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Fossil Seabirds and Changing Marine Environments in the Late Tertiary of South Africa

Storrs L. Olson

FitzPatrick Institute, University of Cape Town, Rondebosch 7700, South Africa.*

Fossil seabirds from early Pliocene (5 Myr ago) deposits in the southwestern Cape Province indicate there was a colder, more sub-Antarctic marine environment in this region in the late Tertiary than at present, thus corroborating and forcibly augmenting similar evidence from molluscs and pinnipeds. The Pliocene seabird fauna included at least four species of penguins (Spheniscidae), an albatross (Diomedeidae), two storm-petrels (Oceanitidae), three species of prions (Pachyptila), *one of which was much larger than any existing member of the genus, several shearwaters* (Puffinus *and relatives), a diving petrel* (Pelecanoides), *a booby* (Sula) *and at least two species of cormorants (Phalacrocoracidae). Gulls and terns (Laridae) were present but it cannot be determined if any of these were truly marine species. With the possible exception of the cormorants and larids, all of the elements of the early Pliocene marine avifauna have either become extinct or have retreated from the Cape region. Relatively few other seabirds, such as the gannet,* Morus capensis, *and the cormorant,* Phalacrocorax carbo lucidus, *have probably established themselves as breeding species in the region subsequently.*

*Fossielseevoëls in Suidwes-Kaaplandse afsettings uit die Vroeë Plioseen (5 miljoen jaar gelede) dui daarop dat daar tydens die Laat Tersiêr in dié gebied 'n kouer, meer subantarktiese mariene omgewing aanwesig was, en dit dien beslis ter bevestiging en versterking van dergelike getuienis aan die hand van molluske en vinpotiges. Die Plioseen-seevoëlfauna het minstens vier pikkewynspesies (Spheniscidae), 'n albatros (Diomedeidae), twee stormswaels (Oceanitidae), twee walvisvoëlspesies (Pachyptila) — waarvan een baie groter was as enige bestaande lid van die genus — verskeie pylstormvoëls (*Puffinus *en verwante voëls), 'n stormduiker (Pelecanoides), 'n malgas (*Sula*) en minste twee spesies duiker (Phalacrocoracidae) ingesluit. Meeue en sterretjies (Laridae) was ook aanwesig, maar daar kon nie vasgestel word of enigeen van hulle egte mariene spesies was nie. Met die moontlike uitsondering van duikers en lariede het al die elemente van die mariene avifauna uit die Vroeë Plioseen uitgesterf of uit Kaapland weggetrek. Betreklik min ander seevoëls, soos die gewone malgas* Morus capensis *en die duiker* Phalacrocorax carbo lucidus, *het hulself heel moontlik sedertdien as broeispesies in die gebied gevestig.*

Introduction

Bones of seabirds (Sphenisciformes, Procellariiformes, and Pelecaniformes) have now been recovered from three late Tertiary sites along the coast of the southwestern Cape Province, South Africa. This paper summarizes the significance of these fossils for understanding past marine environments and their effects on the distribution of seabirds.

The three fossil sites (Fig. 1) are at Ysterplaats air force base, on the outskirts of Cape Town, where only the very poorly preserved remains of three species of penguins were recovered; at Duinefontein, site of the Koeberg nuclear reactor plant, 25 km north of Cape Town; and Langebaanweg, 110 km north of Cape Town, where extraordinary concentrations of vertebrate fossils occur, including a great variety of birds.[1] The Langebaanweg site has been extensively studied, the principal fossiliferous deposits there deriving from the Varswater Formation, which is early Pliocene (5 Myr ago) in age.[2,3] Although the Ysterplaats and Duinefontein sites were originally regarded as Miocene,[4,5] more recent stratigraphic interpretations,[6,7] as well as the species composition of seabirds,[8] indicate that fossils at both localities were probably deposited during the same early Pliocene marine transgression that prevailed during most of the Langebaanweg sequence.

The deposits at Ysterplaats and Duinefontein appear to be purely marine in origin, with those from Duinefontein having been laid down in part in a lagoonal environment with intermittent direct connection to the sea.[9] The species diversity of seabirds at Duinefontein is greater than at Langebaanweg, although many taxa are represented by very fragmentary material, probably of migrant, non-breeding species.

In contrast, the fossils at Langebaanweg accumulated under a variety of conditions, including estuaries protected by islands that could have served as breeding sites for seabirds.[3] As a consequence, bones are generally better preserved at Langebaanweg and the seabird fauna is dominated by concentrations of fossils of relatively few species.

The fossil avifauna

Penguins (Spheniscidae)

At least four species of penguins may be distinguished in the South African Pliocene faunas, with the three largest being represented at Ysterplaats and all four at both Duinefontein and at Langebaanweg. Simpson,[4,5,10-12] who studied much smaller samples than are now available, named each of these species in a different extinct genus. Each of Simpson's specific names remains valid, but there can be no doubt that far too many generic names have been applied to these penguins. I believe that all four fossil species belong to a single genus that is essentially similar to living genera of penguins. This genus combines two possibly primitive postcranial characters now found only in the Antarctic genera *Pygoscelis* and *Aptenodytes*,[13] with a jaw morphology more similar to that in *Spheniscus*, the genus that includes the South African Jackass Penguin, *S. demersus*. (Specimens of the jaw are known only for two of the four fossil species, however.) Thus, we may be dealing with either an extinct genus that shares characters with each of the two major groups of living penguins, or simply with primitive forms of *Spheniscus*.

As the precise relationships of these fossil penguins are at present obscure, their palaeoecological significance is difficult to assess. Nevertheless, the penguin fauna in South Africa was clearly much

*Permanent address: National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560, U.S.A.

more diverse in the early Pliocene, possibly indicating richer food sources such as might have been present with colder waters and increased upwelling. One of the fossil species belongs to a size-class intermediate between the largest living penguins of the genus *Aptenodytes* (15 – 30 kg) and all other living penguins (2 – 6 kg).

Albatrosses (Diomedeidae)

There is only a single bone of an albatross from Langebaanweg, but this is incompletely ossified and may thus indicate breeding in the vicinity.

Storm-petrels (Oceanitidae)

At Langebaanweg there are fairly abundant remains of a species of *Pelagodroma* similar in size and morphology to the living White-faced Storm-petrel, *P. marina,* and that may have been ancestral to it. Storm-petrels are quite small for seabirds and are all but absent from Tertiary marine deposits. Only three other Tertiary fossils of the family have been reported to date, one of which is but the shaft of a humerus of a species the size of *Oceanites oceanicus* from Duinefontein, where fossils of *Pelagodroma* are entirely absent. The accumulations of *Pelagodroma* at Langebaanweg were almost certainly laid down in the vicinity of a breeding site, as they include the incompletely ossified bones of juveniles. Such a site would have been afforded by the islands that lay immediately offshore from Langebaanweg in the early Pliocene (Fig. 1). The modern species of *Pelagodroma* is not a particularly good indicator of surface-water conditions, as it breeds both on sub-Antarctic and subtropical islands. In the Atlantic it occurs in the Salvages, the Cape Verdes, and Tristan da Cunha, and it formerly bred on St Helena and Madeira, where it was probably extirpated during or after the 16th century.[14]

Petrels and Shearwaters (Procellariidae)

From Duinefontein come scant remains of a species of *Procellaria,* a species of *Calonectris,* three species of *Puffinus,* and an apparently extinct fulmarine petrel of uncertain affinities, but intermediate between *Daption* and *Fulmarus* in size. Of these species, only one, a form of *Puffinus* similar in size and morphology to the Short-tailed Shearwater, *P. tenuirostris,* is certainly present at Langebaanweg. Except for the enigmatic fulmarine, similar birds occur regularly as migrants or wanderers in South African waters today, and many of the above species from Duinefontein are likely to have been non-breeding birds. They indicate cold, but not necessarily sub-Antarctic waters.

Of much greater interest is the occurrence of three species of prions of the genus *Pachyptila* at Duinefontein and at Langebaanweg. One of these was a 'giant' form, much larger than any existing member of the genus. This giant prion is the most abundant procellariid at Langebaanweg, where incompletely ossified bones of juveniles were also found, and the species undoubtedly bred in the vicinity. The two other species of *Pachyptila*, both much less common than the largest one, fall within the size range of the modern species of this taxonomically complex genus, from which they cannot readily be distinguished.

Prions are birds of cold waters and although they occur off South Africa in large numbers today, their modern breeding grounds lie entirely within the sub-Antarctic realm, the nearest nesting site to South Africa being at Tristan da Cunha. The breeding of one, and perhaps as many as three, species of *Pachyptila* at Langebaanweg is a strong indication of a colder marine environment off the southwestern Cape in the early Pliocene than at present.

Diving Petrels (Pelecanoididae)

An even better indication, however, are three bones from at least two individuals of a diving petrel (*Pelecanoides*) similar in size to the living form *P. urinatrix exsul.* Diving petrels are likewise sub-Antarctic in distribution and furthermore are sedentary, seldom being found at any great distance from their breeding grounds. As with *Pachyptila,* the nearest modern breeding population of

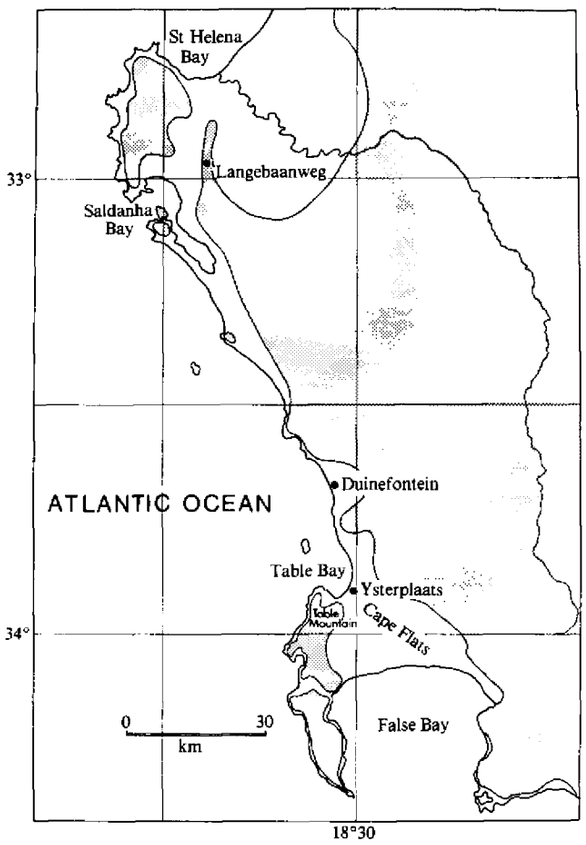

Fig. 1. Map of the southwestern Cape Province showing sites from which Tertiary seabirds have been collected and possible shoreline configuration during the early Pliocene (shaded portions). Note the several large islands that may have been used as breeding sites by early Pliocene marine birds.

Pelecanoides to South Africa today is at Tristan da Cunha, but no diving petrels are currently found in South African waters.

Gannets and Boobies (Sulidae)

The sole sulid in the fossil deposits is a small, rare species of *Sula* known only by four bones from Langebaanweg and one fragment of wing phalanx from Duinefontein. The much larger Cape Gannet, *Morus capensis,* is the only sulid found in Cape waters today. Despite the recent tendency to regard *Morus* as congeneric with *Sula,* these genera are very distinct osteologically and have been so at least since the middle Miocene.[15] Although at least one modern species of *Sula* (*S. variegata*) is restricted to cold waters off western South America, this is a large species, whereas the other, smaller species are all tropical forms. Thus, the small *Sula* at Langebaanweg and Duinefontein may be an indication of some adjacent areas of warm water, as is also suggested by certain fossil molluscs.[3]

Cormorants (Phalacrocoracidae)

The southwestern Cape today is one of only two places in the world (the other being New Zealand) where four species of cormorants co-exist in marine waters. Three of these species are endemic to South Africa. Preliminary analysis of the cormorant fossils[16] indicates the presence of three species at Langebaanweg and probably at Duinefontein as well. The rarest of these is very small, the size of the living Crowned and Reed Cormorants (*Phalacrorax coronatus* and *P. africanus*). The other two are medium-sized species that together are very abundant. These appear to be sibling species that are much more similar to one another osteologically than are the two modern species of medium-sized

cormorants in the Cape region (*Phalacrocorax capensis* and *P. neglectus*). There are no fossils of cormorants as large as the living White-breasted Cormorant (*P. carbo lucidus*), which now occurs throughout much of Africa, including the Cape.

Gulls and Terns (Laridae)

A brief perusal of the charadriiform humeri from Langebaanweg revealed scant representation of a gull about the size of *Larus hartlaubii,* a very worn distal end of a humerus of a larger gull slightly smaller than *Larus dominicanus,* and two species of terns, one about the size of *Sterna sandvicensis* and the other the size of terns in the *Sterna hirundo* complex. There are proximal ends of humeri for one of the terns and the smaller gull; interestingly, both of these appear to be slightly more primitive than modern forms in that the dorsal tricipital fossa is less excavated. This notwithstanding, I would assign the fossils to the modern genera *Larus* and *Sterna,* both of which are quite complex at the species level — to the extent that it would be very difficult to ascertain the precise relationships of the fossil species. Furthermore, as both *Larus* and *Sterna* contain species that may be freshwater, marine or both, the fossils can add little to our understanding of marine conditions and merely tell us that gulls and terns were present in South Africa in the early Pliocene. I have not considered them further in the following section.

Discussion

The basal portion of the Langebaanweg sequence is the so-called Gravel Member (GM).[2,3] This problematical unit is unconformable with the overlying Quartzose Sand Member (QSM) and the Pelletal Phosphate Member (PPM) and is thought to have been deposited during a late Miocene still-stand that predates the terminal Miocene marine regression.[2] Its significance to the present discussion lies in the fact that the invertebrates and sharks from this unit indicate warmer marine temperatures[3] than in the succeeding units.

The QSM and PPM were deposited during an early Pliocene marine transgression resulting from a regressive ice phase in the Antarctic. This followed the terminal Miocene period of maximum ice growth that precipitated the so-called 'Messinian salinity crisis'.[3] Molluscs from the QSM include 'two essentially cold-water species' and, although there are no identifiable molluscs from the PPM, the extinct seal *Homiphoca capensis* occurs in both units. This species is most closely related to Antarctic seals[17] and the greater development of the maxillo-turbinals in the individuals from the PPM has been interpreted as an adaptation to cold, thus indicating either an even colder environment during the deposition of the PPM, or more likely a lag in evolutionary response to continuing cold.[3,17] From the above, Hendey[3] reasoned that 'local sea temperatures at the time of deposition of the QSM were somewhat lower than those prevailing earlier when the GM was laid down, and might have been little different from those of the present (i.e. cold temperate)', and also that 'temperatures remained consistently cold' during the deposition of the PPM.

The seabird fauna from Langebaanweg and Duinefontein strongly supports the above evidence for cold marine temperatures in the Cape region during the early Pliocene. If anything, the presence as breeding birds of such characteristically sub-Antarctic forms as *Pachyptila* and *Pelecanoides,* as well as the much greater diversity of penguins, could be used to argue for even colder marine conditions than prevail at present.

One of the molluscs from the QSM, *Pyrene albuginosa,* would at first seem inconsistent with this interpretation, as this is a warm water species that ranges at present from False Bay to Natal. However, as Hendey[3] points out, the coast near Langebaanweg today is near the 'overlap region' between the Cold and the Warm Temperate marine provinces. In addition, warm water Indian Ocean elements would have had easier access to the Langebaanweg area in the early Pliocene, as the Cape Flats would have been inundated, thus linking False Bay and Table Bay (Fig. 1). The rare presence of a small booby (*Sula* sp.) at Langebaanweg and Duinefontein possibly represents a situation parallel with that of *Pyrene albuginosa,* and this bird is perhaps best regarded as an Indian Ocean intrusive.

The inundation of the Cape Flats has further implications for seabirds, as this would have made islands out of Table Mountain and the other peaks of the Cape Peninsula (Fig. 1). These islands may well have been among the principal nesting grounds of the seabirds that bred in the Cape region in the early Pliocene.

Given the following three points — 1) warmer sea conditions in the Miocene that became colder towards the end of this epoch, 2) the known seabird fauna in the early Pliocene, and 3) the composition of the modern seabird fauna — we can reconstruct something of the history of seabirds in the Cape region from the late Tertiary to the present.

Although it is dangerous to speculate on which seabirds may have been present in the late Miocene solely on the basis of marine temperatures having been warmer then than in the early Pliocene, we would nevertheless expect that such cold-water breeding taxa as *Pachyptila* and *Pelecanoides* may not have been present at all, and penguins may have been less diverse, although a single penguin bone from the Gravel Member indicates that at least one species was present whenever that unit was deposited. Temperatures decreased during the late Miocene, dramatically altering the marine environment and creating favourable conditions locally for cold-water taxa. During the early Pliocene, ocean temperatures remained cold; in addition, sea level rose, thus creating large islands near the Cape that were suitable breeding sites for cold-water seabirds.

The time of origin of the Benguela upwelling system that flows northward along the southwest African coast is now believed to be early late Miocene[18] and an extensive cold-water seabird fauna is unlikely to have developed in the Cape region before that current induced the high marine productivity needed to sustain such a fauna. The Benguela upwelling became progressively more intensive during the Pliocene and Pleistocene.[18] With the establishment of this current and its nutrient-rich waters, penguins, prions and diving petrels were able to move north from higher latitudes and colonize South Africa. It is not known how much speciation of seabirds actually took place in the Cape but it is highly likely that the species of *Pachyptila* and *Pelecanoides,* and perhaps most or all of the penguins, may already have been in existence in the Miocene but at more southerly latitudes and merely moved into South Africa as conditions became suitable.

As indicated by molluscs,[19] marine conditions along the western coast of South America also changed from warm-subtropical in the late Miocene to cool temperate in the early Pliocene. It is therefore quite likely that some of the same species of seabirds that moved into South Africa also moved up the west coast of South America concurrently. In this connection it would be of the greatest interest to compare the early Pliocene seabird fauna of South Africa with that indicated to be present in contemporaneous deposits on the coast of Peru.[20]

Since the early Pliocene, the seabird fauna of the Cape has changed drastically, although we do not know when or why these changes took place. Unless one of the early Pliocene penguins from South Africa is the ancestor of *Spheniscus demersus,* all four species of penguins became extinct; only a single species now occurs in South Africa. As there are no species of Procellariiformes breeding on any African continental island today, all of those that bred in the Cape region in the early Pliocene either retreated to higher latitudes (e.g. *Pelecanoides* and the smaller species of *Pachyptila*) or became extinct (the giant *Pachyptila*). As there is no gannet known from the early Pliocene deposits, we may assume that the ancestors of the Cape Gannet, *Morus capensis*, colonized Southern Africa and speciated since the early Pliocene. The genus *Morus,* with living species in the North Atlantic, South Africa, and Australia/New Zealand, is known from the middle Miocene to the present in the

North Atlantic, and from the middle Miocene to the late Pleistocene in the North Pacific.[15] Nothing is known of the past history of *Morus* in the southern hemisphere, but the evidence from South Africa suggests that the populations there may have been derived from northern oceans since the early Pliocene. The small booby (*Sula* sp.) at Langebaanweg and Duinefontein has disappeared from the Cape since the early Pliocene and either became extinct or evolved into one of the living tropical species of boobies.

Of truly marine birds, only among the cormorants are there species that may have adapted to changing conditions and persisted in the Cape region. Whereas there are four species of cormorants in the present marine avifauna of the Cape, at most three are known in the early Pliocene, although the relationships of the fossil taxa to those still living have not yet been determined. Because of its wide modern distribution and the absence of any very large cormorants in the early Pliocene, *Phalacrocorax carbo* is the species that is most likely to have moved into South Africa since the early Pliocene.

Thus, except for the cormorants, the breeding seabird fauna of the Cape region has completely changed since the early Pliocene, with sub-Antarctic elements having been eliminated or replaced, despite the fact that cold upwelling has persisted in the area since the Miocene. This is paralleled by the seals, in which the extinct monachine *Homiphoca capensis*, with Antarctic affinities, has been replaced by an otariid fur seal, *Arctocephalus pusillus*, whose congeners are found in sub-Antarctic or subtropical waters. The causes of this nearly complete turnover in marine homeotherms are not clear. Fluctuating sea levels during the late Pliocene/Pleistocene glacial and interglacial episodes would certainly have changed the number and configuration of suitable breeding islands and this may have influenced seabird distribution in addition to any changes in the marine environment that Pleistocene events may have caused.

The early Pliocene seabird faunas from South Africa are of interest not only for the insights that they provide into past marine conditions, but also because they constitute the only Tertiary evidence yet available for several sub-Antarctic taxa. For example, the fossils of *Pachyptila, Pelecanoides* and *Pelagodroma* from Langebaanweg and Duinefontein constitute the only Tertiary records for their respective genera. It is hoped that additional palaeontological exploration of marine Tertiary deposits in South Africa will provide us with further information concerning the evolutionary history of seabirds in the southern oceans.

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