AMERICAN MUSEUM
Novitates

PUBLISHED BY THE AMERICAN MUSEUM OF NATURAL HISTORY
CENTRAL PARK WEST AT 79TH STREET, NEW YORK, NY 10024
Number 3395, 29 pp., 9 figures February 19, 2003

A New Specimen of *Pinacosaurus grangeri* (Dinosauria: Ornithischia) from the Late Cretaceous of Mongolia: Ontogeny and Phylogeny of Ankylosaurs

ROBERT V. HILL,[1] LAWRENCE M. WITMER,[2] AND MARK A. NORELL[3]

ABSTRACT

Here we report the occurrence of a juvenile ankylosaur from the Upper Cretaceous locality Ukhaa Tolgod in southern Mongolia. The locality is well known for its exquisitely preserved theropods, mammals, and squamates, but until now has not yielded diagnostic ankylosaur material, although ankylosaur specimens are common at the site. The new specimen consists of a nearly complete skull with associated mandible and osteoderms that exhibits the following ankylosaurid synapomorphies: two pairs of osteodermal ''horns'' projecting from the quadratojugals and squamosals; a wide, triangular skull; a premaxillary beak edge that is not continuous with the maxillary tooth row; and absence of premaxillary teeth. We refer the specimen to *Pinacosaurus grangeri* based on the presence of a large premaxillary sinus, a quadrate not co-ossified with the paroccipital process, and several pairs of accessory openings in the narial region. The new specimen differs from the holotype and other specimens in having five pairs of openings in the narial region, indicating that extensive morphological variability exists in the narial anatomy of *P. grangeri*.

The specimen is identified as a juvenile based on its small size and the incomplete fusion of secondary dermal ossifications to the skull roof, exposing sutural boundaries. Juvenile ankylosaur skulls are rare, but crucial for understanding the basic anatomy of the highly fused and apomorphic adult skull. Morphological data from the new skull and other specimens are

---

[1] Ph.D. Candidate, Department of Anatomical Sciences, State University of New York at Stony Brook, Stony Brook, NY 11794-8081. e-mail: rvhill@ic.sunysb.edu

[2] Associate Professor of Anatomy, Department of Biomedical Sciences and College of Osteopathic Medicine, Ohio University, Athens, OH 45701. e-mail: witmerl@ohio.edu

[3] Curator and Chair, Division of Paleontology, American Museum of Natural History. e-mail: norell@amnh.org

ISSN 0003-0082

added to existing phylogenetic analyses of the Ankylosauria in order to identify diagnostic characters that aid in resolving ankylosaur relationships.

The specimen also provides data on the ontogenetic sequence of secondary dermal ossification. Presence of dermal ossifications covering only the narial region, quadratojugals, and squamosals supports the hypothesis that osteoderms in these areas appear early in ontogeny. Furthermore, two well-developed osteoderms were found in close apposition but unfused to the ventrolateral edges of the mandible. All known mandibles from adult ankylosaurs exhibit fusion of these elements to the underlying bones. Thus, mandibular osteoderms also appear relatively early but do not become fused until much later.

INTRODUCTION

In the early 1920s, the American Museum of Natural History began its Central Asiatic Expeditions marking the advent of intensive paleontological research in the Gobi Desert (Andrews, 1932). The exceptionally well-preserved fossils discovered by these early expeditions included dinosaur eggs and the skeletal remains of Mesozoic mammals, theropods, ceratopsians, and ankylosaurs. The first report of ankylosaurs in Asia was made by Gilmore (1933a), who described a partial right ilium and caudal centrum too fragmentary to name. Soon afterward, however, Gilmore (1933b) named *Pinacosaurus grangeri*, the first new taxon of ankylosaur from Asia, based on a skull, osteoderms, and anterior cervical vertebrae from specimens found at Bayn Dzak.

The last of the Central Asiatic Expeditions took place in 1930, after which date American paleontologists would not return to the Gobi for nearly 60 years (Novacek, 1996; Gallenkamp, 2001). Swedish, Canadian, Polish, and Russian scientists, however, continued to collaborate with their Mongolian and Chinese colleagues, and their expeditions recovered several new taxa of ankylosaurs such as *Talarurus* (Maleev, 1952), *Saichania* and *Tarchia* (Maryańska, 1977), *Amtosaurus* (Kurzanov and Tumanova, 1978), *Shamosaurus* (Tumanova, 1983), and *Tsagantegia* (Tumanova, 1993). More recently described ankylosaur material from China includes *Shanxia* (Barrett et al., 1998), *Tianzhenosaurus* (Pang and Cheng, 1998), and *Gobisaurus* (Vickaryous et al., 2001a).

Despite discoveries of new taxa, *Pinacosaurus grangeri* remains the best known Asian ankylosaur, represented by over 15 specimens (Coombs and Maryańska, 1990), including a nearly complete skeleton, trunk osteoderms, and several well-preserved skulls. Several of these specimens have been found in associations (Jerzykiewicz et al. 1993; Norell, personal obs.) suggesting that these animals may have been social. Young (1935) named *P. ninghsiensis* from the Late Cretaceous of Ningxia Province, China. This taxon is now considered a junior synonym of *P. grangeri*, as is *Syrmosaurus viminicaudus*, which consists of fragmentary remains described by Maleev (1952). Recently, Godefroit et al. (1999) described a new taxon, *Pinacosaurus mephistocephalus*, from the Late Cretaceous of China. This species differs considerably from *P. grangeri* in characters of the narial anatomy and secondary dermal ‘‘horns’’.

American Museum expeditions to the Gobi resumed in 1990, and by 1993 several new fossil localities were discovered, including the richly fossiliferous Ukhaa Tolgod (Dashzeveg et al., 1995). To date, Ukhaa Tolgod has produced approximately 1000 specimens each of mammals and lizards, and abundant remains of theropods, ceratopsians, and ankylosaurs (Gao and Norell, 2000). Here we report the first diagnostic ankylosaur material to be described from Ukhaa Tolgod.

Institutional Abbreviations: **AMNH**, American Museum of Natural History, New York; **DMNH**, Denver Museum of Natural History; **IGM**, Institute of Geology, Ulaan Baatar, Mongolia; **IMM**, Inner Mongolia Museum, Hohhot; **IVPP**, Institute for Vertebrate Paleontology and Paleoanthropology, Beijing; **PIN**, Paleontological Institute, Moscow; **ZPAL**, Institute of Paleobiology (Zaklad Paleobiolgii) of the Polish Academy of Sciences, Warsaw.

GEOLOGICAL SETTING

For over 75 years (Andrews, 1932) vertebrate fossils have been collected from Late

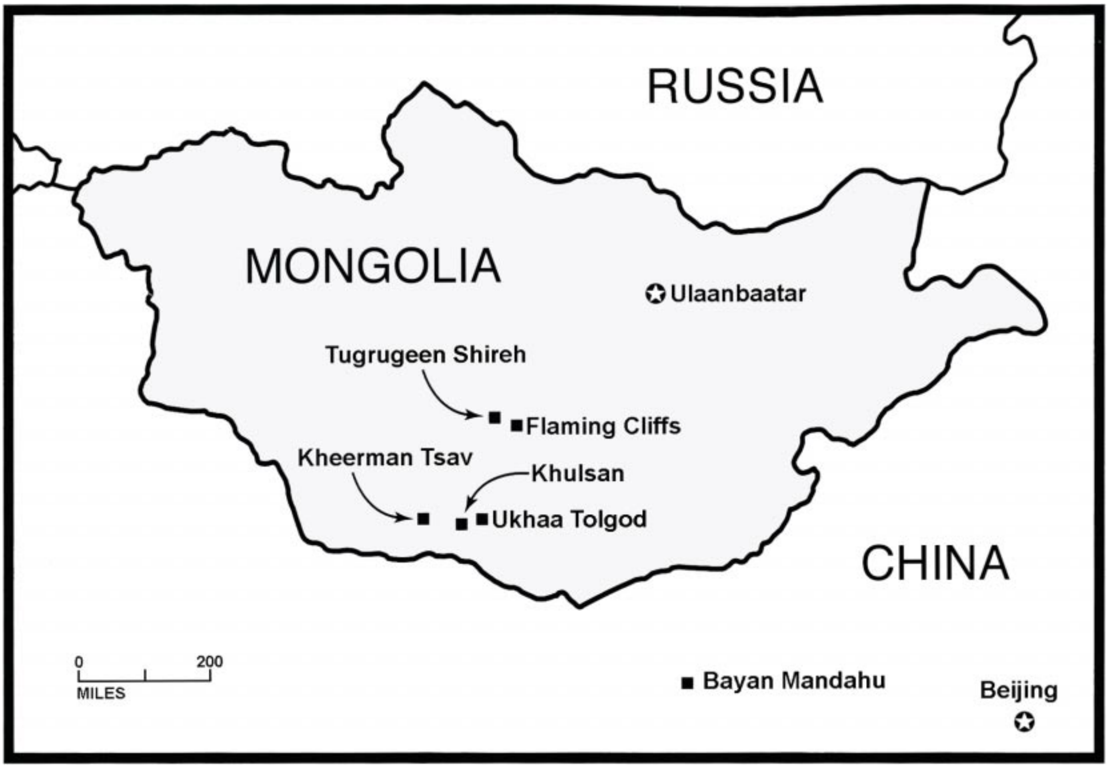


Fig. 1. Map of Mongolia showing major fossiliferous localities, including Ukhaa Tolgod, where the new specimen of *Pinacosaurus grangeri* was found. Modified from Gao and Norell (2000).

Cretaceous localities throughout the Nemegt Basin of southern Mongolia. Most of these localities can be assigned, based on faunal composition and lithology, either to the Middle Campanian Djadokhta Formation or to the Late Campanian Barun Goyot Formation, although precise ages are unknown (see Lillegraven and McKenna, 1986 and Gao and Norell, 2000). Among the most productive of these localities is Ukhaa Tolgod (''brown hills''; fig. 1). Discovered in 1993, the locality has yielded exceptionally well-preserved fossils, including small mammals, lizards, and abundant dinosaur remains (Dashzeveg et al., 1995). The most spectacular finds include fully articulated skeletons of oviraptorids (Clark et al., 2001), some preserved in birdlike brooding postures (Norell et al., 1995; Clark et al., 1999), or with embryos and eggs (Norell et al., 1994). Other dinosaur lineages are represented, including dromaeosaurids, alvarezsaurids, troodontids, ceratopsians, and ankylosaurs (Norell, 1997, Gao and Norell, 2000). The new specimen (IGM 100/1014) was collected at the Camel's Humps locality in the floor of a large quarry on the eastern flank of this escarpment.

The precise stratigraphic and temporal position of Ukhaa Tolgod is not known, as this locality yields mammal specimens previously thought to be unique to each of the two major geological formations in the region (Gradzinski et al., 1977). Gao and Norell (2000) showed that the faunas cannot be distinguished on the basis of fossil lizards, the most common fossil vertebrates recovered at these localities. Thus the distinction between the Djadokhta and Barun Goyot Formations is blurred. However, Dashzeveg et al. (1995) and Loope et al. (1998) have suggested that Ukhaa Tolgod resembles most closely the Flaming Cliffs locality (Bayn Dzak), the type section of the Djadokhta Formation, in its lithology. Both localities are comprised of basal massive sandstones, overlain by thick, highly fossiliferous aeolian deposits, and finally a sequence of fluvial facies consisting of interbedded sandstones, mudstones, and conglomerates.

SYSTEMATIC PALEONTOLOGY

DINOSAURIA OWEN, 1842

ORNITHISCHIA SEELEY, 1887

THYREOPHORA NOPCSA, 1915
(SENSU NORMAN, 1984)

ANKYLOSAURIA OSBORN, 1923

ANKYLOSAURIDAE BROWN, 1908

PINACOSAURUS Gilmore, 1933b
(= *Syrmosaurus* Maleev, 1952)

TYPE SPECIES: *Pinacosaurus grangeri* Gilmore, 1933b.

INCLUDED SPECIES: Type species and *P. mephistocephalus* Godefroit et al., 1999.

AGE AND DISTRIBUTION: ?Late Santonian–Late Campanian of Mongolia and People's Republic of China.

REVISED DIAGNOSIS: Medium-sized ankylosaurid, attaining approximately 5 m in length, with skull longer than wide in adult; premaxillary beak edge not covered by secondary dermal ossifications; large, rostrally facing nares roofed by osteoderms; premaxillary struts define at least two additional openings in narial region, leading to an extensive premaxillary sinus; prominent, hornlike protuberances above orbit formed by lateralmost supraorbital bone; lacrimal incisure (marked pinching of snout in lacrimal region so that the orbits and narial region project laterally beyond the incisure); beak only slightly wider than distance between caudalmost maxillary teeth; quadrate not co-ossified with the paroccipital process; quadrate cotyla lying directly below caudal margin of orbit.

Pinacosaurus grangeri Gilmore, 1933b
(= *P. ninghsiensis* Young, 1935;
Syrmosaurus viminicaudus Maleev, 1952)

HOLOTYPE: AMNH 6523, dorsoventrally crushed skull and mandible with several associated osteoderms, atlas and axis.

TYPE LOCALITY: Djadokhta Formation, Shabarakh Usu, Mongolia (e.g., ''The Flaming Cliffs'').

REFERRED SPECIMENS: Uncataloged IVPP specimens; IGM 100/1014; PIN 614, uncataloged PIN specimens; ZPAL MgD-II/1, ZPAL MgD-II/2, ZPAL MgD-II/7, ZPAL MgD-II/9, ZPAL MgD-II/27, ZPAL MgD-II/31, ZPAL MgD-II/32.

DIAGNOSIS: As for genus; *Pinacosaurus* with squamosal dermal ossifications present as weakly developed pyramids, not long spines as in *P. mephistocephalus*.

DISCUSSION: Abundant material collected by the Sino-Swedish, Polish-Mongolian, Sino-Canadian, and Russian-Mongolian expeditions has been referred to *P. grangeri* or *Pinacosaurus* sp. Most of the cranial material collected by these teams has represented juvenile or subadult individuals. All specimens of *Pinacosaurus* feature the distinctive set of characters found in the holotype, including a highly specialized narial region with at least three pairs of openings, prominent hornlike protuberances above the orbits, and lack of secondary dermal ossifications on the external rostroventral portion of the premaxillary beak. The holotype skull, however, also differs considerably from the numerous subadult crania that have been referred to the genus. The skull is longer than wide, with a narrow premaxillary beak and palate. Maryańska (1977) has attributed this condition to taphonomic processes, but the relatively mild distortion of the pterygoids and premaxillae suggests that the postdepositional reworking of this specimen was limited to dorsoventral crushing. Nevertheless, skulls subsequently referred to *P. grangeri* consistently exhibit the typical ankylosaurid condition of a skull and premaxillary palate that is wider than long.

A narrow skull can be found in more basal thyreophorans such as *Emausaurus ernsti*, *Scelidosaurus harrisonii,* and stegosaurs. The primitive ankylosaurids *Tsagantegia longicranialis* and *Shamosaurus scutatus* also exhibit this condition. The presence of a narrow skull in adult *Pinacosaurus* may be just one indicator of a phylogenetic affinity with these more primitive genera that has previously been obscured, as many of the characters considered diagnostic for the genus (and indeed, for suprageneric ankylosaurian taxa) have been scored from juvenile skulls that do not exhibit all features of the adult. In particular, the exceptionally com-

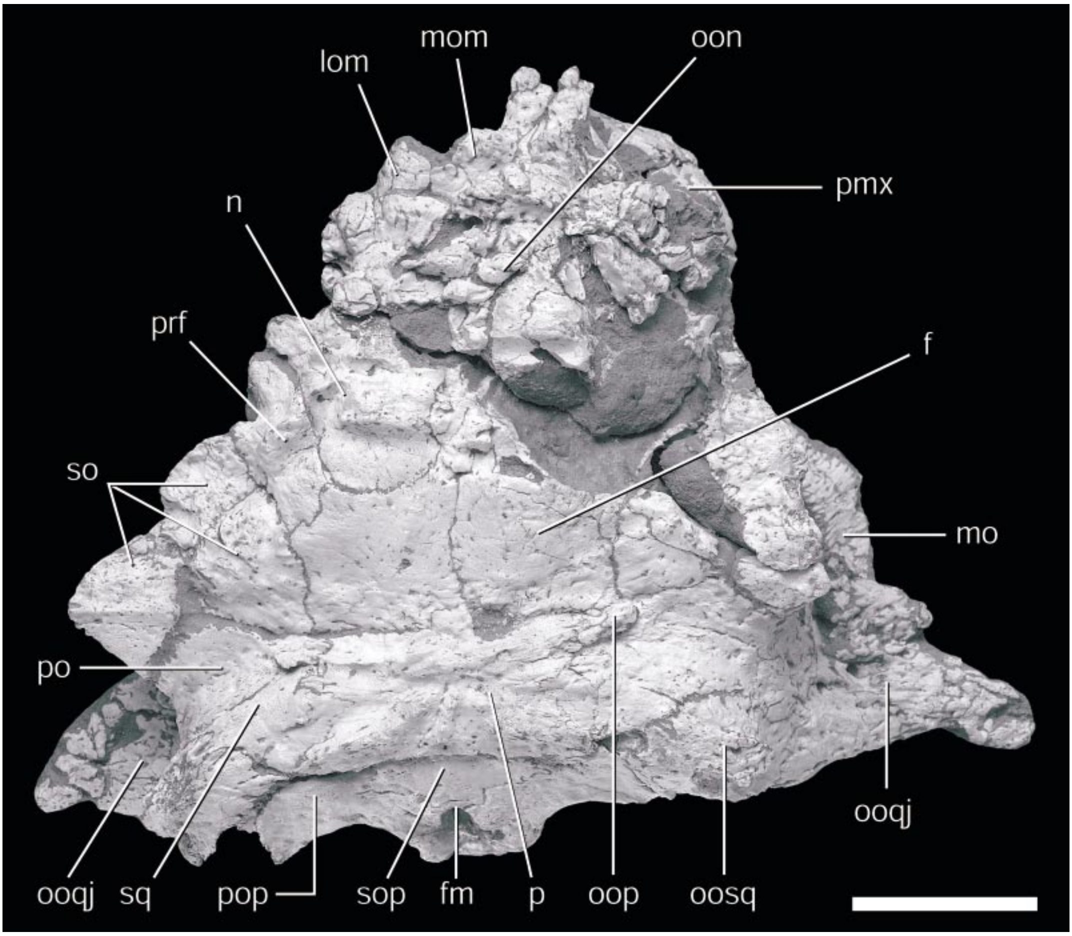


Fig. 2. *Pinacosaurus grangeri*. IGM 100/1014. Dorsal view of skull. See appendix 4 for abbreviations. Scale bar equals 5 cm.

plete skull of *P. grangeri* described by Maryańska (1971; 1977), ZPAL MgD-II/1, is frequently cited as displaying typical ankylosaurid morphology, despite the fact that it represents a juvenile individual (e.g., Sereno, 1986; Coombs and Maryańska, 1990).

DESCRIPTION

General Description: The new specimen (IGM 100/1014) is a nearly complete skull with both hemimandibles preserved intact along with the predentary. The skull has been subjected to some dorsoventral crushing and shearing, and the bones roofing the right antorbital region have been severely broken and lost. The skull is slightly larger than ZPAL MgD-II/1 in all dimensions, and it exhibits greater development of dermal sculpturing over the nasals, which comprise the rostral half of the skull roof. Fusion of secondary dermal ossifications to the more caudal portion of the skull roof has not occurred, and this allows sutural boundaries to be readily identified. The skull was prepared mechanically and the left mandible removed. It was then subjected to computed tomography (CT or CAT scanning), allowing assessment of some structures still located within matrix, although crushing and radiodense mineral deposits complicate interpretation.

Skull Roof (fig. 2): The frontals are subsquare and comprise the central portion of the caudal half of the skull roof. They are in contact with the nasals and prefrontals ros-

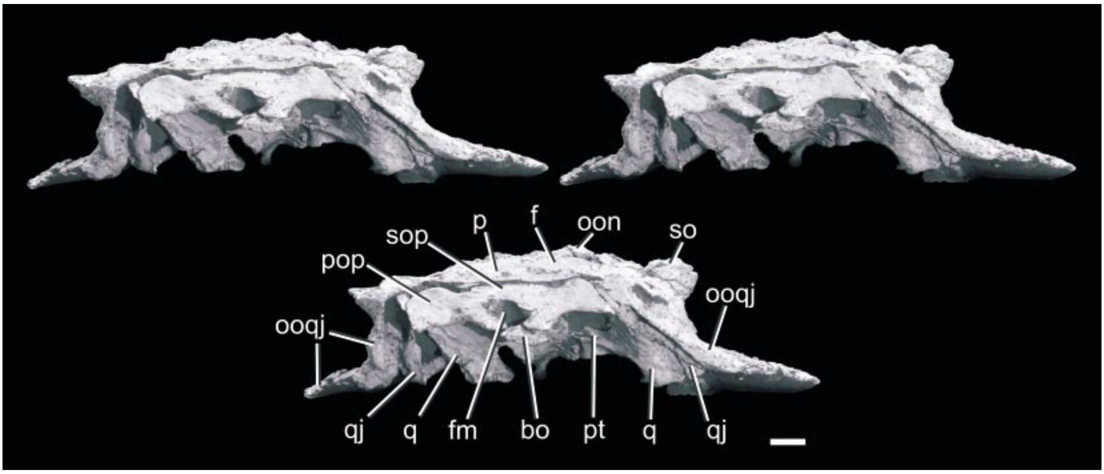


Fig. 3. *Pinacosaurus grangeri*. IGM 100/1014. Stereopairs of skull in occipital view. See appendix 4 for abbreviations. Scale bar equals 2 cm.

trally, and the supraorbitals (= postfrontals of Maryańska, 1971) and postorbitals laterally. Unlike ZPAL MgD-II/1, the parietals are fused, a condition that has been described previously among ankylosaurs only in *Minmi paravertebra* (Molnar, 1996), *Pinacosaurus mephistocephalus* (Godefroit et al., 1999), and *Cedarpelta bilbeyhallorum* (Carpenter et al., 2001); in other ankylosaurids, parietal fusion cannot be assessed due to the sutural boundaries being obscured by overlying osteoderms. Because the other sutures have remained unfused in this individual, fusion of the parietals appears to be the first step in the extensive fusion of the entire skull roof known in adult ankylosaurs. The single, fused parietal element contacts the squamosals and postorbitals laterally. A few small, unfused osteoderms are present at the rostrolateral corners of the parietal, extending laterally over the postorbitals. There is no development of a ‘‘tabular’’ element as described by Maryańska (1971).

The skulls of ZPAL MgD-II/1 and IGM 100/1014 share a wide, equilateral triangular outline in dorsal view, with prominent hornlike supraorbital protuberances (postsupraorbitals of Maryańska, 1971) and much smaller osteoderms extending caudolaterally from the squamosal region. Thus, in both specimens, the widest point of the skull roof is across the supraorbital elements. The dermal skull roof does not extend far enough caudally to obscure the occiput in dorsal view, although this character may be exaggerated by the dorsoventral crushing of the specimen.

OCCIPITAL REGION AND BRAINCASE (fig. 3): The basioccipital is badly crushed dorsoventrally, and much of its original morphology and that of the occipital condyle are difficult to interpret. A saddle-shaped depression on the underside of the basioccipital is present, as in *Nodocephalosaurus* (Sullivan, 1999), but there is no evidence of a distinct ‘‘neck’’ encircling the occipital condyle. The condyle is composed entirely of the basioccipital, and the articular surface appears to have been angled ventrally from the plane of the maxillary tooth rows. As in all ankylosaurs, the occiput of IGM 100/1014 is low and rectangular, and wider transversely than it is high. The small, subrectangular supraoccipital articulates suturally with the exoccipitals, and is largely excluded from the foramen magnum. The exoccipitals are high, rostrocaudally compressed, and appear only loosely associated with the quadrate and squamosal. CT scans confirm that the paroccipital processes are not fused to the squamosal, as in *Saichania,* nor are they fused to the quadrates, as in nodosaurids. The exoccipitals comprise the lateral borders and most of the dorsal border of the foramen magnum. Two small, rugose tuberosities, like those mentioned by Maryańska (1977), lie on the lateral border of the foramen magnum, imme-

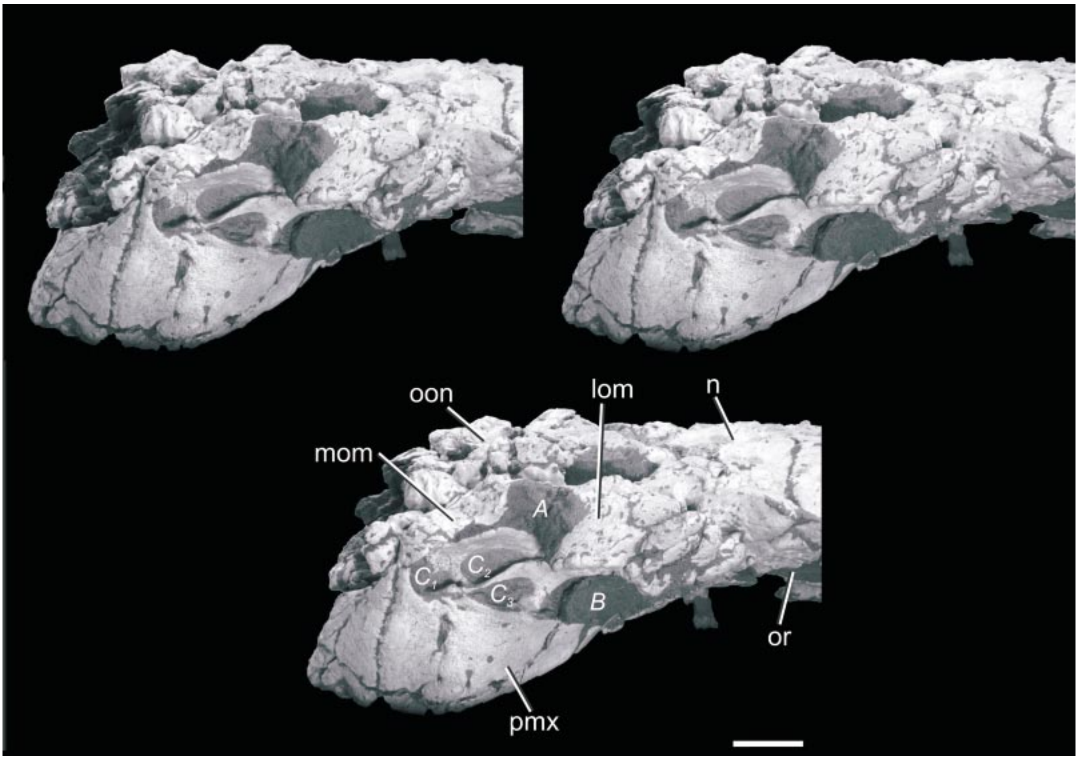


Fig. 4. *Pinacosaurus grangeri*. IGM 100/1014. Stereopairs of narial region in left anterolateral view showing narial apertures and recesses. See appendix 4 for abbreviations. Scale bar equals 2 cm.

diately dorsal to the articulation of the exoccipitals with the basioccipital.

The foramen for the hypoglossal nerve (C.N. XII) can be seen in the lateral edge of the exoccipital near its base. Immediately rostral to this foramen is another foramen for the exit of the glossopharyngeal, vagus, and accessory nerves (C.N. IX–XI). Other details of the braincase can be observed only in the CT scans. Most features are in agreement with Maryańska's (1977) description of ZPAL MgD-II/1, but the intact (i.e., unprepared) nature of much of the braincase of IGM 100/1014 allows clarification of some attributes with CT. For example, the otic vestibule opens broadly to the cranial cavity suggesting that the medial wall of the inner ear is poorly ossified and would have been cartilaginous in life; whether this reflects juvenile status is unknown, although an otic vestibule that is medially open to varying extents has been observed by one of us (L.M.W.) in CT scans of presumably adult *Edmontonia*, *Stegosaurus*, and some other dinosaurs. As perhaps in ankylosaurs generally, the rostrolateral wall of the braincase is strongly ossified, with a stout laterosphenoid broadly contacting the parietal dorsally and with an orbitosphenoid in front that contacts both the parietal and frontal.

NARIAL REGION (fig. 4): The rostral surface and tomial (ventral) margin of the beak is devoid of osteoderms, as is the case in most Asian ankylosaurids. Long caudolateral (maxillary) processes of the premaxillae obscure the most rostral maxillary teeth in lateral view. The dorsal (nasal) processes form an internarial bar that is visible far caudally between adjacent osteoderms. CT scans confirm that the internarial bar is prolonged ventrally as an internasal septum. The CTs reveal occasional gaps in the septum, but these are best attributed to postmortem or postdepositional damage to the septum, which is paper thin in some sections. Contribution of the nasal bone to this septum appears to be relatively slight.

Comparison of available specimens of *Pinacosaurus* reveals variation in the number of openings (real or otherwise, see below) in the narial region. AMNH 6523 and ZPAL MgD-II/1 each have three apparent apertures per side, which, for the sake of discussion, may be labeled *A*, *B*, and *C* (fig. 5). Godefroit et al. (1999) reported four pairs of openings in the holotype of *P. mephistocephalus* (IMM 96BM3/1). The new skull, IGM 100/1014, clearly has five such structures, which are better seen on the left side than on the badly damaged right side. Given that most authors (e.g., Godefroit et al., 1999: 29) regard such narial differences as ‘‘indubitable specific characters’’, further discussion is warranted.

Opening *A* is clearly the entrance to the airway, and represents the ‘‘true’’ bony nostril, as recognized by all modern authors (Maryańska, 1971, 1977; Tumanova, 1987; Coombs and Maryańska, 1990; Godefroit et al., 1999). Gilmore (1933b) regarded *C* as the airway entrance, but we can confirm Maryańska’s (1971, 1977) suggestion that AMNH 6523 preserves *A*. Opening *A* in IGM 100/1014 is very similar to those in ZPAL MgD-II/1 and AMNH 6523 in being bounded dorsally by two osteoderms (or osteodermal masses), with *A* forming an incisure between the two. Similarly, in all these skulls *A* is separated from *C* by a transversely thin, laminar bar of bone that CT scans show is concave medially.

Structure *B* is located caudolaterally fully within the premaxilla. This is the ‘‘gland opening’’ of Maryańska (1977) and Godefroit et al. (1999). In all known skulls, this structure has a well-marked fossa around it. The apparent shape of the structure in ZPAL MgD-II/1 and IMM 96BM3/1 is more or less round, whereas in the holotype and IGM 100/1014 it is larger and more rostrocaudally elongate. Structure *B* in IGM 100/1014 resembles AMNH 6523 and ZPAL MgD-II/1 in being located caudally near the contact with the maxilla, whereas IMM 96BM3/1 is unique in being more rostrally located.

Previous workers have regarded *B* as an aperture, that is, an opening leading internally into the premaxillary (or even maxillary) sinus system (Maryańska, 1971, 1977; Tumanova, 1987; Coombs and Maryańska, 1990; Witmer, 1997a). Godefroit et al. (1999: 24), however, noted that ‘‘this opening is . . . completely closed’’ in IMM 96BM3/1. One of us queried P. Godefroit about the seeming incongruity of a ‘‘closed opening’’, and he replied that indeed structure *B* is not an opening at all, but is ‘‘a depression [rather] than a true opening’’ (personal comm. from P. Godefroit to L.M.W., 30 August 2001). Moreover, Godefroit kindly reexamined IMM 96BM3/1 in China and confirmed ‘‘that our [Godefroit et al., 1999] ‘gland opening’ is completely closed, [forming] some kind of cup-shaped depression’’ (personal comm. from P. Godefroit to L.M.W., 7 November 2001). Close inspection of ZPAL MgD-II/1 failed to reveal conclusive evidence that the margins of the ‘‘opening’’ were not broken, and the possibility must be entertained that a thin bony floor may have been present in structure *B* and subsequently lost. CT scans of IGM 100/1014 are not as conclusive as might be hoped due to crushing and damage, but some slices may support the fossa hypothesis in that a thin wall of bone remains embedded in matrix 6–19 mm medial to the external margin of *B*. The significance here is that a foramen and a fossa are fundamentally different. If *B* is a foramen, as typically conceived, then it represents an additional opening into the premaxillary sinus (with *C* being the other, see below). If *B* is a fossa, however, then it implies a soft-tissue structure residing externally within the nasal vestibule that may have nothing to do with any sinuses. Clearly, CT scans of a well-preserved but generally unprepared specimen are needed.

Determination of the soft-tissue relations and hence function of structure *B* is perhaps moot pending conclusive evidence corroborating or refuting its status as a fossa. Although Maryańska (1971, 1977) regarded it as an aperture, her proposed function for it—housing a nasal salt gland—is actually more consistent with the fossa hypothesis. Osmólska (1979; see also Tumanova, 1987) accepted this gland hypothesis and extended it beyond *Pinacosaurus* to many other dinosaurs. Extant archosaurs and other sauropsids indeed possess a nasal gland that often is in-

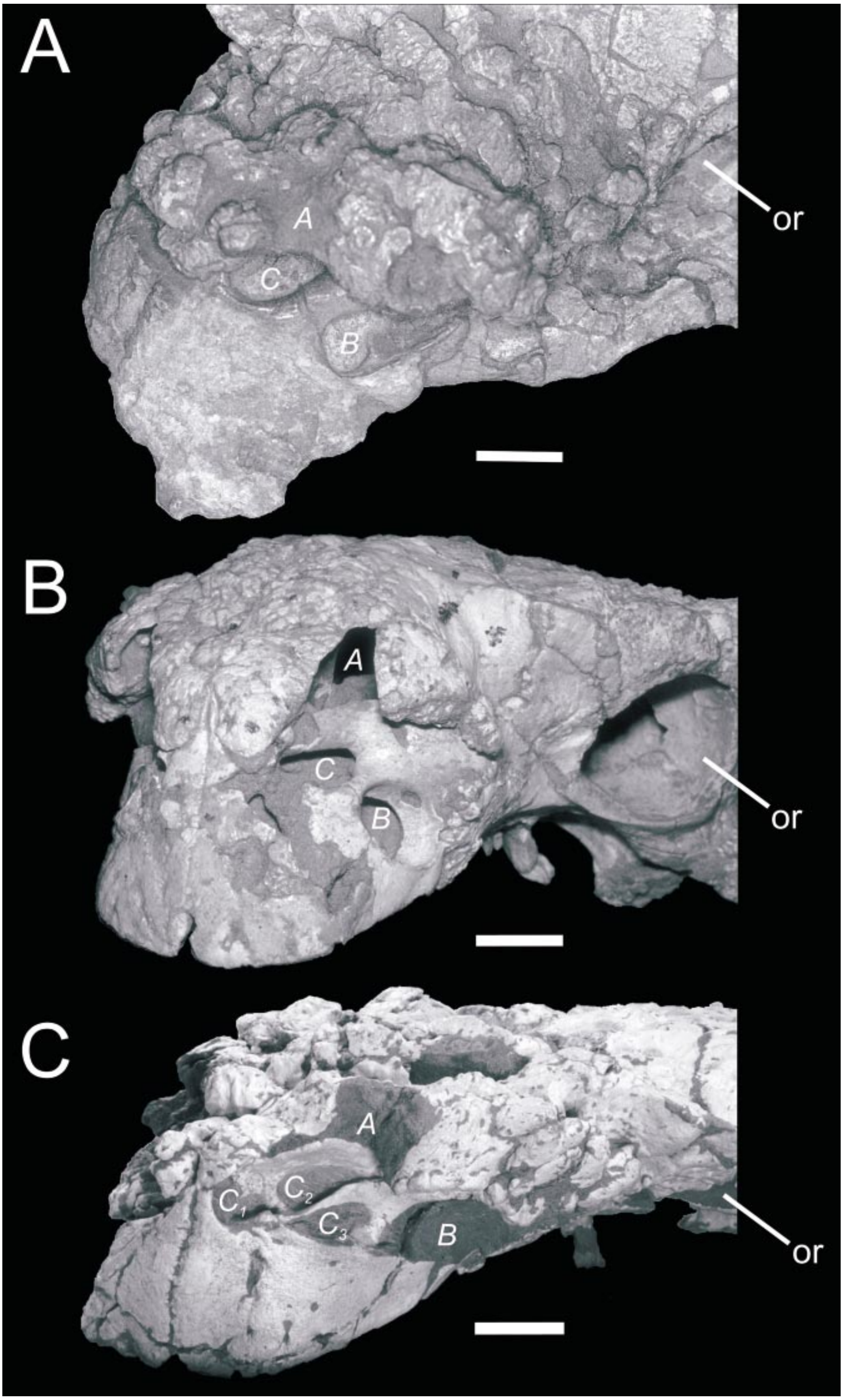


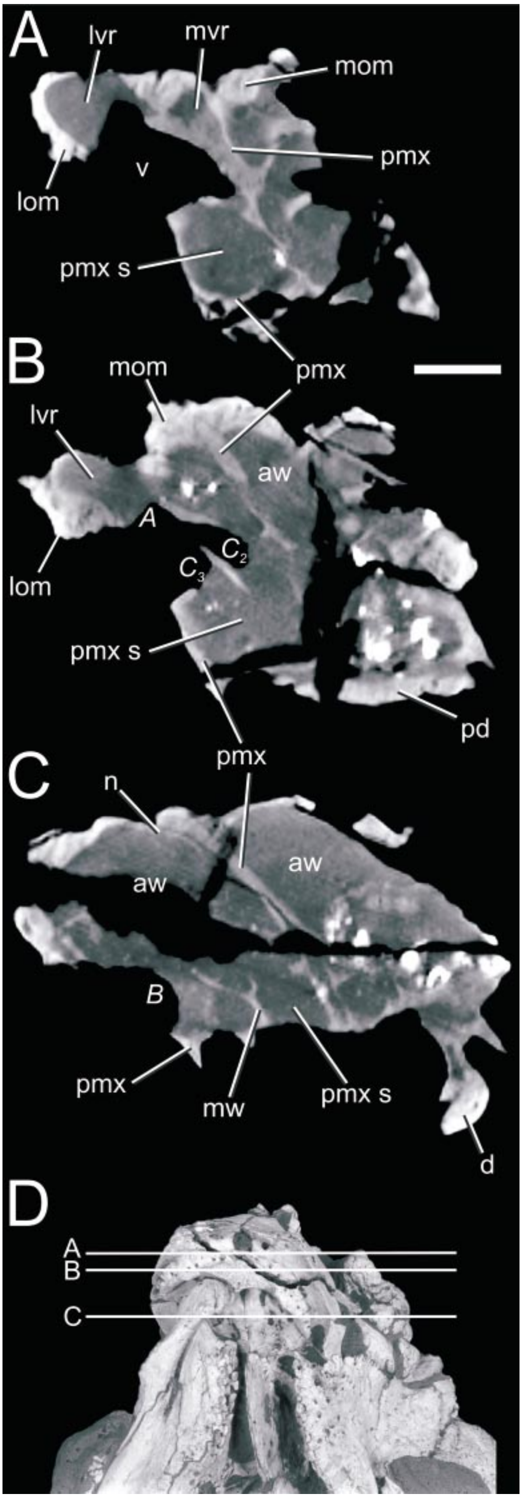
Fig. 5. *Pinacosaurus grangeri*. Narial regions in left anterodorsolateral view showing the diversity and proposed homologies of the narial apertures and recesses. **A,** AMNH 6523. **B,** ZPAL MgD-II/1. **C,** IGM 100/1014. See appendix 4 for abbreviations. Scale bars equal 2 cm.

volved in electrolyte balance and salt excretion; according to Witmer (1995, 1997a), the nasal glands of extant archosaurs (birds and crocodilians) are homologous, as is their position well caudal to the nasal vestibule and premaxilla. Thus, there is ample evidence that dinosaurs such as *Pinacosaurus* had a well-developed nasal gland but that it was not located in the premaxilla. Of course, it is possible that some unknown gland was present, but this hypothesis is probably untestable (Witmer, 1997a). A vascular function for structure *B* is perhaps more likely given that, based on CT studies of ZPAL MgD-II/1 and IGM 100/1014, branches of the maxillary artery open into the structure's caudal margin (see below). Masses of highly vascular narial cavernous (erectile) tissue have been inferred for other extinct archosaurs (Witmer, 2001), and thus *B* may have housed a particularly large mass.

Whereas all known skulls referred to *Pinacosaurus* have a single *A* and *B* on each side, the apertures labeled *C* in figures 4 and 5 are the most variable in number. AMNH 6523 (fig. 5A) and ZPAL MgD-II/1 (fig. 5B) have just a single opening *C* per side, whereas IMM 96BM3/1 has two and IGM 100/1014 (fig. 5C) has three. This variation appears to be real. Based on CT scans of ZPAL MgD-II/1 and IGM 100/1014, we can corroborate Maryańska's (1977) and Tumanova's (1987) observation that aperture *C* opens into a relatively large sinus system within the premaxilla. CT scans of IGM 100/1014 reveals that the ''bony bridge'' (Maryańska, 1971: 48) dividing *A* and *C* in ZPAL MgD-II/1 is actually a thin wall of bone separating the nasal airway (into which *A* opens) from the sinus (into which *C* opens); some workers have regarded this ''bony bridge'' as the septomaxilla (but see below). C_1 in IGM 100/1014 is the smallest of the three *C* apertures and is separated from its contralateral fellow by a thin median septum of premaxilla. This septum is incomplete in some CT slices but probably was intact in life. C_1 overlies the premaxillary sinus rostrally and opens into it caudally. The aperture labeled C_2 in figure 5C (IGM 100/1014) is most comparable to aperture *C* in the other specimens and appears to be the principal opening into the sinus. Aperture C_3 is more horizontal and also opens broadly into the sinus. The variation in the number of *C* openings among the specimens is curious and may represent species-level differences. However, given their opening into a presumably pneumatic sinus and the inherent variability of pneumatic apertures in general (Witmer, 1997a, 1997b), it may be more likely that these are individual variants of little systematic significance. A larger sample is necessary to resolve this issue.

As mentioned above, the bone separating aperture *A* from aperture *C* (or C_2) was regarded by Maryańska (1971) and especially Tumanova (1987) as the septomaxilla. The vomeronasal (VNO, Jacobson's) organ would have been ventral to this bony lamina, according to Tumanova (1987). As additional evidence, both authors cited rostrally placed foramina in the premaxillary palate, which they attributed to the VNO. We join Godefroit et al. (1999) in rejecting this assessment. First, the septomaxilla is an element that has never been reliably identified in any crown-group archosaur. Moreover, our CT scans show complete continuity of the definitive premaxilla with the bone under question, and, again, the bone is a wall between two spaces, not a bridge. The palatal foramina are almost certainly nothing more than the apertures transmitting the vascular anastomosis between the palatal and narial vessels; such anastomoses (with attendant foramina) are a typical feature of amniotes in general and dinosaurs in particular (Witmer, 2001).

Based on CT scans of IGM 100/1014 and ZPAL MgD-II/1, we can identify at least two major premaxillary spaces on each side, the vestibulum nasi (nasal vestibule) and the premaxillary sinus. Scans of IGM 100/1014 (fig. 6) suggest that these two spaces did not communicate broadly, if at all (except to transmit nerves and vessels). There are some gaps in the partitions between the vestibule and sinus, but it cannot be ruled out that these are artifacts of preservation. The nasal vestibule comprises the main airway, conducting inspired air from the fleshy nostril through aperture *A* (the bony nostril) into the main nasal cavity. As mentioned above, two osteodermal masses cover the nasal vestibule, and each osteoderm bears a small recess or sinus associated with the vestibule. The medial of



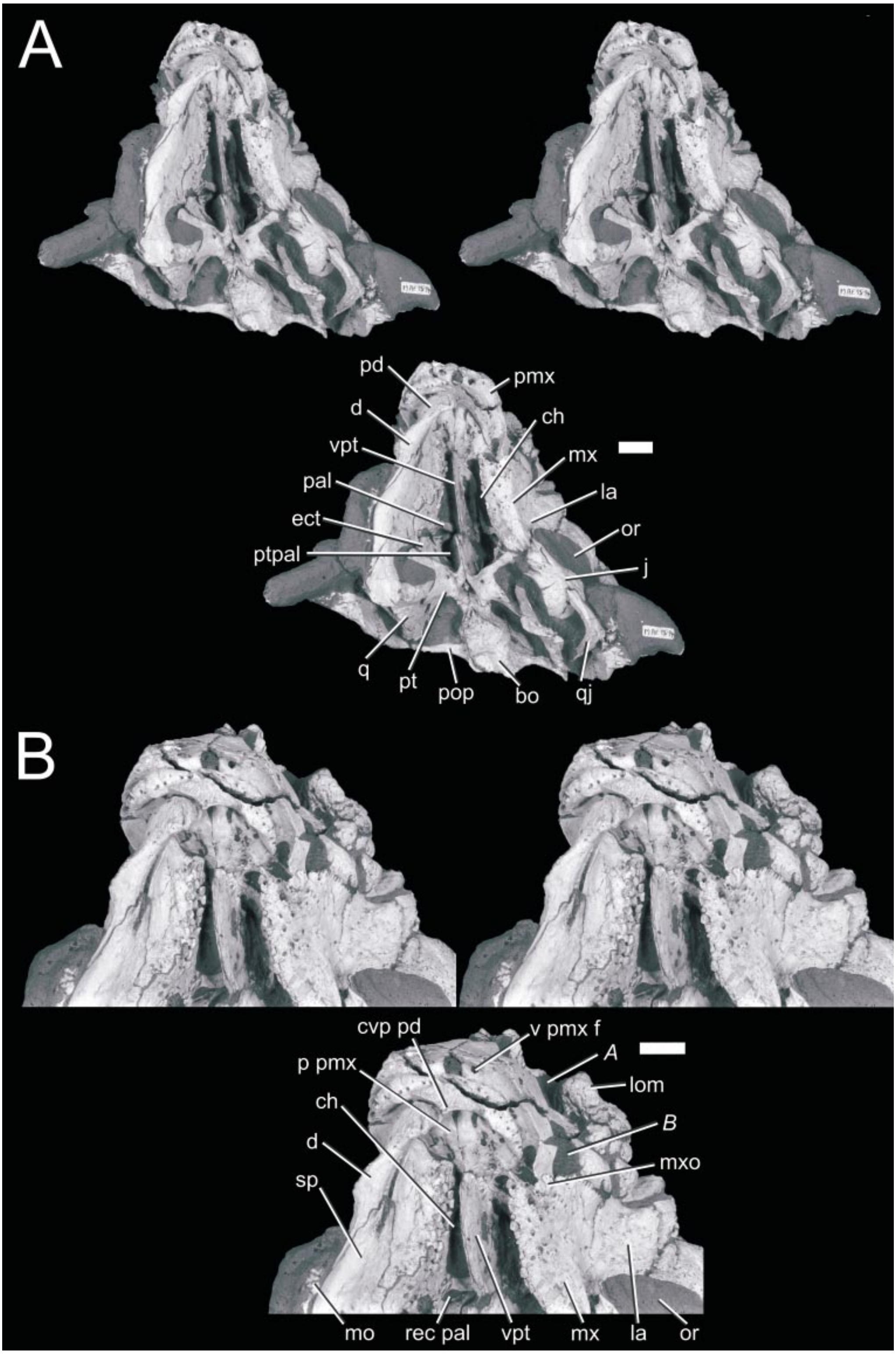
the two vestibular recesses extends far rostrally (at least in ZPAL MgD-II/1), well rostral to *A*, and is floored ventrally by the premaxilla and dorsally by the medial osteoderm. The lateral vestibular recess is housed solely in the lateral osteoderm; the internal surface of the osteoderm is very smooth, commensurate with it being lined with cartilage and/or mucosa, whereas the outer surface is highly sculptured ‘‘surface bone’’. The maxillary neurovascular (dorsal alveolar) canal opens into the floor of the vestibule caudolaterally, just as the canal sends a small branch laterally to open into structure *B* (see above).

The premaxillary sinus is a relatively large cavity. Aperture *C* opens into the sinus rostrally, and the sinus decreases in volume caudally, pinching out caudomedially at the expense of the expanding nasal vestibule. There is no compelling evidence for subdivision within the sinus, despite Maryańska (1977: 120) regarding it as ‘‘multichambered’’. That is, there is virtually no consistent septation within the sinus. As mentioned above, some CT slices of IGM 100/1014 show evidence for a potentially complete medial wall for structure *B*, but, if it truly is a fossa, then this would mean that *B* projects into the sinus and is not topologically a part of it. The assumption has always been that the premaxillary sinus is an air sinus (Coombs and Maryańska, 1990; Witmer, 1999), and this remains the most likely hypothesis.

PALATE (fig. 7): The premaxillary palate is wider than long, parallel-sided, and only slightly rounded at its rostral edge. The new specimen exhibits a flattened premaxillary palate, unlike the strongly ventrally convex condition found in ZPAL MgD-II/1, and the deeply concave palates of adult North American ankylosaurids. This may represent a feature that varies with ontogeny in ankylosaurs.

←

Fig. 6. *Pinacosaurus grangeri*. IGM 100/1014. **A, B, C,** Computed tomographic (CT) slices through the narial region showing internal anatomy and location of sinuses, recesses, and apertures. **D,** Ventral view of skull showing location of slices for A, B, and C above. See appendix 4 for abbreviations. Scale bar equals 2 cm.


A
pd
pmx
d
ch
vpt
mx
pal
la
ect
or
ptpal
j
q
pt
pop
bo
qj
B
cvp pd
v pmx f
p pmx
A
lom
ch
B
d
mxo
sp
mo
rec pal
vpt
mx
la
or

The maxillary tooth rows are deeply inset (emarginated) from the edge of the skull, as is typical of ankylosaurs. The right maxilla is obscured in palatal view by the right hemimandible, which has been crushed against it. The left maxilla, although distorted, is visible, and bears 14 teeth in a straight tooth row. The teeth are leaf-shaped, as is characteristic of many ornithischians, and each one bears vertical striations dividing the crown surface into eight cusps. There is no development of a bandlike cingulum encircling the lower portion of the tooth crowns. There is little to no wear on any of the teeth.

As in ankylosaurs generally (and indeed most thyreophorans), the ventral surface of the skull is dominated by a large palatal vacuity or choanal recess. The choanal recess is bounded by the premaxilla rostrally, the maxilla and ectopterygoid laterally, and the pterygoids caudally. The choana itself is located rostrodorsally within the recess between premaxilla, maxilla, palatine, and the conjoined vomer and pterygoids. The vomers and pterygoids form a narrow, sheetlike palatal keel, which extends ventrally to the level of the maxillary tooth crowns. No clear sutures between vomer and pterygoid can be discerned, even in the CT scans, although the median suture between left and right sides is present throughout its length. The vomeropterygoid flares laterally and dorsally where it contacts the palatine. The palatine in IGM 100/1014 is generally similar to that in ZPAL MgD-II/1 and other ankylosaurians in being recessed dorsally within the choanal recess. There is a peculiar aperture between the palatine and pterygoid located at the dorsomedial juncture of the two bones. Maryańska (1977) referred to this structure as the ‘‘caudal palatal foramen’’, although ‘‘pterygopalatine fenestra’’ is probably more appropriate. The same structures are present in ZPAL MgD-II/1 where they have irregular edges, and it is not clear whether these are preservational artifacts. In IGM 100/1014, however, the right palatine seems to have a complete margin to the fenestra. Likewise, such fenestrae were described and illustrated for *Saichania* (Maryańska, 1977), suggesting they are real. Tumanova’s (1987) identification of fossae, not fenestrae, in this region in *Tarchia*, however, makes the status of pterygopalatine fenestrae in ankylosaurs unclear or at least variable. The palatines of IGM 100/1014 also have several ventral recesses that are presumably pneumatic in origin (Maryańska, 1977). Consistent with the pneumatic interpretation is the fact that the pattern of recesses is asymmetrical and variable among specimens.

The pterygoid bones are retracted caudomedially where they form a more or less transverse lamina that backs the choanal recess. There is a foramen on each side (rostral and caudal) of the transverse lamina. It seems likely that the foramina communicate—Maryańska (1977) assumed they did in ZPAL MgD-II/1—but they do not do so demonstrably in either specimen and CT scans are inconclusive. Assuming they do communicate, they likely transmit the palatine branches of the internal carotid artery and facial nerve. The pterygoid flange is a relatively slender process that broadly contacts the ectopterygoid bone rostrally; it forms much of the rostral margin of the subtemporal fenestra. The ectopterygoid is a relatively small element contacting the maxilla and pterygoid and interposed between the subtemporal fenestra caudally and suborbital fenestra rostrally. The suborbital fenestra in *Pinacosaurus* is reduced to a small foramen between maxilla, ectopterygoid, and palatine. There is a groove running rostrally from the suborbital fenestra that passes just dorsomedial to the teeth (clearer on ZPAL MgD-II/1) and conducted the palatine branch of the palatomaxillary vessels. *Ankylosaurus magniventris* (AMNH 5214) exhibits the same anatomy, and this is perhaps a much more general feature.

The quadrates, although displaced laterally after burial, were vertically oriented and de-

←

Fig. 7. *Pinacosaurus grangeri*. IGM 100/1014. **A,** Stereopairs of whole skull in ventral view. **B,** Stereopairs of anterior part of skull in ventral and slightly left lateral view. See appendix 4 for abbreviations. Scale bars equal 2 cm.

scend directly behind the orbits so that the expanded quadrate cotyla lies just below the caudal border of the orbit. The rostral surface of the quadrate is flat, not deeply excavated as in certain nodosaurids. The dorsoventrally narrow pterygoid ramus of the quadrate in this specimen is an ankylosaurian synapomorphy (Sereno, 1986).

CRANIOFACIAL ORNAMENTATION (figs. 2, 4): There has been considerable debate as to the developmental nature (and terminology) of the ornamentation of the skulls of ankylosaurs (e.g., Maryańska, 1977; Coombs, 1978; Molnar, 1996; Carpenter et al., 2001; Vickaryous et al., 2001b). We generally follow the nomenclature of Vickaryous et al. (2001b), and our studies fully support their contention that cranial ornaments in ankylosaurs develop both as osteoderms that fuse to the skull bones and as elaborations or outgrowths of individual cranial elements. *Pinacosaurus*, particularly ZPAL MgD-II/1, has been an important player in these debates, and IGM 100/1014 provides further information. Sullivan (2000: 218) examined the skull of IGM 100/1014 (then identified by its field number, MAE 95–94) and noted that it was ‘‘totally devoid of cranial osteoderms’’. However, the specimen bears numerous osteoderms overlying the rostral portion of the skull roof. There are also small osteoderms in the vicinity of the parietal, as well as the highly developed quadratojugal ‘‘horns’’. These ossifications can be distinguished from simple dermal sculpturing and rugosities of the existing cranial elements.

In contrast to the relatively smooth frontals, the nasals are highly sculptured and rugose. A prominent ridge runs caudolaterally from the left nasal onto the adjacent prefrontal, and is interrupted only by the suture between these two bones. Thus, even well-developed dermal sculpturing of skull elements does not cross sutural boundaries. In some areas, additional osteoderms overlie the sculptured areas but remain unfused to them. For example, at the rostral tips of the nasals, two oblong dermal rugosities are each capped with a small (~0.5 cm) osteoderm. Additional osteoderms of similar size overlie the nasals farther caudally. These osteoderms have been preserved in situ and are separated from the actual bones of the skull by a thin layer of sandy matrix. At the rostrolateral corners of the parietal, two small, flattened osteoderms are present, crossing laterally onto the surface of the postorbital. Unlike dermal sculpturing, these elements may cross sutural boundaries and overlie more than one cranial element. A final example is a small osteoderm located directly behind the premaxilla and attached to the maxilla that continues the course of the premaxillary tomium. This small osteoderm also is present in ZPAL MgD-II/1, where, as in IGM 100/1014, it can clearly be seen to be a separate element attached to the maxilla because only the left one is present and the element has fallen off on the right side. In older individuals of other ankylosaurid species (the adult *P. grangeri*, AMNH 6523, does not show this region), this osteoderm becomes a much larger structure that is fused to adjacent elements.

MANDIBLE (fig. 8): Both hemimandibles are preserved, as is the slender predentary. The right hemimandible and predentary are still associated with the skull, while the left hemimandible was removed and prepared separately. The mandible features a straight ventral margin in lateral view, with no downturning of the rostral edge as seen in nodosaurids. The coronoid process is low and rounded and does not project above the level of the dentary tooth row. The Meckelian sulcus is deep and communicates caudally with the deep mandibular fossa between the postdentary bones. The predentary is broad and bracket-shaped, with a rudimentary caudoventral process. The predentary bears numerous neurovascular foramina, presumably to serve a rhamphotheca. A subtriangular, rostrocaudally elongate osteoderm is associated with each hemimandible but is not fused to the underlying bone. CT scans confirm that the osteoderm is only loosely attached. This differs from the condition in ZPAL MgD-II/1, in which the postdentary bones are sculptured and rugose, but no osteoderm was found. It also differs from the state in all adult ankylosaurs, in which a large oblong osteoderm is fused to the ventrolateral surface of the mandible. This and other characters noted above indicate that IGM 100/1014 is probably intermediate in age between

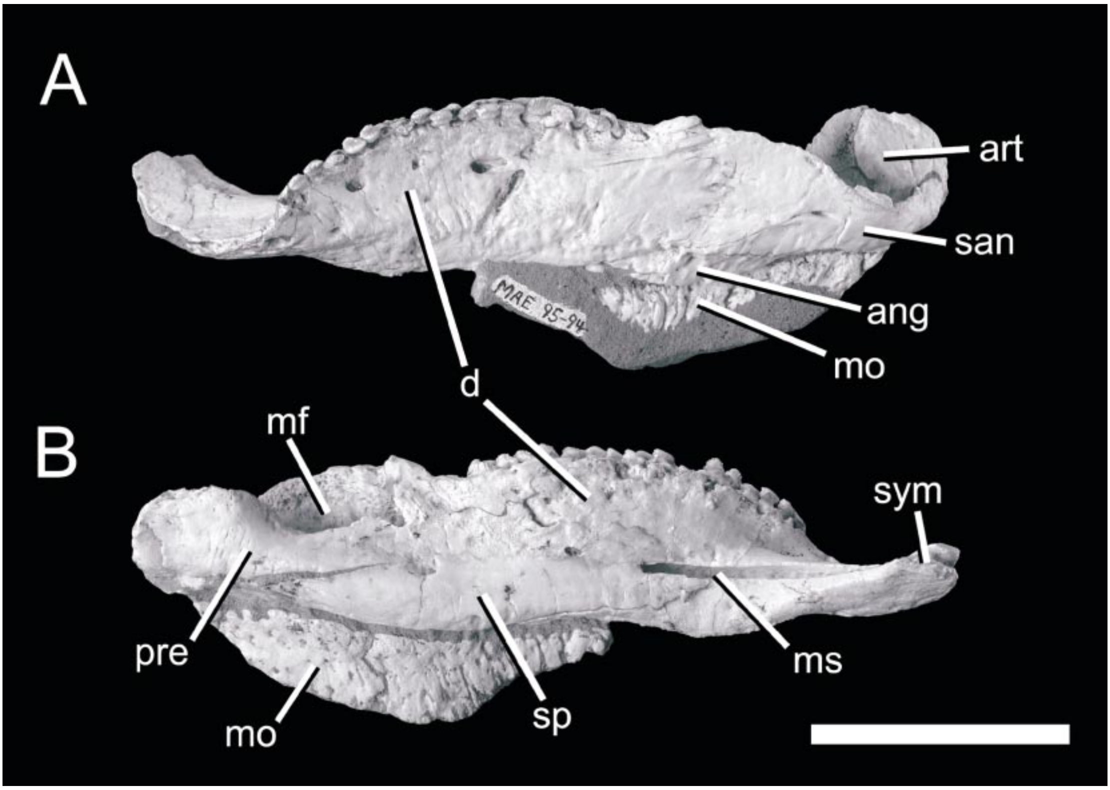


Fig. 8. *Pinacosaurus grangeri*. IGM 100/1014. Left hemimandible in buccal (**A**) and lingual (**B**) views. See appendix 4 for abbreviations. Scale bar equals 5 cm.

the well-known juvenile skull of ZPAL MgD-II/1 and adult ankylosaurs.

PHYLOGENETIC ANALYSIS

Coombs (1978) proposed that all members of the Ankylosauria could be unambiguously assigned to one of two families: the Ankylosauridae or the Nodosauridae. This classification has been widely accepted and is still the preferred classification scheme for ankylosaurs (e.g., Sereno, 1986, 1999; Coombs and Maryańska, 1990). Some recent authors recognize a third clade, Polacanthidae (or Polacanthinae; see Kirkland, 1998; Blows, 2001; Carpenter, 2001), members of which are usually distinguished on the basis of body osteoderm morphology.

Recently, the discovery of new taxa and the subsequent evaluation of new phylogenetic hypotheses have suggested that the relationships among ankylosaurs may actually be far more complex than previously thought. In particular, new species such as *Gastonia burgei* (Kirkland, 1998) and *Gargoyleosaurus parkpinorum* (Carpenter et al., 1998) exhibit a mosaic of traditionally recognized ankylosaurid and nodosaurid characters. Many putatively ‘‘derived’’ characters of these two ankylosaur families may in fact be primitive for the Ankylosauria. For example, one ‘‘derived’’ state possessed by nodosaurids, caudolateral projection of the paroccipital processes, is also present in the primitive ankylosaurid *Gargoyleosaurus*, as is a rostrally sloping quadrate that fuses to the paroccipital process (Carpenter et al., 1998). Conversely, the primitive nodosaurid *Pawpawsaurus* exhibits development of ornamentations over the squamosal (Lee, 1996), resulting in a pair of rudimentary ‘‘horns’’, a character state traditionally considered autapomorphic for the Ankylosauridae. This indicates that the constituent families of the Ankylosauria may have been tra-

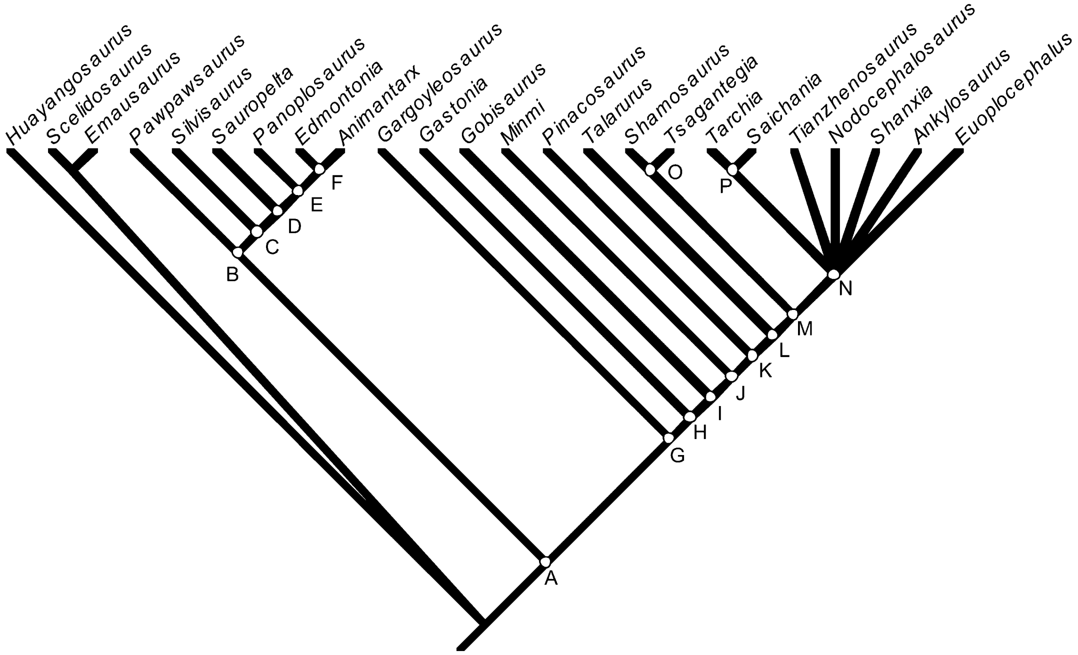


Fig. 9. Strict consensus of 16 equally parsimonious trees found in this cladistic analysis (length = 118 steps; consistency index (CI) = 0.475; retention index (RI) = 0.700; rescaled consistency index (RCI) = 0.332). Node A = Ankylosauria; node B = Nodosauridae; node G = Ankylosauridae. A list of the apomorphies at each lettered node is presented in appendix 3.

ditionally grouped by an abundance of symplesiomorphies, and not entirely by shared derived characters.

MATERIALS EXAMINED: For the collection of character state data, we examined original skulls of *Ankylosaurus magniventris* (AMNH 5895), *Edmontonia rugosidens* (DMNH 468 [= type of *Denversaurus schlessmani*], USNM 11868 [= type of *Palaeoscincus rugosidens*]), *Euoplocephalus tutus* (AMNH 5223, 5328, 5337, 5403), *Gargoyleosaurus parkpinorum* (DMNH 27726), *Nodocephalosaurus kirtlandensis* (SMP VP-900), *Pinacosaurus grangeri* (AMNH 6523, IGM 100/1014, ZPAL MgD-II/1), and *Sauropelta edwardsorum* (AMNH 3035). We also examined high-quality casts of *Animantarx ramaljonesi*, *Ankylosaurus magniventris*, *Gastonia burgei*, *Panoplosaurus mirus*, *Pawpawsaurus campbelli*, *Saichania chulsanensis*, *Scelidosaurus harrisonii*, and *Tarchia gigantea*, as well as original published descriptions of other thyreophoran taxa.

A parsimony analysis of 50 cranial characters was carried out using 21 ankylosaurs and three outgroups as terminal taxa. The analysis was performed using the heuristic search algorithm in PAUP* 4.0b10 (Swofford, 2000) with TBR branch swapping and 100,000 replicates. The basal thyreophorans *Scelidosaurus* and *Emausaurus* and the primitive stegosaur *Huayangosaurus* were fixed as outgroups, and the tree was rooted by comparison to these taxa. Three multistate characters described a distinct morphocline and were therefore treated as ordered characters. These are discussed in appendix 1 (characters 20, 41, and 42). Sixteen equally parsimonious trees of 118 steps were found (consistency index [CI] = 0.475; retention index [RI] = 0.700; rescaled consistency index [RCI] = 0.332). A complete list of character descriptions is presented in appendix 1, the data matrix appears in appendix 2, and a list of apomorphies is found in appendix 3. The matrix is available in electronic form at http://research.amnh.org/vertpaleo/norell.html.

A strict consensus of the 16 most parsimonious cladograms supports certain major divisions of the Thyreophora (fig. 9), but differs considerably from recent phylogenetic analyses of ankylosaurian relationships (e.g., Carpenter et al., 1998; Kirkland, 1998; Hill, 1999; Sereno, 1999; Carpenter, 2001; Vickaryous et al., 2001a), particularly in the interrelationships among ankylosaurids. The analysis recovers a monophyletic ingroup, Ankylosauria, and supports monophyly of two major divisions, Ankylosauridae and Nodosauridae, as proposed by Coombs (1978). Ankylosauria is supported by ten unambiguous synapomorphies (characters 12, 15, 23, 24, 28, 34, 36, 41, 46, and 48; see appendix 1 for descriptions) and four ambiguous synapomorphies (characters 21, 26, 32, and 50). Ankylosauridae is supported by two unambiguous synapomorphies: presence of a premaxillary notch (character 8) and development of secondary dermal ossifications overlying the squamosals (character 42). Nodosaurid monophyly is supported by three unambiguous synapomorphies (characters 31, 38, and 43), and three ambiguous synapomorphies (characters 13, 30, and 49).

Recent studies have supported a monophyletic Polacanthidae (or Polacanthinae) either as a subdivision of Ankylosauridae (Kirkland, 1998) or as the sister taxon to Ankylosauridae (Carpenter, 2001). Taxa considered to be polacanthids are known primarily from postcranial remains, with the notable exceptions of *Gastonia* and *Gargoyleosaurus*, both known from excellently preserved skulls. In the current analysis, as in the analysis of Vickaryous et al. (2001a), *Gastonia* and *Gargoyleosaurus* represent two successively more distant sister taxa to the remaining ankylosaurids; thus, Polacanthidae is here resolved as a paraphyletic assemblage (contra Kirkland, 1998; Carpenter, 2001). It should be noted, however, that this analysis is based only on taxa for which cranial remains are known; inclusion of postcranial characters and taxa represented only by postcranial material may affect this result. This analysis also found the newly described *Gobisaurus* to be a primitive ankylosaurid, but did not preserve a sister taxon relationship between this taxon and *Shamosaurus* (contra Vickaryous et al., 2001a).

Sullivan (1999) proposed a close relationship between the North American ankylosaurid *Nodocephalosaurus* and the Asian taxa *Saichania* and *Tarchia*, based on the shared presence of bulbous, raised osteoderms on the skull roof. However, *Nodocephalosaurus* also shares certain features with North American ankylosaurids such as an arching snout profile (*Tarchia* and *Saichania* exhibit a more level skull roof) and a median osteoderm that overlies the dorsum of the narial region, but does not border the external nares. The current analysis corroborates Sullivan's (1999) interpretation of *Nodocephalosaurus* as a highly derived ankylosaurid, but available data do not allow further resolution of the phylogenetic position of this taxon.

Minmi, the only ankylosaur known from Australia, has been alternatively interpreted as a nodosaurid (Coombs and Maryańska, 1990), a basal ankylosaurid (Hill, 1999; Sereno, 1999), and the most basal ankylosaur, sister taxon to all remaining ankylosaurs (Kirkland, 1998; Carpenter, 2001; although Carpenter [2001: 475] incorrectly interpreted his own cladogram as placing *Minmi* as ''the closest sister group to the Nodosauridae''). The current analysis supports the placement of *Minmi* within Ankylosauridae based on several synapomorphies, including a relatively wide skull, a vertically oriented mandibular ramus of the quadrate, and development of secondary dermal ossifications overlying the quadratojugals.

The position of *Pinacosaurus* in this phylogeny is distinctive in that it has traditionally been considered a highly derived ankylosaurid (e.g., Coombs and Maryańska, 1990; Kirkland, 1998; Carpenter, 2001). This analysis places it basal to a clade containing *Shamosaurus* and *Tsagantegia*, two genera that are considered to be very primitive among ankylosaurids. This may be because the adult *Pinacosaurus* lacks many putatively derived character states that have previously been scored only from the juvenile skull of ZPAL MgD-II/1. For example, the skull of the adult *Pinacosaurus grangeri* (AMNH 6523) is clearly longer than wide, while the juvenile skulls (ZPAL MgD-II/1 and IGM 100/1014) are wider than long. The adult also exhibits weakly developed squamosal protuberances and an occiput that remains visible in dorsal view, and lacks the elaborate cranial ornamentation typical of more highly nested ankylosaurids.

The relationships among five highly derived ankylosaurids (*Ankylosaurus*, *Euoplocephalus*, *Nodocephalosaurus*, *Shanxia*, and *Tianzhenosaurus*) remain enigmatic, owing in part to the fragmentary nature of two of these taxa (*Nodocephalosaurus* and *Shanxia*), and in part to the sutural fusion and apomorphic cranial anatomy of the most derived ankylosaurids.

One hundred bootstrap replicates of the original dataset show 100% support for the ingroup Ankylosauria, and high support for certain smaller clades. Sixty-nine percent of replicates supported the unnamed clade consisting of all ankylosaurids, exclusive of *Gargoyleosaurus* (fig. 9, node H), and 61% supported monophyly of ankylosaurids more highly derived than *Gargoyleosaurus* and *Gastonia* (fig. 9, node I). Monophyly of the Nodosauridae, however, was supported by less than 50% of bootstrap replicates. This may be because certain characters used to unite nodosaurids, such as a long narrow skull and hemispherical occipital condyle, may be primitive for more inclusive clades.

Bremer support (branch support; Bremer, 1994) was also relatively high for the ingroup (eight additional steps were required to collapse Ankylosauria) but lower for less inclusive clades. Three additional steps were required to collapse the clade consisting of *Gastonia* and all other ankylosaurids excluding *Gargoyleosaurus* (fig. 9, node I), and two steps each were required to collapse Ankylosauridae, Nodosauridae, and the clade consisting of all ankylosaurids except *Gargoyleosaurus* (fig. 9, node H). For all other nodes, Bremer support values were less than two steps. These results underscore the fact that while Ankylosauria is robustly supported as a monophyletic group, reliable cranial synapomorphies of its constituent families are few, and support at less inclusive nodes is relatively low.

ONTOGENY

Several ankylosaur specimens have been interpreted as belonging to juvenile individuals. These specimens provide important information about the growth and development of ankylosaurs, but also reveal much about their anatomy in general that cannot be studied in adults. In the first complete description of the pes of *Euoplocephalus*, Coombs (1986) also reported that the specimen (AMNH 5266) belonged to a juvenile or subadult individual. Characters used to distinguish this specimen as such included lack of fusion between the neural arches and vertebral centra, lack of fusion between the sacral ribs and ilia, smooth surfaces on long bones, a femoral head with an indistinct neck, and lack of fusion between the lower leg bones and proximal tarsal bones.

Some of these features were also found in a juvenile nodosaurid specimen from the Paw Paw formation in Texas (Jacobs et al., 1996). The immature nodosaurid exhibited unfused neural arches and pelvic girdle elements, as well as an overall small size and high amounts of spongy bone, even in metaphyseal ossification centers. Examination of this juvenile material was used to evaluate the reliability of certain osteological characters used in phylogeny reconstruction. Jacobs et al. (1996) found that certain typical nodosaurid characters, such as the ventrally angled, offset occipital condyle and proximally located fourth trochanter, could be found in individuals estimated to be just one month old. Other characters, such as the relative proportions of fore and hind limbs, unsurprisingly seem to be subject to ontogenetic changes. Jacobs et al. (1996) interpreted the absence of osteoderms in the juvenile as another hallmark of its immaturity, although the possibility exists that osteoderms were simply not preserved or collected. More recently described material pertaining to juvenile ankylosaurs includes *Anoplosaurus* (Pereda-Suberbiola and Barrett, 1999) and *Liaoningsaurus* (Xu et al., 2001). Although the latter genus includes maxillary fragments, well-preserved crania of juvenile ankylosaurs remain relatively rare.

Maryańska (1971) presented a thorough description of an unusually well-preserved juvenile skull of *Pinacosaurus grangeri* (ZPAL MgD-II/1). Like the Paw Paw juvenile, this skull also lacked the extensive development of osteoderms present in adults. As a result, all sutures between cranial bones remained visible and unfused. With this description, Maryańska (1971) presented the first account of distinct sutural contacts between skull elements in an ankylosaur. Among the novel characters discovered in this unique specimen were the presence of ‘‘tabular’’ and ‘‘postfrontal’’ bones, elements that are absent in most archosaurs. Additionally, Maryańska (1977) later reported a sutural contact between the quadratojugal and postorbital bones. This differs from the condition in all other thyreophorans, in which the caudal process of the jugal intervenes between the two bones. This character has subsequently been widely accepted as diagnostic for Ankylosauria (e.g., Sereno, 1986; Coombs and Maryańska, 1990; Lee, 1996). The interpretation of this character as diagnostic of a more inclusive clade is problematic because the contact has been identified in one juvenile specimen of one species alone.

In his analysis of the phylogenetic position of *Pawpawsaurus*, Lee (1996) coded quadratojugal-postorbital contact as present in ankylosaurids, five species of nodosaurids, and *Pawpawsaurus*, despite the fact that, in the latter genus, the quadratojugal is ‘‘completely fused so precise boundaries cannot be determined’’ (Lee, 1996: 236). Coombs and Maryańska (1990:457) similarly accept the character, even though they assert that ‘‘Sutural boundaries of the skull elements are known from a single ankylosaurid skull.’’ The practice of coding higher taxa based on the character state observed in a single specimen is unjustified, as is the coding of unobservable character states in specimens of other genera. While the contact between quadratojugal and postorbital may indeed diagnose Ankylosauria, the sutural contacts of all other specimens are obscured either by fusion or dermal sculpturing, and are therefore unknown. Thus, this character is best omitted from any list of diagnostic features of ankylosaurs.

The new specimen is slightly larger than ZPAL MgD-II/1 in all dimensions, and it features several characteristics that indicate it is intermediate in age between known juvenile and adult skulls. Many of these characters relate to the development of ornamentations associated with the skull. Postorbital, squamosal, and quadratojugal protuberances are relatively larger in IGM 100/1014 than in other juvenile ankylosaurs, and the orbit is relatively smaller. There is a rugose, sculptured area rostral to the orbits on the dorsal surface of the skull. This condition is intermediate between the smooth nasals of ZPAL MgD-II/1 and the highly fused and rugose skull roof of the adult *Pinacosaurus* (AMNH 6523). Osteoderms associated with the mandible are well developed, but remain unfused to the underlying bones.

The pattern of ornamentations exhibited by this specimen supports the hypothesis that such structures develop first in the squamosal and quadratojugal regions in ankylosaurids (Maryańska, 1977), and that these ossifications grow toward one another, fusing to the dermal skull elements and effectively sealing off the lateral temporal fenestra (Sereno, 1986). Osteoderms overlying the dorsal processes of the premaxillae, and bordering the nares dorsally, also appear early in ontogeny and fuse to the primary skull elements.

The development of rugosities on the caudal extent of the nasal bones in IGM 100/1014 suggests that this region may be the next in the ontogenetic sequence to acquire osteoderms. While not osteoderms themselves, the rugosities may represent spicules of bone that were growing outward to fuse with overlying ossifications in the integument. Having not fused, or perhaps not even completely ossified, the secondary elements in this region may have been lost. A similar pattern of development may be seen in the mandible of ZPAL MgD-II/1, where no osteoderm is preserved, but dermal rugosities line the ventrolateral edges of the postdentary bones. It is possible that an increase in rugosity of the skull bones always precedes extensive mineralization and fusion of secondary dermal elements.

IGM 100/1014 preserves well-developed mandibular osteoderms in situ, which remain unfused to the underlying bones. A roughened area is present on the ventrolateral aspect of the postdentary bones, where the osteoderms presumably would have fused. All mandibles from adult ankylosaurs have a fused, elongate osteoderm in this region. It is clear, then, that these elements appear early in ontogeny, but do not become fused until much later.

CONCLUSIONS

One confounding factor in the analysis of ankylosaur phylogeny is the lack of consensus between authors on certain important characters. The problem of inconsistent coding suggests that some characters may be in need of revision. In addition, characters such as the slope of the quadrate or the orientation of narial opening are continuous characters, which are difficult to code without arbitrarily dividing character states. Clearly these characters need to be reformulated before they can be used effectively in phylogenetic analysis.

Another avenue for future research will be the incorporation of postcranial data into the analysis. Postcranial remains exist for most ankylosaurian genera. Carpenter et al. (1998: 783) suspect that postcranial data will contribute little to phylogenetic analysis, because ‘‘many of the characters separating the two ankylosaur families are cranial.’’ However, as Kirkland (1998) has shown, an entire clade of ankylosaurs may be supported by postcranial characters alone. The addition of postcranial characters may therefore resolve the phylogenetic positions of ambiguously placed taxa, yielding a more robust hypothesis of the interrelationships of ankylosaurs.

Until recently, all ankylosaurid genera were considered monotypic (Sullivan, 1999). The discovery of new specimens of *Pinacosaurus grangeri* and the new species *P. mephistocephalus* (Godefroit et al., 1999) suggests that a reevaluation of all specimens referred to the genus is in order. The specimen described herein is significant because it is developmentally intermediate between known specimens of *P. grangeri*, and therefore represents a contribution to an ontogenetic series of these animals. Continued collection in the fossiliferous Djadokhta-like beds of the southern Gobi Desert may yield a more complete ontogenetic series of these ankylosaurs, similar to the well known series of *Protoceratops andrewsi* collected from the same localities (e.g., Brown and Schlaikjer, 1940; Dodson, 1975).

ACKNOWLEDGMENTS

D. Dashzeveg and other members of the 1995 Mongolian Academy of Sciences–American Museum of Natural History expedition are thanked for collection of the specimen. We thank Kenneth Carpenter and Robert M. Sullivan for access to specimens in their care. Matthew K. Vickaryous and Philip J. Currie provided access to unpublished information. Ed Pederson (AMNH) prepared the specimen. Mick Ellison (AMNH) photographed the specimen and assisted in preparing the figures. We thank Heather Mayle, James Hatton, and O'Bleness Memorial Hospital (Athens, OH) for access to and assistance with CT scanning MAE 100/1014 and ZPAL MgD-II/1. We thank Halszka Osmólska for loan of ZPAL MgD-II/1 to L.M.W. R.C. Ridgley (OU, Athens, OH) assisted with preparation of the stereophotographs. Paul M. Barrett (University of Oxford) and Scott Sampson (University of Utah) reviewed the manuscript and made suggestions for its improvement. Maureen A. O'Leary and Matthew T. Carrano (SUNY–Stony Brook) also commented on early versions of the manuscript. For funding, R.V.H. thanks the Theodore Roosevelt Memorial Fund of the American Museum of Natural History and the Jurassic Foundation; L.M.W. thanks the National Science Foundation (grant IBN-9601174) and the Ohio University College of Osteopathic Medicine; M.A.N. thanks the National Science Foundation (grants DEB 9407999, DEB 9300700, IIS-9874781), the National Geographic Society, the Frick Laboratory Endowment, and the Department of Vertebrate Paleontology at the American Museum of Natural History.

REFERENCES

Andrews, R.C. 1932. The new conquest of Central Asiatic. A narrative of the Central Asiatic expeditions in Mongolia and China 1921–1930. American Museum of Natural History, 678 pp.

Barrett, P.M., Y. Hailu, P. Upchurch, and A.C. Burton. 1998. A new ankylosaurian dinosaur (Ornithischia: Ankylosauria) from the Upper Cretaceous of Shanxi Province, People's Republic of China. Journal of Vertebrate Paleontology 18: 376–384.

Blows, W.T. 2001. Dermal armor of the polacanthine dinosaurs. *In* K. Carpenter (editor), The armored dinosaurs: 363–385. Indianapolis: Indiana University Press.

Bremer, K. 1994. Branch support and tree stability. Cladistics 10: 295–304.

Brown, B. 1908. The Ankylosauridae, a new family of armored dinosaurs from the Upper Cretaceous. Bulletin of the American Museum of Natural History 24: 187–201.

Brown, B., and E.M. Schlaikjer. 1940. The structure and relationships of *Protoceratops*. Annals of the New York Academy of Sciences XL: 133–266.

Carpenter, K. 2001. Phylogenetic analysis of the Ankylosauria. *In* K. Carpenter (editor), The armored dinosaurs: 455–483. Indianapolis: Indiana University Press.

Carpenter, K., C. Miles, and K. Cloward. 1998. Skull of a Jurassic ankylosaur (Dinosauria). Nature 393: 782–783.

Carpenter, K., J.I. Kirkland, D. Burge, and J. Bird. 2001. Disarticulated skull of a new primitive ankylosaurid from the Lower Cretaceous of eastern Utah. *In* K. Carpenter (editor), The armored dinosaurs: 211–238. Indianapolis: Indiana University Press.

Clark, J.M., M.A. Norell, and L.M. Chiappe. 1999. An oviraptorid skeleton from the Late Cretaceous of Ukhaa Tolgod, Mongolia, preserved in an avianlike brooding position over an oviraptorid nest. American Museum Novitates 3265: 1–36.

Clark, J.M., M.A. Norell, and R. Barsbold. 2001. Two new oviraptorids (Theropoda: Oviraptorosauria), Upper Cretaceous Djadokhta Formation, Ukhaa Tolgod, Mongolia. Journal of Vertebrate Paleontology 21: 209–213.

Coombs, W.P., Jr. 1978. The families of the Ornithischian dinosaur order Ankylosauria. Palaeontology 21: 143–170.

Coombs, W.P., Jr. 1986. A juvenile ankylosaur referable to the genus *Euoplocephalus* (Reptilia, Ornithischia). Journal of Vertebrate Paleontology 6: 162–173.

Coombs, W.P., Jr., and T. Maryańska. 1990. Ankylosauria. *In* D.B. Weishampel, P. Dodson, and H. Osmólska (editors), The Dinosauria: 456–483. Berkeley: University of California Press.

Dashzeveg, D., M.J. Novacek, M.A. Norell, J.M. Clark, L.M. Chiappe, A. Davidson, M.C. McKenna, L. Dingus, C. Swisher, and P. Altangerel. 1995. Extraordinary preservation in a new vertebrate assemblage from the Late Cretaceous of Mongolia. Nature 374: 446–449.

Dodson, P. 1975. Quantitative aspects of relative growth and sexual dimorphism in *Protoceratops*. Journal of Paleontology 50: 929–940.

Gallenkamp, C. 2001. Dragon hunter: Roy Chapman Andrews and the Central Asiatic expeditions. New York: Viking Press, 344 pp.

Gao, K., and M.A. Norell. 2000. Taxonomic composition and systematics of late Cretaceous lizard assemblages from Ukhaa Tolgod and adjacent localities, Mongolian Gobi Desert. Bulletin of the American Museum of Natural History 249: 1–118.

Gilmore, C.W. 1933a. On the dinosaurian fauna of the Iren Dabasu Formation. Bulletin of the American Museum of Natural History 67: 23–78.

Gilmore, C.W. 1933b. Two new dinosaurian reptiles from Mongolia with notes on some fragmentary specimens. American Museum Novitates 679: 1–20.

Godefroit, P., X. Pereda-Suberbiola, H. Li, and Z.-M. Dong. 1999. A new species of the ankylosaurid dinosaur *Pinacosaurus* from the Late Cretaceous of Inner Mongolia (P. R. China). Bulletin de l'Institut Royal des Sciences Naturelles de Belgique 69(Suppl. B): 17–36.

Gradzinski, R., Z. Kielan-Jaworowska, and T. Maryańska. 1977. Upper Cretaceous Djadokhta, Barun Goyot and Nemegt Formations of Mongolia, including remarks on previous subdivisions. Acta Geologia Polonica 27: 281–318.

Hill, R.V. 1999. Phylogenetic relationships among Ankylosauria: an analysis of cranial characters. Journal of Vertebrate Paleontology 19: 51A.

Huene, F. von. 1948. Short review of the lower tetrapods. Royal Society of South Africa Special Publications Robert Broom Commemorative Volume: 65–106.

Jacobs, L.L., D.A. Winkler, P.A. Murry, and J.M. Maurice. 1996. A nodosaurid scuteling from the Texas shore of the western interior seaway. *In* K. Carpenter, K.F. Hirsch, and J. Horner (editors), Dinosaur eggs and babies: 337–346. Cambridge: Cambridge University Press.

Jerzykiewicz, T., P.J. Currie, D.A. Eberth, P.A. Johnston, E.H. Koster, and J.-J. Zheng. 1993. Djadoktha Formation correlative strata in Chinese Inner Mongolia: an overview of the stratigraphy, sedimentary geology, and paleontology and comparisons with the type locality in the pre-Altai Gobi. Canadian Journal of Earth Sciences 30: 2180–2195.

Kirkland, J.I., 1998. A polacanthine ankylosaur (Ornithischia: Dinosauria) from the Early Cretaceous (Barremian) of eastern Utah. *In* S.G. Lucas, J.I. Kirkland, and J.W. Estep (editors), Lower and Middle Cretatceous ecosystems. New Mexico Museum of Natural History Bulletin 14: 271–281.

Kurzanov, S.M., and T.A. Tumanova. 1978. The structure of the endocranium in some Mongolian ankylosaurs. Paleontological Journal 3: 369–375.

Lee, Y.-N. 1996. A new nodosaurid ankylosaur (Dinosauria: Ornithischia) from the Paw Paw

Formation (Late Albian) of Texas. Journal of Vertebrate Paleontology 16: 232–245.

Lillegraven, J.A., and M.C. McKenna. 1986. Fossil mammals from the ‘‘Mesaverde’’ Formation (Late Cretaceous, Judithian) of the Bighorn and Wind River basins, Wyoming, with definitions of Late Cretaceous North American land-mammal ‘‘ages.’’ American Museum Novitates 2840: 1–68.

Loope, D.B., L. Dingus, C.C. Swisher III, and C. Minjin. 1998. Life and death in a Cretaceous dune field, Nemegt Basin, Mongolia. Geology 26: 27–30.

Maleev, E.A. 1952. A new family of armored dinosaurs from the Upper Cretaceous of Mongolia. Doklady Akademii Nauk SSSR 87: 131–134. [in Russian]

Maryańska, T. 1971. New data on the skull of *Pinacosaurus grangeri* (Ankylosauria). Palaeontologia Polonica 25: 45–53.

Maryańska, T. 1977. Ankylosauridae (Dinosauria) from Mongolia. Palaeontologia Polonica 37: 85–151.

Molnar, R.E. 1996. Preliminary report on a new ankylosaur from the Early Cretaceous of Queensland, Australia. Memoirs of the Queensland Museum 39: 653–668.

Nopcsa, F. 1915. Die Dinosaurier der Siebenbuergischen Landesteile Ungarns. Mitteilungen. Jahrbuch der Königlich ungarischen geologischen Reichsanstalt. 23: 1–26.

Norell, M.A. 1997. Ukhaa Tolgod. *In* P.J. Currie and K. Padian (editors), Encyclopedia of dinosaurs: 769–770. New York: Academic Press.

Norell, M.A., J.M. Clark, D. Dashzeveg, R. Barsbold, L.M. Chiappe, A.R. Davidson, M.C. McKenna, P. Altangerel, and M.J. Novacek. 1994. A theropod dinosaur embryo and the affinities of the Flaming Cliffs dinosaur eggs. Science 266: 779–782.

Norell, M.A., J.M. Clark, L.M. Chiappe, and D. Dashzeveg. 1995. A Nesting dinosaur. Nature 378: 774–776.

Norman, D.B. 1984. A systematic reappraisal of the reptile order Ornithischia. *In* W.-E. Reif and F. Westphal (editors), 3rd Symposium on Mesozoic Terrestrial Ecosystems, Short Papers: 157–162. Tubingen: Attempto Verlag.

Novacek, M. 1996. Dinosaurs of the Flaming Cliffs. New York: Anchor Books, 367 pp.

Osborn, H.F. 1923. Two Lower Cretaceous dinosaurs of Mongolia. American Museum Novitates 95: 1–10.

Osmólska, H. 1979. Nasal salt glands in dinosaurs. Acta Palaeontologica Polonica 24: 205–215.

Owen, R. 1842. Report on British fossil reptiles. Part II. Reports of the British Association for the Advancement of Sciences 11: 60–204.

Pang, Q., and Z. Cheng. 1998. A new ankylosaur of Late Cretaceous from Tianzhen, Shanxi. Progress in Natural Sciences 8: 326–334.

Pereda-Suberbiola, X., and P.M. Barrett. 1999. A systematic review of ankylosaurian dinosaur remains from the Albian–Cenomanian of England. Special Papers in Palaeontology 60: 177–208.

Seeley, H.G. 1887. On the classification of the fossil animals commonly named Dinosauria. Proceedings of the Royal Society 43: 165–171.

Sereno, P.C. 1986. Phylogeny of the bird-hipped dinosaurs (Order Ornithischia). National Geographic Society Research 2: 234–256.

Sereno, P.C. 1999. The evolution of dinosaurs. Science 284: 2137–2147.

Sullivan, R.M. 1999. *Nodocephalosaurus kirtlandensis*, gen. et sp. nov., a new ankylosaurid dinosaur (Ornithischia: Ankylosauria) from the Upper Cretaceous Kirtland Formation (Upper Campanian), San Juan Basin, New Mexico. Journal of Vertebrate Paleontology 19: 126–139.

Sullivan, R.M. 2000. Reply to Upchurch and Barrett. Journal of Vertebrate Paleontology 20: 218–219.

Swofford, D.L. 2000. PAUP*: phylogenetic analysis using parsimony, version 4.0b10. Sunderland, MA: Sinauer Associates.

Tumanova, T.A. 1983. The first ankylosaur from the Lower Cretaceous of Mongolia. Trudy Sovmestoni Sovetsko-Mongol’skoi Paleontologicheskoi Expeditsii 24: 110–118. [in Russian]

Tumanova, T.A. 1987. The armored dinosaurs of Mongolia. Transactions of the Joint Soviet–Mongolian Paleontological Expedition 32: 1–76. [in Russian, R. Griffith translation]

Tumanova, T.A. 1993. A new armored dinosaur from south-eastern Gobi. Paleontological Journal 27: 119–125.

Vickaryous, M.K., A.P. Russell, P.J. Currie, and X.–J. Zhao. 2001a. A new ankylosaurid Dinosauria: Ankylosauria) from the Lower Cretaceous of China, with comments on ankylosaurian relationships. Canadian Journal of Earth Sciences 38: 1767–1780.

Vickaryous, M.K., A.P. Russell, and P.J. Currie. 2001b. Cranial ornamentation of ankylosaurs (Ornithischia: Thyreophora): reappraisal of developmental hypotheses. *In* K. Carpenter (editor), The armored dinosaurs: 318–340. Indianapolis: Indiana University Press.

Witmer, L.M. 1995. Homology of facial structures in extant archosaurs (birds and crocodilians), with special reference to paranasal pneumaticity and nasal conchae. Journal of Morphology 225: 269–327.

Witmer, L.M. 1997a. The evolution of the antorbital cavity of archosaurs: a study in soft-tissue reconstruction in the fossil record with an analysis of the function of pneumaticity. Memoirs of the Society of Vertebrate Paleontology, Journal of Vertebrate Paleontology 17(suppl. to 1): 1–73.

Witmer, L.M. 1997b. Craniofacial air sinus systems. *In* P.J. Currie and K. Padian (editors), The encyclopedia of dinosaurs: 151–159. New York: Academic Press.

Witmer, L.M. 1999. The phylogenetic history of paranasal air sinuses. *In* T. Koppe, H. Nagai, and K.W. Alt (editors), The paranasal sinuses of higher primates: development, function and evolution: 21–34. Chicago: Quintessence.

Witmer, L.M. 2001. Nostril position in dinosaurs and other vertebrates and its significance for nasal function. Science 293: 850–853.

Xu, X., X.-L., Wang, and H.-L. You, 2001. A juvenile ankylosaur from China. Naturwissenschaften 88: 297–300.

Young, C.C. 1935. On a new nodosaurid from Ninghsia. Palaeontologica Sinica, Series C, 11: 5–27.

APPENDIX 1

CHARACTER LIST

Characters used in this study are described, and the coding of character states explained. Similarity of characters in the current study to those used in previous analyses is noted, citing the author and (where applicable) the character number used in the analysis.

1. **Maximum skull width relative to maximum skull length**: less than (0); greater than (1) (Sereno, 1986; Coombs and Maryańska, 1990; Carpenter et al., 1998, no. 1; Kirkland, 1998, no. 2; Sereno, 1999, no. 94; Carpenter, 2001, no. 2; Vickaryous et al., 2001a, no. 1). Derived ankylosaurids exhibit a condition in which the maximum skull width equals or exceeds its maximum rostrocaudal length. All other thyreophorans possess a skull that is longer than it is wide.

2. **Highest point of skull roof**: caudal to orbits (0); above orbits (1); rostral to orbits (2) (Sereno, 1986; Carpenter et al., 1998, no. 23; Kirkland, 1998, no. 3; Sereno, 1999, no. 99; Carpenter, 2001, no. 3; Vickaryous et al., 2001a, no. 2). Some derived ankylosaurids have a highly arching skull profile that reaches its zenith well rostral to the orbits, when seen in lateral view with the maxillary tooth row horizontal. Others have a skull roof that is relatively level. Nodosaurids and other thyreophorans have a skull roof that slopes gradually rostrally from its highest point in the postorbital region.

3. **Premaxillary palate wider than long**: absent (0); present (1) (Sereno, 1986; Coombs and Maryańska, 1990; Kirkland, 1998, no. 4; Carpenter, 2001, nos.41, 42, 49; Vickaryous et al., 2001a, no. 13). Primitively, thyreophorans have a long, narrow snout that terminates in a narrow beak formed by the premaxillae. This lends the premaxillary palate a shape that is rostrocaudally long and transversely narrow. This condition persists in all nodosaurids. All but the most primitive ankylosaurids exhibit a transverse expansion of the premaxillary palate that is wider than long.

4. **Premaxillary teeth**: present (0); absent (1) (Lee, 1996, no. 19; Carpenter et al., 1998, no. 15; Kirkland, 1998, no. 20; Carpenter, 2001, nos.40, 50; Vickaryous et al., 2001a, no. 17). Primitively, thyreophorans possess teeth in the premaxilla. Premaxillary teeth are not present in derived members of the Nodosauridae and Ankylosauridae.

5. **External nares facing rostrally**: absent (0); present (1) (Coombs and Maryańska, 1990; Carpenter et al., 1998, no. 10; Kirkland 1998, no. 11; Carpenter, 2001, no. 51; Vickaryous et al., 2001a, no. 23). Primitive thyreophorans and stegosaurs have laterally facing external nares. This condition persists in the Nodosauridae and some primitive ankylosaurids. Most derived ankylosaurids have nares that face rostrally. It should be noted that many taxa have nares that seem to face rostrolaterally, and thus an arbitrary decision must be made as to their true orientation. In addition, variation in ossification of the narial osteoderms can affect the orientation of the bony nostril. This character could benefit from an attempt to quantify the position of the naris in space relative to other cranial elements.

6. **Accessory openings in the narial region**: absent (0); present (1) (Sereno, 1986; Coombs and Maryańska, 1990). The external nares are the only openings in the narial region of most thyreophoran taxa. However, in the derived Asian ankylosaurids *Pinacosaurus* and *Saichania*, accessory openings are present, communicating with a sinus in the premaxilla. Struts of bone formed by the premaxillae define a variable number of such openings.

7. **Fused osteoderms present on premaxilla**: absent (0); present (1) (Kirkland, 1998, no. 21). The premaxilla is devoid of osteoderms in primitive thyreophorans and many ankylosaurid taxa. In other ankylosaurids, as well as most nodosaurids, osteoderms are present on the outer surface of the premaxilla.

8. **Rostral edge of premaxilla with broad, ventrally concave notch in rostral view**: absent (0); present (1) (Kirkland, 1998, no. 5; Sereno, 1999, no. 91; Carpenter, 2001, no. 5; Vickaryous et al., 2001a, no. 15). Presence of a ventrally concave premaxillary notch is known in *Gastonia* and *Gargoyleosaurus*. Other thyreophorans exhibit a straight rostral premaxillary margin.

9. **Ventral margin of premaxilla in lateral view**: flat (0); convex (1); concave, resulting in a sharp premaxillary beak (2). Primitively, thyreophorans have a premaxillary beak edge that is flat in lateral view. Certain nodosaurids exhibit a pendulous, rounded premaxillary profile. Some Asian ankylosaurids have a premaxilla that is concave ventrally, forming a sharp beak in lateral view.

10. **Continuous edge formed by the premaxillary beak and maxillary tooth rows**: present (0); absent (1) (Sereno, 1986; Carpenter et al., 1998, no. 14; Kirkland, 1998, no. 6 [in part]; Carpenter, 2001, no. 9). In thyreophorans primitively the edge of the premaxilla grades directly into the tooth rows of the maxilla. This condition persists in nodosaurids, even where the tooth rows are deeply emarginated, and no premaxillary teeth are present. In ankylosaurids, the widening of the premaxillary palate results in a disruption of this continuous edge. This relates directly to other characters, such as width of the premaxilla and obscuring of the rostral maxillary teeth.

11. **Rostralmost maxillary teeth obscured in lateral view by processes of the premaxilla**: absent (0); present (1) (Sereno, 1986; Sereno, 1999, no. 100). The rostralmost maxillary teeth are hidden in lateral view by extensions of the caudoventral edge of the premaxillae in derived ankylosaurids. Nodosaurids and other thyreophorans lack these expanded premaxillary processes, and their rostralmost maxillary teeth are visible in lateral view.

12. **Maxillary tooth rows deeply inset from lateral edge of skull**: absent (0); present (1) (Sereno, 1986; Lee, 1996, no. 4; Carpenter at al., 1998, no. 16; Vickaryous et al., 2001a, no. 22). Stegosaurs and basal thyreophorans resemble other ornithischians in having maxillary tooth rows that are only modestly inset from the lateral edge of the maxilla. The maxillary tooth rows of ankylosaurs are deeply displaced medially (i.e., emarginated) from the edge of the skull.

13. **Maxillary tooth rows deeply concave laterally, outlining an hourglass shape**: absent (0); present (1) (Sereno, 1986; Lee, 1996, no. 8; Carpenter et al., 1998, no. 25; Kirkland, 1998, no. 9; Carpenter, 2001, no. 13; Vickaryous et al., 2001a, no. 18). Within Ankylosauria, nodosaurids exhibit a constriction of the maxillary tooth rows near the premaxillary-maxillary suture that outlines an hourglass shape in the palatal region. Ankylosaurids, as well as other thyreophorans, tend to have straight or very slightly curved tooth rows in the maxillae.

14. **Nasal septum dividing the respiratory passage into two separate bony canals**: absent (0); present (1) (Sereno, 1999, no. 57; Carpenter, 2001, no. 72). In stegosaurs and basal thyreophorans the respiratory passages are confluent above the palate. Ankylosaurs exhibit the development of a bony nasal septum that separates at least part of the respiratory passage into two discrete canals. CTs show, however, that the separation is not complete throughout their length in either nodosaurids or ankylosaurids.

15. **Closure of antorbital fenestra**: absent (0); present (1) (Sereno, 1999, no. 53; Carpenter, 2001, no. 6). In all thyreophorans the antorbital fenestra is reduced by extensions of the lacrimal, maxillary, and jugal bones. In ankylosaurs and derived stegosaurs, the fenestra is completely closed by these bones.

16. **Accessory antorbital ossification(s) completely separating orbit and antorbital cavity**: absent (0); present (1) (Sereno, 1986; Lee, 1996, no. 5; Sereno, 1999, no. 62). In all ankylosaurs, there is at least some development of a bony rostral orbital wall that separates the orbit from the adjacent nasal passage. In some taxa, this wall is solid and completely separates the two cavities. In others, such as *Pawpawsaurus* and *Pinacosaurus*, the rostral orbital wall is perforated so that the orbit is confluent with the nasal passages. Primitive thyreophorans exhibit an open rostral orbital wall.

17. **Median palatal keel composed of the vomer and pterygoid**: absent or weakly developed (0); extending ventrally to level of maxillary tooth crowns (1) (Sereno, 1986; 1999, no. 59). The vomers and pterygoids contribute to a median palatal keel that is flattened mediolaterally. In stegosaurs and basal thyreophorans, this keel is only weakly developed. In ankylosaurs, it extends ventrally, to the level of the maxillary alveolar margin (i.e., to the bases of the tooth crowns).

18. **Extension of the vomerine septum**: incomplete (0); extending to palatal shelves (1); extending to skull roof (2) (Lee, 1996, no. 14; Carpenter et al., 1998, no. 17; Carpenter, 2001, no. 11). In *Scelidosaurus* the sagittal vomerine septum separates the air passages incompletely, such

that the vomer has no contact with bones dorsal or ventral to it. This condition can be found in certain primitive nodosaurids as well. Other nodosaurids possess a septum that reaches as far dorsally as the skull roof, thereby dividing the respiratory tract completely. In ankylosaurids where the condition is known, the vomerine septum reaches the palatal shelves, above which the nasal septum divides the respiratory passageway. It is unclear how this character relates to the presence of a nasal septum and the actual division of the respiratory tract.

19. **Paired premaxillary, maxillary and nasal sinuses**: absent (0); present (1) (Sereno, 1986 [in part]; Coombs and Maryańska, 1990 [in part]; Carpenter, 2001, no. 52; Vickaryous et al., 2001a, no. 26). Paired cranial sinuses are known in certain members of the Ankylosauridae, but can be detected only through fortuitous breakage, sectioning, or CT scans.

20. **Secondary palate**: incomplete or absent (0); present and flat, reaching as far as the second or third maxillary tooth (1); present and composed of two palatal shelves, describing S-shaped respiratory route (2) (Coombs and Maryańska, 1990; Lee, 1996, no. 15; Carpenter et al., 1998, no. 18; Kirkland, 1998, no. 6 and no. 12 [in part]; Carpenter, 2001, nos.56, 71; Vickaryous et al., 2001a, no. 21). Thyreophorans primitively possess a straight and direct respiratory pathway and lack a secondary palate. This condition is retained in primitive nodosaurids and in *Gargoyleosaurus*. Derived nodosaurids like *Edmontonia* show development of a secondary palate that forms the ventral boundary of the respiratory tract. Derived ankylosaurids have a complex system of palatal shelves (comprising a long rostrodorsal shelf and a shorter caudoventral shelf) that describes a sinuous respiratory route.

21. **Pterygoid foramen**: absent (0); present (1) (Lee, 1996, no. 17 [in part]). A small foramen in the ventral surface of the pterygoid is present in many ankylosaurids and certain nodosaurids, such as *Pawpawsaurus*. The function of this foramen is to transmit a neurovascular bundle (see above).

22. **Space between palate and braincase (i.e., interpterygoid vacuity)**: open (0); closed (1) (Lee, 1996, no. 17 [in part]; Sereno, 1999, no. 61). Lee (1996) noted that the space between the palate and braincase is closed in ankylosaurians by the development of vertically oriented pterygoid bones. In *Pawpawsaurus*, however, the space remains open. Lee relates this to the presence of a smaller, more rostrally placed pterygoid foramen that is present in many ankylosaurids. We tentatively retain this character.

23. **Dorsoventrally narrow pterygoid ramus of the quadrate**: absent (0); present (1) (Sereno, 1986). A pterygoid ramus that is dorsoventrally short is thought to be a synapomorphy of the Ankylosauria. The ramus is still laminar and more or less vertical as in tetrapods generally.

24. **Quadrate shaft angled strongly rostroventrally**: absent (0); present (1) (Lee, 1996, no. 10; Carpenter et al., 1998, no. 20; Kirkland, 1998, no. 14). A strong rostroventral slant to the quadrate is present in nodosaurids. This condition may be correlated with the observed ventral inclination of the occipital condyle and other characters related to the head posture thought to have been adopted by nodosaurids (Lee, 1996). Ankylosaurids and other thyreophorans tend to have a vertical, pillarlike quadrate.

25. **Quadrate excavated rostrally**: absent (0); present (1) (Sereno, 1986; Coombs and Maryańska, 1990; Lee, 1996, no. 12; Carpenter, 2001, no. 69; Vickaryous et al., 2001a, no. 38). All ankylosaurs have a quadrate that is rostrocaudally narrow (i.e., ‘‘flattened’’). Nodosaurids exhibit excavation of the rostral surface of the quadrate that may be related to space demands for the attachment of jaw adductor musculature in the infratemporal fossa (Lee, 1996).

26. **Quadrate fused to paroccipital process**: absent (0); present (1) (Carpenter et al., 1998, no. 13; Carpenter, 2001, no. 55; Vickaryous et al., 2001a, no. 39). Many nodosaurids and *Gargoyleosaurus* exhibit fusion of the paroccipital process to the quadrate. In primitive thyreophorans, as well as derived ankylosaurids, there is an abutting or sutural contact.

27. **Paroccipital processes projecting caudolaterally**: absent (0); present (1) (Carpenter et al., 1998, no. 11; Kirkland, 1998, no. 18; Vickaryous et al., 2001a, no. 33). Most ankylosaurids possess paroccipital processes that project laterally, perpendicular to the rostrocaudal axis of the skull. Nodosaurids, however, tend to have paroccipital processes that are angled caudolaterally. This condition is also present in *Gargoyleosaurus*.

28. **Occiput rectangular and wider than high**: absent (0); present (1) (Sereno, 1986; Coombs and Maryańska, 1990; Lee, 1996, no. 1; Sereno, 1999, no. 52; Carpenter, 2001, no. 1). The presence of a rectangular occipital region that is wider than it is high unites the Ankylosauria to the exclusion of all other thyreophorans.

29. **Hemispherical occipital condyle**: absent (0); present (1) (Sereno, 1986 [in part]; Coombs and Maryańska, 1990 [in part]; Lee, 1996, no. 9 [in part]; Carpenter et al., 1998; no. 26; Sereno, 1999, no. 81; Vickaryous et al., 2001a, no. 35). The shape of the occipital condyle varies within Thyreophora, but most can be clearly described as hemispherical or crescentic (reniform). A hemispherical occipital condyle has been consid-

ered a diagnostic character of Nodosauridae, but its presence in certain ankylosaurids suggests this character state may be primitive for Ankylosauria.

30. **Occipital condyle formed exclusively by the basioccipital**: absent (0); present (1) (Sereno, 1986 [in part]; Coombs and Maryańska, 1990 [in part]; Lee, 1996, no. 9 [in part]; Sereno, 1999, no. 82; Vickaryous et al., 2001a, no. 34). In nodosaurids, the occipital condyle is composed exclusively of the basioccipital. This condition is present in some ankylosaurids, but in many the exoccipitals also contribute to the condyle.

31. **Occipital condyle set off from the ventral braincase by a distinct neck**: absent (0); present (1) (Sereno, 1986 [in part]; Coombs and Maryańska, 1990 [in part]; Lee, 1996, no. 9 [in part]; Kirkland, 1998, no. 16; Sereno, 1999, no. 82). The presence of a distinct and constricted ‘‘neck’’ separating the articular surface of the occipital condyle from the braincase has long been considered a diagnostic feature of Nodosauridae. This character is often subsumed by composite characters that describe other morphological features of the occipital condyle. The presence of a neck is difficult to assess in many specimens, and it is sometimes unclear as to whether a neck simply refers to an excavated area around the rostroventral edge of the condyle. We tentatively retain this character.

32. **Occipital condyle angled ventrally from plane of maxillary tooth rows**: absent (0); present (1) (Sereno, 1986 [in part]; Coombs and Maryańska, 1990 [in part]; Lee, 1996, no. 9 [in part]; Sereno, 1999, no. 82; Vickaryous et al., 2001a, no. 36). Most nodosaurids possess an occipital condyle that is angled ventrally at about 50° from the plane of the maxillary tooth rows. Ankylosaurids and other thyreophorans have an occipital condyle that extends caudally from the basicranium in a plane parallel to that of the maxillary tooth rows.

33. **Occipital condyle and paroccipital processes obscured in dorsal view by overhanging skull roof**: absent (0); present (1) (Carpenter et al., 1998, no. 12; Kirkland, 1998 no. 25; Vickaryous et al., 2001a, no. 12). Primitively in thyreophorans the occipital condyle and paroccipital processes are visible in dorsal view. This condition persists in nodosaurids, but the extensive growth of the squamosal dermal ossifications in derived ankylosaurids obscures the occiput when viewed dorsally. This character may change with ontogeny, as juvenile specimens of *Pinacosaurus grangeri* exhibit the primitive condition, while the adult holotype exhibits the derived state.

34. **Closure of supratemporal fenestra**: absent (0); present (1) (Lee, 1996, no. 2; Sereno, 1999, no. 54; Carpenter, 2001, no. 7). The upper temporal fenestra remains open in stegosaurs and in basal thyreophorans. In all ankylosaurs, the upper temporal fenestra is closed by extensions of the squamosal, postorbital, and parietal bones.

35. **Lateral temporal fenestra**: open (0); closed (1) (Carpenter et al., 1998, no. 6). The lateral temporal fenestra is open in primitive thyreophorans and all nodosaurids. Closure of this fenestra occurs in ankylosaurids by fusion of the quadratojugal and squamosal dermal ossifications.

36. **Obliteration of cranial sutures in adults, involving fusion and dermal sculpturing of the outer surface of most of the dermal skull roof**: absent (0); present (1) (Sereno, 1986; Lee, 1996, no. 3; Sereno, 1999, no. 63). Fusion of the dermatocranium such that the sutures are completely obliterated in adults is an autapomorphy of the Ankylosauria. In addition, osteoderms fuse to the dermal skull roof, further obscuring relationships between individual skull bones. In other adult thyreophorans, sutures can be identified, and there is no fusion of secondary dermal elements to the underlying skull table.

37. **Large subcircular dermal ossification covering most of the skull roof between the orbits**: absent (0); present (1) (Sereno, 1986 [in part]; Coombs and Maryańska, 1990 [in part]; Lee, 1996, no. 21; Carpenter et al., 1998, no. 9; Kirkland, 1998, no. 27; Sereno, 1999, no. 84 [in part]; Vickaryous et al., 2001a, no. 8). A large subcircular plate is observed on the skull roof between the orbits in the derived nodosaurids *Edmontonia* and *Panoplosaurus*. Other nodosaurids, ankylosaurids, stegosaurs, and basal thyreophorans lack this plate. It should be noted that not all specimens of *Edmontonia* show development of this plate, the region being covered by two to four smaller ossifications. This indicates that secondary dermal ossifications over the skull roof may be quite variable, and their taxonomic importance may have been oversimplified in previous analyses.

38. **Rostrocaudally narrow dermal ossification along the posterior border of the skull roof**: absent (0); present (1) (Sereno, 1986 [in part]; Lee, 1996, no. 20; Kirkland, 1998, no. 28; Carpenter, 2001, no. 68; Vickaryous et al., 2001a, no. 11). A rostrocaudally narrow plate lines the most caudal edge of the skull roof in many primitive and derived nodosaurids. The plate is absent in ankylosaurids and other thyreophorans.

39. **Pair of large, subrectangular osteoderms at caudal edge of skull roof**: absent (0); present (1). A pair of large, subrectangular osteoderms on the caudal edge of the skull roof is a synapomorphy of the Mongolian ankylosaurids *Tarchia* and *Saichania*.

40. **Raised, polyhedral dermal ossifications**

on skull roof: absent (0); present (1) (Kirkland, 1998, no. 31; Carpenter, 2001, no. 57). The cephalic dermal ossifications of most ankylosaurians are dorsoventrally flattened and thus conform closely to the contours of the underlying skull bones. In the derived Mongolian ankylosaurids *Tarchia* and *Saichania*, and in the recently described North American genus *Nodocephalosaurus*, these ossifications exhibit a great deal of relief, and have been variously described as pyramidal, bulbous, or inflated.

41. **Secondary dermal ossification, projecting ventrolaterally from the quadratojugal region**: absent (0); present and rounded (1); present and wedge-shaped (2) (Carpenter et al., 1998, no. 5; Kirkland, 1998, no. 24; Carpenter, 2001, no. 44; Vickaryous et al., 2001a, no. 7). Most ankylosaurians possess some degree of ornamentation overlying the quadratojugal bones. In nodosaurids, the element is weakly developed or gently rounded. In derived ankylosaurids, however, this ossification is prominent and wedge-shaped and has been referred to by some authors as a jugal ‘‘horn’’ (e.g., Carpenter et al., 1998). A further derived condition exists in *Nodocephalosaurus*, in which the jugal ‘‘horn’’ projects rostroventrally (Sullivan, 1999).

42. **Secondary dermal ossification, projecting caudolaterally from the squamosal region**: absent (0); present as weakly developed pyramid (1); present as prominent, wedge-shaped or pyramidal structure (2); present as narrow, elongated spines (3) (Carpenter et al., 1998, no. 3; Kirkland, 1998, no. 13; Vickaryous et al., 2001a, no. 6). Primitively, thyreophorans lack secondary dermal ossifications on the skull. Dermal ossifications are weakly developed in certain primitive nodosaurids, but ankylosaurids have developed a pair of prominent, wedge-shaped or pyramidal dermal ossifications over the squamosals, forming what some authors call postorbital ‘‘horns’’. These ossifications may join those overlying the quadratojugal along the side of the skull, thereby hiding the lateral temporal fenestra, paroccipital processes, and most of the quadrate in lateral view. However, because certain ankylosaurs exist with closed lateral temporal fenestrae but no squamosal ‘‘horns’’, we consider these to be independent characters.

43. **Median dermal ossification overlying dorsum of nasal region**: absent (0); present (1) (Sereno, 1986 [in part]; Vickaryous et al., 2001a, no. 9). A large, median dermal ossification overlies the nasal region in most nodosaurids, forming the dorsal border of the naris. This condition also occurs in certain ankylosaurids. Other ankylosaurids have a mosaic of small dermal ossifications in this region.

44. **Two pairs of dermal ossifications bordering the external nares**: absent (0); present (1) (Sereno, 1986 [in part]; Carpenter et al., 1998, no. 2). The presence of two pairs (one rostromedial, the other caudolateral) of dermal ossifications bordering the external nares is a condition found only in certain derived members of the Ankylosauridae.

45. **Tooth crowns with cingulum**: absent (0); present (1) (Carpenter et al., 1998 no. 21; Kirkland, 1998 no. 21; Carpenter, 2001, no. 14; Vickaryous et al., 2001a, no. 19). Derived members of the families Ankylosauridae and Nodosauridae possess bandlike cingula around the bases of the maxillary and dentary teeth. The teeth of basal thyreophorans, primitive nodosaurids, and primitive ankylosaurids lack a cingulum.

46. **Closure of external mandibular fenestra**: absent (0); present (1). The external mandibular fenestra is open in *Emausaurus* and in stegosaurs. All ankylosaurs exhibit closure of this fenestra.

47. **Coronoid process very low and rounded, projecting only slightly above the level of the dentary tooth row**: absent (0); present (1) (Sereno, 1986; Carpenter et al., 1998, no. 24; Sereno, 1999, no. 108; Carpenter, 2001, no. 63). The presence of a low coronoid process that barely projects above the level of the dentary tooth row has been considered a synapomorphy of the most derived ankylosaurids (Sereno, 1999). However, the presence of this character state in the basal thyreophoran *Emausaurus* indicates that this may be the primitive condition for ankylosaurs. Nodosaurids possess a more prominent coronoid process.

48. **Elongate osteoderm fused to the ventrolateral aspect of the mandible in adults**: absent (0); present (1) (Sereno, 1986; Coombs and Maryańska, 1990; Sereno, 1999, no. 65; Carpenter, 2001, no. 19). The fusion of a rostrocaudally long osteoderm to the ventrolateral edge of the lower jaw is diagnostic of Ankylosauria. No other thyreophoran exhibits development of an osteoderm in this position. The new juvenile *Pinacosaurus grangeri* skull (IGM 100/1014) has long, subtriangular osteoderms associated with the mandible on both sides. These osteoderms are not, however, fused to the underlying dentary and postdentary bones. This indicates that fusion of osteoderms occurs relatively late in ontogeny, although the osteoderms themselves may already be well developed.

49. **Sinuous ventral margin of mandible, which parallels the sinuosity of the dorsal margin in lateral view**: absent (0); present (1) (Sereno, 1986; Coombs and Maryańska, 1990; Sereno, 1999, no. 85; Carpenter, 2001, no. 62, 75). A sinuous ventral margin of the mandible, ending in a downturned mandibular symphysis, is an au-

tapomorphy of Nodosauridae. Ankylosaurids and other thyreophorans have a relatively straight ventral dentary margin.

50. **Predentary ventral process very short**: absent (0); present (1) (Sereno, 1986; Sereno, 1999, no. 66). The great reduction in the size of the predentary bone led Huene (1948) to coin the term Apraedentalia for the ankylosaurs. Although not completely lacking the bone, as this name suggests, ankylosaurs exhibit reduction, especially in the median ventral process, relative to other thyreophorans.

APPENDIX 2

TAXON-CHARACTER MATRIX[a]

	Character				
	1	1111111112	2222222223	3333333334	4444444445
Taxon	1234567890	1234567890	1234567890	1234567890	1234567890
Scelidosaurus	00?0??????	?00?00???0	??00??00??	???0000000	000000100?
Emausaurus	0000?00?00	00??0?????	???????0??	??00000000	000000100?
Huayangosaurus	0000000000	000?0?1???	0?00?01010	0000000000	0000000000
Gargoyleosaurus	0000000100	01001?1000	???1?1111?	0101010000	220101010?
Gastonia	0111000111	010?1?1??1	1??1??0100	0101010000	11000?????
Gobisaurus	0101110101	11011?1?12	?01011110?	1101110000	110?0?????
Shamosaurus	01010?0021	110?1????1	?????1110?	??11110000	1100?1110?
Tsagantegia	01111?0021	11011?1???	?1?1?10101	?111110000	11001?????
Talarurus	01?11???0?	????11????	??????????	?101110000	210011?11?
Minmi	11????????	010?1?????	???0??0101	0001100000	2100110?0?
Pinacosaurus	0211110001	1101101111	1010100111	0101110000	2P01111101
Tarchia	11111?0021	110?101112	1110100101	0001110011	2300011101
Saichania	1111111021	0101111112	1111?10101	0111110011	2300111101
Tianzhenosaurus	1111100?21	110?1?1???	?????00100	0111110011	22111?????
Nodocephalosaurus	?1?1??1??1	?10?111???	????????11	0??1110001	221???????
Shanxia	??????????	??????????	??????0101	0111?1?000	22????????
Ankylosaurus	1211001001	1101111112	1111000101	0111110000	221101110?
Euoplocephalus	1211110001	1101111112	1111010101	0111110000	2201111101
Pawpawsaurus	0000000000	011?1010?0	1011111111	1101010100	10100?????
Silvisaurus	000000??10	010?11?2?0	?1111?11?1	110111??00	10??11??1?
Sauropelta	00?100????	01??11?2?0	?111111111	1101011100	10?011011?
Panoplosaurus	0001000000	011?11?2?1	?111111111	1101111100	1010111101
Edmontonia	000100?000	011?11?2?1	?111111111	0101011000	101011011?
Animantarx	?2????????	??????????	???1??011?	0101011?00	10???1011?

[a] ? = missing data; 0-3 = character states (see appendix 1); P = polymorphism (states 1 & 3).

APPENDIX 3

APOMORPHY LIST

List of apomorphies for all ingroup taxa. Letters indicate nodes designated in figure 9. As many character states are unknown owing to the non preservation of complete skulls for all taxa, the optimization of some characters is ambiguous. These characters are indicated with an ‘‘a’’ when supported by ACCTRAN or fast optimization, and with a ‘‘d’’ when supported by DELTRAN or slow optimization. Reversals are indicated by a minus sign, and character states other than 0 or 1 are indicated in parentheses. Only characters 20, 41, and 42 were ordered.

Node A (Ankylosauria): 12, 15, 21d, 23, 24, 26d, 28, 30a, 32d, 34, 36, 41, 46, 48, 50d
Node B (Nodosauridae): 13a, 30d, 31, 38, 43, 49a
Node C: 16, 18(2), 22, 37a, 45, 49d
Node D: 4, 37d
Node E: 13d, 20
Node F: −31, 38a
Node G (Ankylosauridae): 8, 42
Node H: 2, 3a, 4, 10, 14a, 18a, 19a, 20, −27a, −29
Node I: 5, 6, 11a, 14d, 19d, −24, 35
Node J: −8a, −26a, −27d, 30d, 41(2), 45
Node K: 3d, −8d, 11d, 18d, 47
Node L: 16, 22a, 24a, −25a
Node M: 9a (2), 22d, 24d, 33
Node N: 1, 20(2), 42(2), 43a, 44
Node O: 9d(2), 26a, 41
Node P: 9d(2), 20a(2), 25a, 39, 40, 42(3), −43a, 44

APPENDIX 4

ABBREVIATIONS

A	aperture *A* in the narial region, homologous to the bony or true external naris
ang	angular
art	articular
aw	airway, nasal passage
B	structure *B* in the narial region
bo	basioccipital
C, C_1, C_2, C_3	aperture *C* in the narial region, divided into subsidiary openings in some skulls
ch	choana
cvp pd	caudoventral process of predentary
d	dentary
ect	ectopterygoid
f	frontal
fm	foramen magnum
j	jugal
la	lacrimal
lom	lateral osteodermal mass covering narial region
lvr	lateral recess of nasal vestibule within lateral osteodermal mass
mf	mandibular fossa
mo	mandibular osteoderm
mom	medial osteodermal mass covering narial region
ms	Meckelian sulcus
mvr	medial recess of nasal vestibule within medial osteodermal mass
mw	possible medial wall to structure *B*
mx	maxilla
mxo	maxillary osteoderm
n	nasal
oon	osteoderms overlying nasal bone
oop	osteoderms overlying parietal bone
ooqj	osteoderms overlying quadratojugal
oosq	osteoderms overlying squamosal
or	orbit
p	parietal
pal	palatine
pmx	premaxilla
pmx s	premaxillary sinus
po	postorbital
pop	paroccipital process
p pmx	palatal process of premaxilla
pre	prearticular
prf	prefrontal
pt	pterygoid
ptpal	pterygopalatine fenestra
q	quadrate
qj	quadratojugal
rec pal	pneumatic recess within palatine bone
san	surangular
so	supraorbital ossification
sop	supraoccipital
sp	splenial
sq	squamosal
sym	mandibular symphysis
v	nasal vestibule
v pmx f	ventral premaxillary foramen
vpt	fused vomeropterygoid element

Recent issues of the *Novitates* may be purchased from the Museum. Lists of back issues of the *Novitates* and *Bulletin* published during the last five years are available at World Wide Web site http://library.amnh.org. Or address mail orders to: American Museum of Natural History Library, Central Park West at 79th St., New York, NY 10024. TEL: (212) 769-5545. FAX: (212) 769-5009. E-MAIL: scipubs@amnh.org

∞ This paper meets the requirements of ANSI/NISO Z39.48-1992 (Permanence of Paper).