Plate Tectonics, Seaways and Climate in the Historical Biogeography of Mammals

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The marsupial and placental mammals originated at a time when the pattern of geographical barriers (oceans, shallow seas and mountains) was very different from that of today, and climates were warmer. The sequence of changes in these barriers, and their effects on the dispersal of the mammal families and on the faunas of mammals in the different continents, are reviewed. The mammal fauna of South America changed greatly in the Pliocene/Pleistocene, when the newly-complete Panama Isthmus allowed the North American fauna to enter the continent and replace most of the former South American mammal families. Marsupial, but not placental, mammals reached Australia via Antarctica before Australia became isolated, while rats and bats are the only placentals that dispersed naturally from Asia to Australia in the late Cenozoic. Little is known of the early history of the mammal fauna of India. A few mammal families reached Madagascar from Africa in the early Cenozoic over a chain of islands. Africa was isolated for much of the early Cenozoic, though some groups did succeed in entering from Europe. Before the climate cooled in the mid-Cenozoic, the mammal faunas of the Northern Hemisphere were much richer than those of today.

Key words: biogeography - mammal dispersal - faunal change

This paper is the result of an invitation to provide an outline of the early history and historical biogeography of mammals that parasitologists might find useful. A more comprehensive account of historical biogeography, geographical change and climatic change during the Mesozoic and Cenozoic can be found in Cox and Moore (2000) and Smith et al. (1994).

DEFINITIONS, WARNINGS AND EXPLANATIONS

The implications of the word "mammal" – Mammals first evolved in the Late Triassic, about 210 mya, and about a dozen different groups of Mesozoic mammal are known to have existed over the following 130 my Their osteological characters are similar to those that we find in the ancestors of the later marsupial and placental mammals, so it is likely that these Mesozoic mammals, too, were hairy and warm-blooded, like their living descendants the monotremes of Australia. They were, almost certainly, also like the latter in being egg-laying, rather than either marsupial or placental in their manner of reproduction. Most were about the size of a mouse, and were insectivorous (i.e. eating invertebrates), though one group became omnivorous and as large as a wood-chuck. The Mesozoic mammals are, however, worth noting because they provided the first opportunity for parasites to become adapted to the mammalian type of physiology.

Mesozoic marsupials and placentals can be distinguished from one another, and from the other Mesozoic mammals, primarily by characteristics of their dentition. Fossil evidence suggests that the two modern groups diverged from one another in the Early Cretaceous, 110-120 mya, but the earliest forms that can be positively identified as belonging to one group or the other are from the Late Cretaceous (for geological time-scale, see Fig. 1) . The placental method of reproduction probably evolved from the marsupial method, rather than directly from the egg-laying method. This implies that the earliest forms that are identified as placental (on the basis of their tooth structure) were probably still marsupial in their method of reproduction.

Times of first appearance of groups - In trying to show the pattern of appearance of the different mammalian orders and families, one can only give the geological level, and corresponding date, of the earliest known specimen; almost certainly, the taxon will in reality have evolved at an earlier date. It is common to find, in non-palaeontological literature, much earlier dates of appearance hypothesized where these better suit the needs of the theory being propounded. But one needs to be prudent in this. In particular, few different types of mammal are known before the end of the Cretaceous, and it is possible that some others may have evolved before that date. But the pattern of first-appear-

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Era	Period	Epoch	Approximate date of commencement in millions of years ago
Cenozoic	Quaternary	Pleistocene	2.4
	Tertiary	Pliocene	5
		Miocene	23
		Oligocene	35
		Eocene	56
		Paleocene	65
Mesozoic	Cretaceous		146
	Jurassic		205
	Triassic		250

The geological time-scale for the Cenozoic and Mesozoic

ances (see Table, derived from data in Benton 1993) does suggest that the radiation of the mammals took place very rapidly after the end of the Cretaceous. This was the time at which the sudden extinction of the dinosaurs removed the restriction on mammalian ecological diversity that predation by the dinosaurs had previously imposed. Until then, the mammals had been limited to being nocturnal, small, insectivorous or frugivorous, probably mainly arboreal, animals whose way of life made them unattractive, inaccessible or invisible as a food-source for dinosaurs, who were much larger and diurnal. A few Cretaceous placentals have been placed in Cenozoic groups that are otherwise composed of large herbivores or carnivores. This is not because the Cretaceous forms were necessarily identical with them in size or diet, but only because they show characteristics which suggest that they may have been ancestral to those Cenozoic groups.

Times of continental fragmentation or collision - The start of the break-up of a continental mass is announced by the appearance of volcanic activity along the line of its future separation into two daughter continents. New volcanic rock is continually produced along this line, so that the two new continents are continually and gradually moved apart. The presence of radio-active minerals in these rocks makes it easy to date them. The band of rocks closest to the line of volcanic activity, which have just appeared from the depths of the earth, contains the youngest rocks, while the band that lies closest to the edge of the continent is the oldest. The age of these oldest rocks therefore indicates the age of separation of the two continents.

The gap between the two separating continents becomes filled by ocean waters, and the rocks become covered by ocean sediments that contain the skeletons of minute marine planktonic organisms. Sometimes the line that separates the two continents is irregular, so that in some areas the two

TABLE

Total numbers of terrestrial mammal families at different periods of time in the Late Cretaceous and early Cenozoic

		Marsupials	Placentals
Late Cretaceous	90-65 my	3	7
Early Paleocene	65-59 my	3	17
Late Paleocene	59-53 my	5	66
Early Eocene	53-45 my	6	91

continents are sliding past one another, instead of simply moving apart – for example, the northern edge of South America moved westwards along the southern edge of West Africa for some time after its eastern edge had separated from Africa. The date of final ending of any land connection between the two continents is then given by the date at which the two marine faunas become united, as shown by the fossil marine planktonic skeletons in the sea sediments.

The date of coalescence of two continents is more difficult to establish, but is indicated by the nature of the rocks laid down between them. As the two continents approach one another, the ocean between them first becomes a shallower sea, and then dries up altogether, and these changes can be detected from the nature of the fossil marine organisms that are laid down in the rocks. But biological contacts between the two areas may begin earlier than the time of union of the continents, because islands may form in the intervening seaway and provide a pathway for dispersal.

Types of faunal link - Biogeographers distinguish three different types of link between faunas or floras. The first is a *corridor*, which contains a wide variety of habitats, so that most types of organism are able to pass through it. The wide expanse of central Asia is a good example of this, forming a corridor linking the faunas of western Europe with those of China. The second is a *filter route*, which contains only a limited variety of habitats, so that only those organisms that can exist in those habitats will be able to disperse through it. The exclusively tropical lowlands of the Panama Isthmus provide a good example of such a link. Finally, a *sweepstakes route* separates areas that are so difficult of access that very few organisms ever succeed in reaching them. The ocean barriers that surround the scattered islands of the Pacific are good examples of this type of link.

THE PHYSICAL BACKGROUND

The outlines and positions of the continents and coastlines from the Mid-Jurassic to the Late Eocene are shown in Fig. 2. The true boundaries of the continents are marked by the edges of the continental shelves, which are separated by the deep oceans. But parts of the continents are often covered by shallow 'epicontinental' seas, which are just as effective as the oceans in forming a barrier to the dispersal of animals and plants. The most important of these were the Obik Sea, which lay just to the west of the Ural Mountains and separated Asia from Europe from the Late Jurassic (160

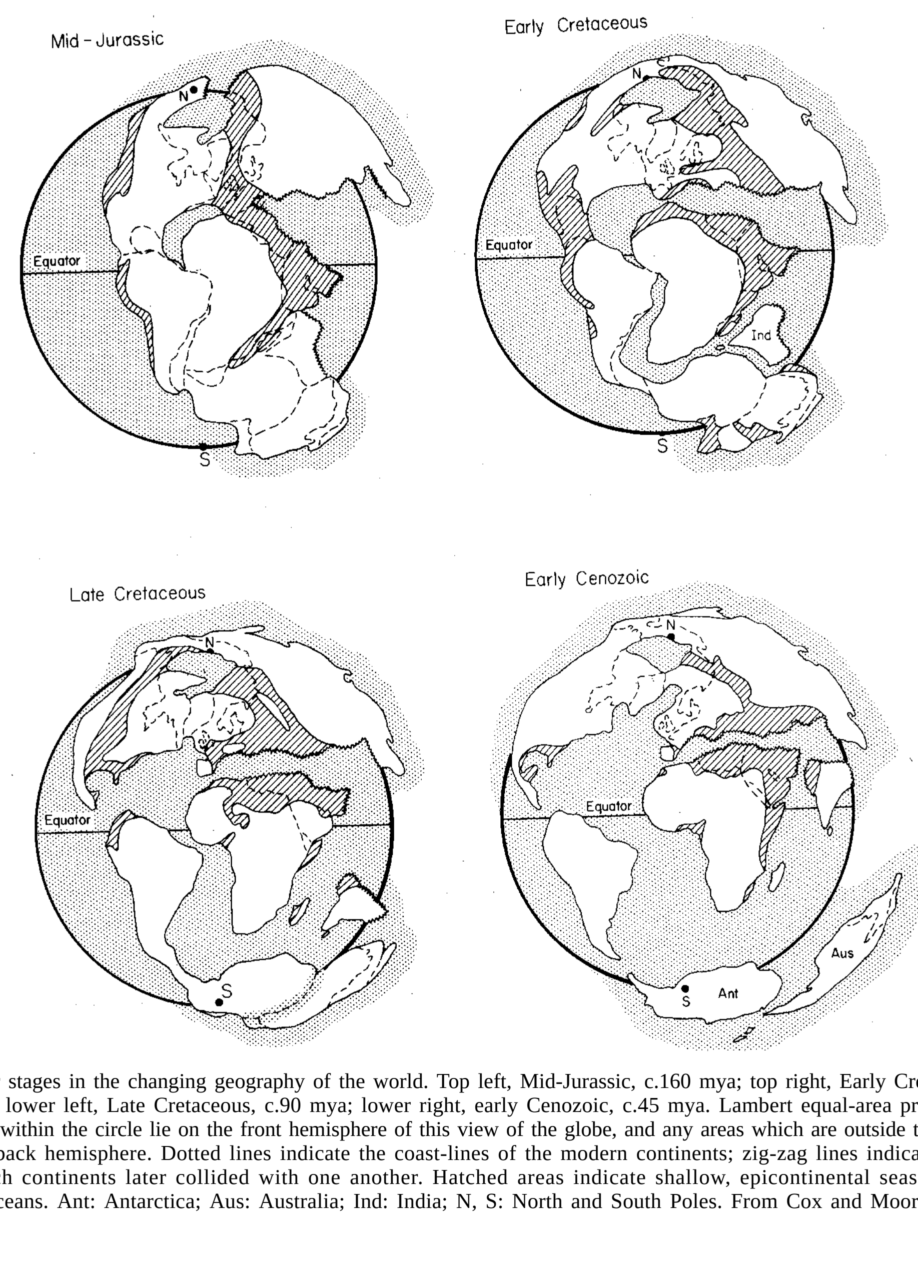

Fig. 2: four stages in the changing geography of the world. Top left, Mid-Jurassic, c.160 mya; top right, Early Cretaceous, c.140 mya; lower left, Late Cretaceous, c.90 mya; lower right, early Cenozoic, c.45 mya. Lambert equal-area projection: areas lying within the circle lie on the front hemisphere of this view of the globe, and any areas which are outside the circle lie on the back hemisphere. Dotted lines indicate the coast-lines of the modern continents; zig-zag lines indicate edges along which continents later collided with one another. Hatched areas indicate shallow, epicontinental seas; stipple indicates oceans. Ant: Antarctica; Aus: Australia; Ind: India; N, S: North and South Poles. From Cox and Moore (1985)

mya) to the Late Cretaceous (65 mya), and the Mid-Continental Seaway, running between the Arctic Ocean and the Gulf of Mexico, which cut North America into two for the whole of the Late Cretaceous (from 105 to 65 mya). The Bering region between Siberia and Alaska is today a flooded plain, in which the depths are mostly only 30-45 m; it has alternated between dry land and seaway in the Late Cretaceous and through much of the Cenozoic, depending on current sea-levels. The combined effect of these seaways and links during the Late Cretaceous was to define two land-masses in the Northern Hemisphere: 'Asiamerica', made up of Asia and western North America, and 'Euramerica', made up of eastern North America, Greenland and Europe (Cox 1974). For much of the Late Cretaceous and early Cenozoic, Europe was merely an archipelago of islands.

It is important to realize that the climate of today is very unusual. The climate of the Mesozoic and early Cenozoic was much warmer than that of today, and was still significantly warmer until the Pliocene, about two million years ago (Fig. 3). This cooling eventually led to the present régime of an extensive covering of polar ice, which in turn caused a great steepening of the rate of temperature change between the equator and the poles. So, in the past, tropical or warm climates extended much further towards the poles. The polar ice-caps have also locked up a great deal of water, so that sea-levels today are comparatively low. Earlier in the Cenozoic, sea-levels were higher, and seas extended far into, or across, the continents, as we shall see. This not only subdivided the continental masses into smaller units of land, but also brought milder, moister and less seasonal climates into the inner regions of these continents.

THE HISTORICAL BIOGEOGRAPHY OF THE MAMMALS

Figure 4 gives an outline of the main events of mammalian dispersal in diagrammatic form. Arrows indicate the directions of dispersal of mammalian families or of continents. Dotted lines indicate the positions of the Bering, Mid-Continental, Labrador, Greenland and Obik Seas, with figures showing the times of opening of each, and arrows indicating whether the sea opened or closed at the time indicated (The 'alpha' symbol at the Bering Sea indicates that it opened and closed a number of times) The position of the Labrador Sea, west of Greenland, is shown as a dotted line, but no further information is given as it is irrelevant to mammalian dispersal. Figures in circles indicate the number of mammalian families present in the area in question, the adjoining figure indicating the relevant time in millions of years. No attempt has been made to give the total numbers of mammal families in the different continents at any period of time later than 55 mya.

The earliest mammals - The earliest, Triassic and Early Jurassic, mammals lived in a world in which there was a single supercontinental landmass, known as 'Pangaea'. Not surprisingly, these mammals spread to all the areas that later dispersed to form today's continents (This is still uncertain in the case of Antarctica and Australia, whose known fossil record is still very incomplete, but it is highly likely).

About 130 mya, in the Middle Jurassic, Pangaea divided into two smaller supercontinents: to the north, 'Laurasia', made up of North America, Europe and Asia, and to the south, 'Gondwana', made up of South America, Africa, India, Antarctica and Australia. The Mesozoic mammals that evolved

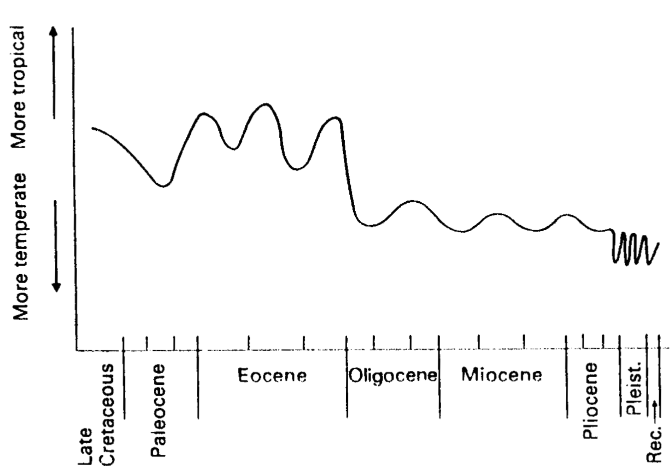

Fig. 3: changes in world temperature levels during the Late Cretaceous and Cenozoic, as suggested by floras from middle latitudes. After Wolfe (1978)

after this date are known only from Laurasia until nearly the end of the Cretaceous (see below).

Mammals in the Americas - The earliest marsupials and placentals are known from Late Cretaceous deposits (c.100 mya) in both the Asian and the western North American parts of Asiamerica (Fig. 4). Dry land still connected the two continents via the Bering region, but fossil floras show that the climate of this region had by then already begun to cool, and that the flowering plants had replaced the ferns, conifers, cycads and ginkgos as the dominant element in the floras. Broad-leaved, deciduous forest covered the region, as far south as c.55^{o}N latitude, and the flora of northern Alaska was one in which the plants died back or survived the winter as seeds (Graham 1999). Never theless, a variety of dinosaurs is known from this area – it is possible that they migrated seasonally, like caribou today. Later in the Cretaceous, c.80 mya, there was still only one family of marsupial (the didelphids, or opossums) in North America, but six families of placental (Fig. 4).

By the Late Paleocene, 55 mya, six families of marsupial and ten families of placental mammal are known from South America. Evidence from marine faunas shows that the Atlantic and Pacific oceans were interconnected in the Late Cretaceous and for much of the Cenozoic, so there was no continuous land connection between North and South America. Nevertheless, a number of families of North American dinosaur, as well as the didelphid marsupials, appear in South America at the end of the Cretaceous, while the diversity of placentals known in South America a little later (see below) implies that they are descended from between two and four lineages that had made the crossing at this same time, at the end of the Cretaceous or earliest Cenozoic. This suggests that the link between the two continents was a pattern of islands, through which dispersal was difficult but not impossible.

After the Late Paleocene, the marsupials underwent little further taxonomic diversification in South America; most of them were small, insectivorous, omnivorous or rodent-like, but one family were carnivores and included forms similar to wolves, sabre-toothed tigers and bears. The placentals diversified much more, into nearly 30 later Cenozoic families. including a variety of herbivorous ungulates, as well as anteaters, armadilloes and sloths – the latter including large terrestrial forms as well as the arboreal genera still extant there. All of these marsupials and placentals made up the oldest mammalian fauna of South America. They were joined, about 30 mya, in the earliest Oligocene, by the New World monkeys and caviomorph rodents that are now characteristic of South America. Since these are not known in the earlier, Paleocene or Eocene fossil faunas, these

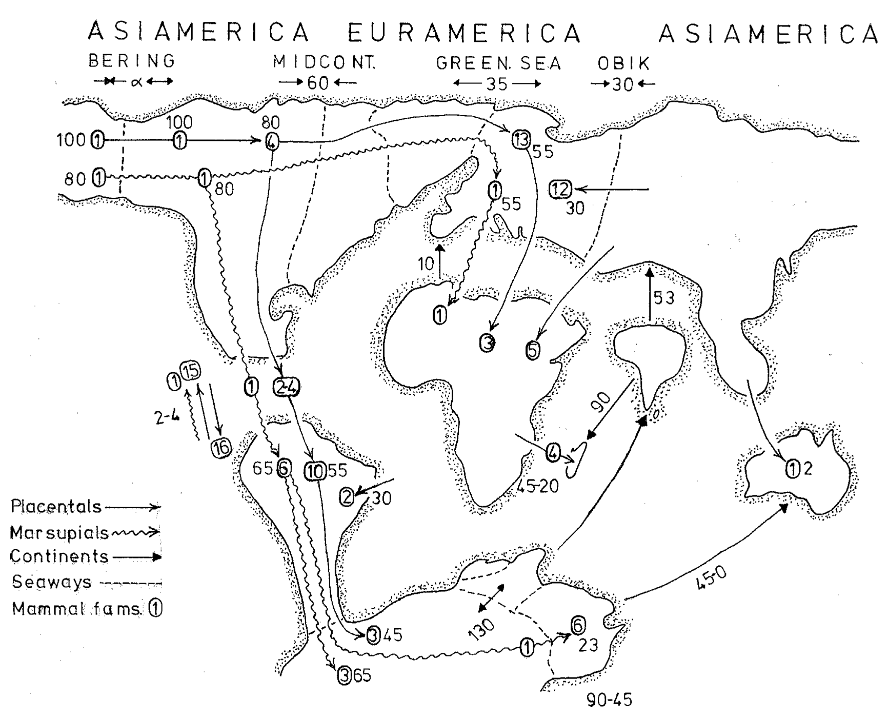

Fig. 4: diagram to illustrate the biogeography of mammals. See text for further details.

two groups must have dispersed to South America some time in the Oligocene, across an ocean gap. Though there has been much debate over where they came from, it is most likely that they came from Africa, where similar monkeys and rodents are known to have existed (George & Lavocat 1993).

The final stage in the development of today's fauna of South American mammals came with the completion of the Isthmus of Panama, which had been developing southwards from North America as an enlarging chain of islands. This took place soon after the Pliocene uplift of the Andes, which doubled their height from 2,000 to 4,000 m and caused major ecological changes in South America. The new land-link led to a the exchange of a variety of mammals between North and South America, known as the "Great American Interchange" (Webb 1985). Though at first the exchange was balanced, 16 families of mammal moving in the two opposite directions, the final result of the competition between the two faunas was very unbalanced. Of the South American mammals, only the didelphids among the marsupials, and the armadillo and the porcupine from the placentals, have survived in North America. In contrast nearly all of the North American families survived in South America – the two interesting exceptions being the elephants and the horses, both of which became extinct in both North and South America (horses were re-introduced to the Americas by Europeans). The most successful of the North American immigrants were the sigmodontine (also known as cricetine) rodents, which diversified into 45 genera in South America.

The passage to Australia - Three families of marsupial are known from the latest Cretaceous rocks of the Antarctic Peninsula, and three families of South American placental are known from the Eocene of the same area (Fig. 4). All of these must have crossed to Antarctica before the Drake Passage between the two continents was broken about 40 mya (The periphery of Antarctica, at least, was still forested until well into the Cenozoic).

Australia first became separate from Antarctica about 90 mya, but the two continents remained fairly close together until they started to separate more rapidly about 45 mya. As in the case of the crossing from North America to South America, only a few groups arrived in Australia, suggesting that, here again, the crossing from one continent to the other took place at a time when the two were separated by a pattern of islands. Unfortunately, we know nothing of the mammal fauna of Australia until the Early Miocene, c.23 mya, by which time six families of marsupial had diversified from what appears to have been only a single family that had crossed from Antarctica. No placental mammals are known from this early Australian mammal fauna. It is therefore more parsimonious to assume that placentals never entered that continent in the early Cenozoic, than to postulate that they did do so but later became extinct in the face of competition from marsupials – a failure that is not known in other instances of competition between the two groups.

By the time, a few million years ago, that the northwards movement of Australia had brought it close to South-East Asia, there were nine families of marsupial in Australia and New Guinea, but few of them succeeded in colonizing any of the islands of the East Indies. During times of low sea-levels, the islands on the South-East Asian continental shelf were united with the mainland, and were colonized by a variety of placentals from there. Rats and bats are the only placental mammals to have crossed all the East Indian islands to reach Australia without human aid. As a result of all this, there are few mammals, either marsupial or placental, in the oceanic islands between South-East Asia and Australia, and this area is best recognized as a transitional region, called 'Wallacea', between the separate Oriental and Australian faunal regions (Cox & Moore 2000).

The mammals of India and Madagascar - Little is known of the early history of the mammal fauna of India. The sub-continent separated from Antarctica about 130 mya, and was rafted northwards (Fig. 4). At first, Madagascar was still attached to India, but the two separated about 90 mya, leaving the former more or less in its present position of the coast of Africa. An island-chain link between Madagascar and Africa existed some time between the Middle Eocene and the Early Miocene, and allowed early types of primate (lemurs), Insectivora (tenrecs), rodents (cricetines) and Carnivora (viverrrids) into the island.

India collided with Asia about 53 mya, but faunal migrations between the two areas may have taken place a little earlier than this across a pattern of intervening islands. India may also have received some mammals from Africa, earlier in its passage northwards.

The mammals of Africa - Africa had been the first part of Gondwana to become separate, when it parted from South America about 100 mya. Though it moved only slowly northwards, it was at first separated from Europe by both shallow seas and also by the mid-latitude belt of aridity. Nevertheless, some placental mammals managed to enter Africa from Europe, perhaps across intervening islands. The record of early Cenozoic African mammals is poor, but early insectivorans, primates and carnivorans are known from African rocks about 55 myold (Fig. 4). A more complete African record begins about 30 mya, and includes two groups. One group consists of early elephants, plus hyraxes (conies), elephant-shrews, aardvarks and the Cape golden mole, while the other (which entered Africa a little later) includes hoofed animals, Carnivora, Insectivora, rodents and the earliest members of the anthropoid primate line that later evolved into apes and human beings.

The Late Cenozoic geographical and biogeographical relationships between Africa and Eurasia are quite complicated (Fig. 5). The first collision between Africa (Arabia) and Asia (Turkey) took place about 19 mya, in the middle of the Early Miocene, when Carnivora, pigs, bovids (cattle, antelope etc.) and cricetid rodents crossed into Africa, while elephants, African carnivores and primates made the reverse journey. The intervening seaway reopened a little later, but finally disappeared 12 mya, when horses appeared in Africa, and rhinoceros, hyaenas and sabre-toothed cats dispersed from Africa to Asia.

The influx of mammals from Asia to Africa about 30 mya took place at the same time as many Asian placentals also entered Europe; both dispersals were the result of lower sea-levels. At this time, the shallow seas between Asia and its neighbours disappeared and the climates of Europe and northern Africa started to become more dry, with the spread of evergreen woodlands, steppe and savanna in Europe (with African rhinoceroses and hippopotamuses). This increasing aridity also led to the appearance of the deserts that now separate the previously-similar tropical mammal faunas of Africa and India, so that such groups as elephants, rhinoceroses and porcupines are represented by different genera in the two areas. Finally, it was only about two million years ago that the enlarging Saharan Desert finally isolated the more southern part of Africa from Europe and North Africa, so that the fauna of North Africa lost most of its African characteristics.

Mammals of the Northern Hemisphere - After the Mid-Continental Seaway dried up, about 60 mya, the mammal faunas of the two halves of North America quickly became uniform, and most of them also crossed to Europe via Greenland (This included the opossum-like didelphid marsupials, which also succeeded in reaching North Africa, but later became extinct both there and in Europe). At that time, the climate of this region had been sufficiently warm for plants that are now found in the sub-tropics of North America and Europe to be able to disperse between the two areas by that route. After the opening of the Greenland Sea between Europe and Greenland, dispersal between Eurasia and North America was exclusively by way of the Bering region. The disappearance of the Obik Sea that had separated Europe from Asia, about 30 mya, and In

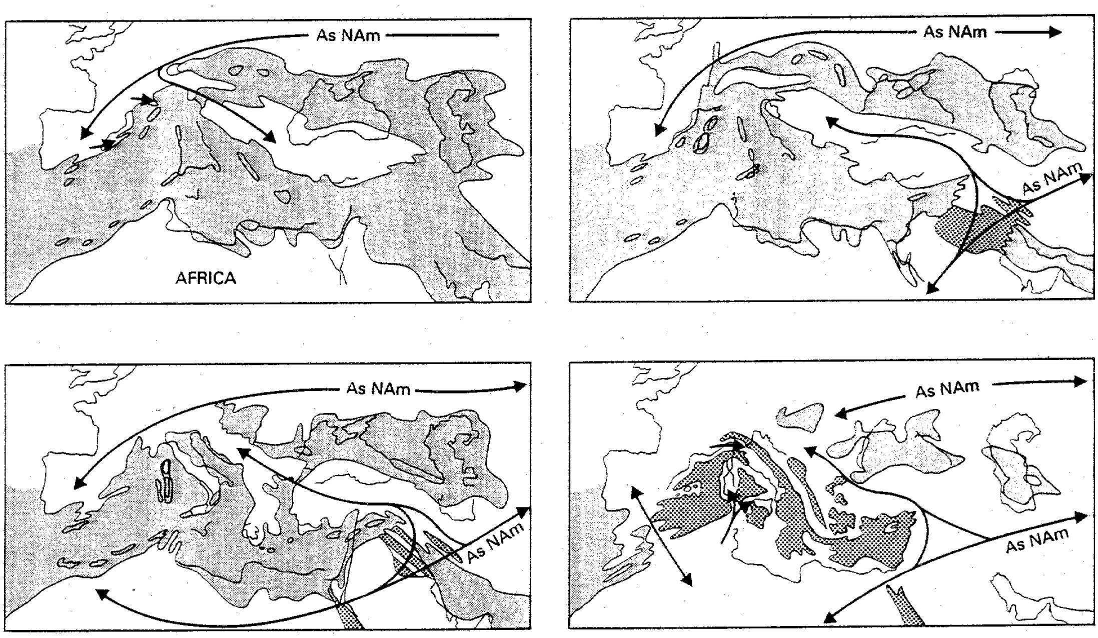

Fig. 4: reconstructions of the Mediterranean area: top left, at the Late Oligocene/Early Miocene boundary; top right, in the middle of the Late Miocene; lower left, the beginning of the Late Miocene; lower right, near the end of the Late Miocene. Light tint indicates sea, dark tint indicates evaporitic deposits laid down as the sea dried up. Arrows show directions of mammal dispersals. As: Asia; NAm: North American. After Steininger et al. (1985)

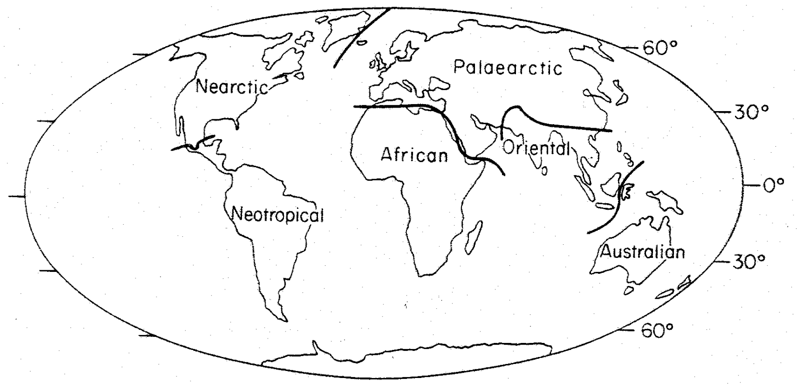

Fig. 6: zoogeographic regions of the world today, based on the distribution of mammals. After Cox and Moore (1993)

the Early Oligocene, allowed Asian mammals into both Europe and Africa (Fig. 4). At this same time, there was a dramatic cooling in the climate of the earth. For example, within one or two million years the mean annual temperature of the Pacific northwest of North America dropped from about 22ºC to about 12ºC, while the mean annual temperature range increased from about 7ºC to nearly 24ºC, so that the climate became much more seasonal, and the annual temperature almost halved. The Bering region therefore became much less congenial as a dispersal route for mammals. When the climate improved again, a little later in the Oligocene, a number of Asian mammals crossed to North America. The final climatic deterioration of the Bering region began in the Miocene and, from then on, most of the mammals that dispersed between the two continents were large, cold-tolerant forms. After the final climatic deterioration in the Pleistocene, only hardy forms such as bison, mountain sheep, mountain goat and musk ox were able to cross. The final break between the two continents, by the incursion of the Bering Sea, took place 1,3000-1,4000 years ago.

The climatic deterioration of the Ice Ages led to the extreme impoverishment of the mammal faunas of the Northern Hemisphere, the more warmth-loving groups becoming restricted to the areas to the south. The chain of geographic barriers that lie immediately to the south of North America and Eurasia (the Panama Isthmus, the deserts of the Sahara and the Middle East, and the Himalayan mountain chain) prevented these mammals from recolonizing the north, and perpetuated the faunal imbalance. Together with the faunal movements described earlier, this led to the pattern of zoogeographic regions that are now recognized (Fig. 6).

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