

I. INTRODUCTION

The origin of diving birds can be traced back to the lower Cretaceous when *Enaliornis* arose. *Enaliornis* was probably the ancestor of Loons and Grebes but it is not until the Oligocene that these two groups can be distinguished in the fossil record.^{1,2} *Hesperornis*, a highly specialized toothed diver from the upper Cretaceous, may also have arisen from the same ancestral stock as Loons and Grebes. *Hesperornis* was a large flightless bird with vestigial wings, and with legs placed far aft, making it improbable that it could move about easily on land. However, it is also possible that Loons and Grebes evolved from a nondiving ancestor, and that the similarities with *Enaliornis* and *Hesperornis* are the result of convergent evolution. This suggestion is not supported by cladistic analysis of these extinct and extant birds, which indicates that they comprise a monophyletic group.³ Furthermore, cladistic analysis indicates that a common ancestor not only gave rise to the above birds but also to the orders Sphenisciformes, Pelicaniformes, and Procellariiformes.

Cormorants and Boobies are believed to have arisen from a Cretaceous bird *Elopteryx*,⁴ but again it is not until the Oligocene that these two groups are separable. The relationship of *Galornis*, a goose-like bird from the lower Cretaceous, to the family Anatidae is questionable^{1,4,5} although true Ducks and Swans of the genera *Anas*, *Aythya*, and *Cygnus* are distinguishable in Oligocene deposits from Europe. Geese and mergansers are represented in the fossil record by the Miocene. By the late Eocene, the majority of water-bird families were in existence, and by the Miocene, the last of the specialized water birds appeared.⁶ The Penguin is no exception. Simpson⁷ showed that by the Miocene Penguins had lost the ability to fly, and their structure was remarkably similar to that of recent Penguins.

It is clear that diving as a mode of life is very old, and that the 100 million or so years that birds have been making their living under water is sufficient time for the evolution of anatomical and physiological traits specific to this way of life.

II. ANATOMICAL AND PHYSIOLOGICAL CORRELATES OF DIVING

A. Anatomical

The mass of the skeleton of birds is frequently reduced by the presence of pneumatic cavities in the larger bones. Birds begin their lives with nonpneumatic, marrow-filled bones, but during incubation and later development the marrow is absorbed and air sacs begin to invade the hollow cavities. The skull is pneumatized by extensions from the nasal and tympanic cavities, whereas the postcranial skeleton receives diverticula from the bronchial system (Figure 1⁸). This has often been claimed to be an adaptation for flight; certainly it must present a problem to diving birds with respect to buoyancy. However, there is evidence to suggest that the body of diving birds is denser than that of nondivers. Portmann⁹ stated that the bones of diving Ducks are less pneumatic than those of nondiving Ducks, and Harrison¹⁰ showed that skull pneumaticity is diminished in diving compared with dabbling Ducks (Figure 1). In the Oldsquaw (*Clangula hyemalis*), the coracoid and scapula are pneumatic, but the bones of the wing and leg are not.¹¹

The degree of pneumaticity varies greatly among species of the order Pelicaniformes. Only the skull and humerus of the Cormorant (*Phalacrocorax carbo*) are pneumatic, but many of the bones of the Gannet (*Aula bassana*) are pneumatic.¹² It is worth noting here that the Cormorant dives from the surface by arching downward and propelling itself with its feet; however, Gannets and Boobies plunge headfirst into the water from heights as great as 100 m.¹³ Furthermore, the Pelican, also a plunger, has many pneumatic bones.¹⁴ Of the birds which dive from the surface, many are known to have poorly pneumatized bones. Casler¹⁵ stated that "the air sacs of the Anhinga penetrate no bones." Pneumaticity is only slight in *Podiceps cristatus*, *Sphenisci*, and *Mergus*, and is completely absent in *Gavia* and