



INTERCONTINENTAL DISTRIBUTION OF MAMMALS AND THEIR IMPORTANCE FOR PALEOBIOGEOGRAPHY OF ASIAN EOCENE

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ABSTRACT

Comparison of the mammalian faunas from the Eocene of Asia, Europe, North America and Africa permits assumptions about the routes of migration of mammals, intercontinental relationships, zoogeographical areas, subareas and certain provinces in Asia.

Mammals prove to be a very convenient object for paleobiogeographical research. Their skeleton fairly accurately reflects their adaptations and close coincidence with specific ecological niches makes them an exceptionally valuable group in solution of paleobiogeographical problems. The morpho-functional analysis of the skeleton permits to reveal a sufficiently adequate functional significance of various features and the function of entire organs, as well as to obtain a clear idea of the character of adaptations, of the ecology and biology, particularly, of feeding and locomotion, habit and habitat. Diversity of ecological types makes mammals good indicators of the landscape and enables to reconstruct the landscape of the past epochs. Thus, utilizing the mammals in paleobiogeographical research, we are able at most to operate with such factors of zoogeographical distribution as food, substrate, temperature, humidity and landscape.

Sufficiently complete up-to-date study of the Eocenic mammals, accumulated information on their systematics, morphology, ecology, geological and geographical distribution make it possible to generalize the available data and to use them in paleobiogeographical research. The available materials being limited, it is possible to characterize only large zoogeographic subdivisions: areas, subareas and certain provinces.

Similarity between the Eocene mammalian fauna in the eastern and western hemispheres suggests the existence at that time of interconnections between the continents. Indisputably, in the Eocene time, there were taking place continental migrations of mammals. Appearance and disappearance of intercontinental relations now made pos-

sible far-reaching migrations and now put in the route of the migrants the insurmountable obstacles.

Our zoogeographical interpretations are based on the comparison of mammalian faunas at the level of families and genera in the Eocene of Asia, North America, Europe and Africa, through identification of their similarities and differences, establishment of endemism, a quantitative calculation of common and endemic forms in different continents, their percentage with respect to the total number of forms, through determination on this basis of the routes and tempi of distribution, obstacles, barriers and exchange of fauna among the continents.

The Asian continent, the most extensive and consolidated of all the northern continents, in the first half of Paleogene showed maximum stability in outlines. In Northern Asia Eocene was the time of proceeding reclamation of dry land in the east and its subsidence in the west. There existed in Central Asia some vast internal depressions, mostly occupied by sea-lakes, characterized by the process of gradual subsidence and accumulation of lacustrine and alluvial-proluvial sediments. Himalayan movements in the late Eocene changed the outline of Asia in the South: the sea regressed on the territory of Asia Minor, the Hindustan peninsula joined up to the Asian mainland, Northern Asia was separated at that time from Europe by an inland sea and a strait extending from Thetis up to the Arctic basin along the eastern slopes of the Ural. This sea and strait for a long time happened to be a natural migration barrier. Only in the early and late Eocene an incidental connection between Asia and Europe was temporarily restored along the Turgai isthmus arising at the

site of the Kustanai elevation, over what is known as the Turgai "bridge". In the north-east, Asia joined up with North America through the Beringian land or a "bridge" that was functioning in the early and late Eocene (Simpson 1947, 1949, 1952; Hopkins 1959, et al.). In the middle-eocene the Beringian "bridge" was flooded by sea (Fig. 1). In the early Eocene there took place a separation of the Asian and African continents. In the middle Eocene during the extensive transgression the sea had submerged North Africa, while in the late Eocene the sea regressed, and in the north-eastern part of Africa the marine conditions gave place to continental ones. The outlines of the European mainland underwent during Eocene repeated changes. Drainage of vast territories in the centre of

Europe during the second half of middle Eocene led to the appearance of large areas of fresh-water and saline-water lakes, lagoons and extensive swamps. In late Eocene intensive tectonic movements within the Alpine geosyncline accounted for plunging of the territory of the Alps, Carpathians, Apennines and for flooding of the Polish-German lowland and the south of European Russia.

Some researchers think that in the early Eocene Europe was connected with Northern America through the North-Atlantic "bridge" passing through Britain, Iceland and Greenland (Kurten, 1966, 1967, et al.). F. Szalay and M. McKenna (1971) assume that this connection was taking place not through Iceland, but that the migration route was lying a great deal to the north, through Green-



Fig. 1. Paleogeographic map of the Eocene Eurasia. 1—sea; 2—coastal lowlands periodically flooded by sea and alluvial-lacustrine low-lands; 3—accumulative plains with a weakly-rough relief; 4—low denudation plains with hilly relief; 5—high denudation plains and ancient highlands with hilly-spurry relief; 6—high plateau and mountain areas; 7—active volcanism regions; 8—land and sea boundaries (after Termier H., Termier G., 1965); 9—North-Atlantic "bridge" (after Szalay, McKenna, 1971).

land—Spitsbergen—elevated shelf of the Barents Sea and Scandinavia (Fig. 2). Break-off of this connection they refer, like B. Kurten (1967), back to the end of the early Eocene and due to this break the similarity of the Cuisian and more later mammals of Europe and North America dropped to a lower level.

The connection between the Western Europe and North Africa, possibly existed in the early Eocene and was achieved through the “filter bridges” in the area of Gibraltar (Crusafont, 1962, et al.) and Caucasus (Pilgrim, 1941). L. K. Gabunia (1957) thinks that the Caucasian “bridge” was functioning in the middle and late Eocene and was connecting Eastern Europe and Forward Asia.

Climate in Eocene was moderately warm, seasonal in Eurasia’s north, subtropical and tropical on Eurasia’s south, North Africa and North America. During Eocene the climate in Eurasia was getting warmer. The climatic conditions in the early Eocene were most favourable for settlement of fauna, since the climatic zones were yet quite weakly differentiated, the distribution of heat and moisture was more uniform and cold periods did not come. In the second half of Eocene it started gradually progressing desi-

ccation of the climate. In Asia an arid zone covered the Central Asia and, partly, Asia Minor. In Central Asia it was related to a continuous reclamation and progressive desiccation, Humid tropical climate was typical of the South Asia and North Africa.

The Eocene floras are characterized by a distinct botanical-geographical zonality. The boundary between the northern Turgai and southern Paltava floristic areas in Eocene shifted northwards (Vakhrameev, 1966; Vakhrameev, Meyen, 1970). All the territory of the north Eurasia was occupied by coniferous and broad-leaved mesophilic forests with a very diversified composition of plants. South of them and in the East of Asia it was prevailing subtropical vegetation (Kornilova, 1966; Kornilova and Fotjanova, 1974). Further to the south Asia’s territory was covered by humid tropical forests (Fig. 3). In mid-Europe forests were represented by mixed southern tropical and moderate leaf-falling elements. South Asia, similarly as South Russia, were covered by a typical Mediterranean vegetation. North American flora was thermophilic. Alaska was the area of subtropical forests and in South America vegetation of the savannah type appeared in middle Eocene (Van der Hammen, 1970). In Greenland evergreen plants were widely spread (Koch,

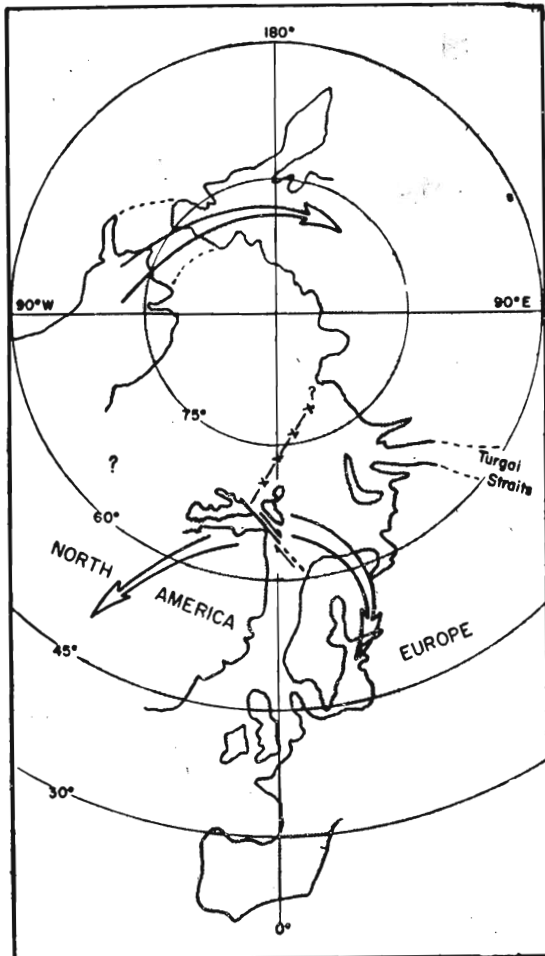


Fig. 2. Migration routes of mammals in Eocene (after Szalay, McKenna, 1971).

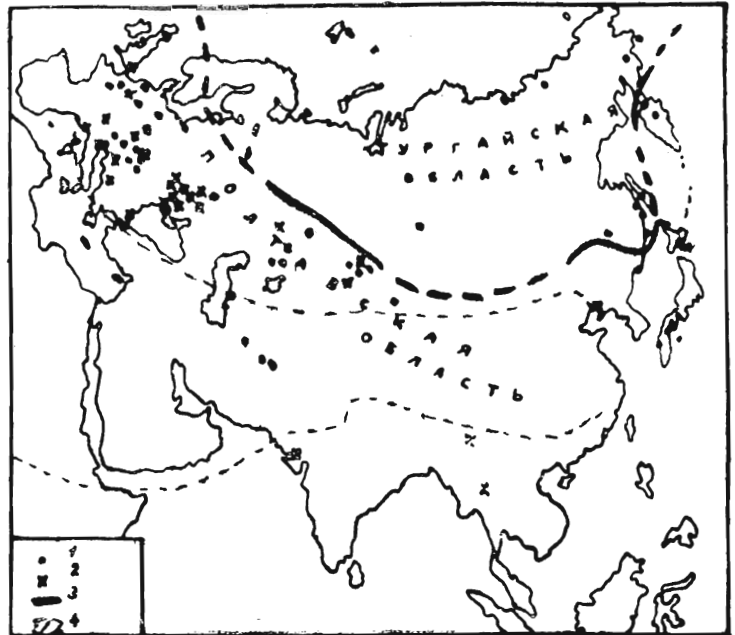


Fig. 3. Position of paleofloristic areas in the Eocene (after V. A. Vakhrameev, 1970).

1964). Tropical forests of the Indo-Malayan type dominated in North America (Boureau, 1956).

Thus, in Eocene there was no complete isolation of northern continents either territorially or with respect to botanical-geographical features. Climatic conditions and floristic zones offered no obstacles to spreading and mixing of faunas in the northern hemisphere, particularly,

in the northern parts of the continents where the main continental "bridges" were, in fact, lying. Merely topographical conditions prevented or contained the migration of the faunas in Eocene. Continental "bridges" with their landscapes (relief, vegetation, etc.) were the very linking elements between the continents, upon which an exchange of faunas was largely dependent. Just the ecological conditions of the "bridges" determined the composition and number of migrants and routes of their travel.

Paleontological study of mammals from different pieces of the Eocene and different continents and regions is very irregular. While the late-Eocene mammals of Asia are studied at present sufficiently well and adequately with the European and North-American mammals, the latter from Asian early and middle Eocene lacks satisfactory information. Therefore most adequate comparative-zoogeographical analysis can now be made of late Eocene only.

Particularly poorly known is Asian early-Eocene fauna. It has been found only in China (provinces Kiangsi, Shantung, Hupeh) (Fig. 4), from whence three orders, Pantodonta, Dinocerata, Perissodactyla, have been described with four families: Coryphodontidae, Prodinoceratidae, Isectolophidae, Helaletidae and five genera: *Coryphodon*, *Eudinoceras*, *Probathyopsis*, *Homogalax* and *Heptodon* (Chow, Tung, 1962; Chow, Li, 1965; Zdansky, 1930).

Incomparably greater research of early-Eocene fauna of mammals from Europe and North America has been made. Of that time it is known from Europe 11 orders, 23 families and 39 genera; from North America—17 orders, 41 families, and 100 genera (Matthes, 1962). Quite noteworthy is the fact that all of the families and genera known in Asia (except for *Eudinoceras*) were also present in the early Eocene of North America and 2 families and 1 genus, in Europe. This confirms the presence in early Eocene of a continental connection between Asia and North America and an active exchange of fauna. This connection was, possibly, realized through the Beringian "bridge". The exchange between Asia and Europe in early Eocene was but limited and this, probably, could be explained by the fact that in the early Eocene it was a barrier for such a migration, the Turgai strait, over which only now and then the connection could be achieved through narrow and periodically broken Turgai "bridge", the latter being limited in territory and, possibly, hardly passable for fauna. On the other hand, in early Eocene there could be observed a striking similarity between the fauna of Western Europe and North America, particularly of its eastern part. In these continents 19 families (about 83% of the European total) and 12 genera (33%) are common. Such a great similarity favours an assumption about the faunistic exchange in early Eocene between Europe and North America, which realized through the North-Atlantic "bridge" connecting the northern part of

the European continent with the East of North America and comprising Greenland (Fig. 2, 4). In early Eocene Europe appeared to be just the eastmost margin of a large mainland and was connected with North America. The southern part of Western Europe at that time formed an archipelago of small islands, only occasionally connecting with the Anglo-Iceland peninsula, and the north of Europe, Russo-Scandia being entirely separated from the western and southern parts with wide straits.

From what has been said above we arrive at a conclusion about existence in early Eocene of the extensive Euro-North-American zoogeographical area, which Western Europe entered as a subarea. Identification of the West-European subarea owes to the presence in Europe of two endemic families (Anoplotheriidae, Lophiodontidae) and 18 endemic general

As regards zoogeographical subdivisions in Asia in early Eocene, we refrain from discussing the subject because of very insignificant factual material available on Asian early-Eocene mammals. As to Africa, no early Eocene mammals are known there at all.

The mammals from Asian middle Eocene are studied better. They have been found in the USSR (Kazakhstan: Zaisan depression, river Obaila, Obailin formation; Taldy-Kurgan region, Andreevka¹); Kirghizia: Maili-Sai and Andarak); in China (Inner Mongolia; provinces Shantung, Hunan, Hupeh); in Pakistan Gada-Kas); in Kalimantan (Fig. 4). Fauna is represented by tillodonts, taeniodonts, rodents, condylarthrs, pantodonts, dinocerats, perissodactyls and artiodactyls. Altogether, 9 orders, 19 families and 28 genera are known from Asian middle Eocene. In Europe—8 orders, 22 families and 54 genera. In North America—13 orders, 30 families and 88 genera. From African middle Eocene one order (Proboscidea) with two families and two genera are known but not found in other continents. The mammalian faunas from middle Eocene of Asia, Europe, and North America are quite comparable. In Asia and Europe 8 families (36% of the European total) and only 2 genera (3.7%) are common; in Asia and North America—11 families (36%) and 3 genera (3.4%). Also middle-Eocene faunas in Europe and North America are different having only 11 common families (36%) and 2 genera (1%). It is to be noted that nearly all of these common families had already been widespread in early Eocene when, they possibly migrated from one continent to another. At the same time, in middle Eocene endemism became very distinct in all the continents. In Asia there were 5 endemic families (30%) and 22 genera (99%); in Europe—8 families (37%) and 49 genera (93%); in North America—12 families (50%) and 85 genera (99%)

¹The mammalian fauna from Andreevka is not yet completely studied and the age of the enclosing deposits has not yet been accurately established; it must be either middle or late Eocene.



Fig. 4. Main localities and migration routes of Eocene mammals in Asia.

A—Main localities of mammals: 1—China, province Kiangsi, Yanshui; 2—China, province Kiangsi, Ninchiashan; 3—China, province Shantung, Wutu; 4—China, province Shantung, Niushan; 5—China, province Hupeh, Ichang; 6—USSR, Kazakhstan, Zaisan depression, river Obaila; 7—Kazakhstan, Taldy-Kurganskaya region, Andreevka; 8—USSR, Kirghizia, Andarak; 9—USSR—Kirghizia, Maili-Sai; 10—Mongolian People's Republic, Khaitshin-Ula; 11—China, Inner Mongolia, Arshanto; 12—China, province Shantung, Hsintai-Hsien; 13—China, province Shantung, Meng-Yin-Hsien; 14—China, province Hunan, Hengyang; 15—Pakistan, Ganda-Kas; 16—Kalimantan, Gunung Sobuman Ulu; 17—USSR, Kazakhstan, Kijn Kerish; 18—USSR, Kazakhstan, Aksoran; 19—USSR, Primorsky territory, Artem; 20—USSR, Kirghizia, Issyk-Kul, Toruaigr; 21—China, Inner Mongolia Irdyn Magna; 22—China, Inner Mongolia, Shara Murun, Ula-Usu; 23—Mongolian People's Republic, Khölobolchi; 24—China, province Honan, Lushih; 25—China, province Yunnan, Iliang; 26—China, province Yunnan, Lunan; 27—China, province Shensi, Lantian; 28—China, province Sinkiang, Luliang; 29—China, province Shansi Yuanchu-Hsien; 30—China, province Hupeh, Yangshi; 31—China, province Kwangsi, Tientong; 32—China, province Kiangsi, Yanshui; 33—Burma, Pondaung; 34—Korea, Hosan; 35—Japan, Hokkaido; 36—Japan, Ube; 37—USSR, Georgia, Vani; B—Land outlines in the Eocene. C—Main directions of migration routes of mammalian fauna.

in Africa, as mentioned above, the entire fauna was endemic.

As seen from the above comparison, in middle Eocene the mammalian faunas in all continents were isolated, with a great number of endemics and practically complete absence of common forms, obviously, due to the break-up of continental contacts through the Beringian, North-Atlantic and Turgai "bridges". All continents of that time were separated from each other and represented independent zoogeographical areas.

It has been amassed a sufficiently adequate and equivalent information on the late-Eocene mammals in all of the continents. In Asia 12 orders, 35 families and 87 genera are known, in Europe—10 orders, 42 families and 85 genera, in North America—14 orders, 47 families and 126 genera, in Africa—5 orders, 8 families and 12 genera.

The finds of late-Eocene mammals in Asia cover a large territory, including the USSR (Kazakhstan: Zaisan depression, Kiin-Kerish¹), Tuzkabal (=Kustov) and Aksyir formations; Kirghizia: Issyk-Kul, Toruaigr; Primorsky territory; Artem (Uglov formation); Mongolia (Khaishin-Ula); China (Inner Mongolia, provinces Honan, Yunnan, Shantung, Shensi, Kiangsi, Kwangsi, Hupeh, Sinkiang); Burma (Pondaung formation); Korea (Hosan coal-field) and Japan (Hokkaido and Ube) (Fig. 4). The fauna is diverse: insectivorous, primates, tillodonts, deltatherids, rodents, carnivorous, lagomorphs, pantodonts, dinocerats, condylarthrs, periossodactyls and artiodactyls. Particularly numerous and diversified are Periossodactyla (10 families) attaining their heyday in late Eocene. Artiodactyla (4 families) are also quite diversified.

At that time in all continents endemic forms were still numerous. In Asia there were 10 endemic families (31%) and 72 genera (85%); in Europe—18 families (43%) and 78 genera (93%); in North America—19 families (42%) and 115 genera (90%); in Africa—6 families (75%) and 8 genera (73%). As seen from these figures, endemism somewhat reduced, in late Eocene as compared to middle Eocene. At the same, time common elements appeared in the faunas of Asia, Europe, North America and Africa. Mostly striking, even though yet insignificant similarity was observed in the mammals of Asia and North America: they had 19 common families (45%) and 12 genera (9%). Appearance of common groups proves the fact that at that time it was taking place the migration of the fauna from one continent to another. As for determining the time and direction of migration, it should be noted that it is very important to registrate the first appearance of a group in one or other continent and time, when it became common to both continents. The latter practically either coincides

or is close to migration time and to be able to determine the direction of the migration route it is important to know, firstly, in which continent the given group had first appeared and, secondly, what are the phylogenetic relations of close genera occurring in either continent.

Thus, after a complete isolation observed in the middle Eocene, it started once again a certain, even though insignificant exchange of fauna between Asia and North America, which seems to be directly connected with a considerable regression of sea and establishment of contacts between the continents. Connection between Asia and North America was realized, probably, across Beringia, while exchange limitations were at that time obviously, accounted for a poor passability of the Beringian dry land; for instance, abundant swamps, lack of food or unfavourable climatic conditions could be a barrier on the way of migrants.

The migration across Beringia occurred, apparently, in two-way direction, but the major part of forms moved from Asia to North America, probably, due to abundance in Asia of diverse biological types occupying different ecological niches, as well as to a great number of eurybiontic forms and ecological analogues largely capable of adapting new conditions and surviving on a new territory.

Presence in the late Eocene of a certain number of common forms in the fauna of Asia and Europe—14 families (33%) and 4 genera (4%)—indicates that the faunistic exchange between this two continents was of negligible value. This connection was accomplished through the Turgai "bridge" but it was insignificant and periodically broke off, what is supported by a sufficient originality and isolation of faunas of two continents.

African late Eocene fauna is highly specific and endemic; however, there are 2 genera of Deltatheridia (*Hyaenodon* and *Pterodon*) which were widely spread at that time in all other continents, i.e. anthracothere (*Rhagatherium*), common with the European one, and *Bothriodon* common with the Asian genus (Andrews, 1906; Simpson, 1945; Arambourg, 1963; Savage, 1965, 1969, et al.). The appearance of these Deltatheridia in African Eocene is quite mysterious. When, whence and in what way did they come to this continent? *Hyaenodon* is abundantly represented in the late Eocene fauna of Quercy (France), while in Asia and North America it became common somewhat later, in Oligocene. African hyenodons by their morphology are mostly close to the European ones; therefore, the migration of this genus from Europe to Africa appears to be most plausible. Another representative of the order Deltatheridia, *Pterodon*, is known from the late Eocene of Asia and North America, whereas in Europe it appeared as early as in middle Eocene. Anthracothere *Bothriodon*, obviously came to Africa from Asia, where the most ancient finds of this genus are known to have been made (in China's late Eocene), while in Europe

¹The age of deposits on the Kiin-Kerish locality is not yet accurately established; it must be either late Eocene or early Oligocene.

and North America *Bothriodon* spread only in Oligocene. *Rhagatherium* is known only in Europe (from middle Eocene) and in Africa (from late Eocene). Thus, most likely that these genera (except for *Bothriodon*) penetrated into Africa from Europe in late Eocene, this, however, being in contradiction to geological and paleogeographical data on the existence of continental connection between Europe and Africa in early Eocene only. The connection was, apparently, realized through the Caucasian 'bridge' (Gabunia, 1957).

Much less similarity, compared to early and middle Eocene, was observed between the faunas of Europe and North America (common 19 families—40%, and 12 genera—9%), which is related to the absence at that time of a connect via the North-Atlantic "bridge".

As seen from the above comparative zoogeographical analysis, in late Eocene the mammalian faunas in all of the continents continued to be specific and endemic, regardless of a certain insignificant exchange. This points to the fact that Asia, Europe, North America and Africa in late Eocene, similarly as in middle Eocene, represented independent zoogeographical areas.

It is worth noting that mammals of Central Asia, Mongolia and northern regions of China revealed much similarity in the composition of subfamilies and genera; these faunas were almost identical, whereas the forms widespread in China's southern regions, Burma, Korea, and Japan were quite specific and showed sharp differences from those of more northern areas. On this base we consider it possible to identify within the Asian zoogeographical area two subareas: North-Asian (Central Asia, Mongolia, North China, Inner Mongolia) and South-Asian (South and East China, Burma, Korea, Japan). This division appears to be quite valid because of the occurrence in Central Asia, Mongolia and China's northern regions of 5 common families (Gobiatheriidae, Brontotheriidae, Deperetellidae, Lophialetidae, Hypertragulidae) and 8 genera (*Gobiatherium*, *Rhinotitan*, *Epimanteoceras*, *Teleolophus*, *Deperetella*, *Lophialetes*, *Breviodon*, *Archaeomeryx*).

The fauna of China's south-east and Burma was extremely peculiar, included numerous endemics and revealed a sharp difference from the Central-Asian and Mongolian fauna (Zdansky, 1930; Young, 1937; Colbert, 1938; Xu, 1962; Chow, 1965, etc.). On this base the South-Asian subarea was singled out; it is characterized by specific insectivorous (*Ictopidium*), tillodonts (*Adapidium*), Primates (*Hoanghoniuss*, *Lantianius*), amynodonts (*Sianadon*), numerous anthracotheres (*Anthracokeryx*, *Anthracosenex*, *Anthracothema*) which are non-existent in the North-Asian subarea.

Within the North-Asian subarea a distinct similarity between the mammals of Kazakhstan and Mongolia has been established, as well as their difference from China's mammals. On this base it seems possible within this subarea to single out, tentatively and very carefully, two

provinces, Middle-Asian-Mongolian and North-Chinese ones. For the former families Brontotheriidae with genera *Epimanteoceras* and *Rhinotitan* and Deperetellidae with genera *Deperetella* and *Teleolophus* were characteristic. On the other hand, it was devoid of some families characteristic of the latter province, namely Deltatheridia (*Sarkastodon*, *Pterodon* and others), rodents (*Advenimus*), carnivorous (*Miacis*), condylarthrs (*Andrewsarchus*, *Hapalodectes*, *Mongolonyx*, *Harpagolestes*), numerous Brontotheriidae, Tapiroidea, Suidae (*Gobiohyus*) and certain anthracotheres (*Ulausodon*).

However, the poor paleontological characteristics of the late-Eocene fauna of Kazakhstan and other regions of Middle Asia make the identification of the above provinces highly hypothetical and provisional, until new materials are obtained and fauna more thoroughly studied.

Thus, summing up what has been said above, it should be concluded that in Eocene the following zoogeographical subdivisions can be identified:

Early Eocene

1. Euro-North-American area:
 - (1) West-European subarea,
 - (2) North-American subarea.

Middle Eocene

1. Asian area,
2. European area,
3. North-American area,
4. African area.

Late Eocene

1. Asian area:
 - (1) North-Asian subarea (Middle Asia, Mongolia, North China):
 - (A) Middle-Asian-Mongolian province (Middle Asia, Mongolia),
 - (B) North-China province (Inner Mongolia, North China),
 - (2) South-Asian subarea (South and East China, Burma, Korea, Japan),
2. European area,
3. North-American area,
4. African area.

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