

Postcranial skeletal pneumaticity and air-sacs in the earliest pterosaurs

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Patterns of postcranial skeletal pneumatization (PSP) indicate that pterosaurs possessed components of a bird-like respiratory system, including a series of ventilatory air-sacs. However, the presence of PSP in the oldest known pterosaurs has not been unambiguously demonstrated by previous studies. Here we provide the first unequivocal documentation of PSP in Late Triassic and earliest Jurassic pterosaurs. This demonstrates that PSP and, by inference, air-sacs were probably present in the common ancestor of almost all known pterosaurs, and has broader implications for the evolution of respiratory systems in bird-line archosaurs, including dinosaurs.

Keywords: avian respiration; flight; Jurassic; Late Triassic; pneumatization; Pterosauria

1. INTRODUCTION

Pterosaurs are among the most iconic of all extinct reptiles and were the first vertebrates to evolve powered flight (Padian 1983). The clade originated by or during the Late Triassic, and the ability of pterosaurs to exploit previously vacant aerial niches led to substantial taxonomic and morphological diversification during their 155+ million years of evolution, culminating in the largest flying organisms of all time (azhdarchids such as *Quetzalcoatlus*, that reached estimated wingspans of up to 12 m). Pterosaur flight was underpinned by a suite of physiological adaptations, including rapid growth rates (Padian *et al.* 2004), possible thermoregulation (Unwin 2005) and a bird-like respiratory system with air-sacs (Claessens *et al.* 2009).

The air-sacs of extant birds form a critical component of the avian respiratory system, permitting flow-through ventilation and exceptionally efficient gas exchange (Duncker 1971). Diverticula of the air-sacs opportunistically pneumatize (invade and hollow out) the vertebrae and limb elements in most volant birds with the effect of reducing skeletal mass; other extant tetrapods lack such postcranial skeletal pneumatization (PSP) and air-sacs (O'Connor 2006).

Electronic supplementary material is available at <http://dx.doi.org/10.1098/rsbl.2009.0139> or via <http://rsbl.royalsocietypublishing.org>.

Postcranial skeletal pneumatization has been used to infer the presence of air-sacs and flow-through ventilation in several extinct Mesozoic bird-line (i.e. ornithodiran) archosaur groups, including non-avian saurischian dinosaurs (e.g. O'Connor & Claessens 2005; O'Connor 2006; Wedel 2007, 2009; Sereno *et al.* 2008), and pterosaurs (Britt 1993; Bonde & Christiansen 2003; Claessens *et al.* 2009).

The distribution of PSP within and among pterosaur species has received relatively little study, though some major features and trends have been established recently (Claessens *et al.* 2009). Previous authors have been unable to identify unambiguous evidence of PSP in stratigraphically early non-pterodactyloid pterosaurs, or 'rhamphorhynchoids', from the Late Triassic and earliest Jurassic (Britt 1993; Bonde & Christiansen 2003; Claessens *et al.* 2009, fig. 4). Here we provide new evidence of PSP in Late Triassic and earliest Jurassic pterosaurs, demonstrating that PSP and, by inference, air-sacs were probably present in the common ancestor of nearly all known pterosaurs and perhaps all ornithodirans.

2. MATERIAL AND METHODS

We studied the material of two Triassic pterosaurs (*Raeticodactylus filisurensis*: BNM 14524, holotype; *Eudimorphodon cf. ranzii*: BSP 1994 I 51; see electronic supplementary material for institutional abbreviations and further details) that had not been examined in previous studies of pterosaur PSP. We also re-examined key specimens (NHM R1034, NHM 41212; GSM 1546) of the earliest Jurassic (Hettangian–Sinemurian) pterosaur *Dimorphodon macronyx*, a member of a lineage that has been identified as the sister group to almost all other pterosaurs (Unwin 2003). See electronic supplementary material for details of criteria used to identify PSP in these specimens.

3. RESULTS

Two mid-cervical vertebrae are preserved in the holotype of *Raeticodactylus filisurensis*: one in dorsal view and one in ventral view. On the posterior half of the neural arch of the latter, a large opening is present on each side (figure 1a). Although the rims of these openings are broken in places, they are complete elsewhere in the same specimen, indicating that these are genuine foramina that appear to communicate with internal chambers. Six anterior dorsal vertebrae are preserved in close association, although the first two are partially obscured by overlying elements. An elongate elliptical foramen with a sharp-edged rim is present on the right lateral surface of the centrum of the third preserved dorsal (figure 1d). Foramina are absent on the centra of the fourth through sixth preserved dorsals. A partial dorsal rib is associated with the most anterior of the preserved dorsal vertebrae. A large elliptical foramen with a well-defined rim is present on the base of the capitulum on the posterior surface of this bone (figure 1b,c), and clearly opens into a larger internal cavity. Similar foramina are absent on the other two well-exposed ribs, both of which are associated with the second most anterior of the preserved dorsals; however, two fossae separated by a low ridge cover much of the posterior surfaces of their proximal ends. Although several of the limb bones (humerus, ulna and femur) of *R. filisurensis* were reported by Stecher (2008) as pneumatic, these elements are only positively identifiable as hollow (as is

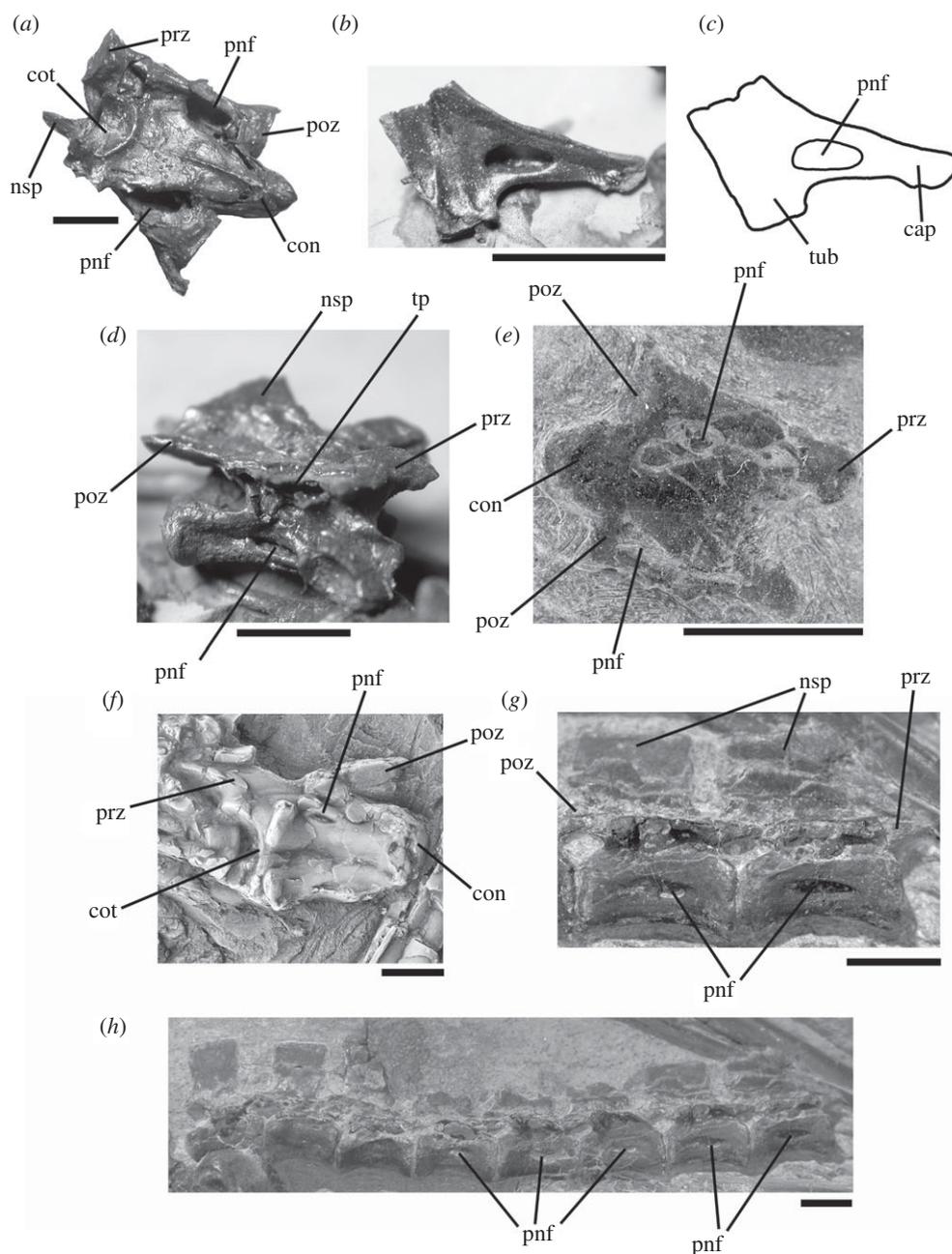


Figure 1. Evidence for postcranial skeletal pneumaticity in early pterosaurs. *Raeticodactylus filisurensis*, BNM 14524: (a) mid-cervical vertebra, ventral; (b,c) anterior dorsal rib, posterior; (d) third preserved dorsal vertebra, right lateral. *Eudimorphodon* cf. *ranzii*, BSP 1994 I 51: (e) mid-cervical vertebra, ventral. *Dimorphodon macronyx*, NHM R1034: (f) cervical vertebra, ventral. *Dimorphodon macronyx*, GSM 1546: (g) dorsal vertebrae 5–6, right lateral; (h) dorsal vertebrae 5–12, right lateral. cap, capitulum; con, condyle; cot, cotyle; nsp, neural spine; pnf, pneumatic foramen; poz, postzygapophysis; prz, prezygapophysis; tp, transverse process. Scale bar, 5 mm.

generally the case for pterosaur long bones, regardless of whether they are pneumatic (Bennett 1996) based upon broken cross-sections; there are no obvious external pneumatic foramina on visible surfaces.

A mid-cervical vertebra of BSP 1994 I 51 (*Eudimorphodon* cf. *ranzii*) is preserved in ventral view (figure 1e). Although heavily crushed and fractured, large (approx. 25% of the maximum anteroposterior length of the centrum) elliptical openings with distinct rims lie close to the posterior end of the neural arch. The openings are similar in position and relative size to those of *R. filisurensis*, with long axes oriented antero-laterally–posteromedially as preserved. There is no

unambiguous evidence for appendicular PSP in BSP 1994 I 51.

Evidence for PSP in *Dimorphodon macronyx* was first noted by Sangster (2003) and is confirmed here. A single large elliptical foramen is visible on the left lateral surface of the centrum of one of the two preserved cervical vertebrae in NHM R1034 (figure 1f). The margins of the foramen are formed by a continuous rim of smoothly curved finished bone, and the long axis of the foramen is oriented parasagittally. The anterior five cervicals are present in a referred specimen (NHM 41212), but are exposed in ventral view only and foramina cannot be recognized. An articulated

sequence of the eight most posterior dorsal vertebrae (dorsals 5–12; Unwin 1988) is present in GSM 1546. Single large elliptical foramina (the largest approx. 35% of the length of the corresponding centrum), located approximately at the midpoint of the exposed right lateral surface of the centrum, are present in dorsals 5–9 (figure 1*g,h*); these foramina have sharp rims and resemble those in *R. filisurensis*. Foramina are absent in dorsals 10–12. Unfortunately, the sacrum of GSM 1546 is too poorly exposed and preserved for the presence or absence of PSP to be determined. No unambiguous appendicular pneumaticity is present in any specimen of *D. macronyx* examined for this study.

4. DISCUSSION

Britt (1993) documented PSP in *Rhamphorhynchus* and Cretaceous pterodactyls, noting that in most pterosaur cervical and dorsal vertebrae ovoid pneumatic foramina were present on each side of the centrum or the ventral surface of the neural arch (see also Bonde & Christiansen 2003). The similarities in size and position among the foramina we have documented in *Eudimorphodon* cf. *ranzii*, *Raeticodactylus filisurensis* and *Dimorphodon macronyx* (figure 1), and those seen in Late Jurassic and Cretaceous pterosaurs (e.g. figure S1, electronic supplementary material), suggests their homology. Britt (1993) additionally documented a large pneumatic foramen on a posterior cervical rib of the Cretaceous pterodactyl *Pteranodon*, in a similar position to the pneumatic foramina present in the ribs of sauropods, theropods and birds. The similarly placed and sized foramen we report on an anterior dorsal rib of *R. filisurensis* is, therefore, probably pneumatic in origin. Our observations suggest that PSP and associated air-sacs were present in the common ancestor of most (possibly all) known pterosaurs (figure S2, electronic supplementary material). The presence of PSP in early pterosaurs suggests that failure to identify PSP in other pterosaur specimens probably reflects unfavourable preservation (e.g. crushing) rather than genuine absence. We are unaware of any pterosaur taxon that unequivocally lacks PSP.

Recent work has demonstrated that strict correlations exist between specific air-sacs and the axial elements that they pneumatize in extant birds (O'Connor & Claessens 2005; O'Connor 2006): the cervical vertebrae/ribs and the anterior to mid-dorsal vertebrae are pneumatized by diverticula of the cervical air-sacs; diverticula of the abdominal air-sacs pneumatize the posterior dorsal, sacral and caudal vertebrae; dorsal vertebrae/ribs are pneumatized directly by the lung. Claessens *et al.* (2009) used this pattern of PSP to infer, 'by analogy', the presence of both cervical and abdominal air-sacs in pterosaur groups. In this approach, the clear evidence for PSP observed in the cervicals and anterior to mid-dorsal vertebrae/ribs (but absent more posteriorly within the dorsal column) of *R. filisurensis* and *D. macronyx* minimally implies the presence of cervical air-sacs. Postcranial skeletal pneumatization has not yet been documented in the postdorsal vertebrae or the appendicular

skeleton of Late Triassic/earliest Jurassic pterosaurs; as a result, there is currently no direct evidence for the presence of abdominal air-sacs in these taxa.

Using particular patterns of PSP in pterosaurs to infer pneumatization by distinct components of an air-sac system would be more robust if pterosaur air-sacs were homologous with those of birds. The distribution of PSP among ornithodirans (figure S3, electronic supplementary material) suggests that PSP in pterosaurs and birds are not homologous; nevertheless, the recognition of evidence for axial PSP (and thus air-sacs) in the common ancestor of most known pterosaurs increases the likelihood that at least non-invading air-sacs were present in the last common ancestor of pterosaurs and birds. Where known, axial pneumatization in the earliest pterosaurs appears to be restricted to the cervical and more anterior dorsal vertebrae. This distribution matches that for PSP in early sauropodomorph and theropod dinosaurs as well as in the early developmental stages of extant birds (Wedel *in press*), and might be interpreted as evidence for the homology of the associated soft tissues. A posterior spread of PSP along the vertebral column in theropod/sauropodomorph evolution recapitulates the development of pneumatization during extant avian ontogeny (Wedel 2007, *in press*). A convergent posterior extension in the extent of PSP may characterize pterosaur evolution, given sacral pneumatization (and inferred abdominal air-sacs) in Cretaceous pterosaurs (Claessens *et al.* 2009).

More compelling evidence for the homology of avian and pterosaur air-sacs could conceivably take the form of pneumatic hiatuses in the vertebral column (Wedel *in press*) and unambiguous PSP in other Triassic archosaurs, including additional pterosaurs. Among extinct non-dinosaurian taxa more closely related to dinosaurs than to pterosaurs (i.e. non-dinosaurian dinosauromorphs), PSP has been cited as absent in one of the best-known taxa, *Marasuchus* (e.g. Britt 1993; Wedel 2007, *in press*). In the probable non-dinosaurian dinosauromorph *Silesaurus opolensis*, cervical and anterior dorsal vertebrae possess exceptionally well-developed and deep external fossae separated from one another by thin bony laminae (Dzik 2003; ZPAL Ab III 411/7), some of which (e.g. the centropost- and centroprezygapophyseal laminae) are otherwise undocumented in non-saurischian archosaurs. Although such fossae/laminae are not unambiguous evidence of PSP (O'Connor 2006), they do require explanation and indicate the pressing need for further work on the origin and early evolution of PSP and the avian respiratory system (see also Gower 2001).

For access to specimens, we thank Jürg Paul Müller and Ulrich Schnepf (BNM), Oliver Rauhut, Adriana López-Arbarello and Katrin Moser (BSP), Rainer Schoch (SMNS), Louise Neep and Paul Shepherd (GSM) and Jerzy Dzik and Tomasz Sulej (ZPAL). Thanks to Brian Andres, Stephen Brusatte, Leon Claessens, Patrick O'Connor, Rico Stecher, David Unwin and Mathew Wedel for discussion and access to unpublished data and to Brian Andres and an anonymous referee for helpful review comments. This work was supported by a NERC small grant (NE/F009933/1).

- Bennett, S. C. 1996 The phylogenetic position of the Pterosauria within the Archosauromorpha. *Zool. J. Linn. Soc.* **118**, 261–308. (doi:10.1111/j.1096-3642.1996.tb01267.x)
- Bonde, N. & Christiansen, P. 2003 The detailed anatomy of *Rhamphorhynchus*: axial pneumaticity and its implications. *Geol. Soc. Lond. Spec. Publ.* **217**, 217–232. (doi:10.1144/GSL.SP.2003.217.01.13)
- Britt, B. B. 1993. *Pneumatic postcranial bones in dinosaurs and other archosaurs*. PhD dissertation, University of Chicago.
- Claessens, L. P. A. M., O'Connor, P. M. & Unwin, D. M. 2009 Respiratory evolution facilitated the origin of pterosaur flight and aerial gigantism. *PLoS ONE* **4**, e4497. (doi:10.1371/journal.pone.0004497)
- Duncker, H. R. 1971 The lung air-sac system of birds. *Adv. Anat. Embryol. Cell Biol.* **45**, 1–171.
- Dzik, J. 2003 A beaked herbivorous archosaur with dinosaur affinities from the early Late Triassic of Poland. *J. Vertebr. Paleontol.* **23**, 556–574. (doi:10.1671/A1097)
- Gower, D. J. 2001 Possible postcranial pneumaticity in the last common ancestor of birds and crocodylians: evidence from *Erythrosuchus* and other Mesozoic archosaurs. *Naturwissenschaften* **88**, 119–122. (doi:10.1007/s001140100206)
- O'Connor, P. M. 2006 Postcranial pneumaticity: an evaluation of soft-tissue influences on the postcranial skeleton and the reconstruction of pulmonary anatomy in archosaurs. *J. Morphol.* **267**, 1199–1226. (doi:10.1002/jmor.10470)
- O'Connor, P. M. & Claessens, L. P. A. M. 2005 Basic avian pulmonary design and flow-through ventilation in non-avian theropod dinosaurs. *Nature* **436**, 253–256. (doi:10.1038/nature03716)
- Padian, K. 1983 A functional analysis of flying and walking in pterosaurs. *Paleobiology* **9**, 218–239.
- Padian, K., Horner, J. R. & De Ricqlès, A. 2004 Growth in small dinosaurs and pterosaurs: the evolution of archosaurian growth strategies. *J. Vertebr. Paleontol.* **24**, 555–571. (doi:10.1671/0272-4634(2004)024[0555:GISDAP]2.0.CO;2)
- Sangster, S. 2003. The anatomy, functional morphology and systematics of *Dimorphodon macronyx* (Diapsida: Pterosauria). PhD dissertation, University of Cambridge.
- Sereno, P. C., Martinez, R. N., Wilson, J. A., Varricchio, D. J., Alcobar, O. A. & Larsson, H. C. E. 2008 Evidence for avian intrathoracic air sacs in a new predatory dinosaur from Argentina. *PLoS ONE* **3**, e3303. (doi:10.1371/journal.pone.0003303)
- Stecher, R. 2008 A new Triassic pterosaur from Switzerland (Central Austroalpine, Grisons), *Raeticodactylus filisurensis* gen. et sp. nov. *Swiss J. Geosci.* **101**, 185–201. (doi:10.1007/s00015-008-1252-6)
- Unwin, D. M. 1988 New remains of the pterosaur *Dimorphodon* (Pterosauria: Rhamphorhynchoidea) and the terrestrial ability of early pterosaurs. *Mod. Geol.* **13**, 57–68.
- Unwin, D. M. 2003 On the phylogeny and evolutionary history of pterosaurs. *Geol. Soc. Lond. Spec. Publ.* **217**, 139–190. (doi:10.1144/GSL.SP.2003.217.01.11)
- Unwin, D. M. 2005 *The pterosaurs from deep time*. New York, USA: Pi Press.
- Wedel, M. J. 2007 What pneumaticity tells us about 'prosauropods', and vice versa. *Spec. Pap. Palaeontol.* **77**, 207–222.
- Wedel, M. J. In press Evidence for bird-like air-sacs in saurischian dinosaurs. *J. Exp. Zool.* (doi:10.1002/jez.513)