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DISPERSION AND TRANSLOCATION OF DUNE SPECIALIST TENEBRIONIDS IN THE NAMIB AREA

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(With 10 figures)

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ABSTRACT

A rich dune-specialised tenebrionid fauna was discovered on two isolated dunes of the southern Namib area. All six species recorded are known from a southern duneland, and three of them also from the central Namib. The southern origin of this fauna is explained by the northward shifting of the dunes. The general pattern of northward expansion of dune specialist biota is shown by the fact that all southern genera reach at least the Kunene in the north; there are genera, however, which start their northward dispersion in the central or northern Namib and are not represented in the south. The enigmatic distribution pattern of these biota could be solved, as well as the areas of origin of genera clarified. The biogeographic evidence also provides evidence for palaeoclimatology and sedimentology in the Namib area.

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FIGURE 9: The northern barchan (no 2) from the foot of the southern one (no 1).

FIGURE 10: The northern barchan (no 2) from the south. Note the closest barchan of group no 9 in the distance.

I. INTRODUCTION AND OBSERVATIONS

A number of tenebrionid species became highly specialised to ultra-psammophilous conditions, (term introduced by Koch (1961:10) for the biome of the vegetationless dunes), and can only be found on the loose sand of barren dunes, some of them associated with the scattered vegetation. Most of these species have developed such structural adaptation characters and habits which prevent them from entering any areas of a different substrate such as consolidated sand, coarse sand or gravel flats, etc. Unfavourable substrate conditions would prohibit them following their typical behavioural pattern of avoiding exposure and predation by diving in loose sand. Similarly the fine bristles and hypertrophic claws promoting their movement on loose sand would break on a coarse substrate, resulting in an obvious disadvantage at re-entering their optimal habitat. Their reproduction would also be severely hampered on a hard substrate from the oviposition to the emergence of the new adult generation. It is likely that any individual of these species would perish if accidentally carried onto such an alien substrate and would have an even smaller chance to give rise to a new generation.

As a matter of fact there is not a single record of an individual of the hyperpsammophilous species being found alive outside of their natural habitat of sand dunes.

The intensive entomological studies in the Namib area initiated by Dr Koch in the early '50s resulted in a wealth of information on these biota. His tabulated fauna list (1962) could since hardly be supplemented, thus the distribution pattern of these species was almost as well known at the time as it is today.

The combination of habitat conservatism and the recognised distribution pattern of genera and species posed problems and intrigued researchers ever since. The scientific dilemma presented appears around two focal points.

a. Problems of speciation of congeneric species which might occur at present on the very same dunes (*Lepidochora*, *Vernayella* and *Onymacris* species).
b. The problem of dispersion of species which now occur in widely separated dune-fields.

The first problem was approached by data collecting to probe the consequent microhabitat selection of congeneric species on various levels and aspect of dunes. Indeed a definite microhabitat preference could be found particularly in *Lepidochora* species. Though to my knowledge a firm statement was not published to this effect, it was claimed that such a stratification of microhabitats might have provided sufficient isolation for successful speciations.

The second problem, the occurrence of conspecific (in other cases congeneric) populations on widely separated dune systems, was explained by "a common and continuous, ancient system of dunes, which later became discontinuous . . ." (Koch, 1961:30).

Later observations and studies suggested however that neither of the explanations is satisfactory. Speciation, supported by vertical stratification on a dune, must be rejected as a possibility. Conspecific populations, inhabiting higher vertical positions on dunes, are more effectively isolated from each other on different dunes, than different species on the same dune. It was also observed that during the change of prevalent wind directions, when the crest and slip-faces of dunes re-arrange, the stratification of species largely breaks down. The conspecific populations take up their positions of preference gradually as the dunes settle down in accord with the new seasonal wind direction. In such circumstances, both the environmental differences, and the chances of population isolations are much too small and much too short to enable any speciation event to occur. Thus the explanation of the common occurrence of two or more congeneric species on the same dune must come from an entirely different quarter.

In the course of the present investigations the term pocket speciation was introduced (Endrödy Younga, 1978:810), and suggested that populations of psammophilous species inhabited accumulating sand pockets (e.g. at river mouths), became adapted to hyperpsammophilous conditions, and achieved thereby isolation from each other. Some of these population isolates, supported by environmental differences, speciated successfully. When the dunelands of the central Namib gradually formed a continuum, the limited distribution areas of these speciated populations became interconnected and colonised each other's territories without genetic interference. It is likely that the currently observed stratified microhabitat selection of the different species on the same dune reflects the sand quality of sand pockets where those species have evolved. But where were those sand pockets of speciation? How did the mixed fauna of the central Namib evolve, and how did the distribution of isolate taxa come about?

No alternative explanation for the disjunct distribution of taxa has been offered since Koch, who invoked the ancient continuity of dune systems to solve the problem (1961:30). The alleged extreme age of the dune-Namib has been disputed in recent years (Endrödy-Younga, 1978:809; 1982), and it was concluded that the massive sand accumulation and dune-sea formation in the central Namib does not date back beyond the late Quarternary period. This new dating of the dune-Namib alters our concept on the origin of its fauna entirely, but actually allows ample time for subsequent re-arrangements of dune systems. Of course one "ancient continuity" could not cause the multitude of different distribution patterns, though an ever changing, kaleidoscope-like recombination of dune systems could. It will be shown that this is not the case either. Events take a much more simple course in nature than we often postulate to them.

THE DISPERSION AND TRANSLOCATION OF BIOTA BY MOVING DUNES

The southern Namib, as defined by Koch (1962:79) is the section of the desert between the Orange and Koichab Rivers. This is largely a hilly gravelly and sandy area with rocky outcrops and with scattered dune-fields from the banks of the Orange River. The duny areas are widely interrupted between north of Oranjemund and Bogenfels, then again between Bogenfels and Pomona. From Prinzenbucht a more or less continuous sandy area with low dunes turns inland in a NNE direction.

I had the opportunity to visit the southern Namib area in the company of Dr Penrith in July 1981. We were on our way southward from Lüderitz.

On the 23rd July two barchan dunes were sighted partly overlying the road. These dunes were isolated by about a kilometre from others to the north and to the west. From there on the road runs for a long distance through a rocky and duneless landscape. On noting this southward isolated position of the dunes we decided to explore them on the route back from Oranjemund. On the afternoon and night of 30th July we collected intensively. The result was staggering. Almost all dune species known from the Bogenfels dunes, some 60 km S of the site *(Lepidochora pilosa, L. discoidalis, L. eberlanzi, Onymacris lobicollis, O. unguicularis, O. laeviceps),* were found in large numbers, but not a single species, hitherto only known from the central Namib dune-sea, even as close as 50 km to the north (Map 1), was present *(Lepidochora argentogrisea, L. kahani, L. porti).*

The problem then was: how and from where did these beetles come to inhabit these isolated dunes? Some change in the position or size of the dunes was clearly indicated by a number of subsequently built roads which now run into the sand walls. I approached the northern dune from the south and noticed that all woody plants on this side were dead and flattened to the gravelly ground. However, on the north side of the large barchan all woody plants were erect and alive. Thus, the dunes seemed to be moving from south to north. The first information from an official (I do not name him, though I warned him of the contrary) was disheartening. I was assured that those dunes did not exist six years ago, and the sand has probably accumulated around a discarded object such as a petrol drum, since.

There was also a line of pegs found on the south side of the northern dune, following approximately the foot of the dune, at a distance of about 15 m. A subsequent exchange of letters and telegrams revealed that the pegs were set by Mr Bom Coetzee in August 1971, moreover not on the south side, behind the dune, but in front of it!

The final proof of the northward movement of the dunes was provided by two sets of aerial maps which were shown to us at the Trigonometrical Survey, Windhoek. The two sets of photos were taken in 1967 and 1978 respectively and show clearly the northward shifting of these barchans and all other dunes shown on them.

Thus the hyperpsammophilous fauna has evidently travelled with the dunes ever since they broke off from the south dunelands, and did not colonise them in their isolated position. Thus the dispersion is not due to the movement of the individuals, away from their oiginal habitats, but to the translocation of their substrate and habitat, the dunes!

II. DISCUSSION

CONCERNING THE BIOTA

Table 1 shows the distribution pattern of dune specialist tenebrionids through the Namib area, between the limits of the desert, the Orange River in the south and the Coroca River in the the north (Angola). In the first column species are marked which were found on the Grillental barchans. The distribution patterns in combination with the discovered Grillental fauna suggest the following conclusions.

	At Grillental	Consecutive sections from south to north: to Koichab	ot Kuiseb	to Huab	to Kunene	to Coroca	North of Coroca	
Lepidochora pilosa Koch 1950	X	X						
diaphana Koch 1950		X						
discoidalis Gebien 1938	X	X	X					
eberlanzi Gebien 1938	X	X	X	X				
argentogrisea Koch 1962			X					
kahani Koch 1962			X					
porti Koch 1962			X					
sp. indet					X			
nocturna Koch 1952						X		
deplanata Tebje 1977						X		
Onymacris lobicollis (Fairmaire 1888)	X	X						non dune sand
laeviceps Gebien 1938	X	X	X					
unguicularis (Haag 1875)	X	X	X	X	X			
plana (Péringuey 1888)		X	X					plant follower
marginipennis (Brême 1840)		X	X	X	X	X		coastal hummocks
bicolor (Haag 1875)					X	X		
langi visseri Koch 1962					X			
langi langi (Guerin 1843)						X	X	
candidipennis (Brême 1840)						X		
Zophosis (Tarsosis) damarensis (Péringuey 1886)	X	X	X	X	X			
stena Penrith 1981					X			
Z. (Cardiosis) eremita (Koch 1950)			X					
fairmairei (Péringuey 1886)			X					
hamiltonuli (Koch 1969)			X					interdune gravel
triangulifera (Gebien 1938)				X				
carpi (Koch 1952)					X			
mouffleti (Deyrolle 1867)						X		
Zophosis (Anisosis) caudata (Deyrolle 1867)				X	X	X		
Vernayella								
ephialtes Koch 1958			X					
pauliani Koch 1962			X					
delabati Koch 1962			X					
noctivaga Koch 1958			X				X	

TABLE 1: Distribution ranges of dune-specialist tenebrionids in the Namib desert.

All genera which are represented in the southern Namib, are also present in the central Namib or even further to the north *(Onymacris, Lepidochora, Tarsosis*[1]*)*. There are, however, genera which start their distribution in the central Namib *(Cardiosis, Vernayella)* or further in the north *(Anisosis)* and do not occur in the southern Namib. Evidently those taxa which evolved in the north could not extend their distribution area to the south.

Conclusion: there was never a dune continuity along the Namib coast since dune specialisation started in tenebrionids. Further the translocation of biota by the means of shifting dunes is an important dispersion factor.

The place of adaptation (or origin) of the species involved can also be determined. The adaptation to hyperpsammophilous conditions occurred in sand pockets in the southern Namib in *Onymacris, Lepidochora* and *Tarsosis*. Similar adaptation occurred in the central Namib in *Cardiosis, Vernayella,* and north of the Swakop River in *Anisosis*.

The continuous dune-sea of the Central Namib can be considered as a hypertrophic microhabitat or "melting pot" of faunal elements of

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[1] Three subgenera of the genus *Zophosis* are discussed *(Cardiosis, Anisosis* and *Tarsosis)*. They represent distinct evolutionary lineages within the genus, and are referred to as genera for convenience in the text, but their systematic position is shown in table 1.

different origin (Endrödy-Younga, 1982: in press). The barren dunes of the central Namib dune-sea are extremely homogeneous with respect to environmental conditions in a very large area, ("hypertrophic microhabitat"). Their expansion to the present degree had a strong homogenising effect on the fauna of the area ("melting pot"). Detailed faunal studies in the central Namib area show that almost all species occur in all parts of the desert between the Koichab (Lüderitz) and Kuiseb Rivers. Differences in distribution are shown in dune stratification, or distance from the sea. These habitat preferences reflect conditions prevailing at the area and time of their speciation.

The populations of *Lepidochora pilosa* and *L. diaphana* will reach the central Namib dune systems by the shifting of their substrate, and will in due course enrich that fauna by two further species. As a matter of fact both species were already collected on the Grasplatz dunes, north of the Aus-Lüderitz road on the same expedition, but have not yet reached the dune fields north of the Koichab River.

The northward shifting of bodies of sand is not uniform by area or time. The Grillental barchans carry only species which are identical with Bogenfels populations in the south (the morphological identities have not yet been assessed for biochemical characters). These populations will reach the northern dune-sea preserving their specific identity. Two species of the genus, *Lepidochora discoidalis* and *L. eberlanzi*, have already successfully colonised the central Namib.

There is, however, indication for earlier translocations and colonisations too. These are by congeneric species which occur only in a more northerly section of the desert than the origin of their genera. Such species are *Lepidochora argentogrisea*, *L. kahani* and *L. porti*. The arrival of the ancestral populations of these species in the central Namib cannot be the result of the currently active translocations, but must have predated them. They can be derived from the stocks of *L. discoidalis* and *L. eberlanzi* (involved in the present translocation) but do not occur in the south.

Dune shifting in the northern Namib is not active at present but must have taken place in the past. Both the distribution of dunes and distribution pattern of species is markedly different in the northern Namib than it was shown to be in the southern and central part of the desert. There is at present no dune shifting in the southern part of the northern Namib, nor is there any sign of present dispersion of biota either. On the evidence of the Grillental dunes, however, the processes which formed the biome of the northern Namib can be recontructed.

The genera *Cardiosis* as well as *Lepidochora* are strictly monophyletic, so that the species in the south have a direct phylogenetic link to those in the north. The genus *Cardiosis* produces a different distribution pattern from that of *Lepidochora*. It does not occur in the southern Namib indicating that it evolved in the central Namib. Its two central Namib species (*C. hamiltonuli* is not a dune species) show a vicariant distribution, *C. eremita* only around Lüderitz, and *C. fairmairei* in the whole area. Three further species of the genus occupy three consecutive northern sections of the desert, from south to north: *C. trianguliféra*, *C. carpi* and *C. mouffleti*, all of them localised to their respective section of the desert (see table 1).

The transformation series of morphological characters of these three species follows the same northerly gradient. It seems to be likely that population fragments of the southern *C. triangulifera* have reached the Huab-Kunene section of the desert, colonised the river-mouth dunes, and somewhere during this translocation process speciated, forming *C. carpi*. At a later stage another population fragment travelled to the north, colonised the Coroca dunes and speciated again, forming *C. mouffleti*.

There is a distinct difference between the chances of speciation during translocations in the southern and northern Namib. One of the explanations might be that there are no barchans in a very long section north of the Swakop River which could promote contemporary translocation in the area today, similar to those in the southern Namib. Thus the colonisation of the northern dune areas by *Cardiosis* populations must have happened in the past, providing the time factor for possible speciation, and without a more or less regular supply of parental populations.

In the southern Namib, however, there is evidence of more or less regular break-off of sand bodies from the southern (Bogenfels) sand masses, testified by groups of barchans along the northward route of movement. These barchans secure a regular supply of southern populations to the colonising northern ones, reducing the chance of effective isolation of the earlier populations. The successfully speciated populations of *Lepidochora argentogrisea*, *L. kahani* and *L. porti* suggested that after the initial colonisation by *L. discoidalis* and *L. eberlanzi* populations in the central Namib there was a break in the sand supply from the south, securing an effective isolation between populations. *Lepidochora nocturna* and *L. deplanata*, also from the *discoidalis* lineage, might have travelled to the north from the central Namib during the same early period of northern colonisation when *Cardiosis* species reached the same area.

It also seems likely that at the time of the central Namib colonisation by ancestral populations of *Lepidochora kahani* and *L. porti,* both from the *eberlanzi* lineage, the colonised area was not covered by a continuous dunesea.

The twofold speciation from the same stock suggests that the colonising populations have landed in different riverine sand pockets, and became isolated not only from the parental populations but also from each other (see in *Cardiosis).* Thus the sand situation in the central Namib at that time must have been very similar to that in the north at present.

The study of the Grillental dunes opens a further aspect to be considered in respect of population-size and speciation. The population density of species on the Grillental dunes appeared to be extraordinary. Though the actual population-sizes were not sampled, they could be confidently estimated at between 100 000 and one million per species on the limited area of the dunes at least in *Lepidochora.* Such population density and population sizes do not favour any speciation, neither during the translocation period nor at the colonisation of a new dune area reached. It seems to be more likely that when the colonisation resulted in speciation, the arriving populations were small, or went through a drastic reduction after they broke away from their area of origin. The present Grillental dunes transport populations northward which are conspecific both with the Bogenfels and partly with the central Namib populations, and are unsuitable for speciation. Thus periods have to be assumed when only smaller populations were transported northward by smaller dunes. This seems to be the case in the northern Namib at present, and also in the past. If sand transportation was ever as active in the north as it is in the south now, we should find conspecific populations regularly in the northern sections. From a sedimentological point of view in such case the Namib north from Swakopmund should be covered more densely and more continuously by dune areas than it actually is.

From a genetical point of view it is interesting to note that the large Grillental populations have not changed since the beginning of their isolation. If conditions of dune movement are presumed as constant, their isolation might be as old as 1500 years and as many generations. This figure is 3000 for conspecific populations which have reached the central Namib from the south already.

The ultimate origin of the dune specialist tenebrionid fauna in the Namib. The dune specialist tenebrionids originate from an ancestral fauna inhabiting the same area prior to the massive sand accumulation. The composition of this ancestral fauna is not known. It is only evident that those groups survived the aridification and psammification (whenever it started), which are preadapted to such conditions. These groups, and primarily the tenebrionids, are predominant components of all sand deserts of the world. Thus from the original fauna of the South West biogeographical zone (Endrödy-Younga, 1978) the aridophilous elements survived, and the psammophilous elements adapted to the expanding sandy conditions. In other words the origin of the dune fauna was a process of gradual sand accumulation and simultaneous adaptation of autochtonous faunal elements. The origin of the primordial, autochtonous elements can be traced back to extra-Namib lineages of the groups involved. Such studies are, however, sometimes difficult due to extreme adaptation, and have hardly been started.

An intriguing question has till now largely been avoided: has the adaptation happened in one or in more different areas of the Namib; and whether dispersion has occurred both southwards and northwards from the adaptation (speciation) centres.

The northward shifting of barchans in the southern Namib, compared with the overall distribution of dune tenebrionids, reveals that dune continuity did not occur before the recent formation of the central Namib dune sea. Further it proves that dispersion has only happened towards the north, as dunes never shift southward in the area.

The absence of some of the genera in southern sections of the desert suggest that adaptation to hyperpsammophilous conditions occurred in different sections: in *Onymacris, Lepidochora,* and *Tarsosis* in the southern Namib, in *Cardiosis* and *Vernayella* in the central Namib and in *Anisosis* in the southern part of northern Namib.

Curiously *Tarsosis* and *Lepidochora* of the southern Namib are first known to occur from Bogenfels some 170 km north from the Orange River. Does it necessarily mean that these genera actually adapted and evolved there, and have never occurred more to the south? It is most likely that the adaptation has happened in the area where massive sand accumulation resulted first in dune formation. Such an event could only occur in conjunction with a major river, where the water transported masses of sand which were later washed ashore by the sea and then blown inland. The only river of such capacity in the area is the Orange, which presumably hes changed its course to the sea frequently, but probably not as far to the north as Bogenfels. In such a case *Lepidochora* might have evolved further to the south; and might, have reached Bogenfels on shifting sand bodies or stretches of dune continua. When, however, dunes disappeared in the south, its populations also disappeared. If at a later stage dune formation occurred anew in the void area, those southerly dunes could not be colonised by *Lepidochora* from the north any longer. There is no indication that *Cardiosis, Vernayella* and *Anisosis* would represent much older adaptations than *Lepidochora*. Therefore it is unlikely that they also have evolved in the Orange area and were translocated to the north, as described above, prior to the appearance of dune specialist *Lepidochora* species.

CONCERNING THE HABITAT

According to the evidence of two sets of aerial photographs all groups of barchans in the Grillental area show a northward shifting. A similar northward shifting is also shown by individual dunes of the continuous dunefields between Prinzenbucht and Pomonahügel.

The rate of northward shifting was measured on the aerial photographs taken at ten year intervals. The movement of ten barchans or groups of barchans (fig. 3) was measured as follows:

dune no 1: 560.5 m
2: 303.0 m
3: 500.0 m
4: 393.9 m
5: 606.0 m
6: 454.5 m
7: 242.4 m
8: 515.1 m
9: 242.4 m
10: 484.8 m

The calculated annual movement thus ranges between 24.2 m and 60.6 m, and gives an average of 43 m.p.a. These figures compare favourably with Torquato's estimate of ± 100 m.p.a. in the Moçamedes area (1970:457).

It can be observed that wind conditions and exposure influence certainly the rate of dune shifting, but probably also the mass of the dune concerned. Barchans, travelling through an elevation, thus being more exposed to the wind move faster (barchans no 1, and no 5) than those which are situated temporarily in the wind-shade of an outcrop (barchans no 2, and no 6). It seems to be likely that smaller bodies of sand (barchans no 8 and no 10) move faster than large ones in similar exposure (barchans no 7 and no 9). It is also evident that barchans of different rate of movement might come into contact with each other, establishing contacts between populations of biota they carry (barchan no 10 joined the group no 9 for 1978). Flanks of barchan groups might also break away. The disintegration of small barchans might occur theoretically, but such an event could not be observed on the aerial photographs. Barchan no 1 reduced in size climbing the outcrop between 1967 and 1978, and gained considerably recently, as it has shifted into the wind-shade of the same outcrop.

It is evident that the individual barchans do not, as a rule, disintegrate and reaccumulate around an object in the wind direction. It can be clearly observed on the aerial photographs, that the southern of the two Grillental dunes travelled over an elevated rocky outcrop. During this period the barchan has reduced in size and has travelled at a higher rate (± 56 m.p.a.), whereas the northern barchan, already on the north side of the outcrop, regained its size and moved at a similar rate to other barchans of the area on flat ground (± 30 m.p.a.). The temporary size reduction and increased rate of movement in the southern barchan is evidently due to the increased wind action on the elevation of the outcrop.

A relative time sequence to sand production, transportation and accumulation in the Namib area, as suggested by the present distribution of dune specialist tenebrionids.

In order to simplify the discussion the data of the genus *Lepidochora* will be taken. Species of this genus occur practically throughout the whole length of the Namib (see table 1). The nine species already described in the genus form two major evolutionary lineages.

The detailed revision of this genus, and the cladistic analysis of its species is yet to be completed, thus the presented derivations are tentative and simplified. The two lineages of *Lepidochora* consist of the following species:

Lepidochora
lineage I: *discoidalis-pilosa-argentogrisea-nocturna-deplanata*
lineage II: *diaphana-eberlanzi-kahani-porti*

The phases of psammification and dune formation:

a. Limited sand supply resulting in sand pocket and dune formation north of the Orange River mouth. The first ancestral species inhabiting these dunes completes the formation of those sand-adaptive characters which are common in all modern species.

b. Limited sand transportation starts towards the north in conjunction with the translocation and speciation of a population fragment of the primordial species. (A similar event must have occurred somewhere in the central Namib area giving rise to the northward dispersion and speciation in *Cardiosis).*

c. A considerably long period of limited or no sand movement (wind conditions?) towards north is assumed, as in both *Lepidochora* and *Cardiosis* the first speciations resulted in the highest morphological diversification, giving rise to evolutionary lineages in both

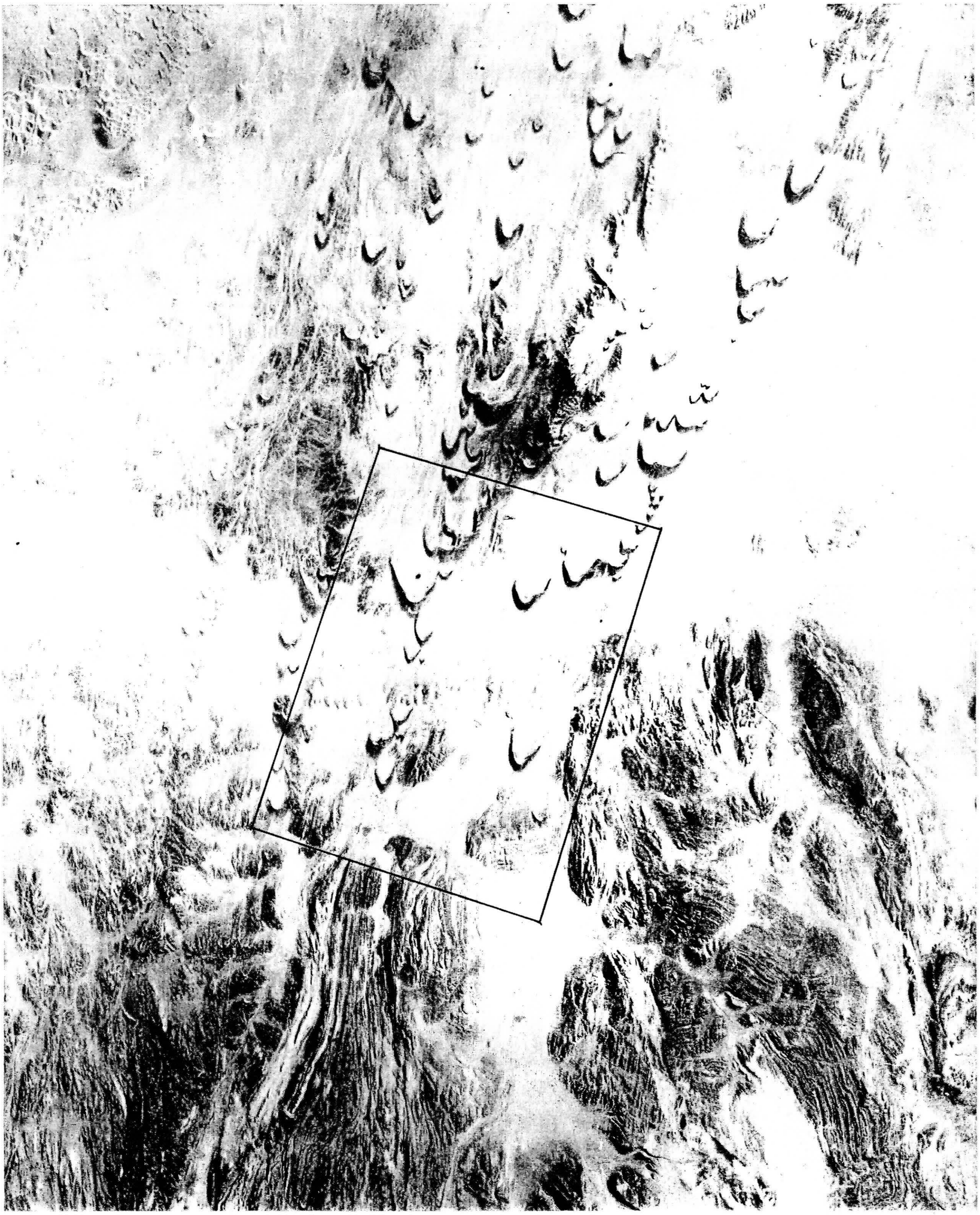

FIGURE 1: Aerial photograph of the northern section of the southern Namib, SE from Lüderitz (see position on fig. 4). The Grillental area, enlarged on figs 2 and 3a is marked.

FIGURE 2: Aerial photograph of the Grillental dunes taken in 1967.

FIGURE 3a: Aerial photograph of the Grillental dunes as taken in 1978.

FIGURE 3b (overprint): Position of the Grillental dunes traced from the earlier (1967) aerial photograph. Dunes no 1 and no 2 are the studied barchans. Dunes no 3 to no 10 were used at measuring the rate of northward shifting in the Grillental area. (North-South length = 5.1 km).

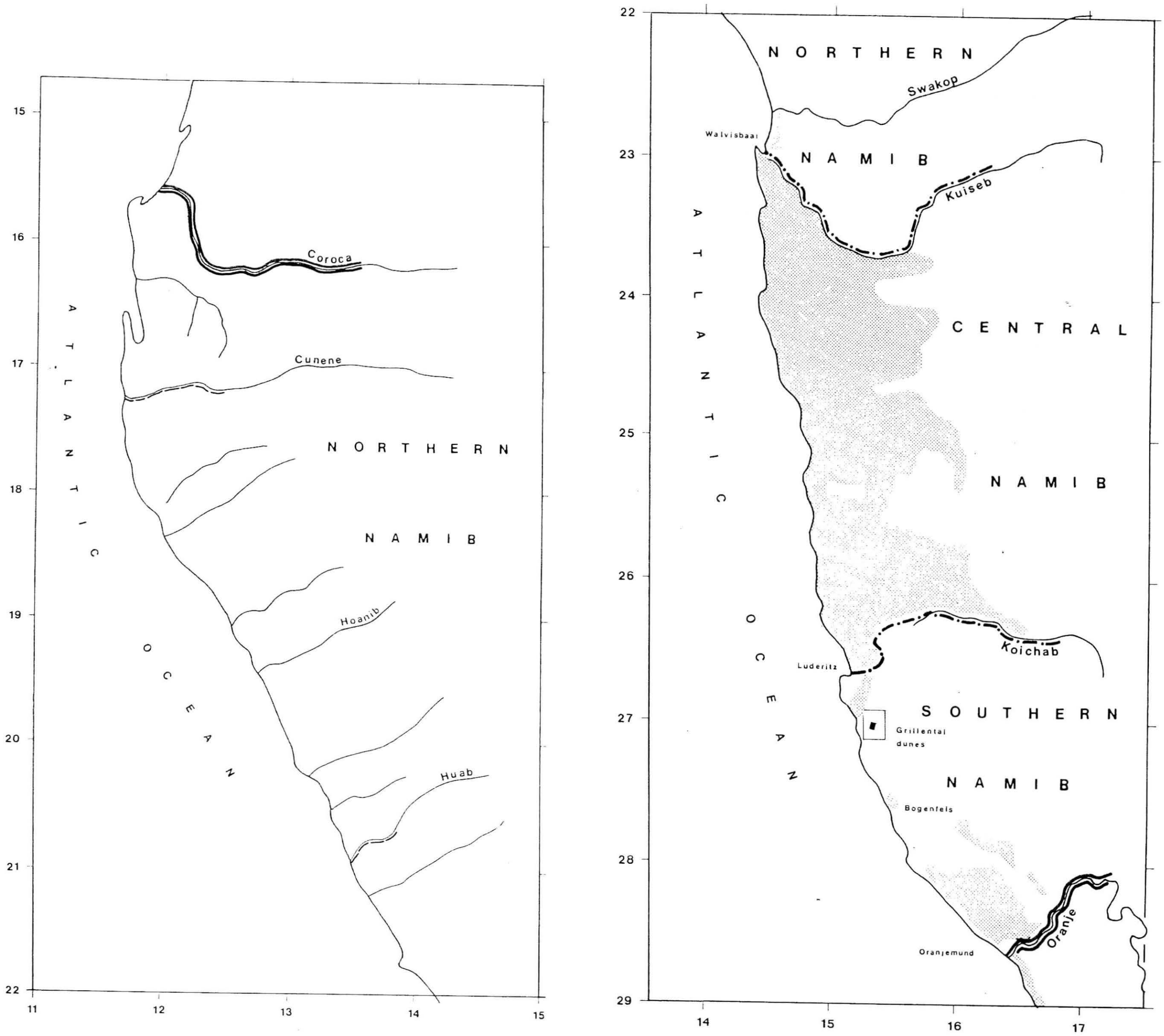

FIGURE 4: Map of the Namib desert showing the main dune areas and rivers. Double heavy lines mark the boundaries of the Namib in the north and in the south. Broken lines-and-dots mark the boundaries between northern, central and southern Namib; and light broken lines the major faunistic areas within the northern Namib.

genera: *L. discoidalis* and *L. diaphana*, and *Cardiosis fairmairei, C. trianguliféra* respectively.

d. It is likely that the period of stagnation was followed by a massive sand accumulation north of the Orange River similar to that at present in the central Namib. It might also be that the very same sand masses were transported to the central Namib in a period of high wind and low sand production activity of the Orange River. It is moreover difficult to assume that the small rivers of the central Namib area with much smaller catchment areas have ever produced more sand than the Orange River.

During the period of massive sand accumulation the distribution areas of the ancestral species of the *Lepidochora* species became connected, and they spread all over the continuous dune areas. *(L. discoidalis* and *L. diaphana* have a common and disjunct distribution area at present in the southern Namib).

e. Northward shifting barchans reach the area of the central Namib importing populations from both lineage-forming ancestral species *(L. discoidalis* and *L. diaphana),* which today, are still present in both sections of the desert. During this period the central

Namib was not yet sand covered, as population isolates could give rise to the endemic daughter species *L. argentogrisea* and *L. kahani, L. porti* respectively.

f. During or after the above period a limited and sporadic northward shifting must have occurred in the northern Namib as well. Population fragments of the *L. discoidalis* lineage have reached the Cunene area giving rise to *L. nocturna* and *L. deplanata*. The repeated translocation and speciation of population fragments from *Cardiosis triangulifera* (Walvis Bay) could have happened during this period or an earlier period of similar conditions, when *Lepidochora* was not present as yet in the northern portions of the central Namib.

g. The following phase has shaped the dune systems and distribution pattern of inhabiting species to the present form. A massive sand accumulation covered practically the whole area of the central Namib between the Koichab and Kuiseb Rivers. In the meantime the dune coverage of the southern Namib became drastically reduced (due to sand production of Orange and wind activity relation). As a result a largely uniform distribution of dune specific tenebrionids developed in the central Namib. Simultaneously the continuous sand fields of the south broke up to form isolated dune areas, all inhabited (as far as they are known) by the same composition of congeneric species.

For some reason the towering sand dunes of the central Namib do not cross the Kuiseb River for some time now, neither do they release sand bodies which could form barchans travelling northards. However, such activity took place in the past as is testified to by the speciated northern populations of *Lepidochora* and *Cardiosis*.

h. At present active sand shifting can be observed in the southern Namib combined with limited sand production. The shifting barchans approach the central Namib dune-sea by approximately 43 m.p.a. and bring southern species with them. These species will enrich the central Namib fauna in due course (if wind conditions do not change in 1 000-1 500 years).

In the central Namib the dune-sea is about to break through at the lower course of the Kuiseb River, threatening the southern suburbs of Walvis Bay. Though drift sand certainly reaches the dune systems north of Walvis Bay and Rooikop, a faunal contact has not yet been established by shifting dune bodies as testified by the still strict vicariance of *Cardiosis fairmairei* (south) and *C. triangulifera* (north).

Sand accumulation and dune formation seems to have been stagnant in the lower part of the northern Namib for a considerably long period of time. There are today no inland dunes between the Swakop and Huab Rivers, they first appear again north from the latter. From the upper section of the desert, however, high sand activity is reported again. From the Hoanib River northwards, accumulating sand is blocking the car-tracks (Möwe Bay), which were still passable two or three years ago (M.J. Penrith, pers. comm.). The northward extension of dune-fields is reported in a rate of ± 100 m.p.a. from the Moçamedes section of the desert in southern Angola (Torquato, 1970:457). From this area, however, no personal observations are available.

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FIGURE 5: The Grillental dunes: no 1 at left, no 2 at right, from the eastern rocky elevation.

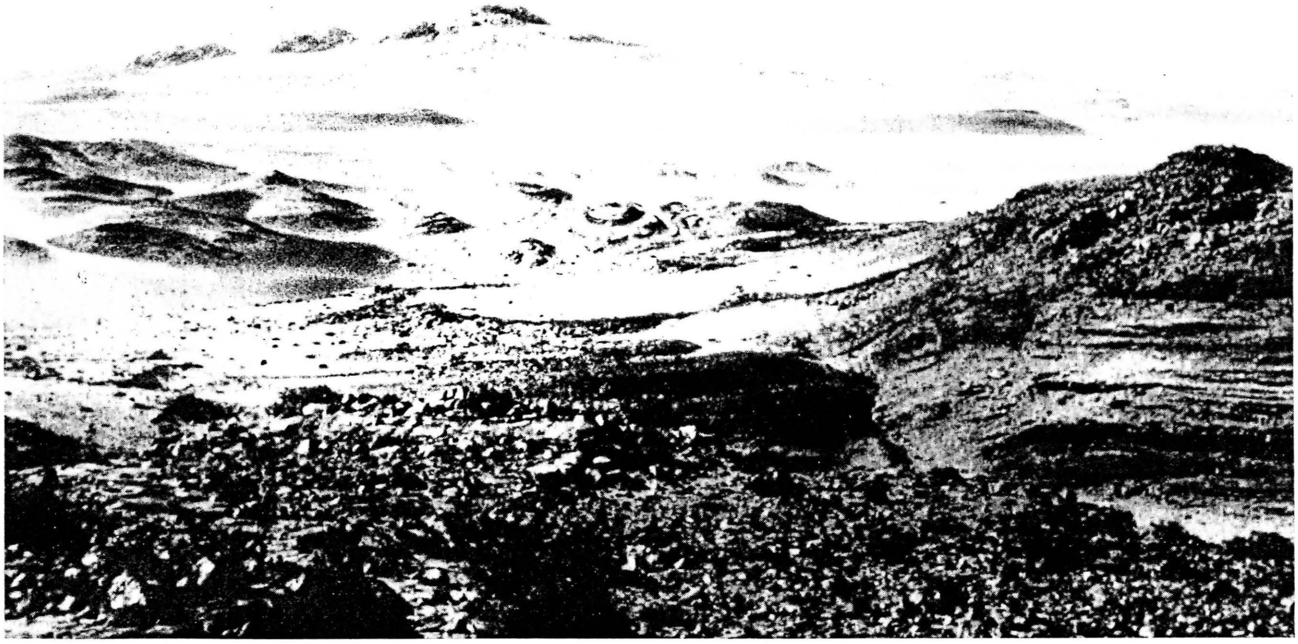

FIGURE 6: Dunes of the barchan group no 9 from the top of the rocky elevation.

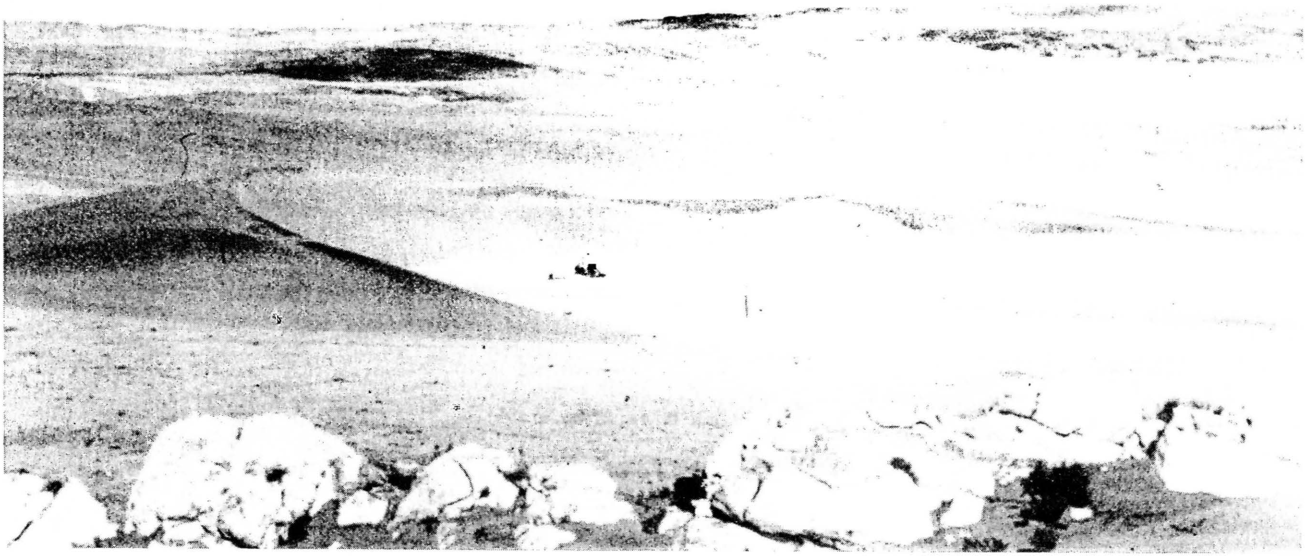

FIGURE 7: The barchan no 1, the southern of the dunes studied. Note the road overlain by the dune at present. The same road bypassed the dune at its eastern flank in 1978 (see fig 3a).

FIGURE 8: The barchan no 2, the northern dune studied. Note the road running today almost into the southern tip of the dune.

figure 9 →
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