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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<sup>1</sup>. 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 <sup>40</sup>Ar/<sup>39</sup>Ar dating<sup>2</sup>.

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<sup>3,4</sup> (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<sup>5</sup>. 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

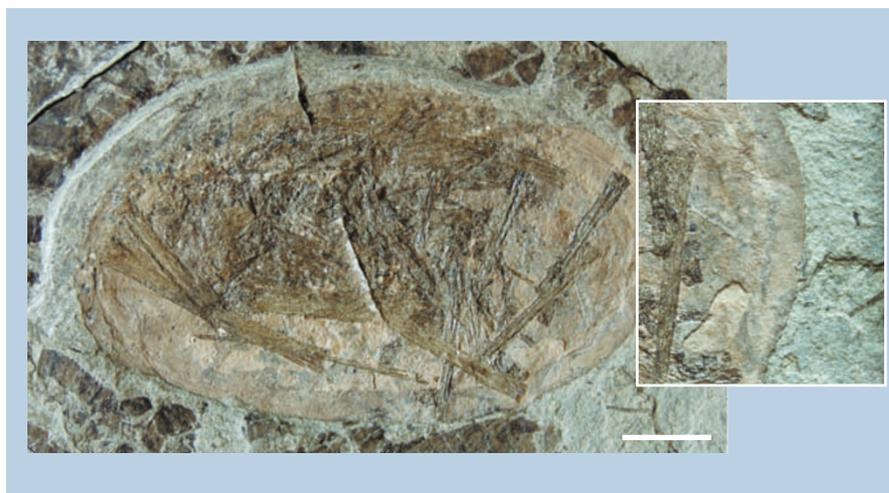


Figure 1 Early Cretaceous pterosaur egg and embryo (JZMP-03-03-2) from the Yixian Formation of Liaoning, China. Scale bar, 1 cm. Inset, magnification of egg boundary (130%) showing the thin, soft shell and no evidence of lamination structures. For composite drawing of the specimen, see supplementary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

with the growth pattern of other pterosaurs<sup>6</sup>.

This specimen seems to be longer and narrower than the previously reported egg<sup>1</sup> (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<sup>7,8</sup> and of some modern amniotes<sup>9</sup>. 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<sup>9</sup>.

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 larvae, 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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