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GEOLOGY AND PALAEOBIOLOGY OF THE NORTHERN SPERRGEBIET, NAMIBIA

by

Dr Martin Pickford[1,2] and Dr Brigitte Senut[2]

[1]Collège de France, and [2]Département Histoire de la Terre, UMR 5143 du CNRS,
Case postale 38, 57, rue Cuvier, 75005, Paris

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Palaeoecological study of the Early Miocene mammals of the Northern Sperrgebiet (Namibia)

Claude Guérin

UFR des Sciences de la Terre, Université Claude Bernard-Lyon I, 27-43 boulevard du 11 novembre 1918, 69622 Villeurbanne Cédex, France
e-mail : Claude.Guerin@univ-lyon1.fr

Four localities of Early Miocene age in the Northern Sperrgebiet, Namibia (Elisabethfeld, Grillental, Langental and Fiskus) combined, have yielded 53 species of mammals. The autecological and synecological studies of this association shows that it corresponds to a countryside that was clearly more forested and more humid than that represented at the basal Middle Miocene site at Arrisdrift, Namibia.

Quatre gisements du Miocène inférieur du Northern Sperrgebiet, Elisabethfeld, Grillental, Langental et Fiskus, ont livré ensemble 53 espèces de Mammifères. L'étude autécologique et synécologique de cette association montre qu'elle correspond à un paysage nettement plus forestier et plus humide que celui du site miocène moyen de Arrisdrift, Namibie.

Introduction

Four Namibian sites of approximately the same age and not very far from each other, Elisabethfeld, Grillental, Langental and Fiskus, have yielded a rich fauna of Early Miocene age. Several species occur in all or most of the four sites. In total the four localities contain 53 mammal species as follows :

- Insectivores and related Orders (Lipotyphla)
Gymnurechinus leakeyi Butler, 1956
Amphechinus rusingensis Butler, 1956
Protenrec butleri Mein and Pickford, 2003
Prochrysochloris cf. *miocaenicus* Butler and Hopwood, 1957
- Macroscelidea
Myohyrax oswaldi Andrews, 1914
Protypotheroides beetzi Stromer, 1922
Miorhynchocyon rusingae (Butler, 1969)
- Rodents
Vulcanisciurus africanus Lavocat, 1973
Protarsomys macinnesi Lavocat, 1973
Parapedetes namaquensis Stromer, 1926
Megapedetes cf *gariepensis* Mein and Senut, 2003
Propedetes efeldensis nov. gen. nov. sp.
Diamantomys luederitzi Stromer, 1922
Pomonomys dubius Stromer, 1922
Phiomyoides humilis Stromer, 1926
Apodecter stromeri Hopwood 1929
Neosciuromys africanus Stromer, 1922
Neosciuromys fractus (Hopwood, 1929)
Bathyergoides neotertiarius Stromer, 1923
Efeldomys loliae nov. gen. nov. sp.
Geofossor moralesi nov. sp.
Microfossor biradiculatus nov. gen. nov. sp.
- Creodonts and Carnivores
Metapterodon kaiseri Stromer, 1924
Metapterodon stromeri Morales, Pickford and Soria 1998
Hyainailouros or *Megistotherium* sp. indet.
Isohyaenodon sp.
Namasector soriae nov. gen. nov. sp.
Ysengrinia sp.
Leptoplesictis senutae nov. sp.
Leptoplesictis namibiensis nov. sp.
Viverridae gen. et sp. indet. I
Afrosmilus africanus (Andrews, 1914)
- Lagomorphs
Austrolagomys inexpectatus Stromer, 1924
- Proboscideans
Eozygodon morotoensis (Pickford and Tassy, 1980)
Gomphotheriidae gen. et sp. indet.
- Tubulidentates
Orycteropus africanus MacInnes, 1956 ou *O. chemeldoi* Pickford, 1975
- Hyracoids
Afrohyrax namibensis nov. sp.
Prohyrax tertiarius Stromer, 1923
- Perissodactyls
Brachypotherium heinzelini Hooijer, 1963
Chilotheridium pattersoni Hooijer, 1971
Aceratherium acutirostratum (Deraniyagala, 1951)
- Artiodactyls
Brachyodus depereti Fourtau, 1918
Brachyodus aequatorialis MacInnes, 1951
Diamantohyus africanus Stromer, 1922
Nguruwe namibensis (Pickford, 1986)
Dorcatherium songhorensis Whitworth, 1958
Dorcatherium sp. cf. *D. moruorotensis* Pickford, 2001
Dorcatherium sp. cf. *D. parvum* Whitworth, 1958
Propalaeoryx austroafricanus Stromer, 1924
Propalaeoryx stromeri nov. sp.
Sperrgebietomeryx wardi Morales, Soria and Pickford, 1999
Namibiomeryx senuti Morales, Soria and Pickford, 1995
Namibiomeryx spaggiarii nov. sp.

Autecological study:

The comments that follow owe a great deal to P. Mein for the small mammals and M. Pickford for many of the larger taxa.

Amphechinus rusingensis is smaller than the extant European hedgehog, *Gymnurechinus* is somewhat larger, *Protenrec* is very small; these three genera were, above all, entomophagous. *Prochrysochloris* is an underground genus which is smaller than the modern European mole.

The three macroscelidids are herbivores : *Myohyrax oswaldi*, hyperhypsodont, weighed about 1 kg; *Protypotheroides*, hypsodont, was appreciably larger, whereas *Miorhynchocyon* is small and brachyodont.

Vulcanisciurus is a small squirrel with brachyodont cheek teeth, indicating a frugivorous-granivorous diet. *Protarsomys*, a granivore, was the size of a mouse. *Megapedetes gariepensis* is smaller than *M. pentadactylus*, its body weight reaching 7 to 8 kg. It was a runner and jumper, with sub-hypsodont cheek teeth indicating an omnivorous diet. *Parapedetes*, hypsodont, was probably a burrower, as it has been found in burrows. *Propedetes* is likely the direct ancestor of extant *Pedetes* with which it shared a similar life style. It weighed 3 to 4 kg, lived in semi-arid areas and fed on fresh grass, roots, buds, fruits, and on occasion, insects. *Diamantomys,* quite hypsodont, weighed somewhat more than 1 kg, and its ecological requirements were likely similar to those of extant *Thryonomys*, which live in grassy hills and savannahs and eat grass, as well as fruit, bark and roots. *Pomonomys*, hypsodont, had closely similar habits, as did *Neosciuromys, N. africanus* weighed more than 1 kg whereas *N. fractus* was somewhat smaller *Phiomyoides* and *Apodecter*, very small, were probably granivores. *Bathyergoides*, weighing less than 1 kg, was brachyodont and was an active burrower, using both its incisors and its head for this activity. *Efeldomys*, very small, was a burrower and fed on roots; *Microfossor* is another underground genus, feeding on roots, and was smaller than extant European moles.

Hyainailouros and *Megistotherium,* which are perhaps synonyms, are hyaenodontid creodonts of very large dimensions which preyed on large ungulates. They weighed in excess of 500 kg and were more widespread than other creodonts.

Metapterodon is a medium sized genus of hyaenodont creodont, most likely forest dwelling ; two species are present in the Northern Sperrgebiet, *M. kaiseri*, from Elisabethfeld, is the smaller, *M. stromeri*, from Langental, is clearly larger (Morales *et al*., this volume). They weighed in the neighbourhood of 10 to 20 kg.

Isohyaenodon sp. is also a forest adapted hyaenodontid, but is smaller than *Metapterodon kaiseri*, and is more hypercarnivorous (Morales *et al*., this volume), weighing less than10 kg.

Namasector soriae is a new genus and species for a Prionogalid creodont. It is the smallest known African creodont (it is smaller than the extant European *Mustela nivalis* and thus weighed less than 100 gm), and is also the most hypercarnivorous (Morales *et al*., this volume).

Ysengrinia sp. is an amphicyonid carnivore. The type species of the genus is from Europe. The species *Y. ginsburgi*, present at Arrisdrift, was larger than a wolf, preyed on suids and medium sized ruminants (Morales *et al*, 1998). The material from Elisabethfeld, Grillental, Fiskus and Langental is slightly smaller than *Y. ginsburgi* (Morales *et al*., 2003; Morales *et al*., this volume), suggesting it preyed on the same kind of animals.

The species of *Leptoplesictis* are small Viverridae resembling extant genets and mongooses. Like the latter, *L. senutae* and *L. namibiensis* were probably terrestrial, forest dwelling and zoophagous/ omnivorous carnivores.

Viverridae gen. et sp. indet. probably had the same ecological requirements as *Leptoplesictis*.

Afrosmilus africanus is a barbourofeline Felidae. It was about the size of an extant lynx (Morales *et al*., this volume).

Austrolagomys inexpectatus is an ochotonid lagomorph, of small size and with very hypsodont teeth.

Eozygodon is a medium sized zygodont Mastodontidae (or Mammutidae) : M. Pickford (2003 a) gives the length and breadth dimension of the M3/ from Auchas Mine as 114.5 x 71.8 mm respectively; for *Mammuthus primigenius* from the Late Pleistocene of Europe the two dimensions range from 203 to 308 mm and from 75 to 112 mm respectively (Guérin and Faure, 1994). This species had a body weight between 4 and 8 tons (Christiansen, 2004). *Eozygodon morotoensis* probably weighed about 1 ton ; it lived in open forest and wooded grassland, and fed on shoots and leaves.

The indeterminate Gomphotheriidae which possessed bunodont cheek teeth probably had a comparable habitat but a more varied diet.

Orycteropus africanus is known from the Early Miocene of East Africa (Rusinga and Mfwangano in Kenya). Its size was about 60% that of extant *O. afer*. *O. chemeldoi*, defined in the Late Miocene deposits of the Ngorora Formation, was about two thirds the size of *O. afer*, with closely similar anatomical features (Pickford, 1975). Extant *O. afer* can reach a weight of 80 kg. It feeds almost exclusively on termites, is nocturnal and excavates extensive burrows. It survives in open savannahs, arid areas and open forest.

Afrohyrax is a medium sized Titanohyracidae, about the size of a small tapir, weighing in at about 100 to 200 kg. Its upper cheek teeth are hypsodont buccally, brachyodont lingually.

Prohyrax tertiarius is a small Pliohyracidae, about a third smaller than *P. hendeyi* (Pickford, 1994) suggesting a body mass of about a dozen kg. Extant

Procavia, the anatomy of which is reasonably similar, are hypsodont and eat a variety of plants including grass, lichen, bark, and fruit. They are rupicole and inhabit rocky areas in savannah and more arid regions.

Brachypotherium heinzelini is a large brachyodont rhinoceros with a hippo-like allure, barrel shaped body and short legs, and was very aquaphilous.

Chilotheridium pattersoni is a small aquaphile rhinoceros, hippopotamoid in appearance, with hypsodont cheek teeth and short legs (Guérin, 2000 and this volume).

Aceratherium acutirostratum is a medium sized, hornless, brachyodont rhinoceros with elongated legs and a tetradactyl manus. It looked somewhat like a tapir and like it, probably lived in humid, more or less swampy forest, (Guérin, 2000).

The two species of *Brachyodus* are large, brachyodont and aquaphile Anthracotheriidae. *B. depereti* is larger than *B. aequatorialis*: the talus of the latter has a lateral height and a distal breadth reaching 108 to 136.4 x 70 to 86 mm respectively, for *B. depereti* these dimensions are 133 to 142 x 73 to 89 mm (Pickford 2003 b). For 12 to 13 extant *Hippopotamus amphibius*, a species whose body weight reaches 3.5 tons, the corresponding dimensions are 87 to 115 x 69 to 88 mm (Faure, 1985). It is possible to envisage that the weight of large *Brachyodus* was about the same order of magnitude as that of *H. amphibius*.

Diamantohyus is a Sanitheriidae. In his description of *D. africanus* from Karungu, Kenya Pickford (1984) figured an upper tooth row (P2/-M3/) 54 mm long, and a talus 26 mm high and 18 mm wide. For the extant European suid *Sus scrofa* the weight of adults ranges from region to region from 50 to 300 kg and the homologous measurements of the tooth row are 100 to 136 mm, the mean for 54 specimens being 120.4 mm, and the mean for the homologous dimensions of the talus are 44.1 and 26.37 mm; these dimensions suggest a body weight between 15 and 45 kg for *D. africanus*.

Nguruwe namibensis is a Kubanochoerinae Suidae; the genus is bunodont with a short face. It is appreciably smaller than *N. kijivium*, with for example an M3/ measuring 14.7 x 11 mm, and an m/3 measuring 14.2 x 8.5 mm (Pickford, 1997). In extant *Sus scrofa*, the M3/ measures 28 to 46 x 15 to 25 mm, with a mean for 43 specimens of 35.94 x 21.27 mm, and the m/3 measures 25 to 44.5 x 12 to 21 mm, with a mean for 60 individuals of 37.42 x 17.26 mm. The body mass of *N. namibensis* was therefore on the order of 10 to 15 kg, and its diet, like that of most suids, was omnivorous.

The Sperrgebiet species of *Dorcatherium* are small Tragulidae with very brachyodont cheek teeth, and they inhabited forest. *Dorcatherium songhorensis* is smaller than *D. piggoti*, and was about the size of extant *Madoqua* with a body weight less than10 kg ; *D. moruorotensis* and *D. parvum* are much smaller, about the same size as a rabbit.

Propalaeoryx are Climacoceratidae Giraffoidea which probably lacked frontal appendages; even though primitive their dentition is already hypsodont. Its body weight was somewhat greater than that of *Sperrgebietomeryx* (Morales *et al*., 1999), probably being on the order of 60 to 70 kg.

Sperrgebietomeryx is with little doubt a Giraffoidea, possibly a Climacoceratidae (Morales *et al*., this volume). Morales *et al.,* (1999) provided the dimensions of the tooth row, the radius and the anterior cannon bones, tibia and talus. The length dimensions of the long bones and the talus correspond more or less to the homologous bones of *Dama dama* but the transverse diameters are smaller than in the deer, only slightly greater than a large roe deer, which allows us to estimate a mean mass for *Sperrgebietomeryx wardi* of about 50 kg.

Species of *Namibiomeryx* are Bovoidea of uncertain family affinities. The genus, already hypsodont (for the epoque ; but brachyodont in comparison with extant bovids) could be the oldest bovid known. *Namibiomeryx senuti* probably had a mass of less than 10 kg as it is smaller than *Namacerus gariepensis*, likely its descendant from the onset of the Middle Miocene, which weighed 10 to 14 kg (Morales *et al*., 2003). *N. spaggiarii* is slightly larger, and was about the same size as the extant steenbok *Raphicerus campestris* and was thus likely to have weighed less than 20 kg.

The mammals from the Northern Sperrgebiet, comprising 53 species, provide evidence of a remarkable biodiversity. Several taxa (the very large creodont, certain small carnivores, most of micromammals, the ruminants *Propalaeoryx*, *Sperrgebietomeryx*, *Namibiomeryx*, evoke a bushy, more or less wooded, savannah, but forest forms are abundant (small and medium sized creodonts, the Viverridae, the two proboscideans, the Suoidea *Diamantohyus* and *Nguruwe* and the three secies of *Dorcatherium*). Most of the micromammals are terrestrial or subterranean, but at least one is a climber/arboreal. Two of the rhinoceroses *Brachypotherium* and *Chilotheridium*, were aquatic, with hippo-like habits, and the third (*Aceratherium*) was aquaphile like tapirs ; the two species of *Brachyodus* were also as aquatic as extant hippos.

Besides the mammals, other higher vertebrates (birds, reptiles) of large size belonged to diverse phytophagous and zoophagous guilds and because of this contribute to the interpretation of the palaeoecology of the region. Next to small tortoises, F. de Lapparent de Broin (this volume) records the large Testudinidae *Namibchersus namaquensis* (Stromer, 1926), a herbivore with a carapace that largely exceeds 80 cm in length. In the Northern Sperrgebiet there also exist two indeterminate species of *Python*, and one of *Crocodylus*, which confirm the humid nature of the environment, and the ostrich *Struthio coppensi* Mourer-Chauviré, Senut, Pickford and Mein, 1996, defined at Elisabethfeld in Namibia, the size of which was ap-

preciably smaller than the extant ostrich, but which, like it, inhabited savannah.

The autecological study thus provides evidence of a mosaic countryside dominated by forest and a humid climate.

Synecological study:

The method utilised is that developed by T. H. Fleming (1973), refined by P. Andrews *et al.,* (1979) and modified by C. Guérin (1998). A locality (or a level in a site) is characterised by a series of four histograms showing in percentage the number of species present grouped according to zoological classification (taxonomic histogram), size (histogram of body weight), feeding adaptations (dietary histogram) and locomotor adaptations.

- The taxonomic histogram has 8 classes corresponding more or less to Orders : R (Rodents), I (Insectivores), Pri (Primates), Ar (Artiodactyls), C (Carnivores plus Creodonts), Per (Perissodactyls), Pro (Proboscidians), A (others).
- The histogram of body weight includes 7 classes : AB = less than 1 kg ; C = 1 to 10 kg; D = 10 to 45 kg; E = 45 to 100 kg ; F = 100 to 200 kg; G = 200 to 1000 kg ; H = more than 1000 kg.
- The dietary histogram comprises 6 classes : En = entomophages; FG = frugivores and granivores; HB = brachyodont herbivores; HH = hypsodont herbivores; Z = carnivores (zoophages); O = omnivores.
- The locomotor histogram includes 6 classes : GT for large terrestrial mammals, subdivided into f (forest), u (ubiquitous) and c (runners); PT for small terrestrial mammals; Gr-Ar for climbers and arboreal species; Aq for aquatic lineages; Ae flying species; Fo for burrowers.

Table 1 indicates the ecological categorisation of each mammal taxon from the Northern Sperrgebiet. Figures 1 to 4 correspond to the four histograms defined above. The systematic histogram (Fig. 1) shows a dominance of rodents, followed by artiodactyls, Carnivores/Creodonts and the category « Others ». Overall, this is typical of relatively open milieux, but the corresponding histogram for Arrisdrift, (Guérin 2003, fig 1 A), with Carnivores/Creodonts dominant, followed by artiodactyls, the class « Others » and then rodents, clearly indicates a more open milieu.

The histogram of body weight (Fig. 2) presents a dominance of class C before classes AB, then D and H; There is thus an elevated number of medium sized species, which translates into the importance of forested zones; furthermore the important number of large species militates in favour of humidity. At Arrisdrift the homologous histogram is markedly different, the dominant classes are in the order AB, D, C and G (Guérin 2003, fig 1 B), the medium sized species are relatively less important, the milieu would have been more open.

The diet histogram (Fig. 3) provides evidence of the primacy of the brachyodont herbivore class (HB) in comparison with that of hypsodont herbivores

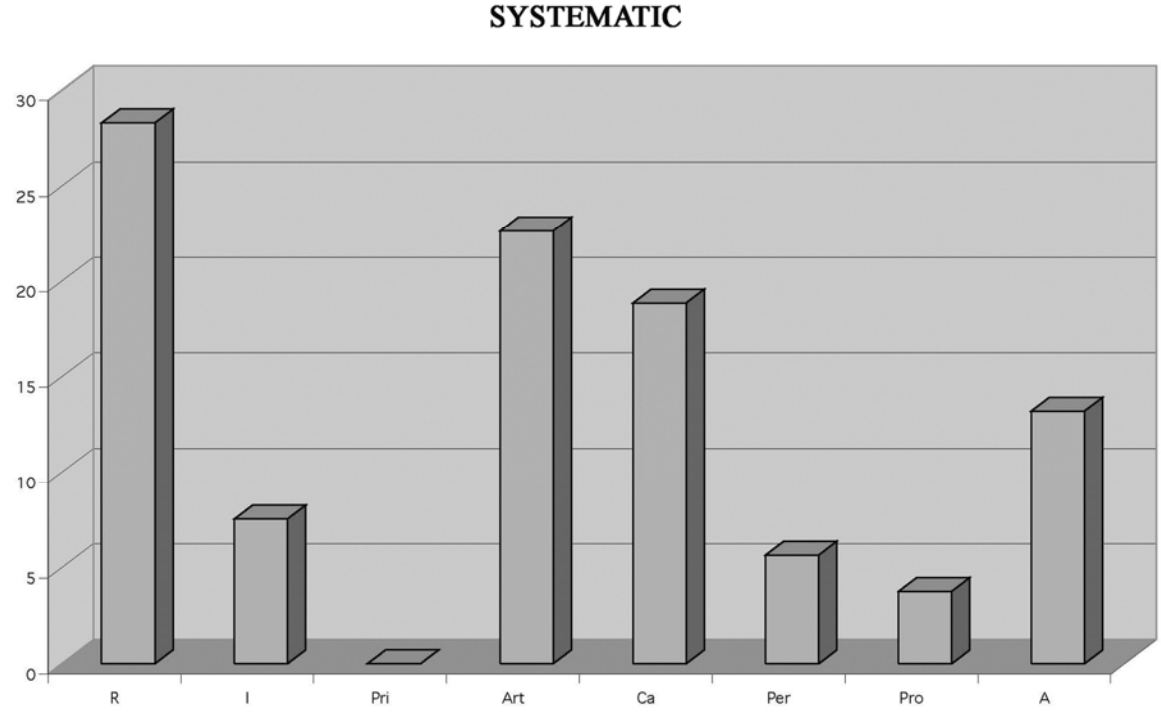

Figure 1. Ecological Histogram of Early Miocene mammals of the Northern Sperrgebiet, Namibia : systematic histogram.

Table 1. Ecological categories of Early Miocene mammals of the Northern Sperrgebiet (for abbreviations, see text).

Species	Systematics	Body weight	Diet	Locomotion
Gymnurechinus leakeyi	I	C	En	PT
Amphechinus rusingensis	I	AB	En	PT
Protenrec butleri	I	AB	En	PT
Prochrysochloris miocaenicus	I	AB	En	Fo
Myohyrax oswaldi	A	C	HH	PT
Protypotheroides beetzi	A	C	HH	PT
Miorhynchocyon rusingae	A	AB	HB	PT
Metapterodon kaiseri	C	D	Z	GT f
Metapterodon stromeri	C	D	Z	GT f
Hyainailourus or *Megistotherium*	C	G	Z	GT u
Isohyaenodon sp.	C	C	Z	GT f
Namasector soriae	C	AB	Z	PT
Ysengrinia sp.	C	D	Z	GT c
Leptoplesictis senutae	C	C	Z	PT
Leptoplesictis namibiensis	C	C	Z	PT
Viverridae indet.	C	C	Z	PT
Afrosmilus africanus	C	D	Z	GT c
Austrolagomys inexpectatus	A	C	HH	PT
Vulcanisciurus africanus	R	AB	HB	Gr-Ar
Protarsomys macinnesi	R	AB	FG	PT
Parapedetes namaquensis	R	AB	HH	Fo
Megapedetes cf. *gariepensis*	R	C	O	PT
Propedetes efeldensis	R	C	O	PT
Diamantomys luederitzi	R	C	HH	PT
Pomonomys dubius	R	C	HH	PT
Phiomyoides humilis	R	AB	FG	PT
Apodecter stromeri	R	AB	FG	PT
Neosciuromys africanus	R	C	HB	PT
Neosciuromys fractus	R	AB	HB	PT
Bathyergoides neotertiarus	R	AB	HB	Fo
Efeldomys loliae	R	AB	HB	Fo
Geofossor moralesi	R	AB	HB	Fo
Microfossor biradiculatus	R	AB	HB	Fo
Eozygodon morotoensis	Pro	H	HB	GT u
Gomphotheriidae indet.	Pro	H	HB	GT u
Orycteropus africanus or *chemeldoi*	A	D	En	GT u
Afrohyrax namibensis	A	F	HH	GT f
Prohyrax hendeyi	A	D	HH	GT u
Brachypotherium heinzelini	Per	H	HB	Aq
Chilotheridium pattersoni	Per	G	HH	Aq
Aceratherium acutirostratum	Per	G	HB	GT f
Brachyodus depereti	Ar	H	HB	Aq
Brachyodus aequatorialis	Ar	H	HB	Aq
Diamantohyus africanus	Ar	D	O	GT f
Nguruwe namibensis	Ar	D	O	GT f
Dorcatherium songhorensis	Ar	C	HB	GT u
Dorcatherium cf. *moruorotensis*	Ar	C	HB	GT f
Dorcatherium cf. *parvum*	Ar	C	HB	GT f
Propalaeoryx austroafricanus	Ar	D	HH	GT c
Propalaeoryx stromeri	Ar	E	HH	GT c
Sperrgebietomeryx wardi	Ar	D	HH	GT c
Namibiomeryx senuti	Ar	C	HH	GT c
Namibiomeryx spaggiarii	Ar	D	HH	GT c

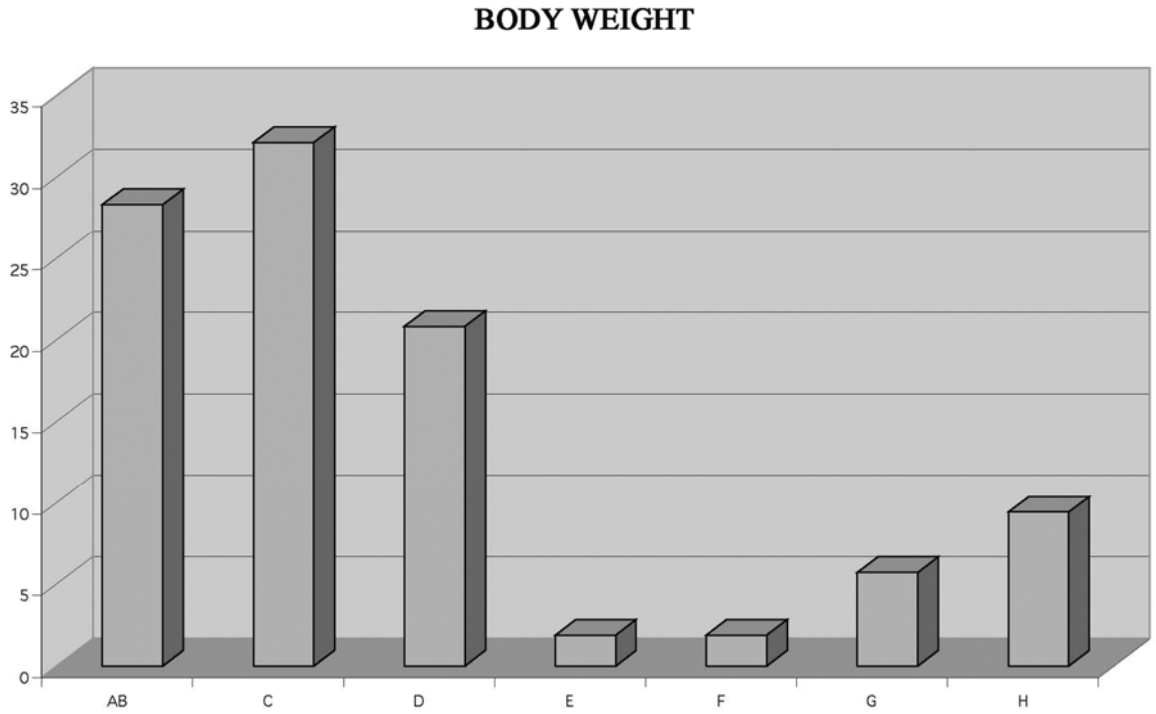

Figure 2. Ecological Histogram of Early Miocene mammals of the Northern Sperrgebiet, Namibia: body weight histogram.

(HH) which follows it, and which is followed in turn by zoophages and entomophages. This is also an indication of a milieu dominated by forest, whereas at Arridrift (Guérin 2003, fig 1 C) the zoophages are more abundant than brachyodont herbivores and hypsodont herbivores, which are equally diverse, follo-

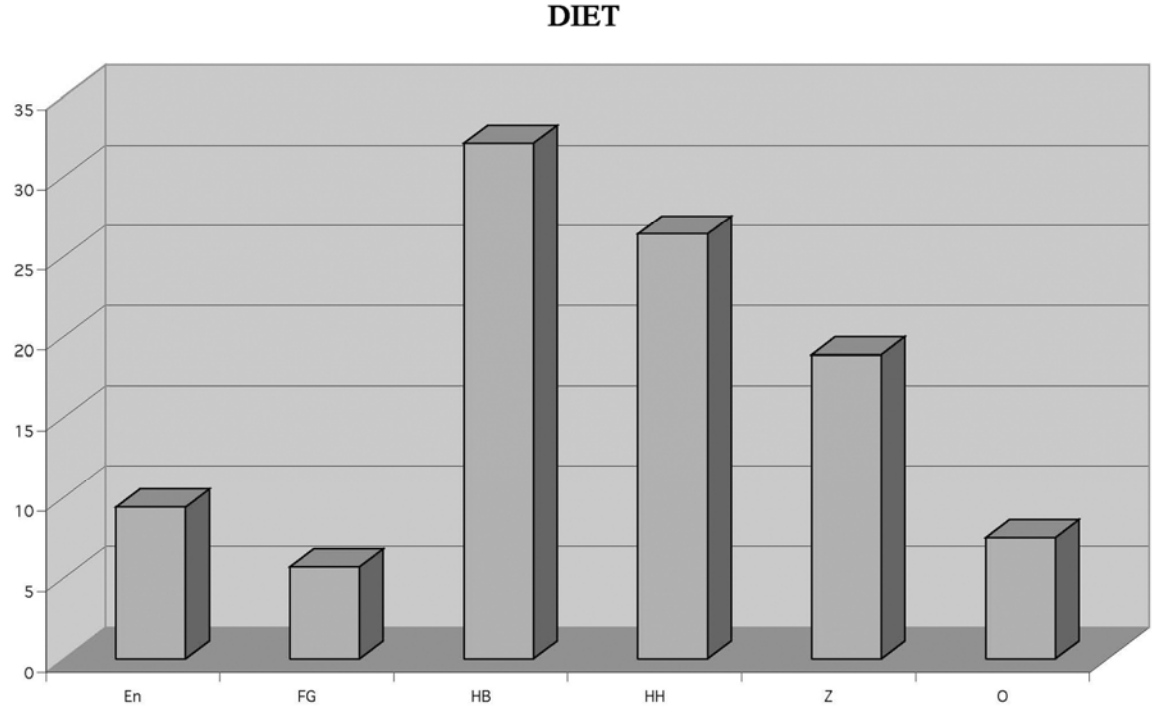

Figure 3. Ecological Histogram of Early Miocene mammals of the Northern Sperrgebiet, Namibia: diet histogram.

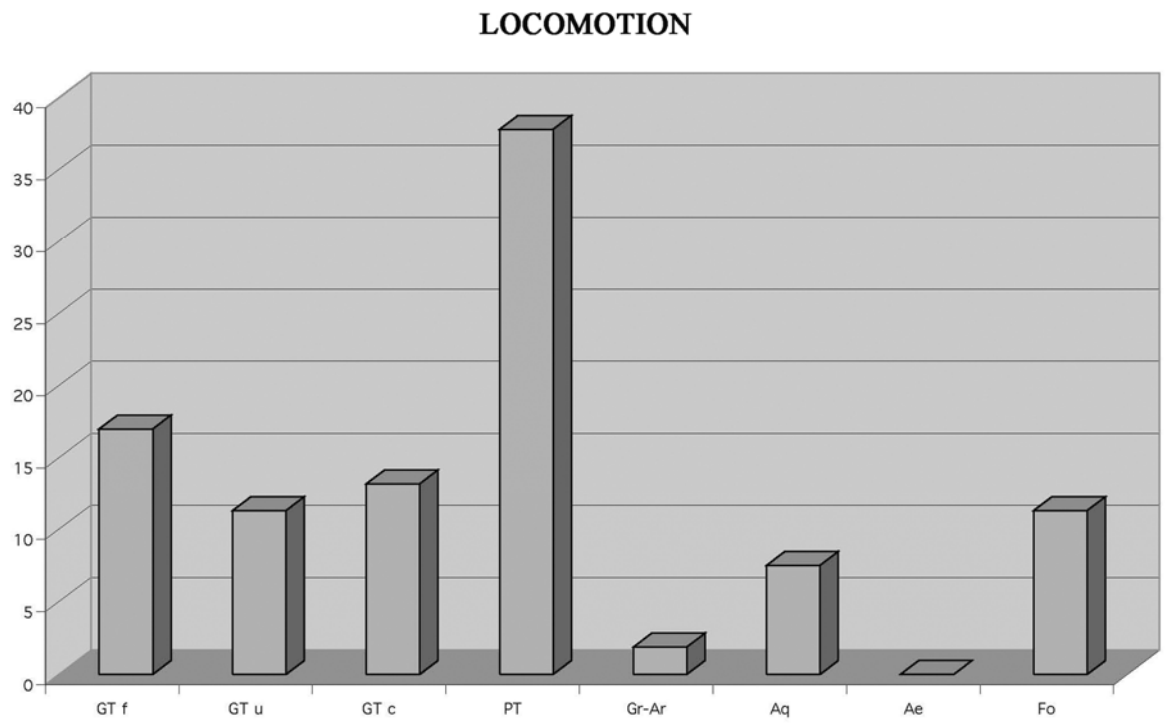

Figure 4. Ecological Histogram of Early Miocene mammals of the Northern Sperrgebiet, Namibia : locomotor histogram.

wed by entomophages, all of which indicate a more open milieu.

The locomotor histogram (Fig. 4) shows that small terrestrial mammals are largely dominant, followed in order by large terrestrial forest species, large terrestrial runners and large ubiquitous terrestrial lineages ; of note is the importance of burrowers (as numerous as the large terrestrial ubiquitous lineages) and in particular, the relatively important quantity of aquatic and aquaphile taxa. At Arrisdrift (Guérin 2003, fig 1 D) small terrestrial mammals are also largely in the majority, but they are followed in order by the ubiquitous terrestrial lineages, large terrestrial runners and large terrestrial forest living species.

In the Northern Sperrgebiet, during the Early Miocene, the palaeoenvironment was therefore dominated by forest (but there were also open zones), and it was frankly humid.

Conclusions

The synecological study and the autoecological study of the fossil mammals accord and complement each other to show that the palaeomilieu of the Northern Sperrgebiet during the Early Miocene was much more wooded and clearly more humid than that of the region of Arrisdrift at the base of the Middle Miocene.

These results confirm that written in 2003 by M. Pickford and B. Senut on the evolution of the climate during the Miocene in the region of the Namib. It was sub-humid around 20 Ma, after which it became semi-arid with summer rainfall between 17.5 and 16 Ma, and then finally clearly arid with winter rainfall.

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