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ORIGINAL ARTICLE

Origin of postcranial skeletal pneumaticity in dinosaurs

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Abstract

The sauropodomorph *Thecodontosaurus caducus* and theropod *Coelophysis bauri* are the earliest known dinosaurs with postcranial skeletal pneumaticity. In both taxa, postcranial pneumatic features are confined to the cervical vertebrae. This distribution of pneumaticity in the skeleton is most consistent with pneumatization by diverticula of cervical air sacs similar to those of birds. Other hypotheses, including pneumatization by diverticula of the lungs, larynx and trachea, or cranial air spaces, are less well-supported.

Key words: dinosaur, pneumaticity, sauropodomorph, theropod, Triassic.

INTRODUCTION

Skeletal pneumaticity, or the phenomenon of having air-filled bones, is not broadly distributed in tetrapods. Among extant taxa, pneumatization of the skull occurs only in archosaurs (crocodilians and birds) and mammals. Pneumatization of the postcranial skeleton is even more limited, and occurs only in birds. Skeletal pneumatization in birds is often assumed to be an adaptation for reducing mass and improving flight performance. It is less commonly recognized that birds inherited postcranial skeletal pneumaticity (PSP) from their non-flying dinosaurian ancestors. PSP in dinosaurs has received little attention until very recently. This paper addresses the origin of PSP in dinosaurs, with the goal of determining what kind of soft-tissue system was responsible for bringing the air into the skeleton.

When we find evidence of pneumaticity in fossil forms, it is fair to ask how the air got into the bones. Left to itself, an enclosed volume of air inside the body will usually dissipate by diffusion into nearby blood vessels. If it is to persist, the air reservoir must be maintained, either by perfusion from a rete mirabile, as in the swim bladders of fish, or by constant connection to the outside. In the case of skeletal pneumatization, a patent sinus ostium or pneumatic foramen is required for normal development (Ojala 1957). Not only must there be a hole in the bone, but there must be an extension of the respiratory or tympanic passages, called a diverticulum, to bring the air from the outside to the pneumatic cavity within the bone.

Pneumatic diverticula may develop from any of four regions of the body: (i) the cranial air spaces, (ii) the larynx and trachea, (iii) the lungs, and, in birds, (iv) the pulmonary air sacs. Conceivably, diverticula from any of these sources could pneumatize portions of the postcranial skeleton. Each of the four regions is therefore a hypothetical source of the diverticula that pneumatized the skeletons of basal dinosaurs. To test these competing hypotheses, I briefly survey the kinds of diverticula that develop from each source in extant sauropsids, predict the pattern of pneumatization that diverticula from each region might be expected to produce, and compare the predicted patterns with the observed patterns of postcranial skeletal pneumatization in basal dinosaurs.

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PNEUMATIC DIVERTICULA IN EXTANT SAUROPSIDS

Diverticula of nasal and tympanic air spaces are present in many extant sauropsids. In testudines and squamates, small cranial diverticula may develop from the nasal cavities or nasopharyngeal ducts (Witmer 1999). In no cases, however, do these diverticula extend into the neck or pneumatize any of the bones of the skull. In contrast, the skulls of crocodilians and most birds are extensively pneumatized by diverticula of both the nasal and tympanic cavities. In a few species of birds, diverticula of the cranial air spaces pass into the neck and may reach as far as the shoulder (King 1966). These cervicocephalic diverticula are intermuscular or subcutaneous. Although they may anastomose with diverticula of the pulmonary air sacs, they do not pneumatize any postcranial bones. If similar diverticula did pneumatize the postcranial skeleton in dinosaurs, they might invade the cervical column at any point, although they might be expected to pneumatize the anterior cervical vertebrae first.

Diverticula of the larynx and trachea are present in some squamates and birds, but absent in crocodilians. Most snakes have a 'tracheal lung'; that is, an expanded tracheal membrane that bears highly vascular parenchymal tissue and functions in gas exchange (Wallach 1998). More conventional tracheal diverticula are also present in some snakes, and they are used to inflate the neck or acoustically modify the hiss (Young 1991, 1992). Laryngeal and tracheal diverticula are also present in a few birds. These diverticula typically form large sacs that lie between the trachea and esophagus or between the trachea and the skin, and they are primarily used in phonation (McLelland 1989). Laryngeal and tracheal diverticula do not pneumatize any bones in extant sauropsids. In fact, given that the membranes of air sacs and diverticula are relatively inelastic and the trachea is mobile (at least in some birds), it may be impossible for tracheal diverticula to invade the vertebral column. If it is possible for tracheal diverticula to pneumatize the skeleton, they could conceivably do so anywhere along the neck.

Among extant vertebrates, diverticula of the lung itself are present only in some birds. In certain lizards and many snakes the posterior portion of the lung may be devoid of parenchymal tissue (Perry 1998). Such regions of the lungs are sometimes referred to as 'air sacs', but they do not ventilate the parenchymal portions of the lungs or give rise to diverticula as do the pulmonary air sacs of birds. In some birds, small diverticula develop from the bronchial branches of the lungs. These diverticula are known to occasionally pneumatize the adjacent thoracic vertebrae and ribs, although pneumatization of these elements by diverticula of the pulmonary air sacs is apparently more common (Müller 1907; O'Connor 2004). The expected pattern of pneumatization in dinosaurs would be the same: diverticula of the lungs should invade the thoracic vertebrae and ribs.

Finally, we must consider the diverticula of the pulmonary air sacs of birds. In most birds there are nine air sacs: a single interclavicular sac and paired cervical, anterior thoracic, posterior thoracic, and abdominal sacs. All of the air sacs give rise to diverticula in at least some species of birds (Duncker 1971). Skeletal pneumatization varies widely within clades and even within populations (Hogg 1984a; O'Connor 2004), and not all of the elements listed here are pneumatized in all taxa. Diverticula of the cervical air sac typically pneumatize the cervical and anterior thoracic vertebrae and their attendant ribs. The sternum, sternal ribs, coracoids, clavicles, scapulae, and humeri are pneumatized by diverticula of the interclavicular air. The anterior and posterior thoracic air sacs give rise to visceral diverticula that lie between the esophagus and pericardium and between the esophagus and liver. Diverticula of the anterior thoracic air sac occasionally pneumatize adjacent sternal ribs. Finally, diverticula of the abdominal air sacs pneumatize the posterior thoracic vertebrae, synsacrum, pelvic girdles, and femora.

The predicted ontogenetic pattern of pneumatization produced by diverticula of pulmonary air sacs depends on which diverticula develop first. The first postcranial bones to be pneumatized in the turkey (*Meleagris gallopavo*) are the sternum and thoracic vertebrae (Cover 1953). In the chicken (*Gallus gallus*), pneumaticity first appears in the humeri and cervical vertebrae (Hogg 1984b). It therefore appears that diverticula of the cervical and interclavicular sacs pneumatize the presacral vertebrae and humeri or sternum, respectively, at about the same time in development. The humeri and sternum are not pneumatized in any non-avian dinosaurs, so we need consider only the relative timing of vertebral pneumatization. In this case, it is clear that the cervical or anterior thoracic vertebrae are pneumatized first; these regions of the spine are pneumatized by diverticula of the cervical air sac. Hogg (1984a) reported that in the chicken cervical vertebrae 5-9 are always pneumatized; the rest of the postatlantal cervical vertebrae are pneumatized in most, but not all, individuals. This suggests that cervicals 5-9 are the first to be pneumatized, and that in a few individuals pneumatization of the neck does not proceed any further.

PATTERNS OF SKELETAL PNEUMATIZATION IN BASAL DINOSAURS

Table 1 Pneumatic diverticula in extant sauropsids and their potential to pneumatize the postcranial skeleton

Source of diverticula	Pneumatize postcranial skeleton in extant forms?	Predicted pattern of postcranial pneumatization in dinosaurs
Cranial air spaces	No	Anterior cervical vertebrae
Larynx and trachea	No	Cervical vertebrae
Lungs	Yes	Thoracic vertebrae and ribs
Pulmonary air sacs	Yes	
Cervical		Cervical or anterior thoracic vertebrae
Interclavicular		Sternum and humerus
Thoracic		Sternal ribs
Abdominal		Synsacrum, pelvis, femur

PSP is present in some "prosauropods" and most sauropods and theropods, but absent in ornithischians and many "prosauropods" (Britt 1993, 1997). (Traditionally, Prosauropoda included all non-sauropod sauropodomorphs[Sereno 1999], but recent analyses suggest that this group is paraphyletic [Yates 2003]. In this paper, I use "prosauropods" to refer to all non-sauropod sauropodomorphs). Further, pneumaticity is well-developed in most pterosaurs. This distribution of the character requires either multiple origins or multiple losses (Fig. 1).

The Late Triassic (Norian) forms *Thecodontosaurus caducus* and *Coelophysis bauri* are the earliest-diverging sauropodomorph and theropod, respectively, with unequivocal evidence of PSP. *Thecodontosaurus caducus* and *C. bauri* may have inherited systems of pneumatic diverticula from a common ancestor, but they are the first representatives of their separate lineages

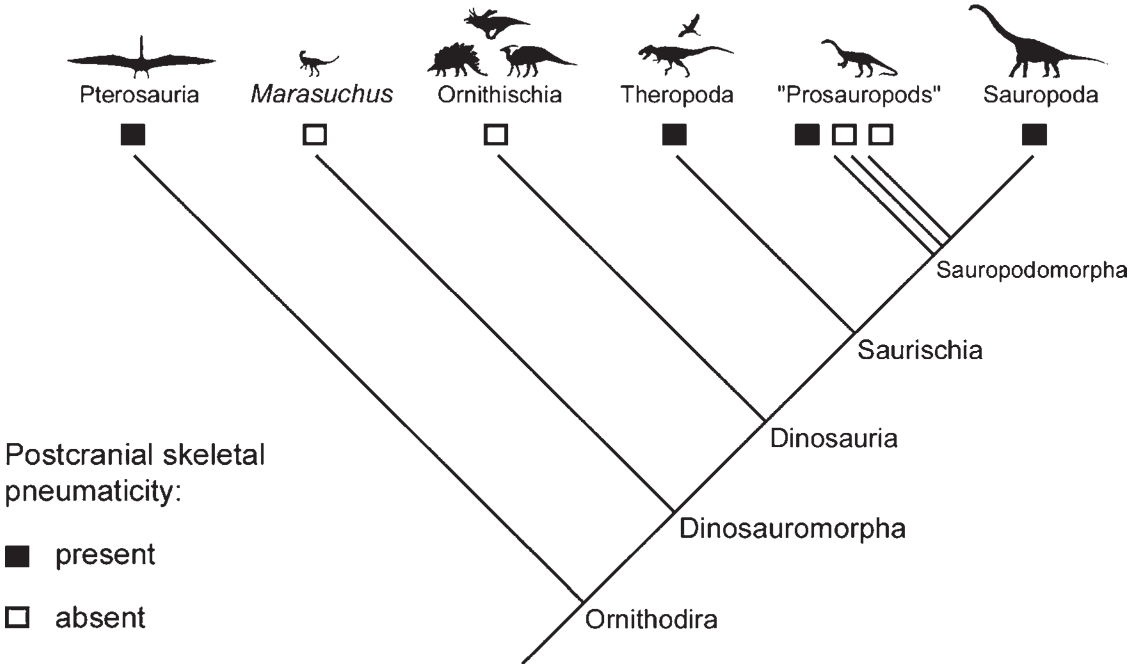

Figure 1 Postcranial skeletal pneumaticity (PSP) in the bird-line archosaurs. Either PSP is primitive for Ornithodira and secondarily lost in some taxa, or it evolved independently more than once. *Coelophysis* and *Thecodontosaurus* are the earliest and most basal members of Theropoda and Sauropodomorpha, respectively, that are known to have PSP. Icons after Sereno 1999.

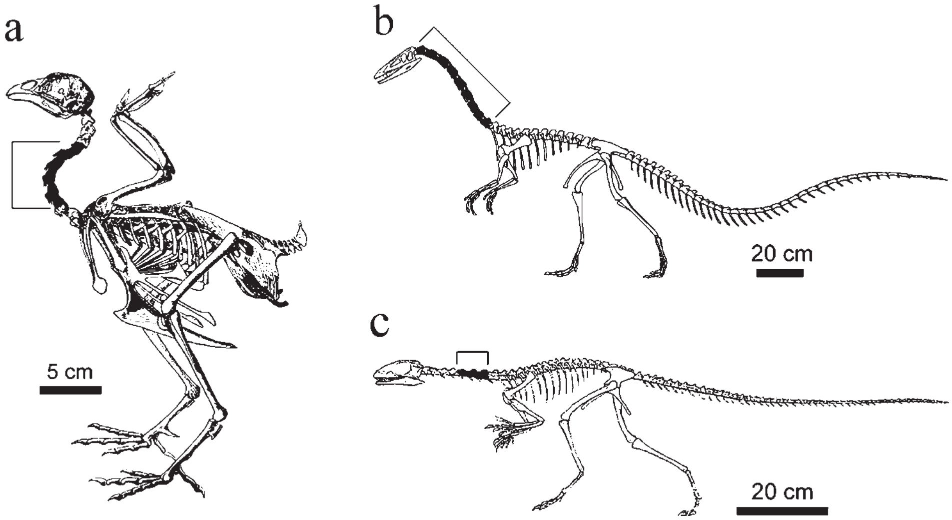

Figure 2 Pneumatic vertebrae in (a) 7-week-old chicken, *Gallus gallus*; (b) *Coelophysis bauri*; and (c) *Thecodontosaurus caducus*. Modified from Storer 1951 (a), Colbert 1989 (b), and Benton *et al*. 2000 (c).

in which the diverticula invaded the postcranial skeleton. *Thecodontosaurus caducus* differs from other species of *Thecodontosaurus*, and from all other prosauropods, in having deep pneumatic fossae in the centra of its cervical vertebrae (Yates 2003). The placement of these cavities on the vertebrae, their invasive nature, and the presence of a distinct margin of bone bounding each cavity, all argue for the interpretation of these cavities as pneumatic in origin. Furthermore, the fossae are present only in cervicals 6-8; thus, the pattern of pneumatization in *Thecodontosaurus* is remarkably similar to the earliest stages of skeletal pneumatization in the chicken (Fig. 2). Pneumatic cavities of this sort do not reappear in sauropodomorphs until the advent of basal sauropods, such as *Shunosaurus*, which have pneumatic cervical vertebrae. *Coelophysis* is the earliest theropod with evidence of PSP. The postaxial cervical vertebrae of *C. bauri* have pneumatic cavities that occupy most of the neural spine and that communicate with the outside through several large foramina (Colbert 1989). *Coelophysis bauri* is similar to more derived theropods, including birds, in having pneumatic cervical vertebrae.

DISCUSSION

Now that the patterns of pneumatization in the earliest dinosaurs with PSP have been established, we can evaluate the four hypotheses outlined here (Table 1). The hypothesis that the patterns of skeletal pneumatization observed in *T. caducus* and *C. bauri* were produced by diverticula of cranial air spaces is not well-supported. Cranial diverticula do not pneumatize postcranial bones in any extant sauropsids, and the most anterior vertebrae of *T. caducus* and *C. bauri* are not pneumatized. Practically any pattern of cervical pneumatization could be produced by diverticula of the larynx and trachea, but these diverticula also do not pneumatize any postcranial bones in extant forms. Diverticula of the lungs sometimes pneumatize the thoracic vertebrae and ribs in birds, but these elements are not pneumatized in *T. caducus* or *C. bauri*.

That leaves the fourth hypothesis, that the PSP of basal saurischians was produced by diverticula of pulmonary air sacs. Diverticula of the air sacs pneumatize many elements of the postcranial skeleton in extant birds. The patterns of pneumatization observed in *Thecodontosaurus* and *Coelophysis* are exactly what we should expect to see if diverticula of cervical air sacs were responsible. In effect, *T. caducus* and *C. bauri* resemble snapshots of the ontogenetic development of PSP in birds (Fig. 2). The patterns of pneumatization present in these taxa show that cervical air sacs and their diverticula were present in both saurischian lineages in the Late Triassic.

PSP in these basal forms is extremely limited. The bone removed by pneumatization accounted for <1% of the total body volume in both *Coelophysis* and *Thecodontosaurus*

(Mathew J. Wedel, unpubl. data), compared to 7-10% for later sauropods and theropods (Wedel 2004). PSP probably did not evolve as an adaptation for lightening the skeleton, although it seems to have been exapted for that purpose later in saurischian evolution.

Furthermore, diverticula did not evolve to pneumatize the skeleton. In the first place, many of the diverticula of birds are visceral, subcutaneous, or intermuscular, and do not pneumatize any bones (Duncker 1971). Skeletal pneumatization cannot be invoked to explain the presence of these diverticula. In the second place, the presence of diverticula is a prerequisite for pneumatization of the skeleton. The immediate ancestors of *Coelophysis* and *Thecodontosaurus* must have already had cervical diverticula. Pneumatization of the cervical series could not happen until these diverticula were already in place, so the diverticula must have evolved for some other purpose.

In terms of evolutionary change, respiratory mechanisms are highly conserved, PSP is highly labile, and diverticula seem to be somewhere in between. All birds have essentially the same lung architecture; the biggest difference among living forms is the presence or absence of a neopulmo (Duncker 1971). On the other hand, PSP varies widely within small clades and even within populations (King 1966; Hogg 1984a; O'Connor 2004). Diverticula appear to be more conserved than PSP (although a dedicated study comparing the evolution of the two is sorely needed). For example, most birds have femoral and perirenal diverticula, but the femur and pelvis are pneumatized only in a subset of those taxa (Müller 1907; King 1966; Duncker 1971).

The evolutionary malleability of lungs, diverticula, and PSP has important implications for the reconstruction of the respiratory system in fossil archosaurs. Most pterosaurs have extensive PSP, although it is not clear whether it is present in any of the Triassic forms (Bonde & Christiansen 2003). The presence of PSP in pterosaurs, sauropodomorphs, and theropods suggests that air sacs were present in the ancestral ornithodiran. For ornithodirans without PSP, including non-dinosaurian dinosauromorphs, ornithischians, and most basal sauropodomorphs, our null hypothesis should be that they had air sacs (because they are bracketed with taxa with PSP) but lacked either PSP or diverticula, not that they lacked air sacs.

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