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# GEOLOGY AND PALAEOBIOLOGY OF THE NORTHERN SPERRGEBIET, NAMIBIA

by

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# Diversification of grazing mammals in southern and equatorial Africa during the Neogene and Quaternary

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It has long been appreciated that mammal dentitions reveal information about diet. A study of African Neogene herbivore dentitions indicates that mammals with grazing adaptations have existed in Africa from the Early Miocene to the Present, suggesting the availability of grass in the environments throughout the period. However, there have been dramatic changes in the mammal communities possessing grazing adaptations. Initially, during the early Miocene the majority of mammals showing such dental adaptations were small, including rodents, macroscelidids and lagomorphs. By Late Miocene times, many medium to large mammals show grazing adaptations, and by the Plio-Pleistocene such adaptations reached a maximum development. These changes are considered to correlate closely with the inferred biomass of grass in the environment, being minimal in Early Miocene forested environments, and maximal in the Plio-Pleistocene steppic grasslands. Detailed examination of the southwest African and eastern African fossil records reveals that grasslands developed considerably earlier in southern Africa than in the equatorial regions. A result of this was that southern African faunas contain a greater diversity of grazing mammals at earlier periods than those in the equatorial zone. Indeed, a number of mammalian lineages adapted to grazing appear to have originated in the south and then spread northwards as environmental conditions opened up there. A number of southern lineages occupied the new equatorial grassland niches before local lineages could adapt to the new conditions. Such local lineages either went extinct or their ranges diminished, a few managing to survive in the central and west African forests.

## Introduction

Phytoliths abound in grasses, considerably more so than in dicotyledons. Herbivores that consume grass leaves and stems expose their teeth to excessive wear, phytoliths having the effect of fine-grained sand paper on the occlusal surfaces of the cheek teeth. Phytoliths are made of silica : 7 on Mho's scale of hardness, while hydroxyapatite has a hardness of 5, ie 100 times softer. Dentine is even softer, ca 4-4.5 on Mho's scale, about the same as cementum.

Mammals that are obligate grass eaters or which include significant amounts of grass in their diet have evolved a variety of strategies for increasing or prolonging tooth life despite excessive wear due to the presence of abundant abrasive opal phytoliths in the grass (Fortelius, 1985; Fortelius and Eronen, 2001; Fortelius and Hokkanen, 2001; Fortelius and Solounias, 2000; Janis, 1988; Janis and Fortelius, 1988; Solounias *et al*., 1994; Van Valen, 1960). Crowns can become hypsodont, the enamel can become folded (plicodont) thereby increasing the length of enamel cutting edge exposed in the occlusal surface. The crown can become invested in a cover of cementum, either incipiently as in *Brachyodus* and *Walangania* or massively as in Elephantidae, the lagomorphs *Austrolagomys* and *Lepus* and the suid *Phacochoerus* among other mammals.

It should be pointed out that it is not only opal phytoliths that play a role in producing excessive wear in mammalian cheek teeth. Open grasslands tend to be rather dusty environments, and clay to silt-sized clasts often blanket near-ground vegetation after wind storms and dust devil activity during the dry season, or sand and silt grains can be deposited on leaves by rain splash during the wet season. Such

lithic deposits adhering to grass leaves probably contribute to tooth wear in a continuous but relatively minor way compared to the daily, long term stresses imposed by opal phytoliths.

In volcanically active areas such as the Kenya Rift Valley, ash eruptions can also lead to widespread deposition of abrasive particles on plants but because eruptions are usually short-lived and erratic in occurrence, their effect on mammalian teeth is generally short-lived. In evolutionary terms, therefore, it would be difficult to discern the effects of volcanic eruptions on dental morphology.

Of greater importance is the environmental role that volcanic activity plays. Eruptions can destroy large tracts of vegetation, either by burying it under lavas, agglomerates and ashes, especially in the immediate vicinity of volcanoes, or by killing it off or altering it due to the hostile chemical environment that such eruptions can produce in the soil profile (Forbes *et al*., 2004). For example, the grassy plains of southern Kenya and northern Tanzania have been maintained at sub-climax vegetation stages over geological time spans, due to the high input of sodium, potassium and calcium into the environment as a result of the eruptions of carbonatite-nephelinite ashes that have blanketed the countryside from time to time. Some of these elements are flushed out of the soil relatively quickly by rain and ground water. Sodium and potassium are two such elements that are rapidly dissolved out of the ashes and soils, and are transported in solution towards lake basins where they contribute to the hyper-alkaline conditions that typify many rift lakes such as Natron and Magadi. Other elements such as calcium can persist in the soil profiles for much longer periods, often forming calcretes where they would normally not occur and

thereby maintaining the conditions in which grasses thrive but large trees cannot grow, or grow only poorly in restricted favourable patches. In East Africa there is evidence that volcanic activity has been altering environments in the vicinity of carbonatite-nephelinite volcanoes since at least the Early Miocene (for example Kisingiri (Forbes *et al.*, 2004) Elgon (Pickford 2002) Napak (Guérin and Pickford, 2003; Pickford, 2004) but it wasn't until the Plio-Pleistocene that activity increased to such an extent in some regions that vegetation over vast areas was kept permanently below its climax stage (Lemagrut, Ol Donyo Lengai and other volcanoes in the Serengeti region of northern Tanzania and southern Kenya have maintained the grassland ecosystem of the Serengeti for several million years).

### Grazing adaptations in mammals

Some Early Miocene small mammals that probably consumed grass developed moderately hypsodont cheek teeth (*Diamantomys, Phthynilla, Pomonomys, Megapedetes*) while others developed extremely hypsodont dentitions without cementum but still retaining roots (*Myohyrax, Protypotheroides*) whereas even others possessed extremely hypsodont cheek dentitions in which the teeth were rootless (*Austrolagomys*). There is often a slight to extensive development of cementum in these lineages, especially the more hypsodont ones (*Austrolagomys*). Few of the eastern and southern African Miocene small mammals with hypsodont teeth developed plicodonty to any great degree, but this condition does occur in some Eurasian lagomorphs (*Prolagus, Trischizolagus*). A few small mammals (*Myohyrax*) developed molarized and hypsodont premolars, another way of increasing the longevity of the cheek tooth battery.

Medium to large mammals that generally live for longer than 5 years compensate for excessive crown wear by a variety of means, some of which are uncommon in small mammals. Hypsodonty, plicodonty, and cementodonty are common to many lineages (Elephantidae, Suidae, Equidae, Rhinocerotidae, Bovidae). Addition of lophs (polylophy) to intermediate molars or to the third molars occurs in several lineages (Proboscideans, Suidae). Hypsodont ectolophs develop in some lineages (Hyracoidea such as *Prohyrax, Parapliohyrax, Pliohyrax, Kvabebihyrax, Postschizotherium*) leaving the lingual cusps of upper molars brachyodont, but this is rare among mammals (*Plagiolophus* is another lineage that employed this strategy). Some lineages, such as bovids and anthracotheres developed increased buccolingual apical to cervical flare of the molars, especially the upper ones (ie the occlusal surface is considerably wider at the cervix than at the apex of the cusps) and some lineages evolved anteroposterior cervical to apical flare of the crowns (ie the crowns are longer apically than at the cervix as in some climacoceratids and the In-

dian suid *Hippohyus* (Pickford, 1987)). As a consequence, mesiodistal length measurements of the occlusal surface of such teeth decrease with increasing wear, whereas the buccolingual breadth measurements increase with increasing wear. Some lineages of mammals molarized the premolars (myohyracids, hyracoids to some extent, rhinocerotids and equids for example). In most of the lineages of Proboscidea and Suidae that developed hypsodont cheek teeth, the enamel thickness was reduced, but the length of enamel cutting edges exposed in the occlusal surface of the crown was increased, either by plication or by the addition of extra lophs to the crowns or by packing more lophs into each unit length of crown. Many mammalian lineages developed cementum cover, and in some of them the surface of the enamel became pustulate (ptychodont as in several Proboscidea including *Afrochoerodon*) or coarsely wrinkled as in *Choerolophodon*, or finely wrinkled (as in the suids *Notochoerus, Metridiochoerus, Phacochoerus,* the anthracothere *Brachyodus* and some proboscideans such as *Loxodonta*). The main function of ptychodonty and choerodonty appears to be the provision of a suitably rugose surface for binding the cementum cover tightly to the enamel in order to prevent chewing forces from shearing the cementum off the enamel. These features are often found together. Phylogenetically, in mammals such as anthracotheres and many pecorans it appears that wrinkling of enamel often developed prior to cementum deposition. In proboscideans the same seems to apply to choerodonty and ptychodonty, early members of lineages with these features possessing light cementum cover (*Afrochoerodon*) while later members (*Choerolophodon*) may have extremely voluminous cementum cover on the cheek teeth.

### Eastern Africa Cainozoic mammals with grazing adaptations

Examination of the Neogene and Quaternary fossil record of tropical Africa reveals that at one time or another, all the dental strategies mentioned above have been employed by at least one, and sometimes several mammalian lineages. However, the record reveals that the distribution of the various strategies for increasing tooth durability through time varied considerably and that they came into play at different times. For instance, very few Early Miocene East African mammals had hypsodont cheek teeth (*Myohyrax*) or cementum (*Austrolagomys, Ougandatherium*) (Guérin and Pickford, 2003) and only a few had wrinkled enamel with a thin, often incomplete cover of cementum (*Brachyodus, Walangania*). By the Pleistocene in contrast, all the strategies for increasing crown life had come into play in numerous lineages of tropical African mammals (Proboscidea, Suidae, Bovidae, Rhinocerotidae, Equidae, Lagomorpha, some rodents (*Pedetes*)).

All of this indicates that the development of

grasslands in East Africa was uneven in rate and kind, but that there was an overall trend for grassland cover to increase with the passage of geological time (Pickford, 2002, 2004). Each mammal lineage that was affected responded at different times and with different combinations of strategies for increasing dental crown life, depending on the vegetation that it could exploit (monocotyledons, dicotyledons) but the overall increase in the employment of such strategies in the fauna provides unequivocal evidence that grasslands increased in area throughout East Africa during the Neogene. This implies that forest and woodland cover decreased correspondingly throughout the same period.

Examination of the East African fossil record in detail shows that the changes were not gradual, but that there were several periods during which accelerated changes took place, and others during which changes were gradual or even stationary. There is no evidence of reversal of the overall trend towards increase in grassland cover, and it seems that this did not happen, although there is no reason, *a priori*, that it shouldn't have done so, at least locally.

It is thus clear that in Eastern Africa the biomass of grass increased throughout the Neogene and Quaternary until it came to dominate huge areas of the region (up to almost 100% grassland cover in some areas such as the Serengeti and Kapiti Plains). The correlate of this is that the biomass of woodland and forest decreased throughout the same period, thereby exerting immense long term pressures on mammalian lineages that were dependent on trees for their survival. The implications for hominoid primates is obvious, since trees provide the principal source of nourishment for such opportunistic omnivores (fruit, nuts, soft leaves) and none of them can survive on a diet of grass (the papionine *Theropithecus* is interesting in this respect, as it is one of the few primates that survives mainly on a diet of grass, albeit predominantly grass seeds and young shoots). Baboons exploit grass corms, but also eat above-ground stems and leaves.

### Southern African Miocene mammals with grazing adaptations

Miocene faunas from the Namib reveal that there must have been grass available as early as ca 21 Ma, but that the region was still well endowed with trees at that time (Ségalen *et al.*, 2002). There is a higher diversity of hypsodont rodents and macroscelidids in the Sperrgebiet (Table 1) than occurred in Early Miocene deposits of East Africa, but there was a lower diversity of medium to large herbivores, the early bovids and climacoceratids being mainly browsers with minor grazing activity.

The common presence of fossil hives of the harvester termite (*Hodotermes*) in the early Miocene deposits of the Sperrgebiet, also indicates that grass must have been present. The overall picture that

emerges is that the region was probably well wooded savannah, possibly like the Grootfontein region in northern Namibia at the present day. Under the climate that prevails today near Grootfontein, calcrete pedogenesis is at its optimal, meaning that thick sheets of calcrete can form in relatively short periods of time (10,000 to 40,000 years). The presence of similar calcretes in the Sperrgebiet, such as for example at Strauchpfütz, supports the suggestion that during the Early Miocene, the Namib was covered in wooded savannah, and that its rainfall was probably between 200 and 760 mm per annum.

The low diversity of medium and large grazers in the Early Miocene faunas of the northern Sperrgebiet suggest that even though grass was available, it was not a dominant vegetation type. As such the main grazers were small vertebrates and termites. Among the vertebrates there were grazing rodents (*Diamantomys*, *Phthynilla*, *Bathyergoides*, *Neosciuromys*, *Parapedetes*, *Propedetes*, and the bathyergid *Efeldomys*) lagomorphs (*Austrolagomys*) and macroscelideans (*Myohyrax*, *Protypotheroides*). Medium to large herbivores were dominated by browsing mammals, such as the ruminants *Dorcatherium*, *Namibiomeryx*, *Sperrgebietomeryx* and *Propalaeoryx* (some of which may have included minor amounts of grass in their diets) the hyracoids *Prohyrax* and *Afrohyrax*, the rhinocerotids, *Brachypotherium*, *Chilotheridium* and *Aceratherium*, the proboscidean *Eozygodon* and the anthracothere *Brachyodus*. The latter genus may have included some grass in its diet, as its teeth show incipient ptychodonty and cementodonty. The small suoids *Nguruwe* and *Diamantohyus* were probably omnivorous, and likely did not include grass in their diets at all. The ostrich *Struthio coppensi* probably consumed grass as well as other plant types. Aepyornithoid eggshells from Elisabethfeld, Grillental and Langental reveal that the bird responsible for them (on the basis of size, it could have been *Struthio coppensi*) included C4 plants in its diet as well as C3 plants (Ségalen *et al.*, 2002).

### Distribution of grasses in Africa

At present, grasses occur in almost all vegetation categories in Africa, but it is in Sahelian type phytochores that they dominate the landscape. In the most humid environments, the Guineo-Congolian rainforest, grasses are confined to the forest understory and occasional glades within the forest, but in any case they make up a minute proportion of the entire vegetative ecosystem. In slightly drier regions where Soudanian phytochores occur (open forest to heavy woodland) grassland is more important and can comprise up to 40% or so of the ground cover. In even drier areas, where Sahelian type phytochores dominate, grasses constitute a significant proportion of the vegetation cover, reaching 100% in particularly favourable areas, but usually having abundant tress and bushes as well as grass. In even drier environments,

Table 1. Feeding categories of Namibian Miocene Mammals

| Locality | Age Ma | Grazers | Mixed graze/browse | Browse | Omnivore |
|---|---|---|---|---|---|
| Langental Grillental, E-Feld | 20 20 21 | *Myohyrax Protypotheroides Parapedetes Propedetes Bathyergoides Diamantomys Neosciuromys Austrolagomys Efeldomys* | *Sperrgebietomeryx Propalaeoryx Namibiomeryx Prohyrax Brachyodus* | *Brachypotherium Aceratherium Afrohyrax Eozygodon* | *Dorcatherium Diamantohyus Nguruwe* Gomphothere |
| Auchas | 19 | *Diamantomys Myohyrax* | *Brachyodus* | *Eozygodon Deinotherium* | *Progomphotherium* |
| Arrisdrift | 17.5 | *Myohyrax Austrolagomys* | *Namacerus Orangemeryx Prohyrax Chilotheridium* Anthracothere | *Deinotherium Namachoerus Diceros* | *Dorcatherium Afromastodon Nguruwe* |
| *D. corbetti* levels | 14 | *Propedetes* | Bovid | Giraffid | Gomphothere |
| *D. wardi* levels | 10 | *Propedetes* | Bovid | Giraffid | Gomphothere |

such as arid steppe, grass cover is generally less than in Sahelian zones, it is more seasonal and large parts of the regions can be covered in bush or may be partially to totally devoid of vegetation. Finally, in desert biotopes, grass cover can be very sporadic, unpredictable and seasonal, and in any case covers only minor parts of the available land surface.

From the above overview of grass distribution in Africa, it is evident that Sahelian type zones are the most favourable for grass growth, and it is in these zones that the greatest number of mammal species will show one or more signs of dental wear stress due to consumption of plants rich in opal phytoliths, and will evolve one or several strategies for minimising or compensating for excessive cheek tooth wear (eg cementum cover) or for extending the life of teeth (eg hypsodonty or polylophy). Indications of such adaptations will appear in many of the mammalian lineages ranging in size from rodents to proboscideans, whereas in such environments bunodont and brachyodont mammals will tend to be relatively rare and of low diversity.

In contrast, the Guineo-Congolian zone is populated by many lineages of mammals that show minimal signs of excessive cheek tooth wear from the presence of opal phytoliths in their diet, and thus most of them will possess bunodont to brachyodont teeth with no cement covering, and weak signs, or no indications at all, of hypsodonty or of polylophy. Furthermore, the biomass of grass in forests is usually small, so it is a relatively minor source of food and can thus support only a limited biomass of herbivores. For this reason, the main grazers in forested regions are small mammals (rodents, lagomorphs) and the occasional bovid or suid (eg *Hylochoerus*). From a palaeontological perspective, it should be possible to determine whether a fauna lived in a humid forest setting, because it will be dominated by bunodont and brachyodont lineages, and if it contains grazers, then these will be dominated by small mammals with a restricted diversity of small or medium sized ruminants, which will in any case show weak adaptations to excessive tooth wear.

At the opposite end of the vegetative spectrum, mammal species adapted to semi-arid to arid environments tend to show evidence of excessive cheek tooth wear, and concomitant evolutionary strategies for extending tooth life, because the dominant vegetation type in such conditions is grass. From the dietary point of view of a herbivore, there is not a great deal of difference between a savannah and a desert, apart from the differences encountered in ensuring access to adequate food supplies. As a general rule, however, the diversity of herbivorous mammals in desert areas is lower than it is in savanna and woodland, and thus the variety of strategies employed for increasing the life of cheek teeth will be more limited than it is in savannas. Because of this, it should be possible by examining the diversity of herbivores and the variety of strategies employed for increasing the life of cheek teeth, to determine whether a fossil locality preserves herbivores from either savanna or desert environments.

## General trends in the development of grazing faunas in the Neogene of Africa

Study of eastern and southern African Miocene faunas reveals that there is a definite order in the development of grazing niches among vertebrates. As grasses started becoming available in sufficient quantities for animals to exploit them on a regular or even on an exclusive basis, it was the small mammals that reacted first in terms of developing hypsodonty and cementodonty. This stage corresponds to Guineo-Congolian forest and the transition zone between

such rainforest and Soudanian dry forest and heavy woodland, in which grass is present but in small quantities or is restricted to clearings within forest.

As grass cover increased at the expense of trees, corresponding to regional mosaics between Guineo-Congolian forest on the one hand, and Soudanian-Zambezian-Somali phytochores on the other, larger mammals began to show dental adaptations to grazing including hypsodonty, cementodonty and plicodonty, but in the initial stages these adaptations were weakly developed. The earliest large mammal to show such adaptations in the Neogene of Africa was the elasmotheriine rhinoceros *Ougandatherium*, known from the Early Miocene of Uganda (Guérin and Pickford, 2003) and Kenya. Medium sized herbivores from the Early Miocene show weak to incipient dental adaptations to grazing, suggesting that grass was a minor or occasional element in their diets. The main lineages involved were *Walangania* in east Africa, and *Namibiomeryx*, *Sperrgebietomeryx* and *Propalaeoryx* in southern Africa. It is stressed though, that the signs for grazing in these genera are weakly developed, meaning that their main food probably consisted of C3 plants. The brachy-hypsodont hyracoid *Prohyrax* shows clear signs of grazing adaptations in the high crowned ectolophs of the cheek teeth. The other hyracoid from the Sperrgebiet (*Afrohyrax*) was probably a committed browser, as it shows no signs of dental adaptations for grazing. During this stage, many small mammals continued to show grazing adaptations in their teeth.

As grass cover increased even further, as Soudanian and related types of phytochores increased in area, more medium sized mammals show signs of grazing adaptations, but these continued to remain quite weakly developed. What appears to have happened is that a greater diversity or ruminants developed, but none of them were extremely hypsodont. The same applies to other large mammals including proboscideans, rhinocerotids, anthracotheres, chalicotheres, hyracoids and suids but, as before, dental adaptations to grazing were moderate, consisting of weakly developed cementodonty, plicodonty, polylophy, and hypsodonty. Strangely, the diversity of small mammals showing grazing adaptations appears to have decreased, perhaps as a result of increased competition from medium sized mammals which increased in diversity at this stage of development of grasslands, as well as increased competition from invertebrates such as harvester termites that played a huge role in grazing but which are less involved in more closed vegetation types (rainfall greater than 750 mm per annum).

It wasn't until grass was the dominant vegetation type, such as occurs in Sahelian and Kalahari-Highveldt phytochores, that many lineages of medium and large mammals show clear and diverse well developed adaptations for grazing. Proboscideans such as elephantids developed polylophy, hypsodonty and cementodonty, whereas others such as anancines,

remained relatively bunodont but developed major cementum deposits on the crowns of the cheek teeth. Even suids, which in more closed vegetation types remained omnivorous or folivorous, began to develop hypsodonty, polylophy, plicodonty and cementodonty, culminating, in the fullness of time, in extreme forms such as *Metridiochoerus* and *Phacochoerus*. In these vegetation types, bovids became even more diverse, and several lineages developed hypsodont teeth with cementum, but seldom very exaggerated plicodonty or increased number of lophs in the cheek teeth. Equids, which were already hypsodont when they colonised Africa at the beginning of the Late Miocene, developed higher cheek teeth, but did not experience any major reorganisations of their dentitions, certainly nothing like those that developed in proboscideans and suids. Rhinocerotids were also rather conservative in terms of dental modifications, with minor plicodonty and cementodonty being developed in *Kenyatherium* and a combination of cementodonty and moderate hypsodonty in ceratotheres. Small mammals adapted to grazing appear to have become even less diverse than in more closed conditions, probably due to increased competition from medium sized grazers and insects that specialise in eating grass.

As conditions become even more open, as in the Sahara-Karroo-Namib phytochores (Fig. 5), the diversity of grazing mammals decreased and no new adaptive dental strategies evolved. This is probably due to the fact that in these phytochores, grass cover is less extensive than in the Sahelian type of phytochore, and it is more seasonal and more patchy in its distribution both in time and in space. In these environments, mammals that include important quantities of grass in their diets are known for the vast size of their territories and their adaptations for long distance migrations in search of sufficient grazing. They also regularly include other vegetation in their diets when it is available, and many show special adaptations for surviving long periods without drinking water.

In summary, there appears to be a close correlation between the development of African phytochores and the animals, especially mammals, that exploited grasses within them. The assemblage of mammals in each phytochore differs from those in neighbouring phytochores. In general, in humid environments where grass is scarce, as in forest and woodland, micromammals comprise the main mammalian grazers. As the grass cover increases, medium sized mammals begin to exploit the grass accompanied by incipient or minor adaptations in large mammals. Termites and other insects that eat grass also increase in diversity, leading to a reduction in the diversity of grazing micromammals. As grassland becomes the dominant vegetation type, such as in Sahelian savanna and steppe, then many medium-sized and large mammals develop dental adaptations for dealing with the effects of abrasion caused by increased ingestion of grass. The range of such adaptations reaches its maxi-
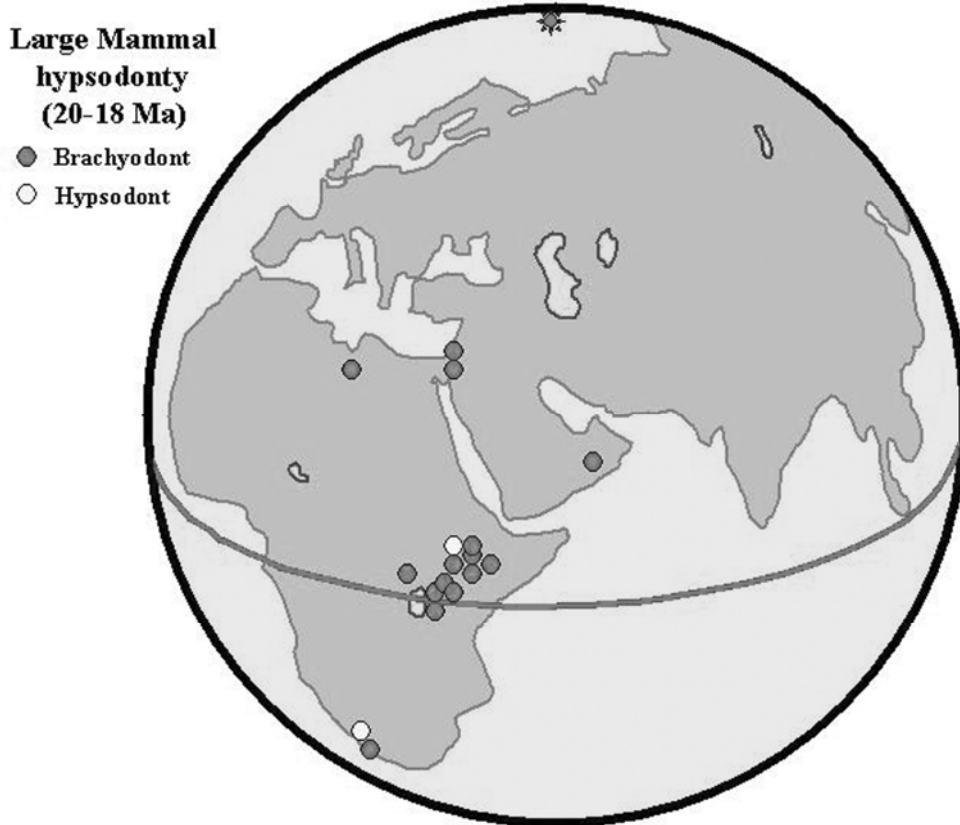
**Figure 1**. Distribution of hypsodont and brachyodont herbivores in Africa from 20-18 Ma. Note the almost equal diversity of browsers/grazers in southern Africa, and the high predominance of browsers over grazers in East Africa.
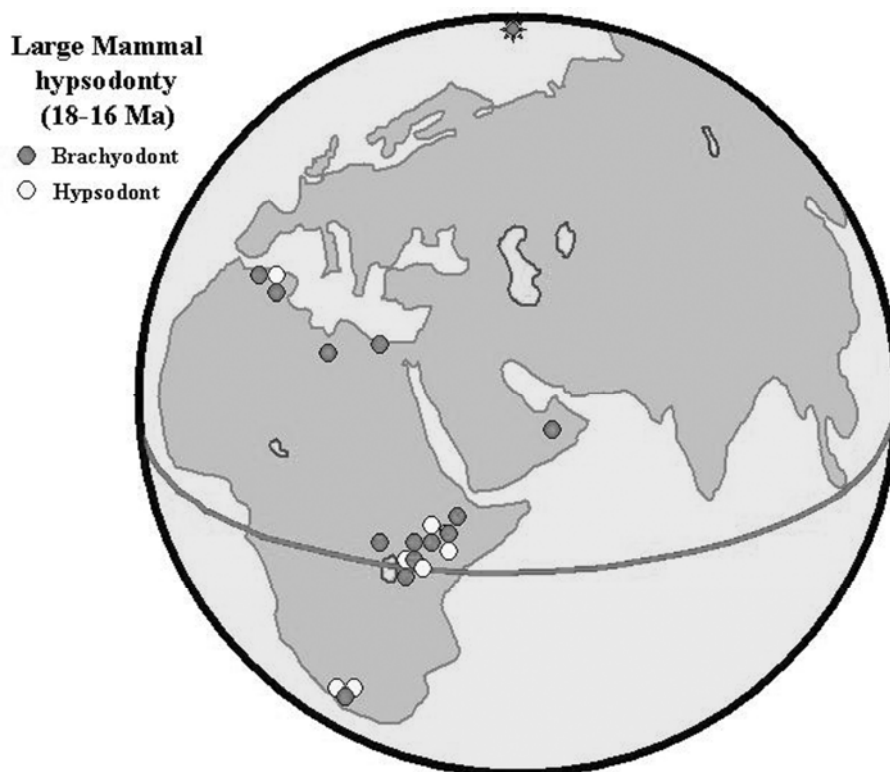


**Figure 2**. Distribution of hypsodont and brachyodont herbivores in Africa from 18-16 Ma. Note the dominance of grazers over browsers in South Africa, compared to the dominance of browsers over grazers in East Africa and North Africa.
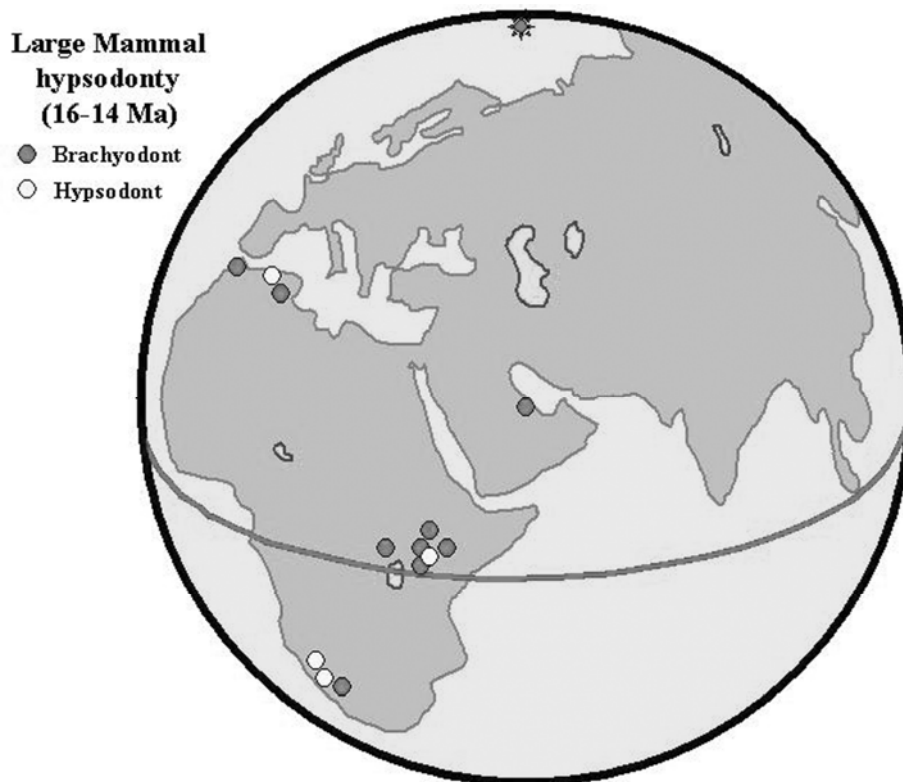
**Figure 3**. Distribution of hypsodont and brachyodont herbivores in Africa from 16-14 Ma. Note the dominance of grazers over browsers in the South compared to the situation in East and North Africa.
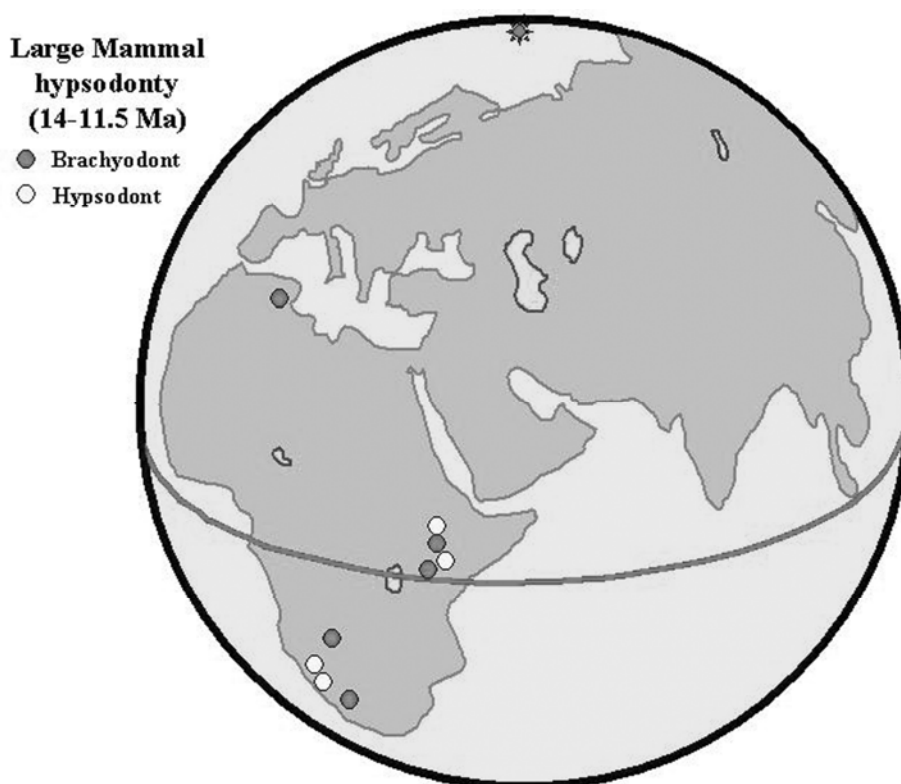
**Figure 4**. Distribution of hypsodont and brachyodont herbivores in Africa from 14-11.5 Ma. Note that the diversity of grazers and browsers in East Africa is more equal during this period than it was in prior periods, and that it approaches the situation that had persited in southern Africa for a long time.

mum, and includes hypsodonty, plicodonty, cementodonty, polylophy and arhizy (ever-growing, rootless teeth) and it includes a maximal diversity of mammals (bovids in particular, but also suids, proboscideans, equids, and rhinocerotids among the medium and large mammals, and some rodents (pedetids, hystricids) and lagomorphs (*Lepus*) among the smaller ones).

The phytochore succession described above corresponds closely to the climatic conditions prevalent in the areas where they occur (mean annual rainfall in particular, but also temperature and seasonality) and

the dental adaptations in each phytochore can be viewed as being related to (and ultimately caused by) climatic conditions that prevail within them. As such the dental adaptations may be used to throw light on palaeoclimates.

### Summary of southern and eastern African grassland ecosystems

The faunas and other data (palaeosols) from southern and eastern Africa reveal that grassland cover developed earlier in the south than in equatorial
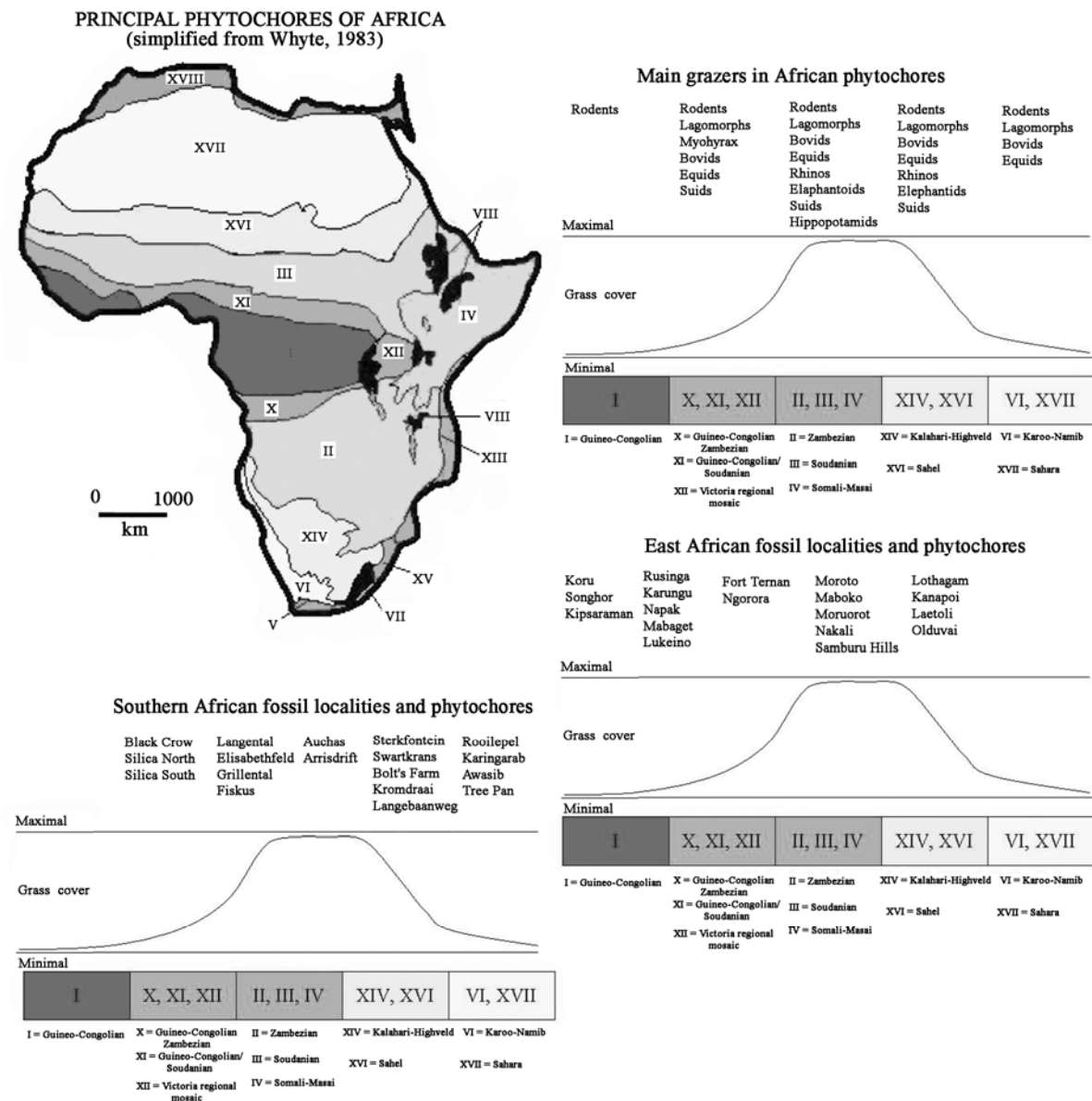


**Figure 5**. Principal phytochores of Africa and the distribution of grazers in these phytochores. The fossil record of grazers in South Africa and East Africa is analysed, and indicates that Southern Africa experienced more open, more arid environments earlier than East Africa did, and this gave southern African mammal lineages a head start in adapting to such ecosystems. When East Africa opened up during the Late Miocene in particular, due to increasing aridity, southern mammal lineages already adapted to arid biotopes simply moved northwards and occupied the available niches before the local lineages could themselves adapt to them.

Africa, and that it has, as a consequence, persisted there longer (Fig. 1 - 5). Not only was the diversity of hypsodont micromammals greater in the south at equivalent periods in the Early Miocene, but also the diversity of medium to large browsing and omnivorous mammals was less than in equatorial Africa. There can be little doubt that in terms of openness of vegetation types (phytochores) the south (at least the southwest where the bulk of the evidence comes from) has largely been in the lead in the African continent. This in turn implies that the south has been more arid and more seasonal for a longer period of time than has the rest of the continent.

The fact that the southern parts of the continent have been more arid, more seasonal, and thus endowed with more open vegetation types, for longer than the rest of the continent, has given many lineages of plants and animals a substantially longer time to adapt to such conditions than has any other part of the continent.

To find comparable histories in other parts of the world, we need to examine mid-latitude Asia and southeastern Europe but these were largely separated from Africa by seaways through much of the Miocene.

It is not surprising therefore, to find that, once arid ecotypes began to occur in East Africa in Middle and Late Miocene times, many lineages of plants and animals from the south simply expanded their territories northwards, displacing local lineages that were afforded inadequate time to adapt to the new conditions before they suffered competition from those lineages that were advancing on them from the south. It was only in the Late Miocene that input from the Eurasian arid areas began to have an important impact on East African faunas, eventually outnumbering advances from the south. Nevertheless, invasions from the south did not cease, several austral lineages of mammals managing to colonise the equatorial parts of the continent during Pliocene and Pleistocene times.

## References

Forbes, M., Bestland, E., Krull, E. and Dicker, D. 2004. Palaeoenvironmental mosaic of *Proconsul* habitats: geochemical and sedimentological interpretation of Kisingiri fossil sites, Western Kenya. *J. Afr. Earth. Sci.,* **39**, 63-79.

Fortelius, M. 1985. Ungulate cheek teeth: developmental, functional and evolutionary interrelations. *Acta Zool. Fennici*, **180**, 1-76.

Fortelius, M. and Eronen, J.T. 2001. Ungulate hypsodonty as a proxy for environmental aridity in the Miocene of Europe. 2nd EEDEN Wksp (Sabadell) *Late Miocene to Early Pliocene environments and ecosystems* Volume of Abstracts, pp. 31-32.

Fortelius, M. and Hokkanen, A. 2001. The trophic context of hominoid occurrence in the later Miocene of western Eurasia - a primate-free view. *In*: L. de Bonis, G. Koufos, and P. Andrews (eds) *Phylogeny of the Neogene Hominoid Primates of Eurasia*, pp. 19-47, Cambridge, Cambridge University Press.

Fortelius, M. and Solounias, N. 2000. Functional characterization of ungulate molars using the abrasion-attrition wear gradient : a new method for reconstructing paleodiets. *Amer. Mus. Novit.*, **3301**, 1-36.

Guérin, C. and Pickford, M. 2003. *Ougandatherium napakense* nov. gen. nov. sp. le plus ancien Rhinocerotidae Iranotheriinae d'Afrique. *Ann. Paléont.,* **89(1)**, 1-35.

Janis, C. 1988. An estimation of tooth volume and hypsodonty indices in ungulate mammals, and the correlation of these factors with dietary preferences. *Mém. Mus. Nat. Hist. Nat. Paris*, **53**, 367-387.

Janis, C. and Fortelius, M. 1988. On the means whereby mammals achieve increased functional durability of their dentitions, with special reference to limiting factors. *Biol. Rev.,* **63**, 197-230.

Pickford, M. 1987. Revision of the Miocene Suidae of the Indian Subcontinent. *Münchener Geowiss. Abh.* A., **12**, 1-91.

Pickford, M. 2002. Early Miocene grassland ecosystem at Bukwa, Mount Elgon, Uganda. *C. R. Palevol*, **1**, 213-219.

Pickford, M. 2004. Palaeoenvironmental reconstruction of Early Miocene hominoid-bearing deposits at Napak, Uganda, based on terrestrial molluscs. *Ann. Paléont.*, **90**, 1-12.

Ségalen, L., Renard, M., Pickford, M., Senut, B., Cojan, I., Le Callonec, L. and Rognon, P. 2002. Environmental and climatic evolution of the Namib Desert since the Middle Miocene: the contribution of carbon isotope ratios in ratite eggshells. *C. R. Geoscience*, **334**, 917-924.

Solounias, N., Fortelius, M. and Freeman, P. 1994. Molar wear rates in ruminants: a new approach. *Ann. Zool. Fennici*, **31**, 219-227.

Van Valen, L. 1960. A functional index of hypsodonty. *Evolution*, **14**, 531-532.