THE CHALICOTHERES AS A BIOLOGICAL TYPE.

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EXTINCT animals occur in the strata of the earth's crust only as skeletons, often fragmentary. The restoration of an animal on the basis of such remains is a difficult task requiring great erudition in the student. It is still more difficult to write the history of the group to which the animal belonged, and the difficulty increases in proportion to the differences of the extinct animal from animals still living. Extinct animals with skeletons very unlike those of recent animals are often a real enigma.

For a long time when only limb bones of *Chalicotherium* were known, the animal was placed among Edentata because its powerful claws suggest those of a sloth. When other parts of the skeleton were found, *Chalicotherium* was placed among the Ungulata in the Perissodactyla, although it differed from all other fossil and living Ungulata [then known] in having claws, not hoofs.

Holland and Peterson (1913) in their monograph bring together a complete list of literature on chalicotheres for the period of 1825-1913. Their detailed quotations give a good idea of previous knowledge of this group of animals. In following years the Chalicotherioidea continued to be studied chiefly by Americans (e.g. Matthew, 1929; Colbert, 1935a, b). Russian literature on Chalicotherioidea is very small in amount for until lately only a few chalicothere bones had been found in Russia. Quite recently, however, the bones of chalicotheres have been found in large numbers in the Tertiary deposits of the Golodnaya Steppe in Southern Kazakhstan. Here the Lower and Upper Tertiary strata are separated by a layer of conglomerate with abundant bones and teeth of mammals. The great majority of these bones belong to a large chalicothere. It has been possible to assemble an almost complete although composite skeleton, to study its elements in detail, and to come to conclusions about the habits of the animal and its phylogenetic relations (Borissiak, in press).

In the skeleton of chalicotheres (Fig. 1), striking features are the rather long neck, the small skull, the comparatively long and thin fore limbs, and the short, massive hind limbs. The feet were digitigrade and the replacement of hoofs by claws was especially well developed on the fore limbs.

In some species of chalicotheres the skull is long and low (like the skull of the horse), but in other species it is short, resembling, in these instances, the skull of a bear. The skull

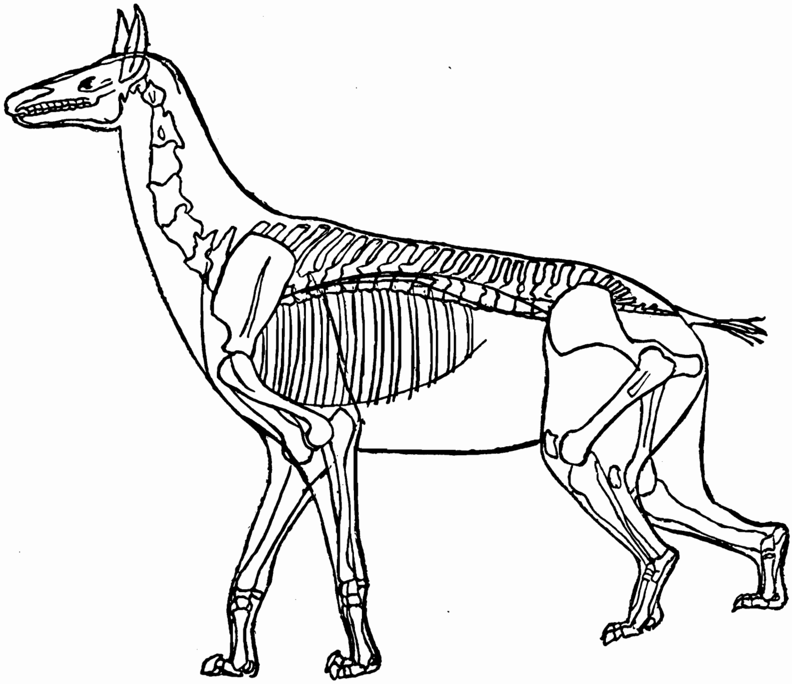

Fig. 1. Restored skeleton of *Phyllotillon betpakdalensis* (Flerov) from the Tertiary of the Golodnaya Steppe.

has characters of primitive Perissodactyla (tapirs, early titanotheres) but also a few characters known only in chalicotheres (e.g. two deep impressions on the sides of the presphenoid). The structure of the cervical section of the vertebral column was very peculiar. It was rather long and at the same time very massive, especially in comparison with the small skull. The vertebral centra were reduced relative to the well developed, flattened neural arches, which bore strong zygapophyses. Such a structure shows that the dorsal muscles of the neck were very strong in comparison with the relatively weak ventral muscles—relations opposite to those observed in typical Perissodactyla.

The structure of the fore limbs, particularly of the manus, was very peculiar and unlike that known in any other mammals. In the most specialized forms, only three of the four digits articulated with the carpus, the fourth and smallest digit being joined to the proximal part of the neighboring digit. The chalicothere carpus was low, with a small, narrow os magnum. The last character distinguishes chalicotheres from horses, the os magnum of which is large, low, and flat, but in this respect chalicotheres are closer to titanotheres. The articulation of the carpus with the fore arm was a transverse arc which per-

Fig. 2. The second digit of the manus of *Phyllotillon betpakdalensis* (Flerov).

mitted considerable swinging of the manus to both sides. Articulation of carpus with metacarpus was very abrupt. On the anterior side of the distal bones of the carpus and on the proximal ends of the metapodials there are rugose swellings for the attachment of strong extensors, while in perissodactyls and in mammals in general limb flexors are usually more strongly developed than extensors. A walking or running animal pushes itself from the ground by flexing its limbs while extensors are used only to bring the limbs to a new place ahead, which is much easier work. The anterior muscles of the chalicothere scapula were also stronger than the posterior. The anterior faces of the metacarpals were evenly convex in all directions, as in some carnivores. The structure of the phalanges was particularly remarkable (Fig. 2). The second digit was stronger than the others (absence of tridactylism). The metacarpal facet of its first phalanx was not on the proximal end, but had moved to the anterior (or dorsal) face of the bone. In other digits this displacement was not so great; the facets here only cut off the anterior edge of the proximal end of phalanges. In other words, the metacarpal and first phalanx of the second digit were joined together at a right angle, not in a straight line. The first and second phalanges were often coössified. The ungual phalanx, again, met the second phalanx at a right angle. In this way was constructed a strong, flat, triangular claw with only slight movements in its parts. The whole digit was bent twice at right angles, forming a very strong hook. This structure was similar in the other digits but not so well developed as in the second. Separate segments of digits were only slightly movable but the digits as a whole had a wide movement owing to the spherical shape of the distal ends of the metacarpals.

The hind feet had in general the same structure but it was not so well developed as in the fore feet: the metatarsals had no distal swellings; the distal facets were not all spherical in shape; etc. The feet were tridactyl with a long middle digit, the metatarsals were more or less shortened, and the whole specialization of the phalanges was less advanced than in the fore feet. The hind feet were more massive than the fore feet; the calcaneum was low; the astragalus was straight-sided and almost without a neck; etc. On the whole, this is a rare case in which the specialization of fore and hind limbs has gone in different directions.

As in all animals, one group of anatomical characters changed constantly as the result of growing specialization in adaptation to the environment, while other inherited characters did not change and were common to all chalicotheres. The latter show the systematic position of the animals and in this case demonstrate that the closest relationship of the chalicotheres is with the titanotheres.

This relationship is particularly shown by the structure of the teeth of chalicotheres, which is similar to that of early and primitive titanotheres in which the upper molar crowns still had transverse lophs connecting the ectoloph with the lingual tubercles (protocone and hypocone). In the later titanotheres, the upper molars lost their transverse lophs. In chalicotheres the upper molars remained the same with surprising conservativeness. The only difference between the earlier and later forms is that the molars were more hypsodont in the latter. In their shape the teeth of chalicotheres represent the best developed browsing type. They were not good for hard grasses, much less for food with remnants of soil, such as bulbs, etc., but were exclusively adapted for soft leaves and branches. The cutting sides of the upper and lower molars worked like sharp scissors, while the strong inner tubercules were for grinding branches and leaves. The structure of the skull was also very similar to that of the early hornless titanotheres, although horns were so typical for the later titanotheres. In the skeleton there are also a great many characters suggestive of titanotheres. In spite of the great specialization of the cervical section of the vertebral column of chalicotheres, the atlas had exactly the same shape as in titanotheres. There is a great similarity in the structure of scapula, humerus, radius, and ulna. The structure of carpus and manus is particularly striking. The small, narrow but high magnum, the very peculiar scaphoid with a small, downwardly directed projection, the abrupt articulation of the phalanges with the carpus, the dilated proximal end of the ulna, the arcuate articulation between the fore arm and the manus—all these characters leave no doubt as to the relationship of the two groups, but weigh against any connection with horses, with which chalicotheres have occasionally been compared because of a certain similarity in the shape of their skulls. (In some restorations, chalicotheres were pictured with horse-like heads and long, curly manes.) The femur had a symmetrical vertical trochlea for the patella. There were also a great many resemblances in the bones of the tarsus. In general the chalicothere pes was more like the titanotheres than was the manus, as a result of the greater specialization of the fore limbs than of the hind limbs in chalicotheres. For example, the pes was typically tridactyl while tridactylism was lost in the manus.

The close relationship of chalicotheres with the early members of the titanothere family gives us an example of the application of Cope's law according to which the origin of a new group is usually from the less specialized forms of the old group.

We pass now to consideration of the characters of the skeleton of chalicotheres dependent on adaptation to their living conditions. New characters in the structure of the skeleton did not, of course, become fully developed at once. They are rather little developed in the Eocene chalicotheres of America and Asia. Even in the Oligocene forms of Europe and Asia they are still not completely expressed.

What were the living conditions that produced such a peculiar structure of the chalicothere skeleton? From the very beginning of the study of chalicotheres many attempts were made to answer this question. The structure of the feet was explained, for example, as an adaptation to digging, to climbing on trees, to catching tree branches in order to bend them to the ground, etc. (Abel, 1920; Gaudry, 1867; Koenigswald, 1932; Matthew, 1929; and others). Some of these ideas, often mutually exclusive, have been abandoned but a few are still accepted.

We have already seen that the neck and fore limbs of chalicotheres had a different structure from typical ungulates. In the neck the strongest muscles were dorsal, which shows that the animal pulled the head and neck upwards and backwards more often than down to the ground. In the fore feet extensors were stronger than flexors, which tells us that the fore feet were used less for walking than for some other work. This brings us to the conclusion that the normal position of the animal was standing on its hind feet while using the fore feet for clinging to the bark of trees when feeding on leaves and tender branches (Fig. 3). The recent goat climbs in this way when hunting after the leaves of large trees. Lifting the fore limbs for such climbing uses the extensors of the whole fore limb from the manus to the scapula. During feeding the head was moved backwards to pick up leaves distant from the trunk of the tree. The small size of the head was favorable for this operation of the neck. Chalicotheres did not embrace the tree trunk with their fore limbs but, in a manner of speaking, walked on the trunk. The manus was particularly well adapted for such "walking." The claw of the second digit was a strong hook which was driven into the bark of the tree more deeply as more pressure was placed on it.[1] Other digits helped the second very effectively, as each of them could change its place on the trunk with ease. Strong extensors not only raised the manus but also made it very stable. The arcuate articulation between the fore arm and the carpus made side movements of the whole manus very easy when the animal was looking for the best place on the trunk.

[1] This principle is used in hooks or hangers that are driven into a wall and support considerable weights.

The structure of the hind limb supplements the preceding picture. During feeding the animal stood on its hind feet only,

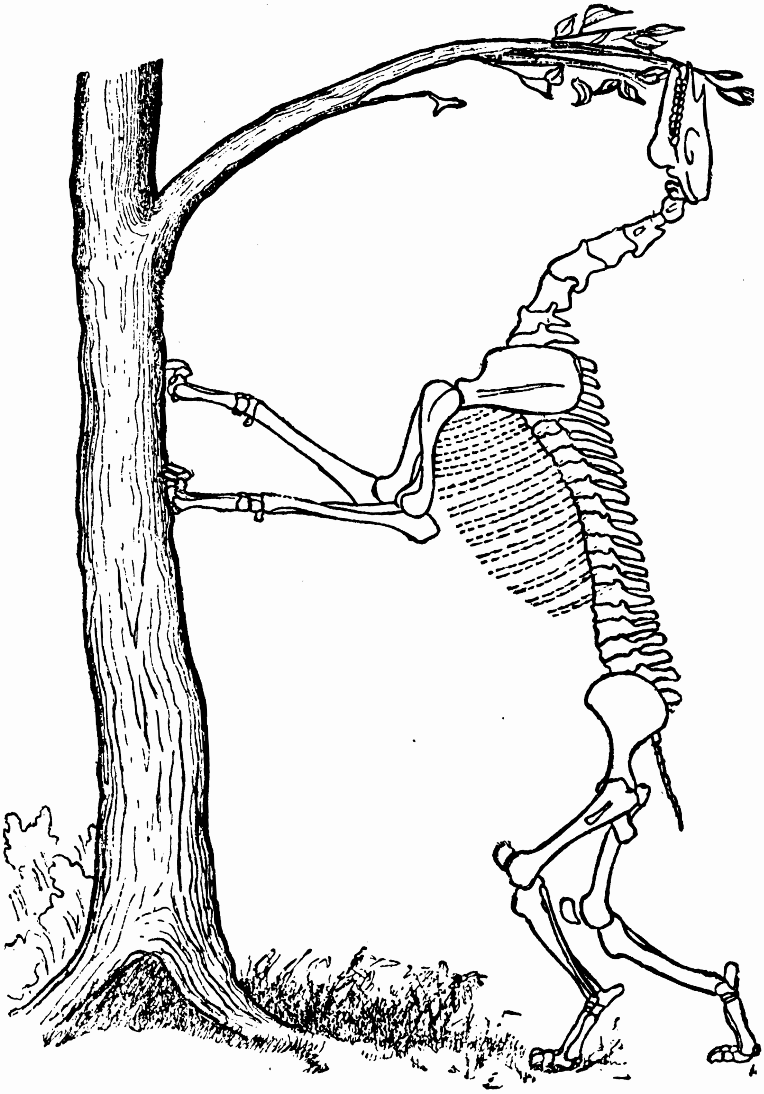

Fig. 3. The posture of the skeleton of *Phyllotillon betpakdalensis* (Flerov) when the animal was feeding.

and these were therefore constructed like the feet of heavy animals and were much heavier than the fore feet. In the forms of later geological age, the hind feet can be compared with the feet of mastodons for massiveness. The astragalus was flattened and moved on the cuboid, the metatarsals were shortened, and the foot was less specialized than the manus. The claws were not so strong and tridactylism was well developed, while in the manus this development was hindered by the structure of the second digit.

Such is the biological type of the chalicotheres as disclosed by the study of their skeletons. This type arose as an adaptation to the environment. This adaptation is of a different degree in chalicotheres of different geological ages, becoming greater and greater with time.

It has been mentioned in the literature that the biological type of the chalicotheres resembles that of the giraffes. The specialization of the two animals was, however, in different directions. The whole skeleton of the giraffe was specialized for feeding on the leaves on the top of trees and did not progress any further. When the chalicotheres had their fore limbs on the ground, as they certainly sometimes did, they would become normal ungulates. Giraffes live in African savannas with scattered groups of trees. Chalicotheres apparently dwelt in dense forests where they had good protection and no competition because of their high adaptation to this environment. Chalicotheres survived through the whole Tertiary and died out only after that period in spite of their generally primitive inherited organization. Titanotheres, from which chalicotheres arose, had already become extinct in the Oligocene when there appeared the (better adapted) rhinoceroses.

The problem of the study of fossils is primarily a morpho-ecological analysis of the fossil skeleton. This analysis enables one to distinguish the rather stable inherited characters from those that were the result of adaptation to the environment. The latter characters permit reconstruction of the biological type of an animal and understanding of its ecological relations. This work is, however, only a preparation for another important task of the paleontologist—discovery of the phylogenetic relations of the given form. This can be done by the comparative study of restored representatives of the group. Such a study permits determination of the phylogenetic relationships of each form in reference to the other representatives of the group, in other words discovery of the place of each form in a common genealogical tree.

The peculiar specialization of the chalicotheres developed gradually. The various representatives of this group, about twenty forms altogether of different geological ages, show different degrees of specialization, which was greater in the forms of later epochs, although we cannot establish an uninterrupted line with gradual modification. On the contrary, practically every form shows some peculiarities comprehension of which is rather difficult, chiefly because the material for study in most cases is very fragmentary. Among these peculiarities is the striking fact that the molar crowns are subquadrate in a few forms but elongated in others. Classification of chalicotheres has generally been based on this character. There have been attempts to bring these variations in the molars into correlation with differences in the structure of the skeletons. Relatively few skeletons are known, however, and associations with the teeth have been only occasionally established. New materials from the Tertiary of the Golodnaya Steppe have showed, however, that all Old World forms are very similar to each other in skeletal structure, whether the molar crowns are short or long. On the other hand, North American forms with long molar crowns, like those of some Asiatic and European forms, have skeletons of quite different type.

It is possible to think of the chalicotheres, after their separation from the titanotheres in the Eocene, as developing further into two separate lines, one in the Old World, and one in the New. Each line developed a number of branches. In Europe there evolved two well defined branches distinguished by the structure of their molars. This is all we positively know on the basis of the present material. Undoubtedly the history of the chalicotheres was much more complicated. A few observations demonstrate that there were subbranches, more especially in the beginning of chalicothere history, which became extinct without leaving any descendants. The genealogical tree of the chalicotheres is composed of several branches, the number of which will increase with discovery of new materials. Each branch of the genealogical tree of the chalicotheres represents a distinct direction of their evolution. The place of every form of chalicothere in this tree depends, first, on its pertinence to one or the other of the two main lines (according to which direction of evolution is typical for this form) and, second, on the degree of specialization. Direction and degree of specialization, like mathematical coördinates, determine the exact place of each form on the corresponding branch. To illustrate these statements we shall bring together information about the best known species of chalicotheres.

The most ancient representative of the Chalicotherioidea is *Eomoropus amarorum*, from the Middle Eocene of Northern America (Osborn, 1913). It was an animal of about the size

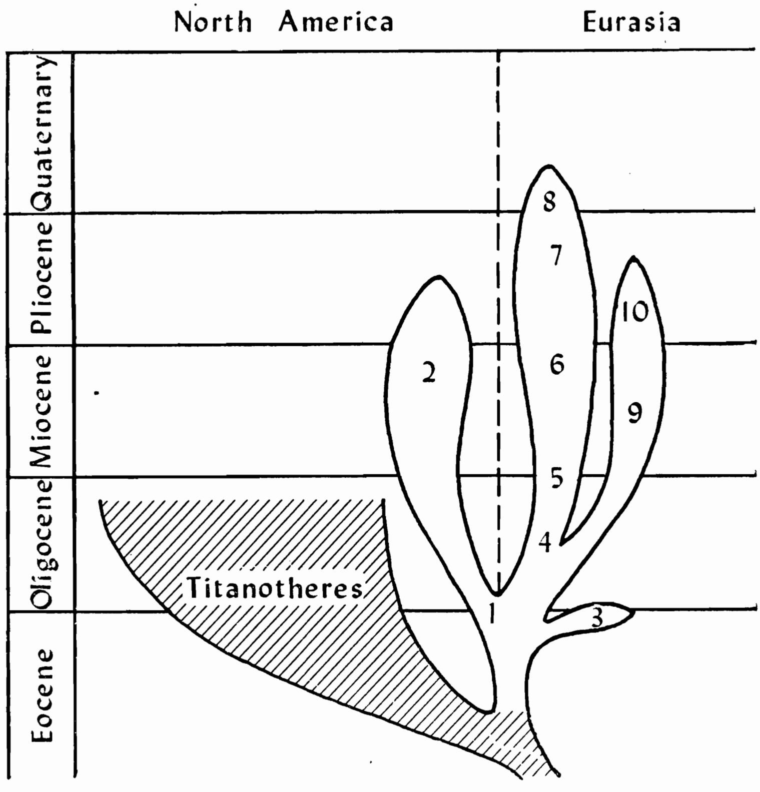

Fig. 4. Phylogenetic scheme of the Chalicotherioidea.
1, *Eomoropus.* 5, *Phyllotillon.* 8, *Postschizotherium.*
2, *Moropus.* 6, *Metaschizotherium.* 9, *Chalicotherium.*
3, *Grangeria.* 7, *Ancylotherium.* 10, *Nestoritherium.*
4, *Schizotherium.*

of the sheep with only insignificant specialization: the cervical vertebra did not show noticeable alterations but the metacarpals had already changed typically for the group in their general shape and joint structure, although they did not yet have callous swellings on the anterior side of the proximal ends. The specialization of the hind feet was still less advanced.

From the Asiatic Eocene isolated teeth are known about which it is not possible to say anything definite. They might belong to *Eomoropus* or to some new genus. At the end of Eocene in Mongolia lived *Grangeria*, a very peculiar form in the structure of its dental apparatus and limbs. *Grangeria* represented an early and short-lived side branch of chalicotheres.

In the Oligocene the European line is represented by several poorly known species of *Schizotherium*, still small animals. A few forms (*S. modicum*) had long molar crowns. The separation of the Chalicotherioidea into those with short and those with long molars had thus begun at this time.

At the end of the Oligocene or beginning of the Miocene in Middle and Southern Asia there lived large chalicotheres with long molars belonging to the genus *Phyllotillon* (Pilgrim, 1912). To this genus belongs *P. betpakdalensis* (See Borissiak, in press; Flerov, 1938), from the Golodnaya Steppe. Owing to the abundant material it is one of the best known chalicotheres. The specialized structure of the skeleton of *P. betpakdalensis* has already been described above. A few bones of *S. turgaicum* from the Middle Miocene of Turgai show remarkable similarity to the bones from the Golodnaya Steppe, but belong to an animal of a smaller size. In this case we have forms of the same branch but with different degrees of specialization determining their respective places on the branch. Another species of *Phyllotillon* lived simultaneously in the valley of the Indus River (Pilgrim, 1912).

In the Miocene also, but a little later than *Phyllotillon betpakdalensis*, there lived in North America *Moropus elatus* (see Holland and Peterson, 1913), a species with long molars very similar to those of *Phyllotillon* and similar also in degree of specialization, but different in the structure of various parts of the skeleton. *Moropus* is a representative of the American chalicothere line.

In the Miocene of Europe lived *Macrotherium*, known from fairly complete fossil remains. *Macrotherium* represents the short-molar branch of Eurasiatic chalicotheres. In spite of its short molars, *Macrotherium* was closer in skeletal structure to *Phyllotillon* than to the American *Moropus* with its long teeth. *Macrotherium* and *Phyllotillon* thus belonged to the same European trunk although to different branches.

In the Pliocene both branches of the European trunk were represented by the largest species of chalicotheres. The form with long teeth is *Ancylotherium* found in the Pikermi Fauna of Greece (Gaudry, 1867). Its hind limbs resemble the limbs of a mastodon in massiveness. The Quaternary representative, *Postschizotherium*, of the same trunk had very strongly developed hypsodont teeth. The branch with short molars was also represented in the Pliocene and Quaternary by big animals.

Such is the history of the chalicotheres as far as it can be represented at the present time. Remains of chalicotheres are still very scarce and it is therefore impossible to make a complete genealogical tree with all branches and subbranches. Altogether we know about fifteen forms which can be placed at different points along a few branches. The task of the paleontologist is to find the position of these points on the branches on the basis of the coördinates as worked out above, and in this way to establish the phylogenetic relationships of the known forms.

We have, however, no basis for connecting these points by lines. This would give the idea of the direct descent of one form from another, which as a rule cannot be proved. In only one case is it possible to show with certainty the pertinence of two forms of different specialization to the same branch. This refers to *Schizotherium turgaicum* and *Phyllotillon betpakdalensis*. This does not mean, however, that one of these forms developed directly from the other and that the two can be connected by a straight line. We prefer to represent the branches as elongated leaves, on which are shown the different forms of chalicotheres according to their mutual relationships.

The study of chalicotheres shows us what paleontology can do for the history of the organic world. We can establish the ecological characters of animals and reconstruct the whole animals. The study of the genera of chalicotheres permits establishment of their phylogenetic relations.

Fossil remains are not complete and paleontology alone cannot decipher the complete history of animals and plants. It needs support from the other biological sciences dealing with recent organisms. But since paleontology alone has all the historical data, its conclusions check the deductions of other biological sciences.

Paleontology has not, however, said its last word. It still lags behind other biological sciences. Not only before but even since Darwin it has usually been in the service of geology, which has always made special demands for paleontological data. Only now are the possibilities of paleontology for the elucidation of many biological problems becoming clear. In the achievement of independence from geology and in becoming a great biological science, Soviet paleontology occupies a leading position.

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