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2 The Seabird Fossil Record and the Role of Paleontology in Understanding Seabird Community Structure

Kenneth I. Warheit

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2.1 INTRODUCTION

Most seabird systems (e.g., species, communities, populations) are large in both temporal and spatial scale. For example, it is now firmly established that many seabird populations and communities are affected by climatic cycles, some of which operate globally and over periods extending from several years to decades (e.g., El Niño–Southern Oscillation and the North Pacific decadal oscillation; see Chapter 7). In general, seabirds are long lived with each bird experiencing a variety of climatic conditions during its lifetime. The longevity of individual seabirds and the fact that these birds live in environments that are affected by large-scale phenomena have prompted a plethora of long-term studies of seabird populations and communities (e.g., Coulson and Thomas 1985, Ainley and Boekelheide 1990, Harris 1991, Wooler et al. 1992). In fact, there is a lengthy history of long-term studies of seabird populations (e.g., Rickdale 1949, 1954, 1957, Serventy 1956) and communities (e.g., Uspenski 1958, Belopol'skii 1961).

The long-term history of seabird systems is even more remarkable when we consider the fossil record. Contrary to "common knowledge," birds have a rather extensive fossil record (Olson 1985a) that is most informative. Owing to the fact that seabirds generally live or lived in depositional environments (e.g., nearshore marine) rather than erosional environments (e.g., upland), the fossil record of seabirds represents a large percentage of the total fossil record of all birds (see Olson

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1985a). Given this relatively good but clearly incomplete fossil record, it is possible to use seabird fossils as a tool not only to study the truly long-term history of seabirds, but also to help interpret the biogeographical patterns and community structure of modern-day seabird systems.

In this chapter, I summarize first the fossil history of seabirds, here defined as Sphenisciformes, Procellariiformes, Pelecaniformes (excluding Anhingidae), Laridae, and Alcidae. This summary includes a comprehensive table (Appendix 2.1) listing each fossil taxon, with its corresponding temporal, spatial, and bibliographic information. I then discuss the importance of fossils and the paleontological record in elucidating many aspects of seabird ecology and evolution. I introduce what fossils can tell us about biology, geography, and time, and provide a series of examples of how the study of seabird fossils presents essential information to our understanding of the long-term and large-scale development of seabird communities. Finally, I conclude with a discussion of the fossil history of the Alcidae. I highlight the Alcidae for several reasons. First, the fossil record of alcids is one of the best fossil records of all seabirds because of the large amount of material that has been collected and described, and the high degree of taxonomic diversity resulting from these descriptions. Second, the alcids encapsulate many of the discussions that are emphasized throughout this chapter. That is, to correctly understand the biogeographic and phylogenetic relationships of alcids requires knowledge of the alcid fossil record. Third, the fossil history of alcids is enigmatic and presents some interesting questions requiring future research.

2.2 THE FOSSIL RECORD OF SEABIRDS

I have provided a list of fossil seabird taxa in Appendix 2.1 (368 entries, including 253 taxa described to species, 28 of which are assigned or have affinities to modern species). Although this list is comprehensive, undoubtedly it is not complete, and it does not include modern seabird taxa found in Pleistocene or Holocene deposits (see Brodkorb 1963, 1967; and Tyrberg 1998 for listing of Pleistocene fossils of modern seabirds). There are at least two published revisions of a fossil taxon (penguins from New Zealand and Antarctica; Fordyce and Jones 1990, Myrcha in press) that were not included in this analysis. In Appendix 2.2, 23 additional fossil taxa are listed that are now considered synonymous with a species listed in Appendix 2.1.

It is tempting to compare the diversity among some higher taxa based on a list of species; however, these species were probably not described using the same set of procedures. For example, one author might feel justified naming a new species based on fragmentary material (e.g., Harrison 1985), while another author might be reluctant to do so or will wait until a greater number of higher quality material is in hand (Olson and Rasmussen 2001). The lack of a standard in describing new fossil species will result in some higher taxa having a greater number of described species than other taxa simply because of authors' biases rather than a product of true morphological diversity. That being said, I will still make some rudimentary comparisons among the higher taxa listed in Appendix 2.1.

Pelecaniformes is the most diverse order in this list in terms of both the number of entries (141) and described species (94). Procellariidae is the most diverse family with 68 entries and 42 described species, followed by the Alcidae (46 entries, 31 species) and Spheniscidae (45 entries, 38 species). The oldest taxon in the list is *Tytthostonyx glauconiticus*, from the late Cretaceous of New Jersey (see Figure 2.1 for time scale), tentatively placed in the Procellariiformes by Olson and Parris (1987). Following this species there are several taxa described from the Paleocene and Eocene, most of which are either archaic penguins or Pelagornithidae, an extinct group of bony-tooth pelecaniforms (see below). In fact, the Paleogene (Paleocene through Oligocene; Figure 2.1) appeared to be dominated by extinct Pelecaniformes (Pelagornithidae and Plotopteridae), Procellariidae, and large-sized penguins (Figure 2.2). Except for *Puffinus* (*P. raemdonckii*, from the early Oligocene of Belgium), modern genera of seabirds do not appear until the early Miocene or 16 to 23 million years ago (mya), and do not become taxonomically diverse until the middle Miocene (11 to 16 mya). The middle Miocene (Fauna I in Warheit 1992; see Figure 2.1) marked the onset

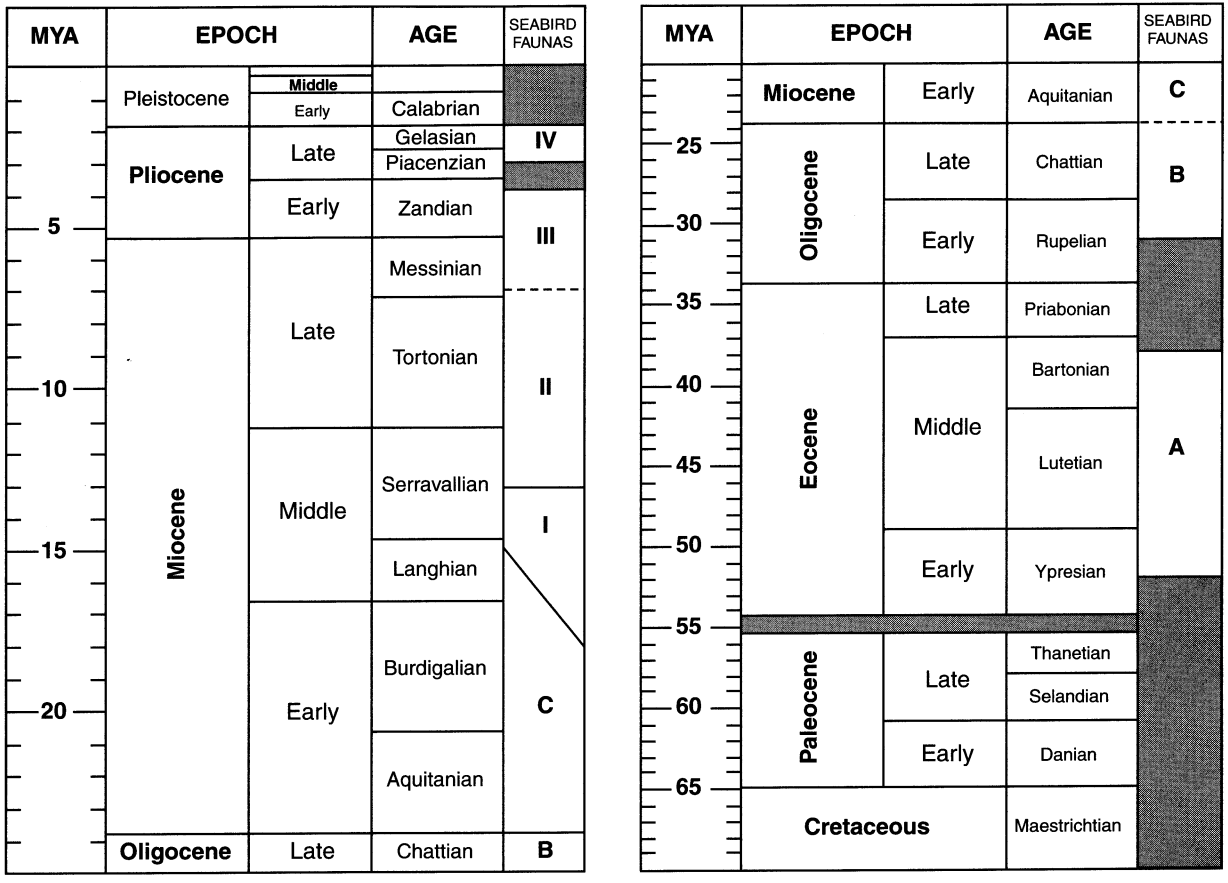

FIGURE 2.1 Cenozoic time scale based on Berggren et al. (1995). Epochs and Ages are divisions of the geologic time scale and correspond to the stratigraphic sequence of rocks and fossils. Epochs and Ages are scaled to absolute time using a combination of paleomagnetic and radioisotopic data. The seabird faunas are from Warheit (1992) and are based on the association of fossil-bearing rock formations from the North Pacific formed during a single, but broadly defined interval of time. The assemblage of seabird fossils from each of these isochronous rock formations is defined as a fauna. See Warheit (1992) for definitions of each of these North Pacific seabird faunas.

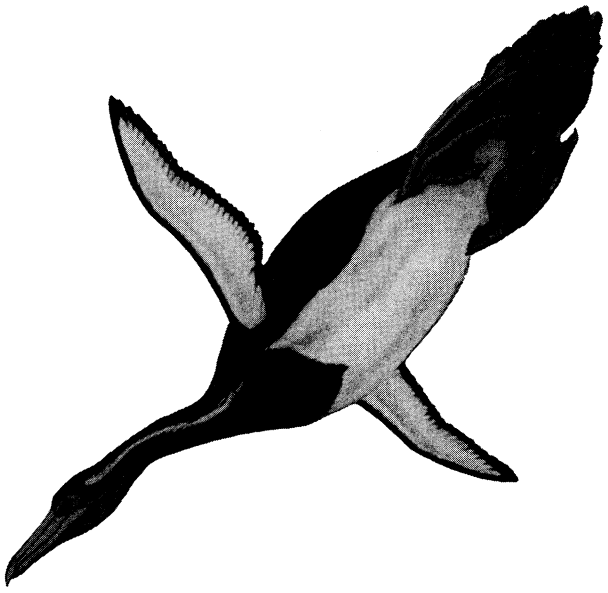

FIGURE 2.2 A reconstruction of one of the largest fossils in the Plotopteridae (Pelecaniformes). This plotopterid was larger than Emperor Penguins and had paddle-like wings similar to penguins. Its hindlimb and pelvic morphology were similar to Anhingas. It used its wings to swim underwater, an adaptation that has evolved several times in birds (Olson and Hasegawa 1979). (After Olson and Hasegawa 1979.)

of a permanent East Antarctic ice cap, a drop in sea level, and an increase in the latitudinal thermal gradient of the world's oceans (Warheit 1992). The steepening of this thermal gradient intensified the gyral circulation of surface currents, and strengthened the coastal and trade winds that promote upwelling (Barron and Bauldauf 1989). Indeed, there appears to be a temporal correlation between these climatic and oceanographic events and the taxonomic diversification of seabirds (see also Warheit 1992).

I discuss some of these issues and other aspects of the seabird fossil record in the next few sections. However, I would like to highlight here two groups of extinct seabirds: Pelagornithidae and Plotopteridae. The Pelagornithidae or pseudodontorns first appeared in the eastern North Atlantic (England) in the late Paleocene and early Eocene (49 to 61 mya) and in the eastern North Pacific and Antarctica in the middle and late Eocene, respectively. This group was truly global in distribution, occurring in fossil deposits in North and South America, Europe, Asia, Africa, New Zealand, and Antarctica, and survived some 57 to 59 million years (Appendix 2.1). The birds were also remarkable in their morphology: gigantic in size, one species was estimated to have a wingspan of almost 6 m (K. Warheit and S. Olson, unpublished data), with bony projections on their rostrum and mandible (Olson 1985a). Their mandible was also composed of a hinge-like synovial joint and lacked a bony symphysis (Zusi and Warheit 1992). Zusi and Warheit (1992) speculated that the birds captured prey on or near the surface of the water while in flight or by lunging while sitting on the water surface. Their extinction is enigmatic, but may be related to fluctuations in local or global food resources (Warheit 1992).

The Plotopteridae were pan-North Pacific in distribution and ranged in size from over 2 m in length to the size of a Brandt's Cormorant (Olson and Hasegawa 1979, Olson 1980, Olson and Hasegawa 1996; Figure 2.2). These seabirds were closely related to sulids, cormorants, and anhingas, but were flightless and possessed paddle-like wings remarkably convergent with those of penguins and flightless alcids (Olson and Hasegawa 1979, Olson 1985a). They disappeared in the early and middle Miocene from the eastern and western Pacific, respectively (Appendix 2.1). Olson

and Hasegawa (1979) and Warheit and Lindberg (1988) considered the evolution and radiation of gregarious marine mammals as a possible cause for the extinction of the plotopterids, while Goedert (1988) suggested that a sharp rise in ocean temperature was a better explanation for their demise (see Warheit 1992 for discussion of both hypotheses).

2.3 THE IMPORTANCE OF SEABIRD FOSSILS

2.3.1 Paleontology and the Structure of Seabird Communities

Press and Siever (1982) define paleontology as "the science of fossils of ancient life forms, and their evolution" and define a fossil as "an impression, cast, outline, track, or body part of an animal or plant that is preserved in rock after the original organic material is transformed or removed." Olson and James (1982a) extended the definition of fossil to also include subfossil bones (bones that have not become mineralized), such as those present in archeological midden sites, and I will adhere to this definition of fossil throughout this chapter. Because fossils, especially seabird fossils, occur in rocks that may also contain the fossiliferous remains of climate-sensitive microorganisms such as foraminiferans, it is possible to associate a particular climatic régime to a particular fossil community. Furthermore, since fossil-bearing rocks also can be placed geographically and dated either relatively or absolutely using a variety of methods, we can associate a fossil with a specific time and place. As such, if fossils are grouped together based on time, they can provide information on what species co-occurred during a specific period and in a specific place, and under the influence of a specific climatic régime. Therefore, fossils are not simply a collection of broken bones, but are in fact treasure troves that provide us with information about the morphology, anatomy, physiology, and behavior of individual organisms, as well as composition of past ecological communities.

Recent and historical processes contribute to the structure of seabird communities today. That is, those that can be measured in ecological time (e.g., predation, competition, dispersal) as well as factors that are measured in geological time (e.g., plate tectonics and the origin of modern oceanic currents), and perhaps random luck (see Jablonski 1986 and Gould 1989 for examples of the importance of random extinctions and historical contingencies, respectively), are responsible for the composition of the seabird communities today. I argue that in order to understand the structure of seabird communities today, we must not only study predation, competition, dispersal, etc., but we must also study fossils. Without incorporating history, an incomplete or a potentially incorrect story is built. To emphasize this point, I provide three examples of how studies of fossils and geological history have contributed essential components to our understanding of seabird communities. The first two examples (North Pacific and South African seabirds) provide information on how continental drift, sea level, and associated changes in climate and oceanography may have been responsible for profound changes in the composition of seabird communities. The final example concerns how the Polynesian colonization of oceanic islands in the Pacific Ocean resulted in extensive extinctions of both land- and seabird taxa prior to European exploration of the Pacific or written history.

2.3.1.1 North Pacific Seabird Communities

I have previously reviewed the fossil history of seabirds from the North Pacific and related this history to plate tectonics and paleooceanography (Warheit 1992). In what follows I highlight some of the findings from this study, focusing primarily on the seabird communities from central and southern California. The California Current upwelling system today is one of the primary eastern boundary systems, and, along with the Benguela and Humboldt upwelling systems of the Southern Hemisphere, currently support abundant and diverse seabird faunas. These three upwelling systems have many of the same types of seabirds. That is, each system has wing-propelled divers (e.g.,

alcids in the north, penguins and diving petrels in the south), foot-propelled divers (cormorants), pelicans, storm-petrels, and gulls, as well as others. Also present in both the Benguela and Humboldt systems are plunge-diving sulids, although there are no sulids, indigenous or otherwise, in the California Current today. It would be possible to develop a series of hypotheses to explain this difference; sulids are present in the Northern Hemisphere and in the North Pacific, and there are breeding sulids as close to the California Current as Baja California. However, developing such hypotheses using only ecological data collected from these communities today would be in error. Sulids existed in the California Current for the better part of nearly 16 million years and were represented by at least 11 to 13 different species (Appendix 2.1; Warheit 1992). Therefore, the question that should be asked is no longer simply "What ecological processes exist that have prevented sulids from occurring in the California Current?" but should also be "Why did sulids become extinct in the California Current, while remaining extant and thriving in other cold water upwelling systems?"

The local extinction of sulids is only one example of a dynamic seabird system. Overall, the seabird communities of the North Pacific in the past are quite different from those that exist today. There are at least 94 species of fossil seabirds in the North Pacific from at least seven distinct seabird "faunas" (Warheit 1992). Most of these species are from extant genera, but there also existed three groups of extinct and somewhat bizarre taxa: Pelagornithidae and Plotopteridae (discussed above), and the mancallids. The mancallids consisted of two, possibly three genera (*Praemancalla*, *Mancalla*, and perhaps *Alcodes*) of flightless alcids with estimated body mass ranging from 1 to 4 kg, compared with a mass of 5 kg for the Great Auk (*Pinguinus impennis*) (Livezy 1988). These were the most abundant seabirds in the California Current from at least 12 mya to the Plio-Pleistocene, especially during the late Pliocene (1.5 to 3 mya; Chandler 1990a), when there were at least three species of *Mancalla* and well over 200 specimens recovered from the San Diego Formation. The flightlessness of mancallids and the Great Auk was convergent in that these two taxa are not considered to be closely related (Storer 1945, Chandler 1990b), and the mancallids were more specialized for wing-propelled diving than the Great Auk, approaching the extreme morphology of penguins (Olson 1985a, Livezy 1988). Mancallids remained extant until the Pleistocene, but became extinct approximately 470,000 years ago (Howard 1970, Kohl 1974), perhaps as a result of competition for terrestrial space with gregarious pinnipeds (Warheit and Lindberg 1988, Warheit 1992).

In its entirety, the seabird history from the California Current upwelling system can be summarized as a transition from archaic pelecaniforms to a fauna closely resembling the system today, consisting of volant alcids, shearwaters, and storm-petrels, but a fauna that also included sulids and flightless alcids. Although competition and predation may have contributed to the various radiations and extinctions that characterized the California Current seabird faunas, the underlying physical process that governed the development of these faunas was the tectonic activities that resulted in the thermal isolation and refrigeration of Antarctica and the uplift of the Isthmus of Panama (Warheit 1992).

2.3.1.2 South African Seabird Faunas

As with the North Pacific seabird communities, there have been significant changes in the composition of the South African seabird faunas during the past several millions of years. Recent seabird faunas in both the North Pacific (in particular California and Oregon) and South African (Atlantic) coasts occur in cold-water upwelling systems. These upwelling systems are a function of continental positions and global circulation patterns, which, in turn, are products of tectonic activities. As such, these upwelling systems have had different characteristics throughout the Tertiary. According to Siesser (1980; in Olson 1983), the Benguela upwelling system off the southwest coast of South Africa did not develop until the early late Miocene. No fossil seabirds have been recovered from deposits prior to the development of this cold water system, but Olson (1983) speculated that since

water temperatures were warmer than those in the Pliocene and today, cold-water taxa were either absent or present in low diversity and abundance. The appearance of the first known South African seabird fauna roughly coincided with a good depositional environment, and, more importantly, with the development of the Benguela system and the production of cold water. Olson (1983, 1985b) concluded that with the progressive development of this cold-water nutrient-rich environment, seabird taxa more typical of cold-water systems moved north from the southerly latitudes near and around Antarctica.

The early Pliocene (5 mya) deposits of South Africa have yielded a diverse seabird fauna consisting of four species of penguins possibly related to *Spheniscus*, an albatross, two species of storm-petrels (*Oceanites*), three species of prions (*Pachyptila*), at least five species of shearwaters (*Procellaria*, *Calonectris*, *Puffinus*), and at least one species each of fulmarine petrel, diving petrel (*Pelecanoides*), and booby (*Sula;* Olson 1983, 1985b,c; Table 2.1). Based on the fossil localities and their depositional environments, and the presence of juvenile individuals in the deposits, Olson (1985b,c) reasoned that this seabird fauna consisted of both breeding and nonbreeding species (see Table 2.1). Although there are similarities between this early Pliocene fauna and South African seabirds today, mostly in terms of the higher taxonomic diversity of the nonbreeding species, there are considerable differences in the diversity of the breeding taxa (Table 2.1). There are no procellariiform taxa currently breeding in South Africa today, although there were at least three species (prion, storm-petrel, diving petrel) breeding locally during the early Pliocene. Olson (1983, 1985b) concluded that, except for the cormorant species, there has been a complete change in the seabird fauna of South Africa from the early Pliocene to today and this faunal turnover was mirrored by a similar turnover in the pinniped fauna. Specifically, taxa with cold-water affinities today and present in South Africa during the early Pliocene have been eliminated from the modern breeding fauna (*Oceanites*, *Pachyptila*, *Pelecanoides*), or are present in the modern fauna, but severely reduced in diversity (*Spheniscus*). This reduction in the number of cold-water species breeding in South Africa from the Pliocene to today is enigmatic because the Benguela cold-water upwelling system has been present off South Africa since the late Miocene. Olson (1983, 1985b) reasoned that the presence of the cold-water system was not the only factor in determining the relative diversity of species, but that a combination of factors contributed to the change in seabird faunas in South Africa. In addition to changes in oceanographic conditions and possible warming of the Benguela Current, it is possible that there were substantial changes in availability of island habitats resulting from fluctuating sea levels during the late Pliocene and throughout the Pleistocene. That is, changes in the height of sea level associated with tectonic activities and polar temperatures affect the availability of breeding habitats by either creating or removing islands. Islands can be created during low sea levels through the emergence of submerged land, or during high sea levels through flooding of low lands and isolation of high lands. The opposite can be true for the destruction of suitable island habitats.

2.3.1.3 Human-Induced Extinction of Seabirds from Pacific Islands

In the previous two examples, the long-term structure of seabird communities appears to have been largely affected by geological processes, namely, those responsible for the development of particular oceanic currents and water temperature, and for changes in relative sea level. However, some of the most profound changes to seabird systems have occurred relatively recently (geologically speaking) and were the direct result of human activities. Steadman (1995) summarized information on the Holocene extinction of birds from Pacific islands resulting from activities of indigenous people from Melanesia, Micronesia, and Polynesia. He determined that approximately 8000 species or populations, mostly flightless rails, became extinct following the geographic expansion of Polynesian populations (the extinction of a local population is here referred to as extirpation; see Steadman 1995). These extinctions and extirpations dramatically reduced the diversity of birds nesting on Pacific islands prior to the arrival of Europeans (and a written history) and, as such,

TABLE 2.1
List of Fossil Seabird Species Described by Olson (1985b,c) from Deposits in South Africa (see text)

Taxon	Number Breeding	
	Fossil[a]	Recent
Sphenisciformes	0	1
Nucleornis insolitus		
Dege hendeyi		
?Palaeospheniscus huxleyorum		
Inguza predemersus		
Diomedeidae	0	0
Diomedea sp.		
Oceanitidae	1	0
Oceanites zaloscarthmus	[b]	
Oceanites sp.		
Procellariidae	1	0
Fulmarinae sp.		
Pachyptila salax	[b]	
Pachyptila sp. B		
Pachyptila sp. C		
Procellaria sp.		
Calonectris sp.		
Puffinus sp. A		
Puffinus sp. B		
Puffinus sp. C		
Pelecanoididae	1	0
Pelecanoides cymatotrypetes	[b]	
Sulidae	0	1
Sula sp.		
Phalacrocoracidae	0	4
Phalacrocorax medium sp. A		
Phalacrocorax medium sp. B		
Phalacrocorax small sp.		

[a] The number of fossil species determined to be breeding is a minimum number and in most cases there are not enough data to determine breeding status.
[b] A fossil species is said to be breeding at a locality if remains of juveniles are found.

send a clear message that our studies of island biogeography *must not* ignore the extinct, prehistoric faunas and floras (Olson and James 1982a). In what follows, I briefly describe some of the changes that occurred to the status and distribution of seabird species throughout the Pacific as a result of the activities of these Pacific island people. This section summarizes the work of H. James, S. Olson, and D. Steadman, and I refer the reader to these original references (Olson and James 1982a,b, 1991, Steadman and Olson 1985, James 1995, Steadman 1995, and references therein). In addition, Harrison (1990) provided a popular account of the interactions between seabirds and humans on the Hawaiian Islands.

James (1995) reviewed the background of prehuman extinction rates for birds on oceanic islands. Although it is not possible to calculate annual turnover rates in species abundance and distribution, as is possible to do for islands today, the fossil record provides the means by which

we can measure long-term biogeographic patterns of seabird species. After reviewing both the Pleistocene and Holocene (i.e., post-Pleistocene) fossil record of birds on Pacific islands, James (1995) and others concluded that bird diversity was relatively stable during the Pleistocene, even during periods of great climatic change, but the number of extinctions increased dramatically following human occupation. For example, on the Hawaiian island of Oahu, James (1987, in James 1995) recorded 17 species of landbirds from Pleistocene deposits. All but two of these species survived a period greater than 120,000 years, during intense global climatic change, including a complete cycle of polar glaciation and deglaciation. However, human activities may have extirpated 13 of these 17 Pleistocene birds during the past thousand years or so (James 1995). In another example, Steadman (1995) described extinction rates in the Galapagos Islands where some 500,000 bones from Holocene deposits have been unearthed; about 90% of these bones predate the arrival of humans. During a period of 4000 to 8000 years prior to human occupation, a maximum of only 3 populations were extirpated from the Galapagos; however, during the few centuries since the arrival of humans, 21 to 24 populations were extirpated (Steadman 1995).

The human-related extinction of birds from islands can be caused by any number of perturbations ranging from direct predation and habitat destruction, to the introduction of non-native predators, competitors, or pathogens (Steadman 1995). On Hawaii, where the extinction of seabird species or populations appears less severe than on the Polynesian islands to the south, Olson and James (1982a) concluded that predation by humans, or collateral predation by their pets, was most important in the extinction of populations or species of flightless and ground-nesting landbirds and burrow-nesting seabirds. However, habitat destruction in the form of clearing of lowland forests was most likely the cause of the extinction of most of the small land bird species. Steadman (1995) added that soil erosion following deforestation also might have eliminated nest sites for burrowing seabirds.

The importance of fossils in understanding modern biogeographic patterns is best demonstrated by the documentation of extinctions and extirpations of birds from these oceanic islands. Steadman (1995 and references therein) stated that the Pacific seabird biodiversity on subtropical and tropical islands is now considerably lower than that on temperate and sub-Antarctic islands, and that this difference in biodiversity has been associated by others with the fact that marine waters in the tropics are less productive. However, Steadman indicated that the difference in seabird diversity between lower and higher latitude islands becomes less when you consider the extinct or extirpated species revealed by the fossil record. For example, on Ua Huka in the Marquesas, the prehistoric diversity of seabirds included at least 7 species of shearwaters and petrels and a total of 22 species of nesting species of seabirds; today there are only four species of seabirds and no breeding shearwaters or petrels (Steadman 1995).

The reduction in biodiversity from the low-latitude Pacific islands is mostly the result of the local extirpation of a population, not the outright extinction of a species. Steadman (1995) stated that there have been few examples of seabird species extinctions throughout Oceania. In the Hawaiian Islands, Olson and James (1991) documented only one extinct species of seabird, *Pterodroma jugabilis*, although there were many examples of local extirpation of populations (Olson and James 1982b). On Henderson Island, Steadman and Olson (1985) showed that although the island still maintains a diverse seabird fauna, *Nesofregatta fuliginosa* is recorded only as a fossil and was most likely eliminated from the island and the rest of the Pitcairn Group of islands because of human activities.

Finally, and perhaps most telling of the prehistoric destruction of Oceania seabird fauna, the fossil record indicates that on Easter Island there were at least 25 species of seabirds including an albatross, fulmar, prion, several species of petrels and shearwaters, a storm-petrel, two species of tropicbirds, a frigatebird, booby, and a suite of tern species (Steadman 1995). Today, 1 of these species is extinct (unnamed Procellariidae), 12 to 15 species no longer occur in or around Easter Island, and only 1 of these 25 species (Red-tailed Tropicbird, *Phaethon rubricauda*) currently breeds on Easter Island (Steadman 1995). Steadman stated (1995, p. 1124) that "Evidently, Easter

Island lost more of its indigenous terrestrial biota than did any other island of its size in Oceania" and that this destruction occurred in a period from 1500 to 550 years ago, during human colonization. In interpreting these data, Steadman assumed that the Polynesians collected the seabirds locally on Easter Island. However, an alternative explanation is that many of these seabird taxa did not breed on Easter Island and the Polynesians captured birds at sea and brought the carcasses back to the island (S. Olson, personal communication). This would inflate the number of "breeding" seabird species on Easter Island if Steadman defined breeding as simply the presence of bones on the island.

2.3.2 The Fossil Record of the Alcidae

The fossil record of the Alcidae is enigmatic when one attempts to reconcile the geographic distribution of certain fossil taxa with that of their modern relatives. For example, while alcid fossils are extremely abundant in western Atlantic deposits (Olson 1985a, Olson and Rasmussen 2001), the overall alcid diversity in the Atlantic was lower than that of the Pacific, and there are no pre-Pleistocene specimens of *Uria* and no fossil specimens of *Cepphus* (see Appendix 2.1). However, while there are relatively few alcid fossils from eastern Pacific deposits except those from the mancallines (see above), alcid diversity was high and there are two fossil species of *Uria* and at least one fossil species of *Cepphus*. In what follows, I briefly review the fossil history of the Alcidae in terms of when and where taxa first appeared (Appendix 2.1, Table 2.2), based on Olson (1985a), Chandler (1990a), Warheit (1992), and Olson and Rasmussen (2001). See Gaston and Jones (1998) for a general account of the fossil record of the Alcidae.

Fossils representing the earliest evolution of the Alcidae are either not described in the literature or their relationships are in question. Storrs Olson (personal communication) stated that a fossil of a "primitive auk" might be present in the London Clay material from the lower Eocene of England, which, if shown to be correct, would represent the earliest known alcid taxon. There are two published accounts of pre-Miocene alcids: *Hydrotherikornis oregonus* from the late Eocene of Oregon (Miller 1931) and *Petralca austriaca* (Mlíkovský and Kovar 1987) from the late Oligocene of Austria. It is unclear if *Hydrotherikornis* is an alcid or a procellariid (see Olson 1985a). Chandler (1990b, p. 73) considered *Hydrotherikornis* to be "a petrel very similar to *Daption*" and he provided one skeletal character to justify this relationship. Chandler (1990b) also doubted the alcid affinities of *Petralca* and placed the taxon in Aves, *Incertae Sedis*; however, he did not examine the specimen but considered the taxon's description by Mlíkovský and Kovar (1987) insufficient to justify placement in the Alcidae.

TABLE 2.2
Distribution of Alcidae and Relative Dates of First Appearance in the Fossil Record (see also Appendix 2.1)

Taxon[a]	Recent Distribution[b]		First Appearance Fossil Record		Comments
	Atlantic	Pacific	Atlantic	Pacific	
Alcini	Yes	Yes	middle Miocene	late Miocene	No *Uria* in Atlantic until Pleistocene
Cepphini	Yes	Yes	—	late Miocene	No *Cepphus* in Atlantic until Recent
Brachyramphini	No	Yes	—	late Pliocene	No *Brachyramphus* in Atlantic
Aethiini	No	Yes	early Pliocene	late Miocene	Only fossil Aethiini in Atlantic
Fraterculini	Yes	Yes	early Pliocene	late Miocene	

[a] Alcini (*Alle, Alca, Uria, Pinguinus, Miocepphus*); Cepphini (*Cepphus, Synthliboramphus*); Brachyramphini (*Brachyramphus*); Aethiini (*Ptychoramphus, Cyclorhynchus, Aethia*); Fraterculini (*Cerorhinca, Fratercula*).
[b] Pacific also includes Bering Sea.

Another 25 to 30 and 8 to 12 million years pass following *Hydrotherikornis* and *Petralca*, respectively, before the appearance of the next fossil alcids, which appear nearly simultaneously in both the western Atlantic and the eastern Pacific (Appendix 2.1, Table 2.2). However, like *Hydrotherikornis* and *Petralca*, these species were not of modern affinities and were described in extinct genera (Appendix 2.1). In the eastern Pacific, there are two alcid fossils known from middle Miocene deposits. The first of these fossils was from Baja, California, and was described as an alcid, but with indeterminate affinities. The second specimen was described in the extinct genus *Alcodes*, whose relationships within the Alcidae are uncertain (Olson 1985a, Chandler 1990b), but was tentatively considered by Howard (1968) to be closely related to the mancallids. In the Atlantic, there existed at least two species of alcids, both described in the extinct genus *Miocepphus*. *Miocepphus* was not closely related to *Cepphus*, as originally described by Wetmore (1940), but was part of the *Alca*-like radiation of Atlantic alcids (Howard 1978, Olson 1985a).

Following this initial middle Miocene radiation, alcid diversity dramatically increased in both the Atlantic and Pacific; however, the radiation within each of the ocean basins did not follow parallel paths (Table 2.2). The radiation in the Atlantic centered within the Alcinae, in particular, birds described as *Alca* (including the extinct genus *Australca*, which Olson and Rasmussen [2001] made synonymous with *Alca*). Of the nine alcid taxa from the late Miocene and early Pliocene deposits of the Atlantic, six are described as Alcini (*Alca*, *Pinguinus*, and *Alle*), while four of these six are considered *Alca* (see Appendix 2.1). The only Alcini missing from the Atlantic at this time was *Uria*. Also present in the Atlantic at this time was *Fratercula* (two species described as having affinities to the *F. arctica* and *F. cirrhata*, respectively) and an Aethiinae of indeterminate relations. During this same time, the situation in the Pacific was quite different, where at least 13 alcid species are recognized (Appendix 2.1) including *Aethia* (1 species), *Uria* (2), *Cepphus* (1), and *Cerorhinca* (2), as well as 7 species of mancallids (*Praemancalla*, *Mancalla*, and *Alcodes*). In addition to these taxa, fossils described as *Alca*, *Synthliboramphus*, and Fraterculini are present. Finally, there are late Pliocene alcid-bearing deposits in the Pacific, but not the Atlantic, and from within these deposits six additional alcid species are described, including two species of *Brachyramphus* and one species each of *Ptychoramphus*, *Synthliboramphus*, *Cerorhinca*, and *Mancalla* (see Appendix 2.1).

Olson and Rasmussen (2001) discussed the biogeographical implications of the Miocene and Pliocene Lee Creek deposits of North Carolina and highlighted two important points related to the history of the Alcidae. First, the two species of *Fratercula* (including *F. cirrhata*) and an unidentified species of Aethiinae in the early Pliocene of North Carolina require some explanation, given the fact that there is only one species of *Fratercula* and no species of Aethiinae in the Atlantic today (Table 2.2). Olson and Rasmussen (2001) considered that both taxa moved from the Pacific to the Atlantic, via the Arctic Ocean, sometime right before or during the early Pliocene. Second, given the possibility of a pre-Pleistocene movement of alcid taxa from the Pacific to the Atlantic, Olson and Rasmussen (2001) speculated that the absence of *Uria* and *Cepphus* from the Atlantic until the late Pleistocene and Recent, respectively, was a result of competition with *Alca*. Olson and Rasmussen (2001) reasoned that until appropriate "niches" became available, a product of the Pleistocene extinction of many of the *Alca* species, *Uria,* and *Cepphus* were unable to colonize the Atlantic.

For the remainder of this section I focus on this second point, and detail several important components of the alcid fossil record that contribute to our understanding of the origin of *Uria*. These components focus on the following four points associated with the fossil record: (1) the presence of *Alca* in the Pacific; (2) the presence and close association of *Uria* and *Cepphus* in the Pacific; (3) the abundance and taxonomic diversity of *Alca* in the Atlantic; and (4) the appearance of *Uria* in the Atlantic during the late Pleistocene. After I detail each of these points, I provide a hypothesis for the biogeographic history of *Uria*.

Howard (1968) described a coracoid and a humerus from late Miocene deposits in southern California as *Alca*. This material is fragmentary and Olson (1985a) was cautious in referring these

specimens to a specific genus. Although Howard was reluctant to assign these fragments to a species or base a description of a new species on this material, she was definitive in her assignment of the fossils to *Alca*. If Howard's identification is correct, *Alca* is no longer restricted to the Atlantic, and this Pacific *Alca* is only slightly younger in age than the first *Alca*-like species from the Atlantic (*Miocepphus*) and older than all other species described to the genus *Alca*. Howard also described two species of murres from Tertiary deposits of California. The older of the two species was *U. brodkorbi* from the Miocene diatomite deposits of southern California and was described by Howard (1981) as a murre comparable in size to the Recent *Uria*. *Uria paleohesperis*, the second *Uria* species described by Howard (1982), was from the late Miocene San Mateo Formation of San Diego County and was younger in age and smaller than *U. brodkorbi*.

The fossil record of *Cepphus* follows closely that of *Uria*. While there are no *Cepphus* fossils from the Atlantic, Howard (1968, 1978) tentatively assigned fossil material from the Miocene of California to this genus. This material is roughly the same age as *U. brodkorbi* and suggests the origin of both taxa may be contemporaneous. In addition, *C. olsoni*, again described by Howard (1982), is from the same fossil locality as *U. paleohesperis*, further emphasizing the temporal and geographic similarity between murres and guillemots.

The most abundant alcid taxon from the Atlantic is *Alca*, in terms of both taxonomic diversity and numbers of specimens recovered. Thousands of *Alca* fossils have been recovered from the early Pliocene Lee Creek deposits of North Carolina (Olson and Rasmussen 2001), from which at least four species, including *A. torda*, are described (see Appendix 2.1). The first and only Atlantic appearance of a fossil correctly identified to *Uria* is *U. affinis*, a single humerus from the Pleistocene of Maine (12,000 years ago), which Olson (1985a) stated is likely referable to one of the extant species. It is clear from the fossil record from the western Atlantic that the Alcini underwent an extraordinary radiation, compared with that of the Pacific, and that this radiation began at essentially the same time as the Pacific radiation of the other alcid clades (Appendix 2.1).

The geographic distribution of fossil *Uria* is enigmatic given *Uria*'s relationships within the Alcini and its current distribution (north Atlantic, north Pacific, and Arctic Oceans; Gaston and Jones 1998). This fossil history has also led to several hypotheses for the evolution of *Uria* (e.g., Olson 1985a, Gaston and Jones 1998, Olson and Rasmussen 2001). These hypotheses generally concern (1) the relationships of *Uria* with the other Alcini, in particular, *Alca*; (2) the ocean of origin of the Alcini and *Uria*; (3) the historical interchange between the Atlantic and Pacific via the Arctic Ocean from the Miocene through the Pleistocene; and (4) the extinction and the loss of diversity of Alcini in the Atlantic. If *Uria* is indeed closely related to *Alca*, as both the morphological (Strauch 1985 and Chandler 1990b) and molecular (Moum 1994, Friesen et al. 1993, 1996) evidence conclusively indicate, and Howard (1968) was correct in identifying *Alca* fossils from the Pacific, the following scenario is most plausible: the Alcini evolved in the Pacific, and quickly moved into the Atlantic where it greatly diversified. In the Pacific, the diversification of Alcini was minimal and centered primarily on the genus *Uria*. *Uria* evolved in the Pacific (or the Arctic) Ocean and moved into the Atlantic sometime between the early Pliocene and the Pleistocene. Alternatively, *Uria* moved into the Atlantic at an earlier date, but remained in northerly latitudes, similar to the distribution of *U. lomvia* today, and therefore would not have occurred in the highly fossiliferous deposits of Lee Creek, North Carolina. I refer the reader to Gaston and Jones (1998) and Olson and Rasmussen (2001) for further discussion of this topic.

2.4 CONCLUSIONS

This has been a brief summary of fossil seabirds and an argument for the importance of fossils in the study of seabird ecology and evolution. Fossils are not simply a collection of bones. People who study fossils are concerned not only with naming and cataloging species. Fossils provide definite information on the history of a taxon or ecological community and, as such, are essential

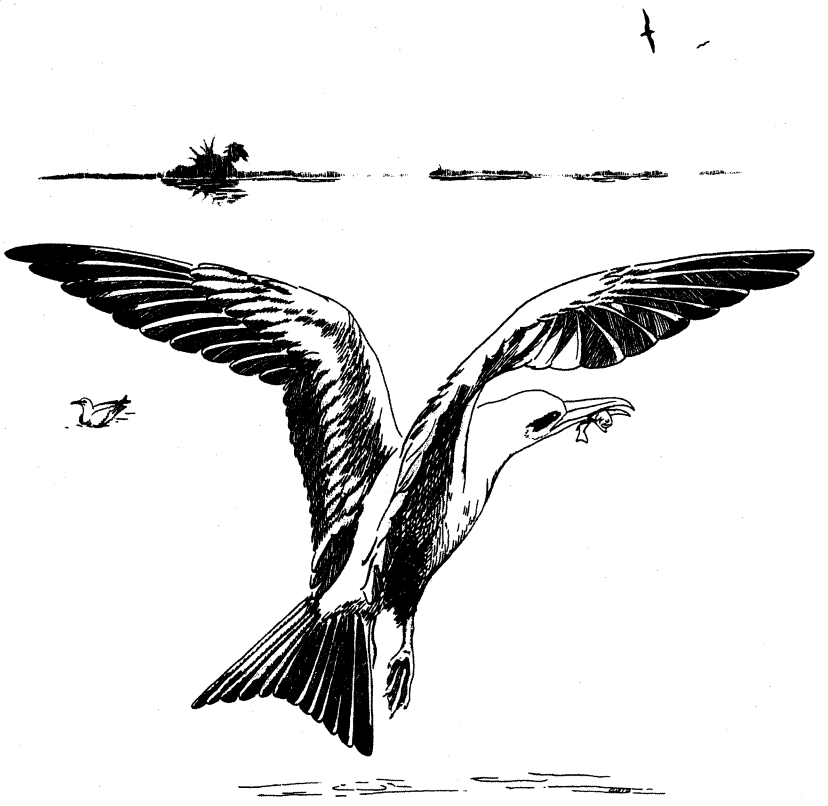

FIGURE 2.3 This reconstruction of an early Eocene frigatebird (*Limnofregata azgosternon*) shows similarities to the tropicbirds which extend to its skeleton. For instance, both have coracoids of the same proportions and a four-notched sternum. (After Olson 1977.)

in our understanding of that taxon or community (Figure 2.3). I have shown that seabird communities in the California and Benguela Currents today are composed of different sets of species from those that existed in the past — related to a combination of geological (e.g., plate tectonics) and ecological (e.g., competition for space with gregarious marine mammals) processes. Therefore, the community structure of the systems today reflects these past processes and these past processes must be considered when evaluating hypotheses concerning this structure. Furthermore, past processes may also be useful in predicting changes in community structure resulting from future short- or long-term events such as habitat alteration and global climate change. Finally, it is quite apparent that we need to consider the fossil history of Pacific islands. Clearly, the seabird composition on these islands scarcely resembles that which existed prior to the expansion of Polynesian populations, and as stated by Olson, Steadman, James, and others, it would be folly to attempt to explain the relative diversity of seabirds there without considering the fossil record.

The fossil record also provides information on the presence and distribution of a particular taxon from times inaccessible to ecological study. We know from the fossil record of the Alcidae that the current distribution of alcid taxa, with *Alca* and *Alca*-like species in the Atlantic and most of the other alcid clades in the Pacific, has existed for many millions of years. Nevertheless, the presence of fossil *Alca* in the Pacific and the absence of fossil *Uria* and *Cepphus* from the Atlantic, for example, deviate from the current distributional patterns and provide important data in our understanding of the evolution of the Alcidae.

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APPENDIX 2.1

List of fossil seabirds

See text and notes at bottom of table for details. [a, d, e]

Genus or higher taxon [b, c]	Species	Cretaceous	Paleocene	Eocene			Oligocene		Miocene			Pliocene		Pleistocene			Holocene	Geographic Region [f]	Specific Locality [f]	Comment [h]	Citation [g]
		latest	late	early	middle	late	early	late	early	middle	late	early	late	early	middle	late					
Charadriiformes																					
Haematopododae																					
Haematopus	*sulcatus*																	w. Atlantic	Florida	1	Olson & Steadman 1979
Haematopus	aff. *palliatus*																	w. Atlantic	N. Carolina		Olson & Rasmussen 2001
Haematopus	aff. *ostralegus*																	w. Atlantic	N. Carolina		Olson & Rasmussen 2001
Stercorariidae																					
Stercorarius	sp. small																	w. Atlantic	Maryland		Olson 1985a
Stercorarius	sp. big																	w. Atlantic	Maryland		Olson 1985a
Catharacta	sp.																	w. Atlantic	N. Carolina		Olson &Rasmussen 2001
Stercorarius	aff. *pomarinus*																	w. Atlantic	N. Carolina		Olson & Rasmussen 2001
Stercorarius	aff. *parasiticus*																	w. Atlantic	N. Carolina		Olson &Rasmussen 2001
Stercorarius	aff. *longicaudus*																	w. Atlantic	N. Carolina		Olson &Rasmussen 2001
Stercorarius	sp.																	w. Atlantic	Florida		Emslie 1995
Stercorarius	*shufeldti*																	e. N. Pacific	Oregon		Howard 1946
Laridae																					
genus indeterminate	sp.																	Paratethys	France		Mourer-Chauviré 1982
Gaviota	*lipsiensis*																	int. Europe	Germany	2	Bochenski 1997
Rupelornis	*definitus*																	e. N. Atlantic	Belgium	3	Olson 1985a
Larus	*pristinus*																	e. N. Pacific	Oregon	4	Olson 1985a
genus indeterminate	sp.																	w. Atlantic	Delaware	5	Rasmussen 1998
Larus	*dolnicensis*																	int. Europe	Bohemia	6	Olson 1985a

APPENDIX 2.1 *(Continued)*

List of fossil seabirds

See text and notes at bottom of table for details. [a, d, e]

Genus or higher taxon [b, c]	Species	Cretaceous	Paleocene	Eocene			Oligocene		Miocene			Pliocene		Pleistocene			Holocene	Geographic Region [f]	Specific Locality [f]	Comment [h]	Citation [g]
		latest	late	early	middle	late	early	late	early	middle	late	early	late	early	middle	late					
Larus	*desnoyersii*								■									Paratethys	France	7	Olson 1985a
Larus	*elegans*								■									Paratethys	France	8	Olson 1985a
Larus	*totanoides*								■									Paratethys	France	8	Olson 1985a
Gaviota	*niobrara*										■							int. N. America	Nebraska		Miller&Sibley 1941
cf. *Larus*	sp.										■							int. N. America	Arizona		Bickart 1990
Larus	sp.										■							Paratethys	Romania		Grigorescu &Kessler 1977
Larus	*elmorei*											■						w. Atlantic	Florida		Olson 1985a
Larus	aff. *argentatus*											■						w. Atlantic	N. Carolina		Olson & Rasmussen 2001
Larus	aff. *delawarensis*											■						w. Atlantic	N. Carolina	9	Olson & Rasmussen 2001
Larus	aff. *atricilla*											■						w. Atlantic	N. Carolina		Olson & Rasmussen 2001
Larus	magn. *ribidundus*											■						w. Atlantic	N. Carolina	10	Olson & Rasmussen 2001
Larus	aff. *minutus*											■						w. Atlantic	N. Carolina		Olson & Rasmussen 2001
Larus	sp.											■						w. Atlantic	N. Carolina		Olson & Rasmussen 2001
cf. *Sterna*	aff. *maxima*											■						w. Atlantic	N. Carolina		Olson & Rasmussen 2001
Sterna	aff. *nilotica*											■						w. Atlantic	N. Carolina		Olson & Rasmussen 2001
Larus	sp.												■					e. N. Pacific	Calif.		Chandler 1990a
Rissa	*estesi*												■					e. N. Pacific	Calif.		Chandler 1990a
Sterna	sp.												■					e. N. Pacific	Calif.		Chandler 1990a
Larus	*perpetuus*												■					w. Atlantic	N. Carolina		Emslie 1995
Larus	*lacus*												■					w. Atlantic	Florida		Emslie 1995
Larus	*robustus*														■	■		e. N. Pacific	Oregon		Brodkorb 1967
Larus	*oregonus*														■	■		e. N. Pacific	Oregon		Brodkorb 1967
Pseudosterna	*degener*															■		w. S. Atlantic	Argentina	11	Olson 1985a
Pseudosterna	*pampeana*															■		w. S. Atlantic	Argentina	11	Olson 1985a

APPENDIX 2.1 *(Continued)*

List of fossil seabirds

See text and notes at bottom of table for details. [a, d, e]

Genus or higher taxon [b, c]	Species	Cretaceous	Paleocene	Eocene			Oligocene		Miocene			Pliocene		Pleistocene			Holocene	Geographic Region [f]	Specific Locality [f]	Comment [h]	Citation [g]
		latest	late	early	middle	late	early	late	early	middle	late	early	late	early	middle	late					
Alcidae																					
Hydrotherikornis	*oregonus*				■													e. N. Pacific	Oregon	12	Olson 1985a
Petralca	*austriaca*							■										Paratethys	Austria		Mlíkovsk& Kovar 1987
genus indeterminate	sp.									■								e. Pacific	Baja Calif.		Demeré et al. 1984
Alcodes	aff. *A. ulnulus*									■								e. N. Pacific	Calif.		Howard & Barnes 1987
Miocepphus	*mcclungi*									■								w. Atlantic	Maryland	13	Olson 1985a
Miocepphus	new sp.									■								w. Atlantic	Maryland		Olson 1984a
Aethia	*rossmoori*										■							e. N. Pacific	Calif.		Howard 1968
Alca	sp.										■							e. N. Pacific	Calif.		Howard 1968
Alcodes	*ulnulus*										■							e. N. Pac ific	Calif.		Warheit 1992
Cepphus (?)	sp.										■							e. N. Pacific	Calif.		Warheit 1992
Cerorhinca	*dubia*										■							e. N. Pacific	Calif.		Warheit 1992
Fraterculini	sp.										■							e. N. Pacific	Calif.		Howard 1978
Praemancalla	*lagunensis*										■							e. N. Pacific	Calif.		Howard 1966
Praemancalla	*wetmorei*										■							e. N. Pacific	Calif.		Warheit 1992
Uria	*brodkorbi*										■							e. N. Pacific	Calif.		Howard 1981
Uria (?)	sp.										■							e. N. Pacific	Calif.		Howard 1978
Aethia (?)	sp.										■	■						e. N. Pacific	Calif.		Warheit 1992
Cepphus	*olsoni*										■	■						e. N. Pacific	Calif.		Warheit 1992
Mancalla	*californicus*										■	■						e. N. Pacific	Calif.		Warheit 1992
Mancalla	cf. *cedrocensis*										■	■						e. N. Pacific	Calif.		Warheit 1992
Praemancalla	cf. *wetmorei*										■	■						e. N. Pacific	Calif.		Warheit 1992
Uria	*paleohesperis*										■	■						e. N. Pacific	Calif.		Warheit 1992
Cerorhinca	*minor*										■	■						e. Pacific	Mexico		Howard 1971
Mancalla	*cedrocensis*										■	■						e. Pacific	Mexico		Warheit 1992
Synthliboramphus	sp.										■	■						e. Pacific	Mexico	14	Howard 1971

APPENDIX 2.1 *(Continued)*

List of fossil seabirds

See text and notes at bottom of table for details. [a, d, e]

Genus or higher taxon [b, c]	Species	Cretaceous: latest	Cretaceous: late	Paleocene: early	Paleocene: middle	Paleocene: late	Eocene: early	Eocene: late	Oligocene: early	Oligocene: late	Miocene: early	Miocene: middle	Miocene: late	Pliocene: early	Pliocene: late	Pleistocene: early	Pleistocene: middle	Pleistocene: late	Holocene	Geographic Region [f]	Specific Locality [f]	Comment [h]	Citation [g]
Mancalla	*diegensis*													■	■				■	e. N. Pacific	Calif.		Warheit 1992
Mancalla	*milleri*													■	■				■	e. N. Pacific	Calif.		Warheit 1992
Alca	*ausonia*													▒	▒					Paratethys & w. Atl.	Italy, N. Carolina	1, 15	Olson & Rasmussen 2001
Aethiinae	sp.													■						w. Atlantic	N. Carolina	16	Olson & Rasmussen 2001
Alca	*antiqua*													■						w. Atlantic	N. Carolina	17	Olson & Rasmussen 2001
Alca	aff. *torda*													■						w. Atlantic	N. Carolina		Olson & Rasmussen 2001
Alca	new sp.													■						w. Atlantic	N. Carolina	18	Olson & Rasmussen 2001
Alle	aff. *alle*													■						w. Atlantic	N. Carolina		Olson & Rasmussen 2001
Fratercula	aff. *arctica*													■						w. Atlantic	N. Carolina		Olson & Rasmussen 2001
Fratercula	aff. *cirrhata*													■						w. Atlantic	N. Carolina		Olson & Rasmussen 2001
Pinguinus	*alfrednewtoni*													■						w. Atlantic	N. Carolina		Olson & Rasmussen 2001
Brachyramphus	*dunkeli*														■					e. N. Pacific	Calif.		Chandler 1990a
Brachyramphus	*pliocenus*														■					e. N. Pacific	Calif.		Warheit 1992
Cerorhinca	*reai*														■					e. N. Pacific	Calif.		Chandler 1990a
Cerorhinca	sp.														■					e. N. Pacific	Calif.		Chandler 1990a
Mancalla	*emlongi*														■					e. N. Pacific	Calif.		Warheit 1992
Ptychoramphus	*tenuis*														■					e. N. Pacific	Calif.		Warheit 1992
Synthliboramphus	*rineyi*														■					e. N. Pacific	Calif.		Chandler 1990a
genus indeterminate	sp.														■					e. N. Pacific	Calif.		Chandler 1990a
Pinguinus	*impennis*															▒	▒	▒	■	e. N. Atlantic	Europe	19	Bochenski 1997
Uria	*affinis*																		■	w. N. Atlantic	Maine	20	Olson & Rasmussen 2001
Pelecaniformes																							
incertae sedis																							
Eostega	*lebedinskyi*				■															Paratethys	Romania	21	Olson 1985a

APPENDIX 2.1 *(Continued)*

List of fossil seabirds

See text and notes at bottom of table for details. [a, d, e]

Genus or higher taxon [b, c]	Species	Cretaceous	Paleocene	Eocene			Oligocene		Miocene			Pliocene		Pleistocene			Holocene	Geographic Region [f]	Specific Locality [f]	Comment [h]	Citation [g]
		latest	late	early	middle	late	early	late	early	middle	late	early	late	early	middle	late					
Liptornis	*hesternus*									■								w. S. Atlantic	Argentina	22	Olson 1985a
Protopelicanus	*cuvierii*												■					e. N. Atlantic	France	23	Olson 1985a
Phaethontes																					
Prophaethon	*shrubsolei*			■														e. N. Atlantic	England	24	Harrison & Walker 1976
Heliadornis	*ashbyi*									■								Atlantic	Maryland, Belgium		Olson 1985d
Heliadornis	*paratethydicus*										■							Paratethys	Austria		Mlíkovsk 1997
Fregatidae																					
Limnofregata	*azygosternon*			■														int. N. America	Wyoming		Olson 1977
Pelecanidae																					
Miopelecanus	*gracilis*								■									Paratethys	France	25	Cheneval 1984
Miopelecanus	*intermedius*									■								int. Europe	Germany	26	Cheneval 1984
Pelcanus	*fraasi*									■								int. Europe	Germany		Olson 1985a
Pelcanus	*schreiberi*											■						w. Atlantic	N. Carolina		Olson 1999
Pelcanus	*odessanus*											■						Paratethys	Ukraine		Olson 1985a
Pelcanus	*cautleyi*											■						India	India		Olson 1985a
Pelcanus	*sivalensis*											■						India	India	27	Olson 1985a
Pelcanus	*halieus*												■					int. N. America	Idaho		Olson 1985a
Pelcanus	*erthrorhynchos*											■	■					e. N. Pacific	Oregon	1	Becker 1987
Pelcanus	*grandicep s*															■		w. S. Pacific	Australia		Brodkorb 1963
Pelcanus	*proavus*															■		w. S. Pacific	Australia		Brodkorb 1963
Pelcanus	*tirarensis*								■	■	■							w. S. Pacific	Australia	28	Miller 1966
Pelcanus	*cadimurka*																■	w. S. Pacific	Australia		Rich & Van Tetes 1981
Pelcanus	*novaezealandiae*																■	w. S. Pacific	Australia	29	Rich & Van Tetes 1981

APPENDIX 2.1 *(Continued)*

List of fossil seabirds

See text and notes at bottom of table for details. [a, d, e]

Genus or higher taxon [b, c]	Species	Cretaceous	Paleocene	Eocene			Oligocene		Miocene			Pliocene		Pleistocene			Holocene	Geographic Region [f]	Specific Locality [f]	Comment [h]	Citation [g]
		latest	late	early	middle	late	early	late	early	middle	late	early	late	early	middle	late					
Pelagornithidae																					
Pseudodontornis	*tenuirostris*		■															e. N. Atlantic	England	30, 35	Harrison 1985
Odontopteryx	*toliapica*			■														e. N. Atlantic	England		Harrison & Walker 1976
Macrodontopteryx	*oweni*			■														e. N. Atlantic	England	31	Harrison & Walker 1976
Dasornis	*londinensis*			■														e. N. Atlantic	England	32, 33	Harrison & Walker 1976
Argillornis	*emuinus*			■														e. N. Atlantic	England	32-34	Harrison & Walker 1976
Argillornis	*longipennis*			■														e. N. Atlantic	England	32-34	Harrison & Walker 1976
Pseudodontornis	*longidentata*			■														e. N. Atlantic	England	35	Harrison & Walker 1976
Argillornis (?)	sp.				■													e. N. Pacific	Washington		Goedert 1989
genus indeterminate	sp.				■													e. N. Pacific	Washington		Goedert 1989
Gigantornis	*eaglesomei*				■													e. Atlantic	Nigeria		Olson 1985a
Pelagornithidae	sp.					■												Antarctic Peninsula	Seymour I.		Olson 1985a
Osteodontornis	*orri*						■		■	■	■							e. N. Pacific	Calif.		Olson 1985a, Warheit 1992
Palaeochenoides	*mioceanus*						■		■									w. Atlantic	S. Carolina		Olson 1985a
Pelagornithidae	sp. small						■											w. Atlantic	S. Carolina	36	Warheit & Olson, unpub. data
Pelagornithidae	sp. medium						■											w. Atlantic	S. Carolina	36	Warheit & Olson, unpub. data
Pelagornithidae	sp. large						■											w. Atlantic	S. Carolina	36	Warheit & Olson, unpub. data
Tympanonesiotes	*wetmorei*						▒			▒								w. Atlantic	S. Carolina	37	Olson 1985a
Cyphornis	*magnus*							■										e. N. Pacific	British Columbia		Olson 1985a
genus indeterminate	sp.							■										w. Atlantic	Delaware		Rasmussen 1998
genus indeterminate	sp.							■										w. N. Pacific	Japan		Okazaki 1989
Osteodontornis	sp.							■										w. N. Pacific	Japan	38	Matsuoka et al. 1998
Pseudodontornis	*stirtoni*							▒				▒						w. S. Pacific	New Zealand	39	Howard & Warter 1969
Pelagornithidae	sp. A								■									w. Atlantic	Maryland	40	Warheit & Olson, unpub. data
Pelagornithidae	sp. B								■									w. Atlantic	Maryland	40	Warheit & Olson, unpub. data

APPENDIX 2.1 *(Continued)*

List of fossil seabirds

See text and notes at bottom of table for details. [a, d, e]

Genus or higher taxon [b, c]	Species	Cretaceous	Paleocene	Eocene			Oligocen		Miocene			Pliocene		Pleistocene			Holocene	Geographic Region [f]	Specific Locality [f]	Comment [h]	Citation [g]
		latest	late	early	middle	late	early	late	early	middle	late	early	late	early	middle	late					
Pelagornis	*miocaeni s*									■								e. N. Atlantic	France		Olson 1985a
Osteodontornis	sp.									■								w. N. Pacific	Japan		Ono & Sakamoto 1991
Osteodontornis	sp.									■								w. N. Pacific	Japan		Ono 1989
Pelagornithidae	sp.										■	■						w. N. Pacific	Japan		Okazaki 1989
Pelagornithidae	sp.										■							w. S. Pacific	New Zealand		Scarlett 1972
Pelagornis	sp. 1											■						w. Atlantic	N. Carolina	41	Olson & Rasmussen 2001
Pelagornis	sp. 2											■						w. Atlantic	N. Carolina	41	Olson & Rasmussen 2001
Pelagornis	sp.											■						e. S. Pacific	Peru		Cheneval 1993
Caspiodontornis	*kobystanicus*						■	■										Paratethys	Caucasus	42	Olson 1985a
Pelagornithidae	sp.											■	■					w. S. Pacific	New Zealand	1	McKee1985
Pseudodontornis	*longirostris*								■	■	■							unknown	unknown	43	Harrison & Walker 1976
Sulidae																					
Sula	*ronzoni*					■												Paratethys	France		Olson 1985a
genus indeterminate	sp. 1							■										w. Atlantic	S. Carolina	44	Warheit & Olson, unpub. data
genus indeterminate	sp. 2							■										w. Atlantic	S. Carolina	44	Warheit & Olson, unpub. data
Empheresula	*arvernensis*							■										Paratethys	France	45	Olson 1985a
Sula	*universitatis*								■									w. Atlantic	Florida	46	Brodkorb 1963
Morus	*loxostylus*								■	■								w. Atlantic	Maryland	47	Olson & Rasmussen 2001
Morus	*vagabundus*									■								e. N. Pacific	Calif.		Warheit 1992
Morus	sp. A									■								e. N. Pacific	Calif.	48	Warheit, unpub. data
Morus	sp. B									■								e. N. Pacific	Calif.	49	Warheit, unpub. data
Morus	*avitus*									■								w. Atlantic	Maryland	50	Olson & Rasmussen 2001
Morus	*atlanticus*									■								w. Atlantic	N. Carolina	51	Olson & Rasmussen 2001
Sula	sp.									■								w. Atlantic	Maryland	52	Warheit & Olson, unpub. data
Morus	*pygmaea*									■								e. N. Atlantic	France	53	Olson 1985a

APPENDIX 2.1 *(Continued)*

List of fossil seabirds

See text and notes at bottom of table for details. [a, d, e]

Genus or higher taxon [b, c]	Species	Cretaceous	Paleocene	Eocene			Oligocene		Miocene			Pliocene		Pleistocene			Holocene	Geographic Region [f]	Specific Locality [f]	Comment [h]	Citation [g]
		latest	late	early	middle	late	early	late	early	middle	late	early	late	early	middle	late					
Morus	*olsoni*									■								Paratethys	Romania		Grigorescu & Kessler 1988
Sarmatosula	*dobrogensis*									■								Paratethys	Romania		Grigorescu & Kessler 1977
Sula	sp.									■								w. N. Pacific	Japan	54	Ono 1983
Sula	sp.									■								w. N. Pacific	Japan	55	Ono & Sakamoto 1991
Morus	*willetti*									■	■							e. N. Pacific	Calif.	56	Warheit 1992
Sula	*pohli*									■	■							e. N. Pacific	Calif.	57	Warheit 1992
Morus	*stocktoni*										■							e. N. Pacific	Calif.	58	Warheit 1992
Morus	*lompocanus*										■							e. N. Pacific	Calif.		Warheit 1992
Morus	*magnus*										■							e. N. Pacific	Calif.		Warheit 1992
Morus	*media*										■							e. N. Pacific	Calif.	59	Warheit 1992
Morus	sp.										■	■						e. Pacific	Mexico		Howard 1971
Sula	*guano*										■	■						w. Atlantic	Florida	60	Brodkorb 1955
Sula	*phosphata*										■	■						w. Atlantic	Florida	60	Brodkorb 1955
Sula	new sp.										■	■						w. Atlantic	Florida	61	Warheit & Becker, unpub. ms
Morus	*peninsularis*											■						w. Atlantic	Florida		Olson & Rasmussen 2001
Morus	new sp. 1											■						w. Atlantic	N. Carolina		Olson & Rasmussen 2001
Morus	new sp. 2											■						w. Atlantic	N. Carolina		Olson & Rasmussen 2001
Sula	new sp. A											■						e. S. Pacific	Peru	62	Cheneval 1993
Sula	new sp. B											■						e. S. Pacific	Peru	62	Cheneval 1993
Sula	new sp. C											■						e. S. Pacific	Peru	62	Cheneval 1993
Sula	sp.											■						e. S. Atlantic	S. Africa		Olson 1985c
Morus	*humeralis*												■					e. N. Pacific	Calif.	63	Chandler 1990a
Morus	*recentior*												■					e. N. Pacific	Calif.	64	Chandler 1990a
Sula	*clarki*												■					e. N. Pacific	Calif.		Chandler 1990a
Sula	sp.												■					e. N. Pacific	Calif.		Chandler 1990a
Morus	*reyanus*															■		e. N. Pacific	Calif.		Brodkorb 1963

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See text and notes at bottom of table for details. [a, d, e]

Genus or higher taxon [b, c]	Species	Cretaceous		Paleocene	Eocene			Oligocene		Miocene			Pliocene		Pleistocene			Holocene	Geographic Region [f]	Specific Locality [f]	Comment [h]	Citation [g]
		latest	late	early	middle	late	early	late	early	middle	late	early	late	early	middle	late						
Sula	*tasmani*																	■	w. S. Pacific	Norfolk I.	65	van Tets et al. 1988
Phalacrocoracidae																						
genus indeterminate	sp.					■	■												Paratethys	France		Mourer-Chauviré 1982
genus indeterminate	sp.						■												Paratethys	Egypt		Rasmussen et al. 1987
Phalacrocorax	*marinavis*								■										e. N. Pacific	Oregon		Shufeldt 1915
Phalacrocorax	*littoralis*								■										Paratethys, int. Eur.	France		Brodkorb 1963
Nectornis	*miocaenus*								■										Paratethys	France	66	Cheneval 1984
Phalacrocorax	*anatolicus*								■										Paratethys	Turkey		Olson 1985a
Phalacrocorax	*lept opus*									■	■								e. N. Pacific	Oregon		Brodkorb 1963
Phalacrocorax	*femoralis*										■								e. N. Pacific	Calif.		Miller 1929
Phalacrocorax	*wetmorei*										■	■							w. Atlantic	Florida		Olson & Rasmussen 2001
Phalacrocorax	*idahensis*										■								N. America	Florida, Idaho		Brodkorb 1963
Phalacrocorax	*brunhuberi*										■								int. Europe	Bavaria	67	Olson 1985a
Phalacrocorax	*intermedius*										■								e. N. Atlantic	France		Brodkorb 1963
Phalacrocorax	*ibericum*										■								e. Atlantic	Spain		Olson 1985a
Phalacrocorax	*lautus*										■								Paratethys	Moldavia		Olson 1985a
Phalacrocorax	*serdicensis*										■								Paratethys	Bulgaria		Bochenski 1997
Phalacrocorax	*goletensis*											■							e. Pacific	Mexico		Howard 1965
Phalacrocorax	sp. large											■							w. Atlantic	N. Carolina	68	Olson & Rasmussen 2001
Pliocarbo	*longipes*											■							Paratethys	Ukraine	69	Olson 1985a
Phalacrocorax	sp.											■							e. S. Pacific	Peru		Cheneval 1993
Phalacrocorax	sp. medium											■							e. S. Atlantic	S. Africa		Olson 1985c
Phala. cf. (*Microcarbo*)	sp.											■							e. S. Atlantic	S. Africa	70	Olson 1985c
Phalacrocorax	*macer*												■						int. N. America	Idaho		Brodkorb 1963
Phalacrocorax	*kennelli*												■						e. N. Pacific	Calif.		Warheit 1992

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Genus or higher taxon [b, c]	Species	Cretaceous	Paleocene	Eocene			Oligocene		Miocene			Pliocene		Pleistocene			Holocene	Geographic Region [f]	Specific Locality [f]	Comment [h]	Citation [g]
		latest	late	early	middle	late	early	late	early	middle	late	early	late	early	middle	late					
Stictocarbo	*kumeyaay*												■					e. N. Pacific	Calif.		Chandler 1990a
genus indeterminate	spp.												■					e. N. Pacific	Calif.	71	Chandler 1990a
Phalacrocorax	sp.												■					w. Atlantic	Florida		Emslie 1992
Phalacrocorax	*filyawi*												■					w. Atlantic	Florida		Emslie 1995
Phalacrocorax	*rogersi*													■				e. N. Pacific	Calif.		Brodkorb 1963
Phalacrocorax	*macropus*														■	■		e. N. Pacific	Oregon		Brodkorb 1963
Phalacrocorax	*pampeanus*															■		w. S. Atlantic	Argentina		Brodkorb 1963
Phalacrocorax	*gregorii*															■		w. S. Pacific	Australia		Brodkorb 1963
Phalacrocorax	*vetustus*															■		w. S. Pacific	Australia		Brodkorb 1963
Phalacrocorax	*auritus*											■	■					N. America	Florida, Idaho	1	Becker 1987
Phalacrocorax	*destefani*											■	■					Paratethys	Italy	1	Brodkorb 1963
Phalacrocorax	*mongoliensis*											■	■					int. Asia	Mongolia	1	Olson 1985a
Phalacrocorax	*reliquus*											■	■					int. Asia	Mongolia	1	Olson 1985a
Phalacrocorax	*chapalensis*											■	■	■	■	■		e. Pacific	Mexico	72	Alvarez 1977
Plotopteridae																					
Phocavis	*maritimus*				■													e. N. Pacific	Washington		Goedert 1988
genus indeterminate	spp.					■	■											w. N. Pacific	Japan	73	Olson & Hasegawa 1996
Plotopterium	*joaquinensis*							■	■									e. N. Pacific	Calif.		Howard 1969
Tonsala	*hildegardae*							■										e. N. Pacific	Washington		Olson 1980
Copepteryx	*hexeris*							■										w. N. Pacific	Japan		Olson & Hasegawa 1996
Copepteryx	*titan*							■										w. N. Pacific	Japan	74	Olson & Hasegawa 1996
genus indeterminate	spp.							■										w. N. Pacific	Japan	75	Olson & Hasegawa 1996
genus indeterminate	sp.							■										w. N. Pacific	Japan	76	Kimura & Sakural 1998
Plotopterium	sp.								■									w. N. Pacific	Japan		Olson & Hasegawa 1985

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Genus or higher taxon [b, c]	Species	Cretaceous		Paleocene	Eocene			Oligocene		Miocene			Pliocene		Pleistocene			Holocene	Geographic Region [f]	Specific Locality [f]	Comment [h]	Citation [g]
		latest	late		early	middle	late	early	late	early	middle	late	early	late	early	middle	late					
Procellariiformes																						
incertae sedis																						
Tythostonyx	*glauconiticus*	■																	w. Atlantic	New Jersey	77	Olson & Parris 1987
Marinavis	*longirostris*			■															e. N. Atlantic	England	78	Harrison & Walker 1977
Diomedeoididae																						
Diomedeoides	*minimus*							■	■										int. Europe	Germany	42	Bochenski 1997
Diomedeidae																						
Plotornis (?)	sp.							■											w. Atlantic	S. Carolina		Olson 1985a
Plotornis	*arvernensis*								■										Paratethys	France	79	Cheneval 1984
Diomedea	*californica*									■	■								e. N. Pacific	Calif.		Warheit 1992
Diomedea	*milleri*									■									e. N. Pacific	Calif.		Warheit 1992
Plotornis	*delfortrii*									■									e. N. Atlantic	France	80	Olson 1985a
Diomedea	*rumana*									■									Paratethys	Romania		Grigorescu & Kessler 1988
Diomedea	sp.										■								e. N. Pacific	Calif.		Warheit 1992
Diomedea	sp.										■	■							e. N. Pacific	Calif.		Warheit 1992
Diomedia	*thyridata*										■								w. S. Pacific	Australia		Wilkinson 1969
Diomedia	sp.										■								w. S. Atlantic	Argentina		Olson 1984b
Phoebastria	aff. *albatrus*											■	■						w. Atl. & e. Pacific	N. Carolina, Calif.	81	Olson & Rasmussen 2001
Phoebastria	aff. *nigripes*											■							w. Atlantic	N. Carolina		Olson & Rasmussen 2001
Phoebastria	aff. *immutabilis*											■							w. Atlantic	N. Carolina		Olson & Rasmussen 2001
Phoebastria	*rexsularum*											■							w. Atlantic	N. Carolina	82	Olson & Rasmussen 2001
Phoebastria	*anglica*											■	■						Atl. & e. N. Pacific	Calif., N. Carol., Engl.	83	Olson & Rasmussen 2001
Diomedea	sp.											■							e. S. Atlantic	S. Africa		Olson 1985b

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Genus or higher taxon [b, c]	Species	Cretaceous	Paleocene	Eocene			Oligocene		Miocene			Pliocene		Pleistocene			Holocene	Geographic Region [f]	Specific Locality [f]	Comment [h]	Citation [g]
		latest	late	early	middle	late	early	late	early	middle	late	early	late	early	middle	late					
Diomedea	sp. B												■					e. N. Pacific	Calif.		Chandler 1990a
Procellariidae																					
Neptuniavis	*minor*			■														e. N. Atlantic	England	84	Harrison & Walker 1977
Neptuniavis	*miranda*			■														e. N. Atlantic	England	84	Harrison & Walker 1977
genus indeterminate	sp.					■												w. Atlantic	Louisiana	85	Feduccia & McPherson 1993
Puffinus	*raemdonckii*						■											e. N. Atlantic	Belgium		Olson 1985a
Frigidafons	*brodkorbi*						■											int. Europe	Germany		Cheneval 1995
Frigidafons	*babaheydariensis*						■	■										Paratethys	Iran	85a	Peters & Hamedani 2000
genus indeterminate	sp. 1							■										w. Atlantic	S. Carolina		Olson 1985a
genus indeterminate	sp. 2							■										w. Atlantic	S. Carolina	86	Olson 1985a
Argyrodyptes	*microtarsus*							■	■									w. S. Atlantic	Argentina	87	Olson 1985a
Puffinus	*micraulax*								■									w. Atlantic	Florida		Olson 1985a
Fulmarus	*miocaenus*								■	■								e. N. Pacific	Calif.		Howard 1984
Puffinus	*inceptor*								■	■								e. N. Pacific	Calif.		Warheit 1992
Puffinus	*mitchelli*								■	■								e. N. Pacific	Calif.		Warheit 1992
Puffinus	*priscus*								■	■	■							e. N. Pacific	Calif.		Warheit 1992
Puffinus	sp.								■	■								e. N. Pacific	Calif.		Warheit 1992
Puffinus	*conradi*								■	■								w. Atlantic	Maryland		Olson 1985a
Puffinus	spp.								■	■	■	■						Atlantic	Maryland & S. Africa	88	Olson 1985a
Puffinus	*aquitanicus*								■	■								e. N. Atlantic	France		Brodkorb 1963
Puffinus	*antiquus*								■	■								e. N. Atlantic	France		Brodkorb 1963
Bulweria?	sp.								■	■		■						w. Atlantic	N. Carolina	89	Olson & Rasmussen 2001
Puffinus(*Thyellodroma*)	sp.								■	■		■						w. Atlantic	N. Carolina	89	Olson & Rasmussen 2001
Puffinus(*Ardenna*)	sp.								■	■		■						w. Atlantic	N. Carolina	89	Olson & Rasmussen 2001
Puffinus	aff. *gravis*								■	■		■						w. Atlantic	N. Carolina	89	Olson & Rasmussen 2001

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Genus or higher taxon [b, c]	Species	Cretaceous	Paleocene	Eocene			Oligocene		Miocene			Pliocene		Pleistocene			Holocene	Geographic Region [f]	Specific Locality [f]	Comment [h]	Citation [g]
		latest	late	early	middle	late	early	late	early	middle	late	early	late	early	middle	late					
Puffinus	sp. A									■								w. N. Pacific	Japan		Ono & Sakamoto 1991
Puffinus	sp. B									■								w. N. Pacific	Japan		Ono & Sakamoto 1991
Fulmarus	*hammeri*										■							e. N. Pacific	Calif.		Howard 1968
Puffinus	*barnesi*										■							e. N. Pacific	Calif.		Warheit 1992
Puffinus	*calhouni*										■							e. N. Pacific	Calif.		Howard 1968
Puffinus	*diatomicus*										■							e. N. Pacific	Calif.		Warheit 1992
Puffinus	*felthami*										■	■						e. N. Pacific	Calif.		Howard 1949
Puffinus	*tedfordi*										■	■						e. Pacific	Mexico		Howard 1971
Calonectris	*krantzi*											■						w. Atlantic	N. Carolina	90	Olson & Rasmussen 2001
Puffinus	aff. *pacificoides*											■						w. Atlantic	N. Carolina		Olson & Rasmussen 2001
Pterodromoides	*minoricensis*											■						Atlantic	Medit., N. Carolina		Olson & Rasmussen 2001
Fulmarus	sp.											■						e. S. Pacific	Peru		Cheneval 1993
Calonectris	sp.											■						e. S. Atlantic	S. Africa		Olson 1985c
Fulmarinae	sp.											■						e. S. Atlantic	S. Africa		Olson 1985c
genus indeterminate	sp.											■						e. S. Atlantic	S. Africa		Olson 1985c
genus indeterminate	sp.											■						e. S. Atlantic	S. Africa	91	Olson 1985b
Pachyptila	*salax*											■						e. S. Atlantic	S. Africa		Olson 1985b,c
Pachyptila	sp. B											■						e. S. Atlantic	S. Africa	92	Olson 1985b,c
Pachyptila	sp. C											■						e. S. Atlantic	S. Africa	93	Olson 1985b,c
Procellaria	sp.											■						e. S. Atlantic	S. Africa		Olson 1985c
Puffinus (*Puffinus*)	sp. A											■						e. S. Atlantic	S. Africa		Olson 1985c
Puffinus (*Puffinus*)	sp. B											■						e. S. Atlantic	S. Africa		Olson 1985b,c
Puffinus (*Puffinus*)	sp. C											■						e. S. Atlantic	S. Africa		Olson 1985c
Calonectris	aff. *borealis*									■		■						w. Atlantic	N. Carolina	94, 95	Olson & Rasmussen 2001
Calonectris	aff. *diomedea*									■		■						w. Atlantic	N. Carolina	94, 96	Olson & Rasmussen 2001
Pachyptila	sp.									■		■						w. Atlantic	N. Carolina	94, 97	Olson & Rasmussen 2001
Procellaria	cf. *parkinsoni*									■		■						w. Atlantic	N. Carolina	94	Olson & Rasmussen 2001

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Genus or higher taxon [b, c]	Species	Cretaceous	Paleocene	Eocene			Oligocene		Miocene			Pliocene		Pleistocene			Holocene	Geographic Region [f]	Specific Locality [f]	Comment [h]	Citation [g]
		latest	late	early	middle	late	early	late	early	middle	late	early	late	early	middle	late					
Procellaria	cf. *aequinoctialis*									■		■						w. Atlantic	N. Carolina	94, 98	Olson & Rasmussen 2001
Pterodroma	magn. *lessonii*									■		■						w. Atlantic	N. Carolina	94	Olson & Rasmussen 2001
Puffinus	aff. *tenuirostris*									■		■						w. Atlantic	N. Carolina	94	Olson & Rasmussen 2001
Puffinus	cf. *puffinus*									■		■						w. Atlantic	N. Carolina	94	Olson & Rasmussen 2001
Puffinus	magn. *lherminieri*									■		■						w. Atlantic	N. Carolina	94	Olson & Rasmussen 2001
Puffinus	*gilmorei*												■					e. N. Pacific	Calif.		Chandler 1990a
Puffinus	*kanakoffi*												■					e. N. Pacific	Calif.		Warheit 1992
Puffinus	sp.												■					e. N. Pacific	Calif.		Chandler 1990a
genus indeterminate	sp.												■					e. N. Pacific	Calif.		Chandler 1990a
Puffinus	*nestori*												■					Paratethys	Ibiza		Olson & Rasmussen 2001
Puffinus	*pacificoides*													■	■	■		e. S. Atlantic	St. Helena I.	99	Olson 1975
Bulweria	*bifax*													■	■	■		e. S. Atlantic	St. Helena I.	99	Olson 1975
Pterodroma	*rupinarum*													■	■	■	■	e. S. Atlantic	St. Helena I.	100	Olson 1975
Puffinus	*holeae*															■		e. Atlantic	Canary I.	101	Walker et al. 1990
Pterodroma	*jugabilis*																■	c. Pacific	Hawaii		Olson & James 1991
Puffinus	*olsoni*																■	e. Atlantic	Canary I.		Olson & Rasmussen 2001
Puffinus	*spelaeus*																■	w. S. Pacific	New Zealand	102	Holdaway & Worthy 1994
Procellariidae	new sp.																■	c. S. Pacific	Easter I.		Steadman 1995
Pelecanoididae																					
Pelecanoides	*cymatotrypetes*											■						e. S. Atlantic	S. Africa		Olson 1985b
Oceanitidae																					
Primodroma	*bournei*			■														e. N. Atlantic	England	103	Harrison & Walker 1977
Oceanodroma	*hubbi*											■	■					e. N. Pacific	Calif.		Miller 1951
Oceanodroma	sp.											■						e. N. Pacific	Calif.		Howard 1978

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Genus or higher taxon [b, c]	Species	Cretaceous	Paleocene	Eocene			Oligocene		Miocene			Pliocene		Pleistocene			Holocene	Geographic Region [f]	Specific Locality [f]	Comment [h]	Citation [g]
		latest	late	early	middle	late	early	late	early	middle	late	early	late	early	middle	late					
Oceanites	*zaloscarthmus*											■						e. S. Atlantic	S. Africa		Olson 1985b
Oceanites	sp.											■						e. S. Atlantic	S. Africa	104	Olson 1985c
Oceanodroma	sp.												■					e. N. Pacific	Calif.		Chandler 1990a
Sphenisciformes																					
Spheniscidae																					
Palaeeudyptes	sp.			■	■													w. S. Pacific	Australia		Simpson 1975
Pachydyptes	*simpsoni*					■												w. S. Pacific	Australia		Jenkins 1974
Pachydyptes	*ponderosus*					■												w. S. Pacific	New Zealand		Simpson 1975
Palaeeudyptes	*marplesi*					■												w. S. Pacific	New Zealand		Simpson 1975
Palaeeudyptes	sp.					■												w. S. Pacific	New Zealand	105	Simpson 1975
Anthropornis	*nordenskjoeldii*					■												Antarctic Peninsula	Seymour I.		Simpson 1975
Anthropornis	*grandis*					■												Antarctic Peninsula	Seymour I.		Simpson 1975
Archaeospheniscus	*wimani*					■												Antarctic Peninsula	Seymour I.		Simpson 1975
Delphinornis	*larsenii*					■												Antarctic Peninsula	Seymour I.		Simpson 1975
Palaeeudyptes	*gunnari*					■												Antarctic Peninsula	Seymour I.		Simpson 1975
Palaeeudyptes	*klekowskii*					■												Antarctic Peninsula	Seymour I.		Myrcha et al. 1990
Wimanornis	*seymourensis*					■												Antarctic Peninsula	Seymour I.		Simpson 1975
genus indeterminate	sp.						■											w. S. Pacific	New Zealand		Simpson 1975
?*Platydyptes*	*marplesi*						▒	▒										w. S. Pacific	New Zealand	106	Simpson 1975
Archaeospheniscus	*lowei*						▒	▒										w. S. Pacific	New Zealand	106	Simpson 1975
Archaeospheniscus	*lopdelli*						▒	▒										w. S. Pacific	New Zealand	106	Simpson 1975
Duntroonornis	*parvus*						▒	▒										w. S. Pacific	New Zealand	106	Simpson 1975
Palaeeudyptes	sp.						▒	▒										w. S. Pacific	New Zealand	106	Simpson 1975
Palaeeudyptes	*antarcticus*						■	■										w. S. Pacific	New Zealand		Simpson 1975

APPENDIX 2.1 *(Continued)*

List of fossil seabirds

See text and notes at bottom of table for details. [a, d, e]

Genus or higher taxon [b, c]	Species	Cretaceous	Paleocene	Eocene			Oligocene		Miocene			Pliocene		Pleistocene			Holocene	Geographic Region [f]	Specific Locality [f]	Comment [h]	Citation [g]
		latest	late	early	middle	late	early	late	early	middle	late	early	late	early	middle	late					
Platydyptes	*novaezealandiae*																	w. S. Pacific	New Zealand		Simpson 1975
genus indeterminate	sp.																	w. S. Pacific	Australia	107	Simpson 1975
Korora	*oliveri*																	w. S. Pacific	New Zealand		Simpson 1975
Platydyptes	*amiesi*																	w. S. Pacific	New Zealand		Simpson 1975
?Paraptenodytes	*brodkorbi*																	w. S. Atlantic	Argentina		Simpson 1972
Arthrodytes	*grandis*																	w. S. Atlantic	Argentina	108	Simpson 1972
Chubutodyptes	*biloculata*																	w. S. Atlantic	Argentina		Simpson 1972
Eretiscus	*tonnii*																	w. S. Atlantic	Argentina	109	Olson 1986
Palaeospheniscus	*patagonicus*																	w. S. Atlantic	Argentina	110	Simpson 1972
Palaeospheniscus	*bergi*																	w. S. Atlantic	Argentina	111	Simpson 1972
Palaeospheniscus	*gracilis*																	w. S. Atlantic	Argentina	112	Simpson 1972
Palaeospheniscus	*wimani*																	w. S. Atlantic	Argentina	113	Simpson 1972
Paraptenodytes	*antarcticus*																	w. S. Atlantic	Argentina	114	Simpson 1972
Paraptenodytes	*robustus*																	w. S. Atlantic	Argentina	115	Simpson 1972
Anthropodyptes	*gilli*																	w. S. Pacific	Australia		Simpson 1975
genus indeterminate	sp.																	w. S. Atlantic	Argentina		Cione & Tonni 1981
?Pseudaptenodytes	*minor*																	w. S. Pacific	Australia		Simpson 1975
Pseudaptenodytes	*macraei*																	w. S. Pacific	Australia		Simpson 1975
genus indeterminate	sp.																	e. S. Pacific	Peru		Cheneval 1993
?Palaeospheniscus	*huxleyorum*																	e. S. Atlantic	S. Africa	116	Olson 1985c
Dege	*hendeyi*																	e. S. Atlantic	S. Africa	116	Olson 1985c
Inguz'	*predemersus*																	e. S. Atlantic	S. Africa	117	Olson 1985c
Nucleornis	*insolitus*																	e. S. Atlantic	S. Africa	116	Olson 1985c
Aptenodytes	*ridgeni*																	w. S. Pacific	New Zealand		Simpson 1975
Marplesornis	*novaezealandiae*																	w. S. Pacific	New Zealand		Simpson 1975
Pygoscelis	*tyreei*																	w. S. Pacific	New Zealand		Simpson 1975

APPENDIX 2.1
Text and Notes

Notes:

[a] Except for the Pelagornithidae and Sulidae, taxa included in this table are based entirely on a review of the literature, in particular Olson (1985a), as well as Bochenski (1997), Brodkorb (1963), Chandler (1990a), Olson and Rasmussen (2001), Warheit (1992), and Simpson (1975). The Pelagornithidae and Sulidae are based on both a review of the literature and unpublished data from Warheit and Olson.

[b] I have not included modern species in this list, except for the Lee Creek fauna, as described by Olson and Rasmussen (2001), or if the modern species is described from a deposit older than Pleistocene. I have also not included a taxon if its affinities are uncertain, but it has been established that the taxon is not a seabird (e.g., *Actiornis anglicus,* see Olson, 1985:207). Furthermore, I have not attempted to sort marine and non-marine deposits; therefore, some of the taxa listed here may have been freshwater/inland species (e.g., perhaps *Phalacrocorax macer*).

[c] The generic identification for some fossils provided in this list may not reflect current taxonomy. For example, most albatross fossils were described in the genus *Diomedea*. Nunn et al. (1996) revised albatross taxonomy, based on a molecular analysis, and the albatross currently inhabiting the north Pacific, for example, are now placed in the genus *Phoebastria*. However, fossil species that would now be placed in *Phoebastria* are listed in this table by their original generic designation (e.g., *Diomedea californica*; see Olson and Rasmussen [2001]), because there has been no formal revision of these taxa.

[d] Each fossil was placed into a specific Epoch (see Figure 2.1) based on the description of the fossil locality in either the original publication or a review article (e.g., Brodkorb 1963, Olson 1985a, Warheit 1992). Fossils that were placed in more than one Epoch are those that occur across several Epochs (solid box) or those with uncertainty as to which Epoch they should be placed (hatched box).

[e] Occasionally, the age of a fossil is revised based on improved stratigraphic or radiometric analyses. I made no attempt here to review the geological literature to determine if there has been a change in the relative or absolute age of any particular fossil since it was originally described or was discussed in a review article. However, if the Age (see Figure 2.1) of a fossil was provided, I established the appropriate Epoch for that fossil based on the most recent Cenozoic geochronology (Berggren et al. 1995; Figure 2.1).

[f] I provided a general locality for each taxon to make evident that these birds occurred in geographic regions more widespread than their specific fossil locality. However, I also provided an example of the more specific locality from which the fossils were recovered. The abbreviations used here are as follows: north (n.), south (s.), east (e.), west (w.), interior (int.), central (c.), Atlantic (Atl.), England (Engl.), Europe (Eur.), Mediterranean (Medit.), California (Calif.), North Carolina (N. Carol.), and island (I.). In addition, Paratethys indicates those areas in relict Paratethys and Tethys Seas (Mediterranean, Black, and Caspian Seas).

[g] Each citation provided here is not necessarily the original reference for the species. For the most part, I have associated a single citation for each taxon listed; that citation will provide additional information for each species, beyond that which I provide in this table, or will point the reader to several additional citations, including the original reference for the species.

[h] The following are the list of comments. Each comment is based on information provided in the citation associated with that taxon, unless noted directly in the comment:

1. Age described as Pliocene.
2. Age described as Oligocene.
3. Affinities not confirmed.
4. Indeterminate affinities - probably not a gull.
5. Rasmussen identified this specimen to the Charadriiformes only, but stated that it was most likely a small species of gull.
6. Probably not *Larus* gull; Mlíkovsk" (1992) considered species as Glareolidae.
7. Probably *Stercorarius*; Mourer-Chauviré (1995) listed as Laridae.
8. Ballmann (1976) considered these species to be gulls but not in *Larus*.
9. Similar to *Larus elmorei*, but slightly larger.
10. Similar to cf. *Larus* from late Miocene-early Pliocene of Arizona.
11. Unlikely to represent extinct taxon.
12. May not be an alcid.
13. *Miocepphus* closely related to *Alca* and not to *Cepphus*.
14. Originally described as ?*Endomychura*.
15. Originally described as *Uria*.
16. Humerus with morphology similar to *Cyclorrhynchus*.
17. Also includes *Australca grandis*; *Australca* is synonymous with *Alca*.
18. Larger than *Alca antiqua*.
19. Also found at Holocene prehistoric sites in both eastern and western Atlantic (Brodkorb 1967).
20. Same size as *Uria lomvia arra*, perhaps specimen is *U. aalge* or *U. lomvia*.
21. Possibly a pelecaniform.
22. Should be placed in Aves *Incertae Sedis*.

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Text and Notes

23. Pelecaniform, but probably not a pelican.
24. Harrison and Walker (1977) created Prophaethontidae for this species.
25. Originally described as *Pelecanus.*
26. May be synonymous with *Miopelecanus gracilis*.
27. Tentatively *Pelecanus*.
28. Age described as from Miocene.
29. Originally described as *Pelecanus conspicillatus novaezealandiae*.
30. Warheit and Olson (unpubl. data) concluded that there are no conclusive data to differentiate this species from *Pseudodontornis longidentata*, and that the two taxa may be synonymous; Olson (1985a) suggested that *Pseudodontornis* may be synonymous with *Pelagornis.*
31. Harrison and Walker established this genus based on characters that cannot be confirmed (Warheit and Olson, unpubl. data). It is most likely that correct genus for this species is *Odontopteryx*.
32. *Dasornis* has taxonomic priority over *Argillornis*. *Dasornis londinensis* and the two species of *Argillornis* may be conspecific and, if so, the species will be referred to as *Dasornis londinensis.*
33. The specimens of *Argillornis* and *Dasornis* cannot be compared because they are described from different skeletal elements.
34. *Argillornis emuinus* and *A. longipennis* are most likely conspecific (Warheit and Olson, unpubl. data).
35. Warheit and Olson (unpubl. data) examined a cast of the specimen and made comparisons with *Macrodontopteryx* and *Dasornis.* Harrison and Walker (1976) have not clearly differentiated this specimen from either *Macrodontopteryx* or *Dasornis,* and therefore, this species may not be valid.
36. Warheit and Olson (unpubl. data) have tentatively determined that there are three species, based on relative size, present in the Chattian deposits of South Carolina; one of these species is an extremely large bird with estimated wingspan of over 18 feet. The taxonomy of pseudodontorns from this locality and age needs to be revised. The "medium-sized" bird is comparable in size to *Palaeochenoides*; the smallest bird is roughly the same size as *Tympanonesiotes*, although it is not entirely clear if that species is a pseudodontorn.
37. Olson states that the age of the specimen is not clearly known and was also uncertain that the taxon is a pseudodontorn.
38. I have not seen this reference; the taxonomic designation, age, and locality were taken from the Zoological Record.
39. The age of this specimen is uncertain; it is younger than early Miocene, but older than late Pliocene (McKee 1985).
40. There are at least two species of pseudodontorns from the middle Miocene deposits of the Chesapeake Bay area. Based on the material in hand, the smaller of the two species is somewhat intermediate in size between the small- and medium-sized birds from the Oligocene of South Carolina, and the larger of the two species is intermediate between the medium- and large-sized species from South Carolina, but closer in size to the medium-sized species.
41. There are two, possibly three species of Pseudodontorns from Lee Creek, and as with the Oligocene birds from South Carolina, these species are diagnosed by size. In an effort to simplify a very confused pseudodontorn taxonomy, Olson and Rasmussen (2001) are referring all the species from late Oligocene and Neogene deposits to the genus *Pelagornis*, which has taxonomical priority over all other pseudodontorn genera from this period.
42. Age described as middle Oligocene, but there is no middle Oligocene (see Figure 2.1).
43. This specimen was originally described in the genus *Odontopteryx*. Lambrecht (1930) established the genus *Pseudodontornis* based on this species. The type specimen for this species is lost and its age and locality are also unknown, although Brodkorb (1963) tentatively listed the species as from the Miocene. Hopson (1964) referred to this species a fragment of a lower mandible from the late Oligocene of South Carolina.
44. There are at least two species of sulids from the Oligocene of South Carolina.
45. Originally described as *Sula*.
46. Warheit and Becker (unpubl. ms) consider this species to be Sulidae, *Incertae Sedis*.
47. Approximately the size of *Morus* sp. A from middle Miocene California (Warheit and Olson, unpubl. data).
48. Approximately the size of *M. loxostyla*.
49. Approximately the size of, or slightly smaller than, *M. lompocanus*.
50. Approximately the size of, or slightly smaller than, *M. willetti* (Warheit and Olson, unpubl. data).
51. Approximately the size of *M. vagabundus* (Warheit and Olson, unpubl. data).
52. Small in size.
53. Originally described as *Sula,* then *Microsula*; *Microsula* synonymous with *Morus* (Olson and Rasmussen, in press).
54. Smaller than *S. pohli*, approximately the size of *M. willetti*, but described as *Sula*.
55. Described as *Sula* (*Microsula*). Maybe conspecific with *Sula* sp. from Japan.
56. Originally described as *Sula*; moved to *Morus* by Warheit (1990).
57. Described originally by Howard (1958) from the early late Miocene (Fauna II of Warheit [1992]). There are specimens of *Sula* from the middle Miocene of California (Fauna I) referred to this species by Warheit (1992). These specimens are slightly smaller than *S. pohli* and may not be conspecific with this species.
58. Originally described as *Paleosula*; moved to *Morus* by Warheit (1990).

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59. Originally described as *Miosula*; moved to *Morus* by Warheit (1990).
60. *Sula guano* and *S. phosphata* are conspecific (Warheit and Becker, unpubl. ms).
61. Large species of *Sula*.
62. Cheneval stated that there were two or three species from the Pisco Formation. Based on skeletal morphometrics (see Warheit 1992), Warheit and Olson (unpubl. data) determined that there are most probably three large-sized species of *Sula,* the smallest of which is the same size or larger than the largest extant booby (*S. dactylatra*).
63. Originally described in the genus *Sula*; moved to *Morus* by Chandler (1990a).
64. Originally described in the genus *Miosula*; moved to *Morus* by Chandler (1990a).
65. Specimens found on Norfolk Island were in association with Polynesian Rat; species may have been seen on Lord Howe Island in 1788.
66. Originally described as *Phalacrocorax*, Cheneval established this new genus for this species.
67. *Phalacrocorax praecarbo* is synonymous with this species.
68. May be referable to a previously described species; perhaps *Phalacrocorax filyawi*.
69. May not be a cormorant.
70. Within size range of *Phalacrocorax* (*Microcarbo*) *coronatus*.
71. Chandler stated that there are at least two additional species of cormorant and shag present in the San Diego Formation.
72. Age described as Pliocene - Pleistocene.
73. Probably early Oligocene, perhaps late Eocene; at least six species, including a species smaller than any of the species from the late Oligocene of Japan.
74. " . . . a species of immense size, being the largest diving bird of any sort ever known to have existed . . . . " (Olson and Hasegawa 1996:750).
75. In addition to the two species of *Copepteryx*, there may be at least an additional four species including another genus in the late Oligocene deposits of Japan.
76. The taxon represented by these fossils may also be included in the material discussed by Olson and Hasegawa (1996). See note 75.
77. This taxon is based on a single specimen (humerus) and is the type for a new family (Tytthostonychidae). Olson and Parris tentatively placed this and an unnamed ulna in the Procellariiformes.
78. Harrison and Walker (1977) placed this species in its own family (Marinavidae).
79. Originally described as *Puffinus*, Olson (1985) said this species was more similar to *Pterodroma*; Cheneval placed the species in *Plotornis*.
80. Olson indicated that this species may have been present in the middle Miocene of Maryland.
81. Olson and Rasmussen made synonymous *Diomedea howardae* (Chandler 1990a) and this species; also known from Pleistocene of Bermuda.
82. *Diomedea* sp. B from Chandler (1990a) may be synonymous with this species.
83. *Diomedea* sp. A from Chandler (1990a) is synonymous with this species. This species may be in the same lineage as *D. californica.*
84. Preliminary analysis by Warheit and Olson (unpubl. data) place these species closer to the Diomedeidae than the Procellariidae.
85. Feduccia and McPherson considered this specimen close in morphology to *Pterodroma*.
85a. I have not seen this reference; the age and location indicated here were taken from the title of the paper.
86. Similar in size and morphology to *Bulweria bulwerii*.
87. Originally described as a penguin.
88. There are many undescribed specimens of *Puffinus* from middle Miocene of Maryland and early Pliocene of South Africa.
89. Age is uncertain, but probably from middle Miocene.
90. Largest species in this genus.
91. Roughly same size of Fulmarinae species from early Pliocene of South Africa; based on the descriptions in Olson (1985b,c), this specimen differs from the preceding undescribed taxon.
92. The available material is indistinguishable from *Pachyptila vittata* and *P. salvini*.
93. Similar in size to the smallest extant *Pachyptila*.
94. Age is uncertain, but probably early Pliocene.
95. Olson and Rasmussen consider this taxon to be a full species rather than a subspecies.
96. Distinguished from *Calonectris borealis* by size.
97. Specimens here are indistinguishable from the medium-sized modern species of *Pachyptila*.
98. Possibly a vagrant given the current distribution of this species and its rarity in the fossil deposit.
99. Age described as Pleistocene.
100. Presumably exterminated after 1502.
101. Species was originally named *Puffinus holei*; Michaux et al. (1991) corrected the spelling of this species to *P. holeae*.
102. The extinction of this species probably resulted from the introduction of *Rattus* by the Polynesians.
103. This species is often omitted from lists or reviews (e.g., Olson 1985a) and its systematic position needs to be reviewed.
104. Smaller sized than *Oceanites zaloscarthmus*.

105. Not *Palaeeudyptes marplesi*.
106. Age described as early to middle Oligocene, but there is no middle Oligocene (see Figure 2.1).
107. There are at least two distinct species.
108. Includes *Paraptenodytes andrewsi*.
109. Originally described by Simpson (1981) as *Microdytes*.
110. Includes *Palaeospheniscus menzbieri*, *P. interruptus*, *P. intermedius*, *P. affinis*.
111. Includes *Palaeospheniscus planus*, *P. rothi*, *Pseudospheniscus planus*, *P. interplanus*, *P. concavus*, *P. convexus*.
112. Includes *Palaeospheniscus nereius*, *P. medianus*.
113. Includes *Palaeospheniscus robustus*.
114. Includes *Isotremornis nordenskjöldi*.
115. Includes *Paraptenodytes curtus*, *Metancylornis curtus*, *Treleudytes crassa*, *T. crassus*.
116. *Spheniscus* or *Inguza*.
117. Perhaps *Spheniscus*.

APPENDIX 2.2
List of Seabird Species

List of seabird species that are now synonymous with a species in Appendix 2.1. The parenthetical number beside each species refers to the Comment in Appendix 2.1

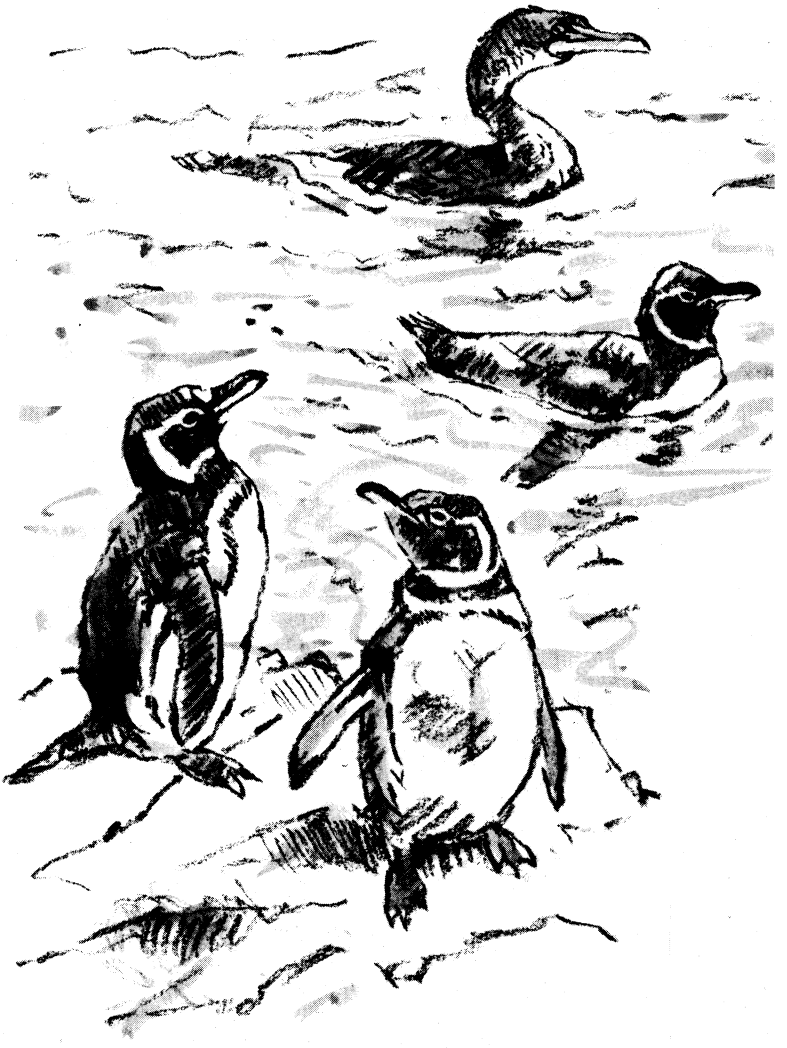
Charadriiformes
Alcidae
Australca grandis (17)

Pelecaniformes
Phalacrocoracidae
Phalacrocorax praecarbo (67)

Procellariiformes
Diomedeidae
Diomedea howardae (81)
Diomedea sp. A Chandler (1990a) (83)

Sphenisciformes
Spheniscidae

Isotremornis nordenskjöldi (114)
Metancylornis curtus (115)
Palaeospheniscus affinis (110)
P. intermedius (110)
P. interruptus (110)
P. medianus (112)
P. menzbieri (110)
P. nereius (112)
P. planus (111)
P. robustus (113)
P. rothi (111)
Paraptenodytes andrewsi (108)
P. curtus (115)
Pseudospheniscus concavus (111)
P. convexus (111)
P. interplanus (111)
P. planus (111)
Treleudytes crassa (115)
T. crassus (115)



Galapagos Penguins and Flightless Cormorant