How pterosaurs bred

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Ninety years have passed since Roy Chapman Andrews returned from his exploration of Mongolia with tales of fossilized dinosaur eggs (1). Fossils interpreted as dinosaur eggs had been described before, but Chapman's crew had found fossils that could only be interpreted as clutches of eggs. Recent fossil evidence of dinosaur reproduction has confirmed that all dinosaurs laid eggs, whereas other Mesozoic groups, such as the aquatic ichthyosaurs, evolved live birth (2). However, the reproductive biology of a key group of extinct Mesozoic species, the flying pterosaurs (see the image), has remained elusive. On page 1197 of this issue, Wang et al. (3) report the largest accumulation of Hamipterus pterosaur eggs found to date. The work is a crucial advance in understanding pterosaur reproduction.

That these flying reptiles even laid eggs was only recently confirmed in 2004, with the report of two eggs from China (4, 5) and one from Argentina (6) that contained well-developed pterosaur embryos. These eggs had thin shells free of the substantial external layer of calcium carbonate that is characteristic of hard-shelled eggs laid by dinosaurs, crocodiles, and birds. Moreover, a skeleton of an adult female of the Chinese pterosaur Darwinopterus was reported a few years ago with a parchment-shelled egg positioned between its legs (7). A more recent report of the counter slab to this specimen shows an imprint of a second egg in the body cavity (8).

Pterosaur eggs thus had soft, parchment-like shells comparable to those laid by modern-day lizards (9). Wang et al.'s study supports this interpretation (3), as does a previous study of a smaller number of eggs from the same site in China (10): The fossilized eggs show little evidence of shell calcification, and many have the characteristic dimpling of dead, dehydrated lizard eggs.

Parchment-shelled eggs need to be buried in a moist substrate to ensure that they do not dry out, thereby killing the embryo; they rely on environmental sources of heat for normal embryonic development. The similarity of pterosaur eggs to lizard eggs means that we can confidently assume that pterosaur eggs were buried. This precludes any form of contact incubation by the parents (as seen in modern birds). However, adults may have attended or defended nests, which would explain the presence of adult skeletons in the specimen reported by Wang et al. The relatively low incubation temperatures associated with environmental sources of heat would have meant a long incubation period, as is now suggested for dinosaurs (11), and hatching of a relatively mature and mobile offspring (as seen in modern reptiles) (9). The accumulation of eggs in the new specimen does not allow conclusions about clutch size to be drawn, but the Darwinopterus find (7, 8) suggests that clutch size was most likely only two eggs.

Wang et al. suggest that Hamipterus nested in colonies. Appropriate nesting environments may have been rare, forcing pterosaurs to adopt colonial nesting through necessity—but it was not without risk. Modern sea turtles nest colonially, but while preparing their own nests, females may inadvertently damage previously dug nests and expose eggs to predators. Perhaps the dimpled pterosaur eggs reported in (3) indicate that Hamipterus also experienced nest damage through intraspecific competition for limited nesting sites.

Unlike in their previous report (10), Wang et al. (3) can confirm that the eggs include pterosaur embryos and can provide details of variation in egg and embryo size. They also investigated potential rates of growth of the posthatching animals found on the same slab by documenting lines of arrested growth in bone sections; this allows the age of the animal to be estimated. Rare in studies of pterosaurs, such data provide insight into posthatching ontogeny in extinct species (12, 13), but care is needed when assessing the ontogenetic stage of embryos (2). Although the authors report on a range of embryonic bones, they provide few replicates to allow assessment of the range of size of the embryos represented; only one bone of the hatchling mentioned by the authors is illustrated.

The authors argue that some embryos were close to hatching with poor bone ossification and no teeth; this would indicate that the hatchlings were unable to feed themselves. However, an alternative perspective is that the embryos were much younger than estimated and not close to hatching and that the lack of growth of teeth is therefore unsurprising; in crocodilians, teeth only arise in the later stages of development (2). Therefore, although the morphological data and observations are better than what has been reported previously, it is important to be cautious and not to infer too many aspects of the life history of Hamipterus from what remains a limited data set.

Wang et al.'s study is remarkable for the number of eggs in association with adults and juvenile pterosaurs that it reports on. This finding provides support for nest-site fidelity, but as the authors suggest, this specimen does not represent the nest site itself, and many questions remain unanswered. Were the eggs buried in sand or covered in vegetation? Was clutch size limited to two? Why are so many of the eggs showing signs of dehydration? Hopefully additional finds of equally spectacular fossils will help us answer such questions for pterosaurs and allow us to paint an increasingly complete picture of reproduction in these extinct species.

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