

A new species of the ankylosaurid dinosaur *Pinacosaurus* from the Late Cretaceous of Inner Mongolia (P.R. China)

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Abstract

A well-preserved articulated skeleton of an ankylosaurian dinosaur from the Late Cretaceous of Bayan Mandahu (Inner Mongolia) is described. The specimen consists of the skull, lower jaws and a great part of the postcranial skeleton, including the cervical armour and tail-club in place. This material is referred to the ankylosaurid genus *Pinacosaurus* GILMORE, 1933. A new species, *P. mephistocephalus*, is erected on the basis of significant differences mainly in the nostril region relative to *P. grangeri* GILMORE, 1933. The new specimen, probably a subadult individual, provides further data about the composition and arrangement of the dermal armour of *Pinacosaurus*. Moreover, the comparisons with both young and adult specimens of *Pinacosaurus* allow a better understanding of ontogenetic changes in this dinosaur.

Key-words: Ankylosauria, *Pinacosaurus*, Late Cretaceous, Inner Mongolia.

Résumé

Le squelette articulé bien conservé d'un dinosaure ankylosaurien provenant du Crétacé supérieur de Bayan Mandahu (Mongolie intérieure) est décrit. Le spécimen comporte le crâne, la mandibule et une grande partie du squelette post-crânien, y compris la cuirasse cervicale et la massue caudale en place. Ce matériel est rapporté à l'ankylosauridé *Pinacosaurus* GILMORE, 1933. Une nouvelle espèce, *P. mephistocephalus*, est érigée sur la base de différences significatives, notamment au niveau du museau, par rapport à *P. grangeri* GILMORE, 1933. Le nouveau spécimen, en l'occurrence un individu subadulte, fournit de nouvelles données quant à la composition et à l'arrangement de la cuirasse dermique de *Pinacosaurus*. De plus, une comparaison entre spécimens immatures et adultes de *Pinacosaurus* permet une meilleure compréhension des variations ontogénétiques chez ce dinosaure.

Mots-clés: Ankylosauria, *Pinacosaurus*, Crétacé supérieur, Mongolie intérieure.

产自中国内蒙古早白垩世地层中
的甲龙科绘龙属一新种

内容提要

本文记述的是产自内蒙古巴彦满达呼地区晚白垩世

地层中的保存完好的甲龙类的关联骨架。这件标本由头骨、下颌骨以及大部分的躯干化石组成,并包括相应的颈部骨甲和尾锤。依据其与谷氏绘龙在鼻孔和眼眶区的显著差别,建立了一个新种——*Pinacosaurus mephistocephalus*, 归属于 Gilmore在1933年所描述命名的甲龙科绘龙属。该新种可能是一个接近成年的个体,它的发现为研究绘龙的骨甲结构和排列方式提供了更进一步的资料。而且,通过绘龙的未成年个体与成年个体的比较研究,可以更好地理解该类恐龙在个体发育方面的变化。

关键词: 甲龙类 绘龙属 新种 上白垩统 内蒙古

Introduction

The ankylosaurid *Pinacosaurus* is a relatively common component of the Late Cretaceous dinosaur faunas of the Gobi Basin (MARYANSKA, 1977; JERZYKIEWICZ & RUSSELL, 1991). GILMORE (1933b) erected *Pinacosaurus grangeri* on the basis of an incomplete skull (AMNH 6523) from the Djadokhta Formation of Bayn Dzak (called Shabarakh Usu in American literature), in Outer Mongolia. This specimen was discovered in 1923 by the second Central Asiatic Expedition of the American Museum (ANDREWS, 1932; GILMORE, 1933b). Other specimens of this species, mainly the skull and associated postcranial skeleton of a juvenile individual (ZPAL MgD-II/1), were collected from the same locality and beds by the Polish-Mongolian Expedition in 1964 (MARYANSKA, 1971) and in other localities of the Mongolian Gobi Basin by the Soviet-Mongolian Expeditions ("*Syrmosaurus viminicaudus*" MALEEVEV, 1952; TUMANOVA, 1987).

In Inner Mongolia (R.P. China), the Bayan Mandahu locality has yielded a herd of young *Pinacosaurus* during field activities undertaken by the Sino-Canadian Dino-

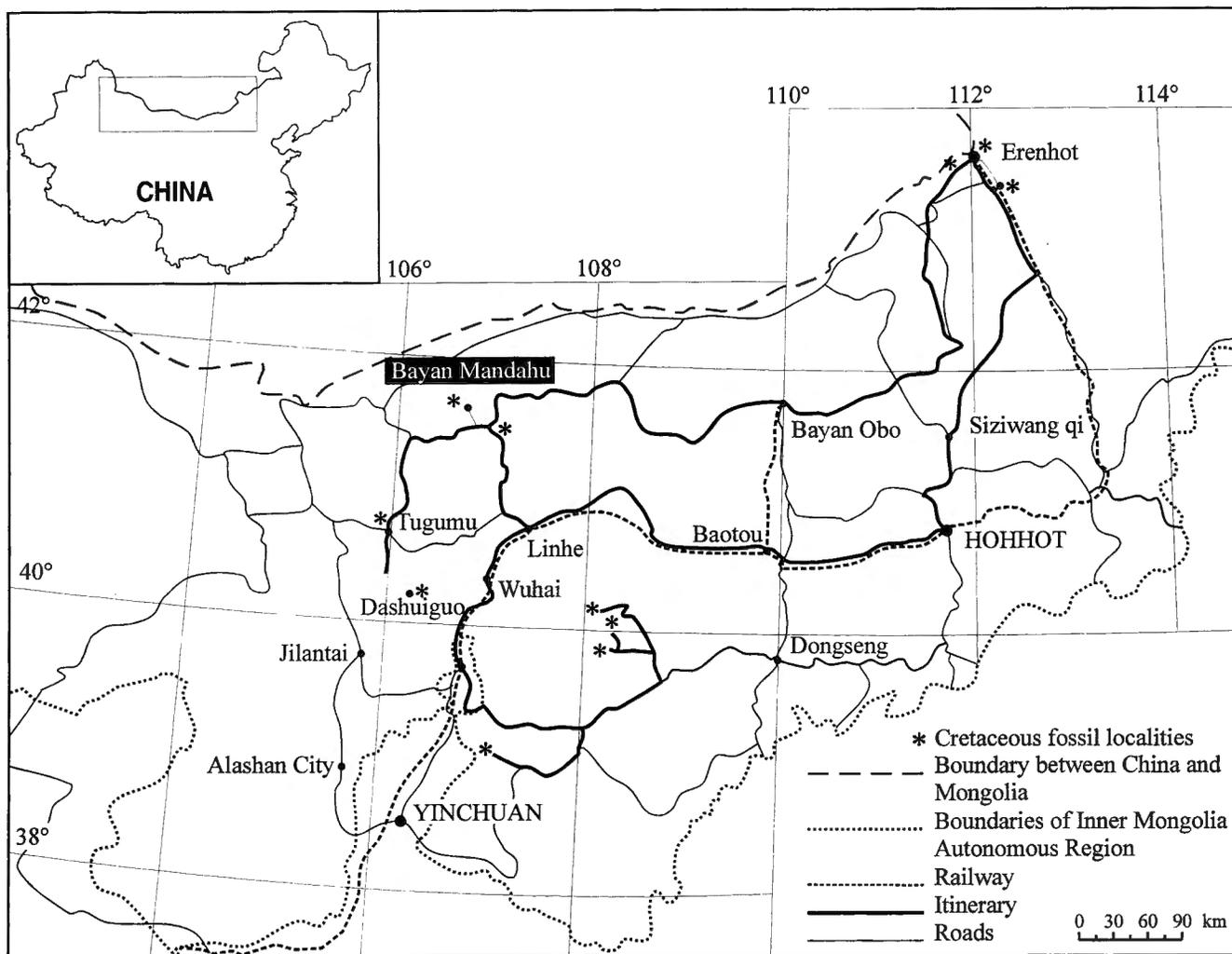


Fig. 1 — Generalized map of the central part of the Inner Mongolia Autonomous Region, showing the itinerary of the Sino-Belgian expeditions in 1995 and 1996. Inset map shows the Inner Mongolia Autonomous Region.

saur Project in 1988 and 1990 (DONG *et al.*, 1989; CURRIE, 1991; DONG, 1992, 1993a). CURRIE (1991) also reported the discovery in 1990 of embryonic remains of *Pinacosaurus* in another site of Inner Mongolia.

A new *Pinacosaurus* specimen from the Bayan Mandahu site is described herein. The specimen, an articulated skeleton with a well-preserved skull, was discovered during the second excavation campaign of the Sino-Belgian Dinosaur Expedition in summer 1996 (GODEFROIT *et al.*, 1998). It represents a new species of *Pinacosaurus*.

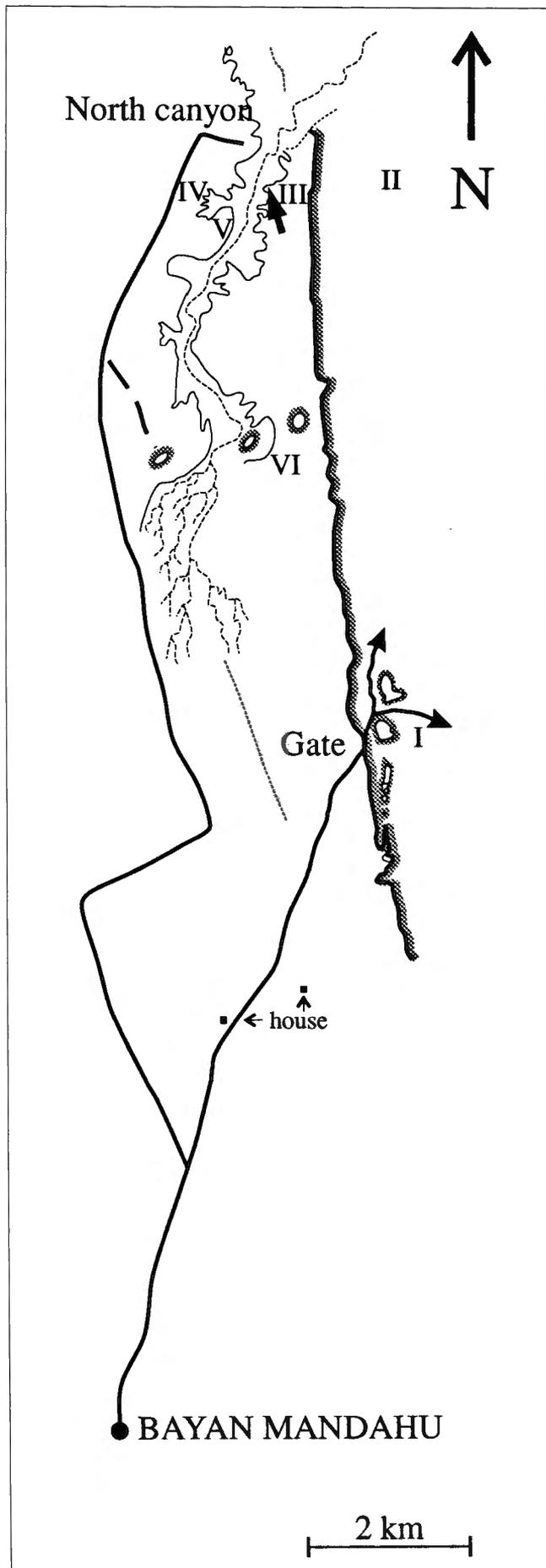
Abbreviations: AMNH, American Museum of Natural History, New York; IMM Inner Mongolia Museum, Hohhot; IRSNB, Institut Royal des Sciences Naturelles de Belgique/ Koninklijk Belgisch Instituut voor Natuurwetenschappen, Brussels; PIN, Palaeontological Institute of the Russian Academy of Sciences, Moscow; PIUU, Paleontologiska Institutionen, University of Uppsala; ZPAL, Zaklad Paleobiologii, Polish Academy of Sciences, Warsaw.

Geological setting

The Bayan Mandahu badlands of Inner Mongolia lie on the northern flank of the Lang Shan (Wolf Mountains), near Urad Houqi, in the southern Gobi Basin (Figures 1 and 2). This site was discovered in 1978 by members of the Inner Mongolia Museum at Hohhot (DONG *et al.*, 1989). Since 1987 field work has been undertaken there by the Sino-Canadian Dinosaur Project (DONG, 1993a) and, more recently, by the Sino-Belgian Dinosaur Expedition (GODEFROIT *et al.*, 1998).

The lithofacies of the Bayan Mandahu Formation are mainly horizontally-bedded red sandstones. Several kinds of deposits, including eolian, interdune, lacustrine, pedogenic and alluvial fans or braid plain, have been distinguished in the sections (EBERTH, 1993). Articulated skeletons are common and occur associated within eolian deposits, whereas rare and fragmentary remains occur within alluvial deposits (JERZYKIEWICZ *et al.*, 1993).

The vertebrate assemblage of Bayan Mandahu includes lizards, amphisbaenians, turtles, crocodylians, dinosaurs



and mammals (DONG, 1992, 1993a; JERZYKIEWICZ *et al.*, 1993). The dinosaurian fauna is dominated by protoceratopsians, mainly *Protoceratops*. *Pinacosaurus*, the only known ankylosaurid of the Bayan Mandahu assemblage, is the second most common dinosaur. Theropods (*Veliciraptor*, *Oviraptor*, *Saurornithoides*) are very rare. *Protoceratops* and *Pinacosaurus* include specimens that represent all ontogenetic stages, including juveniles and embryos (CURRIE, 1991; DONG, 1993a; JERZYKIEWICZ *et al.*, 1993). They primarily occur as articulated and associated skeletons in structureless sandstones. The “standing” position of the skeletons, including the *Pinacosaurus* specimen described herein, suggests that the animals died *in situ* and were probably buried alive during violent sandstorm events (JERZYKIEWICZ *et al.*, 1993). An alternative hypothesis is a rapid deposition on dune-sand alluvial fans during rain storm episodes (see LOOPE *et al.*, 1998). The occurrence of trace fossils such as borings in vertebrate skeletal remains, as these observed in the new *Pinacosaurus* specimen, is a common feature of eolian deposits at Bayan Mandahu (JERZYKIEWICZ *et al.*, 1993). Articulated dinosaur skeletons from the Djadokhta Formation of the Gobi Basin are often extensively bored. Even if the identity of the borers is unknown, it has been suggested that the borings were made by carrion insects (KIRKLAND *et al.*, 1998).

The lower diversity of the vertebrate assemblage and the overall small to moderate size of dinosaurs indicate a stressed palaeoenvironment. The sedimentological data suggest that the Bayan Mandahu redbeds were deposited in a semiarid climate in alluvial to eolian environments (EBERTH, 1993). According to JERZYKIEWICZ *et al.* (1993), the fossil assemblages and lithofacies of the Bayan Mandahu redbeds can be correlated with the type section of the Djadokhta Formation at Bayn Dzak (pre-Aldai Gobi, south-central Mongolia). Since the first description of the Djadokhta beds by BERKEY & MORRIS (1927), the age of this formation has been abundantly discussed by numerous authors. An excellent summary of the conflicting hypotheses is given by LILLEGRAVEN & MCKENNA (1986), who suggest that the Djadokhta Formation could be synchronous of the lower part of the Judithian “North American Land Mammal Age”; according to JERZYKIEWICZ & RUSSELL (1991), this would indicate that the Djadokhta sedimentation began during the middle Campanian and took place during an interval centred on approximately 78 Ma ago. Nevertheless, it must be kept in mind that these conclusions, mainly based on comparisons of vertebrate faunas, remain conjectural by lack of palynofloral, radioisotopic or palaeomagnetic data in the Gobi Basin.

Fig. 2 — Simplified map of Bayan Mandahu area (modified after EBERTH, 1993). Roman numbers indicate the fossil localities excavated during the Sino-Belgian expedition in 1996. The type locality of *Pinacosaurus mephistocephalus* is indicated by an arrow.

Systematic palaeontology

Dinosauria OWEN, 1842
 Ornithischia SEELEY, 1887
 Thyreophora NOPCSA, 1915
 Ankylosauria OSBORN, 1923
 Family Ankylosauridae BROWN, 1908
 Genus *Pinacosaurus* GILMORE, 1933

Type species: *Pinacosaurus grangeri* GILMORE, 1933.

Emended generic diagnosis: Premaxilla excavated by a pair of large and rounded “gland openings”; low sub-rectangular dentary; small edged ossification on the angular area of the mandible reaching the level of the penultimate alveolus; complete reduction of neural arches on caudalmost cervical vertebrae; strongly divergent preacetabular process of ilium; two cervical half-rings composed of three to four fused elements, including oval and low-keeled dorsomedial elements and pointing triangular spines projected ventrolaterally; lightened dermal armour, apparently formed by two longitudinal series of small oval scutes parallel to the vertebral column along the dorsal region.

Remark: The holotype of *Pinacosaurus grangeri* GILMORE, 1933 (AMNH 6523) is a crushed skull of an adult specimen from the Djadokhta Formation of Bayn Dzak (Mongolia). Subsequent diagnosis and description of this species proposed by MARYANSKA (1971, 1977) and COOMBS & MARYANSKA (1990) is mainly based on ZPAL MgD-II/1, the almost complete skull and associated post-cranial skeleton of a juvenile from the same formation and locality, which is regarded to be conspecific to AMNH 6523. Although the latter conclusion cannot be proven with certainty because of the bad state of preservation of the holotype, we have decided to follow it in the present paper.

Pinacosaurus mephistocephalus n. sp.

Holotype: IMM 96BM3/1, a nearly complete articulated skeleton, with cervical dermal armour and tail-club in place. The specimen lies in a natural position, with the limb bones doubled under the body, as is the case of other dinosaur skeletons (e.g., *Protoceratops*) recovered from the sandy beds of the Gobi Basin (JERZYKIEWICZ *et al.*, 1993). The skeleton was not deformed by pressure after burial and there is no evidence of post-mortem transportation. The left arm and a great portion of the left part of the pelvic girdle and hindlimb are missing.

Locus typicus: Quarry SBDE 96BM3 (41°47.269' N; 106°43.573' E; 1239 m alt.), Bayan Mandahu, Urad Houqi Banner, Bayan Nor League, Inner Mongolia Province, P.R. China.

Stratum typicum: Bayan Mandahu Formation, correla-

tive to the Djadokhta Formation, Campanian, Late Cretaceous.

Derivatio nominis: *Mephisto*, abridged name for Mephistopheles, the name in Faust's legend of the devil who made a pact with him; *kephalê* (Greek): head. The head of the holotype of *Pinacosaurus mephistocephalus* reminds a devil's head.

Diagnosis: Two pairs of premaxillary foramina leading to premaxillary sinuses; “gland” opening facing rostrally; both lower and upper premaxillary foramina much smaller than “gland” opening; external nares only visible in dorsal view; orbits circular, as high as long and laterally oriented; no caudodorsal premaxillary process protruding between maxilla and nasal; square-shaped lacrimal; parietal much shorter than frontal; wide frontoparietal process of postorbital; deep frontoparietal depression; scapula relatively short and robust (ratio “proximal width / length” of the scapula = 0.36 in the holotype), with a well-developed acromial process; well-developed deltopectoral crest, extending down the shaft to terminate distal to humeral mid-length; proximal articular head of radius strongly expanded both medio-laterally and cranio-caudally.

Remarks: The diagnosis of *Pinacosaurus mephistocephalus* is mainly based on comparisons with ZPAL MgD-II/1, the best preserved specimen of *P. grangeri*. Both specimens belong to different ontogenetic stages (see below). If the diagnostic value of the first three characters is unquestionable, it cannot be completely excluded that some of the other ones may reflect ontogenetic variation.

Description and comparisons

IMM 96BM3/1 is a well-preserved articulated skeleton, including the skull, lower jaw, most of the vertebral column and the right limbs. The dermal armour is partially preserved *in situ*. It was probably an immature subadult individual of about 3 m long (see below).

Skull comparisons are mainly established with the crushed holotype specimen of *Pinacosaurus grangeri* (AMNH 6523; GILMORE, 1933, figs. 1-3) and a young individual referred to this species (ZPAL MgD-II/1; MARYANSKA, 1971, fig. 1, pls. 6-7; MARYANSKA, 1977, figs. 2-3; pls. 20-25). Other Asian material referred to *Pinacosaurus* has been described by several authors (YOUNG, 1935; MALEEV, 1952, 1954; BUFFETAUT, 1995). Further comparisons are also proposed with other Asian and North American ankylosaurids (BROWN, 1908; MALEEV, 1954, 1956; COOMBS, 1971, 1978, 1986; MARYANSKA, 1971, 1977; CARPENTER, 1982; TUMANOVA, 1977, 1986, 1987, 1993; COOMBS & MARYANSKA 1990; BARRETT *et al.*, 1998; CARPENTER *et al.*, 1998; PANG & CHENG, 1998; SULLIVAN, 1999).

The standardised anatomical nomenclature for dinosaurs recommended by WEISHAMPEL *et al.* (1990: 6) is

Table 1 — Measurements on *Pinacosaurus mephistocephalus* (IMM 96BM3/1), from the Upper Cretaceous of Bayan Mandahu (Inner Mongolia, P.R. China).

I. Skull	
–	Greatest length: 238 mm
–	Length of sagittal axis of the skull: 185 mm
–	Width between squamosal horns: 308 mm
–	Width between quadratojugal horns: 375 mm
–	Width between supraorbital horns: 240 mm
–	Greatest width of premaxilla: 83 mm
–	Width of skull roof, between the rostralmost points of prefrontals: 127 mm
–	Height of the skull, from tip of squamosal horn to base of quadratojugal horn: 143 mm
–	Length of muzzle, from front of orbits to front of skull: 116 mm
–	Length of orbit: 54 mm
–	Width of orbit: 54 mm.
–	Greatest diameter of gland opening: 17.5 mm
–	Distance between gland openings: 18 mm
–	Length of mandible, to the rostralmost point of dentary: 157 mm
–	Greatest width of mandible: 210 mm
–	Greatest depth of mandible: 47 mm
II. Postcranial skeleton:	
–	Length of scapula: 215 mm
–	Proximal width of scapula: 98 mm
–	Distal width of scapula: 77 mm
–	Length of humerus: 200 mm
–	Greatest width of humeral proximal head: 109 mm
–	Greatest width of humeral distal end: 66 mm
–	Length of radius: 98 mm
–	Greatest width of radial proximal head: 68 mm
–	Length of metacarpal I: 42 mm
–	Length of metacarpal II: 39 mm
–	Length of metacarpal III: 38 mm
–	Length of metacarpal IV: 34 mm
–	Length of metacarpal V: 27 mm
–	Length of ilium: 560 mm
–	Greatest width of ilium: 132 mm
–	Length of femur: ca 215 mm

followed in the present paper. Measurements on IMM 96BM3/1 are collected in Table 1.

Skull (Figure 3; Plate 1):

The skull is very similar in shape to that of ZPAL MgD-II/1, the juvenile individual of *Pinacosaurus grangeri*, but clearly larger. It is roughly triangular in dorsal view, wider than long. As usual in ankylosaurs, the antorbital and supratemporal fenestrae are closed (COOMBS & MARYANSKA, 1990). The infratemporal fenestrae are laterally hidden by the quadratojugal ossifications, as is typical in ankylosaurids (COOMBS, 1978). Unlike ZPAL MgD-II/1, IMM 96BM3/1 possesses prominent horns on the squamosal, quadratojugal and supraorbital regions.

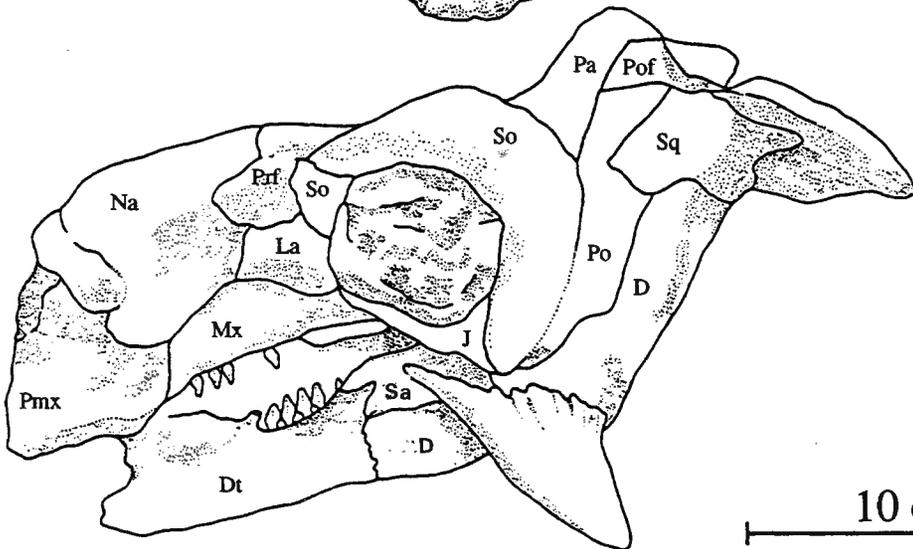
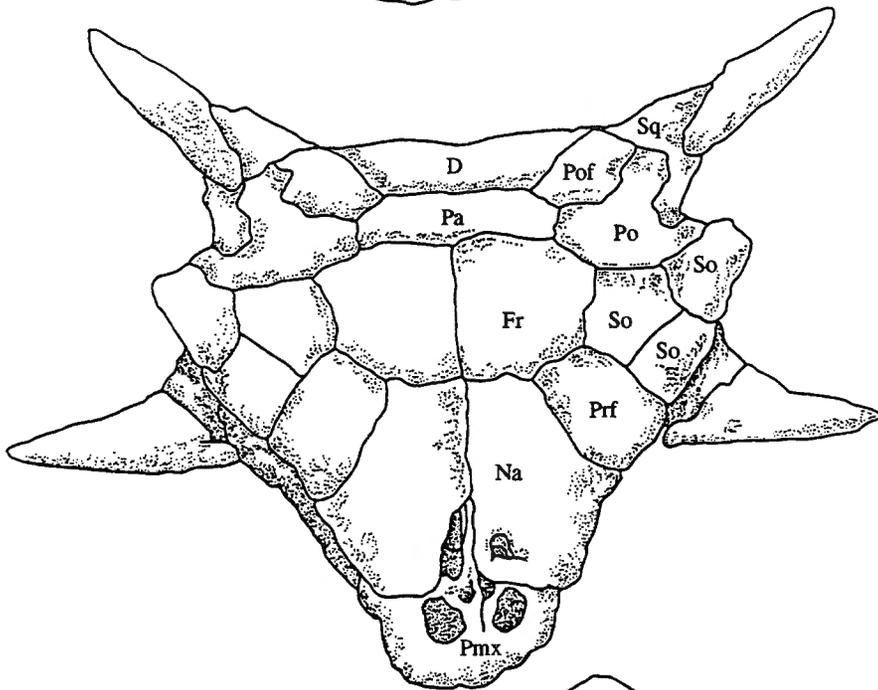
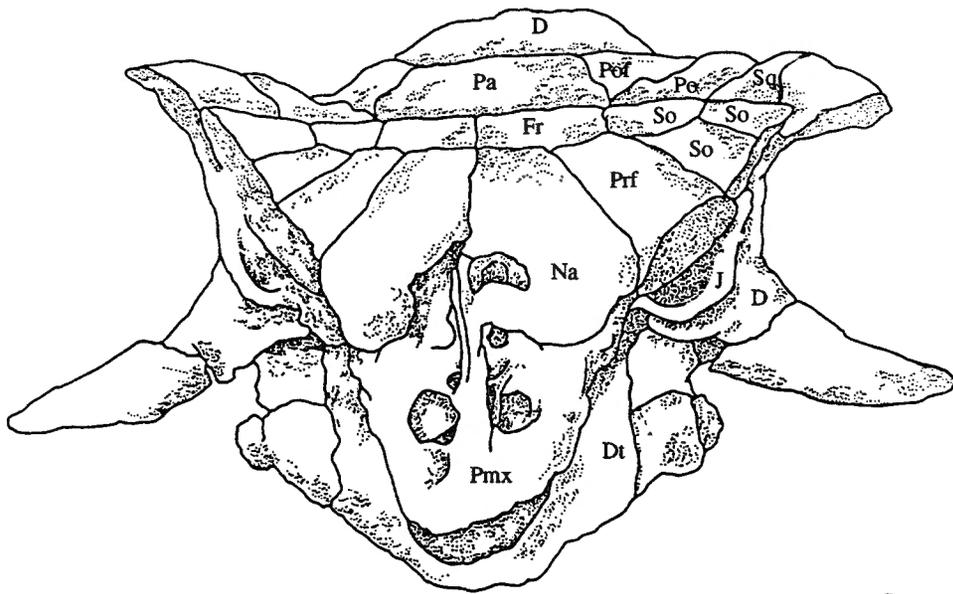
The nomenclature of the skull roof bones followed in the present paper is that established by COOMBS & MARYANSKA (1990: fig. 22.2), which differs slightly from that used by MARYANSKA (1971, 1977).

The **skull roof** of IMM 96BM3/1 is characterized by a marked transverse depression at the level of the fronto-parietal suture and a steep elevation of its caudal part, at the level of the parietal. As usual in ankylosaurids, there is a gentle elevation of the nasals, so that the snout arches above the level of the postorbital skull roof (SERENO, 1986). Unlike adult ankylosaurs, the sutural boundaries of the skull roof bones are visible dorsally and laterally. The sutural pattern of the skull roof closely resembles that of ZPAL MgD-II/1, the only ankylosaurid skull on which sutural boundaries have at present time been described. Nevertheless, differences can be observed, particularly at the rear of the skull. Rugose surfaces due to accretion of secondary ossifications occur in the squamosal, parietal, jugal, supraorbital, premaxillary, nasal and maxillary regions. In *Pinacosaurus*, the skull roof elements are greater and more complicated than in the enigmatic ankylosaur *Minmi* and in the basal thyreophoran *Scelidosaurus* (see MOLNAR, 1996).

The **nasal** is by far the largest bone of the skull roof, forming more than half of the length of the skull. Its rostral portion is intimately fused to secondary dermal ossifications overhanging the premaxillae and forming the roof of the external nares. These secondary dermal ossifications are apparently less developed than in ZPAL MgD-II/1, but this can be due to breakage. Caudally, the transverse naso-frontal suture runs in front of the mid-point of the orbit. The contact with the prefrontal is long, running from the lateral end of the naso-frontal suture to the dorsal portion of the lateral side of the skull. The lateral wall of the nasal successively contacts the lacrimal, the maxilla along a relatively long distance and rostrally the premaxilla.

The **frontals** are approximately square in outline. They are separated from nasals and parietals by transverse sutures. The caudolateral suture with the postorbital is oblique and relatively long. The frontal also contacts the prefrontal rostrolaterally and the medial supraorbital element (postfrontal of MARYANSKA, 1971, 1977) laterally. There is no clear evidence of an ethmoid ossification between the nasals and frontals on the dorsal skull roof, as described in the juvenile specimen ZPAL MgD-II/1 (MARYANSKA, 1971, 1977).

The **parietals** are completely fused, forming a single element. It is much rostro-caudally shorter than the frontals. The caudal half of the parietal plate is covered by a transversely elongated secondary ossification, parallel to the caudal border of the skull roof and extending laterally to contact the squamosals. This element may be regarded as the equivalent, although better developed, of the "tabular" bones of ZPAL MgD-II/1 (MARYANSKA, 1977), as it has similar contacts with surrounding bones. Its caudal border overhangs the occipital region, but is not fused



10 cm

with the supraoccipital. The parietal laterally contacts the postfrontal and the postorbital.

The **prefrontal** significantly contributes to the construction of the skull roof, with a minor contribution to the structure of the lateral wall of the skull. Its rostromedial suture with the nasal is very long. Caudomedially, it contacts the frontal, caudolaterally two of the supraorbital bones and ventrally the lacrimal in an horizontal suture.

The **postorbital** is formed, in external view, by two rami: a dorsal and a lateral one. The dorsal ramus takes part in the caudolateral portion of the skull roof. It is surrounded rostrally by two supraorbital bones, laterally and caudolaterally by the squamosal and caudomedially by the postfrontal. Its frontoparietal medial process is wider than in ZPAL MgD-II/1. The lateral ramus contributes to the postorbital part of the skull. It is caudally bordered by the large quadratojugal dermal plate. It fuses rostrally with the caudolateral supraorbital; their respective limits cannot be correctly substantiated, so that it is not possible to know whether the postorbital participates in the caudal margin and contacts the jugal, as in ZPAL MgD-II/1.

The **postfrontal** (squamosal of MARYANSKA, 1971, 1977) is a small component of the rear of the skull roof surrounded by the parietal, the postorbital and the squamosal. It is excluded from the frontal by the wide frontoparietal process of the postorbital. It is also excluded from the caudal border of the skull roof by the contact between the squamosal and the parietal secondary ossification.

The **squamosal** is roughly triangular in outline and forms the caudolateral edge of the skull. The suture with the postorbital is long, on both the dorsal and lateral sides of the skull. On the other hand, the medial contact with the postfrontal is short. Ventrally, the squamosal lies on the caudolateral plate of the skull. The prominent squamosal horns are subtriangular in shape, slender and distally pointed. They are caudolaterally and slightly dorsally projected. Their basal part is narrow. In dorsal view, the angle between the long axis of the horns and the transverse axis of the skull is about 135° . These ossifications roughly resemble in outline the spike-shaped squamosal horns of *Saichania* (see MARYANSKA, 1977), *Shanxia* (see BARRETT *et al.*, 1998) and, especially, *Tarchia* (see TUMANOVA, 1977, 1987). The homologous ossifications of *Ankylosaurus* (see BROWN, 1908; COOMBS, 1978) and *Gargoyleosaurus* (see CARPENTER *et al.*, 1998) are

large and pyramidal, while those of *Euoplocephalus* are blunt and moderately pointed. The squamosal horns are not developed in *Tsagantegia* and *Shamosaurus* (see TUMANOVA, 1986, 1993).

Three pairs of extra **supraorbitals bones** (postfrontal, presupraorbital and postsupraorbital of MARYANSKA, 1971, 1977; palpebrals of COOMBS, 1972) complete the skull roof, forming the dorsal and caudal orbital margins. The medial supraorbital contacts the frontal, the prefrontal and the postorbital; the rostralateral one contacts the prefrontal and the lacrimal. The caudolateral supraorbital fuses with the postorbital on the lateral wall of the skull; it forms dorsally supraorbital horns, shorter and less laterally projected than the squamosal ones.

A large **secondary quadratojugal plate** forms ventrally the caudolateral border of the skull, externally covering the quadratojugal. Its dorsal border contacts the squamosal and its rostral border forms a long suture with the postorbital. Its ventral portion projects ventrolaterally, supporting a prominent quadratojugal horn. This is the largest of the three pairs of cranial horns. It projects almost horizontally, with the tip slightly directed caudally. Its rostral border is convex, whereas the caudal one is concave. Its dorsal side is rostro-caudally convex and its ventral side is flat to slightly concave. The quadratojugal horns are proportionally broader, less salient and more ventrally projected in *Euoplocephalus*, *Ankylosaurus*, *Shamosaurus*, *Gargoyleosaurus* and, especially, *Tsagantegia*. In *Saichania* and *Tarchia*, the quadratojugal horns are also very prominent and similarly oriented; nevertheless, they are proportionally much broader and less pointed (MARYANSKA, 1977; TUMANOVA, 1977). In *Nodocephalosaurus* SULLIVAN, 1999, the quadratojugal protuberance is projected rostroventrally.

The **orbits** of IMM 96BM3/1 are relatively large (an immature character?), almost rounded, as high as long and laterally oriented. They contrast with those of ZPALMgD-II/1, which have an oval outline, distinctly longer than high and lateroventrally oriented.

The **jugal**, which forms the ventral margin of the orbit, is relatively thin. It progressively becomes mediolaterally wider rearwards. It contacts rostrally the lacrimal on both the lateral side of the skull and inside the orbit; then it overlaps the caudal part of the maxilla. Caudally the jugal contacts the fused postorbital-caudolateral supraorbital. An horizontal wing of the jugal forms the postocular shelf separating the orbit from the mandibular adductor (HAAS, 1969; MARYANSKA, 1977).

The **lacrimal** participates in the rostral margin of the orbit. It is not an elongated rod of bone, as in ZPAL MgD-II/1, but it is rectangular to square-shaped in lateral view. It contacts the prefrontal and the rostralateral supraorbital dorsally, the nasal rostrally, the maxilla ventrally and the jugal caudoventrally. Inside the orbit, the caudal border of the lacrimal is pierced by a large lacrimal foramen; the inner orbital wing of the lacrimal contacts accessory ossifications.

The **maxilla** of IMM 96BM3/1 looks proportionally lower in lateral view than that of ZPAL MgD-II/1. How-

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Fig. 3 — Skull and lower jaw of *Pinacosaurus mephistocephalus* (IMM 96BM3/1), from the Upper Cretaceous of Bayan Mandahu (Inner Mongolia, P.R. China). A: rostral view; B: dorsal view; C: lateral view. Key: D: secondary dermal plates; Dt: dentary; Fr: frontal; J: jugal; La: lacrimal; Mx: maxilla; Na: nasal; Pa: parietal; Pmx: premaxilla; Po: postorbital; Pof: postfrontal; Prf: prefrontal; Sa: Surangular; So: supraorbital; Sq: squamosal.

ever, this character cannot be adequately substantiated and is therefore not included in the specific diagnosis. It contacts the premaxilla rostrally, the nasal rostradorsally and the lacrimal caudodorsally; it reaches the jugal distally. Its rostralateral portion is very rugose. The ventral border of the maxilla forms a deep cheek emargination, as is usual in ankylosaurs (COOMBS & MARYANSKA, 1990). The maxillary teeth have been dislocated and most of them are not preserved *in situ*.

The **premaxilla** is not completely covered by the nasal and accessory dermal plates, so that it is well visible in dorsal view, as in *Pinacosaurus grangeri*, *Euoplocephalus* and *Tianzhenosaurus* (see PANG & CHENG, 1998). In *P. grangeri*, this character is not ontogenetic because it can be observed in both the juvenile ZPAL MgD-II/1 and in the adult AMNH 6523. Dermal ossifications are better developed in the snout area of *Saichania* (see MARYANSKA, 1977, fig. 4), of *Tarchia* (see TUMANOVA, 1977, fig. 1), of *Talarurus* (see TUMANOVA, 1987, fig. 5) and especially of *Ankylosaurus* (see COOMBS, 1978, fig. 1). *Gargoyleosaurus* exhibits a similar dermal development (CARPENTER *et al.*, 1998). In lateral view, the premaxilla of IMM 96BM3/1 forms half of the preorbital part of the skull. The maxillary suture runs vertically in its

ventral part but, contrary to ZPAL MgD-II/1, the premaxilla does not protrude more dorsally as a process wedged between the maxilla and nasal. In ventral view, the premaxillary beak is a little wider than the distance between the caudalmost maxillary teeth, as in *P. grangeri*. In *Tsagantegia*, the beak appears distinctly wider than the distance between the caudalmost maxillary teeth (TUMANOVA, 1993). Both distances appear nearly equal in *Saichania*, *Tarchia* and *Euoplocephalus*. The beak is narrower than the distance between caudalmost maxillary teeth in *Ankylosaurus* and *Gargoyleosaurus*. The premaxillary teeth are absent, as in all ankylosaurids except *Gargoyleosaurus* (see CARPENTER *et al.*, 1998).

The pattern of the **nasal openings** (Figure 4; Plate 2, Fig. 2) is one of the most interesting features in this new specimen. Three pairs of openings have been described in *Pinacosaurus grangeri* (see MARYANSKA, 1971, 1977), but four are present in IMM 96BM3/1. GILMORE (1933) described two pairs of openings in the holotype of *P. grangeri* but, according to MARYANSKA (1971), the third pair may have been crushed together with the cranial roof. Moreover, the disposition of these openings are completely different in IMM 96BM3/1 and ZPAL MgD-II/1. In IMM 96BM3/1, the most ventral opening, which seems equivalent to the "gland" opening of MARYANSKA (1971, 1977), is not located on the side of the muzzle but quite rostrally. This opening is rounded, completely closed and has concave walls. Between the medial border of the "gland" opening and the median nasal septum is a small subtriangular lower premaxillary foramen. This foramen apparently does not communicate with the "gland" opening. The upper premaxillary foramen is oval and much smaller than the ventral "gland" opening, but approximately as large as the lower premaxillary foramen. Both foramina apparently lead to premaxillary sinuses. Dorsally, the large external nares are covered by the dermal ossifications of the nasals. The naris is only visible in dorsal view, whereas this opening can also be seen in ventral view in *P. grangeri*. A premaxillary sheet of bone, here regarded as the septomaxilla of MARYANSKA (1971, 1977), separates the external naris from the upper premaxillary foramen. This sheet of bone is horizontal as in *P. grangeri* but is much more robust than in ZPAL MgD-II/1. Differences in the morphology of nasal openings may be regarded as specific features and suggest a distinction between the Bayan Mandahu specimen and *P. grangeri* (see below). Indeed, the number and distribution of openings through the premaxilla in the external nasal region is taxonomically important within ankylosaurids (MARYANSKA, 1977). *Euoplocephalus*, *Saichania* and *Tianzhenosaurus* have only two pairs of openings; the upper nares of the former are only visible in dorsal view as in IMM 96BM3/1, whereas in *Saichania* they are visible in both dorsal and ventral views as in *Pinacosaurus grangeri*. In *Ankylosaurus*, a rostral and lateral expansion of the dermal ossifications of the nasals covers the premaxillae and restricts the external nares to small openings placed far laterally close to the maxillary suture at the margin of the mouth (COOMBS &

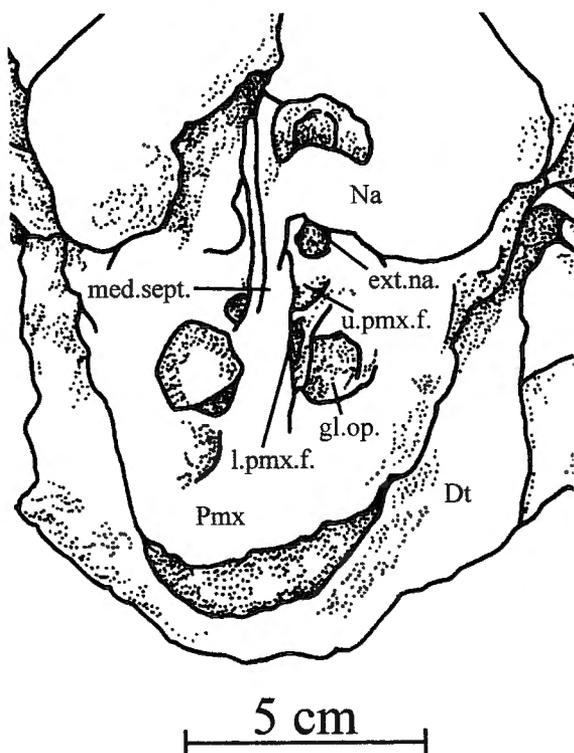


Fig. 4 — Detail of the nasal region of *Pinacosaurus mephistocephalus* (IMM 96BM3/1), from the Upper Cretaceous of Bayan Mandahu (Inner Mongolia, P.R. China). Key: Dt: dentary; ext.na.: external naris; gl.op.: "gland" opening; l.pmx.f.: lower premaxillary foramen; med.sept.: median septum; Na: nasal; Pmx: premaxilla; u.pmx.f.: upper premaxillary foramen.

MARYANSKA, 1990); they are consequently visible only in ventral view (MARYANSKA, 1977).

The **palate** of IMM 96BM3/1 is not visible but, during preparation, a portion of the skull roof was removed and a large part of the palate could be observed in dorsal view (Plate 2, Fig. 1). The palatal vacuities are elongated, but proportionally smaller than those of *Pinacosaurus grangeri*, as observed in AMNH 6523 and ZPAL MgD-II/1. They are limited laterally by the maxillae, caudally and caudomedially by the palatines and rostromedially by the vomers.

The **palatines** are very developed. Rostrally, they form elongated rostral rods that separate the caudal portion of the palatine vacuities. These rods are rostrally separated from each other by the vomers. Caudally, the palatines are highly vaulted and extend laterally to contact the caudolateral part of the maxillae. The palatine surface is pierced by pits and chambers. According to MARYANSKA (1977), this system formed a kind of closed gas-filled cavities. In lateral view, the palatines are rather steeply inclined: their rostral end is placed more ventrally than their caudal end.

The **basicranial and occipital regions** are not available for study. It can nevertheless be observed that the occipital condyle is caudoventrally oriented, as in most Mongolian ankylosaurids except *Saichania*, in which it is ventrally oriented (MARYANSKA, 1977). The occiput, which is completely collapsed, was not fused to the skull roof. This feature suggests that IMM 96BM3/1 is an immature individual, as a wide unossified gap also separates the parietals from the supraoccipitals and paroccipital processes in the juvenile specimen of *P. grangeri* ZPAL MgD-II/1 (MARYANSKA, 1971, 1977).

The **quadrates** of IMM 96BM3/1 are broken but their distal ends still articulate with the lower jaw. As preserved, they were probably vertically and slightly rostrally oriented, like in *P. grangeri* or *Tsagantegia*, so that the quadrate cotylus is located at the same level as the caudal margin of the orbit. In *Saichania*, they are strongly oblique rostrally and the quadrate cotylus is located at the level of the middle part of the orbits (MARYANSKA, 1977). The quadrates are nearly vertical in *Tarchia* (TUMANOVA, 1977).

Mandible (Figure 3; Plate 1):

The mandible is joined together with the skull and is visible in lateral view only. It looks closely similar to that of *Pinacosaurus grangeri*, and clearly different to that of other ankylosaurids such as *Saichania*, *Tarchia*, *Shamosaurus*, *Ankylosaurus* and *Euoplocephalus*, mainly in being distinctly more slender. The dorsal and ventral borders of the dentary are roughly parallel to each other. The coronoid process is very low and rounded, as is typical in ankylosaurids (SERENO, 1986). An ossification is fused laterally to the lower jaw, as in ankylosaurs and *Scelidosaurus* (see GALTON, 1983; NORMAN, 1984). This scute is of small size, reaching the level of the penultimate alveolus as in ZPAL MgD-II/1, and has sharp

borders. It is located on the caudoventral side of the mandible ("angular protuberance" of MARYANSKA, 1977). In *Saichania*, this bone attains half the length of the tooth row and in North-American ankylosaurids, it terminates at about the level of the rostralmost alveolus (MARYANSKA, 1977). Nevertheless, it cannot be excluded that this character may reflect differences in ontogeny. The retroarticular process is very low. Thirteen teeth are preserved in each dentary, but some are apparently missing. MARYANSKA (1971, 1977) counts 15 or probably 16 teeth in the dentaries of ZPAL MgD-II/1. The prementary is missing.

Teeth (Plate 2, Fig. 3):

The maxillary teeth are not well preserved but some teeth are in place on the lower jaw. On the labial side of the crown, the basal cingulum appears better developed than in ZPAL MgD-II/1. The apical cusp is not very developed relatively to the marginal denticles (five on the mesial side and four to five on the distal side). The marginal denticles are well-separated from each other by distinct notches. The crown is ornamented by longitudinal ridges, but this character appears inconstant; on the other hand, no marked grooves can be observed along the crown.

Axial skeleton (Plate 2, Fig. 3):

Although most of the vertebral column of IMM 96BM3/1 is preserved in connection, the vertebrae are poorly preserved, especially in the dorsal region. The cervical armour, part of the dorsal body armour and the tail-club are preserved in place. The first fifteen presacral vertebrae of the column are disposed in a concave-convex structure in lateral view.

The **cervical series** consists of seven to eight vertebrae, including the atlas and axis. The neural arches are fused to the centra, suggesting that the specimen is not a juvenile individual. The atlas and axis are not well exposed, so that it is not possible to know whether they are separate, as occurs in *Pinacosaurus grangeri*, *Shanxia* (see BARRETT *et al.*, 1998), *Tianchisaurus* (see DONG, 1993b) and *Euoplocephalus* (see COOMBS, 1971), or fused as in *Saichania* (see MARYANSKA, 1977). Ossified tendons reach the last cervical vertebrae. The centra are poorly preserved and cannot be accurately described. The neural arches are transversely flattened and very low. They are completely reduced on the caudalmost cervical vertebrae, as in *P. grangeri*. The pre- and postzygapophyses are elongated and divergent in dorsal view. The cervical ribs are visible on the left and right sides but they are not well preserved because of breaking and bioturbation (borings). They are roughly triangular in dorsal view and point laterally, caudally and slightly ventrally. Only the three or four caudalmost cervical ribs are fused to the centrum. The cranial ribs remain free. According to MARYANSKA (1977), the complete reduction of the neural arch of the caudal cervical vertebrae and the elongated zygapophyses

are characters distinguishing the cervical series of *Pinacosaurus* from that of *Saichania*.

The **dorsal series** includes at least ten vertebrae and associated paired ribs. Although partly collapsed, the thoracic cage remains articulated. The caudal part of the dorsal series is incomplete and very badly preserved. All the neural arches are completely hidden by a series of a dozen ossified tendons (Plate 3, Fig. 3), particularly well developed from the sixth dorsal vertebra. The transverse processes are very broad and point obliquely upwards. The dorsal ribs are completely fused to the vertebrae, as is usual in most adult ankylosaurs (COOMBS & MARYANSKA, 1990). The first two pairs are relatively small and slender. The third and fourth pairs quickly increase in size and are strongly oblique caudally, as observed by MARYANSKA (1977) in *Saichania*. From the fifth to the seventh pair, and caudally to the pectoral girdle, the dorsal ribs are very strong and form a very wide and deep thoracic cage. The longest thoracic ribs measure about 40 cm in length, indicating that the thoracic width of the animal was about 80 cm. Their capitular process is very high and cranio-caudally compressed; on the other hand, the lateral part of the ribs is dorso-ventrally compressed. The tuberculum is never developed. In the longest thoracic ribs, the caudal margin forms a dorsal plate-like process, for a better protection of the back of the animal. The caudal dorsal ribs are badly preserved; their size progressively decreases and their proximal portion becomes less angular, with lower capitular processes.

As preserved, the **synsacrum** is composed of eight ossified vertebrae, including at least three dorsosacral centra fused to form a presacral rod, four sacral vertebrae and a sacrocaudal vertebra (Plate 2, Fig. 4). The presacral rod is very incompletely preserved. As compared to the free dorsal vertebrae, the three preserved centra of the presacral rod are relatively long and very compressed laterally. Very long and thin ribs reach the preacetabular part of the ilium. The four sacral ribs are medially co-ossified to the vertebrae and laterally to the ventral side of the ilium, along a distance corresponding to the length of the acetabulum. They are very robust, caudally curved and their lateral portion is particularly enlarged cranio-caudally.

The nearly complete **tail** (Plate 3, Fig. 4) measures about 160 cm in length. Unfortunately, the number of caudal vertebrae cannot be accurately estimated. The proximal caudal vertebrae remain free. Their centra are cylindrical and nearly as high as wide; their articular surfaces are slightly concave. The neural arches are relatively high and rectangular in lateral view. The proximal caudal ribs are robust, straight, dorso-ventrally compressed and slightly expanded at both ends. The first two ribs contact the caudal part of the ilium. Distally, the centra become lower and more elongated; their shape changes from nearly circular to square in cross-section. The transverse processes and ribs quickly disappear completely. As usual in ankylosaurids (COOMBS, 1978), the tail is very rigidified back to its proximal third: the

vertebrae are completely surrounded by a net formed by the very elongated and imbricated successive zygapophyses and haemal spines, as well as by strong ossified tendons.

Pectoral girdle and forelimb (Plate 3, Fig. 2):

The right scapulocoracoid and forelimb are articulated. On the left side, the scapula and the proximal part of the manus are preserved, but the arm is missing. The forelimbs of the animal are folded under the thorax, the palm of the hands facing upwards.

The **scapula** closely resembles that of *Euoplocephalus* (see COOMBS, 1978, fig. 9). The scapular blade is very slightly convex outwards. Its ventral border is very concave, whereas its dorsal border is slightly convex. The distal edge is ventrally bent and is only slightly expanded. The proximal portion of the scapula is characterised by a very prominent acromial process, laterally oriented at right angle to the scapular blade. The glenoid forms an elongated notch at the proximoventral corner of the scapula. The scapula of IMM 96BM3/1 appears proportionally shorter, less convex externally and its acromial process is much more developed than in both juvenile (ZPAL MgD-II/1) and adult (PIN 314-1/7) specimens of *P. grangeri* (see MARYANSKA, 1977, pl. 23, fig. 4; pl. 26, fig. 5). That of *Saichania* is proportionally longer, with a more expanded distal (and proximal?) end (MARYANSKA, 1977, pl. 35, fig. 3). In *Talarurus*, the scapula is relatively long, with a weakly developed acromial process (MALEEVEV, 1954, fig. 7; 1956, fig. 13; MARYANSKA, 1977).

The **coracoid**, ventromedially fused to the scapula, is hidden on the ventral side of the specimen.

The **humerus** is short and relatively robust. Its proximal portion is very expanded medio-laterally and flattened cranio-caudally. The massive head is flanked by a strong medial process and a lateral deltopectoral crest. Although broken, the latter appears much more developed than in *Pinacosaurus grangeri* (see MARYANSKA, 1977, pl. 23, fig. 1; pl. 26, fig. 4), or in *Talarurus* (see MALEEVEV, 1954, fig. 8). The deltopectoral crest of IMM 96BM3/1 extends down the shaft to terminate distally to the humeral mid-length, as in *Saichania* (see MARYANSKA, 1997, pl. 35, fig. 1) and *Shanxia*. The humeral shaft is short and well marked; it is not as flattened as in *Saichania*. The ulnar groove is large, but relatively shallow. As is usual in ankylosaurs (see MARYANSKA, 1977; COOMBS, 1978), the axes of the proximal and distal ends lie at an angle of about 15° to each other, so a slight torsion along the shaft is present.

The **ulna** is very short and rather massive. The olecranon process is a distinct process, but appears less developed than in *Saichania* (see MARYANSKA, 1977, fig. 11C₂). The proximal articular facet for the radius is very extended. In lateral view, the ulnar shaft is relatively long as in *Pinacosaurus grangeri* (see MARYANSKA, 1977, fig. 11B₂), embracing about half of the ulnar length.

The **radius** is distinctly longer than the ulna and is nearly perfectly straight. Its proximal articular end

is slightly concave and strongly expanded both medio-laterally and cranio-caudally, as in *Saichania* (see MARYANSKA, 1977, fig. 11C₃). In *Pinacosaurus grangeri*, the proximal articular surface is very narrow, especially in the juvenile ZPAL MgD-II/1 (MARYANSKA, 1977, fig. 11B₃). Contrary to *Saichania*, the radius of IMM 96BM3/1 appears less expanded distally than proximally.

The **manus** is pentadactyl but the accurate phalangeal formula is not known. None of the carpal elements is preserved in IMM 96BM3/1. *Saichania* and *Talarurus* have also a pentadactyl manus. According to MARYANSKA (1977), the manus of *Pinacosaurus* is longer and more slender than that of *Saichania* and *Talarurus*.

The **metacarpals I-V** are preserved in natural arrangement. All are relatively short and massive. Metacarpals I-II are the longest; metacarpals IV and V are more massive and more flattened palmo-dorsally. The proximal end of the metacarpals is more expanded than the distal one. A rounded oblique crest descends from the proximal head down to the shaft. The distal condyles appear poorly developed.

The **phalanges** are very short and palmo-dorsally flattened. Their proximal articular end is very concave, while the distal one forms convex divided condyles.

Pelvic girdle and hindlimb (Plate 2, Fig. 4):

Only the right **ilium** is preserved and can be described in dorsal view. It displays the typical ankylosaurid characters listed by COOMBS (1978): the postacetabular process is very shortened, whereas the preacetabular process is very elongated and diverges cranially from the vertebral column; both processes are twisted, so that their primitive medial surface faces upwards. The distance between the middle of the sacral vertebrae and the lateral edge of the ilium at the level of the rostral end of the preacetabular process is 37 cm long. The ilium of IMM/96 resembles that of *Pinacosaurus grangeri* in the strong divergence of its preacetabular process, suggesting a very wide basin (MARYANSKA, 1977). According to BUFFETAUT (1995), the preacetabular part of the ilium is straighter and less divergent in other ankylosaurids in which the pelvis is well-known, such as *Euoplocephalus* (see COOMBS, 1978, fig. 13). Nevertheless, it should be noted that the ilium of IMM 96BM3/1 appears less wide than that of PIUU R264, the fragmentary specimen from Shandong described by BUFFETAUT (1995, fig. 1) and referred to as *Pinacosaurus* cf. *grangeri*.

The right **femur** of IMM 96BM3/1 is partly preserved and completely crushed. It looks small, rather slender and perfectly straight, a common feature of ankylosaurs (COOMBS & MARYANSKA, 1990). Both the proximal and distal ends are scarcely expanded. By its slenderness, the femur reminds that of *P. grangeri* (see MARYANSKA, 1977, pl. 24, fig. 1). It also resembles those of *Talarurus* (see MALEEV, 1954, fig. 11; MALEEV, 1956, figs. 21-22) and *Shanxia* (see BARRETT *et al.*, 1998, fig. 8), but is clearly different from the robust femora of *Ankylosaurus*

and *Euoplocephalus* (see COOMBS, 1978, fig. 15). According to BUFFETAUT (1995), the general slenderness of the femur in *Pinacosaurus* is not related to ontogenetic changes, but is truly a taxonomic character, as it can be observed in juvenile (ZPAL MgD-II/1) and adult specimens of *P. grangeri*.

Both **tibiae** and the left **fibula** are also partially visible. They also look rather slender and straight, as is usual in ankylosaurs (COOMBS & MARYANSKA, 1990).

Some **pes** elements are preserved under the pelvic girdle on the left side of the specimen, but they are in a very bad state of preservation. As for the manus, these bones are short and massive.

Dermal armour (Plate 3, Fig. 1):

The **cervical armour** of IMM 96BM3/1 is composed of two half-rings, as is common in ankylosaurids (instead of three transverse rows in nodosaurids). The cranial cervical half-ring is formed by the fusion of three paired plates: the dorsomedial element is large, oval, concave and low-keeled; a lateroventral triangular edged spine, with a convex cranial border and a concave caudal one, projects laterally and slightly caudally; a small irregular scute is located in an intermediate position and fused to the other two elements. A fourth plate is located ventrolaterally relative to the lateral spine: this plate is triangular, edged and horizontal, facing cranio-laterally. Moreover, a thin and elongated stick of bone, pointing caudo-laterally, is supported by the dorsal keel of the dorsomedial plate. A similar stick was apparently present on the lateral side of the intermediate plate. The caudal cervical half-ring is situated approximately at the level of the cervico-dorsal junction. It is larger than the cranial half-ring and is formed by four pairs of fused plates. Medially, two oval scutes are similar in shape to the corresponding plates on the nuchal half-ring, but are slightly larger; they also bore elongated sticks of bones, whose traces can be observed on the dorsal side. Ventrally, an intermediate oval to irregular scute makes the junction with a large, pointed and flattened spine that projects laterally. In contrast to *Euoplocephalus*, the cervical half-rings of *Pinacosaurus*, *Saichania* and *Shamosaurus* (see MARYANSKA, 1977; NORMAN, 1985) are made up of fused keeled plates. In *Saichania*, the cervical yoke is formed by two bony layers and is heavier than that of *Pinacosaurus*, the dorsal and lateral plates being more keeled and sharply pointed (MARYANSKA, 1977, pl. 36, fig. 1) than in the Bayan Mandahu specimen. MARYANSKA (1977) very briefly described the cervical half-rings of *P. grangeri* as two-layered.

The dermal ossifications of the skull and the cervical armour plates are disposed to act as defensive structures. From the skull to the neck, there are three series of dermal elements, each one composed of parallel ossifications: dorsolaterally, the supraorbital protuberances, the squamosal horns and the bony sticks supported by the medial scutes of the cervical half-rings; laterally, the quadratojugal horns and the pointed spines of the two cervical

half-rings; ventrolaterally, the lower jaw ossifications and the sharp ventral scutes of the first cervical row.

Small oval scutes (Plate 3, Fig. 3) are arranged into a longitudinal row on the left side of the body at the level of the sixth, seventh and eighth dorsal vertebrae, between the ossified tendons and the dorsal ribs. A scute similar in size and shape is present on the right side at the level of the seventh vertebra. Erratic and displaced scutes have also been found in the thoracic region. This arrangement suggests that the dorsal armour was composed of a double longitudinal row of scutes disposed medially along the vertebral column. As in *P. grangeri*, there is no evidence of large elements, so that the dorsal armour of IMM 96BM3/1 appears to be lighter when compared to that of *Saichania*, *Euoplocephalus* and *Ankylosaurus*.

A shapeless mass of bony plates has been found at the end of the tail, representing the characteristic ankylosaurid **tail-club**. Although fragmentary, it appears relatively small and slender (Plate 3, Fig. 4). According to CURRIE (1991), the skeletons of *Pinacosaurus* juveniles have some armour elements on the skull and preserve two bands of cervical plates, but the rest of the body seems to have been unprotected and there is no evidence of a tail-club.

Identification and phylogenetic relationships

The specimen IMM 96BM3/1 is a typical Ankylosauria, as it presents the following synapomorphies (COOMBS, 1978; SERENO, 1986; COOMBS & MARYANSKA, 1990): low and flat skull; closed antorbital and supratemporal fenestrae; accessory antorbital ossifications; maxilla with deep, dorsally arched cheek emargination; quadratojugal contacts postorbital; quadrate slanting rostroventrally from the ventral side of the squamosal; ilium rotated into the horizontal plane; neural spines and chevrons of distal caudal vertebrae elongate along the axis of the tail, with extended contacts between haemal spines; extensive dermal armour composed of a series of large plates arranged in rows and a mosaic of small ossicles.

Numerous synapomorphies of both the skull and postcranial skeleton allow us to refer the new specimen from Bayan Mandahu to the family Ankylosauridae rather than to the Nodosauridae (COOMBS, 1978; SERENO, 1986; COOMBS & MARYANSKA, 1990): maximum width of skull greater than length; snout arches above level of postorbital skull roof; external nares divided by a horizontal premaxillary septum; complex secondary palate; sinus-complex developed in the premaxillary-maxillary area; prominent wedge-shaped quadratojugal horns projecting laterally; large wedge-shaped squamosal horns projecting posterolaterally; infratemporal fenestra and quadratojugal hidden in lateral view by quadratojugal and squamosal dermal ossifications; sharp lateral rim and low dorsal prominence for each lateral supraorbital element; flat lateral supraorbital margin above the orbit; very low

coronoid process; two cervical half-rings of armour; short postacetabular process of ilium; ossified tendons surrounding distal caudal vertebrae; terminal tail-club.

The following ankylosaurids are represented in the Late Cretaceous of the Gobi Desert (including the Bayan Shireh, Djadokhta, Barun Goyot and Nemegt formations): *Pinacosaurus grangeri* GILMORE, 1933; *Talarurus plicatospineus* MALEEV, 1952; *Maleevus disparoserratus* (MALEEV, 1952); *Tarchia gigantea* (MALEEV, 1956); *Saichania chulsanensis* MARYANSKA, 1977; and *Tsangantegia longicranialis* TUMANOVA, 1993. *Nomina dubia* include *Sauropites scutiger* BOHLIN, 1953; *Stegosaurides excavatus* BOHLIN, 1953; and *Peishansaurus philemys* BOHLIN, 1953. *Amtosaurus magnus* was described as an ankylosaurid (KURZANOV & TUMANOVA, 1978) but it may be an hadrosaurid (COOMBS & MARYANSKA, 1990). As already pointed out in the description, the specimen IMM 96BM3/1 closely resembles, especially in its skull morphology, *Pinacosaurus grangeri*. Both share the following apomorphies (MARYANSKA, 1977; COOMBS & MARYANSKA, 1990), justifying the attribution of IMM 96BM3/1 to the genus *Pinacosaurus*: presence of paired "gland" openings on the premaxilla; slender mandible with roughly parallel dorsal and ventral margins of the dentary [MARYANSKA (1977) suggested that this peculiar morphology is due to ontogenetic changes, but, with the discovery of IMM 96BM3/1, a taxonomic significance is more plausible]; small edged ossification on the angular area of the mandible reaching the level of the penultimate alveolus; complete reduction of neural arches on caudalmost cervical vertebrae; strongly divergent preacetabular process of the ilium and lightened dorsal armour.

The preceding description has underlined several differences between the skeleton of IMM 96BM3/1 and that of *Pinacosaurus grangeri*, justifying the erection of a new species, *P. mephistocephalus*. The main differences between both species are summarized below:

- Two pairs of premaxillary foramina leading to premaxillary sinuses in *P. mephistocephalus*. One single pair is known in *P. grangeri*.
- The so-called "gland" opening is rostrally located in *P. mephistocephalus*. In *P. grangeri*, this opening is located ventrolaterally.
- The premaxillary foramen is nearly as large as the "gland" opening in *P. grangeri*. In *P. mephistocephalus*, both pairs of premaxillary foramina are much smaller than the "gland" opening.
- In *P. mephistocephalus*, the external nares are only visible in dorsal view. In *P. grangeri* they are also visible in ventral view.
- The orbit is circular, as high as long and oriented laterally in *P. mephistocephalus*. In *P. grangeri*, the orbit is oval, longer than high and oriented ventrolaterally.
- In *P. mephistocephalus*, no caudodorsal process of the premaxilla protrudes between the maxilla and nasal as in *P. grangeri*.
- The lacrimal of *P. mephistocephalus* is square-shaped.

This bone is subrectangular and more elongated in *P. grangeri*.

– In *P. mephistocephalus*, the parietal is much shorter than the frontal. In *P. grangeri*, both are subequal in length.

– The frontoparietal process of the postorbital is wider in *P. mephistocephalus* than in *P. grangeri*.

– The frontoparietal depression parallel to the caudal margin of the skull roof is much deeper in *P. mephistocephalus* than in *P. grangeri*.

– In *P. mephistocephalus*, the scapula is shorter, less convex externally, with a better developed acromial process than in *P. grangeri*.

– In *P. mephistocephalus*, the deltopectoral crest is well-developed and extends down below the shaft to terminate distal to the humeral mid-length. In *P. grangeri*, the deltopectoral crest is less developed and terminates at about the level of the humeral mid-length.

– In *P. mephistocephalus*, the proximal articular end of the radius is strongly expanded both medio-laterally and cranio-caudally. It is very narrow in *P. grangeri*, especially in the juvenile ZPAL MgD-II/1.

The differences in the structure of the external nares are here interpreted as indubitable specific characters. The other characters may be specific too, although an ontogenetic variation within *Pinacosaurus* cannot be excluded. The validity of their taxonomic status must therefore await detailed study of more material from Bayan Mandahu.

The phylogenetical relationships among ankylosaurids are not well understood and a complete cladistic analysis of the Ankylosauridae is not yet available. MARYANSKA (1977) regarded *Pinacosaurus* as an intermediate form between the primitive *Talarurus* and the more advanced forms *Saichania* and *Tarchia* on the basis of the structure of the neurocranium and cranial sinuses. COOMBS & MARYANSKA (1990) recognized two clades within the Ankylosauridae: a “crown” clade including *Ankylosaurus*, *Euoplocephalus* and *Talarurus*, and a sister group consisting of *Pinacosaurus*, *Tarchia* and *Saichania*; *Shamosaurus* is regarded as a basal taxon. The *Pinacosaurus-Saichania-Tarchia* clade was defined by four characters: rostradorsal skull roof covered by 14 to 18 large plates; squamosal horns narrow in dorsal view; laterally flaring naris circular in rostral view; and short premaxillary beak rostral to naris (COOMBS & MARYANSKA, 1990: fig. 22.14). The inclusion of *Talarurus* within the *Euoplocephalus-Ankylosaurus* group is challenged by SULLIVAN (1999: fig. 7), who interpreted it as a basal ankylosaurid; *Talarurus*, *Shamosaurus* and, tentatively, *Tsagantegia* are considered by SULLIVAN (1999) to be an unresolved polytomy and sister taxa to the remaining ankylosaurids because they lack large oval nostrils facing rostrally and divided by a horizontal septum (present on both *Pinacosaurus grangeri* and *P. mephistocephalus*). *Pinacosaurus* lacks the occurrence of an expanded secondary palate, a character shared by *Ankylosaurus*, *Euoplocephalus*, *Sai-*

chania, *Tarchia* and *Nodocephalosaurus* (see SULLIVAN, 1999). Moreover, the presence of bulbous, polygonal, bilateral and symmetrically arranged osteodems over the frontonasal region of the skull roof unites *Saichania*, *Tarchia* and *Nodocephalosaurus*. The North American *Ankylosaurus* and *Euoplocephalus* are the most derived ankylosaurids based on a number of apomorphies listed by COOMBS & MARYANSKA (1990).

It should be noted that SULLIVAN (1999) considered *Tianzhenosaurus youngi* PENG & CHENG, 1998 to be a junior synonym of *Saichania chulsanensis*, and *Shanxia tianzhenensis* BARRETT, HAILU, UPCHURCH & BURTON, 1998 to be an Ankylosauridae *nomen dubium*. Both *Tianzhenosaurus* and *Shanxia* occur in the same formation and the same region, so it is likely that they represent the same taxon (SULLIVAN, 1999). The validity of *Maleevus disparoserratus* (MALEEV, 1952) and *Amtosaurus magnus* KURZANOV & TUMANOVA, 1978 is controversial: both are based on very fragmentary material and *Amtosaurus* may not pertain to the Ankylosauria (COOMBS & MARYANSKA, 1990). Finally, the phylogenetic relationships of the Jurassic taxa *Gargoyleosaurus parkpini* CARPENTER, MILES & CLOWARD, 1998 and *Tianchisaurus nedegoapeferima* DONG, 1993b are currently under debate.

Ontogenetic changes in *Pinacosaurus*

Pinacosaurus is a medium-sized ankylosaur: adult individuals reach about 5 m in length (MARYANSKA, 1977). The juvenile specimens discovered at Bayan Mandahu by the Chinese-Canadian Dinosaur Project measure 1.5 m in length (CURRIE, 1991; JERZYKIEWICZ *et al.*, 1993). IMM 96BM3/1, which comes from the same locality, is about 3 m long. The skull of IMM 96BM3/1 is larger (greatest length 23.8 cm, width 24 cm) than that of the juvenile *P. grangeri* ZPAL MgD-II/1 (length to 18.5 cm and width to 21 cm; MARYANSKA, 1971, 1977), but it is distinctly smaller than that of the holotype specimen AMNH 6523 (skull length to 30.5 cm, width to 34 cm, but these are estimated measurements because the skull is crushed and incomplete).

IMM 96BM3/1 provides new data about the ontogenetic changes in ankylosaurs. According to its size and cranial features, this specimen could be identified as that of an immature individual. In all fully-ossified adult ankylosaurs, the sutural boundaries of the skull bones are obliterated, because of the co-ossification of armour plates or the accretion of secondary epidermal bony deposits (COOMBS & MARYANSKA, 1990). This is also true in *Pinacosaurus*: in AMNH 6523, the holotype of *P. grangeri*, small secondary dermal plates hide the sutural boundaries between the skull bones (GILMORE, 1933). In contrast, the cranial sutural pattern of IMM 96BM3/1 is known, as well as that of the juvenile *P. grangeri* ZPAL MgD-II/1 (MARYANSKA, 1971, 1977). Cranial elements that are uncommon or unknown within the ornithischian dinosaurs can be observed in these

specimens, e.g. a pair of "tabular" bones in the rear of the skull roof and an "ethmoid" bone between the nasals and frontals in ZPAL MgD-II/1, and three extra supra-orbital elements in both individuals. The lack of fusion between the skull roof and the occiput also supports the immature nature of IMM 96BM3/1.

Unlike the juvenile ZPAL MgD-II/1, the specimen IMM 96BM3/1 bears well-developed quadratojugal and squamosal ossifications forming prominent horns. The development and orientation of these horns probably displays an important ontogenetic variability and maybe some sexual dimorphism, as observed in numerous modern bovids and also in ceratopsian dinosaurs (LEHMAN, 1990). The taxonomic value of these structures is therefore difficult to evaluate in the current state of our knowledge.

Several ontogenetic characters of the postcranial skeleton indicate that IMM 96BM3/1 is not a juvenile individual, but probably a subadult (*sensu* MARYANSKA, 1977; GALTON, 1982; COOMBS, 1986): the neural arches of the vertebrae are co-ossified to the centra; the dorsal ribs are fused to the centra; the sacral ribs are firmly fused to the centra and to the ilia; the ossified tendons are very well-developed in the dorsal area and along the distal portion of the tail; finally, the tail-club is well developed.

Distribution of *Pinacosaurus*

Ankylosaurs are usually regarded as good biostratigraphic indicators for Late Cretaceous formations in Mongolia: age assignment based on ankylosaurs agrees with results based on mammals and other groups (MARYANSKA, 1977; TUMANOVA, 1987). *Shamosaurus scutatus* TUMANOVA, 1983, from the Khukhtek Formation (Aptian-Albian: JERZYKIEWICZ & RUSSELL, 1991) of Outer Mongolia is one of the most primitive Asian ankylosaurids (SERENO, 1986; TUMANOVA, 1987). Only *Tianchisaurus nedegoapeferima* from the Middle Jurassic of the Junggar Basin, China (DONG, 1993b) and *Gargoyleosaurus parkini* from the Upper Jurassic of North America (CARPENTER *et al.*, 1998) are older and probably more basal members of the Ankylosauridae. In Inner Mongolia, the Tebch Formation (Barremian - early Aptian: EBERTH *et al.*, 1993) has yielded indeterminate ankylosaurid remains (*Sauroplices scutiger* BOHLIN, 1953). The Bayn Shireh Formation of Outer Mongolia (Cenomanian-Turonian: JERZYKIEWICZ & RUSSELL, 1991) has provided a diversified ankylosaurid fauna, composed of *Talarurus plicatospineus* MALEEV, 1952; *Maleevus disparoserratus* (MALEEV, 1952); *Tsangantegia longicranialis* TUMANOVA, 1993, and *Amtosaurus magnus* KURZANOV & TUMANOVA, 1978. According to JERZYKIEWICZ *et al.* (1993), the Bayan Mandahu Formation of Inner Mongolia and the Djadokhta Formation and equivalents of Outer Mongolia, which have yielded *Pinacosaurus* specimens, are synchronous and Campanian in age. In the overlying Barun Goyot Formation (Campanian: JERZY-

KIEWICZ & RUSSELL, 1991; Late Campanian - Early Maastrichtian: LILLEGRAVEN & FOX, 1986), both *Saichania chulsanensis* MARYANSKA, 1977 and *Tarchia gigantea* (MALEEV, 1956) have been discovered. The latter species is also represented in the Nemegt Formation of Outer Mongolia (Maastrichtian: ROZHDESTVENSKY, 1977; LILLEGRAVEN & MCKENNA, 1986; JERZYKIEWICZ & RUSSELL, 1991).

The geographical distribution of *Pinacosaurus* appears relatively wide in Central Asia. Besides the Djadokhta Formation and equivalent beds of Outer Mongolia and the Bayan Mandahu Formation of Inner Mongolia, other specimens, mainly postcranial bones of *Pinacosaurus nighsiensis* YOUNG, 1935 referred to *P. grangeri* by MARYANSKA (1977), were found in the Alashan Desert of northern Ningxia Province by the Sino-Swedish Expedition in 1932. Outside the Gobi Basin, ankylosaurid remains from the Wangshi Group of Shandong Province in northeastern China have been collected by the Sino-Swedish Expedition in 1923 (WIMAN, 1929) and referred to *Pinacosaurus* cf. *grangeri* by BUFFETAUT (1995). Both the material from Ningxia and Shandong should be referred to *Pinacosaurus* sp., as no specific diagnostic character can be observed. According to BUFFETAUT (1995), *Pinacosaurus* had a rather wide range of habitats, from semiarid conditions at Bayn Dzak and Bayan Mandahu (JERZYKIEWICZ *et al.*, 1993; EBERTH, 1993) to more humid habitats at Shandong (ZHAO, 1992). Reflecting these environmental differences, the vertebrate faunas are also very different in the Gobi Basin formations and in the Wangshi Group with, for instance, numerous *Protoceratops* at Bayn Dzak and Bayan Mandahu, whereas hadrosaurs dominate at Shandong.

The faunal resemblance between the Djadokhta Formation at Bayn Dzak and the Bayan Mandahu Formation is evident, as previously noted by JERZYKIEWICZ *et al.* (1993). The theropod dinosaurs *Saurornithoides mongoliensis* OSBORN, 1924 (CURRIE & PENG, 1993) and *Oviraptor philoceratops* OSBORN, 1924 (DONG & CURRIE, 1996), but also numerous squamate species (GAO & HOU, 1996) occur in both localities. The present paper suggests that the ankylosaur *Pinacosaurus* is represented by different species in the two formations. The large multituberculate mammal *Tombataar* ROUGIER, NOVACEK & DASHZEVEG, 1997 seems also represented by different species in the Djadokhta equivalent strata at Ukhaa Tolgod and at Bayan Mandahu (Rougier, pers. comm., 1997), but this hypothesis requires detailed study of the new specimens discovered by the IMM at Bayan Mandahu (Smith *et al.*, in prep.). Preliminary morphometrical studies on *Protoceratops* skulls from Bayn Dzak and Bayan Mandahu also reveal specific differences between the faunas. If correctly interpreted, these differences may indicate local speciation processes between geographically isolated populations (there is a distance of about 350 km between Bayn Dzak and Bayan Mandahu). These faunal differences may reflect slightly distinct ecological conditions, as suggested by the relative abundance of trionychid turtles at Bayan Mandahu (BRINKMAN &

PENG, 1996). Even so, it is not certain that both formations are strictly synchronous, as no chronostratigraphic scheme based on palynofloral, radioisotopic or palaeomagnetic data has been devised for Late Cretaceous continental sequences in the Gobi Basin.

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PLATE 1

Skull and lower jaw of *Pinacosaurus mephistocephalus* (IMM 96BM3/1), from the Upper Cretaceous of Bayan Mandahu (Inner Mongolia, P.R. China). A: rostral view; B: dorsal view; C: lateral view. Scale bar = 10 cm.

PLATE 2

Pinacosaurus mephistocephalus (IMM 96BM3/1), from the Upper Cretaceous of Bayan Mandahu (Inner Mongolia, P.R. China).

Fig. 1 — Dorsal view of the palate, during preparation of the skull. Scale bar = 10 cm.

Fig. 2 — Right premaxilla in rostral view, four nasal openings are visible. Scale bar = 5 cm.

Fig. 3 — Dentary teeth in lateral view. Scale bar = 5 mm.

Fig. 4 — Dorsal view of the pelvic area. Synsacrum, right ilium and right femur are visible. Scale bar = 20 cm.

Fig. 5 — Thoracic ribs in caudal view. Same scale bar as Fig. 4.

PLATE 3

Pinacosaurus mephistocephalus (IMM 96BM3/1), from the Upper Cretaceous of Bayan Mandahu (Inner Mongolia, P.R. China).

Fig. 1 — Lateral view of the skull and cervical half-rings, showing the defensive structures formed by the dermal ossifications. Scale bar = 10 cm.

Fig. 2 — Lateral view of the right pectoral girdle and forelimb. Scale bar = 10 cm.

Fig. 3 — Detail of the dorsal side of the thoracic region, showing ossified tendons and isolated dermal scutes. Scale bar = 5 cm.

Fig. 4 — Distal end of the tail and tail-club. A: dorsal view; B: ventral view. Scale bar = 10 cm.

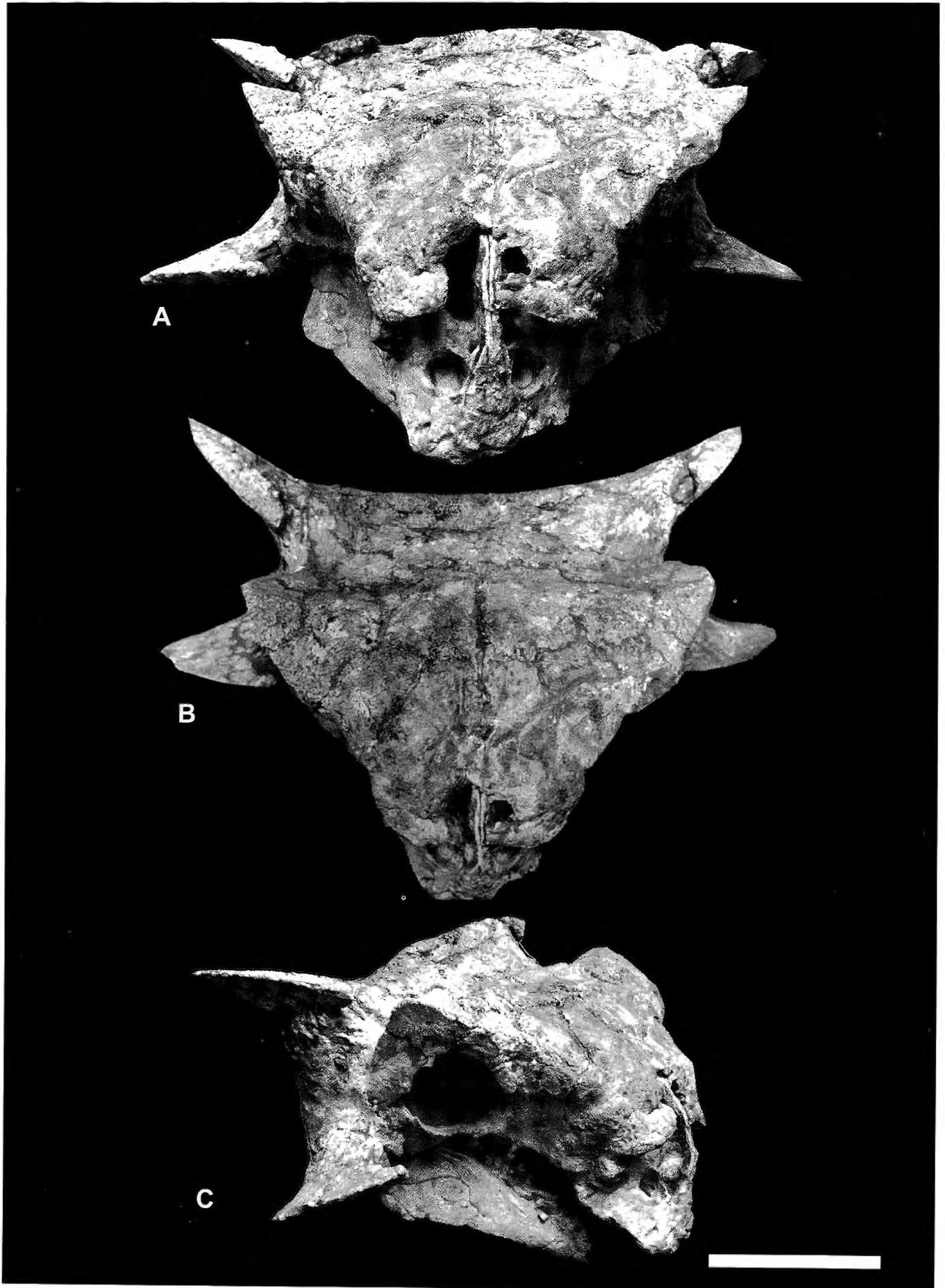


PLATE 1

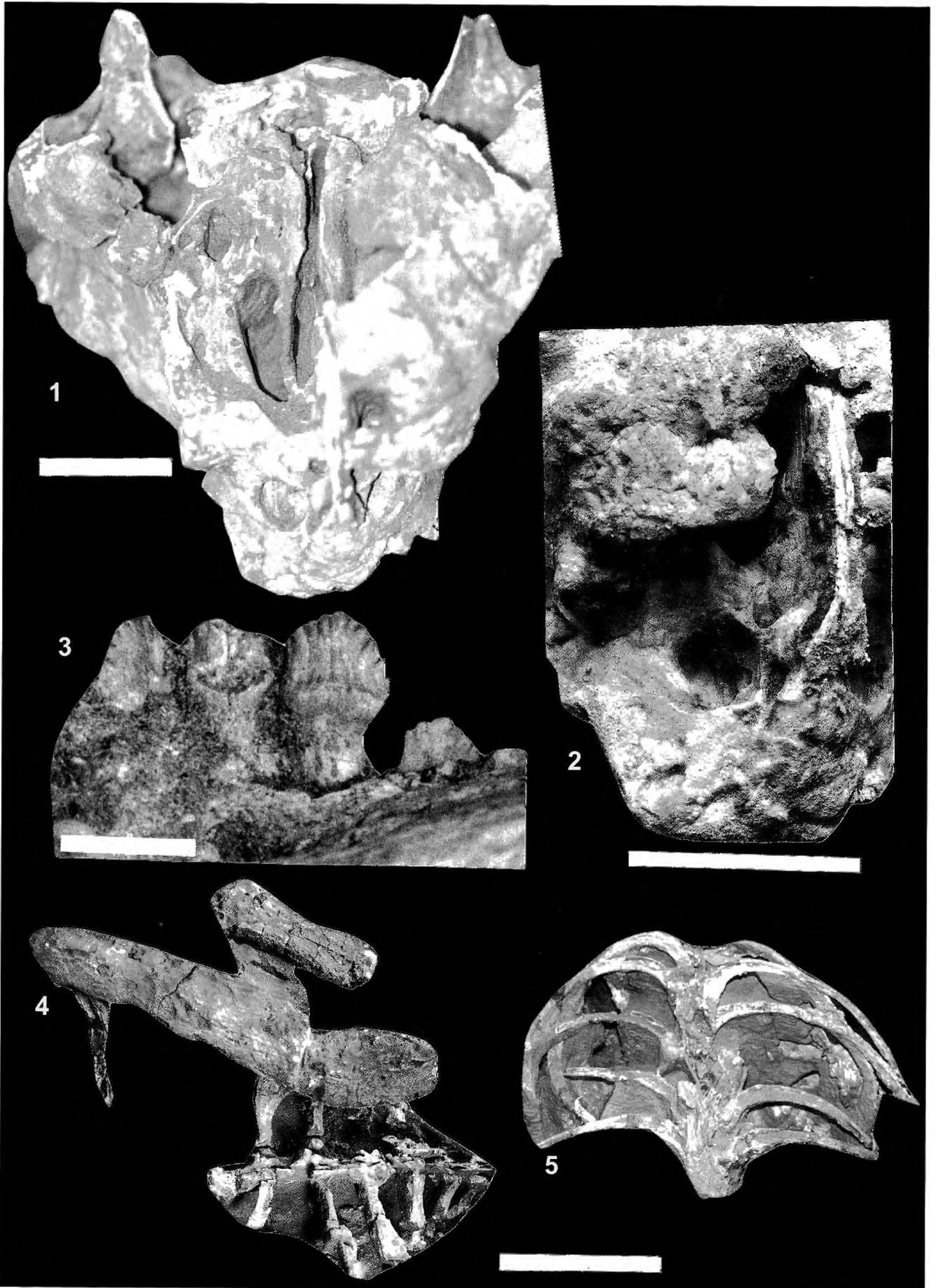


PLATE 2

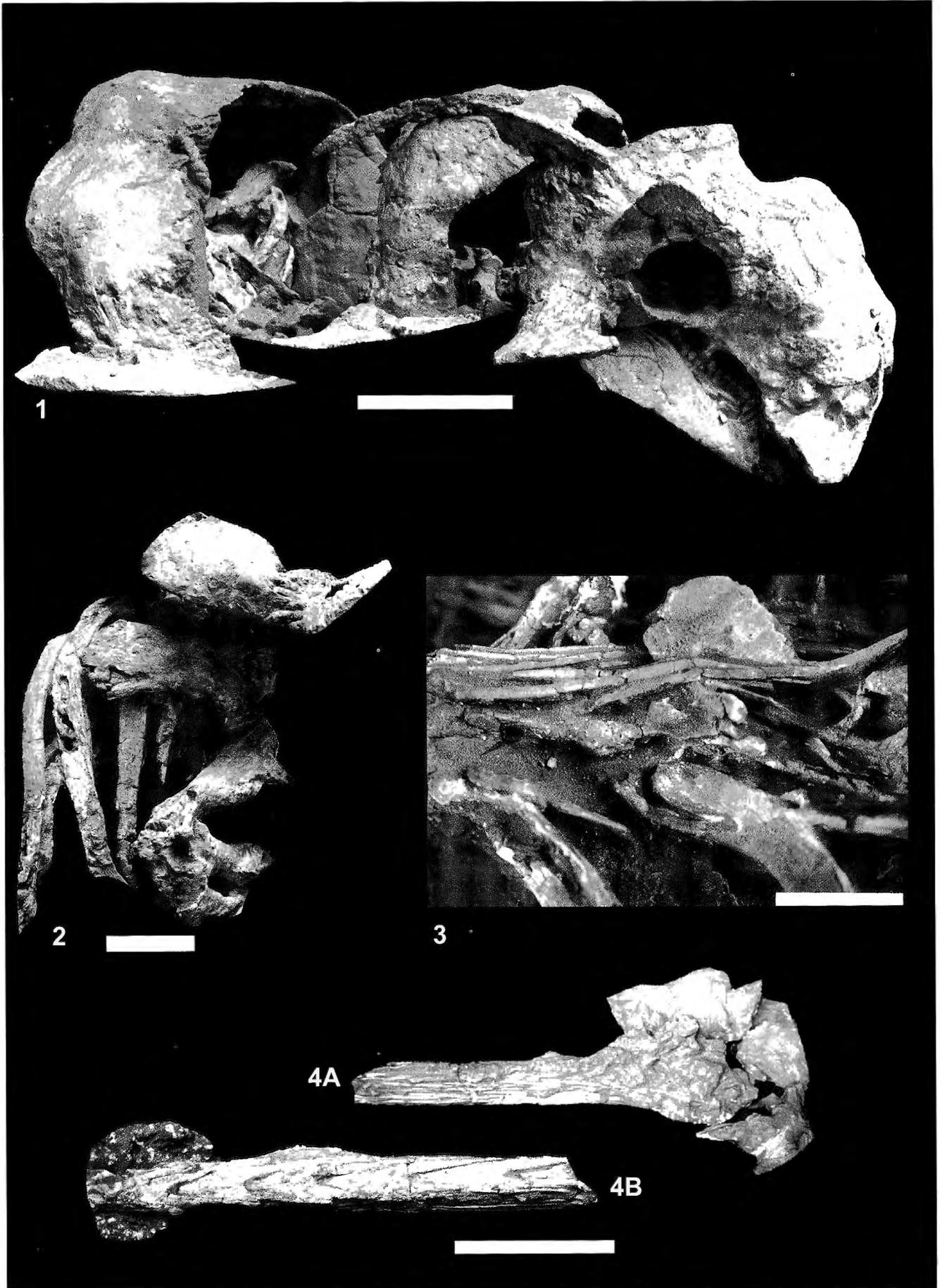


PLATE 3