Acta Soc. Zool. Bohem. **61**: 227–231, 1997
ISSN 0862–5247

Sternal pneumatization in the waterfowl (Aves: Anatidae)

Jiří MLÍKOVSKÝ

Vršovická 11, CZ–101 00 Praha 10, Czech Republic.

Received July 29, 1996; accepted September 16, 1997
Published October 17, 1997

Abstract. Sternal pneumatization in the Anatidae is reviewed. It is shown, that ancestral forms had highly pneumatized sterna. During evolution, sternal pneumaticity has been often reduced, and several diving forms lost is entirely. Presence of additional pneumatic foramina makes it probable, that *Anas* (*Lophonetta*) *specularioides* King, 1828 is not related to the genus *Anas*, but more probably belongs with the core cariamine genera *Cariama*, *Plectropteron* and *Alopochen*.

Sternum, pneumatization, evolution, Aves, Anatidae, world-wide fauna

INTRODUCTION

The waterfowl (Anatidae) is a higly diversified group of birds (Mlíkovský 1987), which is reflected in morphological adaptations. In the present paper I describe variations in the pneumatization of the waterfowl sternum, with special respect to their adaptive and phylogenetic significance.

No detailed study of sternal pneumatization in the waterfowl has been performed so far, although it is well known, that the condition varies among the genera (Verheyen 1955, Woolfenden 1961). Livezey (1986) included data on sternal pneumatization in his phylogenetic analysis of Recent anseriform genera.

The sterna were examined in the comparative collections in the Paleontological Institute of the Russian Academy of Sciences (Moskva), in the Natural History Museum (Paris), and in the author's collection (Praha). Sterna of the Miocene anatid *Mionetta* was studied in the Natural History Museum in Berlin. I was kindly allowed to work in the collections by A. A. Karchu (Moskva), C. Lefèvre (Paris), and B. Stephan (Berlin). I thank them all. See Appendix for the list of examined taxa. Taxonomic arrangement of the waterfowl follows Johnsgard (1979).

STERNAL PNEUMATIZATION

Most of the modern waterfowl have pneumatized sterna with a single pneumatic foramen in the anterior part of the sternal basin (Tab. 1). Additional foramina are present is others, while several waterfowl genera possess non-pneumatic sterna.

Additional pneumatic foramina („lateral foramina") can occur in the sternal basin either along its borders. I found the latter condition in *Coscoroba*, *Anser*, *Branta*, *Alopochen*, *Plectropterus*, and *Anas specularioides*. Hints of these foramina were also present in some individuals from the genera *Dendrocygna* (*bicolor*). In addition to these lateral foramina, also the midline of sternal basin can be perforated. I observed this condition in *Cygnus* (s. str.), and *Cairina*. Hints of the medial perforation were also present in one of two specimens of *Anser cygnoides*, and in *Chloephaga melanoptera*. *Anseranas* has both lateral and medial pneumatic foramina in the sternal basin, but lacks the anterior pneumatic foramen.

Table 1. Patterns of sternal pneumatization in the waterfowl and allied taxa. A – anterior foramen in the sternal basin, B – medial foramina in the sternal basin, C – lateral foramina in the sternal basin, D – foramina on the ventral side of the sternal basin, along keel basis, E – foramen in the frontal edge at manubrium. + = present, (+) = variable, – = absent. Data for taxa marked by an asterisk were derived from Livezey (1986)

	A	B	C	D	E
Phoenicopterus	+	+	+	–	(+)
Chauna	(+)	+	+	–	(+)
Anseranas	–	+	+	–	–
Dendrocygna	+	–	(+)	–	–
Mionetta	–	–	–	–	–
*Thalassornis**	–	–	–		
Cygnus (*Cygnus*)	+	(+)	+	(+)	–
Cygnus (*Olor*)	–	–	(+)	–	–
Coscoroba	+	–	+	+	+
Anser	+	(+)	+	–	–
Branta	+	–	+	–	–
Cereopsis	+	–	–	–	–
*Stictonetta**	+	–	–		
*Cyanochen**	+	–	–		
Chloephaga	+	(+)	(+)	–	–
*Neochen**	+	–	–	–	–
Alopochen	+	–	+	–	–
Tadorna	+	–	–	–	–
Tachyeres	–	–	–	–	–
Plectropterus	+	–	+	–	–
Cairina	+	+	+	–	–
*Pteronetta**	+	–	–	–	–
*Sarkidiornis**	+	–	–	–	–
Nettapus	+	–	–	–	–
Calonetta	+	–	–	–	–
Aix	+	–	–	–	–
Chenonetta	+	–	–	–	–
Amazonetta	+	–	–	–	–
*Merganetta**	+	–	–	–	–
*Hymenolaimus**	+	–	–	–	–
Anas	+	–	–	–	–
A. specularioides	+	–	+	–	–
*Malacorhynchus**	+	–	–	–	–
Marmaronetta	+	–	–	–	–
*Rhodonessa**	+	–	–	–	–
Netta	+	–	–	–	(+)
Aythya	(+)	–	–	–	–
Somateria	–	–	–	–	–
Polysticta	+	–	–	–	–
*Camptorhynchus**				–	
Histrionicus	+	–	–	–	–
Clangula	–	–	–	–	–
Melanitta	–	–	–	–	–
Bucephala	+	–	–	–	–
Mergus	+	–	–	–	–
*Heteronetta**	–	–	–	–	–
Oxyura	–	–	–	–	–
Biziura	–	–	–	–	–

Coscoroba is unique in having pneumatic foramina along the keel basis at the ventral side of the sternal basin.

Rarely, pneumatic foramina are present also in the front of the sternum (*Cygnus*, *Coscoroba*, and *Netta peposaca*). In *Cygnus* (sg. *Olor*), sternal keel is inflated, and contains loop of trachea (see also Wetmore 1951), which enters the keel through the anterior edge.

Non-pneumatic sterna are typical for *Thalassornis*, *Somateria*, *Melanitta*, *Clangula*, *Tachyeres*, *Oxyura*, *Biziura*, and the Miocene *Mionetta*. *Aythya* has a very small anterior pneumatic foramen, which is even absent in some individuals. *Aythya* is apparently at the evolutionary wedge between pneumatic and non-pneumatic sternum.

Close relatives of the Anatidae (Anhimidae and Phoenicopteridae) have highly pneumatized sterna (see Tab. 1).

DISCUSSION

Adaptive significance of sternal pneumatization

All the waterfowl genera, which lack sternal pneumatization, are specialized for diving. Also *Aythya*, which tends to lose pneumatic sterna, is a genus of diving ducks. Not all these genera are closely allied to each other (see Livezey 1986). This makes probable, that diving ducks increase their body density by limiting pneumatization of their skeleton, incl. sternum. However, having non-pneumatic sterna is not a necessary condition for the evolution of diving habits in the waterfowl, because *Mergus*, *Bucephala*, *Histrionicus*, and *Polysticta*, also specialized for diving, have pneumatic sterna. Absence of sternal pneumatization in the Miocene whistling duck *Mionetta* indicates that it evolved diving habits.

Taxonomic implications

Anaseranas has a unique pneumatization pattern of sternum. This is in accord with many other peculiarities it has, and supports its separation from the family Anatidae, advocated earlier by Livezey (1986) and Mlíkovský (1996).

Marked differences in sternal pneumatization between swan subgenera *Cygnus* and *Olor* support the view, that they should be separated at the generic level (cf. Wetmore 1951, Livezey 1986, Mlíkovský & Švec 1986).

Within the Anserinae (sensu Johnsgard 1979), *Cygnus*, *Coscoroba*, *Anser* and *Branta* have highly pneumatized sterna. *Cygnus* (sensu stricto), *Olor* and *Coscoroba* differ from *Anser* and *Branta* in having an additional frontal pneumatic foramen. In the Anatidae, I found this foramen also in the single specimen of *Netta peposaca*. This South American species is sometimes separated at the generic level as *Metopiana*, but no doubts have been casted on its affinities to *Netta*. Study of further specimens of *Netta peposaca* is needed to see, whether frontal pneumatic foramen is a standard character in this species. *Cereopsis* and *Stictonetta* have reduced pneumaticity of sterna, similar to typical Anatinae.

Within the Anatinae, a group of genera, formerly united in the tribe Cairinini (*Alopochen*, *Cairina* and *Plectropteron*) have additional, lateral pneumatic foramina in the sternal basin. This supports their close affinities one to another. Lateral pneumatic foramina in sternal basin are present also in *Anas specularioides*. It is a less known South American duck, often separated at the genus level as *Lophonetta* (Riley 1914, Boetticher 1952, Wolters 1975–1982). Boetticher (1952) placed *Lophonetta* in the neighbourhood of *Tadorna*, but pneumatization patter of sternum provides evidence, that it is more closely related to Cairinini (sensu stricto). *Anas* is a broad, weakly defined genus of generalized ducks (cf. Mlíkovský 1987), and it is well possible,

that unrelated species are still included in it. Previously, this was proven for *Salvadorina waigiuensis* (Mlíkovský 1989).

Different pneumatization patterns in diving ducks indicate, that *Mergus* and *Bucephala* are not closely related to the so-called marine diving ducks (*Melanitta*, *Clangula*, etc.), as is often assumed (e. g. Livezey 1986). This finding supports the conclusions of Brush (1976).

Livezey (1986) listed *Polysticta* among the taxa with non-pneumatic sterna, but the specimen I examined had distinct anterior pneumatic foramen in sternal basin. This might be individual variation, but at least some *Polysticta* individuals still possess pneumatic sterna. This is further character, which separates *Polysticta* from typical eiders of the genus *Somateria* (see also Livezey 1986, Oates & Principato 1994), to which it otherwise appears to be closely related (Woolfenden 1961, Brush 1976, Livezey 1986).

Evolutionary patterns

Screamers, closely related to the Anatidae, have highly pneumatized sterna. This is true also for *Anseranas*, *Cygnus*, and *Coscoroba*, which are generally considered most ancient anatids. This makes highly probable, that ancestral Anatidae had highly pneumatized sterna, with several pneumatic foramina. In the course of evolution, sternal pneumatization became reduced. A single pneumatic foramen is thus characteristic for most of the derived Anatidae. In diving forms, sternum has often lost pneumaticity, presumably in order to increase body density. This state is known already in the ancestral Dendrocygninae (sensu Johnsgard 1979), where *Mionetta* and *Thalassornis* possess non-pneumatic sterna. Obviously, loss of sternal pneumaticity evolved several times in the Anatidae.

Reversal of the common evolutionary pattern, leading from high pneumaticity to its loss, is possible in the Cairinini (sensu stricto). Their sterna are well pneumatized and have additional pneumatic foramina in the sternal basin. In this, proper Cairinini are similar to geese, with which they are apparently unrelated (Woolfenden 1961, Brush 1976, Livezey 1986). Re-gaining high pneumaticity of sternum might be an adaptation to terrestrial life habits of these birds.

CONCLUSIONS

Ancestral Anatidae appear to have had highly pneumatized sterna. Later, pneumatization became reduced in various phyletic lines. Several taxa, specialized for diving, lost sternal pneumatization.

REFERENCES

Boetticher H. von 1952: *Gänse- und Entenvögel aus aller Welt*. Leipzig: Geest & Portig, 95 pp.

Brush A. H. 1976: Waterfowl feather proteins: analysis of use in taxonomic studies. *J. Zool., Lond.* **179**: 467–498.

Johnsgard P. A. 1979: Order Anseriformes. Pp.: 425–506. In: Mayr E. & Cottrell C.W. (eds.): *Check-list of birds of the world. Vol. 1. 2nd ed.* Cambridge: Museum of Comparative Zoology.

Livezey B.C. 1986: A phylogenetic analysis of Recent anseriform genera using morphological characters. *Auk* **103**: 737–754.

Mlíkovský J. 1987: Ecological bases of supraspecific evolution. Pp.: 253–267. In: Pesce-Delfino V. (ed.): *Biological evolution*. Bari: Adriatica Editrice.

Mlíkovský J. 1989: Note on the osteology and taxonomic position of Salvadori's Duck Salvadorina waigiuensis (Aves: Anseridae [Anatidae]). *Bull. British Ornithol. Club* **109**: 22–25.

Mlíkovský J. 1996: Tertiary avifaunas of Europe. *Acta Univ. Carol. – Geol.* **39**: in press.

Mlíkovský J. & Švec P. 1986: Review of the Tertiary waterfowl (Aves: Anseridae) of Asia. *Věst. Čs. Společ. Zool.* **50**: 259–272.

Oates D. W. & Principato J. D. 1994: Genetic variation and differentiation of North American waterrfowl (Anatidae). *Trans. Nebraska Acad. Sci.* **21**: 127–145.

RILEY J. H. 1914: Note on Anas cristata Gmelin. *Proc. Biol. Soc. Washington* **27**: 100.
WETMORE A. 1951: Observations on the genera of the swans. *J. Washigton Acad. Sci.* **41**: 338–340.
WOLTERS H.-E. 1975–1982: *Die Vogelarten der Erde.* Hamburg: Paul Parey, 748 pp.
WOOLFENDEN G. E. 1961: Postcranial osteology of the waterfowl. *Bull. Florida State Mus. Biol. Sci.* **6**: 1–129.

APPENDIX

List of examined species

Taxonomic arrangement of the Anatidae follows Johnsgard (1979). Usually, only one specimen per species was examined. Higher numbers are given in parentheses.

Phoenicopteridae: *Phoenicopterus ruber* Linnaeus, 1758 (5).
Anhimidae: *Chauna chavaria* (Linnaeus, 1766) (9).
Anseranatinae: *Anseranas semipalmata* (Latham, 1798).
Dendrocygninae: *Dendrocygna arborea* (Linnaeus, 1758), *D. javanica* (Horsfield, 1821), *D. bicolor* (Vieillot, 1816), *D. autumnalis* (Linnaeus, 1758), *D. viduata* (Linnaeus, 1766).
Anserinae: *Cygnus* (*Cygnus*) *olor* (Gmelin, 1789) (4), *C. melanocoryphus* (Molina, 1782), *C. atratus* (Latham, 1790), *Cygnus* (*Olor*) *buccinator* Richardson, 1832, *C. cygnus* (Linnaeus, 1758) (2), *C. bewickii*, *C. columbianus* (Ord, 1815), *Coscoroba coscoroba* (Molina, 1782), *Anser anser* (Linnaeus, 1758) (2), *A. albifrons* (Scopoli, 1769) (2), *A. cygnoides* (Linnaeus, 1758) (2), *A. indicus* (Latham, 1790) (3), *A. fabalis* (Latham, 1787) (2), *A. erythropus* (Linnaeus, 1758) (2), *A. caerulescens* (Linnaeus, 1758) (2), *A. rossi* Cassin, 1861, *Branta canadensis* (Linnaeus, 1758), *B. leucopsis* (Bechstein, 1803), *B. ruficollis* (Pallas, 1769), *B. bernicla* (Linnaeus, 1758) (2), *B. sandvicensis* (Vigors, 1834), *Cereopsis novaehollandiae* Latham, 1801.
Tadorninae: *Chloephaga picta* (Gmelin, 1789), *C. melanoptera* (Eyton, 1838), *C. rubidiceps* Sclater, 1861, *C. poliocephala* Sclater, 1857, *Alopochen aegyptiaca* (Linnaeus, 1766), *Tadorna tadorna* (Linnaeus, 1758), *T. tadornoides* (Jardine et Selby, 1828), *T. ferruginea* (Pallas, 1764), *T. variegata* (Gmelin, 1789), *Tachyeres pteneres* (Forster, 1844) (2).
Anatinae: *Plectropterus gambensis* (Linnaeus, 1766), *Cairina moschata* (Linnaeus, 1758), *Nettapus coromandelianus* (Gmelin, 1789), *Calonetta leucophrys* (Vieillot, 1816), *Aix sponsa* (Linnaeus, 1758) (3), *A. galericulata* (Linnaeus, 1758) (2), *Chenonetta jubata* (Latham, 1801), *Anas platyrhynchos* Linnaeus, 1758 (4), *A. poecilorhyncha* Forster, 1781 (2), *A. crecca* Linnaeus, 1758 (2), *A. americana* Gmelin, 1789, *A. strepera* Linnaeus, 1758, *A. querquedula* Linnaeus, 1758 (2), *A. undulata* Dubois, 1837 (2), *A. formosa* Georgi, 1775, *A. acuta* Linnaeus, 1758, *A. bahamensis* Linnaeus, 1758, *A. clypeata* Linnaeus, 1758, *A. falcata* Georgi, 1775 (2), *A. discors* Linnaeus, 1766, *A. rhynchotis* Latham, 1801, *A.* (*Salvadorina*) *waigiuensis* Rotschild et Hartert, 1894, *A.* (*Lophonetta*) *specularioides* King, 1828, *Marmaronetta angustirostris* (Menetries, 1832), *Netta rufina* (Pallas, 1773) (3), *N. peposaca* (Vieillot, 1816), *Aythya valisineria* (Wilson, 1814) (2), *A. fuligula* (Linnaeus, 1758) (4), *A. collaris* (Donovan, 1838) (2), *A. ferina* (Linnaeus, 1758), *A. baeri* (Radde, 1863), *A. affinis* (Eyton, 1838) (2), *A. americana* (Eyton, 1838), *A. marila* (Linnaeus, 1761), *A nyroca* (Gueldenstaedt, 1770).
Merginae: *Somateria spectabilis* (Linnaeus, 1758) (2), *Polysticta stelleri* (Pallas, 1769), *Histrionicus histrionicus* (Linnaeus, 1758), *Clangula hyemalis* (Linnaeus, 1758) (2), *Melanitta nigra* (Linnaeus, 1758) (2), *M. perspicillata* (Linnaeus, 1758), *Bucephala clangula* (Linnaeus, 1758), *B. albeola* (Linnaeus, 1758), *Mergus cucullatus* Linnaeus, 1758, *M. albellus* Linnaeus, 1758 (2), *M. serrator* Linnaeus, 1758, *M. merganser* Linnaeus, 1758.
Oxyurinae: *Oxyura jamaicensis* Gmelin, 1789, *Biziura lobata* (Shaw, 1796) (2).