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Armoured dinosaurs from the Cretaceous of Mongolia

TAT'YANA A. TUMANOVA

Introduction

Ankylosaurs, one of the main suborders of ornithischian dinosaurs, were distributed world-wide in the Mesozoic: their remains are found in Europe, Asia, North and South America, Australia and Antarctica (see Coombs and Maryańska (1990) for the most recent comprehensive review of the group). The earliest representatives of ankylosaurs are known from the Middle Jurassic (Galton, 1980; Dong, 1993), while the latest are Late Cretaceous (Maastrichtian) in age (e.g., Carpenter and Breithaupt, 1986). However, despite its wide distribution and representation by numerous fossil specimens, this group is still not well understood.

In the former USSR remains of ankylosaurs were found in two Lower Cretaceous sites, one in Yakutia (now the Republic Sakha) the other in Buryatia. They have also been recovered from various Upper Cretaceous horizons at 26 localities in Kazakhstan, Uzbekistan (Kyzylkum Desert) and Russia (Ryabinin,1939; Rozhdestvenskii, 1964; Nesov, 1995). These remains are represented by fragmentary material, usually disarticualated bones of the postcranial skeleton, armour, and, typically, teeth.

This article is devoted to the armoured dinosaurs of Mongolia, one of the most representative collections of ankylosaurs from Asia. The first discoveries of Mongolian ankylosaurs were made by the Central Asiatic Expedition of the American Museum of Natural History (1918–1930). Among large numbers of skeletons belonging to various dinosaurs from the highly fossiliferous locality of Bayan Zag, a skull and fragments of the postcranial skeleton of an ankylosaur were collected and later described by Gilmore (1933) as *Pinacosaurus grangeri*. Abundant remains of ankylosaurs were excavated by the Palaeontological Expedition of the USSR Academy of Sciences and described by Maleev (1952a, b, 1954, 1956). Subsequently, new and well preserved ankylosaurs were discovered in the Upper Cretaceous of Mongolia by the Polish–Mongolian Palaeontological Expedition in the years 1963–1971 (Maryańska, 1969; 1971; 1977). Rich collections, including numerous interesting specimens of Upper Cretaceous ankylosaurs and the first Lower Cretaceous representatives of the group were excavated by the Soviet–Mongolian Expedition (now Mongolian–Russian Paleontological Expedition) during the past 20 years (Tumanova, 1977; 1987; 1993; Kurzanov and Tumanova, 1978). Material collected by these two expeditions and described by Maryańska (1977) and Tumanova (1987) are the principal sources for the generic diagnoses of the Mongolian ankylosaurs presented in this chapter.

The currently accepted systematic arrangement of ankylosaurs was developed by Coombs (1971, 1978a), who proposed that ankylosaurs should be divided into two families: Nodosauridae and Ankylosauridae. So far, all ankylosaurs found in Mongolia have been assigned to the family Ankylosauridae.

The oldest mongolian ankylosaur, *Shamosaurus scutatus* (see Figures 26.1–26.3), is the only member of the Ankylosauridae known so far from the Early Cretaceous (Albian–Aptian) of Asia. The construction of the skull of *Shamosaurus* is typical for ankylosaurids, although it also exhibits some plesiomorphic features. For this reason, *Shamosaurus* was placed in a new subfamily, Shamosaurinae (Tumanova, 1987). Owing to errors in the choice of characters, the genus *Saichania* was also included in this subfamily, but this classification of ankylosaurs at the suprageneric level has not been supported by other specialists (e.g. Coomhs and Maryańska, 1990).

Upper Cretaceous ankylosaurs are common in all non-marine regional stratigraphic units. The oldest of these, the Bayanshiree Svita (Cenomanian–Turonian) contains remains of *Talarurus plicatospineus*, *Maleevus disparoserratus*, *Amtosaurus magnus* and possibly *Tsagantegia longicranialis* (see Figure 26.4). The succeeding unit, the Djadokhta Svita (?Late Santonian–Early Campanian), yielded *Pinacosaurus grangeri*, while the slightly younger Baruungoyot Svita (?Middle Campanian) produced *Saichania chulsanensis*. The youngest Mongolian ankylosaur, *Tarchia gigantea*, is known only from the Nemegt Svita (?Middle Campanian–Early Maastrichtian).

Repository abbreviations

AMNH, American Museum of Natural History, New York; GI SPS, Geological Institute, Section of Palaeontology and Stratigraphy, Mongolian Academy of Sciences, Ulaanbaatar; PIN, Palaeontological Institute, Russian Academy of Sciences, Moscow.

The anatomy of ankylosaurs

Ankylosaurs were usually large, reaching up to 7–8 m long, though some adults did not exceed 2.5 m in length. They were quadrupedal animals, heavily constructed, and with a broad body. Ankylosaur skulls are low, wide and rectangular in occipital view, with the long axis horizontal. The antorbital and supratemporal fenestrae are closed and the bones of the skull roof are covered by dermal plates which fuse with the underlying bones in adults, resulting in an even heavier, more massive skull. The special construction of the short neck, wherein the centra of the posterior cervical vertebrae have cranial and caudal faces of different height, enabled the huge weight of the heavy armoured head and dermal 'half-ring' to be supported.

Differences in the size of teeth of the two families (ankylosaurids have smaller teeth) and in the width of the muzzle led Carpenter (1982) to conclude that representatives of the two families employed different modes of feeding. Quite possibly, the nodosaurs, with their narrow muzzles, were more selective in their choice of vegetation, while the broad muzzled ankylosaurids were less so. A similar functional analogy can be found among African ungulates (Carpenter, 1982). In any case, an herbivorous mode of feeding for ankylosaurs seems to be clear, although their long, moveable tongue and some peculiarities in the mobility of the mandibles suggests the possibility that their diet also included insects and larvae (Nopcsa, 1928; Maryańska, 1977; Coombs and Maryańska, 1990).

The pectoral and pelvic girdles, like the limbs, were well adapted to redistributing the body weight. The scapula and coracoid were usually coossified, the ilium was widely expanded in the horizontal plane, and the acetabulum was imperforate. Indeed, the construction of the pelvic girdle is so consistent with quadrupedality that it is difficult to imagine transitional forms from a bipedal ancestor, though according to current models of the monophyletic origin of all ornithischians this must have been the condition of the ancestral form. The short massive limbs were situated beneath the body and moved mainly in a parasaggital plane. The forelimbs were shorter than the hind limbs resulting in a somewhat arch-like dorsal bend in the pelvic region. Coombs (1978b) concluded that ankylosaurs were mediportal, like the rhinoceros and hippopotamus, rather than graviportal like the elephant.

The armour of ankylosaurs consists of flat, keeled or spiked plates arranged in transverse and longitudinal rows. The plates, whose shape, size, height and symmetry vary in different parts of the armour, are surrounded by small, irregular, oval or tubercular ossicles. Distribution of the plates over the armour is also uneven. Usually, the keels of large plates are higher and sharper towards the flanks of the body and the direction of the plate tips differs in alternating longitudinal rows (Maryańska, 1977).

Unlike other thyreophorans, the armour elements of ankylosaurs did fuse to each other. The commonest constructions of the postcranial armour of ankylosaurs, and of Mongolian ankylosaurs in particular, are cervical and pectoral half-rings, each consisting of two bony layers. The deeper half-ring is constructed of fused plates, while the upper layer is formed from three pairs of sharply pointed large plates lying symmetrical to the mid-line. The arrangement of the armour elements follows the same general pattern for each ankylosaur family, but there are distinctive peculiarities in each species. For example, keeled plates with thick and dense walls occur in *Shamosaurus* (Figure 26.11A) and rib and groove ornamentation is found in *Talarurus*, while thin and strongly perforated spine walls are typcial of species of *Tarchia* (Figure 26.11B) and *Saichania*.

The peculiarly constructed tail of ankylosaurs, which could be used as a weapon of defence, is morphologically different in the representatives of both families. In Mongolian ankylosaurs, as in the group as a whole, the proximal part of the tail was flexible while the distal third consisted of a stiff rod formed from coossified posterior caudals in which long prezygapophyses and postzygapophyses overlapped each other up to the heavy, terminal tail club.

Systematic survey

Suborder Ankylosauria Osborn, 1923

Family Ankylosauridae Brown, 1908

Diagnosis (based on Coombs and Maryańska, 1990). Skull broad and triangular in dorsal view. Skull width more or less equal to length. Snout arches above the level of the postorbital skull roof. The caudal process of the premaxilla along the margin of the beak extends lateral to the most medial teeth. Paired sinuses in the premaxilla, maxilla, and nasal. The external nares are divided by a premaxillary septum with a ventral or lateral opening leading into a maxillary sinus. No ridge separating the premaxillary palate from the lateral maxillary shelf. The complex secondary palate twists the respiratory passage into a vertical S-shaped bend. The postorbital shelf, composed of postorbital and jugal bones, extends farther medially and ventrally than in nodosaurids. The lateral supraorbital margin above the orbit is flat. The near-horizontal epipterygoid contacts the pterygoid and prootic. Dorsal surface of the skull roof covered by a large number of small scutes. Scute pattern poorly defined in the supraorbital region. Prominent, wedge-shaped caudolaterally projecting quadratojugal dermal plate. Large, wedge-shaped, caudolaterally projecting squamosal dermal plate. The infratemporal fenestra, paroccipital process and quadratojugal are hidden in lateral view by the united quadratojugal and squamosal dermal plates. There is a sharp lateral rim and low dorsal prominence for each lateral supraorbital element. Coronoid process lower and more rounded than in nodosaurids. Small teeth. Distal caudal vertebrae with centra partially or completely fused and with elongate prezygapophyses that are broad dorsoventrally and elongate postzygapophyses that are united to form a single dorsoventrally flattened, tongue-like process. Haemal arches of distal caudals elongate, with zygapophysis-like overlapping processes and elongate bases that contact to form a fully enclosed haemal canal. Fused sternal plates. Coracoid small relative to scapula. Scapular spine located on extreme anterior edge of scapular blade (see Figure 26.2). Acromion projects laterally and does not project above the dorsal margin of the scapular blade. Postacetabular process of ilium short. Ischium near vertical below acetabulum. Pubis reduced to nubbin and fused to other pelvic elements. Deltopectoral crest and transverse axis through distal humeral condyles in same plane. Fourth trochanter on distal half of femur. Terminal tail club consisting of large pair of lateral plates and two smaller plates. Ossified tendons surround distal caudal vertebrae. Keeled armour plates usually have deep internal hollow (Figure 26.11A).

Shamosaurus Tumanova, 1983

Type species. Shamosaurus scutatus Tumanova, 1983.
Holotype. PIN N 3779/2, complete skull and jaw; Khamaryn Us, Övörkhangai, Dornogov' Aimag; Hühteeg Svita, Lower Cretaceous (Aptian–Albian).
Referred material. In addition to the holotype a partial skull from the holotype locality (Tumanova, 1987) and

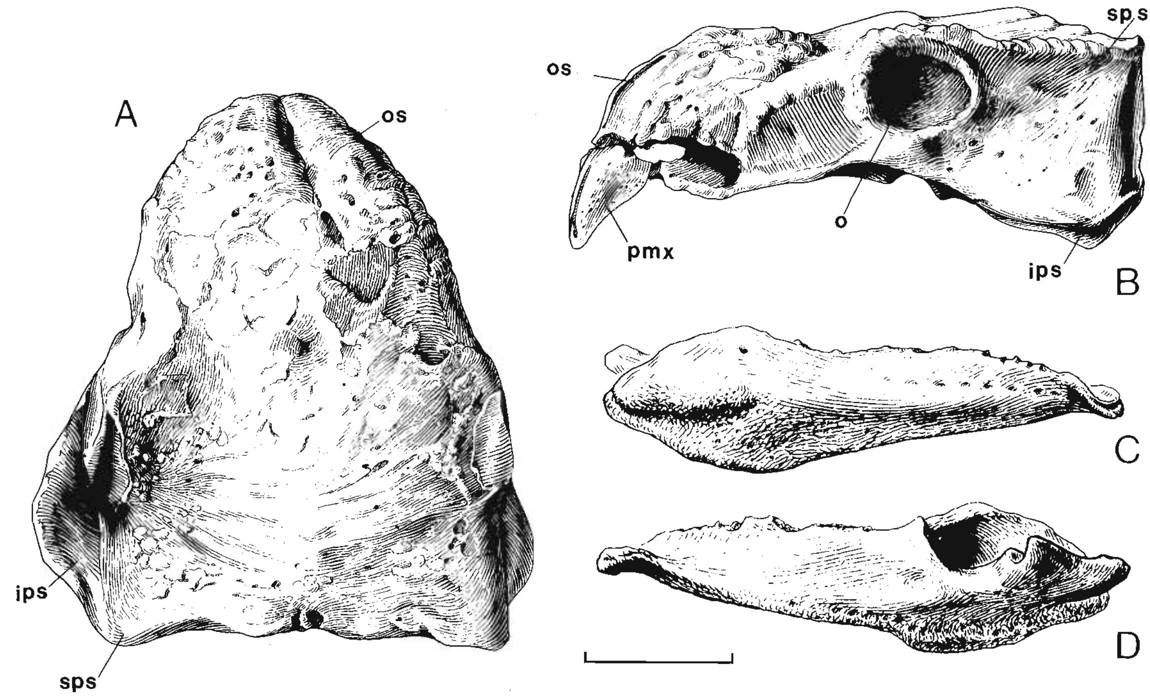

Figure 26.1. *Shamosaurus scutatus*, Tumanova, 1983. PIN 3779/2–1, holotype skull in (A) dorsal and (B) lateral view. Mandible in (C) right lateral and (D) internal view. After Tumanova, 1987, p. 24, fig. 4, p. 42, fig. 12. Abbreviations: ips, quadratojugal (lower postorbital) dermal plate; o, orbit; os, dermal plate; pmx, premaxilla; sps, squamosal (upper postorbital) dermal plate. Scale bar = 100 mm.

an undescribed mandible from Höövör are also referred to this taxon.

Description. The length of the body reaches about 7 m. The skull is up to 360 mm in length and 370 mm width. The dorsal surface of the of the skull was completely covered by osteodermal plates (Figure 26.1) bearing a sculpture pattern of small excrescences. Plates in the posterolateral corners of the skull do not develop into a scute and the quadratojugal and squamosal dermal plates do not hide the quadrate condylus. The anterior part of the snout is oval and narrow, and it is a little narrower than the distance between the posteriormost maxillary teeth. The posterior maxillary shelf is well developed and the ventral surfaces of the palatal bones are inclined laterally. The mandibular condyle of the quadrate is situated behind the posterior margin of the orbit. The occiput is inclined posteriorly and the occipital condyle is oriented ventrally. The quadrate bones and paroccipital process are coossified and the ventral surface of the basioccipital is round and narrow. The walls of armour elements are thick and dense.

Talarurus Maleev, 1952

Type species. Talarurus plicatospineus Maleev, 1952.

Holotype. PIN N 557/91, occipital section of cranium with part of the skull roof. Bayan Shiree, Eastern Gobi desert; Bayanshiree Svita, Upper Cretaceous (Cenomanian-Turanian).

Referred material. A skull roof with occipital section (Kurzanov and Tumanova, 1978) and fragmentary remains of the postcranial skeletons of a number of individuals have been found at the same locality (Maleev, 1952a, b).

Description. The body length of this ankylosaur reached about 4–5 m. The skull (Figure 26.5) is about 240 mm long, and approximately 220 mm wide.

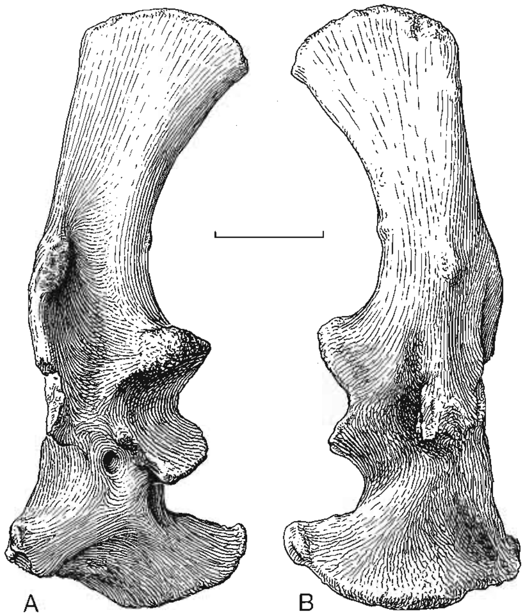

Figure 26.2. *Shamosaurus scutatus* Tumanova, 1983. PIN 3779/2–1, scapulocoracoid in (A) lateral and (B) medial view. Scale bar = 100 mm.

Pyramidal plates occur above and behind the orbits and the entire surface of the skull roof is covered by osteoderms ornamented with small tubercles (Figure 26.5A). The occipital surface is perpendicular to the skull roof and the paroccipital processes are directed a little posterolaterally. The occipital condyle is directed posteroventrally and there is no fusion of the quadrate bones and paroccipital processes. Anterior to the condyle the ventral surface of the basioccipital bears a medial eminence with depressions on both sides. The fundus of the brain cavity is level. The pectoral glenoid is deep and short and the humeral head is situated dorso-terminally. The manus is pentadactyl, the pes tetradactyl. Armour elements bear a 'furrow-rib' type of ornamentation and the tail-club is weakly developed.

Tsagantegia Tumanova, 1993

Type species. Tsagantegia longicranialis Tumanova, 1993.
Holotype (and only known specimen). GI SPS N 700/17, skull; Tsagaan Teeg, Southeastern Gobi; Bayanshiree Svita, Upper Cretaceous (Cenomanian–Turonian).
Description. Large ankylosaur with a body up to 6–7 m long and a skull (Figure 26.4) about 300 mm long and 250 mm wide. The skull roof is covered by numerous small osteoderms with a weakly expressed relief. The upper postorbital spines are not developed and osteoderms do not expand above the occiput. The orbits are situated posterior to the middle of the skull length. The osteodermal ring around the orbit is separated from the other osteoderms by a prominent furrow. The orbit size is slightly reduced due to the presence of the osteodermal ring. The premaxillary beak is trapezoid and the anterior and posterior maxillary shelves are weakly developed. The medial part of the anterior wall of the pterygoid is inclined posteriorly and the basisphenoid and pterygoid are fused. The occipital surface is perpendicular to the skull roof and the lower side of each paroccipital process is directed a little medially, while the distal ends are bent slightly ventrally. The prootic, opisthotic and exoccipital bones are united, but with prominent borders between them. The occipital condyle is wide-oval and directed posteroventrally. The quadrate and paroccipital process are coossified and the mandibular condyle of the quadrate is situated level with the posterior margin of the orbit, or further posteriorly. The ventral surface of the basioccipital bears a central depression, separated by gentle crests from the lateral depressions. The cingulum and lingulum of the maxillary teeth are separated by a vertical furrow.

Maleevus Tumanova, 1987

Type species. Maleevus disparoserratus (Maleev, 1952b)
Holotype. PIN N554/1, fragments of a right and left maxilla; Shireegiin Gashuun, Eastern Gobi Desert; Bayanshiree Svita, Upper Cretaceous (Cenomanian–Turonian).
Referred material. A fragment of a basicranium from the type locality (Figure 26.6).
Description. Anterior maxillary shelf weakly developed and originating from a point near the start of the tooth row. The maxillary teeth have a 'w'-shaped cingulum. The occipital condyle is almost hemispherical

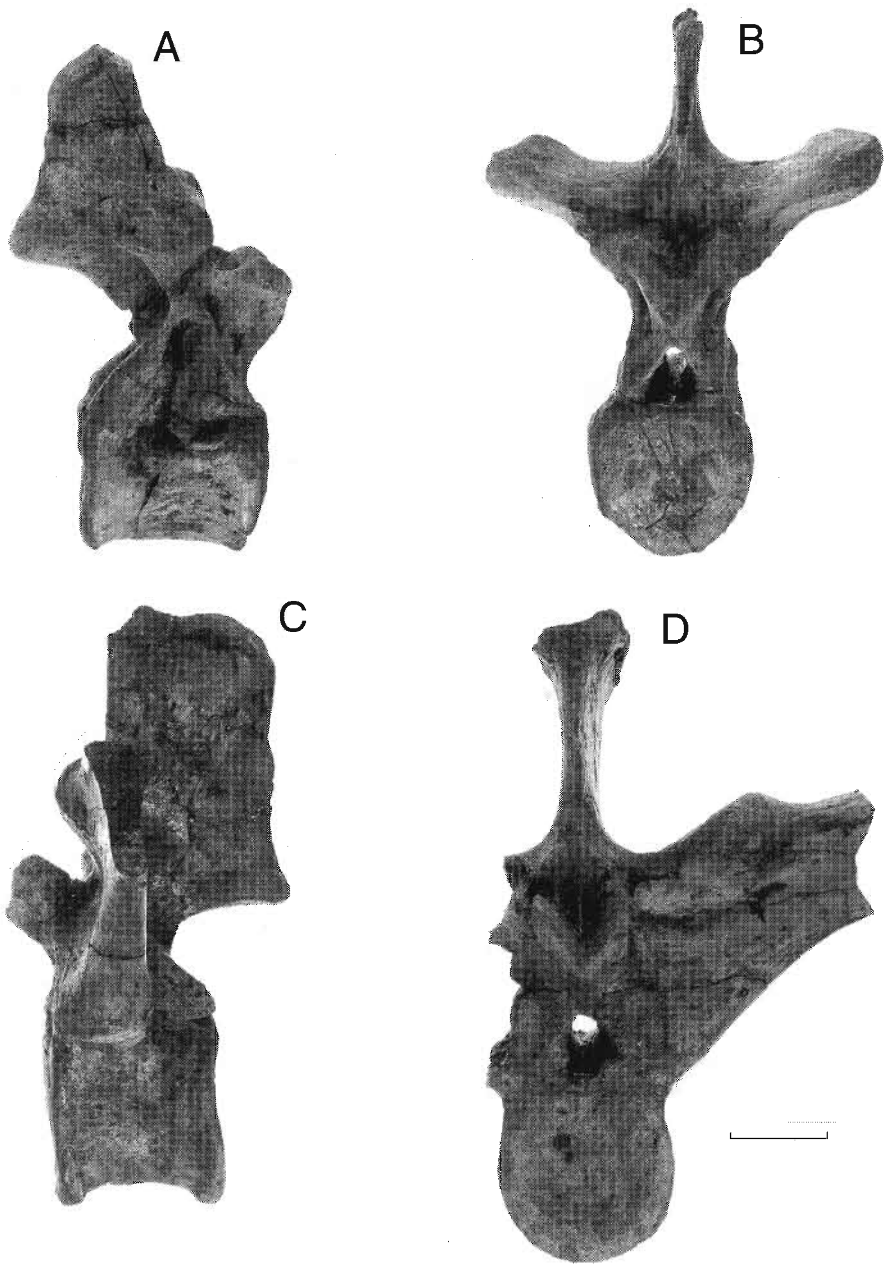

Figure 26.3. *Shamosaurus scutatus*, PIN 3779/2: A-B. Isolated dorsal vertebra in (A) lateral and (B) anterior view. Isolated dorsal vertebra with ankylosed rib in (C) lateral and (D) anterior views. Scale bar = 50 mm.

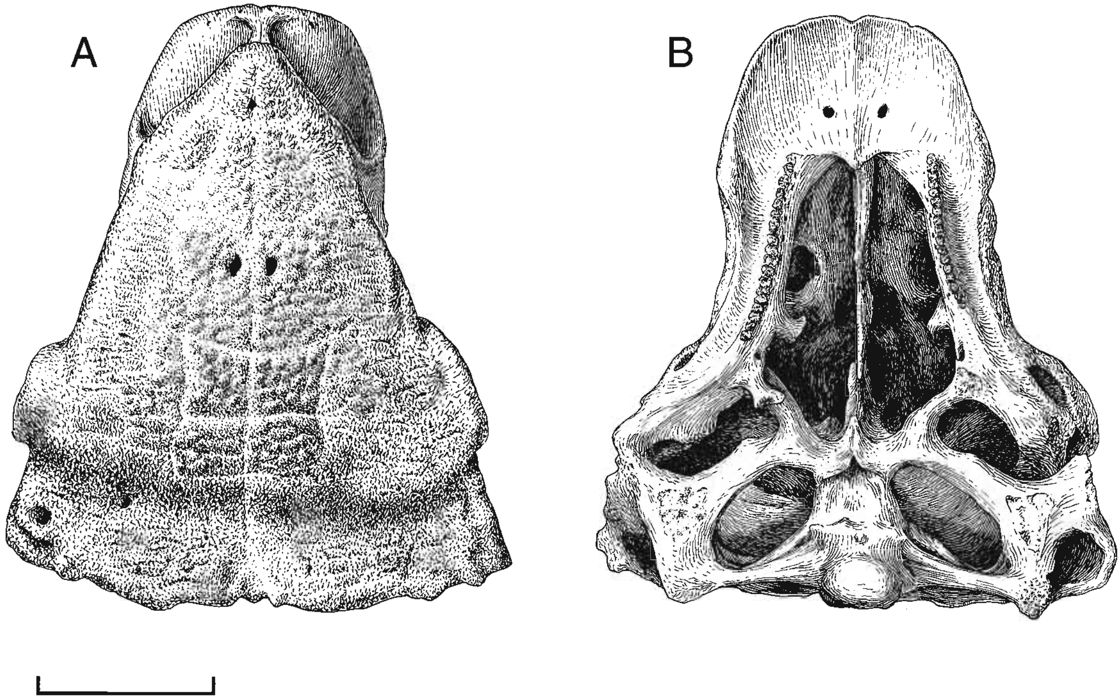

Figure 26.4. *Tsagantegia longicranialis* Tumanova, 1993. GI SPS 700/17, holotype skull in (A) dorsal and (B) palatal view. After Tumanova, 1993. Scale bar = 100 mm.

and ventrally directed. The ventral surface of the basicranium bears two weakly expressed longitudinal ridges which diverge anteriorly (Figure 26.6A). The medial depression upon the basicranium gradually transforms into a depression at the level of the sphenoccipital tubercles. The fundus of the brain cavity is almost level.

Comments. The holotype of this genus was first described by Maleev (1952a, b) under the name of *Syrmosaurus disparoserratus*. However, the type species of this genus, *Syrmosaurus viminicaudus*, proved to be a junior synonym of the genus *Pinacosaurus* and *S. disparoserratus* was assigned by Maryańska (1977) to the genus *Talarurus*. However, as the basicranium of *Syrmosaurus disparoserratus* is different from that of *Talarurus* and as the type material of *Talarurus* does not include the upper jaw, *S. disparoserratus* cannot be assigned to this genus and *Maleevus* was chosen as a replacement name.

Amtosaurus Kurzanov and Tumanova, 1978

Type species. Amtosaurus magnus Kurzanov and Tumanova, 1978.

Holotype (and only known specimen). PIN N 3780/2, brain case (Figure 26.7); Amtgai, Ömnögov', Gobi Desert; Bayanshiree Svita, Upper Cretaceous (Cenomanian–Turonian).

Description. This taxon is represented by a fragmentary basicranium. The occiput is high and the brain cavity is large. The occipital condyle is oval and directed posteroventrally. The ventral surface of the basioccipital bears two gentle longitudinal elevations situated symmetrically on either side of the medial depression (Figure 26.7A). The fundus of the brain cavity is slightly flexed anteriorly.

Pinacosaurus Gilmore, 1933

Type species. Pinacosaurus grangeri Gilmore, 1933.

Holotype. AMNH 6523, incomplete skull and maxilla,

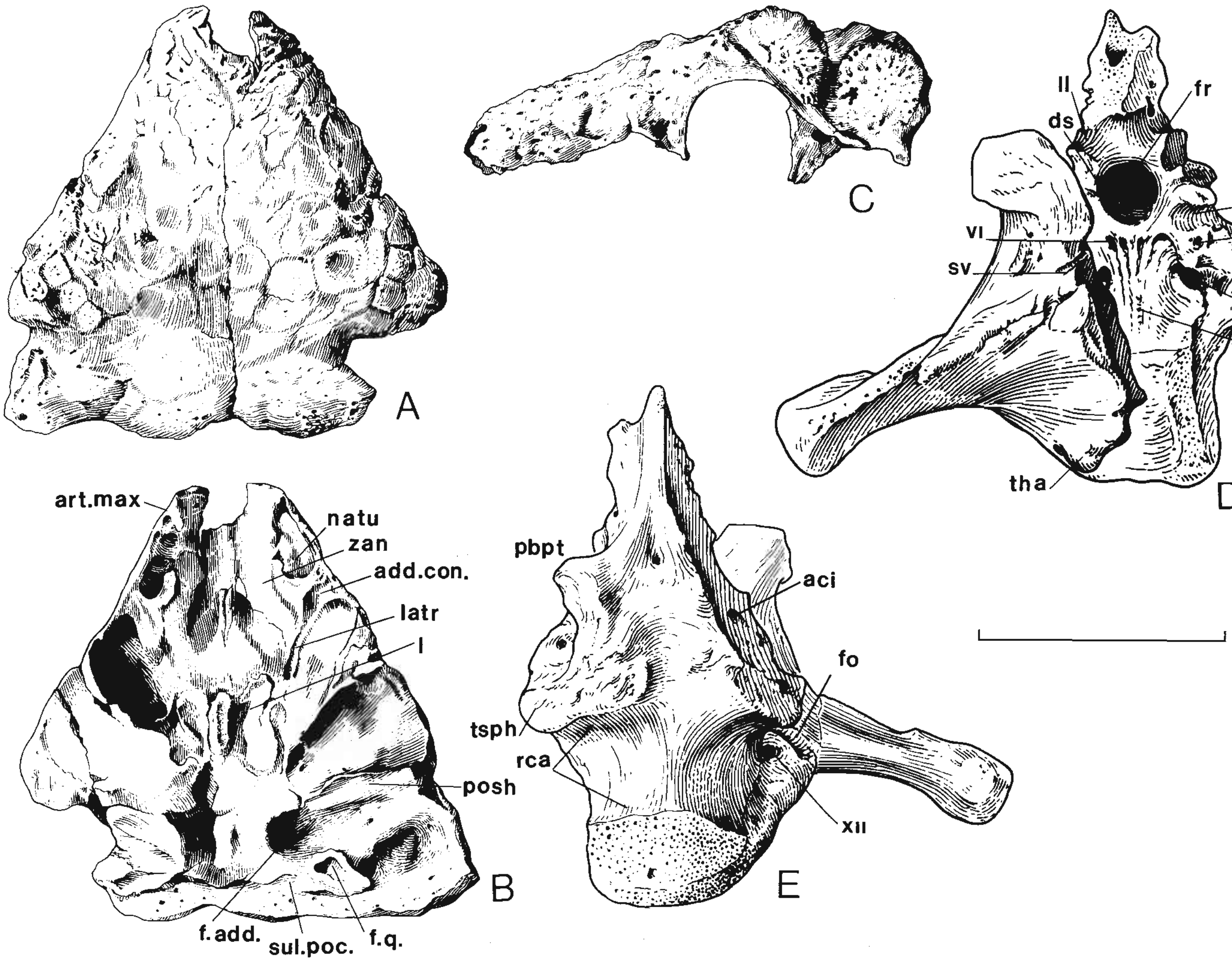

Figure 26.5. *Talarurus plicatospineus* Maleev, 1952. PIN 3780/1, partial skull roof in (A) dorsal, (B) palatal and (C) lateral view. Braincase in (D) dorsal and (E) ventral view. (After Tumanova, 1987, p. 27, fig. 5, p. 36, fig. 7.) Abbreviations: aci, arteria carotis interna; add. con, additus conchae; art. max, maxillary artery; btb, basis trabeculi basalis; ds, dorsum of the Turkish saddle; f. q., fossa for upper process of quadrate; fr, pituitary fossa; fo, fenestra ovalis; l, lagena; latr, lamina transversalis anterior; pbpt, basioccipital process; posh, postocular shelf; natu, nasoturbinals; rca, area for the origin of the M. rectus capiti anterior; sul. poc., sulcus for paroccipital process; sv, sulcus for vein; tha, tubera for neural arches of the first cervical vertebrae; tsph, sphenoccipital tubera; zan, zona annularis; I–XII, cranial nerves. Scale bar = 50 mm.

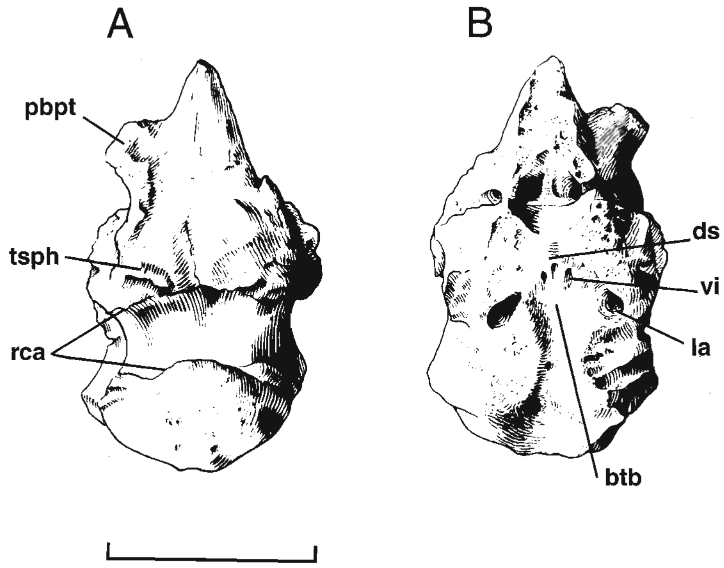

Figure 26.6. *Maleevus disparoserratus* (Maleev, 1952). PIN 554/2–1, partial braincase in (A) ventral and (B) dorsal view. After Tumanova, 1987, p. 39, fig. 10. For abbreviations see Figure 26.5. Scale bar = 50 mm.

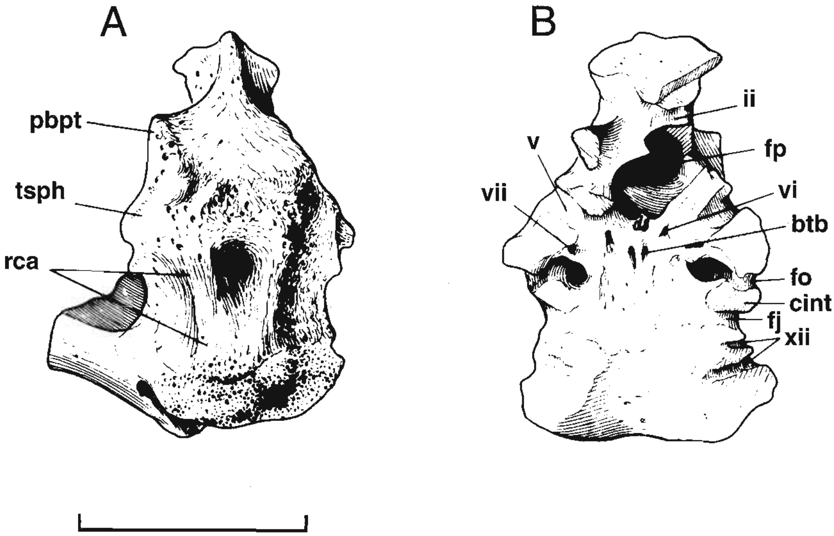

Figure 26.7. *Amtosaurus magnus* Kurzanov and Tumanova, 1978. PIN 3780/2, holotype braincase in (A) ventral and (B) dorsal view. After Tumanova, 1987, p. 38, fig. 9). Abbreviations as in Figure 26.5, and: cint, crista intervenestralis; fj, jugular foramen. Scale bar = 50 mm.

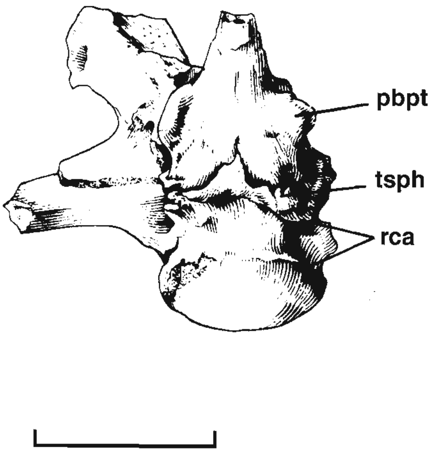

Figure 26.8. *Pinacosaurus grangeri* Gilmore, 1933. PIN 4043, braincase in ventral view. After Tumanova, 1987, p. 37, fig. 8. For abbreviations see Figure 26.5. Scale bar = 50 mm.

first cervical vertebra and some dermal scutes; Bayan Zag, Gobi Desert; Djadokhta Formation, Upper Cretaceous (?Late Santonian–Early Campanian).

Referred material. A well preserved skull and almost complete postcranial skeleton of a young individual, another complete postcranial skeleton (Maleev, 1952a, 1954) and fragmentary remains of postcrania and armour (Maryańska, 1971, 1977) all from the type locality; a basicranium from Baga Tariach (Kurzanov and Tumanova, 1978); an undescribed skull in a concretion from Shilt Uul; and undescribed fragmentary remains of a few individuals from Alag Teeg.

Description. A medium sized ankylosaurid with a body length of about 5 m and a skull 300 mm long and 340 mm wide. The nostrils are divided by a horizontal septum and in a superbly preserved skull there is a third pair of openings that lead into the premaxillary sinus. Ascending processes of the premaxillary bones divide the nostrils, penetrating between the nasal bones and are not covered by osteoderms. Plates above the orbits develop into a longitudinal supraorbital spine consisting of two pyramidal plates and the posterolateral corners of the skull are marked by upper and lower postorbital spines. Osteoderms do not overhang the medial part of the occiput, thus the occipital condyle is visible in dorsal view. The premaxillary beak is quadrato-spherical in shape and broader than the width of the skull between the posteriormost maxillary teeth. Both anterior and posterior maxillary shelves are weakly developed, the palatal bones are elevated, and the medial part of the anterior wall of the pterygoid is inclined anteriorly. The occipital condyle is wide-oval and directed posteroventrally. The contact between the quadrate and the paroccipital process remained unossified. The quadrate bones are slightly inclined anteriorly and the mandibular condyle of the quadrate is located at the level of the posterior margin of the orbit. The ventral surface of the basisphenoid does not exhibit any marked relief (Figure 26.8). The postcranial skeleton (Figure 26.9) is relatively light, the limb

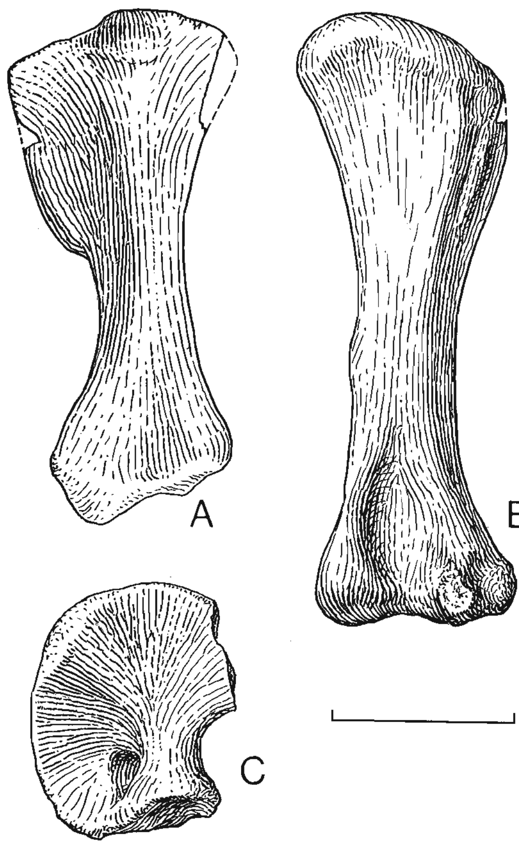

Figure 26.9. *Pinacosaurus grangeri* Gilmore, 1933. PIN 3144. Left humerus (A) in dorsal view. Right femur (B) and coracoid (C) in posterior view. Scale bar = 50 mm.

bones are slender, the manus is pentadactyl and the pes tetradactyl.

Saichania Maryańska, 1977

Type species. Saichania chulsanensis Maryańska, 1977.
Holotype. GI SPS 101/151, skull with mandibles and the anterior part of the postcranial skeleton and armour in natural articulation; Khulsan, Gobi Desert; Baruungoyot Svita, Upper Cretaceous (?Middle Campanian).
Referred material. Fragments of a skull roof and armour from the type locality (Maryańska,1977) and an undescribed skull, mandibles and almost complete postcranial skeleton from Hermiin Tsav.
Description. Large ankylosaur with a body length up to 7 m, and a skull about 450 mm long and 480 mm wide. The skull roof exhibits prominent osteodermal plates and spinous postorbital osteoderms. The nostrils are large, terminally situated, and divided by a horizontal septum. A dorsal opening leads to a respiratory canal and a ventral one to a ventromedial canal which enters the premaxillary sinus. The premaxillary beak has a round-oval shape and is almost as broad as the distance between the posteriormost maxillary teeth. The palatine has strongly developed anterior and posterior maxillary shelves. The medial part of the anterior wall of the pterygoid is inclined anteriorly. The plane of the occiput is perpendicular to the skull roof and the paroccipital processes are low and perpendicular to the skull roof in their upper part, while their lower portion is deflected anteriorly. The occipital condyle is oval, weakly convex and directed ventrally. The quadrate and paroccipital process are coossified. The mandibular cotylus of the quadrate is located at the level of the middle part of the orbit. The anterior and posterior walls of the orbit are heavily ossified. The ventral surface of the basioccipital has no marked relief. The premaxillary bones are partially overlapped by osteoderms growing downward from the nasal bone. Strongly developed secondary plate-like intercostal ossifications occur along the lateroventral side of the trunk. The postcranial skeleton is extremely massive with strong ossification of the sternal complex. The manus is pentadactyl and the tail-club is large.

Tarchia Maryańska, 1977

Type species. Tarchia gigantea (Maleev, 1956).
Holotype. PIN 551/29, a series of caudal vertebrae, metacarpals and phalanges, and fragments of armour plates; Nemegt, Gobi Desert; Nemegt Svita, Upper Cretaceous (?Middle Campanian–Early Maastrichtian).
Referred material. Fragmentary remains of distal parts of tails and fragments of armour from the Nemegt Basin (Maryańska, 1977), an incomplete skull with skull roof, occiput and brain case from Khulsan (Maryańska, 1977) and a well preserved skull (Tumanova, 1977; 1987) with incomplete postcranium.
Description. This is the largest, but stratigraphically, the youngest Mongolian ankylosaur. The body length reached 8 m and the skull (Figure 26.10) was up to 400 mm long and 450 mm wide. The premaxillary part of the snout forms a rounded oval, and is as broad as the distance between the posteriormost maxillary teeth. The anterior and posterior maxillary shelves are well developed. The plane of the palatine bones is horizontally elevated and the anterior wall of each pterygoid is inclined forward. The occiput is inclined slightly posteriorly and the occipital condyle is brachy-oval with a slightly protruding joint surface that is directed posteroventrally. The paroccipital process is high, short, perpendicular to the plane of the skull roof and does not fuse to the quadrate. The mandibular condylus of the quadrate lies at the level of the posterior margin of the orbit. The ventral part of the basioccipital has no marked relief. The height of the foramen magnum exceeds its width, the brain cavity is very high and the openings for the cranial nerves are of large size. The pes is tetradactyl and the tail-club is large.
Comments. The type species of the genus *Tarchia, T. kielanae,* was established on the basis of an incomplete skull with skull roof, occiput and brain case (Maryańska, 1977). However, more comprehensive material has shown that *Dyoplosaurus giganteus* (Maleev, 1956) and *T. kielanae* belong to the same species: *Tarchia gigantea* (Maleev, 1956) (see Tumanova, 1977, 1987; Coombs and Maryańska, 1990).

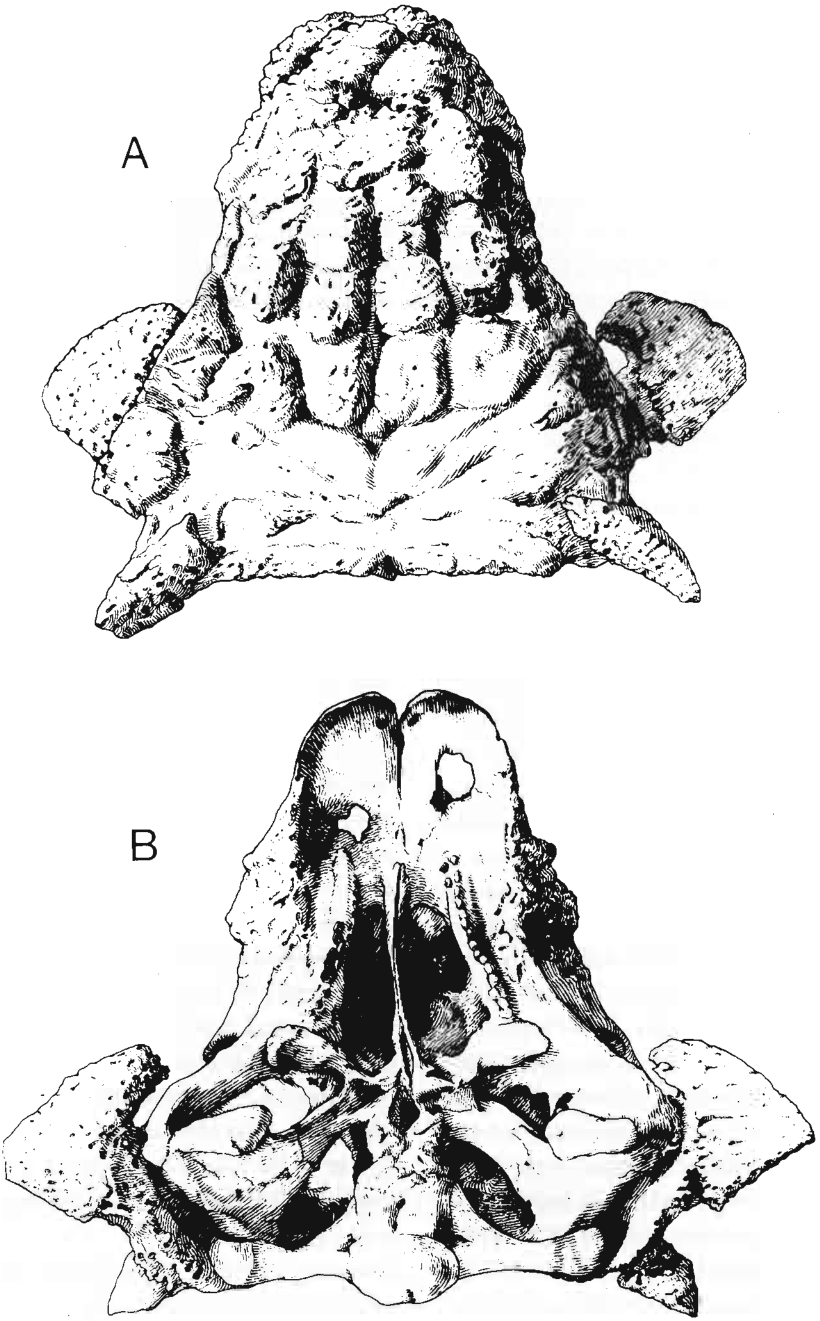

Figure 26.10. *Tarchia gigantea* (Maleev, 1956), PIN 3142/250. Skull in (A) dorsal, (B) palatal and (C) lateral view. Left mandible in (D) external and (E) internal view. Mandible in (F) dorsal view. After Tumanova, 1987, p. 19–21, fig. 3, p. 41, fig. 11. For abbreviations see Figure 26.5, and: art, articular; c, coronoid; f. meck., Meckelian foramen; f. sang, foramen supraangulare; os meck, Meckel's cartilage; pr, retroarticular process; sa, surangular. Scale bar = 100 mm.

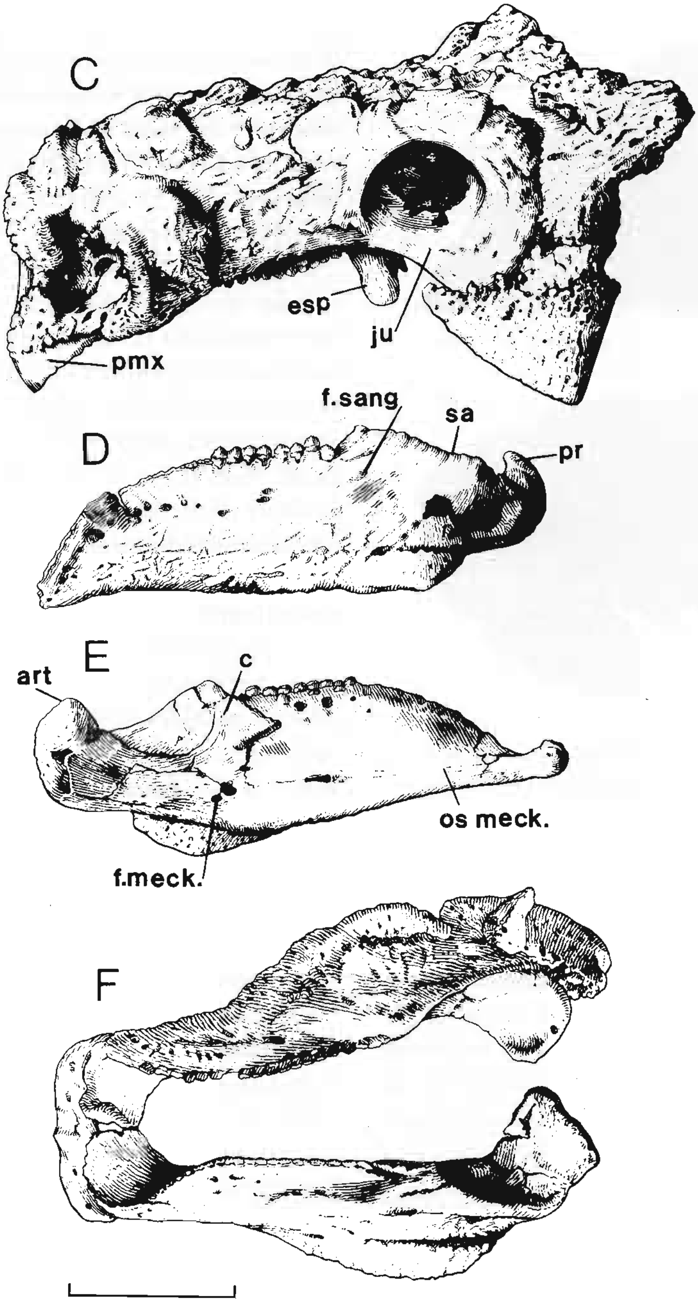

Figure 26.10. (*cont.*)

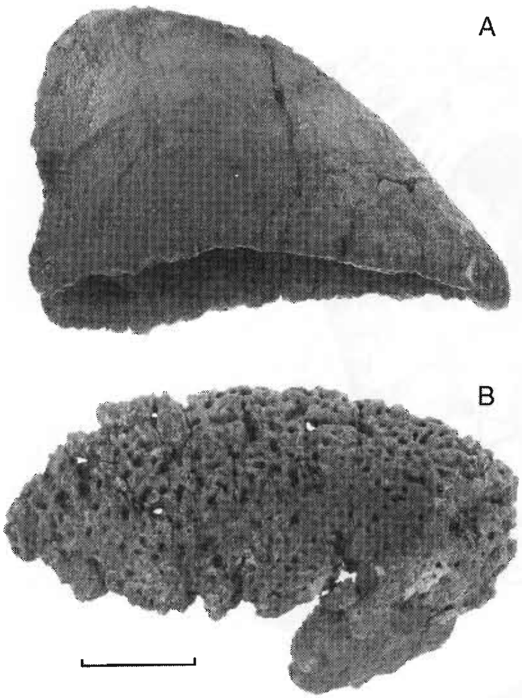

Figure 26.11. Different types of dermal scute surface: (A) *Shamosaurus scutatus* Tumanova, 1983, PIN 3779/2–1, holotype. (B) *Tarchia giantea* (Maleev, 1956), PIN 3142/250. Scale bar = 50 mm.

Discussion

At present, the fossil material of Mongolian ankylosaurs is the most representative for this group in Asia. Ankylosaur remains from the territory of the former Soviet Union (FSU) are fragmentary, scattered and because of the nature of their preservation: mainly teeth, armour and poorly preserved postcranial elements, they cannot be identified to the generic level.

The oldest ankylosaur so far known from Mongolia is *Shamosaurus* from the late Lower Cretaceous (Aptian–Albian). In the Upper Cretaceous assemblages from most of the regional stratigraphic subdivisions usually contain ankylosaurs. Thus they are known from the Cenomanian–Turonian (*Talarurus*, *Amtosaurus*, *Maleevus*) up to the Maastrichtian (*Tarchia*).

The recent discovery of the ankylosaur *Tianchiasaurus nedegoapeferima* (Dong, 1993) in the Middle Jurassic of China has greatly expanded the known time range of ankylosaurs from Asia. Surprisingly, however, although *T. nedegoapeferima* exhibits primitive features of the mandibles and postcranial skeleton, it has a small, flat, tail club that is characteristic for ankylosaurids. Thus all ankylosaurs from Asia seem to belong to the Ankylosauridae.

Besides the Asiatic genera, the Ankylosauridae includes two North American forms: *Euoplocephalus* and *Ankylosaurus*. *Euoplocephalus* is represented by numerous specimens and has the following characters: the external nares face rostrally and are divided by a vertical septum and the width of the beak is equal to or greater than the distance between the caudalmost maxillary teeth. *Ankylosaurus*, the youngest and largest ankylosaurid is distinguished by a strong expansion of the dermal armour in the nasal region that restricts the external nares to small circular openings.

Interrelationships within the Ankylosauridae remain unclear. However, by taking into account the older age of *Shamosaurus*, one can suggest the following general evolutionary transformation in the lineage *Shamosaurus–Ankylosaurus*:

1. quadratojugal and squamosal dermal plates become more horn-like. They are weakly expressed in *Talarurus* (Figure 26.5A, C), *Shamosaurus* (Figure 26.1 A, B), and in *Tsagantegia* (Figure 26.4 A), but are well developed and moderately pointed in *Tarchia* (Figure 26.10 A, C) and *Euoplocephalus*, and take the form of horns in *Ankylosaurus* and *Saichania*;
2. development of the quadratojugal plate tends to hide the mandibular condyle of the quadrate in lateral view;
3. widening of the premaxillary beak;
4. the plane of the orbits rotates forwards while the orbits shift posteriorly;
5. the tooth rows shorten;
6. there is some increase in skull kinetism because of the weakening of the basipterygoid joint: in *Shamosaurus* the pterygoids and basisphenoid were fused, but all isolated basicrania of *Talarurus*, *Maleevus* and *Amtosaurus* exhibit articular surfaces for the contact with the pterygoids.

Some morphological features of *Shamosaurus*, for example, fusion of the quadrate with the paroccipital process can be observed in later ankylosaurs such as *Tsagantegia* and *Saichania*. Often, however, the nature of this contact is rather different: the upper process of the quadrate reaches the skull roof anterior to the paroccipital process and contacts the latter to various degrees: close in *Talarurus*, and, probably, with ligaments in *Tarchia*.

Some features in the morphology of *Shamosaurus* can be considered as intermediate between Ankylosauridae and Nodosauridae. These include: a narrow premaxillary beak; immohile basipterygoidal contact; a quadrate condyle partially visible in lateral view; and a round, vertically oriented occipital condyle. These features suggest that these families are monophyletic and this is strongly supported by the discovery of Jurassic ankylosaurs in North America (Kirkland and Carpenter, 1994; Carpenter *et al.*, 1996). Study of the new Jurassic ankylosaurs may help to clarify phylogenetic relationships, both within families and at the family level.

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