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Possible postcranial pneumaticity in the last common ancestor of birds and crocodylians: evidence from *Erythrosuchus* and other Mesozoic archosaurs

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Abstract Birds and crocodylians (extant archosaurs) have differing, distinctive morphologies. Birds have respiratory airsacs with diverticula that pneumatize the postcranial skeleton, a feature absent in crocodylians. Bony correlates of pneumatic sinuses are known in the vertebrae of some non-avian dinosaurs and in pterosaurs – taxa more closely related to birds than crocodylians. This and the apparent absence of pneumatic postcranial bones in fossil archosaurs more closely related to crocodylians than to birds, has been interpreted as evidence that postcranial pneumaticity is a derived character of birds and their nearest fossil relatives. The presence of apparent osteological correlates of postcranial pneumaticity is here reported in some non-crown-group archosaurs, and some of the fossil taxa more closely related to crocodylians than to birds. This suggests that the last common ancestor of birds and crocodylians might have had a pneumatized postcranium, and that the absence of this feature in crocodylians might be derived.

Archosauria is a diverse clade of diapsids including birds, crocodylians, dinosaurs, pterosaurs, and their fossil relatives. One of the several distinct anatomical features of extant birds is a system of respiratory airsacs, diverticula of which occupy pneumatic sinuses within the appendicular and axial postcranial skeleton (McLelland 1989). The osteological correlates of these avian airsac diverticula have been characterized (Britt 1997), and similar structures have long been known in the vertebrae of pterosaurs and dinosaurs (Meyer 1837; Owen 1856; Seeley 1870). Given these observations, postcranial pneumaticity can be mapped onto a currently orthodox hypothesis of archosaur phylogeny (Fig. 1), and inferred to have been present in the ancestral ornithodiran (Britt 1997). The other extant group of archosaurs, crocodylians, lack postcranial airsacs and associated osteological correlates, and this has been considered or implied to be

a retained plesiomorphy. Additionally, pneumatic vertebrae are reported to be restricted to ornithodirans among archosaurs (e.g. Britt 1997). Here I report possibly pneumatic vertebrae in an extinct non-crown-group archosaur, and in at least some taxa more closely related to

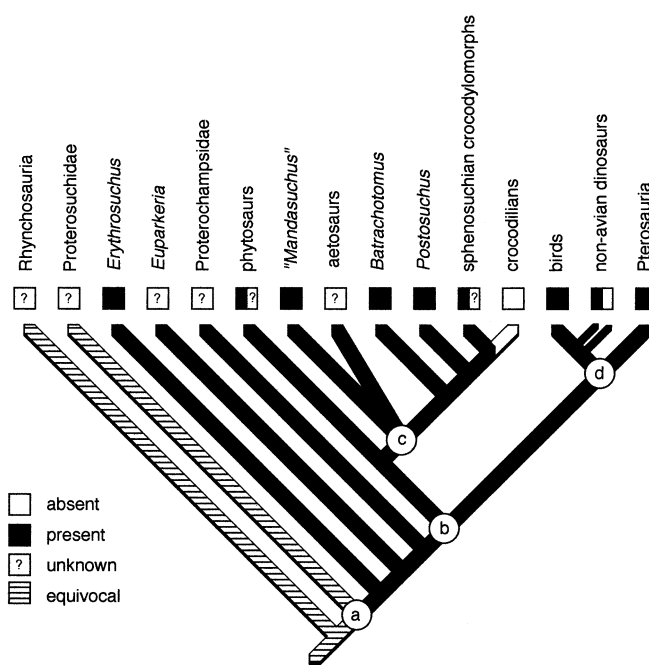


Fig. 1 Currently orthodox (see Gower and Wilkinson 1996) hypothesis of archosaur phylogeny showing relationships among taxa mentioned in text, and depicting a most-parsimonious reconstruction of the evolution of vertebral pneumaticity. This reconstruction is very preliminary. Important caveats include uncertainty surrounding suchian phylogeny, use of parsimony in ancestral character state reconstruction, assumptions that features documented in the text are indicative of vertebral pneumaticity, inadequate understanding of archosaur pneumaticity, incomplete knowledge of vertebral morphology in several taxa, and the crude construction of the “vertebral pneumaticity” character considered here. *Labelled nodes* represent ancestral taxa: **a** ancestral archosaur; **b** ancestral crown-group archosaur (= last common ancestor of birds and crocodylians); **c** ancestral suchian; **d** ancestral ornithodiran

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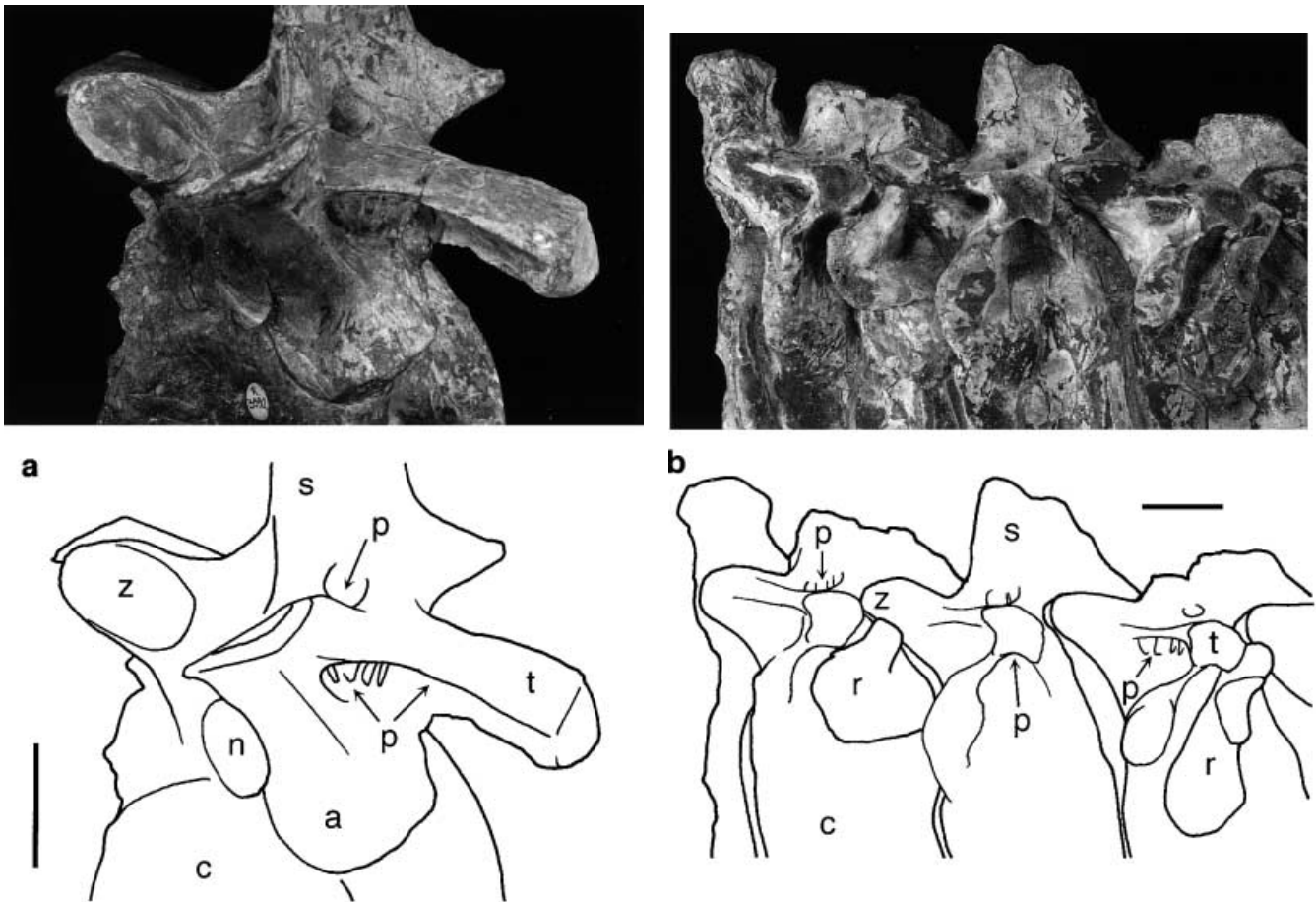


Fig. 2a–c Vertebral fossae in the non-crown-group archosaur *Erythrosuchus africanus*. **a** Dorsal vertebra of BMNH R3592 in left anterolateral and slightly dorsal view; **b** series of dorsal vertebrae of BMNH R8667 in left lateral view; **c** anterior view of broken surface of incomplete, anteriormost preserved vertebra of BMNH R8667, with the anterior aspect of the following vertebra visible in the background. *a* neural arch; *c* centrum; *l* cancellous bone; *m* compact bone; *n* neural canal; *p* possible pneumatic fossa; *r* rib fragment; *s* neural spine; *t* transverse process; *z* zygapophysis. Scale bars 30 mm

crocodilians than to birds. This has important implications for the understanding of the evolution of archosaurian pneumaticity and respiration, and of methods with which to best analyse the evolutionary biology of features in pairs of taxa.

Archosauria is used in its traditional (Juul 1994), rather than crown-group (Gauthier 1986) sense. The terms ‘birds’ and ‘crocodilians’ refer to the crown-groups of these taxa.

Possible pneumatic structures have been discovered in presacral vertebrae of the non-crown-group archosaur *Erythrosuchus africanus*, from the Triassic *Cynognathus* Zone of South Africa. Specimens examined for this study are in The Natural History Museum, London (BMNH). The mid-posterior (but not posteriormost) presacral vertebrae of BMNH R3592 bear what are generally understood to be bony correlates of pneumatization

(Britt 1997); namely structurally complex neural arches that have a series of excavations holding multiple subdivided fossae at the base of the lateral surface of the neural spine, and between lamellae on the anterolateral, ventral, and posterolateral surfaces of the bases of the diapophyses (Fig. 2a). These lamellae are similar to, and potential homologues of, those given various terms in dinosaurs (Osborn 1899; Janensch 1929; see Wilson 1999). Five articulated mid-dorsal vertebrae comprising the smaller BMNH R8667 show the same features as BMNH R3592 (Fig. 2b). Additionally, the first and fifth vertebrae of the series are incomplete, revealing something of the internal extent of the sinuses. Fig. 2c shows that foramina in the fossae at the base of the neural spine pass into the neural arch through outer compact bone, and appear to communicate with paired spaces within cancellous bone. Arch fossae are also present in the mid to posterior cervical vertebrae of BMNH R3592. There is no clear evidence of possible pneumatization in the cervical, sacral and caudal vertebrae of BMNH R3592 or other currently known specimens (see Gower 2001). Unlike in many ornithomirans, the centra of *E. africanus* vertebrae appear to be apneumatic.

The reconstruction of soft tissues in fossils requires caution, and alternative hypotheses should be considered (Witmer 1995). In this instance, clear bilateral asymmetry in the size and subdivision of the neural arch fossae per-

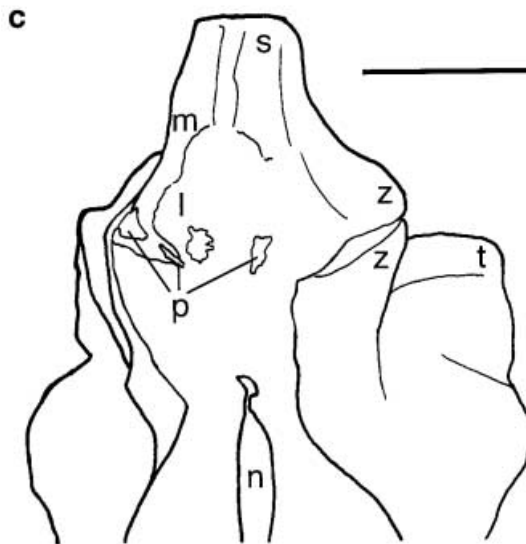


Fig. 2c

haps argue in favour of a pneumatic interpretation over a muscle attachment one, and the size and number of multi-partite fossae concentrated in the diapophyseal area of the neural arch weigh against an exclusively vascular interpretation for all these concavities. Finally, the deep multi-chambered concavities, some of which pierce the neural arch, suggests that the fossae at the base of the diapophyses and neural spine are not merely epiphenomena associated with, for example, development of the lamellae.

Similar possibly pneumatized presacral neural arches are also present in the rauisuchians “*Mandasuchus tanyauchen*” (e.g. BMNH R6793), *Batrachotomus kupferzellensis* (Stuttgart Museum für Naturkunde material, see Gower 1999), and *Postosuchus kirkpatricki* (Chatterjee 1985: 418) – i.e. at least some of the Mesozoic archosaurs more closely related to crocodylians than

birds (Gower and Wilkinson 1996). The presence in rauisuchians of neural arch lamellae has been previously dismissed as a convergence shared with ornithodirans (Wilson 1999). Neural arch fossae separated by lamellae are also present in phytosaurs (Camp 1930) and sphenosuchian crocodylomorphs (Crush 1984; Walker 1990), while pits at the base of neural spines are present in at least one, but not all, species of the non-archosaurian archosauriform clade Rhynchosauria (Dilkes 1995). Clearly a diversity of fossil diapsids and potentially pneumatic features need to be reassessed, and the criteria for identifying pneumaticity re-evaluated.

Two main types of vertebral pneumaticity have been circumscribed for ornithodirans (Britt 1997). Camerate vertebrae have relatively thick bone and several large internal sinuses, whereas camellate vertebrae are thin-walled with numerous small sinuses, giving an often inflated external appearance. The internal sinuses of the vertebrae of *E. africanus* and non-crocodylian suchians are poorly known, but the overall extent of pneumatization, if correctly identified, is clearly not as strongly developed as in the camellate vertebrae of tetanuran theropods, including birds.

If pneumaticity in *Erythrosuchus* and some rauisuchians is accepted and the revised taxonomic distribution mapped onto a consensus hypothesis of archosaur phylogeny (Fig. 1; Gower and Wilkinson 1996), it can be most parsimoniously interpreted that the last common ancestor of birds and crocodylians possessed neural arch pneumaticity. Lack of knowledge about possible pneumaticity in several taxa means that more archosaurs (e.g. proterosuchids, *Euparkeria*, proterochampsids and aetosaurs) need to be re-examined to further test hypotheses that sinuses in the postcranium of, for example, *E. africanus* are pneumatic and homologous with those of birds. More sophisticated pneumatic characters will need to be formulated and the interrelationships of the suchian archosaurs also requires further attention. However, it now seems that although pneumatized centra might be restricted to Ornithodira, pneumatized vertebrae per se may not be a uniquely derived feature grouping birds with other dinosaurs and pterosaurs, and absence of pneumaticity in extant crocodylians (and some dinosaurs) might be derived relative to the archosaur groundplan. Thus it is probably a misleading simplification to state that “the presence of pneumatic vertebrae [and ribs] in theropods is further evidence that birds are theropods” (Britt 1997: 593). Britt (1997) suggested that pneumatic vertebrae were present in the ornithodiran groundplan, but it has also been suggested that the evolution of postcranial pneumaticity in theropod dinosaurs was independent of that in pterosaurs and sauropod dinosaurs (Britt et al. 1998). Reconsideration is needed of the possibility that postcranial pneumaticity evolved more than once among ornithodirans, or indeed among archosaurs as a whole.

Living birds and crocodylians differ in the morphology and action of their respiratory systems. Birds have a flow-through lung, in which airsacs are a key component, and crocodylians have a hepatic piston pump

system. Both systems are unique among living vertebrates, which makes it difficult to infer respiratory modes in extinct archosaurs and to understand how the extant systems evolved. Unsurprisingly then, speculation on lung ventilation mode in fossil archosaurs has become highly contentious (e.g. Ruben et al. 1997; Nassar 1998). Vertebral pneumaticity indicates only the presence of air-filled sinuses in the axial skeleton, it provides no information on their association with body cavity airsacs potentially involved in ventilation. The presence of vertebral pneumaticity in non-crown-group and basal suchian archosaurs suggests that presence alone of similar pneumaticity in non-avian theropods should be used carefully in debates on lung ventilation mode in these taxa. From a Recent perspective, the current fossil evidence indicates that derived features of an avian-like lung were perhaps to some extent present in the last common ancestor of birds and crocodylians.

Previously assumed adaptive advantages of pneumaticity have been questioned, and there is mounting evidence that archosaur pneumaticity evolved independently of flight (Britt 1997; Britt et al. 1998; data presented here), despite being potentially advantageous to fliers. This is consistent with the hypothesis that pneumatic sinuses may result from an opportunistically pneumatizing epithelium and morphogenetic factors (Witmer 1997). In attempting to explain postcranial pneumaticity in early archosauromorphs and its absence in crocodylians, factors probably worth considering include body size and lifestyle. For example, potentially testable hypotheses are that archosaurian postcranial pneumaticity evolved in association with large body size, and was lost in crocodylians as a result of selective pressure to reduce buoyancy in association with the evolution of a semi-aquatic lifestyle. The postcranial skeleton of most Recent birds that dive underwater is poorly pneumatized (McLelland 1989).

That crocodylian postcranial apneumaticity might be a derived archosaurian condition, raises issues concerning the analysis of character evolution in sister-taxon pairs. The previous use of crocodylians as an outgroup demonstrating the derivedness of avian morphology is misleading because both avian and crocodylian anatomy is a combination of plesiomorphies and apomorphies with respect to their last common ancestor. In an analogous situation, Gower and Weber (1998) showed how detailed similarities between bird and crocodylian braincases can be demonstrated to be independently acquired when the morphology of a wide range of fossil archosaurs both from within and outside the crown group is examined. With any pair of taxa (including extant sister-groups), analysis of a wide range of related organisms in association with a phylogenetic hypothesis, is crucial to distinguish homology from convergence and plesiomorphy from apomorphy, and to improve understanding of the origin and evolution of distinctive anatomical systems. Further research of this kind is now required on archosaur postcranial pneumaticity.

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