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DAVID W. E. HONE & ERIC BUFFETAUT (Guest Editors)

Flugsaurier: pterosaur papers in honour of Peter Wellnhofer

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Umschlagbild: Reconstitution of a *Rhamphorhynchus* from the Upper Jurassic of Eichstätt, Bavaria. Concept: P. Wellnhofer; design: R. Liebreich; photograph and collage: M. Schellenberger, L. Geißler, BSPG Munich.

Pterosaur eggshell structure and its implications for pterosaur reproductive biology

By

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Abstract

The recent discovery of pterosaur eggs containing embryos has provided important evidence regarding the structure of pterosaur eggshell. Two eggs, from the same locality and horizon in China, have a shell that appears to have been parchment-like and pliable with no detectable mineralised calcareous component. A third egg, from Argentina, preserves evidence of a single layer of calcite. This is only 30 microns in thickness, however, and thus very much thinner than mineralised layers reported in turtles that lay pliable-shelled eggs. All three examples resemble the parchment-shelled eggs of squamate reptiles, but exhibit variation in the degree of calcification of the outer surface, which also varies between squamate species. It seems unlikely that the parchment-shelled eggs of pterosaurs were incubated by direct contact with the body of a parent because of the risk of crushing the egg. Moreover, the likely high permeability of a parchment-like eggshell would have required burial in a very humid environment, such as sand, soil, or perhaps in mounds of rotting vegetation, to prevent desiccation during incubation. Consequently, pterosaur eggs are likely to have developed in a thermal environment close to ambient temperatures and probably subject to some temperature variation.

Key words: Argentina, China, egg, eggshell, embryo, incubation, pterosaur

Zusammenfassung

Die neueste Entdeckung von Flugsauriereiern, einschließlich Embryos, haben uns wichtige Hinweise über die Struktur von Flugsauriereischalen geliefert. Zwei solche Eier aus China, welche am gleichen Fundort und in der gleichen Schicht gefunden worden sind, besitzen eine biegsame, pergamentartige Schale ohne sichtbare mineralisierte Komponenten. Ein drittes Ei aus Argentinien weist ein dünne Schicht Calcit auf. Diese ist lediglich 30 µm dick und damit viel dünner als die mineralisierten Schichten, wie sie bei Meeresschildkröten gesichtet wurden, die biegsame Eierschalen legen. Alle drei Beispiele ähneln den pergamentschaligen Eiern anderer Schuppenkriechtiere, zeigen allerdings Unterschiede in der Verkalkungsrate der äußeren Hülle, die auch unter Schuppenkriechtierarten variiert. Es ist unwahrscheinlich, dass die pergamentschaligen Eier der Flugsaurier durch direkten Kontakt mit den Körpern der Eltern gebrütet worden sind, da das Risiko einer Beschädigung der Eier besteht. Aufgrund der hohen Permeabilität eines pergamentartigen Eies, wäre ein Vergraben in einer sehr feuchten Umgebung, wie Sand, Erde oder vielleicht in Laub nötig gewesen, um ein Austrocknen während der Brutzeit zu verhindern. Folglich liegt die Vermutung nahe, dass sich die Flugsauriereier in einer thermischen Umgebung entwickelt haben; nahe der Umgebungstemperatur und wahrscheinlich anfällig gegenüber Temperaturschwankungen.

Schlüsselwörter: Argentinien, China, Ei, Eierschale, Embryo, Inkubation, Pterosaurier

1. Introduction

Pterosaurs are an enigmatic group of extinct flying reptiles with a fossil record that extends from the Late Triassic to the end of the Cretaceous (e.g. WELLNHOFER 1991; BENNETT 1999; NAISH & MARTILL 2003; UNWIN 2005). Many aspects of the palaeobiology of this group remain poorly understood, either because of the patchy and incomplete nature of the pterosaur fossil record, or because they are not preserved at all. Such was the case, until recently, for pterosaur reproductive biology, which in the absence of any fossil evidence for pre-hatching stages was confined to speculation, much of it drawing upon ill-founded analogies with birds (e.g. HALSTEAD & HALSTEAD 1985).

In 2004 descriptions of three pterosaur eggs, each with an embryo, were published in the science journal *Nature*. The first of these reported on a well preserved egg, consisting of part and counterpart, measuring 53 by 41 mm (estimated mass of 50 g based on formula for symmetrical elongated crocodilian

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eggs [DEEMING & FERGUSON 1990]) and containing a complete, naturally articulated embryo (WANG & ZHOU 2004; Figs 1, 2). The fossil was found at the locality of Jingangshan in Liaoning Province, China, in lacustrine shales of the Jingangshan beds, which lie within the upper part of the Yixian Formation (WANG & ZHOU 2003) dated at approximately 121 mya (e.g. SMITH et al. 1995; JI et al. 2004) and thus Lower Cretaceous (Aptian) in age (GRADSTEIN et al. 2005). The same locality has yielded several other vertebrates (e.g. ZHANG & JIN 2003; ZHANG & ZHOU 2004; EVANS & WANG 2005; UNWIN et al. 2006) including an avian embryo (ZHOU & ZHANG 2004). Anatomical features, including details of the dentition and the shape of the humerus, and proportions of limb elements, in particular the remarkably short metatarsus, permit IVPP V13758 to be assigned to the Ornithocheiridae (WANG & ZHOU 2004; UNWIN 2005; UNWIN et al. 2006: fig. 5). WANG & ZHOU (2004) and UNWIN et al. (2006) tentatively compared the embryo with *Haopterus gracilis* WANG & LÜ, 2001, an ornithocheirid from the Yixian Formation, but work underway by DMU suggests greater similarity to *Yixianopterus jingangshanensis* LÜ et al., 2006, known from a single incomplete skull and skeleton (JZMP-V-12) found at the same locality and in the same rock sequence as IVPP V13758.

The second pterosaur egg and embryo to be described, JZMP 03-03-2 (JI et al. 2004; UNWIN et al. 2006) was recovered from the same locality and horizon as IVPP V13758 (Figs 1, 3). The eggshell in this specimen, which measures 63.7 by 36.4 mm (estimated mass of 47 g) is, if anything, even better preserved than that of the first egg. Initially, it appeared that the embryo, although originally complete, was more disarticulated than that of IVPP V13758 and possibly at an earlier stage of development (JI et al. 2004; UNWIN et al. 2006). However, restudy of the specimen by one of us (DMU) suggested an alternative interpretation for some limb bones, following on from which it would seem that the embryo was similarly articulated and positioned to that of IVPP V13758. JI et al. (2004) compared JZMP 03-03-2 to *Beipiaopterus chenianus* LÜ, 2003, also from the Yixian Formation, but did not formally assign the embryo to this taxon (contra GRELLET-TINNER et al. 2007). More recently, UNWIN et al. 2006 argued that JZMP 03-03-2 should be assigned to the Ornithocheiridae and possibly to the same taxon as IVPP V13758, which, as mentioned above, is most likely to be *Yixianopterus jingangshanensis*.

A third pterosaur egg with embryo, MHIN-UNSL-GEO V246, was reported by CHIAPPE et al. (2004) from approximately 100 million year old sediments of the Lower Cretaceous (Albian) Lagarcito Formation at Loma del *Pterodaustro*, San Luis Province, central Argentina (Figs 1, 4). At approximately 60 mm in length and 22 mm in width (estimated mass of 16 g) the egg is of similar length to the Chinese specimens, but much narrower and with a much smaller volume (UNWIN et al. 2006). The embryo, uncontroversially identified as *Pterodaustro guinazui* (CHIAPPE et al. 2004; UNWIN et al. 2006: fig. 9; GRELLET-TINNER et al. 2007), is complete, but not quite so well articulated as IVPP V13758, although the pose is remarkably similar (Fig. 1).

Collectively, these three fossils have already provided key insights into pterosaur reproductive biology. For example, UNWIN et al. (2006) used these fossils to demonstrate that some and probably all pterosaurs were oviparous, resolving a long-standing mystery regarding oviparity or viviparity in pterosaurs (WELLNHOFER 1991; UNWIN 2005). In this paper we focus on another significant feature of these fossils, the nature of the eggshell, only brief details of which have appeared so
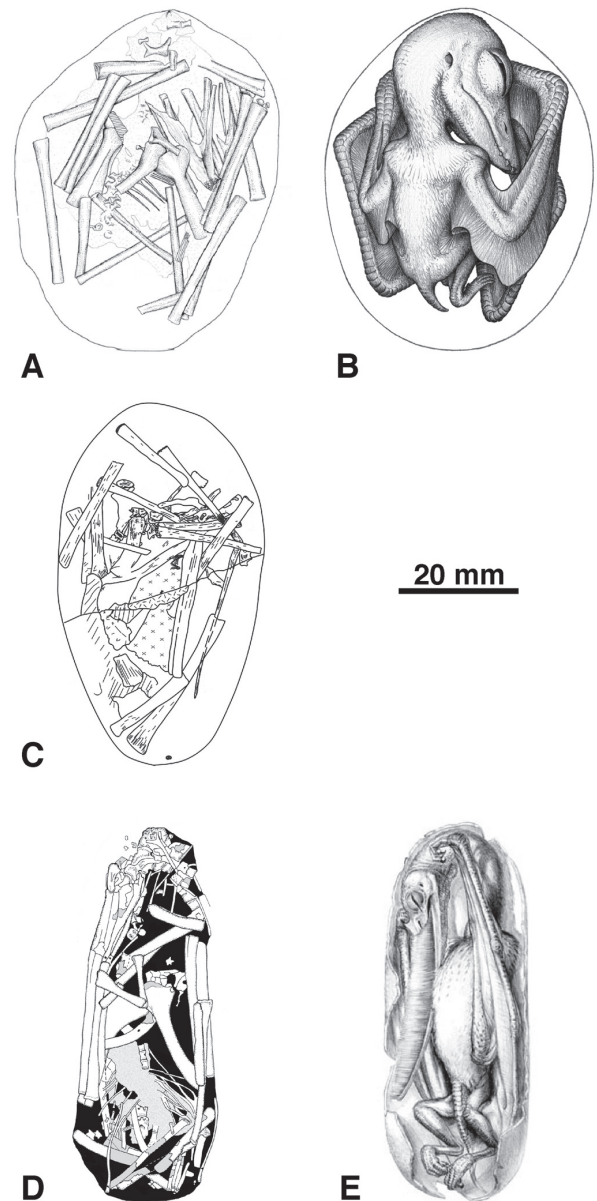
Figure 1: Pterosaur eggs, embryos and restorations of the embryos. **a**: IVPP V13758, Yixian Formation, Lower Cretaceous (Aptian), Jingangshan, Liaoning Province, China. Estimated wingspan of embryo = 250 mm (UNWIN et al. 2006). **b**: restoration of IVPP V13758. **c**: JZMP 03-03-2, Yixian Formation, Lower Cretaceous (Aptian), Jingangshan, Liaoning Province, China. Estimated wingspan of embryo = 295 mm. **d**: MHIN-UNSL-GEO V246, Lagarcito Formation (Lower Cretaceous, Albian), Loma del *Pterodaustro*, San Luis Province, Argentina. Estimated wingspan of embryo = 270 mm (CHIAPPE et al. 2004). **e**: Restoration of MHIN-UNSL-GEO V246. **a**, redrawn with permission from WANG and ZHOU 2004, **b**, from UNWIN et al. 2006, **c**, redrawn with permission from JI et al. 2004, **d** and **e**, redrawn with permission from CHIAPPE et al. 2004.

far (Chiappe et al. 2004; Ji et al. 2004; Wang & Zhou 2004; Unwin et al. 2006; Grellet-Tinner et al. 2007).

Abbreviations: IVPP, Institute for Vertebrate Paleontology and Paleoanthropology, Beijing, China; JZMP, Jinzhou Museum of Paleontology, Jinzhou, Liaoning Province, China; MHIN-UNSL-GEO, Museo de Historia Natural de la Universidad Nacional de San Luis, San Luis, Argentina.

2. Eggshell structure in pterosaurs

2.1 IVPP V13758

The reddish brown colour of the well-preserved eggshell clearly distinguishes it from the light yellow-grey of the background sediment upon which it lies (Fig. 2a). The seemingly smooth texture of the shell also contrasts strongly with the rougher texture of the background sediment although, under the microscope, a fine, even granular texture, described by Wang & Zhou (2004) as a 'papilla-like ornamentation' and
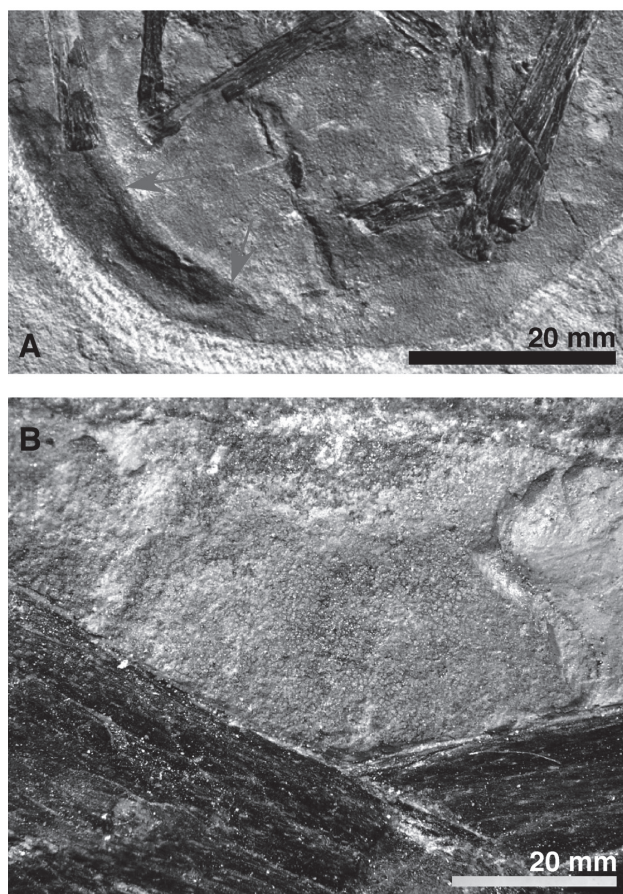
Figure 2: Details of the eggshell of IVPP V13758. **a**: low ridge (arrowed) representing a fold or crease in the shell in the region of the lower terminus of the egg preserved on the main slab. **b**: part of the eggshell preserved on the main slab, illustrating the fine granular texture evident using a low power binocular microscope. Reproduced with permission from Wang Xiaolin and Zhou Zhonghe, IVPP, Beijing, China.

consisting of tiny closely packed tubercles is apparent (Fig. 2b). The free edge of the eggshell (corresponding to its original external surface) can be traced around the entire margin of the egg and it is easy to establish that the eggshell is continuous across the entire fossil.

Several lines of evidence suggest that the original shell is preserved, rather than an impression. A thin, but distinct 'body' to the eggshell can be observed at various locations, for example around the edges of the egg, where fragments of the shell have been lost. In addition, skeletal remains of the embryo generally appear to lie on top of the shell, but there are several examples in which the reverse is seen, wherein bones are overlain by the shell. This indicates that there are two layers of eggshell present in the fossil, as would be expected in a highly compressed specimen where the original shell is preserved. This idea is reinforced by the observation that, at several points, where fragments of one layer have lifted away, a second underlying layer (of the same colour) rather than the sediment, is exposed.

The exact processes by which the eggshell was fossilised are still unclear. Two possible pathways are outlined here, but, undoubtedly, they are not the only solutions. Firstly, mineralisation of the shell fairly soon after burial, possibly facilitated and mediated by partial breakdown of the organic component of the shell. Secondly, wholesale replacement of the shell by, for example, clay minerals after its removal following decay and dissolution.

Two features are of particular importance. First, several low, rounded ridges and ripples are evident at various points on both the part (Fig. 2a) and counterpart. Generally, these features, which correspond to folds or creases in the original shell, are relatively smooth and even, and they do not show any evidence of cracking, fracturing, or crazing as might be expected if the shell were composed of, or contained, a hard calcareous layer. Moreover, such a texture is not evident anywhere else in this specimen, even adjacent to those regions such as the free edges that are likely to have experienced the greatest degree of compression.

It could be argued that a hard calcareous layer was originally present, but was lost through chemical dissolution at some point during diagenesis. Two lines of evidence count against this. First, there is no evidence of such erosion, which is likely to have left pitting, both on the visible surfaces of the eggshell and also on the skeletal remains. Second, calcified structures (bones) are well preserved in the fossil at hand and fossils of molluscs with calcareous shells have also been reported from the same beds at the Jingangshan locality (Ji et al. 2004).

In sum, the features of this fossil provide strong support for the idea that this egg had a relatively soft, parchment-like eggshell. Comparison with eggshell structure of extant oviparous groups suggests that greatest similarity is to be found with the parchment shelled eggs of squamates (Schleich & Kästle 1988; Packard & Demarco 1991; Fig. 5g) although not gekkos, which have a calcareous external layer (Fig. 5e).
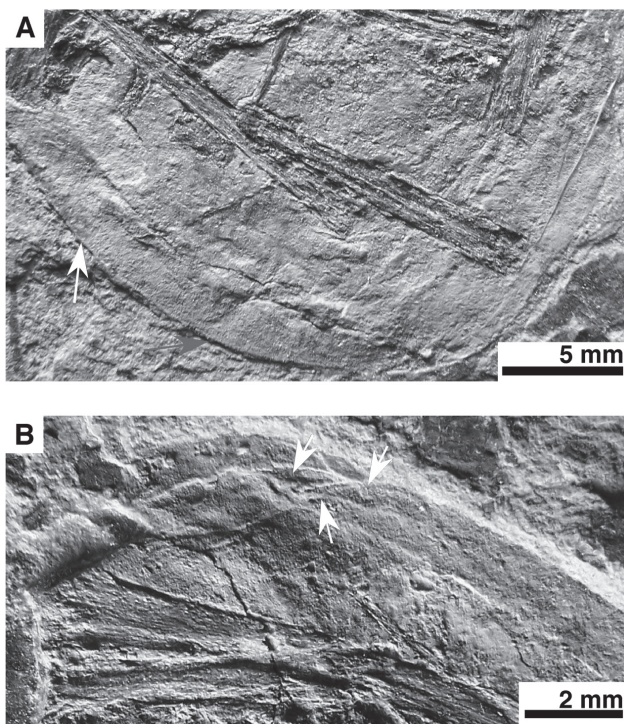
2.2 JZMP 03-03-2

The preservation of the eggshell in this fossil compares closely to that of IVPP V13758 although the specimen, in particular the bones, appears to be a little more heavily com-

pressed. The shell is picked out by a dirty, pinkish brown to dark brown colour, which contrasts with the light grey of the underlying sediment. As for IVPP V13758, to the naked eye, the shell is distinguished by its smooth appearance compared to the sediment upon which it lies (Fig. 3a). At higher magnifications, however, the shell exhibits a fine granular texture as reported for IVPP V13758. The edge of the shell can be easily traced around almost the entire circumference of the egg on the main slab and around the non-fractured part of the egg on the counterslab. The eggshell is continuous across the entire egg except where obscured by overlying bones.

Preservation of the eggshell appears to be identical to that for IVPP V13758, with evidence, for example, where the shell has lifted away from the sediment (visible in the left lower side of Figure 3a), that the eggshell is preserved as a body fossil rather than an impression. Ji et al. (2004) estimate the thickness of the preserved eggshell at 0.25 mm and note that it does not appear to contain laminations or other structures. Presumably, the mode of preservation of the eggshell, mineralisation of existing structures, or replacement by clay minerals, followed a similar pathway to that of IVPP V13758.

The surface of the eggshell bears numerous low ridges, ripples, grooves and edges that represent folds, creases and wrinkles in the original eggshell. A well preserved example is evident adjacent to wing-phalanx one (Fig. 3b). Here, several overlapping creases or folds indicate a region where the eggshell appears to have been slightly distorted, possibly by compressi-

Figure 3: Details of the eggshell of JZMP 03-03-2. **a**: external margin of eggshell (arrowed) bounding lower terminus of egg preserved on the main slab and illustrating that the shell is preserved as a body fossil rather than as an impression. **b**: several overlapping ridges (arrowed) representing folds, or creases, in the eggshell preserved on the counterslab. Reproduced with permission from Jinzhou Museum of Paleontology, Jinzhou, Liaoning Province, China.

on of the egg or possibly through crumpling inward of the shell at this point. Again, there is no evidence of cracking, fracturing or crazing even in regions where the shell has been distorted or suffered the greatest degree of compression around the free edges (Ji et al. 2004). Nor are there any signs of pitting or other evidence to suggest that a calcareous layer was originally present, but subsequently removed by dissolution.

The eggshell of JZMP 03-03-2 would therefore also appear to have been relatively soft and pliable, or parchment-like (Grellet-Tinner et al. 2007) and composed of protein fibres, a conclusion also reached by Ji et al. (2004) who described the shell as "soft and leathery". Again, among extant oviparous vertebrates, this type of eggshell is closest in terms of structural similarity to the parchment-shelled eggs of squamates (Fig. 5g).

2.3 MHIN-UNSL-GEO V246

In this case the eggshell is preserved rather differently from the two eggs described above and consists solely of thin patches of calcareous material (Fig. 4). According to Grellet-Tinner et al. (2007) this fossil may have suffered some diagenetic dissolution as evidenced by the rough, weathered appearance of the outer surface of the eggshell although the extent of the remaining structures show that this was limited.

Scanning electron microscopy reported by Chiappe et al. (2004) and Grellet-Tinner et al. (2007) has revealed that this calcareous layer is only 30 μm in thickness and formed a monolayered eggshell composed of calcium carbonate crystals (Fig. 4b,c). The crystals are blade-like and grouped in V-shaped units that radiate out from a central point at their base. Even assuming some loss of shell due to dissolution, the reported thickness of the remaining eggshell is remarkably thin compared to that of hard-shelled eggs of comparable size of other oviparous vertebrates including turtles, geckoes, crocodilians and birds. It seems likely therefore that for purely mechanical reasons, the calcareous layer was underlain by a protein fibre shell that helped support and maintain the structural integrity of the eggshell.

Grellet-Tinner et al. (2007) argued that the *Pterodaustro* eggshell compared most closely to that of crocodilians, especially alligators. However, there are important differences, most notably in the relative thinness of the eggshell of *Pterodaustro* compared to that of *Alligator mississippiensis*. The latter has eggs measuring 43 by 74 mm (egg mass = 84 g), but with an eggshell that is up to 1 mm thick (Ferguson 1985), some thirty times thicker than the calcareous layer of the *Pterodaustro* egg. Neither does the structure of the *Pterodaustro* eggshell resemble the aragonitic shell units of pliable-shelled turtle eggs (see Schleich & Kästle 1988; Packard & Demarco 1991; Fig. 5a, b), but it is comparable to that observed on some squamate eggs. Whilst parchment-like squamate eggshells are comprised mainly of proteinaceous fibres there is a variable amount of calcium carbonate deposited on the outer surface according to species. In the lizard *Anolis carolinensis*, for example, the calcareous layer is 50 μm thick and in *Agama* species the layer is up to 20 μm thick (Schleich & Kästle 1988). Moreover, deposition of the calcium carbonate is not uniform and forms plaques on the outer surface (Schleich & Kästle 1988; Packard & Demarco 1991).
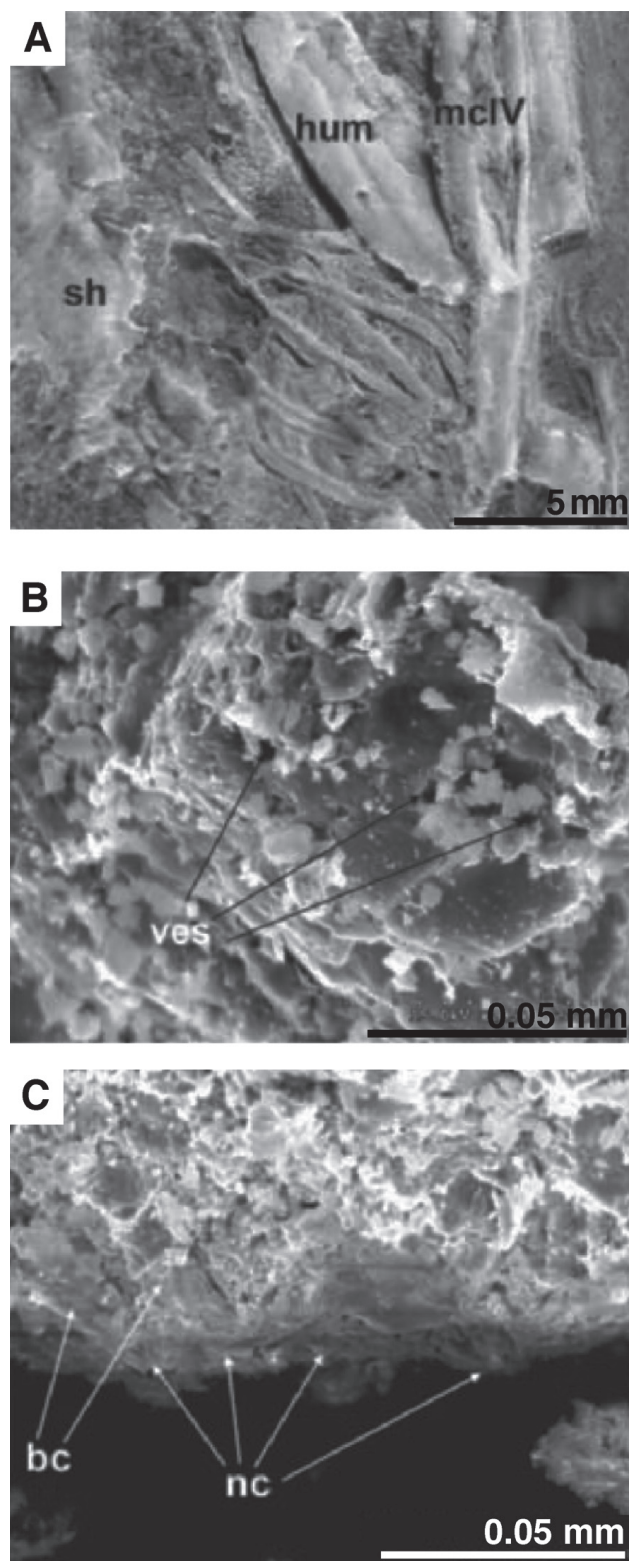
Figure 4: Details of the eggshell of MHIN-UNSL-GEO V246. **a:** patches of eggshell overlying remains of the ribs. **b:** SEM of eggshell in radial section illustrating "vesicles". **c:** SEM of eggshell in radial section illustrating cores and blade-like crystals. **a-c** reproduced with permission from Luis Chiappe. Abbreviations: bc, bladed crystals; hum, humerus; mcIV, fourth metacarpal; nc, nucleation centres; sh, shell; ves, vesicles .

Squamate eggshells form as calcium carbonate crystals from relatively deep in the fibrous shell membrane and so the individual fibres are embedded in the crystals. The "vesicles" described for the *Pterodaustro* egg (Chiappe et al. 2004; Grellet-Tinner et al. 2007) may represent the holes left by such fibres as they decomposed prior to preservation. This, together with the thinness of the calcareous layer on a relatively large egg (*Anolis* eggs weigh 0.25 g [Deeming & Thompson 1991]) suggests that the *Pterodaustro* specimen represents a variant on the parchment-shelled eggs of squamates.

3. Discussion

3.1 Variability in pterosaur eggshell structure

That the eggs of, effectively, two species of pterosaur appear to exhibit quite different eggshell structure may seem surprising. Moreover, as detailed above, this disparity can almost certainly be attributed to real differences in eggshell structure rather than differences that may be due to preservation, such as the loss through dissolution of an outer calcareous layer in the case of the eggs from China. However, such variation need not occasion any surprise since it is well known in several non-avian diapsid groups including chelonians and particularly squamates. Moreover, all species belonging to these groups bury their eggs (with the exception of rigid-shelled gecko eggs [Deeming & Thompson 1991]), lending further weight to the idea that pterosaurs also utilised this incubation strategy. Interestingly, despite far outweighing all these groups in terms of species diversity, extant birds exhibit a remarkable degree of homogeneity in eggshell structure (Board & Sparks 1991), which presumably is imposed upon them by their open-nest incubation strategy.

It is possible that the variability exhibited by pterosaurs represents clade specific adaptations to differing nesting conditions. For instance, the eggs of ornithocheirids may have been laid in nests where the risk of invertebrate predation was lower than the nests of *Pterodaustro*, which invested its eggs with a thicker calcitic layer (see Packard & Packard 1980). Parchment-shelled squamate eggs absorb water during incubation (see Deeming & Birchard 2006) and so the thicker calcareous layer may have helped maintain shell integrity in of *Pterodaustro*. Of course, it is possible that local climatic conditions were important, but these have yet to be established for the environments in which these eggs were laid, buried, exhumed and finally reburied but, should they eventually prove determinable, might help to verify this conjecture.

3.2 Open nest versus burial

Extant oviparous vertebrates exhibit two distinct behavioural modes with regard to the incubation of eggs after oviposition. Extant birds are unusual (compared to other oviparous groups) in that eggs are incubated in open nests (there are exceptions; see Booth & Thompson 1991) and depend upon direct contact with a parent to maintain them at a relatively constant temperature that is (usually) higher than the ambient temperature. Reflecting the mechanical and physical demands of these circumstances, extant birds have hard-shelled eggs

that, moreover, exhibit relatively low vapour conductance values that help to prevent desiccation (e.g. DEEMING 2006). By contrast, most squamates and all chelonians and crocodilians bury their eggs either in vegetation, soil, or in burrows. This helps protect them from predation and, even more importantly, reduces the risk of desiccation, due to the highly porous nature of their eggshells. Parchment-shelled eggs of squamates have water vapour conductance values 200 times that observed in bird eggs of a comparable size (DEEMING & THOMPSON 1991). Pliable-shelled turtle eggs have conductance values 50–80 times higher and even rigid-shelled turtle and crocodilian eggs are 4–10 times more porous than bird eggs of an equivalent size (DEEMING & THOMPSON 1991). Such conductance values mean that unless reptile eggs are in contact with a moist substrate in a humid nest chamber they will lose water (see PACKARD 1991; ACKERMAN & LOTT 2004).

Several lines of evidence suggest that pterosaurs buried their eggs rather than incubating them in open nests. From a purely mechanical point of view it seems highly unlikely that the parchment-shelled eggs found at Jingangshan would have been able to withstand even small loads without becoming distorted or crushed. Consequently, incubation, in a manner analogous to that of birds, can be firmly excluded. The *Pterodaustro* egg appears to have been hard-shelled. However, as noted above, the shell is remarkably thin (as little as only one tenth the thickness of the eggshell in an avian egg of similar dimensions) and it is doubtful that it too could support loads likely to be sustained by the egg during avian-like contact incubation.

The parchment-like morphology of the eggshell correlates well with high vapour conductance values in extant reptiles (and presumably Monotremes, although conductance values have yet to be determined for their eggs). As the calcareous layer becomes more substantial the conductance values drop, but they never reach those exhibited by birds (DEEMING & THOMPSON 1991). These differences in conductance and their relationship with nest type allow us to predict the nesting environment based on eggshell structure and calculation of water vapour conductance. Hence, in dinosaur eggs water vapour conductance values are all high relative to birds (even for non-avian theropods) and so the eggs had to be buried (DEEMING 2006). Structurally, the poorly (or non-) calcified parchment-like eggs of pterosaurs strongly suggest a very high conductance to gases providing clear support for the idea of burial. With a thin calcareous layer the *Pterodaustro* egg may have had lower vapour conductance values than the ornithocheirid eggs. However, these are still likely to have been very high compared to those of birds and even the rigid-shelled eggs of crocodilians and some chelonians.

The nature of the three pterosaur eggs offers only structural comparison and does not allow functional comparison such as calculation of water vapour conductance as a measure of eggshell porosity (e.g. DEEMING 2006). This did not prevent GRELLET-TINNER et al. (2007) from attempting to estimate vapour conductance values for pterosaur eggs by reconstruc-
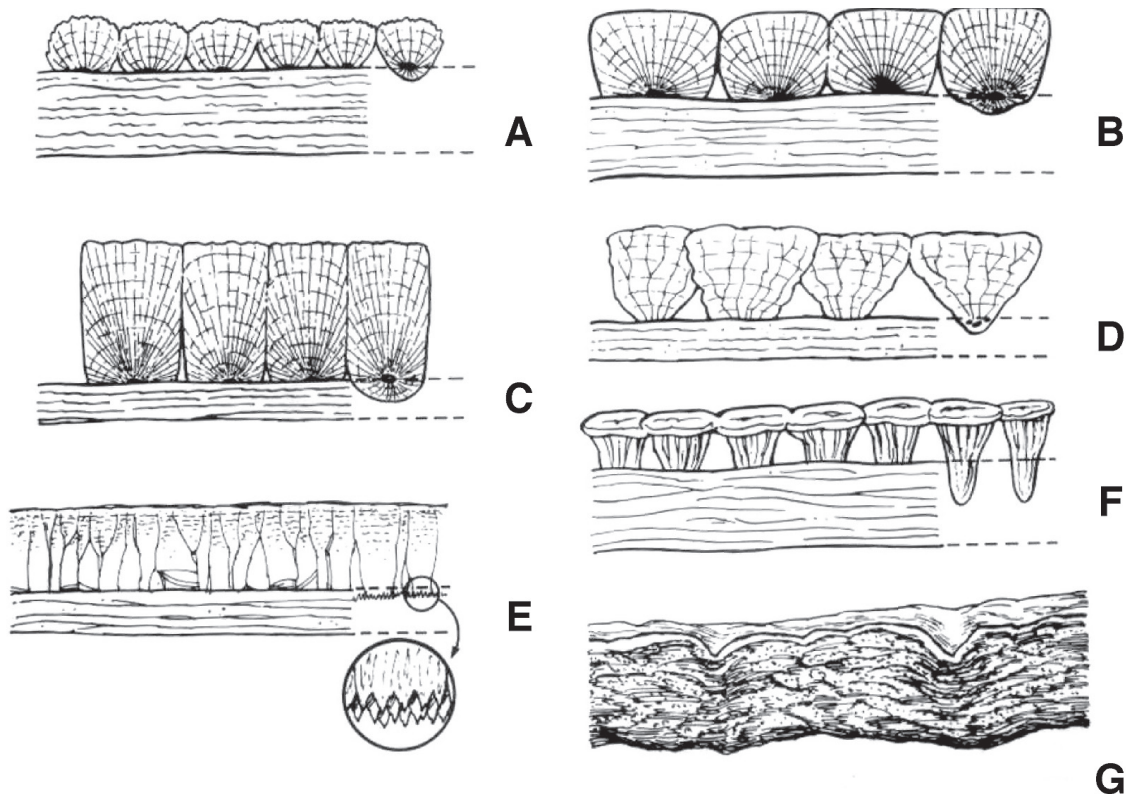
Figure 5: Highly schematic diagrams of reptilian eggshells in cross-section. **a**: pliable-shelled egg of a sea turtle. **b**: pliable-shelled egg of a freshwater turtle. **c**: Rigid-shelled egg of a tortoise. **d**: rigid-shelled egg of a crocodilian. **e**: rigid-shelled egg of a gecko. **f**: parchment-shelled egg of a tuatara. **g**: parchment-shelled egg of oviparous lizard or snake. From PACKARD & DEMARCO (1991), reproduced with permission from Cambridge University Press.

ting their likely volume and fresh egg masses from data collected by HOYT (1976, 1979) for similar sized eggs of birds. Then, using avian regression equations published by AR et al. (1974), they calculated from these volume/mass estimates that if pterosaurs had laid their eggs in open nests they would be predicted to have a rigid shell around 300 μm in thickness for the ornithocheirid eggs and approximately 200 μm for *Pterodaustro*. The calcareous component of the eggshell of the latter is some eight times thinner than the predicted value, while the ornithocheirid eggs lack any calcareous component. This implies much higher vapour conductance values than for eggs laid in open nests, estimated by GRELLET-TINNER et al. (2007) to be 700 times that of birds and 250 times greater than that for crocodilians, in the case of the ornithocheirid egg, and five times higher than typical birds for the *Pterodaustro* egg. However, it is important to realise that this conclusion lacks a strong scientific basis. Firstly, conductance values are not solely determined by shell thickness, but are highly dependent on the thickness and structure of the calcareous layer. A *Python molurus* egg weighs 230 g and has a parchment-like shell with a thickness of 225 μm including an external calcareous deposit of more than 50 μm (SCHLEICH & KÄSTLE 1988), yet its shell conductance is 8,300 mg H_2O per day per Torr, some 36 times greater than a bird egg of equivalent mass (DEEMING & THOMPSON 1991), which would have a shell thickness of 600 μm (AR et al. 1974). By contrast to the calculated values for water vapour conductance of dinosaur eggs by DEEMING (2006), the method employed by GRELLET-TINNER et al. (2007) provides no evident basis for suggesting that the conductance value of the *Pterodaustro* egg would be comparable to that of an extant crocodilian egg.

In summary, there is strong evidence to suggest that, like many other non-avian diapsids (ACKERMAN & LOTT 2004), pterosaurs buried their eggs in mounds of vegetation, or in soil, or possibly in burrows, and that they did this, primarily, to prevent them from desiccating. Other studies (JI et al. 2004; CHIAPPE et al. 2004; UNWIN 2005: UNWIN et al. 2006; GRELLET TINNER et al. 2007) have reached the same conclusion.

3.3 Implications of burial for pterosaur eggs

Aside from obvious benefits, such as concealment from predators, burial may have been advantageous to pterosaurs in several other ways. Relatively high vapour conductance values would have permitted eggs to take up water during incubation (PACKARD 1991; BELINSKY et al. 2004). This has an important implication for pterosaurs: they would not have needed to provision their eggs with a high albumen content to supply the embryo with water during incubation as is the case in rigid-shelled chelonian and crocodilian eggs (BELINKSY et al. 2004). Consequently, this would have reduced the time needed to produce an egg and permitted the production of relatively small eggs whose weight would have been further reduced by the lack of a thick calcareous eggshell. Obviously both of these would be advantageous for fliers such as pterosaurs.

The supposition, that pterosaurs laid relatively small eggs, is consistent with the qualitative observation that pterosaurs appear to have a relatively small pelvis (WELLNHOFER 1991; BENNETT 2001). However, calculating the likely maximum dimensions of the pelvic passage is complicated both by preservation, in that few pelves are preserved uncrushed, and the possibility that pelvic morphology varied between the sexes. BENNETT (1992) has documented the existence of two different pelvic morphs in *Pteranodon*, and argued that the smaller morph, which appears to have a relatively large pelvic canal, represents the female. However, until well preserved uncrushed pelves that can be assigned to females of this or other species of pterosaurs are found, rigorous assessments of pelvic canal dimensions, estimates of likely maximum egg size and comparison of egg size to adult size are not feasible. Further complicating this approach to establishing relative egg size, it is possible that parchment-shelled eggs were capable of sustaining considerable, but non-permanent, distortion during their transition through the pelvic passage, facilitating the production of larger eggs than might otherwise be predicted.

Production of a small egg need not necessarily have adversely affected hatchling fitness. Parchment-shelled squamate eggs absorb water from the nest environment and hatchling mass correlates with the degree of water absorbed (PACKARD 1991). Using an equation from DEEMING & BIRCHARD (2006) we estimate, for example, that a 50 g pterosaur egg with a parchment-shell would have been likely capable of producing a hatchling of 34.5 g (DEEMING & BIRCHARD 2006).

Burial also has important implications for the temperature at which the embryos were incubated (BIRCHARD 2004). Specifically, temperature would have been controlled by the prevailing micro-environment in the nest which, in turn, would have been determined by ambient temperature (ACKERMAN & LOTT 2004). This means that incubation temperatures are likely to have been relatively low, compared to those of birds. This would also have extended the incubation period. In living squamates at 30° C a 50-g snake egg takes ~64 days to incubate compared with ~140 days for a lizard egg (DEEMING et al. 2006). Thus incubation periods for pterosaur eggs of at least two to three months seem likely.

One consequence of this incubation strategy, in extant non-avian diapsids, is precocial offspring that are essentially independent of parental care (see SHINE 1988). This is consistent with evidence from both pterosaur embryos and hatchlings, which suggests that they were already well developed at the point of hatching and highly precocial thereafter (WANG & ZHOU 2004). Unlike bats and almost all birds they may even have been able to fly within hours or days of hatching (UNWIN 2005).

Burial also has implications for physiology. All extant non-avian diapsids are essentially ectothermic heterotherms, a physiological complex that is tightly linked to developmental processes and presumably the thermal conditions under which incubation takes place. The simplest inference that can be made from this is that pterosaurs were also ectothermic heterotherms. This directly contradicts the current consensus (e.g. WELLNHOFER 1991; BENNETT 1999; NAISH & MARTILL 2003; UNWIN 2005) which holds that pterosaurs, if not endothermic homeotherms in exactly the same way as birds and mammals, were certainly much closer to this physiological state than, for example, to the physiological conditions to be found in extant non-avian diapsids. Only further investigation of the reproductive biology and physiology of pterosaurs is likely to resolve this paradox.

Acknowledgements

4. References

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