Intercontinental relationship Europe – Africa and the Indian Subcontinent

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A great number of Miocene genera, and even some species, are cited or described from both Europe and Africa and/or the Indian Subcontinent. In other cases, an ancestor-descendant relationship has been demonstrated. For most of the Miocene, there seem to have been intensive faunal relationships between Europe, Africa and the Indian Subcontinent. This situation may seem normal to us. It is, however, not.

During much of the Tertiary, Africa and India were isolated continents. There were some periods when faunal exchange with the northern continents occurred, but these periods seem to have been widely spaced in time. During a large part of the Oligocene and during the earliest Miocene, Africa and India had been isolated. Endemic faunas evolved on these continents. Families that went extinct in the northern continents during the Paleogene, florished in these southern continents and other families originated. Also in the northern continents evolution went on. The result was that the northern and southern continents had totally different faunas.

Then happened what MADDEN & VAN COUVERING (1976) named the "Proboscidean Datum Event". They apparently believed that it was a single synchronous faunal exchange event between Africa and Eurasia, involving many taxa, including proboscideans. THOMAS (1985) recognized two major phases of faunal exchange. TASSY (1990) showed that the dispersal of the proboscideans was diachronous. The "Datum Event" turns out to be a complex of events (VAN DER MADE 1996, 1997b). These events took place during the Early and Middle Miocene. Faunal exchange between Eurasia and Africa during the Late Miocene is not well documented; the African record is very incomplete. The Indian record is better for the Late Miocene, but nevertheless, relationships between the faunas are not very clear. The events around the latest Miocene Messinian Salinity Crisis are again well studied.

Palaeogeography, global climate and palaeobiogeography

After MN 3, Europe formed one continent with Asia. This land mass extended from Europe, through north Asia to China and SE Asia and is here referred to as Eurasia. This term does not include here SE Europe. At this time, the area north of Crete was land and SE Europe and Anatolia formed a continuous landmass. The Paratethys was large and extended from the valley of the Rhone to the Black Sea, Caspian Sea and further to the east. The Tethys was connected with the Indian Ocean and large part of the Middle East was a shallow sea. During the earliest Miocene, Africa and Arabia formed one continent that had been separated from Eurasia and India for a considerable time. Similarly the Indian Continent had been isolated for a very long period (RÖGL & STEINIGER 1983). Due to this long isolation, the southern continents had endemic faunas.

During the Miocene, the African and Indian plates moved closer to Eurasia causing the further elevation of the Alps, Himalayas and other mountain belts. The Paratethys and Tethys became smaller and extensive areas in the Middle East became shallow seas and finally became land. The area of SE Europe became connected to Eurasia, while the collapse of the area north of Crete separated it from Anatolia. The Red Sea formed, and Arabia became disconnected from Africa. During much of the Miocene, India may have had a contact with Asia at the place of the present Himalayas, but there is little evidence of faunal exchange through this area. The Paratethys was another barrier. Faunal exchange between northern Asia and the southern continents may have occurred through the area between Himalayas and Paratethys.

While plate tectonics gradually changed the geography, sea level fluctuations had more direct effects. Sea level changes were, geologically speaking, instantaneous, and had a magnitude of up to a hundred metres and occasionally successive events had accumulative effects (HAQ et al. 1987). Between 15 and 10.5 Ma ago, sea level dropped in three successive events over two hundred metres (HAQ et al. 1987). Sea level changes were related to global climate; ice accumulation on Antartica was responsible for sea level

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drops (MILLER et al. 1996). While extensive land masses were slowly being formed out of a number of smaller fragments, sea level changes connected and disconnected these areas and allowed for, or inhibitted faunal exchange. The effects of the sea level changes were strongest during the Early Miocene, whereas from the Middle Miocene onward, the land-sea distribution seems to have been less affected and less important in controlling the geographical distribution of mammals.

Changes in global climate had a direct impact on the distribution of species: there are distinct dispersal and extinction events. When, during the Early Miocene, global climate lowered the sea level, and allowed for faunal exchange between Africa and Europe, global climate also permitted Asian animals to disperse into Europe. Late Miocene global climate, may have had effects on sea level, but its effect on the distribution of animals was direct.

Faunal exchange between Europe and Africa and the Indian Subcontinent occurred through SE Europe and Anatolia. Miocene climates do not necessarily have recent equivalents. Nevertheless, certain characters may have been the same: higher temperatures towards the equator, the climate of northern Eurasia may always have been more seasonal with respect to temperature than the central African climate, etc. As we will see in the following sections, the distribution of animals that may have been dependent on some degree of humidity suggests, that the distribution of more and less humid climates during a large part of the Miocene may have shown only a limited variation. In general, the conditions in SE Europe and Anatolia, may have acted as a filter to faunal exchange. There is a well studied pollen record in Anatolia, that is correlated to the MN scale (BENDA & MEULENKAMP 1990); there were important changes in vegetation. Both reasons may explain why certain taxa, did not take part in one faunal exchange event, but were very prominent in a later event.

A peculiar event took place at the end of the Miocene. The connection between the Mediterranean and the Atlantic Ocean was lost. Evaporation in the Mediterranean is greater than the input through precipitation and rivers. The sea level fell by up to several kilometres, and Europe and Asia became connected, allowing for an exchange of terrestrial animals. Since this event caused the formation of extensive salt deposits, it is known as the Messinian Salinity Crisis (HSÜ et al. 1977).

Stratigraphy

MN units or Neogene Mammal Units are widely used for Europe and northern Africa (DE BRUIJN et al. 1992). The MN units do not have a clear definition of the boundaries. It appears that global events, causing major dispersal or extinction events, tend to be within MN units, whereas the transition of one unit to the other is diffuse. Here frequently informal reference will be made to MN 4e (early MN 4), MN 4l (late MN 4) etc. to indicate the part of the MN unit before or after an important dispersal event. In the same way MN 8 may be used instead of MN 7+8. In addition reference is made to continental stages and their biozones: Ramblian (zones Z-A), Aragonian (zones B-G), Vallesian (H-I) and Turolian (J-M) (DAAMS & FREUDENTHAL 1988, VAN DAM 1997). Though these zones are defined with local (Spanish) fauna, the fact that the local faunal events used tend to coincide with global events, makes a more or less precise correlation with a much larger area possible. A number of long profiles, frequently in or correlated to type sections, were sampled for palaeomagnetism in order to date biozones and MN units (KRIJGSMAN et al. 1996). These dates are used here, but differ considerably in the MN 4-6 range as used by for instance STEININGER et al. (1996).

For Africa a series of "faunal sets" were defined (PICKFORD 1981). Like the Spanish zones, these sets tend to capture global events. Many African localities are radiometrically dated (PICKFORD 1986b).

The best record for the Indian Subcontinent is in Pakistan. A series of "faunas" were described from Pakistan, later the names of these "faunas" were applied to the formations from which they were collected and still later, the names have been applied as stages: Bugti, Murree, Kamlial, Chinji, Nagri, Dhok Pathan (SHAH 1984), most of which have been palaeomagnetically sampled and which yielded detailed range charts (BARRY & FLYNN 1990). Collections of older fossils from the Bugti area, include fossils from several levels (PICKFORD 1987), but the bulk of the material is probably from more or less the same age anterior Murree.

A framework of faunal correlations and the study of intercontinental dispersal events were matched to continental-marine tie-points, palaeomagnetic data and radiometric dates, and finally to the eustatic sea level curves of HAQ et al. (1987) (VAN DER MADE 1996, 1997b). Table 45.1 represents stratigraphic data and intercontinental dispersals of mammals.

In this paper, reference will be made to biostratigraphic units and ages, even if an original description of a taxon does not give these data. The references in this section will usually provide the link. If the presence of a taxon in Europe in a particular MN unit is mentioned, but no citation is given, the source is usually DE BRUIJN et al. (1992).

Taxa taking part in faunal exchange

As we have seen above, there have been many dispersals from Eurasia to the southern continents as well as in the other direction. When genera or species dispersed from Africa or the Indian Subcontinent to Europe, nearly always the dispersal routes were through the Middle East, Anatolia and SE Europe. If a genus or species was present in Africa and in the Indian Subcontinent and dispersed to Europe, it is frequently not clear where the colonizing populations came from. In any case, the latest non European populations are likely to have lived in Anatolia, whether the duration was geologically significant or not. Similarly, it frequently cannot be established if a dispersal into the southern continents originated from Europe or Asia.

There are many examples of taxa that originated in some part of Asia and that migrated at the same moment, or at different moments, to Europe and to the southern continents. The presence of such a taxon in these areas does not necessarily mean that there has been a faunal exchange between Europe and Africa or the Indian Subcontinent.

At any moment in palaeontological history, most of the present species are separated from other species by clear morphological and metrical differences. Taking time into account, there is a continuum in morphology and size. Taxonomy subdivides this continuum in species, genera and other taxa. The limits between these taxa are frequently taken at convenient places: at a hiatus in the record, at a moment when evolution went more rapidly, or at a long distance dispersal event. Though the arrival in a new environment may accelerate evolution, the first individuals in the new continent are identical to the populations in the continent of origin. The decision to place the populations that dispersed to the other continent in a different species, genus or tribe, is practical, but disguises the relationships.

In the Indian subcontinent there is virtually no Oligocene and earliest Miocene record. It is here assumed that most of the "Bugti fauna" arrived by migration, this however is not sure. Also in Africa, the latest Oligocene and earliest Miocene fauna is not very well known. Similarly, the record of fossil mammals prior to MN 6 is very restricted in SE Europe and Anatolia, and prior to MN 5 virtually absent, though there is a limited number of micromammal localities.

Insectivora: Insectivores were present in the Paleogene of Africa, but some new families arrived during the Early Miocene (BUTLER 1978a). Several genera of Erinaceidae, presumably of Asian origins, are first cited from Africa (BUTLER 1978a) from localities that are placed in Set I and Set II. Soricidae have been cited from Set II and Set IV localities from Africa, but there are important hiatuses in the record; the origin of these soricids seems to have been Asia (BUTLER 1978a). Talpidae were present in Europe during the Miocene, but did not disperse to the regions south of Anatolia; they did not enter Africa, nor the Indian Subcontinent. They were presumably limited by the extension of "desert soils" (dry soils with a high pH) (VAN DER MADE 1992).

Chiroptera: Chiroptera are already known from the European Paleogene. The record from Anatolia is very incomplete (ENGESSER & ZIEGLER 1996). They have entered Africa prior to the Miocene, but during the Early Miocene and again during the Late Miocene various families of Asian origins entered Africa (BUTLER 1978a).

Primates: The oldest European hominid (or hominoid in the older classifications) remain is from Engelswies and is tentatively placed in *Griphopithecus* by ANDREWS et al. (1996) who also assume a close relationship between *Griphopithecus* and *Kenyapithecus wickeri*. *Griphopithecus* is well known from MN 6e and MN 6l in Anatolia and from MN 6l and MN 7+8 in Central Europe.

Pliopithecus and *Plesiopliopithecus* are likely to have African ancestors, but may have lived some time in SE Europe and Anatolia, before entering Europe in MN 5l.

Dryopithecus entered Europe before MN 9, though the older record is rather poor. There is no evidence that it lived for a longer period outside Africa before entering Europe. It may have entered Europe at the same time as the little suid *Albanohyus*, which has an African record immediately previous to the middle MN 6 dispersal event.

Graecopithecus (= *Ouranopithecus*) is well known from MN 10-11 in Greece and is placed in the Homininae (ANDREWS et al. 1996).

Consensus seems to be growing that *Oreopithecus* is a hominid (ANDREWS et al. 1996). The

Tab. 45.1. Faunal dispersals in the different (sub)continents. The left collumn gives eustatic sea level cycles of HAQ et al. (1987). Four pairs of collumns give the stratigraphy (unit or biozone and the age of its lower boundary in Ma; selected localities with dates in Ma or correlation to the Blow zones; see section on stratigraphy) and the taxa that enter in a particular unit. Thin horizontal lines indicate (predominantly local) stratigraphy, thick horizontal lines mark the dispersal events discussed in this paper. The presumed or possible origin of the taxa is indicated with the following abbreviations: Af = Africa, Am = America, As = Asia, EA = Eurasia, Eu = Europe, ET = the SE European and Anatolian Subcontinent, In = Indian Subcontinent, ME = Middle East. Question marks may indicate doubts on the origin, or on whether this taxon entered in this unit.

CYCLES HAQ et al. (1987)	**Europe**		**SE Europe & Anatolia (& adjacent areas)**		**Indian Subcontinent**		**Africa & Arabia**	
Lower Boundary age	**Stratigraphy** Localities	Entry taxa – origin	**Stratigraphy** Localities	Entry taxa – origin	**Stratigraphy** Localities	Entry taxa – origin	**Stratigraphy** Localities	Entry taxa – origin
TB3.4 5.5 Ma TB3.3 6.3 Ma	**MN 13** **M2-3, 6.1-6.3** Venta del Moro El Arquillo Las Casiones Brisighella	Af – Hippopotamidae Af – *Redunca*? As? – *Agriotherium* ET/Af – *Mesopithecus* Af – *Macaca* In – *Parabos* ET/Af – *Orycteropus*	**MN 13**	Af – *Redunca*?	**Dhok Pathan**	Af – *Hexaprotodon*	**Set VII** Langebaanweg PPM Langebaanweg QSM Lothagam 1C Sahabi	As – *Agriotherium* EA – *Plesiogulo* EA – *Enhydriodon* EA – *Viverra* As – *Felis* ME – *Ancylotherium* In – *Conohyus* II As? – "*Leptobos*" EU/I – *Miotragocerus*
TB3.2 8.2 Ma	**MN 13, M1, 6.8**		**MN 12** Pikermi Samos – Main		**Dhok Pathan**		**Set VII** Lukeino Mpesida	As? – *Cephalophus*? As? – *Ugandax*?
	MN 12, L, 7.7 Concud	ET – *Gazella* ET – *Hispanodorcas* ET – *Palaeoryx* ET – *Protoryx*						
TB3.1 10.5 Ma	**MN 11, K, 8.7**	Af/ET – *Oreopithecus*? Af/ET – *Maremmia*?	**MN 11** Kopran	Af – *Mesopithecus*	**Nagri** Sethi Nagri		**Set VI** Oued Zra Ngerigerowa Nakali U Beglia Fm Ngorora E	In – *Progonomys* In – *Sivachoerus*
	MN 10, J 9.7 Villadecaballs	ET – *Schizochoerus*	**MN 10** Kastellios Hill 9.6-9.3	In – cf. *Dorcabune* Af – *Graecopithecus*				
	MN 9I, I, 10.4 Can Llobateres I La Cantera	ET – *Pliohyrax* In – *Progonomys*	**MN 9I** Loc. 108, 10.3-10.4	In – *Progonomys* In? – *Nisidorcas*? In? – *Prostrepsiceros*?		?Eur – *Conohyus* (Am – *Hipparion*) As? – *Hippopotamodon*		
	MN 9e, H, 11 Can Ponsic Wissberg	As – *Hippopotamodon* (Am – *Hipparion*)	**MN 9e**	As – *Hippopotamodon* (Am – *Hipparion*)				Eu/ET – *Conohyus* I As – *Mellivora* (Am – *Hipparion*)
TB2.6 12.5 Ma	**MN 8, G** San Quirze	As/In? – *Propotamochoerus*	**MN 8** Plakia		**U+M Chinji** Y495 11.03-11.09 Y663 11.03-11.09 Y498 11.09-11.55 Y499 11.55-11.73 Y494 11.86-12.12 Y750 12.46-12.49	Af – *Sivapithecus* As – *Helicoportax* As – *Gazella*	**Set V** Ngorora D 9.8-9.7 Ngorora C 11.9-9.8 Ngorora B 12.3 – 11.9 L Beglia Fm ?Majiwa >11.8 ?Beni Mellal	ET – *Protoryx*
	MN 7, G, 12.5 La Grive		**MN 7** Sariçay					As – *Percrocuta*
	MN 6I, G Manchones I Arroyo del Val Paracuellos III Klein Hadersdorf	ET – *Tethytragus* ET – *Hispanomeryx* ET/As – *Turcoceros* Af – *Dryopithecus* Af – *Albanohyus*	**MN 6I** Çandır Melambes	As? – *Turcoceros*?				
TB2.5 13.8 Ma	**MN 6e, F, 13.75** Sansan	In – *Listriodon*	**MN 6e** Paşalar Prebreza İnönü I	EA – Cervidae As – *Percrocuta* As – *Tethytragus* Af/In – *Kubanochoerus* Af – *Orycteropus* Af – *Pliohyrax* As – *Gazella*? EA/I – *Eotragus*?	**L Chinji** HGSP 8219 HGSP 8425	As – *Protragocerus* As – *Sivoreas* As – *Sivaceros* As – *Kubanotragus* Af – *Orycteropus* EA – Gliridae As? – *Propotamochoerus*	**Set IV** Muryur 13.5 Fort Ternan >12.6 Al Jadidah Nyakach 13.4	As – *Protictitherium* As – *Gentrytragus* As – *Hypsodontus* As – *Protragocerus*
	MN 5I, E, 14 Göriach Ravensburg Pontlevoy Seegraben Münzenberg	Af – *Pliopithecus* Af – *Plesiopliopithecus* ET – *Cricetodon* In – *Conohyus* Af/In – *Sanitherium*	**MN 5I** Mala Miliva Belomechetskaja Rotem Basin Chios					

Tab. 45.1. (continued).

CYCLES HAQ et al. (1987)	**Europe**		**SE Europe & Anatolia (& adjacent areas)**		**Indian Subcontinent**		**Africa & Arabia**	
Lower boundary age	**Stratigraphy** Localities	Entry taxa – origin	**Stratigraphy** Localities	Entry taxa – origin	**Stratigraphy** Localities	Entry taxa – origin	**Stratigraphy** Localities	Entry taxa – origin
TB2.4 15.5 Ma	**MN 5e, D, 16** Engelswies Bézian Baigneaux Lisboa Vb N8/9	Af – Hominoidea As – *Protictitherium*		Taxa listed above may have been present earlier; SE European and Anatolian large mammal record is poor.	**Kamlial** HGSP 8311 HGSP 8223 HGSP 8127	As – Hypsodontinae	**Set IIIb** Maboko sup. >13.8 Ad Dabtiyah	
TB2.3 16.5 Ma	**MN 4l, C, 16.45** Sant Mamet ≥N8 Can Julia ≥N8 Moli Calopa ≥N8 Martí Vell ≥N8 Lisboa IVb ≥N8 Belchatów C 17 Pellecahus	Af – *Deinotherium* Af – *Bunolistriodon* Af – *Dorcatherium* ET – *Megacricetodon* ET – *Fahlbuschia* ET – *Eumyarion* Af/In – *Chalicotherium*		In – Myocricetodontidae	**Kamlial?/Murree?** Fatehgad	Af – *Dionysopithecus* As – *Giraffokeryx*? Af – Pedetidae?	**Set IIIa** Maboko main >14.7 Arrisdrift Moruorot > 16.8 Gebel Zelten Buluk >17.2 Midra-ash-Shamali Kirimun > 15	As – Hypsodontinae As – *Zaraffa* In?/As – *Giraffokeryx* /*Palaeotragus* As – *Africanictis* In – Rhizomyidae In – Myocricetodontidae EA – *Amphicyon* EA – *Ysengrinia* As – *Gazella*?
TB2.2 17.5 Ma	**MN 4e, B, 16.7** Artenay	Af – *Hyanailouros* Af – *Gomphotherium* Af – *Zygolophodon* ET – *Democricetodon*			**Murree?/Bugti?**		**Set II** Mfwangano Karungu 17.5 Rusinga 17.9 Bukwa	As – Soricidae? Eu? – *Luogale* As – *Herpestides* As – *Hemicyon* As? – *Kenyasus* As – *Climacoceras* As – *Hemicyon*
TB 2.1 21 Ma	**MN 3, Z-A** ?Marsolan ?Navère Eggenburg – N5 Maigen – N5 Brüttelen – ≥N5 Beaulieu >17.5 Lisboa II	Af – *Brachyodus*			**Bugti**	Af – *Hemimastodon* Af – *Choerolophodon* Af – *Gomphotherium* Af – *Deinotherium* Af – *Hyainailouros* EA – *Amphicyon* Af – cf. *Geniohyus* As – *Chalicotherium* As – *Phyllotillon* As – *Paraceratherium* EA – *Brachypotherium* EA – *Aceratherium* As – *Chilotherium* Af – *Brachyodus* Af – *Dorcatherium*? As – *Progiraffa* As – Ctenodactylidae EA – Sciuridae EA – Cricetodontidae	**Set I** Langenthal Songhor 19.6 Napak Iriri Koru ±19.5 Mteitei	EA – Erinaceidae EA – Sciuridae As – Ctenodactylidae EA – Cricetodontidae EA – Zapodidae? EA – Dipodidae? EA – *Austrolagomys* EA – *Cynelos* EA – *Leptoplesictis* EA – *Mioprionodon* EA – *Stenoplesictis* As – *Kenyalutra* As – *Kichechia* As – *Legetetia* As – *Afrosmilus* EA – *Chalicotherium* As – *Chilotheridium* EA – *Brachypotherium* EA – *Aceratherium* As – *Nguruwe* As – *Bunolistriodon* EA – primitive Pecora
TB 1.5 22 Ma	**MN 2** Laugnac				Zinda Pir		**Set** 0 Meswa Bridge	

genus is endemic at the Miocene island of Tuscany. In view of the fact that its affinities are not perfectly clear, it is equally possible that it came on the island from Africa, SE Europe and Anatolia or from Europe. The study of the possible origins of other animals on the Tuscany island might shed light on its area of origin.

The cercopithecid *Mesopithecus* decreased in size from MN 11 (*M. delsoni*) to MN 12 (*M. pentelicus*), to MN 13 (*M.* cf. *monspessulanus*) (DE BONIS et al. 1990). The earliest citations are from MN 11 in SE Europe and in Maragheh, Iran and the earliest citations in Europe are from MN 13 (ANDREWS et al. 1996). This suggests, that the entry in Europe is a later dispersal event, either from SE Europe or directly from Africa (during the Messinian Crisis).

The cercopithecid *Macaca* is first cited in Europe from MN 13 in Spain (ANDREWS et al. 1996). The genus is also known from Sardinia. It seems likely, that *Macaca* reached Sardinia during the Messinian crisis (MN 13), though there is no early record of the genus.

Creodonta: Creodonts are a primitive order of carnivores, that declined in Eurasia, but that remained abundant in Africa. In MN 3 the creodont *Hyainailouros* dispersed to the Indian Subcontinent and it is first known from early MN 4 in Europe.

Carnivora: Carnivora are not known from the Paleogene of Africa, starting in the Early Miocene they entered in several waves. Carnivores were probably absent in the earliest Miocene of the Indian Subcontinent. There is no a priori reason to suppose that no European carnivores may have entered Africa and the Indian Subcontinent, though SCHMIDT-KITTLER (1987) assumed that the carnivores entering Africa were of Asian origins. The Amphicyonidae *Cynelos*, *Amphicyon* and *Ysengrinia* were already present in Europe during the earliest Miocene and are cited from Africa, respectively from Set I, Set IIIa and again Set IIIa (SCHMIDT-KITTLER 1987; MORALES et al. in press). *Amphicyon* is cited from Bugti (PILGRIM 1912).

The first appearance of the ursid *Hemicyon* in MN 3 in Europe and in Set II in Africa (SCHMIDT-KITTLER 1987) may well be a single dispersal event and the same is the case for the ursid *Agriotherium*, which appeared apparently simultaneously in Europe in MN 13 (MORALES 1984) and Africa (HENDEY 1981).

The oldest record of the Mustelidae in Africa is *Luogale* from Set II (SCHMIDT-KITTLER 1987). This genus seems to be closely related to *Paragale* from MN 2 in Europe. Lutrinae (*Kenyalutra*) seem to have appeared even earlier in Africa (Set I) than in Europe (MN 4) (SCHMIDT-KITTLER 1987; WILLEMSEN 1990) and both dispersals seem to be independent events. In the latest Miocene, *Plesiogulo* and *Enhydriodon* appeared in Africa (HENDEY 1981). *Plesiogulo* had a previous record in Spain (FRAILE et al. 1997) and the lutrine *Enhydriodon* had a previous record in the Indian Subcontinent and Europe (WILLEMSEN 1990).

Viverridae and Herpestidae had a record in Europe previous to the arrival of *Kichechia*, *Leptoplesictis* and *Mioprionodon* in Africa in Set I and *Herpestides* in Set II (FRAILE et al. 1997, SCHMIDT-KITTLER 1987). *Viverra* with a previous record in Europe appeared in the latest Miocene of Africa (HENDEY 1981).

Stenoplesictidae (= Percrocutidae) probably had a pre-Miocene origin in Asia. *Stenoplesictis*, with felid affinities, first appeared in Africa in Set I and *Africanictis*, with hyaenid affinities, in Set IIIa. In the area of SE Europe and Anatolia Stenoplesictidae appeared in MN 6 and in western Europe in MN 7 (MORALES et al. 1998, WERDELIN 1996).

The hyaenid *Protictitherium* is found in Europe in Bézian (MN 4) (WERDELIN & SOLOUNIAS 1996). The earliest African hyaenids appeared in Set IV (SAVAGE 1978).

The machairodontine felid *Afrosmilus* first appeared in Africa Set I (SCHMIDT-KITTLER 1987) and seems to be closely related to *Pseudaelurus*, which is cited from Europe from MN 3 (FRAILE et al. 1997). It seems likely that both arrived by dispersal from some Asian centre of evolution. The same may be the case with *Felis* which is known from MN 13 in Spain and from equally old deposits in Africa (FRAILE et al. 1997, HENDEY 1981).

Tubulidentata: The origin of the Tubulidentata is in Africa. The earliest aardvarks outside Africa are from MN 6e in Anatolia (FORTELIUS 1990) and from the Chinji Formation in Pakistan (PICKFORD 1978) and are all assigned to the genus *Orycteropus*. The more or less similar age suggest a single dispersal event. *Orycteropus* may have been present in SE Europe and Anatolia till the Upper Miocene (it is very well known from Pikermi and Samos, but it is found in many other localities) and may have dispersed in MN 13 to western Europe (Brisighella).

ALFÉREZ et al. (1988) mentioned a tubulidentate from Córcoles (MN 4, Spain), but PICKFORD (1993) claimed it is a suoid.

Proboscidea: Proboscidea are known from the Eocene of the Indian Subcontinent and Africa and may have originated from a Paleocene Chinese genus (WELLS & GINGERICH 1983). However, by the Early Miocene there was nothing similar to a proboscidean in Eurasia, whereas proboscideans had radiated in Africa. When, during the Early Miocene, Africa became connected after a long time with Eurasia and the Indian Subcontinent, a diverse proboscidean fauna dispersed. *Hemimastodon*, *Gomphotherium* and *Choerolophodon* are present in the Bugti fauna (TASSY 1990). Possibly a little later *Gomphotherium* and *Zygolophodon* appeared in Europe, both are certainly present in MN 4e and are even claimed to be present in MN 3 (BULOT & GINSBURG 1993). *Anancus* appeared in the Late Miocene of Europe and Africa, it is however not sufficiently clear where this genus originated (A.V. MAZO pers. comm.).

The lophodont cheek teeth of *Deinotherium* suggest that it had a specialized diet. *Deinotherium* (or *Prodeinotherium*) is known from Bugti. It reached Europe during the later part of MN 4 and never really entered in China. The later and more limited dispersal of this proboscidean seems to be due to its ecological requirements.

Hyracoidea: The oldest known hyraxes are from the African Oligocene (MEYER 1978). The oldest known hyraxes outside Africa are a form close to *Geniohyus* from Bugti (PICKFORD 1986c) and *Plio-*

hyrax from Pasalar in Anatolia (FORTELIUS 1990), Melambes on Crete and Can Llobateres and other Vallesian European localities (PICKFORD et al. 1997, FISCHER & HEIZMANN 1992). For a long time Melambes was believed to be Vallesian, but it seems much more likely the locality is MN 6 (VAN DER MADE 1996). This gives the impression of a first dispersal towards the Indian Subcontinent in MN 3 and a subsequent dispersal towards SE Europe and Anatolia early in MN 6 and subsequent dispersal towards western Europe in MN 9l.

Perissodactyla: Tapirs were present in Eurasia during the Oligocene and Miocene and the equid *Anchitherium* during the Aragonian and Early Vallesian, but they did not disperse into Africa and the Indian Subcontinent. In the Vallesian, *Hipparion*, also of American origins, dispersed into Eurasia and immediately also into the southern continents.

Chalicotheriidae have their origins in the northern hemisphere and were represented in the earliest Miocene of Europe with *Schizotherium*. When the first connection occurred between Africa the northern and southern continents, *Chalicotherium* moved into Africa and the Indian Subcontinent. At this stage, *Chalicotherium* was not yet present in Europe; it moved into Europe, when the first deinotheres came into Europe. *Phyllotillon* is cited from Bugti and may have given rise to *Ancylotherium*. This group or lineage entered Europe not later than the Middle Miocene and Africa during the Late Miocene (BUTLER 1978b). The group is not well known so that the timing of the dispersals remains dubious.

Rhinocerotidae were present in northern Eurasia during the Oligocene. During the early Miocene they first moved into Africa and the Indian Subcontinent. The initial dispersal into Africa about 21 Ma ago involved four genera (HOOIJER 1978).

Suoidea: *Sanitherium* (= *Diamantohyus*; Palaeochoeridae) first appeared in Set I in Africa and in the Bugti fauna of the Indian Subcontinent (PICKFORD 1984, VAN DER MADE & HUSSAIN 1992) and may have evolved from *Palaeochoerus* or a similar form (VAN DER MADE 1998), which is last known from MN 2 in Europe. In MN 5l, a later stage of evolution of *Sanitherium* entered Central Europe, and was present in Chios.

The origin of the Suidae is in Asia. *Nguruwe* (Listriodontinae) first appeared in Africa in Set I. *Bunolistriodon* appeared in Africa in Set I, the Bugti fauna and later in MN 4l in Europe and China. *Listriodon* evolved in the Indian Subcontinent from *Bunolistriodon* and dispersed in MN 6 to Eurasia (VAN DER MADE 1996).

Cainochoerinae (*Kenyasus*), of unkown origin, entered in Set I Africa. *Albanohyus* is first known from Set IV in Africa and later from MN 7-9 in Europe (VAN DER MADE 1996b).

"Conohyus" sindiense from MN 4l equivalent strata in the Indian Subcontinent is the oldest tetraconodontine known and gave rise to *Conohyus* that dispersed into Europe in MN 5l. During the Vallesian this genus dispersed to Africa, where it gave rise to *Nyanzachoerus*. *"Conohyus" sindiense* evolved into *Sivachoerus* in the Indian Subcontinent and dispersed possibly twice to Africa during the late Miocene, giving rise to several species of *"Nyanzachoerus"* (VAN DER MADE in press).

In MN 8 *Propotamochoerus* (Suinae) dispersed either from Asia or the Indian Subcontinent to Europe. *Hippopotamodon* (= *Microstonyx*), probably of Asian origin, appeared in MN 9 in Europe and in Anatolia and in the Nagri Formation in Pakistan. Suinae did not enter Africa during the Miocene.

Hippopotamoidea: *Brachyodus* of African origin dispersed in MN 3 to Eurasia and the Indian Subcontinent. Hippos evolved in Africa from anthracotheres. *Hexaprotodon* dispersed during the late Miocene to the Indian Subcontinent and a tetraprotodont hippo (placed either in *Hexaprotodon* or *Hippopotamus*) migrated in MN 13 to Europe (VAN DER MADE this volume).

Tragulidae: Tragulidae are primitive ruminants and have their ultimate origin in Eurasia. The oldest *Dorcatherium* is known from Africa from Set 0 (PICKFORD 1986a), possibly from the Bugti fauna (*"Tragulus sivalensis"*; RAZA & MEYER 1984) and from MN 4l in Europe (FAHLBUSCH 1985). *Dorcabune*, with a previous record in the Indian Subcontinent, is probably present in MN 10 in Crete (VAN DER MADE 1997a).

Primitive pecorans: Material from African Set I and II localities was assigned to cf. *Strogulognathus* (= *Eotragus*), *Palaeomeryx*, *Propalaeoryx*, "indeterminate Bovidae", *Gelocus* and *Namibiomeryx* by STROMER (1926), WITWORTH (1958) and HAMILTON (1973) and MORALES et al. (1995) and *"Prodremotherium*(?)" and *"Gelocus*(?)" by PILGRIM (1912) from Bugti probably represent primitive pecorans. The bovoid *Hispanomeryx* is first known from Anatolia from MN 6e (MOYÀ-SOLÀ 1987) and appeared in western Europe in MN 6l.

Bovidae: Citations of very early Bovidae and the great diversity in the primitive forms in Central Asia, Mongolia and China (VISLOBOKOVA 1997) and the sudden appearance of bovids belonging to different subfamilies in Europe, the Indian Subcontinent and Africa, suggest that bovids have their origin in north or central Asia.

The oldest bovids outside north or central Asia are the 18 Ma old boselaphine *Eotragus* from the Indian Subcontinent (SOLOUNIAS et al. 1995) and the *Eotragus* from MN 4e in Europe, both probably coming from north or central Asia. Forms that have been attributed to *Protragocerus* first appeared in Europe in MN 5l, in the Indian Subcontinent in the Lower Chinji Formation and in Africa in Set IV. *Miotragocerus* (= ? *Tragoceridus*) of Eurasian origin entered some 6 Ma ago in Africa (GENTRY 1978). *Sivoreas* entered the Indian Subcontinent 13.8 Ma ago (BARRY & FLYNN 1990) and is found in the Vallesian of Africa (THOMAS 1981).

A number of early citations of *Eotragus* are based on horn cores, that more probably belong to primitive hypsodontinae. This may be the case with a specimen from Gebel Zelten (HAMILTON 1973). Some very hypsodont teeth from Midra-ash-Shamali (WHYBROW et al. 1982), of about the same age, lend support to this idea. The horn core from the Kamlial formation PILGRIM (1939) assigned to *Eotragus*, might also represent a hypsodontine. At present it is not clear, whether the appearance of *Kubanotragus* in MN 5 in the Caucasus and 13.8 Ma ago in Pakistan and *Turcoceros* in MN 6l in Anatolia (KÖHLER 1987, BARRY & FLYNN 1990) present different dispersal events or local evolution from such primitive forms. *Hypsodontus* is known from early MN 5 or MN 6e equivalent localities in Anatolia, Pakistan, southern Russia and Africa (KÖHLER 1987, GENTRY 1978, THOMAS 1984). Less hypsodont specimens from China suggest a dispersal of *Hypsodontus* from China or central Asia towards the other areas some 14 Ma ago.

The short premolars suggest, that a small brachyodont bovid from Ad Dabtiya that GENTRY (1987) assigned to *Eotragus*, might well belong to the hippotragine *Tethytragus* (= *Caprotragoides*). In MN 6e the genus was present in Anatolia and nearly immediately two lineages can be recognized that dispersed to Europe in MN 6l (VAN DER MADE 1994). *Protoryx* evolved in Anatolia from *Tethytragus* and appeared in MN 8 in Africa (KÖHLER 1987). *Gentrytragus* is known from Set IV in Africa and Arabia (GENTRY 1978, THOMAS 1983). *Tethytragus* and *Gentrytragus* (both were formerly placed in *Caprotragoides*) possibly diverged after the dispersal of the first into Anatolia and the second into Africa.

There are early citations of the antilopine *Gazella* (= ? *Homoiodorcas*) from Africa (Set IIIa, IV), the Middle Chinji Formation in Pakistan and possibly from MN 6, but certainly MN 9 in Anatolia (HAMILTON 1973, GENTRY 1978, THOMAS 1984, KÖHLER 1987). *Hispanodorcas* and the hippotragines *Palaeoryx* and *Protoryx* had previous records in Greece and Anatolia (GENTRY & HEIZMANN 1996). These four genera appeared in MN 12 in Spain (NIETO et al. 1997).

From the Vallesian onwards, till nearly the end of the Miocene, the African fossil record is poor, while there is an extremely rich bovid fauna in the Turolian of Greece and Turkey (SOLOUNIAS 1981, KÖHLER 1987, collections in Ankara). But few relationships have been established between these bovids, so that biogeographical interpretations are hazardous.

Giraffidae: The oldest giraffids known are *Teruelia* from MN 2 in Spain (MOYÀ-SOLÀ 1987), *Progiraffa* from Bugti in the Indian Subcontinent (PILGRIM 1912) and *Zaraffa* and *Palaeotragus* from Set III in Africa (CHURCHER 1978), whereas the giraffoid *Climacoceras* is known from Set II (PICKFORD 1981, 1986a), which probably arrived independently from Asia.

Giraffokeryx is cited from the Indian Subcontinent from 16.5 Ma onwards and may have dispersed to SE Europe and Anatolia in MN 5 and Africa in Set IV (BARRY & FLYNN 1990, GENTRY & HEIZMANN 1996, CHURCHER 1978). This gives the impression of a dispersal from the Indian Subcontinent towards Africa and SE Europe late in MN 5. However, doubts have been expressed on determinations based on dental material (MONTOYA & MORALES 1991). *Bramatherium* is cited from the Indian Subcontinent from Aragonian times and appeared in the Turolian in Anatolia (MONTOYA & MORALES 1991). There are a number of other Miocene giraffids, but their relationships and areas of origin are poorely known.

Cervidae: Cervidae first appeared in Europe in MN 3, but did not reach Africa and the Indian Subcontinent during the Miocene.

Lagomorpha: Lagomorpha have their origin in Asia. This is also the case for the Ochotonidae, which later spread to Europe and still later, during the Early Miocene, entered Africa. *Austrolagomys* is cited from Set I (STROMER 1926) and *Kenyalagomys* from Set II (PICKFORD 1986a). The Leporidae did not enter Africa during the Miocene.

Rodentia: Rodentia are very well studied in Europe. The collections from the Indian Subcontinent and Africa are much smaller. Especially for Africa, the available information might be rather incomplete, and therefore it seems better not to treat individual genera (apart from the fact that this would require much more space).

THOMAS (1985) listed as families that dispersed into Africa and Arabia during his NDP1 event: Zapodidae, Sciuridae, Dipodidae, Cricetodontidae and Ctenodactylidae (*Sayimys*) and during the NDP2 event the Gliridae. Cricetodontidae and Sciuridae seem to have their origin in Eurasia (LAVOCAT 1978, THENIUS 1979) and are first recorded from Africa from Set I (PICKFORD 1986a). Dipodidae may have their origin in Europe and entered only in the north of Africa (LAVOCAT 1978). Ctenodactylidae, Sciuridae and Cricetodontidae, all supposedly of Asian origins, dispersed into the Indian Subcontinent during the Early Miocene (DE BRUIJN & HUSSAIN 1984). Data in the time range 21-16.5 Ma are poor, but the available data suggest a major dispersal event around 21 Ma from Asia to Africa and the Indian Subcontinent. DE BRUIJN & HUSSAIN (1984) supposed the Gliridae to have migrated from Europe to the Indian Subcontinent in the Middle Miocene, where they are known from Chinji equivalent levels. The glirid dispersals to the Indian Subcontinent and Africa may form part of a single event.

THOMAS (1985) listed the Pedetidae and Thryonomyidae as dispersing from Africa to Eurasia during the NDP2 event. Pedetidae are first known from Set I localities in Africa (STROMER 1926, PICKFORD 1986). DE BRUIJN & HUSSAIN (1984) listed Pedetidae? from a locality from a Kamlial equivalent level. The family seems to have dispersed towards Eurasia during MN 5/6 (THOMAS 1985) or during the late Miocene (THENIUS 1979). DE BRUIJN & HUSSAIN (1984) indicated that Rhizomyidae dispersed from the Indian Subcontinent to Africa and Myocricetodontidae, of the same geographical origin, to Africa and Anatolia. The localities they cite indicate that the arrival in Africa is not later than MN 4l or Set IIIa, whereas the arrival in Anatolia is not later than MN 6.

The oldest Muridae known are from Pakistan from a locality (DE BRUIJN & HUSSAIN 1984) that is slightly younger than 16.5 Ma. This genus gave rise to *Progonomys* and was replaced by that genus about 11.8 Ma ago (JACOBS et al. 1990). This genus appeared in MN 9 in Anatolia (SEN 1990) and in latest MN 9 in Europe (VAN DAM 1997). *Progonomys* entered Africa in MN 10 (LAVOCAT 1978).

The dispersal events

During the Oligocene and earliest Miocene (MN 1-2; Set 0; "pre-Bugti") Africa and the Indian Subcontinent had endemic faunas. Chapattimyid rodents were present in the Eocene of the Indian Subcontinent and survived there till the earliest Miocene (JACOBS et al. 1981, KUMAR et al. 1996). The primitive ruminant *Leptomeryx* and an anthracothere have been cited from the Oligocene of India (KUMAR et al. 1996). The African faunas of that time include primates, creodonts, tubulidentates, proboscideans and hyracoids. Tragulids were present in the earliest Miocene of Africa and may have been present in the Indian Subcontinent. Eurasian faunas had Carnivora, rhinos, palaeochoerids, suids, primitive pecorans, giraffoids, etc. The subcontinent of SE Europe and Anatolia had been connected with Europe during the Oligocene; the Early Miocene faunas are not well known, but probably showed many resemblances to European faunas.

In the next sections a series of faunal exchange events are treated. Table 45.1 compiles the primary data.

***Brachyodus* event, 21 Ma**: The anthracothere *Brachyodus*, of African origin, entered Europe, Asia and the Indian Subcontinent.

Dispersals into Africa involved a large number of chiropterans, erinaceids, the rodent families Cricetodontidae and Sciuridae, the lagomorph *Austrolagomys*, the amphicyonid *Cynelos*, the viverrids *Kichechia*, *Legetetia*, *Leptoplesictis* and *Mioprionodon*, the stenoplesictid *Stenoplesictis*, the felid *Afrosmilus*, the rhinos *Brachypotherium*, *Aceratherium*, *"Dicerorhinus"* and *Chilotheridium*, the chalicothere *Chalicotherium*, the palaeochoerid *Sanitherium*, the suids *Bunolistriodon* and *Nguruwe* and primitive pecorans, all of Eurasian origins. Possibly at this time the rodent families Dipodidae, Zapodidae and Ctenodactylidae entered Africa.

Dispersals into the Indian Subcontinent included probably the creodont *Hyainailouros*, the proboscideans *Hemimastodon*, *Gomphotherium*, *Choerolophodon* and *Deinotherium*, the hyrax aff. *Geniohyus* and the anthracothere *Brachyodus*, all of African origin. *Dorcatherium* may have been present already or may have come from Africa. The carnivore *Amphicyon*, the rhinos *Paraceratherium* (= ?*Baluchitherium*), *Brachypotherium*, *Aceratherium*, *Chilotherium*, the chalicotheres *Chalicotherium* and *Phyllotillon*, primitive pecorans, the giraffid *Progiraffa* and the rodents Sciuridae, Cricetodontidae and Ctenodactylidae

dactylidae, all of Eurasian origin entered the Indian Subcontinent.

This event took place at the beginning of MN 3, zone Z of the Ramblian, Set I, "Bugti". In numerous places, a regression is documented (Aquitaine, Untere Süsswasser Molasse in central Europe etc.), which is the regression at the onset of the TB2.1 cycle of HAQ et al. (1987). This regression very likely allowed the massive faunal exchange described above.

Creodont event, 17.5? Ma: The creodont *Hyainailouros*, of African origin and the rodent *Democricetodon*, of Anatolian origin dispersed into Europe. The entry of the proboscideans *Gomphotherium* and *Zygolophodon*, of African origin, in Europe might antedate the entry of *Democricetodon*, and thus be in MN 3. However, there are but very few MN 3 localities with proboscideans. Possibly, the localities where these proboscideans are found are very close to or identical in age to the earliest localities with *Democricetodon*.

Soricids, the lutrine *Luogale*, the herpestid *Herpestides*, the ursid *Hemicyon*, the suid *Kenyasus* and the giraffoid *Climacoceras* are first recorded from Set II. The Set II localities are much richer than the Set I localities, it is possible that a number of these taxa were present already before.

At present, it is not sufficiently clear whether there was a single event in Europe, that occurred at the beginning of MN 4 and zone B, nor is it clear whether it is synchronous to the African event at the beginning of Set II. If there was an event, it is related to either the regression of the TB2.2 cycle of HAQ et al. (1987), or to the changes in climate that caused this minor regression.

***Bunolistriodon* event, 16.5 Ma:** The proboscidean *Deinotherium*, the chalicothere, *Chalicotherium*, the suid *Bunolistriodon* and the tragulid *Dorcatherium* with previous records in Africa and the Indian Subcontinent and the cricetids *Megacricetodon*, *Eumyarion* and *Fahlbuschia* of Anatolian origins, dispersed to Europe.

The amphicyonids *Amphicyon* and *Ysengrinia*, felid *Africanictis*, the giraffids *Zaraffa* and *Giraffokeryx* or *Palaeotragus* and the bovid subfamily Hypsodontinae, the first *Gazella*, all of Eurasian origins, and rhizomyid and myocricetodontid rodents, of Indian origins, dispersed to Africa.

The catarrhine *Dionysopithecus* and pedetid rodents, of African origin, and the giraffid *Giraffokeryx*, of Asian origin, dispersed into the Indian Subcontinent.

This event is within MN 4, and at the beginning of zone C of the Aragonian and Set III. It seems to have been allowed for by the regression of the TB2.3 cycle.

Hominid event, 15.5 Ma: A hominid (*Griphopithecus*?), of African origin, entered Europe and possibly the first hypsodontine bovids, of Asian origin, entered the Indian subcontinent. However, these bovids may have been present earlier, since they entered during the previous event in Africa. This event is possibly at the beginning of MN 5, zone D, Set IIIb and the TB2.4 cycle.

***Conohyus/Pliopithecus* event, 14 Ma:** The catharrines *Pliopithecus* and *Plesiopliopithecus*, of African origins, the rodent *Cricetodon*, of Anatolian origin, the palaeochoerid *Sanitherium*, with a previous record in Africa and the Indian Subcontinent, and the suid *Conohyus* of Indian origin entered Europe.

Not later than at this moment, the tubulidentate *Orycteropus* and the hyrax *Pliohyrax*, of African origin, the suid *Kubanochoerus* of Afro-Indian origin and the carnivore *Percrocuta* and cervids dispersed into SE Europe and Anatolia. There is however, virtually no previous large mammal record in the SE European and Anatolian areas. The hyaenid *Protictitherium* and the bovids *Protragocerus*, *Gentrytragus* and *Hypsodontus*, all of Asian origins, entered Africa.

The aardvark *Orycteropus*, of African origin, and the bovids *Protragocerus*, *Sivoreas*, *Sivaceros* and *Kubanotragus*, of Asian origin dispersed into the Indian Subcontinent.

This event is within MN 5 and is at the beginning of zone E, Set IV and the TB2.5 cycle. At this time the Chinji faunal complex was formed.

***Listriodon* event:** The dispersal of *Listriodon*, of Indian origin, to Anatolia and Eurasia seems to be an isolated event at the beginning of MN 6 and zone F.

***Tethytragus* event, 12.5 Ma:** The primitive bovoid *Hispanomeryx* and the bovid *Tethytragus* all with previous records in Anatolia, the suid *Albanohyus* and probably the hominid *Dryopithecus*, of African origin entered Europe. The bovid *Turcoceros* appeared in Europe and in SE Europe and Anatolia; its origin is either local in the latter area or in Asia.

The carnivore *Percrocuta* entered Africa. The bovid *Helicoportax*, of Asian origin, and the hominid *Sivapithecus*, of African origin, entered the Indian Subcontinent.

This event is within MN 6, probably at the beginning of zone G, at the beginning of Set V and the middle Chinji faunal complex and onset of the TB2.6 cycle.

***Propotamochoerus* event**: *Propotamochoerus*, of Asian or Indian origin, entered Europe. KÖHLER (1987) assumed a dispersal of *Protoryx* to Africa in MN 8.

These dispersals did not coincide with a regression. Two cycles (TB2.5-TB2.6) had cumulative effect and global sea level remained very low; probably the sea did not impede any faunal exchange between the major land masses in the Old World. There seem, however, to have been changes in climate in the circum Mediterranean area. In Turkey, the vegetation seems to have changed. The Eskihisar Pollenbild was replaced by the Yeni Eskihisar Pollenbild in MN 8 (BENDA & MEULENKAMP 1990). There were also changes in the vegetation of southern Germany, MN 8 was interpreted as a wetter period (JUNG & MAYR 1980). After a long period of absence, castorids entered again in the Aragonian type area (DAAMS & FREUDENTHAL 1988), suggesting a change towards greater humidity. Such environmental changes may have permitted the dispersal of these taxa.

***Hipparion* event, 11 Ma**: The Equid *Hipparion*, of American origin, entered the Old World and within a short period reached the most distant parts. *Hippopotamodon* (= *Microstonyx*) probably of Asian origin entered in Europe and the Indian subcontinent. *Mellivora,* of Asian/Indian origin, and *Conohyus* of European, Anatolian or Indian origin, dispersed into Africa. The TB3.1 cycle starts with a drop of over 100m sea level. Within the Old World landmasses were connected already, but this event seems to have allowed for a faunal exchange with America.

This event is at the beginning of MN 9, zone H, Set VII and the TB3.1 cycle. It marks the beginning of the Nagri Faunal complex.

Murid event, 9.6 Ma: The murid *Progonomys*, of ultimate Indian origin, and the hyrax *Pliohyrax* dispersed into Europe. Possibly the dispersal of the palaeochoerid *Schizochoerus* was at the same time. All had previous records in Anatolia. There are slightly older citations of *Progonomys* in Europe, but the massive presence of murids that characterises this event is very late in MN 9 or MN 10 (VAN DAM 1997). *Progonomys* and possibly *Sivachoerus* spread at this same moment to Africa. *Dorcabune* may have extended its range from the Indian Subcontinent into Crete.

This event is very late in MN 9 or at the beginning of MN 10, and late in zone I. It seems likely that climatical changes triggered the events.

***Gazella* event, 6.9 Ma**: The bovids *Gazella*, *Protoryx*, *Palaeoryx* and *Hispanodorcas* first appeared in Western Europe in the later part of MN 12 (NIETO et al. 1997) in localities with an estimated age of 6.8-6.9 Ma (VAN DAM 1997). The MN 12-13 boundary is estimated at 6.8 Ma, when certain murids first appear. These murids are still absent in the *Gazella* localities. The bovids have a previous record in SE Europe and Anatolia. This gives the impression, that the appearance of these bovids in Spain is related to the events that marked the MN 12-13 transition.

In Africa, a number of new bovids, including *Cephalophus* and *Ugandax* have their oldest records at about 7 Ma (GENTRY 1978). There are however incertainties about the origin or first occurrence of these bovids.

CERLING et al. (1997) reported on a global vegetation change between 6 and 8 Ma ago; vegetation with a C_3 photosynthetic pathway was replaced by C_4 vegetation, which includes grasses. This was assumed to have occurred due to a decrease of the CO_2 concentration in the atmosphere. The change in vegetation seems to have occurred first at the lower latitudes, whereas Western Europe was not much affected. The changes in vegetation caused important changes in the fauna in Africa, Pakistan and North and South America. Though Europe was much less affected, the appearance of four hypsodont bovids in Spain is worth to be noted.

Hippo event, 6.3 Ma: A hippo (*Hexaprotodon*/*Hippopotamus*), the bovid *Redunca*? and the cercopithecids *Macaca* and *Mesopithecus*, of African origins, the bovid *Parabos*, possibly of Indian origin, and the ursid *Agriotherium*, possibly of Asian origin, entered Europe.

The ursid *Agriotherium*, the mustelids *Plesiogulo* and *Enhydriodon*, the felid *Felis*, and the viverrid *Viverra*, with origins in Eurasia and/or the Indian Subcontinent, the chalicothere *Ancylotherium*, with an origin in the Middle East, the bovids *Leptobos*?, of Asian or Indian origin, and *Miotragoceros*, with a previous record in Europe and SE Europe and Anatolia, and (for the second time) *Conohyus*, of Indian origin, entered Africa. The timing of these dispersals is not very secure, since the previous African fossil record is not very abundant.

Hexaprotodon, of African origin and different from the European hippo, entered the Indian Subcontinent.

This event occurred within MN 13, at the beginning of zone M2 and within the Dhok Pathan unit. There were two regressions during the TB3.3 and 3.4 cycles, causing the events that are known as the Messinian Salinity Crisis. The first regression probably allowed for most of the dispersals. The dispersals towards the Indian Subcontinent are more likely to be related to climatical changes.

Conclusions

The Miocene faunal exchange between Eurasia, Africa and the Indian Subcontinent was intense. Today, these areas are known as the Palaearctic, Ethiopian and Indian bioprovinces. The latter two together are also known as Palaeotropical bioprovince. The recognition of these bioprovinces goes back to SCLATER and WALLACE in the nineteenth century. The Palaearctic is the area north of the arid Sahara-Gobi belt and tends to be seasonal in that it has cold winters and hot summers, the degree depending partially on latitude, and it includes areas with very low temperatures. The Palaeotropic is the area south of the arid belt; it tends to have more of a wet-dry seasonality and includes permanently warm areas. The Ethiopian and Indian bioprovinces are physically separated by the Indian Ocean, but have similar climates. These climates are reflected in the vegetation. Seasonal variations in the supply of fruits and leaves tend to be greater in the Palaearctic, limiting the distribution of folivorous and frugivorous animals.

During much of the Miocene a similar biogeographical pattern seems to have prevailed. As we have seen above, mammals that may have been dependent on some degree of humidity, like tapirs, the equid *Anchitherium*, cervids, moles etc. were present in northern Eurasia, during a long part of the Miocene, but did not enter Africa and India; there may have been an area south of Turkey, that was too arid for them to cross. While there seems to have been an important filter controlling faunal exchange between Eurasia and the southern continents, the data presented above suggest, that faunal relationships between Africa and the Indian Subcontinent were more intense. There are, however, differences between the recent and Miocene patterns, in that the present Holarctic extends into North Africa, whereas this was not the case in the Early and Middle Miocene. PICKFORD & MORALES (1994) claimed that the boundary zone between the Ethiopian and Palaearctic bioprovinces shifted north several times during the Miocene, which would suggest that there are other factors, than the arid belt, limiting faunal exchange between the southern and northern continents. This indeed seems to be the case. Though extinctions are not subject of this paper, it should be mentioned that folivorous animals like tapirs and possibly *Anchitherium* and animals that may have been (partially) frugorivorous, like tragulids and certain primates, became rare or went extinct in Europe during the later part of the Vallesian, when the European climate may have become more seasonal.

The Miocene faunal exchange between Europe (or Eurasia), the block formed by SE Europe and Anatolia, Africa and the Indian Subcontinent occurred in a series of distinct events (table 45.1). The magnitude varies greatly from none (?) to over 20 taxa dispersing into a particular (sub)continent (note that "taxa" as presented here, includes genera, but also whole families). During the Early and Middle Miocene, these dispersal events seem to have been allowed for by low sea level stands, which in turn are caused by a cold global climate, having probably an influence on faunal distribution in its own right. When the Miocene proceeded, the steplike lowering of the sea level (MILLER et al. 1995) caused land masses to become connected, later changes in sea level lost importance in biogeography and climate changes became the driving force controlling patterns of faunal distribution. This is seen in the timing of the dispersal events (see murid and *Gazella* events, table 45.1). The difference with the early Miocene is that changes towards a warm global climate (with high sea level) also caused intercontinental dispersals (as may have been the case in the murids), resulting in more frequent and more complex changes in biogeography.

The "*Brachyodus* event" (about 21 Ma ago, MN 3, Set I, Bugti) is characterized by massive dispersals into the Palaeotropic and only very limited dispersals into the Palaearctic. It is only during the "*Bunolistriodon* event" (MN 4I, Set IIIa), "*Conohyus/Pliopithecus* event" (MN 5I, Set IV, Chinji) and "*Tethytragus* event" when there were important dispersals into the Palaeoarctic. The "*Tethytragus* event" involved also important dispersals into the Palaeotropic. The Upper Miocene record in Africa is rather incomplete, and does not allow for exact timing of the events. It does suggest however, again major dispersals into Africa. The latest Miocene dispersal of hippos of African origin into Europe has received much attention, but is limited to the south of Europe. Correcting for the emblematic dispersal of the hippo to southern Europe, the resulting picture is of a change of the balance of immigration: first the majority of dispersals were into the Palaeotropic, later into the Palaeoarctic and then again into the Palaeotropic. Though there exist differences with the results of PICKFORD & MORALES (1994) in the details of timing of the events and the dominant direction of dispersal at a particular time, both studies support the view that the balance of faunal exchange changed through the Miocene.

Global sea level has been related to global climate and the accumulation of ice masses on continents, in particular on Antarctica, but also to tectonic activity (PARTRIDGE et al. 1995). Whereas global sea level reacts immediately to climate, the relationship may change gradually over longer periods. Tropical soils in Germany, with ages ranging 17-15 Ma, have been interpreted to be caused by the greenhouse effect, caused by high atmospheric CO_2 concentrations (SCHWARZ 1997). Oxigen isotope records suggest relatively warm global climates during the Early and initial Middle Miocene, however, becoming progressively colder during the Middle Miocene (MILLER et al. 1995). This occurred in the period MN 6-9 (14-10 Ma), when the balance was shifting in favor of dispersals towards Africa. There is evidence for a glaciation in Greenland 11 Ma ago (HELLAND & HOLMES 1998).

As mentioned above, seasonality is an important determinant in climate. Large areas of Europe may have had a sufficiently warm and humid and not very seasonal climate during part of the Miocene, to allow the right vegetation to grow for folivorous and frugivorous animals. Another limitation related to seasonality is the reproductive cycle that in the Palaearctic coincides with the seasonal cycle (PICKFORD & MORALES 1994). In any case, a warm and humid seasonal climate may have been less limiting to certain animals than a cold and dry seasonal climate.

The present data are still very incomplete and the "why and wherefore" of the dispersals is frequently not clear. Continued work is necessary to clarify phylogenies and the timing and direction of dispersals and the relationship with the changing flora. These results should be integrated with the rapidly increasing amount of data on global climate, tectonics and sea level. Nevertheless, already an interesting interplay of evolution, climate and tectonics is appearing.

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