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 Vansoniini 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*, Reymond); 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 Vansoniini (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. Somalarabia (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, 1960*a*), 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, 1952*c*). 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 xerophility 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 Somalarabic 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, 1960*a*).

‡ Cf. the following maps of distribution: Stenosini (Koch, 1956); Litoborini (Koch, 1953*c*, 1956); Sepidiina of Molurini (Koch, 1955*a*); Anomalipina and Platynotina of Platynotini (Koch, 1956); Micrantereina and Oncosomina of Drosochrini (Koch, 1958); *Rozonia* (Koch, 1944*a*); *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, Muttilids 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 eurotopic 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 faunae of Tenebrionids may be implied from the following data. Koch (1944*b*) 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, 1960*a*).

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 ascendents.

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, 1950*a*; 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