On the discovery of an oviraptorid skeleton on a nest of eggs at Bayan Mandahu, Inner Mongolia, People's Republic of China

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Abstract: A partial skeleton of *Oviraptor* (which means egg thief), collected at Bayan Mandahu (Inner Mongolia, People's Republic of China) in 1990 was lying on top of a nest of eggs. Of the six known skeletons of this genus from Upper Cretaceous Djadokhtan sediments, this is the second occurrence in which the theropods were interacting with the eggs when they were buried by sand and dust during sandstorms. Two explanations for the association of *Oviraptor* with eggs are that the theropod may have been eating the eggs, or it may have been incubating and protecting them. Evidence presented suggests that the latter hypothesis is more likely. It is also conceivable that the female oviraptorid was in the process of laying eggs when she died.

Résumé : Un squelette partiel d'un *Oviraptor* (qui signifie « voleur d'oeufs »), collecté en 1990 à Bayan Mandahu (Mongolie intérieure, République populaire de Chine), reposait au-dessus d'un nid d'oeufs. Des six squelettes connus de ce genre livrés par les sédiments de la Formation de Djadokhta d'âge Crétacé tardif, c'est la deuxième fois que l'on y trouve des théropodes interagissant avec les oeufs au moment de leur ensevelissement par du sable et de la poussière durant des tempêtes de sable. Deux hypothèses peuvent être formulées pour expliquer l'association de l'*Oviraptor* avec les oeufs, soit que le théropode était à dévorer les oeufs, ou soit qu'il les couvait et les protégeait. Les arguments présentés ici plaident en faveur de la dernière hypothèse. Il est également possible de concevoir que la femelle oviraptoride était en train de pondre les oeufs au moment de son décès.
[Traduit par la rédaction]

内容提要

一九九O年在中华人民共和国内蒙古巴彦满达呼采得一食蛋龙 (*Oviraptor* 意为"偷蛋贼") 的部分骨架。这具标本保存在一窝化石蛋上。在上白垩统 Djadokhta 地层中已发现的六具骨架中，这是此种兽脚类恐龙在与一窝蛋发生某种牵连时被沙暴的尘沙所一起埋葬的第二例。*Oviraptor* 与化石蛋的共生组合有两种可能的解释：其一是这个兽脚类恐龙正在食蛋，其二是它正在孵化或保护这些蛋。本文提供的证据说明后一种解释的可能性更大。另外可以想象，这个雌性食蛋龙也可能是在产蛋过程中死亡。
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Реферат
Частичный скелет Oviraptor (что означает "похититель яиц") был обнаружен в Баян Мандаху (Внутренняя Монголия, Народная Республика Китай) в 1990г. поверх гнезда с яйцами. Из шести известных скелетов данного рода из верхнемеловых осадков Джадохта, это второй случай, когда тероподы во время песчаных бурь были погребены песком и пылью на гнездах яиц. Может быть два объяснения ассоциации Oviraptor с яйцами: терапод мог поедать яйца или

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инкубировать и защищать яйца. Найденные останки свидетельствуют скорее в пользу второй гипотезы. Также возможно, что овирапторид женского пола во время гибели был в процессе откладывания яиц.

[Перевод выполнен для редакции Научно-Исследовательские Журналы]

Introduction

Over 70 years ago, a skeleton of a theropod dinosaur (AMNH 6517) was found with a nest of eggs (AMNH 6508) that were believed to have been laid by *Protoceratops*. The specimens were collected by the Central Asiatic Expeditions of the American Museum of Natural History in the southern Gobi of Mongolia at a site now known as Bayn Dzak. This dramatic and unusual association of specimens was described by Osborn in 1924, who named the theropod *Oviraptor philoceratops*, the "egg seizer with a fondness for ceratopsian eggs." Since then, most palaeontologists have believed that small oviraptorids were egg eaters (Currie et al. 1993). However, Barsbold (1977) proposed that the jaws of oviraptorosaurs were best adapted for crushing the shells of pelecypods, and Smith (1992) suggested that they were the jaws of a herbivore.

A fragmentary oviraptorid skeleton was collected from Bayan Mandahu in Inner Mongolia by the Sino-Canadian expedition of 1990. It came from site 102 (Jerzykiewicz et al. 1993) in the North Canyon. It was evident in the field that the oviraptorid was lying on a nest of eggs, which at the time were assumed to have been laid by a herbivorous dinosaur. *Oviraptor* is not a common animal, and only three skeletons have been recovered from the Djadokhta Formation of Mongolia (Barsbold et al. 1990), so the recovery of three oviraptorid skeletons from the equivalent beds at Bayan Mandahu is noteworthy. Although the sample size is small, the association of *Oviraptor* skeletons and eggs is 33%. Initially, this seemed to be powerful evidence in favour of egg-eating habits for oviraptorids. However, it was also noted that the eggs found with the new specimen were the same size and shape as those found with AMNH 6517, and this suggests an alternate hypothesis. Perhaps *Oviraptor* was not pillaging the nest of another dinosaur, but was protecting its own eggs. Recently, independent evidence came from the discovery of oviraptorid embryo inside a similar type of egg (Norell et al. 1994).

Abbreviations

AMNH, American Museum of Natural History, New York; IGM, Institute of Geology, Mongolia, Ulaan Baatar; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing.

Taxonomy

Dinosauria Owen, 1842
Saurischia Seely, 1888
Theropoda Marsh, 1881
Oviraptorosauria Barsbold, 1976
Oviraptor philoceratops, Osborn 1924

Material

IVPP V9608; a partial skeleton with vertebrae, pectoral girdle, right front limb, and right hind limb. The catalogue number also refers to a partial nest of half a dozen eggs found beneath the skeleton. The skeleton is articulated, and both it and the nest would probably have been complete if it had been discovered before wind, water, and root erosion had destroyed most of it.

Locality and age

Bayan Mandahu, near Urad Houqi in Inner Mongolia; Bayan Mandahu redbeds of the Upper Cretaceous (Campanian).

Description

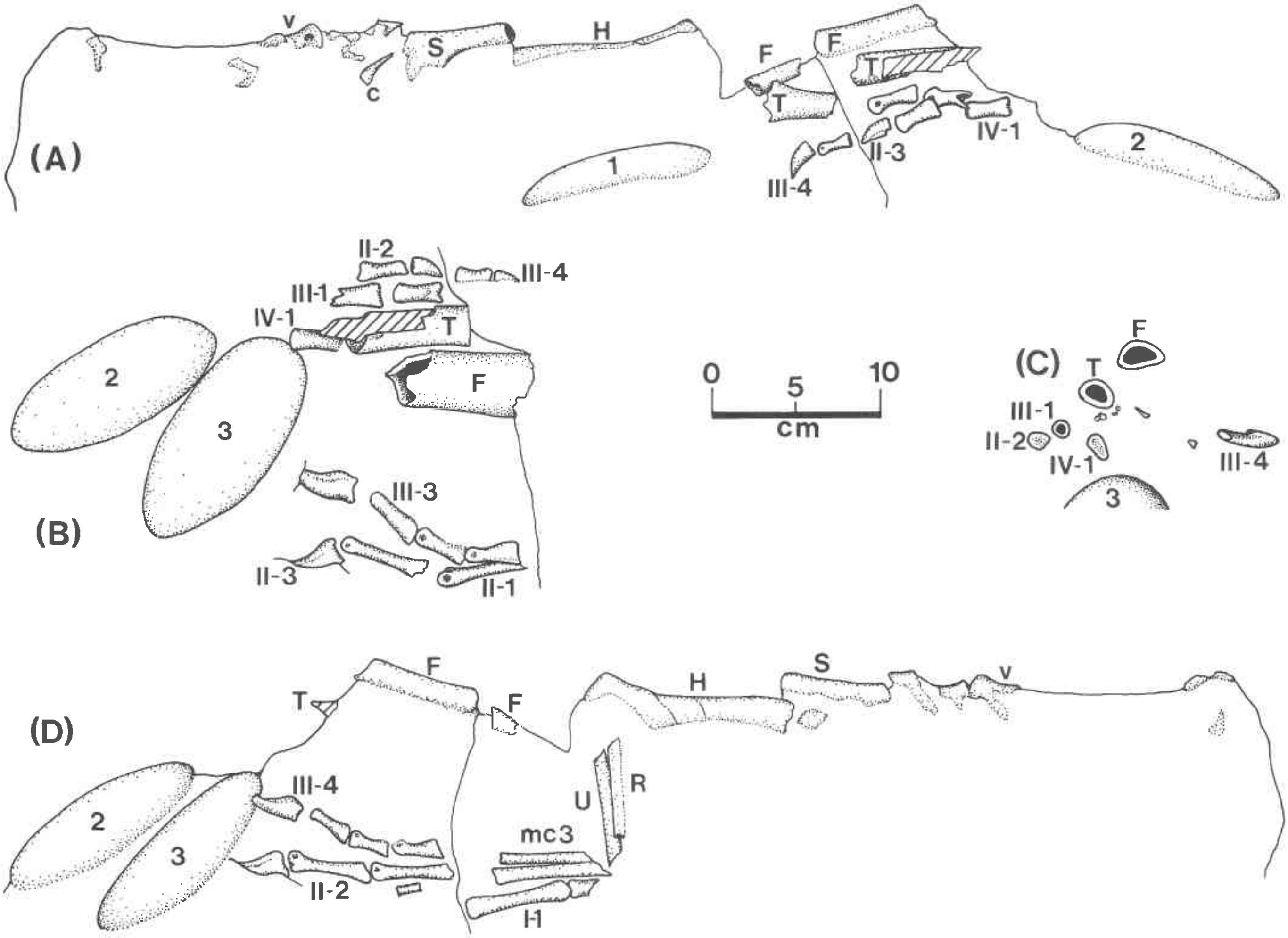
Some fragments (neural arches and spines) of vertebrae are present (Fig. 1), but are not well-enough preserved to merit description. The preserved portion of the right scapula is 80 mm in length, although the element would have been considerably longer in life. Its shaft is relatively narrow (shaft diameter of 12 mm) and is subcircular in section. The distinct anterior edge of the scapula is thickened for the clavicular articulation. A tapering fragment of bone, 38 mm long, anterior to the scapula probably represents the right side of the fused clavicles.

The 168 mm long humerus is relatively thick and strong, with a shaft diameter of 21 mm, and expands distally to 33 mm. The deltopectoral crest is not well preserved, but, as in other oviraptorid skeletons, is restricted to the anterior half of the humerus. The radius and ulna (preserved length is 114 mm) lack the proximal ends, but the forearm was clearly more than 70% of the length of the humerus. As in other oviraptorids, the distal end of the ulna is flattened and is distinctly expanded laterally. The semilunate carpal is in position over metacarpals I and II, but is not well preserved.

As in *Oviraptor* and *Conchoraptor*, but in contrast with *Ingenia*, the first metacarpal (length 32 mm) is less than half the length of the second (82 mm, but incomplete). The preserved portions of the second and third metacarpals are long, and the complete bones were evidently almost equal in length. The incomplete bones are almost half the length of the humerus, which means the specimen cannot be *Ingenia*, because the metacarpus of that genus is only a third the length of the humerus (Barsbold et al. 1990). The second and third metacarpals are closely appressed. Metacarpal II has a shaft width of 12 mm, whereas the shaft of the third metacarpal (incomplete length is 75 mm) is only 8 mm in width.

Digit I includes a complete first phalanx (79 mm), which is comparable in size to that of AMNH 6517. Both ends of the ungual (I-2) are present, but the middle of the bone has been eroded and lost (estimated length is at least 50 mm). The second (II-1 is 60 mm, II-2 is 66 mm, and II-3 is incomplete) and third (III-1 is 38 mm, III-2 is 35 mm, III-3 is 40 mm,

Fig. 1. Oviraptorid skeleton and nest of eggs, IVPP V9608, in left lateral (A), dorsal (B), posterior (C), and right lateral (D) views. C, clavicle; F, femur; H, humerus; R, radius; S, scapula; T, tibia; U, ulna; v, vertebra; mc3, metacarpal 3.



and III-4 is incomplete) digits are close to the same length (with estimated lengths of 165 and 155 mm respectively), the third being only 6% shorter than the second. The penultimate phalanges of the digits are longer than the more proximal phalanges as in *Oviraptor* and *Conchoraptor*. All unguals are recurved, and possess a dorsoposterior ''lip'' as in *Oviraptor*, but not *Conchoraptor*.

The right hind limb is represented by a fragmentary femur, tibia, fibula, and pes (Fig. 1). The femur and tibia are relatively robust in comparison with the forelimbs. The distal end of the femur, 24.5 cm in preserved length, is badly broken. The shaft has a transverse diameter of 3 cm, 2.5 cm of which is made up of the hollow core (Fig. 1C). The 15 cm long fragment of tibia has a diameter of 2.5 cm.

None of the metatarsus has survived, but the second, third, and fourth toes are all represented. There is nothing unusual about the second (33 mm) and third (28 mm) phalanges of digit II, and the third toe is nearly complete (III-1 is 35 mm but incomplete, III-2 is 36 mm, III-3 is 28 mm, and the ungual is 25 mm long but incomplete). As presently prepared, only the first two phalanges of digit IV are exposed, but the rest are probably present. Phalanx IV-1 (30 mm) is easily identified by its concave (not ginglimoid) proximal articular surface (Fig. 1C), which is not perpendicular to the longitudinal axis of the phalanx. Phalanx IV-2 is 27 mm in length. The two preserved unguals are recurved, and are only slightly broader ventrally than dorsally, which is characteristic of oviraptorids.

IVPP V9608 includes six eggs, and fragments of others that were still in position in the nest when it was buried. The eggs are 15 cm long, with short diameters of approximately 5.5 cm. They were laid in a circle in pairs (Figs. 1B, 1D), like so many of the Asian eggs. The longitudinal axes of the eggs are inclined at low angles (13−16°) to the ground (Fig. 1A), and slope away from the centre of the nest. The equatorial region of each egg has linearituberculate ornamentation (variant 1 of Mikhailov 1991), but the polar regions are smooth. Eggshell thickness is less than 1 mm.

Eggshell from the nest was examined using transmitted light microscopy and scanning electron microscopy. The pore system is of the angusticanaliculate type with simple, nonbranching canals. In radial section, two histostructural layers are visible: an inner mammillary layer, and an outer continuous layer (Fig. 2). Shell units are nondistinct, which is a characteristic of the ornithoid basic type and ''ratite'' morphotype (Fig. 2).

Fig. 2. Scanning electron microscope photograph of egg shell from IVPP V9608. Outside of egg shell is towards the top. *c*, continuous layer; *m*, mammilary layer. Scale = 200 μm.

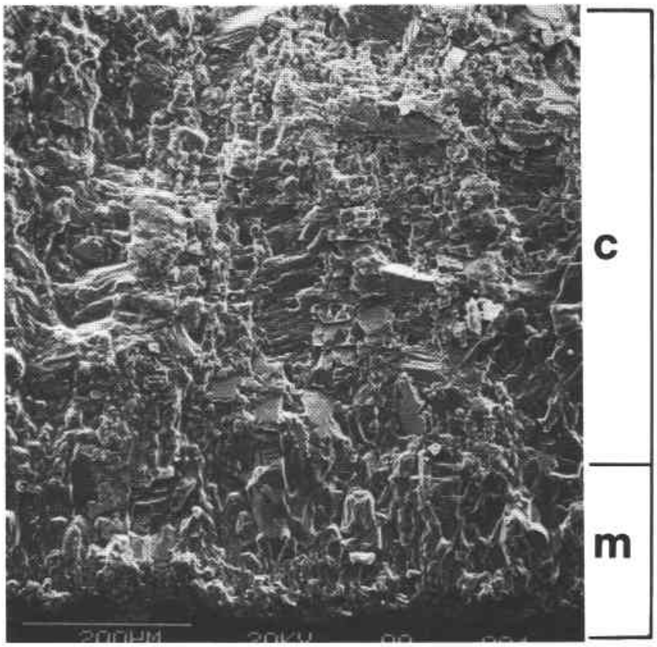
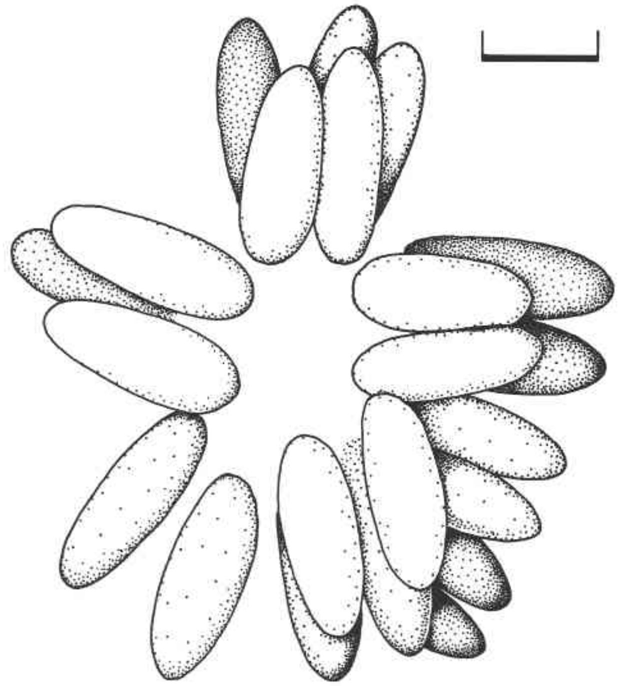


Fig. 3. Nest of elongatoolithid eggs from Mongolia, based on IGM 100/1008. The outlines of some eggs have been restored, but all of the eggs in the drawing are present in the positions shown. Scale bar = 10 cm.



Discussion

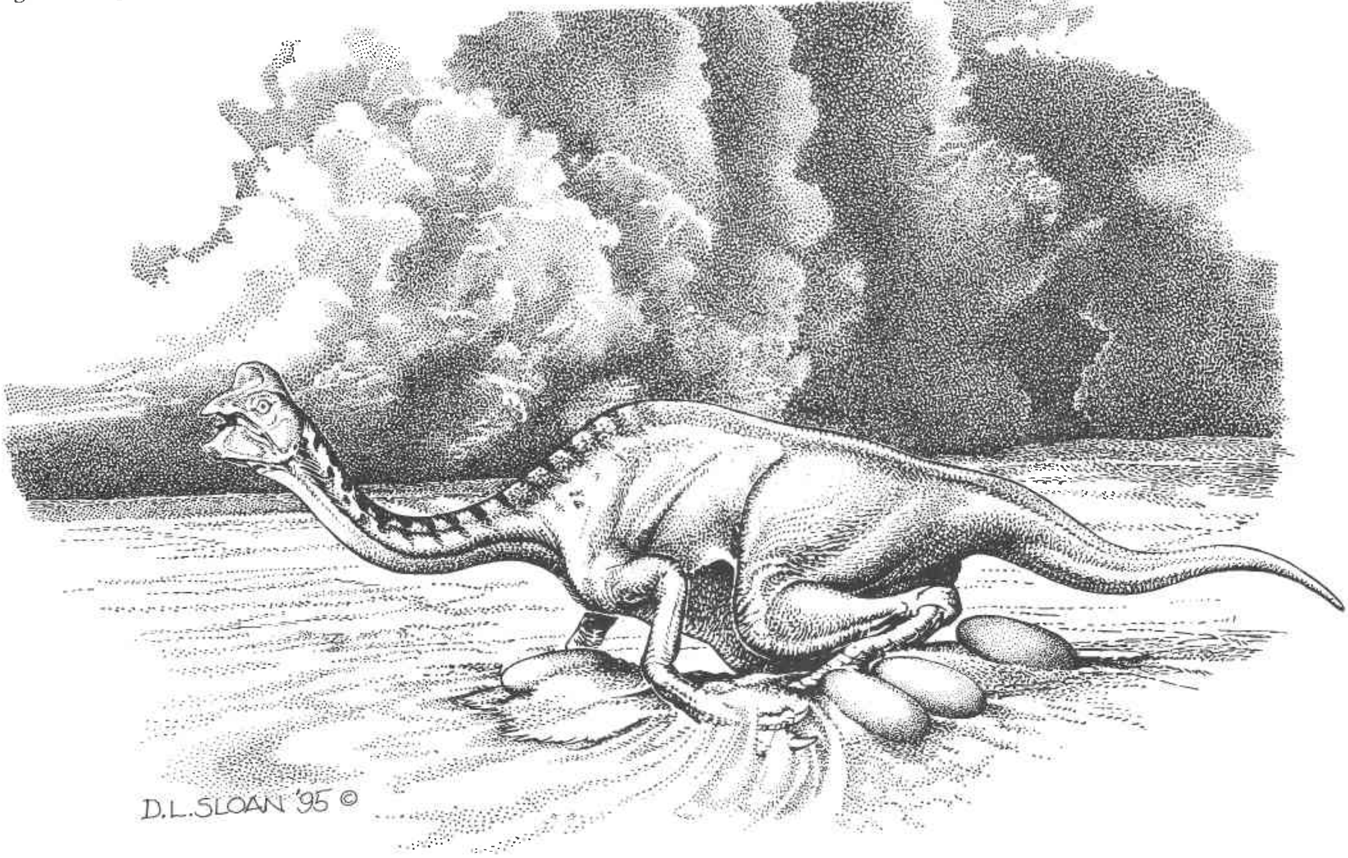
IVPP V9608 has a long forelimb with an elongate tridactylous manus. Digits II and III appear to have been subequal in length, a characteristic found in oviraptorids and ornithomimids. These families are easily distinguished by the structure of the manus (see Barsbold and Osmolska 1990). Three genera of oviraptorids are presently known from the Upper Cretaceous of central Asia, namely *Ingenia, Conchoraptor*, and *Oviraptor*. The length of the forelimb and the morphology of the manus show that IVPP V9608 cannot be *Ingenia*. The presence of a distinct dorsoposterior "lip" on each manual ungual is characteristic of *Oviraptor*, but not *Conchoraptor*. The size and limb proportions of IVPP V9608 fall within the range of variation of known specimens of *O. philoceratops*. For these reasons, the specimen has been identified as *O. philoceratops*, although it is possible that better specimens may ultimately show that the Bayan Mandahu specimens represent a distinct species.

Egg shape, size, shell ornamentation, type of pore system, microstructure, and shell thickness indicate that the eggs found in association with the oviraptorid skeleton are referrable to the parafamily Elongatoolithidae Zhao, 1975. These are elongate eggs with linearituberculate ornamentation in the equatorial region, and relatively thin eggshells. These eggs can be most easily confused with "protoceratopsid" eggs of the P2 group (Mikhailov et al. 1994), which have a similar size, shape, and outer surface ornamentation. The primary difference between these two egg types is the microstructure, which is ornithoid–ratite in the elongatoolithids, and dinosauroid–prismatic in the protoceratopsids (P2 group). Mikhailov (1991) suggested that this form of egg was laid by theropods, although at that time it was difficult to prove this without the presence of embryos in the eggs, or without finding the eggs still present in the maternal dinosaur. The discovery of an oviraptorid embryo in an egg (Norell et al. 1994) clearly shows that oviraptorids laid elongatoolithid eggs with linearituberculate ornamentation and angusticanaliculate pore structure, and indicates that Mikhailov's 1991 identification was correct. The Mongolian eggs are 12 cm long and 6 cm wide with egg shell up to 0.95 mm thick (Norell et al. 1994), and are therefore close to the same dimensions as those of the Chinese eggs.

When IVPP V9608 was discovered, much of the specimen had been lost to erosion. Nevertheless, it is clear that the theropod skeleton was lying on top of the nest, with its hind legs folded underneath the body. The pose of the theropod shows it was trapped in a life pose, sitting on its haunches. Burial was rapid because the body had no opportunity to roll over, and was neither scavenged nor disarticulated. The surrounding sediments are fine-grained, reddish, structureless sandstones interpreted by Eberth (1993) as eolian sands that accumulated in very high energy windstorms. About 500 m from IVPP V9608, similar rocks at about the same level yielded the remains of 12 juvenile *Pinacosaurus* that probably died in a sandstorm (Currie 1989; Jerzykiewicz et al. 1993). It seems likely that the oviraptorid was lying on the nest of eggs when it was buried during a sandstorm. There were similar circumstances surrounding the death and burial of the type specimen of *O. philoceratops* (Osborn 1924).

The right foot is positioned in the centre of the nest (Fig. 1A), where there are no eggs, although the preserved semicircle of eggs lies anterior, posterior, and to the right of the foot. The right arm is folded back, and the hand lies outside of the semicircle of eggs (Fig. 1D) at the same level as the eggs. The belly would have been over the centre of the nest, and the position of the vertebrae suggests that the body

Fig. 4. Interpretation of relationship of oviraptorid and nest of eggs.



was stretched out beyond the nest. The symmetry of the skeleton and nest suggests that the animal was squatting with its feet within the circle of eggs. The back of the right foot is slightly higher in elevation than the eggs (Fig. 1C), although the unguals are at the same level as the eggs (Fig. 1A). This suggests that the centre of the nest had been filled in with sand. The right hand lies outside of the nest and is at the same level as the eggs, indicating that the eggs were probably not buried when the theropod sat on the nest.

The histostructure, shape, and ornamentation of the eggs show that they were laid by a theropod, and the eggs are very similar to oviraptorid eggs with embryonic remains (Norell et al. 1994). Therefore, there is every reason to believe that the eggs of IVPP V9608 are oviraptorid eggs.

Looking at the taphonomic evidence of the site, it is possible to come up with several scenarios to explain the association of the theropod and eggs.

The association of the skeleton and the eggs may have been coincidental. However, specimens found in this type of bedding at Bayan Mandahu usually occur as untransported, isolated skeletons (Jerzykiewicz et al. 1993), so it is unlikely that the association was accidental.

Perhaps the theropod was caught in the act of pillaging a nest of eggs, as was suggested by Osborn (1924). Although only six eggs remain in the nest, there is no evidence of preburial destruction of any of the eggs. Furthermore, a predatory oviraptorid would probably have either consumed or abandoned its food long before it was buried by sand and dust carried by a sandstorm.

Another possibility, and perhaps the most likely, is that the theropod may have been lying on the nest, incubating and (or) protecting the eggs. The position of the skeleton, squatting over the centre of the nest, and the fact that the eggs appear to have been laid by a mature theropod of about the size of IVPP V9608 support this hypothesis. The eggs are the same type (size, shape, and shell morphology) as those associated with the type specimen of *O. philoceratops*, which suggests that it too may have been caring for, rather than pillaging, a nest of eggs.

If the oviraptorid is indeed sitting on the nest, then it suggests that theropods, like their descendants, the birds, incubated and protected their eggs. These instincts must have been very powerful for the animal not to have abandoned the nest as it became buried by sand. But strong maternal instincts offer a more likely explanation than assuming the oviraptorid was consuming the eggs.

There is one other possibility that cannot be tested because too much of the specimen was lost to erosion. The oviraptorid may have been laying eggs when it was buried by sand and dust. The fact that there is no evidence of more than a single layer of eggs supports this hypothesis.

The position of the hind foot in IVPP V9608 and the open centres of this and all other elongatoolitid nests suggest that oviraptorids laid eggs by standing on one spot and turning in a circle.

The arrangement of elongatoolithid eggs in nests has previously led to speculation about egg-laying behaviour. The type of nest that can now be associated with *Oviraptor* was often attributed to *Protoceratops* in the past (Brown and Schlaikjer 1940; Coombs 1989; Thulborn 1992). Complete nests can have more than 30 eggs arranged in a spiral around an open area (Sabath 1991; Mikhailov et al. 1994). The eggs were laid two at a time (Fig. 3), with the female turning in one direction. A nest of these eggs from Bayan Mandahu on display in the Inner Mongolia Museum (Hohhot) shows that the dinosaur turned clockwise as she laid the eggs. The first (lowest) layer is in a circle with a relatively wide radius, but the spiral tightened as additional layers of eggs were laid. The eggs of the lowest layer slope at a low angle away from the centre of the nest (Fig. 1A), but the angle increases in the higher levels. Presumably the decrease in radius and the change in angle reflect changes in orientation of the cloaca as the animal rose higher on her hind legs. The hands may have been used to scoop sand onto the eggs as they were laid. The base of the nest seems to have been at ground level, so the nest itself would have formed a mound (Sabath 1991; Thulborn 1992; Mikhailov et al. 1994).

This egg-laying scenario differs from the interpretation of Sabath (1991) and Mikhailov et al. (1994), who hypothesized that the eggs were laid with a more vertical orientation and were surrounded by vegetation. According to their interpretation, the eggs collapsed into a more horizontal position as the vegetation decomposed. Unfortunately, this hypothesis cannot explain the paired, spiral arrangement of the eggs within the nest and is therefore considered to be less reasonable than the scenario suggested by IVPP V9608.

Although it cannot be determined at this time which scenario is correct, the simplest, most logical explanation is that the *Oviraptor* was sitting on the nest when a sandstorm buried and smothered her (Fig. 4). If this is correct, then IVPP V9608 indicates that at least some theropod dinosaurs may have practised birdlike brooding behaviour.

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