



Evolutionary drivers for flightless, wing-propelled divers in the Northern and Southern Hemispheres

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ABSTRACT

At least four clades of flightless wing-propelled diving birds evolved during the Cenozoic. The most successful, in terms of diversity and evolutionary duration, is the Sphenisciformes, or penguins, which still thrive in Southern Hemisphere waters. Three other groups are now extinct: Plotopteridae (Pelecaniformes); Mancallinae (Charadriiformes), or Lucas auks; and *Pinguinus* (Charadriiformes), or the Great Auk. Two clades include large species, the Plotopteridae, and the Sphenisciformes, in which extinct “giant” forms reached lengths and masses much larger than the living *Aptenodytes forsteri* (Emperor penguin). The extinction of flightless wing-propelled divers, especially giant forms, in the Northern and Southern Hemispheres has been linked to competitive displacement by co-evolving marine mammals. Such an idea is here assessed via taxonomic diversity (i.e., richness) trends from the fossil record reported in the Paleobiology Database. At global to basin scales, flightless divers and marine mammals indeed show contrasting patterns of diversity from the Chattian to the Aquitanian (late Oligocene to early Miocene: 28.4–20.43 Ma); diving birds decrease in diversity with increase in marine mammal diversity, especially Odontoceti. Long-term patterns are not compositional and do not result from scaling effects. Dietary overlap presumably played an important role in any competition, but this aspect is difficult to demonstrate. Marine mammals have similar diversity patterns to each other in both global and regional trends, implying a role for common evolutionary drivers as suggested previously for the evolution of crown Cetacea (or Neoceti). Flightless divers lack common diversity patterns, and show only partial negative correlations, as well as partial similarities, with marine mammal diversity trends. Thus, the evolution of flightless divers was probably governed by a mix of factors, rather than dominated by either physical or biotic drivers.

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1. Introduction

Flightless wing-propelled divers (FWPD) are birds that have abandoned aerial flight, and instead have evolved many adaptations for an aquatic lifestyle that includes underwater flight. Penguins, the only surviving FWPD, have achieved a wide range of morphological adaptations for swimming and diving, with concomitant adaptations in sensory systems and physiology (Stonehouse, 1975; Davis and Darby, 1990; Williams, 1995; Ksepka and Ando, 2011).

In avian Cenozoic history, four groups of birds have evolved as FWPD (Fig. 1): Sphenisciformes, or penguins (Paleocene to Holocene); Plotopteridae (Pelecaniformes, late Eocene to late Miocene); Mancallinae, or Lucas auks (Charadriiformes, middle Miocene to Pleistocene); and *Pinguinus*, or the Great auk (Charadriiformes, Pliocene to Holocene) (Olson, 1985; Hasegawa et al., 1988; Feduccia, 1996; Mayr, 2009; Ksepka and Ando, 2011). Hereafter, the groups

are referred to by their most exclusive names: Sphenisciformes, Plotopteridae, Mancallinae, and *Pinguinus*. These groups show strong morphological convergences linked to underwater flight: for example, the wing elements are shortened, flattened, and anteroposteriorly widened; the humeral head is well-developed; and the acrocoracoid process of the coracoid is elongate and hook-shaped (Storer, 1960; Olson, 1985). Such morphofunctional similarities, and known ecological similarities between Sphenisciformes and *Pinguinus*, suggest that the four groups of birds had the same broad ecological niche (Simpson, 1946; Storer, 1960; Simpson, 1976; Olson and Hasegawa, 1979; Olson, 1985; Olson and Hasegawa, 1996). Storer (1960) proposed parallelism in the aquatic adaptations of Southern Sphenisciformes and Northern *Pinguinus*, prompted by Simpson's (1946) hypothesis on the evolutionary history of Sphenisciformes. Simpson (1946) viewed penguins as originating from volant non-diving sea birds that adopted wing-propelled diving as well as aerial flight (such as modern diving petrels), and then becoming aquatic, non-aerial birds. These concepts are now widely accepted, supported by morphological and molecular phylogenetic reconstructions and fossil records of the

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early forms that retain plesiomorphic characters shared with related volant birds (Olson, 1985; Fordyce and Jones, 1990; Olson and Hasegawa, 1996; Kristoffersen, 2001; Mayr, 2005; Baker et al., 2006; Slack et al., 2006; Clarke et al., 2007; Mayr, 2009; Ksepka and Ando, 2011; Smith, 2011).

The four groups of FWPD have much in common in terms of morphology, broad ecological niche, and early evolutionary history. Cenozoic fossil records show that FWPD lived in all major ocean basins of both the Northern and Southern Hemispheres. However, their current diversities (i.e., taxonomic richnesses) are utterly different geographically: Sphenisciformes still thrive in southern waters, but the three northern FWPD taxa are extinct. Other issues debated for FWPD relate to the body size of giant species, and the timing of their demise. For the Sphenisciformes and Pterodroma, some giant species from the late Eocene to late Oligocene have been reconstructed as much larger than the largest living penguin, the Emperor penguin (*Aptenodytes forsteri*); Miocene or younger giant species have not been reported (Simpson, 1946; Olson, 1985; Warheit and Lindberg, 1988; Ksepka and Ando, 2011; Ksepka et al., 2012). The geographical and temporal patterns prompt crucial evolutionary questions: what factors best explain the extinction of Northern Hemisphere FWPD, and giant forms in general, while leaving penguins in the Southern Hemisphere?

Biotic drivers, particularly involving possible competition with small-sized marine mammals, have been cited to explain the diversity

patterns in the record of FWPD. Such interactions would imply competitive displacement sensu Krause (1986), discussed below. For example, Simpson (1971, 1976) suggested that the extinction of giant penguins was caused by the evolutionary radiation of smaller marine mammals (small odontocete cetaceans, and pinnipeds), with a potential increase in both competition and predation. Olson and Hasegawa (1979) and Olson (1985) considered that the concurrent extinctions of giant Southern Sphenisciformes and Northern Pterodroma might have been caused by the evolution of pinnipedimorphs and odontocetes in the later Oligocene and Miocene, given the potential competition between FWPD and marine mammals of comparable sizes.

Biotic drivers might ultimately reflect physical causes. For example, Warheit and Lindberg (1988) suggested that sea level change led to competition for breeding sites between pinnipeds and Mancallinae, and that the competition could then have caused mancalline extinction, as pinnipeds increased in diversity. Warheit and Lindberg (1988) and Warheit (1992) also suggested that the extinction of large (giant) Sphenisciformes in New Zealand, and Pterodroma in the North Pacific, resulted from competition for breeding sites with pinnipedimorphs in the South Pacific, and with desmatophocids and desmostylians in the North Pacific. Such suggestions are plausible, but none has yet been supported by identifying adequate mechanisms to explain extinction.

The concept of competitive displacement takes its origin from Darwin's (1859) writings on competition: if two taxa are in the same adaptive zone, they would be expected to have structurally similar feeding and locomotory systems, and similar food and habitat requirements. Previous studies have dealt with the categorization of ecological replacements (e.g., competitive displacement and opportunistic displacement) and conditions which define those replacements, as well as actual cases of ecological replacements (Benton, 1983, 1987, 2009; Kitchell, 1985; Krause, 1986; Prevosti et al., 2011). To claim that competition with marine mammals is a possible cause of diversity patterns within FWPD, it must be shown that the process is indeed competitive, not coincidental replacement. The conditions required for competitive displacement involve diversity changes (decline in one group, expansion in the other), temporal and geographic overlap, niche overlap, and lack of concurrent physical change that might otherwise explain the pattern (see discussion below). Among previous studies on diversity changes in FWPD, only the approach by Warheit and Lindberg (1988) meets such conditions. Even then, the time of extinction cited for Mancallinae has been revised from Pliocene to Pleistocene (Hasegawa et al., 1988; Smith, 2011).

In this study, we test the competitive displacement hypothesis involving marine mammal taxa (MM) and FWPD by considering the conditions implied by the hypothesis (see Mode of ecological replacement, under Discussion):

- (1) MM and FWPD show ecological replacement;
- (2) during the replacement, MM and FWPD overlap temporally and geographically;
- (3) during the replacement, MM and FWPD have a negative correlation (decline in FWPD, increase in MM);
- (4) the time span of the replacement is fairly long;
- (5) MM and FWPD are in a similar adaptive zone using common resources;
- (6) the replacement is not associated with changes in physical environment.

If the six conditions are fulfilled, then the pattern and process of replacement must be ecological displacement.

To this end, we considered the generic richnesses over time for MM (Cetacea, Pinnipedimorpha, Archaeoceti [= stem-Cetacea sensu Fordyce and de Muizon, 2001], Odontoceti, Mysticeti, basal Pinnipedimorpha, Phocoidea, and Otarioidea) and FWPD (*Pinguinus*, Mancallinae, Pterodroma, and Sphenisciformes). These taxa were compared through the Cenozoic in light of conditions 1–6, above.

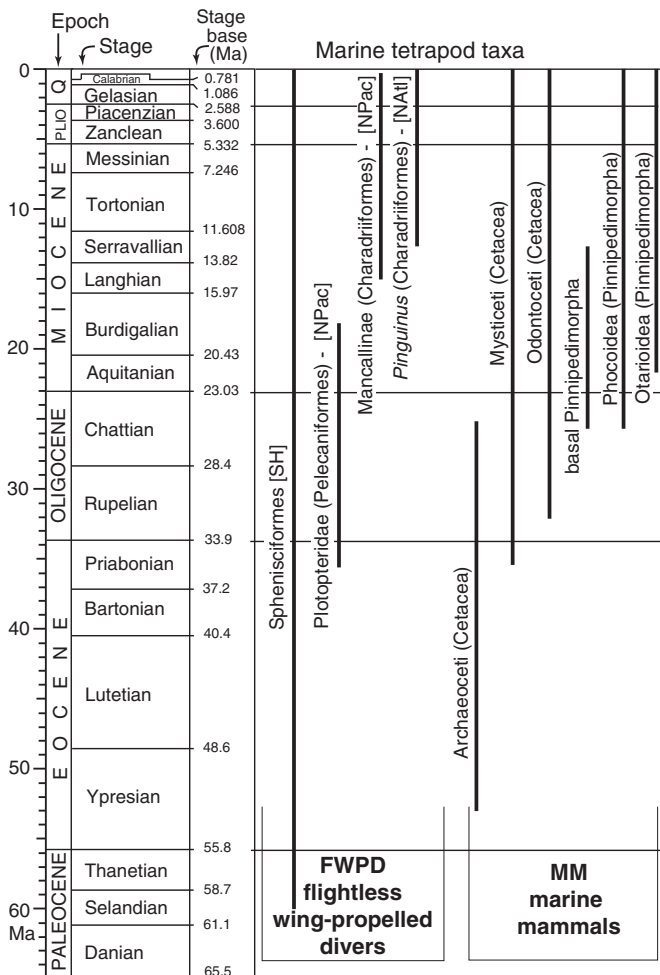


Fig. 1. Age ranges of Cenozoic marine tetrapods: flightless wing-propelled divers and carnivorous marine mammals. SH: Southern Hemisphere, NPac: North Pacific Ocean, NAtl: North Atlantic Ocean.

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