

# Air-filled postcranial bones in theropod dinosaurs: physiological implications and the ‘reptile’–bird transition

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## ABSTRACT

Pneumatic (air-filled) postcranial bones are unique to birds among extant tetrapods. Unambiguous skeletal correlates of postcranial pneumaticity first appeared in the Late Triassic (approximately 210 million years ago), when they evolved independently in several groups of bird-line archosaurs (ornithodirans). These include the theropod dinosaurs (of which birds are extant representatives), the pterosaurs, and sauropodomorph dinosaurs. Postulated functions of skeletal pneumatisation include weight reduction in large-bodied or flying taxa, and density reduction resulting in energetic savings during foraging and locomotion. However, the influence of these hypotheses on the early evolution of pneumaticity has not been studied in detail previously. We review recent work on the significance of pneumaticity for understanding the biology of extinct ornithodirans, and present detailed new data on the proportion of the skeleton that was pneumatised in 131 non-avian theropods and *Archaeopteryx*. This includes all taxa known from significant postcranial remains. Pneumaticity of the cervical and anterior dorsal vertebrae occurred early in theropod evolution. This ‘common pattern’ was conserved on the line leading to birds, and is likely present in *Archaeopteryx*. Increases in skeletal pneumaticity occurred independently in as many as 12 lineages, highlighting a remarkably high number of parallel acquisitions of a bird-like feature among non-avian theropods. Using a quantitative comparative framework, we show that evolutionary increases in skeletal pneumaticity are significantly concentrated in lineages with large body size, suggesting that mass reduction in response to gravitational constraints at large body sizes influenced the early evolution of pneumaticity. However, the body size threshold for extensive pneumatisation is lower in theropod lineages more closely related to birds (maniraptorans). Thus, relaxation of the relationship between body size and pneumatisation preceded the origin of birds and cannot be explained as an adaptation for flight. We hypothesise that skeletal density modulation in small, non-volant, maniraptorans resulted in energetic savings as part of a multi-system response to increased metabolic demands. Acquisition of extensive postcranial pneumaticity in small-bodied maniraptorans may indicate avian-like high-performance endothermy.

*Key words:* pneumaticity, osteological correlates, bird origins, Dinosauria, Theropoda.

## CONTENTS

I. Introduction .....	169
(1) The reptile–bird transition and pneumaticity .....	169
(2) Institutional abbreviations .....	170
II. Postcranial skeletal pneumaticity in extinct non-theropod archosaurs .....	170
(1) Recognising pneumaticity in extinct taxa .....	170
(a) Osteological correlates .....	170
(b) Internal organisation of pneumatic bones .....	172

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(2) Basal archosauriforms .....	173
(3) Pterosaurs .....	173
(4) Sauropodomorph dinosaurs .....	174
III. Physiological implications of postcranial skeletal pneumaticity .....	174
(1) Skeletal pneumaticity and air sacs enable density modulation .....	174
(2) Pneumaticity provides evidence for bird-like ventilatory air sacs and diverticula .....	174
(3) Pneumaticity does not provide evidence for endothermy .....	175
IV. Postcranial skeletal pneumaticity in non-avian theropod dinosaurs .....	176
(1) Anatomy .....	176
(a) Vertebral pneumaticity .....	176
(b) Costal pneumaticity .....	176
(c) Appendicular pneumaticity .....	177
(d) <i>Archaeopteryx</i> .....	177
(2) New data set .....	177
(a) Data collection .....	177
(b) Treating ambiguous evidence .....	178
(3) The distribution of postcranial skeletal pneumaticity in non-avian theropods .....	178
(a) The ‘common pattern’ .....	178
(b) The ‘reduced pattern’ .....	180
(c) The ‘extended pattern’ .....	180
(4) Reconstructing missing data .....	181
(a) Summary .....	181
(b) Interpolation .....	181
(5) Phylogenetic optimisation .....	182
V. Analyses .....	182
(1) General information .....	182
(2) Tests of correlation .....	183
(a) Non-phylogenetically adjusted data .....	183
(b) Phylogenetically adjusted data .....	183
(3) Concentrated changes test .....	185
VI. Discussion .....	186
(1) The evolution of postcranial skeletal pneumaticity in non-avian theropods .....	186
(a) Repeated and conserved patterns .....	186
(b) Skeletal pneumaticity and body size .....	187
(c) Postcranial skeletal pneumaticity as near-‘irreversible’ evolution .....	187
(d) Skeletal pneumaticity and physiological innovation .....	188
(2) Future directions .....	188
VII. Conclusions .....	189
VIII. Acknowledgements .....	189
IX. References .....	189
X. Supporting Information .....	193

## I. INTRODUCTION

### (1) The reptile-bird transition and pneumaticity

Although a relationship between birds and predatory theropod dinosaurs was suggested by Huxley (1868, 1870), it has only recently gained widespread acceptance due to advances in our understanding of non-avian theropod anatomy, discoveries of new fossils, and the application of rigorous numerical methods of phylogeny reconstruction (Ostrom, 1976; Gauthier, 1986; Sereno, 1999; Norell, Clark & Makovicky, 2001; Clark, Norell & Barsbold, 2002; Zhou, 2004; Hu *et al.*, 2009; Xu *et al.*, 2009). This acceptance has precipitated a dramatic expansion of our knowledge of bird origins. Many ‘characteristic’ features of birds first appeared among non-avian dinosaurs and provide a framework for

understanding the evolutionary assembly of avian anatomy and physiology. These include filamentous integumentary structures such as feathers (Chen, Dong & Zhen, 1998; Ji *et al.*, 1998; Xu, 2006; Zheng *et al.*, 2009; Ortega, Escaso & Sanz, 2010), rapid growth rates (e.g. Horner, de Ricqlès & Padian, 1999; Sander, 2000; Erickson, Curry-Rogers & Yerby, 2001; Lee & Werning, 2008; Erickson *et al.*, 2009), medullary bone (a specialised reproductive tissue; Schweitzer, Wittmeyer & Horner, 2005; Lee & Werning, 2008), genomic contraction (Organ *et al.*, 2007; Organ, Brusatte & Stein, 2009), and numerous other anatomical (e.g. Padian & Chiappe, 1998), behavioural (Norell *et al.*, 1995; Norell & Xu, 2004) and locomotor (Gatesy & Dial, 1996; Gatesy, 2001, 2002; Hutchinson, 2001*a, b*; Hutchinson & Allen, 2009) innovations in addition to postcranial skeletal pneumaticity

(e.g. Britt, 1993; O'Connor & Claessens, 2005). Thus, biological distinctions between birds and non-avian dinosaurs are now graded across a lengthy evolutionary transition characterised by the mosaic appearance of bird-like traits. Questions regarding the origins of avian biology are therefore inextricably tied to our understanding of dinosaur biology.

Skeletal pneumaticity arises from invasion of bones by air-filled diverticula of the respiratory system (Müller, 1908; King, 1966; Bremer, 1940; Duncker, 1971; Britt, 1993; O'Connor, 2004). Among extant tetrapods, cranial skeletal pneumaticity is common in archosaurs and mammals (Witmer, 1997, 1999), but pneumatisation of the postcranial skeleton is unique to birds (e.g. Duncker, 1971). Many extinct archosaurs also possessed unambiguously pneumatic postcranial bones (Fig. 1; Owen, 1857, 1859; Seeley, 1870*b*, 1901; Britt, 1993; Wedel, 2003*a*; O'Connor & Claessens, 2005; O'Connor, 2006; Claessens, O'Connor & Unwin, 2009). All such taxa belong to the avian stem lineage Ornithodira (i.e. they are more closely related to birds than to crocodylians). For example, among theropod and sauropodomorph dinosaurs, and pterosaurs, a limited number of cervicodorsal vertebrae are often pneumatic (Britt, 1993; Wedel, 2003*a*, 2007; Butler *et al.*, 2009*b*), and more extensive pneumatisation evolved recurrently in all three groups (Britt, 1993; Xu *et al.*, 2004; O'Connor & Claessens, 2005; Butler *et al.*, 2009*b*; Claessens *et al.*, 2009).

Mass reduction in large-bodied (Cope, 1877; Janensch, 1947; Britt, 1993), and especially flying (Bramwell & Whitfield, 1974; Welty, 1982; Currey & Alexander, 1985), taxa has routinely been employed as a general explanation for the evolution of postcranial skeletal pneumaticity. These hypotheses are supported in a superficial sense by its presence in sauropods, which are uniformly large (Wedel, 2003*a*; Sander *et al.*, 2010), and in the largest non-avian theropods (Xu *et al.*, 2004; Carrano & O'Connor, 2005; O'Connor, 2007; although it is also present in many small theropods). It is prevalent in pterosaurs, especially among larger taxa, which include the largest flying animals ever to have existed on the planet (Claessens *et al.*, 2009). However, the only detailed, species-level study of the evolution of pneumaticity demonstrated that body size correlates only weakly with the proportion of pneumatised skeletal compartments in extant Anseriformes (ducks and geese). Instead, clade-specific patterns and ecological attributes such as foraging behaviour are better predictors of the extent of skeletal pneumatisation (O'Connor, 2004). After exclusion of specialised dive foragers (which have reduced skeletal pneumaticity), data from multiple bird clades show a moderate correlation between body size and the extent of postcranial pneumatisation (O'Connor, 2009,  $r^2 = 0.56$ ). Taking a wider phylogenetic perspective, although the largest extant birds have highly pneumatic skeletons (*Struthio camelus* 120–160 kg; Fowler, 1991; Britt, 1993), their body sizes are substantially smaller than those of most dinosaurs. By contrast, many non-avian theropods and almost all sauropods attained multi-tonne masses but had more limited postcranial skeletal pneumaticity, often restricted to a subset of the presacral vertebrae (especially in

basal taxa; e.g. Madsen, 1976; Sereno *et al.*, 1999; Benson, 2010). This suggests a complex situation in which different body size thresholds, and thus, different selective or physiological regimes, drove the evolution of postcranial skeletal pneumaticity in birds and non-avian dinosaurs.

Non-avian theropods form a paraphyletic grade (Fig. 1E), including bird-like taxa that mark the 'reptile'–bird transition (e.g. Gauthier, 1986; Padian & Chiappe, 1998; Ji *et al.*, 1998; Xu, 2006; Zhang *et al.*, 2008). They occupied a range of body sizes from <0.5 m in length (Xu, Zhou & Wang, 2000; Turner *et al.*, 2007) to >12.0 m (e.g. Coria & Salgado, 1995; Brochu, 2002). A complex pattern of independent increases in the extent of skeletal pneumaticity has been noted (Xu *et al.*, 2004), but not examined in detail. However, it provides a unique opportunity to assess relative pneumaticity in a size-diverse clade quantitatively, and to consider the factors that promoted the early evolution of postcranial skeletal pneumaticity on the evolutionary line leading to birds (Fig. 1E). Our aim is to review the significance of skeletal pneumaticity for understanding extinct ornithodiran biology, to provide detailed data on the distribution of postcranial skeletal pneumaticity in non-avian theropods (see supporting online information, Appendix S1), and examine quantitatively its evolutionary relationship with body size and the onset of avian-like physiology.

## (2) Institutional abbreviations

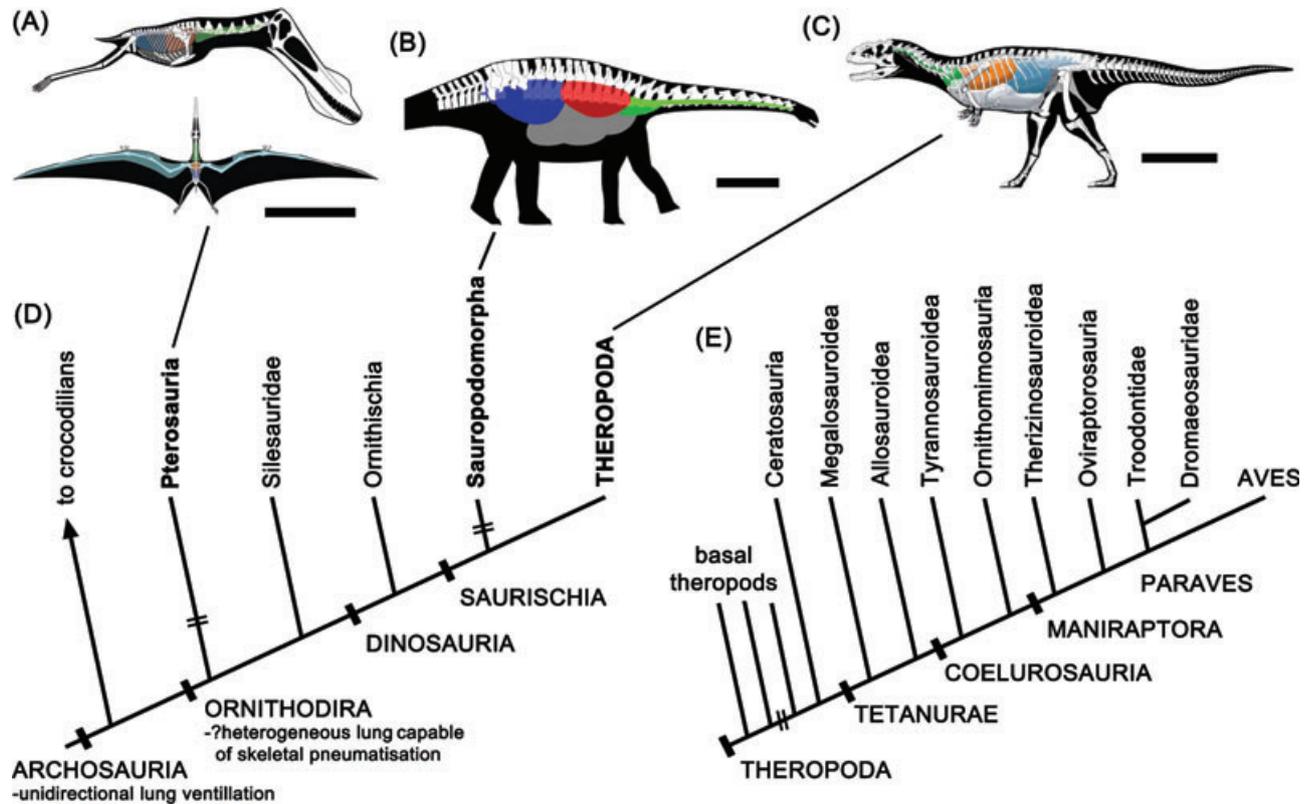
BYU, Brigham Young University Museum of Paleontology, Provo, Utah, U.S.A.; CM, Carnegie Museum of Natural History, Pittsburgh, U.S.A.; FMNH, Field Museum of Natural History, Chicago, U.S.A.; HMN, Humboldt Museum für Naturkunde, Berlin, Germany; MACN, Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia,' Buenos Aires, Argentina; MCNA, Museo de Ciencias Naturales y Antropológicas (J. C. Moyano) de Mendoza, Mendoza, Argentina; MUCP, Museo de Geología y Paleontología, Universidad Nacional del Comahue, Neuquén, Argentina; NHMUK, The Natural History Museum, London, U.K. (formerly BMNH); PVSJ, Instituto y Museo de Ciencias Naturales, San Juan, Argentina; ROM, Royal Ontario Museum, Toronto Canada; UCMP, University of California Museum of Paleontology, Berkeley, U.S.A.; UMNH, Utah Museum of Natural History, Salt Lake City, U.S.A.; USNM, National Museum of Natural History, Smithsonian Institution, Washington DC, U.S.A.

## II. POSTCRANIAL SKELETAL PNEUMATICITY IN EXTINCT NON-THEROPOD ARCHOSAURS

### (1) Recognising pneumaticity in extinct taxa

#### (a) Osteological correlates

A range of observations has been cited as evidence for postcranial skeletal pneumaticity in extinct archosaurs (Owen, 1857, 1859, 1876; Seeley, 1870*a, b*; Cope, 1877;



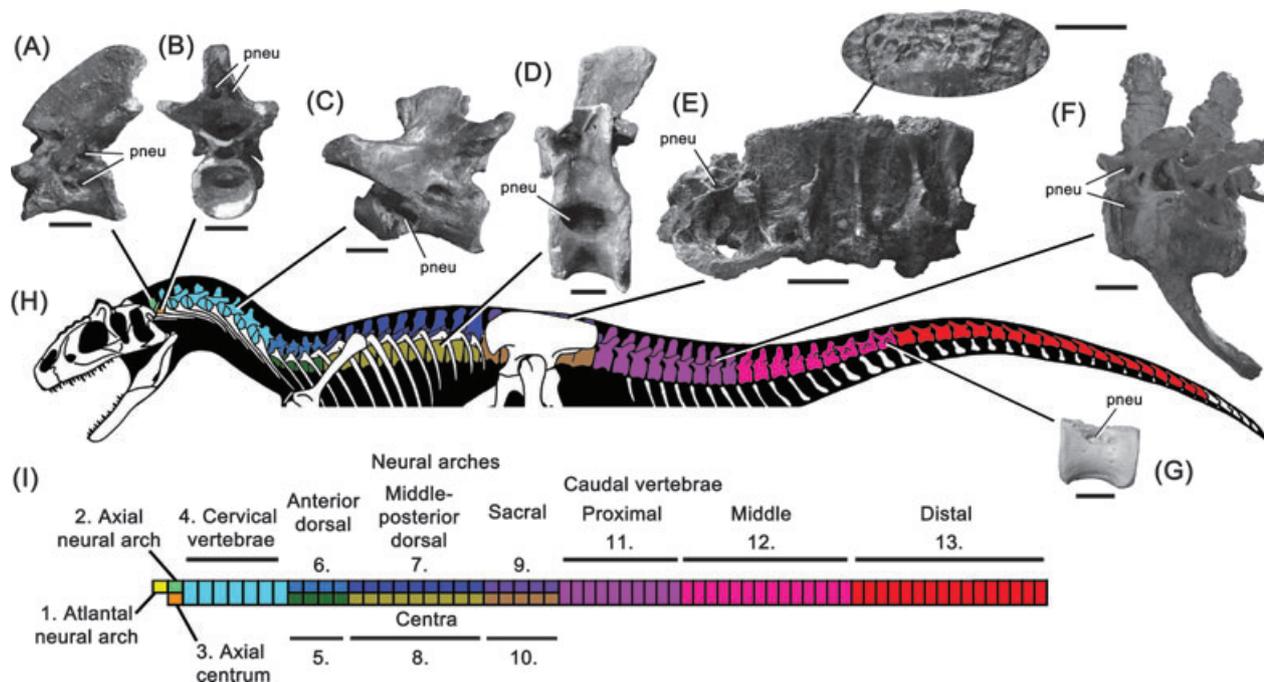
**Fig. 1.** Summary of relationships among bird-line archosaurs (Ornithodira) (D), including theropods (E). The presence of postcranial skeletal pneumaticity in pterosaurs (A), sauropodomorphs (B) and theropods (C) (indicated by bold type in D, and double-line markers in D and E) has led to the recognition of a highly heterogeneous, bird-like lung in these groups, and perhaps all ornithodirans. Modified from Claessens *et al.* (2009) (A), Wedel (2009) (B), and O'Connor and Claessens (2005) (C). Scale bars equal 1 m.

Marsh, 1877; Seeley, 1901; Janensch, 1947; de Beer, 1954). The validity of these observations was only examined recently. Britt (1993) proposed several osteological correlates of vertebral pneumaticity based on an osteological study of the extant ratites *Struthio camelus* and *Dromaius novaehollandiae*. These included large external foramina, external fossae with a crenulated surface texture, well-developed neural arch laminae, thin outer bone walls, broad and smooth or crenulated pneumatic tracks, and internal chambers opening externally *via* foramina. However, O'Connor (2006) noted that several of these features are present in crocodylians, which lack postcranial pneumaticity altogether. External fossae (and associated neural arch laminae) sometimes result from outgrowths of the lungs, but are also often associated with muscle attachments and/or fat deposits. External foramina may accommodate pneumatic diverticula, but often pertain solely to neurovascular soft tissues. Thus, the presence of large internal chambers opening externally *via* large (and thus not simply vascular) foramina has been argued to provide the only unambiguous evidence of skeletal pneumaticity (Fig. 2A–G; Britt, 1997; O'Connor, 2006; Wedel, 2007). We apply this criterion stringently, and thus consider most other features as merely ambiguous evidence of skeletal pneumaticity. This poses particular problems for understanding the early evolution

of postcranial pneumaticity, when unambiguous correlates may not yet have appeared (O'Connor, 2006; Wedel, 2007, 2009). Fortunately, most theropods (and sauropodomorphs and pterosaurs) show abundant, unambiguous evidence of axial skeletal pneumaticity (Britt, 1993; O'Connor & Claessens, 2005; Wedel, 2006; O'Connor, 2006, 2007; Sereno *et al.*, 2008).

Our study concerns the evolution of extensive pneumatisation of vertebrae by pneumatic diverticula of the air sacs. As such, we focus initially on unambiguous evidence of postcranial skeletal pneumaticity (i.e. the presence of distinct foramina that are continuous with large internal chambers within a bone; O'Connor, 2006). In some cases, foramina may be obscured by attached matrix or damage. However, in taxa with camellate pneumatic internal structure (see Section II.1*b*; Britt, 1993; fig. 1 in Wedel 2003*a*; fig. 3 in Wedel, 2003*b*), skeletal pneumaticity can be confirmed by direct observation of broken or abraded surfaces, and areas where internal diverticula penetrate the external bone surface, forming accessory foramina (Fig. 2E).

As reviewed below (see Sections II.1*b*, II.2), it is possible that external structures such as deep fossae and prominent, well-defined neural arch laminae were formed by pneumatic diverticula in at least some taxa. Our analyses focus on non-avian theropod dinosaurs because they comprise the



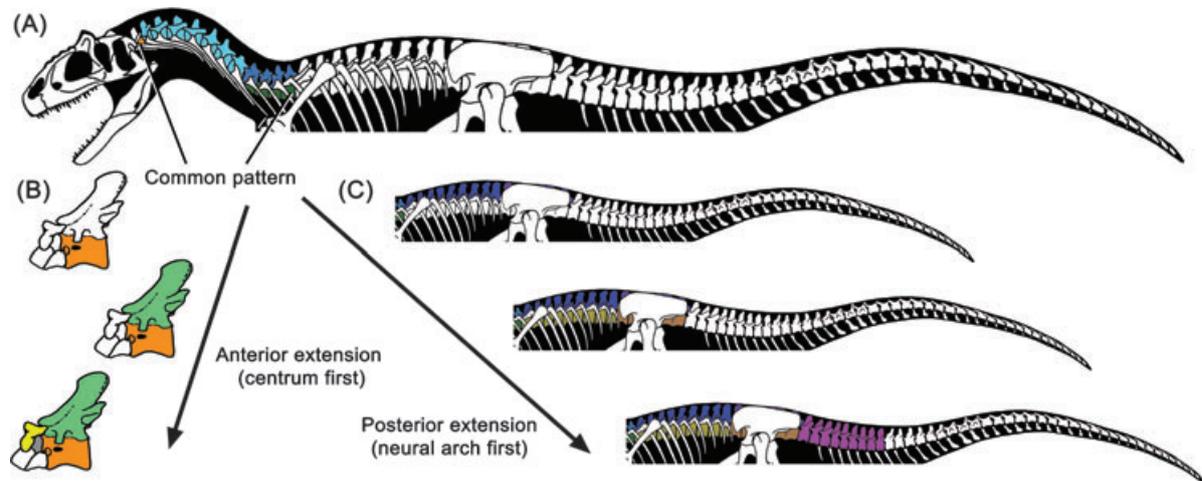
**Fig. 2.** Notional vertebral ‘compartments’ (H–I) and examples of pneumatic vertebrae (A–G). (A–B) *Carnotaurus* axis (MACN-CH 894) in (A) left lateral, and (B) posterior views. (C–G) Other theropod vertebrae in left lateral view: (C) *Baryonyx* cervical vertebra (NHMUK R9951), (D) *Torosaurus* dorsal vertebra (BYU 2008), (E) *Chirostenotes* sacral neural arches (ROM 43250) with enlarged image of internal camellae (scale bar for enlargement equals 20 mm), (F) *Megaraptor* proximal caudal vertebrae (MUCP v 341), (G) cast of *Aerosteon* middle caudal centrum (MCNA PV-3137). (H) Skeletal reconstruction of *Allosaurus* (courtesy of Scott Hartman) and schematic (I) illustrate the vertebrae compartments used in our analysis. Numbering of compartments in I corresponds to that in the text. Abbreviations: pneu, pneumatic opening. Scale bars equal 50 mm unless noted otherwise.

evolutionary line leading to birds. We have assessed the likelihood of a pneumatic origin for some ambiguous correlates of pneumaticity in theropods and conclude that they may be good evidence of pneumaticity (see Section IV.2*b*). However, we do not recommend extrapolating this conclusion to non-theropod taxa without clear justification. The hazards of ambiguous evidence are illustrated by some basal synsids (stem-group mammals), which possess deep fossae on the dorsolateral surfaces of precaudal neural arches (e.g. pl. 25 in Romer & Price, 1940; fig. 8 in Campione & Reisz, 2010) and a prominent, well-defined lamina on the lateral surface of the neural arch that extends anteroventrally from the diapophysis (e.g. *Dimetrodon gigashomogenes*, FMNH UC 112; *Dimetrodon angelensis*, FMNH UR 362). Although these features are strikingly similar to those interpreted as ambiguous evidence for pneumaticity in some extinct archosaurs, it is highly unlikely that pneumaticity was present on the mammalian stem lineage because the complex respiratory tract that enables pneumatisation is a derived feature within archosaurs (see Section III.2).

#### (b) Internal organisation of pneumatic bones

The internal organisation of pneumatic bones has been divided into two categories, originally noted by Longman (1933) and formally defined by Britt (1993). ‘Camerate’ denotes the presence of a small number of large internal

chambers (‘camerae’) within relatively thick-walled bones (Fig. 2D); ‘camellate’ denotes a large number of small, interconnected, internal chambers (‘camellae’) within very thin-walled bones (Britt, 1993, 1997) resulting in an internal honeycomb-like appearance (Fig. 2E). Camerate and camellate morphologies represent end-members of a continuous morphological spectrum, for which Wedel, Cifelli & Sanders (2000) provided a more complex classification. Studies of theropods (Britt, 1993) and sauropods (Britt, 1993; Wedel, 2003*a, b*) have documented a phylogenetic trend of increasingly complex, camellate, architecture, which may confer great mechanical strength (although this has not been tested; Wedel, 2003*b*). Birds, the only surviving theropods, generally exhibit a camellate organisation (e.g. O’Connor, 2006). Phylogenetically basal, unambiguous occurrences of pneumaticity in sauropods and theropods are characterised by camerate vertebral organisation (Britt, 1993; Wedel, 2003*a, b*). More basal taxa in both clades exhibit ambiguous evidence of pneumaticity in the form of deep, localised depressions on the lateral surfaces of the centra, superficially similar to genuinely pneumatic foramina (Colbert, 1989; Britt, 1993; Yates, 2003; Wedel, 2007). Deep depressions also occur as the first stage of skeletal pneumatisation in sauropod ontogeny (Wedel, 2003*b*; Schwarz *et al.*, 2007*b*) and likely therefore represent incipient pneumatisation.



**Fig. 3.** Skeletal reconstruction of *Allosaurus* (A, C) used to demonstrate highly conserved patterns in the evolution of theropod postcranial skeletal pneumaticity. (A) The ‘common pattern’ in which the postaxial cervical vertebrae and anterior dorsal centra are always pneumatised, and the axial centrum and anterior dorsal neural arches are commonly pneumatised (Table 2) indicated by coloured vertebrae, colours correspond to those in Fig. 2H, I; (B) the atlas-axis complex of *Allosaurus* (redrawn from Madsen, 1976) showing the centrum-first progression of anteriorwards evolutionary extensions of vertebral pneumaticity; (C) ‘neural arch-first’ posteriorwards evolutionary extension of vertebral pneumaticity.

## (2) Basal archosauriforms

The presence of postcranial skeletal pneumaticity in basal archosauriforms outside of Pterosauria and Saurischia is controversial. Gower (2001) described neural arch laminae and fossae (with associated foramina) in the Middle Triassic archosauriform *Erythrosuchus* reminiscent of morphological features sometimes identified as pneumatic in saurischian dinosaurs. On this basis, he tentatively interpreted the postcranial skeleton of *Erythrosuchus*, and several crocodile-line archosaurs with similar morphologies, as pneumatic. If correct, then the presence of postcranial skeletal pneumaticity may be plesiomorphic for Archosauria (and thus lost on the evolutionary line leading to crocodiles). However, the interpretation of *Erythrosuchus* as pneumatic has been questioned by later workers (O’Connor, 2006; Wedel, 2007), who noted the apparent absence of unambiguous evidence for postcranial skeletal pneumatisation in the form of large internal chambers. Nesbitt & Norell (2006, p. 1047) noted the presence of ‘true pleurocoels’ on the anterior cervical vertebrae of the Late Triassic crocodile-line archosaur *Effigia*. This statement has subsequently been cited as evidence of postcranial skeletal pneumaticity (Farmer, 2006; Sereno *et al.*, 2008), but Nesbitt (2007) later described this structure as a depression and acknowledged that it only provided ambiguous evidence of pneumaticity. Nonetheless, the possibility that some nonornithomiran archosaurs pneumatised the postcranial skeleton is an intriguing one that is the subject of ongoing research (e.g. Butler *et al.*, 2009a; Butler, Barrett & Gower, 2009b).

## (3) Pterosaurs

von Meyer (1837) first described postcranial skeletal pneumaticity in pterosaurs, and it was recognised by

many subsequent authors (e.g. Owen, 1859; Marsh, 1872; Seeley, 1901; Romer, 1956; Watson, 1974; Howse, 1986). Evidence of pneumaticity has frequently been described in the precaudal vertebrae, especially among Late Jurassic and Cretaceous pterodactyls (Britt, 1993; Claessens *et al.*, 2009), which have camellate organisation. More basal (non-pterodactyl) taxa have received little study. However, the Late Jurassic *Rhamphorhynchus* exhibits pneumatic cervical and anterior dorsal vertebrae and a pneumatic sternum (Britt, 1993: based on Wellnhofer, 1991; Bonde & Christiansen, 2003). Claessens *et al.* (2009) reported pneumatic foramina in the dorsal vertebrae of the late Early Jurassic taxa *Campylognathoides* and *Dorygnathus*, and Butler *et al.* (2009b) described pneumatic foramina in several Late Triassic and earliest Jurassic pterosaurs: located in the mid cervical neural arches, anterior dorsal vertebral centra and an anterior dorsal rib of *Raeticodactylus*, the mid cervical centra of *Eudimorphodon*, and the anterior–middle dorsal centra of *Dimorphodon*. Appendicular bones and more posterior vertebrae and ribs were apparently apneumatic (Butler *et al.*, 2009b), suggesting that pneumaticity was limited to cervical and anterior-middle dorsal vertebrae and cervicodorsal ribs in the earliest pterosaurs.

Seeley (1901) and O’Connor (2006) noted that pneumaticity is common in pterosaur limb bones. However, this is only present in Cretaceous pterodactyls, among which it evolved multiple times independently (reviewed by Claessens *et al.*, 2009): pneumaticity of the pectoral girdle and forelimb was achieved by a ‘postaxial pathway’ in istiodactylids and ornithocheirids, but other clades utilised a ‘preaxial pathway’. Pelvic and hindlimb pneumaticity have been less frequently documented, but were reported in the ornithocheirid *Anhanguera*, the tupuxuarid *Tupuxuara*, and the azhdarchid *Azhdarcho* (Claessens *et al.*, 2009).

#### (4) Sauropodomorph dinosaurs

Sauropodomorpha includes a basal radiation of 'prosauropod' dinosaurs, nested within which are the quadrupedal, herbivorous, long-necked sauropods. Britt (1993) and Wedel (2007) considered most basal sauropodomorphs as lacking evidence of postcranial skeletal pneumaticity (although *Pantyraco*, one of the most basal taxa, has deep pits on the lateral surfaces of the posterior cervical vertebrae that represent ambiguous evidence of pneumaticity; Yates, 2003; Wedel, 2007). However, sauropods have long been recognised as possessing pneumatic vertebrae and ribs (Seeley, 1870a; Cope, 1877; Marsh, 1877; Janensch, 1947, 1950; Romer, 1966; Wilson, 1999). Some basal sauropods exhibit pneumatic cervical and anterior dorsal vertebrae (*Jobaria*; Sereno *et al.*, 1999; Wedel, 2003b). Most neosauropods have pneumatic precaudal vertebrae (Wedel, 2003b; Schwarz & Fritsch, 2006), and within Neosauropoda, diplodocoids and titanosaurs independently acquired pneumatic caudal vertebrae (Britt, 1997; Sanz *et al.*, 1999; Wedel, 2003a) and dorsal ribs (Wilson & Sereno, 1998; Lovelace, Hartman & Wahl, 2007). Pneumatic appendicular bones are rare. However, some titanosaurs (Powell, 1992; Sanz *et al.*, 1999; Xu *et al.*, 2006) possess ilia with a camellate internal architecture, and large internal chambers were described in the ilium of the diplodocoid *Amazonsaurus* (Carvalho, Avilla & Salgado, 2003). Confirmation of these structures as pneumatic awaits discovery of well-preserved specimens with large external foramina (Wedel, 2007).

Sauropod pneumaticity is extensive (Britt, 1993); Wedel (2005) estimated that derived sauropod vertebrae comprised 60% air by volume, comparable to the situation in avian limb bones. Due to their large body size, most hypotheses of the function of sauropod pneumaticity focus on skeletal lightening as an adaptation related to mass reduction (Cope, 1877; Janensch, 1947; Britt, 1993; Schwarz, Frey & Meyer, 2007a), particularly of the extremely long neck (Wedel, 2003b; Sander *et al.*, 2010; Schwarz *et al.*, 2010). It has also been suggested that pneumatic diverticula could provide a lightweight mechanism for support and stabilisation of an extremely long neck, though this remains strictly hypothetical (Akersten & Trost, 2004; Schwarz *et al.*, 2007a; Schwarz & Frey, 2010).

### III. PHYSIOLOGICAL IMPLICATIONS OF POSTCRANIAL SKELETAL PNEUMATICITY

#### (1) Skeletal pneumaticity and air sacs enable density modulation

Skeletal pneumatisation replaces marrow, a heavy, metabolically active tissue, with air, resulting in density reduction and an hypothesised reduction in energetic costs (O'Connor, 2009). Pneumatic bones also have a thinner cortex than apneumatic bones (Currey & Alexander, 1985; Cubo & Casinos, 2000; Fajardo, Hernandez & O'Connor, 2007), further contributing to density reduction (O'Connor,

2006, 2009). Density reduction in response to the problem of weight support on land has been the focus of hypotheses regarding the evolution of skeletal pneumaticity in large dinosaurs, especially sauropods (e.g. Cope, 1877; Janensch, 1947; Romer, 1966; Welty, 1982; Britt, 1993). However, overall mass reduction enabled by pneumatisation also results in energy savings in locomotion and foraging activities (O'Connor, 2009), which could benefit animals of any size, especially those engaging in energy-intensive behaviours such as flight (in birds: Rayner, 1982; Gessaman & Nagy, 1988; Norberg, 1995; O'Connor, 2009). Density reduction of selected portions of the skeleton also provided benefits in ornithodiran evolution. For instance, pneumatisation of cervical vertebrae may have facilitated the evolution of long necks in sauropods (Wedel, 2003b), and is hypothesised to have resulted in substantial energy savings during food acquisition where the non-cervical part of the body remained static (Sander *et al.*, 2010).

Farmer (2006) hypothesised that posterior expansion of the lung in theropods resulted in localised density reductions effecting a ventral shift of the centre of mass, enhancing stability in these bipedal animals. She further suggested that avian air sacs and lung ventilation represented an adaptation for enhancing balance and agility in flight. However, as noted below (see Section III.2), it is likely that posterior expansion of the lung and differentiation into avian-like air sacs occurred early in ornithodiran evolution (Fig. 1D). Thus, if air sacs facilitated the evolution of bipedality and flight in theropods then this represents exaptation of preexisting structures rather than direct adaptation.

#### (2) Pneumaticity provides evidence for bird-like ventilatory air sacs and diverticula

In extant birds, the respiratory system is highly heterogeneous (Hunter, 1774; Duncker, 1978, 1989; Perry, 1983, 2001). The lung is a relatively small, rigid organ fixed to the anterior dorsal vertebrae and ventilated by a system of highly compliant air sacs (Dunker, 1989; Maina, 2000). Almost all gas exchange takes place in the lung (Magnussen, Willmer & Scheid, 1976), which is highly efficient compared to those of mammals (~260%; Brown, Brain & Wang, 1997). Diverticula are finger-like projections from the air sacs that extend throughout the soft tissues of birds, and sometimes invade the bones, resulting in skeletal pneumaticity. Diverticula that invade the skeleton are not pliant and do not help to ventilate the lung.

Many authors have suggested that postcranial skeletal pneumaticity provides evidence of an avian-like respiratory system (e.g. Seeley, 1870b, 1901; Bakker, 1972; Colbert, 1989). This is too simplistic (O'Connor, 2006), but the distribution of pneumaticity among skeletal components does indicate the presence of specific air sacs, homologous with those of birds, in extinct ornithodirans (Wedel, 2003b, 2007; O'Connor & Claessens, 2005; O'Connor, 2006; Claessens *et al.*, 2009; *contra* Ruben *et al.*, 1997, 1999; *contra* Ruben, Jones & Geist, 2003; *contra* Farmer, 2006; *contra* Sereno *et al.*, 2008). The presence of unidirectional air currents was

previously thought to be unique to birds among extant tetrapods, and to have been enabled by caudally located air sacs, which first appeared among extinct ornithomirans (e.g. O'Connor & Claessens, 2005). However, the occurrence of unidirectional air flow in *Alligator* suggests instead that this is primitive for archosaurs (Farmer & Sanders, 2010). Although *Alligator* has a weakly heterogeneous respiratory system, including 'air sac like' regions with reduced parenchymal densities, it does not have true air sacs or postcranial skeletal pneumaticity (e.g. O'Connor, 2006; Farmer & Sanders, 2010). Thus, the primary significance of air sacs in extinct ornithomirans is that they form part of a highly heterogeneous, and possibly highly efficient (Brown *et al.*, 1997) respiratory system (O'Connor, 2006, 2009). An auxiliary benefit of unidirectional lung ventilation is the concomitant reduction of tracheal dead space, which may have enabled the evolution of extremely long necks in sauropods and birds (Wedel, 2003b, 2007; Sander *et al.*, 2010).

Although the lung directly pneumatizes the anterior dorsal vertebrae and adjacent ribs in some birds (O'Connor & Claessens, 2005; O'Connor, 2006), most diverticula responsible for postcranial skeletal pneumaticity arise from the air sacs. Furthermore, particular components of the skeleton are invariably pneumatized by diverticula of specific air sacs. Thus, the cervical air sac diverticula pneumatize the cervical vertebrae and ribs, and the anterior dorsal vertebrae; abdominal air sac diverticula pneumatize posterior dorsal vertebrae, sacral, and caudal vertebrae; and clavicular air sac diverticula pneumatize the sternum, sternal ribs, shoulder girdle and forelimb (O'Connor, 2004; O'Connor & Claessens, 2005). The distribution of pneumatized bones in extant birds parallels that in extinct ornithomirans (O'Connor, 2006): some birds have extremely pneumatic skeletons, but many have only limited postcranial skeletal pneumaticity, often restricted to the cervicodorsal vertebrae and ribs (e.g. O'Connor, 2004, 2009), and some lack postcranial pneumaticity altogether (Owen, 1841; Gier, 1952; O'Connor, 2004, 2009). Regardless of the extent of skeletal pneumaticity, all birds possess the avian respiratory system and associated air sacs and diverticula. Thus, although the presence of pneumatic bones in specific regions of the skeleton provides evidence for specific air sacs (O'Connor & Claessens, 2005), their absence does not provide evidence for the absence of air sacs, or diverticula (O'Connor & Claessens, 2005; O'Connor, 2006; Wedel, 2006, 2007).

Several additional observations suggest that a similar underlying respiratory anatomy gave rise to skeletal pneumaticity in pterosaurs, sauropods, and theropods, including birds:

(1) detailed similarity between the osteological anatomy of pneumatic vertebrae in birds, pterosaurs, and non-avian saurischians, in which the placement of pneumatic foramina is conserved, particularly among phylogenetically basal taxa (O'Connor & Claessens, 2005; O'Connor, 2006);

(2) the regional pattern of acquisition of pneumaticity along the vertebral column in sauropod (Wedel, 2007, 2009), non-avian theropod (O'Connor, 2006; Wedel, 2009), and

pterosaur (see Section II.3, based on data in Butler *et al.*, 2009b) evolution corresponds to that documented in avian ontogeny (Müller, 1908; Bremer, 1940; Cover, 1953; Hogg, 1984a; initially diverticula are present but do not invade the skeleton, subsequently, postaxial cervical and anterior dorsal vertebrae are pneumatized first);

(3) the morphological pattern of vertebral pneumaticity in the theropod *Majungasaurus* (O'Connor & Claessens, 2005; O'Connor, 2006) and the sauropod *Haplocanthosaurus* (Wedel, 2009) suggests pneumaticity proceeding from two independent sources, one located anteriorly (the cervical air sac) and the other adjacent to the posterior dorsal and sacral vertebrae (the abdominal air sac), and is comparable to the pattern of pneumaticity in some individuals of the extant avian *Gallus gallus* (King, 1957; Hogg, 1984b; Wedel, 2003b, 2009: 'pneumatic hiatus').

Thus, there is no reason to doubt that region-specific skeletal pneumaticity evolved in the most recent common ancestor of sauropods and theropods, and perhaps pterosaurs (O'Connor, 2006; Wedel, 2006; Butler *et al.*, 2009b). If this is correct, then the distribution of postcranial skeletal pneumaticity can provide information on the respiratory anatomy of extinct ornithomirans (*contra* Farmer, 2006). Thus, pterosaurs, sauropods and theropods with pneumatic cervical and anterior dorsal vertebrae provide evidence for cervical air sacs, and representatives of these clades with pneumatic posterior dorsal, sacral, caudal or pelvic bones provide evidence of abdominal air sacs. Pneumatic pectoral bones in some theropods (Makovicky, Apesteguía & Agnolin, 2005; Sereno *et al.*, 2008; Ósi, Apesteguía & Kowalewski, 2010) indicate the presence of an interclavicular air sac (O'Connor, 2006).

The distal forelimb bones of some extant birds are pneumatized by subcutaneous diverticula, which arise from the axillary diverticulum of the interclavicular air sac (primarily large-bodied taxa that employ static soaring flight; O'Connor, 2004, 2009). Thus the presence of pneumatic distal forelimb elements in pterosaurs provides evidence for subcutaneous diverticula and an interclavicular air sac (Claessens *et al.*, 2009). These diverticula may even have been fossilized as a 'spongy' layer of subdermal tissue in an exceptionally preserved azhdarchoid wing membrane fragment (Martill & Unwin, 1989; Frey *et al.*, 2003; Claessens *et al.*, 2009).

### (3) Pneumaticity does not provide evidence for endothermy

Several authors have suggested that avian-like respiration, inferred from the presence of postcranial skeletal pneumaticity, provides evidence for endothermy in extinct archosaurs (Seeley, 1870b; Madsen, 1976; Colbert, 1989) (note that air-filled diverticula embedded in rigid skeletal elements are not pliant, and do not participate directly in lung ventilation or gas exchange; but see Warncke & Stork, 1977 on cranial skeletal pneumaticity). This is not clear. For instance, although evaporative cooling has been demonstrated in the highly vascularized trachea of certain

birds (Schmidt-Nielson *et al.*, 1969; Dawson & Whittow, 2000), there is currently no experimental evidence that the air sacs are used for similar purposes (O'Connor, 2006; *contra* Wedel, 2003b). There is therefore no support for hypothesised mechanisms of heat exchange within the air sacs of sauropods (Perry & Reuter, 1999; Perry *et al.*, 2009). However, the complex arrangement of the avian respiratory system allows the lung to be excluded from the respiratory circuit so that air flow through the trachea can be increased to enhance evaporative cooling without the risk of respiratory alkalosis (in *Struthio camelus*: Schmidt-Nielsen *et al.*, 1969; Fowler, 1991; Powell, 2000). Furthermore, a capacity for efficient gas exchange enabled by the lung-air sac system may indicate elevated metabolic potential in ornithomirans (O'Connor & Claessens, 2005; Wedel, 2009; Claessens *et al.*, 2009). At minimum, this is consistent with suggestions that they are physiologically 'intermediate' between birds and more basal reptiles (e.g. Reid, 1997).

#### IV. POSTCRANIAL SKELETAL PNEUMATICITY IN NON-AVIAN THEROPOD DINOSAURS

##### (1) Anatomy

###### (a) Vertebral pneumaticity

Early studies recognised postcranial skeletal pneumaticity in theropods primarily on the basis of pneumatic vertebrae (Owen, 1857; Marsh, 1896; Gilmore, 1920; Madsen, 1976). Britt (1993) and O'Connor (2006, 2007) described a number of distinct locations on the theropod neural arch from which pneumatic foramina could enter the bone. These are similar to those found in extant birds (O'Connor, 2006). By contrast, pneumatic invasion of vertebral centra is achieved by a more limited set of morphologies. In most non-tetanuran theropods pneumatic foramina, if present, are located anteriorly and posteriorly on the lateral surface of the centrum (e.g. Madsen & Welles, 2000; Rauhut, 2003; O'Connor, 2007). These two openings correspond to nutrient foramina that are present in apneumatic vertebral centra, but are rarely described (e.g. Britt, 1993; Zhao *et al.*, 2010). These are sometimes located within a broad, single lateral concavity ('pleurocentral depression') that has sometimes been interpreted as a pneumatic feature, but provides no unambiguous evidence as it is widely distributed among amniotes (O'Connor, 2006). The positional correspondence of pneumatic foramina in pneumatic centra with the nutrient foramina of apneumatic centra suggests that diverticula act to widen pre-existing nutrient foramina, similar to the mechanism documented in extant birds (Bremer, 1940; Britt, 1993; O'Connor, 2006). In the centra of most tetanuran theropods, and rarely among non-tetanurans such as *Liliensternus* (Rauhut, 2003), only the anterior pneumatic foramen is present (Fig. 2C, F). Detailed patterns of the evolution of theropod vertebral pneumaticity are documented in our study.

In basal theropods, vertebral pneumaticity is camerate, consisting of a small number of large internal chambers

(Britt, 1993). An extreme development of this is seen in the megalosauroid *Torvosaurus*, in which the centrum is hollowed by only two (very large) chambers, one on each side (Fig. 2D; Britt, 1991, 1993). Ceratosaurs (e.g. Britt, 1993; O'Connor, 2007), carcharodontosaurian allosauroids (e.g. Britt, 1993; Brusatte, Benson & Hutt, 2008; Sereno *et al.*, 2008), and many coelurosaurs (Fig. 2E; including birds; e.g. Sues, 1997; O'Connor, 2006) show distinctly camellate internal architecture consisting of a large number of small (diameter <10 mm) internal chambers (Britt, 1993).

###### (b) Costal pneumaticity

Many theropods that have extensive vertebral pneumatisation (e.g. middle-posterior dorsal vertebrae are pneumatised) have at least some cervical or anterior dorsal ribs that bear pneumatic foramina, including allosauroids (Madsen, 1976; Currie & Zhao, 1994; Brusatte *et al.*, 2008; Sereno *et al.*, 2008), ceratosaurs (e.g. Madsen & Welles, 2000; O'Connor, 2007), tyrannosaurids (Brochu, 2002), the oviraptorid *Heyuannia* (Lü, 2002), the dromaeosaurid *Deinonychus* (Ostrom, 1969), and the troodontid *Byronosaurus* (Makovicky *et al.*, 2003). However, only rarely are all cervical and anterior dorsal ribs pneumatised (abelisaurid ceratosaurs are an exception: Bonaparte, Novas & Coria, 1990; O'Connor, 2007). It is rare that all ribs are preserved, and in many taxa only a few are known. Thus, scoring the positive absence of pneumatisation in these ribs is difficult, and they are not included quantitatively in the present study.

Middle-posterior dorsal ribs bearing pneumatic foramina are present in some ceratosaurs (Bonaparte *et al.*, 1990; Madsen & Welles, 2000), neovenatorid allosauroids (including megaraptorans; Brusatte *et al.*, 2008; Sereno *et al.*, 2008) and some carcharodontosaurids (*Acrocanthosaurus*: Harris, 1998). It is rare that all middle-posterior ribs are pneumatised and also rare that a large sample of ribs is preserved from a single taxon. Thus, obtaining accurate, quantitative data is only possible for a few taxa that preserve the majority of dorsal ribs and this information was not included in the present study.

Sereno *et al.* (2008) interpreted gastralia of the allosauroid *Aerosteon* as pneumatic. These elements show large, undivided internal chambers and external foramina on the ventral (cutaneous) surface. Pneumatic gastralia are otherwise unknown in non-avian theropods. They are difficult to confirm in *Aerosteon* because the morphology of the external foramina is highly irregular. Although some are suboval and resemble the pneumatic foramina of vertebrae and ribs, others are mediolaterally elongate and continuous with grooves on the ventral surface of the gastralium suggestive of a pathological condition. Furthermore, the large, undivided internal chambers are unlike the highly subdivided, camellate internal structure of other pneumatic bones in *Aerosteon*, and more closely resemble the medullary cavities of apneumatic bones. Thus, confirmation of pneumatic gastralia in non-avian theropods awaits more definitive specimens.

*(c) Appendicular pneumaticity*

Although pneumatic appendicular bones, including the humerus, femur, and pectoral and pelvic girdles, are common in extant birds (Britt, 1993; O’Connor, 2004, 2006, 2009; O’Connor & Claessens, 2005; and also pterosaurs: Claessens *et al.*, 2009) they are rare among more basal theropods. Pneumatic bones of the pectoral girdle and forelimb (Makovicky *et al.*, 2005; Sereno *et al.*, 2008; Wedel, 2009; Ósi *et al.*, 2010) are more widely distributed than those of the pelvis and hindlimb, which are only unambiguously present in extremely pneumatic taxa (those with pneumatic middle caudal vertebrae). The megaraptoran allosauroids *Aerosteon* and *Australovenator* have pneumatic ilia (Sereno *et al.*, 2008; Hocknull *et al.*, 2009), and Lü & Zhang (2005) described a large pneumatic foramen in the femur of the small oviraptorid *Shixinggia*. The furcula of *Aerosteon* may also be pneumatic (see fig. 11B in Sereno *et al.*, 2008). Alternatively, this feature may be pathological as the anterior edge of the putative pneumatic foramen exhibits irregular areas of raised rugose bone (P.M. O’Connor, personal observations; Farke & O’Connor, 2007), and the internal cavity in this element is small and asymmetric. These two features contrast with the situation in pneumatic bones of most birds and other non-avian theropods. Although Colbert (1989) described ‘hollow’ limb bones in the basal theropod *Coelophysis* as pneumatic, large external foramina are absent, precluding pneumaticity and instead indicating a large marrow cavity (Britt, 1993). The rarity of pneumaticity in the theropod hindlimb may reflect the functional constraints of terrestrial locomotion at body sizes above those of most birds, which require strong, weight-supporting hindlimb bones. For instance, most non-diving pelicaniformes are hyperpneumatic and possess pneumatic femora, but the largest taxon *Pelcanus* has an apneumatic femur (whilst retaining pneumaticity in more distal hindlimb bones), which is likely related to the necessity of mediating torsional loads encountered during terrestrial locomotion (O’Connor, 2009).

Due to its rarity, appendicular pneumaticity is not amenable to the study of wide trends in non-avian theropod evolution and it was not scored in the present study. However, it is worth noting at least that pelvic and hindlimb bones are only pneumatized in taxa with the highest levels of vertebral pneumatization. Appendicular pneumatization does not likely conflict with any of the patterns reported here.

*(d) Archaeopteryx*

Because it is the earliest fossil bird, a marker of the ‘reptile’–bird transition, and an icon of evolutionary research, the status of postcranial skeletal pneumaticity in *Archaeopteryx* has been widely discussed (Britt *et al.*, 1998; Christiansen & Bonde, 2001; Mayr *et al.*, 2007; O’Connor, 2007). The distribution of vertebral pneumaticity in *Archaeopteryx* is somewhat uncertain because of incomplete preparation of existing specimens and damage. Britt *et al.* (1998) identified pneumatic foramina in the cervical centra of the ‘Berlin specimen’,

and an anterior dorsal centrum of the ‘Eichstatt specimen’, thereby positing the common pattern for *Archaeopteryx*. Christiansen & Bonde (2001) identified a pneumatic foramen in an anterior dorsal centrum, and a ‘pneumatic’ fossa in the pubis, of the ‘London specimen’. Although it resembles the condition in *Struthio camelus*, the pubic fossa identified as pneumatic by Christiansen & Bonde (2001) does not provide unambiguous evidence of pneumaticity by the criterion applied here (large internal chambers opening externally *via* large foramina; O’Connor, 2006). Furthermore, O’Connor (2007) re-examined the Berlin and London specimens. Of the pneumatic foramina reported in both specimens, he could only confirm that of the fifth cervical centrum of the Berlin specimen. Other reported foramina were obscured by damage and enclosing matrix. Mayr *et al.* (2007), described the new ‘Thermopolis’ *Archaeopteryx* specimen. Although many vertebrae are obscured, this specimen confirms the absence of pneumatic foramina in the caudal and posterior dorsal centra [a dark line on the 13<sup>th</sup> dorsal vertebra represents dendritic mineral growth (see fig. 8A,B in Mayr *et al.*, 2007; fig. 5.152 in Wellnhofer, 2008; R.J. Butler, personal observation)]. Although few unambiguously pneumatic vertebrae are well preserved in *Archaeopteryx*, cervical vertebrae are unambiguously pneumatic, and middle-posterior dorsal and caudal vertebrae are definitely apneumatic. There is currently no consensus on the condition of sacral, anterior cervical and anterior dorsal vertebrae.

**(2) New data set***(a) Data collection*

We collected data for 158 non-avian theropod taxa and *Archaeopteryx*, representing most valid taxa for which known materials were sufficient to score the condition of at least one pneumatic vertebral compartment (Table 1: 131 taxa + *Archaeopteryx*). Twenty-seven of these taxa did not preserve vertebrae and therefore only provided information on body size (femoral length estimates). A written summary of available evidence for pneumaticity in each studied taxon is provided in Appendix S1.

Table 1. Distribution of missing data on the condition of pneumatic compartments among non-avian theropods and *Archaeopteryx*. See Fig. 2I for explanation of numbering of vertebral compartments

Number of missing compartments	0	1	2	3	4	5	6
Frequency	5	4	5	11	9	11	13
Cumulative frequency	5	9	14	25	34	45	58
Number of missing compartments	7	8	9	10	11	12	13
Frequency	13	13	12	13	12	11	27
Cumulative frequency	71	84	96	109	121	132	159

Based on a comprehensive review of published descriptions and photographs, and direct observation of fossil specimens (62 of 159 total taxa; 55 of 131 taxa with data on pneumaticity) (Appendix 1), we scored 159 theropod taxa for femoral length (or an estimate thereof), and the presence of unambiguously pneumatic bones in 13 ‘compartments’ of the axial column (Fig. 2I: the atlantal neural arch (compartment 1), axial neural arch (compartment 2) and centrum (compartment 3), postaxial cervical vertebrae (compartment 4), anterior dorsal centra (compartment 5) and neural arches (compartment 6), middle-posterior dorsal neural arches (compartment 7) and centra (compartment 8), sacral neural arches (compartment 9) and centra (compartment 10), and proximal (compartment 11), middle (compartment 12) and distal (compartment 13) caudal vertebrae. This is a modification of the approach used by O’Connor (2004, 2009) to quantify the extent of skeletal pneumaticity in birds. We selected the present compartments based on empirical observations of the distributions and associations of pneumaticity among non-avian theropods made during this and previous studies (e.g. Britt, 1993). The compartments closely approximate the actual regions of the vertebral column that become pneumatized concurrently in non-avian theropods. Therefore, in most instances, all vertebrae in compartments scored as pneumatic were pneumatized, whereas no vertebrae were pneumatic in compartments scored as apneumatic. One exception is the anterior dorsal centra; in some instances only a few centra were pneumatized.

#### (b) *Treating ambiguous evidence*

Ambiguous evidence of theropod pneumaticity falls into two classes, representing a minute proportion of our data (11 instances; 0.014% of cells for which presence or absence could be scored). This small number of instances is unlikely to affect larger trends in the data and all ambiguous scores were considered as ‘present’ for the following reasons:

(1) Some anterior presacral vertebrae lack pneumatic foramina, instead showing small, but deep, lateral depressions superficially similar to unambiguously pneumatic foramina (e.g. Britt, 1993; Kobayashi & Barsbold, 2005). This occurs in basal theropods such as *Liliensternus*, *Lophostropheus* and ‘*Syntarsus*’ *kayentakatae* (postaxial cervical and anterior dorsal centra) and *Coelophys* (axial centrum), ornithomimids such as *Gallimimus* and *Harpyimimus* (postaxial cervical centra) and *Sinornithomimus* (axial centrum), the megalosauroid *Marshosaurus* (axial centrum) and the dromaeosaurid *Tsaagan* (posterior cervical–anterior dorsal centra).

The positional correspondence of these depressions to the unambiguously identifiable pneumatic foramina of other theropods, particularly close relatives or phylogenetically proximate clades, makes a pneumatic origin very likely. It appears that deep depressions are ‘intermediate’ between the absence of vertebral centrum pneumaticity and an unambiguous presence (i.e. pneumatic foramina). For instance, in *Dilophosaurus* some, but not all, of these fossae

contain large foramina, indicating pneumaticity (UCMP 37302). In *Camotaurus* (MACN-CH 894) two pneumatic foramina are generally present in presacral centra; however, on the right side of the third cervical centrum the anterior ‘foramen’ does not penetrate the bone, but forms a depression.

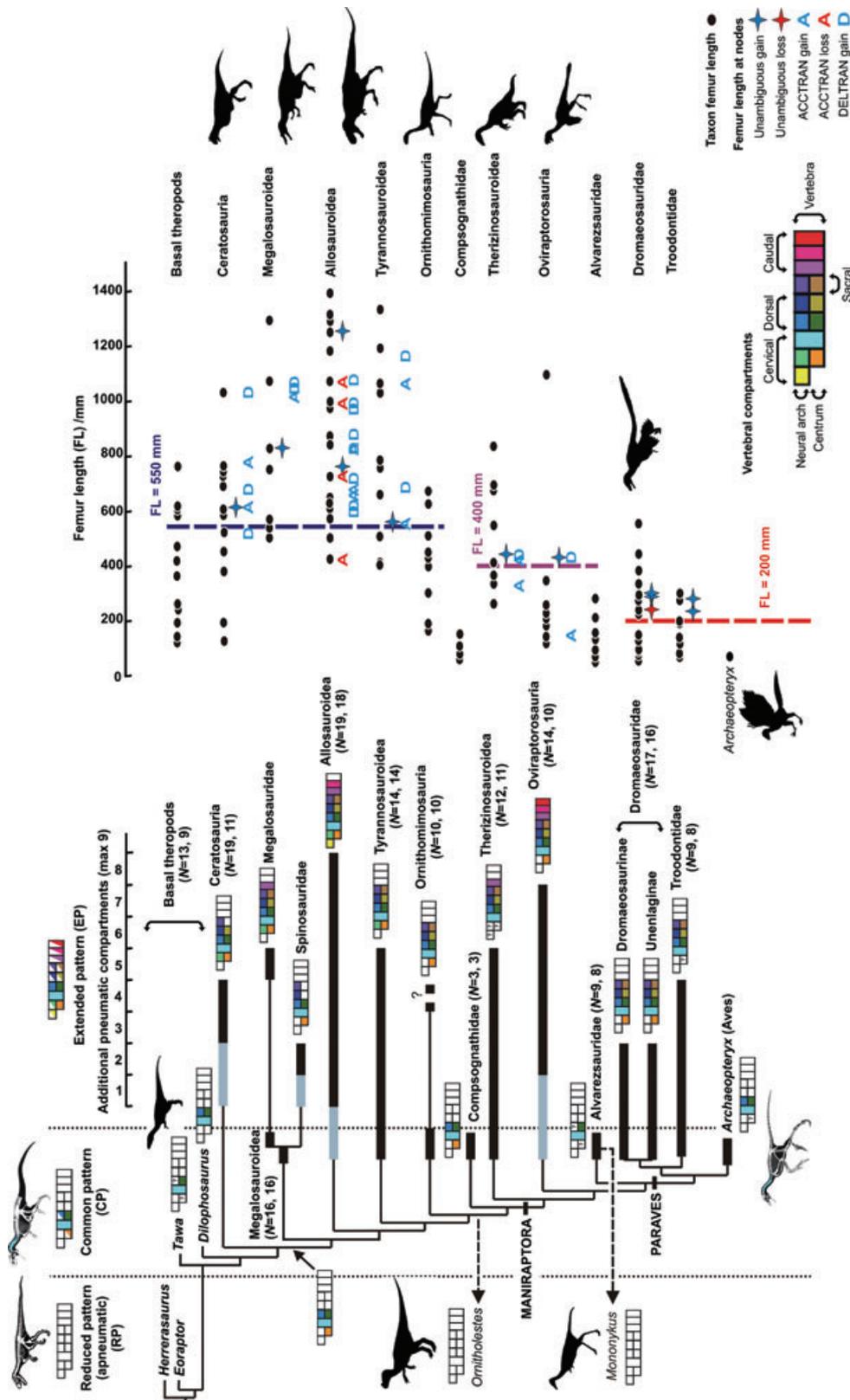
(2) In the megalosauroid *Torvosaurus*, the middle-posterior dorsal neural arch fossae are very deep and often confluent across the midline. The neural arch is effectively reduced to a series of intersecting bony plates (Britt, 1991). Britt (1993) interpreted this as evidence that the spinal cord was enclosed by pneumatic diverticula as in extant birds. However, unambiguous evidence of pneumaticity, large foramina connected to internal chambers (O’Connor, 2006), is lacking. Because all dorsal and some sacral centra are pneumatic in *Torvosaurus*, and because the posteriorwards extension of axial skeletal pneumaticity follows a neural-arch-first pattern in all other theropods (see Fig. 4 and Section IV.3c), we consider it unlikely that the middle-posterior dorsal neural arches of *Torvosaurus* are apneumatic. Thus, the condition in *Torvosaurus* is more plausibly regarded as evidence of pneumaticity rather than of its absence.

### (3) **The distribution of postcranial skeletal pneumaticity in non-avian theropods**

#### (a) *The ‘common pattern’*

Highly conserved patterns are evident in the distribution of unambiguous evidence for pneumaticity (Fig. 3). For instance, of 107 taxa that show any evidence of vertebral pneumaticity, all exhibit postaxial cervical and anterior dorsal centrum pneumaticity where these regions are preserved [Table 2; note that the left side of the 12<sup>th</sup> presacral vertebra is the only pneumatic anterior dorsal centrum in *Elaphosaurus* (HMN Gr. S. 38-44); a few taxa show only ambiguous evidence of anterior dorsal centrum pneumaticity (e.g., basal theropods; see Section IV.2b); possibly pneumatic foramina in the anterior dorsal centra of *Avimimus* are smaller than elsewhere in the vertebral column (Vickers-Rich, Chiappe & Kurzanov, 2002)]. In other words: (1) if any part of the vertebral column is pneumatized, then the postaxial cervical vertebrae and at least some anterior dorsal centra are also pneumatized; (2) if postaxial cervical–anterior dorsal vertebrae are apneumatic, then the whole postcranial skeleton is apneumatic.

Postaxial cervical–anterior dorsal pneumatization therefore represents the ‘common pattern’ (*sensu* O’Connor, 2004, 2009) of non-avian theropod postcranial skeletal pneumaticity (Fig. 3A). Anterior dorsal neural arches and the axial centrum form optional components of the common pattern; only two pneumatic taxa show evidence for the absence of pneumatic anterior dorsal neural arches (*Liliensternus* and *Marshosaurus*; Appendix S1), and pneumaticity of the axial centrum appears early in theropod evolution, but evolves plastically (e.g. Britt, 1993; Rauhut, 2003; Benson, 2010) and is only variably present among individuals of *Allosaurus* (UMNH VP specimens).



**Fig. 4.** The evolution of pneumaticity. (Left) Simplified cladogram, arranged to indicate the number and distribution of pneumatic vertebral compartments in theropod clades [the full cladogram of 137 taxa is shown in Appendix S2, Fig. S1; number of informative taxa from each clade is shown in brackets (e.g.  $N = 14, 10$  for Oviraptorosauria), the second number is the total of those taxa included in the cladogram]. Coloured boxes correspond to pneumatic compartments indicated in Fig. 2, half-filled boxes indicate variable pneumaticity as part of the common (CP), or extended (EP) patterns. The reduced pattern (RP) is apneumatic. Thick horizontal bars indicate within-clade range in the number of EP pneumatic compartments, light-blue portions of bars indicate ambiguously reconstructed states arising from incomplete knowledge of some taxa. Uncertainty within Ornithomimosauria arises from possible sacral pneumaticity in *Ornithomimus sedens* (USNM V 4736). (Right) Femoral length (FL) of taxa with each clade (black circles) and reconstructed FL at nodes for which gains (blue) or losses (red) are optimised unambiguously (stars), or under ACCTRAN (A) or DELTRAN (D). Note the rarity of evolutionary losses. Coloured, dashed lines indicate body size (FL) thresholds above which most instances of pneumaticity occur.

Table 2. Condition of postaxial cervical and anterior dorsal compartments in taxa showing any evidence of vertebral pneumaticity. The postaxial vertebrae and anterior dorsal centra are always pneumatic in taxa with pneumatic postcrania. The anterior dorsal neural arches are almost always pneumatic (there are two exceptions among pneumatised taxa: *Liliensternus* and *Marshosaurus*). Numbers in parentheses denote the compartment number. See Fig. 2I for explanation of numbering of vertebral compartments

Score	Postaxial cervical (4)	Anterior dorsal centrum (5)	Anterior dorsal neural arch (6)
Present	87	60	42
Absent	0	0	2
Ambiguous	4	2	0
Missing data	16	45	63
<b>Total</b> (pneumatic taxa)	107	107	107

(b) *The ‘reduced pattern’*

All four taxa that exhibit apneumatic cervical and/or anterior dorsal vertebrae lack postcranial pneumaticity altogether [*Herrerasaurus* (missing data for zero compartments); *Ornitholestes* (three missing compartments); *Mononykus* (five missing compartments); *Eoraptor* (five missing compartments); PVSJ 512; Novas, 1993; Perle *et al.*, 1994; Chiappe, Norell & Clark, 2002; Carpenter *et al.*, 2005; Appendix S1]. This corresponds to the ‘reduced pattern’, which is common among extant diving birds, and also apparent in the ratite *Apteryx* spp. (O’Connor, 2004, 2009). The absence of postcranial pneumaticity in *Herrerasaurus* and *Eoraptor* is plesiomorphic, whereas pneumaticity appears to have been secondarily lost in *Mononykus* and *Ornitholestes*. The reasons for this are not clear. Despite their small body sizes, neither taxon shows strong evidence of ontogenetic immaturity that might explain the absence or poor development of pneumatic features (e.g. in sauropods: Schwarz *et al.*, 2007b). For instance, the neural arches and centra are articulated in both taxa and the neurocentral sutures appear to be fully closed in *Mononykus* (Chiappe *et al.*, 2002; Carpenter *et al.*, 2005).

(c) *The ‘extended pattern’*

Many non-avian theropods have pneumatic postcranial bones anterior or posterior to those included in the common pattern. This is termed the extended pattern and is approximately equivalent to the ‘expanded’ pattern in birds (O’Connor, 2004, 2009). The extension of skeletal pneumaticity follows conserved patterns both anteriorwards and posteriorwards (Fig. 3B,C). For instance, 26 taxa have a pneumatic axial centrum (an additional four exhibit ambiguous evidence for axial centrum pneumaticity) and nine have a pneumatic axial neural arch (Table 3). All taxa with pneumatic axial neural arches also have pneumatic axial centra (eight taxa) or the condition of the axial centrum

Table 3. Distribution of pneumaticity among anterior cervical elements. There are numerous instances in which the axial centrum is pneumatised but the neural arch is apneumatic, and zero instances in which only the axial neural arch is pneumatised. This indicates that anteriorwards extension of skeletal pneumaticity follows a ‘centrum-first’ pattern. Numbers in parentheses denote the compartment number. See Fig. 2I for explanation of numbering of vertebral compartments

	Axial centrum (3)	Axial neural arch (2)	Atlantal neural arch (1)
Axial centrum also pneumatised	26	8	0
Missing data for axial centrum	—	1	1
<b>Total</b>	26 (+4 ambiguous)	9	1

was not determined (*Skorpiovenator*) (Table 3). This indicates that anteriorwards extension of skeletal pneumaticity follows a ‘centrum-first’ pattern, suggesting that anterior cervical centra must be pneumatised if anterior cervical neural arches are pneumatised (Fig. 3B). Of the analysed theropods, only *Aerosteon* has a pneumatic atlantal neural arch (Serenio *et al.*, 2008) [this is also present in the fragmentary material of *Orkoraptor* (Novas, Ezcurra & Lecuona, 2008), which was not included in our data set]. Unfortunately the axis of *Aerosteon* is not known. However, we predict that the odontoid, axial centrum and neural arch are all pneumatic, as is the case in the related taxon *Neovenator* (Brusatte *et al.*, 2008).

Pneumatisation proceeds posteriorwards from the anterior dorsal vertebrae in a ‘neural arch-first’ pattern (Fig. 3C). This is indicated by the fact that there are no instances in which the middle dorsal–sacral centra are pneumatised without neural arch pneumaticity also being present, but there are many instances in which only the neural arches of these vertebrae are pneumatised (Table 4), and these occur among several independent lineages [spinosaurid megalosauroids (Charig & Milner, 1997; Serenio *et al.*, 1998); sinraptorid allosauroids (Currie & Zhao, 1994); ceratosaurs (Madsen & Welles, 2000; O’Connor, 2007); dromaeosaurids (Norell & Makovicky, 1999); troodontids (Norell *et al.*, 2009)]. This contrasts with the ‘centrum-first’ pattern of anteriorwards extension of pneumaticity. However, in common with the anteriorwards extension, posteriorwards extension along the centra or neural arch series progresses without ‘gaps’: there are no instances in which apneumatic anterior centra or neural arches are succeeded by pneumatic centra or neural arches of a more posterior compartment (Table 4). Although the sacral neural arches of ceratosaurs, sinraptorids and spinosaurids are pneumatised, and these are posterior to apneumatic middle–posterior dorsal centra, this does not break the ‘no gaps’ rule, as the entire dorsal neural arch series is pneumatic in these clades.

Table 4. Distribution of pneumaticity in seven compartments, from the middle–posterior neural arches (7) to the distal caudals (13). Values in bold on the diagonal indicate counts of taxa showing pneumaticity in each compartment. Values above the diagonal are counts of taxa showing evidence for pneumaticity in both compartments [e.g. 17 taxa show evidence of pneumaticity in both the neural arches (7) and the centra (8) of the middle–posterior dorsals; the unaccounted 16 taxa with pneumatic mid-posterior dorsal neural arches are missing data for the mid-posterior dorsal centra]. Values below the diagonal are counts of taxa showing pneumaticity in the succeeding compartment and evidence for absence of pneumaticity in the preceding compartment [e.g. 5 taxa possess pneumaticity in sacral neural arches (9), but show evidence for absence of pneumaticity in the mid–posterior dorsal centra (8)]. Most of these values are zero, and all values are consistent with the observation that posteriorwards extension of axial pneumaticity proceeds in an uninterrupted sequence (‘no gaps’) following a ‘neural arch-first’ pattern. See Fig. 2I for explanation of numbering of vertebral compartments

	Middle–posterior dorsal		Sacral		Caudal		
	Neural arch (7)	Centrum (8)	Neural arch (9)	Centrum (10)	Proximal (11)	Middle (12)	Distal (13)
7.	<b>33</b>	17	9	6	4	3	2
8.	0	<b>28</b>	4	9	6	3	2
9.	0	5	<b>11</b>	5	3	2	2
10.	0	0	0	<b>13</b>	5	2	2
11.	0	0	0	0	<b>12</b>	5	3
12.	0	0	0	0	0	<b>5</b>	3
13.	0	0	0	0	0	0	<b>3</b>

Table 5. Average number of compartments scored as missing data per taxon for all taxa and for informative taxa (those preserving evidence of pneumatisation state) only based on the raw observational data, after interpolation following the patterns noted in the text (A), and after subsequent phylogenetic optimisation (B). Sample size equals 159 unless otherwise indicated (in square brackets)

Missing data/taxon	Direct observation	A: Interpolation + ambiguous => present	B: Phylogenetic optimisation + A
All taxa	7.9	6.0	0.68 (only considering taxa included in tree [137 taxa])
Informative taxa	6.9	4.7	

#### (4) Reconstructing missing data

##### (a) Summary

The complete data set included 159 taxa, among which the average number of compartments scored as missing data was 7.9 out of a maximum of 13 (Tables 1, 5). When taxa for which no compartments could be scored were excluded, this value fell to 6.9. However, the prevalence of missing or ambiguous scores in our data set does not accurately reflect our knowledge of theropod pneumaticity. Missing scores can be estimated based on the highly conserved patterns noted above (see Section IV.3c; Fig. 3). These allow interpolation between compartments for which the condition is known (Section IV.4b), after which the average number of missing data compartments per informative taxon was 4.7 (Table 5). Further estimation of missing data was implemented using phylogenetic optimisation, after which zero compartments were scored as missing data for taxa included in our phylogenetic tree (Section IV.5). It should be noted that

interpolation and phylogenetic optimisation minimise the number of changes hypothesised along phylogenetic lineages. Furthermore, the pneumaticity index (PI; see Section V.1) reconstructed by these methods is likely to be a minimum estimate. Both these properties indicate that our approach is conservative.

##### (b) Interpolation

Following the highly conserved principles that seem to underlie the distribution of axial skeletal pneumaticity in theropods (Fig. 3; see Section IV.3c), we are now able to reconstruct scores for many of the missing cells. Although it is possible that some, as yet undiscovered, theropods may deviate from the patterns reported above, we find that the generally low level of within-clade variability offers great promise for estimating (reconstructing) bin scores for incomplete taxa. Thus, a reliable estimate of missing data in some compartments can be obtained using the following rules:

(1) where pneumaticity is absent in either the postaxial cervical or anterior dorsal centra, all axial compartments can be reconstructed as apneumatic (reduced pattern).

(2) Where pneumaticity is present in any axial compartment, it can also be reconstructed as present in the postaxial cervical and at least some anterior dorsal centra (common pattern).

(3) Anteriorwards extension of axial skeletal pneumaticity follows a ‘centrum-first’ pattern with no gaps: as such, (a) if the axial neural arch is pneumatic then the axial centrum can be reconstructed as pneumatic; (b) if the atlantal neural arch is pneumatic then the axial centrum and neural arch can be reconstructed as pneumatic (Fig. 3B).

(4) Posteriorwards extension of axial skeletal pneumaticity follows a ‘neural arch-first’ pattern (in dorsal and sacral vertebrae) with no gaps in either the neural arch or centrum

Table 6. Summary of phylogenetic optimisation of pneumaticity among vertebral compartments. Na, neural arches. See Fig. 2I for explanation of numbering of vertebral elements

	Atlas		Axis		Cervical	Anterior dorsal		Mid-posterior dorsal		Sacral		Caudal vertebrae		
	Na 1.	Na 2.	Centrum 3.			Centrum 5.	Na 6.	Na 7.	Centra 8.	Na 9.	Centra 10.	Proximal 11.	Middle 12.	Distal 13.
Total changes	1	5	10		3	4	11	10	10	7	5	2	1	
ACCTRAN														
Gains	1	3	2	1	1	1	10	9	9	6	5	2	1	
Losses	0	2	8	2	2	3	1	1	1	1	0	0	0	
DELTRAN														
Gains	1	5	2	1	1	1	11	9	10	7	5	2	1	
Losses	0	0	8	2	2	3	0	1	0	0	0	0	0	

series so: (a) if the middle-posterior dorsal neural arches are pneumatic then the anterior dorsal neural arches can be reconstructed as pneumatic; (b) if the sacral neural arches are pneumatic then all dorsal neural arches can be reconstructed as pneumatic; (c) if middle-posterior dorsal or sacral centra are pneumatised then the corresponding neural arches, and all more anterior dorsal centra and neural arches can be reconstructed as pneumatic; (d) if any caudal vertebrae are pneumatic then all more anterior caudal vertebrae, sacral and dorsal centra and neural arches can be reconstructed as pneumatic (Fig. 3C).

We utilised the data reconstructed by interpolation to study the evolution of pneumaticity *via* the concentrated changes test, and also used it as the basis for phylogenetic optimisation (see Section IV.5).

### (5) Phylogenetic optimisation

Following reconstruction *via* interpolation, we also reconstructed missing data following predictions made by phylogenetic optimisation. Reconstruction of unambiguously optimised states using *Mesquite* 2.72 (Maddison & Maddison, 2009) resulted in a substantially reduced proportion of missing data for 137 taxa included in our phylogenetic tree (0.68 compartments/taxon; Table 5). The few cells remaining undetermined were optimised using ACCTRAN or DELTRAN, resulting in zero missing data. Both data sets were used in tests of correlation between body size (femur length) and the extent of pneumaticity. The optimisations were also inspected visually and are summarised in Fig. 4 and Table 6.

The cervical and anterior dorsal vertebrae (components of the ‘common pattern’) are pneumatised once, early in theropod history, among theropods more derived than *Eoraptor* and *Herrerasaurus* (Fig. 4). Three taxa show partial or total loss of pneumatisation in these compartments; *Mononykus* and *Ornitholestes* lost all postcranial skeletal pneumaticity (Chiappe *et al.*, 2002; Carpenter *et al.*, 2005), and *Marshosaurus* lost pneumaticity of the anterior dorsal neural arches (CM 21704). The axial (second cervical) centrum is also pneumatised early in theropod history, but evolves more plastically, showing a much higher number of losses and possibly multiple independent

gains (Table 6). Further anteriorwards and posteriorwards extension of vertebral pneumatisation (i.e. the extended pattern) each occurred multiple times independently (Fig. 4). Anteriorwards extension occurred in up to five lineages among ceratosaurs, allosauroids (perhaps up to three times), and tyrannosauroids: comprising five independent pneumatisations of the axial neural arch (under DELTRAN) or three pneumatisations with two losses (in allosauroids) under ACCTRAN (Table 6). The atlantal centrum (odontoid) and neural arch were only pneumatised in neovenatorid allosauroids.

Posteriorwards extension of pneumaticity (compartments 7–13; Table 4) occurred numerous times in theropod evolution. The posterior dorsal neural arches were pneumatised in eleven independent lineages (DELTRAN), or perhaps only ten, with a single loss among allosauroids (ACCTRAN). Posterior dorsal centra were pneumatised nine times independently, with a single unambiguous loss recorded in the dromaeosaurid *Velociraptor*, which has apneumatic middle–posterior dorsal centra (Norell & Makovicky, 1999) unlike its closest dromaeosaurine relatives (e.g. Ostrom, 1969). The evolutionary invasion of other compartments is summarised in Table 6. Note that even the caudal vertebrae were pneumatised multiple times in non-avian theropod evolution. This occurred independently among megalosaurids (Britt, 1991; cavernous openings in the laterally surfaces of proximal caudal centra of *Torusaurus* are here interpreted as pneumatic), megaraptoran allosauroids (Calvo *et al.*, 2004; Novas *et al.*, 2008; Sereno *et al.*, 2008; Benson, Carrano & Brusatte, 2010), carcharodontosaurid allosauroids (Stromer, 1931), therizinosauroids (Kirkland & Wolfe, 2001; Zhang *et al.*, 2001; Xu *et al.*, 2002; Zanno *et al.*, 2009) and oviraptorosaurs (Sues, 1997; Xu *et al.*, 2007; A. Balanoff, personal communication, 2010).

## V. ANALYSES

### (1) General information

To test the relationship between body size and the extent of postcranial pneumaticity, we compared femoral length

[FL; a proxy for body size (Christiansen & Farina, 2004; Carrano, 2006)] in millimetres with a pneumaticity index (PI). For many taxa the femoral length of the largest specimens could be measured directly (Appendix S1). For taxa in which the femur is not known, an estimate was made by comparing the size of other preserved elements with those of closely related taxa of similar size for which the femur was known (Appendix S1). Several taxa are only known from subadult individuals. For these, the FL was treated as a minimum value and therefore not used in tests of correlation. FL was log-transformed (base 10) prior to analysis so that proportionally small changes among large-bodied taxa were not overweighted. PI was calculated as the number of compartments that were pneumatized beyond the common pattern (i.e. counting nine compartments: 1–2 and 7–13) divided by the total number of compartments (i.e. nine). For instance, if only the postaxial cervical and anterior dorsal vertebrae were pneumatized then  $PI = 0$ , if the axial neural arch, middle-posterior dorsal and sacral neural arches were additionally pneumatized then  $PI = 3/9 = 0.33$ . Compartments included in the common pattern (compartments 3–6) were not used to calculate the PI as they vary little among non-avian theropods or, in the case of the axial centrum, exhibit intraspecific variation (e.g. *Allosaurus*; UMNH VP specimens). This approach to calculating PI is modified from that employed by O'Connor (2004, 2009) in extant birds. Values of PI were arcsin-transformed prior to analysis. For the correlation and generalised least-squares regression analyses described below (Section V.2), only taxa included in the tree for which femoral lengths of likely adult individuals were known (120 taxa) were included. Two versions of the PI were used.  $PI_A$  was based on scores reconstructed by ACCTRAN optimisation whereas  $PI_D$  used scores generated by DELTRAN optimisation to reconstruct missing data. As noted above (Section IV.4), only a tiny proportion of cells were ambiguously optimised (0.68 cells per taxon or 0.05% of all cells) so  $PI_A$  and  $PI_D$  are highly and significantly correlated (Pearson's  $\rho = 0.889$ ; Spearman's  $r = 0.927$ ;  $P < 0.0001$ ).

Unless otherwise noted, analyses were conducted in R version 2.10.1 (R Development Core Team, 2009). Trees were manipulated and characters optimised in *Mesquite* 2.72 (Maddison & Maddison, 2009).

## (2) Tests of correlation

### (a) Non-phylogenetically adjusted data

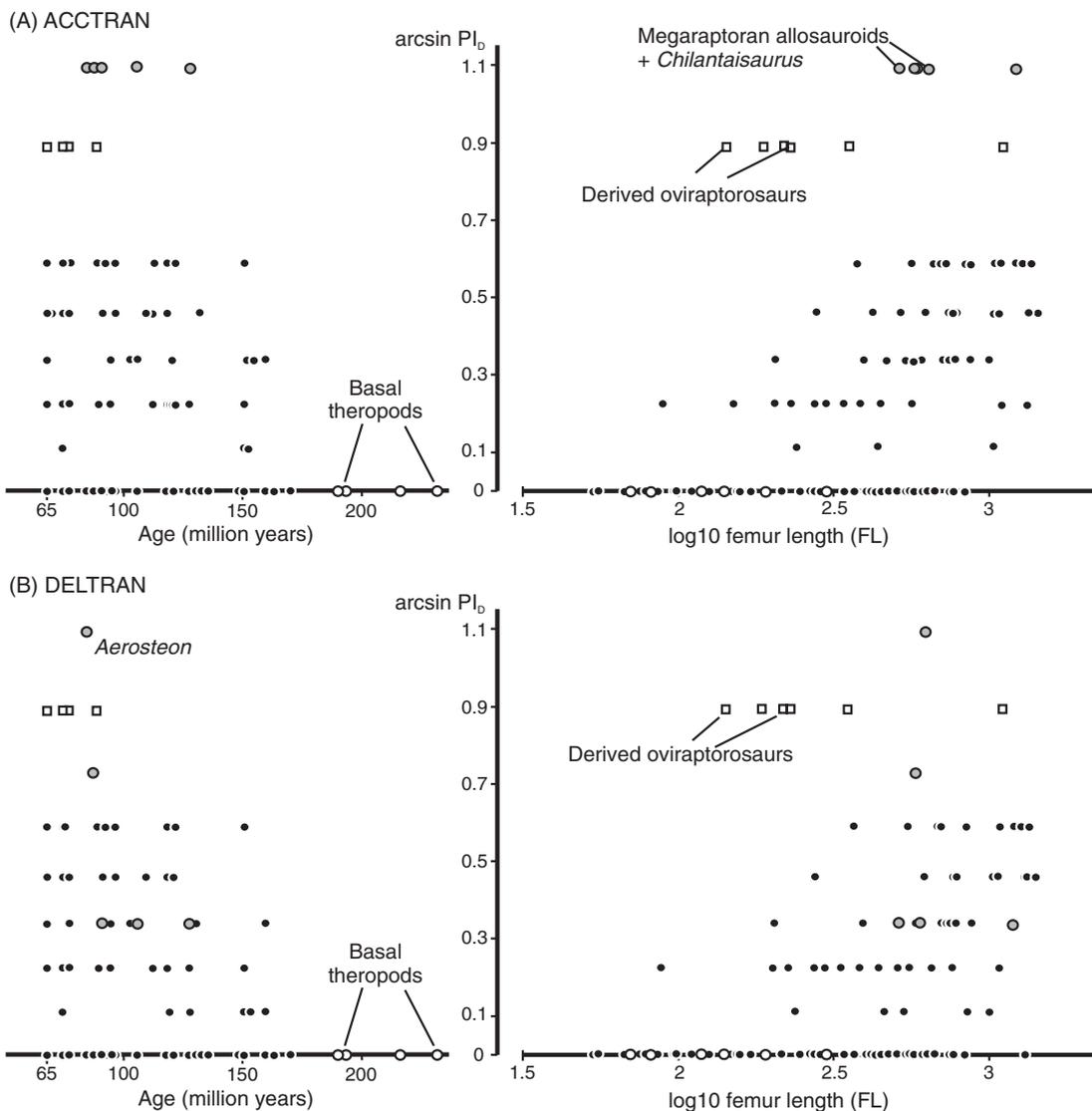
As a preliminary survey of the data we plotted arcsin PI against  $\log_{10}(\text{FL})$ , and geological age (Fig. 5) and tested correlations between these variables using Pearson's  $\rho$ . Both FL and geological age are correlated with PI (Table 7), indicating that larger theropods and geologically younger theropods generally have more pneumatic postcranial skeletons. However, inspection of the plots of geologic age versus PI (Fig. 5) indicates that PI equals zero for all Triassic–Middle Jurassic theropods (>161 million years), and substantially higher variance in PI among Late

Jurassic–Late Cretaceous theropods may be driving the correlation between PI and geological age. Consequently, when the correlation between PI and geological age is tested only for Late Jurassic–Late Cretaceous theropods, correlation coefficients are much reduced, albeit still significantly different from zero (Table 7:  $N = 98$ ; arcsin  $PI_A$  versus age: Pearson's  $rr^2 = 0.06$ ;  $P = 0.012$ ; arcsin  $PI_D$  versus age: Pearson's  $rr^2 = 0.129$ ;  $P = 0.00019$ ).

### (b) Phylogenetically adjusted data

Generalised least squares (Grafen, 1989) was used to test the relationship between body size and PI, accounting for non-independence of taxa using a variance-covariance matrix representing the phylogenetic tree with branch lengths (Appendix S2; Fig. S1; tree file available on request from the authors). This approach is functionally identical to tests of correlation using phylogenetically independent contrasts (Felsenstein, 1985; Garland & Ives, 2000) and was implemented using the R packages APE 2.5-1 (Paradis, Claude & Strimmer, 2004) and NLME 3.1-96 (Pinheiro *et al.*, 2009) following procedural advice provided by G. Hunt (personal communication 2010). The phylogenetic tree used is described in Appendix S2. Temporal branch lengths were estimated based on stratigraphic ages of taxa obtained from *The Paleobiology Database* (downloaded March 2010; most data originally compiled by M.T. Carrano) and checked by R.J. Butler and R.B.J. Benson. Minimum branch length was arbitrarily specified as 3.0 Ma. The tree was non-ultrametric (terminals were not all the same age). Branch lengths were  $\log_e$ -transformed prior to analysis to produce 'standardised' branch lengths as recommended by Garland, Harvey & Ives [1992; for use in independent contrasts analyses; standardisation was verified by inspection of the absolute contrast versus standard deviation plot using the PDAP:PD TREE 1.14 (Midford, Garland & Maddison, 2008) package of *Mesquite*]. A Brownian Motion model of continuous character evolution was applied to calculate the expected covariance between terminals for the generalized least-squares analysis.

The results indicate a statistically significant positive relationship between FL and  $PI_D$  ( $P = 0.0268$ ) (Table 8). The relationship between FL and  $PI_A$  is marginally non-significant ( $P = 0.0507$ ), but very similar to that for FL and  $PI_D$  in all other respects. The ACCTRAN and DELTRAN criteria represent extreme rationales for resolving ambiguous optimisations. It is likely that neither represents the true course of evolution over the entire tree and that the relationship between actual PI and femur length is characterised by values between those for  $PI_A$  and  $PI_D$  and is therefore statistically significant. The low regression coefficients and marginal significance values compared to those for non-phylogenetically adjusted analyses (Section V.2a; Table 7) likely arise for two reasons. (1) Phylogenetically corrected analyses effectively consider independent transitions in FL and PI as data points whereas non-phylogenetically corrected analyses consider individual taxa as data points and therefore draw on



**Fig. 5.** Scatter plots of (A) arcsin  $PI_A$  versus stratigraphic age (left) and  $\log_{10}$  FL, and (B) arcsin  $PI_D$  versus stratigraphic age (left) and  $\log_{10}$  FL.  $PI_A$  and  $PI_D$  are the pneumaticity indices based on scores reconstructed by ACCTTRAN or DELTRAN optimisation, respectively; FL is femur length. A summary of correlation statistics is given in Table 7 and the text. Most theropods are indicated by filled black circles, basal theropods (*cf.* Figs 1, 4) are indicated by unfilled black circles, megaraptoran allosauroids (and *Chilantaisaurus*) are indicated by grey filled circles, and derived oviraptorosaurs with highly pneumatic skeletons are indicated by unfilled black squares. Where  $PI = 0$ , this indicates the common or reduced patterns.

**Table 7.** Correlation coefficients for non-phylogenetically adjusted comparisons between pneumaticity index (PI), femur length (FL) and geological age.  $PI_A$ ,  $PI_D$ , pneumaticity indices based on scores generated by ACCTTRAN and DELTRAN optimisation, respectively. \*, All comparisons significant at  $P < 0.0001$  unless otherwise noted

	Pearson's $\rho$	Spearman's $r$	Kendall's $\tau$
All data ( $N = 120$ )			
Arcsin $PI_A$ versus $\log_{10}$ FL	0.418*	0.503*	0.378*
Arcsin $PI_D$ versus $\log_{10}$ FL	0.381*	0.489*	0.378*
Arcsin $PI_A$ versus age	-0.400*	-0.400*	-0.308*
Arcsin $PI_D$ versus age	-0.447*	-0.462*	-0.361*
Late Jurassic–Late Cretaceous ( $N = 98$ )			
Arcsin $PI_A$ versus age	-0.245; $P = 0.012$	-0.223; $P = 0.023$	-0.169; $P = 0.022$
Arcsin $PI_D$ versus age	-0.359; $P = 0.00019$	-0.333; $P = 0.00055$	-0.253; $P = 0.00065$

Table 8. Details of generalised least-squares regression models for the dependent variable, pneumaticity index (PI), plotted against an explanatory variable, log<sub>10</sub> femur length (FL). d.f. = 120 total; 118 residual. The regression was calculated after accounting for non-independence of phylogenetically related taxa. PI<sub>A</sub>, PI<sub>D</sub>, pneumaticity indices based on scores generated by ACCTRAN and DELTRAN optimisation, respectively

		Coefficient	Standard error	<i>t</i>	<i>P</i>
ArcsinPI <sub>A</sub> versus log <sub>10</sub> FL	Intercept	-0.275	0.151	-1.82	0.0706
	Slope	0.110	0.056	1.97	0.0507
ArcsinPI <sub>D</sub> versus log <sub>10</sub> FL	Intercept	-0.350	0.169	-2.07	0.0404
	Slope	0.140	0.0623	2.24	0.0268

more data (albeit inappropriately, giving a spuriously low *P* value). (2) Phylogenetically corrected analyses test the hypothesis that changes in FL and PI occur simultaneously on the tree. This may not be the case in all instances. Although large body size predisposes the evolution of enhanced pneumaticity (see Section V.3), some large-bodied taxa (e.g. *Megalosaurus*) have PI = 0 (the common pattern) whereas some small-bodied taxa (e.g. *Australovenator*) retain a high degree of postcranial pneumaticity from large-bodied ancestors. In other words, although body size evolution explains some of the variance in the evolution of pneumaticity, other factors such as evolutionary lag, clade-specific patterns, and perhaps ecofunctional traits, may also be important, as in birds (O'Connor, 2004, 2009).

**(3) Concentrated changes test**

The concentrated changes test (Maddison, 1990; Lorch & Eadie, 1999) determines whether changes in one character (the dependent character) are concentrated on branches of the tree that have a particular state of a second character (the independent character). This was implemented using *MacClade* 4.01 (Maddison & Maddison, 2001) to test whether increases in skeletal pneumaticity were more likely to occur on tree branches exhibiting large body size (Figs 4, S1). 'Large-size', the independent variable, was modelled in three ways (Table 9): (A) all taxa and internal nodes with FL > 550 mm were considered as large; (B) all taxa and internal nodes with FL > 400 mm were considered as large; (C) three separate criteria were applied to different sections of the tree, non-maniraptoran taxa and nodes were considered large at FL > 550 mm, non-paravian maniraptoran taxa and nodes were considered large at FL > 400 mm, and paravian taxa and nodes were considered large at FL > 200 mm. The values of FL for this variable model were determined by inspection of the data in Fig. 4.

The FL at nodes was calculated by mapping log<sub>10</sub> FL on the phylogenetic tree incorporating stratigraphic estimates of branch length (Fig. S1; branch lengths not log-transformed) using squared change parsimony in *Mesquite* 2.72 (Maddison & Maddison, 2009) (the resulting values are

Table 9. Concentrated changes test results. Cells containing bold type indicate statistically significant relationships between pneumaticity of compartments and body size (*P* values indicated in parentheses). Numbers before and after the '/' indicate the number of gains and losses respectively, so '1/0' indicates one gain and zero losses on the tree. Columns in which text is grey represent compartments for which too few changes occur to recover a statistically significant result. Cells shaded in grey indicate compartments that form part of the 'common pattern'. See Fig. 21 for explanation of numbering of vertebral compartments. Three separate models were used in the analysis: A, B and C (see text for further details)

Gains/losses on tree	Vertebral compartments											
	1 and 13	2	3	4 and 5	6	7	8	9	10	11	12	
ACCTRAN	1/0	3/2	2/8	1/2	1/3	10/1	9/1	9/1	6/1	5/0	2/0	
DELTRAN	1/0	5/0	2/8	1/2	1/3	11/0	9/1	10/0	7/0	5/0	2/0	
Gains/losses at large size												
A: ACCTRAN	0/0 (1.000)	<b>3/2 (0.026*)</b>	1/4 (0.499)	0/0 (0.358)	0/0 (0.188)	5/0 (0.205)	4/0 (0.276)	6/1 (0.155)	3/1 (0.592)	3/0 (0.433)	1/0 (0.721)	
A: DELTRAN	0/0 (1.000)	<b>5/0 (0.016*)</b>	1/2 (0.134)	0/0 (0.358)	<b>1/0 (0.045*)</b>	6/0 (0.384)	4/0 (0.276)	6/0 (0.267)	4/0 (0.414)	3/0 (0.433)	1/0 (0.721)	
B: ACCTRAN	1/0 (0.576)	3/2 (0.153)	1/4 (0.327)	0/0 (0.214)	0/1 (0.389)	5/1 (0.825)	6/0 (0.121)	6/1 (0.423)	5/1 (0.190)	5/0 (0.056)	2/0 (0.333)	
B: DELTRAN	1/0 (0.576)	5/0 (0.055)	<b>1/2 (0.0315*)</b>	0/0 (0.214)	1/1 (0.168)	8/0 (0.225)	6/0 (0.121)	<b>9/0 (0.023*)</b>	6/0 (0.118)	5/0 (0.056)	2/0 (0.333)	
C: ACCTRAN	1/0 (0.543)	<b>3/2 (0.050*)</b>	1/4 (0.333)	1/0 (0.220)	0/0 (0.0926)	<b>10/0 (0.00012*)</b>	<b>9/1 (0.0028*)</b>	7/1 (0.137)	<b>6/1 (0.022*)</b>	<b>5/0 (0.049*)</b>	2/0 (0.308)	
C: DELTRAN	1/0 (0.543)	<b>5/0 (0.049*)</b>	1/3 (0.141)	1/0 (0.220)	<b>1/0 (0.024*)</b>	<b>11/0 (0.00082*)</b>	<b>9/1 (0.0028*)</b>	<b>9/0 (0.019*)</b>	<b>7/0 (0.013*)</b>	<b>5/0 (0.049*)</b>	2/0 (0.308)	

summarised in Fig. 4). The ‘fix node’ function of *MacClade* 4.01 (Maddison & Maddison, 2001) was then used to designate the state of the independent character on the tree (Fig. S1). Finally, the concentrated changes test (CCT) was implemented in *MacClade* 4.01 for separate dependent characters representing each compartment.

Because the CCT requires a fully resolved tree, the small number of polytomies were resolved arbitrarily. This had no effect on the optimisation of the independent or dependent characters and so should not affect the outcome of the CCT. Significance values represent the probability the observed number of evolutionary gains and losses occurred by a random process (i.e. that as many gains as are observed, or more, occurred on branches showing large body size, and as many losses as observed, or fewer, occurred on those branches by a random process). A small number of nodes were ambiguously optimised for the independent character in each analysis. Therefore, each test was performed twice, once considering only unambiguous presence of the independent variable, and a second test that also incorporated any ambiguously optimised presence. The higher value (i.e. less significant) of these two runs is reported here (Table 9). The large size of the tree (135 taxa) prohibited use of an exact count to determine the distribution of statistical likelihood given the tree topology and distribution of the independent character [see Lorch & Eadie (1999) for an investigation of factors affecting this distribution]. Thus, the distribution was estimated by a simulation of 100,000 replicates, in all of which the ancestral state of the dependent variable was ‘0’. Some compartments lacked sufficient numbers of changes on the tree to recover statistically significant results, even under optimal conditions (all gains and zero losses acquired at large size). This was true for all size threshold models applied to compartments 1, 12 and 13 (atlantal neural arch, middle and distal caudal vertebrae), and for compartment 11 (proximal caudal vertebrae) under threshold model B. Failure to recover statistical significance for these compartments cannot be considered as positive or negative evidence for an association between body size and pneumatisation and the results of these tests are indicated in grey type in Table 9.

The results of the CCTs indicate that increases in pneumatisation of some compartments are statistically significantly concentrated on lineages with large body size (Table 9). The majority of such significant associations are recovered using a variable threshold to define large size (model C). Indeed, under this model, all compartments outside of those included in the common pattern (unshaded cells in Table 9) that exhibit enough changes to recover significant results show evidence that above-threshold size predisposes the evolution of enhanced pneumaticity. The extremely high level of statistical significance relative to those recovered by the other models justifies the increased complexity of the variable threshold model. Evolutionarily, this implies that relative size changes might be at least as important as absolute size changes in terms of affecting biological systems. There is a not a single threshold for all

theropods as predicted under models A or B, which are rejected as they do not obtain a statistically significant fit to the data.

## VI. DISCUSSION

### (1) The evolution of postcranial skeletal pneumaticity in non-avian theropods

#### (a) Repeated and conserved patterns

Our data confirm that patterns in the distribution of pneumaticity in non-avian theropods are similar to those in birds. Non-avian theropods show a ‘common pattern’ in which the postaxial cervical vertebrae, at least some anterior dorsal vertebrae, and occasionally the axial centrum, are pneumatised (Fig. 3). This evolved among primitive theropods more derived than *Eoraptor* and is retained by birds. It also characterises the first appearance of postcranial skeletal pneumaticity in avian ontogeny (Müller, 1908; Cover, 1953; Hogg, 1984a), and both sauropodomorph (Wedel, 2003a, 2007, 2009) and pterosaur (Butler *et al.*, 2009b; Claessens *et al.*, 2009) evolution.

In theropods, the line leading directly to birds is characterised by retention of the common pattern (Fig. 3), which is present in the basal members of most higher clades, likely including *Archaeopteryx* (Britt *et al.*, 1998; O’Connor, 2006; Mayr *et al.*, 2007). [the condition of anterior dorsal vertebrae is uncertain in *Archaeopteryx* (Section IV.1d), but they are predicted as pneumatic by our phylogenetic optimisation (Appendix S1)]. Further pneumatisation (the ‘extended pattern’) evolved independently in at least ten, and perhaps 12, lineages (Fig. 4, Table 6). Eleven of these are included in our data set and summarised in Table 6. The twelfth possible occurrence is represented by the holotype of the ornithomimid *Ornithomimus sedens*, in which the sacral centra bear deep lateral depressions or foramina (Gilmore, 1920). Unfortunately, these are filled with matrix and it is not clear if they represent pneumatic foramina or non-pneumatic depressions (USNM V 4736). Whatever the case, our data indicate a remarkably high number of parallel acquisitions of a bird-like feature in non-avian theropod evolution. An extended pattern also appeared in multiple sauropodomorph and pterosaur clades (Wedel, 2003a; Claessens *et al.*, 2009) emphasising a tendency for ornithomirans to extensively pneumatise the postcranial skeleton.

Anteriorwards extension of skeletal pneumatisation in non-avian theropods follows a ‘centrum-first’ pattern, in which centra are pneumatised before neural arches (Fig. 3B). By contrast, posteriorwards extension of pneumaticity follows a ‘neural arch-first’ pattern (Fig. 3C). Although there is currently no compelling explanation for these patterns, zero exceptions were documented among non-avian theropods. This high degree of conservatism during numerous independent acquisitions of extended pneumaticity supports the inference of a common underlying respiratory system in all non-avian theropods, because when this system invades

the skeleton it does so in a repeated, predictable sequence. Available data on extant avian pneumaticity are not resolved to the level of centra and neural arches, but instead consider whole vertebra (O'Connor, 2004, 2009) so it is currently not clear whether extant birds show the same detailed patterns as non-avian theropods.

There are no 'gaps' (instances in which apneumatic compartments are interposed between two pneumatic compartments). Furthermore, during the present study we did not find any instances of an unambiguously apneumatic vertebra or vertebrae interposed between pneumatic vertebrae ('pneumatic hiatus'). Pneumatic hiatuses occasionally occur in chickens when diverticula from different air sacs fail to anastomose (King, 1957; Hogg, 1984b). Wedel (2009) described a hiatus in the sacrum of the sauropod *Haplocanthosaurus*, and suggested that this provided evidence for multiple sources of pneumatisation, and thus multiple air sacs (Wedel, 2003b). The apparent absence of unambiguous hiatuses among non-avian theropods suggests that patterns of change in the size of pneumatic foramina may be the best evidence for the presence of multiple sources of pneumatisation. These patterns were described in *Majungasaurus* by O'Connor & Claessens (2005) and O'Connor (2006, 2007), who also observed that the same patterns in extant birds arose from the fact that pneumatic features closer to air sacs are generally larger.

#### (b) Skeletal pneumaticity and body size

There is a weak, but significant, correlation between our pneumaticity index and the body size proxy of femur length (FL) (Fig. 5, Table 7). This demonstrates that larger non-avian theropods generally exhibit more extensive vertebral pneumaticity, but that size alone does not fully explain the distribution of this trait. This is consistent with the existence of large-bodied taxa that primitively retain the common pattern, and small-bodied taxa with extremely pneumatic skeletons (Fig. 5; e.g. Sues, 1997; Vickers-Rich *et al.*, 2002; Benson, 2010). Furthermore, a regression line calculated after accounting for the non-independence of phylogenetically related taxa shows only a marginally significant fit (Table 8). This indicates that evolutionary changes in body size and pneumatisation do not always occur simultaneously, suggesting an evolutionary lag. Correspondingly, taxa such as noasaurid ceratosaurs (Carrano, Sampson & Forster, 2002; Carrano, Loewen & Sertich, 2011), some megaraptoran allosauroids (Benson *et al.*, 2010), and possibly derived oviraptorosaurs (Sues, 1997; Vickers-Rich *et al.*, 2002), retain the highly pneumatic skeleton of their larger-bodied relatives (e.g. Madsen & Welles, 2000; Xu *et al.*, 2007; Benson & Xu, 2008) despite having secondarily evolved smaller size. However, among non-maniraptoran theropods, extended pneumaticity is only ever gained at large body size (FL > 550 mm), whereas in non-paravian maniraptorans gains occur at moderate sizes (FL > 400 mm), and in paravians they occur at relatively small sizes (FL > 200 mm) (Fig. 4). The concentrated changes test (Maddison, 1990) indicates that this distribution is significantly different from

random (Table 9), and is thus independent of phyletic size decrease in coelurosaurs noted by Carrano (2006) and Turner *et al.* (2007). This is illustrated by many 'small' non-maniraptoran theropods (primarily basal theropods, ceratosaurs, tyrannosauroids, and ornithomimosauroids), which are larger than most maniraptorans but do not accrue any evolutionary increases in skeletal pneumatisation. Thus, large body size drives the evolution of enhanced pneumaticity in basal theropods, likely in response to gravitational demands related to mass support. However, our results suggest that selection for skeletal mass reduction in the form of pneumaticity occurred at much smaller body sizes among derived, bird-like theropods. This is similar to the situation in birds such as ratites (which are also derived theropods, and do not fly), most of which have a highly pneumatised vertebral column, despite their small size compared to many basal theropods.

#### (c) Postcranial skeletal pneumaticity as near-'irreversible' evolution

Evolutionary reductions in the extent of skeletal pneumatisation are rare (Table 6). Only four losses are unambiguously optimised (Fig. 4, Table 6): in *Mononykus*, *Ornitholestes*, *Marshosaurus* (which has apneumatic anterior dorsal neural arches) and *Velociraptor* (which has apneumatic middle-posterior dorsal centra). A small number of further losses are ambiguously optimised among allosauroids. It is possible that once pneumatic diverticula are integrated into the skeletal system it is difficult to return to an apneumatic condition without incurring maladaptive negative functional or developmental consequences. This hypothesis is difficult to test in the absence of combined developmental and functional studies of avian pneumaticity (see below). However, an evolutionary lag in the acquisition of pneumatisation among large-bodied theropod lineages (see Sections V.2, V.3) is also consistent with the hypothesis that pneumatisation is a 'difficult' evolutionary step.

The high likelihood of evolutionary gain over loss could plausibly result in a 'phylogenetic ratchet', whereby temporally longer lineages have more pneumatic bones. This does not appear to be the case (Table 7). An increase in the maximum extent of vertebral pneumatisation occurred abruptly during the Late Jurassic when the extended pattern originated in multiple lineages; notably, a similar transition occurred in multiple clades of pterydactyloid pterosaurs and sauropodomorphs at about this same time (Wedel, 2003a; Claessens *et al.*, 2009). However, an increase in the minimum level of pneumatisation that would be required to demonstrate a directed evolutionary trend (McShea, 1994) did not occur, suggesting that this instead indicates that different lineages followed different evolutionary trajectories (Fig. 5). Given the very high frequency of evolutionary gains in pneumaticity over losses, it seems difficult to explain how theropods maintained a low minimum level of pneumatisation over extended geological intervals (>100 million years). However, a relatively small-bodied lineage (leading to birds) gave rise to multiple clades of larger-bodied theropods that experienced relatively high rates of

turnover (Bakker *et al.*, 1992; Carrano, 2006). Thus the main line of theropod evolution consistently comprised small-bodied taxa, and thus did not accrue extensive postcranial pneumatization.

(d) *Skeletal pneumaticity and physiological innovation*

The evolution of extensive pneumatization at relatively small body sizes has been considered as a weight-saving adaptation for energetically demanding flight, especially in large birds (van Tyne & Berger, 1976; Welty, 1982; Currey & Alexander, 1985; O'Connor, 2009) and pterosaurs (Claessens *et al.*, 2009). However, because this occurs widely among derived, bird-like theropods (maniraptorans), its origin preceded avian flight. A direct physiological role (e.g. evaporative cooling) for skeletal pneumatization has not been demonstrated (O'Connor, 2006). However, pneumatization replaces heavy, metabolically active bone and marrow with air, reducing metabolic energy consumption and locomotion costs (e.g. Currey & Alexander, 1985; Cubo & Casinos, 2000; Fajardo *et al.*, 2007). O'Connor (2009) demonstrated that relative body size explained some of the variance in skeletal pneumatization of extant birds, but that clade-specific patterns and ecofunctional traits were better predictors of relative pneumaticity. For instance, static soaring taxa from multiple clades evolved hyperpneumaticity, and distantly related dive foragers such as diving ducks, penguins and loons evolved reduced pneumaticity. These correlations are related to energy savings associated with locomotion and foraging (Lovvorn & Jones, 1991; Lovvorn, Jones & Blake, 1991; O'Connor, 2009). This shows clearly that energy savings derived from skeletal pneumatization can be substantial for highly active animals, regardless of body size. It is likely then, that maniraptoran (including avian) skeletal pneumatization reflects the demands of an increasingly high-performance metabolic regime, which places a premium on energy conservation (e.g. Liem *et al.*, 2001).

Non-avian dinosaurs possessed avian-like anatomical, behavioural and physiological traits, many of which are associated with increased metabolic potential (e.g. Ji *et al.*, 1998; Erickson *et al.*, 2001; O'Connor & Claessens, 2005; Xu, 2006; Organ *et al.*, 2007). Nonetheless, inferring the physiology of extinct dinosaurs is difficult, and it is possible that many had 'intermediate' metabolic regimes. Coelurosaurs, including maniraptorans, possess a body-covering pelage composed of branching, hollow filaments that likely provided insulation (e.g. Xu, 2006) (some other dinosaurs have possibly homologous, non-branching integumentary structures; Zheng *et al.*, 2009). This suggests that they may have been endothermic, but additional physiological indicators have been lacking (Xu, 2006). Our study indicates the selective forces that shaped the evolution of skeletal pneumatization in non-avian maniraptorans are similar to those in birds (O'Connor, 2004, 2006). This is consistent with the presence of an intensive, and possibly avian-like metabolic regime (i.e. endothermic homeothermy) only in derived theropods, and complements wider observations of avian-like features in maniraptorans.

(2) **Future directions**

We have provided detailed, species-level data on non-avian theropod postcranial skeletal pneumaticity using the Pneumaticity Index (PI) as a metric of the extent of skeletal pneumatization. We relied on the presence of large external foramina continuous with internal chambers as 'unambiguous' evidence of pneumaticity, an admittedly conservative approach for assessing this trait in fossil forms. A more comprehensive understanding of the evolution of skeletal pneumaticity requires additional detailed numerical studies of extant and extinct avian clades, particularly stem neornithine groups, which have received only minimal attention in this regard.

The continued refinement of explicit morphological criteria and the application of such criteria to more basal ornithodiran and non-ornithodiran archosaurs (e.g. pseudosuchians; see Gower, 2001) are essential for characterising pneumatization within non-theropod clades and for assembling robust evolutionary hypotheses concerning the distribution of skeletal pneumaticity among archosaurs more generally. Future studies will reveal whether the highly conserved patterns observed here in non-avian theropods are also conserved in other groups. They may also indicate whether similar adaptive patterns characterise the evolution of pneumaticity across all ornithodirans. Pterosaurs are an important comparative data point because, like birds, they comprised mainly (or entirely in the case of pterosaurs) flying taxa. One obstacle to understanding the detailed distribution of pterosaur pneumaticity is the poor preservation of many specimens, which ironically often results from the presence of many fragile, thin-walled pneumatic bones (Claessens *et al.*, 2009; Butler *et al.*, 2009b). Sauropodomorphs have received relatively more attention (Wedel, 2003a, b, 2006, 2007, 2009), but also lack detailed, species-level data and may have been subject to different adaptive processes than theropods due to their higher average body sizes (e.g. Carrano, 2006). One remaining question in dinosaur biology is why the highly successful and diverse ornithischian dinosaurs apparently did not evolve postcranial skeletal pneumaticity, despite being deeply nested within Ornithodira. There are currently few clues, if any. However, hypotheses governing the evolution of pneumaticity in ornithodirans must also explain its absence in ornithischians.

Future studies may incorporate data on the relative pneumatization of individual bones to provide absolute, quantitative estimates of skeletal mass reduction such as those provided by Wedel (2005). To be possible, this will require computed tomographic scans to visualise the internal structures of pneumatic bones from many taxa. Such studies should first be conducted in extant forms in which accurate volume-mass relationships may be accurately determined. Finally, additional, detailed studies on structural and functional biomechanics (e.g. Fajardo *et al.*, 2007) and basic physiological implications (e.g. the significance for energy consumption) of skeletal pneumaticity in extant birds may clarify hypotheses regarding these traits in extinct taxa.

A better understanding of the cellular and tissue-level developmental mechanisms underlying skeletal pneumaticity would be extremely valuable (see O’Connor, 2009). Pneumaticity arises from a complex interplay among developmentally disparate tissue systems (e.g. pulmonary, muscular, skeletal) of the body, the end result of which is typified by extreme interspecific variability even among closely related avian taxa. As such, the characterisation of these mechanisms in extant birds would provide the necessary evolutionary developmental context for (1) understanding larger-scale phyletic patterns observed in various archosaurian lineages, and (2) developing hypotheses related to eco-functional attributes in now extinct forms (e.g. body size evolution). The lung-air sac system of birds and its ability to pneumatize the skeleton represents an extremely complex system, and until recently has remained enigmatic, but ongoing studies are essential for ground-truthing hypotheses about extinct forms.

## VII. CONCLUSIONS

(1) We collected data on body size and the extent of postcranial skeletal pneumatisation in 158 non-avian theropod taxa and *Archaeopteryx*. Postcranial skeletal pneumaticity evolved early in theropod evolution and is retained in birds. Patterns in the evolution of non-avian theropod pneumaticity provide our only opportunity to understand the early evolution of this characteristically ‘avian’ trait.

(2) Non-avian theropods exhibit a ‘common pattern’ in which the postaxial cervical and anterior dorsal vertebrae, and occasionally the axial centrum, are pneumatised. This is similar to that of birds, pterosaurs and sauropodomorphs, suggesting that the underlying respiratory anatomy, which is not preserved in fossils, was similar among all ornithomirans (bird-line archosaurs).

(3) The common pattern is retained on the line leading to birds, but more extensive pneumatisation evolved up to 12 times in independent lineages. This highlights a remarkably high number of independent acquisitions of a bird-like feature in non-avian dinosaurs.

(4) Highly conserved patterns in the evolutionary extension of skeletal pneumaticity exist among multiple theropod lineages: anteriorwards extensions proceed according to a ‘centrum-first’ pattern whereas posteriorwards extensions occur ‘neural-arch first’. It is currently difficult to explain these patterns but zero exceptions were observed.

(5) Body size correlates only weakly with the extent of skeletal pneumatisation. However, evolutionary increases in pneumatisation are concentrated among large-bodied lineages of basal theropods, and occur in increasingly smaller-bodied lineages among maniraptorans, and especially paravians (including birds; e.g. O’Connor, 2009). Thus, relaxation of the relationship between body size and pneumatisation preceded the origin of birds and cannot be explained as an adaptation for flight.

(6) Evolutionary losses of skeletal pneumaticity are very rare, perhaps due to functional constraints. This results in high levels of skeletal pneumaticity in some small-bodied clades derived from large-bodied ancestors such as noasaurid ceratosaurs, megaraptoran allosauroids, and perhaps aviraptorosaurs.

(7) The early evolution of postcranial skeletal pneumatisation in theropods was likely driven by weight savings in response to gravitational constraints. Skeletal mass reduction in small, non-volant, maniraptorans likely formed part of a multi-system response to increased metabolic demands. Acquisition of extensive postcranial pneumaticity in small-bodied maniraptorans may indicate avian-like high-performance endothermy.

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## IX. REFERENCES

- AKERSTEN, W. & TROST, C. H. (2004). Air sac diverticula as passive support devices in birds and saurischian dinosaurs: an overlooked biomechanical system. *Journal of Morphology* **260**, 275.
- BAKKER, R. T. (1972). Anatomical and ecological evidence of endothermy in dinosaurs. *Nature* **238**, 81–85.
- BAKKER, R. T., SIEGWARTH, J., KRALIS, D. & FILLA, J. (1992). *Edmarka rex*, a new, gigantic theropod dinosaur from the middle Morrison Formation, Late Jurassic of the Como Bluff outcrop region. *Hunteria* **2**(9), 1–24.
- BENSON, R. B. J. (2010). A description of *Megalosaurus bucklandii* (Dinosauria: Theropoda) from the Bathonian of the UK and the relationships of Middle Jurassic theropods. *Zoological Journal of the Linnean Society* **158**, 882–935.
- BENSON, R. B. J., CARRANO, M. T. & BRUSATTE, S. L. (2010). A new clade of archaic large-bodied predatory dinosaurs (Theropoda: Allosauroidae) that survived to the latest Mesozoic. *Naturwissenschaften* **97**, 71–78.
- BENSON, R. B. J. & XU, X. (2008). The anatomy and systematic position of the theropod dinosaur *Chilantaisaurus tashikouensis* Hu, 1964 from the Early Cretaceous of Alanshan, People’s Republic of China. *Geological Magazine* **145**, 778–789.
- BONAPARTE, J. F., NOVAS, F. E. & CORIA, R. A. (1990). *Camotarsus sastrei* Bonaparte, the horned, lightly built carnosaur from the Middle Cretaceous of Patagonia. *Natural History Museum of Los Angeles County, Contributions in Science* **416**, 1–42.
- BONDE, N. & CHRISTIANSEN, P. (2003). The detailed anatomy of *Rhamphorhynchus*: axial pneumaticity and its implications. In *Evolution and Paleobiology of Pterosaurs* (eds E. BUFFETAUT, J.-M. MAZIN), pp. 217–232. Geological Society, London.
- BRAMWELL, C. D. & WHITFIELD, G. R. (1974). Biomechanics of *Pteranodon*. *Philosophical Transactions of the Royal Society of London B* **267**, 503–581.
- BRIMER, J. L. (1940). The pneumatization of the humerus in the common fowl and the associated activity of the theelin. *Anatomical Record* **77**, 197–211.

- BRITT, B. B. (1991). Theropods of Dry Mesa Quarry (Morrison Formation, Late Jurassic), Colorado, with emphasis on the osteology of *Torosaurus tanneri*. *Brigham Young University Geology Studies* **37**, 1–72.
- BRITT, B. B. (1993). *Pneumatic postcranial bones in dinosaurs and other archosaurs*. PhD thesis, University of Calgary.
- BRITT, B. B. (1997). Postcranial pneumaticity. In *Encyclopedia of Dinosaurs* (eds P. J. CURRIE, K. PADIAN, E. NICHOLLS), pp. 590–593. Academic Press, San Diego.
- BRITT, B. B., MAKOVICKY, P. J., GAUTHIER, J. & BONDE, N. (1998). Postcranial pneumatization in *Archaeopteryx*. *Nature* **395**, 374–376.
- BROCHU, C. A. (2002). Osteology of *Tyrannosaurus rex*: insights from a nearly complete skeleton and high-resolution computed tomographic analysis of the skull. *Society of Vertebrate Paleontology Memoir* **7**, 1–138.
- BROWN, R. E., BRAIN, J. D. & WANG, N. (1997). The avian respiratory system: a unique model for studies of respiratory toxicosis and for monitoring air quality. *Environmental Health Perspectives* **105**, 188–200.
- BRUSATTE, S. L., BENSON, R. B. J. & HUTT, S. (2008). The osteology of *Neovenator salerii* (Dinosauria: Theropoda) from the Wealden Group (Barremian) of the Isle of Wight. *Palaeontographical Society Monograph* **162**(631), 1–75.
- BUTLER, R. J., BARRETT, P. M., ABEL, R. L. & GOWER, D. J. (2009a). A possible ctenosauriscid archosaur from the Middle Triassic Manda Beds of Tanzania. *Journal of Vertebrate Paleontology* **29**, 1022–1031.
- BUTLER, R. J., BARRETT, P. M. & GOWER, D. J. (2009b). Postcranial skeletal pneumaticity and air-sacs in the earliest pterosaurs. *Biology Letters* **5**, 557–560.
- CALVO, J. O., PORFIRI, J. D., VERALLI, C., NOVAS, F. E. & POBLETE, F. (2004). Phylogenetic status of *Megaraptor namunhuaquii* Novas based on a new specimen from Neuquén, Patagonia, Argentina. *Ameghiniana* **41**, 565–575.
- CAMPIONE, N. E. & REISZ, R. R. (2010). *Varanops brevirostris* (Eupelycosauria: Varanopidae) from the Lower Permian of Texas, with discussion of varanopid morphology and interrelationships. *Journal of Vertebrate Paleontology* **30**, 724–746.
- CARPENTER, K., MILES, C., OSTROM, J. H. & CLOWARD, K. (2005). Redescription of the small maniraptoran theropods *Ornitholestes* and *Coelurus* from the Upper Jurassic Morrison Formation of Wyoming. In *The Carnivorous Dinosaurs* (ed. K. CARPENTER), pp. 49–71. Indiana University Press, Bloomington.
- CARRANO, M. T. (2006). Body size evolution in the Dinosauria. In *Amniote Paleobiology* (eds M. T. CARRANO, T. J. GAUDIN, R. W. BLOB, J. R. WIBLE), pp. 225–268. University of Chicago Press, Chicago.
- CARRANO, M. T., LOEWEN, M. A. & SERTICH, J. W. (2011). New materials of *Masiakasaurus knopfleri* Sampson, Carrano, and Forster, 2001, and implications for the morphology of the Noasauridae (Theropoda: Ceratosauria). *Smithsonian Contributions to Paleobiology* **95**, 1–53.
- CARRANO, M. T. & O'CONNOR, P. M. (2005). Bird's-eye view. *Natural History* **114**, 42–47.
- CARRANO, M. T., SAMPSON, S. D. & FORSTER, C. A. (2002). The osteology of *Masiakasaurus knopfleri*, a small abelisauroid (Dinosauria: Theropoda) from the Late Cretaceous of Madagascar. *Journal of Vertebrate Paleontology* **22**, 510–534.
- CARVALHO, I. S., AVILLA, L. S. & SALGADO, L. (2003). *Amazonasaurus marahensis* gen. et sp. nov. (Sauropoda, Diplodocoidea) from the Lower Cretaceous (Aptian–Albian) of Brazil. *Cretaceous Research* **24**, 697–713.
- CHARIG, A. J. & MILNER, A. C. (1997). *Baryonyx walkeri*, a fish-eating dinosaur from the Wealden of Surrey. *Bulletin of the Natural History Museum, Geology Series* **53**, 11–70.
- CHEN, P.-J., DONG, Z.-M. & ZHEN, S.-N. (1998). An exceptionally well-preserved theropod dinosaur from the Yixian Formation of China. *Nature* **391**, 147–152.
- CHIAPPE, L. M., NORELL, M. A. & CLARK, J. M. (2002). The Cretaceous, short-armed Alvarezsauridae. In *Mesozoic Birds: Above the Heads of Dinosaurs* (eds L. M. CHIAPPE, L. M. WITMER), pp. 87–120. University of California Press, Berkeley.
- CHRISTIANSEN, P. & BONDE, N. (2001). Axial and appendicular in *Archaeopteryx*. *Proceedings of the Royal Society of London B* **267**, 2501–2505.
- CHRISTIANSEN, P. & FARINA, R. A. (2004). Mass prediction in theropod dinosaurs. *Historical Biology* **16**, 85–92.
- 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**(2), e4497 (doi:10.1371/journal.pone.0004497).
- CLARK, J. M., NORELL, M. A. & BARSBOLD, R. (2002). Cladistic approaches to the relationships of birds to other theropod dinosaurs. In *Mesozoic Birds: Above the Heads of Dinosaurs* (eds L. M. CHIAPPE, L. M. WITMER), pp. 31–60. University of California Press, Berkeley.
- COLBERT, E. H. (1989). The Triassic dinosaur *Coelophysis*. *Museum of Northern Arizona Bulletin* **57**, 1–160.
- COPE, E. D. (1877). On a gigantic saurian from the Dakota Epoch of Colorado. *Paleontological Bulletin* **25**, 5–10.
- CORIA, R. & SALGADO, L. (1995). A new giant carnivorous dinosaur from the Cretaceous of Patagonia. *Nature* **377**, 224–226.
- COVER, M. S. (1953). Gross and microscopic anatomy of the respiratory system of the turkey. III. The air sacs. *American Journal of Veterinary Research* **14**, 239–245.
- CUBO, J. & CASINOS, A. (2000). Incidence and mechanical significance of pneumatization in the long bones of birds. *Zoological Journal of the Linnean Society* **130**, 499–510.
- CURREY, J. D. & ALEXANDER, R. M. (1985). The thickness of the walls of tubular bones. *Journal of Zoology* **206**, 453–468.
- CURRIE, P. J. & ZHAO, X.-J. (1994). A new carnosaur (Dinosauria: Theropoda) from the Jurassic of Xinjiang, People's Republic of China. *Canadian Journal of Earth Sciences* **30**, 2037–2081.
- DAWSON, W. R. & WHITTOW, G. C. (2000). Regulation of body temperature. In *Sturkie's Avian Physiology*, 5th edition (ed. G. C. WHITTOW), pp. 343–390. Academic Press, San Diego.
- DE BEER, G. (1954). *Archaeopteryx lithographica*. British Museum of Natural History, London.
- DUNCKER, H.-R. (1971). The lung air sac system of birds. *Advances in Anatomy, Embryological and Cell Biology* **45**, 1–171.
- DUNCKER, H.-R. (1978). Functional morphology of the respiratory system and coelomic subdivisions in reptiles, birds and mammals. *Proceedings of the Zoological Society of Germany, Jena* **72**, 91–112.
- DUNCKER, H.-R. (1989). Structural and functional integration across the reptile-bird transition: locomotor and respiratory systems. In *Complex Organismal Functions: Integration and Evolution in Vertebrates* (eds D. B. R. WAKE, G. ROTH), pp. 147–169. John Wiley & Sons, New York.
- ERICKSON, G. M., CURRY-ROGERS, K. & YERBY, S. (2001). Dinosaur growth patterns and rapid avian growth rates. *Nature* **412**, 429–433.
- ERICKSON, G. M., RAUHUT, O. W. M., ZHOU, Z., TURNER, A. H., INOUE, B. D., HU, D. & NORELL, M. A. (2009). Was dinosaurian physiology inherited by birds? Reconciling slow growth in *Archaeopteryx*. *PLoS One* **4**(10), e7390 (doi:10.1371/journal.pone.0007390).
- FAJARDO, R. J., HERNANDEZ, E. & O'CONNOR, P. M. (2007). Postcranial skeletal pneumaticity: a case study in the use of quantitative microCT to assess vertebral structure in birds. *Journal of Anatomy* **211**, 138–147.
- FARKE, A. A. & O'CONNOR, P. M. (2007). Pathology in *Majungasaurus crenatissimus* (Theropoda: Abelisauridae) from the Late Cretaceous of Madagascar. *Society of Vertebrate Paleontology Memoirs* **8**, 180–184.
- FARMER, C. G. (2006). On the origin of avian air sacs. *Respiratory Physiology and Neurobiology* **154**, 89–106.
- FARMER, C. G. & SANDERS, K. (2010). Unidirectional airflow in the lungs of alligators. *Science* **327**, 338–340.
- FELSENSTEIN, J. (1985). Phylogenies and the comparative method. *American Naturalist* **125**, 1–15.
- FOWLER, M. E. (1991). Clinical anatomy of ratites. *Journal of Zoo and Wildlife Medicine* **22**, 204–227.
- FREY, E., TISCHLINGER, H., BUCHY, M.-C. & MARTILL, D. M. (2003). New specimens of Pterosauria (Reptilia) with soft parts with implications for pterosaurian anatomy and locomotion. In *Evolution and Paleobiology of Pterosaurs* (eds E. BUFFETAUT, J.-M. MAZIN), pp. 233–266. Geological Society, London.
- GARLAND, T., HARVEY, P. H. & IVES, A. R. (1992). Procedures for the analysis of comparative data using phylogenetically independent contrasts. *Systematic Biology* **41**, 18–32.
- GARLAND, T., JR & IVES, A. R. (2000). Using the past to predict the present: confidence intervals for regression equations in phylogenetic comparative methods. *American Naturalist* **155**, 346–364.
- GATESY, S. M. (2001). The evolutionary history of the theropod caudal locomotor module. In *New Perspectives on the Origin and Early Evolution of Birds* (eds J. GAUTHIER, J. F. GALL), p. 333–350. Peabody Museum of Natural History, New Haven.
- GATESY, S. M. (2002). Locomotor evolution on the line to modern birds. In *Mesozoic Birds: Above the Heads of Dinosaurs* (eds L. M. CHIAPPE, L. M. WITMER), p. 432–447. University of California Press, Berkeley.
- GATESY, S. M. & DIAL, K. P. (1996). Locomotor modules and the evolution of avian flight. *Evolution* **50**(1), 331–340.
- GAUTHIER, J. A. (1986). Saurischian monophyly and the origin of birds. *Memoirs of the California Academy of Science* **8**, 1–55.
- GESSAMAN, J. A. & NAGY, K. A. (1988). Transmitter loads affect the flight speed and metabolism of homing pigeons. *The Condor* **90**, 662–668.
- GIER, H. T. (1952). The air sacs of the loon. *The Auk* **69**, 40–49.
- GILMORE, C. W. (1920). Osteology of the carnivorous Dinosauria in the United States National Museum, with special reference to the genera *Antrodemus* (Allosaurus) and *Ceratosaurus*. *Bulletin of the United States National Museum* **110**, 1–154.
- 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.
- GRAFEN, A. (1989). The phylogenetic regression. *Philosophical Transactions of the Royal Society of London B* **326**, 119–157.
- HARRIS, J. D. (1998). Reanalysis of *Acrocanthosaurus atokensis*, its phylogenetic status, and implications, based on a new specimen. *Bulletin of the New Mexico Museum of Natural History and Science* **13**, 1–75.
- HOCKNULL, S. A., WHITE, M. A., TISCHLER, T. R., COOK, A. G., CALLEJA, N. D., SLOAN, T. & ELLIOTT, D. A. (2009). New mid-Cretaceous (latest Albian) dinosaurs from Winton, Queensland, Australia. *PLoS One* **4**(7), e6190 (doi:10.1371/journal.pone.0006190).

- HOGG, D. A. (1984a). The development of pneumatization in the postcranial skeleton of the domestic fowl. *Journal of Anatomy* **139**, 105–113.
- HOGG, D. A. (1984b). The distribution of pneumatization in the skeleton of the adult domestic fowl. *Journal of Anatomy* **138**, 617–629.
- HORNER, J. R., DE RICQLÈS, A. J. & PADIAN, K. (1999). Variation in dinosaur skeletochronology indicators: implications for age assessment and physiology. *Paleobiology* **25**, 295–304.
- HOWSE, S. C. B. (1986). On the cervical vertebrae of the Pterodactyloidea (Reptilia: Archosauria). *Zoological Journal of the Linnean Society* **88**, 307–328.
- HU, D., HOU, L., ZHANG, L. & XU, X. (2009). A pre-*Archaeopteryx* troodontid theropod from China with long feathers on the metatarsus. *Nature* **461**, 640–643.
- HUNTER, J. (1774). An account of certain receptacles of air, in birds, which communicate with the lungs, and are lodged both among the fleshy parts and in the hollow bones of those animals. *Philosophical Transactions of the Royal Society of London* **64**, 205–213.
- HUTCHINSON, J. R. (2001a). The evolution of femoral osteology and soft tissues on the line to extant birds (Neornithes). *Zoological Journal of the Linnean Society* **131**, 169–197.
- HUTCHINSON, J. R. (2001b). The evolution of pelvic osteology and soft tissue on the line to extant birds (Neornithes). *Zoological Journal of the Linnean Society* **131**, 123–168.
- HUTCHINSON, J. R. & ALLEN, V. (2009). The evolutionary continuum of limb function from early theropods to birds. *Naturwissenschaften* **96**, 423–448.
- HUXLEY, T. H. (1868). On the animals which are most nearly intermediate between birds and reptiles. *Annals and Magazine of Natural History* **4**, 66–75.
- HUXLEY, T. H. (1870). Further evidence of the affinity between the dinosaurian reptiles and birds. *Quarterly Journal of the Geological Society* **26**, 12–31.
- JANENSCH, W. (1947). Pneumatizität bei Wirbeln von Sauropoden und anderen Saurischien. *Palaeontographica, Supplement* **7**(3), 1–25.
- JANENSCH, W. (1950). Die Wirbelsäule von *Brachiosaurus brancai*. *Palaeontographica, Supplement* **7**(3), 27–92.
- JI, Q., CURRIE, P. J., NORELL, M. A. & JI, S.-A. (1998). Two feathered dinosaurs from northeastern China. *Nature* **393**, 753–761.
- KING, A. S. (1957). The aerated bones of *Gallus domesticus*. *Acta Anatomica* **31**, 220–230.
- KING, A. S. (1966). Structural and functional aspects of the avian lungs and air sacs. *International Review of Genetics and Experimental Zoology* **2**, 171–267.
- KIRKLAND, J. I. & WOLFE, D. G. (2001). First definitive therizinosauroid (Dinosauria; Theropoda) from North America. *Journal of Vertebrate Paleontology* **21**, 410–414.
- KOBAYASHI, Y. & BARSBOLD, R. (2005). Anatomy of *Harpymimus okladnikovii* Barsbold and Perle 1984 (Dinosauria; Theropoda) of Mongolia. In *The Carnivorous Dinosaurs* (ed. K. CARPENTER), pp. 97–126. Indiana University Press, Bloomington.
- LEE, A. H. & WERNING, S. (2008). Sexual maturity in growing dinosaurs does not fit reptilian growth models. *Proceedings of the National Academy of Sciences of the U.S.A.* **105**, 582–587.
- LIEM, K. F., BEMIS, W. E., WALKER, W. F. JR. & GRANDE, L. (2001). *Functional Anatomy of the Vertebrates*. Brooks/Cole, U.S.A.
- LONGMAN, H. A. (1933). A new dinosaur from the Queensland Cretaceous. *Memoirs of the Queensland Museum* **10**, 131–144.
- LORCH, P. D. & EADIE, J. MCA. (1999). Power of the concentrated changes test for correlated evolution. *Systematic Biology* **48**, 170–191.
- LOVELACE, D. M., HARTMAN, S. A. & WAHL, W. R. (2007). Morphology of a specimen of *Supersaurus* (Dinosauria, Sauropoda) from the Morrison Formation of Wyoming, and a re-evaluation of diplodocid phylogeny. *Arquivos do Museu Nacional, Rio de Janeiro* **65**, 527–544.
- LOVVORN, J. R. & JONES, D. R. (1991). Body mass, volume, and buoyancy of some aquatic birds, and their relation to locomotor strategies. *Canadian Journal of Zoology* **69**, 2888–2892.
- LOVVORN, J. R., JONES, D. R. & BLAKE, R. W. (1991). Mechanics of underwater locomotion in diving ducks: drag, buoyancy and acceleration in a size gradient of species. *Journal of Experimental Biology* **159**, 89–108.
- LÜ, J.-C. (2002). A new oviraptorosaurid (Theropoda: Oviraptorosauria) from the Late Cretaceous of southern China. *Journal of Vertebrate Paleontology* **22**, 871–875.
- LÜ, J.-C. & ZHANG, B.-K. (2005). A new oviraptorid (Theropoda: Oviraptorosauria) from the Upper Cretaceous of the Nanxiong Basin, Guangdong Province of southern China. *Acta Palaeontologica Sinica* **44**, 412–422.
- MADDISON, W. P. A. (1990). A method for testing the correlated evolution of two binary characters: are gains or losses concentrated on certain branches of a phylogenetic tree? *Evolution* **44**, 539–557.
- MADDISON, W. P. & MADDISON, D. R. (2001). MACCLADE: Analysis of Phylogeny and Character Evolution. Sinauer Associates Inc., Sunderland, Massachusetts.
- MADDISON, W. P. & MADDISON, D. R. (2009). Mesquite: a modular system for evolutionary analysis. Version 2.72. <http://mesquiteproject.org>.
- MADSEN, J. H., JR. (1976). *Allosaurus fragilis*: a revised osteology. *Utah Geological and Mineralogical Survey Bulletin* **109**, 3–163.
- MADSEN, J. H., JR. & WELLES, S. P. (2000). *Ceratosaurus* (Dinosauria, Theropoda) a revised osteology. *Miscellaneous Publications of the Utah Geological Survey* **2**, 1–80.
- MAGNUSSEN, H., WILLMER, H. & SCHEID, P. (1976). Gas exchange in air sacs: contribution to respiratory gas exchange in ducks. *Respiratory Physiology* **26**, 129–146.
- MAINA, J. N. (2000). Comparative respiratory morphology: themes and principles in the design and construction of the gas exchangers. *The Anatomical Record B* **261**, 25–44.
- MAKOVICKY, P. J., APESTEGUÍA, S. & AGNOLIN, F. L. (2005). The earliest dromaeosaurid from South America. *Nature* **437**, 1007–1011.
- MAKOVICKY, P. J., NORELL, M. A., CLARK, J. M. & ROWE, T. (2003). Osteology and relationships of *Byronosaurus jaffei* (Theropoda: Troodontidae). *American Museum Novitates* **3402**, 1–32.
- MARSH, O. C. (1872). Discovery of additional remains of Pterosauria. *American Journal of Science, series 3* **11**, 507–509.
- MARSH, O. C. (1877). Notice of new dinosaurian reptiles from the Jurassic Formation. *American Journal of Science* **14**, 514–516.
- MARSH, O. C. (1896). The dinosaurs of North America. *United States Geological Survey Annual Report* **1894–1895**, 133–244.
- MARTILL, D. M. & UNWIN, D. M. (1989). Exceptionally well-preserved pterosaur wing membrane from the Cretaceous of Brazil. *Nature* **340**, 138–140.
- MAYR, G., POHL, B., HARTMAN, S. & PETERS, D. S. (2007). The tenth skeletal specimen of *Archaeopteryx*. *Zoological Journal of the Linnean Society* **149**, 97–116.
- McSHEA, D. W. (1994). Mechanisms of large-scale evolutionary trends. *Evolution* **48**, 1747–1763.
- MEYER, H. von. (1837). Die Bayreuthen Petrefakten-Sammlungen. *Neues Jahrbuch für Mineralogie, Geognosie, Geologie und Petrefakten-Kunde* **1837**, 314–316.
- MIDFORD, P. E., GARLAND, T., JR. & MADDISON, W. (2008). PDAP:PDTree package for Mesquite, version 1.12. [http://mesquiteproject.org/pdap\\_mesquite/](http://mesquiteproject.org/pdap_mesquite/).
- MÜLLER, B. (1908). The air-sacs of the pigeon. *Smithsonian Miscellaneous Collection* **50**, 365–414.
- NESBITT, S. J. (2007). The anatomy of *Effigia okeefeae* (Archosauria, Suchia), theropod-like convergence, and the distribution of related taxa. *Bulletin of the American Museum of Natural History* **302**, 1–84.
- NESBITT, S. J. & NORELL, M. A. (2006). Extreme convergence in the body plans of an early suchian (Archosauria) and ornithomimid dinosaurs (Theropoda). *Proceedings of the Royal Society of London B* **273**, 1045–1048.
- NORBERG, U. M. (1995). How a long tail and changes in mass and wing shape affect the cost of flight in animals. *Functional Ecology* **9**, 48–54.
- NORELL, M. A., CLARK, J. M., CHIAPPE, L. M. & DASHZEVEG, D. (1995). A nesting dinosaur. *Nature* **378**, 774–776.
- NORELL, M. A., CLARK, J. M. & MAKOVICKY, P. J. (2001). Phylogenetic relationships among coelurosaurian dinosaurs. In *New Perspectives on the Origin and Evolution of Birds* (eds J. GAUTHIER, L. F. GALL), pp. 49–67. Yale University Press, New Haven.
- NORELL, M. A. & MAKOVICKY, P. J. (1999). Important features of the dromaeosaurid skeleton II: information from newly collected specimens of *Velociraptor mongoliensis*. *American Museum Novitates* **3282**, 1–45.
- NORELL, M. A., MAKOVICKY, P. J., BEVER, G. S., BALANOFF, A. M., CLARK, J. M., BARSBOLD, R. & ROWE, T. (2009). A review of the Mongolian Cretaceous dinosaur *Sauromithoides* (Troodontidae: Theropoda). *American Museum Novitates* **3654**, 1–63.
- NORELL, M. A. & XU, X. (2004). A troodontid dinosaur from China with avian-like sleeping posture. *Nature* **431**, 838–841.
- NOVAS, F. E. (1993). New information on the systematics and postcranial skeleton of *Herrerasaurus ischigualastensis* (Theropoda: Herrerasauridae) from the Ischigualasto Formation (Upper Triassic) of Argentina. *Journal of Vertebrate Paleontology* **13**, 400–423.
- NOVAS, F. E., EZCURRA, M. D. & LECUONA, A. (2008). *Orkoraptor burkei* nov. gen. et sp., a large theropod from the Maastrichtian Pari Aike Formation, Southern Patagonia, Argentina. *Cretaceous Research* **29**, 468–480.
- O'CONNOR, P. M. (2004). Pulmonary pneumaticity in the postcranial skeleton of extant Aves: a case study examining Anseriformes. *Journal of Morphology* **261**, 141–161.
- 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. *Journal of Morphology* **267**, 1199–1226.
- O'CONNOR, P. M. (2007). The postcranial axial skeleton of *Majungasaurus crenatissimus* (Theropoda: Abelisauridae) from the Late Cretaceous of Madagascar. *Society of Vertebrate Paleontology Memoir* **8**, 127–162.
- O'CONNOR, P. M. (2009). Evolution of archosaurian body plans: skeletal adaptations of an air-sac-based breathing apparatus in birds and other archosaurs. *Journal of Experimental Zoology A* **311**, 504–521.
- 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.
- ORGAN, C. L., BRUSATTE, S. & STEIN, K. (2009). Sauropod dinosaurs evolved moderately sized genomes unrelated to body size. *Proceedings of the Royal Society, B* **276**, 4303–4308.
- ORGAN, C. L., SHEDLOCK, A. M., MEADE, A., PAGEL, M. & EDWARDS, S. V. (2007). Origin of avian genome size and structure in non-avian dinosaurs. *Nature* **446**, 180–184.
- ORTEGA, F., ESCASO, F. & SANZ, J. L. (2010). A bizarre, humped Carcharodontosauria (Theropoda) from the Lower Cretaceous of Spain. *Nature* **467**, 203–206.
- ÓSI, A., APESTEGUÍA, S. & KOWALEWSKI, M. (2010). Non-avian theropod dinosaurs from the early Late Cretaceous of central Europe. *Cretaceous Research* **31**, 304–320.

- OSTROM, J. H. (1969). Osteology of *Deinonychus antirrhopus*, an unusual theropod from the Lower Cretaceous of Montana. *Bulletin of the Peabody Museum of Natural History* **30**, 1–165.
- OSTROM, J. H. (1976). *Archaeopteryx* and the origin of birds. *Biological Journal of the Linnean Society* **8**, 91–182.
- OWEN, R. (1841). On the anatomy of the Southern *Apteryx* (*Apteryx australis*, Shaw). *Transactions of the Zoological Society of London* **2**, 257–301.
- OWEN, R. (1857). Monograph on the fossil Reptilia of the Wealden and Purbeck formations. Part III: Dinosauria (*Megalosaurus*). *Palaeontographical Society Monographs* **9**(34, for 1855), 1–26.
- OWEN, R. (1859). Monograph on the fossil Reptilia of the Cretaceous formations. Supplement No. 1. Pterosauria (*Pterodactylus*). *Palaeontographical Society Monographs* **11**(47, for 1857), 1–19.
- OWEN, R. (1876). Monograph on the fossil Reptilia of the Wealden and Purbeck Formations. Supplement 7. Crocodilia (*Poikilopleuron*). Dinosauria (*Chondrosteosaurus*). *Palaeontographical Society Monographs* **30**(136), 1–7.
- PADIAN, K. & CHIAPPE, L. M. (1998). The origin and early evolution of birds. *Biological Reviews* **73**, 1–42.
- PARADIS, E., CLAUDE, J. & STRIMMER, K. (2004). APE: analysis of phylogenetics and evolution in R language. *Bioinformatics* **20**, 289–290.
- PERLE, A., CHIAPPE, L. M., BARSBOLD, R., CLARK, J. M. & NORELL, M. A. (1994). Skeletal morphology of *Mononykus olecranus* (Theropoda: Avialae) from the Late Cretaceous of Mongolia. *American Museum Novitates* **3105**, 1–29.
- PERRY, S. F. (1983). Reptilian lungs: functional anatomy and evolution. *Advances in Anatomy, Embryology and Cell Biology* **79**, 1–81.
- PERRY, S. F. (2001). Functional morphology of the reptilian and avian respiratory systems and its implications for theropod dinosaurs. In *New Perspectives on the Origin and Early Evolution of Birds* (eds J. GAUTHIER, L. F. GALL), pp. 429–441. Peabody Museum of Natural History, New Haven.
- PERRY, S. F., CHRISTIAN, A., BREUER, T., PAJOR, N. & CODD, J. R. (2009). Implications of an avian-style respiratory system for gigantism in sauropod dinosaurs. *Journal of Experimental Zoology* **311A**, 600–610.
- PERRY, S. F. & REUTER, C. (1999). Hypothetical lung structure of *Brachiosaurus* (Dinosauria: Sauropoda) based on functional constraints. *Mitteilungen aus dem Museum für Naturkunde der Humboldt-Universität Berlin, Geowissenschaftliche Reihe* **2**, 75–79.
- PINHEIRO, J., BATES, D., DEBROY, S., SARKAR, D. & R CORE TEAM (2009). nlmc: Linear and Nonlinear Mixed Effects Models. *R package version 3.1*–93.
- POWELL, F. L. (2000). Respiration. In *Sturkie's Avian Physiology*, 5<sup>th</sup> edition (ed. C. G. WHITTOW), pp. 233–264. Academic Press, New York.
- POWELL, J. E. (1992). Osteología del noroeste Argentino. In *Los Dinosaurios y Su Entorno Biotico: Actas del Segundo Curso del Paleontología en Cuenca* (eds J. L. SANZ, A. D. BUSCALONI), pp. 165–230. Instituto Juan de Valdes, Cuenca, Argentina.
- R Development Core Team. (2009). A language and environment for statistical computing. <http://www.R-project.org>.
- RAUHUT, O. W. M. (2003). The interrelationships and evolution of basal theropod dinosaurs. *Special Papers in Palaeontology* **69**, 1–213.
- RAYNER, J. M. V. (1982). Avian flight energetics. *Annual Reviews in Physiology* **44**, 109–119.
- REID, R. E. H. (1997). Dinosaurian physiology: the case for “intermediate dinosaurs”. In *The Complete Dinosaur* (eds J. O. FARLOW, M. K. BRETT-SURMAN), pp. 449–473. Indiana University Press, Bloomington.
- ROMER, A. S. (1956). *Osteology of the Reptiles*. University of Chicago Press, Chicago.
- ROMER, A. S. (1966). *Vertebrate Paleontology*, 3<sup>rd</sup> edition. University of Chicago Press, Chicago.
- ROMER, A. S. & PRICE, L. I. (1940). Review of the Pelycosauria. *Special papers of the Geological Society of America* **28**, 1–538.
- RUBEN, J. A., DAL SASSO, C., GEIST, N. R., HILLENIUS, W. J., JONES, T. D. & SIGNORE, M. (1999). New evidence for pulmonary function and metabolic physiology of theropod dinosaurs. *Science* **283**, 514–516.
- RUBEN, J. A., JONES, T. D. & GEIST, N. R. (2003). Respiratory and reproductive paleophysiology of dinosaurs and early birds. *Physiological and Biochemical Zoology* **76**, 141–164.
- RUBEN, J. A., JONES, T. D., GEIST, N. R. & HILLENIUS, W. J. (1997). Lung structure and ventilation in theropod dinosaurs and early birds. *Science* **278**, 1267–1270.
- SANDER, P. M. (2000). Long bone histology of the Tendaguru sauropods: implications for growth and biology. *Paleobiology* **26**, 466–488.
- SANDER, P. M., CHRISTIAN, A., CLAUS, M., FECHNER, R., GEE, C. T., GRIEBELER, E.-M., GUNGA, H.-C., HUMMEL, J., MALLISON, H., PERRY, S. F., PREUSCHOF, H., RAUHUT, O. W. M., REMES, K., TUTKEN, T., WINGS, O. & WITZEL, U. (2010). Biology of the sauropod dinosaurs: the evolution of gigantism. *Biological Reviews*. (doi: 10.1111/j.1469-185X.2010.00137.x)
- SANZ, J. L., POWELL, J. E., LEOEUFF, J., MARTINEZ, R. & PEREDA, X. (1999). Sauropod remains from the Upper Cretaceous of Laño (north-central Spain). Titanosaur phylogenetic relationships. *Estudios del Museo de Ciencias Naturales de Alva 14*(numero especial 1), 235–255.
- SCHMIDT-NIELSEN, K., KANWISHER, J., LASIEWSKI, R. C., COHN, J. E. & BRETZ, W. L. (1969). Regulation and respiration in the ostrich. *The Condor* **71**, 341–352.
- SCHWARZ, D. & FREY, E. (2010). Is there an option for a pneumatic stabilization of sauropod necks?—An experimental and anatomical approach. *Palaeontologica Electronica* **11**(3), 17A: 26p.
- SCHWARZ, D., FREY, E. & MEYER, C. A. (2007a). Pneumaticity and soft-tissue reconstructions in the neck of diplodocoid and dicraeosaurid sauropods. *Acta Palaeontologica Polonica* **52**, 167–188.
- SCHWARZ, D. & FRITSCH, G. (2006). Pneumatic structures in the cervical vertebrae of the Late Jurassic Tendaguru sauropods *Brachiosaurus brancai* and *Dicraeosaurus*. *Ecologiae Geologicae Helvetica* **99**, 65–78.
- SCHWARZ, D., IKEJIRI, T., BREITHAUPT, B. H., SANDER, P. M. & KLEIN, N. (2007b). A nearly complete skeleton of an early juvenile diplodocid (Dinosauria: Sauropoda) from the Lower Morrison Formation (Late Jurassic) of north central Wyoming and its implications for early ontogeny and pneumaticity in sauropods. *Historical Biology* **19**, 225–253.
- SCHWARZ, D., MEYER, C. A., FREY, E., MANZ-STEINER, H.-R. & SCHUMACHER, R. (2010). Mechanical implications of pneumatic neck vertebrae in sauropod dinosaurs. *Proceedings of the Royal Society B* **277**, 11–17.
- SCHWEITZER, M. H., WITTMAYER, J. L. & HORNER, J. R. (2005). Gender-specific reproductive tissue in ratites and *Tyrannosaurus rex*. *Science* **308**, 1456–1460.
- SEELEY, H. G. (1870a). On *Ornithopsis*, a gigantic animal of the pterodactyle kind from the Wealden. *Annals and Magazine of Natural History (series 4)* **5**, 279–283.
- SEELEY, H. G. (1870b). *The Ornithosauria*. Deighton, Bell & Co., Cambridge.
- SEELEY, H. G. (1901). *Dragons of the air*. D. Appleton, New York.
- SERENO, P. C. (1999). The evolution of dinosaurs. *Science* **284**, 2137–2147.
- SERENO, P. C., BECK, A. I., DUTHEIL, D. B., GADO, B., LARSSON, H. C. E., LYON, G. H., MARCOT, J. D., RAUHUT, O. W. M., SADLEIR, R. W., SIDOR, C. A., VARRICCHIO, D. D., WILSON, G. P. & WILSON, J. A. (1998). A long-snouted predatory dinosaur from Africa and the evolution of spinosauroids. *Science* **282**, 1298–1302.
- SERENO, P. C., BECK, A. L., DUTHEIL, D. B., LARSSON, H. C. E., LYON, G. H., MOUSSA, B., SADLEIR, R. W., SIDOR, C. A., VARRICCHIO, D. J., WILSON, G. P. & WILSON, J. A. (1999). Cretaceous sauropods and the uneven rate of skeletal evolution among dinosaurs. *Science* **286**, 1342–1347.
- SERENO, P. C., MARTINEZ, R. N., WILSON, J. A., VARRICCHIO, D. J., ALCOBER, O. A. & LARSSON, H. C. E. (2008). Evidence for avian intrathoracic air sacs in a new predatory dinosaur from Argentina. *PLoS One* **3**(9), e3303 (doi:10.1371/journal.pone.0003303).
- STROMER, E. (1931). Wirbeltier-Reste der Baharije-Stufe (unterstes Cenoman). 10. En Skelett-Rest von *Carcharodontosaurus* nov. gen. *Abhandlungen der Bayerischen Akademie der Wissenschaften. Mathematisch-naturwissenschaftliche Abteilung* **9**, 1–23.
- SUES, H.-D. (1997). On *Chirostenotes*, a Late Cretaceous oviraptorosaur (Dinosauria: Theropoda) from western North America. *Journal of Vertebrate Paleontology* **17**, 698–716.
- TURNER, A. H., POL, D., CLARKE, J. A., ERICKSON, G. M. & NORELL, M. A. (2007). A basal dromaeosaurid and size evolution preceding avian flight. *Science* **317**, 1378–1381.
- TYNE, J., VAN & BERGER, A. J. (1976). *Fundamentals of Ornithology*. Second Edition. John Wiley and Sons, New York.
- VICKERS-RICH, P., CHIAPPE, L. M. & KURZANOV, S. (2002). The enigmatic bird-like dinosaur *Animus portentosus*. In *Mesozoic Birds* (eds L. M. CHIAPPE, L. M. WITMER), pp. 65–86. University of California Press, Berkeley.
- WARNEKE, G. & STORK, H. G. (1977). Biostatische und thermoregulatorische Funktion der Sandwich-Strukturen in der Schädeldecke der Vögel. *Zoologische Anzeiger* **199**, 251–257.
- WATSON, D. M. S. (1974). Pterodactyls past and present. *Philosophical Transactions of the Royal Society B* **267**, 583–585.
- WEDEL, M. J. (2003a). The evolution of vertebral pneumaticity in sauropod dinosaurs. *Journal of Vertebrate Paleontology* **23**, 344–357.
- WEDEL, M. J. (2003b). Vertebral pneumaticity, air sacs, and the physiology of sauropod dinosaurs. *Paleobiology* **29**, 243–255.
- WEDEL, M. J. (2005). Postcranial skeletal pneumaticity in sauropods and its implications for mass estimates. In *The Sauropods: Evolution and Paleobiology* (eds J. A. WILSON, K. CURRY-ROGERS), pp. 201–228. University of California Press, Berkeley.
- WEDEL, M. J. (2006). Origin of postcranial skeletal pneumaticity in dinosaurs. *Integrative Zoology* **2**, 80–85.
- WEDEL, M. J. (2007). What pneumaticity tells us about ‘prosauropods’, and vice versa. *Special Papers in Palaeontology* **77**, 207–222.
- WEDEL, M. J. (2009). Evidence for bird-like air sacs in saurischian dinosaurs. *Journal of Experimental Zoology A* **311**, 611–628.
- WEDEL, M. J., CIFELLI, R. L. & SANDERS, R. K. (2000). Osteology, paleobiology, and relationships of the sauropod dinosaurs *Sauroposeidon*. *Acta Palaeontologica Polonica* **45**, 343–388.
- WELNHOFER, P. (1991). *The Illustrated Encyclopedia of Pterosaurs*. Crescent Books, New York.
- WELNHOFER, P. (2008). *Archaeopteryx: der Urvogel von Solnhofen*. Verlag Dr. Friedrich Pfeil, München.
- WELTY, J. C. (1982). *The Life of Birds*. Saunders College Publishing, Philadelphia.

- WILSON, J. A. (1999). A nomenclature for vertebral laminae in sauropods and other saurischian dinosaurs. *Journal of Vertebrate Paleontology* **19**, 639–653.
- WILSON, J. A. & SERENO, P. C. (1998). Early evolution and higher-level phylogeny of sauropod dinosaurs. *Society of Vertebrate Paleontology Memoir* **5**, 1–68.
- WITMER, L. M. (1997). The evolution of the antorbital cavity of archosaurs: a study in soft-tissue reconstruction in the fossil record with an analysis of the function of pneumaticity. *Memoirs of the Society of Vertebrate Paleontology* **3**, 1–73.
- WITMER, L. M. (1999). The phylogenetic history of paranasal air sinuses. In *The Paranasal Sinuses of Higher Primates: Development, Function and Evolution* (eds T. KOPPE, H. NAGAI, K. W. ALT), pp. 21–34. Quintessence, Chicago.
- XU, X. (2006). Feathered dinosaurs from China and the evolution of major avian characters. *Integrative Zoology* **1**, 4–11.
- XU, X., CLARK, J. M., MO, J., CHOINIERE, J., FORSTER, C. A., ERICKSON, G. M., HONE, D. W. E., SULLIVAN, C., EBERTH, D. A., NESBITT, S., ZHAO, Q., HERNANDEZ, R., JIA, C.-K., HAN, F.-L. & GUO, Y. (2009). A Jurassic ceratosaur from China helps clarify avian digital homologies. *Nature* **459**, 940–944.
- XU, X., NORELL, M. A., KUANG, X., WANG, X., ZHAO, Q. & JIA, C. (2004). Basal tyrannosauroids from China and evidence for protofeathers in tyrannosauroids. *Nature* **431**, 680–684.
- XU, X., TAN, Q., WANG, J., ZHAO, X.-J. & TAN, L. (2007). Gigantic bird-like dinosaur from the Late Cretaceous of China. *Nature* **447**, 844–847.
- XU, X., ZHANG, X.-H., SERENO, P., ZHAO, X.-J., KUANG, X.-W., HAN, J. & TAN, L. (2002). A new therizinosauroid (Dinosauria, Theropoda) from the Upper Cretaceous Iren Dabasu Formation of Nei Mongol. *Vertebrata Palasiatica* **40**, 228–240.
- XU, X., ZHANG, X., TAN, Q., ZHAO, X. & TAN, L. (2006). A new titanosaurian sauropod from Late Cretaceous of Nei Mongol, China. *Acta Geologica Sinica* **80**, 20–26.
- XU, X., ZHOU, Z. & WANG, X. (2000). The smallest known non-avian theropod dinosaur. *Nature* **408**, 705–708.
- YATES, A. M. (2003). New species of the primitive dinosaur *Thecodontosaurus* (Saurischia: Sauropodomorpha) and its implications for the systematics of early dinosaurs. *Journal of Systematic Palaeontology* **1**, 1–42.
- ZANNO, L. E., GILLETTE, D. D., ALBRIGHT, L. B. & TITUS, A. L. (2009). A new North American therizinosauroid and the role of herbivory in 'predatory' dinosaur evolution. *Proceedings of the Royal Society of London B* **276**, 3505–3511.
- ZHANG, F., ZHOU, Z., XU, X., WANG, X. & SULLIVAN, C. (2008). A bizarre Jurassic maniraptoran from China with elongate ribbon-like feathers. *Nature* **455**, 1105–1108.
- ZHANG, X.-H., XU, X., ZHAO, X.-J., SERENO, P., KUANG, X.-W. & TAN, L. (2001). A long-necked therizinosauroid dinosaur from the Upper Cretaceous Iren Dabasu Formation of Nei Mongol, People's Republic of China. *Vertebrata Palasiatica* **39**, 282–290.
- ZHAO, X.-J., BENSON, R. B. J., BRUSATTE, S. L. & CURRIE, P. J. (2010). The postcranial skeleton of *Monolophosaurus jiangi* (Dinosauria: Theropoda) from the Middle Jurassic of Xinjiang, China and a review of Middle Jurassic Chinese theropods. *Geological Magazine* **147**, 13–27.
- ZHENG, X.-T., YOU, H.-L., XU, X. & DONG, Z.-M. (2009). An Early Cretaceous heterodontosaurid dinosaur with filamentous integumentary structures. *Nature* **458**, 333–336.
- ZHOU, Z. (2004). The origin and early evolution of birds: discoveries, disputes, and perspectives from fossil evidence. *Naturwissenschaften* **91**, 455–471.

## X. SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article.

**Appendix S1.** Supplementary data file containing scores for compartmental pneumaticity, femur lengths, and justification of scores for 159 taxa.

**Appendix S2.** Composite cladogram and accompanying explanation and references.

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