

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 Klinghardtsberge, 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.).