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## Minute theropod eggs and embryo from the Lower Cretaceous of Thailand and the dinosaur-bird transition

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**Abstract** We report on very small fossil eggs from the Lower Cretaceous of Thailand, one of them containing a theropod embryo, which display a remarkable mosaic of characters. While the surficial ornamentation is typical of non-avian saurischian dinosaurs, the three-layered prismatic structure of the eggshell is currently known only in extant and fossil eggs associated with birds. These eggs, about the size of a goldfinch's, mirror at the reproductive level the retention of small body size that was paramount in the transition from non-avian theropods to birds. The egg-layer may have been a small feathered theropod similar to those recently found in China.

### Introduction

Recent discoveries from the Lower Cretaceous of China coupled with phylogenetic studies predict that, besides the

acquisition of feathers, retention of a basal small body size was paramount in the transition from non-avian theropods to birds (Xu et al. 2000; Zhang et al. 2002; Xu et al. 2003; Zhou 2004). Hypothetically, the retention of a small body size in theropods should also have been mirrored at the reproductive level by equally small eggs. However, no theropod egg clearly associated with skeletal material displaying such a minute size had yet been discovered, all currently known such associations corresponding to fairly large-bodied terminal taxa (Norell et al. 2001; Varricchio et al. 2002; Makovicky and Grellet-Tinner 2000). We report here the discovery of extremely small eggs with a theropod embryo *in ovo* in the Lower Cretaceous of Thailand, that display a remarkable mosaic of avian and non-avian theropod eggshell characters, supporting the retention of a small body size at this critical evolutionary transition.

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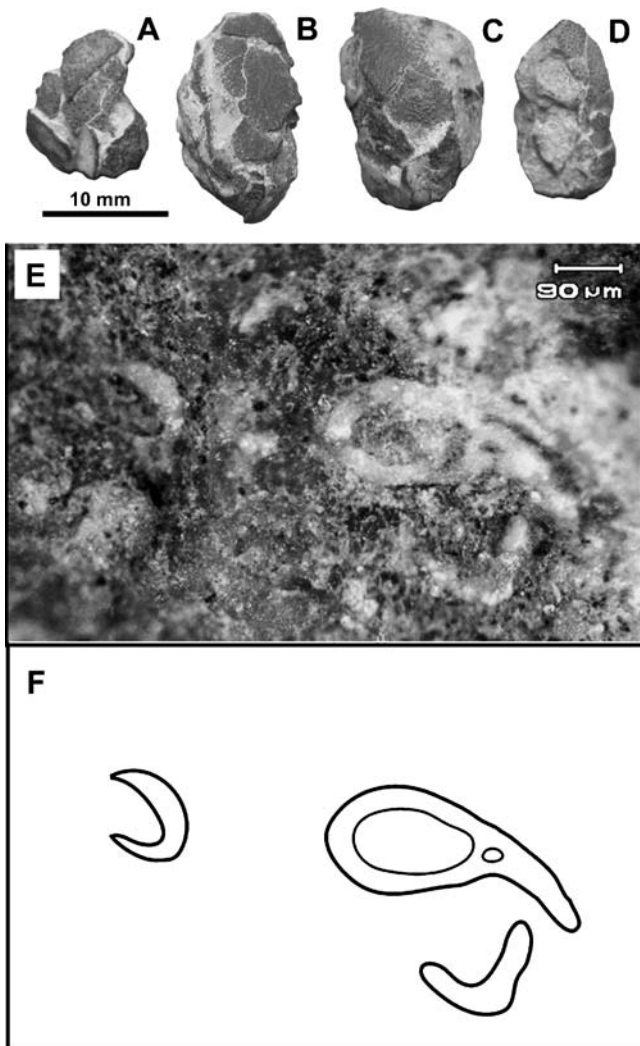
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## Description

Four fossil eggs (Sahat Sakhon Dinosaur Research Center of the Thai Department of Mineral Resources, SK1-1 to SK1-4) were found in 2002 and 2003 on an outcrop of red siltstones of the Early Cretaceous (Racey et al. 1996) Sao Khua Formation at Phu Phok, in Sakhon Nakhon Province, northeastern Thailand. As they were surface-collected, together with abundant bones and teeth of various fishes and tetrapods (Buffetaut et al. 2003) eroding out of the sediment, no evidence of nesting structure could be discovered, but they are likely from the same clutch, as they all come from the same small area and are morphologically identical (Fig. 1a). As shown by their cross-sections, these eggs

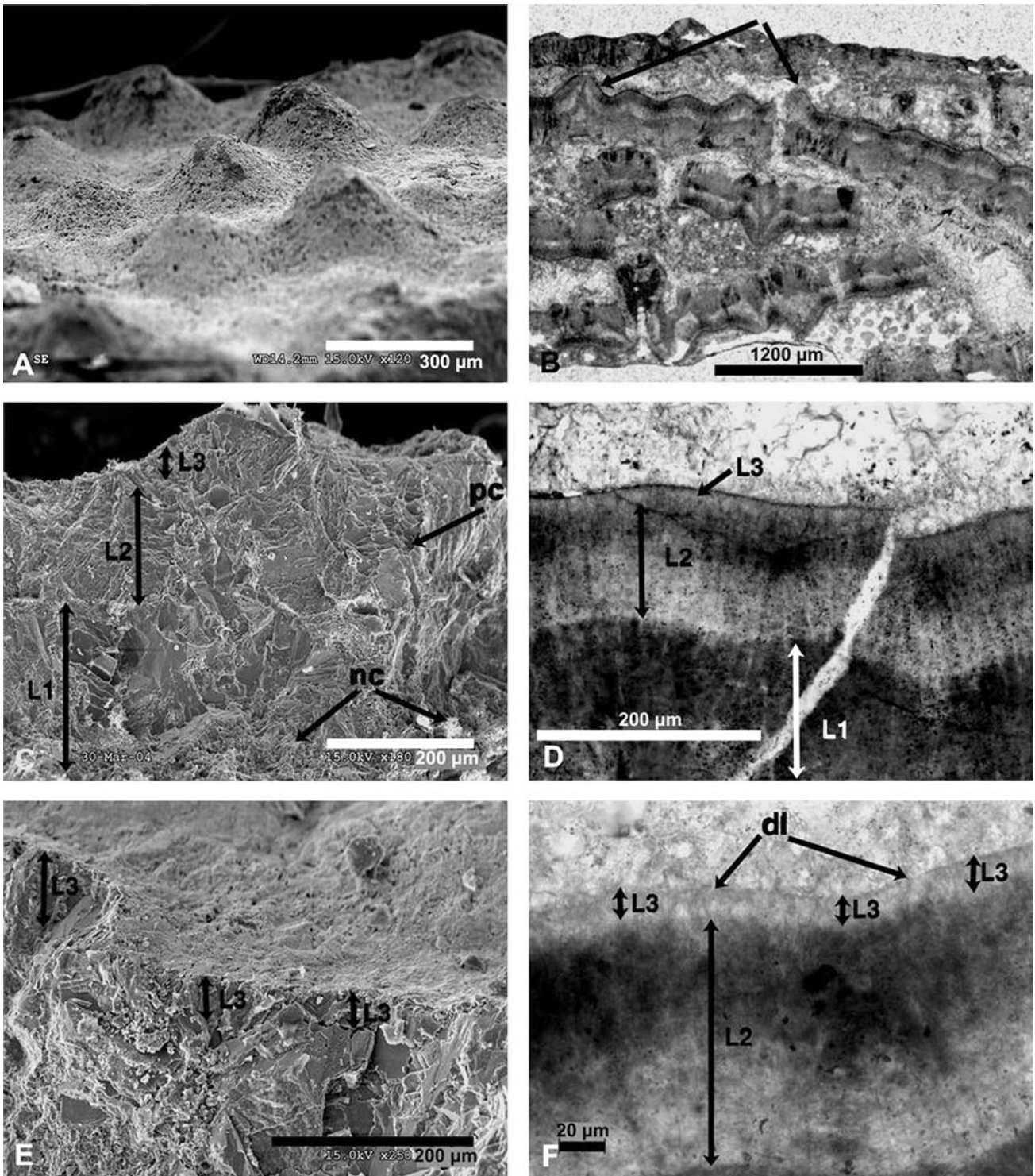


**Fig. 1** Eggs and embryo from the Sao Khua Formation (Early Cretaceous) at Phu Phok, Thailand. (A–D) Four eggs from the Early Cretaceous Sao Khua Formation at Phu Phok, northeastern Thailand (Sahatsakhon Dinosaur Research Centre, SK1-1 to SK1-4). The nodular surficial ornamentation of the eggshell is visible. Eggs SK1-1 (B) and SK1-2 (C) still partly show the original oval shape of the eggshell, whereas SK1-3 (A) and SK1-4 (D) are more incomplete and crushed. Scale bar: 10 mm. (E,F) Embryonic bones visible in cross-section inside egg SK1-1: photograph (E) and explanatory sketch (F)

have undergone crushing, but two of them are sufficiently well preserved to assess their original size and shape. The asymmetric, oval shape best compares with that of *Gallus gallus*, thus departing from the bauplan of other positively identified non-avian theropod eggs, and their dimensions of 18 mm (length) by 11 mm (equatorial diameter) with an estimated (Sabath 1991) volume of 1.15 cm<sup>3</sup> match those of *Carduelis carduelis* (Goldfinch) or *Parus major* (Great Tit). Sufficient eggshell fragments have slid on top of each other to indicate that cracking occurred after burial, and early lithification of the sediment apparently prevented extensive flattening of the shell (Mueller-Töwe 2002). Crushing was followed by calcite re-deposition, as attested by cathodoluminescence observations and in light microscopy by a faint black line outlining the outer surface of the shell and delimiting a calcitic epitaxial growth possibly of microbial origin.

The shell thickness, without the surficial ornamentation, averages 354 µm, a value very similar to that of the much more voluminous *Gallus gallus* eggs and 30% more than that of an ornithothoracine bird from the Late Cretaceous of Argentina (Schweitzer et al. 2002). The outer surface ornamentation is markedly nodular (Fig. 2), as in many non-avian dinosaur eggs (Mikhailov 1997; Grellet-Tinner 2004). The taller nodes average 183 µm, while the smaller and more numerous ones are twice smaller (92 µm). Pore-like fissures at the level of the taller nodes are likely the result of compression during a late diagenetic phase rather than being of biological origin. Although cathodoluminescence observations indicate one and possibly two diagenetic phases, the resulting ultrastructural replacement did not alter the eggshell microstructure and three prismatic structural layers are still visible in radial section (Fig. 2), a character presently known to be synapomorphic to Mesozoic Ornithothoraces and more modern birds (Grellet-Tinner 2000), as opposed to the two-layered condition seen in non-avian theropod eggs (Grellet-Tinner and Chiappe 2004). The innermost layer (1) is poorly preserved and only a few truncated crystals are visible at its base. The width and cross-section of some of these crystals show that they are not acicular but blade-like as in troodontids and known avialans. Layer 1 averages 207 µm and is thicker than layer 2 (136 µm), which is not a common feature in modern birds or in the known non-avian theropods but is shared with the Late Cretaceous egg from Neuquen, Argentina, which contains an ornithothoracine embryo (Schweitzer et al. 2002). Layer 3 is conspicuous and is 32 µm thick.

Fossil eggs can only be taxonomically identified with certainty by embryos *in ovo* or by the preservation of a gravid female dinosaur with shelled eggs in its reproductive system (Sato et al. 2005). Recent discoveries of a variety of fossil theropod eggs containing embryonic material, or in direct association with adult skeletons, have provided reliable documentation on the taxonomic significance of egg morphology and eggshell microstructure in allosauroids (Mateus et al. 1997), oviraptorosaurs (Norell et al. 2001), troodontids (Varricchio et al. 2002), dromaeosaurids (Makovicky and Grellet-Tinner 2000) and possibly therizinosaurs (Manning et al. 2000), as well as



**Fig. 2** Eggshell microstructure of the Phu Phok eggs. **A** SEM of the nodular surficial ornamentation. Note the bimodal distribution of the height of the nodes. This type of ornamentation has previously been reported in elongatoolithid eggs, a parataxonomic family that has been traditionally associated with non-avian theropods. **B** Thin section of an entire egg. Note the multilayered and multidirectional arrangement of the eggshell fragments indicative of a compression of the egg, as it was still whole. Black arrows point to some of the taller and rarer surficial nodes. **C** SEM picture of eggshell radial section. Note the distinct presence of three eggshell structural layers, a pore canal and eggshell units broken at their base, leaving only a

conical stub at their point of origination. **D** Thin section of eggshell radial section. As for the SEM picture, note the presence of the three structural eggshell layers and also of a black diagenetic line (dl) here interpreted as bacterially mediated micrite. **E** SEM picture showing eggshell structural layer 3 in more detail. **F** Thin section showing the difference of crystallographic orientation between L2 and L3. Note also the presence of the micrite diagenetic line on the outer eggshell surface. *Abbreviations:* L1, L2, L3: eggshell structural layers 1 to 3; pc, pore canal; nc, nucleation centres of eggshell units; dl, diagenetic line

enantiornithine birds (Schweitzer et al. 2002), although only a few specimens were diagnostic enough to allow identification at the generic or specific level. However, most of these non-avian specimens are associated with derived members of maniraptoran taxa (Novas and Pol 2005; Xu et al. 2002) and thus are biased toward relatively large body size, a remark which also applies to most known very early birds, including *Archaeopteryx* and *Confuciusornis* (Chiappe and Witmer 2002). Nevertheless, the maniraptorans *Citipati osmolskai* and *Troodon formosus*, for which egg/embryo associations allow precise identifications (Norell et al. 2002; Varricchio et al. 2002), already exhibit incipient avian reproductive traits, with their asymmetrical eggs indicating the presence of a proto air cell, and monoautochronic ovideposition. However, their eggs are at least 200 times more voluminous than the first well-attested ornithothoracine eggs (Schweitzer et al. 2002) and 400 times bigger than the Phu Phok eggs. Moreover, they do not exhibit either the typical avian oval shape (Grellet-Tinner 2000) associated with the asymmetry caused by the presence of a fully developed avian air cell, or the three-layered eggshell, both typical of known Mesozoic and modern bird eggs (Schweitzer et al. 2002; Grellet-Tinner 2000), and of the Phu Phok eggs.

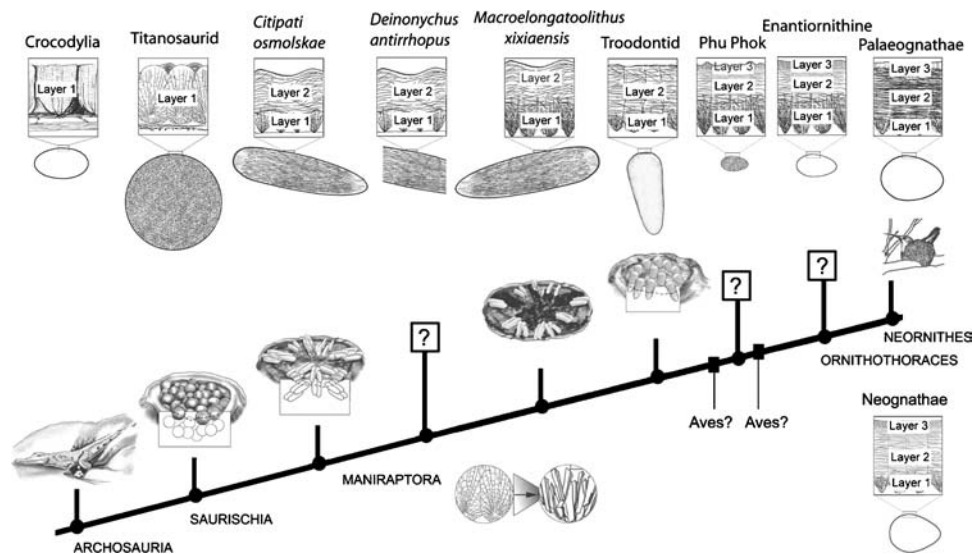
### Embryonic bones

Inside one of the eggs from Phu Phok (SK1-1), three small bones can be seen in section (Fig. 1b, c) in the hard partly

calcitic siltstone matrix, which fills the crushed shell. Further preparation of such extremely delicate fossils would be highly hazardous, and scanning attempts have not been successful because of the lack of density difference between the matrix and the embryonic bones. One of the bones just shows the outline of a hollow subcircular shaft. The other two appear to be associated in what may be roughly their original anatomical position. The larger bone shows a hollow oval shaft continued on one side by a long curved tapering process. In section, its greatest dimension is 0.37 mm (at the level of the process). The associated bone is subcrescentic in cross-section. The hollow nature of the bones is consistent with referral to Theropoda, but anatomical identification is difficult, which limits the significance of these embryonic remains for the interpretation of the eggs.

### Implications for the dinosaur-bird transition

Extant bird eggs are sequentially ovideposited from only one functioning ovary. They vary greatly in mass from 1500 to 0.86 g (Rahn et al. 1975) and in shape from pseudo-spherical to pear-shaped (Proctor and Lynch 1993), but still display the typical avian asymmetrical shape. Egg shape and size are the result of a compromise between environmental forces that have influenced the evolution of a species and the morphology of the hen pelvis (Carpenter 1999). As there is a relation between egg weight and adult body weight in birds (Rahn et al. 1975), and a



**Fig. 3** Character mapping and graphic representation of evolutionary trends in eggs and egg-laying from basal archosaurs (here represented by crocodylians) to modern birds. This diagramme is based on fossil specimens selected for a high degree of association between eggs and skeletons. From top to bottom: eggshell microstructure (showing an evolutionary increase in the number of structural layers), egg shape (from symmetrical to asymmetrical because of the presence of an aircell) and nesting structures (when known). Neornithes (modern birds) have a three-layered eggshell, which is prismatic in the Palaeognathae (above), while it is aprismatic (*sensu* Grellet-Tinner and Chiappe 2004) in the Neognathae (below). The

insert at bottom center shows the evolution of bladed calcite crystals from an acicular state during oogenesis in modern birds. The diagram reveals a pattern uniting nesting structures with egg shape, number of structural layers, and reproductive behaviours, from archaic and simple structures to more elaborate features. Within this pattern, the Phu Phok eggs appear to be more bird-like than those of troodontids, but less so than those of enantiornithine birds. With the information at hand, it is still impossible to decide whether they were laid by a non-avian theropod with advanced avian features or by a primitive bird more basal than enantiornithines

strong correlation between canal opening of a gravid female and maximum diameter of eggs, the very small size of the Phu Phok eggs indicates that they were laid by a very small animal. Its body size may have been comparable to that of a modern goldfinch if its reproductive system was similar to that of modern birds, or slightly larger if this theropod had retained two functioning ovaries (a primitive character), as the ratio of egg volume to adult weight would be smaller in this case. Among the known fossils from the Sao Khua Formation, a few bones of a small theropod were tentatively referred to a compsognathid (Buffetaut and Ingavat 1984), but this animal was too large to have laid such small eggs. However, very small maniraptorans similar to *Microraptor zhaoianus* (Xu et al. 2000) and *Epidendrosaurus ningchengensis* (Zhang et al. 2002), from Chinese formations that are roughly contemporaneous (Zhou et al. 2003) with the Sao Khua Formation, could easily have laid the Phu Phok eggs.

To date, the Early Cretaceous theropod eggs from Phu Phok, by their size and mosaic of eggshell structural characters, differ from any reported other eggs that have been taxonomically identified. Beyond the fact that they match the egg size of small extant passerine birds, they display avian characters in their avian oval shape and their eggshell microstructure. The eggshell has a prismatic structure with three structural layers, where layer 1 is considerably thicker than layer 2 (Schweitzer et al. 2002). Among theropod eggs clearly associated with skeletal remains, this combination of characters has hitherto been found only at the phylogenetic level of Ornithothoraces (Schweitzer et al. 2002; Grellet-Tinner 2004), yet the eggshell also retains a surficial ornamentation typical of non-avian saurischians (Grellet-Tinner 2004), not observed in known ornithothoracine eggs. By their oological characters, the Phu Phok eggs are thus phylogenetically more derived than those of oviraptorids (Norell et al. 2001) and troodontids (Varricchio et al. 2002), but not as avian as those of known ornithothoracine birds (Schweitzer et al. 2002; Grellet-Tinner 2004) (Fig. 3). By their mosaic of avian and non-avian characters, the Phu Phok eggs indicate either the acquisition of some oological avian characters prior to the theropod-bird transition if they belong to a non-avian coelurosaur, or the retention of some non-avian eggshell characters in primitive avialans if they were laid by a bird. Be that as it may, they advocate that the dinosaur-bird transition was characterized by mosaic evolution at the reproductive level. Furthermore, they advocate the retention of a body size similar to that of very small theropods during the dinosaur-bird transition, a hypothesis that is congruent with phylogenetic analyses and has been recently documented by the discovery of small feathered arboreal maniraptorans in the Chinese Early Cretaceous Lagerstätten.

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