Dinosaurs - Without the Sensation*
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In the 1920s the American Museum of Natural History mounted an expedition into Mongolia to search for evidence of the Central Asian origins of man. They discovered the skeletons of predatory and herbivorous dinosaurs. These discoveries became a scientific sensation: until that time dinosaurs had been discovered in Europe, North America, and Africa. In the late 1940s a paleontologist expedition from the Academy of Sciences of the USSR under the direction of scientist and author I. A. Efremov discovered one of the most bountiful dinosaur graveyards in the Late Cretaceous deposits of the Nemegt basin. This graveyard yielded the skeletons of giant predatory and duck-billed dinosaurs that became some of the most spectacular exhibits at the Paleontological Museum in Moscow.

Since 1969, the Joint Soviet-Mongolian Paleontological Expedition has worked every year in the Gobi Desert. During these 20 years more than 30 nearly complete skeletons have been discovered (many of these are now on display at museums in Moscow and Ulan Bator). Along with these skeletons a large number of bone fragments, skin impressions, entire eggs and clutches, and shell fragments have also been discovered. From these discoveries 16 new species of dinosaur have been defined, some of which remain to be studied. It was revealed that these are animals from the same large taxonomic groups that were already known from discoveries in other continents. Only the prosauropods, which had been discovered previously in the Late Triassic of Eurasia, Africa and America, and the ceratopsians, whose remains have been found in Upper Cretaceous deposits of North America, were absent.

We have found Mongolian dinosaur bones only in Cretaceous deposits. Judging by these remains, the dinosaurs had already become numerous and diverse in the Lower Cretaceous. The herbivorous ornithopods and ankylosaurs (armored dinosaurs) were in the majority, somewhat fewer were the predatory theropods. The Upper Cretaceous deposits were even more bountiful: we did not expect to find so many species and such a vast number of bones. In terms of the number of dinosaurs in the fauna, the Gobi region of Mongolia may equal that of the entire North American continent.

The most abundant material gathered in Mongolia allowed us to trace the evolution of two large dinosaur groups—theropods and ornithischians—and to sometimes understand the ecological reasons that led to the appearance of many smaller taxonomic units.

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It was difficult to presume that in almost every evolutionary line of bipedal theropods, i.e., capable of moving on only their two hind legs, that an entire series of avian features would distinctly manifest themselves: some had morphological features similar to the famous "first bird" *Archaeopteryx*, and others had features similar to birds.

A small group of theropods that was almost lacking in avian features, the tyrannosaurs, were the largest predators that ever lived on Earth. These animals were as much as 13 m long and walked on powerful hind legs. The first discoveries were made in the Upper Cretaceous deposits of North America and they were no less diverse in Mongolia. It has been revealed only very recently that they fed not only on live prey, but on carrion as well. Some features of their structure give us reason to think that they were good swimmers.

The ornithomimosaurs, or ostrich-like dinosaurs, have long been known from American discoveries. Instead of teeth they had a horny rostrum, and long forelimbs that ended in a tridactyl hand that they could have used to capture prey. But in America these were only specialized, morphologically monotypic forms; in Mongolia they are unexpectedly diverse—from primitive forms with several slightly developed teeth to forms with a powerful avian rostrum. Some Mongolian ornithomimosaurs moved on two legs, similar to modern marsh birds. Others, with large laws on their hands, could probably have traveled on four legs.

The Mongolian discoveries provided new data about the morphology of various small theropods that could eat different foods and live in diverse environments: typical dromaeosaurs and oviraptors that could live in water and on land had a massive horny rostrum to crush hard vegetation like nut shells or mollusk shells.

We have observed skeletal fragments of therizinosaurs and segnosaurs related to theropods, which to this day have been found nowhere else but Mongolia. We have studied them carefully but many of their morphological features remain a mystery. For example, what function did the hypertrophied forelimbs of *Therizinosaurus*, with flat claws more than a meter long, serve? Or the horny rostrum (which, by the way, is extremely widespread among dinosaurs) and small curved teeth of the erlikosaurs and segnosaurs? We assume that these theropods changed their diet to social insects or even vegetation.

Despite their common structure, the theropods were nevertheless quite diverse morphologically. This is apparently due to the variety of their ecological niches. If we make our judgments based on their morphological features, the theropods cannot be thought of as exclusively predators: some of them could have fed on carrion, others on mollusks, a third group on insects, and a fourth group was apparently omnivorous.

These conclusions are important and interesting in their own right, although I believe it is even more interesting that the possibility for substantiating the origins of avian flight and of the birds themselves has been revealed. Over the last decade renewed interest in this important, unresolved paleontological problem has been aroused, and a unique model has been found among the Mongolian theropods that may be used to trace the evolutionary changes that led to birds. This is the specialized group of avimimids, which had avian and theropod features in almost equal measure.

In the previous century naturalists began looking for bird ancestors and the mechanisms that gave them the ability to fly. T. Huxley thought bird ancestors began to fly after they had mastered gliding, by leaping from tree to tree. Thus arose the "arboreal" theory that is still supported by most specialists today. Not long afterward, the American S. Williston advanced the "ground" theory in which birds began as bipedal cursorial dinosaurs: as they ran and leapt, they helped themselves by flapping their forelimbs, which gradually evolved to wings.

In either theory the birds are linked with *Archaeopteryx*—the most ancient feathered reptile (from the Upper Jurassic of western Europe), which is sometimes called the first bird. Adherents of one hypothesis consider it an aerial animal, other consider it a ground animal. It is now apparent that the contradictory interpretations of *Archaeopteryx*'s morphology do not resolve the problem of bird origins. In my view this will be helped by the "ornithization" of *Avimimus* that occurred over a long period of time.

In many of its skull and skeletal features it is similar to the small theropods, but some morphological features show that *Avimimus* had developed a feathered covering. Thanks to the special structure of the ulnar articulations, when the extremities flexed, the forearm automatically rotated around the long axis and flexed the carpometacarpal joint. The movements of the various joints are connected in exactly the same way in all flying birds, which promoted the folding and unfolding of the wings and flight feathers. *Avimimus* metacarpals are compacted into a powerful formation—a clasp that exists only in birds and attaches the large primary flight feathers. According to other features the wings themselves were short and wide (with long secondary flight feathers) and poorly adapted to flight. *Avimimus* probably could only take wing like modem chickens, tinamous, and water rails while hunting or when in danger, but it remained a cursorial bipedal theropod and only attempted to master the air as a means of travel. But these attempts could hardly have been successful if *Avimimus* had not been warm-blooded— flight is an extremely energy-consumptive activity and requires an intense metabolism. The possibility that many of the small cursorial theropods were warm-blooded has not been excluded.

The Mongolian material allows us to refine the genetic links among birds. The morphological commonality of theropods, especially *Avimimus*, with birds may attest to direct genetic links between these groups or to their parallel development. There are practically no explicit signs of kinship other than the structure of the forearm, which is identical with that of birds. *Avimimus* was probably a parallel branch of theropods that led to the flying forms. In my view the evolutionary branch to birds must have come from theropods, but from far more ancient forms than *Avimimus*.

Although *Avimimus* would not have been a direct ancestor of birds, it and others undoubtedly led a unique lifestyle and consequently acquired a unique structure (feathering, wings) that was affiliated with flight. The path that led to the manifestation of wings and feathers was similar. The direct ancestors of birds, such as the cursorial bipedal theropods, especially *Avimimus*, learned to fly not by climbing trees and gliding downward, but merely by running along the ground. Consequently, bipedal locomotion preceded flight with no intermediate arboreal stage. This is easy to understand if we consider that the rudiments of wings provided locomotor advantages—running and leaping became more stable. The morphological bias of *Avimimus* confirms that we must look for the bird ancestors among ground-dwelling forms.

Another large group of Mongolian reptiles is the ornithischians. During the Lower Cretaceous the most widespread of these were the small bipedal ornithopods—psittacosaurs, which had a rostrum much like that of parrots. They were probably lakeshore dwellers because we have found their skeletons in lake deposits, less frequently in river deposits.

At the same time, and also by the lakeshores, lived the iguanodonts, which for unknown reasons abandoned the areas inhabited by psittacosaurs (their remains have not been found together). Interestingly, the single Mongolian species of iguanodont is assigned to a new genus that was transitional between ornithischians and duck-billed dinosaurs.

A large number of the skeletons found in Upper Cretaceous deposits are those of duck-billed dinosaurs (hadrosaurs). All things considered, their habitats were their graveyards and their bones saturated the rock. The hadrosaurs found in Mongolian deposits were fewer (four genera) than in the North American deposits (15 genera) and they were more primitive. The most ancient of these were mid-sized (5–6 m long) and combined the features of the flat-headed and helmeted forms.

Among the most interesting discoveries are the ankylosaurs. Some of their morphological features: the large osseous "club" at the end of the tail that was used as a defensive weapon, the skin ossifications on the sides, and spines that had numerous traces of blood vessels (grooves or channels), are unusual. The blood flow rate of the ankylosaurs varied, whereby they varied the rate at which they exchanged heat with the environment; i.e., they possessed a primitive, passive temperature-regulating system. On the strength of all the taphonomic data (frequent accumulation of skeletons) and morphological features (wide, f1at ribs, the end phalanges of the digits similar to hooves) the ankylosaurs are closer, in terms of their lifestyle, to the hippopotamus rather than the purely land-dwelling animals as some specialists have suggested. The work of our expedition has increased the number of known ankylosaur genera to nine. Because only two genera of dinosaur from the family have been found in North America, and they are evolutionally younger, we are forced to conclude that the most ancient of these appeared in Asia.

Unexpectedly bountiful in terms of the number of species were the protoceratopsians—members of the horned dinosaurs (ceratopsians). This form is basically 1.5–2 m long with a small horn on its nose or without and an osseous "collar" covering the neck. But giant forms whose skull is more than a meter long have been found. From the number of genera in this family and in the family of true horned dinosaurs, we may assume that both groups dominated the local fauna almost equally. Although it has not yet been established who were the ancestors of the homed dinosaurs (psittacosaurs were closest to them of all), there are compelling reasons to think they arose in Central Asia as a number of hornless forms and later spread eastward, becoming the true horned dinosaurs in America.

Some of the Gobi deposits were very rich in eggshells and entire clutches. Interestingly, according to the data of K. E. Mikhailov, our co-worker at the Institute, the microstructure of the eggshells of predatory dinosaurs are identical to those of modern birds. This is yet another feature that supports the phylogenetic similarity of theropods and birds.

From the egg clutches of theropods, sauropods (sauropterygia), hadrosaurs and various protoceratopsians that have been preserved, we can make some judgments about how the various dinosaur forms behaved. Sauropod, like the modern sea turtles, apparently laid their eggs randomly in a shallow pit dug in the ground; protoceratopsian clutches were more complex: very long eggs were laid in pairs in a circle in two or three layers, or laid vertically (for better gas exchange), and apparently were laid with vegetation, otherwise they could not have survived. The clutches of predatory dinosaurs were probably like the nest-incubators of the modem Australian weed chickens. Many dinosaurs laid their eggs in the same location for several years in succession. Parental care was not alien to theropods: in one clutch we found small bones of different animals, apparently the remains of food that was bought to the young.

Having examined, albeit briefly, the diversity of dinosaurs and their characteristics, we will now turn to their evolutionary history. To do this we will compare the dinosaurs from Central Asia and North America. These continents were not separated by the Bering Strait during the Cretaceous Period; hence there was no impediment to them resettling and migrating from one continent to the other. The truth is that, judging by the Late Cretaceous Mongolian dinosaurs, they moved from Asia eastward.

The fauna of Mongolia is in many ways similar to that of America at the level of order and superfamily. For example, the same groups have been discovered in the Nemegt basin as in Montana or Alberta: diverse predatory dinosaurs, duckbills, armored, horned, and others. Mainly among theropods are there endemic groups. But starting from families, essential differences manifest themselves: if one group of dinosaurs or another had developed mainly on one continent and their closest relatives were few in number, then the opposite situation occurred on the other continent. Thus, the protoceratopsians were dominant in Central Asia (two more species were found there) and members of the ceratopsian families, if there were any, were in the minority. Eight species of true horned dinosaurs were found in North America, but only two species of protoceratopsian. The ankylosaurs were widespread in Asia and extremely rare in America where other armored dinosaurs—nodosaurs—were dominant, but generally unknown in Asia. On the whole, ornithischian dinosaurs were more diverse and numerous in America, but in Asia it was theropods that were more numerous and diverse. There is no satisfactory explanation as yet for this phenomenon, but possibly, the monotony of the physical and geographical conditions of Central Asia during the Cretaceous was thus reflected. During this period the local climate and landscape were quite different than in North America. The habitats of Mongolian dinosaur were much farther from the sea, where the seasons were more distinct and the climate more severe and arid.

The climate became especially hot and arid at the end of the Early Cretaceous. The psittacosaurs and iguanodonts that also lived in water basins prevailed among the fauna of this period, and the others (theropods, stegosaurs, ornithopods, ankylosaurs) were encountered with roughly the same frequency. Apparently a large number of weakly flowing lakes with irregular mode and slight grassy vegetation along the shores (the main food of psittacosaurs) was the reason for their widespread habitation.

At the beginning of the Late Cretaceous the climate became wetter, and the number of forms associated with water—hadrosaurs (as the crocodiles)—increased and settled widely in low swampy ravines, and the variety of theropods and ankylosaurs increased.

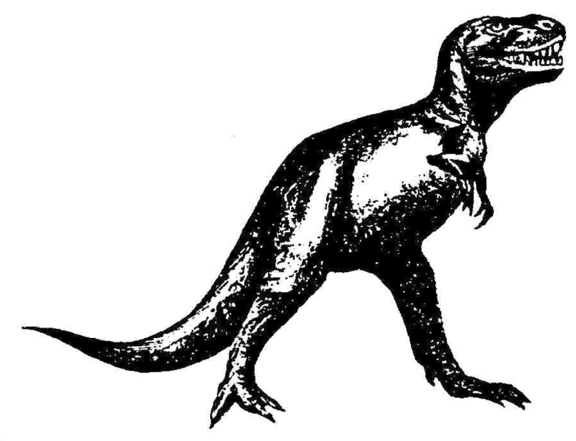
In the arid and semiarid climate that was later established, hadrosaurs almost disappeared, and protoceratopsians dominated the fauna: theropods, ankylosaurs, and sauropods became rare. It is quite conceivable that protoceratopsians were the ecological analogs of psittacosaurs: they had similar jaw and tooth structures and were equally widespread under similar paleogeographic circumstances.

Afterward a new cycle of wetting set in, and a network of rivers appeared, although the lakes remained (one of which existed at the site of the largest deposit in the Nemegt basin). The fauna achieved its greatest diversity: theropods, hadrosaurs, ankylosaurs, sauropods and other reptiles became numerous. Surprisingly, it was not hadrosaurs, which were capable of living in water or on land, that dominated, but theropods, among which numbered the largest predators—tarbosaurs—which apparently captured prey in the water. Somewhat smaller were the ornithomimosaurs—*Gallimimus*. In comparison with previous centuries in the Cretaceous, the relationship of predatory and herbivorous animals changed drastically during this time period. A number of specialists have used this relationship in modern mammal societies, along with some features in the skeletal structure, and have concluded that the large predatory dinosaurs were warm-blooded. The composition of the Nemegt fauna, however, in which predators clearly dominated, contradicts this confusion.

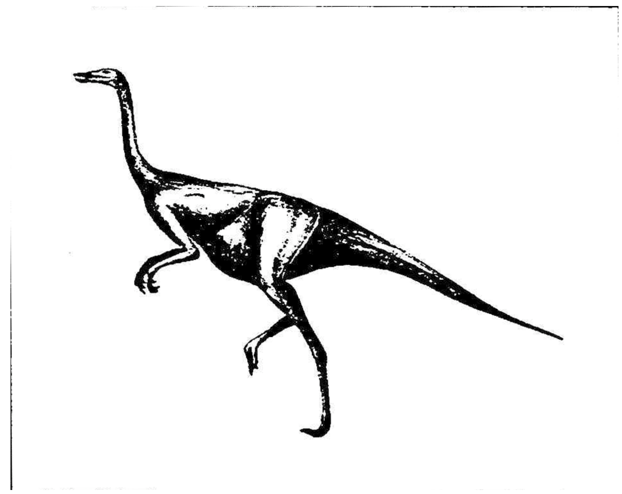
And last, without which no discussion of Mongolian dinosaurs would be complete, is the problem of their extinction—a problem that non-specialists love to discuss. Unfortunately, the material discovered by our expeditions does not provide any grounds even for us, specialists, to draw unique conclusions. The fact is that to this day there are no known remains of dinosaurs who were the last of their kind that lived at the boundary between the Cretaceous and the Paleogene. There are extremely few deposits of this age other than two small portions, which contain extremely poor paleontological material—only eggshells and a few oviraptorid bones. In all of the Mongolian deposits dated to the end of the Cretaceous and the sections upward, the number of dinosaur bones decreases significantly. For this reason there is no basis for a natural extinction of the species (the "lifetime" of a species is estimated to be roughly 1.2 million years) that would replace catastrophic extinction.

The dinosaur burial grounds have been fairly thoroughly studied over the last two decades. This does not mean, however, that Mongolia has nothing further to offer. Almost every season in the field yields discoveries of new species. We do not delude ourselves with hopes of finding unknown giants such as the tarbosaur, but smaller members of new species will undoubtedly be discovered. The study of material accumulated during the last twenty years goes on. The Mongolian dinosaur differ from others in several features that may seriously influence our concepts of this group of fossilized reptiles.

FIGURES

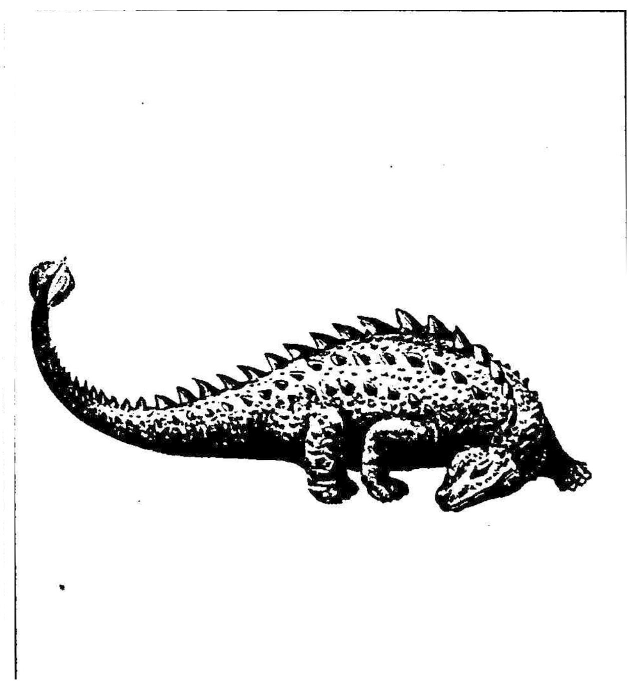


Tarbosaurus—one of the largest predatory dinosaurs.



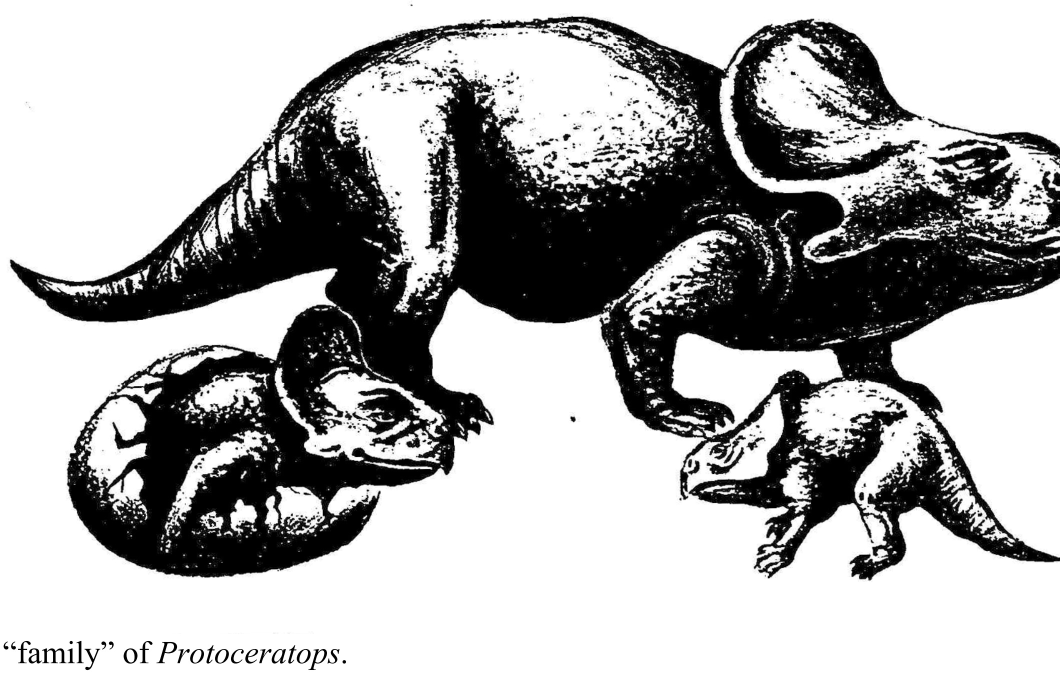
Gallimimus—an ostrich-like dinosaur.

Avimimus—looks like a bird but its skeleton is theropod.

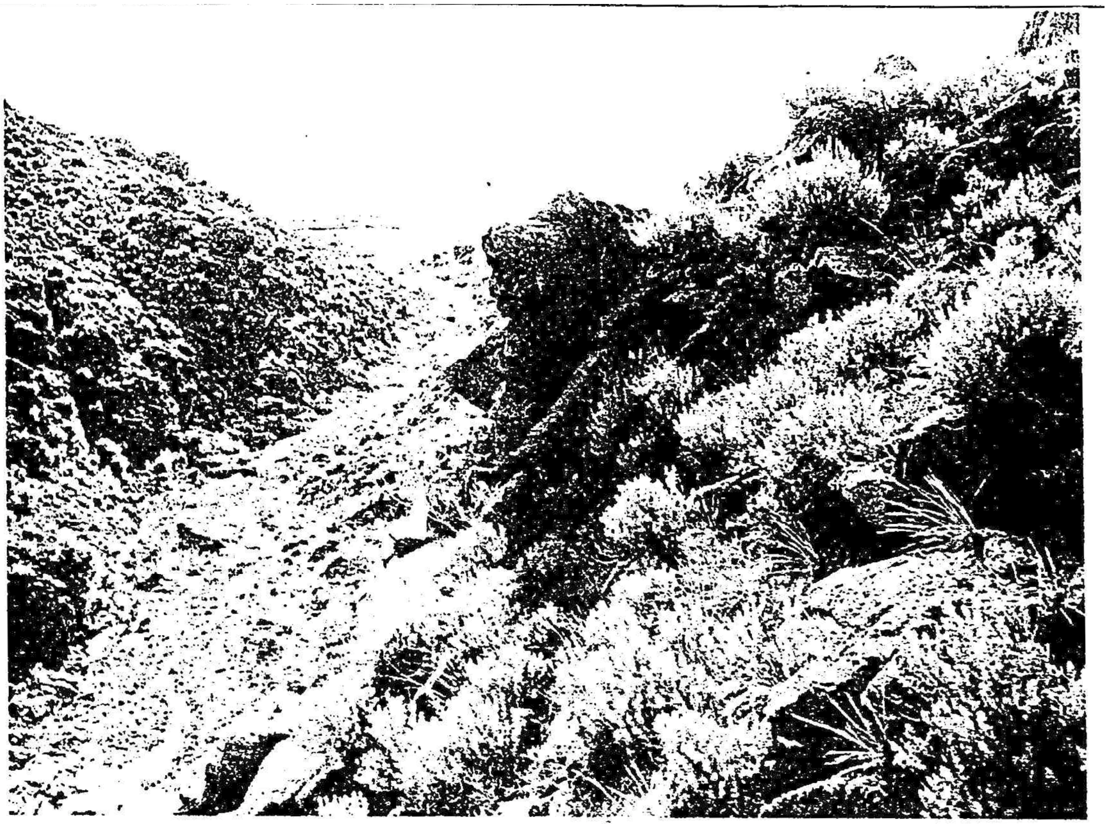


Ankylosaurus, with numerous bony spines on its body and a “club” at the end of its tail.

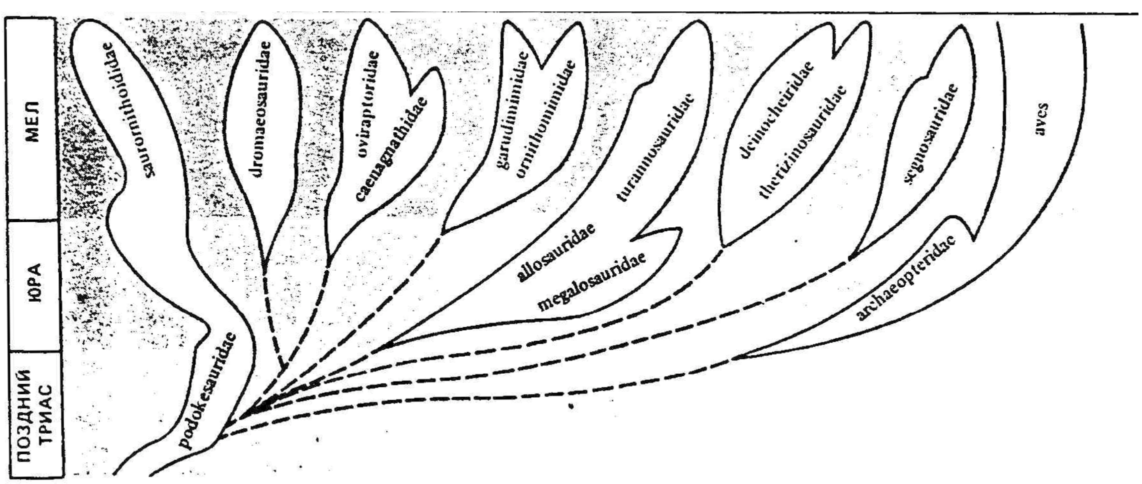
Psittacosaurus (right) is related to the ornithischians, a hadrosaur (center) is related to the duck-bills, and an iguanodont (left) belongs to a species that was transitional between the ornithischian and duck-billed dinosaurs.



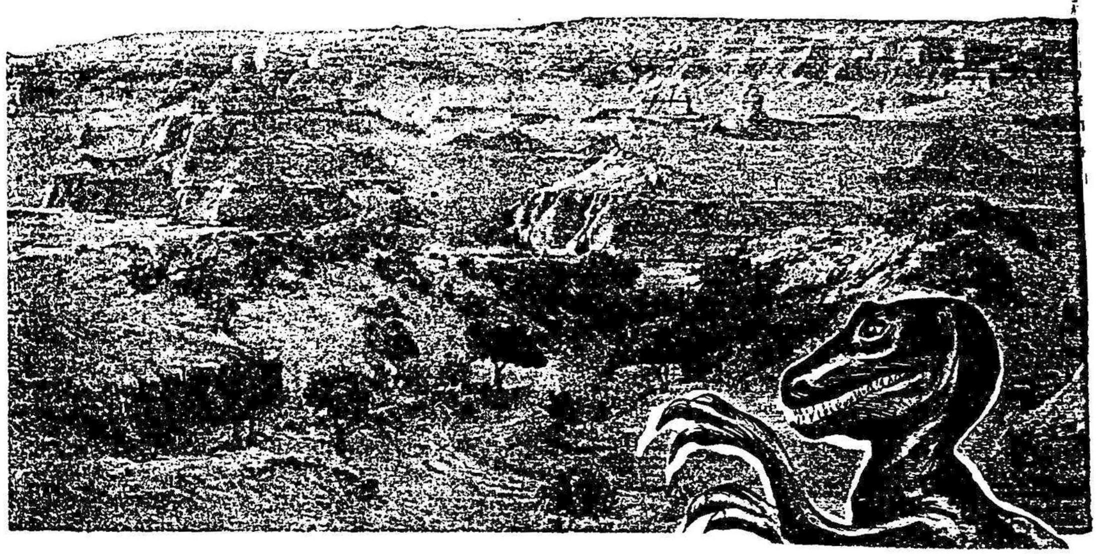
A “family” of *Protoceratops*.



The Khuren Dukh deposit, containing the remains of dinosaurs and flying reptiles. Photo by A. A. Morkovkin.



Phylogenetic diagram of the theropod families. The dark line indicates the theropod groups whose bones have been found in Mongolia. From *Morphology, Phylogeny, and Classification of Dinosaurs*, by S. M. Kurzanov, Moscow, 1988; with supplementary material from *Predatory Dinosaurs of the Mongolian Upper Cretaceous*, by R. Barsbold, Moscow, 1983.
Key: (a) Cretaceous; (b) Jurassic; (c) Late Triassic.



Khermin Tsav—the largest deposit of Upper Cretaceous vertebrates.