. dept., NMBH26926, (1♀ BMSA); Hopefield (crossed out), **Saldanha Bay**, (33.01S 17.57E), // ix.(19)60 // (1♂ SAMC); ZAMBIA: **Monze**, (*ca.* 16.16S 27.29E), xii.1988, C.R. Owen, (2♂ DNSM), *idem*, but ii.1989, (1♀ 3♂ DNSM).

Scarabaeus (Pachysoma) hippocrates (MacLeay, 1821)

(Figures 4, 19, 37, 54, 58)

Pachysoma hippocrates MacLeay, 1821: 507; MacLeay, 1833: 55; Castelnau 1840: 68; Péringuey 1902: 77; Gillet 1911a: 6; Ferreira 1953a: 16; Ferreira 1961: 23; Ferreira 1966: 57; Ferreira 1969: 21; Holm and Scholtz, 1979; 230. Holotype: No locality (1♂ BMNH).

Pachysoma macleayi Castelnau, 1840: 68: Ferreira 1961: 23; Holm and Scholtz, 1979; 230.

Pachysoma hessei Ferreira, 1953a: 18; Ferreira 1961: 23; Ferreira, 1969: 21; Holm and Scholtz, 1979; 230. Holotype: Namaqualand, Wallekraal (1♂ SAMC).
Scarabaeus hippocrates (MacLeay): Mostert and Holm, 1982: 275.

Diagnosis. Clypeus bidentate, genae and clypeal edge unserrated and continuous (figure 19); protibial spurs bifurcate in both sexes, males have ventral inner edge of protibia elbowed and serrated (this characteristic varies clinally from very marked south of the Olifants River to absent in specimens from the north (i.e. Port Nolloth) (figures 37a,b); metatarsal claws longer than last tarsal segment; genitalia as in figures 58a,b,c.

Distribution, Habitat and Conservation. Coastal southwestern South Africa, recorded from Cape Town, Bloubergstrand (33°48'S 18°27'E) to Port Nolloth (29°15'S 16°53'E) in Namaqualand (figure 4). Their habitat preference includes vegetated soft to firm sand of coastal hummocks and hillocks, the periphery of dune systems, and river beds and banks. *S. (P.) hippocrates* occur within the West Coast National Park and the proposed Groen-Spoeg National Park. Habitat modification threatens certain populations of *S. (P.) hippocrates*, viz. those of Bloubergstrand and Port Nolloth.

Comments on locality data. The Sneeukop (33°07'S 19°37'E), (5000ft) locality near Wellington, is probably due to an incorrectly labelled specimen. This specimen was collected by Dr K.H. Barnard, who worked at the SAMC from 1911-1964. Dr Barnard was a keen mountaineer, who collected and described 10 species of the high altitude specialist *Colophon* Gray (Lucanidae). Endrödy-Younga (1988), revised *Colophon* and the only locality label resembling the above is for *Colophon stokoei* from 'Upper Snoukop, Wellington, 4500-5000ft., January, K.H.Barnard & R.Primos'. Additionally, Endrödy-Younga (1988) records that '...the data published by Barnard are not consistent with those of the labels...' suggesting that Barnard was not a stickler for detail. No other *S. (Pachysoma)* specimens were collected by Dr Barnard. This single male agrees with *S. (P.) hippocrates* from Bloubergstrand near Cape Town. Sneeukop is well outside the established coastal distribution range of all *S. (Pachysoma)* species, and no *S. (Pachysoma)* have been reliably collected from high altitudes (1525 m). The Bain's Kloof pass to Wellington was visited by JDUGH and the only remotely suitable habitat for *S. (Pachysoma)* is along the sandy river beds of the Wit and Bobbejaan rivers.

Morphological variation. The *hippocrates* species complex contains three species, viz. *S. (P.) hippocrates, S. (P.) glentoni* and *S. (P.) endroedyi*. It was suspected that the distribution of *S. (P.) hippocrates* extends from Cape Town to the Olifants River while *S. (P.) hessei* occurs north of the Olifants River to Port Nolloth. This suspicion was tested, but no distinct change was found in the aedeagal morphology across this potential barrier (Olifants River). Individual aedeagi from disjunct populations, e.g. Port Nolloth (29°15'S 16°53'E) and Modder River (33°28'S 18°20'E) differ significantly, but when all populations were examined there is only evidence of a gradual clinal change. Furthermore, the populations comprising the cline exhibit very slight unique genitalic and other morphological features. This suggests that *S. (P.) hippocrates* is currently undergoing speciation. Furthermore, within a population the male genitalia can show distinct differences. For example in the Port Nolloth and Sand Kop (29°42'S 17°06'E) populations the development of a spine on the left paramere is variable.

Examination of the external morphology revealed the same trend, but evidently *S. (P.) hippocrates sensu lato* includes a main-cline composed of four subclines (listed below) within it. The main cline (for the entire geographic range of *S. (P.) hippocrates*) varies in the following features: (1) aedeagal morphology; (2) variation in size, large in the south to smallest in the north; (3) variation in the expression of the dimorphic elbowed protibia, very slight in the north to very marked in the south. Further detailed examination of all specimens revealed four subclines within *S. (P.) hippocrates*, i.e. excluding the sister species [*S. (P.) aesculapius, S. (P.) endroedyi* and *S. (P.) glentoni*]. These populations may be isolated by river courses (i.e. natural barriers) and include: (1) a Cape Town to Lambert's Bay population, distinguished by large size and dimorphic protibia; (2) an Olifants to Groen River population, recognizable by a reduction in the dimorphism of the protibia, and the presence of waxy indument on the periphery of the elytra; (3) a Groen to Buffels River population, characterised by an even smaller difference in the protibia between sexes, and no waxy indument; (4) a Buffels River to Port Nolloth (possibly extending to the Holgat River, but as yet unconfirmed), characterised by small size, practically no dimorphism of the protibia, but very orange setal colour in mature sclerotized specimens (teneral specimens of other populations may have this colour). Thus, no consistent and easily recognizable suite of characters could be found to justify the existence of *S. (P.) hessei* at subspecific or specific level. To divide *S. (P.) hippocrates* into four subspecies would make identification very difficult for a nonspecialist. I therefore choose to regard *S. (P.) hippocrates* as a species with distinct south to north clinal variation, and consequently the synonymy of *S. (P.) hessei* with *S. (P.) hippocrates* is maintained.

Biology. S. (P.) hippocrates occur sympatrically with *S. (P.) aesculapius* south of the Olifants River, and with *S. (P.) striatus* north of the Olifants River. Of 36 nests excavated by JDUGH, five contained only pellets, six contained both detritus and pellets while 25 contained only detritus. This suggests that *S. (P.) hippocrates* prefers detritus. Two separate attempts were made to breed *S. (P.) hippocrates* in the lab. Three pairs between (1.ix.1996-23.i.1997) and six pairs between (9.ix.1998-4.xii.1998) of *S. (P.) hippocrates* were placed in round 25l buckets and 5l square bread bins respectively. Sand, detritus and dry pellets from their collection site were used. They dug burrows, foraged regularly, but did not breed.

Comments. S. (P.) hippocrates is very similar to *S. (P.) glentoni* (see diagnosis of these species for the differences) but is easily and reliably differentiated by the male genitalia and geographic distribution.

Types. The holotype of *Pachysoma hippocrates* has no locality label, but the type locality is recorded by MacLeay (1821) as Cap. Bonae Spei. It is a large (length 35.20 mm; width 22.34 mm) specimen with very worn protibia, and its genitalia were first dissected by JDUGH for this study. Holm and Scholtz (1979) suspected it came from the southern extreme of the species' distribution. The size and male genitalia confirm their suspicion, however, it does not match any labelled material from the southern populations, except a single male labelled C. Bon Spei that conforms to it in size, microsculpture and identical male genitalia.

Ferreira (1953a), lists the holotype, allotype and twelve paratypes of *Pachysoma hessei* in the SAMC collection, and one paratype in the CPMM collection. Holm and Scholtz (1979) were only able to trace the holotype, allotype and two paratypes in the SAMC collection. The remaining ten paratypes from the SAMC were discovered during reorganisation (1993 onwards) of the collection (see Cochrane 1995).

Type material examined (Σ14 spec. [5], 3♀ 11♂, 9♂ diss.). **SOUTH AFRICA**: HOLOTYPE ♂, *Pachysoma hippocrates* MacLeay: [1] *Hippocrates* (written onto faded white traingle) / 58.60. (written onto blue disk) / Type (printed on white disk, surrounded by a red circle) / *Pachysoma hippocrates* (Kirby MS), Type McLeay. (written onto now faded white paper) / *Pachysoma hippocrates* M'Lea, Holotype (written onto white rectangular card, surrounded by a red line, UPSA label) / *Pachysoma hippocrates* Holotype dissected J.duG. Harrison 1998 / (1♂ BMNH). HOLOTYPE ♂, *Pachysoma hessei* Ferreira: Wallekraal, Namaqualand, (30.22.05S 17.37.05E) // Mus., Expd., Oct.1950. // (printed locality label) / Holotypus, ♂, *Pachysoma Hessei*, 1951, Maria C. Ferreira / *Pachysoma hessei* Ferreira (= *hippocrates* M'Leay), det. Holm & Scholtz 1978, (written onto UPSA holotype label) /, (1♂ SAMC), *idem*, but / Allotypus, ♀, *Pachysoma Hessei*, 1951, Maria C. Ferreira /, *Pachysoma hessei* Ferreira (=*hippocrates* M'Leay), det. Holm & Scholtz 1978, (written onto UPSA paratype label) /, (1♀ SAMC), PARATYPES: *idem*, but Type, SAM/Ent. 2678, (printed onto green card), (8♂ SAMC), (1♂ TMSA), {1 CPMM}; Wallekraal, Namaqualand, (30.22.05S 17.37.05E), S.A.M., Oct.1950 (written) / Type, SAM/Ent. 2678 /, (1♀ SAMC), (1♀ TMSA).

Additional material examined (Σ308 specs. [45], 92♀ 185♂, 77♂ diss., 5uns., 26eth., 81p.). **SOUTH AFRICA**: Western Cape; **Abrahamskraal farm**, 33.14S 18.09E, 25.viii.1983, E-Y:1976B, groundtraps with faeces bait 70 days, Endrödy, Penrith, (4♂ TMSA); **Atlantis** Area, (*ca.* 33.35S 18.27E), 30.xii.1985, Owen, (1♀ TMSA); near Atlantis, (*ca.* 33.35S 18.27E), 8.x.1986, C.R.Owen, BM 1987-57, (2♀ 1♂ BMNH); **Bloubergstrand**, (33.48S 18.27E), 25.xi.1964, A.L.Capener, (1♂ SANC); Piketberg D., **Bottel Fontein 11**, near Brakkuil, 32°30'S 18°23'E, 19-20.xii.1996, J.duG.Harrison, site 208, vegt. sand rises, soft white sand, (1♀ abdomen with 4 legs TMSA); Hopefield D., Langebaan, West Coast National Park, **Bottelary 353**, 33°07'05S 18°05'12E, 21.xii.1996, J.duG.Harrison, site 210, vegt. yellow sand, (1♀ BMNH); Bottelary 353, 33°09'10S 18°07'22E, 21.xii.1996, J.duG.Harrison, site 212, vegt. white sand, (5♂ BMNH), (2p SANC); Bottelary 353, 33°07'06S 18°05'23E, 21.xii.1996, J.duG.Harrison, site 213, vegt. white sand, (1♂ BMNH); Bottelary 353, 33°09'24S 18°05'51E, 22.xii.1996, J.duG.Harrison, site 214, vegt. dune, white sand, (1♀ BMNH); Bottelary 353, 33°08'04S 18°04'50E, 22.xii.1996, J.duG.Harrison, site 215,vegetated dune, white sand/humus, (1♀ BMNH), (5p SANC); **C. Bon Spei** (Cape of Good Hope), (written onto white paper) / Fry Coll., 1905-100. (printed onto white paper) / (point mounted male genitalia dissected here) /

Pachysoma AEsculapius. Oliv., P.B.Spei., (written onto white paper), (1 ♂ TMSA); **Darling**, C.C. (33.23S 18.23E), x.(19)05, L. Péringuey, (1♂ SANC), (2♀ 1♂ SAMC); Darling, C.C. (33.23S 18.23E), 1905, L. Péringuey, (1♂ SANC), (2♂ SAMC), (1♂ TMSA); Darling, C.C. (33.23S 18.23E), (19)05, J.M.Baiu ?, (2♂ UPSA), (1♀ 5♂ SANC), (4♀ 6♂ SAMC), (2♂ MGMK), (2♀ 2♂ TMSA); Darling, (33.23S 18.22E), (19)06, H.M.Dudley, (spelling ?), (1♂ DNSM), (2♀ 1♂ SAMC); **Donkergat**, (Postberg Nature Reserve 33.05S 18.00E), (or near Atlantis 33.39S 18.30E), 1.v.1983, M.Stiller, (1♀ USSA); **Elandsbay Forestry**, 32.18S 18.21E, 28.viii.1981, E-Y:1853B, groundtraps with meat bait 60 days, Endrödy-Younga, (1♀ 1♂ TMSA); Hopefield D., West Coast National Park, **Geelbek 360**, 33.10S 18.08E, 7-8.xi.1996, T.J.Robinson, (2♀ 10♂ UPSA); Hopefield D., West Coast National Park, Geelbek, 33.10S 18.08E, 17-18.ix.1987, (1♀ 2♂ BMSA), 28-29.ix.1987, (2♀ 5♂ SANC), 13-14.x.1987, (1♀ 2♂ ZMHB), 20-21.x.1987, (1♀ 1♂ MNHN), A.L.V.Davis / Ex. cattle dung baited pitfall, Fynbos thicket mosiac, Sand; Geelbek Forestry, 33.12S 18.08E, 25.viii.1983, E-Y:1975B, groundtraps with banana bait 70 days, Endrödy, Penrith, (1♀ TMSA); Langebaan, 12km Farm Geelbek, (*ca.* 33.16S 18.10E), 11-13.x.1978, sand shrubland, A.L.V. Davis (1♀ SANC); Langebaan, 12km SE Farm Geelbek, (*ca.* 33.16S 18.10E), 30.vii.1979, A.L.V. Davis, DRU2660, (1♂ SANC); Geelbek 360, 33°13'07S 18°08'52E, 21.xii.1996, J.duG.Harrison, site 211, vegt. dunes, white sand, (2♂ SMWN);Geelbek 360, 33°11'35S 18°08'49E, 23.xii.1996, J.duG.Harrison, site 218, active dunes, white sand, (1p SANC); **Hopefield**, (Saldanha Bay crossed out), 33.04S 18.21E // ix.1960 // (1♂ UPSA), (2♀ 2♂ SAMC); *idem*, but / compared to type *P. hippocrates* MacLeay, Holm & Scholtz, no locality, worn protibia, (1♀ TMSA); **Klein Klipheuwel**, 32.14S 18.26E, 26.viii.1981, E-Y:1851B, hand-collected around traps at setting, Endrödy-Younga, (1♀ TMSA); Clanwilliam, nr. Lambert's Bay, **Kookfontein 88**, 32°03'54S 18°22'39E, 16.xii.1996, J.duG.Harrison, site 205, vegt. dune, firm yellow sand, (1♂ TMSA); **Lambert's Bay**, 9km N, (*ca.* 32.07.05S 18.22.05E), 28.ix.1974, Houston, Davis, Tribe, (1♂ SANC); Lambert's Bay, 6km E, 32.06S 18.24E, 1.ix.1979, E-Y:1628, white dunes day, Endrödy-Younga, (1♂ TMSA); **Langebaan**, Cape, (33.06S 18.02E), 1.x.1977, N.J.Duke, (2♂ TMSA); Leipoldtville, 12km W, (*ca.* 32.12S 18.23E), 27.iv.1976, Davis & Aschenborn, DRU2283, (2♀ SANC); **Modder River 721**, 33.28S 18.20E, 13-14.x.1987, (1♂ TMSA), 20-21.x.1987, (1♀ 1♂ TMSA), 10-11.xi.1987, (1♂ SAMC), 28-29.xi.1987, (2♂ UPSA), A.L.V. Davis / Ex. cattle dung baited pitfall, Fynbos thicket, sand; **Saldanha Bay**, C.C., (33.07S 17.52E), 1913, (2♀ SAMC); Saldanha, (33.03S 17.58E), x.(18)92, (1♂ SAMC); **Stofbergsfontyn 365**, 33°10'16S 18°03'02E, 22.xii.1996, J.duG.Harrison, site 216, behind 1° dunes, white sand, (1♂ BMNH) (4♂ 1p SANC); Stofbergsfontyn 365, 33°11'25S 18°04'12E, 22.xii.1996, J.duG.Harrison, site 217, behind 1° dunes, white sand, (1♀ 2♂ 10p SANC); **Velddrif**, 3km E, 32.46S 18.14E, 31.viii.1981, E-Y:1870, groundtraps with faeces bait, Endrödy-Younga, (1♂ TMSA); **Vredenburg**, (32.52.05S 17.52.05E), 10.vii.1944, (NMBH 3681), (1♂ BMSA); **Ysterfontein** (Clanwilliam), (32.07.05S 18.37.05E), (Saldanha Bay crossed out) // ix.1960 // (2♀ SAMC); **Yzerfontein**, 8km N, 33.15S 18.11E, 25.viii.1983, E-Y:1978B, ground traps with meat bait 70 days, Endrödy, Penrith, (4♂ TMSA); No locality data, (4x BMNH). Synonym of *Scarabaeus (Pachysoma) hippocrates*, i.e. *Pachysoma hessei* Ferreira, 1953a.

SOUTH AFRICA: Northern Cape; Namaqualand; Dembergdraai F., (Groen Rivers Valley 504), 30.47S 17.43E, 24.viii.1979, sand blown hill, E-Y:1590, leg Endrödy-Younga, (3♂ TMSA); Dembergdraai F., (Groen Rivers Valley 504), 30.47S 17.43E, 24.viii.1979, groundtraps, 63 days with meat bait, E-Y:1589B, leg Endrödy-Younga, (2♂ TMSA); Dembergdraai F., 30.47S 17.43E, 18.ix.1994, E-Y:3014B, Endrödy-Younga & Bellamy, groundtraps with banana bait for 7 days, (1♀ 1♂ TMSA); Dembergdraai F., 30.48S 17.43E, 19.ix.1994, E-Y:3021, Endrödy-Younga & Bellamy, on red sandy ground, (1♂ TMSA); **Gemsbok Vlakte Farm** (498), 30.30S 17.29E, 30.viii,1977, hand-collected, dunes, day, E-Y:1361 Endrödy-Younga, (2♂ TMSA); **Graskom,** 30.18S 17.23E, 15-18.ix.1982, S.Louw, NM8642, (1♂ BMSA); same data but, M.-L. Penrith / H54563, (1♀ 1♂ SMWN); **Karroevlei**, Van Rhynsdorp, (Karoovlei, Klein Kogel Fontein 148), 31.06S 17.51E, 13.x.1948, (1♀ SAMC); **Hondeklipbay**, 16km E, (*ca.* 30.21S 17.26E), ix.1991, C.R.Owen, (1♀ 1♂ COCS); **Kommandokraal Farm** (624), 31.30S 18.12E, 30.viii.1979, hand-collected on sand, E-Y:1622, Endrödy-Younga, (1♂ TMSA); Kommandokraal Farm W (624), 31.29S 18.11E, 23.ix.1994, E-Y:3035, E-Y: Endrödy-Younga & Bellamy, on ground, (1♀ TMSA); Kommandokraal Farm (624), 31.30S 18.12E, 22.ix.1994, E-Y:3033, Endrödy-Younga & Bellamy, on sandy ground, (4♀ 5♂ TMSA); **McDougall's Bay**, 4km S of Port Nolloth, 29.17S 16.53E, 29.xi.1994, Scholtz, Chown, Klok (2♂ UPSA), (3♂ TMSA); **Port Nolloth**, 29.15S 16.53E, xi.1994, Scholtz, Chown, Klok (13p SANC); Port Nolloth, 29.22.05S 16.52.05E, 1911, C.L.Biden, (1♂ SAMC); **Quaggafontein** (478), 30.13S 17.33E, 29.viii.1977, E-Y:1353, hand-collected, day, Endrödy-Younga, (2♀ TMSA); Quaggafontein (478), 30.13S 17.33E, 29.viii.1977, E-Y:1356B, groundtraps, 60 days, with meat bait, Endrödy-Younga, (1♂ TMSA); **Rooidam Farm,** (Wit Water 557), 31.04S 17.48E, 26.ix.1994, E-Y:3046, white vegetated dunes, Endrödy & Bellamy, (3♂ TMSA); Rooidam Farm, (Wit Water 557), 31.02S 17.46E, 20.ix.1994, E-Y:3026, ground and light, Endrödy-Younga, (1♂ TMSA); **Strandfontein Farm,** (Strand Fontein 499), 30.33S 17.22E, 3.ix.1977, E-Y:1374, hand-collected, dunes, day, Endrödy-Younga, (1♀ TMSA); **Soutpan**, 10km E., (near Salt River mouth), 31.15S 17.59E, 13.ix.1987, E-Y:2493, in cattle grid, Endrödy-Younga, (1♀ 1♂ TMSA); No locality data, Dr. Smith, S.Afr. 44-6 (1 BMNH).

SOUTH AFRICA: Northern Cape; Namaqualand; De Dam 541, 30°52'06S 17°45'24E, 4.xii.1996, J.duG.Harrison, site 173, dead in mud, firm yellow sand, (1p SANC); **De Klipheuvel 435**, near Soutfontein, 30°39'40S 17°34'55E, 1.xii.1996, J.duG.Harrison, site 163, sand plain fynbos, yellow sand near vegetated dunes, (1♂ TMSA); **De Witflacte 551**, near Hardevlei, 30°52'50S 17°45'50E, 4.xii.1996, J.duG.Harrison, site 174, vegetated dune, firm/soft yellow sand, (1p SANC); **Driekop 500**, 30°36'34S 17°27'41E, 30.viii.1996, J.duG. Harrison, site 78, vegetated old dune, yellow sand, (2p SANC); Driekop 500, 30°35'09S 17°31'06E, 30.viii.1996, J.duG.Harrison, site 80, Bitter River bank, yellow sand, (1♂ 2p SANC); **Graafwater, Farm 156**, 31°22'38S 18°01'23E, 6.xii.1996, J.duG.Harrison, site 186, firm Y. sand plain, nr. vegt. dunes (1♀ 3♂ 1p SANC); **Groen River, Roode Heuvel 502**, 30°45'24S 17°38'24E, 4.xii.1996, J.duG.Harrison, site 168, Groen River bank, red sand, (1♂ SAMC); **Kanoep 491**, nr. Swartfontein, 30°26'41S 17°25'41E, 22.xi.1996, J.duG.Harrison, site 150, Spoeg R. bed, white sand banks, (5♂ SANC), (2♂ TMSA); Kanoep 491, near Swartfontein, 30°28'22S 17°26'37E, 23-24.xi.1996, J.duG.Harrison, site 151, Bitter R. Dunes, dune periphery, white sand, (1p SANC); Kanoep 491, near Swartfontein, 30°28'14S 17°26'23E, 23-24.xi.1996 J.duG.Harrison, site 151a, Bitter R. Dunes, interdune slack, white/red sand, (1♀ 2♂ SMWN); **Klein Duin 154**, 29°13'01S 16°57'45E, 29.vii.1996, J.duG.Harrison, site 23, vegetated rise bf. white dunes, dead, (2p SANC); Klein Duin 154, 29°13'17S 16°57'49E, 29.vii.1996, J.duG.Harrison, site 24, white sand dunes, (2p SANC); Klein Duin 154, 29°13'04S 16°57'54E, 29.vii.1996, J.duG.Harrison, site 26, white sand dunes, vegetated slack, (4p SANC); **Kleinsee, Sand Kop 322**, 29°40'07S 17°07'22E, 1.viii.1996, J.duG.Harrison, site 30, vegetated dune, yellow sand, (4♀ 1♂ BMNH) (3p SANC); Kleinsee, Sand Kop 322, 29°42'40S 17°06'51E, 3-6.viii.1996, (4♀ 7♂ UPSA) (2p SANC), 22.viii.1996, (1♀ 4♂ SAMC) (14eth. TMSA) (8p SANC), J.duG.Harrison, site 31, vegetated dune, yellow sand; **Kleinsee, Honde Vlei 325**, 29°45'25S 17°13'11E, 7.viii.1996, J.duG.Harrison, site 32, vegetated dune, yellow sand, (1♂ TMSA); Kleinsee, Sand Kop 322, 29°39'55S 17°10'34E, 28-30.x.1996, Harrison & Scholtz, site 113, vegetated dune, red sand, (12♀ 18♂ UPSA) (17p SANC); Kleinsee, Sand Kop 322, 29°40'16S 17°08'05E, 28.x.1996, Harrison & Scholtz, site 114, firm yellow sand plain, (1p SANC); near **Koingnaas**, 30°02'41S 17°12'44E, 12.viii.1996, Harrison & Scholtz, site 41, DeBeers Game Farm, vegetated dune, white sand, (1p SANC); Koingnaas 475, 30°13'37S 17°19'00E, 3.ix.1996, J.duG.Harrison, site 82, Swartlintjiesrivier bank, yellow sand, (1♂ UPSA); Koingnaas 475, 30°13'20S 17°18'46E, 22.xi.1996, J.duG.Harrison, site 141, Swartlintjies R. bank, yellow sand, (9eth. TMSA); **Kourootje 316**, 29°45'07S 17°20'39E, 9.viii.1996, Harrison & Scholtz, site 37, yellow sand, vegetated dune near, (1p SANC); Kourootje 316, near Komaggas, 29°46'44S 17°22'22E, 10.xi.1996, J.duG.Harrison, site 121, sand plain fynbos, vegt. dune y/r sand, (1♂ 2eth. TMSA); **Kwaas 501**, 30°43'39S 17°31'23E, 14.viii.1996, Harrison & Scholtz, site 47, Vegt. dune, yellow soft sand, (2♀ SMWN); Kwaas 501, 30°42'38S 17°34'36E, 1.xii.1996, J.duG.Harrison, site 164, sand plain fynbos, yellow sand, (1♀ SAMC); **Roode Heuvel 502**, 30°44'23S 17°34'27E, 21.vii.1996, J.duG.Harrison, site 10, sand plain fynbos, red sand, (1♂ 1p SANC); **Rondabel 542**, 30°49'01S 17°46'07E, 4.xii.1996, J.duG.Harrison, site 170b, vegetated dune, soft yellow sand, (2♀ 1♂ 1p SANC); **Samsons Bak 330**, near Kleinsee, 29°55'22S 17°13'34E, 20.xi.1996, J.duG.Harrison, site 130, firm yellow sand, near vegt. dune, (1p SANC); Sand Kop 322, 29°39'55S 17°10'34E, 19.viii.1996, J.duG.Harrison, site 62&113, vegetated dune, red sand, (1♂ BMSA); **Somnaasbaai, Somnaas 474**, 30°09'S 17°13'E, 20.x.1996, J.duG.Harrison, site 101, white sand nr. active white dunes, (1p SANC); **Soutfontein** 'Dorp', De Klipheuvel 435, 30°36'S 17°35'E, 3.ix.1996, J.duG.Harrison, site 84, Bitter River Bed, (1eth. TMSA); **Strand Fontein 499**, 30°33'S 17°25'E, 20.vii.1996, J.duG.Harrison, site 6, Bitter River Dunes, interdune slack, (1p SANC); Strand Fontein 499, 30°33'45S, 17°26'25E, 13.viii.1996, Harrison & Scholtz, site 43&44, Bitter River Dunes, white sand, (1p SANC); Strand Fontein 499, Bitter R. Dunes, 30°32'28S 17°26'18E, 29.viii.1996, J.duG.Harrison, site 75, interdune slack, white/red sand, (1p SANC); Strand Fontein 499, Bitter River Dunes, 30°32'42S 17°25'45E, 14.ix.1996, J.duG.Harrison, site 91, dune periphery, soft white sand, 2m high shrubs, (1♀ SANC); Strand

Fontein 499, Bitter River Dunes, 19.x.1996, Cameron Mocke, site 102, (1x SANC); Strand Fontein 499, 30°33'32S 17°25'34E, 24-25.xi.1996, J.duG.Harrison, site 152, Bitter River, foredunes nr. sea, soft white sand, (4♀ 3♂ ZMHB); Strand Fontein 499, 30°34'00S 17°26'51E, 24.xi.1996, J.duG.Harrison, site 153, Bitter R. Dunes, vegt. white sand, (1♂ UPSA); Strand Fontein 499, Bitter R. Dunes S., 30°33'57S 17°26'37E, 26-27.xi.1996, J.duG.Harrison, site 155, dune periphery, soft white sand, (1♂ UPSA); Strand Fontein 499, Bitter River Dunes, 30°32'28S 17°26'18E, 4.ix.1996, J.duG.Harrison, (1♀ UPSA); **Wit Water 557**, near Kotzesrus, 31°01'18S 17°46'33E, 5.xii.1996, J.duG.Harrison, site 177, Brak River, yellow sand bank, (1♀ 1p SANC); Wit Water 557, near Rooidam, 31°02'29S 17°46'46E, 5.xii.1996, J.duG.Harrison, site 179, vegetated dune, yellow sand, (1♂ 4p SANC); **Zonnekwa 328**, near Kleinsee, 29°50'56S 17°13'23E, 20.xi.1996, J.duG.Harrison, site 127, vegetated dune, yellow sand, (1♀ TMSA); **Zoutpan 471**, near Koingnaas, 30°05'51S 17°19'05E, 21.xi.1996, J.duG.Harrison, site 137, sand plain fynbos, yellow sand near vegt. dunes, (1p SANC); S.Afr: Vredendal D., **Graafwater**, Farm 156, 31°22'38S 18°01'23E, 6.xii.1996, J.duG.Harrison, site 186, firm Y. sand plain, nr. vegt. dunes, (1♀ 3♂ UPSA); Vredendal D., **Kommandokraal**, on Farm 624, near Koekenaap, 31°29'58S 18°11'47E, 8-9.xii.1996, J.duG.Harrison, site 191, vegetated dune, yellow sand, (1♂ TMSA); Vredendal D., Kommandokraal, on Farm 624, near Koekenaap, 31°29'02S 18°10'08E, 10.xii.1996, J.duG.Harrison, site 193, vegetated dune, yellow sand, (1p SANC); Kommandokraal, 31.31S 18.13E, 100m, 23.ix.1985, AVEvans, CLBellamy, (1♂ UPSA); Vredendal D., **Skilpadvlei**, Farm 620 near Koekenaap, 31°34'05S 18°12'06E, 11.xii.1996, J.duG.Harrison, site 194, vegetated dune, yellow sand, (1♀ 1♂ UPSA) (2p SANC).

A single specimen from the following locality may be incorrectly labelled because it occurs outside the species' established range: **SOUTH AFRICA**; **Sneeukop**, Wellington, (*ca.* 33°07'05S 19°37'05E), 5000ft, // xi.1922, K.H.Barnard //, (1♂ SAMC).

Scarabaeus (Pachysoma) glentoni Harrison, Scholtz and Chown **sp. n.**

(Figures 5, 20, 38, 55, 59)

Description.

Size (mm). Body length, mean ♂29.70; ♀29.12; range ♂26.72-36.28; ♀25.54-31.98. Pronotal width, mean ♂19.16; ♀17.71; range ♂16.38-22.96; ♀15.78-18.58 (n = 12♂ 12♀). Colour. Cuticle black, setae rufous, antennal clubs golden.

Head (Dorsal) (figure 20). Clypeus bidentate, teeth rounded and separated by V-shaped incision; clypeal and genal margins unserrated, almost continuous, separated at clypeal-genal suture by small incision; whole head finely granular, becoming punctate around periphery; large setiferous granules adjacent eye and genae; posterior edge of genae rounded. *(Ventral).* Rim of setae on clypeus and genae edge; clypeal teeth raised into two ridges separated by hollow depression, posterior raised rim with single pointed tooth; line of setae on either side of clypeal ridges; mandibles robust, mentum bilobed, each lobe with stiff setae pointing forwards; antennae lamellate, 9-segmented, club composed of last 3 segments.

Pronotum. Head amplected into prothorax; anterior lateral edge, irregularly notched, posterior lateral edge, serrate from setal fringe; setal fringe, long on outside edge tapering to short medially; disc globose; midline area unsculptured, centrally widened to form unsculptured diamond-shape; adjacent disc deeply punctate, anterior edges granular; distinct patch of fine granules on posterior lateral edge; posterior edge curved inwards.

Legs; Protibia (Dorsal) (figure 38b). Quadridentate, teeth pointed, curved downwards, apical surface smooth, basal half transversely furrowed; serrations between teeth; proximal half of protibia with smooth undulations, basal half smooth and continuous; medial setiferous carina; setal border on inner and proximal outer edges, long; setae between teeth, short; inner edge markedly deflected medially; spurs short, stout, bifid and curved downwards. *(Ventral)* (figure 38a). Apical surface of teeth smooth; outer surface scattered with shallow broad punctures, inner edge with fine granules; medial inner lateral edge deflected downwards and bordered with row of irregular but distinct setiferous knobs; medially at base of protibia are 2 rows, outer composed of small setiferous knobs (about 4-5) while inner of carina, both merge into inner protibial deflection. *Mesotibia.* Short and robust, outer edge with 3 bands of seta, inner edge with 2 bands; mesospur slightly spatulate (figure 55), apex forms blunt point; tarsal insertion slightly sub-apical; 2 almost equal in length tarsal claws, both longer than last tarsal segment. *Metatibia (Dorsal).* Medial ridge, proximal side smooth, distal side with long setal brush; spurs thin, pointed, round in cross section, slightly deflected in centre; 2 equal and curved tarsal claws; claws almost equal to just longer than last tarsal segment. *(Lateral).* 3 curved setal brushes on the tibia.

Elytra. Elytra fused, humeral callus absent; well-developed sub-elytral ridge; elytral rim broad; 6 faint striae per elytron, most visible when viewed laterally; 6 interstriae per elytron with rows of irregularly spaced, fine, setiferous granules.

Abdomen. Mesocoxae contiguous, mesosternal ridge absent; abdominal sternites with single row of setiferous granules becoming irregularly spaced as sternite widens laterally; bilobed protuberances in males (absent in females) on lateral edge of sternites 2,3,4, (numbered 1-6 from metacoxae) only.

Pygidium. Dorsoventral midline unsculptured; sides scattered with small granules, bilateral smooth rim around edge of pygidium.

Aedeagus. Short, asymmetrical, see figures 59a,b,c.

*Female.*Differs from male as follows; Protibia (Ventral). Proximal carina very reduced at (X 40); inner lateral edge with slight deflection, and row of anterior facing setiferous notches (X 40). Abdomen. Width of the last abdominal sternite, broad at pygidium; prominent protuberances on sternites 3-5, absent.

Comments. S. (P.) glentoni is externally virtually indistinguishable from *S. (P.) hippocrates.* The male genitalia provide the most reliable character for distinguishing these two species (figures 59a,b,c vs. 58a,b,c). Externally *S. (P.) glentoni* is distinguished from *S. (P.) hippocrates* by the narrow almost parallel sided mesotarsal spurs (figure 54 vs. 55), and a distinct patch of granules on the posterior of the pronotum. The localised distribution of *S. (P.)*

glentoni (figures 5a,b) as opposed to the much wider distribution of *S. (P.) hippocrates* (figure 4), separates the two species. Very abraded mesospur of *S. (P.) hippocrates* (figure 54 unabraded), resemble the narrow mesospurs of *S. (P.) glentoni* (figure 55 unabraded), care should be taken not to confuse the two species on this character.

Distribution, habitat and conservation. Localised to north of Lambert's Bay and south of the Olifants River, extending inland to Clanwilliam (figure 5a,b). Known habitats include the firm vegetated sand of river banks (Olifants and Groot-Sandleegte Rivers) and coastal hummocks. *S. (P.) glentoni* has not been collected in or around larger dunes, and does not occur within any proclaimed conservation area.

Biology. S. (P.) glentoni was observed collecting detritus, which was dragged forward to preconstructed burrows. A single male was observed at its burrow entrance, releasing what was probably pheromone. The beetle adopted a head down position, and using the hind legs, it would rhythmically stroke its abdominal sternites and then flick its legs backwards. This action was interspersed by short breaks (5-10 s), where the hind legs were held outstretched, but not moved. This behaviour was also observed in *S. (P.) gariepinus* and *S. (P.) hippocrates.*

Etymology. Named for a keen naturalist, Mr Jon Glenton, who encouraged JDUGH's interest in biology from an early age. Mr Glenton provided the Land~Rover that enabled JDUGH to collect this new species.

Type material examined (Σ120 specs., 31♀ 89♂, 18♂ diss., 15♂eth.). **SOUTH AFRICA**: HOLOTYPE ♂, S.Afr., SW Cape, Nortier Farm, 32.03S-18.19E / 25.8.1981; E-Y:1847, day, red sand, leg. Endrödy-Younga (1♂ TMSA); *idem* but, ALLOTYPE ♀ (1♀ TMSA); 108 PARATYPES: S.Afr., SW Cape, Nortier Farm, 32.03S-18.19E / 25.8.1981; E-Y:1847, day, red sand, leg. Endrödy-Younga (4♀ 7♂ TMSA), (1♀ 1♂ BMNH), *idem* but, SAM-COL-A043134 (1♀ 2♂ SAMC); S.Afr., SW Cape, Nortier Farm, 32.03S-18.19E / 23.8.1981; E-Y:1840, day, red sand, leg. Endrödy-Younga (2♀ 5♂ TMSA); S.Afr., SW Cape, Nortier Farm, 32.03S-18.19E / 25.8.1981; E-Y:1845, groundtraps, leg. Endrödy-Younga / groundtrap with faeces bait (1♂ TMSA). S.Afr: Vredendal D., nr. Strandfontein, De Boom 273, Skerpklip, 31°45'31S 18°20'55E, 12-14.xii.1996, leg. J.duG.Harrison / Univ.Pret.Zoo&Ento., J.duG,Harrison 1996, site 199 No.., Grootsandleegte R. Bank, Y/R sand, (2♀ 4♂ SANC), (2♀ 4♂ ZMHB), *idem* but, T1425 (5♂ SMWN), (4♂ eth. TMSA); S.Afr: Vredendal D., nr. Strandfontein, De Boom 273, Skerpklip, 31°45'18S 18°17'38E, 14.xii.1996, leg. J.duG.Harrison / Univ.Pret.Zoo&Ento., J.duG,Harrison 1996, site 200, No.., Grootsandleegte R.Bed, white sand, (1♀ TMSA); S.Afr: Vredendal D., nr. Strandfontein, Byneslaagte 274, Onderputs, 31°47'29S 18°22'59E, 14.xii.1996, leg. J.duG.Harrison, site 202, Grootsandleegte R., Y. firm sand plain, (5♂ MNHN), (6♂ BMNH), *idem* but, T306 (5♂ BMSA); S.Afr: Vredendal D., nr. Strandfontein, Byneslaagte 274, Onderputs, 31°47'01S 18°22'11E, 14-15.xii.1996, leg. J.duG.Harrison, site 203, Grootsandleegte R., Y. firm sand plain, (3♀ TMSA), (1♂eth. TMSA); S.Afr: Vredendal D., Fonteintjie 466, near Witwater, 31°55'17S 18°22'08E, 15.xii.1996, leg. J.duG.Harrison, site 204, sand rise, yellow sand, (1♀ 4♂ SANC), (1♂ UPSA), (10♂eth. TMSA); S.Afr: Vredendal D., Fonteintjie 466, near Witwater, 31°54'58S 18°21'37E, 15.xii.1996, leg. J.duG.Harrison, site 204a, sand rise, yellow sand, (5♂ TMSA), (1♀ 2♂ UPSA), (2♀ 2♂ COCS) *idem* but, SAM-COL-A043135 (3♀ 5♂ SAMC), *idem* but, T1425 (2♀ 5♂ SMWN); S.Afr: Clanwilliam, nr. Lambert's Bay, Kookfontein 88, 32°03'54S 18°22'39E, 16.xii.1996, leg. J.duG.Harrison / Univ.Pret.Zoo&Ento., J.duG,Harrison 1996, site 205 No.., Vegt. dune, firm yellow sand (1♀ 1♂ TMSA); S.Afr. C.P. 12km N., of Clanwilliam, (*ca.* 32.06S 18.50E), 14 October 1981, VB Whitehead / SAM-COL-A043133 (1♀ SAMC); S.Afr: Clanwilliam, 11.7km W, *ca.* 32.10S 18.47E, 5.viii.1997, C.R.Owen (3♀ 1♂ TMSA); (No locality data) / Ferreira Collection / NMBH3677 / National Museum of Bloemfontein, Dept. Entomology / 234 (written in blue ballpoint on yellow card, possibly by Ferreira) / T306 (1♂ BMSA).

Scarabaeus (Pachysoma) endroedyi Harrison, Scholtz and Chown **sp. n.**

(Figures 5, 21, 39, 56, 60)

Description.

Size (mm). Body length: mean ♂22.92; ♀24.28; range ♂20.66-24.70; ♀22.30-26.40. Pronotal width: mean ♂14.54; ♀14.20; range ♂12.78-15.98; ♀12.84-15.18 (n = 12♂ 12♀). *Colour*. Cuticle black; elytral indument grey-white to brown; antennal club golden; seta rubescent to brown.

Head(Dorsal) (figure 21). Clypeus bidentate; teeth short, apex rounded, separated by smooth V-shaped incision; genal and clypeal edge unserrated, almost continuous, separated at genal-clypeal incision; head finely granular, setose granules restricted to genae and posterior of head between eyes. (Ventral). Rim of setae around clypeal and genal edge; clypeal teeth raised into 2 ridges, posterior rim, with single pointed tooth; mandibles robust, mentum bilobed, stiff setae pointing forward on lobe; lamellate antennae, 9-segmented, club formed by last 3 segments, which are covered with fine golden setae; ventral eye smaller than dorsal eye.

Pronotum. Head amplected into prothorax; concavity bordered by bilateral rim; anterior lateral edge, unequally notched; posterior lateral edge, serrate from setal fringe; fringe, long on outer edge tapering to short medially; disc globose and setiferously granula-punctate; medial diamond-shape and posterior lateral edges, finely shagreened.

Legs; Protibia (Dorsal) (figure 39b). Quadridentate, teeth pointed, curved downward, apical surface smooth, basal half transversely furrowed; blunt serrations between and proximal to teeth, becoming smooth on proximal half of protibia; medial setiferous carina; setal border, long on inner edge and proximal outer edge, short between teeth; inner edge, deflected inwards medially; spur weakly bifid and curved downward. (Ventral) (figure 39a). Surface granular, apical section of teeth smooth; proximal carina and single row of setae dissipate before proximal tooth; inner edge deflected downwards, bordered with row of irregular, distinct knobs. *Mesotibia*. Mesotibia short and robust; outer edge with 3 bands of seta; spurs slightly spatulate, apex blunt; tarsal insertion slightly sub-apical; 2 unequal tarsal claws, both shorter than last tarsal segment. *Metatibia* (Dorsal). Proximal side of medial ridge smooth, distal side with long setal brush; spurs thin, apex pointed, round in cross section, slightly deflected in centre; 2 equal and curved tarsal claws, shorter than or almost equal to last tarsal segment. (Lateral). 3 curved setal brushes on tibia.

Elytra. Fused, humeral callus absent; well-developed sub-elytral ridge and rim; elytra bordered by band of indument; 6 striae per elytron, scattered with minute, irregular setose granules.

Abdomen. Mesocoxae contiguous, mesosternal ridge absent; abdominal sternites with single row of setiferous granules becoming irregularly spaced as sternite widens laterally; bilobed protuberances in males (absent in females) on lateral edge of sternites 2,3,4, (numbered 1-6 from metacoxae) only.

*Pygidium.*Irregularly speckled with small granules; bilateral smooth rim around edge of pygidium.

Aedeagus. Parameres short, asymmetrical, see figures 60a,b,c.

Female. Differs from male as follows; Protibia (Ventral). Proximal carina and single row of setae very reduced at (X 40); inner lateral edge with slight deflection, and row of anterior facing setiferous notches (X 40). Abdomen. Width of the last abdominal sternite, broad at pygidium; prominent protuberances on sternites 3-5 wanting.

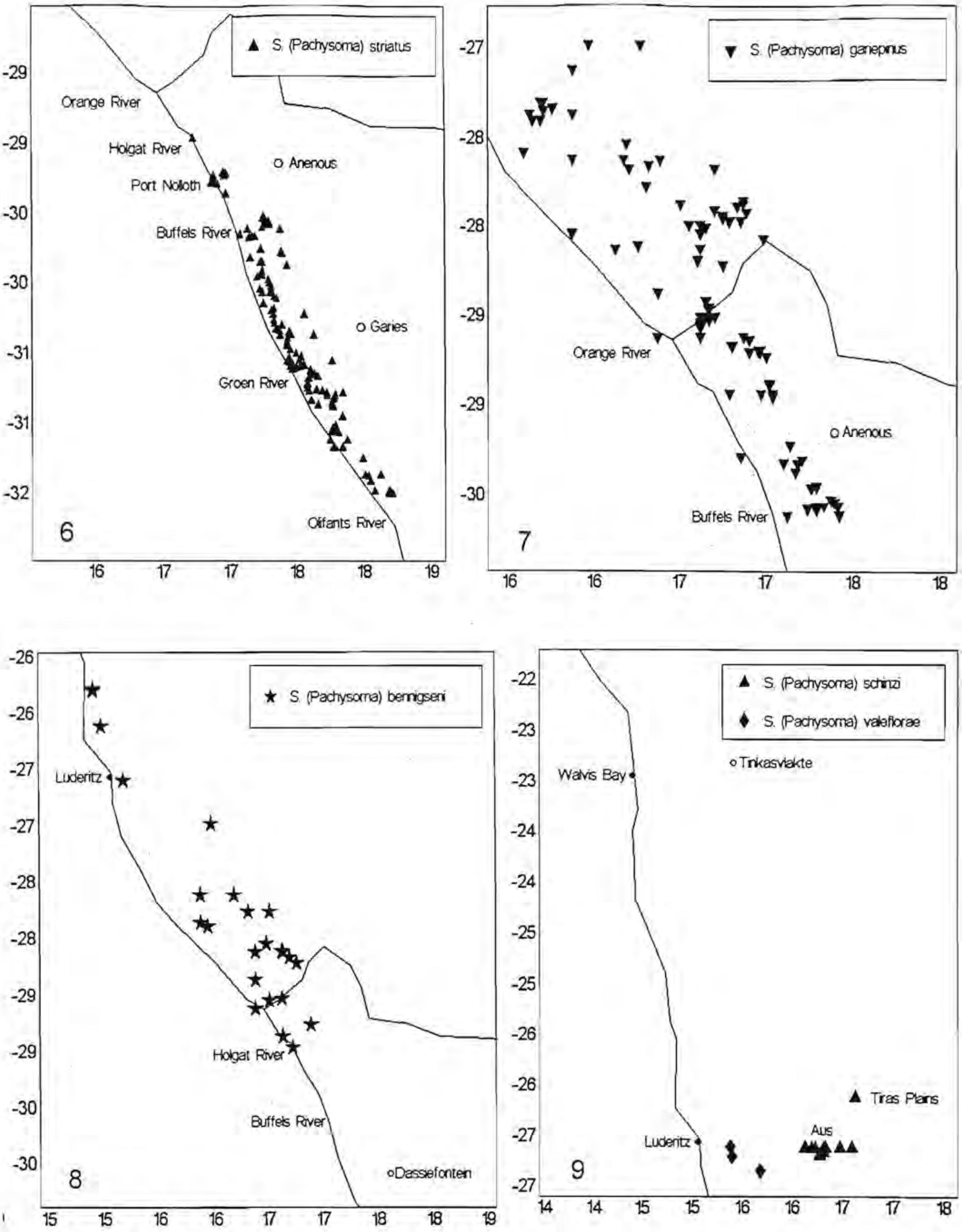
Comments. The smallest species within the *hippocrates* species complex. Similar to *S. (P.) hippocrates* but with elytral indument like *S. (P.) striatus* and *S. (P.) gariepinus*. The sympatric population of *S. (P.) hippocrates* also exhibits elytral indument, but to a lesser degree. The two species are easily distinguished as *S. (P.) hippocrates* is larger and has metatarsal claws longer than the last tarsal segment, while *S. (P.) endroedyi* metatarsal claws are shorter.

Distribution, habitat and conservation. Restricted to southwestern South Africa, occurring just north of the Olifants River. The localised distribution (figures 5a,b) might be an artifact of the absence of roads passing through their habitat (thus preventing easy collection), or lack of suitable habitats further northwards. Preferred habitats include the vegetated firm sand of coastal hillocks and sand dunes. This species does not occur within a proclaimed conservation area. The increase in recreational development around Strandfontein (31°45'S 18°14'E), and Koekenaap (31°32'S 18°14'E) potentially threatens the future survival of this species.

Biology. Seven nests of this species were excavated by JDUGH. One contained pellets and six contained a combination of detritus and pellets. *S. (P.) endroedyi* thus may be a mixed dung and detritus feeder. All specimens were collected during daylight. Their foraging behaviour is typical of *S. (Pachysoma)*. The larvae are unknown.

Etymology. Named for the late Dr Sebastian Endrödy-Younga, who recognised this species as new and collected most of the type series. JDUGH is indebted to Sebastian for encouraging and guiding his interest in beetle collecting and systematics.

Type material examined (Σ135 spec.[0], 47♀ 88♂, 16♂ diss.). **SOUTH AFRICA**: HOLOTYPE ♂, S.Afr: Namaqualand, **Kommandokraal** farm, 31.30S-18.12E / 23.9.1994; E-Y:3033, on sandy



FIGS. 6-9. Distribution of *Scarabaeus (Pachysoma)* species in South Africa and Namibia. Questioned locality records or range extensions are shown by an open circle. (6) *S. (P.) striatus*; (7) *S. (P.) gariepinus*; (8) *S. (P.) bennigseni*; (9) *S. (P.) schinzi* and *S. (P.) valeflorae*.

ground, Endrödy & Bellamy, (1♂ TMSA); *idem*, but ALLOTYPE ♀, (1♀ TMSA); *idem*, but PARATYPES, (2♀ 4♂ BMNH), (12♀ 23♂ TMSA), (2♂ UPSA), (2♂ MNHN), (2♂ ZMHB), *idem*, but T307 (2♂ BMSA), *idem*, but T1424 (2♂ SMWN); S.Afr., Namaqualand, Kommandokraal Frm., 31.30S-18.12E / 30.8.1979; E-Y:1622, singled on sand, leg. Endrödy-Youngae, (2♂ TMSA); S.Afr., Namaqualand, **Koekenaap**, 31.32S-18.14E / 30.8.1979; E-Y:1623, red dunes night, leg. Endrödy-Youngae, (2♂ TMSA); S.Afr., Namaqualand, Koekenaap, 31.32S-18.14E / 31.8.1979; E-Y:1624, red dunes day, leg. Endrödy-Youngae, (4♀ 5♂ TMSA); S.Afr., Namaqualand, Koekenaap, 31.32S-18.14E / 31.8.1979; E-Y:1625, groundtraps, 59 days, leg. Endrödy-Youngae / groundtraps with banana bait (1♂ TMSA), *idem*, but groundtraps with meat bait (1♂ TMSA); *idem*, but groundtraps with faeces bait (1♂ TMSA); South Africa: Cape, Kommandokraal, 31.31S-18.13E, 100m, 23-IX-1985, AVEvans, CLBellamy / T1424 (2♀ 4♂ SMWN); S. Africa, C.P. , Kommandokraal 624, Vredendal, 31°30'S, 18°12'E / 23 Sept. 1985, Louw, v. Rensburg, NMBH 15818 / T307 (1♀ BMSA); Kommandokraal, Cape, R.S.A., 31°30'S. 18°12'E., 19 Sept. 1982, M.-L.Penrith / H54679 / T1424 (1♀ SMWN); S.Afr.; W Cape, KommandokraalfarmW (sic), 31.29S-18.11E / 23.9.1994; E-Y:3035, on ground, Endrödy & Bellamy (5♂ TMSA); S.Afr; Namaqualand, **Koekenaaphilldunes** (sic), 31.32S-18.14E / 23.9.1994; E-Y:3032, groundtraps, 3 days, Endrödy & Bellamy / groundtraps with banana bait (1♂ TMSA); S.Afr; SW Cape, Koekenaap dunes, 31.32S 18.14E / 22.9.1994; E-Y:3030, ground & hummocks, Endrödy & Bellamy (6♀ 3♂ TMSA), *idem*, but SAM-COL-A043137 (6♀ 3♂ SAMC); S.Afr: Vredendal D., **Graafwater on Farm 156**, 31°22'38S 18°01'23E, 6.xii.1996, leg. J.duG.Harrison / Univ.Pret.Zoo&Ento., J.duG.Harrison 1996, Site 186 No.., firm Y. sand plain, nr. veget. dunes (1♂ TMSA); S.Afr: Vredendal D., **Elsie Erasmus Kloof 158**, 31°24'46S 18°02'30E, 7-8.xii.1996, leg. J.duG.Harrison / Univ.Pret.Zoo&Ento., J.duG.Harrison 1996, site 188 No.., vegt. 'old' dune, yellow sand, (2♀ 4♂ BMNH), *idem*, but T1424 (2♀ 4♂ SMWN); S.Afr: Vredendal D., Kommandokraal, on Farm 624, near Koekenaap, 31°29'58S 18°11'47E, 8-9.xii.1996, leg. J.duG.Harrison / Univ.Pret.Zoo&Ento., J.duG.Harrison 1996, site 191 No.., vegetated dune, yellow sand, (1♂ SANC); S.Afr: Vredendal D., Kommandokraal, on Farm 624, near Koekenaap, 31°29'02S 18°10'08E, 10.xii.1996, leg. J.duG.Harrison / Univ.Pret.Zoo&Ento., J.duG.Harrison 1996, site 193 No.., vegetated dune, yellow sand, (1♀ 2♂ SANC); S.Afr: Vredendal D., **Vleitjies, Farm 620** near Koekenaap, 31°34'53S 18°10'15E, 11.xii.1996, leg. J.duG.Harrison / Univ.Pret.Zoo&Ento., J.duG.Harrison 1996, site 195 No.., Olifants R. vegt., dune/bank, red sand, (2♀ 5♂ SANC); S.Afr: Vredendal D., Vleitjies, Farm 620 near Koekenaap, 31°34'53S 18°10'56E, 12.xii.1996, leg. J.duG.Harrison / Univ.Pret.Zoo&Ento., J.duG.Harrison 1996, site 196 No.., Olifants R., vegt. dune, soft red sand / T307 (2♀ 1♂ BMSA).

Scarabaeus (Pachysoma) striatus (Castelnau, 1840)

(Figures 6, 22, 40, 61)

Pachysoma striatum Castelnau, 1840: 68; Péringuey 1902: 81; Gillet 1911a: 6: Ferreira 1953a; 36: Ferreira 1961:24; Holm and Scholtz, 1979; 233. [Holotype lost?], type locality Cape.

Pachysoma marginatum Péringuey, 1888: 92; Péringuey, 1902: 77; Gillet 1911a: 6: Ferreira, 1953a: 22; Ferreira 1961: 24; Ferreira, 1966: 58; Ferreira 1969: 21. Lectotype ♂, Port Nolloth (1♂ TMSA).

Irrorhotides fryi Shipp. 1896: 116; Ferreira, 1953a: 22; Ferreira 1961: 24. {Holotype ?}, {Type in Frey collection? NHMB}.

Scarabaeus striatus (Castelnau): Mostert and Holm, 1982: 275.

Diagnosis. Clypeus bidentate, genal and clypeal edge unserrated and almost contiguous (figure 22). Protibia and metatibia sexually dimorphic, protibial spurs simple in both sexes (figures 40a,b). Pronotum with a hook on outer posterior edges. Elytra striated, elytral rims with band of waxy indument. Metatarsal claws shorter than last tarsal segment.

Distribution, Habitat and Conservation. Distributed from the Holgat to the Olifants River (figure 6). Preferred habitats include the firm consolidated sand of vegetated coastal hummocks, hillocks, dunes and river banks. Contained within the proposed Groen-Spoeg National Park.

Comments on locality data. The Holgat River Mouth record extends the known distribution of *S. (P.) striatus* about 30 km northwards. The high security mining area between Kleinsee and Port Nolloth accounts for the lack of records here. This area was surveyed early in the season of 1996, but only dead specimens of *S. (P.) striatus* were found on Oubeep 173 at 29°21'55S 16°57'32E.

Garies and Anenous Pass fall outside the expected coastal distribution of *S. (P.) striatus* (figure 6). These specimens were probably collected closer towards the coast, but the closest inland locality known was used to record their location.

Morphological variation. Elytral sculpture, body size and the expression of indument in *S. (P.) striatus* vary within and between populations. Very small females of *S. (P.) striatus* from Dembergdraai (30°47'S 17°43'E) and Rooidam (31°04'S 17°48'E) were thought to represent a new species (Endrödy-Younga pers. comm.). However, upon examination they conform in all aspects to typical female *S. (P.) striatus.*

Biology. Refer to Scholtz (1989) for a detailed study on the foraging and burrow construction of this species. Of 28 burrows excavated by JDUGH, 26 contained only dry dung pellets while two contained both detritus and pellets. This suggests that *S. (P.) striatus* is predominately a dry pellet feeder rather than a detritus feeder. Scholtz (1989) found that the natural forage of the Port Nolloth population of *S. (P.) striatus* was rodent pellets. However, the vast majority of the pellets excavated by JDUGH were sheep, but even small fragments of dry ostrich dung were collected. Thus it appears that *S. (P.) striatus* will collect any suitable dry dung that it can relocate.

S. (P.) striatus were successfully bred under lab conditions on two separate occasions. Four pairs 1.ix.1996-23.i.1997 and six pairs 9.ix.1998-4.xii.1998 of *S. (P.) striatus* collected from Strand Fontein (30°33'S 17°26'E), were placed in round 25l buckets and 5l square bread bins respectively. Sand, dry sheep pellets and detritus from their collection site (Strand Fontein Farm in Namaqualand) were provided. They dug burrows, foraged regularly, and bred successfully. The 1996 sample produced two third-instar larvae (prepupa), one pupa and one teneral adult. Two third-instar larvae (prepupa) and one pupa were bred in 1998. No evidence of the use of a brood pear to contain the larvae was found in *S. (Pachysoma)*. Which is additionally confirmed by the larval morphology because the characteristic hump defining all dung ball confined larvae is absent in *S. (Pachysoma) striatus* and *S. (Pachysoma) gariepinus* larvae. When excavated the larvae were in clean moist sand a few centimetres from the closest nest evidence (i.e. larval or adult frass and/or a decomposed dung plug). The pupae were surrounded by a fragile casing constructed from sand grains cemented together. This suggests that *S. (Pachysoma)* larvae are open nest feeders that move away from their nests as prepupae, before pupating in clean sand. The nature of the larval food itself needs to be verified, as no larvae were found in a nest. However, the possibilities include the rehydrated dung pellets or detritus provisioned by the adults, or they might feed on the adult faeces (i.e. already processed dung and detritus).

Klemperer and Lumaret (1985) studied the nesting biology of *Geotrupes (Thorectes) sericeus* (Geotrupidae) a flightless species restricted to sandy coastal dunes in western France. Their study provides valuable insight into the biology of flightless species nesting in sand and feeding on dry dung. Female *T. sericeus* lay an egg at the terminal end of a chamber before provisioning it with a plug of unhomogenized dry rabbit pellets. The egg chamber is thus outside the dung mass and the larvae are free-living. Related species *T. albarracinus* and *T. laevigatus,* which nest in soil have their egg chamber contained within the homogeneous brood mass of sheep dung (Klemperer and Lumaret 1985). It is worth determining whether *S. (Pachysoma)* females also lay their eggs at the terminal ends of the food chamber, away from the food itself. This is very likely as Klemperer and Lumaret (1985) suggest that '...ovipositing outside the brood mass may have a selective advantage where nests are made during the wet season in sandy environments. Water is more likely to drain away from a chamber in sand, but an egg inside a dung mass is more likely to 'drown'. This is because the dung mass will retain water by capillary suction...' (Scholtz 1989 shows this capillary action with dry pellets used by *S. (P.) striatus*). Other Geotrupidae that nest in sand, viz. *Typhaeus typhoeus* and *Ceratophyus hoffmannseggi* always oviposit outside the brood chamber (Klemperer and Lumaret 1985). *T. sericeus* pupate inside the original brood chamber but *Typhaeus typhoeus* that prefer sandy soils (Brussaard and Visser 1987) pupate in the surrounding sand (Main 1917), as observed in *S. (Pachysoma)*.

Comments. Similar to *S. (P.) gariepinus,* but differentiated by the distinct posterior pronotal hooks.

*Types.*Castelnau's (1840) description of *Pachysoma striatum* suggests a single female specimen was examined (length 9 lig width 6 lig). The line (lin. or lig.) equals one-twelfth of an inch (Torre-Bueno 1989). Thus, this specimen measured about 19.08 mm long and 12.72 mm wide. The type locality was recorded as 'Cap de Bonne-Espérance' and the specimen was deposited in the collection of M.Gory.

Based on Castelnau's (1840) description of *P. striatum* only, Péringuey (1900) remarked that *P. striatum* represented either a small specimen of *Pachysoma hippocrates* or that *P. striatum* might be identical to *Pachysoma marginatum*. Holm and Scholtz (1979) were unable to find the type of *Pachysoma striatum* Castelnau, and suggest it is probably lost. Because *P. striatum* was the closest species in size, morphology, and distribution to *P. marginatum* (20-25 mm long 14-16 mm wide), Holm and Scholtz (1979) synonymised *P. marginatum* with *P. striatum*. However, the possibility does exist that *S. (P.) endroedyi* sp.n. is what Castelnau (1840) described as *Pachysoma striatum*. *S. (P) endroedyi* was not known to Holm and Scholtz (1979) and occurs sympatrically with *P. striatum*, overlaps in size with *P. striatum* and has elytral indument like *P. striatum*. However, without the holotype of *P. striatum*, and only the short description by Castelnau (1840) no further conclusions can be made.

Péringuey's (1888) description of *Pachysoma marginatum* includes references to both sexes, lists a range in body size (length 20-25 mm; width 14-16mm) and mentions that *P. marginatum* is 'pretty common at Port Nolloth, Namaqualand'. These observations suggest that several specimens were examined. He deposited the types in the SAMC collection and in his personal collection. According to Cochrane (1995), Dr Hesse removed all suspected types from Péringuey's private collection, labelled them with green (holotype) and orange (paratypes) labels and deposited them in the SAMC collection. The only possible type material listed by Ferreira (1953a) are three males from Port Nolloth collected by Warden, dated between 1885 to1899. Only one undated specimen from this series was examined from the UPSA collection. Holm and Scholtz (1979) were unable to find any labelled type material and rightfully designated the earliest collected specimen from Port Nolloth as the male lectotype. Subsequently however, two specimens from the type locality both determined in Péringuey's hand, one older than the designated lectotype and the other not dated were discovered in the SAMC and DMSA collections respectively. These specimens are designated here as paralectotypes. A single pinned aedeagus labelled in Péringuey's hand as follows: '*Pachysoma marginatum*, armature of ♂', was also discovered in the SAMC (refer to discussion on *S. (P.) denticollis* types). This aedeagus probably originates from the holotype of *P. marginatum*, which appears to be lost. Because a lectotype has already been designated by Holm and Scholtz (1979) this aedeagus is designated as paralectotype of *P. marginatum*.

Type material examined (Σ4 specs. [1], 1♀ 3♂, 1♂ diss.). **SOUTH AFRICA**: LECTOTYPE ♂, *Pachysoma marginatum* Péringuey, designated by Holm and Scholtz (1979): Pt. Nolloth, (29.17S 16.51E), 29.11.(18)85 / *Pachysoma marginatum* Péringuey, Lectotype, Holm and Scholtz 1978, (1♂ TMSA). PARALECTOTYPES 1♀ 1♂ 1♂ aedeagus, designated here: Cape, Port Nolloth, (29.17S 16.51E) // Rev. G.H.Fisk, Dec v. 1884 //, / ♀ (written by Péringuey? on white paper, now faded) / *Pachysoma marginatum* LP (written by Péringuey on white paper, now faded), (1♀ SAMC); Pt. Nolloth, L.Namaqua. (written on white paper, now faded) / *Pachysoma marginatum* (written by Péringuey on white paper, now faded) / Durban Museum (printed on white card), (1♂ SAMC); *Pachysoma marginatum* armature of ♂ (written by Péringuey), (male genitalia mounted onto white card with a brass minuten), (1♂ aedeagus only SAMC).

Additional material examined (Σ759 specs. [86], 275♀ 439♂, 4♂diss., 45eth., 137p.). **SOUTH AFRICA**: **Buffels river valley**, 29.35S 17.17E, 4.x.1976, E-Y:1256, on sandy hill, Endrödy-Younga, (2♂ TMSA); Buffels rivier valley, 29.35S 17.17E, 31.viii.1976, E-Y:1197, groundtraps 33 days, Endrödy-Younga, (1♀ 1♂ TMSA); Buffels rivier, 29.55S 17.39E, 27.x.1977, E-Y:1397, on red ground, Endrödy-Younga, (1♀ TMSA); **Dembergdraai**, 30.47S 17.43E, 24.viii.1979, E-Y:1590, sandblown hill, Endrödy-Younga, (2♂ TMSA); Dembergdraai, 30.47S 17.43E, 26.x.1979, E-Y:1656, on hard red sand, Endrödy-Younga, (1x TMSA); Dembergdraai, 30.47S 17.43E, 18.ix.1994, on ground, day, E-Y:3015, Endrödy-Younga & Bellamy, (1♀ 5♂ TMSA); Dembergdraai farm, 30.47S 17.43E, 19.ix.1994, groundtraps 6 days, hand-collected around traps at setting, E-Y:3019, Endrödy-Younga, (6♀ 2♂ TMSA); Dembergdraai, 30.48S 17.43E, 19.ix.1994, on red sandy ground, E-Y:3021, Endrödy-Younga & Bellamy, (1♀ TMSA); **Eiland Punt Noord 549**, 30.52S 17.39E, 25.viii.1996, A.Mackenzie, (1♀ UPSA); **Geelduine**, 30.04S 17.14E, 16-18.vi.1987, J.Irish, E.Marais, (1♀ 2♂ SMWN); **Gemsbok Vlakte Farm**, 30.30S 17.29E, 30.viii.1977, E-Y:1361, hand-collected, dunes, day, Endrödy-Younga, (1♀ 1♂ TMSA); Gemsbok Vlakte Farm, 30.30S 17.29E, 28.x.1977, E-Y:1399, hand-collected, dunes, day, Endrödy-Younga, (1♂ TMSA); **Graskom**, 30.18S 17.23E, 15-18.ix.1982, M-L.Penrith, H54563, (4♀ 17♂ SMWN); Graskom 610, 30.18S 17.23E, 15-18.ix.1982, S.Louw, NMBH 8641, (2♀ 17♂ BMSA); **Groenriviermond**, (*ca.* 30.50S 17.36E), 30.ix.1972, H.D.Brown, E.Koster, A.Prinsloo, (3♀ SANC); Groenrivier Mouth, 30.50S 17.36E, 3.ix.1977, E-Y:1379, hand-collected, dunes, night, Endrödy-Younga, (1♂ TMSA); Groenrivier, 30.50S 17.36E, 29.x.1977, E-Y:1402, hand-collected, white dunes, Endrödy-Younga, (1♀ 5♂ TMSA), Groen River, (*ca.*30.50S 17.36E), viii.1990, C.R.Owen, (3x COCS); Groen River, (*ca.*30.50S 17.36E), 10.ix.1997, A.Mackenzie, (4x UPSA); **Grootmis**, 20km E, (*ca.* 29.37.05S 17.07.05E), 4.x.1972, H.D.Brown, E.Koster, A.Prinsloo, (1♀ SANC), **Holgat River Mouth**, 28.58S 16.43E, 25-27.ix.1988, J.Irish, E.Marais, (2♀ 3♂ SMWN); **Hondeklipbay**, 12 km E, 30.21S 17.25E, 30.viii.1977, E-Y:1359, groundtraps with faeces bait, 58 days, Endrödy-Younga, (1♀ TMSA); Hondeklipbay, 16km E, (*ca.*30.21S 17.26E), 24.x.1986, C.R.Owen, (2x COCS); Hondeklipbaai, 6km E, SE3017Ad, (30.22.05S 17.22.05E), 27.ix.1974, Houston, Davis, Tribe, (1x SANC); 7km WNW of Wallekraal on road to Hondeklip Bay, (*ca.* 30.22S 17.27E), 14-16.ix.1992, F.W. & S.K. Gess, (1♀ 1♂ AMGH); **Karroovlei**, (31.22.05S 18.07.05E), 13.x.(19)48, (1♂ SAMC); **Katdoringvlei**, 31.07S 17.52E, 27.viii.1979, hand-collected on sand, E-Y:1604, Endrödy-Younga, (1♀ 1♂ TMSA); Katdoringvlei, 31.07S 17.52E, 28.x.1979, E-Y:1664, hand-collected on sand, day, Endrödy-Younga, (5♀ 2♂ TMSA); **Klein Kogel Fontein**, 31.10S 17.50E, 27.viii.1979, E-Y:1607, hand-collected, Endrödy-Younga, (3♂ TMSA); **Kleinsee**, (29.39S 17.04E), xii.(19)48, J.H.Power, (1♀ 1♂ AMMM); Kleinzee, 12km E, 29.36S 17.14E, 4.ix.1987, E-Y:2474, ground & vegetation, Endrödy-Younga, (1♀ 3♂ TMSA); **Koingnaas**, 1km NE, 30.11S 17.19E, 100m, 3.ix.1986, AVEvans, CLBellamy, (3♀ 4♂ UPSA); **Kommandokraal 624**, Vredendal, 31.30S 18.12E, 23.ix.1985, Louw, v.

Rensburg, NMBH 15818, (1♂ BMSA); Kommandokraal Farm W, 31.29S 18.11E, 23.ix.1994, E-Y:3035, on ground, Endrödy-Younga & Bellamy, (2♀ 10♂ TMSA); **Kotzersrus**, 30.57S 17.50E, 23.viii.1979, E-Y:1581, white dunes, day, Endrödy-Younga, (7♀ 16♂ TMSA); Kotzersrus, 30.57S 17.50E, 23.viii.1979, E-Y:1583B, groundtraps with faeces bait, 62 days, Endrödy-Younga, (1♀ TMSA); **Namaq.L.** C.L.L. Biden, 1911, (1♀ SAMC); **Port Nolloth**, (29.17S 16.51E), Nov.(18)90, (1♂ SAMC); Pt. Nolloth, (29.17S 16.51E), B.Warden, (1♂ SAMC); Port Nolloth, (29.17S 16.51E), 1911, C.L.Bidens, (1♀ TMSA), (1♂ UPSA), (5♂ SAMC); Port Nolloth, (29.17S 16.51E), viii.1911, C.L.Biden, (3♂ SAMC), (1♂ 1♀ SANC); Port Nolloth, (29.17S 16.51E), x.1911, Lightfoot, (2♀ 1♂ SAMC); Pt. Nolloth, (29.17S 16.51E), x.1911, R.M.Lightfoot, (1♂ UPSA); Port Nolloth, (29.17S 16.51E), ix.(19)21, Name?, NM9025, Donation Natal Museum, (1x BMSA); Port Nolloth, (29.17S 16.51E), xi.(19)40, (1x SANC); Port Nolloth, C.P., (29.17S 16.51E), 22.xi.1948, Koch & van Son, (1♀ 1♂ TMSA); Port Nolloth, (29.17S 16.51E), v.(19)53, C.Koch, (2♀ 1♂ TMSA); Port Nolloth Dunes, 29.14S 16.57E, 4.x.1976, E-Y:1257, hand-collected, on dunes, Endrödy-Younga, (2♂ TMSA); Port Nolloth, (29.17S 16.51E), 2.x.1981, V.B. Whitehead, (1♂ SAMC); Port Nolloth, (29.17S 16.51E), 27.xi.1986, C.H.Scholtz, (1♀ UPSA); Port Nolloth, McDougall's Bay, 29.17S 16.52E, 27.xi.1986, C.H. Scholtz, (6♀ 14♂ UPSA); Port Nolloth, 4km S, McDougall's Bay, 29.17S 16.53E, 29.ix.1994, Scholtz, Chown, Klok, (1♂ UPSA); **Quaggafontein**, 30.13S 17.33E, 28.viii.1977, E-Y:1352, hand-collected, at night, Endrödy-Younga, (1♀ 4♂ TMSA); Quaggafontein, 30.13S 17.33E, 29.viii.1977, E-Y:1353, hand-collected, day, Endrödy-Younga, (22♀ 15♂ TMSA); Quaggafontein, 30.13S 17.33E, 29.viii.1977, E-Y:1356, ground traps, with faeces bait, 60 days, Endrödy-Younga, (2♂ TMSA); Quaggafontein, 30.13S 17.33E, 29.viii.1977, E-Y:1356a, ground traps, with meat bait, 60 days, Endrödy-Younga, (10♀ 2♂ TMSA); Quaggafontein, 30.13S 17.33E, 29.viii.1977, E-Y:1356b, ground traps, with meat bait, 60 days, Endrödy-Younga, (4♀ 2♂ TMSA); Quaggafontein, 30.13S 17.33E, 29.viii.1977, E-Y:1357, hand-collected, at night, Endrödy-Younga, (1♀ TMSA); Quaggafontein, 30.13S 17.33E, 29.viii.1977, E-Y:1354, groundtraps 60 days, Endrödy-Younga, (1♀ TMSA); **Rooidam farm**, 31.04S 17.48E, 25.viii.1979, E-Y:1599, hand-collected, sandy hill, Endrödy-Younga, (1♀ TMSA); Rooidam farm, 31.04S 17.48E, 26.viii.1979, E-Y:1602, yellow sand, day, Endrödy-Younga, (3♀ 15♂ TMSA); Rooidam farm, 31.04S 17.48E, 26.viii.1979, E-Y:1603, yellow sand, night, Endrödy-Younga, (2♀ 1♂ TMSA); Rooidam farm, 31.04S 17.48E, 20.ix.1994, E-Y:3026, ground & light, Endrödy-Younga & Bellamy, (4x TMSA); Rooidam farm, 31.04S 17.48E, 21.ix.1994, E-Y:3027E, ground traps with faeces bait for 5 days, Endrödy-Younga, (19x TMSA); Rooidam Farm, 31.04S 17.48E, 21.ix.1994, E-Y:3027G, ground traps for 5 days, Endrödy-Younga & Bellamy, (3x TMSA); Rooidam Farm N, 31.02S 17.46E, 21.ix.1994, E-Y:3028E, ground traps with faeces bait for 5 days, Endrödy-Younga, (3♀ 1♂ TMSA); Rooidam Farm, 31.04S 17.48E, 26.ix.1994, E-Y:3046, white vegetated dunes, Endrödy & Bellamy, (3♀ 6♂ TMSA); **Rondawel** Farm, 30.47S 17.50E, 4.ix.1977, E-Y:1381, hand-collected, Endrödy-Younga, (1♀ TMSA); **Soutpan**, 20km E, 31.15S 17.32E, (in sea, try 18.32E) 31.vii.1989, cattle grid on road, E-Y:2631, Endrödy & Klim., (2♂ TMSA); Soutpan, 10km E, 31.15S 17.59E, 13.ix.1987, in cattle grid, E-Y:2493, Endrödy-Younga, (4♀ 2♂ TMSA); **Thong-**

Gys Dunes, 29.32S 17.14E, 23-25.ix.1988, J.Irish, E,Marais, (4♂ SMWN); **Tities Baai**, 3km NW, 31.10S 17.46E, 28.viii.1979, hand-collected, E-Y:1614, Endrödy-Younga, (2♂ TMSA); **Wallekraal**, (30.22.05S 17.37.05E), Namaqualand, SAM, x.1950, (9♀ 11♂ SAMC), (3♀ 4♂ UPSA) *idem*, but NMBH 3682 (1♀ 1♂ BMSA,); **Witduin**, 29.52S 17.25E, 23.ix.1988, J.Irish, E.Marais, (3♀ 1♂ SMWN); **Strandfontein farm**, 30.33S 17.22E, 3.ix.1977, E-Y:1374, hand-collected, dunes, day, Endrödy-Younga, (3♂ TMSA); **Strandfontein farm**, 30.33S 17.22E, 3.ix.1977, E-Y:1376, groundtraps, with banana bait, 56 days, Endrödy-Younga, (3♂ TMSA); No label data, (9x SAMC), (1x SANC).

All material below, unless otherwise specified, was collected by J. du G. Harrison, and is listed in chronological order by site number: **S.Afr: Namaqualand**, Koingnaas, Somnaas 474, 30°08'49S 17°14'36E, 16.vii.1996, site 2, active white dunes, interdune slack, (2♀ 2♂ 1p SANC); Port Nolloth, McDougall's Bay, 29°17'17S 16°52'56E, 18.vii.1996, site 3, coastal hummocks, white sand, (1♀ 1♂ 3eth. TMSA); Port Nolloth, McDougall's Bay, 29°17'36S 16°53'59E, 18.vii.1996, site 4, coastal hummocks, white sand, (1♂ TMSA); S.Afr: Namaqualand, Strand Fontein 499, 30°33'S 17°25'E, 20.vii.1996, site 6, Bitter River Dunes, interdune slack, (2♀ 2p SANC); Roode Heuvel 502, 30°44'57S 17°34'24E, 21.vii.1996, site 9, red sand; (1♂ 1p SANC); Buffels River Complex, Oubeep 173, 29°21'55S 16°57'32E, 22.vii.1996, site 13, coastal hummocks, white sand, (3p SANC); Stryd Rivier 188, 29°34'28S 17°16'49E, 24.vii.1996, site 15, firm red sand, Buffels River, (1p SANC); Stryd Rivier 188, 29°33'46S 17°17'02E, 24.vii.1996, site 16, red sand, Buffels River, (1p SANC); Stryd Rivier 188, 29°33'46S 17°17'02E, 26.vii.1996, site 19, red sand, Buffels River, (1♂ SANC); Stryd Rivier 188, 29°33'37S 17°16'55E, 27.vii.1996, site 20, red sand nr. Buffels River, (2♀ 1p SANC); Roode Vley 189, 29°34'01S 17°15'42E, 27.vii.1996, site 21, blowout, red sand, vegetated dune, (12♀ 4♂ UPSA) (2p SANC); Klein Duin 154, 29°13'01S 16°57'45E, 29.vii.1996, site 22, white sand, vegetated dune, (3p SANC); Klein Duin 154, 29°13'04S 16°57'54E, 29.vii.1996, site 26, white sand dunes, vegetated slack, (1♀ 2♂ TMSA) (1p SANC); Kleinsee, Sand Kop 322, 29°39'54S 17°09'12E, 30.vii.1996, site 29, vegetated dune, blowout, red sand, (2p SANC); Kleinsee, Honde Vlei 325, 29°45'25S 17°13'11E, 7.viii.1996, site 32, vegetated dune, yellow sand, (2♀ 2♂ SAMC) (1p SANC); Roode Vley 189, 29°34'01S 17°15'42E, 9.viii.1996, Harrison & Scholtz, site 21/36, blowout, red sand, vegetated dune, (1♀ SAMC); Port Nolloth, Klein Duin 154, 29°12'46S 16°56'35E, 11.viii.1996, Harrison & Scholtz, site 38, white sand, dune periphery, (5p SANC); Port Nolloth, Klein Duin 154, 29°12'44S 16°56'17E, 11.viii.1996, Harrison & Scholtz, site 39, white sand, dune periphery, (1p SANC); Elands Klip 333, 29°57'45S 17°11'19E, 12.viii.1996, Harrison & Scholtz, site 40, DeBeers Game Farm, vegetated dune, yellow sand, (2♂ 2p SANC); near Koingnaas, 30°02'41S 17°12'44E, 12.viii.1996, Harrison & Scholtz, site 41, DeBeers Game Farm, vegetated dune, white sand, (1♀ SAMC); near Wallekraal, Avontuur 488, 30°23'47S 17°25'21E, 13.viii.1996, Harrison & Scholtz, site 42, red sand, (1♀ 3p SANC); Strand Fontein 499, 30°33'45S 17°26'25E, 13.viii.1996, Harrison & Scholtz, site 43/44, Bitter River dunes, white sand, (3♀ 3♂ ZMHB), (4p SANC); Strand Fontein 499, 30°34'08S 17°27'21E, 13.viii.1996, Harrison & Scholtz, site 45, Klipheuwel House, drowned, (1♀ SAMC); Dermbergdraai, 504, 30°46'S 17°41'E 14.viii.1996, Harrison & Scholtz, site 49, Groen R. bank RHS, red sand, (2p SANC); De Klipheuvel 435, 30°39'43S 17°38'45E, 15.viii.1996, Harrison & Scholtz, site 52, sand plain Fynbos, red sand, (1♂ 1p SANC); De Klipheuvel 435, 30°38'47S 17°37'40E, 15.viii.1996, Harrison & Scholtz, site 53, red sand, (12♀ 2♂ SMWN); Soutfontein, 435, 30°36'54S 17°35'41E, 15.viii.1996, Harrison & Scholtz, site 54, Bitter River Bed, (1♂ SANC); Strand Fontein 499, 30°31'13S 17°31'30E, 15.viii.1996, Harrison & Scholtz, site 57, red sand, (2♀ 1♂ BMSA); Sand Kop 322, 29°39'55S 17°10'34E, 19.viii.1996, site 62/113, vegetated dune, red sand, (1♂ BMSA); Avontuur 488, nr. Hondeklipbaai, 30°20'11S 17°21'27E, 27.viii.1996, site 68, vegetated dunes, yellow sand, (1p SANC); Strand Fontein 499, Klipheuwel House, 30°34'08S 17°27'21E, 28.viii.1996, site 69, (1♀ SANC); Strand Fontein 499, Bitter R. Dunes, 30°33'01S 17°26'21E, 28.viii.1996, site 71, interdune slack, white/red sand, (1♀ 1♂ UPSA); Strand Fontein 499, Bitter R. Dunes, 30°33'37S 17°26'14E, 28.viii.1996, site 72, interdune slack, white/red sand, (2♂ MNHN); Strand Fontein 499, Bitter R. Dunes, 30°32'28S 17°26'18E, 29.viii.1996, site 75, interdune slack, white/red sand, (4♀ 8♂ SAMC), (4p SANC); Strand Fontein 499, Bitter R. Dunes, 30°32'S 17°26'E, 29.viii.1996, site 77, dune slope, firm white sand, (1♀ BMNH); Driekop 500, 30°36'34S 17°27'41E, 30.viii.1996, site 78, vegetated old dune, yellow sand, (3p SANC); Driekop 500, 30°35'29S 17°31'03E, 30.viii.1996, site 79, vegetated old dune, yellow sand, (1p SANC); Driekop 500, 30°35'09S 17°31'06E, 30.viii.1996, site 80, Bitter River Bank, yellow sand, (5p SANC); Sandkraal exit gate, Soutfontein to Baievlei Rd., 30.viii.1996, site 81,yellow sand, (1p SANC); Zand Kraal 434, 30°33'S 17°45'E, 3.ix.1996, site 83, Bruinkop, yellow firm sand, (1♂ SANC); Strand Fontein 499, 30°32'42S 17°30'30E, 4.ix.1996, site 87, yellow sand, undulating plain, (1♂ SANC); Kleinsee, Sand Kop 322, 29°39'55S 17°10'34E, 28-30.x.1996, Harrison & Scholtz, site 113, vegetated dune, red sand, (10♀ 55♂ 6p UPSA); Kleinsee, Sand Kop 322, 29°40'16S 17°08'05E, 28.x.1996, Harrison & Scholtz, site 114, firm yellow, sand plain, (6♂ SAMC), (2p SANC); Stryd Rivier 188, 29°34'09S 17°17'00E, 31.x.-1.xi.1996, Harrison & Scholtz, site 115, red sand & gravel, (3♀ 2♂ SANC); *idem*, but 9.x.1997, Harrison & Davis, (1x UPSA); Stryd Rivier 188, 29°32'52S 17°14'57E, 9.xi.1996, site 119, vegetated dune, red sand, (6eth. TMSA); Stryd Rivier 188, 29°31'29S 17°14'23E, 9.xi.1996, site 120, vegetated dune & blowout, red sand, (1♀ 4♂ SMWN); Kourootje 316, near Komaggas, 29°46'44S 17°22'22E, 10.xi.1996, site 121, Sandplain Fynbos, vegt. dune Y/R sand, (1♂ 16eth. TMSA); Rooivlei 327, near Kleinsee, 29°48'58S 17°08'31E, 19.xi.1996, site 124, vegetated dune, yellow sand, (2♂ BMSA); Zonnekwa 328, near Kleinsee, 29°50'48S 17°13'08E, 20.xi.1996, site 126, large vegt. dune, yellow sand, (1♀ 2♂ BMNH); Zonnekwa 328, near Kleinsee, 29°50'56S 17°13'23E, 20.xi.1996, site 127, vegetated dune, yellow sand, (1p SANC); Zonnekwa 328, near Kleinsee, 29°51'08S 17°13'59E, 20.xi.1996, site 128, interdune slack, firm W/R sand, (3♀ 8♂ BMSA); Samsons Bak 330, near Kleinsee, 29°54'38S 17°13'47E, 20.xi.1996, site 129, interdune slack, firm W/R sand; (1♀ SANC); Samsons Bak 330, near Kleinsee, 29°55'22S 17°13'34E, 20.xi.1996, site 130, firm yellow sand, near vegt. dune, (2♀ SAMC); Elands Klip 333, near Kleinsee, 29°56'40S 17°13'46E, 21.xi.1996, site 131, soft yellow sand, (1♀ SAMC); Heidons 335, near Kleinsee, 29°58'44S 17°16'31E, 21.xi.1996, site 132, plain behind dunes, yellow sand, (10♀ 4♂ UPSA) (14eth. TMSA); Heidons 335, near Kleinsee, 29°59'45S 17°17'21E, 21.xi.1996, site 133, plain behind dunes, yellow sand, (1♀ 1♂ 1p SANC); Heidons 335, near Kleinsee, 30°01'16S 17°17'50E, 21.xi.1996, site 134, plain behind dunes, yellow sand, (2♀ BMNH); Heidons 335, near Kleinsee, 30°02'47S 17°17'42E, 21.xi.1996, site 135, plain behind dunes, yellow sand, (1♀ 2♂ SANC); Heidons 335, Heidons, 30°03'58S 17°17'35E, 21.xi.1996, site 136, vegetated dune, yellow sand, (1♀ 1♂ SAMC); Zoutpan 471, near Koingnaas, 30°05'51S 17°19'05E, 21.xi.1996, site 137, Sandplain Fynbos, yellow sand, near vegt. dune, (1♂ BMSA); Zoutpan 471, near Koingnaas, 30°06'35S 17°20'12E, 21.xi.1996, site 138, red sand plain, (2♂ SANC); Koingnaas 475, 30°13'20S 17°18'46E, 22.xi.1996, site 141, Swartlintjies R. Bank, yellow sand, (1♂ 6x eth. TMSA); Zwart Lintjes R. 484, nr. Koingnaas, 30°15'41S 17°19'11E, 22.xi.1996, site 142, yellow sand, (3♀ SMWN); Zwart Lintjes R. 484, nr. Koingnaas, 30°16'59S 17°19'23E, 22.xi.1996, site 143, coastal plain nr. Y. vegt. D., biocrust, (1♀ SANC); Avontuur 488, nr. Hondeklipbaai, 30°19'50S 17°19'57E, 22.xi.1996, site 144, coastal plain nr. Yellow Vegt. Dunes, (1♀ 1♂ MNHN); Avontuur 488, nr. Hondeklipbaai, 30°20'03S 17°21'03E, 22.xi.1996, site 145, vegetated dune, yellow sand, (1♀ 3♂ ZMHB); Avontuur 488, nr. Hondeklipbaai, 30°20'18S 17°21'53E, 22.xi.1996, site 146, vegetated dune, yellow sand, (1♀ 2♂ SANC); Avontuur 488, nr. Wallekraal, 30°23'49S 17°25'21E, 22.xi.1996, site 147, firm red sand, (8♂ BMNH); Kanoep 491, nr. Swartfontein, 30°24'47S 17°25'03E, 22.xi.1996, site 148, firm red sand, (1♂ 1p SANC); Kanoep 491, nr. Swartfontein, 30°26'00S 17°25'10E, 22.xi.1996, site 149, yellow/red sand, (1♂ BMSA); Kanoep 491, nr. Swartfontein, 30°26'41S 17°25'41E, 22.xi.1996, site 150, Spoeg R. Bed, white sand banks, (2♀ 2♂ SMWN); Kanoep 491, near Swartfontein, 30°28'22S 17°26'37E, 23-24.xi.1996, site 151, Bitter R. Dunes, dune periphery, white sand, (18p SANC); Kanoep 491, near Swartfontein, 30°28'14S 17°26'23E, 23-24.xi.1996, site 151a, Bitter R. Dunes, interdune slack, white/red sand, (2♀ 11♂ BMNH), (3♀ 11♂ SANC); Strand Fontein 499, Bitter R. Dunes S., 30°32'19S 17°26'29E, 26.xi.1996, site 154, interdune slack, red/white sand, (4♀ 5♂ BMNH); Strand Fontein 499, Bitter R. Dunes S., 30°33'57S 17°26'37E, 26-27.xi.1996, site 155, dune periphery, soft white sand, (1♀ 1♂ BMNH); Strand Fontein 499, Bitter R. dunes S., 30°35'20S 17°26'44E, 1.xii.1996, site 156, dune periphery, white sand, (1♀ ZMHB); Driekop 500, 30°36'28S 17°27'53E, 1.xii.1996, site 157, coastal plain, yellow sand, (1♀ 1♂ ZMNB); Driekop 500, 30°36'15S 17°28'26E, 1.xii.1996, site 158, coastal plain, yellow sand, (8♀ 2♂ SANC); Driekop 500, 30°35'54S 17°29'16E, 1.xii.1996, site 159, vegetated dune, yellow sand, (1♀ 2♂ BMSA); De Klipheuvel 435, 30°35'S 17°33'E, 1.xii.1996, site 160, sand, (1♂ SMWN); De Klipheuvel 435, near Soutfontein, 30°38'43S 17°35'33E, 1.xii.1996, site 161, Sandplain Fynbos, yellow sand near vegetated dunes, (1♀ 1♂ SAMC); De Klipheuvel 435, near Soutfontein, 30°40'25S 17°34'55E, 1.xii.1996, site 162, Sandplain Fynbos, yellow sand near vegetated dunes, (5♂ UPSA); Kwaas 501, 30°42'38S 17°34'36E, 1.xii.1996, site 164, Sandplain Fynbos, yellow sand, (2♂ SANC); Kwaas 501, 30°43'29S 17°34'21E, 1.xii.1996, site 165, Sandplain Fynbos, yellow sand, (4♂ TMSA); Klip Kuil 547, near Groenrivier, 30°46'04S 17°34'59E, 1.xii.1996, site 166, yellow sand, (2♂ TMSA); Groen River, Roode Heuvel 502, 30°45'24S 17°38'24E, 4.xii.1996, site 168, Groen

River Bank, red sand, (1♂ SANC); Rondabel 542, 30°47'59S 17°46'39E, 4.xii.1996, site 169, Groen River Bank, red sand, (2♀ 2♂ SANC); Rondabel 542, 30°49'01S 17°46'07E, 4.xii.1996, site 170a, firm red sand, (3♂ 4p SANC); Branduin 543, 30°49'51S 17°45'36E, 4.xii.1996, site 171, dead in mud, firm red sand, (3♀ 1♂ BMSA), (11p SANC); De Dam 541, 30°51'14S 17°45'13E, 4.xii.1996, site 172, red sand plain, (1♀ 4♂ SAMC); De Dam 541, 30°52'06S 17°45'24E, 4.xii.1996, site 173, dead in mud, firm yellow sand, (3♀ 6♂ BMNH), (3♀ 4♂ SMWN), (10p SANC); De Witflacte 551, near Hardevlei, 30°52'50S 17°45'50E, 4.xii.1996, site 174, vegetated dune, firm/soft yellow sand, (2♀ 5♂ UPSA) (11p SANC); Varsfontein 554, near Kotzesrus, 30°56'57S 17°50'04E, 5.xii.1996, site 175, Brak River Bank, red/yellow sand, (1♀ 1♂ 1p SANC); Wit Water 557, near Kotzesrus, 31°01'03S 17°47'04E, 5.xii.1996, site 176, Brak River Bank, firm sand, (1♀ SAMC); Wit Water 557, near Kotzesrus, 31°01'18S 17°46'33E, 5.xii.1996, site 177, Brak River, yellow sand bank, (2♂ 9p SANC); Strandfontein 559, near Waterval, 31°01'46S 17°45'44E, 5.xii.1996, site 178, Brak River Bank, (1♂ BMNH); Wit Water 557, near Rooidam, 31°02'29S 17°46'46E, 5.xii.1996, site 179, vegetated dune, yellow sand, (1♀4♂ 8p SANC); Strandfontein 559, near Waterval, 31°03'15S 17°45'07E, 5.xii.1996, site 180, Brak River Bank, red sand, (2♂ TMSA); Tities Baai 560, near Brak R. mouth, 31°06'54S 17°44'28E, 5.xii.1996, site 181, firm yellow sand, near sea, (2♀ 3♂ BMNH); **S.Afr: Vredendal District**, Graafwater, Farm 156, 31°22'12S 17°59'54E, 6.xii.1996, site 185, red sand plain, (2♂ SANC); Graafwater, Farm 156, 31°22'38S 18°01'23E, 6.xii.1996, site 186, firm Y. sand plain, nr. vegt. dunes, (2♀ 1♂ SANC); Elsie Erasmus Kloof 158, 31°24'46S 18°02'30E, 7-8.xii.1996, site 188, vegt. 'old' dune, yellow sand, (1♀ 9♂ SANC); Elsie Erasmus Kloof 158, Skaapvlei, 31°28'47S 18°04'08E, 8.xii.1996 site 190, firm red sand, (1♂ SANC); Kommandokraal, on Farm 624, near Koekenaap, 31°29'02S 18°10'08E, 10.xii.1996, site 193, vegetated dune, yellow sand, (8♀ 1♂ SANC); **S.Afr: Namaqualand**, Kourootje 316, nr. Komaggas, 29.46.51S 17.22.55E, 9.x.1997, Harrison & Davis, site 220, vegetated dune, yellow sand, (1p UPSA), Koingnaas 475, 30.11.45S 17.18.17E, 10.x.1997, Harrison & Davis, site 221, (1x UPSA).

Specimens from the following localities may be incorrectly labelled because they are outside the species' established range: **SOUTH AFRICA**: **Anenous**, (Anenous Pass, Steinkopf), (29°14'S 17°40'E), 25.ix.(19)25, leg. name?, donation Natal Museum, NM 9025, (1♀ 3♂ BMSA); **Garies**, (30°30'S 18°00'E), Namaland, Schlechler, (1♂ SANC).

Scarabaeus (Pachysoma) gariepinus (Ferreira, 1953)

(Figures 7, 23, 41, 62)

Pachysoma gariepinus Ferreira, 1953a: 23; Ferreira 1961: 24; Ferreira, 1969: 21; Holm and Scholtz, 1979: 231. Holotype: Namaqualand, Holgat. (1♂ TMSA).

Scarabaeus gariepinus (Ferreira): Mostert and Holm, 1982: 275.

Diagnosis. Clypeus bidentate, but vestigeal outer clypeal teeth sometimes present; genal and clypeal edges serrate (figure 23); protibia not dimorphic with simple protibial spurs (figure 41); band of indument on elytral and pronotal outer edges; metatarsal claws shorter than last tarsal segment; genitalia illustrated in figures 62a,b.

Distribution, habitat and conservation. S. (P.) gariepinus is distributed on either side of the Orange River (figure 7). The southern most extent of *S. (P.) gariepinus* distribution in South Africa coincides with the Buffels River (29°33'S 17°24'E), while *S. (P.) gariepinus* occurs to Agub Mountain (26°59'S 15°58'E) in Namibia. The preferred habitat of *S. (P.) gariepinus* is firm consolidated sand of dunes, river banks and inland flats. No specimens were collected (by JDUGH) from dunes south of the Orange River, but only from inland sandy flats, river banks and the bases of sandblown outcrops. North of the Orange River *S. (P.) gariepinus* appears to have a closer association with dunes. Northern populations of *S. (P.) gariepinus* occur within the Namib-Naukluft Park.

Comments on locality data. Specimens from Brandvlei, Kakamas, and the Groen River Mouth all occur outside the established distribution range of *S. (P.) gariepinus*, and are probably incorrectly labelled specimens. However, the Kakamas record could be evidence that *S. (P.) gariepinus* can move inland along the Orange River.

Morphological variation. The following attributes of *S. (P.) gariepinus* vary within and between localities: size; elytral sculpture; indument; and size of the mesipisternal protuberance. The Namaqualand populations (south of Orange River) are characterised by smaller body size and red indument, while the Namibian populations are generally larger in body size with their indument stained white to grey. Specimens' from Rosh Pinah (27°53'S 16°50'E) have very white indument and smooth elytra lacking distinct interstriae and granules. However, their genitalia conform to the typical *S. (P.) gariepinus* form.

A distinct mesepisternal protuberance (MEP), previously not mentioned by other authors, was noticed in specimens of *S. (P.) gariepinus* from Namibia. To determine if the MEP differentiated *S. (P.) gariepinus* into one species on either side of the Orange River it was examined in all available material. The MEP varies within and between populations and sexes. It appears larger in males and especially large males while smaller in females. It varies from virtually no expression in the Namaqualand populations to being well defined in the Namibian populations. For example, it is slightly expressed in some males but no females in populations close to the Buffels River, (e.g. Wolfberg). It becomes markedly more defined in *S. (P.) gariepinus* populations near Port Nolloth, while Hohenfels (Namibia) populations have it well expressed. The MEP clearly suggests a cline from south to north and supports the variation seen within *S. (P.) gariepinus* as attributable to one species. Further support for the continuity of the Namaqualand and Namibian populations is provided by male genitalia and elytral sculpture.

Biology. Holm and Scholtz (1979) observed *S. (P.) gariepinus* collecting *Oryx gazella* pellets that they dragged forward one at a time to their burrows. Mostert and Holm (1982) reported that 'When fresh horse droppings were presented to *Scarabaeus gariepinus* specimens in their natural surroundings, they would cut out a ball about 20 mm in diameter and roll it backwards in the same way as do the fully winged *Scarabaeus* species'. This exact experiment was repeated in Namaqualand but *S. (P.) gariepinus* only showed interest in the horse dung when it was dry. Only then would they break off a small piece of dry dung using their protibia and clypeus and drag it with their hind legs to their preconstructed burrow. Of the 17 nests excavated by JDUGH; nine contained only dry dung pellets; three contained only detritus; while five contained both pellets and detritus. This suggests that *S. (P.) gariepinus* is predominately a dry pellet feeder.

S. (P.) gariepinus were successfully bred in captivity and three larvae were obtained. Larval observations and comments concur with *S. (P.) striatus* above.

Comments. S. (P.) gariepinus superficially resemble *S. (P.) striatus* females, but the two species are easily separated as *S. (P.) striatus* has a hook on the posterior lateral pronotal edge that is absent in *S. (P.) gariepinus*.

Types. Ferreira (1953a), designated a holotype (♂), allotype (♀) and 55 unsexed paratypes in her description of *Pachysoma gariepinum*. These types were deposited as follows: holotype, allotype and 51 paratypes in the TMSA collection; three paratypes in the UPSA collection; and one paratype in the CPMM collection. The three UPSA paratypes have subsequently been deposited in the TMSA, while no material from the CPMM collection in Mozambique was borrowed by Holm and Scholtz (1979) or in this revision. Holm and Scholtz (1979) noted that the holotype and most of the paratypes could be traced in the TMSA collection, although not labelled as such. Fortunately, Ferreira (1953a) listed the respective numbers of specimens from each locality, except the Holgat locality. However, via subtraction twelve paratypes were from Holgat. The allotype was not labelled, and since there are ten females from Holgat it becomes untraceable.

To add to the confusion of the type series, two separate series from Holgat dated 23.xi.(19)48 and 2.ix.1950 exist. Only the 1948 date is recorded in Ferreira's (1953a) description, although some of the specimens from 1950 also bear Ferreira's paratype labels. As these specimens (i.e. Holgat 1950) were not published as types, they are invalid. I have taken the opportunity of having all available type material together to label traced paratypes. These labels are printed on yellow card copying Ferreira's format and spelling verbatim. None of Ferreira's (1953a) original labels were removed. Thus, of the original 55 paratypes, 46 are traced and labelled as such.

Type material examined (Σ47 spec. [50], 20♀ 28♂, 14♂ diss.). **SOUTH AFRICA**: HOLOTYPE ♂, *Pachysoma gariepinus* Ferreira: Holgat, (28.56S 16.47E), NW C.P., 23.xi.(19)48, Koch & V. Son, / Tipo *Pachysoma gariepinus* 1951 M.C.Ferreira (written in red ink on white rectangular card with a black frame), (1♂ TMSA), (Allotype not marked, therefore untraceable). PARATYPES: *idem*, (10♀ 3♂ TMSA); Anenous, (29.14S 17.40E), 15.xi.1933, G. v. Son, (9♂ TMSA), *idem*, but / VII, 950 /, (1♂ TMSA); Brandkaross, (written in pencil, possibly from Gaerdes collection), (28.28S 16.40E), (1♀ 1♂ TMSA), *idem*, but / NMBH3685 / 203 /, (1♂ BMSA); 12m S of Grootderm, (*ca.* 28.37.05S 16.37.05E), (Groot Derm 10), 11.ix.1950, G.van Son, C.Koch, (1♀ TMSA); Oograbies, (29.13S 17.08E), L. Namaquald., 30.viii.(19)50, C.Koch, G. van Son, (3♀

5♂ TMSA); Oograbies, (29.13S 17.08E), (written in black ink), (1♀ 1♂ TMSA); Ograbies, (29.13S 17.08E), (written in black ink), (1♂ TMSA); Pt Nolloth, (29.17S 16.51E), Warden, S. / *Pachysoma gariepinus* Fer. 1951, M.C.Ferreira (written on white paper in black ink, black border around rectangle), (1♀ TMSA); Pt. Nolloth. C.C., (29.17S 16.51E), R.M.Lightfoot, Pt. Nolloth. C.C. / *Pachysoma marginatum* / *Pachysoma gariepinus* Fer. 1951, M.C.Ferreira (written on white paper in black ink, black border around rectangle), (1♀ TMSA); Pt Nolloth, (29.17S 16.51E), 1885, (1♀ SAMC). NAMIBIA: Namib, sens. Eberlanz, (1♀ 2♂ TMSA); *idem*, but Eberelanz (1♂ TMSA); Oranjemund, SWA, (28.33S 16.37E), 21. 6 or 8.(19)42, (1♂ TMSA).

Additional material examined (Σ453 specs. [16], 188♀ 235♂, 11♂ diss., 13uns., 17eth., 20p.). **SOUTH AFRICA**: Northern Cape; Namaqualand, **Brandkaross**, (28.28S 16.40E), v.1953, Dr. C.Koch, NMBH 3685, (1♂ BMSA); Brandkaross, Richtersveld, (28.28S 16.40E), 9.ix.(19)50, C.Koch, G.van Son, (Not published paratype, see Ferreira 1953 pub. and specimens totals, acc: J.Harrison 1999), (1♂ TMSA); Richtersveld, Brandkaross Farm, 28.30S 16.39E, 24.viii.1989, E-Y:2667, sandblown hill, night, Endrödy & Klimaszew., (1♀ TMSA); Richtersveld, Brandkaross, 3km SE, 28.30S 16.42E, 30.ix.1991, E-Y:2815, sandy valley, hand-collected, Endrödy-Younga, (2♀ 8♂ TMSA); Richtersveld, Brandkaross, Oranje, 3km SW, 28.30S 16.39E, 4.viii.1989, E-Y:2629, sandblown hill, day, Endrödy & Klimaszew., (3♂ TMSA); Richtersveld, Brandkaross, Oranje, 3km SW, 28.30S 16.39E , 2.viii.1989, E-Y:2625, sandy hill, night, Endrödy & Klimaszew., (1♂ TMSA); **Buffels River Valley**, 29.35S 17.17E, 3.x.1976, hand-collected, Endrödy-Younga, E-Y:1252, (1♀ TMSA); **Grasvlakte**, 28.56S 17.02E, 8.ix.1987, red dunes day, Endrödy-Younga, E-Y:2483, (1♀ TMSA); **Grootmis**, 20km E, (*ca.* 29.37.05S 17.07.05E), 4.x.1972, H.D.Brown, E.Koster, A.Prinsloo, (2♀ 5♂ SANC); **Holgat**, (28.56S 16.47E), L. Namaquald., 2.ix.1950, C.Koch, G.van Son, (Not published paratype, see Ferreira 1953 pub. and specimens totals, acc: J.Harrison 1999), (6♀ 3♂ TMSA); Holgat, 18km E, 28.56S 16.58E, 5.ix.1987, red dunes, day, Endrödy-Younga, E-Y:2476, (1♂ TMSA); **Jakkalsputs**, SE2816Db, (28.37.05S 16.52.05E), 19,21.xi.1975, H31996, (3♀ 3♂ SMWN); Jakkalsputs, 28.42S 16.54E, 350m, 15-16.ix.1985, A.V.Evans, C.L.Bellamy, (5♀ 5♂ UPSA); Jakkalsputs, 28.38S 16.54E, (16.54E and not 18.54E as on label), 9-11.ix.1982, S.Louw, NMBH 8473, (2♀ 2♂ BMSA); **Port Nolloth**, (29.17S 16.51E), 1885, (1♀ SAMC); Port Nolloth, 36mls E, (*ca.* 29.15S 17.32E at base of Anenous pass), viii.1925, O.Hughes, 1791, Donation Natal Museum, NMBH 9025, (2♀ BMSA); Port Nolloth, 22-23km SE, 29.19S 17.06E, 150m, 15.ix.1984, C.L.Bellamy, (1x UPSA); Port Nolloth, 22km E, (*ca.* 29.18S 17.12E), 31.viii.1986, A.V.Evans, (5♀ 9♂ UPSA); **Steenbok** 165, nr. Sononderberg, 29.22S 17.10E, 250m, 1.ix.1986, A.Evans, C. Bellamy, (2♂ UPSA); **Witpütz**, (Witputs 27.36S 16.41E), 21.2.(19)63 / Gaerdes (typed) / H25895 / (1♂ SMWN); **Wolfberg**, (probably *ca.* 29.37S 17.25E), Cape, ix.1989, C.R.Owen, (3x COCS), (2♀ 3♂ DNSM).

Specimens collected by J.duG.Harrison in chronological order: **S.Afr: Namaqualand, Stryd Rivier** 188, 29°34'28S 17°16'49E, 24.vii.1996, J.duG.Harrison, site 15, firm red sand, Buffels River, (2p SANC); **Dikgat** 195, 29°34'46S 17°14'04E, 26.vii.1996, J.duG.Harrison, site

18, red sand, Buffels River, (1♀ SAMC); Stryd Rivier 188, 29°34'09S 17°17'00E, 9.viii.1996, Harrison & Scholtz, site 35, firm red sand plain, (1♀ SAMC); **Wolfberg** 187, 29°32'17S 17°23'23E, 25.viii.1996, J.duG.Harrison, site 63, Buffels R. Bank, coarse sand, (1♀ SAMC); **Gemsbok Vlei** 158, 29°19'14S 17°10'46E, 25.viii.1996, J.duG.Harrison, site 65, flat red sand plain, (4eth. TMSA), (15p SANC); **Drooge Kraal** 180, 29°27'S 17°17'E, 5.ix.1996, J.duG.Harrison, site 88, red sand plain, (1♀ TMSA); Drooge Kraal 180, 29°27'21S 17°15'23E, 5.ix.1996, J.duG.Harrison, site 89, red sand plain, (2♂ TMSA); near Beauvallon, **Groot Derm 10**, 28°31'12S 16°39'49E, 25.x.1996, J.duG.Harrison, site 105, 'waaisand', (1♀ TMSA); **Farm 600, Holgat R.**, 28°41'26S 16°57'43E, 26.x.1996, J.duG.Harrison, site 107, coarse red sand, (3♀ 2♂ BMNH), (3♀ 2♂ ZMHB), (3♀ 2♂ SMWN), (13eth. TMSA), (2p SANC); Farm 600, Holgat R., 28°41'42S 16°57'29E, 26.x.1996, J.duG.Harrison, site 107a, coarse red sand, (1♀ TMSA); Farm 600, Holgat R., 28°41'36S 16°57'02E, 26.x.1996, J.duG.Harrison, site 108, vegetated dunes, red sand, (2♀ 3♂ SAMC); **Farm 600, Kuboes to Lekkersing road**, 28°43'26S 16°59'50E, 26.x.1996, J.duG.Harrison, site 109, vegetated red sand, (1♀ SANC); Farm 600, Kuboes to Lekkersing road, 28°52'47S 17°00'53E, 26.x.1996, J.duG.Harrison, site 110, vegt. loam near yellow sand rise, (2♀ 1♂ SANC); **Farm 600, Geel Pan**, 28°53'06S 17°00'54E, 26.x.1996, J.duG.Harrison, site 111, vegetated red sand, (1♂ SANC); Farm 600, Bakenskop, 28°57'11S 17°01'59E, 26.x.1996, J.duG.Harrison, site 112, vegetated dune, red sand, (1♀ 1♂ SANC); Stryd Rivier 188, 29°34'09S 17°17'00E, 31.x.-1.xi.1996, Harrison & Scholtz, site 115, red sand & gravel, (19♀ 11♂ UPSA), (1p SANC); **Bontekoe 197**, 29°33'34S 17°19'44E, 4.xi.1996, J.duG.Harrison, site 116, Buffels R. Valley, coarse river sand, (2♀ 2♂ SANC); **Staan Hoek 198**, 29°31'34S 17°22'09E, 9.xi.1996, J.duG.Harrison, site 118, Buffels R. Valley, red river sand, (1♀ 1♂ SANC); **Nuttabooi 199**, Langhoogte to Komaggas Rd., 29°33'47S 17°24'25E, 9.x.1997, Harrison & Davis, site 219, Buffels R. Valley, red river sand, (1x UPSA).

NAMIBIA: Agub Mt., 26.59S 15.58E, Diamond Area 1, 12-13.viii.1983, J.Irish, E.Griffin, H56627, (2♂ SMWN); 22mls W Udabib, **Aurusberg W**, (27.39S 16.19E), 20.xi.1962, H.D.Brown, W.Fürst, (1♂ TMSA) (Udabib: cannot trace); Aurusberge, (=Aurus Mts.), Diamond Area 1, (27.39S 16.19E), 22.x.1974, H.D.Brown, (1♂ SANC); Aurus Dunes nr. Aurusvlei, 27.40S 16.12E, 23.iv.1988, R.Oberprieler, (3♀ 6♂ SANC); **Bogenfels**, 20km E, 27.35S 15.35E, 25.vii.1981, sandy gravelly flat, Endrödy-Younga, E-Y:1799, (1♀ TMSA); **Chamias**, 45km S, SE2816Aa, (28.07.05S 16.07.05E), vii.1978, Izak Bruwer, UP, (1♂ SANC); **Daberas Dunes**, (28.13S 16.45E), Gt. Namaqualand, v.1953, C.Koch, (2♂ TMSA); **Diamond Area 1**, 27.52S 16.30E, 17.viii.1983, J.Irish, E.Griffin, H56715, (1♂ SMWN); Diamond Area 1 at 28.02S 15.52E, 16-29.ix.1994, E.Marais, Pres. pitf. traps (2♀ 2♂ SMWN); **Hohenfels** 15mls E Oranjemund, (*ca.* 28.37.05S 16.37.05E), 19.xi.1962, H.D.Brown & W.Fürst, (3♀ 1♂ TMSA); Hohenfels, 28.30.05S 16.37.00E, 01-07.xi.1994, Scholtz, Chown & Klok, (15♀ 26♂ UPSA), (5x BMNH), (2♀ 2♂ ZMHB); **Kegelberg**, Diamond Area 1, 27.37S 16.23E, 27.ix.1994, E.Marais, (3♀ SMWN); **Klinghardtberge**, Spitzkuppe Süd, Diamond Area 1, (27.20S 15.45E), 9.x.1974, H.D.Brown, (1♀ 7♂ SANC); Klinghardtberge, 10km SE, SE2715Bd3, (27.22.05S 15.52.05E), vii.1982, E.Holm, (1♂ TMSA), (1♀ 5♂ UPSA); SE of Klinghardtberge, SE2715Db2, (27.37.05S

15.52.05E), vii.1982, E.Holm, (1x TMSA); NE of Klinghardtberge, SE2715Bb2, (27.07.05S 15.52.05E), i.1983, E.Holm, (2♀ TMSA); Klinghardt Mt., (27.20S 15.45E), 22.x.1977, V.B.Whitehead, (2♂ SAMC); Klinghardt Mt., (27.20S 15.45E), 1977, J.Boomker, (1♀ 1♂ TMSA), (1♀ SANC); Klinghardt Mts., at 27.20S 15.45E, Diamond Area 1, 3-6.ix.1980, S.Louw, M-L.Penrith, H42441, (5♀ 4♂ SMWN); Klinghardt Mt., 27.18S 15.41E, Diamond Area 1, 29-30.vii.1981, M-L.Penrith, H43463, (1♀ SMWN); Klinghardt Mt., 27.18S 15.42E, 29.vii.1981, sandy valley, day, Endrödy-Younga, E-Y:1808, (2♀ 2♂ TMSA); Klinghardt Mt., at 27.21S 15.42E, Diamond Area 1, 2-4.x.1982, M-L. Penrith, J.Irish, H54956, (2♀ 10♂ SMWN); Klinghardt Mt., W at 27.24S 15.38E, Diamond Area 1, 1-4.x.1982, M-L.Penrith, J.Irish, H54886, (1♂ SMWN); Klinghardt Mt., 27.18S 15.42E, 21.viii.1989, sandy ground, day, Endrödy & Klimaszew., E-Y:2659, (9♀ 11♂ TMSA); Klinghardt Mt., 27.18S 15.42E, 21.viii.1989, ground traps 3 days, Endrödy & Klimaszew., E-Y:2677b, (1♂ TMSA); **Mac Millian's Pass**, 9mls NE Rosh Pinah, (*ca.* 27.51S 16.52E), 24.ix.1968, H.D.Brown, (1♂ TMSA); **Manganese Mine**, Richtersveld, 28.40S 16.48E, 10.x.1976, hand-collected, Endrödy-Younga , E-Y:1270, (1♀ 1♂ TMSA); **Namaskluft 88**, Lüderitz at 27.55S 16.53E, 31.viii.1989, S.Louw, ex Mesems, NMBH28069, (1♂ BMSA); **Nieu-Tsaus**, Lüderitz District, 26.59S 16.16E, 16.viii.1990, E.Marais, C.Roberts, (1♀ SMWN); **Obib Dunes**, 28.00S 16.39E, 17.ix.1973, hand-collected, dune, night, Endrödy-Younga, E-Y:116, (1♂ TMSA); Obib Dunes, 28.00S 16.39E, 18.ix.1973, on dunes, diurnal, Endrödy-Younga, E-Y:117, (7♀ 3♂ TMSA); Obib Mt. Camp, 27.59S 16.33E, 19.ix.1973, on flowers, Endrödy-Younga, E-Y:123, (2♀ 4♂ TMSA); Obib Dunes, 28.11S 16.36E, 20.ix.1973, faeces trap, day, Endrödy-Younga, E-Y:128, (6♀ 3♂ TMSA); Obib Dunes, 28.11S 16.36E, 20.ix.1973, around camp, Endrödy-Younga, E-Y:129, (1♀ TMSA); Obib Dunes E at 28.02S 16.37E, Lüderitz, 16-20.ix.1973, H14397, (1♀ SMWN); Obib Mts/Dunes, SE2816Ba, (28.07.05S 16.37.05E), Diamond Area 1, 28-30.x.1977, Coll. S.Louw, M-L.Penrith, H35117, (2♀ 2♂ SMWN); Obib Dunes, West edge, (*ca.* 28.06S 16.15E), 8.ix.1980, on dunes, Whitehead, (2♂ SAMC); Obib Dunes, Lüderitz at 27.59S 16.37E, 3.ix.1991, R.Archer, NMBH28116, (3♀ 5♂ BMSA), *idem*, but Obibwasser (1♂ BMSA); **Oranjemund**, 10km NE, Lüderitz, SE2816Da, (*ca.* 28.37.05S 16.37.05E), 19.ix.1973, H14546, (1x SMWN); Oranjemund, 10km N, (*ca.* 28.22.05S 16.22.05E), vii.1978, E.Holm, (2♂ SANC); Oranjemund, SE2816Cb, (28.37.05S 16.22.05E), vii.1979, J.A.Irish, UP, (1♀ SANC); NE of Oranjemund, SE2816Cb2, (28.37.05S 16.22.05E), vii.1982, E.Holm, (2♀ 1♂ TMSA), (1♂ UPSA); Oranjemund, 28.32S 16.37E, 28.vii.1981, sandy hills, day, Endrödy-Younga , E-Y:1805, (4♀ 1♂ TMSA); Oranjemund, 28.33S 16.37E, Diamond Area 1, 27-28.vii.1981, M-L.Penrith, H43524, (1♂ SMWN); Oranjemund, (28.33S 16.37E), i.1991, N.Larsen, (1♂ SAMC); Oranjemund, Diamond Area 1, 28.34S 16.27E, 15.ix.1994, E.Marais, dung traps, (6♀ 2♂ SMWN); **Rechtersveld**,.(ambiguous), SWA, 1922, G.E. Smith, 1799, Donation Natal Museum, NMBH9025, (2♀ BMSA); **Rosh Pinah**, 22mls N, (*ca.* 27.40S 16.42E), Lüderitz Dist., 21.ix.1968, H.D.Brown, (1♂ TMSA); Rosh Pinah, 27.53S 16.50E, 14.ix.1973, hand-collected on ground, Endrödy-Younga, E-Y:103, (1♀ TMSA); Rosh Pinah, 27.53S 16.50E, 15.ix.1973, E-Y:110, hand-collected around camp, Endrödy-Younga, (1♂ TMSA); Rosh Pinah, 28.04S 16.59E, 15.ix.1973, hand-collected, Endrödy-Younga, E-Y:110, (2♂ TMSA); Rosh Pinah, 27.53S 16.50E, 22.ix.1973, faeces traps, Endrödy-Younga, E-Y:139, (2♂ TMSA); Rosh Pinah, **Namaskluft**, (27.53S 16.50E), 17.xi.1975, SAM, V.B.Whitehead, (1♂ SAMC), *idem*, but 14.xi.1975, (1♀ SAMC); Rosh Pinah, Lüderitz, 27.56S 16.45E, 2.ix.1989, S.Louw, under plants, NMBH 27944, (2♂ BMSA); Rosh Pinah, (south of landing strip), Lüderitz, 27.57S 16.45E, 1.ix.1989, S.Louw, NMBH 31079, (1♂ BMSA); Rosh Pinah, 10km NW, Lüderitz District, 27.54S 16.42E, 13.viii.1990, C.Roberts, E.Marais, (1♀ 4♂ SMWN); Rosh Pinah, 2km ESE, Lüderitz District, 27.58S 16.47E, 13.viii.1990, E.Marais, C.Roberts, (1♂ SMWN); Rosh Pinah, 7.6km E, (*ca.* 27.58S 16.51E), 11.viii.1992, C.R.Owen, (1♀ COCS); **Roter Kamm**, 27.46S 16.18E, 24.iv.1988, R.Oberprieler, (1♀ 2♂ SANC); Roter Kamm, Diamond Area 1, Lüderitz District, 27.46S 16.18E, 25-30.vi.1989, C.S.Roberts, (2♀ 4♂ SMWN); **Sargdeckel**, Klinghardt Mts., SE2715Bc, (27.22.05S 15.37.05E), Diamond Area I, 22-25.x.1977, Coll. M-L. Penrith, S.Louw, H34992, (3♀ 2♂ SMWN); Sargdeckel, Klinghardt Mts., 27.24S 15.41E, Diamond Area I, 1-2.x.1982, M-L. Penrith, J.Irish, H54903, (3♀ 8♂ SMWN); **Skilpadberg**, Diamond Area 1, 28.27S 16.40E, 14.xi.1992, Huns Exp. '92, (1♀ SMWN); Skilpadberg, Diamond Area 1, 28.25S 16.39E, 18.ix.1994, E.Marais, at light, (1♀ SMWN); **Uguchab Riv.**, Diamond Area 1, 27.37S 16.10E, 14-15.viii.1983, J.Irish, E.Griffin, H56680, (2♀ 1♂ SMWN); Uguchab River nr. Aurusberg, 27.32S 16.11E, 22.iv.1988, R.Oberprieler, (1x SANC); Between **Zebrafontein & Obib**, (*ca.* 27.52.05S 16.52.05E), Gt. Namaquald., v.1953, C.Koch, (1♀ TMSA).

Specimens from the following localities may be incorrectly labelled because they are outside the species' established range: SOUTH AFRICA: **Brandvlei**, (30.13S 17.29E Brandvlei Farm), (30.28S 20.30E, Calvinia), (Brandsevlei, 29.525S 18.52E, Gamoep), viii.1937, (1♂ TMSA); **Groenrivermond**, (30.50S 17.36E), 30.x.1972, H.D.Brown, E.Koster, A.Prinsloo, (2♂ SANC); **Kakamas**, (28.52.05S 20.37.05E), 1992, R.O.C., (2♀ USSA).

Scarabaeus (Pachysoma) bennigseni (Felsche, 1907)

(Figures 8, 24, 42, 63)

Pachysoma bennigseni Felsche, 1907: 274; Péringuey, 1908: 556; Gillet, 1911a: 6; Ferreira, 1953a: 35; Ferreira 1961: 22; Ferreira, 1966: 59; Ferreira, 1969: 20; Holm and Scholtz, 1979: 235. [Holotype]: Orange River [1x SMTD].

Pachysoma granulatum Ferreira, 1953b: 2; Ferreira 1961: 23; Ferreira, 1966: 59; Ferreira, 1969: 20. Holotype: Namtib (1♂ TMSA).

Scarabaeus bennigseni (Felsche): Mostert and Holm, 1982: 275.

Diagnosis. Clypeus quadridentate, outer clypeal teeth reduced in size and deflexed outwards; genae serrated and discontinuous from clypeus (figure 24); protibia hardly sexually dimorphic, protibial spurs sinusoidal in males and straight in females (figure 42); small (length 23 mm; width 14.24 mm), black; elytra granular to smooth, markedly flat and deeply striate; metatarsal claws equal in length to last tarsal segment.

Distribution, habitat and conservation Coastal species occurring from just south of the Orange River (i.e. Holgat River mouth) to Spencer Bay north of Lüderitz (figure 8). The northern population is conserved within the Namib-Naukluft Park, but the central and southern populations occur within Diamond Area 1 and Alexkor mining property, respectively. Preferred habitats include coastal sand dunes and sand flats on unstable to compacted sand.

Comments on locality data. The Dassiefontein / Sneeukop locality record on the escarpment near Kamieskroon is very unlikely (figure 8). This locality falls well out of the confirmed range of *S. (P.) bennigseni* and is a record that is both further inland and at a higher elevation than expected for this coastal sand plain to sand dune species. The genitalia of this single male are typical of *S. (P.) bennigseni*.

Morphological variation. S. (P.) bennigseni occurs on both sides of the Orange River, which is a potential barrier between the two populations. Examination of external features and male genitalia reveals no evidence that these allopatric populations represent separate species. South of the Orange River *S. (P.) bennigseni* has smoother elytra and specimens are larger, while north of the river they are smaller but with well-defined elytral interstriae and distinct granular elytral sculpture. Within populations the elytral sculpture varies only slightly, unlike *S. (P.) gariepinus* and *S. (P.) striatus*. This minor morphological difference is clinal and consistent with that seen throughout *S. (Pachysoma)* species.

*Biology.*According to Holm and Scholtz (1979) foraging and tunnelling are very similar to *S. (P.) gariepinus*. A single nest was excavated by JDUGH at Jam Pan that contained a mixture of detritus and dung pellets. The larvae are unknown.

Comments. S. (P.) bennigseni superficially resembles *S. (P.) denticollis* (black form), but lacks dimorphic protibia.

*Types.*Although Felsche (1907) records only a single length (20 mm) in his description of *Pachysoma bennigseni* he lists two collections (Collection Felsche and Collection Bennigsen) in which material is deposited, which suggests more than a single type specimen. Holm and Scholtz (1979) examined the holotype from Oranjefluss (Orange River) in the SMTD collection.

Ferreira (1953b) described *Pachysoma granulatum* and subsequently (Ferreira 1966) synonymised it with *Pachysoma bennigseni*. Holm and Scholtz (1979) only mention the holotype, allotype and four paratypes for *P. granulatum*. The type series of *P. granulatum* comprised 29 specimens (Ferreira 1953b). Twenty-six types are in the TMSA collection, while the remaining three are reputed to be in the BMNH and CPMM collections. There are two sets of specimens from the type locality (i.e. Daberas dunes) which could create confusion in the future (see type and additional material examined). The type series (9♀ 17♂) is labelled with handwritten locality labels while the second series (9♀ 11♂) has printed labels.

Type material examined (Σ26 specs. [7], 9♀ 17♂, 1♂ diss.). **NAMIBIA**: HOLOTYPE ♂, *Pachysoma granulatum* Ferreira: S. Great Namaq., Daberas dunes, (28.13S 16.45E), v.1953, C.Koch (written on faded white card) / (male genitalia point mounted) / Holotype, *Pachysoma granulatum* ♂, M.C.Ferreira, 1953 (written on white card) / Holotypus, *Pachysoma granulatum*, M.C.Ferreira sp.n. (Endrödy-Younga label), (1♂ TMSA); Allotype ♀, *idem*, but / Alotype (sic) *Pachysoma granulatum* ♀, M.C.Ferreira, 1953 (written on white card) / Allotypus, *Pachysoma granulatum*, M.C.Ferreira sp. n. (Endrödy-Younga label), (1♀ TMSA). PARATYPES: *idem*, but Paratipo (red ink) *Pachysoma granulatum*, M.C.Ferreira (written on white card, all the paratypes are labelled by both Ferreira and Endrödy-Younga), (8♀ 16♂ TMSA); [2 BMNH]; {1 CPMM}.

Additional material examined (Σ137 specs. [24], 49♀ 87♂, 4♂ diss., 1uns.). **SOUTH AFRICA**: Northern Cape; Namaqualand, **Alexander Bay**, 10km S, SE2816Ca, (28.37.05S 16.07.05E), vii.1978, E.Holm, (1♀ UPSA); Alexander Bay, Jam Pan, State L. 1, 28.38.59S 16.32.14E, 24.x.1996, J.duG.Harrison, site 103, periphery of pan, white sand, (1♀ SAMC); **Boegoeberg-South**, 28.46S 16.53E, 28.ix.1988, E.Marais, J.Irish, (1♀ 2♂ SMWN); Richtersveld, **Holgat Mouth**, 28.58S 16.43E, 1.ix.1976, E-Y:1199, hand-collected fr. hummocks, Endrödy-Younga, (1♂ TMSA).

NAMIBIA: **Agate Beach**, Lüderitz, (26.36S 15.10E), 19.i.1973, M.K.Jensen, extensive dune field with much *Stipagrostis sabulicola*, (1♂ TMSA), (1♂ SMWN); **Agub Mt.**, 26.59S 15.58E, Diamond Area 1, 12-13.viii.1983, J.Irish, E.Griffin, H56628, (1♀ 7♂ SMWN); **Blueberge**, 2km E, 26.07S 14.58E, 18.i.1974, E-Y:297, on and between dunes, day, Endrödy-Younga, (2♂ TMSA); **Boegoeberg**, 27.54S 15.56E, Diamond Area I, 20-21.viii.1983, J.Irish, E.Griffin, H56778, (2♂ SMWN); **Daberas dunes**, (28.13S 16.45E), Gt. Namaqualand, v.1953, C.Koch, (labels printed in black onto white card, 19 labels in one font, 1 label in a larger font, not part of the original type series of *Pachysoma granulatum*), (9♀ 11♂ TMSA), btw. Rooi Lepel-Daberas Dunes, (*ca.* 28.07S 16.37.05E = Rooilepel, Oranjemund; 28.15S 16.38E = Rooilepel, Obib), Gt. Namaqualand, v.1953, C.Koch, (2♂ TMSA) Daberas Gate, 8km E, 28.33S 16.30E, Diamond Area I, 26-27.x.1980, C.G.Coetzee, H42554, (1♀ SMWN); Lüderitz Dist., **Eccles dunes**, 27.55S 16.38E, 18.ix.1997, compacted sand, Marais & Kirk-Spriggs, (1♀ 3♂ SMWN); SE of **Klinghardtberge**, SE2715Db2, (*ca.* 27.33.53S 15.55.58E), vii.1982, E.Holm, (9♂ TMSA), (4♂ UPSA); **Obib Dunes**, West Edge, (*ca.* 28.07.05S 16.22.05E), 8.ix.1980, on dunes, Whitehead, (2♂ SAMC); Obib Dunes, W at 28.03S 16.28E, Diamond Area 1, 7-9.ix.1980, S.Louw, M-L. Penrith, H42503, (2♀ 3♂ SMWN); Obib Dunes, 28.10S 16.41E, Diamond Area 1, 19.viii.1983, J.Irish, H56755, (1♀ 1♂ SMWN); Obib Mts/Dunes, SE2816BA, (28.07.05S 16.37.05E), Diamond Area 1, 28-30.x.1977, Coll. M-L. Penrith, S.Louw, H35118, Ala 5 gg 161, (1♂ SMWN); **Oranjemund**, SE2816Cb2, (28.37.05S 16.22.05E), vii.1982, E.Holm, (4♀ 6♂ UPSA), *idem*, but NE of Oranjemund, (1♂ UPSA); SE of Oranjemund, SE2715Db2, (27.37.05S 15.52.05E), vii.1982, E.Holm, (1x UPSA); Oranjemund, 10km N, SE2816Ad, (28.22.05S 16.22.05E), vii.1978, E.Holm, (1♀ 2♂ SANC), (1♂ UPSA), (1♀ 1♂ TMSA); Oranjemund, SE2816CB, (28.37.05S 16.22.05E), vii.1978, Izak Bruwer, UP, (1♀ SAMC); Oranjemund Dunes, Diamond Area 1, 28.32S 16.27E, 16.ix.1994, E.Marais, (1♀ 2♂ SMWN); **Rietvlei**, SE2816Dc, (*ca.* 28.52.05S 16.37.05E [in sea]), xi.1978, J.A.Irish, (1♂ SANC); **Rooiduine nr Obibberge**, 28.07S 16.37E, 25.iv.1988, R.Oberprieler, (3♂ SANC), (1♀ UPSA); **Roter Kamm**, 27.46S 16.18E, 24.iv.1988, R.Oberprieler, (3♀ 3♂ SANC); **Saddle Hill**, (*ca.* 25.53S 14.56E), i.1966, (1♂ TMSA); **Saddle Hill North**, 25.48S 14.54E, Diamond Area 2, 7.xii.1989, E.Griffin, on dunes, (2♀ SMWN); **Skerpioenkop**, Diamond Area 1, 27.46S 16.30E, 26.ix.1994, E.Marais, (8♀ 4♂ SMWN), (1♀ 1♂ BMNH), (1♀ 1♂ ZMHB); **Spencer Bay Water**, 25.47S 14.54E, 14.i.1974, E-Y:285, hand-collected, day, Endrödy-Younga, (7♀ 8♂ TMSA); **Uguchab Riv.**, 27.37S 16.10E, Diamond Area 1, 14-15.viii.1983, J.Irish, E.Griffin, H56681, (1♂ SMWN).

Additional material listed in Holm and Scholtz (1979): **Buchuberg**, (Boegoeberg), Lüderitz, SE2715Dd, 27.52.05S 15.52.05E, 1972, C.J.C. (SMWN); **Spencer Bay**, Noordhoek, Brakvlei, SE2514Dd, (25.52.05S 14.52.05E), 17.i.1973, (UPSA); Oranjemund, Lüderitz, SE2816Cb, (28.37.05S 16.22.05E), 25-27.xi.1972, (SMWN).

A single specimen from the following locality may be incorrectly labelled because it occurs outside the species' established range: SOUTH AFRICA: Namaqualand, **Dassiefontein & Sneeukop**, 30.09S 17.59E, 20-22.ix.1988, J.Irish, E.Marais, (1♂ SMWN).

Scarabaeus (Pachysoma) schinzi (Fairmaire, 1888)
(Figures 9, 25, 43, 64)

Pachysoma schinzi Fairmaire, 1888: 178; Péringuey 1902: 80; Felsche 1907: 273; Gillet 1911a: 6; Ferreira 1953a: 26; Ferreira 1961: 24; Ferreira 1966: 59; Ferreira 1969: 21; Holm and Scholtz 1979: 235. [Holotype]: No locality [1♂ MNHN].

Scarabaeus schinzi (Fairmaire): Mostert and Holm, 1982: 275.

Diagnosis. Sexual dimorphism of head marked (figure 25a,b), males with bifid clypeal horns (figure25b); protibia serrated between and proximal to protibial teeth (figure 43a,b), distance between second and third protibial teeth (especially in male) greater than between other protibial teeth; elytra smooth, with no sub-elytral ridge; metatarsal claws shorter than last tarsal segment.

Distribution, habitat and conservation Confined to the gravel plains around Aus on the Huib-Hoch Plateau (figure 9). *S. (P.) schinzi* has a very restricted distribution and its conservation status is unknown. *S. (P.) schinzi* is not contained within any conservation area.

Comments on locality data. The Tinkasfläche specimens collected by Gaerdes occur well out of the confirmed distribution range of *S. (P.) schinzi.* Irish (1995) examined Gaerdes original diaries and verified that Gaerdes confused the name's Tinkasfläche (22°53'S 15°23'E) with Tiras Plains (26°08'S 16°38'E) before about 1967. The Tiras Plains (to the north of Aus) are well within the expected distribution of *S. (P.) schinzi.*

Morphological variation. Size of the clypeal horns varies slightly, but the shape is consistent within the species.

*Biology.*Biology unknown. Louw (label data) collected *S. (P.) schinzi* under plants, and according to Owen (pers. comm.) *S. (P.) schinzi* feeds on vegetation (presumably fallen flower petals and detritus).

During September of 1950 Koch and van Son collected 88 females and 70 males of *S. (P.) schinzi* from Aus. This represents the longest series ever collected for any *S. (Pachysoma)* species and forms 84% of available material for *S. (P.) schinzi*. Subsequently only 10 females and 21 males have been collected. Possible reasons for this apparent lack of material since 1950 might include the following: (1) an artifact of collectors' activities and objectives; (2) the unpredictable activity period of *S. (P.) schinzi* a consequence of unpredictable rainfall near Aus; (3) habitat modification around Aus.

The ratio between females and males (1.25♀:1♂) suggests the Aus population sampled in 1950 was at an early stage in their breeding cycle. All 158 specimens collected are mature individuals (no tenerals are present) and the protibial and clypeal wear on some specimens suggests that this sample represented only mature adults most probably of at least one to two years (seasons) old. The small numbers of subsequently collected *S. (P.) schinzi*, could be the result of the large sample taken in 1950. Especially as the restricted distribution range (figure 2d) and low vagility of *S. (P.) schinzi* reduces the potential for recolonization. If this is the case, future coleopterists should refrain from over collecting any local population of *S. (Pachysoma)*. The larvae are unknown.

Comments. Rare in collections, probably due to their limited distribution and an activity period linked to unpredictable rainfall (but also see biology). *S. (P.) schinzi* straddles the boundaries between the Desert, Nama-Karoo and Succulent Karoo Biomes (Rutherford and Westfall 1994) on the Huib-Hoch Plateau.

Types.Fairmaire (1888) described only the male of *Pachysoma schinzi*, a single body length (29 mm) suggests one specimen was examined from 'Namaqua-Land'. Felsche (1907) noted the differences between the sexes and described the female of *P. schinzi*.

Type material. **NAMIBIA**: [HOLOTYPE ♂], *Pachysoma schinzi* Fairmaire: Namaqua-Land, [1♂ MNHN]. Holm and Scholtz (1979) suspect the holotype comes from the vicinity of Aus.

Additional material examined (Σ189 specs. [192], 98♀ 91♂, 5♂ diss.). **NAMIBIA**: **Augustvelde** 42, Lüderitz Distr., 26.38S 16.18E, 13-30.ix.1994, E.Marais, Pres. pitf. traps, (1♀ 2♂ SMWN); **Aus**, Gt. Namaqualand, (26.41S 16.16E), 17.ix.1950, C.Koch, G.van Son, (3♀ 3♂ UPSA), (76♀ 55♂ TMSA),(2♀ 1♂ SAMC), *idem*, but NM3676, (7♀ 10♂ BMSA), (1♂ TMSA); Aus, (26.41S 16.16E), S.W. Prot., Dr. Knobel, (1♂ SAMC); Aus, 6-12km W, (26.38S 16.13E to 26.38S 16.11E), 4.ii.1974, Davis & Kirsten, DRU1409, (2♀ 2♂ SANC) (1♂ SAMC); Aus, 5km NE, 26.37.05S 16.07.05E, 4.ii.(19)74, Davis & Kirsten, DRU1410, (1♀ 1♂ SANC); Aus, (26.41S 16.16E), 30.ix.1987, C.R.Owen, (2♀ 2♂ BMNH); South Inland, Aus 20-30km E, 26°37'S 16°28'E, 18.ix.1987, E-Y:2504, ground and stones, Endrödy-Younga, (1♀ 3♂ TMSA); **Lüderitz**, 5km N of Aus, 26.37S 16.19E, 12.viii.1997, Kirk-Spriggs & Marais, dung trap sample, (1♂ SMWN); **Plateau Farm**, 22mls E Aus, (26.37S 16.35E), 14-17.i.1972 / Southern African Exp., BM 1972-1, (2♀ BMNH); **Rosh Pinah**, 155km on Aus Rd., Lüderitz, 26.40S 16.18E, 30.viii.1989, S.Louw, under plants, NMBH27927, (1♀ NMBH); **Kubub 15**, Lüderitz Distr., 26.42S 16.16E, 13-30.ix.1994, E.Marais, Pres. pitf. traps, (6♂ SMWN); **Tinkasfläche, (= Tiras plains**, *ca.* 26.07.05S 16.37.05E), 25.XI.(19)62 / compared to type of *P.valeflorae* Ferreira, clypeal horns further apart, longer, Holm and Scholtz 1979, (1♂ TMSA). Tinkasfläche, (= Tiras plains, *ca.* 26.07.05S 16.37.05E), 25.XI.(19)62 / Gaerdes (typed) / H25892, (1♂ SMWN). Irish (1995), using Gaerdes diary verified the confusion by Gaerdes between the names Tinkasfläche (SE2215Cd) and Tiras Plains (SE2616Ba) prior to about 1967.

Scarabaeus (Pachysoma) valeflorae (Ferreira, 1953)

(Figures 9, 26, 44, 65)

Pachysoma valeflorae Ferreira, 1953a: 28; Ferreira 1961: 24; Ferreira, 1966: 59; Ferreira, 1969:22; Holm and Scholtz, 1979: 235 (subjective synonym of *Pachysoma schinzi* Fairmaire).Holotype: Haalenberg, Namibia (1♂ TMSA).

Diagnosis. Sexual dimorphism of the head marked between sexes (figures 26a,b); male has two clypeal horns, anterior edges of genae produced into distinct point (figures 26a,b); no serrations between or proximal to protibial teeth (figures 44a,b); small and slightly built in comparison to *S. (P.) schinzi*.

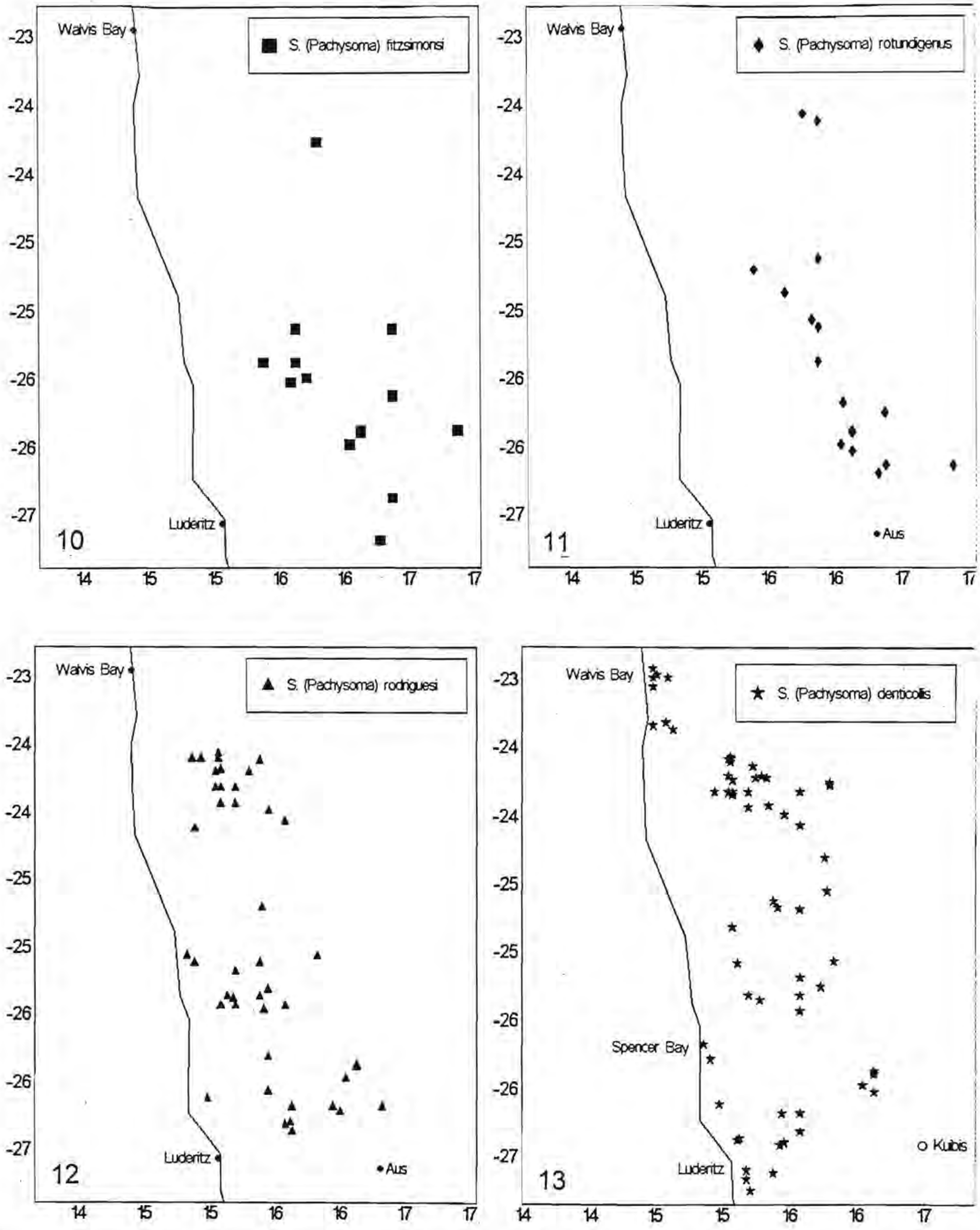
Distribution, habitat and conservation. S. (P.) valeflorae occurs at the boundary between the Desert and Succulent Karoo Biome on the coastal plain (figure 9), (Rutherford and Westfall 1994). It is probably restricted to the sand dunes between Elizabeth Bay and Grasplatz (see figure 4 in Endrödy-Younga 1986). Its conservation status is unknown.

Comments on locality data. Refer to *S. (P.) schinzi* for a discussion on the Gaerdes Tinkasfläche locality.

Morphological variation. The holotype is the largest specimen among the limited material examined. *S. (P.) valeflorae* is smaller and slighter than *S. (P.) schinzi.* Sizes of the male clypeal horns differ slightly in the five males examined, but the diagnostic shape is consistent.

Biology. Biology unknown.

Comments. Ferreira (1953a) based her description of *Pachysoma valeflorae* on the male holotype. Holm and Scholtz (1979) examined two male specimens of *S. (P.) valeflorae* from Haalenberg and Rotkop. The third male specimen, labelled Tinkasfläche, which Holm and Scholtz (1979) attributed to *S. (P.) valeflorae* represents a confusing locality record (see comments on locality data for *S. (P.) schinzi* above), but can now be placed close to Aus at Tiras Plains (26°07'S 16°37'E). Based on the available material, Holm and Scholtz (1979) synonymised *S. (P.) valeflorae* with *S. (P.) schinzi* stating that, with material from Rotkopf and Tinkasfläche now available, *S. (P.) valeflorae* is obviously the western extreme of a cline. A very limited amount of new material, (i.e. the first known female and three males) conform with typical *S. (P.) valeflorae. S. (P.) valeflorae* can be distinguishing from *S. (P.) schinzi* by the following characters: (1) the shape and size of the clypeus, anterior edges of genae produced into distinct points (figures 26a,b); (2) males, equal spacing between the second and third



FIGS. 10-13. Distribution of *Scarabaeus (Pachysoma)* species in Namibia. Questioned locality records or range extensions are shown by an open circle. (10) *S. (P.) fitzsimonsi*; (11) *S. (P.) rotundigenus*; (12) *S. (P.) rodriguesi*; (13) *S. (P.) denticollis*.

protibial teeth (figure 44b); (3) no serrations between or proximal to the protibial teeth (figures 44a,b); (4) a localized coastal distribution (figure 9); (5) small body size (the holotype is the largest specimen available); (6) smooth elytra; (7) and stouter, shorter aedeagi (figures 65a,b,c).

The final word on the status of *S. (P.) valeflorae* will only be possible when material from near Tsaukaib and Garub is collected (that is if *S. (P.) valeflorae* occurs at these sites?). This area is either the transition zone between the two species, or an ecological barrier of unsuitable or very marginal habitats. *S. (P.) valeflorae* is very close to *S. (P.) schinzi*, and potentially could be considered a subspecies of *S. (P.) schinzi*. This was obviously evident to Ferreira who considered the name *Pachysoma similis* (unpublished) before choosing *Pachysoma valeflorae* instead. Based on the limited available material, I find no evidence for a clinal gradation in morphology between *S. (P.) valeflorae* and *S. (P.) schinzi* and subsequently reinstate *S. (P.) valeflorae* to specific level.

Types.Pachysoma valeflorae was described from a single male specimen, currently in the TMSA collection. Koch and van Son collected the holotype on the 23.ix.1950, but a few days previously (17.ix.1950) they had collected the 158 *S. (P.) schinzi* from Aus.

Type material examined (1♂ diss.). **NAMIBIA**: HOLOTYPE ♂, *Pachysoma valeflorae* Ferreira: 10m W of Haalenberg, (26.37.05S 15.22.05E), Gt. Namaqualand, 23.ix.1950, Koch & van Son / Holotypus ♂, *Pachysoma similis* (sic) det.M.C. Ferreira, 1951 / Holotypus, *Pachysoma valeflorae* sp.n. M.C.Ferreira (Endrödy-Younga label), (1♂ TMSA).

Additional material examined (Σ5 specs. [1], 1♀ 4♂, 3♂ diss.). **NAMIBIA**: **Diamond Area 1**, 26.51S 15.40E, 11.viii.1983, J.Irish, H56792, (1♀ SMWN); **Rotkop**, (26.43S 15.23E), 10.x.1995, C.R.Owen (2♂ SMWN), (1♂ TMSA); Rotkop, 22mls E of Lüderitz, (26.37.05S 15.22.05E), 22.xi.1929 / S.W.Africa, R.E.Turner, Brit. Mus. 1930-113, (damaged teneral), (1♂ BMNH).

Scarabaeus (Pachysoma) fitzsimonsi (Ferreira, 1953)

(Figures 10, 27, 45, 66)

Pachysoma fitzsimonsi Ferreira, 1953a: 20; Ferreira 1961: 22; Ferreira 1966: 58; Ferreira 1969: 21; Holm and Scholtz 1979: 234. Holotype: Namtib, Namibia (1♂ TMSA).

Scarabaeus fitzsimonsi (Ferreira): Mostert and Holm, 1982: 275.

Diagnosis. Clypeus quadridentate, outer clypeal teeth reduced in size (figure 27); protibia hardly dimorphic with simple protibial spurs (figure 45); sub-elytral ridge usually present but faint; inner metatarsal claws slightly shorter than outer metatarsal claw; metatarsal claws shorter than last tarsal segment; male genitalia in figures 66a,b.

Distribution, habitat and conservation. This species occurs east of the central dune area (figure 10), on the sandy flats of the pro-Namib (Holm and Scholtz 1979). *S. (P.) fitzsimonsi* occurs within the Namib-Naukluft Park.

Comments on locality data. The single record from the far east of the Namib Desert (23°53'S 16°07'E), is a considerable range extension northwards for the distribution of *S. fitzsimonsi*. Suspicion of a new species was unconfirmed as the single male matches *S. (P.) fitzsimonsi* in all aspects, including the faint sub-elytral ridge and genitalia typical of the species. This locality record requires confirmation.

Morphological variation. Two females, one each from Haibvlakte and Numabis Pan have no sub-elytral ridge, a character used by Holm and Scholtz (1979) to separate *S. rotundigenus* from *S. (P.) fitzsimonsi*. A male from Haibvlakte does, however, have a sub-elytral ridge and genitalia typical of *S. fitzsimonsi*. This suggests, possible dimorphism in expression of the sub-elytral ridge, but no other *S. (P.) fitzsimonsi* females examined confirm this possibility

Biology. The biology of *S. (P.) fitzsimonsi* is unknown. However, based on the hind leg morphology their foraging behaviour and food choice should not differ from that of *S. (P.) rodriguesi* (dung pellets) or *S. (P.) denticollis* (dung pellets and detritus). The short metatarsal claws of *S. (P.) fitzsimonsi* suggest pellet feeding rather than detritus feeding and adaptation to a firm substrate rather than soft dune sand (see Koch 1961, 1962a,b, 1969, Lawrence 1969, Newlands 1972, Endrödy-Younga 1982a, and Henschel 1997 for evidence of this morphological change in other taxa). *S. (P.) fitzsimonsi* is thus probably predominately a dry pellet feeder. Evidence to support this claim comes from Davis (pers. comm.) who recalls finding sheep pellets in the burrows when he excavated the Weissenborn specimens. The larvae are unknown.

Comments. Easily confused with *S. (P.) rotundigenus* but *S. (P.) fitzsimonsi* is distinguished by having simple protibia in both sexes, short metatarsal claws, and apical insertion of the mesotarsi and metatarsi on the tibia. The sub-elytral ridge in *S. fitzsimonsi* cannot be used as the only character to distinguish between these two species (see morphological variation).

Types. All the types are in the TMSA collection. The holotype and allotype have no date on their locality label, but the paratypes are dated 17.ix.1950.

Type material examined (Σ4 specs. [4], 2♀ 2♂, 2♂diss.). **NAMIBIA**: HOLOTYPE ♂, *Pachysoma fitzsimonsi* Ferreira: Namtib, 70m NW of Aus, (*ca.* 25.52.05S 16.52.05E), Gt. Namaqualand, (no date), C.Koch, G.van Son / Holotipo *Pachysoma FitzSimonsi*, ♂, M.C.Ferreira, 1951 (written by Ferreira in red ink on white card, surrounded by a black rectangular border) / Holotypus *Pachysoma fitzsimonsi*, M.C.Ferreira sp.n. (written by Endrödy-Younga onto TMSA Ferreira label), (aedeagus and pygidium on a separate pin), (1♂ TMSA); *idem*, but /Alotipo *Pachysoma FitzSimonsi*, ♀, M.C.Ferreira, 1951 / Allolotypus *Pachysoma fitzsimonsi*, M.C.Ferreira sp.n., (1♀ TMSA). PARATYPES: Aus, Gt. Namaqualand, (26.41S 16.16E), 17.ix.1950, C.Koch, G.van Son / Para-Tipo *Pachysoma FitzSimonsi*, M.C.Ferreira, (1♀ 1♂ TMSA).

Additional material examined (Σ26 specs. [29], 11♀ 15♂, 5♂ diss.). **NAMIBIA**: **Aus**, 30km N to **Helmeringhausen**, SE2616Ad, (*ca.* 26.22.05S 16.22.05E), 7.x.1979, E. Holm & C.H. Scholtz, (1♀ UPSA); **Haibvlakte**, 25.29S 15.42E, Diamond Area 2, 5-6.iv.1986, J.Irish, H65260, (1♀ 1♂ SMWN); **Kanaän 104**, SE2516Cc, (*ca.* 25.52.05S 16.07.05E), Lüderitz, 22-27.vi.1976, S.Louw, M-L. Penrith, H32992, plains, grass & dunes, (3♀ 4♂ SMWN), (1♀ TMSA); Kanaän 104, 25.53S 16.07E, Lüderitz, 15-21.x.1976, S.Louw, M-L. Penrith, H33338, (2♀ 1♂ SMWN); Farm **Namtib**, 112km NW Aus via Farm Neisip, (*ca.* 25.52.05S 16.07.05E), 5.ii.1974, Davis & Kirsten, DRU1413, (1♀ 1♂ SANC); Namtib Dunes, 25.58S 16.02E, 2.viii.1981, E-Y:1818, night, veget. dunes, Endrödy-Younga, (1♀ TMSA); **Numabis Pan**, 25.31S 15.35E, Diamond Area 2, 7.iv.1986, J.Irish, H65359 (1♀ SMWN); **Uri Hauchab**, (*ca.* 25.22.05S 15.22.05E), 4.vii.1976, (1♂ UPSA); Farm **Weissenborn**, SWA, 100km NW Aus via Farm Neisip, (*ca.* 25.07.05S 16.22.05E),5.ii.1974, Davis & Kirsten, DRU1411, (2♂ UPSA), (3♂ SANC), (1♂ SAMC).

Additional localities listed in Holm and Scholtz (1979): **Awasib Dunes** E, (*ca.* 25.07.05S 15.37.05E), Lüderitz, 29-30.I.1974, (SMWN); **N-Awasib**, (*ca.* 25.22.05S 15.37.05E), 4.vii.1976, Dept. Entomology, Univ. Pretoria (UPSA); **Farm Spesbona**, 184 km N Aus via Farm Neisip, (*ca.* 25.37.05S 16.22.05E), 5.xi.1974, Davis & Kirsten, (SANC).

A single specimen from the following locality may be incorrectly labelled because it occurs outside the species' established range. NAMIBIA: **Namib Desert**, far east, 23.46S 15.47E, Praetorius, 9.ii.1981, 10h30, 1DV, south breeze, high fog, C5477, (1♂ SMWN).

Scarabaeus (Pachysoma) rotundigenus (Felsche, 1907)

(Figures 11, 28, 46, 67)

Pachysoma rotundigena Felsche, 1907: 273; Péringuey 1908: 555; Gillet 1911a: 6; Holm and Scholtz 1979: 236. [Holotype]: Sinclair, S.W.A. [1x SMTD].

Neopachysoma rotundigena (Felsche): Ferreira, 1953a: 43; Ferreira 1961: 25; Ferreira 1966: 60; Ferreira 1969: 25; Zunino 1977: 15.

Scarabaeus rotundigenus (Felsche): Mostert and Holm, 1982: 275.

Diagnosis. Clypeus quadridentate, outer clypeal teeth reduced in size; genae rounded and finely serrated (figure 29); protibia dimorphic, protibial spurs bifid in both sexes (figure 46); elytra smooth and shiny with no sub-elytral ridge; tarsal insertion sub-apical; metatarsal claws longer than last two tarsal segments; male genitalia as in figures 67a,b.

Distribution, habitat and conservation. This species occurs in the vegetated marginal inland dunes of the southern Namib dune area (Holm and Scholtz 1979), (figure 11). The very long tarsal claws and enlarged tibial setal brushes suggest *S. (P.) rotundigenus* is adapted to soft dune sand. Conserved within the Namib-Naukluft Park.

Comments on locality data. The three specimens from the SE corner of the Namib-Naukluft Park extend the known distribution for *S. (P.) rotundigenus* northwards (figure 11). Collected independently these specimens probably reflect real occurrence rather than incorrectly labelled specimens. The most northerly record of *S. (P.) fitzsimonsi* is from near this locality. As *S. (P.) fitzsimonsi* and *S. (P.) rotundigenus* occur close to one another in the south, these overlapping range extensions corroborate these new records.

Morphological variation. The three (2♀ 1♂) most northerly specimens (SE of Namib-Naukluft Park) match in all morphological attributes, including male genitalia to that of *S. (P.) rotundigenus*.

Biology. Biology unknown. However, they occur in vegetated dunes where detritus readily accumulates around the base of plants. This habitat and their long metatarsal claws suggest a detritus feeding diet. The larvae are unknown.

Comments. Easily confused with *S. (P.) fitzsimonsi*, but differentiated by the absence of a sub-elytral ridge, sub-apical insertion of the tarsi on the tibia, and long metatarsal claws.

Types. A body length of 26 mm is given by Felsche (1907) in the description of *Pachysoma rotundigena*, suggesting that he only examined one specimen. However, two collections (Collection Felsche and Collection Bennigsen, Berlin) are listed as having material, suggesting more than one specimen was examined (Felsche 1907).

Type material {>?2 spec.}. **NAMIBIA**: [HOLOTYPE], **Sinclair**, (25.44S 16.22E), D.S.W. Afrika, [1x SMTD].

Additional material examined (Σ50 specs. [33], 19♀ 31♂, 4♂diss.). **NAMIBIA**: Namib plain, 70mls N **Aus**, (ambiguous), 1.v.1972, L.& O. Prozesky, (1♂ TMSA); E **Awasib**, SE2515Bb1, (*ca.* 25.03.53S 15.48.53E), 11.vii.1976, UP, (1♀ UPSA), (1♀ SAMC); **Excelsior 59**, Lüderitz, SE2616Ab, (*ca.* 26.07.05S 16.22.05E), 1-4.vii.1979, S.Louw, M-L. Penrith, H39170, (1♀ 2♂ SMWN); SW of **Helmeringhausen**, SE2616Ab3, (*ca.* 26.10.58S 16.18.53E), vii.1978, E.Holm, (1♀ 1♂ UPSA), (2♀ 3♂ SANC); **Kanaän**, SE2516Cc, (25.52.05S 16.07.05E), 19-20.i.1985, UP Ent. Dept., (2♂ UPSA); Kanaän 104, 25.53S 16.07E, Lüderitz, 15-21.x.1976, S.Louw, M-L. Penrith, H33338, (1♀ SMWN); Kanaän 104, SE2516Cc, (*ca.* 25.53S 16.07E), Lüderitz, 25.iv.-2.v.1977, M-L. Penrith, S.Louw, H34749, (4♂ SMWN), (1♂ UPSA); Kanaän 104, SE2516Cc, (*ca.* 25.53S 16.07E), Lüderitz, 22-27.vi.1976, S.Louw, M-L. Penrith, H32992, (2♀ 9♂ SMWN); Farm Kanaän, 25.53S 16.07E, 7.v.1977, E-Y:1323, hand-collected on dunes, S.Mothlasedi, (1♀ 2♂ TMSA); **Namtib Dunes**, 25.58S 16.02E, 8.viii.1989, E-Y:2640, dunes, day, Endrödy & Klimaszew., (1♂ TMSA); Namtib Dunes, 25.58S 16.02E, 2.viii.1981, E-Y:1817, sandflat, day, Endrödy-Younga, (1♀ TMSA); Namtib, 70mls NW of Aus, SE2516Cc, (*ca.* 25.52.05S 16.07.05E), Gt. Namaqualand, C.Koch, G. van Son, (2♀ TMSA); **Sossusvlei**, (24.42S 15.23E), x.1965, W.D.Haacke, (1♀ UPSA), (1♂ TMSA); Sossusvlei, (24.42S 15.23E), 7.iv.1996, D.Wellmann, 2nd Yr. Coll., (1♀ UPSA); **Tiras Dunes**, 26.01S 16.07E, Lüderitz District, 8.iv.1986, J.Irish, (1♀ SMWN); Farm **Vergenoeg**, 25.40S 16.03E, 28.iii.1986, E.Holm & E.Marais, (1♀ 2♂ UPSA); **Wolwedans 144**, Maltahöhe Distr., SE2515Bb, (*ca.* 25.07.05S 15.52.05E), i.1990, Z.Cooper, (1♂ SMWN).

Additional localities listed in Holm and Scholtz (1979); **Gorrasis 99**, Lüderitz, SE2515Bd, (*ca.* 25.22.05S 15.52.05E), 25-31.i.1974, (SMWN); **Kanaän 104**, Lüderitz, SE2516Cc, (*ca.* 25.53S 16.07E), 6-7.x.1972, (SMWN); **Koichab East**, SE2616Bb, (*ca.* 26.07.05S 16.52.05E), vii.1978, Dept.Ento. (UPSA); **Sesriem 137**, Maltahöhe, SE2415Dc, (*ca.* 24.52.05S 15.37.05E), 5-6.IV.1972, (SMWN); Sesriem Dunes, SE2415Db, (*ca.* 24.37.05S 15.52.05E), 5.v.1972, I.O.Prozesky, (TMSA).

Specimens from the following localities may be incorrectly labelled because they are outside the species' established range: NAMIBIA; SE corner of Namib Desert Park, nr. **Knamhoek** Farm, SE2315Db, (*ca.* 23.37.05S 15.52.05E), 860m, 15.ii.1974, L.Lyneborg, vegetated, moving dunes / Zool. Museum DK Copenhagen / (1♀ UPSA); **Namib Park**, SE corner, 23.34S 15.45E, 26.xi.1974, E-Y:496b, groundtraps for 105 days, with ferm. banana bait, Endrödy-Younga, (1♀ 1♂ TMSA).

Scarabaeus (Pachysoma) rodriguesi (Ferreira, 1953)

(Figures 12, 29, 47, 68)

Neopachysoma rodriguesi Ferreira, 1953a: 44; Ferreira 1961: 25; Ferreira 1966: 60; Ferreira 1969: 25; Zunino 1977: 15. Holotype: Namtib, Namibia (1♂ TMSA).

Pachysoma rodriguesi (Ferreira): Holm and Scholtz 1979: 237.

Scarabaeus rodriguesi (Ferreira): Mostert and Holm 1982: 275.

Diagnosis. Head with prominent tubercle on frons (figure 29); protibia sexually dimorphic, spurs strongly bifid (figures 47a,b); posterior pronotal margins with sharp points on either side; large, shiny and reddish black in colour; metatarsal claws long; male genitalia illustrated in figures 68a,b.

Distribution, habitat and conservation. Restricted to the central Namib dune area (figure 12). Their morphology reflects adaptation to ultrapsammophilous conditions of the central dune sea. *S. (P.) rodriguesi* is contained within the Namib-Naukluft Park.

Comments on locality data. Holm and Scholtz (1979) mentioned the curious record along the Buffels River. They noted that the single female collected, did not differ significantly from the northern population, except in having the tubercle on the frons reduced. The size of the tubercle on the frons varies within and between sexes from the same population and thus does not constitute a population specific character. Recent extensive field work along the Buffels River yielded no *S. (P.) rodriguesi* and confirms the suspicion by Holm and Scholtz (1979) that this specimen is incorrectly labelled.

Morphological variation. The size of the protuberance on the frons varies in both the 13 females and in the 11 males in the material of *S. (P.) rodriguesi* from 20 miles south of Gobabeb.

Biology. Holm (1970) and Holm and Scholtz (1979), give detailed accounts of the biology of *S. (P.) rodriguesi.* To summarize, the species collects *Oryx* and hare pellets that are dragged forward to their preconstructed burrows, but no use of detritus is mentioned. *S. (P.) rodriguesi* has been observed mating above ground in the afternoon (Holm and Scholtz 1979). The larvae are unknown.

Comments.S. (P.) rodriguesi is an unmistakable large central Namib species, with only very large specimens of *S. (P.) hippocrates* and *S. (P.) glentoni* matching it in size.

*Types.*Ferreira (1953a) described *Pachysoma rodriguesi* from five specimens, four of which she deposited in the TMSA collection and one paratype in the CPMM collection. All the types are currently in the TMSA collection. The date is omitted from the printed locality labels, while the holotype has a separate label with the date (26.ix.1953) on it. Ferreira (1953a) records the date of collection of the type series as the 26.ix.1950. Considering the description of *P.rodriguesi* was published in 1953, I suspect the date of collection was the 26.ix.1950, rather than 26.ix.1953 as recorded on the holotype.

Type material examined (Σ5 specs. [5], 1♀ 4♂, 3♂diss.). **NAMIBIA**: Holotype ♂, *Neopachysoma rodriguesi* Ferreira: Namtib, 70m NW of Aus, (*ca.* 25.58S 16.02E), Gt. Namaquald., C.Koch, G.van Son / 26.ix.1953 (written in pencil on faded white paper) / Holotipo *Neopachysoma Rodriguesi* M.Cornita Ferreira, 1950 (written in red ink on white card, with a black border around the label) / Holotypus *Neopachysoma rodriguesi* M.C.Ferreira sp.n. (written by Endrödy-Younga on TMSA Ferreira label), (1♂ TMSA); (aedeagus of the holotype is point mounted on a separate pin, but labelled *idem*); Allotype ♀, *idem*, but Alotipo (sic) *Neopachysoma Rodriguesi* M.Cornita Ferreira, 1950 (written in red ink on white card, with a black border around the label) / Allotypus *Neopachysoma rodriguesi* M.C.Ferreira sp.n. (written by Endrödy-Younga on TMSA Ferreira label), (1♀ TMSA). Paratypes: *idem*, but Paratipo (sic) *Neopachysoma Rodriguesi* M.Cornita Ferreira, 1950 (written in red ink on white card, with a black border around the label) / Paratypus *Neopachysoma rodriguesi* M.C.Ferreira sp.n. (written by Endrödy-Younga on TMSA Ferreira label), (3♂ TMSA).

Additional material examined (Σ93 specs. [37], 44♀ 49♂, 3♂diss). **NAMIBIA**: **Aus**, 46km NW, (*ca.* 26.11S 15.37E), 18.ix.1996, C.R.Owen, (2♂ COCS), (1♂ TMSA); E. **Awasib**, SE2515Bb1, (25.03.53S 15.48.53E), 11.vii.1976, U.P., (1♂ UPSA), (1♂ SANC); N. Awasib, 2515Bc3, (25.25.58S 15.33.53E), 4.vii.1976, UP, (1♂ UPSA), (1♂ SANC); Awasib Sand Dunes, (25.25.58S 15.33.53E), southern Namib, 15.v.1969, H.D.Brown, (3♀ SANC), *idem*, but NMBH3684, (1♂ BMSA); **Blueberg**, 2km E, 26.07S 14.58E, 18.i.1974, E-Y:297, on and between dunes day, Endrödy-Younga, (2♂ TMSA); **Diamond Area 2**, 25.28S 15.24E, 23.v.1983, J.Irish, H57740, (1♂ SMWN); **St. Francis Bay**, SE2514Bb1, (25.03.53S 14.48.53S), 8.vii.1976, UP, (1♀ SANC); **Guinasibberg**, SE2515Ab, (25.07.05S 15.22.05E), 17.i.1985, UP, (1♀ UPSA); W. Guinasibberg, SE2515Ad2, (25.18.53S 15.25.58E), 6.vii.1976, UP, (1p UPSA); **Gobabeb**, 10mls S of, (*ca.* 23.42S 15.02E), iii.1968, E.Holm, (3♀ 2♂ TMSA); Gobabeb, 20mls S of, (*ca.* 23.49S 15.02E), vi.1967, E.Holm, (13♀ 11♂ TMSA); Gobabeb, (23.34S 15.03E), ii.1977, R.Tilson, (1♂ SMWN); S. Gobabeb, SE2315Ca3, (23.40.58S 15.03.53E), 14.vii.1976, UP, (1♂ UPSA); Gobabeb, 23.34S 15.03E, 22.viii.1982, E-Y:1919, hand-collected, dune valley, day, Endrödy-Younga, (1♂ TMSA); nr. **Harus**, (25.23S 15.10E), southern Namib, 10.v.1969, H.D.Brown, (1♀ TMSA); nr. Harus Mts, (25.23S 15.10E), southern Namib, 9.v.1969, H.D.Brown, NMBH3683, (1♂ BMSA); SW of **Helmeringhausen**, SE2616Ab3, (26.10.58S 16.18.53E), vii.1978, E.Holm, (2p UPSA); Farm **Kanaan**, 25.53S 16.07E, 7.v.1977, E-Y:1323, hand-collected on dunes, S.Mothlasedi, (1♂ TMSA); **Koichab**, SE2615Bc1, (26.18.53S 15.33.53E), vii.1982, E.Holm, (2♂ UPSA); Koichab, SE2615Bb4, (26.10.58S 15.55.58E), vii.1982, E.Holm, (1♀ UPSA); Koichab Pan, (26.18S 15.36E), vii.1978, E.Holm, (2♂ UPSA); Namib Desert, SWA, (2♀ 1♂ TMSA); **Namib-Expedition**, SE2315Cc3, (23.55.58S 15.03.53E), i.1977, Holm, Kirsten & Scholtz, (1♀ UPSA); Namib-Expedition, SE2515Aa4, (25.10.58S 15.10.58E), i.1977, Holm, Kirsten & Scholtz, (1♀ SANC); Namib-Expedition, SE2515Ac4, (25.25.58S 15.10.58E), i.1977, Holm, Kirsten & Scholtz, (1♀ SANC); Namib-Expedition, SE2515Cd2, (25.48.53S 15.25.58E), i.1977, Holm, Kirsten & Scholtz, (1♀ SANC); **Namtib Dunes**, 35mls E, Neisip, (*ca.* 26.13S 15.59E), Aus Dist., 1.v.1972, L. & O.Prozesky, (2♂ TMSA); Namtib Dunes, 25.58S 16.02E, 8.viii.1989, E-Y:2640, dunes, day, Endrödy-Younga, (1♀ TMSA); Namtib Dunes, 25.58S 16.02E, 2.viii.1981, E-Y:1817, sand flat, day, Endrödy-Younga, (1♂ TMSA); **Natab**, 10mls E, (*ca.* 23.36S 16.16E), Central Namib, 28.iv.1969, H.D.Brown, (3♂ TMSA); Natab, 15mls E, (*ca.* 23.36S 14.51E), Central Namib, 28.iv.1969, H.D.Brown, (1♀ TMSA); Natab, 23.36S 15.03E, 6.xi.1976, W.J.Hamilton, C1221, (1♀ SMWN); **Sossusvlei**, (24.42S 15.23E), x.1965, W.D.Haacke, (1♀ TMSA); **Tsondab**, SE2415Ba1, (24.03.53S 15.33.53E), 11.vii.1975, // day, dune foot // (1♀ UPSA); NE Tsondab Plains, SE2315Cc2, (23.48.53S 15.10.58E), 15.vii.1976, UP, (1♀ UPSA), (3♀ SANC); SE Tsondab Plains, SE2315Cc4, (23.55.58S 15.10.58E), 15.vii.1976, UP, (1♂ UPSA), (2♂ SANC), (1♂ SAMC); Tsondab Plains, N fringe, 15mls S of Natab, (*ca.* 23.42S 15.17E), 20.iv.1969, M.Pond, (2♀ 2♂ SMWN), *idem*, but 10:00-17:30, (1♀ SMWN), *idem*, but C2896, (1♂ SMWN); Tsondab Vlei, 23.59S 15.26E, 13.i.1975, E-Y:542B, ground baited faeces traps, 1 day, Endrödy-Younga, (1♀ TMSA); N **Uri-Hauchab**, SE2515Ac3, (25.25.58S 15.03.53E), 6.vii.1972, UP, (1♀ UPSA); **Ururas**, 90km SSE, SE2414Bb, (24.07.05S 14.52.05E), 14.x.1979, Holm & Scholtz, (1♂ UPSA); SE2615Ab2, (26.03.53S 15.25.58E), 8.vii.1980, UP, (1♂ UPSA).

Additional locality data from Holm and Scholtz (1979); **Awasib**, 9km W, SE2515Ad, (*ca.* 25.22.05S 15.22.05E), 8.vi.1969, (SMWN); Dunes nr. **Harus**, SE2515Ac, (*ca.* 25.22.05S 15.07.05E), Lüderitz, 9.v.1969, (SMWN); **Harusberg**, SE2515Ac, (*ca.* 25.22.05S 15.07.05E), v.1969, (SMWN); **Homeb** 10mls ESE Gobabeb, SE2315Cb, (*ca.* 23.37.05S 15.22.05E), 23-25.i.1972, (BMNH); **Koichab Pan**, SE2615Bc, (*ca.* 26.22.05S 15.37.05E), 20.i.1966, (SMWN); **Koichab West**, SE2615Bc, (*ca.* 26.22.05S 15.37.05E), vii.1978, E.Holm, (UPSA); **Lüderitz**, SE2514Bb, (*ca.* 25.07.05S 14.52.05E), 17.ix.1971, (SMWN); **Sossusvlei**, Lüderitz, SE2413Cb, (*ca.* 24.37.05S 13.22.05E), 6.iv.1974, W. Wendt, H. Roth, (SMWN); N **Tsondab Plains**, SE2315Cc1, (*ca.* 23.48.53S 15.03.53E), 14.vii.1976, (UPSA).

A single specimen from the following locality may be incorrectly labelled because it is outside the species' established range: SOUTH AFRICA; Northern Cape, Namaqualand;

Buffelsriver Valley, 29.35S 17.14E, 31.viii.1976, E-Y:1197B, groundtraps for 33 days, Endrödy-Younga, (1♀ TMSA).

Scarabaeus (Pachysoma) ***denticollis*** (Péringuey, 1888)

(Figures 13, 30, 48, 69)

Pachysoma denticolle Péringuey, 1888: 93; Péringuey, 1902: 77; Gillet, 1911a: 6; Holm and Scholtz, 1979: 239. Lectotype: Walfish Bay, Namibia (1♂ SAMC).

Neopachysoma denticolle (Ferreira), 1953a: 37; Ferreira 1961: 25; Ferreira, 1966: 60; Ferreira, 1969: 25; Zunino, 1977: 15; Holm and Scholtz, 1979: 239; Mostert and Holm, 1982: 277.

Neopachysoma penrithae Zunino, 1977: 15; Holm and Scholtz, 1979: 239. Holotype: Lüderitz, Namibia (1♀ SMWN).

Scarabaeus denticollis penrithae (Zunino): Mostert and Holm, 1982: 277.

Diagnosis. Clypeus quadridentate, outer clypeal teeth smaller than medial teeth; genae finely serrated (figure 30); protibia sexually dimorphic, protibial spurs bifid in males simple in females (figures 48a,b); elytra orange to black, deeply striate, striae smooth to granular; metatarsal claw longer than last tarsal segment; male genitalia as in figures 69a,b.

Distribution, habitat and conservation. Restricted to the coastal and inland dunes of the central Namib (figure 13), and conserved within the Namib-Naukluft Park. Holm (1970) suggests they prefer semi-stable sand and dune streets.

Comments on locality data. The Mata Mata locality (Kalahari Gemsbok National Park), is without doubt due to a labelling error. The Kuibis record also occurs out of the established distribution range for *S. (P.) denticollis*.

Morphological variation. Refer to comments on *S. (P.) denticollis penrithae*.

Biology. S. (P.) denticollis feeds mainly on hare and *Oryx* dung which are dragged as single pellets to their preconstructed burrows. They are also reported to collect dead insects, mice and chameleon droppings and vegetable matter (grass blades, *Monsonia* sp. leaves etc.) (Holm 1970, Holm and Scholtz 1979). Here the forage is picked up with the hind legs and held against the underside of the abdomen (Holm and Scholtz 1979), while the beetle runs on the front four legs.

Comments. Zunino's (1977) description of *Neopachysoma penrithae* is based on two females from the southern Namib. Holm and Scholtz (1979) noted it was difficult to evaluate the characters proposed by Zunino due to the lack of material, but suggested three possibilities to account for the morphological differences: (1) the southern extreme of a cline; (2) a subspecies; (3) hybrids between *S. (P.) denticollis* and *S. (P.) bennigseni*. They however choose to synonymies *S. penrithae* with *S. (P.) denticollis*. Having examined 22 additional specimens of *S. penrithae*, from three localities, Mostert and Holm (1982) concluded it had become 'fairly certain that *S. penrithae* Zunino is a subspecies of *denticolle* Péringuey, with a very limited distribution (parapatric with the typical form) in the triangle between Kolmanskop, Lüderitzbucht and Spencer Bay' (see figure 4d). Mostert and Holm (1982) also mention that 'specimens collected on scattered dunes between Kolmanskop and Koichab pan were clearly intermediate between *penrithae* and *denticolle* in all the diagnostic characters given by Zunino (1977)'. This suggests a cline rather than a distinct subspecies. Unfortunately, Mostert and Holm (1982) did not examine any black specimens from the north of *S. (P.) denticollis* distribution (Walvis Bay), nor was *S. (P.) denticollis penrithae* included in their key.

Zunino (1977) used the following differences to separate *S. (P.) denticollis* from *S. penrithae*: (1) shape of the median clypeal teeth, (2) elytral sculpture; (3) colouration of elytra; (4) size of the epipleura and pseudo-epipleura.

To assess the validity of retaining *S. (P.) denticollis penrithae* as a subspecies these characters were investigated in the 211 available specimens. The following was found: there is no consistent significant difference in the size or shape of the median clypeal teeth between the northern and southern populations of *S. (P.) denticollis*, the holotype of *S. penrithae* represents an individual where the outer two clypeal teeth are deflexed outwardly more than usual in southern specimens; granular elytral interstriae define the southern population more reliably than elytral colour. However, although most series of *S. (P.) denticollis penrithae* exhibit this character, it is variably expressed within and between the southern populations. For example, in the seven individuals from SE2615Ad4 (26°26'S 15°26'E), elytral sculpture varies in expression and is not as marked as in the six individuals from 30km N of Lüderitz (26°22'S 15°07'E); both the northern (Walvis Bay at 22°58'S 14°30'E) and southern populations (Lüderitz at 26°36'S 15°10'E) of *S. (P.) denticollis* have elytras that range in colour from completely black to a dark orange. The presence of black *S. (P.) denticollis* at both ends of the species distribution, but absent in the centre of its range has not been reported previously (see Holm and Kirsten 1979). Specimens with one black and one orange elytron further substantiate the variability of elytral colour. The disjunct occurrence of individuals with black elytra indicates that its use as a diagnostic character has no standing and should be avoided. Zunino (1977) however, used the black elytra of *S. penrithae* as a diagnostic feature for the species; the epipleura and pseudo-epipleura are broader in the southern populations, but do not constitute grounds for erecting a subspecies. The large female holotype has particularly wide elytra, and consequently large epipleura and pseudo-epipleura; while no substantial difference was found in the male genitalia between the northern and southern samples examined.

To retain *S. (P.) denticollis penrithae* as a subspecies would necessitate the description of two additional subspecies to account for the central Namib and northern Namib populations. *S. penrithae* represents the southern morphological variation within *S. (P.) denticollis*, which is no greater than that expressed in the central (small, always orange) and northern (medium sized, black to orange with smooth interstriae) populations. *S. (P.) denticollis penrithae* is thus regarded as synonymous with *S. (P.) denticollis*.

Types. Péringuey's (1888) description of *Pachysoma denticolle* gives no range for size, and mentions a single locality (Walfish Bay) and collector (Mr P. Nightingale), which suggests he probably based his description on a single specimen (see Péringuey's description of

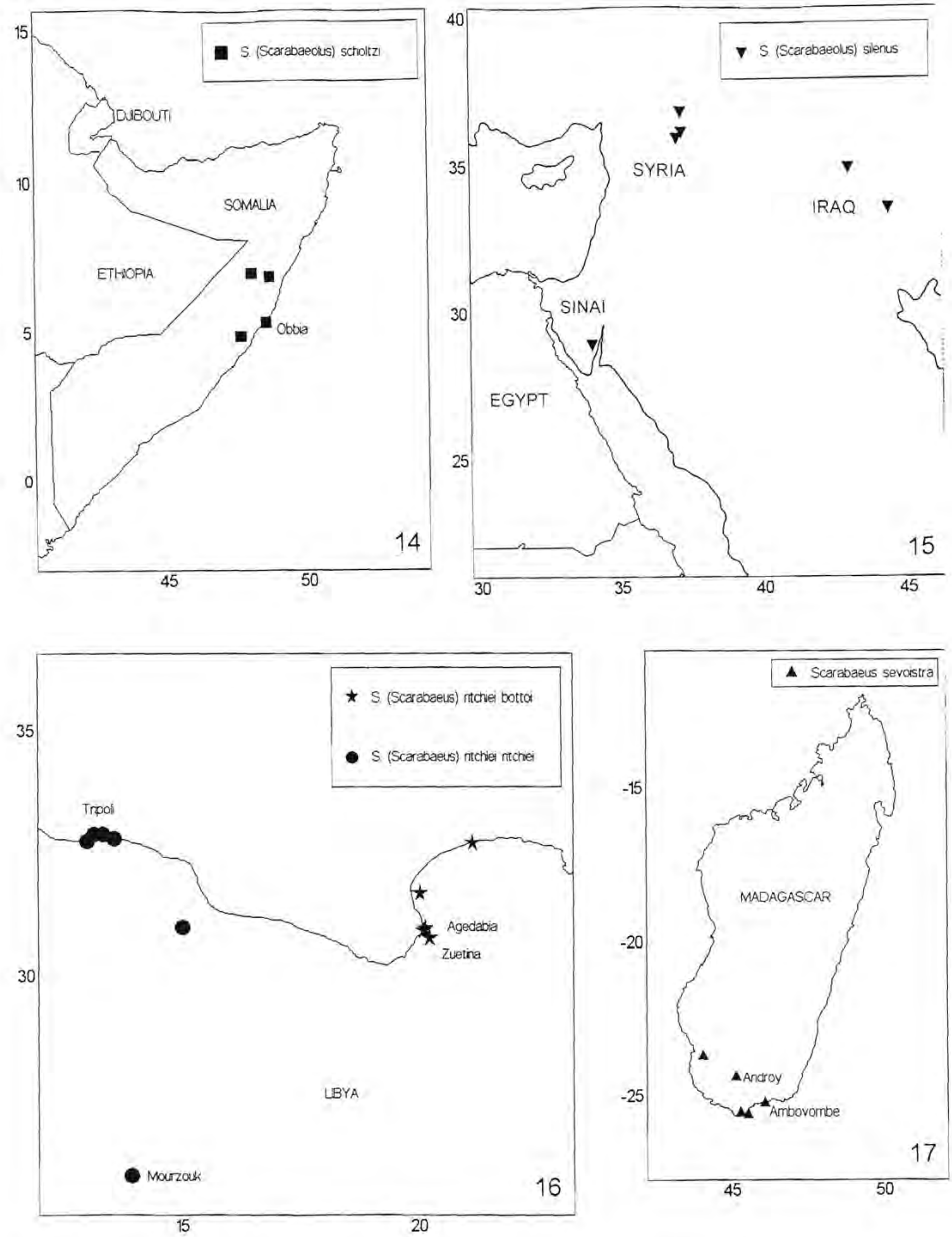
Pachysoma marginatum under *S. (P.) striatus* above for the opposite situation). However, Péringuey's type label is on a male labelled 'Ganab C.Wilmer', while the Walfish specimen lacks a type label. This situation led Holm and Scholtz (1979) to designate the Walfish specimen as lectotype, although the Ganab specimen bears the type label.

Péringuey is renowned for inconsistently or not labelling type specimens (see Cochrane 1995 for a discussion). Reexamination of all available evidence suggests that the lectotype (Walfish) designated by Holm and Scholtz (1979) is in fact the original holotype. Evidence for this includes the following: (1) of all potential type material examined, only the Walfish specimen is dated [Dec. (18)85] before the publication date (1888) of the species. The Ganab specimen bearing the type labels is dated 2.(18)89, which excludes it as a possible type; (2) Péringuey (1902) includes four diagrams (plate 7, figures 31-34) of *Pachysoma* aedeagi. *P. denticolle, P. marginatum, P. hippocrates* and *P. aesculapius* are illustrated, which comprise the only illustrations in Péringuey's papers (1888, 1902, 1908) of *Pachysoma* genitalia. The only dissected *Pachysoma* aedeagi attributable to Péringuey in the SAMC collection (Péringuey Collection) includes only the above four species all labelled in his handwriting. These separately mounted genitalia were probably used for the above illustrations, but can they be matched to specimens?; (3) the potential type specimens include one male from Walfish Bay (1♂) and a pair from Ganab (1♂ 1♀). The only specimen previously dissected and lacking its genitalia is the Walfish Bay specimen (lectotype). Thus, the aedeagus labelled *P. denticolle* by Péringuey is probably from this Walfish specimen; (4) Péringuey (1902) in his 'Catalogue of the Coleoptera of South Africa' provides a new description for *P. denticolle* (the 1888 and 1902 descriptions are strikingly different). In which he mentions the female of *P. denticolle* for the first time, gives a range in body length (16-17mm; width 11mm) and records the distribution as Damaraland. The pair labelled Ganab, Damaraland was probably used for the second description, and possibly this is when Péringuey labelled the Ganab male as type.

This evidence substantiates the choice by Holm and Scholtz (1979) of the Walfish Bay Nightingale specimen as lectotype, but suggests that the Walfish Bay Nightingale specimen is probably the original holotype of *Pachysoma denticolle*. Short of submitting a query to the Zoological Commission, I retain the original lectotype designation, but designate the aedeagus as a paralectotype.

Type material examined (Σ2 spec. [2], 1♀ 1♂, 1♂diss.). **NAMIBIA**: LECTOTYPE ♂, *Pachysoma denticolle* Péringuey designated by Holm and Scholtz 1979: Walfish B, (22.58S 14.30E), Dec. (18)85 (date hard to see) // Nightingale //, / *Pachysoma denticolle*, LP (written in black ink by Péringuey on faded white card) / *Pachysoma denticolle* Péringuey Lectotype, Holm and Scholtz, 1978, (1♂ SAMC); PARALECTOTYPE ♂, *Pachysoma denticolle* Péringuey designated here: (aedeagus mounted with a brass minuten on white card) / *Pachysoma denticolle* LP (1♂ aedeagus SAMC). HOLOTYPE ♀, *Neopachysoma penrithae* Zunino: Lüderitz, SE 2615 Ca, 19 Oct 1970 / H5483 / Holotypus, *Neopachysoma penrithae* mihi, M.Zunino 1977 / (female genital slide labelled) *Neopachysoma penrithae* Zunino, Holotypus, (1♀ SMWN). Paratype: Suid. Namib / H2889, {1♀ MZTI}.

Additional material examined (Σ209 specs. [78], 85♀ 105♂, 8♂diss., 19uns., 1p.). **NAMIBIA**: **Agate Beach**, (26.36S 15.10E), Lüderitz, 19.i.1973, extensive dune field with much *Stipagrastis sabulicola*, M.K.Jensen, (1♂ UPSA); Agate Beach, Lüderitz, SE2615Ca2, (*ca.* 26.33.53S 15.10.58), vii.1978, E.Holm, (1x UPSA); **Awasib Dunes** E at 25.15S 15.43E, Lüderitz, 29-30.i.1974, H17188, Zunnio genital slide, (1♀ UPSA); N Awasib, SE2515Bc3, (*ca.* 25.25.58S 15.33.53E), 4.vii.1976, UP, (1♀ 1♂ UPSA), (1♀ SANC); E Awasib, SE2515Bb1, (*ca.* 25.03.53S 15.48.53E), 11.vii.1976, UP, (1♂ UPSA), (3♂ SANC), (1♀ SAMC); **Blueberge**, 2km inland, 26.07S 14.58E, 18.i.1974, hand-collected, E-Y:297, Endrödy-Younga, (1 TMSA); Damaral., **Ganab**, (23.06S 15.29E), 2.(18)89., // C.Wilmer //, / *Pachysoma denticollis* (sic) type ♂ L P / Type (printed in black onto red card), (1♂ SAMC); (*idem*, but female, with no C.Wilmer on reverse of label, label illegible without other legible label), (1♀ SAMC); **Gobabeb**, (23.34S 15.03E), 408m, 17.iv.1967, (2♀ 2♂ TMSA); Gobabeb, 2mls S., (*ca.* 23.35S 15.02E), 8.iv.1967, Holm, (1♂ TMSA); Gobabeb, 10mls S, (*ca.* 23.42S 15.02E), iii.1968, E.Holm, (1♀ TMSA); Gobabeb, 20mls S, (*ca.* 23.49S 15.02E), vi.1967, E.Holm, (1♀ 2♂ TMSA); Gobabeb, 15km S., 23.44S 15.04E, Diamond Area 2, 14-15.v.1984, J.Irish, H.Liessner, H60772, (1♀ 1♂ SWWN); Namib-Naukluft Park, dunes near Gobabeb, 23.34S 15.03E, iii.1983, R.Oberprieler, (2♂ SANC); SE **Guinasibberg**, SE2515Bc1, (*ca.* 25.18.53S 15.33.53E), 4.vii.1976, UP, (1♀ UPSA), (2♀ SANC); N Guinasibberg, SE2515Ba3, (*ca.* 25.10.58S 15.33.53E), 5.vii.1976, UP, (3♀ UPSA), (2♀ 1♂ SANC), (1♀ SAMC); **Homeb**, 2mls upstream Kuiseb W bank, (*ca.* 23.38.05S 15.13.00E), x.1967, W.J.Hamilton, (includes dung pellet, the size of beetles abdomen), (1♀ TMSA); Namib between Lüderitz & **Hottentotsbay**, (*ca.* 26.23S 15.06E), 10.i.1974, E-Y:274, hand-collected, Endrödy-Younga, (1♂ UPSA); Farm **Kanaän,** 25.53S 16.07E, 7.v.1977, hand-collected on dunes, E-Y:1323, S.Mothlasedi, (1♀ TMSA); Kanaän, 25.52S 16.07E, 2.iv.1976, M.K.Seely, well vegetated red dunes, C1241, (1♂ SMWN); Kanaän 104, SE2516Cc, (25.52S 16.07E), Lüderitz, 22-27.vi.1976, S.Louw, M-L. Penrith, H32993, (14♀ 9♂ SMWN), (2 UPSA); Kanaän 104, SE2516Cc, (25.52S 16.07E), Lüderitz, 25.iv-2.v.1977, M-L. Penrith, S.Louw, H34748, (1♀ 2♂ SMWN); **Koichab Pan**, SE2615Ba3, (*ca.* 26.10.58S 15.33.53E), vii.1978, E.Holm, UP, (2♂ UPSA), (1♂ SANC); Koichab, SE2615Bc1, (*ca.* 26.18.53S 15.33.53E), vii.1982, E.Holm, (1♀ 1♂ UPSA); **Kolmanskop**, 6km SE, 26.45S 12.15E, 5.viii.1989, shifting dunes, day, Endrödy-Younga & Klim., (orange to black), (7 TMSA); **Kolmanskop**, SE2615Cb, (26.37.05S 15.22.05E), 6.x.1979, E.Holm, C.H.Scholtz, (2 UPSA); **Lüderitz**, 30km N, SE2615Ac, (26.22.05S 15.07.05E), 5.x.1979, E.Holm, C.H.Scholtz, (dark form), (2♀ 1♂ UPSA), (3♂ SANC); Lüderitz, SE2615Ca4, (26.40.58S 15.10.58E), 16.vii.1975, UP, (1♂ UPSA); **Namib Desert**, 25.05.05S 15.06.00E, (v.v. of SE on label), 20.vii.1976, *S.sabilicola* covered sandy street, M.K.Seely, C1234, (1♂ SMWN); Namib Desert, 23.45S 15.47E, 8.ii.1981, far east census, 11:30hrs, slipface pit traps, Osberg, C5250, (1♀ SMWN); Namib Desert, 23.46S 15.47E, far east, 29.v.1981, morning middune, Praetorius, C5429, (1♂ SMWN); Namib, 1948, (probably Gaerdes coll.), (1♀ 1♂ TMSA); Namib Desert, **Noctivaga,** 23.43S 15.14E, 22.vi.1981, middune, moderate N wind, clear, 12h25, Praetorius, C5514, (1♀ SMWN); Namib Desert, **Miss Cluckies Fley**, 23.43S 15.19E, 25.v.1981, middune, 16h30, Praetorius, C5501, (1♀ SMWN); (Namib Desert), far east, 23.46S 15.47E, 17.iv.1982, 11h00, midslope, Hamilton, C5711, (1♂ SMWN); **Namib Exped.**, SE2415Cc1, (24.48.53S 15.03.53E), i.1977, Holm, Kirsten & Scholtz, (1♂ UPSA); Namib Exped., SE2615Ab4, (26.10.58S 15.25.58E), i.1977, Holm, Kirsten & Scholtz, (dead faded specimen), (1♂ UPSA); **Namtib Dunes**, 25.58S 16.02E, 8.viii.1989, E-Y:2640, dunes, day, Endrödy-Younga & Klim., (3♀ 1♂ TMSA); Namtib, 70mls NW of Aus, (SE2516Dd), (*ca.* 25.52.05S 16.52.05E), Gt. Namaqualand, C.Koch & van Son, 26.ix.1953, (4♀ 11♂ TMSA); **Natab**, 23.36S 15.03E, 10.xii.1976, L.W.Powrie, C1237, (1♀ SMWN); Natab, 23.35S 15.03E, 25.viii.1976, M.K.Seely, C1236, (1♀ SMWN); Dunes S of **Rechenberg**, 30mls NE Lüderitz, (*ca.* 26.24S 15.27E), ix.1963, W.D.Haacke, (1♀ 2♂ TMSA); **Sandwich Bay**, SE2314Bc1, (*ca.* 23.18.53S 14.33.53E), 7.vii.1975, day, beach, UP, (1♂ UPSA); Sandwich Harbour, (23.20S 14.28E), 28.xii.(19)62, W.Criess, (all black), (4♀ 1♂ TMSA), (1♀ SANC); **Sesriem Dunes**, (24.33S 15.46E), 5.v.1972, Prozesky, (1♀ 2♂ TMSA); **Sossusvlei**, SE2415Cb, (24.37.05S 15.22.05E), 4.vii.1978, L.A.Wessels, (3♂ UPSA), (1♀ SANC); Sossusvlei, SE2415Da3, (24.40.58S 15.33.53E), 14.vii.1975, UP // night, dune //, (1♂ SANC); Sossusvlei, 24.40S 15.24E, 14.viii.1989, E-Y:2649, dunes, day, Endrödy-Younga & Klim., (2♀ 2♂ 6 TMSA); Sossusvlei, Namib-Naukluft Park, 24.18S 15.45E, 7.xii.1992, M.Pusch, (1♀ SMWN); **Spencerbay**, N-hook, 25.40S 14.51E, 11.i.1974, hand-collected, day, E-Y:278, Endrödy-Younga, (1 TMSA); **Spencer Bay Water**, 25.47S 14.54E, 14.i.1974, hand-collected on dunes, E-Y:286, Endrödy-Younga, (1♀ TMSA); **Tiras Dunes**, 26.01S 16.07E, Lüderitz District, 8.iv.1986, J.Irish, (1♀ 1♂ SMWN); **Tsondab** Plains, N fringe, 15mls S of Natab, (*ca.* 23.42S 15.17E), 20.iv.1969, M.Pond, (1♀ 6♂ SMWN); Tsondab Flats, 23.55S 15.20E, 8.vii.1975, M.K.Seely, C1238, (1♂ SMWN); Tsondab Flats, 23.55S 15.20E, 8.vii.1975, M.K.Seely, C1239, (1♂ SMWN); Tsondab Flats, 23.50S 15.04E, Diamond Area 2, 15.v.1984, J.Irish, H.Liessner, H61048, (1♀ SMWN); Tsondab, SE2315Dc1, (23.48.53S 15.33.53E), 12.vii.1975, day, dune, UP, (1♀ UPSA); Tsondab, SE2415Ba1, (24.03.53S 15.33.53E), 11.vii.1975, day, dune foot, UP, (1p UPSA); SE Tsondab Plains, SE2315Cc4, (23.55.58S 15.10.58E), 15.vii.1976, UP, (1♀ 1♂ UPSA); N Tsondab Plains, SE2315Cc1, (23.48.53S 15.03.53E), 14.vii.1976, UP, (1♀ 1♂ UPSA), (1♂ SANC); NE Tsondab Plains, SE2315Cc2, (23.48.53S 15.10.58), 15.vii.1976, UP, (1♀ 1♂ UPSA), (1♀ 3♂ SANC); W Tsondab Plains, SE2314Dd2, (23.48.53S 14.55.58E), 15.vii.1976, UP, (1♀ SANC); Tsondabvlei, Namib-Naukluft Park, at 23.59S 15.27E, 2-26.viii.1989, dunes, day, S.Louw, NMBH 27864, (1♀ BMSA); **Uri Hauchab**, 25.21S 15.16E, 21.vii.1976, M.K.Seely, C1235, (1♂ SMWN); N Uri Hauchab, SE2515Ac2, (25.18.53S 15.10.58E), 6.vii.1976, UP, (2♂ UPSA), (2♂ SANC); **Walfisch. B.**, (22.58S 14.30E), J.Drury, (19)08, (1♂ SAMC); Walvisbai, 8km S of town, 22.59S 14.35E, 19.xi.1974, E-Y: 487, sandy flat, Endrödy-Younga, (orange to black), (2♀ 11♂ TMSA); Walvis Bay, 22.55S 14.28E, 8.iv.1981, S.Braine, (black), (1 SANC); **Wortel**, 23.03S 14.28E, 8.i.1977,



FIGURES 14-17. Distribution of flightless *Scarabaeus (Scarabaeolus)* and *Scarabaeus (Scarabaeus)* species in Africa, the Middle East and Madagascar. (14) *S. (Scarabaeolus) scholtzi* in Somalia; (15) *S. (Scarabaeolus) silenus* in Sinai, Syria, and Iraq; (16) *S. (Scarabaeus) ritchiei* in Libya; (17) *S. (Scarabaeus) sevoistra* in Madagascar. See figure 2 for distribution of *S. (Scarabaeus) cancer* in Angola.

M.K.Seely, C1240, (1♂ SMWN); SE2615Ad4, (26.25.58S 15.25.58E), 10.vii.1980, UP, (2♀ 1♂ UPSA), (4♀ SANC).

Additional localities listed in Holm & Scholtz (1979); **Koichab West**, SE2615Bc, (*ca.* 26.22.05S 15.37.05E), vii.1978, E.Holm, UP, (UPSA); **Namib Exped.**, SE2515Cd2, (*ca.* 25.48.53S 15.25.58E), i.1977, Holm, Kirsten & Scholtz, (UPSA); **Sesriem 137**, Maltahöhe, SE2415Dc, (*ca.* 24.52.05S 15.37.05E), 5-8.iv.1972, (SMWN).

Untraced locality: C1242, (originally from DRU Gobabeb), (1 SMWN). Multiple / ambiguous locality: Homeb / Tsonda(b)vlei, Namib Desert Park, Walvisbaai, SE2315Ca/c, 13.vi.1974, C2898, (1♀ SMWN); Which could be;Ca=23.37.05S 15.07.05E;Cc=23.52.05S 15.07.05E;Homeb=23.39S 15.10E;Tsondabvlei=23.57S 15.24E;Walvisbaai=22.58S 14.30E; No data, (1 TMSA), (2 UPSA).

Specimens from the following locality may be incorrectly labelled because they are outside the species' established range: SOUTH AFRICA; **Mata Mata**, S.Kalahari, (25.47S 20.00E), vi.1956, C.Koch, (2♀ 2♂ TMSA); NAMIBIA: **Kuibis**, (26.41S 16.52E), iv.1933, G.v.Son, (1♂ SANC).

Species of flightless Scarabaeini in the subgenera *Scarabaeus (Scarabaeus)* and *Scarabaeus (Scarabaeolus)*

Key* to the species of flightless *Scarabaeus (Scarabaeus)* and *S. (Scarabaeolus)*

1 Two tarsal claws on all tarsi; one mesotibial spur .... ***S. (Scarabaeus)*** Linnaeus 2

– Two tarsal claws on all tarsi; two mesotibial spurs, second spur greatly reduced in size .... ***S. (Scarabaeolus)*** Balthasar 3

2 (1) Profemora much enlarged and bearing well-pronounced spines; body size large (Holotype 48 mm long); only recorded from Angola .... ***S. (Scarabaeus) cancer*** (Arrow)

– Genae with clearly defined point in front, genal margin smooth and regular; mesocoxae semi-contiguous; distribution centred on coastal Libya .... ***S. (Scarabaeus) ritchiei*** (MacLeay)

– Mentum with ventral protuberance; elytra short; aedeagus symmetrical; distributed in semiarid SW of Madagascar .... ***S. (Scarabaeus) sevoistra*** (Alluaud)

3(1) Genae with clearly defined anterior point, genal margin irregular, may have secondary genal points; Mesopotamian distribution .... ***S. (Scarabaeolus) silenus*** (Gray)

– Genae without anterior points, smooth lateral margins of clypeus and genae separated by incision between genae and clypeus; aedeagus symmetrical; only recorded from Somalia . . . . **S. (Scarabaeolus) scholtzi** Mostert & Holm

*Key modified from Mostert and Holm (1982).

Scarabaeus (Scarabaeolus) scholtzi Mostert and Holm, 1982
(Figures 14, 31, 49, 70)

Scarabaeus (Scarabaeolus) scholtzi Mostert and Holm, 1982: 276.
Mnematium scholtzi (Mostert and Holm, 1982): Carpaneto and Piattella, 1988: 269.

Diagnosis. Clypeus quadridentate, outer clypeal teeth half size of medial teeth, medial teeth separated by broad 'U' shaped gap; genal and clypeal edges unserrated, and separated by an incision at genal-clypeal suture (figure 31); protibia quadridentate, serrations between and proximal to teeth (figure 49); elytra fused, humeral callus absent, no sub-elytral rim, small elytral rim, elytral striae very faint; second mesotibial spur, vestigeal which places this species in subgenus *Scarabaeolus* (Mostert and Scholtz 1986); metatarsal claws, shorter than last tarsal segment; aedeagus symmetrical (figure 70a,b).

Distribution and habitat. Endemic to the coastal plains of Somalia (figure14), occurring in what is also known as the Somali-Chalbi Desert (Costa 1995). Koch (1961) includes a photograph by C.F. Hemming (who collected the type series of *S. (Scarabaeolus) scholtzi*) of Somalian dunes, east of Berbera. This picture possibly depicts likely habitat for *S. (Scarabaeolus) scholtzi*.

Morphology. The head of *S. (Scarabaeolus) scholtzi* resembles that of *Sceliages* species in shape. The mesocoxae of *S. (Scarabaeolus) scholtzi* are completely contiguous as with all *Pachysoma* species, but unlike *Pachysoma* the mesosternal ridge is still present as a distinct hump.

Biology. The mouthparts of *S. (Scarabaeolus) scholtzi* do not appear be adapted for feeding on dry dung or detritus as in *S. (Pachysoma)* species. The epipharynx of *S. (Scarabaeolus) scholtzi* and *Sceliages brittoni* are strikingly similar in morphology. Towards the end of the wet season on the Namaqualand coast, dead millipedes became abundant in certain sandy areas. As *Sceliages brittoni* feeds mainly on dead millipedes, perhaps *S. (Scarabaeolus) scholtzi* has a similar diet which could account for the convergence in epipharyngeal morphology. It seems possible that dead millipedes could be an abundant, localized, but short lived food resource for a flightless beetle?

Comments. Dr Charles Koch visited Somalia in 1958 and collected an abdomen with elytra of a flightless Scarabaeini. Ferreira (1966) examined this abdomen and suggested without reasons that it came from a *Pachysoma* species. Holm and Scholtz (1979) were unable to find this elytron in the TMSA collection and queried how Ferreira (1966) determined it to be a *Pachysoma* rather than a *Mnematium*. Mostert and Holm (1982) were also unable to trace this elytron, but mentioned that it probably belonged to *S. (Scarabaeolus) scholtzi*. The abdomen was discovered in the BMSA collection (which curates some of Ferreira's collection). It consists now of two complete elytra and all the abdominal sternite. Although labelled from Somalia, the specimen was puzzling because the head and thorax were that of *S. (Scarabaeus) ritchiei*. However, due to the distinct mesosternal ridge, and a protuberance on the outer edge of the last abdominal sternite, characters which are absent in *S. (Scarabaeus) ritchiei*, the abdomen was determined to be that of *S. (Scarabaeolus) scholtzi*. Further examination revealed that the *S. (Scarabaeus) ritchiei* pronotum and head were glued to the *S. (Scarabaeolus) scholtzi* abdomen, suggesting a previous mismatch. The parts of the two species have been separated and the *S. (Scarabaeolus) scholtzi* abdomen deposited in the TMSA collection.

Types. Mostert and Holm (1982) record 13 type specimens, but only 11 were traced. The BMNH and UPSA collections are listed by Mostert and Holm (1982) as having two paratypes each, while only one paratype was found in each of these collections.

Type material examined (Σ11 uns. specs., 1♂ diss.). **SOMALIA**: HOLOTYPE ♂; NE. Afr. Somali Rep, 52 km NE El Den, (04.53N 47.38E), coastal plain / 28.10.1971, Hemming T 238 / Holotype, *Scarabaeus scholtzi* Mostert & Holm 1982, (1♂ TMSA). PARATYPES: *idem*, but Paratype, *Scarabaeus scholtzi* Mostert & Holm 1982, (1x BMNH), (6x TMSA), (1x UPSA); Somali Rep., 90 km N. Obbia on Geriban road, (06.53N 48.38E) / T 240 2.xi.1971, C.F. Hemming / Paratype, *Scarabaeus scholtzi* Mostert & Holm 1982, (2x TMSA).

Additional material examined (1x abdomen). **SOMALIA**: Obbia, (Hobyo), (05.21.05N 48.31.32E), SOMALIA, Mudugh., (Mudug, Gobolka), (07.00N 48.00E), viii.1958, C. Koch, (1x abdomen TMSA).

Scarabaeus (Scarabaeolus) silenus (Gray, 1832)

(Figures 15, 32, 50, 71)

Mnematium silenus Gray, 1832: 40; Felsche 1907: 275; Balthasar 1935: 27; Balthasar 1963: 141; Ferreira 1969: 28.

Mnematidium silenus (Gray): Reitter 1894: 183.

Scarabaeus rotundipennus Holdhaus, 1919: 54.

Mnematium rotundipenne (Holdhaus): Balthasar 1935: 28; Balthasar 1963: 141; Ferreira 1969: 28.

Pachysoma rotundipenne (Holdhaus): Holm and Scholtz 1979: 226.

Pachysoma silenus (Gray): Holm and Scholtz 1979: 227.

Scarabaeus (Scarabaeolus) silenus (Gray): Mostert and Holm, 1982: 277.

Diagnosis. Clypeus quadridentate, teeth pointed and almost equal in size, separated by equal gap, genal anterior apex produced into distinct tooth (figure 32); protibia quadridentate, serrations between and proximal to teeth, proximal serrations' coarse; spurs simple, males with inner edge of protibia serrated (figure 50); Sub-elytral rim present, small elytral rim, striae very faint, humeral callus absent; metatarsal claws about half length of last tarsal segment; mesocoxae semi-contiguous (> 1.5 mm), with prominent depression between mesocoxae, anterior to which is prominent mesosternal ridge; male genitalia simple (figures 71a,b).

Distribution. Recorded from the Sinai Peninsula, Aleppo in Syria, Anah and Baghdad in Iraq to Saudi Arabia (figure 15). Probably associated with the Tigris and Euphrates Rivers in Iraq, which extend into Syria as the Al Furat River.

Morphology. The vestigeal second mesotibial spur, which places this species in the subgenus *Scarabaeolus*, is very hard to see. Some specimens of *S. (Scarabaeolus) silenus* examined had lost (open socket visible) their vestigeal spur, the spur is however present in the species.

Biology. Unknown. The mouthpart morphology appears intermediate between that of wet dung feeding *Scarabaeus* and dry dung feeding *Pachysoma*, which suggests a mixed diet of both wet and dry food.

Comments. The inclusion of this species in the subgenus *Scarabaeolus* (*sensu* Mostert and Holm 1982, Balthasar 1965), requires further investigation.

No difference was found between *S. silenus* (distribution centred on the Sinai Peninsula and Saudi Arabia) and its synonym *S. rotundipenne* (distribution centred on Iraq and Syria).

Types. Balthasar (1963) was unable to locate the holotype. Mostert and Holm (1982) examined the holotype, which is housed in the SMTD collection.

Type material examined (1 uns. spec.). SYNTYPE, **ARABIA**: Silenus Ol.* Arab. Ol. (written onto faded yellow card) / 8889 / (1x ZMHB).

Additional material examined (Σ8 uns. specs.). **EGYPT**: Egypt; S.W. Sinai, 10.1.1948, (29.00N 34.00E), H.Field / H.Field B.M. 1954-393 / (6x BMNH), (1x TMSA); **IRAQ**: Persia / 71.30 / (1x BMNH).

Published locality data (in italics). **IRAQ**: *Ana* (Anah), 34.28N 41.56E; *Baghdad*, 33.20.19N 44.23.38E, *Baghdad*, (Muhafazat), 34.00N 43.46E. **SYRIA**: *Aleppo*, (Halab, Muhafazat), 36.00N 37.00E, (Halab), 36.12N 37.10E; *Nahye* (Bayi), untraced.

Scarabaeus (Scarabaeus) ritchiei (MacLeay, 1821)

(Figures 16, 33, 51, 72)

Mnematium ritchiei MacLeay, 1821: 506; Reiche 1841: 212; Reiche 1842: 93; Reitter 1894: 183; Ferreira 1961:26; Balthasar 1963: 138. Holotype: Mourzouk (1 BMNH).

Scarabaeus (Mnematium) ritchiei (MacLeay): Bedel 1892: 282.

Mnematium ritchiei ritchiei MacLeay: Gridelli 1930: 324; Zunino 1984: 96.

Mnematium ritchiei bottoi Gridelli, 1930: 324; Zunino 1984: 96.

Pachysoma ritchiei (MacLeay): Holm and Scholtz, 1979: 226.

Scarabaeus (Scarabaeus) ritchiei (MacLeay): Mostert and Holm, 1982: 275.

Diagnosis. Clypeus quadridentate, clypeal teeth pointed and separated by 'U' shaped depression; posterior edge of genae without pointed flange, genae unserrated, but produced into an extra tooth on anterior edge (figure 33); protibia quadridentate, serrations between and proximal to teeth, spurs simple (figure 51); sub-elytral ridge and rim small, elytral striae vary from faint to distinct between specimens, humeral calli absent; metatarsal claws shorter than last tarsal segment (LTS), and approximately equal to width of LTS; male genitalia simple (figure 72a,b).

Distribution and habitat. Coastal vegetated sand dunes (Balthasar 1963) in Libya (figure 16).

Comments on locality data. The type locality for *Mnematium ritchiei*, i.e. Mourzouk (Murzuq or Marzuq) when compared to most of the coastal locality records, is far inland (figure 16). The distribution maps of Balthasar (1963) and Mostert and Holm (1982) do not show this clearly. The town Murzuq is close to the 'Sahara Murzuq', which are presumably inland sand dunes. There are no locality records joining the two subspecific populations of *S. (Scarabaeus) ritchiei*, but one would expect their distributions to have been continuous at some previous time along the coastline.

Morphological variation. Gridelli (1930) described the subspecies *Mnematium ritchiei bottoi*, which has a Cyrenacian distribution (figure 16). Schatzmayr (1937) synonymised it with *M. ritchiei*. Zunino (1984), using male genitalia and differential reduction of the hind wings recognised the two subspecies as valid. Because only specimens from Tripoli (31°00'N 15°00'E) were examined, no comment can be made on the validity of *S. (Scarabaeus) ritchiei bottoi*. However, from experience with coastal *S. (Pachysoma)* species one would expect a degree of clinal variation across the geographic range of flightless *S. (Scarabaeus) ritchiei*.

Biology. Biology unknown. Various authors have assumed that *S. (Scarabaeus) ritchiei* rolls ball like flying *Scarabaeus* (e.g. Balthasar 1963). The mouthpart morphology appears intermediate between that of wet dung feeding *S. (Scarabaeus)* and dry dung feeding *S. (Pachysoma)*, which suggests a mixed diet of both wet and dry food.

Comments. The size of the mesosternal ridge and hind wing buds (see Zunino 1984) suggests that *S. (Scarabaeus) ritchiei* have not been flightless for as long as *S. (Pachysoma)* species. There is no marked setal development, a typical adaptation for dealing with soft dune sand.

Types. *Mnematium ritchiei* was described from a single specimen that is now in the BMNH collection ('The only specimen known of this interesting insect is now in the British

Museum...'. MacLeay 1821). MacLeay (1821) includes the following data about the specimen, 'Mourzouk, October 1819, D.Ritchie', but this is not on the label itself.

Type material examined (1♂). LECTOTYPE ♂, *Mnematium ritchiei*, MacLeay: Vigor's Type ('Vigor's' written, 'Type' typed, on white disk surrounded by a red circle) / *Ritchii* ML / (written, on now faded white paper) / Babary. (not traced), Capt. Lyon. (typed) / 59.57, Vigors Coll. (typed), (1♂ BMNH).

Additional material examined (Σ26 uns. specs., 2♂ diss.). **LIBYA**: Tripoli, Lyb., (31.00N 15.00E), NMBH11654,55,56,57, (4 BMSA); Tripolis, (31.00N 15.00E), 06 (6 UPSA); Tripolis / Coll. C. Felsche Kauf 20, 1918, (1 SMTD); Tripolis, (3 ZMHB); Tripolitaine, (31.00N 15.00E), Envir. de Tripoli , Alluaud...1899 / Nevinson Coll. 1918-14 (6 BMNH), *idem*, but 302, (1 BMNH); Tripolis / Fry Coll. 1905-100, (4 BMNH); Tripoli, (2 BMNH).

Published locality data. *Scarabaeus ritchiei ritchiei* (MacLeay), Tripolitan Distribution. **LIBYA**; *Mourzouk* (Murzuk; Murzuq), 25.55N 13.55E; *Pirazzoli* (untraced); *d'Orbigny* (untraced). *Scarabaeus ritchiei bottoi* (Gridelli), Cyrenaican Distribution. **LIBYA**; *Sidi Mesri* (untraced, but) Sidi Kasar, 32.42.42N 21.07.55E; *Sidi ben Nur*, Sidibennur (Sidi Bu an Nur), 31.41N 20.01E, (Sidi Abu an Nur), 32.48N 13.36E); *Zuetina* (Az Zuwaytinah), 30.57.15N 20.07.18E, 30.55N 20.05E; *Agedabia*,(Ajdabiya), 30.45.33N 20.13.23E; *En-Ngila*, (An Najilah), 32.45N 13.02E; *Tagiura*, (Tajura), 32.52.54N 13.21.02E.

Scarabaeus (Scarabaeus) sevoistra Alluaud, 1902

(Figures 17, 34, 52, 73)

Scarabaeus sevoistra Alluaud, 1902: 250.
Neateuchus sevoistra (Alluaud): Gillet, 1911b: 309.
Neomnematium sevoistra (Alluaud): Janssens, 1938: 71; Paulian, 1953: 27; Paulian and Lebis, 1960: 13; Ferreira 1961: 26; Mostert and Holm 1982: 275.
Scarabaeus (Scarabaeus) sevoistra Alluaud: Mostert and Holm 1982: 275.

Diagnosis. Clypeus quadridentate, clypeal teeth pointed, but blunt ended; clypeus and genae punctate-striate; small protuberance on frons (figure 34); protibia quadridentate, and markedly sexually dimorphic; no serrations between or proximal to protibial teeth, male protibia, serrated on inner edge and with prominent inward protuberance distally (figure 52), spurs simple in both sexes; pronotal disc smooth, but impressed with circular punctures; shortest elytral length to pronotal length ratios of any flightless Scarabaeini; very faint sub-elytral ridge, elytral rim and striae faint; no metatarsal claws were available for examination. Paulian (1960) includes a habitus diagram where the mesotarsal claws are shorter than the last tarsal segment, but the metatarsus are not illustrated. Male genitalia illustrated in figures 73a,b.

Distribution and habitat. Only recorded from the southwest of Madagascar, in semiarid bush veld (figure 17).

Comments on locality records. Mostert and Holm (1982) map *Scarabaeus sevoistra* in the north east of Madagascar. According to the NIMA GEOnet Names Server (Roher 1999) there are 60 Marovato, four Ambovombe, and eight Androy localities in Madagascar. However, Faux Cap (Betany) is used only once in Madagascar, and thus all localities were chosen from the semiarid bush veld of southwestern Madagascar.

Morphology. S. (Scarabaeus) sevoistra differs from the other flightless Scarabaeini in that the head resembles *Kheper* species. The absence of serrations on the outer edge of the protibia, is another characteristic of *Kheper* species. The mesotarsal claws are typical of *Scarabaeus* species, i.e. two curved claws, but no metatarsal claws were available for examination. A single metatarsal claw would place this species with *Kheper* rather than *Scarabaeus*. Mesocoxae semi-contiguous (0.58 mm; 1♀), and separated by a depression. Mesosternal ridge present, but more reduced than *S. (Scarabaeus) ritchiei*, *S. (Scarabaeolus) silenus* and *S. (Scarabaeolus) scholtzi.*

*Biology.*Foraging and feeding biology unknown. However, the mouthpart morphology suggests wet dung feeding.

Comments. S. (Scarabaeus) sevoistra is one of three Scarabaeini recorded from Madagascar, the other two species include *Scarabaeus radama* Fairmaire, 1895 which morphologically is a typical flying *Scarabaeus.* While *Madateuchus viettei* Paulian, 1953 which Mostert and Scholtz (1986) synonymised with *Scarabaeus* has characteristics placing it with *Kheper* (three protibial teeth) and *Scarabaeus* (two tarsal claws).

Types. Alluaud (1902) described the species from a single specimen (length 22 mm), collected in the Analavondrove region at Androy in February 1901 by Dr J. Decorse. Ferreira (1961) lists the holotype in the MNHN collection.

Material examined (Σ2 specs., 1♀ 1♂). **MADAGASCAR**; Marovato (25.32S 45.16E), Ambovombe Distr. (25.10S 46.05E or 25.12S 46.04E), i.1956, leg. C.Koch, (1♀ TMSA), *idem*, but / Museum Frey München / NMBH11652, (1♂ BMSA). The male specimen is badly damaged, has only one complete protibia and its aedeagus has been lost.

Published locality data. **MADAGASCAR**; Type locality, *Androy*, 24.21S 45.07E or 23.41S 44.03E; *Faux Cap* (or Betany), 25.34S 45.31E.

Scarabaeus (Scarabaeus) cancer (Arrow, 1919)

(Figures 1, 2, 35, 53, 74)

Mnematium cancer Arrow, 1919: 433; Boucomont 1925: 116; Ferreira 1961: 26; Balthasar 1963: 139; Ferreira 1969: 28.

Pachysoma cancer (Arrow): Holm and Scholtz 1979: 227.

Scarabaeus cancer (Arrow): Mostert and Holm 1982: 278.

Diagnosis. Clypeus quadridentate, clypeal teeth pointed, (both specimens examined are worn, so shape of apex of clypeal teeth cannot be determined); genae extended laterally, anterior edge produced into a point (also worn), posterior edge coarsely serrate, dorsal surface with scattered setiferous punctures (figure 35); protibia quadridentate, (no sign of serrations between worn protibial teeth), edge irregular below protibial teeth (figure 53); profemur enlarged, spined, procoxae with large spines on anterior edge; spurs simple in both sexes; very faint sub-elytral ridge, elytral rim larger, humeral calli absent, anterior edge of elytra rounded, striae faint; metatarsal claws were absent in both specimens, but Arrow (1919) describes tarsi and claws as 'both pairs of tarsi are rather broad and the claws are minute, short, straight, and not divergent'; mesocoxae contiguous, deep depression separating them; mesosternal ridge absent; male genitalia illustrated in figures 74a,b.

Distribution and habitat. Only recorded from the Kwatiri and Longa rivers in Angola (Boucomont 1925), (figures 1,2). Based on the distribution of the other flightless Scarabaeini (figures 1,2), one would expect this species to occur in the coastal dunes north of the Kunene River, i.e. the Mocamedes Desert. The known distribution of *S. (Scarabaeus) cancer* suggests rather an association with inland rivers. Sand bodies near these rivers would be a likely place to look for *S. (Scarabaeus) cancer.*

Comments on locality data. When Arrow (1919) described *Mnematium cancer* he remarked, 'A single specimen of the extraordinary insect here represented, bearing no label to record its origin or habitat, was in the collection of the late BG. Nevinson, recently presented to the British Museum by his son. Probably, like its nearest allies, it inhabits the western part of southern Africa, possibly the Bihé district of Angola, from where Mr. Nevinson received other interesting beetles'. As the BMNH collection currently has two specimens, *S. (Scarabaeus) cancer* was obviously collected again as the female does not have a BMNH locality label. Boucomont (1925) records two localities in the Kubango District of Angola, where *S. (Scarabaeus) cancer* was collected. The female in the BMNH possibly comes from this expedition.

Morphology. S. (Scarabaeus) cancer is hard to place within the Tribe Scarabaeini. The profemora and procoxae suggest it evolved from a *Pachylomerus* like ancestor. The asymmetrical aedeagus and two tarsal claws place it closer to *Scarabaeus*. While the shape of the head is very similar to *S. (Scarabaeus) ritchiei, S. (Scarabaeolus) silenus* and the flying *S. (Scarabaeus) multidentatus*, placing it within the *Mnematium / Mnematidium* species group. The degree of morphological change that has occurred since wing loss, is similar to *Pachysoma*, i.e. contiguous mesocoxae, mesosternal ridge absent, fused elytra, rounded anterior elytral edge. The mouthparts of *S. (Scarabaeus) cancer* are closer to *Pachysoma* than to *Mnematium* species. Which could be a result of their geographical proximity and an equal lapse in time since wing loss?

Biology. The biology of this species is unknown. However, based on the biology of other Scarabaeini one could expect *S. (Scarabaeus) cancer* to behave and forage like *Pachylomerus femoralis* (see Tribe 1976) or *Scarabaeus catenatus* (see Sato 1997, 1998). Both these flying species have very short mesocoxal distances, which is probably an adaptation or pre-adaptation to a multi-foraging strategy, and enlarged profemora. The mouthpart morphology of *S. (Scarabaeus) cancer* is closest to *S. (Pachysoma)* species, which suggests dry dung feeding or at least both dry and wet feeding. Collected during April and May 1913.

Comments. Arrow (1919) refrained from placing *S. (Scarabaeus) cancer* in its own genus, because of the unsatisfactory character of several genera within the Scarabaeini at the time. Holm and Scholtz (1979), suggested that if any species warranted a separate genus *S. (Scarabaeus) cancer* would. Mostert and Holm (1982), discussed *S. (Scarabaeus) cancer* as *incertae sedis* but placed it within *Scarabaeus sensu lato*. The temptation to create a new genus is great, probably because of the large body size and spectacular profemora of *S. (Scarabaeus) cancer*. *S. (Scarabaeus) cancer* warrants a separate genus no more than *S. (Scarabaeus) sevoistra* or *S. (Scarabaeolus) scholtzi* (which are just as unique, but much smaller). Flying species seemingly warranting their own genera includes; *S. galenus*, *S. multidentatus*, and *S. proboscideus*.

Eighty years after the description of *S. (Scarabaeus) cancer*, a well-supported decision on the generic placement of this species can still not be made. Progress has been compounded by the lack of specimens (only two known) and biological information for *S. (Scarabaeus) cancer*. With the advent of molecular biology, molecular data (if ever *S. (Scarabaeus) cancer* is recollected) should be added to the morphological before a decision is made regarding the origin or generic placement of *S. (Scarabaeus) cancer*. As the last known collection of this species was 86 years ago, and the area where they occur is probably mined, this might never be possible.

Types. *Mnematium cancer* was described from the single male holotype, housed in the BMNH collection (Arrow 1919).

Type material examined (1♂ diss.). HOLOTYPE ♂, **ANGOLA**: (No type locality, but Bihé (Kuito) District at 12.23S 16.56E suspected) / Holotype (white paper disk with a red circle, 'Holotype' typed in black) / Nevinson Coll. 1918-14 / *Mnematium cancer* type Arrow / Aedeagus point mounted / *Mnematium cancer* ♂ Arrow, M.E. Bacchus, det. 1975, Holotype, (1♂ BMNH).

Additional material examined (1♀ diss.). **ANGOLA**: (No locality data), / *Mnematium cancer* Arrow, det. R.J.W. Aldridge 1978 / *Pachysoma cancer* (Arrow) det. Holm & Scholtz 1978 / (1♀ BMNH).

Published locality data. **ANGOLA**: River Kwatiri (15.50S 20.10E), 1200 m, April 1913; River Longa (15.20S 18.50E), 1200 m, May 1913.

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Appendix 1a. Checklist of the species of *Scarabaeus (Pachysoma)*

Scarabaeus (Pachysoma) aesculapius Olivier, 1789.
= Ateuchus barbatus Thunberg, 1818.
= Pachysoma validum Boheman, 1857.
Scarabaeus (Pachysoma) bennigseni (Felsche, 1907).
= Pachysoma granulatum Ferreira, 1953b.
Scarabaeus (Pachysoma) denticollis (Péringuey, 1888).
= Neopachysoma penrithae Zunino, 1977.
Scarabaeus (Pachysoma) endroedyi Harrison, Scholtz & Chown **sp. n.**
Scarabaeus (Pachysoma) fitzsimonsi (Ferreira, 1953a).
Scarabaeus (Pachysoma) gariepinus (Ferreira, 1953a).
Scarabaeus (Pachysoma) glentoni Harrison, Scholtz & Chown **sp. n.**
Scarabaeus (Pachysoma) hippocrates (MacLeay, 1821).
= Pachysoma macleayi Castelnau, 1840.
= Pachysoma hessei Ferreira, 1953a.
Scarabaeus (Pachysoma) rodriguesi (Ferreira, 1953a).
Scarabaeus (Pachysoma) rotundigenus (Felsche, 1907).
Scarabaeus (Pachysoma) schinzi (Fairmaire, 1888).
Scarabaeus (Pachysoma) striatus (Castelnau, 1840).
= Pachysoma marginatum Péringuey, 1888.
= Irrorhotides fryi Shipp, 1896.
Scarabaeus (Pachysoma) valeflorae (Ferreira, 1953a).

Appendix 1b. Checklist of the species of flightless Scarabaeus (Scarabaeolus)

Scarabaeus (Scarabaeolus) scholtzi Mostert and Holm, 1982.
Scarabaeus (Scarabaeolus) silenus (Gray, 1832).
= Scarabaeus rotundipennus Holdhaus, 1919.

Appendix 1c. Checklist of the species of flightless Scarabaeus (Scarabaeus)

Scarabaeus (Scarabaeus) cancer (Arrow 1919).
Scarabaeus (Scarabaeus) ritchiei ritchiei (MacLeay, 1821).
Scarabaeus (Scarabaeus) ritchiei bottoi (Gridelli, 1930).
Scarabaeus (Scarabaeus) sevoistra (Alluaud, 1902).

Index to genera, subgenera, species, subspecies and synonyms

Valid names in **bold**; synonyms in roman. Page numbers: key in parentheses; species heading first.

CHAPTER 4

CONCLUSION AND SUMMARY

The cladistic analysis of *Scarabaeus (Pachysoma)* MacLeay reveals that *Pachysoma* represents a derived clade of the large and variable genus *Scarabaeus* Linnaeus. Desert animals are renowned for exhibiting an array of behavioural, physiological and morphological adaptations to their environment (Louw and Seely 1982, Cloudsley-Thompson 1983, 1991, Wilson 1989, Costa 1995, Somme 1995, Henschel 1997). Thus when one considers the selective effect of an arid environment, it is not surprising that *S. (Pachysoma)* evolved from a *Scarabaeus/Mnematium*-like ancestor adapted to the specific environmental conditions of the Namib Desert. Their dragging foraging strategy, diet of dry dung and detritus, reduced mesocoxal distance and well-developed psammophily and aptery are all indications of the biological and morphological changes that *S. (Pachysoma)* species have undergone. This specialisation is also evident in the flying genera of the tribe Scarabaeini that appear to have radiated into other feeding niches. These include *Kheper*, *Drepanopodus* and *Scarabaeus (Scarabaeus)* as predominately wet dung feeders; *Scarabaeus (Scarabaeolus)* as wet dung and carrion feeders; *Sceliages* as millipede feeders and *Pachylomerus* with a mixed diet of wet dung, fruit and carrion.

The morphological ancestor of *S. (Pachysoma)* (see figure 1 in chapter 2), undoubtedly similar to a *Mnematium* species, must have inhabited arid areas. *Mnematium*, unlike *S. (Pachysoma)*, has not undergone such extensive morphological and biological adaptation to their xeric environment. This is evident from their mouthpart morphology, intermediate between dry and wet dung feeding. Additionally, *Mnematium* species show slight psammophilous adaptation (i.e. long leg setae and spatulate mesospurs as present in *S. (Pachysoma)*), and the degree of morphological reduction is slight. For example, degree of brachyptery varies among *Mnematium cancer*, *Mnematium silenus* and *Mnematium ritchiei* while in *S. (Pachysoma)* species it is uniformly advanced.

The polyphyletic origin of wing loss (figure 1 chapter 2) displayed in the tree topology supports hypotheses proposed by Holm and Scholtz (1979) and Mostert and Holm (1982), that aptery has evolved more than once within the Scarabaeini. Consequently there is no justification for the Pachysomina subtribe composed of four flightless groups, *Pachysoma, Neopachysoma, Mnematium* and *Neomnematium* (see Ferreira 1953). This is evident by the size of *Mnematium* wing buds in *M. ritchiei* (see Zunino 1984), semi-contiguous mesocoxae in *M. silenus* and presence of a mesosternal ridge in *M. ritchiei* and *M. silenus*. Based on figure 1 in chapter 2, elevating *Pachysoma* to generic level would make the genus *Scarabaeus* paraphyletic. Unfortunately, *Scarabaeus* is still paraphyletic with the continued recognition of *Kheper, Drepanopodus* and *Sceliages*. However, for practical purposes *Pachysoma* is proposed as a subgenus of *Scarabaeus*. The inclusion of *Scarabaeus (Scarabaeolus) scholtzi* and *M. silenus* (*sensu* Mostert and Holm 1982) in the subgenus *Scarabaeolus* (*sensu* Balthasar 1965) makes *Mnematium* polyphyletic and is thus regarded as synonymous with *Scarabaeus*. Lacking synapomorphies for *Neomnematium* and *Neopachysoma*, these genera are included as synonyms with *Scarabaeus (Scarabaeus)* and *Scarabaeus (Pachysoma)*, respectively. It is beyond the scope of this study to alter the generic status of *Kheper*, *Sceliages* and *Drepanopodus*, but their retention as valid genera makes *Scarabaeus* paraphyletic, and a system of subgenera to include them within *Scarabaeus* is thus suggested to future workers.

Five modes of food relocation have been recorded in the Scarabaeini. The four main clades of the cladogram (figure 1 chapter 2) include one or more of these relocation strategies. Of interest is that the 'super-telecoprid' *Kheper*, which only roll, is apical, while taxa with more than one form of relocation behaviour are more basal in the tree (e.g. *Pachylomerus*, *Scarabaeus galenus* and *Scarabaeus catenatus*), while the *Pachysoma* clade represents derived draggers. A morphological change associated with aptery is a reduction in the mesocoxal distance (see Scholtz 1981). However, taxa with reduced mesocoxal distance also have aberrant or multi-strategy relocation behaviours. Thus, there may be an association between the mesocoxal distance and the predominant mode of foraging.

A sandy substrate is required by *S. (Pachysoma)* species to rehydrate their dry food, but flying taxa with aberrant relocation strategies (*Pachysoma* which drag food forward can also be classified as aberrant relocators in the telecoprid sense) also prefer a sandy substrate (see Sato 1997).

Scarabaeus (Pachysoma) are restricted to the semiarid to arid coastal sands of southern Africa (see figure 1 chapter 3). The remaining flightless Scarabaeini have also been recorded from similar xeric areas (see figure 2 chapter 3), suggesting an association between wing loss and aridity in the Scarabaeini.

The subgenus contains 13 species, of which 2 are described as new. Types (lectotype and paralectotypes) are designated and rediscovered types listed in the abstract of chapter 3 and discussed in that same chapter. The revision illustrates the clinal morphology of most *S. (Pachysoma)* species. The large number of *Scarabaeus (Pachysoma) hippocrates* specimens examined, covering most of their range, is an especially good example of the clinal gradation of morphology over their distribution. Unless detected, this can lead to misinterpretations of species boundaries. For example, the proposed species, *Neopachysoma penrithae* Zunino and subspecies *Scarabaeus (P.) denticollis penrithae*, represent the southern extreme of a clinal population when sufficient material is available for study (see *S. (P.) denticollis* comments in chapter 3). *Scarabaeus (Pachysoma) glentoni* and *Scarabaeus (Pachysoma) endroedyi* appear to represent a vicariance speciation event, with the Olifants River as the boundary separating these species and two populations of *S. (P.) hippocrates*. *S. (P.) glentoni* is especially interesting as this species hardly differs from *S. (P.) hippocrates* externally, but has male genitalia that are strikingly different (see figures 58a,b,c and 59a,b,c in chapter 3).

To date, nine of the 13 species of *S. (Pachysoma)* have been observed only dragging dry dung and detritus forward (see species' biology in chapter 3). Although, there is a single record of *Scarabaeus (Pachysoma) gariepinus* making and rolling a dung ball from fresh dung (Mostert and Holm 1982). However, not once during six months of field work was this observed, even when fresh dung was offerred. However, the foraging strategies as exbited by *S. galenus* (Tribe 1976, Halffter and Halffter 1989, Doube 1990, Ybarrondo and Heinrich 1996) and *S. catenatus* (Sato 1997, 1998) suggest that modification of ball rolling could lead to dragging.

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OPSOMMING

Die filogenetiese geldigheid van *Pachysoma* MacLeay, 1821, word kladisties ondersoek. Die kladistiese analise van 64 volwasse karakters van 37 taksa sluit wat alle genera van die Scarabaeini (behalwe die monotipiese *Madateuchus* Paulian, 1953) insluit, dui aan dat sommige huidig erkende genera (nl. *Sceliages* Westwood, 1837; *Kheper* Janssens, 1940; en *Drepanopodus* Janssens, 1940) 'n polifiletiese oorsprong het. *Pachysoma* behels 'n monofiletiese klade van hoogs gevorderde ('derived') *Scarabaeus* Linnaeus, 1758. Om nomenklaturale stabiliteit in die Scarabaeini te bevorder is dit wenslik om *Pachysoma* as 'n subgenus van 'n uitgebreide genus *Scarabaeus* Linnaeus, 1758 te beskou. *Neopachysoma* Ferreira, 1953; *Mnematium* MacLeay, 1821 en *Neomnematium* Janssens, 1938 word behou as sinonieme van *Scarabaeus sensu latu*. Die unieke biologie van *Pachysoma* word geïnterperteer in die lig van aanpassings tot droë toestande, en is deels afkomstig van balrolgedrag en voeding op nat mis. Daar word gepostuleer dat die verdorring van die Namibwoestyn die evolusie van *Pachysoma* vanaf 'n *Scarabaeus*-tipe voorouer geïnisiëer het, terwyl duinbewegings hul huidige verspreiding verklaar. Dit blyk dat die evolusie van vlugloosheid bemiddel word deur 'n verwantskap tussen droë mis- en detritusvoeding, uitsonderlike hervestigingstrategieë, en die teenwoordigheid in droë, sanderige habitatte. Die evolusionêre geskiedenis van *Pachysoma* word bespreek aan die hand van die filogenetiese analise, geografiese verspreidings, biologie, substraat, en voedselversamelingsstrategie.

Die subgenus *Scarabaeus (Pachysoma)* MacLeay word hersien. Al 13 spesies van die subgenus is endemies tot die weskus van suidelike Afrika. 'n Sleutel tot al die spesies is saamgestel en hul verspreidings is gekarteer. Twee nuwe spesies, *Scarabaeus (Pachysoma) endroedyi* en *Scarabaeus (Pachysoma) glentoni*, word van die suid-westelike Kaap Provinsie beskryf. Die subspesie *S. (P.) denticollis penrithae* (Zunino) word gesinoniemiseer met *S. (P.) denticollis denticollis* (Péringuey). Die sinonimie van *S. (P.) hessei* (Ferreira) met *S. (P.) hippocrates* (MacLeay) word bevestig. *Scarabaeus (P.) valeflorae* (Ferreira), voorheen gereken 'n sinoniem van *S. (P.) schinzi* (Fairmaire) word herstel as 'n geldige spesie. Die vermiste tipereeks van *S. (P.) hessei* (Ferreira) word nagespeur. 'n Lektotipe word aangewys vir *S. (P.) aesculapius* Olivier, en drie paralektotipes word aangewys vir *S. (P.) marginatus* (Péringuey). Aantekeninge oor die tipereekse, verspreidingsrekords, morfologiese variasie en bekende biologie van al die vluglose Scarabaeini word gegee. 'n Oorsiglys van die geldige spesies en die sinonieme van *Pachysoma, Neopachysoma, Mnematium* en *Neomnematium* word ingesluit.

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