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An Oviraptorid Skeleton from the Late Cretaceous of Ukhaa Tolgod, Mongolia, Preserved in an Avianlike Brooding Position Over an Oviraptorid Nest

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ABSTRACT

The articulated postcranial skeleton of an oviraptorid dinosaur (Theropoda, Coelurosauria) from the Late Cretaceous Djadokhta Formation of Ukhaa Tolgod, Mongolia, is preserved overlying a nest. The eggs are similar in size, shape, and ornamentation to another egg from this locality in which an oviraptorid embryo is preserved, suggesting that the nest is of the same species as the adult skeleton overlying it and was parented by the adult. The lack of a skull precludes specific identification, but in several features the specimen is more similar to *Oviraptor* than to other oviraptorids. The ventral part of the thorax is exceptionally well preserved and provides evidence for other avian features that were previously unreported in oviraptorids, including the articulation of the first three thoracic ribs with the costal margin of the sternum and the

presence of a single, ossified ventral segment in each rib as well as ossified uncinat processes associated with the thoracic ribs. Remnants of keratinous sheaths are preserved with four of the manal claws, and the bony and keratinous claws were as strongly curved as the manal claws of *Archaeopteryx* and the pedal claws of modern climbing birds. The skeleton is positioned over the center of the nest, with its limbs arranged symmetrically on either side and its arms spread out around the nest perimeter. This is one of four known oviraptorid skeletons preserved on nests of this type of egg, comprising 23.5% of the 17 oviraptorid skeletons collected from the Djadokhta Formation before 1996. The lack of disturbance to the nest and skeleton indicate that the specimen is preserved in the position in which the adult died. Its posture is the same as that

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commonly taken only by birds among tetrapods that brood their nest, and its close proximity to the eggs indicates that the nest was not covered,

indicating that the behavior of sitting on open nests in this posture evolved before the most recent common ancestor of modern birds.

INTRODUCTION

Among the most surprising and revealing specimens collected from Upper Cretaceous Djadokhta-like beds in Mongolia by the joint American Museum of Natural History–Mongolian Academy of Sciences expeditions are those of the peculiar dinosaurs of the Oviraptoridae (Norell and Clark, 1997). Unlike the skulls of most other nonavian theropods, the unusually short, often highly pneumatized skull of oviraptorids lacks teeth and may bear a crest, resembling superficially the skull of the living cassowary. The abundance of oviraptorid specimens at the extraordinarily rich locality of Ukhaa Tolgod (Dashzeveg et al., 1995) is most unexpected in light of their rarity in other deposits (Barsbold et al., 1990). This wealth of new material already has answered a 75 year old enigma, and the specimen described here played a crucial role in this story (Norell et al., 1994).

The bizarre and poorly preserved holotype specimen of *Oviraptor philoceratops* was discovered at Bayn Dzak (the “Flaming Cliffs”) by the American Museum’s Central Asiatic Expedition in 1923, fortuitously encountered while excavating the first dinosaur nest found at this famous locality (Andrews, 1932). Because eggs similar to those in this nest are abundant at Bayn Dzak, and because of the preponderance of skeletal material of *Protoceratops andrewsi* at this locality, the eggs were identified as belonging to *Protoceratops* (Osborn, 1924). The skeleton overlying the nest therefore presented an enigma. To explain this association, Henry Fairfield Osborn (Osborn, 1924) speculated that the adult animal had been preserved while robbing the nest (although there was no evidence to indicate predation), hence he endowed it with a name meaning “egg seizer fond of ceratopsians.”

For many years the identity of the eggs as those of *Protoceratops* was accepted with little doubt. In recent years this identification was questioned (Sabath, 1991; Mikhailov, 1991),

but only circumstantial evidence for reidentifying the eggs was forwarded. The discovery of Ukhaa Tolgod in 1993 provided the evidence crucial to deducing a definitive answer—an oviraptorid embryo within the same type of egg as those beneath the *Oviraptor philoceratops* holotype (Norell et al., 1994). With this reidentification of the eggs the association of the skeleton with eggs of its own kind became explicable as evidence of parental care, rather than predation.

The specimen described here, IGM 100/979 (mistakenly labeled 100/972 in fig. 1 of Norell et al., 1995), provides further evidence that this association is indeed a result of parental behavior. The specimen (fig. 1) was discovered in 1993, and after its preparation a preliminary note was published (Norell et al., 1995). A second specimen on a nest was collected from Ukhaa Tolgod in 1995 (see Webster, 1996), and another from correlative beds at Bayan Mandahu in Inner Mongolia, China, was reported by Dong and Currie (1996). These three specimens and the *O. philoceratops* holotype provide compelling evidence that the close association between adults and nests in Oviraptoridae has a biological explanation.

The specimen is remarkably intact, and in addition to its importance in preserving this individual’s relationship to the nest it provides important new data on the thoracic skeleton in oviraptorids. Many of these features were revealed by preparation following publication of the preliminary note, and thus were not reported or illustrated there. Oviraptorids are among the closest relatives of Avialae, the group comprising *Archaeopteryx*, extant birds, and related taxa (Aves of some other authors: see Gauthier, 1986), and these new features help determine the precise relationships of oviraptorids among Theropoda and the homology of these features.

Institutional abbreviations: AMNH—American Museum of Natural History, New York; IGM—Mongolian Institute of Geolo-

gy, Ulaan Baatar; **IVPP**—Institute of Vertebrate Paleontology and Paleoanthropology, Beijing; **MAE**—field numbers of the collections made by the Mongolian Academy of Sciences—American Museum of Natural History expeditions to the Gobi Desert.

GEOLOGIC SETTING OF THE FIND

The specimen is from a thick-bedded sandstone in the lower part of the local section at the Ankylosaur Flats sublocality, Ukhaa Tolgod. These sediments and the fauna they entomb closely resemble sediments and assemblages at localities in the Djadokhta Formation, such as Bayn Dzak and Bayan Mandahu, but some similarities with the fauna of the Barun Goyot Formation have also been noted (Dashzeveg et al., 1995; Gao and Norell, 1996). Currently the stratigraphic relationships of this locality relative to other localities, especially the type section of the Barun Goyot Formation, are unclear and under study (L. Dingus et al., in prep.).

At Ukhaa Tolgod, the specimen was collected from a unit with a lithology that has been described elsewhere as a "structureless sandstone" and interpreted as eolian in origin (e.g., Eberth, 1993). In the Djadokhta Formation at Ukhaa Tolgod this facies initially was interpreted as eolian in origin (Dashzeveg et al., 1995). Recently, Loope et al. (1998) reinterpreted these deposits as representing low-energy debris flows from eolian deposits that formed thick alluvial fans. The source of these deposits was an extensive field of stabilized sand dunes that destabilized when inundated with water during large rainstorms. They interpreted the ancient Ukhaa Tolgod environment as dominated by large, stabilized sand dunes separated by interdunal environments such as small, ephemeral ponds. Loope et al. (1998) suggested that sand flowed at relatively low energy from the dunes into the interdunal zone following large rainstorms. The low-energy flows covered dead, or dying, animals and may have entombed smaller animals in burrows. Low-energy depositional conditions may therefore be responsible for the excellent preservation of the Ukhaa Tolgod fossils, including IGM 100/979.

As with many of the specimens from

Ukhaa Tolgod, traces of burrowing invertebrates are preserved with the skeleton. They are recognizable mainly because they are more strongly cemented than the surrounding matrix and are lighter in color. Five burrows were exposed during preparation, including a long burrow on the dorsal surface of the sternal plates (fig. 2). These burrows are filled with white particles which may be pieces of digested bone, and two in the shoulder region are nearly white. Four of the five are slightly curved, but the smallest one is straight. One is preserved above the right coracoid, one to the left of the fourth digit of the left pes, and another between the right ischium and right pes, and one was removed from above a right ventral rib just behind the right sternal plate. Most are similar in shape, ranging from 3–4 cm in length and 4–8 mm in diameter, but the one above the sternum is over 6 cm long (fig. 2). Although other evidence of contemporaneous fossil arthropods at Ukhaa Tolgod (Loope et al., 1998) and other Djadokhta localities (see Johnston et al., 1996) may be from the taxon responsible for the burrows, it is also possible that burrows associated with IGM 100/979 were formed significantly after deposition of the bed in which it is buried.

The age of the Djadokhta Formation at Ukhaa Tolgod and elsewhere in Mongolia and China currently is not constrained by radiometric dates, marine invertebrates, or paleomagnetic polarity patterns. Comparisons of the vertebrates suggest a correlation with the late Campanian to early Maastrichtian marine invertebrate stages (Lillegraven and McKenna, 1986; Jerzykiewicz and Russell, 1991). However, the Darabasa Formation of Kazakhstan has a mammalian fauna similar to that of the Djadokhta Formation and is interbedded with Early Campanian marine invertebrates (Averianov, 1997).

DESCRIPTION THE SKELETON

The skeleton (fig. 1) is incompletely exposed, as further preparation would compromise the integrity of the specimen or endanger bones by removing their support. Missing are nearly the entire vertebral column, the skull, and the ilia and left femur. The



Fig. 1. IGM 100/979, in dorsal view. See Appendix for abbreviations.

exposed portions comprise a complete right forelimb; a partial left forelimb including the proximal end of the humerus, the distal ends of the radius and ulna, and all the bones of the manus; the nearly complete furcula; the ventral portion of both scapulae fused with the coracoids; the left and right sternal plates; what appears to be the ventral part of a vertebral centrum in the shoulder region; the distal ends of the ischia and pubes; the distal end of the right femur and the proximal half of the tibia and fibula in articulation; the right pes distal to the middle of the metatarsals (the second and third digits are not exposed); the left fibula, tarsus, and pes in articulation, and what may be a fragment of the proximal end of the tibia; and a series of

gastralia and the distal ends of seven pairs of ribs. Most of the bones are uncrushed except the right radius, ulna, femur, and tibia. Remnants of the keratinous claws of the manus are preserved on the ends of the second and third unguals on the right side and the first and third ungual on the left side.

PECTORAL GIRDLE AND FORELIMB: The furcula (fig. 3) is missing the distal half of its left side and a small part of the distal tip of its right side, which is otherwise preserved in articulation with the right scapula. It is completely fused, with no indication of a suture between the two clavicles. It is a robust bone that curves posterodorsally at its distal end (as preserved on the right side). The broken edge of the left side of the bone reveals

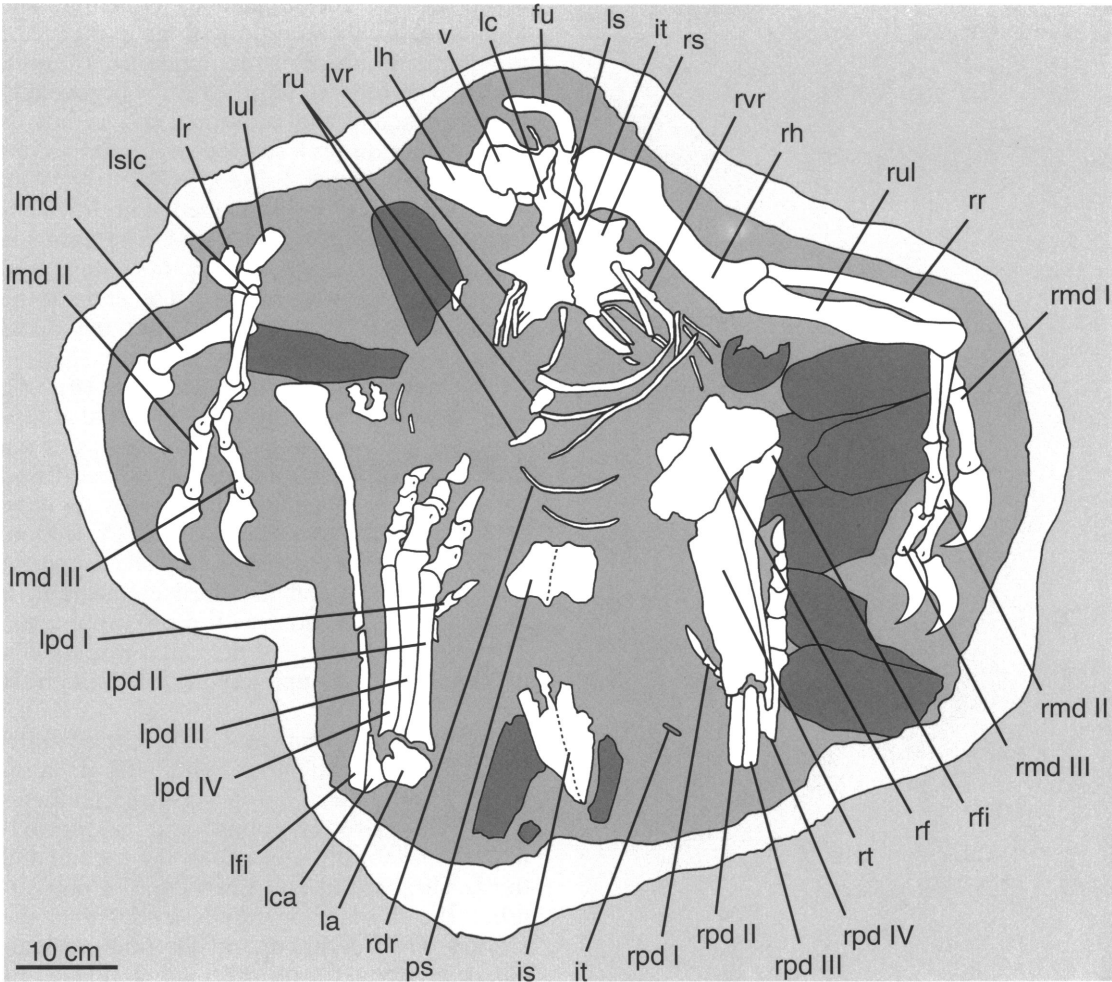


Fig. 1.—Continued.

no indications of a pneumatic space within it, as is found in the furcula of many birds. The distal end flattens where it articulates with a distinct shelf on the anterior edge of the scapula. An unusually long, dorsoventrally flat hypocleidium extends posteroventrally from the midline of the furcula, directly toward the sternum (fig. 3). It is nearly half as long as is each half of the furcula. It tapers distally from a broad base, and is about twice as long as the base is wide.

Remnants of the scapulae are poorly preserved. A well-developed shelf is preserved on the anterior edge of both elements dorsal to the glenoid fossa, and the furcula articulates with this shelf on the right side. The

shelf is nearly horizontal and dorsally concave, with a well-developed semicircular rim anteriorly.

The right coracoid is partly exposed and the left is almost completely exposed in medial view. The exposed portion is similar in size and shape to that of other oviraptorosaurs (Barsbold et al., 1990), which is more elongate ventrally than in basal theropods, forming a quadrangular shape in medial and lateral views. The articulation with the sternum is exposed only on the left side, where the coracoid has been displaced slightly anterodorsally. The coracoid contacts the sternum along the anterior edge near the midline.

The humerus (fig. 4) has a well developed



Fig. 2. IGM 100/979, invertebrate trace on the dorsal surface of the sternal plates. Anterior end of skeleton toward top.

deltoid crest, extending nearly the proximal third of the bone. Opposite the deltoid crest, near the medial edge of the humerus, is a low prominence, the ventral (internal) tuberosity. Only the anterior surface of the distal end is exposed.

The shaft of the only complete ulna, the right, is apparently broken and healed, as indicated by an expanded area two-thirds of the way down the shaft with a rugose surface. A deep longitudinal groove medial to the rugose area may also be due to this injury, but

could also be accentuated by crushing. The ulna is relatively straight with no evidence of bowing, and there is no evidence of quill knobs. The olecranon process is only weakly developed, and the proximal end is not as robust as in an undescribed oviraptorid skeleton from Ukhaa Tolgod, IGM 100/1002. The distal end is expanded into a well-formed, convexly rounded end. The radius is slightly more slender than the ulna, and shows no evidence of injury. The ends of the radius are not well exposed, but the distal third has a slight dorsal bend to the shaft.

The carpals are poorly exposed (fig. 4). The large distal ("semilunate") carpal is separated slightly from the proximal ends of the metacarpals, and could not have been fused to them. The left element appears to have rotated somewhat out of position. A second, smaller carpal is preserved laterally, opposite the proximal end of the third metacarpal. It is triangular in shape, with a proximal apex. There is no evidence of proximal carpals, but this area is not completely exposed on either side.

The manus comprises only three digits (figs. 5, 6), homologous with I-III in comparison with other Theropoda. The first metacarpal is relatively robust and is approximately one-third the length of the second and third. The second and third parallel one another, the third being more slender than the second. The lateral edge of the first metacarpal is in contact with the medial surface of the second, but as preserved on both sides the third articulates on the ventrolateral, rather than lateral, edge of the proximal end of the second. The proximal end of the third metacarpal is well developed rather than being reduced as in some oviraptorids (such as *Ingenia*).

The digital formula of the manus is 2-3-4-X-X. The first digit is about two-thirds the length of digits II and III (including metacarpals), which are equal in length. The proximal phalanx of the first digit is long and robust, similar in length to, but more robust than, metacarpals II and III. The proximal and medial phalanges of the second digit are also elongate, each being approximately two-thirds the length of the proximal phalanx of digit I. The proximal two phalanges of the third digit are smaller, each being approxi-

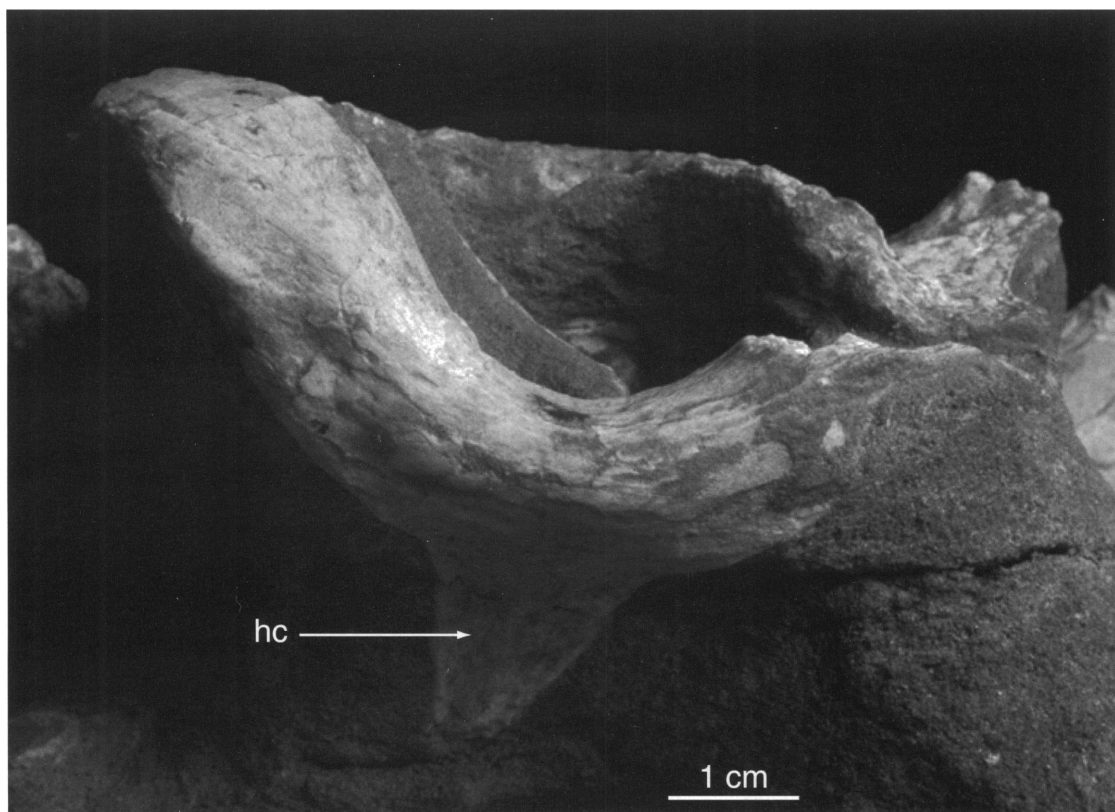


Fig. 3. IGM 100/979, furcula in anterodorsal view. Note the elongate, flat hypocleidium (hc).

mately one third the length of the proximal phalanx of digit I. The penultimate phalanx of digit III is approximately 25% longer than the proximal phalanges.

The articulations between the proximal phalanges and the metacarpals indicate that little rotation was possible. The surfaces are not well rounded, and they do not extend far beyond the minimum area over which the two bones contact. The articulations between the phalanges, however, are all strongly convexo-concave and extend beyond the minimum area of contact, indicating a much greater degree of anteroposterior rotation.

The manal claws are strongly curved, deep, and laterally compressed with well developed flexor tubercles. The proximal end of unguals II and III has a well-developed lip dorsal to the articular surface. The groove for the claw sheath on each side is situated near the ventral edge proximally and rises to the dorsal surface distally, being symmetrically

placed on both sides. The claw of digit I is larger than that of digit II (89 mm in greatest length versus 77 mm), which is larger than that of digit III (71 mm).

Remnants of the unossified, presumably keratinous, part of the claw are preserved on the second and third unguals on the right side and the first and third ungual on the left side. They indicate that the keratinous claw extended significantly beyond the end of the bone. In all four cases the keratin is preserved as a thin ribbon of fibrous tissue dorsal to the end of the ungual, suggesting that this region of the claw differed from others in some way (perhaps in density or thickness of the keratin). (A small clump of white material beneath the ungual of left digit III near its tip may also be from the keratinous claw.) The longest example is on right digit II, although the distal part of the keratin is separated by a large gap from the proximal part. The total length of the tissue, including the

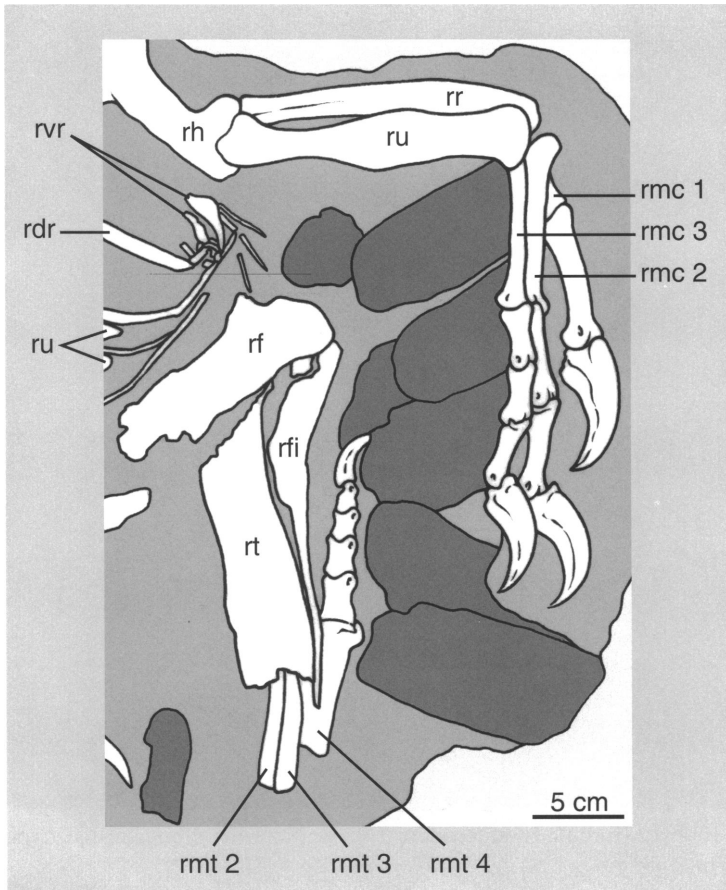


Fig. 4. IGM 100/979, right fore and hindlimbs on nest in dorsal view. Note pairing of eggs. Photographed prior to preparation of sternum. See Appendix for abbreviations.

gap, is 32 mm, and it extends 23 mm beyond the end of the bone in a direction continuous with the curvature of the dorsal edge of the claw.

PELVIS AND HINDLIMB: Only the distal part of the pubes are preserved, and their distal ends are not exposed (fig. 1). In cross section the lateral part of each bone is subcircular, and a thin lamina extends medially towards the midline. The two bones are strongly sutured into a midline symphysis, forming a relatively flat anterior surface. Proximally the medial edge of each bone becomes more posteriorly oriented, creating a concavity on the anterior surface of the symphysis, and presumably a pubic apron posteriorly. The orientation of the bones is similar to the position of these bones in articulated pelvises of oviraptorids, nearly vertical but projecting

somewhat anteroventrally. The pubic boot is not exposed and must occupy the region in the center of the nest.

The distal end of the ischium (fig. 7) is expanded and the two bones form a horizontal symphysis with a deeply concave dorsal surface. The ischia are in firm contact over the length of the symphysis (116 mm), and the suture involves a complex interdigitation of large processes and concavities in a sinusoidal pattern. An ischial symphysis has not been reported in any other oviraptorid specimen (Barsbold et al., 1990). The bone thins dramatically distally, in the posterior third of the symphysis, and ventrally along the midline. The preserved portion of the ischia lies distal to the region an obturator process would be expected.

The distal end of the right femur is too



Fig. 4.—Continued.

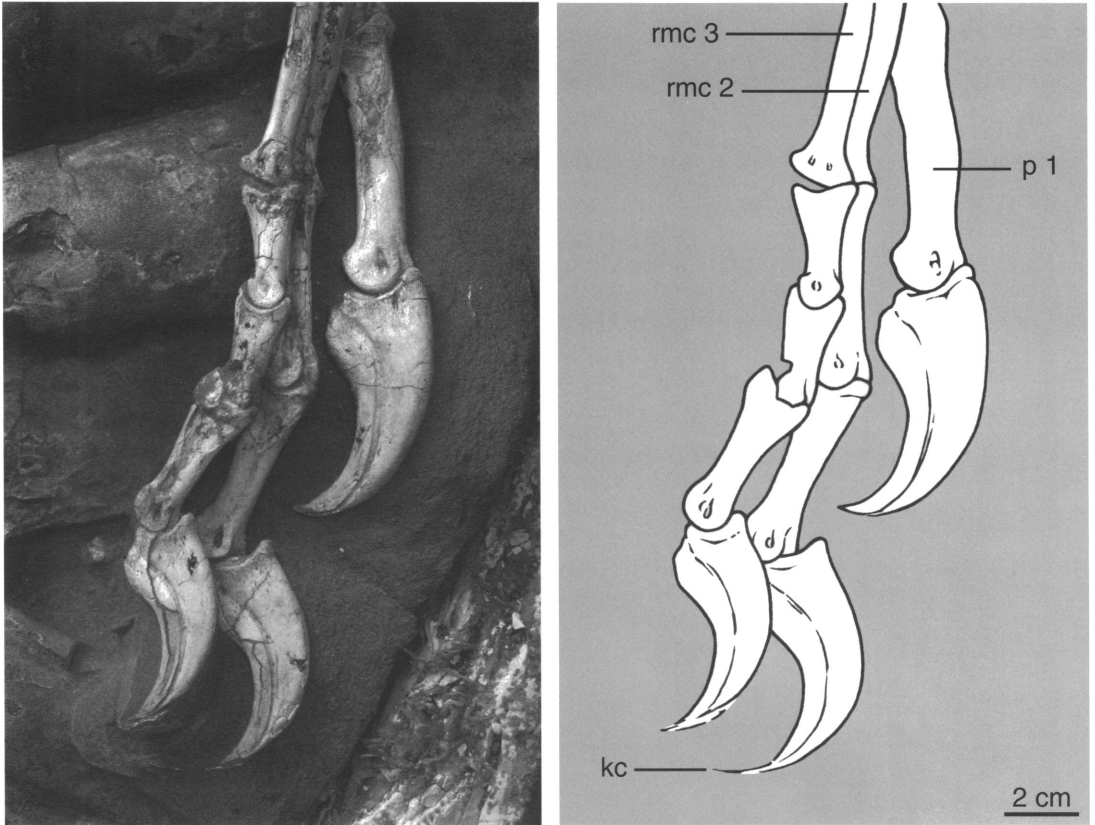


Fig. 5. IGM 100/979, right manus in lateral view. Note remnant of keratinous claw on digit II and III unguals. See Appendix for abbreviations.

poorly preserved to offer reliable evidence of its original condition. It is crushed dorsoventrally (fig. 8).

The proximal end of the right tibia is partly covered by the femur, but a strong lateral deflection proximally indicates the presence of a lateral cnemial crest. The shaft is crushed and exhibits few features of interest.

Both fibulae exhibit a distinct bend approximately one-third of the way down the shaft, some (but not all) of which may be due to post-depositional distortion. The portion proximal to the bend expands proximally and is mediolaterally flattened, articulating with the lateral cnemial crest of the tibia. Distal to the bend, the fibula becomes extremely slender, and it extends to the tarsus to contact the calcaneum (fig. 9).

The poorly preserved left proximal tarsals indicate that the calcaneum is fused to the astragalus distally but not proximally. The

ascending process of the astragalus is a broad sheet of bone that would have covered the entire anterior surface of the distal end of the tibia, but it is unclear how far along the tibia it extended proximally. The distal tarsals are not exposed, presumably lying beneath the proximal tarsals.

As in other Theropoda, the proximal end of the first metatarsal is greatly reduced. Metatarsals II–IV are similar to each other in size, and only the proximalmost part of metatarsal III narrows between II and IV, although much less so than in, for example, Troodontidae. None of the metatarsals are fused to one another. Metatarsal III is slightly longer than IV, which is slightly longer than II. The articulating surfaces on the distal ends of these metatarsals are smooth and do not show a ginglymoid condition. They extend anterodorsally onto the shaft, indicating the capacity for at least limited digitigrade pos-

ture. Metatarsal I articulates on the postero-medial edge of metatarsal II three-fourths of the way down its shaft, and is preserved in what appears to be its natural position on both feet. Its distal end is twisted anteriorly, so that the toe is not reversed as it is in many birds. The splintlike metatarsal V is exposed on the left side, and is approximately one-third the length of metatarsal III. It articulates with metatarsal IV on its posterolateral edge, and extends proximally to the same level as metatarsals II–IV.

The digital formula of the pes is 2-3-4-5-0. The relative lengths of the complete digits are $\text{III} > \text{IV} > \text{II} > \text{I}$. The phalanges are short and robust with strongly curved articulation surfaces. The unguals are broad and robust, with very deep grooves for the keratinous claw. The unguals are stout and only weakly curved ventrally except that of the first toe.

AXIAL SKELETON: The only vertebra preserved, located between the scapulae, is too poorly preserved to provide significant information.

The two sternal plates (fig. 10) are very well preserved, exposed in dorsal view, and are generally similar to those of other oviraptorids with paired elements (Barsbold, 1981). They abut along the midline, without overlapping. The right plate is slightly longer anteriorly than the left, but otherwise the exposed portions of both sides are symmetrical across the midline. The anterior edge of each plate is concave anterolaterally, and the coracoid articulates with only a small area near the midline. The medial edge of each plate is straight without indentations, although anteriorly it is obscured by the trace fossil covering most of this region. The lateral edge is complex but is dominated by two lateral processes: an anteriorly placed one with a posterolateral costal margin, and a blunt, posteriorly placed process comparable to the lateral xiphoid process (or trabecula) on the sternum of many avians.

The anterior process has a concave anterior edge and a straight posterolateral edge, forming a triangle in dorsal view. The anterior edge is smooth, while the posterolateral edge is thick, rugose, and with several expansions. The first three ventral ribs (i.e., the ventral segments of the thoracic ribs) are preserved in contact with this edge on the left

plate and very close to this edge on the right, and they undoubtedly articulated to these irregularities. The fourth ventral rib terminates far from this surface (11.5 cm from it on the right side), and its distal end tapers to a point rather than being expanded like the first three ribs, strongly suggesting it did not articulate with the costal margin of the sternum.

On the right side, which is better exposed, the more posterior of the two lateral processes is square, terminating in an antero-posteriorly broad, gently rounded edge, and it extends further laterally than the anterior process. Its anterior edge is short and slightly concave anteriorly, and the posterior edge is straight and continuous medially with the posterior edge of the plate. The posterior edge of the plate is somewhat irregular but is much thinner than the costal margin, and there is no evidence for the articulation of ribs. Near the midline the sternal plate has a short, broad posterior process.

Only the ventral portions of the posteriormost cervical rib and the first six thoracic ribs are preserved, but they are nearly undisturbed and preserved in exceptional detail. These seven ribs are folded backward anterior to the pubes on the right side, which is the basis for this description because the left ribs are incompletely exposed (fig. 10). The second through fourth preserved ribs articulate with the sternum, and because the thoracic series is typically defined to begin with the first rib that articulates with the sternum (e.g., Romer, 1956: 227) they belong to this series. The posteriormost cervical is thinner than the first thoracic, but is comparable in thickness to the second thoracic.

A separate ventral (sternal) segment is present in the first three dorsal ribs and articulates ventrally with the sternum (fig. 10). The fourth thoracic rib has a ventral segment that does not articulate with the sternum, and it tapers to a point ventrally. The fifth and sixth ribs lack ventral components, and there is no indication of an articulation surface distally for a cartilaginous segment. All of the ventral rib segments are well ossified, as is evident from cancelous bone exposed within the ventral end of several segments and the presence of haversian systems (fig. 11).

The articulation surfaces between the ventral and dorsal rib segments are expanded



with nearly flat articulation surfaces (fig. 10). They are separated from each other by several millimeters of matrix, suggesting the presence of connective tissue between them. All of the ventral rib segments are flattened in the same directions as the corresponding dorsal component to the rib. They are preserved close to one another, as a bundle, and the ventral end of each is expanded where it meets the sternum. The ventral segment of the first dorsal rib is the stoutest and shortest, and is straight. The left ribs are preserved in articulation with the sternum (those on the right are displaced a few centimeters posteromedially), and the robust ventral segment of the first thoracic rib is the most lateral of the three articulating on the costal margin of the sternal plate (as inferred in *Sinraptor*; Currie and Zhao, 1993). The ventral segments of the second and third thoracic rib are progressively longer and thinner and have a distinct medial bend near the articulation with the dorsal segment (exposed only on the right side). The ventral segment of the fourth thoracic rib is much shorter and tapers to a point, and it is preserved far from the sternum (see above), indicating it did not articulate with it.

The fourth, fifth, and sixth thoracic ribs are progressively shorter than those articulated with the sternum, but because they are incomplete proximally their actual lengths are not known. Nevertheless, the dramatic shortening in these ribs and the lack of disturbance to the skeleton strongly suggest that the rib cage was anteroposteriorly short in comparison with, for example, crocodylians.

Associated with the dorsal segments of the first four preserved ribs are four mediolaterally flattened uncinat processes that expand ventrally (fig. 12). The uncinat processes are all incomplete dorsally but their proportions suggest they were at least as long as in *Velociraptor* (see Norell and Makovicky, in press). The posterior edge is straight and the anterior edge is concave anteriorly. They are preserved extending posterodorsally over the lateral surface of the rib posterior to them,

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Fig. 6. IGM 100/979, left manus in lateral view. Note remnant of keratinous claw (kc) on unguals of digits I and III and strong curvature of claw.

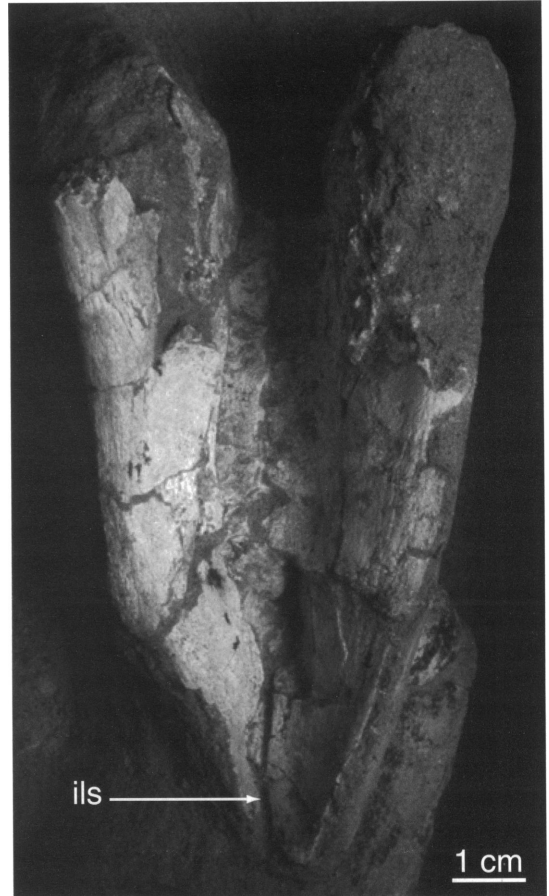


Fig. 7. IGM 100/979, ischia in dorsal view, anterior toward the top of the figure. Note ischial symphysis (is) and apposition of ischia and egg.

with the expanded base abutting the rib anterior to them.

A few segments of gastralia are partly exposed near the ventral midline beneath the ventral ribs and sternal plates and anterior to the left pes. They continue anteriorly beneath the sternal plates, and are easily distinguished from the ventral ribs by their smaller diameter, complex articulations, and lack of articulation with the edge of the sternum. Four segments exposed behind the posterior edge of the right sternal plate converge anteromedially and are much larger than seg-

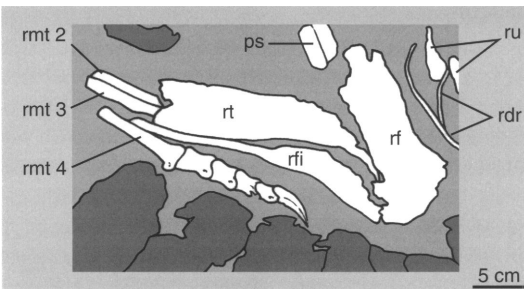


Fig. 8. IGM 100979, right hindlimb in dorso-lateral view. Note close proximity of fourth digit and egg. See Appendix for abbreviations.

ments exposed more posteriorly. Otherwise they are similar to those of *Dromaeosauridae* (Norell and Makovicky, 1997).

THE NEST

Fifteen eggs are partially exposed beneath the skeleton, but a similar number are estimated to remain unexposed in the matrix. The nest appears to be intact, and with a few exceptions breakage is consistent with compression of the sediment rather than preburial disturbance because there is little displacement of the fragments. All of the exposed

eggs are horizontal or subhorizontal, aligned radially within the nest, and, as exposed beneath the right arm, arranged in at least two layers. The remaining thickness of the block beneath the lower layer suggests that no more than two layers are present beneath the right arm, but the bottom of the nest is not exposed. Eight eggs are arranged in pairs (figs. 1, 4), and all may be paired. Where eggs are exposed in two layers, beneath the specimen's right forelimb, matrix is absent between some areas of the juxtaposed eggs, but an egg in the upper layer beneath the left manus is suspended at least partly by matrix and not by the lower layer of eggs. Furthermore, at least one pair of eggs in the upper layer is situated farther away from the center of the nest than the eggs upon which they rest (fig. 4), unlike the arrangement of at least two other nests of this type (Dong and Currie, 1996). Most of the center of the nest is not exposed, but there is no evidence for eggs in the center at the same level as the uppermost eggs exposed further out from the center.

The eggs are elongate, parallel sided, with

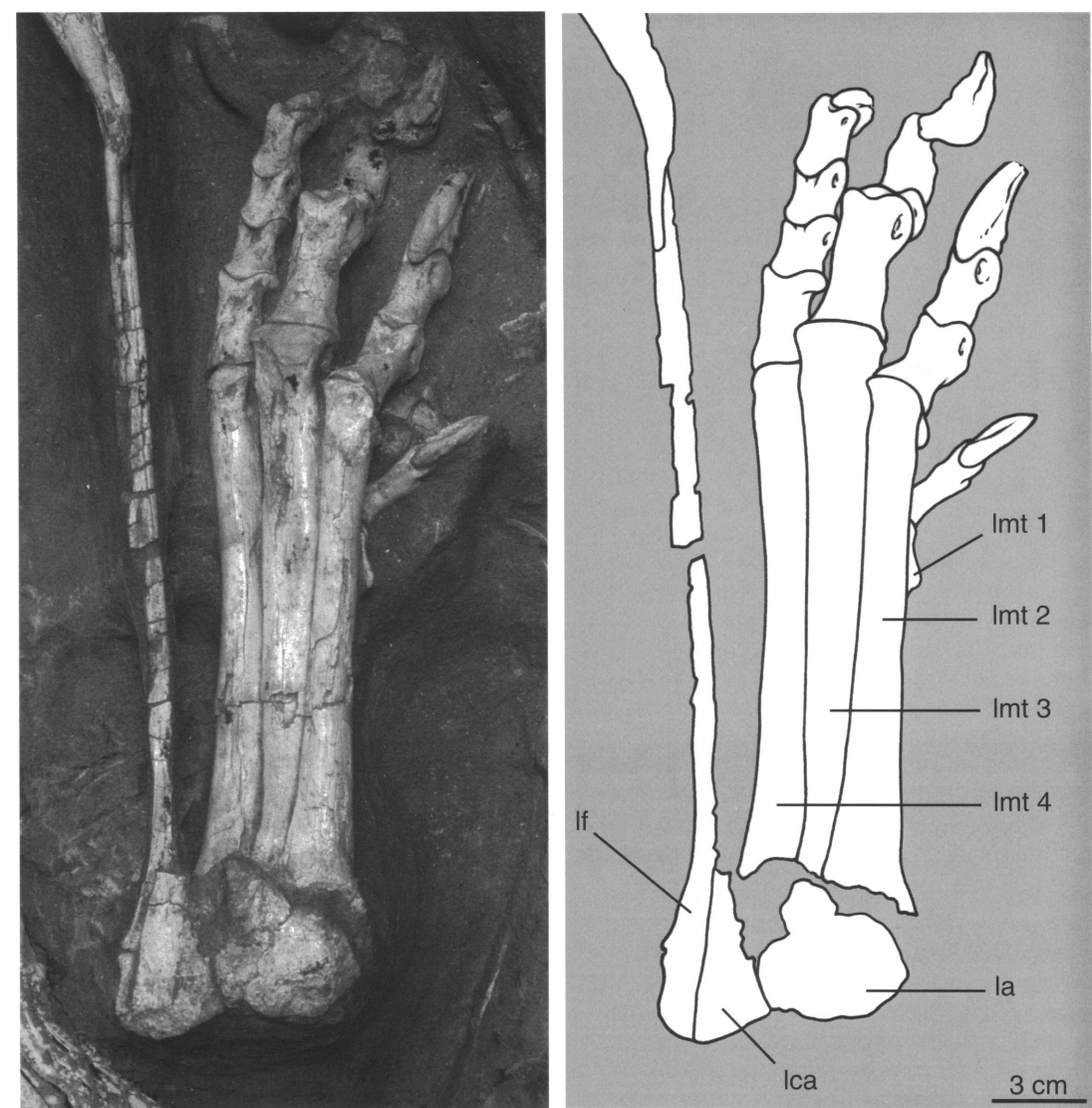


Fig. 9. IGM 100/979, left fibula and tarsus in posterior view, left pes in dorsal view. Note egg fragments beneath unguals. See Appendix for abbreviations.

rounded ends of similar shape, a shape termed elongatoolithid (Mikhailov et al., 1994). Although previously we implied that they are less rounded at one end than the other (Norell et al., 1995), in those eggs where both ends are exposed they are symmetrical. The outer surface has a series of longitudinally oriented fine ridges that grade into dimples or smooth areas at the poles. None of the well-exposed eggs show indications of hatching or predation, nor are

bones visible in the few in which the interior is exposed. Two eggshell fragments, near the left ischium, suggest the presence of a broken egg, but this area is insufficiently exposed to interpret definitively. A histologic study of the egg shell will be published elsewhere (Bray et al., in press).

None of the eggs are exposed in their entirety, so all of their dimensions cannot be measured accurately. A pair of eggs beneath the right manus differ in their width, one be-

ing only 6.5 cm wide, the other 7.2, and the difference is likely due to the effects of crushing. An egg beneath the left carpus is nearly completely exposed, and as preserved is at least 18 cm in length, but less than 19 cm.

Eggs are not preserved within the pelvic region, much of which is missing. If the animal had been in the act of laying an egg or preparing to do so, it is expected that one or two would be preserved here. The incompleteness of the pelvis makes this assessment uncertain, but to have been lost to erosion an egg must have been "floating" in matrix well above the ischiadic symphysis.

There is no evidence from the outlying sediments as to the shape or size of the nest, although little sediment was removed with the block. There is no obvious structure to the sediments, nor changes in macroscopic details away from the eggs (however, they have not been studied microscopically). There is also no evidence for plant matter in the nest, but as the sediments are highly oxidized and poorly consolidated with large pore spaces it is unclear whether it could have survived diagenesis and the percolation of ground water (D. Loope, pers. comm.), and plant remains are not known from the Djadokhta Formation at Ukhaa Tolgod.

POSTURE OF THE SKELETON ON THE NEST

The most remarkable aspect of the skeleton is the birdlike posture in which it is preserved (figs. 1, 13). The body would have completely covered the nest, with the abdominal region over the center, and both limbs are placed in positions nearly symmetrical across the midline. The positions of the tibia, fibulae, femur, pelvis, and ribs suggest that the body was shifted slightly to the left of center, lying on the left side of its chest, rather than being exactly symmetrical. Furthermore, the right forelimb is shifted medially, and the proximal end of the humerus has come to lie near the midline. This shifting of the body and right forelimb to the left suggest that the sediment deposited upon the skeleton may have come toward the animal from its right hand side.

The gastralia, ventral ribs, and apparently the sternal elements rest directly on eggs. An

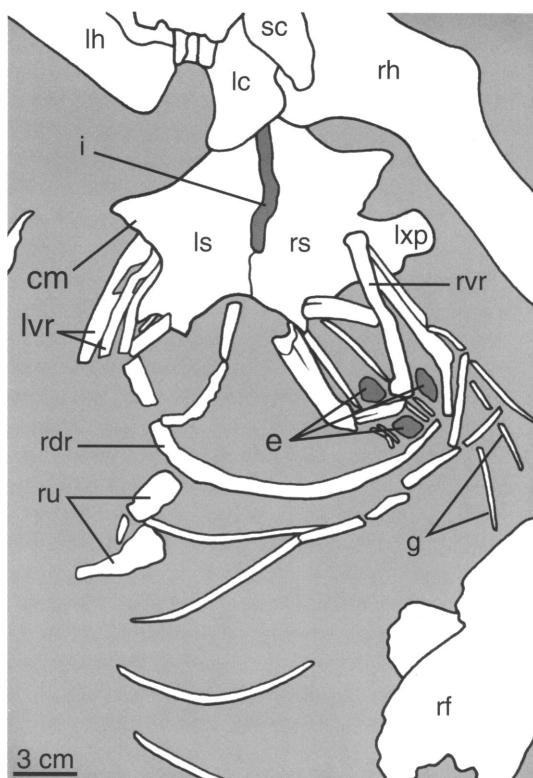


Fig. 10. IGM 100/979, sternal plates in dorsal view, anterior toward top of figure. Note the articulations of the three ventral rib segments with the sternum, dislocated slightly posteriorly on the right side but intact on the left. Also note the apposition of the gastralia and ventral ribs with a partially exposed egg posterior to the right sternal plate. See Appendix for abbreviations.

egg is exposed beneath the ribs and gastralia immediately posterior to the right sternal element (fig. 10), and the bones rest directly on the egg surface. The more posterior ribs are above the highest level of eggs, suggesting that the center of the nest may have been filled.

The forelimbs extend laterally and then posteriorly to overlie the perimeter of the nest (fig. 1). The humeri extend laterally and slightly posteriorly from the glenoid fossa. The right antebrachium is extended, but the distal ends of the left indicate that the elbow on that side was flexed about 90°. The right carpus is strongly flexed, but the left is only slightly flexed. The hands are strongly pronated and lay on their medial surface, and



Fig. 10.—Continued.

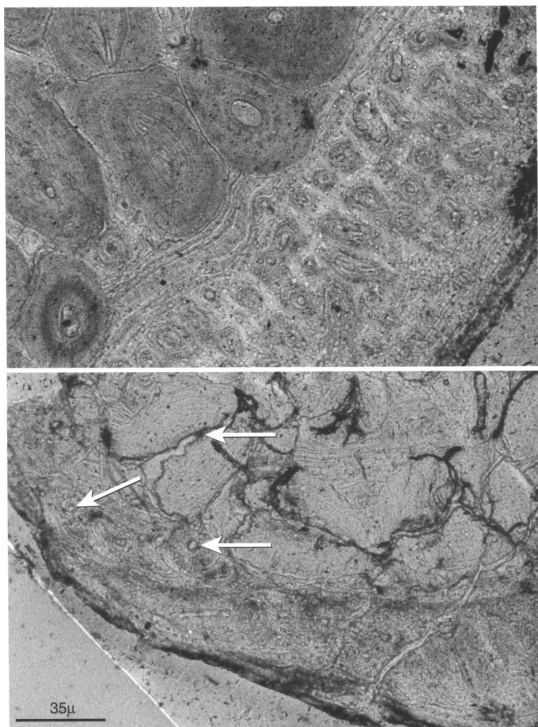


Fig. 11. IGM 100/797, thin sections of a dorsal segment of a thoracic rib (top) and a ventral segment of the left first thoracic rib (bottom). Note the presence in both of osteons with a central lacuna, identified by arrows in the ventral rib section, indicative of ossification rather than calcification.

the ventral displacement of the first and third metacarpals relative to the second is most likely due to the vertical compression that came to bear after deposition. The right carpus rests on top of, or very close to, an egg, but the left forearm is several centimeters above the level of the eggs.

The ischia lie directly on top of an egg, and the pubes extend into the matrix anterior to this egg, toward the center of the nest. The pubes have not been completely exposed, but the preserved portions are from the pubic symphysis and therefore near the ventral end of the bone. Although the expanded "boot" at the end of the bone is not evident, the pubes probably do not extend much further ventrally than their exposed portions.

Both legs are oriented parasagittally with the knee and ankle joints strongly flexed. The toes of digits II-IV on the left pes are flexed

in several places (at the base of phalanges II-1, III-2, and IV-5), while the fourth toe of the right side is completely extended (the second and third are not exposed). The bones of the left pes are intermixed with pieces of egg shell, and the fourth toe of the right pes is less than 1 cm from an egg beneath it.

The skeleton shows little indication of disturbance after deposition. All of the exposed elements are in their natural articulations, and the few cases in which they are slightly separated (e.g., the ungual of left pedal digit III) are to the limited extent consistent with postdepositional compaction. The region showing the greatest disturbance is the shoulder girdle, where the coracoids are separated from the sternal elements and the furcula is moved anteriorly, apparently due to a medial movement of the right, and to a lesser extent the left, forelimbs.

DISCUSSION

PHYLOGENETIC AFFINITIES OF THE SKELETON

The precise identification of IGM 100/979 is made difficult by the lack of a skull and vertebrae, but several features allow identification both to Oviraptoridae and to a group within it. Skeletons of Oviraptoridae are common at Ukhaa Tolgod (Dashzeveg et al., 1995), and at least two taxa are present (Clark and Norell, in prep.). Oviraptoridae are members of the theropod group Coelurosauria, but do not belong to the largest group of coelurosaurs, the birds (i.e., Avialae).

The coelurosaurian affinities of the skeleton are evident from the presence of elongate forelimbs, the absence of manus digit IV and the presence of the semilunate carpal (Gauthier 1986). Among nonavian Coelurosauria, only Dromaeosauridae, Therizinosauridae, Troodontidae and Oviraptorosauria (including Oviraptoridae) are known to have a subquadrangular coracoid (Gauthier, 1986; Russell and Dong, 1993; Sues, 1997). Dromaeosaurids and Oviraptorosauria both have two broad sternal plates that are sometimes fused (Barsbold, 1983; Norell and Makovicky, 1997), but dromaeosaurids have an opisthopubic pelvis, a thinner fibula, metatarsals II-IV with ginglymoid distal ends, a retractable second pedal digit with a greatly en-

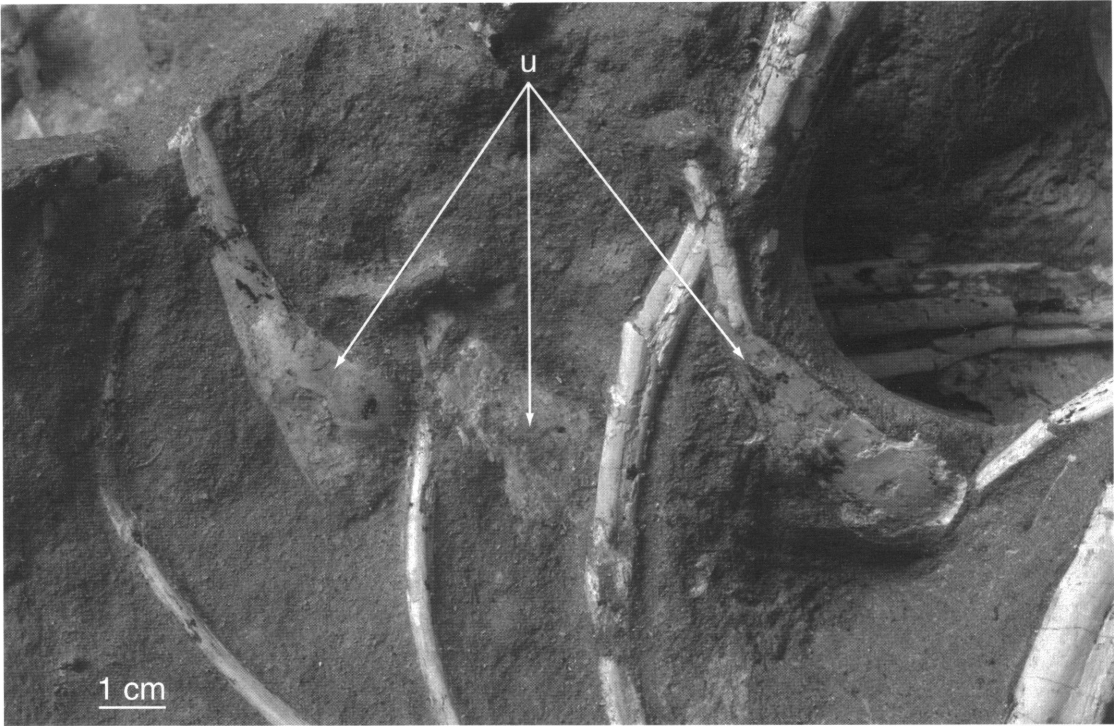


Fig. 12. IGM 100/979, dorsal segments of right thoracic ribs and associated uncinata processes in right dorsolateral view, anterior to the right.

larged claw, and shallower manal claws with asymmetric grooves for the keratinous sheath. The manus also differs in having a shorter third digit relative to the second, and a more slender, slightly bowed third metacarpal. The deep, strongly curved manal claws of this specimen, with a dorsal lip over the articulating surface, are similar only to those of oviraptorosaurians and troodontids

(Currie, 1990). However, troodontids have an extremely reduced third metatarsal, an unusually robust fourth metatarsal, and a retractable second pedal digit (Osmólska and Barsbold, 1990), and are reported to lack a furcula, the clavicles instead being slender and paired (Russell and Dong, 1993).

Oviraptoridae and the poorly known Caenagnathidae (including *Chirostenotes*, *Caen-*

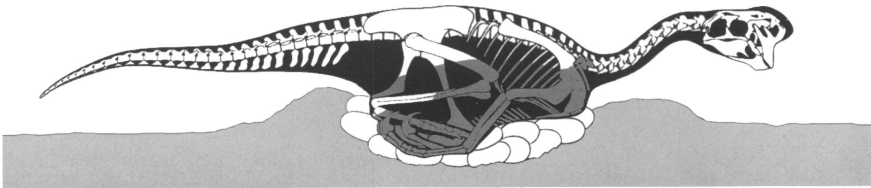


Fig. 13. Schematic reconstruction of the oviraptorid as it might have appeared on the nest in lateral view, based on the posture of the skeletal remains of IGM 100/979. The preserved portion of the skeleton is shaded darker than the reconstructed portion. The arrangement of eggs in the nest is in part hypothetical, because most of the nest is not exposed, and the degree to which the outer parts of the nest were buried is hypothetical.

agnathasia, and *Elmisaurus*; Sues, 1997) and *Microvenator* (Makovicky and Sues, 1998) together comprise Oviraptorosauria (Osmólska and Barsbold, 1990). Many postcranial elements are unknown for Caenagnathidae, and the relationships of *Microvenator* are uncertain, limiting the unambiguous diagnosis of Oviraptoridae. Nevertheless, the metatarsals of Caenagnathidae differ from those of Oviraptoridae and IGM 100/979 in that metatarsal III is much narrower dorsally, and in *Elmisaurus rarus*, at least, the proximal metatarsals are fused together with the distal tarsals (Osmólska, 1981). Furthermore, manus digits II and III are subequal in length and robustness in Oviraptoridae (Barsbold et al., 1990), as they are in this specimen, but in Caenagnathidae and most other Coelurosauria (with the exception of ornithomimosaurs) digit III is shorter and more gracile than digit II (Gauthier, 1986). The only known skeleton of *Microvenator celer* shares few elements in common with IGM 100/979, but the deltopectoral crest of the humerus of *Microvenator* is shorter and less pronounced (Makovicky and Sues, 1998).

Oviraptoridae are unique among nonavian theropods in the shape of their furcula, but this element is not known in Caenagnathidae or *Microvenator*. A furcula is present in several nonavian theropods (Currie and Zhao, 1993; Norell et al., 1997; Chure and Madsen, 1996; Makovicky and Currie, 1998), but in Oviraptoridae it is particularly robust and often has a distinct hypocleidium (Barsbold, 1983), as on this specimen. Among theropods the most similar furcula is that of *Archaeopteryx* (de Beer, 1954) and *Confuciusornis* (Peters, 1996; Chiappe et al., submitted), although these (unlike that of many birds) lack a hypocleidium. The hypocleidium of IGM 100/979 is longer than in any described oviraptorid, but this delicate process may have been lost or damaged in other specimens.

Of the three named genera of Oviraptoridae—*Oviraptor*, *Ingenia*, and *Conchoraptor*—the skeleton of *Ingenia* is the most specialized. The manus of *Ingenia* is unusual in that digit I is nearly as long as digit II, and metacarpal I is half as long as the metacarpal II, rather than being one third the length of metacarpal II as in *Oviraptor* and most other

Coelurosauria (Barsbold, 1981; Barsbold et al., 1990), features that are absent in IGM 100/979. The sternum of *Ingenia* also has a less developed lateral trabecula than does that of *Oviraptor* (Barsbold, 1983, fig. 15). The postcranial skeleton of *Conchoraptor* also lacks the specializations of *Ingenia* (Barsbold et al., 1990), but the numerous specimens of this taxon preserved in the Mongolian Institute of Geology are all much smaller than those of IGM 100/979, whereas several specimens of *Oviraptor* are of a similar large size, much larger than any other oviraptorosaurian. Pending revision of this group based upon the new material from Ukhaa Tolgod, the present evidence therefore suggests that IGM 100/979 is an oviraptorid most closely related to *Oviraptor*.

The specimen also presents some features differing from conditions in other Oviraptoridae. The posterolateral flattening and bending of the furcula and the horizontal orientation of the shelf on the anterior edge of the scapula with which it articulates are similar to, but more developed than, these regions in *Oviraptor philoceratops* (IGM 100/42). The strongly sutured ischial symphysis is also unique among oviraptorid specimens, but the bone along the symphysis is very thin and therefore easily damaged, and none of the known oviraptorid skeletons with complete ischia are as large as this one.

PHYLOGENETIC AFFINITIES OF THE EGGS

Many types of eggs are known from the Djadokhta Formation of Mongolia (Mikhailov et al., 1994), but the identification with particular groups of vertebrates is tentative for all except the single type for which diagnostic embryonic remains are known. The single exception (IGM 100/971) is an oviraptorid embryo preserved within an incomplete egg from Ukhaa Tolgod (Norell et al., 1994). The eggs of IGM 100/979 are similar in all respects to the egg with the oviraptorid embryo.

A parataxonomy of eggs and eggshell has been developed by Zhao (e.g., 1975), and Mikhailov (1991) identified histologic morphotypes correlated with this taxonomy. The eggs of IGM 100/979 are of the type classified as elongatoolithid in Zhao's system as

modified by Mikhailov, based upon their large size, elongate shape with parallel or sub-parallel sides, and sculpture pattern ("discretituberculate") of nodes and short longitudinal ridges on the long edges and nodes on the ends. The eggs from the nest (AMNH 6508) beneath the holotype of *Oviraptor philoceratops* at Bayn Dzak (Norell et al., 1994) and those from beneath the oviraptorid skeleton at Bayan Mandahu (Dong and Currie, 1996) are also of this type.

The eggs of IGM 100/979 are unusually long, at least 18 cm in length. Elongatoolithid eggs are generally 15–17 cm long (Mikhailov et al., 1994); those from Bayan Mandahu are only 15 cm in length, and the eggs from beneath the *O. philoceratops* holotype (AMNH 6508) are 14 cm long (although crushing may have shortened them by up to 2 cm). The egg from Ukhaa Tolgod with the oviraptorid embryo (IGM 100/971) was cited as being only 12 cm long (Norell et al., 1994), but it is too incomplete to estimate its length accurately.

Because of the paucity of embryonic remains in fossil eggs the precise identity of most is unclear, and the taxonomic level at which elongatoolithid eggs are diagnostic may extend beyond Oviraptoridae. Furthermore, the only known embryo is incomplete, and cannot be identified below the family level. The skull and mandible of the embryo possess the short, vertical rostrum, edentulous margins, and tall mandible that distinguish oviraptorids from all other theropods. The mandible is much shorter and taller than that of caenagnathids, placing it within the Oviraptoridae. Unfortunately, the lack of dorsal roofing bones and evidence of the manus (which may be covered by the rest of the skeleton) precludes more precise identification.

POTENTIAL SKELETAL HOMOLOGIES WITH AVIALAE

This specimen is significant in providing new information concerning the ventral part of the thorax and the keratinous claws in oviraptorids, and in suggesting that oviraptorids behaved in ways similar to their living relatives, birds. The ribs and sternum provide evidence for features hitherto poorly known in

Oviraptoridae and unknown or rare in other close relatives of birds: a single ossified ventral rib segment in the first four thoracic ribs, the articulation of three ribs with the costal margin of the sternum, and ossified uncinat processes. The specimen also confirms features noted previously in other oviraptorids (Barsbold, 1981), such as the articulation of the coracoid with the anterior, rather than lateral, edge of the sternum and the presence of a robust furcula.

The pattern of rib segmentation in IGM 100/979, with a single, ossified ventral segment, is remarkably similar to the pattern in the ribs of birds and unlike that in crocodylian ribs. In the thoracic rib cage of nonavian reptiles, such as crocodylians, one or two cartilaginous segments are present between the ossified dorsal rib and the sternum, but they do not ossify (Parker, 1868; Hoffstetter and Gasc, 1969). In crocodylians, the first 9 or (in *Gavialis*) 10 thoracic ribs have two cartilaginous segments ventral to the dorsal rib (i.e., three segments in all), whereas the following two ribs lack the intermediate element. The two ventral segments calcify in some individuals, but they are not reported to ossify (e.g., they do not have haversian systems). The ribs of birds, however, have only one ventral segment, and it is well ossified (Bellairs and Jenkin, 1960). An apparently ossified, single ventral rib segment is present in fossils of some basal avialans (e.g., *Iberomesornis*, *Confuciusornis*, and *Hesperornis*) although they are not discernible on any known specimen of *Archaeopteryx*.

Ossified ventral ribs were identified tentatively in the dromaeosaurid *Deinonychus* on the basis of isolated elements (Ostrom, 1969: 84–86), in the dromaeosaurid *Velociraptor* (Barsbold, 1983: 34), and in the basal troodontid *Sinornithoides* on the basis of CT scans of an articulated skeleton (Russell and Dong, 1993). Comparing *Deinonychus* with crocodylians, Ostrom tentatively inferred the presence of two ventral segments in *Deinonychus*, but the isolated elements he studied do not provide evidence sufficient to reach this conclusion, especially considering the evidence of only a single ventral segment in their relatives, birds and oviraptorids. An ossified ventral segment is definitively present in *Velociraptor* (Norell and Makovicky, in

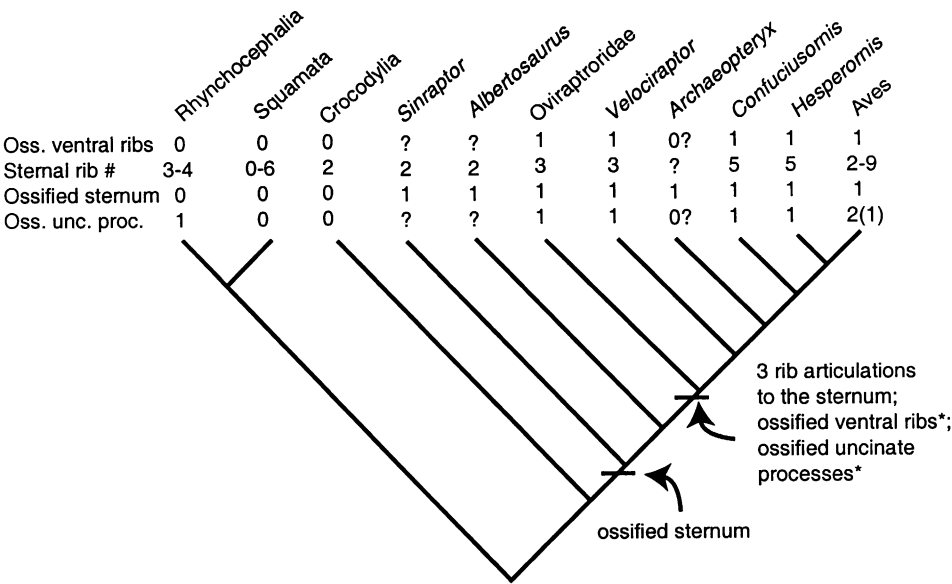


Fig. 14. Cladogram of relationships among theropod taxa with well-preserved sternal regions and distribution of osteological characters discussed in the text, and the level at which selected features are synapomorphous (under DELTRAN optimization). Relationships are supported by the analyses of Gauthier (1986), Holtz (1994), and Sues (1997), and the interpretation of Currie and Zhao (1993). **Ossified ventral ribs**: rib ossification confined to dorsal segment (0) or both dorsal and ventral rib segments ossified (1); **Sternal rib number**: number of rib articulations to the body of the sternum (the praesternum); **Ossified sternum**: sternum unossified (0) or ossified (1); **Ossified uncinat processes**: ossified uncinat processes absent (0), present and separate from ribs (1), present and fused to ribs (2). Parentheses indicate the occurrence in a group of a condition that is most simply interpreted as secondarily derived, asterisk indicates characters that apply to more inclusive groups under different optimization procedures. Sources: Parker, 1868; Marsh, 1880; Fürbringer, 1888; Howes and Swinnerton, 1901; Lambe, 1917; Hoffstetter and Gasc, 1969; Currie and Zhao, 1993; Wellnhofer, 1993; Norell and Makovicky, in press; Chiappe et al., submitted.

press), but is not otherwise reported in non-avian Coelurosauria.

The ventral segments on IGM 100/979 definitively confirm the presence of these structures in nonavian theropods, and they corroborate the identification of these elements in *Deinonychus*, at least one example of which is similar in shape and has expanded ends (Ostrom, 1969: fig. 52b). The absence of these elements in other taxa may be an artifact of ontogenetic sampling, preservation, or the manner in which they were collected. In any case, the presence of ossified ventral rib segments is a synapomorphy of birds with a group including at least oviraptorids and dromaeosaurids among dinosaurs (fig. 14).

The articulation of three ribs with the sternum in IGM 100/979 is significant in com-

parison with the typically larger number in birds and the smaller number in more basal theropods. In birds a variable number of ribs articulate with the sternum, but with a single exception it is greater than two. The number of rib attachments to the avian sternum is reported to range from 2 in some species of Dinornithidae (moas) to 9 in, for example, *Cygnus* (Fürbringer, 1888: table 21). The sternum of some moas is reported to have facets for only two ribs, but those of other species in this family are reported to have three (Owen, 1879; Oliver, 1949). The relationships of moas, within Paleognathae (Lee et al., 1997), imply that the condition of having only two rib articulations represents an evolutionary reversal from a larger number of articulations, given that tinamous, neo-gnaths, and basal avialans, where known

(e.g., *Hesperornis* and *Ichthyornis*, Marsh, 1880; *Confuciusornis*, Chiappe et al., submitted), have a larger number. In *Archaeopteryx* a sternum is preserved on only one specimen (Wellnhofer, 1993), and it is too poorly preserved to determine the number of rib articulations.

In the few nonavian theropods for which this feature is known (*Albertosaurus* and *Sinraptor*), distinct facets for only two rib articulations are evident on the sternum (Lambe, 1917; Currie and Zhao, 1993). The sternum is known in representatives of all of the other major groups of dinosaurs (Sauropodomorpha, Thyreophora, Ornithopoda, and Marginocephalia), but it is unclear how many ribs attach (Weishampel et al., 1990). A specimen of *Velociraptor mongoliensis* from Tugrugeen Shireh (IGM 100/976) has three closely appressed ventral ribs preserved adjacent to the right side of the right sternal plate (Norell et al., 1997; Norell and Makovicky, in press), providing evidence that three ribs articulated with the sternum in this taxon as well. The articulation of more than two ribs with the sternum in the oviraptorid specimen described here and in *Velociraptor* therefore is a synapomorphy of these two taxa with birds, but the lack of information about the distribution of this feature among other extinct Coelurosauria greatly limits its implications at this time.

In crocodylians (Parker, 1868; Hoffstetter and Gasc, 1969), the first two thoracic ribs articulate (via cartilaginous segments) with the broad body of the cartilaginous sternum (the praesternum of Parker, 1868), and the following 6 or 7 ribs articulate with a much narrower posterior extension (the mesosternum of Parker, 1868). In extant birds, ribs articulate only with the anterior part of the lateral edge of the broad, ossified sternal plate, and a structure similar to the mesosternum of crocodylians is absent (Parker, 1868; Fürbringer, 1888). The ossified sternum of theropods (including birds) is therefore most comparable to the body (praesternum) of the crocodylian sternum, and the presence of two ribs in articulation with the sternum in basal theropods and with the body of the sternum in crocodylians in consequence establishes this as the primitive condition for Archosauria.

The precise phylogenetic relationships among theropods is disputed, but all recent studies (Currie and Zhao, 1993; Holtz, 1994; Sues, 1997) indicate that oviraptorosaurs and dromaeosaurids are more closely related to extant birds than are tyrannosaurids, and tyrannosaurids are more closely related to a group comprising these taxa than is *Sinraptor*. The optimization of the number of rib articulations to the sternum on a cladogram of these phylogenetic relationships (fig. 14) indicates that (1) two rib articulations with the ossified portion of the sternum is plesiomorphic for Theropoda, (2) three rib articulations with the sternum is a synapomorphy of dromaeosaurids, oviraptorids, and Avialae (and perhaps some other coelurosaurians more closely related to them than to tyrannosaurs and more basal dinosaurs), and (3) the higher number of sternal articulations in many birds is an evolutionary increase.

The identification of the costal margin of the sternum allows for a more precise understanding of the morphology of this structure in oviraptorids (see Barsbold, 1981, for descriptions of other oviraptorid sternae). The costal margin is in a position comparable to that of most birds, on the anterior half of the lateral surface, rather than posteriorly as in crocodylians and lepidosaurs. Although there is a great deal of variation among birds in the morphology of the lateral edge of the sternum there is often a lateral or posterolateral process immediately posterior to the costal margin, termed the external xiphoid process of the lateral xiphisternum by Parker (1868) and Bellairs and Jenkin (1960) but identified as the lateral trabecula by Fürbringer (1888) and Baumel and Witmer (1993). The posterior of the two lateral processes of the sternum described above in IGM 100/979 is in this same position, and its similarity with the structure in extant birds and the presence of a similar process in some basal avialans (e.g., *Concornis*; Sanz et al., 1995) is sufficient to hypothesize that it may be homologous among these taxa. The absence of such a process in alvarezsaurids (Perle et al., 1994) suggests that this feature may have been lost and regained in the course of avialan evolution, however.

The articulation of the coracoid to the anterior edge of the sternum is a further feature

that oviraptorids and some other nonavian theropods share with birds. In crocodylians and lepidosaurs the coracoid articulates along the lateral surface of the sternum, whereas in birds it articulates along the anterior edge (Parker, 1868). The sternum is poorly known in dinosaurs, but in Ankylosauria (Coombs, 1990) and *Iguanodon* (Norman, 1980) the coracoid contacts the anterolateral edge of the sternum (Coombs, 1990) whereas in sauropods it is unclear where the coracoid articulates (McIntosh, 1990). In *Sinraptor* (Currie and Zhao, 1993), *Albertosaurus* (Lambe, 1917), and the dromaeosaurid *Velociraptor* (Norell et al., 1997; Norell and Makovicky, in press), as well as in other oviraptorids (Barsbold, 1981), the articulation is with the anterior edge of the sternum.

The presence of ossified uncinat processes in IGM 100/979 broadens the taxonomic distribution of this character within Theropoda (fig. 14). Free uncinat processes associated with the thoracic ribs are present in *Velociraptor* (Paul, 1988; Norell and Makovicky, in press) and in some basal avialans, being especially well developed in *Hesperornis regalis* (Marsh, 1880), *Confuciusornis* (Chiappe et al., submitted) and *Chaoyangia* (Hou and Zhang, 1993). In extant birds these elements develop independent of the rib but usually fuse to it, except in *Apteryx* and penguins where they remain free (Parker, 1868; Fürbringer, 1888; Bellairs and Jenkin, 1960). The incomplete elements preserved on this specimen are similar to those of *Velociraptor* but are more expanded ventrally. Those of *Hesperornis* are as broad ventrally but are shorter. Although the evidence presented by IGM 100/979 for identifying these as uncinat processes is not definitive, owing to its incompleteness dorsally, at least one other oviraptorid specimen from Ukhaa Tolgod, IGM 199/1002, a nearly complete articulated skeleton, preserves similar elements interlaced with the ribs, corroborating this identification.

The evolution of uncinat processes in diapsids is somewhat ambiguous, as they are present and ossified in birds and the basal lepidosaur *Sphenodon*, present but unossified in crocodylians, and altogether absent in extant squamates (Parker, 1868; Howes and Swinnerton, 1901; Hoffstetter and Gasc,

1969; Bellairs and Jenkin, 1960). Uncinat processes are not reported in nontheropodan diapsids nor in *Archaeopteryx*, but it is difficult to ascertain whether the apparent absence of these elements is actually due to the vagaries of preservation because it requires exceptional preservation to differentiate these elements from the ribs proper. In any case, the elements in IGM 100/979 are similar to the elongate elements in basal birds such as *Hesperornis* rather than to the short, unossified elements of crocodylians, and the distribution of elongate, ossified uncinat processes indicates that it is a synapomorphy of Avialae and a more inclusive group of dinosaurs including oviraptorids and dromaeosaurids (fig. 14).

In extant birds, movements of the rib cage and sternum are critical to the passage of air through the specialized respiratory system (McLelland, 1989), and it has been suggested that this respiratory system was absent in nonavian theropods (Ruben et al., 1997). The presence in oviraptorids of ossified uncinat processes, a furcula, ossified ventral ribs in articulation with a broad, ossified sternum, and an anteriorly placed coracoid-sternum articulation, on the other hand, suggests that these animals were capable of the movements required by the avian respiratory system. Cataloging the osteological components of the avian respiratory mechanism does not constitute a critical test of the biomechanical capabilities of these structures, however, and demonstrating the capability of a behavior is not equivalent to demonstrating that the behavior was present. There is at present no strong evidence for the detailed morphology of the respiratory system in nonavian dinosaurs worthy of detailed consideration. In any case, the assertion that ossified ventral rib segments and a broad sternum are absent in nonavian theropods (Ruben et al., 1997) is false, and the inference that a respiratory system like that of avians was absent in these taxa is not supported by any reliable evidence (the interpretation of incompletely prepared soft tissue residue in *Sinosauropteryx* notwithstanding).

The remains of the keratinous claws of the manus are the first reported for an oviraptorid, and indicate a highly curved claw (Chiappe, 1997). The curvature of the kera-

tinous pedal claws of living birds and its relationship to lifestyle was studied by several authors, most recently Feduccia (1993), in an attempt to interpret the lifestyle of *Archaeopteryx* and other theropods. Feduccia noted that in *Archaeopteryx* the curvature of the pedal claws is similar to that of perching birds, and the curvature of the manal claws is similar to that of climbing birds. Using Feduccia's method of measuring curvature, the claw of digit II on the right side of IGM 100/979 spans a minimum of 160° , similar to the manal claws of *Archaeopteryx* and the pedal claws of climbing birds (Chiappe, 1997). Furthermore, the bony manal claws of the dromaeosaurids *Deinonychus* (Ostrom, 1969) and *Velociraptor* (Barsbold, 1983; Norell and Makovicky, in press) are as strongly curved as that of IGM 100/979. This suggests either that *Deinonychus* and oviraptorids were climbers, or that there was no correlation between claw curvature and climbing behavior in these taxa. Correlations between form and function are a dubious means of inferring behavior, because form does not always indicate behavior where this relationship can be examined in extant taxa (Lauder, 1995), and we are unaware of any evidence that tests critically the climbing abilities of oviraptorids and dromaeosaurids. In any case, the lack of curvature in the manal claws of nonavian theropods reported by Feduccia (1993) is contradicted by this specimen.

IMPLICATIONS OF THE SPECIMEN FOR OVIRAPTORID BEHAVIOR

The specimen described here presents rare evidence of behavior in an extinct animal, but the interpretation of behavior in fossils is more speculative than in living organisms. Because behavior—self-initiated movement of living organisms—cannot be observed directly in fossils it must be inferred, and these inferences involve untestable assumptions beyond those involved in observing behavior in living organisms. However, the success of studies of insect nests, spider webs, and written languages demonstrates that the products of behavior are interpretable, and in some ways more easily interpreted than is the behavior producing them because they can be observed repeatedly without being affected.

The position of IGM 100/979 strongly evokes the posture taken by birds while sitting on their nests, and the occurrence of four specimens directly on nests among the first thirty excavated oviraptorid skeletons indicates that this association is the result of a consistent behavior of these animals, so a careful consideration of its implications is necessary. We review other specimens here, because a discussion of other specimens of oviraptorids preserved on nests is critical to corroborating the evidence provided by our specimen.

(1) AMNH 6517, the holotype of *Oviraptor philoceratops* Osborn, 1924. The specimen is from the Djadokhta Formation at Bayn Dzak. The skeleton is missing the hind limbs, but the anterior part of the skeleton is preserved lying on its side rather than in a posture similar to that of IGM 100/979. Osborn (1924) noted that the skull was preserved four inches above the nest, but the precise position of the skeleton over the nest is unclear because they were separated during preparation. The nest from beneath the skeleton (AMNH 6508) is incomplete, comprising only 15 eggs when collected (two of which were not intact). The preserved portion of the nest indicates that the eggs were arranged in pairs and in at least three tiers, and the preserved semicircular pattern suggests the nest was originally circular.

(2) IVPP specimen V9608, described by Dong and Currie (1996). Most of the skeleton is absent, but preserved are several vertebral fragments and portions of the right fore and hind limbs overlying six elongatoolithid eggs. There is no indication among the preserved bones that the skeleton or nest was incomplete before erosion, but the eggs occur in only one layer. The limb elements indicate the skeleton was in a posture similar to that of IGM 100/979, with the arm around the perimeter of the nest and the pes in the center of the nest.

(3) An unprepared skeleton from Ukhaa Tolgod, field number MAE 95-97. As exposed in the field, the specimen consists of much of a skeleton (except the skull) overlying a nest that may be complete. Although incompletely exposed, the eggs have discretuberculate sculpturing on the poles similar to that of elongatoolithid eggs. A photograph

of the specimen was published by Webster (1996: 80).

In the most recent review of *Oviraptoridae*, Barsbold et al. (1990) listed the total number of specimens known at that time from all formations as 13, including the first one ever collected, AMNH 6517. Dong and Currie (1996: 632) reported that three specimens of oviraptorids were collected from the Djadokhta Formation at Bayan Mandahu by the Sino-Canadian Dinosaur Project, including IVPP V9608. The American Museum of Natural History–Mongolian Academy of Sciences expeditions in 1991 and 1992 collected three oviraptorid specimens from the Barun Goyot Formation at Ikh Khongil (also known as Nemegt) and Khermeen Tsav, and in 1993 discovered the wealth of fossils at Ukhaa Tolgod (Dashzeveg et al., 1995). A complete census of oviraptorids from Ukhaa Tolgod must await preparation of all of the theropod material collected thus far, but the two specimens overlying eggs collected in 1993 and 1995 were among the first 12 specimens collected that were identifiable as oviraptorid (including one embryo). Thus, the four oviraptorid skeletons overlying nests were among the first 30 adult specimens of this family collected, a ratio of 13.3%. If only the remains from the structureless sandstones of the Djadokhta Formation are considered, then the four specimens on nests are among only 17 adult specimens collected before 1996, a ratio of 23.5%.

The state of preservation of IGM 100/979 indicates that it was little disturbed after the death of the animal, and its posture is likely that taken by the animal as it died (fig. 1). The skeleton is remarkably complete and exhibits no evidence of scavenging or other disturbance after death that would have altered the posture of the skeleton (other than the worm burrows, which are unlikely to have altered it significantly). This is unusual for vertebrate fossils, which are often disarticulated and show other evidence of transportation, such as hydrodynamic wear. Both the skeleton and the nest are so little disturbed as to leave little doubt that they were not transported after death and, thus, that the position in which they are preserved reflects the position of the skeleton when it died.

The sedimentology of the deposits from

which this specimen and the three other oviraptorids directly overlying nests were collected suggest sudden burial, and represent an environment in which the animal could plausibly have been living (rather than one to which it was carried after death). All are from similar facies of the Djadokhta Formation, a facies termed a structureless sandstone (Eberth, 1993). Although such sandstones often are continuous laterally with crossbedded sandstones, indicative of sub-aerial, eolian deposition, there is no evidence of crossbedding within them. The lack of internal structure to these sandstones, which may reach 15 m in thickness, has been interpreted as the result of sudden accumulations of wind-borne sand (Eberth, 1993). A recent model suggests instead that these structureless sandstones were deposited as mass movements from standing dunes during rain, rather than wind, storms (Loope et al., 1998).

Regardless of which of these two depositional models is correct, the horizontal orientation of the nest and skeleton, the lack of disturbance to them, and their occurrence within a single bed of structureless sandstone indicate that they were in place before burial and then covered by a flow. The common occurrence of apparently undisturbed nests of dinosaur eggs in the sandstones of the Djadokhta Formation (Mikhailov et al., 1994), and to a lesser extent that of undisturbed, articulated skeletons (which, unlike the nest, may be transported as a unit when the carcass has not decomposed), indicate that the sandstones formed the substrate of the environment in which the adult oviraptorids lived.

The direct apposition of the skeleton on the nest in IGM 100/979 provides strong evidence that the nest was not completely covered. The adult skeleton is separated from the eggs in most places by little sediment, and in some areas (e.g., the right carpus, left pedal digits, right fourth pedal digit, ischial symphysis, and sternal elements) they are in contact or nearly in contact. The position of the posterior ribs, pubes, and the medial part of the right foot above sediments in the middle of the nest indicate that the center of the nest was not open.

Unfortunately, it is not possible to deter-

mine precisely how much of the nest was buried, because the sediments forming the nest are not distinguishable from those that later buried them with the skeleton. Furthermore, although most parts of the forelimbs are separated from the top of the nest by several centimeters of sediment it is unclear that this necessarily implies these areas of the nest were covered by this sediment, because it could have been deposited as the animal was being buried. During burial it is much less likely that sediment was removed from between the skeleton and nest to bring them closer together, rather than added to separate them, so the separation of the skeleton and nest probably indicate the minimal amount of separation (except for the relatively minor compaction of the sediments).

The precise relationship between the skeleton and nest is known at present for only one other nesting oviraptorid, IVPP V9608. Because several skeletal elements are at or below the level of the eggs, Dong and Currie (1996) infer that the nest was not buried. They also infer from the position of the feet, in the center of the nest but at the same level as the top of the eggs, that the center of the nest was filled in. Although the skeleton is incomplete, the preserved portions are in positions similar to those of IGM 100/979, indicating a symmetrical posture.

The symmetrical posture exhibited by IGM 100/979 and by IVPP V9608 is similar to the position birds take when they sit on nests (Skutch, 1976; Campbell and Lack, 1985). Other oviraptorid skeletons from the structureless sandstones of Ukhaa Tolgod that are not on nests are not in this position, lying instead on their sides with the limbs extended in various positions (e.g., IGM 199/1002). Indeed, we are unaware of any non-avian dinosaur specimens other than IGM 100/979 and IVPP V9608 preserved in precisely this posture.

The similarity between the posture of these two specimens with the posture of birds is clear, but the important question is whether they are homologous—is this condition “the same” as a result of their close evolutionary relationship? The inference of homology between behaviors shared among living organisms is no more problematic than is the interpretation of morphological homologues

(Wenzel, 1992; Greene, 1994), because both are based upon the simplest interpretation of similarities shared among groups of taxa (Rieppel, 1994). Because of its ephemeral nature, however, behavior is more difficult to document (e.g., Drummond, 1981; Miller, 1988). Sampling is a critical issue because the condition in all relevant taxa—including those supposedly lacking the behavior—must be ascertained. These problems are exacerbated in the fossil record, because in addition to the more speculative documentation of behavior it offers, sampling is biased by unknown factors related to the genesis of the geologic deposits in which they are preserved, and the taxonomic identity of the organism is often poorly resolved or, in the case of trace fossils, conjectural. Nevertheless, these considerations should not necessarily exclude the use of fossil evidence of behavior in comparative studies if they offer reliable evidence of particular behaviors.

Among extant oviparous reptiles parental care of eggs after deposition is common and taxonomically widespread only in archosaurs. Parents remain close to their eggs after they are laid, in some cases in direct contact with them, in birds (Kendeigh, 1952), crocodylians (Magnusson et al., 1989; Thorbjarnarson, 1996), and some squamates (Tinkle and Gibbons, 1977; Shine, 1988) but not in turtles (Shine, 1988) or *Sphenodon* (Moffat, 1985). Because parental care is pervasive in mammals (although only one group is oviparous) and is common and widespread among amphibians (Duellman and Trueb, 1994), it may be primitive for the Tetrapoda.

Optimizing these conditions to a cladogram of tetrapod relationships (fig. 15), the condition in Squamata is critical to determining whether parental care of eggs was lost in Reptilia and then re-evolved in some Squamata and in Archosauria or whether instead it was lost independently in turtles, rhynchocephalians, and within Squamata. If the distribution of this feature among squamates implies that it evolved in the common ancestor of the entire group, then the two alternatives just mentioned are equally parsimonious. If, however, it is simpler to infer that parental care was not present in the common ancestor of squamates then parental care is most parsimoniously considered to have

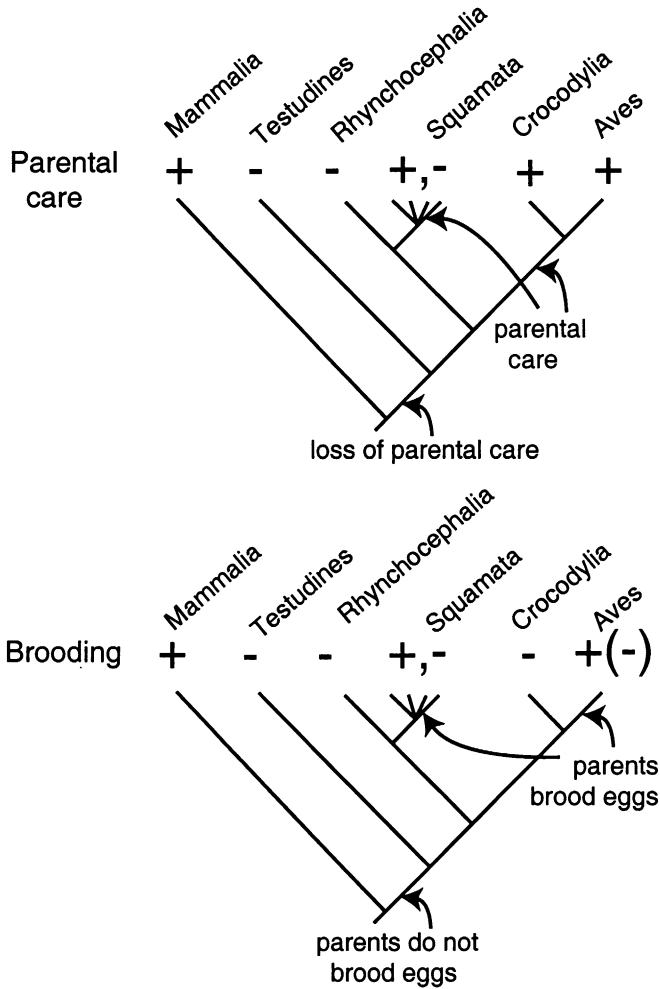


Fig. 15. Cladogram of relationships among extant Reptilia illustrating character distributions and inferences of homology discussed in the text, and the level at which they are synapomorphous (under DELTRAN optimization). Relationships are supported by the analysis of Eernisse and Kluge (1993). **Above:** Presence or absence of parental care of eggs after deposition. Note that this assumes the condition in Squamata to be variable; it is one of two equally parsimonious optimizations if brooding is inferred to be plesiomorphic for Squamata, the other being separate losses of brooding behavior in Testudines, Rhynchocephalia, and some Squamata. **Below:** Presence or absence of direct contact between parent and eggs after deposition (i.e., brooding). Parentheses indicate the occurrence in a group of a condition that is most simply interpreted as secondarily derived. Conditions refer only to oviparous taxa (i.e., monotremes, all testudines, both species of Rhynchocephalia, most squamates, and all archosaurs). Sources: Shine, 1988; Moffat, 1985; Collias and Collias, 1984.

been lost in the common ancestor of Reptilia and re-evolved in the Archosauria (fig. 14). Among Squamata, parental care of eggs is known to occur in Iguaninae, the scincid genus *Eumeces*, Anguidae, the teiid genus *Tupinambis*, Varanidae, Boidae, Colubridae, and Elapidae (Tinkle and Gibbons, 1977; Shine,

1988). Unfortunately, because of the cryptic behavior of most squamates it is unclear whether the absence of reports of parental care in the other 98% of squamate species (Shine, 1988) is due to the absence of this behavior or to insufficient opportunities for observation of these species. Taken at face

value (i.e., assuming brooding is absent in those groups for which it has not been reported), the distribution of brooding behavior in squamates implies that it evolved separately in each of these groups. However, the actual distribution of this behavior among squamates is undoubtedly broader. It is therefore uncertain whether parental care is plesiomorphic for Squamata, and this is how we have treated this group in optimizing this character to the relationships of amniotes (fig. 14).

If parental care is a synapomorphy of archosaurs, the crocodylian condition might mistakenly be considered to represent the primitive condition for the group. But the primitive condition for Archosauria comprises only those features of parental care common to both crocodylians and birds that are absent in outgroups. Thus, crocodylian parental care may include specializations of Crocodylia, just as parental care of birds involves specializations of Aves identifiable by their absence in crocodylians and other avian outgroups.

A specialized form of parental care is the brooding of eggs, in which the parent brings its body into direct contact with the eggs for prolonged periods of time. In the two archosaur groups, only bird parents are known to habitually brood their eggs, typically by resting directly on top of the nest (Skutch, 1976; Campbell and Lack, 1985; Gill, 1995). Crocodylian eggs are instead buried en masse either within a convex mound or a hole (Greer, 1970; Thorbjarnarson, 1996) covered by sediment that in some cases is mixed with plant debris. Although crocodylian parents (most commonly the female) often stay near the nest and, in some species at least, often lie on the side of the nest (Cott, 1961, 1971), they are not reported to lie directly on eggs (which are buried) or with the body centered on the nest (Magnusson et al., 1989). There is, thus, no evidence for brooding, or even for a consistent position or orientation of the adult's body relative to the nest. Crocodylian behavior is difficult to study in the wild, and the possibility that this particular behavior occurs occasionally cannot be dismissed entirely, but sufficient field studies and numerous observations of captive animals indicate that in crocodylians, unlike in birds, sitting on the center of the nest and covering the

eggs with the body is not a consistent part of the behavioral repertoire.

Among birds, with a few interesting exceptions (e.g., megapodes), one or both parents habitually sit directly on their eggs, and, again with only a few interesting exceptions (e.g., emperor penguins), take a characteristic posture over the nest (Campbell and Lack, 1985). The body is centered over the nest with the hind legs folded beneath, the abdomen contacts the eggs broadly, and often the forelimb is folded back along the sides of the body. In extant birds this behavior usually involves a brooding patch, a highly vascularized area on the abdomen over which the feathers are shed and body heat is transferred to the eggs more efficiently than elsewhere on the body. Brooding behavior is present in tinamous and ratites (although the latter lack a brooding patch) as well as in the putatively most basal neognath taxa (Campbell and Lack, 1985), and is therefore primitive for modern birds.

Although it is possible that oviraptorid nests were buried and occasionally uncovered (a behavior exhibited by the Egyptian plover; Howell, 1979), there is no compelling evidence that any oviraptorid nest was ever completely buried. It is unlikely that evidence is forthcoming for specimens without nesting adults, given the difficulty of distinguishing the sediments in which the nest was deposited from those that later came to bury them. In any case, because open nests are present in basal ratites and neognaths (Collias and Collias, 1984, appendix 1) and the oviraptorid nest provides evidence that in this group the nest was open at least some of the time during the brooding period, it corroborates the hypothesis that an open nest is the plesiomorphic condition for extant Aves.

The presence of two oviraptorid adults directly on nests suggests that adults of this taxon habitually sat on nests, but it does not necessarily imply that they were endothermic and provided heat to the eggs on a regular basis, as birds do through their brooding patch. There is no evidence available to test this hypothesis, and the assumption that the behavior associated with brooding and the act of brooding itself was correlated in oviraptorids is just that—an untestable assumption.

It has been suggested that the posture in this specimen is similar to that occasionally taken by crocodylians (Geist and Jones, 1996), but few similarities are apparent on close comparison. Indeed, the differences between the many different postures taken by crocodylians and that of IGM 100/979 are so obvious—the latter lies over the center of the nest in direct contact with eggs and with its legs folded beneath it and its arms spread around the perimeter of the nest—that this suggestion is easily dismissed.

The decidedly nonrandom pattern in which the eggs within oviraptorid nests are arranged also provides evidence of the behavior involved in their deposition. The pairing of eggs within nests of this type (i.e., elongatoolithid) strongly suggests that each pair was laid simultaneously using both oviducts (Varicchio et al., 1997). The arrangement of the pairs of eggs is also highly structured, much more so than the positions of eggs in crocodylian nests. The pairs of eggs are spaced around the perimeter of a circle in two layers, with a central area devoid of eggs. We considered the circular arrangement of the eggs to be evidence of manipulation by an adult after deposition (Norell et al., 1995), but alternatively it could be the result of highly precise positioning by the mother, standing in the middle of the nest, during the egg laying process (Dong and Currie, 1996). It is unclear if there is any evidence that could falsify either of these hypotheses.

It has been suggested that the pairing of eggs in oviraptorid nests is evidence either that they were laid at intervals of one day or more ("monoautochronic ovulation") or in a much shorter period of time, but there is no strong evidence against either alternative. Deposition of the eggs on more than one day, as in birds, was advocated by Varicchio et al. (1997), who cited in support the pairing of eggs in lizards and an abnormal duck that laid pairs of eggs over long time intervals. It is unclear why the pairing of eggs necessarily precludes more rapid deposition, however, given our lack of information about the reproductive biology of oviraptorids. The alternative scenario, in which the eggs were laid at one time, is supported mainly by a nest in which the pairs of eggs are arranged in a spiral pattern, with gradual changes in

position between pairs (Dong and Currie, 1996). Although this pattern suggests continuity in the process of egg deposition, and is plausible, it is also possible that the mother (or mothers) simply aimed well when they returned to the nest over time. It is again unclear that any evidence is available that could refute either of these hypotheses.

The behavior of egg turning, in which birds manipulate the eggs after they have been laid, is common to nearly all living birds and, as far as is known, to all that directly brood their eggs (Campbell and Lack, 1985; Deeming, 1991). It has been suggested that the apparent partial burial of the eggs in oviraptorid nests "preclude[s] the possibility of egg rotation as in birds" (Varicchio et al., 1997: 249), and indicates the absence of a structure—chalazae, fibers that support the embryo within the egg—correlated with this behavior. As discussed above, it is uncertain to what extent the eggs were buried while the adult was alive, but in any case it is unclear why burial of the eggs necessarily precludes periodic unburying and rotation. The repeated burial of eggs by the Egyptian plover (Howell, 1979) demonstrates the possibility of this behavior, and although the large number of eggs in oviraptorid nests would require a great deal of activity to rotate all of them, there seems no reason to consider egg turning to have been impossible or improbable in the absence of information about oviraptorid metabolism and behavior. Indeed, which of the more unusual behaviors exhibited by living animals would be deemed unlikely if only their effects were known?

Stronger evidence against egg rotation is the pairing of the eggs, because rotation of the eggs would presumably disrupt this pattern, assuming it to have been created when the eggs were laid. It is of course possible that the eggs were laid so soon before their terminal burial that rotation had not yet taken place, or that the pairing was due to precise parental manipulation after egg turning, so at best the hypotheses of paired oviducts and egg turning are only weakly tested by the observation of egg pairs.

There remain many obvious desiderata for understanding these fossils. In addition to the unanswered questions just surveyed, we do not know the sex of the adults on the nests,

their precise genealogical relationship to the eggs (e.g., whether more than one set of parents contribute to the nest), how often and for how long adults attended the nest, what was the gestation period of the eggs, or how long hatchlings stayed in the nest. It is tempting to speculate, but a more fruitful approach is to continue searching the sands of Ukhaa Tolgod and elsewhere for specimens that will provide evidence that might address these questions.

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APPENDIX: ABBREVIATIONS USED IN
ILLUSTRATIONS

cm	costal margin of sternum	lt	lateral trabecula of sternum
e	egg	lul	left ulna
fu	furcula	lvr	left ventral rib
g	gastralia	pl	proximal phalange, digit I of right manus
hc	hypocleidium	ps	pubic symphysis
i	invertebrate burrow	rdr	dorsal segment of right thoracic rib
is	ischial symphysis	rf	right femur
it	invertebrate trace	rfl	right fibula
kc	keratinous claw remnant	rh	right humerus
la	left astragalus	rmc1-3	metacarpals of right manual digits I-III
lca	left calcaneum	rmdI-III	right manus digits I-III
lfi	left fibula	rmt1-4	metatarsals of right pedal digits I-IV
lh	left humerus	rpdl-IV	right pedal digits I-IV
lmdI-III	left manus digits I-III	rr	right radius
lmt1-4	metatarsals of left pedal digits I-IV	rs	right sternal plate
lpd I-IV	left pedal digits I-IV	rsc	right scapula
lr	left radius	rt	right tibia
ls	left sternal plate	ru	right uncinatc process
lsc	left scapula	rul	right ulna
lslc	left semilunate carpal	rvr	ventral segment of right thoracic rib
		v	vertebra

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