THE MORPHOLOGICAL UNIQUENESS OF ANKYLOSAURIA

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The first discoveries of Ankylosauria were made in Europe [11,15]. Because of a number of similarities in the skull structures of Ankylosauria and Stegosauria, their quadrupedal nature, and armored spines these animals were classified as a group of Stegosauria. It was only later, due to the study of more complete discoveries, that the armored dinosaurs were put into a separate subdivision and ranked with the Stegosauria and Ceratopsia [9,10,14,16].

Recent studies [3-6,12,13] have revealed that Ankylosauria are an ornithischia group distinguished from other ornithischian dinosaurs not only by the morphology of their teeth but by their armor and pronounced structural features.

From her study of Mongolian Ankylosauria T. Maryanska notes [13] that Ankylosauria are similar to Stegosauria in pelvic structure but differ from other quadrupedal dinosaurs: she proposes the acetabular depression closed primarily in the Ankylosauria whereas the partial closure of this structure in the ceratops occurred secondarily. Maryanska also notes a number of features in the skull of the Ankylosauria that are atypical of dinosaurs.

W. Coombs [6] points to the strong structure of the hip girdle in armored dinosaurs. He draws attention to the unusual structure of the ilia in Ankylosauria. The ilia grow in a horizontal plane and are markedly lengthened and broadened in the pre-acetabular region and the pubic bones are small and rectangular with a short posterior projection and have no anterior projection (a pubis has not been found intact in the

Mongolian Ankylosauria that Coombs did not study). Coombs adds the strong hardening of the orbit walls and the formation of a postorbital shelf (Fig. 1a) to the specific features of Ankylosauria skulls.

Additional features affecting mainly the skull of the Mongolian Ankylosauria have been observed in studying data obtained over several years by the SSMPE (expansion unknown) and archived at the Palaeological Institute of the Academy of Sciences of the Soviet Union. These features more strongly emphasize the morphological uniqueness of Ankylosauria.

It was formerly thought that the superior temporal fenestrae of Ankylosauria were covered by osteoderms [7]. However, there are distinct junctions on the roof of the skull of a young Pinacosaurus (ZPAL Mg-II/1). Superior temporal fenestrae were not observed on this animal. That is to say that if the reconstruction of the Pinacosaurus skull [12] is accurate, then the absence of the superior temporal fenestrae may bear full witness to the possibility that not only were they overgrown with osteoderms but with uniquely dermal bones. However, the junctions on the indicated skull are in an unusual location and the bones, particularly in the posterior area of the top, have an unusual configuration (Fig. 2). Therefore, it is possible that they fullly correspond to no more than isolated areas of osteoderms that are fused with the bones below them. With age the complete separation between these regions disappeared externally, they became thicker, and the surface became uneven – the characteristic skull top of the adult Ankylosauria was formed. Thus, the available data do not resolve the question of whether or not the absence of superior temporal fenestrae in Ankylosauria is a primary or a secondary development. These data do, however, make certain the proposition that not only osteoderms, but the intrinsic dermal bones participated in covering them over.

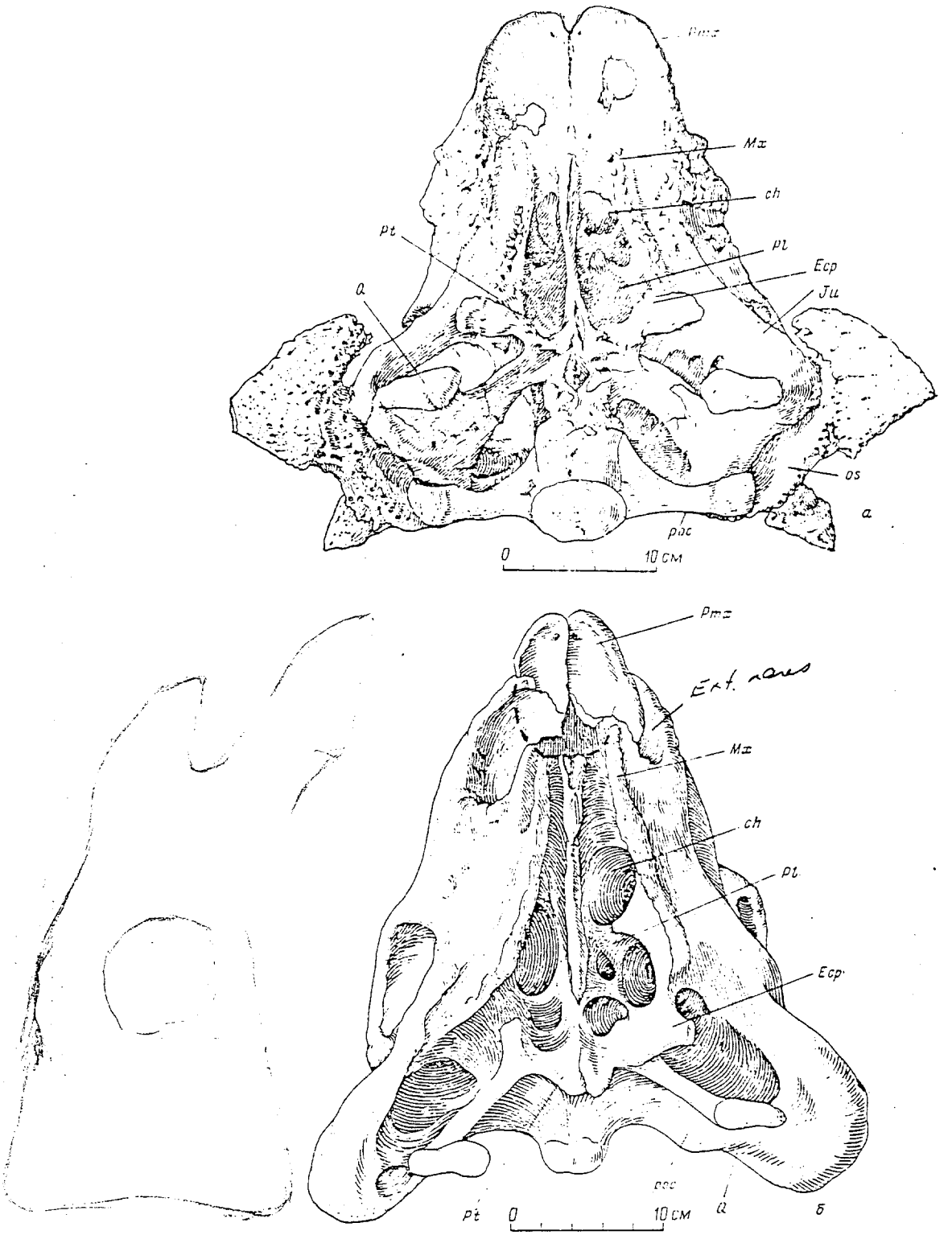

Fig. 1. Ankylosauria skull from the ventral side. *a*) Tarchia, *b*) Shamosaurus.

Legend: *ch*) choanae, *Ecp*) ectopterygoid bone, *Ju*) jugalia, *Mx*) jawbones, *os*) osteodermal growth, *Pl*) pterygoid bones, *Pmx*) palate bones, *poc*) paroccipital lobes, *Pt*) premaxillar bones, *Q*) quadrate bones.

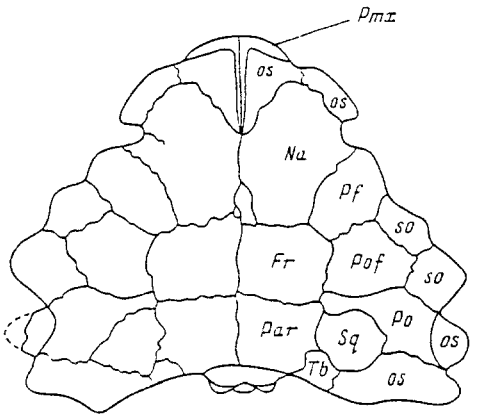

Fig. 2. Top of a Pinacosaurus skull from the dorsal side (compiled by Maryanska, 1977, pg. 102, Fig. 2A).

Legend: *Fr*) frontal bones; *Na*) nasal bones; *Par*) parietal bones; *Pf*) prefrontal bones; *Pmx*) premaxillar bones; *Po*) postorbital bones; *Pof*) postfrontal bones; *So*) supraorbital bones; *Sq*) squamosal bones; *Tb*) tabular bones; *os*) osteodermal growths.

There are no visible traces of the fenestrae on the ventral surface of the skull top where only the apex of an adductoral well is found in the form of a slight depression having gently sloping edges between the bases of the posterior eye wall and the paroccipital lobe. In contrast with Palaeosuchus, whose superior temporal opening is covered by osteoderms, a well-defined ridge at the base of a previous opening is visible from the ventral side, the ventral surface of this region is smooth in Ankylosauria and there is no visible bone-osteoderm contact. The result is that even this feature may not be a criterion for explaining the primariness of the presence or absence of superior temporal fenestrae in the skulls of Ankylosauria.

The lower temporal opening in Ankylosauria is covered by an osteoderm that hangs externally from the squamosal bone and is visible only from behind. It is visible in Nodosaurs from the side as a notch in the posterior side edge of the skull. In the occipital view, the lower temporal opening in Ankylosauria has elliptical contours and was formed by the postorbital and quadratojugal bones from the front and below and by the quadrate and, obviously, squamosal bones from behind and above. In addition, the distal end of the paroccipital lobe plays a role in housing of lower temporal opening.

Features in the structure of the Ankylosauria endocranium significantly distinguish it from the same region in the skull of other dinosaurs. In most dinosaurs (as well as most of the Archosauria) the morphologically ventral surface of the main occipital bone and the basisphenoid are rotated backwards so that the base of the skull is sharply curved ahead of the basipterygoidal lobes. As a result, the brain box makes a very distinct impression. As a rule, the basypterigoidal lobes are slightly lowered. The angle formed by the base of the skull and and a line at the bottom of the endocranial plane is as much as 50-55°.

In Ankylosauria the brain box is low, the base of the skull is not curved, the ventral surface of the main occipital bone and the basisphenoid is rotated upward as in the non-Archosaurian reptiles, the basipterigoidal lobes protrude only slightly and connect with the spheno-occiptal nodes (Fig. 1a). The angle between the base of the skull and the indicated line is not more than 15-17°. If shortening of the basipterigoidal lobes is explicitly linked with achinetism (?) of the skull, then it becomes more complicated to explain why a relatively straight base of the skull is preserved in Ankylosauria.

The brain box of Ankylosauria contains another feature that distinguishes them from typical dinosaurs and which, from the functional point of view, is difficult to explain: in Ankylosauria the interior carotid artery is along the dorsal surface of the basipterigoidal lobes [2], whereas in most dinosaurs it is more central, beneath the lobes [1].

The possibility of pterygoids intergrowing with the basipterygoidal lobes is said by Coombs [4] to be peculiar to the Nodosauria, but we have found this phenomenon in several Ankylosauria (Saichania, Shamosaurus: Fig. 1b), which further distinguishes the Ankylosauria from the other ornithischian dinosaurs (unfortunately, the nature of the basipterygoidal articulation has not been described for Stegosauria, which makes it impossible to affirm anything about this group).

The structure of the posterior quadrate region of the Ankylosauria skull, which is unusual for dinosaurs, calls attention to itself. In spite of the strong resemblance of the structures in this region, the absence of a contact for the quadrate bones with the paroccipital lobes in typical dinosaurs is clearly defined. As a rule, the squamosal bone plate in them is located between the vertical quadrate bone and the paroccipital lobe. In all of the known Ankylosauria this connection shifts to the opisthotic bone. Here the quadrate bones only approach the top of the skull, touching the forward part of the paroccipital lobes (Ankylosaur, Euoplocephalus, Talarurus, Pinacosaur, Tarchia: Fig. 1a) or the lower edges of the paroccipital lobes intergrow with the upper quadrate bones (Saichania, Shamosaurus: Fig. 1b and all Nodosauria); in other cases both types of connection exist (Shamosauria from Khamryn-Usa, PIN No. 3779/1).

The outlines, the form and the contacts of the squamosal bones in Ankylosauria also exhibit several differences from those found in typical dinosaurs in which these bones are usually narrow, are located in the buccal region and reach, on the dorsal surface of the top of the skull, only the upper edge of the paroccipital lobes. In Ankylosauria, though, the bones used as squamosal bones are very strongly distributed dorsally along the top of the skull (Fig. 2); not excluded is that the growth of the squamosal bones is in part connected with their ingrowth with a portion of the osteoderm and the covering of the superior temporal opening; the ventral surface of the squamosal bones has pits for the upper lobes of the quadrate bones (if complete ingrowth does not occur) as it does with all the other ornithischian dinosaurs (Ornithopoda, Stegosauria, Ceratopsia). However, the squamosal bone plate, which separates the quadrate bone from the paroccipital lobe in other dinosaurs, is diminished in Ankylosauria to the lower transverse ridge and the paroccipital lobe is laid into a furrow in the squamosal bone that covers its upper edge and continues somewhat behind it.

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It is not easy to evaluate the significance of the aforementioned morphological features. Some of them may be explained by the development of an osteodermal cover for the skull and the loss of kipetism (?) (features of the basipterygoidal articulation, the connection of the quadrate bones with the paroccipital lobes). It is interesting to note that crocodiles are also characterized by an akinetic (?) skull, the connection for the quadrate bones is also displaced with the sqamosal bones not to the paroccipital lobes, but to the prootic bones. Yet the connection of the quadrate bones with the ear capsule (?) does not exclude the possibility of a streptostylin (?): thus, the in birds the prootic connection with the quadrate bones coincides with a well defined streptostylin (?). The absence of superior temporal fenestrae may also be connected with the development of an osteodermal cover. It is more difficult to explain the absence of a distinct curve at the base of the skull in Ankylosauria – the ventral surface of the main occipital bone and the basisphenoid are turned downward in them as in primitive reptiles and not backward as in all of the typical Archosauria, including even the Triassic pseudosuchia of the type Erythrosuchus. It is possible that this feature will enable us to propose an even more profound distinction between the Ankylosauria and ornithischian dinosaurs than is ordinarily allowed. However, the absence of a dinstinct curve of the brain box in the images of the skull of primitive ornithischia such as the Pisanosaur and the Hypsilophodon [8] compels us to refrain from drawing more definite conclusions on this topic and makes further research necessary.

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