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Proboscidean dispersals from Africa towards Western Europe

Proboscideans of African origins dispersed towards Western Europe during two distinct periods: browsing forms did so between some 18.5 and 14 Ma and grazers between some 2.7 and 0.8 Ma ago. The earlier dispersals occurred when Western Europe had a warmer and less seasonal climate than today, the later dispersals occurred at moments of fundamental global climatic change when open landscapes increased in Europe. Between 8 and 6 Ma ago, the changing environment caused African Proboscidea to adapt to grazing. It is this adaptation that allowed them to enter again Western Europe.

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INTRODUCTION

From the Miocene onwards, proboscideans are well known from most continents. Since the beginning of this century, their origin is supposed to be in Africa. Describing material from the Fayum, Andrews (1904, 1906), proposed for the first time that the origin of the proboscideans is in the African *Moeritherium*. Schlesinger (1912) determined *Mastodon angustidens* in the lower Miocene of Algeria. Matsumoto (1924) supposed that the zygodonts descended from *Palaeomastodon* and the bunolophodont elephantoids from Phiomia, both from the Palaeogene of Africa. This idea was followed by Tobien (1978).

Berggren & Van Couvering (1974) and Madden & Van Couvering (1976) popularised the 'Proboscidean Datum Event'. This event was supposed to be a major faunal exchange between Africa and Eurasia during the Early Miocene. This 'event' attracted much discussion about when it happened and which taxa where involved. Tassy (1990) and Antunes (1990) showed that the initial dispersal of the proboscideans was diachronous and that there was more than one dispersal event. Thomas (1985) supposed that there were two major faunal exchanges and Van der Made (1996) recognised up to six dispersal events between Africa, northern Eurasia, the Indian Subcontinent and the area formed by SE Europe and Anatolia. These events ranged in age between 21 and 12.5 Ma. The proboscideans that have been assumed to disperse from Africa include *Hemimastodon*, *Gomphotherium*, *Zygolophodon*, *Choerolophodon*, *Platybelodon*, and *Deinotherium*.

The entry of *Mammuthus* (or '*Archidiskodon*') in Europe coincides with that of *Equus* and is considered to be an important stratigraphical marker (Azzaroli *et al.* 1988). This event is believed to have occurred some 2.7 Ma ago (Sardella *et al.* 1998). The dispersal of *Elephas antiquus* towards Europe has

aroused much less interest, possibly because this species has often been confused with *Mammuthus*. Though the possibility of other dispersals will be discussed below, an interesting pattern arises: the proboscidean dispersal events towards western Europe form two clusters, one in the Early-Middle Miocene and one in the Late Pliocene and Pleistocene. It is the aim of this paper to establish which dispersals occurred and when they occurred, and to study their context.

THE TAXA

Hemimastodon
Hemimastodon is known only from two teeth from Bugti, described by Pilgrim (1908) and Tassy (1988). The exact age is not well known, but the bulk of the fauna might be as old as 21 Ma (Van der Made 1996). A phylogenetic analysis by Tassy (1990) suggests that *Hemimastodon* is the sister taxon of the Elephantoidea. The primitive character of these teeth is in line with an old age, but is not sufficient ground to assume that the taxon was present in the Indian Subcontinent prior to the major Early Miocene faunal exchange at about 21 Ma; though primitive, the taxon may have come from Africa.

Gomphotherium
Historically *Gomphotherium*, being a bunodont elephantoid, has been traced back to Phiomia (Tobien 1976, 1978). Many authors supposed an evolution from *Gomphotherium* to *Tetralophodon* to *Anancus* (Schlesinger 1917; Lehmann 1950; Mottl 1969; Tobien 1978), though Tassy (1985) did not accept this lineage. Material from Portugal that has been considered intermediate between *Gomphotherium* and *Tetralophodon* (Antunes & Mazo 1978), was considered to be platybelodont (Tassy 1985). Both *Gomphotherium* and *Tetralophodon* have been reported from Eppelsheim, Germany (Lehmann 1950; Tobien 1980, 1996), but in SW Europe, this association has never been found (Mazo 1977, 1996). *Gomphotherium* and *Tetra-*

lophodon are cited from the Turolian of China (Tobien *et al.* 1986, 1988; Guan 1996).

A skull and mandible from the Upper Miocene of Hohenwarth in Austria were interpreted as intermediate between *Tetralophodon* and *Anancus* (Zapfe 1957) and many isolated teeth have been considered as intermediate (Schlesinger 1917; Lehmann 1950; Mottl 1969; Tobien 1978). Material from Concud has been assigned to *Anancus* or a closely related form (Lehmann 1950; Bergounioux & Crouzel 1958; Mazo 1977) and has an age of 6.8 Ma (Van Dam 1997). Material from the Late Miocene of Perim (Tassy 1986) might be among the oldest material, but the exact age is not known. Material from Mpesida, Kenya has an estimated age of 6.4-6.0 Ma (Kalb *et al.* 1996) and material from Langebaanweg QSM and Sahabi is slightly younger. The age of these localities was controversial, but a revision of the Tetraconodontinae suggests that the age might be about 5.5 Ma (Van der Made 1999a), though the possibility even exists that one of the localities might be in regressive sediments deposited during the TB3.3 cycle of Haq *et al.* (1997). Even if a simple lineage is not accepted, there is no consensus on the time and place of origin of the latter two genera. Tobien (1972, 1973) has interpreted some remains from western Europe that originally were placed in *Gomphotherium*, as primitive platybelodonts. Tassy (1984) essentially followed this idea, but introduced the name *Archaeobelodon* for these proboscideans and tentatively assigned material from Legetet to this genus (Tassy 1984). Astibia & Mazo (1988) and Mazo (1996) assign the western European material to *Gomphotherium*.

Of all the forms treated above, *Gomphotherium* is the only one that experienced dispersal from Africa to Western Europe, that is beyond discussion. There is a temporal gap between Phiomia and the earliest *Gomphotherium*. Material from Legetet (Africa; Set I, MN3 equivalent; faunal sets Pickford 1981; MN units - Mein 1990, De Bruijn *et al.* 1992) and material from Bugti (Pakistan; MN 3

equivalent) has been assigned to *Gomphotherium* (Pickford & Andrews 1981; Pilgrim 1912). In Europe the genus is cited from Navère (France; late MN 3; Bulot & Ginsburg 1993) and Artenay (France; early MN 4; Ginsburg & Antunes 1966; Tassy 1977a) and from an MN3 equivalent locality in Japan (Takai 1954 as cited by Tassy 1990). Qiu *et al*. (1999, p. 445) believe that indeterminate proboscideans were present in China in MN 2. However, the arguments for an age comparable to MN2 are not convincing and MN 3 age seems more likely. The first determinable Chinese proboscidean is *Gomphotherium* (Qiu *et al*. 1999) of MN 4 age. The most accepted opinion holds that *Gomphotherium* evolved in Africa and dispersed during MN3 to the Indian Subcontinent, in MN 3 (early/late?) to China and Japan, and late in MN3 or at the MN3-4 transition to Western Europe.

Deinotherium
Deinotheres are found in Africa, the area of SE Europe and Anatolia, and the Indian Subcontinent. The smaller forms are often placed in *Prodeinotherium* and the larger (and later) forms in *Deinotherium*. Different species of both genera are cited from the different (sub)continents, which either implies multiple dispersals or a polyphyletic origin of *Deino-therium*. For the time being, we assign all deinotheres to *Deinotherium*. The origin of the deinotheres is assumed to be in Africa (Osborn 1936). The earliest record outside Africa is in Bugti (Pakistan; Pilgrim 1908) and might be as old as 21 Ma (Van der Made 1996). Deinotheres arrived later in Europe (Tassy 1990) and are found in localities like Artesilla (Spain; Aragonian zone C or late MN4; Azanza *et al*. 1993). The entry in Europe is supposed to have happened 16.5 Ma ago (Van der Made 1996).

Zygolophodon
The oldest true zygodont known is *Eozygodon* from Meswa Bridge (Kenya; 22 Ma; Tassy & Pickford 1983), and is related to

Zygolophodon. Meswa Bridge is older than the first major Miocene faunal exchange between Africa and Eurasia. During the Late Miocene *Mammut* replaced *Zygolophodon* in Europe and northern Asia. A skull from (probably) the Odessa region was interpreted as intermediate form (Kubiak 1972).

A dispersal of *Zygolophodon* from Africa to Europe and Asia is widely accepted, though the opinions differ on when this may have happened. Some authors (Tobien 1976, 1996; Tassy 1977b, 1996) think that *Zygolophodon* arrived in Europe together with *Gomphotherium*, while others (Stehlin 1926; Gaziry 1976; Mazo 1977) think that the teeth of this age that are attributed to *Zygolophodon*, are morphological variants of *Gomphotherium*. A mandible fragment of *Gomphotherium* from Paracuellos 5 (province of Madrid; MN6) has a p4 and a m1 with zygodont and a m2 with bunodont morphology (Mazo 1985, 1996), suggesting that identifications based on isolated specimens are disputable. For Tassy (1985) *Zygolophodon* is present in the Orleanean of France and Spain, though not in Portugal. The oldest locality where it is cited is in Marsolan (Tassy 1977b), which is placed in MN3 and where *Brachyodus onoideus* is present (Bulot & Ginsburg 1993). Within MN3 *Brachyodus intermedius* evolved into *B. onoideus*, which implies that Marsolan is in the later part of MN3. From early MN6 onwards the presence of *Zygolophodon* in Europe is indisputable (Elgg, Switzerland; Schinz 1824). *Zygolophodon* is described or cited from the Orleanian and Vallesian of China (Tobien *et al*. 1988; Guan 1996) and Kazakhstan (Gabunia 1981; Tassy 1985).

Choerolophodon, Platybelodon
The oldest record of *Choerolophodon* is possibly from Buluk (Kenya; dated 17,2 Ma; Tassy 1990). The genus is known from Bugti (Lydekker 1884a,b). However this 'locality' has many levels, including the Middle Miocene and the exact provenance of the material is often not known (Pickford 1988). The oldest extra-African record is in Chios

(Greece; MN5; Tobien 1980), it is also known possibly from the Kamlial Formation and certainly from the Chinji Formation (Lydekker 1884a,b; Tassy 1983). The presence of *Choerolophodon* in China (Tobien *et al*. 1984; Guan 1996), has been doubted (Tassy 1994). Both Chios and the base of the Chinji Formation are believed to be about 14 Ma old and the base of the Kamlial Formation might be as old as 16.5 Ma (Van der Made 1996). Though the genus has been cited from Spain (Bergounioux & Crouzel 1958), this material is currently considered to be milk dentition of *Anancus* (Mazo 1977, 1996).

The oldest record of *Platybelodon* is from Loperot (Kenya, MN4 equivalent; Tassy 1990). The oldest extra-African record of the genus is from Shanwang and Tongxin (China; Guan 1996) and Belometchetskaya (southern Russia; Gabunia 1973). Shanwang is correlated to MN 5 (Qui *et al*., 1999). Suids indicate that Belometchetskaya is older than Dingjiaergou (in the lower level at Tongxin) and that both are MN5 equivalent (Guan & Van der Made 1993; Van der Made 1996). The possible existence of a primitive platybelodont *Archaeobelodon* has been discussed above.

The available data suggest that *Choerolophodon* originated in Africa and dispersed not later than 14 Ma ago, possibly even earlier, but probably not earlier than 16.5 Ma ago, to the Indian Subcontinent and the area of SE Europe and Anatolia. Also *Platybelodon* might be of African origin and dispersed about 14 Ma ago to the Caucasus area, Asia and the Indian Subcontinent. None of these forms reached Western Europe.

Mammuthus

The oldest record of *Mammuthus* is from Langebaanweg QSM in South Africa (Maglio & Hendey 1970; Kalb *et al*. 1996). The age of this locality has been controversial, the suids suggesting an aberrant age (Hendey 1981), but a recent revision of the Tetraconodontinae resolved the problem (Van der Made 1999a) and the locality might have an age of 5.5 Ma. Radulescu & Samson (1994) claim

the presence of *Mammuthus* at about 3 Ma in Cernatesti and Tulutesti (Rumania). The oldest citations from Western Europe are from Huelago, with an age of some 2.7 Ma (Mazo 1989; Van der Made & Mazo 2001), Montopoli, with an age close to 2.58 Ma (Italy; Azzaroli *et al*. 1988; Sardella *et al*. 1998) and the Red Crag (England; Lister 1996) at about 2.5-3 Ma.

Elephas

The oldest record of *Elephas* is *E. ekorensis* from Ekora and Kanapoi, with an age of over 4 Ma (Maglio 1970; Beden 1979; Fitch & Miller 1976). *Elephas* first appeared in the Indian Subcontinent with *Elephas planifrons* 3.3 Ma ago (Hussain *et al*. 1992). One of the oldest citations of *Elephas antiquus* in Western Europe is from Huescar, Spain (Mazo 1989). Huescar is placed in the latest Early Pleistocene, between some 0.9 and 1 Ma (Sesé *et al.* 2001). *E. antiquus* was also correctly cited from Soleilhac, France (Bout 1964). This locality is placed in the early Middle Pleistocene (Roebroeks & Van Kolfschoten 1995).

THE DISPERSAL EVENTS

The Early Miocene setting

During the late Oligocene and early Miocene Africa was separated from Eurasia by the Tethys, and many mammals, including proboscideans, evolved in isolation. Also the Indian Subcontinent was isolated. The fossil record of this period is poor in both areas, and it is not known whether, or how much faunal exchange may have occurred between both areas. While tectonics slowly drove Africa and India closer to Eurasia, an important and abrupt sea level low stand at around 21 Ma produced a land connection between these areas and a major faunal exchange occurred. From this time on sea level low stands allowed from repeated dispersal events. Accumulative sea level lowering during the late Middle Miocene resulted in more permanent land connections; whereas

initially the combination of climatical changes and sea level controlled faunal dispersal events, after some 11 Ma ago, the importance of sea level was reduced (Haq *et al*. 1987; Van der Made 1996, 1999; Miller *et al*. 1995; Rögl 1998; Rögl & Steininger 1983; Thomas 1985).

Initially, the majority of dispersals were from Eurasia to the southern (sub)continents. Most of the time, this was the predominant direction of dispersal, though between 17.5 and 12.5 Ma and around 5 Ma ago, dispersals to the north were common (Thomas 1985; Pickford & Morales 1994; Van der Made 1996, 1997, 1999b). Changes in composition of Spanish rodent faunas around 14 Ma ago, have been interpreted as resulting from a major climatical event coeval to a major change in marine oxygen isotope values (Van der Meulen & Daams 1992). Taxa of (sub)-tropical origins or taxa that are limited by minimum temperatures or seasonality started to go extinct in Europe from about 12.5 Ma onwards, whereas they lived on longer in areas more to the south (Van der Made 1992, 1993, 1997, 1999b). The dominant direction of dispersals and the duration of taxa with tropical origins or dependence on temperature may be indicative of climate at a particular time. It has been hypothesised that Europe had a tropical climate during part of the Early and Middle Miocene (Pickford & Morales 1994), alternatively, the European climate may have been simply warmer or less seasonal than in the present (Van der Made 1999b).

Initial dispersal to the Indian Subcontinent - about 21 Ma

During the initial faunal exchange event, at least 15 genera of large mammals and many small mammals of Eurasian origin entered Africa and India (Van der Made 1999b), this corresponds more or less to Thomas' (1985) NDP1 dispersals towards the Afro-Arabian plate. This dispersal event is supposed to have occurred during the sea level low stand of the TB2.2 cycle of Haq *et al*. (1987) (Van der Made 1996). Not later than at this

moment, deinotheres, *Hemimastodon* and *Gomphotherium* reached the Indian Subcontinent and the latter genus may have reached China and Japan. There is no evidence for a proboscidean dispersal to Europe. The only large mammal of African origin that reached Europe in this initial event is the anthracothere *Brachyodus* (Van der Made 1999b). During the same event it reached India, and possibly Japan where it was found with *Gomphotherium* (Takai 1954 as cited by Tassy 1990) and Siberia (Vislobokova 1994) as well.

Gomphotherium-dispersal towards Europe - about 17.5 Ma

The first proboscideans that reached Europe did so during the later part of MN3 or at the MN3-4 transition and include *Gompho-therium* and perhaps *Zygolophodon*. The rodent *Democricetodon* (of Anatolian origin), the carnivore *Hyanailouros* (of African origin), and the bovid *Eotragus* and the suoid *Taucanamo* (both of Asian origins) entered Europe at the MN 3-4 transition, around 17.5 Ma ago and at about the same moment a number of taxa of Eurasian origins entered Africa. (Van der Made 1996, 1999b). The proboscidean localities of Marsolan and Navère seem to be slightly older than the entry of *Democricetodo*n in western Europe (Bulot & Ginsburg 1993), or at least do not have this rodent. The question is whether the time difference is important.

Deinotherium-dispersal towards Europe - about 16.5 Ma

Deinotherium entered Europe when also the rodents *Megacricetodon*, *Eumyarion* and *Fahlbuschia* (of Anatolian origins) and the chalicothere *Chalicotherium*, the suid *Bunolistriodon* and the tragulid *Dorcatherium* (all with a previous record in Africa and the Indian Subcontinent) entered western Europe. About five mammal genera entered Africa. Some mammals, both of African and Asian origins entered the Indian Subcontinent, including the primate *Dionysopithecus*. This

dispersal event corresponds largely to Thomas' (1985) NDP1 dispersals to Eurasia and is believed to be allowed for by the sea level low of the TB2.3 cycle of Haq *et al*. (1987) (Van der Made 1996, 1999b). A hominoid, possibly *Griphopithecus* (Andrews *et al*. 1996), dispersed to Europe either during this or another event 15.5 Ma ago (Van der Made 1999b). That event did however not involve any Proboscidea. The dispersals to the north were more important than those to the south and this is the time when Europe has been interpreted to have had a tropical climate (Pickford & Morales 1994). The northward migrations might reflect the tendency towards the climatic optimum.

The possible *Zygolophodon*-dispersal - about 14 Ma

As discussed above, there are different opinions on the first European *Zygolophodon*; the genus is either supposed to have been present late in MN3/early in MN4, or in the earlier part of MN 6. In the latter case it may have entered in the major MN5 dispersal event, when the primates *Pliopithecus* and *Plesiopliopithecus*, of african origins, the suoids *Sanitherium* (with a previous record in Africa and the Indian Subcontinent) and *Conohyus* (of Indian origin) and the rodent *Cricetodon*, of Anatolian origin, entered Europe. At this time *Platybelodon* dispersed towards the area extending from the Black Sea area to northern China and *Choerolophodon* entered SE Europe, an important faunal exchange took place. Hyraxes and aardvarks, of African origins, spread towards SE Europe and the hyraxes to the Indian Subcontinent as well. Several bovid genera of Asian origins dispersed towards Africa, the Indian Subcontinent and SE Europe. This event has been related to the sea level low stand at the onset of the TB2.5 cycle of Haq *et al*. (1987) some 14 Ma ago (Van der Made 1996, 1999b) and corresponds partially to Thomas' (1985) NDP2 dispersals towards Eurasia.

Later Middle Miocene to Early Pliocene dispersal events

An event 12.5 Ma ago, involved several dispersals from Africa towards western Europe (Van der Made 1996, 1999b), but none of proboscideans. At the same time, there were a number of local and total extinctions in Europe (Van der Made 1992, 1993). Animals that are limited by minimum temperatures, such as crocodiles, disappeared from central Europe, but lived on more to the south. *Dorcatherium*, that was represented by four species in Europe, decreased its species diversity to one, but remained diverse in the Indian Subcontinent. Several lineages that had been present in Europe for millions of years went extinct. Later dispersal events were predominantly towards Africa (Vrba 1995; Van der Made 1999b), though during the latest Miocene there were again relatively many dispersals from Africa towards Europe, but there is no convincing evidence that these involved proboscideans. The oxygen 18 isotope curves from the Atlantic suggest high temperatures during the late Early and early Middle Miocene, a very important drop between some 14 and 12.5 Ma and a gradual further decrease towards the present. These curves have been related to faunal events (Bonifay 1980; Pickford 1987; Van der Meulen & Daams 1992).

The Plio-Pleistocene setting

The late Pliocene and Pleistocene are characterised by climatic fluctuations of increasing magnitude and length. These fluctuations caused important biogeographical reorganisations. The relation between astronomical (Milankovic) cycles and climate has been known for a long time, but it is in recent years that great advances have been made in the recognition of these cycles in geology and paleontology. The cycles are changes in the shape of the orbit and the orientation of the axis of the earth. The eccentricity of the orbit, the obliquity the earth's axis relative to the plane of the orbit, and the precession of the equinoxes are subject to cycles with durations

of some 100, 40 and 20 ka respectively (Foucault 1993). The shorter cycles have a greater impact on higher latitudes. Before some 2.7 Ma ago, the 20 ka cycle had a greater influence on global climate, after that date the 40 ka cycle became dominant and after some 1 Ma ago the 100 ka cycle (deMenocal 1995). Important biogeographical reorganisations occurred around 2.7 and 1 Ma ago, whereas the period inbetween was relatively stable.

Mammuthus dispersal - about 2.7 Ma

Mammuthus entered Western Europe slightly before 2.6 Ma, possibly about 2.7 Ma ago. Around this date important changes occurred. Large mammals that dispersed into western Europe at this time include the equid Equus, the deer *Eucladoceros*, the bovid *Leptobos etruscus*, and of course the proboscidean *Mammuthus*. Several of these animals, including *Mammuthus*, are typical of open habitats. More or less simultaneously, forest animals, like *Tapirus* and *Mammut* went extinct. The dispersal of *Equus*, of American origin, is traditionally related to a first cold period in a series that lead to the severe glaciations of the Middle and Late Pleistocene. The accumulation of continental ice caused a sea level low stand, allowing for the crossing of the Bering Strait by *Equus*.

Another change that occurred at this time, is the southward shift of the limits of the Palearctic bioprovince. This is well reflected in the distribution of the deer. Deer originated in Asia, entered Europe some 21 Ma ago, maintained the southern limit of their distribution within Anatolia till some 2.5/2.7 Ma ago, when they entered the Indian Subcontinent and North Africa (Maglio 1978; Hussain *et al*. 1992; Barry & Flynn 1990). Lagomorphs first entered the Indian Subcontinent (Steensma & Hussain 1992). It has been hypothesised that Cervidae, Talpidae, the equid *Anchitherium* and Tapiridae have been limited for millions of years in their southward expansion by an area that was too arid for them to cross (Van der Made 1992).

The arid belt that runs at present from the north of Africa to the Middle East and continues into central Asia may have been present in some form for a long time, but it may have been more permeable to mammal dispersals 2.7 Ma ago. These changes are probably related to the growing importance of the 40 ka cycle, causing periods of a greater seasonality and lower temperatures. Lower temperatures directly affect the degree of aridity, though other mechanisms may have acted on the environment, causing biogeographical adjustments.

Elephas dispersal - about 0.8 Ma

Elephas (*Palaeoloxodon*) entered Europe some 0.8 Ma ago. As we have seen, between about 1.2 and 0.8 Ma ago the 100 ka eccentricity cycle posed itself as the dominant cycle forcing the climate and the impact of the glaciations on the European environment became gradually stronger. Species from different environments sharing a tolerance for cold periodically lived together as the 'glacial fauna'. With the successive glaciations, they adapted to the unique glacial environment. Species with a lesser tolerance for cold formed the 'interglacial fauna' but lived during the glaciations in refugia in southern Europe. Whereas the separation into 'glacial' and 'interglacial' faunas seems to have occurred after 0.8 Ma, when the 100 ka cyclicity was well established, the transition period between some 1.2 and 0.8 was characterised by the appearance of a number of new taxa. These taxa do not seem to have evolved in Western Europe, consequently they must have dispersed from an area outside (western) Europe. Using paleomagnetism in combination with biostratigraphy, the dispersals can tentatively be arranged in three clusters.

Just before 1.07 Ma. Localities that are supposed to be only slightly older than the Jaramillo event include Venta Micena and Pirro Nord. Traditionally these localities have been located around 1.2 Ma, though there is no objective way to estimate their exact age.

Taxa that first appear in these localities inclu-
de the cervid *Eucladoceros giulii* and the
bovids *Bison degiulii*, *Soergelia minor*,
Praeovibos sp. (?) and *Capra alba*. All taxa
were probably typical of dry and/or open
landscapes, though some of the bovids may
have been inhabitants of more mountainous
environments while other bovids and the
large cervid are likely to have preferred
plains. Probably all these taxa have their ori-
gins in Asia or Eastern Europe.

1.07 - 0.78 Ma. Localities that are as old as
the Jaramillo event, or slightly younger, such
as Untermassfeld, Vallonet, Atapuerca TD4-6,
etc. have the first records of a number of spe-
cies that still live, as well as others extinct
now. These taxa include: the hyaenid
Crocuta, the felids *Panthera leo* and *Panthera
pardus*, the suid *Sus scrofa*, the deer
Capreolus (?) and *Cervus elaphus*, and bovids
of the *Bison menneri/voigtstedtensis* group.
The carnivores have their ultimate origin in
Africa, but were prior to 1.07 Ma present in
the Middle East. The ungulates have their ori-
gin in northern Asia or Eastern Europe. The
suid and the deer are more typical of a tem-
perate closed environment. Whereas the hya-
enid is more typical of an open environment.

Shortly after 0.78 Ma. Localities that are not
very much younger than 0.8 Ma include
Voigtstedt, Süssenborn, Bad Frankenhausen,
Hundsheim, Huescar etc. Taxa that first
appear in these localities include the probos-
cidean *Elephas antiquus*, the rhinos
Coelodonta, *Stephanorhinus hundsheimensis*
and *Stephanorhinus kirchbergensis*, the cer-
vids *Megaloceros soleilhacus* (?), *Megalo-
ceros savini* and *Rangifer* and the bovids
Hemitragus bonali, *Praeovibos priscus*,
Ovibos suessenbornensis and *Soergelia elisa-
bethae*. Most of these animals may have pre-
ferred an open landscape, though this is pro-
bably not the case for S. *kirchbergensis*.
Hemitragus was probably more typical of the
mountainous environments. The deer, rhinos
and bovids probably had their origin in Asia

or eastern Europe. *Coelodonta*, *Rangifer* and
some of the bovids seem to have appeared
earlier in Germany and Austria than in France
and have been interpreted as belonging to the
glacial fauna, though their glacial adaptations
may not yet have been fully developed at this
early stage. *S. kirchbergensis* is considered to
belong to the interglacial fauna. This suggests
the possibility of more than one event.

The vast majority of taxa that dispersed
into Western Europe were typical of open
landscapes. This does not seem to be reflec-
ted in an equivalent number of extinctions of
animals that preferred closed habitats, but in
an increase in biodiversity. It seems therefore
that the European landscape became progres-
sively more open, though closed habitats con-
tinued to exist. The entry of *Elephas antiquus*
forms part of these changes. Between about
2.7 and 0.8 Ma *Mammuthus* was the only
elephantine in Europe, but after the entry of
Elephas it became part of the developing gla-
cial faunas, whereas the latter became part of
the interglacial faunas. It is possible that the
opening of the landscape allowed for a
second elephantine species in Europe, follow-
ed by an adaptation of each lineage to a diffe-
rent environment, the newcomer ending up
with the less severe 'interglacial niche'.

**DISPERSALS, EVOLUTION AND
EUROPEAN ENVIRONMENT**
Figure 1 indicates the distribution in time of
proboscideans in Western Europe. Thick lines
represent the range of groups or lineages of
proboscideans, dots indicate the approximate
age of the type locality of the type species of
a genus. Dispersals of proboscideans from
Africa towards Western Europe occurred in
two clusters about 17.5, 16.5 and possibly 14
Ma ago and about 2.7 and 0.8 Ma ago. The
figure also indicates eustatic sea level after
Haq *et al*. (1987). The earliest three dispersal
events are separated by periods of isolation of
Africa. After two successive and cumulative
drops at 14 and 12.5 Ma sea level remained
low, save for a short period after 5 Ma, and
the land connection between Africa and

Eurasia became probably permanent. It is noteworthy that in the long period between 12.5 and 2.7 Ma, when land connections did exist, no dispersals could be demonstrated, neither around 21 Ma ago. The availability of land connections was a prerequisite, but it was apparently not the real factor controlling migrations most of the time.

It is evident that the earlier dispersals occurred during high temperatures as indicated by the isotope record (Fig. 1). The period between 17.5 and 14 Ma ago had a climatic optimum, between some 14 and 12.5 Ma a

dramatic drop in temperature occurred. The later dispersals occurred when temperatures were lower. Temperature itself was probably not a limiting factor. As proboscideans are very large animals, it is to be expected that they are less sensitive to temperature, but temperature may have acted on the environment and in this way it could have been a limiting factor. The proboscideans that dispersed towards western Europe are not only two groups according to the time of dispersal, but also according to masticatory adaptations. The proboscideans that reached Western
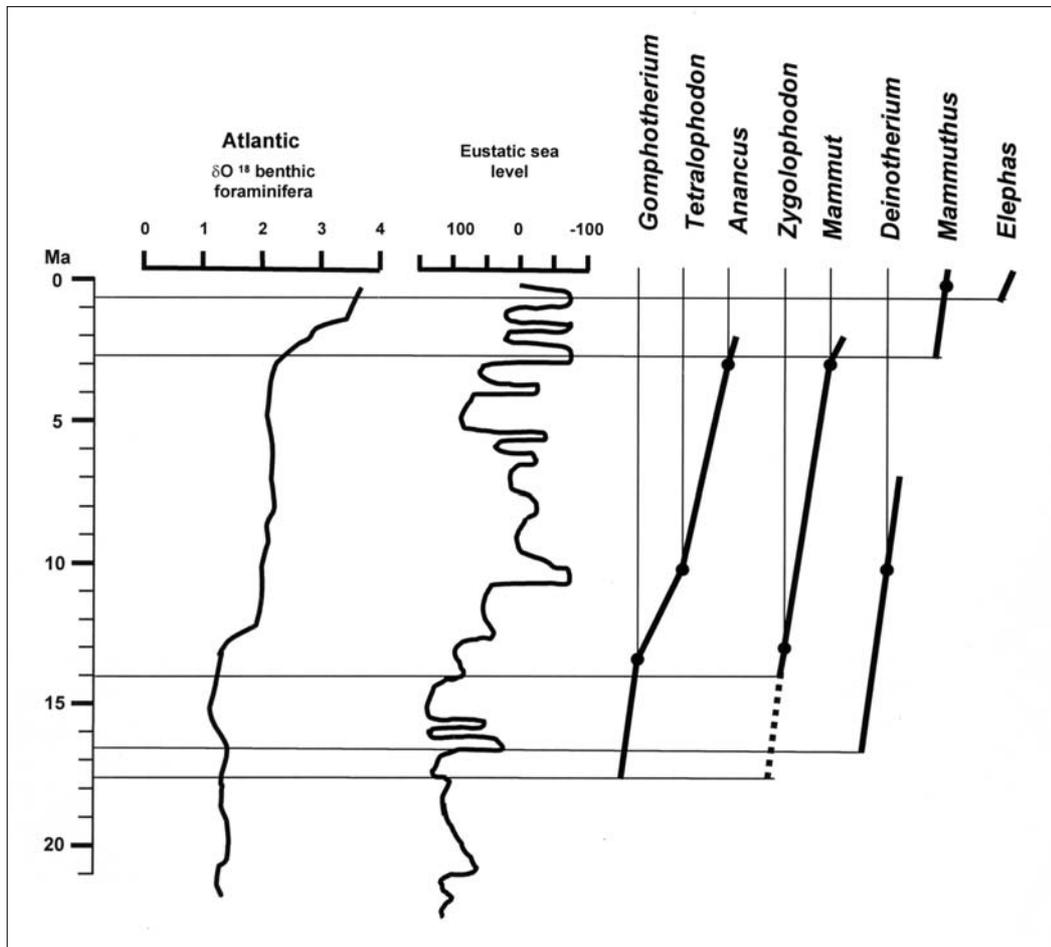

Figure 1 Oxygen isotope records (after Flower & Kennett 1993) and eustatic sea level (after Haq *et al.* 1987) and range chart of the Proboscidean genera in Western Europe. Dots refer to the position of the type localities of the type species. The range of the *Gomphotherium-Tetralophodon-Anancus* and *Zygolophodon-Mammut* groups are indicated as if two lineages, though speciation events may have occurred within each group.

Europe between some 17.5 and 14 Ma ago had low crowned cheek teeth, wide cusps or crests, thick enamel, relatively few cementum, relatively short M3 and at some time in life had premolars and molars in use. These proboscideans were probably browsers that may have eaten hard, but not very abrasive food. They may have eaten fruit. *Deinotherium* and the *Zygolophodon-Mammut* group were probably folivorous. *Anancus* may have evolved in the Palaearctic from earlier migrants and acquired longer molars, particularly the M3, and lost its premolars. This suggests that it adapted to a diet poorer in nutrients, so that greater amount of food had to be ingested. The proboscideans that reached Europe between 2.7 and 0.8 Ma ago, had high-crowned cheek teeth, with antero-posteriorly compressed cusps, valleys filled with cementum, thin enamel and elongate molars, in particular elongate M3. These animals were grazers. This type of dentition evolved in Africa some 6 Ma ago.

The browsing proboscideans entered Western Europe, when a large number of animals of (sub)tropical origins did so too. Up to four species of *Dorcatherium* (Tragulidae) entered Europe at the same time as *Deinotherium*. Living tragulids tend to be frugivorous and to a lesser extend folivorous (Kingdon 1989). The suid *Bunolistriodon* was folivorous (Hunter & Fortelius 1994; Van der Made 1996). The primates *Griphopithecus*, *Pliopithecus*, *Plesiopliopithecus* and *Dryopithecus* were probably frugivorous and folivorous. Tropical environments have the year round fruit and leaves, while environments with cold winters don't. This may have been a limiting factor to dispersal. Around 12.5 Ma a number of animals went extinct in western Europe, that either had migrated earlier towards the north, or that were sensitive to temperature. Crocodiles went extinct in central Europe, tragulid species diversity dropped from four to one, whereas diversity remained high in the Indian Subcontinent, and the last members of the *Bunolistriodon meidamon* lineage, that had disappeared already around

14 Ma from Europe, went extinct in Anatolia (Van der Made 1992, 1993, 1996). Still some animals of southern origins migrated northward and some of those that had done so before, still lingered on.

The next important climatical change is the 'Mid-Vallesian Crisis', when seasonality became more accentuated (Van Dam 1997; Fortelius *et al*. 1996; Van der Made 1990). This is probably the reason that suoid species diversity in Europe dropped markedly; in lower Vallesian localities five to six suoid species may be found together, but in younger localities rarely more than one. This marked the end of the Cainochoerinae, Listriodontinae and Tetraconodontinae in Europe, three suid subfamilies that have their oldest record in the tropics and it also was the end for the European Schizochoerinae (ranges after Van der Made 1990; taxonomy after Van der Made 1997; see also Fortelius *et al*. 1996). All but the Listriodontinae lived on in the tropics and the Tetraconodontinae became very diverse there. Other groups were also affected, for instance European mainland primates went extinct. Around 7-8 Ma ago, the last European tragulids and deinotheres went extinct. Thus, many of the lineages of tropical origins that entered Europe before 12.5 Ma ago went extinct after that date. It is likely that this is related to the effect of decreasing temperatures and increasing seasonality on the vegetation. It became probably progressively more difficult for frugivores and folivores to come through the winter.

Vegetation with a C4 photosynthetic pathway is favoured by low atmospheric CO_2 levels compared to that with a C3 pathway, and includes grasses. Carbon 13 isotope records suggest that such vegetation started becoming important at low latitudes between 5 and 8 Ma ago, while this happened much later at high latitudes (Quade *et al*. 1989; Cerling 1992; Cerling *et al*. 1993, 1997). Carbon isotopes in tooth enamel show that deinotheres maintained a pure C3 diet, while other herbivores shifted to a C4 dominated diet (Cerling *et al*. 1997). When the vegeta-

tion changed in the tropics, proboscideans there adapted to grazing and evolved hypsodont cheek teeth, with thin enamel, a high number of plates, much cementum, etc. It is this adaptation that allowed proboscideans to enter and survive in Europe and northern Asia. The exact timing of their dispersals coincides with important climatical changes, suggesting that it were these changes that triggered the dispersals.

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