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DISTRIBUTIONAL AND PHYLOGENETIC STUDIES ON INDIAN FOSSIL MAMMALS. III

A CLASSIFICATION OF THE CHALICOTHERIOIDEA

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INTRODUCTION

The chalicotheres are aberrant perissodactyls having teeth like the teeth of the titanotheres, but having, in the advanced forms at least, clawed feet. Because of this anomalous association of grazing teeth with digging feet, rather than with cursorial feet, the chalicotheres have been of great interest to students of mammalian morphology and taxonomy for many years. Naturally, from the time of the first discovery of chalicotherine remains, the taxonomic position of these curious mammals has been a subject of considerable controversy among palaeontologists and zoölogists.

For many years the students of fossil vertebrates did not realize that the chalicotherine skulls and feet, discovered in European and Asiatic deposits, were representative of one kind of animal. Consequently the skulls or teeth were described separately from the feet, and they were variously classified. The feet were almost always identified as belonging to some giant edentates.

Even after Filhol's recognition of the fact that the feet and the skulls, so long regarded as belonging to different animals, in reality were from one animal, there were differences of opinion as to the relationships of the chalicotheres to each other and to other perissodactyls.

Naturally, these divergences of opinion led to the formulation of several systems of classification for the chalicotheres. It is hardly necessary to attempt here a detailed review of the history of research on the Chalicotherioidea, since Holland and Peterson in their Memoir of 1914 give a fairly complete account of the work of various authors from the time of Cuvier on. There will be, however, a presentation of several of the outstanding classifications of the chalicotheres in this paper, and these will be compared to the system of classification now under consideration.

The classification to be set forth below has been briefly outlined in a recent paper, but the bases on which it was founded have not heretofore

been discussed.[1] The detailed discussion of the classification advocated in the following pages, and the evidence in favor of it, is the purpose of the information contained in this paper.

Desirability of a Separate Superfamily Chalicotherioidea

Until Filhol made the important discovery that *Macrotherium* is a true perissodactyl with aberrant feet, there had been a variety of views expressed as to the relationships of the chalicotheres. Of course it was recognized by the early students of the group that these animals, as known from the skulls and teeth, should be classified with the ungulates. (As pointed out above, the feet were not associated with the skulls or teeth, and were supposed to be representative of giant edentates.) Huxley, in 1870, placed *Homalodotherium* from South America with *Chalicotherium* as an "anoplotheroid." In 1872 Gill regarded the chalicotheres as members of the Artiodactyla, while in 1873 Gaudry placed them among the Pachydermata. Marsh, in 1874, pointed out the resemblances between the chalicotheres and the titanotheres, and in this regard he came nearer to a true realization of their relationships than did the authors that preceded him. In 1881 Cope placed the chalicotheres near the Tapiridae and the Menodontidae, in the Perissodactyla, and in 1887, after Filhol had announced the association of the skull of *Chalicotherium* with the feet of *Macrotherium*, this same author proposed the erection of a new order, the Ancylopoda, for the reception of the chalicotheres.

The separation of the chalicotheres into a distinct order was accepted with reservations by Osborn in 1893. Finally in 1898, Osborn proposed the division of the Perissodactyla into five superfamilies, and one of these was named the Chalicotherodea. Subsequent authors have, for the most part, considered the chalicotheres as constituting a separate group of equal rank with the other perissodactyl groups.

Recently, in 1931, Simpson has reduced the chalicotheres to family status and placed them in the superfamily Brontotherioidea.[2] This opinion, it seems to me, is not justified, and the evidence bearing on it will be presented in the following paragraphs.

If we begin by comparing the most primitive chalicotheres with the most primitive titanotheres we find that the resemblances between them are indeed striking. This is due to the fact that they are primitive, and all primitive perissodactyls are very much like each other—as was especially stressed by Dr. W. D. Matthew many times over.

[1] Colbert, E. H. 1934. Bull. Amer. Mus. Nat. Hist., LXVII, pp. 353–355.
[2] Simpson, G. G. 1931. Bull. Amer. Mus. Nat. Hist., LIX, p. 282.

Naturally *Eomoropus*, the most primitive chalicothere, is very much like *Lambdotherium* and *Eotitanops*, the earliest titanotheres, and in turn it is like *Eohippus*, the earliest horse. All of these genera are characterized by their relatively small size, low primitive skulls, brachyodont teeth and their undifferentiated feet. These are characters that show their common origin; they are characters to be expected in any primitive perissodactyl.

A comparison between the more advanced forms of the chalicotheres and the titanotheres will show how these two groups separated from each other during the course of their phylogenetic development, each following a different kind of anatomical development. In the chalicotheres the skull became rather horse-like, the neck was elongated, the legs became long, the front legs being longer than the hind legs, and the feet remained short and developed claws. On the other hand the titanotheres showed a trend toward the growth of excrescences on the skull (although this did not occur in all of the genera), the body tended to get heavy and the limbs were heavy. The feet had hoofs and were quite different from the feet of the chalicotheres. In both groups the teeth remained very similar to each other. In both groups there was a various reduction in the incisors. The chief differences in the cheek teeth are that in the chalicotheres the hypocone is attached to the metaloph, whereas in the titanotheres the hypocone is always quite separate.

In spite of the similarities of the teeth in the chalicotheres and the titanotheres, the differences in the skull, skeleton, and feet seem too profound to warrant a grouping of these forms in a single superfamily.

A Comparison of Classifications

There have been several attempts at a classification of the chalicotheres, the most outstanding of which have been those of Holland and Peterson (1914), von Zittel as revised by Smith Woodward (1925), Matthew (1929), and von Koeningswald (1932).

Holland and Peterson (1914), in their monograph entitled "Osteology of the Chalicotheroidea," presented the following arrangement for the chalicotheres.

Order Ungulata
Suborder Perissodactyla
Superfamily Chalicotheroidea
Family Chalicotheriidae
Subfamily Schizotheriinae
Genera *Schizotherium*

Pernatherium
Eomoropus
Phylotillon
Subfamily Moropodinae
Genera *Moropus*
Nestoritherium
Subfamily Macrotheriinae
Genera *Macrotherium*
Chalicotherium
Circotherium

In the earlier editions of von Zittel's 'Text Book of Palaeontology' no attempts were made to subdivide the chalicotheres; the genera were listed under one heading. In Smith Woodward's revision of 1925, however, the following arrangement of the group was presented.

Order UNGULATA
Suborder PERISSODACTYLA
Family Chalicotheriidae
Subfamily Schizotheriinae
Genera *Schizotherium*
Pernatherium
Eomoropus
Phylotillon
Subfamily Moropodinae
Genera *Moropus*
Nestoritherium
Subfamily Macrotheriinae
Genera *Macrotherium*
Chalicotherium
Circotherium

Obviously this classification has been adapted, without change, from the work of Holland and Peterson. The only difference to be noted is in the fact that no superfamily designation is used.

In 1929 Dr. W. D. Matthew classified this group along somewhat different lines. His arrangement is presented below.

Family Chalicotheriidae
Subfamily Eomoropinae
Genera *Eomoropus*
Subfamily Chalicotheriinae
A.—Brachyodont Series

Genera?*Olsenia*
?*Pernatherium*
Schizotherium
Macrotherium
Chalicotherium
Circotherium

B.—Hypsodont Series

Genera *Schizotherium* (tentative for certain species)
Moropus
Phylotillon
Nestoritherium

This classification designed by Matthew is a great improvement over the previous classifications, for it not only is a better expression of the interrelationships of the various genera of chalicotheres, but it is also distinctive in that it embodies certain concepts of taxonomic and phylogenetic significance that had not been realized by other authors.

Dr. Matthew pointed out a fact that other authors had seemingly missed, namely that *Eomoropus* differs far more from the later Tertiary chalicotheres than they do from each other. Consequently he divided the family Chalicotheriidae into two subfamilies, one containing *Eomoropus*, and the other containing all of the later Tertiary genera. This second subfamily, the Chalicotheriinae, he again split, into two series, A and B, based on the brachyodonty and the hypsodonty of the teeth respectively. In making this division of the Chalicotheriinae it may be possible that Matthew fell into one error by placing the genus *Schizotherium* in the same group with *Macrotherium* and *Chalicotherium* (series A of his classification). It would seem that *Schizotherium* is more truly referred to the second series, along with *Moropus*, *Phylotillon*, and *Ancylotherium*. Evidence in favor of this statement will be brought out below.

Of course, Matthew had especially in mind *Schizotherium pilgrimi*, a form of Lower Miocene age in which the molars are brachyodont and quadrate as in *Macrotherium*. This species would certainly fall into Matthew's series A. A close examination of the figure of *S. pilgrimi* would seem to show, however, that this form may not belong to the above-mentioned genus, but that it may rather be a primitive chalicotherine directly ancestral to *Macrotherium*. The questionable relationship of *Schizotherium pilgrimi* was recognized by Forster Cooper and by Matthew.[1]

[1]Matthew, W. D. 1929. Bull. Amer. Mus. Nat. Hist., LVI, p. 518.

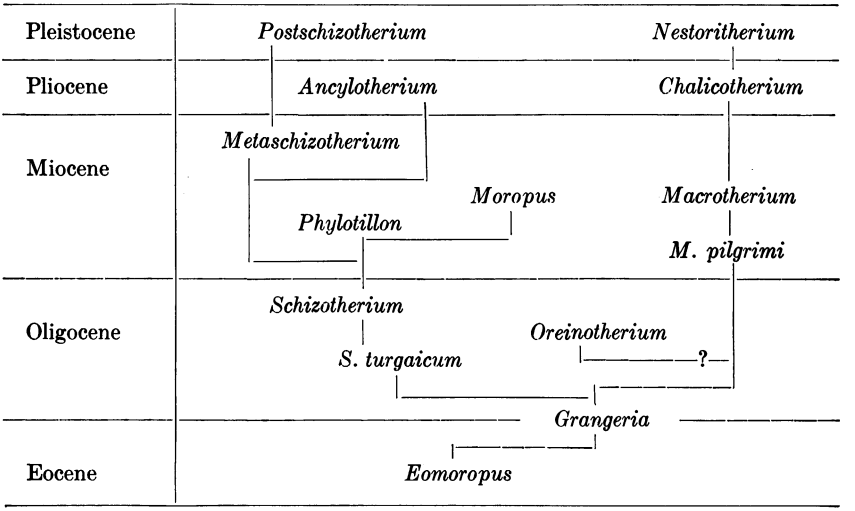
"*Schizotherium pilgrimi* [is] certainly not the milk dentition of *Phylotillon*, and has every appearance of being permanent dentition of a brachyodont chalicothere of quite small size and very primitive construction of the teeth, the anterior transverse crest being more normally developed and protocone less isolated and less shifted in position than in any Miocene genus. I suspect that Cooper's identification indicates that *Schizotherium* belongs, some species at least, in the chalicotherine series as defined below, as the earliest stage of its development."

Dr. Matthew's statement, quoted above, bears directly on the question of the relationships of *Schizotherium turgaicum* Borissiak, an Oligocene form from eastern Asia. This species was originally described as belonging to the genus *Schizotherium*, but Koenigswald in 1932 referred it to *Macrotherium*, especially on the basis of its quadrate, brachyodont upper molars.

A close scrutiny of the figures of *S. turgaicum* leads to the conclusion that this form is not a *Macrotherium*, as was supposed by Koenigswald, but rather is a much more primitive genus, possibly more primitive even than *Schizotherium*. *S. turgaicum* shows certain characters that relate it to the Eocene chalicotheres, *Eomoropus* and *Grangeria*. The quadrate upper molar may be a primitive character inherited from an Eocene ancestor such as *Eomoropus*. In the lower molars the metastylid is distinct, being rather separated from the anterior spur from the hypoconid—a primitive character found in most of the early Eocene perissodactyls. In the hind foot of *S. turgaicum* the astragalus is narrow, and its trochlea is relatively deep, as in the primitive Eocene perissodactyls. On the other hand, the neck of the astragalus is reduced, an advanced character, and its lower articular surface has a facet for the navicular only. In this last feature *S. turgaicum* shows a decided trend toward the *Moropus* type of astragalus. The metapodials of *S. turgaicum* are long, and in general they show a definite trend toward the long foot characteristic of *Moropus* and related genera. The phalanges are rather primitive.

Thus we see that *Schizotherium turgaicum* is a primitive Oligocene chalicothere, showing many primitive heritage characters retained from its Eocene ancestors, but developing certain habitus characters that show a definite trend toward the typical Oligocene *Schizotherium* of Europe and Asia. If *S. turgaicum* is of the genus *Schizotherium*, then we must suppose that the genus shows two broad stages of development, an earlier one retaining many holdovers of Eocene heritage characters, and a later one in which the primitive characters are for the most part lost, and the definitive *Schizotherium* habitus characters are established.

It may be that *Schizotherium turgaicum* is a form close to the stem of the schizotherine branch of chalicotheres, just as *Grangeria gobiensis*, recently described, is a primitive chalicothere approaching the beginnings of the chalicotherine branch. This conclusion is suggested by a study of the astragalus in these forms, and although single characters are never to be taken as the absolute evidence for phylogenetic relationships, still in the case under consideration these single characters carry a considerable degree of weight. *S. turgaicum* has no cuboid facet on the astragalus, which makes it like *Moropus* and other schizotherine chalicotheres; *Grangeria* has a very small cuboid facet on the astragalus, and this foreshadows the condition typical of *Chalicotherium* and related genera. On the other hand, the teeth of *S. turgaicum* are much more primitive than the teeth of the typical *Schizotherium*, so we have good reason to think that this eastern Asiatic form is less advanced in its phylogenetic development than are the characteristic Oligocene species of *Schizotherium*. The above suggested relationships may be represented in the following manner.



Turning now to the classification formulated by von Koenigswald in 1932, we see that the genus *Schizotherium* is grouped with *Moropus*, *Phylotillon*, etc., which would seem to be the correct expression of its relationships.

Family Chalicotheriidae
Subfamily Eomoropinae
Genus *Eomoropus*
Subfamily Chalicotheriinae
Genera *Chalicotherium*
[Including
Macrotherium
Schizotherium turgaicum
Schizotherium pilgrimi]
Nestoritherium
[Including
Circotherium]
Subfamily Schizotheriinae
Genera *Schizotherium*
Metaschizotherium
Colodus [Referring to *Ancylotherium pentelici*]
Phylotillon
Moropus
Postschizotherium

In his original classification, von Koenigswald listed the various species under the several genera.

This classification, evidently based on Matthew's classification of 1929, contains certain inconsistencies. The genus *Grangeria*, named by Zdansky in 1930, is omitted. The genus *Macrotherium* is suppressed, and its species are considered as belonging to the genus *Chalicotherium*, a change the validity of which may be doubted. The name *Colodus* is revived for *Ancylotherium pentelici* (*Nestoritherium pentilici*), notwithstanding the fact that *Colodus* is properly referable to *Atelodus pachygnathus*. Then again, von Koenigswald made his two subfamilies Chalicotheriinae and Schizotheriinae equal in rank to his subfamily Eomoropinae, in spite of the fact that Matthew had pointed out the necessity of regarding them as of lesser value than the Eomoropinae. In this regard, von Koenigswald overlooked the important fact that the two subdivisions of advanced chalicotheres are much more like each other than they are like the primitive subfamily, Eomoropinae, which would of course call for a recognition of them as lesser divisions in the classification of the chalicotheres.

A Classification of the Chalicotherioidea

With the foregoing considerations in mind we may now turn to the question of the classification being proposed in the present paper. A few preliminary remarks may be in order at this point.

The earliest known chalicotheres are of Middle to Upper Eocene age, and are found in North America and in Asia. As indicated above, Dr. Matthew pointed out the fact that these primitive chalicotheres are in reality more nearly like the Eocene titanotheres and the other primitive perissodactyls than they are like the later chalicotheres. These Eocene forms are characterized by unspecialized skulls and feet, and a primitive perissodactyl dentition with the canines well developed.

As the chalicotheres continued into the Oligocene and into the later Tertiary, they would seem to have split into two well-defined groups. One group, typified by *Schizotherium* and *Moropus*, is characterized by a rather elongated skull, elongated, hypsodont cheek teeth, a skeleton in which the fore and the hind limbs are of subequal length, and feet having long metapodials. The other group typified by *Macrotherium* and *Chalicotherium*, is characterized by a skull in which the facial portion is short, the cheek teeth are quadrate and brachyodont, a skeleton in which the fore limbs are longer than the hind limbs, and feet having short metapodials and flattened phalanges.

This twofold division of the advanced chalicotheres would seem to be a natural one, for when it is tested in the light of our present available knowledge it would seem to hold true. Therefore, on the basis of the division of the chalicotheres into a primitive group and two advanced groups the following classification is presented. It is really a slight modification of Matthew's classification of 1929.

Order Perissodactyla
- Superfamily Chalicotherioidea
  - Family Chalicotheriidae
    - Subfamily Eomoropinae
      - Genera *Eomoropus*
        Grangeria
    - Subfamily Chalicotheriinae
      - Tribe Chalicotherini
        - Genera *Chalicotherium*
          Macrotherium
          Nestoritherium
          Oreinotherium

Tribe Schizotherini
Genera *Schizotherium*
Metaschizotherium
Moropus
Phylotillon
Ancylotherium
Postschizotherium
Incertae Sedis
Pernatherium

A more detailed presentation of this classification is now offered.

Order PERISSODACTYLA
Superfamily Chalicotherioidea
Family Chalicotheriidae

Cheek teeth bunoselenodont; last upper premolars with two outer and one inner cusp, last lower premolars with double crescents; upper molars with W-shaped ectoloph, with protoloph connecting protocone and paracone, and metaloph connecting metacone and hypocone; lower molars doubly crescentic with a separate metastylid, and the third lower molar without a talonid except in the primitive genera. Auditory bulla large; orbit open behind; strong postglenoid and paroccipital processes; foramen lacerum anterius and foramen rotundum enclosed in a common vestibule; alisphenoid canal present; mandible with a broad ascending ramus. Cervical vertebrae keeled. Pelvis elongated; femur with or without third trochanter. Distal face of the astragalus articulating with the navicular and cuboid or with the navicular only. Manus either tetradactyl or tridactyl; pes tridactyl; distal ends of metapodials with convex articulating surfaces; terminal phalanges deeply bifid, except (?) in the primitive genera.

Subfamily **Eomoropinae**

Primitive and of small size. Quadrate, brachyodont molars, with protoloph connecting protocone and metacone, and metaloph connecting paracone and hypocone; lower molars with a separate metastylid; third lower molar with a talonid. First upper premolar and both upper and lower canines present; lower canine more or less in series with the incisors; incisor formula variable. Manus tetradactyl; pes tridactyl; astragalus with or without a cuboid facet (in *Grangeria* and *Eomoropus* respectively). Metapodials and phalanges not highly modified as in the later chalicotheres. Limbs subequal in length.

EOMOROPUS Osborn, 1913

Eomoropus amarorum (Cope)—Generic type. Washakie formation, Upper Eocene, Wyoming.

Eomoropus annectens Peterson. Uinta formation, Upper Eocene, Utah.

Eomoropus quadridentatus Zdansky. Ludian, Upper Eocene, Honan, China.

Eomoropus major Zdansky. Ludian, Upper Eocene, Honan, China.

Eomoropus minimus Zdansky. Ludian, Upper Eocene, Honan, China.

GRANGERIA Zdansky, 1930

Grangeria canina Zdansky—Generic type. Lower Oligocene (?), Shantung, China.

Grangeria gobiensis Colbert. Irden Manha formation, Upper Eocene, Inner Mongolia.

Subfamily **Chalicotheriinae**

Advanced genera of large size. Premaxillaries often, if not always edentulous. Canines and first upper premolar absent; upper molars quadrate to elongate; no third lobe on the last lower molar. Manus and pes highly modified; femur with third trochanter.

Tribe **Chalicotherini**

Advanced genera of medium to very large size. Quadrate, brachyodont upper molars, with ectoloph bent lingually beyond the median line of the tooth; molar indices usually above 90; metastylid reduced in lower molars. Manus and pes tridactyl, manus longer than pes; trapezium wanting; astragalus with a cuboid facet; articulating faces of the proximal phalanges tending to be parallel with the long axis of the bone; claws short; limbs unequal, the forelegs being much longer than the hind legs.

CHALICOTHERIUM Kaup, 1833

Chalicotherium goldfussi (Kaup)—Generic type. Pontian, Lower Pliocene, Eppelsheim, Germany.

Chalicotherium antiquum (Kaup). Pontian, Lower Pliocene, Eppelsheim, Germany.

NESTORITHERIUM Kaup, 1859

Nestoritherium sivalense (Falconer and Cautley)—Generic type. Upper Siwaliks, Lower Pleistocene, India.

?*Nestoritherium sindiense* (Lydekker). Manchar beds, Mio-Pliocene, Sind.

Nestoritherium sinense (Owen). Lower Pleistocene, Wanhsien, China.

MACROTHERIUM Lartet, 1837

Macrotherium sansaniense Lartet—Generic type. Sarmatian, Upper Miocene, Sansan, France.

Macrotherium grande Lartet. Sarmatian, Upper Miocene, Sansan, France.

Macrotherium magnum Lartet. Sarmatian, Upper Miocene, Sansan, France.

Macrotherium giganteum Gervais. Sarmatian, Upper Miocene, Sansan, France.

Macrotherium secundarium Filhol. Sarmatian, Upper Miocene, Sansan, France.

Macrotherium minus Lartet. Sarmatian, Upper Miocene, Sansan, France. [The foregoing species are probably synonymous.]

Macrotherium rhodanicum Deperet. Upper Miocene, La Grive St. Alban, France.

Macrotherium salinum Forster Cooper. Chinji zone, Lower Siwaliks, Lower Pliocene, India.

Macrotherium pilgrimi (Forster Cooper). Bugti beds, Lower Miocene, Baluchistan.

Macrotherium turgaicum (Borissiak). Oligocene, Siberia.

Macrotherium brevirostris Colbert. Tung Gur formation, Upper Miocene, Inner Mongolia.

Macrotherium matthewi (Holland and Peterson). Pawnee Creek formation, Middle Miocene, Colorado.

OREINOTHERIUM Russell, 1934

Oreinotherium bilobatum (Cope)—Generic type. Cypress Hills beds, Lower Oligocene, Saskatchewan.

Tribe **Schizotherini**

Advanced genera of medium to very large size. Elongated, hypsodont molars, with ectoloph tending to be vertical, thus making the tips of the paracone and metacone on or outside of the median line of the tooth; molar indices usually below 90; metastylid not reduced. Manus tetradactyl, pes tridactyl; trapezium present; astragalus articulating with navicular only; articulating facets of proximal phalanges inclined to median axis of bones; limbs subequal in length.

SCHIZOTHERIUM Gervais, 1876

Schizotherium priscum (Gaudry)—Generic type. Phosphorites, Oligocene, France.

Schizotherium modicum (Gaudry).—Phosphorites, Oligocene, France.

Schizotherium ingens (Filhol). Phosphorites, Oligocene, France.

Schizotherium wetzleri (Kowalevsky). Aquitanian, Oligocene, France.

Schizotherium avitum Matthew and Granger. Ardyn Obo formation, Oligocene, Mongolia.

METASCHIZOTHERIUM von Koenigswald, 1932

Metaschizotherium fraasi von Koenigswald—Generic type. Upper Miocene, Germany and France.

Metaschizotherium bavaricum von Koenigswald. Upper Miocene, Germany.

POSTSCHIZOTHERIUM von Koenigswald, 1932

Postschizotherium chardini von Koenigswald—Generic type. Pleistocene, Nihowan, China.

PHYLOTILLON Pilgrim, 1910

Phylotillon naricus (Pilgrim)—Generic type. Bugti Beds, Lower Miocene, Baluchistan.

MOROPUS Marsh, 1877

Moropus distans Marsh—Generic type. Harrison formation, Lower Miocene, Nebraska.

Moropus elatus Marsh. Harrison formation, Lower Miocene, Nebraska.

Moropus senex Marsh. Harrison formation, Lower Miocene, Nebraska.

Moropus cooki Barbour. Harrison formation, Lower Miocene, Nebraska.

Moropus maximus Holland and Peterson. Harrison formation, Lower Miocene, Nebraska.

Moropus hollandi Peterson. Harrison formation, Lower Miocene, Nebraska.

Moropus petersoni Holland. Harrison formation, Lower Miocene, Nebraska.

Moropus parvus Barbour. Harrison formation, Lower Miocene, Nebraska.

[The foregoing species probably, for the most part, are synonymous.]

Moropus merriami Holland and Peterson. Virgin Valley formation, Middle Miocene, Nevada.

Moropus oregonensis (Leidy). Bridge Creek beds, Miocene, Oregon.

ANCYLOTHERIUM Gaudry, 1863

Ancylotherium pentelici (Gaudry and Lartet)—Generic type. Pontian, Lower Pliocene, Pikermi, Greece and Samos Island.

Of Uncertain Position

Pernatherium rugosum Gervais. Eocene, France.

THE EVOLUTION OF THE CHALICOTHERES

The chalicotheres would seem to have had their beginnings as small, unspecialized perissodactyls in North America. *Eomoropus amarorum* from the Eocene of Wyoming, a genus very close to the primitive titanotheres, is our first record of a definitely ancestral chalicothere. During the closing stages of the Eocene period the descendants of *Eomoropus* migrated from North America to Asia, probably by way of a trans-Bering land bridge, and in the oriental continent they spread over a broad area, enjoying a long period of untrammeled development. These primitive chalicotheres persisted through the uppermost stages of the Eocene in Asia and held over into the lower stages of the Oligocene, and they may be regarded as rather directly descended from *Eomoropus* of North America. They are represented by two genera, namely *Eomoropus* and *Grangeria*.

From these generalized Eocene chalicotheres two specialized phylogenetic branches arose and developed through the middle and upper portions of the Tertiary epoch. One of these groups, the Chalicotherini, typified by quadrate, brachyodont upper cheek teeth and short feet, was mainly Eurasiatic in its distribution. It enjoyed a long period of phylogenetic evolution through the Miocene and the Pliocene and into the Pleistocene, and it spread throughout Europe and Asia. It would seem, also, that in the Miocene certain members of this group (*Macrotherium*) crossed from Asia to North America.

The other group, the Schizotherini, typified by hypsodont, elongated cheek teeth and long feet, inhabited both Eurasia and North America. In the Oligocene the members of this group are well defined in Eurasia, but whether they were present in North America or not, is a question difficult to decide at this time. Chalicothere remains in the Oligocene of North America are extremely rare, to say the least. In the Miocene, however, we find members of this group in the Old World (*Phylotillon*) and in the New World (*Moropus*). This line persisted through the Lower Pleistocene in Europe and Asia.

Did the chalicotheres originate in North America, migrate to Asia, and then become extinct in America, only to reappear in a subsequent counter-migration from Asia. Our present knowledge of the distribution of the group would lend some weight to this idea. For instance, *Eomoropus* appears in the Eocene in North America, and slightly later in the Upper Eocene or Lower Oligocene of Mongolia and China. Then through the Oligocene we have no very conclusive records of chalicotheres in North America, although their remains are relatively common in Europe and Asia. Finally the two branches of advanced chalicotheres are found in North America, where they persist for but a short time. In Eurasia, however, these two branches of advanced chalicotheres undergo a considerable degree of adaptive radiation, and persist until and through the early Pleistocene.

Cope described "*Chalicotherium*" *bilobatum* from the Oligocene of Saskatchewan, on the basis of a very fragmentary specimen. Russell has recently made this species the type of a new genus, *Oreinotherium*. Unfortunately the status of this form is still a matter of some doubt.

Perhaps there was a series of migrations and counter migrations between North America and Asia. Perhaps the Old World was the center of adaptive radiation for the advanced chalicotheres, whereas the New World offered a haven for certain immigrant and restricted forms.

Of course these suppositions are little more than tentative specula-

tions. It must be admitted that the lack of chalicotheres in the Oligocene of North America is purely circumstantial, dependent on the chances of discovery and consequently is not a real index as to the presence or the absence of the group in the New World. If some really well-preserved remains of the Schizotherini were to be found in the Oligocene of North America, we would be justified in regarding *Moropus* as a truly autochtonous type, but until such a discovery is made, the possibility of *Moropus* being an immigrant form, descended from *Schizotherium* of Eurasia, remains strong. At any rate, from the above considerations, we may conclude that the chalicotheres form a group of North American origin, but primarily of Eurasiatic radiation.

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