

Evolution of Archosaurian Body Plans: Skeletal Adaptations of an Air-Sac-Based Breathing Apparatus in Birds and Other Archosaurs

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ABSTRACT Living birds represent the only extant sauropsid group in which pulmonary air sacs pneumatize the postcranial skeleton. Notable in this regard is an extraordinary degree of variability, ranging from species that are completely apneumatic to those characterized by air within the entire postcranial skeleton. Although numerous factors (e.g., body size) have been linked with “relative” pneumaticity, comparative studies examining this system remain sparse. This project sought to (1) characterize whole-body patterns of skeletal pneumaticity in distantly related neognath birds and (2) evaluate putative relationships among relative pneumaticity, body size and locomotor specializations. Pneumaticity profiles were established for 52 species representing 10 higher-level groups. Although comparisons reveal relatively conserved patterns within most lower-level clades, apparent size- and locomotor-thresholds do impart predictable deviations from the clade norm. For example, the largest flying birds (vultures, pelicans) exhibit hyperpneumaticity (i.e., pneumaticity of distal limb segments) relative to smaller members of their respective clades. In contrast, skeletal pneumaticity has been independently lost in multiple lineages of diving specialists (e.g., penguins, auks). The application of pneumaticity profiling to extinct archosaurs reveals similar trends in body size evolution, particularly when examining patterns of pneumaticity in a size-diverse assemblage of pterosaurs (flying “reptiles”). As a fundamental organizing system, skeletal pneumaticity may play a role in relaxing constraints on body size evolution by allowing volumetric increases without concomitant increases in body mass. Not only might this be critical for taxa (birds, pterosaurs) exploiting the energetically costly aerial environment, but could be beneficial for any large-bodied terrestrial vertebrates such as the dinosaurs. *J. Exp. Zool.* 311A:504–521, 2009. © 2009 Wiley-Liss, Inc.

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From the smallest birds to the largest dinosaurs, archosaurs represent one of the most morphologically diverse clades of tetrapods. Extant members alone (crocodilians and birds) display a tremendous range of morphologies and physiologies, establishing the putative end-members of the metabolic spectrum among amniotes generally. Moreover, by inclusion of extinct members of the group, archosaurs demarcate perhaps the greatest body size range among all terrestrial tetrapods, ranging in size from the ~1.8 g bee hummingbird (Dunning, '93) to the giant sauropod dinosaurs, the largest of which are estimated to approach or exceed 100 tonnes (Mazzetta et al., 2004; Upchurch et al., 2004).

The potential impact of postcranial skeletal pneumaticity (air-filled bones) on body size evolu-

tion has been obliquely addressed in a number of studies (e.g., Cope, 1877; Müller, '08; King, '66; Carrano and O'Connor, 2005; O'Connor, 2006 and references therein; Schwarz and Fritsch, 2006), typically in discussion points that lack quantitative comparative data (although see O'Connor, 2004; Wedel, 2005). Whereas explicit scaling studies have yet to be performed regarding the impact of whole-body postcranial skeletal pneu-

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matization, basic physics dictates that an air-filled volume will have a lower mass (as a function of reduced density) than an equal sized volume filled with marrow. A growing number of studies have also documented that the cortex of pneumatic bone is thinner relative to that observed in apneumatic bone (Currey and Alexander, '85; Cubo and Casinos, 2000; Fajardo et al., 2007), suggesting another mechanism by which bone specific volume-mass relationships may be altered in the context of pneumatization. Hence, in a volume constant model, the lower mass of an air-filled element would require less energy to move through the environment during normal activities such as locomotion, assuming that the structural/mechanical integrity of an air-filled bone is sufficient to withstand physiological loads (e.g., joint- and ground-reaction forces, site-specific tendon and ligament forces) generated during life.

Given that postcranial skeletal pneumaticity is variable among species, even within a given clade (see Crisp, 1857; King, '66; O'Connor, 2004), with more- or less of the postcranial skeleton air-filled in different taxa, the system is ideally suited for conducting pattern analysis and exploring potential mechanisms related to body size evolution within extant birds. Framed within this context, it is also possible to evaluate basic hypotheses related to body size evolution in extinct archosaurian lineages exhibiting pneumaticity of the postcranial skeleton such as nonavian saurischian dinosaurs and pterosaurs.

Pulmonary air sacs and postcranial pneumaticity

Whereas most sauropsid clades include members with "air sac" like regions of the pulmonary system (Fig. 1A), living birds are the only one in which air sacs represent the sole compliant portion of the system and serve to move air through a relatively volume-constant parabronchial lung (Duncker, '71, '74; Perry, '83, '98; Brackenbury, '87). Moreover, birds are the only extant sauropsids in which pulmonary air sacs pneumatize elements of the postcranial skeleton (Fig. 2), thereby allowing a direct correlation between skeletal morphology and pulmonary structure (Bremer, '40; King, '57; O'Connor, 2004). Evidence of postcranial skeletal pneumaticity has also been identified in a number of now extinct archosaurian lineages (Fig. 1B), most notably among the pterosaurs and saurischian

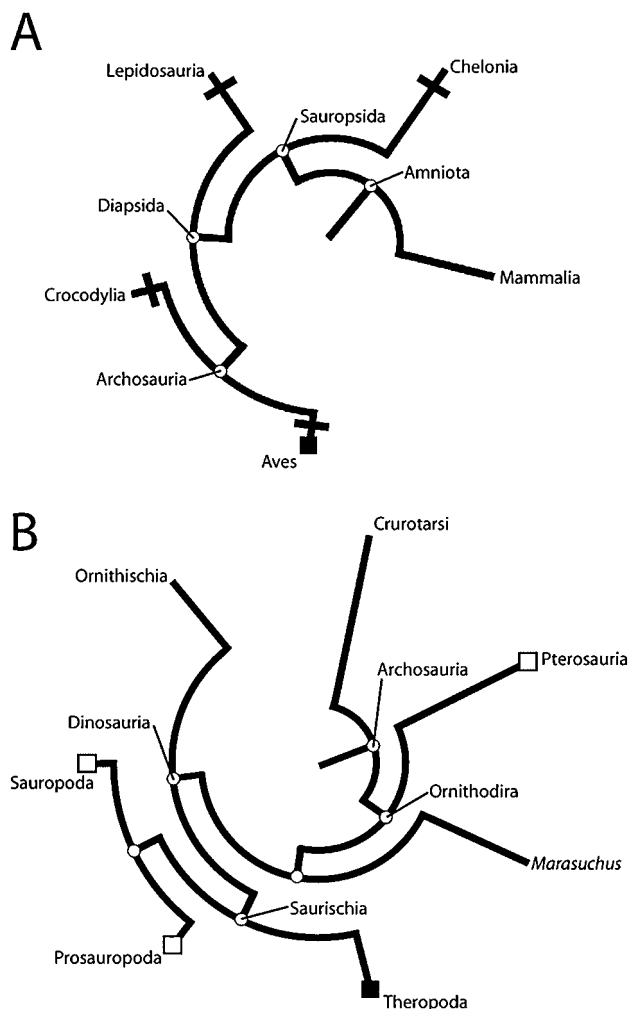


Fig. 1. Phylogenetic hypotheses of key amniote (A) and archosaurian (B) taxa with increased levels of pulmonary heterogeneity (black rectangles) and those clades in which pneumaticity of the postcranial skeleton is present (black terminal squares) or inferred (open squares). Phylogenetic hypotheses based on Gauthier ('94), Brochu (2001), and Irmis et al. (2007).

dinosaurs (e.g., Janensch, '47; Britt, '93; Wedel, 2003; O'Connor, 2006).

Pneumatic features of the postcranial skeleton remain the benchmark by which hypotheses of pulmonary structure in extinct forms can be based. Using extant bird postcranial skeletal morphology as the basis for comparison (Fig. 2), cortical bone foramina that communicate with large internal cavities in bone represent evidence for an air-sac-based pulmonary system (see O'Connor, 2006). Similar morphology in fossils may be used for different types of structural and functional inference, related in turn to tissue-, organ-, and whole organism-level organization.

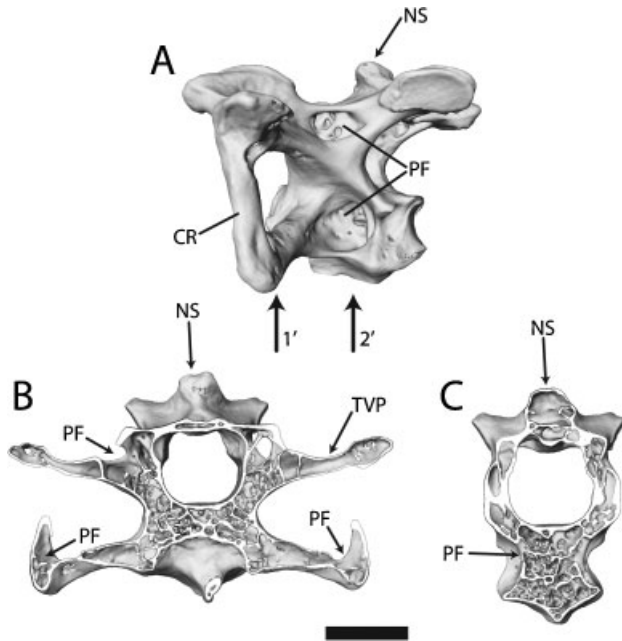


Fig. 2. Osteological features related to pneumatic invasion by the pulmonary system in extant birds. Middle cervical vertebra of a Great Skua (*Catharacta skua*, CM 11606) in left lateral (A) and sectional (B, C) views. Scale bar = 0.5 cm. (A) MicroCT rendering of vertebra to illustrate pneumatic foramina in cortical bone surface. (B, C) Sectional views indicated by arrows 1' (B) and 2' (C) in A to highlight continuity of pneumatic foramina in cortical surface with large, thin-walled chambers inside pneumatic bone. CR, cervical rib; NS, neural spine; PF, pneumatic foramen; TVP, transverse process.

For example, postcranial skeletal pneumaticity minimally results from tissue interactions between the skeletal and pulmonary systems, indicating the presence of a dynamic pneumatic epithelium capable of expanding into the skeleton (Bremer, '40; Hogg, '84). This further allows one to hypothesize the presence of a heterogeneously partitioned pulmonary system, one with distinct gas exchange (lungs) and ventilatory (air sacs/diverticula) components, and provides insight into the basic anatomical configuration of the post-tracheal respiratory system (Perry, 2001; O'Connor, 2006). This in turn provides a foundation by which functional attributes (e.g., compliance) may be modeled and/or how the musculoskeletal system may have influenced ventilatory function. See Perry (2001), Wedel (2003, this volume), O'Connor and Claessens (2005), O'Connor (2006), Claessens et al. (2009) and Perry et al. (this volume) for recent efforts using inferences related to postcranial skeletal pneumaticity in the context of extinct archosaurian respiratory evolution.

Nonrespiratory aspects of pulmonary air sacs

The physiological (e.g., gas-exchange capacity) implications of different pulmonary structure/function relationships in sauropsids have been explored in detail, both historically (e.g., Duncker, '71, '78; Perry, '83, '98; Maina, 2000, 2002, 2006, and references therein), and as part of this volume for various individual taxa. Less work has focused on the nonrespiratory benefits and/or trade-offs of different types of pulmonary organization (although see Duncker, '89), particularly in those taxa with an air-sac-based pulmonary apparatus. More generally, avian air sacs and their associated diverticula are known to function in aspects of vocalization (Lockner and Murrish, '75; Dantzker et al., '99; Plummer and Goller, 2008), visual displays (Murie, 1867, 1868; Honess and Allred, '42; Akester et al., '73) and have been hypothesized (although not formally tested) to play a role in, among other things, thermoregulation (Bignon, 1889) and impact protection during diving behavior (Richardson, '39). Perhaps most impressive is the degree to which the air sac system interacts with and modifies the postcranial skeleton in birds and the variability that exists when comparing one species with another in this regard.

Although generalizations (e.g., reduced pneumaticity in diving forms) regarding the variability of avian postcranial skeletal pneumaticity are numerous (e.g., King, '66; Welty, '79; McLelland, '89), the topic has only recently received detailed, phylogenetically informed consideration. In the first quantitative comparative study of pneumaticity in birds, O'Connor (2004) documented a common pattern of pneumaticity in anseriform birds (ducks, geese, swans) in which the cervicothoracic vertebral column was pneumatized by diverticula of the cervical and abdominal air sacs and the lungs. This was identified as the common anseriform pattern, with repeated, independent deviations from it including both reductions and expansions in different clades. One repeated pattern included a reduction (mergines) or total absence (oxyurines, *Thalassornis*) of postcranial skeletal pneumaticity in ducks that regularly employ diving as part of their primary foraging strategy (O'Connor, 2004). This work also identified a correlation between relative pneumaticity and body size, with a slight positive relationship observed between a metric developed for characterizing whole body skeletal pneumaticity (i.e., the

pneumaticity index, PI) and body mass. It was observed that, as body size (mass) increased, more individual elements of the postcranial skeleton were pneumatized.

These observations serve as the basis for this work in assessing whether patterns of skeletal pneumaticity in anseriforms are generally applicable to birds as a whole. Thus, the osteological manifestation of the interplay between pulmonary and skeletal systems represents the focus of this paper, whereby extant birds are used as a testing ground for assessing hypotheses related to body plan evolution. The basic hypothesis addressed in this study can be conceptualized as follows: Larger-bodied (i.e., larger whole-body volume) members of a given clade will exhibit more pneumatic postcranial bones than smaller-bodied clade members. Moreover, given the diversity in locomotor behaviors (e.g., diving) appreciated among different bird groups, relationships between body size and postcranial skeletal pneumaticity may be decoupled in favor of other factors. To further explore these concepts, birds from numerous clades of nonpasseriform neognaths were surveyed to examine relationships among body size, locomotor specialization(s) and relative postcranial skeletal pneumaticity.

MATERIALS AND METHODS

An examination of postcranial skeletal and soft-tissue anatomy of selected species from ten traditional avian ordinal groupings (Livezey and Zusi, 2007) was conducted, including concentrated analyses of Anseriformes (ducks, geese, swans), Charadriiformes (waders, terns, gulls), and Pelecaniformes. Selected species within Ciconiiformes (storks, herons), Falconimorphae (hawks, New and Old World vultures), Gruiformes (bustards), Coraciiformes (hornbills), Sphenisciformes (penguins), Gaviiformes (loons), and Podicipediformes (grebes) were also examined as part of this study (Appendix). This approach was designed to capture a diverse phylogenetic sample (Tables 1 and 2) of nonhyphen:passeriform neognaths, including multiple clades characterized by a large range of body sizes and locomotor/foraging specializations (e.g., diving, soaring). Comparisons within different clades were used to assess relationships between the amount of skeletal pneumaticity and body size and diving behavior.

Following methods outlined in O'Connor (2004), individual specimens were scored for the presence or absence of skeletal pneumaticity in discrete

anatomical units of the postcranial skeleton (Table 2). Twelve anatomical units were defined and included four regions of the vertebral column (cervical, thoracic, synsacral, and caudal), the sternum, and ribs (taken as a single unit) from the axial skeleton. The appendicular skeleton was partitioned as the pectoral girdle, humerus, distal forelimb, pelvic girdle, femur, and distal hind limb as distinct anatomical units. Museum skeletal specimens were examined for the presence of pneumatic foramina, whereas whole-body pulmonary injection specimens were examined for the presence of latex within skeletal elements. A species-specific pneumaticity index (PI) was established by totaling the number of individual anatomical units exhibiting evidence of pneumaticity and dividing this sum by 12 (Table 2). Body mass data, when not available for individual specimens, were taken from species- and sex-specific means (when appropriate) provided in Dunning ('93).

Body mass data were \log_{10} transformed and species-specific PIs (i.e., percentages) were arcsin transformed prior to analyses following protocols outlined in O'Connor (2004). A regression analysis was conducted to evaluate correlative relationships between PI and body mass. As the PI is a composite value for the proportion of the skeleton pneumatized (based on presence-absence data), and not an exact quantification of total bone volume to air volume, regression analyses were used to identify trends between body size and relative pneumaticity, and not to test slope assumptions associated with specific scaling models (e.g., McMahon, '75). Thus, the goal of such analyses was to assess whether slopes were significantly different from 0, and when present, to identify correlation coefficients and the directionality of any trends.

Although it has long been appreciated that relatedness of species (i.e., phylogeny) may overestimate relationships among study variables (e.g., Felsenstein, '85; Harvey and Pagel, '91; Harvey and Purvis, '91), this study does not incorporate an explicit phylogenetic comparative approach (e.g., independent contrasts). The sampling strategy employed herein specifically targeted only selected members of distantly related clades. As such, the comparisons used represent heuristic approaches for identifying trends in disparate clades of birds, with the goal of identifying future research directions aimed at characterizing scaling relationships related to whole-body pneumatization. For a detailed, phylogenetically in-

TABLE 1. Basic characteristics of clades examined in study

Taxon	Common name	Body mass range (kg)	Locomotor category	Foraging specialization
Sphenisciformes	Penguins	1.11–45.00	Flightless	Pursuit diving (from surface)
Podicipediformes	Grebes	0.13–1.48	F/BFL	Pursuit diving (from surface)
Gaviiformes	Loons	0.99–6.40	F/BFL	Pursuit diving (from surface)
Pelecyaniformes				
Anhingidae	Snake birds	0.95–1.85	F/SS	Pursuit diving (from surface)
Phalacrocoracidae	Cormorants	0.55–4.1	F/FG	Pursuit diving (from surface)
Pelecanidae	Pelicans	3.17–13.6	SS	Splash diving
	Gannets, Boobies	0.85–3.6	SS (DS?)	Splash diving
	Tropicbirds	0.33–0.75	SS	Surface foraging
	Frigatebirds	0.75–1.67	SS	Surface foraging
Anseriformes				
Anhimidae	Screamers	2.0–5.0	SS	Nonspecialized
Anatidae				
Oxyurini	Stiffetails	0.36–0.87	F	Pursuit diving (from surface)
Anatini	Dabbling ducks	0.34–1.8	F	Surface foraging
Anserini	Geese/swans	0.88–14.3	F	Surface foraging
Charadriiformes				
Alcidae	Auks	0.07–1.2	F/BFL	Pursuit diving (from surface)
Jacanidae	Jacanas	0.04–0.23	F	Surface foraging
Rostratulidae	Painted snipes	0.07–0.16	F	Surface foraging
Charadriidae	Plovers	0.03–0.30	F	Surface foraging
Scolopacidae	Sandpipers	0.02–0.04	F	Surface foraging
Sternidae	Terns	0.05–0.70	F/DS	Splash diving
Ciconiiformes				
Ardeidae	Herons	0.25–4.75	F/FG	Surface foraging
Ciconiidae	Storks	2.0–9.0	F/FG/S	Surface foraging
Falconimorphae				
Cathartidae	New World vultures	0.95–14.2	SS	Nonspecialized
Old World vultures		1.54–12.5	SS	Nonspecialized
Gruiformes				
Otididae	Bustards	0.68–10.90	FG	Nonspecialized
Coraciiformes (Bucerotiformes)				
Bucerotidae	Hornbills	0.083–6.18	FG	Nonspecialized

BFL, burst flapping; DS, dynamic soaring; F, flapping flight; FG, flap-gliding; SS, static soaring. Body mass data from Dunning ('93) and Kemp ('95) and locomotor categories based on Videler (2005). Taxonomic framework developed from recent phylogenetic surveys of Livezey and Zusi (2007) and Hackett et al. (2008).

formed analysis of anseriform birds, see O'Connor (2004).

Phylogenetic hypotheses used for contextual purposes and character mapping were provided by recent morphological (Livezey and Zusi, 2007) and molecular (Hackett et al., 2008) analyses focused on higher-level relationships among neornithine birds.

Micro-computed tomography of skeletal elements (Fig. 2) was conducted on a General Electric eXplore Locus in vivo micro-CT scanner at the Ohio University μ CT Facility. All elements were scanned at 85 kVP, 400 mA, and slice thicknesses of either 0.092 mm or 0.045 mm, depending on the absolute size of the specimen in question. VFF and DICOM images were assembled into 3-D

visualizations using GE MicroView 2.1.2 and AMIRA 4.1, respectively.

Institution abbreviations: American Museum of Natural History, New York (AMNH); Carnegie Museum of Natural History, Pittsburgh (CM); Field Museum of Natural History, Chicago (FMNH); Justus-Liebig University, Giessen, Germany (JLUG); National Museum of Natural History, Washington D.C. (NMNH); Ohio University Vertebrate Collections, Athens (OUVC); Transvaal Museum, Pretoria, South Africa (TM).

RESULTS

Among most birds examined, vertebrae at the cervicothoracic junction are the most commonly

TABLE 2. Postcranial pneumaticity profiles for avian taxa examined in study

	CeV	TV	SV	CaV	ST	CO	Pct	Hu	DFL	Plv	Fe	DHL	PI
Sphenisciformes	-	-	-	-	-	-	-	-	-	-	-	-	0.00
Podicipediformes	-	-	-	-	-	-	-	-	-	-	-	-	0.00
Gaviiformes	-	-	-	-	-	-	-	-	-	-	-	-	0.00
Pelecaniformes													
<i>Anhinga</i>	-	-	-	-	-	-	-	-	-	-	-	-	0.00
Phalacrocoracidae*	-	±	-	-	±	-	-	±	-	-	-	-	0.25
<i>Pelecanus</i>	+	+	+	+	+	+	+	+	+	+	-	+	0.92
<i>Sula/Morus</i>	+	+	+	+	+	+	+	+	+	+	+	-	0.92
<i>Fregata</i>	+	+	+	-	+	+	+	+	+	+	+	-	0.83
<i>Phaethon</i>	+	+	+	-	+	+	+	+	+	+	+	-	0.83
Ciconiiformes													
<i>Ardea</i>	+	+	+	-	+	+	-	+	-	-	-	-	0.50
<i>Ixobrychus</i>	+	+	+	-	+	+	-	+	-	-	-	-	0.50
<i>Botaurus</i>	+	+	+	-	+	+	-	+	-	-	-	-	0.50
<i>Ciconia</i>	+	+	+	+	+	+	+	+	-	+	+	-	0.83
<i>Mycteria</i>	+	+	+	+	+	+	+	+	-	+	+	-	0.83
<i>Epihippiorhynchus</i>	+	+	+	+	+	+	+	+	-	+	+	-	0.83
<i>Leptoptilos</i>	+	+	+	+	+	+	+	+	+	+	+	-	0.92
Falconimorphae													
Strigiformes	+	+	+	+	+	+	+	+	-	+	-	-	0.75
Cathartidae	+	+	+	+	+	+	+	+	+	+	+	-	0.92
<i>Sagittarius</i>	+	+	+	+	+	+	+	+	-	+	+	-	0.83
<i>Accipiter</i>	+	+	+	+	+	+	+	+	-	+	+	-	0.83
<i>Gyps</i>	+	+	+	+	+	+	+	+	+	+	+	-	0.92
Otitidae													
<i>Otis</i>	+	+	+	+	+	+	+	+	+	+	+	-	0.92
Bucerotiformes													
<i>Tockus</i>	+	+	+	+	+	+	+	+	+	+	+	-	0.92
<i>Bucorvus</i>	+	+	+	+	+	+	+	+	+	+	+	+	1.00
Anseriformes													
Anhimidae	+	+	+	+	+	+	+	+	+	+	+	+	1.00
<i>Oxyura</i>	-	-	-	-	-	-	-	-	-	-	-	-	0.00
<i>Anser</i> *	+	+	+	-	±	±	±	+	-	+	-	-	0.67
<i>Anas</i> *	+	+	+	-	±	±	-	+	-	+	-	-	0.58
For detailed Anseriform analysis see O'Connor (2004)													
Charadriiformes													
Alcidae	-	-	-	-	-	-	-	-	-	-	-	-	0.00
Jacaniidae*	+	+	-	-	-	-	-	-	-	-	-	-	0.17
Rostratulidae*	+	+	-	-	-	-	-	-	-	-	-	-	0.17
Scolopacidae*	+	+	-	-	-	-	-	-	-	-	-	-	0.17
Charadriidae*	+	+	-	-	-	-	-	-	-	-	-	-	0.17
Sternidae*	+	+	-	-	-	-	-	-	-	-	-	-	0.17
Glareolidae*	+	+	-	-	-	-	-	-	-	-	-	-	0.17

*Pneumaticity limited to 1–3 vertebrae at the cervicothoracic junction

CaV, caudal vertebrae; CeV, cervical vertebrae; CO, costal elements; DFL, distal forelimb elements; DHL, distal hind limb elements; Fe, femur; Hu, humerus; Pct, pectoral girdle elements; Plv, pelvic girdle elements; ST, sternum; SV, sacral vertebrae; TV, thoracic vertebrae. Symbols: +, pneumatic; -, apneumatic; ±, variable pneumaticity. * indicates the maximum PI value of a clade in which pneumaticity is variable.

pneumatized regions of the postcranial skeleton (Fig. 3B). In many cases (e.g., charadriiform waders) this was the only region of the skeleton exhibiting pneumaticity (Table 2). Although O'Connor (2004) identified a common pattern among anseriform birds with portions of the cervicothoracic vertebral column pneumatized, the broader survey conducted herein reveals

that this may represent a more common pattern, at least in small to medium body-sized taxa (e.g., species <1.2 kg). The PI values encompassed within this phenotype range between 0.12 and 0.24. Birds of larger body size and/or with specialized locomotor behaviors (e.g., diving, soaring) pneumatize fewer (PI < 0.12) or additional (PI > 0.24) elements of the postcranial

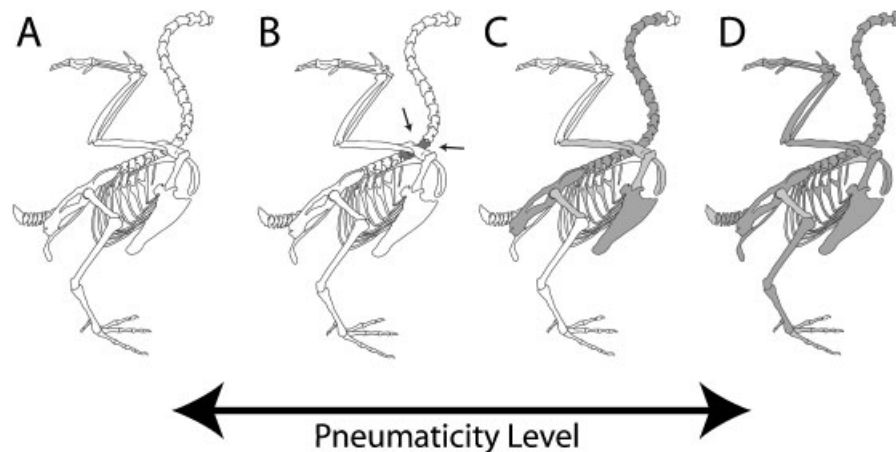


Fig. 3. Skeletal schematics of four major pneumaticity phenotypes exhibited among extant birds. (A) Reduced pattern (RP) represented by taxa (e.g., penguins) lacking postcranial pneumaticity; (B) common pattern (CP) represented by taxa (e.g., shorebirds) with pneumaticity restricted to portions of the cervicothoracic vertebral column; (C) expanded pattern (EP) represented by taxa (e.g., geese) with pneumaticity extending throughout the postcranial axial skeleton, limb girdles and proximal limb elements; and (D) hyperpneumaticity pattern (HP) represented by taxa (e.g., pelicans, vultures) with pneumaticity extending throughout both postcranial axial and appendicular skeletons, including distal elements of the limbs. Pneumatic portions of the skeleton indicated by dark gray shading; areas of light gray shading indicate elements that exhibit variability in pneumaticity even when adjacent elements are pneumatic. Underlying arrow emphasizes the continuous nature of the relationship among the four pneumaticity phenotypes.

skeleton (Fig. 3; Table 2), mirroring observations in anseriforms. Importantly, the deviations from this pattern are repeated in disparate clades of neognath birds (Fig. 4A and B). It is important to note that such repeated deviations are apparent regardless of whether morphological (Livezey and Zusi, 2007) or molecular datasets (Hackett et al., 2008) were used in generating the phylogenetic hypothesis (see the occurrence of RP in Fig. 4A and B).

An examination of neognath diving specialists (e.g., penguins, loons, grebes) reveals a complete absence of postcranial skeletal pneumaticity ($PI = 0$) in these taxa (Figs. 3A and 4; Table 2). The three clades are invariant in this regard, with all species of each group lacking pneumaticity of the postcranial skeleton (Fig. 5A; Appendix). Among pelecyaniform birds the darters (*Anhinga*) and cormorants (*Phalacrocorax*) exhibit reduced levels of postcranial pneumaticity (Figs. 4C and 5B), and the auks (Alcidae) among charadriiform birds do not pneumatize the skeleton (Table 2). In these cases, not only are the apneumatic taxa (*Anhinga*, auks) dedicated dive foragers but they are nested within higher-level groups of birds that exhibit pneumatic postcranial bones (Fig. 4C). It is significant to note that pneumatic diverticula are still present adjacent to skeletal tissues in apneumatic diving forms (e.g., auks,

penguins), but that diverticula do not penetrate the bones (personal observation; see Discussion below).

Body size and relative pneumaticity

A synoptic survey of nonpasseriform neognaths was undertaken to identify any taxon with evidence of pneumaticity of the appendicular skeleton (Fig. 3C), particularly those taxa with pneumatic invasion of elements distal to the elbow and knee joints (Fig. 3D). Among the surveyed birds, proximal appendicular pneumaticity was identified in at least some members of the following clades: Anseriformes, Pelecaniformes, Ciconiiformes, Gruiformes (Otididae), Falconiformes, and Coraciiformes (~Bucerotiformes) (see Table 2 for representative examples). Distal extremity pneumaticity (Fig. 3D), hereafter referred to as hyperpneumaticity ($PI > 0.83$), was restricted to certain members of the following groups: storks, bustards, hornbills, New and Old World vultures, screamers among anseriform birds, and pelicans and their allies (Figs. 4 and 5). In these cases, pneumatic foramina were identified in at least one of the following elements: ulna, radius, carpometacarpus, tibiotarsus, tarsometatarsus, or phalanges (manual or pedal) (Fig. 6C). Storks, bustards, vultures, and the non-*Pelecanus*

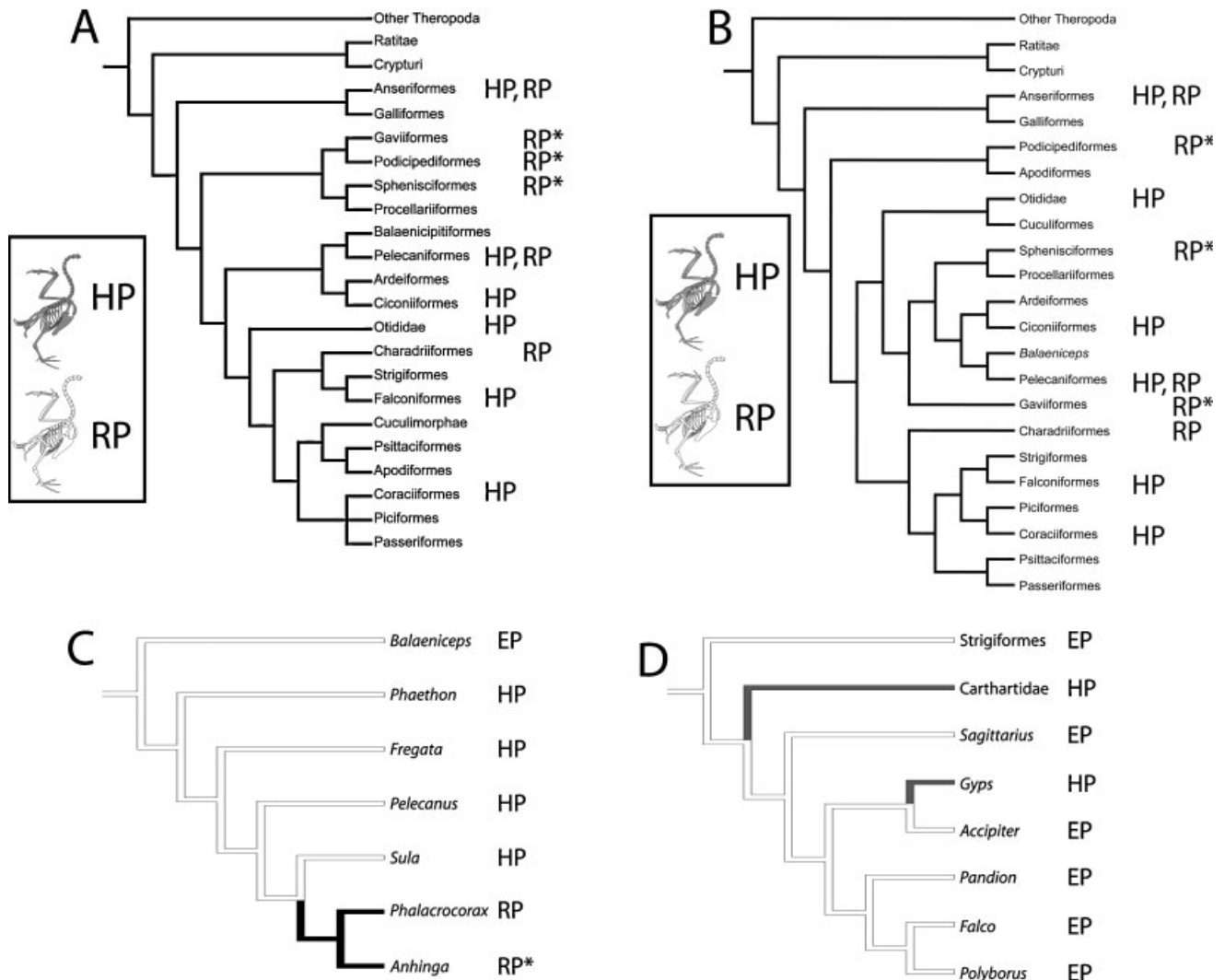


Fig. 4. Phylogenetic hypotheses used for character mapping of both reductions (RP) and extreme expansions (HP) of postcranial pneumaticity profiles among extant avians. (A) Global avian topology from morphology-based analysis of Livezey and Zusi (2007). (B) Global avian topology based on molecular hypothesis of Hackett et al. (2008). (C) Clade-specific hypothesis of pelecaniiform birds. (D) Clade-specific hypothesis of falconimorph birds. Phylogenetic context for C and D provided by the recent morphology-based analysis of Livezey and Zusi (2007). EP, expanded pneumaticity pattern; HP, hyperpneumaticity pattern; RP, reduced pneumaticity pattern. Black shading in C indicates a reduction in pneumaticity; gray shading in D indicates an increase in pneumaticity. Note: an asterisk indicates pneumaticity state invariance in terminal taxa.

pelecaniiforms restrict distal limb pneumaticity to forelimb elements, whereas screamers, hornbills, and the genus *Pelecanus* pneumatize both distal fore- and hind-limb elements (Table 2).

Generally hyperpneumatic these taxa represent the largest flying birds alive today (by body mass) (Table 1), and when within-clade variability exists, are the largest members of their respective clades (Fig. 5). For example, among storks distal forelimb pneumaticity is limited to the Marabou stork (*Leptoptilos crumeniferus*), a species that ranges in body mass between 5.6 and 8.9 kg and is the

largest member of the clade. Other, smaller-bodied members of the group (e.g., *Ephippiorhynchus*, *Mycteria*, *Ciconia*) do not pneumatize elements distal to the elbow or knee (Table 2). Similarly, among pelecaniiform birds, only *Pelecanus* (3.17–13.6 kg body mass range) pneumatizes both distal fore- and hind-limb elements, whereas other, smaller pelecaniiform birds restrict distal limb pneumaticity to the forelimb (Figs. 4C and 5B).

Old and New World vultures have developed hyperpneumaticity independently in concert with

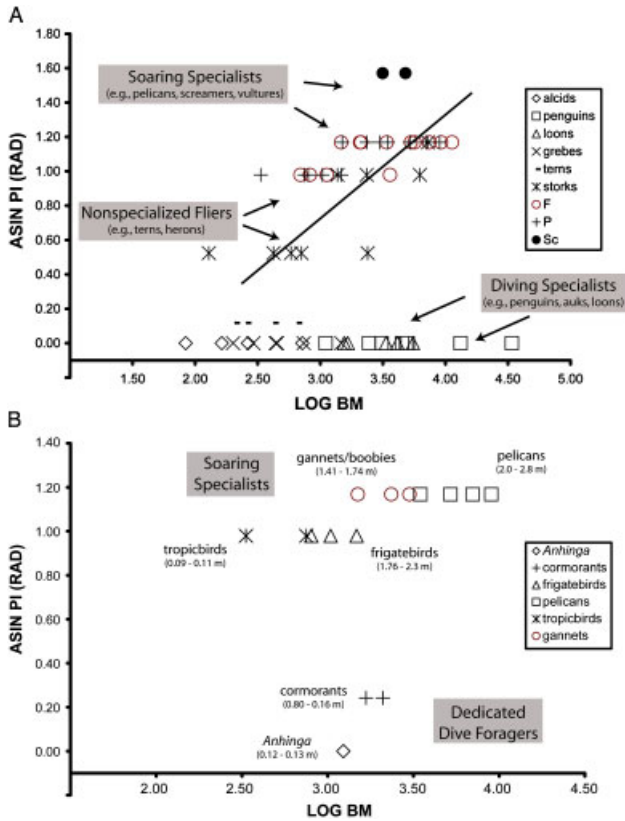


Fig. 5. Bivariate plots of arcsin-transformed pneumaticity index (ASIN PI) regressed on log body mass (LOG BM) in extant birds. Arcsin values expressed in radians. (A) Multi-clade dataset; ($n = 37, y = 0.49x - 0.66, R^2 = 0.56$). (B) Expanded peleciform dataset, with wingspan range indicated for each taxon. F, falconimorphs; P, pelicaniforms; Sc, screamers.

large body size among falconimorph birds (Figs. 4D and 5; Table 2). The body mass range of both clades represents local maxima relative to their respective sister falconimorphs (Fig. 4D). Note the recent analysis of Livezey and Zusi (2007) posits both groups of vultures as falconimorphs. The use of an alternative phylogenetic hypothesis (e.g., Seibold and Helbig, '95) positing a sister-taxon relationship between New World vultures and Ciconiiformes yields a similar result of independently derived hyperpneumaticity in the two groups.

An analysis of PI regressed on body mass for the assembled dataset (excluding subsurface dive foragers; e.g., penguins) reveals a significant ($P < 0.05$), positive correlation between the two traits ($n = 37, y = 0.49x - 0.66, R^2 = 0.56$). Neither within clade nor phylogenetically controlled analyses were conducted due to a sampling protocol that sought diverse representation among neognath birds as a whole.

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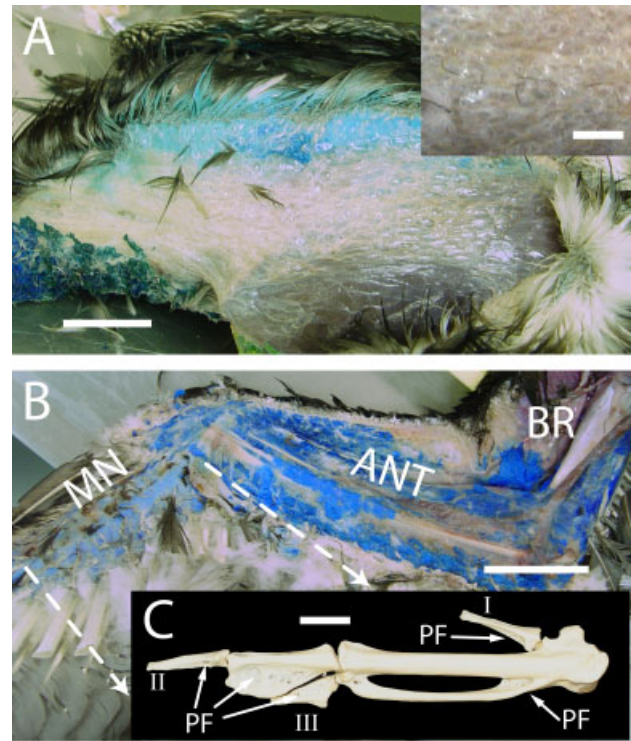


Fig. 6. Subcutaneous air sac diverticula and distal limb pneumaticity in birds. (A) Gross dissection of a partially in-filled thoracic subcutaneous diverticulum in a brown pelican (*Pelecanus occidentalis*, OUV C 10211), ventral view (head to the left)—inset shows close-up of meshwork morphology typical of subcutaneous diverticula. (B) Gross dissection of distal forelimb subcutaneous diverticular network in a turkey vulture (*Cathartes aura*, OUV C 10493), right forelimb, ventral view. (C) Carpometacarpus and phalanges of a turkey vulture (*C. aura*, OUV C 9648) for comparison with (B) to highlight pneumatic foramina in distal forelimb bones, right carpometacarpus and phalanges, ventral view. Blue color in photographs indicates the extent of in-filled latex following the negative pressure pulmonary injection protocol outlined in O'Connor (2004). Dashed arrows indicated reference position of C relative to B. ANT, antebrachium; BR, brachium; CMC, carpometacarpus; MN, manus, PF, pneumatic foramen; I, alular digit; II, major digit; III, minor digit. Scale equals 5 cm in A and B, 2 cm in A (inset) and C.

The soft-tissue anatomy of hyperpneumaticity

An examination of hyperpneumatic taxa indicates that distal limb bones are causally linked with an extensive subcutaneous air sac diverticulum (or series of diverticula). Gross dissection of representative peleciform (*Pelecanus*, *Sula*), bucerotid (*Bucorvis*, *Tockus*), and carthartid (*Cathartes*) birds reveal the existence of widespread diverticular networks intercalated throughout the subcutaneous space (Fig. 6; see Appendix for taxa available for soft-tissue analy-

sis). Latex-injection preparations of the pulmonary apparatus indicate that the origin of bone-pneumatizing diverticula is located in the lower (i.e., posttracheal) portion of the respiratory tract. Subcutaneous diverticular networks originate from the axillary diverticulum (O'Connor, 2004; Fig. 3) of the interclavicular (~clavicular) air sac. See O'Connor (2004, 2006) for a nomenclature and figures of individual air sacs and diverticula.

Not only do the clades in the previous section reveal the independent acquisition of distal limb pneumaticity in relatively large-bodied neognath birds, but most taxa also employ static soaring as a dominant flight mode to remain aloft (Table 1). That is, these species exploit ambient wind currents (thermals, updrafts, etc.) to maintain lift instead of actively flapping to do so. The bucerotids (hornbills) remain the sole exception among hyperpneumatic forms in this regard, in that they use intermittent bouts of flap-gliding as their dominant locomotor mode.

DISCUSSION

The variability in postcranial skeletal pneumaticity documented above, particularly in the context of the number of apparent functional correlates (e.g., the repeated loss of skeletal pneumaticity in diving forms), suggests that the interplay between the skeletal and respiratory systems serves multiple biological roles. The avian lung-air sac system is unique among amniotes with regard to anatomical organization (Duncker, '71), flow-dynamics (Bretz and Schmidt-Nielsen, '71; Piiper and Scheid, '85), and gas exchange potential (Maina, 2000, 2006 and references therein). Moreover, the very nature of increased pulmonary heterogeneity (i.e., air sac/diverticula development) has allowed birds to co-opt the respiratory apparatus to influence the fundamental tissue properties, shape, and size of the postcranial skeleton. The ability to pneumatize selected portions of the postcranial skeleton allows for differentially altering the density of individual bones, which in turn could influence energy expenditure associated with basic processes such as locomotion (e.g., individual bone/limb kinematics, whole body energetics) and foraging (Lovvorn and Jones, '91; Lovvorn et al., '91).

Decoupling volume-mass relationships: lessons from birds

From the sample examined herein, four major pneumaticity phenotypes have been designated

among extant birds (Fig. 3). The vast majority of small-bodied forms exhibit pneumaticity in restricted portions of the vertebral column, a pattern herein referred to as the common avian pattern (CP; Fig. 3B). The diversity of shorebirds (waders) and other small-bodied neognaths typify this phenotype, with taxa restricting pneumaticity to a few (~2–3) vertebrae at the cervico-thoracic junction (Table 2). Certain anseriforms (O'Connor, 2004) and larids (personal observation) also exhibit this pattern, with varying amounts of the vertebral column pneumatized. A number of diving specialists (e.g., auks, penguins, anhingas) exhibit reductions from CP and are completely apneumatic, representing the reduced pattern (RP; Fig. 3A). In contrast, many other clades expand upon CP, variably pneumatizing additional portions of the postcranial axial skeleton (e.g., sternum, ribs), limb girdles, and occasionally, proximal limb bones (humerus, femur). This represents the expanded pattern (EP; Fig. 3C) and characterizes the state in many anseriforms (nondiving ducks, geese; O'Connor, 2004), galliforms, columbiforms, and medium-sized members of a number of other groups (e.g., hawks, falcons, storks, herons, etc.; Table 2). It is only the largest members of selected clades that further expand pneumaticity into distal elements of the fore-, and more rarely, hind limbs, thereby characterizing the hyperpneumaticity pattern (HP; Fig. 3D). This is extremely rare among neognath birds generally, and appears restricted to large-bodied groups that regularly employ static soaring as a primary locomotor mode (Table 1) and in the case of the large-headed hornbills, a unique combination of flap-gliding and soaring.

Further underscoring the plasticity associated with postcranial pneumatization is the repeated loss of pneumaticity (reduced pattern, RP) in distantly related groups of diving birds (Fig. 4). Specifically, birds that employ sustained diving from the surface as part of their foraging repertoire (e.g., penguins, loons, auks, darters, diving ducks) have reduced skeletal pneumaticity altogether, likely in response to demands for reduced buoyancy (O'Connor, 2004; also see Lovvorn and Jones, '91; Wilson et al., '92). These taxa are nested within higher-level clades that exhibit postcranial skeletal pneumaticity, suggesting that the development of skeletal pneumatization has been restricted in these forms. In contrast, aerial plunge divers such as pelicans and terns have not reduced pneumaticity like the surface divers noted

above, and some forms (e.g., pelicans) even exhibit increased levels of pneumaticity. These taxa are categorized as splash divers, whereby birds dive from relatively low heights (~6–7 m) to capture prey items near the air–water interface; hence a need for reduced buoyancy may not be as important. Moreover, the elaborate subcutaneous air sac network in some large-bodied aerial divers (brown pelicans) has been hypothesized to function in impact protection during the contact phase between the air and water (Richardson, '39).

Such interspecific variability in postcranial pneumaticity, not to mention the wide-spread independent acquisition of both reductions and expansions (Fig. 4), strongly suggest that this system is under the control of some form of signaling mechanism. For example, it would appear that the system responds as certain size/mass thresholds are reached in birds (see below). More specifically, data presented in this work on flying birds indicate that as body mass increases, more individual elements of the postcranial skeleton are pneumatized. Not surprisingly, it also appears that a suite of other changes (e.g., behavior, morphology of wing profiles) characterize taxa at the upper end of the body mass range for flying birds. For example, virtually all of the largest flying birds (by mass) use static soaring as their primary flight mode.

The patterns identified herein suggest that pneumaticity of the avian postcranial skeleton may release structural constraints on body size evolution in the group by decoupling typical volume–mass relationships that encumber other animals (i.e., ones without a heterogeneously partitioned pulmonary system). In other words, the ability to differentially alter the density of the postcranial skeleton, one of the single heaviest constituent tissues of the amniote body, may have significantly influenced the avian radiation since the middle of the Mesozoic. At minimum three other Mesozoic archosaurian lineages (theropod and sauropod dinosaurs, pterosaurs) have previously exploited a generally similar pulmonary system (Wedel, 2005; O'Connor, 2006). Many nonavian theropod, and in particular, most sauropod dinosaurs exceeded the upper size limit attained by any known terrestrial vertebrate (extant or extinct), whereas hyperpneumatic aerial pterosaurs exceeded the largest known birds by estimates of 5–7 m as measured by wingspan (see Pneumaticity Profiles below).

Controls on skeletal pneumatization: systemic, local, or both?

Exactly what dictates (1) the stimulus–response relationship between the pulmonary and skeletal systems (e.g., site-specific osteoclast recruitment), (2) the developmental timing of epithelial expansion, and (3) whether it is mediated by systemic (e.g., hormonal) or local (e.g., biomolecular gradients) regulators (or both) remains unknown. It is known that active pneumatization of the skeleton in birds occurs after hatching (Hogg, '84; Schepelmann, '90; Brackmann, '91). However, although ontogenetic studies in the chicken (Hogg, '84) have documented the timing of whole-bone pneumatization, they have otherwise not explored the cellular or molecular processes related to the expansion of epithelium into and throughout the interior bones. It is only recently that researchers have started to explore the distribution of osteoclasts (and their associated signaling molecules) in the context of primate skeletal pneumatization (e.g., Smith et al., 2005), thereby opening up the potential for applying similar approaches aimed at investigating avian postcranial skeletal pneumatization.

Given the wealth of unknown factors related to the development of avian postcranial pneumaticity data from whole-body pattern analysis and even individual bone characteristics provide interesting observations for promoting the development of future studies. For example, gross dissection of diving specialists (e.g., auks) reveals that although the postcranial skeleton is not air-filled, pneumatic diverticula are still positioned adjacent to the skeleton. Hence, the lack of skeletal pneumaticity in these forms is not merely the result of inhibited diverticular development. Moreover, diving specialists are typically apneumatic throughout the entire postcranial skeleton (Table 2), not to mention portions of the cranial skeleton (see Witmer, '90), suggesting the involvement of a systemic regulatory mechanism.

A number of examples also suggest that local (i.e., bone-specific) regulatory mechanisms may exist for controlling pneumaticity. For example, in contrast to the hyperpneumatic static soaring birds (e.g., pelicans, vultures), large-bodied, dynamic soaring birds (e.g., albatrosses) do not pneumatize distal limb elements although they do exhibit pneumaticity of the vertebral column typical of other birds in this size class (personal observation). Instead, distal forelimb elements (e.g., ulnae, carpometacarpi) retain thick cortical

bone and are filled with marrow. It has been demonstrated that long bone pneumaticity results in reduced resistance to bending (Cubo and Casinos, 2000; Curry, 2002). As such, it is interesting to speculate that the highly energetic setting (i.e., one possibly representing a less predictable loading environment) encountered by dynamic soaring birds would favor bone strength over the decreased density obtained via pneumatization. By contrast, static soaring typically occurs in relatively slow moving thermals (Videler, 2005), whereby bone loading would be much more predictable generally, and birds would have more time to modify the attitude of the flight control surfaces in the case of increasing and potentially dangerous loading situations.

Another example to support the concept of bone-specific signaling of pneumatization is found within the postcranial skeleton of pelicans. *Pelecanus* is unique among hyperpneumatic neognath birds in exhibiting pneumaticity of the entire forelimb, yet only within the distal most hind limb elements (Table 2). Although the tibiotarsus and tarsometatarsus are pneumatic, the more proximally positioned femur is apneumatic and marrow-filled, even though pneumatizing diverticula surround the latter bone. This is not a spurious observation based on a low sample size (see Appendix), but appears to be a trait characterizing *Pelecanus* among the nondiving pelecarniforms, with other members of the clade (e.g., *Sula*, *Morus*, *Fregata*) exhibiting pneumatic femora. Similar to the situation hypothesized above for dynamic soaring birds, it may be the case that bone-specific feedback (e.g., osteocyte-mediated strain detection; Lanyon, '93) may play a role in restricting the pneumatization process. As the avian femur is known to experience predominantly torsional loads when in contact with the substrate (Main and Biewener, 2007), the absence of femoral pneumaticity in the pelican may be related to the necessity of mediating loads encountered during terrestrial locomotion in *Pelecanus*, the largest member of the clade. Ongoing research examining relationships among whole-bone morphometrics, cross-sectional geometry, histology, and mechanical strength testing in the specific context of pneumaticity (e.g., Rasmusson and O'Connor, 2007), along with integrated studies examining bone response to different loading situations (e.g., Main and Biewener, 2007), will no doubt provide novel perspectives on the complex interplay between pneumatic epithelial and skeletal tissues. Finally, perhaps

most interesting would be studies aimed at identifying mechanisms related to either systemic or local control of the skeletal pneumatization process. Not only would such an endeavor venture into a different areas of developmental biology (e.g., identifying the molecular signaling pathways involved) but would no doubt lead into exciting evolutionary-developmental biology questions related to clade diversification as those pathways evolve.

Extinct archosaurs: pneumaticity profiles in saurischian dinosaurs and pterosaurs

Whereas detailed comparative studies similar to those conducted on birds are not possible for most fossil groups, being limited by both sample size and completeness of individual specimens, it remains possible to evaluate roughly similar questions in some extinct archosaurian lineages. For example, nonavian theropod dinosaurs have been surveyed previously (e.g., Britt, '93; O'Connor and Claessens, 2005), but with most of the emphasis on patterns of pneumaticity in relation to soft tissue reconstruction and pulmonary evolution. However, Carrano and O'Connor (2005) and O'Connor (2006, 2007) discussed the presence of increased pneumaticity in larger-bodied nonavian theropods, including tyrannosaurids and carcharodontosaurids, suggesting that some of the general principles related to body size evolution in birds may apply to their nonavian theropod relatives. Supporting this assertion is that in tyrannosaurids, smaller-bodied clade members pneumatize fewer elements of the postcranial skeleton than larger-bodied forms (Xu et al., 2004). Similarly, Wedel (2003) attempted to characterize the variability of skeletal pneumaticity in sauropodomorph dinosaurs. This work documented clade-level evolution of pneumatic features in sauropodomorphs, with anatomically restricted skeletal pneumaticity in basal members of the group and increased levels of pneumaticity in derived forms. Unfortunately, the absolute and large size of virtually all skeletally mature sauropod dinosaurs is such that it likely exceeds any theoretical size threshold for pneumaticity, thus most derived forms pneumatize most of the vertebral column (Wedel, 2003, 2005).

The extinct pterosaurs ("flying reptiles") represent another example of an archosaurian group exhibiting evidence of postcranial skeletal pneumaticity (Bonde and Christiansen, 2003; Unwin, 2006; Claessens et al., 2009), and perhaps one that

represents a more interesting comparison for the information detailed above for birds. First, basal pterosaurs were small-bodied forms (i.e., wingspans <2.5 m) that were either (1) apneumatic or (2) pneumatized restricted portions of the postcranial axial skeleton at the cervicothoracic junction. This is noteworthy in its similarity to patterns identified in basal sauropods and theropods (O'Connor, 2007; Wedel, 2007) and in many groups of small-bodied birds (Table 2; O'Connor 2004). Patterns of enhanced skeletal pneumaticity, including pneumatization of distal forelimb elements, was independently acquired in at least two groups (e.g., Ornithocheiroidea, Azhdarchoidea) of large-bodied pterodactyloid pterosaurs. Each clade is typified by members with wingspans greater than 3 m, and in extreme cases, spans approaching 10 m. Hence, whole-body pneumaticity patterns in the largest pterosaurs mirror those patterns identified in the largest flying birds, further underscoring the potential impact of postcranial skeletal pneumatization for influencing body size evolution in archosaurs. Claessens et al. (2009) provide detailed analyses of respiratory evolution and body-size evolution in pterosaurs.

As nonavian theropod and sauropodomorph dinosaur groups both represent nonvolant forms, any necessity for density reduction, and thus, a decoupling of standard volume-mass relationships, may pale in comparison for the need in aerial forms such as birds (Rayner, '82; Gessaman and Nagy, '88; Norberg, '95). However, from an energetics perspective (Bennett, '85), the ability to pneumatize any portion of the postcranial skeleton could be beneficial to an organism, whether it be ground dwelling, arboreal, aerial, or any combination thereof.

Finally, this paper has been limited to an examination and discussion of postcranial skeletal pneumaticity, as it is typically the skeleton that is preserved in the vast majority of fossils specimens. However, given the exceptional skeletal evidence for a heterogeneously partitioned pulmonary

apparatus in saurischian dinosaurs and pterosaurs, it is important to note that such pulmonary systems in extant sauropsids also occupy a significant volume of the body cavity (see Duncker, '79; Perry, '83; Duncker and Güntert, '85). Thus, whole body mass estimates in fossil archosaurs (e.g., Wedel, 2005, 2007; Schwarz and Fritschs, 2006) and any associated energetic considerations for whole body mechanics (e.g., turning inertia [Carrier et al., 2001], cost of transport [Nishii, 2006]) or thermoregulation (Perry et al., this volume) must account for those portions of the anatomy (e.g., intrathoracic and intraabdominal air sacs) not predicted to directly impact skeletal morphology in preserved fossils of these taxa. For example, recent modeling efforts (Hutchinson et al., 2007) have explicitly attempted to model locomotor biology in extinct archosaurs using a range of estimates for whole trunk density based on different models of pulmonary structure.

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APPENDIX: LIST OF SPECIMENS USED IN THE STUDY

Species identification		Collection information	
Pelecaniformes			
<i>Anhinga</i>	<i>anhinga</i>	NMNH	225790
<i>Anhinga</i>	<i>anhinga</i>	NMNH	622528
<i>Anhinga</i>	<i>anhinga</i>	NMNH	322081
<i>Anhinga</i>	<i>anhinga</i>	CM	14313

<i>Anhinga</i>	<i>anhinga</i>	CM	14362
<i>Anhinga</i>	<i>anhinga</i>	CM	261889
<i>Anhinga</i>	<i>anhinga</i>	CM	907
<i>Anhinga</i>	<i>anhinga</i>	CM	203
<i>Anhinga</i>	<i>anhinga</i>	OUV	10435
<i>Phalacrocorax</i>	<i>aristotelis</i>	JLUG*	<i>n</i> = 7
<i>Phalacrocorax</i>	<i>pencilillatus</i>	CM	10810
<i>Phalacrocorax</i>	<i>auritus</i>	CM	7425
<i>Phalacrocorax</i>	<i>auritus</i>	NMNH	561035
<i>Phalacrocorax</i>	<i>auritus</i>	OUV	10431
<i>Phalacrocorax</i>	<i>auritus</i>	OUV	10436
<i>Phalacrocorax</i>	<i>auritus</i>	OUV	10437
<i>Phalacrocorax</i>	<i>auritus</i>	OUV	9772
<i>Phalacrocorax</i>	<i>auritus</i>	OUV	10479
<i>Phalacrocorax</i>	<i>auritus</i>	OUV	9771
<i>Phalacrocorax</i>	<i>auritus</i>	OUV	10291
<i>Phalacrocorax</i>	<i>auritus</i>	OUV	10234
<i>Phalacrocorax</i>	<i>auritus</i>	OUV	10241
<i>Phalacrocorax</i>	<i>auritus</i>	OUV	10233
<i>Phalacrocorax</i>	<i>auritus</i>	OUV	10505
<i>Phalacrocorax</i>	<i>auritus</i>	OUV	10482
<i>Sula</i>	<i>dactylatra</i>	NMNH	289144
<i>Sula</i>	<i>dactylatra</i>	CM	8270
<i>Sula</i>	<i>serrator</i>	NMNH	612654
<i>Morus</i>	<i>bassana</i>	NMNH	554787
<i>Morus</i>	<i>bassana</i>	NMNH	614826
<i>Morus</i>	<i>bassana</i>	CM	1161
<i>Morus</i>	<i>bassana</i>	CM	12175
<i>Morus</i>	<i>bassana</i>	CM	21320
<i>Morus</i>	<i>bassana</i>	OUV	10434
<i>Morus</i>	<i>bassana</i>	OUV	10492
<i>Fregata</i>	<i>magnificans</i>	CM	5133
<i>Fregata</i>	<i>magnificans</i>	CM	203
<i>Fregata</i>	<i>magnificans</i>	CM	907
<i>Pelecanus</i>	<i>occidentalis</i>	OUV	10211
<i>Pelecanus</i>	<i>occidentalis</i>	AMNH	21610
<i>Pelecanus</i>	<i>occidentalis</i>	CM	13035
<i>Pelecanus</i>	<i>occidentalis</i>	CM	13033
<i>Pelecanus</i>	<i>occidentalis</i>	CM	10374
<i>Pelecanus</i>	<i>occidentalis</i>	OUV	10494
<i>Pelecanus</i>	<i>occidentalis</i>	OUV	10478
<i>Pelecanus</i>	<i>occidentalis</i>	OUV	10484
<i>Pelecanus</i>	<i>occidentalis</i>	OUV	10433
<i>Pelecanus</i>	<i>occidentalis</i>	OUV	10494
<i>Pelecanus</i>	<i>occidentalis</i>	OUV	10440
<i>Pelecanus</i>	<i>occidentalis</i>	OUV	10430
<i>Pelecanus</i>	<i>erythrorhynchus</i>	SBU	103985
Procellariiformes			
<i>Calonectris</i>	<i>sp</i>	OUV	10438
<i>Phoebastria</i>	<i>immutabilis</i>	OUV	10483
<i>Phoebastria</i>	<i>immutabilis</i>	OUV	10481
<i>Phoebastria</i>	<i>immutabilis</i>	OUV	10486
<i>Phoebastria</i>	<i>immutabilis</i>	OUV	10224
<i>Phoebastria</i>	<i>immutabilis</i>	OUV	10448
<i>Phoebastria</i>	<i>immutabilis</i>	OUV	10439
<i>Phoebastria</i>	<i>immutabilis</i>	OUV	10480
<i>Phoebastria</i>	<i>immutabilis</i>	OUV	10225
<i>Phoebastria</i>	<i>immutabilis</i>	OUV	10509
Charadriiformes			
<i>Alca</i>	<i>torda</i>	JLUG*	<i>n</i> = 6
<i>Alca</i>	<i>torda</i>	CM	S-396

<i>Aethia</i>	<i>crstatella</i>	CM	S-11196
<i>Aethia</i>	<i>crstatella</i>	CM	S-15847
<i>Aethia</i>	<i>crstatella</i>	CM	S-15848
<i>Aethia</i>	<i>crstatella</i>	CM	S-15850
<i>Aethia</i>	<i>pusilla</i>	CM	S-11727
<i>Aethia</i>	<i>pusilla</i>	CM	S-11728
<i>Aethia</i>	<i>pusilla</i>	CM	S-15851
<i>Aethia</i>	<i>pusilla</i>	CM	S-15852
<i>Aethia</i>	<i>pusilla</i>	CM	S-15853
<i>Aethia</i>	<i>pusilla</i>	CM	S-15854
<i>Alle</i>	<i>alle</i>	CM	S-6919
<i>Fratercula</i>	<i>arctica</i>	JLUG*	<i>n</i> = 4
<i>Fratercula</i>	<i>arctica</i>	CM	S-398
<i>Fratercula</i>	<i>arctica</i>	CM	S-11794
<i>Fratercula</i>	<i>cirrhata</i>	CM	S-10807
<i>Fratercula</i>	<i>cirrhata</i>	CM	S-11779
<i>Uria</i>	<i>aalge</i>	JLUG*	<i>n</i> = 4
<i>Uria</i>	<i>aalge</i>	CM	S-399
<i>Uria</i>	<i>aalge</i>	CM	S-2030
<i>Uria</i>	<i>aalge</i>	CM	S-8011
<i>Uria</i>	<i>lomvia</i>	CM	S-14970
<i>Uria</i>	<i>lomvia</i>	CM	S-15846
<i>Cephus</i>	<i>columba</i>	CM	S-8252
<i>Cephus</i>	<i>columba</i>	CM	S-11083
<i>Cephus</i>	<i>grylle</i>	CM	S-14342
<i>Cephus</i>	<i>grylle</i>	CM	S-14344
<i>Synthliborhamphus</i>	<i>antiquus</i>	CM	S-11556
<i>Ptychoramphus</i>	<i>aleuticus</i>	CM	S-8203
<i>Ptychoramphus</i>	<i>aleuticus</i>	CM	S-8204
<i>Cyclorhynchus</i>	<i>psittacula</i>	CM	S-15836
<i>Bradyrhampus</i>	<i>marmoratus</i>	CM	S-2041
<i>Bradyrhampus</i>	<i>marmoratus</i>	CM	S-8127
<i>Cerorhinca</i>	<i>moncerata</i>	CM	S-5119
<i>Cerorhinca</i>	<i>moncerata</i>	CM	S-8126

See O'Connor and Duncker (2007) for a comprehensive list of Charadriiform birds

Anseriformes

<i>Anhima</i>	<i>cornuta</i>	NMNH	2476
<i>Anhima</i>	<i>cornuta</i>	NMNH	345217
<i>Chauna</i>	<i>torquata</i>	NMNH	345619

See O'Connor (2004) for a comprehensive list of anseriform birds

Sphenisciformes

<i>Spheniscus</i>	<i>humboldti</i>	CM	10810
<i>Spheniscus</i>	<i>dermeris</i>	OUGC	10288
<i>Spheniscus</i>	<i>dermeris</i>	JLUG*	<i>n</i> = 2
<i>Aptenodytes</i>	<i>patagonicus</i>	JLUG*	<i>n</i> = 1
<i>Aptenodytes</i>	<i>forsteri</i>	CM	11600
<i>Pyposcelis</i>	<i>adeliae</i>	OUGC	9649

Podicipediforms

<i>Podiceps</i>	<i>crstatatus</i>	JLUG*	<i>n</i> = 7
<i>Podiceps</i>	<i>ruficollus</i>	JLUG*	<i>n</i> = 2

Gaviiforms

<i>Gavia</i>	<i>immer</i>	OUGC	10563
<i>Gavia</i>	<i>immer</i>	OUGC	10407
<i>Gavia</i>	<i>immer</i>	OUGC	10467
<i>Gavia</i>	<i>immer</i>	CM	16102
<i>Gavia</i>	<i>arctica</i>	JLUG*	<i>n</i> = 1

Falconimorphae

<i>Cathartes</i>	<i>aura</i>	OUGC	10284
<i>Cathartes</i>	<i>aura</i>	OUGC	9648
<i>Cathartes</i>	<i>aura</i>	OUGC	10493
<i>Buteo</i>	<i>jamaicensis</i>	OUGC	9789

<i>Bubo</i>	<i>virgineatus</i>	OUV	10485
Ciconiiformes			
<i>Ardea</i>	<i>herodias</i>	OUV	9765
<i>Ardea</i>	<i>herodias</i>	OUV	10542
<i>Ardea</i>	<i>herodias</i>	CM	10805
<i>Ardea</i>	<i>herodias</i>	CM	3207
<i>Ardea</i>	<i>herodias</i>	CM	3356
<i>Scopus</i>	<i>umbretta</i>	CM	11572
<i>Ephippiorhynchus</i>	<i>senegalensis</i>	USB	103801
<i>Leptiptilos</i>	<i>crumeniferus</i>	USB	118743
<i>Mycteria</i>	<i>americana</i>	CM	911
<i>Mycteria</i>	<i>americana</i>	CM	13026
<i>Ciconia</i>	<i>abdimii</i>	CM	1213
<i>Ixobrychus</i>	<i>exilis</i>	CM	11026
<i>Botarus</i>	<i>lentiginosus</i>	CM	1392
<i>Botarus</i>	<i>pinnatus</i>	CM	8655
<i>Botarus</i>	<i>pinnatus</i>	CM	10296
Coraciiformes			
<i>Bucorvis</i>	<i>leadbeateri</i>	AMNH	3953
<i>Bucorvis</i>	<i>leadbeateri</i>	CM	2457
<i>Bucorvis</i>	<i>leadbeateri</i>	TM	76018
<i>Tockus</i>	<i>erythrorhynchus</i>	TM	60543
<i>Tockus</i>	<i>erythrorhynchus</i>	TM	60545
<i>Tockus</i>	<i>erythrorhynchus</i>	TM	60547

JULG* indicates number (*n*) of specimens available for direct examination. Shaded cells indicate those specimens available for subcutaneous air sac study.

LITERATURE CITED

- Akester AR, Pomeroy DE, Purton MD. 1973. Subcutaneous air pouches in the Marabou stork. *J Zool Lond* 170:493–499.
- Bennett AF. 1985. Energetics and locomotion. In: Hildebrand M, Bramble D, Liem K, Wake D, editors. *Functional vertebrate morphology*. Cambridge: Harvard University Press. p 173–184.
- Bignon F. 1889. Contribution a L'etude de la pneumatocite chez les oiseaux. *Mem Soc Zool France* II:260–320.
- Bonde N, Christiansen P. 2003. The detailed anatomy of *Rhamphorhynchus*: axial pneumatocity and its implications. In: Buffetaut E, Masin J-M, editors. *Evolution and palaeobiology of pterosaurs*. London, Geol Soc Spec Pub 17. p 217–232.
- Brackenbury JH. 1987. Ventilation of the lung-air sac system. In: Seller TJ, editor. *Bird respiration*. Boca Raton: CRC Press. p 39–70.
- Brackmann F. 1991. Das erythropoetische Knochenmark der europäischen Wachtel: Verteilung und volumen bei Wachstum und pneumatisation des Skeletts. Ph.D. Thesis. Institut für Anatomie und Zytobiologie. Giessen, Justus-Liebig Universität.
- Bremer JL. 1940. The pneumatization of the humerus in the common fowl and the associated activity of theelin. *Anat Rec* 77:197–211.
- Bretz WL, Schmidt-Nielsen K. 1971. Bird respiration: flow patterns in the duck lung. *J Exp Biol* 54:103–118.
- Britt B. 1993. Pneumatic postcranial bones in dinosaurs and other archosaurs. Ph.D. Dissertation. University Calgary, Canada.
- Brochu CA. 2001. Progress and future directions in archosaur phylogenetics. *J Paleontol* 75:1185–1201.
- Carrano MT, O'Connor PM. 2005. Bird's eye view. *Nat Hist* 114:42–47.
- Carrier DR, Walter RM, Lee DV. 2001. Influence of rotational inertia on turning performance of theropod dinosaurs: clues from humans with increased rotational inertia. *J Exp Biol* 204:3917–3926.
- Claessens LPAM. 2005. The evolution of breathing mechanisms in the Archosauria. Ph.D. Dissertation. Harvard University, USA.
- Claessens LPAM, O'Connor PM, Unwin DM. 2009. Respiratory evolution facilitated the origin of pterosaur flight and aerial gigantism. *PLOS One* 4:e4497. DOI:10.1371/journal.pone.0004497
- Cope ED. 1877. On a gigantic saurian from the Dakota Epoch of Colorado. *Paleontol Bul* 25:5–10.
- Crisp E. 1857. On the presence or absence of air in the bones of birds. *Proc Zool Soc Lond* 1857:215–220.
- Cubo J, Casinos A. 2000. Incidence and mechanical significance of pneumatization in the long bones of birds. *Zool J Linn Soc* 130:499–510.
- Curry JD. 2002. *Bones: structures and mechanics*. Princeton: Princeton University Press. p 436.
- Currey JD, Alexander RM. 1985. The thickness of the walls of tubular bones. *J Zool (Lond)* 206:453–468.
- Dantzker MS, Deane GB, Bradbury JW. 1999. Directional acoustic radiation in the strut display of male sage grouse *Centrocercus urophasianus*. *J Exp Biol* 202:2893–2909.
- Duncker H-R. 1971. The lung air sac system of birds. *Adv Anat Embryol Cell Biol* 45:1–171.
- Duncker H-R. 1974. Structure of the avian respiratory tract. *Resp Physiol* 22:1–19.
- Duncker H-R. 1978. Functional morphology of the respiratory system and coelomic subdivisions in reptiles, birds and mammals. *Verh Dtsch Zool Ges* 1978:99–132.

- Duncker H-R. 1979. Coelomic cavities. In: King AS, McLelland J, editors. Form and function in birds, Vol. I. London: Academic Press. p 39–67.
- Duncker H-R. 1989. Structural and functional integration across the reptile-bird transition: locomotor and respiratory Systems. In: Wake DBR, Roth G, editors. Complex organismal functions: integration and evolution in vertebrates. New York: John Wiley & Sons. p 147–169.
- Duncker H-R, Güntert M. 1985. The quantitative design of the avian respiratory system—from hummingbird to mute swan. In: Nachtigall W, editor. Biona Report 3—Biology and Related Natural Sciences. p 361–378.
- Dunning JB, editor. 1993. CRC handbook of avian body masses. Boca Raton: CRC Press. 371p.
- Fajardo RJ, Hernandez E, O'Connor PM. 2007. Postcranial skeletal pneumaticity: a case study in the use of quantitative microCT to assess vertebral structure in birds. *J Anat* 211:138–147.
- Felsenstein J. 1985. Phylogenies and the comparative method. *Am Nat* 125:1–15.
- Gauthier JA. 1994. The diversification of the amniotes. In: Prothero DR, Schoch RM, editors. Major features of vertebrate evolution, short courses in paleontology: no 7. Knoxville, TN: Paleontological Society. p 129–159.
- Gessaman JA, Nagy KA. 1988. Transmitter loads affect the flight speed and metabolism of homing pigeons. *Condor* 90:662–668.
- Hackett SJ, Kimball RT, Reddy S, Bowie RCK, Braun EL, Braun MJ, Chojnowski JL, Cox WA, Han K-L, Harshman J, Huddleston CJ, Marks BD, Miglia KJ, Moore WS, Sheldon FH, Steadman DW, Witt CC, Yuri T. 2008. A phylogenomic study of birds reveals their evolutionary history. *Science* 320:1763–1768.
- Harvey PH, Pagel MD. 1991. The comparative method in evolutionary biology. Oxford: Oxford University Press. 239p.
- Harvey PH, Purvis A. 1991. Comparative methods for explaining adaptations. *Nature* 351:619–624.
- Hogg DA. 1984. The development of pneumatisation in the postcranial skeleton of the domestic fowl. *J Anat* 139:105–113.
- Honess RF, Allred WJ. 1942. Structure and functions of the neck muscles in inflation and deflation of the esophagus in the sage cock. *Wyom Game Fish Depart Bul* 2:5–12.
- Hutchinson JR, Ng-Thro-Hing V, Anderson CF. 2007. A 3D interactive method for estimating body segmental parameters in animals: application to the turning and running performance of *Tyrannosaurus rex*. *J Theor Biol* 246:660–680.
- Irmis RB, Nesbitt SJ, Padian K, Smith ND, Turner AH, Woody D, Downs A. 2007. A late triassic dinosauriform assemblage from New Mexico and the rise of dinosaurs. *Science* 317:358–361.
- Janensch W. 1947. Pneumatizität bei Wirbeln von Sauropoden und Anderen Saurischiern. *Palaeontogr Supp* 7:1–25.
- King AS. 1957. The aerated bones of *Gallus domesticus*. *Acta Anat* 31:220–230.
- King AS. 1966. Structural and functional aspects of the avian lungs and air sacs. *Int Rev Gen Exp Zool* 2:171–267.
- Kemp A. 1995. The hornbills. Oxford: Oxford University Press. p 1–302.
- Lanyon LE. 1993. Osteocytes, strain detection, bone modeling and remodeling. *Calc Tiss Int* 53:S102–S107.
- Livezey BC, Zusi RL. 2007. Higher-order phylogeny of modern birds (Theropoda, Aves: Neornithes) based on comparative anatomy. II. Analysis and discussion. *Zool J Linn Soc* 149:1–95.
- Lockner FR, Murrish DE. 1975. Interclavicular air sac pressures and vocalizations in mallard ducks *Anas platyrhynchos*. *Comp Biochem Physiol A* 52:183–187.
- Lovvorn JR, Jones DR. 1991. Body mass, volume, and buoyancy of some aquatic birds, and their relation to locomotor strategies. *Can J Zool* 69:2888–2892.
- Lovvorn JR, Jones DR, Blake RW. 1991. Mechanics of underwater locomotion in diving ducks: drag, buoyancy and acceleration in a size gradient of species. *J Exp Biol* 159:89–108.
- Main RP, Biewener AA. 2007. Skeletal strain patterns and growth in the emu hindlimb during ontogeny. *J Exp Biol* 210:2676–2690.
- Maina JN. 2000. Comparative respiratory morphology: themes and principles in the design and construction of the gas exchangers. *Anat Rec: New Anat* 261:25–44.
- Maina JN. 2002. Some recent advances on the study and understanding of the functional design of the avian lung: morphological and morphometric perspectives. *Bio Rev* 77:97–152.
- Maina JN. 2006. Development, structure, and function of a novel respiratory organ, the lung–air sac system of birds: to go where no other vertebrate has gone. *Bio Rev* 81:545–579.
- Mazzetta GV, Christiansen P, Fariña RA. 2004. Giants and bizarres: body size of some southern South American Cretaceous dinosaurs. *Hist Biol* 16:71–83.
- McLelland J. 1989. Anatomy of the lungs and air sacs. In: King AS, McLelland J, editors. Form and function in birds, Vol. 4. London: Academic Press. p 221–279.
- McMahon TA. 1975. Using body size to understand the structural design of animals: quadrupedal locomotion. *J Appl Physiol* 19:619–627.
- Müller B. 1908. The air-sacs of the pigeon. *Smith Misc Coll* 50:365–414.
- Murie J. 1867. On the tracheal pouch of the emu (*Dromaeus novaehollandiae*). *Proc Zool Soc Lond* 1867:405–415.
- Murie J. 1868. Observations concerning the presence and function of the gular pouch in *Otis kori* and *Otis australis*. *Proc Zool Soc Lond* 1868:471–477.
- Nishii J. 2006. An analytical estimation of the energy cost for legged locomotion. *J Theor Biol* 238:636–645.
- Norberg UM. 1995. How a long tail and changes in mass and wing shape affect the cost of flight in animals. *Func Ecol* 9:48–54.
- O'Connor PM. 2004. Pulmonary pneumaticity in the postcranial skeleton of extant aves: a case study examining Anseriformes. *J Morphol* 261:141–161.
- O'Connor PM. 2006. Postcranial pneumaticity: an evaluation of soft-tissue influences on the postcranial skeleton and the reconstruction of pulmonary anatomy in archosaurs. *J Morphol* 267:1199–1226.
- O'Connor PM. 2007. The postcranial axial skeleton of *Majungasaurus crenatissimus* (Theropoda: Abelisauridae) from the Late Cretaceous of Madagascar. *Soc Vert Paleon Membr* 8:127–162.
- O'Connor PM, Claessens LPAM. 2005. Basic avian pulmonary design and flow-through ventilation in non-avian theropod dinosaurs. *Nature* 436:253–256.

- O'Connor PM, Duncker H-R. 2007. Postcranial pneumaticity in charadriiform birds: re-examining relationships among skeletal pneumaticity, body size, and diving behavior. *Int Comp Biol* 47:e214.
- Perry SF. 1983. Reptilian lungs: functional anatomy and evolution. *Adv Anat Embryol Cell Biol* 79:1–81.
- Perry SF. 1989. Mainstreams in the evolution of vertebrate respiratory structures. In: King AS, McLelland JM, editors. *Form and function in birds*, Vol. 4. New York: Academic Press. p 1–67.
- Perry SF. 1998. Lungs: comparative anatomy, functional morphology, and evolution. In: Gans C, Gaunt AS, editors. *Biology of the reptilia: visceral organs*. Ithaca: Society for the Study of Amphibians and Reptiles. p 1–92.
- Perry SF. 2001. Functional morphology of the reptilian and avian respiratory systems and its implications for theropod dinosaurs. In: Gauthier J, Gall LF, editors. *New perspectives on the origin and early evolution of birds*. New Haven, CT: Peabody Museum of Natural History. p 429–441.
- Piiper J, Scheid P. 1985. Airflow pathways in the avian respiratory tract. *Bird flight—vogelflug: Biona Report 3—Biology and Related Natural Sciences*. p 335–349.
- Plummer EM, Goller F. 2008. Singing with reduced air sac volume causes uniform decrease in airflow and sound amplitude in the zebra finch. *J Exp Biol* 211:66–78.
- Rasmusson EL, O'Connor PM. 2007. Morphology of the forelimb skeleton and locomotory behavior in birds: Pelecaniformes and Procellariiformes. *J Morphol* 268:1122.
- Rayner JMV. 1982. Avian flight energetics. *Ann Rev Physiol* 44:109–119.
- Richardson F. 1939. Functional aspects of the pneumatic system of the California brown pelican. *Condor* 41:13–17.
- Schepelmann K. 1990. Erythropoietic bone marrow in the pigeon: development of its distribution and volume during growth and pneumatization of bones. *J Morphol* 203: 21–34.
- Schwarz D, Fritsch G. 2006. Pneumatic structures in the cervical vertebrae of the Late Jurassic Tendaguru sauropods *Brachiosaurus brancai* and *Dicraeosaurus*. *Ecol Geol Helv* 99:65–78.
- Seibold I, Helbig AJ. 1995. Evolutionary history of new and old World vultures inferred from nucleotide sequences of the mitochondrial cytochrome b gene. *Phil Trans Roy Soc Lond B* 150:163–178.
- Smith TD, Rossie JB, Cooper GM, Mooney MP, Siegel MI. 2005. Secondary pneumatization of the maxillary sinus in callitrichid primates: insights from immunohistochemistry and bone cell distribution. *Anat Rec* 285A: 677–689.
- Unwin DM. 2006. *Pterosaurs: from deep time*. New York: Pi Press. p 352.
- Upchurch P, Barrett PM, Dodson P. 2004. *Sauropoda*. In: Weishampel DB, Dodson P, Osmolska H, editors. *The dinosauria*, 2nd edition. Berkeley, UC Press. p 259–322.
- Videler JJ. 2005. *Avian flight*. Oxford: Oxford Ornithology Series. p 258.
- Wedel MJ. 2003. The evolution of vertebral pneumaticity in sauropod dinosaurs. *J Vert Paleon* 23:344–357.
- Wedel MJ. 2005. Postcranial skeletal pneumaticity in sauropods and its implications for mass estimates. In: Curry Rogers KA, Wilson JA, editors. *The Sauropods: evolution and paleobiology*. Berkeley: UC Press. p 201–228.
- Wedel MJ. 2007. What pneumaticity tells us about “prosauropods”, and vice versa. *Spec Pap Paleon* 77: 207–222.
- Welty JC. 1979. *The life of birds*. Philadelphia: Saunders College. p 623.
- Wilson RP, Hustler K, Ryan PG, Burger AE, Nöldeke EC. 1992. Diving birds in cold water: do Archimedes and Boyle determine energetic costs? *Am Nat* 140:179–200.
- Witmer LM. 1990. The craniofacial air sac system of Mesozoic birds (Aves). *Zool J Linn Soc* 100:327–378.
- Xu X, Norell MA, Kuang X, Wang X, Zhao Q, Jia C. 2004. Basal tyrannosauroids from china and evidence for protofeathers in tyrannosauroids. *Nature* 431:680–684.