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THE TENEBRIONID BEETLES OF SOUTH WEST AFRICA

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South West Africa appears on the map as a very tidy entity; bounded on the west by the Atlantic Ocean, and on the south by the Orange River, while the eastern and northern boundary lines—with the exception of the Kunene River in the north-west—were apparently drawn neatly across the landmass with pencil and ruler. Nature, however, does not recognize artificial limitations, and South West Africa is part—and certainly the driest part—of the arid system comprising the Kalahari, the Karroo, Namaqualand and the Namib. If we exclude the Cape Region this vast area roughly coincides with the western half of southern Africa.

Precipitation and geographical structure together determine the composition of the fauna and flora of South West Africa. The quality of rainy seasons and the average rainfall decrease from north-east to south-west, falling from 760 to 30 mm. or even to nil in the Namib desert. The rainy season (where such exists) occurs in summer, except for a few restricted areas along the lower reaches of the Orange River, which receive their rain in winter.

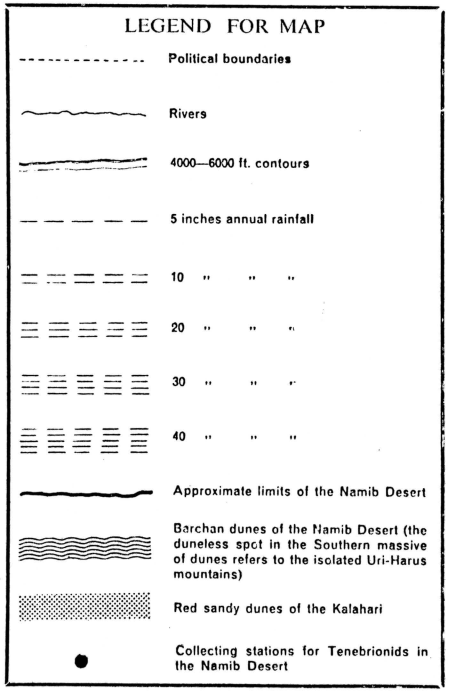
Geographically South West Africa falls naturally into three longitudinal sections, themselves part of the physiographic regions of the South West African Highlands, the Kalahari and the Namib. The irregularly shaped eastern section is the largest; it comprises part of the Kalahari basin (which protrudes in a westerly direction in the north), the eastern plains of the Kaokoveld, Ovamboland, the Etosha and Okavango areas, the Kaukau-Kungveld and the Caprivi Strip. In the south it also includes the region of the lower Orange River, which is really a transitional area shared by the Kalahari and the Namib. In the middle section we find the Otavi highlands, the Kaokoveld mountains, Damaraland and Great Namaqualand, which, for the greater part, belong to the South West African highlands. The third, or western section, comprises the Namib Desert coastal belt, which defies political boundaries by extending across the Kunene River to the north, and across the Orange River to the south.

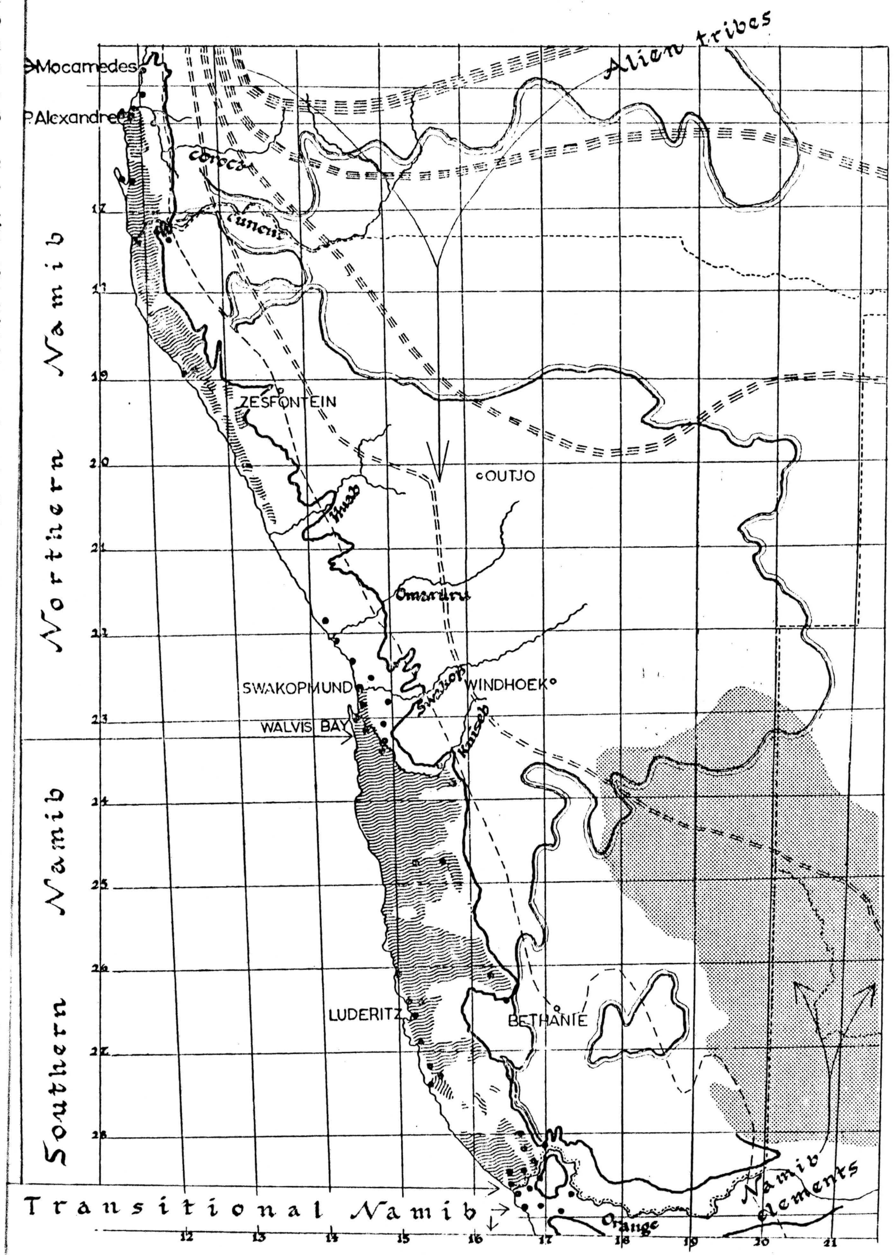
Wide range of latitude, variable rainfall and the consequent aridity of the land, together with extremes of temperature, have resulted in a highly specialized fauna and flora, adapted to survival in conditions of extreme heat and dryness—everywhere in South West Africa the bare soil shows between plants. As one would expect, vegetation changes gradually, from subtropical savannah in the north-east to pure desert without vegetation in the south-west. Mixed savannah and mopane bush are found in the northern Kalahari section which is subtropical; the rest of the Kalahari and the highlands are thornveld areas. Towards the west, the vegetation gradually assumes a desertic character, decreasing in quality till we find scrub and shrub types on the sloping marginal areas of the highlands, together with sub-desertic grass. This gives place to desert grass which fades away entirely on the sand dunes and gravel plains of the Namib.

To sum up briefly, the country from the point of view of vegetation may be divided by a diagonal line from Benguela in the north-west to Port Elizabeth in the south-east, forming an eastern Kalahari portion which has affinities with the Sudanese-Angolan phytogeographic Region (cf. MONOD, 1957), and a western, very endemic Karroo-Namib portion. Research on the Tenebrionid beetles found in these two areas confirms the correctness of this definition.

A few notes on the Tenebrionidae in general are necessary before discussing the Tenebrionid beetles of South West Africa and their adaptation to local conditions. These insects form part of the Coleoptera (beetles), the largest order existing in the animal kingdom. The size of this order (which dates back to Permian times) is astounding. So far, about 400,000 species have been described, equal to about one-third of all known animals. The Tenebrionids form the largest family of the heteromerous section of Polyphaga, and constitute about 5 per cent of the Coleoptera. They are rarely predators, but live peacefully, feeding either on dead or decaying animal or vegetable matter, or upon plants. They are usually black in colour and are remarkable for a very great variation in body-form. Another very striking feature is their amazing power of adaptation to every type of condition; probably the variation in the form of body is closely linked with this feature. During their long evolutionary past, these beetles penetrated into each ecological niche as it became available, and it is likely that bodily form became adapted to each circumstance as it arose and developed.

Leaving aside systematic division, Tenebrionids can be divided into two sections; the winged and the wingless species, two-fifths belonging to the former and three-fifths to the latter. The winged species are usually members of primitive tribes found in pan-tropical forest, or of various groups of very wide to world-wide distribution. Of the wingless species, a few groups live in wood and humus found in forests, but nearly all of them are very localized ground-beetles, amazingly well adapted to hot, dry conditions, viz. xerophilous insects. Owing to their power of adaptation and their tendency to become highly specialized, these beetles have established themselves in all the desert areas of the world, and have become so resistant to extremes of heat and aridity that they can tolerate conditions that are fatal to most other forms of life.





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South West Africa being mainly hot and arid, one would expect to find such wingless, ground-dwelling species there, and, in fact, they form almost 95 per cent of the Tenebrionid population. They are dependent on the soil in and on which they live, but soil and vegetation vary considerably, sometimes within a small area; they have therefore developed a high degree of specialization in conformity with the geographic, climatological and botanic conditions of each area. On account of their amazing adaptability to and tolerance of heat and dryness, the relative number of species and even of individuals in the fauna of South West Africa increases progressively as conditions become more and more adverse to other forms of life, until in the extremely arid parts of the Namib which are devoid of vegetation these beetles play a dominant and basic role.

Considering South West Africa as an entity, there are certain Tenebrionids which are widely distributed over the whole of the area. These are the xerophilous tribes Molurini, Cryptochilini, Adesmiini, Asidini, Eurychorini, Zophosini, Tentyriini, Platynotini, Drosochrini, Scaurini, Caenocrypticini, as well as the Stizopina and Stenolamina of Opatrini. They are the basic elements of the Tenebrionid fauna of South West Africa. Their inherited power of adaptation to excessive heat and drought is proved by several facts: they are the only ancestral groups by which the extremely xerophilous fauna of the Namib has been formed; the number of species decreases considerably towards the less arid area of the northern Kalahari; with the exception of the endemic Caenocrypticini and the two last mentioned South African tribes of Opatrini, they are all present also in the dry parts of distant North Africa, but the Tentyriini, Adesmiini, Cryptochilini and Scaurini are not found in the near-by eastern section of South Africa which is comparatively humid.

Immigrant tribes, well represented in the eastern section of southern Africa, have penetrated into the less dry parts of South West Africa. From the north, east and south-east came Stenosini, Litoborini, Anomalipina and Platynotina of Platynotini, Micrantereina and Oncosomina of Drosochrini, Sepidiina of Molurini, and many genera of tropical origin such as *Ethmus*, *Macropoda* and *Zambesmia* of *Adesmia*, *Rozonia* etc. None of these is to be found in the more arid areas, however; in no case have they extended farther southwards than the approximate latitude of the southern slopes and escarpments of the Damaraland highlands, or into the Namib. To a small extent infiltration by Cape and Namaqualand tribes (e.g. Oncotini, Pythiopini, etc.) also took place in the southern part of Great Namaqualand.

From the point of view of the Tenebrionid fauna, it is extremely interesting to compare and contrast the Namib with the rest of South West Africa. As we have seen, only the basic South West African tribes are to be found in the Namib, in which, furthermore, there has been an amazing development, both in quality and quantity, of specific, generic, subtribal and even tribal endemism. Beyond the confines of the Namib, we find a proliferation of species—which is due also to the occurrence of the additional immigrant tribes and genera—but the endemism of genera is poor, and there is none of tribal or even subtribal rank. In the central highlands, however, there seems to be a certain indigenous structure of Tenebrionid fauna. Apart from the infiltration of alien tribes, this area has a close relationship with the Kalahari, but is particularly remarkable for the richness of its stone-loving and rock-dwelling Tenebrionid fauna.

To this fauna belong various genera such as *Rhammatodes*, *Asphaltesthes*, *Rozonia* etc., which seem to be endemic to the South West African Highland Region. They have infiltrated along river beds into the Namib as well as the Kalahari. The extremely stone-loving (petrophilous) genus *Afrinus* from the Karroo has even reached the heights of the isolated Brandberg. It is noteworthy that many sand-loving (psammophilous) Kalahari Tenebrionids occur in the highlands without having changed generically, sometimes not even specifically.

The Namib desert is not a homogeneous area, but consists of litoral sands, sandy dunes, stony and sandy plains and dry river beds (where water may be found at varying depths below the surface). It may also be divided further into the True Namib, north of the Orange River, and the Transitional Namib of Little Namaqualand in the south. Tribes or genera that occur in both areas may be regarded as the basic elements of the Namib Tenebrionids; these are the Vansonini, the genus *Onymacris* of Adesmiini, *Pachynotelus*, and chains of specialized genera belonging to the Zophosini, Caenocrypticini, and the *Stips* group of Eurychorini.

The True Namib comprises the main section of the coastal desert, from the Orange River almost as far north as Mocamedes in Angola.[1] An outstanding feature is the area of ever-shifting "barchan" dunes which give a lunar aspect to the landscape. This dune system is very sharply defined by the Orange River in the south and the ancient, dry Coroca River of Angola in the north; elsewhere in Africa such dunes are found only in the Sahara and eastern Somalia. Although frequently interrupted by gravelly, hardsoil surfaces devoid of vegetation, or by sandy-grass valleys, the typical feature of this terrain is the barren sand, waterless and usually without vegetation. Nevertheless the Tenebrionid fauna is amazingly rich.

In the True Namib occurs an almost entirely endemic psammophilous Tenebrionid fauna which in the barchan dunes becomes typically insular. The unique stag-beetle-like Calognathini and the blind to small-eyed Dactylocalcarina of Zophosini, as well as the highly specialized genera *Lepidochora*, *Vernayella*, *Onychosis*, *Cardiosis*, *Tarsosis*, *Entinopoda*, *Namibomodes* and many others, form the basic elements; they occur over the whole region and are strictly endemic to it, in exactly the same way as is e.g. the characteristic reptile *Palmatogecko*. They include the extraordinary number of about 35 endemic genera and several hundred endemic species so far discovered.[2] As regards species inhabiting hardsoil surfaces the exact limits of the True Namib fauna have not yet been defined in the east, but are sharply defined in the north and south. The dune species, however, appear to be wholly confined to their dunes; probably they could not exist elsewhere.

[1] This statement is well documentated from the point of view of the fauna, but does not agree with the physiographic extension and subdivision of the Namib (cf. WELLINGTON, 1955).

[2] In comparison with these numbers, the Tenebrionid fauna of North African and Saharan territories appears to be very poor. E.g. in Tripolitania, the Fezzanese desert included, occur 202 species and subspecies of Tenebrionids, of which 63 species and 3 genera are endemic (KOCH, 1937); from Morocco which participates in the Mediterranean, Atlasic-Baetic, Atlantic and Saharan faunae, 711 species and subspecies (viz. one-seventh of all Moroccan Coleoptera) are known, but only about 100 forms occur in the Sahara of southern Morocco (cf. KOCHER, 1958).

The True Namib is sharply divided into Northern and Southern Namib, and this division is reflected in the distribution of the Tenebrionids. Between Swakopmund and the Huab River there is a wide area of country devoid of barchan dunes; one would expect this to be the dividing line, but the distribution of the Tenebrionids does not confirm this. Since the "white" (see below) Tenebrionids, endemic to the Northern Namib, also occur in the dunes south of Walvis Bay, the former bed of the Kuiseb River seems to be a more acceptable line of demarcation until more data is available.

The Southern Namib is the sandier of the two sections. Between the Kuiseb River and the Bogenfels area there is a vast region of barchan dunes ranging in altitude from sea-level to the 4,000 ft. contours, sometimes towering up above the plain to heights of about 1,000 ft. There are also, in this "Unübersehbares Dünenmeer" of the former German cartographers, isolated mountains and outcrops of rock "drowning in sand", and salt areas formed by the oozing away of rivers coming down from the highlands. The Tenebrionid fauna differs from that of the Northern Namib in several respects. There are no "white" species, but the composition of genera and species appears to be notably richer. To mention only a few of the many endemic genera of this area we find the blind *Dactylocalcar* and *Syntyphlus*, the speedy *Cerosis* of the grit valleys between dunes, and the *Fossiolochile*, *Arthrochora*, *Archinamibia*, *Psammogaster*, *Periloma* of the sandy dunes.

Here evolved also the *Lepidochora* and *Vernayella*, which probably are the most characteristic of all nocturnal Namib dwellers. They show remarkably great proliferation of species, not only latitudinally and longitudinally, but also vertically in respect to the height of the dunes. The species from the yellow-brown sublitoral dunes of Walvis Bay differ from the species found in the continental reddish sand found in the same area; Kuiseb area species differ from those occurring in the Sossus Vlei or in the southern Bogenfels area. Still more remarkable was the discovery of four different species on one dune in the Kuiseb-knee area; one species was always found near the top of the dune, two in the sand of the lee-side, and the fourth on the harder grit-like sand at the bottom of the very same dune—a truly remarkable instance of specialization and adaptation to the micro-ecologic diversity of biotope.

The crest of high dunes is composed of continuously shifting ("smoking") sand which naturally is completely devoid of vegetation, yet harbours an abundant population of "under-sand" Tenebrionids—a phenomenon which has not been found in any other desert in the world. During the day *Tarsosis*, *Cardiosis* and certain *Onymacris* were recorded, and *Lepidochora*, *Vernayella* etc. at night.

In the Northern Namib Tenebrionids follow roughly the same distribution pattern as *Welwitschia*, beginning at the Kuiseb River and ending suddenly at Moçamedes, beyond which species of the South West African Highland type take the place of the Namib species. This northern section of the True Namib contains the specialized, endemic genera *Calosis*, *Anisosis*, *Ophthalmosis*, *Protodactylus*, *Microderopsis*, *Namibismus* etc., and the very remarkable "white" Tenebrionids that belie their name by the pale to snowy-white coloration of their elytra. Some other Tenebrionids have whitish scales, hairs etc., but these "white" species are the

only Coleoptera yet discovered with a white cuticle.[1] They occur over the whole of the Northern Namib on both hard ground and on dune sand, and belong to the phylogenetically distant tribes and genera *Onymacris*, *Stenocara* and *Calosis*. At Porto Alexandre three different species of "white" *Onymacris* were found on the same dune together with a "white" *Calosis*. It may therefore be inferred that the white coloration is a case of extreme and sympatric convergence due to factors (of terrain etc.) which are to be found only in the Northern Namib.

The sandy Transitional or Pro-Namib (cf. KOCH, 1952) 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 into the red sands of the south-western Kalahari. None of the highly specialized genera of the True Namib has been found here, with the exception of *Vansonium* and the southernmost species of *Onymacris*. The fauna is quite different in composition from that of the True Namib, being a complex mixture of Namaqualand, Namib and Kalahari elements, although belonging in many cases to the same phylogenetic lines such as Cryptochilini, Zophosini and the *Stips* group of Eurychorini. Generic and specific endemism is very marked. There has been, however, a certain amount of interchange of Kalahari and Namib elements in the lower Orange River area, and also in Great Namaqualand. In the latter area it seems likely that "bridges" of wind-blown sand enabled psammophilous Namib elements to cross to the adjacent Kalahari sand dunes. Among others, *Onymacris multistriata*, *Stips*, *Cimicichora* and *Heliophosis* may be mentioned as occurring there.

The ecology of the dune Tenebrionids is extremely interesting, since a very rich and varied fauna inhabits a large area which, at first sight, appears to be so unfavourable, even hostile, to most forms of life. How can beetles even exist, let alone proliferate, in barren sand with no vegetation and the minimum of rainfall, rapid and extreme fluctuations of temperature and intense solar radiation? After careful study of the area and its beetle population, the answer was found in wind and the inherent adaptability of these Tenebrionids.

Due to the Benguela current, the coastal Namib desert is an area of continual winds, blowing alternately from the south-west and east. On the existence of these winds depends all the Tenebrionid life of the dunes, and in particular that of the many extremely errant species of the vegetationless part which are no longer connected with vegetation, but just dwell anywhere in the sea of sand.

The cool south-west wind blows in from the sea and is laden with moisture which forms mist and dew, especially at night, when it raises the relative air moisture to saturation point. The easterly land wind carries organic matter which is dropped on the dunes. Thus the one supplies the water, the other the food.[2] In this respect the biotope of the Namib dunes may be compared with the deep sea of the ocean, for the primary life of both depends on the importation of food from outside.

[1] KUEHNELT, 1957, has found that the white coloration is not due to a pigment, but is caused by the unorientated reflection of light by the numerous microscopical bubbles of air which are enclosed in the exocuticula. Hence the white colour comes about in the same way as in snow, white flowers or white scales of butterflies.

[2] The very great importance of wind for the supply of food in deserts was emphasized for the first time by G. SCORTECCI, 1940, in his magnificent opus on the biology of the Sahara desert.

Relatively few diurnal species exist in such a harsh environment (of *Onymacris*, *Stenocara*, *Calognathus*, *Pachynotelus*, all Zophosina and others), but they often appear gregariously in great individual numbers.[1] The different species react variously to heat, radiation and evaporation, from which they are protected by the development of additional characters of body formation. Among the most notable of these adaptations are a marked thickening of the integument, connate sutures, swollen elytra combined with a larger space beneath the elytra, and usually very elongate legs which make rapid movement possible during the short intervals of direct exposure, and also carry the body at a high level above the heated surface of the sand. Of course the degree of light-loving (photophilous) disposition is also very variable and there can be observed all transitional phases of Tenebrionids which prefer twilight (crepuscular species), or shade (umbriphilous species), or even need the direct sunlight as stimulus (heliotactic species). The velocity of the heliotactic species of these diurnal, dune Tenebrionids is simply amazing, and it seems that the modified spur-like armatures on the legs allow for a better grip on the moving sand, while the frequently observed asymmetry of the spurs of claws may facilitate locomotion on the "quasi-fluid oblique planes". Many of these runners are also rapid diggers, to which activities we can add jumping and ball-like rolling in the Zophosina, and in *Cardiosis* even peculiar semi-volant movements by making use of the current of the wind. The formation "sand-shoes" (viz. compressed feet which are provided with brushes of bristles with a broom-like action) occurs in both the diurnal and nocturnal species.

We were unable, however, to confirm any theories on mimetic or pale coloration of desert Tenebrionids in connection with protection from enemies or better reflexion of heat respectively, for the "white" Tenebrionids of the Northern Namib live under exactly the same biotic conditions as do the black Tenebrionids of the Southern Namib, moreover the "white" Tenebrionids cannot support higher temperatures than the black ones (cf. BOLWIG, 1957), while the often soil-coloured (homochromous) secretory layer on the body surface in many *Zophosis* may correctly be interpreted as a means of protection from evaporation rather than as cryptic mimicry.

Nocturnal species are considerably more numerous, and include all *Lepidochora*, *Vernayella*, *Caenocrypticus*, *Stips*, *Arthrochora*, *Archinamibia*, *Psammogaster*, *Periloma*, *Brinckia*, *Namibomodes*, *Uniungulum*, *Vansonium* and many others. They are exposed to a much lesser degree of evaporation, and to no direct heat and solar radiation, the influence of which—in their dormant state during the day—they can regulate deliberately by changing position in the depth of the sand. In accordance with this different climatological environment their morphological structures are opposed in many ways to those of the diurnal species. Very often the elytra are loosely jointed to the body and no longer close hermetically the respiratory space beneath elytra, the pigmentation of the cuticle becomes reduced or vanishes altogether (the body therefore assuming a pale yellowish to testaceous colour), in many cases the elytra assume a semi-transparent (diaphanous) appearance (e.g. in *Uniungulum*, some *Pterostichula*, *Caenocrypticus*, etc.), in others (e.g. *Lepidochora*) the elytra change from opaque during the day or dry nights to diaphanous during moist nights (hygrophaneity), and also the very frequently met occurrence of surface secretion during the moist night or squamiform vestiture may be connected with the hygroscopic property of these sculptural structures. In some genera (e.g. *Namibomodes*, *Brinckia*) the cuticle of the whole body produces a secretion of an adhesive nature to which grains of sand stick, forming thus a thick layer of probably increased hygroscopic property; *Stips stali*, again, stores the wet sand on dish-like sculptural cavities on the surface of the body. Although based on the same principles, the legs show important points of dissimilarity from the diurnal dune species. As the nocturnal species have to retire and dig themselves to considerable depths in the sand during the hot day (while the diurnal species merely hide underneath the cool and wet surface of the sand during the night), many of these nocturnal species are therefore potential diggers, exhibiting most intricate armatures on legs and, in almost all cases, protective cilia on the sides of the body. In this connection I may only mention the peculiar formation of the legs in *Lepidochora*, in which, in addition to the normal feet, supplementary webbed, sand-swimming "feet" have developed by means of the finger-like (multi-digitate) modification of the normally spur-like apical armatures of the tibia (calcaria). The asymmetry of the ungual spurs can be observed also in the nocturnal species (*Namibomodes* and *Vernayella*), but reaches, under otherwise hypertrophic conditions, the highest possible degree of atrophy in *Uniungulum*, in which the outer spur of the claws has disappeared altogether. With the exception of a few crepuscular cases in *Lepidochora* all the nocturnal species are extraordinarily photophobic to artificial light during the night; they stop moving almost at once when they become aware of light. They are moderately fast to slow in their movements, except for the *Vernayella* which we were able to observe rapidly racing on the "oblique planes" as long as they were not disturbed by light.

Also very specialized are the permanently "under-sand" species such as *Dactylocalcar* and *Syntyphlus*, as well as all the early stages of Tenebrionids (larvae and pupae). The loss of pigmentation and eyes, the hypertrophy of sense-bristles, are common to all, but, while in the adult of *Dactylocalcar* the legs are spoon-shaped, the belly is strikingly swollen (physogastric) and the sub-elytral cavity expanded, in the larvae there are additional leg-like appendages (urogomphi) on the anal sternite, and locomotory and defensive armatures on the anal tergite (pygopod).

A brief review such as this can do no more than indicate the amazing richness of the Tenebrionid fauna of the Namib and its high degree of endemism. The limited exploration so far carried out shows that the endemic tribes, genera and species far outnumber those found in other deserts of the world, and in no other desert do we find species showing such extreme specialization and adaptation. This leads to the conclusion that this richness and endemism is due to the long and undisturbed duration of the peculiar climate and conditions obtaining in the Namib. The Sahara has experienced alternating pluvial and arid periods (cf. MONOD, 1942), the Somalia and Madagascar barren dunes (which we have found to be devoid of all indigenous life) are of comparatively recent formation (cf. also AZZAROLI, 1957), but the Namib climate and

[1] In literature we very often find references to the scarcity of individual occurrence of insects in deserts. These statements need rectification and certainly do not hold good for the Tenebrionids, as we sometimes found the dunes simply swarming with *Onymacris*, *Lepidochora*, *Vernayella*. About similar observations in the Gobi desert cf. REYMOND, 1938, in the Sahara SCORTECCI, l.c.

The great frequency of mist and dew provides enough water to satisfy the metabolism of such highly adapted and xerophilous beings as the Namib Tenebrionids. We must also take into consideration the comparatively slow process of dehydration in a foggy desert in general, the hygroscopic property of the organic fragments (cf. BUXTON, 1924, 1932), and the hygroscopic nature of sand in general.[1] And sand is the sole medium of the dune Tenebrionids, in which they live either permanently, as in their blind early or even adult stages, or temporarily, as diurnal or nocturnal adults.

The wind-blown and constantly renewed supply of organic matter consists of insects, living or dead, and parts of plants. These fragments are continuously mixed with sand at the "smoking" crests of the dunes. Still more falls and accumulates on the sloping lee sides, which are also moister than the less steep windward slopes on account of the run-off concentration of all available precipitation. At some sites the organic substances concentrate on the lee side and form gradually a layer which develops finally into a rather compact substratum of dried, sub-fossilized, humus-like detritus underlying the foot of the dune.[2]

A habitat with such peculiar features could, however, only be exploited to the full by creatures in which inherent adaptability had been developed to the highest degree of specialization.[3] In the dune species, the body appears to have been transformed into a mechanism which is able to move on sand, to burrow into sand, in most cases also to move under the surface in the sand, but in particular to move on, and to burrow horizontally into, the oblique surfaces of the lee slopes of the dune. The astounding variety in morphological structures such as the complex, spur-like armatures on the legs, the protecting ciliation on the sides of the body and many others, may readily be explained by the mechanical laws of locomotion on and in the "quasi-fluid inclined planes" of the dunes. Many other peculiarities of body formation can be referred to as hygroscopic and protective structures, such as secretory layers and squamiform vestiture on the surface, loosely jointed or connate sutures, etc.[4]

The high degree of speciation is certainly due to the great diversity of ecological niches, in particular those offered by the very variable micro-composition and granularity of sand. There is little doubt that the discovery that barren sand represents an ecological niche for a rich fauna of Tenebrionids deserves the greatest attention, for this hostile biotope 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, 1939).

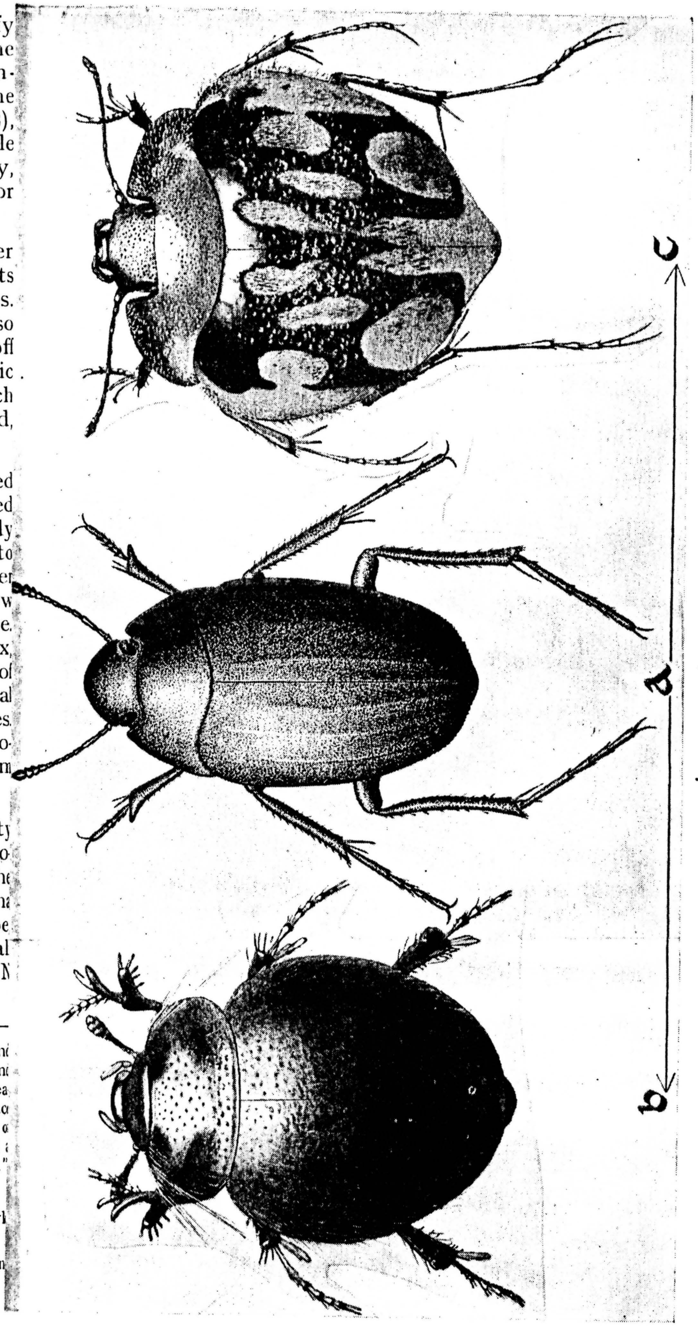

FIGURE 1.—Specialization of Namib Tenebrionids.

(a) A species of the ascendent genus *Zophosis* from Damaraland; it does not differ much in its general appearance from several hundred other species which occur over the whole of Africa, the Mediterraneum and the Indian deserts.

(b) and (c)—Species of two of the descendent Namib genera. (b) *Dactylocalcar caecus*, an anophthalmous "under-sand" Zophosin of the dunes. (c) *Cardiosis fairmairei* of Zophosini, an errant, heliotactic runner and diver of the sand of the "smoking" crest portions of dunes.

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[1] BAGNOLD, 1954, writes literally: "The best soil is undoubtedly blown sand which is relatively clean of fine dust particles between the grains. Water can descend very quickly through this soil since its anti-wetting property is low and its permeability high. Owing to capillary tension a given charge of water applied at the surface of dry sand will sink to a certain depth and no more, the depth being something of the order of eight times the immediate precipitation. Water which has reached a depth of 20 to 30 cm. remains as a moist unsaturated zone for several years . . ."

[2] Cf. KAISER, 1926; KOCH, 1953 and 1955.

[3] About the ecology of shifting desert sand and its insects cf. the recent remarkably well documentated monograph by F. PIERRE, 1958.

[4] About the adaptive morphology of desert Tenebrionids cf. GEBIEN, 1938 and 1939, PIERRE, l.c., KOCH, 1958, etc.

Relatively few diurnal species exist in such a harsh environment (of *Onymacris*, *Stenocara*, *Calognathus*, *Pachynotelus*, all Zophosina and others), but they often appear gregariously in great individual numbers.[1] The different species react variously to heat, radiation and evaporation, from which they are protected by the development of additional characters of body formation. Among the most notable of these adaptations are a marked thickening of the integument, connate sutures, swollen elytra combined with a larger space beneath the elytra, and usually very elongate legs which make rapid movement possible during the short intervals of direct exposure, and also carry the body at a high level above the heated surface of the sand. Of course the degree of light-loving (photophilous) disposition is also very variable and there can be observed all transitional phases of Tenebrionids which prefer twilight (crepuscular species), or shade (umbriphilous species), or even need the direct sunlight as stimulus (heliotactic species). The velocity of the heliotactic species of these diurnal, dune Tenebrionids is simply amazing, and it seems that the modified spur-like armatures on the legs allow for a better grip on the moving sand, while the frequently observed asymmetry of the spurs of claws may facilitate locomotion on the "quasi-fluid oblique planes". Many of these runners are also rapid diggers, to which activities we can add jumping and ball-like rolling in the Zophosina, and in *Cardiosis* even peculiar semi-volant movements by making use of the current of the wind. The formation "sand-shoes" (viz. compressed feet which are provided with brushes of bristles with a broom-like action) occurs in both the diurnal and nocturnal species.

We were unable, however, to confirm any theories on mimetic or pale coloration of desert Tenebrionids in connection with protection from enemies or better reflexion of heat respectively, for the "white" Tenebrionids of the Northern Namib live under exactly the same biotic conditions as do the black Tenebrionids of the Southern Namib, moreover the "white" Tenebrionids cannot support higher temperatures than the black ones (cf. BOLWIG, 1957), while the often soil-coloured (homochromous) secretory layer on the body surface in many *Zophosis* may correctly be interpreted as a means of protection from evaporation rather than as cryptic mimicry.

Nocturnal species are considerably more numerous, and include all *Lepidochora*, *Vernayella*, *Caenocrypticus*, *Stips*, *Arthrochora*, *Archinamibia*, *Psammogaster*, *Periloma*, *Brinckia*, *Namibomodes*, *Uniungulum*, *Vansonium* and many others. They are exposed to a much lesser degree of evaporation, and to no direct heat and solar radiation, the influence of which—in their dormant state during the day—they can regulate deliberately by changing position in the depth of the sand. In accordance with this different climatological environment their morphological structures are opposed in many ways to those of the diurnal species. Very often the elytra are loosely jointed to the body and no longer close hermetically the respiratory space beneath elytra, the pigmentation of the cuticle becomes reduced or vanishes altogether (the body therefore assuming a pale yellowish to testaceous colour), in many cases the elytra assume a semi-transparent

[1] In literature we very often find references to the scarcity of individual occurrence of insects in deserts. These statements need rectification and certainly do not hold good for the Tenebrionids, as we sometimes found the dunes simply swarming with *Onymacris*, *Lepidochora*, *Vernayella*. About similar observations in the Gobi desert cf. REYMOND, 1938, in the Sahara SCORTECCI, l.c.

(diaphanous) appearance (e.g. in *Uniungulum*, some *Pterostichula*, *Caenocrypticus*, etc.), in others (e.g. *Lepidochora*) the elytra change from opaque during the day or dry nights to diaphanous during moist nights (hygrophaneity), and also the very frequently met occurrence of surface secretion during the moist night or squamiform vestiture may be connected with the hygroscopic property of these sculptural structures. In some genera (e.g. *Namibomodes*, *Brinckia*) the cuticle of the whole body produces a secretion of an adhesive nature to which grains of sand stick, forming thus a thick layer of probably increased hygroscopic property; *Stips stali*, again, stores the wet sand on dish-like sculptural cavities on the surface of the body. Although based on the same principles, the legs show important points of dissimilarity from the diurnal dune species. As the nocturnal species have to retire and dig themselves to considerable depths in the sand during the hot day (while the diurnal species merely hide underneath the cool and wet surface of the sand during the night), many of these nocturnal species are therefore potential diggers, exhibiting most intricate armatures on legs and, in almost all cases, protective cilia on the sides of the body. In this connection I may only mention the peculiar formation of the legs in *Lepidochora*, in which, in addition to the normal feet, supplementary webbed, sand-swimming "feet" have developed by means of the finger-like (multi-digitate) modification of the normally spur-like apical armatures of the tibia (calcaria). The asymmetry of the ungual spurs can be observed also in the nocturnal species (*Namibomodes* and *Vernayella*), but reaches, under otherwise hypertrophic conditions, the highest possible degree of atrophy in *Uniungulum*, in which the outer spur of the claws has disappeared altogether. With the exception of a few crepuscular cases in *Lepidochora* all the nocturnal species are extraordinarily photophobic to artificial light during the night; they stop moving almost at once when they become aware of light. They are moderately fast to slow in their movements, except for the *Vernayella* which we were able to observe rapidly racing on the "oblique planes" as long as they were not disturbed by light.

Also very specialized are the permanently "under-sand" species such as *Dactylocalcar* and *Syntyphlus*, as well as all the early stages of Tenebrionids (larvae and pupae). The loss of pigmentation and eyes, the hypertrophy of sense-bristles, are common to all, but, while in the adult of *Dactylocalcar* the legs are spoon-shaped, the belly is strikingly swollen (physogastric) and the sub-elytral cavity expanded, in the larvae there are additional leg-like appendages (urogomphi) on the anal sternite, and locomotory and defensive armatures on the anal tergite (pygopod).

A brief review such as this can do no more than indicate the amazing richness of the Tenebrionid fauna of the Namib and its high degree of endemism. The limited exploration so far carried out shows that the endemic tribes, genera and species far outnumber those found in other deserts of the world, and in no other desert do we find species showing such extreme specialization and adaptation. This leads to the conclusion that this richness and endemism is due to the long and undisturbed duration of the peculiar climate and conditions obtaining in the Namib. The Sahara has experienced alternating pluvial and arid periods (cf. MONOD, 1942), the Somalia and Madagascar barren dunes (which we have found to be devoid of all indigenous life) are of comparatively recent formation (cf. also AZZAROLI, 1957), but the Namib climate and conditions have apparently remained stable since the Benguela current drew close to the coast line. According to geological evidence this occurred millions of years ago during the Cretaceous Period, when the Polyphaga beetles had already made considerable evolutionary progress. Probably at about the time that the Namib sands originated, species of all the basic South West African tribes began their infiltration into this area, and started along the path of specialization and adaptation. As the dunes grew and their area expanded, these beetles became more and more specialized, and more and more sharply differentiated from the Tenebrionid fauna beyond the confines of the desert.

Nevertheless they can all be traced back phylogenetically to the original and basic South West African ancestral tribes. Representatives of identical tribes and even genera today inhabit the dunes of the Sahara and even of the far-distant Gobi, but the actual place of origin of these pan-desertic groups is still an unsolved riddle.

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