Some aspects of abundant life in the vegetationless sand of the Namib Desert dunes*

Positive psammotropism in Tenebrionid-beetles

C. Koch

In memory of my friend the late Prof. F. S. Bodenheimer, who guided my investigations in the desertic fauna of Israel as far back as 1933.

One of the most remarkable features of the Namib Desert is found in the combination of the vegetationless (or *ultra-desertic*) barrenness of its sandy dunes and plains with an extraordinary richness of its Tenebionid fauna — a statement which certainly seems to be somewhat contradictory and is unknown of other deserts. In spite of its small size (only one-thirtieth of the size of the Sahara), the large extent of vegetationless soils, and the fact that exploration so far has been confined to a few collecting stations in the marginal areas, the composition of the known fauna is richer than in the Sahara, and distinguished by the complete, practically insular endemism; there are known several hundred species and about 90 genera of wingless ground-Tenebrionids; of these, 2 tribes, approximately 35 genera and more than 200 species, are endemic to the section of the *True Namib* (**) alone.

According to soil surfaces we can divide the Namib into three longitudinal sections which more or less follow each other from the coast towards the highlands; these sections are the littoral sands, the barchan dunes and the consolidated to rocky soil surfaces of the plains. To them have to be added special biotopes such as the hygrophilous or halophilous strata of river beds, pans, etc.

A special eco-fauna of Tenebrionids corresponds to each of these sections. The most remarkable of these biotopes is without doubt that of the dune systems, which are peculiar to the *True Namib,* for the greater part vegetationless, and harbour the most specialized and endemic elements of the Namib fauna. The strictly dune-loving species are wholly confined to the dunes and 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.

The main habitats which exist in these dunes, and to which the respective inhabitants have reacted in a convergent manner, are the following:—

(*) With 2 maps, 8 text-figures and 10 plates, pp. 76- 92, at the end of volume.

(**) This is the part of the Namib Desert, which stretches from the Orange River as far northwards as a few miles north of Mocamedes (about the biogeographic division of the Namib, cf. KOCH, 1960). Cf. maps.

(a) Grassy dunes, viz. portions of the barchan dunes which bear more or less scattered vegetation (such as *Aristida*-grasses, „narras" or *Acanthosicyos horrida,* etc.); these portions are usually situated in the marginal areas of the dune system. This habitat is favoured by the category of the *plant-followers,* the life of which, in one way or the other, appears to be connected with the existence of active vegetation. They are not necessarily phytophagous (or plant-eating) insects, but are attracted or move or gravitate towards a plant centre.

(b) The barren dunes and vegetationless slope and crest portions of grassy dunes. The barren sand of desertic dunes in general, which is devoid of any macroflora, was believed to be devoid also of all other life (except for bacteria, microfungi and microalgae). With the exception of 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 become adapted to this extreme biotope may be defined and referred to by the term *ultra-psammophilous* (*), for they no longer depend on active plant life, but just live 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 strikingly modified species of all Namib Tenebrionids, such as *Lepidochora, Cardiosis, Tarsosis, Anisosis, Vernayella,* many *Onymacris* and others.

The primary elements responsible for the environment of the dune-dwellers may be ultimately condensed to these two, sand and wind, with active vegetation playing a part, but not necessarily a fundamental role. The loose sand represents the readily penetrable, "*quasi-fluid*" medium, with which the dune-dwellers are in continuous contact during their whole life cycle. The wind, however, changes the sand into an optimum biotope, not only on account of wind-borne importation of moisture (from the sea) and alimentary matter (from the hinterland), but also by its moulding of the sand into the rolling continuity of the "*inclined planes*" of the dunes (†), a configuration which is chiefly responsible for the creation of

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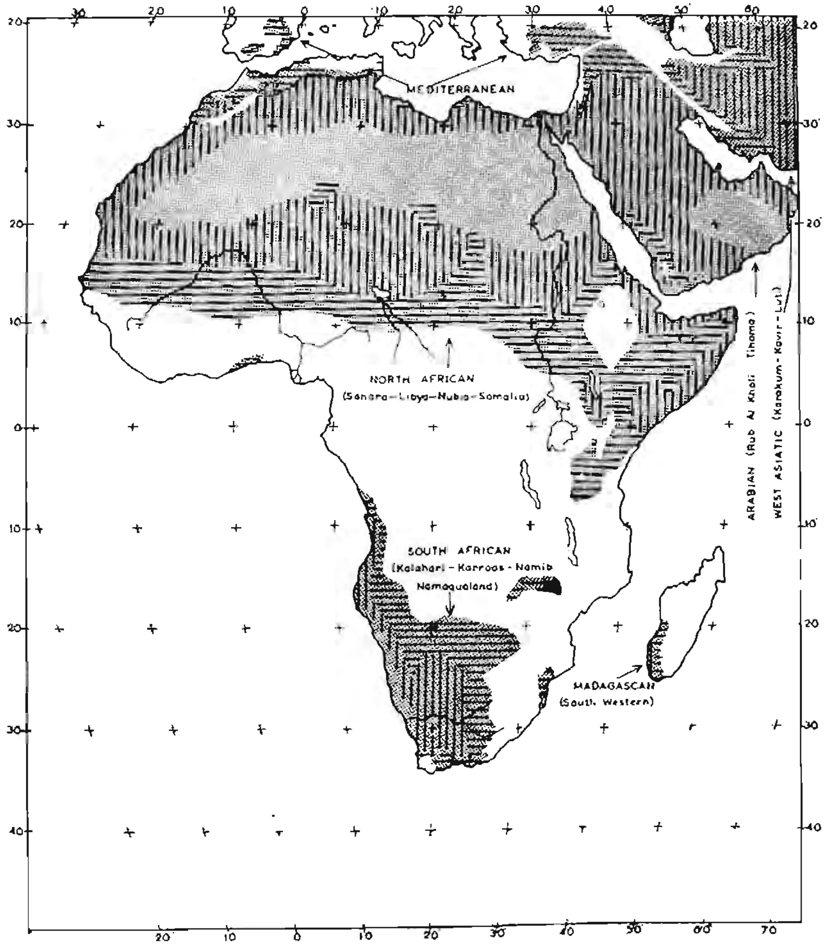
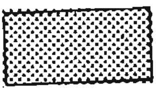
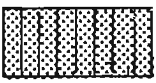
(*) *Ultra-psammophilous* = loving vegetationless (ultra-desertic) sand.

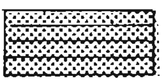
(†) This is the "Unübersehbares Dünenmeer" of the former German cartographers, with dune craters reaching a depth of 300 ft. and the dunes rising as high as 1,000 ft. from the floor of valley (e.g. at the Sossus Vlei of the *Southern Namib*), a height which competes with the maximal heights of the Sahara dunes (e.g. 300 m, south of Murzuq in the Fezzanese Erg of the Libyan Desert).



Map 2
Distribution of arid homoclimates on the African continent (after MEIGS).


: *Extremely arid* (at least one year without rain); to such *extremely arid* zones belong only the Namib, the central part of the Sahara, the coastal area of south-western Arabia and the Rub' Al Khali Desert in the south-eastern part of Arabia.


: *Arid* (with reference to THORNTHWAITE'S precipitation-evaporation system in relation to the needs of plants; practically 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).

favourable conditions of life, such as the catchment and preservation of precipitation, shade, and other factors mentioned below (Plate II).

Although the Namib belongs homoclimatically to the extremely arid deserts because of the merely episodic nature of the rainfall, and the very low average rainfall figures (which are said to vary from 30 mm to nil), some reasons of environment which favourably influence and prevent the dehydration of the dune-dwellers may be quoted as follows: -

(a) The moisture-storing nature of sand as medium, in connection with underground humidity. Owing to capillary tension, water which has reached a depth of 20 to 30 cm remains a moist, unsaturated zone for several years, since no evaporation can take place from the moment the capillaries of water are broken and no longer communicate with the soil surface (BAGNOLD, WALTER);

(b) The *inclined planes* of the dune-configuration make possible the run-off concentration of all available precipitation. WALTER has measured the water produced by fog on an inclined roof of a house of 60 sqm. surface during a month in Swakopmund; he collected about 250 l. of water. In correlation with the moisture-storing properties and the high degree of permeability of pure, coarse dune-sand, the great frequency of fog (more than 200 days p.a., even within a distance of 35 km from the coast), and the enormous extension of the surface of the *inclined planes* in the dune-systems, these data may have a remarkable bearing on the possibilities for life not only of the adults but in particular of the permanently "under-sand" early stages of the *ultra-psammophilous* species, by the formation of almost permanent strata of "under-sand" moisture at the bottom of the leeward slopes of the dunes.

(c) The angle of inclination of the *planes* acts as a very effective protection from insolation and evaporation, if brought into relation, on the one hand with the vertical angle by which the dune-dwellers enter immediately into a considerable relative depth, and on the other hand with the angle of sun-radiation which, during the daily cycle, couples increases of heating with decreases in penetration, thus diminishing to a great extent the hostile conditions reigning at the zenithal angle. As the meridional and nocturnal temperatures on and above the surface of the sand are extremely high and extremely low respectively, but are of a fairly constant medium degree under the surface, immediate relief from heat — due to the vertical angle of the burrowing dune-dweller — becomes evident. As the larvae of deserticolous Tenebrionids were found in different soil substrata of level plains, at a depth ranging from 5 to 60 cm from the surface

(HAFEZ & MAKKI), we may readily infer that, under the particularly favourable conditions of the *inclined planes* of *quasi-fluid* dune-sand, the depth of a constant microclimate can be reached under all circumstances.

(d) The angle of inclination of the *planes* provides also for a remarkable increase in the shaded surface of the dune soil on account of the daily solar rhythm. Thus the *inclined planes*, though bare of any objects that could provide suitable shade, offer nevertheless similarly favourable shade conditions to those found in plains with vegetation and rocks.

(e) The *inclined planes* are also accumulation centres for the wind-borne alimentary matter, on account of aerodynamic processes.

(f) The hygroscopic property of the dry organic fragments (BUXTON, PIERRE, FIORI). These findings may be of particular importance in connection with the subterraneous detritus stringers, often found at the floor of the leeward slopes of the dunes.

(g) In the case of the *plant-followers*, the active vegetation with its favourable shade conditions and high water content, influencing in particular the sand and detritus mixture between the roots, where the *stationary plant-followers* (e.g. *Caenocrypticus*) and the early stages of the *errant plant-followers* (e.g. *Onymacris rugatipennis)* live. Shrub shade temperatures in the Egyptian desert, for example, were found to be considerably below the soil surface temperature at any hour of the day and during almost all months, especially in the hot season (HAFEZ & MAKKI).

The dune species are, like all other members of the Tenebrionid family, omnivorous, but are particularly attracted by any substance with increased watery content. Their fundamental food supply, however, (whether active vegetation is involved or not), is the wind-borne organic matter, because this is always present. In the case of the *ultra-psammophilous* species these organic fragments seem to represent the sole sustenance, except eventually for some microflora(*). The constantly renewed supply of organic matter consists of insects, living or dead, and parts of plants, all hurled across the barren dunes by the continental, easterly wind. The fragments are continuously mixed with sand, particularly at the "smoking" crests of dunes, but still more fall and accumulate on the sloping leeward sides. Samples of dune-sand from the coastal part of the *Northern Namib* revealed 36,3% of organic matter

(*) LOGAN cit.: "Even in the totally plantless areas such as the shifting sand dunes, flies, Tenebrionid beetles and lizards are to be found. What constitutes a base of chain of food supply the writer cannot state. Perhaps it lies in microflora present within the sands and gravel."

(BRINCK). At some sites this organic debris concentrates on the leeward sides and forms gradually a layer which develops finally into a rather compact substratum of dried, subfossilized detritus underlying the foot of the dunes (KAISER, KOCH, 1953 and 1955, BRINCK). The water of metabolism, however, is produced by oxidation of even this extremely desiccated food.

Phylogenetically all the dune Tenebrionids of the Namib, without any exception, are strictly xerophilous by inheritance, belonging throughout to xerophilous tribes(*). The high degree of their common ancestral xerophility can clearly be proved as follows:—

(a) All the dune species are direct descendants of the arid fauna of the Kalahari-Karroo-Namaqualand biogeographical system;

(b) The ancestral groups participate in the distant faunae of the Sahara-Sindic influenced parts of North Africa, but are absent from the more humid eastern half of Southern Africa, though this region closely adjoins the arid Kalahari-Karroo-Namaqualand area geographically;

(c) None of the non-xerophilous (subxerophilous, mesophilous, hygrophilous) groups are represented, although such tribes have penetrated into the northern part of the South West African highlands from the north, east and south-east via a Trans-Bechuana distributory bridge (KOCH, 1960);

(d) With the biotic conditions in South West Africa ranging from sub-tropical to ultra-desertic, the 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 composing the entomo-fauna increases progessively 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, the *ultra-psammophilous* species play a dominant and basic role of life.

In the dune Tenebrionids of the Namib a great importance must be attached to the daily rhythm of life. Taking into consideration the apparently hostile daylight conditions of the dunes on the one hand, and the reputed propensity for adaptibility in the dune Tenebrionids on the other, we would expect many of these Tenebrionids to have changed over to nocturnal habits, in order to benefit by the absence of insolation and heat and the presence of night-moisture — views which in fact have been expressed very often in literature on deserts.

(*) These xerophilous tribes and subtribes are: Adesmiini (cf. Plates V, VI and IX), Zophosini (cf. Plates IV and VIII), Cryptochilini (cf. Plate IX), Calognathini (cf. Plate VII), Vansoniini (cf. Plate VII), Eurychorini (cf. Plates I and V), Tentyriini, Molurini, Caenocrypticini (cf. Plate X), and Stizopina of Opatrini.

With a few remarkable exceptions(*), however, the adaptive properties of these insects do not seem to be so far reaching as to change impulses which are inherent in phylogenetic stems such as tribes or subtribes as a whole. On the contrary, we find that it is just in the extreme fauna of the vegetationless dunes that the number of diurnal *ultra-psammophilous* species and genera surpasses that of the nocturnal ones. In the two diurnal tribes Adesmiini and Zophosini (which are diurnal but not necessarily heliophilous and dune-loving by inheritance), an evolutionary development has taken place which has reached the highest degree of heliotactic activity in the *ultra-psammophilous* dune-dwellers of the Namib; neither in the Sahara nor in the Gobi have these tribes gained access to the dune-biotope.

The diurnal species appear a short while after sunrise, when the sand has been heated up sufficiently, and retire again into the sand at about sunset, with the cooling down of the surface temperature of sand. The reversed rhythm takes place in the case of nocturnal species, in accordance also with the appearance of the night-moisture. Surfacing from and burrowing into the sand are carried out in an identical manner by both the diurnal and the nocturnal dune species. This process is fast and can be compared often to a kind of surfacing-diving rather than to fossorial movements, in that the body first puts itself into a vertical position towards the usually inclined surface and then propels itself between the fast moving grains of sand.

Reasons for the resistance to heat, insolation and evaporation seem to be readily found in the behaviour of these heliotactic dune-runners, in close association with morphological structures and physiological patterns. Though the intervals of direct exposure may vary, they are very frequently interrupted by diving under the surface of the sand; the diving affords an immediate and efficient relief from the effects of exposure, as the endo-climatic conditions of the sand are very different from the sunlight conditions on the open sand, particularly so, since a considerable and micro-climatically favourable depth is immediately reached on account of the vertical angle of the dive into the *inclined planes* of sand (cf. p. 12). The locomotion of the diurnal forms is characterized by the development of considerable speed (as is the case in all heliotactic ground animals). It does not seem, however, that speed has any serious bearing on protection from exposure, with the probable exception of the increased cooling action of the wind, and the shortening of the intervals of direct contact between the heated surface of the sand and the tactile sense bristles of the tarsi. We have watched the diurnal dune-runners developing the identical degree of speed on cool and cloudy days as on hot, sunny ones; the nocturnal *Vernayella*

(*) *Epiphysa* of Adesmiini (cf. Plate VI), *Fossilochile* of Cryptochilini, Dactylocalcarina of Zophosini (cf. Plate VIII), and *Vansonium* (cf. Plate VII).

(cf. Plate X) race on the *quasi-fluid* surface of the *inclined planes* of the dunes during cold nights as fast as do the heliotactic *Cardiosis* on hot days; we have also watched groups of *ultra-psammophilous Onymacris* remaining exposed to the full impact of insolation for long intervals, when feeding on the leeward side of the dunes where the heated air usually stagnates on account of its situation out of the wind(*).

The nocturnal species, and all the early "under-sand" stages of the dune-dwellers in general, are exposed to a much lesser degree of evaporation, and to no direct heat and solar radiation, the influence of which — in their dormant phase during the day — they can regulate deliberately by changing position in the depth of the sand. They are, however, not alone in their enjoyment of the night-moisture, as the diurnal runners also seem to store the same during their dormant phase (during which they become motionless and quite stiff), which usually takes place not in the depth, but just underneath the wet surface of the sand. The nocturnal species are comparatively slow-moving, with the unique exception of the only known nocturnal runners in the genus *Vernayella* (cf. Plate X). They are all strictly photophobic insects; on becoming aware of an artificial light they either slow down to practically a stand-still or quickly dive into the sand.

The Tenebrionids of the Namib have reached a remarkable degree of adaptive change in morphological structures. In order to judge these manifestations correctly, however, we must remember that all Namib Tenebrionids, and this without any exception, are components of strictly xerophilous groups (cf. p. 14), and are therefore a priori adapted to the life in areas of great aridity by the development of certain organisation-characters. The latter must be sharply distinguished from adaptive morphological features of a non-phylogenetical, homo-morphological or secondary nature, due to a phylogenetically independent evolution under parallel conditions of the milieu, usually occurring convergently in unrelated groups.

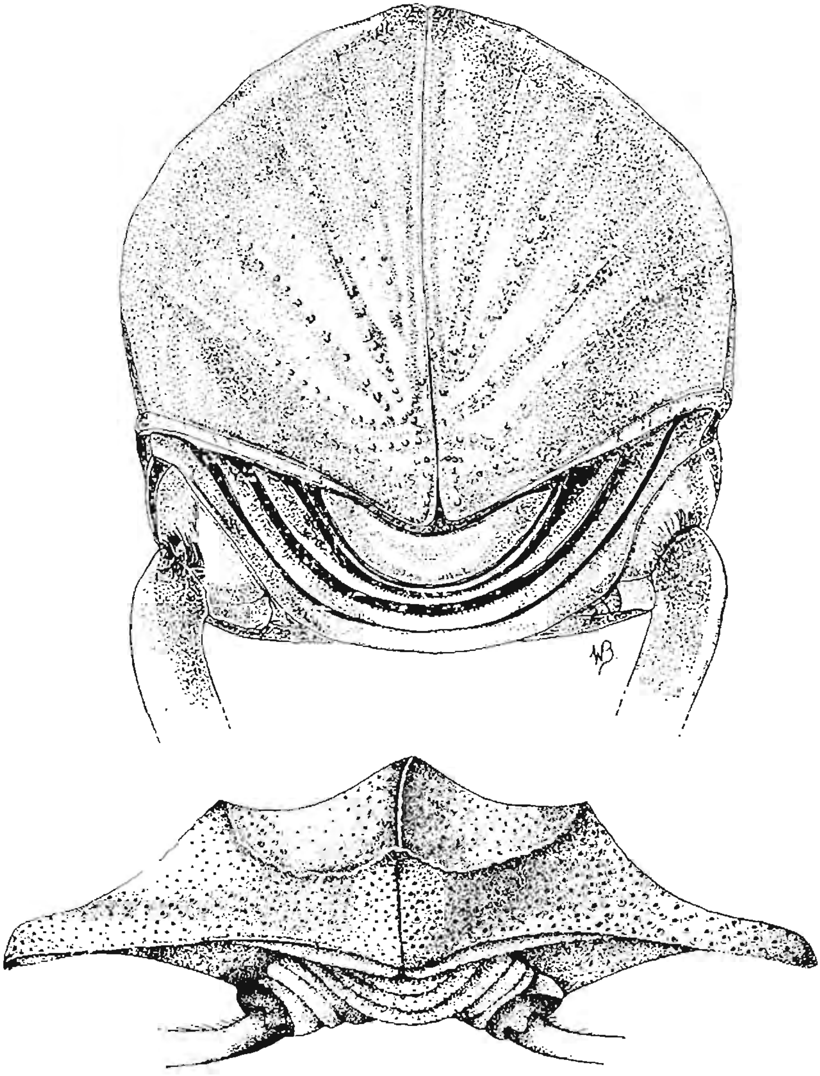
As stated above, the daily rhythm of the dune-dwellers of the Namib is based strictly on an ancestral disposition. Accordingly, the common ancestral structures indicate a protection from insolation and evaporation in the diurnal tribes (†) on account of the hermetic

(*) Cf. HAFEZ & MAKKI, on heat stupor and resistance to high temperature in the Egyptian *Adesmia bicarinata*, cit.: "The beetles were unaffected when they were left under gradually rising temperature of the soil surface and they died when it reached 50° to 53° C. The same conclusion was arrived at in the laboratory. When the beetles were left at high temperatures such as 48, 52, 58 and 62° C, they fell into a state of heat stupor after 150, 32, 6 and 4 minutes, respectively."

(†) The diurnal tribes are the Adesmiini (cf. Plates V, VI and IX), Zophosini (cf. Plates IV and VIII), Cryptochilini (cf. Plate IX), and Calognathini (cf. Plate VII).

fig. 1

To the wide range of variability in the subelytral volumen of dune-species. Caudal aspect of body:—



Above. — *Onymacris unguicularis* HAAG, a heliotactic *ultra-psammophilous* species, with extreme convexity of elytra and consequent increase of the subelytral cavity.

Below. — *Stips stali* (HAAG), a nocturnal *plant-follower*, showing the extreme complanation of elytra and consequent reduction of the subelytral cavity.

connation of body sutures in association with the disappearance of the elytral hypomera and only pygidial mobility, while they imply moisture-storing to practically hygroscopic properties in the nocturnal tribes(*) because of the open body-sutures, more or less loosely jointed parts of the body, the development of hypomera in the pleural formation of the elytra connected with abdominal mobility, and the frequently depigmented, softened sclerotization and a peculiar hygrophaneity of the cuticle. There are only a few exceptions from this rule in the diurnal groups, since the Dactylocalcarina, Vansoniini and *Fossilochile* of Cryptochilini have changed to nocturnal habits; but in all these cases the primary or constitutional organisation-structures have been maintained in spite of extreme secondary modification.

Contrary to indications found in literature, all other adaptive structures occur in both diurnal *and* nocturnal species.

An increase (e.g. in the diurnal *Onymacris* and nocturnal *Epiphysa*) or a reduction (e.g. in the diurnal *Calognathus* and the nocturnal *Stips*) in the volume of the subelytral cavity ("pseudophysogastry") is found therefore in both diurnal and nocturnal species, though the increase is often quoted to imply a protection from heat in deserticolous Coleoptera, as the air used for respiration is believed to pass first through the subelytral cavity and is thus possibly cooled and moistened before entering the spiracles. Comparing e.g. the width-height ratio of body in the extremely convex *Onymacris unguicularis* and the extremely complanate *Stips stali* (see Plate V), both occurring together in the barchan dunes of the *Southern Namib* (see fig. 1), the former is to the latter as is 1 to 0,25; in both species the convexity and complanation of body are primitive organisation-structures which are peculiar to the respective tribes Adesmiini and Eurychorini. But there are cases known, in which the reduction of the subelytral cavity by the complanation of body in dune-dwellers is decidedly a secondary adaptive feature, as e.g. in the male of *Onymacris plana* (see Plate VI).

The thickness of the cuticle, which is often referred to as a protection from insolation or enemies, is almost general in the diurnal species and less frequent in the nocturnal ones, although a particularly high degree of sclerotization can be observed in some nocturnal species such as *Epiphysa* (cf. Plate VI) and *Stips* (cf. Plate V).

A pale "desert colouration" can be observed in some of the diurnal *and* nocturnal species; it is therefore not a peculiarity of the diurnal deserticolous Tenebrionids, as frequently quoted in literature, in connection with reflection of radiation. With the exception of the unique white to yellowish structural colour of the elytra (cf. Plate IX) in some Tenebrionids from the *Northern Namib* (*"white" Onymacris, Calosis* and *Stenocara eburnea* [see Plate IX], this pale colour

(*) The nocturnal tribes are the Vansoniini, Eurychorini, Tentyriini, Molurini, Caenocrypticini and Stizopina of Opatrini.

is produced by derivatives of the cuticle, viz. either white hairs or scales (e.g. in the diurnal *Calognathus* [cf. Plate VII and *Pachynotelus* cf. Plate IX, or in the nocturnal *Vansonium* cf. Plate VII, *Fossilochile* and *Lepidochora* cf. PlateI], or a whitish, yellowish, brownish, brick-red to violet, pulverulescent secretory substance (Zophosini, Adesmiini), which can assume a somewhat waxy to elongately stringy consistence in some Eurychorini. This secretory substance is also responsible for some cases of homochromous colouration, effected either by the accidentally identical tint of this substance (some Zophosini), or in a perfect manner by the adhesive properties of some kind of colourless substance to which particles of sand stick (e.g. the diurnal *Heliophosis* and the nocturnal *Namibomodes, Brinckia,* etc.).

Entirely black species are numerous among the diurnal, but less frequent in the nocturnal dune-Tenebrionids. On the other hand there are no depigmented diurnal dune-species known, while the greater part of the nocturnal species are depigmented, viz. of the characteristic yellowish to testaceous colour of chitin, but containing melanogen in their cuticle.

The unique white colour of the unpigmented elytra of the *Onymacris* from the *Northern Namib, Calosis* and *Stenocara eburnea* (see Plate IX), is caused by the unorientated reflection of light by the numerous microscopic bubbles of air which are enclosed in the exocuticula (KÜHNELT). All hypotheses such as protection from insolation (GEBIEN), or protection from enemies on account of the "homochromous" colouration (PÉRINGUEY, GEBIEN), may have to be rejected. We should be able to conclude the "white" elytra either offer no protection from radiation on account of the absence of pigment, or are better protected than the black elytra, since white colour reflects, and black colour absorbs, radiation — if BOLWIG had not proved experimentally that the "white" Tenebrionids cannot support higher temperatures than the black ones. BODENHEIMER, who studied the degree the rays of various wave-lengths in the solar spectrum are able to pierce the dead part of the integument of insects and reptiles, found the integument to be normally fairly well protected against penetration into its living tissues, irrespective of colour; furthermore he found a striking similarity in the transmission trend through all colours and integumental structures, as well as the general non-transmittance of ultra-violet rays. Finally, we must also remember that the "white" Tenebrionids do not differ in their behaviour from the normally black diurnal species, that they occur together with the black species, nor is the environment of the *Northern Namib* fundamentally different from that reigning in the *Southern Namib.* There may be some truth in GEBIEN's suggestion that the absence of melanogen and melanin may be associated with factors of suppression, which may exist in the sole and very restricted area of the occurrence of the "white" Tenebrionids (viz. in the *Northern Namib*).

All dune-species of the Namib are apterous. Apterism is commonly believed to represent an adaptation to life in deserts and other areas exposed to wind, since flying insects are supposed not to withstand the extreme aerodynamic conditions prevailing in deserts. However, in all dune-species of the Namib the atrophy of wings is a common ancestral organisation-character of the tribes to which they belong, and is found also in con-tribal and even con-generic, mesophilous to hygrophilous species living e.g. in tropical rain forests. On the other hand there are many Heterocera, Diptera and Hymenoptera occurring in the dunes, which do not show any signs of atrophy of the wings.

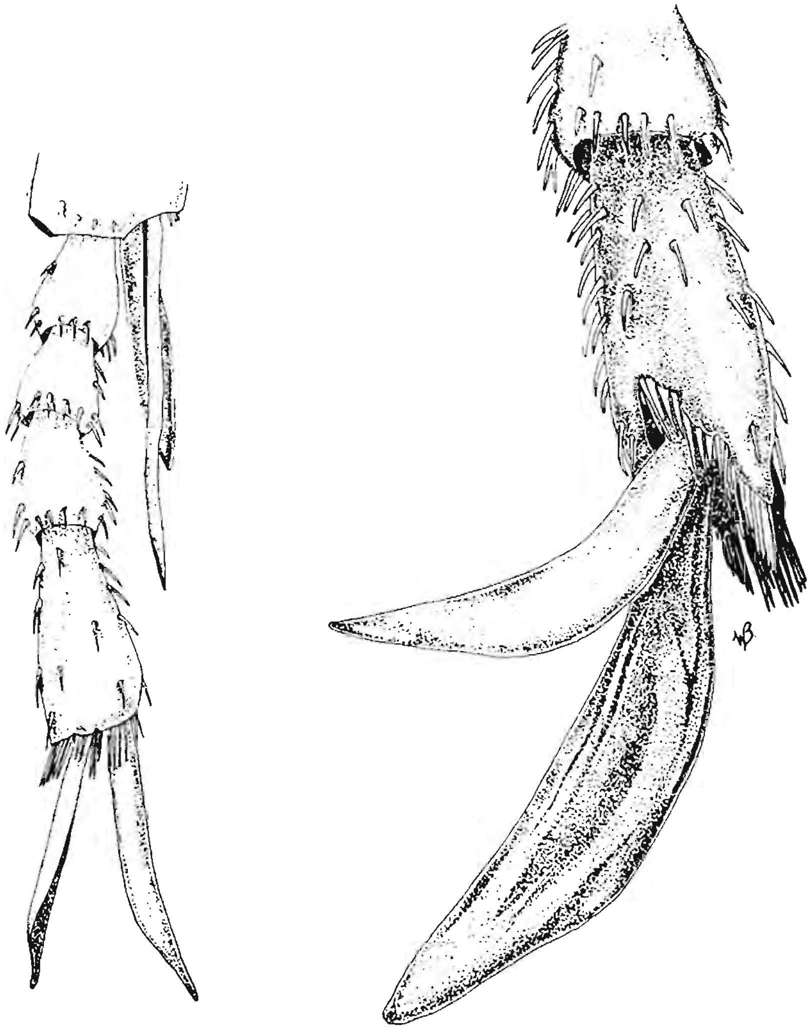
With regard to the size of body, there are no essential differences between diurnal and nocturnal Tenebrionids of the Namib. In both the range of size varies from about 1½ to 40 mm, but on an average the diurnal species are larger. Based on investigations into the laws of transpiration, it was assumed that only large and medium-sized Tenebrionids can live in an arid milieu, while the small species depend exclusively on an environment of a high degree of humidity (MARCUZZI). However, the smallest species known of the diurnal Zophosini live in the Namib Desert (viz. *Microsis* [see Plate IV], *Protodactylus, Carpiella,* etc.); they vary in size from just above 1 to 4 mm and compare well by these minimum dimensions with the nocturnal Namib Caenocrypticini, such as the ultra-psammophilous *Vernayella* (cf. Plate X) and others.

Most of the secondary morphological adaptations of the dune-dwellers are related to the legs in connection with locomotion on and in the *quasi-fluid* sand on the *inclined planes* of the dunes (see figs. 2 to 8). Generally these modifications consist of a hypertrophic development of the tactile armatures which are in continuous contact with the loose grains of sand (e.g. sense bristles, coronula, calcaria, claws), as well as of an extension of the gripping surface of the feet. Many of these structures have been observed so far only in the dune species of the Namib; e.g. the rather general atrophy of the outer or the inner spur of claws (under otherwise hypertrophic conditions of the armatures, e.g. cf. Plates IV and X), which occurs in a convergent manner with many different and unrelated genera(*) and can go so far that the outer spur appears to be lacking altogether in the intermediate and posterior legs of *Uniungulum;* or the multidigitate tibial calcaria (see fig. 5 and Plate I) in the nocturnal *Lepidochora,* a peculiar formation of the legs, in which, in addition to the normal tarsus, supplementary, webbed "sand-swimming" feet have developed by means of a finger-like extension of the normally spiniform calcaria; or the sudden development of four instead of the usual two calcaria in *Dactylocalcar,* of which the two true calcaria have become modified to extraordinarily enlarged and foliaceous

(*) These genera belong to the tribes Zophosini, Adesmiini, Eurychorini, Molurini and Caenocrypticini.

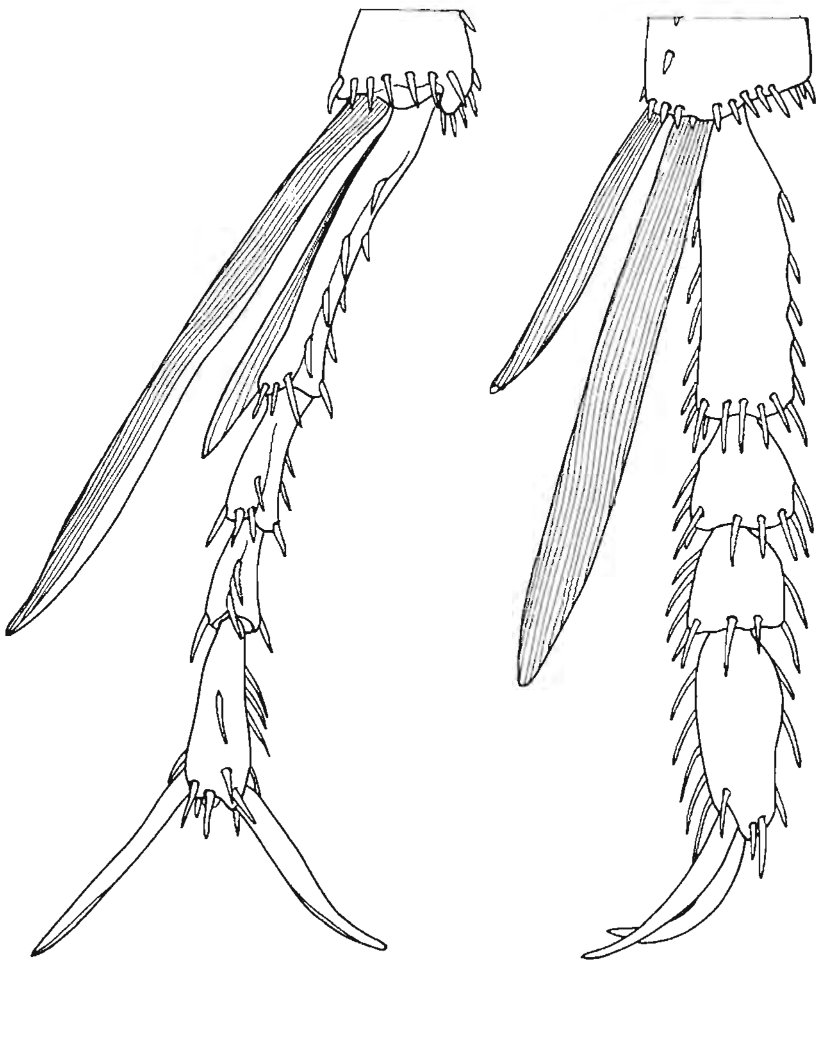
figs. 2 to 8
To the adaptive structures of the legs in dune-species.

fig. 2



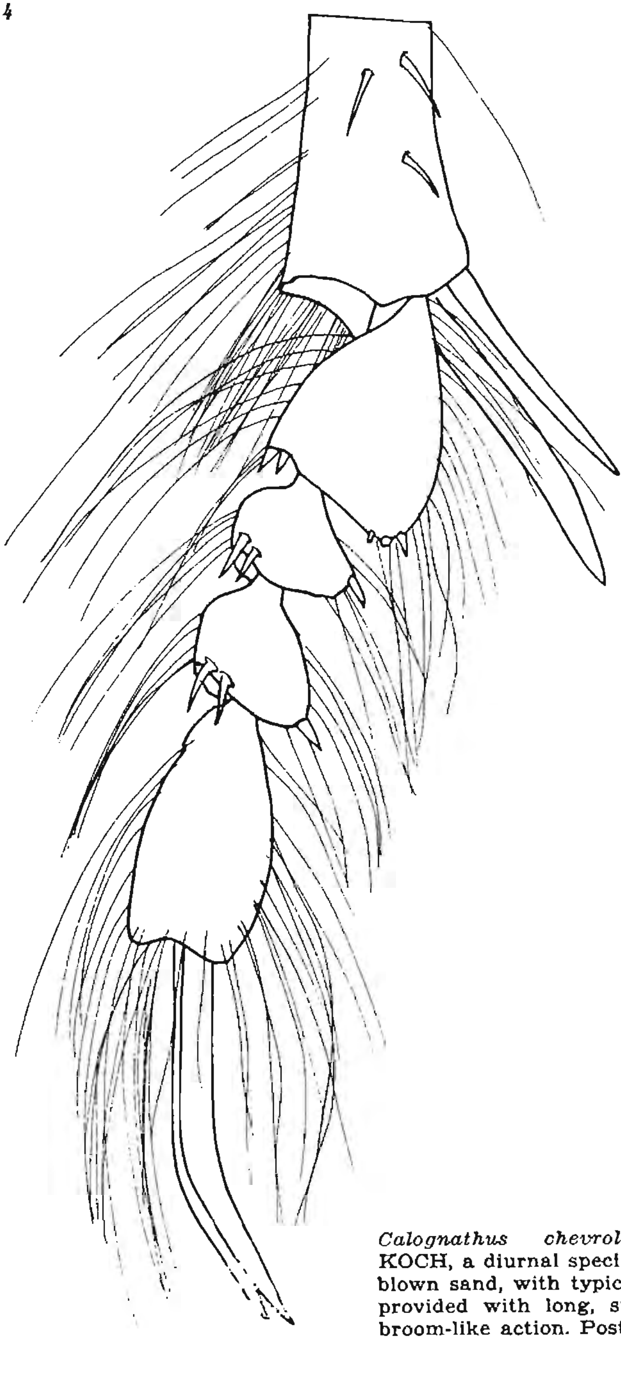
Onymacris unguicularis HAAG, a heliotactic *ultra-psammophilous* species, with hypertrophy of the tibial calcaria, coronula of the ungual socket and unequally developed claws. *Left.* — Posterior tarsus. *Right.* — Ungual segment of posterior tarsus, strongly magnified.

fig. 3



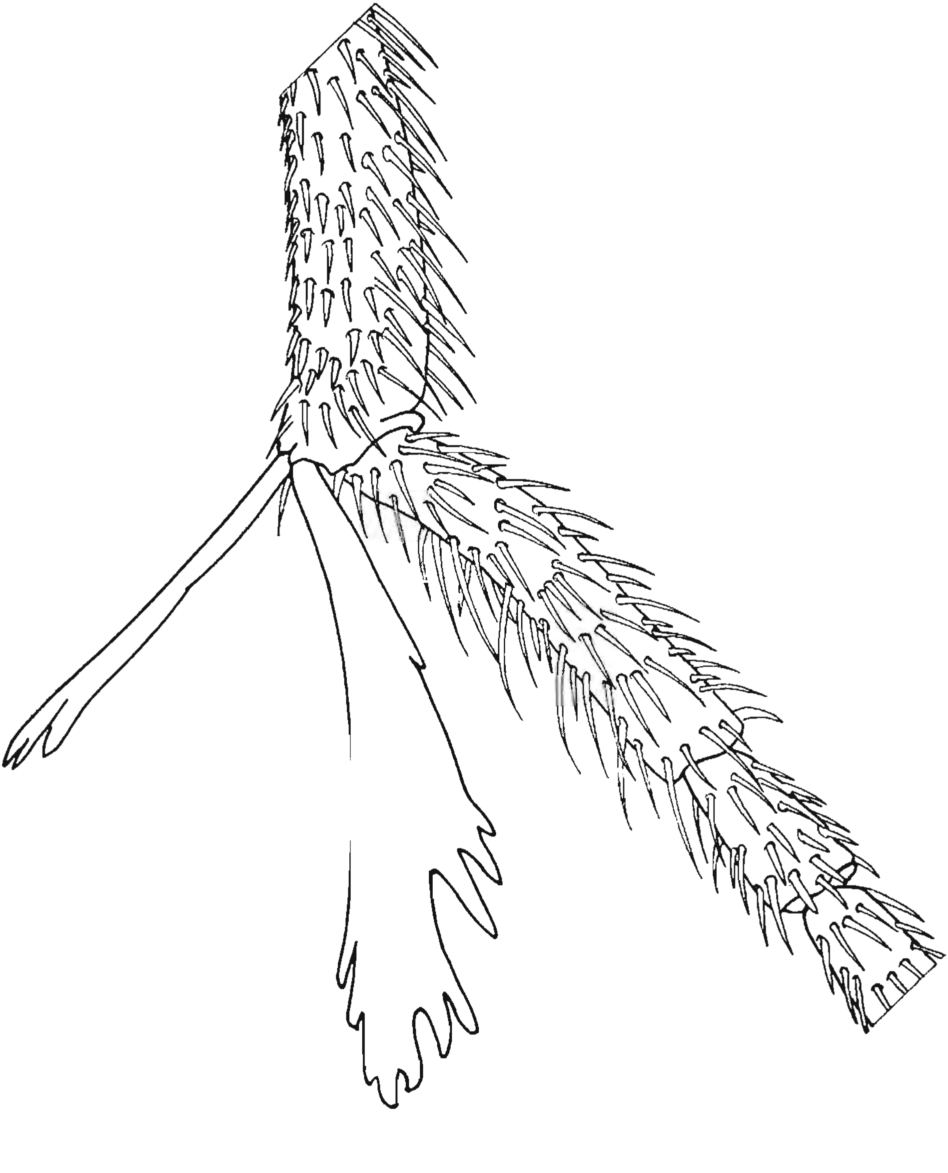
Eustolopus calcaratus GEBIEN, a heliotactic *ultra-psammophilous* species, showing hypertrophic tibial calcaria, combined with laterally compressed, sand-shoe-like posterior tarsi. *Left.* — Posterior tarsus, upper surface, with portions of the inner lateral surface exposed. *Right.* -- Posterior tarsus, lateral surface.

fig. 4



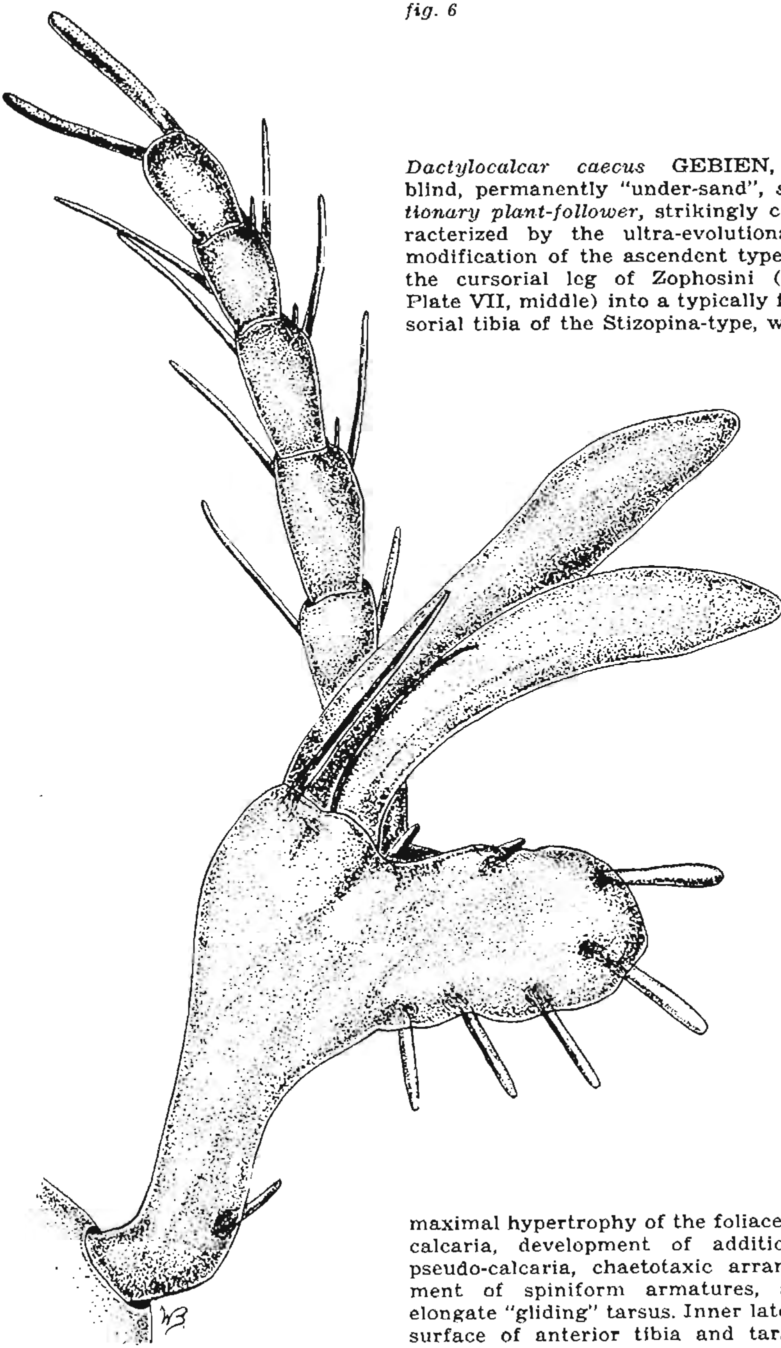
Calognathus chevrolatii eberlanzi KOCH, a diurnal species tunnelling in blown sand, with typical "sand-shoes" provided with long, silky bristles of broom-like action. Posterior tarsus.

fig. 5



Lepidochora eberlanzi GEBIEN, one of the representatives of a nocturnal *ultra-psammophilous* genus, characterized by the hypertrophic development of tactile bristles and the finger-like extension of the normally spiniform tibial calcaria. Posterior leg, apical portion of tibia with calcaria and proximal segments of tarsus.

fig. 6



Dactylocalcar caecus GEBIEN, a blind, permanently "under-sand", *stationary plant-follower*, strikingly characterized by the ultra-evolutionary modification of the ascendent type of the cursorial leg of Zophosini (see Plate VII, middle) into a typically fossorial tibia of the Stizopina-type, with maximal hypertrophy of the foliaceous calcaria, development of additional pseudo-calcaria, chaetotaxic arrangement of spiniform armatures, and elongate "gliding" tarsus. Inner lateral surface of anterior tibia and tarsus.

figs. 7 — 8

Primitive fossorial legs of the only two Stizopina of the Namib dunes. Anterior tarsus and tibia.

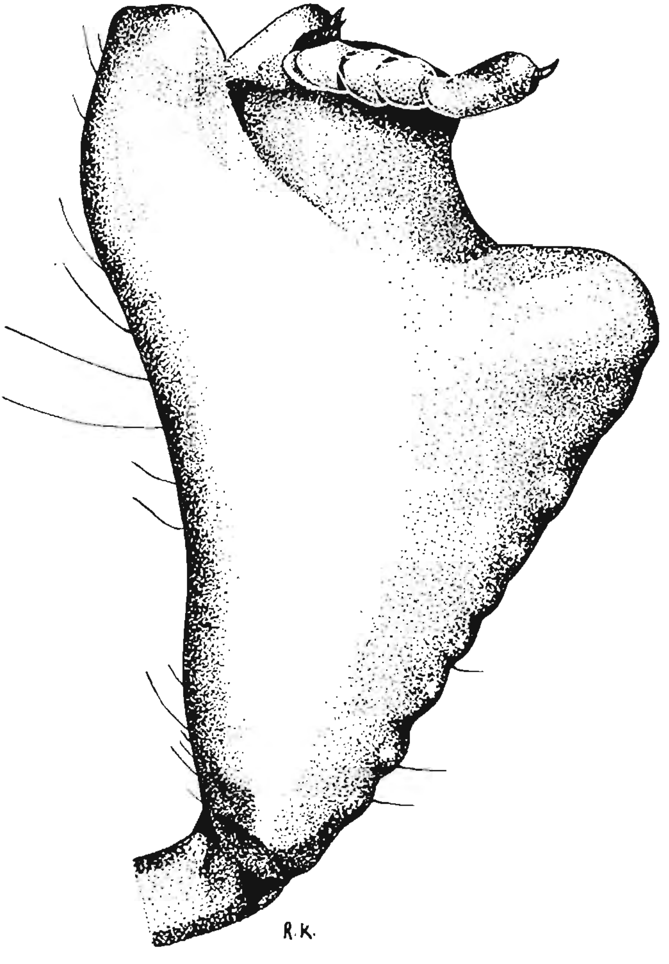


fig. 7 — Psammogaster malani KOCH.

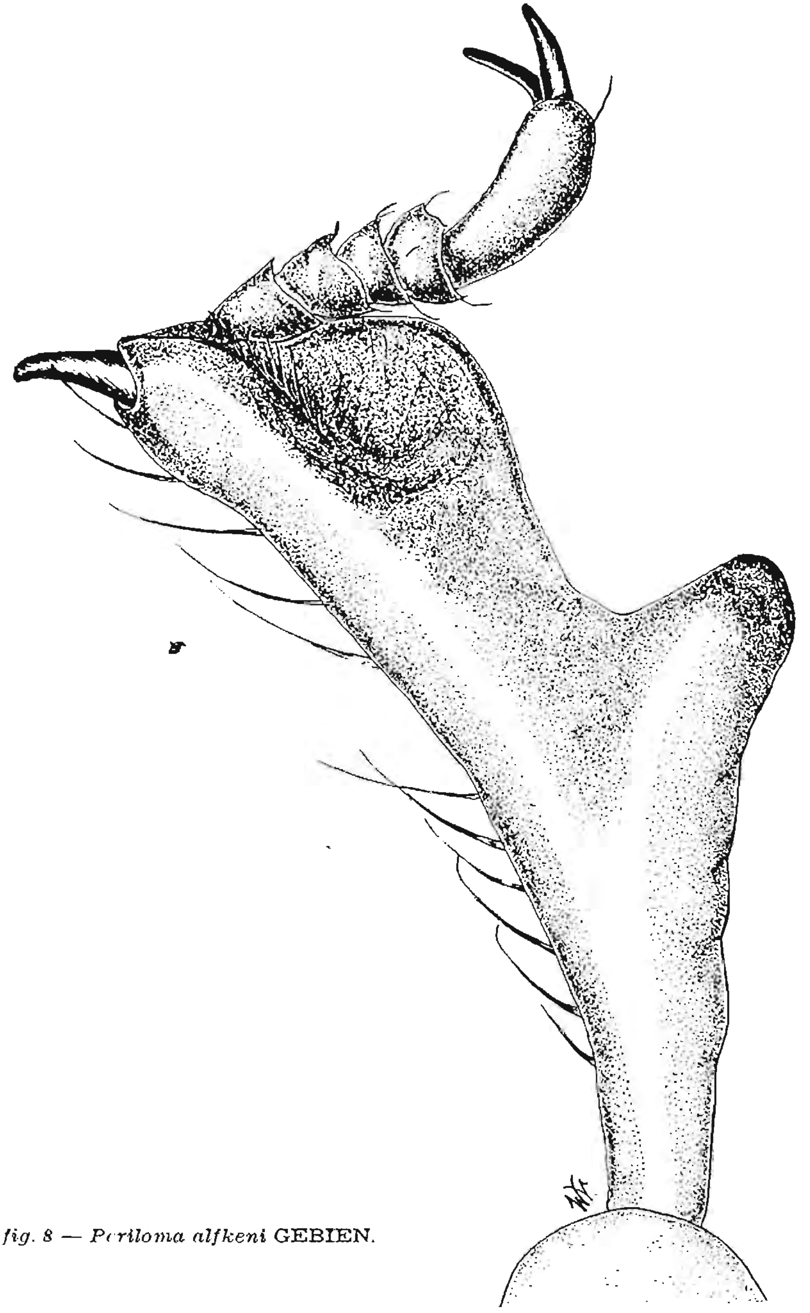


fig. 8 — Periloma alfkeni GEBIEN.

structures (see fig. 6). The usually cursorial legs of the Adesmiini and Zophosini have undergone the most striking changes; in some species they have changed to "diving-surfacing" (but not fossorial) legs, in others (e.g. *Cardiosis*) to "gliding" legs (cf. Plates IV, VIII and X), while they have become typically fossorial legs (see fig. 6) only in *Dactylocalcar* (typically fossorial legs of shovel-like action occur otherwise among the dune-dwellers only in some Stizopina, e.g. *Psammogaster* [see fig. 7], but in this case the fossorial leg has been maintained as a primitive organisation-feature which is peculiar to many Opatrini).

The striking modification of the cursorial legs into "gliding" legs occurs exclusively in *ultra-psammophilous* groups, such as the heliotactic *Cardiosis* (cf. Plates IV and VIII) or the nocturnal *Vernayella* (cf. Plate X). As opposed to the cursorial leg (cf. Plate V), in which the elongation of the femur and tibia is correlated with an abbreviation of the tarsus, the reversed ratio characterizes the "gliding" leg on account of the extraordinary elongation of the sand-contacting tarsus but shortening of the tibia and femur. In some *Vernayella* the intermediate tarsus is twice the length of the respective tibia; this formation is certainly connected closely with the very rapid and somewhat gliding movements on the surface-sand of the *quasi-fluid* leeward slopes of dunes, recalling the Heteroptera of Veliidae, Gerridae and Hydrometidae, which all move — in a similar way -- rapidly on the undulate surface of water.

Mention should be made also of the laterally compressed feet in the Calognathini, Vansoniini and some Adesmiini; such "sand-shoes" (see figs. 3 and 4) are known to occur also in Tenebrionids of other arid areas of Africa (e.g. Sahara) and are connected undoubtedly with digging and tunnelling in blown sand, and of broom-like action on account of dense brushes of bristles.

Statements in literature, which refer to the extreme elongation of the cursorial legs in the Adesmiini of the Namib dunes, have to be rejected; they are based on an incorrect report by GEBIEN who indicates as a classical example the extraordinarily elongate legs of *Stenocara phalangium* (which stretch to more than three times the length of body), see Plate V. This species, however, does not live in the dunes, but on the grassy plains with a consolidated soil surface. The legs of the true dune Adesmiini, though certainly of an elongate type, are considerably shorter, e.g. those of *Stenocara desertica* are quite three times shorter than those in *Stenocara phalangium*. Thus, locomotion by great speed does not seem to be correlated necessarily with an elongation of the legs.

Another feature of great peculiarity is the almost complete atrophy of the eyes in some of the dune-species, such as *Dactylocalcar caecus* (see Plate VIII) and *Syntyphlus subterraneus*. These are the only cases known in the Tenebrionids of the world, in which anophthalmy occurs in psammophilous groups.

The morphology of the few larvae studied does not agree with the generalising conclusions at which PIERRE arrived by the study of the dune-larvae from the north-western Sahara. There is no conformity with regard to a hypertrophic development of tactile sense bristles, and in none of the cases was it possible to interprete this vestiture as a character of adaptation to the life in sandy dunes. For instance the derivatives of the cuticle are subidentically developed in the larvae of the three ecologically very different Adesmiini *Onymacris unguicularis, Stenocara eburnea* and *Epiphysa flavicollis,* although the first is heliotactic and *ultra-psammophilous,* the second diurnal and living on gravelly or sandy plains, while the last mentioned species occurs on hard soils, also rocks, and is of nocturnal habits. On the other hand, of the three sympatric, ecologically subidentical, *ultra-psammophilous Lepidochora*-species *kahani, porti* and *discoidalis*. the larvae of the two former species possess a strikingly dense and elongate vestiture which, again, *discoidalis* lacks entirely. The morphological differences between the larvae of *ultra-psammophilous* species (such as *Onymacris unguicularis* and *laeviceps*) and those of *plant-followers* in the dunes (e.g. *Onymacris rugatipennis* and *plana*) were found to be much less conspicuous than expected and confined rather to a differentiation in the arrangement of the bristle-pattern on legs and pygidium.

If we compare the richness, endemism and specialization of the Tenebrionids of the Namib dunes with the Tenebrionid fauna of other dune regions on the African continent, we find that the sandy dunes of the Sahara apparently lack those *ultra-psammophilous* inhabitants of the vegetationless biotope of the dunes. There are no *ultra-psammophilous* species either in the red dunes of the southern Kalahari, but only *plant-followers*. We were also unable to observe any indigenous life at all on the small dunes of the semi-desertic area in south-western Madagascar, or on the barren, shifting barchan dunes of Somalia, though the latter form considerably extended systems in the coastal area of former British Somaliland (cf. Plate III), are situated in an area of good seasonal rainfall in the Benadir Province, and are exposed to a high degree of moisture from the Indian Ocean in the Mijertain.

These findings may entitle us to conclude that the richness and endemism of the Namib fauna do not depend so much on a given quality of biota, but are rather the result of the long and undisturbed duration of these special biota. This does not imply that the sand of the dunes may be very ancient but certainly means that desertic conditions have prevailed over an extraordinarily long period. and implies in particular the factor of erosion and consequent production of loose sand and dunes. We must also assume that the configuration of the dune systems has changed over the ages and differed considerably from the recent extension of the dunes. This is proved beyond doubt by the striking fact of generic and sometimes even specific identity of strictly dune-loving and also *ultra-psammophilous* Tenebrionids of widely separated dune-systems. So identical genera and often identical species populate the dune systems of the *Southern* and *Northern Namib,* although, based on the recent configuration, both systems are separated by a very wide duneless area stretching from the Kuiseb to the Huab Rivers. As strictly dune-loving species depend for their dispersal on the medium of *quasi-fluid,* shifting sand — (cf. fish, which can move only in water) — we must conclude that they originated in a common and continuous, ancient system of dunes, which later became discontinuous, probably on account of certain climatic changes.

Before concluding the present outlines, we must emphasize the fact that the multitude of biological problems, as met with in this desert, have hardly been scratched. The high degree of peculiarity of the Namib follows from its great and undisturbed age in association with the quite unique climatic conditions, culminating in the development of a complex *ultra-psammophilous* fauna of the vegetationless sand. This peculiarity becomes very evident, if we try to apply to the life in the Namib the general biological rules as derived from the many careful scientific investigations into the life in other deserts of the world. They are found to be opposed to our observations, according to the following rough scheme.

Morpho-ethological adaptations, assumed to occur generally in deserticolous Tenebrionids, based on connections found to exist between the reaction to humidity (hydric equilibrium) and the milieu (as listed by MARCUZZI).	**Observations on the morphology and behaviour of Namib Tenebrionids.**
Increase in the volumen of the subelytral cavity (protection from heat and transpiration).	Subelytral cavity varying from extreme (e.g. *Onymacris,* see fig. 1) to practically non-existent (e.g. *Stips,* see fig. 1); extreme subelytral cavity occurring also in nocturnal species enjoying a high degree of night-moisture (e.g. *Epiphysa,* cf. Plate VI).

Dark colour of the integument, due to the presence of melanogen and melanin in the cuticle (various theories concerning protection from radiation, stimulation of metabolism by absorption of actinic rays, etc.).	Colouration varying from entirely black (cf. Plates V and VI) and a high percentage of melanogen and melanin in the cuticle (diurnal and nocturnal species), through yellow to reddish-brown (cf. Plates I and X), with a lesser percentage of pigment (depigmented, only nocturnal species), and through pale and whitish produced by derivatives of the pigmented cuticle (diurnal and nocturnal species, cf. Plates I VII and IX), to structurally white and unpigmented elytra (diurnal species occurring exclusively in the *Northern Namib*, cf. Plate IX).
Generally nocturnal habits (enjoyment of night-moisture, absence of direct insolation, etc.).	Extremely heliotactic and otherwise diurnal species outnumbering the nocturnal ones.
Fossorial legs in larvae and often adults.	Fossorial legs occur in the larvae of practically all ground Tenebrionids, whether living in deserts or tropical rain forests. In adults typically fossorial legs have been observed only in a few Stizopina (see figs. 7, 8), however, not as an adaptive but a phylogenetic organisation-character; the modification of the constitutional Zophosini-cursorial leg into an adaptive, typically fossorial leg is known only of the permanently under-sand *Dactylocalcar caecus* (see fig. 6 and Plate VIII).
Large body size (protection from transpiration).	Body varying from large and medium-sized to extremely small (smallest forms of Tenebrionidae) in both diurnal and nocturnal species.

Comparatively small spiracles.	No observations.
Frequently shortened and broadened shape of body in the larvae.	Larvae usually very slender and elongate (Adesmiini, Zophosini, etc.), rarely dilated and shortened (e.g. *Lepidochora*).

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REFERENCES QUOTED:

BAGNOLD, E. A. — 1954. The physical aspects of dry desert. *Biol. Deserts, London,* 7—12.

BODENHEIMER, F. S. — 1954. Problems of physiology and ecology of desert animals. *Biol. Deserts, London,* 162—167.

BOLWIG, N. — 1957. Experiments on the regulations of body temperature of certain Tenebrionid beetles. *J. ent. Soc. S. Afr.,* 20: 454—458.

BRINCK, P. — 1956/57. The food factor in animal desert life. — *B. Hanström Zool. Pap., Lund,* 120—137.

BUXTON, P. A. — 1924. Heat, moisture, and animal life in deserts. *Proc. roy. Soc.,* B, 96: 123—131.

FIORI, G. — 1957. Ecologia ed ethologia dell'entomofauna dello Uadi Caam. *Boll. Ist. Ent. Univ. Bologna,* 22: 1.

GEBIEN, H. — 1938. Die Tenebrioniden der Namibwüste Südwestafrikas. *Abh. naturw. Ver. Bremen,* 30: 20—107.

HAFEZ, M. & MAKKI, A. M. M. — 1959. Studies on desert insects in Egypt. — III. On the bionomics of *Adesmia bicarinata. Bull. Soc. ent. Egypte,* 52: 89—113.

HESSE, A. J. — 1938. Some adaptive responses of insect life to semi-arid conditions in South Africa. *S.Afr. J. Sci.,* 35; 69—91.

KAISER, R. — 1926. *Die Diamantenwüste Südwest-Afrikas.* Berlin, 2, 856pp.

KOCH, C. — 1953. S.A. Tenebrionidae. — XXI. On some new endemic Opatrinae from the Namib Desert. *Ann. Transv. Mus.,* 22: 231—252.

— 1955. The fauna of the Namib Desert. *Bull. Transv. Mus.,* 2: 4—5.

— 1960. The Tenebrionid beetles of South West Africa. *Bull. S. Afr. Mus. Ass.,* 7: 73—85.

KÜHNELT, W. — 1957. Weiß als Strukturfarbe bei Wüstentenebrioniden. *S. B. öst. Akad. Wiss., math.-nat.,* 1, 166: 103—112.

LOGAN, R. F. — 1960. The Central Namib Desert. *Publ. Nat. Acad. Sci. Washington,* 758, 162pp.

MARCUZZI, G. — 1960. Rapporti tra equilibrio idrico e ambiente nei Coleotteri Tenebrionidi. *Arch. zool. (ital.), Napoli,* 45: 325—342.

PÉRINGUEY, L. — 1885. First contribution to the South African coleopterous fauna. *Trans. S. Afr. phil. Soc.,* 3: 74—149.

PIERRE, F. — 1958. Ecologie et peuplement entomologique des sables vifs du Sahara nord-occidental. *Publ. Centr. Rech. Sci. biol., Paris,* 1, 332pp.

WALTER, H. — 1937. Die ökologischen Verhältnisse in der Namib-Nebelwüste. *Jb. wiss. Bot.,* 84: 58—222.

OPSOMMING:

In teenstelling tot die heersende toestande in ander woestyne gaan die onvrugbaarheid van die sanderige duine gepaard met 'n buitengewone ryk Tenebrionid-fauna. Die spesies wat hulself aangepas het by die uitermatige biotoop van vegetasielose sand kan omskryf en na verwys word as *ultra-psammophilous*, omdat hulle heeltemal onafhanklik is van aktiewe plantegroei, en oorals in die onvrugbare sandstreke voorkom sonder die neiging om deur plante of enige ander sentrale doelwit aangelok te word. Die grondbestanddele van die habitat van hierdie *ultra-psammophilous* Tenebrionidae word saamgevat in twee elemente, nl. sand en wind. Die los sand verteenwoordig die maklik deurdringbare *kwasie vloeibare* medium, terwyl die wind die sand na 'n optimum biotoop verander nie alleenlik deur die invoering van vogtigheid en voedingstowwe (nl. organiese deeltjies) nie, maar ook deur die vorming van die sand in die golwende onafgebrokenheid van die *afdraande oppervlaktes* van die duine; 'n formasie wat hoofsaaklik verantwoordelik is vir die skepping van geskikte lewenstoestande, tewete die opvangs en bewaring van waterneerslae, skaduwee, optimum endoklimaat van die sand, ens.

Melding van 'n paar van die morfologiese, fisiologiese en etologiese aanpassingsvermoës tot hierdie besondere lewensvoorwaardes is gemaak. Daar is bevind dat die algemene biologiese reëls wat na navorsing in ander woestyne opgestel is, op die Namibwoestyn nie van toepassing is nie. Die *ultra-psammophilous* Tenebrionidae speel 'n dominante en basiese rol in die samestelling van die fauna van Suidwes-Afrika onder omstandighede wat biologies uiters sleggesind is soos in die plantelose duine van die Namibwoestyn gevind word. Hierdie kewers is die direkte afstammelinge van die fauna van die Karroo—Kalahari—Namakwaland systeem. Ons kom dus tot die gevolgtrekking dat die rykdom en inheemsheid van die fauna van die Namibwoestyn nie soseer afhanklik van 'n sekere hoeveelheid biota is nie, maar meerendeels voorvloeiende is uit die lang en onverstore duurtyd van hierdie spesiale biota.

ZUSAMMENFASSUNG:

Im Gegensatz zu den in anderen Wüsten herrschenden Bedingungen, weist das vegetationslose Dünenmeer der Namib einen außerordentlichen Reichtum an Tenebrioniden („Schwarzkäfern") auf, welche diesem Biotop eigentümlich sind. Für diese Arten wird die ökologische Bezeichnung *„ultra-psammophil"* geprägt; sie hängen nicht mehr, wie die *Pflanzen-Folger* der Dünen, von aktiver Vegetation ab, sondern leben irgendwo in der vegetationslosen Leere der Sanddünen, ohne um irgendein zentrales Objekt (z. B. Pflanze oder Stein) zu gravitieren. Die primären Umweltfaktoren dieser *ultra-psammophilen* Arten können zuletzt zurückgeführt werden auf nur zwei, nämlich Sand und Wind: der lose Flugsand stellt das leicht durchdringliche, *quasi-flüssige* Medium dar, während der Wind den toten Sand in einen optimalen Biotop verändert, nicht nur auf Grund der von ihm eingeführten Feuchtigkeit und Nahrung (letztere in Form von organischer Substanz aus dem Hinterland), sondern auch durch die durch ihn bedingte Umformung des Sandes in die wellige Kontinuität der *schiefen Ebenen* der Dünen — eine Konfiguration, welche in der Hauptsache verantwortlich ist für die Schaffung von günstigen Lebensbedingungen, wie z. B. das Auffangen jeglicher Art von Niederschlag, Bildung von Schatten, optimales Endo-Klima des Sandes, etc.

Auf einige der morphologischen, physiologischen und ethologischen Anpassungserscheinungen an diese besonderen Lebensbedingungen und zahlreiche, auffallende Abweichungen von den allgemeinen, biologischen Regeln über Wüstenleben, wird hingewiesen. Die *ultra-psammophilen* Tenebrioniden stellen die dominierenden Elemente in der Zusammensetzung der südwestafrikanischen Fauna unter extrem-lebensfeindlichen Bedingungen (vegetationsloser Sand) dar, ihre Abstammung kann auf die ursprünglichen Bewohner des Trockengebietes von Karroo—Kalahari Namaqualand zurückgeführt werden, und sie verdanken ihre Entstehung weniger der Qualität der speziellen Lebensbedingungen als dem ungeheuren Alter und ungestörtem Bestand derselben.

Plates to article:—

C. Koch, Some aspects of abundant life in the vegetationless sand of the Namib Desert dunes (cf. pp. 8—34).

Explanation to Plate I

Lepidochora kahani KOCH, discovered in the dunes figured on Plate II, one of the numerous species of the nocturnal to crepuscular and *ultra-psammophilous Lepidochora* which populate the vegetationless dunes from the Orange River northwards as far as Porto Alexandre in southern Angola. The body is more or less strongly complanate, the depigmented and hygrophaneous cuticle densely covered with white scales (strongly magnified, below), and the anterior margin of head serrate (magnified contours, above), while the tibial calcaria are extended, finger-like and multi-digitate (magnified, below).

Plate I (painting A. von Peez, Brixen)

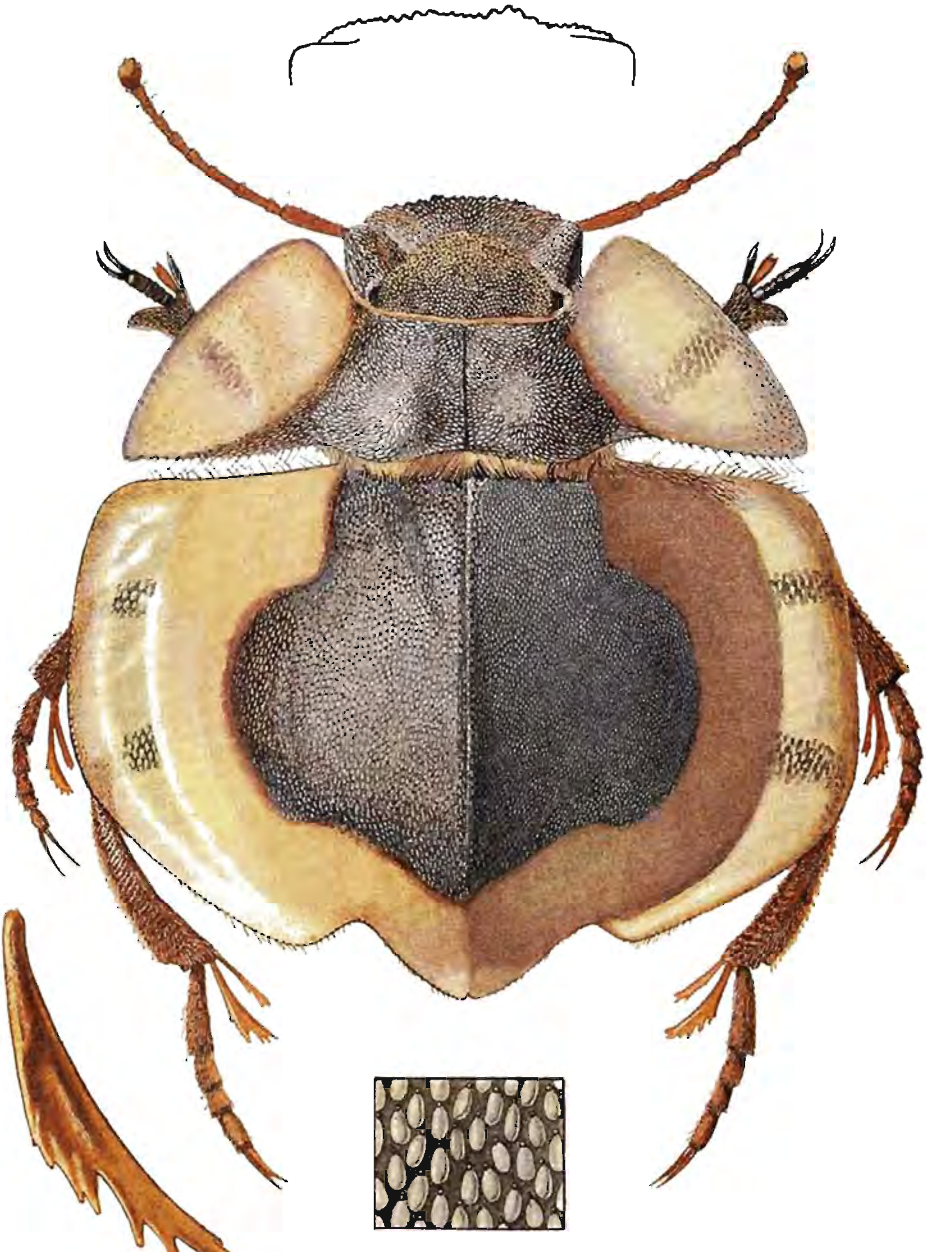
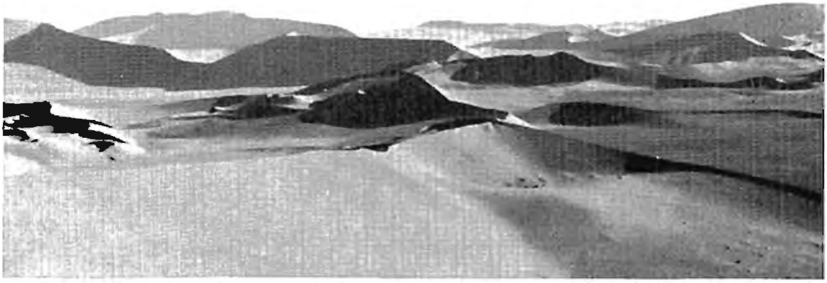
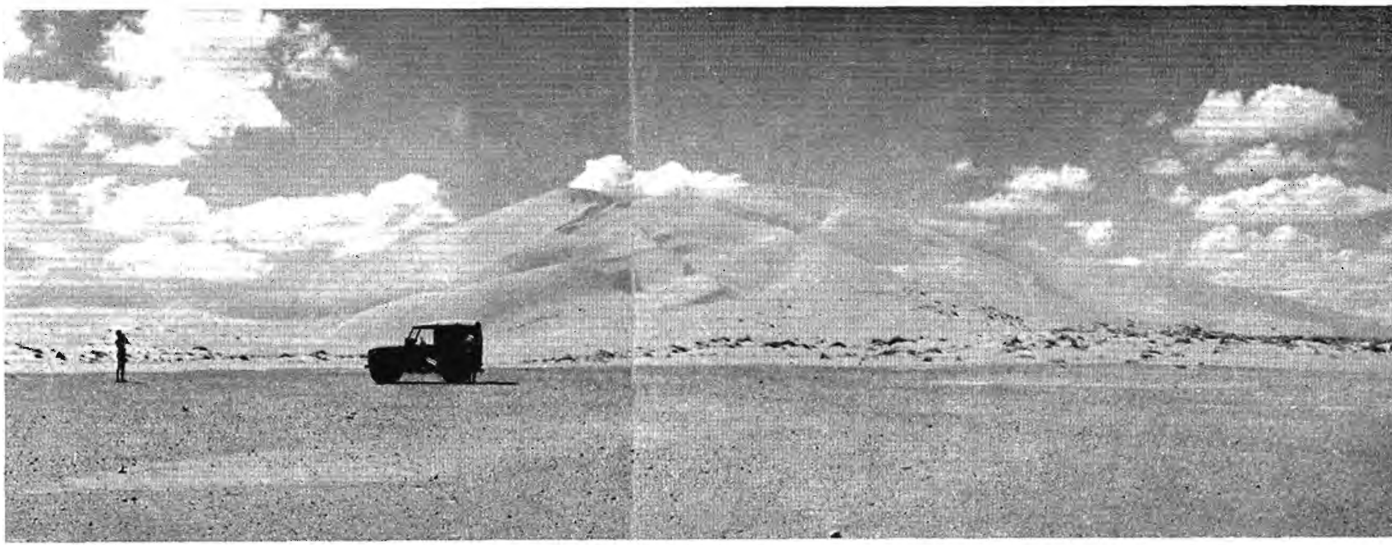


Plate II (phot. K. T. Lilier, Saarland)



Configuration of the *inclined planes* in the barren dunes of the *Southern Namib* (Sossus Vlei area). Note the favourable shade conditions at the *quasi-fluid* leeward slopes, where most of the *ultra-psammophilous* species (both heliotactic and nocturnal ones, in adult as well as early stages) are concentrated.

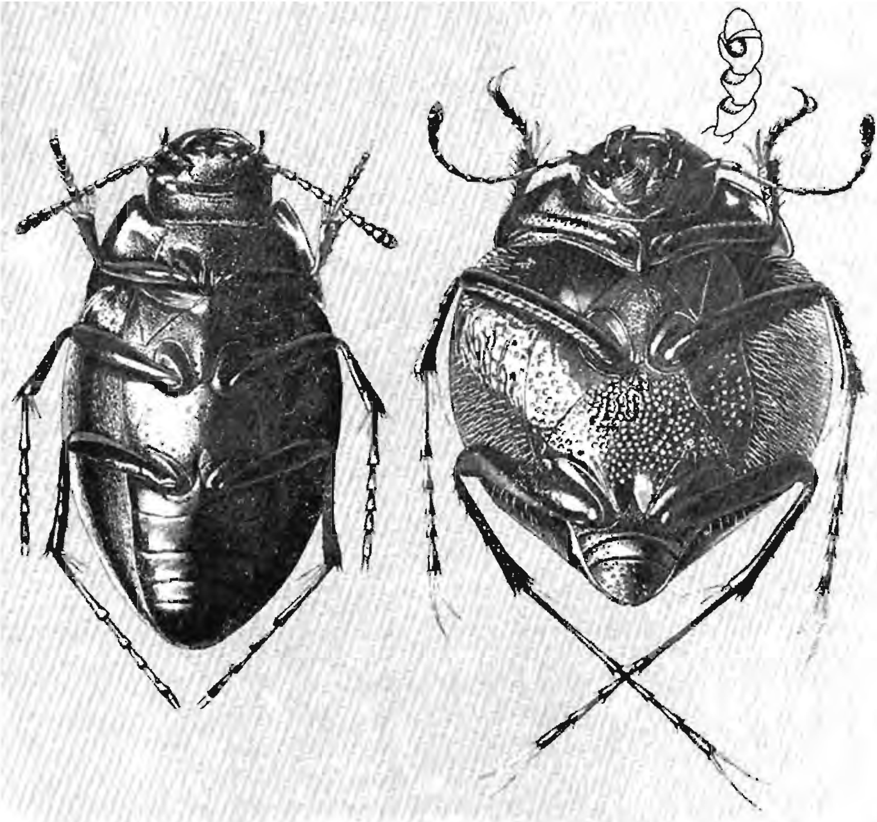
Plate III (phot. C. F. Hemming, Nairobi)



System of high barren dunes in the coastal area of former British Somaliland (east of Berbera). Contrary to the development of a rich *ultra-psammophilous* fauna in the Namib dunes, these Somalian dunes are devoid of any *ultra-psammophilous* life, harbouring only a few *errant plant-followers* of Saharan origin.

Plate IV (paintings A. von Peez, Brixen)

Modifications of body structures in connection with *ultra-psammophilous* and heliotactic life habits and development of great, "semi-volant" speed.



Left. *Microsis vilhenai* KOCH, a heliotactic species living in blown sand of the *Northern Namib.* The formation of the underside of body does not differ much from that of the ascendent *Zophosis;* in the legs the tendency for a change to the "gliding" type can be seen in the moderate elongation of the tarsi.

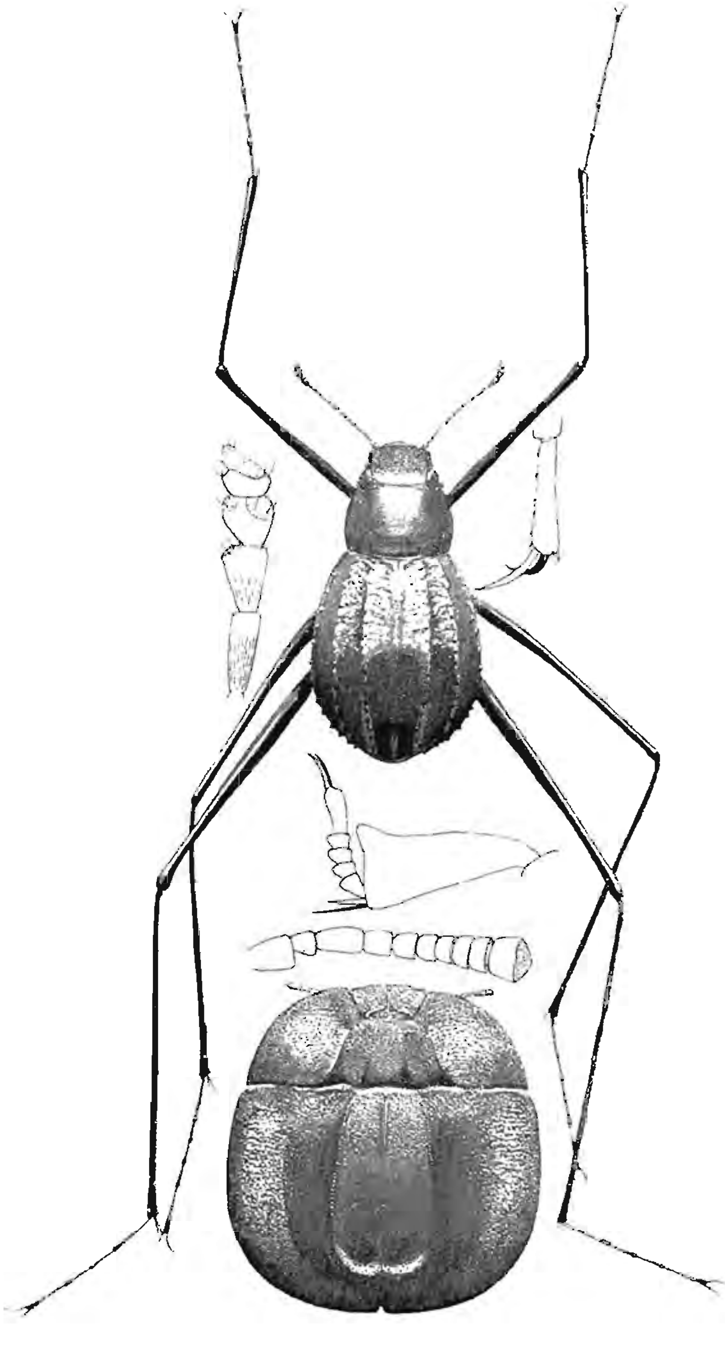
Right. — *Cardiosis moufleti* DEYROLLE, a greatly heliotactic and *ultra-psammophilous* species of the *quasi-fluid* leeward slopes and "smoking" crests of the barren dunes *(Northern Namib).* Endowed with an extraordinary speed of cursorial and diving movements, the underside of body is strongly convex and dilated, the metasternum characterized by its considerable extension in association with the subtelescopic contraction of the abdomen, the legs are transformed into typical "gliding" legs through the extraordinary elongation of the intermediate and posterior tarsi, the posterior coxae are powerful, and the tibial calcaria and claws are hypertrophic, the latter with abbreviate inner spur.

Explanation to Plate V

Above. *Stenocara phalangium rufofemoratum* KOCH, an extraordinarily fast, heliotactic runner of the grassy and sandy plains of the *Southern Namib*, carrying the body high above the heated surface of the sand. Body with large subelytral cavity; the legs exceedingly elongate (stretching to three times the length of body), with atrophied armatures, calcaria and claws, and of typically cursorial proportions on account of the shortened tarsi.

Below. *Stips stali* (HAAG), a strongly sclerotized, black, nocturnal and *errant plant-follower* of the dunes. Body contracted and very complanate, with reduced subelytral cavity; the legs are very short, of subfossorial type, moving underneath, and concealed by, the disc-like dilation of the dorsum of body. Hitherto the complanation of body has been interpreted as an adaptation to petrophilous life habits (e.g. HESSE quoting *Stips* as an example); however, in *Stips* the complanation of body represents a primitive organisation-feature occurring in both the petrophilous and psammophilous species.

Plate V (paintings H. John, Bad Nauheim)
Extremes in shape of body and appendages in two Namib species.



Explanation to Plate VI

Left. — *Onymacris plana plana* PÉRINGUEY, a heliotactic, dimorphic and *errant plant-follower* (narras) of the barchan dunes. A male specimen with umbrella-like complanation of elytra and consequent reduction of the subelytral cavity as a secondary modification; in the female the elytra have maintained their high degree of convexity as a primitive organisation-feature peculiar to the genus *Onymacris* (cf. also text fig. 1, above); legs with hypertrophic tibial calcaria and claws.

Right. — *Epiphysa louwrensi* KOCH, a psammo-petrophilous species of the coastal plains south of Luderitz. This species, though closely related to the diurnal Adesmiini in both its adult and early stages, has changed to strictly nocturnal habits but under preservation of the primitive organisation-structures as occurring in all the diurnal Adesmiini, namely the hermetic connation of the sutures and the very strong sclerotization of the body, as well as the extremely increased volumen of the subelytral space; note the moderately elongate tibial calcaria and claws as compared with the respective parts of body in the dune species figured at left. During daytime, this species and most of the other *Epiphysa* are found hiding under stones, a behaviour which, on account of the extreme convexity of body, appears to be contradictory to the general assumption that petrophilous Tenebrionids are characterized by a complanation of body (see also remarks to Plate III).

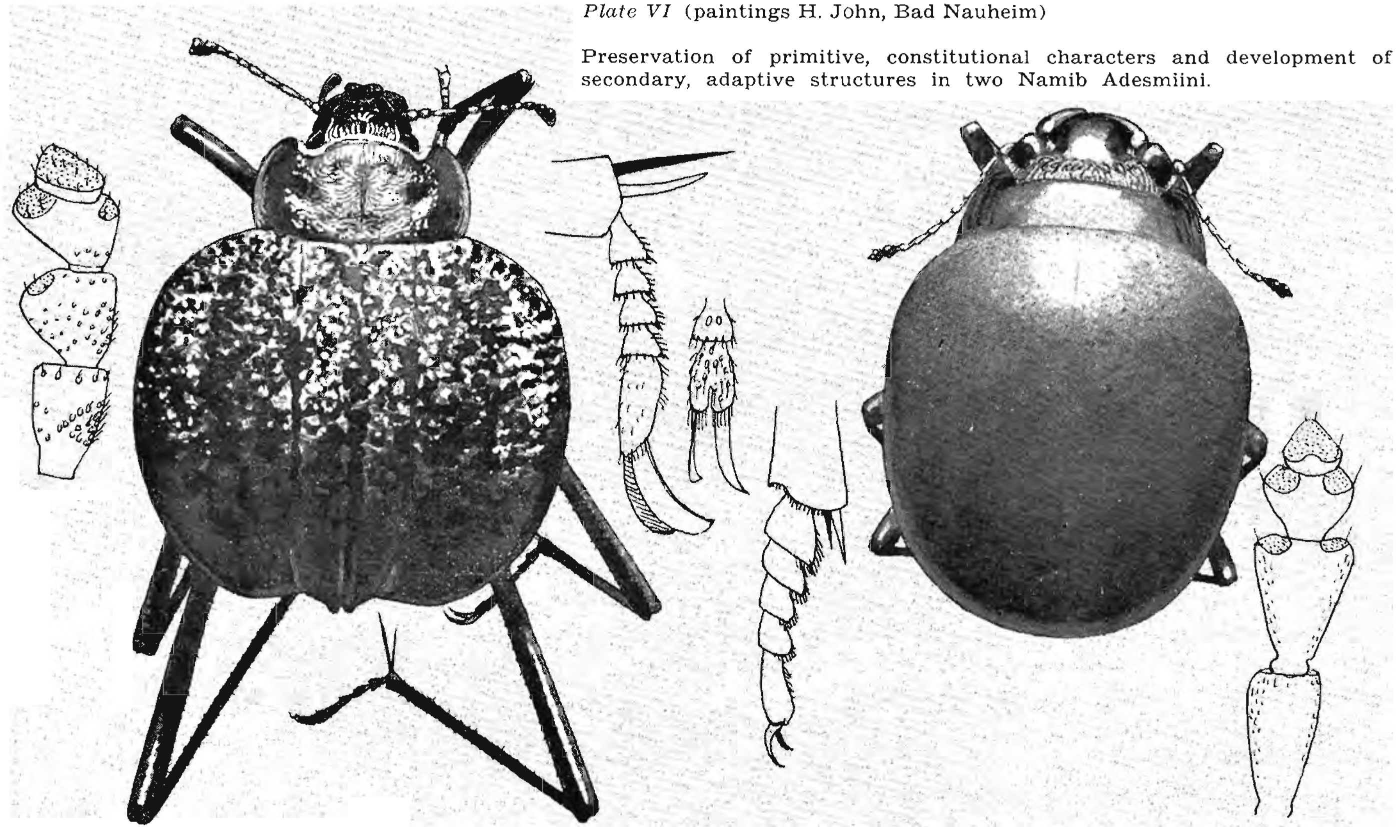


Plate VI (paintings H. John, Bad Nauheim)

Preservation of primitive, constitutional characters and development of secondary, adaptive structures in two Namib Adesmiini.

Explanation to Plate VII

Left. A male of *Calognathus chevrolatii eberlanzi* KOCH, belonging to a diurnal and errant species of the *True Namib*, which tunnels in blown sand and the fore-dunes. Body of complanate formation and covered with white and transparent squamiform derivatives of the cuticle, the legs with "sand-shoes"; strikingly characterized by the stag-beetle-like hypertrophy of the mandibles in the male. Specimens of this species were watched carrying small leaves and seeds of plants into their burrows, as was frequently observed also in *Gonopus* of Platynotini (BRINCK) and *Parastizopus* of Stizopina (Opatrini). At right, the normally developed ninth, tenth and eleventh segments of antennae

Right. - A male of *Vansonium bushmanicum* KOCH, a nocturnal, psammo-petrophilous species occurring in the *Transitional Namib* and the *Southern Namib*, tunnelling in blown sand under stones. Body greatly convex, the cuticle entirely clothed with a continuous layer of imbricate, whitish scales, the antennae with atrophied and connate three apical segments, the sutures of body hermetically closed, the eyes with erect scales between the acinose corneal facets, and the legs with "sand-shoes". At *right*, distal segments of antennae, with the normally developed seventh and eighth segments, but the last segment formed by a club which is composed of the connate ninth, tenth and eleventh segments.

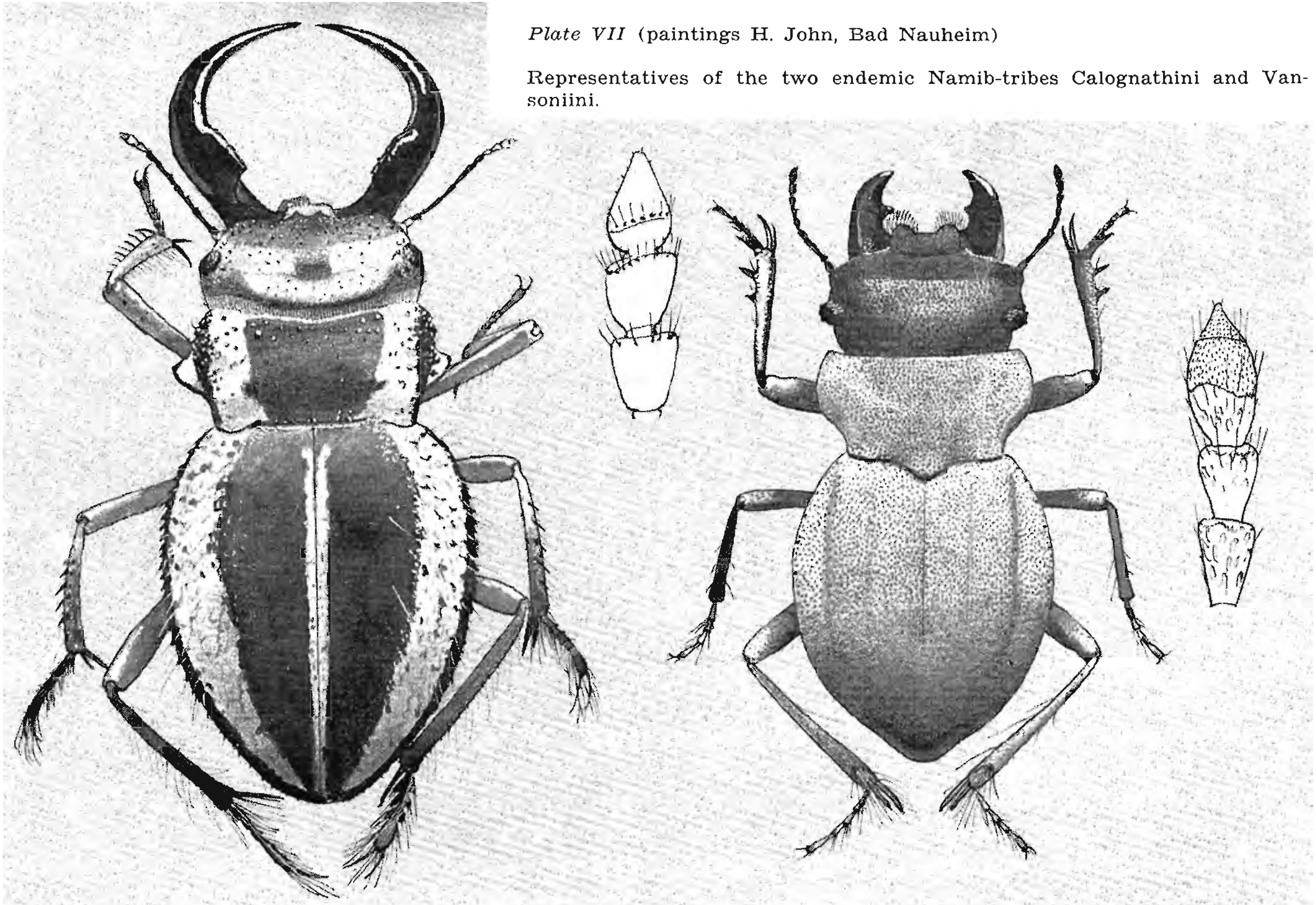


Plate VII (paintings H. John, Bad Nauheim)

Representatives of the two endemic Namib-tribes Calognathini and Vansoniini.

Explanation to Plate VIII

Middle. — A representative of the ancestral, primitive and diurnal genus *Zophosis*, occurring with several hundred, homogeneous species all over the African continent, but absent from the vegetationless portion of Namib-dunes. Eyes well-developed; legs cursorial, with subequally long claws and moderately elongate tarsi which are not longer than tibiae; antennae moderately elongate; body flattened to moderately convex; elytra shoulderless.

Right. — *Cardiosis fairmairei* PÉRINGUEY, a representative of the highly heliotactic and *ultra-psammophilous* genus *Cardiosis* which is endemic to the vegetationless dunes of the *True Namib*. The *Cardiosis* are Zophosini, which have responded to the *ultra-psammophilous* biotope by very striking, secondary modifications of body structures. The body is subglobular, extremely convex above and below, with protruding humeral portion, and the deepened sculptural patches on elytra are filled with a dense layer of a pulverulescent secretory substance of a sulphureous tint; the cursorial legs of *Zophosis* have become changed to the "gliding" type on account of the elongation of the tarsi which are decidedly longer than the tibiae; the antennae are very thin and very elongate; the claws are unequally long; and the eyes of very large size.

Left. — *Dactylocalcar caecus* GEBIEN, a subterraneous, blind, *stationary plant-follower* of the barchan dunes of the *Southern Namib*. This species is the only known representative of Zophosini, which has changed to nocturnal and probably permanently "under-sand" habits. It deviates extremely from the ascendent and primitive *Zophosis*-type by striking secondary, adaptive structures, such as anophthalmy, typically fossorial legs with shovel-like dilation of the contracted anterior tibiae, tarsi of the "gliding" type and hypertrophic armatures (cf. text fig. 6), shortened antennae, ciliate pronotum, and the extremely convex, subglobular body.

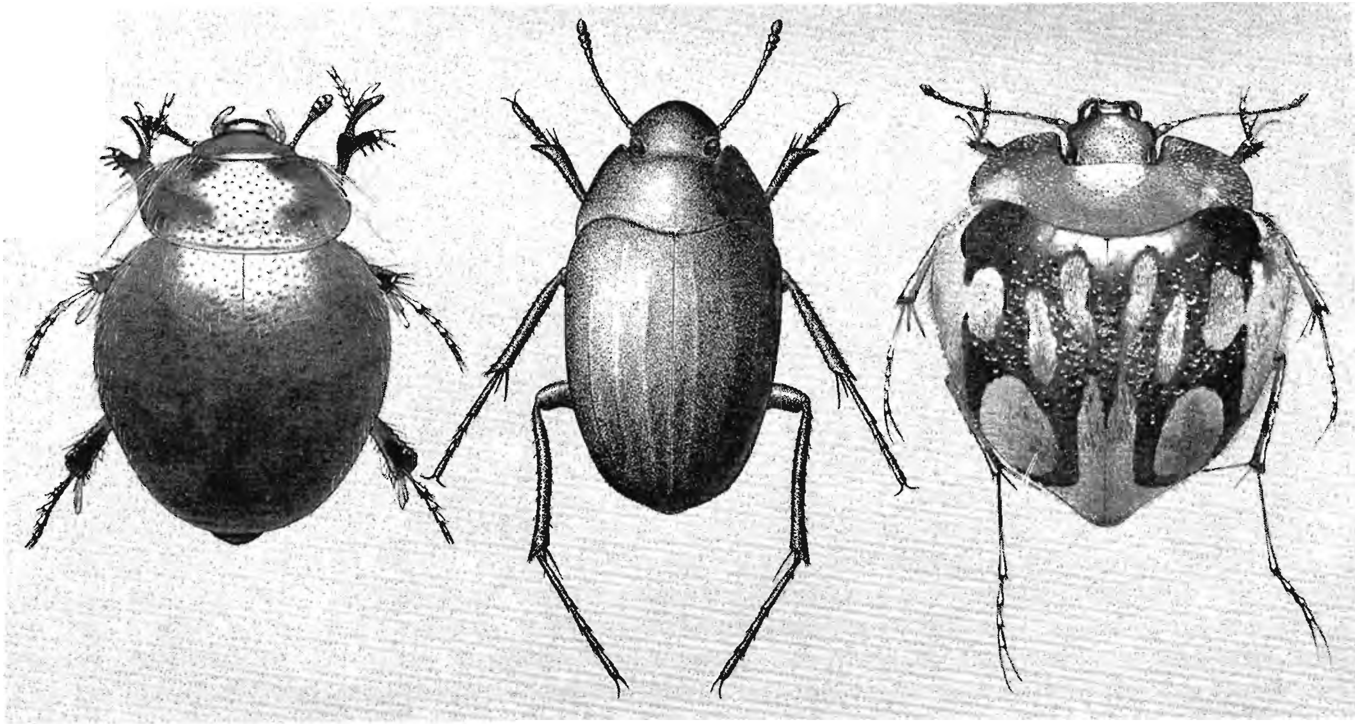


Plate VIII (paintings H. John, Bad Nauheim)
Modifications in the dune Zophosini, in connection with *ultra-psammophilous* and highly heliotactic, as well as permanently "under-sand" (or nocturnal) life habits respectively.

Explanation to Plate IX

Left. — *Stenocara eburnea* PASCOE, a diurnal to heliotactic runner of the plains, rock outcrops and mountains of the south-western part of the *Northern Namib*. It is a representative of the "white" Tenebrionids being strikingly characterized by the unpigmented and structurally white elytra; in the world this group of peculiar and convergent Tenebrionids is met with exclusively in the *Northern Namib*.

Right. — *Pachynotelus herminiferus* KOCH, a diurnal Cryptochilini-species of the sandy plains and dry river beds of the Roessing area *(Northern Namib)*. In this case the white colouration is produced by a thick layer of imbricate scales (strongly magnified, below). Note also the hypertrophy of tibial calcaria and the broom-like ciliation of tarsi.

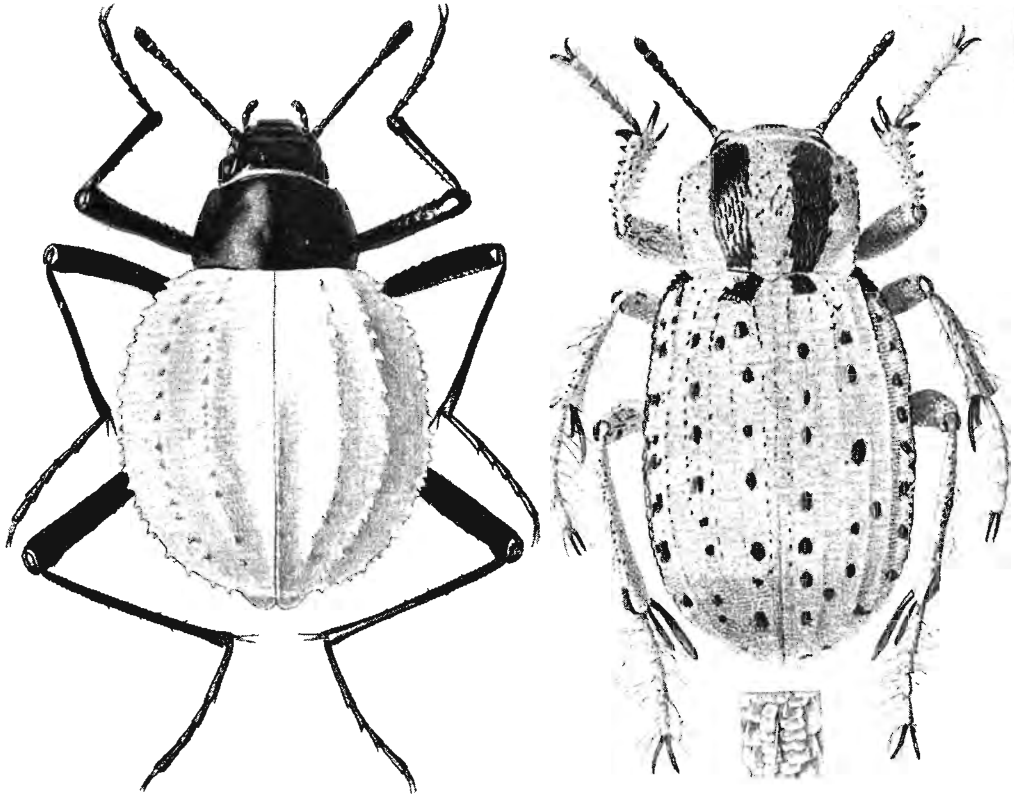
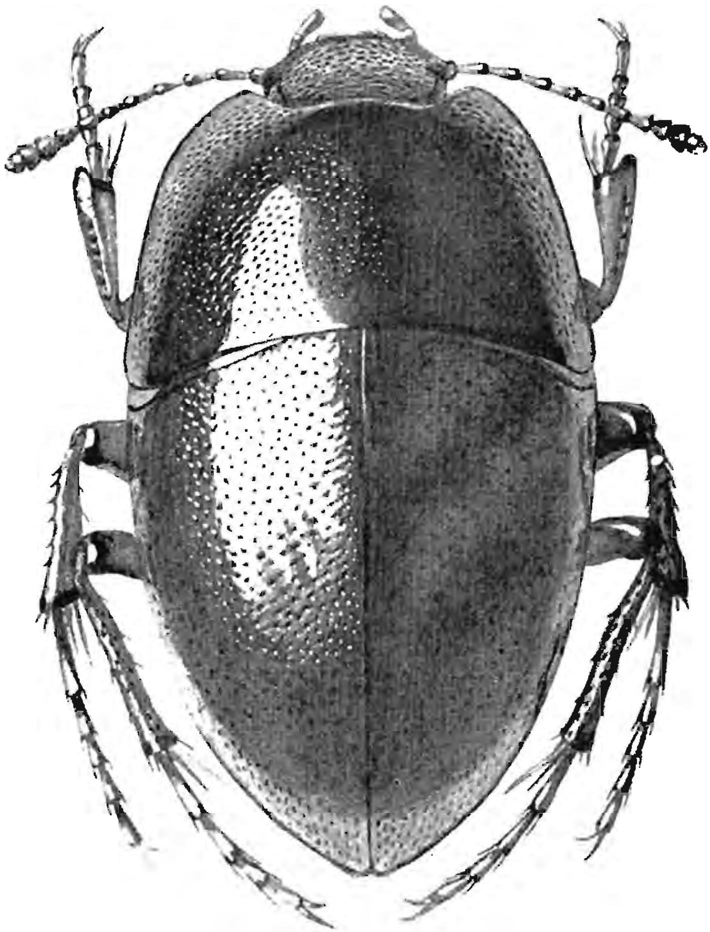


Plate IX (after paintings A. von Peez, Brixen) White colouration.

Plate X (after a painting A. von Peez, Brixen)

Modifications of body structures in connection with *ultra-psammophilous* but nocturnal life habits and development of great, "gliding" speed.



Vernayella noctivaga KOCH, a representative of the only known nocturnal runners *Vernayella* which are endemic to the vegetationless dunes of the *True Namib*. Although being entirely unrelated to the Zophosini (belonging to the Caenocrypticini), the *Vernayella* exhibit a certain degree of structural parallelism with their diurnal counterparts, viz. the *Cardiosis* of Zophosini; as in the *Cardiosis*, the legs are of the "gliding" type, characterized by the elongation of tarsi and the unequal length of claws. The cuticle is depigmented, varying from shiny and polished to hygrophaneous, diaphanous and opaque.