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A revision of the endemic south-western African dung beetle subgenus *Scarabaeus (Pachysoma)* MacLeay, including notes on other flightless Scarabaeini (Scarabaeidae: Scarabaeinae)

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The subgenus *Scarabaeus (Pachysoma)* MacLeay, 1821, is revised. All 13 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 south-western Cape are described. The subspecies *S. (P.) denticollis penrithae* (Zunino) is synonymized with *S. (P.) denticollis denticollis* (Péringuey). The synonymy of *S. (P.) hessei* (Ferreira) with *S. (P.) hippocrates* (MacLeay) is confirmed. *Scarabaeus (Pachysoma) 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.

Introduction

The genus *Pachysoma* MacLeay, 1821, was last revised by Holm and Scholtz (1979). In a study that focused on all the flightless Scarabaeini, Mostert and Holm (1982) synonymized *Pachysoma* with *Scarabaeus* Linnaeus, 1758, and elevated *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

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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)* (see Harrison *et al.*, unpublished). Holm and Scholtz (1979) included the species of *Mnematium* MacLeay, 1821, within *Pachysoma*. Their system is not followed here, because *Mnematium*, *Neomnematium* Janssens, 1938, and *Mnematidium* Ritsema, 1889, are included within *Scarabaeus sensu lato* (see Harrison *et al.*, unpublished). All subsequent use of *Pachysoma* herein is at the subgeneric level.

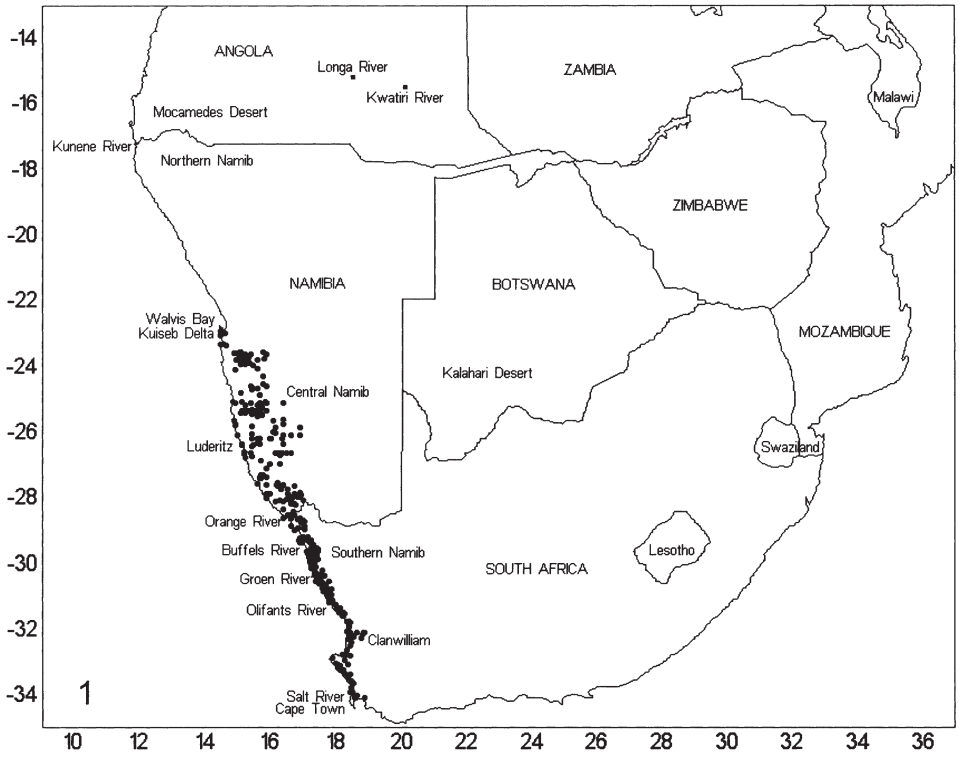
Scarabaeus (Pachysoma) currently comprises 13 species endemic to the sandy coastline from Cape Town (33°56′S, 18°28′E) in South Africa to Walvis Bay (22°58′S, 14°30′E) in Namibia (figure 1). The northerly distribution of *S. (Pachysoma)* is abruptly halted at the Kuiseb River (23°03′S, 14°27′E), which marks the end of the sandy central Namib dune sea. The southern and easterly limits of *S. (Pachysoma)* are, however, 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)* species, *S. (Pachysoma)* species do not make dung balls but collect dry dung pellets and detritus, which they drag forward to preconstructed burrows (refer to Harrison *et al.*, unpublished 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 re-examined. 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, personal communication), and access to previously unavailable material (see Harrison, 1999).

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 on to 1:250 000 Topocadastral maps. Collecting efforts were thus focused 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

FIGS 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*).


ANGOLA
Longa River
Kwatiri River
ZAMBIA
Malawi
Mocamedes Desert
Kunene River
Northern Namib
ZIMBABWE
NAMIBIA
BOTSWANA
Walvis Bay
Kuiseb Delta
MOZAMBIQUE
Kalahari Desert
Central Namib
Luderitz
Swaziland
Orange River
Buffels River
Southern Namib
Lesotho
SOUTH AFRICA
Groen River
Olifants River
Clanwilliam
Salt River
Cape Town
1
-14
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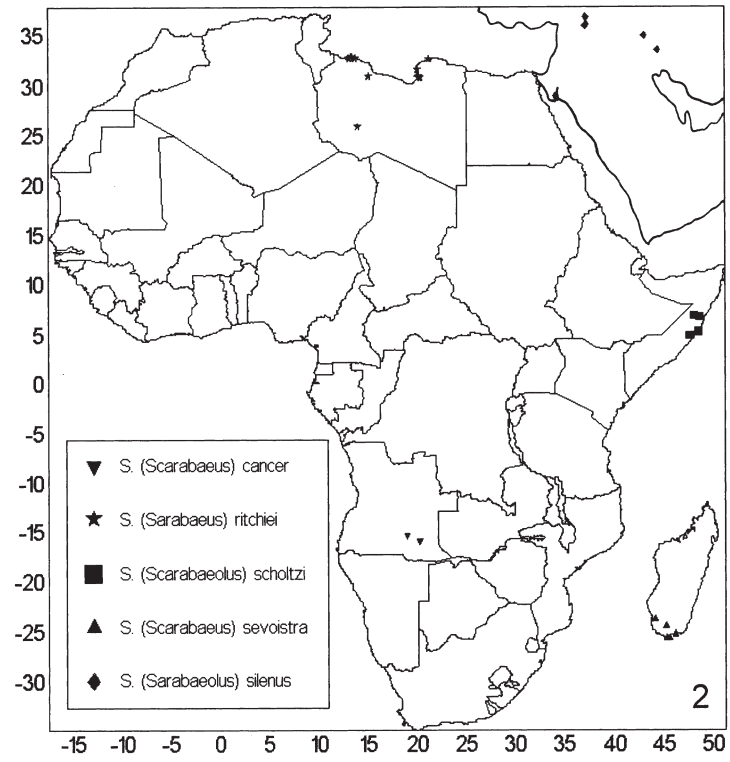
-34
10 12 14 16 18 20 22 24 26 28 30 32 34 36


S. (Scarabaeus) cancer
S. (Sarabaeus) ritchiei
S. (Scarabaeolus) scholtzi
S. (Scarabaeus) sevoistra
S. (Sarabaeolus) silenus
2
35
30
25
20
15
10
5
0
-5
-10
-15
-20
-25
-30
-15 -10 -5 0 5 10 15 20 25 30 35 40 45 50

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.

Material and methods

Material examined is in the following depositories; acronyms, unless marked by an asterisk, follow Arnett *et al.* (1999): AMGS, Albany Museum, Grahamstown, South Africa; BMNH, The Natural History Museum, London, UK; 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, Kimberley, 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 was dry pinned specimens. However, fragments of dead specimens were collected and often represent the only evidence that a species of *S. (Pachysoma)* 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: presence (in ♀) or absence (in ♂) 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 in ♂; broad in ♀). Locality data for the additional material examined is not included here, but is available from the authors or Harrison (1999).

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.

Types. Ferreira (1953a, 1953b) 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 we 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 on to 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 on to 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 'O Sneeukop'.

Morphology. Terminology used follows Lawrence and Britton (1991), and Torre-Bueno (1989). Using external morphology specimens were sorted into morpho-species, 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, whereas 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) coloration from the sand type of microsculpture, pronounced elytral

rim and elytral intervals. Care should be taken to focus on the actual microsculpture 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 dependent 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, 1996, personal communication).

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 3 min 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 on to 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 discernible; (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–c, 64–65a–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 remarks will be added here. We believe *Scarabaeus (Pachysoma)* MacLeay represents a derived branch of *Scarabaeus* (see Harrison *et al.*, unpublished), 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 south-western 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 horn-like 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)	*S. (P.) schinzi* (Fairmaire)
–	No serrations between or proximal to protibial teeth (figure 44)	*S. (P.) 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	*S. (P.) 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	*S. (P.) 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) . . . . . *S. (P.) denticollis* (Péringuey)
– Protibia without internal projections opposite sub-apical outside serration (figure 42); elytra markedly flat and deeply striate . . *S. (P.) bennigseni* (Felsche)

8(6) Elytra smooth, shiny; protibia with sub-apical projection on inside (figure 46) . . . . . *S. (P.) rotundigenus* (Felsche)
– Elytra striate; pronotum and elytra greyish black with band of indument around outer margin; protibia not dimorphic, spur simple (figure 41) . . . . . *S. (P.) 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) . . . . . *S. (P.) 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) . . . . . *S. (P.) 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 . . . . . *S. (P.) endroedyi* sp. n.
– Metafemur with two dense, semicircular combs of bristles on the underside . . . . . *S. (P.) 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) . . . . *S. (P.) aesculapius* Olivier

*Key modified from Holm and Scholtz (1979).

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

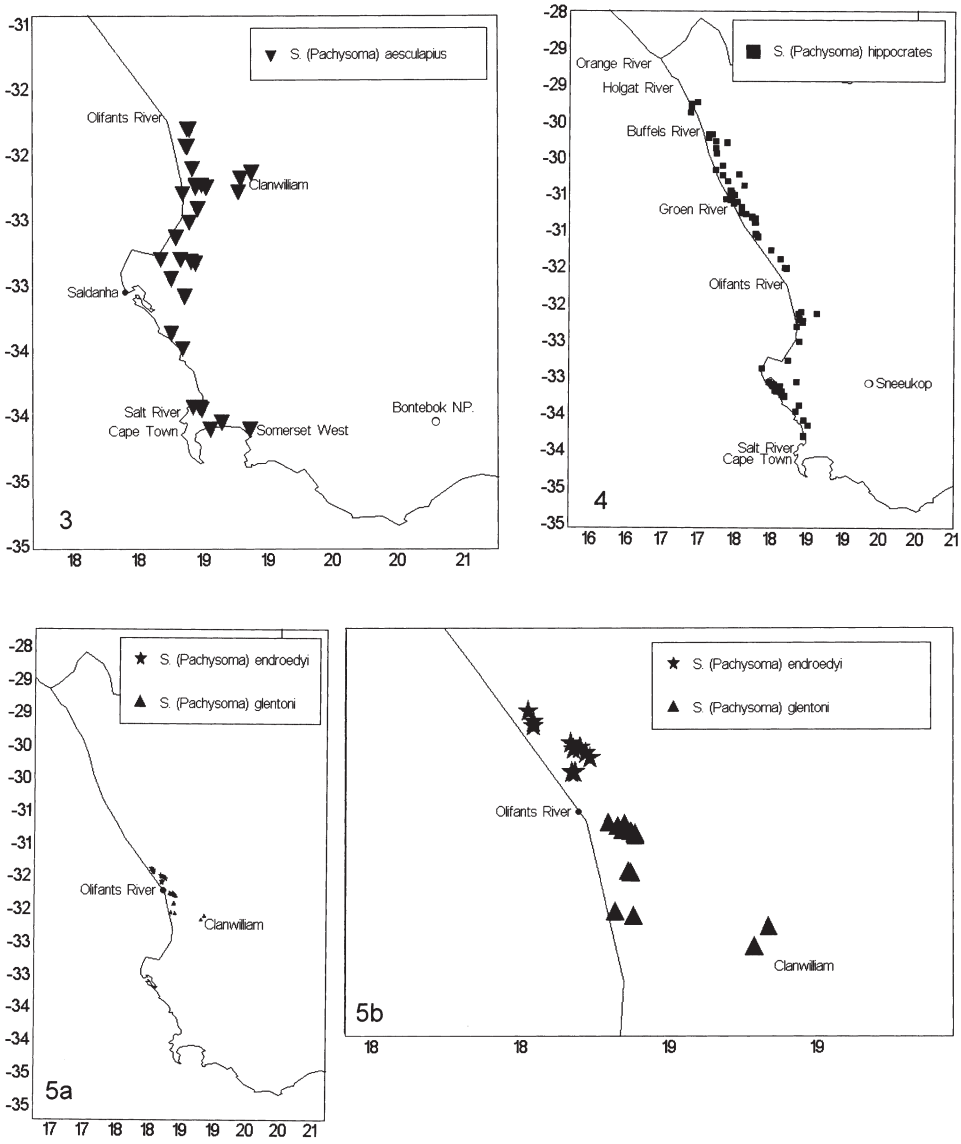
Scarabaeus aesculapius Olivier, 1789: 154; Olivier, 1790: 172; Hausmann 1807: 252; Mostert and Holm, 1982: 275. Lectotype designated here: no locality (1♂ BMNH).

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.



FIGS 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.

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, 1999, personal communication).

Scarabaeus (Pachysoma) 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. We 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 J. du G. Harrison (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 habit 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* from Leipoldtville in morphology. 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 (1996, personal communication) 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 (near the Olifants River) (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. We 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 characterized 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 27 mm, width 19 mm) 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* recorded the clypeus as quadridentate (Thunberg, 1818), whereas 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) mentioned 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 a.m.), and late afternoon (*ca* 16:00–18:00 p.m.). 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 (see label data in type material below). 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 borrowed a specimen or specimens from Olivier, which MacLeay then labelled as his type (i.e. MacLeay's type) or compared Olivier's specimen with *P. aesculapius* material in the BMNH, before labelling it as his type (i.e. MacLeay's type). As Olivier's types are considered lost, this specimen either came from the Olivier series or was at least compared to Olivier's 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 (2 uns. NHRS), (1♀ BMNH). An additional female paralectotype (see type material for label data) is however in the TMSA collection.

Type material examined (3 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 on to 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 from South Africa (Σ173 specs [42], 61♀ 107♂, 28♂ diss., 5uns., 2eth., 7p.).

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–c.

Distribution, habitat and conservation. Coastal south-western 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. *Scarabeus (Pachysoma) 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) (5000 ft) locality near Wellington, is probably due to an incorrectly labelled specimen. This specimen was supposedly collected by Dr K. H. Barnard, who worked at the SAMC from 1911 to 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'. However, a comparison of Barnard's handwritten locality labels on *Colophon* specimens in the SAMC with that on the Sneeukop *S. (P.) hippocrates* specimen reveals that the writing is not Barnard's, which additionally suggests a mislabelling. 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 *S. (P.) 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, whereas *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, characterized 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), characterized 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 non-specialist. We 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. Scarabaeus (Pachysoma) 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 and 25 contained only detritus. This suggests that *S. (P.) hippocrates* prefers detritus. Two separate attempts were made to breed *S. (P.) hippocrates* in the laboratory. Three pairs (between 1 September 1996 and 23 January 1997) and six pairs (between 9 September 1998 and 4 December 1998) of *S. (P.) hippocrates* were placed in round 25 litre buckets and 5 litre 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) listed the holotype, allotype and 12 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 10 paratypes from the SAMC were discovered during reorganization (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 on faded white traingle) / 58.60. (written on blue disk) / Type (printed on white disk, surrounded by a red circle) / *Pachysoma hippocrates* (Kirby MS), Type McLeay. (written on now faded white paper) / *Pachysoma hippocrates* M'Lea, Holotype (written on white rectangular card, surrounded by a red line, UPSA label) / *Pachysoma hippocrates* Holotype dissected J. du G. 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 on 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 on UPSA paratype label) /, (1♀ SAMC), PARATYPES: *idem*, but Type, SAM/Ent. 2678, (printed on green card), (8♂ SAMC), (1♂ TMSA), {1x 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 from South Africa (Σ308 specs [45], 92♀ 185♂, 77♂ diss., 5uns., 26eth., 81p.).

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.

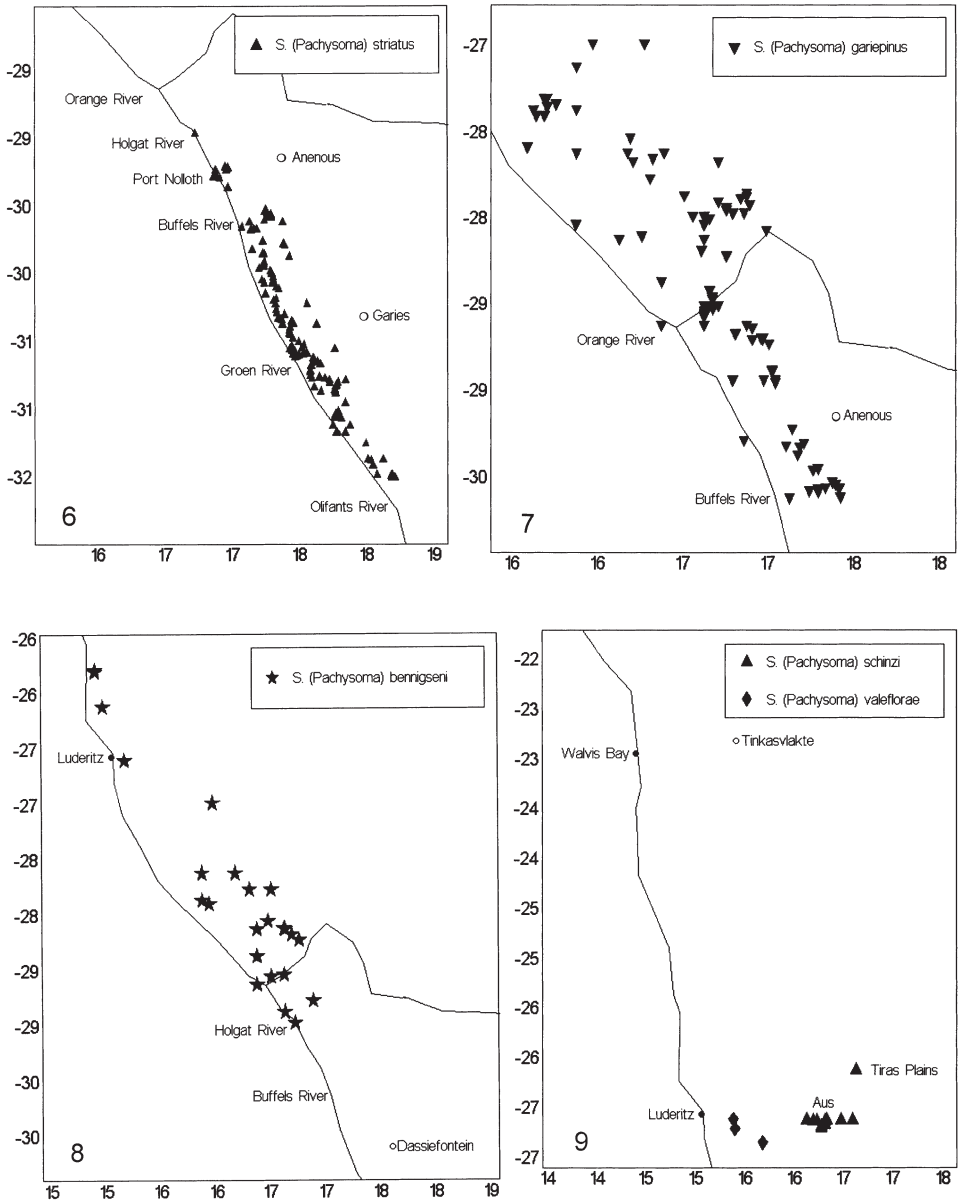
Head (figure 20). *Dorsal*: clypeus bidentate, teeth rounded and separated by V-shaped incision; clypeal and genal margins unserrated, almost continuous, separated at clypeal–genal suture by small incision; whole head finely granular, becoming punctate around periphery; large setiferous granules adjacent 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, nine-segmented, club composed of last three 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. *Protibia, 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 two rows, outer composed of small setiferous knobs (about four or five) while inner of carina, both merge into inner protibial deflection. *Mesotibia*: *s*hort and robust, outer edge with three bands of seta, inner edge with two bands; mesospur slightly spatulate (figure 55), apex forms blunt point; tarsal insertion slightly sub-apical; two 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; two equal and curved tarsal claws; claws almost equal to just longer than last tarsal segment. *Metatibia, lateral*: three curved setal brushes on the tibia.

Elytra. Elytra fused, humeral callus absent; well-developed sub-elytral ridge; elytral rim broad; six faint striae per elytron, most visible when viewed laterally; six 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



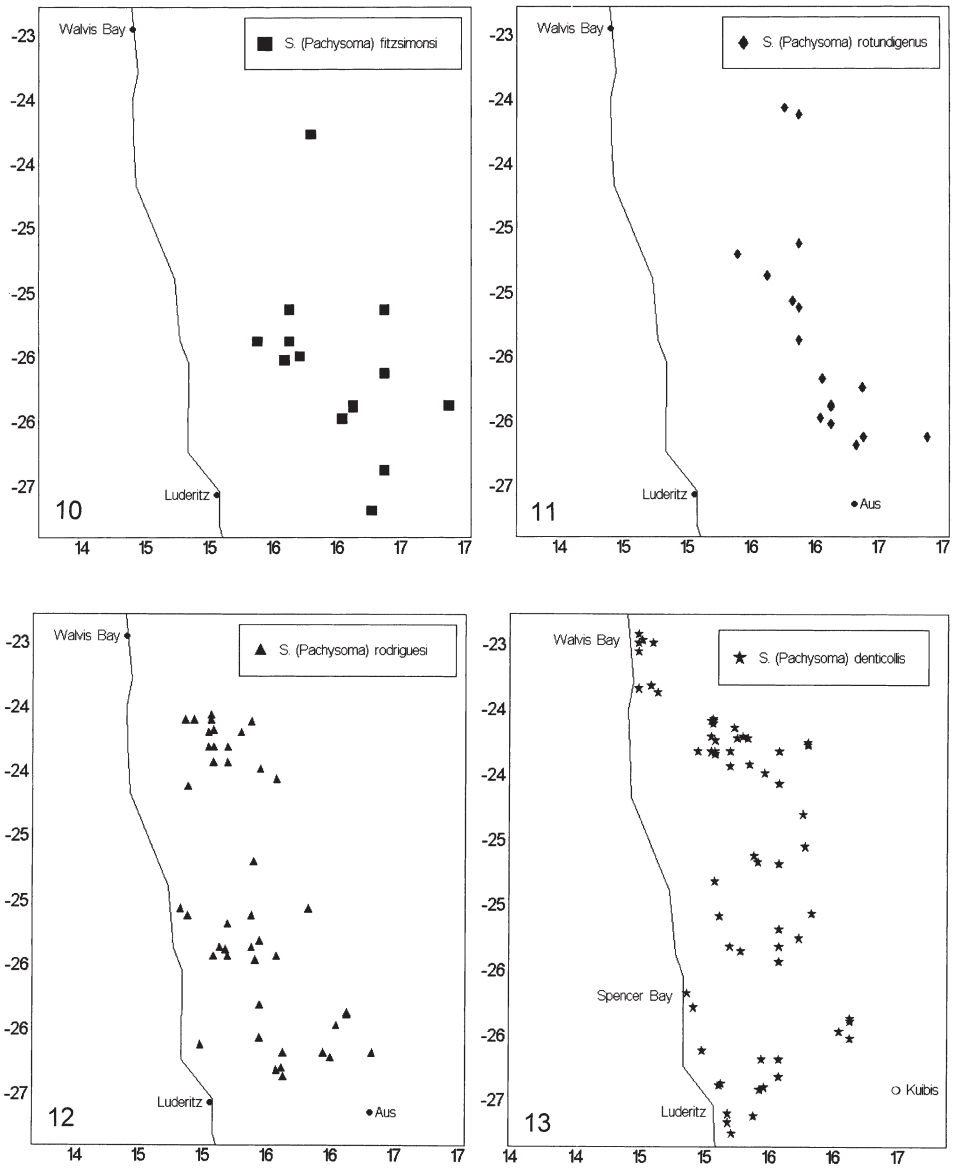
FIGS 6–9. Distribution of *Scarabaeus (Pachysoma)* species in South Africa and Namibia. Questioned locality records or range extensions are shown by an open circle. (6) *S. (P.) striatus*. (7) *S. (P.) gariepinus*. (8) *S. (P.) bennigseni*. (9) *S. (P.) schinzi* and *S. (P.) valeflorae*.

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 figure 59a–c.

Female. Differs from male as follows; Protibia (ventral). Proximal carina very



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*.

reduced at (×40); inner lateral edge with slight deflection, and row of anterior facing setiferous notches (×40). Abdomen. Width of the last abdominal sternite, broad at pygidium; prominent protuberances on sternites 3–5, absent.

Comments. *Scarabaeus (Pachysoma) glentoni* is externally virtually indistinguishable from *S. (P.) hippocrates.* The male genitalia provide the most reliable character for distinguishing these two species (figure 59a–c vs 58a–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 localized distribution of *S. (P.) glentoni* (figure 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. Localized 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. *Scarabaeus (Pachysoma) 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 (Σ124 specs, 35♀ 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, (4♀ 4♂ SANC), (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, (5♀ 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.

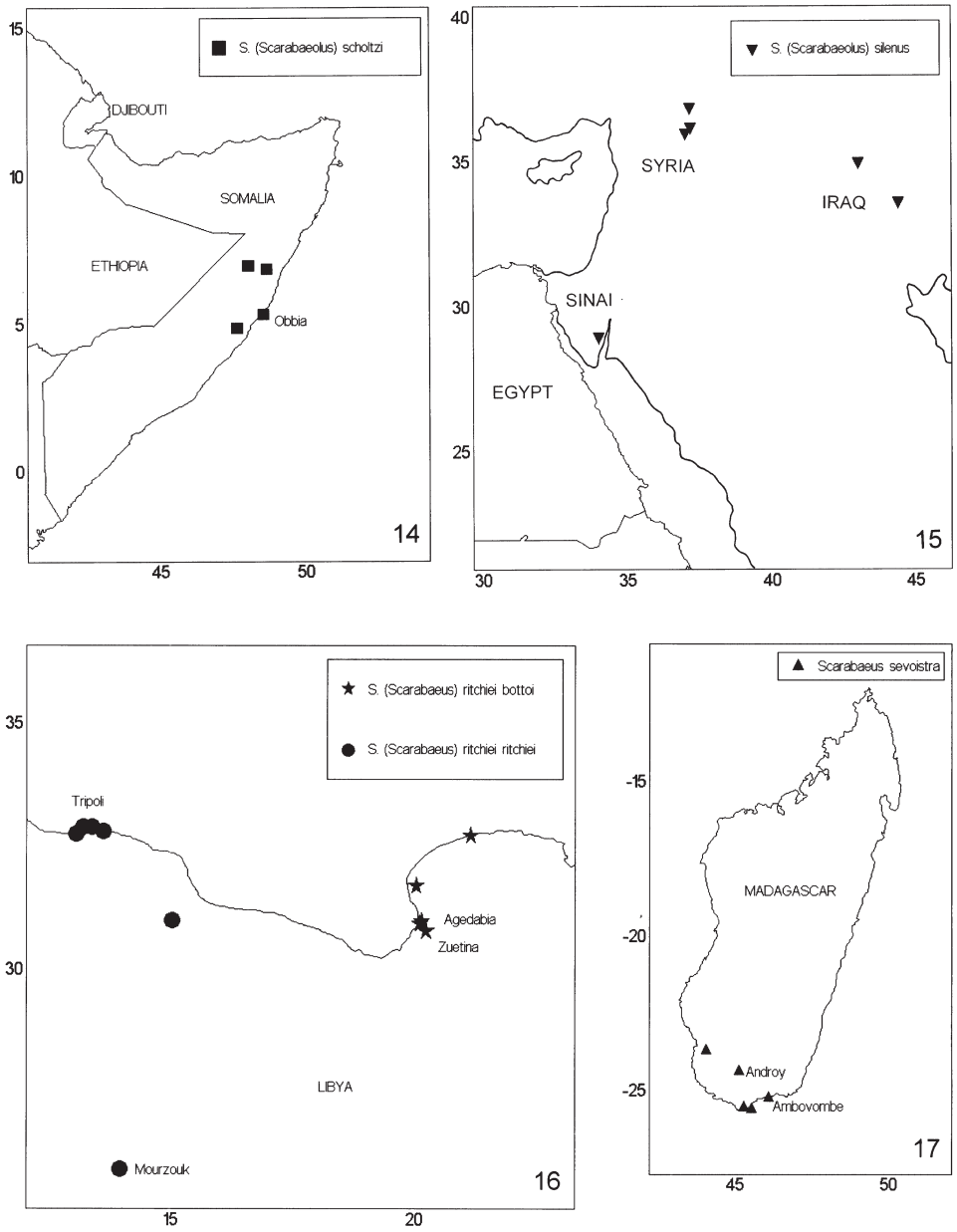
Head (figure 21). *Dorsal*: clypeus bidentate; teeth short, apex rounded, separated by smooth V-shaped incision; genal and clypeal edge unserrated, almost continuous, separated at genal–clypeal incision; head finely granular, setose granules restricted to genae and posterior of head between eyes. *Ventral*: rim of setae around clypeal and genal edge; clypeal teeth raised into two ridges, posterior rim, with single pointed tooth; mandibles robust, mentum bilobed, stiff setae pointing forward on lobe; lamellate antennae, nine-segmented, club formed by last three 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. *Protibia*, v*entral* (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 three bands of seta; spurs slightly spatulate, apex blunt; tarsal insertion slightly sub-apical; two 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; two equal and curved tarsal claws, shorter than or almost equal to last tarsal segment. *Metatibia, lateral*: three curved setal brushes on tibia.

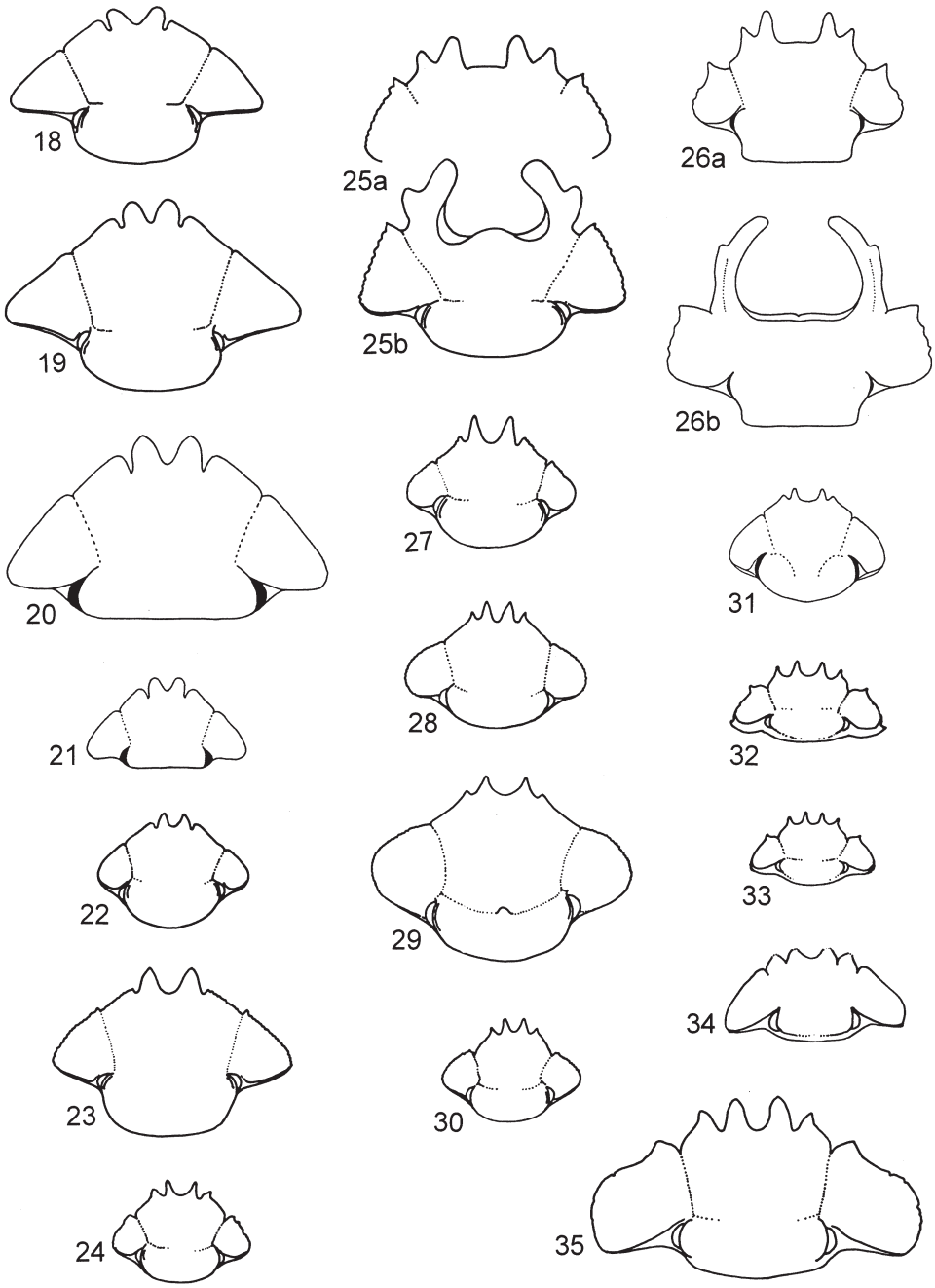
Elytra. Fused, humeral callus absent; well-developed sub-elytral ridge and rim; elytra bordered by band of indument; six striae per elytron, scattered with minute, irregular setose granules.

Abdomen. Mesocoxae contiguous, mesosternal ridge absent; abdominal sternites



FIGS 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.

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.



FIGS 18–35. (18–30) 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.) gapiepinus*. (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*. (31, 32) Head of flightless *Scarabaeus (Scarabaeolus)* species in dorsal view. (31) *S. (Scarabaeolus) scholtzi*. (32) *S. (Scarabaeolus) silenus*. (33–35) Head of flightless *Scarabaeus (Scarabaeus)* species in dorsal view. (33) *S. (Scarabaeus) ritchiei*. (34) *S. (Scarabaeus) sevoistra*. (35) *S. (Scarabaeus) cancer*.

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

Aedeagus. Parameres short, asymmetrical, see figure 60a–c.

Female. Differs from male as follows: Protibia, ventral: proximal carina and single row of setae very reduced at (×40); inner lateral edge with slight deflection, and row of anterior facing setiferous notches (×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 south-western South Africa, occurring just north of the Olifants River. The localized distribution (figure 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 recognized 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 specs [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 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 (figure 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 (28°58′S, 16°43′E) 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, 1996, personal communication). 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 laboratory conditions on two separate occasions. Four pairs (1 September 1996 to 23 January 1997) and six pairs (9 September 1998 to 4 December 1998) of *S. (P.) striatus* collected from Strand Fontein (30°33′S, 17°26′E), were placed in round 25 litre buckets and 5 litre 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) synonymized *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 14–16 mm) 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 and 1899. 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 on to white card with a brass minuten), (1♂ aedeagus only SAMC).

Additional material examined from South Africa (Σ759 specs [86], 275♀ 439♂, 4♂ diss., 45eth., 137p.).

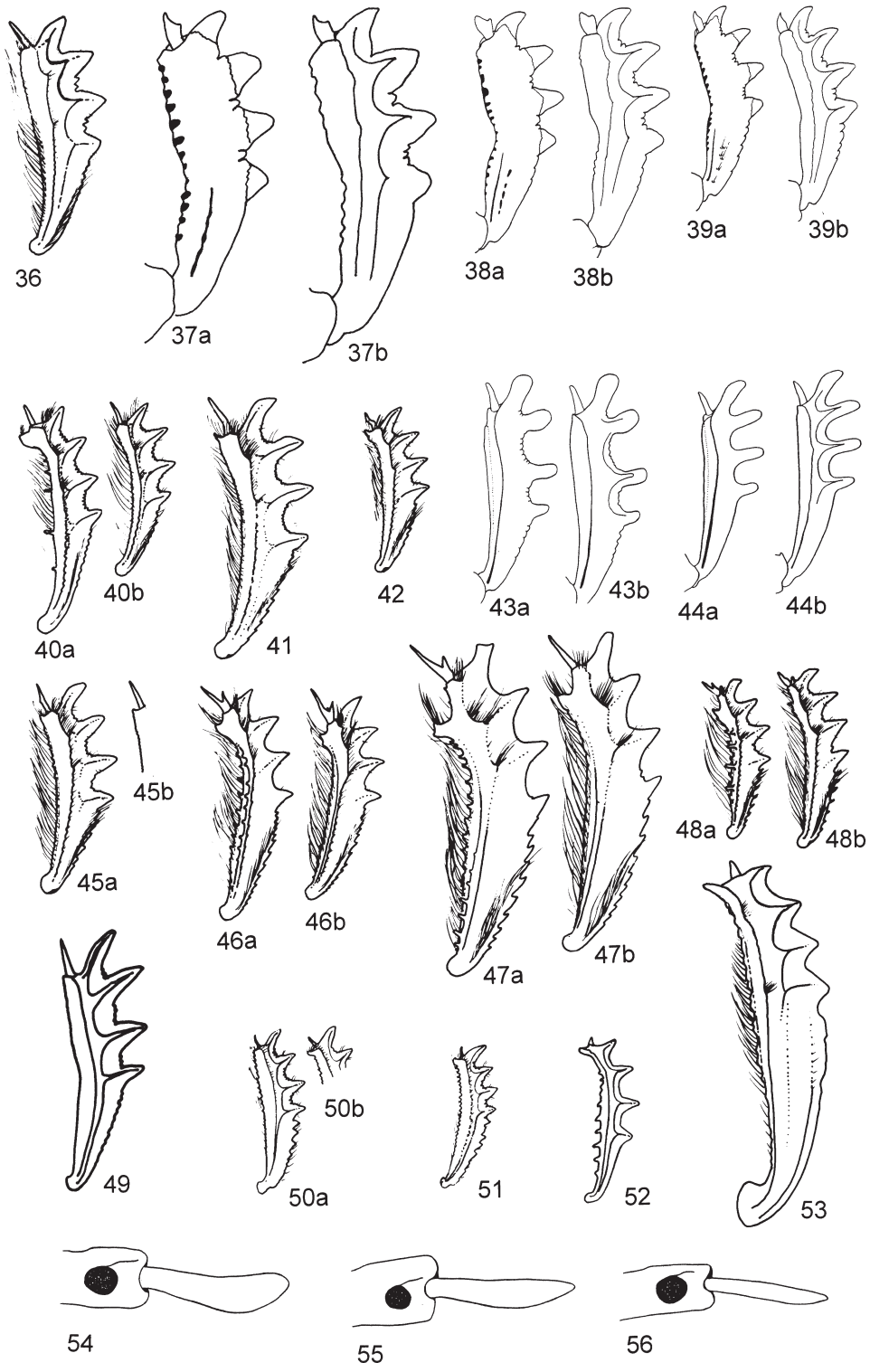
Scarabaeus (Pachysoma) gariepinus (Ferreira, 1953)
(figures 7, 23, 41, 62)

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 figure 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

FIGS 36–56. (36–48) Protibia of *Scarabaeus (Pachysoma)* species in dorsal view, unless otherwise indicated. (36) *S. (P.) aesculapius*. (37) *S. (P.) hippocrates*: (a) ventral, (b) dorsal view. (38) *S. (P.) glentoni*: (a) ventral, (b) dorsal view. (39) *S. (P.) endroedyi*: (a) ventral, (b) dorsal view. (40) *S. (P.) striatus*: (a) male, (b) female. (41) *S. (P.) gapiepinus.* (42) *S. (P.) bennigseni.* (43) *S. (P.) schinzi*: (a) male, (b) female. (44) *S. (P.) valeflorae*: (a) male, (b) female. (45) *S. (P.) fitzsimonsi*: (a) male, (b) female. (46) *S. (P.) rotundigenus*: (a) male, (b) female. (47) *S. (P.) rodriguesi*: (a) male, (b) female. (48) *S. (P.) denticollis*: (a) male, (b) female. (49, 50) Protibia of flightless *Scarabaeus (Scarabaeolus)* species in dorsal view. (49) *S. (Scarabaeolus) scholtzi*. (50) *S. (Scarabaeolus) silenus*: (a) male, (b) female. (51–53) Protibia of flightless *Scarabaeus (Scarabaeus)* species in dorsal view. (51) *S. (Scarabaeus) ritchiei.* (52) *S. (Scarabaeus) sevoistra*. (53) *S. (Scarabaeus) cancer*. (54–56) Mesospurs. (54) *S. (P.) hippocrates*; (55) *S. (P.) glentoni*; (56) *S. (P.) endroedyi.*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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 characterized 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 12 paratypes were from Holgat. The allotype was not labelled, and since there are 10 females from Holgat it becomes untraceable.

To add to the confusion of the type series, two separate series from Holgat dated 23 November (19)48 and 2 September 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. We 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 from South Africa and Namibia (Σ453 specs [16], 188♀ 235♂, 11♂ diss., 13uns., 17eth., 20p.).

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 [1uns. 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) synonymized it with *Pachysoma bennigseni*. Holm and Scholtz (1979) only mention the holotype, allotype and four paratypes for *P. granulatum*. The type series

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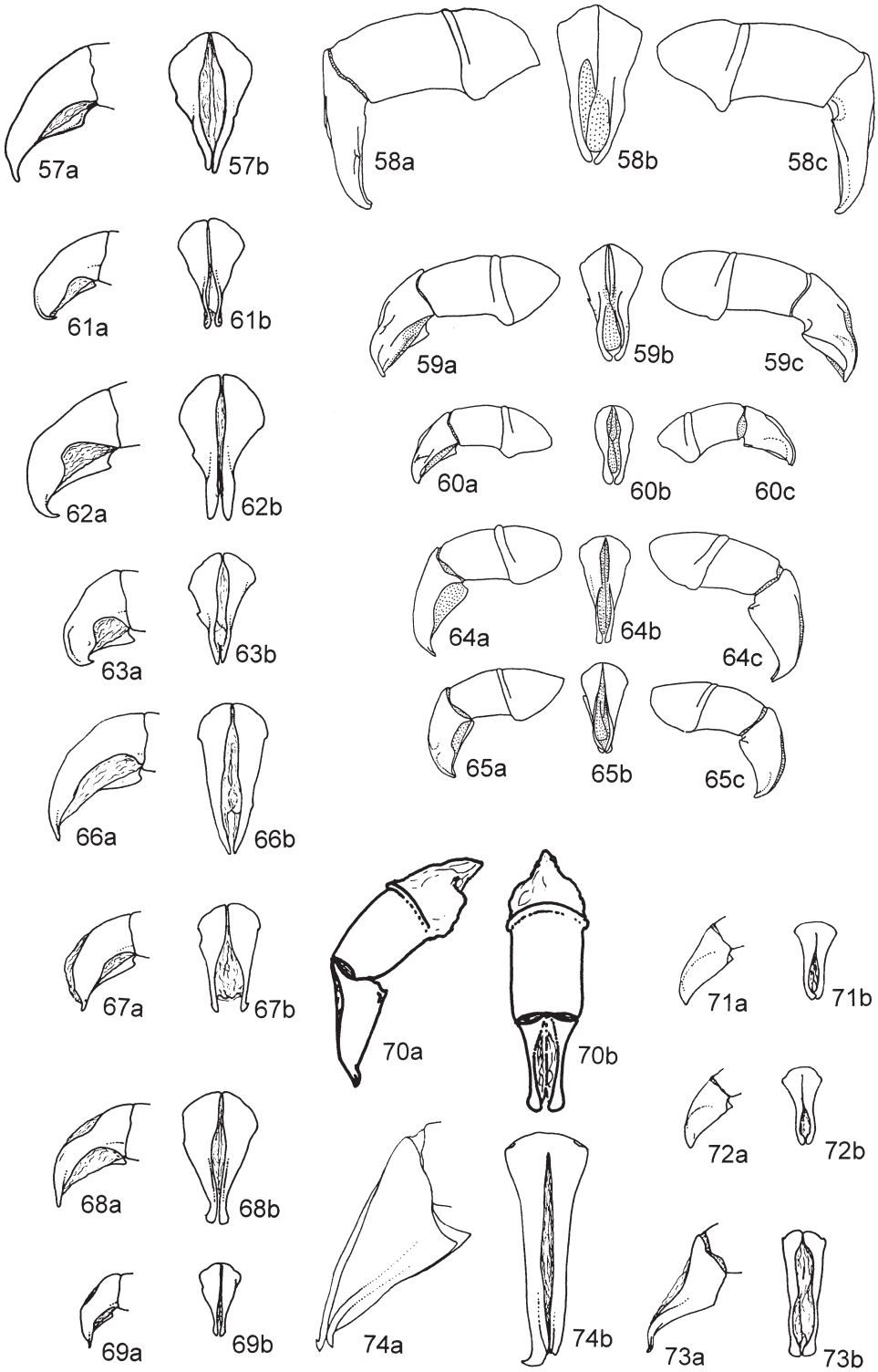
FIGS 57–74. Roman letters (a, b, c) represent: (a) lateral left paramere, (b) anterior view, (c) lateral right paramere. (57–69) Aedeagi of *Scarabaeus (Pachysoma)* species. (57a, b) *S. (P.) aesculapius.* (58a–c) *S. (P.) hippocrates*. (59a–c) *S. (P.) glentoni*. (60a–c) *S. (P.) endroedyi*. (61a, b) *S. (P.) striatus*. (62a, b) *S. (P.) gapiepinus*. (63a, b) *S. (P.) bennigseni*. (64a–c) *S. (P.) schinzi*. (65a–c) *S. (P.) valeflorae.* (66a, b) *S. (P.) fitzsimonsi*. (67a, b) *S. (P.) rotundigenus*. (68a, b) *S. (P.) rodriguesi*. (69a, b) *S. (P.) denticollis.* (70, 71) Aedeagi of flightless *Scarabaeus (Scarabaeolus)* species. (70a, b) *S. (Scarabaeolus) scholtzi*. (71a, b) *S. (Scarabaeolus) silenus*. (72–74) Aedeagi of flightless *Scarabaeus (Scarabaeus)* species: (72a, b) *S. (Scarabaeus) ritchiei*. (73a, b) *S. (Scarabaeus) sevoistra*. (74a, b) *S. (Scarabaeus) cancer.*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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. 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); [2uns. BMNH]; {1uns. CPMM}.

Additional material examined from South Africa and Namibia (Σ137 specs [24], 49♀ 87♂, 4♂ diss., 1uns.).

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 (figure 25b); 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 (26°41′S, 16°16′E) 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* (figure 9).

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 (1997, personal communication) *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 1–2 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 from Namibia (Σ189 specs [192], 98♀ 91♂, 5♂ diss.).

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 (figure 26a, b); male has two clypeal horns, anterior edges of genae produced into distinct point (figure 26a, b); no serrations between or proximal to protibial teeth (figure 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 six 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) synonymized *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 females and five males) conforms 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 (figure 26a, b); (2) males, equal spacing between the second and third protibial teeth (figure 44b); (3) no serrations between or proximal to the protibial teeth (figure 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 (figure 65a–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, we 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 23 September 1950, but a few days previously (17 September 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 from Namibia (Σ7 specs [1], 2♀ 5♂, 3♂ diss.).

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 figure 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. However, 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, 1962b, 1969; Lawrence, 1969; Newlands, 1972; Endrödy-Younga, 1982; 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 (1999, personal communcation) 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 September 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 on to 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 from Namibia (Σ26 specs [29], 11♀ 15♂, 5♂ diss.).

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. [1uns. 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 figure 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 {>uns. 2 spec.}. NAMIBIA: [HOLOTYPE], Sinclair, (25.44S 16.22E), D.S.W. Afrika, [1uns. SMTD].

Additional material examined from Namibia (Σ50 specs [33], 19♀ 31♂, 4♂ diss.).

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 (figure 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 figure 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 September 1953) on it. Ferreira (1953a) records the date of collection of the type series as 26 September 1950. Considering the description of *P. rodriguesi* was published in 1953, we suspect the date of collection was the 26 September 1950, rather than 26 September 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. Namaqauld., 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 from Namibia (Σ93 specs [37], 44♀ 49♂, 3♂ diss).

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 (figure 48a, b); elytra orange to black, deeply striate, striae smooth to granular; metatarsal claw longer than last tarsal segment; male genitalia as in figure 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. Scarabaeus (Pachysoma) 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 synonymize *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) coloration 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 30 km 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 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). Re-examination 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 (16–17 mm; width 11 mm) 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, we 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 from Namibia (Σ209 specs [78], 85♀ 105♂, 8♂ diss., 19uns., 1p.).

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

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 semi-arid 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 and 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 to 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* species. 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 sternites. 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 (Σ11uns. 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, (1uns. BMNH), (6uns. TMSA), (1uns. 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, (2uns. TMSA).

Additional material examined from Somalia (1uns. abdomen).

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 (figure 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. 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).

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* Balthasar, 1965; Mostert and Holm, 1982), requires further investigation.

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 (1uns. spec.). SYNTYPE: ARABIA: Silenus Ol.* Arab. Ol. (written on to faded yellow card) / 8889 / (1uns. ZMHB).

Additional material examined from Egypt and Iraq (Σ8uns. specs).

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.
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) synonymized it with *M. ritchiei*. Zunino (1984), using male genitalia and differential reduction of the hind wings, recognized 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* roll balls 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 from Libya (Σ26uns. specs, 2♂ diss.).

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 figure 73a, b.

Distribution and habitat. Only recorded from the south-west of Madagascar, in semi-arid 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 semi-arid bush veld of south-western 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 shared with *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) synonymized 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 from Madagascar (Σ2 specs, 1♀ 1♂).

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 figure 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.

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*. However, *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). While flying species seemingly warranting their own genera include *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°23′S, 16°56′E 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 from Angola (1♀ diss.).

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Appendix

Checklist of the species of Scarabaeus (Pachysoma) MacLeay

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 and Chown sp. n.
Scarabaeus (Pachysoma) fitzsimonsi (Ferreira, 1953a).
Scarabaeus (Pachysoma) gariepinus (Ferreira, 1953a).
Scarabaeus (Pachysoma) glentoni Harrison, Scholtz and 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).

Checklist of the species of flightless Scarabaeus (Scarabaeolus) Balthasar

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

Checklist of the species of flightless Scarabaeus (Scarabaeus) Linnaeus

Scarabaeus (Scarabaeus) cancer (Arrow 1919).
Scarabaeus (Scarabaeus) ritchiei ritchiei (MacLeay, 1821).

Scarabaeus (Scarabaeus) ritchiei bottoi (Gridelli, 1930).
Scarabaeus (Scarabaeus) sevoistra Alluaud, 1902.

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