Palaeontology

Smart-winged pterosaurs

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Why did ancient flying reptiles have so much processing-power in the back of their brain? To provide highly responsive flight control, is an answer to emerge from an innovative analysis of pterosaur skulls.

Brains, not surprisingly, are rarely fossilized, leaving a large gap in our knowledge of the anatomy of most extinct organisms. Fortunately, in some vertebrates — mammals, birds, dinosaurs and pterosaurs — the brain fits so tightly into the braincase that its external features are faithfully reflected by the contours of the inner surface of the bones that enclose it. Unfortunately, opportunities to recover these data from fossil material are infrequent and often involve destructive techniques, thereby excluding many valuable specimens from consideration.

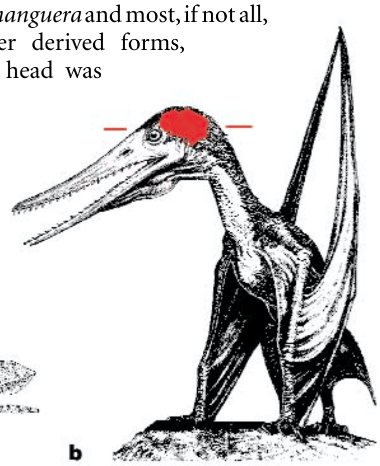
High-resolution X-ray computed tomography, which has proved extremely helpful elsewhere in palaeontology[1], offers the possibility of looking inside braincases and generating a digital cast without damaging the fossil. Witmer and colleagues[2] have successfully applied this new technique to two kinds of pterosaur (see page 950 of this issue). These are a poorly understood group of flying reptiles that flourished during the Mesozoic (between 251 million and 65 million years ago) and which remain the subject of controversy[3]. The new work clarifies several aspects of pterosaur neural anatomy, and prompts some startling new ideas regarding their locomotion and behaviour.

Witmer *et al.* looked at rare, uncrushed skulls of two specimens. One was of *Rhamphorhynchus*, a long-tailed, crow-sized creature from the Upper Jurassic (163–144 million years ago). The other was of *Anhanguera*, a large, short-tailed form dating to the Lower Cretaceous (144–97.5 million years ago). In trade jargon, *Rhamphorhynchus* and *Anhanguera* are respectively 'basal' and 'derived' — loosely put, 'primitive' and 'advanced'.

The new findings confirm earlier studies[4,5] showing that pterosaurs had a remarkably bird-like brain — for example, it had reduced olfactory lobes and large, laterally displaced optic lobes. This suggests that, like modern birds, pterosaurs were usually more interested in what they could see than what they could smell. The pterosaur brain seems to have been relatively small when scaled against body mass, however, with the brains of both *Rhamphorhynchus* and *Anhanguera* plotting below the limits for extant birds. Witmer *et al.* propose, convincingly, that this is primarily related to differing ancestries: birds inherited their grey matter from relatively big-brained theropod dinosaurs[6], whereas pterosaurs inherited theirs from relatively small-brained archosaurs[7].

The most striking results concern brain structures called floccular lobes and semi-circular canals. Floccular lobes extend out and backwards from the rear part of the brain and are exceptionally large in pterosaurs, while semi-circular canals encircle the floccular lobes and are involved in balance. In living vertebrates the orientation of the semi-circular canals, in particular the lateral canal, relates directly to the 'alert' position usually adopted by the head during locomotion and other behaviours. Exploiting this association, Witmer *et al.* show that, whereas the head posture of *Rhamphorhynchus* and probably all basal pterosaurs was normally horizontal, in *Anhanguera* and most, if not all, other derived forms, the head was

a



b

Figure 1 **Ground truth? Pterosaur head orientations inferred by Witmer *et al.*[2], and their interpretation in terms of posture when on the ground.** a, **The horizontal alignment of the lateral semi-circular canal, indicated by the red line, is consistent with a crouching posture and forward-directed head in basal pterosaurs, represented by *Rhamphorhynchus*.** b, **In derived forms such as *Anhanguera*, the reorientation of the canal can be interpreted in terms of an upright position and a downward-pointing head. (Pterosaurs redrawn from ref. 10 and not to scale.)**

directed sharply downwards at about 30°.

This is an elegant piece of work. But explaining the difference in head orientation is not easy. Maybe, suggest Witmer *et al.*, it relates to the large cranial crests borne by many derived pterosaurs, including *Anhanguera*, which could have affected skull aerodynamics during flight and required some repositioning of the head. But this is inconsistent with the recent discovery of large cranial crests in several basal pterosaurs[8,9], and their occasional absence in *Anhanguera* for instance. Alternatively, could head depression be related to feeding? *Anhanguera* and other derived pterosaurs have been interpreted as aerial fish-catchers[10], a feeding style that would have benefited from a downward-directed skull — especially as it may have permitted some stereoscopy, enabling accurate judgement of distance to a moving target. Again, however, there are inconsistencies. Many derived pterosaurs, such as the flamingo-like, filter-feeding form *Pterodaustro*, were not airborne fishers. But several basal forms were, as a specimen of *Rhamphorhynchus* with a fish in its belly eloquently testifies. Yet they still fished successfully with their level heads.

A more persuasive answer to this problem lies on the ground (Fig. 1). Like their reptilian ancestors, basal pterosaurs with their relatively short arms were condemned to walk with the body and head in a near-horizontal position, aligned with the lateral semi-circular canal. By contrast, functional studies[11] suggest that derived forms used their relatively long arms to prop themselves upright. But because they still needed to see in front of them as they walked, this required some restructuring of the skull and its posture, one consequence of which would have been reorientation of the semi-circular canals.

Attractive as they are, these ideas do not address the extraordinarily large size of the floccular lobes in pterosaurs. Witmer *et al.* suggest that this region of the brain may have been responsible for coordination of the head, eye and neck, permitting gaze-stabilization during flight. Such an ability would have been useful for aerial hunters that relied primarily on sight. But not all pterosaurs had such a lifestyle, so this is not an entirely satisfactory explanation.

Far more convincing, in my view, is Witmer and colleagues' proposal that the floccular lobes were responsible for processing large volumes of sensory data generated by the wing membranes. This is a plausible idea, because in other vertebrates the floccular lobes receive sensory inputs from skin and muscles. New, extraordinarily well-preserved pterosaur material from Germany[12] and China[13] shows that the wing membranes were highly complex, containing structural fibres, blood vessels and a fine network of muscles. These features would have given the wings the ability to collect and transmit sensory information about local conditions within the membranes, enabling pterosaurs to build up a detailed map of the forces experienced by the wings from moment to moment. Processing via the floccular lobes could have allowed them to respond very rapidly, through localized contraction or relaxation of muscle fibres within the membrane and coordination with fore- and hind-limb movement. Equipped with their 'smart' wings, pterosaurs would have had excellent flight control. Despite their antiquity, they could even have outperformed modern birds and bats. ■

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