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An Embryonic Oviraptorid (Dinosauria: Theropoda) from the Upper Cretaceous of Mongolia

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ABSTRACT

An embryonic oviraptorid skeleton is described within an egg from the Late Cretaceous Djadokha Formation of Ukhaa Tolgod, Mongolia. The specimen comprises the ventral part of the skull and most of the mandible, a poorly preserved axial skeleton missing most of the tail, and portions of the forelimbs, shoulder girdles, pelvis, and hindlimbs. The skull is readily referable to the theropod dinosaur clade Oviraptoridae on the basis of several skull specializations (edentulous, vertically oriented premaxilla, a sinusoidally shaped lower jaw, and an unusual articulation of the vomer and premaxilla), and the postcranial skeleton is consistent with this identification. The egg is equivalent in overall shape and microstructure to those found beneath several oviraptorid skeletons recovered from the same formation. The skeleton is well ossified and, in comparison with ossification patterns in living Aves, the evidence suggests that this species was closer to the precocial end of the precocial-altricial spectrum of developmental patterns.

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INTRODUCTION

In July of 1993, during the third year of a joint paleontological project between the American Museum of Natural History and the Mongolian Academy of Sciences (Novacek, et al., 1994), a field party discovered an embryonic dinosaur. The embryo (IGM 100/971) (figs. 1, 3, 4) was found at Xanadu (Norell, 1997a), a sublocality of the exceedingly rich Ukhaa Tolgod locality (Dashzeveg et al., 1995, Norell, 1997b, Loope et al., 1998) in south-central Mongolia (fig. 2).

Norell et al. (1994) presented a preliminary description of the embryo. Circumstances surrounding its discovery were further commented on by Clark (1995) and Norell and Clark (1997). In short, the embryo was found in an eroded nest of several eggs lying in a circular pattern, as is typical of other oviraptorid clutches (Brown and Schlaikjer, 1940; Sabath, 1991; Mikhailov et al., 1994; Clark et al., 1999). One side of the egg had completely eroded away, exposing many of the bones, and the egg was broken into three pieces. The largest egg portion contains most of the preserved skeleton (fig. 3); a few tarsal elements were found in a smaller fragment (fig. 4), while a third piece contains no osseous material. Associated with the embryo were the remains of two small theropod skulls (Norell et al., 1994). Eggshell samples were sectioned and examined using a variety of histological techniques (Norell et al., 1994; Bray et al., submitted).

The specimen can be assigned to the Oviraptoridae based on several features. As in oviraptorids, some basal avialans,⁴ and dromaeosaurids, the foot has a fully developed third metatarsal that is not "pinched" proximally. A complete furcula is present in the pectoral girdle, and it is robust as in oviraptorids (Barsbold, 1981, 1983; Clark et al., 1999), unlike the more slender condition in *Velociraptor* (Norell et al., 1997; Norell and Makovicky, 1999). The unique skull of ovi-

raptorids provides the definitive evidence for referral of IGM 100/971 to the Oviraptoridae. Although poorly preserved, the skull maxillae and mandibles are edentulous, the premaxilla is oriented almost vertically, the outline of the lower jaw forms a severe sinusoidal wave, and the vomer forms an unusual articulation with the premaxilla on the roof of the mouth. All of these characters are present only in the Oviraptoridae (Barsbold, 1981, 1983; Barsbold et al., 1990; Clark et al., submitted).

Unlike eggs containing theropod embryos from China (Manning et al., 1997; Currie, 1996), IGM 100/971 is completely filled with sediment that is identical to the matrix surrounding the egg. This implies that the egg was cracked and infilled before lithification of the surrounding sediments. Presence of a double layer of eggshell (fig. 5) also suggests that the egg was broken and that some of its shell rearranged not long after burial and before the surrounding matrix fixed the elements in place. Dong and Currie (1993) suggested that such breakage is a critical element in the preservation of embryos, because it allows the egg contents to run out of the egg before enzymatic activity associated with decomposition destroys the fragile embryonic bones. However, the apparently unbroken eggs from China containing a wide variety of taxa seem to contradict this, at least for specimens at one locality (Manning et al., 1997; Currie, 1996). In the case of IGM 100/971, the fact that the skeletal elements are preserved in exquisite articulation indicates that the egg was filled in with matrix prior to decomposition of the connective tissue holding these articulations together.

The implications of this specimen as compared to other Cretaceous eggs from Central Asia was immediately apparent (Norell et al., 1994; Clark, 1995; Norell and Clark, 1997). The shell is identical in both ultrastructure and microstructure to many eggs found at other Mongolian and Chinese localities (Norell et al., 1994; Bray et al., submitted). Notable are those found associated with the type specimen of *Oviraptor philoceratops* at the Flaming Cliffs by American Museum Central Asiatic Expeditions in 1923 (Andrews, 1932). Soon after their discovery, these eggs were assigned to the ubiquitous *Protocera-*

⁴The term avialan (Avialae) is used throughout for the group including all of the descendants of the last common ancestor of *Archaeopteryx lithographica* and modern Aves. Aves is used for the crown group composed of all of the descendants of the last common ancestor of the extant diversity.



Fig. 1. IGM 100/971 showing the exterior of the egg.

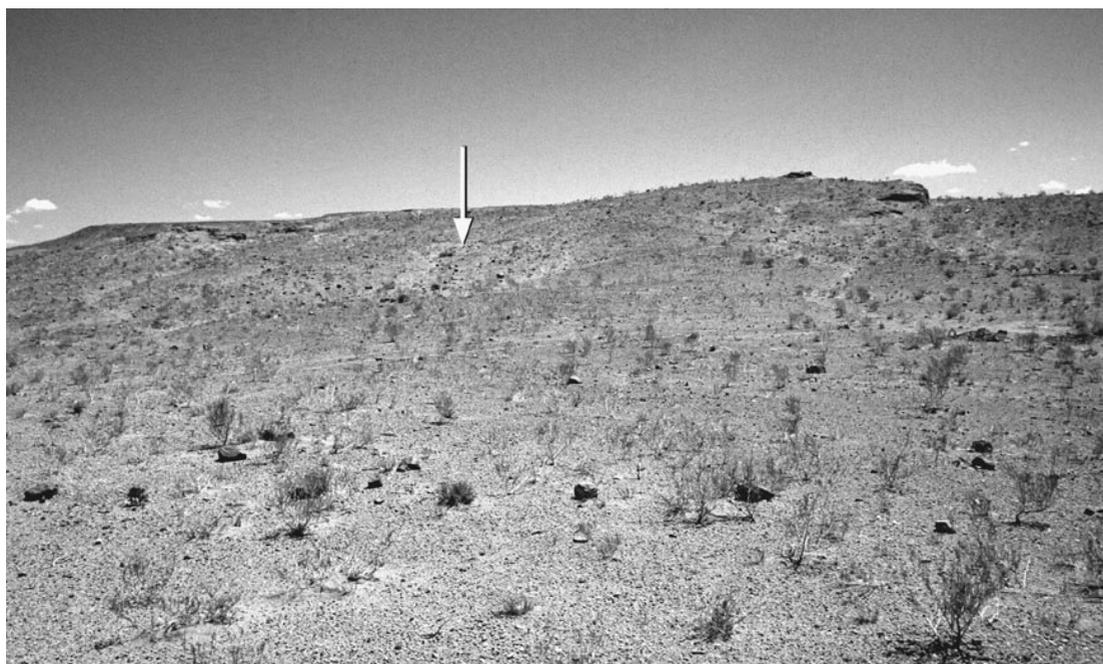


Fig. 2. The Ukhaa Tolgod Xanadu site looking east. The site of the IGM 100/971 find is indicated with an arrow.

tops andrewsi (Osborn, 1924). *Oviraptor philoceratops*, as its name implies, was interpreted as dying in the act of predated on the nest. However, it is fair to point out that Osborn (1924:7) cautioned that the name he proposed for the specimen “may entirely mislead us as to its feeding habits and belie its character”.

Through the years, the interpretation of *Oviraptor philoceratops* as egg eater and *Protoceratops andrewsi* as nest builder has been challenged by a few authors. Sabath (1991) and Mikhailov (1991) suggested theropod affinities based on eggshell histology. Nevertheless the familiar image of *Protoceratops andrewsi* standing near a nest of eggs is a common one in both the popular and scientific literature and is even captured in museum displays (fig. 6). The find of an oviraptorid embryo inside a “*Protoceratops*” egg modified this interpretation (Clark, 1995; Norell and Clark, 1997). Subsequent reports (Norell et al., 1995; Dong and Currie, 1996; Clark et al., 1999) of oviraptorids sitting on nests in brooding positions have enhanced this view and allowed reinterpretation of the *Oviraptor philoceratops* type specimen as a probable parent directly associated with the nest.

GENERAL DESCRIPTION

The embryo lies within the egg in a fetal position (fig. 3), with the head tucked forward next to the knees, as in crocodiles (Reese, 1915). This differs from the condition in modern birds where the head is tucked back beneath the arm (see Elzanowski, 1981). Little disarticulation of the elements has occurred. The head is located near the short axis of the egg, with its mandibles appressed against the shell. The cervical and thoracic vertebrae generally follow the arc defined by the egg apex, and the arms and shoulder girdle lie just below the head. The pelvis lies on the opposite side of the egg from the snout, and the hind leg is flexed with the knee lying just below the chin of the animal. The foot is also flexed and lies parallel to the long axis of the tibia. No caudal vertebral elements are preserved in the specimen; consequently the orientation of the tail cannot be ascertained.

Unfortunately much of the skeleton has been lost to weathering. The following elements are preserved:

- Egg fragment 1 (fig. 3) is the largest fragment, containing most of the preserved skeletal elements.
- Egg fragment 2 (fig. 4) is a small fragment from the caudal pole of the egg. This fragment contains a few tarsal bones.
- Egg fragment 3 is a piece of shell devoid of any osseous elements.

Numerous fragments were found near the embryo, and are likely from the same nest, but cannot be associated specifically with the embryo.

DESCRIPTION

SKULL

The skull is extremely fragmentary due to erosion of the dorsal elements, with only the dorsal surface of the palate, quadrates, premaxillae, and braincase floor exposed (fig. 7). The preserved elements are extremely well ossified, but many sutures are poorly defined.

The premaxillae are paired and form a beak with sharp edges at the end of the skull (fig. 8). The surface of this beak is rugose, suggesting that a horny covering may have been present. The anterior or nasal process is a small ridge of bone that is oriented nearly perpendicular to the horizontal axis of the skull. Just posterior to the base of the nasal process, is a small fossa. On the right premaxilla, the external narial opening is not preserved. The left premaxilla preserves much of the narial border except dorsally. The narial opening is elliptical with a subvertical, slightly posterodorsally inclining long axis. Inside the oral cavity, the premaxillae meet at the midline, forming an extensive and complete secondary palate with the maxilla.

The dorsal surface of the palatal rami of the premaxillae is poorly preserved. Posteriorly, the paired maxillae meet the premaxillae in a transverse suture. A thin premaxillary process contacts the premaxilla along the midline. Posteriorly, the maxilla borders the large choana. The palatal surface forms

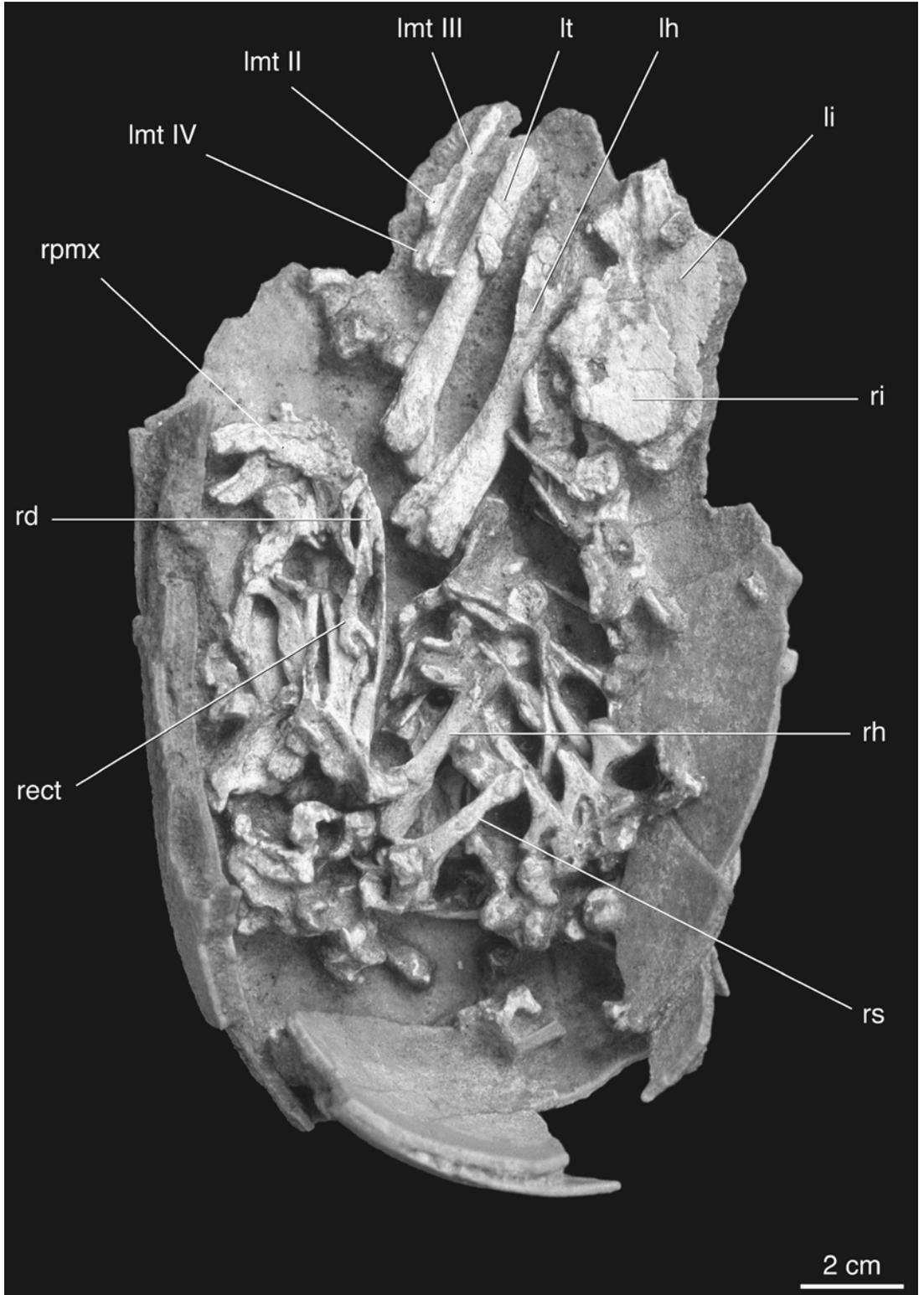


Fig. 3. Egg fragment 1—the main part of the IGM 100/971. Abbreviations are given in appendix 1.

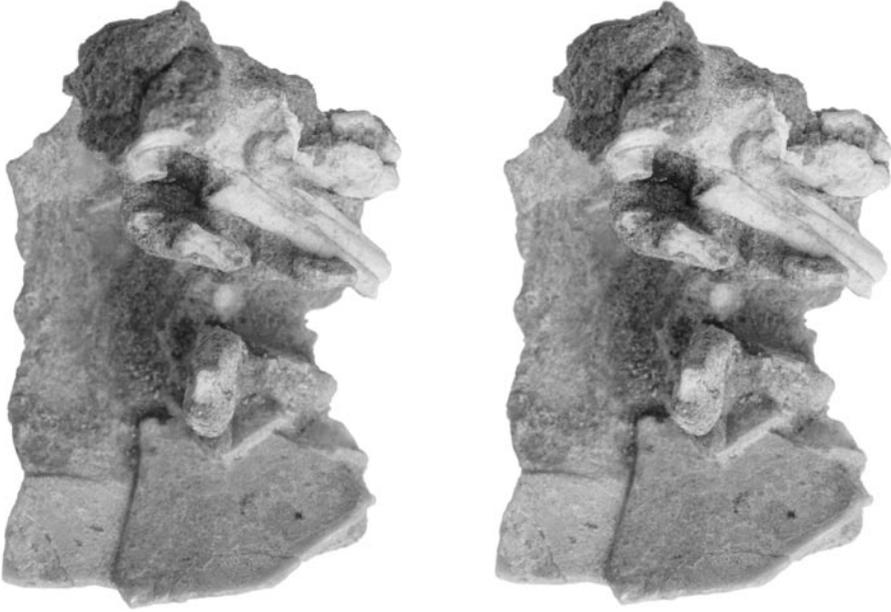


Fig. 4. Egg fragment 2—the right pes of IGM 100/971. Abbreviations are given in appendix 1.

gentle longitudinal ridges on each side of the midline. Posteriorly, along the midline at the intermaxillary suture is the contact surface for the vomer, which is unpreserved. In oviraptorids, this articulation is a complex one, where the vomer interdigitates with the maxilla via a large median process and paired lateral processes that are splayed diagonally in an anterolateral orientation. On the ventral surface of the skull it is this unusual articulation that contributes to the large “bumps” on the palate that have been confused with teeth (Paul, 1988: 376), but are actually ventromedial processes of the maxillae that lie between the lateral process of the vomer and its median articulation with the maxilla.

Dorsal to the palatal process of the maxilla is the ascending or narial process of this bone. Only the internal surface of the narial process can be observed, and the left is better preserved than the right. The ventral and anterior border of the antorbital fenestra is present on the left maxilla. Just ventromedial to the antorbital fenestra on the right side is a shallow fossa that may enclose the maxillary pneumatic sinus. Posteriorly, the maxillary contact with the jugal is not preserved, and both jugals are absent.

The left palatine is poorly preserved, and

only its medial ascending process is present. It is attached to a small plate of bone that represents the palatine surface. Anteriorly, it is covered by a fragment of maxilla. Posteriorly, it contacts the pterygoid and ectopterygoid.

Just medial to the posterior edge of the palatine is a small vertically oriented lacrimal fragment where it forms the preorbital bar. It lies at the posterior apex of the choana, just lateral to the vomerine process of the left pterygoid.

The left ectopterygoid can be observed in dorsal view. It is hook-shaped and forms the anterior and anteromedial boundary of the tiny subtemporal fenestra. Anterolaterally, the ectopterygoid forms a triple junction with the palatine and the maxilla. In this region, just anterior to the dorsal apex of the jugal process of the ectopterygoid, lies a tiny palatal fenestra. The jugal process broadens slightly where it would contact the unpreserved jugal. Posteriorly, the ectopterygoid broadens where it overlies the pterygoid. Posteromedially, the pterygoid process of the ectopterygoid overlaps the pterygoid, contributing to the pterygoid flange.

Both pterygoids are preserved in articulation with the braincase and the quadrates.

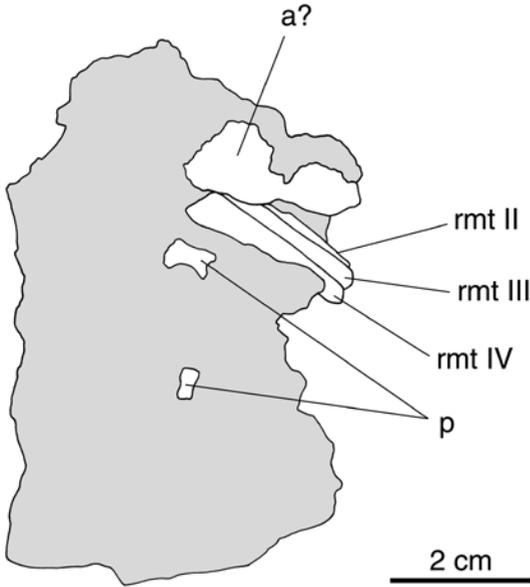


Fig. 4. Continued.

The pterygoids converge anteriorly, nearly meeting at their vomerine processes, and delimit a narrow interpterygoid vacuity. The pterygoid is broad anteriorly, posterior to the vomerine process, and narrows just anterior to the basiptyergoid articulation. The pterygoid flange is small. Just anterior to the small basiptyergoid articulation, the pterygoid elevates dorsally and with the pterygoid process of the quadrate forms a large vertical flange. This elevated area anterior to the braincase is perforated by a large foramen exiting anteriorly. The sutural connection

with the quadrate is not apparent. However, elements of the quadratopterygoid flange curve ventral to the braincase, defining a large chamber between the braincase wall and the flange.

As in adult oviraptorids, the quadrates are massive, and even at this early stage of development they appear to be fused with the pterygoids. The quadrates are extremely thick anteroposteriorly. The anterior surface of the quadrate, just dorsal to the articular surface, is concave. Correspondingly, the posterior surface is convex, giving the articular ramus a slightly forward pointing orientation.

On the floor of the braincase only the basi-sphenoid is preserved. The basioccipital should have survived erosion, but may have been separated from the skull and may be among the unidentified quadrangular bone fragments posterior to the skull. Anteriorly, a well preserved basisphenoid rostrum lies between and dorsal to the pterygoids. The parasphenoid rostrum extends anteriorly to just beyond the level of the posterior margin of the ectopterygoid's pterygoid process. At the dorsal base of the parasphenoid, the hypophyseal fossa is filled with matrix. Posterior and ventral to the braincase floor lies a pair of oval articular surfaces. These represent articulations with the unpreserved basi-occipital.

Both mandibles are present and in loose articulation (the right mandible is dislocated medially, and the left is flattened out exposing its medial surface). Like the premaxillae,

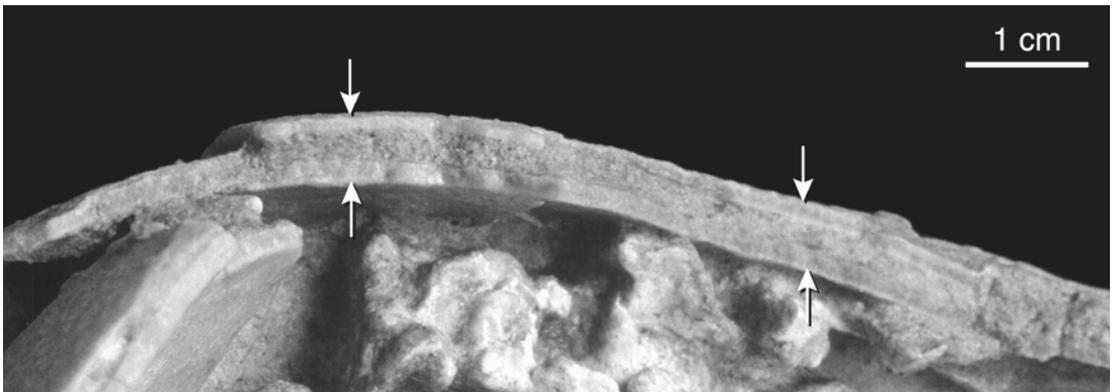


Fig. 5. Egg fragment 1 showing the double layer of eggshell caused by postmortem crushing.



Fig. 6. Although refuted by evidence, museum displays and popular accounts often show *Protoceratops andrewsi* associated with oviraptorid eggs and nests. This example from the American Museum of Natural History shows two *Protoceratops* in the vicinity of a nest. This mount was created in 1935 to highlight the findings of the first reported dinosaur nests by the museum's Central Asiatic Expeditions.

and in contrast to the condition seen in adult oviraptorids, the dentaries are not fused at the symphysis. The mandibular fenestra is large. Anteriorly the mandibular fenestra is elliptical and posteriorly it is truncated by the anterodorsal-posteroventrally directed margin of the surangular. As in oviraptorids generally, the articular fossa is low relative to the extremely convex, arching dorsal margin of the mandible. The toothless dentaries form the anterior half of the mandible. The dorsal margin is sinusoidal in lateral view and the ventral surface is flat, becoming convex at the symphysis. Inside the mouth, a broad shelf forms an anterior floor of the oral cavity near the midline at the symphysis.

Posteriorly, the dentary forms the anterior apex of the mandibular fenestra. A dorsal process arches posteriorly to join the surangular dorsal to the mandibular fenestra, although its dorsalmost part is not preserved on the right side and it is poorly exposed on the left side. A poorly preserved ventral process extends posteriorly to contact the surangular at the posterior end of the mandibular fenestra. The lateral surface of the bone

is crenulated in the symphyseal area, suggesting the presence of a horny beak surrounding the mouth.

In oviraptorids, the surangular is a large bone that makes up an extensive part of the lateral surface of the mandible. The surangular rises to a peak on the dorsal surface of the mandible just posterior to the level of the posterior end of the mandibular fenestra. The medial surface of the surangular is concave. The suture between the surangular and the articular is indistinct. The posterolateral surface of the mandible displays a depression anterior to its cranial articulation that is typical of adult oviraptorids.

VERTEBRAE

The vertebrae are poorly preserved throughout the embryo. However, representatives of all vertebral regions are present.

Only a single cervical vertebra can be identified with certainty (fig. 9), lying just posterior to the skull. It comprises a neural arch separated from its accompanying centrum. Apparently, and unlike those in adult

oviraptorids, the cervical rib was not fused to the neural arch. Well-formed anterior and posterior zygapophyses can be seen. The remaining cervical vertebrae and cervical ribs are only preserved as amorphous lumps of bone.

A few fragmentary dorsal vertebrae are scattered through the egg. Those that are best preserved lie in the pelvic region and therefore represent posterodorsals (fig. 10). The neural arches are separated from the centra and are unpreserved, except as featureless fragments lying near the rib heads. The centra are medially constricted giving the centrum an anterodorsally concave appearance. The dorsal surfaces of the centra are exposed, and the entrances to deep, probably pneumatic, cavities are visible.

Behind and anterior to the right ilium is a string of three centra that may be sacrals. The vertebrae are laterally compressed and separated from their neural arches. The sacral centra are fused to each other. Unfortunately other aspects of sacral anatomy are either unpreserved or cannot be exposed.

The pole of the egg that housed the posteriormost part of the animal is not preserved. A few tiny vertebrae, presumably posterior caudals, are preserved just anterior to the snout of the animal adjacent to the tibia (fig. 10), and one may lie in the mouth. These bones are extremely spongy, but they show a medial constriction and, although difficult to orient, seem to possess zygapophyseal structures.

RIBS

Well-ossified, but fragmentary thoracic ribs are preserved adjacent to corresponding vertebral segments. Although no exposed individual rib is preserved in its entirety, several rib fragments from the mid-thoracic area are visible. On these the heads are well-ossified and the capitulum and tuberculum of each individual rib are widely separated. Throughout the column the ribs are proximally flat, taking on a more circular cross-sectional shape distally. Just anterior to the pelvis, small but well-ossified ribs are present.

FORELIMB AND PECTORAL GIRDLE

A well-developed furcula is present (fig. 9). It is small, robust, and boomerang shaped. In anterior view, it is flat and, at the apex, straplike. The clavicular rami broaden and gently curve posterodorsally. There is no indication of an interclavicular suture, or a corresponding furcular apophysis, between lateral clavicular moieties, although in adult oviraptorids a hypocleidium is present (Clark et al., 1999).

Both scapulae are preserved, although only the most extreme proximal end of the left scapula is exposed (figs. 3, 9). The broken right scapula indicates that the scapular blade is straplike and ventrally concave. The head of the scapula, which articulates with the coracoid, is observed in both right and left elements. The width of the scapula increases dramatically at this articulation. Posteriorly, the scapula contributes to a large, deep glenoid fossa. The acromion is separated from the coracoid tubercle by a shallow longitudinal groove to which the furcula attaches. Ventral to the scapulae, between these bones and the eggshell, are several small, poorly preserved plates of bone that may represent fragments of the left coracoid. The right coracoid is disarticulated from the scapula and lies perpendicular to it. It is poorly preserved ventrally and is perforated by a centrally located coracoid foramen.

The proximal three-quarters of the right humerus is preserved, with the lateral surface exposed. The ventral surface of the proximal left humerus is exposed below an unpreparable mass of bones (figs. 3, 9). The proximal head of the humerus is greatly expanded relative to the shaft, suggesting the development of a large internal tuberosity. The head is formed of unfinished bone. On the humeral shaft, just distal to the head, a rugose area may represent the insertion point for the deltoid muscle. The deltopectoral crest is well formed distally. However, it is not continuous with the humeral head (as in adult theropods), being separated from it by a shallow trough. The medial surface of the proximal end of the left humerus is visible. The surface is anteroventrally concave and may have served as the insertion area for the pectoralis muscle.

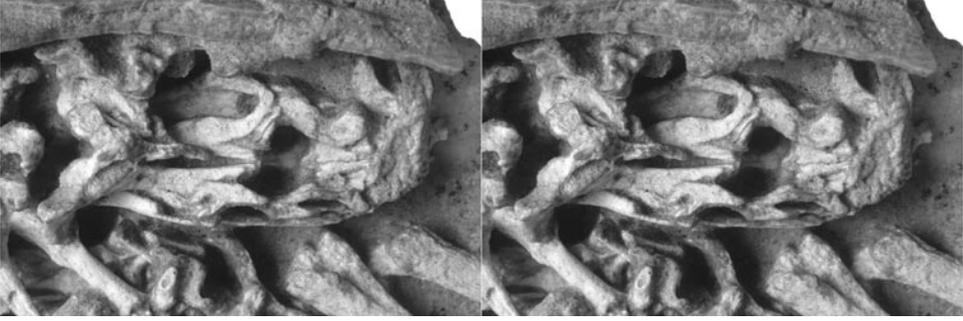


Fig. 7. The skull of IGM 100/971 in dorsal view. The anterior right lateral surface of the skull is visible due to oblique crushing on the palate. Abbreviations are given in appendix 1.

Only the most proximal fragments of the right radius and ulna are preserved. These elements are so fragmentary that they display no recognizable morphology, and apparently their proximal articular surfaces were formed of unfinished bone.

THE PELVIS AND HINDLIMB

The only preserved pelvic bones are portions of both ilia (fig. 10). The ilia are disarticulated, and it is impossible to tell if they were well-ossified to the sacral vertebral elements. The bones themselves are extremely thin, with smooth surfaces. The fragmentary elements suggest that the lateral surface was dorsoventrally high in comparison with adults ascribed to the smaller new species from Ukhaa Tolgod (Clark et al., submitted). The anterior blade of what appears to be the right ilium is preserved with its lateral side

visible. This surface is smooth and gently concave and is slightly raised dorsal to the acetabulum. Just ventral to the shallow anterior notch, the pubic peduncle is small and indistinct. However, this may be a preservational artifact.

On the left ilium, the ischiac peduncle forms the posterior border of the acetabulum and posteriorly it forms the posteroventral margin of a shallow posterior notch. A small ridge extending posteriorly is probably an early developmental manifestation of the medial blade (posterior blade of Welles, 1984); the ventral surface of this ridge therefore represents the channel for the caudofemoralis muscle.

The left hindlimb is nearly complete. The only remaining element of the right hindlimb is the tarsus preserved in egg fragment 2 (fig. 4). The proximal end of the femur is weath-

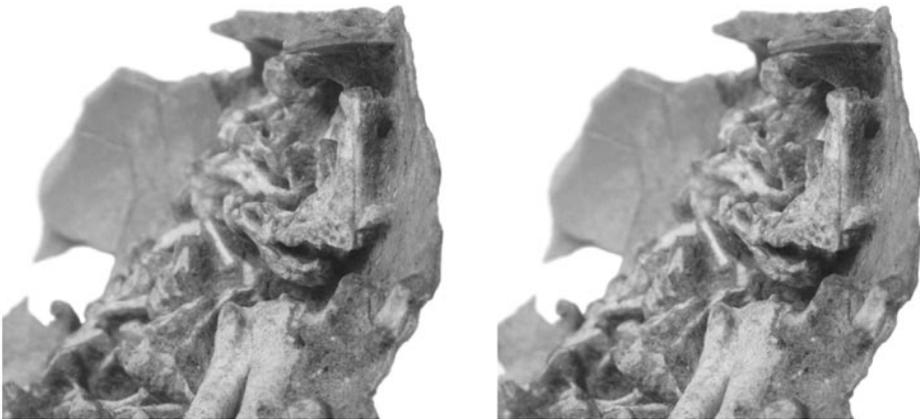


Fig. 8. The skull and left knee of IGM 100/971. The skull is in anterior view showing the mandibular symphysis and the suture between the premaxillae. Abbreviations are given in appendix 1.

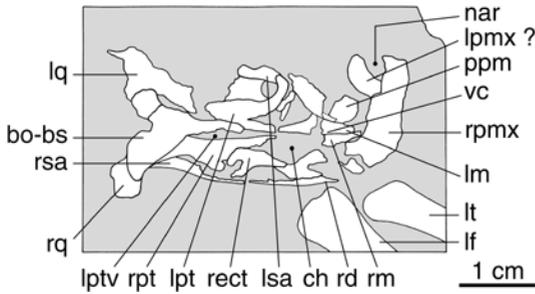


Fig. 7. Continued.

ered, and the femoral heads are absent. This is probably accentuated by incomplete ossification of the bone end. Just distal to the position of the femoral head lies a small concavity, posteriorly delimited by a small ridge that makes up the fourth trochanter. The femoral shaft is anteroposteriorly bowed. The anterior surface of the distal end of the femur is hidden. Buttresses for the lateral and medial condyle delimit a deep and well-defined popliteal fossa on the posterior surface. The distal surface is unfinished, although three distinct protuberances can be seen. Two of these correspond to the medial and lateral condyles. The third, lying posteromedial to the lateral condyle, corresponds to the ectocondylar tuber seen in adult oviraptorids.

The left tibia and fibula are preserved on IGM 100/971 fragment 1, except for their distalmost portions. The tibia is straight, shaftlike, and circular in cross section. The subtriangular proximal surface is unfinished. A small, but recognizable cnemial crest is

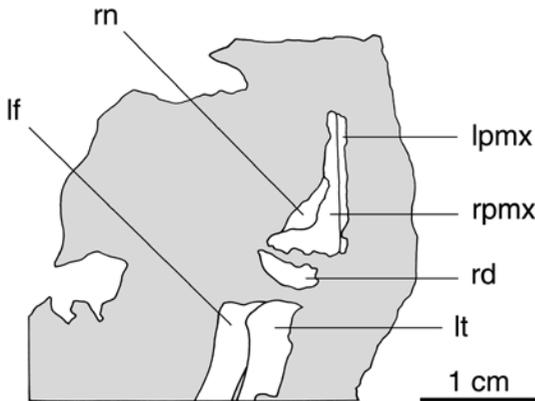


Fig. 8. Continued.

visible medially. Proximally, the fibula is expanded and extends the entire length of the preserved proximal part of the tibia.

A small bone fragment lying adjacent to the proximal end of the tarsus on IGM 100/971 fragment 2 probably represents the astragalus (fig. 4). Not much of this element is preserved. However, it lies adjacent to the proximal end of the tarsus and seems to have a finished articular surface. If our interpretation of this element is correct, the area of fragmented bone lying in a more proximal position is the ascending process of the astragalus, which in life lay on the anterodistal surface of the tibia.

The proximal portion of the right tarsus is preserved on fragment 2 (fig. 4) and the distal extremity of the left tarsus is exposed on fragment 1 (fig. 10). The right tarsus is exposed in anterior view, while the left tarsus is exposed in dorsal view. The three primary metatarsal bones (MT II, III, and IV) are nearly equal in size distally. They are suboval or nearly circular in cross section, indicating that the metatarsus does not display the arctometatarsalian condition. The proximal ends of the metatarsal bones are unfinished bone. MT IV is expanded proximally. MT III is narrow and displays an anterolateral surface where it contacts MT IV just distal to the proximal end of the tarsus. The distal metatarsus, although heavily worn, shows that MT III is the longest metatarsal. MT II is very fragmentary, consisting of only a small splint of bone lying adjacent to MT III. MT IV is more complete, although its slightly bulbous end is composed of unfinished bone. The distal end of MT III is also expanded and composed of unfinished bone. Near the distal metatarsus are several small lumps of indistinct bones that may represent pedal phalanges at an early, but unrecognizable stage of development.

EGGSHELL MORPHOLOGY

The morphology and histology of the eggshell of this specimen have been briefly described by Norell et al. (1994) and in more detail by Bray et al. (submitted). In short, the egg is elongatoolithid and is covered with longitudinal, or linearituberculate ridges. In all aspects of ultra and microstructure, the

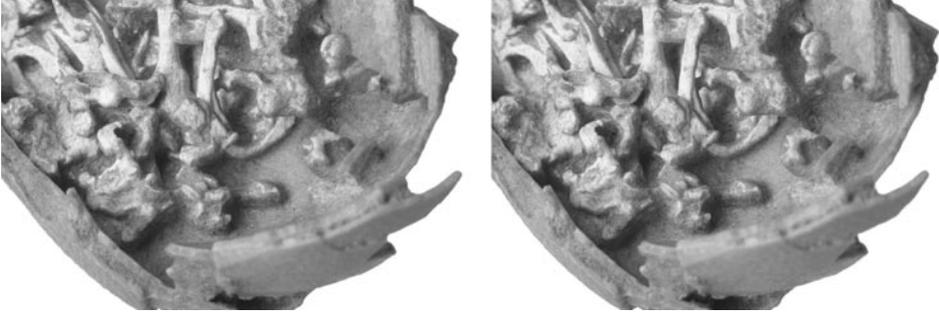


Fig. 9. Detail of the basicranium, cervical vertebra, and shoulder region of IGM 100/971. Abbreviations are given in appendix 1.

egg is identical to those considered by Mikhailov et al. (1994) to be of the ornithoid basic type and ratite morphology of the traditional egg parataxonomy, in their E1 group. This is the same type of egg that is found beneath several adult oviraptorid skeletons (Norell et al., 1994; Clark et al., 1999), including two skeletons at Ukhaa Tolgod.

An interesting weathering phenomenon has occurred in which the sculptured surface of the eggshell (fig. 1) has become reversed. In unworn eggshell, the horizontal growth lines of the egg lie parallel to the surface of the egg, mirroring the profile of the sculptural ridges and valleys. In the worn eggshell the "original ridges have weathered below the level of the original valleys thus giving the appearance of 'ridges' in place of the original 'valleys' and a flattened valley texture to the sites of the actual ridges" (Bray et al., submitted).

COMPARISONS WITH ADULT OVIPTORID TAXA

Because of the extremely specialized nature of the oviraptorid skull, referral of IGM 100/971 to this taxon can be made with confidence. However, because the Gobi Desert boasts an extensive oviraptorid diversity, referral to any specific taxon within this family is problematic. At least four taxa are known to occur in Upper Cretaceous rocks of this region, variously ascribed to the Djadokhta and Barun Goyot Formations (Barsbold et al., 1990), and two new species are known from the Djadokhta Formation at Ukhaa Tolgod (Clark et al., submitted). However, published diagnoses for oviraptorid taxa are far from adequate. This problem is confounded by the fact that little is known of changes to the oviraptorid skeleton during ontogeny.

Many of the differences among oviraptorid skull morphologies concern the presence of

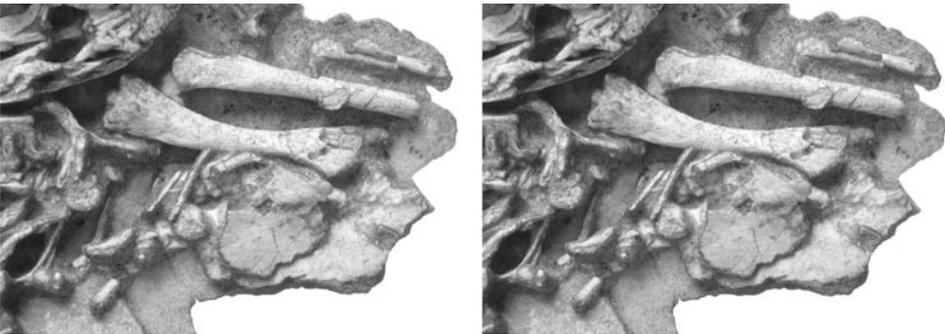


Fig. 10. Detail of the pelvis and hind limb of IGM 100/971. Abbreviations are given in appendix 1.

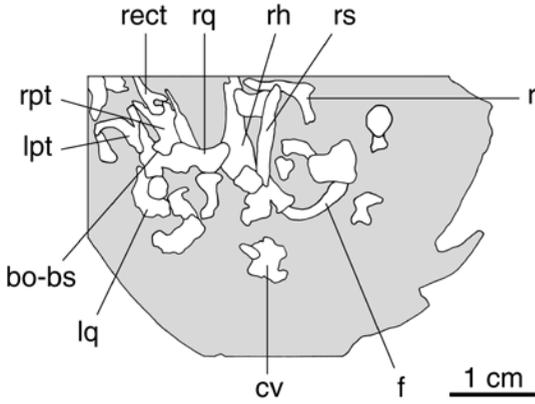


Fig. 9. Continued.

a crest along the dorsal midline of the skull in some specimens. Unfortunately, small sample sizes hinder our understanding of this crest as either intraspecific (e.g., sexually dimorphic) or interspecific. In any case, a lack of a crest in any small oviraptorid specimens is suspicious, suggesting that a crest might develop very late in ontogeny.

Although the dorsal region of the skull is not preserved in IGM 100/971, the premaxilla does suggest affinities with a certain group of oviraptorids. In noncrested forms like *Ingenia yanshinii*, an unnamed small taxon from Ukhaa Tolgod (Clark et al., submitted), and *Conchoraptor*, the anterior margin of the premaxilla is oriented posterodorsally, giving the snout a somewhat pointed profile. In *Oviraptor* (including *O. mongoliensis*) and a second unnamed large taxon from Ukhaa Tolgod (Clark et al., submitted), the anterior border of the premaxilla is oriented almost vertically, perpendicular to the plane of the ground, giving the skull a box-

like appearance. IGM 100/971 displays the latter morphology, with a nearly vertical premaxilla. We therefore tentatively refer it to the new large species from Ukhaa Tolgod.

Robust furculae are characteristic of oviraptorids, and their presence can be documented with certainty in *Oviraptor*, *Ingenia yanshinii*, and two undescribed forms from Ukhaa Tolgod (Barsbold, 1981; Clark et al., 1999; Clark et al., submitted). A furcula is known in several other theropod taxa (Norell et al., 1997; Makovicky and Currie, 1998, Xu et al., 1999, Burnham et al., 2000). In IGM 100/971, the furcula is dorsoventrally compressed and nearly flat in cross section. This is in contrast to the condition seen in adult oviraptorids, where the furcula is subcircular in cross section (Clark et al., 1999), and in this aspect resembles *Archaeopteryx* and other basal avialans, as well as the dromaeosaurs *Bambiraptor* and *Sinornithosaurus*. It differs from the more gracile furcula of *Velociraptor* (Norell et al., 1997).

PATTERNS OF OSSIFICATION AND DEVELOPMENTAL STRATEGIES

The discovery of IGM 100/971 provides the opportunity to compare patterns of ossification in an embryo of a nonavian dinosaur with those of living Aves. Perhaps most significant is the high degree of ossification of the skeleton of IGM 100/971. Although comparisons with Aves are complicated by the fact that the precise embryonic stage of IGM 100/971 is unknown and that in some instances its incompleteness may reflect preservational instead of ontogenetic factors, the observed degree of ossification of this fossil embryo at least falls toward the higher end of the spectrum observed for Aves very close to parturition. Ossified and well-defined ends of bones, such as the scapula, appear not to be present in living precocial hatchlings (Starck, 1993, 1994). In fact, most living hatchlings remain largely cartilaginous and poorly ossified, although it is known that the amount of ossification is greater in Aves with a precocial rather than an altricial mode of development (Starck, 1993, 1994; Starck and Ricklefs, 1998). For example, Starck (1994) calculated that the osseous mass of a precocial hatchling of Barred Buttonquail (*Turnix*

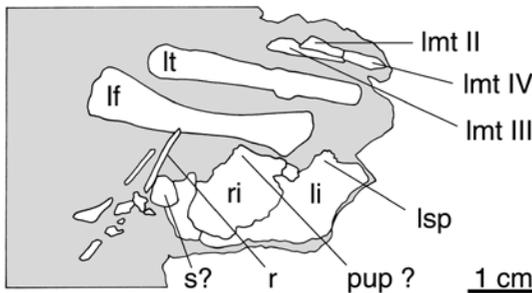


Fig. 10. Continued.

suscitator) ranges between 15.5 and 25.3% of the total skeletal tissue while that of an altricial hatchling Budgerigar (*Melopsittacus undulatus*) represents between 7.2 and 13.3% of the skeleton.

The high degree of ossification of IGM 100/971 is particularly evident in the skull, where even sutures are generally undistinguished (e.g., quadrate and pterygoid, surangular and angular). As in Aves (Hogg, 1980; Starck, 1993) and other nonavian dinosaurs (Chiappe et al., 1998), the degree of ossification of the skull of IGM 100/971 appears to be greater than that observed in the postcranial elements, where most bones, especially those from the limbs, have unfinished ends. Other aspects of the pattern of ossification of IGM 100/971 also agree with that observed in extant Aves. The well-ossified furcula of IGM 100/971 suggests that this element ossified early in embryogenesis, as in extant Aves (Russell and Joffe, 1985; Starck, 1994). For example, in the Common Quail (*Coturnix coturnix*), the Barred Buttonquail (*Turnix suscitator*), and the Common Kestrel (*Falco sparverius*), the furcula ossifies prior to most of the remaining skeleton (Starck, 1993: figs. 15B, 16B, 17B). The absence of sternal plates in IGM 100/971, which are large and well-ossified in adult oviraptorids (Clark et al., 1999), may indicate that, as in Aves, the centers of ossification of the sternum were inactive in embryonic stages (Hogg, 1980). Alternatively, the sterna may have been present but not preserved. The absence of symphyseal fusion between the dentaries is perhaps the most obvious difference between the pattern of ossification of IGM 100/971 and that of living birds. In the latter, the rostral ossification centers of the dentaries are nearly fused from the beginning of ossification (Jollie, 1957) and these two bones form a solid coossified symphysis at hatching (Hogg, 1980).

The wide spectrum of morphological, physiological, behavioral, and locomotory features of hatchlings of extant Aves is usually subdivided into four developmental categories [additional subdivisions are used by some authors; see Starck and Ricklefs (1998)]: precocial (e.g., megapods, tinamids, phasianids, anatids), semiprecocial (e.g., larks, stercorariids), semialtricial (e.g., raptors,

ciconids, ardeids), and altricial (e.g., psittacids and passeriforms). Precocial hatchlings are feathered, capable of finding their food, locomotorily active, and nidifugous; altricial hatchlings are naked and blind, unable to independently feed, incapable of locomotion, and consequently, nidicolous. "Superprecociality" represents the precocial extreme of the precocial-altricial gradient (Starck and Ricklefs, 1998). Superprecocial neonates (e.g., megapods) are completely independent and in some instances are able to fly the same day they have hatched. The semiprecocial and semialtricial developmental modes are intermediate categories of the precocial-altricial spectrum. Several authors (Elzanowski, 1981; Geist and Jones, 1996) have attempted to correlate the degree of ossification or the histology of dinosaur fossil embryos with specific developmental postnatal strategies of extant Aves. Elzanowski (1981), for example, regarded the high degree of ossification of certain Late Cretaceous embryos, usually attributed to the enantiornithine *Gobipteryx minuta*, as indicative of superprecociality, and proposed that this was the ancestral developmental mode of Aves.

In a histological study of extant Aves and nonavian dinosaurs, Geist and Jones (1996) argued that nonavian dinosaurs were precocial rather than altricial. Embryogenetic studies of Aves, however, have shown that the relative degree of ossification is a weak indicator of developmental modes (Starck, 1993; Starck and Ricklefs, 1998), thereby raising objections to these specific correlations. Although the degree of ossification of precocial hatchlings is significantly greater than that of altricial hatchlings, the degree of ossification of superprecocial, precocial, and semiprecocial hatchlings differs little (Starck, 1993). Furthermore, the degree of ossification of altricial embryos is comparable to that of other embryos for the first three-quarters of their embryogenesis (Starck, 1993), and the specific developmental stages of fossil embryos are hard to evaluate.

The distribution of specific developmental strategies among living birds strongly supports precociality, and not superprecociality, as the ancestral developmental mode of Aves (Starck, 1993; Chiappe, 1995). Most species of basal Aves (e.g., paleognaths, galliforms,

anseriforms) exhibit varying degrees of precocial behaviors (Starck and Ricklefs, 1998). Thus, the superprecocial strategy of megapods and a few other galliforms must be derived (contra Elzanowski, 1981). Hatchling crocodylians are also precocial (in a broad sense, because the avian categories are inapplicable for crocodylians). Thus, Geist and Jones' (1996) conclusions are not surprising given our knowledge of the developmental strategies and phylogenetic relationships of living archosaurs. Optimization of this character in archosaurs clearly supports the notion that a certain degree of precociality was primitive for all nonavian dinosaurs as well as for basal Aves; altriciality, however, may have evolved independently in certain lineages of nonavian dinosaurs (Starck and Ricklefs, 1998). The high degree of ossification of the skeleton of IGM 100/971 supports the idea that oviraptors were not altricial, although without indicating a specific developmental strategy. In particular, the ossified state of its sacrum and tail is significant, because one of the differences between the patterns of ossification of altricial Aves and those of other developmental modes is the fact that the sacrum of the former does not ossify until postnatal stages. Thus, it is likely that the development of oviraptorid neonates was closer to the precocial than to the altricial side of the precocial-altricial spectrum of its extant counterparts.

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APPENDIX 1

- a? possible astragalus
bo-bs basioccipital/basisphenoid
ch choana
cv cervical vertebra
f furcula
IGM Institute of Geology, Mongolia
lf left femur
lh left humerus
li left ilium
lm left maxilla
lmt II left metatarsal II
lmt III left metatarsal III
lmt IV left metatarsal IV
lpmx right premaxilla
lpt left pterygoid
lptv left pterygoid vacuity
lq left quadrate
lsa left surangular
lsp left sacral process
lt left tibia
nar nares
p phalanges
ppm palatal process of premaxilla
pup pubic peduncle
r ribs
rd right dentary
rect right ectopterygoid
rh right humerus
ri right ilium
rm right maxilla
rmt II right metatarsal II
rmt III right metatarsal III
rmt IV right metatarsal IV
rn right narial opening
rpmx right premaxilla
rpt right pterygoid
rq right quadrate
rs right scapula
rsa right surangular
s? possible sacral vertebrae
vc vomer contact

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