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EARLY PLIOCENE PROCELLARIIFORMES  
(AVES)  
FROM LANGEBAANWEG,  
SOUTH-WESTERN CAPE PROVINCE,  
SOUTH AFRICA

By  
STORRS L. OLSON

Cape Town      Kaapstad

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EARLY PLIOCENE PROCELLARIIFORMES (AVES) FROM  
LANGEBAANWEG, SOUTH-WESTERN CAPE PROVINCE,  
SOUTH AFRICA

By

STORRS L. OLSON

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(With 7 figures and 5 tables)

[MS accepted 14 June 1984]

ABSTRACT

Eight species of sea-birds of the order Procellariiformes are identified among the fossils collected from early Pliocene deposits at Langebaanweg, south-western Cape Province, South Africa. All four living families of Procellariiformes are represented, including an albatross (Diomedidae), a new species of *Oceanites* ('*Pelagodroma*', Oceanitidae), five species of Procellariidae, including three species of *Pachyptila*, one of which is described as new, and a new species of diving petrel (Pelecanoididae). At least three of these species appear to have been breeding in the area, indicating that cold Temperate or Subantarctic oceanic conditions were present in the south-western Cape in the early Pliocene. The specimens of *Oceanites*, *Pachyptila*, and *Pelecanoides* provide the first Tertiary records for these genera. Most taxa are very similar to and perhaps ancestral to living species, with the principal exception of a giant form of *Pachyptila* that represents a previously unknown lineage.

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INTRODUCTION

Among the abundant fossils of terrestrial and aquatic birds from the early Pliocene deposits at Langebaanweg (P. Rich 1980) are remains of at least eight species representing each of the four families of the strictly marine order Procellariiformes (albatrosses, storm-petrels, shearwaters, and diving petrels). The only other site in South Africa from which Tertiary procellariiform fossils have been recovered is at Duinefontein, also in the south-western Cape and of approximately equivalent age (Olson in press *a*). The palaeoceanographic significance of the marine birds from these early Pliocene faunas is dealt with in a more general overview (Olson 1983), the scope of the present paper being mainly systematic.

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The geology and chronology of the Langebaanweg sequence have been detailed by Henzey (1981*a*, 1981*b*, 1982). These deposits formed during an early Pliocene period of marine transgression, under a variety of estuarine and fluvial conditions that resulted in the accumulation of remains of both marine and terrestrial organisms. The Langebaanweg sequence comprises two lithostratigraphic units, the Quartzose Sand Member (QSM) and the Pelletal Phosphorite Member (PPM). The PPM consists of channel deposits in two different beds, 3aS and 3aN, the latter of which truncates the former and is thus younger, at least where palaeontological excavations were undertaken. Both the QSM and PPM are time-transgressive so that whereas parts of the QSM are older than parts of the PPM, this relationship does not hold throughout the entire sequence (see Henzey 1981*b*: 32, fig. 8). There is sufficient evolutionary time represented between the older and younger portions of the sequence for morphological changes to have taken place within some species of mammals, e.g. the seal *Homiphoca capensis* (De Muizon & Henzey 1980).

Most of the individuals of Procellariiformes come from the QSM deposits (Table 5), indicating that this unit probably had a somewhat stronger marine influence than the PPM deposits. The composition of species and individuals of marine birds and the preservation of the bones themselves contrast with more typical marine deposits such as at Duinefontein, and indicate that at least the more abundant species were probably breeding in the vicinity, where they could have taken advantage of nearby islands that were created by the higher sea levels of the early Pliocene (Olson 1983).

Fossil specimens described here are in the collections of the division of Cenozoic Palaeontology of the South African Museum; all fossil specimen numbers are prefixed by the acronym SAM-PQ, which has been omitted here for the sake of brevity.

## SYSTEMATICS

### Order Procellariiformes

#### Family Diomedelidae

#### Genus *Diomedea* Linnaeus, 1758

#### *Diomedea* sp.

#### *Material*

Proximal end of left tarsometatarsus L12005, from the Quartzose Sand Member of the Varswater Formation at Langebaanweg.

#### *Discussion*

This single bone is the only evidence to date of albatrosses from the Tertiary of South Africa. The specimen is porous proximally and hence is from a juvenile individual and may indicate breeding in the vicinity. The proximal width is 17.3 mm, the specimen being from a species approximately the size of the living *Diomedea melanophris*.

Although albatrosses today are predominantly birds of southern oceans, there are but two other Tertiary records from the Southern Hemisphere—a fragmentary rostrum from the late Miocene of Victoria, Australia, described as *Diomedea thyridata* (Wilkinson 1969), and a single toe bone of a larger species from the early late Miocene near the Valdez Peninsula, Argentina (Olson 1984). This contrasts with the much better representation of albatrosses in the Northern Hemisphere where fossils are known from the late Oligocene into the Quaternary (Olson in press *b*).

### Family **Oceanitidae**

#### Subfamily Oceanitinae

Both on osteological and myological grounds, the storm-petrels fall into two very distinct groups that are best ranked as subfamilies (see Klemm 1969). The more specialized of these, to which all the fossils from Langebaanweg clearly belong, is the Oceanitinae, characterized by very short, stout humeri, ulnae, and femora, and greatly elongated tibiotarsi and tarsometatarsi. Five genera are customarily admitted among the species in the Oceanitinae (e.g. Jouanin & Mougín 1979), but I am unable to discern any osteological basis for considering either *Pelagodroma* Reichenbach, 1853, or *Garrodia* Forbes, 1881, to be distinct from *Oceanites* Keyserling & Blasius, 1840. *Pelagodroma marina* and *Garrodia nereis* resemble each other and differ from *Oceanites oceanicus* and *O. gracilis* in having the rostrum longer and more slender and the ridge of bone between impressions of the supraorbital glands narrower, but neither of these characters can be regarded as being of generic importance. Hence the first two are included in *Oceanites* as *O. marinus* (Latham) and *O. nereis* (Gould), respectively.

Within the Oceanitinae, there is an evolutionary trend towards greater size and increasing specialization of the tarsometatarsus and toes for locomotion across the surface of the water. In *Oceanites* this can be described as paddling, whereas *Fregatta* and *Nesofregatta* use the feet to bound rapidly across the surface, often against strong head winds (D. G. Ainley, Point Reyes Bird Observatory, pers. comm.). The trend for morphological specialization for such locomotion reaches its extreme in *Nesofregatta fuliginosa*, which is the largest species in the family and in which the distal end of the tarsometatarsus is expanded and the toes are greatly flattened, being fused by the skin of the web into a nearly inflexible paddle. The two species of *Fregatta* are more or less intermediate in these respects between *Oceanites* (*sensu lato*) and *Nesofregatta*. Within *Oceanites*, *O.* ('*Pelagodroma*') *marinus* shows perhaps the greatest tendency towards the specializations of *Fregatta* and *Nesofregatta*.

#### Genus *Oceanites* Keyserling & Blasius, 1840 (*sensu lato*)

All the storm-petrel bones from Langebaanweg are referable to a single species of Oceanitinae that differs from *Fregatta* in having the tibiotarsus and tarsometatarsus proportionately longer and much more slender. It differs from

*Nesofregatta* in lacking the distinctly flattened and expanded distal end of the tarsometatarsus and thus agrees with *Oceanites* in the broad sense as defined above.

*Oceanites zaloscarthmus* sp. nov.

Figs 1–2

*Material*

*Holotype*: L25214, complete right humerus (Fig. 1A), from the Quartzose Sand Member of the Varswater Formation at Langebaanweg, Cape Province, South Africa.

*Paratypes*: In addition to the holotype, 175 other specimens are referred to this species. These consist of 2 right and 2 left coracoids; 6 complete, 7 proximal, and 11 distal right humeri; 6 complete, 5 proximal, and 17 distal left humeri; 6 complete and 2 distal right ulnae; 4 complete, 3 proximal, and 4 distal left ulnae; 2 proximal left carpometacarpi; 4 right and 6 left femora; 14 distal right, 3 proximal left, and 16 distal left tibiotarsi; 2 complete, 17 proximal, and 10 distal right tarsometatarsi; 1 complete, 13 proximal, and 13 distal left tarsometatarsi. A list of specimen numbers with exact provenance within the Langebaanweg quarry is kept at the South African Museum and is also available from the author. The two carpometacarpi were found in unsorted material and some of the femora were in amongst the Passeriformes, so additional specimens of the species will doubtless be found in the material that has already been collected.

*Measurements of holotype*

Total length 24,80 mm; length from distal end of pectoral crest to distal extent of dorsal condyle 17,70 mm; width of shaft at midpoint 2,20 mm; distal width 4,80 mm. (Measurements to nearest 0,05 mm.)

*Measurements of paratypes*

See Table 1.

*Diagnosis*

Much larger and more robust than *Oceanites oceanicus*, *O. gracilis*, or *O. ('Garrodia') nereis*. Very similar in size and morphology to *O. ('Pelagodroma') marinus* but (1) brachial fossa of humerus much shallower and less extensive; (2) olecranon better developed (nearly absent in *O. marinus*); (3) carpal tubercle of ulna more pointed, less expanded and less triangular; (4) distal end of ulna not rotated ventrally; (5) shafts of hindlimb elements more robust; (6) femur less curved in lateral and medial views; (7) wings of inner and outer trochleae of tarsometatarsus less prominent and not as expanded to the sides.

*Distribution*

Early Pliocene Varswater Formation (QSM, PPM 3aN, PPM 3aS) at Langebaanweg, south-western Cape Province, South Africa.

TABLE 1  
Skeletal measurements (to nearest 0,05 mm) of fossil and living species of *Oceanites* ('*Pelagodroma*').

	<i>O. zaloscarthmus</i> sp. nov.			<i>O. marinus</i> (n = 3*)	
	n	range	mean	range	mean
CORACOID					
Length from head to midpoint of sternal end	3	13,35-13,60	13,50	13,80-14,00	13,90
Shaft width at midpoint	4	1,60-1,95	1,75	1,45-1,70	1,55
HUMERUS					
Total length	10	24,80-26,50	25,75	24,30-25,15	25,00
Length from distal end of pectoral crest to dorsal condyle	21	17,55-19,65	18,75	17,50-18,55	18,10
Shaft width at midpoint	30	1,90-2,50	2,25	1,95-2,10	2,00
Distal width	35	4,25-5,25	4,75	4,60-4,75	4,65
ULNA					
Total length	5	22,60-23,50	23,10	22,10-22,95	22,60
Length from distal lip of ventral cotyla to distal end	9	20,95-21,95	21,50	20,45-21,45	21,10
Shaft width at midpoint	14	1,75-2,20	2,00	1,80-1,90	1,85
Distal width	18	3,20-3,85	3,40	3,30-3,55	3,40
CARPOMETACARPUS					
Proximal depth	2	4,85-4,90	4,90	4,90-5,00	4,95
FEMUR					
Total length	8	16,20-17,50	16,65	17,00-17,25	17,15
Proximal width	7	4,10-4,40	4,30	4,00	4,00
Shaft width at midpoint	10	1,70-1,90	1,80	1,65	1,65
Distal width	2	3,75-3,95	3,85	3,70-4,20	3,90
TIBIOTARSUS					
Distance from proximal articular surface to distal end of fibular crest	3	11,55-13,80	12,75	12,65-14,05	13,25
Distal width	24	3,55-3,85	3,70	3,50-3,65	3,60
TARSOMETATARSUS					
Total length	3	40,40-41,80	40,90	39,05-40,45	39,95
Proximal width	29	3,90-4,55	4,35	4,20-4,35	4,30
Shaft width at midpoint	14	1,70-2,10	1,85	1,60-1,67	1,65
Distal width	24	4,25-4,80	4,45	4,45-4,50	4,50

\* Two skeletons from Peru and one from South Africa.

#### Etymology

Greek *zale*, surging sea, and *skarthmos*, skipping; essentially a rephrasing of the word *pelagodroma*.

#### Remarks

Except for the distinguishing features of the humerus and ulna, the differences between *Oceanites zaloscarthmus* and *O. marinus* are very minor and

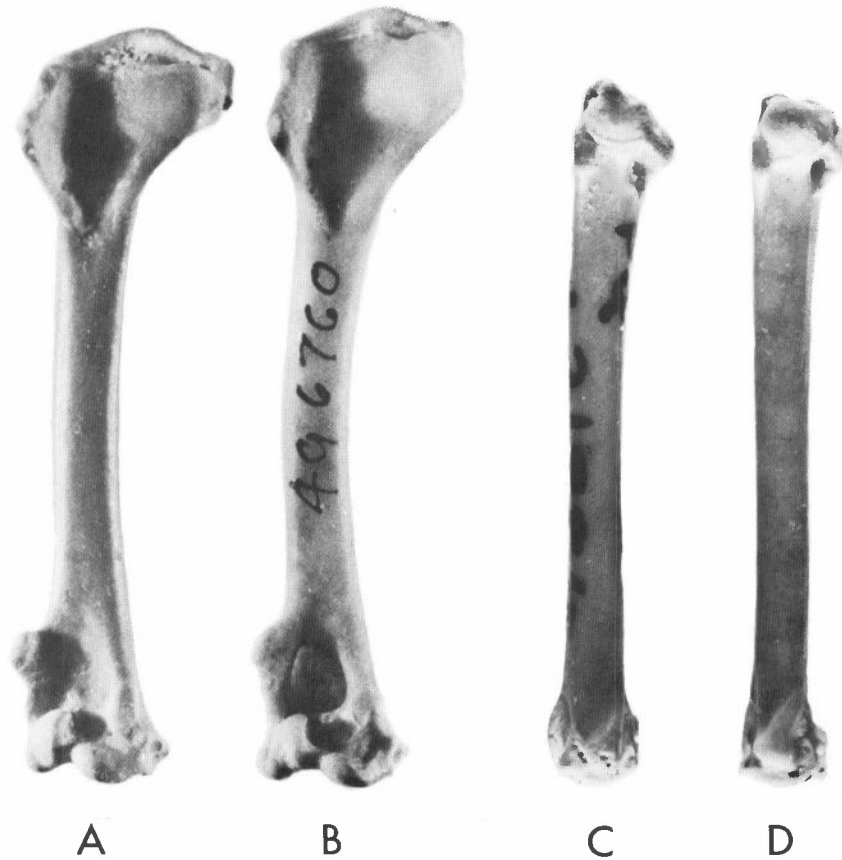


Fig. 1. Wing elements of *Oceanites* ('*Pelagodroma*'). A. *O. zaloscarthmus* sp. nov., holotype, L25214, right humerus, cranial aspect. B. *O. marinus*, USNM 496760, right humerus, cranial aspect. C. *O. zaloscarthmus* sp. nov., L21994, left ulna, cranial aspect. D. *O. marinus*, USNM 496760, left ulna, cranial aspect. All figures  $\times 3$ .

it is likely that the Langebaanweg species is ancestral to the living form. A more specialized condition in the latter is the curious rotation of the distal end of the ulna ventrally (Fig. 1C, D) with respect to the 'standard anatomical position' (Baumel 1979: 5). This is best appreciated when the ulnae are viewed resting on the caudal (trailing) surface (i.e. with the secondary papillae downward—see Fig. 1C, D). The deepening of the brachial fossa of the humerus and the reduction of the olecranon in *O. marinus* may possibly be correlated with the ventral rotation of the distal end of the ulna.

The fossils from Langebaanweg constitute only the fourth reported Tertiary occurrence of the family Oceanitidae. The others consist of two specimens from the late Miocene of California referred to the genus *Oceanodroma* (see Howard



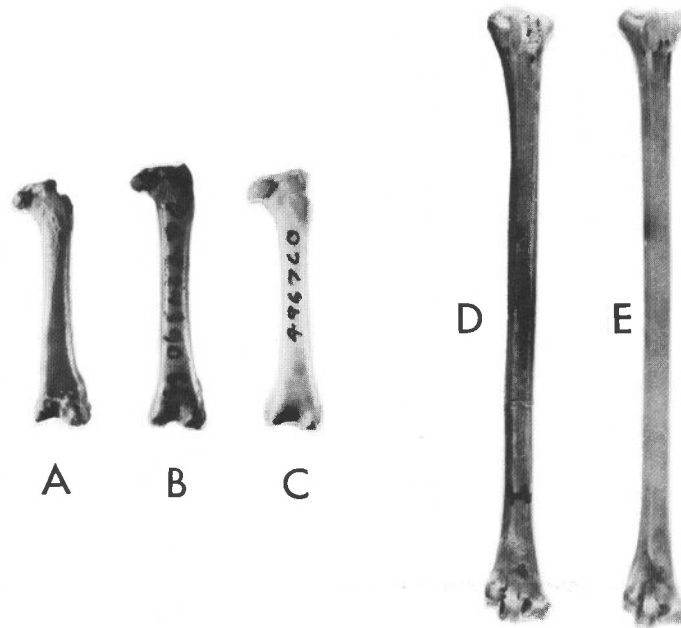


Fig. 2. Hindlimb elements of *Oceanites* ('*Pelagodroma*').  
 A-B. *O. zaloscarthmus* sp. nov., L24405, L24390U, left femora in cranial aspect showing variation in size and robustness. C. *O. marinus*, USNM 496760, left femur, cranial aspect. D. *O. zaloscarthmus* sp. nov., L24386Q, right tarsometatarsus, plantar aspect. E. *O. marinus*, USNM 496760, right tarsometatarsus, plantar aspect. All figures  $\times 2$ .

1978), and the shaft of a humerus the size and shape of that of *Oceanites oceanicus* from Duinefontein (Olson in press *a*). Despite the relative abundance of *Oceanites zaloscarthmus* at Langebaanweg, the species is entirely absent at Duinefontein. This may reflect differences in the depositional environment at these two sites. That so many bones of *O. zaloscarthmus* were concentrated at Langebaanweg is an almost certain indication that the species was breeding close by, probably on the islands lying immediately offshore from the Langebaanweg site (Hendey 1981*b*, 1982; Olson 1983, in press *a*). The probable presence of a breeding colony is also indicated by incompletely ossified bones of young, though possibly volant, individuals among the fossil sample.

The living species *Oceanites marinus* is rather widely distributed, nesting on islands in waters that lie in warm Subantarctic and especially in cool Subtropical waters. Although the species disperses widely in the non-breeding season, it has not as yet been recorded from South African waters (Clancey 1980; Harrison 1983). There are breeding populations on islands around western and southern Australia, in the New Zealand region, and in the Atlantic in the Salvages, Cape Verdes, and Tristan da Cunha (Jouanin & Mougin 1979). The species was once

abundant at St. Helena, probably until after the arrival of man in the sixteenth century (Olson 1975), and bones are also known from Madeira and Porto Santo (Harald Pieper, Zoologisches Museum, Kiel, pers. comm.). The species disappeared in relatively recent times from Amsterdam Island in the Indian Ocean (Jouanin & Paulian 1960), probably as the result of introduced predators (Murphy & Irving 1951). The absence of *O. marinus* in the Benguela Current off South Africa is the more curious considering that the species is quite abundant in the Peru Current off South America, which would seem to present similar conditions. This might be due in part to the extirpation of the population on St. Helena, although one might expect birds from Tristan da Cunha off South Africa as well.

#### Family **Procellariidae**

##### Genus *Pachyptila* Illiger, 1811

The prions (*Pachyptila*) are unique among the Procellariidae in having the bill greatly expanded and equipped with lamellae for filtering small prey items. The tongue and hyoid apparatus are correspondingly enlarged and housed in a distensible gular sac. With the exception of the very tip of a rostrum, however, cranial elements of *Pachyptila* have not yet been identified from Langebaanweg and fossils from there are assigned to this genus on the basis of characters of the humerus, which in *Pachyptila* has a short, blunt ectepicondylar spur (processus supracondylaris dorsalis) in combination with a very deep brachial fossa, terete shaft, and lack of expansion of the ventral epicondylar area. The humerus of *Pachyptila* is most similar to that of *Halobaena*, but in that genus the ventral epicondylar area is slightly expanded and the ectepicondylar spur is deeper proximo-distally.

##### *Pachyptila salax* sp. nov.

Figs 3–5, 6A

#### *Material*

*Holotype*: L25187, complete left humerus (Figs 3A, 6A) from the Quartzose Sand Member of the Varswater Formation at Langebaanweg, Cape Province, South Africa.

*Paratypes*: In addition to the holotype, 202 other specimens are referred to this species. These consist of 3 complete, 1 scapular, and 1 sternal ends of right coracoids; 8 complete, 4 scapular, and 1 sternal ends of left coracoids; 1 nearly complete, 14 proximal, and 16 distal right humeri; 1 nearly complete, 7 proximal, and 13 distal left humeri; 4 proximal and 4 distal right ulnae; 2 complete, 2 proximal, and 4 distal left ulnae; 3 proximal and 1 distal right carpometacarpi; 2 complete and 2 proximal left carpometacarpi; 1 complete and 3 proximal right femora; 3 complete, 3 proximal, and 1 distal left femora; 11 right and 5 left distal ends of tibiotarsi; 7 complete, 13 proximal, and 7 distal right tarsometatarsi; 5 complete, 9 proximal, and 8 distal left tarsometatarsi. With less certainty,



Fig. 3. Wing elements of *Pachyptila*. A. *P. salax* sp. nov., holotype, L25187, left humerus, caudal aspect. B. *P. vittata*, SAM-ZO56746, left humerus, caudal aspect. C. *P. salax* sp. nov., L22224, left ulna, dorsal aspect. D. *P. vittata*, SAM-ZO56746, left ulna, dorsal aspect. All figures  $\times 2$ .

4 scapulae, 2 fragments of sterna, the distal end of a radius, and 25 pedal phalanges are assigned to this species on the basis of size. A list of specimen numbers with exact provenance within the Langebaanweg quarry is kept at the South African Museum and is also available from the author.

*Measurements of holotype*

Total length 73,1 mm; length from head to proximal lip of brachial fossa 62,5 mm; length from distal end of pectoral crest to distal end of dorsal condyle 54,7 mm; proximal width through dorsal and ventral tubercles 12,7 mm; width and depth of shaft at midpoint 4,3 and 3,7 mm; distal width 9,3 mm.

*Measurements of paratypes*

See Tables 2 and 3.

*Diagnosis*

Much larger than any known species of *Pachyptila* (Table 2). Apart from size, there are few postcranial characters that will distinguish between the species of *Pachyptila*, although in *P. salax* the carpal tubercle of the ulna appears less pointed and slightly more proximally situated, the alular metacarpal and extensor process are more perpendicular to the shaft rather than slanting proximally, and the shaft of the tarsometatarsus appears to be relatively stouter.

*Distribution*

Early Pliocene Varswater Formation (QSM, PPM 3aN, PPM 3aS, and Duynfontyn Members) at Langebaanweg and Duinefontein, south-western Cape Province, South Africa.

*Etymology*

Greek *salax*, a sieve, in allusion to the filtering apparatus characteristic of the living members of this genus. The name is a masculine noun in apposition and there is no implied allusion to the pejorative Latin adjective of the same orthography.

*Remarks*

*Pachyptila salax* is so much larger than any of the living taxa in the genus (Table 2), regardless of their status, that there can be no question of its specific distinctness. It was a giant among prions and adds an entirely new dimension to our concept of radiation within *Pachyptila*. Although prions the size of *P. salax* may have been endemic to South Africa, it seems likely that birds of this size class would have been more widely distributed in the past and have become extinct everywhere since the early Pliocene.

It is unfortunate that there is not more of the bill known for *P. salax*. The tip of a rostrum that is tentatively referred to this species (Fig. 5A, C) is not sufficient even to suggest how much the rest of the bill may have been expanded. Compared

TABLE 2  
Measurements (mm) of living and fossil taxa of *Pachyptila*.

Measure- ment No.	<i>turtur</i> n = 3		<i>crassi- rostris</i> n = 1		<i>belcheri</i> n = 8		<i>desolata</i> n = 11		<i>sp. C</i> n = 3		<i>salvini</i> n = 8		<i>vittata</i> n = 5		<i>sp. B</i> n = 1		<i>salax</i> sp. nov.	
	range	mean	range	mean	range	mean	range	mean	range	mean	range	mean	range	mean	range	mean	range	mean
1	52,2-54,8	53,6	56,9	55,9	54,5-57,0	55,9	54,8-60,0	57,5	—	—	56,1-59,0	57,7	58,4-61,1	59,6	—	—	—	73,1
2	2,7-3,0	2,9	3,2	3,4	3,3-3,7	3,4	3,1-3,7	3,4	—	—	3,4-3,9	3,6	3,6-3,8	3,7	—	—	4,1-4,8	4,4
3	6,2-6,9	6,6	7,5	7,5	7,3-7,9	7,5	7,1-7,8	7,5	6,3-7,4	6,8	7,5-8,1	7,8	7,9-8,3	8,1	7,8	—	8,9-10,1	9,5
4	49,4-54,3	51,6	55,0	53,3	51,6-55,2	53,3	52,4-59,2	55,9	—	—	54,0-57,7	56,2	58,3-61,9	60,2	—	—	72,7-75,0	73,9
5	26,8-29,2	28,2	30,2	29,5*	28,8-30,1	29,5*	28,6-31,3	30,1	—	—	29,2-31,7	30,3	31,5-33,8	32,7	—	—	37,4-39,5	38,5
6	22,9-24,2	23,9	25,9	23,6*	22,8-24,5	23,6*	23,5-24,8	24,3*	—	—	23,8-26,2	24,8	25,3-26,0	25,7*	—	—	30,6-32,9	31,8
7	32,0-33,2	32,5	34,7	32,8	31,2-34,3	32,8	31,8-34,1	33,0	—	—	30,9-34,8	32,8	33,3-35,2	34,2	—	—	36,5-39,2	37,6

\* n = one less than listed above.

Measurements are: 1. length of humerus; 2. shaft width of humerus at midpoint; 3. distal width of humerus; 4. length of ulna; 5. length of carpometacarpus; 6. length of femur; 7. length of tarsometatarsus.

TABLE 3  
Additional measurements (mm) of *Pachyptila salax* sp. nov.

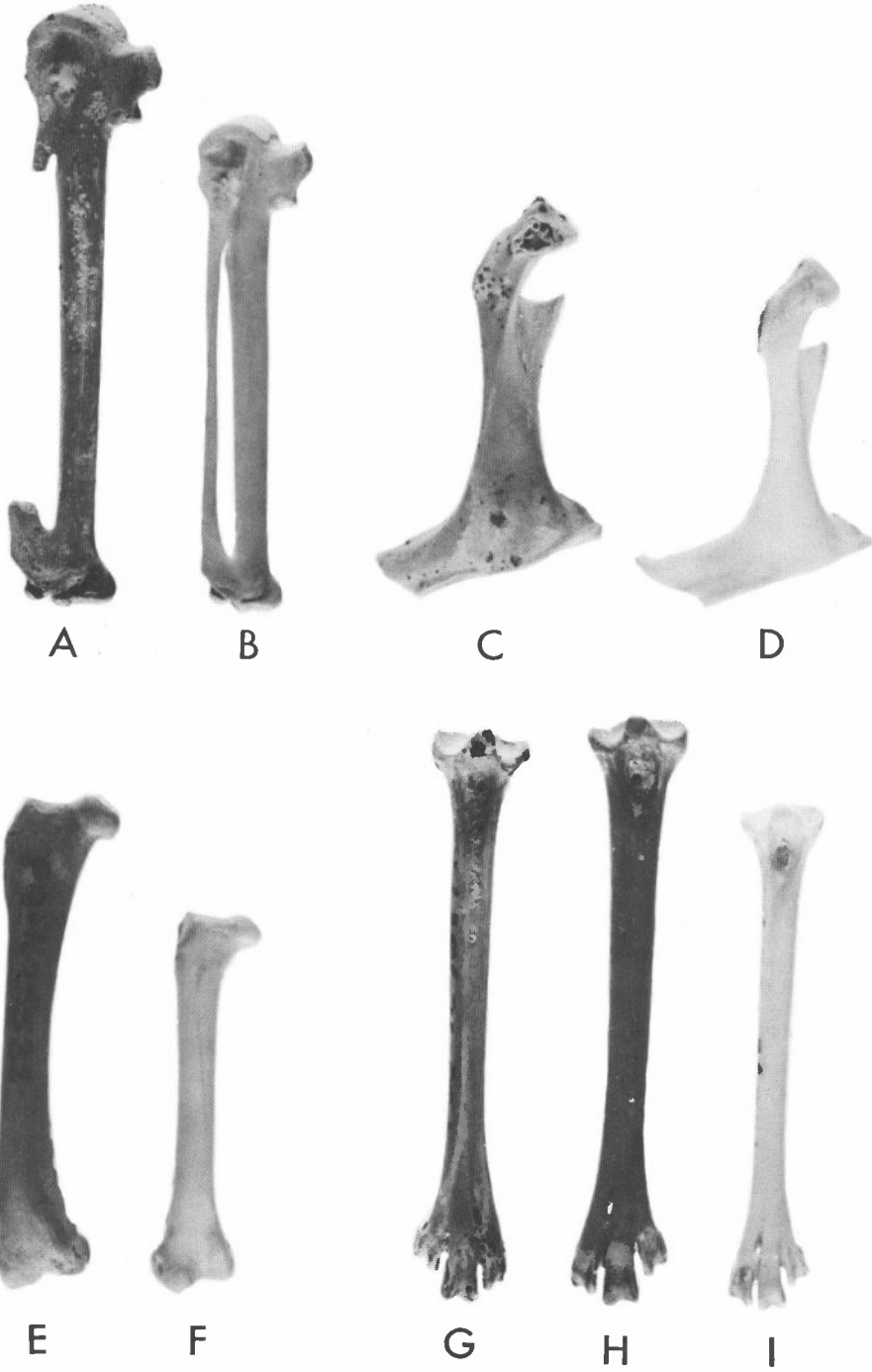
	n	range	mean
<b>CORACOID</b>			
Length from head to medial angle	9	22,4–24,2	23,3
<b>HUMERUS</b>			
Proximal width through dorsal and ventral tubercles	6	12,5–13,3	12,9
Length from distal end of pectoral crest to dorsal condyle	4	52,2–54,7	53,7
Length from head to proximal lip of brachial fossa	3	62,5–65,3	64,2
<b>ULNA</b>			
Proximal width	7	5,7–6,5	6,2
Distal width	6	5,5–5,9	5,7
<b>CARPOMETACARPUS</b>			
Proximal depth	3	8,9–9,2	9,1
Proximal width	5	6,9–7,3	7,1
Distal width	2	6,5–6,5	6,5
<b>TIBIOTARSUS</b>			
Distal width	12	5,1–5,5	5,4
<b>TARSOMETATARSUS</b>			
Proximal width	30	5,8–6,8	6,4
Shaft width at midpoint	19	2,4–3,1	2,6
Distal width	22	5,6–6,7	6,2

with *P. vittata*, the rostral tip of *P. salax* is markedly broader and considerably less decurved.

On size alone there are at least three species of *Pachyptila* in the Langebaanweg fauna and also at Duinefontein (Olson in press *a*). *Pachyptila salax* is larger than any other species in the genus, *Pachyptila* species B (see p. 138) is the size of the two largest living taxa, *P. vittata* and *P. salvini*, and *Pachyptila* species C (see p. 138) falls within the size ranges of the four smaller living taxa (Table 2). It is possible that more than one species could be included under *Pachyptila* species C. The available specimens of *Pachyptila* species B and C, all postcranial, are insufficient to determine anything more than that at least two species are represented. Although these fossils cannot be distinguished from living taxa, they cannot be assigned to a particular living taxon nor can one

(facing page)

Fig. 4. Skeletal elements of *Pachyptila*. A. *P. salax* sp. nov., L28203U, left carpometacarpus, ventral aspect. B. *P. vittata*, SAM-ZO56746, left carpometacarpus, ventral aspect. C. *P. salax* sp. nov., L28174C, right coracoid, ventral aspect. D. *P. vittata*, SAM-ZO56746, right coracoid, ventral aspect. E. *P. salax* sp. nov., L25531, right femur, cranial aspect. F. *P. vittata*, SAM-ZO56746, right femur, cranial aspect. G. *P. salax* sp. nov., L20691M4, left tarsometatarsus, cranial aspect. H. *P. salax* sp. nov., L24397, right tarsometatarsus, cranial aspect (note variation in robustness of shaft). I. *P. vittata*, SAM-ZO56746, right tarsometatarsus, cranial aspect. All figures  $\times 2$ .



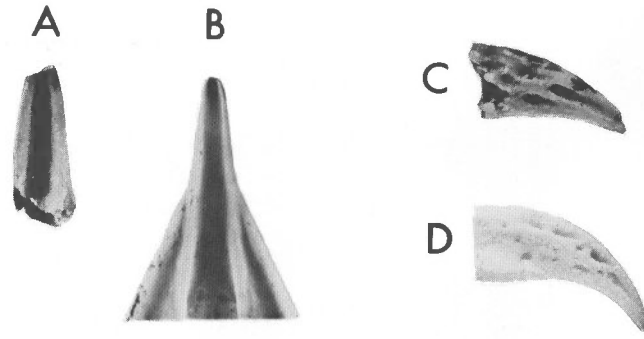


Fig. 5. Rostral tips (premaxillae) of *Pachyptila*. A. *P. salax* sp. nov., L28857, ventral aspect. C. Same, lateral aspect. B. *P. vittata*, SAM-ZO56746, ventral aspect. D. Same, lateral aspect. All figures  $\times 2$ .

assume that the fossils actually were conspecific with any taxon now in existence.

The South African occurrences provide the first fossil record to date for the genus *Pachyptila*. The concentration of bones of *P. salax* at Langebaanweg and the presence of incompletely ossified bones, probably from pre-fledging individuals, show that at least *P. salax*, if not the other species of *Pachyptila*, was breeding in the vicinity of Langebaanweg. This indicates that Subantarctic or at least cool Subtropical marine conditions probably existed nearby. Today, most breeding colonies of *Pachyptila* are on islands in Antarctic or Subantarctic waters. The only colonies north of the Subtropical Convergence are at Tristan da Cunha, St. Paul and Amsterdam islands, and in the northern part of New Zealand, all of which lie quite near the Subtropical Convergence.

The systematics of the modern species of *Pachyptila* are quite complex and a consensus on the number of species that should be recognized has not been reached. The divergence in views is exemplified by Harper (1980), who continues to recognize the six species that have commonly been accepted, and Cox (1980), who advocates reducing the number to three (though his argument leads to only two species). Consideration of the osteology of *Pachyptila* makes it doubtful that the number of species can be as few as three. Were Cox correct, some of the species of *Pachyptila* would exhibit a degree of morphological plasticity with few parallels among sea-birds.

Fleming (1941) attributed much of the speciation process in *Pachyptila* to the effects of Quaternary climatic events. Whereas it is likely that some of the differentiation between populations that has caused problems in assessing relationships among living taxa may have arisen as late as the Quaternary, we have seen that considerable divergence and radiation had already taken place in *Pachyptila* by the early Pliocene. It seems probable, therefore, that the principal species lineages in *Pachyptila* arose prior to the Quaternary.





Fig. 6. Left humeri (except C, distal end of right humerus) of *Pachyptila* in cranial aspect. A. *P. salax* sp. nov., holotype L25187. B. *P. vittata*, SAM-ZO56746. C. *Pachyptila* species B, L25577. D. *Pachyptila* species C, L24386D, I. E. *P. desolata*, SAM-ZO56324. All figures  $\times 2$ .

*Pachyptila* species B

Fig. 6C

*Material*

Distal end of right humerus, L25577DF; proximal end of right humerus, L42830D.

*Distribution*

Early Pliocene Varswater Formation (QSM, PPM 3aS, and Duynfontyn Members) at Langebaanweg and Duinefontein, south-western Cape Province, South Africa.

*Remarks*

This species is the size of *Pachyptila vittata* or *P. salvini*, the two largest living members of the genus, and cannot be distinguished from either on the basis of available material. See remarks under *P. salax*.

*Pachyptila* species C

Fig. 6D

*Material*

Complete left humerus, L24386D, I; distal ends of left humeri, L25776BO, L25575B; distal end of right humerus, L25579G2.

*Distribution*

Early Pliocene Varswater Formation (QSM and Duynfontyn Members) at Langebaanweg and Duinefontein, south-western Cape Province, South Africa.

*Remarks*

This species is the size of the smaller living taxa of *Pachyptila* but the material is not otherwise diagnostic—see remarks under *P. salax*. Nine pieces of ulnae, two coracoids, and the distal end of a tibiotarsus are from procellariids too small for *Pachyptila salax*. These most likely belong to one or the other of the smaller species of *Pachyptila*.

Genus *Puffinus* Brisson, 1760

Subgenus *Puffinus* Brisson, 1760

*Puffinus* sp.

*Material*

Distal end of right humerus, L25577CF; proximal end of left humerus, L56198; right coracoid, L25481.

*Distribution*

Early Pliocene Varswater Formation (QSM, PPM 3aN, and Duynfontyn Members) at Langebaanweg and Duinefontein, south-western Cape Province, South Africa.

*Remarks*

This is '*Puffinus* species B' of the Duinefontein fauna. It is similar in morphology to the living short-tailed shearwater, *Puffinus tenuirostris*, and was about the same size, although perhaps slightly smaller. It is illustrated and is discussed more fully elsewhere (Olson in press *a*).

Procellariidae gen. et sp. indet.

*Material*

Left coracoid, L28440J.

*Distribution*

Early Pliocene, Quartzose Sand Member of the Varswater Formation at Langebaanweg, south-western Cape Province, South Africa.

*Remarks*

This specimen is from a procellariid larger than *Pachyptila salax* and smaller than the preceding species; thus it represents an additional taxon for Langebaanweg. The bone differs qualitatively from any of the species of *Puffinus* and is compatible in size with the enigmatic species of fulmarine from Duinefontein (Olson in press *a*).

Family **Pelecanoididae**

Genus *Pelecanoides* Lacépède, 1799

The flattened alcid-like humerus and the distinctive lateral reflection of the head of the coracoid make the three bones discussed below unmistakably referable to the monogeneric family of diving petrels. All three fossils appear to belong to a single species that differs only in minor details from living species of *Pelecanoides*.

*Pelecanoides cymatotrypetes* sp. nov.

Fig. 7

*Material*

*Holotype*: Complete left humerus, L14564 (Fig. 7A) from the Quartzose Sand Member of the Varswater Formation at Langebaanweg, Cape Province, South Africa.

*Paratypes*: Proximal end of left humerus lacking internal tuberosity, L28469T; left coracoid lacking parts of procoracoid and sternocoracoidal processes, L28855.

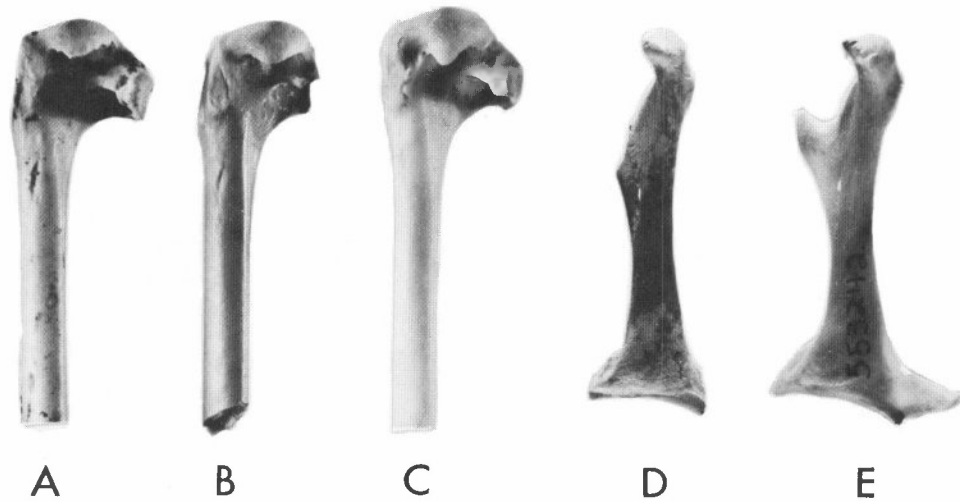


Fig. 7. Proximal portions of left humeri in caudal aspect (A-C) and left coracoids in ventral aspect (D, E) of *Pelecanoides*. A. *P. cymatotrypetes* sp. nov., holotype, L14564. B. *P. cymatotrypetes* sp. nov., L28469T. C. *P. urinatrix exsul*, USNM 553240. D. *P. cymatotrypetes* sp. nov., L28855. E. *P. urinatrix exsul*, USNM 553242.

#### *Measurements of holotype*

Total length 43,2 mm; proximal width 9,2 mm; shaft width and depth at midpoint 3,4 and 2,1 mm; distal width 7,1 mm.

#### *Measurements of paratypes*

See Table 4 for measurements of coracoid.

#### *Diagnosis*

Differs from living species in lacking the distally projecting protuberance on the caudal surface of the head of the humerus; ventral tubercle in ventral view shorter and deeper. Coracoid with head projecting more ventrally and less medially than in living species.

#### *Distribution*

Early Pliocene, Quartzose Sand Member of the Varswater Formation at Langebaanweg, south-western Cape Province, South Africa.

#### *Etymology*

Greek *kyma*, wave, and *trypetes*, borer, from the habit of the living species of flying straight through the crests of waves. The name is a masculine noun in apposition.

TABLE 4  
Measurements (mm) of living and fossil taxa of *Pelecanoides*.

Species	n	Humerus length	Coracoid length from head to midpoint of sternal facet
<i>P. cymatotrypetes</i> sp. nov.	1	43,2	24,6
<i>P. urinatrix exsul</i>	2	43,0; 44,1	23,2; 24,4
<i>P. urinatrix chathamensis</i>	1	40,6	21,8
<i>P. urinatrix</i> subsp. (Argentina)	1	42,1	22,9
<i>P. magellani</i>	2	43,3; 44,8	23,4; 25,1
<i>P. georgicus</i>	1	39,3	21,4

#### Remarks

This species is very similar to living forms except for the less extensive ossification of the head of the humerus, in which respect it is probably primitive. In size it is similar to *Pelecanoides urinatrix exsul* or *P. magellani*, but the bones are stouter than in the latter and the resemblances of the fossil are greatest to *P. u. exsul*.

The three bones of *P. cymatotrypetes* provide the only Tertiary record of the Pelecanoididae. A supposed Tertiary occurrence of *Pelecanoides* in New Zealand was subsequently shown to be Quaternary in age (T. Rich *et al.* 1979). Modern diving petrels are confined to cold Temperate or Subantarctic waters. None has been recorded from South Africa (Clancey 1980) and the nearest breeding colony is at Tristan da Cunha. Although considered to be 'sedentary' (Jouanin & Mougin 1979), high densities of diving petrels may occur some 1 300 to 1 600 km from the nearest land (D. G. Ainley, pers. comm.). They are nevertheless not as vagile as other members of the order.

#### DISCUSSION

Despite the fact that at present the order Procellariiformes is far more diverse in the Southern Hemisphere, its fossil record has hitherto been largely confined to the Northern Hemisphere, where the taxa represented consist mainly of albatrosses and a diversity of shearwaters of the genus *Puffinus* (Olson in press *b*). The early Pliocene deposits at Langebaanweg and at Duinefontein (Olson in press *a*) thus provide our first important insights into the procellariiform fauna of the southern oceans in the late Tertiary, as well as the first Tertiary records for the genera *Oceanites*, *Pachyptila*, and *Pelecanoides*.

The fossils available from deposits in the Northern Hemisphere seem to indicate that evolution within the Procellariiformes proceeded rather slowly from the Miocene onward, with species' lineages persisting for long periods with relatively little morphological change. Being extremely vagile, procellariiforms

adapted to particular oceanic conditions probably moved with them whenever global climatic changes caused shifts in surface water temperatures or salinities. Thus these birds have been able to remain with a 'stable' environment over long periods of geological time.

The Benguela Current and the cold upwelling associated with it did not originate until early late Miocene (Siesser 1980). It is therefore unlikely that a procellariiform fauna with such characteristically Subantarctic elements as seen at Langebaanweg and Duinefontein could have become established in South Africa before then. These species almost certainly did not just appear *de novo*, however, and were therefore probably present at higher latitudes during the Miocene and merely moved into southern Africa when conditions there became suitable (Olson 1983).

The history of certain marine organisms in South Africa may thus have close parallels with those on the western coast of South America. Zinsmeister (1978) has suggested a correlation between the formation of the West Antarctic ice sheet and the disruption of major current patterns in the Southern Hemisphere, which sent cold currents up the Pacific coast of South America and permitted cold-water faunas to expand northward out of the higher latitudes. The situation with South African sea-birds would appear to agree with Zinsmeister & Feldmann's (1984) view of the higher southern latitudes as a centre of origin for numerous animals that evolved early in the Tertiary but that did not disperse to middle latitudes until the Neogene.

Of the eight species of Procellariiformes at Langebaanweg (Table 5), six do not differ in any major way from living species and each could possibly be ancestral to some existing form. This is certainly true of *Oceanites zaloscarthmus* and *Pelecanoides cymatotrypetes*, which are very likely to be on a direct line with *O. marinus* and *P. urinatrix*, respectively. The material of *Diomedea*, *Puffinus*,

TABLE 5

Distribution of bones of Procellariiformes in the various units of the Varswater Formation at Langebaanweg. Number of specimens in first column, minimum number of individuals in parentheses. Pedal phalanges tentatively assigned to *Pachyptila salax* are not included. The material from PPM 3aS may include some specimens redeposited from the QSM.

	QSM	PPM 3aS	PPM 3aN
<i>Diomedea</i> sp.	1 (1)	— —	— —
<i>Oceanites zaloscarthmus</i>	147 (35)	20 (7)	9 (6)
<i>Pachyptila salax</i>	187 (33)	8 (6)	8 (6)
<i>Pachyptila</i> species B	1 (1)	1 (1)	— —
<i>Pachyptila</i> species C	4 (3)	— —	— —
<i>Pachyptila</i> spp. B or C	9 (3)	1 (1)	2 (1)
Procellariidae, gen. & sp. indet.	1 (1)	— —	— —
<i>Puffinus</i> sp.	2 (1)	— —	1 (1)
<i>Pelecanoides cymatotrypetes</i>	3 (2)	— —	— —
TOTAL	355 (80)	30 (15)	20 (14)

and the two smaller species of *Pachyptila* is too incomplete for confident assessment, but nevertheless presents nothing to suggest that any of these taxa represent lineages with no living descendants.

The coracoid of the unidentified genus of Procellariidae, if from the same species as the enigmatic fulmarine from Duinefontein, might indicate an extinct lineage. The most interesting of the procellariiform taxa at Langebaanweg is *Pachyptila salax*, which represents a totally extinct line of giant prions. Why this largest species in the genus should have become extinct while smaller species have remained diverse and abundant in the Subantarctic realm is not readily apparent.

Only two of the procellariiforms at Langebaanweg, *Oceanites zaloscarthmus* and *Pachyptila salax*, are abundantly represented and appear to be more than incidental. Bones of juvenile individuals of both of these species are present in the Langebaanweg deposits and both were thus probably breeding in the vicinity, as may also be presumed for *Pelecanoides cymatotrypetes* because of the more sedentary nature of the modern members of this genus. The procellariiform fauna at Langebaanweg, having formed at or near the site of breeding colonies, thus contrasts with those, such as at Duinefontein and at most localities in the Northern Hemisphere, where diversity is higher due to the presence of migrant and wintering species, but numbers of individuals per species are lower.

The great preponderance of specimens and individuals of Procellariiformes at Langebaanweg is in the QSM rather than in the channel deposits of the PPM (Table 5). As these are strictly marine taxa, this reflects either a more marine depositional environment in the QSM or at least an enhanced probability in the QSM of post-mortem transportation of sea-birds from a more purely marine situation. The minimum numbers of individuals in Table 5 were calculated by regarding specimens from each collecting site within the quarry as a separate sample, which perhaps has the potential of yielding too high a value. Considering that we are dealing with minima anyway, it is doubtful that this has exaggerated the number of individuals that contributed bones to the total fossil sample. Under conditions of terrestrial deposition it was found that the relative abundance of species of Procellariiformes on St. Helena Island did not differ significantly whether calculated by total number of specimens or minimum number of individuals (Olson 1975).

The fossil Procellariiformes and other sea-birds indicate the presence of cold waters off the Atlantic coast of South Africa in the early Pliocene. Since that time, Procellariiformes have ceased to breed in South Africa, and, in fact, no species of this order breeds on any continental African island today. Because the Benguela Current still provides cold upwelling off the southern African coast, the cause of the apparent retreat of certain species to higher latitudes and the extinction of other species, such as *Pachyptila salax* and several penguins (Olson 1983), is not readily perceived. Certainly the change in size, number, and character of suitable breeding islands that came about as a result of falling sea-levels would very likely have had a marked effect on Procellariiformes. This would be particularly true for burrowing species because the sea-bird islets that

remain in the Cape region today are largely devoid of soil in which to burrow. Nevertheless, many species of Procellariiformes nest exposed on the ground or in crevices in rocks and would seemingly have been less severely affected by geomorphological changes in islands.

Not only has there been a nearly complete turnover and restructuring of the marine avifauna of the Cape region since the early Pliocene (Olson 1983), but the same holds true for pinnipeds as well. The seal *Homiphoca capensis*, which has its nearest affinity with the Antarctic crab-eater seal *Lobodon carcinophagus* (see De Muizon & Hendey 1980), was abundant at Langebaanweg in the Pliocene but since then has become extinct and has been replaced by the fur seal *Arctocephalus pusillus*, whose congeners are found in Subantarctic and Subtropical waters as well as the Antarctic. Such a pattern does not seem explicable solely by changes in the nature of offshore islands.

Very likely there was a combination of factors responsible for the pronounced changes in the fauna of marine homeotherms observed since the early Pliocene in South Africa. Present evidence suggests that oceanographic conditions have not remained stable and have become less advantageous for organisms that are now characteristic of colder waters at higher latitudes.

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