Argentinian unhatched pterosaur fossil

New pterosaur-egg features add to our understanding of these extinct flying reptiles.

Our knowledge of the eggs and embryos of pterosaurs, the Mesozoic flying reptiles, is sparse. Until now, the recent discovery of an ornithocheirid embryo from 121-million-year-old rocks in China[1] constituted the only reliable evidence of an unhatched pterosaur. Here we describe an embryonic fossil of a different pterosaur from the Early Cretaceous lacustrine deposits of Loma del Pterodaustro (the Lagarcito Formation, which is about 100 million years old) in central Argentina. This new fossil provides insight into the eggshell morphology, early growth and nesting environments of pterosaurs.

The specimen (MHIN-UNSL-GEO-V 246; see Fig. 1 and supplementary information) is split into two slabs, with its articulated bones preserved as an aggregate (22 × 60 mm) in an oval shape. The porous appearance of the bone surface, the minimal ossification of the ends of the limb bones, and the absence of fusion between the sacral vertebrae and between the scapula and coracoid provide size-independent support of the specimen's early ontogenetic age[2,3]. The skeleton is also preserved in the curled position typical of embryos[4] — forelimbs folded against the body, hindlimbs flexed and skull facing caudally, rostrum tucked under a wing — as opposed to the spread-out configuration seen in most preserved pterosaur skeletons, including those of early juveniles[3].

The proportionally large skull and the long forelimbs, with their robust metacarpals IV carrying elongated phalanges, identifies the specimen as a pterosaur[5]. Within the pterosaur group, the metacarpal:humerus ratio of greater than 0.8, the subequal lengths of the femur and metacarpal IV, and the proximally placed, D-shaped deltopectoral crest of the humerus, support the specimen's placement among the pterodactyloids[6,7]. Pterosaurian fossils collected so far at Loma del Pterodaustro belong to the filter-feeding pterodactyloid *Pterodaustro guinazui*[8]. This specimen is indistinguishable from both juvenile and mature specimens of *Pterodaustro* — with its long, slender snout and evidence of filament-like mandibular dentition[8].

The relative sizes of limb elements of the specimen, which give an estimated wingspan of 27 cm, are similar to those of early juvenile specimens of *Pterodaustro* and agree well with allometric observations based on a growth series of this taxon indicating negative and positive allometry for the proximal (humerus and ulna) and distal (metacarpal IV) portions of the wing, respectively[9]. The correspondence between the wing proportion of the specimen and those of previously published juveniles of *Pterodaustro*[9] indicates a near-hatching stage of the former and a hatchling state of the latter, and suggests that neonatal growth rates were minimal.

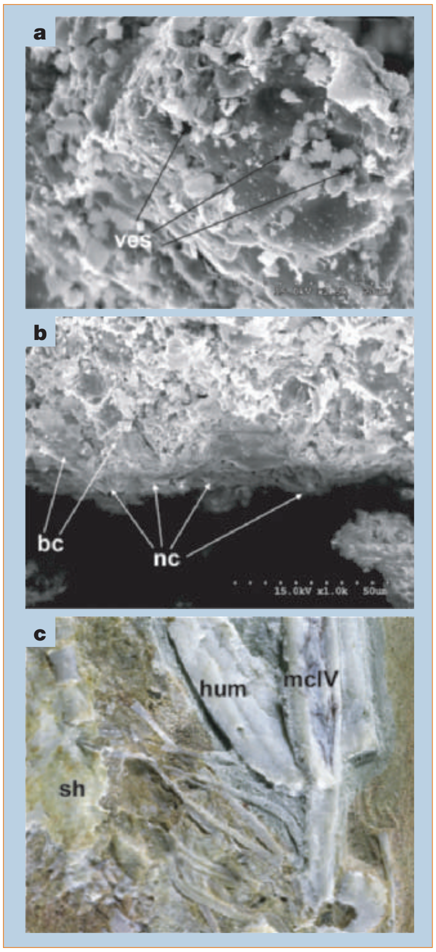

Figure 1 Shell around a pterosaurian embryo from the Early Cretaceous period in Argentina (specimen MHIN-UNSL-GEO-V 246). **a,b,** Scanning electron micrographs of radial sections of the eggshell: note the nucleation centres and bladed crystals at the apex of the V-shaped eggshell units, and micrometre-sized vesicles (ghost protein) on the surfaces. **c,** Detail showing the eggshell and general preservation of the bones. Abbreviations: bc, bladed crystals; hum, humerus; mcIV, metacarpal IV; nc, eggshell nucleation centres; sh, eggshell; ves, vesicles. For composite drawing of the entire specimen, see supplementary information.

A smooth, carbonatic material of biotic origin covers portions of the specimen and displays features of an eggshell, indicating that the new fossil is contained within an elongated egg (Fig. 1). Although the eggshell is somewhat weathered, it is extremely thin — about 30 μm in thickness. Scanning electron microscopy reveals that it consists of a single layer of calcite, with crystals radiating from a basal point and forming V-shaped eggshell units, similar to the eggshell of archosaurs (including birds), whose units radiate from an organic core[10]. Preserved crystals near the nucleation centres also exhibit the blade shape that is characteristic of most archosaurian lineages.

No information on egg morphology was recovered with the previously reported pterosaurian embryo from China[1]. Our specimen, however, shows that pterosaurs shared with extant archosaurs and chelonians an eggshell composed of a single layer of juxtaposed carbonatic crystals[11], but they differed from chelonians in that they laid calcitic eggs with blade-shaped crystals[12]. The new fossil shows that pterosaurian eggs also differ from the hard-shelled eggs of squamates (geckos in particular), which lack nucleation cores and V-shaped eggshell units[12].

At Loma del Pterodaustro, individuals of *P. guinazui* vary greatly in size — wingspans range between 27 and 300 cm. Such a range, together with the presence of embryonic and neonate remains[9], suggests that a nesting ground was nearby. Palaeoenvironmental reconstructions, combined with the remarkably low diversity of Loma del Pterodaustro — fish are the only vertebrates other than the hundreds of *Pterodaustro* fossils — suggest that this pterosaur inhabited an environment unsuitable for most other tetrapods, in agreement with reconstructions of this filter-feeding pterosaur as an ecological analogue of the flamingo. Furthermore, the association of the specimen with remains of early juveniles, subadults and adults of *Pterodaustro*[8,9] agrees with previous inferences of parental care in pterosaurs[13].

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Palaeontology

Pterosaur egg with a leathery shell

The recent discovery of a pterosaur egg with embryonic skeleton and soft tissues from the Yixian Formation confirmed that the flying pterosaurs were oviparous[1]. Here we describe another pterosaur egg whose exquisite preservation indicates that the shell structure was soft and leathery.

The new pterosaur egg with its embryo (JZMP-03-03-2; Fig. 1 and supplementary information) was collected from the Jingangshan Beds of the Yixian Formation in the Jingangshan area of Liaoning, China. Both this and the earlier pterosaur egg (IVPP V13758) are from beds of Early Cretaceous age, estimated to be 121 million years old by $^{40}Ar/^{39}Ar$ dating[2].

The presence of the pteroid bone and the long wing-phalanges and wing-metacarpals within the egg shows that JZMP-03-03-2 is an embryonic pterosaur[3,4] (for composite drawing, see supplementary information). The ilium and tibia are completely preserved, but the pubis, pteroid and dorsal vertebrae are only partially ossified. The pteroid has a slightly bent proximal end. The forelimb bones have embryonic characteristics, such as longitudinal shallow grooves on the shaft. The humerus is robust and complete, with a length of 17 mm; the deltopectoral crest is only weakly ossified. The radius and ulna (about 26 mm long) are straight and much longer than the humerus.

The right- and left-wing metacarpals are both well developed and are 13.3 mm long — about 53% of the ulna length. There are only three wing phalanges, as in the pterodactyloid *Beipiaopterus* from the Yixian Formation[5]. The robust first wing phalanx has a length of 15.8 mm, which is slightly longer than that of the wing metacarpal. The second wing phalanx narrows distally, and at 22.7 mm is much longer than the first; the third wing phalanx is 26.8 mm. The ratio of the combined length of wing phalanges to humerus is 3.84, which is lower than the ratio of 5.08 found in the adult specimen of *Beipiaopterus*. The difference in wing-finger length to humerus between JZMP-03-03-2 and the adult *Beipiaopterus* is consistent with the growth pattern of other pterosaurs[6].

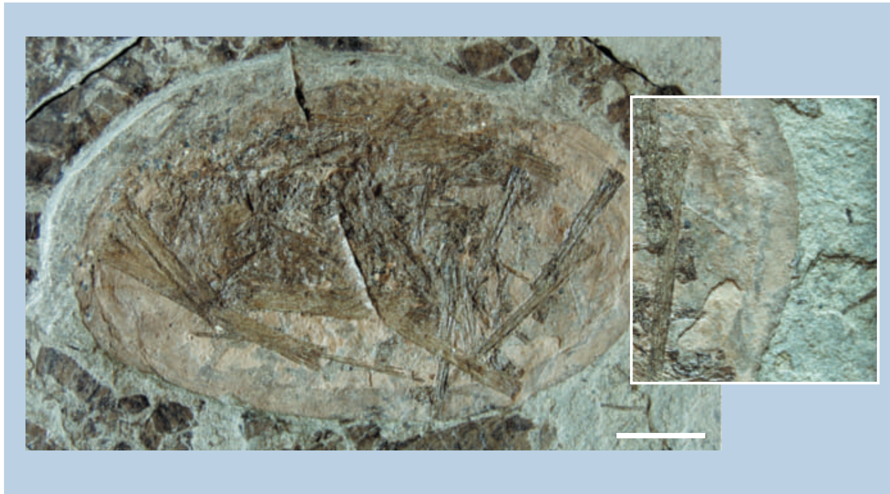

Figure 1 Early Cretaceous pterosaur egg and embryo (JZMP-03-03-2) from the Yixian Formation of Liaoning, China. Scale bar, 1 cm. Inset, magnification of egg boundary (130%) showing the thin, soft shell and no evidence of lamination structures. For composite drawing of the specimen, see supplementary information.

This specimen seems to be longer and narrower than the previously reported egg[1] (63.7 mm and 36.4 mm maximum length and width, respectively). Most skull elements (except four curved and needle-like teeth) are poorly ossified. Because of differences in some characters of the JZMP-03-03-2 and IVPP V13758 embryos (such as their shape and size for developmental stage), we suggest that the two eggs contain embryonic skeletons that belong to different pterosaur taxa.

The matrix in the interior of the egg is yellowish-brown; the embryonic skeleton is greyish-brown. The thin shell is brown-to-dark-brown and contrasts with the matrix surrounding the eggshell. The eggshell appears to be very thin (about 0.25 mm; Fig. 1, inset) and has no lamination in its microstructure. We did not detect the inner mammillary layer or the outer squamous layer formed of calcite crystallites that form the standard structural components of the hard eggshells of dinosaurs[7,8] and of some modern amniotes[9]. Neither the part nor the counterpart of this pterosaur eggshell show any of the sharp fractures that are typical of broken, hard eggshells.

Because calcareous shells of molluscs are present in the same shale, we can rule out the possibility that the absence of a calcareous shell in this specimen might have been caused by diagenetic dissolution post mortem. Our observations indicate that this pterosaur egg from Yixian had a soft, leathery shell, similar to those widely found among sphenodonts, squamates, crocodiles and turtles[9].

This pterosaur egg specimen is preserved in grey lacustrine tuffaceous shales with horizontal bedding, together with typical freshwater fossils such as fish, turtles, conchostracans, insect larvals, ostracods, gastropods, plants and lizards. Both sedimentary and palaeontological evidence indicates that the site of burial of these eggs was a low-energy palaeoenvironment. But the shallow lake, to which these eggs were transported after death, is not the original nest site, which was likely to have been a lake beach or mud-flat.

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