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GEOLOGY AND PALAEOBIOLOGY OF THE NORTHERN SPERRGEBIET, NAMIBIA

by

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Palaeoecology, palaeoenvironment and palaeoclimatology of the Sperrgebiet, Namibia

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Stromer (1926) concluded that the faunas from the northern Sperrgebiet were of a steppic nature. The present study indicates that the area was more vegetated and more humid than envisaged by Stromer. The terrestrial gastropods are useful indicators of climate, and those from the Early Miocene deposits of the northern Sperrgebiet suggest that the region was close to a winter rainfall belt, but not necessarily within it, in contrast to its present day winter rainfall regime. The freshwater snails indicate that water bodies in the region were generally unstable, which concords with the overall aspect of aridity that the terrestrial faunas indicate. The presence of calcareous concretions of pedogenic origin at several sites, some forming continuous sheets (calcretes) as for example at Strauchpfütz, indicate that the region was not arid or hyper-arid, but more likely semi-arid to sub-humid. It certainly was not forested, but was most likely savanna, with denser stands of riparian vegetation along rivers and around water bodies such as ponds. It was only after the Early Miocene that hyper-arid conditions were established in the area, along with a predominantly winter rainfall climatic regime.

Introduction

Right from the start of studies on the faunas of the northern Sperrgebiet, inferences were made about the palaeoenvironments represented in the area. Stromer (1926), for instance, concluded that the faunas were of steppic affinities or as he called them "Steppenfaunen" and other authors have generally agreed (Braestrup, 1935; Hamilton and Van Couvering, 1977; Hendey, 1984; Pickford and Senut, 2000).

This paper examines the palaeoecology and palaeoenvironment of the northern Sperrgebiet from various perspectives, including pedogenesis, faunal indications, dental adaptations, and studies of terrestrial and freshwater molluscs and insect bioconstructions. It complements the article by Guerin (2008) based on autecological and synecological studies of the same faunas, and concludes that during the Early Miocene the Sperrgebiet was likely sub-humid with wooded savannah and forest patches, and enjoyed a summer rainfall regime, but with a winter rainfall belt not far away.

Dental adaptations

A study of dental adaptations reveals a high occurrence of hypsodont types in the Early Miocene mammal faunas of the northern Sperrgebiet, particularly among the small mammals. Hypsodonty is rarer among the medium and large mammals, some being relatively brachyodont (*Sperrgebietomeryx*, *Namibiomeryx*) or even bunodont (*Dorcatherium*, *Nguruwe*, *Diamantohyus*). Among the hypsodont forms are those in which the teeth still retain roots such as *Protypotheroides* and those that are arhyzic, such as *Austrolagomys inexpectatus*. Brachy-hypsodonty is quite common, this term describing teeth that are brachyodont on one side of the tooth and hypsodont on the other, the hypsodont side being circular in mesial and distal profile rather than pillar-like as in completely hypsodont teeth. The normal kind of brachy-hypsodonty is encountered in *Prohyrax tertiarius*, in which it is the lingual cusps of upper molars that are brachyodont, and the buccal cusps high and curved. In rodents, the opposite is the case, with the buccal cusps of upper molars being low and the lingual one high and circular in profile. Among the latter form are members of at least two separate families, Diamantomyidae and Bathyergidae. Cementum is present in the teeth of *Protypotheroides*, *Austrolagomys*, and *Pomonomys dubius*. What emerges from this study is that a higher proportion of the small herbivores from the Sperrgebiet possesses hypsodont teeth, some with cementum, than occurs in contemporaneous deposits in East Africa. The conclusion is hard to escape that many of the Early Miocene Sperrgebiet mammals, principally small mammals, were subsisting on grass, or included grass in their diets on a regular basis. Nevertheless, it seems that fruits must have been available in the region, because at least three medium-sized mammals have dentitions suggestive of occasional or frequent frugivory (*Nguruwe namibensis*, *Diamantohyus africanus*, *Dorcatherium songhorensis*) and several mammals suggest that leaves must have been available on a year round basis (*Afrohyrax*, bovids, climacoceratids, *Eozygodon*, brachypothere).

Differences in representation of species at various sites

The faunal lists for the main fossil localities in the northern Sperrgebiet are more or less similar, but the representation of species at them is not. For example, *Diamantomys luederitzi* is rare at Langental, but common at Grillental and Elisabethfeld. In contrast, *Pomonomys dubius* is very common at Langental, but rare at Elisabethfeld and unknown at Gril-

Table 1: Dental adaptations of Sperrgebiet mammals

Namibian Early Miocene Fauna	**Dental type**
Myohyrax oswaldi	Extremely hypsodont, arhyzic
Protypotheroides beetzi	Extremely hypsodont with cementum
Metapterodon kaiseri	Sectorial
Metapterodon stromeri	Sectorial
Namasector	Ultra-sectorial
Amphicyonidae	Sectorial
Austrolagomys inexpectatus	Extremely hypsodont with cementum, arhyzic
Protenrec sp.	Brachyodont with pointed cusps
Amphechinus sp.	Brachyodont with pointed cusps
Parapedetes namaquensis	Extremely hypsodont
Propedetes sp.	Extremely hypsodont
Bathyergoides neotertiarius	Inverse brachy-hypsodont
Neosciuromys africanus	Inverse brachy-hypsodont
Phthinylla fracta	Bunodont
Phiomyoides humilis	Bunodont
Apodecter stromeri	Bunodont
Phiomys andrewsi	Bunodont
Diamantomys luederitzi	Hypsodont
Pomonomys dubius	Inverse brachy-hypsodont with cementum
Protarsomys	Bunodont
Gomphothere	Bunodont
Eozygodon morotoensis	Lophodont
Prohyrax tertiarius	Normal brachy-hypsodont
Afrohyrax namibensis	Brachyodont, no cementum
Chilotheridium pattersoni	Hypsodont
Aceratherium	Brachyodont
Brachypotherium heinzelini	Brachyodont
Brachyodus depereti	Brachyodont semi-selenodont
Diamantohyus africanus	Bunodont with selenodont tendency
Nguruwe namibensis	Bunodont
Dorcatherium songhorensis	Brachyodont with bunodont tendency
Dorcatherium pigotti	Brachyodont with bunodont tendency
Dorcatherium moruorotensis	Brachyodont with bunodont tendency
Propalaeoryx austroafricanus	Brachyodont, selenodont
Sperrgebietomeryx wardi	Brachyodont, selenodont
Namibiomeryx senuti	Brachyodont, selenodont

lental. Frogs are common at Langental and Grillental, but are rare at Elisabethfeld. *Parapedetes namaquensis* is common at Elisabethfeld, but unknown at Grillental and Langental. *Prohyrax tertiarius* and *Diamantohyus africanus* are more common at Langental than they are at Elisabethfeld and Grillental. Tortoises are very common at Elisabethfeld, but rarer at Grillental and Langental. Ruminants are common at all sites.

The question naturally arises whether these inter-site differences are due to chronological or to ecological differences. Minor differences in the sediments are evident, with the Langental silts and sands being heavily overprinted by pedogenesis, whereas the Elisabethfeld and Grillental ones are less affected by soil forming processes. But in general, the fossil-bearing deposits at these localities are fine grained and accumulated in shallow valleys, some with minor amounts of standing water (Grillental, Langental) and others with mainly overbank facies (Elisabethfeld). There seems to be no clear pattern related to ecology. For example, of the two localities which yield many frog bones, one (Langental) is poor in *Diamantomys* while the other (Grillental) is rich in their remains.

Termite hives

At Grillental and Fiskus, several termite hives were found. They are usually preserved as half-metre diameter ball-like or ring-like structures and are comprised of numerous irregular horizontal ovaloid cells arranged one above the other and side by side. They have been described as the ichnospecies *Namajenga mwichwa*. In the Sperrgebiet they invariably occur in green silts or in aeolian sands. Research on extant termite hives suggests that these structures were made by a species of *Hodotermes* and have nothing to do with the termites (*Psammotermes*) that occur at present in the Namib Desert. The latter build quite different, and much smaller diameter and taller tube-like hives. If the determination is correct, then this would not only support the inference that the region was not desert, but was semi-arid to sub-humid during the Early Miocene, and would also tend to support the conclusion that it enjoyed a summer rainfall regime. The mean annual rainfall was probably less than 750 mm, since extant *Hodotermes* do not occur in regions where rainfall is greater than this. The main food of *Hodotermes* is grass, which accords with the evidence afforded by the study of dental morphology of the Sperrgebiet mammals which indicates that grass was a readily available food resource.

Pedogenesis

The fossiliferous sediments at Langental are mottled green-brown with layers of calcareous nodules, sometimes disposed in hexagonal patterns, at others in discontinuous thin sheets and vertical veins. The overall aspect of the deposits is of a relatively mature palaeosol with development of calcrete nodules.

In Glastal, calcareous nodules in silts are better developed than at Langental, but do not form continuous sheets of calcrete. In this respect, Glastal, which is between Langental and Strauchpfütz, is intermediate in calcrete pedogenesis between Langental with weaker development, and Strauchpfütz where it is well developed.

At Strauchpfütz, there are four major superposed carbonate layers separated from each other by green/brown mottled marls, often with calcareous nodules. Although there is evidence, such as the localised presence of freshwater gastropods and some patches of limestone with vertical hollows representing moulds left by water margin plants, that some of the limestone accumulated in a paludal setting, most of them appear to be pedogenic in origin, and are thus calcretes. This interpretation provides support for the idea that the region was not arid or hyper-arid during the Early Miocene, but was at the most semi-arid, with rainfall probably over 200 mm per year, and it may even have been sub-humid with as much rainfall as 750 mm per year.

Today, similar nodular calcretes and calcrete crusts form extensively in Namibia in semi-arid and sub-humid settings such as the region around the Otavi Mountains in the north. Given enough time with stable geomorphological conditions, pedogenic calcareous nodules grow and coalesce to form large masses of calcrete and eventually a continuous calcrete crust or horizon. Such calcretes tend not to form in really arid or hyper-arid conditions such as those that prevail in the true Namib Desert where rainfall is less than 100 mm per annum, but are best developed in neighbouring semi-arid areas such as steppe and savanna where rainfall is over 200 mm but less than 750 mm per year.

Palaeoclimate

During the Early Miocene, the northern Sperrgebiet was semi-arid with a summer rainfall regime (the winter rainfall zone was not far away, probably to the south of the Orange River). There were unstable water bodies (seasonal swamps and rivers) and the country was relatively open woodland with plenty of grass. By the onset of the Middle Miocene in contrast, the region had become hyper-arid with a winter rainfall regime. Hyper-aridity has continued to the present day, with minor semi-arid interludes during the Pleistocene.

The southern trade winds which sweep the coast of Namibia and South Africa have dominated the climate of the Sperrgebiet since the onset of the Middle Miocene, as shown by the prevalence of north dipping avalanche slopes in palaeodunes of the Namib, but bergwinds began to play an important role in the Namib during the Late Miocene (Ségalen *et al.*, 2004).

The importance of the history of polar ice caps in moulding the climate of the Sperrgebiet cannot be over-emphasised. Upwelling of cold water along the coast of southwestern Africa and the position of the South Atlantic anticyclone are by far the most important factors determining the climate of the region, and both of these are in turn related to the presence of the Antarctic Ice Sheet. Growth of this ice sheet to continental size occurred towards the end of the Early Miocene, and its effects were to shift the world's eco-climatic belts northwards. The Sperrgebiet which was in the southern sub-tropical zone during the Early Miocene, became part of the southern temperate zone as this zone expanded northwards about 17 Ma. Its rainfall regime changed from summer dominated to winter dominated at this time, as shown by changes in the terrestrial gastropods and termites. Hyper-arid conditions set in over the Namib from about 16 Ma, partly due to the northwards shift of the temperate zone, but mainly because of the establishment of cold upwelling water cells along the coast, and desert conditions have prevailed in the coastal strip ever since.

Expansion of the Arctic Ice Cap during the Late Miocene had dramatic effects on world climates, floras and faunas, but the Central Namib, already being a desert, was not greatly affected. The only significant climatic change that occurred in the region was the onset of frequent bergwinds, which began to play an important geological role from about 8 Ma which continues to the present day (as witnessed by the presence of ancient dunes with west and south dipping avalanche slopes). Bergwinds (or east winds) are vigorous masses of air that descend from the high plateau of Namibia and South Africa during the winter months when large cold masses of air accumulate on the plateau and flow westwards down valleys, warming as they descend. At present, sufficiently voluminous masses of cold air large enough to feed the bergwind system for two or three days at a time, only accumulate on the plateau during the winter months. The onset of abundant palaeobergwinds during the Late Miocene suggests that prior to this the winters in Namibia were not cool enough for such voluminous cold air masses to form. Global cooling during the Miocene, which culminated in the expansion of the Arctic Ice Sheet, may have been critical for producing conditions suitable for regular bergwinds to occur in Namibia.

Conclusions

There can be little doubt that during the Early Miocene, the northern Sperrgebiet was semi-arid with a summer rainfall regime. Hyperarid conditions did not prevail until the base of the Middle Miocene, some 17-16 Ma. Not only does the fauna support this conclusion, as was already inferred by Stromer (1926), but also the palaeosols, which often contain pedogenic carbonate nodules, or are even comprised of calcrete sheets, confirm the semi-arid to sub-humid climatic regime under which they accumulated. The terrestrial gastropods indicate that a winter rainfall zone was not far off, but that the northern Sperrgebiet itself was not within this climatic category, which was presumably further south during the Early Miocene. By the onset of the Middle Miocene the same region was well within the area affected by winter rainfall.

The shift from summer to winter rainfall and from semi-arid to hyper-arid climate occurred about 17-16 Ma, and was probably caused by the expansion of the Antarctic Ice Cap to continental proportions.

An important aspect of the presence of semi-arid climate in the Sperrgebiet since the Early Miocene, and, as a consequence, of open, unstable environmental conditions, is that animals and plants living there have had ample time to adapt to such conditions. Grazing adaptations in the dentition are well developed in several of the Sperrgebiet mammals, whereas, during the same period in East Africa, there were fewer mammals adapted to grass eating. A consequence of the precocious onset of aridity in southern Africa, is that herbivores living there have had much longer to adapt to such conditions than those living in the tropics which were, at that time more humid and more stable. As the environment in East Africa became more open and unstable during the Middle Miocene and especially during the Late Miocene and Plio-Pleistocene, a number of southern African lineages of vertebrates that were adapted to such conditions, spread northwards and occupied the newly open areas before any of the local lineages could themselves adapt to them. The biogeographic history of several lineages of reptiles, terrestrial birds, and mammals shows this quite clearly, including crocodiles, ostriches, dassies and antelopes.

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