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Evolution of the Cenozoic marine avifaunas of Europe

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(With 3 figures and 1 table)

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Abstract

The fossil record of the Cenozoic marine birds from European seas is summarized. Three main phases in the evolution of this avifauna are discerned, namely the Paleocene-Eocene, Oligo-Miocene, and Pliocene-Recent ones. These phases coincide with major changes in climate evolution. A key event was the "Messinian Crisis" in the late Miocene, which none of the local seabirds survived. The modern marine avifauna of the Mediterranean Sea is of post-Miocene origin.

Keywords: Palaeogene, Neogene, Paratethys, Tethys, sea birds, fossil record, Aves

Introduction

Cenozoic deposits of Europe and adjacent regions have yielded considerable numbers of bird remains, including those of seabirds (Mlíkovský 1996, 2002a; Tyrberg 1998, 1999; see also Mlíkovský 1992b; Warheit 2002; Mayr 2005). Seabirds are an ecologically important group of birds characterized by their dependence on the marine environment (Harrison 1985; Schreiber & Burger 2002; Gaston 2004). Their record in European seas ranges from the late Paleocene to the Recent. The term "European seas" is used throughout this paper for a region currently ranging from the Azores in the west to the Ural Mountains and the Caspian Sea in the east, Svalbard in the north and northern Africa in the south. This area was largely covered by the Tethys Sea in the early Tertiary, but moving continents caused repeated local sea regressions and transgressions, which eventually led to the current appearance of the region with much land and less sea. Changing sea and land extensions markedly influenced the occurrence of both marine and land animals here (e.g. Rögl 1998, 1999a, b; Harzhauser et al. 2007, and references cited therein). This paper summarizes our current knowledge of fossil seabirds in the "European seas", with a focus on the composition of local marine avifaunas and their zoogeographical relationships.

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Material & Methods

This paper is based on the review of the Cenozoic birds of Europe by Mlíkovský (2002a) and additional (usually more recent) publications. Families are understood here in a broad sense (see Mlíkovský 2002a). However, different authors vary in their opinions as to the extent of individual families. To avoid confusion, I added the abbreviation "s. l." (sensu lato) to family names where appropriate. For a faunal analysis, such as this one, it is of less import whether a taxon is treated as a subfamily or a closely related family. An optimistic approach to the taxonomic identities of fossil taxa was adopted here, i.e. I treated fossils as correctly identified unless their identity was considerably doubted by me or other authors (see Mlíkovský 2002a and below). Nonetheless, many fossil bird taxa are clearly of dubious identity, especially the Palaeogene birds (Olson 1985a; Mlíkovský 2002a).

The present paper is limited to those bird families that presumably include only seabirds. Various other families, such as divers (Gaviidae) or cormorants/shags (Phalacrocoracidae), include both marine and freshwater forms. The latter families are omitted here because it is impossible to definitively determine whether a particular species was a freshwater or a marine bird. The geological context in which the fossils were found is of little aid here because decidedly non-marine birds, such as quails, were found in marine deposits (e.g. Mlíkovský 1992a; Göhlich 2003), while proper seabirds can be found in non-marine deposits (e.g. Stewart 2002).

The geographic position of localities at which fossil seabirds were found is shown in maps (figs 1-3). Considering the rapid changes in the extent of land and seas during the Cenozoic in this region and that each map covers a long period, I refrained from mapping the localities on palaeomaps, believing that such maps would be misleading.

Stratigraphy follows Legendre & Lévêque (1997) for the Palaeogene (MP zones), Steininger (1999) for the Neogene (MN zones), and Mlíkovský (2002b) for the Quaternary.

Systematic overview

Procellariidae s. l.

The oldest procellariids of European seas are known from the early Eocene of Grand Daoui, Morocco (Gheerbrant et al. 2003; unidentified, tentatively referred), and from the early Eocene (MP 8-9) of the island of Sheppey, England, from where *Primodroma bournei* Harrison & Walker, 1977 was described (Harrison & Walker 1977). Procellariid affinities of the allegedly procellariid genus *Neptuniavis* Harrison & Walker, 1977 from the early Eocene (MN 8-9) of the island of Sheppey were doubted by Mlíkovský (2002a), and Mayr et al. (2002, see also Mayr 2008) removed it to the Pelagornithidae s. l.

The Oligocene record of procellariids includes *Diomedeoides brodkorbi* (Cheneval, 1995) from the early Oligocene (MP 22) of Frauenweiler, Germany (Mayr 2002), and the middle Oligocene (MP 23-24) of Froidefontaine, France (Cheneval 1995), and *Diomedeoides lipsiensis* (Fischer, 1983) from the middle Oligocene (MP 23-24) of

Fig. 1. Distribution of marine birds in European seas during the Paleocene (■) and the Eocene (●). 1 – Grand Daoui, 2 – Island of Sheppey, 3 – Nederokkerzeel, 4 – Etterbeek, 5 – Messel, 6 – Grand Daoui, 7 – Cluj-Napoca.

Espenhain, Germany (Fischer 1983, 1985, 1997; Mayr 2002). *Gaviota* (= *Diomedeoides*) *lipsiensis* was originally described by Fischer (1983) as a gull, but Mayr (2002) recognized its procellariiform affinities, suggesting at the same time that bones from the same locality described by Fischer (1983, 1985) as "?*Rupelornis definitus*" Van Beneden, 1871, and *Diomedeoides minimus* Fischer, 1985, respectively, all belong to a single species, to which the name *Diomedeoides lipsiensis* (Fischer, 1983) is applicable. *Rupelornis definitus* Van Beneden, 1871 from the middle Oligocene (MP 23-24) of Rupelmonde, Belgium (Van Beneden 1871), is of doubtful taxonomic position (see Mlíkovský 2002a, and references cited therein), but Mayr et al. (2002) suggested that it is a petrel similar to *Diomedeoides*. A partial skeleton from the late Oligocene (MN 25-30) from Litenčice, Czech Republic, has been tentatively identified as a petrel (R. Gregorová, pers. communication 2008). The Miocene record is limited to the oldest part of this period and includes *Diomedeoides brodkorbi* (Cheneval, 1995) from the early Miocene (MN 1) of Weisenau-AS, Germany (Cheneval 1995; specimen tentatively referred), and *Plotornis arvernensis* (Milne-Edwards, 1896) from the early Miocene (MN 2a) of Saint-Gérand-le-Puy, France (Shufeldt 1896, Cheneval 1984). The Miocene record is completed by an uncertain record (based on a fragmentary ulna)

Fig. 2. Distribution of marine birds in European seas during the Oligocene (■) and the Miocene (●). 1 – Rupelmonde, 2 – Gannat, 3 – Froidefontaine, 4 – Frauenweiler, 5 – Espenhain, 6 – Thalbergschichten, 7 – Traun-Pucking, 8 – Litenčice, 9 – Perekishkul, 10 – Anwerp, 11 – Léognan, 12 – Saint-Gérand-le-Puy, 13 – Penedo Norte, 14 – Lanzarote, 15 – Weisenau, 16 – Grund, 17 – Vösendorf, 18 – Sankt-Margarethen (tentatively included), 19 – Credința

of *Diomedea rumana* Grigorescu & Kessler, 1988 from the middle Miocene (MN 8) of Credința, Romania (Grigorescu & Kessler 1988).

The next oldest procellariids were first recorded in European seas from the Pliocene. The record includes *Pterodromoides minoricensis* Seguí et al., 2001 from the early or middle Pliocene of Punta Nati on the island of Menorca, Balears (Seguí et al. 2001a; see Seguí et al. 2001b and Alcover 2001 for the corrected age of this species, which was originally described as being of the late Miocene age). It also includes *Phoebastria anglica* (Lydekker, 1891) from the late Pliocene (MN 16-17) of Foxhall, Orford and Covehithe, England (Lydekker 1891; Harrison & Walker 1978; Olson & Rasmussen 2001; Dyke et al. 2007), unidentified procellariids from the late Pliocene (MN 17) of Ahl al Oughlam, Morocco (Geraads 2006), and *Puffinus nestori* Alcover, 1989 from the late Pliocene (MN 18) of Ca Na Reia on the island of Eivissa, Spain (Alcover 1989). The Quaternary record includes two fossil species: *Puffinus olsoni* McMinn et al., 1990 from various late Pleistocene deposits on the islands of Lanzarote and Fuerteventura, Canary Islands (McMinn et al. 1990), and *Puffinus holeae* Walker et al., 1990. The latter was found in various late Pleistocene localities on the island of Fuerteventura, Canary

Fig. 3. Distribution of marine birds in European seas during the Pliocene (■) and the Pleistocene (●). Only sites in which fossil species were found are shown for the Pleistocene. 1 – Covehithe, 2 – Orford, 3 – Foxhall, 4 – Kattendijk, 5 – Ahl al Oughlam, 6 – Ca Na Reia, 7 – Punta Nati, 8 – Orciano Pisano, 9 – Figueira Brava, 10 – Lanzarote, 11 – Fuerteventura.

Islands (WALKER et al. 1990; OLIVER 2001; SÁNCHEZ MARCO 2003), and the late Pleistocene to early Holocene of Figueira Brava, Portugal (MOURER-CHAUVIRÉ & ANTUNES 2000). Otherwise, only extant species of petrels were recorded from the Quaternary of European seas (see TYRBERG 1998, 1999; MLÍKOVSKÝ 2002a).

Pelagornithidae s. l.

A number of bird bones excavated from the early Eocene (MP 8-9) deposits of the island of Sheppey, England, were attributed to pelagornithid birds (BOWERBANK 1854; OWEN 1870, 1873, 1878, 1880; HARRISON & WALKER 1976a, 1977; MAYR 2008) and the following species were described: *Argillornis emuinus* (BOWERBANK, 1854), *Dasornis londinensis* OWEN, 1870, *Odontopteryx toliapica* OWEN, 1873, *Argillornis longipennis* OWEN, 1878, *Macrodontopteryx oweni* HARRISON & WALKER, 1976, and *Pseudodontornis longidentata* HARRISON & WALKER, 1976. In addition, the genus *Neptuniavis* HARRISON & WALKER, 1977 with two species (*Neptuniavis miranda* HARRISON & WALKER, 1977 and *Neptuniavis minor* HARRISON & WALKER, 1977), originally created for allegedly procellariid birds (HARRISON & WALKER 1977), probably represents pelagornithid birds (MAYR et al. 2002; MAYR 2008). OLSON (1985a) and MLÍKOVSKÝ

(2002a) indicated that a smaller number of pelagornithid species is represented in the Shelley deposits than recognized by HARRISON & WALKER (1976a). MAYR (2008) made a first step in revising the material, lumping large-sized species *Dasornis londinensis* OWEN, *Argillornis longipennis* OWEN, and *Neptuniavis miranda* HARRISON & WALKER with *Dasornis emuinus* (BOWERBANK). Unidentified pelagornithids were tentatively reported from the early Eocene of Grand Daoui, Morocco (GHEERBRANT et al. 2003). Pelagornithids were recorded also from the middle Eocene (MP 11-13) of Etterbeek, Belgium, where *Argillornis emuinus* (BOWERBANK, 1854) and tentatively *Argillornis longipennis* OWEN, 1878 were identified (DOLLO 1909), i.e. *Dasornis emuinus* (BOWERBANK) (sensu MAYR 2008).

The Oligocene record is limited to *Caspiodontornis kobystanicus* ASLANOVA & BURČAK-ABRAMOVIČ, 1982 from the late Oligocene (MP 25-30) of Perekishkul, Azerbaijan (ASLANOVA & BURČAK-ABRAMOVIČ 1982, 1999).

The Neogene record is similarly meagre. A sternum of a large pelagornithid was found in the early/middle Miocene of Penedo Norte, Portugal (MAYR et al. 2008). Eggshell fragments from the late (?) Miocene of the island of Lanzarote, Canary Islands, were tentatively attributed to pelagornithids (GARCÍA TALAVERA 1990), and *Pelagornis mauretanicus* MOURER-CHAUVIRÉ & GERAADS, 2008 was described from the late Pliocene (MN 17) of Ahl al Oughlam, Morocco (MOURER-CHAUVIRÉ & GERAADS 2008). If correctly dated, the latter species represent the youngest fossil record of pelagornithids worldwide.

Phaethontidae s. l.

The phaethons were recorded in European seas during two well-separated periods: Ancient phaethons, sometimes classified as a separate family – Prophaethontidae – were recorded from the Paleocene to middle Eocene. The record includes *Lithoptila abdounensis* BOURDON et al, 2004 from the late Paleocene (MP 6) of Grand Daoui, Morocco (BOURDON et al. 2004), another phaethon – *Phaetusavis pelagicus* – from the early Eocene (MP 7) of Grand Daoui, Morocco (BOURDON et al. 2007), *Prophaethon shrubsolei* ANDREWS, 1899 from the early Eocene (MP 8-9) of Sheppey Island, England (ANDREWS 1899; HARRISON & WALKER 1976b, 1977), and an unnamed form from the middle Eocene of Nederokkerzeel, Belgium (MAYR & SMITH 2002).

Thereafter, there is no trace of phaethons in European seas until the genus *Heliadornis* appeared in the middle Miocene; it survived until the lower part of the late Miocene according to our current knowledge. The record includes *Heliadornis ashbyi* OLSON, 1985 from the middle Miocene (MN 7-8) of Antwerp, Belgium (OLSON & WALKER 1997; see also OLSON 1985b), and *Heliadornis paratethydicus* MLÍKOVSKÝ, 1997 from the late Miocene (MN 10) of Vösendorf, Austria (MLÍKOVSKÝ 1997).

Fregatidae

Only a tentative record of frigate birds from European seas has been reported so far. It is from the early Eocene of Grand Douai, Morocco (GHEERBRANT et al. 2003).

Sulidae

The oldest sulid record is *Eostega rectirostris* (Mayr, 2002) from the middle Eocene (MP 11) of Messel, Germany (Mayr 2002; Mlíkovský 2007), being followed by *Eostega lebedinskyi* Lambrecht, 1929 from the late Eocene (MP 17-20) of Cluj-Manastur, Rumania (Lambrecht 1929, 1933; Mlíkovský 2007; age corrected according to V.A. Codrea & V. Matyas, pers. communication 2008). The Oligocene record is limited to *Empheresula arvernensis* (Milne-Edwards, 1867) from the late Oligocene (MP 30) of Gannat, France (Milne-Edwards 1867-1868; Harrison 1975a, b; Cheneval 1984), and to an indeterminate sulid from the late Oligocene of the Thalbergschichten, Germany (Darga et al. 1999).

The Miocene record seems to be somewhat richer. It includes *Empheresula arvernensis* (Milne-Edwards, 1867) from the early Miocene (MN 2a) of Saint-Gérand-le-Puy, France (Cheneval 1984), and *Enkurosula pygmaea* (Milne-Edwards, 1874) from the early Miocene (MN 2-3) of Léognan, France (Milne-Edwards 1874), and from the middle Miocene (MN 5) of Grund, Austria (Göhlich 2003 and Daxner-Höck et al. 2004; sub *Microsula pygmaea*). It also includes *Sarmatosula dobrogensis* Grigorescu & Kessler, 1977 and *Morus olsoni* Grigorescu & Kessler, 1988, both from the middle Miocene (MN 8) of Credința, Romania (Grigorescu & Kessler 1977, 1988). Unfortunately, European Miocene sulids lack a modern taxonomic revision (see also Mlíkovský 2002a), which prevents a closer evaluation of this record.

The Pliocene record is limited to undescribed specimens from the late Pliocene (MN 17) of Ahl al Oughlam, Morocco (Geraads 2006). The Quaternary record is limited to the modern *Morus bassanus* (Linnaeus, 1758) (see Tyrberg 1999).

Alcidae

The pre-Messianian record of alcids from European seas is limited to *Petralca austriaca* Mlíkovský, 1987 from the late Oligocene (MP 30) of Traun-Pucking, Austria (Mlíkovský 1987).

Next records are known from the early Pliocene onwards, including *Alca stewarti* Martin et al., 2000 from the early Pliocene (MN 14) of Kattendijk, Belgium (Martin et al. 2000), and *Alca ausonia* (Portis, 1889) from the middle Pliocene (MN 15-16) of Orciano Pisano (Portis 1889; Olson & Rasmussen 2001). Both these species belong in the modern genus *Alca* Linnaeus, 1758. In addition, as yet unidentified auks were reported from the late Pliocene (MN 17) of Ahl al Oughlam, Morocco (Geraads 2006). The Quaternary record includes the extinct Great Auk *Alca impennis* Linnaeus, 1758, and extant species (see Tyrberg 1999; Mlíkovský 2002a).

Absent families

The families listed above were recorded in the Cenozoic European seas, while the following families of seabirds lack any record from European seas: Penguins (Spheniscidae s. l.) have been widespread in southern seas since the Paleocene until the present, but they never reached northern seas (see e.g. Ksepka et al. 2006 for their geographic history). Similarly, the Plotopteridae, a family of flightless marine birds known from

the Oligocene and Miocene of the North Pacific (Olson & Hasegawa 1979; Warheit 1992, 2002), never reached the North Atlantic and European seas.

Avifaunal evolution

This chapter is based on the "Systematic overview" (above), where relevant references are given. For a summary of the results see table 1. The geographic distribution of records from particular periods is given in figs 1-3.

Paleocene

The Paleocene record of marine birds from European seas is limited to the Phaethontidae s. l. (*Lithoptila*).

Eocene

The Eocene marine avifauna was rather rich in European seas. It included early phaethons (*Prophaethon*), early petrels (*Primodroma*), early gannets (*Eostega*), pelagornithids (*Dasornis*, *Odontopteryx*, *Pseudodontornis*, and *Macrodontopteryx*), and perhaps Fregatidae (indet., tentatively referred).

Oligocene

The Oligocene marine avifauna of European seas does not share any genera with the European Eocene avifauna, which indicates severe extinctions at the Eocene/Oligocene boundary, perhaps caused by rapid warming (e.g. Zachos et al. 2001). Procellariids (*Diomedeoides*, *Rupelornis*) were most frequently found. In addition, the following families were recorded: Alcidae (*Petralca*), Pelagornithidae s. l. (*Caspiodontornis*), and Sulidae (*Empheresula*). A late Oligocene record of a *Diomedeoides* petrel from Babaheydar, southwestern Iran (Peters & Hamedani 2000), is a first paleornithological hint that marine avifaunas of the Indian Ocean and European seas were not significantly different from each other in the Oligocene, but more data for the Indian Ocean are needed to assess the relationships more adequately. On the other hand, the absence of the Plotopteridae, well known from the Oligocene of the northern Pacific Ocean, indicates that a barrier for seabirds existed at that time between the northern Pacific Ocean and the European seas, although it remains unclear what represented this barrier.

Miocene

The marine avifauna of European seas in this period included procellariids s. l. (*Rupelornis*, *Diomedeoides*, *Plotornis*, ?*Diomedea*), sulids (*Empheresula*, *Enkurosula*, *Morus*, *Sarmatosula*), phaethons (*Heliadornis*), and pelagornithids (indet.). In addition, a diver (*Gavia schultzi* Mlíkovský, 1998), found in the middle Miocene (MN 7) marine deposits of Sankt-Margarethen, Austria (Mlíkovský 1998), is a good candidate for a seabird. However, its inclusion among the seabirds is uncertain because modern *Gavia* divers inhabit both fresh and saltwater. The record ranges from MN 1 to MN 10, whereas no seabirds were recorded from the younger part of the late Miocene (MN 11-13), which coincides with the Messinian Crisis (e.g. Popov et al. 2006; Gladstone et al. 2007).

Family (s.l.)/Genus	Paleocene		Eocene				Oligocene		Miocene					Pliocene		Pleistocene/ Recent
	Early	Late	Ypresian	Lutetian	Bartonian	Priabonian	Stampian	Chattian	Agenian	Orleanian	Astaracian	Vallesian	Turolian	Ruscinian	Villanyian	
	1-5	6	7-10	11-13	14-16	17-20	21-24	25-30	1-2	3-5	6-8	9-10	11-13	14-15	16-18	19-20
Spheniscidae																
Procellariidae			■				■	■	■		■ ?			■	■	■
*Primodroma**			■													
*Diomedeoides**							■		■							
*Plotornis**									■							
Diomedea											■ ?					
*Pterodromoides**														■		
Phoebastria															■	
Puffinus															■	■
Fulmarus																■
Pterodroma																■
Bulweria																■
Calonectris																■
Hydrobates																■
Pelagodroma																■
Oceanodroma																■
Pelagornithidae*			■	■				■			■ ?	?			■	
*Dasornis**			■	■												
*Odontopteryx**			■													
*Macrodontopteryx**			■													
*Pseudodontornis**			■													
*Neptuniavis**			■													
Caspiodontornis								■								
*Pelagornis**															■	
Phaethontidae		■	■								■	■				
*Lithophila**		■														
*Prophaethon**			■													
*Heliadornis**											■	■				
Fregatidae			■ ?													
Sulidae				■		■		■	■	■	■				■	■
*Eostega**				■		■										
*Empheresula**								■	■							
*Enkurosula**									■ ?	■						
*Sarmatosula**											■					
Morus											■					■
Plotopteridae*																
Alcidae								■						■	■	■
*Petralca**								■								
Alca														■	■	■
Uria																■
Alle																■
Cepphus																■
Fratercula																■

Tab. 1. Occurrence of seabird families and genera in the Cenozoic European seas. See text for exact data and for comments on the validity of involved genera. Note that family records include also specimens not identified to genus level. Fossil taxa are marked with an asterisk (*).

The Miocene marine avifauna of European seas shows similarities with contemporary marine avifaunas on the western, i.e. North American, coasts of the North Atlantic (see Olson & Walker 1997; Rasmussen 1998; Olson & Rasmussen 2001).

Pliocene

The Pliocene record is limited to Atlantic shores and the western part of the Mediterranean Sea. It includes Procellariidae s. l. (*Phoebastria*, *Puffinus*, *Pterodromoides*), Alcidae (*Alca*), and Pelagornithidae (*Pelagornis*). This avifauna markedly differs from the Miocene one, which indicates that the European marine avifauna did not survive the Messinian Crisis.

Quaternary

Only modern species and the recently extinct Great Auk were recorded from the Quaternary deposits and are or were known as recent breeders at European seas. The record includes (vagrants and accidental breeder omitted) the Procellariidae (*Fulmarus*, *Pterodroma*, *Bulweria*, *Calonectris*, *Puffinus*, *Hydrobates*, *Oceanodroma*), Sulidae (*Morus*), and Alcidae (*Uria*, *Alle*, *Alca*, *Cepphus*, *Fratercula*) (Hagemeijer & Blair 1997; Tyrberg 1998, 1999; Sánchez Marco 2004). The breeding occurrence of these birds is now largely limited to Atlantic shores and Atlantic islands (Hagemeijer & Blair 1997; Zotier et al. 1999). The Mediterranean Sea is inhabited only by *Puffinus*, *Calonectris* and *Hydrobates* petrels, while no proper seabirds (from families covered in this paper) are currently breeding in the Black and Caspian Seas (Hagemeijer & Blair 1997; Zotier et al. 1999; Brooke 2002).

Štegman (1948) suggested that modern marine avifaunas of the Mediterranean, Black, Caspian and Aral Seas are relics of the Tethys avifauna. His opinion is not supported by the present data. Instead, there is no evidence that seabirds survived the Messinian Crisis in European seas (see above). The paleontological data presented here, zoogeographical data (Voous 1976), as well as molecular data (Wink et al. 1993; Heidrich et al. 1996, 1998; Cagnon et al. 2004; Gómez-Díaz et al. 2006) suggest that modern seabirds spread to the Mediterranean Sea from the North Atlantic only after the Messinian Crisis, and that relevant speciation events are all post-Miocene in age.

Summary

European seas were inhabited by seabirds from the Paleocene onwards and – expectedly – their presence and diversity depended on sea conditions. The data available indicate that three main phases in the evolution of local marine avifaunas can be distinguished: (1) Paleocene-Eocene, (2) Oligocene-Miocene, and (3) Pliocene-Recent (tab. 1). Major breaks in the evolution of these avifaunas seem to coincide with major climatic events (Zachos et al. 2001), but the fossil record of marine birds here is still too meagre to allow for a detailed resolution of their evolution.

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