Basic avian pulmonary design and flow-through ventilation in non-avian theropod dinosaurs

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Birds are unique among living vertebrates in possessing pneumaticity of the postcranial skeleton, with invasion of bone by the pulmonary air-sac system[1–4]. The avian respiratory system includes high-compliance air sacs that ventilate a dorsally fixed, non-expanding parabronchial lung[2,3,5,6]. Caudally positioned abdominal and thoracic air sacs are critical components of the avian aspiration pump, facilitating flow-through ventilation of the lung and near-constant airflow during both inspiration and expiration, highlighting a design optimized for efficient gas exchange[2,5–8]. Postcranial skeletal pneumaticity has also been reported in numerous extinct archosaurs including non-avian theropod dinosaurs and *Archaeopteryx*[9–12]. However, the relationship between osseous pneumaticity and the evolution of the avian respiratory apparatus has long remained ambiguous. Here we report, on the basis of a comparative analysis of region-specific pneumaticity with extant birds, evidence for cervical and abdominal air-sac systems in non-avian theropods, along with thoracic skeletal prerequisites of an avian-style aspiration pump. The early acquisition of this system among theropods is demonstrated by examination of an exceptional new specimen of *Majungatholus atopus*, documenting these features in a taxon only distantly related to birds. Taken together, these specializations imply the existence of the basic avian pulmonary *Bauplan* in basal neotheropods, indicating that flow-through ventilation of the lung is not restricted to birds but is probably a general theropod characteristic.

Recent studies of non-avian theropod dinosaurs, the extinct ancestors of living birds[11,13], have proposed a crocodylian-like pulmonary system with a hepatic-piston model of ventilation[14–17]. These studies counter long-held views[9–10,12] that pneumatic vertebrae in theropods resulted from an avian-like pulmonary air-sac system (Fig. 1). Pneumatic postcranial bones are present in all clades of non-avian theropods (Fig. 2)[9,12–13] and are typically restricted to the axial skeleton (for example, the vertebrae and ribs). Moreover, the locations of pneumatic foramina within bones are virtually identical between theropod dinosaurs and extant birds (Fig. 3). However, explicit statements about higher-level pulmonary organization and functional hypotheses for ventilating a pulmonary air-sac system in theropods have been speculative at best. Models[18,19] proposed for the evolution of the avian pulmonary apparatus postulate a cranial to caudal developmental sequence for air sacs in the theropod lineage, with the caudal components critical for establishing flow-through ventilation predicted to occur only in derived coelurosaurs.

Correlations between regional pneumaticity and specific air sacs in both birds and theropods have long remained ambiguous[9,10,16,17,20], particularly with regard to the extent of the vertebral column pneumatized by the cervical air-sac system. However, results from this study indicate that regional patterns of axial pneumaticity can be unequivocally associated with specific components of the air-sac system, and include both cervical and abdominal diverticula in addition to the lung itself. An examination of 234 air-sac-injected birds reveals the following invariant patterns: first, cervical air-sac diverticula (Fig. 1) pneumatize cervical vertebrae and ribs and the cranialmost thoracic (dorsal) vertebrae; second, abdominal air-sac diverticula invade caudal, synsacral and caudalmost thoracic vertebrae; and third, in most birds the lung itself pneumatizes adjacent thoracic vertebrae and ribs (see Supplementary Table 1). Other air sacs (Fig. 1) either do not pneumatize the skeleton (for example the caudal thoracic sac) or variably invade the sternum, sternal ribs, shoulder girdle and forelimb elements (for example the cranial thoracic, clavicular sacs). In no cases do cervical air-sac diverticula extend caudally along the column to pneumatize vertebrae beyond the middle thoracic series. This is significant because it has been asserted[16,17] that all pneumatization of the vertebral column in birds and non-avian theropods results from cervical air-sac diverticula, thereby ignoring the dominant role of abdominal air sacs and the lung for pneumatization of the postcranial axial skeleton.

An evaluation of postcranial pneumaticity in non-avian theropods reveals consistent regional patterns similar to those of living birds. A recently recovered spectacularly preserved specimen[12,21] of the basal neotheropod *Majungatholus atopus* (UA 8678) reveals the presence of pneumatic vertebrae in cervical, thoracic (dorsal) and sacral regions of the vertebral column (Figs 3 and 4). Pneumatic foramina in cervical vertebrae and ribs are consistent with pneumatization by cervical air-sac diverticula (Fig. 4b, f). Notably, the cervical ribs have the relatively largest pneumatic foramina known among non-avian theropods[21]. Pneumaticity of vertebral centra in the thoracic series is limited to the first four vertebrae (Fig. 4c), whereas neural arches are pneumatized throughout the entire region (Fig. 4d). This pattern of pneumaticity in thoracic centra is widespread in theropods, probably reflecting pneumatization by a firmly attached, dorsally positioned lung in the cranial half of the thorax. Pneumaticity of caudal thoracic and sacral vertebrae is restricted to neural arches and is consistent with pneumatization by abdominal air-sac diverticula (Fig. 4e). A reduction in both size and number of neural arch foramina in thoracic vertebrae 12 and 13, along with enhanced pneumaticity of sacral neural arches, indicates two different sources of pneumatization: one source for the thoracic region and one for the sacral region.

The general pattern of pneumaticity in *Majungatholus* is expressed throughout Theropoda (see Supplementary Table 1), being evident in representatives of all major neotheropod clades (Fig. 2). Sacral pneumaticity is present in at least some members of abelisauroid, spinosauroid, allosauroid, ornithomimid, tyrannosauroid and maniraptoran clades, indicating a consistent and widespread pattern of pneumatic invasion by caudally located air sacs in non-avian theropods. The postcranial pneumaticity observed in non-avian theropods implies the potential for a degree of pulmonary air sac development similar to that observed only in living birds.

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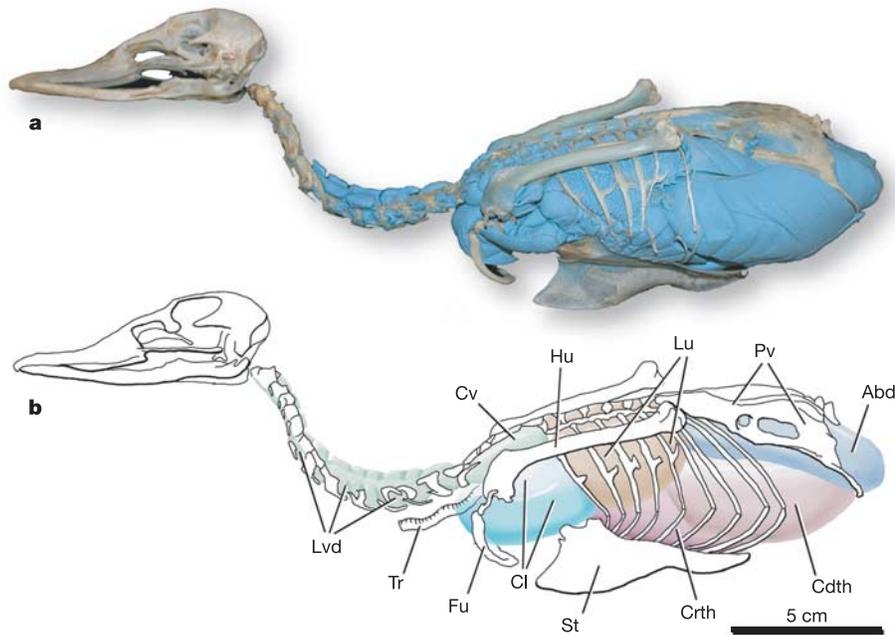
Figure 1 | **Pulmonary air-sac system in a bird.** **a**, Latex injection (blue) of the pulmonary system in a duck (*Anas crecca*), highlighting the extent of air sacs throughout the body. **b**, Main components of the avian flow-through system (ribs have been illustrated in their proper anatomical positions).

Abd, abdominal air sac; Cdth, caudal thoracic air sac, Cl, clavicular air sac; Crth, cranial thoracic air sac; Cv, cervical air sac; Fu, furcula; Hu, humerus; Lu, lung; Lvd, lateral vertebral diverticula; Pv, pelvis; Tr, trachea.

Skeletal and soft-tissue specializations in the cranial half of the avian trunk maintain a near-constant volume of the pulmonary cavity[2,5,6]. Movements of the sternum, ribs and pectoral girdle change trunk volume to create pressure differences that drive ventilatory airflow[2,6,22,23]. Cineradiographic (high-speed X-ray film) studies of skeletal and visceral kinematics during lung ventilation show greater expansion of the ventrocaudal trunk, with a larger ventral excursion of the caudal sternal margin relative to the cranial sternal margin (see Supplementary Table 2 and Supplementary Movie 1). As a result, the largest ventilatory volume changes are produced caudal to the exchanger (lung), establishing the necessary pressure gradient required for flow-through ventilation.

Skeletal adaptations consistent with an avian-like aspiration pump are already present in basal neotheropods, including a relatively rigid thoracic vertebral column with accessory hyposphene–hypantra articulations and a robust cranial thorax. In the cranial ribcage, the vertical arrangement of the diapophysis and parapophysis, the two vertebral joints that articulate with the two heads of each rib, ensures a rigid and relatively incompressible skeletal framework around the pulmonary cavity. The orientation of the vertebrocostal articulations gradually changes to a horizontal position between thoracic vertebrae 4 and 9, thereby allowing larger lateral excursions of the more caudally positioned ribs. The greater capacity for lateral excursion of these ribs in theropods, along with movements of the gastralial apparatus, a system recently proposed to work as a ventrally positioned accessory aspiration pump[24], provides a mechanism for establishing greater volumetric changes in the caudal half of the theropod trunk, a key characteristic essential for establishing flow-through ventilation in birds[6–8].

Postcranial pneumatic features have also been identified in the extinct large-bodied sauropod dinosaurs and flying pterosaurs[3,9,12,25]; the ability to pneumatize the skeleton might therefore be an ornithodiran synapomorphy. However, inferences related to pulmonary organization and ventilation are necessarily limited in non-theropod groups because they lack extant descendants that can be used as reference taxa. Moreover, the possibility that pulmonary air sacs also functioned in non-respiratory capacities[9,12,25] (for example, density

reduction) might be particularly important in these large-bodied and flying taxa, meriting further research.

We predict that in any biophysical model for the evolution of flow-through ventilation, areas of increased lung compliance must initially be located caudal to the gas-exchange portion of the pulmonary
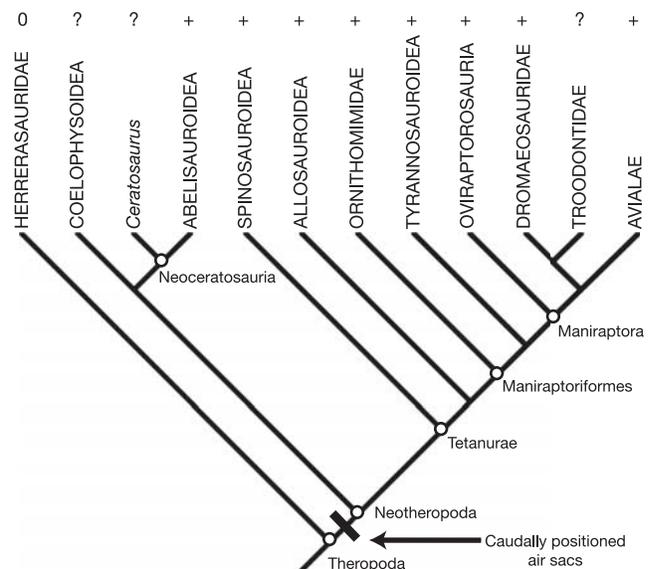

Figure 2 | **Proposed relationships of theropod taxa used in study (modified from references 11 and 13).** A plus sign indicates a theropod clade for which sacral pneumaticity has been inferred, indicating the presence of abdominal air sacs and diverticula; zero indicates the absence of sacral pneumaticity; and a question mark indicates an ambiguous pneumaticity state. Although regional variation exists in skeletal pneumatic features (for example, reduced thoracic pneumaticity in some deinonychosaurs)[26], this variation mirrors levels observed in extant birds and probably reflects the variety of factors known to influence relative pneumaticity such as body size and clade specificity[4,12].
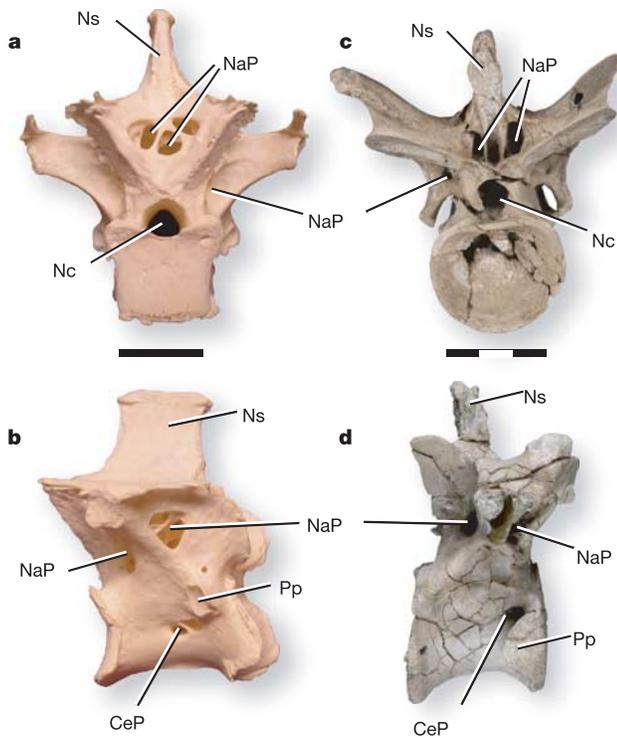
Figure 3 | Vertebral pneumaticity in avian and non-avian theropods.
Comparisons between a bird (**a**, **b**) and theropod dinosaur (**c**, **d**) in caudal (**a**, **c**) and right lateral (**b**, **d**) views, illustrating the topological similarity of pneumatic features. **a**, **b**, Cranial thoracic vertebra of a sarus crane (*Grus antigone*, SBU AV104063). **c**, **d**, Mid-cervical (**c**) and cervicothoracic (**d**) vertebra of an abelisauroid theropod (*Majungatholus atopus*, UA 8678). Scale bar, 1 cm (**a**, **b**) and 3 cm in (**c**, **d**). CeP, central pneumatic foramen; NaP, neural arch pneumatic foramen; Nc, neural canal; Ns, neural spine; Pp, parapophysis.

apparatus. It is only when higher-compliance air sacs are positioned caudal to the lung that air will be moved through it on ventilation. An initial cranial position for air sacs, as has been predicted previously for theropods[18,19], would result only in expansion/contraction of the cranial air sac, and would serve little role in ventilating a caudally positioned lung. Ancillary evidence for this model comes from extant non-avian sauropsids that also possess similarly heterogeneous pulmonary systems. Although not serving ventilatory roles, nor pneumatizing the postcranial skeleton, air sacs or diverticular complexes develop on the caudal end of the lung in chameleons, varanids and snakes[3,6], indicating that the caudalmost region of the sauropsid lung might be relatively plastic. Sacral pneumaticity in theropod dinosaurs, the basis for inferring caudally positioned air sacs, is consistent with a 'caudal origin model' and establishes the potential for flow-through ventilation in the dinosaurian ancestors of living birds.

Flow-through ventilation of the lung provides numerous potential benefits, including increased tidal volume, decreased anatomical dead space, and airflow past gas-exchange tissues during both inspiration and expiration. High-compliance pulmonary systems also use less energy for ventilation[2,3,5] and require relatively small adjustments of the body wall[2,5–8]. Together these traits highlight a system with the potential for high gas exchange efficiency. Although our model does not predict the specific type of intrapulmonary air flow in non-avian theropods (unidirectional versus bidirectional), it does establish both pulmonary and skeletal prerequisites required for flow-through ventilation, a plausible early stage in the evolution of the highly derived avian pulmonary apparatus.

Recent studies of non-avian theropod dinosaurs have documented several features once thought solely to characterize living birds, including the presence of feather-like integumentary specializations[26], rapid, avian-like growth rates[27,28], and even bird-like behaviours captured in the fossil record[29,30]. Either implicitly or explicitly, these studies have linked anatomical, physiological or behavioural inferences with an increased metabolic potential,
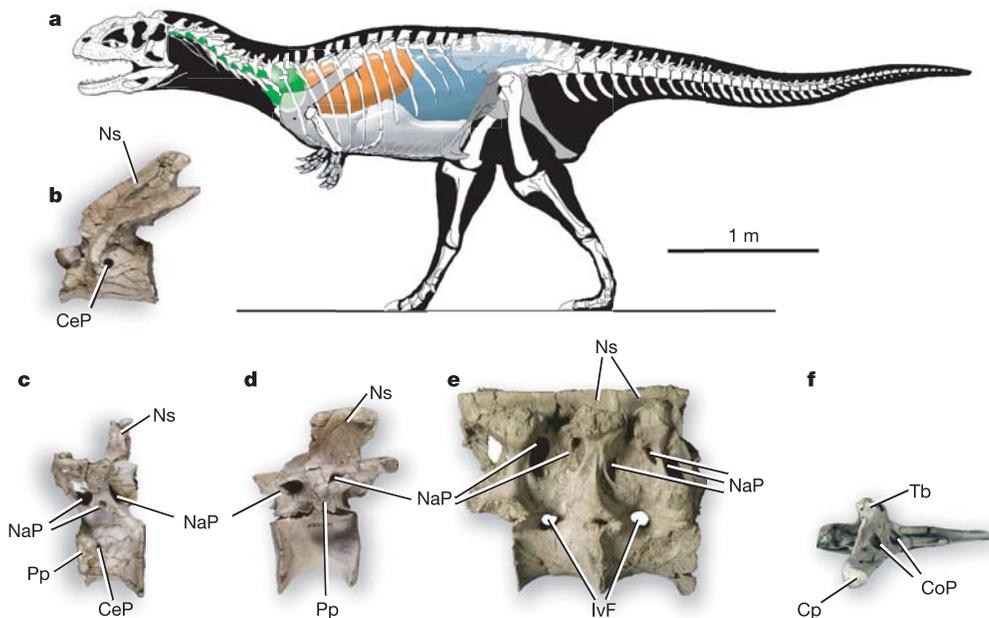

Figure 4 | Reconstruction of pulmonary air-sac system in *Majungatholus atopus* (based on UA 8678/FMNH PR 2278/2100 (ref. 21)). **a**, Pulmonary components based directly on vertebral morphology in UA 8678 include the following: cervical system (green), lung (orange) and abdominal system (blue). In modern birds, clavicular and thoracic air sacs are also present (see Fig. 1); their placement here (indicated in light grey), combined with the overlapping nature of other components, represents tertiary-level inferences emphasizing the uncertainty surrounding the reconstruction of soft tissues

not constrained by osteological evidence. Unknown skeletal elements are indicated by dark grey shading. **b–f**, Vertebrae (**b–e**) and rib (**f**) of UA 8678 illustrating pneumatic features. **b**, Second cervical; **c**, first thoracic; **d**, ninth thoracic (reversed); **e**, sacral complex, left lateral view; **f**, left ninth cervical rib, medial view (reversed). CeP, central pneumatic foramen; CoP, costal pneumatic foramen; Cp, capitulum; IvF, intervertebral foramen; NaP, neural arch pneumatic foramen; Ns, neural spine; Pp, parapophysis; Tb, tuberculum.

suggesting that if not bird-like in metabolism, theropods were at least 'more similar' to birds than to reptiles. Our study indicates that basal neotheropods possessed the anatomical potential for flow-through ventilation of the pulmonary system, emphasizing the early evolution of respiratory adaptations that are consistent with elevated metabolic rates in predatory dinosaurs.

METHODS

Birds used in pulmonary studies were salvage specimens obtained from wildlife rehabilitators and museums. All cineradiographic experiments were conducted in accordance with state and institutional guidelines. A detailed taxonomic list of included taxa and pulmonary injection and cineradiographic protocols is given in the Supplementary Information.

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