

A nesting dinosaur

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A SPECTACULAR fossil specimen that suggests the presence of an avian type of nesting behaviour in oviraptorids, a clade of non-avian maniraptoran theropods, is reported here. The substantial evidence indicating that birds are a type of theropod dinosaur has led to copious discussion concerning the origin and possible presence of advanced avian reproductive behaviour in non-avian dinosaurs. Although the inference of behaviour from fossils is problematic, some remarkable discoveries, such as the incontrovertible evidence of dinosaur nests¹, and more controversial claims made on the basis of dinosaur nesting grounds² and juvenile morphology³, hint at the occurrence of advanced reproductive behaviour in a variety of non-avian dinosaurs. But there is no direct fossil evidence implying advanced parental systems such as those found in modern birds. The closest associations between presumed parents and nests occur in oviraptorid dinosaurs from Late Cretaceous deposits of the Gobi Desert^{4,5}. The specimen described here is the first preserved well enough to determine its precise relationship with the nest. It is a large oviraptorid positioned over a nest of oviraptorid eggs in the same posture taken by many living birds when brooding. This provides the strongest evidence yet for the presence of avian brooding behaviour in non-avian dinosaurs.

Other *Oviraptor* discoveries have been found associated with nests^{4,5}, including the first discovery of *Oviraptor* at the Flaming Cliffs in 1923⁴, and it has been suggested previously that perhaps these individuals were defending or incubating their nests⁵. At the time of the original discovery in 1923, the eggs were thought to belong to *Protoceratops andrewsi*, the most common dinosaur in those deposits. This led to the eponymous suggestion that *Oviraptor* died while scavenging the eggs. The recent discovery of an oviraptorid embryo⁶ within the type of egg associated with

the *Oviraptor philoceratops* holotype suggests instead that this individual's proximity to the nest was related to parental care rather than to predation.

The specimen (IGM 100/979) (Fig. 1) was collected at Ukhaa Tolgod, a Late Cretaceous fossil locality in South Central Mongolia^{7,8}, during the 1993 segment of the Mongolian Academy of Sciences/American Museum of Natural History of Paleontological Project. To preserve spatial relationships definitively the entire specimen was collected in a single large block. No eggs were exposed on the surface, indicating that the entire nest as preserved was collected.

At Ukhaa Tolgod, remains of oviraptorids are the most common theropod elements encountered, rivalling ankylosaurs as the most common dinosaur discovered at this locality⁷. Like most specimens from Ukhaa Tolgod, the specimen shows no evidence of transportation after death, and is preserved in a facies hypothesized to be deposited by large sandstorms⁷. The specimen is of a large individual, although it is not outside the range of Ukhaa Tolgod oviraptorids. The skull, vertebrae, tail and dorsal pelvic bones, and proximal parts of both hindlimbs are missing, yet the majority of the remaining elements including the gastralia and ribs are preserved (Fig. 1).

The maniraptoran affinity of this specimen is shown by the presence of a semilunate carpal that is firmly secured to metacarpals I and II⁹. The clavicles are fused forming a stout furcula, a feature typical of oviraptorids¹⁰. IGM 100/979 has a forward-pointing pubis and metatarsal III is not pinched proximally by II and IV; digit three in the hand is gracile as is typical of many maniraptorans. Differences in manual proportions have been used to differentiate oviraptorid taxa^{10,11}. In *Oviraptor* and *Conchoraptor*, digits II and III are subequal in length and longer than digit I, whereas all three digits are nearly equal in length in *Ingenia*. Furthermore, the digits of *Oviraptor* are longer and thinner than in other oviraptorids and the taxon uniquely displays large, laterally compressed, recurved claws, with extremely large flexor tubercles as expressed in IGM 100/979. The specimen displays several pathologies, including a right ulna that was broken and healed during life.

IGM 100/979 is the best preserved and most complete oviraptorid specimen of any yet found on a nest, and offers the first evidence of the precise position of the skeleton to the nest (Fig. 2). Both hindlimbs are tightly folded (Fig. 1c), with the feet and the lower legs nearly parallel to one another. The feet lay atop and adjacent to eggs on the inner perimeter of the circle defined

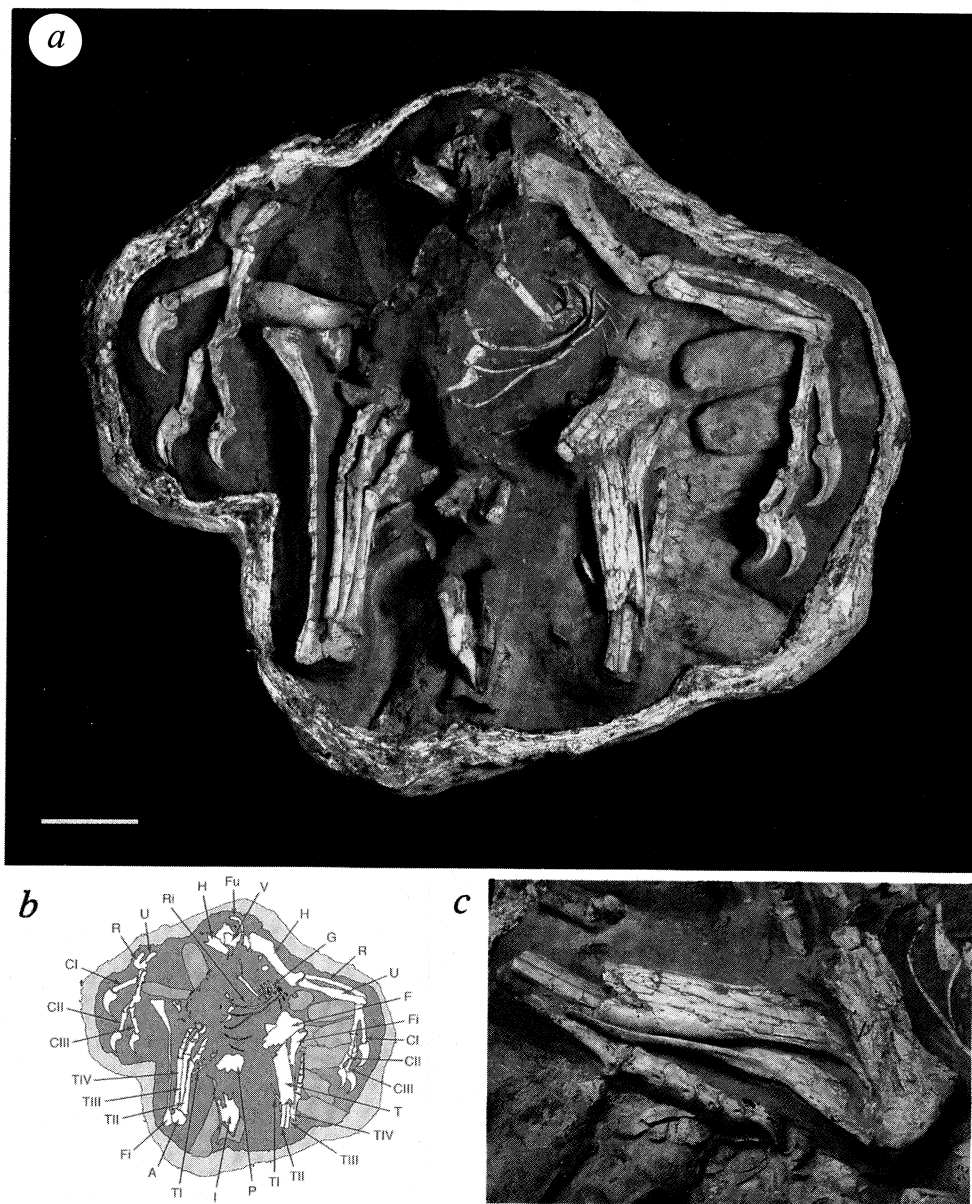


FIG. 1 a, Specimen photograph of IGM 100/972. Scale bar, 10 cm. b, Schematic map of the specimen. Exposed eggs are indicated in blue. CI-III, Manual digits; F, femur; Fi, fibula; Fu, furcula; G, gastralia; H, humerus; I, ischium; P, pubis; R, radius; Ri, ribs; S, scapula; T, tibia; TI-IV, tarsal elements; U, ulna; V, vertebrae. c, Detail of the right pes of IGM 100/972 showing close association between the *Oviraptor* and the eggs.

by the nest (Fig. 1c). The pubis lies in the direct centre of the nest, and the ischia (which are fused distally) lay more posteriorly atop the posteriormost eggs. Anteriorly, gastralia just posterior to the shoulder girdle lie in contact with eggs. The front limbs are directed posteriorly, with both arms wrapped around the nest. The claws on the hands are directed inward. Evidence of soft tissue preservation, unusual for sandstone matrices, is apparent at the tips of the manual claws (Fig. 3).

The eggs in the nest are arranged in a circular pattern, with the broad end of the egg pointing towards the centre of the nest. In places they occur in two levels. Fifteen eggs are visible; however, additional eggs are undoubtedly present in areas that could not be prepared without damage to the skeleton. From the spacing and distribution of the visible eggs, it can be estimated that about 22 eggs filled the nest, a number typical of nests that can be referred to oviraptorids¹². Individual eggs measure 18 cm long by 6.5 cm wide although post-mortem vertical compression may influence these measurements to a small degree. Egg surfaces are ornamented with small ridges that run parallel to the long axes, and their shape can be characterized as elongatoolithid¹³. Eggshell morphology is identical to an egg containing an oviraptorid embryo⁶ and those associated with other oviraptorid skeletons^{4,5}.

Although other nests containing eggs with an identical eggshell morphology are common in the area, none was discovered close enough to suggest the occurrence of a communal nesting colony as has been postulated for the ornithomimid *Maiasaura*^{2,14}.

Other factors could possibly account for the association found in IGM 100/979. The nature of fossil preservation at Ukhaa Tolgod (no apparent post-mortem transportation), the near life pose of the oviraptorid skeleton on the nest, and the positive association of these eggs suggest strongly that this is not a chance occurrence. Another possibility is that the animal perished while in the act of laying eggs in the nest. This seems obviated by the lack of eggs inside the body cavity. Furthermore, the neat systematic arrangement of this and other oviraptorid nests



FIG. 2 Reconstruction of *Oviraptor* on nest shortly before death.



FIG. 3 Detail of manual claw of digit I. Arrow shows traces of soft tissue preservation and extent of horny covering of the unguis. Scale bar, 1 cm.

implies that the eggs were manipulated¹⁵ by the parents into a specific configuration after laying as in living birds.

Brooding behaviour (by which we refer only to the behaviour of sitting on nests) is exhibited by living birds to varying degrees and in diverse ways among the different groups¹⁵. However, in all but exceptional cases (nest parasites, mound builders) an individual (usually both sexes in neognaths¹⁶) rests directly upon the eggs for prolonged periods of time during their maturation. In palaeognaths the nest is typically attended by males¹⁶ (in both sexes in ostriches¹⁵). This behaviour is associated with thermoregulatory incubation. Very exceptionally, some extant ectotherms are also known to brood their nests (pythons¹⁷) where this behaviour is also correlated with maintenance of a constant, higher than ambient temperature during incubation. Although strongly suggestive, this does not imply that brooding behaviour and endothermy are necessarily correlated. Brooding behaviour may have developed as a mechanism for shading the eggs (common in arid-land birds^{15,18}), or as an advanced system of egg protection for ground nests that was later co-opted within birds in parallel with their metabolic evolution. Their phylogenetic distribution indicates that both endothermy and brooding behaviour are primitive characteristics among modern birds.

The occurrence of multiple specimens of large oviraptorids associated with nests suggests that (1) they were the parents of the nests, (2) that like other archosaurs they habitually stayed close to the nest, and (3) with the addition of IGM 100/992, that they brooded their nests. Unfortunately the nature of the fossil record limits the testing of these hypotheses. However, the sedimentary context of IGM 100/979 and its death position relative to the nest provide compelling evidence of an *Oviraptor* sitting on a clutch of eggs in a position homologous to the

brooding posture displayed by many modern birds. This finding provides the strongest evidence yet that modern avian brooding behaviour evolved long before the origin of modern birds and among non-avian maniraptoran theropods. □

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Apoptosis and increased generation of reactive oxygen species in Down's syndrome neurons *in vitro*

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DOWN'S syndrome (DS) or trisomy 21 is the most common genetic cause of mental retardation¹. Development of the DS brain is associated with decreased neuronal number and abnormal neuronal differentiation^{2–7}, and adults with DS develop Alzheimer's disease^{8,9}. The cause of the neurodegenerative process in DS is unknown. Here we report that cortical neurons from fetal DS and age-matched normal brain differentiate normally in culture, but DS neurons subsequently degenerate and undergo apoptosis whereas normal neurons remain viable. Degeneration of DS neurons is prevented by treatment with free-radical scavengers or catalase. Furthermore, DS neurons exhibit a three- to fourfold increase in intracellular reactive oxygen species and elevated levels of lipid peroxidation that precede neuronal death. These results suggest that DS neurons have a defect in the metabolism of reactive oxygen species that causes neuronal apoptosis. This defect may contribute to mental retardation early in life and predispose to Alzheimer's disease in adults.

Primary mixed cultures of human neurons and astrocytes were established from 16–19 weeks' gestation fetal DS and normal cerebral cortex as previously described¹⁰. DS and normal human neurons survived plating and elaborated axons and dendrites to a similar extent during the first 5–7 days in culture (Fig. 1a). However, after 7 days in culture, DS cultures began to show neurodegenerative changes, including neuronal shrinkage, vacu-

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