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**Cranial pneumatization in the Phalacrocoracidae.**—In certain regions of the cranium in birds, air spaces separate inner and outer layers of dense, ossified bone. In many cases, these pneumatic areas (“ossified bone” [sic] of earlier studies—see Serventy et al. 1967) are contiguous with cranial air sacs, but precise functions are still being debated (Harrison 1957, Warneke and Stork 1977, Winkler 1979). Pneumatization occurs late in development and has been used to assess cranial maturation (Winkler 1979); its relationship with age, however, is not well understood, and its reliability as an age index is uncertain (cf. Serventy et al. 1967, McNeil and Burton 1972, Sugimori et al. 1985).

The relationship of the bursa of Fabricius with age has been well-documented, and its size is used regularly to assess chronological age (see Gower 1939, Linduska 1943, Kirkpatrick 1944). Davis (1947) and McNeil and Burton (1972) consequently examined the relationship between cranial ossification and bursa size, but found differing results. Davis qualitatively assessed bursa size and cranial ossification in 110 species in 31 families, and although he found widely varying results, he felt that degree of cranial ossification was directly correlated with age. McNeil and Burton found no such relationship among ossification, pneumatization, and age in 21 species of shorebirds, but determined that bursa size tracked chronological age as it did in other birds.

During the course of a phylogenetic study of the Phalacrocoracidae (Siegel-Causey 1988), I was able to obtain data on cranial pneumatization patterns in 15 taxa in the family. Where possible, I measured bursa size, extent of pneumatization, and various skull dimensions. I examine here the phylogenetic patterns of cranial pneumatization in the Phalacrocoracidae and the relationship between the extent of cranial pneumatization, bursa size (age), and body size.

*Methods.*—All skeletal measurements were done on museum specimens obtained from various collections. Species of Phalacrocoracidae used in this study and sample sizes are: Reed Cormorant (*Phalacrocorax africanus*, 15), Little Pied Cormorant (*P. melanoleucos*, 21), Brandt’s Cormorant (*P. penicillatus*, 4), Black-faced Cormorant (*P. fuscescens*, 2), Olivaceous Cormorant (*P. olivaceus*, 50), Double-crested Cormorant (*P. auritus*, 57), Little

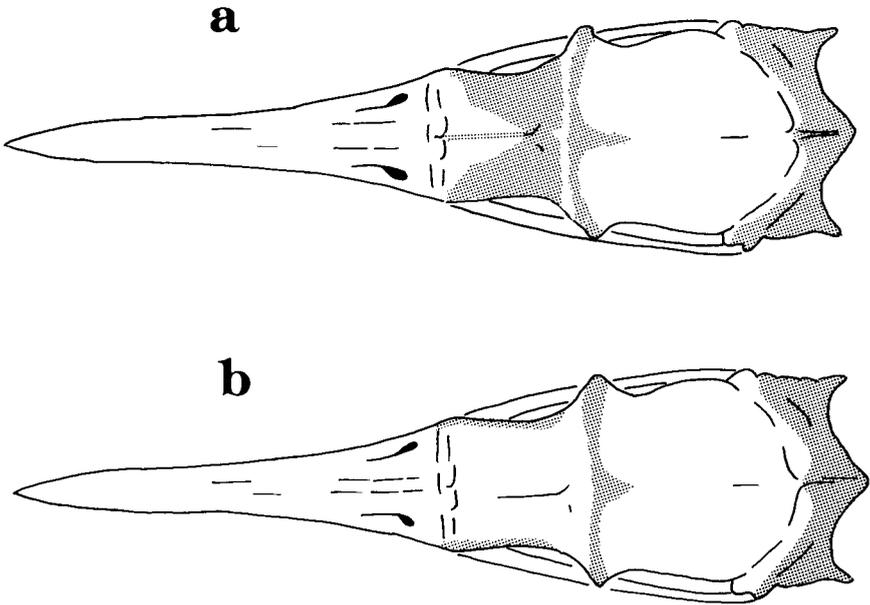


FIG. 1. Pneumatization patterns of phalacrocoracid skulls. A) Cormorants (Phalacrocoracinae); B) Shags (Leucocarboninae). Shaded area represents pneumatic bone.

Black Cormorant (*P. sulcirostris*, 3), Pied Cormorant (*P. varius*, 4), Great Cormorant (*P. carbo*, 11), Socotra Cormorant (*P. nigrogularis*, 3), Cape Cormorant (*P. capensis*, 4), Imperial Shag (*P. atriceps*, 112), Rock Shag (*P. magellanicus*, 73), Pelagic Cormorant (*P. pelagicus*, 10), and Red-legged Shag (*P. gaimardi*, 30). A list of specimens and data is available from the author.

Skulls were measured by dial calipers to a 95% replicated accuracy of  $\pm 0.1$  mm. Length and width of bursa of Fabricius were measured in the field to nearest mm by dial calipers with indeterminate accuracy. I visualized the extent of pneumatized bone by back illumination: nonpneumatic bone in the Phalacrocoracidae is translucent, while pneumatized bone is opaque (see Serventy et al. 1967, Fig. 1 in Stork 1970). Multivariate analyses were performed using BMDP statistical programs (Dixon 1985). Cases with missing data for the variables under analysis were excluded.

**Results.**—Among all phalacrocoracids examined, I observed only two qualitative patterns of pneumatization. In the Reed, Little Pied, Brandt's, Black-faced, Olivaceous, Double-crested, Pied, Little Black, and Great cormorants, all members of the Phalacrocoracinae (Siegel-Causey 1988), the major centers of cranial pneumatization were the mastoid, the dorsal cranial strut, and the posterior half of the frontal (Fig. 1A). Pneumatic bone in the anterior half of the frontal was restricted to a lateral triangular region on both sides and to three narrow strips. Two of them were located laterally along each edge and one medially at the juncture of the optic septum and the frontal. The lateral extent of pneumatized bone within the frontal was correlated with cranium length in Double-crested (DCC) and Olivaceous (OC) cormorants (DCC:  $r = 0.71$ ,  $P < 0.001$ ; OC:  $r = 0.51$ ,  $P < 0.001$ ), and with

the width of the frontal (DCC:  $r = 0.675$ ,  $P < 0.001$ ; OC:  $r = 0.55$ ,  $P < 0.001$ ). Sample sizes of other cormorants were insufficient for analysis.

In Socotra, Cape, Imperial (IS), Rock (RS), Pelagic, and Red-legged shags (RLS), all members of the Leucocarboninae (Siegel-Causey 1988), the centers of cranial pneumatization were the same as in the first group of species except for the frontal (Fig. 1B). Pneumatized frontal bone was restricted in these species to a narrow lateral strip on each side (IS:  $\bar{x} = 1.43 \pm 0.54$  [SD] mm; RS:  $\bar{x} = 1.56 \pm 0.81$  mm; RLS:  $\bar{x} = 0.91 \pm 0.75$  mm). The width of the lateral strip was correlated with cranium length ( $r = 0.52$ ,  $P < 0.001$ ) and frontal width ( $r = 0.61$ ,  $P < 0.001$ ) only in the Imperial Shag. Frontal pneumatization was not correlated with cranium length nor frontal width in Rock, Pelagic, or Red-legged shags; sample sizes of other shags were insufficient for analysis.

In all cases where I could measure bursa size, the extent of pneumatized frontal bone was uncorrelated with bursa area when the log-linear effects of size (frontal width) were removed (OC:  $r = 0.44$ , IS:  $r = 0.01$ , RLS:  $r = 0.11$ , RS:  $r = -0.09$ , RLS:  $r = 0.11$ ).

*Discussion.*—In his survey of cranial pneumatization in birds, Winkler (1979) placed cormorants implicitly into the group B pattern, which included ardeids, gruiforms, falconiforms, galliforms, and larids. In this group pneumatized bone is restricted somewhat to the lateral and ventral parts of the cranium, with dorsal areas corresponding to the cerebellar prominences of the brain remaining apneumatic. The only study to examine pneumatization in cormorants explicitly was by Harrison (1957), who, judging by the appearance of the illustration (Fig. 6 in Harrison 1957), unfortunately used a juvenile specimen of *P. carbo*.

Pneumatization of the cranium in adult phalacrocoracids proceeds from three centers: the mastoid (see Fig. 6 in Harrison 1957), dorsal cranial strut (see Fig. 4 in Winkler 1979), and frontal. These pneumatized areas are similar in other Pelecaniformes (Harrison 1957, Winkler 1979), but only the first two centers have been examined previously. The frontal pneumatization pattern is the only one that varies phylogenetically in the Phalacrocoracidae, and it seems to be directly related to the shape of the nasal gland depression on the dorsal surface of the frontal. In cormorants (Phalacrocoracinae), the glands are bilobed and small relative to the size of the frontal; in shags (Leucocarboninae), the glands are single-lobed and large (Siegel-Causey, unpubl. data). In all other pelecaniformes, gland shape is small and bilobed; the pneumatization patterns are more complex but generally follow that seen in the Phalacrocoracinae (Harrison 1957). Therefore, the pneumatization pattern in the Leucocarboninae is a derived condition, and supports the previous findings that shags are the most derived members of the family (Siegel-Causey 1988).

Pneumatized frontal bone occurs only in areas not occupied by the gland depression, and its extent is correlated directly with cranial size, but not age (as measured by bursa size). Either cranial pneumatization in cormorants is not age-related, as previous studies have demonstrated for other birds (McNeil and Burton 1972, Winkler 1979), or bursa size does not correlate with age in phalacrocoracids. At present, neither alternative can be disproved.

Various functions have been hypothesized for cranial pneumatization: strength (Chapin 1949, McNeil and Burton 1972), flight speed (Harrison 1964), "mode of life" (Harrison 1957, 1964), thermoregulation (Warneke and Stork 1977), and structural accommodation (Winkler 1979). Full reviews of these and other hypothesized functions can be found in Harrison (1964) and Winkler (1979). The first three hypotheses are not completely separable and many exceptions can be found. For example, heavily pneumatized crania are a feature of birds which hammer their beaks into substrate when feeding (e.g., Picidae), but high-diving waterbirds (e.g., Pelecaniformes) that experience high impact stress have relatively lesser pneumatized skulls, and many passerines which experience neither (e.g., *Parus*, *Hirundo*, *Sitta*) have completely pneumatic crania.

Harrison (1964) predicted that slow-flying species would have the greatest amount of

pneumatization, but McNeil and Burton (1972) documented many cases in the Charadrii where the opposite was true. "Mode of life" is harder to define, and thus difficult to test as a hypothesis, but Harrison (1957, 1964) concluded that diving birds had the least amount of cranial pneumatization, presumably as a means to minimize cranial buoyancy and internal air spaces. Until more rigorous criteria for this hypothesis can be developed, its status remains indeterminate.

Warneke and Stork (1977) hypothesized that increased cranial pneumatization assisted in thermoregulation. They observed a proportionate increase in feather-ruffling during cold weather in juvenile passerines compared to adults, and associated it with lessened cranial pneumatization in younger birds. Such an explanation is *ad hoc* and proximate, and furthermore no such pattern is seen in waterbirds which will incur much greater heat loss while in water. Other explanations relating to diving depth, swimming or flight speed, flight acceleration, foraging technique, etc. suffer similar fates.

Winkler (1979) surveyed pneumatization patterns in 287 species, and hypothesized that simultaneous structural accommodation of internal (i.e., brain, eyes, glands, etc.) and external (muscle attachment, cranial shape) features was the ultimate explanation for the presence of pneumatized bone. Thus, rugose projections for attachment of muscle or aponeuroses (e.g., the crotophyte or temporal crests of phalacrocoracids) can be maintained without undue weight or cranial deformation of internal cavities. The absence of pneumatized bone within the frontal gland depression allows the nasal gland to fit within the orbit which is otherwise occupied by the eyes. The external (ventral) surface of the frontal thus remains streamlined, which is an important consideration in pursuit divers such as cormorants and shags.

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**Historical status of Harlequin Ducks wintering in eastern North America—a reappraisal.**—Vickery (1988) concluded that “Harlequin Ducks (*Histrionicus histrionicus*) in eastern North America are now and have historically been quite rare and of local distribution.” While there is no doubt that this adequately describes the present situation, there is evidence to suggest that formerly this sea duck was more common there. Phillips (1925), Palmer (1949, 1976), and Todd (1963) clearly stated that numbers of Harlequin Ducks had declined over the periods they considered. Phillips (1925) supported his contention that Harlequin Ducks had declined considerably up to the early parts of the present century in Atlantic Canada by quoting Langille (1884) and Dresser (1871–81), who made reference to hundreds in specific areas of the maritime provinces. Downs (1888) considered them rather common in winter in Nova Scotia. References to New Brunswick may be interpreted as unclear; however, Herrick (1873) considered Harlequin Ducks common in winter in the late 1800s in the Grand Manan archipelago. Peters and Burleigh (1951) noted that the Harlequin Duck in Newfoundland had “. . . become much reduced in numbers during recent years. It has now become so rare that it should receive protection for all times.” Peterson and Fisher (1955) observed “. . . hundreds of Harlequin Ducks . . .” at one site on Cape St. Mary’s, an area that anecdotal information indicates to have supported thousands in winter.

Christmas Bird Counts (CBC) from 1979–80 to 1987–88 disclosed a pattern of decline for Cape St. Mary’s, Newfoundland ( $r = -0.701$ ;  $P < 0.02$ ), and for Nova Scotia, where sightings have declined significantly since the mid 1970s ( $r = -0.575$ ;  $P < 0.02$ ) when those counts first incorporated sites such as Port Hebert, which consistently supported small numbers of wintering Harlequin Ducks.

The present scarcity of sightings of Harlequin Ducks in the Gulf of St. Lawrence may not be indicative of former numbers as Comeau (1909) noted rapid declines in numbers wintering near Pointe des Monts. Rowdon (1969), quoted in McNeil et al. (1973), believed that Harlequin Ducks were once fairly common on the Magdalen Islands. Significant winter concentrations (hundreds) were reported for Anticostic Island (Brewster 1884) for the 19th