

An ankylosaurid (Ornithischia: Ankylosauria) braincase from the Upper Cretaceous Bissekty Formation of Uzbekistan

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Abstract

An ankylosaurid braincase from the Upper Cretaceous Bissekty Fm. (Upper Turonian-Coniacian) at Dzharakuduk, central Kyzylkum Desert (Uzbekistan), is most similar to the braincase of *Amtosaurus magnus* from the upper part of the Upper Cretaceous Bainshire Fm. of Amtgai (Mongolia) in the structure of the ventral surface of the basioccipital, presence of a triangular anterior projection on the *dorsum sellae*, and dorsal position of the *fenestra ovalis* relative to the jugular foramen. It is referred to a new species, *Amtosaurus archibaldi* n. sp., which differs from *A. magnus* in having three instead of two foramina for the passage of branches of *N. hypoglossus* (XII), a smaller angle between the ventral surfaces of the basioccipital and basisphenoid (90° rather than 120°), and the more posterior position of the basipterygoid processes. *Amtosaurus* is an additional element shared by the Bissekty and upper Bainshire vertebrate assemblages. The alleged Campanian age for the Iren Dabasu Fm. is based on inadequate evidence, and this unit is more likely Late Turonian to ?Coniacian in age. The upper part of the Bainshire Fm. is Turonian-Santonian in age.

Key-words: Dinosauria, Ankylosauria, *Amtosaurus*, Late Cretaceous, Uzbekistan, Mongolia

Résumé

Une boîte crânienne d'ankylosaurien a été récoltée dans la Formation de Bissekty d'âge Crétacé supérieur (Turonien supérieur - Coniacien) à Dzharakuduk dans la partie centrale du désert de Kyzylkum (Uzbekistan). Elle est fort semblable à la boîte crânienne d'*Amtosaurus magnus* de la partie supérieure de la Formation de Bainshire (Crétacé supérieur) à Amtgai (Mongolie) par la structure de la surface ventrale du basioccipital, la présence d'un prolongement triangulaire antérieur sur le *dorsum sellae* et la position dorsale de la *fenestra ovalis* par rapport au foramen jugulaire. Elle est attribuée à une espèce nouvelle, *Amtosaurus archibaldi* n. sp., qui diffère d'*A. magnus* par la présence de trois, et non de deux, foramina pour le passage des branches de *N. hypoglossus* (XII), par un angle formé par les surfaces ventrales du basioccipital et du basisphénoïde plus petit (90° et non 120°), et par la position plus postérieure des processus basiptérygoïdes. *Amtosaurus* est un nouvel élément commun aux assemblages de vertébrés de la Formation de Bissekty et de la partie supérieure de la Formation de Bainshire. L'âge campanien avancé pour la Formation d'Iren Dabasu se base sur des preuves insuffisantes; un âge Turonien à ?Coniacien est plus vraisemblable. La partie supérieure de la Formation de Bainshire est d'âge Turonien-Santonien.

Mots-clefs: Dinosauria, Ankylosauria, *Amtosaurus*, Crétacé supérieur, Uzbekistan, Mongolie

Резюме

Мозговая коробка анкилозавриды из верхнемеловой биссектинской свиты (верхний турон – коньяк) Джаракудука, центральная часть пустыни Кызылкум (Узбекистан), наиболее похожа на мозговую коробку *Amtosaurus magnus* из верхнемеловой байнширэнской свиты местонахождения Амтгай (Монголия) по структуре ventральной поверхности основной затылочной кости, присутствию треугольного переднего отростка на *dorsum sellae* и дорзальному положению *fenestra ovalis* относительно яремного отверстия. Мозговая коробка из Узбекистана отнесена к новому виду *Amtosaurus archibaldi* n. sp., который отличается от *A. magnus* наличием трех вместо двух отверстий для выхода подъязычного нерва (XII), меньшим углом между ventральными поверхностями основной затылочной и основной клиновидной костей (90° вместо 120°), более задним положением базиптеригонидных отростков. *Amtosaurus* является еще одним общим элементом между биссектинским и байнширэнским комплексами позвоночных. Предполагаемый кампанский возраст для формации Ирэн-Дабасу основан на недостаточных данных и эта формация, скорее всего, имеет поздний туронский - ?коньякский возраст. Верхняя часть байнширэнской свиты имеет турон-сантонский возраст.

Ключевые слова: Dinosauria, Ankylosauria, *Amtosaurus*, поздний мел, Узбекистан, Монголия

Introduction

Ankylosaurs are a distinctive group of armoured ornithischian dinosaurs with an almost worldwide distribution during the Cretaceous Period. In Asia, their skeletal remains are common in the Cretaceous continental strata of Mongolia and China, often including complete skulls and skeletons (MARYAŃSKA, 1977; TUMANOVA, 1987, 2000; BARRETT *et al.*, 1998). By contrast, ankylosaurian remains have been frequently found on the territory of the former USSR, but are generally very fragmentary and represented by isolated teeth, postcranial bones, or osteoderms. Ankylosaurian fossils have been confidently identified from the Upper Albian?-Lower Cenomanian Khodzhakul Fm. in the southwestern Kyzylkum Desert, Uzbekistan (Khodzhakul I, Sheikhdzheili II, Chelpyk), the Upper Turonian-?Coniacian Bissekty Fm. in the central Kyzylkum Desert, Uzbekistan (Dzharakuduk, Taikar-

shi, Kulkuduk, Tyulantash, Tamdy-Truba), the Coniacian-?Santonian Kynyr Fm. in the central Kyzylkum Desert, Uzbekistan (Dzhalpakshi, Zhaldyrbas-Takyr), the Santonian Yalovach Fm. in northern Tajikistan (Kansai, Kyzylpilyal), the Santonian Syuk-Syuk Fm. in southern Kazakhstan (Kyrkkuduk), the Santonian-?Campanian Koturbulak Fm. in central Kazakhstan (Koturbulak), unnamed Santonian-?Campanian strata in eastern Kazakhstan (Karacheku), unnamed Campanian-?Maastrichtian strata in the central Kyzylkum Desert, Uzbekistan (Shatyrtube II), and Maastrichtian Tsagayan Fm. in the Amur Province, Russia (Kundur) (RIABININ, 1939; MARYAŃSKA, 1977; MARKEVICH *et al.*, 1994; NESSOV, 1995; TUMANOVA, 2000). As is evident from this list, ankylosaurs were widely distributed in what is now Middle Asia and Kazakhstan and are found at a number of stratigraphic levels, which makes this region potentially important for the understanding of the evolutionary history of these dinosaurs in Asia. However, any detailed study is hindered by the fragmentary nature of the material. NESSOV (1995, pp. 20-21) observed changes in the osteoderm and tooth structure of ankylosaurs at the Cenomanian-Turonian boundary: osteoderms change from nearly flat, small, polygonal dermal plates, frequently adjacent to other plates (NESSOV, 1995, pl. 4, figs. 2, 3), to large, longitudinally elongated osteoderms with a ventral concavity (NESSOV, 1995, pl. 4, figs. 4-6), and tooth types

with a distinct constriction between the root and crown (NESSOV, 1995, pl. 4, fig. 10) are replaced by teeth lacking such a constriction (NESSOV, 1995, pl. 4, fig. 11). He has interpreted this change as a replacement of the Shamosauridae [sic] by the Ankylosauridae.

This paper presents a description of an almost complete braincase of an ankylosaurid dinosaur from the Upper Cretaceous Bissekty Fm. at Dzharakuduk, Central Kyzylkum Desert, in Uzbekistan (Fig. 1). This specimen was discovered by Oleg Tsaruk in September 1998 during fieldwork of the joint Uzbek-Russian-British-American-Canadian project (URBAC-98). This braincase is the most complete and important ankylosaurian specimen discovered in Middle Asia to date, and, for the first time, permits a more precise systematic assessment of the Bissekty ankylosaur, which was previously known only from osteoderms and teeth. Furthermore, being exceptionally well preserved, the fossil provides new data on the evolution of the braincase in Ankylosauria. The Bissekty specimen was compared to the braincases of the nodosaurids *Silvisaurus condrayi* EATON, 1960 from the Lower Cretaceous (Albian) Dakota Fm. of Kansas (EATON, 1960), *Pawpawsaurus campbelli* LEE, 1996 from the Lower Cretaceous (Albian) Paw Paw Fm. of Texas (LEE, 1996), and *Struthiosaurus austriacus* BUNZEL, 1871 from the Upper Cretaceous (Campanian-? Maastrichtian) Gosau beds of Austria (PEREDA-SUBERBIOLA & GALTON, 1994), as well as the

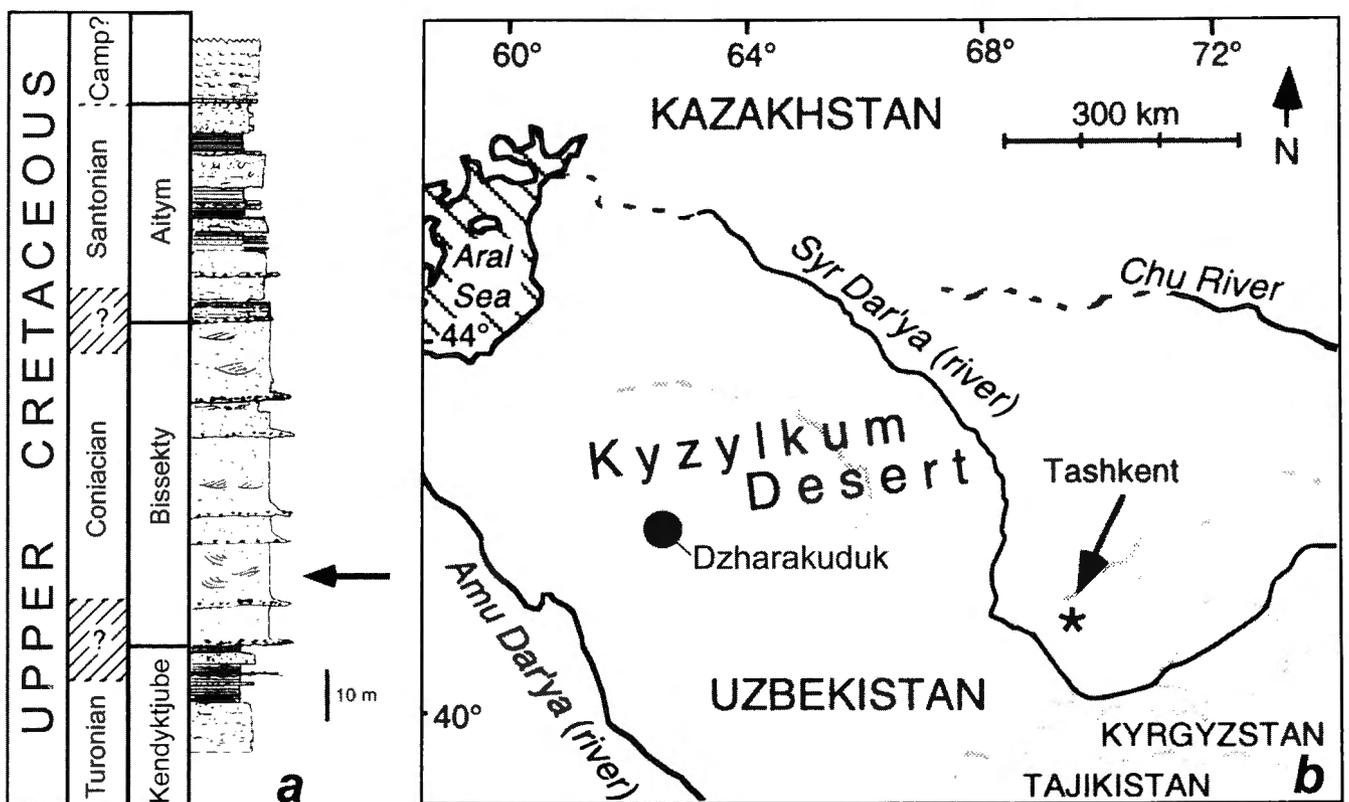


Fig. 1 — Geological (a, indicated by arrow) and geographical (b, Dzharakuduk, Uzbekistan, indicated by solid dot) location of the *Amtosaurus archibaldi* n.sp. holotype specimen (modified after ARCHIBALD *et al.*, 1999, figs. 1, 2). The Bissekty Fm. is fluvial and the Kandyktjube and Aitym formations are marginally marine.

braincases of the ankylosaurids *Shamosaurus scutatus* TUMANOVA, 1983 from the Lower Cretaceous Dzunbain Fm. of Mongolia (TUMANOVA, 1983, 1986), *Tsagantegia longicranialis* TUMANOVA, 1993 from an unnamed ?Upper Cretaceous formation in Mongolia (TUMANOVA, 1993), *Talarurus plicatospineus* MALEEV, 1952b, *Amtosaurus magnus* KURZANOV & TUMANOVA, 1978, and *Maleevus disparoserratus* (MALEEV, 1952a) from the Upper Cretaceous Bainshire Fm. of Mongolia (KURZANOV & TUMANOVA, 1978; TUMANOVA, 1987), *Pinacosaurus grangeri* GILMORE, 1933 from the Upper Cretaceous Djadokhta Fm. of Mongolia (MARYANSKA, 1971, 1977), *Saichania chulsanensis* MARYANSKA, 1977 and *Tarchia kielanae* MARYANSKA, 1977 from the Upper Cretaceous Barun Goyot Fm. of Mongolia (MARYANSKA, 1977), *Tarchia gigantea* (MALEEV, 1956) from the Upper Cretaceous Nemegt Fm. of Mongolia (TUMANOVA, 1977), *Shanxia tianzhensis* BARRETT *et al.*, 1998 from the Upper Cretaceous Huiquanpu Fm. of China (BARRETT *et al.*, 1998) [possibly synonymous with *Tianzhenosaurus youngi* PANG & CHENG, 1998 from the same formation and region, see PANG & CHENG (1998), SULLIVAN (2000), and UPCHURCH & BARRETT (2000)], cf. *Polacanthus* sp. from the Lower Cretaceous of England (NORMAN & FAIERS, 1996), *Gastonia burgei* KIRKLAND, 1998 from the Lower Cretaceous Cedar Mountain Fm. of Utah (KIRKLAND, 1998), and *Nodocephalosaurus kirtlandensis* SULLIVAN, 1999 from the Upper Cretaceous Kirtland Fm. of New Mexico (SULLIVAN, 1999). With the exception of *Amtosaurus magnus*, all these taxa will only be referred to by their generic names below.

The specimen described in this paper is housed in the Paleoherpetological Collection of the Zoological Institute, Russian Academy of Sciences, Saint Petersburg (abbreviated ZIN PH).

Systematic palaeontology

Ornithischia SEELEY, 1887

Ankylosauria OSBORN, 1923

Ankylosauridae BROWN, 1908

Amtosaurus KURZANOV & TUMANOVA, 1978

Amtosaurus archibaldi n. sp.

Figs. 2, 3.

Holotype: ZIN PH 1/16, braincase.

Etymology: In honour of Prof. J. David ARCHIBALD (San Diego State University, San Diego, USA), the leader of the URBAC project.

Type locality and horizon: Dzharakuduk (N 42°06'21", E 62°37'45"), Central Kyzylkum Desert, Uzbekistan. Lower part(?) of the Bissekty Fm., Upper Cretaceous (Upper Turonian-Coniacian) (Fig. 1).

Diagnosis: Differs from *Amtosaurus magnus* KURZANOV & TUMANOVA, 1978 by having three rather than two exits

for *N. hypoglossus* (XII), a smaller angle between the ventral surfaces of the basioccipital and basisphenoid (90° rather than 120°), and the basiptyergoid processes being more posteriorly placed.

Description

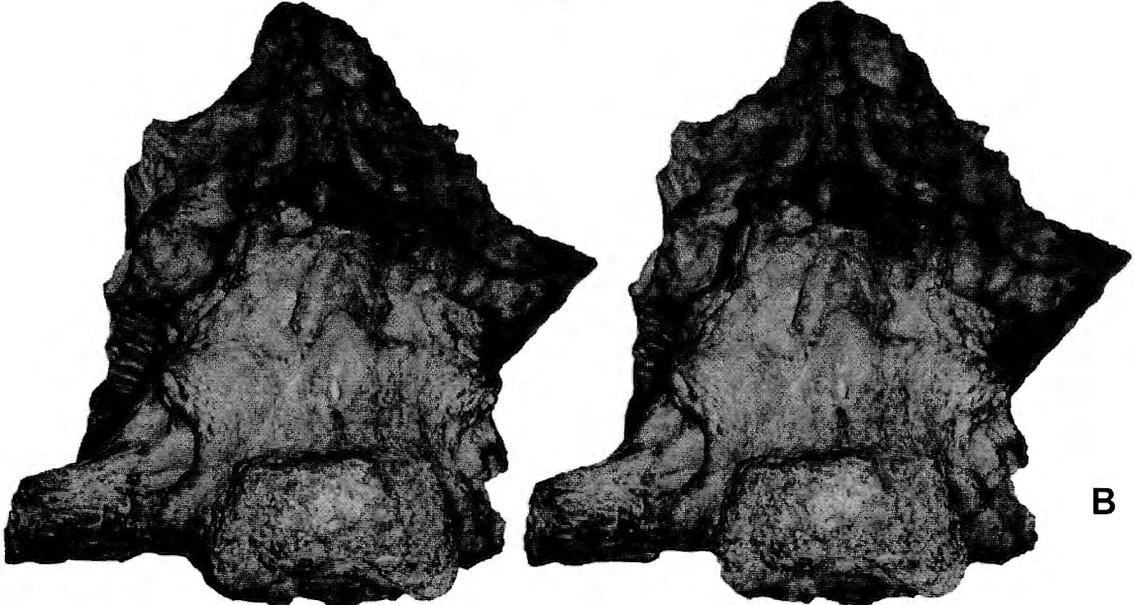
The braincase is fully ossified, and the bones of the skull roof are completely fused to it. In most cases, the sutures have been obliterated. On the other hand, both basal tubera and the right basiptyergoid process, the occipital condyle, and possible the distal tip of the right paroccipital process were not completely ossified. The openings for cranial nerves and blood vessels are relatively large. There is a distinct suture separating the basioccipital and exoccipital on the right side, extending along the preserved part of the paroccipital process (Fig. 2D). As evident from the known data on ankylosaur ontogeny (e.g. COOMBS & MARYANSKA, 1990; GODEFROIT *et al.*, 1999) all these characters suggest that this specimen represents a not yet fully mature individual. It is interesting that ossification was asymmetrical, the right side appearing "less mature" than the left side: there is a suture between the basioccipital and exoccipital, the basiptyergoid process is not ossified, and the occipital condyle was apparently less ossified on the right side.

Skull roof: The posterior portion of the skull roof is broken off. The preserved dorsal surface of the skull is not covered by osteoderms. It is almost flat and bears numerous irregularly distributed small to medium-sized pits. At the posterior margin, there is a short longitudinal groove, extending along the midline for about 12 mm, and dividing anteriorly into two grooves, which are directed anterolaterally and diverge at a right angle (Fig. 2A). Similar grooves are present in *Talarurus* (MALEEV, 1956, fig. 1) and *Tarchia* (TUMANOVA, 1977, fig. 1a) on the posterior portion of the skull roof free of osteoderms. In the latter taxon they diverge at a greater angle.

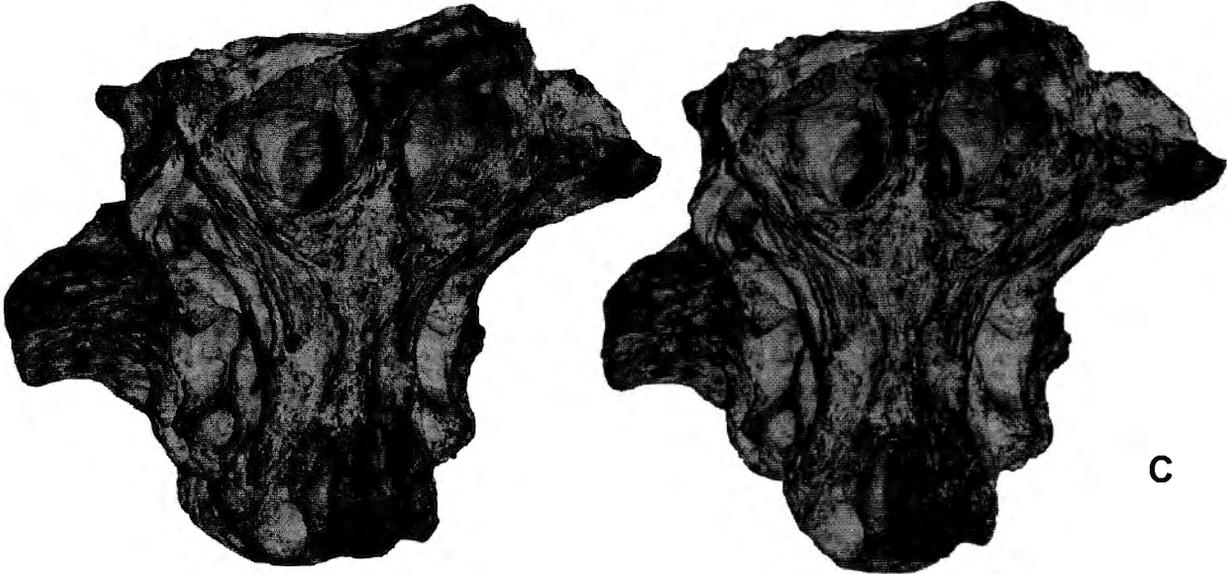
Occiput: The occipital surface is inclined at the angle of about 125° to the dorsal surface of the skull. The occipital condyle is directed posteroventrally and barely projects beyond the occipital plane. Its articular surface is crescent-shaped and transversely elongated: its height is 24.3 mm, its width 38.3 mm. The relatively small *foramen magnum* is oval, with a vertical diameter of 19 mm and a horizontal diameter of 23.3 mm. It is dorsally bordered by two flat surfaces for articulation with the proatlas(?) or atlas ("proatlas facet" of CARPENTER *et al.* [1998, fig. 1] or "proatlas shelf" of CARPENTER *et al.* [1999, fig. 2B]). Just dorsal to these surfaces, there are asymmetrical, transversely oriented presumably venous sulci, which terminate near the midline in small foramina. Similar sulci have been reported for *Tsagantegia* (TUMANOVA, 1993, p. 97). Another possibility is that these openings are for the first spinal nerve (dorsal root), which in *Talarurus* lies below the "proatlas facet" (KURZANOV & TUMANOVA, 1978, fig. 1a). This possibility will be proved, if "proatlas facets" in ankylosaurs turn to be the proatlantal elements fused with the skull, as PEREDA SUBERBIOLA & GALTON (1994) suggested previously;



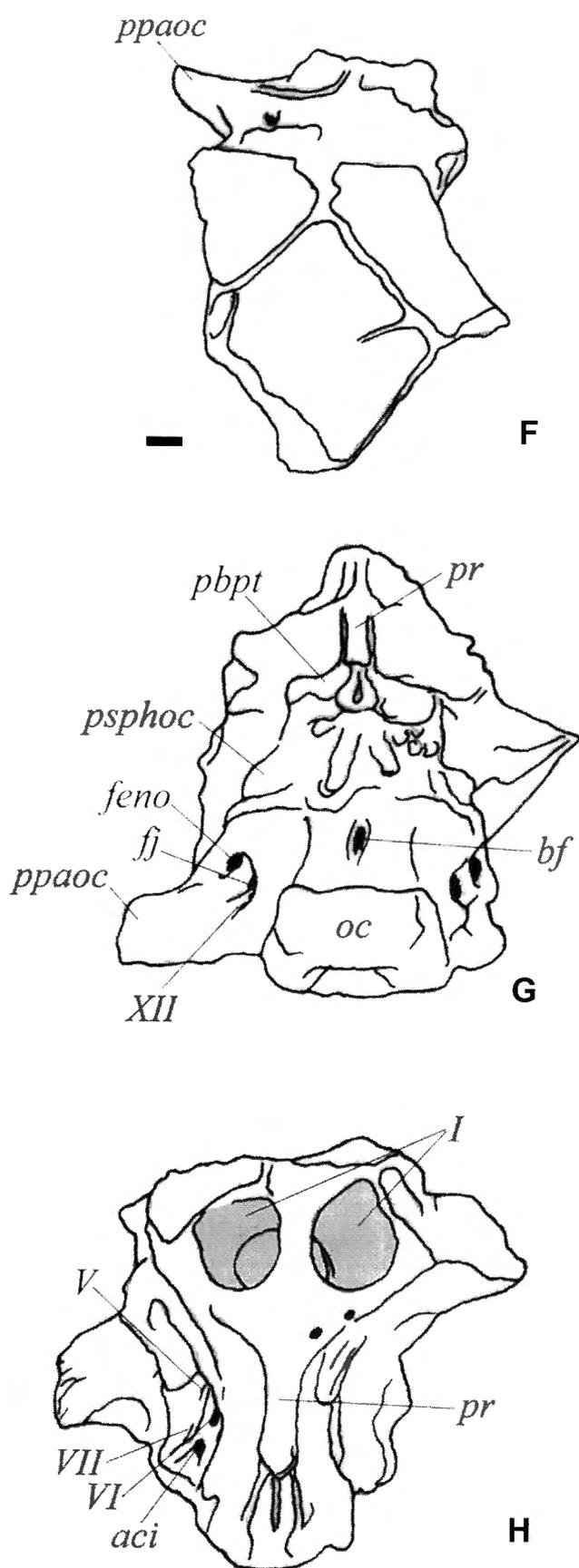
A



B



C



usually the proatlantal elements are assumed to be lost in Thyreophora (MAKOVICKY, 1997, p. 583). Much larger openings, the posttemporal fenestrae ("posttemporal foramina" of LEE, 1996, p. 238, figs. 4, 9), served for the passage of a vein (ROMER, 1997, p. 65; possibly the *vena capitis dorsalis*, see NORMAN & FAIERS, 1996, p. 304, fig. 1), lie dorsal to those sulci. The posttemporal fenestrae are also asymmetrical, the right one being almost twice as large as the left. This passage opens internally in the subtemporal fossa above the ear capsule outside the side wall of the braincase and has three smaller openings on its medial side. At least two of latter openings led to the endocranial cavity. This passage extends along the anterodorsal margin of the paroccipital process. The preserved portion of the paroccipital process is short and narrow; it distinctly decreases in thickness towards the distal end, which apparently was not completely ossified. On the posterior surface of the paroccipital surface, at the level of the *foramen magnum* mid-height, there is a small circular depression, possibly for the cranial attachment of the *rectus capitis posterior* muscle. In *Pawpawsaurus* similar depressions are placed above the *foramen magnum* (LEE, 1996, p. 238).

Braincase: The basioccipital is broad on its ventral side. It is flattened along the midline and concave laterally. The longitudinal ridges bordering the lateral depressions for insertion of *M. rectus capitis anterior* are weakly developed. The ventral surface of the basioccipital is deeply concave anteroposteriorly and faces almost directly ventrally. There is a very deep and short fissure on the basioccipital along midline, placed in a large shallow depression. A similar foramen was found in a juvenile *Pinacosaurus*, and a similar depression ("pouch") was described for *Saichania* (MARYAŃSKA, 1977, p. 110), *Tsagantegia* (TUMANOVA, 1993, p. 97), and *Nodocephalosaurus* (SULLIVAN, 1999, fig. 5B). In an adult specimen of *Tarchia*, this becomes a large gap opening into the endocranial cavity (MARYAŃSKA, 1977, p. 110). Such a foramen or depression seems to be characteristic for most Asiatic ankylosaurs (TUMANOVA, 1987, p. 39). Anterior to this depression, the surface of the bone is eroded. This part may not have been ossified. The position of the suture between the basioccipital and exoccipital indicates that exoccipital made no contribution to the occipital condyle, unlike in *Pinacosaurus* (MARYAŃSKA, 1977, p. 109), *Tianschisaurus* (DONG, 1993, p. 260), and *Minmi* (MOLNAR, 1996, fig. 12). The exits for branches of *N. hypoglossus* (XII) are entirely within the basioccipital, close to contact with the exoccipital. In *Pinacosaurus* and *Pawpawsaurus*, the reverse is present: the foramen lies within the exoccipital, just above the contact with basioccipital (MARYAŃSKA, 1977, p. 110; LEE, 1996, fig. 10). Ventral to the suture, the *crista interfenestralis* separates the *foramen jugulare* and *fenestra ovalis*. The jugular foramen, which served for the passage of cranial nerves IX-XI and *V. jugularis*, is located in the ventral base of the proximal part of paroccipital process, within the basioccipital. It is separated from the two ventral exits of XII only by a thin bony

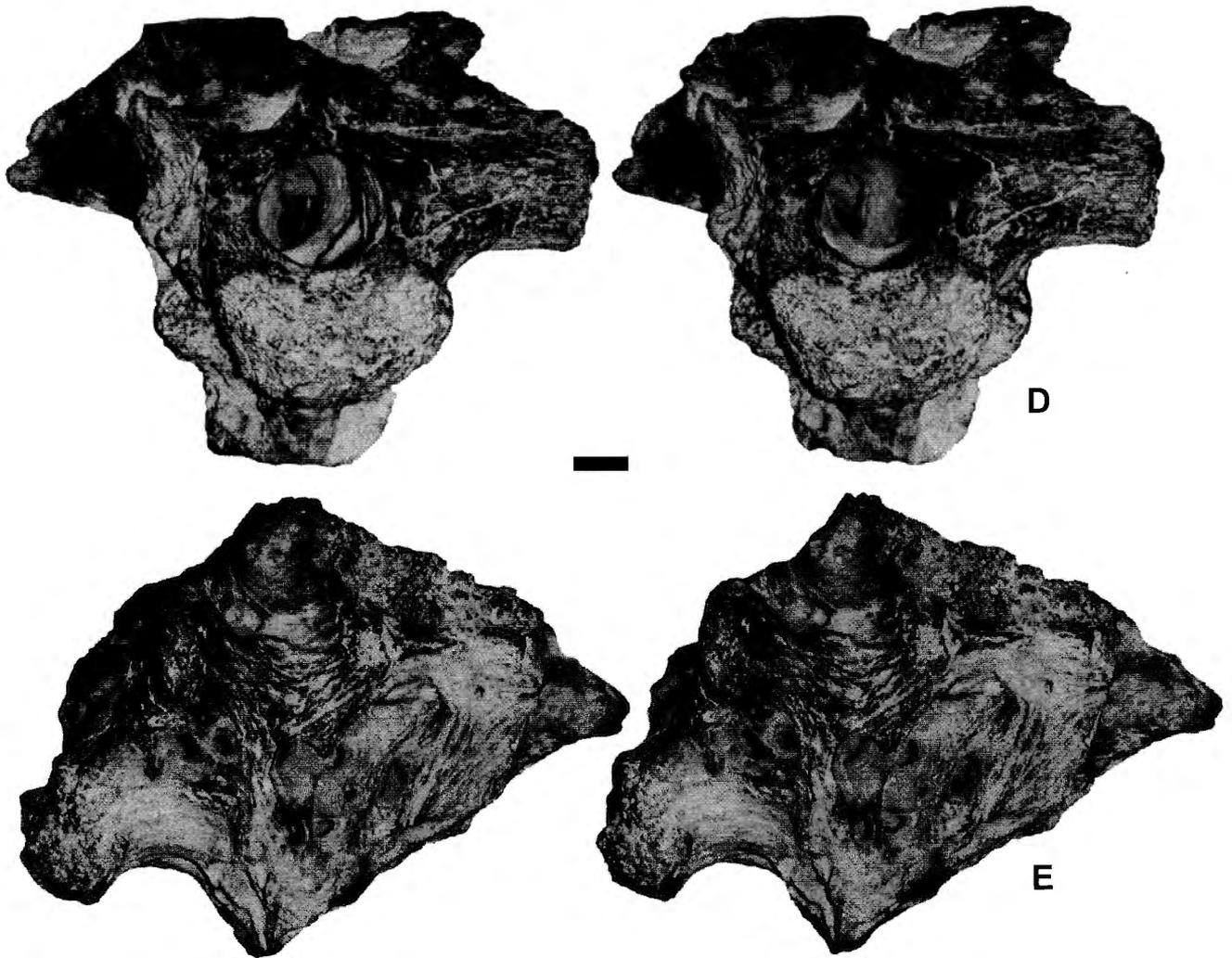


plate. The *crista interfenestralis* extends anterolaterally to the dorsal part of the sphenoccipital process. It is less developed than in *Shanxia* (BARRETT *et al.*, 1998, fig. 6). The *crista interfenestralis* completely separates the *fenestra ovalis* and *foramen jugulare* and is thick as in *Amtosaurus magnus* (KURZANOV & TUMANOVA, 1978, fig. 2; in that paper, the foramina are mislabeled on the figures: the anterior foramen is the *fenestra ovalis* and the posterior the *foramen jugulare*), and *Shanxia* (BARRETT *et al.*, 1998, fig. 6). In *Talarurus*, the *crista interfenestralis* is much more weakly developed and separates the foramina only ventrally (KURZANOV & TUMANOVA, 1978, fig. 1b). In *Saichania*, *Tarchia* and *Gastonia* the two foramina are confluent (TUMANOVA, 1987, p. 39; KIRKLAND, 1998, fig. 2A). Just posterior to the *foramen jugulare*, there are three openings for branches of *N. hypoglossus* (XII), gradually increasing in size from the anterior (ventral) to the posterior (dorsal). These canals are separated only by the thin bony laminae. In *Talarurus* and *Amtosaurus* (KURZANOV & TUMANOVA, 1978, figs. 1b, 2g), there are only two openings for XII, the posterior one being noticeably larger; in *Talarurus*, they also separated

by a considerable distance. Although in the holotype of *Amtosaurus magnus* the area anterior to these foramina is not preserved, *N. hypoglossus* (XII) has only two passages, as is apparent from a dorsal view of the endocranial cavity (KURZANOV & TUMANOVA, 1978, fig. 2). In cf. *Polacanthus* (NORMAN & FAIERS, 1996, figs. 2, 3) also there are two openings for XII, but they are of similar size. At least two openings for XII were present in *Gastonia* (KIRKLAND, 1998, fig. 2B). On an endocranial cast of *Euoplocephalus* (COOMBS, 1978b, fig. 1) there are three distinct branches of XII, which gradually increase in size from anterior to posterior, exactly as in ZIN PH 1/16. In *Pinacosaurus*, there is a single foramen for XII and a separate *foramen jugulare* (MARYAŃSKA, 1977, p. 110). In *Saichania* and *Tarchia* (MARYAŃSKA, 1977, fig. 7, pl. 27, fig. 3; TUMANOVA, 1977, p. 96), there is one small foramen posterior to the *fenestra ovalis*, which was interpreted as the exit for IX-XII. Taking into the account the reduction of the *crista interfenestralis* mentioned above, it is more likely that the larger anterior foramen is a combined *fenestra ovalis* and *foramen jugulare* and the small posterior foramen is a single opening for XII (see

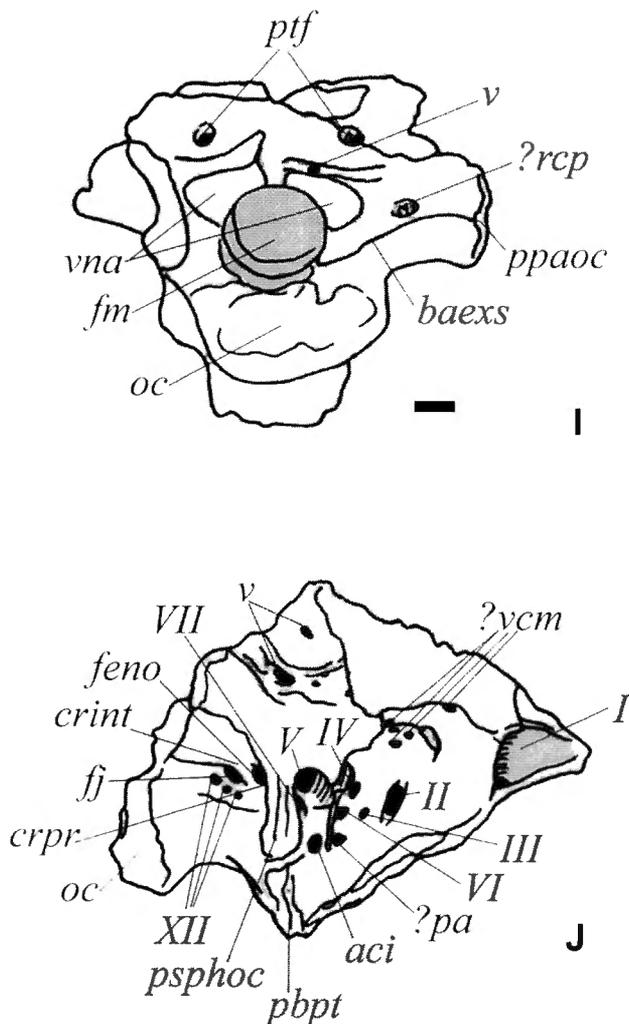


Fig. 2 — *Amtosaurus archibaldi*, n. sp., ZIN PH 1/16, holotype. Bissekty Formation (Upper Cretaceous), Dzharakuduk, Uzbekistan. Braincase in dorsal (A, F), ventral (B, G), anterior (C, H), posterior (D, I), and lateral (right) (E, J) views. Stereo pairs (A-E) and outline drawings (F-J). Abbreviations: aci - internal carotid artery, baexs - basioccipital-exoccipital suture, bf - basioccipital ventral fissure, crint - crista interfenestralis, crpr - crista prootica, feno - fenestra ovalis, fj - jugular foramen, fm - foramen magnum, oc - occipital condyle, pa - palatine artery, pbpt - basipterygoid process, ppaoc - paroccipital process, pr - parasphenoidal rostrum, psphoc - sphenooccipital process, ptf - posttemporal fenestra, rcp - rectus capitis posterior muscle attachment, v - vein, vna - contact area for first vertebra neural arch on exoccipital, vcm - vena cerebialis media, I-VII and IX-XII - cranial nerves. Scale bar equals 1 cm.

also TUMANOVA, 1987, p. 39). The *crista prootica* (Fig. 2E) is very short and weak, unlike the long crest in *Shanxia* (BARRETT *et al.*, 1998, fig. 6). The basioccipital and basisphenoid are meeting at the angle of about

90° (120° in *Amtosaurus magnus*, 150° in *Talarurus*; TUMANOVA, 1987, p. 39). The two bones are separated on the lateral side by a robust ridge, bearing the unossified surfaces of the basal tuber and, more ventral, the basipterygoid process. These processes are separated by a groove for *A. carotis cerebialis*, which entered the braincase through the opening (internal carotid foramen) just anterior to this groove (Fig. 2E). In *Nodocephalosaurus* the internal carotid foramen is distinctly larger and placed noticeably more anterior relative to the basioccipital-basisphenoid suture (SULLIVAN, 1999, figs. 3, 5A). Dorsal to the internal carotid foramen, there is a large depression bearing two openings, a large anterior for *N. trigeminus* (V) and a much smaller posterior one for *N. facialis* (VII). A similar common depression for the foramina for the passage of nerves V²⁻³ and VII is present in *Saichania* (MARYAŃSKA, 1977, fig. 7). In *Pawpawsaurus* (LEE, 1996, fig. 10) and cf. *Polacanthus* (NORMAN & FAIERS, 1996, fig. 2) openings for V and VII are not placed in the common depression and more widely separated. In ZIN PH 1/16 the short bony canal for V is subdivided laterally by short ventral and dorsal ridges into two parts, indicating separation of *N. trigeminus* into an anterior *ramus ophthalmicus* (V¹), directed anterolaterally, and a posterior *ramus maxillaris et mandibularis* (V²⁻³), directed laterally. A distinct groove going ventrally from the opening for VII apparently was for the *ramus palatinus* of VII.

The basipterygoid process (which is ossified on the left side; Fig. 2B, E) is massive and short. Apparently, the basisphenoid-pterygoid contact was still potentially mobile, as in a young specimen of *Pinacosaurus* (MARYAŃSKA, 1977, p. 111). Anterior to the foramen for the internal carotid artery, there is a large opening, possibly for the palatine artery (compare with MARYAŃSKA, 1977, fig. 7 and NORMAN & FAIERS, 1996, figs. 1, 2). According to KURZANOV & TUMANOVA (1978, figs. 1b, 1g) this foramen is for the pituitary vein. Dorsal to that there are three foramina for the passage of cranial nerves III, IV, and VI (Fig. 2E). The topography of the exits for these nerves is essentially as in *Saichania* (MARYAŃSKA, 1977, fig. 7) and similar to that in cf. *Polacanthus* (NORMAN & FAIERS, 1996, fig. 2). Possibly in cf. *Polacanthus* the opening designated for III is actually for VI (thought by NORMAN & FAIERS to be passing through the common foramen with the palatine artery), and opening for III, which should be rather small, is not preserved on that specimen; this would increase the similarity between cf. *Polacanthus* and ZIN PH 1/16. In ZIN PH 1/16 the complex of openings III, IV, and VI is situated just posteriorly to a depression, bearing a large foramen for the exit of II and separated from this depression by a prominent ridge. In contrast, in *Saichania*, the foramina for these nerves are placed posteroventrally to the exit for *N. opticus* (II) (MARYAŃSKA, 1977, fig. 7). Well dorsal to the foramen for *N. trochlearis* (IV), there are several small foramina, at least some of them possibly served for the *vena cerebialis media* (see NORMAN & FAIERS, 1996, fig. 2). The parasphenoid is completely fused with the basisphenoid. The parasphenoid rostrum is broken off (Fig. 2B). It

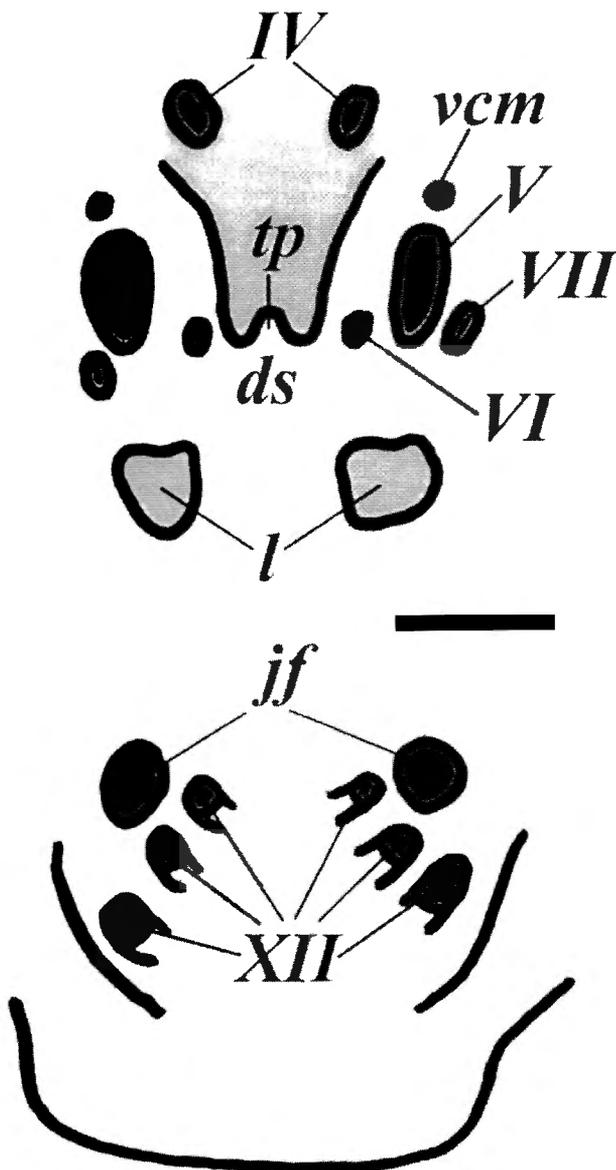


Fig. 3 — *Amtosaurus archibaldi*, n. sp., ZIN PH 1/16, holotype. Bissekty Fm. (Upper Cretaceous), Dzharakuduk, Uzbekistan. Sketch view of the ventral floor of the cranial cavity (dorsal surface of basioccipital and basisphenoid). Abbreviations: ds - dorsum sellae, fj - jugular foramen, l - lagena, tp - triangular projection, vcm - vena cerebialis media, IV, V, VI, VII, and XII - cranial nerves. Scale bar equals 1 cm.

terminates 20 mm before the posterior margin of the basisphenoid. The foramina for *N. olfactorius* (I) are very large (Fig. 2B, C). The endocranial cavity is highest at the middle part. Its ventral floor is flat and smooth, somewhat rises dorsally at the pituitary fossa, as in *Amtosaurus magnus* (TUMANOVA, 1987, p. 39) and cf. *Polacanthus* (NORMAN & FAIERS, 1996, fig. 3). The anterior wall of the dorsum sellae is inclined forward, forming an acute angle with the posterior (dorsal) wall. The dorsum sellae forms a short triangular anterior projection along the midline,

overhanging the pituitary fossa (Fig. 3). This structure is exactly the same as in *Amtosaurus magnus* (KURZANOV & TUMANOVA, 1987, fig. 2), but is absent in *Talarurus* (KURZANOV & TUMANOVA, 1987, fig. 1) and *Maleevus* (TUMANOVA, 1987, fig. 10) from the same formation. The lateral wings of the dorsum sellae are directed anterolaterally. At the posteromedial end, they bear the foramen for *N. abducens* (VI) (Fig. 3). The similarly broad and high dorsum sellae is also found in *Saichania* (MARYAŃSKA, 1977, p. 111) and *Maleevus* (TUMANOVA, 1987, fig. 10). In *Pinacosaurus* (MARYAŃSKA, 1977, pl. 20, fig. 3) and *Tarchia*, the dorsum sellae is low and narrow and the foramen for VI is situated on the lateral wall of the pituitary fossa (MARYAŃSKA, 1977, p. 111). The canal for the passage of VI is anterolaterally directed. Dorsal to the opening for VI, there is a large foramen for *N. trigeminus* (V), and, just posterior to it, there is a short fissure for *N. facialis* (VII). There is no visible basis trabeculi basalis, as described in *Talarurus* and *Amtosaurus magnus* (KURZANOV & TUMANOVA, 1987, figs. 1, 2) and in *Maleevus* (TUMANOVA, 1987, fig. 10). Anterior to the sella turcica, there is a large transverse groove for *N. opticus* (II; optic chiasma). The inner ear is open on the lateral wall of the brain cavity, but details cannot be elucidated without further dissection of the specimen. The large lagena is situated just ventromedially to the fenestra ovalis.

COMPARISONS

The braincase ZIN PH 1/16 is referable to the Ankylosauria by the presence of the following derived characters (MARYAŃSKA, 1977; TUMANOVA, 1981, 1987; COOMBS & MARYAŃSKA, 1990; SERENO, 1999):

- 1) bones of the skull roof fused together and to the braincase;
- 2) ventral wall of basioccipital facing ventrally rather than posteriorly;
- 3) basipterygoid processes short and closely approaching sphenoccipital processes;
- 4) internal carotid artery passing dorsal to basipterygoid process.

The articular surface of the occipital condyle is crescent-shaped rather than hemispherical; the condyle lacks a neck and is directed posteroventrally rather than ventrally, which suggest ankylosaurid rather than nodosaurid affinities of this material. The topology of the openings for cranial nerves and vessels in ZIN PH 1/16 corresponds exactly to an endocranial cast of the North American ankylosaurid *Euoplocephalus* described by COOMBS (1978b). In nodosaurids the structure of the jugular foramen is more primitive. In *Silvisaurus* a separate jugular foramen is absent and cranial nerves IX-XI have separate exits from the braincase (EATON, 1960, fig. 5; IX is mislabeled as "XI"; CARPENTER & KIRKLAND, 1998, fig. 14). In *Pawpawsaurus* there are two closely adjoined foramina, a smaller posterior for *vena jugularis posterior* and a larger anterior for IX-XI (LEE, 1996, fig. 10). Furthermore, in *Silvisaurus* the exits for V and VII are placed noticeably more anteriorly, between the exits for

IV and VI (EATON, 1960, fig. 5). In *Pawpawsaurus* distribution of these openings is nearer the condition of ZIN PH 1/16 and other ankylosaurids. The single foramen for the jugular vein and IX, X, and XI, as well as a relatively posterior position of the openings for V and VII in cf. *Polacanthus* (NORMAN & FAIERS, 1996), advocates for attribution of Polacanthinae to Ankylosauridae rather than to Nodosauridae, as was recently suggested by KIRKLAND (1998). Another similarity between cf. *Polacanthus* and ankylosaurids such as *Amtosaurus*, is a very large opening for the olfactory nerve (NORMAN & FAIERS, 1996, p. 304). In the nodosaurid *Pawpawsaurus* the canal for the olfactory nerve is narrow (LEE, 1996, p. 239). This possibly was correlated with a relatively simple respiratory passage in nodosaurids compared with the more complicated respiratory system with numerous sinuses in ankylosaurids (COOMBS, 1978a, figs. 5, 6).

The Bissekty ankylosaur differs from *Tianschisaurus*, *Shamosaurus*, *Maleevus*, *Pinacosaurus*, and *Nodocephalosaurus* in the possession of an occipital condyle with a crescent-shaped articular surface, from *Shamosaurus*, *Talarurus*, *Maleevus* and *Saichania* in the posteroventral orientation of the occipital condyle, from *Talarurus*, *Pinacosaurus*, and *Tarchia* in the greater horizontal diameter of the *foramen magnum*, from *Pinacosaurus*, *Saichania*, and *Tarchia* in the presence of more than one foramen for the passage of *N. hypoglossus* (XII), from *Pinacosaurus* and *Tarchia* by the *dorsum sellae* being pierced by *N. abducens* (VI), from *Saichania* by a single endocranial exit for V, from *Shanxia* by the occipital condyle lacking a neck and the *crista interfenestralis* and *crista prootica* being much smaller. The Bissekty ankylosaur is most similar to *Amtosaurus magnus* in sharing four distinctive characters listed in both the original diagnosis (KURZANOV & TUMANOVA, 1978, p. 92) and the revised diagnosis (TUMANOVA, 1987, p. 17) for the latter taxon:

1. there are two longitudinal, sloping ridges on the ventral surface of basioccipital, symmetrically placed relative to the longitudinal median depression on the basioccipital, and extending from the occipital condyle toward the sphenoccipital processes;
2. the *dorsum sellae* has a triangular anterior projection toward the *sella turcica*;
3. the *fenestra ovalis* is placed somewhat dorsally to the level of *foramen jugulare*;
4. the endocranial openings are relatively large.

The first character is found also in *Tsagantegia*; all other known Asian ankylosaurs have a different structure of the ventral surface of the basioccipital. The second and third characters are not found in any other Asian ankylosaur; we considered them as autapomorphies of *Amtosaurus* and thus refer the Bissekty ankylosaurid to that genus. The fourth character is of uncertain phylogenetic significance. The attribution of *Amtosaurus magnus* to Ankylosauria was questioned by COOMBS & MARYAŃSKA (1990), who considered it as a possible hadrosaurid, and this unfounded inference was widely cited in literature, especially in more popular papers. The discovery of ZIN

PH 1/16, which is more complete than the *A. magnus* holotype, confirms the attribution of *Amtosaurus* to the Ankylosauria.

All the characters distinguishing *A. archibaldi* n. sp. from the type species, *A. magnus* can be considered as plesiomorphies. This is not surprising in view of a somewhat greater stratigraphic age of the Bissekty Fm. relative to that of the upper part of the Bainshire Fm. The holotypes of both species also differ in size, ZIN PH 1/16 being approximately 1.4 times smaller in comparable dimensions, but this may merely reflect the individual age of the latter.

DISCUSSION

Morphology: Derived nodosaurids and ankylosaurids independently acquired an occipital condyle composed entirely of the basioccipital (SERENO, 1999). An exoccipital contribution to the occipital condyle among Ankylosauridae is present in the Middle Jurassic *Tianschisaurus* (DONG, 1993, p. 260), possibly in the Early Cretaceous *Shamosaurus* (TUMANOVA, 1986), and in the Late Cretaceous *Pinacosaurus* (MARYAŃSKA, 1977, p. 109). In *Amtosaurus archibaldi* n. sp., there is a posterior projection of the exoccipital toward the occipital condyle along the margin of the *foramen magnum*. In this respect, *A. archibaldi* n. sp. is intermediate between primitive and more derived Ankylosauridae.

The Asian ankylosaurids show a morphological sequence in the reduction of number of the exits for *N. hypoglossus* (XII) from three (*A. archibaldi* n. sp.) to two (*Talarurus*, *A. magnus*) and finally to a single small foramen (*Pinacosaurus*, *Saichania*, *Tarchia*). The North American *Euoplocephalus* had three distinct branches of XII on an endocast (COOMBS, 1978b, fig. 1) and three exits for this nerve on the braincase (LEE, 1996, p. 238). *A. archibaldi* n. sp. is primitive in this respect relative to known Asian taxa, but possibly not to North American ankylosaurids (Ankylosaurinae). In polacanthine ankylosaurids (cf. *Polacanthus*, *Gastonia*) were two openings for XII (NORMAN & FAIERS, 1996, fig. 2; KIRKLAND, 1998, fig. 2). This may suggest, that the single opening for XII in *Silvisaurus* (EATON, 1960, fig. 5) and *Pawpawsaurus* (LEE, 1996, fig. 10), if correctly interpreted, was possibly independently acquired. In *Struthiosaurus*, judging from the endocasts (PEREDA-SUBERBIOLA & GALTON, 1994, fig. 5), there were one or two openings for XII.

A similar morphological trend shows transformation of the *fenestra ovalis* and jugular foramen, from two separate openings (ZIN PH 1/16, *Amtosaurus magnus*, *Shanxia*, *Pinacosaurus*) to partially joined foramina subdivided by a ventral ridge (*Talarurus*), and to a single opening (*Gastonia*, *Tsagantegia*, *Saichania*, and *Tarchia*). This sequence is also stratigraphic, except *Pinacosaurus* from the Djadokhta Fm., which is more primitive in this respect than *Talarurus* from the older Bainshire Fm. (see below).

The structure of the braincase is well known in Asian ankylosaurids (KURZANOV & TUMANOVA, 1978; TUMANOVA, 1987; BARRETT *et al.*, 1998) but virtually unknown to

date for North American ankylosaurids (not described for *Gargoylesaurus*, *Gastonia*, *Euoplocephalus*, and *Ankylosaurus*; not adequately preserved in *Nodocephalosaurus*). The braincase described here is one of the best specimens known to date for the Ankylosauria.

Phylogeny: The first Asian records of ankylosaurs were referred to Nodosauridae (WIMAN, 1929; GILMORE, 1933; YOUNG, 1935; RIABININ, 1939). They are referable to Ankylosauridae, as was demonstrated by MARYAŃSKA (1971, 1977) and COOMBS (1978) on the basis of new material from Mongolia. The oldest Asian ankylosaur, the Middle Jurassic *Tianschisaurus*, is only known from an incomplete specimen (DONG, 1993) resembling nodosaurids in the possession of a hemispherical, ventrally oriented occipital condyle. Similarly, the Early Cretaceous *Shamosaurus* shares with nodosaurids some plesiomorphic traits (e.g., rostrum narrow anteriorly, occipital condyle oriented ventrally), but also both groups have some highly specialized characters in common, such as the fusion of the pterygoid-basisphenoid contact and of the contact between the quadrate and paroccipital process. Both these characters are also present in *Saichania*, and the latter character is found in *Tsagantegia* (TUMANOVA, 1987, 1993). The fusion of the quadrate to the paroccipital process has also been reported for the Late Jurassic *Gargoylesaurus parkpini* from North America, which is considered an ankylosaurid (CARPENTER *et al.*, 1998; SERENO, 1999). This character may be plesiomorphic for Ankylosauria. The systematic position of *Shamosaurus* is uncertain, mostly because some of its important morphological details (e.g., structure of the nasal passage, arrangement of osteoderms on skull roof) have not yet been adequately described. Currently *Shamosaurus* is considered an ankylosaurid (TUMANOVA, 1987; KIRKLAND, 1998; SULLIVAN, 1999).

TUMANOVA (1983) proposed Shamosaurinae to incorporate *Shamosaurus* and *Saichania*, mostly based on the characters mentioned above. Later she considered the Shamosaurinae as monotypic; on her phylogenetic scheme, this group is paraphyletic (TUMANOVA, 1987, fig. 14). SULLIVAN (1999) considered *Shamosaurus*, *Talarurus*, and *Tsagantegia* as primitive ankylosaurids forming unresolved polytomy to the more derived "crown-group" ankylosaurids. The analysis by KIRKLAND (1998, fig. 3) placed *Shamosaurus* outside the clade Polacanthinae + Ankylosaurinae.

The phylogenetic schemes for Ankylosauria presented by MARYAŃSKA (1977, fig. 12) and TUMANOVA (1987, fig. 14) are basically similar, but differ in two main features:

- 1) *Saichania* is derived from *Pinacosaurus* by MARYAŃSKA and from *Shamosaurus* (not known before 1983) by TUMANOVA, and
- 2) the North American *Euoplocephalus* and *Ankylosaurus* are derived from *Talarurus* by MARYAŃSKA and from *Pinacosaurus* by TUMANOVA.

If *Euoplocephalus* had three exits for *N. hypoglossus* (XII), as suggested by its endocranial cast (COOMBS, 1978b), it (and its presumed descendant *Ankylosaurus*)

more likely originated from an ankylosaurid of the evolutionary level represented by *Amtosaurus archibaldi* n. sp., having three separate exits for the nerve XII. These taxa cannot be derived from *Pinacosaurus* or any Barun Goyot or Nemegt ankylosaurid, all of which have a single exit for XII (contra KIRKLAND, 1998, fig. 3). It is not clear, whether *Euoplocephalus* and *Ankylosaurus* were derived from the North American Early Cretaceous shamosaurine and polacanthine ankylosaurids, recently discovered (CARPENTER & KIRKLAND, 1998; KIRKLAND, 1998), or from an Asian immigrant. If the latter is correct, this migration event may have taken place in Late Santonian - Early Campanian times. This interval was the warmest period in the high latitudes for the whole Cretaceous (e.g. WOLFE & UPCHURCH, 1987; ZAKHAROV *et al.*, 1999), increasing interchange between western North American and Asian vertebrate faunas, making it possible for thermophilous animals to pass through the Bering bridge. However, the recent discovery of the Late Campanian North American *Nodocephalosaurus*, which forms a distinct clade with *Saichania* and *Tarchia* (SULLIVAN, 1999), may suggest another wave of intercontinental migration, occurring in Late Campanian times.

The Late Cretaceous (Early Campanian) *Pinacosaurus* is one of the most archaic taxa among known Asian ankylosaurids. It displays some of the primitive characters found in nodosaurids (occipital condyle formed by the basioccipital and exoccipital, articular surface of occipital condyle hemispherical); this is possibly the reason for its original reference to the Nodosauridae (GILMORE, 1933). From the later Barun Goyot and Nemegt ankylosaurids, *Pinacosaurus* differs by separated *fenestra ovalis* and jugular foramen, which allies it with the Bainshire and Bissekty taxa. On the whole, the Djadokhta vertebrate assemblage is characterized by presence of some very archaic taxa that are not known from the older Bainshire assemblage, such as bainguid lizards and protosuchian crocodyliforms (JERZYKIEWICZ & RUSSELL, 1991). Possibly during relatively cool Bainshire times, these archaic taxa persisted in a refugium in southern Asia. During Late Santonian to Early Campanian times, considerable warming led to their distribution extending far to the north, encompassing Central Asia. This idea is in line with the suggested early Campanian age for the Djadokhta fauna (AVERIANOV, 1997).

Biostratigraphic significance: NESSOV (1995, 1997) correlated the Bissekty vertebrate fauna with the vertebrate assemblages from the upper part of Bainshire Fm. in Mongolia and Iren Dabasu Fm. in northern China and considered these formations of Turonian-Coniacian age. There are six genera of terrestrial vertebrates common to all these faunas: the turtles *Adocoides*, *Trionyx*, and *Lindholmimys*, the crocodyliform *Shamosuchus*, the tyrannosaurid *Alectrosaurus*, and the ornithomimid *Archaeornithomimus* (CURRIE & EBERTH, 1993; NESSOV, 1995, 1997; SUKHANOV, 2000). *Alectrosaurus*, *Archaeornithomimus*, *Adocoides* and *Lindholmimys* in Mongolia are not known from the younger Djadokhta, Barun Goyot and Nemegt faunas (JERZYKIEWICZ & RUSSELL, 1991). In

Middle Asia, *Adocoides* and *Lindholmemys* are also known from the Santonian deposits of Kazakhstan and Tajikistan (NESSOV, 1997). Other vertebrates might be of biostratigraphic importance at the species level, but turtles appear to be the most promising in this respect (NESSOV, 1997; DANILOV, 1999; SUKHANOV, 2000; DANILOV & SUKHANOV, 2001). There are other taxa shared by the Bissekty and Iren Dabasu faunas, but not recorded from the upper Bainshire fauna: the turtle *Khunnuchelys* and the ornithomimid dinosaurs *Bactrosaurus* and *Gilmoreosaurus* (BRINKMAN *et al.*, 1994; NESSOV, 1995). However, from the upper part of Bainshire Fm. at Baynshin Tsav, skeletal remains of a “hadrosaurine” and a “lambeosaurine” have been reported (NORMAN & KURZANOV, 1997), which increases the similarity between these three faunal assemblages. In the present paper, another common element between the Bissekty and upper Bainshire faunas, the ankylosaurid *Amtosaurus* is reported. On the other hand, the Iren Dabasu and upper Bainshire faunas share the ankylosaurid *Talarurus* (CURRIE & EBERTH, 1993, tab. 1). Both these ankylosaurid taxa are not known outside these three stratigraphic units and may have a reasonable biostratigraphic value.

CURRIE & EBERTH (1993, p. 140) suggested that the age of the Iren Dabasu fauna may be in fact “as young as Campanian”, and this view has been widely cited in the literature. However, this opinion is based only on two theropod genera, *Saurornithoides* and *Avimimus*, which were said to occur in the Iren Dabasu and later assemblages (Djadokhta and Barun Goyot), but were not found in any Bainshire locality. The skeletal remains of theropod dinosaurs from the Iren Dabasu Fm., upon which the opinion by CURRIE and EBERTH is based, have not yet been described, and the attribution of the material to these genera remains to be supported. It appears that the identification of *Saurornithoides* in the Iren Dabasu fauna is based on isolated metatarsals (CURRIE & EBERTH, 1993, tab.1). CURRIE (2000, p. 443) stated that “... many iso-

lated avimimid bones have been collected for more than 70 years from the Irendabasu Fm. ... and in 1975 at Baishin Tsav.” This material remains mostly undescribed. KURZANOV (1987, p. 68, fig. 36) figured a theropod femur from Iren Nor (Iren Dabasu), collected by the Sino-Soviet paleontological expeditions, which he referred to as an “avimimid”. It differs in a number of details from the femur of the holotype of *Avimimus portentosus* KURZANOV, 1981 (KURZANOV, 1987, fig. 19) and apparently is not referable to this species, which is known from the Barun Goyot Fm. RYAN *et al.* (2001, p. 95A) referred to the Iren Dabasu avimimid as *Avimimus portentosus* in the title of their abstract, but in the text they stated that it is only “congeneric” with the Djadokhta species. This challenges the view of CURRIE & EBERTH (1993) concerning the possibly Campanian age of the Iren Dabasu fauna. The evidence at hand indicates that the Bissekty Fm. of the central Kyzylkum Desert is roughly equivalent in age to the Iren Dabasu Fm. of Inner Mongolia and to the upper part of the Bainshire Fm. in the eastern Gobi Desert. The age of the Bissekty Fm. is now estimated as late Turonian - Coniacian or as late Turonian (ARCHIBALD *et al.*, 1999). A similar age estimate is likely for the Iren Dabasu Fm. The upper part of the Bainshire Fm. may be somewhat younger, Turonian – Santonian (see also HICKS *et al.*, 1999). The more primitive nature of *Amtosaurus archibaldi* n. sp. from the Bissekty Fm. compared to *A. magnus* from the upper Bainshire Fm. supports this assessment.

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References

- ARCHIBALD, D., SUES, H.-D., AVERIANOV, A., DANILOV, I., REZVYI, A., WARD, D., KING, C. & MORRIS, N., 1999. New paleontologic, biostratigraphic, and sedimentologic results at Dzharakuduk (U. Cret.), Kyzylkum Desert, Uzbekistan. *Journal of Vertebrate Paleontology*, **19** (suppl. to 3): 29A-30A.
- AVERIANOV, A.O., 1997. New Late Cretaceous mammals of southern Kazakhstan. *Acta Palaeontologica Polonica*, **42**: 243-256.
- BARRETT, P.M., YOU, H., UPCHURCH, P. & BURTON, A.C., 1998. A new ankylosaurian dinosaur (Ornithischia: Ankylosauria) from the Upper Cretaceous of Shanxi Province, People's Republic of China. *Journal of Vertebrate Paleontology*, **18**: 376-384.
- BRINKMAN, D.B., NESSOV, L.A. & PENG, J., 1994. *Khunnuchelys* gen. nov., a new trionychid (Testudines: Trionychidae) from the Late Cretaceous of Inner Mongolia and Uzbekistan. *Canadian Journal of Earth Sciences*, **30**: 2214-2223.
- BROWN, B., 1908. The Ankylosauridae, a new family of armoured dinosaurs from the Upper Cretaceous. *Bulletin of the American Museum of Natural History*, **24**: 187-201.
- BUNZEL, F., 1871. Die Reptilfauna der Gosau-Formation in der Neuen Welt bei Wiener-Neustadt. *Abhandlungen der k. u. k. geologischen Reichsanstalt Wien*, **5**: 1-18.
- CARPENTER, K. & KIRKLAND, J.I., 1998. Review of Lower and Middle Cretaceous ankylosaurs from North America. In: LUCAS, S.G., KIRKLAND, J.I. & ESTEP, J.W. (Editors), Lower and Middle Cretaceous Terrestrial Ecosystems. *New Mexico Museum of Natural History and Science Bulletin*, **14**: 249-270.
- CARPENTER, K., KIRKLAND, J.I., BURGE, D. & BIRD, J., 1999. Ankylosaurs (Dinosauria: Ornithischia) of the Cedar Mountain Formation, Utah, and their stratigraphic distribution. In: GILLETTE, D. (ed.), Vertebrate Paleontology in Utah. *Utah Geological Survey Miscellaneous Publications*, **99-1**: 243-251.

- CARPENTER, K., MILES, C. & CLOWARD, K., 1998. Skull of a Jurassic ankylosaur (Dinosauria). *Nature*, **393**: 782-783.
- COOMBS, W.P., Jr., 1978a. The families of the ornithischian dinosaur order Ankylosauria. *Palaeontology*, **21**: 143-170.
- COOMBS, W.P., Jr., 1978b. An endocranial cast of *Euoplocephalus* (Reptilia, Ornithischia). *Palaeontographica*, **A161**: 176-182.
- COOMBS, W.P., Jr. & MARYAŃSKA, T., 1990. Ankylosauria. In WEISHAMPEL, D.B., DODSON, P. & OSMÓLSKA, H. (Editors), *The Dinosauria*. University of California Press, Berkeley, pp. 456-483.
- CURRIE, P.J. 2000. Theropods from the Cretaceous of Mongolia. In: BENTON, M.J., SHISHKIN, M.A., UNWIN, D.M. & KUROCHKIN, E.N. (Editors), *The Age of Dinosaurs in Russia and Mongolia*. Cambridge University Press, Cambridge, pp. 434-455.
- CURRIE, P.J. & EBERTH, D.A., 1993. Palaeontology, sedimentology and palaeoecology of the Iren Dabasu Formation (Upper Cretaceous), Inner Mongolia, People's Republic of China. *Cretaceous Research*, **14**: 127-144.
- DANILOV, I.G., 1999. The ecological types of turtles in the Late Cretaceous of Asia. *Proceedings of the Zoological Institute RAS*, **281**: 107-112.
- DANILOV, I.G. & SUKHANOV, V.B., 2001. New data on lindholmemydid turtle *Lindholmemyx* from the Late Cretaceous of Mongolia. *Acta Palaeontologica Polonica*, **46**: 125-131.
- DONG, Z., 1993. An ankylosaur (ornithischian dinosaur) from the Middle Jurassic of the Junggar Basin, China. *Vertebrata Palasiatica*, **31**: 257-266.
- EATON, T.H., 1960. A new armoured dinosaur from the Cretaceous of Kansas. *Paleontological Contributions, University of Kansas*, **8**: 1-24.
- GILMORE, C.W. 1933. Two new dinosaurian reptiles from Mongolia with notes on some fragmentary specimens. *American Museum Novitates*, **679**: 1-20.
- GODEFROIT, P., PEREDA SUBERBIOLA, X., LI, H. & DONG, Z., 1999. A new species of the ankylosaurid dinosaur *Pinacosaurus* from the Late Cretaceous of Inner Mongolia (P.R. China). *Bulletin de l'Institut royal des Sciences naturelles de Belgique, Sciences de la Terre*, **69** – Suppl. B: 17-36.
- HICKS, J.F., BRINKMAN, D.L., NICHOLS, D.J. & WATABE, M., 1999. Paleomagnetic and palynologic analyses of Albian to Santonian strata at Bayn Shireh, Burkhan, and Khuren Dukh, eastern Gobi Desert, Mongolia. *Cretaceous Research*, **20**: 829-850.
- JERZYKIEWICZ, T. & RUSSELL, D.A., 1991. Late Mesozoic stratigraphy and vertebrates of the Gobi Basin. *Cretaceous Research*, **12**: 345-377.
- KIRKLAND, J. I., 1998. A polacanthine ankylosaur (Ornithischia: Dinosauria) from the Early Cretaceous (Barremian) of eastern Utah. In: LUCAS, S.G., KIRKLAND, J.I. & ESTEP, J.W. (Editors), *Lower and Middle Cretaceous Terrestrial Ecosystems. New Mexico Museum of Natural History and Science Bulletin*, **14**: 271-281.
- KURZANOV, S. M., 1981. [On unusual theropods from the Upper Cretaceous of the MPR.] *Trudy Sovmestnoi Sovetsko-Mongol'skoi Paleontologicheskoi Ekspeditsii*, **15**: 39-50 (In Russian).
- KURZANOV, S. M., 1987. [Avimimididae and the problem of the origin of birds.] *Trudy Sovmestnoi Sovetsko-Mongol'skoi Paleontologicheskoi Ekspeditsii*, **31**: 1-92 (In Russian).
- KURZANOV, S. M. & TUMANOVA, T. A., 1978. [On the structure of endocranium in some ankylosaurs of Mongolia.] *Paleontologicheskii Zhurnal*, **1978** - 3: 90-96 (In Russian).
- LEE, Y.-N., 1996. A new nodosaurid ankylosaur (Dinosauria: Ornithischia) from the Paw Paw Formation (late Albian) of Texas. *Journal of Vertebrate Paleontology*, **16**: 232-245.
- MAKOVICKY, P. 1997. Postcranial axial skeleton, comparative anatomy. In: CURRIE, P.J. & PADIAN, K. (Editors), *Encyclopedia of Dinosaurs*. Academic Press, San-Diego, London, etc., pp. 579-590.
- MALEEV, E. A., 1952a. [A new family of armoured dinosaurs from the Upper Cretaceous of Mongolia.] *Doklady Akademii Nauk SSSR*, **87**: 131-134 (In Russian).
- MALEEV, E. A., 1952b. [A new ankylosaur from the Upper Cretaceous of Mongolia.] *Doklady Akademii Nauk SSSR*, **87**: 273-276 (In Russian).
- MALEEV, E. A., 1956. [Armoured dinosaurs of the Upper Cretaceous of Mongolia.] *Trudy Paleontologicheskogo instituta AN SSSR*, **62**: 51-91 (In Russian).
- MARKEVICH, V.S., BOLOTSKY, Y.L. & BUGDAEVA, Y.V., 1994. [Kundur locality of dinosaurs in Amur River region.] *Tikhookeanskaya geologiya*, **6**: 96-107 (In Russian).
- MARYAŃSKA, T., 1971. New data on the skull of *Pinacosaurus grangeri* (Ankylosauria). *Palaeontologia Polonica*, **25**: 45-53.
- MARYAŃSKA, T., 1977. Ankylosauridae (Dinosauria) from Mongolia. *Palaeontologia Polonica*, **37**: 85-151.
- MOLNAR, R.E., 1996. Preliminary report on a new ankylosaur from the Early Cretaceous of Queensland, Australia. *Memoirs of the Queensland Museum*, **39**: 653-668.
- NESSOV, L.A., 1995. [Dinosaurs of Northern Eurasia: New Data about Assemblages, Ecology and Paleobiogeography.] *Izdatelstvo Sankt-Peterburgskogo universiteta*, St. Petersburg, 156 pp. (In Russian).
- NESSOV, L.A., 1997. [Cretaceous Nonmarine Vertebrates of Northern Eurasia.] *Izdatelstvo Sankt-Peterburgskogo universiteta*, St. Petersburg, 218 pp. (In Russian).
- NORMAN, D.B., & FAIERS, T., 1996. On the first partial skull of an ankylosaurian dinosaur from the Lower Cretaceous of the Isle of Wight, southern England. *Geological Magazine*, **133**: 299-310.
- NORMAN, D.B. & KURZANOV, S.M., 1997. On Asian ornithopods (Dinosauria: Ornithischia). 2. *Arstanosaurus akkurganensis* Shilin and Suslov, 1982. *Proceedings of the Geologists' Association*, **108**: 191-199.
- OSBORN, H.F., 1923. Two Lower Cretaceous dinosaurs from Mongolia. *American Museum Novitates*, **95**: 1-10.
- PANG Q., & CHENG, Z., 1998. [A new ankylosaur of Late Cretaceous from Tian-zhen, Shanxi.] *Progress in Natural Sciences*, **8(3)**: 326-334 (In Chinese).
- PEREDA-SUBERBIOLA, J., & GALTON, P. M., 1994. A revision of the cranial features of the dinosaur *Struthiosaurus austriacus* Bunzel (Ornithischia: Ankylosauria) from the Late Cretaceous of Europe. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, **191**: 173-200.
- RIABININ, A. N., 1939. [The Upper Cretaceous vertebrate fauna of South Kazakhstan. I. Reptilia. Part. 1. Ornithischia.] *Trudy Tsentral'nogo nauchno-issledovatel'skogo geologo-razvedchnogo Instituta*, **118**: 3-39 (In Russian).
- ROMER, A.S., 1997. *Osteology of the Reptiles*. Krieger Publishing Company, Malabar, Florida, xxvii+772 pp.
- RYAN, M. J., CURRIE, P. J. & RUSSELL, A.P., 2001. New material of *Avimimus portentosus* (Theropoda) from the Iren Dabasu

- Formation (Upper Cretaceous) of the Erenhot region of Inner Mongolia. *Journal of Vertebrate Paleontology*, **21** (suppl. to 3): 95 A.
- SEELEY, H.G., 1887. On the classification of the fossil animals commonly named Dinosauria. *Proceedings of the Royal Society of London*, **43**: 165-171.
- SERENO, P. C., 1999. The evolution of dinosaurs. *Science*, **284**: 2137-2147.
- SUKHANOV, V. B., 2000. Mesozoic turtles of Middle and Central Asia. In: BENTON, M.J., SHISHKIN, M. A., UNWIN, D. M. & KUROCHKIN, E. N. (Editors), *The Age of Dinosaurs in Russia and Mongolia*. Cambridge University Press, Cambridge, pp. 309-367.
- SULLIVAN, R.M., 1999. *Nodocephalosaurus kirtlandensis*, gen. et sp. nov., a new ankylosaurid dinosaur (Ornithischia: Ankylosauria) from the Upper Cretaceous Kirtland Formation (Upper Campanian), San Juan Basin, New Mexico. *Journal of Vertebrate Paleontology*, **19**: 126-139.
- SULLIVAN, R.M., 2000. Reply to Upchurch and Barrett. *Journal of Vertebrate Paleontology*, **20**: 218-219.
- TUMANOVA, T.A., 1977. [New data on the ankylosaur *Tarchia gigantea*.] *Paleontologicheskii Zhurnal*, **1977-4**: 92-100 (In Russian).
- TUMANOVA, T.A., 1981. [On the morphological peculiarity of ankylosaurs.] *Paleontologicheskii Zhurnal*, **1981-3**: 124-128 (In Russian).
- TUMANOVA, T.A., 1983. [A first ankylosaur from the Lower Cretaceous of Mongolia.] *Trudy Sovmestnoi Sovetsko-Mongol'skoi Paleontologicheskoi Ekspeditsii*, **24**: 110-118 (In Russian).
- TUMANOVA, T.A., 1986. Skull morphology of the ankylosaur *Shamosaurus scutatus* from the Lower Cretaceous of Mongolia. In: TAQUET, P. & SUDRE, C. (Editors), *Les Dinosauriens de la Chine à la France. Muséum d'Histoire Naturelle de Toulouse, France et Muséum d'Histoire Naturelle, Chongqing, PR China*, pp. 73-79.
- TUMANOVA, T.A., 1987. [The armoured dinosaurs of Mongolia.] *Trudy Sovmestnoi Sovetsko-Mongol'skoi Paleontologicheskoi Ekspeditsii*, **32**: 1-80 (In Russian).
- TUMANOVA, T.A., 1993. [On a new armoured dinosaur from southeastern Gobi.] *Paleontologicheskii Zhurnal*, **1993-2**: 92-98 (In Russian).
- TUMANOVA, T.A., 2000. Armoured dinosaurs from the Cretaceous of Mongolia. In: BENTON, M.J., SHISHKIN, M.A., UNWIN, D.M. & KUROCHKIN, E.N. (Editors), *The Age of Dinosaurs in Russia and Mongolia*. Cambridge University Press, Cambridge, pp. 517-532.
- UPCHURCH, P. & BARRETT, P.M., 2000. The taxonomic status of *Shanxia tianzhenensis* (Ornithischia, Ankylosauridae); a response to Sullivan (1999). *Journal of Vertebrate Paleontology*, **20**: 216-217.
- WIMAN, C., 1929. Die Kreide-Dinosaurier aus Schantung. *Palaeontologia Sinica*, **C, 6**: 1-67.
- WOLFE, J. A. & UPCHURCH, G. R. JR., 1987. North American nonmarine climates and vegetation during the Late Cretaceous. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **61**: 33-77.
- YOUNG, C. C., 1935. On a new nodosaurid from Ninghsia. *Palaeontologia Sinica*, **C, 11**: 1-34.
- ZAKHAROV, Y. D., BORISKINA, N. G., IGNATYEV, A. V., TANABE, K., SHIGETA, Y., POPOV, A. M., AFANASYEVA, T. B. & MAEDA, H., 1999. Palaeotemperature curve for the Late Cretaceous of the North Western Circum-Pacific. *Cretaceous Research*, **20**: 685-697.

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