Re-evaluation of the eggshell structure of eggs containing dinosaur embryos from the Lower Jurassic of South Africa

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Some of the oldest known dinosaur eggs with embryos were reported from Lower Jurassic sediments of South Africa’s Elliot Formation. The osteological data from the embryos suggest that the eggs were laid by dinosaurs, and the presence of skeletal materials of the sauropodomorph Massospondylus carinatus at the egg-producing locality prompted the tentative hypothesis of a prosauropod parentage for these eggs. Original analysis of eggshell microstructure, however, suggested that they shared crocodilian characteristics. Re-evaluation of eggshell microstructure suggests that the ‘crocodilian’ characteristics of the eggshell are instead artefacts of diagenesis. The available data from the eggs and embryos suggest that the clutch is probably dinosaurian in origin, but no particular dinosaurian lineage can be identified as the egg-layer.

The first clutch of Mesozoic eggs containing embryos was collected more than twenty years ago from the Rooidraai locality in Golden Gate Highlands Park, South Africa. The Elliot Formation crops out throughout the area, and although the sediments exposed at Rooidraai were once thought to be Late Triassic in age, they are now regarded as Early Jurassic. The Elliot Formation preserves a rich terrestrial vertebrate fauna, with the remains of the prosauropod dinosaur Massospondylus carinatus found to be relatively common at Rooidraai. The Rooidraai embryos were originally attributed to dinosaurs on the basis of cranial features of one of them. The eggs were later identified as ‘probably prosauropod’, but more interestingly, the eggshell structure was described as sharing characteristics with the eggs of crocodilians. The shells were described as consisting of ‘broadly wedge-shaped and ill-defined units’ and so were thought to be ‘seemingly more similar to crocodilian than to avian eggs’. The reconstruction provided by Grine and Kitching reaffirmed these statements. If the fossil eggs and embryos from Rooidraai are indeed attributable to prosauropod dinosaurs, they would fill an enormous gap in our knowledge of eggs, eggshell structure, and early development in dinosaurs, as ornithopod eggs and embryos are now known only from Late Cretaceous hadrosaurs, theropod eggs with embryos from Late Jurassic and Late Cretaceous avetheropods (sensu Padian et al.), and sauropodomorph eggs with embryos from Late Cretaceous titanosaurids.

It is now accepted that fossil eggshell structure has phylogenetic implications. For example, dinosaur eggshell can be distinguished from that of crocodilians by the presence of acicular (radial)-tabular wedges, and theropod eggshell from that of other dinosaurs by the presence of two structural zones. Therefore, the crocodilian-like units reported by Grine and Kitching in probable prosauropod eggshell contrasts with the current understanding of dinosaur eggshell structure and warrants further investigation of the Rooidraai eggs. Here we re-examine the structure of eggshell from the same egg that was described by Grine and Kitching in order to identify any diagnostic characteristics of the Rooidraai eggshell, and to determine whether these features are shared with the eggshells of the major archosaurian groups.

The original clutch of six consisted of what in life were probably spherical to subspherical eggs. Eggshell samples were removed from BP/1/5347b (from next to the sample taken by Grine and Kitching) and examined both in thin section and using scanning electron microscopy (SEM). The thickness of the eggshell ranges from 75–120 µm. The microscopic analyses reveal no recognizable shell units that comprise archosaurian eggshell. The irregular blocky and wedge-like structures within the shell (as shown in Fig. 1A,B) may represent recrystallized calcite. X-ray diffraction analysis confirmed that the shell consists of calcite.

The subspherical shape of the eggs is shared with those of titanosaurid sauropods and ornithopods among dinosaurs, whereas crocodilian and non-avian theropod eggs tend to be elongate. There appear to be no features, other than the shape and the calcite composition, that are diagnostic of the Rooidraai eggshell. The absence of shell units or zonation in the eggshell, which are present in the eggshell of all known archosaurian reptiles, implies that the Rooidraai eggs have been altered diagenetically. Furthermore, the preserved shell thickness is significantly less than what would be expected for a crocodilian or avian egg of an equivalent volume. Whether this represents

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Fig. 1. A. Scanning electron micrograph of eggshell (below black arrows) from BP/1/5347b; B, magnification of A showing blocky texture of the recrystallized eggshell.
the true shell thickness is uncertain, although the unexpected thinness could also be attributed to diagenesis12,13 rather than to resorption by the embryo, as suggested by Grine and Kitching.1

The reconstruction of the eggshell structure provided by Grine and Kitching (ref. 3, Fig. 24) illustrates a distinctly crocodilian morphology, with horizontal stratification and shell units composed of broad, divergent wedge-like structures. The microstructure of the eggshell shown in their SEM micrographs is less convincing, and appears to be more like the blocky and wedge-like structures shown in Fig. 1B, which we interpret as recrystallized calcite.

The poor preservation of BP/1/5347b makes it impossible to draw comparisons between the Rooidraai eggshell and that of other archosaurs. The interpreted spherical to subspherical shape of the eggs1 is suggestive of sauropodomorph or other archosaurs. The interpreted spherical to subspherical structure of the eggshell shown in Fig. 1B, which we interpret as recrystallized calcite.

The reconstruction of the eggshell structure provided by Grine and Kitching do indeed represent the original structure of the eggshell, wedges are found in crocodilian, theropod, sauropod and hadrosaur eggshell and are thus, at the very least, apomorphic for archosaurs. The "herringbone pattern" described as a shared characteristic between the Rooidraai and avian eggshells actually represents a cleavage pattern of calcite and is considered to have no taxonomic significance.11

In conclusion, the eggshell from Rooidraai provides little information of taxonomic value beyond the original identification by Kitching that the eggs are dinosaurian in origin. Careful preparation and study of the embryos preserved within the eggs will allow a more specific classification within the Dinosauria.

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Another, oldest member of the hominid family line

A mainly French team, led by Michel Brunet of the University of Poitiers, has reported the discovery of the most primitive hominid genus and species yet found (Brunet M. et al. A new hominin from the Upper Miocene of Chad, Central Africa. Nature 418, 145-151; 2002). Described as another turning point in our recognition of human origins, the fossil cranium, a lower jaw fragment and several teeth but with all postcranial material missing were located in the Toros Menalla fossiliferous area of the Djourab Desert of northern Chad, some 2500 km to the west of the East African Rift Valley that in its turn has provided so many specimens of early man. Brunet and his colleagues call this oldest and most primitive known member of the hominin clade Sahelanthropus tchadensis.

Absolute dating of Sahelanthropus is not possible because of the absence of associated material with the necessary isotopic or magnetic properties. Matching the fossil fauna found at the Toros Menalla site with its counterparts at two locations in Kenya, however, permitted the researchers to conclude that the Chad fossils are between 6 and 7 million years old (Vignaud P. et al. Geology and palaeontology of the Upper Miocene Toros Menalla hominid locality, Chad. Nature 418, 152-155; 2002). The faunal and sedimentological evidence at the find site fossil fish and plants compatible with a gallery forest bordering a lake suggests that Sahelanthropus lived close to a large body of water but not far from a sandy desert. ‘Our Chad ancestor displays various features such as the size and character of the teeth and the shape of the face that are similar to later hominids including Kenyanthropus and Homo. In other respects, however, including a small brain size, the fossil exhibits primitive features. Bernard Wood writes: ‘...from the back it looks like a chimpanzee, whereas from the front it could pass for a 1.75 million year old advanced australopith’. Brunet et al. note that the ‘observed mosaic of primitive and derived characters evident in Sahelanthropus indicates its phylogenetic position as a hominid close to the last common ancestors of humans and chimpanzees.’ This implies that the divergence of the chimpanzee and human lineages must have occurred before 6 Myr. It remains to be seen how closely related the Chad cranium is to that of another recently discovered hominin of comparable age - the 6 Myr old Orrorin from Kenya, for which unfortunately little craniodental material is known (Pickford M. and Senut B. ‘Millennium Ancestor’, a 6 million year old bipedal hominin from Kenya. S. Afr. J. Sci. 97, 22; 2001).