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Armored Dinosaurs of the Upper Cretaceous of Mongolia
Family Ankylosauridae
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Contents

| | |
|--|----|
| I. Brief historical outline of Ankylosaur research | 52 |
| II. Systematics section..... | 53 |
| Suborder: Ankylosauria | |
| Family: Ankylosauridae Brown, 1908 | |
| Genus: <i>Talarurus</i> Maleev, 1952 | 54 |
| <i>Talarurus plicatospineus</i> Maleev | 56 |
| Genus: <i>Dyoplosaurus</i> Parks, 1924..... | 78 |
| <i>Dyoplosaurus giganteus</i> sp. nov. | 79 |
| III. On some features of Ankylosaur skeletal structure..... | 85 |
| IV. Manner of life and reconstruction of external appearance of <i>Talarurus</i> | 87 |
| V. Phylogenetic remarks and stratigraphic distribution of Mongolian Ankylosaurs | 89 |
| Bibliography..... | 91 |

The paleontological expedition of the Academy of Sciences of the USSR in 1948-1949 discovered and investigated a series of sites of armored dinosaurs in the territory of the Mongolian Peoples Republic (Efremov, 1949, 1950, 1953). Besides primitive *Syrmosaurids* (Maleev, 1952b), there were discovered the remains of a new specimen of the family Ankylosauridae.

The discovery of the specimen of this family in Mongolia created an extreme scientific interest in clarifying the geological and geographical distribution of these dinosaurs.

The greatest diversity of forms is found in the final phases of the Cretaceous period. Such delimitation of vertical distribution indicates that the blossoming of their evolution preceded in a comparatively short interval of time. They were remnants representing the suborder Ankylosauria, which attained its blossoming at the end of the Mesozoic. Except for *Polacanthus* from the Wealdian of England and fragmentary finds from the Upper Cretaceous of France and Lower Austria, the distribution of more specimens was restricted to the North American continent.

The investigation of new sites allows us to analyze the problem of the origin and distribution of different groups of armored dinosaurs of Asia and to characterize more fully the paleofaunistic continental strata of the Cretaceous period of Mongolia.

The current paper presents the result of research into new representatives of the family of ankylosaurs from the uppermost levels of the Cretaceous of Mongolia, the previous accounts of which was given to me (Doklady AN SSSR, 1952n).

Illustrations for the paper are by the artist P. V. Sivkov.

I. BRIEF HISTORICAL OUTLINE OF ANKYLOSAUR RESEARCH

The first scientific data concerning the nature of ankylosaurs dates back to the beginning of the fortieth decade of the 19th Century, when Mantell (Mantell, 1833) described the genus *Hylaeosaurus* from separate skeletal remains and armor spines discovered in Lower Cretaceous deposits of England (Weald). This author had in his hands fragmentary remains and therefore could not give a full characteristic description of their genus.

At the end of the 1870s and the beginning of the 1890s, information on the armored dinosaurs of the Lower Cretaceous of Europe was substantially increased. In 1867, a paper by Huxley appeared, which supplied the detail characteristics of the genus *Acanthopholis* from the Weald of England. Here it was pointed out that the cranium of *Acanthopholis* does not have temporal cavities as do later ankylosaurs, the armor consists of separate carinate spines which are distributed in symmetrical rows on the skin surface. In 1881, a paper was published by Hulke, in which was reported information on *Polacanthus* from the Lower Cretaceous of England; in the paper the structure of the armor and the axial skeleton were described in detail. *Polacanthus* had massive compact bony armor, which consisted of united polygonal plates. The external surface of the armor was decorated with sharp bony spines.

In the beginning of the twentieth century, Nopcsa (1918) described new collections of ankylosaurs from the Lower Cretaceous of France and lower Austria. We obtain the earliest information on armored dinosaurs of North America from the papers of Leidy (1856), who described fragmentary dental remains from the Upper Cretaceous of Montana and classified them as a separate species of the genus *Palaeosincus*.

Especially new sites were described from the province of Alberta and the states of Montana and Wyoming. In 1901, Lucas described and illustrated remains of the skeleton of *Hoplitosaurus* from the Upper Cretaceous of South Dakota. A year later Lambe's (1902) paper appeared, in which remains of *Sterecephalus* from the Upper Cretaceous of Alberta. In 1905 there appeared a paper of Williston, in which there was reported a brief characterization of the genus *Stegopelta* from the Upper Cretaceous of Wyoming. Later, in 1908, a paper was published by Brown (1908) with a detailed description of *Ankylosaurus magniventris* from the Upper Cretaceous of Montana. In this paper, the author described and illustrated the cranium, the axial skeleton and the armor. Based on a sharp difference of *Ankylosaurus* from the majority of the European ankylosaurs, he separated a new family of Ankylosauridae, to which belong all North American forms, and the genus *Polacanthus* from the Weald of England.

Starting from 1920 there appeared a series of papers by Sternberg (1921), Parks (1924), Nopcsa (1928), Gilmore (1930) and Lambe (1931), with descriptions of new collections from different points of North America. These papers added greatly to the information previously available about the nature of armored dinosaurs; a description of the cranium, the teeth and the armor was provided, seven new genera and a few species were described. It should be noted that descriptions of new species and often even of separate genera were produced from findings of separate teeth or poorly determined fragmentary remains, without comparative analysis with earlier well-known forms, which led to unnecessary formation of some "new" species. Nopcsa (1928) made an attempt to look over the systematics of armored dinosaurs, On the basis of his own classification, he examined the size of the cranium, the amount of bony plates covering the cranium, and the size of the first cervical vertebrae. All armored dinosaurs having a small cranium without a temporal cavity he assigned to the first group, in which he placed *Acanthopolis*, *Hylaeosaurus*, *Steogceras*, *Struthiosaurus*, *Troodon*. In the second group he placed those genera, the specimens of which had a large cranium covered above with multiple plates and

spines. With this group he classed almost all ankylosaurs of North America: *Ankylosaurus*, *Palaeoscincus*, *Hierosaurus*, *Stegopelta*, *Nodosaurus*, *Hoplitosaurus*, and the genus *Polacanthus* from the Lower Cretaceous of England. In the third group Nopcsa isolated three genera - *Panoplosaurus*, *Dyoplosaurus*, and *Polacanthoides*, in which the cranium is covered above with five large plates.

Such classification of armored dinosaurs did not have a sufficient basis and did not record further indications. By contemporary systematics, Nopcsa's first group consists of the family Acanthopholidae. The second and third group of armored dinosaurs, which have between them more general characteristics in structure of the cranium, armor and post-cranial skeleton, are joined to the family Ankylosauridae.

Investigation of the armored dinosaurs of Central Asia, if we do not consider the short memorandum of Gilmore (1933) and the references of Riabinin (1939), begins with the papers of the Mongolian Paleontological Expedition of the AN SSSR in 1946-1949, which uncovered some sites of Upper Cretaceous ankylosaurs in Mongolian Territory.

II. SYSTEMATIC SECTION

Suborder ANKYLOSAURIA

Family ANKYLOSAURIDAE Brown, 1908

Diagnosis: Ankylosauridae are large quadruped dinosaurs. The cranium is massive, short, and wide, of triangular shape. The top of the cranium is covered with multiple bony plates and spines. The teeth are of stegosaurid type, with oval-lanceolate crown of striated sculpture. The vertebrae are entire on both sides. The neck is short. The sacrum is long, and encloses from five to nine vertebrae. The body is flattened, broad, covered with heavy bony armor, which consists of united bony plates.

Comparison. In skeletal structure, Ankylosauridae are readily distinguished from other ankylosaurs. The structure of the cranium and armor distinguishes them from the family Acanthopholidae. The latter family has a small cranium, triangular in form. Its longitudinal axis forms a right angle with the set of the neck. The dermal armament - the armor - consists of round or oval-carinate plates and spines, not coalescing into solid shells.

The difference, as opposed to Syrmosauridae, consists of the fact that in the following the light armor consists of complete bony spines of varied shapes arranged in symmetrical rows on the skin surface. The ribs in the lumbar region do not fuse with the transverse outgrowths of the vertebrae. The sacrum is short and consists of three vertebrae.

Contents of Family: The family Ankylosauridae consists of the following genera: *Hoplitosaurus*, *Polacanthus*, *Polacanthoides*, *Ankylosaurus*, *Edmontonia*, *Dyoplosaurus*, *Euoplocephalus*, *Hierosaurus*, *Nodosaurus*, *Palaeoscincus*, *Panoplosaurus*, *Scolosaurus*, *Stegopelta*, *Anodontosaurus*, *Pinacosaurus*.

In Cretaceous deposits in Mongolia, new specimens of the family were discovered - a new genus *Talarurus* and species *Dyoplosaurus giganteus* sp. nov.

Geographical Distribution - Remains of ankylosaurids were found in Cretaceous sites in Europe, Asia and North America.

Geological Age: Lower - Upper Cretaceous.

Genus *TALARURUS* Maleev, 1952

Talarurus: Maleev, 1952 B, Dokl. AN SSSR, vol. 87, no. 2, p. 273.

Type Genus. *Talarurus plicatospineus* Maleev, 1952.

Diagnosis: Large quadruped dinosaurs with heavy armor. The cranium is not large, of trapezoidal shape. On the top of the cranium there are many covering bones. The cervical vertebrae are short and high. The dorsal vertebrae are long, centra are high; articular surfaces are flattened. Lumbar ribs (4-5) are firmly joined by the lateral processes of the vertebrae. The scapula is twice as long as the humerus. The articular cavity is large, of circular shape, extended cranio-caudally. The humerus is somewhat longer than the tibia, and double the length of the radius. The ratio of the humerus to the femur is 3:2.

The ilia are long, U-shaped, greatly expanded and broadened in the acetabular region. The sacrum consists of nine vertebrae: four sacral, four lumbar, and one caudal. The front feet are shorter than the rear feet. The digits terminate in flat ungulate phalanges. The tail is long (20-25 vertebrae). The front caudal vertebrae are short with high centra, the rear ones are thin, lower, with greatly developed neural and hemal arches, by means of which they are strongly united to each other and form the impact section of the tail ("club"). The armor consists of bony plates which are carinate in shape, 20-50 mm in thickness, united longitudinally along the longitudinal axis of the plates with each other and forming cervical, dorsal and pelvic scuta. On the external surface of the scuta are located hollow bony spines of corrugated sculpture, which compose the external ornamentation of the armor. Average length of the skeleton with cranium not less than 4.5 - 5 m.

Comparison: On the comparison of *Talarurus* with other genera of the Suborder Ankylosauria, it is necessary to mention first of all that in type of cranial structure, the axial skeleton and the armor, this form is shown to be a typical specimen of the family Ankylosauridae.

The heavy armor, the considerable sacralization of the vertebrae (nine vertebrae), ankylosis of the ribs with transverse processes of the vertebrae determine the affiliation of *Talarurus* with the family Ankylosauridae.

Among the most completely known Cretaceous Ankylosaurids: *Polacanthus* (Lower Cretaceous of England), *Palaeoscincus*, *Panoplosaurus*, *Scolosaurus*, *Dyoplosaurus*, *Euoplocephalus*, *Ankylosaurus* (Upper Cretaceous of North America), the closest to *Talarurus* in structure of the cranium, the axial skeleton and armor is the genus *Ankylosaurus* B. Brown (1905) (Upper Cretaceous of North America, Lance Formation of Montana and the Edmonton Formation of Alberta).

On the other hand, *Talarurus* differs from *Ankylosaurus* and many other genera of the family Ankylosauridae. The most important differences of these genera from *Talarurus* are as follows:

Ankylosaurus (Upper Cretaceous of North America) has a more massive cranium - the width of the rear border of the cranium is 700 mm. and the external armor spines are absent. The armor of *Ankylosaurus* consists of low carinate-shaped plates.

Dyoplosaurus and *Scolosaurus* (Upper Cretaceous of North America) are larger than *Talarurus*. For these forms the armor is sturdier and consists of thick plates of polygonal shape. External spines of the armor have smooth sculpture.

Euoplosaurus (Upper Cretaceous of North America) is distinguished by larger dimensions of the skull and large convexity of the frontal-parietal regions. The width of the rear border is 450 mm. The armor consists of lower carinate plates which coalesce into a compact shell. External armor spines are absent.

Polacanthus (Lower Cretaceous of England) has thicker armor, not divided into separate segments as in *Talarurus*. The inner surface of the armor is closely united with the dorsal surface of the ribs. The armor spines are smooth. The sacrum is very short - six vertebrae.

Palaeoscincus (Upper Cretaceous of North America) differs from *Talarurus* in its more massive cranium, which considerably exceeds the width of the previously mentioned: the width of the rear border of *Palaeoscincus* is 470 mm; of *Talarurus*, 350 mm. The armor is not segmented and consists of polygonal plates, on which are distributed smooth carinate spines.

Table 1. Correlation of some skeletal elements of *Talarurus* and other ankylosaurs of the family Ankylosauridae (in millimeters).

| item | <i>T. plicatospinus</i> | <i>Ankylosaurus magneventris</i> | <i>Dyoplosaurus acutosquameus</i> | <i>Paleoscincus rugosidens</i> | <i>Panoplosaurus mirus</i> | <i>Polacanthus foxi</i> | <i>Scolosaurus cutleri</i> |
|----------------------------|-------------------------|----------------------------------|-----------------------------------|--------------------------------|----------------------------|-------------------------|----------------------------|
| usual length scapula | 600 | 600 | unknown | unknown | 440 | unknown | 560 |
| glenoid | 105 | 175 | unknown | unknown | 110 | unknown | 130 |
| usual width glenoid | 50 | 140 | unknown | unknown | unknown | unknown | 70 |
| usual length humerus | 335 | unknown | unknown | 110 | 130 | unknown | 440 |
| femur | 470 | unknown | unknown | unknown | unknown | unknown | 600 |
| tibia | 248 | 270 | unknown | 385 | 385 | unknown | 445 |
| number of sacral vertebrae | 9 | 9 | unknown | 9 | 6 | 6 | 6 |
| number of caudal vertebrae | unknown | unknown | 23 | unknown | unknown | 6 | 28 |
| form of armor | solid carapace | solid carapace | solid carapace | solid carapace | solid carapace | solid carapace | solid carapace |

Panoplosaurus (Upper Cretaceous of North America) differs in structure and number of covering elements of the skull - plates of different shapes, of large dimensions, not more than five in number; *Talarurus* has small plates, many in number. The sacrum of *Panoplosaurus* is short, about six vertebrae. The structure of its armor is unknown.

The characteristics listed above are so important that they go beyond the scope of species differences and provide a firm basis for singling out the armored dinosaurs from Bayn-Shire as an independent genus *Talarurus* Maleev. In Table I is shown the relationship of skeletal elements of different ankylosaur species which pertain to the genus indicated above.

General Observations: The discovery at Bayn Shire of armored dinosaurs which match up with armored dinosaurs of North America at the very same evolutionary level and which are very similar to the genus *Ankylosaurus*, known from the Upper Cretaceous (Lance Formation, Hell Creek strata, Montana; Edmonton Formation of Alberta), indicates the close similarities of the dinosaur fauna of Mongolia and the USA, This faunal similarity suggests the possibility of developing a correlation of formations by considering their similarity in geological age and on this basis determine the age of the strata for *Talarurus* as the latter fragments of the Upper Cretaceous, which correspond for now, it seems to the Upper Senonian.

Species Content.: The genus *Talarurus* contains, so far, a single species - *T.plicatospinus* Maleev, 1952.

Geographical Distribution. Central Asia.

Sites: Mongolian Peoples Republic, Bayn-Shiren, 130 km. SW of the Aimag Center of Sayn Shand.

Geological age: Upper Cretaceous.

Talarurus plicatospineus Maleev, 1952

Talarurus plicatospineus: Maleev, 1952 B, Dokl. AN SSSR, vol. XXXVII (37), No. 2.. P. 273.

Type Species. Fragment of skull (rear section of cranium, occipital region, base of skull) and postcranial skeleton (PIN, no. 557-3).

Species diagnosis: Contained in diagnosis of genus *Talarurus*.

DESCRIPTION

Skull: At the present time, no less than six morphological types of armored dinosaur skulls are known: *Scelidosaurus*, *Stegosaurus*, *Troodon*, *Panoplosaurus*, *Dyoplosaurus*, *Ankylosaurus*. Generally, the skull of *Talarurus* (Fig. 1.) resembles the skull of *Ankylosaurus* and *Euoplocephalus*. The rear section of cap is moderately arched in a front-to-rear direction and from side to side (Fig.2). On either side, this convex surface borders on the oblique surface of the lateral section, which drops down obliquely outward and downward (Fig. 3). Judging from the shape of the preserved part, the front profile of the skull was, apparently, wide and somewhat rounded.

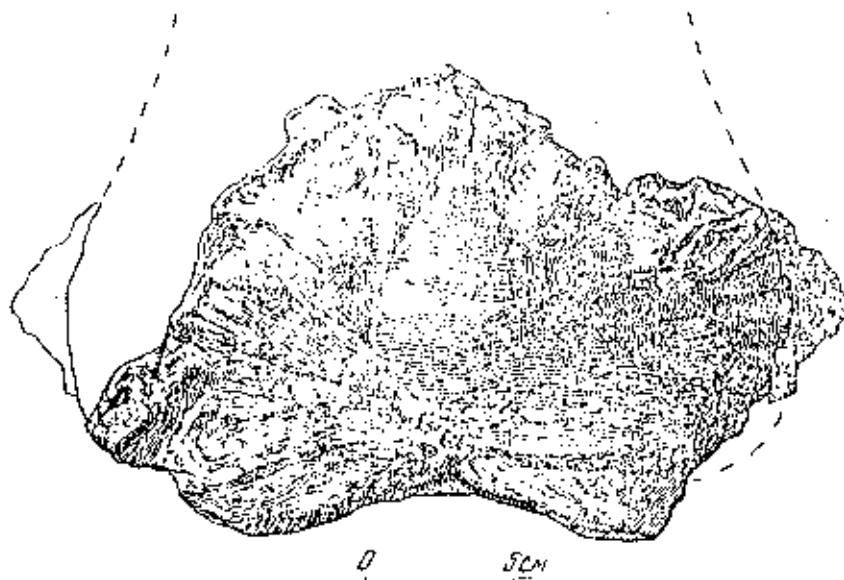


Fig. 1. *Talarurus plicatospineus*. Dorsal section of cranium from above. PIN 557-3

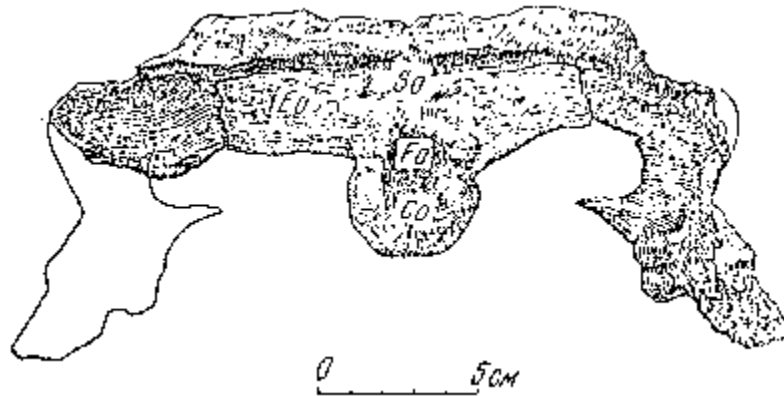


Fig. 2. *Talarurus plicatospineus*. Cranium from rear. Co – condylus occipitalis; d- dermal element of lateral section of cranium; Eo – exoccipitalis; Fo – foramen occipitale magnum; So – supraoccipitale. PIN 557-3

Ossified dermal plates cover the surface of the skull cap and sides of the cranium in such a way that they completely conceal all outlines of the cerebral bones. The covering plates are of different polygonal shapes: tetragonal, pentagonal, and hexagonal. The external surface of the plates are pitted by multiple depressions.

The ventral surface of the skull cap (Fig. 3) is divided by multiple chambers arranged symmetrically, which, during the life of the animal, were filled with air, similar to the sinus of the elephant head.

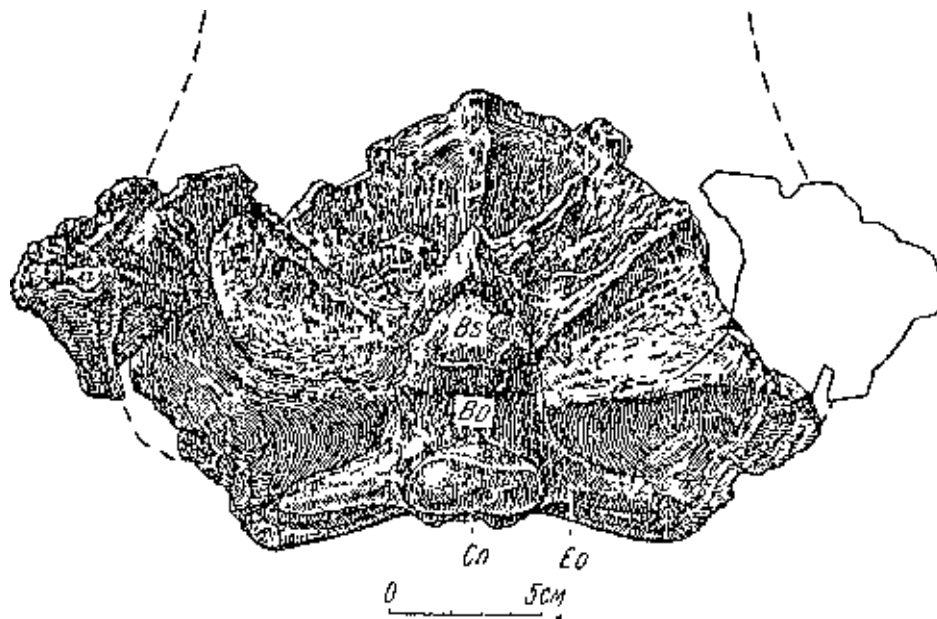


Fig. 3. *Talarurus plicatospineus*. Dorsal section of cranium from below. PIN 557-3. Cranium from rear. Co – condylus occipitalis; Bo – basioccipitale; Bs – Basisphenoideum.

Considering the investigation of the cranium from the rear, the occipital section turns out to be free of dermal covering elements, but the whole structure was united by seams so that it is impossible to distinguish precisely the boundaries of separate bones (Fig. 2). The occipital condyle is large, ventrally inclined from the longitudinal axis of the cranium, just as a link with the longitudinal cervical axis of the cranium forms an obtuse angle with the longitudinal axis of the first and second cervical vertebrae. This, undoubtedly, is the result of the separate structure of the cervical vertebrae, which form an elevation under the angle with the trunk neck, as it was described for *Syrmosaurus* (Maleev, 1952b).

The articular surface of the condyle has an almost spherical shape, the largest diameter is diagonal.

The basal occipital bone (basioccipitale) is short, wide in transverse diameter almost rectangular (fig 3, Vo), Its external surface, in front of the condyle, is deeply concave longitudinally and convex transversely. The upper surface midway is concave and forms the lower section of the large occipital opening (foramen occipitale magnum). The large occipital opening is oval in shape. It is larger in the transverse diameter than in the vertical. Laterally from the condyle and somewhat above it are distributed the lateral occipital bones (exoccipitalia); their lower borders take part in the formation of the upper half of the occipital condyle. The upper occipital bone (supraoccipitale) is not large.. Its lower section is slightly convex and forms the upper boundary of the large occipital opening (foramen occipitale magnum). The basal sphenoid bone (basisphenoideum) is long, triangular in shape (Fig. 3 Bs).

SPINAL COLUMN

The cervical vertebrae (30-60, Fig. 4). The full series of cervical vertebrae has not yet been seen in even one armored dinosaur from the Upper Cretaceous. Nopcsa (1928) described eight cervical vertebrae of a *Scolosaurus* skeleton in the British Museum. Gilmore (1914) describes 12 cervical vertebrae from *Stegosaurus*. The exact number of cervical vertebrae for *Talarurus* is impossible to establish, since the atlas, epistrophe and portion of the latter vertebrae of this series are absent. Those having cervical vertebrae (30-60) in structure are almost unique and, except for a few, differ in dimensions.

In cervical vertebrae the body is short, amphicoelous, deeply depressed laterally in the middle and expanded at the ends. The cross-sectional diameter of the body exceeds the vertical. The hemal crest is poorly expressed. The anterior articular surface is more depressed.; it has a depressed spoon like shape, with some ventral inclination. The posterior articular surface is more completely flat and somewhat tapered in a caudoventral direction. The neural arch is high. On its dorsal surface it has a sloping crest, gradually rising and passing into a firm spinous process and expanding in a transverse direction. The cerebral channel is large, oval in cross sectional view. The prezygapophyses are more weakly developed than the postzygapophyses, spread widely apart and dorso-medially



Fig. 4. *Talarurus plicatospineus*. Fourth cervical vertebra, lateral view. PIN 557-3

exposed at the articular surfaces. The posterior processes are distributed below the anterior ones, are greatly extended to the rear and separated by a deep cut. Their articular facets are drawn together and turned centro-laterally. In the articular series of such vertebrae the neck is forced to bend upward. The transverse processes are short, with tapering diapophyses. The costal [=rib] facet (edge) is well discernible on the anterior edge of the body for joining with the end of the rib. The size of the vertebrae increases at the rear, the diapophyses are somewhat longer and higher, the costal facets project more strongly, the neural canal becomes larger, but an increase in height of the dorsal processes does not occur.

Dorsal Vertebrae. The vertebral bodies are long and amphicoelous, deeply depressed in the middle of the sides (Fig. 5). The articular surfaces are broad and slightly depressed. The transverse diameter of the body is greater than the vertical diameter. The anterior articular surface is more depressed than the posterior surface (Fig. 6), which indicates a slight mobility of the spinal column and a large curvature of the back. On the vertical surface of the front half of the vertebra there is a well-developed keel. Posteriorly, this keel disappears, and the lower section of the body becomes obtusely rounded. The neural arch is low and massive. Its height is 1.5 times less than the height of the body. The transverse processes are wide, moderate in length, inclined obliquely upward. On the ventral side of the process, there is a deep depression for the purpose of a firm union with the rib. The vertebral processes of the posterior section of the dorsal column are fused with the ribs, so that the boundary between the two elements is very hard to discern (Fig. 7). The pleuropophyses are large, depressed, distributed on the upper half of the body and on the base of the arch. The neural channel on the anterior dorsal vertebrae is large, oval in cross-section; on the posterior dorsal vertebrae it is laterally compressed and is of smaller size. The prezygapophyses form channels [=troughs] by their union [along the midline]. Their articular facets are rotated medially. The posterior articular processes are folded downward, tightly joined together medially. The articular facets are depressed and inclined [=face] laterally; they form a

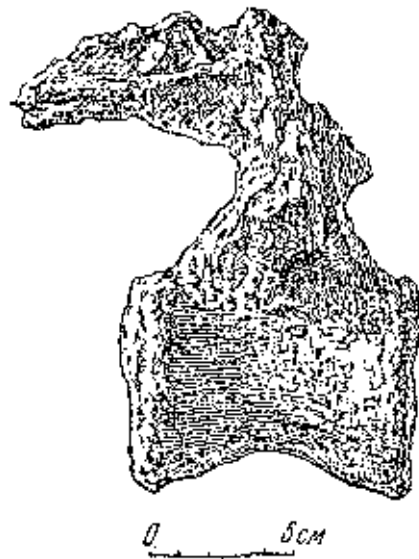


Fig. 5. *Talarurus plicatospineus*. Dorsal vertebra, lateral view. PIN 557-3



Fig. 6. *Talarurus plicatospineus*. Dorsal vertebra, anterior view. PIN 557-3

dowel-shaped joint with the prezygapophyses of the following vertebrae. Such a joining of vertebrae greatly restricts lateral motion. The spinous processes for all spinal and lumbar vertebrae have a scapulate form, somewhat expanding and thickening at the upper end. The size of the vertebral body and the height of the neural arches gradually decrease towards the rear.

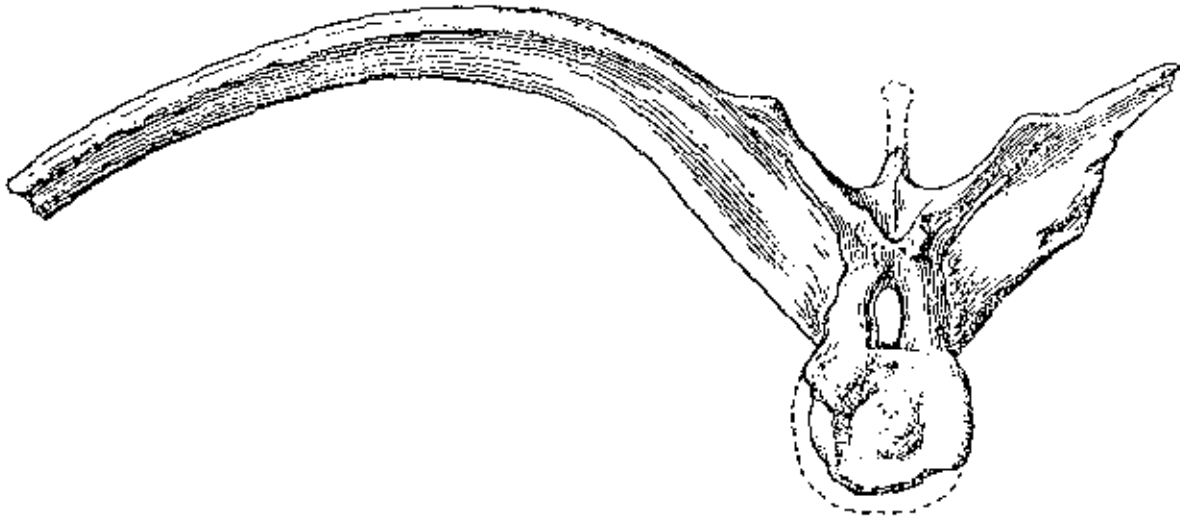


Fig. 7. *Talarurus plicatospineus*. Lumbar vertebra with ribs in natural articulation. PIN 557-3

Sacral Section of the Vertebra. The sacrum of *Talarurus* consists of four sacral vertebrae, the sacrum proper; four pre-sacral or sacro-lumbar vertebrae; and one caudal vertebra. All the vertebrae are fused together in an intricate complex of nine vertebrae - the synsacrum. Such a number of vertebrae occur in *Ankylosaurus* (Brown, 1908), *Nodosaurus* (Lull, 1921), *Palaeoscincus* from the Upper Cretaceous of North America (Leidy, 1856; Gilmore, 1930) and other armored dinosaurs. This indicates that the pelvic girdle is reinforced by the addition of the presacral and first caudal vertebrae.

The first sacral vertebra has detached ribs; therefore, it appears to be one of a series of presacral vertebrae. The next vertebra is united to the sacral vertebrae by means of neural processes and the short ribs, which are in contact with the diapophyses. The sacral vertebrae are similar to all the others in the spinal column - solid, amphicoelous, gradually increasing in size front and back; they are low, vertically compressed, having a rounded ventral surface with projecting keel. The sacral ribs are thick, short, horizontally inclined, with widening proximal and distal ends. The proximal end is ankylosed with the vertebra body, but the distal end forms a sacrocostal union of articulation with the ilium. To accomplish this union, 4 pairs of ribs take part.

The diapophyses of the sacral vertebrae are strongly developed, inclined downwards and form the bone partition with the sacral ribs, which form the walls around the sacral fenestrae. These fenestrae are restricted by the centra medially, but by the expanded ends of the sacral ribs outwardly, which are united with the inner surface of the ilium. The neural canal is wide, and oval in cross-section. The spinal processes are short, with expanding vertices, extending above the ilium. All the spinal processes are closely fused to each other and form a thick bony slab.

Caudal Section of the Spine. These are represented by isolated vertebrae from all sections of the tail; we may surmise that the entire tail of *Talarurus* apparently consisted of no less than 25 to 30 vertebrae. The anterior caudal vertebrae are short, high; their articular surfaces are depressed

and are extended to a greater height than depth. The centrum surfaces are deeply

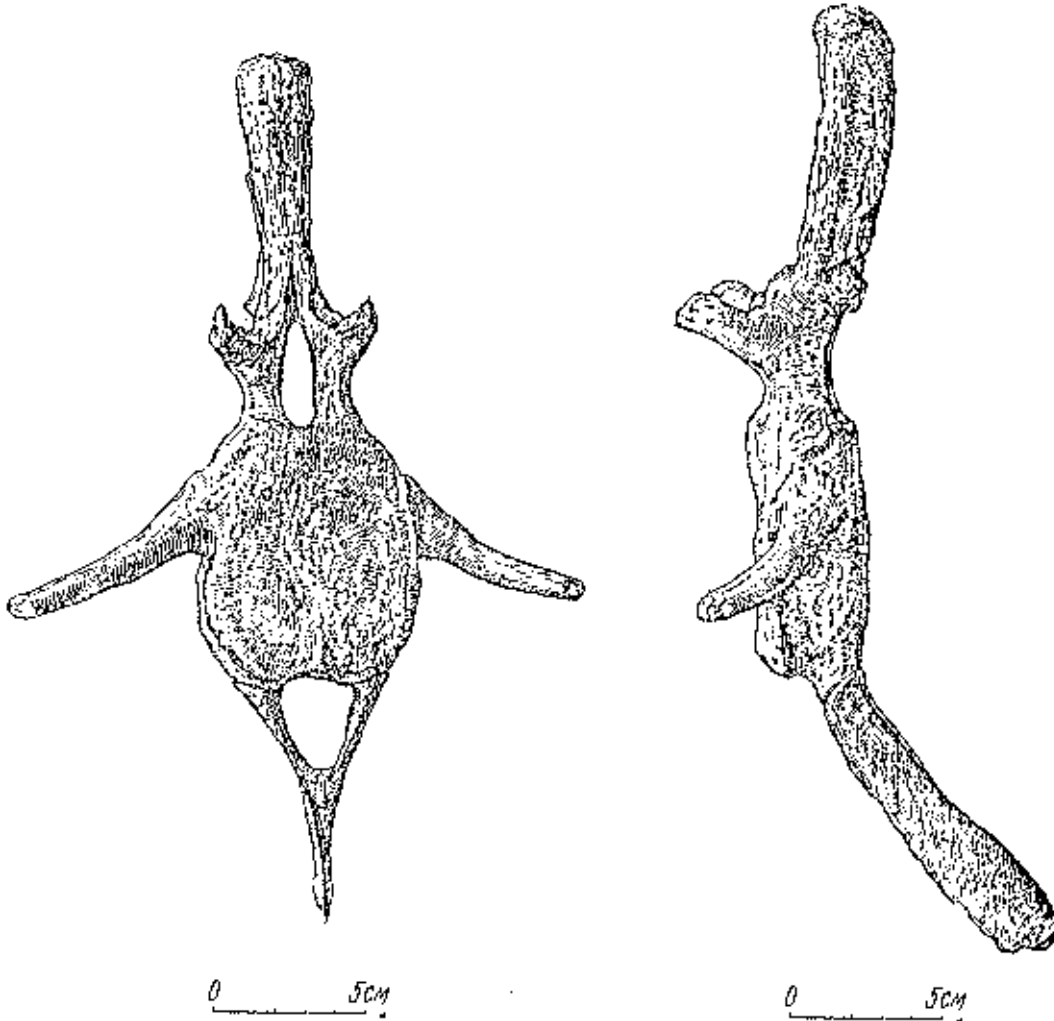


Fig. 8. *Talarurus plicatospineus*. First caudal vertebra, anterior view. PIN 557-3

Fig. 9. *Talarurus plicatospineus*. First caudal vertebra, lateral view. PIN 557-3

notched (Figs. 8 and 9). The lateral processes are long, obliquely inclined in a forward direction and almost reach the external surface of the postacetabular process of the ilium. The transverse processes of the following vertebrae are shortened and do not reach the ilium. Their size gradually decreases towards the rear. The neural arch is high and massive. Its height is equal to half the centrum height. The neural canal is large, triangular in shape, greatly enlarged and depressed at the base of the arch.

The prezygapophyses on the anterior caudal vertebrae are more developed than the postzygapophyses, widely distributed and turned toward the articular areas in a dorso-medial direction. The posterior processes are located above the anterior ones. Their articular edges are slightly compressed and rotated laterally.

The spinal processes (Fig. 8) are high, triangular in shape and slightly rounded in cross section, terminating in an expanded blunt apex.

The chevrons (Fig. 9) are long, wedge-shaped, with expanding proximal termini; they are independently connected with part of the posterior half of the centrum. The hemal canal is large, triangular in cross section. The entire coalition of chevrons with the vertebrae bodies is only evident in the posterior section of the tail (Fig. 10).

The vertebrae of the middle tail section are longer than the preceding ones. The transverse processes branch out horizontally from the upper part of the vertebra. Their size gradually decreases toward the rear; the smallest transverse processes are found on the last free vertebrae.

The spinous processes are greatly flattened and inclined to the rear.

The vertebrae of the rear half of the tail (10 - 15) are long, low, amphicoelous, greatly depressed laterally midway and broadened at the ends (Fig. 10).

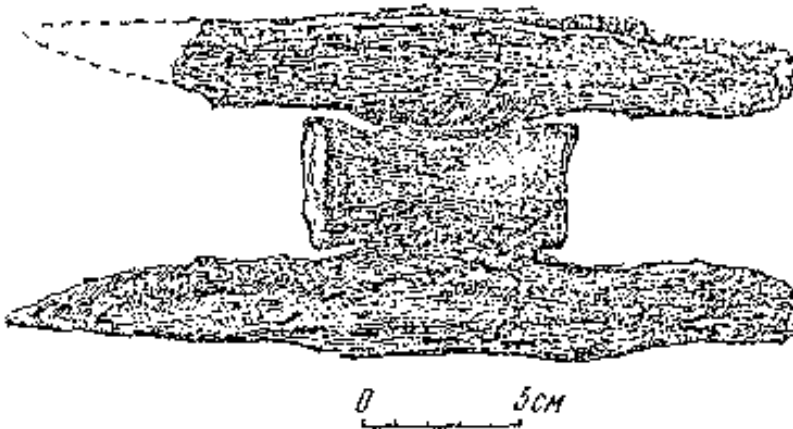


Fig. 10. *Talarurus plicatospineus*. Vertebra of the posterior caudal section, lateral view. PIN 557-3

The cross-section diameter is somewhat larger than the vertical. The spinous processes on all vertebrae are reduced and combined with the neural arch, so that the process borders are impossible to isolate (Fig. 10).

The walls of the neural arch in the anterior section are broken and greatly drawn forward, forming long forked and split zygapophyses (Fig. 11). The postzygapophyses section of the arch is compressed and has a wedge-shaped cusp. The cerebral canal appears as a narrow slot and is open above at its greatest extent. The hemal arch is lower, of rounded shape. Such a structure of the neural and hemal arches causes an almost immovable union of vertebrae by the bilateral articulation of the postzygapophyses section of the arch of the preceding vertebra being completely enveloped by the prezygapophyses section of the next one, but the constricted wedge-shaped section of the hemal process enters the V-shaped sculptured section (Fig. 11). The series of such vertebrae forms the percussive section of the tail, a “club” reaching a length of over one meter. All the vertebrae of this series are covered by a large number of extremely well developed ossified sinews, which conceal the borders of the separate vertebrae and increase the weight and elasticity of the percussive section of the tail.



Fig. 11. *Talarurus plicatospineus*. Vertebra of the posterior caudal section in natural articulation. PIN 557-3

The particularly great number of large tendons extends to the lateral regions, where they are arranged in winding rows, similar to that described for the Mongolian *Syrmosaurids* (Maleev, 1954).

Table 2. Dimensions of cervical vertebrae, dorsals, and caudals (in millimeters) measurements

| | vertebrae | | | | | | |
|----------------------------------|-----------|-----|---------|------|---------|---------|---------|
| | cervicals | | dorsals | | | caudals | |
| | III | IV | I | VIII | XV | I | IX |
| longest centrum length | 65 | 67 | 89 | 101 | 100 | 40 | 60 |
| longest centrum width | 60 | 71 | 80 | 75 | 75 | 80 | 75 |
| greatest height with neural arch | 116 | 173 | 156 | 215 | unknown | 230 | unknown |

RIBS

There are numerous rib fragments which represent every body segment, except for the cervicals.

The thoracic ribs are massive, wide, arched, with well-developed tubercula and capitula (Fig. 12). The gap between the tuberculum and capitulum is shallow and long. The tuberculum is fixed and aligned with the articular surface slightly rearwards and inwards, almost at the same angle as the curvature of the upper part of the rib. The upper section of the rear border of the rib (from the rising vertex) stretches rearwards and forms a deep concavity in which are placed vessels and nerves. Along the anterior surface of the rib runs a pronounced muscle groove.

On the upper section of the rib, on the approximate level of the upper point of the arch, there is a small rough region, serving as a place of attachment of powerful musculature. At a spot between the middle and the distal ends there is a slight protuberance (Fig. 12) which appears to correspond morphologically to the hook-shaped processes (pr. uncinati) of alligators and crocodiles.

The upper part of the rib in cross-section has an elliptical shape, distally it has a T-shape. The length of the rib ranges from 50 cm to 1 m; the width ranges from 3 to 6 cm (Fig. 12). The anterior thoracic ribs are tapered distally and are slightly ground down. The thoracic ribs are connected with the transverse processes of the vertebrae independently and they rise in their curvature to such a height, so that at the highest point of the arch they reach the summit of the spinal process, which thus forms a very wide spine and a large body size.

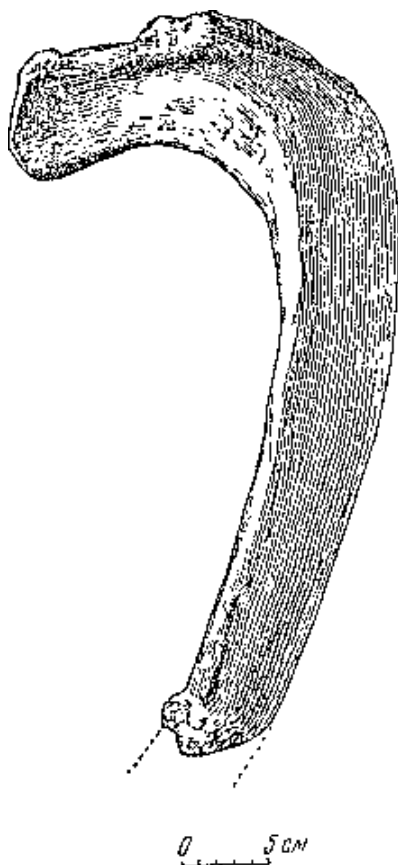


Fig. 12. *Talarurus plicatospineus*. Rib, lateral view. PIN 557-3

The lumbar ribs, in contrast to the dorsal, are wider; even in the vicinity of the spinal column their width reaches 4-5 cm. The distal ends are partially covered by the inner border of the preacetabular part of the ilium, for which reason the first lumbar rib seems longer, but the next one seems shorter.

Almost all the lumbar ribs (4-5 pair) are tightly joined with the neural arch from the capitulum to the tuberculum, so that the suture is very difficult to detect. By such a union of lumbar ribs, great durability and immobility of the body supports the heavy armor equipment of the rear section of the body (see Fig. 7). The following lumbar rib is not very much changed. It is narrow near the spinal column and wide at the ilium.

In this connection, it is extremely close to the following sacral ribs, but they all approach the internal surface of the ilium where they form the rest of the ilio-costal juncture. The sternum is broad, triangular in shape, and consists of a pair that have grown together, of which all three sides are of almost equal length. The front end of the sternum is tapered, the rear end is greatly widened and drawn out in an angle into long lateral processes.

The external (ventral) surface of the sternum is convex and has a well-expressed longitudinal keel.

The internal (dorsal) surface is deeply concave in the middle, rounded ovally and swollen laterally.

The cranial and caudal ends of the sternum were apparently cartilagenous and are not preserved.

THE HUMERAL ZONE

The scapula is a massive oar-shaped bone (Fig. 13). The upper part of it is strongly inclined to the rear, just as the lobe forms on the dorsal surface of the thoracic ribs. The anterior [=dorsal] border of the scapula is thickened and curved. The lobe [=blade] is wide and strongly inclined inwards. The dorsal border is thin, semi-oval in outline. The external (ventral) surface is convex, smooth, without any noticeable irregularities; the dorsal surface is strongly flexed and has a series of elongated grooves, especially visible in the lower part. Distally, the scapula expands and greatly increases, forming the upper half of the fossa glenoidalis. On a level with the fossa glenoidalis, the front border of the scapula is bent outward in the form of a semi-oval protuberance which probably is homologous with the acromial process of the higher vertebrates. Immediately behind this protuberance there is a slight concavity, which served, apparently as the place of attachment of m. deltoideus.

Near the union with the coracoid, the posterior border of the scapula is bent very much outwards below the obtuse angle at the lobe. The coracoid is large and massive (Fig. 13). Its length is equal to half the length of the scapula. At the proximal end it closely adheres to the distal section of the scapula, forming the lower half of the fossa glenoidalis. The boundary which unites the scapula and coracoid is clearly visible on the midline of the fossa glenoidalis. The front border of the coracoid is thin, coarsely irregular, and is reminiscent in some respects of the upper border of the scapula. This indicates that during

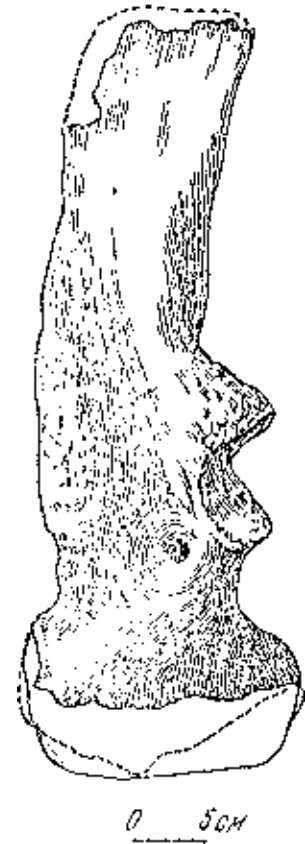


Fig. 13. *Talarurus plicatospineus*. Left scapula, lateral view. PIN 557-3

the life of the animal it had a very large cartilaginous section, which was united to the coracoid. The middle part is deeply concave within and slightly inclined backwards, so that its external surface is almost inclined forwards. The rear boarder is greatly thickened, flexed in an arch and rounded in oval shape. The foramen coracoideum is large, oval in shape, inclined diagonally within and rearwards to the external surface, rising slightly to the suture of coracoid and scapula. Below, the surface of the coracoid is somewhat convex in width, and forms a projecting externally obtuse angle with the upper section.

The fossa glenoidalis is large, rounded in shape. Its major axis reaches 105 mm, and runs parallel to the major axis of the scapula. The minor axis is 50 mm. The internal wall in cross-section forms an obtuse angle. The upper wall is longitudinally concave. The external border is rounded convexly and is somewhat >squeezed= in the dorsal direction, particularly in the anterior section. The lower portion is slightly curved transversely. The external border projects dorsally to some degree.

Dimensions of the Humeral Region Bones (In Millimeters) of *Talarurus*

Scapula

| | |
|--|-----|
| Scapula length to upper border of f. glenoidalis | 350 |
| Width of the proximal end | 152 |
| Thickness of the proximal end | 49 |
| Width of the distal end | 163 |
| Thickness of the distal end | 47 |

Coracoid

| | |
|---|-----|
| Length of coracoideum from lower border of f. glenoidalis | 145 |
| Width of the proximal end | 162 |
| Thickness of the proximal end | 40 |
| Width of the distal end | 158 |
| Thickness of the distal end | 9 |

Fossa glenoidalis

| | |
|---|-----|
| Total (overall) length (from the upper border of the scapula to the lower border of coracoid) | 105 |
| Width in horizontal direction | 50 |
| Depth | 65 |

ANTERIOR EXTREMITIES

The humerus is massive, wide, with greatly expanded proximal portion, shaped like a concave oval-triangular plate, rounded at the upper edges (Fig. 14). The anterior edge of the humerus has a sturdy delta-shaped crest (crista deltoidea) with an anterior thickness up to 2.5 - 3 cm, beginning below the head and passing through the middle of the bone at the narrowest point of the shaft, where it fuses with the entepicondylar border of the distal section. With this crest, the width of the humerus reaches 17 cm. The rear border of the shoulder is thicker and has a strong, but short processus medialis up to 3 cm thick. Between the deltoid crest and the processus medialis, the midsection of the bone is longitudinally curved (Fig. 14). On the ventral side of this section there is a wide sloping concavity (Fig. 15). The humeral head is large, rounded in shape, slightly drawn out in a front-to-rear direction, and projects somewhat outward, directed slightly rearwards. Its ventral border is almost a straight line and only slightly bent downward at the place of greatest bulge, the dorsal border is flexed and at the bulge it is sharply bent as if detached. At the base of the deltoid crest, the humeral body is constricted in a trihedral-prismatic cross

section, slightly twisted in the vertical plane. The distal end of the humerus is less expanded than the proximal. Its dorsal surface is slightly concave midway and convex at the border. On its

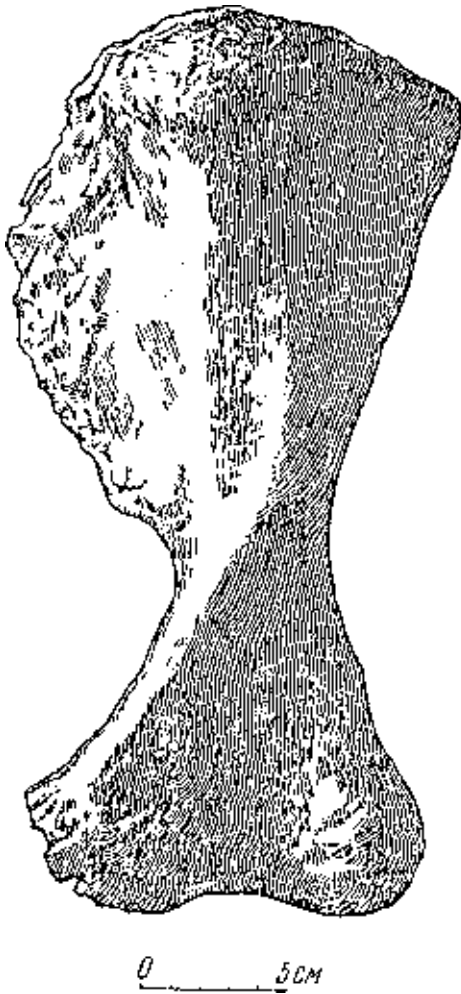


Fig. 14. *Talarurus plicatospineus*. Left humerus, from above. PIN 557-3

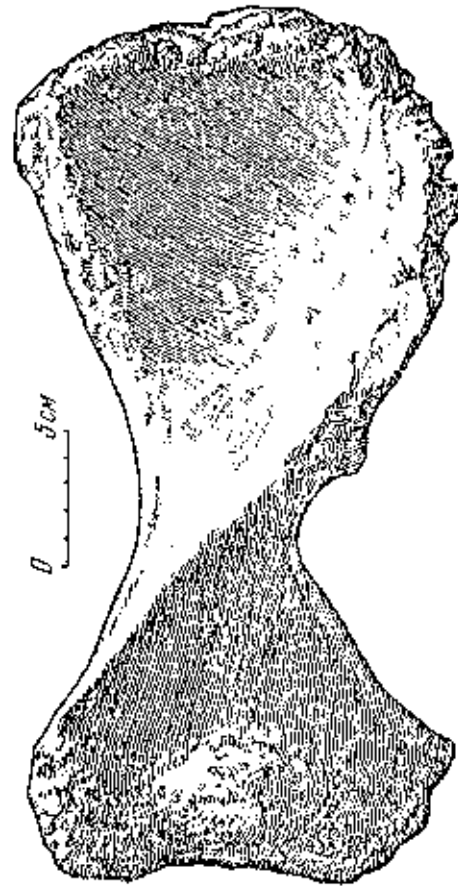


Fig. 15. *Talarurus plicatospineus*. Left humerus, from below. PIN 557-3

proximal border, there projects a small epicondylus radialis, and on the postaxial border, the epicondylus ulnaris. The internal surface is flexed transversely from border to border. The articular surface for articulation with the lower arm has the shape of a cylinder divided by a small constriction in a massive ovoid condylus radialis and a somewhat smaller, almost round condylus ulnaris.

The radius is not large, has wide and thick ends, especially the distal, which is greater than the distal end of the ulna (Fig. 16). The length of the radius is 61 mm shorter than that of the ulna; the maximal thickness is 60 mm. The anterior surface is slightly flexed and tapered inward. The ulnar surface is transversely expanded and is very coarse at the point of contact with the ulna. The bone in the proximal section is oval in cross-section and the central section is almost round; the distal section is triangular. The proximal articular surface is oval in outline, greatly

elongated in an antero-posterior direction, and concave (dish shaped). The rear convex side of the upper end of the radius closely conforms to the depression for it on the anterior surface of the ulna. The distal articular surface is more convex. Its external border slopes slightly forward, the ulnar and radial borders are curved in an oval.



Fig. 16. *Talarurus plicatospineus*. Left radius, lateral view. PIN 557-3

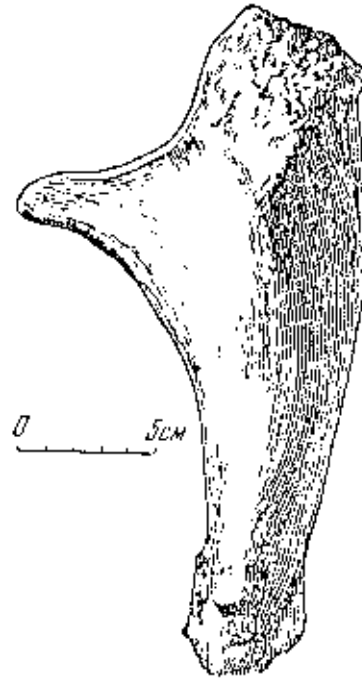


Fig. 17. *Talarurus plicatospineus*. Left ulna, lateral view. PIN 557-3

The ulna is massive, short, greatly widened at the proximal end and gradually tapering at the distal end (Fig. 17). The smallest transverse diameter of the ulna equals 50 mm. The ratio of the length of the humerus to the ulna is 1:2. The external surface of the bone is convex and very uneven in the proximal section. The central section is compressed and slightly twisted along the axis. The proximal end has a triangular shape and on the surface, facing the radius is located a deep incisura radialis, which completely covers the upper end of the radius. The processus olecranon is very massive and overhangs outside and above. Half of its surface is occupied by a tapered facet of the ulnar joint. On the inner or radial surfaces near the distal end there is a depressed, coarse region - the place of attachment of a ligament. The distal end is slightly widened and less thick; its articular surface tapers in the direction of the anterior side.

The carpus - Elements of the carpus were not preserved. The metacarpus (Mc1 - Mc5) consists of five bones almost identically in size (Fig. 18).

Mc1 is a short and wide bone, somewhat compressed in front and widened at the ends. The proximal end has a triangular outline and on the side bordering Mc2, slightly concave within. The surface for articulation with the carpal elements is somewhat convex and slightly rough. The distal end is wider than the proximal. The transverse diameter is considerably greater than the vertical. The articular surface with the first phalangeal digit is convex in an antero-

posterior direction and slightly sloped toward the external border. The rear surface is slightly flattened and transversely concave at the proximal end.

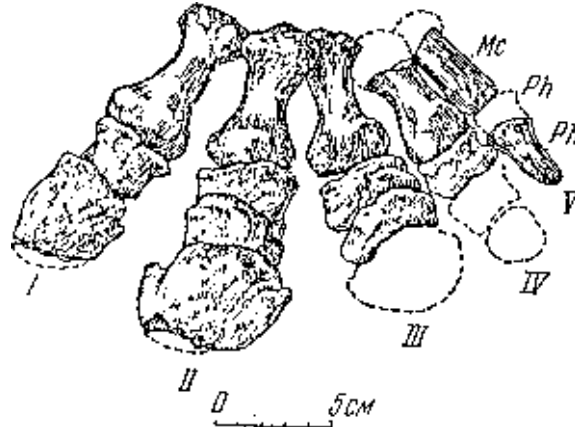


Fig. 18. *Talarurus plicatospineus*. Wrist cluster from above. PIN 557-3. Mc – metacarpalia; Ph – Phalanges; I-V - digits

On the lateral surfaces of the distal articular are distributed ligamentous fossulae, bordered above by small bundles of nodules. The palmar surface at the proximal end is extremely convex; at the distal end it is depressed.

Mc2 Long and very narrow end, compressed at the proximal section and widened distally. The proximal end has an oval shape; its surface is rough and slightly tapered. The distal articular surface is widened transversely and strongly convex in a front-rear direction.

Mc3 - The most massive bone of this series. Its body is moderately compressed in front and greatly broadened at the end. The proximal end is triangular in shape, with the top inclined upwards. The articular surface is convex in front and inclined to the sides in the form of two equal facets, designated for segmentation from the radiale and intermedium. The distal end is thick and has a strongly convex articular surface with the first phalangeal digit.

The rear surface of the bone on the proximal end is concave lengthwise; on the distal end, curved in an oval shape. The palmar surface is concave transversely and has a small irregularity for attachment of a ligament.

Mc4 - has the proportions of Mc2. The bone body is laterally compressed in front and widened at the ends, especially in the distal end. The articular facet for the first phalangeal digit has the appearance of a bar with a small groove in front, dividing it into two articular spaces, of which the medial is rather large.

Mc5 - a very weak element of the metacarpal series. The body of the bone is moderately compressed, the distal end is slightly widened and rounded into an oval shape.

Phalangeal formula: I - 2; II - 3, III - 3, IV - 3, V - 2. The proximal phalanx Ph1 of the first digit is the largest element of that series of bones. It is larger in width than in length. The proximal articular surfaces is deeply concave transversely, the distal one is convex. The palmar surface is flattened and slightly concave in a transverse direction.

The phalanges of the second row Ph2 are short in the second and third digits and wide. The articular surface with the first phalanx is deeply concave transversely. The distal surface is convex vertically and concave transversely. The palmar surface is concave and in a small leaf-shaped growth extended rearwards under the lower surface of the first phalanx.

The ungulate phalanges are depressed and hoof-shaped. While the animal lived they were

covered with corneous sheaths. The proximal end of the phalanx is widened and has a concave articular surface divided by a small projecting crest into two articular depressions, of which the medial is more depressed. The digital end is tapered and rounded into an oval. The rear surface is convex and very coarse, especially in the proximal section. The palmar surface is depressed and smoother.

Table 3. Bone Dimensions of Anterior Limbs

| Measurement | Humerus | Radius | Ulna | Mc1 | Mc2 | Mc3 | Mc4 |
|-------------------------------|---------|--------|-------|-------|-------|-------|---------|
| Length | 335 | 164 | 225 | 59 | 65 | 67 | Unknown |
| Largest proximal width of end | 165 | 70 | 112 | 30 | 41 | 41 | Unknown |
| Thickness of above | 80 | 60 | 95 | 40 | 21 | 24 | Unknown |
| Largest distal width | 140 | 75 | 35 | 35 | 32 | 33 | 28 |
| Thickness of Above | 68 | 61 | 49 | 25 | 27 | 29 | 18 |
| Cross-section at midpoint | 60x60 | 35x34 | 45x37 | 18x15 | 16x20 | 20x18 | 21x16 |

PELVIC GIRDLE

The ilium is very massive and is characterized by a large extension in front and a limiting contraction of the postacetabular section, which scarcely reaches 1/3 the length of the anterior section (Fig. 19). On lateral observation, the bone is bent from side to side and in a front-rear direction. The preacetabular section is long, wide, moderately thickened, somewhat narrow in front and terminates in a rounded truncated end. The acetabular section is comparatively short, abruptly twists in a transverse direction and terminates in a large dome-shaped widening which forms the basic section of a vertical depression, where the rear expanded border projects especially strongly for union with the ischium. The pubic base occupies a more forwards position and is imperceptibly developed. The axial depression [=acetabulum] is small, round in shape, inclined almost vertically downward. The ventral surface of the bone differs from the central concavity and is curved to the lower border, which is recurved somewhat externally and slightly upwards, forming on the acetabular section a powerful 'antitrochanter' for attaching caudo-femoral musculature. The dorsal surface is convex and has a small roughness, which becomes more pronounced on the axial depression and grows larger. Above the axial depression [=acetabulum], the bone is deeply concave within and on this spot it joins with the widened bones of the sacral ribs, forming an immovable or costal union [=sacral yoke]. The postacetabular section is short, wide, almost triangular in shape, very closely approaches the spinal column and unites with the transverse processes of the first caudal vertebrae.

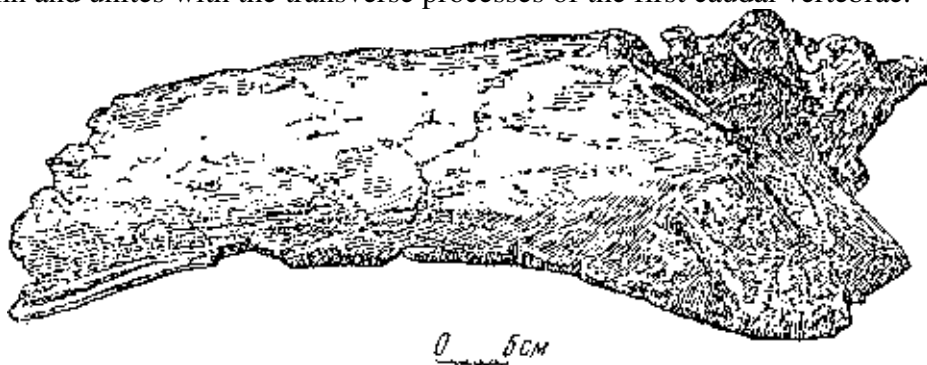


Fig. 19.. *Talarurus plicatospineus*. Ilium with dorsal surface. PIN 557-3

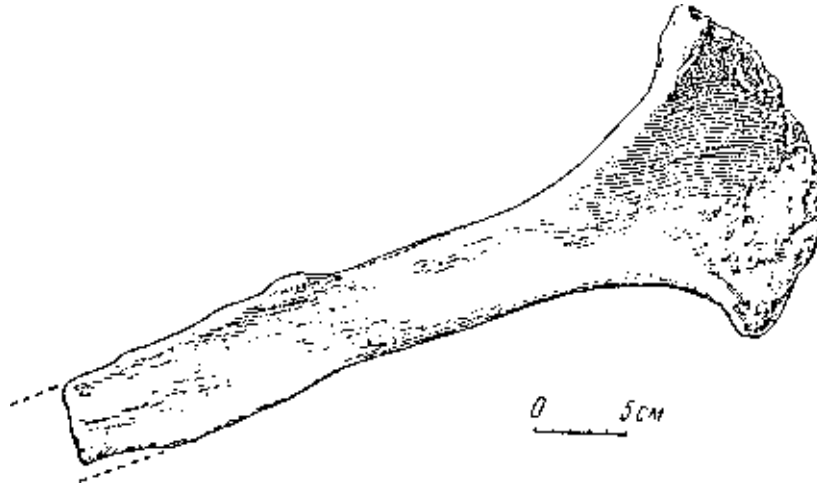


Fig. 20. *Talarurus plicatospineus*. Ischium with external surface. PIN 557-3

The ischium is comparatively long, flat, almost triangular in outline, widened at the proximal end and gradually contracts posteriorly towards the distal end (Fig. 20). The acetabular border is oval-convex and has two articular facets: the front, the smaller, for joining with the pubis, and the rear, extended for joining with the ilium. Between these facets the extended bone surface is very concave within and forms the rear section of the axial depression [=acetabulum]. Below the proximal end, the bone is transversely flattened and slightly flexed within. At the bend, the bone has a small rough area for fastening of ligaments. On the inside, the bone surface is transversely convex. There is no data whether there was symphysis with the ischium of the opposite side; probably there was cartilaginous union. The pubis is practically unknown; on the side of the axial depression [=acetabulum] there is a small fragmentary bone, which demonstrates that this element of the pelvis was of undetermined dimensions.

Table 4. Pelvic Bone Dimensions(in millimeters)

| | Measurements | Ilium | Ischium |
|-------------------------------|--------------|-------|---------|
| Greatest length | 1000 | 500 | |
| Width - Proximal end | 170 | 173 | |
| Width - Distal end | 245 | 61 | |
| Length of Preacetabular sect. | 600 | - | |
| Length of Post acet. Sect. | 240 | | |

REAR EXTREMITIES

The femur is massive and wide (Fig. 21). Its body is evenly expanded and slightly compact in anteriorly and posteriorly. The ratio of the femur to the humerus is 2:3, The proximal end is widened and thick. The head is massive and almost not separated by a collar [=neck] from the body of the bone. A greater trochanter fuses with a lesser [=anterior] one and is not separate from the head, so that the proximal rugose surface of the following one is continuously elongated and covers the upper surface of the greater trochanter. On the lower side of the femur, at the level of approximately half the length, there is a small region with a rough surface --the fourth

trochanter.

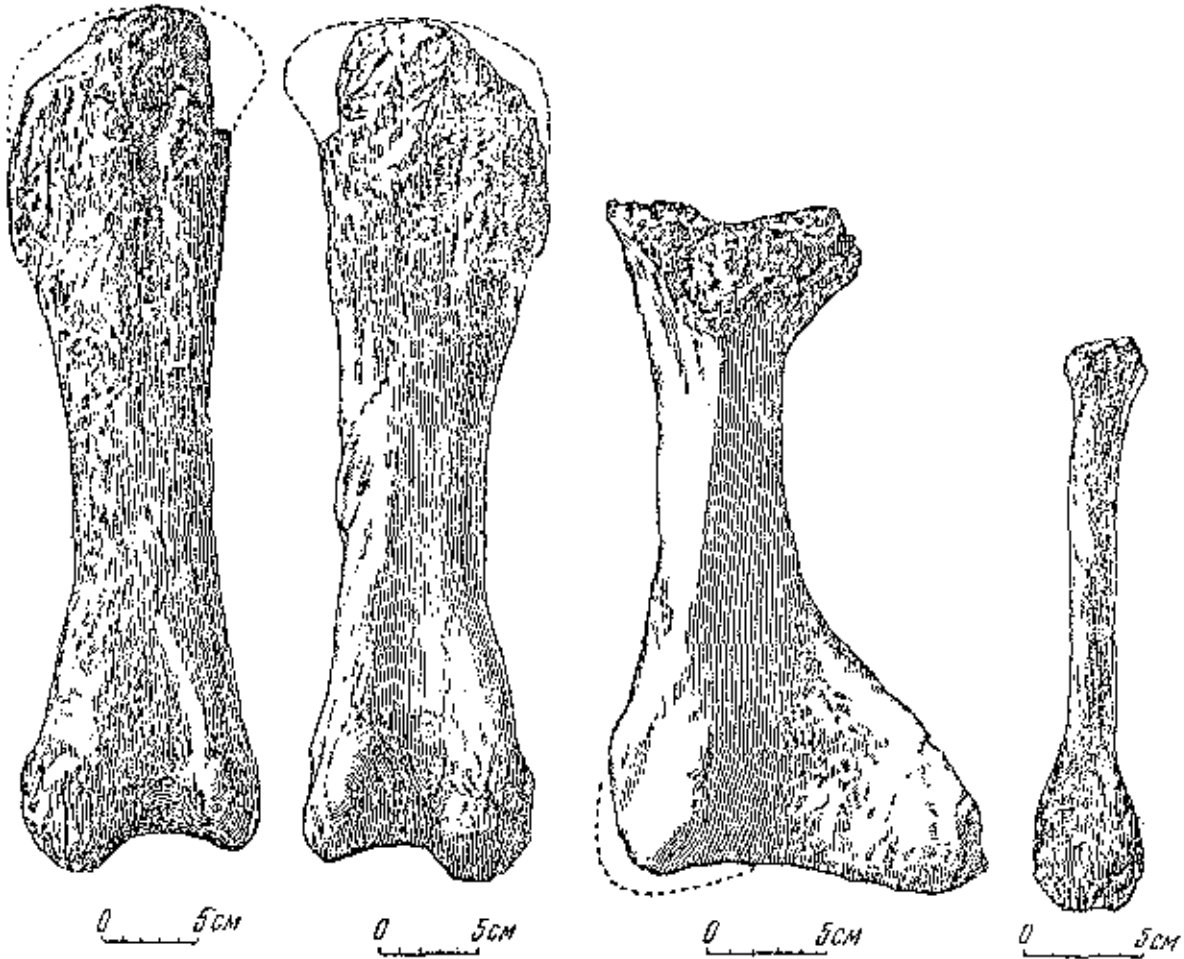


Fig. 21. *Talarurus plicatospineus*.
Right femur from
front. PIN 557-3

Fig. 22. *Talarurus plicatospineus*.
Right femur from
rear. PIN 557-3

Fig. 23. *Talarurus plicatospineus*.
Left tibia from
front. PIN 557-3

Fig. 24. *Talarurus plicatospineus*.
Left tibia from
rear. PIN 557-3

The upper surface of the femur is devoid of any unevenness or crest, only on its distal region is there a triangular depression - the fossa patellaris, along which ran the tendon of the muscles, the extensors of the tibia.

The distal end of the femur is transversely wider than in the anteroposterior direction; the articular section is well developed. The large epicondylus tibialis and epicondylus fibularis are slightly tapered above and strongly project over the f. patellaris, their separator. On the lower surface of the femur there is a large elongated depression - the fossa m. poplitei, under which partitions project of a wide intercondylar fissure (fossa intercondyloidae), a large condylus tibiale and the slightly smaller condylus fibularis, on the surface of which runs a short fissure for the tendinous muscles that bend the leg (Fig. 22). On the lateral surfaces of both condyles, there are uneven coarse patches for attachment of the bundles of the knee joint.

The tibia is short, wide, compressed in front and greatly widened at the ends (Fig. 23).

The ratio of the femur to the tibia is 2:3. The front surface of the bone is convex and has a well defined knee crest - the crista tibiae, which shifts distally in the medial direction and dwindles to nothing. The proximal end is wider in the anteroposterior direction than in the transverse. Its external border is slightly extended [=i.e., fibular process] for reception of the proximal end of the fibula. The distal end is greatly widened transversely. The [distal] articular surface for articulation with the tarsal elements has the appearance of a cylinder, separated at the front by a wide constriction on the more massive section of articulation with the astragalus and on the lesser - for joining with the calcaneus.. Above the junction with the calcaneus, there is a small concavity with a slightly wrinkled surface; on it borders the distal end of the fibula. The rear surface on the upper section is convex and has a powerful blunted crest (crista posterior tibiae), in the distal section it is flattened and slightly concave lengthwise.

The fibula is short, straight, with thin shaft and widening at the ends (Fig. 24). The ends are arranged relative to each other in such a way that their largest diameters form a right angle. The tibial surface of the proximal end is concave, agreeing with the surface of the tibia. On the rear surface, close to the center of the bone, there is a small rough section for fastening of ligaments. The distal end is thicker than the proximal, its internal surface is very rough.

The elements of the tarsus were not preserved.

The metatarsus (Mt1 - Mt4) consists of four strong firm bones (Fig. 25). Mt1 is somewhat shorter than the others. The bone is slightly tapered in the middle and widened at the end. The proximal end is thickened and has concave articular surfaces for joining with the tarsal elements. The distal end is wider than the proximal. Its transverse diameter is twice as long as the vertical diameter. The surface for linking with the first phalanx of the digit is convex and medially rather skewed.

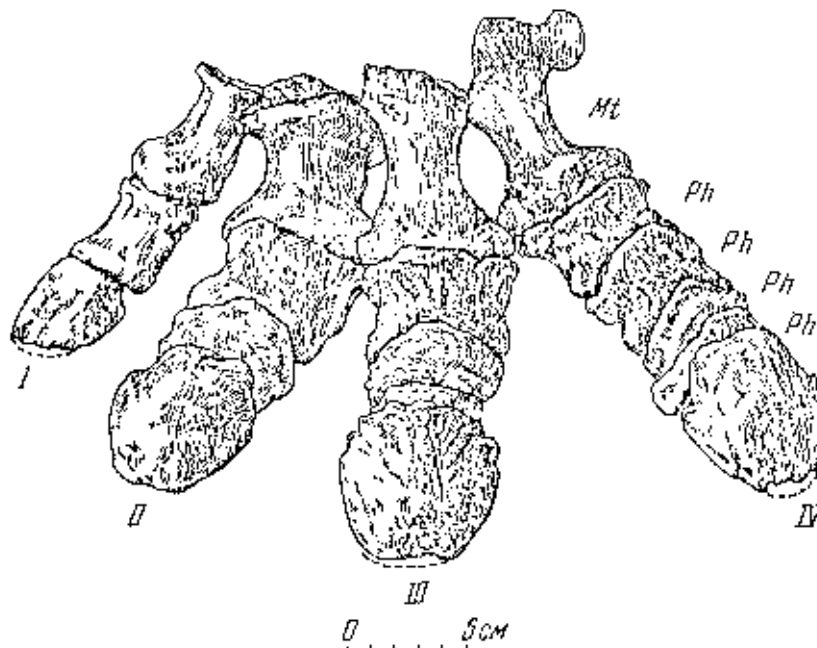


Fig. 25. *Talarurus plicatospineus*. Foot from above. PIN 557-3. Mt-metatarsals; Ph- Phalanges; I-IV – digits.

Mt2 is a massive, short bone, greatly compressed in a front-rear direction and thickened at the ends. The vertical diameter of the proximal end is a great deal larger in the transverse

direction. The articular surface is transversely concave and at the edges has a powerful tuberosity for attaching ligaments. The distal end is wider transversely than vertically. The articular surface is convex in a front-rear direction and drawn upwards, where it terminates in a strong tuberosity for attachment of ligament. The surface on the edge is concave and there is no irregularity. The volar [=sole] surface is very depressed (flattened), concave in the distal section transversely and very rough throughout its length.

Mt3 is longer than Mt2. The bone is greatly compressed laterally. The proximal end is thick. Its vertical diameter is twice that of the transverse diameter. The articular surface is greatly extended in a front-rear orientation, concave transversely and slightly uneven. The distal end is wider transversely than vertically. The articular surface is convex and greatly extended upward at the rear edge of the bone. The lower section of this surface is joined with the first phalanx of the digit, while the upper is left free. The edge is slightly concave in a front-rear direction and convex transversely, the volar [=sole] is flattened and slopes laterally.

Mt4 is less massive than Mt3. The bone is very compact laterally midway and expanded at the ends. The proximal end has a triangular shape and the upper end is turned downward. The articular surface is stretched in an anteroposterior direction and is somewhat concave transversely. The distal end is very flat and widened transversely. The articular surface is shaped like a bar, with a large extension on the lower side of the bone. The dorsal surface is concave in a front-rear direction and flattened transversely. The volar surface is flattened and sloped greatly to the side.

The complete phalangeal formula for the rear extremities of armored dinosaurs is undetermined. Based on the material provided at our disposal, we may propose the following phalangeal formula: I - 2, II- 3, III- 4, IV - 5 (Fig. 25).

The phalanges of the first row Ph1 in all four digits are shorter, thicker, comparatively heavier than in the wrist. Their width is twice the length. The proximal articular surface is concave top to bottom and transversely extended. The distal surface is convex and divided by a wide contraction into two facets, of which the medial is more developed. On the lateral surfaces, at the distal articular surface, are placed ligamentous depressions, bounded above by small ligamentous tubercles. The border surfaces of the phalanx are somewhat flattened and gently sloping in a lateral direction. The volar surface is transversely concave, slightly uneven; on the distal end there are two deep ligament depressions.

The phalanges of the second row, Ph2, are short and wide. The surface of articulation with the first phalanx is deeply concave in a transverse direction and divided by a small truncated crest on two articular depressions, of which the medial is more depressed. The distal surface is vertically convex and transversely concave. The border surface is concave longitudinally and extended rearwards by a small protuberance on the articular surface of the first phalanx. The volar surface is concave and slightly coarse.

The phalanges of the third and fourth rows (Ph3 and Ph4) are represented by very short but wide bones. Their width is 2.5 times greater than the length. The proximal articular surface is concave from the top downwards and divided by a small crest into two facets of equal size. The distal surface is vertically convex and transversely concave.

The clawed phalanges are flattened, ungulate in shape. In size they greatly surpass the clawed phalanges of the wrist. The proximal end of the phalanx is widened and has concave articular surface with an overhanging crest for fastening the sinews of the common extension of the digits, *m. extensor digitalis communis*. The distal end is somewhat compressed, curved in an oval shape. The dorsal surface is convex and very rough, with a few elongated fissures for

fastening the blood vessels. The volar surface, on its proximal section, is slightly convex and has two small depressions for fastening the deeply flexed digits - m. flexor profundus, on the distal section, it is flattened and rather rough. During the creature's life, the corneous sheath, which covered the phalanges, comprised the thick and massive hooves.

Table 5. Bone dimensions of rear limbs of *Talarurus* (in millimeters)

| Measurement | Femur | Tibia | Fibula | Mt1 | Mt2 | Mt3 | Mt4 |
|------------------------|-------|-------|--------|---------|-----|-----|-----|
| Greatest length | 470 | 298 | 267 | unknown | 81 | 89 | 87 |
| Width proximal end | 131 | 100 | 60 | unknown | 57 | 40 | 47 |
| Width distal end | 125 | 150 | 53 | 39 | 67 | 53 | 51 |
| Thickness proximal end | 87 | 130 | 29 | unknown | 82 | 76 | 67 |
| Thick distal end | 129 | 68 | 16 | 26 | 35 | 36 | 32 |

ARMOR OR PROTECTIVE EQUIPMENT

The protective equipment of *Talarurus* consisted of solid, compact bony armor, which was made up of plates (figs. 26 and 27) of navicular shape, of a thickness of 20 to 50 mm, joined longitudinally by means of slightly movable seams and forming cervical, spinal and pelvic scutes. On the external surface of the scutes, which are on the lateral surface of the limbs and tail, are located complete bony spines with apparently corrugated walls, comprising the external ornament of the armor (figs. 31 and 32).



Fig. 26. *Talarurus plicatospineus*.
Armor plate from above. PIN 557-3



Fig. 27. *Talarurus plicatospineus*.
Armor plate, side view. PIN 557-3

To understand these formations morphologically and functionally, we must distinguish three structural elements of the armor.

The first element is made up of comparatively flexible skin, in which numerous small

ossifications are contained. Parts of the skin were located between separate scutes of the armor and, besides, covered the whole peritoneal region.

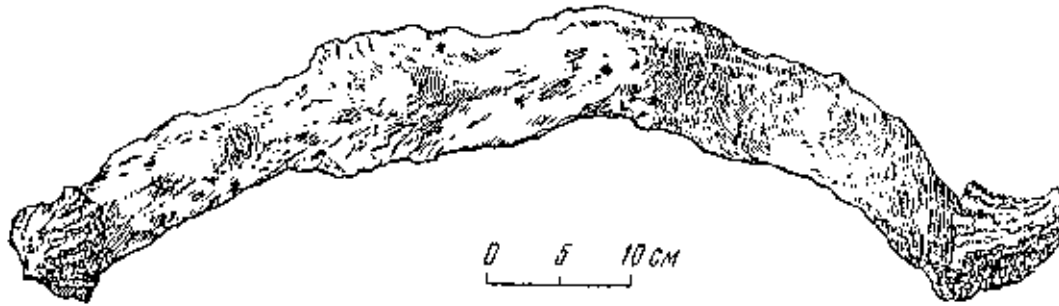


Fig. 28. *Talarurus plicatospineus*. Section of spinous carapace of armor, viewed from above. PIN 557-3

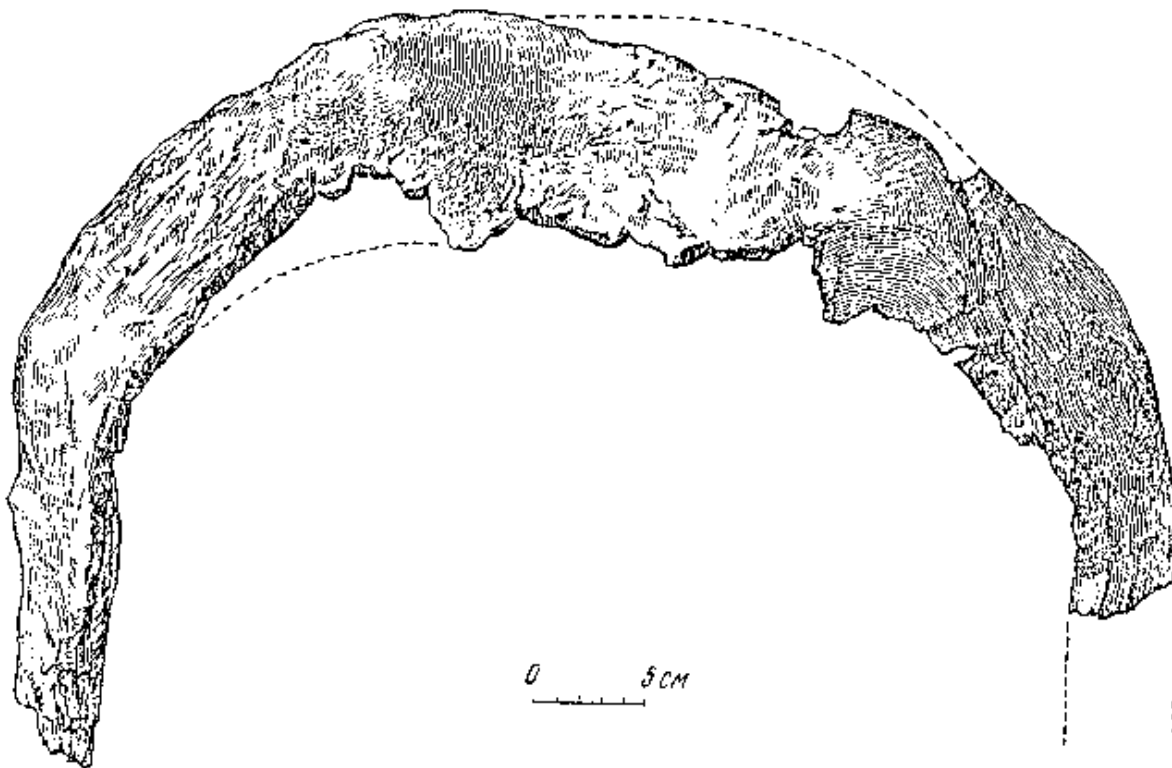


Fig. 28. *Talarurus plicatospineus*. Section of pelvic carapace of armor, viewed from above. PIN 557-3

The second element consisted of thick bony plates of navicular shape, 10-30 cm in length and 10-15 cm in width (figs. 26-27). The external surface of the plates are very convex in the middle and completely skewed on the edges. On the entire surface are located many depressions and furrows for blood vessels. The anterior and posterior borders of the plates are very coarse and are terminated by small papilla-shaped growths, which were joined to sections of granulated hide. Their internal surface is rough and very concave, shaped like an elongated groove. The lateral edge is uneven, with different kinds of serrations and depressions, by means of which the

plates are united to each other, forming scutes of arch-like form (Fig. 28-29). These scutes are of low mobility and covered the neck, back and pelvic regions of the animal. Between them ran narrow bands of granulated skin and, therefore, the body outwardly appeared laterally segmented. The third element consisted of whole bony scutes, forming the external ornament of the armor. The scutes differed in shape, but mostly they were triangular and conical in shape (Fig. 30 - 31).

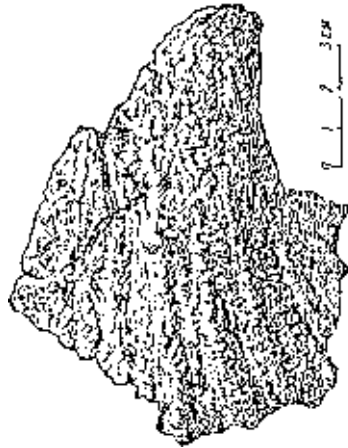


Fig. 30. *Talarurus plicatospineus*. Spine of armor. PIN 557-3



Fig. 31. *Talarurus plicatospineus*. armor spine . PIN 557-3

The back spines are massive and wide, sharp at the ends. Their basic shape is oval. The greatest height of a spine is 15 cm. The external surface of these spines are covered by elongated, as if corrugated, creases and small pits. The spines are arranged symmetrically on the surface of the scutes and are firmly united with the convex section of the leathery plates.

Leathery armament of the neck. The first section of the neck was, apparently, covered by very narrow bands of granular skin, on which were sequentially arranged two cervical scutes, covering the neck from above and laterally. Each scute consisted of not less than six separate plates, on the convex surface of which were spines. Especially sharp spines were located on the scutes of the lateral section.

Protective armament of the torso. On the front and rear sections of the torso, the armament is different. The front, the more mobile section, consists of 6 to 7 transverse segments (scutes; Fig. 28). The heavier rear section covered the lumbar-sacral region and consists of one or two large segments (Fig. 29-32).

The armor segments of the front half of the torso consist of no less than from 10-12 plates on the external surface of which are located sharp spines of conical shape (Fig. 28). The largest cranial-caudal length (width) of the spine is 12-15 cm; the largest transverse length is 1-1.5 M. The intervals between transverse segments were united by bands of granular hide, the cranial-caudal length (width) of which is 3-5 cm.

The sacro-lumbar scute is the most massive section of the entire armor. It consists of 10 large plates of a thickness of 30-50 mm (Fig. 29). The front border of the scute is concavely

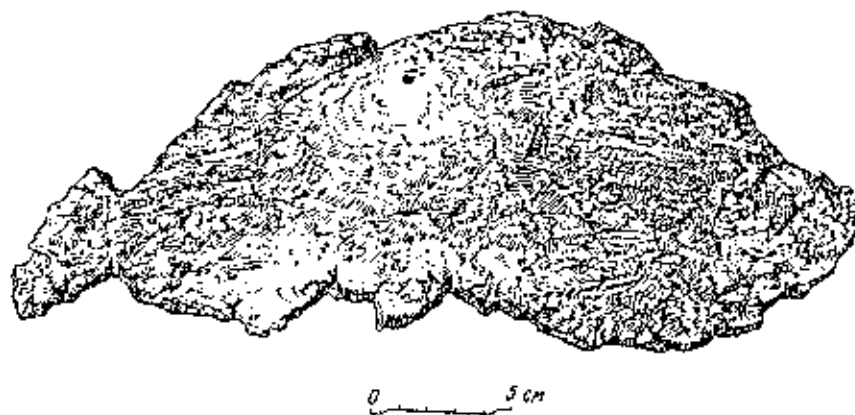


Fig. 32. *Talarurus plicatospineus*. section of pelvic armor spine from above. PIN 557-3

sloping in a transverse direction, the caudal border is convex. On the exterior and interior surfaces of the plates there are located large cavities and furrows for vessels. The largest cranial-caudal length (width) of the scute is 20 cm.

The tail was, probably, enclosed in bony rings, on the side of which were located sharp triangular spines, similar to what we observe in the gigantic glyptodonts.

MATERIAL: Fragment of skull and postcranial skeleton No. 557-3 PIN AN SSSR. With the 1948 excavation in the northeast section of a cliff at Bayn-Shire, in a cone of red calcareous clay, there were uncovered remains of three incomplete skeletons of armored dinosaurs. The material was represented by a fragment of a skull (the rear section of the skullcap, occipital region, base of the skull), cervical, spinal, sacral and caudal vertebrae, bones of the pelvis and of the humeral region, bones of the front and rear limbs, ribs, multiple bony plates and spines, which comprised the external armor of the animal.

The bones are well preserved, black in color due to oxides of magnesium, greatly mineralized and mixed with protracted maceration. Near at hand from the right side of the excavation [=quarry] in the southwest section of the cliff, in grains of clayey sand and the sand clays of the layer's central section were found more broken remains of two more skeletons of such dinosaurs. Among these remains were found pelvic bones and bones of the shoulder region, bones of the front and rear limbs, spinal and caudal vertebrae, fragments of ribs and bony plates of armor. Based on measurements of the bones, the remains of a skeleton of lesser size were separated, which belong to a young specimen of this species. The bones are well preserved, of yellowish-gray color with reddish tinge. Besides the listed remains, at this level of location there are found separate remains of Trachodons and carnivorous dinosaurs.

Comparison of materials from the first and second excavations indicated that all bones fall into the classification of individuals of almost the same age, of one genus and species, to the exclusion of the remains of the young specimen mentioned above.

Geologic Age - Upper Cretaceous.

Genus *DYOPLOSAURUS* Parks, 1924

Dyoplosaurus: Parks, W. A., Univ. Toronto, studies, Geol. Sec. 18, 1924

TYPE GENUS; *Dyoplosaurus acutosquameus* Parks, 1924

DIAGNOSIS. Large quadruped dinosaurs with heavy armor. The skull is not large, triangular in shape, slightly greater in length than in width. Lamellar leathery ossifications completely cover the surface of the skullcap and sides of the cranium. The rear border of the skullcap is deviated with rows of small spines. The ribs are massive. Between the central rib and its distal end there is a rough spot, morphologically similar to the hook-like outgrowths of other reptiles. The first caudal vertebrae are short and high. The vertebrae of the rear half of the tail are long, narrow, fused to the body, forming a solid 'hammer' or 'club' not less than 1 meter in length.

COMPARISON. In cranial structure, *Dyoplosaurus* slightly resembles *Panoplosaurus* (Upper Cretaceous of North America) in its possession of a small skull covered on top by five large bony plates. All the other examples of the family Ankylosauridae, *Ankylosaurus*, *Hierosaurus*, *Nodosaurus*, *Palaeoscincus*, *Scolosaurus* (Upper Cretaceous of North America), *Talarurus* (Upper Cretaceous of Mongolia), *Hoplitosaurus*, *Polacanthus* (Lower Cretaceous of England) have large crania covered by numerous small plates.

Dyoplosaurus differs greatly from all other ankylosaurs in the structure of the armor spines. Not one of the known genera has a similar sculpture of the spines, having very thin bony plates pitted externally and internally with multiple pits and channels for blood vessels. All this sets *Dyoplosaurus* apart as an independent genus of the family Ankylosauridae.

Species Content: Genus *Dyoplosaurus* includes two species: *Dyoplosaurus acutosquameus* Parks, 1924 and *Dyoplosaurus giganteus* sp. nov.

Geographical Distribution: Representatives of genus *Dyoplosaurus* discovered from Mongolia, Nemget site and North America, Alberta province.

DYOPLOSAURUS GIGANTEUS sp. nov. [now *Tarchia gigantea*]

TYPE SPECIES. Isolated caudal vertebrae of the anterior half of the tail in quantity of 12 pieces (from II to XIII), armor spines, metatarsal bones and phalanges of digits; no. 551-29, PIN AN SSSR.

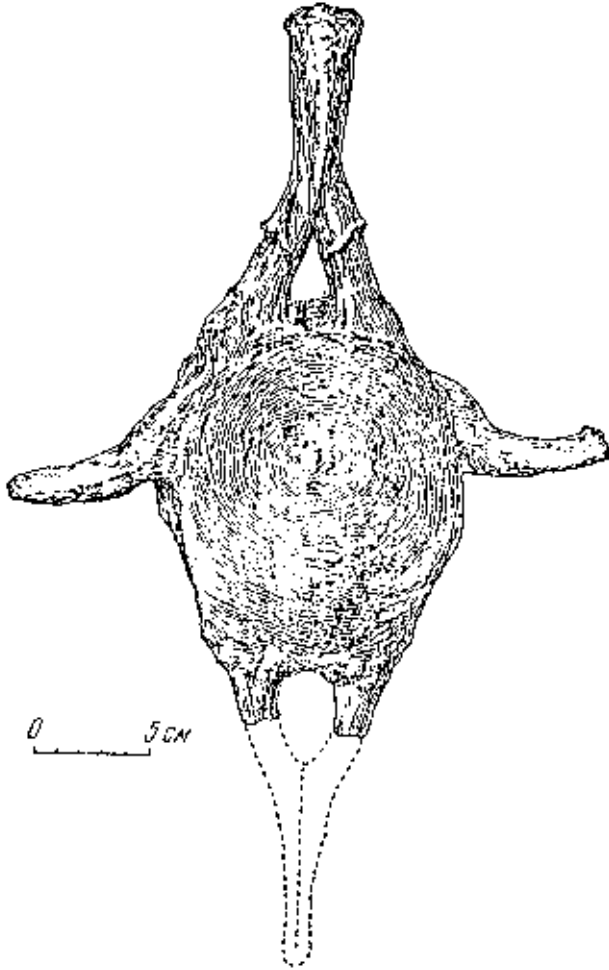
DIAGNOSIS. The anterior caudal vertebrae are short, high, amphicoelous. Chevrons are massive, scapular in shape, firmly attached to the rear half of the body of the corresponding vertebra. The rear caudal vertebrae are long, low. The metatarsal bones are short, wide. The clawed phalanges are thick, hooflike in shape. The spines of the armor are sharp, thin walled. The external surfaces of the spines are pitted with multiple depressions and channels for blood vessels (Fig. 37-40).

DESCRIPTION

There are 12 vertebrae in the anterior half of the tail, which indicate that the tail of *Dyoplosaurus giganteus* was comparatively short and consisted of 22-25 vertebrae.

The first caudal vertebrae are short, high; the articular surfaces are slightly depressed and extended to a greater height than width (Fig. 33). The centrum sides are rounded and less compressed than in the other armored dinosaurs. The transverse processes are long, horizontal, sharp at the ends and slightly folded [angled forwards] anteriorly, their size gradually decreases posteriorly, where they assume the form of small bumps that project from the upper part of the vertebrate body. The neural arch is massive, high. Its height is almost equal to the centrum's height. The neural channel is large, of triangular cross section, slightly widened and hollow at the base of the arch. The prezygapophyses on the first caudal vertebrae are more developed than the

postzygapophyses, which are widely separated and revolve dorsomedially by means of articular areas. The r postzygapophyses are somewhat higher than the prezygapophyses. Their articular areas [of the postzygapophyses] are drawn together and face laterally. The spiny processes [=neural spines] are high, of rectangular shape, slightly curved in cross-section and terminate in a thickened top.



weakly depressed and almost platycoelous. The transverse processes are reduced and represented

Fig. 33. *Dyoplosaurus giganteus* sp. nov. Second caudal vertebra, from rear. PIN 551-29

by small crests. The smallest transverse process is found on the XII vertebra. The neural arch is low; the cerebral canal is small, oval in outline. The spinous processes are crest-shaped, very compressed laterally and sharply inclined to the rear. The prezygapophyses are massive, widely distributed and strongly lengthened forward and projected to almost half the body length. The postzygapophyses are reduced and fused with the lateral surface of the spinous processes, where they appear as small, barely perceptible areas which scarcely project on the body the spinous processes. The hemal arch is low, long (Fig. 35). The hemal process is not apparent and mixes with the upper section of the arch. The front section of the arch is V-shaped and greatly extended forward, the rear is wedge shaped and constricted. The hemal canal is low and curved; below it is covered for almost all its extent by the bony walls of the arch.

Such a structure of the neural and hemal arch causes an almost immobile union of the

The chevrons are long, carinate, closely joined with the rear half of the corresponding vertebra's body. The hemal channel is large and triangular in cross-section. Subsequent caudal vertebrae, from IV to X, gradually increase in length and decrease in height. The transverse processes sharply decrease and assume the appearance of small tubercles, which are distributed on the first section of the vertebra body. The neural arch is low and wide. The spinous processes are extremely widened and inclined to the rear. On the ventral surface of the vertebrae runs a deep longitudinal depression, which widens gradually to the rear and increases in depth. The chevrons are massive, carinate, linked independently with the rear section of the corresponding vertebra. The hemal channel is large, oval in outline.

The next vertebrae, from X to XIII, are much greater in length compared to the preceding ones (Fig. 34). Their bodies are low and wide. The cross-section diameter of the centrum is twice as wide as the vertical one. The articular surfaces are

vertebrae by a two-fold articulation, wherein the postzygapophyses section of the arch of the preceding vertebra is completely embraced by the prezygapophyses section of the subsequent vertebra, but the wedge-shaped tapered section of the hemal arch of the preceding vertebra enters a V-shaped incised section of the arch of the subsequent one. A series of such vertebrae form a percussion section of the tail - "the club", which reached a length of not less than 1 meter.

The metatarsus (Mt2-Mt4) appears as a solid, strong bone (Fig. 36). Mt2 is the most massive bone of this series. The bone is moderately compressed in the middle and very wide at the ends. The vertical diameter of the proximal end is somewhat greater than the transverse diameter. The articular surface has an oval outline, slightly concave transversely and has a small rough area at the edge for fastening the ligaments. The distal end is wider than the proximal end. Its transverse diameter is three times greater than the vertical diameter. The area for articulation with the first phalanx of the digit curves in a front-rear direction and is somewhat extended above, where it terminates in a strong tuberosity. The back area is concave in a front-rear direction, transversely convex and has no irregularity. The volar area in the proximal section is convex and has a very rough area; in the distal section it is longitudinally concave in the middle and inclined to the side.

Table 6. Correlation of caudal vertebrae measurements of *Dyoplosaurus giganteus* sp. nov., and other ankylosaurs of the Family Ankylosauridae (in millimeters).

| measurement | <i>D. gigantea</i> | | | <i>D. acutosquameus</i> | <i>Talarurus plicatospineus</i> | <i>Palaeoscincus rugosidens</i> | | |
|-----------------------------------|--------------------|-----|---------|-------------------------|---------------------------------|---------------------------------|-----|-----|
| | II | XI | XIII | | | II | XI | XIV |
| greatest length | 53 | 80 | 129 | 60 | 40 | 49 | 56 | 52 |
| greatest width | 116 | 105 | 100 | 70 | 80 | 103 | 85 | 86 |
| greatest height | 135 | 95 | 60 | 75 | - | - | - | - |
| greatest height with neural spine | 300 | 150 | unknown | unknown | 230 | 200 | 187 | 135 |

Table 7. Dimensions of caudal vertebrae of *Dyoplosaurus giganteus* (in millimeters)

| measurements | caudal vertebrae | | | | | | | | | | | | |
|--|------------------|-----|-----|-----|-----|-----|-------|-----|-----|-----|-----|-------|--|
| | II | III | IV | V | VI | VII | VII I | IX | X | XI | XII | XII I | |
| greatest length | 53 | 60 | 68 | 69 | 71 | 74 | 76 | 80 | 80 | 93 | 111 | 129 | |
| greatest width with transverse process | 270 | 250 | 200 | 180 | 150 | 135 | 130 | 125 | 125 | 117 | 105 | 100 | |

| | | | | | | | | | | | | |
|-----------------------------------|----|----|----|----|----|----|-----|----|----|----|----|----|
| greatest height | 13 | 13 | 12 | 11 | 11 | 10 | 105 | 10 | 95 | 85 | 68 | 60 |
| | 5 | 0 | 5 | 5 | 5 | 8 | | 0 | | | | |
| greatest height with neural spine | 30 | 29 | - | - | - | 23 | - | - | - | 15 | - | - |
| | 0 | 5 | | | | 0 | | | | 0 | | |

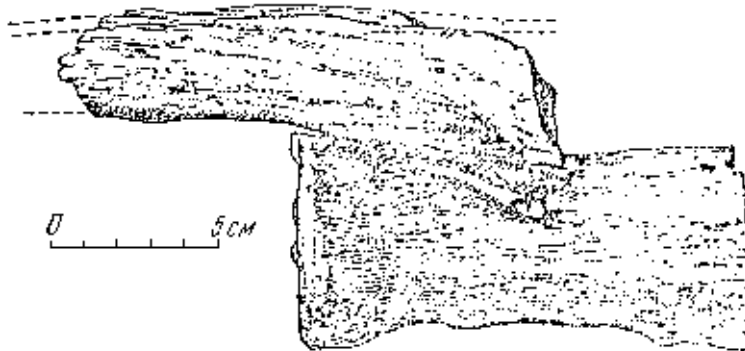


Fig. 34. *Dyoplosaurus giganteus* sp. nov. Thirteenth caudal vertebra, side view. PIN 551-29

Mt3 is less massive than Mt2. The bone is greatly compressed in a dorso-ventral direction and widens at the ends. The proximal end has an oval outline, and laterally surrounds Mt2 completely, tapered. The articular surface is lengthened transversely and is somewhat concave in the middle. The distal end is not so wide as the proximal end. The articular surface is of cylindrical shape, with a large extension on the upper surface of the bone. The spinous area is slightly concave in front-rear direction and transversely flattened. The volar surface is longitudinally concave and very rough for attachment of ligaments.

Mt4 is longer than Mt2 and M3. The bone is very compact laterally and widens at the ends. The proximal end is thickened. The distal end is wider transversely than vertically. The articular surface is cylindrical in shape, with a large extension on the lower side of the bone. The spinous surface is convex transversally and has no irregularity. The volar surface on the proximal section is convex and very rough, extensively concave on the distal part.

The full phalangeal formula for *Dyoplosaurus giganteus* is unknown. (Figs. 35-36). The phalanges of the first row Ph1. The second and fourth digits are short and flat. Their width is twice the length. The proximal articular surface is deeply concave above and below and transversely extended. The distal surface is convex and divided by a wide construction on two facets, of which the medial is more developed. On the lateral surfaces, by the distal articular surface, are located ligamental depressions, restricted above and below by large ligamental tubercles. The spinous surface of the phalanx is somewhat thickened and fully compressed laterally; the volar surface is concave transversely and rather coarse.

The clawed phalanges are massive unguals that are short for the size of the animal, and were covered by even more blunt corneous sheaths (Fig. 36). In size they very greatly exceed all preceding phalanges and are almost not inferior in size to the metacarpal bones. The proximal end is very wide transversely and has a concave articular surface for joining with the preceding phalangeal digit. The distal end of the phalanx is rather constricted and ovaly rounded. The spinous surface is convex and very rough, with some elongated furrows and numerous cavities for blood vessels. On the side of the phalanx emanate large bundles of pits for securing the

sinews of



Fig. 35. *Dyoplosaurus giganteus* sp. nov.
Haemal arch of thirteenth caudal vertebra, from
below. PIN 551-29



Fig. 36. *Dyoplosaurus giganteus* sp. nov. Foot
PIN 551-29

the general digit extensors, m. extensor digitalis communis. The volar surface is slightly concave in an anteroposterior direction and very rough, where there are usually two small pits for deeply anchoring the flexors of the digits - m. flexor profundus.

Table 8. Dimensions of rear limb bones of *Dyoplosaurus giganteus* (in millimeters)

| measurement | mt2 | mt3 | mt4 | ungual digit |
|------------------------|-----|-----|---------|--------------|
| greatest length | 80 | 70 | unknown | 85 |
| width distal end | 70 | 95 | 37 | 62 |
| thickness proximal end | 75 | 48 | 50 | 40 |
| thickness distal end | 28 | 37 | 32 | 12 |

Defensive Weapons. The defensive weapons of *Dyoplosaurus giganteus* sp. nov. were preserved only in the form of separate spines, which were found together with the caudal vertebrae. In form, these spines are divided into five separate types.

1. Huge spines of triangular shape with rounded corners and widened bases (Fig. 37). The outer side of the spine is slightly convex and largely pitted with numerous depressions and small channels leading within, the inner side is concave and deeply sculptured. The greatest

length of a spine from front to rear is 190 mm, the greatest vertical diameter is 180 mm, the greatest transverse diameter is 50 mm. These spines were distributed, apparently, on the lower border of the lateral surface of the tail.

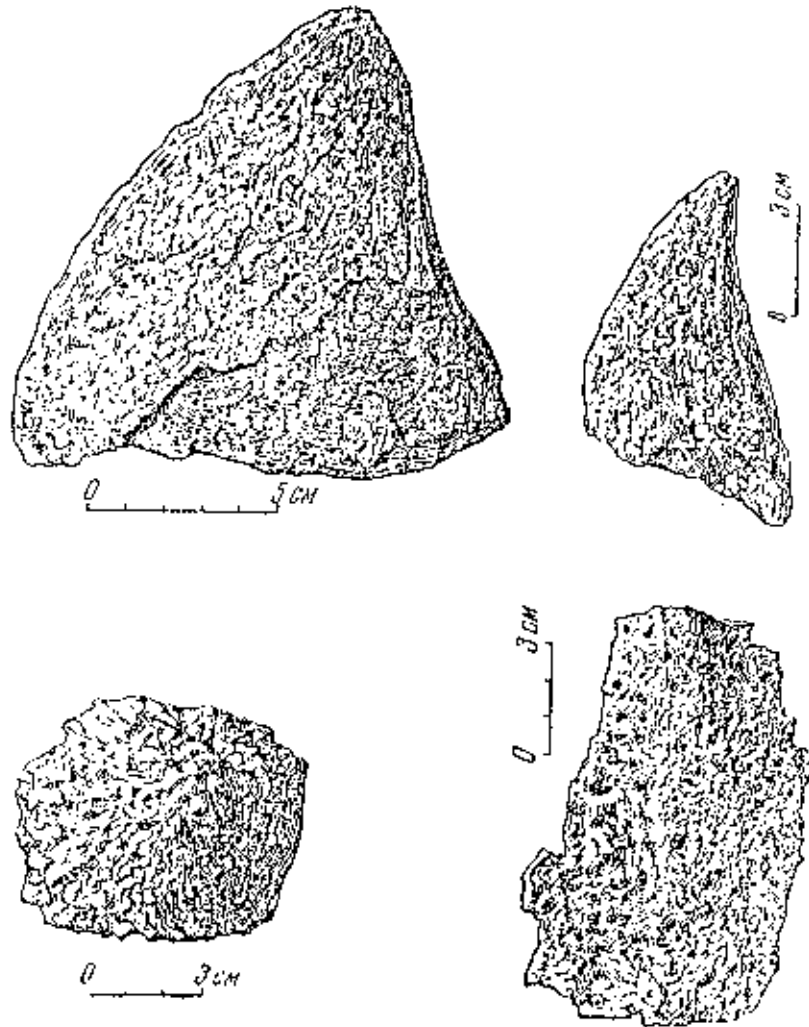


Fig. 37-40. *Dyoplosaurus giganteus* sp. nov. armor spines. PIN 551-29

2. Smaller sharp-pointed spines of triangular shape, with very sharp tip and slightly widened base (Fig. 38); they had very thin walls and were very similar to spines of the first type of sculpture. The greatest length of spine in a front-rear direction is 60 mm, the greatest vertical diameter is 95 mm; the largest transverse diameter is 26 mm. These spines were distributed, apparently, in the intermediate space between spines of the first type.

3. The smaller spines of triangular shape with blunted tips. The lateral areas are almost symmetrical and are sculptured with small depressions and channels, leading within. The greatest spinous length in front-rear direction is 95 mm. The greatest vertical diameter is 80 mm, the greatest cross-section diameter is 30 mm. They were located more dorsally than spines of the first type and constituted a second parallel row.

4. Spines of conical shape with very widened base and truncated top. The external surface is very rough; it has many depressions and channels (Fig. 39). The greatest spine length is 55 mm, the greatest height is 65 mm. These spines were distributed, apparently, on the interval

between spines of the first and second rows and constituted the third parallel row.

5. The long spines of trapezoid shape with greatly widened bases and sharply expressed dorsal crest (Fig. 40). The lateral areas of the cover are compressed and sculptured with many pits and channels. The inner surface of the spines is slightly concave transversely and is extremely coarse. The location of these spines correspond to the medial row which runs on the dorsal surface of the tail.

Comparison. In comparing *Dyoplosaurus giganteus* sp. nov. with many other species of the family Ankylosauridae, one must first state that in the characteristics of the caudal vertebral structure and armor spines, this species is a typical representative of a suborder of ankylosaur. High, massive caudal vertebrae, with dense increase of chevrons and armor spines, which have a unique sculpture, determine the affiliation of the remains described to the genus *Dyoplosaurus*. But the *Dyoplosaurus* from Mongolia differs somewhat from *D. acutosquameus* which was discovered later (Upper Cretaceous of North America) in having very large measurements of the caudal vertebrae, which are larger than the caudal vertebrae of all other ankylosaurs. All of this compelled us to assign the Mongolian armored dinosaur to a new species of the genus *Dyoplosaurus* - *D. giganteus* sp. nov. (gigantic dinosaur).

General observations. The discovery of armored dinosaurs of the type *Dyoplosaurus* in Nemegt broadens our concept of dinosaur fauna of the Mesozoic of Central Asia and demonstrates that in the contents of this fauna are contained different faunistic complexes which contain major varieties of ecological types. Among these are not only carnosaur, hadrosaur, sauropods, but also many ankylosaurs, found together with ceratopsids, in more open geographic ranges of bedrock edges, marshy forests and river valleys.

The evolutionary level of *Dyoplosaurus* from Nemegt corresponds to *Panoplosaurus*, *Dyoplosaurus acutosquameus* and *Scolosaurus*, which are known from the middle level of the Upper Cretaceous of North America (Belly River Formation of Alberta). This, no doubt, indicates the Upper Cretaceous age of *Dyoplosaurus giganteus* sp. nov. and admits the possibility of considering the Nemegt deposits to be almost the same age with Belly River, which may be a little older than the deposits at Bayn-Shire.

Material. Twelve caudal vertebrae (II-XIII?) inclusively, with partially preserved neural and hemal arches. Three metatarsal bones (Mt2-Mt4), phalanges of the first row, digits II and IV, a phalangeal claw and some separate armor spines. The bones are yellow in color, well preserved, and collected in 1949. Collection No. 551-29, PIN AN SSSR. Caudal vertebrae II to XIII (from 29/1 to 29/12); armor spines (from 29/13 to 29/23), metatarsal bones (from 29/24 to 29/26), phalangeal digit (from 29/27 to 29/30).

III. SOME STRUCTURAL FEATURES OF ANKYLOSAUR SKELETONS

Armored dinosaurs or ankylosaurs belong to the suborder Ornithischia and, consequently, they possess a large part of the traits of ornithischian dinosaurs. In contrast to bipedal and unprotected specimens of the suborder, the armored forms were quadrupedal and protected either by solid bony armor or by a row of separate bony plates and spines. These forms appear, not without grounds as armadillo-like dinosaurs or "reptilian tanks", just as in all reptiles, omitting tortoises, they were fully protected by armor. They have no analogues among contemporary vertebrates and therefore the functional character of their skeleton presents special difficulties.

The skull has some features of primitive colylosaurs (*Pareiasaurus*) but has also characteristic traits which are typical only for armored dinosaurs; for example, the presence of large, air-bearing cavities similar to the sinuses of an elephant head, distinctly lightening the

whole head and producing a complex structure of the skullcap, so that its strength is much increased.

The occipital condyle is inclined ventrally from the long axis of the skull, so that while attached to the neck the longitudinal axis of the skull forms with the longitudinal axis of the first and second cervical vertebrae an obtuse angle. Such an articulation certainly is revealed as the result of particular structure of the cervical vertebrae, forming a rising spot beneath the angle with the cervical body.

The front articular surfaces of the smaller [cervical] vertebrae are slightly concave and are inclined vertically, the rear surfaces are tapered and depressed below the front surfaces. Near the articular series of such vertebrae, a peculiar curve was produced and a deviation of the neck upwards, in consequence of which the head was continually raised. The neck movements were possible in a dorso-ventral direction, while the range of the rise was greater than that of the descent. The rising of the neck and head was a very significant biological feature, increasing the radius of observation, features essential to the creatures, which were of very insignificant height of limbs and a wide flat body. This feature was developed in some other morphological forms in large degree for such flat-bodied forms, as in the contemporary *Echinoryncus* lizards of the desert - *Moloch*, *Phrynosoma*, etc.

The extremely peculiar vertebrae structure of the trunk. The vertebra bodies are massive, wide; the transverse diameter of the centrum exceeds the vertical diameter. The front articular surfaces are deeper than the rear ones.

The prezygapophyses and postzygapophyses are well developed and form a link "pivot or hinge". They are extended greatly to the rear of the vertebrae center. All of these features are evidence of the lack of mobility of the spinal column and the extreme curve of the spine. The peculiar union of the ribs with the transverse processes of the vertebrae, by which the dorsal edge of the cervical ribs enters into the furrow on the transverse process, also greatly strengthens the vertebral column and thorax generally.

For the extremely wide and flat thorax of *Talarurus*, this reinforcement of the ribs is especially significant. The entire coalescence of the ribs of the lumbar region with the transverse processes of vertebrae greatly reinforces this region of the back bone and gives rise to a firmer basis for support of especially heavy armor covering the pelvic section of the body. With the presence of heavy body armor, no doubt, there occurs the strengthening of the pelvic girdle, which results from the entrance into the structure of the sacrum of many sacral vertebrae and the first caudal vertebra.

The most interesting structure is the limb structure of *Talarurus*. Ankylosaurs have the most massive humerus of all other ornithischian dinosaurs, which is doubtless connected with their quadrupedal manner of motion. The large dimensions of the humerus, the large deltoid crest, the peculiar location of the head, together with the form of the articular channel, which is stretched in a cranio-dorsal direction, demonstrate that the front limbs of *Talarurus* were curved and the humerus was oriented horizontally.

The femur, compared to that of the typical ornithischian, was subjected to strong alterations. The interval between the head and the greater trochanter is not expressed; the lesser [=anterior] trochanter developed very slightly and was fused with the greater; the fourth trochanter was almost completely reduced and had the appearance almost of a small rough area. These changes in the femur are thus linked with quadruped locomotion.

The wrist and foot were greatly developed. The metacarpal and metatarsal wrists are short and wide; the phalanges of the digits are massive; the claws are flat, of ungulate form.

The presence of wide and flat clawed phalanges indicate that the digits are distributed parallel to the ground and formed in this way an angle with the metacarpal elements. This, it seems, indicates the plantigrade manner of walk of ankylosaurs.

The caudal structure of *Talarurus* was most unique. The vertebrae of the anterior half of the tail are short, high, and permit motion in both the dorsal and lateral direction. The vertebrae of the rear section of the tail are low, long and linked almost immovably by means of a special spinous joint, by which the postzygapophyses section of the arch of the preceding vertebra is completely enveloped by the zygapophyses section of the next vertebra, but the wedge-shaped constricted section of the hemal process of the preceding vertebra enters a V-shaped incised section of the following vertebra.

As a whole, the entire section of the tail lost mobility of the separate vertebrae and was converted in a functional way to its own class of 'mallet' or 'club', with a length not less than 1 meter. The blows from such a 'club' caused a motion of the front half of the tail, which is very similar to analogous adaptations in the gigantic glyptodonts (Scott, 1937). Large and small spines and numerous ossified tendons further increased the weight and resilience of the tail section blows.

IV. MANNER OF LIFE AND RECONSTRUCTION OF THE APPEARANCE OF *TALARURUS*

The results of skeletal studies presented above make it possible for us to come to some conclusions about the appearance and way of life of the dinosaur described.

Talarurus plicatospineus was a massive animal, of heavy structure, generally resembling the gigantic glyptodont of the Cenozoic era, but was even larger (Fig. 41).

The neck was somewhat extended ahead of the body and somewhat raised upward. The creature possessed a relatively small head, protected above and at the sides by various forms of spines and bony plates, which gave it a fantastic appearance and, it seems, served as a secure protection.

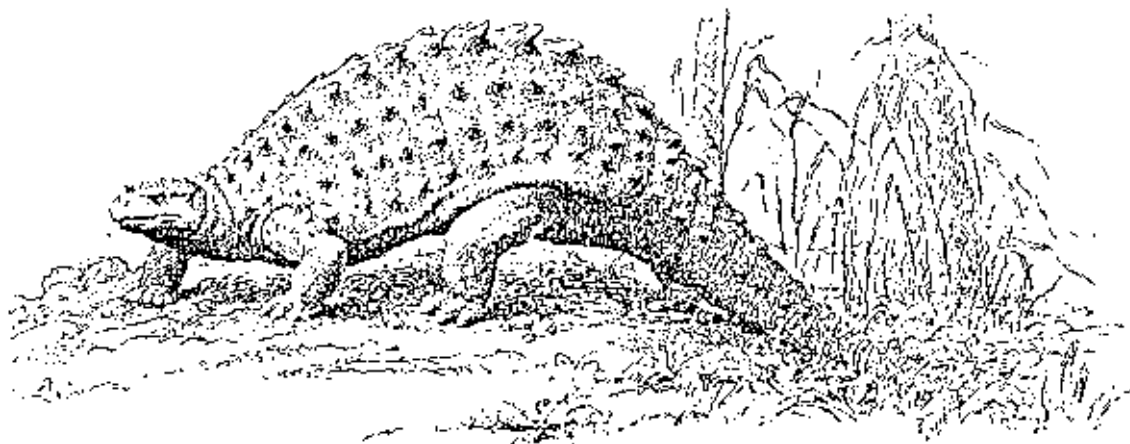


Fig. 41. *Talarurus plicatospineus*. Reconstruction of outer appearance. Artist N.O. Yanshinov.

Short lower jaws were provided with simple lance-shaped teeth, with short, flattened, crowns and poorly notched cutting edges. The torso was wide and low, attaining a length of 2.5-3 meters. The greatest body width in the midsection and the beginning of the sacral region reaches from 1.3-1.5 meters. The height of the creature and front limbs could not be greater than 1 meter,

because the fossa glenoidalis was probably not located higher than 40-50 cm from the ground. A small variation between the sizes of the femur and the humerus indicates that the rear section of the body was raised only a little higher than the front.

The massive legs are greatly projected sideways. The wrist had five digits; the fifth digit was much more poorly developed than the rest. The rear foot had four toes. The toes terminated in flat phalanges of ungulate shape. The entire spine and lateral sections of the body were covered with heavy bony armor, consisting of separate bony scutes, between which are located segments of granular hide. This covering supplemented sharp bony spines, which added to the animal an even more formidable appearance. The tail was enclosed in bony rings and equipped with sharp spines.

In order to reconstruct the way of life of *Talarurus*, our knowledge of the conditions and makeup of terrestrial and aquatic fauna of that time is still insufficient. Besides the armored dinosaurs of the type of *Talarurus*, there existed numerous herbivorous dinosaurs of the trachodont type, and also gigantic predatory dinosaurs of *Tyrannosaurus* type and lesser predators of the *Ornithomimus* type. Remains of all these creatures were abundantly present in sites and are encountered almost in one bone layer.

Naturally, we may not propose that there was one and the same place of habitation for all elements of this fauna, but doubtless their areas were in close contact. The analysis of adaptations in the skeleton of *Talarurus* leads us to the conclusion that this creature inhabited dry land. The wide flat trunk, the massive polydigital limbs terminating in flat ungulate phalanges, the heavy armored tail, the uniform bony armor, which consisted of plates of 30-50 mm thickness, undoubtedly reveal adaptation to inhabiting open areas of dry land.

Contemporary spinous lizards: *Moloch*, *Phrynosoma*, *Zonarus*, *Uromastix*, which inhabit arid and semi-arid regions of Africa, Australia, and America, are very small in size and of flat bodily form. The flat body form shows the adaptive adjustment for life in open, bright places; a creature forced to the substratum, escapes the attention of predators. The body of *Talarurus* was constructed so that our assumptions about the habitation of armored dinosaurs in open, bright places are even more strengthened.

The presence of solid bony armor of several centimeters thickness allowed ankylosaurs to adopt not only shady areas of river and lake shores, but also more distant open and dry areas, where the armor protected them from excessive heat and attacks of predatory dinosaurs, the areas of distribution of which were probably adjacent, etc. The simple tapering shape of the teeth with low flattened crown and notched cutting edge rules out feeding on tough vegetation. The claws of *Talarurus* do not have special adaptation for digging; consequently the latter may not live on juicy subterranean parts of plants, such as tubers, onions and roots. For a single genus, there might have been only succulent food plants, with frail external covering.

All the things presented above allow us to conclude that at the end of the Upper Cretaceous, ankylosaurs could utilize open continental regions of Central Asia similar in physico-geographic and climatic conditions to contemporary regions of Africa; as, for example, the Congo Basin and Zambezi, the Nile Delta, where they may find food, and feed on every kind of succulent vegetable.

V. PHYLOGENETIC OBSERVATIONS AND STRATIGRAPHIC DISTRIBUTION OF MONGOLIAN ANKYLOSAURS

The ankylosaurs of the Upper Cretaceous of Mongolia, represented by two groups, sharply differ in degree of their evolutionary development: on one hand, the primitive armored

dinosaurs of the family *Syrmosauridae* (Maleev, 1954), is characterized by the presence of thin armor, which consists of symmetrically distributed bony spines which do not coalesce with each other and do not form thick bony 'armor' plates, and with little sacralization of the backbone, with absence of coalescence of the ribs with transverse processes of the vertebrae; on the other hand, the genuine *Ankylosauridae*, with heavy armor, consisting of thick bony plates and spines, of great sacralization of the spinal column (11 sacral vertebrae) and the presence of ankylosed ribs with transverse processes. The first were described from the sites at Ulan-osh (Maleev, 1952a), Bayn-Dzak, Shiregin-gashun. The designation of the sites belong to different stratigraphic levels and includes the following fauna:

1. Site Ulan-osh. In faunal content, herbivorous dinosaurs of the genus *Psittacosaurus* predominate, which are close to the primitive *syrmosaurids* in evolutionary level.
2. Site Bayn-Dzak. In the red sand desert of the site were irregularly dispersed bones and complete skeletons of *syrmosaurids* (in rare accumulations and separate assemblages). Here were found remains of *Syrmosaurus viminicaudus* (Maleev, 1952a) and of small vegetarian dinosaurs of the genus *Protoceratops* and small predatory dinosaurs of the family *Ornithomimidae*.
3. Site Shiregin-gashun. In the sand of north central residual rocks were found separate remains of armored dinosaurs of the genus *Syrmosaurus* (*S. disparoserratus*), of small predatory dinosaurs of the family *Ornithomimidae* and separate bones of trachodonts, sauropods and carnosaurs.

The presence of primitive armored dinosaurs of the genus *Syrmosaurus* and small predatory dinosaurs of the family *Ornithomimidae* clearly demonstrates that the fauna of the given sites are almost identical and, in fact, show one faunistic complex in different stages of development.

The original (most ancient) stage of this complex presented the fauna of Ulan-osh, the age of which is established by the presence of *Psittacosaurus* found only in the lower Cretaceous of Mongolia - Ondai-Sair and the Oshi Formation (Artsa Bogdo).

The *syrmosaurid* fauna of Bayn-Dzak, by the presence of the ceratopsid genus *Protoceratops*, known only from the lower part of the Upper Cretaceous of Mongolia, determines the geological age of the strata with *Syrmosaurus viminicaudus* remnants of the age. Apparently, the indicated layers correspond to the contemporary formation of Dzakokht, i.e., the lowest level of the Upper Cretaceous of Mongolia, lower than every known Upper Cretaceous sites of Europe and North America.

The presence of trachodontids in the fauna of Shiregin-gashun, known from the highest level of the Cretaceous, establishes this fauna as the youngest, but also indicates that *Syrmosaurus* also entered other faunistic complexes of a higher level than those met with in Bayn-Dzak. The age of Shiregin-gashun is determined as the Middle Senonian and corresponds to the Belly River formation of the USA from which strata also are known trachodonts and armored dinosaurs. It is possible that this segment of the Upper Cretaceous was the last significant period of for specimens of the family *Syrmosauridae* in Mongolia, after which the dinosaur fauna complexes were generally replaced by later ankylosaurs.

Genuine ankylosaurs of the family *Ankylosauridae* are absent in lower strata. They emerge somewhat later in the middle of the Upper Cretaceous in the faunistic complex with trachodonts and large carnosaurs (Nemsget site, *Dyoplosaurus giganteus* sp. nov.).

The degree of evolutionary development of armored dinosaurs of Bayn-Shire, from which the genus *Talarurus* was known, consists of Upper Cretaceous ankylosaurs of the genus *Ankylosaurus*, known from the highest strata of the Cretaceous of the USA, the Lance Formation,

the strata of Hell Creek, Montana. This coincidence makes it possible to determine the geological age of *Talarurus* by later sections of the Upper Cretaceous, which correspond to the age of the Upper Senonian. Ankylosaur strata is thicker at Bayn-Shire and appear to be the highest layers of the Upper Cretaceous bone bed of Mongolia known up to the present time.

Table 9. Stratigraphic Distribution of Armored Dinosaurs of the Cretaceous of Mongolia

| Age | Site | Faunal Characteristics |
|------------------|----------------------------------|---|
| Upper Cretaceous | Bayn-Shire (ankylosaur layer) | <i>Talarurus plicatospineus</i> , Trachodonts, tortoises |
| | Nemegt | <i>Saurolophus</i> , Carnosauria, <i>Dyoplosaurus giganteus</i> sp. nov. |
| | Shiregen-gashun | <i>Syrmosaurus</i> <i>disparoserratus</i> , trachodonts, small carnivores |
| | Byan-Dzak | <i>Syrmosaurus viminicaudus</i> , <i>Protoceratops</i> , small carnivores |
| Lower Cretaceous | Ulan-osh, Oshi-Nuru | <i>Psittacosaurus</i> sp. |

The appearance of the greatest variety of armored dinosaur forms in Asia, apparently fell within the middle of the Upper Cretaceous (Shiregin-gashun, Nemget, Bayn-Shire), when only in Mongolia there lived no less than three to five species, consisting of two separate families, Syrmosauridae and Ankylosauridae.

It is characteristic that in this length of time there was a great variety of predatory dinosaurs of different sizes which apparently fed on armored dinosaurs as indicated by traces of teeth excellently preserved in many vertebrae of *Talarurus* skeletons.

The presence of primitive syrmosaurids amid Mongolian ankylosaurs much older than the Upper Cretaceous armored dinosaurs of North America and Europe, allows us to assume that Upper Cretaceous ankylosaurs originated in the Asiatic continent from which they then migrated to the east and to the west.

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