THE FUNCTION AND EVOLUTION OF THE SUPRAORBITAL PROCESS IN DUCKS

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The anterior margin of the orbit in ducks is formed by the lacrimal bone, which articulates with the anterolateral margin of the frontal bone and the posterodorsal corner of the maxillary process of the nasal bone. The evolution of this bone in birds generally has been dealt with recently by Cracraft (Amer. Midl. Naturalist, 80: 316, 1968), whose terminology for the parts of the lacrimal bone is followed here. In many ducks the posterodorsal corner of the lacrimal is marked by a small tubercle, which serves as the site of attachment of the anterior end of the orbital membrane, a sheet of connective tissue that covers and protects the dorsal aspect of the eyeball. In some forms this tubercle has become elongated to form a stout, finger-like projection, the supraorbital process. This appears to provide mechanical protection to the eyeball and salt gland (Figure 1). Table 1 lists the occurrence and degree of development of this process in the skulls of all living genera of ducks.

Correlation with Feeding and Locomotor Habits

In the following discussion, data on feeding habits are from Delacour (The waterfowl of the world, vols. 1–3, London, Country Life Ltd., 1954, 1956, 1959). Table 1 shows that the supraorbital process is developed significantly only in certain groups of ducks that feed underwater. It is absent or rudimentary in the Tadornini, Cairinini, and Anatini, which are primarily surface feeders, but also in *Merganetta armata*, the Torrent Duck, which feeds underwater. In the Aythyini it is fairly well-developed in several species of *Aythya*, which are excellent divers, but is rudimentary in *Netta peposaca*, which is more of a surface feeder. It is also rudimentary in the Canvasback, *Aythya valisineria*, which dives for vegetation. Among the Mergini the supraorbital process is highly developed in eiders (*Polysticta, Somateria*), scoters (*Melanitta*), and Long-tailed Duck (*Clangula hyemalis*), all of which feed mainly on invertebrates taken from the bottom. It is also fairly large in the Harlequin Duck, *Histrionicus histrionicus*, which feeds on invertebrates, often in turbulent waters. In contrast, the process is absent or rudimentary in the Bufflehead and goldeneyes (*Bucephala*) and the closely related mergansers (*Mergus*). These species are largely carnivorous, the mergansers eating mostly fish. Among the stifftail ducks (Oxyurini) the supraorbital process is undeveloped in both the Black-headed Duck (*Heteronetta atricapilla*) and the Ruddy Duck (*Oxyura jamaicensis*) which feed mainly on vegetation, and

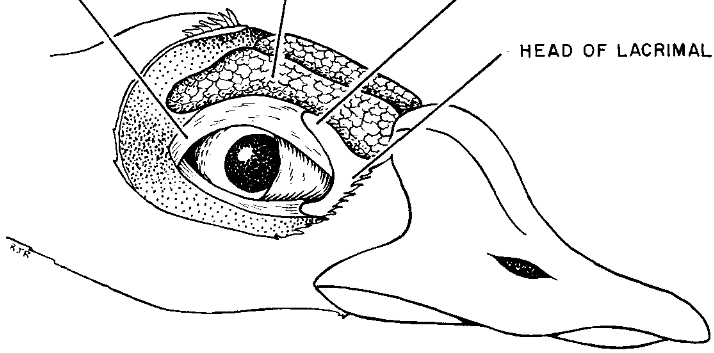

Figure 1. Lacrimal bone and adjacent structures in a male King Eider, *Somateria spectabilis*.

in the carnivorous Musk Duck (*Biziura lobata*). In the steamer ducks (Tachyerini) the process is quite large, resembling that in the eiders. Both groups feed widely on marine invertebrates.

In general, the supraorbital process is most highly developed in those forms that feed on the bottom and that might be likely to damage the eye by abrasion against underwater objects such as the hard shells in mollusk beds. Freshwater divers that feed on plants or invertebrates in the soft mud of ponds or lakes are probably less subject to such injury. The mergansers, which pursue fish in open water, are less exposed to the possibility of such eye injuries.

Evolution

The most recent studies of waterfowl evolution (e.g. Johnsgard, Waterfowl/their biology and natural history, Lincoln, Univ. Nebraska Press, 1968, p. 3) suggest that the Oxyurini, Mergini, Aythyini, and Tachyerini arose independently from some Anatini-like, surface feeding ancestral group. Hence specialization for diving and underwater food-gathering arose at least four times in the history of the Anatinae, and the development of an elongated supraorbital process presumably occurred three times. It is not clear why this structure did not arise in such bottom-feeding forms as the Oxyurini or *Merganetta armata.* Perhaps the necessary genetic changes upon which selection could operate simply never took place.

The question arises as to whether the elongated process should be considered homologous in the different groups of ducks. It is generally held

TABLE 1

OCCURRENCE AND SIZE[1] OF THE SUPRAORBITAL PROCESS IN DUCKS

Species	No.	Actual length		Relative length[2]	
		Range	Mean	Range	Mean
TADORNINI					
Cyanochen cyanopterus	1	Rudimentary[3]			
Chloephaga melanoptera	2	Absent			
Neochen jubatus	1	Rudimentary			
Alopochen aegyptiacus	1	Absent			
Tadorna tadornoides	1	Rudimentary			
TACHYERINI					
Tachyeres patachonichus	2	3.3–17.0	10.2	14–75	44
T. pteneres	1	6.3–7.0	6.7	24–25	24.5
T. brachypterus	1	8.4	8.4	–	49
CAIRININI					
Plectropterus gambensis	1	Absent			
Cairina moschata	2	Rudimentary			
Pteronetta hartlaubi	1	Rudimentary			
Sarkidiornis melanotos	1	Absent			
Nettapus coromandelianus	1	Rudimentary			
Callonetta leucophrys	1	Absent			
Aix sponsa	4	Absent			
Chenonetta jubata	2	Absent			
Amazonetta braziliensis	1	Absent			
ANATINI					
Merganetta armata	1	Absent			
Hymenolaimus malacorhynchus	1	Absent			
Anas crecca	5	Absent or rudimentary			
A. gibberifrons	3	Absent or rudimentary			
A. platyrhynchos	5	Absent or rudimentary			
A. rubripes	2	Rudimentary			
Malacorhynchus membranaceus	3	Rudimentary			
Marmaronetta anguirostris	1	Absent			
AYTHYINI					
Rhodonessa caryophyllacea	1	Rudimentary			
Netta peposaca	2	Rudimentary			
Aythya valisineria	4	Rudimentary			
A. americana	5	0.7–1.8	1.3	3–9	6
A. marila	3	1.1–2.3	1.6	6–12	8
A. affinis	5	1.3–2.7	2.1	7–14	11
MERGINI					
Somateria mollisima	4	4.7–8.9	6.2	18–33	25
S. spectabilis	3	4.6–5.2	4.9	19–23	21
S. fischeri	4	6.0–8.2	6.7	25–34	28
Polysticta stelleri	5	3.0–3.6	3.3	16–19	18
Histrionicus histrionicus	3	1.8–2.7	2.2	10–14	12
Clangula hyemalis	5	2.6–4.1	3.4	13–19	16
Melanitta nigra	3	3.7–5.0	4.6	18–24	22
M. perspicillata	5	2.3–4.0	3.2	13–18	15
M. fusca	5	2.6–4.0	3.1	12–19	15

[1] Measurements in mm.

[2] This is the actual length divided by the width of the orbit and expressed as a percentage. The mean relative length is most useful for the purpose of comparing the development of the process in different species.

[3] The process is considered rudimentary if less than 1.5 mm. in length.

TABLE 1 (*Continued*)

Species	No.	Actual length		Relative length[2]	
		Range	Mean	Range	Mean
Bucephala albeola	4	Absent or rudimentary			
B. islandica	1	Absent			
B. clangula	4	Absent			
Mergus albellus	1	Rudimentary			
M. serrator	5	Rudimentary			
M. merganser	3	Absent or rudimentary			
OXYURINI					
Heteronetta atricapilla	2	Absent or rudimentary			
Oxyura jamaicensis	5	Absent or rudimentary			
Biziura lobata	3	Absent or rudimentary			

that homology occurs when the condition or feature is also found in a form ancestral to the groups under discussion. As it is believed that the different tribes of diving ducks evolved separately from a surface-feeding ancestry, the condition would not be considered homologous by this definition alone. It seems probable that in each case this advanced condition resulted by parallel evolution from a common ancestral structure, the tubercle of attachment of the orbital membrane. Bock (Amer. Naturalist, 47: 265, 1963) suggests that, in closely related forms, features that appear to be homologous may have evolved independently in groups whose common ancestor possessed a precursor of the advanced condition. This

TABLE 2

FAMILIES AND SPECIES OF BIRDS EXAMINED IN ADDITION TO THOSE IN TABLE 1

Spheniscidae:	*Pygoscelis adeliae; Spheniscus humboldti; S. magellanicus; S. mendiculus; Megadyptes antipodes; Eudyptula minor; Aptenodytes forsteri.*
Gaviidae:	*Gavia adamsii; G. arctica; G. immer; G. stellata.*
Podicipedidae:	*Aechmophorus major; A. occidentalis; Centropelma micropterum; Podiceps auritus; P. caspicus; P. cristatus; Podilymbus podiceps.*
Diomediidae:	*Diomedea exulans; D. immutabilis; D. nigripes.*
Procellariidae:	*Daption capensis; Macronectes giganteus; Pterodroma leucopterus; Pachyptila forsteri.*
Pelecanoididae:	*Pelecanoides garotii.*
Pelecanidae:	*Pelecanus conspicillatus.*
Sulidae:	*Sula dactylatra.*
Phalacrocoracidae:	*Nannopterum harrisi.*
Anhingidae:	*Anhinga novae-hollandiae.*
Fregatidae:	*Fregata magnificens.*
Anseranatidae:	*Anseranas semipalmata.*
Anatidae:	*Anser albifrons; Branta canadensis; B. bernicla; Cygnus atrata; Coscoroba coscoroba; Dendrocygna autumnalis; D. bicolor.*
Rallidae:	*Fulica americana.*
Heliornithidae:	*Heliornis fulica.*
Alcidae:	*Pinguinus impennis; Uria aalge; Cerorhinca monocerata.*
Cinclidae:	*Cinclus mexicanus.*

would indicate that the descendent groups share an evolutionary potential inherited from the ancestor, and the advanced condition should then be considered to be homologous. The supraorbital process in ducks appears to be such a case.

In order to ascertain whether a similar development has occurred in other groups of aquatic birds, I surveyed the skulls of representative species of a wide variety of orders (Table 2). In most cases no structure exists comparable to the elongated supraorbital process of ducks, although some penguins and grebes have a rudimentary process that presumably functions as a place of attachment of the orbital membrane. Albatrosses (*Diomedea*) and some Procellariidae (*Daption, Pterodroma*) have a short, blunt process that may provide protection similar to that suggested for ducks. A short process also is present in the Finfoot, *Heliornis fulica.* Among Anatidae other than true ducks (Anatinae), a process of more than rudimentary size was found only in the swanlike *Coscoroba coscoroba.* Its significance in this nondiving, surface-feeding species is not known.

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