THE GENUS *SISYPHUS* LATR.
(COLEOPTERA:SCARABAEIDAE)
IN SOUTHERN AFRICA

By

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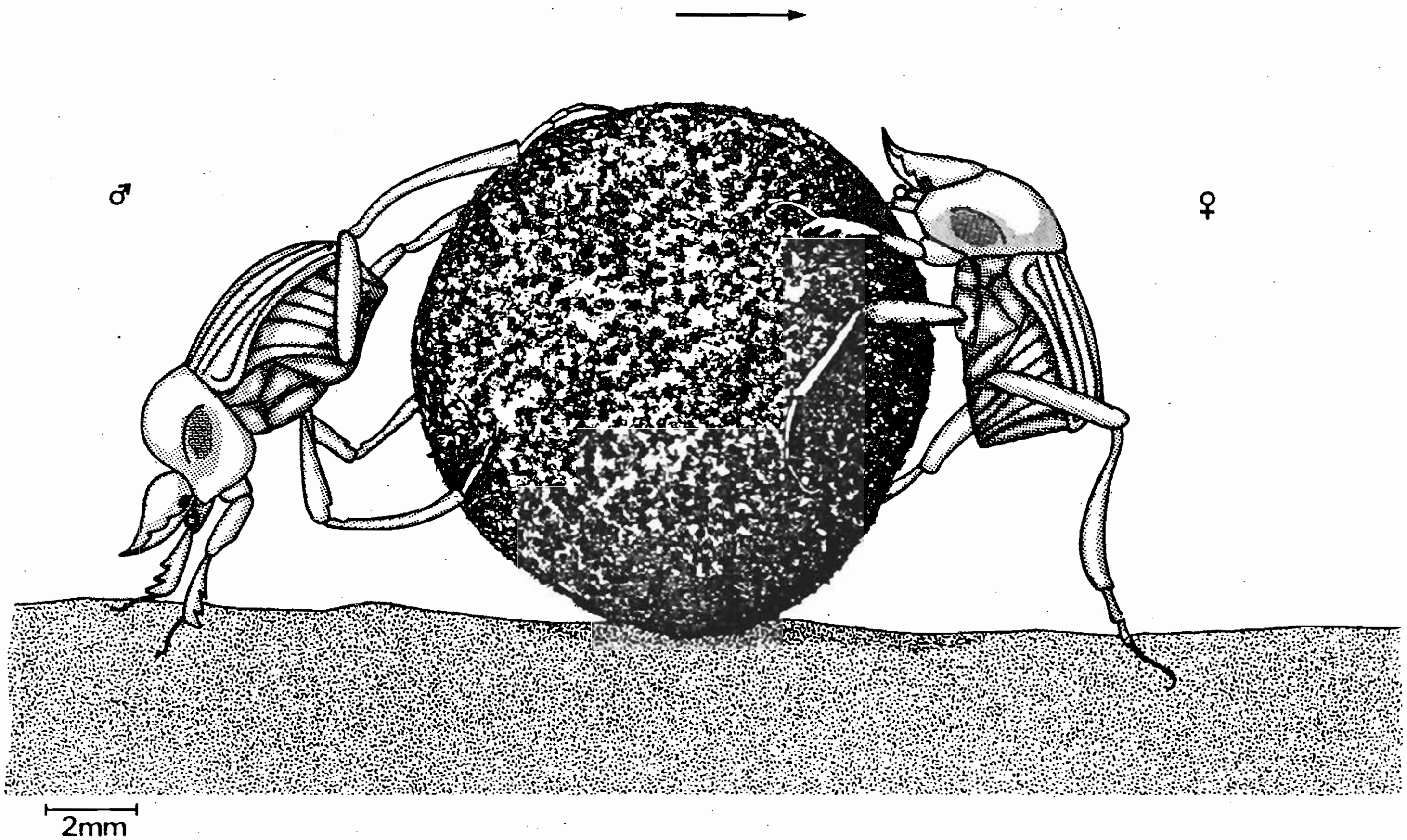

A pair of Sisyphus infuscatus Klug co-operating in rolling a brood ball.

(Arrow shows direction of movement)

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1 INTRODUCTION

Breeding in Scarabaeinae, the predominantly coprophagous subfamily of the Scarabaeidae, falls into three categories (Bornemissza 1969);

endocoprid:	breeding in the food source (usually dung),
paracoprid:	breeding near or at the food source (usually dung),
telecoprid:	removing part or all of the food material (also usually dung) some distance from the source and then utilizing it for breeding.

The genus *Sisyphus*, of the subfamily Scarabaeinae, falls into the telecoprid category. All the *Sisyphus* species make dung balls from dung pads, roll them away and then use them for breeding. The extraordinarily long meso- and metathoracic legs, characteristic of this genus, are well adapted for this ball making and rolling function. The frontispiece shows a pair of these beetles, co-operating in rolling a potential brood ball, in the positions characteristic of the genus. The roles of the male and female may, however, be reversed. The distribution of this genus includes Africa, Indo-China, Europe and South America, the last area probably through introduction by Man (Haaf, 1955). There are no *Sisyphus* species in Australia (Halffter and Matthews, 1966), or any other Scarabaeinae which are efficient in the utilization of soft bovine-type dung (Bornemissza, 1960; Waterhouse, 1974). It is because of this fact that the study of this genus and most other dung beetle genera concerned with bovine-type dung, began. Since the indigenous Australian Scarabaeinae are specialists in the utilization of the hard pellet-like droppings of marsupials, they are unable to utilize successfully bovine dung. With the introduction of cattle and horses into Australia came the problem of dung pollution in pastures. It has been estimated (Bornemissza, 1960) that domestic cattle in Australia produce about 33 million tons of dung (dry weight) annually, resulting in the loss of 300,000 of pasture land each year from the accumulation of dung pads. In addition, two introduced fly species, the bushfly, *Musca vetustissima* Walker and the buffalo fly, *Haematobia exigua* de Meijere, which are dung breeders, have become serious pests. In Africa the natural dung beetle fauna recycles the pasture nutrients and destroy the breeding places of the dung breeding flies by breaking up and burying the dung pads, sometimes within 24 hours of their being dropped.

The Australian Commonwealth Scientific and Industrial Research Organization set up the Dung Beetle Research Unit (hereafter referred to as the "Unit") under Dr. G.F. Bornemissza, in South Africa in 1970 to study African, European and Asian dung beetles. Suitable species are being sent to Australia to be released in various areas, eventually providing a fauna to cover as many ecological situations as possible in the vast cattle farming expanses of Australia. Careful study has to be undertaken prior to release in Australia to ensure that only species of adequate reproductive potential, dung disposing potential and of known habitat and food preferences are introduced. The beetles should be easily cultured in the laboratory, quickly establish themselves in the field and not compete significantly with one another or the native dung beetle fauna, which are specialized in the utilization of marsupial faecal pellets. New species to be introduced into Australia, therefore, should show a clear preference for bovine-type dung and not pellet-like droppings. Species with a wide distribution, colonizing several ecologically different areas, are being especially selected, since this means greater tolerance of the species to changing conditions and also, finally, fewer species will have to be introduced.

Very little was known of the general biology of the *Sisyphus* species prior to the establishment of the Unit in South Africa. The only species investigated in any detail up until this time was *S. schaefferi* (L.), a European species, by Prasse (1957 a-c; 1958; 1960). During the initial breeding programmes of Bornemissza in South Africa and through this study it became evident that several *Sisyphus* species were relatively prolific breeders and had a wide distribution. They are also of specific interest because, since they are ball rollers, they tend to colonize the external perimeters of the dung pads, often immediately after the dung pads are dropped. The perimeters of the pads, while they are still fresh, are also preferred by the dung-breeding flies, for egg laying. Thus the *Sisyphus* species "strike the first blow" at controlling the fly population by shredding the dung and destroying or exposing the fly eggs to desiccation. *Sisyphus* species do tend to shred up most of the pad rather than bury it and so are not as important for recycling nutrients as they are for making the dung unsuitable for oviposition by the flies and lessening, to a great extent, the chance of the fly larvae completing their life history in the dung. By shredding up pads, *Sisyphus* does not pose a serious threat of competition to other dung beetle genera. This is because *Sisyphus*, and many other dung beetle genera, as mentioned by Halffter and Matthews (1966) have a mechanism for aggregating in large numbers in some dung pads while they are often completely absent in other similar pads in the same area. This means that *Sisyphus* will shred up a certain percentage of pads in a field and leave the others almost completely free for the utilization of other dung beetles which occur sympatrically.

Most of the known African *Sisyphus* species (24 out of 37) occur in southern Africa. Efforts have, therefore, been concentrated on those species occurring south of the Zambezi and this study will be concerned with and refer to those species only.

The validity and identity of 20 of the 24 known species have been established while the four remaining species have been morphologically isolated but not named. The study of the taxonomy of the genus is presented in the first section of this thesis to prove the authenticity and identity of the species being discussed in the thesis. The section following taxonomy is on distribution. Most of the *Sisyphus* species are distributed over a large part of southern Africa, though sometimes only in small isolated pockets. This wide distribution means that in most areas, two to ten species are sympatric. Superficially, these sympatric species seem to be highly competitive with one another. A major function of this study is, therefore, the investigation of this apparent interspecific competition as regards the behaviour and biology of the different species with emphasis on eight species occurring sympatrically in the Mkuzi Game Reserve, Zululand. A general section on the biology of the genus, however, precedes the section investigating competition. An evaluation of the species, as possible species for introduction into Australia, is included at the end of the summary tables.

This preliminary study does not nearly complete the investigation of the genus *Sisyphus*. It shows the possible use for Australia of these small coprophagous insects and also the potential of study in the vast and as yet, little explored fields of behaviour, ecology and physiology in this genus and other dung beetle genera.

2 TAXONOMY

Preliminary biological investigations into the species of the genus *Sisyphus* in southern Africa, revealed that there were several more valid species than mentioned in recent reviews of the genus (Haaf, 1955; Ferreira, 1972). For the selection of potential species for Australia and for any detailed biological investigation to be undertaken, it was necessary to be able to isolate and preferably also positively identify, the *Sisyphus* species. Their taxonomy had, therefore, to be completely revised. For this purpose the type material and original descriptions of all the species possibly occurring in southern Africa were sought. Type material of three of these species could not be traced through the 31 European and American institutes contacted. The original descriptions of all 24 species and their synonyms were examined.

The *Sisyphus* species, shown during the study, to occur in southern Africa are listed below. Species considered by me to be synonyms, are listed in brackets below the appropriate species. Decisions on the validity of species were based on the examination of the type material, where available, over 2 000 *Sisyphus* specimens in the Unit's collection and biological observations on most of the species. The type material and specimens of the Unit's collection examined, are listed at the end of this section. In addition to this material, several *Sisyphus* specimens from other institutes were examined which included species not found in southern Africa. The reasons and some evidence for the decisions on the species listed, is provided in the discussion following the list. The major morphological differences, as further evidence of the validity of the species, are in the key to the southern African *Sisyphus* species, presented in this section. All figures relating to the taxonomy of *Sisyphus* are together at the end of the key. The major morphological differences, together with further morphological characters, including sexual differences, colour and size ranges, are summarized in the first of the summary tables (table 8.1).

The genus *Sisyphus* was divided into two subgenera by Müller (1942) with the erection of the subgenus *Neosisyphus*. The two subgenera, *Sisyphus* and *Neosisyphus* have been found to be morphologically and biologically valid taxa and useful in this study. The species listed, therefore, have been separated accordingly. Where there is still uncertainty concerning the identity of a species, the species involved is included in a species group. The species within one group have close morphological and biological affinities.

SUBGENUS *SISYPHUS*

S. muricatus (Olivier 1789)
✓*S. fasciculatus* Boheman 1857
✓*S. alveatus* Boucomont 1935
✓*S. impressipennis* van Lansberge 1886
    (*transvaalensis* Péringuey 1908 syn. nov.)
    (*callosipes* Arrow 1909)

S. SEMINULUM GERSTAECKER SPECIES GROUP

S. seminulum Gerstaecker 1871

(*nanniscus* Péringuey 1902)

✓*S.* species *X* (unidentified)

✓*S.* species *Y* (unidentified)

S. COSTATUS (THUNBERG) SPECIES GROUP

✓*S. costatus* (Thunberg 1818)

(*crispatus* Gory 1833 syn. nov.)

(*gazanus* Arrow 1909 syn. nov.)

✓*S. sordidus* Boheman 1857

(*natalensis* Balthasar 1968 syn. nov)

S. caffer Boheman 1857

✓*S. ?goryi* von Harold 1859

SUBGENUS *NEOSISYPHUS*

S. tibialis Raffray 1877

✓*S. mirabilis* Arrow 1927

S. kuehni Haaf 1955

S. quadricollis Gory 1833

✓*S. fortuitus* Péringuey 1902

✓*S. spinipes* (Thunberg 1818)

(*hessii* Gory 1833)

(*atratus* Klug 1855)

(*appendiculatus* Boheman 1857)

✓*S. infuscatus* Klug 1855

(*bornemisszai* Ferreira 1972)

S. rubrus Paschalidis 1974

S. macrorubrus Paschalidis 1974

S. BARBAROSSA WIEDEMAN SPECIES GROUP

S. barbarossa Wiedeman 1825

(*rugosus* Gory 1833 syn. nov.)

S. calcaratus Klug 1855

(*rubripes* Boheman 1857 syn. nov.)

✓*S. confrater* Kolbe 1914

S. species *A* (new species, unnamed)

The two subgenera can be separated best by the characters given in the key (first couplet). In addition, species of the subgenus *Sisyphus* appear more "hairy" than those of *Neosisyphus*. This character has not been used in keying out the two subgenera as it is not possible to define, although it is the most striking difference between them. The sexual differences between the two species also vary. In *Neosisyphus* the hind trochanter in the male is almost always projected into a spine (fig. 10) often very long; the hind trochanter of the female is usually never projected (fig. 8) or only to a very short spine. In *Sisyphus* the trochanter is never extended into a spine in the male or female (figs 5 and 7) with the possible exception of a west African species *S. angulicollis* Felsche which was not examined. In the males of *Sisyphus* the ventral edge of the hind tibia has a row of "tubercles" (fig. 7) in most species, while in the female this edge is serrated (fig. 5).

2.1 DISCUSSION ON THE STATUS OF THE SPECIES.

SUBGENUS *SISYPHUS*

S. muricatus (Olivier,) figs 11 and 54.

Olivier, 1789 : 188; Gory, 1833 : 7-8; Péringuey, 1902 : 105-6; Arrow, 1927 : 458; Haaf, 1955 : 367-8; Ferreira 1972 : 801.

There has been no previous confusion over the validity and identity of this distinctive species which has only been collected in South Africa. The type has been examined.

S. *fasciculatus* Boheman, figs 12 and 55.

Boheman, 1857 : 192; Péringuey, 1902 : 106;
Haaf, 1955 : 367; Ferreira, 1972 : 799.

There has been no previous confusion over the validity and identity of this distinct species which has also only been found in South Africa. The type collected in "Caffraria" (Cape Province) has been examined and it agrees entirely with the original description.

S. alveatus Boucomont, fig. 56.

Boucomont, 1935 : 279-280; Haaf, 1955 : 361;
Ferreira, 1972 : 792.

S. alveatus was described by Boucomont from Kenya in 1935. Haaf (1955) gives its distribution as being: the Comoro Islands, former Spanish Guinea and Ethiopia. Ferreira (1972) agrees with the distribution given by Haaf. Several specimens, identical with the type of *alveatus* have, however, been collected by the Unit in the Transvaal and Rhodesia. Several more specimens, previously unrecognized as *alveatus* were found in the Transvaal Museum, Pretoria. These specimens were collected in the Transvaal and Mozambique. This is the first time, therefore, that *alveatus* has been recorded as occurring in southern Africa.

S. impressipennis van Lansberge, figs 14, 15 and 57.

S. impressipennis van Lansberge, 1886 : 73; Arrow, 1927 : 462; Haaf, 1955 : 362-364.

S. transvaalensis Péringuey, 1908 : 557-8; Arrow, 1927 : 462; Haaf, 1955 : 364-5; Ferreira, 1972 : 807-810. Syn. nov.

S. callosipes Arrow, 1909 : 517-8; 1927 : 462; Haaf, 1955 : 365.

In 1886 van Lansberge described *impressipennis* from Angola. One male and three female syntypes have been examined. The male was designated as lectotype since it agrees completely with the original description. Two of the females seem to be of another unknown species as they differ consistently in several characters from the male lectotype, and from over 200 specimens of *impressipennis* in the Unit's Collection. In 1908 Péringuey described *transvaalensis* from the northern Transvaal (Soutpansberg). The male holotype of *transvaalensis* has been examined and it is identical to the type of *impressipennis*, so *transvaalensis* is a synonym of that species. Arrow described *callosipes* in 1909 from Nyassaland (Malawi) and Mashonaland (Rhodesia). One male and one female syntype have been examined. They agree with Arrow's description but are also identical to *impressipennis*. *S. callosipes* is therefore also a synonym of this species.

Haaf (1955) synonymized *impressipennis* with *crispatus* Gory. *S. transvaalensis* was therefore considered the valid species. Ferreira (1972) also accepted *transvaalensis* as the valid species. *S. impressipennis*, however, as seen from lectotype and description of *impressipennis* and the description and figure of *crispatus* is a different species, having characteristic projections on the hind femora in males and females (figs 14 and 15) which are entirely lacking in *crispatus*.

S. SEMINULUM GERSTAECKER SPECIES GROUP.

This species group is characterized by the cleft between the two anterior clypeal spines (fig. 18) and the scattered hair pattern on the pygidium (fig. 17).

Haaf (1955) grouped the species supposedly having these characteristics as follows:

(1) *costatus* (Thunberg 1818) with the synonyms:
rugosus Roth 1851
seminulum Gerstaecker 1871
latus Boucomont 1928

(2) *ocellatus* Reiche 1847 with its supposed smaller subspecies,
nanniscus Péringuey 1902.

Ferreira (1967 and 1972) followed Haaf's decisions.

Examination of the type of *rugosus* Roth from Abyssinia and the type of *latus* Boucomont from Cameroons, revealed that they are different species and that specimens of neither species are known from southern Africa. *S. rugosus* Roth belongs to the *costatus* species group and since the name *rugosus* was used for the species *Sisyphus rugosus* by Gory in 1833, its use for Roth's species was not permissible. Arrow (1909) also stated that *rugosus* Roth was a preoccupied name. However, because *latus* and *rugosus* Roth are not known to occur in southern Africa, they will not be considered further in this study.

S. costatus does not fit into the *seminulum* species group but is typical of another group of species in southern Africa, in which there is a broad, flat area between anterior clypeal spines (fig. 19) and the hairs on the pygidium are in a trident-shaped pattern (fig. 16). *S. costatus* will be discussed within this group. *S. costatus* is not the same species as *rugosus*, *seminulum* or *latus* as revealed from the examination of the types of all four species. All four are distinct species.

S. seminulum Gerstaecker figs 3, 17, 18 and 58.

S. seminulum Gerstaecker, 1871 : 49, 1873 : 127; Arrow 1927 : 465; Janssens, 1938 : 29 ; Haaf, 1955 : 355-6; Ferreira, 1972 : 796.

nanniscus Péringuey, 1902 : 107-8;

ocellatus subspecies *nanniscus* Péringuey in Arrow, 1909 : 518-9; Haaf, 1955 : 357-8; Ferreira, 1967 : 75; 1972 : 806.

S. seminulum was described from a single female type specimen collected in Zanzibar. This type has been examined and it has the clypeus and pygidium hair pattern (figs 18 and 17) which characterizes its species group. The type is identical to over 200 specimens in the Unit's collection which came from Kenya, Rhodesia, Mozambique and South Africa. *S. seminulum* is therefore a valid species, occurring in southern Africa.

In 1902 Péringuey described *nanniscus* from Durban. The type of *nanniscus* has been examined and is identical to that of *seminulum*. The descriptions of the two supposed species also agree. *S. nanniscus* is, therefore, a synonym of *seminulum*. Haaf (1955) considered *nanniscus* to be a small subspecies of *ocellatus* Reiche 1847. He mentions that Arrow (1927) and Janssens (1938) considered *nanniscus* to be a synonym of *seminulum* but rejects this decision. Ferreira (1967 and 1972) supports Haaf. I have been unable to find the type of *ocellatus* but have seen the original description and figure. At hand, however, are two specimens from Nyassa (Mozambique) and Abyssinia (Ethiopia), identified by Haaf in 1954 as *ocellatus*. One of these was also determined as *ocellatus*, by Arrow. These two specimens, however seem to be of different species but neither could be considered closely related to *seminulum (nanniscus)*. They are all three different species. Reiche's figure of *ocellatus* shows denuded spots on the pronotum. In the two specimens identified by Haaf as *ocellatus*, these spots are obvious but in *seminulum (nanniscus)* they are hardly descernible. Therefore, while one of the two supposed specimens of *ocellatus* is probably that species, it is highly unlikely that *seminulum* is a subspecies of *ocellatus* but until the type of *ocellatus* is examined, I cannot be certain.

S. species *X* (Unidentified), figs 23 and 59.
S. species *Y* (Unidentified), figs 24 and 60.

These two species have the denuded spots on the prothorax, mentioned by Arrow (1909) as being characteristic of *ocellatus*. One of these two species could be *ocellatus* and the other would then be a new species. Both species occur in southern Africa. *S.* species *X* seems identical with the specimen at hand determined by both Haaf and Arrow as *ocellatus.* If species *X,* or species *Y,* is *ocellatus* then this would be a new locality record for *ocellatus* as Haaf (1955) gives its distribution as not extending further south than East Africa.

S. COSTATUS (THUNBERG) SPECIES GROUP

This group is characterized by the broad, shallow space between the anterior pair of clypeal spines (fig. 19) and the trident-shaped pattern of hairs on the pygidium (fig. 16). *S. costatus* was described in 1818 by Thunberg. The second species of this group to be described was *S. crispatus* Gory, in 1833. There has been much argument about the status of *crispatus* and the species which should be synonomized with it. (Péringuey, 1902; Arrow, 1909, 1927; Haaf 1955; Ferreira, 1967 and 1972).

Haaf (1955) synonymized five species with *crispatus:*

sordidus Boheman 1857
caffer Boheman 1857
goryi von Harold 1859
pygmaeus Klug 1862
impressipennis van Lansberge 1886.

Ferreira (1972) in addition to these synonyms, considers *S. gazanus* Arrow 1909 to be very close to *crispatus.* The type of *crispatus,* said by Gory (1833) to be in the collection of Chevrolat, has not been seen since 1900. In 1927 Arrow wrote "I consider *S. crispatus* unidentified, pending the discovery of Chevrolat's specimen." This is still the situation. Gory's description and figure of *crispatus* are not clear enough to identify this species positively. However, in the Hope Collection, Oxford, where the rest of Gory's *Sisyphus* specimens are kept, are four specimens over a label, probably written by Gory, which reads "*Sisyphus crispatus*, Dej. Cap. B. Sp." In his paper Gory (1833) refers to *crispatus* as *crispatus* Dejean and gives its locality as the Cape of Good Hope = Cap. B. Sp. These Oxford specimens were, therefore, probably seen by Gory but whether they were part of his original material described, is doubtful. These specimens have been examined and are identical to *costatus*. This identification agrees with Gory's figure of *crispatus* since tufts of hairs around the elytra (fig. 21), characteristic of all the species in the *costatus* group except *costatus* itself, are not present. Three more specimens labelled "*crispus* Dej. C.B.Sp." are in a private collection in Italy, near Turin. Péringuey (1902) said he examined the type of *crispatus* from Genova, which is very near the location of the three specimens. At present these specimens are being examined in Italy for me by Dr. Mario Zunino of the University of Turin. When his comments are received, concerning the specimens of *crispatus*, a definite decision can probably be made on its validity.

During this study, for the sake of clarity and easy reference, the names of the supposed synonyms of *crispatus* i.e. *sordidus*, *caffer* and *goryi*, found to be different species, will be used as if they are a valid species and *crispatus* will be synonymized with *costatus*. Although unlikely, one of these species could be a synonym of *crispatus*.

S. impressipennis does not belong to this species group, as already discussed, but is itself a valid species with which *transvaalensis* and *callosipes* have been synonymized.

Although Klug designated a type for *pygmaeus*, in his description of this species (1862) he states that he is only providing the new name, *pygmaeus*, for the species described by Gory (1833) as *hirtus* (a name used by Wiedeman in 1825 for an Indian *Sisyphus* species). However, *hirtus* Gory had already been renamed by von Harold in 1859 as *goryi*, so the name *pygmaeus* and the type designated as such by Klug, are entirely invalid and will not be considered further.

S. costatus (Thunberg), figs 13 and 61.

S. costatus (Thunberg), 1818 : 412; Arrow, 1927 : 458; Haaf, 1955 : 355-6; Ferreira, 1972 : 794, 795.

S. crispatus Gory, 1833 : 13. Syn. nov.

S. gazanus Arrow, 1909 : 518, 1927 : 461-2; Haaf, 1955 : 361-2; Ferreira, 1972 : 799. Syn. nov.

One specimen of *costatus*, determined in Thunberg's own hand, has been examined. The head of this specimen of *costatus* is missing but examination of the rest of the body leaves no doubt that this specimen is the same as those collected by the Unit in the Transvaal and Natal. One syntype of *gazanus* and the original description have been examined. *S. gazanus* is the same species as *costatus* and therefore is a synonym of *costatus*. Both supposed species have the trident-shaped hair pattern on the pygidium (fig. 16), no tufts of hair visible around the edges of the elytra and have many long hairs, tapering to fine points, on the prothoracic episternum.

S. costatus was considered by Haaf (1955) to have a cleft between the two anterior spines of the clypeus, as in *seminulum* (fig. 18). It is obvious from his supposed re-description of *costatus* that he had misidentified the species. Ferreira (1972) also misidentified this species.

S. sordidus Boheman, figs 5, 6, 7, 19, 21 and 62.

S. sordidus Boheman, 1857 : 194; Péringuey, 1902 : 106-7; Haaf, 1955 : 362-4; Ferreira, 1972 : 82.

S. natalensis Balthasar, 1968 : 954. Syn. nov.

One male specimen determined as *sordidus* in Boheman's own hand was examined. No type material labelled as such is known to exist for this species. This specimen examined, agrees with Boheman's description of *sordidus* and is identical to specimens of a distinct species collected by the Unit, mostly from low-lying areas in southern Africa. The male holotype of *natalensis* has been examined and it is identical to *sordidus*.

S. caffer Boheman, figs 16, 20, 22 and 63.

Boheman, 1857 : 195; Péringuey, 1902 : 106-7; Haaf, 1955 : 362-4; Ferreira, 1972 : 82.

One male specimen labelled as type and determined as *caffer* in Boheman's hand has been examined. This is a different species to *sordidus*, most obvious from the different shapes of the heads (figs 19 and 20) and the aedeagi (figs 62 and 63). Specimens of *caffer* have been collected mostly from the high lying areas of the Cape, Natal, Orange Free State and Transvaal.

S. goryi von Harold, fig. 64. (*S. ?goryi* Harold, fig. 65).

S. goryi von Harold, 1859 : 224; Péringuey, 1902 : 106-7; Arrow, 1927 : 460; Haaf, 1955 : 362-3.

S. hirtus Gory, 1833 : 14; Arrow, 1909 : 518-9; 1927 : 460; Haaf, 1955 : 362-3.

S. pygmaeus Klug, 1862 : 219; Haaf 1955 : 362-3.

When Gory published the species name *hirtus* in 1833 it had already been used by Wiedeman in 1825 for an Indian *Sisyphus* species. Von Harold, therefore, re-named *hirtus* Gory as *goryi* in 1859. Péringuey synonymized *caffer* and *sordidus* with *goryi* but the type of *goryi* has been examined and compared to Boheman's specimen of *sordidus* and type of *caffer*. These are three different species, as seen from their aedeagi (figs 62, 63 and 64) and other morphological characters, given in the key and summary tables. Haaf (1955) and Ferreira (1972) also incorrectly stated that these three species are all synonyms of *crispatus*.

S. goryi was originally described from Senegal (as *hirtus*) by Gory, in 1833. A specimen of von Harold, inadmissably labelled as the "type" of *goryi* came from the Cape. Examination of specimens similar to *goryi* collected from Nigeria, Kenya, Mozambique, Rhodesia and South Africa show a wide range of body length (4,5 to 8 mm). There are small morphological variations among these specimens (over 300 specimens examined) including variations in the aedeagi. None of these differences are large or consistent enough to separate these specimens into different species without first doing cross breeding experiments and biological studies. The specimens collected in southern Africa differ slightly from those collected in Kenya and Nigeria and also from the type of *goryi* but seem to be the same as von Harold's specimen. It is not certain however, that the southern African specimens are indeed of a single species. In this study, the southern African specimens are regarded as belonging to the species *?goryi*.

SUBGENUS *NEOSISYPHUS*

S. tibialis Raffray, figs 26, 41 and 66.

Raffray, 1877 : 312; Haaf, 1955 : 379-380;
Ferreira, 1972 : 841-4.

One specimen of this distinct species was collected by G.F. Bornemissza at Bosbokrand, in the eastern Transvaal. This single specimen leads to the tentative claim that this species occurs in southern Africa. Haaf (1955) gave the distribution of *tibialis* as being Abyssinia (Ethiopia) and East Africa. Ferreira (1972) added Kenya to these areas. Several specimens of *tibialis* from Kenya have been examined. The type has not been seen and the specimens mentioned here were determined from the unmistakable original description and figures.

S. mirabilis Arrow, figs 25, 40 and 67.

S. mirabilis Arrow, 1927 : 458-9; Haaf, 1955 : 380; Ferreira, 1972 : 825.

S. spinipes Gory, 1833 : 8; Arrow, 1927 : 458-9.

The new name *mirabilis* was provided by Arrow in 1927 for the species *spinipes* of Gory, a name pre-occupied in 1818 by *Sisyphus spinipes* (Thunberg). No further argument over the validity and identity of this distinctive species exists in the literature. The type and original description have been seen. *S. mirabilis* is only known from South Africa and Mozambique.

S. kuehni Haaf, figs 52, 53 and 68.

Haaf, 1955 : 373-4; Ferreira, 1972 : 822-5.

A male paratype and the original description of this recently described, rather rare species have been examined. Several more specimens listed at the end of this section have also been examined. The distribution of *kuehni* seems restricted to South Africa.

S. quadricollis Gory, figs 35 and 69.

Gory, 1833 : 9; Haaf, 1955 : 373.

The male holotype and original description of this rare species have been examined. Only a single female specimen of *quadricollis* has been collected during the Unit's field trips. This species also, is only known to occur in South Africa (Cape Province).

S. fortuitus Péringuey, figs 33, 43 and 70. (*S. near fortuitus* Péringuey, figs 44 and 71).

Péringuey, 1902 : 103; Haaf, 1955 : 371-2;
Ferreira, 1972 : 85, 820.

Péringuey described *fortuitus* from Natal (Durban). According to Haaf (1955) the type of *fortuitus* designated presumably by Péringuey, did not bear the same locality

(Durban) and morphological characters mentioned by Péringuey. This supposed type was, Haaf maintains, actually a specimen of *spinipes* and its aedeagus did not correspond to the aedeagus drawn of *fortuitus*, by Péringuey. Haaf, therefore, in 1954 designated a lectotype of *fortuitus* with the locality of Durban, from Péringuey's material. This lectotype has been examined and it agrees with Péringuey's description and figure of the aedeagus. Péringuey's supposed original type has also been examined. It is a specimen of *infuscatus* determined in Péringueys hand as *fortuitus* but the printed, red type label on the pin is not of the kind used by Péringuey. Several other type specimens of Péringuey from other genera, were examined and these all had the word "type" written on the determination label in Péringueys hand. There was no printed, red type label. There is no evidence, therefore, that Péringuey designated the *infuscatus* specimen as the type of *fortuitus*. No other specimens of *fortuitus* determined by Péringuey, could be found. Therefore, since the specimen designated by Haaf as lectotype of *fortuitus*, agrees with the description, figure and locality data given by Péringuey for *fortuitus*, Haaf's lectotype must be considered as the type specimen of this species.

Haaf (1955) gives *fortuitus* a distribution of Natal, French Guinea and Cameroons. Ferreira adds the Cape Province to this distribution. The figures drawn by Haaf of the middle legs of *fortuitus*, are from a specimen collected in French Guinea. These show a prominant spine distally, on the ventral ridge of the femur. In 63 southern African specimens of *fortuitus* examined this spine was not as prominent nor of the same shape (fig. 43). However, Bornemissza collected several specimens of a species which is very similar to *fortuitus*, in Nigeria but it has the femoral spine (fig. 44) as in Haaf's figures and is not like that of the southern African *fortuitus* specimens. The aedeagi (figs 70 and 71) are also different. It is probable, therefore, that *fortuitus* (*sensu* Haaf) is actually two species. *S. fortuitus* (*sensu* Péringuey) is probably a southern African species. This could be confirmed by the examination of material occurring outside southern Africa which was determined by Haaf as *fortuitus* and also by attempted crossbreeding of live, southern and west African material.

S. spinipes (Thunberg), figs 4, 32, 39, 50 and 72.

S. spinipes (Thunberg), 1818 : 411; Péringuey, 1902 : 103-4 (as *S. quadricollis* Gory); Arrow, 1927 : 458-9; Haaf, 1955 : 368-370; Ferreira, 1972 : 837, 839, 841.

S. hessii Gory, 1833 : 11; Péringuey, 1902 : 103; Haaf, 1955 : 368.

S. atratus Klug, 1855 : 651; Arrow, 1927 : 459; Haaf, 1955 : 368-370.

S. appendiculatus Boheman, 1857 : 190; Péringuey, 1902 : 103; Haaf, 1955 : 368-9.

The holotype of *hessii;* holotype and one paratype of *atratus;* type of *appendiculatus* (determined in Boheman's own hand) and a male specimen of *spinipes* determined in Thunberg's hand, have been examined. They are all of the same species. *S. hessii, atratus* and *appendiculatus* are all, therefore, synonyms of *spinipes*. Péringuey (1902) first synonymized *hessii* and *appendiculatus* with *spinipes*, which he incorrectly identified as *quadricollis*. Arrow (1927) synonomized *atratus* with *spinipes*. Haaf (1955) and Ferreira (1972) came to these same conclusions. *S. trochantericus* Fairmaire 1891 was considered a synonym of *spinipes* by Haaf (1955). The type and original description of *trochantericus* have been examined and it is a valid species, not occurring in southern Africa.

S. infuscatus Klug, figs 42, 51 and 73.

S. infuscatus Klug, 1855 : 651; Péringuey, 1902 : 104 (as *S. atratus* Klug); Arrow, 1927 : 459; Haaf, 1955 : 368-370; Ferreira, 1967 : 84; 1972 : 814-818.

S. bornemisszai Ferreira, 1972 : 85, fig. 279.

Arrow (1927) synonymized *infuscatus* with *spinipes*. Haaf (1955) and Ferreira (1967) did the same. During the initial part of this study specimens of *infuscatus*, not known at that time to be of this species, but found to differ from *spinipes*, were given to Ferreira in March 1972 for identification. From these and further specimens, Ferreira (1972) named a new species *bornemisszai*. However, just before the description of *bornemisszai* went into press, Ferreira received the type of *infuscatus*. This was identical to *bornemisszai*. The description and discussion of the species *bornemisszai* was, therefore, changed to put *infuscatus* as the valid species name. The figure (279) labelled *bornemisszai*, was, however, published as such and so the name *bornemisszai* exists as a synonym of *infuscatus*. I have examined the holotype and paratype of *infuscatus* and they are of a valid species, not synonymous with *spinipes*, as seen from the aedeagi (figs 72 and 73) and other characters. *S. infuscatus* also occurs in southern Africa.

S. rubrus Paschalidis, figs 31, 38, 49 and 74.

S. rubrus Paschalidis, 1974 : 299-301.
S. rubripes Boheman *sensu* Péringuey, 1902:101-2.
S. rubripes Péringuey in Arrow 1927 : 461, 464;
Haaf, 1955 : 370-1; Ferreira, 1972 : 829, 831, 834.

Péringuey (1902) first described this species which he misidentified as *rubripes* Boheman 1857. Haaf (1955) realized that the species described by Péringuey was a new species but Haaf referred to the new species as "*rubripes* Péringuey." Ferreira (1972) also used this name which was invalid since the species name, *rubripes*, had been used for a *Sisyphus* species by Boheman in 1857. Paschalidis (1974) therefore, published a discussion of this new species and gave it the species name of *rubrus*. A reprint of this paper is bound in with this thesis.

S. macrorubrus Paschalidis, fig. 75.

Paschalidis, 1974 : 301-3.

This species is very closely related, morphologically and biologically to *rubrus* and was previously considered as being the same species as *rubrus*. Paschalidis (1974) separated *rubrus* and *macrorubrus* on morphological, distributional and biological grounds. Morphologically the two species are very similar but their size ranges, although overlapping are different and their aedeagi (figs 74 and 75) are very different. *S. rubrus* and *macrorubrus* occur sympatrically in a few areas but while *rubrus* occurs almost throughout South Africa, Rhodesia, Mozambique and also in Kenya, *macrorubrus* is only known from the Orange Free State.

Paschalidis (1974) carried out crossbreeding experiments with the two species which showed conclusively that both *rubrus* and *macrorubrus* were valid species since they could not interbreed.

S. BARBAROSSA WIEDEMAN SPECIES GROUP

This species group is characterized by its dark brown to black colour and the absence of any cuticular projections on the ventral ridge of the middle femur or tibia (figs 36 and 37). There are six known species in this group. Two of these species, *armatus* Gory 1833 and an unidentified species collected by Dr. Bornemissza in Nigeria, do not occur in southern Africa. The males of the six species are relatively easy to identify but the females are very similar and difficult to separate.

S. barbarossa Wiedeman, figs 27, 30, 46 and 76.

S. barbarossa Wiedeman, 1825 : 23; Arrow, 1927 : 458; Haaf, 1955 : 368-9.

rugosus Gory, 1833 : 12; Péringuey, 1902 : 104-5 (as *spinipes* (Thunberg)); Arrow, 1927 : 457, 460; Haaf, 1955 : 377-9; Ferreira, 1967 : 81-2; 1927 : 835, 837. Syn. nov.

Arrow (1927) and Haaf (1955) considered *barbarossa* as a synonym of *spinipes*. The female type of *barbarossa* and male type of *rugosus* have been examined. They are of the same species but not the same as *spinipes*. Therefore *barbarossa* is a valid species and *rugosus* is a synonym of *barbarossa*.

S. calcaratus Klug, figs 8, 9, 10, 28, 37 and 78.

S. calcaratus Klug, 1855 : 651; 1862 : 219; Péringuey, 1902 : 103-4; Arrow, 1927 : 459; Haaf 1955 : 377-9; Ferreira, 1967 : 81; 1972 : 86.

S. rubripes Boheman, 1857 : 193; Haaf, 1955 : 376-7; Ferreira, 1967 : 77; 1972 : 84.

S. calcaratus was synonymized with *spinipes* by Péringuey in 1902. Arrow (1927), however, said that *calcaratus* was a valid species. Haaf (1955) and Ferreira (1967 and 1972) have synonymized *calcaratus* with *barbarossa* (which they called *rugosus*). I regard *calcaratus* as a valid species, entirely different to *spinipes* but close morphologically and behaviourally to *barbarossa*. *S. barbarossa* and *calcaratus* differ most in their body lengths (*calcaratus* 5,5 - 8 mm : *barbarossa* 7,5 - 10 mm) and shape of aedeagi (figs 76 and 78). Haaf gave the size range for *barbarossa* as 6,5 to 10 mm, thus he probably included *calcaratus* specimens in his measurements and redescription. The two species also have different geographical distributions, as illustrated in section 3.

Cross breeding tests were made to confirm the species status of *calcaratus* and *barbarossa*. Six males and seven females of each species were individually paired in the following combinations:

3 pairs of : *barbarossa* male + *calcaratus* female
3 pairs of : *calcaratus* male + *barbarossa* female
3 pairs of : *barbarossa* male + *barbarossa* female
3 pairs of : *calcaratus* male + *calcaratus* female

and one female of each species was isolated.

All beetles used were between two weeks and one month old and females had already been mated, so they could lay several fertile eggs without being mated again. The pairs were observed for the number of fertile eggs produced, i.e. those which hatched or had developing embryos. Most of the *calcaratus* females died before they stopped laying fertile eggs because they had reached the end of their natural adult lives, but the results for *barbarossa*, which lives considerably longer, are recorded in figure 1. After 75 days the females with *calcaratus* males stopped laying fertile eggs after producing an average of ten each. The other three females with *barbarossa* males continued laying fertile eggs, an average total of 25, until they died, between 114 and 140 days after the investigation started. The first female which was paired with the *calcaratus* male, died after 114 days. Therefore they had not stopped laying fertile eggs after 75 days because they had reached the end of their natural adult lives. The control female also stopped

FIG 1

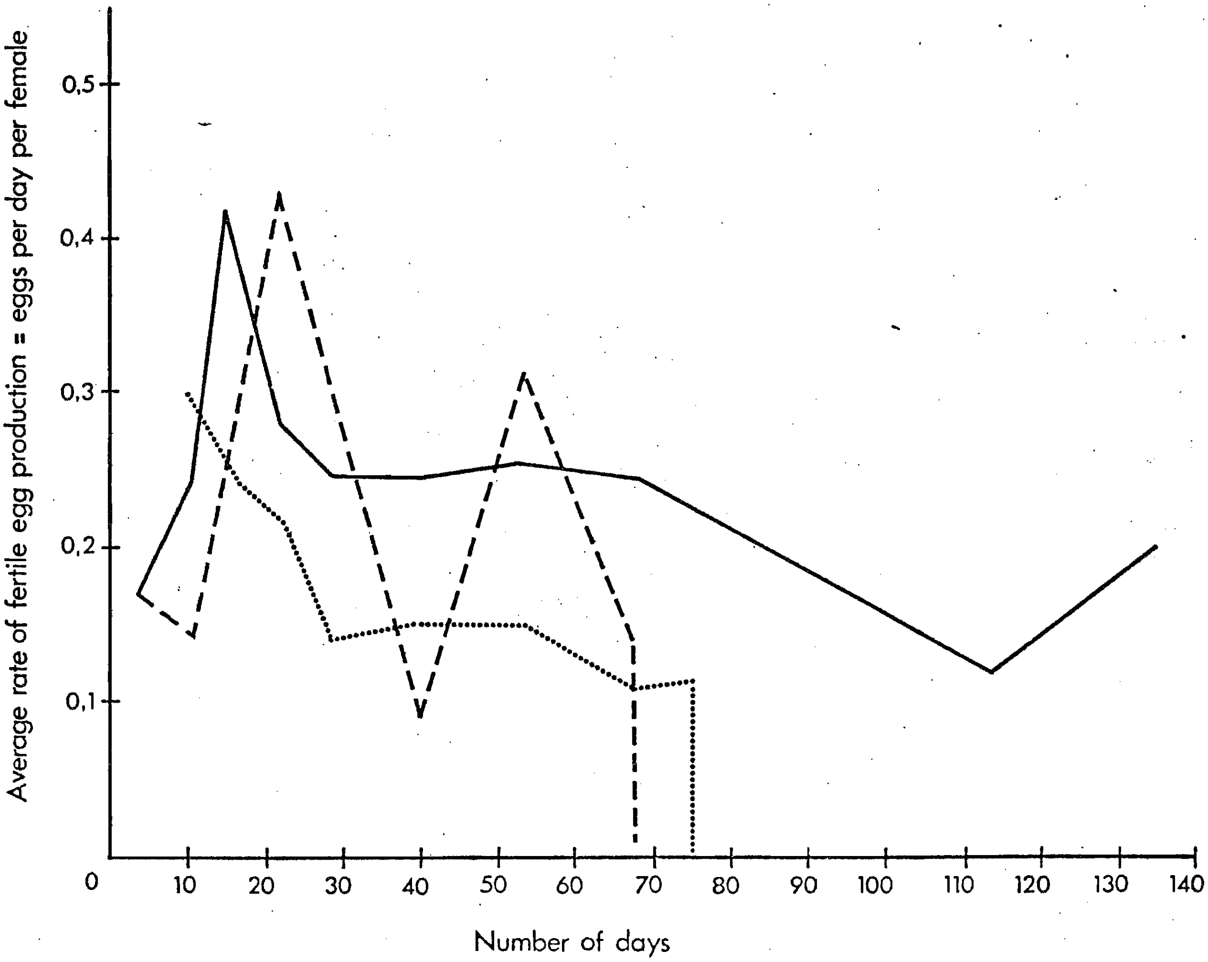
The fertile egg production when *S. barbarossa* Wiedeman females are paired with males of the same species or those of *S. calcaratus* Klug.

<u>KEY</u>

Solid line = *barbarossa* male and female (three pairs)

broken line = *barbarossa* female and *calcaratus* male (three pairs)

dotted line = control *barbarossa* female with no male.


Average rate of fertile egg production = eggs per day per female
0,5
0,4
0,3
0,2
0,1
0
10
20
30
40
50
60
70
80
90
100
110
120
130
140
Number of days

1

laying fertile eggs after 70 days, having laid 16 fertile eggs. This indicates that the *calcaratus* males were unable to fertilize the eggs of the *barbarossa* females, being of a different species. Size differences were not responsible for the failure to mate, since individuals closest to the overlap of the size ranges of each species were used and the body length differences were within the differences existing in the normal range for the species.

Biologically these two species differ mostly in that *calcaratus* has three to four adult generations per summer season and *barbarossa* has only one to two generations. This is because all *barbarossa* eggs laid from the middle of December will only produce adults the following October. They overwinter as larvae. In *calcaratus* eggs laid until the end of February can produce adults within the same season. The adults of *barbarossa* are relatively long lived (about seven months) while those of *calcaratus* live for about four months.

From the morphological and biological data and the distributional data in the next section, there can be little doubt that *calcaratus* is a different species to *barbarossa*.

After examination of the female type, *rubripes* Boheman was found to be identical to *calcaratus*. *S. rubripes* was synonymized by Haaf (1955) with *armatus* Gory. Ferreira (1967 and 1972) supported this decision. Examination of the types of *rubripes* (female), *armatus* (male) and *calcaratus* (male) showed that *rubripes*, besides other characters, had the semi-erect, black hairs on the elytra (fig. 28) characteristic of *calcaratus* and not the curling light red-brown hairs (as in fig. 27) of *armatus*, or the other species in the *barbarossa* group. *S. rubripes* is, therefore, a synonym of *calcaratus* and not of *armatus*.

Within the species *calcaratus* there seems to be variation of several morphological characters including the shape of the aedeagus. This is especially noticeable with specimens collected in South Africa compared to those collected in Rhodesia and Mozambique, although within one series collected near Messina, Transvaal, the same variations exist. When breeding *calcaratus* through several generations in the laboratory, from material originally collected at one locality, all the females (29) produced fertile eggs. Of nine filial females from parental stock collected at various localities, including Messina and Mkuzi, only five produced fertile eggs. This suggests that there may be more than one species included, at present, under the species name *calcaratus*. More detailed experimental work and careful morphological investigation is needed before any definite conclusions can be reached since, if there is more than one species involved, they are very closely related and will be difficult to distinguish.

S. confrater Kolbe, figs 29, 36, 45 and 79.

Kolbe, 1914 : 317; Haaf, 1955 : 376-7;
Ferreira, 1967 : 77; 1972 : 84, 812-4.

The species *confrater* was previously identified as *armatus* as seen from material at hand determined by Haaf and the figures drawn by Ferreira (1972) supposedly of *armatus*. The male holotype of *armatus* from Senegal, has been compared to the male type and male paratype of *confrater* from Tanganyika (Tanzania) and they are two different species. They differ in that the projection on the ventral femoral ridge of the hind leg in the male is angular and prominent in *confrater* while the hind trochanter is relatively short (fig. 45); in *armatus* males, the femoral projection is hardly developed (fig. 48), while the hind trochanter is long (fig. 48). The aedeagi of *armatus* and *confrater* also differ (figs 79 and 80).

S. setiger Roth 1851 was also synonymized by Haaf (1955) and Ferreira (1967 and 1972) with *armatus*. The female holotype of *setiger* has been examined and it is not the same as *confrater*. *S. confrater* is therefore a valid species occurring in southern Africa.

S. species *A*.

Only one male specimen of this species has been examined. Morphologically it is very close to *rugosus*. The shape of the hind femoral projection and hind trochanter of the male are different (figs 46 and 47) as are the aedeagi (figs 76 and 77). Further specimens of this species are needed, preferably live material for cross-breeding experiments, before the validity of this species can be established beyond a doubt. It could then be more fully described and named.

2.2 KEY TO THE SPECIES IN SOUTHERN AFRICA

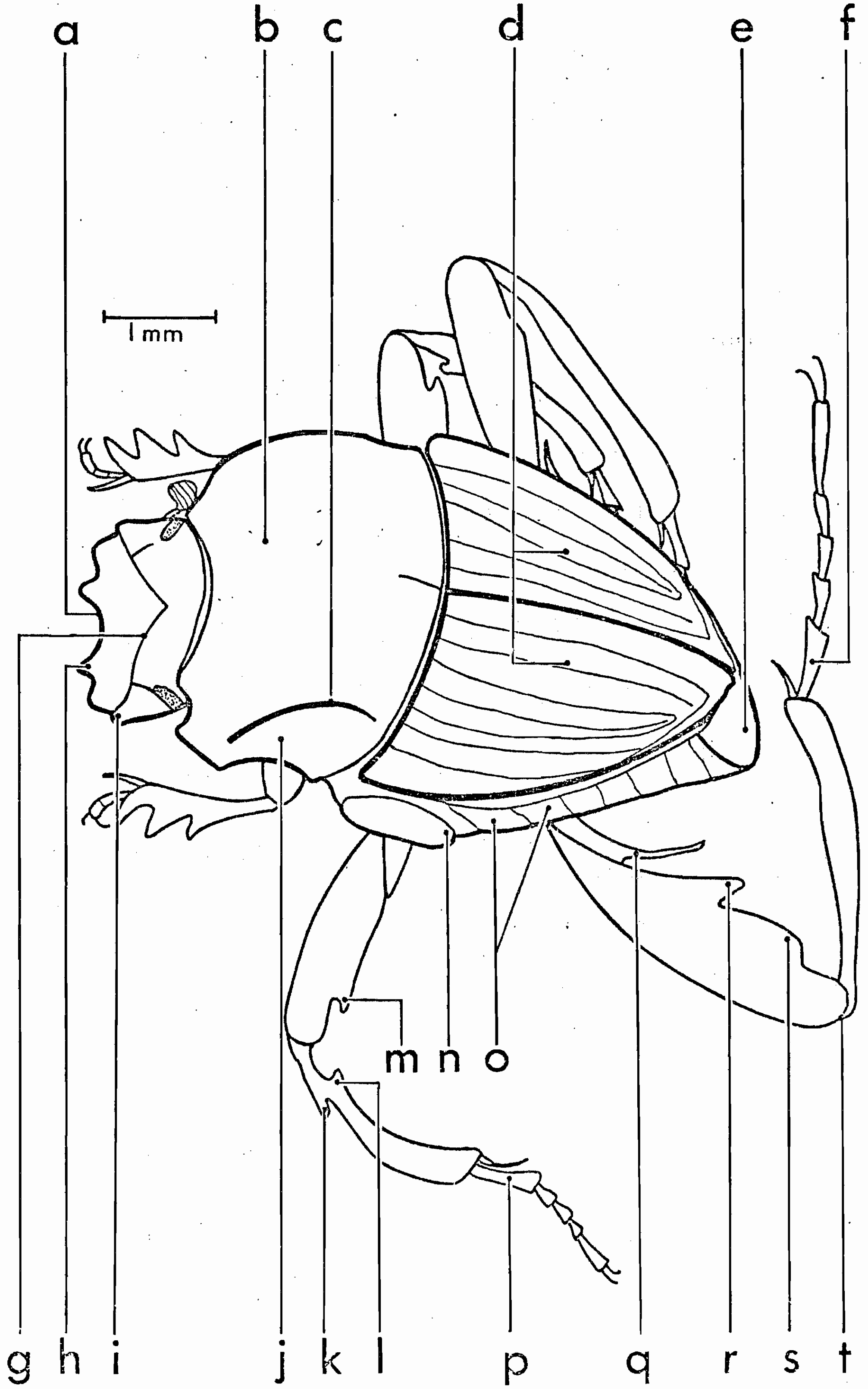
S. species *A* is the only known species not to be included in this key since only one male specimen has been examined which is not sufficient material on which to base any species characteristics. Figure 2 is of a generalized adult *Sisyphus*, which shows the positions of the key characters used. Body length measurements used in the key (and summary tables) are taken from the anterior edge of the clypeus (head deflexed) to the end of the elytra. Body length varies considerably within one species and has been used more as an indication of the size range of the species than as a definite morphological character. Where shape of the clypeus is used as a character to distinguish species it must be noted that the shape of the clypeal spines can vary with age, from abrasion and therefore other characters, when given, should be considered together, or even in preference to those regarding the shape of the clypeal spines. The number and/or locality given in brackets in the legend to the figures at the end of the key, refers to the locality and specimen number of the specimen from which the figure was drawn. Unless otherwise stated all these specimens are in the Unit's collection and are therefore, listed with their locality details at the end of this section of taxonomy.

FIG 2

Hypothetical *Sisyphus* specimen showing the location of key morphological characters. (dorso-lateral aspect).

a. Area between anterior pair of clypeal spines.
b. Pronotum.
c. Lateral prothoracic ridge.
d. Central area of elytra.
e. Pygidium.
f. First tarsal segment of hind leg.
g. Epicranial suture.
h. Anterior clypeal spine.
i. Posterior clypeal spine.
j. Prothoracic episternum.
k. Cuticular projection (or spine) proximally on dorsal ridge of middle tibia.
l. Cuticular projection (or spine) proximally on ventral ridge of middle tibia.
m. Cuticular projection (or spine) distally on ventral ridge of middle femur.
n. Coxa of middle leg.
o. Abdominal segments.
p. First tarsal segment of middle leg.
q. Trochanter of hind leg.
r. Cuticular projection (or spine) in the middle of the ventral ridge of hind femur.
s. Flat cuticular projection distally on ventral ridge of hind femur.
t. Insertion of hind tibia into hind femur.

2



1 Complete lateral prothoracic ridge present, separating pronotum from prothoracic episternum (fig. 3). "Comb" of strong setae on ventral edge of first tarsal segment of middle and hind legs, usually more pronounced on tarsus of middle leg (fig. 6) than hind leg (fig. 5) Subgenus *Sisyphus* 2

Lateral prothoracic ridge hardly developed and flattened anteriorly and posteriorly (fig. 4). No "comb" of strong setae on ventral edge of first tarsal segment of middle or hind legs. Strong setae usually present on tarsal segments but not in straight lines and not on ventral edge (figs 8 and 9). Subgenus *Neosisyphus* 12

2 Hairs on elytra grouped in distinct tufts (fig. 12) 3

Hairs on elytra distributed in longitudinal rows never forming tufts (fig. 13) 5

3 Hair on pronotum grouped in tufts .... *S. fasciculatus*

Hair on pronotum not in tufts 4

4 Pronotum extended each side of the head, forming pronounced angular projections in the male (fig 11), less pronounced in the female, Body length 8,5 - 11,5 mm .... *S. muricatus*

Pronotum with no such projections. Body length 3,5 - 5,5 mm .... *S. alveatus*

5 Femur of hind leg with anvil-shaped projection in the male (fig. 14) and a similar but evenly rounded projection in the female (fig. 15) .... *S. impressipennis*

Femur of hind leg with no such projections (figs 5 and 7) 6

6 Clypeus with cleft between anterior pair of spines (fig. 18) and hair on pygidium random (fig. 17) *S. seminulum* species group 7

Clypeus with broad, shallow area between anterior pair of spines (fig. 19) and hair on pygidium in trident-shaped pattern. (fig. 16) *S. costatus* species group 9

7 Hairs on pronotum fine and interspersed with bald patches forming a symmetrical pattern on the pronotum. Head shape fig. 23 or 24. Body length 3,5 - 8 mm 8

Hairs on pronotum not fine and form no obvious pattern. Head shape fig. 18. Body length 3 - 4,5 mm .... *S. seminulum*

8 Head shape fig. 23. Body length 6 - 8 mm. Aedeagus fig. 59 .... *S.* species *X*

Head shape fig. 24. Body length 3,5 - 5,75 mm.
Aedeagus fig. 60 .... *S.* species *Y*

9 Tufts of hairs present on the abdomen around the edges of the elytra (figs 21 and 22). Well spaced short/medium length hairs on prothoracic episternum 10

No tufts ofhairs around edges of elytra. Many long hairs on prothoracic episternum.
.... *S. costatus*

10 Sides of head rounded (fig. 19). No pair of "pockets" containing long hairs on ventral surface, – between middle coxae. Hairs on elytra, numerous tending to form bunches, are not in single file but are still in longitudinal rows. Tufts round edges of elytra of curling short, thick hairs. (fig. 21)
.... *S. sordidus*

Sides of head almost parallel (fig. 20). Pair of "pockets" containing long hairs present on ventral surface, between middle coxae. Hairs on elytra usually in single file, within longitudinal rows, not in bunches. Tufts around elytra of semi-erect long, fine hairs (fig. 22) or medium length and thickness 11

11 Hair distinct red-brown colour especially on pronotum and elytra and the tufts round elytra, which are of semi-erect, long, fine hairs (fig. 22). Aedeagus fig. 63. ...... *S. caffer*

Hair yellow, especially tufts around elytra, which are of medium length and thickness. Aedeagus fig. 65 .... *S. goryi*

12 Femur and tibia of middle leg with no cuticular spines or projection on ventral ridge (figs 36 and 37).
S. barbarossa species group 13

Tibia and/or femur of middle leg with cuticular spine or projection on ventral ridge (figs 38 and 42) 15

13 Femur of hind leg with sharply pointed spine on ventral ridge in the male (figs 10 and 46). Spine absent in the female. Hairs in centre of elytra black and erect, with only the tips curling over (fig. 28) or if hairs of light red-brown colour and curling (fig. 27), then dorsal area of head almost entirely matt and a depressed triangular or Y-shaped area devoid of hairs present, posterior to and including the epicranial suture (fig. 30) 14

Femur of hind leg with blunt, triangular spine on ventral ridge of the male (fig. 45). Spine absent in the female. Hair on elytra light red-brown and curling at ends (fig. 27) but dorsal surface of head almost entirely with glossy sheen and epicranial suture making only a V-shaped depression around which the cuticle is well pitted and usually has hairs (fig. 29) .... *S. confrater*

14 Hair in central area of elytra, light red-brown curling and well spaced (fig. 27). Usually dark brown to black beetles with elytra of lighter colour than pronotum. Body length 7,5 - 10 mm. Aedeagus fig. 76 .... *S. barbarossa*

Hair on central area of elytra usually black and erect with tip just bent over (fig. 28). Body usually entirely black, legs may be of lighter colour than pronotum and elytra. Body length 5,5 - 8,0 mm. Aedeagus fig. 78. .... *S. calcaratus*

15 Tibia of middle legs with cuticular projections on dorsal ridge and sometimes on ventral ridge (figs 40 and 41) 16

Tibia of middle legs with no projections on dorsal ridge as above. Projections on ventral ridge only or none at all (figs 38 and 42) 17

16 Entirely black species. No "boils" present on pygidium (*cf*. figs 25 and 26)....... *S. mirabilis*

Brown to light brown species. A pair of "boils" present on pygidium (fig. 26) .... *S. tibialis*

17 Elytra "cut away" at side (fig. 35) .... *S. quadricollis*

Elytra not "cut away" at side (fig. 34) 18

18 Hind femur produced distally on ventral ridge into a flat, rounded projection, which constricts before the insertion of the tibia; more obvious in the male (fig. 52) but also clearly evident in the female (fig. 53) .... *S. kuehni*

Ventral ridge of hind femur with no such projection in the male or female 19

19 Middle tibia with spine proximally on ventral ridge (figs 38 and 39). Male with blunt spine on ventral ridge of hind femur or none at all (figs 50 and 49) 20

Middle tibia without prominent spine proximally on ventral ridge; a "shelf" is formed where tibia narrows abruptly to insert into femur (fig. 42). Male has a sharp spine mid-ventrally on the hind femur (fig. 51). Female without such a spine. .... *S. infuscatus*

20 Head shape as in fig. 33; posterior pair of spines rounded. Male has no cuticular projections on ventral ridge of hind femur. Usually entirely brown to dark brown species .... *S. fortuitus*

Head shape as in figs 31 or 32, posterior pair of clypeal spines pointed. If entirely brown beetle then male with spine on hind femur (fig. 50) or if male has no such spines (fig. 49) then beetle is brown to light orange-brown in colour with lengthened hind trochanter of the male and legs of both sexes of a lighter colour than the pronotum 21

21 Proximal spine on ventral ridge of middle femur tending to point distally or at right angles to the femur (fig. 38). Brown to light orange- or yellow-brown beetle with legs of lighter colour than the pronotum. Hind femur of male and female without cuticular projection on ventral ridge (fig. 49) 22

Proximal spine on middle femur tending to point proximally (fig. 39). Usually entirely brown to dark brown species. Hind femur of male with spine on ventral ridge (fig. 50). Female has indications of a spine or nothing at all.
.... *S. spinipes*

22 Body length 7,2 - 10,2 mm. Aedeagus fig. 75.
.... *S. macrorubrus*

Body length 6,5 - 9,5 mm. Aedeagus fig. 74.
.... *S. rubrus*

2.3 FIGURES OF MORPHOLOGICAL CHARACTERS

FIGS 3 - 10

Subgeneric differences in morphology.

Fig. 3 S:*S. seminulum* Gerstaecker; head and prothorax lateral aspect (2/6). Arrow shows complete lateral, prothoracic ridge.

Fig. 4 N:*S. spinipes* Thunberg; head and prothorax. lateral aspect (656/1). Arrow shows incomplete lateral, prothoracic ridge.

Fig. 5 S:*S. sordidus* Boheman, female; left hind trochanter, femur, tibia and first two tarsal segments; inner aspect (1321/3).

a - trochanter, not elongated.
b - ventral tibial ridge serrated.
c - "comb" of setae.

Fig. 6 S:*S. sordidus* Boheman, male; first tarsal segment right middle leg; inner aspect. (1039a/1). Arrow shows "comb" of setae on ventral ridge.

Fig. 7 S:*S. sordidus* Boheman, male; right hind trochanter, femur and tibia; inner aspect (1039a/1).

a - trochanter not elongated.
b - "tubercles" on ventral ridge of tibia.

Fig. 8 N:*S. calcaratus* Klug, female; left hind trochanter, femur, tibia and first two tarsal segments; inner aspect (1321/2).

a - trochanter not extended.
b - no "comb" setae.

Fig. 9 N:*S. calcaratus* Klug, male; first tarsal segment of right middle leg; inner aspect (1321/1). Arrow shows setae not in "comb".

Fig. 10 N:*S. calcaratus* Klug, male; left hind trochanter, femur and tibia; inner aspect. (1321/1)

a - elongated trochanter.
b - sharp spine on ventral ridge of femur.

S = *Sisyphus:*

N = *Neosisyphus:*

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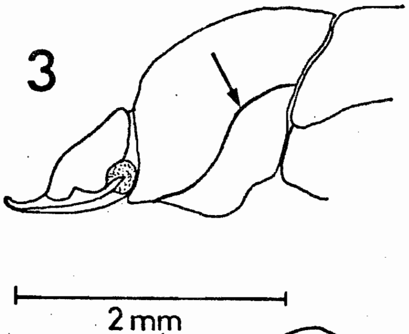

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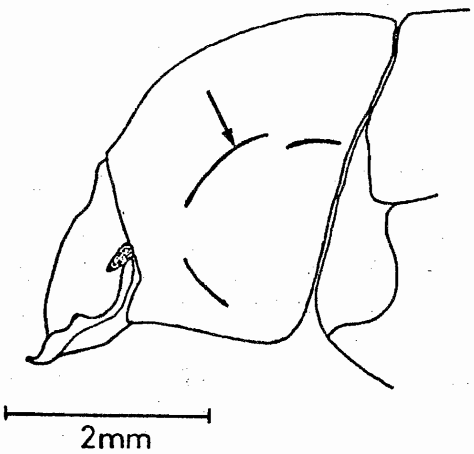

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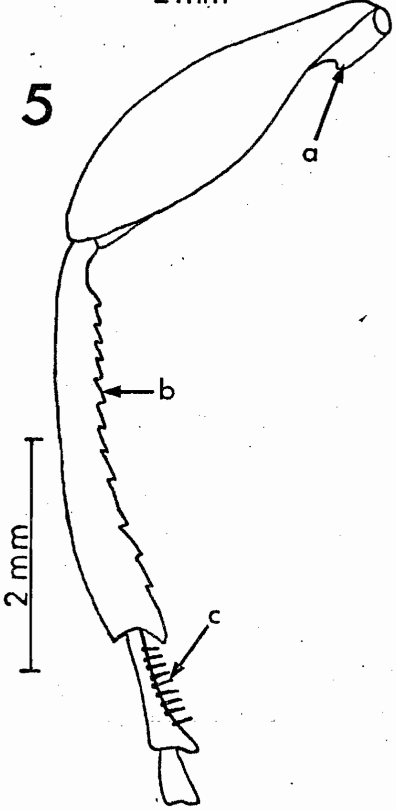

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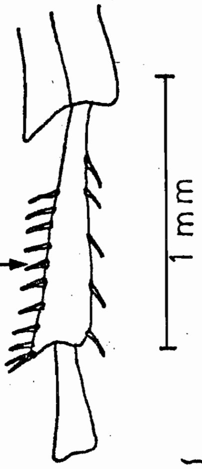

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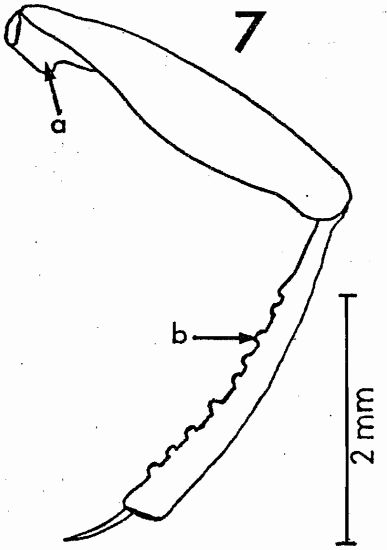

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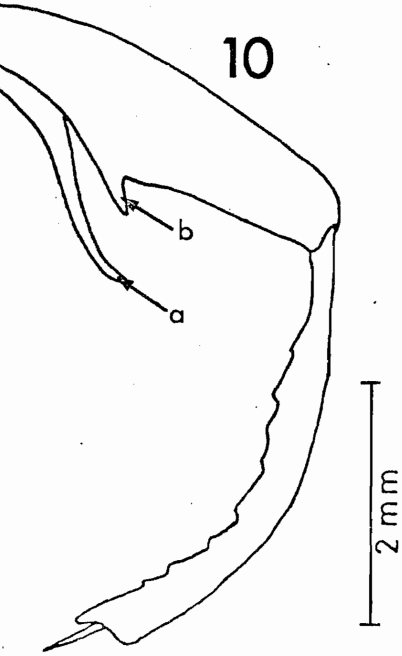

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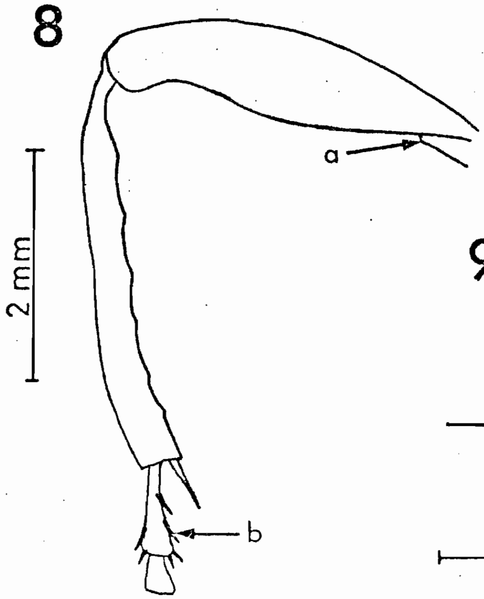

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FIGS 11 - 20

Morphological characters of the species in the subgenus *Sisyphus*.

Fig. 11 *S. muricatus* (Olivier), male; head and prothorax; dorsal aspect (528a/1). Arrow shows pronotal projection.

Fig. 12 *S. fasciculatus* Boheman; elytrum and abdomen; left side, lateral aspect (2/5). Arrow shows hairs arranged in tufts on elytrum.

Fig. 13 *S. costatus* (Thunberg); elytrum and abdomen; left side, lateral aspect (943/1). Arrow shows hairs arranged in longitudinal rows on elytrum.

Fig. 14 *S. impressipennis* van Lansberge, male; right hind femur; inner aspect (394/1). Arrow shows anvil-shaped projection.

Fig. 15 *S. impressipennis* van Lansberge, female; right hind femur; inner aspect (396/1). Arrow shows rounded projection.

Fig. 16 *S. caffer* Boheman; pygidium, elytra and abdomen; posterior aspect (942/1). Arrows show trident-shaped hair pattern of pygidium.

Fig. 17 *S. seminulum* Gerstaecker; pygidium, elytra, and abdomen; posterior aspect (2/6). Arrows show random hair pattern on pygidium.

Fig. 18 *S. seminulum* Gerstaecker; head; dorsal aspect (2/6). Arrow shows cleft between anterior clypeal spines.

Fig. 19 *S. sordidus* Boheman; head; dorsal aspect (1321/3).

a - flat area between anterior clypeal spines.
b - sides of head rounded.

Fig. 20 *S. caffer* Boheman; head; dorsal aspect (942/1). Arrow shows straight sides of head.

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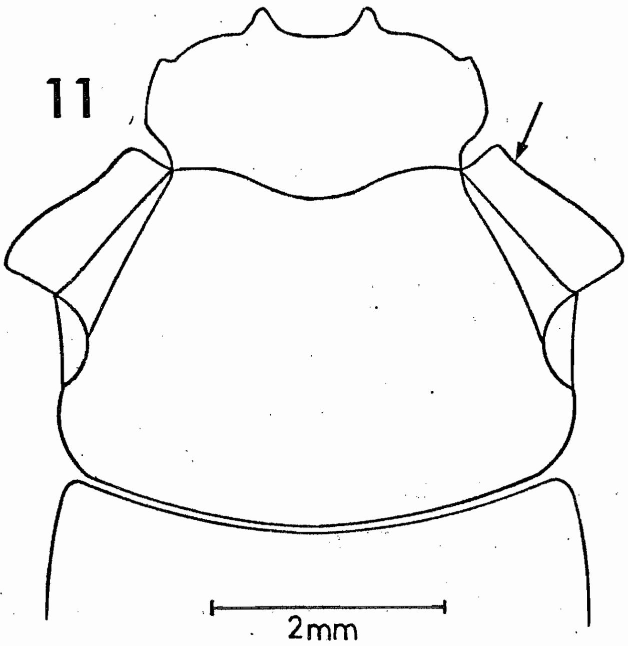

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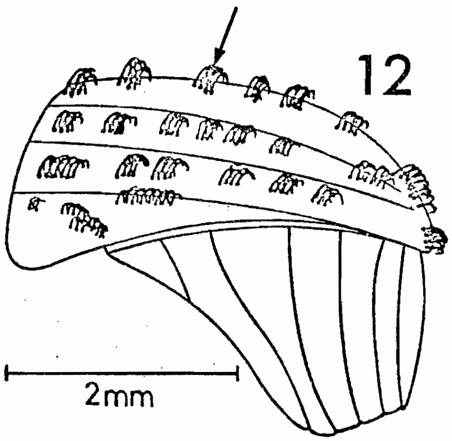

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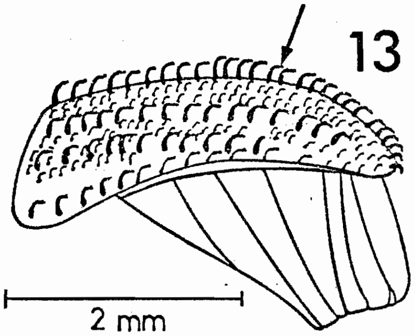

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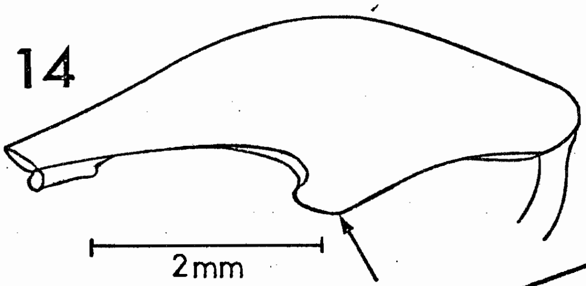

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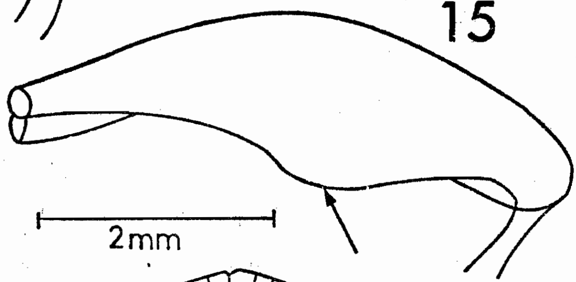

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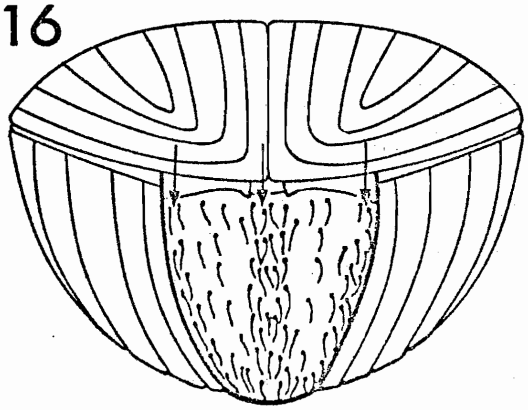

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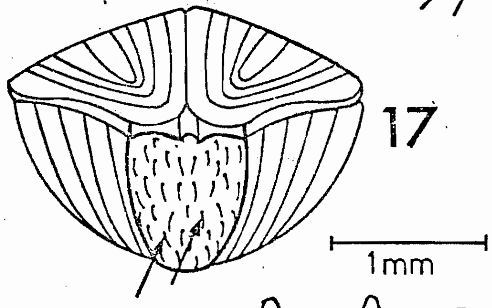

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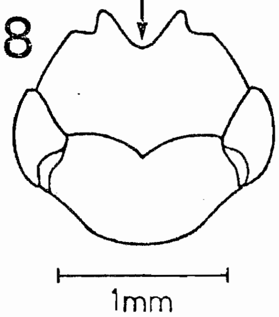

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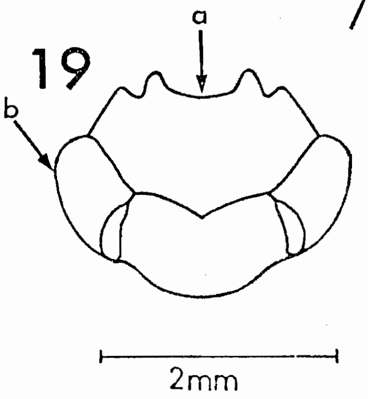

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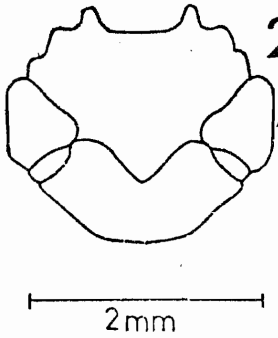


FIGS 21 - 26

Morphological characters of species in the subgenera *Sisyphus* and *Neosisyphus*.

Sisyphus

Fig. 21 *S. sordidus* Boheman; elytrum; dorsal aspect (1321/3).
a - elytrum,
b - abdomen,
c - tufts of hairs on edge of abdomen.

Fig. 22 *S. caffer* Boheman; elytrum; dorsal aspect (942/1).
a - elytrum,
b - abdomen,
c - tufts of hairs on edge of abdomen.

Fig. 23 *S.* species *X;* head; dorsal aspect (2/7). Arrow shows area of difference in shape of head.

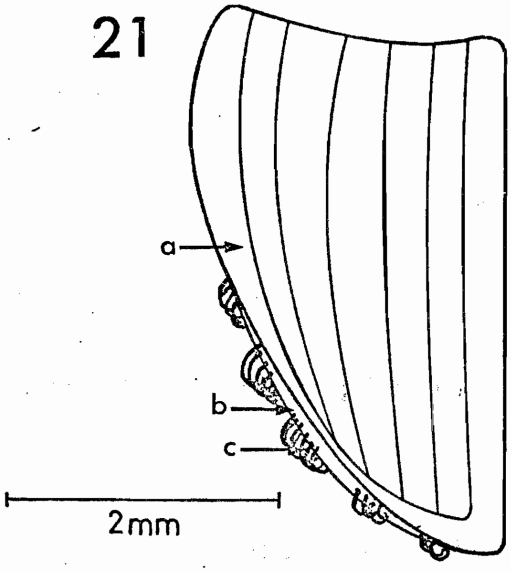
Fig. 24 *S.* species *Y;* head; dorsal aspect (348/1). Arrow shows area of difference in shape of head.

Neosisyphus

Fig. 25 *S. mirabilis*. Arrow; pygidium, elytra and abdomen; posterior aspect (2/2). Arrow shows pygidium simple, has no "boil" (*cf.* fig. 26).

Fig. 26 *S. tibialis* Arrow; pygidium, elytra and abdomen; posterior aspect (1153/2). Arrows show pair of "boils" on pygidium.

21



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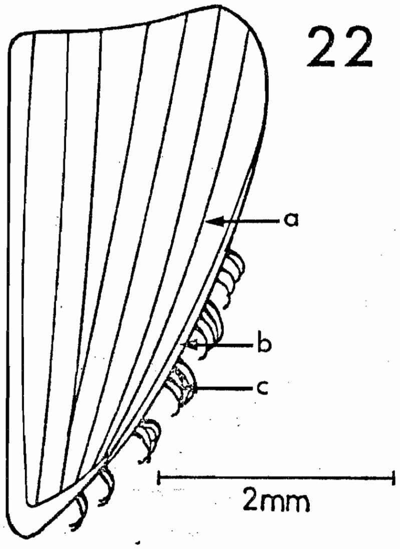

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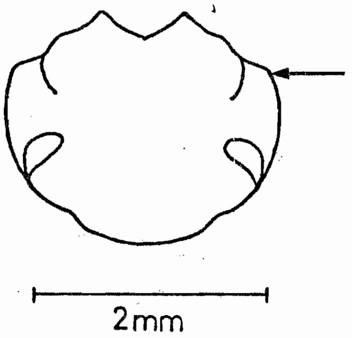

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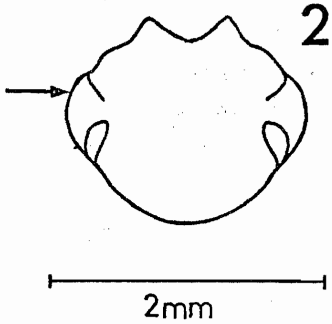

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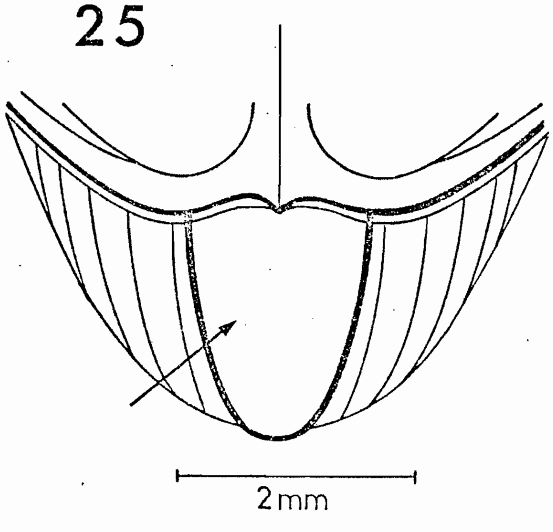

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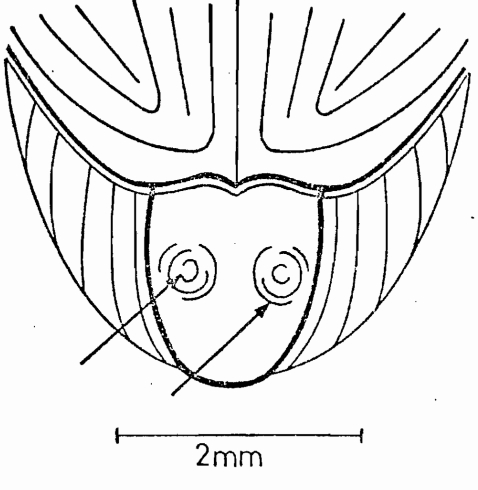


FIGS 27 - 35

Morphological characters of species in the subgenus *Neosisyphus*.

Fig. 27 *S. barbarossa* Wiedeman; hairs on central area of right elytrum; lateral aspect (173/1).

Fig. 28 *S. calcaratus* Klug; hairs on central area of right elytrum; lateral aspect (1321/1).

Fig. 29 *S. confrater* Kolbe; head; dorsal aspect (341/1). Arrow shows V-shaped epicranial suture.

Fig. 30 *S. barbarossa* Wiedeman; head; dorsal aspect (173/1). Arrow shows epicranial suture tending to form Y-shape.

Fig. 31 *S. ruburs* Paschalidis; head; dorsal aspect (♀ - paratype 462/1). Arrow shows pointed posterior clypeal spine.

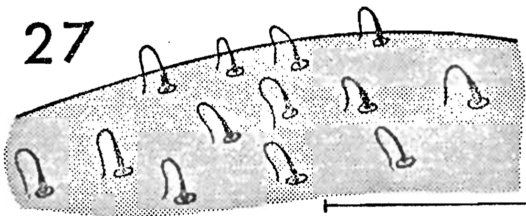
Fig. 32 *S. spinipes* (Thunberg); head; dorsal aspect (10/1). Arrow shows pointed posterior clypeal spine.

Fig. 33 *S. fortuitus* Péringuey; head; dorsal aspect (47/1). Arrow shows rounded posterior clypeal spine.

Fig. 34 *S. fortuitus* Péringuey; elytrum and abdomen, right side; lateral aspect (47/1). Arrow shows elytrum straight at side not "cut away".

Fig. 35 *S. quadricollis* Gory; elytrum and abdomen; right side lateral aspect (210/1). Arrow shows elytrum "cut away" at side.

27



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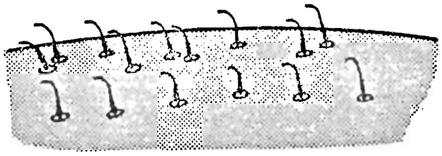

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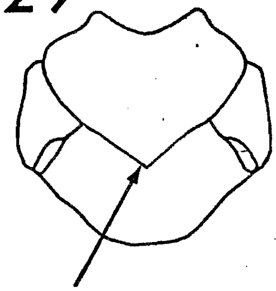

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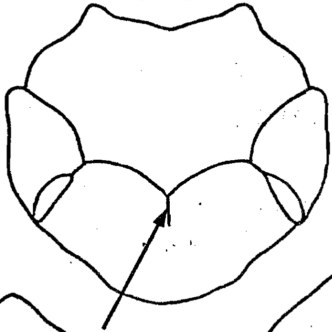

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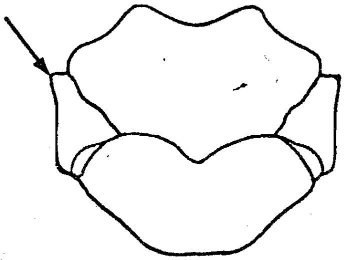

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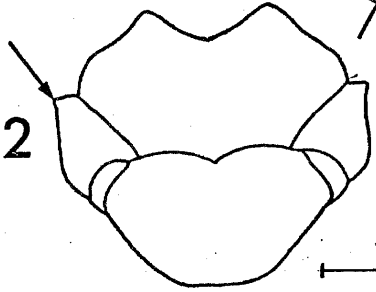

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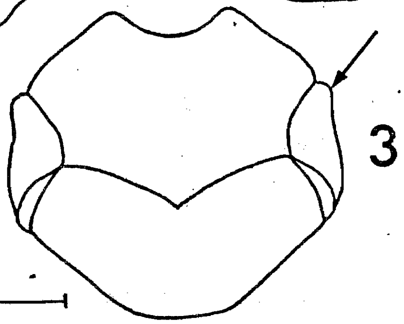

fig. 29-33

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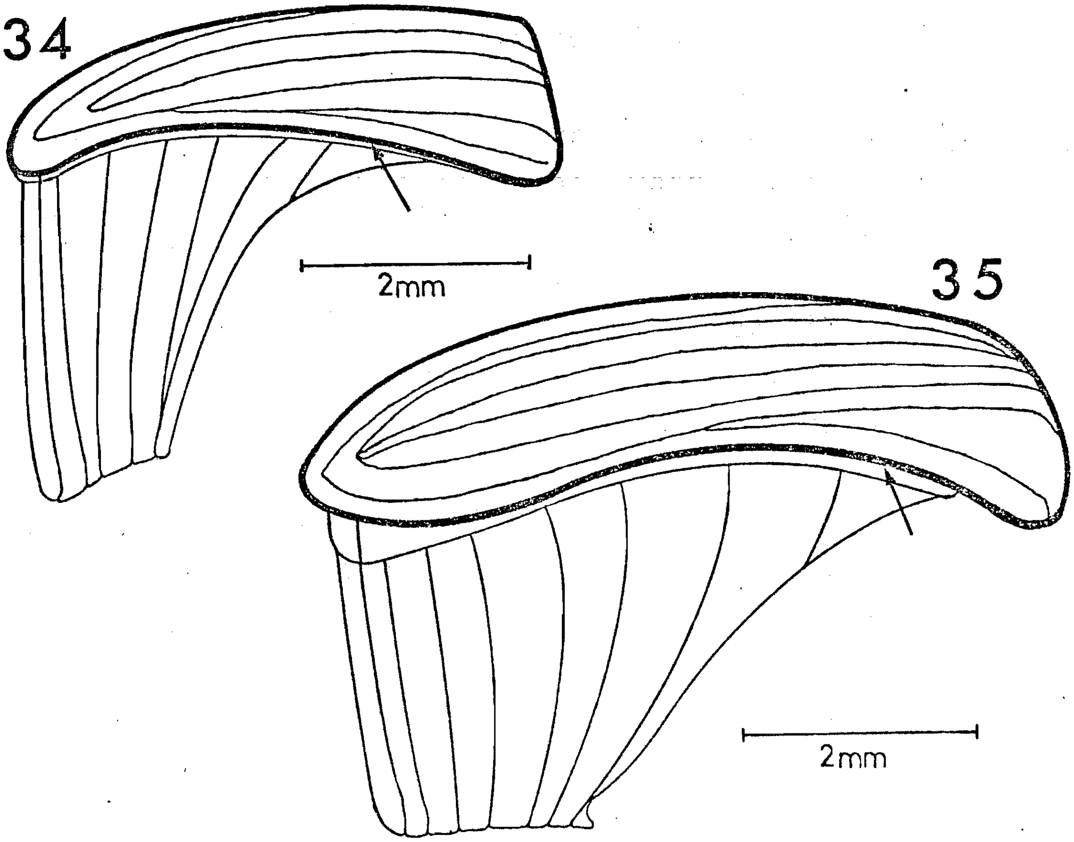

FIGS 36 - 44

Morphological characters on middle femur and tibia in the species of *Neosisyphus*. (There are no sexual differences on the middle legs.) All figs of right middle leg, inner aspect. Arrows indicate points of difference between species.

a - presence or absence of spine on femur.
b - presence or absence of spine on tibia, ventral ridge
c - presence or absence of spine on tibia, dorsal ridge.

Fig. 36 *S. confrater* Kolbe, male (341/1).

Fig. 37 *S. calcaratus* Klug, female (1321/2).

Fig. 38 *S. rubrus* Paschalidis, female (female - paratype 462/1)

Fig. 39 *S. spinipes* (Thunberg), female (656/1).

Fig. 40 *S. mirabilis* Arrow, male (2/2).

Fig. 41 *S. tibialis* Raffray, female (1153/2).

Fig. 42 *S. infuscatus* Klug, male (2/3).

Fig. 43 *S. fortuitus* Péringuey, male (47/1).

Fig. 44 *S. near fortuitus* Péringuey, male (Jos (32 km NE), Nigeria, 26 VII 1974, G.F. Bornemissza/1).

FIGS 45 - 53

Morphological characters on hind trochanter, femur and tibia in the species of *Neosisyphus*. All figs of right hind leg; inner aspect. Arrows indicate points of differences.

a - trochanter.
b - projection on ventral femoral ridge

Fig. 45 *S. confrater* Kolbe, male (341/1).

Fig. 46 *S. barbarossa* Wiedeman, male (173/1).

Fig. 47 *S.* species *A*, male (349/1).

Fig. 48 *S. armatus* Gory, male (male - holotype).

Fig. 49 *S. rubrus* Paschalidis, male (311/1).

Fig. 50 *S. spinipes* (Thunberg), male (10/1).

Fig. 51 *S. infuscatus* Klug, male (2/3).

Fig. 52 *S. kuehni* Haaf, male (56a/1).

Fig. 53 *S. keuhni* Haaf, female (56a/2).

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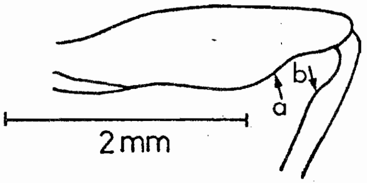

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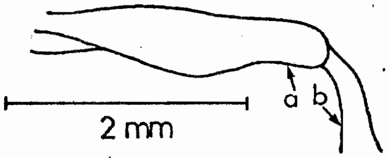

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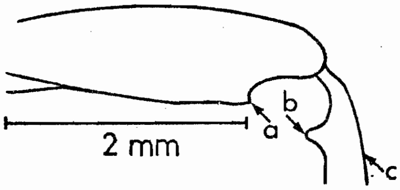

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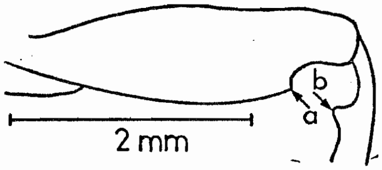

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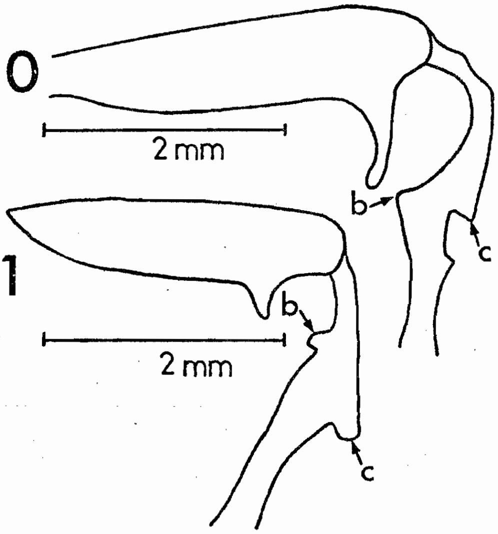

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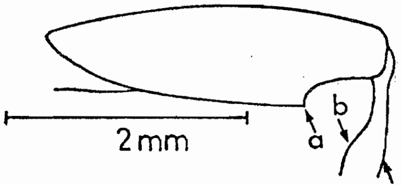

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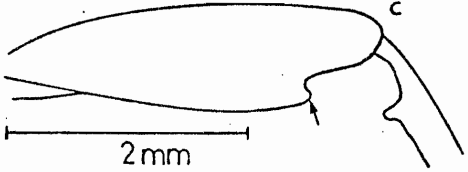

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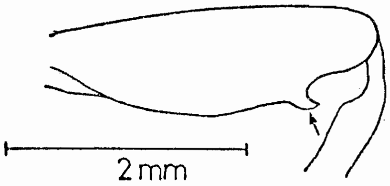

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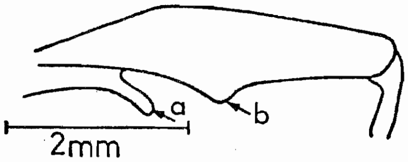

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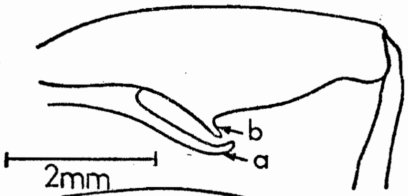

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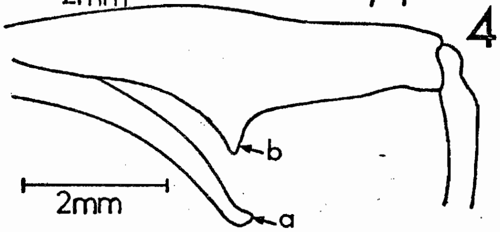

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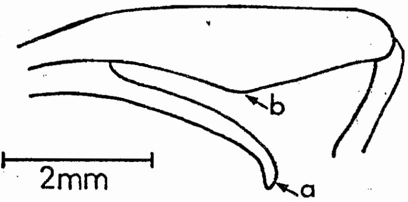

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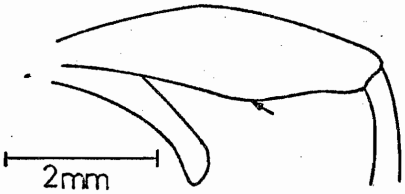

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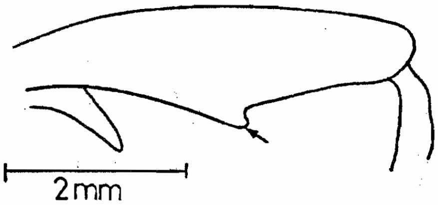

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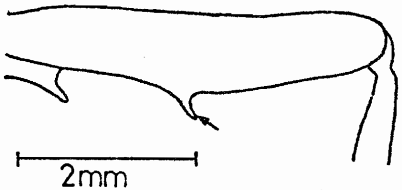

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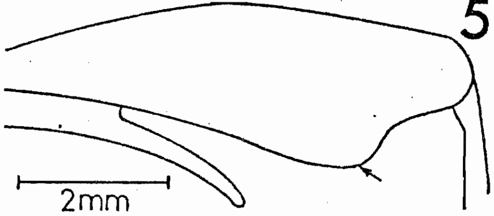

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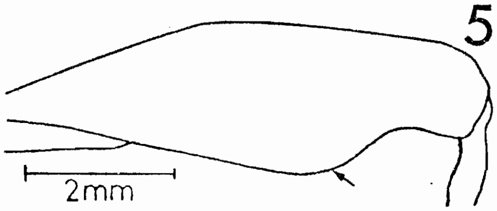

FIGS 54 - 65

Characteristic shape of the distal segment of the aedeagus in species of the subgenus *Sisyphus*. All aedeagi drawn from lateral aspect. Dorsal profile of shaded area is variable in shape as this area is not heavily sclerotized, as is the unshaded area.

Fig. 54	*S. muricatus* (Olivier) (528/1).
Fig. 55	*S. fasciculatus* Boheman (2/4).
Fig. 56	*S. alveatus* Boucomont (306/1).
Fig. 57	*S. impressipennis* van Lansberge (394/1).
Fig. 58	*S. seminulum* Gerstaecker (5/1).
Fig. 59	*S.* species *X* (2/7)
Fig. 60	*S.* species *Y* (348/1).
Fig. 61	*S. costatus* (Thunberg) (943/1).
Fig. 62	*S. sordidus* Boheman (Specimen det. Boheman "Pt. Nat. Tarniers", in Riksmuseet, Stockholm).
Fig. 63	*S. caffer* Boheman (male - type, in Riksmuseet, Stockholm.)
Fig. 64	*S. goryi* von Harold (male - type, in Hope Collection Oxford University Museum.)
Fig. 65	*S. ?goryi* von Harold (von Harold's "type" specimen of *"goryi"*. "Cap bon Sp." in Museum National d' Histoire Naturelle, Paris.)

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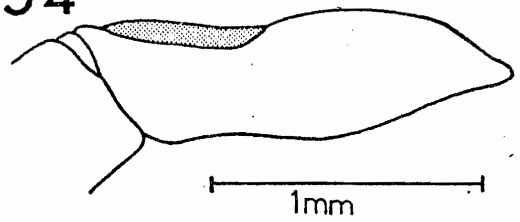

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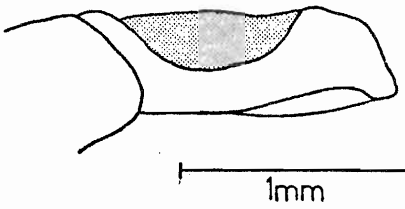

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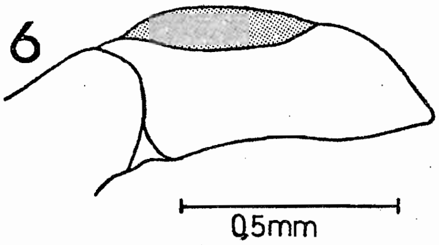

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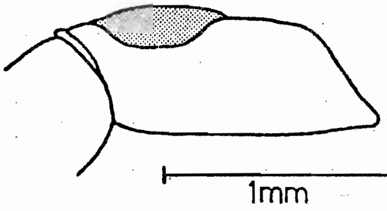

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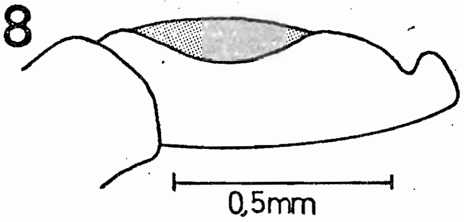

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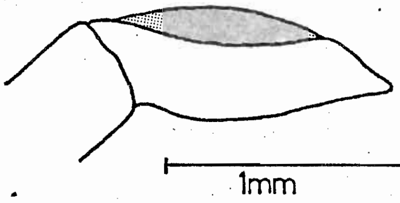

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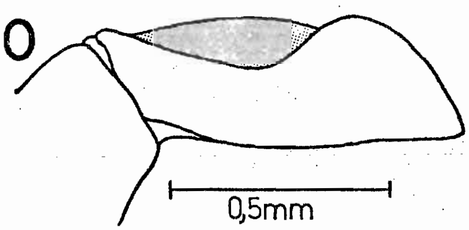

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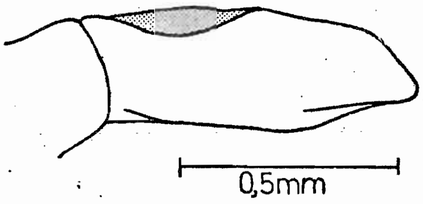

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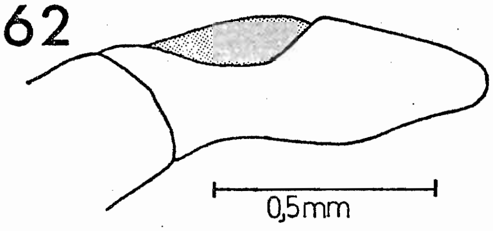

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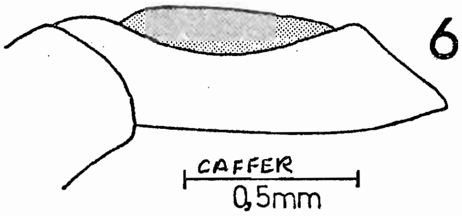

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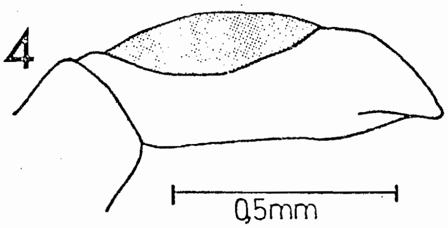

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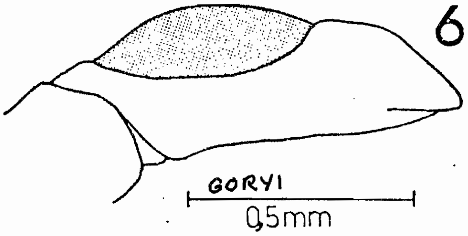


FIGS 66 - 80

Characteristic shape of the distal segment of the aedeagus in species of the subgenus *Neosisyphus*. All aedeagi drawn from lateral aspect. Dorsal profile of shaded area is variable in shape. Striped areas are of soft tissue, not sclerotized.

Fig. 66 *S. tibialis* Raffray (1153/1).

Fig. 67 *S. mirabilis* Arrow (2/1).

Fig. 68 *S. kuehni* Haaf (56a/1)

Fig. 69 *S. quadricollis* Gory (Leipoldtville-Elands Bay, Mus. Exp., Nov. 1948; det E. Haaf, 1954; det K.M. Paschalidis 1974; in South African Museum, Cape Town.)

Fig. 70 *S. fortuitus* Pēringuey (47/1).

Fig. 71 *S. near fortuitus* Pēringuey (Jos (32 km NE) Nigeria, 26 VII 1974, G.F. Bornemissza/1).

Fig. 72 *S. spinipes* (Thunberg) (10/1).

Fig. 73 *S. infuscatus* Klug (2/3).

Fig. 74 *S. rubrus* Paschalidis (male - holotype).

Fig. 75 *S. macrorubrus* Paschalidis (male - holotype).

Fig. 76 *S. barbarossa* Wiedeman (173/1).

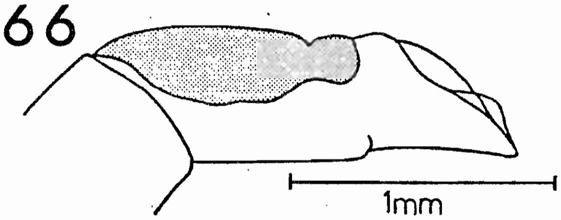
Fig. 77 *S.* species *A*, (349/1).

Fig. 78 *S. calcaratus* (1321/1).

Fig. 79 *S. confrater* Kolbe (341/1)

Fig. 80 *S. armatus* Gory (Coll. C. Felsche, Kauf 20, 1918, Senegambien; det. K.M. Paschalidis, 1974; in Staatliches Museum für Tierkunde, Dresden).

66



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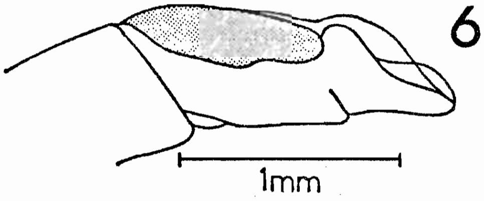

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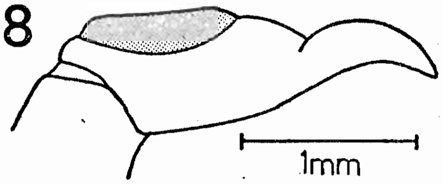

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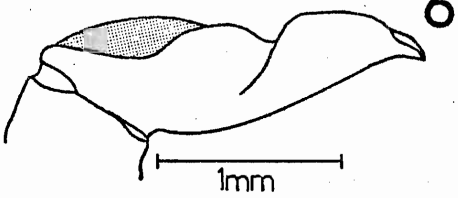

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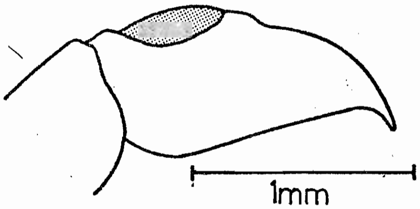

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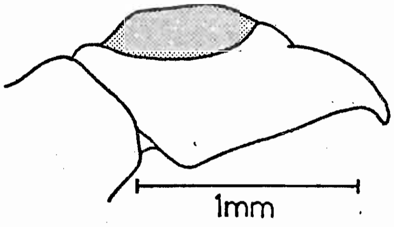

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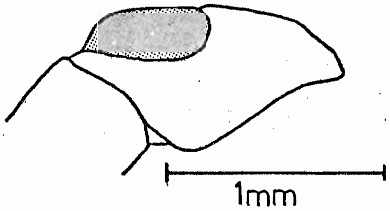

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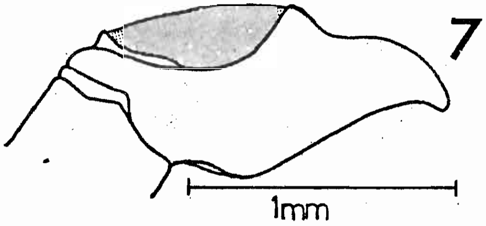

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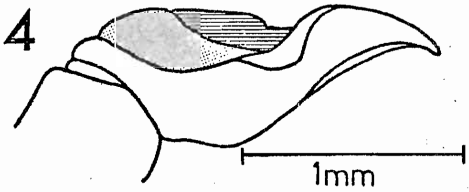

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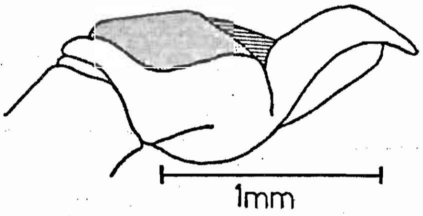

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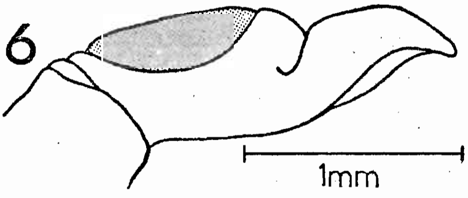

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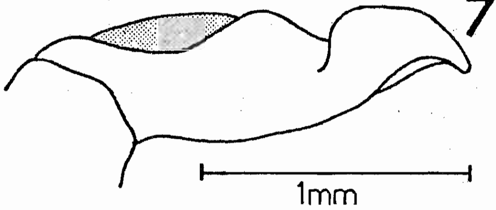

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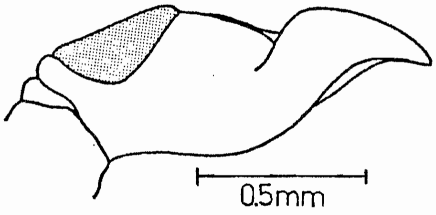

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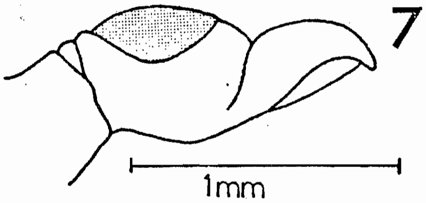
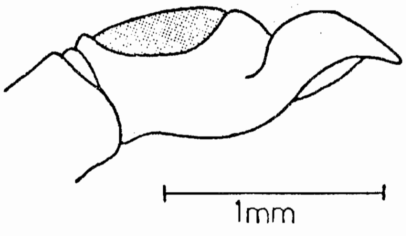


80



2.4 REFERENCE MATERIAL EXAMINED

Locality numbers refer to those on the Unit's lists. Which state the vegetation, soil and dung type on which the beetles were collected.

SUBGENUS *SISYPHUS*

MURICATUS (OLIVIER)

TYPE: in Hope Department of Entomology, University Museum, Oxford

Locality	Date	Collecter	Locality Number	Number of males/females	
SOUTH AFRICA:					
Mt. Sheba, E. Tvl.	5.II.71	Bornemissza & Aschenborn	58	-	1
Mt. Sheba, E. Tvl.	Jan 74	G.F. Bornemissza	1296	17	27
Pilgrims Rest Tvl.	6.II.71	Bornemissaza & Aschenborn	61	-	1
Bergen (10 mi S) S.E. Tvl.	1.IV.72	A.A. Kirk	610	1	1
Knysna C.P.	23.X.71	Bornemissza & Kirk	528	2	1
Laboratory Bred	Emerged Dec 72	Bornemissza & Aschenborn	528a	1	-

FASCICULATUS BOHEMAN

TYPE: male, from Caffraria (Cape Province South Africa), in Naturhistoriska Riksmuseet, Stockholm.

SOUTH AFRICA:

Umfolozi G.R. Natal	1-6/7. X. 70	Bornemissza & Kirk	2	3	6
Umfolozi G.R. Natal	24.V.71	H.H. Aschenborn	266	-	1
Nelspruit (20km W) E. Tvl.	15.II.73	Aschenborn & Temby	1004	1	-

ALVEATUS BOUCOMONT

TYPE: female, from Kibwezi (Kenya), in Museum National, d'Histoire Naturelle, Paris.

SOUTH AFRICA:

Belfast E.Tvl	2.II.71	Bornemissza & Aschenborn	51	1	-
Belfast (14km E) E. Tvl.	16.I.73	A.L.V. Davis	909	-	2

Pongola (30kms W) Natal	24.II.73	K.M. Paschalidis	1043	-	1
RHODESIA:					
Kyle G.R.	2.I.72	Bornemissza & Kirk	306	1	3
MOZAMBIQUE:					
Gondola (10mi E)	9.I.72	Bornemissza & Kirk	327	-	1

IMPRESSIPENNIS VAN LANSBERGE

LECTOTYPE: male, from Humpata (Angola) in Rijksmuseum van Natuurlijke Historie, Leiden.

Holotype of *transvaalensis* Péringuey : male, in South Africa Museum, Cape Town.

Syntypes of *callosipes* Arrow : one male and one female, in British Museum (Natural History), London.

SOUTH AFRICA:					
Pafuri (Picnic Spot) K.N.P., Tvl.	23.I.73	Bornemissza & Temby	1060	1	-
RHODESIA:					
Kyle G.R.	2.I.72	Bornemissza & Kirk	307	2	1
Biriwiri Riv. Bridge	5.I.72	Bornemissza & Kirk	319	3	3
Penhalonga (Hawk's Head Farm)	7.I.72	Bornemissza & Kirk	324	1	-
Kariba (10mi N)	3.II.72	A.A. Kirk	356	6	4
Victoria Falls	8.II.72	Bornemissza & Kirk	373	2	2
Victoria Falls	11.II.72	Bornemissza & Kirk	378	15	31
Victoria Falls	11.II.72	Bornemissza & Kirk	382	31	13
Victoria Falls	11.II.72	Bornemissza & Kirk	388	3	7
Victoria Falls	11.II.72	Bornemissza & Kirk	390	6	9
Victoria Falls	11.II.72	Bornemissza & Kirk	391	3	4
Victoria Falls	11.II.72	Bornemissza & Kirk	392	4	2
Victoria Falls	11.II.72	Bornemissza & Kirk	393	-	2
Victoria Falls	11.II.72	Bornemissza & Kirk	394	5	11

Victoria Falls	11.II.72	Bornemissza & Kirk	395	6	12
Victoria Falls	11.II.72	Bornemissza & Kirk	396	11	8
Victoria Falls (7 mi W)	11.II.72	Bornemissza & Kirk	380	-	1
MOZAMBIQUE:					
Gondola (10mi E)	9.I.72	Bornemissza & Kirk	327	-	1
Gorongosa N.P.	11-28.I.72	G.F. Bornemissza	328	-	1
Gorongosa N.P.	11-28.I.72	G.F. Bornemissza	330	1	-
Gorongosa N.P.	11-28.I.72	G.F. Bornemissza	335	1	-
Gorongosa N.P.	22.I.72	Bornemissza & Kirk	338	1	16

SEMINULUM GERSTAECKER

TYPE: female, from Zanzibar, in Museum für Naturkunde der Humboldt, Berlin, D.D.R.

Holotype of *nanniscus* Péringuey, in South African Museum, Cape Town.

SOUTH AFRICA:				No. of specimens
Umfolozi G.R. Natal	1-7.X.70	Bornemissza & Aschenborn	1	1
Umfolozi G.R. Natal	1-7.X.70	Bornemissza & Aschenborn	2	27
Umfolozi G.R. Natal	1-7.X.70	Bornemissza & Aschenborn	5	22
Umfolozi G.R. Natal	24.V.71	H.H. Aschenborn	264	2
Umfolozi G.R. Natal	24.V.71	H.H. Aschenborn	266	2
Umfolozi G.R. Natal	24.V.71	H.H. Aschenborn	267	3
Umfolozi G.R. Natal	24.V.71	H.H. Aschenborn	268	3
Umfolozi G.R. Natal	21/26. VIII.71	Bornemissza & Insley	489	1
Umfolozi G.R. Natal	25.VIII.71	Bornemissza & Insley	492	5
Umfolozi G.R. Natal	25.VIII.71	Bornemissza & Insley	496	6
Umfolozi G.R. Natal	25.VIII.71	Bornemissza & Insley	499	8
Umfolozi G.R. (Bl. Umf. Riv) Natal.	25.VIII.71	Bornemissza & Insley	500	1

Umfolozi G.R. Natal	24.XI.71	Bornemissza, Olsen, Davis	474	4
Umfolozi G.R. Natal	28.III.72	K.M. Olsen	564	1
Umfolozi G.R. (Sontuli loop) Natal	28.III.72	K.M. Olsen	566	9
Umfolozi G.R. Natal	11.X.72	K.M. Olsen	690	2
Mkuzi G.R. (Msinga Hide) Natal	27.III.72	K.M. Olsen	561	1
Mkuzi G.R. (Masundweni Riv.) Natal	27.III.72	K.M. Olsen	562	4
Mkuzi G.R. (Hides) Natal	16.X.72	K.M. Olsen	693	1
Mkuzi G.R. (Vulture Pan) Natal	24.XII.72	A.L.V. Davis	891	3
Mkuzi G.R. (Vulture Pan) Natal	22.II.73	K.M. Paschalidis	1036	1
Mkuzi G.R. (Msinga Hide) Natal	22.II.73	K.M. Paschalidis	1039	1
Mkuzi G.R. (Msinga Hide) Natal	3-4.XII.73	K.M. Paschalidis	1321	7
Ndumu G.R. (Ficus Forest) Natal	16/17.X.72	K.M. Olsen	695	4
Hluhluwe G.R. (Vervaneni?Loop)	21.II.73	K.M. Paschalidis	1034	1
Castle Gorge (41mi W Pretoria) Tvl.	5.XII.70	G.F. Bornemissza	48	1
Nelspruit (35mi W) Tvl.	6.V.72	Bornemissza & Insley	654	6
Nelspruit (10mi W) Tvl.	7.V.72	Bornemissza & Insley	655	1
Bosbokrand E. Tvl.	6.II.71	Bornemissza & Aschenborn	63	1
Bosbokrand (2km E) E. Tvl.	14.V.73	G. & P. Bornemissza	1124	2

Punda Milia (30km NE Masanje) K.N.P. Tvl.	23.III.71	Bornemissza & Temby	1058	1
Pafuri (Picnic Spot) K.N.P. Tvl.	23.III.73	Bornemissza & Temby	1060	18
Pafuri K.N.P. Tvl.	15.III.72	A.A. Kirk	594	4
Somerset East (East) C.P.	10.III.71	H.H. Aschenborn	198	1
RHODESIA:				
Umtali (15mi S)	20.IV.71	Bornemissza & Aschenborn	131	9
Umtali (13mi S)	20.IV.71	Bornemissza & Aschenborn	132	1
Birchenough Bridge (30mi W)	21.IV.71	Bornemissza & Aschenborn	147	6
Birchenough Bridge	4.I.72	Bornemissza & Kirk	314	1
Lundi (5mi N)	23.IV.71	Bornemissza & Aschenborn	157	1
Lundi (5mi N)	23.IV.71	Bornemissza & Aschenborn	158	5
Lundi (5mi N)	31.XII.71	Bornemissza & Kirk	302	9
Dett (4mi NW)	12.II.72	Bornemissza & Kirk	399	5
Chipinga (8mi NW)	5.I.72	Bornemissza & Kirk	318	1
Biriwiri Riv. Bridge	5.I.72	Bornemissza & Kirk	319	6
Penhalonga (Hawk's Head Farm)	7.I.72	Bornemissza & Kirk	324	3
MOZAMBIQUE:				
Changalane	24.VII.70	V. Ferreira	15	2
Gorongosa N.P.	11-28.I.72	G.F. Bornemissza	330	2
Gorongosa N.P.	11-28.I.72	G.F. Bornemissza	332a	1
Maputo Elephant Res. (opp. gate)	18.IX.73	K.M. Paschalidis	1183	1
KENYA:				
Sultan Hamud (122km NW Mombasa)	27.VI.73	A. Macqueen	1171	4

Mariakani (35km NW Mombasa)	28.VI.73	A. Macqueen	1174	3

SPECIES *X*

SOUTH AFRICA:

				male	female
Umfolozi G.R. Natal	1-7.X.70	Bornemissza & Aschenborn	2	3	10

SPECIES *Y*

SOUTH AFRICA:

Umfolozi G.R. Natal	1-7.X.70	Bornemissza & Aschenborn	2	3	3
Umfolozi G.R. Natal	25.VIII.71	Bornemissza & Insley	496	1	1

MOZAMBIQUE:

Gorongosa N.P.	11-28.I.72	Bornemissza & Kirk	328	1	-
Dondo (5mi NW)	19.I.72	Bornemissza & Kirk	344	1	3
Dondo (5mi NW)	19.I.72	Bornemissza & Kirk	342	8	9
Beira (15mi N)	19.I.72	Bornemissza & Kirk	348	5	-

COSTATUS (THUNBERG)

Female specimen, det. Thunberg, in University of Uppsala, Sweden.

Specimens of *crispatus* Gory (4) collected from Cape Province, in Gory collection, Hope Department of Entomology, University Museum, Oxford.

SOUTH AFRICA:

				No. of specimens
Newcastle (32km N) Natal	27.I.73	Bornemissza & Insley	944	5
Perdekop (4kms S) Natal	27.I.73	Bornemissza & Insley	943	1
Piet Retief (31 mi NW) S.E. Tvl.	31.III.72	K.M. Olsen	569	1
Pilgrims Rest (7mi W) E. Tvl.	6.II.71	Bornemissza & Aschenborn	60	1
Pilgrims Rest E. Tvl.	6.II.71	Bornemissza & Aschenborn	61	5
Swartberg (2km N) N.E. CP.	6.II.73	A.L.V. Davis	987	1
George (10km SW) C.P.	3.II.73	A.L.V. Davis	970	2

SORDIDUS BOHEMAN

Male specimen determined in Boheman's hand, from "Caffraria" (Cape Province, South Africa), in Naturhistoriska Riksmuseet, Stockholm.

SOUTH AFRICA:

Hluhluwe G.R. Natal	1-7.X.70	Bornemissza & Aschenborn	7	1
Hluhluwe G.R. Natal	1-7.X.70	Bornemissza & Aschenborn	9	4
Ndumu G.R. Natal	23.II.73	K.M. Paschalidis	1041	2
Mkuzi G.R. (Msinga Hide) Natal	22.II.73	K.M. Paschalidis	1039	9
Mkuzi G.R. (Vulture Pan) Natal	24.XII.72	A.L.V. Davis	871	1
Mkuzi G.R. Natal	23-24.II/ 2-3.III.72	S.R. Herd	1005	2
Pretoriuskop (Rhino Camp) K.N.P. Tvl.	7.III.72	A.A. Kirk	571	8

RHODESIA:

Umtali (13mi S)	20.IV.71	Bornemissza & Aschenborn	132	3
Glen Clova (10 mi E)	21.IV.71	Bornemissza & Aschenborn	140	1

MOZAMBIQUE:

Joao Belo	24.VII.70	G.F. Bornemissza	12	1
Dondo (5mi NW)	19.I.72	Bornemissza & Kirk	347	3
Gorongosa N.P.	22.I.72	Bornemissza & Kirk	338	1
Gondola (10mi E)	9.I.72	Bornemissza & Kirk	327	2
Beira (15mi N)	19.I.72	Bornemissza & Kirk	349	35

CAFFER BOHEMAN

TYPE: male, from "Caffraria" (Cape Province, South Africa), in Naturhistoriska Riksmuseet, Stockholm.

SOUTH AFRICA:

Tonquani (50mi W Pretoria) Tvl.	11.XII.71	Bornemissza & Insley	438	2
Standerton (8km S) Tvl.	27.I.73	Bornemissza & Insley	942	3

Bloemfontein (9km NE) OFS	4.I.73	H.H. Aschenborn	826	1
Ladybrand (Maseru Rd) OFS	27.XI.70	Bornemissza Aschenborn	35	2
Ladybrand OFS	27.XI.70	Bornemissza & Aschenborn	35a	1
Wepener (15mi S) OFS	3.III.71	H.H. Aschenborn	168	3
Vredefort OFS	29.XI.70	G.F. Bornemissza	45	2
Fouriesburg (22km N) OFS	11.I.73	H.H. Aschenborn	873	1
Kroonstad (26kms N) OFS	30.I.73	A.L.V. Davis	949	1
Sasolburg (9km SE) OFS	3.I.73	H.H. Aschenborn	821	1
Ladysmith (23km NE) Natal	12.I.73	H.H. Aschenborn	881	1
Frere (2mi W) Natal	4.XII.71	A.A. Kirk	447	4
Estcourt (29km N) Natal	7.II.73	A.L.V. Davis	993	2
Perdekop (4km S) Natal	27.I.73	Bornemissza & Insley	943	1
Newcastle (32km N) Natal	27.I.73	Bornemissza & Insley	944	1
Ermelo (4-9km N) Natal	28.I.73	Bornemissza & Insley	948	1
Tsolo (5kms NW) Transkei	5.II.73	A.L.V. Davis	983	1
Queenstown (30mi S) CP	5.III.71	H.H. Aschenborn	172a	7
Tarkastad (17mi E) CP	30.X.71	Bornemissza & Kirk	540	1
Aliwal North (East) CP	3.III.71	H.H. Aschenborn	178	1
Aliwal North (North) CP	3.III.71	H.H. Aschenborn	179	1
Aliwal North (22mi S) CP	4.III.71	H.H. Aschenborn	177	1
Aliwal North (8mi W) CP	3.III.71	H.H. Aschenborn	180	1
Aliwal North (6mi S) CP	3.III.71	H.H. Aschenborn	176	2
Cathcart (5mi S) East CP	5.III.71	H.H. Aschenborn	173	2

GORYI VON HAROLD

TYPE: male, of *hirtus* Gory, in Hope Department of Entomology, University Museum, Oxford.

NIGERIA:

Jos (32km NE)	26.VII.74	G.F. Bornemissza	1533	13

?GORYI VON HAROLD: male, "type" specimen of *goryi* von Harold, from Cape Province South Africa, in Museum National, d'Histoire Naturelle, Paris.

SOUTH AFRICA:

Rust de Winter (15km W) Tvl.	10.II.73	Bornemissza & Insley	1003	5
Phalaborwa (30km SE) Tvl.	17.I.73	A.L.V. Davis	914	1
Barberton E. Tvl.	8.XII.70	H.H. Aschenborn	27	1
Gravelotte (5mi E) E. Tvl.	9.II.71	Bornemissza & Aschenborn	66	3
Rustenburg (22km W) Tvl.	9.I.73	A.L.V. Davis	894	4
Pietersburg (42km E) Tvl.	18.I.73	A.L.V. Davis	921	1
Zeerust (32km E) W. Tvl.	9.I.73	A.L.V. Davis	895	1
Zeerust (8km SW) W. Tvl.	9.I.73	A.L.V. Davis	896	2
Hoedspruit (18 km SE) E. Tvl.	17.I.73	A.L.V. Davis	913	3
Pienaars Riv. Dam (26km NE Pretoria) Tvl.	14.I.73	Bornemissza & Insley	930	1
Castle Gorge (42mi W Pretoria) Tvl.	29.V.71	Bornemissza & Insley	283	1
Castle Gorge (42mi W Pretoria) Tvl.	15.V.71	Bornemissza & Insley	283	2
Castle Gorge (41mi W Pretria) Tvl.	5.XII.70	G.F. Bornemissza	48	1
Castle Gorge (40mi W Pretoria) Tvl.	20.II.71	Bornemissza & Insley	82	3
Skukuza area KNP Tvl.	20.III.73	Bornemissza & Temby	1048	1
Pongola (30kms W) Natal	24.II.73	K.M. Paschalidis	1043	4
Hluhluwe Natal	25.V.71	H.H. Aschenborn	258	1
Mkuzi G.R. (Vulture Pan) Natal	24.XII.72	A.L.V. Davis	891	3

Umfolozi Natal	24.V.71	H.H. Aschenborn	256	1

BOTSWANA:

Chobe N.P.	10.II.72	Bornemissza & Kirk	376	1

RHODESIA:

Various localities and collectors	151

MOZAMBIQUE:

Various localities and collectors	86

KENYA:

Various localities, collected A Macqueen	55

TIBIALIS RAFFRAY

SOUTH AFRICA:				male	female
Bosbokrand (5km SW) Tvl.	20.X.72	G.F. Bornemissza	721	-	1
KENYA:					
Naivasha (North)	21.VI.73	A. Macqueen	1153	1	2
Kikuyu (Mguga Res. Sta.)	22.VI.73	A. Macqueen	1158	1	-

MIRABILIS ARROW

TYPE: female of *spinipes* Gory, in Hope department of Entomology, University Museum, Oxford.

SOUTH AFRICA:

Dukuduku For. Res. Natal	Feb. 71	Brown, Wessels Koster	-	-	1
Umfolozi G.R. Natal	24.V.71	H.H. Aschenborn	256	-	1
Umfolozi G.R. Natal	1-7.X.70	Bornemissza & Aschenborn	2	4	4
Umfolozi G.R. Natal	1-7.X.70	Bornemissza & Aschenborn	5	-	1
Mkuzi G.R. (Msinga Hide) Natal	27.III.72	K.M. Olsen	561	1	-
Mkuzi G.R. (Msinga Hide) Natal	3-4.XII.73	K.M. Paschalidis	1321	25	19
Hluhluwe G.R. Natal	30.III.72	K.M. Olsen	567	1	-

KUEHNI HAAF

PARATYPE: male, from Estcourt, Natal, in British Museum (Natural History), London.

SOUTH AFRICA:

Belfast Tvl.	2.II.71	Bornemissza & Aschenborn	51	2	-

Mt. Sheba E. Tvl.	Jan 74	G.F. Bornemissza	1296	-	1
Mt. Sheba (7mi N) E. Tvl.	4.II.71	Bornemissza & Aschenborn	56a	1	1
Paterson (7mi W) C.P.	6.III.71	H.H. Aschenborn	183	-	1

QUADRICOLLIS GORY

TYPE: male, in Hope Department of Entomology, University Museum, Oxford

SOUTH AFRICA:

Middelburg (15mi S) C.P.	11.III.71	H.H. Aschenborn	210	1	-
Leipoldtville-Elands Bay, C.P.	Nov. 1948	Museum Exp.	+	1	-

+ in South African Museum, Cape Town

FORTUITUS PERINGUEY.

LECTOTYPE: male, det. E. Haaf, 1954, from Durban, Natal, in South African Museum, Cape Town.

SOUTH AFRICA:

Umfolozi G.R. Natal	1-7.X.70	Bornemissza & Aschenborn	2	3	2
Umfolozi G.R. Natal	1-7.X.70	Bornemissza & Aschenborn	1	1	1
Hluhluwe G.R. Natal	1-7.X.70	Bornemissza & Aschenborn	7	-	1
Bergville Natal	4/5.XII.71	A.A. Kirk	449	-	3
Umfolozi G.R. Natal	24.XI.71	Bornemissza, Olsen, Davis	472	1	2
Umfolozi G.R. Natal	24.XI.71	Bornemissza, Olsen, Davis	473	2	3
Umfolozi G.R. Natal	24.XI.71	Bornemissza, Olsen, Davis	474	4	-
Mkuzi G.R. Natal	25.XI.71	Bornemissza, Olsen, Davis	479	1	-
Mkuzi G.R. (Masundweni Riv.) Natal	27.III.72	K.M. Olsen	562	1	-
Eshowe (East) Natal	25.XII.73	A.L.V. Davis	893	-	1
Mkuzi G.R. (Msinga Hide) Natal	3-4.XII.73	K.M. Paschalidis	1321	3	1
Umfolozi G.R. Natal	24.V.71	H.H. Aschenborn	266	1	-
Pretoria (30mi W) Tvl.	5.XII.70	G.F. Bornemissza	47	1	-

Castle Gorge (42mi W Pretoria) Tvl.	4.XII.71	Bornemissza & Insley	437	1	-
Tonquani Gorge (50mi W Pretoria) Tvl.	11.XII.71	Bornemissza & Insley	438	3	1
Piet Retief (31mi NW) Tvl.	31.III.72	K.M. Olsen	569	1	-
Zeerust (8km SW) W. Tvl.	9.I.73	A.L.V. Davis	896	-	1
Tonquani Gorge (80km W Pretoria) TVL.	13.I.73	Bornemissza & Insley	929	1	2
Bosbokrand (2km SE) E. Tvl.	14.V.73	G. & P. Bornemissza	1124	-	2
Bluegumspoort (Louis Trichardt area) N. Tvl.	17/18.II 72	A. A. Kirk	598	-	1
Middelburg (13mi E) Tvl.	31.V.71	H.H. Aschenborn	275	-	1
Knysna (5km E) C.P.	2.II.73	A.L.V. Davis	966	-	1
RHODESIA:					
Umtali (15mi S)	20.IV.71	Bornemissza & Aschenborn	131	1	-
Penhalonga (5mi NE)	31.I.72	A.A. Kirk	354	3	5
Biriwiri Riv. Bridge	5.I.72	Bornemissza & Kirk	319	-	3
Chipinga (8mi NW)	5.I.72	Bornemissza & Kirk	318	1	-
Silversteams Riv. Bridge (3mi N)	5.I.72	Bornemissza & Kirk	321	-	1
Penhalonga (Hawk's Head Farm)	7.I.72	Bornemissza & Kirk	324	3	-

SPINIPES (THUNBERG)

Male specimen, det. Thunberg, in University of Uppsala, Sweden.

Type of *hessii* Gory, male, in Hope Department of Entomology, University Museum, Oxford.

Type of *atratus* Klug, male, in Museum für Naturkunde der Humboldt, Berlin D.D.R.

Type of *appendiculatus* BOHEMAN, male, in Naturhistoriska Riksmuseet, Stockholm.

SOUTH AFRICA:

Umfolozi Natal	1-7.X.70	Bornemissza & Aschenborn	2	-	1
Hluhluwe Natal	1-7.X.70	Bornemissza & Aschenborn	7	4	2

Ladysmith (10mi N) Natal	9.X.70	Bornemissza & Aschenborn	10	4	-
Hluhluwe Natal	1-7.X.70	Bornemissza & Aschenborn	9	5	9
Umfolozi G.R. Natal	24.XI.71	Bornemissza, Olsen, Davis	473	1	2
Mkuzi G.R. Natal	24.XI.71	Bornemissza, Olsen, Davis	479	-	1
Mkuzi G.R. (Masundweni Riv.) Natal.	27.III.72	K.M. Olsen	562	-	1
Eshowe (East) Natal	25.XII.73	A.L.V. Davis	893	-	1
Mkuzi G.R. (Msinga Hide) Natal	1-3.XII.73	K.M. Paschalidis	1321	9	-
Mposa Natal	21.V.71	H.H. Aschenborn	254	7	3
Stanger Natal	21.V.71	H.H. Aschenborn	253	1	2
Mtubatuba (4mi N) Natal	22.V.71	H.H. Aschenborn	263	4	2
Somkele Natal	25.V.71	H.H. Aschenborn	257	7	3
Umfolozi Natal	1-6.X.70	Bornemissza & Aschenborn	1-5	-	1
Port Edward (7mi N) Natal	19.V.71	H.H. Aschenborn	241	1	1
Malelane (5mi W) E. Tvl.	8.XII.70	H.H. Aschenborn	25	4	1
Numbi Gate E. Tvl.	4.II.71	Bornemissza & Aschenborn	56	34	17
Bosbokrand E. Tvl.	6.II.71	Bornemissza & Aschenborn	63	13	8
Bosbokrand (5mi N) E. Tvl.	6.II.71	Bornemissza & Aschenborn	63a	4	1
Louis Trichardt (11mi N) Tvl.	14.XII.71	K.M. Olsen	462	1	-
Acornhoek (5mi W) E. Tvl.	2.XI.71	H.D. Brown	424	-	5
Nelspruit (35mi W) Tvl.	6.V.72	Bornemissza & Insley	654	1	1
Nelspurit (10mi W) Tvl.	7.V.72	Bornemissza & Insley	655	1	-
Barberton (8m N) Tvl.	7.V.72	Bornemissza & Insley	656	-	1
Nelspruit (20km W) E. Tvl.	31.X.72	A.L.V. Davis	724	-	1

Carolina (4mi S) E. Tvl.	29.V.71	H.H. Aschenborn	271	-	1
Moedig E. Tvl.	30.V.71	H.H. Aschenborn	273	1	1
Punda Milia (70km SW KNP gate) NE Tvl.	26.IV.73	I.D. Temby	1132	1	-
Peddie (3mi S) East CP	6.III.71	H.H. Aschenborn	174	-	2
Queenstown (30mi S) CP	5.III.71	H.H. Aschenborn	172a	1	-
Kingwilliams Town (20mi S) CP	6.III.71	H.H. Aschenborn	182	1	1
Stutterheim (15mi S) CP	6.III.71	H.H. Aschenborn	188	1	-
Idutywa Transkei	19.V.71	H.H. Aschenborn	244	1	1
Butterworth Transkei	19.V.71	H.H. Aschenborn	245	3	6
Knysna (7mi W) CP	30.IV.72	K.M. Olsen	640	1	-
RHODESIA:					
Inyazura (5mi E)	8.IV.71	Bornemissza & Aschenborn	100	1	1
Umtali (15mi S)	20.IV.71	Bornemissza & Aschenborn	131	1	-
Chipinga (10mi N)	21.IV.71	Bornemissza & Aschenborn	135	-	5
Inyazura (9km S)	13.XI.72	A.L.V. Davis	760	-	1
Penhalonga (5mi NE)	31.I.72	A.A. Kirk	354	2	1
Penhalonga (Hawk's Head Farm)	7.I.72	Bornemissza & Kirk	324	1	3
MOZAMBIQUE:					
Machipanda (7mi E)	10.V.71	Bornemissza & Aschenborn	94	1	-
Vila Pery (5mi E)	10.IV.71	Bornemissza & Aschenborn	95	13	5
Gorongosa mts. (2,300ft)	15.IV.71	Bornemissza & Aschenborn	105	9	3
Vila de Manica (3mi E)	10.IV.71	Bornemissza & Aschenborn	108	-	1
Beira (10mi NW)	16.IV.71	Bornemissza & Aschenborn	117	-	3
Gorongosa N.P.	12.IV.71	Bornemissza & Aschenborn	118	-	1

Muda	16.IV.71	Bornemissza & Aschenborn	124	1	-
Beira (6mi N)	17.IV.71	Bornemissza & Aschenborn	125	28	21
Beira (4mi N)	17.IV.71	Bornemissza & Aschenborn	126	7	3
Maputo Elephant Res. (opp. gate)	18.IX.73	K.M. Paschalidis	1183	2	1
Beira (15mi N)	19.I.72	Bornemissza & Kirk	349	2	1
Dondo(6mi SE)	19.I.72	Bornemissza & Kirk	346	8	4
Machipanda (5mi E)	8.I.72	Bornemissza & Kirk	325	6	6
Gorongosa N.P.	11-28.I.72	G.F. Bornemissza	341	1	-

KENYA:

Darajani (210km SE Nairobi	25.VI.73	A. Macqueen	1163	1	-
Sultan Hamud 122km NW Mombasa)	27.VI.73	A. Macqueen	1171	2	-

INFUSCATUS KLUG

TYPE: male and paratype female, in Museum für Naturkunde der Humboldt, Berlin, D.D.R.

SOUTH AFRICA:

Umfolozi Natal	1-7.X.70	Bornemissza & Aschenborn	2	7	2
Hluhluwe Natal	1-7.X.70	Bornemissza & Aschenborn	9	2	-
Umfolozi G.R. Natal	24.XI.71	Bornemissza, Olsen, Davis	473	1	2
Mtubatuba (3mi N) Natal	21-26.VIII. 71	Bornemissza & Insley	488	1	2
Mkuzi G.R. (Masundweni loop) Natal	27.III.72	K.M. Olsen	562	2	-
Somkele Natal	25.V.71	H.H. Aschenborn	257	-	1
Umfolozi Natal	1-6.X.70	Bornemissza & Aschenborn		2	4
Umfolozi G.R. Natal	24.V.71	H.H. Aschenborn	264	1	-
Mkuzi G.R. (Msinga Hide) Natal	3-4.XII.73	K.M. Paschalidis	1321	5	2

Malelane (5mi W) E. Tvl.	8.XII.70	H.H. Aschenborn	25	-	1
Messina (5mi N) N. Tvl.	15.XII.71	K.M. Olsen	464	-	1
Letaba KNP Tvl.	12.III.72	A.A. Kirk	588	3	3
Letaba (31mi N) KNP Tvl.	13.III.72	A.A. Kirk	590	1	1
Letaba KNP Tvl.	11.III.72	A.A. Kirk	587	5	9
Gravelotte (5mi E) E. Tvl.	9.II.71	Bornemissza & Aschenborn	66	-	2
Cathcart (5mi S) East CP	5.III.71	H.H. Aschenborn	CG	1	-
Somerset East (15mi E) East CP	10.III.71	H.H. Aschenborn	CIa	2	1
Somerset East (East) East CP	10.III.71	H.H. Aschenborn	CU	1	-
RHODESIA:					
Birchenough Bridge	3.I.72	Bornemissza & Kirk	313	-	1
Kyle G.R.	2.I.72	Bornemissza & Kirk	311	-	1
MOZAMBIQUE:					
Beira (6mi N)	17.IV.71	Bornemissza & Kirk	125	7	9
Beira (4mi N)	17.IV.71	Bornemissza & Kirk	126	1	1
Maputo Elephant Res. (opp. gate)	18.IX.73	K.M. Paschalidis	1183	-	1
Gorongosa N.P.	11-28.I.72	G.F. Bornemissza	335	2	-
Gorongosa N.P.	11-28.I.72	Bornemissza & Kirk	330	6	-
KENYA:					
Nairobi (40km SE Lukenya Rd)	24.IV.73	A. Macqueen	1159	-	1
Sultan Hamud (22km NW Mombasa)	27.VI.73	A. Macqueen	1171	2	6

RUBRUS PASCHALIDIS

HOLOTYPE: male, South Africa.

Castle Gorge, 42mi W) Tvl.	15.V.71	Bornemissza & Insley	283	94	65

PARATYPES: SOUTH AFRICA: Durban, Natal, III.1888, (1 female), "*S. rubripes* Pér., Lectotype, det. E. Haaf, 1954".

Castle Gorge (42mi W Pretoria) Tvl.	15.V.71	Bornemissza & Insley	283	12	6
Castle Gorge, (42mi W Pretoria) Tvl.	19.VI.71	Bornemissza & Insley	283	7	6
Bergen S.E. Tvl.	1.VI.72	A.A. Kirk	609	2	1
Louis Trichardt (11mi S) Tvl.	4.XII.71	K.M. Olsen	462	2	4
Bosbokrand Bridge (5mi N) E. Tvl.	6.II.71	Bornemissza & Aschenborn	63a	36	25
Bosbokrand Bridge E. Tvl.	6.II.71	Bornemissza & Aschenborn	63	21	15
Vryburg (15mi E Leeuwrand Farm) CP	7.X.72	R. Kluge	678	1	-
Mafeking (9mi E) CP	22.V.72	A.L.V. Davis	618	1	-
Aliwal North (22mi S) CP	4.III.71	H.H. Aschenborn	177	2	-
Umtata (10mi N) Transkei	19.V.71	H.H. Aschenborn	246	2	3
Vredefort (20mi S) OFS	3.XI.71	Bornemissza & Kirk	555	2	1

MOZAMBIQUE:

Vila Pery (5mi E)	10.IV.71	Bornemissza & Aschenborn	95	1	2

RHODESIA:

Sebakwe,	1901	D. Dods		2	-

(det. Péringuey as *rubripes* Boheman, det. Haaf, 1954, as *rubripes* Péringuey)

Sebakwe,	1902	D. Dods		3	1

(det. Péringuey as *rubripes* Boheman, det. Haaf, 1954, as *rubripes* Péringuey).

Holotype and paratypes in National Collection of Insects, Pretoria and paratypes in South African Museum, Cape Town, and CSIRO collection, Pretoria.

ADDITIONAL MATERIAL:

RHODESIA:

Kyle G.R.	3.I.72	Bornemissza & Kirk	311	1	-

VARIOUS LOCALITIES: 779 specimens, in CSIRO collection, Pretoria.

MACRORUBRUS PASCHALIDIS

HOLOTYPE/ male, SOUTH AFRICA.

Vanstadensrus OFS	10.XII.71	A. A. Kirk	457	-	-

PARATYPES: 33males and 23 females, SOUTH AFRICA:

Vryburg (24km SW) North CP	8.XI.73	I.D. Temby	1251	1	-

Kimberley (25mi S) CP	14.X.71	Bornemissza & Kirk	506	1	-
Aliwal North (mi W) CP	3.III.71	H.H. Aschenborn	180	2	1
Aliwal North (North) CP	3.III.71	H.H. Aschenborn	181	2	-
Aliwal North (6mi S) CP	3.III.71	H.H. Aschenborn	176	5	-
Aliwal North (East) CP	3.III.71	H.H. Aschenborn	178	2	2
Zastron (2mi W) OFS	3.III.71	H.H. Aschenborn	170	2	3
Zastron (21mi N) OFS	12.V.72	K.M. Olsen	649	1^{+}	1^{+}
Wepener (22mi N) OFS	11.V.71	H.H. Aschenborn	202	1	2
Wepener (19mi S) OFS	11.V.71	H.H. Aschenborn	218	1	-
Wepener (North) OFS	3.III.71	H.H. Aschenborn	167	2	1
Ladybrand (16mi S) OFS	2.III.71	H.H. Aschenborn	162	2	2
Ladybrand (Maseru Rd) OFS	27.IX.70	Bornemissza & Aschenborn	35	$4+1^{+}$	$2+1^{+}$
Caledon Riv (3mi W Maseru) OFS	2.III.71	H.H. Aschenborn	163	3	2
Bloemfontein (11mi N) OFS	3.IX.71	Bornemissza & Aschenborn	553	1	2
Rouxville OFS	1.XI.71	Bornemissza & Aschenborn	547	1	1

SOUTH WEST AFRICA:

Outjo (15kmN)	10.IV.74	H.H. Aschenborn	1472	1	3

+ = in South African Museum, Cape Town.

ADDITIONAL MATERIAL: SOUTH AFRICA:

Vryburg (24km SW) North CP	8.X.73	I.D. Temby	1251	-	1
Kimberley (25mi S) CP	14.X.71	Bornemissza & Kirk	506	3	1
Aliwal North (Hotsprings) CP	13.V.71	H.H. Aschenborn	222	2	-
Aliwal North (6mi S) CP	3.III.71	H.H. Aschenborn	176	2	1
Aliwal North (8mi W) CP	3.III.71	H.H. Aschenborn	180	-	2

Middelburg (15mi S) CP	11.III.71	H.H. Aschenborn	210	-	1
Wepener (South) OFS	3.III.71	H.H. Aschenborn	166	-	2
Caledon Riv. (Near Maseru) OFS	2.III.71	H.H. Aschenborn	164	-	31
Wepener (15mi S) OFS	3.III.71	H.H. Aschenborn	168	5	1
Zastron (2mi W) OFS	3.III.71	H.H. Aschenborn	170	-	1
Rouxville (South) OFS	3.III.71	H.H. Aschenborn	169	1	-
Wepener (22mi N) OFS	11.V.71	H.H. Aschenborn	202	1	-
Bloemfontein (9km NE) OFS	4.I.73	H.H. Aschenborn	826	1	-
Ladybrand (16mi S) OFS	2.III.71	H.H. Aschenborn	162	1	-
Ficksburg (12mi S) OFS	10.V.71	H.H. Aschenborn	200	2	-
Ladybrand (Maseru Rd) OFS	27.XI.70	Bornemissza & Aschenborn	35	2	1
Ladybrand OFS	27.XI.70	Bornemissza & Aschenborn	35	13	8
Bloemfontein (11mi N) OFS	3.XI.71	Bornemissza & Kirk	553	3	2
Vredefort (20mi S) OFS	3.XI.71	Bornemissza & Kirk	555	1	-
Zastron (21mi N) OFS	12.V.72	K.M. Olsen	649	-	-

BARBAROSSA WIEDEMAN.
TYPE: female, from Cape Province, in Universitetets Zoologiske Museum, Copenhagen

Male type of *rugosus* Gory, in Hope Department of Entomology, University Museum, Oxford.

SOUTH AFRICA:

Pilgrims Rest (7mi W) E. Tvl	6.II.71	Bornemissza & Kirk	60	-	1
Belfast E. Tvl	2.II.71	Bornemissza & Aschenborn	51	1	-
Piet Retief (6mi SE) SE. Tvl	26.XI.71	Bornemissza, Olsen, Davis	482	-	1
Belfast (15mi E) Tvl	6.V.72	Bornemissza & Insley	652	1	-
Sabie (East) E. Tvl.	9.X.73	A.L.V. Davis	1224	-	1
Lothair SE. Tvl	29.V.71	H.H. Aschenborn	272	1	-

Grahamstown (9km NE) CP	2.I.73	K.M. Paschalidis	997	-	3
Caledon (26km SE) West CP	11.X.73	I.D. Temby	1260	1	-
Cathcart (5mi S) East CP	5.III.71	H.H. Aschenborn	173	3	3
Somerset East (15mi E) CP	1.III.71	H.H. Aschenborn	207	1	-
Middelburg (15mi S) CP	11.III.71	H.H. Aschenborn	210	-	1
Queenstown (North) CP	5.III.71	H.H. Aschenborn	172	-	1
Avontuur South CP	8.III.71	H.H. Aschenborn	192	-	1
Ladybrand (7mi W) OFS	6.II.71	Bornemisssza & Aschenborn	35	1	-
Ladybrand OFS	27.XI.70	Bornemisssza & Aschenborn	35a	-	3
Witsieshoek OFS	6.XII.71	A.A. Kirk	452	-	1
Tweespruit (37km E) OFS	9.X.73	K.M. Paschalidis	1269	1	-
Ladybrand (16mi S) OFS	2.III.71	H.H. Aschenborn	162	1	-
Caledon Riv. (3mi W Maseru) OFS	2.III.71	H.H. Aschenborn	163	1	1
Wepener (North) OFS	3.III.71	H.H. Aschenborn	167	2	1
Zastron (2mi W) OFS	3.III.71	H.H. Aschenborn	170	-	1
Fouriesburg OFS	12.IV.71	C. Cilliers	289	-	1

SPECIES *A*

MOZAMBIQUE:

Beira (15mi N)	19.I.72	Bornemisssza & Kirk	349	1	-

CALCARATUS KLUG

TYPE: male and 3 male paratypes, in Museum für Naturkunde der Humboldt, Berlin, D.D.R.

SOUTH AFRICA:

Mkuzi G.R. (Msinga Hide) Natal	25.XI.71	Bornemisssza, Olsen, Davis	479	-	1
Mkuzi G.R. Msinga Hide Natal	3-4.XII.73	K.M. Paschalidis	1321	7	5
Zebediela Tvl	7.XII.70	H.H. Aschenborn	31	1	-
Sabie E. Tvl.	6.II.71	Bornemisssza & Aschenborn	62	1	-

Messina (5mi N) Tvl.	6.II.71	Bornemissza & Aschenborn	77	20	12
Castle Gorge (40mi W Pretoria) Tvl	20.III.71	Bornemissza & Aschenborn	82	1	-
Letaba KNP Tvl.	11.III.72	A.A. Kirk	587	2	1
Pretoriuskop KNP (Rhino Camp) Tvl.	7.III.72	A.A. Kirk	571	-	1
Letaba KNP Tvl.	12.III.72	A.A. Kirk	588	1	2
Vivo (2mi E) N. Tvl	19.III.72	A.A. Kirk	601	1	-
Waterpoort, (3mi E) Tvl.	19.III.72	A.A. Kirk	605	-	1
Shingwidzi KNP (10 mi NE)	14.III.72	A.A. Kirk	612	2	1
Castle Gorge (42km W Pretoria) Tvl.	29.V.71	Bornemissza & Insley	283	-	1
Pietersburg (37mi N) Tvl.	18.II.72	Bornemissza & Insley	417	1	-

RHODESIA:

Umtali (15mi S)	20.IV.71	Bornemissza & Aschenborn	131	1	-
Victoria Falls (29mi E)	12.II.72	Bornemissza & Aschenborn	397	1	-
Penhalonga (Hawk's Head Farm)	7.I.72	Bornemissza & Aschenborn	324	2	1
Victoria Falls	11.II.72	Bornemissza & Aschenborn	393	-	1
Gwelo Area	6.II.72	Bornemissza & Aschenborn	364	1	-

MOZAMBIQUE:

Gorongosa NP	11-28.I.72	Bornemissza & Aschenborn	330	1	-

CONFRATER KOLBE

TYPE: male and male paratype, in Museum für Naturkunde der Humboldt, Berlin, D.D.R.

Type of *rubripes* Boheman, female, in Naturhistoriska Riksmuseet, Stockholm.

SOUTH AFRICA:

Mkuzi G.R. Natal	25.XI.72	Bornemissza, Olsen, Davis	479	1	-
Pilgrims Rest E. Tvl.	6.II.71	Bornemissza & Aschenborn	61	-	1
Dullstroom (7mi SE) E. Tvl.	11.III.72	K.M. Olsen	429	-	1

Piet Retief (6mi SE) SE. Tvl.	26.XI.72	Bornemissza, Olsen, Davis	482	1	-
Piet Retief (31mi NW) SE. Tvl.	31.III.72	K.M. Olsen	569	1	-
Badplaas (20mi NE) E. Tvl.	7.V.72	Bornemissza & Insley	657	-	1
Pilgrims Rest (West) E. Tvl.	3.IX.72	Davis, R. & A. Klug	671	1	-
Pilgrims Rest (Caravan Camp) E. Tvl.	9.X.72	Bornemissza & Insley	680	2	3
Pilgrims Rest (5km E) E. Tvl.	8.X.73	A.L.V. Davis	1223	-	1
Stutterheim (15mi S)	6.III.71	H.H. Aschenborn	188	2	1
Idutywa Transkei	19.V.71	H.H. Aschenborn	244	2	-
Kei Riv. Bridge Transkei	19.II.71	H.H. Aschenborn	242	1	-

RHODESIA:

Salisbury (15mi E)	8.IV.71	Bornemissza & Aschenborn	90	-	1
Umtali (22mi N)	9.IV.71	Bornemissza & Aschenborn	128	-	1
Fort Victoria (25mi N)	7.IV.71	Bornemissza & Aschenborn	152	-	1
Penhalonga (5mi NE)	31.I.72	A.A. Kirk	354	1	2
Makuti (40mi S)	3.II.72	A.A. Kirk	355	1	-
Penhalonga (5mi NE)	31.I.72	A.A. Kirk	354	1	2

MOZAMBIQUE:

Machipanda (7mi E)	10.IV.71	Bornemissza & Aschenborn	94	-	1
Vila Pery (5mi E)	10.IV.71	Bornemissza & Aschenborn	95	4	1
Vila de Manica (3mi E)	10.IV171	Bornemissza & Aschenborn	108	-	1
Dondo (6mi SE)	19.I.72	Bornemissza & Aschenborn	346	1	-
Gorongosa NP	11-28.I.72	Bornemissza & Aschenborn	341	1	-
Gorongosa NP	22.I.72	Bornemissza & Aschenborn	338	1	-
Gorongosa NP	11-28.I.72	Bornemissza & Aschenborn	330	-	1

ANGOLA:

Jau, Huila Dist. (5mi SW)	15.IV.71	H.D. Brown	-	-	1

In South African Museum, Cape Town:

collected Kolbe 1899, det. E. Haaf 1954, as *armatus* Gory, 1 male.

3 DISTRIBUTION AND SEASONAL OCCURRENCE

All data on the distribution and seasonal occurrence of *Sisyphus* in southern Africa, have been derived with few exceptions, from the material in the Unit's collection and material collected for breeding purposes. Lists of specimens in the Unit's collection are at the end of section 2. Figure 81 shows the collecting sites visited by members of the Unit from October 1970 to May 1974. Many of these sites have been visited at least once during the months when the *Sisyphus* adults are most active (September to April). Figures 82 to 88, represent the known distribution of *Sisyphus* in southern Africa. They show that the vast majority of *Sisyphus* species are found on the eastern half of the sub-continent, i.e. in the areas with a medium to high, (500-1250 mm) average annual rainfall, which falls mostly in summer or throughout the year. Distribution in winter rainfall areas is very restricted. *S. rubrus* (fig. 86) is the most widespread and abundant species. Its distribution ranges from areas with 300 to 400 mm average annual rainfall and maximum temperatures exceeding 44°C (near Messina, N. Tvl.), to areas with 1500 to 1750 mm average annual rainfall (just east of Machipanda, Mozam.) and the minimum winter temperatures of -5°C (near Ermelo, S.E. Tvl.). *S. rubrus* occurs at sea level and in areas over 1200 metres above sea level. In contrast, *mirabilis* (fig. 84) has only been found at three places, all game reserves near each other in Zululand. At each dung beetle collection site, vegetation, soil and dung type were recorded. The *Sisyphus* species have shown few preferences with regard to these factors. Soil texture varies in areas they are found, often for one species, from clay to coarse, gravel-type sand. Since these species are telecoprids and do not burrow as much, or as deeply as paracoprids, soil texture would not be expected to influence them to any great extent. Relative acidity or alkalinity of the soil was not recorded. Its effect on distribution is, therefore, not known. In areas where dung of several types of animals is available, e.g. game reserves, individual *Sisyphus* species have been found on many dung types, from those with a fine consistency such as buffalo dung or comparatively dry impala pellets, to the very coarse dung of white rhino. No clear dung preferences have emerged from collection data where there have been sufficient records for the evaluation of an individual species. Vegetation has a marked effect on the distribution of some species. *S. seminulum* (fig. 82), *impressipennis, fasciculatus* (fig. 88) and *mirabilis* (fig. 84) have been collected almost exclusively in forest or woodland. The other *Sisyphus* species have been collected in vegetation ranging from thick riverine forest to overgrazed, treeles pastures. Therefore, it is probably a combination of altitude and climatic factors and in some cases vegetation as well, rather than soil or dung types, which determine the distribution of the species.

The reason for the choice of the Mkuzi Game Reserve as an experimental site, is also evident from the figures. Ten species have been found there and seven of these in large numbers. The distribution of these species either centres on Mkuzi, e.g. *rubrus* (fig. 86) and *spinipes* (fig. 85) or Mkuzi is their southern limit e.g. *calcaratus* (fig. 87) and *sordidus* (fig. 83), or their distribution is limited to the general area only e.g. *mirabilis* (fig. 84).

Figure 89 illustrates the known seasonal occurrence of the species but only species collected on more than two occassions, are shown. These records show a peak of occurrence in spring, summer and autumn (September to April) but since few collecting trips were made in June, July and August, these records are incomplete and are only indications of the seasonal distribution for the species.

Figure 89 indicates that the species of the subgenus, *Sisyphus,* excluding *seminulum,* are not active during winter as are those of *Neosisyphus* and including *seminulum.* In *Neosisyphus,* individuals of *spinipes* have been collected earlier at the beginning of the summer season (21st August), than for example, *fortuitus* (1st October). This suggests that *spinipes* appears in the field first, which gives it an advantage at that time as regards competition from other *Sisyphus* species. However, between the beginning of October and the end of March (summer months) all the *Sisyphus* species are found, most of them throughout this period.

The partial ecological isolation of species is evident from these data on distribution and seasonal occurrence but it has been shown here that during the summer several species in many areas will be sympatric and possibly competing with one another. Further investigations recorded in the following sections, besides supplementing these distributional data, will show how a complex combination of several different factors, including distribution, contribute to the final measure of isolation achieved by the species of *Sisyphus* in southern Africa, which reduces competition between them to a minimum.

FIGS 81 - 88

ung beetle collection sites and the distribution of *Sisyphus* species in southern Africa. Collecting sites less than 10 kms apart are represented as a single point. Game reserves here several collections were made, are drawn in as a whole.)

ig. 81 Sites at which dung beetles have been collected during the Unit's field trips from October 1970 to May 1974. Position of Mkuzi Game Reserve ringed.

ig. 82 Distribution of the species in the *S. seminulum* species group.

ig. 83 Distribution of species in the *S. costatus* species group (excluding *?goryi* since it is not certain if more than one species is involved).

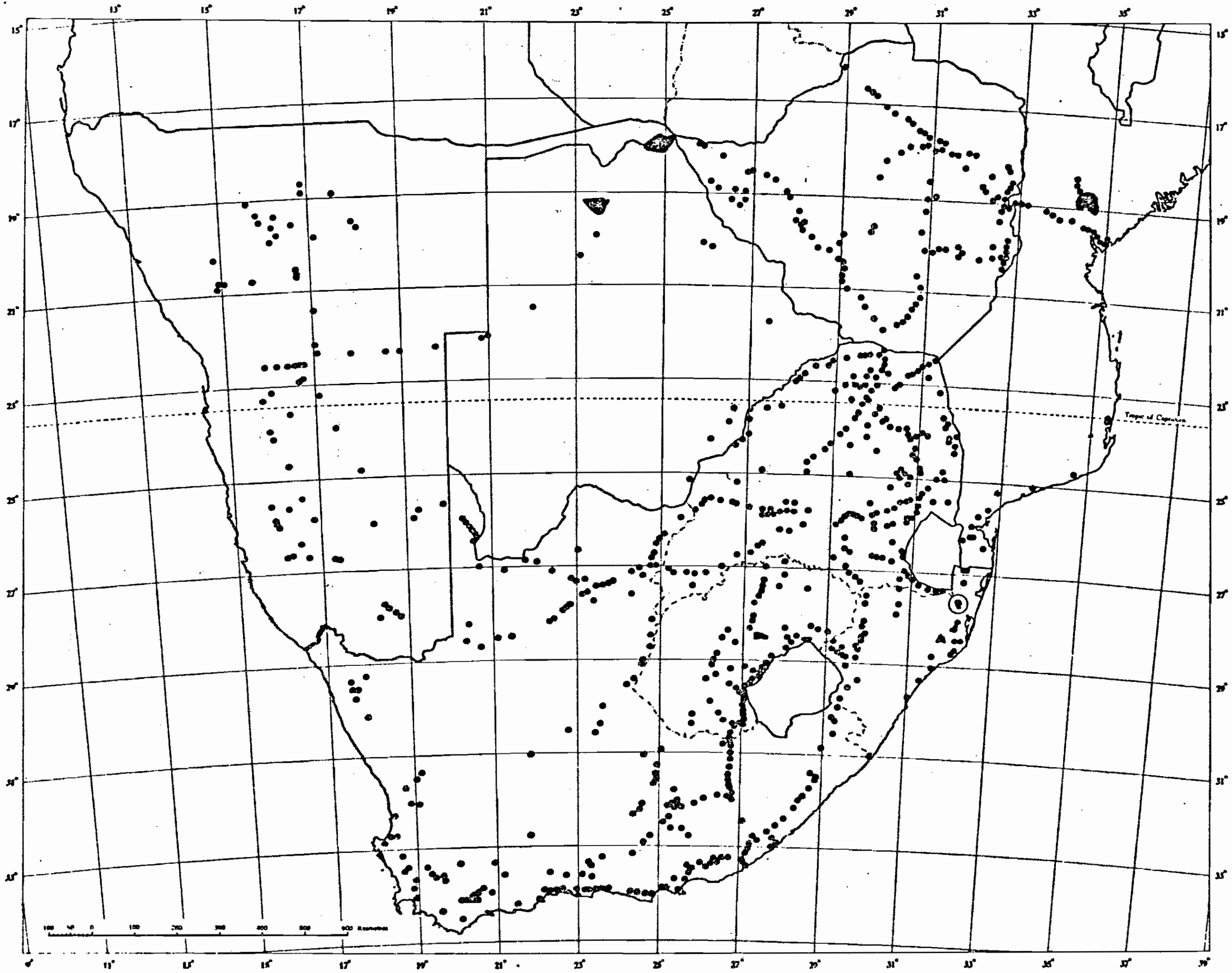
ig. 84 Distribution of *S. mirabilis*, *S. fortuitus* and *S. infuscatus*.

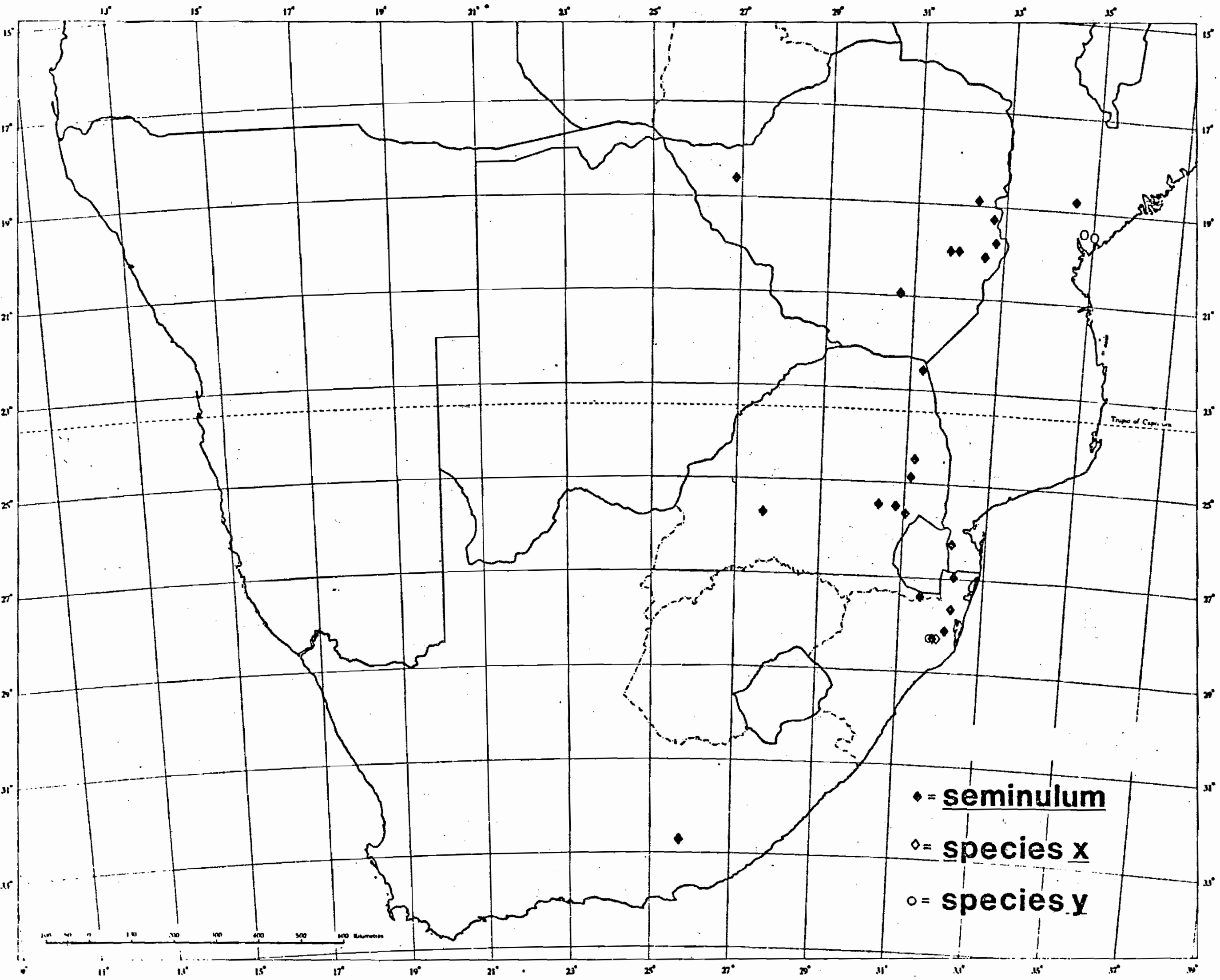
ig. 85 Distribution of *S. spinipes*.

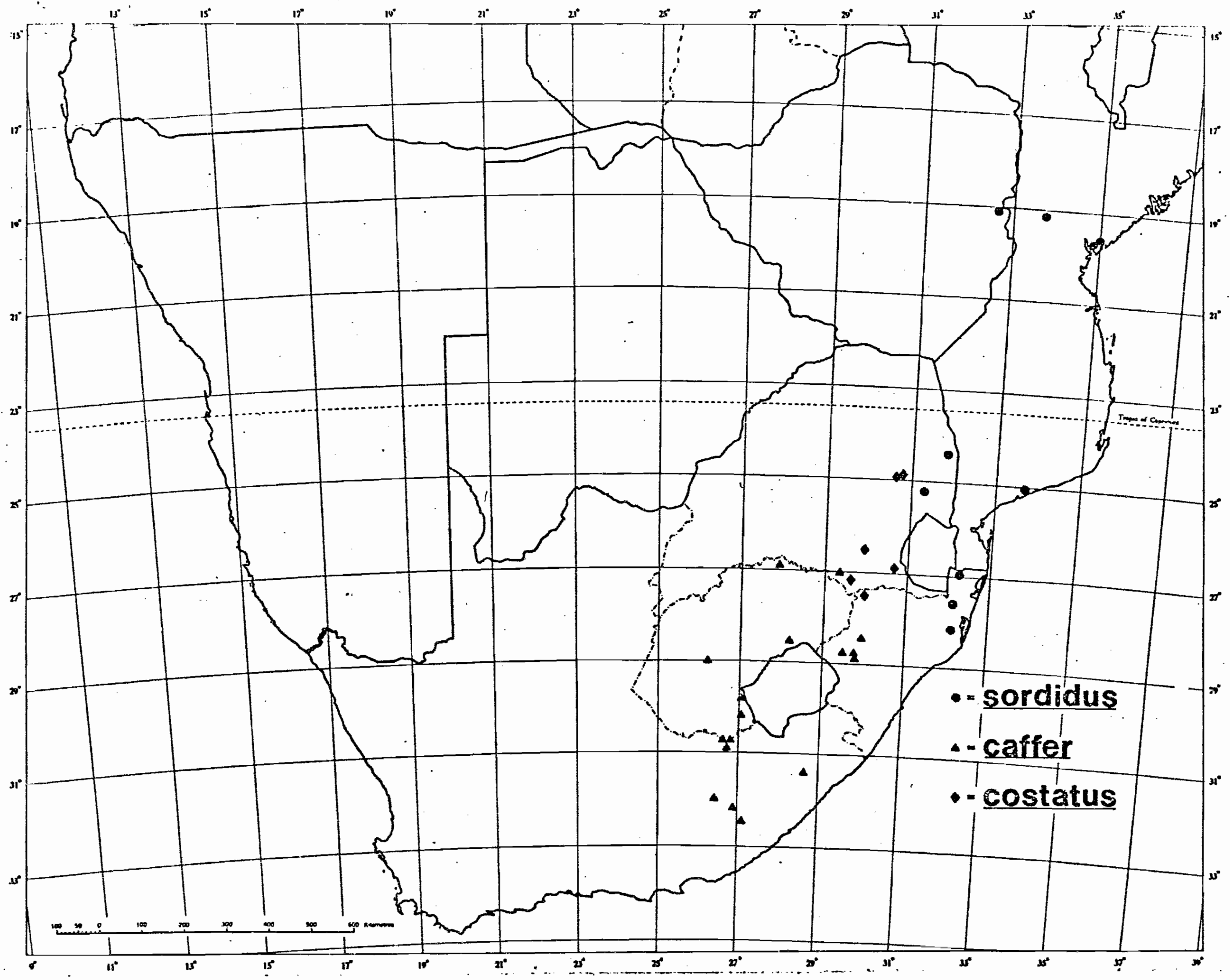
ig. 86 Distribution of the sibling species *S. rubrus* and *S. macrorubrus*.

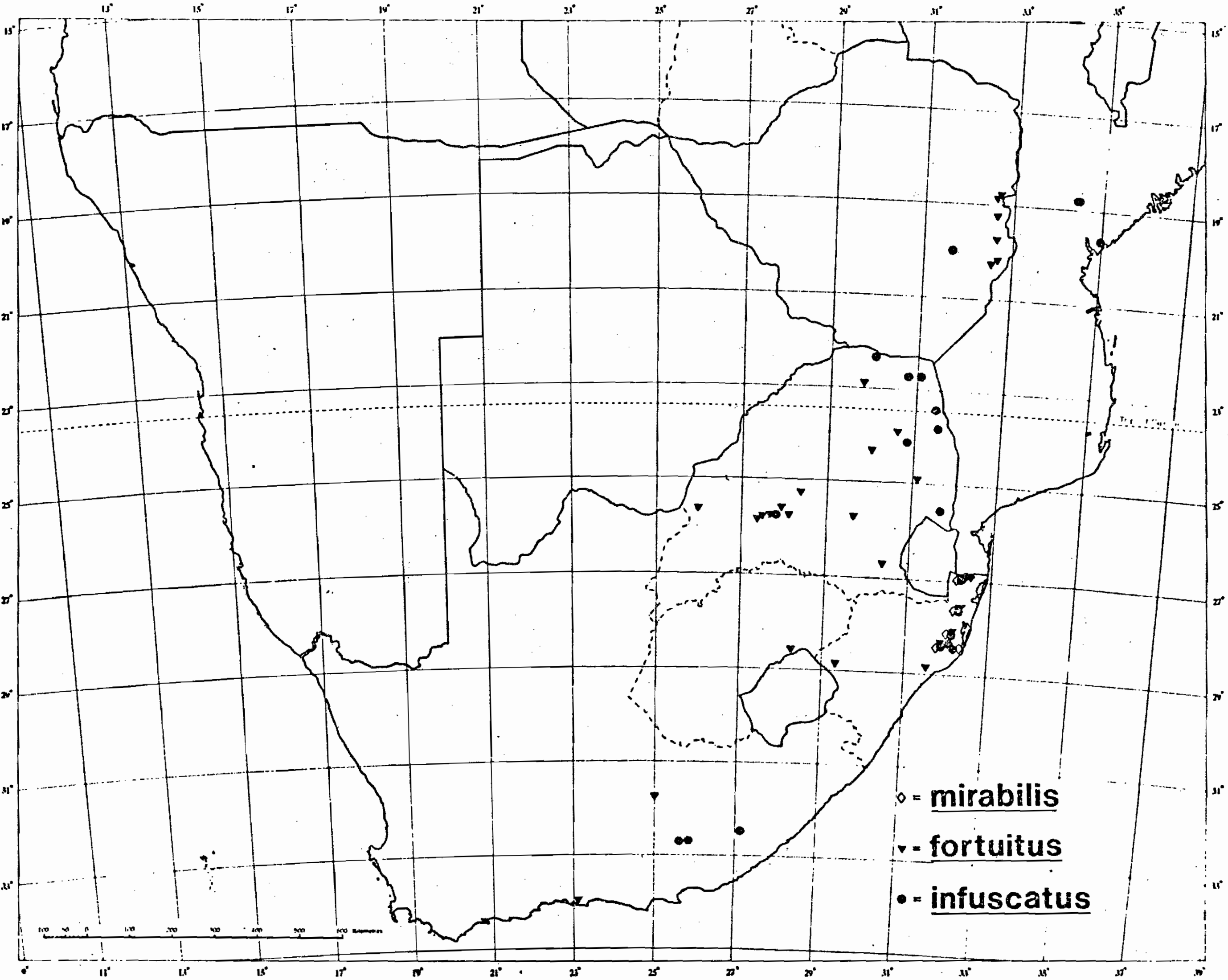
ig. 87 Distribution of species in the *S. barbarossa* species group.

ig. 88 Distribution of seven uncommon *Sisyphus* species, or those with a limited distribution.


13°
15°
17°
19°
21°
23°
25°
27°
29°
31°
33°
35°
Tropic of Capricorn
100 50 0 100 200 300 400 500 600 Kilometres
9°
11°
13°
15°
17°
19°
21°
23°
25°
27°
29°
31°
33°
35°
37°
39°

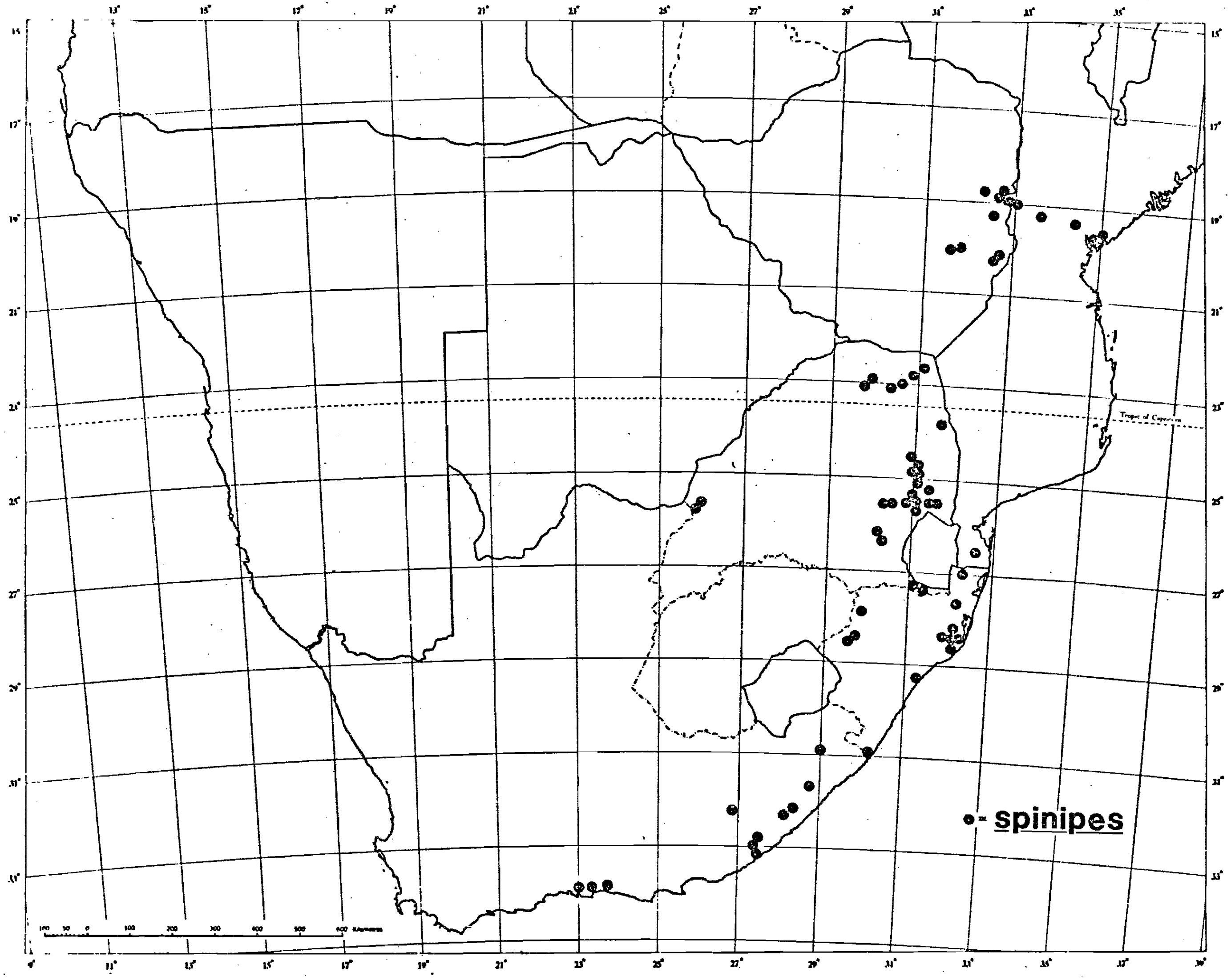

◆ = seminulum
◇ = species x
○ = species y
Tropic of Capricorn
Kilometres

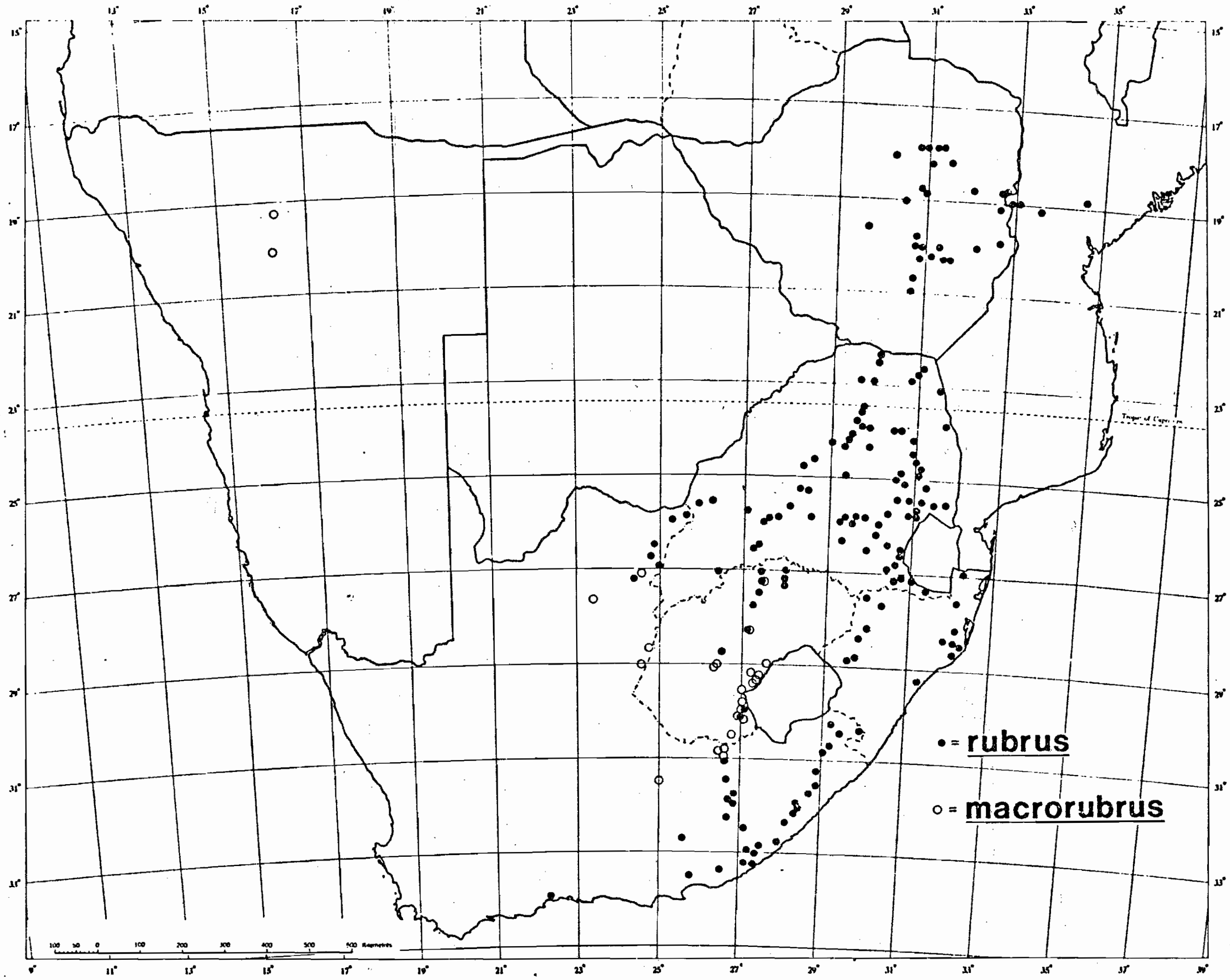

● - sordidus
▲ - caffer
◆ - costatus
Tropic of Capricorn

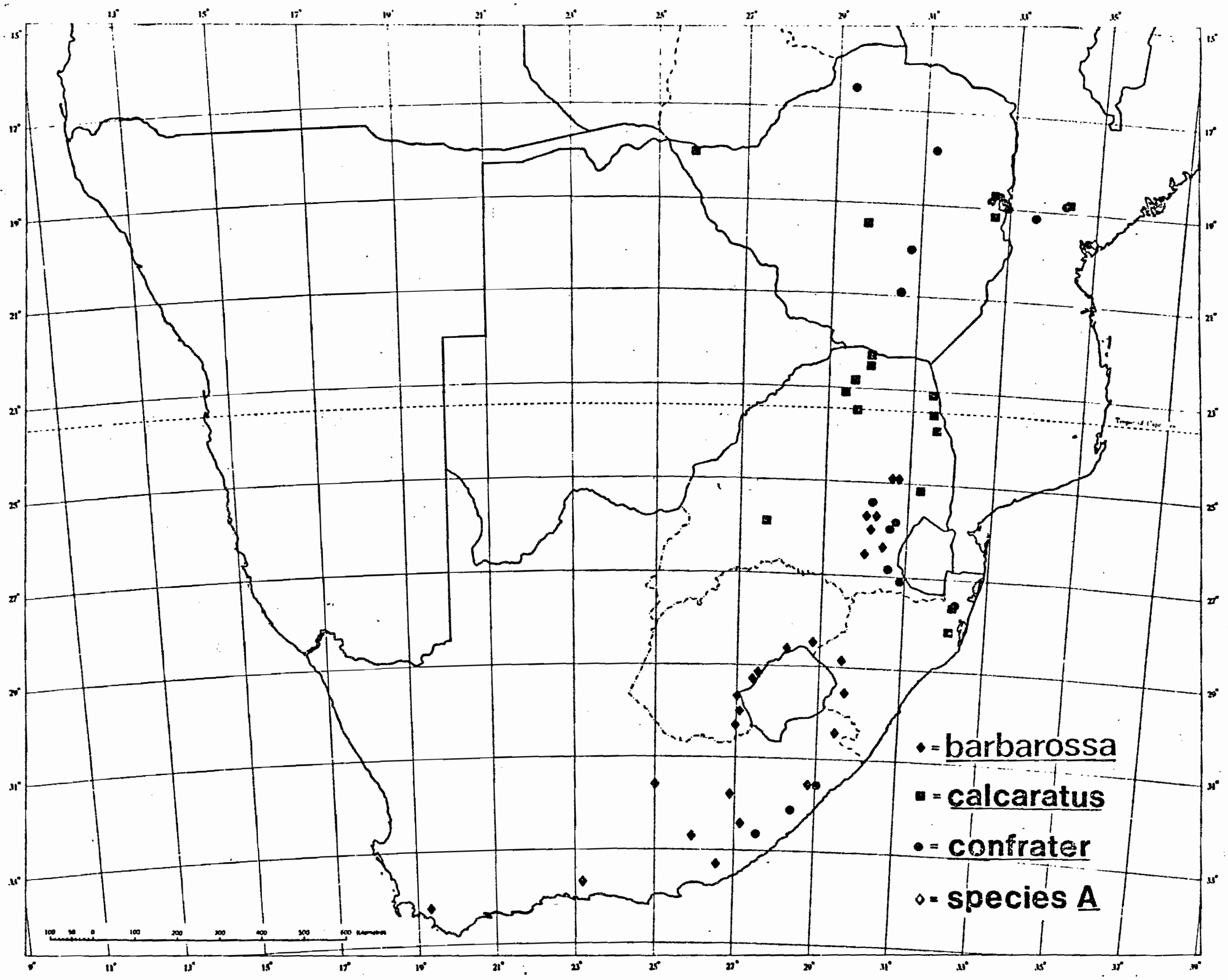
13°
15°
17°
19°
21°
23°
25°
27°
29°
31°
33°
35°
◇ = mirabilis
▼ = fortuitus
● = infuscatus

84

85




● = rubrus
○ = macrorubrus
Tropic of Capricorn



◆ = barbarossa
▣ = calcaratus
● = confrater
◇ = species A
Tropic of Capricorn
100 50 0 100 200 300 400 500 600 Kilometres

87

88

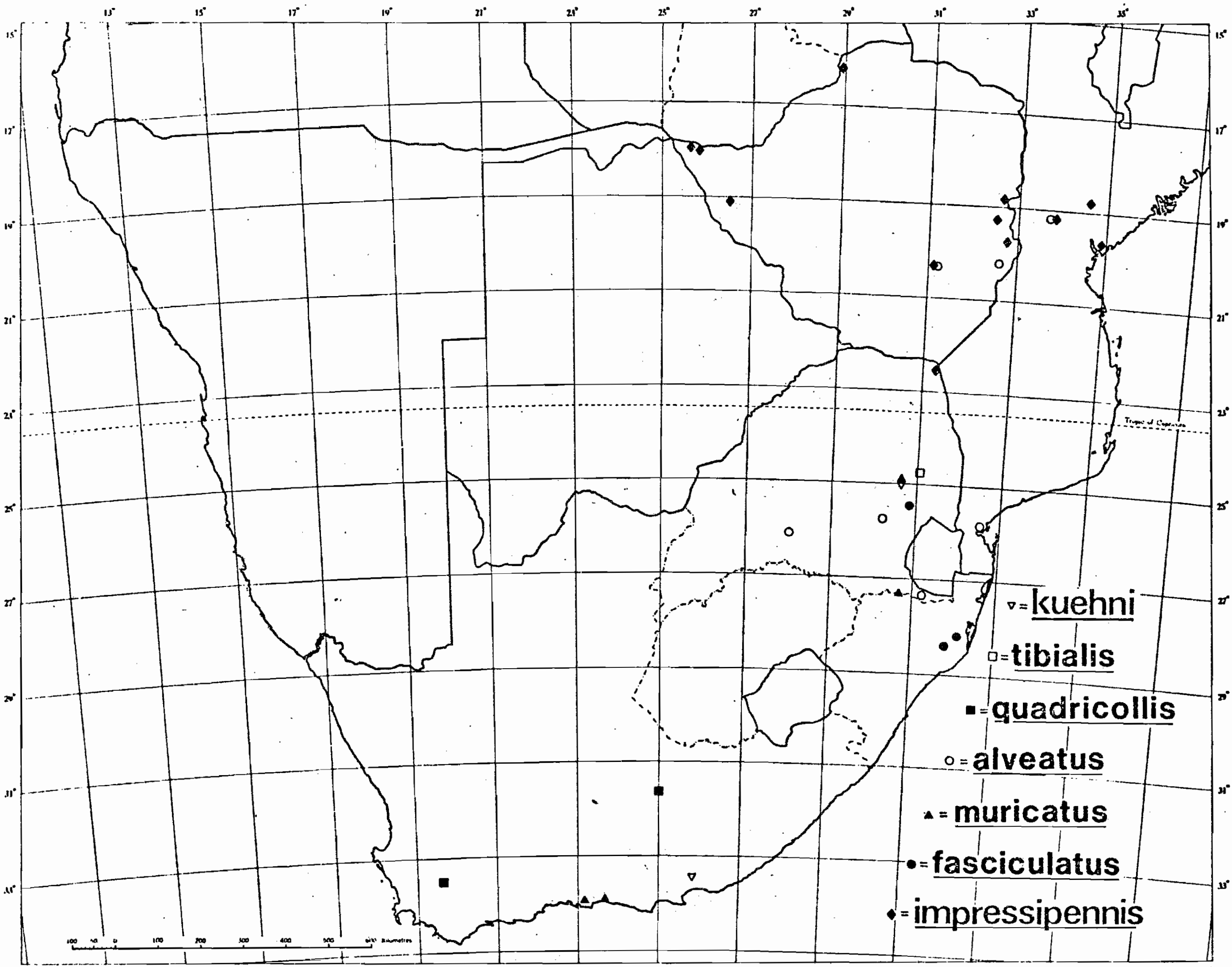
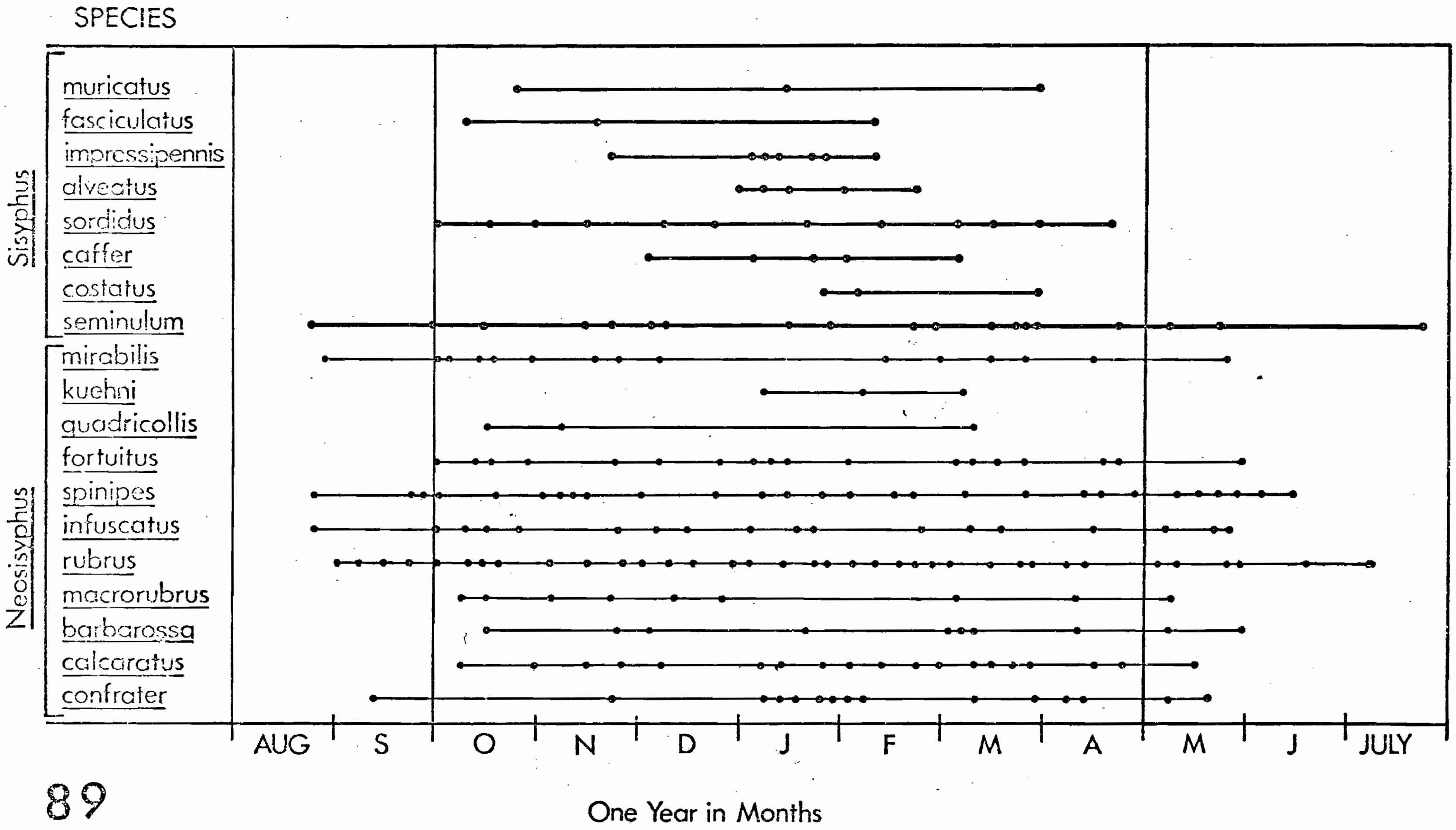

▽ = kuehni
□ = tibialis
■ = quadricollis
○ = alveatus
▲ = muricatus
● = fasciculatus
◆ = impressipennis
Tropic of Capricorn
Kilometres

FIG 89

Seasonal occurrence of *Sisyphus* species in southern Africa, obtained from cumulative field data collected between October 1970 and May 1974. *Sisyphus* field activity starts each year in early spring (end of August/beginning of September) and is most obvious from the end of September until the end of April, the period represented between the two vertical lines in this figure. (Collections of individual *Sisyphus* species made less than four days apart, are represented as a single point.


SPECIES
Sisyphus
muricatus
fasciculatus
impressipennis
alveatus
sordidus
caffer
costatus
seminulum
Neosisyphus
mirabilis
kuehni
quadricollis
fortuitus
spinipes
infuscatus
rubrus
macrorubrus
barbarossa
calcaratus
confrater
AUG
S
O
N
D
J
F
M
A
M
J
JULY
One Year in Months

4 MATERIALS AND METHODS

4.1 Laboratory cultures

Most of the techniques for breeding dung beetles had already been developed by Dr. G.F. Bornemissza, in Australia. They were adapted to suit the particular needs of this genus.

The *Sisyphus* cultures were kept in a laboratory which was heated when necessary by a thermostatically controlled convection heater. No cooling was found to be necessary. Laboratory temperature regimes were kept as close as possible to those of the experimental area in the Mkuzi Game Reserve, as indicated in Table 1. The mean daily temperatures are given for summer (October to March) and winter (May to August).

Table 1: Comparison of temperatures in the Mkuzi Game Reserve and in the laboratory, from October 1971 to December 1973.

		Mkuzi	Laboratory
Summer	Mean Daily Maximum	31,8°C	30,3°C
	Mean Daily Minimum	19,5 °C	20,4 °C
Winter	Mean Daily Maximum	25,6 °C	25,0 °C
	Mean Daily Minimum	12,5 °C	15,8 °C

Relative humidity in the laboratory was not controlled and varied widely from 20% to 96% in summer and 15% to 83% in winter depending on watering regimes in the laboratory. Relative humidity was, however, usually above 50%. Temperatures and humidity in the laboratory were monitored with a thermohygrograph and maximum and minimum temperatures were also recorded. Normally, lighting in the laboratory was natural daylight from large windows.

Adult beetles for observation were paired within four days after emergence and placed in small, individually labelled celluloid containers, (fig. 90). Single pairs placed in larger square containers (25 x 17,5 cm) but with the same depth (8 cm) showed a marked reduction in ball production. For example, four pairs of *mirabilis* showed a reduction of 61,4% in ball production over 29 days, compared with two pairs which were left in the small circular containers. These small circular containers were found to be the most suitable for individual pair rearing.

The dung used was from pasture fed cattle and was collected fresh (within five hours of being voided) in the early morning to lessen chances of contamination by beetles in the field. This dung contained about 80% water (by weight). A small quantity of water was mixed in the dung collected to facilitate shaping of the pads in the containers. The dung then contained about 85% water. Beetles were given fresh dung every three to four days in summer and four to six days in winter. Dung was removed from the breeding containers when the water content had dropped to between 35% and 50%. Dung colonized by *Sisyphus* in the field (observed for *rubrus* and *?goryi*) varied from 86% to 35% water content and *rubrus* was observed making brood balls in dung from 80% to 50% water content, which is typical for most *Sisyphus* species. Soil used was a standard mixture of two parts river sand, four parts river loam and one part shredded peat-moss. This mixture is the standard used by the Unit. Soil moistures varied from 4% to 13% water content (by weight) for adult *Sisyphus* cultures.

FIGS 90 AND 91

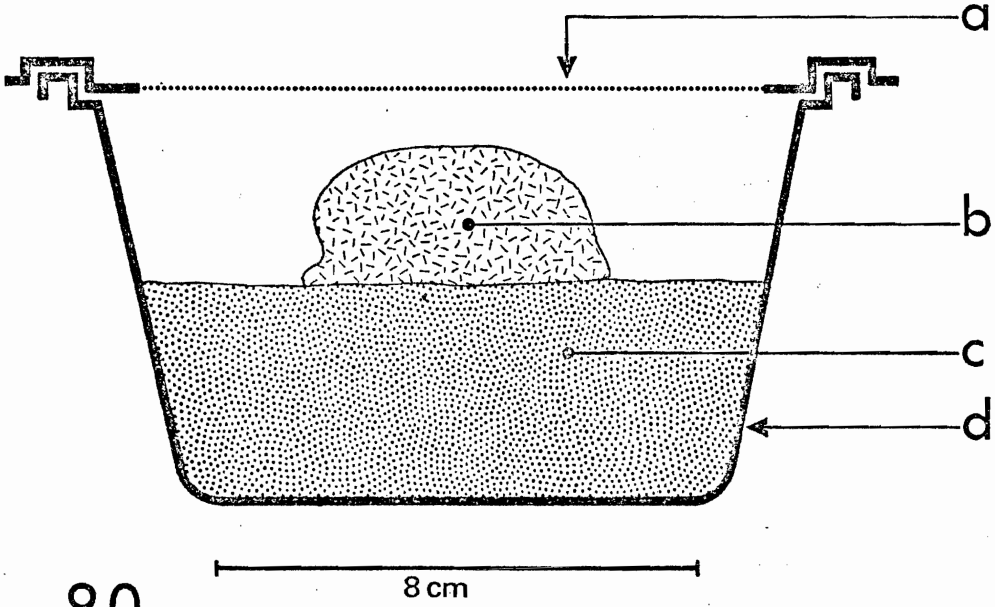
Containers for rearing of live material in the laboratory

Fig. 90 Vertical section of container for individual adult pair rearing.

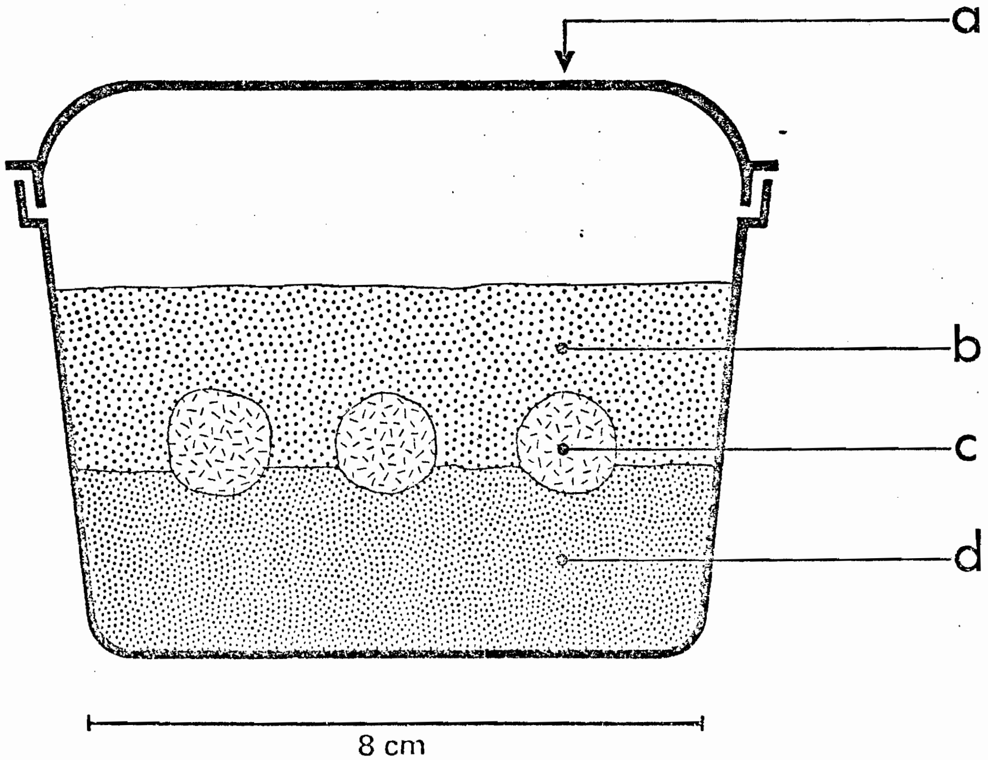
a - nylon netting of lid.
b - dung.
c - well packed soil.
d - container.

Fig. 91 Vertical section of container for rearing of immature stages in brood balls.

a - loosely fitting transpartent lid.
b - loosely packed soil.
c - brood ball.
d - well packed soil.



90



91

Total Numbers of adult pairs observed from emergence, or collection, until death, are listed in table 2. All biological data are based on these pairs and supplemented in some species where results were not substantial, by data from mass cultures.

Brood balls collected from the mass culture or individual pairs were buried in soil in a plastic container (fig. 91). This method of closed container rearing of immature stages was developed in preference to screened top containers used previously by the Unit, because of high mortality of larvae, pupae and teneral adults in the brood balls, resulting from difficulties with soil moisture regulation in the open containers. With the use of closed containers the number of adults emerging from the brood balls (one egg is laid in each ball) increased from 20% to 70% of the total number of brood balls set. Soil moisture in these closed containers was maintained at a lower level than that used for adult rearing. It varied from 3% to 8% water content for all species. Containers were checked regularly for emerging adults, although the newly emerged beetles could live for a few days, without food, in these containers. The total numbers of adults per species which emerged in the laboratory and on which emergence records are based, are listed in table 3.

Table 2: Number of individual pairs and individuals in mass cultures, observed in laboratory

Sisyphus				*Neosisyphus*			
Species	No. of laboratory bred pairs	No. of field collected pairs	Approx. no. of individuals in mass cultures	Species	No. of laboratory bred pairs	No. of field collected pairs	Approx. no. of individuals in mass cultures
S. muricatus	4	1	20	*S. tibialis*	12	11	-
S. fasciculatus	17	6	40	+*S. mirabilis*	29	10	300
S. impressipennis	2	11	-	*S. kuehni*	-	2++	-
+*S. seminulum*	22	10	200	+*S. fortuitus*	19	8	50
+*S. sordidus*	10	6	200	+*S. spinipes*	35	11	300
S. costatus *S. caffer* *S. ?goryi*	-	-	50	+*S. infuscatus*	20	-	100
				+*S. rubrus*	38	-	200
				S. macrorubrus	3	10	100
S. species *Y*	-	1	-	*S. barbarossa*	4	3	40
				+*S. calcaratus*	38	3	200
				S. confrater	5	-	50

(+ = the 8 Mkuzi species)

(++ = information on one pair supplied by G.F. Bornemissza)

Table 3: Numbers of adults which emerged in the laboratory

Species	Total No. emerged	No. of males	No. of females
S. muricatus	8	4	4
S. fasciculatus	39	18	21
S. impressipennis	.11	7	4
+*S. seminulum*	196++	?	?
+*S. sordidus*	21++	?	?
other *S. costatus* group species	14++	?	?
S. tibialis	71	32	39
+*S. mirabilis*	350	175	175
S. kuehni	7	2	5
+*S. fortuitus*	122	54	68
+*S. spinipes*	237	108	129
+*S. infuscatus*	232	112	120
+*S. rubrus*	267	131	136
S. macrorubrus	32	15	17
S. barbarossa	18	9	9
+*S. calcaratus*	338	160	178
S. confrater	120	65	55

(+ = the 8 Mkuzi species)

(++ = As it was not possible to sex every specimen positively by morphological characters on emergence, numbers of males and females have not been given.)

4.2 FIELD WORK

Sisyphus specimens were collected during all the Unit's field trips, mainly for the reference collection but because of the difficulties in recognizing the individual species, especially in the field, all specimens found were usually brought back to the laboratory for identification. In this way large serial collections of species were made. There was no set sampling routine. Time spent in an area depended on the amount of dung beetle activity and varied from

15 minutes to over two hours. *Sisyphus* specimens were collected from the dung pads, or as they landed on, or near them. Pads inspected were mostly relatively fresh, usually less than five days old. In areas where there was little suitable dung available for inspection but evidence of good previous activity, fresh dung pads were put down from a supply of dung carried on the trips. Beetles coming to these pads were then collected.

Traps were also set to catch dung beetles for general distribution data, and for monitoring *Sisyphus* populations in Mkuzi. For trapping *Sisyphus* and other dayfliers traps as shown in figure 92 were found to be the most effective. The bait in the traps was dung. The dung beetles are strongly attracted by olfaction to this source of food and breeding materials (Halffter and Matthews, 1966). Although the dung in the trap was out of sight, this did not decrease the effectiveness of the traps, since vision seems to play no part in the location of dung (Heymons and von Lengerken, 1929). Six permanent traps were set at the selected experimental site in the Mkuzi Game Reserve, arount the Msinga Hide and were constructed as in figure 93. These were very similar in construction and operation to those used by the Unit generally for trapping. The area of the permanent traps which was used in monitoring the dung beetle population and for field experiments, was a wooded area around a water hole and had sandy soil. The six traps were in operation from February 1973 until April 1974. They were set around 6 a.m. one day by a Natal Parks Ranger and were collected at the same

FIGS 92 AND 93

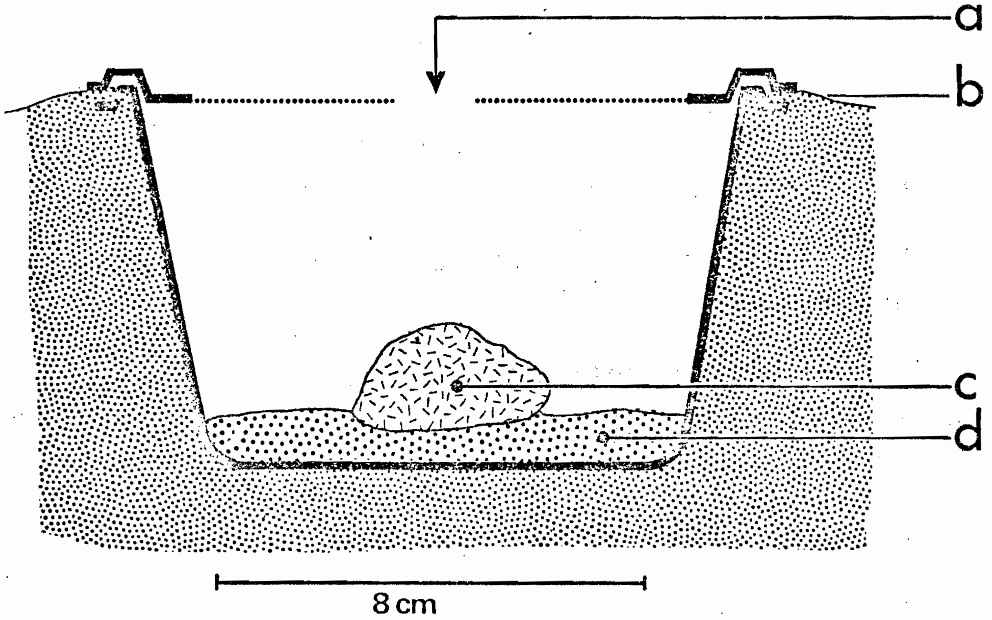
Field traps for dung beetles.

Fig. 92 Vertical section of temporary trap used for hourly monitoring of day flying dung beetles.

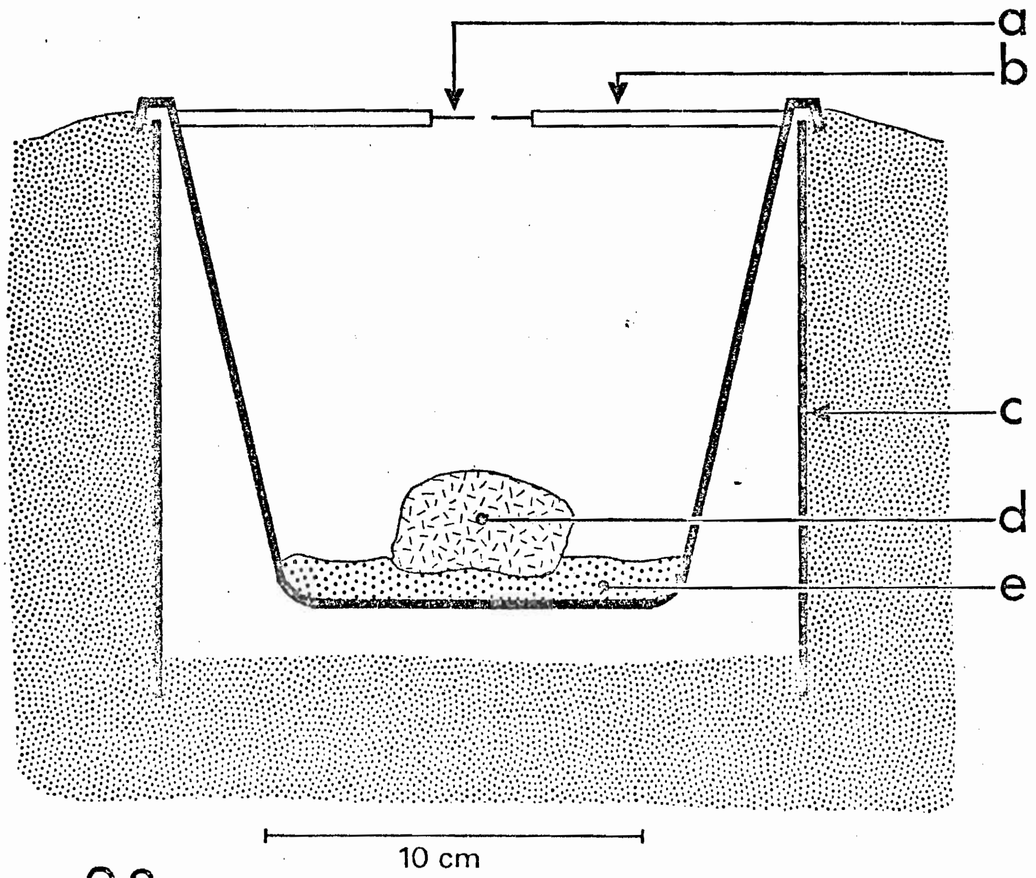
a - hole in netting
b - surface of ground
c - dung bait
d - sand

Fig. 93 Vertical section of one of six traps at permanent sites in Mkuzi Game Reserve.

a - soft polythene strips to prevent escape of trapped beetles.
b - clear perspex lid.
c - circular iron "collar" permanently in ground in trap position.
d - dung bait.
e - sand.



92



93

time on the following day. The contents of each trap were placed in individually labelled containers and posted to Pretoria where the beetles were identified. This was repeated usually once every two weeks in summer and once a month in winter.

Sisyphus activity was further investigated by intensive collections in the Zululand reserves during November 1971, March 1972, October 1972, February 1973, May 1973, December 1973 and April 1974. During the December 1973, and April 1974 trips, hourly traps were operated at the experimental site between 7 a.m. and 5 p.m. These were of the type shown in figure 92. Over the same period in December, pads of cow dung, placed at the same site, were continually monitored for beetle activity from 7 a.m. to 5 p.m. Smaller pads were put down at intervals during one day to investigate aggregation in different *Sisyphus* species and other genera.

5 GENERAL BIOLOGY OF THE GENUS

Sisyphus is a genus of dung ball rolling beetles. They are all day flying and breed most actively in summer. Figure 94 is a diagrammatic representation of the life history of *Sisyphus*, from egg to adult. Most dung beetles have similar life histories but there are many variations in the formation of broods and duration of stages.

5.1 PRE-REPRODUCTIVE PERIOD

Sisyphus adults usually emerge from their brood balls during the warmer part of the day. The sex ratio is approximately 1 : 1 as determined from the laboratory emergences (table 3) and field collected material (section 2.4). The male is fertile at emergence. The female undergoes a feeding period which lasts from one to three weeks, before oviposition begins. This feeding period may however, last ten months in species which do not breed during winter. The sexes feed separately, on the liquid part of the dung and the mouth parts of the adult dung beetle have become adapted for this purpose. Most of the mouthparts have become membraneous except the molar areas of the mandibles which are modified to grind food particles to a few microns in size (Halffter and Matthews, 1966). After the initial feeding period, the female of the *Sisyphus* species copulates several times with different males, over a period of days. Then often with the co-operation of a male, the first brood ball is formed by the female from the dung.

FIG 94

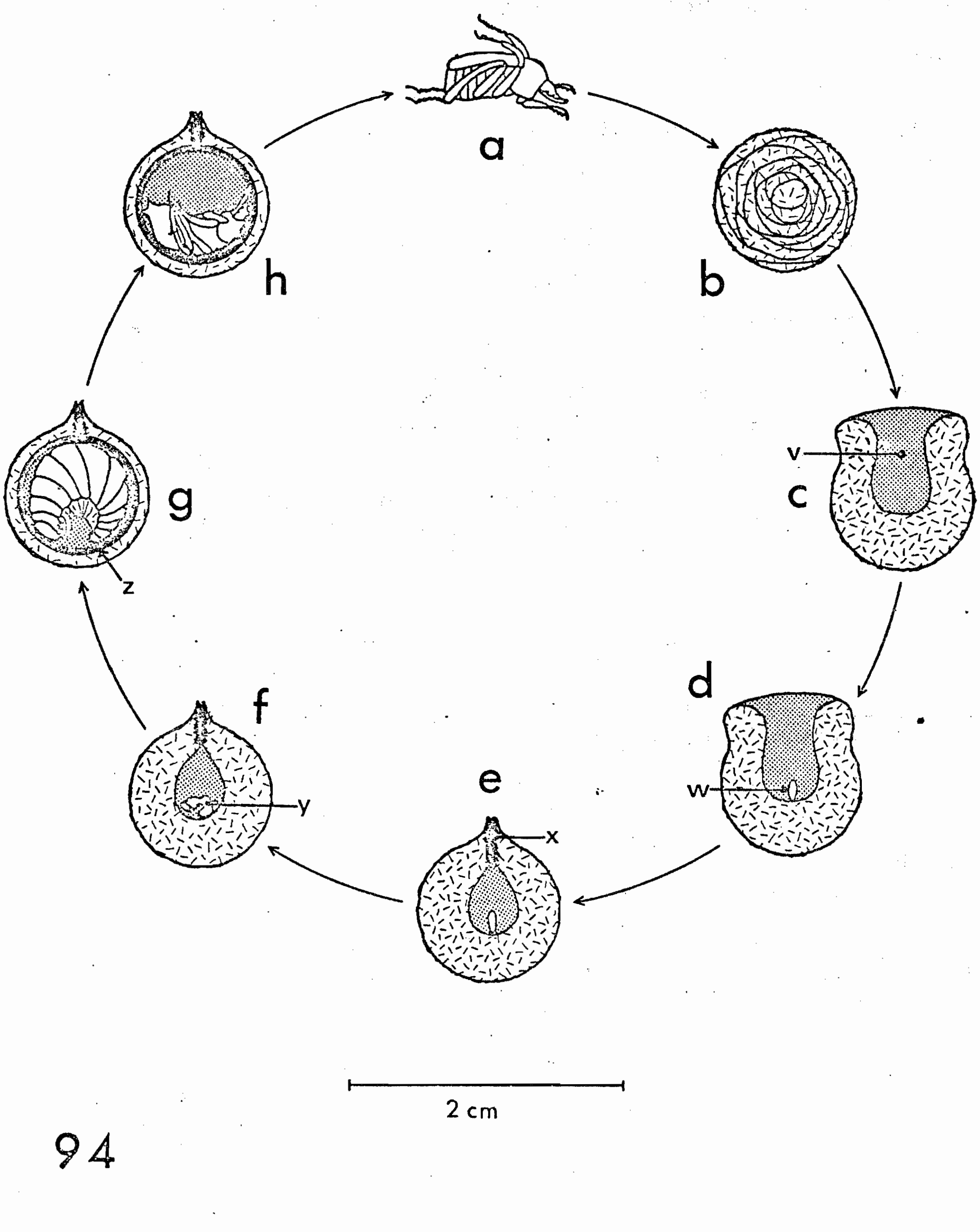
Generalized life history of *Sisyphus* species and their sequence of brood ball formation. (Brood balls drawn in vertical section).

a. Adult emerges and feeds on fresh dung.
b. First brood ball is formed from dung pad, is rolled away and in some species is buried at this stage.
c. Female forms egg chamber in ball.
d. Female lays egg in chamber.
e. Female closes egg chamber and in the remaining species ball is buried at this stage.
f. Egg hatches, larva feeds.
g. Three larval instars are completed. Third (final) instar larva is the usual immature overwintering form.
h. Pupa- stage is reached after a short prepupal stage in which the gut is emptied and the body shrinks.

Duration of stages

a-b. Emergence to first brood ball: either five to 30 days or over six months.
b-e. Completing one brood ball: usually within six hours.
e-f. Egg laid to larva hatches: four to 27 days.
f-g. Hatching to mature third instar larva: three weeks to several months.
g-h. Larva to pupa: either one week or several months.
h-a. Pupa to adult: within three weeks.

v = egg chamber
w = egg
x = tunnel of loosely packed dung where chamber has been closed.
y = newly hatched larva.
z = faecal shell.


a
b
v
c
d
w
e
x
f
y
g
z
h
2 cm

5.2 REPRODUCTIVE PERIOD

Reproductively active females are often found feeding or mating with a male in the dung. The female is usually responsible for initiating brood ball making. Unmated females, if kept isolated in the laboratory, sometimes make a few brood balls after an extended feeding period. These may contain infertile eggs, or no eggs at all. Isolated males of *mirabilis* make brood balls and this might apply to other species in the subgenus *Sisyphus*. Comingnan (1928) considers ball making to be initiated by tactile and olfactory stimuli. In *Scarabaeus semipunctatus* Fabricius, by holding dung over non-nutritive pulp and applying ammonia to the antennae, he got the beetles to make balls of the pulp. Balls will not be made until a certain threshold of olfaction is reached, however. Puzanova-Malysheva (1956) found in another species of *Scarabaeus* that the material offered must contain at least 50% dung to initiate ball making. The ball rollers also seem sensitive to the weight of the ball. Puzanova-Malysheva (1956) offered *Scarabaeus sacer* Linnaeus a dung ball of the correct size but containing a lead weight. This ball was torn apart, the weight removed, and the ball then made up again. Using the same species she demonstrated that any shape of dung offered to individuals will be moulded into a round ball of the correct size. Halffter and Matthews (1966) sum up these observations, saying "we thus see that the beetles have an acute awareness of the exact shape, size and weight of the masses they are handling, and an ability to cope with a wide variety of situations regarding the ball, indluding some which must very seldom be encountered under natural conditions".

In summer the brood balls of the *Sisyphus* species are usually made during the cooler parts of the day, (15-25°C) which are early morning or late afternoon and evening. In winter, balls are made during the warmer periods (15-25°C) which may be later in the day. If the male is with the female, he will mate with her during this ball making. Brood balls are formed usually under or at the edge of the dung pad, by *Neosisyphus*, from a small core of about 25% of the final diameter of the ball. Onto this core successive layers of dung are added using prothoracic legs. The metathoracic legs are considered to act as callipers for judging ball diameter (Halffter and Matthews, 1966). Hingston (1923) found with *Gymnopleurus miliaris* Fabricius, also a telecoprid, that if one hind leg was removed the beetle could no longer form a spherical ball. The same has been observed with the female beetles in the present study, strengthening the contention that in *Sisyphus*, the female has the major role in ball making and shaping. The diameter of the completed brood ball, besides being dependent on the size of the beetle, is also species specific as illustrated from previous literature by Halffter and Matthews (1966). Table 4 indicates that the ball/beetle ratio for seven southern African species of *Sisyphus* differs in the individual species.

Table 4: Ball diameter/beetle body length; means and ranges for seven *Sisyphus* species (Mean ball diameter divided by mean beetle body length = ratio)

Species	Mean of ratios calculated for individual females	Range of ratios	Mean female body length in mm	No. females measured	Mean ball diameter in mm	No. balls measured
barbarossa	1,45	1,31 - 1,54	9,2	11	13,5	83
calcaratus	1,45	1,30 - 1,60	7,1	14	10,6	92
infuscatus	1,58	1,53 - 1,67	8,1	7	13,6	72
fortuitus	1,60	1,50 - 1,70	10,2	11	17,1	74
rubrus	1,63	1,53 - 1,72	7,3	6	14,7	39
mirabilis	1,68	1,52 - 1,78	9,5	9	16,2	62
spinipes	1,93	1,80 - 2,01	8,4	7	17,6	48

When the brood ball is completely formed from the dung it is rolled away by the pair, as shown in the frontispiece, or by the female alone. If both are co-operating the male usually pushes and the female pulls the ball but this can be changed when trying to overcome obstacles. On her own, the female will either push or pull the ball, pushing it when the terrain is even and pulling when obstructions or difficulties are encountered.

A "pirate" female of the same or different species, may challenge another female for her ball, or two males may fight for the ball or compete for the female on the ball. Especially between males, this combat is agressive and one male may chase another some distance from the female and ball while the female rolls her ball away alone. If the stolen ball is smaller than that specifically used by the "pirate" female, she may take it back to the dung and add to it or steal another ball and add it to the first. If the ball is too big she will cut it down to size with her front legs. Direction of rolling from the dung, as observed in 66 pairs of *seminulum* at the Umfolozi Gamer Reserve, Zululand, was apparently haphazard as regards position of the sun and slope of the ground. Matthews (1963) has demonstrated , however, that slope of the ground, wind direction and position of the sun have a positive influence on the direction of balls rolled by *Canthon pilularius* (L). More detailed investigation could reveal the influence of these factors on *Sisyphus* species. The pairs of *seminulum* observed, generally rolled their balls in straight lines from the dung source. Matthews (1963) also noted this for *Canthon pilularis* (L). The advantage of this seems to be obvious, as discussed by Halffter and Matthews (1966), i.e. the beetle can get its ball farthest from the dung source and possible competition, as soon as possible. After rolling the ball for a distance which may be several centimeters to several metres, depending on the terrain and species involved, the ball is either buried, usually under an object, or placed up in grass stems or twigs (figs 95 and 96).

In two species which bury their brood balls, *rubrus* and *calcaratus*, the choice of the actual burial site by the female, was investigated in the laboratory. A total of four pairs of each species were used. Two pairs of each species were placed in one of two containers of 64 x 38 cm

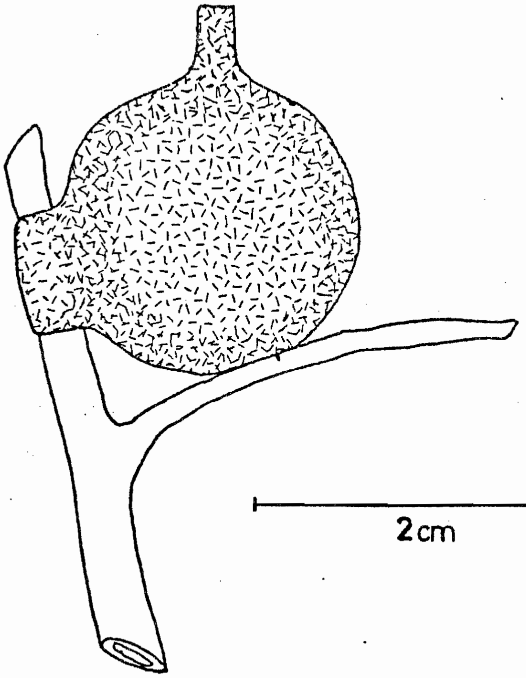
FIGS 95 AND 96

Brood ball deposition sites.

Fig. 95 A completed brood ball of *S. spinipes* cemented onto twig, as an example of a brood ball left in the vegetation. Only balls of *spinipes* have been observed to be cemented with dung onto the vegetation.

Fig. 96 A brood ball of *S. calcaratus* buried under the edge of a stone, as in several other *Sisyphus* species.

a - stone
b - soil
c - excavated soil
d - brood ball



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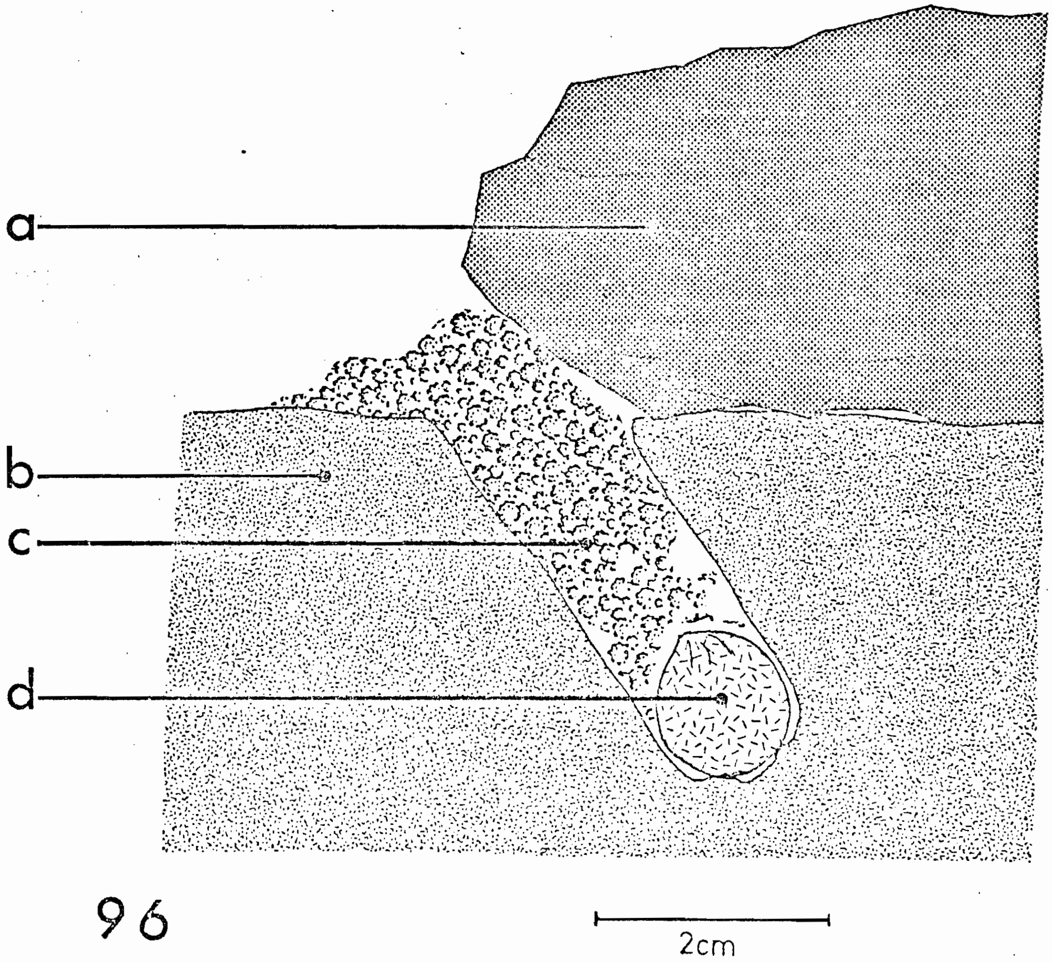


96

and with a depth of 20 cm. They contained 8 cm of soil. Four different types of possible burial sites were offered in various combinations, in the containers. These four sites were:

(a) moist soil under stones;

(b) exposed moist soil (not under cover);

(c) dry soil under stones;

(d) exposed dry soil.

Each test ran for about ten days. Three different combinations of sites were used but the choice of all four sites was repeated three times with the positions of sites interchanged. The numbers of balls buried at the different sites are recorded in table 5.

Table 5: Results of brood ball burial investigation in *rubrus* and *calcaratus*.

Combination of burial sites offered	Number of balls buried in each site.											
	a=moist soil under stones			b=exposed moist soil			c=dry soil under stones			d=exposed dry soil		
	+*rub*	++*calc*	Total	*rub*	*calc*	Total	*rub*	*calc*	Total	*rub*	*calc*	Total
a,b,c and d	20	20	40	2	0	2	3	1	4	0	1	1
b and d	-	-	-	8	6	14	-	-	-	0	0	0
b,c and d	-	-	-	2	7	9	5	12	17	0	1	1

+*rub* = *rubrus* ++*calc* = *calcaratus*

The results in table 5 show that the females have a preference for burying their brood balls in moist soil under stones (40/47 balls). The females selected exposed moist soil (14 balls) only if the other choice was exposed dry soil (0 balls). When dry soil under stones was offered in addition to exposed moist and dry soil the females preferred the covered area (17 balls) although some females still selected the exposed moist soil (9 balls). The advantages gained for the survival of the immature stages, by these preferences is obvious.

In *calcaratus*, ball burial behaviour of 29 females in individual pair containers (fig. 90) was observed as regards the soil moisture in the containers. In the laboratory *calcaratus* does not always bury its brood balls. When the soil had a water content of 0-3% then 73% of the total number of balls recorded (175) were buried. At water contents from 3-15% the percentage ball buried remained at about 50% (total number of balls recorded : 598). The site of ball burial in the container, either under the dung, or between dung and the side of the container i.e. in uncovered soil, was recorded for a total of 325 balls. Table 6 records the numbers of balls buried at these sites, according to the water content of the soil at the time of burial.

Table 6: Site of brood ball burial for *calcaratus* in individual pair containers with soil of different moistures.

Water content in soil	% of balls buried under dung	% buried between dung and side (in uncovered soil)	Total number of balls recorded.
0 to 3%	100	0	93
4 to 7%	85,7	14,3	140
8 to 11%	80,9	19,1	47
12 to 15% (saturated soil)	46,7	53,3	45

The results in table 6 show that balls are buried in a more protected place if the soil is not wet. *S. calcaratus* females also tend to bury more of their balls, (73% as against 50%) when the soil is relatively dry, indicating that the female responds behaviourally to the environmental conditions existing at the time she is rolling the brood ball.

In some species the egg is laid in the ball before burial e.g. *calcaratus* but in others, including *rubrus* and those taking their balls into grass stems and twigs, the egg is laid after deposition. The sequence for oviposition is shown in figure 94 (stages b-g) and the male, if with the female will mate with her but not assist her during the formation and closure of the egg chamber. The single egg laid is usually stuck lightly to the bottom wall of the egg chamber by a soft dark secretion produced by the female, which also lines the entire egg chamber. Halffter and Matthews (1966) speculate that this layer may be antibiotic, to protect the egg from mould growth. In the laboratory up to three eggs have been found in one ball. This would not normally occur in the field since the female leaves the ball after oviposition, for a new dung pad. In all *Sisyphus* species the position of brood ball closure (fig. 94e) can be detected either by an obvious tip, in those species which carry their balls into grass stems, or a cap or small point in species which bury their balls. Figure 97 illustrates the variation in the completed brood ball shape and size among *Sisyphus* species. Halffter and Matthews (1966) suggest that the area where the brood balls of ball rolling genera have been closed which contains a tunnel of less firmly packed dung (fig. 94e), could be for air exchange. This tunnel is present

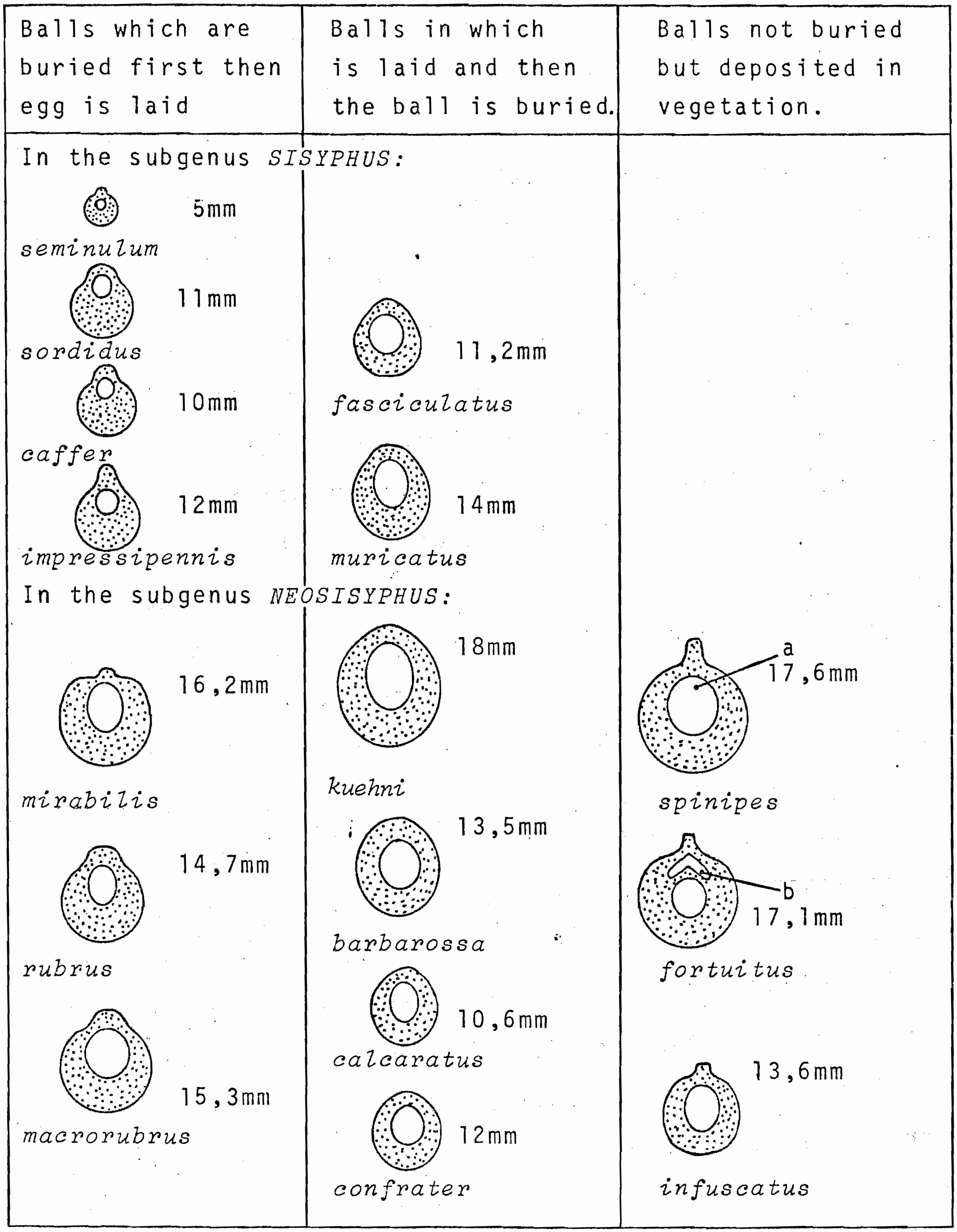


Fig. 97 : Variation in shapes, position of egg chamber, and mean diameter of brood balls of 16 *Sisyphus* species, arranged according to the sequence of their ball construction.
a = egg chamber   b = air chamber
(All brood balls drawn in vertical section, cut surface of dung is shaded.)

in *Sisyphus* broods and in addition *fortuitus* has an actual air chamber above the egg chamber (fig. 97).

The duration of each stage in brood ball production varies between individual females and species but the total period for producing one complete brood ball is not more than six hours in all the species of *Neosisyphus*. In the species of the subgenus *Sisyphus* brood ball formation and burial is completed within this time but oviposition may be completed in some species only after a considerably longer period.

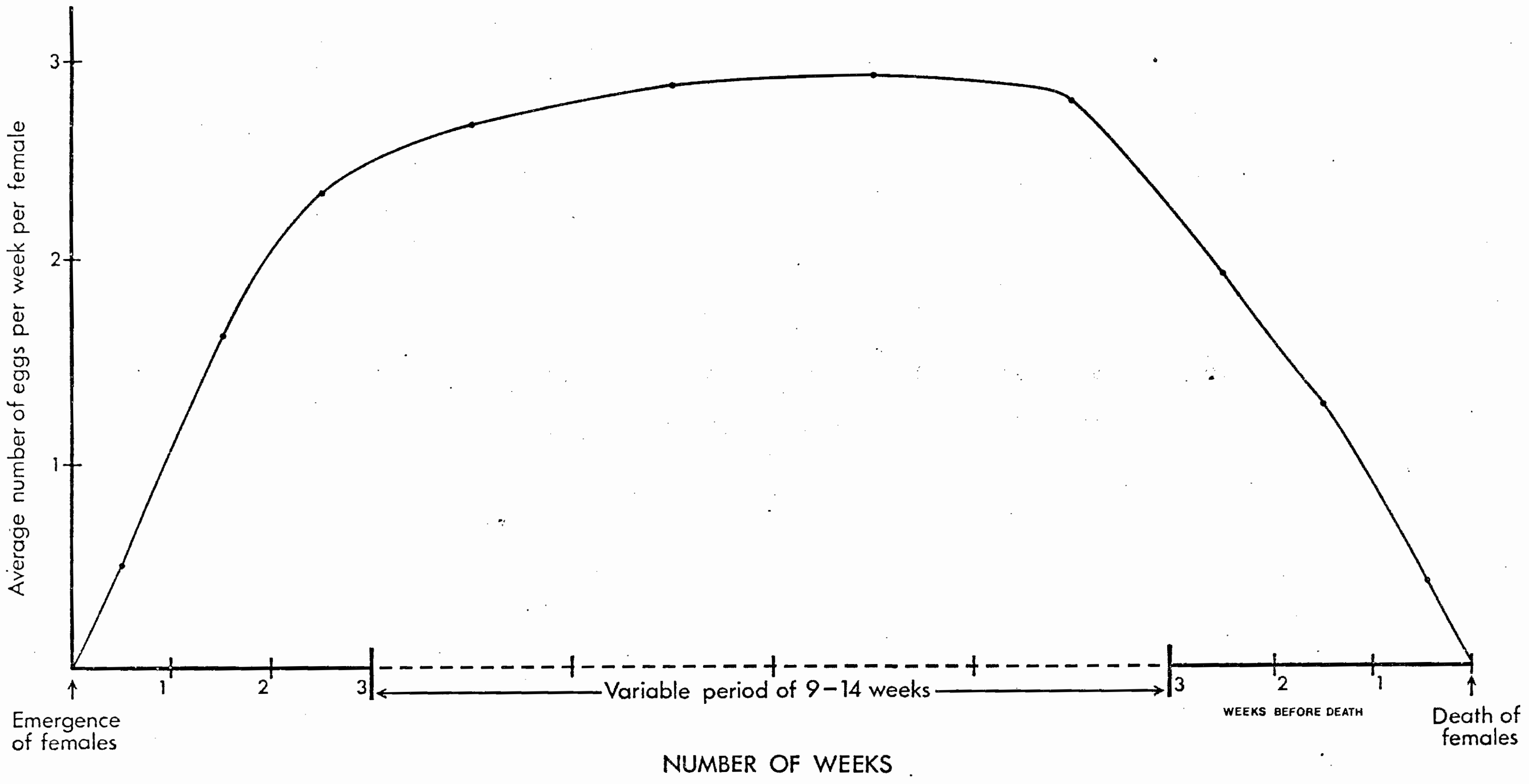
Most females of the genus *Sisyphus* can lay several eggs between matings but mate far more often than necessary to maintain normal fertile egg production. For *rubrus* it has been estimated that the female is mated about four times for each egg laid but the female can lay twenty fertile eggs between each mating. The female is always receptive to mating. This is an advantage in low populations since every time a male is encountered, mating can take place. Copulation usually lasts for 15 to 20 minutes in *Sisyphus schaefferi* (L), a European species. With its brood ball underground this species seems to copulate continually (Prasse 1958). Observations on southern African *Sisyphus* species show that these exhibit similar behaviour. Whether each mating fills the seminal vesicle and subsequent seemingly successful matings are not completed, or if each mating fills part of the vesicle, is not known.

Females usually do not lay more than one egg per day and often a day or more is spent feeding before the next egg is laid, although the female may have produced a brood ball each day for several days in succession, previously. The method of breeding in itself results in the utilization of a relatively large part of the day for a single brood ball to be completed. Therefore, usually not more than one egg can be laid per day. In addition, dissection of females showed that the single left ovary consisting of one ovariole, probably typical of all Scarabaeinae (Halffter and Matthews, 1966), does not produce mature eggs at the rate of those genera which can lay four eggs per day and which have a faster method of dung burial and brood making, e.g. the paracoprids *Eunoiticellus intermedius* (Reiche) and *Onitis alexis* Klug, (laboratory observations). The rate of egg production in *Sisyphus* varies very little during the period of peak egg production as shown in figure 98. A few weeks before the death of the female the egg production rate drops sharply and usually for the last four to ten days of her life, the female produces no eggs. During the build up and decline of egg production a few incomplete brood balls, without eggs, may be made.

The effect of temperature on the rate of egg production was investigated in the eight Mkuzi species. Twenty individuals of *sordidus* and *seminulum* were used and eight pairs each of *calcaratus*, *rubrus*, *spinipes*, *infuscatus*, *fortuitus* and *mirabilis*. All beetles used were between one and two months old. The beetles were all left in their experimental containers for the first four days, at normal laboratory temperatures (21-27°C). Half of the pairs were then subjected to a series of lower temperatures and the other half to higher temperatures. Temperatures were changed on

FIG. 98

Average rate of egg production from emergence to death for 13 females of *calcaratus*, during summer (October to February).


Average number of eggs per week per female
3
2
1
1
2
3
Variable period of 9–14 weeks
3
2
1
WEEKS BEFORE DEATH
Emergence of females
Death of females
NUMBER OF WEEKS

every fourth day, at the same time. The results of this experiment are recorded in table 7.

The number of balls produced by the females of *sordidus* and *seminulum* were too low for any conclusions to be made so these two species have not been included in table 7.

Table 7: Results of an experiment to investigate the effect of different temperatures on the egg production rate of six species of *Neosisyphus*.

Temperature range	No of balls/♀/in 4 days
15,5 - 22,5°C	0,5
20 - 22°C	0,63
21 - 27°C	1,13
20 - 30°C	1,41
28 - 37°C	2,18
35 - 44°C	2,45

As could be expected these results show that the breeding rate (rate of egg production) is increased with an increase in temperature. Comignan (1928) observed in a species of *Scarabaeus* that when temperatures increased to more than 30°C, the beetles burrowed into the dung and stayed there. The species of *Neosisyphus* examined not only seem to be tolerant of higher temperatures but produced eggs at a faster rate. This increase of breeding rate, even at temperatures between 35 and 44°C seems to contradict laboratory and field observations that brood balls are made by the *Neosisyphus* species during the cooler (15-25°C) parts of the day i.e. early morning and late afternoon. These facts suggest that time of day is involved in determining the ball making period, and this may overrule any control by temperature under certain conditions.

There are one to five generations of adults per year depending on the species and the relative severity of the seasons.

5.3 FLIGHT, DUNG LOCATION AND FOOD PREFERENCES

All the *Sisyphus* species are strong diurnal fliers. They fly to find suitable dung and mates. Dung beetles, e.g. *Onthophagus gazella* (F) have been recorded as having flown long, unbroken distances, up to 30 kms and since the introduction of *O. gazella* into Australia, in 1967, it has dispersed so that 80 km gaps between its initial release sites in northern Australia have been closed (Anonymous, 1972). *Sisyphus* species may fly similar distances, though no records exist so far. This ability to fly long distances means that the potential dispersion of the species is great and the population level at any one place may vary depending on immigration or emigration. Thus, measuring population levels in one area may not reflect the rate of emergence and death of a particular species but rather changes in the suitability of the area.

The actual flight, take off and landing of *Sisyphus schaefferi* has been studied in detail by Prasse (1960). This species tends to fly into the wind at a height of about 1,5 - 2 metres. It flies relatively short distances (40 - 60m) at a time, resting on the ground or vegetation between flights. The maximum air speed has been estimated by Prasse (1960) to be 5-6 metres/second. Preparation for flight in *S. schaefferi* takes an average time of 0,39 seconds excluding the preliminary "pumping" of the abdomen. The preparation sequence consists of "pumping" the abdomen three to ten times, lifting the middle legs so that the tarsi point upwards, lifting the elytra into the position for flight and then spreading the wings. Prasse considers that the middle tarsi, while being in the upward position, act as air-speed and turn indicators during flight. The species of *Sisyphus* observed in the present study undergo similar flight preparations. Prasse (1957a) observed in *S. schaefferi* that when the food source is detected the beetles drop to the ground about 1 to 1,5 m from the dung and undertake the final search by walking. This is not the case with the *Sisyphus* species observed in the field which land very near the dung pad or actually on it. This suggests a more controlled flight than that attributed to the telecoprid tribe, Scarabaeini, by Halffter and Matthews (1966).

There is little doubt, from the earlier observations on other genera mentioned by Halffter and Matthews (1966), that the dung is located by olfaction, using mainly the laminate antennae over long distance and the maxillary palpi at close range. Vision does not seem to be involved in the location of food. (Heymons and von Lengerken, 1929).

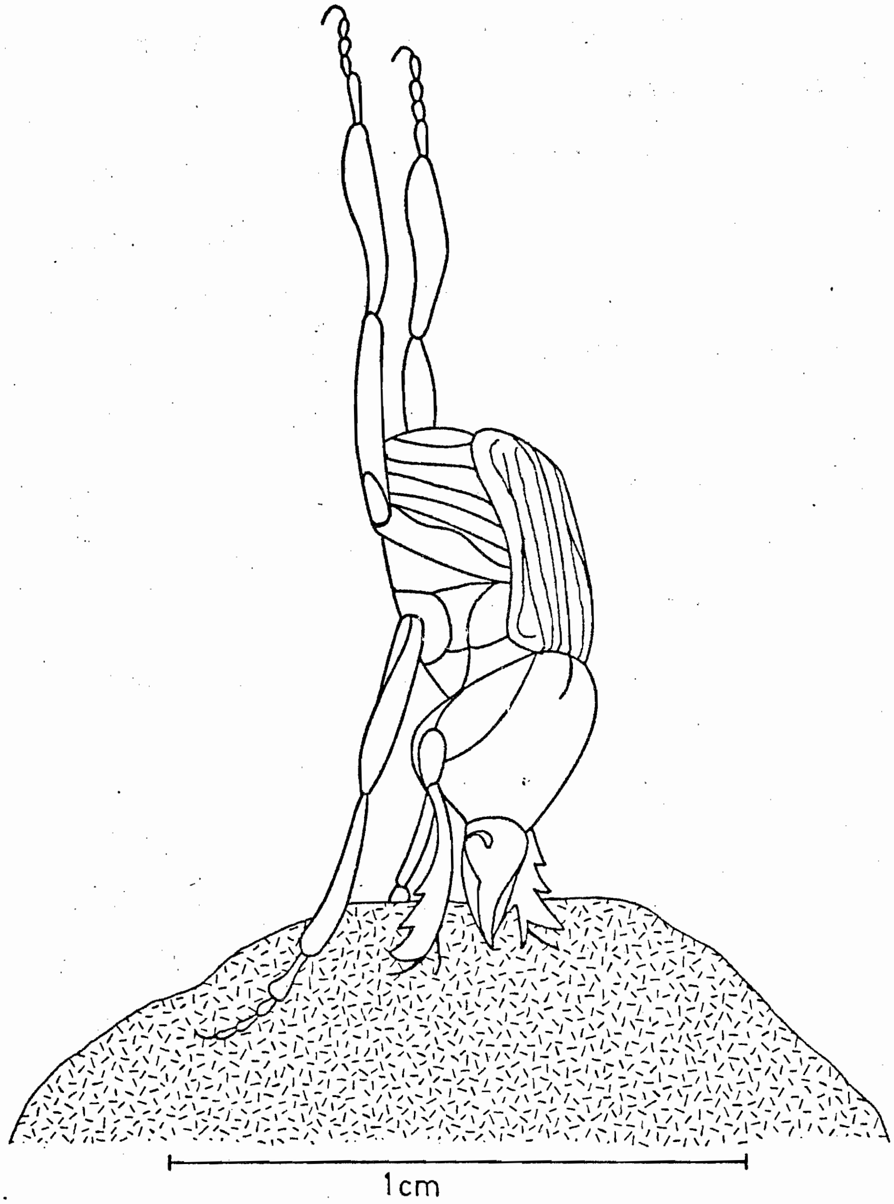
Dung just voided and up to one day old is usually colonized by *Sisyphus* and a wide variety of dung types are utilized ranging from rhinoceros dung to the pellets of impala. Food preferences were investigated in the laboratory. The eight Mkuzi species were used. In the laboratory portions of about 40 cc of rhinoceros, impala and cattle dung were offered as well as a similar amount of soft or rotting banana, tomato, meat and dead third instar larvae of *Onitis* Fabricius. The food types were offered in various different combinations to a total of ten females and five males of each of the six *Neosisyphus* species, plus 20 *seminulum* and 20 *sordidus*. The experiment ran for four days. A definite preference was shown for the cattle dung. A total of 24 balls were made from this dung. One ball was made from the rhino dung by *spinipes*, three impala pellets and two *Onitis* larvae were buried but not utilized for feeding or breeding and one ball was formed from the tomato by *rubrus*. The decaying meat was used for feeding but not broken up, possibly because it was not sufficiently decayed; the rhino dung in the same experimental container was, however, completely shredded and dried before the beetles went to the meat. From this experiment it seems that only in unusual circumstances would anything besides dung be used for breeding or play any part in competition between species, and dung with a consistency of cattle dung rather than that of rhino or impala is preferred.

These investigations into food preference were preliminary and still need to be followed up.

An additional factor in the location of dung pads is a suspected aggregation pheromone released by individuals of the same species, or genus already in or on a dung pad. That a pheromone is involved in *Sisyphus* is based on observations in the field, laboratory and experimental evidence from other genera. Halffter and Matthews (1966) mention that selective colonization of certain dung pads, leaving other identical pads untouched in the same field has been observed in several genera of dung beetles, e.g. *Onthophagus*, *Ateuchus*, *Canthon* and *Gymnopleurus*. This selective colonization results in the aggregation of a particular species in one pad, while few of none are found in surrounding pads. G.D. Tribe (pers. comm.) has found that in the ball rolling genus *Kheper* Janssene, a pheromone is secreted by the beetle while at the dung and is accompanied by a characteristic attitude. A similar attitude has been observed in the laboratory for *Sisyphus transvaalensis* males (fig. 99). *S. sordidus* and *fasciculatus* also remain motionless on the dung with the end of their abdomens raised. In *Neosisyphus* no characteristic attitude has been observed but aggregation in certain dung pads in the field is common among these species and is probably brought about by a pheromone. The function of this agregation is probably for the purpose of mating. In addition, when a pad is heavily colonized by one species, other species, especially of different genera, tend to be excluded and therefore competition with them is avoided.

5.4 IMMATURE STAGES

The eggs of *Sisyphus* as with all Scarabaeinae observed, are relatively large, soft and yolky. The chorion is not hard. This is probably because, in the dung brood, the egg does not need mechanical protection. Eggs laid take 8 - 14 days to hatch in summer(at 19-29°C) and 15 to 29 days in winter (at 14-24°C). There is no overwintering in the egg stage. The effect of temperature and relative humidity on embryonic developmental time, was investigated in eight *Sisyphus* species. The eggs used were placed on compacted soil in covered petri dishes. One set were



99 S. impressipennis, male, in "pheromone release attitude" on top of dung pad

d/

on moist soil, the other on air dried soil. A total of 131 eggs were used for this investigation and 81,8% of these hatched. The number of days recorded between egg laying and hatching are shown in table 8.

Table 8: Maximum and minimum number of days needed for eggs of the eight Mkuzi *Sisyphus* species to hatch in summer, winter and at high or low relative humidity.

Species	100% Relative Humidity	10% to 35% Relative Humidity
	No. of days	No. of days
Summer 19-29°C++		
seminulum	5-8	+
sordidus	8	+
calcaratus	7-8	9-15
spinipes	8-9	10-11
rubrus	8-10	11
mirabilis	8-10	+
infuscatus	8-10	10-15
fortuitus	10-14	15-21
Winter 14-24°C+++		
seminulum	19-21	+
sordidus	+	+
calcaratus	20-24	+
spinipes	18-26	19-25
rubrus	15-21	+
mirabilis	17-20	27
infuscatus	19-27	26
fortuitus	25-29	26-29

\+ No data available. ++ Eggs laid on 10th November
+++ Eggs laid 20th July.

Of the 93 eggs kept at 100% relative humidity, 83,8% hatched and of the 38 at 10-35% relative humidity, 76,3% hatched. Therefore, while delaying hatching up to seven days in summer, low relative humidity seems to have little effect on the mortality of the embryos within the eggs. Part of the total mortality (18,2%) must have been caused by injury to the eggs and also, some eggs may not have been fertile. The eggs of these species seem therefore to be resistant to des~~s~~iccation. In the field, the eggs would seldom be exposed to relative humidities below 35% since they would hatch, especially if the ball is buried, before the brood ball could dry out. The moist dung of the ball keeps the egg chamber at an almost constant 100% relative humidity. Low temperatures as might be expected, delayed hatching, up to 11 days. There was no difference in egg mortality at winter temperatures (18,2%) as compared to that at summer temperatures (18,4%). Between the time taken for *seminulum* eggs to hatch, 5-8 days (in summer) and that taken for *fortuitus* eggs, 10-14 days (in summer) lies the range for the each of the *Sisyphus* species investigated.

The larvae, in contrast to the adults, have strong chewing and crushing mouth parts and feed on the solid dung material. The hind gut of Scarabaein~~id~~e larvae has a similar enlargement to that of phytophagous Scarabaeid larvae for which this enlargement serves as a chamber for the bacterial fermentation of cellulose (Halffter and Matthews, 1966) The hind gut enlargement in Scarabaeinid larvae may serve the same purpose but this enlarged portion also stores larval excrement which can be used for repairing the brood ball if a hole should develop. (Halffter and Matthews, 1966).

The larvae are eyeless, rather sluggish, their body is "C" shaped and has a dorsal hump consisting of all or some of the first six abdominal segments. These characters are common to almost all Scarabaeinae. The hump is very important for giving the larva mobility within the brood and allowing it to feed. It braces itself against the walls of the ball using the hump and the end of the last abdominal segment which is flattened. This leaves the head and anterior end of the body free and in a position for feeding. The larva re-ingests some of its faeces while feeding but most of its excrement is not ejected. The larva eventually makes a spherical chamber in the brood by its constant movements in all directions. The size of the chamber is "tailored" by the larva to its size and if it is too big or to small the larva is not able to move or feed. The larva is, however, able to correct the size of the chamber if artificially enlarged, using its faeces (Prasse, 1957c).

There are three larval instars in all Scarabaeinae (Halffter and Matthews, 1966). In *Sisyphus* these three larval instars can take less than 30 days to complete in summer but if the ball dries out or temperatures drop, as winter approaches, it may be up to 300 days before pupation occurs. The fully developed third instar larva is the usual immature overwintering stage in all *Sisyphus* species. Moisture is necessary throughout the larval instars, so that they can be completed in the shortest possible time in summer. An experiment was carried out to investigate the effect of moisture. Batches of brood balls of six species were placed, either in air dried soil, in water saturated soil, or in soil with the normal water content i.e. about 6%. A similar number of balls was used for each species in each soil moisture type, making up a total of 187 balls with eggs. The brood balls, were made between 27th October and 7th November 1973 and were set in soil or dried out from 8th November 1973. Forty-two days after 8th November the dry broods were watered and the wet ones allowed to dry out to normal moisture. A total of 82 adults emerged, and this included all the species in each of the three categories. Figure 100 shows the result of this experiment: that the minimum period required for completion of the immature stages was extended during the time the balls were kept dry. The period over which most of the beetles 78 to 84%) emerged, was about 25 days. The spread in emergences exists because six different species were involved, each with its individual period necessary for larval development. In addition, within one experimental container balls may be drier than others, or eggs laid a few days earlier or later resulting in some variation in emergence times.

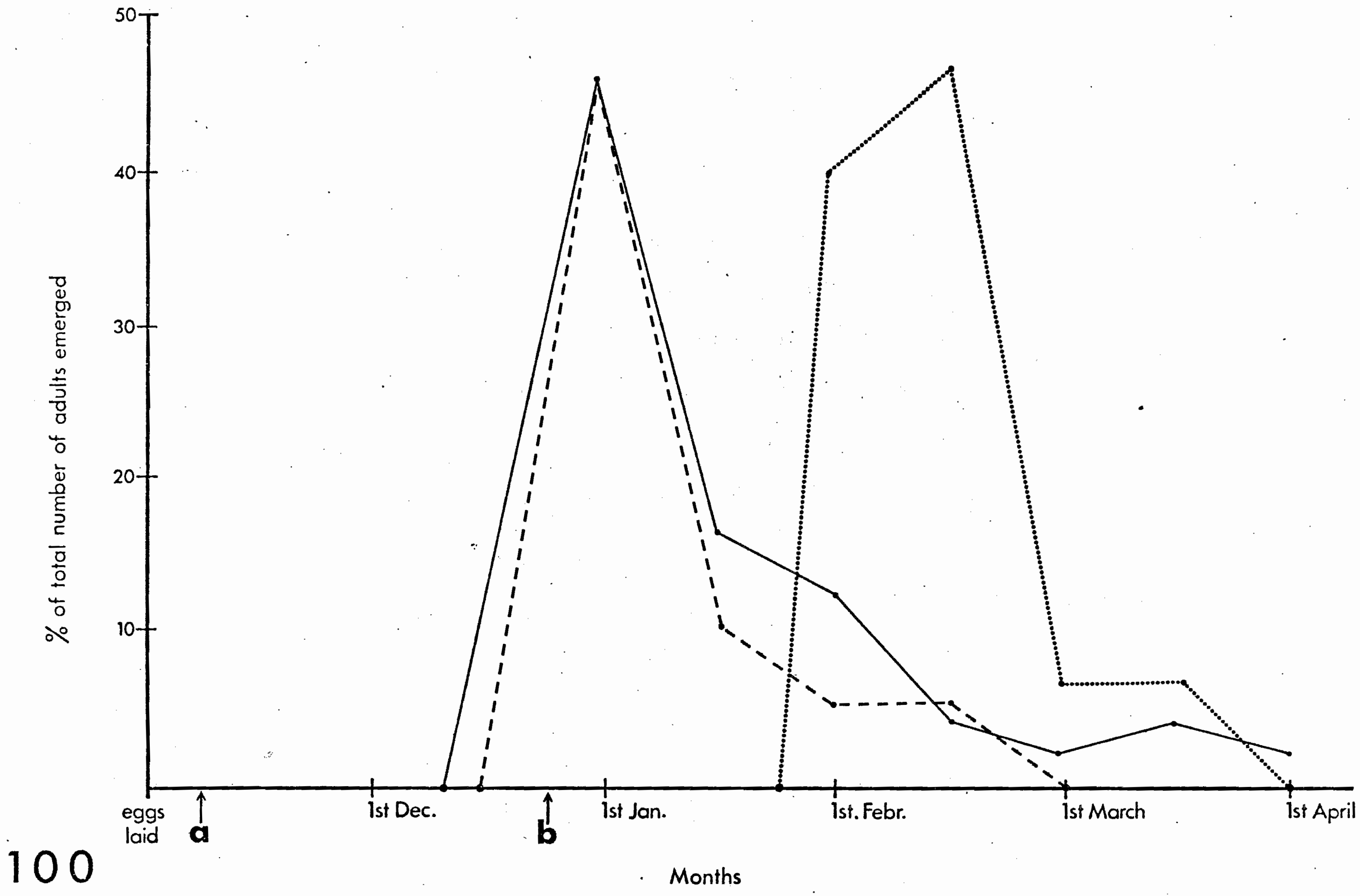
Prolonged excess moisture (over 12%) can kill the immature stages. Table 9 shows further results of the experiment with dry, wet and normal soil previously described for the data in figure 100.

FIG 100

Period required for completion of immature stages if brood balls are initially kept dry, wet or normal moisture soil.

Arrow a : when balls were saturated or dried out.
Arrow b : when dry balls were re moistened
(for further details see text)

<u>Key</u> : Solid line = broods in normal soil
Broken line = broods in saturated soil.
Dotted line = broods in dry soil.


50
40
30
20
10
% of total number of adults emerged
eggs laid
a
1st Dec.
b
1st Jan.
1st. Febr.
1st March
1st April
Months

100

Table 9: Number of adults emerging from brood balls buried in dry soil, wet soil and soil with normal moisture.

Soil type	No of balls set	% adults emerged	% larvae alive and overwintering after 200 days	Total % survived (= adults + larvae)
Dry	53	28,3%	15,1%	43,4%
Wet	53	34,0%	1,9%	35,9%
Normal	81	60,5%	8,6%	69,1%

A high percentage of those dying, which are originally in dry soil, resulted from overwetting of the broods after the 50 day dry period. This was evident from the high number of large, third instar larvae which were found dead in their broods. These could not have reached that size before the broods were dried out, so they had survived the dry period only to be killed by excess moisture. It can be said, therefore, that excess moisture and not the lack of moisture causes more deaths in the immature stages of *Sisyphus*.

Resistance of the larvae to desiccation was investigated in the eight Mkuzi *Sisyphus* species. A total of 80 larvae were used, most in the first and second instar and a few in the third instar. The first instar larvae used were removed from the brood balls as eggs and so had never fed. The larvae or eggs were placed individually in 7 mm diameter gelatine capsules and these were set up in a rack on a shelf in the laboratory. The capsules were, therefore, exposed to the fluctuations of temperature and relative humidity in the laboratory. Relative humidity varied from 30 to 80% and temperatures from 15°C to 32°C. Figure 101 shows the survival of these larvae. The high initial number of deaths (within 14 days) was probably caused by injury to the larvae when placed in the capsules. Although the numbers of larvae alive slowly decreased, considering that they were in an artificial and relatively unprotected environment when compared to the brood ball, to have survived at all means that the larvae themselves must have a well developed mechanism to resist dessiccation. A control set of 18 larvae, also initially kept in capsules, were put into artificial dung broods (fig. 102) at intervals during the experiment and their development was observed. Of these 18 larvae, eight emerged as full sized adult specimens after being in dung for 42-58 days. In addition, three were still alive and overwintering as fully developed third instar larvae after 160-230 days, two larvae died during their third instar and five larvae died within six days of being in the dung, probably because the dung was too wet or the larvae were injured. The eight adults which emerged had developed from larvae placed in capsules during the first, second and third instar. Therefore, it is possible for all instars of *Sisyphus* to resist dessiccation during dry periods and then complete their development to emerge as viable adults when the brood is re-moistened.

The dry periods in the above experiments were mostly over summer months. Such dry periods may occur in the field but longer dry periods occur in the field during winter. Resistance to desiccation in winter was investigated in seven *Sisyphus*

FIG 101

Graph showing the survival of *Sisyphus* larvae in individual gelatine capsules.

(80 larvae were originally placed in capsules; as larvae died the number of remaining live larvae dropped over 170 days until only three were left alive).

FIG 102

Diagram of third instar larvae in artificial observation brood in petri dish.

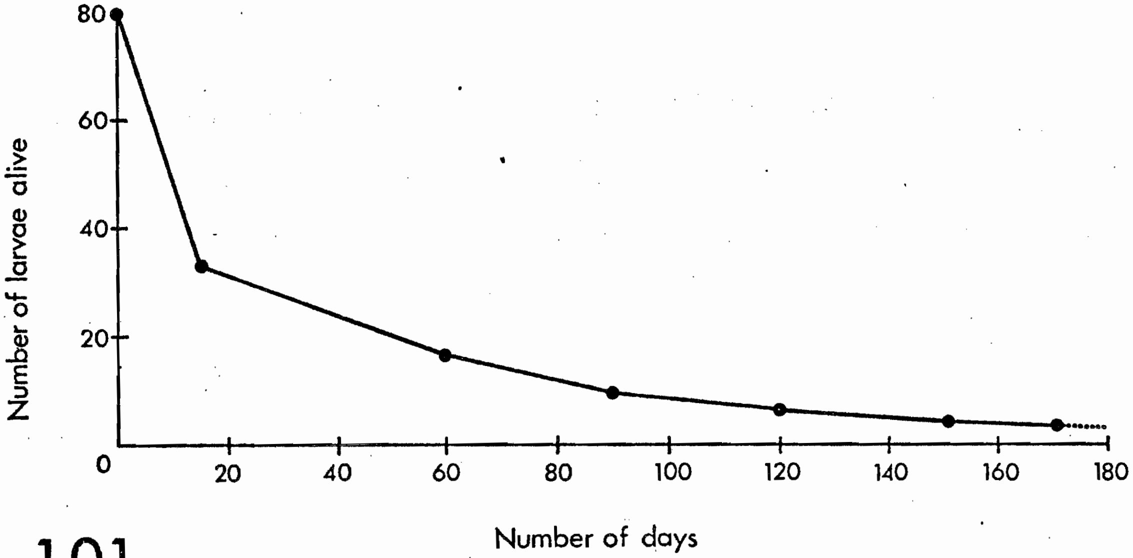
(Petri dish and brood drawn in vertical section).

a - larva

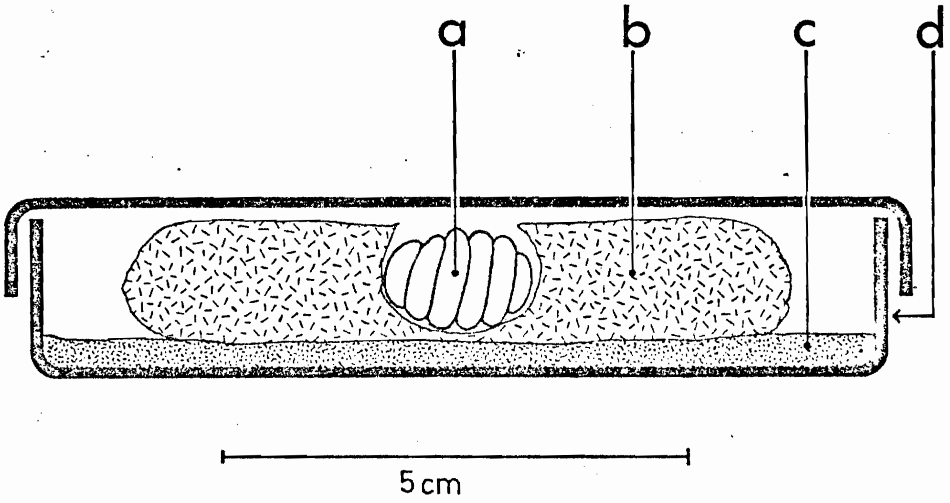
b - dung

c - moist soil

d - petri dish


80
60
40
20
0
Number of larvae alive
20
40
60
80
100
120
140
160
180
Number of days

101


a
b
c
d
5 cm

102

species. A total of 159 brood balls were dried out from 30th March 1973. They had been made from 5th to 28th March 1973. The balls contained larvae of all three instars. All three instars will overwinter at any stage of their growth if temperatures are too low, or the ball too dry for them to complete their development. Any temporary rise in temperature, or wetting of the brood will allow them to develop, even in winter, until they are fully developed third instar larvae. The completely dry experimental balls were left for 136 days in dry soil, until 13th August when they were re-buried, after wetting, in soil of normal moisture. Adults began emerging 59 days later, which was 20 to 55 days after control individuals of the same species began emerging from control broods which had been kept moist from when they were made and throughout all or most of the winter. These control broods were also moistened on 13th August. A total of 59,7% of the previously dry broods produced viable adults. This percentage is close to the usual number of emergences obtained from broods kept in normal soil moisture and tended over relatively short periods in summer, e.g. those recorded in table 9 (69,1% emergence). The larval stages of *Sisyphus*, therefore, can resist desiccation over long periods, including over winter and can emerge finally as viable adults.

Duration of the larval stage is also dependent on temperature, as could be expected. If temperatures remain low, as in winter, although the third instar larva may be fully developed, it will not pupate. Overwintering third instar larvae have fat stored in their bodies and will pupate when temperatures rise. The following example shows that at the beginning of summer, increased temperatures stimulate pupation. Eighty-seven broods of *mirabilis* containing eggs laid in April and May 1973, were buried in normal moisture soil in two separate containers. Both sets were allowed to dry out slowly but not completely. Development from egg to adult in summer takes about two months. Adults from these broods, however, were expected to emerge only at the beginning of September, after overwintering. On 13th August one set of broods was watered for the first time while the other was not. The broods were not watered again. Between the 1st and 7th of September the first 11 adults had emerged from the watered broods. Between the 6th and 7th September the first five adults had emerged from the broods not watered. Therefore no increase in moisture was necessary to stimulate pupation and the eventual emergence of the adult. Excess moisture, as in soil with more than 12% water, has been observed to kill pupae by rotting them. In the brood ball, the pupa is protected against this danger. A hard faecal shell is made inside the remainder of the dung ball, by the final instar larva before it overwinters or pupates. This gives protection against loss of moisture as well as the chamber getting saturated. The pupa of *Sisyphus* and other Scarabaeinae, in addition, has several projections on its dorsal surface, which has contact with the brood. These projections hold the pupa off the surface and therefore decrease the possibility of rotting through contact with a saturated surface.

Moisture plays a most important part in facilitating the emergence of the adults from the brood balls. The larvae pupate if temperatures are suitable but if the broods are dry and hard many of the adults will not be able to escape and will have to wait until the balls are softened by rain. How long the adults can wait in the brood ball is not known. When checking brood balls after emergences have stopped, dead adults are frequently found in broods, which were dry and hard. The adult, therefore, cannot live indefinitely in the brood ball. After wetting containers of broods which have been dry, adults may start to emerge within a few days. A few adults have been observed escaping from hard, completely dry balls.

There is no overwintering in the pupal stage in *Sisyphus*. If a larva pupates the adult will emerge after two to three weeks. Moisture affects the duration of the immature stages as well as temperature but more important, moisture affects ultimate survival. For this reason *Sisyphus* species are not found in very dry areas (below 200mm average annual rainfall) and very wet areas (above 2000mm), since they will not be able to survive successfully such prolonged dry periods (sometimes two years in these areas) and especially, prolonged wet periods. The adult beetles too, are not able to withstand indefinite periods of wet or drought.

5.5 SUBGENERIC DIFFERENCES

The subgenera *Sisyphus* and *Neosisyphus*, are morphologically and biologically valid taxa. Biologically, however, *seminulum* (subgenus *Sisyphus*) is intermediate between the two subgenera.

The most obvious biological difference between the subgenera is that in summer, all species of *Sisyphus*, including *seminulum*, make food balls from the dung, roll these away, bury them and then feed on them. They do not feed at the dung source for any length of time as do *Neosisyphus* which never roll food balls but remain feeding in the dung for at least three hours, but usually more than twelve hours. The food balls made by species of *Sisyphus* are usually of a rougher shape and smaller size than their brood balls. These food balls are, however, a consistent size within a species. They are actually small lumps of dung quickly shaped and cut from the dung pad by the beetle, using mostly its spade-like clypeus and front legs. In winter, however, *Sisyphus* species may feed in the dung and tend not to make food balls.

The construction of brood balls also seems to differ in the two subgenera. *Neosisyphus* makes brood balls starting from a core of dung onto which successive layers are added and the egg chamber is formed almost in the centre of the ball as in figure 94(b). In *Sisyphus* however, including *seminulum*, brood balls are cut out as a whole from the dung as with the food ball but are more compact and uniform in shape, since more time is taken over forming them from the dung. The egg chamber is near the tip of the brood (fig. 97). It is possible that the buried brood ball is completely remade and compacted before the egg chamber is constructed , the egg laid and the chamber is closed. *S. schaefferi* follows this pattern (Prasse 1957b). *S. fasciculatus* and *muricatus* do not remake their balls, which resemble those of *Neosisyphus* (fig. 97).

Neosisyphus fly to new pads during the hottest part of the day (12-3 p.m.) and make their brood balls in the early morning or late afternoon. *Sisyphus*, excluding *seminulum* however, fly to fresh dung just before and after peak daily temperatures are reached. They make their brood and food balls during this time (9a.m. - 12p.m. and 3p.m. - 5p.m.). At no time during summer do *Sisyphus* individuals remain at the pad for any length of time. They spend most of their adult lives in the soil. *Neosisyphus* individuals spend most of their adult lives in the dung pad, only leaving with a brood ball or to colonize fresh dung.

Before flying off from an old pad, *Neosisyphus* species and *seminulum* clean themsleves of adhering dung and then paint the entire sides of their bodies using the metathoracic legs, with a white secretion, emerging as a drop of fluid from the anal opening. The function of this secretion was not investigated in any detail. The secretion, as seen from dissecctions seems to originate from the malphigian tubules. No species of *Sisyphus* except *seminulum* were observed to cover themselves with dung, or utilize this secretion in this manner. When reaching a fresh dung pad the *Neosisyphus* species and *seminulum*, cover themselves, especially dorsally, with dung.

Sisyphus also differs from *Neosisyphus* in that the former subgenus excluding *seminulum*, does not breed during winter. What actually causes the females of the subgenus *Sisyphus*, which were breeding during the summer, to stop during April and overwinter as non-breeding adults was not investigated. It is probably either temperatures, photo period or a combination of both. The same stimuli probably again initiate their breeding during the following spring. All adults of the subgenus *Sisyphus* which emerged after the middle of December, did not breed until the following summer. The non-breeding females, of *fasciculatus*, were subjected to various temperatures during winter but did not start breeding until the end of September as did a set of control females kept under normal laboratory temperatures. Only one female of *fasciculatus* emerged at the beginning of December (7th Dec., 1972). This female began producing eggs ten days later. It seems therefore, that the females which did not reach reproductive maturity (about two weeks after emergence) before the December solstice (22nd December) did not breed during that same summer but overwintered and bred during the following summer. The major control of egg production in this generation seems, therefore, to be photoperiod.

In order to investigate if, in the field, there was an overwintering generation of *Sisyphus* which had bred the previous season, the wearing of the dentition of the fore tibia of *sordidus* caught in traps in Mkuzi, was examined. Worn down dentition is a sign of age and would show that the beetles had been active for some time before being caught. During February/March, 1973 214 *sordidus* were caught and in the following spring, September/October 113 were caught. No *sordidus* were seen in the field from and including April to August. Worn tibia recorded were those in which the "teeth" on the outer edge of the fore tibia were shorter than the width of the base, whereas in those which were not, or little worn, the teeth were longer than the width.

Percentages recorded were:

February/March : Worn - 39%
Not worn - 61%
September/October : Worn - 34,5%
Not worn - 65,5%

These results show that there are overwintering adults which survive the winter and therefore can breed during the following summer, which may be their first or second breeding season.

The survival of adults during winter, which is usually very dry in the areas where the *Sisyphus* species occur, was investigated. Seventeen individuals of the subgenus *Sisyphus* and 39 of *Neosisyphus* were put together in a container with dry soil and a few stones for four weeks (23rd July to 20th August 1973)at temperatures fluctuating between 12 to 26°C daily. These beetles were given only enough dung on which to feed on and not enough to moisten appreciably the soil in the container. A control of 87 *Sisyphus* and 105 *Neosisyphus* individuals was fed the same amounts of dung but kept in containers with moist soil. Several species were used but in the same proportions in experiment and control containers. During the four week period one of the 17 experimental *Sisyphus* died but 31 of the 39 experimental *Neosisyphus* died. Of the control only 15 of the 105 *Neosisyphus* died and none of the *Sisyphus* individuals died. These results indicate that the species of the subgenus *Sisyphus* are far more able to survive the dry winter periods than the *Neosisyphus* species. This could be physiological but probably is also because of the behaviour of the *Sisyphus* species, burrowing into the soil usually under objects and remaining quiescent, while the

Neosisyphus are more exposed to the environment as they usually remain actively breeding. Throughout most of the winter, the adults of *Sisyphus* bury into the ground and only come up to feed occasionally, or not at all. All *Neosisyphus* species and *seminulum* are on the other hand, obligatory breeders from emergence to death. 'There is usually no adult overwintering in this subgenus. Adults emerging late in summer will breed during the winter at a rate slower than that of the summer.

These facts concerning the two subgenera show that they differ considerably in their biology. They are not sufficiently different morphologically, however, to be separated into two genera and also, *seminulum* links them together biologically, being intermediate between *Sisyphus* and *Neosisyphus*.

6 VARIATION BETWEEN SPECIES RELATED TO COMPETITION

The preceeding sections on distribution and general biology have shown the variation existing among *Sisyphus* species and indicate that the eight Mkuzi species are representative of the genus. While differences do exist, there is still however, much overlap of distribution and biology. These eight species will be dealt with almost exclusively in the following section, to explain how *Sisyphus* species, when sympatric, can still be individually successful in spite of their sympatry and apparent competition for dung.

Competition in this study refers mainly to competition for dung, i.e. its availability for breeding and thus propagation of the species. Scarcity of dung does not only lower the immediate brood ball production but may considerably reduce the fecundity of the females, as illustrated in the following example. In late August 1971, at the very beginning of the breeding season, over 300 *spinipes* were collected by G.F. Bornemissza, in Zululand. These were kept crowded together and given only just sufficient dung for feeding and not for breeding. After three weeks over 100 females of these were paired with males and placed in individual containers. These females began to produce brood balls within two days. When collected in the field these beetles were not breeding and were, therefore, probably collected very soon after their emergence. The individual pairs in the laboratory produced a mean total 27 broods per female. Thirty-five filial pairs bred in the laboratory at similar temperatures, produced a mean total of 43 broods per female. This suggests that the very congested females, through excessive crowding, had their overall fecundity reduced. The food spectrum experiment described in section 5.3, showed that other material such as rotting meat and fruit can be used for feeding in cases of stress in *Sisyphus* but these are not suitable for normal breeding, so cannot replace dung in this respect and alleviate competition for breeding material when dung is limited.

Competition for dung can be overcome in two ways;

(1) through behaviour, by avoiding individuals occupying the same habitat and requiring the same materials for living and breeding, or

(2) through biology and ecological preferences thereby avoiding the population peaks of other populations with the same preferences for food and breeding requirements.

6.1 VARIATIONS IN BEHAVIOUR

Competition between individuals of sympatric species, active at the same time of the season would take place:

(1) if they had coinciding patterns of diurnal activity,

(2) if they colonized the same areas of the same dung pads, or

(3) used the same sites for brood ball deposition.

6.1.1 Patterns of Diurnal Activity

Diurnal activity patterns were investigated in the laboratory and field. In the laboratory the beetles recorded as being "active" were those which had left the dung and were flying, or on the soil surface, preparing for flight, in order to find and colonize a new dung pad. In the field "active" beetles recorded were those which had been flying and had just colonized a fresh pad or entered a trap. In the laboratory the summer activity of the eight Mkuzi species was recorded once every one or two hours, from 7 a.m. to 7 p.m. over six consecutive days in November 1973 and nine consecutive days in February 1973. Each day during these periods fresh dung was placed in the experimental containers, which also contained the dung from the previous two days. The containers used in the November experiment measured 21 by 34 cm. and had a depth of 18 cm. and in the February experiment they were 36 by 45 cm. with a depth of 21 cm. During both periods one species was used per container. Six pairs of each *Neosisyphus* species were observed in November and 25 *seminulum* and 30 *sordidus* individuals. In February four pairs of each *Neosisyphus* species and *sordidus* were observed and also 20 *seminulum* individuals. In addition, from July 1971 to October 1972, activity of individual pairs (listed in table 2) was recorded each time the dung in the containers was changed.

The total numbers of beetles observed during each one or two hour observation period during the experiments or from individual pairs in the laboratory and on which activity patterns have been based, are recorded in table 10.

Table 10: Total numbers of beetles observed in each one or two hour period during diurnal activity observations in the laboratory, on the eight Mkuzi *Sisyphus* species, in summer and winter.

Summer				Winter		
Period of observation	Total no. of each *Neosisyphus* species observed	Total no. of *seminulum* observed	Total no. of *sordidus* observed	Period of observation	Total no. of *Neosisyphus* observed	Total no. of *Sisyphus* observed
7-8am	132	120	258	8-10am	87	8
8-10am	144	220	252	10-11am	114	0
10-12pm	160	340	276	11-12pm	81	4
12-1pm	72	160	108	12 -1pm	16	4
1-2pm	84	160	174	1 -2pm	68	16
2-3pm	100	200	190	2 -3pm	95	36
3-4pm	100	100	190	3 -4pm	303	4
4-6pm	92	180	220	4 -6pm	77	24

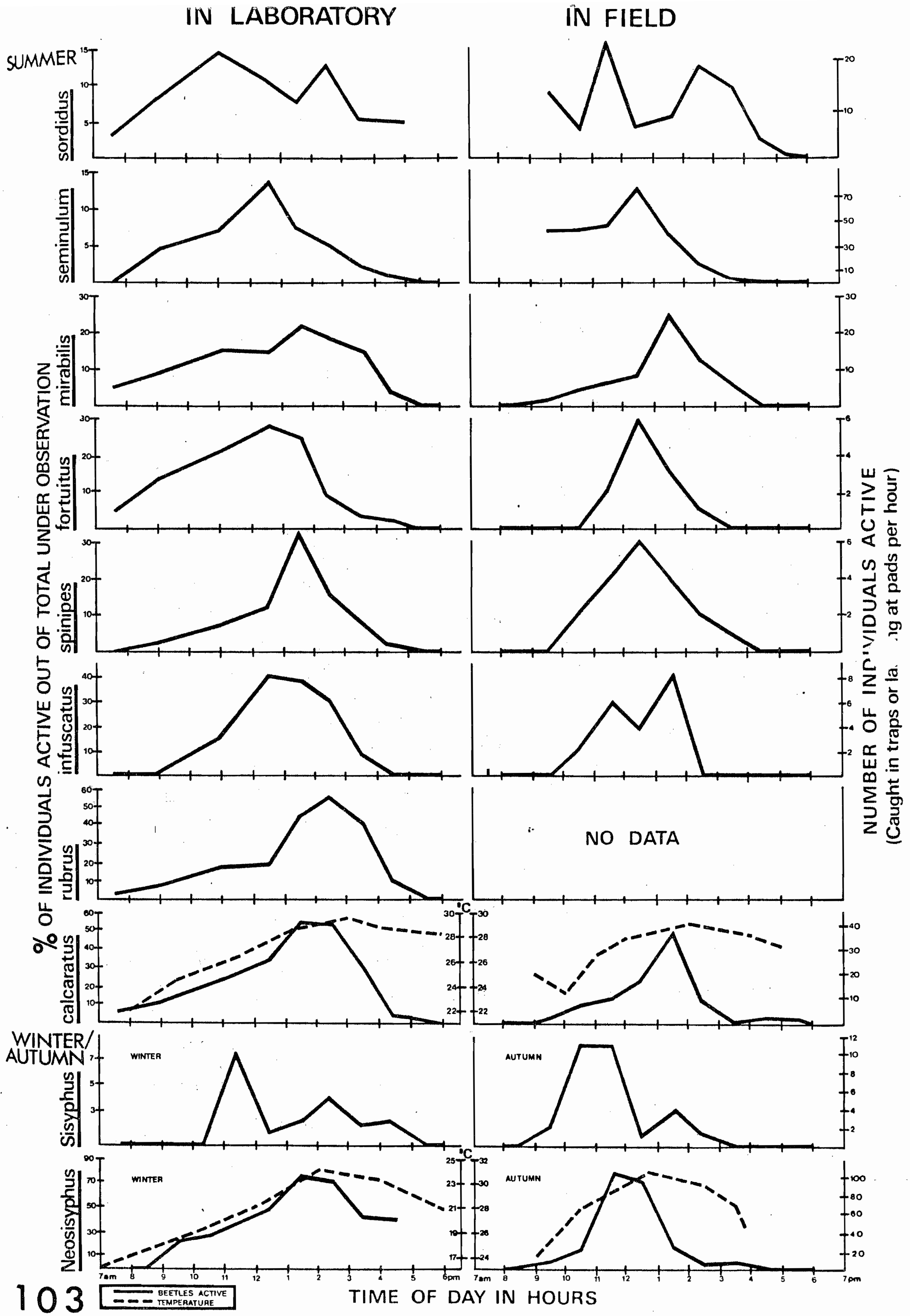
Diurnal activity in the field, (in Mkuzi) was recorded over three consecutive days in December (summer) and two days in late April (autumn) for seven species (*rubrus* was not found in Mkuzi during the 1973/74 season). The activity in the field was monitored using eight traps (fig. 92), containing horse or cattledung. These traps were reset hourly and were in operation from 8a.m. to 5p.m. In addition, in December, beetles coming to or leaving three pads, of one litre cattle dung each, under constant daily observation, were recorded. The results of the laboratory and field observations on diurnal activity are recorded in figure 103. Only one graph has been drawn for the autumn and winter activity of the species of *Sisyphus* and one graph for *Neosisyphus*, since the activity peaks of individual species were very close. The activity of individual species in the laboratory and field is very similar, for most species. *S. spinipes* and *infuscatus* are the only species which show differences in the position of their peaks of activity as regards the laboratory and field records. In the field, however, few *spinipes* or *infuscatus* were observed (a total of 19 and 16 respectively). Therefore, since the laboratory data show the same pattern of activity as that in the field, for other species where more individuals were observed, the laboratory data for these two species are probably more representitive. Males and females have not been separated since they show very similar activity patterns but some males may take to the wing before the females, especially if the female is completing a brood ball.

The biggest difference in diurnal activity patterns is that between *sordidus (Sisyphus)* and the *Neosisyphus* species together with *seminulum*. *S. sordidus* has two activity peaks, one before and one after the maximum daily temperature is reached. Between the two peaks of *sordidus* activity, lie the maximum activity periods of the other seven species. Each of these species has its definite time of peak activity, which may be the same as for other species. In summer this spread of activity peaks means that one species which has an earlier peak activity period, will tend to colonize a certain number of pads earlier than other species. The aggregation phenomenon will enhance this species-specific pad colonization effect, resulting in the "contagious colonization" of dung pads. This selective colonization of pads was further investigated in Mkuzi in December 1973. Five pads of about 100 g cattle dung

FIG 103

Results of observations on the diurnal activity of the eight Mkuzi *Sisyphus* species under laboratory, field, summer and winter conditions.

Graphs drawn with broken lines are of the temperatures during each observation period i.e. summer in the laboratory; winter in the laboratory; summer in the field and autumn in the field.



IN LABORATORY
IN FIELD
SUMMER
sordidus
seminulum
mirabilis
fortuitus
spinipes
infuscatus
rubrus
NO DATA
calcaratus
°C
WINTER/AUTUMN
WINTER
AUTUMN
Sisyphus
Neosisyphus
% OF INDIVIDUALS ACTIVE OUT OF TOTAL UNDER OBSERVATION
NUMBER OF INDIVIDUALS ACTIVE
(Caught in traps or la ng at pads per hour)
7am
8
9
10
11
12
1
2
3
4
5
6pm
7pm
TIME OF DAY IN HOURS
BEETLES ACTIVE
TEMPERATURE

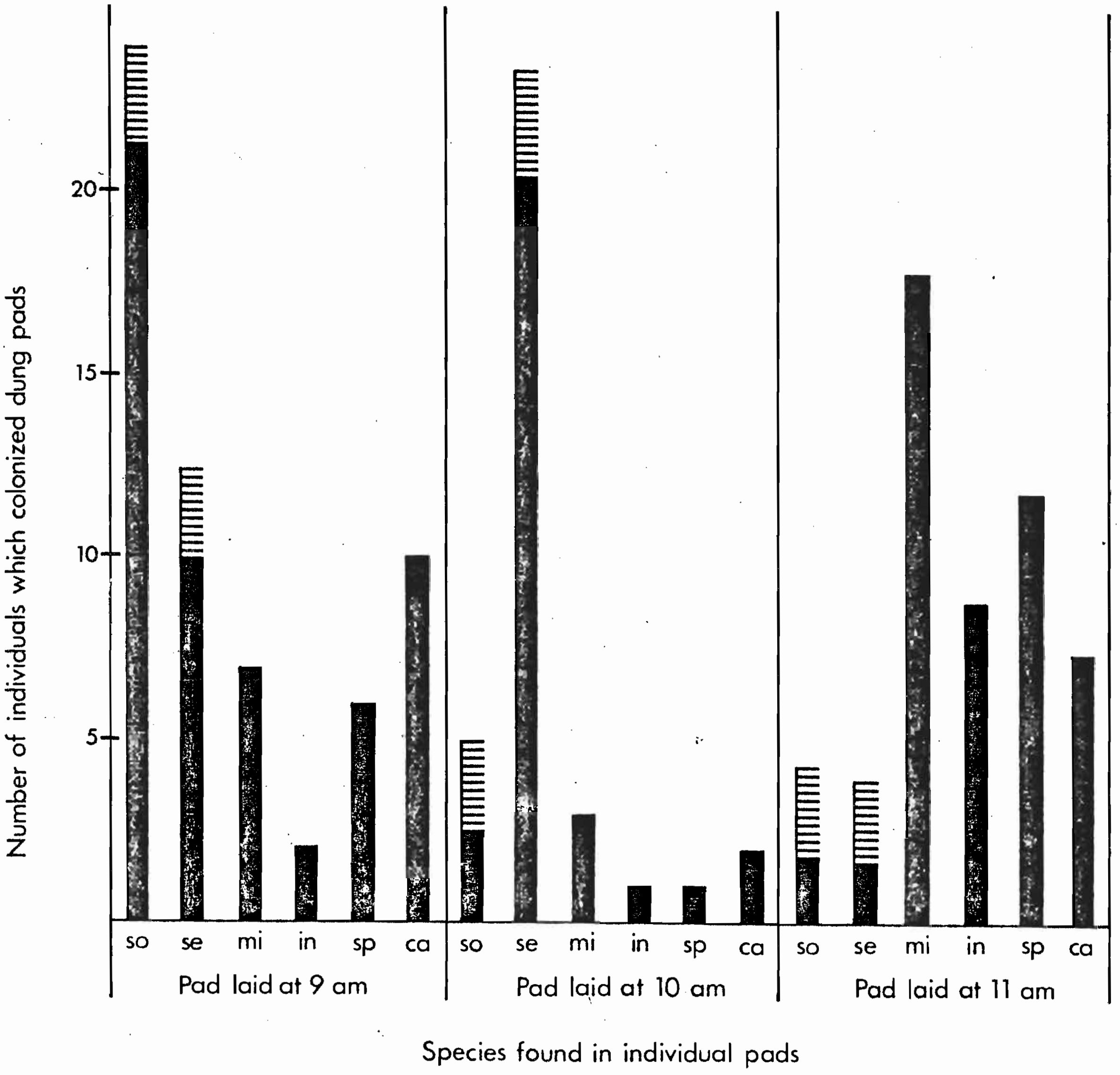
each, were laid at nine, ten, eleven a.m., and one and two p.m. Beetles colonizing them were recorded. Few beetles other than of *Sisyphus* species came to these pads, so these are not mentioned. The numbers of individuals of *Sisyphus* species colonizing the pads are recorded in figure 104. The pad laid at 9 a.m. was soon colonized by *sordidus*, which has the earliest activity peak (11 a.m. to 12 p.m.). Individuals of this species do not remain at the dung for long but make and roll their balls immediately (within four to ten minutes of reaching the dung source). Some *seminulum* also colonized this pad. They made and rolled their balls away immediately as did *sordidus*. *S. seminulum*, however, which has its peak activity between 12 and 1 p.m., colonized the 10 a.m. pad more heavily. When the numbers of active *infuscatus*, *mirabilis*, *spinipes* and *calcaratus*, which have activity peaks between 1 and 2 p.m., started to build up around 12 p.m. they began to colonize the 11 a.m. pad which had very few *sordidus* or *seminulum*. By 1 p.m. most *sordidus* had left the 9 a.m. pad, with their balls but several *seminulum* were still active on the 10 a.m. pad. The *infuscatus*, *mirabilis*, *spinipes* and *calcaratus*, which were reaching their peak activity period, also colonized the abandoned 9 a.m. pad. Accurate numbers of *sordidus* and *costatus* were not obtained since the pads were not under constant observation and some individuals came to the pads, made and rolled their balls away between recordings. Since the *Neosisyphus* species remained in the pad after reaching it, they could be counted accurately by breaking up the pads at the end of the day. During this experiment, however, the day became cloudy and cool before 2 p.m. so the

FIG 104

Results of an experiment to show selective colonization of dung pads by six Mkuzi *Sisyphus* species.

(Since accurate numbers of *sordidus* and *seminulum* could not be obtained, the columns representing these species are broken at the top.)

so = *sordidus*
mi = *mirabilis*
sp = *spinipes*
se = *seminulum*
in = *infuscatus*
ca = *calcaratus*



Number of individuals which colonized dung pads
20
15
10
5
so
se
mi
in
sp
ca
so
se
mi
in
sp
ca
so
se
mi
in
sp
ca
Pad laid at 9 am
Pad laid at 10 am
Pad laid at 11 am
Species found in individual pads

the number of *Neosisyphus* recorded is not as high as usual and the colonization of different pads by different individual species was not as marked as previously observed. The 1 and 2 p.m. pads contained very few beetles and so have not been included in figure 104. If the day becomes cloudy and cool before reaching its usual maximum temperature, the numbers of *Neosisyphus* active that day will be relatively low while more *sordidus* and *seminulum*, which do not fly during the maximum heat of the day, will be active over a longer period.

In species of *Neosisyphus*, the first day that fresh dung is dropped or offered and colonized in the field or laboratory, all the individuals remain feeding in the dung and no brood balls are made. On the day after colonization the beetles not actually breeding, will leave the dung pad and those individuals remaining to breed will make brood balls either during the morning or late afternoon. The actual time of brood ball making also seems to vary according to the species. Figure 105 shows the different periods of ball making observed for the eight Mkuzi species during summer in the field and laboratory. The periods marked for each species on figure 104, are those when the majority of balls were made. Brood ball making could be initiated at other times of the day especially if the temperatures were cooler than usual. These differences in ball making times, not only reduce competition for dung if the species are in the same pad, but reduce combat over newly formed brood balls.

FIG 105

Diagram to show the periods over which the eight species of *Sisyphus* at Mkuzi were observed making brood balls in the laboratory and field, during summer.

Broken lines indicate where ball making was observed in isolated cases but could possibly be more frequent during that period.

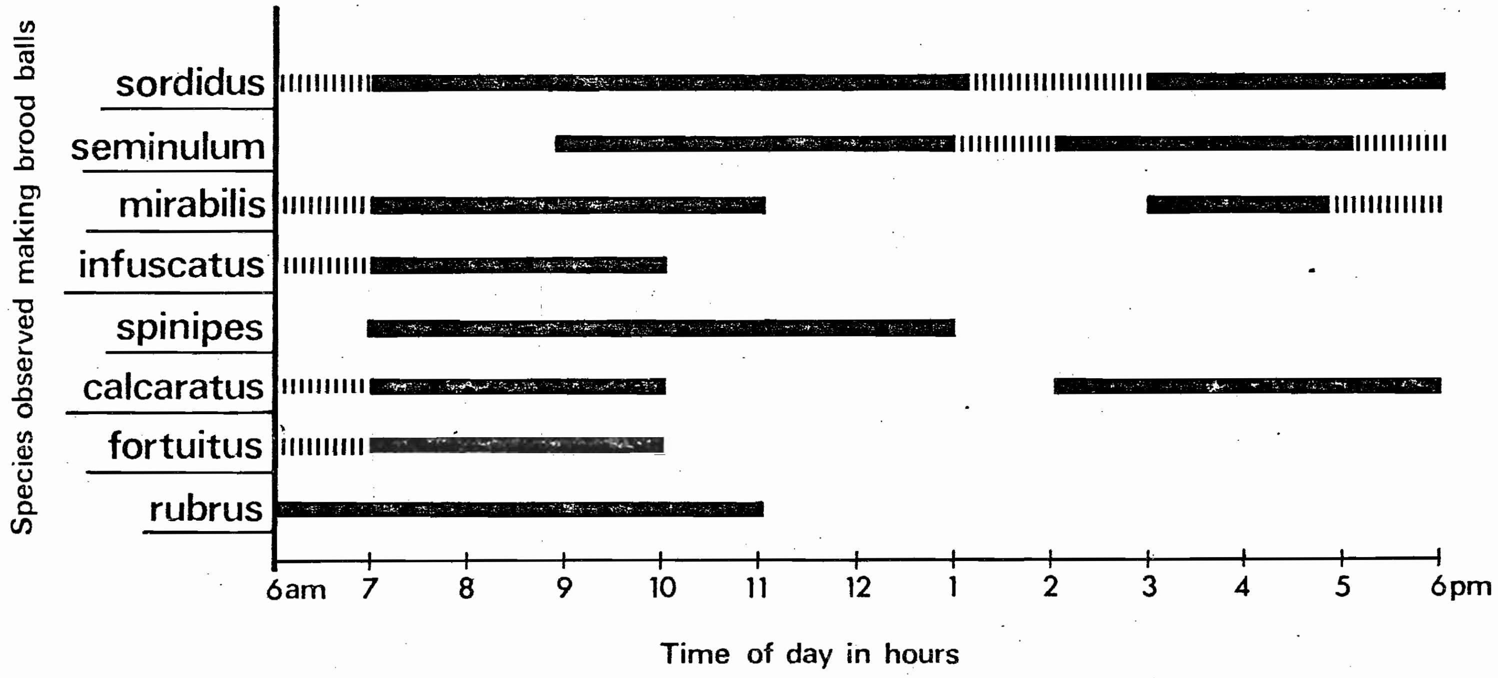
6.1.2 Colonization of Pads in Different Locations and certain Areas of these Pads.

Besides some degree of temporal isolation, however, spatial isolation was also evident in the eight Mkuzi species. The area where the dung is dropped i.e. in the sun or shade will have an effect on the number of *Sisyphus* species and relative number of individuals colonizing it. Males and females showed the same behaviour in this regard and therefore the totals of males plus females ofeach of the six species caught in traps (fig. 92) (four in the sun and four in the shade) in Mkuzi, over five days, are recorded in table 11.

Table 11: Numbers and percentages of adults of six *Sisyphus* species in Mkuzi, caught in traps in the sun or traps in the shade.

Species	% in sun	% in shade	Total no. recorded
sordidus	72,5	27,5	120
seminulum	0,5	99,5	395
mirabilis	17,9	82,1	28
infuscatus	65	35	20
spinipes	100	0	5
calcaratus	70	30	100

From the results in table 11 it is evident that *seminulum* shows almost exclusive preference for the shade. The two specimens in traps in the sun were caught between 3 and 4 p.m. when temperatures and insolation were decreasing. *S. sordidus* and *calcaratus* showed a preference for dung in the sun but about one third also went to dung in the shade. The numbers recorded of *mirabilis* are low but further field observations


Species observed making brood balls
sordidus
seminulum
mirabilis
infuscatus
spinipes
calcaratus
fortuitus
rubrus
6am
7
8
9
10
11
12
1
2
3
4
5
6pm
Time of day in hours

substantiated this preference shown towards the shade. Similarly, *infuscatus* and *spinipes* tended to colonize dung in the sun more heavily but also went to that in the shade.

Different areas of the dung pad itself are colonized by individual species for their brood or food ball making. Three major areas of dung pad colonization have been observed. They are: deep into the edge of the pad, just in or under the edge of the pad, or at the edge or on the surface of the dung. *S. sordidus* and *seminulum* make their food and brood balls at the edge of the pad or in crevices on its surface. *S. calcaratus* makes its balls at the edges of the pad, *mirabilis* and *infuscatus* just under or in the edge of the pad, while *fortuitus, spinipes* and *rubrus* utilize an area deeper into the dung pad. These different areas colonized are often not as noticable when a pad is very heavily colonized and is shredded and flattened. The various species will, however, still be found in different areas of these flattened pads. Those usually at, or just in the edge will remain there, while those going deeper into the edge will be found towards the middle of flattened pads.

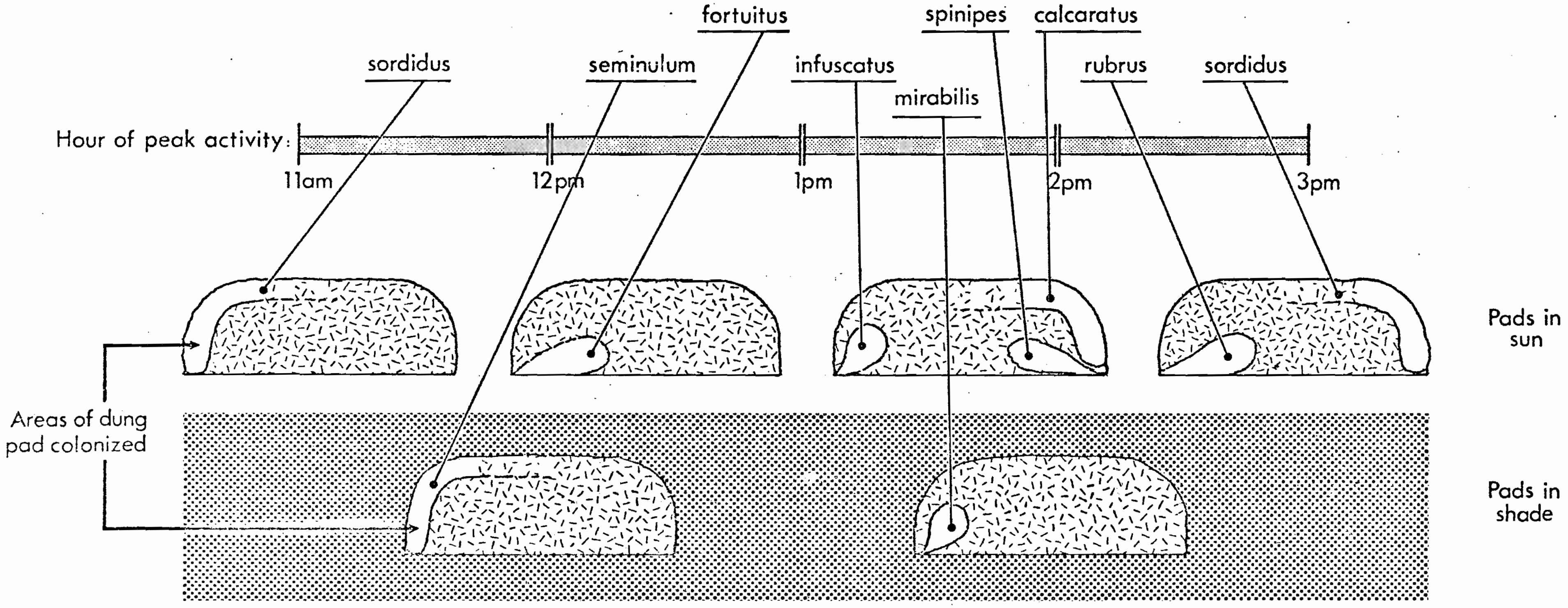
From this knowledge of the different areas and sites of the dung preferred, together with the differences in peak dung colonization periods, a diagrammatic representation of species isolation at the dung source itself, can be drawn up. Figure 106 is a model of the colonization of individual pads by different species which serves to illustrate those behavioural mechanisms of species isolation which minimize competition.

6.1.3 Sites of Brood Ball Deposition

All eight Mkuzi species have been observed making and depositing their balls in the field. Two major areas are selected for brood ball deposition. *S. spinipes, infuscatus* and *fortuitus* drag their balls into twigs or grass stems. Here they make their egg chamber, oviposit, close the balls and then leave the brood ball up in the vegetation (fig. 95). The other *Sisyphus* species bury their balls usually under objects. By utilizing two very different areas for oviposition, the species reduce competition for balls at the deposition site. This competition is further reduced by the fact that different species may be seeking an area to deposit their balls at slightly different times (fig. 105). In addition, combat between beetles at the deposition site will not be as high as that at the pad, since each breeding beetle at the site should have its own ball.

FIG 106

Diagrammatic representation of how the eight sympatric *Sisyphus* species in Mkuzi achieve partial ecological isolation according to their diurnal activity peak, their choice of dung pads in certain positions and the utilization of particular areas of these pads.


fortuitus
spinipes
calcaratus
sordidus
seminulum
infuscatus
rubrus
sordidus
mirabilis
Hour of peak activity:
11am
12pm
1pm
2pm
3pm
Pads in sun
Areas of dung pad colonized
Pads in shade

6.2 VARIATIONS IN BIOLOGY

The major biological differences in the genus *Sisyphus*, between the two subgenera of *Sisyphus* have been discussed in section 5. There are, however, further points of difference within each subgenus. Biological variation between species, which has been found to affect competition with other species includes variations in:

(1) the duration of the immature stages and the seasonal period over which adults emerge;

(2) the reproductive biology of the adult female and the length of the adult female life.

6.2.1 The Duration of the Immature Stages and the Emergence of Adults.

There are differences in the duration of the egg stage in the various species, as indicated in table 8 but these differences are too small to be important as regards minimizing competition with other species.

All *Sisyphus* species overwinter as larvae but some larvae also pupate and become adults in the same summer season in which the egg was laid. There is, therefore, much variation in the length of the larval stage but this variation in age between overwintering larvae and those which pupate and become adults before the winter, is very similar for all species. Most species, however, have several generations of adults within one season and this period, from egg to adult within the season, varies between species. Table 12 shows the duration of the immature stages, completing their development within one season, as obtained from laboratory data.

Table 12: Mean and range of days necessary for each of the eight Mkuzi *Sisyphus* species to complete their development from egg to adult within one season, in the laboratory during summer. (October to March).

Species	Mean number of days	Range of days recorded	Total no. of emergences
sordidus	66,2	55-77	11
seminulum	47,1	30-72	120
mirabilis	77,3	60-140	90
fortuitus	73,2	56-91	14
spinipes	51,8	43-75	83
infuscatus	53,7	42,83	66
rubrus	64,0	35-113	60
calcaratus	59,7	38-110	99

Table 12 shows that there is a large range in the duration of the immature stages in summer within one species. Differences in temperature at different times of the season would be partly responsible for this as well as different water content of the soil in the brood ball containers. These two factors cannot, however be responsible for such large fluctuations (e.g. *rubrus* 35 to 113 days) and often broods in the same container, with eggs laid over a few days, produce adults over a period of 40 days. The biological advantages of scattered emergences in as unpredictable environment as those found in southern Africa, as opposed to a single burst of emergences, is obvious.

The period over which adults emerge during the year will also allow an increase of, or restrict the population growth, depending on its length. The overwintering larvae of all eight Mkuzi species pupate in spring or early summer and the adults emerge about two to three weeks later. There is variation, however, between species, in exactly when pupation takes place and therefore, when the adults subsequently begin emerging. The adult emergences recorded after the 1973 winter for seven of the eight Mkuzi species are shown in figure 107. Only two emergences of *sordidus* (in September) were recorded from overwintering larvae and so *sordidus* is not presented in figure 107. Since the adults of *sordidus*, being a species of the subgenus *Sisyphus*, do not breed in winter but overwinter as adults and most of the eggs laid produce adults within the same season, there are relatively fewer overwintering larvae than in the *Neosisyphus* species or *seminulum*. However, the adults of *sordidus*, after the winter, became active again, in the laboratory, towards the end of August (food ball making recorded from 27th August) and began breeding towards the end of September (recorded from 24 th September). *S. sordidus*, therefore, according to laboratory observations, together with *mirabilis*, the females of which take 10 to 14 days to mature after emergence, are the first of the eight species to become reproductively active at the beginning of the summer season. *S. fortuitus* is the last to follow, about six weeks later. While the numbers of emergences recorded for *calcaratus* and *rubrus* (fig. 107) are too low to be taken as anything more than indications, together with the graphs of the other five species, they do show that there are differences in time between the peak emergences of species, from spring and through the first two months of summer. Competition between species during this period would therefore, be reduced.

FIG 107

Graphs of cumulative percentages of adult emergences in the laboratory at the beginning of summer, for seven Mkuzi *Sisyphus* species. Numbers in brackets after the species name represent the total number of emergences recorded for that species.

In the laboratory, emergences of adults stop at different times at the end of summer in the various species Together with the different onset of emergences at the beginning of summer, this gives more or less species specific periods of adult emergence during the year. These periods, based on records of emergences from broods of all eight Mkuzi species kept under the same conditions in the laboratory, are illustrated in figure 108. Emergences are almost continuous throughout this period since by the time all the adults of one generation have emerged, those of the next generation have begun to emerge. In *fortuitus*, however, the second generation of adults is incomplete (period of emergence shown by broken line in figure 108). Of the eggs laid by the first generation of adult *fortuitus* (from overwintering larvae) only a small percentage produce adults within the same season, as shown in table 13, was compared to *mirabilis* which has an almost complete second generation.

Table 13: Percentages of *fortuitus* and *mirabilis* individuals which completed their immature development within one season compared to those which overwintered as larvae. Eggs of both species were laid at the same time intervals during the observation period: November 1972 to mid-February 1973. For each species emergences within the same season were from eggs laid in November, December, January and February.

Species	% emerged within the same season	% overwintered, emerged next season	Total number emerged
fortuitus	12,9	87,1	62
mirabilis	90	10	50

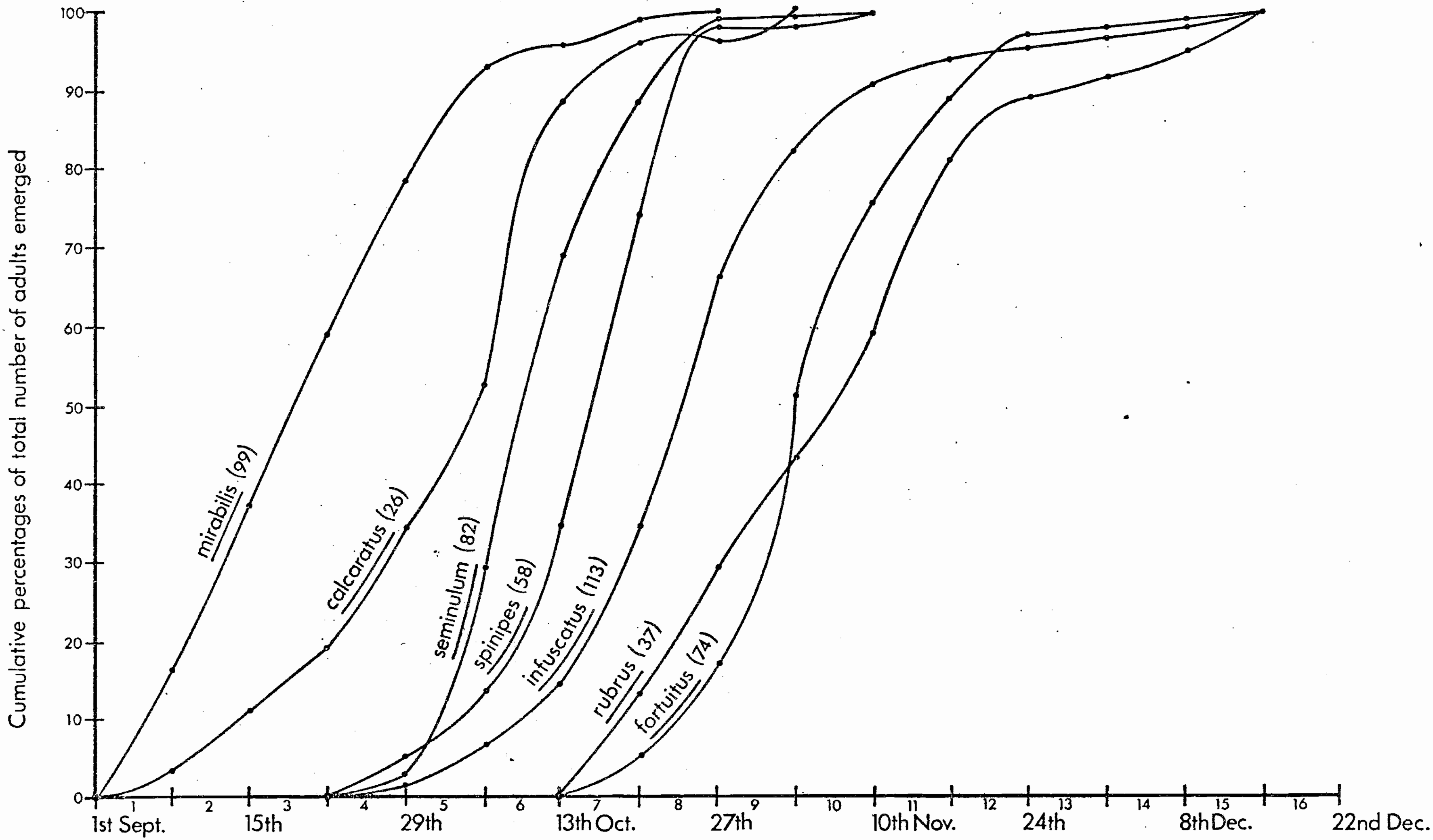

Cumulative percentages of total number of adults emerged
100
90
80
70
60
50
40
30
20
10
0
mirabilis (99)
calcaratus (26)
seminulum (82)
spinipes (58)
infuscatus (113)
rubrus (37)
fortuitus (74)
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
1st Sept.
15th
29th
13th Oct.
27th
10th Nov.
24th
8th Dec.
22nd Dec.
Weeks: 1st September - 22nd December

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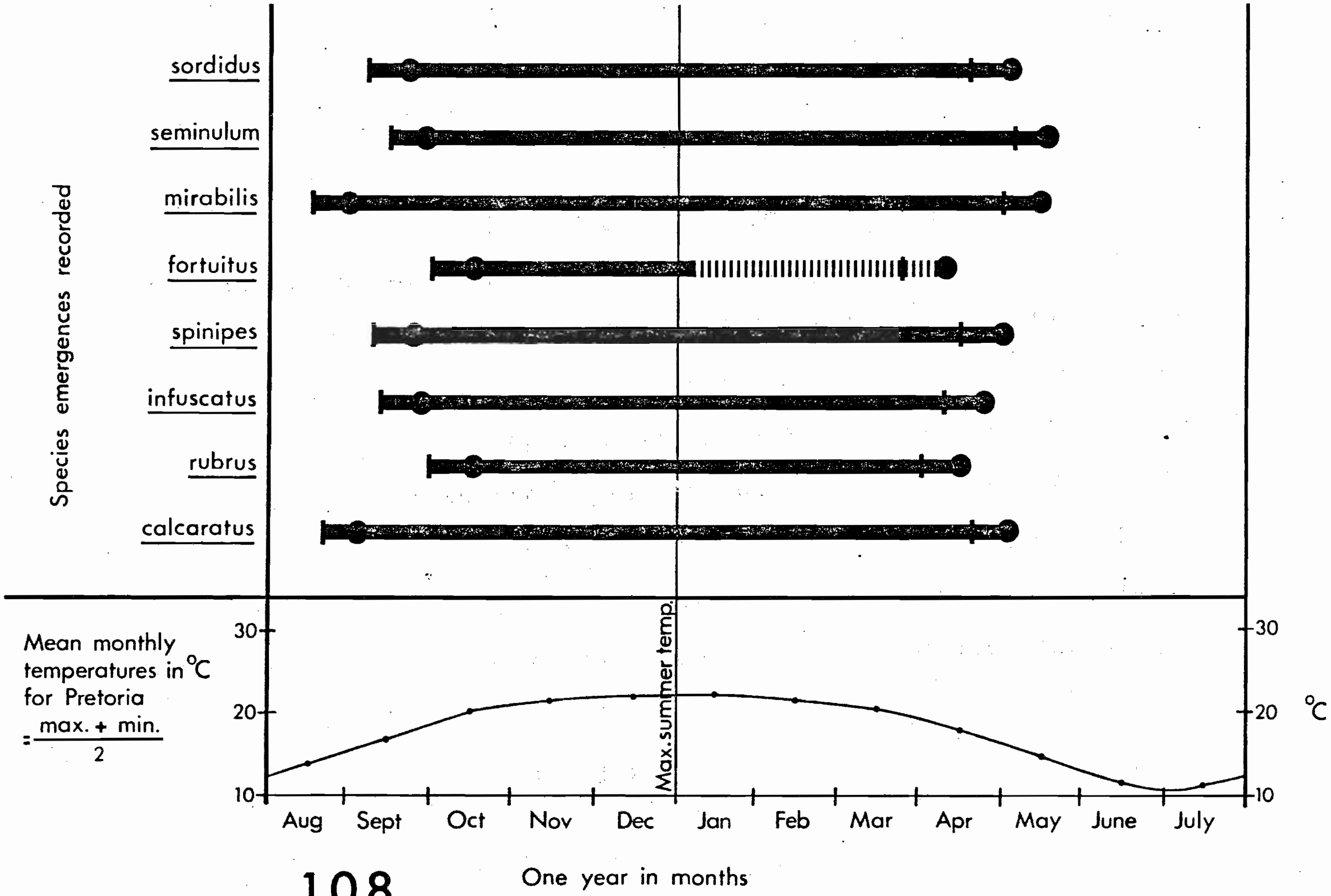
FIG 108

Diagram of the seasonal period of emergence in the laboratory of the eight Mkuzi *Sisyphus* species. Horizontal line between dots is the period between the first and last adult emergences. Horizontal line demarcated by short vertical line represents the estimated period from when the first larva pupates until the last pupates during the season. The broken line (for *fortuitus*) represents the emergence period of the relatively few individuals of the partial second generation. The mean monthly temperatures for the year in Pretoria as recorded by the Weather Bureau from 1903 to 1943, are given as indications of temperature differences.


Species emergences recorded
sordidus
seminulum
mirabilis
fortuitus
spinipes
infuscatus
rubrus
calcaratus
Mean monthly temperatures in °C for Pretoria = max. + min. / 2
30
20
10
°C
Max. summer temp.
Aug
Sept
Oct
Nov
Dec
Jan
Feb
Mar
Apr
May
June
July
One year in months

S. mirabilis has the longest immature development time (77,3 days) recorded for the eight *Sisyphus* species, yet the majority (90%) of its larvae, from eggs laid during the same period as those of *fortuitus*, completed their immature development and became adults in the same season (table 13). The effect of temperature on the number of individuals of the second generation emerging within the same season, was investigated in *fortuitus*. From 3rd April 1974 a container (A) of 30, third instar *fortuitus* larvae, which had begun overwintering were taken from the normal breeding room and kept at 28-33°C. Another container (B) of 30 similar larvae, was left in the normal breedingroom at 16-26°C as a control. The last *fortuitus* adult to emerge in the laboratory, under normal conditions, was on 20th February 1974. On 30th April 1974 the first adult emerged from A. A total of 12 adults emerged up until 10th May 1974, when the container was returned to the normal breeding room. No adults emerged from B, the control. On 10th October the broods in A and B were opened. Eight third instar, overwintering larvae were found in A and 18 in B. Increasing the temperature, therefore, made larvae of container A pupate and finally emerge as adults 70 days after normal laboratory emergences had ceased. The differences in seasonal emergence periods between species are also controlled by temperature. As in *fortuitus*, if temperatures are raised after emergences of the other species have stopped at the end of summer, beetles will again begin to emerge. This was done with *rubrus* and *calcaratus* and adults emerged throughout the winter months (May to August).

Each species seems to have a critical temperature below which the mature third instar larvae will not pupate. This is indicated by the results in figure 108, in that those species which begin emerging earlier in the season e.g. *mirabilis* stop emerging later than the other species. Considering that the emergence of the adults takes place about two weeks after pupation, the period of pupation for each species (fig. 108) is seen to begin and end roughly at the same temperature on either side of the maximum summer temperatures, at the end of December. Further emergence records would probably show up this trend more positively. As a result of this control by temperatures, these periods of emergence can be very variable in the field for any one season. The different emergence peaks at the beginning of summer may be considerably condensed. If there is a prolonged dry period the emergence patterns will also be affected since many of the adults would then not be able to escape from their brood balls when ready to do so. This frequently happens in summer rainfall areas when the spring or summer rains are late after a dry winter. When the late rains do come, the species will all begin emerging together.

Considering the different number of days required for immature development (table 12) and the seasonal period over which adults emerge in each species (fig. 108), it is evident that each species will have different numbers of adult generations within one season the numbers of generations recorded in the laboratory for each of the eight Mkuzi species, are contained in table 14.

Table 14: Number of generations of breeding females for the eight Mkuzi *Sisyphus* species, as obtained from laboratory data.

Species	Number of generations
sordidus	1 + 1 incomplete
seminulum	4
mirabilis	3
fortuitus	1 + 1 incomplete
spinipes	3 + 1 incomplete
infuscatus	3
rubrus	3 + 1 incomplete
calcaratus	3 + 1 incomplete

Incomplete generations shown in table 14 are those in which the numbers of emerging adults were not greater than those of the previous generation. The second generation was complete in most species. Some of the eggs laid by this generation of adults and most of the eggs laid by the third generation (in *spinipes*, *rubrus* and *calcaratus*) did not develop into adults until the next season.

6.2.2 The Reproductive Biology and Longevity of the Adult Female

Table 14 shows that *sordidus* has only one complete and one incomplete generation per season although the recorded mean duration of the immature stages is 66,2 days and the period of adult emergence is about 250 days. This reduction in generations is a result of the biology of the adults and not the larvae, as in *fortuitus*. Eggs of almost all the first generation of *sordidus* produce adults within the same season. All females emerging after mid December, however, as in the subgenus *Sisyphus* (except *seminulum*), feed only occasionally and do not reproduce.

They spend much of their time in the soil until the following spring when they mate and begin laying eggs. Therefore this species is only able to produce a partial second generation of breeding adults in one season, i.e. those which emerge before mid-December.

The number of individuals in a population can be built up during one season by having several generations of breeding adults during that season. From table 14 it would seem that *fortuitus* and *sordidus* (only one complete generation) do not have this potential to build up as large populations as the other six species. The reproductive biology and longevity of the females, however, can also be responsible for accelerating population growth. The laboratory data, obtained between January 1971 and October 1974, from individual pairs, on reproductive potential, rate of egg production and female longevity are recorded in table 15. The number of eggs laid and the longevity of the females emerging in summer (from September to January) and therefore, breeding mostly over the warmer months, are recorded separately from those emerging later in the summer or autumn (February to May). The rates of egg production (eggs/female/day) were calculated from the means for each month, obtained from four to 19 females, each breeding over 18-31 days of the month. The summer rate was calculated from the means for October to March and the winter rate was for April to August. The longevity of the males of each species was very similar to that of the females, e.g. of 18 *rubrus* "summer" females, the mean longevity was 116,8 days and the mean for the corresponding 18 males was 112,3 days. The variations in the longevity of the males have not, therefore, been included in table 15. The differences were found to be unimportant as regards competition.

Table 15: [+]No filial life histories of *sordidus* were completed by the time of writing, so ranges of eggs laid per female were calculated from reproductive rate and estimated longevity of 16 field collected and filial females. There are no "winter" *sordidus* females, which emerge at the end of summer and breed mostly during winter.

[++]"Summer" females of *sordidus* were those which emerged during the season, before mid-December and began breeding within a few weeks. These may die at the end of the season (after ± 200 days) or live to overwinter and breed again in the next season (living up to 500 days).

[+++]"Winter" females of *sordidus* were those which emerged after mid-December and only bred after overwintering. These may die during their first breeding season (after ± 300 days) or may overwinter again and then breed into a second season (living up to ± 700 days).

Table 15: The number of eggs per female, rate of egg production and female longevity of the eight Mkuzi species as recorded in the laboratory, during summer and winter.

Species	Total number of eggs/female						Mean rate of egg production (balls/♀/day)		Longevity of females (days)					
	"Summer" ♀♀			"Winter" ♀♀					"Summer" ♀♀			"Winter" ♀♀		
	Mean	Range	No ♀♀	Mean	Range	No ♀♀	In summer	In winter	Mean	Range	No ♀♀	Mean	Range	No ♀♀
sordidus	-	10-20^{+}	-	-	-	-	0,053	0	-	±200-500^{++}	-	-	±300-700^{+++}	-
seminulum	26,0	10-37	19	17,5	17-18	2	0,38	0,26	125,2	109-159	12	186,0	-	2
mirabilis	46,8	21-64	23	46,2	39-57	7	0,48	0,21	144,1	60-200	23	214,6	120-265	7
fortuitus	54,5	29-91	16	57,5	46-69	3	0,53	0,23	153,5	92-220	16	201,0	90-268	3
spinipes	43,7	17-56	18	34,5	10-60	11	0,63	0,25	104,2	78-137	18	153,2	190-202	11
infuscatus	56,4	16-81	11	36,2	16-49	6	0,83	0,37	114,1	45-174	11	127,3	61-187	6
rubrus	36,4	15-55	18	24,8	30-34	5	0,51	0,19	116,8	50-173	18	148,6	84-183	5
calcaratus	41,2	18-60	20	25,5	25-26	2	0,39	0,13	133,6	107-183	11	221,0	196-246	2

The ranges in the numbers of eggs laid and the longevity of the females, which are interdependent, are large. Very large numbers of females would be needed therefore, to produce accurate data. These data, recorded in table 15, are presented as indications of the possible biological characters which contribute to the ecological isolation of the species. The ranges and especially means, given in table 15, indicate that the eight species produce different total numbers of eggs, produce these at different rates and live for a different number of days. The numbers of "winter" females observed were mostly too small to make any definite comparisons with "summer" females but the winter females do seem to live longer and in six of the species the total number of eggs produced is decreased in the "winter" females. The rates of egg production are decreased in winter as could be expected. *S. calcaratus* shows the biggest reduction in breeding rate in winter (by 67%) and *seminulum* the smallest (31,9%). This could be expected since *calcaratus* tends to occur in higher numbers in drier, hotter areas (e.g. Messina, N. Tvl.) and prefers dung pads in the sun while *seminulum* is not found in as dry or as hot areas in Messina and it colonizes, almost exclusively, dung in the shade. The other six species show very similar reductions in rate, during winter, i.e. from 56% to 63%.

It can be seen from table 15, that *sordidus*, although has only one complete adult generation a year, the population growth can be just as great as in the *Neosisyphus* species and *seminulum* because it can live for longer than these species (200 to 700 days compared to 45 to 268 days).

The major population growth of *sordidus*, however, would be from season to season and not within one season, since the generations would accumulate mostly over successive seasons. In each field population of *sordidus*, from mid-December, there are actually six generations of adults present which fall into four distinct population groups:

(a) Adults which emerged as the first and second generation of the previous season, bred prior to overwintering and in the present season are breeding for the second time.

(b) Adults which emerged after mid-December of the previous season as the second generation of that season but did not breed before overwintering and are breeding during the present season for the first time.

(c) Adults which emerged as the first or second generation before mid-December of the present season and are breeding.

(d) Adults which emerged after mid-December of the present season and are not breeding.

Of these generations only one complete generation and one incomplete generation have emerged and bred within the same season (group c) but early in the season (September) the population groups a and b, which after overwintering, will begin breeding and so boost the population of newly emerged beetles.

S. fortuitus, as opposed to *sordidus*, breeds at a relatively high rate (0,53 eggs/♀/day compared to 0,053 of *sordidus*) and *fortuitus* lived longer than the other *Neosisyphus* species. Therefore, although, *fortuitus* has only one complete generation a year, during the summer a large "bank" of eggs are laid, most of which will only emerge as adults at the beginning of summer. This gives rise to a large initial population of the species in November, when the other *Neosisyphus* species have not yet been able to build up their numbers through a second generation.

From tables 14 and 15 it can be seen that each species has one or more biological characteristic which would rapidly increase the population (e.g. several generations or high breeding rate) but each species also has at least one biological characteristic which could be considered as inhibiting rapid population growth (e.g. few generations or slow breeding rate). Table 16 summarizes these different characteristics and gives the month of the seasonal population peak which would develop from these interacting characters, if conditions remained favourable and fairly constant within the season.

The population monitoring traps operating from February 1973 to April 1974, in Mkuzi, described under material and methods (section 4), only caught four of the eight *Sisyphus* species in numbers large enough to evaluate relative seasonal population fluctuations. Not more than 18, usually none at all, of the other species were caught during any one month. The four species caught in sufficient numbers were *sordidus*, *seminulum*, *mirabilis* and *calcaratus*. The total number of beetles in the fortnightly summer catches often differed greatly due to the weather conditions prevailing at the time of trapping. For January and March therefore, no reliable records exist. For the comparison of species caught in the other months, percentages have been used for the individual species since the absolute numbers are not reliable. Table 17 shows the results of this field trapping.

Table 16:

X denotes characteristic present for that species.

f:+ = start to emerge in August; others in September.

ff:+ = mean rate over 0,8; - = rate under 0,4 eggs/♀/day.

fff:+ = 4 full generations per season; others = 3.

ffff:+ = mean adult life over 130 days; others under 120.

Table 16: Biological characteristics tending to increase or inhibit population numbers and the resultant seasonal population peaks of the eight *Sisyphus* species in Mkuzi.

Species	Positive Characteristics				Negative Characteristics				Month of potential population peak
	Become active early in season (Aug/Sep) *f*	High breeding rate (0,3-0,9 eggs/♀/day) *ff*	Several generations per season (3-4) *fff*	Long adult life in summer (over 200 days)	Become active late in season (Oct)	Slow breeding rate (less than 0,9 eggs/♀/day)	Few generations per season (less than 2 full)	Short adult life (in summer 105-154 days) *ffff*	
sordidus	X+			X		X	X		Oct
seminulum	X	X -	X +					X	Apr
mirabilis	X +	X	X					X +	Feb
fortuitus		X			X		X	X +	Nov
spinipes	X	X	X					X	March
infuscatus	X	X +	X					X	March
rubrus		X	X		X			X	March
calcaratus	X +	X -	X					X +	March

Table 17: Field populations of four *Sisyphus* species in Mkuzi as found in traps set twice monthly from May 1973 to April 1974. The type of dung bait used each month is given.

Species	%.of total number caught							
	May-Sept	Oct	Nov	Dec	Jan	Feb	March	April
sordidus	0	61,0	47,8	25,3	-	39,1	-	10,9
seminulum	0	15,5	25,8	38,7	-	39,8	-	75,9
mirabilis	0	19,2	18,0	15,5	-	18,4	-	3,7
calcaratus	0	4,3	8,1	20,5	-	2,7	-	9,6
Total catch for month	0	727	161	380	-	550	-	294
Type of dung used	Horse	Horse	Horse	Cattle	Horse	Horse	Horse	Horse and cattle

S. sordidus and *seminulum* show population peaks (in October and April) relative to the other species, which agree with the predicted peaks in table 16, derived from laboratory data. The records in table 17 for *mirabilis*, show no clear population peak but the relative numbers of individuals were similar from October to February, then they had decreased by April. This suggests that a population peak existed between October and February. For *calcaratus* a population peak is shown in December which contradicts the laboratory data, suggesting a peak in March. However, the December captures were made using cattle dung as bait, while those in October, November and February, when considerably fewer *calcaratus* were collected (2,7-8,1% as opposed to 20,5%), were from horse dung. In April half horse and half cattle dung was used and 9,6% of the four *Sisyphus* species caught were *calcaratus*. *S. sordidus*, which has previously shown a preference for horse dung was caught in relatively lower numbers in December when cattle dung was used, than in November or February when horse dung was used. The different percentages of *calcaratus* could, therefore, be influenced by dung preference and not really represent the relative population of *calcaratus* present at the time.

No dung beetles were caught during the 1973 winter (May-August) which was exceptionally dry as was the previous summer. The 1973/74 summer rains only came at the end of September and so no beetles were caught until October. No evidence of the possible differences in the field appearances of *Sisyphus* species at the beginning of the season could, therefore, be recorded.

These field data recorded in table 17 suggest that the laboratory data collected on the biology of these four species and probably on the other *Sisyphus* species, are reliable as an indication of activity in the field. The same conclusion can be reached for the laboratory and field observation on the behaviour of the species. These laboratory data, therefore, can be used in considering the suitability of the species for transfer to Australia.

One major difference, however, between the laboratory and field data has been complete disappearance of the *Neosisyphus* species and *seminulum* in Mkuzi during winter. This was first observed during the 1973 winter which was preceeded by an exceptionally dry summer and this drought was thought to be the explanation. The 1973/74 summer and the 1974 winter, however, were considerably wetter but no *Sisyphus* were seen in Mkuzi in July and August. It was suspected that the species had a shorter adult life in the field. However, when examining the fore tibia of *calcaratus* and *sordidus* collected in traps set in Mkuzi (for G.D. Tribe) on 16th September 1974, it was found that two of the 11 *calcaratus* caught had very worn dentition on the fore tibia. This wearing is a sign of old age in the adults. At the beginning of September traps were set in the same area and no *Sisyphus* were caught. The wearing of the tibia to the extent observed could not have taken place within the two weeks between trapping. The only other explanation and one which would also explain the winter disappearance of the *Neosisyphus* species in the field in winter, seems to be that under certain unfavourable conditions, these species will also stop breeding and overwinter as adults, as do the species of the subgenus *Sisyphus*. This suggests that the adults of *Neosisyphus*, in addition to the larvae, are not as susceptible to changing environmental conditions as initially accepted but are able to adapt behaviourally and biologically to adverse periods in the field and survive these to reproduce when conditions are more favourable.

7 NATURAL ENEMIES AND COMPETITION FROM OTHER GENERA

In a study of insects intended for a biological control programme besides investigating biology and distribution, it is also necessary to look at natural enemies. Very little work has been done in this respect for dung beetles and no data are known to exist for any of the *Sisyphus* species. During the present study only superficial and preliminary observations on the natural enemies of dung beetles were made. These will be briefly discussed, together with a few other cases recorded by various workers. Some data on the field and laboratory activity of other dung beetle genera have been collected and this serves to outline the extent of their competition with *Sisyphus*.

7.1 NATURAL ENEMIES

Since most of the *Sisyphus* species spend a large amount of their time on or just under the dung or soil surface and either lay eggs in balls on the soil surface, or buried a few inches in the soil, they are vulnerable to parasites and predators.

Several times in the field endocoprid larvae, have been found to be parasitised by a species of *Bombylius* (Diptera : Bombylidae) and in one case by a species of the superfamily Chalcidoidea (Hymenoptera) (A.L.V. Davis, pers. comm.).

Many mites are found on the adults and dead or dying eggs, larvae and pupae of all dung beetle genera. It has not been established whether the mites are only attacking dying individuals or are primarily responsible for their deaths.

Various birds e.g. crowned guinea fowls and mammals e.g. baboon, have been implacated as predators of dung beetles (G.D. Tribe, pers. comm.). In southern Africa, however, there is no known proven case of a vertebrate preying selectively or heavily on dung beetles.

Two invertebrate predators of dung beetles are known. Species of Histeridae (Coleoptera) living in dung have been seen to attack and kill the adult dung beetles (G.F. Bornemissza, pers. comm.). In Mkuzi several individuals of an asilid species (Diptera) were observed waiting on the vegetation near dung pads and then catching small *Onthophagus* individuals on the wing, as they were about to land on the dung pads. The asilids returned to the vegetation with their prey, sucked out their body contents, discarded the empty "shell" and prepared for another attack. Several times they tried to catch individuals of *calcaratus* but did not suceed as the beetles were probably too large. The asilids could have caught individuals of the smaller species, *seminulum*, but the asilids were only observed to "hunt" at pads in the sun, while *seminulum* flies almost exclusively to pads in the shade.

Fungus is often found growing on dead adults, eggs, larvae and pupae. Whether this is primary or secondary is not known. It has been shown, however, that there are diseases attacking at least the egg stage of dung beetles. The trachea of the fully formed embryo in the egg have been observed to blacken. These embryos failed to hatch and died within the egg. This could be the result of a disease attacking the embryonic larva itself, or through an inability of the larva to hatch, caused by a change in the chorion due to disease.

These examples show a wide range of possible natural enemies of the genus *Sisyphus*.

7.2 COMPETITION FROM THE GENERA

The paracoprid genera, e.g. *Onitis* Fabricius, *Copris* Müller, *Heliocopris* Hope, *Onthophagus* Latreille and *Euoniticellus* Janssens tend to bury the dung, working from underneath the pad and therefore are less inclined to disrupt the ball making activities of the *Sisyphus* species when they are together in the same pad, than other telecoprid genera e.g. *Pachylomera* Korby, *Kheper* Janssens, *Scarabaeus* L, *Gymnopleurus* Illiger, *Allogymnopleurus* Janssens and *Garreta* Janssens. Several individuals of *Heliocopris neptunus* Boheman, however, have each been observed in the Umfolozi Game Reserve, Zululand to "demolish" overnight, a litre dung pad which was colonized by *Sisyphus* species during the previous day. These *Heliocopris* could carry *Sisyphus* individuals away with them in the dung and these *Sisyphus* could ultimately die in the *Heliocopris* burrow. The para- and telecoprid species, however, also tend to colonize certain dung pads selectively and tend to avoid those colonized by *Sisyphus*. In addition the differences in behaviour and biology between species of other genera and *Sisyphus* species are far greater than those found to exist between the *Sisyphus* species themselves. A few species of *Scarabaeus* and *Kheper*, for example, are night or crepuscular fliers (G.D. Tribe, pers. comm.) as are several species of *Onitis*, *Heliocopris*, *Copris* and *Onthophagus*. Some species of these genera also show a strong preference for one dung type, e.g. horse or sheep.

Other telecoprid genera observed are similar to the subgenus *Sisyphus* in that they make and roll their balls away almost immediately on reaching the dung and so spend most of their adult lives away from the food source. Therefore, the ball rolling activity of other telecoprid day fliers which could cause the most disruption of *Sisyphus* breeding activity, takes place during the warmer parts of the day when the *Neosisyphus* species have finished their early morning ball making activity and not yet started any late afternoon or evening activity. A total of 195 *Allogymnopleurus thalassinus* were observed, for example flying to dung and making balls between 10 a.m. and 3 p.m. in Mkuzi, over three days in December. Few individuals (17) were seen flying outside this period.

The seasonal activity periods of some of the other telecoprid species also differ from those of the *Sisyphus* species. In Mkuzi, at the experimental site, seven other telecoprid species were found, belonging to six different genera. Their relative seasonal activity as obtained from the Mkuzi traps is recorded in table 18.

Table 18: Seasonal field activity periods of seven telecoprid species, other than *Sisyphus*, in Mkuzi from May 1973 to April 1974, as obtained from traps set twice monthly.

Genus and species	Period of Activity	No individuals caught
Kheper nigroaeneus (Boheman)	Early October to April	150
Kheper Lamarcki (M'Leary)	November to April	23
Pachylomera femoralis (Kirby)	late October to April	9
Scarabaeus zambesianus Pēringuey	October to April	1+
Allogymnopleurus thalassinus (Klug)	late October to February	527
Gymnopleurus sp.	late October to December	20
Garreta nitens (Olivier)	late October to December	91

+This specimen was caught in April but many were collected by G.D. Tribe and I.D. Temby in October 1973. This *Scarabaeus* is a crepuscular flier (G.D. Tribe, pers. comm.) so did not come to traps already colonized by *Sisyphus* and other day fliers.

These telecoprid species seem to have only one complete adult generation per season. As in the species of the subgenus *Sisyphus* the adults stop breeding in April and overwinter. *A. thalassinus* and *G. nitens* were bred in the laboratory and these females (over 100 of each species) showed the same activity period as they did in the field (table 18). By the end of February all the females of these two species had stopped producing eggs. This was observed over two seasons (1970/1971 and 1973/1974). The adults emerging in December, from eggs originally laid in the same season did not breed but overwintered and became active during the next summer.

Therefore, while all the *Sisyphus* species investigated seem to utilize the same dung types, are all day fliers and are active together at least in the last two-thirds of the season, some species of other genera have definite dung preferences, have diurnal activity periods varying over 24 hours and may only be active over half of the summer season. A more detailed investigation into these other genera, especially telecoprid genera, would probably show several more differences. Even from this very preliminary investigation, therefore, it seems that other genera pose less of a threat of competition to the *Sisyphus* species than the *Sisyphus* species do to each other.

8 SUMMARY TABLES

Table 8.1 : MORPHOLOGY

Table 8.2 : DISTRIBUTION AND SEASONAL OCCURRENCE

Table 8.3 : ADULT BEHAVIOUR

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Table 8.5 : SUITABILITY OF SPECIES FOR AUSTRALIA

Data in brackets is either estimated or calculated from incomplete data, unless otherwise indicated.

N/A = not applicable

\- = no, or insufficient, data available.

TABLE 8.1 : MORPHOLOGY

SPECIES	CHARACTERS OF SPECIES GROUPS	SPECIFIC CHARACTERS WITHIN GROUPS	BODY LENGTH IN MM. (MEANS GIVEN FIRST, RANGES IN BRACKETS; THEN NUMBERS OF INDIVIDUALS MEASURED)	SEXUAL DIFFERENCES (MOST PROMINANT CHARACTER OF MALE, WHICH DIFFERS FROM FEMALE)	COLOUR RANGES	FIG. NUMBER OF AEDEAGUS
MURICATUS	HAIR ON ELYTRA IN TUFTS	HAS PRONOTAL PROJECTION; BODY LENGTH MORE THAN 8MM:	♂ :10,5(8,9-11,5)20 ♀ :10,4(8,5-11,3)32	HAS PROJECTION ON VENTRAL RIDGE, HIND FEMUR	ENTIRELY BLACK	54
FASCICULATUS		TUFTS PRESENT ON PRONOTUM	♂ :8,0(6,5-8,8)4 ♀ :8,0(7,5-8,3)7	HAS "BRUSH" OF HAIRS ON VENTRAL OF HIND TIBIA	ENTIRELY BLACK	55
ALVEATUS		BODY LENGTH LESS THAN 6MM.	♂ :4,9(—)2 ♀ :4,4(3,5-5,1)7	HAS "TUBERCLES" ON VENTRAL RIDGE OF HIND TIBIA	ENTIRELY BLACK	56
IMPRESSIPENNIS	SHAPE OF HIND TIBIAL PROJECTION (FIGS 14 : 15)		♂ :9,2(7,5-11,2)71 ♀ :8,6(6,7-10,2)161	HAS ANGULAR PROJECTION ON VENTRAL RIDGE OF HIND FEMUR	ENTIRELY DARK BROWN TO BLACK	57
SEMINULUM	FRONT OF CLYPEUS CLEFT; HAIRS ON PYGIDIUM RANDOM	HEAD SHAPE (FIG. 18)	♂& ♀:3,8(3,0-4,4)84	NO VISIBLE EXTERNAL DIFFERENCE	RED-BROWN TO DARK BROWN LEGS AND ELYTRA LIGHTER	58
SPECIES *X*		HEAD SHAPE (FIG. 23)	♂& ♀:6,9(6,0-8,1)13	HAS "TUBERCLES" ON VENTRAL RIDGE OF HIND TIBIA	ENTIRELY BLACK	59
SPECIES *Y*		HEAD SHAPE (FIG. 24)	♂& ♀:4,5(3,6-5,5)34	HAS "TUBERCLES" ON VENTRAL RIDGE OF HIND TIBIA	ENTIRELY BLACK	60
COSTATUS	FRONT OF CLYPEUS BROAD FLAT; HAIRS ON PYGIDIUM IN "TRIDENT"-SHAPED PATTERN.	NO ABDOMINAL HAIR TUFTS	♂& ♀:5,6(5,1-6,2)18	HAS "TUBERCLES" ON VENTRAL RIDGE OF HIND TIBIA	USUALLY ENTIRELY BLACK; ELYTRA MAY BE RED-BROWN IN COLOUR	61
SORDIDUS		SIDES HEAD ROUNDED (FIG. 19)	♂& ♀:6,4(5,5-7,3)76	HAS "TUBERCLES" ON VENTRAL RIDGE OF HIND TIBIA	ENTIRELY BLACK	62
CAFFER		VENTRAL HAIR POCKETS PRESENT AND HAIRS OF RED-BROWN COLOUR	♂& ♀:7,2(6,1-7,8)45	HAS "TUBERCLES" ON VENTRAL RIDGE OF HIND TIBIA	ENTIRELY BLACK	63
?GORYI		VENTRAL HAIR POCKETS PRESENT AND HAIRS OF YELLOW	♂& ♀:5,9(4,9-7,9)136	HAS "TUBERCLES" ON VENTRAL RIDGE OF HIND TIBIA	ENTIRELY BLACK	65
TIBIALIS	PROJECTION ON DORSAL SURFACE OF MIDDLE TIBIA	"BOILS" ON PYGIDIUM PRESENT	♂ :9,7(9,3&10,0)2 ♀ :8,8(—) 2	HAS PROMINANT SPINE ON VENTRAL RIDGE, HIND FEMUR	LIGHT BROWN TO DARK BROWN	66
MIRABILIS		NO "BOILS" ON PYGIDIUM	♂ :9,9(8,3-11,1)31 ♀ :9,7(8,4-10,6)26	HAS PROMINANT SPINE ON VENTRAL RIDGE, HIND FEMUR	ENTIRELY BLACK	67
KUEHNI	SHAPE OF HIND FEMORAL PROJECTION (FIGS 52 ; 53)		♂ :10,8(9,6-11,9)3 ♀ :12,3(11,5-13,0)3	TROCHANTER IS EXTENDED TO FORM A SPUR	DARK BROWN; ELYTRA OF A LIGHTER RED- BROWN COLOUR	68
QUADRICOLLIS	PROJECTIONS ONLY ON VENTRAL SURFACE OF MIDDLE TIBIA AND FEMUR	SIDES ELYTRA "CUT AWAY"	♂ :11,3(—)1 ♀ :11,2(—)1	TROCHANTER IS EXTENDED TO FORM A SPUR	DEEP RED- TO ORANGE BROWN; ELYTRA LIGHTER THAN PRONOTUM	69
FORTUITUS		MALE NO HIND FEMORAL SPINE; POSTERIOR CLYPEAL SPINES ROUNDED	♂ :10,5(9,0-11,5)33 ♀ :10,0(9,0-11,5)26	TROCHANTER IS EXTENDED TO FORM A SPUR	ENTIRELY DARK BROWN	70
SPINIPES		POSTERIOR CLYPEAL SPINES POINTED	♂ :8,6(6,5-10,0)175 ♀ :8,6(6,5-9,7)103	HAS PROMINENT SPINE ON VENTRAL RIDGE, HIND FEMUR	USUALLY ENTIRELY BROWN TO DARK BROWN	72
INFUSCATUS		NO SPINE VENTRALLY ON MIDDLE TIBIA	♂ :8,1(6,7-9,0)38 ♀ :8,2(6,8-9,1)39	HAS PROMINANT SPINE ON VENTRAL RIDGE, HIND FEMUR	BROWN TO YELLOW- OR ORANGE BROWN; LEGS LIGHTER DORSALLY	73
RUBRUS		SHAPE OF MIDDLE FEMORAL SPINE; AEDEAGUS (FIG. 74)	♂ :7,6(6,6-9,0)153 ♀ :7,8(6,5-9,5)93	TROCHANTER IS EXTENDED TO FORM A SPUR	BROWN TO LIGHT YELLOW- OR ORANGE BROWN; LEGS ALWAYS LIGHTER	74
MACRORUBRUS		SHAPE OF MIDDLE FEMORAL SPINE; AEDEAGUS (FIG. 75)	♂ :9,1(7,2-10,2)74 ♀ :9,1(7,8-10,0)42	TROCHANTER IS EXTENDED TO FORM A SPUR	BROWN TO LIGHT YELLOW- OR ORANGE BROWN; LEGS ALWAYS LIGHTER	75
BARBAROSSA	NO PROJECTIONS DORSALLY OR VENTRALLY ON MIDDLE TIBIA OR FEMUR	EPICRANIAL SUTURE IN Y-SHAPED DEPRESSION;	♂ :9,5(8,5-10,0)13 ♀ :8,9(7,9-9,8)20	HAS PROMINANT SPINE ON VENTRAL RIDGE, HIND FEMUR	DARK BROWN TO BLACK HAS A SILKY SHEEN; ELYTRA MAY BE LIGHTER	76
SPECIES *A*		SHAPE OF MALE HIND FEMORAL SPINE (FIG. 47)	♂& ♀:10,9(—)1	HAS PROMINANT SPINE ON VENTRAL RIDGE, HIND FEMUR	BLACK	77
CALCARATUS		SEMI-ERECT HAIRS IN MIDDLE OF ELYTRA	♂ :7,1(5,9-8,0)45 ♀ :6,8(5,7-7,5)27	HAS PROMINANT SPINE ON VENTRAL RIDGE, HIND FEMUR	USUALLY ENTIRELY BLACK, HAS A SLIGHT SILKY SHEEN	78
CON[illegible]ER		EPICRANIAL SUTURE IN V-SHAPED DEPRESSION.	♂ :7,8(6,[illegible])20 ♀ :7,3(6,3-7,9)20	HAS PROMINANT SPINE ON VENTRAL RIDGE, HIND FEMUR	USUALLY ENTIRELY BLACK, SILKY SHEEN	79

TABLE 8.2 : DISTRIBUTION AND SEASONAL OCCURRENCE IN SOUTHERN AFRICA

SPECIES	SOUTH AFRICA: WESTERN CP	SOUTHERN CP	CENTRAL CP	NORTHERN CP	NORTH-EASTERN CP	EASTERN CP	OFS: EASTERN BORDER	OFS: REMAINDER	NATAL	ZULULAND	SE TVL	E TVL	S TVL	SW TVL	KNP UP TO PHALABORWA	N & NE TVL	SWA: ETOSHA AREA	RHODESIA: NORTH WESTERN	NORTHERN	CEN. HIGHLANDS	CEN & S. LOWLANDS	EASTERN	MOZAMBIQUE: SOUTHERN	CENTRAL COASTAL	CENTRAL INLAND	AVERAGE ANNUAL RAINFALL OVER MAJORITY OF DISTRIBUTION. HIGH=OVER 750MM MEDIUM=500-750MM LOW=BELOW 500MM	ALTITUDE OVER MAJORITY OF DISTRIBUTION HIGH=OVER 140M MEDIUM=1000-1400M LOW=BELOW 100 METERS	TEMPERATURE^X HOT=± 34°C-10°C MEDIUM=± 29°C-5°C COLD=± 25°C-0°C (X BASED ON AVERAGE DAILY MAX. AND AVERAGE DAILY MIN. FOR THE HOTTEST AND COLDEST MONTHS RESP.)	RANGE OF VEGETATION TYPES	SEASONAL OCCURRENCE AS FROM FIELD DATA
MURICATUS		+									+	+														HIGH	LOW-HIGH	MEDIUM	GRASSLANDS	OCT-MARCH
FASCICULATUS										+		+														MEDIUM	LOW	HOT	WOODLAND-FOREST	OCT-FEB
ALVEATUS												+	+								+	+	+		+	MEDIUM-HIGH	LOW-HIGH	COLD-HOT	GRASSLANDS	JAN-FEB
IMPRESSIPENNIS																+		+	+		+	+		+	+	LOW-MEDIUM	LOW-MEDIUM	MEDIUM-HOT	WOODLAND-FOREST	NOV-FEB
SEMINULUM						+				+	+	+	+			+		+			+	+		+	+	LOW-MEDIUM	LOW-MEDIUM	HOT	WOODLAND-FOREST	AUG-JULY
SPECIES *X*										+																MEDIUM	LOW	HOT	WOODLAND	-
SPECIES *Y*										+														+		MEDIUM-HIGH	LOW	HOT	WOODLAND	-
COSTATUS									+		+	+														MEDIUM-HIGH	MEDIUM-HIGH	COLD-MEDIUM	GRASSLAND	JAN-MARCH
SORDIDUS										+					+							+	+	+	+	MEDIUM-HIGH	LOW	HOT-MEDIUM	TREELESS SCRUB OR WOODLAND	OCT-APRIL
CAFFER					+	+	+	+	+		+															MEDIUM-HIGH	MEDIUM-HIGH	COLD-MEDIUM	GRASSLAND	DEC-MARCH
? GORYI										+		+	+	+	+	+		+	+	+	+	+		+	+	LOW-HIGH	MEDIUM-LOW	MEDIUM-HOT	TREELESS SCRUB OR GRASSLAND - WOODLAND	NOV-MAY
TIBIALIS												+														HIGH	LOW	HOT	SHRUB/WOODLAND	-
MIRABILIS										+																MEDIUM-HIGH	LOW	HOT	WOODLAND-FOREST	AUG-MAY
KUEHNI						+						+														HIGH	LOW-HIGH	MEDIUM-COLD	GRASSLANDS	JAN-MARCH
QUADRICOLLIS	+		+																							LOW	LOW	COLD	SCRUB OR GRASSLANDS	OCT-MARCH
FORTUITUS		+	+				+		+	+	+	+	+	+		+						+				LOW-HIGH	LOW-HIGH	COLD-HOT	TREELESS SCRUB OR GRASSLANDS-WOODLAND	OCT-MAY
SPINIPES		+			+	+			+	+	+	+		+	+	+					+	+	+	+	+	MEDIUM-HIGH	LOW-MEDIUM	COLD-HOT	TREELESS SCRUB OR GRASSLANDS-WOODLAND	AUG-JUNE
INFUSCATUS						+				+			+		+	+					+			+	+	MEDIUM-HIGH	LOW-MEDIUM	MEDIUM-HOT	TREELESS SCRUB OR GRASSLANDS-WOODLAND	AUG-MAY
RUBRUS		+			+	+	+	+	+	+	+	+	+	+	+	+				+	+	+			+	LOW-HIGH	LOW-HIGH	COLD-HOT	TREELESS SCRUB OR GRASSLANDS-WOODLAND	SEPT-JULY
MACRORUBRUS			+	+	+		+	+									+									LOW-MEDIUM	MEDIUM-HIGH	MEDIUM-COLD	GRASSLANDS-SAVANNAH	OCT-MAY
BARBAROSSA	+	+	+		+	+	+		+																	MEDIUM-HIGH	MEDIUM-HIGH	COLD-HOT	GRASSLANDS-SAVANNAH	OCT-MAY
SPECIES *A*																								+		HIGH	LOW	HOT	SAVANNAH	-
CALCARATUS										+		+			+	+		+		+		+			+	LOW-MEDIUM	LOW-MEDIUM	MEDIUM-HOT	TREELESS SCRUB OR GRASSLAND-WOODLAND	OCT-MAY
CONFRATER						+				+	+	+							+	+	+	+		+	+	MEDIUM-HIGH	LOW-MEDIUM	COLD-HOT	TREELESS SCRUB OR GRASSLAND-WOODLAND	SEPT-MAY

SPECIES *A*																								+		HIGH	LOW	HOT	SAVANNAH	-
CALC TUS										+		+			+	+		+		+		+			+	LOW-MEDIUM	LOW-MEDIUM	MEDIUM-HOT	TREELESS SCR GRASSLAND-WC	OCT-MAY
CONFRATER						+				+	+	+							+	+	+	+		+	+	MEDIUM-HIGH	LOW-MEDIUM	COLD-HOT	TREELESS SCRUB OR GRASSLAND-WOODLAND	SEPT-MAY

TABLE 8.3 : ADULT BEHAVIOUR

SPECIES	MAKES FOOD BALLS (=+) OR FEEDS AT DUNG (=X)	PAINTS ITSELF WITH WHITE SECRETION AND COVERS ITSELF WITH DUNG, OR NOT	PERIOD OF BROOD-BALLS MAKING ACTIVITY A= + 10AM-12PM & POSSIBLY ALSO 2-4PM. B= ± 6-11AM & POSSIBLY ALSO 4-6PM	HOURS OF PEAK DUNG COLONIZATION ACTIVITY	AREA OF DUNG USED FOR MAKING BROOD-BALLS	SHAPE OF BROOD BALL WHEN COMPLETED AFTER OVIPOSITION (f=SEE FIG. 97 FOR ILLUSTRATION)	WHEN, DURING BROOD MAKING SEQUENCE, OVIPOSITION TAKES PLACE	WHERE BROOD BALL IS DEPOSITED
MURICATUS	+	NO	A	10AM-12PM	IN SURFACE LAYER OF PAD	ORANGE-SHAPED^f	BEFORE BURIAL	BURIED DOWN TO 5CM
FASCICULATUS	+	NO	A	10AM-12PM	SURFACE	ORANGE-SHAPED^f	BEFORE BURIAL	BURIED DOWN TO 5CM
ALVEATUS	(+)	(NO)	(A)	(10AM-12PM)	(SURFACE)	-	-	-
IMPRESSIPENNIS	+	NO	A	10AM-12PM	SURFACE	PEAR-SHAPED^f	AFTER BURIAL	BURIED IN CHAMBER 2-5CM DEEP
SEMINULUM	+	YES	9AM - 1PM	12-1PM	SURFACE	DOME ON SPHERE^f	AFTER BURIAL	BURIED TO 5CM DEEP
SPECIES *X*	(+)	(NO)	(A)	(10AM-12PM)	(SURFACE)	DOME ON SPHERE	-	-
SPECIES *Y*	(+)	(NO)	(A)	(10AM-12PM)	(SURFACE)	DOME ON SPHERE	-	BURIED
COSTATUS	+	NO	(A)	(10AM-12PM)	(SURFACE)	DOME ON SPHERE	AFTER BURIAL	BURIED
SORDIDUS	+	NO	A	11AM-12PM & 2-3PM	SURFACE	DOME ON SPHERE^f	AFTER BURIAL	BURIED 2-5CM DEEP
CAFFER	+	NO	(A)	(10AM-12PM)	(SURFACE)	DOME ON SPHERE^f	AFTER BURIAL	BURIED
? GORYI	+	NO	(A)	(10AM-12PM)	(SURFACE)	DOME ON SPHERE	AFTER BURIAL	BURIED
TIBIALIS	X	YES	B	(1-3PM)	IN EDGE OF DUNG PAD	SPHERE	AFTER BURIAL	BURIED UNDER OBJECTS; 4-10CM DEEP
MIRABILIS	X	YES	B	1-2PM	JUST IN EDGE	SPHERE WITH VERY SHORT TIP^f	AFTER BURIAL	
KUEHNI	X	YES	B	(12-3PM)	IN EDGE OF PAD	ORANGE-SHAPED^f	BEFORE BURIAL	-
QUADRICOLLIS	(X)	(YES)	(B)	(12-3PM)	(IN EDGE)	-	-	-
FORTUITUS	X	YES	B	12-1PM	DEEP INTO EDGE	SPHERE WITH TIP^f	AFTER DEPOSITION	DEPOSITED IN VEGETATION
SPINIPES	X	YES	B	1-2PM	DEEP INTO EDGE	SPHERE WITH LONG TIP^f	AFTER DEPOSITION	DEP. & CEMENTED TO VEGETATION
INFUSCATUS	X	YES	B	1-2PM	JUST INTO EDGE	SPHERE WITH TIP^f	AFTER DEPOSITION	DEPOSITED IN VEGETATION
RUBRUS	X	YES	B	2-3PM	DEEP INTO EDGE	SPHERE WITH FLAT DOME^f	AFTER BURIAL	BURIED UNDER OBJECTS;
MACRORUBRUS	X	YES	B	(12-3PM)	DEEP INTO EDGE	SPHERE WITH FLAT DOME	AFTER BURIAL	4-10 CM DEEP
BARBAROSSA	X	YES	B	(12-3PM)	IN SURFACE LAYER	ORANGE-SHAPED^f	BEFORE BURIAL	BURIED 1-5CM OR LEFT ON SURFACE
SPECIES *A*	(X)	(YES)	B	(12-3PM)	(SURFACE)	-	-	-
CALCARATUS	X	YES	B	1-2PM	SURFACE	ORANGE-SHAPED^f	BEFORE BURIAL	JUST BURIED, TO 5 CM DEEP
COI TER	X	YES	B	(12	SURFACE	ORANGE-SHAPED^f	BEFORE BURIAL	USUALLY BURIED; JUST 3CM

TABLE 8.4 : BIOLOGY OF IMMATURE AND ADULT STAGES

SPECIES	NUMBER OF DAYS TAKEN FOR EGGS TO HATCH IN SUMMER. RANGE GIVEN FIRST THEN NUMBER OF EGGS RECORDED IN BRACKETS	DURATION OF IMMATURE STAGES IN SUMMER (EGG TO ADULT)(MEANS IN DAYS)	PERIOD OVER WHICH ADULTS EMERGE IN SUMMER IN THE LAB. + = ADULTS EMERGING AFTER MID-DEC NOT BREEDING UNTIL NEXT SUMMER	NUMBER OF ADULT GENERATIONS PER SEASON (INC=INCOMPLETE GENERATION IN WHICH LESS ADULTS THAN PRESENT GENERATION EMERGE)	REDUCTION IN GENERATIONS CAUSED BY NON-BREEDING, NEWLY EMERGED FEMALES, OR BECAUSE EMERGENCES CEASED	NUMBER OF EGGS PRODUCED PER FEMALE IN SUMMER (MEANS)	RATE OF EGG PRODUCTION: EGGS/FEMALE/DAY IN SUMMER (MEANS)	FEMALE LONGEVITY, EMERGING EARLY IN SUMMER (MALES VERY SIMILAR) (MEANS IN DAYS)	OVERWINTER AS NON-BREEDING ADULTS, OR NORMALLY BREED DURING WINTER	ADULTS VERY RESISTANT TO DESSICATION IN SUMMER AND WINTER
URICATUS	-	58,0	? - APRIL	1+1 INC	FEMALES	14,0	0,13	395,0	NON-BREEDING	YES
SCICULATUS	-	60,0	? - MAY	1+1 INC	FEMALES	18,0	0,16	390,0	NON-BREEDING	YES
LVEATUS	-	-	-	-	-	-	-	-	NON-BREEDING	YES
RESSIPENNIS	-	48,0	-	1+1 INC	FEMALES	-	0,19	(OVER 270)	NON-BREEDING	YES
MINULUM	5 - 8 (10)	47,1	END SEP-MAY	4	N/A	26,0	0,38	125,2	BREEDS	NO
ECIES *X*	-	-	-	-	-	-	-	-	(NON-BREEDING)	-
ECIES *Y*	-	-	-	-	-	-	-	-	(NON-BREEDING)	-
STATUS	-	-	-	1+1 INC	FEMALES	(10-20)	(±0,05)	(OVER 200)	NON-BREEDING	YES
RDIDUS	8 (1)	66,2	SEP - MAY	1+1 INC	FEMALES	(10-20)	0,053	(200-500)	NON-BREEDING	YES
FFER	-	(60-70)	-	1+1 INC	FEMALES	(10-20)	(±0,05)	(OVER 200)	NON-BREEDING	YES
ORYI	-	(60-70)	-	1+1 INC	FEMALES	(10-20)	(±0,05)	(OVER 200)	NON-BREEDING	YES
BIALIS	-	65,0	-	(3)	N/A	28,0	0,47	80,0	BREEDS	NO
RABILIS	8-10 (8)	77,3	END AUG-MAY	3	N/A	46,8	0,48	144,1	BREEDS	NO
EHNI	-	-	(OCT-FEB)	1+1 INC	EMERGENCES	-	0,38	-	BREEDS	NO
DRICOLLIS	-	-	-	-	-	-	-	-	(BREEDS)	-
TUITUS	10-14 (6)	73,2	OCT-APRIL BUT VERY FEW AFTER DEC	1+1 INC	EMERGENCES	54,4	0,53	153,5	BREEDS	NO
VIFES	8 - 9 (8)	51,8	END SEP-MAY	3+1 INC	N/A	43,7	0,63	104,2	BREEDS	NO
USCATUS	8 -10 (7)	53,7	OCT-APRIL	3	N/A	56,4	0,83	114,1	BREEDS	NO
RUS	8 -10 (4)	64,0	OCT-APRIL	3+1 INC	N/A	36,4	0,51	116,8	BREEDS	NO
RORUBRUS	-	64,8	(OCT-APRIL)	(3+1 INC)	N/A	(OVER 30)	0,40	(OVER 90)	BREEDS	NO
BAROSSA	-	(50-60)	OCT-FEB	1+1 INC	EMERGENCES	42,0	0,37	208,2	BREEDS	NO
CIES A	-	-	-	-	-	-	-	-	(BREEDS)	-
ARATUS	7-8 (5)	59,7	SEP-MAY	3+1 INC	N/A	41,2	0,39	133,6	BREEDS	
FRATER		55,1	SEP-MAY	(3)	N/A	43,0	[illegible]	139,0	BREEDS	NO

ARBAROSSA	-	(50-60)	OCT-FEB	1+1 INC	EMERGENCES	42,0	0,37	208,2	BREEDS	NO
SPECIE	-	-	-	-	-	-	-	-	(BREEDS)	-
CALCARATUS	7-8 (5)	59,7	SEP-MAY	3+1 INC	N/A	41,2	0,39	133,6	BREEDS	NO
CONERATER	-	55,1	SEP-MAY	(3)	[illegible]	43.0	0.18	139.0	BREEDS	NO

TABLE 8.5 : SUITABILITY OF THE SPECIES FOR AUSTRALIA

+ CHARACTER FAVOURABLE: 0 CHARACTER UNFAVOURABLE
++ CHARACTER VERY FAVOURABLE: 00 CHARACTER VERY UNFAVOURABLE

(COLUMN HEADINGS GIVE THE CHARACTERIST
DESIRED IN THE SPECIES FOR INTRODUCTI

SPECIES	MORPHOLOGICALLY DISTINCT SPECIES	VARIED, WIDE DISTRIBUTION	OCCURS IN SUFFICIENT NUMBER TO ESTABLISH A LABORATORY BREEDING POPULATION	IMMATURE STAGES COMPLETED IN A SHORT TIME	ADULT EMERGENCES IN THE LABORATORY OVER A LONG PERIOD	SEVERAL GENERATIONS OF ADULTS PER SEASON	NUMBER OF GENERATIONS INCREASED BY MAINTAINING HIGH TEMPERATURES	ADULTS LONG-LIVED	EACH FEMALE PRODUCES A LARGE NUMBER OF EGGS	EGGS PRODUCED AT A HIGH RATE	ADULTS BREEDING INTO WINTER IN THE FIELD AND LABORATORY	ADULTS VERY RESISTANT TO DESSICATION	LEVELS OF SUITAB OF THE SPECIES 1 HIGHLY RECOMM 2 RECOMMENDED 3 FOR LATER CON TION OF LIMIT VALUE 4 OF VERY LIMIT 5 UNSUITABLE
MURICATUS	++	0	+	+	+	00	0	++	0	0	0	++	4
ASCICULATUS	++	0	+	+	+	00	0	++	0	0	0	++	3
ALVEATUS	++	0	0	-	-	-	-	-	-	-	-	-	5
MPRESSIPENNIS	+	+	+	+	+	00	0	++	0	0	0	++	4
SEMINULUM	+	+	+	++	++	++	+	0	+	+	+	0	2
SPECIES *X*	+	0	0	-	-	-	-	-	-	-	-	-	5
SPECIES *Y*	+	0	0	-	-	-	-	-	-	-	-	-	5
COSTATUS	+	0	0	+	+	00	0	++	00	00	0	++	5
SORDIDUS	+	+	+	+	+	00	0	++	00	00	0	++	3
CAFFER	+	+	+	+	+	00	0	++	00	00	0	++	3
? *GORYI*	0	++	+	+	+	00	0	++	00	00	0	++	3
TIBIALIS	++	+OUTSIDE SA	+	+	+	+	+	0	+	+	+	0	2
MIRABILIS	++	0	+	+	++	+	+	+	+	+	+	0	3
KUEHNI	+	0	0	-	0	0	-	+	-	+	+	0	5
UADRICOLLIS	+	0	0	-	-	-	-	-	-	-	-	-	5
ORTUITUS	0	+	+	+	0	0	+	+	++	++	+	0	2
SPINIPES	0	++	+	+	+	++	+	0	+	++	+	0	1
NFUSCATUS	0	+	+	+	+	++	+	0	++	++	+	0	2
RUBRUS	0	++	+	+	+	+	+	0	+	+	+	0	1
ACRORUBRUS	0	+	+	+	+	+	+	0	+	+	+	0	2
ARBAROSSA	0	+	+	+	0	0	+	+	+	+	+	0	2
SPECIES *A*	0	0	0	-	-	-	-	-	-	-	-	-	5
ALCAP TUS	0	+	+	+	++	++	+	0	+	+	+	0/+	2
ONFR ER	0	+	+	+	+	+	+	0	+	+	+	0	3

9 DISCUSSION

This general study of the southern African species in the genus *Sisyphus* was largely a preliminary investigation. The aim was to isolate and identify species involved and to investigate their behaviour and biology. Many questions concerning the mechanisms influencing their behaviour and biology have arisen during this study but it would take several more years of research to answer these questions. The aims of this project, however, have been achieved. Firstly, the taxonomy of the species has been completely revised. From the summary tables of the differences in morphology, distribution, behaviour and biology between the species, the validity of these species is clearly established. Overall the number of known valid *Sisyphus* species in southern Africa has been increased from 17 to 24.

The basic knowledge of behaviour, biology and ecology of the *Sisyphus* species, which has come from this study has made it possible for these species to be assessed for introduction into Australia. In table 8.5 of the summary tables, after the tabulation of their favourable and unfavourable characteristics, the 24 species have been grouped according to their suitability as species to be sent to Australia. The species highly recommended for Australia have been selected mainly on whether they have been found in relatively large numbers in several areas in the field, have bred at a reasonable rate (over 0,25 balls/female/day) in the laboratory, and did not overwinter as non-breeding adults. A total of nine species (groups 1 and 2 of table 8.5 have been highly recommended for Australia. These species are; group 1: *spinipes*, *rubrus*, (eggs both already sent to Australia); group 2: *seminulum*, *tibialis*, *fortuitus*, *infuscatus*, *macrorubrus*, *barbarossa* and *calcaratus*. Six more species (group 3 of table 8.5) should also be considered but the subgenus *Sisyphus* species of this group would probably be difficult to breed in the laboratory unless the non-breeding overwintering stage of the adults can be broken. The species of group 3 would probably be of a more limited value to Australia since they are not as numerous in the field as the species of groups 1 and 2, or have restricted distributions. Nine species (groups 4 and 5) were found to be of very limited potential, or totally unsuitable, mostly because they have never been found in large numbers in the field and/or have a very restricted distribution. The species suggested for Australia can now be studied in more detail in the light of the findings of this preliminary study.

From the distributional and seasonal occurrence data it is evident that eventually the more common species, which have been recommended for Australia, will be sympatric in several areas over a large part of the summer season if they are introduced into Australia. Through differences in behaviour and biology, however, it seems that these species reduce competition with one another sufficiently to allow them to co-exist succesfully. Since the *Sisyphus* species recommended for Australia do have different trends in distribution, behaviour and biology, each one fills a different ecological niche, each of which will contribute to the aim of the "Dung Beetle Project", i.e. to fill as many ecological situations as possible in Australia.

The question of competition between sympatric species is probably more complex than suggested by the data and arguments presented in section 6. Intraspecific competition and relative abundance also need to be considered. Competition between the *Sisyphus* species is most disadvantegeous when it results in the combat over brood balls at the dung source. Severe competition here would seriously interfere with the reproduction of the species. Therefore, it seems that intraspecific competition could also disrupt the breeding activity of the species. Some of the biological characters given in table 16 (e.g. slowbreeding rate of few adult generations) would seem to be effective in limiting population growth within one season. However, from the maximum numbers which build up during the season, the initial level of the population of the next season would be determined. Therefore over succesive seasons there seems to be potentially unlimited population growth. This control of the population growth within one season, would reduce the intraspecific competition, without seriously reducing the ability of the species population to establish itself again in the next season. If the population does become too large over succesive favourable seasons, then the overcrowding resulting could reduce the fecundity of the females. This has been observed in *Sisyphus* for *spinipes*, described in the introduction to section 6. Intraspecific competition has been observed to reduce the rate of egg production considerably in the laboratory but to find out at what population size and in which circumstances intraspecific competition begins to affect seriously the success of the species in the field would still require intensive investigation.

In Mkuzi, four of the eight species *sordidus*, *seminulum*, *mirabilis* and *calcaratus* occur in large numbers while there are relatively few *fortuitus*, *spinipes*, *infuscatus* and *rubrus*. The four species occurring sympatrically in large numbers, suggesting similar habitat preferences, are behaviourally and biologically distinct species. These four species would have the least amount of competition between each other. Therefore, they seem to have evolved different behavioural and biological patterns in order to co-exist successfully in a similar, preferred habitat. The four species occurring in low numbers are more similar to each other and *calcaratus*, in behaviour and biology. Since they are in low numbers they will be more seriously affected by interspecific competition and since they are biologically and behaviourally similar, they could be displaced, or displace each other, from the Mkuzi area. This would not be severely detrimental to these species, however, since they occur in other areas more favourable for them in large numbers where fewer or no other *Sisyphus* species exist. If conditions in Mkuzi change, these species could re-colonize this marginal area from individuals in the main area of their distribution.

This study has revealed that several *Sisyphus* are suitable for transfer to Australia. If introduced into Australia, they have excellent chances of establishing themselves successfully in the field, without seriously competing with one another. They should contribute to the control of the fly pests and to a lesser extent, reduce pasture damage in Australia.

10 SUMMARY

1 Twenty four species of the genus *Sisyphus* known in southern Africa are listed with their synonyms and their taxonomy is discussed.

2 A key to the adults of 23 of these species is given.

3 The known distribution of 23 species and seasonal occurrence of 19 species are illustrated and briefly discussed.

4 The general biology of the genus *Sisyphus* is discussed and the major behavioural and biological differences between the two subgenera *Sisyphus* and *Neosisyphus*, are given.

5 The laboratory and field investigation into variations in behaviour and biology in eight species occurring in the Mkuzi Game Reserve, with regards to interspecific competition, is presented.

6 The known possible natural enemies of *Sisyphus* are mentioned and the extent of competition from other genera, based on field and laboratory observations, is outlined.

7 Summary tables of all data with a final tabulated evaluation of the suitability of species for introduction into Australia is given.

8 Nine species have been highly recommended for Australia. Six more species could be considered but most of these still need further investigation. The remaining nine species were found to be unsuitable for transfer to Australia.

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