translated by Robert Welch

THE FIRST ANKYLOSAURUS FROM THE LOWER CRETACEOUS OF MONGOLIA

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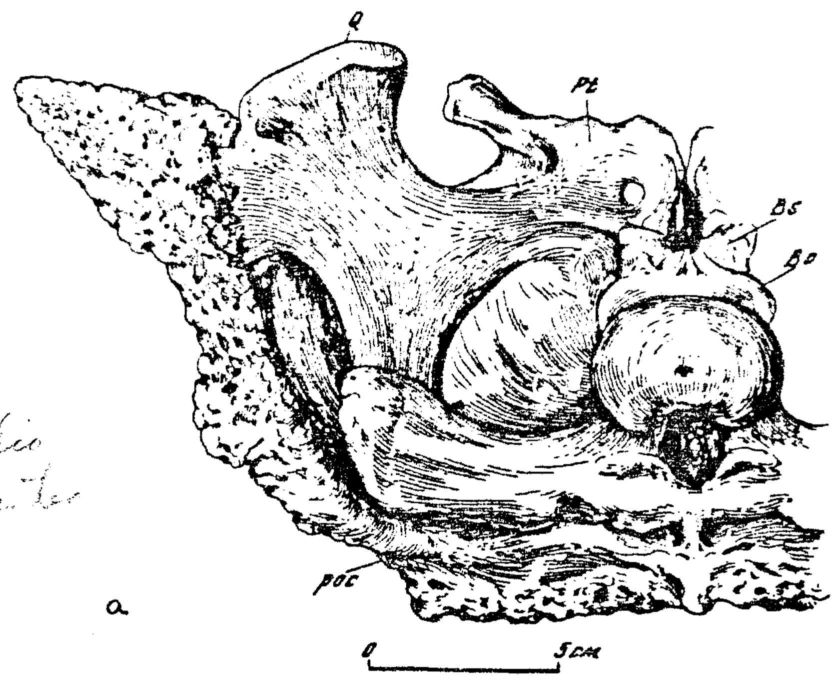
The armored dinosaurs are a component of the faunal complexes in practically all of the Upper Cretaceous continental deposits of Mongolia. Somewhat more rare are discoveries of ankylosauria in Lower Cretaceous deposits. Even more unique was the 1977 discovery of a complete and well preserved armored dinosaur skull in the Dzunbain formation deposits of the Lower Cretaceous at Khamryn-Us in the south-east Gobi desert. Along with the skull were found incomplete parts of the postcranial skeleton and a large number of osteodermal shields, including previously unknown elements of ankylosaur armor – "triads".

Features were revealed in the skull structure of the Lower Cretaceous ankylosaurus that are characteristic of the family Ankylosauridae to which all of the previously known Mongolian dinosaurs are belong. However, because of individual features such as the narrow snout, the contact of the quadrate bones with the paroccipital lobes and some others we separated this new ankylosaur and the previously known Saichainia into a new subfamily. In this regard the subfamily Ankylosaurinae comprises all of the other known ankylosaurs.

FAMILY ANKYLOSAURIDAE
Subfamily Shamosaurinae Subfam. Nov.

Diagnosis. Ankylosaurids with a tapered forward end of the snout; the anterior wall of the pterygoids slopes gently backward, the pterygoids fuse rigidly with the basisphenoid, the interpterygoidal cavity is small, the quadrate bones fuse with the lower edge of the paroccipital lobes (Fig. 1b), the occipital condyle changes from a broad oval to a circular shape.

Tarchia gigantea



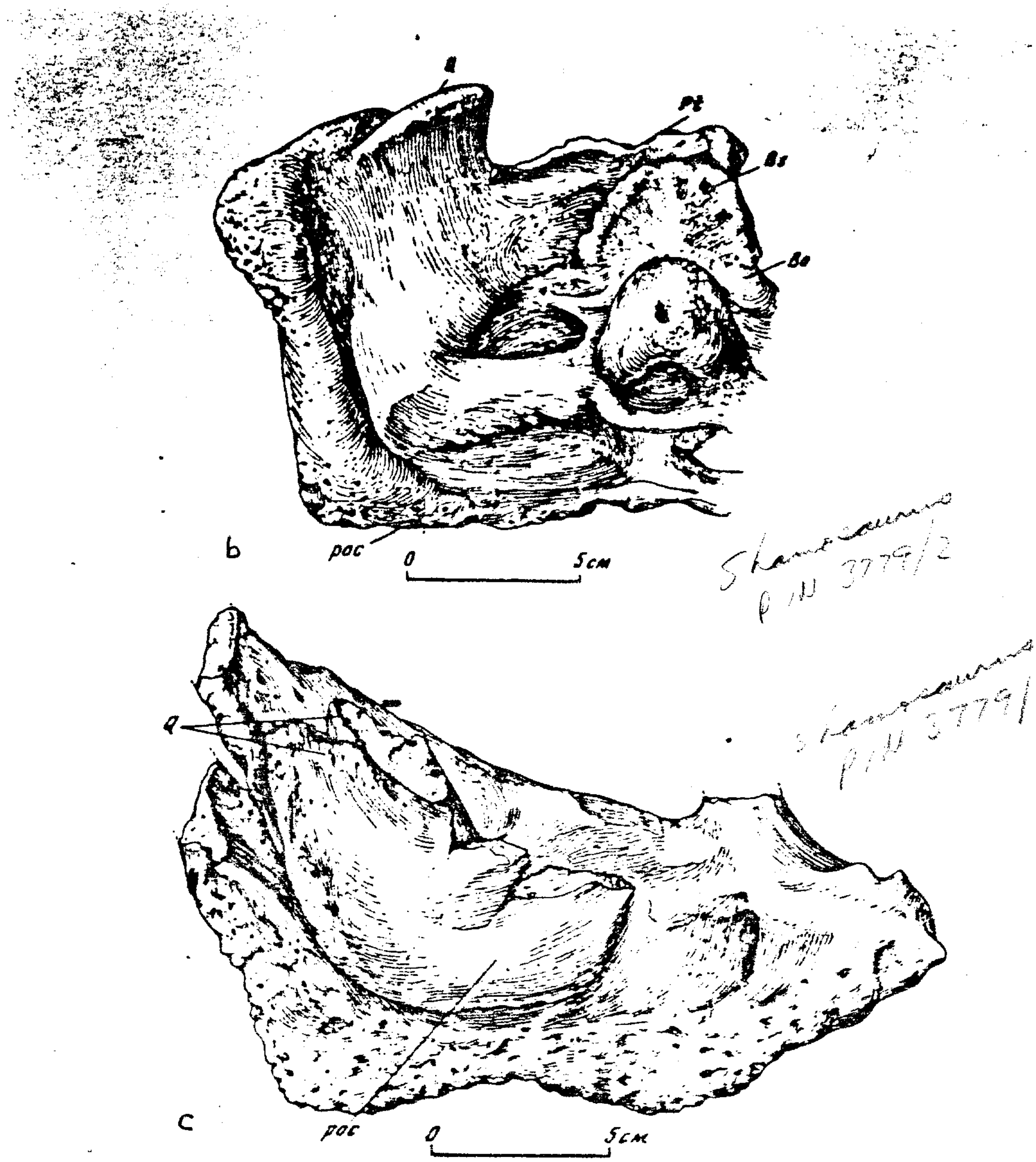
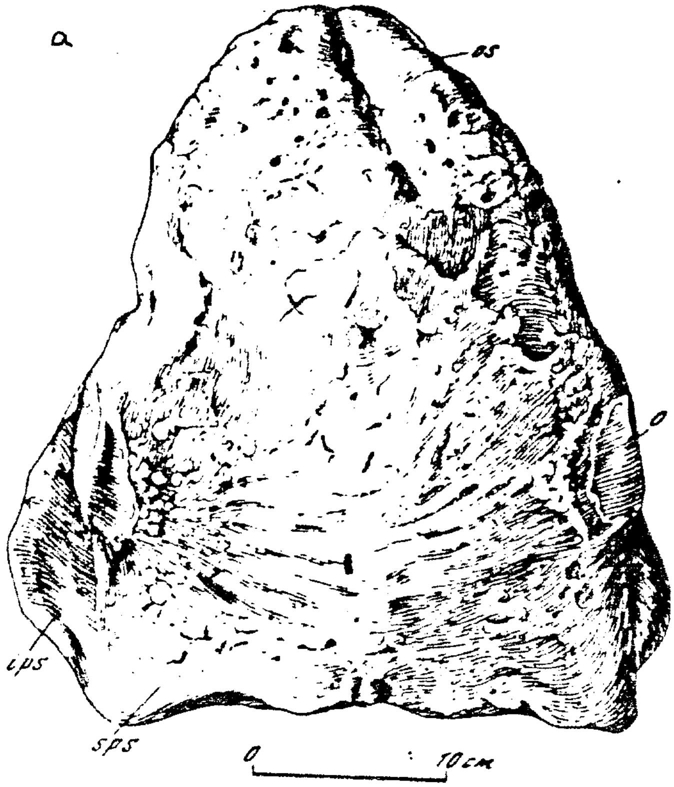


Fig. 1. Views of the contact between the quadrate bones and the paroccipital lobes and pterygoids with the brain box.
a) Tarchia gigantea, PIN collection 3142/250; b) Shamosaurus scutatus, PIN collection 3779/2; c) Shamosaurus, PIN collection 3779/1. Bo – occipital condyle; Bs – basisphenoid bone; poc – paroccipital lobes; Pt – pterygoid bones; Q – quadrate bones.

Composition of the subfamily. Two genuses: Saichainia, Shamosaurus.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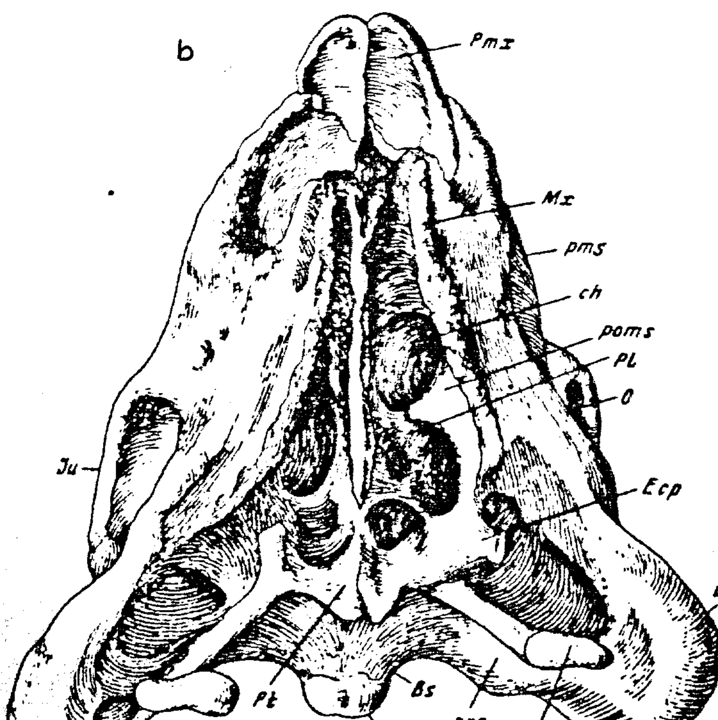
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Comparison. Distinguished from the Ankylosaurinae by narrower premaxillae; complete fusion and ossification of the contact between the quadrate bones and the paroccipital lobes; fusion of the pterygoids with the basisphenoid (Fig. 1); smaller interpterygoidal cavity; the broad oval or circular, ventrally oriented occipital condyle.

Distribution. Cretaceous period, Mongolian People's Republic.

Shamosaurus gen. nov.

Characteristic species. Shamosaurus scutatus, Lower, Cretaceous, Dzunbain formation, Khamryn-Us, South-east Gobi desert, Mongolian People's Republic.

Diagnosis. Large ankylosaur having the roof of its skull completely covered with finely grained osteodermal shields, the postorbital osteoderms do not coalesce into spines, laterally the osteodermal covering does not close the quadrate condyle region, the orbits are located at the middle of the skull line and are directed almost entirely to the side (Fig. 3b), the upper region of the premaxillae are covered with osteodermal growths, the forward region of the snout is a narrow oval shape and is much narrower than the distance between the back teeth of the upper jaw, the rear maxillar shelf is well developed, the ventral surface of the palate bones is sloped laterally, the jaw articulation is far behind the rear edge of the orbit, the plane of the condyle is sloped to the rear, the occipital condyle is oriented ventrally, the ventral surface of the basioccipital bone is narrow and circular.

Comparison. Shamosaurus scutatus differs from Saichainia in that the postoccipital osteoderms did not acquire the form of spines; the osteodermal cover did not descend laterally to the level of the quadrate condyle, whereas in Saichainia it cannot be seen from the side, by orbits that are oriented laterally and not antelaterally; and by a narrower premaxillar region that is much narrower than the distance between the back teeth of the upper jaw.

Species composition. The genus is monotypical.

Distribution. Lower Cretaceous period, Mongolian People's Republic.

Shamosaurus scutatus sp. nov.
Fig. 2

The species is named from the Latin word scutatus – armed with shields.

Holotype – Paleontological Institute of the USSR collection #3779/2, skull; Lower Cretaceous, Dzunbain formation; Khamryn-Us, South-east Gobi desert, Mongolian People's Republic.

Description. Skull is 36 cm long, 26 cm wide in the orbit region. Behind the orbits the maximum width – the distance between the lower postorbital shields – is 37 cm. In plan view the skull is a triangle. The top of the skull is somewhat convex as viewed from the front and, starting from the supraorbital region looks like a rectangle the short sides of which are formed by the keels of the supraorbital and upper postorbital shields.

The bony nostrils are large and terminal. The orbits are of average size and are situated laterally and directed strictly to the sides (Figs. 2,3).

Upper temporal fenestrae were not observed. The lower fenestrae were covered by an overhanging osteodermal complex so that the quadrate condyle was visible from the side.

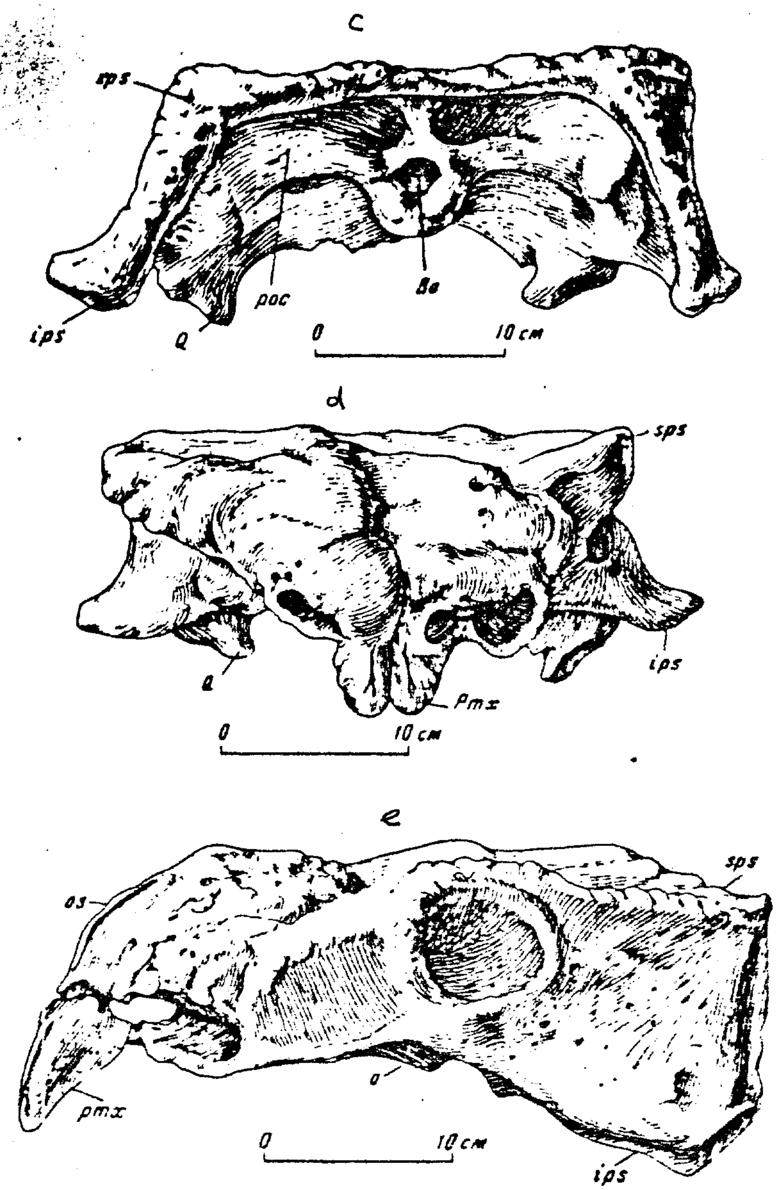

Fig. 2. Shamosaurus skull, PIN collection 3779/2. a) from above; b) from below; c) from the side; d) from behind.
Ch – choanae; Ecp – exterior pterygoid bones; ips – lower postorbital shields; ju – jugalia; Mx – maxillar bones; Os – osteodermal growth; Pl – palatal bones; Pmx – premaxillar bones; pms – forward maxillar shelf; poms – posterior maxillar shelf; sps – upper postorbital shields.
See Fig. 1 for other nomenclature.

The entire surface of the top of the skull (Fig. 2a) was covered with a solid osteodermal cover that had no distinctive contour and an uneven, fine grainy or serrated sculpture. The cover transitioned smoothly into shields that have no contour boundaries. The supraorbital shields are low and long, with a keel that runs from front to back. From behind, their keel transforms into the forward rib of the pyramidal upper postorbital shields. Shields of this type are called traditional by analogy with other ankylosaurids but the fact is that they look like low pyramids with apexes that correspond to the posterior nodes of the skull and with three ribs that are directed forward to the center of the top of the skull and laterally downward. The lower postorbital shields are of a more typical form. Between the overall osteodermal cover and the shield itself is a boundary which is probably a remnant of the attachment of a horny cover. The shields are carinate and directed to the sides. The keel is extended from the front to the back. The shield is formed of unequal sides: to the rear its height increases. The lower side of the shield is a horizontal surface, the upper is a gently sloping concave surface.

The only bones that are free of the osteodermal cover from the outside are the premaxillar bones that form the tapered end of the snout and border the nostrils from the front downward. This area of the skull was somewhat more damaged but inasmuch as it is possible to judge, these bones were covered by osteoderms high between the nostrils and did not emerge at the surface of the top of the skull as in Tarchia.

Palatal surface. The forward edge of the premaxillar bones is a narrow oval. Medially at the seam between the praemaxillaria and near the cusp of the notch there is a pair of openings that proceed inward to the rear. These openings probably served as exits for the ethmoid branch of the trigeminal nerve (Y_1).

The boundary between the premaxillar and maxillar bones was destroyed; therefore, we cannot make any judgments regarding the nature of the contact. The boundaries and features of the remaining bones on the palatal surface likewise cannot be commented upon due to their poor degree of preservation and, in addition, their rigid fusion. It is therefore not worthwhile to speak specifically about the bones but about their arrangement, basing our commentary on the only skull of a young ankylosaur-pinacosaur whose bones were relatively free of osteoderms (Maryanska, 1971).

The upper jaw bones are long and their forward region expands medially to form a well defined forward maxillar shelf that begins approximately at the level of the middle of the tooth row. The rear maxillar shelf is also well developed and is oriented in a laterally inclined plane as in Euoplocephalus and Saichainia. Because of this the suborbital opening is located on this plane between the upper jaw bones that frame it from the front and laterally, the palatal bones medially, and the ectopterygoidal bones from behind. The suborbital opening is very large.

Unique to shamosaurus is the length of its tooth row, which is greater than that in all of the known large ankylosaurs.

Laterally, the jaw bones bound the palatal cavities in which the palatal bones reside high above the oral cavity. The forward edge of the palatal bones frames the bony choanae from behind. The side edge of the choanae bounds the postorbital opening and they make contact with the rear maxillar shelf.

The vomers are the medial extension of the premaxillar bones on the palatal surface and they merge into a thin vertical septum that separates the palatal depressions. The septum has probably been formed on the vomers from behind by the palatal processes of the pterygoids.

The pterygoidal processes serve as the posterior wall of the palatal depressions and form, perpendicular to the septum and palatal processes of the pterygoids, a vertical structure that comprised the vomers and the palatal processes of the pterygoids. The interpalatal depression was, probably, very small. The pterygoids are rigidly fused to the brain box creating the impression that it was pressed into the vertical structure of the pterygoidal processes (Figs. 1b, 2b). A similar type of contact is seen in representatives of the nodosaurids but is not characteristic of the Ankylosauridae. Because of the abbreviation of the entire quadrate-pterygoid branch, the quadrate processes of the pterygoids are relatively tall and short in comparison with other ankylosauria. The upper forward area of the pterygoids is formed by short exterior pterygoid bones.

Ossification of the palatoquadrate bar. The quadrate bones are wide, flat, triangular and inclined somewhat forward. The wide band of the pterygoidal process runs forward and inward to fuse with the pterygoids (Fig. 1b). The dorsal end of the quadrate bone rises to the top of the skull fusing with the lower and forward regions of the paroccipital lobe. It is interesting to note that collection 3779/1 taken from the same site contains an incomplete skull of what is most likely another shamosaurus but in this skull are two branches at the dorsal end of the quadrate bone: the first branch runs parallel to the paroccipital lobe to the top of the skull as is seen in most ankylosauria; the second branch fuses with its lower edge. Apparently, the degree of fusion between the quadrate bones and the paroccipital lobes was governed by the intensity at which the cartilage in this area ossified during the animal's lifetime.

One more very short process of the quadrate bones is directed laterally to combine with the quadratojugal bone.

The lower articulation surface of the quadrate bones looks like an oval whose long axis is oriented at a right angle to the long axis of the skull.

Brain box. The basisphenoid is short, massive and slightly ossifying. The sphenoccipital lobes are very close to the basipterygoidal processes. The basisphenoidal complex looks as if it was shifted into the pterygoids.

The occipital bone is wide (Fig. 2d). The occipital foramen is large, one-third the height of the occipital bone, elongated in the horizontal direction.

The paroccipital lobes are wider in the distal region and go forward in the proximal region which causes the osteodermal edge of the top of the skull to somewhat overhang the medial area of the occipital bone. The occipital condyle is circular, the articulation surface is directed almost ventrally.

On the ventral surface of the basioccipital bone, between the condyle and the sphenoccipital lobes is a surface for the attachment of m. m. recticapitis anteriores. The configuration differs widely among the various genuses of ankylosaurids and in shamosaurus is a comparatively narrow, convex, ventrally circular surface.

Lower jaw. The lower jaw of shamosaurus is long and narrow. The surface of the outside of the jaw is uneven, obviously, due to the osteodermal covering. A narrow spine extends along the lower edge, completely covering the area of the angular bone.

The coronoid process is low and slight, as it is in all ankylosauria. The coronoid bone, however, is fairly large. It overhangs on the dentary bone by its front end and extends along the rear half of the tooth row as a narrow tongue.

Commentary. Owing to the discovery of Lower Cretaceous ankylosaurus and clarification of the morphology of Shamosaurus skull it is now possible to offer a proposal regarding the relationships between the two families of ankylosauria and a more detailed phylogenetic construction (Fig. 4). These questions had previously been considered unresolved (Coombs, 1978) because the extraction of families from one another hindered specific indices of the skull of known representatives such as the convergence of the upper ends of the quadrate bones with the paroccipital lobes in Nodosaurids and the horn-shaped osteodermal shields at the posterolateral nodes of the top of the skull, side temporal fenestrae closed by osteoderms, a complex system of accessory sinuses in the nasal cavity, and the club at the end of the tail in ankylosaurids.

Several features in the skull of shamosaurus reflect their relative similarity with the nodosaurids and attest to the well-known intermediacy of the shamosaurus skull structure between both families. These features are: 1) a comparatively narrow snout; 2) the lack of even a small fraction of kinetism: complete fusion of the quadrate bones with the paroccipital lobes and the pterygoids with the brain box; 3) a circular, ventrally oriented occipital condyle, and; 4) incomplete covering in the lateral aspect of the quadrate condyle by an osteoderm. Shamosaurus, however, being the oldest of the known ankylosaurids, is in its overall structure representative of the family. Changes in the morphology of its skull have occurred that are typical of the ankylosaurids. One branch of the nodosaurids has retained its initial features: open lower temporal fenestrae, but early nodosaurids that were contemporary of shamosaurus had premaxillar teeth (Silvisaurus; Eaton, 1960). In the later family members only the ridges that bound the premaxillar bone with the beginning of each tooth row remain and in ankylosaurids the premaxillar teeth have disappeared altogether. Obviously, these features determine the "primitiveness" of the nodosaurids; i.e., the nodosaurid-like animals may be seen as a hypothetical ancestor of the ankylosauria.

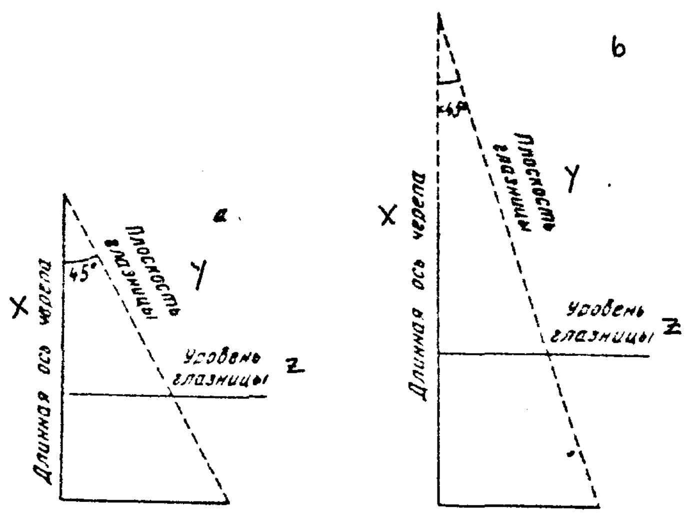

Fig. 3. Diagram showing the location and angle of rotation of the orbit. a) in tarchia; b) in shamosaurus.
x) long axis of skull; y) orbit plane; z) orbit level.

With the discovery of Shamosaurus, ankylosauria have been separated into two groups according to skull morphology. The first group contains Upper Cretaceous Saichainia (Maryanska, 1977) and Lower Cretaceous Shamosaurus, which have intermediate for the two families features in the skull structure that are atypical of ankylosaurids: a relatively narrow premaxillar region in the snout, quadrate bones fused with the paroccipital lobes, pterygoids fused with the brain box, and a small pterygoidal pit. The second group includes all of the other Mongolian ankylosauria.

Obviously, the first group is most similar in morphology to the nodosaurids which, apparently, were close to their ancestors. In evolving to the Shamosaurinae changes occurred in the morphology of the skull such as some widening in the postorbital region, the lateral temporal fenestrae being closed by osteodermal plates, the transformation of the osteoderms at the posterolateral nodes of the skull into what resembles horns. The palate of typical ankylosaurids, beginning with the shamosaurinae, is distinguished by the transverse orientation of the pterygoids and ectopterygoids. The occipital condyle in Shamosaurus and the nodosaurids is turned downwards but lacks the "neck" on which it sits in the nodosaurids, i.e., it is pushed somewhat into the base of the endocranium. Saichainia may be considered a descendant of Shamosaurus. In this case the following transformations took place along the shamosaurus – saichainia line: the premaxillar region of the snout widened; the osteodermal plates grew further downward from the squamosal bones to the closure of the quadrate condyle; the osteoderms at the posterolateral nodes of the skull transformed into spines; the orbits relocated further to the rear and their plane rotated somewhat forward (Fig. 3); of a secondary palate developed; the jaws grew shorter and the alveolar edge grew correspondingly longer. However, the nature of the contacts between the quadrate bones and the paroccipital lobes and between the pterygoids and the brain box did not change. The ankylosaurinae proper could probably be derivatives of this line. But in evolving to the new branch, at the root of which is talarurus (the oldest of the known late Cretaceous ankylosaurinae), the nature of the contact between the quadrate bones and the paroccipital lobes and between the pterygoids and the brain box changed and the size of the interpterygoidal depression increased, along with the same changes that took place in the aforementioned branch. The upper processes of quadrate bones in these ankylosauria did not fuse with the lower region of the paroccipital lobes but made contact with them from the front side, abutting them in varying degree: flatly in talarurus and in a young Mongolian ankylosaur – tarchia – the contact was apparently made at the ligaments (Fig. 1a). At the basipterygoidal processes in all ankylosaurinae are articulation facets at which the basipterygoidal articulation was achieved. The apexes of both branches – saichainia and tarchia – are very similar in external appearance, which, apparently, is an example of homeomorphy.

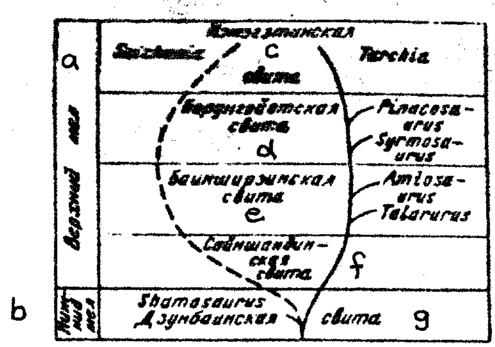

Fig. 4. Phylogenetic diagram showing the interrelationships between the Mongolian ankylosaurids.
a) Upper Cretaceous; b) Lower Cretaceous; c) (illegible) formation; d) Baryngaist formation; e) Bainshirzin formation; f) Sainshandin formation; g) Dzunbain formation.

Besides the enumerated fundamental trends in the Talarurus – Tarchia branch, the following fundamental trends were noted (Maryanska, 1977; Coombs, 1978): an increase in the size of the animals and strengthening of the armor, further consolidation of the armor. The large size of Shamosaurus completely corresponds to that of the most recent members of this branch and a fairly high degree of consolidation of the elements of Shamosaurus exoskeleton – the same two half-rings: neck and shoulder, that is found in the later Saichainia and Tarchia, as well as a thin supersacral osteodermal shield; additionally different constructions from the fusing armor elements are encountered that are not seen in the other Mongolian ankylosauria ("triads"). Apparently we must assume that there are comparatively unimportant forms in the Shamosaurus-Saichainia branch that have armor made up of individual, nonfusing osteodermal elements that gave rise to the talarurus branch (particularly the anklyosaurinae).

LITERATURE CITED

1. Coombs, W. "The families of the ornithischian dinosaur order Ankylosauria" Paleontology, vol. 21, pt.1, pp. 143-170, 1978.
2. Maryanska, T. "New data on the skull" in: Results of the Polish-Mongolian palaeontological expeditions, Pt. III, Pinacosaurus grangeri (Ankylosauria), Palaeontol. pol. No. 25, pp. 45-53, 1971.
3. Maryanska, T., "Ankylosauridae – Dinsoauria from Mongolia" in: Results of the Polish-Mongolian palaeontological expeditions, Paleontol. pol., No. 37, pp. 65-151, 1977.