

THE ORIGIN AND AFFINITIES OF AFRICAN MAMMAL FAUNAS

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ABSTRACT. The paper summarizes quantitatively the land mammal faunas of Africa and four adjoining regions of Eurasia at successive stages through the Tertiary. Venn diagrams are used to show the changing degrees of similarity between the regions, and deductions are attempted on the relation of the African plate to the Eurasian and Indian plates.

THE African plate has formed a recognizable land mass at least since the late Mesozoic. The Riff-Riff in Morocco is the only significant Tertiary addition. Madagascar and the Arabian peninsula are the only major areas detached and neither possesses Tertiary mammals. From the evidence of the Tertiary mammal faunas an attempt is made to assess the extent and duration of contact or proximity of the African plate with the Eurasian plates across the Tethys sea. The three most probable areas for intercontinental crossings are Morocco-Iberia, Tunisia-Sicily-Italy, and routes from north-east Africa through the Arabian peninsula. For the migration of land mammals, these routes need not necessarily possess full land bridges; a chain of islands is adequate. For instance the presence of Pleistocene elephants in Africa, Europe, Asia, North and South America bears witness to their ability to traverse divers terrains. The living Asian elephant *Elephas indicus* is found in India, Burma, Malaysia, and on the island of Sumatra, but not on any of the other East Indies islands (except Borneo where it was introduced); Sumatra is 30 miles from the Malayan peninsula. In the Pleistocene elephants got as far as New Guinea, presumably when the sea levels were much lower.

Williams (1955) recorded how an elephant which had been one of a herd introduced into the South Andaman Island was some twelve years later found on the largest of the northern islands; the journey involved a 200-mile walk and three crossings of open sea at least a mile wide and usually with a swell.

As well as land bridges and island chains, colonization can be due to chance dispersal over wide stretches of sea. For example Madagascar has been isolated from Africa throughout the Tertiary; it is 1000 miles long and 300 miles from the African shores. No pre-Pleistocene mammals are known, and excluding the extinct Pleistocene hippopotamus, six families are represented in the Pleistocene and Recent Malagasy fauna, only three present in Africa. The exclusively Malagasy families are the primates Lemuridae, Indridae, and Daubontoniidae. Two of the other groups present, rodents and carnivores, are represented on Madagascar by sub-families unknown in Africa. The insectivore family Tenrecidae is recorded from the Early Miocene of East Africa, but otherwise is exclusively Malagasy. The invasions are probably post-Early Miocene and the isolation and lack of competition has enabled the stocks to radiate into a variety of niches. In the Pleistocene faunas of Mediterranean islands there are many species that are unknown on the adjacent

continents, but most of the genera are common to Africa or Europe; the Mediterranean islands are closer to the mainland masses and have not been isolated for so long a period as has Madagascar.

The chances of colonization are dependent on many variables, of which size of the island, distance from the mainland, climatic regime, and the distribution of rivers and sea currents are all important parameters. A floating island of vegetation from a river mouth with small mammals living on it has a poor chance of reaching and colonizing a small distant island, but a much greater chance of success should there be an adjacent continental mass. The later situation probably arose repeatedly during the Tertiary as the African plate moved north narrowing the Tethyan sea. The presence of the same genera, and in some cases of the same species, in Africa, Europe, and Asia at various times during the Tertiary and Pleistocene, points to periods of close proximity of the plate margins. It is in this light that the faunal evidence is examined.

The emphasis is on the evidence from Africa, and the other continental masses are considered only in so far as they are relevant to the theme. The Tertiary mammal record in Africa has many gaps, both in time and space, and as new sites are discovered the picture may alter radically. No sites are known in Africa with faunas of Palaeocene, Early Eocene, Mid Oligocene or Late Oligocene age. Nevertheless the record is on average better than that of Asia, though poor when compared with Europe.

PALAEOGENE

In attempting to establish likely migration routes across Tethys it is necessary to analyse the faunas of Africa together with those of various parts of Eurasia. The biggest problem in quantifying the data is the sporadic nature of the evidence, sporadic in time interval, in geographic distribution, and in taxonomic representation. For this reason it is impossible to subdivide the African faunas. While Tertiary mammal faunas of Africa are largely confined to North and East Africa, the Arabian peninsula is the most significant area with respect to possible migration routes. Unhappily there is an almost complete lack of evidence in this area; mammals crossing Arabia from Europe or Asia could move westward or southward, or both.

In Europe the faunas of Iberia are separated for analysis. The Pyrenees have acted as a filter limiting migrations, and so if mammals crossed Tethys from Morocco, this would be reflected in the Iberian fauna. It would likewise be desirable to separate off the Balkans from the rest of Europe, but the evidence is so scanty for most of the Tertiary that it would be a pointless exercise. As a formerly isolated plate, the Indian subcontinent must be considered separately, and with it the faunas of the Siwaliks. The equivalent facies on the northern face of the Himalayas have unfortunately yielded almost no Tertiary mammals; a few *Hipparion* teeth are recorded from the Chirchik valley, near Tashkent, and an anthracothere is known from the Ladakh district of Kashmir (Dixit, pers. comm.).

To express succinctly the relationships of the faunas Venn diagrams have been used. The data cannot be analysed further because of the many gaps and biases in the record. The degree of similarity is used as a measure of mutual exchange between the defined areas, and depicted with arrows on the maps. It will be noted that the

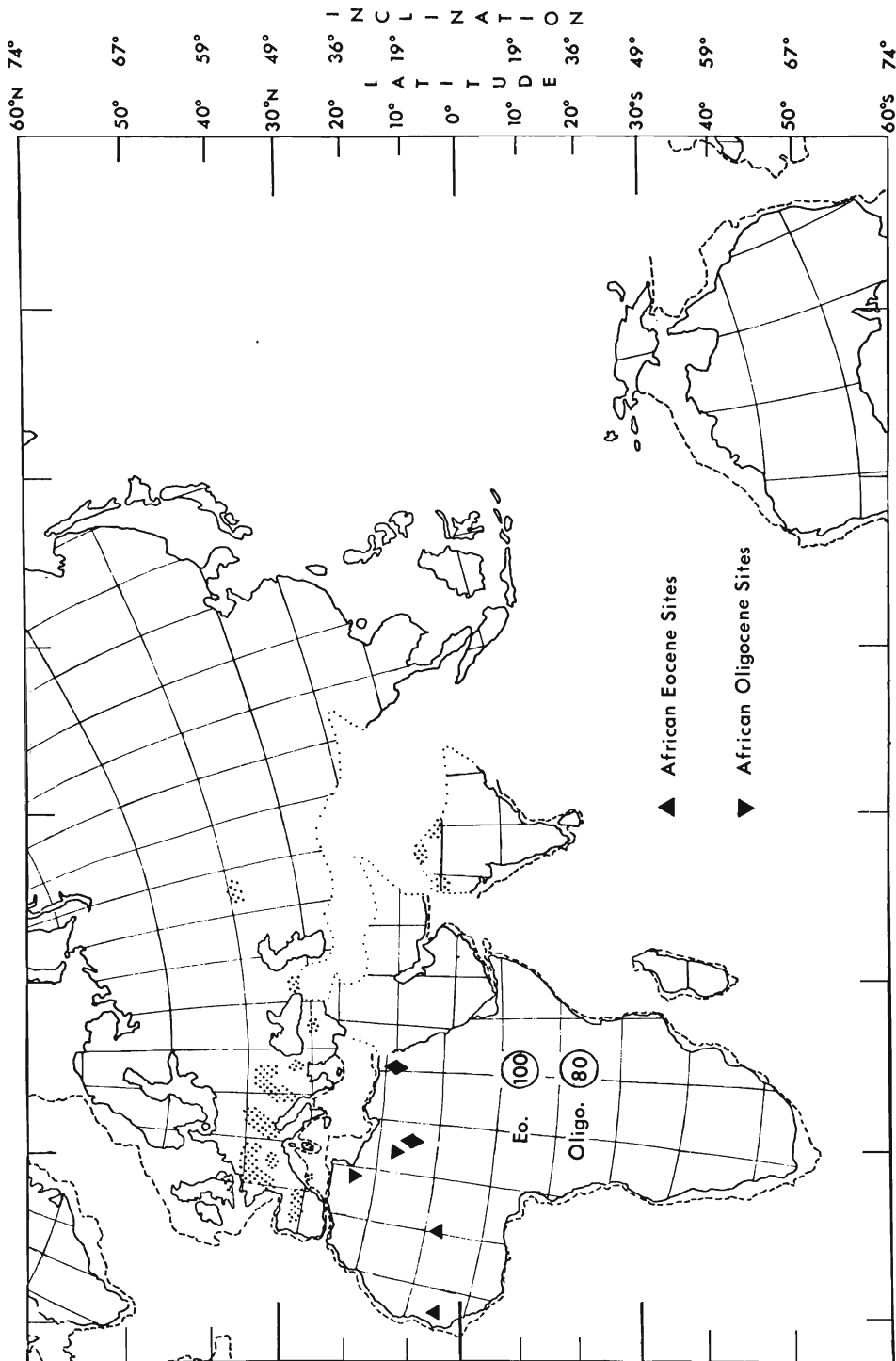
arrows are double ended; routes may operate in one direction for some species and in the opposite direction for other species.

The Eocene and Oligocene mammal faunas of Africa are so endemic and so limited in taxonomic range and geographic distribution that no useful comparisons can be made with other continents, hence a Venn diagram would be meaningless and no arrows are placed on the map (text-fig. 1).

Excluding a few specimens in the Triassic and one in the Jurassic, the earliest mammals in Africa occur in deposits of Mid-Eocene age. All are situated north of the equator and except in Egypt all sites have but one species. The only two orders of mammals present are both aquatic, Cetacea and Sirenia. Cetacean remains are known from Gebel Mokattam in Egypt and from Ameki in Nigeria; the genera are different and although a sea connection may have persisted from Cretaceous and Palaeocene times, the cetacean evidence does not aid the solution of the problem. Sirenian remains are known from Libya, Egypt, and Somalia; the Libyan and Egyptian faunas are generically distinct; those of Somalia are only rib fragments. With the exception of a single bone from the Lower Eocene of the London Basin, the earliest cetacea are those African species of Mid-Eocene age, and by Late Eocene times whales are known from eastern North America. Likewise the earliest Sirenia are of Mid-Eocene age, those of Africa together with *Prosastomus* from Jamaica, and by Late Eocene times they are found in eastern North America and Europe. Thus the evidence of the aquatic mammals suggests migrations across the Atlantic. The only Eocene aquatic mammals east of Suez are sirenian rib fragments from Somalia (Savage 1969) and Jordan (McGugan, pers. comm.). Sahni and Mishra (1972) report a cetacean, *Protocetus*, from the Middle Eocene of Kutch; the genus is well known from the Fayum of Egypt.

Eocene

Land mammals of Mid Eocene are unknown from Africa, and even in the Late Eocene our knowledge is limited to one order, Proboscidea. The Late Eocene levels of the Gebel Mokattam in Egypt appear to be little different from earlier levels with a similar fauna of sirenians and cetaceans. However, the deltaic and littoral facies of the Qasr es Sagha Formation in the Fayum, Egypt, yields proboscideans in addition to cetaceans and sirenians (Simons 1968), and a similar fauna is also known from Dor el Talha in Libya (Savage 1969). The two proboscidean genera described are *Moeritherium* and *Barytherium*. *Moeritherium* is the earliest and most primitive member of the order; it probably resembled the pigmy hippopotamus in build and size, and had a preference for semi-aquatic habitat. *Barytherium* was as large as an Indian elephant, had deinotherium-like molars and hippopotamus-like incisors. Simons (1968) reported an anthracothere and a hyaenodont, neither identifiable to generic level. Additionally a tooth fragment of *Moeritherium* is recorded from Senegal and another from Mali. The Proboscidea appear to share with the Sirenia ancestry from a condylarth stock that invaded Africa, probably during the Palaeocene. The wholly endemic nature of the Eocene land fauna (Table 1) suggests a long period of isolation of Africa after the initial chance dispersal of ancestral stock. Proboscideans not only appear to have originated in Africa, but remained isolated there until early Miocene times.



TEXT-FIG. 1. Sites of Eocene and Oligocene land mammals in Africa and adjoining areas of Tethys, with percentage of endemic African genera.

TABLE 1. Distribution of African land mammal taxa

Age	Orders		Families		Genera		Genera endemic to Africa
	Total	African	Total	African	Total	African	%
U. Eocene	1	1	2	2	2	2	100
L. Oligocene	8	3	15	10	31	25	80
L. Miocene	11	2	31	9	70	52	74
U. Miocene	9	1	23	5	38	21	55
Pliocene	9	0	21	1	41	20	50
Pleistocene	10	8	38	7	123	85	69
Recent	9	1	42	12	212	167	78

Oligocene

African sites containing mammal faunas of Oligocene age are no more numerous than those of the Eocene, and the two richest localities are Gebel Qatrani Formation, Fayum, and the upper marls of Dor el Talha, Libya. Other minor localities are found at Gebel bon Gobrine, Tunisia, and Zella in central Libya. It is unfortunate that only in the North have deposits containing Eocene and Early Oligocene land mammals been found. Presumably the vast land mass of the African continent supported at least as varied a fauna as is found at the Fayum and Dor el Talha, if not more rich, but there is no evidence at all to show what evolutionary processes were going on in the hinterland. A sirenian at Bedeil in Somaliland might indicate that the lower part of the Aden Gulf was beginning to open.

In all thirty-one genera are recorded, of which twenty-five are exclusively African; the evidence points to a radiation of endemic stocks and immigration of new stocks from Eurasia, without any African stocks emigrating. The following is a summary of the taxa:

- Group I Exclusively African at ordinal, familial, and generic levels:
- Proboscidea *Moeritherium, Barytherium, Palaeomastodon, Phiomia*
 - Embrithopoda *Arsinoitherium*
 - Hyracoidea *Pachyhyrax, Saghatherium, Geniohyus, Bunohyrax, Megalohyrax, Titanohyrax*
- Group II Exclusively African at familial and generic levels, but orders known from earlier horizons outside Africa:
- Primates *Parapithecus, Apidium, Propithecus, Aegyptopithecus, Aeolopithecus, Oligopithecus*
 - Rodentia *Metaphiomys, Phiomys, Paraphiomys, Gaudeamus, Phiocricetomys*
 - Insectivora *Metabodotes, Ptolemaia*
- Group III Exclusively African only at specific level; one genus among the creodonts (*Metasinopa*) is also exclusively African:
- Creodonta *Metasinopa, Apterodon, Pterodon, Hyaenodon*
 - Artiodactyla *Mixtotherium, Rhagatherium, Brachyodus.*

Group I comprises taxa evolved from endemic Eocene ancestors. Those in Group II comprise taxa that evolved in Africa from ancestors that crossed from Eurasia sometime before the Early Oligocene, probably during the Eocene. Group III comprises stocks that made the crossing only a short time before the period in which they are found. Contemporary faunas of Europe and Asia are very different from those of the Fayum; the former are characterized by anthracotheres, entelodonts, titanotheres, and palaeotheres. The carnivorous creodonts have widespread distributions; *Hyaenodon* is known from Early Oligocene deposits of western Europe, China, and North America as well as from North Africa. *Pterodon* is present in Late Eocene beds of Mongolia and North America. *Apterodon* is found outside Africa in Early and Mid-Oligocene strata of western Europe. Only three ungulates are common to Africa and Europe in Early Oligocene; *Mixtotherium* and *Rhagatherium* are rare in Mid Eocene to Early Oligocene sites of France. The third genus *Brachyodus* also occurs in France, and in Late Oligocene extended its range into Pakistan.

Three ecological groups of mammals can now be recognized in the Oligocene: entirely aquatic mammals such as the Cetacea and Sirenia; the water-side mammals such as the early proboscideans and the anthracotheres, and the first real spread of true land mammals, which were presumably washed as carcasses into the deltaic and near-shore localities from which they are now recovered.

During Early Oligocene times the African mammalian fauna is still largely endemic, 80% at generic level. The fact that the traffic was all one way into Africa, argues strongly against any land bridge. The creodonts are so widespread that little can safely be deduced from them. With only three herbivorous genera reaching Africa, chance dispersal seems a likely explanation; two of them are anthracotheres and the family is usually thought to have been water-frequenting. The African Oligocene families of rodents, primates, and insectivores could have evolved there from chance dispersal in earlier times; the affinities of the African and Eurasian faunas are too weak to suggest any likely route across Tethys.

NEOGENE

Although the Palaeogene faunas of Africa appear to be fairly simple and easily understood, this is an over-simplification of the facts. With the Neogene, the complexity of the faunal interpretations become more and more obvious. Even in the Eocene the later pattern is beginning to emerge of COMMUNICATION—ISOLATION—EVOLUTION—COMMUNICATION, etc. This pattern is to recur time and time again throughout the Tertiary and locally in the Quaternary until the present day, with each period of time producing more and more complex intermingling of faunas from adjacent continents, and complementary complications among the new faunas of the adjacent countries. Cooke (1968) covers many of these points and produces maps, tables, and charts which amply demonstrate these complexities. Since Cooke's paper was prepared, much new work has proceeded on African faunas covering all ages, enabling some new ideas and interpretations on the origins and affinities of the fauna.

Even during times when faunal movements were possible to or from Africa and

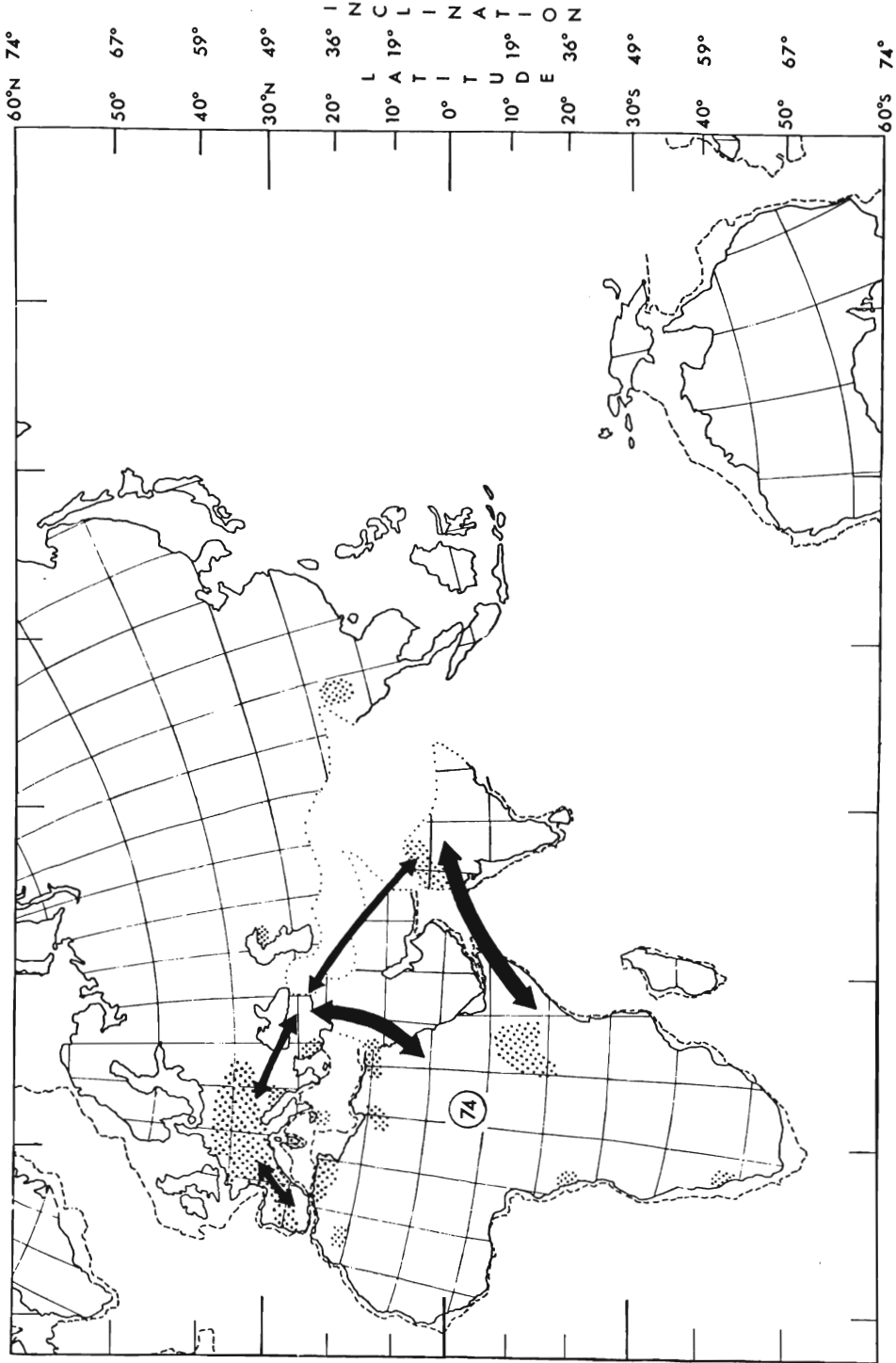
its adjacent continents, the route or routes were sometimes of a very temporary nature such as island chains or narrow corridors across which only certain types of land mammal could travel. At other times routes were not only wider and more complete, but various routes were open at any one time, so that a variety of exchanges with several areas may have been possible. After a period of evolution and diversification during isolation not necessarily all elements of a fauna will travel along any newly opened corridor; it may be that only a few genera in a family will migrate, so that with each interchange the similarities between faunas of one area and another will be weakened.

It is probable that there was little sedimentation inland during the Palaeogene and until the tectonic activity began on a major scale during the Miocene, conditions were rarely suitable for the preservation of land vertebrates. There is a gap of several million years in our record of African mammal faunas between those of the Early Oligocene of North Africa and those of the 'Lower Miocene' deposits which are more widespread on the continent, and are no longer restricted to off-shore and deltaic areas. Rifting in the Red Sea area causing Arabia to part from Africa appears to date from the Miocene thus restricting faunal interchange between the two areas, although the barrier at this stage in time may have been confined to a series of water-filled depressions along the line of the faulting. In East Africa Miocene faulting is evident in the Kavirondo area of western Kenya, accompanied by volcanic activity (Bishop 1967). This has an important bearing on both the preservation of the fauna by the alkaline sediments, and also the production of biotite-rich pyroclastic sediments which can be used in radiometric dating. North African Miocene deposits are formed from deltaic and fluvial sediments similar to those of the Oligocene. Sites of similar age in the Congo and South West Africa are also fluvial and dated by comparison of faunal assemblages. Localities such as Gebel Zelten in Libya; Moghara, Wadi Faregh, and Siwa (Hamilton, in press) in Egypt indicate that the southern shore of Tethys has moved north since the Oligocene, being not far from its present-day position in the east, but some 200 miles south of the Mediterranean shore in the Sirte basin of Libya.

Early Miocene

The Early Miocene faunas are the most prolific of the Tertiary faunas in terms of number of specimens, species, and sites (see text-fig. 2). Table 1 records 70 genera of which 52 are exclusively African during the Early Miocene; the endemism is still strong, 74% at generic level, but markedly less so than in the Oligocene.

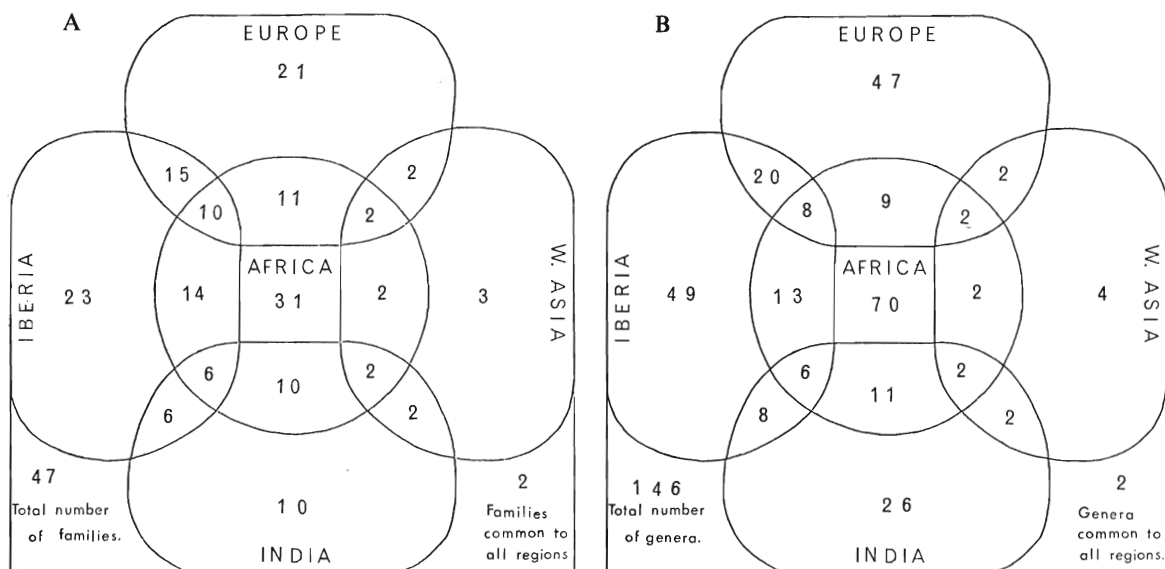
The picture at ordinal level shows considerable changes from that of the Oligocene (Table 1). Embrithopoda have become extinct and Lagomorpha, Carnivora, Tubulidentata, and Perissodactyla have been added. Out of 11 orders only Hyracoidea and Tubulidentata are exclusively African at this period. The family changes are striking; the number has doubled since the Oligocene, but the number of exclusively African families remains about the same. The important changes in the families are the appearance of 23 immigrant families, including insectivores, creodonts, rhinoceroses, anthracotheres, pigs, and bovids. All these families have an earlier history in Europe and Asia; three previously endemic proboscidean families emigrate



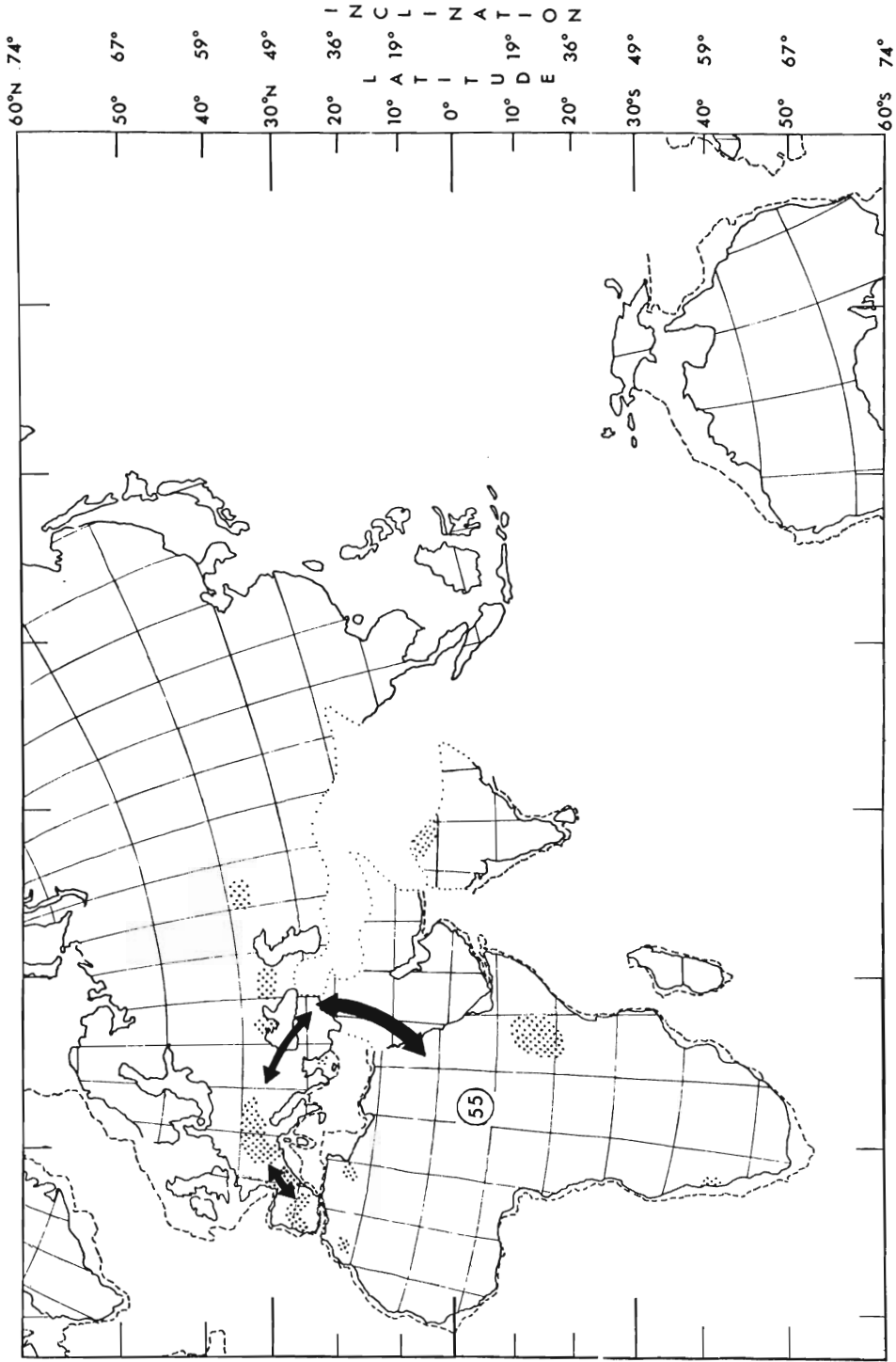
TEXT-FIG. 2. Sites of Early Miocene land mammals in Africa and adjoining areas of Tethys, with percentage of endemic African genera. Arrowed bars indicate affinity at generic level of 50% or more.

across Tethys; each is represented by one genus (*Gomphotherium*, *Zygodon*, and *Deinotherium*). In the case of the immigrant families, while genera are common to Europe, Asia, and Africa, no species are found to cross the Tethys. In contrast the emigrant genera each has a widely distributed species. *Gomphotherium angustidens* is recorded from East and North Africa, Spain, France, Germany, eastern Europe, Pakistan, and even Japan. *Zygodon turicensis* occurs in Algeria and Spain. *Deinotherium hobleyi* from East and North Africa is very similar and almost identical to *D. cuvieri* from France and Spain, to *D. hungaricum* from eastern Europe, and to *D. pentapotamiae* from Pakistan.

The two best-known Early Miocene faunas approximating to Africa are those of the Iberian peninsula and the Bugti Hills in Pakistan. The Iberian fauna contains 49 genera of which 13 occur in Africa. The Bugti fauna (with Fatehjang) contains 26 genera of which 11 occur in Africa (Savage 1967). The Iberian and Bugti faunas share 8 genera in common (text-fig. 3). From western Asia only four genera are known, but two of these occur in Africa. A site in the Negev of Israel has yielded a few mammals, including *Gomphotherium* and *Deinotherium*. During the Early Miocene Israel was part of the African plate and so this does not constitute a Tethyan crossing. A site near Izmir in Turkey has yielded a *Gomphotherium angustidens* and *Deinotherium* sp.; another site at Ust Urt on the north-east shore of the Caspian has yielded a *Gomphotherium* sp. From Adi Ugru in Eritrea, Vialli (1966) has recorded *Deinotherium*, cf. *hobleyi*. These are the only sites which give any positive clues to the migration routes across Tethys in the Early Miocene. Out of 146 genera recorded from the Early Miocene, only *Gomphotherium* and *Deinotherium* are known from all five regions.



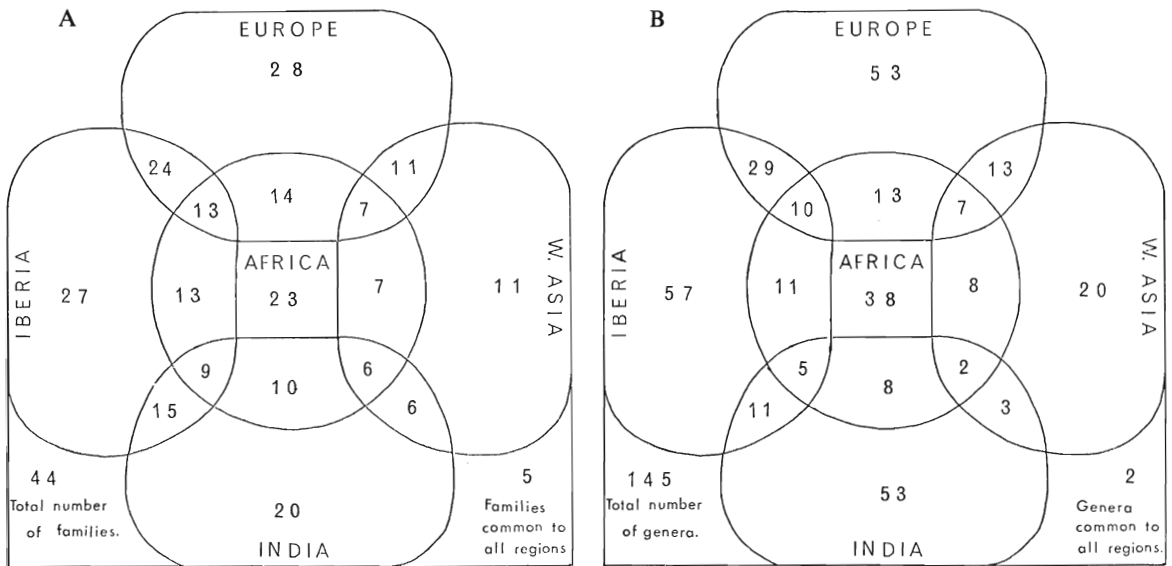
TEXT-FIG. 3. Frequency distribution of Lower Miocene land mammals. A, families; B, genera.



TEXT-FIG. 4. Sites of Middle and Late Miocene land mammals in Africa and adjoining areas of Tethys, with percentage of endemic African genera. Arrowed bars indicate affinity at generic level of 50% or more.

Middle and Late Miocene

The Middle and Late Miocene faunas of Africa (text-fig. 4) are not readily distinguishable and so are taken together. There are several localities in north-west Africa, but the majority of sites contain only a sparse fauna. Of the localities in East Africa, that of Fort Ternan is the most important; the beds have been dated at 14 million years and there are marked differences with the earlier Miocene faunas. Gomphotheres are still abundant, but deinotheres are absent here, though they persist in other areas. Again anthracotheres are absent from Fort Ternan, though present in North Africa and India. Ruminants are prolific, with bovids and girafids showing affinities with India in particular, and Iberia to a lesser extent. Compared with the earlier Miocene, there is little change at ordinal level; Lagomorpha and Tubulidentata are lacking from the record, but this is probably due to gaps in collecting rather than actual absence. No new orders appear and only the Hyracoidea remain exclusively African. At family level (text-fig. 5), only 5 out of the 23 families present are exclusively African; Cercopithecidae, Oreopithecidae, and Hippopotamidae are new families making a first appearance and probably evolved from endemic African ancestors. Phiomysidae and Procaviidae continue from the Early Miocene as exclusively African. Two previously African families, Pedetidae and Pongidae, now have representatives in Europe and Asia. Cricetidae, Sciuridae, and Gliridae are known in Europe in the Early Miocene and now appear in Africa for the first time. Hyaenidae and Ctenodactylidae are first found in the Middle and Upper Miocene of Africa and Asia, and may have originated in Africa from endemic stocks. Thus the record shows probably 5 families evolving in Africa, 3 immigrating and 4 emigrating, including 2 of the newly evolved families.



TEXT-FIG. 5. Frequency distribution of Upper Miocene land mammals. A, families; B, genera.

Only 38 genera are known compared with 70 from the Early Miocene, and the endemics are reduced to 55%. When we compare the African faunas with those of the Iberian and Indian peninsulas we see a similar degree of affinity. Vindobonian faunas are well represented in Spain and in the Chinji beds of the Siwalik Hills in Pakistan and India. In Spain 57 genera are recorded, of which 11 occur in Africa; in India 53 genera are recorded of which 8 occur in Africa. Iberia and India show 11 genera in common, of which 5 also occur in Africa (text-fig. 5).

But it is with western Asia that the strongest links are to be found, mainly founded on sites in Kazakhstan; out of 20 genera recorded almost half are known in Africa. The data for African affinities suggests that the closest links were with western Asia, while by comparison those with Iberia and India were relatively weak. The total number of genera recorded, 145, is almost identical to that for the Early Miocene; again only two genera are common to all five regions, namely *Gomphotherium* and *Protragocerus*.

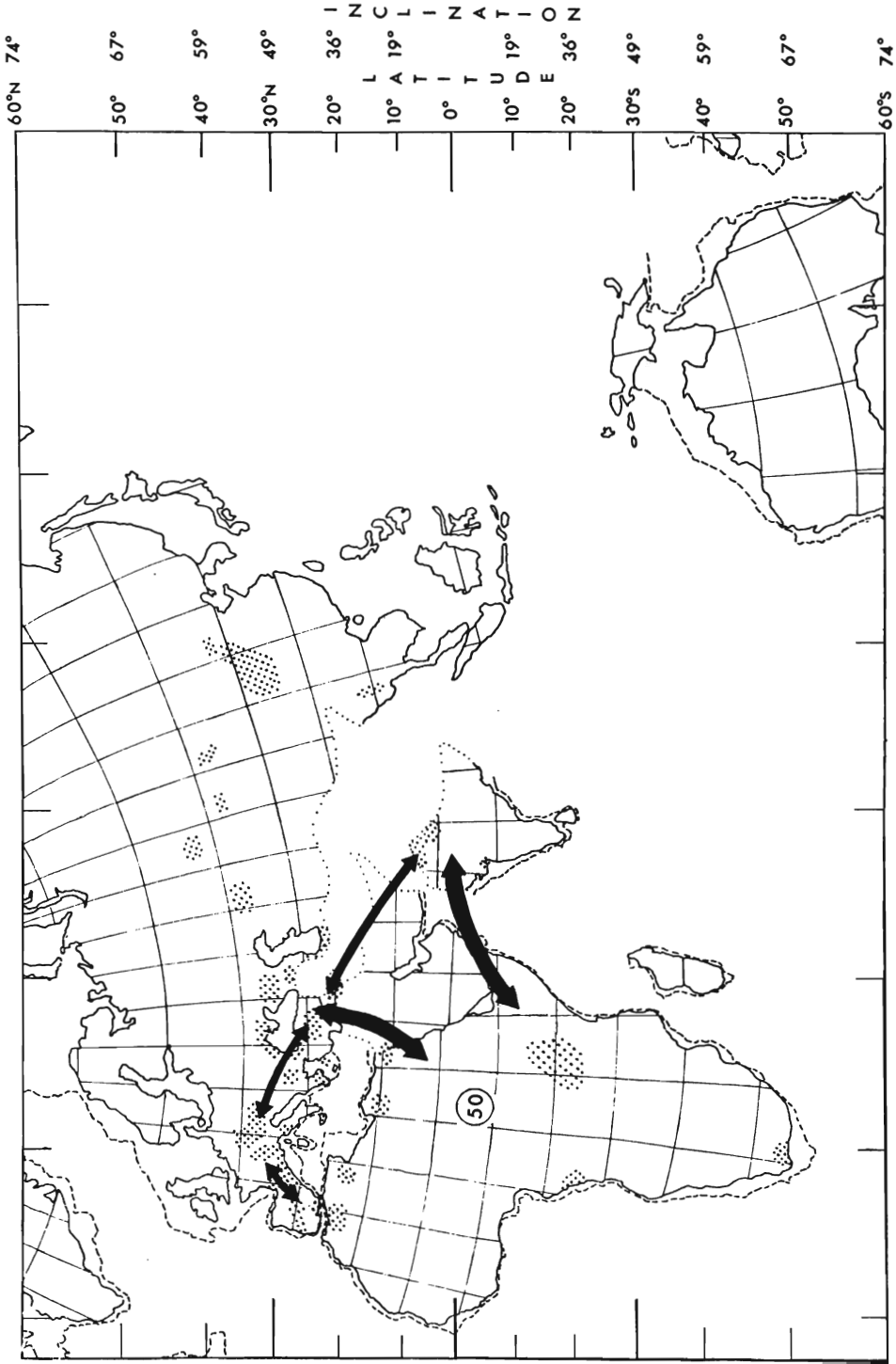
Pliocene

It is in the period of the Pliocene and Pleistocene (text-fig. 6) that most new discoveries have been made in recent years, in Kenya and Tanzania in East Africa and in Tunisia in the north-west. The Pliocene of Africa has not been recognized until comparatively recently, partly due to some localities having been thought of as Miocene, and others as Pleistocene. With new excavations and radiometric dating it is now clear that many localities are truly Pliocene.

The faunal picture in the Late Miocene was of mammals having much in common with those of the earlier faunas, but enriched by and enriching the faunas of other continents; at the end of the Miocene the mammalian faunas take on a rather different aspect, and one in which for the first time can be seen the direct ancestors of the modern African fauna. The differences between the faunas of North and East Africa become wider, although there is still similarity between the two areas. The Sahara plays an increasing role as a faunal barrier. The elevation of the Suez Isthmus and other routes across Tethys gives the North African mammals a more European aspect in the Pleistocene. With the formation of the Red Sea rift, routes from Africa into Europe are pushed further north, although there was probably still a route across southern Arabia into India, at least until the beginning of the Pleistocene.

At ordinal level there is almost no change from the Miocene, save that the Tubulidentata are no longer exclusively African. The number of African families (text-fig. 7) is about the same as in Late Miocene times, but only the Macroscelididae are exclusively African. The gomphotheres continue to diversify, along with suids, bovids, and primates. The hippopotamids evolve to replace the anthracotheres in East Africa, the equids in form of *Hipparion* enter Africa from Asia and are first recorded in North African sites. The last of the hyaenodontid creodonts is seen in East Africa, with a contemporary survivor in India. The generic record bears striking resemblance to that of the Miocene in terms of total numbers and in being about 50% endemic. Iberia, Europe, western Asia, and India all have fuller generic representation than Africa, and on balance the relationships between Africa and the other regions are about the same, with stronger links apparent across Eurasia than across Tethys. Out of a total of over 200 genera, only five are common to all

AFRICAN MAMMAL FAUNAS

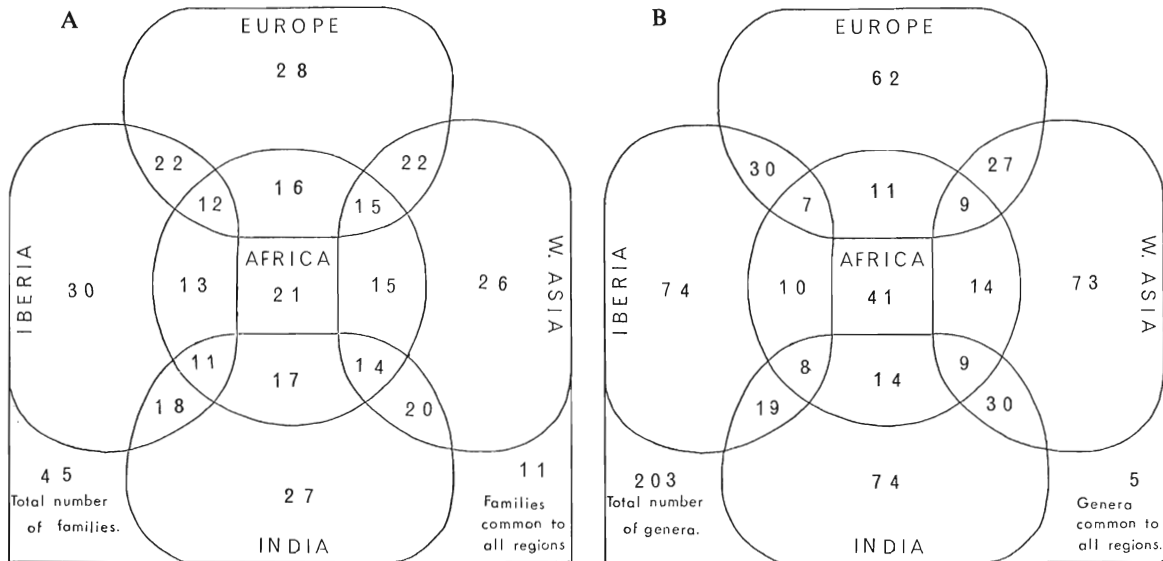


TEXT-FIG. 6. Sites of Pliocene land mammals in Africa and adjoining areas of Tethys, with percentage of endemic African genera. Arrows bars indicate affinity at generic level of 20% or more.

five regions; these are *Gomphotherium*, *Deinotherium*, *Ictitherium*, *Hipparion*, and *Hippopotamus* (text-fig. 7).

From Late Pliocene times onward the African fauna becomes more and more isolated into separate groups in various parts of the continent, and small areas can give some clue to regional changes in topography and climate. The evidence for faunal exchange with Europe in the Pleistocene gets more and more slender, until the African continent becomes completely isolated again at the end of the Pleistocene. The last mammals of the tropical African fauna to enter Europe may have been the Hippopotamidae, the Elephantidae, and some large carnivores which managed to survive in even the British Isles until the last glaciation. The pigmy faunas of the Mediterranean islands have been thought of as originating from mainland Europe, becoming gradually smaller and smaller in size as the habitat was impoverished. It is just possible that some of this pigmy fauna, such as *Hippopotamus minutus* from Malta, may have evolved only slightly from one of the small forms known in Africa during the Pleistocene, reaching the islands from the south; however, no pigmy elephants are known in the African fauna, so their origin is unknown.

The number of Pleistocene and Recent mammal families is well up on the Pliocene, as also is the proportion of endemics (Table 1). As might be expected the generic records are also vastly greater than for any previous time interval; that for the Pleistocene is treble the Pliocene record, and the Recent total is almost double that of the Pleistocene. Endemism increases appreciably, so that today it is higher than at any time since the Oligocene. This endemism is remarkable in view of the close proximity of the African plate to Eurasia, especially at the north-west and north-east extremities, and the high degree of endemism is best seen as a reflection of the effectiveness of the Sahara as a barrier to animal migration.



TEXT-FIG. 7. Frequency distribution of Pliocene land mammals. A, families; B, genera.

CONCLUSIONS

In spite of severe gaps in the fossil record, over-all trends in changing faunas can be deduced. The Eocene faunas are wholly endemic, and there is decreasing endemism through Oligocene and Miocene times to reach a minimum in the Pliocene. The most frequented routes for emigration and immigration seem usually to have been via western Asia and India. During Pleistocene and Recent times endemism rose rapidly, almost reaching the level of the Oligocene, and the reasons for this are to be found not in the geographic isolation of Africa, but rather in the climatic barrier of the Sahara.

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