

THE TENEBRIONIDAE OF SOUTHERN AFRICA

XXXI. COMPREHENSIVE NOTES ON THE TENEBRIONID
FAUNA OF THE NAMIB DESERT

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(With 7 plates, 7 maps and 2 lists)

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INTRODUCTION

SINCE 1948 frequent trips have been made to the Namib Desert, including various diamond, game and native areas, by kind permission of the Administrations of South-West Africa and Angola, the South African Mines Department, as well as the Consolidated Diamond Mines of South-West Africa, the South West African Industrial Diamonds Ltd. and the Angolan Diamond Company.

These trips were timed in such a way that they covered the seasonal changes, being undertaken during all months of the year, and touching on

all major bio-geographic and ecological sections of the Namib. Their chronological succession is as follows:

(a) October to December 1948, to the southern part of the Southern Namib (between Oranjemund and Luderitz) and the Transitional Namib (coast of northern Little Namaqualand, the lower Orange River area, Bushmanland and south-western Kalahari); sponsored by the University of California, State Alluvial Diggings, Consolidated Diamond Mines of South-West Africa, General Motors S.A. Ltd. and Shell S.A. Ltd. (cf. Koch, 1950a).

(b) October to November 1949, to the Transitional Namib and the southern part of the Southern Namib, as in (a), but with a long stay for ecological field work in the barchan dunes at Hottentot Bay; sponsored by the institutions and industrial undertakings mentioned above as in (a) (cf. Koch, 1952c).

(c) September to December 1950, to the Transitional Namib, the Richtersveld and the southern and central parts of the Southern Namib, between Luderitz, Aus and the Koichab River; sponsored by the institutions and industrial undertakings mentioned in (a) (cf. Koch, 1952c).

(d) May to July 1951, to the Skeleton Coast of the Northern Namib and adjacent areas of the Kaokoveld; sponsored by Mr B. Carp (cf. *Transv. Mus. Rep.* 1952).

(e) August to October 1951, to the Angolan part of the Northern Namib; sponsored by Dr L. K. Marshall, the Peabody Museum of Harvard University and Smithsonian Institution (cf. *Transv. Mus. Rep.* 1952).

(f) February to March 1953, to the Transitional Namib and the Richtersveld; sponsored by Mr B. Carp (cf. *Transv. Mus. Rep.* 1953).

(g) April to May 1953, to the southern part of the Southern Namib (between Oranjemund and Aus) and the lower Orange River area of the Transitional Namib; sponsored by the State Alluvial Diggings (cf. *Transv. Mus. Rep.* 1954).

(h) May to August 1954, to the southern and Angolan parts of the Northern Namib; sponsored by the late Mr A. S. Vernay and assisted by Dr L. K. Marshall (cf. Koch, 1958, and *Transv. Mus. Rep.* 1955).

(i) October to November 1955, to the Transitional Namib and the Richtersveld; sponsored by Mr B. Carp and the State Alluvial Diggings (cf. *Trans. Mus. Rep.* 1956).

(j) August to October 1956, to the Cunene River area of the Northern Namib (Kaokoveld and south-western Angola); sponsored by Mr G. Visser (cf. *Transv. Mus. Rep.* 1957).

(k) May 1956, and February 1957, to the south-western Kalahari as parts of the Transitional Namib; sponsored by the S.A. National Parks Board (cf. *Transv. Mus. Rep.* 1957).

(l) September to November 1957, to the northern part of the Southern Namib (Tsauchab and Kuiseb Rivers areas) and to the southern part of the Northern Namib (between Swakopmund and the Mesum Mountains); sponsored by Messrs A. Honig, B. Carp and A. F. Port (cf. *Transv. Mus. Rep.* 1958).

(m) May to June 1959, to the northern part of the Southern Namib (Kuiseb River area); sponsored by Mr B. Carp and the Export Division of the 'Volks-wagenwerk G.m.b.H.' (cf. Koch, 1962, and *Transv. Mus. Rep.* 1960).

The object of all these trips was to widen our knowledge of the fauna of the Namib Desert, to which, probably on account of its reputed barrenness and inaccessibility, very little attention had previously been paid. Although much has already been published on the taxonomy of the material collected—consisting mainly of articles on the Tenebrionid beetles, other insects, Apterygota, Arachnoidea and reptiles—large numbers of as yet undescribed species are preserved in the collections of the Transvaal Museum.

In spite of the many collecting trips undertaken, only a superficial knowledge of this fauna has so far been gathered owing to the scattered nature of the collecting stations which were more or less confined to mar-

ginal areas,† and the fact that it has not been possible to work out in detail considerable portions of the material belonging to groups that are taxonomically very obscure. Nevertheless, a modest attempt is here being made to give some comprehensive notes on the fauna of Namib Tenebrionids for the following two reasons:

(a) The Namib Desert is one of the least known but most remarkable faunistic areas of the African continent. There is no publication which deals with the Namib as a whole from any one aspect. We are fortunate, however, in there being some magnificent contributions of fundamental status that deal with parts of the Namib, such as the geology of the southern part of the Southern Namib by Kaiser, the plant ecology of the extra-dune Namib around Swakopmund by Walter, the thesis on the Tenebrionid beetles of the Luderitz and Swakopmund areas by Gebien (1938), and the recent monograph on the 'Central Namib' by Logan.

An examination of the scientific literature on deserts in general, discloses scarcely any mention of the Namib Desert, although many such publications are of a high scientific standard. Taking into account the great importance of problems of aridity and deserts in the world—which is emphasized by the existence of a special UNESCO Advisory Committee on Arid Zone Research, the 'Centre de Recherches Sahariennes du Centre National de la Recherche Scientifique' in France and institutional research on sand dune systems in the United States‡—it is surprising that no references to the Namib Desert appear in the publications of such institutions.

(b) With the gradual progress of our field research on the Tenebrionid fauna of the Namib, in association with experimental work, observations and breeding of postembryonal stages in the insectarium, more and more insight has been gained and proof has accumulated that the barren dune system or the vegetationless parts of the barchan dunes represent a most remarkable and hitherto unobserved biotope of optimum conditions for certain xerophilous Tenebrionids (and other macro-animals). In order to establish a comprehensively documented background for the correct interpretation of this new desertic feature, the condensation of many of our independent observations is considered necessary, if only for the sake of obviating the need to consult the many widely scattered and very specialized publications.

The fact that the problems of aridity have recently received particular attention in South Africa,§ is due in particular to Acocks's eminent thesis on the status of aridity and the progress of desertification in South Africa.

† Our collecting stations in the Namib are marked with a ▲ on the maps 3-7 to the present paper.

‡ Cf. Symposium on Sand Dune Systems, presented at the Annual Meeting of American Association for the Advancement of Science, December 1959, Chicago.

§ Frommurze gives an extensive bibliography on hydrological research in arid and semi-arid areas in South Africa and Angola, of which the following references may be quoted as dealing critically with the desertification of these areas:

SENATE, UNION OF SOUTH AFRICA (1914). *Select Committee Report on Droughts, Rainfall and Soil Erosion*. Cape Town, S.C. 2.

DROUGHT COMMISSION (1923). *Final Report of the Drought Investigation Commission*. Pretoria: Government Printer.

KANTACK, F. E. (1930). The alleged desiccation of South Africa. *Geogr. J., Lond.*, 76.

PAULSMEIR, H. J. C. (1946). *Is South Africa drying up?* Windhoek.

KOROT, I. F. (1948). An investigation into the evidence bearing on recent climatic changes over southern Africa. *Irrig. Dep. S.A. Mem.*

With regard to the Namib Desert itself, however, credit is due to Mr F. Eberlanz and Dr A. M. Weber for having aroused public interest by the creation of local Namib museums in Luderitz and Swakopmund respectively. Several articles on the peculiar pattern of life in the Namib dunes† have found a remarkable response in wider scientific circles, and now, on the initiative of Dr V. F. FitzSimons, Director of the Transvaal Museum, the project of the establishment of a special Research Station in the Namib Desert has taken definite shape through the kind authorization of the South-West African Administration and the close cooperation of the Transvaal Museum, the State Museum at Windhoek, the Section of Nature Conservation of the South-West African Administration, and the South-West African Scientific Society. Preliminary proposals to this effect, dating back to 1957, have been acclaimed not only by competent South African institutions and scientists, such as the S.A. Council for Scientific and Industrial Research, the Transvaal Museum,‡ the S.A. Museums Association,§ the S.A. Association for the Advancement of Science,|| the Zoological Society of Southern Africa,¶ etc., but also by international science.

Acknowledgments. Our gratitude is due to the S.A. Council for Scientific and Industrial Research, the Director and Board of Trustees of the Transvaal Museum, and the above-mentioned generous sponsors of field trips, for the great assistance which made possible this co-ordinated research in taxonomy, ecology and ontogeny over a prolonged period.

DIVISIONS OF THE NAMIB IN CORRELATION WITH THE FAUNA OF TENEBRIONIDAE

Remarks. A * in front of names refers to new genera, species and subspecies described in the following paper (pp. 107-159). In the present text and lists of species (pp. 79-85) the names of authors of systematic units have been omitted, but can readily be found by consulting the bibliographic index on pp. 86-93.

† Cf.:

KOCH, C. The fauna of the Namib Desert (*Bull. Transv. Mus.* 2, 1955, pp. 4-5, 1 photo).
BRINCK, P. The food factor in animal desert life (*Zool. Pap. B. Hanström, Lund*, 1956, pp. 120-37, 8 figs.).

KOCH, C. Die Namibdünen und ihre Tierwelt ('*Der Kreis*', Windhoek, May 1959, pp. 198-200, 1 photo, 1 colour plate).

KOCH, C. The Tenebrionid beetles of South-West Africa. Read at the Annual Meeting of the S.A. Museums Association, May 1959 (*S.A. Mus. Ass. Bull.* 7, 1960, pp. 73-85, 1 map, 3 figs.).

PROZESKY, O. P. M. Birdlife at Sandwich Harbour (*Bull. Transv. Mus.* 4, 1960, pp. 2-3, 3 photos).

HOESCH, W. Über die Tierwelt im Gebiet der südwestafrikanischen Wanderdünen. (*Natur u. Volk*, 90, pp. 252-64, 14 figs.).

‡ Cf. FITZSIMONS, V. F. Report on the project of a Namib Desert Research Station (*Transv. Mus. Rep.* 1961, 6, p. 2).

§ Cf. Proceedings of Twenty-third Annual General Meeting of the S.A. Museums Association (*S.A. Mus. Ass. Bull.*, 1959, in particular Paulian, R. & Koch, C., cit. pp. 21-2).

|| Cf. LAWRENCE, R. F. The sand-dune fauna of the Namib Desert (*S.A. J. Sci.* Sept. 1959, pp. 233-9, 3 figs.).

¶ Cf. BRAIN, C. K. Proposed Namib Desert Research Station (*Zool. Soc. S.A.* 1, 1959, p. 32, 1 photo).

(1) *Definition of area*

The Namib Desert may be considered as the only true desert in that part of Africa lying in the Southern Hemisphere. It is a foggy, coastal desert and in this respect comparable only to the South American Atacama Desert, as in both the development of desertic phenomena is due to cold oceanic currents.

When compared with the 8,000,000 km.² occupied by the Sahara Desert (Drouhin, Pierre), the Namib, with a roughly estimated area of only 270,000 km.², is a dwarf only one-thirtieth the size of the former (cf. map 1). But in spite of its small size, it shows edaphic features of an ultra-desertic status (absence of macro-vegetation)† similar to those found in the Sahara; such are, for example, massifs of barren dunes, sandy and gravel plains without or with only very scattered, desertic vegetation, and salty pans, which correspond almost exactly to the Saharan terms of *Erg*, *Reg* and *Sebkha* respectively.

The unfavourable biotic conditions typifying the true desert of the torrid zones, viz. the irregular and very low rainfall in association with intense evaporation, are also similar. It is evident, however, that they are of a less hostile quality because of an additional factor of precipitation in the form of mist from the sea, which, in one way or the other, may help to adjust the merely episodic quality of rainfall, by reducing the degree of the evaporation of all precipitation and that of the transpiration of the fauna and flora.

According to Meigs's homoclimatic classification of the arid zones of the world, the Namib Desert is defined as an extremely arid‡ but mild§ desert without a distinct season of precipitation, characterized by the temperature index 22.§ Among the extremely arid deserts of the world a similar homoclimate is shown only by the likewise mild Atacama Desert (temperature index 23); the remaining extremely arid deserts are either hot deserts (temperature index 24) such as the Sahara, the Arabic Rub' al-Khali and the North American Mohave and Sonoran Deserts, or the cold winter Takla Makan Desert in Turkestan (temperature index 03).

The Namib (cf. map 2) is a coastal desert, which attains a width of approximately 100 miles at some places, and extends along the Atlantic Ocean roughly for 1300 miles from the Olifants River in Little Namaqualand (Republic of South Africa), through the whole of South-West Africa to as far northwards as Moçamedes in the south-western part of Angola.|| There are no sharp limits in

† Since all classification terms for degrees of aridity relate to vegetation, the term 'ultra-desertic' is used in the present paper for such areas of the desert, in which no natural and active macro-flora exists (e.g. the barren sandy dunes and vegetationless plains of the Namib).

‡ In regard to moisture, Meigs subdivides the arid climates of the world as follows (cf. map 1):

Extremely arid, based on rainfall records which show at least one year without rain, with no regular seasonal rhythm of rainfall.

Arid, (with reference to Thornthwaite's precipitation-evaporation system in relation to the needs of plants) those areas in which the rainfall is not adequate for crop production.

Semi-arid, (based upon Thornthwaite's system) areas with sufficient rainfall for certain types of crops, and where grass is an important element of the natural vegetation.

§ In regard to temperatures, Meigs's arid zones are classified as *hot* (indices 24, 33, 34), *mild* (indices 22, 23), *cool winter* (indices 12, 13, 14) and *cold winter* (indices 02, 03, 04). The first digit of these temperature indices represents the coldest month and the second digit the warmest month based on mean monthly temperatures. The digits read as follow: 0 = below 0° C.; 1 = 1-10° C.; 2 = 10-20° C.; 3 = 20-30° C.; 4 = above 30° C.

|| This statement is well documented from the point of view of the fauna in the south (Koch, 1952c) and north (Koch, 1958). It agrees fairly well with the physiographic extension of the Namib as indicated by Wellington, but not with Meigs's homoclimatic map of the eastern hemisphere. On this map the Namib is indicated as ending in the north just south of the border of South-West Africa, at about Rocky Point; this is incorrect and must be rectified, as the Angolan Namib not only faunistically and physiographically, but also climatologically, does not differ from the South-West African part of the Northern Namib.

the east, however, and we may accept the 2000 ft. contour of the South African maps (or the 600 m. contour of the South-West African maps) as the more or less arbitrary limitation of the coastal low ground, except for areas in Great Namaqualand, where the extension of the barchan dunes clearly determines the desertic nature of the country, although the dunes rise considerably above the 2000 ft. contour, reaching inland in some places to 4000 ft. (cf. map 2).

(2) *Composition, xerophilous character and origin of the Namib Tenebrionidae*

In regard to both the degree and the extent of aridity, the Namib is the extreme component of the arid Kalahari-Karroos-Namaqualand phyto-geographical system (Monod, 1957; cf. map 1). In close agreement with this definition the fauna of the Tenebrionids is composed almost entirely of very xerophilous groups.

If we exclude the indifferent, widely diffused and usually alate groups—such as psammophilous representatives (e.g. *Anemia* of Melanimini) or the inhabitants of hygrophilous strata (e.g. *Gonocephalum*) or those of arboreous biotopes (Strongyliini, Praogenini, † *Epitragina* of Tentyriini, etc.)—the analysis of the composition of this fauna establishes the fact that all Tenebrionids of the Namib, without exception, belong to such tribes or subtribes as are distributed over the whole of South-West Africa and south-western Angola. These tribes and subtribes may be regarded, for convenience sake, as the basic groups of Southern West Africa (viz. South-West Africa plus south-western Angola, cf. Koch, 1958). These basic groups are the Cryptochilini, Tentyriini, Scaurini, Caenocrypticini, Adesmiini, Eurychorini, Zophosini, as well as the subtribes Hypomelina, Oxurina and Phanerotomeina of Molurini, Gonopina of Platynotini, Drosochrina of Drosochrini, Stizopina and Stenolamina of Opatrini; the two endemic tribes Calognathini and Vansonini may be here included, as they are linked phylogenetically with the Cryptochilini.

The prevailing xerophilous disposition of these groups is readily proved by their distribution pattern, ‡ which has kept strictly to regions with low to moderate precipitation. The following are the characteristic outlines of this distribution:

(a) All groups are absent from the neighbouring South-East African Province (see Koch, 1958), except for the two extra-Guinean tribes Zophosini and Eurychorini, and the Ethiopian (or Tropic African) Phanerotomeina of Molurini. The reason for this unusually constant pattern is simply the increased humidity of the South-East African Province, where the rainfall exceeds 20 in., this area being inhabited mainly by subtropical and mesophilous Tenebrionids.§

† We consider *Praogena* Laporte and several closely allied genera the representatives of a tribus proper (viz. Praogenini *sensu novo*), on the basis of various hitherto unobserved characters such as the constant occurrence of a stridulatory gula of the Platynotini and Oncotini type (cf. Koch, 1956), the pleural structure of the elytra, which deviates greatly from that in the other Strongyliini, etc.

‡ Cf. the following maps of distribution: Cryptochilini (Koch, 1952*b*); Tentyriini (Koch, 1955*a*); Caenocrypticini (Koch, 1952*c*); Adesmiini (Koch, 1944-48, 1952*c* and 1955*a*, Raymond); Eurychorini (Koch, 1952*a* and Brown); Molurini (Koch, 1955*a*); Hypomelina, Oxurina and Phanerotomeina of Molurini (Koch, 1955*a*); Gonopina of Platynotini (Koch, 1956); Drosochrina of Drosochrini (Koch, 1958); Stizopina and Stenolamina of Opatrini (Koch, 1956); Calognathini and Vansonini (Koch, 1955*a*).

§ There is no uniform terminology for classifying a territory according to degrees of humidity and aridity (Meigs). Drouhin proposes for North-West Africa the following definitions: humid zone, over 500 mm. of rain p.a.; semi-arid zone, between 500 and 100 mm.; arid zone proper, less than 100 mm. Emberger's quotient representing the dryness of the arid regions of North Africa = $100R/[(M+m)(M-m)]$ (R is the normal total annual rainfall; M is the normal maximum temperature of the hottest month; and m is the normal minimum temperature of the coldest month). Simaika, using Emberger's

(b) If, however, we check the distribution of those groups which range beyond the borders of the Southern African Subregion, viz. Cryptochilini, Tentyriini, Scaurini, Adesmiini, Eurychorini, Zophosini, Drosochrina, Phanerotomeina and also Stizopina,† we find that they all occur also in the desertic to subdesertic Palaearctic, Mediterranean and Eremian Subregions, or at least in the north-easternmost part of the Tropical African Subregion, viz. Somal Arabia (Cryptochilini, Phanerotomeina and the Stizopina-like *Clitobius*-group of Opatrina); four of these groups display even Saharo-Sindic tendencies (Tentyriini, Adesmiini, Zophosini and the *Clitobius*-group).

Thus the ancestral groups by which the Tenebrionid fauna of the Namib has been formed can be considered strictly xerophilous, as they participate in the fauna of the Saharo-Sindic influenced parts of North Africa (cf. Koch, 1960a), in spite of their absence from the South-East African Province, which closely adjoins the arid Kalahari-Karroos-Namaqualand area geographically.

Furthermore, none of the subxerophilous to mesophilous (alien Southern West African) groups is represented in the fauna of the Namib. These alien tribes have penetrated into the northern part of South-West Africa from the north, east and south-east via a Trans-Bechuana distributory bridge (cf. Koch, 1952c). In no case, however, have they expanded farther southwards than the approximate latitude of the southern escarpment of the Damaraland highlands, or farther westwards than the escarpment of the Kaokoveld and Chella mountains. These alien groups are the Stenosini, Litoborini and Heterotarsini, as well as the subtribes Sepidiina of Molurini, Anomalipina and Platynotina of Platynotini, Micrantereina and Oncosomina of Drosochrini, Emmallina and Sclerina of Opatrini, and also a great number of tropical and subtropical genera of the basic tribes, such as *Ethmus*, *Stenethmus*, *Rozonia*, *Macropoda* and *Zambesmia* of *Adesmia*, etc.‡

About 98% of all Namib Tenebrionids are apterous species. The remaining 2% are alate species which belong, with the exception of some *Cyphostethe*, *Derosphaerius* and *Oppenheimeria* (Epitragina) and *Anemia* (Melanimini), to arboreous tribes of Pan Tropical origin, and restricted in the Namib to the few more hygrophilous strata such as river-beds, pans, etc.

It must be remembered that the Tenebrionids are plentifully represented in ultra-deserts as well as in tropical rain-forests.§ In this exceedingly wide range of adaptation to every possible terrestrial biotope, however, they do not differ from some other coleopterous families such as e.g. the predatory Carabids which, though greatly preferring very humid to pseudo-aquatic ecological niches, prey on Tenebrionids in deserts also (e.g. *Mantichora*, *Anthia*, *Graphipterus*, etc.). What is remarkable in the Tenebrionids, however, is the extraordinary increase

formula as a base, accepts for North-East Africa the following scheme: 0-200 mm. desert conditions, 200-400 mm. arid conditions, 400-800 mm. semi-arid conditions.

In the present paper we have adopted Marcuzzi's scheme of classification (1956) which relates the xerophily of Tenebrionids with the amount of precipitation as follows:

- xerophilous elements—0-500 mm. of precipitation;
- subxerophilous elements—500-1100 mm. of precipitation;
- mesophilous elements—more than 1100 mm. of precipitation.

† Recently a fauna of hitherto unknown apterous genera of the *Clitobius*-group of Opatrina has been discovered in the Somal Arabian area of Somalia, which forms a clear link with the Stizopina, so far believed to represent an autochthonous element of the Southern African Subregion (Koch, 1960a).

‡ Cf. the following maps of distribution: Stenosini (Koch, 1956); Litoborini (Koch, 1953c, 1956); Sepidiina of Molurini (Koch, 1955a); Anomalipina and Platynotina of Platynotini (Koch, 1956); Micrantereina and Oncosomina of Drosochrini (Koch, 1958); *Rozonia* (Koch, 1944a); *Macropoda* and *Zambesmia* of *Adesmia* (Koch, 1944-48).

§ We very often find in literature the Tenebrionid beetles erroneously defined as drought-loving insects in general.

in the relative number of species (and individuals) in a given fauna of animals in relation to the increase in the factors of aridity pertaining within the respective area. But, of course, in the Tenebrionids also the absolute number of species is higher in biotopes offering generally optimum conditions of life, such as the equatorial rain-forests, than it is in deserts. The reasons that, nevertheless, the number of xerophilous world species surpasses that of the hygrophilous and mesophilous species are the prevalence of factors of aridity in the torrid zones of the world and the greater speciation of xerophilous Tenebrionids. The latter are very sensitive to climatological, edaphic and vegetational conditions, and also to geographic and ecologic isolation on account of their apterism.

In the apterous ground Tenebrionids of the Namib the xerophilous properties appear to have reached the highest possible degree. This statement follows from a quantitative study of the entomological fauna of South-West Africa. With the biotic conditions ranging there from subtropical to ultra-desertic, these Tenebrionids have developed in a reversed ratio to the general rules of life optima, for it has been found that the relative number of species in the composition of the fauna increases progressively with the increase of the bio-hostile phenomena of aridity, until, under ultra-desertic conditions, as met with in the vegetationless biotopes of the Namib Desert, they play a dominant and basic role of life.†

During the ages of evolution, the Tenebrionids were thus able to turn to their advantage the ultra-desertic biotope of the barren sandy dunes, which, although hostile to macro-life in general, appears to offer them a multitude of ecological niches.

From observations in the field, which were carried out at various sites, the following example of the composition of the fauna of the interior and vegetationless part of the dunes near Rooibank (lower Kuiseb river area) may be given:

(a) One species of a lizard of which only the foot prints could be tracked; probably *Aporosaura anchietae*.

(b) Dune termites, spiders, Muttillids and *Lepisma*, of each one species.

(c) Thirteen species of Tenebrionids which are strictly indigenous to the vegetationless part of the dunes, viz. *Lepidochora discoidalis*, **kahani*, **porti* and *eberlanzi parva*, *Onymacris unguicularis* and *laeviceps*, *Cardiosis fairmairei*, *Tarsosis damarensis*, *Cerosis hereroensis*, *Dactylocalcar caecus*, *Vernayella noctivaga*, *ephialtes* and **delabati*. Moreover, the individual numbers of almost all these species happened to range in quasi-gregarious proportions, while the other animals, except for the termites and *Lepisma*, occurred in solitary specimens.

We must also emphasize the striking richness of the specific composition and the high degree of endemism of the Tenebrionid fauna of the Namib. Although exploration has so far been carried out at comparatively few collecting stations, we find that the number of endemic tribes, genera and species, as well as that of genera and species in general, apparently surpass by far that of other deserts.

Excluding the alate, arboreous and eutopic species, the Namib fauna is composed of several hundred species and about ninety genera of apterous ground Tenebrionids, of which two tribes, approximately thirty-five genera and almost 200 species, are endemic to the True Namib section alone. Since no comprehensive figures are available from other deserts of the world, we have to rely for comparison on some available figures of non-ecologic but political territories of a more or less arid status. However, the comparative poorness of the respective faunas of Tenebrionids may be implied from the following data. Koch (1944b) quotes the number of species for the following Mediterranean, North African

† Cf. also Marcuzzi (1960): 'It is possible to identify the prevailing climate of a given region basing on the percentage with which the Tenebrionids are represented within the whole of the coleopterous fauna or the whole of the insect fauna, so that we can speak of a "Tenebrionid index".'

and Saharan countries: Dalmatia 73, Crete 66, Greece 160, Asia Minor 220, Palestine 144, Egypt 267, Cyrenaica 140 and Tunisia 260. In Tripolitania, including the Fezzanese desert, 202 species and subspecies occur, of which three genera and sixty-three species are endemic (Koch, 1937). From the heterogeneous territory of Morocco, which participates in the Mediterranean, Atlasic-Baetic, Atlantic and Saharan faunae, 711 species and subspecies are recorded by Kocher, but only about 100 forms occur in the Saharan part of this country.

The sandy dunes of the Sahara lack also those Tenebrionids of the biotope of the vegetationless part of the dunes, and the process of adaptive morphological change appears to have just started when compared with the excessive modifications in the Namib species. We were unable to find any indigenous life at all, either on the small dunes of the semi-desertic area in south-western Madagascar, or on the barren barchan dunes of Somalia, though the latter are situated in an area of good seasonal rainfall in the Benadir Province, and are exposed to a high degree of sea moisture from the Indian Ocean in the Mijertain (Koch, 1960a).

These findings may enable us to conclude that the richness and endemism of the Namib fauna do not depend on a given quality of biota, but are rather the result of the long and undisturbed duration of these special biota. In contrast to the Sahara, which has undergone various alternating pluvial and arid periods (Monod, 1942; Scortecci, 1940), and to the decidedly recent age of the Somalian dunes (Azzaroli, 1957), one assumes that the Namib has not experienced any pluvial period worth mentioning since the oceanic Benguela current drew close to the coast. According to geological evidence this occurrence dates back to the Cretaceous Period (Kaiser, 1926), a time in which the Poliphaga beetles (to which the Tenebrionids belong) were already well on the way of evolution (Jeannel, 1946). At this time probably, and in close association with the origin of the Namib sand, the process of adaptation to life in ever-shifting sand was initiated by those species of all the basic Southern West African tribes, which ventured to migrate from their indigenous biotope to the sands. This process gradually progressed together with the growth and extension of dunes, continuously filling all newly originating ecological niches until it led to the recent endemism which is expressed in extreme morphological differentiation in sharpest contrast to the neighbouring extra-Namib ascendants.

The great evolution of the specialized elements of the Namib Fauna may thus be attributed to the millions of years of undisturbed desert conditions. In spite of remarkable deviations from the morphology of the ascendent type, they can all be traced back phylogenetically to the basic Southern West African tribes, the distribution pattern of which keeps strictly to arid and desertic regions in Africa and partially also in Asia. Many representatives of the Adesmiini, Zophosini, Epitragina and Tentyriina of Tentyriini today populate identical formations of sandy dunes in the Namib, the distant Sahara and the very distant Gobi; in some cases even the identity of Saharo-Sindic genera, such as *Cyphostethe*, with Southern African groups of species has been proved by recent research (Koch, 1950a; Gridelli, 1953). On the other hand, several tribes, such as the Eurychorini, Molurini, Cryptochylini, Drosochrini, etc., clearly indicate a Tropic African if not Southern African origin.

(3) *Biogeographic divisions of the Namib (cf. map 2)*

Based on an analysis of the distribution pattern of Tenebrionids, the Namib can be divided rather sharply into biogeographic latitudinal sections. Taking into consideration the dominant role these insects play in the fauna of the Namib, it is possible that the proposed division may prove to be more generally applicable.

Endemic genera, which occur in all sections, may be considered as basic

elements of the Namib and in some cases have gained access to the sands of the south-western Kalahari. Such basic genera are **Brinckia*, *Pachynotelus*, *Onymacris*, *Caenocrypticus* and *Carchares*. Only one species is known to occur in all sections, viz. the sublittoral *Carchares macer*.

Various groups of genera and tribes can be placed in the same category on account of their close inter-generic or inter-tribal phylogenetic relationship. These are the group of the two endemic tribes Calognathini-Vansoniini, the chain of extra-*Zophosis* Namib genera of Zophosini,† the *Stips*-group of Eurychorini,‡ and in a slightly wider sense also the Caenocrypticini. They occur all over the area, but their generic components are confined to various sections or to the south-western Kalahari (e.g. *Heliophosis* of Zophosini).

A. True Namib

In general literature, including Gebien's thesis (1938), this is the area which is referred to simply as 'Namib'.

Whereas the southern and northern limits of the Namib as a whole are obscure because of the transitional character of the fauna in the respective peripheral areas, the True Namib shows sharply defined border lines by means of natural faunistical barriers, such as the Orange River in the south and the Angolan Coroca River in the north. These limits may have to be extended for exceptional cases to the Holgat River of Little Namaqualand in the south and to Moçamedes in the north, but in general are of considerable reliability. The faunistical barrier effect of the Cunene River is negligible (cf. Koch, 1958), but in previous literature we frequently find the Cunene cited as representing either the northern border of the Namib (also in Gebien) or the north-western limits of the Southern African Region.

Thus the True Namib comprises the main section of the Namib and is well distinguished by the presence of systems of ever-shifting, sandy dunes of the barchan type, which originate exactly at the northern bank of the Orange River and end as abruptly at the southern bank of the Coroca River.

The degree of endemism of this section is extraordinary; there are more than thirty endemic genera and 200 endemic species of Tenebrionids. According to Gebien, a similarly high degree of endemism can be observed only in the fauna of ancient islands, and there is no other continental area known which can compete with the Namib in this respect.

The endemic genera *Namibomodes*, *Calognathus*, *Eustolopus*, *Lepidochora*, *Cardiosis*, *Tarsosis*, *Vernayella* and *Onychosis* may be regarded as the primary elements of the True Namib. With the exception of the sublittoral *Onychosis*, they are strictly confined to the dune area, but are spread over all dune systems of the area, thus ignoring faunistical barriers of otherwise considerable validity, such as river-beds like the Koichab, Kuiseb, Huab or Cunene, as well as intervening and isolating hard-soil spaces, of which the most extensive is the gravelly and sandy plain between the Kuiseb and Huab Rivers.

A specific identity of Tenebrionids living in the Southern as well as in the Northern Namib can be proved in several cases. These are **Brinckia debilis*, *Onychosis gracilipes*, *Carchares macer*, *Namibomodes serrimargo*, *Eustolopus octoseriatus*, *Tarsosis damarensis*, *Caenocrypticus phaleroides* and *Vernayella noctivaga*. Of these species the three first mentioned are inhabitants of the sublittoral biotope, and their spreading northwards can be readily explained by the more or

† This chain is composed of the following genera: *Calosis*, *Heliophosis*, *Cardiosis*, *Tarsosis*, *Antisosis*, *Ophthalmosis*, *Onychosis*, *Gyrosis*, *Cerosis*, *Dactylocalcar*, *Protodactylus* and **Carpiella*.

‡ To the *Stips*-group belong the genera *Lepidochora*, *Stips* (olim *Steira*), *Cimicichora*, *Cimicia* and *Arthrochora*.

less continuous expansion of their biotope. Only historic reasons, however, can be applied to the phenomenon of identity in the five last mentioned species. Being strictly bound to the biotope of the barchan dunes, they have not changed even subspecifically, in spite of the great discontinuity of the recent configuration of the dune systems. Subspecific changes can be reported only of *Calognathus chevrolatii*, while the remainder of dune species is endemic to the different dune systems.

Of other animals we may mention here the reptile *Palmatogecko rangei*. Its distribution corresponds well to that of the above primary Tenebrionids, as it spreads over all dunes in the True Namib and agrees with *Calognathus* also in the crossing of the Orange River. Its less stenotopic character, however, is revealed by its expansion across the Coroca River to Moçamedes, an area which lacks the barchan dunes proper and to which consequently none of the true dune Tenebrionids has migrated.

A secondary split of the True Namib into two markedly differentiated faunistic subdivisions, however, appears to be due to the barrier effect of the Kuiseb River. Here the system of the dunes of the southern section—except for the system of coastal dunes between Walvis Bay and Swakopmund—stops suddenly at the southern bank of the river, with isolated dune-systems reappearing only north of the Huab River (cf. map 2). Schultze and also Gebien emphasized the profound difference between the vegetation and fauna of the Luderitz area and that of the Swakopmund district. Jaeger took the Kuiseb River to represent the geomorphological division between the northern and the southern sections of the Namib. Mertens, however, in concordance with Walter and on the basis of the South-West African reptiles, considered the Swakop River to be the faunistic dividing line between the two sections. Our studies on the Tenebrionids do not agree with this view, as many species just follow the continuous hard-soil surfaces which extend from Porto Alexandre, or even Moçamedes, right through to the Kuiseb River. It appears that this distribution pattern is confirmed also, for example, by the dispersal of *Welwitschia*, or *Pachydactylus kochii* in the reptiles.

(a) *Southern Namib*. This part of the True Namib is the more sandy of the two sections. It is characterized by the immense continuity of the dune system between the Koichab and the Kuiseb Rivers; this system dissolves into more or less isolated dunes in the south between the Koichab and the Orange Rivers.

The dunes of the northern part, in respect of continuous expansion and height, can only be compared with those of the Sahara; they stretch from south to north for about 300 miles and attain a maximal width of about 100 miles at various latitudes; they can rise as high as 1000 feet from the floor of a valley (e.g. at the Sossus Vlei), a height which competes with the maximal heights of the Saharan dunes (e.g. 300 m. of the dunes of the Libyan desert, south of Murzuq in the Fezzan).

Among other characteristic features of this section are the limited areas occupied by the sandy plains between the dunes and the escarpment of the highlands, isolated mountains and rocky outcrops which are partly or entirely invaded by wind-blown sand, and salty pans which have originated from the seeping away of rivers from the highlands.

The limits of the Southern Namib are formed by the Orange River in the south and the Kuiseb River in the north. Attention must be drawn, however, to a correction of these boundaries in the north-west, where, in close proximity to the coast, the dunes have crossed the recent bed of the Kuiseb River and protrude northwards as far as Swakopmund (cf. map 4). This north-western arm of the dunes—which geomorphologically is considered to belong to the Southern Namib (Jaeger)—harbours quite a special fauna which, on account of the occurrence of

the southernmost representative of the 'white'† Tenebrionids and *Stenocara brunripes*, both of the Northern Namib, appears to be the only known transitional area between the Southern and the Northern Namib. In this area, although adjoining the continental part of dunes, are found also several endemic species such as *Cardiosis triangulifera* and *Lepidochora eberlanzi parva* (cf. Pl. XV), occurring together with dune species from the Southern Namib, such as *Onymacris unguicularis, plana* and *rugatipennis, Vernayella ephialtes* and others.

Endemic to the Southern Namib are the following genera: **Uniungulum, Fossilochile, Archinambia, Gyrosis, Cerosis, Dactylocalcar, Pythiopus, Periloma, Nemanes, Psammogaster* and *Syntyphlus*; of these *Gyrosis, Nemanes* and *Periloma* have crossed the Orange River to a negligible extent, while, with the exception of *Nemanes* and *Pythiopus* occurring on hard soil, all the species of these endemic genera are dune dwellers.

The extreme specific endemism and the great and often sympatric, speciation are reasons to suspect the Southern Namib to be the probable centre of evolution of the Namib Tenebrionids. Gebien has already numbered thirty-five endemicspecies.

There are indications that the large area of the Southern Namib is composed of three faunistically differentiated regions. A major faunistical subdivision seems to be created by the Koichab River (cf. map 3), while the area south of Luderitz,‡ which includes the dune system around the Klinghardtberge, shows a different composition of fauna connected also with the Transitional Namib.

In the list of the species of the Southern Namib (pp. 79-81) I have referred to the Koichab River as a faunistical division, while species which are not endemic to the Southern Namib are marked with °.

(b) *Northern Namib.* The Northern Namib extends from the Kuiseb River northwards to a few miles beyond Moçamedes. Its main characteristics are the wide expansion of more or less vegetationless, gravelly and sandy plains, the remarkable frequency of river-beds running from the highlands to the sea, the discontinuous configuration of the dune system,§ and biologically the endemic and sympatric occurrence of *Welwitschia mirabilis* and the 'white' Tenebrionids.

The 'white' Tenebrionids occur over the whole of the Northern Namib, whether on hard ground or wind-blown sand, and are placed in phylogenetically distant tribes and genera (viz. *Onymacris* and *Stenocaru* of Adesmiini, and *Calosis* of Zophosini). Their range of distribution starts within the faunistically critical, north-western part of the southern dunes, south of Walvis Bay, and at the northern bank of the Kuiseb River. Here we encounter *Onymacris marginipennis palgravei* on the coastal dune, and *Stenocara eburnea* and *Calosis amabilis* on all hard-soil faces, whether in between the coastal dunes or on the plains; they have expanded to a variable extent towards the north and on their route have crossed all rivers, including the Swakop River. *Onymacris langi* is the northernmost species of these 'white' Tenebrionids and is endemic to the Moçamedes desert.

Welwitschia is in accord with the 'white' *Calosis* and the depigmented *Protodactylus* ecologically as well as zoogeographically, as both spread from the Kuiseb River to about Moçamedes, but occur exclusively on consolidated soil faces but not in the dunes.||

It should be emphasized that no 'white' Tenebrionids occur in the remainder

† In the present paper the term 'white' refers to all those Tenebrionids which are distinguished by the white to yellowish white, structural, colour pattern of the more or less unpigmented elytral cuticle (cf. Pl. XIV).

‡ Viz. the 'Wannennamib' (cf. Kaiser).

§ Logan omits to mention the occurrence of sandy dunes in the Northern Namib, leaving the reader under the impression that such dunes are peculiar only to the Southern Namib.

|| Brinck's statement, that *Welwitschia* grows in the sandy dunes in the southern part of its distribution, is incorrect.

of the Namib (nor elsewhere) and that all the many forms of *Onymacris* in the Northern Namib are 'white' without exception.

The generic endemism of the Northern Namib scarcely shows any lesser degree of development than the Southern Namib, but differs in its composition by the predominance of the extra-dune genera over the dune genera. The following are the endemic genera: *Palpomodes*, *Microderopsis*, *Namibismus*, *Eutichus*, *Calosis*, *Anisosis*, *Ophthalmosis*, *Protodactylus*, **Carpiella*. Of these genera only *Namibismus*, *Anisosis* and *Ophthalmosis* are dune dwellers.

With regard to the faunistical importance of rivers in this area, the following facts may be stressed. North of the Huab River we find the re-appearance of the barchan dune biotope coupled with the re-appearance of some of the dune genera which we know from the Southern Namib, viz. *Pachynotelus*, *Caenocrypticus*, *Namibomodes*, *Calognathus*, *Eustolopus*, *Lepidochora*, *Cardiosis*, *Tarsosis* and *Vernayella*, as well as the typical barchan dune *Onymacris*, to which must be added the three above-mentioned endemic genera *Namibismus*, *Anisosis* and *Ophthalmosis*. The greater influence of the Coroca River as a barrier follows from the many genera which do not cross it towards the north, but occur also north of the Cunene River; these are **Brinckia*, *Pachynotelus*, *Calognathus*, *Lepidochora*, *Cardiosis*, *Orychosis*, *Calosis*, *Ophthalmosis*, *Anisosis*, *Vernayella*, *Palpomodes* and *Microderopsis*. There are few genera which, coming from the south, have not extended across the Cunene River; these are *Caenocrypticus*, *Carchares*, *Namibomodes*, *Eustolopus*, *Eutichus* and **Carpiella*.

Contrary to the gradual petering out of Namib elements in the southern peripheral area south of the Orange River (Transitional Namib), the typical Namib fauna comes to a rather abrupt end in the northern peripheral area at about Moçamedes. There are only three Namib genera left which expand as far northwards as Moçamedes, viz. *Namibismus*, *Onymacris* and *Protodactylus*. On the other hand, the Moçamedes desert is invaded by a great number of elements of the South-West African highland fauna (e.g. *Rhammatodes*, *Asphaltesthes*, etc.), and species of subtropical or tropical origin (of the genera *Hanstroemium*, *Ethmus*, the *vialis*-group of *Psammodes*, *Gnophota*, etc.).

The complicated faunistical conditions of the Northern Namib are well reflected by the great speciation and endemism which takes place within this area, as well as by the distribution pattern of the respective species. In the list of the species of the Northern Namib (pp. 82-85), those species marked with ° are not endemic to the area.

B. Transitional Namib

The sandy Transitional Namib stretches southwards from the Orange River approximately as far as the Olifants River, into parts of north-western Little Namaqualand and Bushmanland, and merges in the north-east with the red sands of the south-western Kalahari.

With the exception of some notes on a biogeographic division of the Namib (Koch, 1952c), there are no references in the literature available to me pointing to this area representing a faunistical part of the Namib.† Gebien also does not mention a prolongation of the Namib fauna across the Orange River. In 1952 I established roughly the same division as is discussed in the present publication, but proposed for this southernmost part the biogeographic term 'Pro-Namib'. Later, however, I recalled that the term 'Vor-Namib', in an ecogeographic sense, is frequently used in German literature for the inner, longitudinal portion of the

† Physiographically this area is regarded as a component of the Namib by Wellington, and also on Meigs's homoclimatic map it is indicated as belonging to the extremely arid area of the Namib Desert.

Namib as opposed to the outer or coastal portion (Gebien, Mertens, etc.). In order to avoid any misunderstanding I have proposed the biogeographic term 'Transitional Namib' instead (Koch, 1960b) for this area, which also roughly corresponds in extent to the physiographic unit of the same denomination as defined by Wellington.

The Transitional Namib is a typically transitional area, which is characterized by a very complex and mixed fauna composed of Cape, Namaqualand, Namib and Kalahari elements.

The degree of endemism is very great, but the Cape and Namaqualand elements prevail by far. They belong to the Oncotini, Pythiopiini, Tentyriini, Molurini, Cryptochilini, and Stizopina and Stenolamina of Opatrini. Their endemic development and speciation reach a peak in the lower Orange River area and the Richtersveld, where very highly specialized and localized species occur, such as the spectacular *Psammodes diabolica* (cf. Pl. XII) and *egregia*, *Parapachynotela johni*, etc. Although living close to the Orange River, these Namaqualand elements have not migrated into the True Namib across the river. In a few very exceptional cases a migration across the river has taken place, but the species involved have not extended farther northwards than the area adjacent to the Orange River. A remarkable subspecific differentiation was observed in *Psammodes diabolica*, with the typical form occurring on the southern bank of the river and the subspecies **tactilis* on the opposite northern bank.

The true Namib elements are confined to the coastal sands and to the small and frequently isolated, sandy dunes of the Orange River depression. Along this route they have often entered the dunes of the south-western Kalahari; they may also have reached this area by means of bridges of wind-blown sand in Great Namaqualand, at such places where the Kalahari dunes draw into comparatively close proximity to the Namib dunes.

Although none of the many highly specialized genera of the True Namib has been found, except for *Vansonium*, the typical Namib elements are well represented. All the basic Namib genera are present (**Brinckia*, *Pachynotelus*, *Onymacris*, *Caenocrypticus*, *Carchares*); endemic genera, which can be readily traced back phylogenetically to the Namib elements, are *Cimicichora*, *Cimicia* and *Heliophosis*, while *Cimiciopsis* is found also in the southern portion of the Southern Namib.

The most characteristic endemic Namib species of this area are the following: **Brinckia *oograbiensis*, **serratina* and *vaga* (coastal sands); *Phanerotomea verecundum*, *roriferum* and *globosum* (coastal sands); *Pachynotelus leopardinus*, *cutulus*, *haagi*, *garipepinus* and *scaccarium* (lower Orange River area); *Onymacris paiva* with the subspecies *schencki*, *confluens* and *conjuncta* (coastal sands), *boshimana* (Bushmanland) and *multistriata* (south-western Kalahari); *Cimiciopsis atra* (coastal sands); *Stipsostoma holgatensis*; *Stips cassidoides* (lower Orange River area); *Cimicichora gigantea* (lower Orange River area), *crenulata* (Bushmanland) and *hessei* (south-western Kalahari); *Cimicia spinipes* (coastal sands and lower Orange River area); *Heliophosis kalaharica* (south-western Kalahari); *Caenocrypticus bushmanicus* (Bushmanland); *Carchares gracilis* (Namaqualand), etc.

Of species which are common to both Transitional and Southern Namib the most remarkable is *Vansonium bushmanicum* from Bushmanland, together with the subspecies **namibense* so far known from the Southern Namib but only north of the Koichab River. Further such species are, among others, **Brinckia insularis*, *Onymacris lobicollis* and *hottentota*, if we do not consider those endemic species of the Southern Namib which, though having crossed the Orange River, remain confined to its southern bank (e.g. *Calognathus chevrolatii* f.t., *Periloma alfkeni*, *Pachynotelus dimorphus*, *Nemanes expansicollis*, etc.).

(4) *Ecological divisions of the Namib*

According to edaphic features we can divide the Namib into three longitudinal sections which lie next to one another from the coast towards the highlands. These sections are the littoral sands, the barchan dunes and the consolidated sand to rocky soil surfaces of the plains. To these have to be added special biotopes such as the more hygrophilous or halophilous strata of river-beds, pans, etc.

A special eco-fauna of Tenebrionids corresponds to each of these sections.

A rough longitudinal division of the Namib has been accepted also from the point of view of climatology, viz. into an outer section or coastal and true fog belt, and an inner Namib which is the inland area gradually rising towards the slopes of the highlands. This is roughly based on the characteristic precipitation formula of the Namib, correlating the increase of rainfall with the decrease of sea mist from the coast eastwards. Although this division has been applied by various authors, such as Walter to the vegetation, Gebien to the Tenebrionids, Mertens to the reptiles, etc., it seems to be of a lesser importance for the ecology of the apterous ground Tenebrionids than are edaphic features. According to the distribution pattern of many Namib-Tenebrionids, these beetles are somewhat indifferent to the degree of air moisture but depend very much on the soil conditions. Various dune Tenebrionids such as *Lepidochora*, *Arthrochora*, *Stips stali*, *Namibomodes*, *Onymacris*, etc., occur not only under the conditions of a high degree of air moisture as met with close to the coast (e.g. Luderitz, Rooibank, Swakopmund), but were found also in areas far out of the fog belt, e.g. at Namtib, a site which is situated quite 80 miles from the sea (cf. map 3). The same seems to apply to various reptiles; *Palmatogecko rangei* has been observed on the practically littoral sands of Luderitz and Moçamedes, but also in the marginal area of the barchan dunes opposite the farm Arib (north-west of Abbabis), viz. about 80 miles inland from the coast as the crow flies (cf. map 4). Similar cases can be reported also of animals living on consolidated gravel grounds; *Stenocara eburnea* believed to be confined to the coastal area, was collected recently as far inland as the Mesum Mountains, while the gecko *Pachydactylus kochii* has been noted at Cape Cross as well as the inland station Gobabeb.

A. *Littoral sands*

As opposed to the eastern (or Indian) coast, the Atlantic coast of Africa is very poor in Tenebrionids pertaining to the circum-African littoral sand fauna proper.

On the eastern coast the proliferation of the littoral genera is remarkable, consisting of *Trachyscelis*, *Macrotrachyscelis*, *Plesioderes*, *Cornopterus*, *Nesocaedius*, *Corinta*, *Ammobius*, *Freyula*, *Diaderma*, *Heterocheira*, *Diphyrhynchus*, certain species of *Falsammidium* and the subgenus *Apteroclitobius* of *Clitobius* (cf. Koch, 1960a). Some of these Indian elements have expanded along the eastern and Mediterranean coasts of the continent as far as southern Morocco in the north-west (viz. *Trachyscelis*, *Ammobius* and *Nesocaedius*), and to the south-eastern Cape Province in the south (*Cornopterus*).

The Atlantic elements, however, are very poorly represented and are confined to the genera *Ammidium* and *Falsocaedius*, to which *Phaleriderma*, an endemic genus of the littoral sands of the Cape Province, can be added.

In conformity with this development the Namib lacks any specialized element of the circum-African littoral sand fauna; there is only *Ammidium namibense* from the tropical part of the Atlantic coast, which has expanded southwards as far as the Skeleton Coast. There are also species of the indifferently psammophilous genera *Caedius* and *Clitobius* (s.str.), while the tidal Phaleriini of worldwide distribution are represented by the phyto-sarcophagous genus *Pachyphaleria*.

This genus is endemic to the whole west coast of Southern Africa and, in appearance, recalls to an amazing extent the Phaleriini-genus *Phalerisida* from the Chilean coast.

There are, however, quite a number of species belonging to continental groups, which have become adapted to the biotope of littoral and sublittoral sands. They are all endemic to the Namib, but found only on sites where the coast forms a littoral plain; they strictly avoid the barchan dunes, however, and are absent even from sites where these dunes drop directly to the sea (e.g. north of Hottentot Bay). Such species of strictly littoral habits are **Brinckia debilis*, *vaga*, **serratina* and *insularis*, *Onychosis gracilipes*, *Carchares macer*, etc. **Brinckia insularis* is one of the few species known to occur also on the small Namib islands; it was discovered on Possession Island, but was later collected again on the mainland.

Another group shows less strictly littoral tendencies in representing a link between the littoral and dune habitats. To this group belong, among others, *Carchares granulosa* and the stem of the 'white' *Onymacris* of the Northern Namib. *Onymacris marginipennis*, with its subspecies *palgravei* and *nigropunctata*, as well as *Carchares granulosa*, are found only in close proximity to the coast, on wind-blown sand or at the foot of marginal dunes, as long as there is vegetation. In many cases *Onymacris marginipennis* was observed to agree in its habitat with that of the strictly littoral **Brinckia debilis*, e.g. on the sands of the small and isolated beach of Henties Bay.

The other species of the 'white' *Onymacris* (viz. *candidipennis*, *bicolor*, *brincki* and *langi*) keep generally in proximity to the coast, but some of them (*candidipennis*, *bicolor marshalli* and *brincki*) have conquered also the barchan dunes, and in some places have spread inland as far as there exists a continuity of wind-blown sand which is not separated from the coastal dunes by any kind of hard-ground barrier. The apparently quite abnormal occurrence of the 'white' *Onymacris *visseri* in the mountains of the Kaokoveld can be explained by the above reasons. This species lives on the blown sand of the N'Gola flats in the Marienfluss depression, which is flanked on either side by the Hartmann Mountains in the west and the Baynes Mountains in the east. The parts of the Marienfluss depression, however, where *Onymacris visseri* occurs, are situated still within the 600 m. contour and form 'river-pockets' of low ground, which communicate with the low ground of the coastal Namib by the way of the Cunene River depression in the north and penetrate southwards between the mountains round the northern slopes of the Hartmann Mountains (cf. map 6). A parallel case of dispersal can be reported of *Protodactylus*, the type species of which (*opticus*) was known from the Moçamedes desert, while another species (**sanctae-mariae*) was recently discovered also in the N'Gola flats of the Marienfluss depression.

B. *Barchan dunes*

This biotope is peculiar to the True Namib and harbours the most autochthonous elements of the Namib fauna. An analysis of the strictly dune-loving Tenebrionids shows that they all belong to endemic species and in most cases also to endemic genera. It seems that these strictly dune-loving species are unable to migrate back to the adjacent, extra-dune soil surfaces which, even if formed by sand, may differ from the coarse dune-sand in composition, compactness and granularity. Thus the dune species are wholly confined to the dunes and can probably not exist elsewhere.†

† Dune Tenebrionids, which were kept in the insectarium on artificial or river sand, soon damaged the armatures of legs and lost the tactile sense bristles and lateral cilia of body; in the *Lepidochora* the knife-sharp lateral margin of elytra became pierced and broken in places.

Endemic genera of the barchan dune section are the following: *Namibomodes*, **Uniungulum*, *Calognathus*, *Fossilochile*, *Archinamibia*, *Eustolopus*, *Namibismus*, *Lepidochora*, *Arthrochora*, *Cardiosis*, *Tarsosis*, *Anisosis*, *Ophthalmosis*, *Dactylocalcar*, *Gyrosis*, *Cerosis*, *Periloma*, *Psammogaster*, *Syntyphlus* and *Vernayella*. Strictly endemic dune species have been developed also in genera which, in one way or the other, are diffused also outside the true barchan dunes. Such genera are *Phanerotomea*, *Pachynotelus*, *Onymacris*, *Stenocara*, *Stips* and *Caenocrypticus*. Of the several hundred species of the psammophilous Pan African genus *Zophosis* not a single one has gained access to the dunes, nor do I know of any Tenebrionid species which occurs on the sand of dunes and also on other soils.

While many of the endemic genera are monotypical, the speciation in others is remarkably high, with *Lepidochora* composed of nine different forms, *Vernayella* and *Namibomodes* each numbering four species, *Cardiosis* ten forms, etc. In the genera mentioned, and also *Onymacris* and *Pachynotelus*, a split into two to four sympatric species has often taken place, due probably to the adaptive response of the respective forms to subtle differences in the conditions of ecological niches.

The main ecological niches which exist in the barchan dune area, and to which the respective inhabitants react in a convergent manner, are the following:

(a) Portions of the barchan dunes which bear more or less scattered vegetation, such as dune grasses, *Narras* (*Acanthosicyos horrida*), etc.; these portions are usually situated in the marginal area of the dune systems, or are formed by smaller, undulating grassy dunes in front of the big and barren dunes.

This niche is favoured by a great number of dune Tenebrionids. They are plant-followers (Koch, 1952c) or plant-satellites (Pierre, 1958), as their life, in one way or the other, appears to be connected with the existence of plants. They are not necessarily phytophagous insects but, as opposed to the inhabitants of the barren portion of the dunes, may be best characterized by the name of 'gravitaters', as they are attracted, move or gravitate towards a plant centre. According to the manner in which they react to this milieu, they occur in the Namib dunes in the two following categories.

(α) *Errant plant-followers* (cf. Pl. XIII). These are all those species which, during the active ethological state of daily rhythm, move around between or underneath the plants, and retire into the sand below the plant for the interval of their daily dormant state. A typical example of such an errant plant-follower is *Onymacris plana*. It is a daylight and considerably heliotactic sand-runner of the barchan dunes, living always close to some plant and frequently taking intermittent shelter in the half-shade of this plant during the day, but digging itself into the sand underneath the plant at sunset for the period of its nocturnal dormant state.

Many of the diurnal and also the nocturnal dune Tenebrionids can be placed in this category, such as *Namibomodes*, *Archinamibia*, *Namibismus*, *Arthrochora*, *Ophthalmosis*, *Gyrosis*, *Stips stali* and of the genus *Onymacris* the species *plana*, *lobicollis*, *subelongata*, *rugatipennis* (cf. Pl. XIII), *marginipennis* and *langi*.

(β) *Stationary plant-followers*. The species of this category appear to be more intimately connected with the plant than those of the preceding group. They usually live in gregarious populations in the sand underneath the plant, generally between the roots, and surface from the sand only occasionally, without moving too far away from the plant. In this behaviour they recall the Tenebrionids of the circum-African littoral sand fauna and are all also nocturnal, or permanently 'under-sand' insects. Typical representatives are, for example, *Caenocrypticus deserticus*, *phaleroides* and *peezi*, *Periloma alfkeni*, *Psammogaster malani* and, so far as I was able to observe, also *Dactylocalcar caecus* and probably *Syntyphlus subterraneus*. The early stages of these species, and probably also of those of the preceding group, may belong to these stationary plant-followers.

(b) The barren dunes and vegetationless slope and crest portions of grassy dunes. Until recently the barren sand of the desertic dunes in general, which is devoid of any macro-flora, was believed to be devoid also of all other life, except for bacteria, micro-fungi and micro-algae (cf. Kilian & Feher on the micro-life of the Saharan sands). With the exception of observations which we have carried out in the Namib Desert, there is no mention in literature of this so-called hostile biotope representing in fact an optimal ecological niche for a whole group of Tenebrionids.

The species which have adapted themselves to this extreme biotope may be defined and referred to by the term *ultra-psammophilous* (Koch, 1961), for they no longer depend on active plant life, but just dwell anywhere in the barren wastes of sand, without necessarily being attracted by plants, or gravitating towards any other central object.

To these ultra-psammophilous dune-dwellers belong the most specialized of all Namib Tenebrionids, viz. all *Lepidochora* (cf. Pl. XV), *Cardiosis*, *Tarsosis*, *Anisosis*, *Vernayella*, and of *Onymacris* the species *unguicularis* (cf. Pl. XIII) with its subspecies *polita*, *laeviceps*, *brincki*, *candidipennis* and *bicolor* with its subspecies *marshalli*.

(c) Some greatly specialized genera cannot be assigned to any of the above-mentioned categories, and seem to react to various further ecological niches. *Calognathus chevrolatii*, *Vansonium bushmanicum* **namibense*, *Cerosis hereroensis* and **Uniungulum* **hoeschi*, for example, have been observed to live in barren sand, but under variously different conditions. *Calognathus* and *Vansonium bushmanicum* **namibense* occur in close proximity to the marginal area of the barchan dunes, in wind-blown sand which invades the foot of the big dunes or rocky outcrops and hills; they have never been observed within the barchan dune system, and it seems that they display somewhat petro-psammophilous habits. **Uniungulum* has been discovered in the grassy marginal area of dunes, but does not seem to be attracted by vegetation. Quite a special ecological niche is occupied by *Cerosis*, which we observed regularly within the true, barren barchan dunes, but exclusively in the run-off valleys between the dunes, on a more compact sand of somewhat grit-like granularity.

C. Sandy to gravelly plains, with isolated rocky outcrops and hills

The principal characteristics of this section† are the hard consistency of the soil (sandy, gravelly, rocky or partially covered by blown sand), and the wide extension of flat, low ground. This low ground is almost continuous but considerably constricted by the great expansion of the barchan dunes in the Southern Namib; it is divided by a great number of river-beds in the Northern Namib, and expands right to the coast line in the dune-less southern portion between the Swakop and Huab Rivers.

Although physiographically clearly delimited in the east by the natural borders formed by the escarpments of the highlands (Jaeger),‡ this part is the least sharply defined of the ecological sections of the Namib. The 2000 ft. (or 600 m.) contours, which were accepted as eastern border lines, do not coincide in most cases with the natural faunistical limits. The plains often rise gradually above the 2000 ft. contour, and various enclaves of the highlands, such as isolated hills and portions which have broken away from the escarpment, keep below this contour. Thus, on the one hand a great number of faunistical elements of the highlands

† See parts of the 'Inner Namib' and the 'Outer Namib' of Walter, and 'Vor-Namib' of Gebien, Mertens and others.

‡ Geomorphologically Jaeger includes the whole of the coastal incline in the Namib, as opposed to the highlands delimited by the escarpment in the west.

have expanded far down and westwards on to the low ground of the Namib, while, on the other hand, several Namib elements have penetrated in the midst of the highlands by means of 'river-pockets'.

Generally, however, the true and endemic Namib elements of the low ground are readily recognizable by the fact that they do not occur in the highlands proper, while many highland species descend to the low ground and are frequently met with right at the foot of the barchan dunes (e.g. species of the genera *Renatiella* (cf. Pl. XIV), *Herpiscius*, *Rhammatodes*, *Asphaltesthes*, *Drosochrus*, *Nicandra*, *Psectes*, *Zophosis*, *Stips dohrni* **namibensis*, etc.).

Of typical and endemic Namib forms living on the plains, mention is made here only of all the 'white' *Calosis*, the 'white' *Stenocara eburnea* (cf. Pl. XIV); the genera *Nemanas*, *Microderopsis*, **Carpiella*, *Palpomodes*, *Protodactylus*, together with *Stenocara phalangium* and *velox*, *Stipsostoma sculpta*, *Stips dohrni* **namibensis*, *Gyrosis* **moralesi*, as well as localized species of *Zophosis*, *Stenolamus*, *Lornamus*, *Drosochrina* and *Stizopina*. The ecological niches occupied by these Tenebrionids vary in indefinite ways according to geomorphological and vegetation biotopes.

Ultra-deserticolous tendencies seem to prevail in some species, such as *Stenocara eburnea* and *phalangium*, *Calosis amabilis*, *lundholmi* and *tricolor*, *Gyrosis* **moralesi* and several *Zophosis*, which are not attracted by plants, and pass their dormant phase in the sand or under small pebbles. Deviations from this behaviour may be due to various factors, such as seasonal rhythm, etc. Thus we found large numbers of individuals of *Stenocara eburnea* under *Salsola* plants on the quartz-grit plains between the Omaruru River and the Lagoon-Mountains, while the same species, on the gravelly flats north-east of Rooibank, was observed to be typically errant, and did not take shelter under the scattered *Arthraerna leubnitziae* plants which represented the only vegetation on these otherwise barren plains.

Psammophilous plant-followers are *Stenocara phalangium*, the *Palpomodes* and *Protodactylus*, the two former being errant, the latter almost stationary and also penetrating into the marginal area of dunes in the Porto Alexandre desert.

Typically petrophilous insects are *Microderopsis*, *Rhammatodes*, *Asphaltesthes*, *Lornamus* and many *Drosochrina*; several species of *Rhammatodes* and *Asphaltesthes* show subcavernicolous habits and live in eroded caves or in cracks of rock surfaces. Wind-blown accumulations of dry grass fragments and other detritus are the habitat of **Carpiella*, *Stenolamus* and various *Stizopina* and *Cryptochilini*. Some adelostomoid Eurychorini are myrmecophilous, while *Stips dohrni* **namibensis* and *Stipsostoma sculpta* seem to prefer the abandoned burrows of rodents and reptiles.

LIST OF THE SPECIES OF THE SOUTHERN NAMIB

Between Orange and Koichab Rivers Between Koichab and Kuiseb Rivers

MOLURINI

<i>Phanerotomea gibberosulum</i>	<i>Phanerotomea gibberosulum</i>
<i>sericicolle</i>	
<i>imbricatum</i>	
<i>Psammodes diabolica</i> * <i>tactilis</i>	
<i>schultzei</i>	
<i>eberlanzi</i>	
<i>lossowi</i>	<i>Psammodes kuisup</i>
<i>Namibomodes rubra</i>	◦ <i>Namibomodes serrimargo</i>
◦ <i>serrimargo</i>	* <i>zarcoi</i>
	* <i>maculicollis</i>
◦ <i>Brinckia insularis</i>	◦ <i>Brinckia debilis</i>
	* <i>Uniumgulum</i> * <i>hoeschi</i>

Between Orange and Koichab Rivers

Between Koichab and Kuiseb Rivers

Calognathus chevroletii f.t.
chevr. eberlanzi

CALOGNATHINI

Calognathus chevr. eberlanzi

VANSONINI

Vansonium bushmanicum **namibense*

CRYPTOCHILINI

Parapachynotela eberlanzi
Pachynotelus granaticollis
leucimus
namibensis
longipilis
◦*dimorphus* (1)
strigicollis f.t.
comma f.t.
*comma niveus**Pachynotelus strigic. junior**comma damarensis*
albonotatus
albostrigatus
streya
**kuehnelti*
*Fossilochile rufa**Onymacris lobicollis*
laeviceps
unguicularis f.t.
unguic. polita
plana f.t.
plana debilis
rugatipennis

ADESMIINI

Onymacris laeviceps (2)
unguicularis f.t.*plana* f.t.*rugatipennis*
*subelongata**Eustolopus calcaratus*
◦*octoseriatus*
◦*Physosterna cribripes*
◦*Stenocara inaffectata*
◦*bethanica*
phalangium f.t.
Epiphysa louwrensi◦*Eustolopus octoseriatus* (3)
◦*Physosterna cribripes**Stenocara phalang. rufofemorata* (4)*Cimiciopsis castleae*
◦*Cimicia spinipes*
Stips stali
Arthrochora arenicola
Lepidochora pilosa
diaphana
discoidalis f.t.

eberlanzi f.t.

EURYCHORINI

Stips stali (5)
Arthrochora arenicola (6)*Lepidochora discoidalis* f.t.
*disc. *argentogrisea*
eberlanzi parva
**kahani*
portiStipsostoma sculpta*
Eurychora alaticollis

TENTYRIINI

Archinamibia peezi (6)*Afrinus adamantinus*
namibensis
◦*Asphaltesthes impressipennis*
◦*Rhammatodes aequalipennis*
Derosphaerius humilis◦*Rhammatodes aequalipennis*
Derosphaerius humilis
◦*Cyphostethe tau cavipectus*

Between Orange and Koichab Rivers

Between Koichab and Kuseib Rivers

ZOPHOSINI

*Cardiosis eremita**Cardiosis fairmairei* f.t.
fairmair. namtibensis
*fairmair. freyi**fairmair. luederitzensis**triangulifera* f.t.
triang., reducta°*Tarsosis damarensis*
°*Onychosis gracilipes*
Gyrosis orbicularis°*Tarsosis damarensis*
°*Onychosis gracilipes*
Gyrosis orbicularis
moralesiCerosis hereroensis*
Hesseosis adamantina
Zophosis solivaga
*namibensis**Cerosis hereroensis* (6)*Dactylocalcar caecus* (6)

SCAURINI

Carchares granulosa
°*macer**Carchares granulosa*
°*macer*

PYTHIOPINI

Pythiopus cornutipectus

ONCOTINI

°*Ograbies campi*
Hirtograbies namibensis
longipilis
°*Stridigula plamiuscula*

STIZOPINA (OPATRINI)

Parastizopus diehli
°*lithopsophilus*°*Parastizopus balneorum**Periloma alskeni*
*Nemanis expansicollis**Psammogaster malani*
Syntyphlus subterraneus

STENOLAMINA (OPATRINI)

Stenolamus malacodermus

GONOPINA (PLATYNOTINI)

°*Gonopus tibialis*°*Gonopus tibialis*

PHALERIINI

°*Pachyphaleria capensis*°*Pachyphaleria capensis*

CAENOCRYPTICINI

Caenocrypticus deserticus
°*phaleroides*°*Caenocrypticus phaleroides* (6)
peezi°*Fitzsimonsium cymbium*°*Vernayella noctivaga*
ephialtes
**pauliani*
**delabati*

DROSOCHRINA (DROSOCHRINI)

*Nicandra spinulosa**New records:* (1) Also north of the Orange River (Daberas dunes).(2) *Onymacris laeviceps* spreads northwards as far as Gobabeb (also at the Tsauchab River and Sossus Vlei).

(3) Collected also in the dunes near Gobabeb.

(4) Very common also on the grit plains at the southern side of the Kuseib River, near Gobabeb.

(5) *Stips stali* has been collected everywhere on the dunes of the Southern Namib, from about Haalenberg northwards as far as Walvis Bay.(6) Recently the following species were collected also at the Tsauchab River, Sossus Vlei, Gobabeb and Rooibank: *Arthrochora aremicola*, *Archinamibia peezi*, *Cardiosis fairmairei* f.t. and *freyi*, *Cerosis hereroensis*, *Dactylocalcar caecus* and *Caenocrypticus phaleroides*.

LIST OF THE SPECIES OF THE NORTHERN NAMIB

Between Kuiseb and Huab Rivers Between Huab and Cunene Rivers Between Cunene and Coroca Rivers North of Coroca River

MOLURINI

Phanerotomea cordiventre

Phanerotomea dubiosum
argenteofasciatum
Psammodes sellatus subsp.
uriae
°*Synhinba cordiforme*

Palpomodes physoptera f.t.
halophila
°**Brinckia debilis*

Namibomodes serrimargo
Palpomodes physoptera f.t.

°*Synhinba cordiforme*
Palpomodes phys. angolensis

rudebecki
°**Brinckia debilis*

°**Brinckia debilis*
Somaticus welwitschi
°*Ethmus vernayi* f.t.

Somaticus welwitschi

CALOGNATHINI

Calognathus chevrol. atricolor

CRYPTOCHILINI

Pachynotelus herminiferus

Pachynotelus machadoi f.t.
machadoi tigrum

Pachynotelus machadoi laevimargo

lineatus

ADESMIINI

Onymacris marginipennis
subsp. *palgravei*

Onymacris marginipennis f.t.

Onymacris marginipennis
subsp. *nigropunctata*
bic. marshalli

bicolor f.t.
brincki
**visseri*

candidipennis

Onymacris longi

°*Physosterna globosa* f.t.
glob. epiphysoides
glob. scherzi
cribripes

°*Eustolopus octoseriatus*

°*Physosterna cribripes*

°*Physosterna cribripes*

Between Kuiseb and Huab Rivers

Between Huab and Cunene Rivers

Between Cunene and Coroca Rivers

North of Coroca River

ADESMIINI (cont.)

Stenocara brunnipes f.t.
depressa f.t.
eburnea
°*velox*

Stenocara brunn. pluricostata
depr. dissoluta

°*velox*

Stenocara desertica

dilaticornis

dilaticornis

Stenocara machadoi
°*nervosa*
Stenodesia marshalli
°*Metriopus kunenensis karakul*

Stenodesia marshalli
Metriopus kunenensis f.t.
°*Renatiella fettingi*

Stenodesia marshalli
Metriopus kunenensis f.t.

Renatiella gebieni
°*Alogenius robinsoni*
cavifrons semigranulatus
Epiphysa ciliata

°*Alogenius robinsoni*

°*Alogenius robinsoni*

EURYCHORINI

°*Stips dohrni* **namibensis*

°*Stips dohrni* **namibensis*

Stips dorsocostata

Stips dorsocostata

°*Eutichus wahlbergi*

°*Eurychora batesi*
°*angolensis*

°*Eurychora batesi*
°*angolensis*

°*Eurychora batesi*
°*angolensis*
Platysemodes benguelensis

Psaryphulum damara

°*Psaryphulum machadoi*

TENTYRIINI

Microderopsis benguelensis (1)

Microderopsis benguelensis

Microderopsis benguelensis
Asphaltesthes complicans
subsp. *laevigatus*

°*Asphaltesthes costatus* f.t.

°*Asphaltesthes afrogermanicus*

Rhammatodes striatulus
speluncarius f.t.
spelunc. mocamedinus
machadoi
oasis
moufleti
carinatus
deserticus
°*quadricollis*

Rhammatodes deserticus

°*Rhammatodes quadricollis*
longicorn. sceletosorae

Between Kuiseb and Huab Rivers	Between Huab and Cunene Rivers	Between Cunene and Coroca Rivers	North of Coroca River
	TENTYRIINI (cont.)		
◦ <i>Rhammatodes aequalipennis</i> ◦ <i>subcostatus</i> ◦ <i>tagenesthoides</i>	◦ <i>tagenesthoides</i> ◦ <i>Gnophota anthr. colpotoides</i> ◦ <i>Rozonia infranotata</i>	◦ <i>Gnophota anthracina</i> f.t. ◦ <i>semirugosa</i> <i>Namibismus castaneus</i>	◦ <i>Gnophota anthracina</i> f.t. ◦ <i>semirugosa</i> <i>Namibismus castaneus</i>
	ZOPHOSINI		
<i>Calosis amabilis</i> f.t. <i>amab. swakopensis</i>	<i>Calosis lundholmi</i> <i>Cardiosis carpi</i> ◦ <i>Tarsosis damarensis</i> <i>Anisosis caudata</i>	<i>Calosis tricolor</i> <i>Cardiosis moufleti</i> <i>Anisosis caudata</i> <i>Ophthalmosis longipes</i> ◦ <i>Onychosis gracilipes</i> <i>Microsis wilhenai</i>	<i>Calosis tricolor</i>
◦ <i>Onychosis gracilipes</i>	◦ <i>Onychosis gracilipes</i>		◦ <i>Microsis transbechuana</i>
◦ <i>Zophosis dorsata</i> <i>deveva</i> <i>gaerdesi</i> <i>damarina</i> <i>mniszzechi</i>	<i>Zophosis saltans</i> ◦ <i>greeni</i> ◦ <i>himba</i> <i>kunenensis</i>	<i>Zophosis braini</i> <i>elongata</i> <i>sexcostata</i>	<i>Zophosis kunenensis</i> <i>braini</i> <i>Zophosis angolensis</i> <i>mocamedina</i> ◦ <i>bebeana</i> <i>trigo</i> <i>striatimargo</i> <i>pubescens</i>
<i>Protodactylus</i> * <i>giessi</i>			

Between Kuiseb and Huab Rivers	Between Huab and Cunene Rivers	Between Cunene and Coroca Rivers	North of Coroca River
	ZOPHOSINI (cont.)		
	<i>Protodactylus</i> * <i>sanctae-mariae</i>		<i>Protodactylus opticus</i>
* <i>Carpiella</i> * <i>latisterna</i>		SCAURINI	
◦ <i>Carchares macer</i> ◦ <i>Herpiscius bisbicostatus</i>	◦ <i>Carchares macer</i>		<i>Herpiscius robinsoni</i>
		STIZOPINA (OPATRINI)	
◦ <i>Parastizopus balneorum</i>			◦ <i>Stizopus laticollis</i>
	◦ <i>Ammidium namibense</i>	OPATRINA (OPATRINI)	
<i>Gonocephalum kolbei</i>		◦ <i>Ammidium namibense</i>	◦ <i>Ammidium namibense</i>
		STENOLAMINA (OPATRINI)	
	<i>Stenolamus brincki</i>		<i>Stenolamus machadoi</i> <i>filum</i> <i>deserticus</i>
◦ <i>Gonopus tibialis</i> <i>pliciventris</i>	◦ <i>Gonopus tibialis</i>	GONOPINA (PLATYNOTINI)	
		◦ <i>Gonopus tibialis</i>	◦ <i>Gonopus tibialis</i>
		LITOBORINI	
		CAENOCRYPTICINI	
◦ <i>Lornamus damara</i>	◦ <i>Caenocrypticus phaleroides</i>		◦ <i>Lornamus dividiopsis</i>
		DROSOCHRINA (DROSOCHRINI)	
<i>Drosochrus vernayanus</i> <i>desolatus</i>		◦ <i>Vernayella noctivaga</i>	◦ <i>Drosochrus crenulatus</i>
◦ <i>Nicandra michaelsemi</i> <i>Diestecopus histrio</i> <i>gracilipes</i>	<i>Nicandra desertica</i>		
		<i>Diestecopus martinsi</i>	<i>Diestecopus martinsi</i>

New records. (1) Recently we have collected *Microderopsis benguelensis* also in the area between the Kuiseb and the Huab Rivers, where it seems

widely spread (Cape Cross, Gobabeb, Rooibank, *Welwitschia*-plain in Game Reserve no. III, etc.).

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Afrinus Fairmaire, 1888 (Gebien, 1937; Koch, 1952c)
 adamantinus Koch, 1950a (Koch, 1952c)
 namibensis Koch, 1952c
Alogeni Gebien, 1910 (Haag, 1875b; Koch, 1951a; Ferreira, 1955a)
 cavifrons semigranulatus Koch, 1951a
 robinsoni Koch, 1951a
Ammidium Erichson, 1843 (Koch, 1959a)
 namibense Koch, 1959a.
Ammobius Guerin, 1846 (Koch, 1950c; Espanol, 1956; Koch, 1959a)
Anemia Laporte, 1840 (Gebien, 1937, 1938; Koch, 1956)
Anisosis Deyrolle, 1867 (Chatanay, 1921; Koch, 1958)
 caudatus Deyrolle, 1867 (Koch, 1952c, 1958)
 ANOMALIPINA Koch, 1956
Apteroclitobius Koch, 1960a
Archinamibia Koch, 1952c
 peezi Koch, 1952c (Ferreira, 1955a)
Arthrochora Gebien, 1938 (Koch, 1952c)
 arenicola Gebien, 1938 (Koch, 1952c)
Asphaltesthes Kraatz, 1865 (Koch, 1941, 1950a, 1952c)
 afrogermanicus Koch, 1941 (Koch, 1943, 1950a, 1952c)
 complicans laevigatus Koch, 1952c
 costatus Erichson, 1843 (Koch, 1950a, 1952c)
- Caedius* Mulsant & Rey, 1859 (Espanol, 1944; Koch, 1950c, 1959a, 1960a)
 CAENOCRYPTICINI Koch, 1958
Caenocrypticus Gebien, 1920 (Koch, 1950c, 1952c, 1958)
 bushmanicus Koch, 1950c (Koch, 1952c)
 deserticus Koch, 1950c (Koch, 1952c)
 peezi Koch, 1958
 phalerooides Koch, 1950c (Koch, 1952c)
 CALOGNATHINI Lacordaire, 1859 (Gebien, 1937; Koch, 1950a, 1955a)
Calognathus Guerin, 1836 (Koch, 1950a)
 chevrolatii chevrolatii Guerin, 1836 (Koch, 1950a, 1952c; Ferreira, 1955b)
 chevrolatii eberlanzi Koch, 1950a (Gebien, 1938; Ferreira, 1951; Koch, 1952c)
 chevrolatii atricolor Pic, 1912 (Koch, 1952c)
Calosis Deyrolle, 1867 (Chatanay, 1921; Koch, 1958)
 amabilis Deyrolle, 1867, (Koch, 1952c, 1958)
 amabilis brunnilineata Koch, 1952c (Koch, 1958)
 amabilis swakopensis Koch, 1952c (Koch, 1958)
 lundholmi Koch, 1952c (Koch, 1958)
 tricolor Deyrolle, 1867 (Koch, 1952c, 1958)
 tricolor albescens Koch, 1952c (Koch, 1958)
Carchares Pascoe, 1887 (Gebien, 1920, 1937, 1938; Koch, 1958)
 gracilis Peringuey, 1886
 granulosa Peringuey, 1886 (Gebien, 1920)
 macer Pascoe, 1887 (Gebien, 1920)
Cardiosis Deyrolle, 1867 (Chatanay, 1921; Koch, 1952c, 1958)
 carpi Koch, 1952c (Ferreira, 1953b)
 erenita Koch, 1950a (Koch, 1952c)
 fairmairei Peringuey, 1886 (Koch, 1950a; Ferreira, 1951; Koch, 1952c; Ferreira, 1954)
 fairmairei freyi Kulzer, 1949 (Koch, 1952c)
 fairmairei luederitzensis Koch, 1952c (Koch, 1950a)
 fairmairei namtibensis Koch, 1952c

- mouffleti* Deyrolle, 1867 (Koch, 1952*c*, 1958)
triangulifera Gebien, 1938 (Koch, 1952*c*)
Cerosis Gebien, 1920 (Koch, 1958)
hereroensis Gebien, 1920 (Gebien, 1938; Koch, 1952*c*, 1958)
Cimicia Fairmaire, 1891 (Koch, 1952*a*)
spiripes Fairmaire, 1891 (Koch, 1952*a*; Ferreira, 1955*a*)
Cimicichora Koch, 1952*a*
crenulata Koch, 1952*a*
gigantea Koch, 1952*a*
hessei Koch, 1952*a*
Cimiciopsis Koch, 1952*a*
atra Koch, 1952*a*
castleae Koch, 1952*a*
Clitobius Mulsant & Rey, 1859 (Español, 1944; Koch, 1959*a*, *b*, 1960*a*)
Corinta Koch, 1950*c* (Español, 1956; Koch, 1959*a*, 1960*a*)
Cornopteris Koch, 1950*c* (Koch, 1959*a*, 1960*a*)
Cryptocarpus Koch, 1952*c* (Koch, 1958)
 CRYPTOCHILINI Solier, 1840 (Haag, 1872; Gebien, 1937; Koch, 1952*b*, 1953*a*, 1955*a*, 1957*b*)
Cyphostethe Marseul, 1867 (Koch, 1950*a*, 1952*c*)
gigantea Koch, 1950*a*
tau cavipectus Koch, 1952*c*
- Dactylocalcar* Gebien, 1938 (Koch, 1958)
caecus Gebien, 1938 (Koch, 1952*c*; Ferreira, 1953*b*; Koch, 1955*a*, 1958, 1960*b*)
 DACTYLOCALCARINA Koch, 1958
Derosphaerius Westwood, 1889 (Koch, 1950*a*)
Diaderma Koch, 1960*a*
Diestecopus Solier, 1848 (Koch, 1958)
gracilipes Koch, 1958
histrion Koch, 1958
martinsi Koch, 1958
Diphyrhynchus Fairmaire, 1849 (Gebien, 1922; Koch, 1935; Gebien, 1937; Koch, 1953*b*, 1956, 1960*a*)
 DROSOCHRINA Koch, 1958
 DROSOCHRINI Koch, 1958
Drosochrus Erichson, 1843 (Koch, 1958)
crenulatus Erichson, 1843 (Koch, 1958)
desolatus Koch, 1958
vernayanus Koch, 1958
- EMMALLINA Koch, 1956
Epiphysa Blanchard, 1845 (Gebien, 1937; Koch, 1951*a*; Ferreira, 1954)
ciliata Bates, 1872
barbata Koch, 1951*a*
latisterna Koch, 1951*a*
lowrensi Koch, 1951*a*
 EPITRAGINA Koch, 1955*a*
Ethmus Haag, 1873 (Koch, 1953*c*, 1955*a*, 1958)
vernayi Koch, 1958
Eurychora Thunberg, 1791 (Haag, 1875*c*; Koch, 1952*a*)
alaticollis Gebien, 1938
angolensis Haag, 1875*c*
batesi Haag, 1875*c*
 EURYCHORINI Haag, 1875*c* (Gebien, 1937; Koch, 1952*a*, 1955*a*)
Eustolopus Gebien, 1938
calcaratus Gebien, 1938 (Koch, 1951*a*)
octoseriatus Gebien, 1938 (Koch, 1951*a*, 1952*c*; Ferreira, 1955*a*)
Eutichus Haag, 1875*c* (Koch, 1952*a*)
wahlbergi Haag, 1875*c* (Koch, 1952*a*, 1953*d*)

- Falsammidium* Koch, 1960a
Falsocaedius Espanol, 1943 (Koch, 1959a, 1960a)
Fitzsimonsium nom.nov. for *Fitzsimonsia* Koch, 1955c (Koch, 1958)
cymbium Koch, 1955c
Fossilochile Koch, 1952b
rufa Koch, 1952b
Freyula Koch, 1959b (Koch, 1960a)
- Gnophota* Erichson, 1843 (Koch, 1943, 1944a, 1950a)
anthracina Erichson, 1843 (Koch, 1944a)
anthracina colpotoides Koch, 1944a (Koch, 1950a; Ferreira, 1955a)
semirugosa Kraatz, 1865 (Koch, 1944a)
Gonocephalum Solier, 1834 (Espanol, 1944; Gridelli, 1945, 1948)
kolbei Gridelli, 1945 (Gridelli, 1948)
- GONOPINA Koch, 1956
Gonopus Latreille, 1829 (Gebien, 1920, 1937, 1938; Koch, 1953e; Ferreira, 1955a; Koch, 1956)
pliciventris Gebien, 1920
tibialis Fabricius, 1798
Gyrosis Gebien, 1920 (Koch, 1958)
orbicularis Deyrolle, 1867 (Chatanay, 1921; Gebien, 1920, 1938; Koch, 1958)
- Hanstroemium* Koch, 1953d (Koch, 1956)
adelostomoides mocamedinum Koch, 1956
adelostomoides bicornutum Koch, 1953f (Koch, 1956)
- Heliophosis* Koch, 1952c (Koch, 1958)
kalaharica Koch, 1952c (Koch, 1958)
- Herpiscius* Solier, 1836 (Gebien, 1920; Koch, 1958)
bisbicostatus Gebien, 1920
robisoni Koch, 1958
- Hesseosis* Koch, 1958
adamantina Koch, 1958
- Heterocheira* Lacordaire, 1859 (Gebien, 1937; Koch, 1953b, 1956, 1960a)
- HETEROTARSINI Koch, 1956
Hirtograbies Koch, 1953e (Koch, 1956)
campi Koch, 1953e
longipilis Peringuey, 1908 (Koch, 1953e)
namibensis Koch, 1953e
- HYPOMELINA Koch, 1955a
- Lepidochora* Gebien, 1938 (Koch, 1950a, 1952a)
diaphana Koch, 1950a (Koch, 1952c)
discoidalis Gebien, 1938 (Koch, 1950a; Ferreira, 1951)
eberlanzi Gebien, 1938 (Koch, 1950a, 1952c)
eberlanzi parva Koch, 1958
nocturna Koch, 1952c (Koch, 1958)
pilosa Koch, 1950a (Koch, 1952c)
- LITOBORINI Antoine, 1941 (Espanol, 1945; Koch, 1953c, 1956)
Lornamus Koch, 1952c (Koch, 1958)
damara Koch, 1958
dividiopsis Koch, 1952c
- Macropoda* Solier, 1835 (Kuntzen, 1914-16; Koch, 1944-48)
Macrotrachyscelis Pic, 1925 (Koch, 1953g, 1960a)
- MELANIMINI Koch, 1956
Metriopus Solier, 1835 (Kuntzen, 1914-16; Gebien, 1937, 1920)
kunenensis Koch, 1951 (Koch, 1952c)
kunenensis karakul Koch, 1952c
- MICRANTEREINA Koch, 1958
Microderopsis Haag, 1875a (Koch, 1950a)
benguelsensis Haag, 1875a (Koch, 1952c)

- Microsis* Koch, 1958
transbechuana Koch, 1958
vilhenai Koch, 1958
- MOLURINI Solier, 1843 (Haag, 1871, 1873, 1875*a*; Koch, 1951*b*, 1952*d*, 1953*c*, *d*,
f, 1955*a*, 1958)
- Namibismus* Koch 1952*c*
castaneus Koch, 1952*c* (Ferreira, 1954)
- Namibomodes* Koch, 1952*d* (Koch, 1958)
serrimargo Gebien, 1938 (Ferreira, 1953*b*; Koch, 1958)
- Nemanus* Fairmaire, 1888 (Gebien, 1938)
expansicollis Fairmaire, 1888 (Gebien, 1938)
- Nesocaedius* Kolbe, 1915 (Español, 1956; Koch, 1960*a*)
- Nicandra* Fairmaire, 1888 (Koch, 1958)
desertica Koch, 1958
michaelseni Gebien, 1920 (Koch, 1958)
spinulosa Koch, 1958
- Ograbies* Peringuey, 1899 (Koch, 1953*e*)
campi Koch, 1953*e*
- ONCOSOMINA Koch, 1958
- ONCOTINI Koch, 1953*e* (Koch, 1956)
- Onychosis* Deyrolle, 1867 (Chatanay, 1921; Koch, 1958)
- onguilipes* Deyrolle, 1867 (Gebien, 1920, 1938; Koch, 1952*c*, 1958)
- Onymacris* Allard, 1885 (Haag, 1875*b*; Kuntzen, 1914-16; Gebien, 1937)
bicolor Haag, 1875*b* (Kuntzen, 1914-16; Gebien, 1938; Koch, 1952*c*)
bicolor marshalli Koch, 1952*c* (Koch, 1958)
boshimana Peringuey, 1886 (Koch, 1951*a*)
brincki Koch, 1952*c*
candidipennis Breme, 1840 (Breme, 1841; Allard, 1885; Kuntzen, 1914-16;
 Gebien, 1938; Koch, 1952*c*)
hottentota Peringuey, 1886 (Kuntzen, 1914-16; Gebien, 1938)
laeviceps Gebien, 1938 (Koch, 1951*a*)
langi Guerin, 1843; Allard, 1885; Kuntzen, 1914-16; Gebien, 1938; Ferreira,
 1951; Koch, 1952*c*, 1958)
lobicollis Fairmaire, 1888 (Kuntzen, 1914-16; Gebien, 1938; Koch, 1951*a*)
marginipennis nigropunctata Koch, 1952*c*
marginipennis palgravei Peringuey, 1885 (Kuntzen, 1914-16; Gebien, 1938;
 Koch, 1952*c*)
multistriata Haag, 1875*b* (Allard, 1885; Kuntzen, 1914-16; Gebien, 1938,
 Koch, 1951*a*)
paiva Haag, 1875*b* (Allard, 1885; Peringuey, 1885, 1886; Kuntzen, 1914-16;
 Koch, 1951*a*)
paiva confluens Haag, 1875*b* (Kuntzen, 1914-16; Koch, 1951*a*)
paiva conjuncta Haag, 1875*b* (Peringuey, 1886; Kuntzen, 1914-16; Koch, 1951*a*)
paiva disjuncta Koch, 1951*a*
paiva schencki Kuntzen, 1914-16 (Koch, 1951*a*)
plana Peringuey, 1886 (Kuntzen, 1914-16; Gebien, 1938; Koch, 1951*a*; Ferreira,
 1953*a*, 1955*a*)
plana debilis Koch, 1951*a*
rugatipennis Haag, 1875*b* (Allard, 1885; Peringuey, 1885, 1886; Kuntzen,
 1914-16; Gebien, 1938; Koch, 1951*a*)
subelongata Gebien, 1938 (Koch, 1951*a*)
unguicularis Haag, 1875*b* (Allard, 1885; Peringuey, 1885, 1886; Kuntzen,
 1914-16; Gebien, 1938; Koch, 1951*a*)
unguicularis polita Gebien, 1938 (Koch, 1951*a*)
- OPATRINA Koch, 1956 (Español, 1958; Koch, 1960*a*)
- OPATRINI Español, 1944 (Koch, 1956)
- Oppenheimeria* Koch, 1952*c*
- OXURINA Koch, 1955*a* (Koch, 1952*d*)

- Pachynotelus* Solier, 1840 (Haag, 1872; Gebien, 1920, 1937, 1938; Koch, 1952*b*)
albonotatus Haag, 1872 (Koch, 1952*b*)
albostrigatus Haag, 1872 (Koch, 1952*b*)
catulus Koch, 1952*b*
comma Gebien, 1920 (Koch, 1952*b*)
comma damarensis Koch, 1952*b*
comma niveus Koch, 1952*b*
dimorphus Koch, 1952*b*
gariepinus Koch, 1952*b*
granaticollis Gebien, 1920 (Koch, 1952*b*)
haagi Peringuey, 1899 (Gebien, 1920; Koch, 1952*b*)
herminiferus Koch, 1958
kaszabi Koch, 1952*b*
leopardinus Koch, 1952*b*
leucinus Koch, 1952*b*
lineatus Haag, 1878 (Koch, 1952*b*)
longipilis Gebien, 1920 (Koch, 1952*b*)
machadoi Koch, 1952*b* (Koch, 1958)
machadoi laevimargo Koch, 1952*b*
machadoi tigrinum Koch, 1958
namibensis Koch, 1952*b*
scaccarium Koch, 1952*b*
streyi Koch, 1952*b*
strigicollis Gebien, 1920 (Koch, 1952*b*)
strigicollis junior Koch, 1952*b*
- Pachyphaleria* Gebien, 1920
capensis Laporte, 1840 (Chevrolat, 1878; Gebien, 1920)
- Palpomodes* Koch, 1952*d* (Koch, 1958)
halophila Koch, 1958
physoptera Gebien, 1920 (Koch, 1952*d*; Ferreira, 1953*b*; Koch, 1958)
physoptera angolensis Koch, 1958
rudebecki Koch, 1952*d* (Koch, 1958)
- Parapachynotela* Koch, 1952*b* (Koch, 1957*b*)
eberlanzi Gebien, 1938 (Koch, 1952*b*)
johni Koch, 1957*b*
- Parastizopus* Gebien, 1938 (Gebien, 1938-42; Koch, 1953*h*)
balnearum Peringuey, 1908 (Gebien, 1920; Gebien, 1938)
diehli Gebien, 1938 (Koch, 1953*h*)
lithopsophilus Koch, 1953*h*
- Periloma* Gebien, 1938 (Koch, 1953*h*, 1956)
alfkeni Gebien, 1938 (Koch, 1953*h*)
- Phaleriderma* Koch, 1953*e*
- PHALERIINI Mulsant, 1854; Gebien, 1938-42; Ferreira, 1955*a*
- Phalerisida* Kulzer, 1959
- Phanerotomea* Koch, 1958 (Koch, 1952*d*; Solier, 1843)
argenteofasciatum Koch, 1953*f*
cordiventre Haag, 1871 (Gebien, 1937; Koch, 1952*d*, 1958)
dubiosum Peringuey, 1899 (Gebien, 1937, 1938; Koch, 1952*d*, 1958)
gibberosulum Peringuey, 1908 (Gebien, 1937, 1938; Koch, 1952*d*)
imbricatum Koch, 1952*d*
roriferum Koch, 1952*d*
sericicolle Koch, 1952*d*
verecundum Peringuey, 1899 (Gebien, 1937, 1938; Koch, 1952*d*)
- PHANEROTOMEINA Koch, 1958 (Koch, 1952*d*, 1955*a*)
- Physosterna* Allard, 1885 (Gebien, 1937)
cribripes Haag, 1875*b* (Allard, 1885)
globosa Haag, 1875*b* (Allard, 1885; Koch, 1951*a*)
globosa epiphysoides Peringuey, 1885 (Koch, 1951*a*)
globosa scherzi Koch, 1951*a*
- PLATYNOTINA Koch, 1956
- PLATYNOTINI Koch, 1956

- Platysemodes* Strand, 1935 (Haag, 1875*c*; Koch, 1952*a*)
benguelensis Haag, 1875*c* (Koch, 1952*a*)
- Plesioderes* Mulsant & Rey, 1860 (Gebien, 1922, 1938-42; Koch, 1950*c*, 1959*a*, 1960*a*)
- Praogena* Laporte, 1840 (Mäklin, 1863; Gebien, 1942-44)
- Protodactylus* Koch, 1952*c* (Koch, 1958)
opticus Koch, 1952*c* (Ferreira, 1953*b*; Koch, 1958)
- Psammodes* Kirby, 1818 (Haag, 1871; Gebien, 1937; Koch, 1952*d*, 1955*a*)
diabolica Koch, 1952*d* (Koch, 1955*a*)
eberlanzi Koch, 1952*d*
egregia Haag, 1871 (Peringuey, 1886; Gebien, 1937; Koch, 1955*a*)
kuisup Peringuey, 1908 (Gebien, 1920, 1937)
lossowi Koch, 1952*d*
schultzei Peringuey, 1908 (Gebien, 1937; Koch, 1955*a*)
sellatus Haag, 1875*a* (Gebien, 1937; Koch, 1953*f*)
sellatus wriai Koch, 1953*f*
vialis Burchell, 1822 (Haag, 1871; Gebien, 1937; Koch, 1955*a*)
- Psammogaster* Koch, 1953*h* (Koch, 1956)
malani Koch, 1953*h*
- Psaryphulum* Koch, 1952*a*
damara Koch, 1952*a*
machadoi Koch, 1952*a*
- Psectes* Hesse, 1935 (Gebien, 1942-44; Koch, 1958)
- Pygmaeodes* Koch, 1952*d* (Koch, 1958)
- PYTHIOPINI Koch, 1955*b* (Koch, 1956)
- Pythiopus* Koch, 1952*c* (Koch, 1955*b*, 1956)
cornutipectus Koch, 1952*c*
- Renatiella* Koch, 1944-48 (Koch, 1951*a*)
gebiemi Koch, 1944-48 (Koch, 1951*a*)
- Rhamatodes* Haag, 1875*a* (Koch, 1941, 1950*a*, 1952*c*)
- Aequalipennis* Peringuey, 1899 (Gebien, 1920; Koch, 1950*a*, 1952*c*)
carinatus Haag, 1875*a* (Koch, 1941, 1950*a*, 1952*c*)
cataractus Koch, 1950*a* (Koch, 1952*c*)
deserticus Koch, 1952*c*
holgatensis Koch, 1950*a* (Koch, 1952*c*)
longicornis Haag, 1875*a* (Koch, 1941, 1943, 1950*a*, 1952*c*)
longicornis sceletosorae Koch, 1952*c*
machadoi Koch, 1952*c*
moufleti Haag, 1875*a* (Koch, 1941, 1950*a*, 1952*c*)
oasis Koch, 1952*c*
quadricollis Fairmaire, 1902 (Koch, 1941, 1943, 1950*a*, 1952*c*)
speluncarius Koch, 1952*c*
speluncarius mocamedinus Koch, 1952*c*
striatulus Koch, 1941 (Koch, 1950*a*, 1952*c*)
subcostatus Koch, 1941 (Koch, 1950*a*, 1952*c*)
tagen esthoides Koch, 1941 (Koch, 1950*a*, 1952*c*)
- Rozomia* Fairmaire, 1888 (Gebien, 1920; Koch, 1944*a*, 1952*c*)
halli Koch, 1952*c*
inframotata Koch, 1952*c*
- SCAURINI Solier, 1836 (Reitter, 1914; Gebien, 1937; Koch, 1958)
- SCLERINA Koch, 1956
- SEPIDIINA Koch, 1955*a* (Koch, 1958)
- Somaticus* Hope, 1840 (Koch, 1955*a*)
welwitschi Koch, 1955*a* (Koch, 1958)
- Stenethmus* Gebien, 1937 (Koch, 1952*d*, 1955*a*)
- Stenocara* Solier, 1835 (Haag, 1875*b*; Reitter, 1916*a*; Gebien, 1920)
bethanica Koch, 1951*a*
brunnipes Haag, 1877 (Peringuey, 1904; Gebien, 1920)

- brunnipes pluricostata* Koch, 1952c
depressa Haag, 1875b (Gebien, 1920)
depressa dissoluta Koch, 1952c.
desertica Koch, 1952c
dilaticornis Koch, 1950a (Koch, 1952c)
eburnea Pascoe, 1866 (Haag, 1875b; Gebien, 1920; Koch, 1958)
inaffectata Gebien, 1920 (Koch, 1950a)
machadoi Koch, 1950a
nervosa Haag, 1879 (Koch, 1952c)
phalangium Gebien, 1920 (Koch, 1950a)
phalangium rufofemorata Koch, 1950a (Ferreira, 1951, 1953a)
velox Peringuey, 1886 (Koch, 1950a)
Stenodesia Reitter, 1916a (Gebien, 1937; Koch, 1952c)
marshalli Koch, 1952c
 STENOLAMINA Koch, 1956
Stenolamus Gebien, 1920 (Koch, 1953d, f, 1955b)
brincki Koch, 1953d (Koch, 1953f, 1955b)
deserticus Koch, 1953f (Koch, 1955b)
filum Koch, 1953f (Koch, 1955b)
machadoi Koch, 1953f (Koch, 1955b)
malacodermus Koch, 1955b
 STENOSINI Lacordaire, 1859 (Koch, 1940, 1943)
Stips Koch, 1950b (Koch, 1952a; Westwood, 1837; Haag, 1875c; Gebien, 1920)
cassidoides Gebien, 1920 (Koch, 1952a)
dorsocostata Fairmaire, 1902 (Gebien, 1920; Koch, 1952a)
gebieni Hesse, 1935 (Koch, 1952a)
stali Haag, 1875c (Koch, 1952a)
Stipsostoma Koch, 1952a (Brown, 1958)
sculpta Gebien, 1920 (Koch, 1952a; Brown, 1958)
 STIZOPINA Koch, 1956 (Gebien, 1938)
Stizopus Erichson, 1843 (Mulsant & Rey, 1859; Gebien, 1938; Koch, 1956)
laticollis Erichson, 1843 (Mulsant & Rey, 1859)
Storthocnemis Karsch, 1881 (Gridelli, 1933; Koch, 1937)
 STRONGYLIINI Lacordaire, 1859 (Gebien, 1942-44)
Symphochora Koch, 1952a.
Synhimba Koch, 1952d
cordiforme Haag, 1871 (Koch, 1952d)
Syntyphlus Koch, 1953h (Koch, 1956)
subterraneus Koch, 1953h

Tarsocnodes Gebien, 1920 (Koch, 1952d)
Tarsosis Gebien, 1920 (Koch, 1958)
damarensis Peringuey, 1886 (Gebien, 1920, 1938; Koch, 1952c, 1958)
 TENTYRIINA Koch, 1955a (Solier, 1835; Gebien, 1937)
 TENTYRIINI Koch, 1955a (Koch, 1950a)
Thorictophasis Koch, 1950c
Trachyscelis Latreille, 1809 (Gebien, 1938-42; Koch, 1953g, 1960a)

 VANSONIINI Koch, 1955a
Vansonium Koch, 1950a
bushmanicum Koch, 1950a (Koch, 1955a)
Vernayella Koch, 1958
ephialtes Koch, 1958
noctivaga Koch, 1958

Zambesmia Koch, 1944-48
 ZOPHOSINA Koch, 1958
 ZOPHOSINI Solier, 1834 (Deyrolle, 1867; Chatanay, 1916, 1921; Gebien, 1920;
 Koch, 1958)

- Zophosis* Latreille, 1802 (Solier, 1834; Deyrolle, 1867; Reitter, 1916*b*; Chatanay, 1916; Gebien, 1920; Chatanay, 1921; Gebien, 1937; Koch, 1958)
angolensis Erichson, 1843 (Deyrolle, 1867; Chatanay, 1921; Koch, 1958)
bebeana Koch, 1958
braini Koch, 1958
damarina Peringuey, 1908 (Gebien, 1920; Chatanay, 1921; Koch, 1958)
dorsata Peringuey, 1892 (Chatanay, 1921)
elongata Deyrolle, 1867 (Chatanay, 1921; Koch, 1958)
greeni Koch, 1958
himba Koch, 1958
kunenensis Koch, 1958
mniszewski Deyrolle, 1867 (Chatanay, 1921)
mocamedina Koch, 1958
namibensis Peringuey, 1908 (Chatanay, 1921)
pubescens Chatanay, 1914 (Chatanay, 1921; Koch, 1958)
saltans Koch, 1958
sexcostata Deyrolle, 1867 (Chatanay, 1921; Koch, 1958)
solivaga Koch, 1958
striatimargo Koch, 1958
trigo Koch, 1958
viridilimbata Chobaut, 1899 (Reitter, 1916*b*; Koch, 1937)

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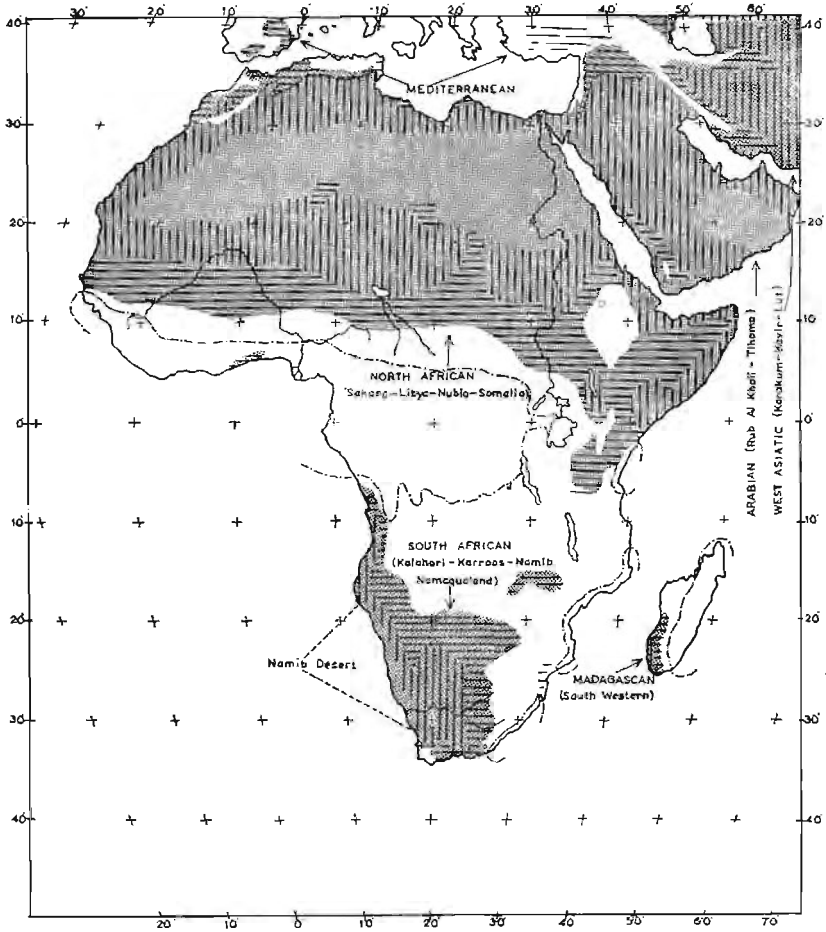
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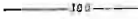
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Map 1. Distribution of arid homoclimates in Africa. (After Meigs; Monod, 1957.)

-  Semi-arid
-  Arid
-  Extremely arid (in the South African arid zone: Namib Desert; in the North African arid zone: Sahara Desert; in the Arabian arid zone: Rub Al Khali Desert)
-  Limits of Guinean forest regions (Congo-Indic forest)

Maps 3-7. Topography of the Namib Desert and hinterland. (Maps 4-6, after the South-West African 1:800,000 map, 1955 edition [Surveyor General, Windhoek]. Map 3, after the same and the South African 1:500,000 map [Trigonometrical Survey Office, Pretoria]. Map 7, after the following maps: Beetz, W. (1938), *Klimaschwankungen und Krustenbewegungen in Africa südlich des Äquators von der Kreidezeit bis zum Diluvium* (*Geogr. Ges. Hannover, Sonderveröffentlichung*, 3); Gossweiler, J. & Mendonca, F. A. (1939), *Carta Fitogeográfica 1:200,000* [*Gov. Geral de Angola*]; Ministerio das Colonias (1935), *Carta de Angola 1:1,500,000*.)

 Contours. In South-West Africa: 300, 600 and 900 m contours (maps 3-6); in the Union of South Africa: 2000-foot contour (map 3); in Angola: 2000-foot contour (map 3) north of the Cunene River; 400 and 1000 m contours (map 7).



Highlands. Delimited by the 1200 m contour in South-West Africa and the Union of South Africa (maps 3-6), by the 1000 m contour in Angola (map 7).



Rivers



Pans



Faunistical border lines of the Namib



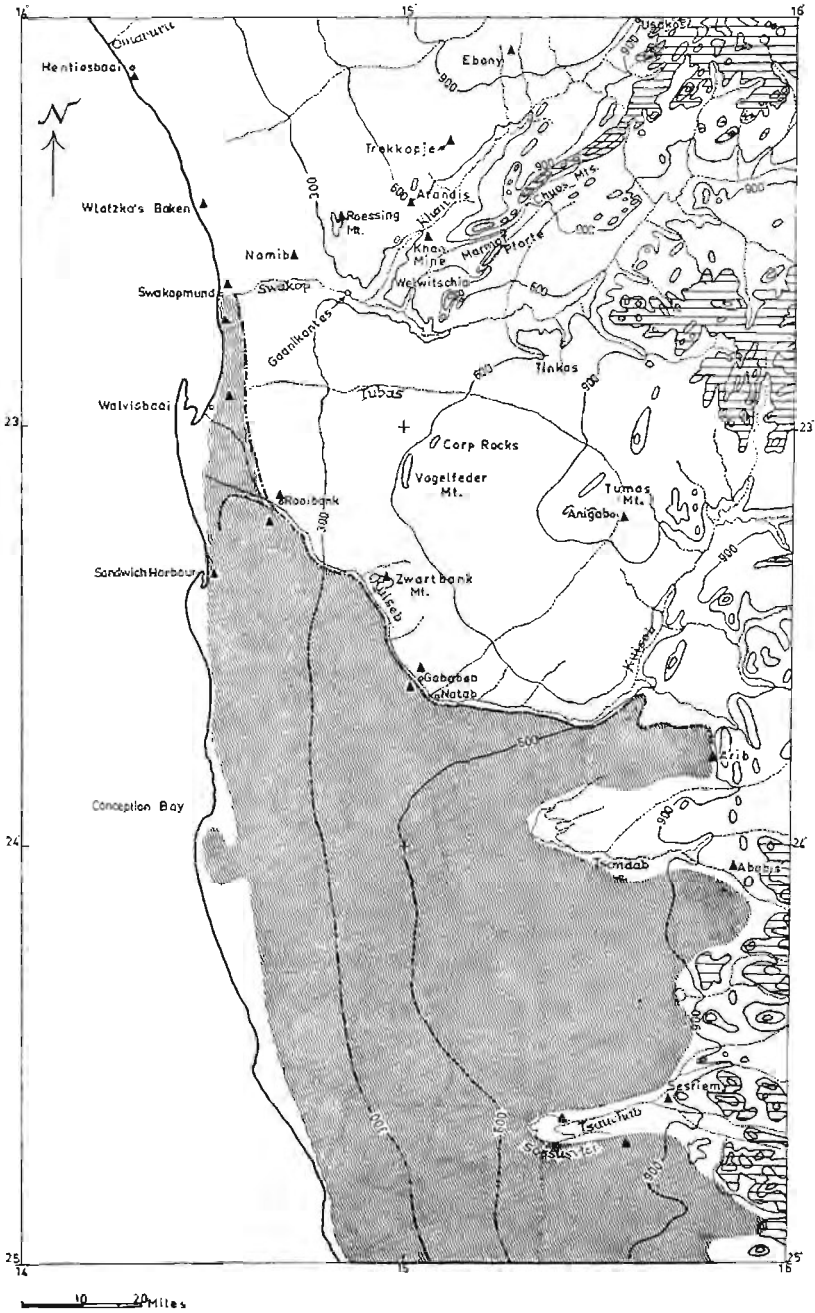
Collecting stations for Tenebrionidae



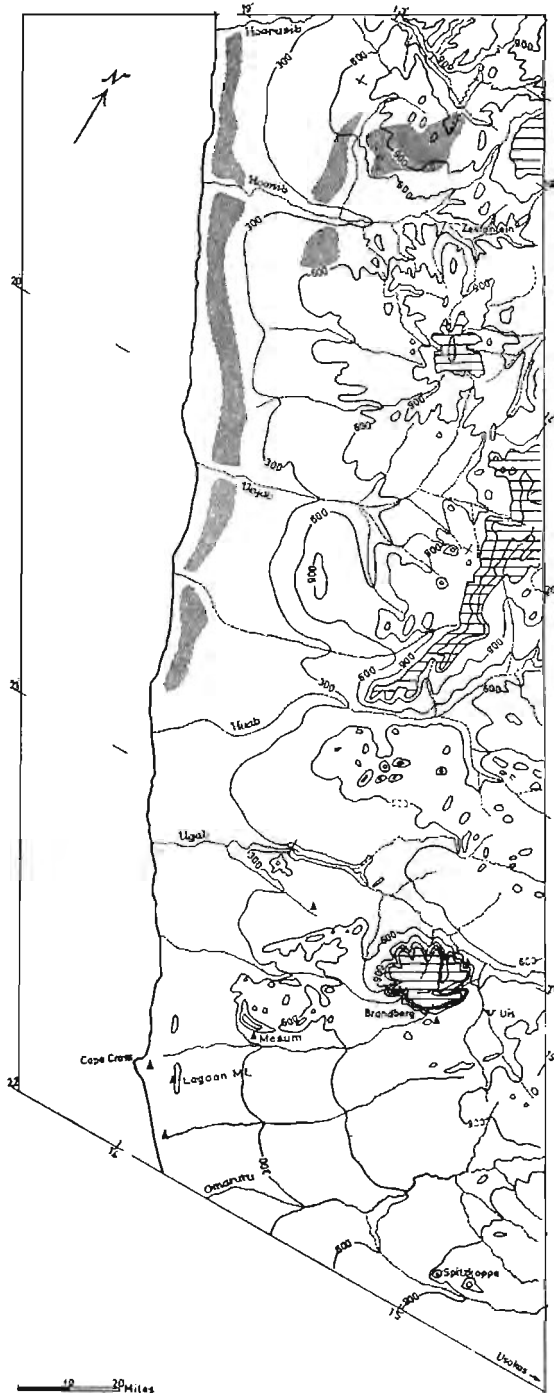
Systems of barchan dunes in the True Namib



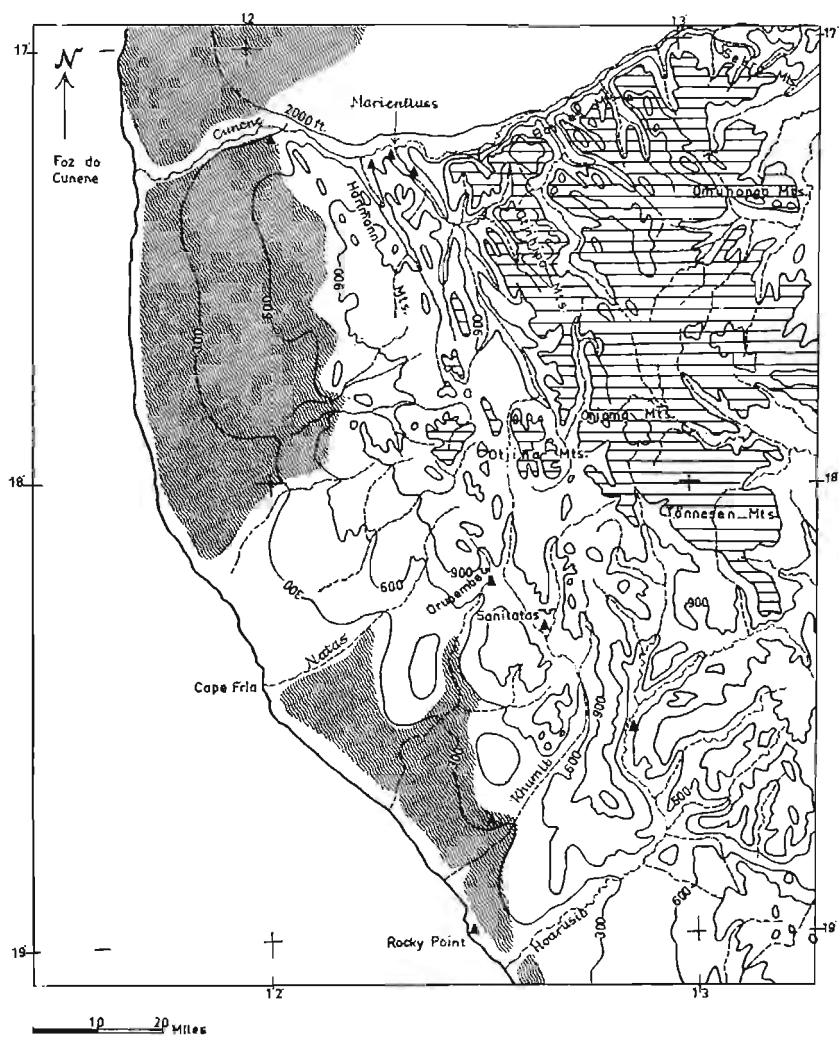
Blown sand and small dunes of the Transitional Namib



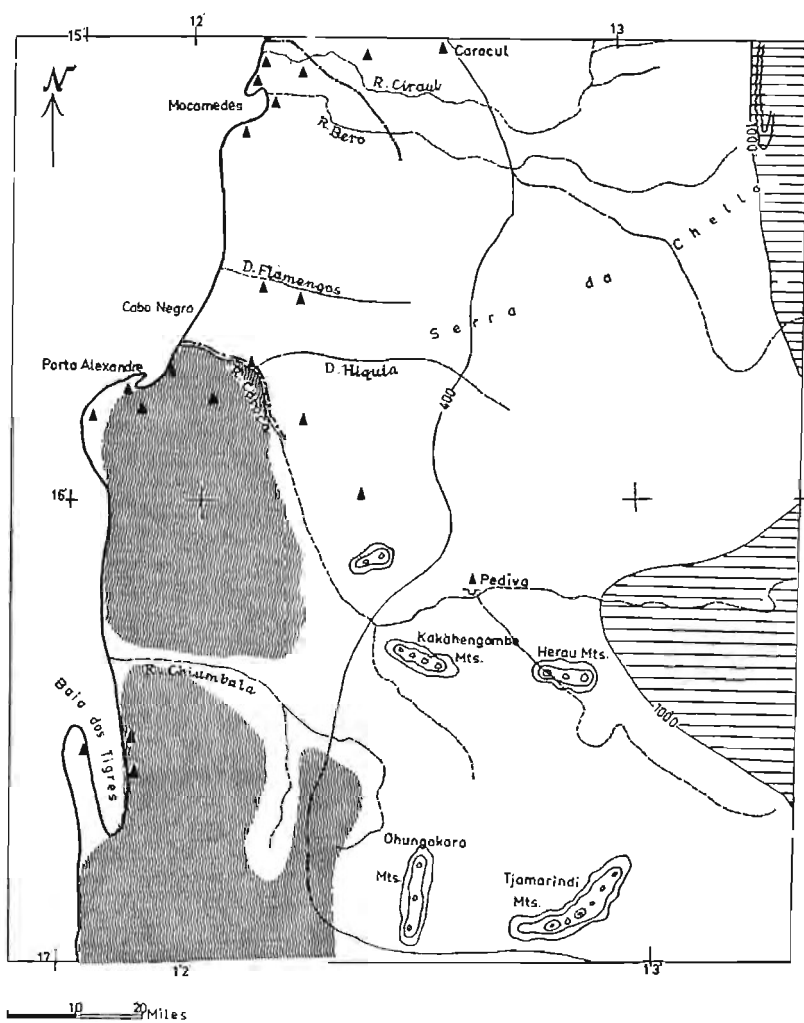
Map 4. Northern part of the Southern Namib and southern part of the Northern Namib.



Map 5. Central part 1 (south) of the Northern Namib.



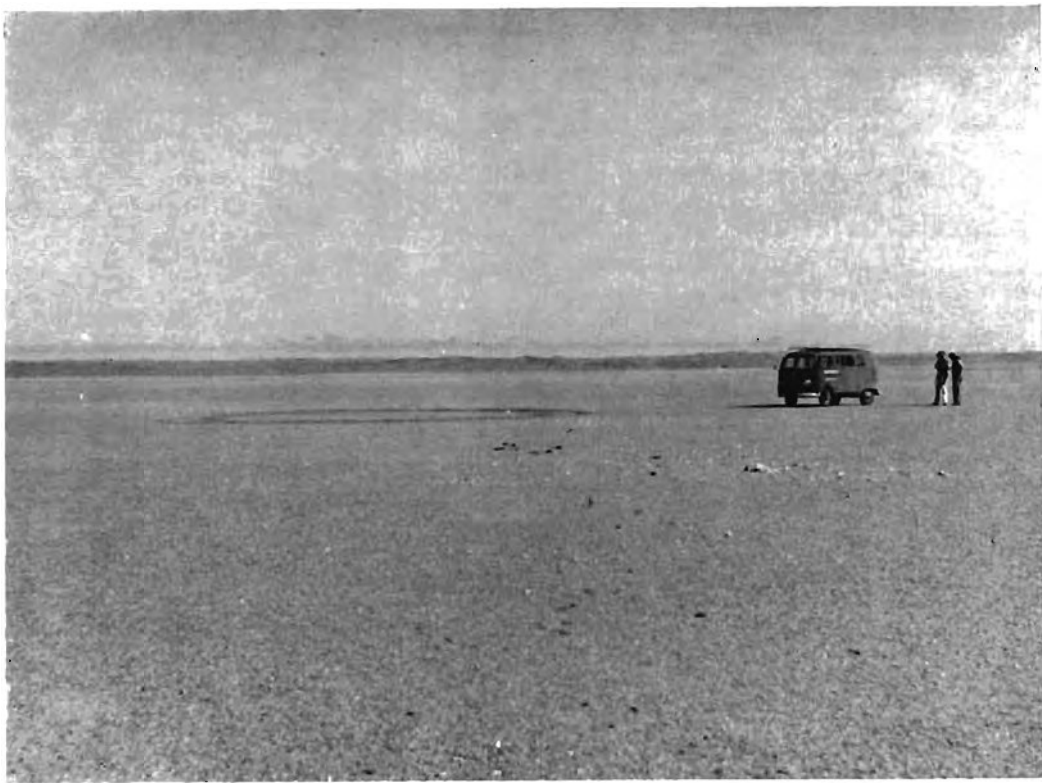
Map 6. Central part 2 (north) of the Northern Namib.



Map 7. Northern part of the Northern Namib.



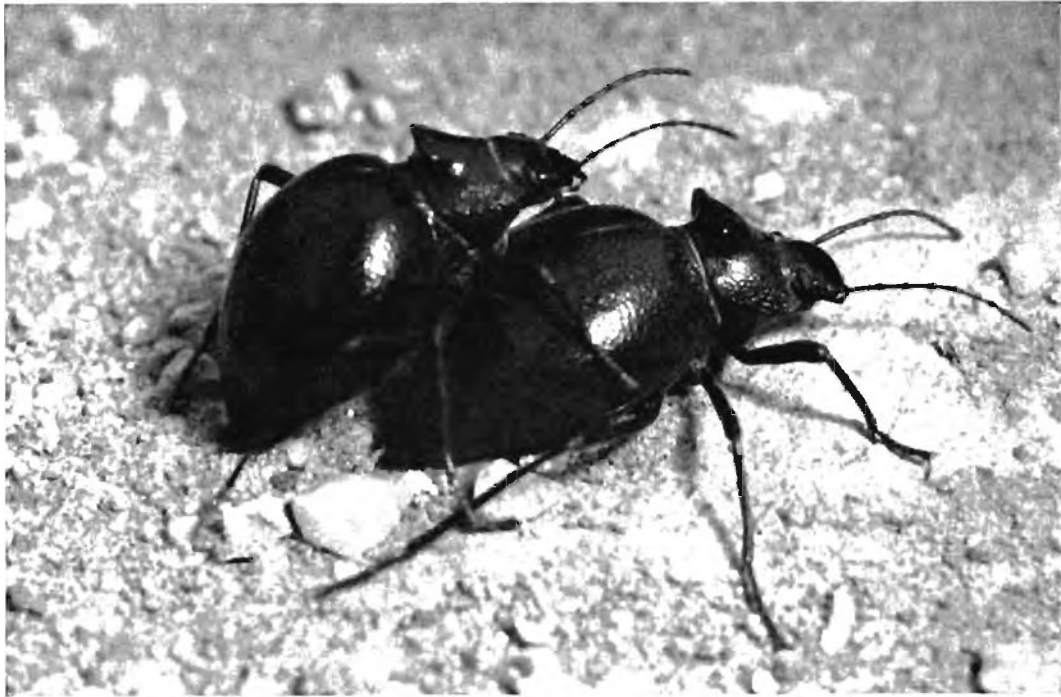
Biotope of the vegetationless dunes. Marginal dunes of the Southern Namib system, at the southern bank of the Kuiseb River, close to Gobabeb. In the background the densely wooded Kuiseb-bed which sharply separates the dunes from the vegetationless gravel plains (background). At right the sharp and 'smoking' crest of a dune. (Photo C. K. Brain.)



Biotope of the vegetationless gravel plains. Perfectly flat plain of the southernmost portion of the Northern Namib, north-west of Gobabeb. On the horizon is the margin of the dune system of the Southern Namib, above a layer of sea mist. The Kuiseb-bed, which runs along the margin of the dunes, is not shown, as it is situated in a depression. (Photo C. K. Brain.)



Biotope of an exotic, densely wooded Namib river-bed. Forest of Acacia giraffa and albida in the Kuiseb-bed, close to Gobabeb. This forest-gallery separates very sharply the vegetationless dunes in the south from the practically vegetationless gravel plains in the north. (Photo C. K. Brain.)

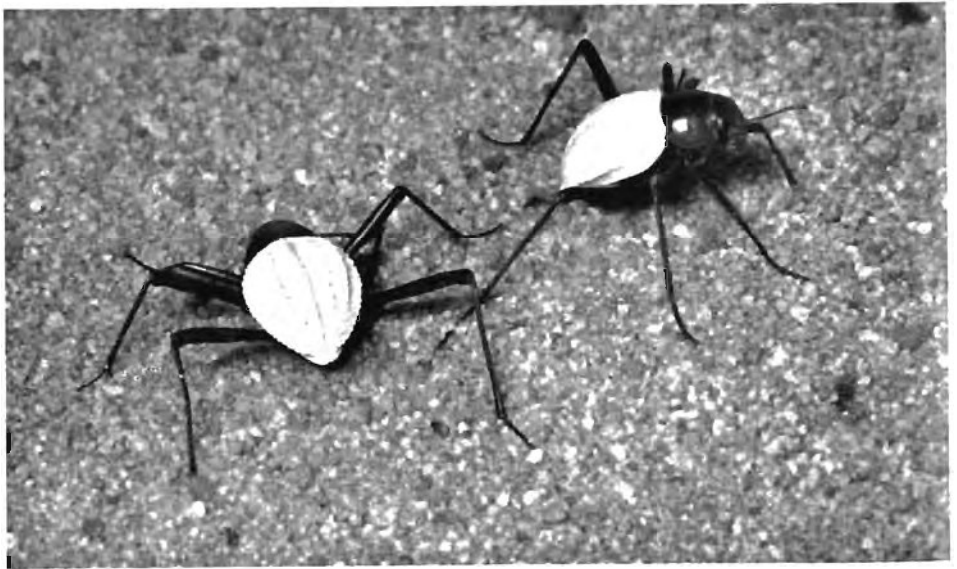


Psammodes diabolica Koch, f.t. A very peculiar, endemic species of the northernmost part of the *Transitional Namib* (lower Orange River area); nocturnal and psammo-petrophilous. (Transv. Mus. Insectarium. Photo C. K. Brain.) $\times 2$.



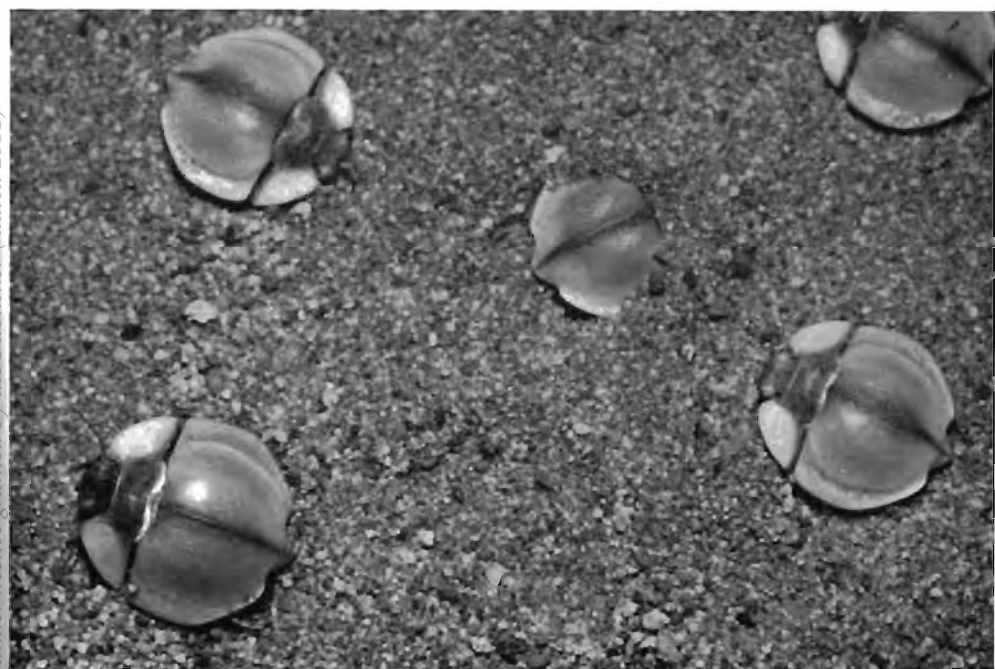
ABOVE. *Onymacris longicaularis* Haag, f.t., an ultra-psammophilous and highly heliotactic runner of the vegetationless dunes of the *Southern Namib*. Female specimen burrowing. (Transv. Mus. Insectarium. Photo L. Schulze.) $\times 1.8$.

BELOW. *Onymacris rugatipennis* Haag, an errant plant-follower of the dunes of the Southern Namib; heliophilous. Male specimen in pursuit of the female. (Transv. Mus. Insectarium. Photo L. Schulze.) $\times 1.8$.



ABOVE. *Renatiella (Spongesmia) scrobipennis* (Haag), a slow-moving, diurnal but umbriphilous species of the Kalahari and the Highlands of South-West Africa, extending westwards into the Namib on all hard soils. (Transv. Mus. Insectarium. Photo L. Schulze.) $\times 2.6$.

BELOW. *Stenocara eburnea* Pascoe, one of the characteristic 'white' Namib Tenebrionids. A heliotactic, fast runner of the gravel plains and mountains of the southern part of the Northern Namib. (Transv. Mus. Insectarium. Photo L. Schulze.) $\times 2.6$.



ABOVE. *Physosterna globosa* (Haag), f.t. (on right) and subsp. *epiphyroides* (Peringuey) from the southern portion of the Northern Namib. Extremely convex, diurnal but umbriphilous runners populating the sand of the Kuiseb-bed forest. (Transv. Mus. Insectarium. Photo L. Schulze.) $\times 1.8$.

BELOW. *Lepidochora eberlanzi* subsp. *parva* Koch, an ultra-psammophilous and strictly nocturnal Eurychorin from the vegetationless dunes between Walvis Bay and Swakopmund. Hygrophanous, depigmented and of complanate body shape. Centre specimen burrowing. (Transv. Mus. Insectarium. Photo L. Schulze.) $\times 2.2$.