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AN EARLY PLIOCENE MARINE AVIFAUNA FROM DUINEFONTEIN, CAPE PROVINCE, SOUTH AFRICA

By

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Cape Town Kaapstad

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By

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(With 3 figures and 1 table)

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ABSTRACT

Late Tertiary marine deposits of the Varswater Formation at Duinefontein, Cape Province, South Africa, have yielded remains of 16 or 17 species of sea-birds (Sphenisciformes, Procellariiformes, Pelecaniformes) and one land-bird (Galliformes, Phasianidae). Most of the sea-birds are characteristic of cold waters, indicating that these deposits are probably no older than late Miocene, the age of origin of the Benguela upwelling, and the species composition of the marine avifauna correlates well with nearby early Pliocene deposits at Langebaanweg. Differences between the sea-bird faunas at these two sites may be related to differences in the depositional environments.

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INTRODUCTION

During the construction of the Koeberg nuclear power station in 1978, fossiliferous sediments were exposed in two excavations at Duinefontein farm on the coast 30 km north of Cape Town. Vertebrates recovered here consist of marine birds, cetaceans, sharks, and bony fishes, as well as a small terrestrial component including ungulate, lagomorph, snake, and turtle remains (Rogers 1979). To date, the only study of any of the vertebrates from this site is Simpson's (1979*b*) report on six penguin bones, identified as belonging to two species, only one of which, *Nucleornis insolitus*, was represented by sufficiently diagnostic material to merit naming. Since then, many more avian fossils have been obtained, so that now there are over 70 reasonably diagnostic bones of penguins from at least four species, as well as specimens assignable to 12 or 13 species of

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Procellariiformes and Pelecaniformes, and a single fragment of a francolin bone (Phasianidae, Galliformes), the last being the only terrestrial bird in the fauna.

Although many of the specimens are very fragmentary and can be identified only tentatively, the fauna nevertheless provides important new information on the distribution and occurrence of sea-birds in the late Tertiary of the South Atlantic. All fossil specimens are in the collections of the section of Cenozoic Palaeontology at the South African Museum and specimen numbers are preceded by the acronym SAM–PQ, here omitted for brevity.

SYNOPSIS OF THE GEOLOGY AND AGE OF TERTIARY SEA-BIRD SITES IN THE CAPE PROVINCE

Tertiary sea-birds have been obtained from three localities (Fig. 1) in the south-western Cape Province—Duinefontein, Ysterplaat, and Langebaanweg (Olson 1983). As the first two of these sites have in the past been attributed incorrectly to the Miocene (Simpson 1973, 1979*b*), it is appropriate to review here some of the new stratigraphic and faunal information altering that interpretation. Simpson, of course, is blameless in referring to the Duinefontein and Ysterplaat sites as Miocene, for he relied entirely on preliminary assessments that had been communicated to him. Nevertheless, the belief that the penguin fossils from these sites were Miocene in age probably affected his taxonomic conclusions to some degree.

The best known of the above sites is Langebaanweg, the stratigraphy and mammalian fauna of which has been exhaustively treated by Hendey and others in numerous papers (see Hendey 1981*a*, 1981*b*, 1982, and references therein). Virtually all sea-bird fossils from Langebaanweg come from two extremely fossiliferous units of the Varswater Formation that are early Pliocene (5 Ma) in age (Hendey 1981*a*, 1981*b*, 1982). Fossils were deposited under a variety of estuarine, palustrine, and fluviatile conditions. The vertebrates, although dominated by terrestrial forms, have a strong marine component that includes sharks, seals, and whales, as well as sea-birds. The marine avifauna consists for the most part of numerous individuals of relatively few species that probably bred on nearby islands (Olson 1983, 1985).

In the revised view of the stratigraphy of the Duinefontein sediments, the beds containing fossil birds are now considered to belong to the Duynefontyn Member of the Varswater Formation (Dingle *et al.* 1983, modified from Rogers 1979). The bird remains were apparently deposited during the same early Pliocene marine transgression during which the Langebaanweg deposits were formed. The deposits are 8,2 to 8,5 m below present sea level. The environmental setting at the time of deposition is thought to have been a lagoon sheltered by a barrier spit that was breached by storm or spring tides (Rogers 1979). This interpretation accords with the fact that some of the bird bones are fairly well preserved, whereas others are heavily worn. The avifauna consists almost entirely

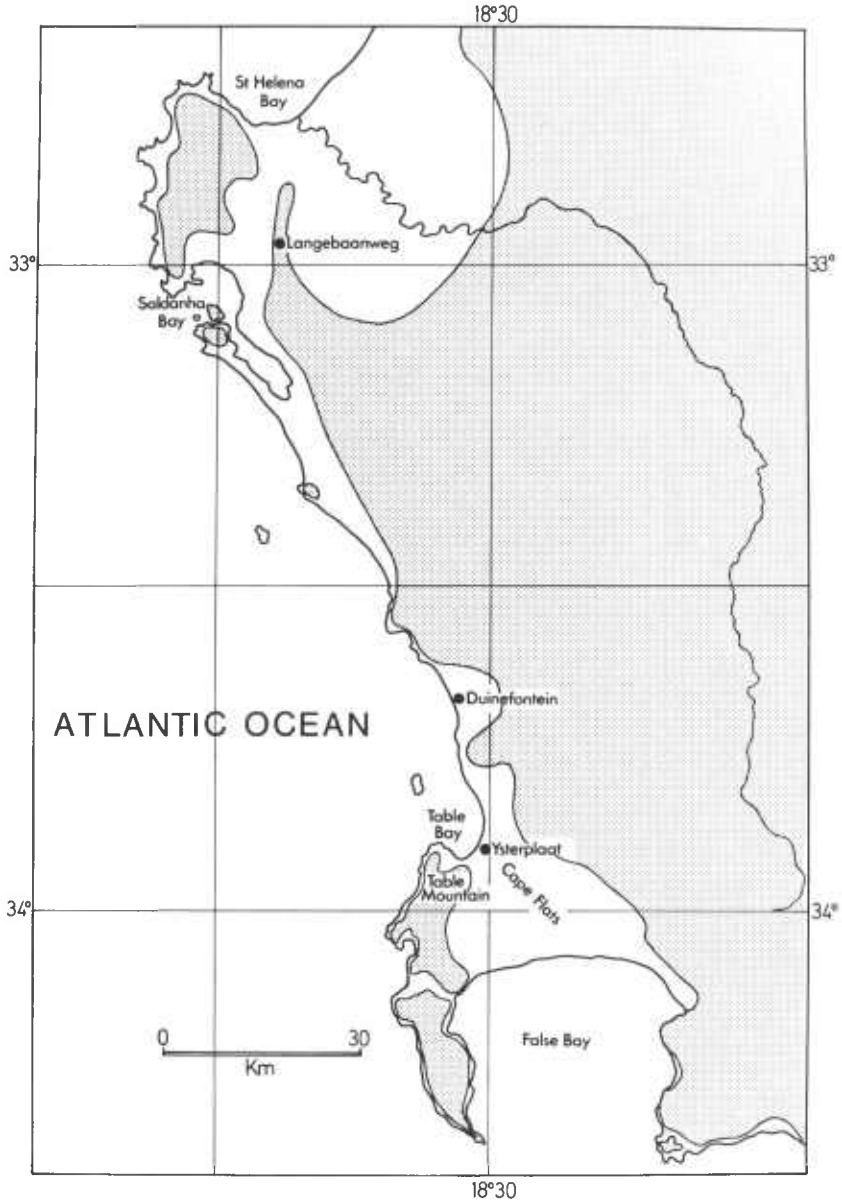

Fig. 1. Tertiary sea-bird localities in the south-western Cape Province showing their relationship to possible shoreline configuration (shaded portion) in the early Pliocene (modified from Olson 1983).

of pelagic species, a number of which may have been non-breeding migrants. This indicates direct access to the open ocean, at least at times. Of the 16 or 17 species in the Duinefontein fauna, 10 to 12 appear to be shared with Langebaanweg, which is further evidence of their probable contemporaneity.

The deposits at Ysterplaat Air Force Base, on the outskirts of Cape Town, are at 10 m above sea level and 1,5 km from the present coastline. Tankard (1975*a*, 1975*b*) assigned the Ysterplaat deposits to his Saldanha Formation, the type section of which is much farther north on Hoedjiespunt in Saldanha Bay. This formation was erected by Tankard 'as a convenience to accommodate all phosphate rock-bearing horizons in the western Cape', the assumption at the time being that all such phosphate rocks were Miocene in age, whereas subsequently 'it has been shown that thick phosphate rock units occur in the upper part of the Varswater Formation' (Dingle *et al.* 1979: 91). Consequently, 'the original definition of the Saldanha Formation, as a lithostratigraphic unit distinct from the Varswater Formation, cannot be demonstrated with present data, and . . . the use of the term "Saldanha Formation" [should] be discontinued' (Dingle *et al.* 1979: 81). Because the assumption that phosphatic rocks must be Miocene was erroneous, because there was no real basis for assigning the Ysterplaat deposits to the Saldanha Formation in the first place, and because the existence of such a formation cannot be demonstrated, there is no basis for considering the Ysterplaat deposits to be Miocene in age. These deposits appear to be purely marine in origin, the only vertebrate fossils present being those of penguins, whales, and sharks. The penguin material is in very poor condition, although part of it provided the basis for the species Simpson (1973) named *?Palaeospheniscus huxleyorum*. As far as the material permits, the three species of penguins at Ysterplaat appear to be the same as the three largest species common to both Duinefontein and Langebaanweg. There is no evidence at present that the Ysterplaat fossils are not of approximately equivalent age.

Thus, new stratigraphic revisions, as well as the nature of the marine avifauna, indicate that all three sites in the south-western Cape from which fossil sea-birds have been recovered are likely to be early Pliocene in age, the deposits all probably having formed at some phase of the same sea-level cycle. On the basis of molluscs from the Gravel Member underlying the Varswater Formation at Langebaanweg, Hendey (1981*a*, 1981*b*) postulated that late Miocene marine temperatures were warmer than during the deposition of the succeeding early Pliocene sediments. Furthermore, Siesser (1980) has shown that the Benguela Current and its associated cold upwelling did not originate off the south-western coast of Africa until the early late Miocene. The marine avifaunas from Duinefontein and Langebaanweg contain a number of Subantarctic, cold-water species of Procellariiformes as well as a diversity of penguins (Olson 1982, 1985, in prep.). Such assemblages would have been unlikely to have been present prior to the origin of the colder waters and increased marine productivity that the Benguela upwelling would have provided; hence these fossils would not be older than late Miocene in any case.

SYSTEMATICS

Order SPHENISCIFORMES

Family **Spheniscidae**

There are at least four species of penguins from Duinefontein, corresponding to the four species named from South Africa by Simpson (1971, 1973, 1975, 1979*b*). These species, however, were described in four different extinct genera, whereas it is now believed that all probably belong to a single genus (Olson in prep.). This genus is either distinct from all living genera but closely related to *Spheniscus*, or the South African fossil penguins are actually primitive forms of *Spheniscus* and should be referred to that genus. In the former case, the generic name *Inguza* Simpson (1979*a*) would apply. A decision on the generic status of these penguins would perhaps be facilitated by examination of early Pliocene penguins from Peru (see De Muizon 1980, 1981). Rather than creating new combinations at this point, each species has been listed in the genus in which it was last placed by Simpson, with the generic name in quotes to indicate present uncertainties.

'Nucleornis' insolitus Simpson, 1979

Material

Holotype: right tarsometatarsus, MBD4. Paratype: right tarsometatarsus, MBD3. Specimens referred herein: worn proximal end of left coracoid, MBD215; distal end of left radius, MBD399; proximal ends of right radii, MBD7, MBD161; distal end of right ulna, MBD304 + MBD160; shafts of left femora, MBD318, MBD532; shaft of right tibiotarsus, MBD320; worn metatarsal (probably R4), MBD219. Minimum number of individuals, 2.

Remarks

This species is the largest of the South African fossil penguins and is larger than any living penguin except the two species of *Aptenodytes*. It is the only species for which Duinefontein is the type-locality. The two tarsometatarsi studied by Simpson (1979*a*) remain the only really diagnostic specimens, although a few others from Duinefontein, Ysterplaat, and Langebaanweg are assigned to this species on size alone.

'Dege' hendeyi Simpson, 1975

Material

Worn right radius lacking distal end, MBD303; shaft of left tibiotarsus, MBD533.

Remarks

This rare species is intermediate in size between *'Nucleornis' insolitus* and *'?Palaeospheniscus' huxleyorum*. The only reasonably diagnostic material is from

Langebaanweg, the type-locality, with fragmentary specimens from Duinefontein and Ysterplaat being referred on size.

'?Palaeospheniscus' huxleyorum Simpson, 1973

Material

Fragment of right mandibular ramus, MBD201; right clavicle, MBD419 [possibly too large for this species]; fragmentary right coracoids including at least the glenoid area, MBD153, MBD154, MBD214, MBD310, MBD313, MBD528; fragmentary left coracoids including at least the glenoid area, MBD2, MBD152, MBD308, MBD311, MBD312; sternal ends of left coracoids, MBD203, MBD307; proximal ends of right humeri, MBD296, MBD527; shafts of right humeri, MBD207, MBD211, MBD297; distal ends of right humeri, MBD210, MBD294; complete left humerus, MBD151; complete left ulna, MBD202; complete right radius, MBD302; proximal end of right radius, MBD129A; left radius lacking distal end, MBD305; distal end of left radius, MBD129B; ulnare, MBD418; alar phalanx, MBD314; complete right femur, MBD92; proximal ends of right femora, MBD300, MBD301; distal ends of right femora, MBD157, MBD315, MBD400, MBD471; shafts of right femora, MBD218, MBD535; fragmentary tibiotarsi, MBD212, MBD213, MBD316, MBD515; complete left tarsometatarsus, MBD292; shaft of left tarsometatarsus, MBD468. Minimum number of individuals, 6.

Remarks

This species is somewhat larger than the largest individuals of the living South African penguin *Spheniscus demersus*. Originally described from Ysterplaat, it is the most abundant penguin at Duinefontein and the second most abundant at Langebaanweg, where most of the material was incorrectly attributed to the larger species *'Dege' hendeyi* by Simpson (1975).

'Inguza' predemersus (Simpson, 1971)

Material

Right mandibular articulation, MBD322; right quadrate, MBD342; scapular end of left coracoid, MBD155; complete right humerus, MBD295; shaft of right humerus, MBD10; shafts of left humeri, MBD11, MBD70; distal end of left humerus, MBD530; complete left ulna, MBD159; right radius, MBD204; complete right carpometacarpus, MBD293; shaft of right tibiotarsus, MBD319; left tibiotarsus lacking proximal end, MBD1; shaft of left tarsometatarsus lacking fourth metatarsal, MBD487. Minimum number of individuals, 3.

Remarks

This is the commonest penguin at Langebaanweg, the type-locality, and is the second most abundant penguin at Duinefontein, although it was not

recovered at Ysterplaat. It is a small species, somewhat smaller than *Spheniscus demersus*, to which it was originally thought to be ancestral (Simpson 1971).

In addition to numerous unidentifiable scraps of penguin bone, there are specimens that seem to be too large for *'Inguza' predemersus* and too small for *'?Palaeospheniscus' huxleyorum*: fragmentary right coracoids, MBD309, MBD401; shaft of right femur, MBD317; distal end of right femur, MBD534; shaft of right tibiotarsus, MBD158; distal end of left tibiotarsus, MBD298. These fossils cannot be assigned positively, nor can it be stated with certainty that they represent a fifth species. Some bones from Langebaanweg are also of this size.

Order PROCELLARIIFORMES

Family **Oceanitidae**

Subfamily Oceanitinae

Oceanites sp.

Material

Shaft of right humerus with distal portion of scar for M. pectoralis, MBD260.

Remarks

Although very fragmentary, this specimen comes from a species much smaller than any other bird known from Duinefontein and is sufficiently diagnostic for assignment to the short-winged subfamily Oceanitinae of the Oceanitidae. It is from a bird smaller than *Oceanites zaloscarthmus*, a species common at Langebaanweg (Olson 1985), and agrees in size and details with the living species *Oceanites oceanicus*.

Family **Procellariidae**

Fulmarinae, gen. et sp. indet.

Fig. 2

Material

Distal end of right humerus, MBD334.

Remarks

This is one of the better-preserved specimens from the Duinefontein site and is quite singular in its morphology. The very deep brachial fossa and triangular, proximally pointing ectepicondylar spur (processus supracondylaris dorsalis) give it a strong superficial resemblance to a gull (Laridae); yet the lack of distinct tricipital sulci, the more expanded and rounded ventral epicondylar area, and the heavier shaft in ventral view show that it cannot be a gull and must belong in the Procellariidae. The shortness of the ectepicondylar spur, the deep brachial fossa, and the less flattened and expanded ventral epicondylar area suggest that this bird belongs with the 'fulmarine' group of petrels, rather than with *Procellaria, Calonectris*, or *Puffinus*. In size it is intermediate between the smaller *Daption* on

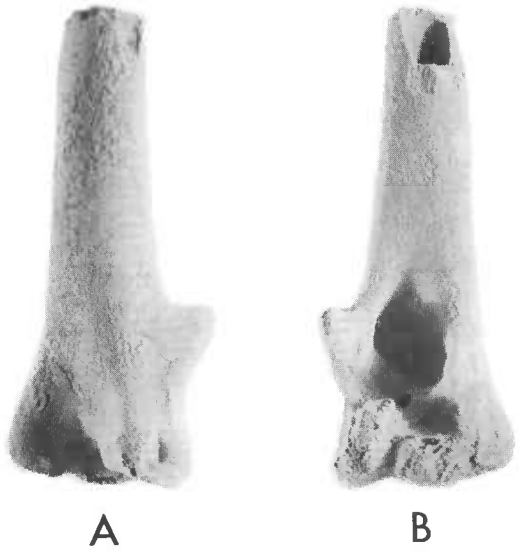

Fig. 2. Distal end of right humerus of Fulmarinae, gen. et sp. indet., MBD334. A. Caudal aspect. B. Cranial aspect. ×2.

the one hand, and the larger *Fulmarus–Thalassoica* on the other. Of these genera, it is more similar to *Daption* in not having the brachial depression extending as far proximally. It differs from these genera, as well as from *Pagodroma, Halobaena*, and *Pachyptila*, in the shape of the ectepicondylar spur and in the deeper brachial fossa. If correctly referred to the fulmarine petrels, this specimen would represent a species in a size-class that has become extinct. A coracoid from Langebaanweg may also be referable to this species because it is too large for the largest species of *Pachyptila* yet is not referable to the genus *Puffinus* or any of its close relatives (Olson 1985).

Pachyptila salax Olson, 1985

Material

Incomplete distal end of right humerus, MBD261; incomplete distal end of left humerus, MBD253; pieces of shaft of right humerus, MBD149, MBD246; proximal end of left carpometacarpus, MBD463; distal end of left carpometacarpus, MBD237; fragment of right coracoid, MBD387; proximal end of left tarsometatarsus, MBD410. Minimum number of individuals, 2.

Remarks

The specimens listed here belong to a species smaller than any of the other procellariids in the fauna except the two following. The only reasonably

diagnostic specimen is MBD261, which, although lacking the condyles, has the ectepicondylar spur and part of the brachial fossa remaining. The spur is short and rounded and the brachial fossa is deep, as in *Pachyptila*, and the specimen agrees in size and other details with the giant species *Pachyptila salax* that dominates the procellariiform fauna at Langebaanweg (Olson 1985). The other material from Duinefontein is referred to this species solely on the basis of size.

Pachyptila species B

Material

Distal end of left humerus, MBD546.

Remarks

This specimen is from a species of *Pachyptila* the size of *P. vittata*, the largest of the living species of the genus. It is indistinguishable from a comparable specimen from Langebaanweg (Olson 1985).

Pachyptila species C

Material

Right coracoid, MBD322; shaft of left humerus, MBD464; shaft of right humerus, MBD339.

Remarks

This species is smaller than *P. vittata* and is similar in size to the smaller living species *P. desolata*, being smaller than any of the other procellariids in the Duinefontein fauna. The coracoid is the only reasonably well-preserved specimen, the others being included only on size. This species would be of the same size as the smallest species of *Pachyptila* from Langebaanweg.

Procellaria sp.

Material

Shaft of left humerus with most distal part of pectoral crest and scar for M. pectoralis, MBD86 + 86C.

Remarks

This specimen is assigned to the genus *Procellaria* (including *Adamastor*) on size alone, the members of this genus being much smaller than *Macronectes* and markedly larger than any of the other forms of Procellariidae. The fossil also agrees with *Procellaria* in the pronounced, wide distal scar for M. pectoralis. This is the first Tertiary record of the genus *Procellaria*.

Calonectris sp.

Material

Right carpometacarpus lacking minor metacarpal and distal end, MBD144; worn distal end of right tarsometatarsus, MBD324.

Remarks

These specimens are from a large shearwater slightly larger than *Calonectris diomedea* or *Puffinus gravis*. The alular metacarpal is decidedly notched and thus very unlike *Fulmarus, Daption*, or *Macronectes*. In size and robustness of shaft, MBD144 is most similar to *Calonectris diomedea*, although the pisiform process is more reduced in the fossil.

Puffinus (Puffinus) species A

Fig. 3A

Material

Complete right ulna, MBD545; shaft of right humerus, MBD564; shaft of left humerus, MBD336.

Remarks

The ulna cited here is the most complete of the diagnostic procellariiform fossils from Duinefontein, lacking only part of the olecranon. The shaft is very short, thick, and curved compared to the ulnae in modern species of *Puffinus* of comparable size. The distal portion of a shaft of a humerus is tentatively assigned here as it is much compressed but larger than in either of the other two species of *Puffinus* from Duinefontein.

Puffinus (Puffinus) species B

Fig. 3B, C

Material

Distal end of left humerus, MBD12; shafts of left humeri, MBD407, MBD496; distal ends of right humeri, MBD146, MBD244, MBD497; shafts of right humeri, MBD565, MBD407; distal end of left tibiotarsus, MBD458; distal end of left tarsometatarsus, MBD13. Minimum number of individuals, 2.

Remarks

This species has the very flattened humerus characteristic of the subgenus *Puffinus*. It is nearest to the living species *P. tenuirostris* in size and morphology but appears to be slightly smaller. A few bones from Langebaanweg (e.g. Fig. 3B) have also been assigned to this species (Olson 1985).

Fig. 3. Wing elements of *Puffinus*. A. *Puffinus* species A, MBD545, right ulna, ventral aspect. B–D. Distal ends of right humeri, cranial aspect. B. *Puffinus* species B, L25577F (Langebaanweg). C. *Puffinus* species B, MBD244 (Duinefontein). D. *Puffinus* species C, MBD337. All figures × 2.

Puffinus (Puffinus) species C

Fig. 3D

Material

Distal end of right humerus, MBD337; shaft of right humerus, MBD86; shaft of right ulna, MBD566; proximal end of left ulna, MBD541. Minimum number of individuals, 2.

Remarks

These fossils appear to be from a species of *Puffinus* smaller than *Puffinus (P.)* species B and similar in size to *P. p. puffinus* but not having the shaft as compressed or the brachial depression as reduced as in that species. Morphologically it is thus more like a small version of *P. tenuirostris*.

Medium-sized indeterminate Procellariidae

Among the remaining specimens from Duinefontein are 13 fragments of humeri, 5 of ulnae, 6 of carpometacarpi, 4 scapulae, 1 coracoid, and 6 basal phalanges of the major digit of the wing that can be assigned to the Procellariidae. Among the species recognized from Duinefontein, these specimens are too large for any *Pachyptila* and too small for *Calonectris* or *Procellaria*, but they are not otherwise sufficiently diagnostic to be assigned to any of the four medium-sized species recognized here, or to permit the recognition of any additional species.

Order PELECANIFORMES

Family **Sulidae**

Sula sp.

Material

Proximal half of phalanx 1 of major digit of wing, MBD340.

Remarks

This specimen comes from a sulid much smaller than the living Cape gannet *Morus capensis* and is thus likely to be referable to the same small species of *Sula* that is known from Langebaanweg (Olson 1983). The material from Langebaanweg is so scanty that it does not merit detailed treatment in a separate publication, and therefore will be dealt with here.

The four specimens of *Sula* sp. from Langebaanweg consist of two sternal ends of right coracoids from the Pelletal Phosphorite Member (Bed 3aS) and the scapular end of a coracoid and distal end of a humerus from the Quartzose Sand Member. These represent a minimum of four individuals. Measurements of these specimens are as follows: coracoid—head to sternal lip of glenoid facet 20,1 mm, length and width of glenoid facet 10,8 × 6,5 mm, length and width of furcular facet 7,3 × 6,0 mm, depth through sternal facets 8,6 mm; humerus—greatest

diagonal diameter of brachial depression 14,2 mm, length of dorsal condyle 8,7 mm.

These specimens differ from *Morus* and resemble *Sula* in the following characters: much more expanded ventral lip and smaller dorsal lip of the sternal facet of the coracoid; more rounded rather than ovoid furcular facet; dorsal condyle of humerus not noticeably hooked. Compared to the modern species of *Sula*, the South African species is small, falling within the lower part of the size range of the living species *Sula sula* but slightly exceeding in size the smallest individuals of that species from the Central Pacific. The material is too fragmentary for detailed comparisons with living species and although the fossil form was fairly similar to *Sula sula* it differs in having the dorsal lip of the sternal facet of the coracoid narrower and the brachial depression of the humerus shallower.

It has been suggested that this species of *Sula* may have been an incidental warm-water element in the early Pliocene fauna of the south-western Cape, for which there is precedent among molluscs as well (Olson 1983). The only sulid in the Cape region today is the endemic gannet *Morus capensis*, a much larger form for which no antecedent has been found in the Langebaanweg or Duinefontein deposits. The modern species of *Morus* are found in the cool-temperate waters of the North Atlantic, South Africa, Australia and New Zealand. The genus also persisted into the late Pleistocene in the North Pacific but died out there subsequently. In the Miocene and Pliocene of the western North Atlantic, the sulid fauna consisted mainly, if not entirely, of a variety of species of *Morus* differing greatly in size, suggesting that the species of *Sula* were mainly of tropical distribution at that time, as they are today. Thus, I would postulate that *Morus* probably did not disperse to the Southern Hemisphere until after the early Pliocene. The discontinuous distribution of the three living species reflects the discontinuity of suitable habitat. Dispersal between these widely disjunct breeding ranges appears to present few problems for these strong-flying birds, as documented by the numerous instances of vagrant individuals of one species being found in breeding colonies of another (Crawford *et al.* 1983).

Family **Phalacrocoracidae**

Fossil cormorants from Langebaanweg are treated by James (in prep.), whose identifications are followed here.

Phalacrocorax sp., medium-sized

Material

Cranial end of right scapula, MBD540; scapular end of right coracoid, MBD242; part of humeral end of right coracoid, MBD252; shafts of right coracoids, MBD382, MBD567; shaft and sternal end of left coracoid, MBD383; proximal end of right humerus, MBD326; proximal ends of right ulnae, MBD249,

MBD412; proximal end of left ulna, MBD247; distal ends of left ulnae, MBD338, MBD403; proximal end of left radius, MBD404; proximal end of left carpometacarpus, MBD327; shaft and distal end of right carpometacarpus, MBD196; distal end of left carpometacarpus, MBD329; proximal end and shaft of left femur, MBD243; proximal ends of left femora, MBD145, MBD248; proximal end of right tarsometatarsus, MBD417. Less diagnostic specimens that probably also belong to this species: part of humeral end of left coracoid, MBD385 (small); shaft of right humerus, MBD333A; abraded distal end of left tarsometatarsus, MBD235 (small). Minimum number of individuals, 3.

Remarks

This material is considered to be conspecific with the species from Langebaanweg described by James (in prep.), although a few very minor points of osteological difference do exist between the Duinefontein and Langebaanweg samples. James (in prep.) discusses the evolutionary relationships of this fossil species.

The amount of size variation in bones of medium-sized cormorants from Duinefontein is comparable to that observed in the much larger sample of fossil cormorants from Langebaanweg. The proportion of larger and smaller individuals of this species differs among the major stratigraphic members of the Varswater Formation at Langebaanweg, suggesting that a larger and a smaller population of the species may have coexisted on the South African coast during the early Pliocene (James in prep.). If this view is correct, then it is apparent that individuals from both populations were deposited at Duinefontein as well as at Langebaanweg.

Phalacrocorax cf. *(Microcarbo)* sp.

Material

Distal end of left ulna, MBD245.

Remarks

This ulna is small enough to fall within the size range of *Phalacrocorax (Microcarbo) coronatus*, the living endemic marine 'microcormorant' of South African waters. Unfortunately, the specimen is not sufficiently diagnostic to allow positive identification. An examination of variation in long bones of recent *Phalacrocorax capensis* showed that the distal end of the ulna is especially likely to be atypically small in odd individuals (James in prep.). The chance that this bone belonged to just such an odd individual of the medium-sized cormorant cannot be entirely ruled out.

Nevertheless, as the presence of a small cormorant in southern Africa during the late Pliocene is affirmed by two bones from the Varswater Formation at Langebaanweg (James in prep.), the ulna from Duinefontein could well belong to the same species.

Order GALLIFORMES

Family **Phasianidae**

Francolinus sp.

Material

Scapular end of right coracoid, MBD544.

Remarks

The most abundant bird at Langebaanweg is a medium-sized species of francolin (Rich 1980) about the size of *Francolinus africanus*. Although the single specimen from Duinefontein is not diagnostic at the species level within the genus *Francolinus*, it is nevertheless identical with coracoids of the abundant francolin at Langebaanweg and very likely referable to the same species.

DISCUSSION

Previous to the South African discoveries, there was practically nothing known about sea-birds in the Tertiary of the Southern Hemisphere, apart from numerous reports of fossil penguins and a few bones of pseudotoothed birds (Pelagornithidae, Pelecaniformes—see Olson in press). Hence the Duinefontein fauna, despite the relative paucity of specimens and their poor preservation, represents a significant addition to our knowledge of Tertiary marine birds.

The species composition at Duinefontein is contrasted with that of marine birds at Langebaanweg and Ysterplaat in Table 1. The differences between these sites are probably due almost entirely to the nature of the depositional environment. That at Ysterplaat was most likely a high-energy beach deposit, as only the very dense, durable bones of the three larger species of penguins were found, and these are heavily abraded. At Duinefontein, conditions for preservation were somewhat better, probably reflecting the alternation between beach and lagoon postulated by Rogers (1979).

The five species found at Duinefontein that are absent at Langebaanweg (*Oceanites* sp., *Procellaria* sp., *Calonectris* sp., *Puffinus* spp. A and C) are all likely to have been non-breeding migrants that died at sea and washed ashore. Representatives of each of these genera occur regularly in Cape waters today (Brooke 1981). *Oceanites oceanicus* and *Procellaria aequinoctialis*, which may be closest to the species of *Oceanites* and *Procellaria* at Duinefontein, occur in Antarctic and cold Subantarctic waters during summer, but move northward to Subtropical waters of high productivity, including those off South Africa, in the southern winter. *Calonectris diomedea*, on the other hand, breeds in Subtropical waters of the North Atlantic and occurs regularly in Subtropical waters off South Africa in the southern summer. If such patterns of distribution had been established by the early Pliocene, it might indicate that deposition at Duinefontein was not restricted to a particular season of the year.

TABLE 1

Distribution of fossil Spheniscifformes, Procellariiformes, and Pelecaniformes in the southwestern Cape Province (based on the present paper; Olson 1985, in prep.; James in prep.). YS = Ysterplaat, DF = Duinefontein, LG = Langebaanweg, GM = Gravel Member, QSM = Quartzose Sand Member, PPM = Pelletal Phosphorite Member (Beds 3aN and 3aS). See Hendey (1981*b*) for terminology of the Langebaanweg sequence.

Species	YS	DF	LG GM	LG QSM	LG PPM 3aS	LG PPM 3aN
'Nucleornis' insolitus	×	×	—	—	—	×
'Dege' hendeyi	×	×	×	×	×	×
'?Palaeospheniscus' huxleyorum	×	×	—	×	×	×
'Inguza' predemersus	—	×	—	×	×	×
Diomedea sp.	—	—	—	×	—	—
Oceanites sp.	—	×	—	—	—	—
Oceanites zaloscarthmus	—	—	—	×	×	×
Fulmarinae, gen. et sp. indet.	—	×	—	?	—	—
Procellaria sp.	—	×	—	—	—	—
Calonectris sp.	—	×	—	—	—	—
Pachyptila salax	—	×	—	×	×	×
Pachyptila species B	—	×	—	×	×	—
Pachyptila species C	—	×	—	×	—	—
Puffinus species A	—	×	—	—	—	—
Puffinus species B	—	×	—	×	—	×
Puffinus species C	—	×	—	—	—	—
Pelecanoides cymatotrypetes	—	—	—	×	—	—
Sula sp.	—	×	—	×	×	—
Phalacrocorax medium sp.	—	×	—	×	×	×
Phalacrocorax small sp.	—	?	—	—	—	×

Puffinus spp. B and C might be analogous to *Puffinus griseus* and *P. puffinus*, each of which occurs as a migrant in Cape waters today. These modern species breed in the Southern and Northern hemispheres respectively. Both of the modern species are somewhat more specialized in wing morphology than the Pliocene forms, whose similarities to *Puffinus tenuirostris* may be due to shared primitive characters and may not necessarily indicate close relationship with that strictly Pacific species. *Puffinus* sp. A seems not to have any close living relatives and may represent an extinct lineage, the oceanographic preferences of which could not then be inferred. Not much can be said about the enigmatic fulmarine except that in the Southern Hemisphere the fulmarines breed only in Antarctic or Subantarctic waters. Of possible relatives, *Daption* and *Fulmarus* occur regularly off the Cape today.

Three species of marine birds are found only at Langebaanweg and are absent at Duinefontein. However, because *Diomedea* sp. and *Pelecanoides cymatotrypetes* are known only from one and three bones, respectively, their absence from Duinefontein is probably attributable to chance alone. It is not at all clear why albatrosses should be so scarce or absent in these deposits, considering

their relative abundance in Neogene marine deposits in the Northern Hemisphere and given the abundance of albatrosses in South African waters today.

Another matter is the complete absence of the storm-petrel *Oceanites zaloscarthmus* at Duinefontein, whereas at Langebaanweg it is the second most abundant procellariiform bird (Olson 1985). Only three other fossils of Oceanitidae have so far been reported from Tertiary marine deposits anywhere (Olson 1985, in press), so the Langebaanweg collections have increased the total world sample by a factor of nearly 60. The very small size, the highly pelagic nature of their existence, and the non-diving habits of storm-petrels probably contribute to their scarcity as fossils. For so many remains to be recovered from Langebaanweg argues for exceptional circumstances of fossilization. In this case, these storm-petrels probably died in the quiet waters of an estuary in the vicinity of a breeding island (Olson 1983, 1985), circumstances that would have reduced the likelihood of deposition of pelagic, offshore migrant species, thus accounting in part for the differences in species composition observed between Duinefontein and Langebaanweg.

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REFERENCES

BROOKE, R. K. 1981. The place of South Africa in the world of seabirds and other marine animals: 135–147. *In*: COOPER, J. *ed. Proceedings of the Symposium on Birds of the Sea and Shore*. Cape Town: African Sea-bird Group.

CRAWFORD, R. J. M., SHELTON, P. A., COOPER, J. & BROOKE, R. K. 1983. Distribution, population size and conservation of the Cape gannet *Morus capensis*. *S. Afr. J. mar. Sci.* **1**: 153–174.

DINGLE, R. V., LORD, A. R. & HENDEY, Q. B. 1979. New sections in the Varswater Formation (Neogene) of Langebaan Road, south-western Cape, South Africa. *Ann. S. Afr. Mus.* **78**: 81–92.

DINGLE, R. V., SIESSER, W. G. & NEWTON, A. R. 1983. *Mesozoic and Tertiary geology of southern Africa*. Rotterdam: Balkema.

HENDEY, Q. B. 1981*a*. Geological succession at Langebaanweg, Cape Province, and global events of the late Tertiary. *S. Afr. J. Sci.* **77**: 33–38.

HENDEY, Q. B. 1981*b*. Palaeoecology of the late Tertiary fossil occurrences in 'E' Quarry, Langebaanweg, South Africa, and a reinterpretation of their geological context. *Ann. S. Afr. Mus.* **84**: 1–104.

HENDEY, Q. B. 1982. *Langebaanweg. A record of past life*. Cape Town: South African Museum.

JAMES, H. F. In prep. Fossil cormorants (Aves: Phalacrocoracidae) from Cape Province, South Africa.

MUIZON, C. DE. 1980. Des baleines dans le désert! *In*: *Muséum National d'Histoire Naturelle: Récits et Découvertes*: 183–190. Paris: Fernand Nathan.

MUIZON, C. DE. 1981. Les vertébrés fossiles de la Formation Pisco (Pérou). Première partie: Deux nouveaux Monachinae (Phocidae, Mammalia) du Pliocène du Sud-Sacaco. *Trav. Inst. fr. Etud. andines* **22**: 1–161. *In: Recherches sur les grandes Civilisations*, Mém. N° 6. Paris: A.D.P.E.

OLSON, S. L. 1983. Fossil seabirds and changing marine environments in the late Tertiary of South Africa. *S. Afr. J. Sci.* **79**: 399–402.

OLSON, S. L. 1985. Early Pliocene Procellariiformes (Aves) from Langebaanweg, south-western Cape Province, South Africa. *Ann. S. Afr. Mus.* **95**: 123–145.

OLSON, S. L. In press. The fossil record of birds. *In:* FARNER, D., KING, J. & PARKES, K. C. *eds*. *Avian biology*. Vol. 8. New York: Academic Press.

OLSON, S. L. In prep. A revision of South African fossil penguins (Aves: Spheniscidae).

RICH, P. V. 1980. Preliminary report on the fossil avian remains from late Tertiary sediments at Langebaanweg (Cape Province), South Africa. *S. Afr. J. Sci.* **76**: 166–170.

ROGERS, J. 1979. The sedimentary succession at the Koeberg nuclear power station, Melkbosstrand. *Abstr. 18th Congr. geol. Soc. S. Afr.* **1**: 310–322.

SIESSER, W. G. 1980. Late Miocene origin of the Benguela upswelling [*sic*] system off northern Namibia. *Science* **208**: 283–285.

SIMPSON, G. G. 1971. Fossil penguin from the late Cenozoic of South Africa. *Science* **171**: 1144–1145.

SIMPSON, G. G. 1973. Tertiary penguins (Sphenisciformes, Spheniscidae) from Ysterplaats, Cape Town, South Africa. *S. Afr. J. Sci.* **69**: 342–344.

SIMPSON, G. G. 1975. Notes on variation in penguins and on fossil penguins from the Pliocene of Langebaanweg, Cape Province, South Africa. *Ann. S. Afr. Mus.* **69**: 59–72.

SIMPSON, G. G. 1979*a*. A new genus of late Tertiary penguin from Langebaanweg, South Africa. *Ann. S. Afr. Mus.* **78**: 1–9.

SIMPSON, G. G. 1979*b*. Tertiary penguins from the Duinefontein site, Cape Province, South Africa. *Ann. S. Afr. Mus.* **79**: 1–7.

TANKARD, A. J. 1975*a*. The marine Neogene Saldanha Formation. *Trans. geol. Soc. S. Afr.* **78**: 257–264.

TANKARD, A. J. 1975*b*. The late Cenozoic history and palaeoenvironments of the coast margin of the south-western Cape Province, South Africa. Rhodes University: Unpublished Ph.D. thesis.