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THE ARMORED DINOSAURS OF THE CRETACEOUS PERIOD IN MONGOLIA (Family Syrmosauridae)

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INTRODUCTION

The armored dinosaurs of the various levels of the Upper Cretaceous period occupy an important position among the few Mesozoic reptiles found by the Paleontological Expedition of the Academy of Sciences of the USSR in the Mongolian People's Republic during the period 1948-1949.

Up to this time these animals were known to be part of the Lower Cretaceous epoch in England and the Upper Cretaceous epoch in North America. A few fragmentary finds were made in the Upper Cretaceous in France and Lower Austria. Armored dinosaurs were first found in Mongolia by the paleontological expedition of the Academy of Sciences of the USSR.

The discovery of these new deposits is of great stratigraphic and paleogeographic interest because it sheds light on the history of this interesting group of dinosaurs in Central Asia and makes it possible to draw some conclusions regarding the age of the rock masses containing these remains.

This article is a summary of a study of a new group of armored dinosaurs from the lower levels of the Upper Cretaceous in Mongolia. A preliminary description of these dinosaurs was given by Maleev in "Reports of the Academy of Sciences of the USSR" in 1952.

SYNOPSIS OF THE HISTORY OF THE STUDY OF ARMORED DINOSAURS

The first discoveries of armored dinosaurs of the suborder Ankylosauria were made in 1853 by Mantel (cited by Zittel, 1932) from fragments of the lower jaw and armor scales found in the Lower Cretaceous in England (Wealden stage), who described the genus *Hylaeosaurus*. Mantel had only insignificant fragments and could therefore not explain the exact characteristics of the genus he had described.

Several works appeared in the second half of the 19th century (Huxley, 1867 - cited by Zittel, 1932) in which two more European Ankylosauria were described. In 1918 Nopsca (cited by Zittel, 1932) described a new collection from the Lower Cretaceous in France and Lower

Austria. Brown (1908) gave a thorough description of the ankylosauria, which from studying the skull of *Troodon validus* and *Acanthopholis,* assigned all of the European ankylosauria (*Acanthopholis*, *Hylaeosaurus*, *Struthiosaurus*, *Rhodonosaurus*) to the independent family Acanthopholidae.

The North American armored dinosaurs were revealed in the second half of the 19th century when in 1856 Leidy (cited by Zittel, 1932) described their remains from Upper Cretaceous deposits in Montana. The remains of armored dinosaurs discovered in Alberta, Montana, and Wyoming were especially rich.

In 1851 Lucas (cited by Zittel, 1932) described and imaged the remains *Hopoplitosaurus* found in South Dakota. Lambe (1902) described the remains of a skeleton found in Alberta, assigning it to the genus *Sterocephalus*. Williston (1905) very briefly described remains found in Wyoming, assigning them to the genus *Stegopelta*. Brown (1908) described *Ankylosaurus magniventris* found in Montana and provided images of the skull, the axial skeleton, and armor. On the basis of the marked distinction of *Ankylosaurus* from the European Ankylosauria he isolated a new family Ankylosauridae, to which *Polacanthus* from the Wealden stage in England and all of the North American forms are related. At approximately the same timw Wieland (1908) described the remains of armor from Niobrara (Kansas), relating them to the order *Hierosaurus*.

Sternberg described the remains of *Panoplosaurus* from Alberta in 1921. In 1924 parks (cited by Zittel, 1932) very briefly described *Dyoplosaurus* from these same levels.

Beginning in 1928, a number of articles written by Nopsca (1928) and Lambe (1931) (both cited by Zittel, 1932) and by Gilmore (1930) described new collections from various sites in the United States. These articles extended prior knowledge of the structure of the armored dinosaurs: the skull, teeth, and armor were described, seven new genera and species were described.

All of the enumerated works have major shortcomings: 1) a surficial description of the remains without clarification of the functional features and lifestyle of the animals; 2) the species, and all too often the individual genera, were haphazardly separated based on descriptions of the different teeth or poorly defined fragmentary remains, no comparative analysis with previously known forms was done and the vertical distribution was not taken into consideration.

CLASSIFICATION

Suborder Ankylosauria

Family Syrmosauridae Maleev, 1952

Diagnosis of the Family[1]. Large, four-legged dinosaurs with light defensive armor consisting of individual symmetrically distributed scales. The body is very flat and broad as in the Upper Cretaceous Ankylosauria. The teeth are stegosauroid, with a lamellar flat crown having channeled sculpture [=rugose]. Because of the flat body, the head has a distinctive adaptation for elevating, which is expressed as a unique structure of the cervical vertebrae - the articulation surfaces have been twisted so that the rear surface of the vertebra is depressed below the front surface and is almost parallel to it. The dorsal vertebrae are long, with low centra and are slightly flat at the ends. The torso ribs do not attach to the transverse processes of the vertebrae. The

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[1]This identification was made by studying the postcranial skeleton of *Syrmosaurus viminicaudus*. Maleev, 1952

pelvis is stegosauroid. The iliac bones are quite wide and thick in the postacetabular region, as in the Ankylosauria. The sacrum consists of three true sacral vertebrae. The front legs are shorter than the hind legs. The digits end with hoof-like formations (the end phalanges). The tail is long (35-40 vertebrae). The rear tail vertebrae (15-20) are rigidly attached to one another, forming a long "club". The overall length of the skeleton and skull is 4-5 meters.

Comparison. A comparison of the syrmosaurids with the known genera of the family Acanthopholidae reveals the following essential differences.

The fundamental differences are contained in the structure of the teeth, the axial skeleton, and the armor.

Syrmosaurid teeth are distinguished by the low crown height, the more pronounced flatness of the crown and the slight serration of the cutting edge. The vertebrae are distinguished by their length and by the structure of the neural arch. The neural arch is high and the diapophyses are long. The low degree of sacralization in the back - three true sacral vertebrae - distinguishes the Syrmosauridae from all of the known genera of the suborder.

The structure of the syrmosaurid tail is distinguished by the large number of vertebrae that form the tail, by the symmetrical distribution of the spines, and by the formation of an "club" at the end of the tail.

A comparison with representatives of the Ankylosauridae family revealed that:

1.The teeth are distinguished by the lamellar shape of the crown, its small size, and the nature of the sculpture.
2. None of the known Ankylosauridae had the similarly shaped first cervical vertebrae (third, fourth) that have the centra articular surfaces skewed relative to one another. These vertebrae are of the typical structure in Ankylosauria.
3. The dorsal vertebrae have small centra, a high neural arch, a high spinal process [=neural spine], and long diapophyses.
4. Although the torso ribs are very similar to the ribs of Ankylosauria, they differ by the absence of irregularities on the dorsal side of the rib.
5. The lumbar ribs have no union with the transverse processes of the vertebrae.
6. The bones of the girdles and extremities are very similar to those of the Ankylosauria in most features, but much smaller.
7. The small degree of sacralization of the vertebrae - in all, three sacral vertebrae - distinguishes the syrmosauroids from all of the other known Ankylosauria. In these the sacrum has from five to nine large vertebrae.
8. The pelvic bone is very similar to that of the armored omithopod *Scelidosaurus* (Owen, 1861) and the *Stegosaurus* (Owen, 1875), but is very different from the pelvic bones of Ankylosauria of the Upper Cretaceous in which the ilium is trough-shaped and is oriented almost horizontal relative to the lengthwise axis of the sacrum.
9. Syrmosaurids are sharply distinguished from all of the other Ankylosauria by their cutaneous defense that consists of hollow carinoform bony spines arranged in rows on the surface of the skin, with no interconnection between them and without thick bony plates - "armor".
10. The tail structure of the syrmosaurids is very similar to that of several Ankylosauria (*Dyoplosaurus*, *Scolosaurus*), but differs from them by the large number of vertebrae in the tail, the absence of the solid bone rings that enveloped the tail,

and sharp spines at the end of the "club".

It is apparent from the preceding comparison that representatives of the syrmosaurid family are in general similar to the known Acanthopholidae and Ankylosauridae families and differ in many features in the structure of their armor, axial skeleton, extremities, pelvis, sacrum, and tail. These differences from the aforementioned families are so pronounced that they exceed the differences of the species within the genera, the differences of the genera within the families, and extend beyond the family. This provides a complete foundation to consider the syrmosaurids a unique line of development among the Ankylosauria and to classify them as an independent family, Syrmosauridae Maleev, 1952, which includes the primitive armored dinosaurs of Asia that occupy an intermediate place between the armored Ankylosauria of the Upper Cretaceous and the spiny Ankylosauria of the Lower Cretaceous strata.

Composition of the family. The syrmosaurid family includes the primitive armored dinosaurs of the Lower and Upper Cretaceous in Mongolia, presented for the moment as the unique genus *Syrmosaurus* Maleev, 1952. The diagnosis of the family, genus, and species has is based on the most typical features of the typical family species - *Syrmosaurus viminicaudus* (slow moving, woven-tailed lizard: δγρμζ - slow moving, creeping; viminicaudus - woven-tailed).

General comments. The discovery of syrmosaurid remains in the Djadokhta Formation in Bayn Dzak and with the remains of herbivorous dinosaurs of the genus *Protoceratops*, stratigraphically confined to the lowest layers of the Upper Cretaceous, only confirms their geological antiquity and makes it possible to date the geological age of the syrmosaurids to the lower horizontals of the Upper Cretaceous, lower than all of the known Upper Cretaceous deposits in Europe and North America that correspond to the lows of the Cenomanian.

Distribution. Syrmosaurid remains are found in the Bayn Dzak, Shiregin Gashun, and Ulan Osh deposits in the Mongolian People's Republic. Lower-Upper Cretaceous.

Table 1. Relationship Between Elements of the Skeleton of *Syrmosaurus viminicaudus* and Other Members of the Family Ankylosauridae.

	Units of measure	*Syrmosaurus viminicaudus*	*Ankylosaurus magniventris*	*Dyplosaurus acutosquameu*s
Overall length of scapula	mm	400	600	Unknown
Overall length of fossa glenoidales	mm	104	175	Unknown
Overall width of fossa glenoidales	mm	56	140	Unknown
Overall length of humerus	mm	300	Unknown	Unknown
Overall length of tibia	mm	270	270	Unknown
Overall number of sacral vertebrae	units	3	9	Unknown
Overall number of tail vertebrae	units	35-40	unknown	28
Type of armor		Rows of scales	Continuous	Continuous

Table 1 - continuous

	Units of measure	*Palaeoscincus rugosidens*	*Panoplosaurus mirus*	*Polacanthus foxii*	*Scolosaurus cutleri*
Overall length of scapula	mm	Unknown	410	Unknown	Unknown
Overall length of fossa glenoidales	mm	Unknown	110	Unknown	Unknown
Overall width of fossa glenoidales	mm	Unknown	Unknown	Unknown	Unknown
Overall length of humerus	mm	410	430	Unknown	Unknown
Overall length of tibia	mm	3-5 [sic]	3-5 [sic]	Unknown	Unknown
Overall number of sacral vertebrae	units	9	6	6	Unknown
Overall number of tail vertebrae	units	Unknown	Unknown	Unknown	28
Type of armor		Continuous	Continuous	Continuous	Continuous

Genus *Syrmosaurus* Maleev, 1952

Syrmosaurus: Maleev, 1952. Reports of the Academy of Sciences, vol. 87, No. 1.

Genus type specpies - *Syrmosaurus viminicaudus* Maleev, 1952.

Diagnosis of the Genus[2]. The teeth are stegosauroid, with a low lamellar crown with rugose sculpture. The cutting edge of the crown has 8-10 serrations. The cervical vertebrae are long and the articulated surfaces of the centers are angled so that the rear surface of the vertebra is below the front surface and almost parallel to it. The dorsal vertebrae are on with low centra and slightly flat at the ends. The neural arches and diapophyses are high. The torso ribs are loosely connected with the transverse processes vertebrae. The pelvis is stegosauroid. The iliac bones in the preacetabular region are long and very wide and thick in the acetabular region. The postacetabular region is short and wide. The pubic bone is slightly developed narrow and thin. The sacrum comprises three vertebrae. The forelegs are shorter than the hind legs. The wrist has five digits (the fifth digit is significantly reduced). The rear foot has three digits. The tail is long, 35-40 vertebrae. The vertebrae are entwined with numerous chords of ossified tendons. The posterior tail vertebrae are rigidly connected to each other, forming a long "club" that is equipped at its end with a striking member made of skin spines that have grown together. The armor consists of individual carinate bone spines arranged in symmetrical rows on the upper and side surfaces of the neck, the torso, the exterior side of the extremities, and the tail. The unique knife-like spines arranged flatwise at the end of the tall form an "axe". The overall length of the skeleton is-4.5 meters.

Comparison. Only one genus, *Syrmosaurus* Maleev, 1952, appears in the family.

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[2]This identification was made by studying the postcranial skeleton of *Syrmosaurus viminicaudus*. Maleev, 1952

Species composition. The genus *Syrmosaurus* includes the following species: *Syrmosaurus viminicaudus* Maleev, 1952, *Syrmosaurus viminicaudus* Maleev, 1952 sp., and *Syrmosaurus disparoserratus* Maleev, 1952.

Distribution. Representatives of the genus *Syrmosaurus* have been found in the Bayn Dzak, Shiregin Gashun, Ulan Oshih deposits in the Mongolian People's Republic. Lower-Upper Cretaceous.

Syrmosaurus viminicaudus Maleev, 1952

Holotype.[3] Postcranial skeleton and crown of tooth. Collection No. 614 of the Paleontological Institute of the Academy of Sciences of the USSR.

Species diagnosis. *S. viminicaudus* conforms with the genus diagnosis *Syrmosaurus*. Description. The teeth are stegosauroid. Each tooth consists of a laterally compressed vertically channeled crown with a serrated edge and a long cylindrical root. The exterior surface of the crown is convex vertically, whereas the interior surface is slightly concave. A rounded frill [=cingulum] at the base of the crown is more protruding on the exterior surface. The cutting edge of the crown is divide into eight serrations. The root is cylindrical (Fig. 1).

Fig. 1. *Syrmosaurus viminicaudus* Maleev,1952 Tooth viewed from the interior side. 10x.

Cervical vertebrae (third, fourth) (Fig. 2a, b). The body of the vertebra is slightly tapered from the sides in the middle and wide at the ends. The front articulated surface looks like a flat spoon with a sharp ventral incline. Its horizontal diameter [=width] is greater than its vertical. The rear articulater surface is platycoelous and slightly tapered in the caudoventral direction. The neural arch is high. A sloped ridge runs along its [neural arch] dorsal surface and gradually increases to form a triangular spinous process [=neural spine]. The prezygapophyses are less developed than the rear ones [i.e., postzygapophyses], are widely spread with articulation facets that are rotated dorsomedially. The postzygapophyses are curved like an arch, markedly extend posteriorly, and are separated by a deep notch. Their articulation facets are close together and are rotated ventrolaterally. The transverse processes [=diapophyses] are slightly developed. The neural canal is high and egg-shaped in cross-section. In contrast to the preceding [vertebrae], the 5th 6th and 7th cervical vertebrae are short and high, the length of the centrum is equal to its height. The articulation surfaces have a rounded amphicoelous shape. The transverse processes [diapophyses] are more developed and are directed horizontally. The ventral ridge is well defined.

Thoracic and lumbar vertebrae are amphicoelous. The bodies of the vertebrae are long and low. The length of the centrum is more than twice the height. The neural arch is 1.5-2 times that of the centyrum. The prezygapophyses are directed forwards and slightly upward, spread widely, and the articulation facets are rotated medially. The postzygapophyses are very elongated, extending beyond the caudal edge [of the centrum] by half the centrum length. The articulation facets [of the postzygapophyses] are connected and rotated laterally. The transverse processes form an arch and rise upward steeply. They are wide at the base and narrow slightly at the ends. A wide groove for the dorsal edge of the proximal area

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[3]This skeleton was found along with remains of small herbivorous dinosaurs of the genus Protoceratops and Cretaceous carnivores of the group Ornithominidae

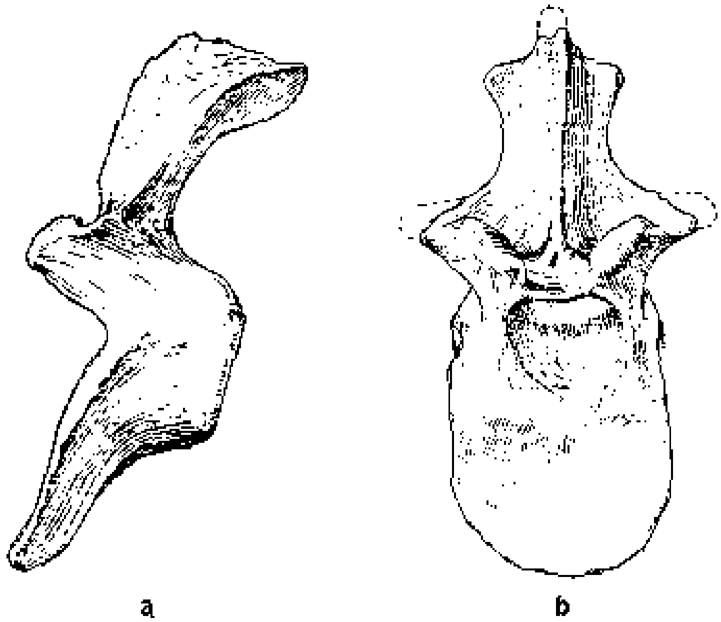

Fig. 2. *Syrmosaurus viminicaudus*, third neck vertebra. a) from the side, b) from the front. 1/2 actual size.

of the rib runs along the ventral side of the process. The length of the vertebrae and the height of the neural arch gradually decreases toward the rear. The last four vertebrae, which may be assigned to the lumbar (20th, 21th, 22nd, 23rd), are joined together by their centra [=synsacrum]. All of the dorsal vertebrae support long curved ribs.

The sacral region of the vertebral column consists of three vertebrae that are joined together (Fig. 3). The centra are thick and markedly wide in front and behind. The neural arches

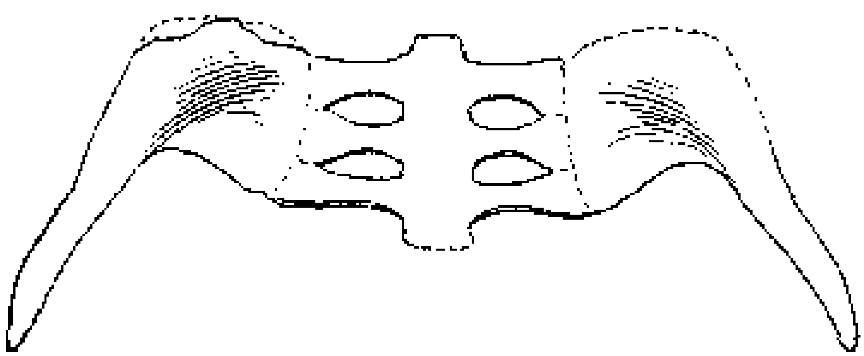

Fig. 3. *Syrmosaurus viminicaudus*. Diagram of the pelvic girdle

are low. The neural canal is low and circular in cross section. Each transverse process is conjoined with a short sacral rib into a single unit.

The tail region of the vertebral column consists of 35-40 vertebrae and is 2.1 meters long (Fig. 4). The vertebrae in the front half of the tail (from the 1st to the 17th) are amphicoelous: the centra are short and wide, the articulation surfaces are flat. The neural arch is low. The neural canal is narrow and rectangular in cross section.

The neural spines are high, their apexes are inclined backward and slightly curved (convex anteriorly). The transverse processes are narrow, are inclined anteriorly and their lengths decreases gradually posteriorly. The haemal arches have well-developed hammer-shaped haemal processes and are attached to the surface of the centra from below. The haemal canal is high and triangular shaped. Its height is 1.5 times that of the neural canal.

The vertebrae in the rear half of the tail, starting from the 18^{th}, gradually increase in length and grow thinner, the articulation surfaces of the centra flatten and acquire a platycoelous shape.

The spinous processes diminish and merge with the neural arch. The arch walls along the front region of the neural arches are separate and extend forwards, forming long Y-shaped prezygapophyses. The postzygapophyses region of the arch is compressed and wedge-shape, tapering to a point. The neural canal looks like a narrow slit and is open from above for most of its extent. The haemal arch is much more developed than the neural arch. The haemal process is shaped like a ridge. The front region of the haemal process has a V-shaped notch and is extended forwards. The rear region narrows in a wedge-shape. The haemal canal is low and circular shaped.

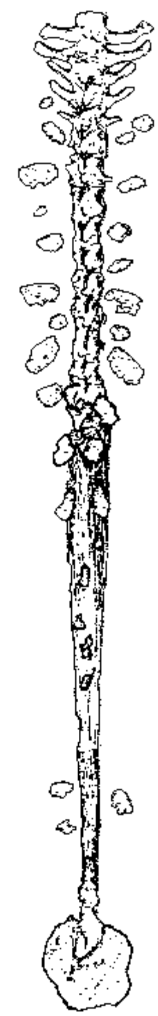

Fig. 4. *Syrmosaurus viminicaudus*. Tail skeleton viewed from the ventral side. 1/12 actual size.

The structure of the neural and haemal arches creates an almost immobile vertebrae joint that is created by the double articulation of the postzygapophyseal portion of the arch of one vertebra completely surrounding the prezygapophyseal portion of the next vertebra, and the wedge-shaped region of the haemal process projects into the V-shaped notch region. The last three tail vertebrae lack neural and haemal arches and are fuse together to produce a rod-shaped ossification, the end of which is a club that consists of three spines (Fig. 4). The lateral spines of this club (on each side of the ossification) are trapezoidal in shape and are oriented with their expanded base towards the centra of the fused vertebrae and with the sharp ridges projecting laterally. The terminal spine is triangular, with rounded angles at the base, and is oriented so that its sides fuse with the rear edges of the lateral spines, and the apex fuses with the distal end of the ossification.

On the whole, the club on the tail is reminiscent of a double-edged "axe" (27 x 19 cm in size) the handle of which is the last three modified vertebrae and the cutting edges are the sharp ridges of the lateral spines.

All of the vertebrae in the rear half of the tail are intertwined with numerous ossified tendons that conceal the limits of the individual vertebrae. Among these are tendons 400 mm long that pass along the midline of the lateral sides in the anterior portion. These tendons are 8.5 mm thick at the front end and 2.5 mm thick in the rear end. These tendons start round in cross-section and become semi-oval towards the posterior end. Above and below these are tendons 250 mm long, varying in thickness from 5 to 2.5 mm and shaped like the tendons along the dorsal and ventral surface of the vertebrae. Further back are tendon cords 130 mm long and varying in thickness from 4.5 to 2.5 mm, and then tendons 270 mm long and thickness varying from 3 to 2 mm. All these tendons intertwine among themselves at the ends to form an extraordinary elliptical "sheath", surrounding the centra. On the dorsal side of this "sheath" is an open interstice 1.5-2 mm wide from which the neural spines project. Interstices 2-3 cm wide for the haemal arches are found on the ventral side.

Spinous processes were not preserved on the spinal vertebrae.

Table 2. Dimensions of the Cervical Dorsal and Caudal Vertebrae

Measurement	Units of measure	3rd cervical	6th cervical	4th dorsal	8th dorsal	15th dorsal	1st caudal	9th caudal
Length of centrum	mm	91	50.5	74.5	72.5	69	54	44
centrum, anterior width	mm	57	-	55	55	-	57	55
centrum, posterior width	mm	59	-	59.5	59.5	-	53	48
centrum height	mm	39.5	58.5	41	41	-	41	37
Height of neural arch	mm	36.5	37	65	65	-	-	-
Height of centrum with spinous process	mm	71	-	-	-	-	97	85

Ribs. On the whole, the cervical ribs are small and increase rapidly in size posteriorly The proximal part of each rib is wide and separated by a shallow notch which divide it into two processes. One of the processes, rotated ventromedially, is the head of the rib. It is thick at the end with a rounded platform for articulation with the corresponding platform on the lateral surface of the vertebra arch. The other process - a tubercle that runs in the dorsal direction, has no such thickening but has at its end an ellipsoidal articulation platform for the transverse process. The front surface of the rib is slightly convex and the rear side is concave. The distal ends of the first ribs gradually taper and each rib is wedge-shaped.

Each dorsal rib is long, curved in an arch and semi-ovoid in cross section (Fig. 5). The

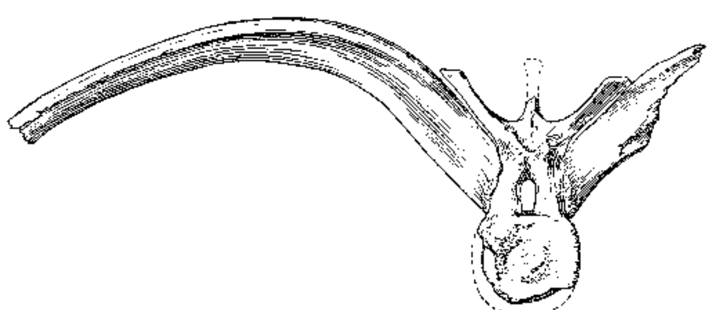

Fig. 5. *Syrmosaurus viminicaudus*. Dorsal vertebra with rib in its natural attachment. 1/3 actual size.

proximal region is thick and wide, the center region is tapered, and the distal end is wide and flat. In contrast with the cervical ribs, the notch between the head and the tubercle is long and shallow. Along the front surface of the rib is a small muscle groove and along the rear is a more developed groove along which the vessels and nerves pass. The distal ends of the ribs are apparently connected with wide, well-developed sternal cartilage.

On the ribs from the posterior region of the torso, the structure of the proximal region is much like the sternal ribs, but is much shorter and less curved. The distal end is more pointed. The sacral ribs are short, thick columns compressed laterally in the middle and very wide at the ends. The proximal end of each rib is tightly fused with the transverse process. The notch that separates the head and the tubercle is absent. The distal, less thick end of the hollow rib is tapered toward the iliac bone, with an irregular cartilaginous surface for connecting with it.

The sternum is a wide triangle, 22 x 30 cm in size (Fig. 6). It consists of two symmetrical bones are fused along the medial edges. Its front end is tapered and its rear end is wide and extended at the corners into long lateral processes that are formed by extension of the sides. The exterior surface of the sternum is slightly convex with a carina 20 mm tall (Fig. 6a). The interior surface is deeply concave in the center and tapered at the edges (Fig. 6b). The sternum itself is porous and the lateral and rear edges, which look like broad semi-oval strips were, apparently,


a b

Fig. 6. *Syrmosaurus viminicaudus*. a) sternum, from the exterior, b) sternum, from the interior. 1/5 actual size.

cartilaginous and not preserved.

The scapula is a massive oar-shaped bone (Fig. 7). Its blade is wide and markedly concave inward. The dorsal edge has a semi-oval shape. Distally, the blade narrows slightly and then, after a small constriction [=scapular neck] widens and thickens, forming the upper region of the glenoid cavity. Above the glenoid cavity, the front edge is curve outward as a semi-oval projection which, by its location, corresponds to the pr. acromion in the higher vertebrates.

In the lower area of the distal region from the exterior and interior side, are slight depressions - points of attachment for m. deltoideus.

Coracoid. In general, the coracoid looks like an irregular tetrahedron, i.e., a wedge-like taper on the rear side. It is intimately attached proximally to the scapula forming the lower half of

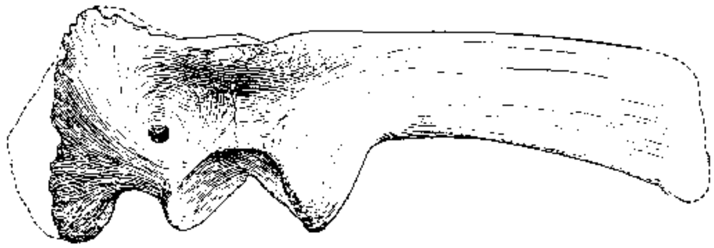

Fig. 7. *Syrmosaurus viminicaudus*. Scapula from the side. 1/3 actual size.

the glenoid cavity[4]. In front of the glenoid cavity, the upper region of the coracoid is deeply concave - this is where the foramen coracoideum is seen as an oval-shaped opening that is directed diagonally into and behind [medially] the coracoid. The glenoid region of the coracoid narrows downward, is somewhat tapered in the dorsal direction and is slightly concave. The lower surface of the coracoid is somewhat concave along its width and with the upper region forms an outward projecting obtuse angle. From the interior side, the surface of the coracoid is U-shaped concave in the horizontal plane. The glenoid cavity (fossa glenoidalis) is U-shaped and open from the side and from behind. Its interior wall in cross-section makes an obtuse angle that is nearly a right angle. The upper wall is a lengthwise concave surface. The outside edge is convex curved as if it had been squeezed out in the dorsal direction, particularly in the center region. The lower wall is flat. The exterior edge projects dorsally.

Dimensions of scapula for *Syrmosaurus viminicaudus* (in mm)

Scapula	
Length of scapula to upper edge of fossa glenoidalis	400
Width of proximal end	90
Thickness of proximal end	11.5
Width of distal end	100
Thickness of distal end	64
Coracoid	
Length of coracoid from lower edge of fossa glenoidalis	200
Width of proximal end	65
Thickness of proximal end	79.5
Width of distal end	75
Thickness of distal end	20
Fossa Glenoidalis	
Overall length (from upper scapular edge to lower coracoidal)	104
Width horizontal	56
Depth	47

Front Extremities. The humerus is a massive, wide bone with a very wide proximal

[4] The boundary between the scapula and the coracoid is well defined on the middle horizontal of the glenoid cavity.

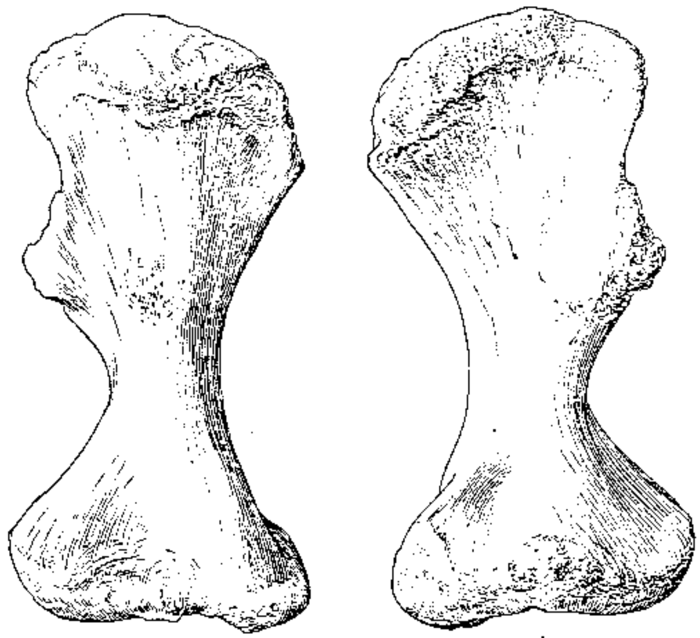

Fig. 8. *Syrmosaurus viminicaudus*. a) Left humerus seen from the dorsal [=posterior] side; b) Left humerus seen from the ventral [=anterior] side. 1/3 actual size.

region that looks like a concave, oval-triangular wafer. The head is large and slightly thick in comparison. The front edge of the humerus has a wide processus lateralis [=deltopectoral crest] that measures 10-12 mm thick from the front, that begins near the lower edge of the head and proceeds to the narrow area in the middle of the shaft, where it merges with the entepicondylar edge of the distal region. The rear [medial] edge of the humerus is thicker, with a strong, but short processus medialis up to 20 mm thick. Between both processes, the middle of the bone is lengthwise convex (Fig. 8a). A concavity is seen in this region on the ventral side [=anterior] (Fig. 8b). The head of the humerus looks like a convex semi-oval. The ventral edge of the humeral head is almost straight and is only slightly curved downward at the thickest spot, as if it had been squeezed. The middle of the humerus is tapered, with a three-sided prismatic cross-section that is somewhat curled in the vertical plane. The distal end of the humerus is narrower than the proximal end . The dorsal [=posterior] surface [of the distal end] is slightly concave in the middle and convex at the edges. A small epicondylus radialis projects from the proximal edge and a epicondylus ulnaris projects from the post-axial edge of the dorsal surface. The ventral [=anterior] surface is convex in the middle and concave at the edges. The articular surface for articulation with the foreleg looks like a cylinder divided by a small constriction into the massive oval shaped condylus radialis and the somewhat smaller, almost circular condylus ulnaris.

The radius is a small columnar bone with a wide proximal [=distal] and a narrower distal [proximal] ends (Fig. 9a [radius is upside down and was described that way]). The anterior surface of the bone is slightly concave. The ulnar surface is flat transversely with pronounced irregularities where it connects with the ulna. The radius is triangular in cross-section in the proximal [=distal] region (the narrow side toward the radial edge), an almost circular cross-section in the middle and oval cross-section in the distal [=proximal] region. The proximal

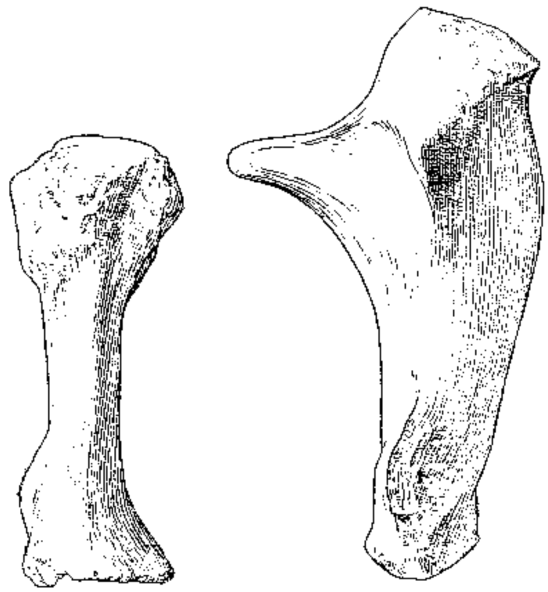

Fig. 9. *Syrmosaurus viminicaudus.* a) Left radius seen in lateral view; b) Left ulna in lateral view. ½ actual size. [the radius is upside down]

[=distal] articulation surface is oval, markedly extended toward the ulna and is slightly concave. The distal [=proximal] articular surface is more rounded, slightly tapered anteriorly, and to the inside its interior edge is thick and oval-convex.

The ulna is triangular in cross-section, wide at the proximal end and tapers gradually toward the distal end. The middle of the bone is slightly bent and curled [=twisted] along its axis. The proximal end is oval and on the side toward the radius has a deep incisura radialis. On the ulnar edge [=medial side] is a well developed processus olecranon that projects backwards [=forwards] and upward, and in a radial direction is a tapered surface for the elbow joint. The distal end is slightly wide and thick, the articulation surface is tapered front and to the side.

Carpus. The intermedium is small (35 mm), convex-oval in shape. The ulnar surface is concave and the metacarpal surface is convex.

Metacarpus. The metacarpals, Mc1- Mc4 are small, almost equal in length and almost identical in form. The discussion which follows relates to any of the metacarpal bones of the 1st, 2nd, 3rd, and 4th digits. The body of each bone is oblate from front to back, and thick at the proximal end. Towards the distal end it gradually tapers and becomes thinner. The proximal end has a wide articulation area, slightly concave in the anteroposterior direction. Ligamental nodules project in the palmar direction from the articulation area.

The back surface of the metacarpal is convex in the transverse direction and smooth. The palmar surface is flatter, with two irregularities for attaching ligaments. The distal end is not as thick as the proximal end. The articulation surface looks like a cylinder with a channel in the middle that divides it into two articulation areas, from which the medial area is somewhat larger. On the lateral sides, at the distal articulation surface, are the ligament pits and above them small ligamental nodules. Mc5 is much weaker than Mc1- Mc4.

Phalanges. Ph1 is a small ossicle, oval in shape and 2 cm long. The articulation surface for the metacarpal is slightly concave. The distal surface is convex, with a small lengthwise groove in the center.

Ph2 is a short bone compressed from the sides along the middle and expanded at the ends. Its width is1.5 times its length. The proximal end is thick, with a concave articulation area extended in transverse direction. The back surface is convex and smooth. The palmar surface is flat, with a small irregularity for attaching ligaments. The distal end is less flat than the proximal end. The articulation surface of the distal end looks like a cylinder with a channel in the middle.

Ph3 is a small bone, with a triangular profile. The proximal end is wide with a deep articulation area. The distal end is tapered and rounded.

The ungual is small and oval shaped. The proximal end has an almost half-moon concave articulation surface, with a small protruding ridge for attaching the tendons (m. extensor digitalis communis). The distal end is semi-oval in shape. The back surface of the phalanx is convex with five vascular vessel grooves which travel inward. The palmar surface is flat, with a prominent irregularity for attaching m. flexor profundus.

Table 3. Dimensions of the Bones of the Front and Rear Extremities.

Measurement	Units of measure	Humerus	Radius	Ulna	Femur	Tibia	Fibula
Overall length	mm	300	145.5	225	400	270	270?
Greatest width of proximal end	mm	135.5	31.5	52.5	102	84.5	32.5
Thickness of proximal end	mm	50.5	51.5	50.5	34.5	94	21.5
Greatest width of distal end	mm	132.5	29.5	49.5	138	102	-
Thickness of distal end	mm	36	24	26.5	52.5	41	-
Cross section in the middle	mm	54x48	29.5x27	35x27.5	35x27.5	42x41.5	26x19

Pelvic girdle. The ilium is massive, bow-shaped, and very wide and thick at the rear end. The preacetabular region is slightly tapered and has an elongated front that reaches the 17^{th} vertebra. The acetabular region is comparatively short and ends in a large dome-shaped expansion forming the dorsomedial wall of the cotyloid [=acetabular] cavity. The ventral surface of the bone is distinguished by being concave in the middle and convex at the ventral edge, which is curved outwards and somewhat upward to form in the acetabular region a powerful "antitrochanter" for attaching m. iliofemoralis and m. iliotrochantericus. The dorsal surface [above the acetabulum] is convex with a small irregularity that proceeds to the acetabular region in a strong callosity.

The ischium is small and wedge-shaped (Fig. 10a). The outside surface of the bone is slightly convex and smooth; the interior side is concave with a lengthwise irregularity for attachment of the m. ischiotrohantericus, m. puboischio-tibialis, m. pubo-ischiofemoralis and m. flexor tibialis (Fig. 10b).

The acetabular (proximal) end of the ischium is wide and elongated into two angular processes: The posterior process is short for articulating with the ilium and the anterior process is long for articulating with the pubis. Between these processes, the external surface is concave and

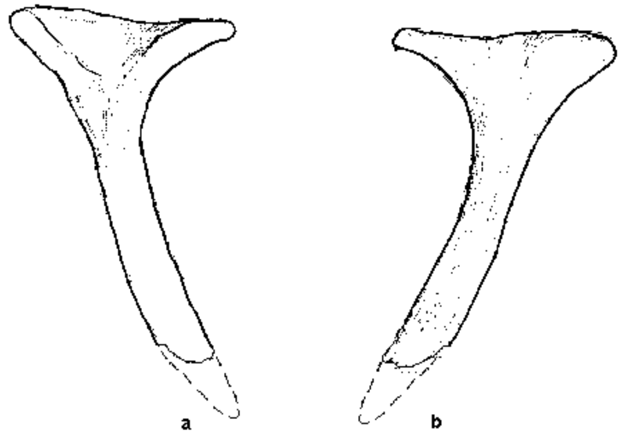

Fig. 10. *Syrmosaurus viminicaudus*. a) Ischium from the exterior side; b) Ischium from the interior side.1/3 actual size.

comprises the rear-medial region of the cotyloid [=acetabular] cavity. In the distal direction, the bone gradually tapers and is slightly bent in the medial direction, forming a narrow symphysis with the bone paired to it.

The pubis was so poorly preserved that it is impossible to describe it. Judging by the number of pieces that were preserved, we may assume that the pubis was slightly developed.

Rear extremities. The femur is much more developed than the humerus (Fig. 11). The center of the bone is oval in cross section. The proximal end is wide and thick. The head and the trochanters (trochanter major and trochanter minor) were not preserved. There is a small tubercle, approximately one third up from the bottom of the femur, with an irregularity - the fourth trochanter. The upper [=anterior] side of the femur is devoid of any irregularities or ridges; in the distal region there is only a triangular depression (fossa patellaris) along which ran the tendons for the muscles that flex the tibia. The distal end of the femur is thick and the articulation region is well developed. The large epicondylus tibialis and epicondylus fibularis are tapered slightly upward [=anteriorly], projecting prominently above [=beyond] the fossa patellaris that separates them. An identical depression that looks like a triangular well - fossa m. popliteal - is

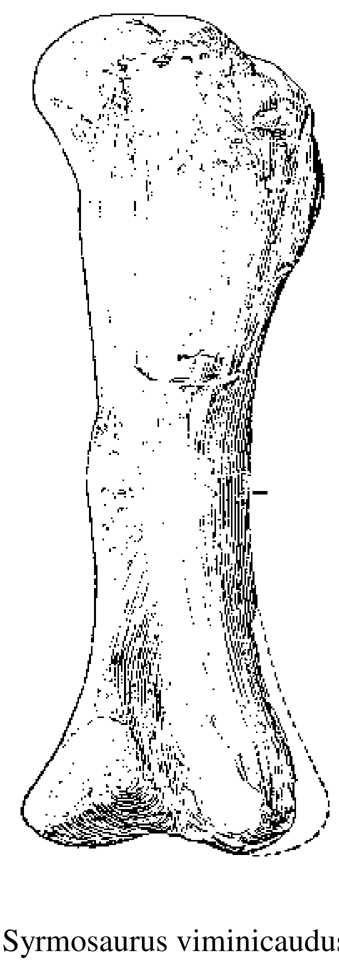

Fig. 11. Syrmosaurus viminicaudus. Right femur. 1/4. actual size.

present on the lower [=posterior] side of the femur, and separating by a fossa intercondyloidea the large, protruding condylus tibialis and the somewhat smaller condylus fibularis. The lateral sides of both condyles have nodular irregularities for attachment to the knee articulation. A preliminary study of the late ankylosaurids from Bayn Shire in which the extremities bones were well preserved allows us to presume that the following structure existed in the unpreserved areas of the *Syrmosaurus* femur: the interstice (neck) between the head and the greater trochanter is not manifest, the lesser [=anterior] trochanter blends with the large, the fourth trochanter is weakly developed.

The tibia is a massive bone, with triangular cross section slightly curved along its length and wide at the proximal and distal ends. The front surface of the bone is convex with a well defined crista tibiae, which is distally displaced in the lateral direction and dwindles to nothing. On the fibular side, in the proximal region, is a small callosity where the proximal head of the fibula makes contact. The rear surface is slightly curved and compressed from the sides to form the convex region of the powerful crista on the rear of the tibia that widens and flattens distally. The distal region of the rear surface is flat, with a large lengthwise, triangular concavity.

The fibula is almost as long as the tibia, but much thinner and wide in the proximal region. The front surface of the fibula is convex and quite smooth. The rear surface in the proximal region is lengthwise concave and flat in the distal region.

Elements of the tarsus were not preserved.

Metatarsals. Judging by the fragments that have been preserved the metatarsal bones were more massive than the metacarpals. Mt3 is more developed than Mt2 and Mt4. The distal end of Mt3 is very wide, with a convex articulation surface for the first row of phalanges.

Phalanges. This description of the phalanges of the digits on the rear extremities is made from fragments of the third digit, which was better preserved than the others. Ph1 is a short bone, compressed in the middle and wide at the ends. It is as long as it is wide. The proximal end is thick with a concave articulation surface for the Metatarsal. The back surface is flat with a small irregularity for attaching the tendons. The distal end is less flat than the proximal. The articulation surface looks like a cylinder with a channel in the middle.

Ph2- is a small oval bone. The proximal end is thick with a deeply concave articulation surface for Phi. The distal articulation surface is cylindrical with a wide reduction in width in the middle.

The ungual phalanx - Ph3 - has, as its name suggests, an ungual-shape. It is three times the size of the ungual phalanx in the manus. The proximal end is thick with a half-moon shaped concave articulation surface with a protruding ridge for attaching the tendons for m. extensor digitalis communis. The distal end is oval. The back surface of the phalanx is convex and small branches or angles protruding from both sides of the proximal end. The palmar surface is flat, with a distinct irregularity for attaching the m. flexor profundus.

Armor. The armor consists of individual carinate bony spines arranged in symmetrical rows on the upper and lateral surfaces of the neck, torso, exterior sides of the extremities and tail. The spines are hollow bony elements in various shapes (Fig. 12). In the most general characterization, they are hollow cones, tetrahedra, and triangular prisms. The exterior surface of the spine has a large number of depressions within which small channels that are directed inward. The interior [=ventral] surface of the bone is very pitted. The spines can be put into ten groups depending upon their shape and their topographical distribution on the animal:

1. Dorsal line on the neck. The spines are 35-40 mm long, 21 mm high, lambda-shaped

[λ], with a high dorsal ridge. The lateral sides form between themselves an obtuse angle.

2. Lateral surface of the neck. The spines are 30-50 mm long,14.5 mm high, shaped like an irregular triangle with a low dorsal ridge, a sharp front edge and flat rear edge. The sides come together at an acute angle.
3. Front edge of the shoulder and lateral surface of the scapula. The spines are 50-55 mm long, 18 cm high, shaped like an arrow, with a low dorsal ridge.
4. Dorsal surface of the shoulder. The spines are 80-85 mm long, 43 mm high, shaped like an irregular triangle, with a curvolinear dorsal ridge. The sides come together at an acute angle.
5. Dorsal surface of the front region of the torso. The spines are 35-80 mm long, 31.5 mm high, shaped like an irregular triangle with a high dorsal ridge. At the vertex of the spine the direction of the sides forms a right angle.
6. Lateral surface of the anterior region of the torso. The spines are 70-80 mm long, 28 mm high, shaped like an irregular triangle with a low dorsal ridge and sharp front edge.
7. Dorsal surface of the posterior region of the torso. The spines are 80-120 mm long, 60 mm high, shaped like an irregular triangle with a high dorsal ridge. The sides come together at an acute angle.
8. Lower edge of the lateral surface of the torso. The spines are 80-200 mm long, knife-like, with a sharp outer edge.
9. Lateral surface of the tail. The spines are 45-75 mm long, 22-30 mm high, shaped like an irregular triangle, with a high dorsal ridge and sharp front edge. The lateral sides come together at an acute angle.
10. The ventral surface of the tail was covered with individual scaphoid plates that became flatter in the rear half of the tail, growing together to form the "handle" of the "club".

Fig. 12. *Syrmosaurus viminicaudus*. Armor spines. 1/3 actual size.

Comparison. *Syrmosaurus viminicaudus* differs from the following two species of this genus in insignificant details that are seen in the structure of the teeth. There are no known postcranial skeleton [for these other species].

Distribution. Bayn Dzak (Shabarak Usu), Southern Gobi, 100 km northwest of the Aimak center Dalan Tszadagad, Mongolian People's Republic. Age was dated to the lower horizon of the Upper Cretaceous period.

Material for Study. Postcranial skeleton, collection No. 614, Paleontological Institute of the Academy of Sciences of the USSR. Overall skeleton length is 4.5 m. The skeleton was prepared from the ventral side (Fig. 13), but laid at its discovery site in normal position - dorsals

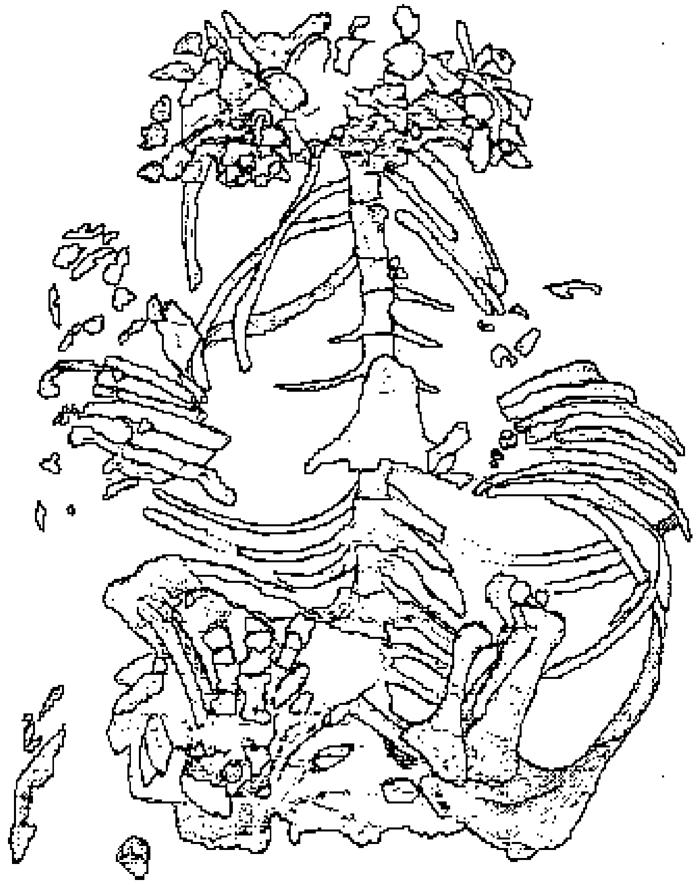

Fig. 13. Syrmosaurus viminicaudus. Overall view of the prepared skeleton. 1/25 (1/12 ?) actual size.

upward. The skull and first three neck vertebrae were missing. A broken tooth crown, practically the entire spinal column, with ribs in their natural position, bones of the extremities, and part of the armor were preserved. The cervicals, pectoral, and first caudal vertebrae were badly deformed, the neural arches and their processes were partially destroyed. Only two fragments of the cervical ribs were preserved. The dorsal ribs were badly crushed and the distal ends were broken off. The scapular regions were partially destroyed and the coracoids were crushed. The bones of the extremities were badly deformed, the proximal and distal ends were destroyed.

Of the armor, 72 complete spines and 27 fragments were preserved. Of these, 39 were found in the anterior region of the skeleton and lay in disorder immediately below the bones of the shoulder region and the front extremities. The largest spines were clearly oriented to the outside of the forelimbs, from the head of the shoulder to the elbow. Fragments of the long, knife-like spines laid on the on the sides of the mid-region of the torso - nine on the right side and 18 on the left. On the left side of the pelvic region lay seven large spines. Along the tail, on the right and left sides, lay about 13 spines.

The description of the arrangement of the skeletal parts confirms that the animal was buried in sedimentation with its neural spines upward and all four extremities bent under the torso, tail extended, and, apparently, the neck extended. The weight of the semi-dispersed skeleton forced the sternum and the ribs to settle on the extremities and their limbs, which were partially twisted from their natural position and deposited in the plane of the body up to the backbone. Only those armor spines that were on the extremities were preserved because they were shielded by the body of the animal from destruction and water erosion from above. Not a single spine from the upper side of the torso remained intact. All of the bones in the skeleton are white, porous, and weathered, showing traces of atmospheric action prior to burial. However, the nature of the destruction of the joints and the surfaces of many of the bones is so unique that it cannot be explained by weathering alone. It is likely that the cartilaginous portions of many bones were destroyed prior to their burial by microorganisms or insects.

Syrmosaurus sp.

Holotype. Fragment of the left and right half of the lower jaw. Collection No. 753 of the Paleontological Institute of the Academy of Sciences of the USSR.

Diagnosis of species. The teeth are stegosauroid, with a low lamellar crown and grooved sculpture. The cutting edge of the crown is divided into eight serrations. The root of the tooth is cylindrical. No postcranial skeleton is known to exist.

Description. A fragment 15 mm in size belongs to the right half of the lower jaw. Two teeth were located within the 15 mm portion on the dental edge, only one tooth was preserved. A fragment 19 mm in size belongs to the same half of the jaw. Three teeth were located within the 19 mm portion on the dental edge. A fragment 22 mm in size belongs to the left half of the jaw. Five teeth were located within the 22 mm portion on the dental edge, only one tooth was preserved. The teeth (Fig. 14) are stegosauroid with a low lamellar crown and channeled sculpture. The exterior surface of the crown is slightly convex, the interior side is concave. The cutting edge is divided into eight serrations. The apical serration is better developed. Along one side of it are four serrations, along the other side are three serrations. The root of the tooth is cylindrical.

Fig. 14. *Syrmosaurus* sp. Fragment from the lower jaw. Actual size.

Comparison. Complete similarity was observed between the teeth of *Syrmosaurus* sp. and those of *Syrmosaurus viminicaudus* from Bayn Dzak: they have the same shape and crown size, the same number of serrations along the edge of the crown, the apical serration is in the same location. Because of these similarities, the remains discovered must without doubt be related to the undefined species of the genus *Syrmosaurus* - *Syrmosaurus* sp.

General comments. During a visit to the Ulan Oshih deposit in 1946, incomplete remains of herbivorous dinosaurs form the genus *Psittacosaurus* and small predatory dinosaurs from the group Ornithomimidae (parts of the extremities, vertebrae, teeth, skull fragments) were collected in the lower part of the upper third of the excavation (in the vertical center of the remnant). Among these remains were found the jaw fragments of an armored dinosaur.

The presence of *Syrmosaurus* and Cretaceous predatory dinosaurs from the group Omithomimidae in the fauna of Ulan Oshih shows that the fauna of Ulan Oshih is generally similar to that of Bayn Dzak (in this case and others Syrmosauridae and Omithomimidae). Because of the similarities of thefauna, we may correlate the strata of Ulan Oshih with the deposits of Bayn Dzak and date these strata to the lower horizontal of the Upper Cretaceous epoch. The remains of *Psittacosaurus*, however, known only in the Lower Cretaceous compels us to revise the proposed dating and relate the bone-bearing layers of Ulan Oshih to the upper part of the Lower Cretaceous or the transitional between the Lower and Upper Cretaceous.

Distribution. The Ulan Oshih deposit is 200 km north-east of Dalan Tszadagad, 30 km north-west of the Dagshiuin Khuduk well, Mongolian People's Republic. Upper Cretaceous (?) epoch.

Material for study. A fragment of the right side of the lower jaw 15 mm in size. A fragment of the left side of the jaw 22 mm in size. Bones of a yellowish color, badly silicified. Collected 1946.

Syrmosaurus disparoserratus Maleev, 1952

Holotype. Fragments of the right and left half of the lower jaw. Collection No. 554 of the Paleontological Institute of the Academy of Sciences of the USSR. Collected 1949[5].

Diagnosis. The lower jaw is short and narrow. The symphyseal edge is turned outward, the alveolar edge is elevated. The teeth are stegosauroid, with a low lamellar crown and rugose sculpture. The number of serrations on the cutting edge of the crown is not the same for every tooth: from three to five serrations on each side of the apical serration.

Description. The jaw fragments of S. disparoserratus have the following features. A fragment 110 mm in size belongs to the right half of the jaw. On a section of the dental edge 90 mm long was space for 18 teeth, seven were preserved. A fragment 75 mm in size is the rear section of the left half of the jaw. On a section of the dental edge 55 mm long was space for 11 teeth, two were preserved. A fragment 37 mm in size is the front edge of the left half of the jaw containing six teeth within a 26 mm section. The lower jaw (mandibula) (Fig. 15) is low and short and the cross section at the center is triangular. The front edge of the symphysis end is turned outward. The alveolar end is elevated. The teeth are not differentiated, are stegosauroid and arranged in a curvolinear manner on the interior edge. Each tooth comprises a laterally compressed, vertically channeled crown that has a crenulated edge and a long cylindrical root. The outside surface of the crown is slightly convex vertically, whereas the inside is slightly concave. At the base of the crown is a rounded frill [=cingulum] that is more pronounced on the outside surface. The number of serrations on each tooth is not the same for every tooth: from three to five serrations on each side of the apical serration. The apical serration is more developed than the others and lies on the center vertical line.

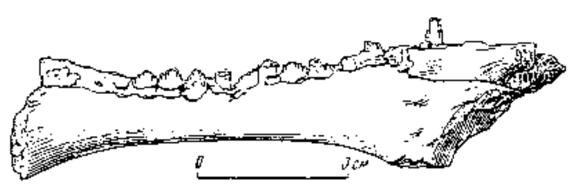

Fig. 15. *Syrmosaurus disparoserratus* Maleev, 1952. Fragment of the right half of the lower jaw. 2/3 actual size.

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[5]From data by I. A. Efremov who first visited the site in 1946 and found in the fauna of Shiregin Gashun the remains of Cretaceous predatory dinosaurs from the group Omithomimidae, large sauropods, trachodonts, and camosaurs.

Comparison. The teeth of *S. disparoserratus* show a close similarity to those of *Syrmosaurus* found in the Bayn Dzak and Ulan Oshih deposits and described by Maleev: the same number of serrations (8-10) on the edge of the crown, the same shape and size of crown, the same location for the apical serration. The teeth of *Syrmosaurus disparoserratus* differ from those of *Syrmosaurus viminicaudus* and *Syrmosaurus* sp. by the number of serrations on the cutting edge of the crown. All teeth are different and have a different number of serrations: there are from three to five serrations on each side of the apical serration. This distinction allowed us to relate the Shiregin Gashun remains to a new species of the genus *Syrmosaurus*, which, because of the nature of the crowns of the teeth, was named *S. disparoserratus* - "of varied serrations". It is possible that *S. disparoserratus*, which is very similar to *S. viminicaudus* in the form of its teeth, differs from it in minor details in the postcranial skeleton, which, to date has not been discovered.

General comments. The presence of trachodont remains in the fauna of Shiregin Gashun eliminates the possibility of equating the geological age of *S. disparoserratus* to that of *S. viminicaudus*. At the same time it does provide some basis for equating Shiregin Gashun to higher horizons than Bayn Dzak of the Cretaceous that correspond to the middle Cenomanian and the Belly River formation in the USA from which the armored dinosaurs and trachodonts are known.

Distribution. The Shiregin Gashun deposit is 350 km west of the Aimak center Dalan Tszadagad, between the Nemegetu and Baga Bogdo ranges, Mongolian People's Republic. Upper Cretaceous period.

Material for study. A fragment of the right half of the lower jaw 110 mm in size, with preserved teeth. A fragment of the left half of the lower jaw 75 mm in size. A fragment of the left half of the lower jaw 37 mm in size. The bones were well preserved, gray in color, badly silicified. Collections of 1949.

FUNCTIONAL FEATURES OF THE SYRMOSAUROID SKELETAL STRUCTURE

From our study of the preserved portions of the skeleton we may propose the following features of its structure:

1. The unique form of the first cervical vertebrae (3^{rd}, 4^{th}?) with obliquely set articulation surfaces, shows that in its normal position, the neck was turned upward and the head elevated. Neck motion was possible in mostly the dorsoventral direction and the upward sweep was greater than the downward.

2. Well developed cervical ribs and the very amphicoelous nature of the other cervical vertebrae limited the lateral movement of the neck.

3.The slope of the neck and head, like a lever applied on one side of the cranial support, increased the force required to bend the spinal column and thereby created in it a large curvature in the dorsal direction. This, of course, was an important biomechanical moment that diminished the force available to extend the spine. This force arose because of the weight of the enormous, flat torso. The bending strength of the neck and head was, of course, small because the head of *Syrmosaurus* was, apparently, small. Lacking spinal rigidity, a large heavy head would drastically increase the bending force. On the other hand, the heavy weight of the head drastically lowered the motive power of the front limbs, making it difficult for the animal to move. Consequently, the existence of a large, heavy head on a flat bodied creature, such as *Syrmosaurus*, would have been a biomechanical absurdity.

4. The high neural arches and neural spines on the dorsal vertebrae, along with the relatively slight development of the vertebra centra, caused the spinal column to be very rigid in order to resist extending and bending, while simultaneously reducing the weight of the spinal column. A completely analogous situation is a board set on its side - incomparably more rigid to flexure than when laid flat.

5. The high development and unique position of the zygapophyses of the dorsal vertebrae, which were joined by the complete envelopment of the postzygapophysis of one vertebra by the prezygapophysis of the one behind it guaranteed stability against twisting.

6. The reinforced union of the ribs with the transverse processes on the vertebrae, accomplished by inserting the dorsal edge of the rib neck into the furrow on the transverse process, gave the spinal column and rib cage additional strength against deformation. This reinforcement was particularly important for the unusually wide and flat rib cage of *Syrmosaurus* (see Fig. 5).

7. The fusion of the last four torso vertebrae and the first sacral vertebra ensured that the sacral region of the spinal column was rigid and immobile, which was important because it was not well developed in comparison with the pelvic girdle and the powerful rear limbs.

8. The lengthening of the preacetabular region of the ilium (up to the 17^{th} vertebra) and positioning it parallel to the axis of the spinal column increased the length of the region to which the pelvic-femur musculature was attached. This made it possibile for the legs to have a long stroke in the front direction - motion that was important for digging into sand.

9. Features of the glenoidal and acetabular cavities and the shape of the articulation surfaces of the humerus and femur show that these bones were located almost horizontal relative to the lower limbs. Thus, the extremities supported the body from the sides. Below the elbow and knee joints the forearm and shin were almost vertical. The lift of the body off the ground for locomotion was insignificant and required great muscular strength. The animal's belly almost always dragged along the ground. The limbs moved as follows: the humerus and femur moved front and backward in an almost horizontal plane, with some rotation in the elbow and knee joints. At the same time the right rear foot swung, the left front foot carried the front and conversely, the swing of the right front extremity coincided with the forward motion of the left rear.

10. The loose articulation of the vertebrae in the front half of the tail allowed it to move in dorsal and lateral directions. The change in the neural and haemal arches in the vertebrae of the rear half of the tail created an almost immobile connection between them. This connection was achieved by means of a two-sided articulation wherein the postzygapophyseal region of the arch of a vertebra was completely enveloped by the prezygapophyseal region of the one behind it, and the wedge-shaped region of the haemal process entered the V-shaped notch. As a whole, the entire posterior half of the tail was immobile, transforming it into a "club" (1.3 m long) that was equipped at its end with two long, knife-like spines that formed a two-edged "axe" acting in the horizontal plane.

Blows were delivered by moving the front half of the tail, similar to that of the glyptodons - *Glyptodon clavipes*, very similar in the defensive function of the tail and in its construction to *Syrmosaurus*.

The superior development of the haemal arches in comparison with the neural arches in the tail vertebrae and the presence of large strands of ossified tendons on the lower lateral side of the tail surface speaks of the great strength of the musculature that set it into motion.

Fig. 16. *Syrmosaurus viminicaudus*. Reconstruction of the exterior view.

All of the enumerated features in the structure of *Syrmosaurus* skeleton developed as the result of adapting to the conditions of existence. It would be extremely interesting to study the skeleton of modern flat-bodied spined lizards, especially *Phrynosoma*. Undoubtedly, we could create an analogy with the structure of *Syrmosaurus* in a number of features, but, it seems sensible, on a somewhat different morphological basis.

A RECONSTRUCTION OF *SYRMOSAURUS* EXTERIOR VIEW

In spite of the poorly preserved skeletal elements, we can come close to a fairly complete representation of what the dinosaur looked like when it was alive.

Syrmosaurus viminicaudus was a massive land animal similar in overall appearance to the modern spined desert lizards of the genus *Phrynosoma* and *Moloch* but much larger. It had a small head, short, strong neck, short, barrel-shaped torso 2-2.5 m long, and a large tail 2.1 m long. The overall length of the animal was as much as 5 m, with the height of its front region not more than 1 m, probably less. These are the fundamental features of *Syrmosaurus* appearance (Fig. 16). The head and neck were raised upward to increase the field of vision, and the very wide and flat torso is like that the modern *Phrynosomia,* but in even greater degree. The low, short jaws were filled with lancet-like teeth that had a low, flat crown, and slightly serrated cutting edges. The forelimbs were shorter than the hind limbs, and the manus had five digits (the fifth was significantly reduced). The back feet had three digits. The digits terminated in flat, unguals. The armor consisted of separate, oval-shaped, cariniform, bony spines (probably equipped with a corneous cover when the animal was alive) arranged in symmetrical rows on the upper and lateral surfaces of the neck, torso, exterior sides of the extremities and tail. Special knife-like spines arranged flatwise at the end of the tail formed a striking "axe".

THE SYRMOSAURID LIFESTYLE

The lifestyle of *Synnosaurus* cannot be explained in sufficient detail because of the lack of a skull. The source material from which we can construct some preliminary assumptions is the postcranial skeleton and some data regarding the genesis of the deposit.

A wide, short torso; strong, multidigit feet; digits that terminate in ungular phalanges, a heavy, defensively equipped, uniquely armored body - all are undoubtedly adaptations to life in open areas of dry land. The wide, flat shape of the humerus and femur and their almost horizontal position, and the insignificant size of the legs in comparison with the size of the torso show that *Syrmosaurus* had the ventral portion of its body in contact with the ground when it moved. This means of locomotion is characteristic of slow moving land quadrupeds. The flat ungular phalanges of the digits counteracted the legs sinking into soft soil, but made movement through sand possible. The simple, lancet-like shape of the teeth, with their low flat crown and slightly serrated cutting edge, shows that the basic food of the syrmosaurids could only have been soft vegetation having a soft outer shell. This vegetation, under the conditions of a landscape with uncovered sand dunes (the syrmosaurid deposit in Bayn Dzak) might have grown abundantly along the banks of a slowly flowing river and the marshy shells of the delta regions. Visibly, places such as these, with subaerial sand dunes, were a biotope for *Syrmosaurus* in Mongolia (Efremov 1948, 1949, 1950). The mastery of similar biotopes, for the most part being open areas of dry land, meant that the syrmosaurids adapted to digging into the sand. The means by which they dug was similar to what is observed in modern spiny desert lizards of the genera *Moloch*, *Phrysonoma* and *Zonurus*; i.e., the animal creates a small depression in the sand by moving its torso back and forth and then uses its front and rear extremities to rake the sand to the sides of its body, leaving only a small area of its back exposed. This method of digging is seen in almost all desert reptiles and, apparently, evolved as a response to environmental factors protecting lightly defended animals having no continuous bony armor from serious overheating and attack by predatory dinosaurs and serving as a reliable camouflage.

In contrast to the syrmosaurids, the later Upper Cretaceous Ankylosauria of the genera *Ankylosaurus*, *Palaeoscincus*, *Scolosaurus*, etc. evolved to master more open areas of dry land frequently remote from river banks and marshy delta areas. The influence of their habitat caused ankylosaurids to develop a more rigid axial skeleton and heavy bony armor that achieved thicknesses of 100 mm in some of them. Armor such as this reliably protected the ankylosaurids from serious overheating and obviously served as a good defense against the attack of predatory dinosaurs, the ranges of which were, if not analogous, then almost contiguous.

THE GEOLOGICAL AGE AND STRATIGRAPHIC DISTRIBUTION OF THE MONGOLIAN SYRMOSAURIDS

Analysis of the fauna data obtained from the deposits shows that the syrmosaurids were buried with herbivorous dinosaurs of the genus *Psittacosaurus*, ceratopsids of the genus *Protoceratops*, and Cretaceous predatory dinosaurs of the group Omithomimidae (Bayn Dzak, Ulan Oshih), trachodonts and ornithomimids (Shiregin Gamush). The discovery of syrmosaurids and ornithomimids together shows that the fauna from all three deposits are almost identical and are, in essence, one faunal complex at different stages of its development. The earliest stage is represented by Ulan Oshih, the age of which is determined from the presence of *Psittacosaurus,* which is known only from the Mongolian Lower Cretaceous - Ondai Sair, and the Osh and Artsu Bogdo Formations. Because of this, the geological age of *Syrmosaurus* sp. may be dated to the Lower Cretaceous epoch. However, the presence of Ornithomimidae - known from the Upper and Lower Cretaceous - compels us to revise the dating somewhat and consider the bone-bearing layers of Ulan Oshih to be the upper part of the Lower Cretaceous, or transition layers between the Lower and Upper Cretaceous. If further discoveries of syrmosaurs, like those found in Ulan Oshih, prove to be similar to *Syrmosaurus viminicaudus* from Bayn Dzak, then the Ulan Oshih layers can be correlated with the Bayn Dzak layers or some others.

The similarity of the syrmosaurids and omithomimids sets the faunal stage of Bayn Dzak as almost contemporaneous with that of Ulan Oshih. However, the presence of ceratopsids of the genus *Protoceratops*, known only from the lower horizons of the Upper Cretaceous of Mongolia compels us to date the geological age of *Syrmosaurus viminicaudus* to these horizons, which correspond to the Djadokhta Formation (the lowest horizons of the Mongolian Upper Cretaceous, which are lower than all of the known Upper Cretaceous deposits in Europe and North America).

The presence of trachodontids, known from the higher horizons of the Cretaceous, in the Shiregin Gashun fauna, define this stage as the most recent and shows that *Syrmosaurus* appeared in still other faunal complexes and in higher horizons - higher than the Ulan Oshih and Bayn Dzak horizons. The Shiregin Gashun horizon corresponds to the middle Cenomanian period and the Belly River Formation in the USA that contain trachodonts and armored dinosaurs. It is possible that this interval in the Upper Cretaceous was the last time that members of the family Syrmosauridae were alive in Mongolia. Afterwards, they were replaced in the general complex of dinosaur fauna by true Ankylosauria from the family Ankylosauridae found in Bayn Shire.

Table 4. Geological Distribution of the Armored Dinosaurs from the Cretaceous Period in Mongolia and North America.

		Mongolia			North America				
		Deposit and stratigraphic horizon		Fauna	Alberta		Montana		
					Formation	Fauna	Formation		Fauna
Upper Cretaceous	Danian Stage (Laramie)	Bayn Shire	Ankylosaurid horizon	*Talarurus plicatospineus*			Lance	Hell Creek	*Ankylo-saurus*
	Senonian	Nemegt		*Saurolophus* Carnosauria	Edmonton	*Ankylosaurus Anodontosaurus*			
	Cenomanian	Shiregin Gashun		*Syrmosaurus disparoserratus*	Belly River	*Scolosaurus Palaeoscincus Dyoplosaurus*	Judith River		*Palaeo-scincus*
		Bayn Dzak	Djadokhta	*Srymosaurus viminicaudus*					
Lower Cretaceous	Albian	Ultan Osh	?	*Syrmosaurus* sp.					

CONCLUSIONS

Analysis of the geological and geographical distribution of Cretaceous ankylosaurs shows that, with the exception of *Polacanthus* from the Wealden stage in England and two fragmentary finds from the Upper Cretaceous in France and Lower Austria, most representatives of the suborder were restricted to the North American continent. In the Cretaceous deposits in the USA they are found with ceratopsids: *Ceratops*, *Leptoceratops*, *Brachyceratops*, *Monoclonius*, *Styracosaurus*, *Arhinoceratops*, *Anchiceratops*, *Torosaurus* and *Triceratops*. *Syrmosaurus* are found in the lower horizons of the Upper Cretaceous in Mongolia, which is geologically much older than all of the known deposits of Ankylosauria in Europe and North America. Buried with them are small herbivorous dinosaurs of the genus *Psittacosaurus*, Cretaceous ceratopsids of the genus *Protoceratops* and predatory dinosaurs of the group Ornithomimidae. This is principally another fauna complex that points to the great geological age of the syrmosaurids in comparison with members of the family Ankylosauridae that were known up until now.

Without precondition, the Mongolian syrmosaurids are a new, previously unknown form of armored dinosaurs living in Central Asia during Cretaceous time. As a comparative analysis of its skeleton has shown, this form of dinosaur is much older than all of the known representatives of the suborder and is therefore set into its own independent family of Asiatic armored dinosaurs - Syrmosauridae, for the time being with only the unique genus *Syrmosaurus*. It is possible that the syrmosaurids are representatives of a group of those ancestral forms from which the true ankylosaurs of the Upper Cretaceous, nicknamed "lizard tanks" for the strong bony armor around their body, developed. The presence of syrmosaurids in the lower horizontals of the Cretaceous and true ankylosaurids in the high horizons of the Cretaceous (Bayn Shire) of Mongolia allow us to propose that Central Asia was the birthplace of the Upper Cretaceous ankylosaurs and that during that period they migrated to the northeast through the Bering Strait region and disseminated in North America.

Thus, the Mongolian deposits settle the question of the presence of Ankysloauria in early and later phases of the Cretaceous period in Asia, and introduce new data regarding the history of their development and distribution in the Old World.

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