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NEOGAEORNIS WETZELI LAMBRECHT, A CRETACEOUS LOON FROM CHILE (AVES: GAVIIDAE)

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INTRODUCTION

The fossil bird *Neogaeornis wetzeli* was described as a new genus and species by Lambrecht (1929), based on a right tarsometatarsus collected in 1923–1924 by W. Wetzel from the Upper Cretaceous Quiriquina Formation of Chile. The specimen shows the laterally compressed shaft and retracted inner trochlea typical of birds that are highly specialized for foot-propelled diving. Consequently, Lambrecht (1929) compared this fossil with loons (Gaviiformes), grebes (Podicipediformes), and the Cretaceous diving birds *Hesperornis, Baptornis,* and *Enaliornis.*

Lambrecht (1933) placed *Neogaeornis, Enaliornis,* and *Baptornis* in his order Colymbo-Podicipediformes, along with loons and grebes. This was preceded by the order Hesperornithiformes, containing only *Hesperornis.* Brodkorb (1963) placed *Enaliornis* in the Gaviiformes and *Neogaeornis* and *Baptornis* in the Podicipediformes, while maintaining *Hesperornis* in a different subclass.

Not until the important work of Martin and Tate (1976) were the relationships among the Cretaceous and modern divers clarified. Martin and Tate determined that none of the Cretaceous divers were closely related to modern loons and grebes. Within the Hesperornithiformes, they recognized three families: Enaliornithidae for *Enaliornis* from the Lower Cretaceous of England, Hesperornithidae for *Hesperornis* from the Upper Cretaceous of North America, and Baptornithidae for *Baptornis,* a more primitive genus than *Hesperornis,* also from the Upper Cretaceous of North America. Without examining the holotype, they tentatively included *Neogaeornis wetzeli* in the Baptornithidae.

The Hesperornithiformes are not otherwise known outside of North America and none of those yet found are younger than Campanian. The Gaviiformes are unknown outside the northern hemisphere and their fossil record extends only as far back as the late Eocene (Olson, 1985). The cosmopolitan Podicipediformes are unknown before the early Miocene (Olson, 1985). Thus *Neogaeornis* has considerable temporal and biogeographic importance regardless of its identity. After more than 60 years, a reappraisal of the type specimen is appropriate.

SYSTEMATIC PALEONTOLOGY

Class AVES Linnaeus, 1758
Order GAVIIFORMES Wetmore and Miller, 1926
Family GAVIIDAE Allen, 1897

Genus *NEOGAEORNIS* Lambrecht, 1929

Type species—*Neogaeornis wetzeli* Lambrecht, 1929, by monotypy.

NEOGAEORNIS WETZELI Lambrecht, 1929
Figure 1

Holotype—GPMK 123, right tarsometatarsus lacking proximal articular surface and inner trochlea. The distal surface of the middle trochlea is eroded and the entire distal end of the bone is much cracked and repaired, such that the natural configuration of the remaining trochlcae is probably altered. When received, the specimen was considerably filled in and encrusted with molding compound and glue, so that details were greatly obscured. This material was removed as much as was possible without endangering the integrity of the specimen. Casts made prior to this operation will not be particularly accuratc.

Type Locality—Cliff at west end of Bahía San Vicente, on the southern point of Península Tumbes, Province of Concepción, Chile.

Horizon—Quiriquina Formation, Arauco Group, Upper Cretaceous. The marine Quiriquina beds rest unconformably on Paleozoic rocks and are unconformably overlain by Eocene continental sediments (Riccardi, 1988). The ammonites in these deposits belong to taxa elsewhere restricted to strata of either Campanian or Maastrichtian age (or both) and consequently the Quiriquina Formation is regarded as "Campanian/Maastrichtian" (Biró-Bagóczky, 1982; Riccardi, 1988), although in the correlation chart of Riccardi (1988: table 17) it is placed largely in the Maastrichtian.

Referred Material—A second tarsometatarsus was tentatively referred to *Neogaeornis wetzeli* by Oliver Schneider (1940). This was from the vicinity of Cerro del Conejo (also known as Cerro de las Pulgas or Cerro del Camarón) at 36°46'S, 73°15'W, in the area known as Vegas de Gualpén on the Bahía San Vicente and thus almost certainly is also from the Quiriquina Formation to judge from associated Cretaceous invertebrates. This specimen has never been illustrated or discussed, other than being listed by Brodkorb (1963), and is given no further consideration here.

Measurements of Holotype—Total length as preserved, 58.4 mm; estimated total length, 63.0 mm; width and depth of shaft at midpoint, 3.5 × 5.3 mm. The overall size of the specimen indicates a bird somewhat smaller than the smallest living species of Gaviidae, the Red-throated Loon (*Gavia stellata*), and approximately the size of the extant Red-necked Grebe (*Podiceps grisegena*).

Comparisons—Among the characters that Martin and Tate (1976) used to define the Hesperornithiformes were the absence of proximal foramina in the tarsometatarsus and the absence of a hypotarsus. Although the proximal end is badly abraded in the holotype of *Neogaeornis wetzeli,* on the posterior surface there is a distinct remainder of a medial cal-

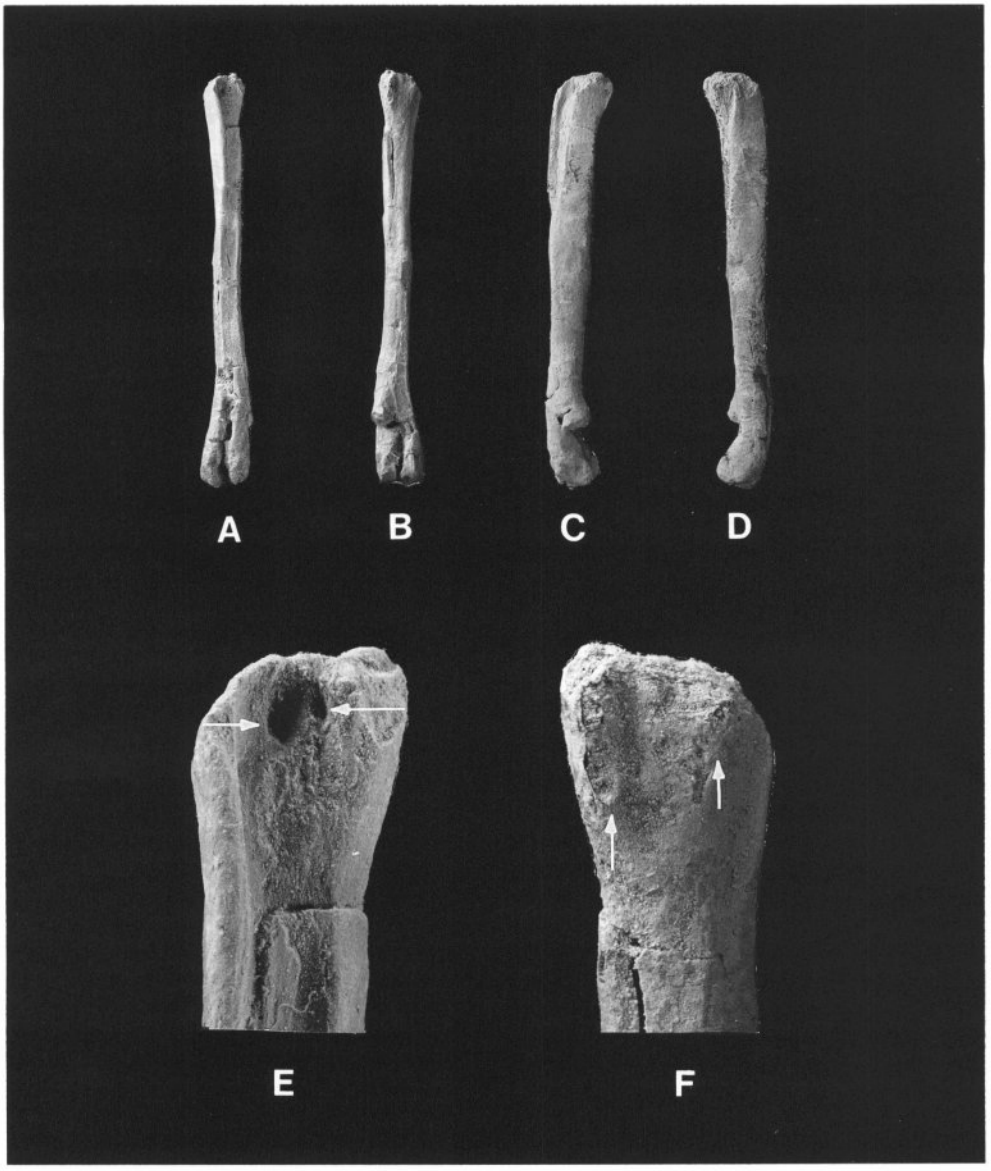

FIGURE 1. *Neogaeornis wetzeli,* holotype (GMPK 123), right tarsometatarsus: **A**, anterior; **B**, posterior; **C**, medial; **D**, lateral; **E**, anterior view of proximal end showing the proximal foramina (arrows); **F**, posterior view of proximal end showing the remains of calcaneal ridges of the hypotarsus (arrows). **A–D**, natural size; **E–F**, 5×.

caneal ridge with a vague suggestion of a groove lateral to it, as well as a faint indication of a lateral calcaneal ridge (Fig. 1F). Thus, *Neogaeornis* had a hypotarsus. Furthermore, on the anterior surface there are two distinct proximal foramina (Fig. 1E). The posterior opening of the medial foramen can also be detected (it is not evident in the photographs because it is filled in with matrix), but that for the lateral foramen appears to be obscured by breakage. The presence of a hypotarsus and of proximal foramina preclude the assignment of *Neogaeornis* to the Hesperornithiformes. Furthermore, the entire bone is much more gracile and laterally compressed than in any of the Hesperornithiformes.

Neogaeornis thus must belong to the radiation of modern birds. It is now generally recognized that specializations for foot-propelled diving have evolved independently in loons, grebes, and Cretaceous divers, so that these three groups are only convergently similar in hindlimb structure (Olson, 1985; Raikow, 1985). Although it is conceivable that some other group entirely may have given rise to *Neogaeornis* during the Mesozoic, this would be difficult to determine from a tarsometatarsus alone. Nevertheless, there are no modern birds as specialized for foot-propelled diving as loons and grebes, so that given the highly derived structure of the foot of *Neogaeornis,* the genus could not be placed among any other Recent taxa.

The holotype of *Neogaeornis wetzeli* is similar to loons (Gaviiformes) and differs from grebes (Podicipediformes) in the following characters: shaft more laterally compressed with

the proximo-anterior portion of the external side produced as a distinct crest; trochleae narrower; distal foramen and base of the internal trochlea more elevated (situated more proximad).

In grebes, the outer trochlea extends farther distally than the middle trochlea, whereas in loons the opposite is true. In the holotype of *Neogaeornis*, these trochleae are about equal in extent, but this may be an artifact of preparation, as the middle trochlea appears to have been broken entirely free and reattached somewhat more proximally than its natural position. Thus the original configuration of the trochleae may have been more loonlike than is now apparent.

The fossil differs from the tarsometatarsus of modern loons mainly in the markedly more distal placement of the distal foramen. In this respect, however, it is not unlike the early Miocene loon *Colymboides minutus* from the Aquitanian of France (Storer, 1956:fig. 2).

The identification of *Neogaeornis* as a loon is greatly strengthened by Chatterjee's (1989) discovery of a partial skeleton of a loon (including skull parts) in the Upper Cretaceous Lopez de Bartodano Formation of Seymour Island, Antarctica. This specimen, which I have examined, is unquestionably a loon referable to the modern family Gaviidae, and may possibly even be referable to *Neogaeornis*.

From a geographical standpoint, a Late Cretaceous grebe in Chile would at first seem more reasonable than a loon. Grebes have been postulated to have arisen in the Southern Hemisphere and do not appear in the Northern Hemisphere until the Miocene (Olson, 1989). Furthermore, the greatest modern diversity of grebes is in South America (Storer, 1967). Conversely, extant loons, as well as all of their previous fossil record, are confined to the northern portions of the Northern Hemisphere.

Nevertheless, because there may be a much closer relationship between loons and penguins (which are confined to the Southern Hemisphere) than had previously been admitted, especially when the morphology of the Eocene penguins of Antarctica is considered (Olson, 1985), the presence of Mesozoic loons in the Southern Hemisphere does not seem so anomalous. *Neogaeornis* is of startlingly modern aspect for a Mesozoic bird. It would suggest that the most recent common ancestor of penguins and loons existed prior to the Late Cretaceous. It may also fit a pattern observed in molluscs and other marine organisms whereby taxa originated at high latitudes in the Southern Hemisphere and dispersed northward in the Early Tertiary (Zinsmeister, 1982).

In summary, the foot-propelled diving bird *Neogaeornis wetzeli*, from the Upper Cretaceous of Chile, definitely does not belong among the Hesperornithiformes. Doubtless the Mesozoic age of this fossil is the principal reason for its ever having been associated with that order. Its similarities to modern loons are such that it may be placed in the order Gaviiformes and in the modern family Gaviidae.

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