

Pulmonary Pneumaticity in the Postcranial Skeleton of Extant Aves: A Case Study Examining Anseriformes

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ABSTRACT Anseriform birds were surveyed to examine how the degree of postcranial pneumaticity varies in a behaviorally and size-diverse clade of living birds. This study attempts to extricate the relative effects of phylogeny, body size, and behavioral specializations (e.g., diving, soaring) that have been postulated to influence the extent of postcranial skeletal pneumaticity. One hundred anseriform species were examined as the focal study group. Methods included latex injection of the pulmonary apparatus followed by gross dissection or direct examination of osteological specimens. The Pneumaticity Index (PI) is introduced as a means of quantifying and comparing postcranial pneumaticity in a number of species simultaneously. Phylogenetically independent contrasts (PICs) were used to examine the relationship between body size and the degree of postcranial pneumaticity throughout the clade. There is a high degree of similarity (i.e., clade-specificity) within most anseriform subgroups. As a whole, Anseriformes demonstrate no significant relationship between relative pneumaticity and body size, as indicated by regression analysis of body mass on PI. It is apparent, however, that many clades of diving ducks do exhibit lower PIs than their nondiving relatives. By exclusion of diving taxa from analyses, a significant positive slope is observed and the hypothesis of relatively higher pneumaticity in larger-bodied birds is only weakly supported. However, low correlations indicate that factors other than body size account for much of the variation observed in relative pneumaticity. Pneumaticity profiles were mapped onto existing phylogenetic hypotheses. A reduction in the degree of postcranial pneumaticity occurred independently in at least three anseriform subclades specialized for diving. Finally, enigmatic pneumatic features located in distal forelimb elements of screamers (Anhimidae) result from invasion of bone by a network of subcutaneous air sac diverticula spreading distally along the wings. *J. Morphol.* 261:141–161, 2004. © 2004 Wiley-Liss, Inc.

KEY WORDS: pneumaticity; air sacs; postcranial skeleton; Aves; Anseriformes

It has long been recognized that birds have modified the basic tetrapod skeletal plan by such mechanisms as the loss of teeth and various bones, fusion of limb segments (e.g., carpometacarpus), and extreme pneumatization of both cranial and postcranial skeletal elements. These modifications are typically regarded as mass-reducing adaptations to a

flying lifestyle (Currey and Alexander, 1985; Bühler, 1992).

Pneumaticity of the avian postcranial skeleton results from invasion of bone by extensions from the lung and air sac system, a trait unique to birds among living amniotes (Duncker, 1989). Further, it has been observed that the extent, or degree, of pneumaticity varies greatly between different groups of birds (Crisp, 1857; Bellairs and Jenkin, 1960; King, 1966; McLelland, 1989). However, previous studies are necessarily limited in that they have 1) discussed pneumaticity in a relative, qualitative fashion (e.g., one group vs. another); 2) examined only one or a few species; 3) examined domesticated animals exclusively; and/or 4) lacked the necessary phylogenetic context required to make broader statements and comparisons.

The current understanding of avian postcranial pneumaticity relies on numerous generalizations presented in review chapters and textbooks that usually discuss the entire avian respiratory apparatus (Welty, 1979; McLelland, 1989; Proctor and Lynch, 1993), with specific comments concerning postcranial pneumaticity often restricted to one or two paragraphs at the end of an article or chapter (although see King, 1966). Most research focusing on postcranial pneumaticity has examined domesticated species. Such studies have provided an excellent anatomical framework for the relationship between specific bones and particular air sacs (Müller, 1908; King, 1957; Rigdon et al., 1958; Hamlet and Fisher, 1967; Hogg, 1984a,b), but have not ade-

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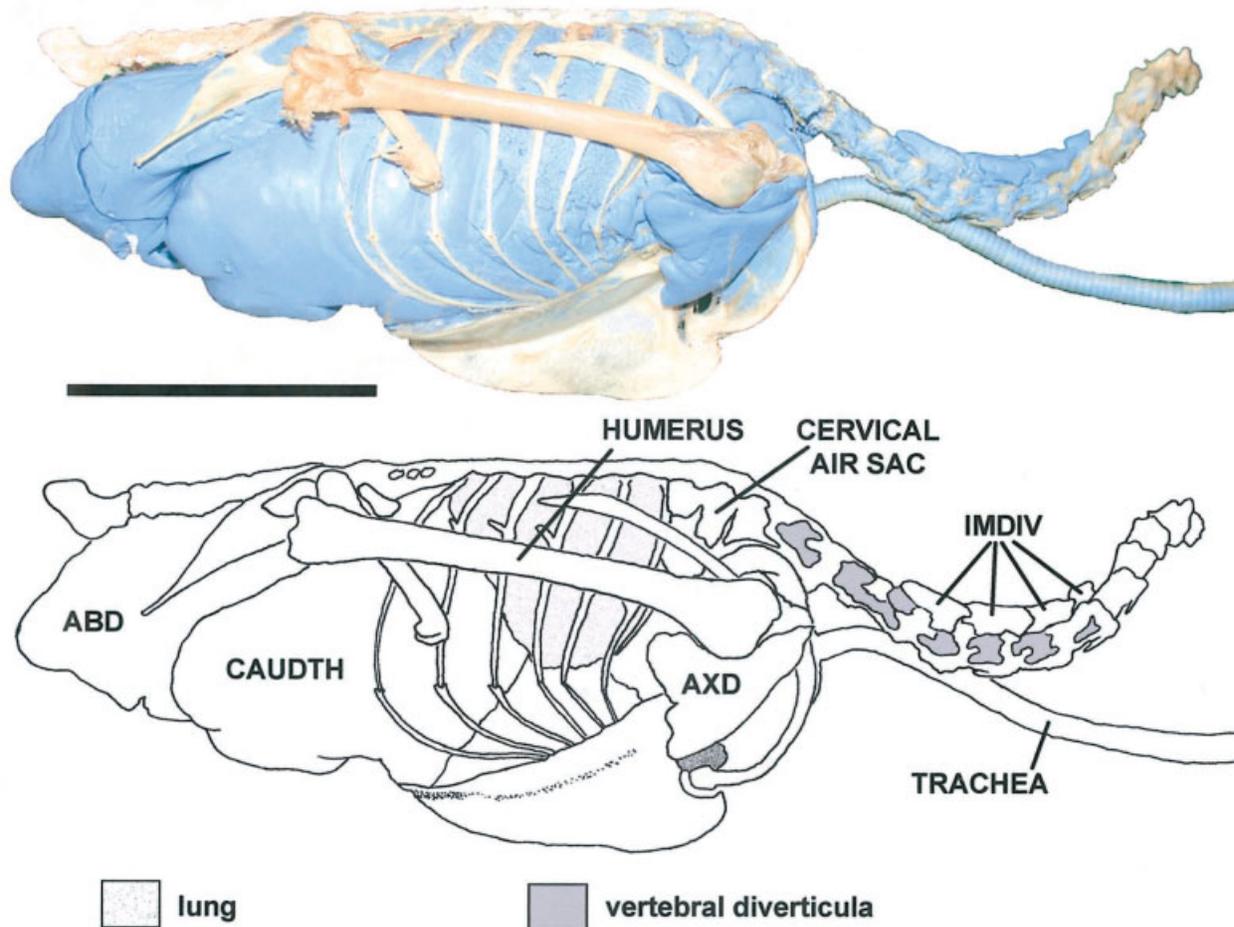


Fig. 1. Blackheaded gull (*Larus ridibundus*). Skeletal-latex preparation demonstrating extent of lung and air sacs, right lateral view. Note the axillary diverticulum (AXD) of the clavicular air sac located on the ventral aspect of the shoulder joint and vertebral diverticula (dark shading) on the lateral aspect of the cervical vertebral column. Also note intermuscular diverticula (expanding from vertebral diverticula) positioned on the dorsal aspect of the neck. ABD, abdominal air sac; AXD, axillary diverticulum; CAUDTH, caudal thoracic air sac; IMDIV, intermuscular diverticula. Scale bar = 5 cm.

quately assessed interspecific variability of this system in birds.

This study provides the first survey of postcranial pneumaticity among a selection of neognath groups, with a focus on the anseriform clade. Data were obtained by: 1) examination of specimens in which the lung and air sac system had been injected with latex, followed by maceration of all soft tissues; and 2) examination of osteological specimens in museum collections. The former method allows a direct assessment of which bones are pneumatized by specific air sac diverticula and, perhaps more importantly, causally associates bony morphology (e.g., foramina) with a specific soft-tissue system. Osteological correlates (*sensu* Witmer, 1995) of the pulmonary air sac system can be identified and used in cases where soft-tissue analysis is not feasible. Further, this permits the construction of species-specific pneumaticity profiles for taxa of interest from museum skeletal

collections, thus allowing for a more taxonomically diverse comparative sample.

BACKGROUND Avian Air Sac System

Among extant amniotes, birds are unique in the design of the pulmonary apparatus. The avian lung is a rigid structure that changes little in volume during respiration, while a series of thin-walled, distensible air sacs are connected to its surface (Figs. 1, 2; Bretz and Schmidt-Nielsen, 1971; Duncker, 1971, 1974; Lasiewski, 1972; Piiper and Scheid, 1985). Pulmonary air sacs consist of poorly vascularized, epithelial expansions that grow from the lung surface prior to hatching and are attached to a series of intrapulmonary bronchi (Locy and Larsell, 1916a,b; Smith et al., 1986). Air sac compliance facilitates lung ventilation (i.e., movement of

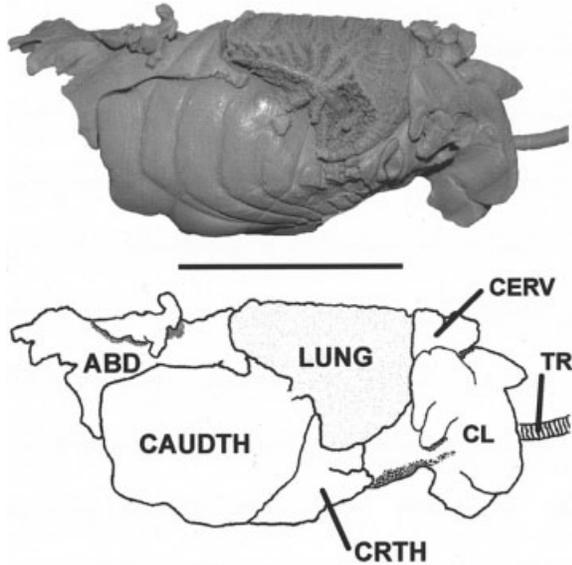


Fig. 2. Blackheaded gull (*Larus ridibundus*). Latex cast of isolated pulmonary system to demonstrate the relative positions and sizes of the lung and air sacs, right lateral view. ABD, abdominal air sac; CAUDTH, caudal thoracic air sac; CERV, cervical air sac; CL, clavicular air sac; CRTH, cranial thoracic air sac; TR, trachea. Scale bar = 5 cm.

air to and from the exchange surfaces within the lung) during the respiratory cycle by allowing changes in air sac volume that respond to dynamic intrathoracic and intraabdominal pressures induced by movements of the body wall (Brackenbury, 1987; Fedde, 1987; Boggs et al., 1997, 1998, 2001).

Most birds possess one single and four paired air sacs, which are typically divided into cranial and caudal groups (Fig. 2; Müller, 1908; Duncker, 1971). The cranial group consists of the paired cranial thoracic and cervical sacs and the (usually) single clavicular (=interclavicular) sac. The caudal series comprises the paired caudal thoracic and abdominal sacs. However, variations of this basic plan occur in some species (McLelland, 1989; also see Duncker, 1971, for an extensive review of major air sac organization in different avian clades).

Whereas main air sacs reside within the body cavity, an elaborate network of epithelium-lined outgrowths (=pneumatic diverticula) extends from the sacs to invade various regions of the body (Fig. 3; Müller, 1908; Groebels, 1932; King, 1966). Pneumatic diverticula intercalate throughout both soft and skeletal tissues of the body. These can be organized into one of the four following categories: visceral, intermuscular, subcutaneous, and intraosseous diverticula. Functional and/or systematic studies of certain diverticula have been examined elsewhere (e.g., Bignon, 1889; Richardson, 1939; Salt and Zeuthen, 1960; Duncker, 1971; Dantzker et al., 1999). As this study is concerned with variability in skeletal pneumaticity, the remainder of the article fo-

cuses on those diverticula directly related to pneumatization of the postcranial skeleton, the intraosseous diverticula.

Coincident with localized resorption of cortical bone, intraosseous diverticula invade skeletal elements by epithelial expansion through the cortical surface and throughout the medullary space. As pneumatization progresses, there is a corresponding decrease in the marrow content of many bones (Schepelmann, 1990; Brackmann, 1991). While this process is typically regarded as a weight-reducing specialization for flight (Bühler, 1992), it should be noted that many forms of flightless birds (e.g., the nonapterygid ratites) have extremely pneumatic postcranial skeletons (Hunter, 1774; Bellairs and Jenkin, 1960; Bezuidenhout et al., 1999).

Identification of Osseous Pneumaticity

Although many early anatomists noted the air-filled nature of avian postcranial bones, Hunter (1774) was the first to list criteria to distinguish pneumatic from nonpneumatic bone. Pneumatic bones: 1) have lower specific gravity; 2) are less vascularized; 3) contain relatively less oil than nonpneumatic bones (in response to the absence of the fatty marrow in the former); and 4) contain apertures (i.e., pneumatic foramina) for the passage of pneumatic diverticula into the medullary cavity (Fig. 4, PF).

These criteria provide a basis for distinguishing pneumatic from nonpneumatic bone, but other workers have put forth additional features indicative of pneumaticity. Müller (1908) described pneumatic bones as lighter in color than nonpneumatic bones and with thin enough cortical bone as to be "virtually transparent" in some cases. Müller also emphasized that although the size and shape of pneumatic foramina vary from taxon to taxon, the locations of foramina remain relatively constant. This consistent placement of foramina is interpreted as necessary in order to create a hole "where the pressure, traction, and torsion are least" (Müller, 1908:391). In other words, he posited that pneumatic foramina are positioned in order to minimize the chances of jeopardizing the structural or mechanical integrity of a given bone.

Additionally, Witmer (1990) pointed out that not all pneumatic bones actually have pneumatic foramina on their surfaces. In his study of craniofacial pneumaticity in archosaurs, he distinguished between intramural and extramural pneumatization. Intramural pneumatization occurs when pneumatic diverticula directly invade bone via foramina present on the bone's surface. In contrast, extramural pneumatization occurs when a bone is pneumatized indirectly, via the expansion of pneumatic cells through a line of fusion (i.e., across a suture) with adjacent pneumatic bone. As an example, Witmer

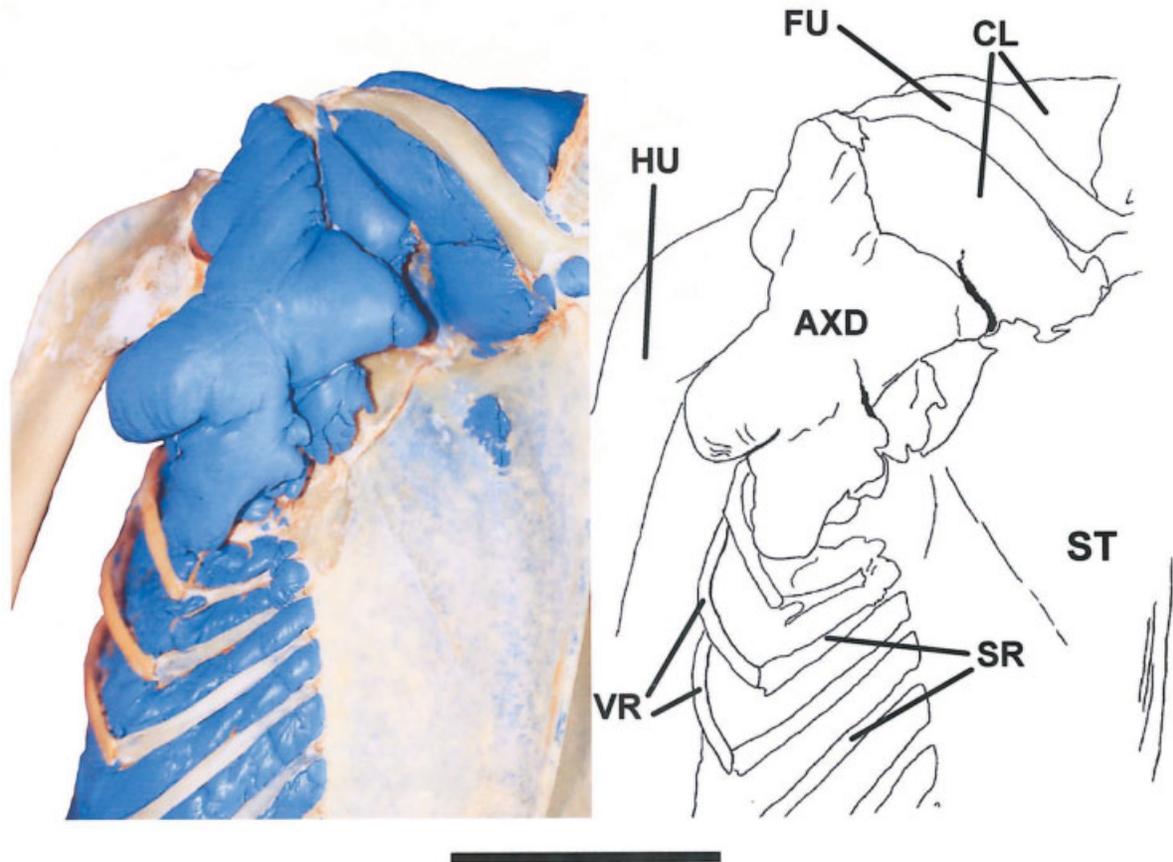


Fig. 3. Mute swan (*Cygnus olor*). Skeletal-latex preparation demonstrating axillary diverticulum on the ventral surface of the right shoulder joint, ventral view (cranial is to the top of image). Numerous diverticula originate from the clavicular air sac and pneumatize the humerus and pectoral girdle elements. AXD, axillary diverticulum; CL, clavicular air sac; FU, furcula; HU, humerus; SR, sternal ribs; ST, sternum; VR, vertebral ribs. Scale bar = 10 cm.

(1990) described the case in which the parietal bone is pneumatized indirectly by pneumatic diverticula expanding from within the squamosal bone. Extramural pneumatization has also been described in the avian postcranial skeleton between adjacent, fused vertebrae (King and Kelly, 1956; King, 1957; Hogg, 1984a,b).

Further, pneumatic diverticula may not actually invade bone via a foramen, but may still impress osteological markers on the surface in the form of an excavation or fossa (Witmer, 1990). Pneumatic diverticula adjacent to bone may partially invade the bone and leave depressions, sometimes with trabecular struts bridging the space. The distinction between fossa and foramen in this case is the presence of a distinct rim of cortical bone on the latter.

Postcranial Pneumaticity—Anatomical Distribution

Generally, pneumaticity of the appendicular skeleton is limited to girdle elements and proximal limb bones, whereas pneumatic invasion of the postcra-

nial axial skeleton involves the vertebral column in addition to the ribs and sternum (Fig. 5). Müller (1908) examined pigeons (*Columba livia*) via latex injection of the pulmonary system in an attempt to characterize the air sacs as well as to document the extent of postcranial pneumaticity. Diverticula of the clavicular air sac pneumatize the humerus, sternum, sternal ribs, and pectoral girdle elements. Vertebral diverticula originating from cervical air sacs invade cervical and cranial thoracic vertebrae and their associated ribs. Diverticula from abdominal air sacs are responsible for pneumatization of femora and coxal elements in addition to caudal thoracic and synsacral vertebrae. The dorsal position of the avian lung within the thoracic cavity and its close proximity to thoracic vertebrae and ribs often promotes invasion of these elements directly from lung diverticula adjacent to the bone. Until recently, it was generally accepted that cranial and caudal thoracic air sacs play no role in the pneumatization process, based on the absence of diverticula from these sacs (Müller, 1908). It should be noted, however, that in certain species (e.g., *Melospittacus un-*

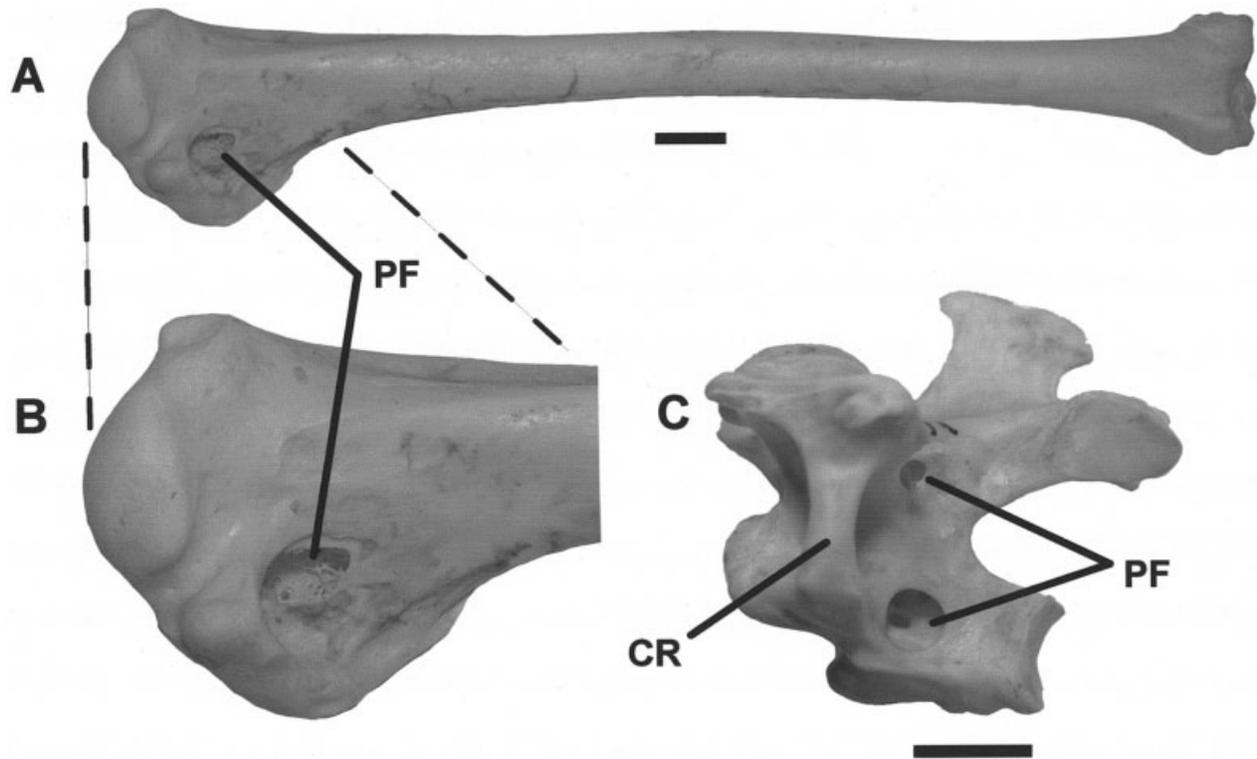


Fig. 4. Osteological features related to pneumatic diverticula. Scale bars = 1 cm. **A:** Black-necked swan (*Cygnus melancoryphus*). Humerus-caudal view, proximal end facing toward left of image (CM S-201). **B:** Close-up view of proximal end of **A** (CM S-201). **C:** Upland (Magellan) goose (*Chloephaga picta*, CM S-10464). Cervical vertebra, left lateral view. Note the presence of pneumatic foramina within both the centrum and neural arch. CR, cervical rib; PF, pneumatic foramen.

dulates) cranial thoracic air sacs pneumatize sternal ribs (Evans, 1996). Given the relative paucity of studies specifically examining postcranial skeletal pneumaticity, particularly in nondomesticated taxa, it is expected that variations on the basic plan will be revealed as more groups are studied.

Few authors have described pneumatic invasion of the limb skeleton beyond the proximal segments (i.e., distal to humeri or femora). Hunter (1774) asserted that air sac diverticula penetrate into antebrachial and carpal elements of the pelican. Owen (1835) also described this condition in pelicans. Additionally, Bellairs and Jenkin (1960) reported pneumatic phalanges in hornbills. However, most recent studies generally posit that pneumaticity occurs exclusively within propodial elements (McLelland, 1989). In a study of 87 species of birds, Crisp (1857:219) found "that in no bird that I have examined was air found in the bones of the extremities beyond the humeri and femora." He further noted that although distal limb elements are not truly pneumatic, they often are thin-walled, tubular structures lacking marrow and an extensive trabecular network, and thus superficially resemble pneumatic bones. He did not offer any suggestions as to how this state was achieved or what significance, functional or otherwise, it holds.

Several reports (e.g., Fisher, 1946; Bellairs and Jenkin, 1960) of distal limb pneumaticity have relied exclusively on osteological surveys of the taxa of interest, rather than soft-tissue studies. It is worth mentioning that previous studies using pulmonary injection methodology have failed to document invasion of distal limb elements by air sac diverticula (e.g., King, 1956; King and Kelly, 1956; Hogg, 1984b).

Interspecific Variability in Pneumaticity

Two main topics of discussion surrounding postcranial pneumaticity relate to the influence of body size and diving on the relative degree of pneumaticity between species. First, it is commonly stated that larger-bodied birds are relatively more pneumatic than smaller-bodied ones (Müller, 1908; Bellairs and Jenkin, 1960; King, 1966; McLelland, 1989). Explanations typically revolve around the extreme energetic requirements of flying organisms and how a reduction in mass is critical for such animals.

Additionally, many authors note a reduction or absence of pneumaticity in diving forms (e.g., penguins, loons, diving ducks; Gier, 1952; Bellairs and Jenkin, 1960; King, 1966; Jones and Furilla, 1987;

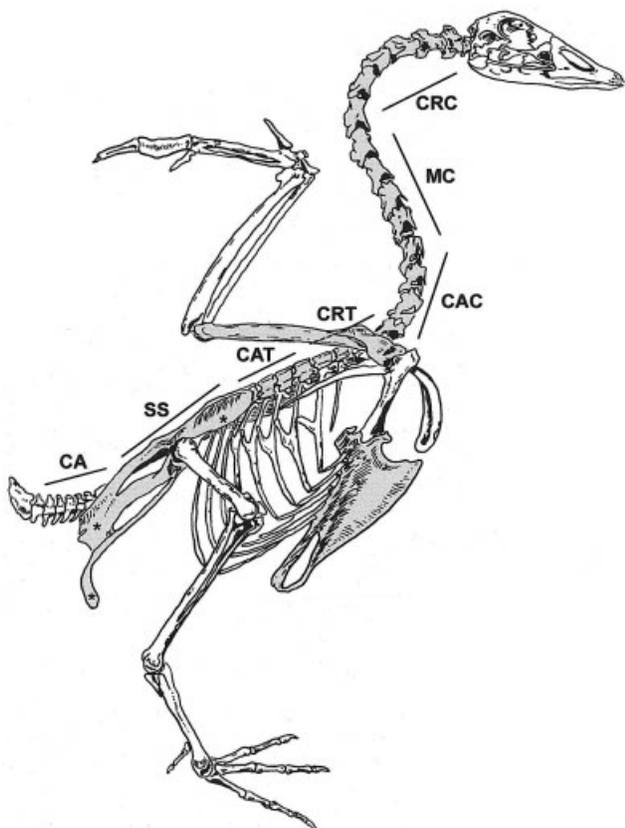


Fig. 5. Diagram showing postcranial bones commonly pneumatized (light gray shading) and those bones rarely pneumatized (no shading) in extant birds. Also illustrated are composite anatomical units (AUs) (e.g., fused coxal elements and regions of the vertebral column) used for study. Vertebrae: CA, caudal; CAC, caudal cervical; CAT, caudal thoracic; CRC, cranial cervical; CRT, cranial thoracic; MC, middle cervical; SS, synsacral. Due to the fusion of individual coxal bones (indicated by * in figure) in extant birds, coxae were scored as a single AU. Note: Pneumatic bones are variable from species to species and the shading represents the common pattern observed in many members of extant Anseriformes (skeleton modified from Komarek, 1979).

McLelland, 1989; Livezey, 1995b). Similar to the previous arguments regarding body mass, reduced pneumaticity in diving species is most often interpreted as an energy-saving adaptation in forms that propel themselves beneath the water surface while foraging. Instead of using energy to counteract pneumaticity-induced buoyancy, diving species can focus on obtaining food.

Hypothesized influences of both diving and body size on pneumaticity involve aspects of energy savings related to different types of locomotion (i.e., either flying or diving). However, an explicit quantitative assessment of pneumaticity is lacking among previous studies of postcranial pneumaticity. Thus, the main goal of this project includes a quantitative assessment of postcranial pneumaticity among the taxonomically diverse Anseriformes, with specific hypotheses related to the influence of

both diving behavior and body size and their relationship with observed differences in the degree of pneumaticity between species.

MATERIALS AND METHODS

Anseriform birds were selected as the focal clade to test hypothesized influences on the relative amount of postcranial pneumaticity. Aside from having one of the better-resolved phylogenies among living birds (e.g., see Livezey, 1997c, and references therein), this group possesses members that span a large body size range and also exhibit a number of subgroups specialized for diving. For this study, species are designated as divers if 1) underwater locomotion plays a dominant role in their foraging strategy, and 2) they possess morphological features consistent with diving specializations (e.g., elongate hind limbs; see Livezey, 1995b,c; 1996b; McCracken et al., 1999). All major clades within Anseriformes were sampled ($n = 157$ specimens from 101 species representing 37 genera (~66% of known anseriform species diversity—see Appendix)). Specimens from other neognath groups were also examined to provide both phylogenetic outgroup and functional comparative samples for anseriform taxa.

Materials examined included skeletal specimens in museum collections and salvaged whole specimens prepared via pulmonary injection procedures designed to delimit the extent of the air sac system and diverticular network. Specifically, latex injection of the pulmonary apparatus followed by gross dissection allows a direct assessment of those bones pneumatized by air sac diverticula, as colored latex is observable through the cortical surface (Figs. 1, 3). In elements with thicker cortical bone (e.g., coracoids), it was often necessary to use a probe to pierce the cortical surface in order to observe the internal state (i.e., presence or absence of latex) of each bone.

Specimens examined for this project include those housed in the following collections: American Museum of Natural History, New York (AMNH); Carnegie Museum of Natural History, Pittsburgh (CM); Justus-Liebig Universität, Giessen, Germany (JLUG); Michigan State University Museum, East Lansing (MSU); Ohio University Vertebrate Collections, Athens (OUVC); Transvaal Museum, Pretoria, South Africa (TM); United States National Museum of Natural History, Washington DC (NMNH).

Pulmonary Injection Protocol

Injected specimens were either 1) prepared in the Department of Biomedical Sciences at Ohio University, or 2) examined in the collections of Professor H.-R. Duncker (Institute of Anatomy and Cell Biology at Justus-Liebig Universität, Giessen, Germany). In both cases specimens were prepared in a hypobaric injection chamber specifically designed for injection of the pulmonary system. Procedures for infilling of the pulmonary apparatus are modified from the work of Duncker and colleagues (Duncker et al., 1964; Duncker and Schlüter, 1964). A brief overview is presented here and a more detailed protocol will be presented elsewhere.

Frozen specimens acquired from either museum collections or wildlife rehabilitators were thawed overnight. After attaching plastic tubing to the trachea via cyanoacrylate adhesives, the specimen was placed inside the injection chamber. The tubing was attached to a standard laboratory vacuum pump. A second tube connected the chamber directly to the vacuum pump. In a stepwise manner, the chamber and then the specimen were evacuated to a pressure of 20 mmHg. Both chamber and specimen were brought back to atmospheric pressure and the procedure was repeated twice to thoroughly evacuate residual air from the pulmonary system. Upon reaching 20 mmHg for the third time, the line connecting the trachea to the vacuum pump was clamped off, cut, and attached to a funnel filled with Ward's Biological Latex (37W2581). Using the negative pressure environment in both the specimen and the chamber, latex was allowed to slowly

TABLE 1. Anatomical Units (AUs) and abbreviations used for derivation of Pneumaticity Index (PI)

<u>Composite units</u>	
CRC, Cranial Cervical Vertebrae*	MC, Middle Cervical Vertebrae*
CAC, Caudal Cervical Vertebrae*	CRT, Cranial Thoracic Vertebrae
CAT, Caudal Thoracic Vertebrae	SS, Sacsacral Vertebrae
CA, Caudal Vertebrae	VR, Vertebral Ribs
SR, Sternal Ribs	CX, Fused Ilium-Ischium-Pubis
DLE, Distal Limb Segments (i.e., bones distal to elbow or knee joints)	
<u>Individually scored units</u>	
CC, coracoids; FU, furculae; FM, femora; HU, humeri; SC, scapulae; ST, sterna	

*Cervical ribs were scored with their respective vertebrae, as they are fused in extant birds.

enter the specimen via the line attached to the trachea. This was done in a controlled manner using adjustable tubing clamps, as infusion of too much latex too rapidly can render the specimen useless.

Upon completion of the injection procedure, the specimen was refrigerated in a 15% solution of acetic acid to assist in curing the latex. Localized injection of 15% acetic acid rapidly decreased the time of latex curing. Subsequent to setting of the latex, specimens were dissected and examined for the presence of latex in bones (Fig. 1). This procedure has the added benefit of demonstrating both the extent of the main air sacs as well as the relationships of air sac diverticula to various tissues (e.g., bone, musculature, or skin).

Data Collection

In order to examine interspecific patterns of postcranial pneumaticity, individual elements were scored for the presence or absence of either latex (in the case of injected specimens) or pneumatic foramina (in the case of skeletons). Anatomical units (AUs) were established to allow comparisons between taxa with substantially different vertebral counts. As an example, the number of cervical vertebrae present in anseriform taxa ranges from 16 to 23, along with known intraspecific variation in vertebral number in certain species (Woolfenden, 1961). With this in mind, the vertebral column was divided into seven functional regions in a manner similar to that proposed by Boas (1929) and Zusi (1962) (Fig. 5). These consisted of cranial, middle, and caudal cervical, cranial and caudal thoracic, sacral, and caudal vertebral regions. Each region was then scored for the presence or absence of injected latex or pneumatic foramina. In order to assign a positive assessment of pneumaticity for a given AU, at least one element within that region must exhibit pneumaticity.

Furthermore, fused elements (e.g., coxae, cervical vertebrae and cervical ribs) were scored as single units since extramural pneumatization commonly occurs in avian skeletal tissues (King, 1957; Hogg, 1984b). Given the apparent rarity of pneumaticity beyond proximal limb segments, the presence of distal limb pneumaticity was scored as a single unit. See Table 1 for a complete list of anatomical units used for the quantitative portion of this study. In cases where intraspecific differences in pneumaticity were observed, a species maximum was established to account for differential filling of latex and intraspecific variability known to exist in certain taxa (e.g., *Gallus*; Hogg, 1984a).

Pneumaticity Index (PI)

In order to assess pneumaticity among a large number of species, a quantitative measure of relative pneumaticity is required. Previous discussions of postcranial pneumaticity are often general in nature, with discussions concerning one, two, or a few species (Ulrich, 1904; McLeod and Wagers, 1939; King, 1956; Rigdon, 1959; Hogg, 1984b). The Pneumaticity Index (PI) is introduced as a means to quantify pneumaticity for a given species and to allow comparisons among multiple species simultaneously.

Data derived through these means are also amenable to statistical analysis (see below). In order to generate the PI for a given species, specimens were scored for the presence of pneumatic postcranial elements (i.e., within AUs) to create the numerator of the index. Subsequently, this number was divided by 17 (the total AUs for extant birds used in this study—see Tables 1, 2, and Fig. 5 for further details) to produce the PI.

$$\frac{\# \text{ Pneumatic AUs}}{\text{Total \# AUs}} = \text{PNEUMATICITY INDEX}$$

For example, the Canada goose (*Branta canadensis*) has a species score of 12 pneumatic AUs, thus yielding a PI of 0.71. Pneumaticity in either side of bilateral AUs was sufficient to be scored as present in that AU. That is, it was not required that both humeri be pneumatic in order to include that element in the species score. However, it should be noted that pneumatization usually occurs bilaterally (although occasional bilateral asymmetry has been documented in domesticated species: e.g., Hogg, 1984a,b).

The PI does not take into account partial pneumatization of an element, and thus it provides no measure of the extent of pneumaticity within a given AU. The goal of this work, however, is to examine large-scale differences between species and higher-level clades of birds. Further, it should be noted that injected specimens seldom demonstrated partial infilling of latex in a given element. In fact, when present, partial filling appears to result more from incomplete injection of latex than an actual representation of a partially pneumatized bone (pers. obs.).

Statistical Approaches

To examine the relationship between pneumaticity and body size among different species, extant members of the anseriform clade were examined within both ahistorical (e.g., species-based OLS regression analysis) and historical (e.g., phylogenetically independent contrasts) contexts. Regression analyses of body mass on PI were performed on the whole anseriform dataset, in addition to subclades within Anseriformes. Additionally, due to the (presumed) overwhelming influence of diving on pneumaticity, analyses were also performed on the anseriform dataset excluding all diving specialists (as defined by nonpneumatic characteristics). Body mass estimates for species were taken from published literature compiled by Dunning (1993). As the PI generates percentages, these data were arcsin-transformed prior to analysis (Sokal and Rohlf, 1995). Body mass data were log₁₀ transformed prior to analysis.

In order to examine the influence of phylogeny on the relationship between body size and pneumaticity, phylogenetically independent contrasts (PICs) were performed on the same dataset, including subgroups within Anseriformes. Due to the nonindependence of species' values (Harvey and Pagel, 1991; Harvey and Purvis, 1991; Purvis and Rambaut, 1995), comparisons utilizing both historical and ahistorical approaches may elucidate the relative influence of phylogeny on a given relationship between variables. Relationships obtained using phylogenetically inde-

TABLE 2. Pneumaticity profiles for anseriform taxa examined

Taxon	n	CRC	MC	CAC	CRT	CAT	SS	CA	VR	SR	ST	HU	SC	CC	FU	FM	CX	DLE	BM (g)	PI	D/ND
<i>Chauna chavaria</i> *	3	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	4800	1.00	ND
<i>Anhima cornuta</i>	2	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	3150	1.00	ND
<i>Anseranus semipalmata</i>	3	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	-	2070	0.88	ND
<i>Dendrocygnini</i>	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	680	0.00	D
<i>Thalassomis leuconotus</i>	1	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	-	1150	0.41	ND
<i>Dendrocygna arborea</i>	2	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	-	732	0.53	ND
<i>Dendrocygna arcuata</i>	1	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	-	828	0.47	ND
<i>Dendrocygna autumnalis</i>	1	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	-	710	0.53	ND
<i>Dendrocygna bicolor</i>	1	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	-	792	0.53	ND
<i>Dendrocygna eytoni</i>	2	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	-	800	0.53	ND
<i>Dendrocygna guttata</i>	2	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	-	525	0.53	ND
<i>Dendrocygna javanica</i>	2	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	-	690	0.53	ND
<i>Dendrocygna viduata</i>	2	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	-	3308	0.65	ND
<i>Anserini</i>	2	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	-	2578	0.71	ND
<i>Anser anser</i> *	2	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	-	3150	0.71	ND
<i>Anser albifrons</i> *	1	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	-	1964	0.76	ND
<i>Anser cygnoides</i>	1	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	-	2600	0.76	ND
<i>Anser erythropus</i>	1	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	-	1307	0.71	ND
<i>Anser indicus</i>	1	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	-	2630	0.76	ND
<i>Branta bemiela</i>	1	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	-	3614	0.71	ND
<i>Branta caerulescens</i>	1	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	-	1294	0.71	ND
<i>Branta canadensis</i>	1	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	-	1970	0.65	ND
<i>Branta ruficollis</i>	1	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	-	5650	0.71	ND
<i>Branta sandvicensis</i>	2	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	-	6650	0.71	ND
<i>Cygnus atratus</i> *	4	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	-	9350	0.71	ND
<i>Cygnus columbianus</i> *	5	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	-	4700	0.74	ND
<i>Cygnus cygnus</i>	2	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	-	10650	0.71	ND
<i>Cygnus melancoriphus</i>	2	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	-	2367	0.59	ND
<i>Cygnus olor</i> *	9	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	-	3560	0.65	ND
<i>Sarkidiornis melanota</i>	1	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	-	4228	0.41	D
<i>Plectropterus gambensis</i>	1	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	-	1152	0.59	ND
<i>Tachyerini</i>	2	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	-	1182	0.53	ND
<i>Tachyeres pteneres</i>	2	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	-	1230	0.53	ND
<i>Tadornini</i>	3	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	-	839	0.53	ND
<i>Tadorna tadorna</i> *	1	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	-	129	0.47	ND
<i>Tadorna cana</i>	1	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	-	1300	0.53	ND
<i>Tadorna ferruginea</i>	1	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	-	1520	0.53	ND
<i>Tadorna radjah</i>	1	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	-	1862	0.53	ND
<i>Tadorna tadomoides</i>	1	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	-	2900	0.65	ND
<i>Tadorna variegata</i>	1	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	-	2781	0.59	ND
<i>Cyanochen cyanopterus</i>	1	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	-	2200	0.65	ND
<i>Alopochen aegyptiacus</i>	1	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	-	2000	0.59	ND
<i>Chloephaga melanoptera</i>	1	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	-	344	0.47	ND
<i>Chloephaga picta</i>	2	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	-			
<i>Chloephaga poliocephala</i>	1	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	-			
<i>Chloephaga rubriceps</i>	1	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	-			
<i>Malacorhynchus membranaceus</i>	2	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	-			

TABLE 2. (Continued)

Taxon	n	CRC	MC	CAC	CRT	CAT	SS	CA	VR	SR	ST	HU	SC	CC	FU	FM	CX	DLE	BM (g)	PI	D/ND
<i>Histrionicus histrionicus</i>	1	-	-	+	+	+	-	-	-	-	-	-	-	-	-	-	-	-	622	0.18	D
<i>Melanitta deglandi</i>	1	-	-	+	+	+	-	-	-	-	-	-	-	-	-	-	-	-	950	0.12	D
<i>Clangula hyemalis</i>	2	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	873	0.18	D
<i>Bucephala clangula</i>	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	900	0.00	D
<i>Mergellus albellus</i> *	2	-	-	-	+	+	-	-	-	-	-	-	-	-	-	-	-	-	610	0.06	D
<i>Lophodytes cucullatus</i>	1	-	-	+	+	+	+	-	-	-	-	+	-	-	-	-	-	-	610	0.35	D
<i>Mergus merganser</i> *	2	-	-	+	+	+	+	-	-	-	-	+	-	-	-	-	-	-	1470	0.41	D
<i>Mergus serrator</i>	1	-	+	+	+	+	+	-	-	-	-	+	-	-	-	-	+	-	1021	0.47	D

+ indicates pneumatic bone, - indicates apneumatic bone.

Body mass data from Dunning, 1993.

*Species examined via latex or polyester resin injection studies. BM (g), body mass in grams; CA, caudal vertebrae; CAC, caudal cervical vertebrae; CAT, caudal thoracic vertebrae; CC, coracoid; CRC, cranial cervical vertebrae; CRT, cranial thoracic vertebrae; CX, fused coxal elements; D/ND, diving/nondiving species; DLE, distal limb elements; FM, femora; FU, furculae; HU, humeri; MC, middle cervical vertebrae; n, sample size; PI, pneumaticity index; SR, sternal ribs; SS, synsacral vertebrae; ST, sternum; VR, vertebral ribs.

pendent contrasts are predicted to have less explanatory power for a given relationship (e.g., body size vs. PI) than are species-based regressions due to the removal of inherited similarity (Nunn and Barton, 2001). Further, if contrasts-based regressions demonstrate a significant relationship (i.e., slope $\neq 0$) between variables, it implies the relationship between variables occurred multiple times over the history of the group under study.

Phylogenetically independent contrasts were performed using CAIC (Comparative Analysis by Independent Contrasts) v. 2.6.8 for the Apple Macintosh (Purvis and Rambaut, 1995). CAIC was chosen over other methods (e.g., PHYLIP, Felsenstein, 1993) to examine correlated character evolution because it can analyze categorical variables (e.g., diving vs. nondiving) and it is also able to contend with incompletely resolved (i.e., polytomous) nodes (Purvis and Rambaut, 1995; Garland et al., 1999). Branch lengths were set equal to 1.0 for this analysis. Body mass—PI comparisons were examined in CAIC using “crunch” mode (Purvis and Rambaut, 1995). As with other nondirectional comparative methods (i.e., cross-sectional methods of Garland et al., 1999), comparisons are made between phylogenetically equivalent taxa (e.g., daughter taxa of a given node or between equivalent nodes of the phylogeny) and not between a reconstructed ancestral state and its dependent taxa (Harvey and Purvis, 1991).

Character mapping of PI and other traits were constructed using MacClade v. 4.0 (Maddison and Maddison, 2000). Phylogenetic hypotheses of Anseriformes utilized for both CAIC analysis and character mapping were provided by the recent analyses by Ericson (1997) and Livezey (1991, 1995a–d, 1996a–c, 1997a–c).

TESTING HYPOTHESES INVOLVING PNEUMATICITY

As mentioned above, Anseriformes serve as the focal group for this study based on the following criteria: 1) members span a large range of body masses, 0.304–10.65 kg; 2) phylogenetic relationships of the members are well resolved; and 3) some members of the group employ specialized diving behavior during foraging.

Based in large part on qualitative statements in the avian morphology literature, the two main hypotheses examined in this study can be summarized as follows:

1) The relationship between pneumaticity and body size

H₁: Pneumaticity Index (PI) increases with increasing body mass among species examined.

Regression analyses of body mass on PI seek to identify potential relationships between overall size and relative pneumaticity. Interspecific differences in pneumaticity may result in refutation of the null hypothesis if slopes from regression analyses are significantly different from zero. A positive slope significantly different from zero would support statements by previous workers of increased pneumaticity in larger-bodied birds. The purpose of this study is to examine broad patterns in relative pneumaticity, not to address specific scaling relationships between pneumaticity and body size. Thus, slopes significantly different from zero indicate either positive ($b > 0$) or negative ($b < 0$) trends between the two variables. Other than testing significance of slopes relative to zero, specific predictions for slope values not equal to zero (e.g., as in scaling studies) were not examined in this analysis.

2) The relationship between pneumaticity and diving behavior

H₁: Pneumaticity Index (PI) decreases with increasing diving behavior exhibited by species examined.

Regression analyses of the anseriform dataset both with and without diving members seek to identify potential functional relationships between the two variables. For example, if nondiving species exhibit relatively higher pneumaticity indices than diving forms, one would expect an increase in slope values by exclusion of the latter group. It should be noted that most members of the anseriform clade exhibit some form of diving or partial submersion while foraging. For the purpose of this work, diving

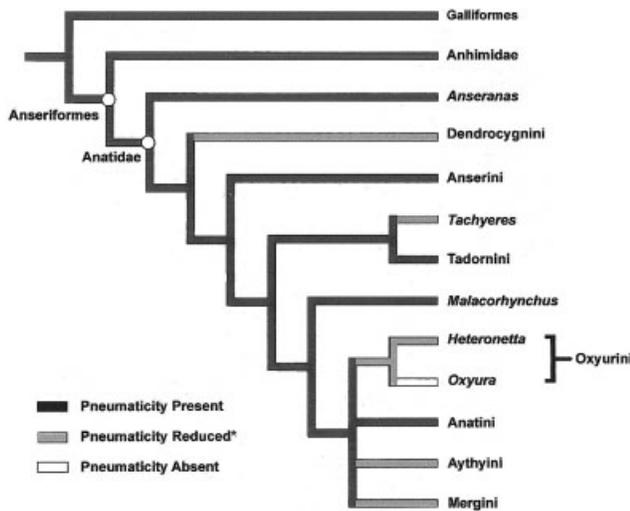


Fig. 6. Phylogenetic hypothesis of major anseriform taxa with relative pneumaticity mapped onto cladogram. Anseriform in-group relationships are based on Livezey (1997a,c). *The reduced pneumaticity category (gray shading) includes clade members that range from the common anseriform condition to completely apneumatic postcrania. A reduction in postcranial pneumaticity has occurred at least three times among the anseriform group, and possibly more, depending on resolution of the polytomy that includes the Anatini, Aythyini, Mergini, and Oxyurini clades.

species were defined by behavioral observations and morphological features other than those related to pneumaticity (Raikow, 1970; Livezey, 1995b,c, 1996b; McCracken et al., 1999). Of course, the null hypothesis for either diving or body size relationships can be formally stated as:

H_0 : Pneumaticity Index (PI) does not vary as a function of diving characteristics or size differences among species examined.

RESULTS

Among anseriform taxa examined, the most commonly pneumatized anatomical units (AUs) are caudal cervical and thoracic vertebrae. In most taxa, other regions of the precaudal vertebral column, sterna, humeri, and coxal elements are also pneumatic (Fig. 5). Less common pneumatic AUs are vertebral and sternal ribs and pectoral girdle elements. Very rarely (two of 101 species) are free caudal vertebrae (including the pygostyle), hind limb elements, and distal forelimb bones pneumatic. When ribs (sternal or vertebral) are pneumatic, there is a general trend of decreasing pneumaticity from cranial to caudal along the rib series. Thus, in most anseriform taxa examined a common pattern of postcranial pneumaticity is apparent, with the following skeletal elements involved: precaudal vertebrae, sterna, coxal elements, and humeri. Clade-specific patterns emerge with partitioning of Anseriformes into its constituent subclades (Table 2; Figs. 6, 7A–C). Table 2 also provides body mass estimates (published species' means) for species utilized in the study.

Anhimidae—The basally positioned screamers exhibit the maximum development of postcranial pneumaticity among anseriform taxa examined. Notable features of anhimids are the presence of pneumatic furculae, scapulae, coracoids, caudal vertebrae including the pygostyle, and sternal and vertebral ribs (although see *Anseranas semipalmata*, below). Additionally, the two species of screamers (*Chauna chavaria* and *Anhima cornuta*) are unique among anseriform birds in possessing pneumatic distal forelimb elements and pneumatic hind limb bones. For example, in *Anhima cornuta* (the horned screamer: CM 18588, NMNH 345217), radii, ulnae, femora, and tibiotarsi in addition to elements of the manus and pes are pneumatic.

Anseranas semipalmata—The magpie goose exhibits the general anseriform pattern as the basal-most member of the Anatidae (Anseriformes minus the Anhimidae). Enhancements of this pattern include pneumaticity of all pectoral girdle elements, vertebral and sternal ribs, and caudal vertebrae, similar to the condition observed in screamers. However, unlike screamers, *A. semipalmata* does not possess pneumatic hind limb or distal forelimb elements or a pneumatic pygostyle.

Dendrocygnini—The whistling and white-backed ducks display the typical anseriform pattern in having pneumatic precaudal vertebrae, sterna, humeri, and coxae. The only exceptions among the eight *Dendrocygna* species examined are a lack of pneumatic sterna in *D. arborea* and *D. autumnalis*. *Thalassornis leuconotus*, the white-backed duck, stands out among the group in having a postcranial skeleton lacking pneumaticity altogether (PI = 0; Fig. 7A).

Anserini—In addition to possessing the general anseriform pattern, the relatively large-bodied swan and geese species variably pneumatize pectoral girdle elements and vertebral and sternal ribs. Aside from the screamers and *Anseranas*, anserine species are the only anseriform taxa to pneumatize furculae and vertebral ribs.

Tadornini—Twelve species of sheldgeese and shelducks examined generally follow the common anseriform plan of pneumaticity. The only deviations from this pattern are the presence of pneumatic sternal ribs in the four *Chloephaga* species examined. Two species of *Tadorna* (sister taxa *T. tadorna* and *T. radjah*) also displayed minimal pneumaticity of sternal ribs.

Oxyurini—Of the stiftail ducks examined, all deviate from the general anseriform pattern by variable reduction in the number of pneumatic elements (Fig. 6). The three *Oxyura* species totally lack pneumatic postcranial elements. *Heteronetta atricapilla* (the black-headed duck), the sister taxon of *Oxyura*, exhibits reduced pneumaticity relative to the general pattern (e.g., it lacks pneumatic sterna and cranial cervical vertebrae), but retains pneumatic

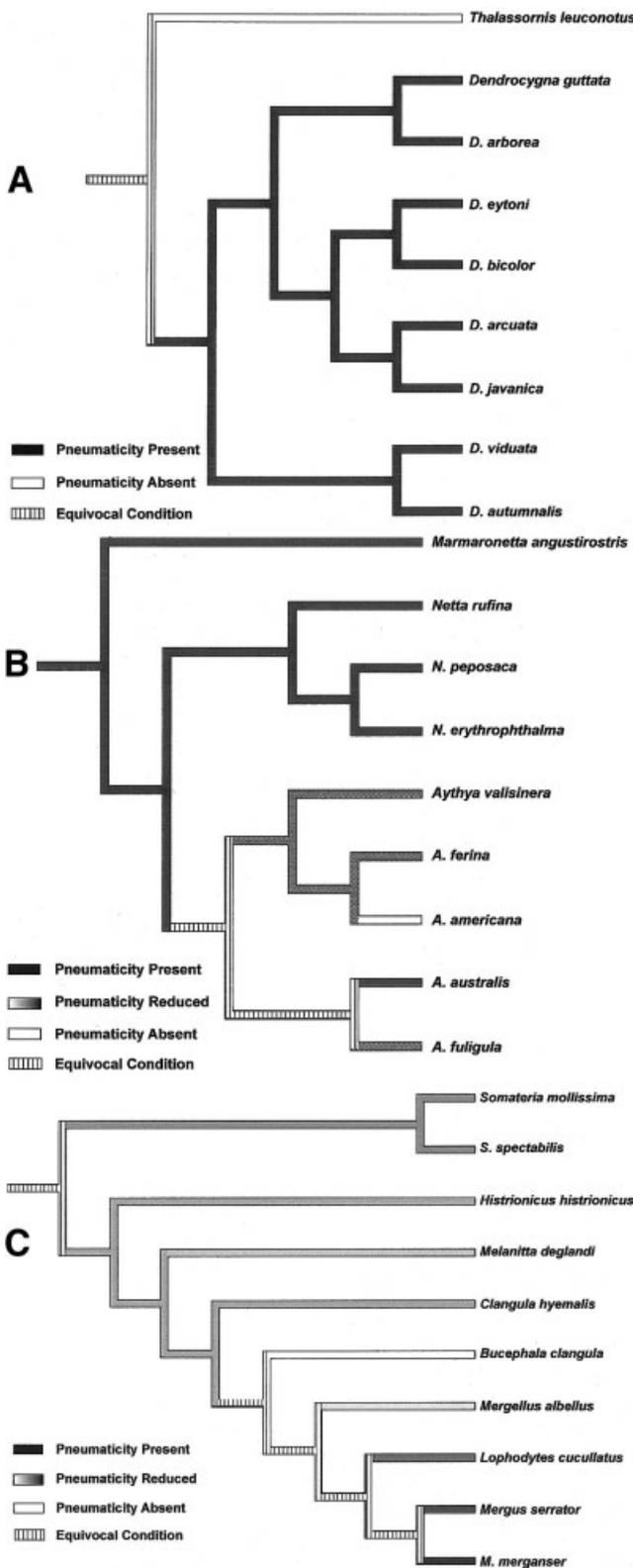


Figure 7

humeri, coxae, and sacral, thoracic, and caudalmost cervical vertebrae.

Anatini—Dabbling ducks seldom depart from the general anseriform pattern and generally exhibit pneumaticity of the precaudal vertebral column, sterna, coxae, and humeri. Deviations do occur in a few non-*Anas* anatines (e.g., *Cairina*, *Callonetta*) and exist as species-specific increases in pneumaticity of pectoral girdle elements. However, as an example of generic uniformity, the 24 species of *Anas* examined were virtually invariant in bones pneumatized. Only a single specimen of *Anas cyanoptera* deviated in having two pneumatic left mid-sternal ribs.

Aythyini—Of nine pochard species examined, there exists considerable variation in pneumatic postcranial elements (Fig. 7B). The basally positioned *Marmaronetta angustirostris*, and three congeneric species comprising its sister genus, *Netta*, all exhibit the common anseriform pattern. However, the five species belonging to the genus *Aythya* range from a complete lack of pneumaticity (e.g., *A. americana*) to a pattern similar to the non-*Aythya* aythyines (e.g., *A. australis*). *A. fuligula*, *A. ferina*, and *A. valisineria* are nearly apneumatic, with involvement of the cranial thoracic and caudal cervical vertebrae only.

Mergini—The sea ducks also display a wide range of pneumaticity in the postcranial skeleton (Fig. 7C). In general, the group exhibits less pneumaticity than the common anseriform pattern, with an absence of pneumaticity in cranial cervical vertebrae, humeri and sterna. *Bucephala clangula* totally lacks pneumatic postcranial elements, and *Histrionicus*, *Melanitta*, and *Clangula* have pneumaticity limited to the mid-portion of the vertebral column, similar to the pochards *Aythya fuligula* and *A. ferina*. Only in the genus *Mergus* is the general anseriform pattern

Fig. 7. Phylogenetic hypotheses of specific anseriform clades with relative pneumaticity mapped onto the cladogram—relative pneumaticity is indicated by gradations of gray with darker shading indicative of higher relative pneumaticity. **A**: Dendrocygnini (whistling and white-backed ducks), based on Livezey (1995a). Note the uniform degree of pneumaticity among all species examined except the completely apneumatic, basally positioned *Thalassornis leuconotus*. **B**: Aythyini (pochards), based on Livezey (1996b). While all members of the group engage in diving behavior, the variable distribution of pneumaticity characteristics suggests a more complex relationship between relative pneumaticity and the behavioral trait (e.g., dive-based foraging) traditionally used to define the group. Further, relationships between body size and pneumaticity are also clouded when examined in this one clade of anseriform birds—the small-bodied *Marmaronetta angustirostris* (<500 g) displays the average anseriform pattern, while the large-bodied *Aythya valisineria* (1,200 g) displays reduced postcranial pneumaticity. **C**: Mergini (sea ducks), based on Livezey (1995d). Similar to the situation observed among aythyine taxa (**B**), the traditionally defined “diving” sea ducks also display a wide range of pneumaticity states.

TABLE 3. Log-arsin least-squares regressions of body mass on pneumaticity index compared with independent contrast regressions in Anseriformes and subclades within the group

Comparison	Ordinary least squares			Phylogenetic independent contrasts		
	b	r ²	n	b	r ²	n ₁
Global Anseriformes	0.54*	0.18	85	0.20	0.04	81
Anatidae	0.50*	0.14	83	0.15	0.02	79
Anatidae minus divers	2.82*	0.48	59	1.02*	0.13	58
Anatini	1.6	0.08	24	0.39	0.01	23
Anserini	0.001	0.005	14	0.33	0.01	13

n, sample size, n₁, number of contrasts. *Slope significantly different from zero for at least $P < 0.05$ level.

approached, although the two *Mergus* species examined (*M. merganser* and *M. serrator*) still lack pneumaticity of the cranialmost cervical vertebrae.

Body Size, Diving, and Relative Pneumaticity

Regression analyses (OLS) and phylogenetically independent contrast (PIC) comparisons of body mass on pneumaticity index (PI) were performed on the entire anseriform dataset and on specific subclades within Anseriformes (Table 3). Anseriform taxa were also examined as a function of locomotor (diving and soaring) specializations (Fig. 8). Whereas there is an area of overlap between dedicated diving and nondiving taxa (Fig. 8, PI range 0.65–0.80), diving forms tend to have lower PI values. Additionally, the soaring screamer species (anhimids) stand out among all taxa examined in possessing the highest PI values. Due to the apparent influence of diving on pneumaticity (i.e., lower PIs in divers), additional analyses of body mass and relative pneumaticity were performed on reduced datasets with diving species excluded (Fig. 9B; Table 3).

Whereas a global anseriform regression of body mass on PI results in a significant ($P < 0.001$) slope of 0.54, a contrast regression results in a nonsignificant slope ($P = 0.07$) of 0.20, emphasizing the relative influence of phylogeny on the relationship (Table 3; Fig. 9A). Upon exclusion of the two large-bodied, extremely pneumatic screamer species, OLS regression and contrast slopes decrease to 0.50 ($P < 0.001$) and 0.15 ($P = 0.17$), respectively. Similar to the relationship observed for the whole anseriform dataset, OLS regression results in a slope significantly different from zero, while the contrast slope does not (Table 3).

By excluding dedicated diving taxa (aythyines, mergines, oxyurines, and *Thalassornis*) from the anatid analysis, OLS regression and independent contrast slopes are 2.82 ($P < 0.001$) and 1.02 ($P < 0.001$), respectively. In contrast to the earlier two comparisons, both OLS and contrast regressions re-

sult in positive slopes significantly different from zero. Analyses of traditional tribe-level taxa (tadornines, anatines, and anserines) result in nonsignificant slopes for all groups examined (Table 3). Characteristic to all analyses are low r^2 values (r^2 ranges 0.14–0.48, OLS, and 0.02–0.13, PIC).

Pneumaticity in Select Nonanseriform Groups

Most recent (and traditional) phylogenetic analyses suggest a sister-taxon relationship between Anseriformes and Galliformes (e.g., Galloanserae or Galloanserimorphae) representing a basal neognath clade (Livezey, 1997a; Livezey and Zusi, 2001). Select galliform birds including chicken (*Gallus*), turkey (*Meleagris*), pheasant (*Phasianus* and *Chrysolophus*), and partridge (*Perdix*) were examined via latex injection of the pulmonary system (Appendix). These were used to establish a pneumaticity profile to represent a general galliform condition. Galliformes are strikingly similar to the common anseriform pattern with regard to postcranial pneumaticity. Pneumatic elements commonly include precaudal vertebrae, sterna, and, more variably, sternal ribs, humeri, pectoral girdle, and coxal elements. Unlike the condition in most Anseriformes, at least some galliform taxa (e.g., *Gallus gallus*, *Chrysolophus pictus*) commonly exhibit pneumatic vertebral ribs, albeit only cranial ones.

Nonanseriform diving taxa examined included penguins (*Spheniscus* sp., *Aptenodytes* sp., *Eudyptes cristatus*), loons (*Gavia* sp.), grebes (*Podiceps* sp.), and pelecarniforms (*Pelecanus* sp., *Phalacrocorax*

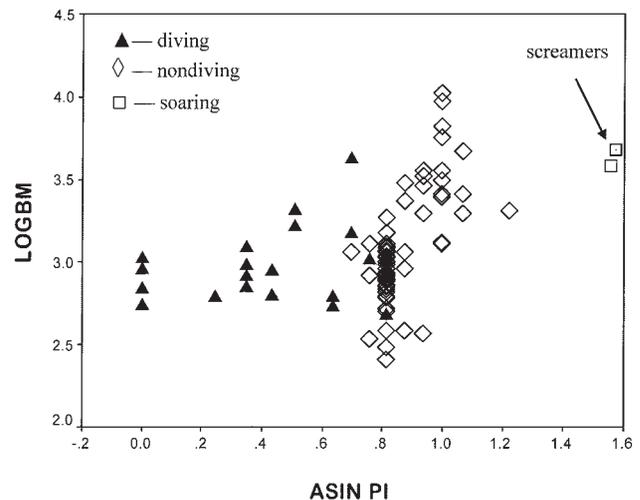


Fig. 8. Bivariate plot of log body mass (LOGBM) and arcsin-transformed Pneumaticity Index (ASIN PI). In this figure, taxa are sorted by diving (▲), nondiving (◇), and soaring (□) characteristics (see text for additional discussion). Arcsin values for this and all subsequent graphs are expressed in radians.

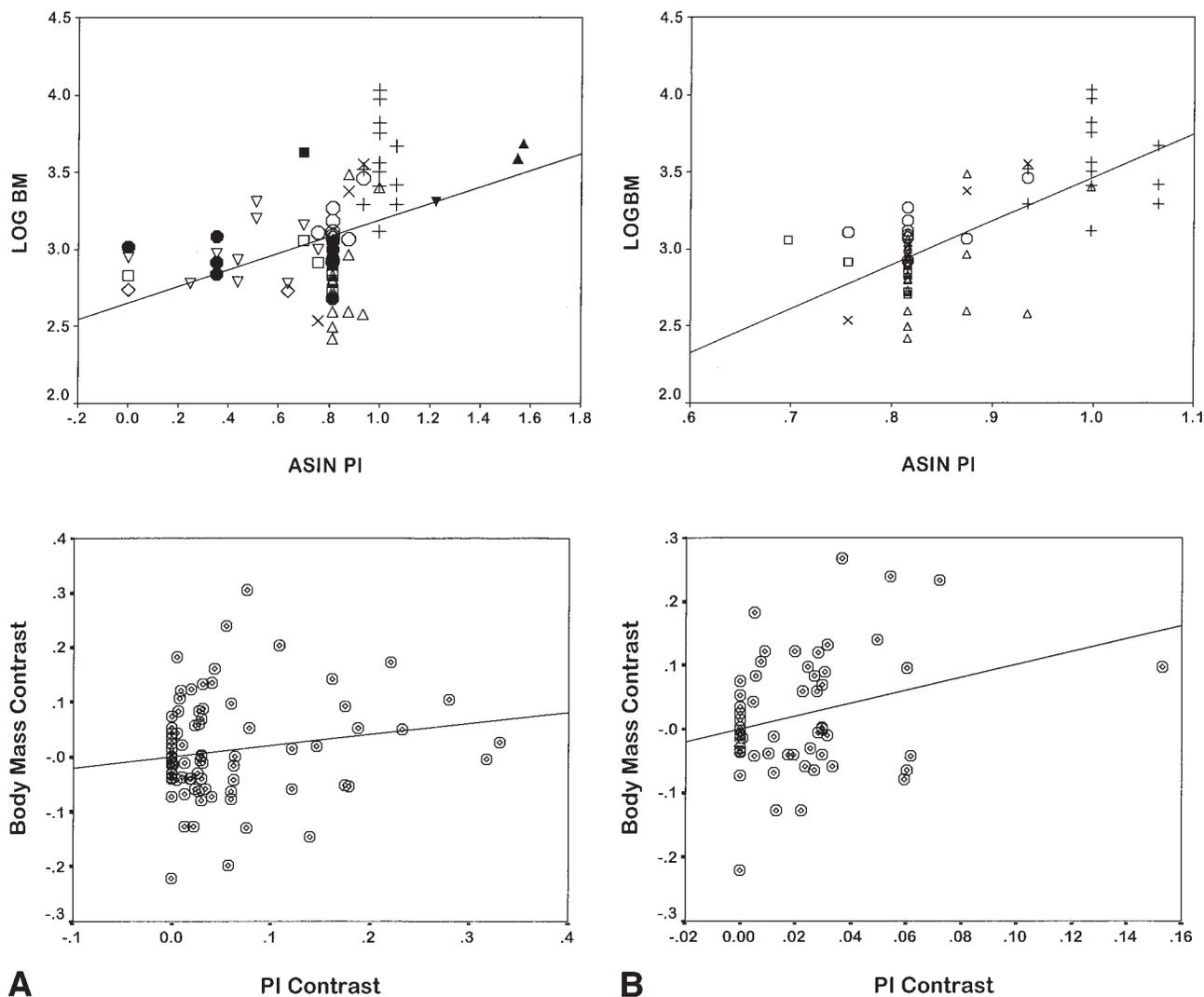


Fig. 9. Bivariate plots of log body mass (LOGBM) regressed on arcsin-transformed Pneumaticity Index (ASIN PI) and contrast comparisons for each variable. Symbols refer to the following taxonomic affiliations: \blacktriangle , Anhimidae; \blacktriangledown , *Anseranas semipalmata*; \square , Dendrocygnini; $+$, Anserini; \blacksquare , *Tachyeres*; \circ , Tadornini; \diamond , Oxyurini; \triangle , Anatini; \bullet , Aythyini; ∇ , Mergini; \times , Other (e.g., *Malacorrhynchus membranaceus*, *Plectropterus gambensis*, *Sarkidornis melanota*). **A:** Global anseriform dataset. Ordinary least-squares regression values (top plot): $n = 85$, $b = 0.54$ ($P < 0.001$), $r^2 = 0.18$. Independent contrast regression values (bottom plot): $n = 81$, $b = 0.20$ ($P = 0.07$ NS), $r^2 = 0.04$. **B:** Anatidae excluding diving and soaring specialists. Ordinary least-squares regression values (top plot): $n = 59$, $b = 2.82$ ($P < 0.001$), $r^2 = 0.48$. Independent contrast regression values (bottom plot): $n = 58$, $b = 1.02$ ($P < 0.05$), $r^2 = 0.13$.

sp.). In general, most species completely lacked pneumatic foramina in any postcranial skeletal elements. However, in both *Spheniscus* and *Phalacrocorax* specimens, large pneumatic-like fossae were observed on the lateral surface of vertebral centra at the cervico-thoracic transition. These were observable in only one or two vertebrae.

In contrast, however, is the extreme development of postcranial pneumaticity in certain pelecaniform birds (e.g., *Pelecanus* sp., *Sula bassana*). Similar to the condition in screamers, most elements of the postcranial skeleton are pneumatic, including distal forelimb bones and the entire hind limb skeleton. In these taxa it is possible to demonstrate the presence

of extensive subcutaneous air sac diverticula associated with the distal forelimb and hind limb pneumatic features.

DISCUSSION

This study sought to extricate the relative effects of phylogeny, body size, and diving behavior reported to influence the degree of postcranial pneumaticity among living bird species. Diving habit and clade specificity appear as primary factors related to differential development of postcranial pneumaticity. In general, there is a reduction in the amount of

pneumaticity among diving forms relative to non-divers. However, there is a considerable amount of variability even among diving taxa examined (see below). Further, there appears to be little support for a relationship between relative pneumaticity and body size, at least among the anseriform birds surveyed. While this study does not address specific scaling issues (e.g., volumetric comparisons between taxa exhibiting different degrees of pneumaticity), it does provide baseline data on relative pneumaticity and can be used for future comparative studies addressing specific scaling hypotheses.

General Anseriform Pattern

There is considerable variability in the amount of the postcranial skeleton pneumatized among extant Anseriformes, ranging from complete lack of pneumaticity in certain diving forms (e.g., *Oxyura*) to the hyperpneumatic condition observed in screamers (Anhimidae). However, many groups display a common pattern in the extent of postcranial pneumaticity (Fig. 5). Deviations from this pattern usually result as reductions in pneumaticity in specialized diving taxa.

This common pattern includes pneumaticity of the following anatomical units: precaudal vertebrae, sterna, humeri, and coxae. Groups displaying this pattern include most whistling ducks (*Dendrocygna*), shelducks (*Tadorna*), and non-*Cairina* anatines. Increases from this basic pattern involve pneumatization of sternal ribs and pectoral girdle elements. Groups exhibiting such increases include geese and swans (e.g., *Anser*, *Branta*, *Cygnus*) and sheldgeese (*Chloephaga*, *Alopochen*, *Cyanochen*). Other taxa that deviate from the common pattern include the magpie goose (*Anseranas semipalmata*) and the screamers, both of which pneumatize virtually all costal and pectoral girdle elements. Further, anhimids are unique as the only anseriform group to pneumatize distal forelimb and hind limb elements (see Distal Limb Pneumaticity section).

Body Size

It is commonly stated that body size is the primary factor influencing the extent of pneumaticity throughout the avian postcranial skeleton (Bellairs and Jenkin, 1960; McLelland, 1989). OLS regressions of body mass on pneumaticity index for all Anseriformes or the Anatidae suggest a positive relationship between body size and relative pneumaticity (Table 3). However, this relationship is nonsignificant when analyzed via phylogenetically independent contrasts (PICs). As predicted by PIC analysis, relationships between variables are less well supported, and it indicates that historical factors account for a proportion of the relationship observed between body mass and relative pneumatic-

ity. Only when the anatids are examined with diving taxa excluded does a positive relationship between body size and pneumaticity remain after PIC analysis. However, the extremely low correlation suggests that additional factors must be influencing this relationship, and that body size alone does not account for different pneumaticity profiles observed between species.

The examination of lower-level clades (e.g., traditionally defined tribes—Anatini, Anserini) results in nonsignificant slopes for analyses of body mass and relative pneumaticity (Table 3). As an example, 24 species of *Anas* are virtually invariant in the development of pneumaticity as measured by the PI, although spanning a body mass range from 0.326–1.25 kg (Table 2). Perhaps even more striking is the overall similarity of pneumaticity among 15 anserine (geese and swans) species as exemplified by *Branta ruficollis* at 1.294 kg and *Cygnus olor* at 10.65 kg. Differences observed between anatines and anserines revolve around pneumatization of pectoral girdle elements and sternal ribs in the latter group, suggesting that clade identity, rather than body size, may influence relative pneumaticity (see below). Future work incorporating other bird groups may further elucidate relationships between body size and pneumaticity.

Diving Behavior

Diving specializations among certain anseriform clades have long been recognized and include caudally positioned hind limbs and elongation of individual hind limb elements (Raikow, 1970; Livezey, 1995a–d, 1996b; McCracken et al., 1999). Additionally, diving taxa often show a reduction in pneumaticity of the postcranial skeleton. However, pneumaticity-specific characters used in phylogenetic analyses are usually limited to the sternum and humerus and not the entire postcranial skeleton (e.g., see Livezey, 1995a). Postcranial skeletal pneumaticity is also reduced or absent in some nonanseriform neognath diving taxa. For example, a reduction in pneumaticity is observed in loons, penguins, grebes, and alcid charadriiform birds (e.g., *Alca torda*, see Appendix). Furthermore, typically pneumatic cranial bones (e.g., quadrates) are not pneumatized in *Gavia*, *Spheniscus*, and certain alcid charadriiform birds (Witmer, 1990), thereby supporting a general trend of reduced pneumaticity (even of the head skeleton) in diving forms.

Diving adaptations are found among a number of anseriform taxa, including *Thalassornis leuconotus*, oxyurines, aythyines, and mergines (McCracken et al., 1999). Given the current understanding of phylogenetic relationships among higher-level anseriform taxa, reduction in postcranial pneumaticity associated with diving clades has evolved separately at least three times, if not more, depending on how

relationships among the oxyurine-anatine-aythyine-mergine groups are resolved (see Fig. 6).

Although the traditionally defined groups of diving ducks display a reduction in pneumaticity from the common anseriform pattern, they do so quite variably. For example, aythyines are represented by basal members exhibiting the general pattern, with more derived members displaying variable reductions in pneumaticity (Fig. 7B). A similar condition is observed among oxyurines, with the basalmost species being relatively more pneumatic than derived members of the group (Fig. 6). As an example, all three *Oxyura* species examined completely lack pneumatic postcranial elements, with *Heteronetta* exhibiting pneumatic vertebrae and humeri. Mergines, on the other hand, lack any pattern related to relative pneumaticity throughout the clade (Fig. 7C). Taxa included range from the completely apneumatic *Bucephala clangula* to the condition in the genus *Mergus*, in which the common pattern of anseriform pneumaticity is approached.

Dendrocygnines display the common anseriform pattern of pneumaticity throughout the postcranial skeleton. The one exception to this observation is found within the basalmost member, *Thalassornis leuconotus*, which totally lacks pneumatic postcranial elements (Fig. 7A). Livezey concluded that diving adaptations evolved three separate times among the dendrocygnines (i.e., *T. leuconotus*, *Dendrocygna viduata*, and the *D. arcuata*—*D. javanica* clade (Livezey, 1995a; fig. 4 therein). A reduction in overall postcranial pneumaticity coincides with his assertion of diving specializations for *T. thalassornis*. In contrast, the relationship between postcranial pneumatic and other morphological or behavioral traits used to identify diving *Dendrocygna* species is less well understood and requires further examination.

In general, it appears that traits unrelated to pneumaticity diagnose much more inclusive clades of divers than do pneumatic characters (e.g., oxyurines, aythyines; Fig. 7B). In other words, hind limb adaptations related to diving arise primitively among diving clades and reductions in postcranial pneumaticity are found within more derived taxa. Future studies examining diving ability and its relationship to postcranial pneumaticity are necessary to further refine the relationship between the two characteristics. For example, how does differential diving ability (e.g., depth attained, duration of dive, etc.) correlate with pneumaticity among different diving duck species?

Other Diving Birds

Anseriform birds are not the only neognath group with diving specialists. In fact, many higher-order avian groups consist almost exclusively of diving members (e.g., Sphenisciformes—penguins,

Podicipediformes—grebes, Gaviiformes—loons, alcid Charadriiformes, phalacrocoracid Pelecaniformes; Perrins and Middleton, 1986). An examination of select taxa of sphenisciform, podicipediform, gaviiform, and phalacrocoracid birds confirm earlier observations of a general lack of pneumaticity among postcranial skeleton elements (see Appendix for taxa examined). Whereas most of the above-mentioned taxa lack pneumatic postcranial elements altogether, it was observed that one or two vertebrae at the cervicothoracic transition are commonly pneumatic in certain taxa (e.g., cormorants, penguins). In these cases, pneumaticity was identified by the presence of large foramina or fossae located in the lateral surface of vertebral centra. These were associated directly with cervical air sacs. Similar foramina in diving-adapted anseriforms were not observed.

Distal Limb Pneumaticity

The most extreme development of postcranial pneumaticity among anseriform taxa is found within the basalmost clade, the screamers (Anhimidae). These birds are the only anseriform taxa to pneumatize distal forelimb and hind limb elements. They are also the only anseriform species to possess an extensive network of subcutaneous air sac diverticula (Groebels, 1932; McLelland, 1989). During this work, screamer specimens were not available for dissection studies to assess the means by which distal limb bones are pneumatized. However, subcutaneous-induced pneumaticity of distal limb elements has been observed in other neognath taxa (e.g., *Sula bassana*, *Pelecanus occidentalis*) (Owen, 1835; O'Connor, 2001). Gross dissection of pelican specimens has revealed subcutaneous diverticular networks associated with distal limb pneumatic features in these birds (O'Connor, 2001). Such a correlative observation provides an anatomical hypothesis to account for the presence of distal limb pneumatic features in screamers. That is, based on the presence of subcutaneous diverticula and distal limb pneumaticity in other taxa, it is plausible to view this as a mechanism by which distal limb elements are pneumatized in screamers. From a functional perspective, screamers are the only anseriform taxa to regularly utilize soaring flight (i.e., the use of thermals and not muscle energy to remain aloft for long periods of time). Perhaps distal limb pneumaticity merely reflects an attempt to further reduce mass, particularly of the extremities, in taxa performing such specialized locomotor behaviors.

The observation that most recent studies (e.g., McLelland, 1989) have failed to adequately discuss distal limb pneumaticity probably results from its relative rarity among extant birds and/or methodological limitations of most air sac injection procedures. For example, whereas screamers are known

to possess subcutaneous air sac diverticula extending over much of the body surface, an examination of injected specimens of *Chauna chavaria* revealed only minimally injected subcutaneous diverticula near the base of the neck. This suggests that standard methods of air sac preparations may lack the appropriate resolution necessary to examine such diverticular networks and that novel approaches must be developed for this task. Work by the author is currently under way to elucidate the specific soft-tissue relationships of distal forelimb pneumatic features in addition to addressing the functional role of distal limb pneumaticity in different neognath groups (e.g., bucerotids, cathartids, pelecanids).

Pneumaticity Among Anseriform Groups

Based on the condition in basal anseriform taxa (Anhimidae, *Anseranas*) and the purported sister-group of anseriforms (Galliformes), some degree of postcranial pneumaticity is primitive for the clade as a whole (Fig. 6). Of interest within the group is the relatively expansive degree of pneumaticity among screamers and, to a lesser extent, the magpie goose (*Anseranas semipalmata*; Table 2). Both taxa exhibit pneumaticity far exceeding that found in other extant anseriform groups. This may indicate a general decrease in postcranial pneumaticity throughout early-diverging clades (i.e., anhimids to *Anseranas* to non-*Anseranas* anatids). Alternatively, basal non-*Anseranas* anatids (e.g., dendrocygnines) may better represent the primitive condition of the group, which is more similar to most galliform birds examined. Thus, expanded pneumaticity in the basal groups Anhimidae and *Anseranas* may represent autapomorphic conditions for those taxa. Examination of fossil anseriform taxa (e.g., *Presbyornis*, *Cnemiornis*) will no doubt refine ideas about relative pneumaticity at the base of the anseriform radiation. However, until more work (e.g., see the preliminary analysis of Livezey and Zusi, 2001) is done to resolve higher-level neognath relationships (e.g., determination of the sister-group of the Galloanserae), an assessment of the outgroup pneumaticity profile remains ambiguous for reference to the basal anseriform condition.

Among non-*Anseranas* anatids, clade-specific patterns emerge as the dominant factor influencing the relative degree of postcranial pneumaticity (Table 2; Fig. 9A,B). This is particularly noticeable in such diverse clades as anserines and anatines. While perhaps not as strongly demonstrated, clade-specific patterns are also apparent in the dendrocygnines (excluding *Thalassornis*) and tadornines.

The most within-clade variability observed in pneumaticity occurs among diving groups (mergines, aythyines; Fig. 7B,C). Generally, diving taxa exhibit a reduction in postcranial pneumaticity. However, it is difficult to assess how much re-

duction is present. Perhaps a more appropriate conclusion to draw from these data is that diving taxa do reduce pneumaticity relative to their nondiving sister taxa. However, the degree to which pneumaticity is reduced varies tremendously, as exemplified by the situation in mergines (Fig. 7C).

CONCLUSIONS

In general, anseriform birds are characterized by clade-specific patterns in the extent of postcranial pneumaticity derived from pulmonary air sacs. However, many anseriform taxa converge upon a common pattern that includes pneumatization of precaudal vertebrae, sterna, humeri, and coxal elements. Deviations from this pattern include clade-specific pneumatization of sternal ribs and pectoral girdle elements (e.g., anserines) or a general reduction in pneumaticity in diving forms.

The relationship between body size and relative pneumaticity has marginal support, at least among the size-diverse clade of anseriform birds. By the exclusion of diving taxa from the Anatidae, there does exist a positive relationship between relative pneumaticity and body size (i.e., larger-bodied birds are slightly more pneumatic than smaller-bodied birds). However, low correlations indicate that factors other than body size account for a substantial proportion of the observed relationship.

Among the many diving groups (e.g., oxyurines, aythyines, mergines), there appears to be a general reduction in pneumaticity relative to the common anseriform pattern. However, this reduction is variable both between and within clades of diving ducks. Nonpneumatic characters (e.g., elongate hind limb elements) diagnose more inclusive clades of diving ducks than do pneumatic features, and it appears that changes in pneumaticity occur subsequent to changes in other morphological and behavioral systems related to diving. Thus, the precise relationship of reduced pneumaticity to diving remains somewhat enigmatic. Distal limb element pneumaticity in the soaring screamers is likely the result of invasion of bone by subcutaneous air sac diverticula, similar to the condition observed in other neognath taxa (e.g., pelicans).

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APPENDIX. Taxa examined in study

ANSERIFORM TAXA Species	Museum Location and Number
<i>Chauna chavaria</i> *	JLUG (1), NMNH 346634, NMNH 226110
<i>Anhima cornuta</i>	CM 18588, NMNH 345217
<i>Anseranas semipalmata</i>	CM 10809, NMNH 347638, NMNH 621019
<i>Thalassornis leucotis</i>	CM S-16484, CM S-16470, CM-S 15865
<i>Dendrocygna arborea</i>	NMNH 226455
<i>Dendrocygna arcuata</i>	CM 16466, CM 14756
<i>Dendrocygna autumnalis</i>	NMNH 430491
<i>Dendrocygna bicolor</i>	NMNH 224797
<i>Dendrocygna eytoni</i>	NMNH 343182
<i>Dendrocygna guttata</i>	NMNH 491367, CM 14752
<i>Dendrocygna javanica</i>	CM 15138, CM 15139
<i>Dendrocygna viduata</i>	CM 15799, CM 14884
<i>Anser anser</i> *	JLUG (2)
<i>Anser albifrons</i> *	JLUG (1), MSU 29903
<i>Anser cygnoides</i>	CM S-15744
<i>Anser erythropus</i>	CM S-15878
<i>Anser indicus</i>	CM S-16440
<i>Branta bernicla</i>	CM 5047
<i>Branta canadensis</i>	CM 9894
<i>Branta caerulescens</i>	CM 11047
<i>Branta ruficollis</i>	CM S-2070
<i>Branta sandvicensis</i>	CM 14428, CM S-14947
<i>Cygnus atratus</i> *	CM 1435, JLUG (3)
<i>Cygnus columbianus</i> *	CM 1214, CM 9198, CM 15725, JLUG (2)
<i>Cygnus cygnus</i>	CM S-1339, NMNH 492481
<i>Cygnus melancoriphus</i>	CM S-201, NMNH 428167
<i>Cygnus olor</i> *	CM 10532, JLUG (7), NMNH 557526
<i>Sarkidiornis melanota</i>	MSU 4760
<i>Plectropterus gambensis</i>	CM S-16483
<i>Tachyeres pteneres</i>	CM S-15768, CM S-13399
<i>Tadorna tadorna</i> *	CM 14951, CM 15722; JLUG (1)
<i>Tadorna cana</i>	CM 15672
<i>Tadorna ferruginea</i>	CM 14235
<i>Tadorna radjah</i>	CM 15742
<i>Tadorna tadornoides</i>	CM 11813
<i>Tadorna variegata</i>	CM 15813
<i>Cyanochen cyanopterus</i>	CM 15047
<i>Alopochen aegyptiacus</i>	MSU 6213
<i>Chloephaga melanoptera</i>	CM S-16159
<i>Chloephaga picta</i>	CM S-10464, CM S-13748
<i>Chloephaga poliocephala</i>	CM 13466
<i>Chloephaga rubidiceps</i>	CM 16477
<i>Malacorhynchus membranceus</i>	CM 15020, CM 15021
<i>Heteronetta atricapilla</i>	CM 15684
<i>Oxyura jamaicensis</i>	CM 11005, CM 16480
<i>Oxyura leucocephala</i>	CM 16480
<i>Oxyura vittata</i>	CM 14943
<i>Aix galericulata</i> *	JLUG (1)
<i>Aix sponsa</i> *	JLUG (1), OUV 9421, OUV 9663
<i>Pteronetta hartlaubii</i>	CM 15674, CM 14520
<i>Cairina moschata</i> *	CM 4991, CM 8265; JLUG (1)
<i>Cairina scutulata</i>	CM 14922
<i>Chenonetta jubata</i>	CM 15042
<i>Nettapus coromandelianus</i>	CM 16155
<i>Nettapus pulchellus</i>	CM 15747
<i>Amazonetta brasiliensis</i>	CM 14758
<i>Callonetta leucophrys</i>	CM 16151
<i>Anas specularis</i>	CM 13467
<i>Anas capensis</i>	CM 15876
<i>Anas strepera</i>	CM 16617
<i>Anas penelope</i>	CM 15716
<i>Anas americana</i>	CM 11133
<i>Anas sparsa</i>	CM 951
<i>Anas rubripes</i>	CM 5025
<i>Anas platyrhynchos</i> *	CM 10463, CM 2661, JLUG (1)
<i>Anas undulata</i>	CM 15866
<i>Anas luzonica</i>	CM 16084

APPENDIX. (Continued)

ANSERIFORM TAXA	
Species	Museum Location and Number
<i>Anas superciliosa</i>	CM 15879
<i>Anas poecilorhyncha</i>	CM 16473
<i>Anas cyanoptera</i>	CM 15670
<i>Anas discors</i>	CM 15102
<i>Anas platalea</i>	CM 15118
<i>Anas clypeata</i>	CM 11989
<i>Anas gibberifrons</i>	CM 14757
<i>Anas erythrorhyncha</i>	CM 16476
<i>Anas flavirostris</i>	CM 13465
<i>Anas georgica</i>	CM 16428
<i>Anas querquedula</i>	CM 15114
<i>Anas formosa</i>	CM 15956
<i>Anas crecca</i> *	CM 15988, CM 15738, JLUG (2)
<i>Anas falcata</i>	CM 15867
<i>Marmaronetta angustirostris</i>	CM 14753, CM 11178
<i>Aythya americana</i>	NMNH 500894
<i>Aythya australis</i>	NMNH 556840
<i>Aythya ferina</i> *	JLUG (1), NMNH 431534, NMNH 318431
<i>Aythya fuligula</i> *	JLUG (2)
<i>Aythya valisineria</i>	NMNH 499407, NMNH 610674
<i>Netta erythrophthalma</i>	NMNH 612022
<i>Netta peposaco</i>	NMNH 500892
<i>Netta rufina</i>	NMNH 621198
<i>Somateria mollissima</i>	NMNH 499635
<i>Somateria spectabilis</i>	NMNH 561211
<i>Histrionicus histrionicus</i>	CM 11605
<i>Melanitta deglandi</i>	CM S-2037
<i>Clangula hyemalis</i>	CM 10806, CM 14368
<i>Bucephala clangula</i>	CM 5076
<i>Mergellus albellus</i> *	JLUG (1)
<i>Lophodytes cucullatus</i>	CM 10343, CM 14565
<i>Mergus merganser</i> *	JLUG (1)
<i>Mergus serrator</i>	CM 5055
NONANSERIFORM TAXA	
<i>Struthio camelus</i> *	AMNH 1727, OUV 9422
<i>Pheasianus colchicus</i> *	OUVC 9664
<i>Chrysolophus pictus</i> *	JLUG (3)
<i>Gallus gallus</i> *	JLUG (5), OUV 9419, OUV 9420
<i>Melagris gallopavo</i> *	JLUG (1)
<i>Perdix perdix</i> *	JLUG (2)
<i>Spheniscus humboldti</i>	CM 10810
<i>Spheniscus demeris</i> *	JLUG (2)
<i>Aptenodytes patagonicus</i> *	JLUG (1)
<i>Aptenodytes forsteri</i>	CM 11600
<i>Eudyptes cristatus</i> *	JLUG (1)
<i>Gavia immer</i>	CM S-16102
<i>Gavia arctica</i> *	JLUG (1)
<i>Podiceps cristatus</i> *	JLUG (7)
<i>Podiceps ruficollis</i> *	JLUG (2)
<i>Phalacrocorax aristotelis</i> *	JLUG (7)
<i>Phalacrocorax auritus</i>	CM 7425
<i>Phalacrocorax penicillatus</i>	CM 10810
<i>Pelecanus erythrorhynchus</i> *	JLUG (2)
<i>Pelecanus occidentalis</i> *	AMNH 21610
<i>Sula bassana</i> *	CM T-21320, JLUG (3)
<i>Alca torda</i> *	JLUG (6)
<i>Fratercula arctica</i> *	JLUG (4)
<i>Uria aalge</i> *	JLUG (4)
<i>Diomedea immutabilis</i>	NMNH 498120
<i>Bucorvus leadbeateri</i>	AMNH 3953, CM S-2457, TM 76018
<i>Tockus erythrorhynchus</i>	TM 60543, TM 60547, TM 60545

AMNH, American Museum of Natural History, New York; CM, Carnegie Museum of Natural History, Pittsburgh; JLUG, University of Giessen, Germany; MSU, Michigan State University Museum, East Lansing; NMNH, National Museum of Natural History, Washington D.C.; OUV, Ohio University Vertebrate Collections, Athens; TM, Transvaal Museum, Pretoria, South Africa.

Numbers in parentheses indicate the number of injected specimens studied at JLUG.

*Specimens prepared via latex or polyester resin injection.