Supplement to *Koedoe* 1984: 153-165

NOTES ON THE COLEOPTEROUS FAUNA OF THE KALAHARI

edited by

E. HOLM

Department of Entomology
University of Pretoria
Pretoria
0002

Abstract – Three essays on aspects of the beetle fauna of the Kalahari are presented. The first deals with the problem of defining the Kalahari zoogeographically. Two hundred distribution maps of species from three beetle families were analysed to outline the region (I). The second compares the ground-living beetles of the Kalahari to those of the Namib, with reference to faunistic composition and ecological niches (II). The third investigates the origin of the sand-adapted tenebrionid beetles of the Kalahari, with special reference to the tribes Adesmiini and Zophosini (III).

Introduction

The lack of a precise definition of the Kalahari region makes meaningful discussion of its fauna or ecology difficult. The first paper in this contribution on the coleopterous fauna of the Kalahari attempts to define the Kalahari on the basis of species distribution maps of three beetle genera from three different families.

Very few specific studies on the Kalahari insect fauna are available, compared to *e.g.* the extensive work on Namib insects. (For recent bibliographies on the latter see Holm & Scholtz 1980 and Wharton & Seely 1982). Apart from the few papers from which the following contributions are drawn, all information on Kalahari beetles is contained in taxonomic revisions which invariably cover much larger regions than the Kalahari *sensu stricto*. Even in these papers information on the coleopterous Kalahari component is usually scarce and distribution records few and far between. As far as we could establish, the position is similar in other insect orders.

There can be little doubt that the ground-living beetle fauna is one of the most important ecological components of the Kalahari system, as it is in the Namib. The only ecological study of this faunal component is a descriptive pattern and niche analysis by Louw (1983), of which extracts are given below. A follow-up of this work with quantitive ecological studies should certainly be a priority of research in the Kalahari ecosystem.

There is obviously a need for an intensive survey of the insects of the Kalahari. Taxonomic studies could contribute much to our understanding of the history and ecology of the region through illuminating the ancestry and relationships of the fauna, degrees of endemism, the diversities at species and higher taxonomic levels and the zoogeography. Some of these possibilities are indicated in the paper by Penrith below.

Part I

THE BOUNDARIES OF THE KALAHARI REGION AS DERIVED FROM DISTRIBUTION MAPS OF THREE BEETLE GENERA

E. HOLM and C. H. SCHOLTZ
Department of Entomology
University of Pretoria
Pretoria
0002

As an ecological biome the Kalahari is hard to define because it seems to grade into savanna in the west, north and east and into Karroo in the south. It is therefore not surprising that there seems to be no consensus as to the boundaries of the region loosely described as the Kalahari.

We approached this question not from an ecological, but from a zoogeographical angle. For our analysis we used the published distribution maps of the 93 *Acmaeodera* (Buprestidae) species (Holm 1978), 42 *Trox* (Trogidae) species (Scholtz 1980) and 65 *Graphipterus* (Carabidae) species (Basilewsky 1977) recorded from southern Africa. These genera were selected because they represent ecologically widely different families (Buprestidae: woodborers, Trogidae: carrion-feeders and Carabidae: predators, respectively), and because recent revisions with adequate distribution maps were available. Distribution limits were drawn around the recorded localities of each species using a method that compensates for poorly collected areas. This method is fully described in Holm & Scholtz (*in press*) & De Klerk & Scholtz (*in prep.*).

Two-hundred individual species maps were classified into three categories. The first category included maps of species that occur mainly within the general region usually described as Kalahari (Fig. 1).

The second category included maps of all species that do occur in the Kalahari, but have the major part of their geographic distribution outside this area (Fig. 2). The third category consisted of maps of those species that occur outside the Kalahari (or enter it only very marginally) (Fig. 3). The species representation of the three genera in categories one to three was rather similar (*Acmaeodera* 67%, 21% and 3%; *Trox* 86%, 10% and 5%; *Graphipterus* 69%, 26% and 5%). All three genera are clearly predominantly savanna groups, and are also poorly represented in tropical and desert areas elsewhere on the African continent.

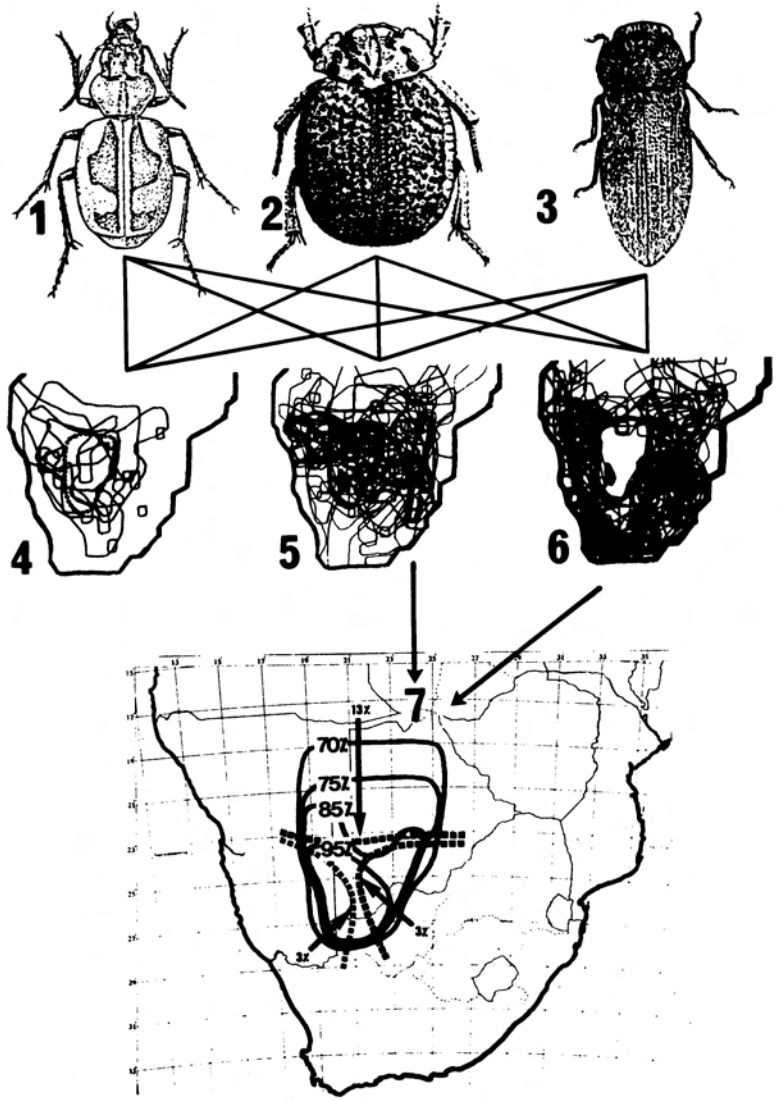

Fig. 1. *Graphipterus* sp. (from Basilewsky 1977).

Fig. 2. *Trox* sp.

Fig. 3. *Acmaeodera* sp.

Fig. 4. Superimposed distribution limits of species from all three genera occurring mainly within the hypothesized Kalahari (dotted line).

Fig. 5. Superimposed distribution limits of species from all three genera occurring mainly outside, but with substantial instrusion into the hypothesized Kalahari (heavy line).

Fig. 6. Superimposed distribution limits of species from all three genera outside the hypothesized Kalahari (heavy line), or entering it marginally.

Fig. 7. Exclusion contours based on Figs. 5 and 6. Percentages of species intruding up to the dotted limits from the various directions are given on the arrows.

Category 1: The combined maps of the few species that are mainly endemic to the Kalahari do not produce any clear pattern. There is a tendency to extend into savanna regions to the west, north and east (Fig. 4).

Category 2: The species intruding into the Kalahari show a more clearly defined savanna-distribution cutting across the northern Kalahari. Progressively fewer are represented towards the south-west of the region (Fig. 5).

Category 3: The combined maps of excluded or virtually excluded species form a very clearly defined boundary around the Kalahari (Fig. 6).

The maps of categories two and three were then analyzed to draw contours around the areas which exclude progressively higher percentages of species from 70% to 95% (Fig. 7). On the same map, the percentage of all species intruding into the region from various directions (up to the dotted limits) are given on arrows.

Discussion

Since the three genera investigated are ecologically and phylogenetically unrelated and yet produced similar results, it is probable that the zoogeographical limits derived from them have a fairly general significance.

The summarizing Fig. 7 allows the following conclusions:

1. Zoogeographically the Kalahari seems to be well defined in the south, but grades into savanna in the north.
2. There are few species common to the Kalahari on the one hand and the Karoo and Namaqualand regions on the other. In contrast virtually all Kalahari species also occur in the savanna regions.
3. On the zoogeographical evidence provided, the Kalahari therefore clearly represents a special extension of the savanna regions of the Trans-Botswana corridor (Endrödy-Younga 1978). This extension becomes progressively more differentiated from the typical savanna towards the south west, reaching its most defined state in the area surrounding the Kalahari Gemsbok Park.
4. Whatever ecological affinities there may be between the Kalahari and other arid regions in southern Africa (Karoo, Namaqualand, Namib), these are not borne out by zoogeographical affinities in the three genera investigated.

Acknowledgements

Both authors acknowledge grants from the CSIR and the University of Pretoria towards this study.

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Part II

COMPARISON OF THE FAUNISTICS AND ECOLOGICAL PATTERNS OF THE GROUND-LIVING BEETLE FAUNAS OF THE KALAHARI AND NAMIB DESERT

S. V. d. M. LOUW

National Museum
P.O. Box 266
Bloemfontein
9300

The ground-living beetle faunas of the Namib Desert and Kalahari were compared in a one-year (1976-77) survey with lines of pit-traps covering the main habitats. The Kalahari site was about 50 km west of Aroab (26° 28′S, 19° 33′E), while the Namib site was on Kanaän 104 (25° 52′S, 16° 07′E). A total of 92 traps were used in the two sites.

The complete methods and results of the survey are published elsewhere (Louw 1983). Some of the findings of special interest and bearing on the faunistics and ecology of the Kalahari can be summarized as follows:

1. *Ecological niches.* The available niches for ground-living beetles in the Kalahari and Namib dunes were remarkably similar, with the important exception of the absence of dune slip faces in the Kalahari. While some ecologically very equivalent beetles could therefore be found in the ground-living faunas of the two areas, none of these pairs of equivalents agreed at species level and all but one were in different genera (Table 1).

Table 1

Biological equivalents between the Namib and Kalahari living Tenebrionidae

KALAHARI	NAMIB
Cimicichora hessei *	*Arthrocora arenicola* *
Zophosis jacoti **	*Zophosis hereroensis* **
Tarsocnodes ?tarsalis **	*Lepidochora discoidalis* *
	Vernayella pauliani *
Miripronotum prominoculatum *	*Uniungulum hoeschi* *
Somaticus regalis	*Onymacris rugatipennis alboetessellata* **
Onymacris multistriata **	*Onymacris plana plana* **
Metriopus hoffmannseggi **	*Onymacris boschimana subelongata* **
Renatiella scrobipennis **	*Cauricara phalangium rufofemorata* **
Parastizopus armaticeps **	*Stipsostoma sculpta; Stips stali* **
*Iugidorsum cumstriis**	*Sulcipectus levis* *

*: Endemic genera

**: Endemic species

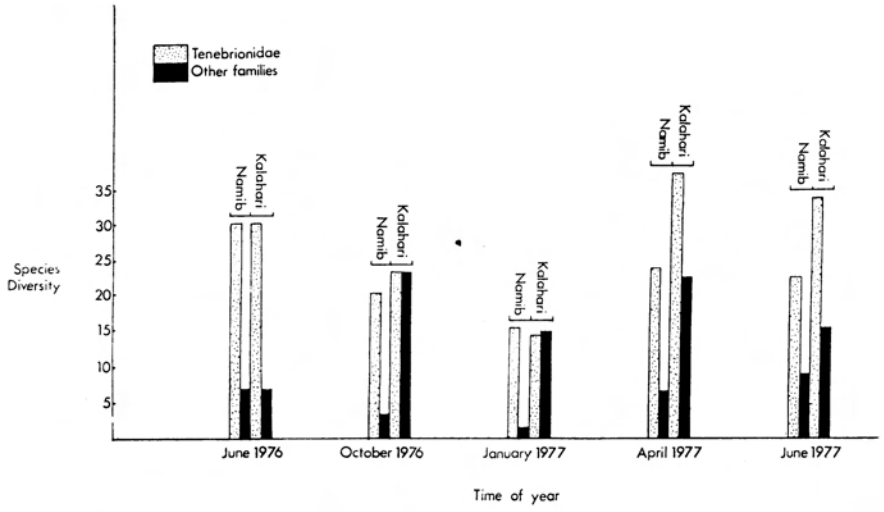

Fig. 1. Composition of apterous Coleoptera populations at main study sites in the Namib and Kalahari deserts.

Namib beetles generally had narrower habitat niches than their less stenoceous Kalahari counterparts, but a few very specialized Kalahari species were also recorded (e.g. *Miripronotum prominoculatum* Louw which only occurs on dune crests at ambient temperatures of lower than 5 °C).

2. *Diversity*. With 37 genera and 51 species of ground-living beetles, the Kalahari site had a significantly greater diversity than the Namib site (29 genera and 45 species). Sixty percent of species in the Kalahari were tenebrionids, against 80% in the Namib. The higher diversity in the Kalahari could largely be attributed to more non-tenebrionids in the summer months (Fig.1).
3. The dominant species in the ground-living beetle community were tenebrionids in the Namib and carabids in the Kalahari.
4. Both systems had a high degree of endemism among the ground-living beetles, with no species common to both areas. At generic level, however, there was considerable overlap.

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Part III

ORIGIN OF SAND-ADAPTED TENEBRIONID BEETLES OF THE KALAHARI

MARY-LOUISE PENRITH

Transvaal Museum
P.O. Box 413
Pretoria
0001

The extensive fixed dunes that cover most of the Kalahari have been mapped by Lancaster (1980, 1981). These dunes vary from sparsely vegetated in the south-western Kalahari to heavily clothed with savanna vegetation in the northern areas. As yet, no complete study of the Tenebrionidae of the Kalahari has been made, but preliminary studies at various sites in the south-western Kalahari, coupled with general collecting over a wider area, indicate that beetles of the family

Tenebrionidae are well represented in the Kalahari, and that an endemic psammophilous element of the tenebrionid fauna is well developed. The family Tenebrionidae is generally well represented in desert areas of the world. Three dune areas in the south-western Kalahari yielded 54, 37 and 32 species of Tenebrionidae respectively; at each site one third or more of the species recorded were sand specialists endemic to the Kalahari.

At tribal and subtribal level, the composition of all the tenebrionid fauna of southern African dune areas is similar. Below tribal level, the Kalahari psammophilous tenebrionid fauna includes several endemic lineages: two subgenera and two large species groups of Zophosini, a genus of Eurychorini, three genera of Molurini, and a genus of Opatrini (subtribe Stizopina). A number of lineages of wider distribution have sand-adapted members endemic in the Kalahari.

In order to investigate the relationships and possible origin of the sand-adapted Kalahari tenebrionids, the Zophosini and Adesmiini have been studied, since recent revisions are available and phylogenies have been established for these groups (Penrith 1977, 1979, 1980, 1981a, 1981b, 1982, 1983, *in prep.*) Since among the south-western African Tenebrionidae the sand-adapted lineages or species are always relatively derived, it is possible to trace their relationship back to less specialized species or groups. Four lineages of Zophosini that are dominant elements in the psammophilous Kalahari fauna and three species of Adesmiini are considered. These are the subgenera *Heliophosis* and *Sabulophosis* of the genus *Zophosis*, the *Zophosis deyrollei* and *Z. michaelis* species groups of the subgenus

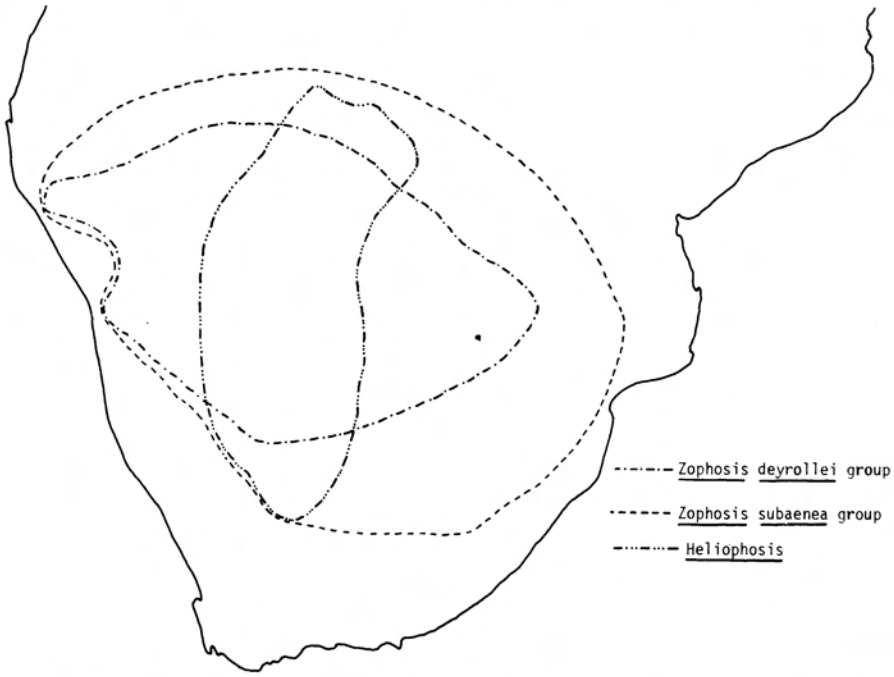

Fig. 1. Distribution of *Heliophosis*, *Zophosis deyrollei* group, and *Z. subaenea* group.

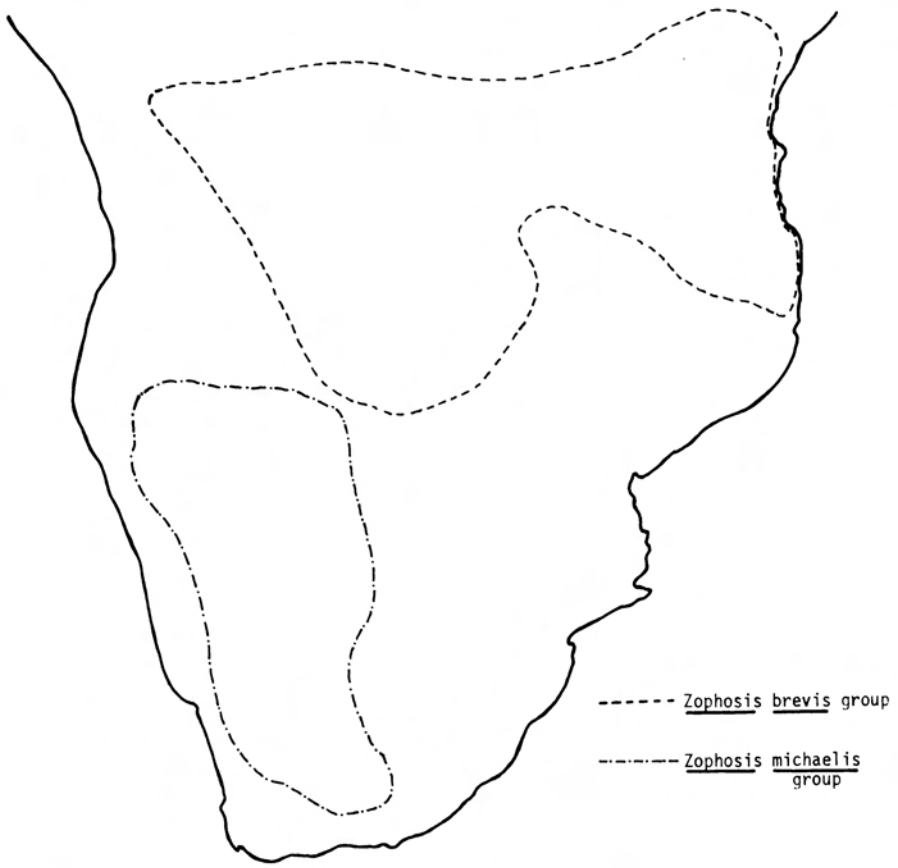

Fig. 2. Distribution of *Zophosis michaelis* and *Z. brevis* groups.

Zophosis, and *Onymacris multistriata*, *Stenocara kalaharica* and *Metriopus (Ceradesmia) albicollis*. In total, 56 species of Zophosini, of which 36 are endemic, and 19 species of Adesmiini, of which 10 are endemic, are recorded from the Kalahari. The non-endemic species have a wider distribution that includes adjacent areas. Most commonly they extend further westward into the margins of the Namib; several are savanna species that occur further north and east, and among the Zophosini in particular there are many elements shared with the Karoo, to the south. All the endemic species are tolerant of a deep sand substratum and may be found on the dunes, as is the case with many of the species of wider distribution. The present study was restricted to species that are found exclusively on dunes or in deep windblown sand.

The most derived of the four lineages of *Zophosis* studied is *Heliophosis*, with four species distributed in the western Kalahari (Fig. 1). An ancestor is considered to be a species similar to *Zophosis subaenea* of the subgenus *Zophosis*, belonging to a species group of *Zophosis* that is widespread in central southern Africa, with its centre of distribution in the Kalahari. The *Z. deyrollei* group, with seven species, has a wider, trans-Kalahari distribution, with two species also in the sands of the pro-Namib; it is probably derived from members of the same group as gave rise to *Heliophosis*. The *Z. michaelis* group, with 10 species, extends both into the northern pro-Namib and into the Karoo (Fig. 2). On shared apomorphic features it seems likely to be derived from a group of *Zophosis* sp. *s.s.* that is wide-spread in central and eastern Africa. The subgenus *Sabulophosis,* with eight species distributed across the Kalahari and penetrating the northern pro-Namib and Namaqualand to the west and the transitional highveld zone to the east (Fig. 3) to a limited extent, has a very different origin from the first three lineages, being derived from the subgenus *Hologenosis* (see Penrith 1982b). Certain shared apomorphic characters indicate a common origin with the *Zophosis burkei* group of *Hologenosis,* which is distributed from East Africa across the Kalahari, and includes an endemic Kalahari psammophilous species, *Z. rufipennis*.

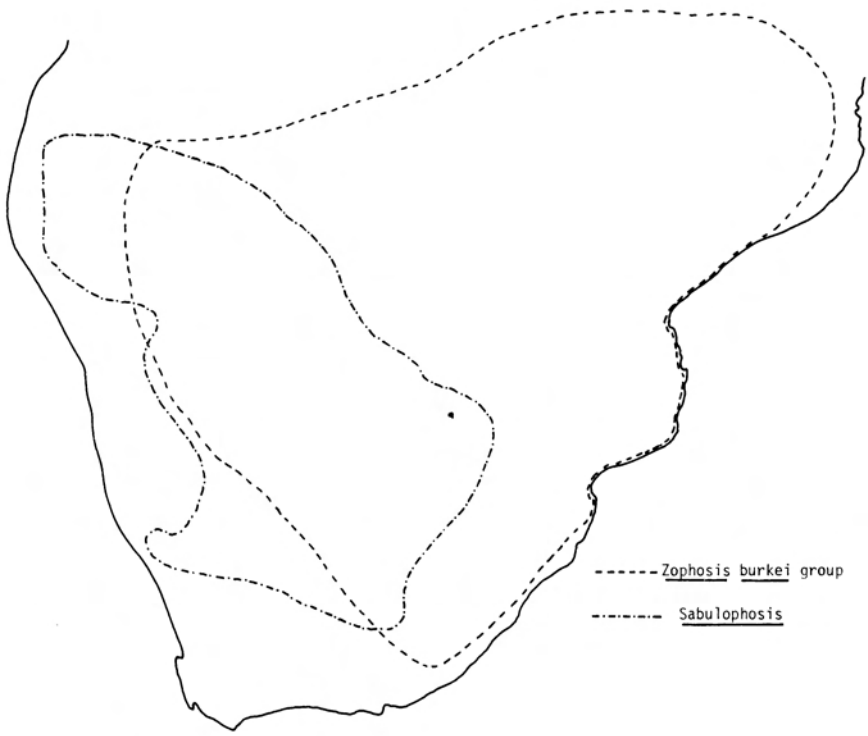

Fig. 3. Distribution of *Sabulophosis* and *Zophosis burkei* group.

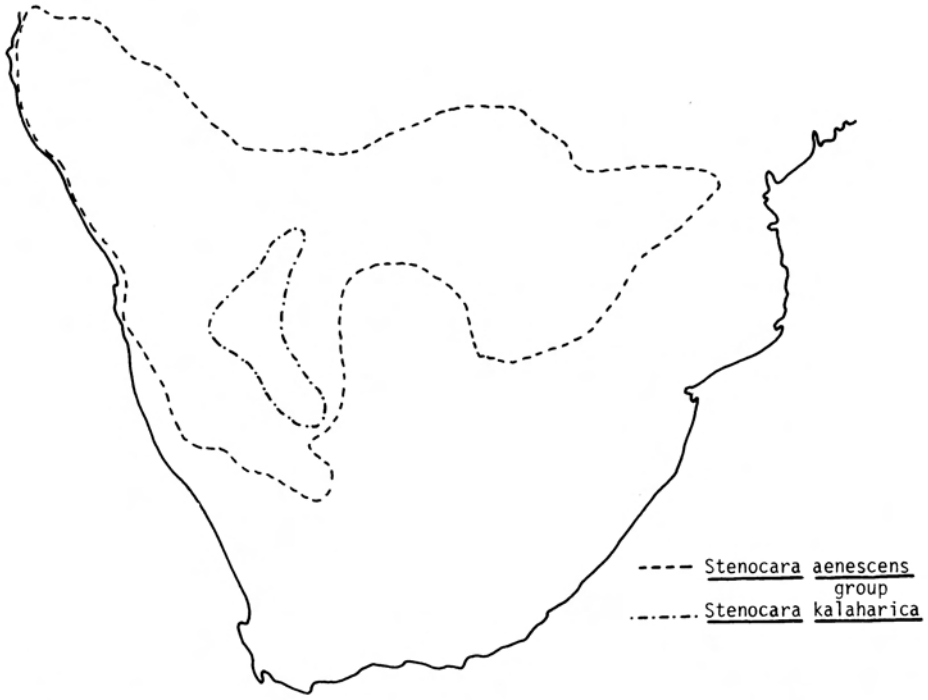

Fig. 4. Distribution of *Stenocara kalaharica* and *Stenocara aenescens* group.

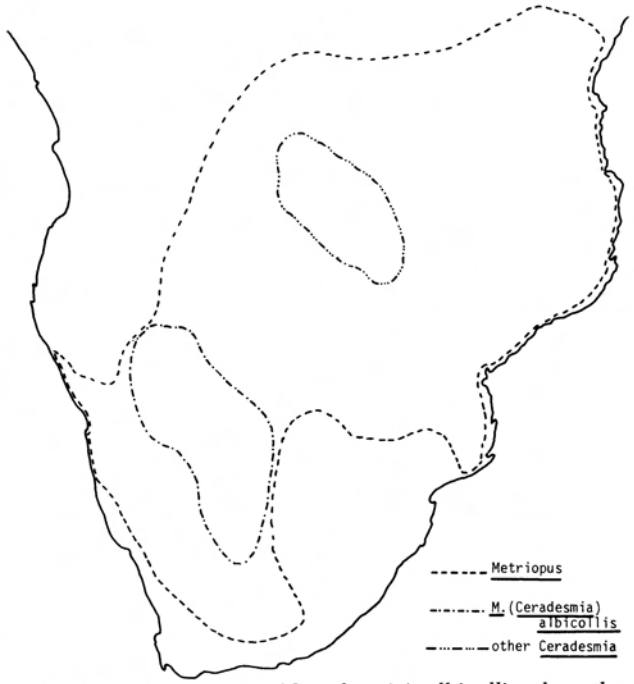

Fig. 5. Distribution of *Metriopus (Ceradesmia) albicollis*, the other two species of *Ceradesmia*, and of the genus *Metriopus*.

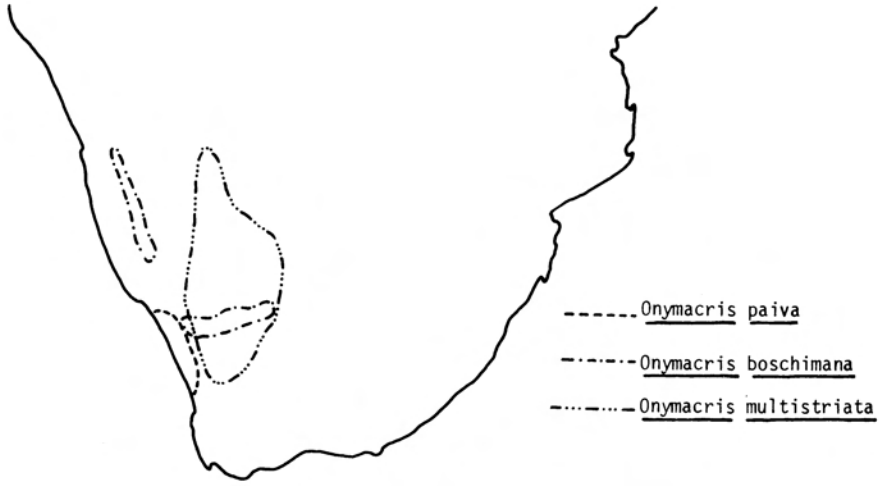

Fig. 6. Distribution of *Onymacris multistriata, O. boschimana,* and *O. paiva.*

The Adesmiini are as a tribe less psammophilous than the Zophosini, the genus *Onymacris* being the only whole lineage that shows a strong preference for sand. *Stenocara kalaharica* is distributed in the western Kalahari (Fig. 4), and is probably derived from the *Stenocara aenescens* group, with a trans-Kalahari distribution. *Metriopus albicollis* is rather more widely distributed (Fig. 5). It belongs to the subgenus *Ceradesmia,* of which it is the most derived of the three species. The other two species occur further north in central Africa. *Ceradesmia* is the most derived subgenus of *Metriopus,* whose general distribution is broadly southern and eastern African (Fig. 5).

In contrast to the probable Kalahari origin of *Stenocara kalaharica* and *Metriopus albicollis, Onymacris multistriata,* the third Kalahari dune adesmiine, clearly has a south-western origin. It is an apomorphic species with the tibiae compressed and flattened, a condition in the genus approached only in *O. boschimana*, which occurs in two subspecies with an apparently discontinuous distribution in northern Namaqualand and the Namib (Fig. 6). The two species are likely to have arisen from species similar to the Namaqualand *Onymacris paiva*. The derivation of *Onymacris multistriata* from a south-western Namaqua group is probably parallelled in the Kalahari by a species of *Pachynotelus* of the tribe Cryptochilini.

The evidence from the phylogeny of the Zophosini and Adesmiini suggests that psammophilous forms have tended to develop locally from whatever suitable ancestral stocks were available in the area during times when aridification increased sand deposition and accumulation. Geological evidence indicates that the Kalahari sands are of considerable age, so that even in moist conditions stocks of tenebrionids with a high tolerance or preference for sandy substrata would be

favoured. When aridification produced dune conditions, evolution of psammophiles might be rapid. The high degree of endemism of the sand-adapted Kalahari Tenebrionidae (at species level, apart from marginal penetration into and from adjacent areas along the somewhat ill-defined boundaries, there are no elements shared with other areas) emphasizes the local nature of their evolution. This is further supported by the present-day distribution of ancestral groups, which is diverse and indicates several different areas of origin for the Kalahari psammophilous tenebrionids. The ancestral groups of *Heliophosis, Sabulophosis,* the *Zophosis deyrollei* group and *Stenocara kalaharica* have a trans-Kalahari distribution; the ancestral stocks of the *Z. michaelis* group and *Metriopus albicollis* occur further north, in central Africa, while the ancestors of *Onymacris multistriata* originated to the south-west, in Namaqualand. The pattern of evolution of psammophilous Tenebrionidae postulated by Endrödy-Younga (1982) for the Namib is probably true in general for sandy areas, although mechanisms of dispersal would probably differ in the Kalahari.

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