

23. Radionov, V. F., Bryazgin, N. N. & Aleksandrov, Y. I. *The Snow Cover of the Arctic Basin* (Gidrometeoizdat, St. Petersburg, 1996).
24. Babko, O., Rothrock, D. A. & Maykut, G. A. Role of rafting in the mechanical redistribution of sea ice thickness. *J. Geophys. Res.* **107**, doi:10.1029/1999JC000190 (2002).
25. Wadhams, P. & Horne, R. J. An analysis of ice profiles obtained by submarine sonar in the Beaufort sea. *J. Glaciol.* **25**, 401–424 (1980).
26. Lindsay, R. W. & Rothrock, D. A. Arctic sea ice leads from advanced very high resolution radiometer images. *J. Geophys. Res.* **100**, 4533–4544 (1995).
27. Bourke, R. H. & McLaren, A. S. Contour mapping of Arctic Basin ice draft and roughness parameters. *J. Geophys. Res.* **97**, 17715–17728 (1992).
28. Haas, C. & Eicken, H. Interannual variability of summer sea ice thickness in the Siberian and central Arctic under different atmospheric circulation regimes. *J. Geophys. Res.* **106**, 4449–4462 (2001).
29. Gregory, J. M. *et al.* Recent and future changes in Arctic sea ice simulated by the HadCM3 AOGCM. *Geophys. Res. Lett.* **29**, doi:10.1029/2001GL014575 (2002).
30. Eicken, H., Tucker, W. B. & Perovich, D. K. Indirect measurements of the mass balance of summer Arctic sea ice with an electromagnetic induction technique. *Ann. Glaciol.* **33**, 194–200 (2001).

Acknowledgements We thank the European Space Agency for the provision of ERS data, and the National Snow and Ice Data Centre for submarine and passive microwave data. We also thank J. Mansley for assistance with data processing, and D. Wingham for comments. This work was supported by the UK Natural Environment Research Council and the European Union.

Competing interests statement The authors declare that they have no competing financial interests.

Correspondence and requests for materials should be addressed to S.L. (swl@cpom.ucl.ac.uk).

Neuroanatomy of flying reptiles and implications for flight, posture and behaviour

Lawrence M. Witmer¹, Sankar Chatterjee², Jonathan Franzosa³ & Timothy Rowe³

¹Department of Biomedical Sciences, College of Osteopathic Medicine, Ohio University, Athens, Ohio 45701, USA

²Museum of Texas Tech University, Box 43191, Lubbock, Texas 79409, USA

³Jackson School of Geosciences, University of Texas, Austin, Texas 78712, USA

Comparison of birds and pterosaurs, the two archosaurian flyers, sheds light on adaptation to an aerial lifestyle. The neurological basis of control holds particular interest in that flight demands on sensory integration, equilibrium, and muscular coordination are acute^{1–8}. Here we compare the brain and vestibular apparatus in two pterosaurs based on high-resolution computed tomographic (CT) scans from which we constructed digital endcasts. Although general neural organization resembles birds, pterosaurs had smaller brains relative to body mass than do birds. This difference probably has more to do with phylogeny than flight, in that birds evolved from nonavian theropods that had already established trends for greater encephalization^{5,9}. Orientation of the osseous labyrinth relative to the long axis of the skull was different in these two pterosaur species, suggesting very different head postures and reflecting differing behaviours. Their enlarged semicircular canals reflect a highly refined organ of equilibrium, which is concordant with pterosaurs being visually based, aerial predators. Their enormous cerebellar floccular lobes may suggest neural integration of extensive sensory information from the wing, further enhancing eye- and neck-based reflex mechanisms for stabilizing gaze.

The first vertebrate fliers were pterosaurs, an exclusively Mesozoic group that most workers¹⁰ regard as close relatives of Dinosauria within Archosauria (Fig. 1a). Pterosaurs were lightly built,

and their fossils are rare and often badly crushed. Virtual endcasts derived from CT scans of nearly complete skulls of two pterosaurs (Fig. 1)—the more basal *Rhamphorhynchus* and the pterodactyloid *Anhanguera*—are the most complete to date (Fig. 2; see Methods

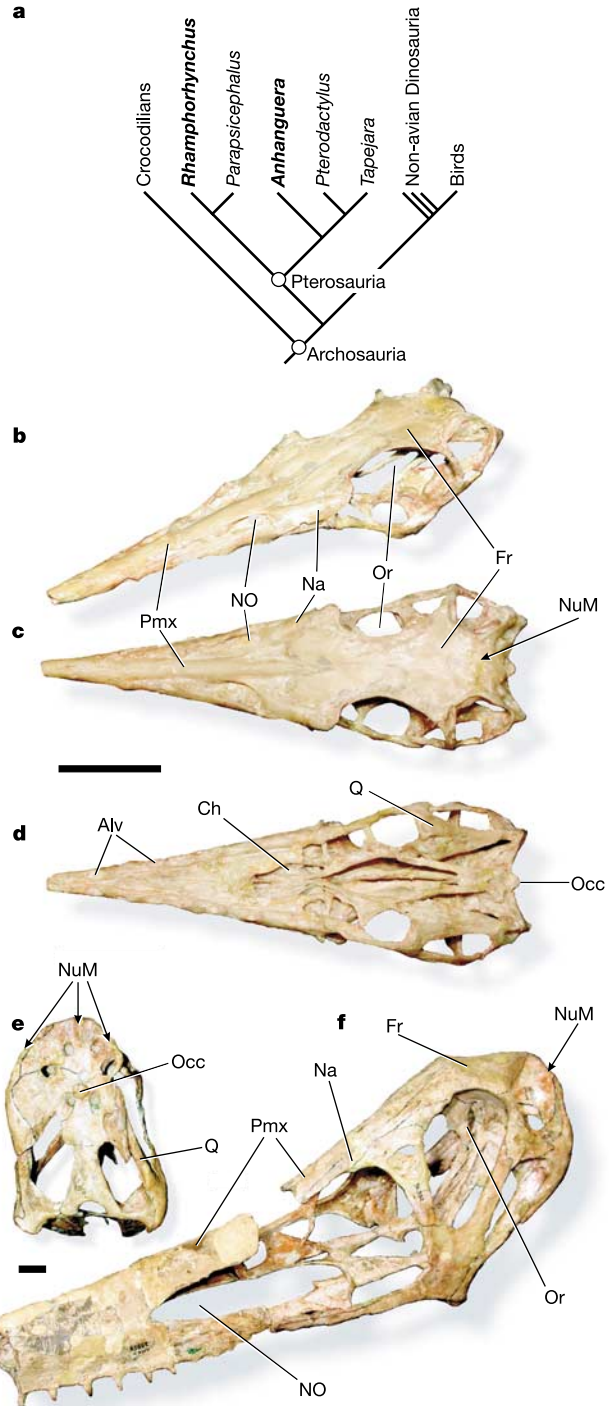


Figure 1 Relationships and skulls of pterosaur taxa. **a**, Cladogram of taxa mentioned in text and including pterosaurs for which endocast data are available. Topology based on ref. 19. **b–d**, *Rhamphorhynchus muensteri* (CM 11434, Jurassic, Germany) in left rostradorsolateral (**b**), dorsal (**c**), and ventral (**d**) views. **e, f**, *Anhanguera santanae* (AMNH 25555, Cretaceous, Brazil) in caudal (**e**) and left rostradorsolateral (**f**) views. Scale bar equals 20 mm. Alv, alveoli; Ch, choana; Fr, frontal; Na, nasal; NO, narial opening (confluent with antorbital fenestra in *Anhanguera*); NuM, area of attachment of nuchal (neck) musculature; Occ, occipital condyle; Or, orbit; Pmx, premaxilla; Q, quadrate.

and Supplementary Information). They confirm some previous findings of birdlike attributes^{1–8}: expansion of the cerebrum and cerebellum, displacing the enlarged optic tecta (lobes) ventrolaterally; small olfactory areas; and enlarged flocculi (cerebellar auricles) (Fig. 2). Despite these structural similarities, the brains of *Rhamphorhynchus* and *Anhanguera*, relative to body mass, do not fall within the range of extant birds, although they were enlarged relative to extant nonavian reptiles^{4,5,11} (Fig. 3; see Methods). Moreover, comparisons of total brain mass do not reveal differences in relative size of brain components (and hence underlying neural organization). For example, the enormous flocculi of pterosaurs probably outweighed the optic tecta, whereas the reverse is certainly true in birds.

Nevertheless, pterosaurs do possess a number of avian neuro-anatomical traits that may well be associated with the sensory and coordination functions necessary for flight. Jerison⁴ suggested that avian brains were relatively larger than those of pterosaurs because birds evolved in the environmentally complex and neurologically challenging arboreal habitat that required greater neural processing and hence greater mass. That may be true, but another factor is that birds and pterosaurs had different phylogenetic starting points: pterosaurs evolved from relatively very small-brained basal archosaurs, whereas birds evolved from theropod dinosaurs that had already initiated a substantial trend of brain expansion^{5,9}.

The virtual endocasts include the semicircular canals (Fig. 2), which had previously been only partially known for one pterosaur, *Parapsicephalus*¹. The entire osseous labyrinth is preserved bilaterally in *Anhanguera* and the large majority of it is preserved in *Rhamphorhynchus*. The semicircular canal system is greatly expanded, with the long canals encircling the flocculus. Its general arrangement closely resembles that of birds and some other dinosaurs⁵, but, whereas it is relatively modest in these groups, the

vestibular apparatus is relatively much larger in the pterosaurs. The well preserved osseous labyrinths in *Rhamphorhynchus* and *Anhanguera* provide an opportunity to test behavioural hypotheses of head orientation and posture. Researchers tend to reconstruct the head orientation of extinct animals with the skull's long axis (often the jawline) horizontal. Animals, of course, adopt a variety of head postures. There is a rich and taxonomically diverse literature supporting a robust empirical relationship between the planar elevation of the lateral semicircular canal and preferred head orientation^{12–16}. Determining 'preferred' head posture may seem problematic at first, but most vertebrates adopt a very stereotyped 'alert' posture^{13,17} and, moreover, retain this posture through a variety of behaviours¹⁵. Most studies agree that this preferred head orientation involves maintaining the lateral semicircular canal approximately level with the horizon (that is, 0° inclination) or elevated slightly in the front (5–10° inclination)^{12–16}.

Applying a conservative 5° inclination to pterosaurs shows that the long axis of the skull of *Rhamphorhynchus* indeed has a more or less horizontal orientation, as is typically portrayed⁶. However, bringing the lateral semicircular canal of *Anhanguera* to a position of 5° inclination results in the skull's long axis being strongly down-turned (Fig. 4c). This dramatically different posture impacts on behavioural hypotheses relating to feeding and locomotion, perhaps allowing lateral scanning movements of the head (that is, in the plane of the lateral canals) to operate with optimal sensitivity¹³ or perhaps even simply allowing for a less obstructed view and greater overlap of the visual fields (binocular vision; Fig. 4e). Differences in head orientation may correlate with differences in body posture during terrestrial quadrupedal locomotion in that *Rhamphorhynchus*, with its relatively shorter forelimbs, must have adopted a more horizontal trunk, whereas *Anhanguera* had longer forelimbs and so had a more upright body posture^{6,18,19}, which in turn required a compensatory down-turning of the head. The aerody-

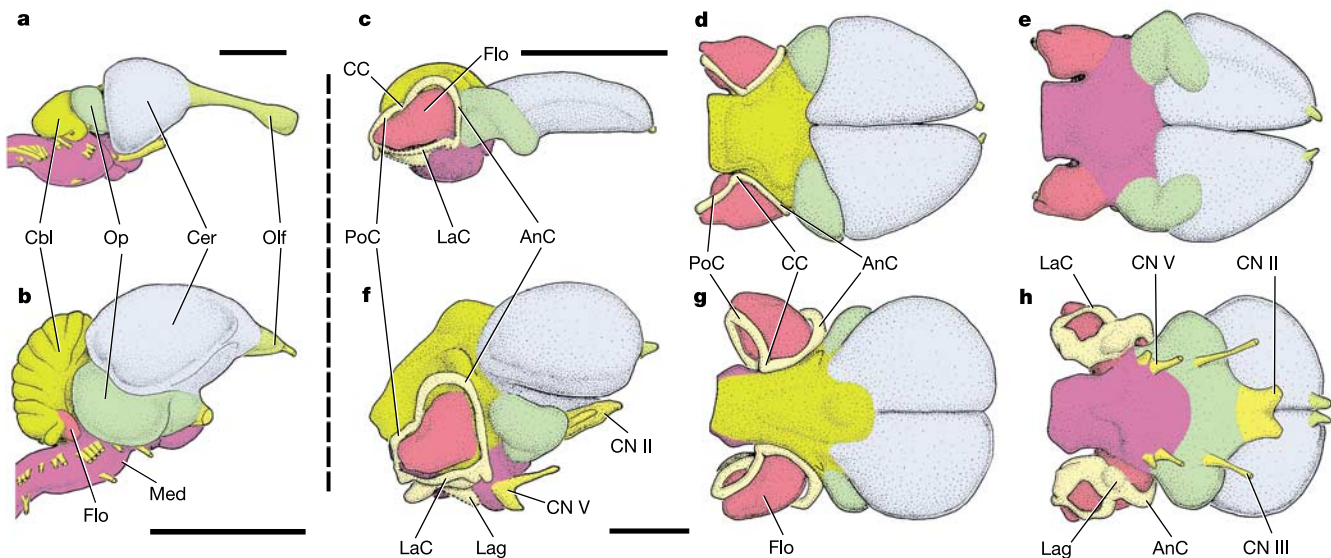


Figure 2 Endcasts and labyrinths of pterosaurs compared to brains of extant archosaurs. **a**, Brain of the crocodylian archosaur *Alligator mississippiensis* in right lateral view. **b**, Brain of the avian archosaur *Columba livia* (pigeon) in right lateral view. **c–e**, Endocast and osseous labyrinth of *Rhamphorhynchus muensteri* in right lateral (**c**), dorsal (**d**), and ventral (**e**) views. **f–h**, Same of *Anhanguera santanae* in right lateral (**f**), dorsal (**g**), and ventral (**h**) views. Major areas of the brain are labelled for the alligator and pigeon, and the corresponding regions of the endocasts are given the same colour. The lagenar (cochlear) regions of both pterosaurs and some parts of the lateral semicircular canal of *Rhamphorhynchus* were not included in the virtual endocasts but were reconstructed from

the raw slice data. Some details of the ventral portion of the virtual endocast of *Rhamphorhynchus* were not well enough preserved to allow unequivocal reconstruction. **a** and **b** modified from originals^{29,30}. Scale bars equal 10 mm. AnC, anterior semicircular canal; Cbl, cerebellum; CC, crus communis; Cer, cerebrum; CN II, cranial nerve II (optic nerve); CN III, cranial nerve III (oculomotor nerve); CN V, cranial nerve V (trigeminal nerve); Flo, flocculus (cerebellar auricle); LaC, lateral (horizontal) semicircular canal; Lag, lagena (cochlea); Med, Medulla; Olf, olfactory lobe (bulb); Op, optic lobe (tectum); PoC, posterior semicircular canal.

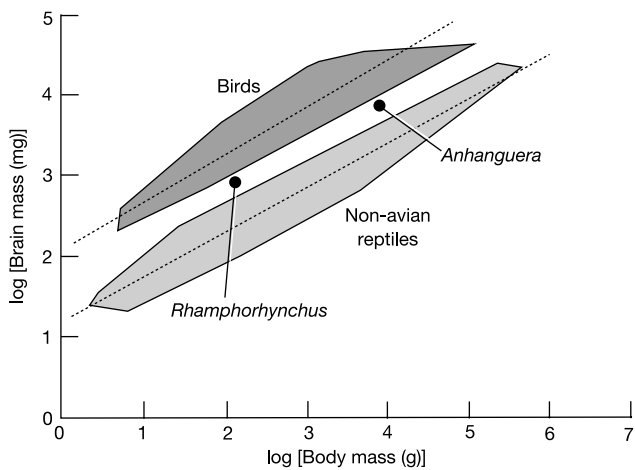


Figure 3 Relative brain size in pterosaurs compared to birds and other reptiles. Brain mass (using endocast mass as a proxy) in *Rhamphorhynchus muensteri* and *Anhanguera santanae* is relatively large in comparison to similarly sized reptiles, but does not fall within the range of extant birds. Data for taxa other than the pterosaurs derive from Hurlbert²⁸; see Methods for details and equations.

namic effects of a declined versus a perhaps more streamlined horizontal head orientation have not been fully assessed, but merit consideration¹⁸, particularly given the great length of the skull of *Anhanguera* and the fact that the bill bears a crest. It is worth noting that the occiput bears an extensive and robust attachment surface for neck musculature, and the cervical vertebrae are similarly stout (Fig. 1e–f). Thus, the head and neck appear to have been well-adapted to resist the large sagittal bending moments induced by aerodynamic forces in the declined head posture model (Fig. 4c). *Rhamphorhynchus*, by comparison, appears to have had only

modest neck musculature (Fig. 1c). Also, whereas the skull of *Rhamphorhynchus* is broad dorsally, the skull of *Anhanguera* is narrow and more triangular in cross-section (Fig. 4e), such that a declined head posture may incur less drag than might be suggested by a lateral view¹⁸.

The most striking and divergent aspect of pterosaur neuroanatomy is the space devoted to the sense of equilibrium. Comparing lateral views of the brains and semicircular canals of the two pterosaurs to that of a bird (for example, pigeon) shows that the labyrinth of pterosaurs occupies fully twice as much area, relatively, as the bird. This expansion in pterosaurs is all the more remarkable considering that birds themselves, relative to mammals, have enlarged labyrinths²⁰. The avian expansion has generally been associated with flight and the attendant requirements for balance and control in a three-dimensional aerial environment²¹. Semicircular canals sense angular acceleration (that is, head rotation), and canals with larger radii have increased sensitivity¹⁶. Moreover, animals (for example, birds and primates) with larger canals have been shown to be generally more aerobic or acrobatic^{16,21,22}. Thus, labyrinth expansion in pterosaurs is to be expected, although perhaps not to the extent observed here.

The great enlargement of the flocculus in pterosaurs, on the other hand, although reported previously^{2,5}, has not been widely appreciated. In extant nonavian reptiles, the flocculus is inconspicuous, whereas in birds and many other dinosaurs, the flocculus is larger and housed in a small bony recess. In *Rhamphorhynchus* and *Anhanguera*, however, the flocculus is larger than the optic tectum, forming a prominent lobe projecting from the caudolateral corner of the cerebellum (Fig. 2). The virtual endocasts allow quantification of relative floccular size. In *Rhamphorhynchus* and *Anhanguera*, the flocculi occupy about 7.5% of total brain mass, whereas in birds their relative mass is much less (1–2%). No other vertebrate group has so expanded the flocculus. In fact, the enlarged semicircular canals could be an epiphenomenon of primary floccular enlargement in that the canals are apparently

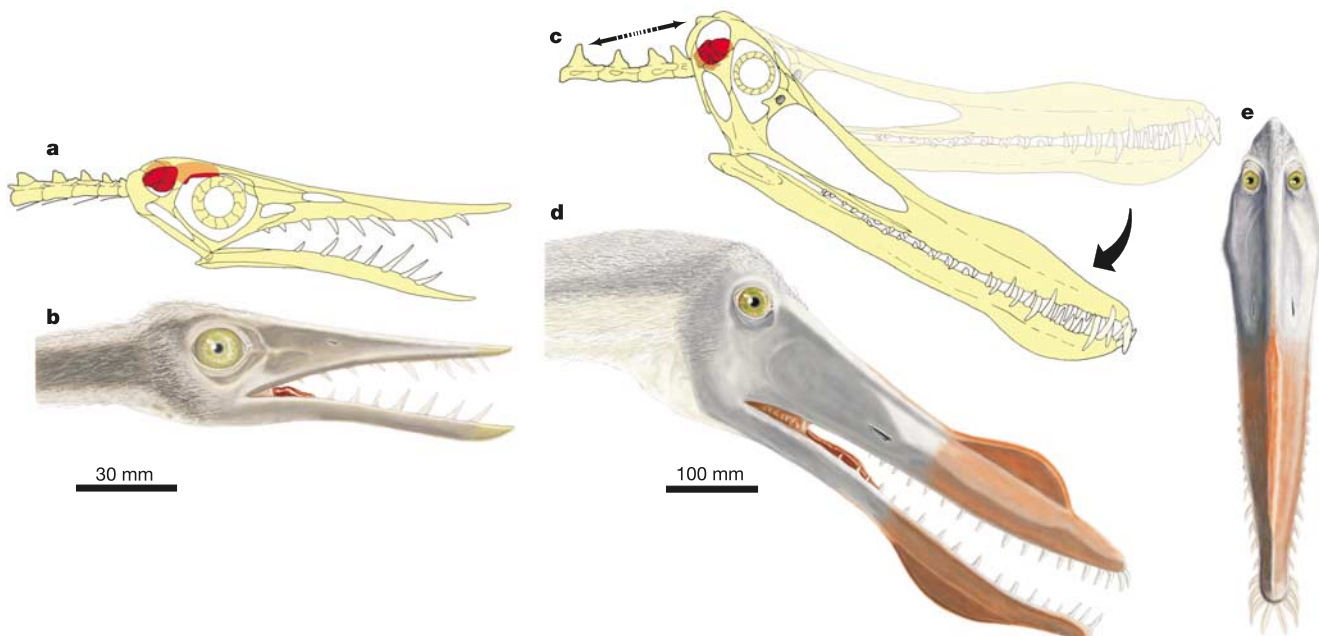


Figure 4 Skull and head postures of pterosaurs. **a, b**, *Rhamphorhynchus muensteri* skull (**a**) and restored head (**b**) in side view. **c–e**, *Anhanguera santanae* skull (**c**) and restored head in side (**d**) and front (**e**) views. Brains (endocasts) are indicated in red in **a** and **c**. In **c**, the declination of the skull (curved arrow) from horizontal (pale) reflects a head

posture with the lateral canal inclined 5° above horizontal. The double-headed arrow in **c** indicates the well-developed neck muscles that would have prevented excessive sagittal deflection of the head caused by aerodynamic drag. **a** and **c** modified from originals^{25,26}.

constrained to encircle the flocculus.

The flocculus has important connections with the vestibular system (via brainstem nuclei), the eye muscles (which are approximately coplanar with the canals), and, in some taxa, the neck muscles^{23,24}. This circuitry is best understood in the context of the vestibulo-ocular (VOR) and vestibulocollic (VCR) reflexes whereby coordination of head, eye and neck movements ensures stabilization of an image on the retina, preventing blurring^{16,24}. These reflexes allow a cheetah or a hawk to maintain a rock-steady gaze as it pursues its prey. Because some of the processing takes place in the flocculus, it would seem that pterosaurs devoted (perhaps even diverted) considerable neural resources to the integration of these gaze-stabilization mechanisms. Enhancement of such mechanisms seems reasonable in these two visually oriented pterosaurs given their apparent foraging style of aerial fish-eating^{6,25,26}.

However, there is no reason to believe that pterosaurs were more agile or aerobic than birds (including avian aerial piscivores), and hence the size of the flocculus and semicircular canals remains enigmatic. Under the principle of proper mass (the amount of neural tissue in a structure is proportional to the amount of processing⁴), it would seem that the flocculus of pterosaurs was the site of neural processing unlike that seen in extant vertebrates, suggesting that an explanation should be sought among the unusual features of pterosaurs, such as the large, skin-covered flight membrane of the wing. In birds and mammals, the flocculus receives inputs carrying proprioceptive and cutaneous information (with a relay in the inferior olivary nucleus)²⁴. Thus, the pterosaur flocculus may have processed an unusually high volume of proprioceptive and somatosensory information associated with the wing membrane that stretched between the limbs, as well as with the limb joints themselves, consequently having a direct impact on the VOR/VCR and flight control. Support for enhanced proprioceptive input from pterosaur wings comes from the recent finding that the flight membrane incorporated muscle and tendon²⁷, which would have sent proprioceptive (muscle spindle) fibres back to the central nervous system, potentially for integration in the flocculus. Thus, the enlarged flocculus may be causally linked to the pterosaur integumentary wing membrane, with the wing providing to the flocculus potentially massive amounts of sensory data on attitude and body orientation, resulting in enhanced compensatory reflexes for maintaining the fixation of gaze upon a target. □

Methods

Imaging

Information on the brains of extinct organisms has traditionally come from naturally occurring endocasts of the brain cavity¹, latex endocasts^{7,8} made after the rock has been removed, and reconstructions of ground thin-sections of skulls⁴. We used a newer, noninvasive technique employing X-ray computed tomography (CT) to reconstruct a digital or 'virtual' endocast from the transverse CT slices of the brain cavity and vestibular apparatus. One skull each of *Rhamphorhynchus muensteri* (CM 11434; from the Upper Jurassic Solnhofen Lithographic Limestones of southern Germany) and *Anhanguera santanae* (AMNH 25555; from the Lower Cretaceous Santana formation of northeastern Brazil) was acid-prepared to remove surrounding matrix and then CT-scanned. *Rhamphorhynchus* was scanned along the coronal axis for a total of 476 slices, each slice 0.25-mm thick, with an interslice spacing of 0.2 mm (for a slice overlap of 0.05 mm). *Anhanguera* was scanned along the coronal axis for a total of 595 slices, each slice 0.50-mm thick with an interslice spacing of 0.45 mm (for a slice overlap of 0.05 mm). Raw slice data, reconstructed skulls, and virtual endocast animations are provided in the Supplementary Information.

Relative brain size calculations

Allometric scaling of brain mass (M_{Br}) and body mass (M_{Bd}) provides a means of comparing relative brain size. Jerison³ facilitated comparison by devising a simple metric, the encephalization quotient (EQ), which is a ratio of actual brain mass to the predicted brain mass (based on allometry) for the animal's reference group (for example, mammals, reptiles). We employ Hurlburt's²⁸ modifications of Jerison's method, such that for reptiles, $EQ = M_{Br}/(0.155(M_{Bd})^{0.53})$, whereas for birds, $EQ = M_{Br}/(0.117(M_{Bd})^{0.59})$. We use the avian equation to estimate the pterosaur EQs because pterosaur brains filled the endocranial cavity (as in birds, but unlike in reptiles). Mass estimation for *Rhamphorhynchus* (CM 11434) and *Anhanguera* (AMNH 25555) was complicated by lack of associated postcranial skeletons. We obtained body masses from comparably sized complete skeletons: *Rhamphorhynchus muensteri* (SMF R4128²⁵) and *Anhanguera piscator*

(NSN-PV 19892²⁶). Using a principal-components analysis method for estimating body mass¹⁸, M_{Bd} for *Rhamphorhynchus* is 136 g, and M_{Bd} for *Anhanguera* is 7,600 g. Brain volume (determined from CT) multiplied by density (1.036 g cm⁻³) yields M_{Br} of 0.83 g for *Rhamphorhynchus* and 7.72 g for *Anhanguera*. EQ is 0.39 for *Rhamphorhynchus* and 0.34 for *Anhanguera*. Plotting log-transformed values on Hurlburt's²⁸ graph of brain versus body-mass shows that these pterosaurs fall between the reptile and avian polygons, with their EQs below those of birds (Fig. 3).

Received 14 March; accepted 2 September 2003; doi:10.1038/nature02048.

1. Newton, E. T. On the skull, brain, and auditory organ of a new species of pterosaurian (*Scaphognathus purdoni*), from the Upper Lias near Whitby Yorkshire. *Phil. Trans. R. Soc. Lond. B* **179**, 503–537 (1888).
2. Elinger, T. Das Gehirn der Pterosaurier. *Z. Anat. Entwicklungsgesch.* **82**, 105–112 (1927).
3. Elinger, T. The brain of *Pterodactylus*. *Am. J. Sci.* **239**, 665–682 (1941).
4. Jerison, H. J. *Evolution of the Brain and Intelligence* 482 (Academic, New York, 1973).
5. Hopson, J. A. In *Biology of the Reptilia* Vol. 9 *Neurology A* (eds Gans, C., Northcutt, R. G. & Ullink, P.) 39–146 (Academic, New York, 1979).
6. Wellnhofer, P. *The Illustrated Encyclopedia of Pterosaurs* 192 (Crescent, New York, 1991).
7. Bennett, S. C. The osteology and functional morphology of the Late Cretaceous pterosaur *Pteranodon*. Part I. General description of osteology. *Palaontogr. Abt. A* **260**, 1–112 (2001).
8. Wharton, D. S. *The Evolution of the Avian Brain* 343. PhD thesis, Univ. Bristol (2002).
9. Larsson, H. C. E., Sereno, P. C. & Wilson, J. A. Forebrain enlargement among nonavian theropod dinosaurs. *J. Vert. Paleontol.* **20**, 615–618 (2000).
10. Brochu, C. A. Progress and future directions in archosaur phylogenetics. *J. Paleontol.* **75**, 1185–1201 (2001).
11. Kellner, A. W. A. Description of the braincase of two Early Cretaceous pterosaurs (Pterodactyloidea) from Brazil. *Am. Mus. Novit.* **3175**, 1–34 (1996).
12. Lebedkin, S. Über die Lage des Canalis semicircularis lateralis bei Säugern. *Anat. Anz.* **58**, 447–460 (1924).
13. Duijm, M. On the head posture of some birds and its relation to some anatomical features. *Proc. Koninkl. Nederl. Akad. Wetensch. C* **54**, 202–211, 260–271 (1951).
14. Blanks, R. H. L., Curthoys, I. S. & Markham, C. H. Planar relationships of semicircular canals in the cat. *Am. J. Physiol.* **223**, 55–62 (1972).
15. Erichsen, J. T., Hodos, W., Evinger, C., Besette, B. B. & Phillips, S. J. Head orientation in pigeons: postural, locomotor and visual determinants. *Brain Behav. Evol.* **33**, 268–278 (1989).
16. Spoor, F. & Zonneveld, F. Comparative review of the human bony labyrinth. *Yearbook Phys. Anthropol.* **41**, 211–251 (1998).
17. de Beer, G. R. How animals hold their heads. *Proc. Linn. Soc. Lond.* **159**, 125–139 (1947).
18. Chatterjee, S. & Templin, R. J. Posture, locomotion and paleoecology of pterosaurs. *Geol. Soc. Am. Spec. Pap.* (in the press).
19. Unwin, D. M., Lü, J. & Bakhurina, N. N. On the systematic and stratigraphic significance of pterosaurs from the Lower Cretaceous Yixian Formation (Jehol Group) of Liaoning, China. *Mitt. Mus. Naturk. Berlin Geowiss. Reihe* **3**, 181–206 (2000).
20. Jones, G. M. & Spels, K. E. A theoretical and comparative study of the functional dependence of the semicircular canal upon its physical dimensions. *Proc. R. Soc. Lond. B* **157**, 403–419 (1963).
21. Turkewitsch, B. G. Zur Anatomie des Gehörorgans der Vögel (Canales semicirculares). *Z. Anat. Entwicklungsgesch.* **103**, 551–608 (1934).
22. Spoor, F., Bajjal, S., Hussain, S. T., Kumar, K. & Thewissen, J. G. M. Vestibular evidence for the evolution of aquatic behavior in early cetaceans. *Nature* **417**, 163–166 (2002).
23. Butler, A. B. & Hodos, W. *Comparative Vertebrate Neuroanatomy: Evolution and Adaptation* 514 (Wiley-Liss, New York, 1996).
24. Winship, I. R. & Wylie, D. R. W. Zonal organization of the vestibulocerebellum in pigeons (*Columba livia*): I. Climbing fiber input to the flocculus. *J. Comp. Neurol.* **456**, 127–139 (2003).
25. Wellnhofer, P. Die Rhamphorhynchoidea (Pterosauria) der Oberjura-Plattenkalke Süddeutschlands. Teil I. Allgemeine Skelettmorphologie. *Palaontogr. Abt. A* **148**, 1–33 (1975).
26. Kellner, A. W. A. & Tomida, Y. Description of a new species of Anhangueridae (Pterodactyloidea) with comments on the pterosaur fauna from the Santana Formation (Aptian-Albian), northeastern Brazil. *Nat. Sci. Mus. Monogr.* **17**, 1–135 (2000).
27. Tischlinger, H. & Frey, E. Ein *Rhamphorhynchus* (Pterosauria, Reptilia) mit ungewöhnlicher Flughalterhaltung aus dem Solnhofener Plattenkalk. *Archaeopteryx* **20**, 1–20 (2002).
28. Hurlburt, G. R. *Relative Brain Size in Recent and Fossil Amniotes: Determination and Interpretation* 250. PhD thesis, Univ. Toronto (1996).
29. Romer, A. S. *Osteology of the Reptiles* 772 (Univ. Chicago Press, Chicago, 1956).
30. Proctor, N. S. & Lynch, P. J. *Manual of Ornithology* 340 (Yale Univ. Press, New Haven, 1993).

Supplementary Information accompanies the paper on www.nature.com/nature.

Acknowledgements D. S. Berman (Carnegie Museum of Natural History) and J. Maisey (American Museum of Natural History) agreed to the loan and preparation of the pterosaur specimens. M. Atanassov assisted with body mass estimates and other morphometrics. Z. Zheng acid-prepared the fossils. M. Colbert, J. Humphries, R. Ketcham, and J. Maisano assisted with the CT scanning, data processing, and web delivery. Figures were drafted by R. Ridgely (Figs 2 and 3a, c) and K. McQuilkin (Fig. 3b, d, e and Fig. 4). We thank G. R. Hurlburt and D. S. Wharton for sharing data in their doctoral dissertations. We thank G. R. Hurlburt, P. M. O'Connor, E. Weber, and D. S. Wharton for fruitful discussion of pterosaurs and neuroscience, and R. J. Templin for providing aerodynamic expertise. The manuscript benefited from comments provided by D. M. Unwin & S. C. Bennett. Funding was provided by NSF grants to L.M.W. and T.R. and by Texas Tech University to S.C.

Competing interests statement The authors declare that they have no competing financial interests.

Correspondence and requests for materials should be addressed to L.M.W. (witmerL@ohio.edu).