SYSTEMATICS OF THE SUBTRIBE SCARABAEINA LATREILLE, 1802 (COLEOPTERA : SCARABAEIDAE)

BY

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RÉSUMÉ

The taxonomic history of Scarabaeini, and the morphological and biological features characteristic of members of this tribe, is discussed. Each subtribe of Scarabaeini is briefly reviewed, and a key to the subtribes is provided. The sub=tribe Scarabaeina is more fully discussed prior to its sys=tematic assessment.

A new flightless species, Scarabaeus scholtzi spec. nov. is described, and the taxonomic position of the flightless spe=cies within Scarabaeina is evaluated. It is concluded that these species do not represent one or more monophyletic groups, but are the consequence of adaptation by species of Scarabaeus L. to localised conditions of extreme aridity and, possibly, windi=ness. The genera Pachysoma M'Leay and Neomnematium Janssens, in which the flightless species are contained, are consequently synonymised with Scarabaeus L.

The validity of the genera Mnematidium Ritsema, Neateuchus Gillet and Madateuchus Paulian is assessed. As no definitive autopomorph could be found for each of these genera, they are synonymised with Scarabaeus L.

The genus Pachylomera Kirby is emended to Pachylomerus Bertoloni.

The genera of Scarabaeina, as redefined in this work, are reviewed and a key to these genera is provided. A phylogeny and classification of the genera is proposed, based largely on cladistic principles.

The thesis is illustrated with 169 photographs, drawings and maps.

SAMEVATTING

Die taksonomiese geskiedenis van Scarabaeini, en die morfologiese en biologiese eienskappe wat kenmerkend van lede van hierdie tribus is, word bespreek. Elke subtribus van Scarabaeini is kortliks saamgevat, en 'n sleutel tot die subtribusse word voorsien. Die subtribus Scarabaeina word meer breedvoerig bespreek, met die oog op die sistematiese evaluering en ontleding daarvan.

'n Nuwe vluglose species van die subtribus Scarabaeina word beskryf en die taksonomiese geldigheid van die vluglose species binne Scarabaeina word in oënskou geneem. Daar word tot die gevolgtrekking gekom dat hierdie species nie een of meer monofiletiese groepe verteenwoordig nie, maar eerder die gevolg is van aanpassing deur verskeie *Scarabaeus* species by plaaslike omstandighede, hoofsaaklik dorheid, en miskien ook winderigheid. Die genera *Pachysoma* M'Leay en *Neomnematium* Janssens, waarin die vluglose species geplaas was, word dus sinonieme van *Scarabaeus* L.

Die geldigheid van die genera *Mnematidium* Ritsema, *Neateuchus* Gillet en *Madateuchus* Paulian word ondersoek. Aangesien geen unieke outapomorf vir elkeen van hierdie genera gevind is nie, word die genera as sinomiene van *Scarabaeus* L. geplaas.

Die genus *Pachylomera* Kirby word geëmendeer tot *Pachylomerus* Bertoloni.

Die genera van Scarabaeina, soos herdefinieer in hierdie werk,

word in oënskou geneem en 'n sleutel tot dié genera word voorsien. 'n Filogenie en klassifikasie van bogenoemde genera word voorgestel, hoofsaaklik gebaseer op kladistiese beginsels.

Die verhandeling word met 169 tekeninge, kaarte en foto's geillustreer.

1. INTRODUCTION

1.1 INTRODUCTION

The subtribe Scarabaeina consists of five genera of tele=coprid dung beetles confined to the Old World. Bornemissza (1969) divided scarabaeine dung beetles into three beha=vioural groups: i) endocoprids, which nest within the dung pad; ii) paracoprids, which nest below or next to the dung pad but have tunnels connecting the nest and the dung pad; iii) telecoprids which roll or carry dung away from the pad, and have no further contact with the dung pad. _Scarabaeus_ L. and _Kheper_ Janssens occur throughout most of Africa, southern Europe and Asia, while _Drepanopodus_ Janssens, _Sceliages_ Westwood and _Pachylomerus_ Bertoloni are restricted to the southern regions of Africa. The distribution of the subtribe is closely associated with the presence of large herbivores, high ambient temperatures and soil conditions which allow for the excavation of burrows (Halffter & Matthews 1966, Tribe 1976).

Although certain species, such as _Scarabaeus sacer_ L., are well known and have been studied in depth (Fabre 1911, Hey=mons & van Lengerken 1929), the subtribe as a whole has re=ceived only cursory taxonomic, and even less biological and phylogenetic, treatment. The brachypterous species of Scar=abaeina were considered by previous authors to represent one or more distinct genera within the subtribe (Ferreira 1969, Holm & Scholtz 1979). Examination of all known brachypterous species, their disjunct distribution, and evidence of occasional brachyptery in other scarabaeoid genera, suggests that the brachypterous condition could have arisen repeatedly as a result of adaptation to a localised set of extreme ecological conditions, and thus may not represent one or more unique lineages that would justify generic status.

Secondly, certain genera such as <u>Neateuchus</u> Gillet and <u>Madateuchus</u> Paulian, when viewed in isolation seem to justify generic status, but within the scope of <u>Scarabaeus sensu lato</u>, this status appears dubious.

Thirdly, no phylogenetic tree or cladogram of the subtribes of Scrabaeini, or the genera of Scarabaeina, has ever been published, although Janssens' synopsis of the subtribes of Scarabaeini seems to attempt some reflection of the relationship of these subtribes (Janssens 1949).

Publications dealing with Scarabaeina have either been entirely taxonomic, or have dealt only with isolated species groups. Even in the case of the taxonomic studies, the subtribe as it is presently understood, has not been dealt with. Ferreira (1969), in the most comprehensive taxonomic work to date, dealt only with the species that occur south of the Sahara desert, while the excellent publication of Janssens (1940) excluded a number of the known genera.

The purpose of this study was consequently to investigate the phylogenetic position of the brachypterous species of Scarabaeina in relation to the macropterous species, to re=

assess the generic classification of the Scarabaeina, to analyse the phylogeny of the subtribe and its genera, and to revise, update and collate as much taxonomic and general information about the subtribe as possible.

1.2 MATERIAL AND METHODS

The material consisted largely of museum specimens housed in the collections of the UP, DRU, TM and NCI. Additional material was obtained from the other institutions mentioned in the list of abbreviations at the end of this section. Various species were personally collected and observed in the field, especially *Scarabaeus gariepinus* (Ferreira) and *Drepanopodus proximus* (Péringuey).

The work is essentially a morphological study of the species of Scarabaeina, with the subsequent analysis and classification based on cladistic (*sensu* Hennig 1965) principles. Apart from the external features, the shape and form of the aedeagus was of major importance.

To remove the aedeagi, the specimens were placed in boiling water for a few minutes. This enabled one to flap open the pygidium at the tergal membrane by cutting the membrane between the penultimate abdominal sternite and the pygidium. Once this was done, the aedeagus could be removed with a pair of forceps through the resultant opening. The pygidium was then swung closed. No glue was needed to keep it in its original position and the specimen was not damaged in any other way.

For microscopic examination and photographic purposes, the best method of mounting the aedeagi was found to be by inserting the point of a long, sharp cardboard triangle into the base of an aedeagus, after a small amount of water soluble glue had been placed on the tip of the triangle. By mounting the triangle on an insect pin and then holding the pin in a gem clamp placed under the microscope, the aedeagus could be held stationary and consequently viewed and photographed from any angle.

1.3 ABBREVIATIONS OF INSTITUTIONS FROM WHICH MATERIAL WAS OBTAINED

BM - British Museum (Natural History), Cromwell Road, London, SW7 5BD, England.

DRE - Staatliches Museum für Tierkunde, DDR-801, Dresden, Augustusstrasse 2, Democratic Republic of Germany.

DRU - Dung Beetle Research Unit of the CSIRO, Private Bag X5, Lynn East 0039, South Africa.

GEN - Museo Civico di Storia Natuale "G. Doria", Via Brigata Liguria N.9, 16121 Genova, Italy.

MUN - Zoologische Sammlung der Bayerische Staates, Maria-Ward Strasse 1B, D8000 Munich, West Germany.

NM - National Museum, P O Box 266, Bloemfontein 9300, South Africa.

NCI - National Collection of Insects, Plant Protection Research Institute, Private Bag X134, Pretoria 0002, South Africa.

PAR - Museum National D'Histoire Naturelle,
45 bis Rue de Buffon, Paris, France.

SAM - South African Museum, P O Box 61, Cape Town 8000,
South Africa.

SIS - Hùsares 1079 - CC21, 1642 San Isidro,
Pcia Buenos Aires, Argentina.

TM - Transvaal Museum, P O Box 413, Pretoria 0001,
South Africa.

UP - Department of Entomology, University of Pretoria.
Pretoria 0002, South Africa.

WIEN - Naturhistorisches Museum Wien, Burgring 7,
A1014 Vienna, Austria.

2. TRIBE SCARABAEINI

Scarabaeini Péringuey 1900: 21; Gillet 1911: 4; Janssens 1938: 1, 2; 1940: 13; 1949: 24; Ferreira 1953: 3, 4; 1961: 21,228; Balthasar 1963: 136; Halffter & Matthews 1966: 259; Matthews 1974: 1.

Ateuchides Reiche,1841(a): 221; 1841(b): 59; 1842: 22; Westwood 1847: 225; Lacordaire 1956: 64; Lansberge 1874: 177; Harold 1879: 35.

Ateuchidae Burmeister, 1846: 27.

Ateuchini Erichson, 1847: 788; Péringuey 1900: 21.

Scarabaeini Péringuey, 1900: 21; Gillet 1911: 4; Janssens 1938: 1, 2; 1940: 13; 1949: 24; Ferreira 1953: 3, 4; 1961: 21, 228; Balthasar 1963: 136; Halffter & Matthews 1966: 259; Ferreira 1969: 16; Matthews 1974: 1.

2.1 TAXONOMIC HISTORY

Although the name Scarabaeini is of relatively recent origin (Péringuey, 1900), the tribe was more or less defined by Reiche (1842) in his classification of Scarabaeinae, when he distinguished Ateuchides - with slender hind tibia, from Coprides - with distally dilated hind tibia.

Lacordaire (1856) divided the Scarabaeinae, which he referred to as the tribe Coprides, into the same two groups, which he then designated as subtribes. He further divi=

ded the Ateuchides (Scarabaeini) into four groups: Ateuchides, Gymnopleurides, Deltochilides and Minthophilides. The characters used for defining these groups were the width of the epipleura and the presence or absence of protarsi.

The next major classification of Coprides (Scarabaeinae) was by van Lansberge (1874). He maintained the Ateuchides and Coprides of Reiche (1842) and Lacordaire (1856). Although he was not the first author to use the character, Lansberge stressed the importance of the alignment of the mesocoxae in the definition of the major groupings within the Scarabaeini, as well as the relative lengths of the first and second mesotarsal segments. Both these characters are still of key importance in present classification systems. The three main divisions, called tribes, within Lansberge's Ateuchides were the true Ateuchides (with strongly oblique mesocoxae), the Canthonides (with moderately oblique mesocoxae) and the Sisyphides (with mesocoxae parallel and very widely separated). As these characters and groups are still of major importance today, Lansberge can be regarded as the initiator of modern scarabaeine classification.

The true Ateuchides, which concern us here, included the section Eucranides (brachypterous species represented by the South American subtribe Eucraniina, the African genera *Pachysoma* M'Leay, *Neopachysoma* Ferreira and *Mnematium* M'Leay, the Madagascan genus *Neomnematium* Janssens), and the section Ateuchides (representing the winged genera of the present subtribes Scarabaeina and Gymnopleurina).

Lansberge's tribal categories were adopted and built upon by Péringuey (1900), whose system was in turn used by Gillet (1911) in the Coleopterorum Catalogus. Janssens (1949) modified and updated the system into a stable, logical classification which has formed the basis of all subsequent scarabaeine taxonomic work of any consequence (Balthasar 1963; Halffter & Matthews 1966; Ferreira 1969; Matthews 1972, 1974).

2.2 MORPHOLOGY

Janssens (1940) distinguished the following features as characteristic of the Scarabaeini:

i) meso- and metatibia relatively long and thin, not distally flared, or with a gradual increase in diameter and metatibia usually curved;

ii) protibial spur articulating with tibia;

iii) meso- and metafemora elongated;

iv) tarsal segments 1-4 not, or slightly, widened;

v) scutellum invisible or very small;

vi) antennae 8- or 9-segmented;

vii) very little sexual dimorphism;

viii) generally diurnal;

ix) evolutionarily advanced because of their ball-rolling and nidification behaviour.

Janssens (loc. cit.) subdivided the Scarabaeini into six subtribes; viz. Canthonina, Alloscelina, Sisyphina, Gymnopleurina, Scarabaeina and Eucraniina. Halffter & Matthews (1966) agreed with Janssens' assessment that Scarabaeini is an advanced group, stating that they believed it to be a homogeneous, behaviourally advanced group which split off early in scarabaeine history, probably from saprophagous ancestors. Halffter & Matthews record Eurysternina as an additional subtribe, but its taxonomic position is still unclear and it is consequently not included in the review of Scarabaeini subtribes in section 2.5.

2.3 BIOLOGY

Although the species of Scarabaeini are generally ball-rolling dung beetles, many exceptions occur on the specific, generic, and even subtribal levels. Deviations from the coprophagous rule include general and specialised necrophagy, and commensalism with ants and termites. The major trends in the biology of species within Scarabaeini will be mentioned in the following review of the subtribes of Scarabaeini.

2.4 DISTRIBUTION

Members of the Scarabaeini occur in all the biogeographical regions, but the tribe is poorly represented in the northern latitudes.

The breakdown of genera according to Halffter & Matthews (1966), is roughly as follows:

Nearctic region	4
Palearctic region	4
Oriental region	12
Australasian region	16
Ethiopian region	27
Neotropical region	37

From the above data it would appear that the tribe is of west-Gondwanan origin. Analysis of subtribal distribution patterns (Matthews 1974, 1976 and the present work) seems to support this conclusion.

2.5 REVIEW OF SUBTRIBES OF SCARABAEINI

2.5.1 Canthonina

A very large subtribe consisting of some 69 genera with a tropical and subtropical Gondwanan distribution, but particularly abundant in South America (33 genera). Australia has 16 genera, Africa 10, and seven genera occur on Madagascar and Mauritius.

The canthonines are characterised by widely separated, slightly oblique mesocoxae, the sides of the pronotum being regularly curved and not compressed as in Sisyphina, the presence of protarsi in most species except the flightless ones, and nine-segmented antennae.

The feeding habits of the subtribe were analysed in some detail by Halffter & Matthews (1966). The subtribe contains coprophages, copro-necrophages and necrophages. Often predominantly coprophagous or predominantly necrophagous species are found within the same genus, e.g. *Malagoniella* Martinez. The main conclusion to be drawn from these data is that insects which are attracted to the breakdown products of the organic components in dung could conceivably be attracted to similar breakdown products in decaying animals. I observed this on various collecting trips when usually coprophagous *Scarabaeus* species were attracted to pit-traps baited with decaying meat.

Matthews (1974) mentioned the ability of certain canthonines to utilise dried faecal pellets by burying them at the depth of the moisture line in the soil. It is assumed that moisture seeping into the pellets revives bacterial and fungal activity, these micro-organisms in turn serving as food for the beetles. This strategy is probably also employed by those xerophilous Scarabaeina species which are known to utilise dried pellet dung.

The brooding behaviour of the canthonines is more or less typical of the Scarabaeini, i.e. the construction at the food sources of a brood ball which is then rolled away and buried. Matthews (1974) noted that a number of Australian genera are apparently unable to construct a brood ball al=

though they are able to roll a pellet of dung, which is their usual food and brood source. One genus, Cephalodesmius Westwood, is able to detach a portion from a larger faecal mass, this portion not being shaped and rolled, but carried in the forelegs. These observations help to clarify the position of the South American eucraniine species which exhibit similar methods of dung transport. Because of this behaviour Halffter & Matthews were loath to place the eucraniines with the other telecoprid groups. This phenomenon also warns against a too strict behavioural classification, as exceptions to behavioural rules abound within the Scarabaeini.

2.5.2 Alloscelina

A small, little-studied subtribe of myrmecophilous and termitophilous species occurring in the Ethiopian and Oriental zoogeographical regions.

The alloscelines are morphologically adapted for their myrmeco- and termitophilous existence, being small (± 7 mm), globose and short-legged. They have slightly oblique mesocoxae, reminiscent of the species of Scarabaeini, and Gymnopleurina, but have eight antennal segments, whereas the latter subtribes have nine segments.

The following allosceline genera have been found in association with ants and termites:

> _Alloscelus_ Boucomont - with _Dorylus_ ants;
> _Megaponerophilus_ Janssens - with _Megaponera_ ants;
> _Ponerotrogus_ Silvestri - with _Ponera_ ants;
> _Haroldius_ Boucomont - with _Pheidole_ and _Diacomma_ ants;
> _Afroharoldius_ Janssens - with termites.

Apart from the fact that they are myrmeco- or termitophiles, nothing more is known about the biology of these beetles. No feeding behaviour has been observed. It is assumed that they feed on the remains of the food left by their hosts, which include some notoriously aggressive carni=vores such as the driver ants (_Dorylus_). The mechanism by which the beetles themselves are protected from these ants is not known.

2.5.3 _Sisyphina_

A small but widely distributed subtribe containing three genera. Their area of distribution includes the Ethiopian, Oriental, Neotropical and Australasian zoogeographical re=gions, and the Indian Ocean island of Mauritius. The si=syphines are generally found in open savanna, but also inhabit certain forest and montane regions.

The Sisyphina are characterised by the following morpholo=gical features:

i) eight-segmented antennae;
ii) the presence of protarsi;

iii) widely separated, parallel mesocoxae;

iv) pronota having flat, vertical sides;

v) elongate, filiform meso- and metatarsi;

vi) triangular (heart-shaped) elytra when viewed from above.

The sisyphines are generally coprophagous, preferring moist bovine dung. Some myrmecophily, especially with the ant genus *Pheidole*, has also been recorded. The "*Reifungsfrass*" - a period of maturation feeding after overwintering - is about three months for the genus *Sisyphus* Latrielle while for *Neosisyphus* *pygmaeus* Klug on Mauritius, it appears to be slightly more than a month (Vinson 1947). Adults emerge in middle to late summer and overwinter in deep burrows. Thus the adult is almost a year old when sexual activity commences.

Sisyphus species are good fliers, and search for dung by means of short rapid flights of ± 50 metres (Prasse 1960). They are very adept ball-makers and-rollers, also being able to construct a large ball from smaller pellets. *Sisyphus* species, in common with those of *Scarabaeus*, require a minimum temperature of about 21°C before ball-rolling commences. Rapidity and skill of rolling increase with temperature up to a maximum of about 30°C. In contrast to *Scarabaeus*, the female appears to be the more active partner in co-operative ball-rolling.

In _Sisyphus_ (_Neosisyphus_) Müller and certain other species, the brood-ball is coated with clay, but not buried, while in the remaining _Sisyphus_ species the balls are buried without a clay shell, or with only a thin layer of soil. _Sisyphus_ _quadricollis_ Gory, a South African species, attaches its brood-ball to a grass stem (Arrow, 1931).

2.5.4 _Gymnopleurina_

Gymnopleurina is a relatively small subtribe of four genera confined to the Old World. Species of Gymnopleurina are found in grassland savanna and in forest savanna throughout Africa, Asia and southern Europe.

The oblique mesocoxae of the gymnopleurines are similar to those of the species of Scarabaeina. For this reason they were at one stage classified with the Scarabaeina. They have subsequently been placed in a subtribe of their own, because of the presence of protarsi, which are lacking in the Scarabaeina species. Another morphological similarity to the Scarabaeina is the loss of the second mesotibial spur in two sub-genera of _Gymnopleurus_ Illiger. This appears to be a specialization associated with ball-rolling.

The gymnopleurines are coprophages, with distribution and feeding habits similar to the scarabaeines which will be discussed in more detail later. Arrow (1931) reported collecting specimens of *Paragymnopleurus* Shipp in rotten fruit.

Arrow (*op. cit.*) stated that in parts of Africa, *Gymnopleurus* species are used as models for mimicry by other dung-beetles of the genera *Onthophagus* Latreille and *Phalops* Erichson. The reason for this mimicry has not been established.

2.5.5 *Eucraniina*

This small subtribe, consisting of only three genera, (*Eucranium* Brullé, *Glyphoderus* Westwood and *Anomiopsoides* Blackwelder) is confined to a small area of the Neotropical region, where the species occur almost exclusively in dry, sandy areas of Argentina.

All the eucraniines are flightless and xero-psammophilous, with an appearance almost identical to that of the flightless *Scarabaeus* species which occur in similar habitats. The genus *Glyphoderus* Westwood is unusual in having marked sexual dimorphism, with the males having large pronotal horns, while the females have little more than a median pronotal depression. Both sexual dimorphism, and complexly sculptured pronota are rarely found within the Scarabaeini, but the above conditions do occur separately in the wingless *Scarabaeus* species such as *S.* *(schinzi)* Fairmaire, which displays marked sexual dimorphism in the development of the clypeal teeth, and in *S.* *rodriguesi* (Ferreira) and *S.* *denticolle*, (Péringuey) which have moderately sculp=

tured pronota. Apart from general appearance, the species of Eucraniina and Scarabaeina also share the oblique con= dition of the mesocoxae, the absence of protarsi, the shape of the protibia, and the four protibial dentations.

For the above reasons, Eucraniina appears to be the sub= tribe closest to Scarabaeina, while the simple aedeagus and unreduced second mesotibial spur are plesiomorphic conditions which would place the Eucraniina close to the ancestral stock from which Scarabaeina arose.

The eucraniines are telecoprid in their nidification be= haviour. While they have not been observed to construct a ball at the food-source, a sphere is constructed prior to egg-laying. The dung is carried from the food-source to the burrow in the forelegs, in much the same way as a person would carry a large bundle of washing. Many eucra= niines have the inner clypeal teeth shaped like a pitch-fork (Fig. 128), which suggests that the clypeal teeth aid in securing and carrying the lump of dung in this manner.

2.5.6 Scarabaeina

The subtribe Scarabaeina has an Old World distribution, occurring throughout Africa, Asia, the Middle East and southern Europe. Three species also occur on Madagascar. The habitats occupied by species of Scarabaeina range from moist savanna through drier habitats to desert regions.

The species of Scarabaeina are characterised by oblique, closely set mesocoxae; nine-segmented antennae, absence of protarsi and the presence of three pairs of forward projecting dentations on the head; two pairs on the clypeus and one pair formed by the anterior angles of the genae. These cephalic dentations play a role in "cutting off" a portion of dung from a larger mass. In some species that rely on pellet dung which does not require this cutting function, the dentations may be reduced to a greater or lesser extent.

The Scarabaeina represent a branch of telecoprid dung beetles which have flourished in a region where herbivore dung has been plentiful and the habitat suitable for the development of the telecoprid method of nidification. Opportunistic necrophagy has been observed in some of the xerophilous *Scarabaeus* L. species, as well as in some of the *Sceliages* Westwood species, which are often found rolling a portion of millipede along in the same manner as a dung-ball would be treated. It would thus appear that telecoprid nidification behaviour can be used successfully for foods other than dung.

INCERTAE SEDIS

2.5.7 Eurysternina

Eurysternina is a monotypic subtribe containing only the genus *Eurysternus* Dalman. The subtribe has a Neotropical distribution occurring in the tropical forests of Mexico and Gautemala.

No description or analysis of the morphology of this sub=tribe could be obtained. Halffter & Matthews (1966) only mentioned that they placed eurysternines in Scarabeini be=cause of the shape of their hind legs.

Ohaus (1909) stated that _Eurysternus_ species carry dung on their flattened backs, holding the dung in position with the middle legs while walking with the front and hind legs. No ball-rolling has been observed amongst any of the eury=sternine species. Brood-balls are formed, however. _Eurysternus_ _plebejus_ Harold leaves its brood-balls on the surface of the soil. The balls are apparently coated with a layer of clay for protection. Very similar behaviour has been observed in some Sisyphina species, the completed ball eventually being attached to a stalk of grass. The egg-chamber is centrally located in the brood-ball and the egg is attached to the wall of the chamber by a dark-colou=red cement (Arrow 1931). Two adults of _Eurysternus_ _magnus_ Laporte have been found in a chamber excavated directly un=der a pat of cow dung (Halffter & Matthews 1966). This is reminiscent of paracoprid behaviour, rather than the tele=coprid behaviour normally associated with Scarabaeini.

Because of the uncertain status of this subtribe, it is not included in the phylogenetic assessment of the genera of Scarabaeini.

2.6 KEY TO THE SUBTRIBES OF SCARABAEINI

1 (2) Meso- and metatibiae long and thin, not distally flared (Fig. 92) - Scarabaeini - 3

2 (1) Meso- and metatibiae short and stout, distally flared (Fig. 93) ....non-Scarabaeini

3 (4) Mesocoxae more or less parallel, separated by more than one mesocoxal length (Fig. 97).. 5

4 (3) Mesocoxae oblique, separated by less than one mesocoxal length (Fig. 98) 9

5 (6) Pronotum laterally compressed (Fig. 99); metatarsi conspicuously long and filiform; elytra triangular or heart-shaped from above ....Sisyphina

6 (5) Pronotum not laterally compressed; metatarsi not conspicuously long and filiform 7

7 (8) Antennae eight-segmented, with the exception of genus <u>Afroharoldius</u> in which antennae are nine-segmented; protarsi always present .... Alloscelina

8 (7) Antennae nine-segmented; protarsi present or absent; lateral fold of elytra wide; metatarsi laterally compressed..........Canthonina

9 (10) Protarsi present (Fig. 95); elytra laterally sinuate near base, exposing pleura (Fig. 100) .... Gymnopleurina

10 (9) Protarsi absent; elytra not laterally sinuate 11

11 (12) Tarsi bearing one or two claws (Fig. 96); single mesotibial spur, exceptionally two; fully-winged or brachypterous ... Scarabaeina

12 (11) Tarsi without claws, two conspicuous mesotibial spurs (Fig. 94); always brachypterous .... Eucraniina

3. SUBTRIBE SCARABAEINA LATRIELLE

Ateuchides Lacordaire, 1956 (Ateuchides *vrais pars*); Lansberge 1874 (*pars*); Gillet 1911.

Scarabaeides Péringuey, 1900 (*pars*); Gillet 1911; Ferreira 1953.

Scarabaeinae Kolbe, 1905.

Scarabaeina Janssens, 1949; Ferreira, 1961; Halffter & Matthews 1966, Ferreira 1969; Pachysomides Ferreira 1953.

Pachysomina Ferreira 1961; 1966; 1969 (*pars*).

3.1 TAXONOMIC HISTORY

The sense in which Gillet (1911) used the taxon Scarabaeides Lacordaire is the first clear exposition of the subtribe Scarabaeina as it is understood at present. Because of the southern African distribution of most of the genera in the subtribe, Péringuey (1900) included, by implication, all the present genera except *Neomnematium* Alluaud (from Madagascar) and *Mnematidium* Ritsema (from Syria) in his definition of the Scarabaeides taxon. Péringuey also included *Gymnopleurus* Illiger, now excluded because of the presence of protarsi which are absent in the other genera.

Péringuey used the closely set, oblique coxae as the main characteristic of the Scarabaeides. Gillet (1911), in his catalogue, does not furnish criteria for his taxa, but it appears that Péringuey's (1900) system was followed.

Janssens (1949), in his synopsis of the classification of Scarabaeidae, was the first to use the term Scarabaeina for the subtribe.

The subtribe Pachysomina Ferreira, containing the brachypterous species of Pachysoma M'Leay was synonymised with Scarabaeina by Holm & Scholtz (1979).

3.2 MORPHOLOGY

The morphological features that are mentioned in the literature as the most characteristic of the subtribe are the following:

- i) mesocoxae oblique and closely set (separated by half the length of the mesocoxa or less);
- ii) antenna nine-segmented;
- iii) protarsi absent;
- iv) tarsi with one or two claws (Figs. 157-162);
- v) scutellum invisible or very reduced;
- vi) one or two mesotibial spurs (Figs. 113, 114, 127).

These characters will be discussed in the description which follows. HEAD: Usually armed with six triangular, more or less recurved teeth, the inner four of which are on the clypeus, while the outer pair is formed by the anterior angles of the genae. The median pair is often ventrally subcarinate or toothed. (Species with these characteristics used to comprise the redundant genus Sebasteos

Westwood.) Depending on the shape of the genae, the outer pair of teeth may be more or less absent (some southern wingless Scarabaeus species), or have the appearance of an extra pair of teeth (Scarabaeus multidentatus Klug). The surface of the head and genae is punctured, the punctures being elongate and contiguous on the clypeus and the edges of the genae, but becoming sparse and granulate towards the base of the head, which always has a more or less distinct transverse ridge running across it. Transverse lines also run medially from the antero-medial corner of each eye but fade without meeting. Between and slightly in front of these two lines, a single, median tubercle is usually found. Scarabaeus L. has two tubercles placed side by side. The condition of the mentum varies from being evenly rounded, to having a median ridge (Kheper spp.), to bearing a large tooth (Scarabaeus proboscideus Guérin). There is a correlation between the sizes of the tubercles or ridges on the mentum and those on the frons. The eyes are divided into upper and lower halves by the canthus of the genae and always have a superciliary ridge. The size of the eyes, both dorsal and ventral but especially the latter, is directly related to whether the species is diurnal or crepuscular (very few, if any species of Scarabaeina are stricly nocturnal), the eyes of the crepuscular species being conspicuously large and often having a milky appearance in museum specimens. The mouthparts of all species of Scarabaeina are reduced and membranous. Maxillary palpi four-segmented, with a longitudinal groove along the inner side of the apical segment in all genera except *Sceliages*. Antenna nine-segmented, basal segment as long as the following five segments, the terminal three segments forming the club.

PRONOTUM: The pronotum is as broad or broader than the elytra and always convex, ranging from slightly convex (e.g. *Pachysoma* spp., *Scarabaeus rubripennis*), to very convex (e.g. *Sceliages* spp., *Scarabaeus convexus*). Evenly granulate or punctulate, moderately sculptured in a few cases (e.g. *Scarabaeus rodriguesi* (Ferreira), *S. denticolle* (Péringuey), *Pachylomerus* spp., *Kheper lamarcki* (M'Leay)), but never with pronotal horns or elaborate sculpturing as found in other scarabaeines, including some of the closely related species of Eucraniina.

THORAX: The scutellum is indistinct in most species and very small in the few species in which it is visible. Species are fully-winged in the great majority of cases, but brachypterous species occur randomly in dry, sandy regions throughout the distribution range of the subtribe (Fig. 8). Aptery, or more correctly brachyptery, as wing vestiges are always present, occurs in the subtribes Scarabaeina and Eucraniina. The brachypterous species of Scarabaeina were consolidated into a single genus, *Pachysoma* M'Leay by Holm & Scholtz (1979), while the exclusively wingless South American species of Eucraniina are divided into the genera *Eucranium* Brullé, *Glyphoderus* Westwood and *Anomiopsoides* Blackwelder.

These eucraniines all occur in hot, sandy areas, but as no winged forms occur, it is not possible to compare the morphology and biology of the macropterous and brachypterous species of Scarabaeina. The morphology and biology of macropterous and brachypterous species of Scarabaeina appear to differ only in so far as the species have become adapted to local conditions, of which brachyptery is the most obvious adaptation. The reasons for brachyptery will be discussed later. The elytra of the fully-winged species have a rectangular appearance, being slightly ampliate laterad of the humeral calli and tapering slightly towards the pygidium. The elytra are only slightly convex except along the posterior portion of the elytral suture where convexity increases as the elytra turn down towards the pygidium. In brachypterous species the elytra are more or less evenly rounded and convex both transversely and longitudinally. The elytra are always laterally carinate, with two parallel carinae running along the dorsolateral margin of each elytron. In some of the brachypterous species e.g. *Pachysoma rodriguesi* Ferreira these supra-marginal carinae are so close together as to have the appearance of a single carina, while in *Kheper* species the two carinae characteristically diverge abruptly just next to the humeral callus. The pygidium is exposed, obtusely triangular and punctulate or granulate. The aedeagus may be simple, symmetrical (*Drepanopodus* spp., some *Scarabaeus* spp.), more or less complex, symmetrical *Pachylomerus* spp., some *Kheper* spp., some *Scarabaeus* spp.), or asymmetrical (Sceliages spp., some Scarabaeus spp., some Kheper spp.).

LEGS: The plesiomorphic condition of the protibia within Scarabaeina, as determined by comparison to the Eucraniina, is with four large external dentations, with smaller serra=tions between and proximal to these dentations. In Kheper spp., the serrations have disappeared completely, and the proximal dentation is reduced (Fig. 155). In the remain=ing genera some measure of serration on the protibia is al=ways present, but as the protibiae are the major burrowing organs, the serrations are often worn away, especially in Pachylomerus species. The condition of the proximal den=tation is variable, being reduced in all the Sceliages species and many of the Scarabaeus species, but only in one of the observed species (including those in the BM), namely Scarabaeus caffer (Boheman), has the proximal den=tation been completely resorbed. In the case of Scarabaeus multidentatus Klug the proximal serrations are particular=ly large, giving the appearance of the protibia having more than the usual four dentations, but the dentations are easily distinguished from the serrations by being larger and having a dorsal carina which the serrations lack (Fig. 151). The profemora of members of one genus, Pachy=lomerus Bertoloni, are extraordinarily well-developed, being grossly enlarged, especially in the males. Scarabaeus cancer (Arrow) is the only other species of Scarabaeina that exhibits an unusual enlargement of the profemora, the remaining species tending to have normal or slender profemora. The mesothoracic legs are of use in determining phylogenetic relationship. The mesocoxae of Scarabaeina species tend to be closely set, being less than half a mesocoxal length apart, except for the mesocoxae of species of *Sceliages* which all exceed this half coxal width. *Sceliages* species also differ from other Scarabaeina species in having a large second mesotibial spur (Fig. 113), whereas in the majority of species the second spur is absent. In the few species where the second spur does occur it is vestigial, being no more than one-fifth the size of the first (Fig. 114). The point of insertion of the tarsus on the tibia of the mesothoracic leg is variable. The plesiomorphic condition is insertion at the distal extremity of the tibia but in extreme cases, such as *Drepanopodus* species, the insertion is halfway along the length of the tibia. *Sceliages* is the only genus in which all species exhibit the plesiomorphic condition, *Pachylomerus* and *Kheper* species showing a moderate proximal shift, while *Scarabaeus* shows all the conditions from plesiomorphic to apomorphic, but never as extreme as in the species of *Drepanopodus*. Each genus of Scarabaeina has a tarsal structure peculiar to it. In *Sceliages* the tarsus is relatively short, with the tarsal segments laterally flared, and having two claws of equal size (Fig. 157). The remaining genera have more slender, elongated tarsi. In *Scarabaeus* two equal tarsal claws are found but the tarsal segments are never flared as in *Sceliages*. *Pachylomerus* species have two small, unequal tarsal claws (Fig. 161), while in Kheper and Drepanopodus only one tarsal claw is present (Figs.160, 162). In the former genus the claw is reasonably stout and the tarsus moderately hirsute, while in Drepanopodus the claw is recessed and small (Fig. 160), and the tarsus very hirsute. The tarsal hairs of the psammophilous species of Scarabaeina, such as Drepanopodus, often form "sandshoes" (Fig. 160) which apparently help to distribute weight on the soft substrate in much the same way as snowshoes do. Finally, the character of 'no tarsal claws' mentioned by Janssens (1949) for some Scarabaeina members was not found in the species examined, apparently occurring only in the Ethiopian species Scarabaeus tonckeri Boucomont. The absence of tarsal claws, plus the presence of two large, equal mesotibial spurs, are the main features separating the flightless species of the South American subtribe Eucraniina from Scarabaeina, especially from the brachypterous species of the latter.

3.3 BIOLOGY

3.3.1 Feeding and nesting behaviour

In general, the species of Scarabeina are telecoprid dung beetles, utilizing the dung of large herbivores, especially that of bovids. Food and brood balls are fashioned from moist dung by detaching a quantity of dung from a larger mass by means of the clypeus and protibia, then shaping the removed portion into a ball. These balls are rolled some distance from the dung-source before being buried prior to being used as food by the adult, or as food and shelter for the developing larva.

Although it is probably correct to state that most species of Scarabaeina prefer to use the dung of large herbivores, some degree of opportunism is displayed under desert conditions. Holm & Scholtz (1979) noted that Scarabaeus denticolle (Péringuey) utilises not only hare, mouse and chameleon dung, but even drags vegetable matter such as leaves and grass into its burrows.

Necrophagy has been observed in another desert species, Scarabaeus rubripennis (Boheman), (Holm, pers. comm.), while it appears that the Sceliages species use millipede carcasses as food or brood source as I, and various other workers, have observed these beetles rolling pieces of millipede along in the same way in which a ball of dung would be rolled. The reasons for this seemingly aberrant behaviour are discussed under the relevant generic section (4.3.1).

In contrast to the ball-rolling behaviour of the Scarabaeina species, members of the Eucraniina, the outgroup which appears most closely related to Scarabaeina, apparently do not roll the detached portion of dung, but carry it in the forelegs (Halffter & Matthews, 1966), aided in some species by the elongated clypeal teeth which act as a kind of pitchfork in securing the dung being carried e.g. Eucranium arachnoides Brullé and Anomiopsoides cavifrons Burmeister (Fig. 128). E. arachnoides has been observed carrying horse manure in this way (Burmeister 1861 cited in Kolbe 1905). Horse manure, being relatively dry and friable, may not be suitable for shaping and rolling in the normal manner in any case. A. cavifrons and A. furciferum Burmeister have been observed carrying rodent pellets (small, oblong and unsuited for moulding into a ball?) in the same way (Martinez, 1945).

3.3.2 Diel activity patterns

The majority of Scarabaeina species are diurnal, but several crepuscular species are found in Kheper and Scarabaeus. The crepuscular habit seems to be a highly evolved condition, with very characteristic phenotypic features associated with it. The most obvious of these are large eyes (Figs.123, 124), which often take on a milky appearance after death; large body size; rufous hair (as opposed to black) on all parts of the body; and the presence of pheromone-disseminating metatibial brushes on males. The presence of pheromone glands on the abdominal sternites is characteristic of many of the crepuscular species of both Kheper and Scarabaeus, the advantage of such an olfactory attractant in poor light conditions being quite obvious. The presence of these glands was first described by Tribe (1975, 1976). The size of the glands and metatibial brushes seems to correlate with the degree of crepuscular/nocturnal activity of the species, the largest brushes and glands occurring in the most nocturnal species. All Kheper species have pheromone brushes, although only three southern African species, K. lamarcki (M'Leay), K. cupreus (Castelnau) and K. prodigiosus (Erichson), appear to be strictly crepuscular (Tribe 1976). The presence of pheromone glands in Kheper species thus appears to be a case of preadaptation for crepuscular activity, as pheromone glands are also present in at least two of the four crepuscular Scarabaeus species mentioned by Tribe (1976).

3.4 DISTRIBUTION

While the subfamily Scarabaeinae is represented in all six zoogeographical regions, examination of the distribution patterns within the subfamily shows it to be predominantly Ethiopian and Oriental.

As all scarabaeine tribes are abundantly represented in the Ethiopian region while the other regions show a lower tribal and specific diversity, it seems likely that the subfamily Scarabaeinae had a Gondwanan origin. For the same reasons, the tribe Scarabaeini is also thought to have had a Gondwanan origin (Matthews 1974). The subtribe Scarabaeina is confined to the Old World, in contrast to such related cosmopolitan subtribes as Sisyphina and Canthonina. The overall distribution of Scarabaeina exhibits an arid pattern while the Scarabaeina genera show a marked southern distribution, with only two genera (as redefined in the present work), namely Scarabaeus and Kheper, occurring north of the 10th degree N. latitude.

The taxonomic outgroup of the Scarabaeina appears to be the South American subtribe Eucraniina, which occurs in arid regions of Argentina, similar to south-western Africa where the most plesiomorphic species of Scarabaeina are found. The distribution data suggest that _Sceliages_ Westwood had a southern centre of speciation (south of 25° S. latitude), while _Scarabaeus_ L. and _Drepanopodus_ Janssens had arid, south-western centres of speciation, _Pachylomerus_ Bertoloni a moister, more central southern African centre of speciation, and _Kheper_ Janssens a moist south-eastern centre of speciation.

Apart from the above, the following factors regarding the distribution of both genera and species of Scarabaeina should be borne in mind.

i) _Uneven collecting of material_

Certain parts of Africa such as southern Africa and East Africa have been much more thoroughly sampled than other regions. In a recent study of the distribution of five beetle families representing some 30 genera, 500 species and 6000 distribution records, only about 800 of the nearly 1600 degree squares in sub-Saharan Africa yielded any results at all (Holm & Scholtz pers. comm.)

ii) _Temperature_

According to Tribe (1976) temperature directly influences such activities as flying time and pheromone release, and also plays a role in the seasonal fluctuations in numbers of telecoprid scarabaeines. He found that telecoprids usually occur in regions with an "effective temperature" (Stuckenberg, 1969) above 15°C. Effective temperature is the biologically meaningful temperature at a given location, based on the greater fluctuation of temperature with increasing altitude, the biological importance of the summer months, the duration of the warm period and the temperatures at the beginning and end of this period. Regions with an E.T. of 15-19°C are classified as "warm to very warm".

iii) Rainfall

Rainfall affects the distribution of telecoprids in a number of ways.

a) Mean annual rainfall - the genus Kheper appears to occur only in areas with a minimum annual rainfall of 200mm and a maximum of 1000mm, while Pachylomerus also occurs in areas with a relatively high rainfall. On the other hand, the drier regions of southern Africa (100-400mm/yr) are inhabited mainly by the small Scarabaeus (Scarabaeolus) species.

b) Rainfall season - Fabre noted at the turn of the century that a certain quantity of rain was required before Scarabaeus species were able to escape from their underground brood-balls. Apart from softening the soil, rainfall must coincide with temperatures warm enough for beetle activity. For these reasons, Scarabaeina numbers in winter rainfall areas are relatively low.

iv) Soil type

Soil types affect the distribution of dung beetles both directly and indirectly. The majority of telecoprids occur in areas with sandy soils (Soil Map of South Africa, 1973). Even within a relatively small area such as Mkuzi Game Reserve, species of Scarabaeina are found mainly in the sandy areas of the reserve (Tribe 1976). Kheper bonellii (M'Leay) occurs in the south-western Cape Province in littoral and near-littoral sand. Although this is a winter rainfall region and K. bonellii is active in summer, it is not dependent on rainfall in summer to release it from the soil, as no hard crust forms on the surface of the ground, and the sand retains enough moisture to allow escape from the brood-ball in spring.

An indirect effect of soil type on beetle distribution is the vegetation that a given soil can support, which in turn will determine the distribution of the herbivores on which the dung beetles are dependent.

v) Interrelationship with herbivores

As scarabaeines are for the most part morphologically and behaviourally very specialised coprophages, the distribution and abundance of these beetles are largely reflections of the availability of suitable dung. The large-scale extermination of indigenous mammals, introduction of domestic animals, erection of fences, and modern farming practise must have had striking effects on dung beetle distribu=

tion, although it may take some time for these changes to become apparent. A species in which these effects are well demonstrated is *Circellium bacchus* F., a large flightless canthonine which relies on an abundant supply of elephant or rhinoceros dung in compensation for its greatly reduced mobility. Distribution records show that this species used to occur sympatrically with elephants and rhinoceroses throughout most of southern Africa, but at present it is restricted almost exclusively to the Addo Elephant Park in the Eastern Cape Province. This beetle is further restricted by occurring only on sandy soils, and by the fact that it is an extremely slow breeder, producing a single brood-ball per female per season (Tribe, 1976).

Conversely, scarab species which previously utilized buffalo dung may actually be able to increase their distribution range by making use of cattle dung as a substitute. A case in point seems to be *Pachylomerus opacus* Lansberge, which was recently collected at Nylsvley Nature Reserve in the northern Transvaal, after having previously been recorded only from the north-western Cape Province and Botswana.

4. SYSTEMATIC SECTION

4.1 APTERY WITHIN SCARABAEINA

4.1.1 Introduction

The flightless species of the subtribe Scarabaeina were in=vestigated in an attempt to update and clarify their taxo=nomic status. Recent publications such as Balthasar (1963) and Holm & Scholtz (1979) expressed misgivings about the validity of the genera to which these species had been assigned.

Wing reductions, associated with scarabaeine species occur=ring in arid, sandy areas, is documented from as far afield as South America (Halffter & Matthews, 1966) and Australia (Matthews, 1974), as well as south-western Africa, Madagas=car and the Middle East (see Fig. 8).

In South America and Australia brachyptery has occurred in at least three and six scarabaeine genera respectively. In the Old World, four genera viz. *Mnematium*, *Pachysoma*, *Neomnematium* and *Neopachysoma*, were each created to accom=modate one or more of the flightless species.

The distribution and phenotype of these species argue against a monophyletic origin of the brachypterous condi=tion, but none of the species exhibits an autapomorph in=dicative of a phylogeny distinct from the other species of the genus *Scarabaeus*. As the distribution of *Scarabaeus* embraces all the distributions of the flightless Old World species, it was concluded that the latter represent brachypterous species of Scarabaeus, rather than uniquely derived genera.

A key, with illustrations, to all the flightless Old World Scarabaeina species is provided.

4.1.2 Status of the Genera Pachysoma M'Leay and Neomnematium Janssens with a description of a new species of Scarabaeus L.

4.1.2.1 Genus Pachysoma M'Leay (syn. nov. ad Scarabaeus L.)

Pachysoma M'Leay, 1821: 507. Type-species Pachysoma hippocrates M'Leay.

Mnematium M'Leay, 1821: 506. Type-species Mnematium ritchiei M'Leay.

Irrorhotides Shipp, 1896: 116. Type-species Irrorhotides fryi Shipp.

Neopachysoma Ferreira, 1953: 37. Type-species Pachysoma denticolle Péringuey.

Holm and Scholtz (1979) synonymised Neopachysoma Ferreira and Mnematium M'Leay with Pachysoma M'Leay, pointing out that the characters on which the subtribe Pachysomina Ferreira was based, namely brachyptery, absence of humeral calli, semi-contiguous mesocoxae and short metasternum, were not demonstrably synapomorphic; consequently the subtribe Pachysomina has no phylogenetic justification.

It was suggested that the brachypterous condition may have been acquired independently by the various species and that the absence of humeral calli, and the short metasternum, were the results of wing reduction. Similar reductions can be seen in another scarabaeoid genus containing fully-winged and brachypterous species, namely *Trox* M'Leay (Scholtz 1981).

The likelihood that the semi-contiguous condition of the mesocoxae in *Pachysoma* is due to wing-reduction is borne out by the fact that the species in which it does not occur, *P. rotundipenne*, P. silen... has the lowest rating for morphological reductions and developments of the 13 *Pachysoma* species examined (Holm & Scholtz, 1979). This implies that the *Pachysoma* species are descended from a scarabaeine beetle with non-contiguous mesocoxae, functional wings, humeral calli and a relatively long metasternum. As the species of *Pachysoma* do not differ in any significant way from those of *Scarabaeus* (*sensu lato*), except for the four characters mentioned, the retention of the genus *Pachysoma* (*sensu* Holm & Scholtz 1979) does not appear justified on morphological grounds, unless a synapomorphic character proving a unique derivation can be found.

Unfortunately, the previously known species are all so closely related that the suspected polyphyletic nature of the characters associated with the brachypterous condition could not be verified. The new species described in this paper, as well as *P. silenus* has, however, proved to belong to the subgenus *Scarabaeolus*, due to the presence of a second mesotibial spur, which is the main characteristic used in separating the subgenera *Scarabaeus* and *Scarabaeolus* (Balthasar 1965; Ferreira 1969). They show all the characters of *Pachysoma* (*sensu* Holm & Scholtz) and therefore make that genus untenable within the present framework of generic classification of the tribe.

Lastly, the only positive argument for retaining *Pachysoma*, the peculiar behaviour and biology (Holm & Scholtz 1979), has become suspect as a valid synapomorph through observations of the behaviour of *Pachysoma gariepinus* (see *S. gariepinus* below).

I therefore recommend that *Pachysoma* (and its synonyms) be regarded as a synonym of *Scarabaeus*.

4.1.2.2 Genus *NEOMNEMATIUM* Janssens (*syn. nov.* ad *Scarabaeus* L.)

Neomnematium Janssens, 1938: 71. Type-species *Scarabaeus sevoistra* Alluaud.
Scarabaeus Alluaud 1902: 250-251 (pars).
Neateuchus Gillet 1911: 7 (pars).

Neomnematium Janssens is a monotypical genus containing *N. sevoistra* Janssens (1938) removed this species from the genus *Neateuchus*, claiming that the presence of a protuberance on the mentum was due to convergence with the other species of *Neateuchus*, rather than common ancestry - the protuberance of *N. sevoistra* is short and simple while those of the *Neateuchus* species are long and bifid. The presence of a symmetrical aedeagus in *N. sevoistra*, as against the asymmetrical aedeagi of the *Neateuchus* species, lends further support to this assertion.

While recognising the similarity between *N. sevoistra* and species of *Mnematium*, Janssens preferred to create a new genus, *Neomnematium*, for this species - apparently because of the protuberance on the mentum. Another *Scarabaeus* species, *S. zambesianus*, however, has a mentum very similar to *N. sevoistra*. The symmetrical aedaegus of *N. sevoistra* is also found in *S. scholtzi spec. nov.* and *S.* (*Scarabaeolus*) *rubripennis*.

I therefore conclude that *N. sevoistra* has no demonstrably unique apomorphs which justify a genus separate from *Scarabaeus*.

The synonymy of the genus *Scarabaeus* (according to Gillet (1911), Balthasar (1963) and the new synonyms listed in this work) is given in section 4.3.2.

The synonymy of *Pachysoma* and *Neomnematium* with *Scarabaeus* affects the following combinations:

Scarabaeus (*s.str.*) *aesculapius* Olivier;
S. (*s.str.*) *ritchiei* (M'Leay);
S. (*s.str.*) *hippocrates* (M'Leay) *comb. nov.*

S. (*Scarabaeolus*) *silenus* (Gray) *comb*. *nov*.

S. (*s*. *str*.) *striatus* (Castelnau);

S. (*s*. *str*.) *denticolle* (Péringuey) *comb*. *nov*;

S. (*s*.*str*.) *schinzi* (Fairmaire);

S. (*s*.*str*.) *sevoistra* Alluaud;

S. (*s*.*str*.) *bennigseni* (Felsche);

S. (*s*. *str*.) *rotundigena* (Felsche);

S. (*s*. *str*.) *cancer* (Arrow);

S. (*s*. *str*.) *fitzsimonsi* (Ferreira);

S. (*s*.*str*.) *gariepinus* (Ferreira);

S. (*s*.*str*.) *rodriguesi* (Ferreira).

The synonomies and other data for these species remain as in Holm & Scholtz (1979).

4.1.2.3 Subgenus *SCARABAEOLUS* Balthasar

Scarabaeolus Balthasar, 1965: 14.

Scarabaeus (*Scarabaeolus*) *scholtzi* *spec*. *nov*. (Figs. 1-8)

Holotype: Somali Republic: NE Afr. Somali Rep., 52 km NE El Den, coastal plain, (NE 04 47 Dc), 28.x.1971, Hemming (TM).

Paratypes: 10 ditto (2 BM, 7 TM, 1 UP): 2 Somali Rep., 90 km N. Obbia on Geriban road, (NE 06 48 Dc), 2.xi 1971, C.F. Hemming (1 TM, 1 UP).

Description

COLOUR: Black. SIZE: Length 15-18mm width (pronotum) 10-13mm. HEAD: Slightly wider than long, medially glab=

rous but genae and rest of clypeus bearing scattered setiferous punctures; median clypeal projections short, with distance between approximately twice the length of each projection; smooth lateral margins of clypeus and genae form a more or less continuous line as in _S_. _aesculapius_ but clearly separated by an incision between clypeus and genae. PRONOTUM: Disc frontal profile more convex than lateral profile, smooth with irregular, small punctures; posterior margin evenly convex between outer angles; antero-lateral margins slightly convex, serrulate and narrowing sharply from outer angles to anterior margin; head recess in anterior margin deep and closely applied to basal margin of head. ELYTRA: Humeral angles round, calli absent; surface smooth; costae faint, elytral profile evenly convex in length and width. APPENDAGES: Maxillary palpi with terminal segment approximately three times the length of the penultimate segment (Fig. 4).
LEGS: Mesotibia with two distinct unequal spurs, the longer one approximately three times the length of the other (Fig. 7). VENTER: Smooth and glabrous except for a sparse line of setae running transversely across anterior half of last abdominal sternite. MALE GENITALIA: Simple, symmetrical (Figs. 5 and 6).

Discussion

This species belongs to the subgenus _Scarabaeolus_, which is characterised by the presence of a second mesotibial spur. The mysterious elytron mentioned by Ferreira (1966), and commented on by Holm & Scholtz (1979), probably belongs to this species.

In the possession of a second mesotibial spur, this species is similar to *Scarabaeus silenus*, but the examined specimens of S. *scholtzi* are much smaller than those of *S. silenus*. Apart from size, it can also be distinguished from the latter species by the absence of anterior genal projections and the presence of a transverse ridge across the base of the elytra.

Scarabaeus (*Scarabaeolus*) *silenus* (Gray) *comb. nov.*
(Figs. 8, 16, 69-72).

Holotype: DRE

Type locality: Arabia

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

Mnematidium silenus Reitter 1894: 183

Scarabaeus rotundipennis Holdhaus, 1919: 54.

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

Pachysoma rotundipenne: Holm & Scholtz 1979: 226 *syn. nov.*

Pachysoma silenus: Holm & Scholtz 1979: 227 *syn. nov.*

In his description of *Scarabaeus rotundipennis*, Holdhaus (1919) distinguishes *S. rotundipennis* from *S. ritchiei*, while *S. silenus* is not mentioned. He was apparently not aware of the latter species. The only difference between the holotypes of *S. silenus* and *S. rotundipennis* is the irregular genal margin of the former compared to the smooth genal margin of the latter. Specimens from S.W. Sinai, however, have all the intermediate conditions. I therefore synonomise *S. rotundipennis* with *S. silenus*.

The species has been collected from the confluence of the Tigris and Euphrates rivers in Iraq, Halab (Aleppo), the Sinai Peninsula and the north-eastern regions bordering the Red Sea (Balthasar 1963, plus material examined).

Although *Scarabaeus silenus* and *S. ritchiei* are very similar, *S. silenus* can be distinguished by the following features: (i) the presence of a second mesotibial spur (also present in *S. scholtzi*, fig. 7); (ii) non-contiguous mesocoxae, (iii) a distinct break in the inner peripheral setation of the mesotibia opposite the insertion of the tarsus - the second tibial spur is located in, or just next to, the distal clump of setae. *S. silenus* is also generally larger than *S. ritchiei* (lengths 18-25mm and 16-20mm respectively) and clearly separated geographically (Fig. 8).

MATERIAL EXAMINED: (17 unsexed specimens). SYRIA: Alep (Halab), NE 36 37 Cc, le Moult. IRAQ (PERSIA): Baghdad, NE 33 44 Cb. (ex Coll. R.O. Berthur) (PAR); Nahÿe (Ba ÿi)-Ana (Anah), NE 35 43, Mesopot. Exp. Nat. O.V., 1910, Pietschmann (PAR) EGYPT: S.W. Sinai, NE 29 34, 10.i.1948, H. Field (BM).

4.1.2.4 Subgenus SCARABAEUS Linneaeus

Scarabaeus (s.str.) gariepinus (Ferreira) comb. nov.
(Figs. 8, 21, 57-59.)

This species occurs around the mouth of the Orange River extending some 100 km north and south of the river and at least 70 km inland.

In an attempt to test the behavioural evidence for my suspicion that the Pachysoma species were in fact nothing but brachypterous Scarabaeus species, a field investigation was undertaken in November 1980.

The dung available to these xerophilous scarabs is almost entirely in the form of pellets, in the case of S. gariepinus usually the droppings of Oryx gazella (gemsbuck) and Antidorcas marsupialis (springbuck). These small dry pellets are held between the hindlegs only, and dragged forward as opposed to the backward rolling of the larger, wet dung balls constructed by other Scarabaeus species, which use both middle and hind legs to manipulate the ball.

When fresh horse droppings (collected at Oranjemund) were presented to S. 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.

Scarabaeus (s.str.) denticolle (Péringuey) comb. nov.
(Figs. 8, 14, 30-34).

Scarabaeus (*s*. *str*.) *denticolle* *penrithae* (Zunino)
stat. *nov*.

Neopachysoma *penrithae* Zunino, 1977: 15.
Pachysoma *penrithae* Holm & Scholtz, 1979: 230 (*P*. *denticolle*).

The status of the taxon *penrithae* Zunino which was tentatively held to be synonymous with *Scarabaeus* *denticolle* by Holm & Scholtz (1979), has since then become clear through intensive collecting in the area near Lüderitzbucht. Good series from Kolmanskop and localities between Lüderitzbucht and Hottentotsbaai all conformed to the typical *penrithae*, but 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) and Holm and Scholtz (1979). It has thus become fairly certain that *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.

Additional material examined (9 specimens): 30 km N. Lüderitz, SE 26 15 Ac. 5.x.1979, Holm & Scholtz (UP); Kolmanskop, SE 26 15 Cb. 6.x.1979, Holm & Scholtz (UP) (intermediates to *denticolle* *s*.*str*.) (13 specimens): SE 26 15 Ad. Dept. Entomology exp. (UP).

Scarabaeus (*s*.*str*.) *fitzsimonsi* (Ferreira) *comb*. *nov*.
(Figs. 8, 11, 39-42).

NEW LOCALITY RECORD: NAMIBIA: Aus. (30 km N), SE 26 16 Ad. 7.x.1979, Holm & Scholtz (UP).

Scarabaeus (*s.str.*) *rodriguesi* (Ferreira) *comb. nov.* (Figs. 8, 9, 35-38).

NEW LOCALITY RECORD: NAMIBIA: 90 km SSE Ururas, SE 24 14 Bb, 14.x.1979, Holm & Scholtz (UP).

INCERTAE SEDIS

4.1.2.5 *Scarabaeus cancer* (Arrow) *comb. nov.* (Figs. 8, 18 54-56)

Holotype: BM.

Type locality: Not reported when species was originally described, but Arrow suspected that it came from the Bihé district of Angola.

Mnematium cancer Arrow, 1919: 433; Balthasar 1963: 139; Ferreira 1969: 28.

Pachysoma cancer: Holm & Scholtz 1979:227.

Only the type specimen of this species could be obtained. Its position within the subtribe Scarabaeina remains unclear. The profemora of *Scarabaeus cancer* are very similar to those of the *Pachylomera* species. The aedeagus of *S. cancer*, however, is asymmetrical and ventrally extended (Fig. 55), while the aedeagi of the *Pachylomera* species are symmetrical and not ventrally extended.

Until more material is available and the status of the other genera within the Scarabaeina has been revised, I suggest that *S. cancer* should provisionally be included in the genus *Scarabaeus* (*sensu lato*).

4.1.3 Key to the flightless species of *Scarabaeus*

1 (2) One spur at distal end of mesotibia (*Scarabaeus s. str.*) 3

2 (1) Two spurs at distal end of mesotibia (*Scarabaeus* (*Scarabaeolus*)) 27

3 (4) Profemora much enlarged and bearing well-pronounced spines - very large species (Type 48 mm in length)...*S.*(*S.*) *cancer* (Arrow)

4 (3) Profemora not much enlarged, without well-pronounced spines 5

5 (6) Elytra rounded, without ridge on base......... 7

6 (5) Elytra with sharp ridge on base...............19

7 (8) Anterior margin between median clypeal points convex to straight (Figs. 19-20) - sexual dimorphism marked, the male with the clypeal points strongly produced into horn-like structures (Fig. 20). Distance between second and third protibial dentations notably greater than between others (Fig. 60......*S.*(*S.*) *schinzi* (Fairmaire)

8 (7) Anterior margin between median clypeal points concave............................... 9

9 (10) Frons with a prominent tubercle between the eyes (Fig. 9) - specimens large, shiny, black, with a median and two lateral longi=

tudinal depressions on pronotal disc.................*S*.(*S*.) *rodriguesi* (Ferreira)

10 (9) Frons without a tubercle 11

11 (12) Outer margin of genae smooth and rounded (Fig. 13), protibial spur simple - male protibia modified, with internal projec= tion at the apex (Fig. 50) ....*S*.(*S*.) *striatus* (Castelnau)

12 (11) Outer margin of genae serrated, irregular or angular, protibial spur simple or bifurcate 13

13 (14) Pronotum with a median and two oblique lateral depressions on disc................... 15

14 (13) Pronotal disc evenly rounded.................. 17

15 (16) Protibia with a small but distinct denti= culate projection on the apex, laterad of the protibial spur - specimens mostly with orange on elytra, the males only with the protibial spur bifurcate and protibia with two rows of long spines on the inside (Figs. 30-31) .... *S*.(*S*.) *denticolle* (Péringuey)

16 (15) Protibia without a projection on the apex - elytra markedly flat and deeply striate.... .... *S*.(*S*.) *bennigseni* (Felsche)

17 (18) Elytra smooth, shiny, protibial spur bifurcate - protibia with a subapical projection on the inside (Figs. 43-44)
.... S.(S.) rotundigena (Felsche)

18 (17) Elytra striate, protibial spur simple - pronotum and elytra greyish-black with a band of indument around the outer margin; protibia simple (Fig. 57)......
.... S.(S.) gariepinus (Ferreira)

19 (20) Mentum with a ventral protuberance, elytra short, aedeagus symmetrical.....
.... S.(S.) sevoistra Alluaud

20 (19) Mentum without a ventral protuberance, aedeagus asymmetrical...................... 21

21 (22) Protibial spur bifurcate (Figs. 63-65), metatarsal claws as long as last segment or longer ....S.(S.) hippocrates (M'Leay)

22 (21) Protibial spur simple, metatarsal claws much shorter than last tarsal segment....... 23

23 (24) Metatibia with no transverse combs of bristles on the underside............
.... S.(S.) fitzsimonsi (Ferreira)

24 (23) Metatibia with two dense, semicircular transverse combs of bristles on the underside.............................. 25

25 (26) Genae straight in front, without any points, and hardly separated from clypeus by an incision, with a smooth outer edge (Fig. 23)......... S.(S.) aesculapius Olivier

26 (25) Genae with a clearly defined point in front, genal margin smooth and regular. Mesocoxae semi-contiguous...... S.(S.) ritchiei (M'Leay)

27 (28) Genae with a clearly defined point in front, genal margin irregular, may have secondary genal points................. S. (Scarabaeolus) silenus (Gray)

28 (29) Genae without anterior point, smooth lateral margins of clypeus and genae form a more or less continuous line but clearly separated by an incision between genae and clypeus (Fig. 1) Aedeagus symmetrical (Figs. 5-6) ....S. (Scarabaeolus) scholtzi spec. nov.

4.1.4 Phylogenies of the flightless Scarabaeus species

4.1.4.1 The North African species

The morphological similarity between Scarabaeus silenus and S. ritchiei is so marked that they were, for a time, thought to be the same species (Reitter, 1894). They can, however, be clearly distinguished by the presence of a vestigial second mesotibial spur in S. silenus, while this spur is lacking in S. ritchiei. According to Balthasar's

(1965) classification, the presence of the second mesotibial spur places *S. silenus* in the subgenus *Scarabaeolus*, while *S. ritchiei* belongs in the subgenus *Scarabaeus*.

While this classification is accepted, the case in point suggests that either brachyptery or the loss of the second mesotibial spur must have occurred more than once, and that the phylogenetic distance between *Scarabaeus silenus* and *S. ritchiei* is less than that expected for subgenera, since neither of the two characters constitutes a conclusive synapomorph.

Mnematidium multidentatum, a fully-winged species, shows a marked resemblance to *Scarabaeus ritchiei*. The characters used in the generic definition of *Mnematidium*, namely the large proximal protibial serrations and the angular lateral margins of the genae, are of doubtful validity. The fact that the aedeagi of *M. multidentatum* and *S. ritchiei* are almost identical enhances the probability that these two species constitute sister groups.

4.1.4.2 The Somalian species

Scarabaeus scholtzi does not resemble any of the other flightless species, nor any of the winged species examined. As relatively few winged *Scarabaeus* species from that region were examined, however, the probability of a winged species closely related to *S. scholtzi* cannot be excluded.

4.1.4.3 The Angolan species

Scarabaeus cancer is the only flightless species that occurs in Angola. The phylogeny of this rare species remains uncertain, since its overall size and profemora are similar to those of *Pachylomera* species, while the tarsal claws and aedeagus resemble those of the *Scarabaeus* species.

4.1.4.4 The South West African species

According to Holm & Scholtz (1979), *Scarabaeus ritchiei* and *S. silenus* have undergone the least morphological evolution of the flightless species examined by them. Therefore, it is not surprising that a winged species, *Mnematidium multidentatum*, exists which closely resembles these species. Unfortunately, no such close winged relatives are known for the brachypterous south-western African species.

The most obvious difference between the flightless and the fully-winged south-western African species, apart from the rounding of the elytra due to brachyptery, is found in the shape of the clypeal and genal teeth. A possible reason for this difference is that in the winged *Scarabaeus* species, the teeth on the clypeus and genae are used in "cutting" off a piece of dung from the larger mass, prior to shaping it into a ball. The dung used by the flightless species is invariably in the form of pellets, i.e. "ready-made" balls, thus the function of the clypeal and genal teeth becomes obsolete, allowing more evolutionary flexibility in the form of these teeth to evolve.

While it is difficult to correlate the flightless species with extant winged ones, it is clear that species groups exist within the ten flightless south-western African species.

The most obvious grouping, based on overall similarity and apparent synapomorphies such as protibial and aedeagal form (see also Holm & Scholtz, 1979), is as follows:

The *aesculapius* group: *S. aesculapius*, *S. hippocrates*, *S. rotundigena*.
The *schinzi* group: *S. schinzi*, *S. fitzsimonsi*.
The *striatus* group: *S. striatus*, *S. gariepinus*.
The *denticolle* group: *S. denticolle*, *S. rodriguesi*, *S. bennigseni*.

4.2 SYSTEMATICS OF MACROPTEROUS TAXA OF SCARABAEINA

4.2.1 Status of the genera *Mnematidium* Ritsema, *Neateuchus* Gillet and *Madateuchus* Paulian

4.2.1.1 MNEMATIDIUM Ritsema

Mnematidium Ritsema, 1889: 207; Shipp 1895: 40; Gillet 1911: 7; Arrow 1919: 433; Balthasar 1935: 28; Janssens 1938: 8, 69, 70; Janssens 1940: 55; Balthasar 1963: 143.

Ateuchus Weber *sensu* Klug 1845: 41 (*pars*) ; *A.* (*Mnematidium*) Shipp 1895: 40.

Octodon Lansberge 1874: 183.

Scarabaeus (*Neoctodon*) Bedel 1892: 282.

TYPE SPECIES: *Ateuchus multidentatus* Klug

MATERIAL EXAMINED. (1 male, 2 unsexed specimens).
EGYPT: Suez Canal, (NE 31, 32), 1969, J. Couyat (PAR).
ISRAEL: Tel Aviv, (NE 32, 34), 20.iv.1933, C. Koch (NM);
Jaffa, (NE 32 34), (no collector's name or date) (NM).

TAXONOMIC HISTORY. *Mnematidium multidentatum* (Klug) was originally described as an *Ateuchus* Weber (present-day *Scarabaeus* L.) species by Klug 1845, in what appears to be the second publication to mention this species. The possibility of an intermediate publication in which *Ateuchus multidentatus* was reallocated to *Mnematium* is not unlikely but no reference to such a publication could be found. Lansberge (1874) in turn proposed the genus *Octodon* to accommodate this species. Ritsema (1889) collated and emended Lansberge's publications, and described the genus *Mnematidium* for this species as *Octodon* was a preoccupied name in the mammalia. Bedel (1892), in his revision of Palaearctic *Scarabaeus* species, assigned *M. multidentatum* Klug to *Scarabaeus*, placing it alone in his newly-established subgenus *Neoctodon*.

Reitter (1894) added to the general confusion by raising *Neoctodon* Bedel to generic status, together with '*Mnematidium*', while actually having in mind *Mnematium* M'Leay. This error was pointed out by Shipp (1895a), who then accorded subgeneric status to *Mnematidium* Ritsema, within the genus *Ateuchus*. In a revision of the genus

Ateuchus a few months later (Shipp 1895b), no mention is made of Mnematidium at all.

The next mention of this genus was by Gillet (1911), who listed Mnematidium as a genus in the Coleopterorum Catalogus. All subsequent authors have maintained the generic status of Mnematidium, although Arrow (1919) stated that he could find no adequate grounds for separating Mnematidium from Sebasteos Westwood, the latter now a synonym of Scarabaeus.

MORPHOLOGY. The morphological characters in which M. multidentatum differs most from Scarabaeus species are the following:

i) relatively long protibia with basal serrations almost as large as the dentations (Fig. 151);

ii) genae laterally expanded and angular, giving the appearance of an extra pair of clypeogenal teeth (Fig. 117).

It is from the second character that the synonymised generic names Octodon and Neoctodon are derived.

In all other respects, M. multidentatum has a general Scarabaeus facies.

BIOLOGY. Balthasar (1963) stated that M. multidentatum was to be found on sparsely-vegetated dunes in desert regions, and that its biology was apparently similar in all respects to that of the true ('echten') *Scarabaeus* species.

PHYLOGENY AND DISTRIBUTION. As long ago as 1919, Arrow expressed the opinion that there were no valid grounds for separating *Mnematidium* from *Sebasteos* (now a synonym of *Scarabaeus*). Although the genus was upheld by Janssens (1940), the protibial and genal conditions appear to be grade differences of conditions found in closely related species. The protibial dentations in all specimens examined were clearly distinguishable from the proximal serrations, as the dentations are not only significantly larger, but also have a dorsal carina which the serrations lack.

Secondly, the condition of the genae is very similar to that found in *Scarabaeus silenus* (Gray) and, especially, *S. cancer* (Arrow) (Fig. 83). The genae of a number of other species of *Scarabaeus* also show a marked plasticity of form, so that the expanded condition of the genae in *M. multidentatum* must be accorded low taxonomic weight.

The generic status of *Mnematidium* is further weakened by the typical *Scarabaeus*-like condition of the other morphological features of taxonomic value, especially the aedeagus, tarsi, tarsal claws and infra-clypeal denticulations. *Mnematidium* is consequently synonymised with *Scarabaeus* (*sensu lato*).

According to Balthasar (1963) Scarabaeus multidentatus occurs along the southern and south-eastern Mediterranean coastal regions, from Tunis in the west to Haifa in the east. The species also occurs on the Sinai peninsula and along the north-eastern coastal regions of the Red Sea.

4.2.1.2 NEATEUCHUS Gillet

Neateuchus Gillet, 1911(a): 309; 1911(b): 38; Janssens 1938: 8, 70; 1940: 56; Ferreira 1969: 64.
Ateuchus Guérin 1844: 73 (pars); Boheman 1860: 22 (pars).
Scarabaeus Péringuey 1888: 92 (pars); 1900: 30, 51 (pars); Felsche 1907: 276 (pars); Péringuey 1908: 554 (pars).

TYPE SPECIES: Ateuchus proboscideus Guérin

MATERIAL EXAMINED. (6 males, 2 females, 29 unsexed specimens, UP): BOTSWANA: 35 km S of Kang, Botswana, SE 23 22 Dd, 23.i.1978, Holm, Jacobs, Kirsten, Scholtz. NAMIBIA: 10 km NE Rosh Pinah, SE 27 16 Dc, 3.xii.1980, Univ. of Pretoria; 40 km ex Stampriet - Gochas, S.W.A., SE 24 18 Ba, 25.i.1981, Univ. of Pretoria; Vreemdelings=poort, SE 24 15 Dd, 22.i.1980, University of Pretoria; SO of Klinghardtsberge SE 27 15 Db, vii.1982., E. Holm. SOUTH AFRICA: Cape Province: Ca 20 km ENE Port Nolloth, SE 29 17 Aa, 30.xi.1980, University of Pretoria; Mata Mata, SE 25 20 Cc, 7.i.1980, University of Pretoria; Floradora Ranch, N. Cape Province, SE 27 22 Ba, 26.i.1981, Univer=sity of Pretoria; Frylinkspan, SE 27 22 Ba, 5.i.1980, University of Pretoria; 10 km Dwarskersbos, Cape Province, SE 32 18 Bb, 20.xii.1977, E. Holm; Twee Rivieren, SE 26 20 Bc, 6.i.1980, University of Pretoria.

TAXONOMIC HISTORY. *Neateuchus* was described by Gillet (1911), to accommodate three *Scarabaeus* species, *S. proboscideus* (Guérin), *S. rixosus* Péringuey, and *S. sevoistra* Alluaud, with the generic characters given as the closely set mesocoxae and the presence of a protuberance on the mentum.

Janssens (1938) removed *N. sevoistra* from *Neateuchus* and described the genus *Neomnematium* to accommodate this species arguing that the protuberance on the mentum of *N. sevoistra* was different in form and not monophyletic with those of the other species of *Neateuchus*. This classification has remained unchanged up to the present.

MORPHOLOGY. Apart from the protuberance on the mentum, species of *Neateuchus* have no autapomorphs to distinguish them from species of *Scarabaeus*. The first generic character mentioned by Gillet, namely the closely set mesocoxae, is found in many other *Scarabaeus* species, especially *S. cristatus* Fab. which, apart from lacking the protuberance on the mentum, is virtually identical to *N. proboscideus*.

BIOLOGY. No published reference to the biology of *N. proboscideus* could be found. However, the distribution records show it to be xero- and psammophilous, while the rufous body hair and large eyes suggest that it has a crepuscular activity pattern similar to that recorded by Tribe (1976) for the almost identical *Scarabaeus zambesianus* Péringuey.

PHYLOGENY AND DISTRIBUTION. In describing the genus *Neateuchus*, Gillet relied solely on the presence of the protuberance on the mentum for the definition of the taxon. The second character which he used, namely the closeness of the mesocoxae to each other is, by his own admission, very similar to the condition found in the genera *Mnematium* M'Leay and *Mnematidium* Ritsema, which were synonymised earlier in this work with *Scarabaeus* L. The condition of the protuberance on the mentum is, however, variable both intra- and interspecifically, which largely nullifies the taxonomic significance of this character.

In *Neateuchus proboscideus* the protuberance is bifid, and varies in length (and shape) from 1,8mm to 2,6mm in two specimens of equal size (30mm), while in *Neateuchus rixosus* (Péringuey), the protuberance is described as being simple and much shorter in all cases than *N. proboscideus*.(Neither the type specimen nor any other specimens of this southern African species could be traced. As no further specimens have apparently been collected since it was described by Péringuey in 1900, it would appear that the species was probably based on small specimens of *N. proboscideus* which does occur within the designated distribution of "Southern Rhodesia, Middle Limpopo".)

In Scarabaeus sevoistra (originally included in the genus Neateuchus) the protuberance is also short, simple and different in shape from that of N. proboscideus. When N. proboscideus is compared to Scarabaeus zambesianus Péringuey and S. cristatus F., the close relationship between these species becomes apparent. Janssens (1940) declared that apart from the protuberance in Neateuchus specimens, they were identical in all respects to S. cristatus, while in the slightly squatter S. zambesianus the incipient condition of the protuberance on the mentum is obvious (Fig. 124). Other similarities between S. sevoistra, S. zambesianus, S. cristatus and N. proboscideus are as follows:

i) overall size;
ii) shape and width of head;
iii) fulvous hair;
iv) smooth punctulate pronotum;
v) length and shape of tarsal segments;
vi) length and shape of tibia and tibial spurs, and protibial dentation;
vii) reduction of serrations between protibial dentations;
viii) greater or lesser development of protuberances on frons and mentum;
ix) similarly shaped antennal lamellae.

From the above it is deduced that the shape of the mentum in these Scarabaeus species is variable, and that even allowing for the monophyletic origin of the protuberance on the mentum in three species, the general apomorphic states of these species do not represent a taxon distinct from the genus Scarabaeus. Consequently the genus Neateuchus is synonymised with Scarabaeus.

4.2.1.3 MADATEUCHUS Paulian

Madateuchus Paulian, 1953; 1960; Halffter & Matthews 1966.

TYPE SPECIES: Madateuchus viettei Paulian

MATERIAL EXAMINED. MADAGASCAR: 1 ♀ Fôret de 1' Ankarafantsika xi, 1951 (P. Viette), Holotype; xiii, 1956 (P. Griveaud), 2 specimens (1 ♀, 1 ♂).

TAXONOMIC HISTORY. The genus and species were described by Paulian in 1953, and featured again by him in Fauna de Madagascar Vol. XI in 1960. The only other reference to this monotypic genus was in a list of Scarabaeina genera in Halffter & Matthews (1966).

MORPHOLOGY. The distinguishing characters used in both the genus and species descriptions are the presence of protuberances on the frons and mentum, and of a reduced proximal dentation on the protibia, giving the impression of only three dentations instead of the four normally found in Scarabaeus species.

The morphology of Madateuchus viettei Paulian, including the taxonomically important aedeagus, is very similar in all other respects to that of the species of *Scarabaeus*.

BIOLOGY. Nothing has been published about the biology of this species, but the large eyes and rufous pubescence suggest that it is a crepuscular species. It is also unusual in apparently occurring in a forested area, as scarabaeines are normally found in savanna and desert biomes.

PHYLOGENY AND DISTRIBUTION. The genus and species des= criptions of *M. viettei* were based on a single female specimen. The lack of a male specimen for purposes of the original description was a major short-coming, as the aedeagus is a character of great importance in scarabaeine taxonomy. The aedeagal form has proved to be typical of that found in *Scarabaeus* species (Figs. 121, 122).

In the reduction of the proximal protibial dentations and convex median borders of the inner clypeal teeth, *Madateuchus viettei* resembles some of the *Kheper* species. However, *M. viettei* differs from the latter in the possession of two tarsal claws instead of one, and the presence of serrations between the protibial dentations. The presence of a reduced protibial tooth is also not unique within *Scarabaeus*. While *Scarabaeus* species usual= ly have four large, relatively even-sized protibial denta= tions, the size of the proximal dentation shows great variation. In at least one examined species, *S. caffer* (Boheman), it is as reduced as that of *M. viettei*.

The other slightly unusual features of *M. viettei* such as protuberances on the frons and/or mentum are also shared by *Scarabaeus* species such as *S. cristatus* F. and *S. zambesianus* Péringuey. The phylogenetic significance of the protuberance on the frons is further weakened by the fact that it is a sex-related character, being uncharacteristically absent in the males as it is normally the female scarabaeines which have the simpler cephalic condition.

The seemingly pointed abdomen of *M. viettei* figured in both publications dealing with this species (Paulian 1953; 1960), is due to the pygidium of the type specimen having been bent back and therefore being visible from above. The elytra have, in fact, the typical *Scarabaeus* shape.

Lastly, in describing the new genus, Paulian does not contrast it with *Scarabaeus*; nor does he mention what he considers to be the most important features for the establishment of the new genus, except by implication in his key to the Madagascan Scarabaeini. These characters are those discussed above, so that the maintainance of the genus *Madateuchus* seems untenable and it is consequently synonymised with *Scarabaeus*.

4.3 REVIEW OF THE GENERA OF SCARABAEINA

4.3.1 SCELIAGES Westwood

Sceliages Westwood, 1837: 12; 1838: 159; Lacordaire 1856: 66; Lansberge 1874; Shipp 1895: 37; Péringuey 1900: 22, 62;

Gillet 1911: 15; Paulian 1934: 58; Ferreira 1961: 63; zur Strassen 1965: 219, 220; Ferreira 1969: 75, 76;
Parascarabaeus Balthasar, 1961: 174.

TYPE SPECIES: *Sceliages iopas* Westwood

TAXONOMIC HISTORY. Although the genus *Sceliages* Westwood was described in 1937, literature on this genus is limited, due probably to the restricted distribution of the species of *Sceliages*. Misidentification of *Sceliages* species usually resulted in their being placed in the genus *Ateuchus* Weber or *Scarabaeus* L., with the relatively recent *Parascarabaeus* Balthasar (1961) being the only full generic synomyn of *Sceliages* to date. The description of *Parascarabaeus* as a separate genus is probably due to a single mislabelled specimen of *Sceliages augias* Gillet, which gave its location as Tonkin (a region of Pakistan). All other specimens of *Sceliages* spp. have been collected only in the southern half of Africa. The frequent assignment of *Sceliages* specimens to *Scarabaeus* may also have contributed to the paucity of literature concerning *Sceliages*.

The paper by zur Strassen (1965) is the only detailed study of *Sceliages* since Shipp (1895), although Gillet (1911) and Ferreira (1960) listed all the known species and synonyms. Unfortunately zur Strassen (1965) does not figure any of the aedeagi of the *Sceliages* species - usually a very helpful taxonomic character - nor does he feature any consistent distinguishing character for all the species of

Sceliages, thus making analysis and identification of species very difficult.

MORPHOLOGY. Sceliages is the genus within the Scarabaeina which appears to have undergone the least morphological evolution, i.e. all the character-states found in the remaining genera can be derived from a Sceliages-like ancestor, with the exception of the more or less complex symmetrical aedeagus found in some species of various genera. The Sceliages species have a simple, asymmetrical aedeagus virtually identical to that of many Scarabaeus species. For reasons which will be discussed later, the similarity between Sceliages and Scarabaeus aedeagi appears to be due to convergence rather than synapomorphy. Morphological features used in the literature for identifying Sceliages species are the following:

i) two well-developed mesotibial spurs; the inner spur smaller than the outer, but still much larger than the same spur found in Scarabaeus species of the subgenus Scarabaeolus Balthasar;

ii) the shape of the antennal club; the apical segment is contained in the cup-shaped second segment while both these terminal segments are in turn contained in the larger cup-shaped third segment;

iii) the distally flared basal segments of the tarsi, giving them a triangular shape when viewed from above or below;

iv) the relatively wide separation of the mesocoxae - by more or less half the length of a mesocoxa. This distance is approximately twice as large as that found in the other genera within _Scarabaeina_;

v) elytra, pronotum and head smooth and unsculptured;

vi) pronotum very convex, head deflexed.

BIOLOGY. In spite of the genus having been described nearly 150 years ago, no published reference to the biology of any species of _Sceliages_ could be found. From personal observa=tion and communication with other coleopterists, it is well established that most or all _Sceliages_ species are, in fact, "telecoprid" necrophages, meaning that they are carrion-feeders which exhibit the typical telecoprid behaviour of rolling the food or brood material away from the food-source. To do this the portion of millipede is manipulated with the middle and hind legs, while the beetle rolls it backwards in the characteristic head-down "pushing" position adopted by most scarabaeine dung-beetles. While this behaviour has often been observed by both amateur and professional entomologists, no-one has reported what the fate of the detached portion of millipede is.

Dr Prozesky-Schulze (pers. comm.) has suggested that _Sceliages_ species may use the gut-content of the millipede, as she has observed millipedes feeding on dung. At the same locality she also observed _Sceliages_ specimens rolling kudu dung-pellets. It would thus appear that at least some species of Sceliages are facultative necrophages, utilizing dung in the absence of millipede remains. The fact that crushed millipedes serve as good bait for attracting Sceliages specimens suggests that there is a marked degree of specificity for this food or brood source. Fabre (1911) observed that Scarabaeus species often differentiate between the type of dung used for food and that used for breeding purposes. This may be the case with Sceliages species, dung being used for food while millipede remains are reserved for use as brood material. It seems unlikely that only the gut-content of these millipede portions would suffice as brood material, as suggested by Dr Prozesky-Schulze.

Various references to scarabaeines making use of myriapod remains are found in the literature. Luederwaldt (1911) mentioned Deltochilum significum L. rolling a dead and dry diplopod, while Péringuey (1901) quoted a Mr Marshall as stating that Onthophagus praestans Péringuey was only found under dead millipedes. Scarabaeus rubripennis (Boheman) exhibits wider necrophagy (Holm pers. comm.), not confined to arthropods, as do several Onthophagus Latrielle species, while some Onthophagus species are also attracted to vegetable matter (Halffter & Matthews 1966).

The above-mentioned examples serve to illustrate that although members of scarabaeine taxa are usually stenophagous the euryphagy displayed by members of Sceliages is within the broad scarabaeine pattern.

PHYLOGENY AND DISTRIBUTION. As mentioned previously the species of *Sceliages* in many ways represent "prototypes" of the other genera of Scarabaeina, especially *Scarabaeus*. While *Sceliages* was described and maintained as a genus largely because of the possession of a large second meso=tibial spur (cladistically a plesiomorph and therefore in=valid as a taxonomic character), the synapomorphic condi=tion of the antennal club, the inner clypeal teeth, and the aedeagus of species of *Sceliages* suggest that the genus is valid.

The validity of *Sceliages* as a genus is strengthened by the aberrant biology of these beetles. While necrophagy occurs sporadically in Scarabaeini, and even in *Scarabaeus*, it would appear that *Sceliages* represents a morpologically and behaviourally monophyletic group which justifies gene=ric status within Scarabaeina.

The genus has a southern African distribution (zur Strassen 1965), being recorded from the Cape Province in the south to Zaïre in the north. Balthasar (1961) described the synonymous genus *Parascarabaeus* from Asia but, as explained earlier, that was probably due to a mislabelled specimen.

4.3.2 SCARABAEUS Linnaeus

Scarabaeus Linnaeus, 1758: 345; Lansberge 1874: 182; Bedel 1892: 281; Reitter 1893(a): 161; 1893(b): 37, 40; Péringuey 1900: 23; Gillet 1911: 7; Arrow 1931: 38; Balthasar 1935: 28; Ferreira 1953: 4; 1945: 380;

Balthasar 1963: 144; Janssens 1940: 14; 1941: 1; Paulian 1941: 50; zur Strassen 1967: 130; Ferreira 1969: 30.

TYPE SPECIES: *Scarabaeus sacer* L.

Actinophorus Creutzer, 1799: 79.

Ateuchus Weber, 1801: 10; Lacordaire 1856: 66; Shipp 1894: 254, 289, 309; 1895: 39, 40, 218.

Heliocantharus M'Leay, 1821: 497; 1833: 49.

Mnematium M'Leay, 1821: 506; 1833: 54; Lansberge 1874: 182, 184; Balthasar 1935: 23, 27; Janssens 1938: 8, 71; 1940: 6; Ferreira 1953: 5; 1961: 26; Balthasar 1963: 137, 138, 139; Ferreira 1969: 26, 27, 28; Holm & Scholtz 1979: 226.

TYPE SPECIES: *Mnematium ritchiei* M'Leay

Pachysoma M'Leay, 1821: 507; 1833: 55; Reiche 1841: 212; 1842: 65, 87, Tab. 6, Fig. 7; Lacordaire 1850: 66, 68; Janssens 1938: 8, 71; Ferreira 1953: 3, 6, *pl*. 3; 1961: 21; 1966: 57; 1969: 17-20; Holm & Scholtz 1979: 226,227. *syn*. *nov*.

TYPE SPECIES: *Pachysoma hippocrates* M'Leay

Sebasteos Westwood, 1847: 226; Kolbe 1895: 333; Shipp 1895: 218. Péringuey 1900: 25,26.

TYPE SPECIES: *Sebasteos galenus* Westwood

Octodon Lansberge, 1984: 183. *syn*. *nov*.

TYPE SPECIES: *Ateuchus* *multidentatus* Klug

Mnematidium Ritsema, 1889: 207; Shipp 1895: 39, 40; Gillet 1911: 7; Arrow 1919: 433; Balthasar 1935: 28; Janssens 1938: 8, 69, 70; 1940: 13, 55; Balthasar 1963: 138, 143. *syn*. *nov*.

TYPE SPECIES: *Ateachus* *multidentatus* Klug

Parateuchus Shipp, 1895: 221.

TYPE SPECIES: *Scarabaeus* *palemo* Olivier

Irrorhotides Shipp, 1896: 116, 117. *syn*. *nov*.

TYPE SPECIES: *Pachysoma* *striatum* Castelnau

Neateuchus Gillet, 1911(a): 309; 1911(b): 7; Janssens 1938: 8, 70; 1940: 14, 56; Ferreira 1952: 259; 1953: 4; 1961: 49; 1969: 64,66.

TYPE SPECIES: *Ateuchus* *proboscideus* Guérin

Neomnematium Janssens, 1938: 7, 71; Paulian 1953: 26, 27; 1960: 13; Ferreira 1961: 26.

TYPE SPECIES: *Scarabaeus* *sevoistra* Alluaud

Madateuchus Paulian, 1953: 24-27; 1960: 11. *syn*. *nov*.

TYPE SPECIES: *Madateuchus* *viettei* Paulian

Neopachysoma Ferreira, 1953: 4, 37; 1961: 25; 1966: 60; 1969: 24; Holm & Scholtz 1979: 226. *syn*. *nov*.

TYPE SPECIES: *Pachysoma denticolle* Péringuey

MATERIAL EXAMINED. *S. alienus* (Péringuey) (1); *S. ambiguus* (Boheman) (1); *S. bohemani* (Harold) (10); *S. caffer* (Boheman) (4); *S. canaliculatus* Fairmaire (1); *S. catenatus* (Gerstaecker) (1); *S. clanceyi* Ferreira (1); *S. convexus* (Hausman) (2); *S. cristatus* F. (1); *S. damarensis* Janssens (3); *S. flavicornis* (Boheman) (20); *S. galenus* (Westwood) (5); *S. gangeticus* (Castelnau) (1); *S. goryi* Castelnau (24); *S. interstitialis* (Boheman) (1); *S. intricatus* (F.) (2); *S. laticollis* L. (1); *S. parvulus* (Boheman) (57); *S. radama* (Fairmaire) (4); *S. rubripennis* (Boheman) (69); *S. rugosus* (Hausman) (2); *S. rusticus* (Boheman) (70); *S. satyrus* (Boheman) (28); *S. zambesianus* Péringuey (11).

TAXONOMIC HISTORY. The name *Scarabaeus* enjoys pre-eminence in coleopteran nomemclature as it is, in fact, the Latin word for beetle, probably derived in turn from the Greek word *Karabos* of the same meaning. The formal use of *Scarabaeus* as a genus name dates from Linnaeus' *Systema Naturae* (Ed. X) of 1758, with *Scarabaeus sacer* recorded as the type species. Many of the genera established by Linnaeus were later found to be closer to the modern family taxon, which led to many new genera being created for the various taxonomic groups within the original genus. Shipp (1894) argued that the name *Ateuchus* Weber be used instead of *Scarabaeus*, which was applied by Linnaeus to represent the whole family of lamellicorns, i.e. Scarabaei=

dae. However, as Linnaeus had designated a type species, Shipp's reasoning was not valid. In his original description of Ateuchus, Weber did not designate a type species, which contributed to the subsequent confusion regarding the validity of Ateuchus. Ateuchus Weber was synonymised with Scarabeus by Péringuey (1900), but he does not furnish any reason for the synonymy. The genus Ateuchus, referring to American species, appears in the modern literature; Halffter & Matthews (1966) listed it as part of the tribe Coprini. The many others synonyms of Scarabaeus are a reflection of inadequate research, poor communications, lack of a uniform system such as the International Code of Zoological Nomenclature, and the variation found within this successful and widely-distributed genus.

MORPHOLOGY. As Scarabaeus dominates the subtribe in number of species, distribution and variety of morphological form, Scarabaeus species often appear almost identical to members of other Scarabaeina genera. Furthermore, there is no single character by which Scarabaeus can be unequivocally separated from other genera of Scarabaeina. The characters most consistently mentioned in the literature in regard to Scarabaeus are the following:

i) body winged;

ii) head six-dentate (often referred to as clypeus being six-dentate, although in fact the clypeus bears four teeth, while the anterior angles of the genae account for the remaining pair of teeth);

iii) anterior femora of normal size;

iv) protibia bearing four more or less even-sized dentations, with serrations between, and proximal to, dentations;

v) mentum simple and evenly rounded;

vi) aedeagus asymmetrical;

vii) mesocoxae closely set;

viii) mesotibia bearing only one spur, or having the second spur no larger than one-fifth the size of the first;

ix) tarsi more or less filiform, with two even-sized articulating claws.

All other characters mentioned in the literature show a greater or lesser deviation within _Scarabaeus_, as many of these characters are in all probability not of mono=phyletic origin but rather reflections of adaptations to local conditions, or represent extremes of morphological characters which exhibit a more or less continuous gradient of plasticity within the genus. For these reasons certain of the above-listed characters such as points i, ii, v, and vi are also invalidated in the present revision.

Although there appears to be no single morphological character by which _Scarabaeus_ can be unequivocally sepa=rated from other Scarabaeina genera, the shape of the tarsi and claws (point ix) is the character which most nearly approaches such a criterion, while points viii and ix together do provide an unambiguous means of identification.

BIOLOGY. The first observations of *Scarabaeus* biology date back some 5000 years to the time of the Pharoahs when *Scarabaeus sacer* L. and other *Scarabaeus* and *Kheper* species were revered as objects of religious significance.

The foundation of modern dung-beetle ethology and biology was laid by Jean Henri Fabre with the publication of his *Souvenirs Entomologiques*, especially volumes V and VI (1897, 1899). In these studies, *Scarabaeus* and *Copris* species were Fabre's favourite insects. Further studies of *Scarabaeus* biology were conducted by Goggio (1926) and Heymons and van Lengerken (1929, 1953). Although the above-mentioned studies were of a very high standard, the number of species studied was small, so that at present no idea of the uniformity or heterogeneity of *Scarabaeus* biology can be arrived at, except from brief personal ob=servation or communication with fellow coleopterists, and from more generalized studies of dung-beetles such as those by Halffter and Matthews (1966) and Tribe (1976).

The salient points to emerge from the above sources are the following:

i) *Scarabaeus* species are highly specialised tele=coprid (ball-rolling) coprophages, which in a few instances exhibit opportunistic necrophagy.

ii) The genus is predominantly diurnal, but a few species are specialised for crepuscular ac= tivity.

iii) Great variety is shown in the type and consis= tency of dung used. Moist large-herbivore dung is used very widely, but the pellet dung of sheep and antelope is preferentially used by some species (Goodman 1928), while human excre= ment also attracts many species.

iv) A great many Scarabaeus species exhibit marked xerophily and thermophily, with accompanying behavioural and morphological changes under extreme conditions (see reference to aptery and method of pellet rolling in some desert species).

v) The large number of species, great phenotypic range, and the wide distribution of the genus, suggests a long historial existence and remarkable success within the coprophagous niche.

LIFE-CYCLE. The Scarabaeinae in general, and the Scarabaeini in particular, are characterised by a highly specialised method of nidification. The broad outlines of the Scarabaeus life-cycle are as follows:
Emergence of the new adult from the underground brood-ball occurs after the first rains of spring. According to Fabre (1911), moisture is of cardinal importance in the softening of the extremely hard shell of the brood-ball.

If sufficient rain is lacking the beetles are unable to emerge and consequently die of starvation inside the ball. Emergence is followed by a period of maturation-feeding ('Reifungsfrass').

Sexual activity begins after the Reifungsfrass. Nuptial activity usually commences once a male is in possession of some dung (Tribe, 1976). When the two sexes meet, the female adopts a submissive attitude, whereas if two males meet they will challenge each other and combat often ensues. After the initial challenge, the male and female briefly touch antennae before the female is accepted by the male, prior to construction and rolling of the "nuptial ball". The nuptial ball is constructed almost entirely by the male, the female either following a few centimetres behind the male, or clinging to the ball. The ball may be rolled from 36cm to many metres, the shorter distance being exceptional.

The dung-ball is referred to as a nuptial ball because it is apparently used solely to attract the female (if the ball is removed from the male, the female abandons him), and is consumed by the breeding pair prior to, and after copulation. The female then constructs, rolls and buries another dung-ball from which some six to ten brood-pears, each containing a single egg, are fashioned. The female remains underground with these brood-pears for the duration of the larval development period. The pear-shape of the brood-balls is due to the egg chamber being formed on the surface of the completed sphere. The egg-chamber is formed by the female making a depression on the surface of the ball and then drawing up the area around the depression into walls, mixed with soil, so as to enclose the egg in a small "igloo". By feeding on the surface of the brood-balls and coating them with her own faecal material, the female inhibits fungal invasion (Halffter & Matthews 1966, Tribe 1976). The larvae store their faecal material in a hump formed by the enlarged colon, and this material is excreted just before the pre-pupal stage. Faeces are also used by the larvae to coat the inside of the pupal cell or to carry out emergency repairs in the event of the brood-ball being damaged, while a similar layer is added by the female on the outside. As these layers dry they form a protective and anti-fungal layer around the pupa. Emergence is usually followed by a short period of feeding, after which the female and F1 offspring burrow into the soil where they overwinter. Scarabaeus species are usually univoltine, but some of the smaller species may be bi-voltine.

This method of nidification is so successful that only one ovariole of a single ovary is functional in these species, with no more than 12 ova being produced per season in many cases (Halffter & Matthews 1966).

PHYLOGENY AND DISTRIBUTION. Cladistic analysis of the genera of Scarabaeina suggests that Scarabaeus is the second most plesiomorphic genus after Sceliages (Table 1), but whereas the latter is restricted in number of species and in distribution, Scarabaeus dominates the subtribe in both these respects, accounting for more than 70% of all species and having a distribution range at least three times larger than the other Scarabaeina genera, with the exception of Kheper Janssens, which occurs in most of the moister regions of the Scarabaeus distribution.

Because of the relatively large number of superficially different species of Scarabaeus, a number of subgenera have been proposed at various times (Bedel 1892; Péringuey 1900; Balthasar 1965). The modern literature contains no dis=cussion of the validity of the earlier subgenera. Janssens (1940) merely mentioned the subgenera (Scarabaeus s. str., Ateuchetus Bedel and Parateuchus Shipp) in passing. Balthasar (1965) described the subgenus Scarabaeolus, and lowered the genus Kheper Janssens to subgeneric status. Zur Strassen (1967) reinstated Kheper as a genus, and as he was unable to locate the vestigial second mesotibial spur which Balthasar had used as the main subgeneric character for describing Scarabaeolus, he did not attempt a further subgeneric classification of Scarabaeus.

Ferreira (1969) recognized only two subgenera, namely Scarabaeolus Balthasar and Scarabaeus s. str. Because of the extremely vestigial condition of the second mesotibial spur, the validity of Scarabaeolus appeared somewhat dubious, as it seemed likely that such a small, non-functional structure could disappear completely within a particular species, resulting in that species being placed, incorrectly, in another subgenus. Conversely, the presence of a vestigial second mesotibial spur is a plesiomorphic condition (compared to species in which it has been lost), and its presence in two or more species may be due as much to convergence as to monophyly (indeed, this condition of the second mesotibial spur is also found in some members of the subtribe Gymnopleurina). Investigation has revealed that the species of Scarabaeolus may well constitute a monophyletic group, as they share a number of character states, apart from the presence of a vestigial second meso=tibial spur.

These character states include the distance between the lateral elytral carinae, the position of the tarsus on the metatibia, size of the tarsal claws, and overall size. The group also has a relatively limited distribution, the majority of species occurring south of 10°C. latitude and west of 25°E. longitude. The relatively few species occurring outside the region probably spread along the Somalia south west African route (Endrody-Younga 1978).

A number of species that share the condition of the elytral carinae, tarsal position on the metatibia, over=all size and distribution, do not possess the vestigial mesotibial spur. As suggested earlier, the loss of such a small, non-functional structure is almost inevitable. These species are consequently included in Scarabaeolus, necessitating a redefinition of this subgenus as follows:

i) Lateral edge of elytra rounded, with elytral carinae widely separated (Fig. 115) and not, or only slightly, projecting past the sides of the abdomen. Carinae running parallel along the full length of the elytra. (These characters do not apply to the flightless species, *S. silenus* and *S. scholtzi*, as brachyptery has led to a changed elytral shape);

ii) most species possess a vestigial second mesotibial spur (Fig. 114);

iii) end of metatibia blunt, with tarsus inserted very close to base of tibial spur, and having the tarsal claws about as long as the distal tarsal hairs. The latter condition is shared by some non-Scarabaeolus species, but these are easily recognized by the sharp, overhanging elytral edge and the lack of a vestigial second mesotibial spur.

The subgeneric status of the non-Scarabaeolus species is still unclear, as I was unable to find reliable apomorphs that could constitute subgeneric characters. This appears to have been the case in the most recent revisions of *Scarabaeus* (zur Strassen 1967, Ferreira 1969), as zur Strassen expressed doubt about the validity of *Scarabaeolus* - being unable to locate the vestigial mesotibial spur - and did not attempt a subgeneric classi=fication himself, while Ferreira placed all the non-*Scarabaeolus* species in *Scarabaeus* *s*. *str*.

In spite of the difficulty in establishing subgenera, the majority of non-Scarabaeolus species fall easily into one of two groups; the first group being those species with relatively blunt metatibia with the tarsus inserted very close to the base of the tibial spur (i.e. the sub=genus *Ateuchetus* Bedel, excluding the *Scarabaeolus* species), while the second group includes those species in which the metatibia is distally extended and flattened, with the tarsus inserted about one to two tarsal widths from the base of the tibial spur.

The shape of the tibial extremeties is, however, subject to functional adaptation (e.g. in sand-dwelling species), and the distance between the tarsal insertion and the base of the tibial spur shows a continuous inter-specific varia=tion, making the delimitation of sub-genera on these grounds alone unjustified.

Scarabaeus has by far the widest distribution of the genera of Scarabaeina, occurring throughout most of Africa, southern Europe, the Mediterranean region, the Middle East and Asia. Based on Tinley's (1975) classification of African biomes, members of *Scarabaeus* occur in all African terrestrial biomes, with the exception of forests, but the genus displays an overall arid distribution. The subgenus *Scarabaeolus* especially, has a relatively restricted desert to arid savanna distribution, while the remaining species show a wider, more varied distribution covering desert, arid savanna, moist savanna, Palaeartic temperate and Afrotemperate biomes.

4.3.3 DREPANOPODUS Janssens

Drepanopodus Janssens, 1940: 73; Ferreira 1952: 267, 268; 1953: 78; 1961: 50, 51; Halffter & Matthews 1966: 260; Ferreira 1969: 67.

TYPE SPECIES: *Ateuchus costatus* Wiedeman

MATERIAL EXAMINED. *D. costatus* (Wiedeman) (11); *D. proximus* (Péringuey) (23).

TAXONOMIC HISTORY. *Drepanopodus* was described, together with *Kheper*, by Janssens (1940) to accommodate former *Scarabaeus* species. The species of *Kheper* and *Drepanopodus* proved to have only one tarsal claw whereas all other *Scarabaeus* species possess two even-sized tarsal claws. The single-clawed species sort easily into their respective genera as each genus has very distinct apomorphs, which will be discussed in later sections. *Drepanopodus* has been upheld as a genus in all the important studies since 1940.

MORPHOLOGY. As mentioned previously, *Drepanopodus* species bear a close resemblance to those of *Scarabaeus*. In his original description of *Drepanopodus*, Janssens distinguished the single-clawed *Scarabaeus*-like species (*Kheper* and *Drepanopodus*) from the double-clawed true *Scarabaeus* species, while further splitting *Drepanopodus* from *Kheper* due to the high insertion of the tarsus into the mesotibia in the *Drepanopodus* species (Fig. 127).

Other ways in which *Drepanopodus* species differ from those of *Kheper* are the presence of a visible scutellum, a simple symmetrical aedeagus and in having serrations between the protibial dentations. The latter condition is shared by species of *Scarabaeus* and *Sceliages*, thus lack of these serrations serves as an easy way of distinguishing *Kheper* from the other Scarabaeina genera in the field.

BIOLOGY. Species of *Drepanopodus* occur in extremely arid regions. The food location and burial behaviour of *D. proximus* (Péringuey) was observed at Obib Dunes (SE 28 16) in south-western Namibia during November 1980. Approximately 300g of horse droppings were placed out at 09h00 on a sandy gravel plain with hardly any visible vegetation. November is one of the driest months of the year in this region. There was virtually no air movement at the time, and no specimens of Drepanopodus in evidence, yet within five minutes several specimens of D. proximus were circling the bait. Beetles could be seen approaching with a minimum of zig-zagging from distances of more than a hundred metres, and locating the dung in two or three minutes once they were within some ten metres of the dung source.

The activity of the beetles was nothing short of frantic. A beetle would take command of a dropping and defend it vigorously, even against interfering human fingers. Within seconds a piece of dung would be cut out of the dropping, using the sharp clypeal teeth, and rolled back=wards in the usual telecoprid head-down attitude. The distance from the dung source at which the dung was buried varied from about half a metre to some ten metres.

Prior to excavation of a burrow, the dung ball was positioned directly behind the beetle, so that the sand from the burrow was pushed over the ball as soon as excava=tion commenced. Excavation was effected by scraping sand under the body with the protibia, then turning around and "butting" the little heap further away from the burrow. Once a depth of a few centimetres was reached, the dung ball was retrieved from the mound of loose sand and fur=ther excavation continued by digging away the soil beneath the ball.

Circumstances did not permit further observation, nor the establishment of the depth of the burrows.

Drepanopodus proximus occurs sympatrically with a brachypterous *Scarabaeus* species, *S. gariepinus*. Both species utilised the horse droppings very readily, although the droppings of the gemsbuck, *Oryx gazella* are probably the most common source of dung for both species. The burrows of *S. gariepinus* were found to be approximately 30 to 40 cm deep.

D. proximus and *S. gariepinus* appear to represent two extremes of adaptation to desert conditions, the former being an extremely good flier while the latter is flightless.

PHYLOGENY AND DISTRIBUTION. While *Drepanopodus* appears to be phylogenetically close to *Scarabaeus*, the apomorphic condition of the tarsal claws and the very high mesotarsal insertion in the species of *Drepanopodus* represent a distinct break with the morphological spectrum of the species of *Scarabaeus*. The generic status of *Drepanopodus* is consequently maintained.

The symmetrical aedeagus and general facies of the species of *Drepanopodus* is similar to that of *Scarabaeus rubripennis* (Boheman) which is also a desert-dwelling species, occurring some 200 kilometres further north than *D. proximus*. The general morphological condition of *S. rubripennis* is plesiomorphic within the genus, suggesting that

Drepanopodus probably split off early in Scarabaeus his=tory, but diverged only slightly from the early Scarabaeus facies.

The two Drepanopodus species are psammophilous and xero=philous, with D. costatus (Wiedeman) occurring in the northern Cape Province and Orange Free State and D. proximus occurring further west in Namaqualand and Southern Namibia, with a small area of overlap in the vicinity of the Augrabies Falls.

4.3.4 PACHYLOMERUS Bertoloni

Pachylomerus Bertoloni, 1949; Shipp 1896.
Scarabaeus Kirby 1828; Scarabaeus (Pachylomera) Péringuey 1900.
Pachylomera Lansberge 1874a; 1874b; Gillet 1911; Janssens 1938; 1940; Ferreira 1952; 1953; 1961; Halffter & Matthews 1966; Ferreira 1969.

TYPE SPECIES: Scarabaeus femoralis Kirby

MATERIAL EXAMINED. P. femoralis (Kirby) (23); P. opacus Lansberge (11).

TAXONOMIC HISTORY. Kirby (1928), incorrectly quoted as the author of the genus by all authors of this century, described femoralis merely as a distinct species ('type') of Scarabaeus. Bertoloni (1849) established the genus Pachylomerus, which Lansberge (1874a) emended or misspelt as Pachylomera femorata Kirby when he described P. opaca.

His failure to bracket the author name probably led later authors to believe that Kirby was the author of the genus as well as the species.

According to Article 32(a) of the Code, (correct original spelling) *Pachylomera* is a *lapsus calami*, not a synonym of *Pachylomerus*. The original spelling of the genus name is consequently reinstated.

Shipp (1896) appears to be the only author from 1849 to the present to use the original spelling of the genus name, also emending *Pachylomera opaca* to the correct form of *Pachylomerus opacus*.

Péringuey (1900) gave *Pachylomerus* subgeneric status within *Scarabeus*, but Janssens (1938, 1940) and Ferreira (1952, 1953, 1969) reinstated it as a genus.

MORPHOLOGY. The following morphological features are characteristic of this genus:

i) greatly enlarged profemora, especially males;
ii) two small recessed tarsal claws (Fig. 161);
iii) a relatively complex, symmetrical aedeagus (Figs. 141, 142);
iv) broad, flat, sculptured pronotum (Fig. 107);
v) elytra only slightly convex.

BIOLOGY. The biology of *Pachylomerus femoralis* was investigated by Tribe (1976). The gist of his findings is as follows:

The species is diurnal and is active throughout the day. Although Halffter & Matthews (1966) postulated that these beetles would be unable, because of their enlarged profemora, to roll dung-balls in the normal telecoprid way, this is not the case. They do, however, exhibit a limited type of telecopry in that only the brood-balls are apparently rolled away, while feeding occurs at the dung-pad. Within Scarabaeina, it is more usual for both brood- and food-balls to be rolled away.

When a dung-pad is located, a sloping burrow about 120cm long and 20cm deep is constructed by a single beetle of either sex within 30cm of the dung-pad. On completion the burrow is provisioned with a number of brood-balls made in the usual telecoprid way by using the clypeus and forelegs to remove and hold the ball. The ball is butted with the head or rolled backwards to the entrance of the burrow and then pushed inside with the head. _P_. _femoralis_ vigorously defends a large portion of the dung-pad and the area between the burrow and the dung-pad. The powerful profemora and tibia are equipped with sharp spines on the inner surfaces, and any intruding scarab is grabbed and held in these forelegs, with the spines pressed against it with great force. Upon release the victim immediately flees.

Once the burrow has been provisioned the beetle adopts a head-stand stance and releases an attractive pheromone from pores in the abdominal sternites. The pheromone is dispersed by brushing off the powdery carrier with the hindlegs. Although the hindlegs of Pachylomerus species are hirsute, there are no special brushes for dissemina=ting the pheromone as there are in all species of Kheper and some of those of Scarabaeus.

It appears that both sexes of Pachylomerus species possess pheromone glands, while these glands are restricted to the males in species of Scarabaeus and Kheper. As the burrows are constructed close to a dung-pad, the dung probably serves as the primary attractant. A beetle arriving at the dung-pad after the burrows have been provisioned will then be attracted by the pheromone to the burrow of a beetle of the opposite sex. The breeding and development of immature stages of the life-cycle of these beetles has not been documented.

PHYLOGENY AND DISTRIBUTION. While the enlarged profemora are the most conspicuous morphological character of the species of Pachylomerus, there is marked sexual dimorphism in the size of the profemora, the males usually having much larger profemora than the females. The phylogenetic significance of this character is consequently lessened, but the sexual dimorphism is in itself an apomorph, and the species of Pachylomerus possess a number of other phylo=genetically sound apomorphs, such as a highly evolved aedea=gus, recessed tarsal claws and a broad, sculptured pronotum, which justify the generic status of Pachylomerus.

Pachylomerus shares a number of apomorphs with *Kheper* (Table 1). These two genera appear to be reasonably close phylogenetically, and morphologically much more highly envolved than *Sceliages*, *Scarabaeus* and *Drepanopodus*.

Tribe (1976) stated that the distribution of *P. femoralis* coincided with the Kalahari sandveld, but examination of the collections of UP, DRU, NCI and TM, showed the species to be distributed throughout the sandy savanna areas of southern Africa and as far north as the equator. The distribution of *P. opacus* (Lansberge) was thought to be confined to the arid north-western Cape Province and southern Botswana, but large numbers of this species have recently been collected on the Nylsvley Nature Reserve in the Northern Transvaal region. Rainfall, season, sporadic collection and local fluctuations in the numbers of a particular species, are just a few of the factors contributing to the incomplete distribution records which are available for most species of Scarabaeina. It seems likely that *P. opacus* also has a wider distribution than even this new locality reveals.

4.3.5 KHEPER Janssens

Kheper Janssens, 1940: 14, 59; Ferreira 1952: 5; 1953(b): 3; 1961: 52, 233; Ferreira 1969: 56.

Scarabaeus (*Kheper*) Balthasar 1963: 145; Halffter & Matthews 1966: 260.

TYPE SPECIES: *Ateuchus aegyptiorum* Latrielle

MATERIAL EXAMINED. *K. cupreus* (Castelnau) (11); *K. intermedius* (Gillet) (1); *K. lamarcki* (M'Leay) (33); *K. nigroaeneus* (Boheman) (41); *K. prodigiosus* (Erichson) (11); *K. subaeneus* (Gillet) (26).

MORPHOLOGY. While there is a great resemblance between *Scarabaeus* and *Kheper* species, the latter may be easily distinguished by the following features:

- i) no serrations between, or proximal to, protibial dentations;
- ii) reduced proximal protibial tooth;
- iii) single, fixed tarsal claw, similar to *Drepanopodus*;
- iv) spurs of meso- and metatibia inflected;
- v) aedeagus distally expanded; symmetrical or asymmetrical;
- vi) many species have a purplish/green metallic appearance.

TAXONOMIC HISTORY. Kheper was described by Janssens (1940) in his monograph of Scarabaeus and related genera, to accomodate all but two of the former Scarabeaus species bearing only one tarsal claw. The two remaining single-clawed species were also placed in a newly erected genus, namely Drepanopodus. The Kheper species share a number of apomorphs which are lacking in the Drepanopodus species. This separation of Kheper from Drepanopodus and from Scarabaeus has remained valid. Balthasar (1963) relegated Kheper to subgeneric status and this was echoed by Halffter & Matthews (1966), but the latter work was merely a reflection of the latest publication dealing with this group, being essentially a biological study rather than a taxonomic one. Ferreira (1969) accorded full generic status to Kheper on the same grounds as Janssens had, and this status is maintained in the present study for reasons that will be discussed in the succeeding sections.

BIOLOGY. The biology of Kheper nigroaeneus as described in some detail by Tribe (1976) is given below. It appears to be typical of most Scarabaeus and Kheper species (Davis, pers. comm). As telecoprids, Kheper specimens detach pieces of wet herbivore dung from a larger mass and shape the detached pieces into spherical balls, which are then rolled some distance from the source before being consumed, or buried as brood-balls. Breeding activity is initiated only if a male Kheper is in possession of some dung.

All the males of southern African species of Kheper, and of certain Scarabaeus species, possess an attractant pheromone produced in glands lying behind the anterior abdominal sternites. The volatile pheromone is released from paraffin hydro-carbon tubules which are extruded like toothpaste from a tube through pores in the sternites. The pheromone is further dispersed into the air by the male who, after lowering his head and raising his abdomen, brushes off the carrier and pheromone in little puffs by means of special mesotibial brushes.

When the male perceives the female by her movement, he challenges her by raising his head and forelegs, and ad=vancing towards her. She responds by lowering her head and forelegs. A male, on the other hand, responds by raising his head and forelegs, which usually results in combat. After a brief touching of antennae, the male accepts the female and they set about preparing a brood-ball, the male cutting out the ball while the female com=pacts it with her protibiae. The female clings to the dung-ball while it is rolled away from the dung-pad. When the male finds a suitably soft and damp spot, he excavates a shallow depression into which he rolls the ball. The burying is completed by the male continuing to dig beneath the dung-ball, the ball slowly sinking lower and lower. The female pats the ball with her forelegs and tries to keep the ball free of loose sand. Once the ball is buried, copulation takes place below-ground.

After copulation, the female constructs an egg-chamber, a conical projection on the surface of the brood-ball, which she coats with a dark liquid of oral or anal origin. Halffter & Matthews (1966) consider this liquid to have antibiotic properties in the coprid species. The male emerges from the brood-chamber after about four days, while the female remains with the brood-ball, feeding at a reduced rate on the outside of the brood-ball, even when the ball is eventually covered with her own faecal matter.

Inside the ball, the larvae of *Kheper* and *Scarabaeus* spp. store their faecal material in the colon until the prepupal stage, when it is used to coat the inside of the pupal chamber.

The female remains brooding until the emergence of the new adult. Her constant feeding helps to keep the brood-ball free from mould, while the faecal matter also appears to have an inhibiting effect on fungal growth. The female removes the conical projection on the egg-chamber in the early stages of larval development, leaving a thin area in the wall of the brood-ball. The adult usually emerges through this part.

On emergence in January or February (midsummer), the F_1 beetles have no food in their gut and very little fat reserves. The remainder of the summer is spent in feeding. No laboratory specimens have been observed to attract a mate during this period. Between February and April, the

F_1 beetles burrow into the soil again to overwinter until spring, when they re-emerge in response to increasing temperature and rainfall. Spring emergence is followed by a further period of maturation feeding, the beetles not being sexually mature yet. During this period all beetles show aggression as they fight for possession of dung. After some three weeks, the maturation feeding ends, and the breeding phase begins.

PHYLOGENY AND DISTRIBUTION. While all species of *Kheper* closely resemble the winged *Scarabaeus* species, the former share a complex of apomorphs (Table 1) which suggests a monophyletic origin, and a great enough phylogenetic distance from *Scarabaeus* to justify a separate genus. Cladistically, *Kheper* appears to be the most apomorphic genus within Scarabaeina.

The genus has a wide distribution, the majority of species occurring in the Ethiopian zoogeographical region, but also extending into the Palaearctic and Oriental regions. Tribe (1976) analysed the distribution of the southern African scarabaeine species in some detail. He concluded that the major ecological factors in the distribution of the *Kheper* species were bushveld vegetation, sandy soil, an "effective temperature" above 15°C, and a summer rainfall with an annual minimum and maximum of 200 and 1000mm respectively. These conditions are normally met with in the 150-500 metre altitude range in southern Africa, but may extend to 2000 metres in the tropics.

4.4 KEY TO THE GENERA OF THE SUBTRIBE SCARABAEINA

1 (2) Conspicuous second mesotibial spur, at least half the length of the outer spur (Fig.113) .... *Sceliages* Westwood

2 (1) Second mesotibial spur absent or vestigial, less than one-fifth the length of the outer spur (Fig. 114)......................... 3

3 (4) Insertion of mesotarsus halfway along length of mesotibia (Fig. 127); elytral carinae widely separated (Fig. 115), often reddish-brown; tarsi bearing only one claw (Fig. 160) .... *Drepanopodus* Janssens

4 (3) Insertion of mesotarsus at, or close to, end of mesotibia (Fig. 114).................... 5

5 (6) Profemora conspicuously enlarged; two unevenly reduced, recessed tarsal claws (Fig. 161)................ *Pachylomerus* Bertoloni

6 (5) Profemora not conspicuously enlarged........... 7

7 (8) Tarsi bearing only one claw (Fig. 162), no serrations between, or proximal to, protibial dentations, proximal protibial tooth reduced (Fig. 155).............. *Kheper* Janssens

8 (7) Tarsi bearing two equal claws (Fig. 158); serrations between and/or proximal to protibial dentations (Fig. 148)....*Scarabaeus* L.

Note: The genus *Circellium* Latrielle, until recently included in Scarabaeina, was moved to Canthonina by Cambefort (1978).

5. PHYLOGENY OF THE GENERA OF SCARABAEINA

5.1 INTRODUCTION

The cladistic principles outlined by Hennig (1965), as modified by subsequent authors, were used in the phylogenetic analysis of the genera of Scarabaeina. The terminology adopted is that of Ashlock (1971).

While the argument about cladistic analysis, and more especially cladistic classification, is still raging (Patterson 1980, and many others), the line of concensus running through the argument is that the cladistic method of analysis can be a useful tool or guiding principle (not an only tool, or a religion) in the analytical kit of the taxonomist. It is hopefully as such that it has been used in this work.

The holophyly of Scarabaeina was assessed by comparison with the other subtribes of Scarabaeini. By means of this comparison, the taxonomic outgroup (sister group) of Scarabaeina was determined and the method of outgroup comparison (Watrous & Wheeler, 1981) was then used in allocating plesiomorphic or apomorphic status to the taxonomic characters of the species of Scarabaeina.

The principal morphological characters used in the analysis and classification of the genera are summarised in Table 1. From this table it is evident that apomorphies occur in each genus. Analysis of these apomorphies suggests that most of them are autopomorphs, even though occurring in more than one genus (i.e. convergence), but a small number of them are likely to be synapomorphies. In theory, if the taxonomic characters have been correctly chosen and the synapomorphies correctly identified, a pattern should be revealed from which a number of possible phylogenetic configurations can be drawn, with the most parsimonious of these configurations being accepted as the most likely phylogeny.

Ultimately, however, the choice of taxonomic characters, and the decision as to which phylogenetic configuration represents the greatest parsimony, remains subjective (with or without cladistic analysis).

TABLE 1: CHARACTERS USED IN THE CLADISTIC ANALYSIS OF THE GENERA OF SCARABAEINA

Character	Plesiomorphic state	Apomorphic state	Assignment of the different states to the respective genera				
			Sceliages	*Scarabaeus*	*Drepanopodus*	*Pachylomerus*	*Kheper*
1. Antennae	basal lamella of club ovate and slightly concave	basal lamella of club cup-shaped and deeply concave	A_1	P	P	P	A_2
2. Mesosternum	smooth	furrowed	P	P-A	A	A	A
3. Mesocoxae	widely separated	closely set	P	A	A	A	A
4. Pheromone glands	absent	present	P	P-A	P	A	A
5. Aedeagus	simple, symmetrical	complexly symmetrical	A_1	P-A	P	A_2	A_3
6. Elytral carinae	close	wide apart	P	P-A	A	P	P
7. Protibia	externally serrated	serrations lacking	P	P	P	P	A
8. Profemora	not enlarged	enlarged	P	P(-A)	P	A	P

A = Apomorphic; A_{1-3} different (probably independently derived) apomorphic states; (-A) *S. cancer* only; P = Plesiomorphic.

TABLE (continued)

Character	Plesiomorphic state	Apomorphic state	Assignment of the different states to the respective genera				
			Sceliages	*Scarabaeus*	*Drepanopodus*	*Pachylomerus*	*Kheper*
9. Second mesotibial spur	large	vestigial	P	A	A	A	A
10. Mesotibial insertion	apical	subapical	P	A	A_1	A_2	A_2
11. Metatibial insertion	apical	subapical	P	P-A	A_1	A_2	A_2
12. Tibial extremeties	flared	parallel	P	A	A	A	A
13. Tarsal claws	two	one	P	P	A_1	P	A_2

A = Apomorphic; A_{1-3} different (probably independently derived) apomorphic states;

(-A) *S. cancer* only; P = Plesiomorphic.

5.2 ANALYSIS

Eucraniina was accepted as the taxonomic outgroup of Scarabaeina because the following characters appeared to be synapomorphic with those of Scarabaeina:

i) oblique, closely-set mesocoxae
ii) slender, quadridentate protibia
iii) protibia lacking a tarsus
iv) elytra seven-striated, (except in species of the genus Eucranium, which have eight striae)

The species of Gymnopleurina, included in Scarabaeina by Péringuey (1900), also have oblique mesocoxae, but appear to be phylogenetically further from Scarabaeina than Eucraniina as the gymnopleuimes have tridentate protibia, tarsi on the protibia and nine-striated elytra.

The species of Eucraniina generally have more plesio=morphic characters than Scarabaeina, except for the fact that all Eucraniina lack tarsal claws (Fig. 94). Thus they possess distally flared meso- and metatibia with the mesotibia always bearing two large spurs (Fig. 94), and simpler symmetrical aedeagi than those of Scarabaeina (Figs. 129-130).

A major limitation in the use of Eucraniina as a taxo=nomic outgroup is the fact that all the eucraniines are brachypterous, which restricts their usefulness as plesiomorphic "models" for the predominantly macropterous species of Scarabaeina.

Where characters in Eucraniina have been affected by changes associated with brachyptery (characters 2, 3 & 6 of Table 1), Gymnopleurina, as the next closest subtribe to Scarabaeina, was used to determine the relative plesio- or apomorphy of these characters.

Sceliages Westwood appears to be the genus closest to the hypothetical common ancestor of the genera of Scarabaeina. Although species of _Sceliages_ have asymmetrical aedeagi very similar to those of some species of _Scarabaeus_, this asymmetry is relatively simple and is probably due to convergence rather than synapomorphy, as the species of _Sceliages_ have retained plesiomorphies not found in even the most plesiomorphic species of _Scarabaeus_.

Scarabaeus L. appears to be the next most plesiomorphic genus after _Sceliages_. Within the scope of Scarabaeina, _Scarabaeus_ is a large (± 100 spp.), heteromorphic genus, with many species exhibiting one or more apomorphic characters but these appear to be autapomorphs as no species or group of species exhibits a large complex of these apomorphs.

The most plesiomorphic _Scarabaeus_ species appear to be close to _S. rubripennis_ Boheman which is small, diurnal, with a symmetrical aedeagus and bearing a second mesotibial spur, while S. goryi Castelnau which is large, crepuscular, with large eyes and rufous pubescence, complex, assymmetrical aedeagus, and a single mesotibial spur, is representative of the most apomorphic species of Scarabaeus.

Species of Drepanopodus Janssens resemble the more plesiomorphic species of Scarabaeus such as S. rubripennis but differ from these species in possessing synapomorphies such as a single tarsal claw (Fig. 160) and having the meso- and metatarsi implanted far up on the tibiae (Fig. 127), while the tarsi of the plesiomorphic species of Scarabaeus are implanted at the distal extremities of the tibiae.

The complex symmetrical aedeagus found in the species of Pachylomerus Bertoloni is the most important autapomorph of this genus. Of the eight apomorphies shared by Pachylomerus and Kheper some are no doubt autapomorphs while others are synapomorphic for both genera, as it is unlikely that all the shared apomorphs are the result of convergence. As these two genera are also the only ones in Scarabaeina which have complex symmetrical aedeagi, it seems reasonable to assume that this condition and a number of the shared apomorphies may have existed in a common ancestor.

The abdominal pheromone glands may also be a synapomorph of both genera, but as a few Scarabaeus species also possess these glands, their phylogenetic significance for

Pachylomerus and Kheper is lessened since the possibility exists that they could have developed independently in each of these genera.

Kheper Janssens in many ways appears to represent the next major step in the evolution of the genera of Scarabaeina. Not only are the species of Kheper the most apomorphic of those within Scarabaeina but in contrast to Pachylomerus, which is limited to two species and confined to roughly the southern half of Africa, there are some 21 species of Kheper, with a distribution extending from southern Africa to Asia. This suggests that new niches have been, or are being, successfully invaded by members of this genus.

The most important apomorphs of the species of Kheper are the complex symmetrical and asymmetrical aedeagi, the lack of protibial serrations, the presence of a stout single tarsal claw, and the reduction of the proximal protibial dentation. While the species of Drepanopodus also possess a single tarsal claw and share a number or lesser apomorphs with Kheper species, the simple, symmetrical aedeagi, lack of pheromone glands and general plesiomorphic facies of the Drepanopodus species make it unlikely that the single tarsal claw is synapomorphic with that of the Kheper species.

5.3 CLASSIFICATION

The classification of the evolutionary units of Scarabaeina, as identified by cladistic analysis, departs from cladistic theory in two respects.

Firstly, the classification is not a mirror image of the cladogram in the sense that each successive dichotomy is not ranked lower than the preceeding one, i.e. "upward" ranking from the genus level has been employed, rather than "downward" ranking from the common ancestor of the subtribe. The Linnaean system of classification does not allow for the large number of groups and subgroups which a strictly cladistic classification would require, while the additional categories would provide no more information than that already contained in the cladogram. This problem is recognised by many "pure" cladists (Scoble, pers. comm.), and the recent literature reveals an active search for solutions to the problems of cladistic higher classification.

The second departure from cladistic theory is the retention of *Scarabaeus* as a paraphyletic genus. In all major taxonomic revisions to date, *Scarabaeus* has been defined as consisting of those species having two equal tarsal claws, and serrations between and proximal to the protibial dentations. Within Scarabaeina, these are plesiomorphic characters. In terms of cladistic theory, taxa cannot be recognised on the basis of shared plesiomorphs.

Scarabaeus can be distinguished from *Sceliages* on valid cladistic grounds, but not from *Drepanopodus*, *Pachylomerus* and *Kheper*. As *Scarabaeus* is the most plesiomorphic of these four genera, cladistically *Drepanopodus*, *Pachylomerus* and *Kheper* should be lumped with *Scarabaeus*. This does not solve the problem, however, as the same difficulties will arise in the definition of the subgenus *Scarabaeus* *s*. *str*. The only justification for such a taxonomic change would be that the recognition of a subgenus on the grounds of shared plesiomorphs would be a slightly lesser "sin" than it is in the case of a genus, but this is far out=weighed by the unnecessary confusion caused by the lowering of three sound and well-established genera to subgeneric status.

The cladistic requirement of a definitive apomorph for every taxon is based on the assumption that there can be no surviving ancestor after a phylogenetic split has occurred, and that all phylogenetic splits are reflected in relatively gross, observable, external apomorphic structures in the adult organism. The infallibility of these two assumptions has not been proved, and has been opposted by many authors, amongst others Mayr (1974) especially in the event of allopatric speciation.

Drepanopodus, Pachylomerus and Kheper all exhibit marked shifts away from the "normal" Scarabaeus niche, - see discussion of genera for details. This suggests that the pressure on the "normal" Scarabaeus niche in the event of these phylogenetic splits would have been minimal, thereby increasing the chances of survival of the ancestral species.

The results of the cladistic analysis are summarised in Figs. 163 and 164.

> WHAT CONCLUSIONS ARE WE TO DRAW FROM THIS....? SIMPLY THIS: OUR TRUTHS ARE BUT PROVISIONAL; ASSAILED BY THE TRUTHS OF TOMORROW, THEY BECOME ENTANGLED WITH SO MANY CONTRADICTORY FACTS THAT THE LAST WORD OF KNOWLEDGE IS DOUBT.
>
> JEAN HENRI FABRE

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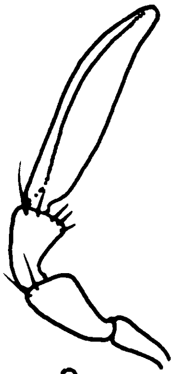
Figs. 1-7 *Scarabaeus scholtzi spec. nov.* 1. Dorsal view of *S. scholtzi.* 2. Dorsal view of left maxillary palp. 3 Dorsal view of right protibia. 4. Dorsal view of left metatarsus. 5-6. Aedeagus. 5. Lateral view from right side. 6 Dorsal view. 7. Ventral view of left mesotibia to show second tibial spur.



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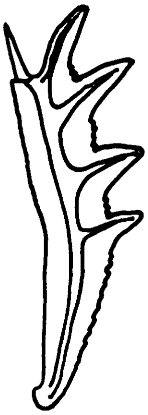

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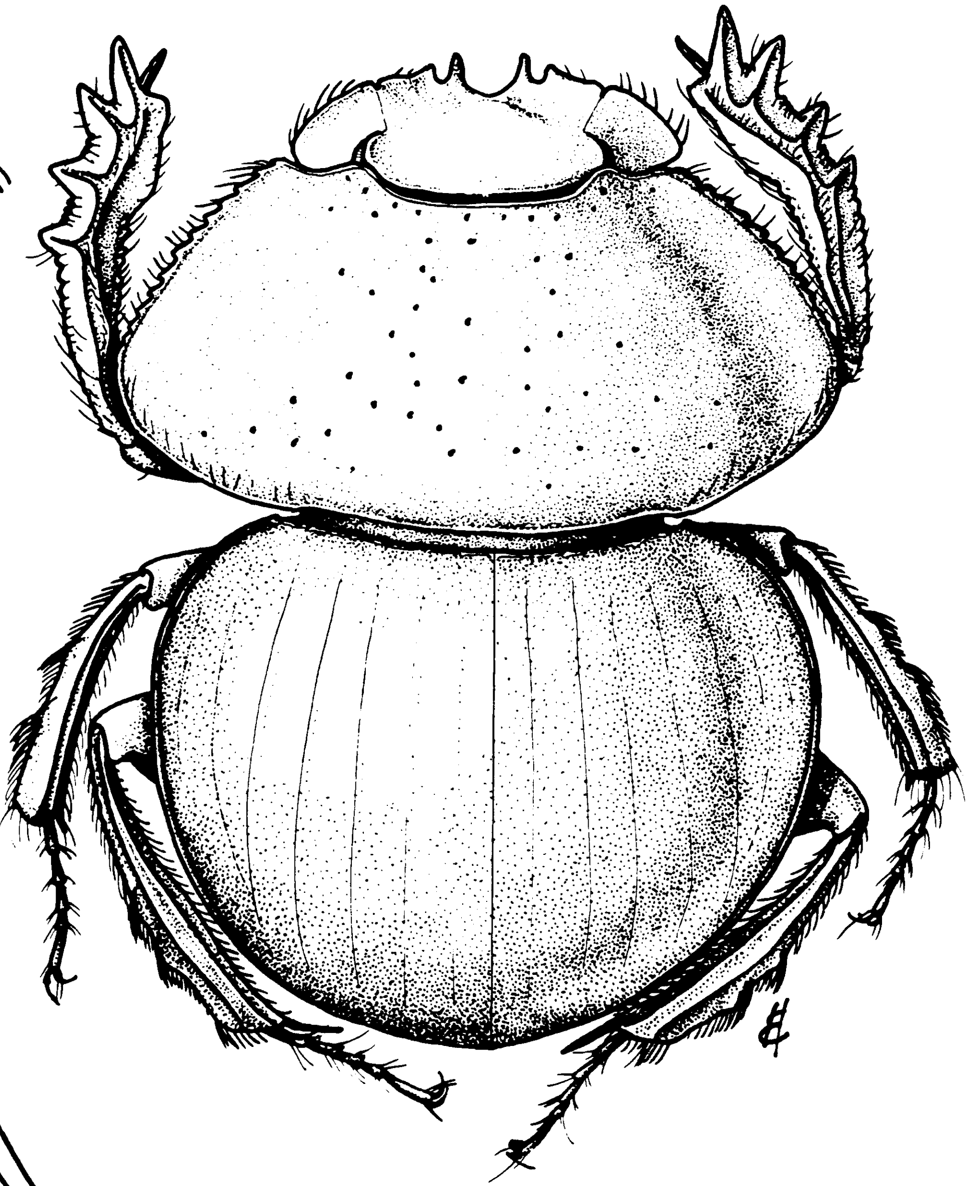

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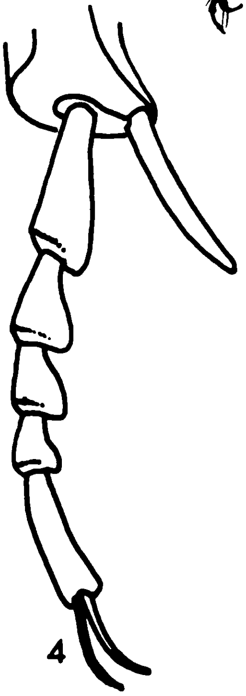

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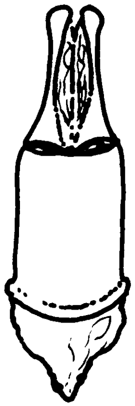

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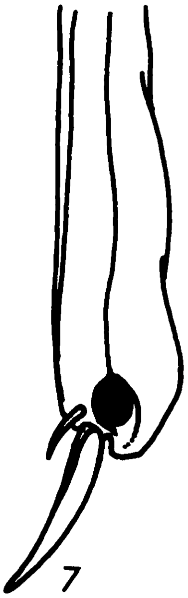

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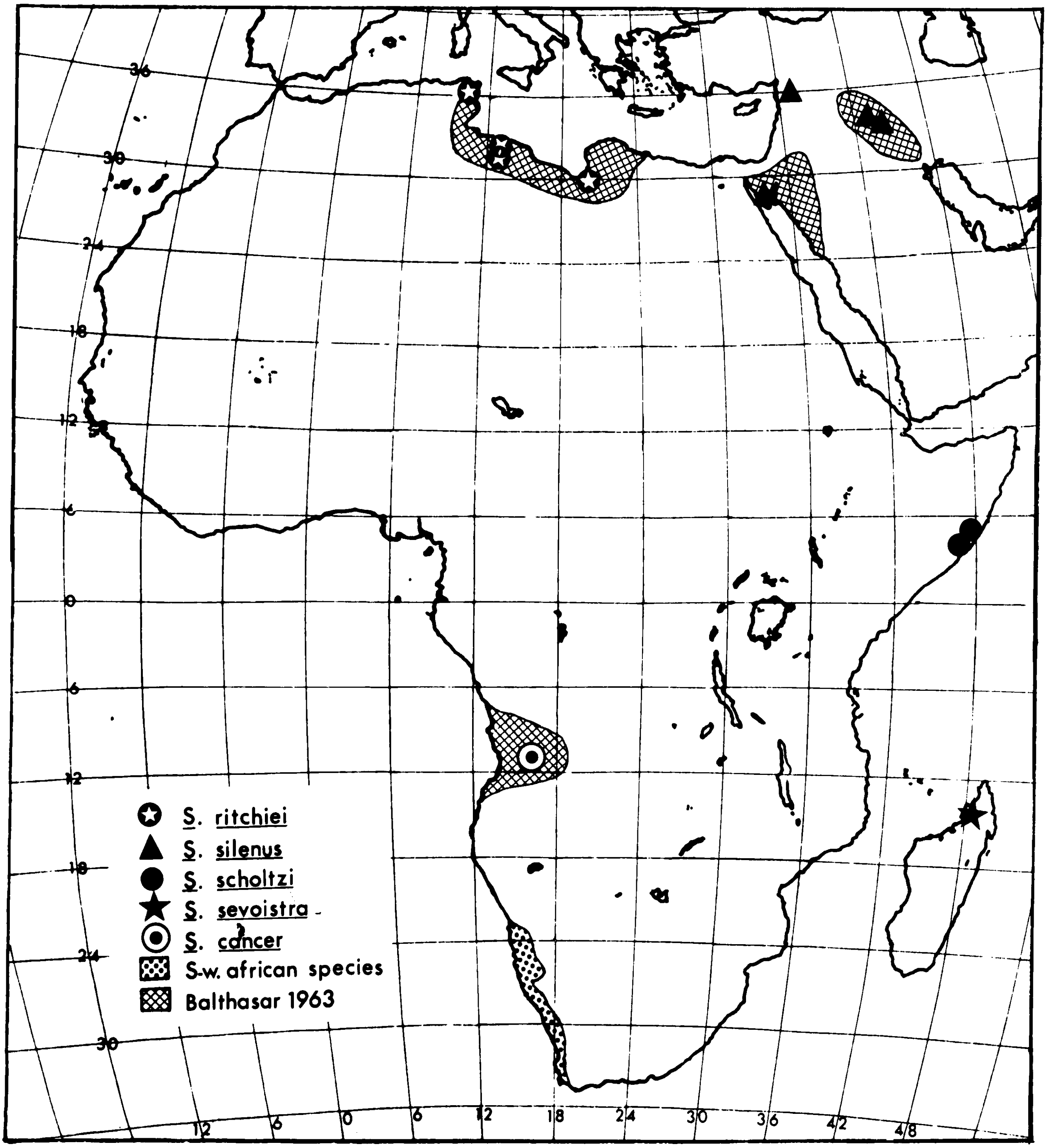
Fig. 8. Distribution map of flightless *Scarabaeus* species.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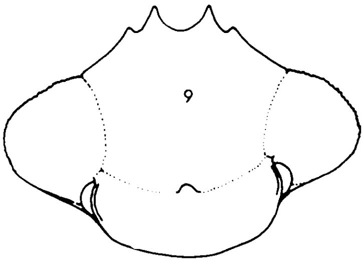
42
48
S. ritchiei
S. silenus
S. scholtzi
S. sevoistra
S. cancer
S-w. african species
Balthasar 1963

Figs. 9-23. Dorsal view of heads of flightless *Scarabaeus* species (After Holm & Scholtz 1979).

9. *S. rodriguesi*. 10. *S. rotundigena*.
11. *S. fitzsimonsi*. 12. *S. bennigseni*.
13. *S. striatus*. 14. *S. denticolle*.
15. *S. ritchiei*. 16. *S. silenus*.
17. *S. sevoistra*. 18. *S. cancer*.
19-20. *S. schinzi*. 19. Female. 20. Male.
21. *S. gariepinus*. 22. *S. hippocrates*.
23. *S. aesculapius*. (*S. scholtzi* - see Fig. 1)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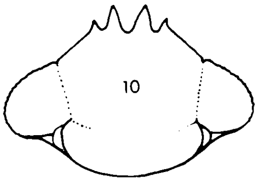
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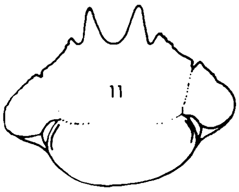
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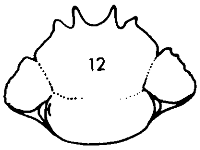
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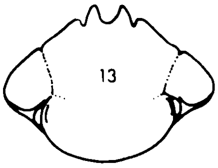
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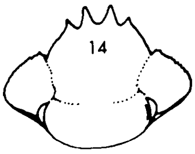
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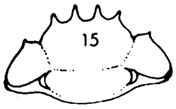
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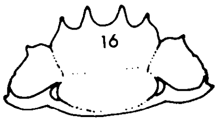
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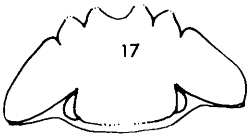
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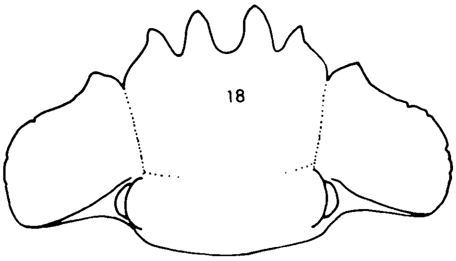
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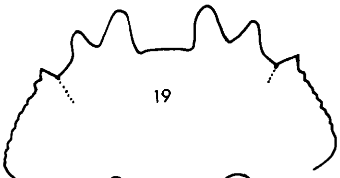
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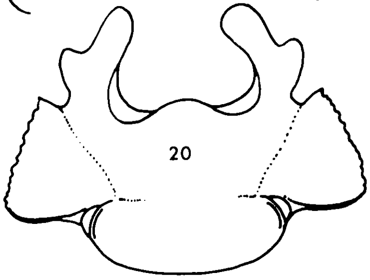
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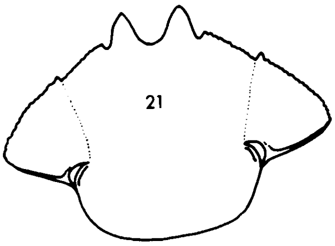
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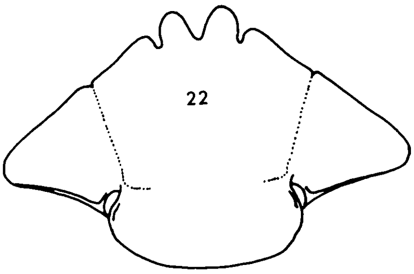
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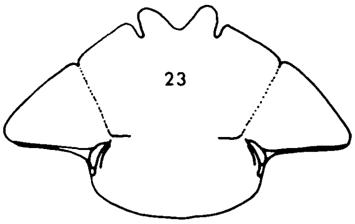
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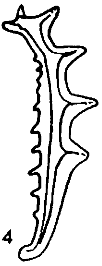
Figs. 24-75: Tibiae (dorsal view) and aedeagi of flightless *Scarabaeus* species. (After Holm & Scholtz, 1979) 24-26 *S. sevoistra*. 24. Protibia male. 25. Aedeagus lateral. 26. Aedeagus dorsal. 27-29. *S. aesculapius*. 27. Protibia. 28. Aedeagus lateral. 29. Aedeagus dorsal. 30-34. *S. denticolle*. 30. Protibia male. 31. Protibia female. 32. Aedeagus lateral. 33. Aedeagus dorsal. 34. Aedeagus lateral (ssp. *penrithae*). 35-38. *S. rodriguesi* 35. Protibia male. 36. Protibia female. 37. Aedeagus lateral. 38. Aedeagus dorsal. 39-42. *S. fitzsimonsi*.39. Protibia male. 40. Distal end protibia female. 41. Aedeagus lateral. 42. Aedeagus dorsal. 43-46. *S. rotundigena*. 43. Protibia male. 44. Protibia female. 45. Aedeagus lateral. 46. Aedeagus dorsal. 47-49. *S. bennigseni*. 47. Protibia. 48. Aedeagus lateral. 49. Aedeagus dorsal. 50-53. *S. striatus*. 50. Protibia male. 51. Protibia female. 52. Aedeagus lateral. 53. Aedeagus dorsal. 54-56. *S. cancer*. 54. Protibia. 55. Aedeagus lateral. 56. Aedeagus dorsal. 57-59. *S. gariepinus*. 57. Protibia. 58. Aedeagus lateral. 59. Aedeagus dorsal. 60-62. *S. schinzi*. 60. Protibia male (with distance 'a' less in female). 61. Aedeagus lateral. 62. Aedeagus dorsal. 63-68. *S. hippocrates*. 63. Protibia male. 64. Protibia female. 65. Protibia male (northern species, from Wallekraal). 66. Aedeagus lateral (from Wallekraal). 67. Aedeagus dorsal (from Wallekraal). 68. Aedeagus dorsal (from Darling). 69-72. *S. silenus*. 69. Protibia female. 70. Distal end of protibia male. 71. Aedeagus lateral. 72. Protibia male. 74. Aedeagus lateral. 75. Aedeagus dorsal.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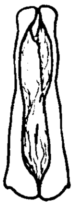
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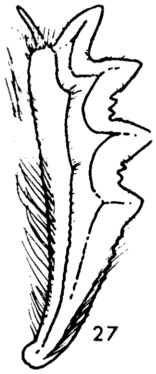
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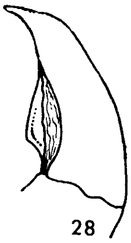
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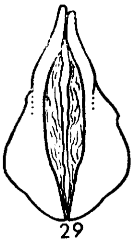
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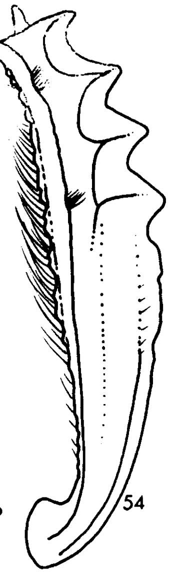
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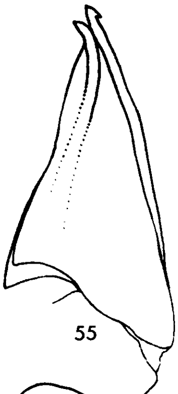
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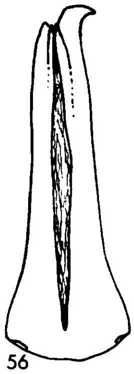
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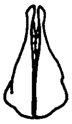
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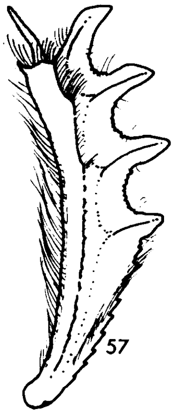
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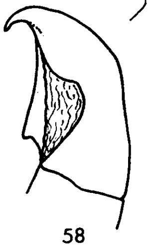
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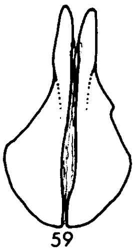
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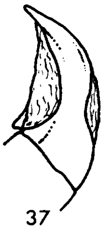
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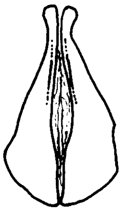
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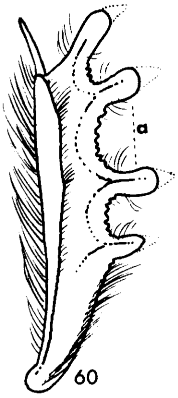

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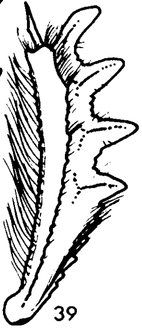
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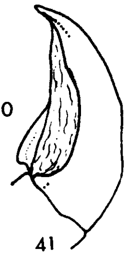
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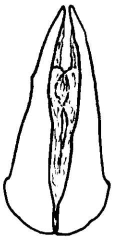
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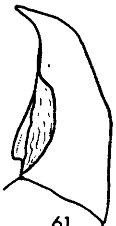
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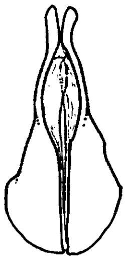
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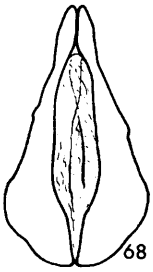
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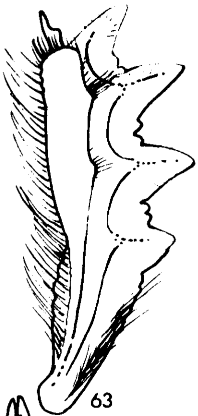
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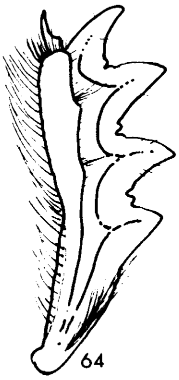
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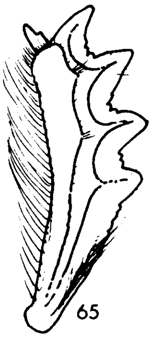
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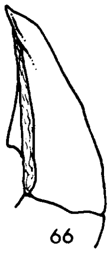
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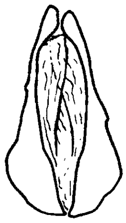
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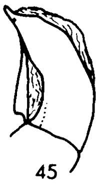
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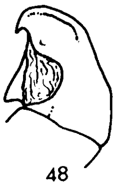
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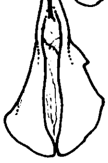
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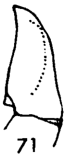
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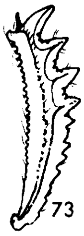
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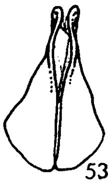
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Figs. 76-91. Brachypterous species of *Scarabaeus* L.
(± natural size)

76. *S. gariepinus* (Ferreira) *comb. nov.*
77. *S. aesculapius* Olivier.
78. *S. rotundigena* (Felsche) *comb. nov.*
79. *S. striatus* (Castelnau) *comb. nov.*
80. *S. rodriguesi* (Ferreira) *comb. nov.*
81. *S. denticolle* (Péringuey) *comb. nov.*
82. *S. schinzi* (Fairmaire) *comb. nov.* - female
83. *S. cancer* (Arrow) *comb. nov.*
84. *S. schinzi* (Fairmaire) *comb. nov.* - male.
85. *S. bennigseni* (Felsche) *comb. nov.*
86. *S. hippocrates* (M'Leay) *comb. nov.*
87. *S. fitzsimonsi* (Ferreira) *comb. nov.*
88. *S. silenus* (Gray) *comb. nov.*
89. *S. ritchiei* (M'Leay) *comb. nov.*
90. *S. scholtzi spec. nov.*
91. *S. sevoistra* Alluaud.


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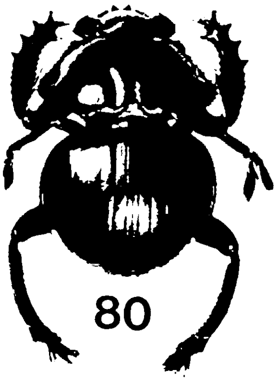
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Figs. 92-100. Distinguishing features of subtribes of Scarabaeini

92. Slender tibia typical of members of Scarabaeini.

93. Flared tibia typical of non-Scarabaeini scarabs.

94. Eucraniina sp. Mesotibial extremity and tarsus, showing large second spur and lack of tarsal claws.

95. Gymnopleurina sp. - dorsal view of protibia showing three protibial dentations and presence of protarsus.

96. Scarabaeina sp. - slender tarsus typical of subtribe.

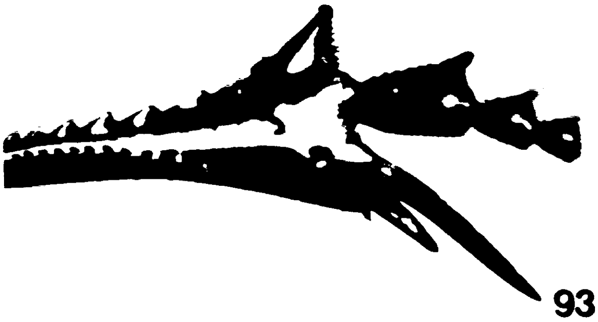
97. Widely separated parallel mesocoxae typical of non-Scarabaeini scarabs.

98. Closely positioned, oblique mesocoxae typical of members of Scarabaeini.

99. Sisyphina sp. - lateral view of pronotum showing flattened lateral border.

100. Gymnopleurina sp. - dorso-lateral view of elytron showing sinuate lateral margin exposing pleura.

92



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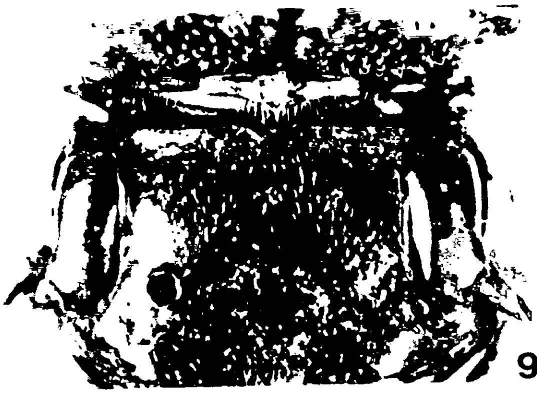

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Figs. 101-102. Representative Eucraniina species.

101. *Eucranium arachnoides* Brullè

102. *Anomiopsoides cavifrons* Burmeister

Figs. 103-105. Representative *Scarabaeus* species.

103. *Scarabaeus multidentatus* (Klug) *comb. nov.*

104. *Scarabaeus goryi* (Castelnau)

105. *Scarabaeus rusticus* (Boheman)

Figs. 106-110. Representative Scarabaeina species.

106. *Kheper lamarcki* (M'Leay)

107. *Pachylomerus femoralis* Bertoloni

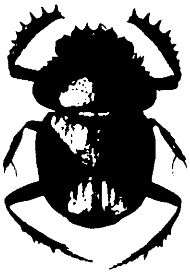
108. *Scarabaeus proboscideus* (Guérin) *comb.nov.*

109. *Sceliages hippias* Westwood

110. *Drepanopodus proximus* (Péringuey)


101


102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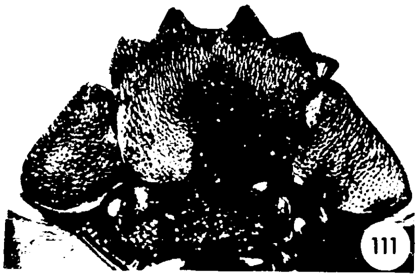
Figs. 111-130. Features of Scarabaeina and Eucraniina species.

111. *Scarabaeus proboscideus* (Guérin) *comb. nov.* - dorsal view of head.
112. *Scarabaeus zambesianus* Péringuey - view of head, showing similarity to that of 111.
113. *Sceliages* sp. - mesotibial extremity, showing large second mesotibial spur.
114. *Scarabaeus* (*Scarabaeolus*) sp. mesotibial extremity, showing vestigial second mesotibial spur.
115. *Scarabaeus* (*Scarabaeolus*) sp. - lateral view of elytron, showing widely separated elytral carinae.
116. *Scarabaeus s. str.* sp. - lateral view of elytron, showing closely placed elytral carinae.
117. *Scarabaeus multidentatus* (Klug) *comb. nov.* dorsal view of head, showing laterally expanded genae forming "fourth pair" of "dentations".
118. *Scarabaeus viettei* (Paulian) *comb. nov.* - dorsal view of head.
119. *S. viettei* - dorsal view of male protibia.
120. *S. viettei* - dorsal view of female protibia.
121. *S. viettei* - lateral view of aedeagus.
122. *S. viettei* - dorsal view of aedeagus.
123. *Scarabaeus proboscideus* (Guérin) *comb. nov.* - lateral view of head.
124. *Scarabaeus zambesianus* Péringuey - lateral view of head, showing incipient protuberance on mentum, and overall similarity to *S.proboscideus*.
125. *Scarabaeus multidentatus* (Klug) *comb. nov.* ventral view of head showing relatively small eyes of diurnal species.
126. *Scarabaeus zambesianus* Péringuey - ventral view of head showing relatively large eyes of crepuscular species.
127. *Drepanopodus sp.* - mesotibial extremity showing high insertion of tarsus on tibia.
128. *Anomiopsoides cavifrons* Burmeister - dorsal view of head showing "pitch-fork"-like clypeal dentations.
129. *Eucranium arachnoides* Brullé - aedeagus, lateral view.
130. *Eucranium arachnoides* Brullé - aedeagus, dorsal view.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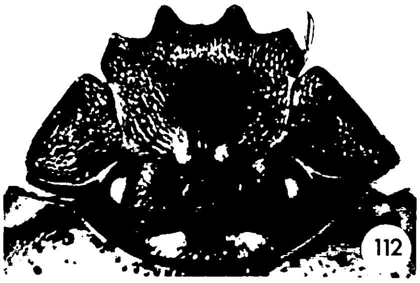
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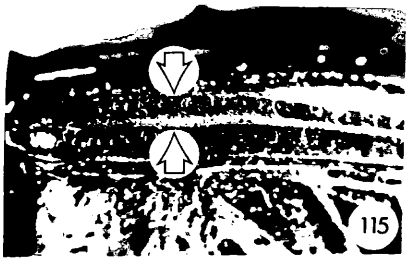
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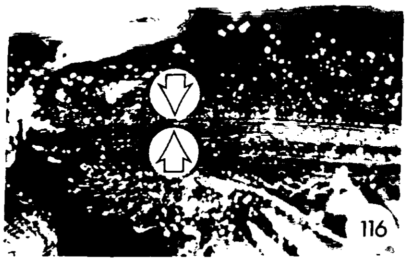
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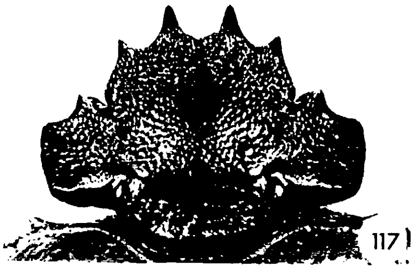
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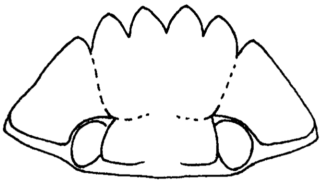
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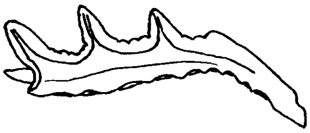
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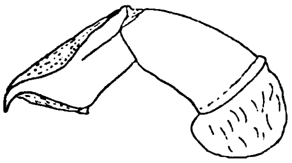
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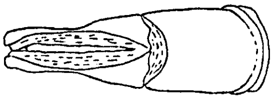
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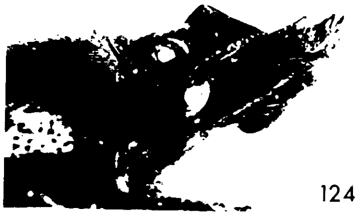
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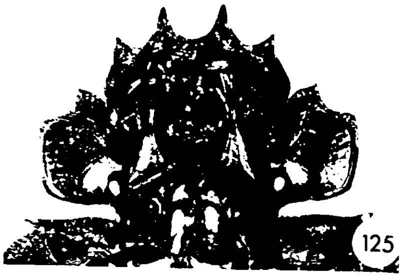
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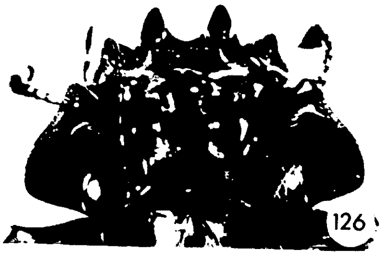
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Figs. 131-146: Scarabaeina spp. aedeagi

131-132. Sceliages hippias Westwood.

133-134. Drepanopodus proximus (Péringuey)

135-136. Scarabaeus multidentatus (Klug) comb. nov.

137-138. Scarabaeus proboscideus (Guérin) comb. nov.

139-140. Scarabaeus zambesianus Péringuey

141-142. Pachylomerus femoralis Bertoloni

143-144. Kheper subaeneus (Harold)

145-146. Kheper cupreus Castelnau


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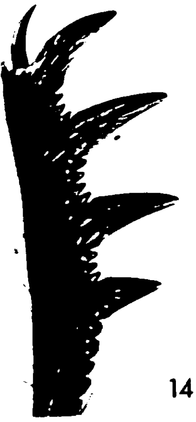
Figs. 147-162. Protibiae and metatarsi of Scarabaeina and Eucraniina species

147. *Sceliages* sp.
148. *Scarabaeus* (*Scarabaeolus*) *rubripennis* (Boheman)
149. *Scarabaeus proboscideus* (Guérin) *comb*. *nov*.
150. *Scarabaeus caffer* (Boheman)
151. *Scarabaeus multidentatus* (Klug) *comb*. *nov*.
152. *Scarabaeus ritchiei* (M'Leay) *comb*. *nov*.
153. *Drepanopodus proximus* (Péringuey)
154. *Pachylomerus femoralis* Bertoloni
155. *Kheper cupreus* (Castelnau)
156. *Anomiopsoides cavifrons* Burmeister
157. *Sceliages hippias* Westwood
158. *Scarabaeus* (*Scarabaeolus*) *rubripennis* (Boheman)
159. *Scarabaeus satyrus* (Boheman)
160. *Drepanopodus proximus* Péringuey
161. *Pachylomerus femoralis* Bertoloni
162. *Kheper cupreus* (Castelnau)


147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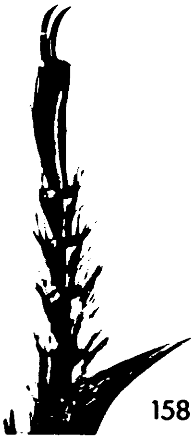
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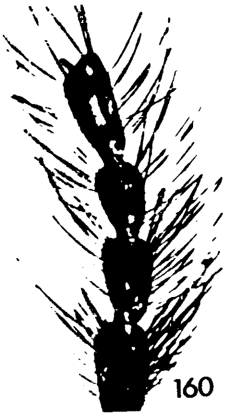
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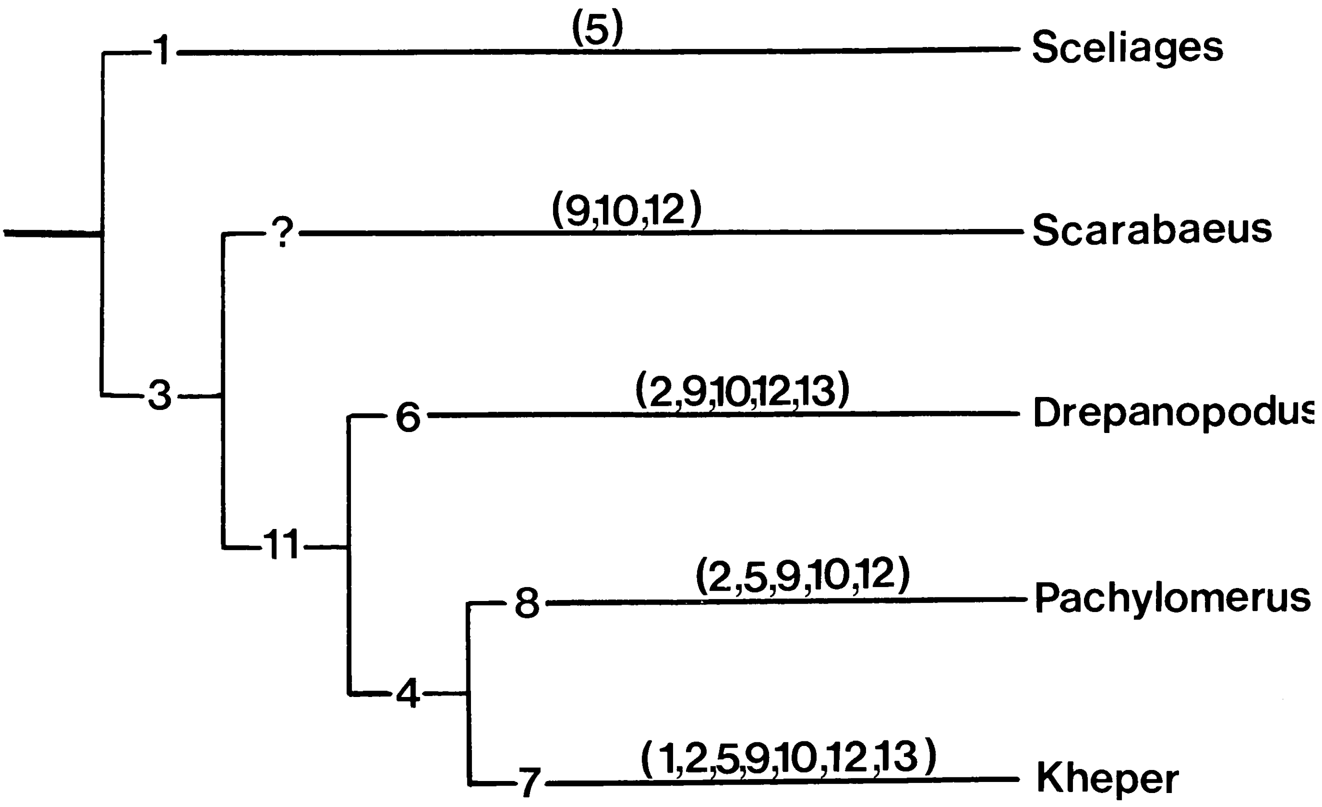
Fig. 163. Possible phylogeny of the genera of Scarabaeina. Numbers refer to apomorphies mentioned in Table 1.

Fig. 164. Phylogram of the genera of Scarabaeina. Area represents number of species, deviation from the vertical represents species diversity.


1
(5)
Sceliages
?
(9,10,12)
Scarabaeus
3
6
(2,9,10,12,13)
Drepanopodus
11
8
(2,5,9,10,12)
Pachylomerus
4
7
(1,2,5,9,10,12,13)
Kheper

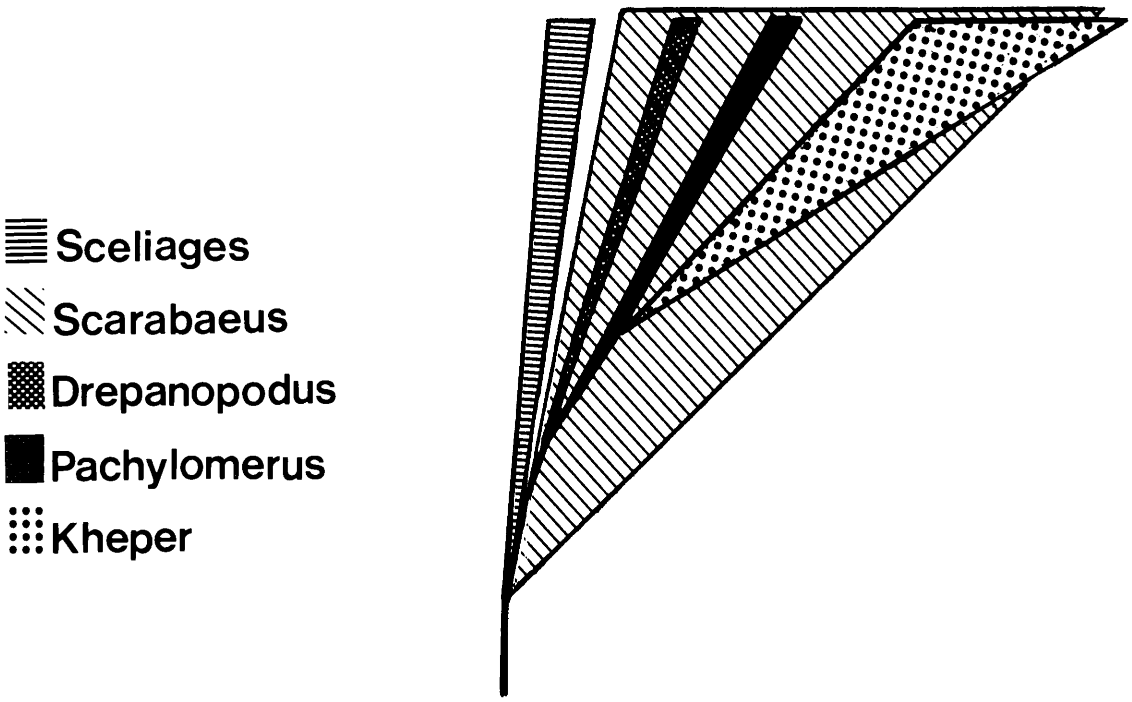

Sceliages
Scarabaeus
Drepanopodus
Pachylomerus
Kheper

Fig. 165. Recorded distribution of species of *Scarabaeus* Linnaeus

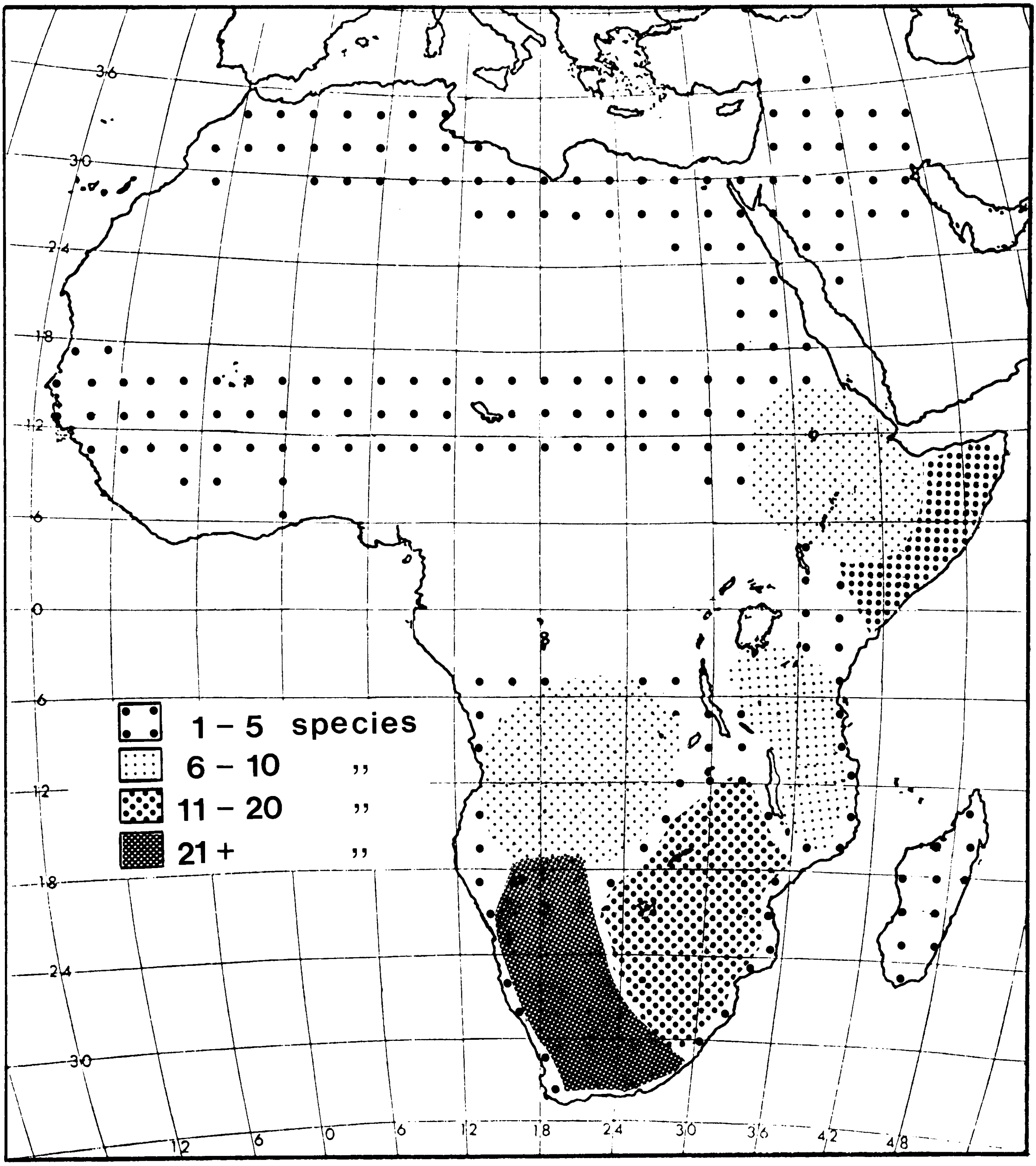

1 – 5 species
6 – 10 ,,
11 – 20 ,,
21 + ,,
36
30
24
18
12
6
0
6
12
18
24
30
12
6
0
6
12
18
24
30
36
42
48

Fig. 166. Recorded distribution of species of <u>Kheper</u> Janssens

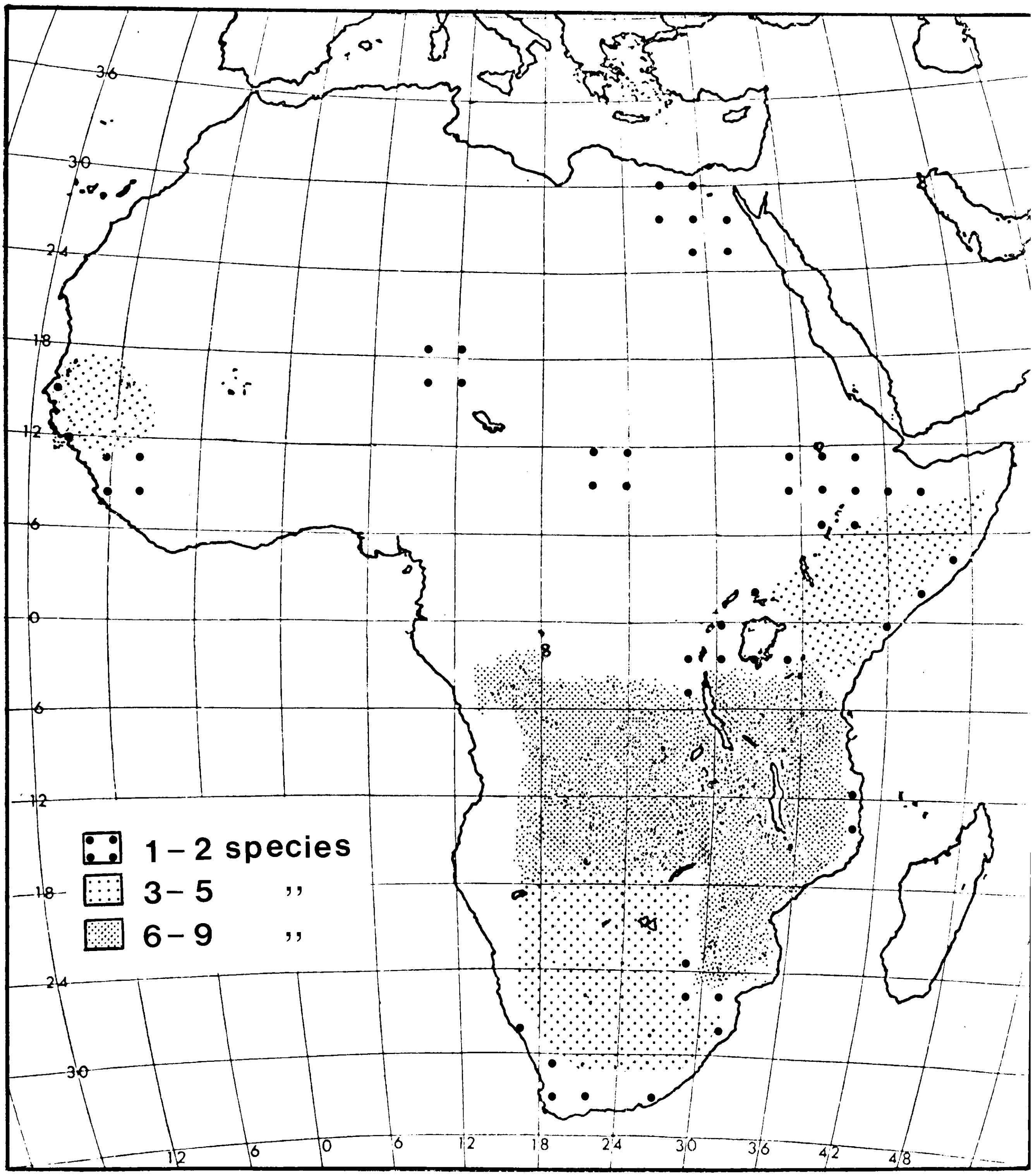
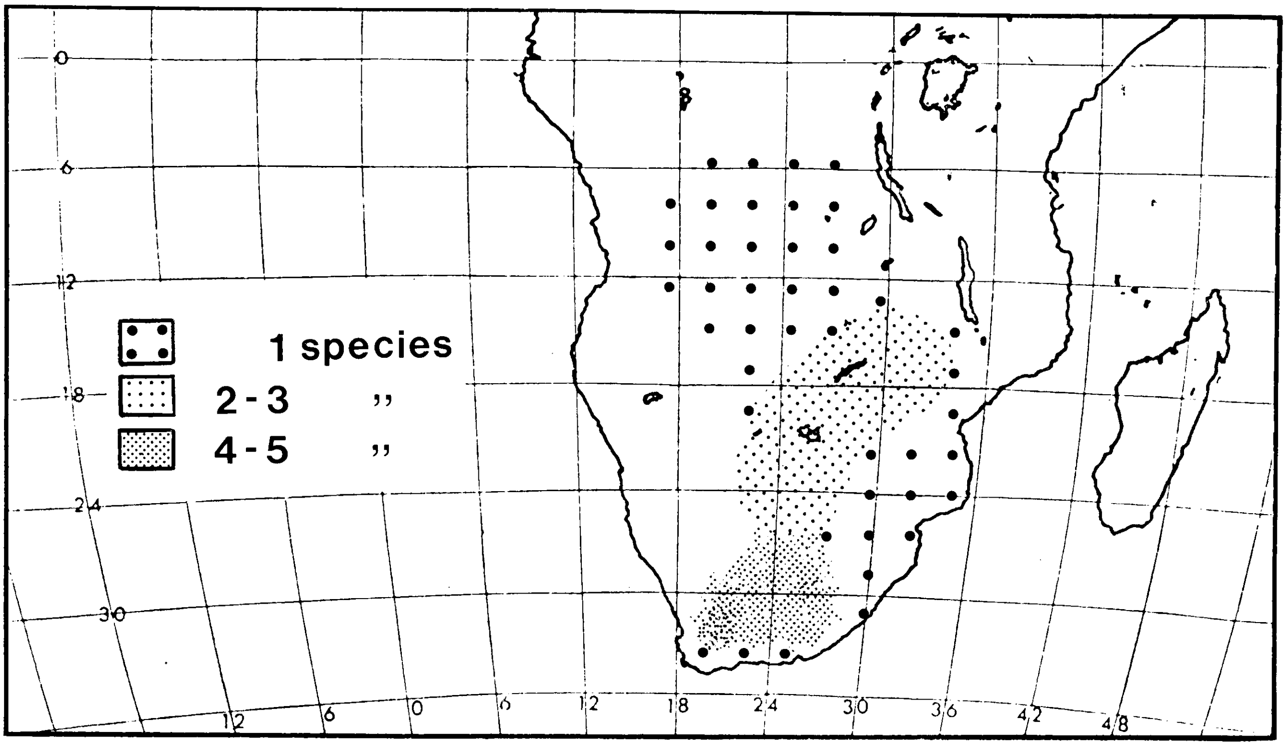
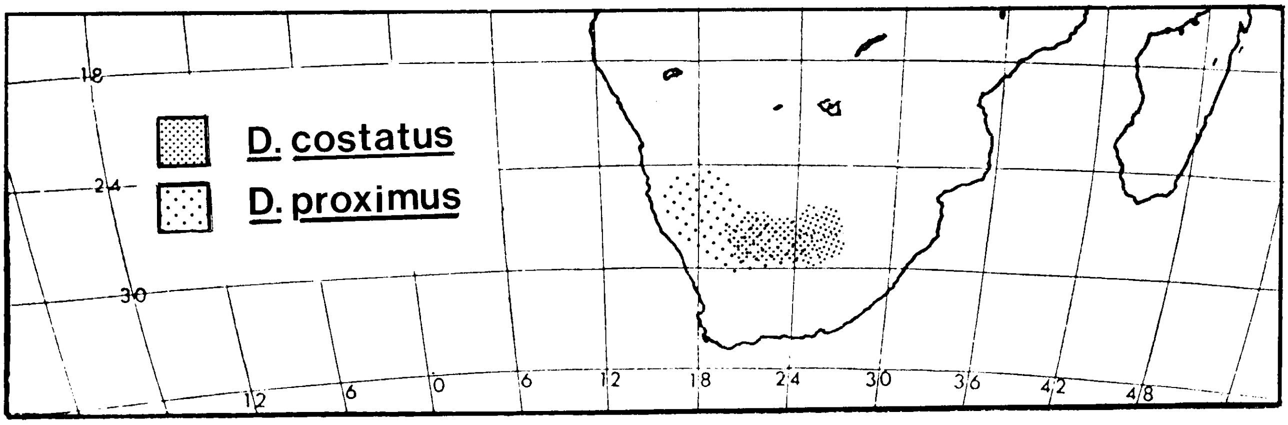

36
30
24
18
12
6
0
6
12
18
24
30
1 – 2 species
3 – 5 ,,
6 – 9 ,,
12
6
0
6
12
18
24
30
36
42
48

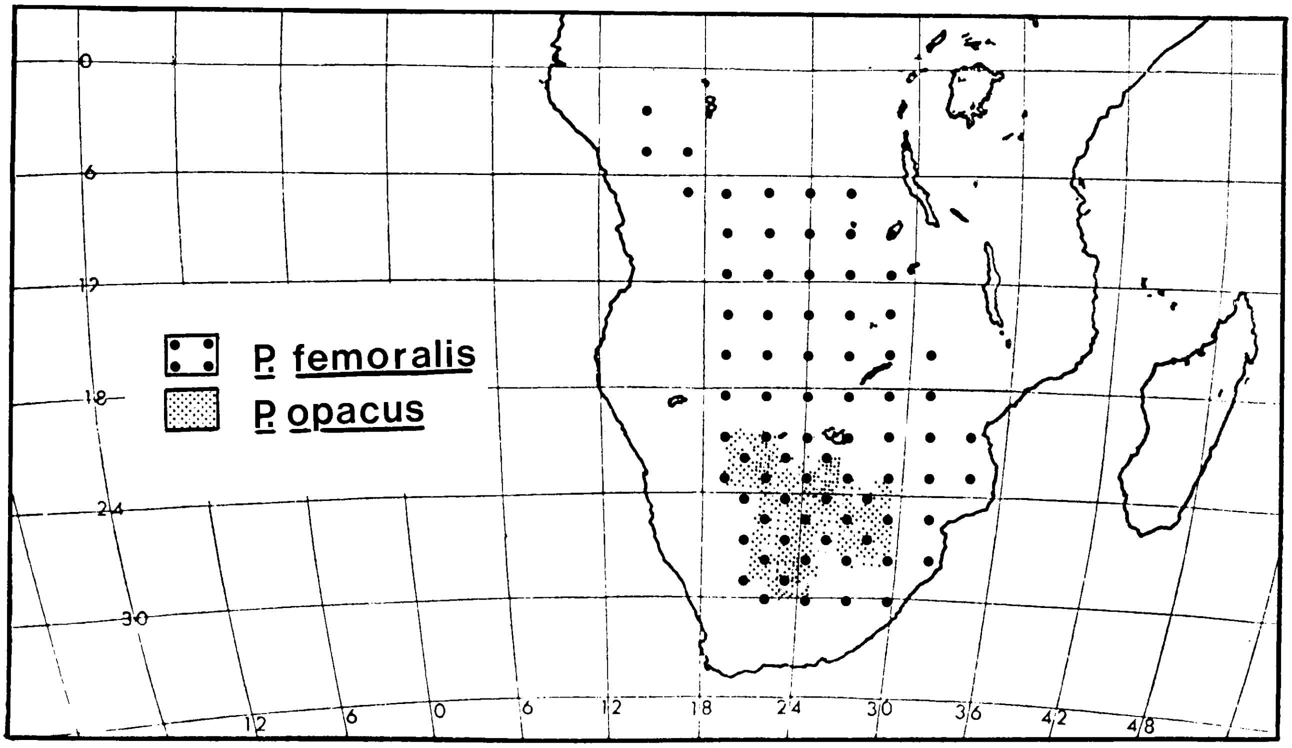
Fig. 167. Recorded distribution of species of *Sceliages* Westwood.

Fig. 168. Recorded distribution of species of *Drepanopodus* Janssens

Fig. 169. Recorded distribution of species of *Pachylomerus* Bertoloni


1 species
2 - 3 ,,
4 - 5 ,,
0
6
12
18
24
30
12
6
0
6
12
18
24
30
36
42
48


D. costatus
D. proximus
18
24
30
12
6
0
6
12
18
24
30
36
42
48


P. femoralis
P. opacus
0
6
12
18
24
30
12
6
0
6
12
18
24
30
36
42
48