

## A NEW GIANT PENGUIN FROM THE EOCENE OF AUSTRALIA

by R. J. F. JENKINS

ABSTRACT. *Pachydyptes simpsoni* sp. nov., a 'giant' fossil penguin, is described from fragmentary remains found at two levels in the Upper Eocene, Blanche Point Marls, South Australia. The remains from the lowest level immediately predate the first appearance of the index coccolith *Isthmolithus recurvus* Deflandre and are amongst the oldest well-dated penguin bones known.

Comparison with the largest modern penguin *Aptenodytes forsteri* Grey suggests that the fossil species probably stood about 140 cm tall. Its coracoid was relatively short compared to this modern species, one cervical vertebra relatively longer, and the wing length similar proportionally. Penguins are considered to have evolved from flying birds (Simpson 1946, 1971a) and the short coracoid is interpreted as supporting this. The inferred relatively long neck may have been inherited from the volant ancestor of the penguins or represent an early specialization. The length of the wing reflects its function as a propulsive organ in water and reinforces the suggestion by Simpson that 'all the basic locomotory adaptations of the Spheniscidae were virtually complete in the late Eocene'.

The need for precise stratigraphic data in analysing the palaeoecology of fossil penguins is emphasized, and so far as is possible, *P. simpsoni* and other Eocene fossil penguins are placed in a context of biostratigraphic, biogeographic, and palaeoclimatic data. This suggests that the Eocene penguins from Australasia lived in seas with surface water temperatures of about 12–16 °C. They are interpreted as recording northward penetration of Antarctic populations, perhaps to a palaeolatitude of 45° S.

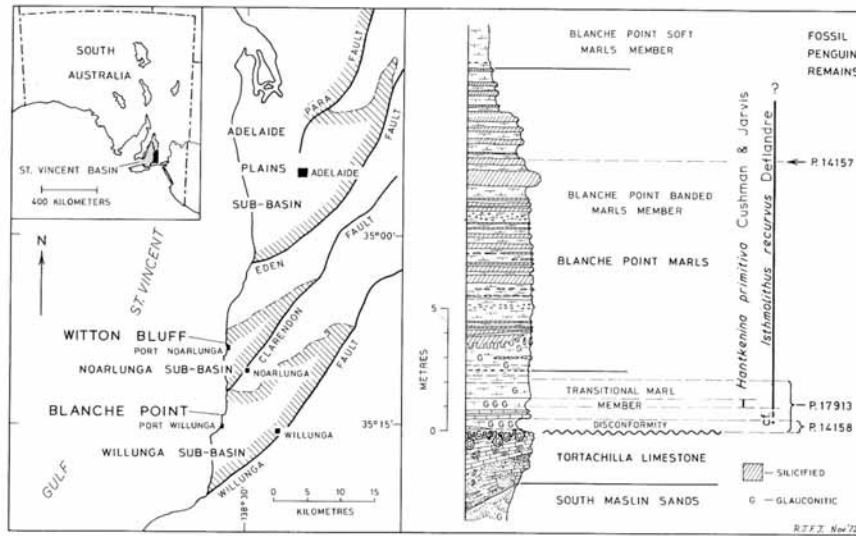
In May 1968 several fossil penguin bones were discovered by Messrs. Bret Robinson and Harry Eames in the Blanche Point Marls (Reynolds 1953) at Blanche Point, 37 km SSW. of Adelaide, South Australia (text-fig. 1). The Blanche Point Marls are of Upper Eocene age (Lindsay 1969; Ludbrook 1969). Further bones were collected by Dr. M. R. Walter, Bureau of Mineral Resources, Canberra, and myself at a subsequent excavation made at the point of initial discovery.

Two other bones collected at Blanche Point (apparently in association) in October 1932 by Mr. L. W. Parkin, now Director of the Australian Mineral Foundation, Frewville, Adelaide, were kindly made available by Emeritus Professor M. F. Glaessner, of the University of Adelaide. These bones also proved to be from a fossil penguin and are here considered conspecific with those discovered in 1968.

Another small bone fragment was collected by a student during a teaching excursion to Blanche Point in June 1971 and is here tentatively referred to the same species.

Twenty-six fossil penguin bones, all found isolated, have been documented or described previously from the Tertiary of Australia (Glaessner 1955; Simpson 1957, 1959, 1965, 1970). These bones are from the south-eastern part of the continent (mainland).

The first fossil penguin remains identified from Australia, a humerus from Witton Bluff, 11 km north of Blanche Point (text-fig. 1), was reported by Finlayson (1938) who considered that the bone most closely resembled a humerus of *Palaeudyptes* Huxley, 1859, from the New Zealand Tertiary. Glaessner (1955) recorded his own discovery of a fossil penguin tibiotarsus immediately south of Witton Bluff in the upper part of the Blanche Point Banded Marls Member (Reynolds 1953) of the Blanche Point Marls, and indicated that Finlayson's bone was from the Transitional Marl



TEXT-FIG. 1. Locality maps and stratigraphic column measured from the Eocene section exposed in the sea-cliffs at Blanche Point. The known ranges of key planktonic index fossils in this section and the stratigraphic levels of the fossil penguin remains described in this paper are indicated. The Tortachilla Limestone varies in thickness and it and the Blanche Point Marls are virtually conformable.

Member (Reynolds, *op. cit.*) of the Blanche Point Marls. These bones were studied by Simpson (1957) who identified the humerus as *Palaeudytes cf. antarcticus* Huxley, 1859 and the tibiotarsus as *P. cf. antarcticus*? Both bones are presently referred by Simpson (1971a) to *Palaeudyptes* sp. indet.

Glaessner (1955) also recorded the occurrence of two Oligocene penguin bones, a damaged humerus and an incomplete small femur, from the Gambier Limestone near Mount Gambier, South Australia. Simpson (1957) described the humerus as Gen. et sp. indet. A and the femur as Gen. et sp. indet. B. Planktonic foraminiferal studies made on samples from the same or the probable locality of these bones suggest a dating within the *Globigerina labiacrassata* zone of Ludbrook and Lindsay (1969), in terms of local zonation, or approximately equivalent to zone P. 19/20 of Blow (1969, 1970), with respect to tropical biostratigraphy (Dr. B. McGowan, pers. comm.). Coccolith assemblages from the same samples, kindly examined by Mr. S. Shafik, were suggestive of a late Middle Oligocene age (late Rupelian).

A new genus and species, *Anthropodytes gilli*, was erected by Simpson (1959) for a humerus which Gill (1959) reported from Miocene deposits exposed by the Glenelg River in western Victoria. Investigations which I have made on the planktonic foraminifera in samples from the locality of this bone indicate a dating within the *Globigerinoides trilobus trilobus* zone of Ludbrook and Lindsay (1969), or Lower Miocene.

Simpson (1965, 1970) documented the occurrence of twenty fossil penguin bones

from Beaumaris, Victoria, and one penguin bone from Spring Creek, near Minhamite, Victoria. An approximately late Miocene age was ascribed to these materials (Simpson 1970). The approximately late Miocene deposit with which the penguin bones from Beaumaris are associated (the Black Rock Formation) rests disconformably on sediments of Lower to Middle Miocene age (Gill 1957; Kenley 1967). The penguin remains are apparently from the bed of remanié phosphatic nodules which occurs at the base of the Black Rock Formation, and it seems probable that at least some of the bones may have been derived from the underlying pre-late Miocene rocks. The bone from near Minhamite, an incomplete humerus, was made the holotype of a new genus and species, *Pseudaptenodytes macraii* Simpson, 1970. The bones from Beaumaris were identified as *P. macraii*, ?*P. minor* Simpson, 1970, and Spheniscidae gen. et sp. indet.

None of the remains discussed above resemble the bones described in the present work. The materials dealt with here are catalogued in the palaeontological collection of the South Australian Museum, Adelaide, and the registration numbers given in the text pertain to this collection.

#### SYSTEMATIC PALAEONTOLOGY

Order SPHENISCIFORMES Sharpe, 1891

Family SPHENISCIDAE Bonaparte, 1831

Genus PACHYDYPTES Oliver, 1930

*Type species. Pachydyptes ponderosus* Oliver, 1930, by original designation.

- 1930 *Pachydyptes* Oliver, p. 85.
- 1946 *Pachydyptes* Oliver; Simpson, p. 41 (synonymy).
- 1952 *Pachydyptes* Oliver; Marples, p. 35.
- 1971a *Pachydyptes* Oliver; Simpson, p. 365 (revised diagnosis).

*Remarks.* Three genera of closely similar, very large or 'giant' fossil penguins are currently recognized from the Early Tertiary, *Palaeodyptes* Huxley, 1859, *Anthropornis* Wiman, 1905, and *Pachydyptes* Oliver, 1930. Bones referred to *Palaeodyptes* are known from the Upper Eocene and Oligocene of the South Island of New Zealand, the Upper Eocene and (late Middle) Oligocene of southern, mainland Australia (Simpson 1971a), and from Seymour Island, off the Antarctic Peninsula, in sediments dated tentatively on the basis of cetacean remains and their penguin fauna as being possibly late Eocene (Simpson 1971b). *Anthropornis* is identified only from these same deposits on Seymour Island (Simpson 1971b). Prior to the present study *Pachydyptes* was considered to include only the type species *P. ponderosus* from the Totara Limestone (Gage 1957) at Oamaru, Otago Province, southern New Zealand (Simpson 1971a). The Totara Limestone (in the usage of Gage 1957 and Simpson 1971a) is dated by recent planktonic foraminifera and coccolith studies as extending from possibly the latest Kaiatan, through the Runangan and into the Whaingaroan, in terms of New Zealand marine stages, or Upper Eocene to Lower Oligocene (Jenkins 1971; Edwards 1971).

Simpson (1971a, 1971b) drew attention to the problem of the validity of the distinctions made between the three above-mentioned genera. Simpson (1971a, footnote p. 347) points out the close resemblance between *Pachydyptes* and *Anthropornis*

and suggests that the two are only tentatively distinct. Nevertheless, Simpson (1971*b*) continues to distinguish all three genera but comments that 'had the separation not already been made, . . . [he] would hesitate to separate the genera now'. He indicates that their type-species are quite distinct and concludes 'it appears that *Pachydyptes*, *Anthropornis*, and *Palaeudyptes* are related genera and form a close morphological sequence in that order'; this order was 'not phylogenetic as *Pachydyptes* and *Palaeudyptes* are at least partly contemporaneous and *Anthropornis* may well be also'.

The bones described in the present work most closely resemble their counterparts in *Pachydyptes ponderosus*. However, they are less robust than the bones of *P. ponderosus* and in this and several other respects approach bones referred to *Anthropornis* and *Palaeudyptes*, thus lending further emphasis to the intergradational series evident between the early 'giant' penguins. Nevertheless, the bones of *P. ponderosus* and the new fossil species seem as similar as in any other two fossil penguin species assigned to a single genus, and in features such as the extremely large head of the humerus, the great width of the shaft of this bone, and the lengthened or expanded *pectoralis secundus* and *pectoralis tertius* muscle insertions, appear distinct from other known fossil penguins. It thus seems justifiable to maintain the taxon *Pachydyptes* and to include the present species with it.

*Pachydyptes simpsoni* sp. nov.

Plates 37-39; text-fig. 2*a*

Named for Professor George Gaylord Simpson, a most eminent palaeontologist and leading student of penguin evolution.

*Material.* The holotype, P.14157*a-g*, was discovered by Messrs. Robinson and Eames and consists of the following bones: (*a*) greater portion of left coracoid; (*b*) eroded head of right humerus; (*c*) broken head of left humerus; (*d*) right radius with the extremities damaged; (*e*) left carpometacarpus with the first metacarpal broken away; (*f*) left proximal phalange of second digit; (*g*) a damaged and distorted vertebra, possibly the twelfth. All of the bones occurred in a single 20-cm-thick stratum within an area of about half a square metre. Hence the assemblage almost certainly represents one individual.

The paratype material, P.14158*a, b*, collected by Mr. Parkin, consists of two bones: (*a*) badly broken proximal two-thirds of the right humerus; (*b*) proximal end of right radius.

The specimen P.17913 collected in 1971 is a small fragment of a bone shaft and is interpreted as being broken from the proximal part of a rib.

*Preservation.* The bones consist either of the natural skeletal material or are partly phosphatized. The matrix of the holotype, P.14157, consists of irregularly silicified, but otherwise poorly indurated marl.

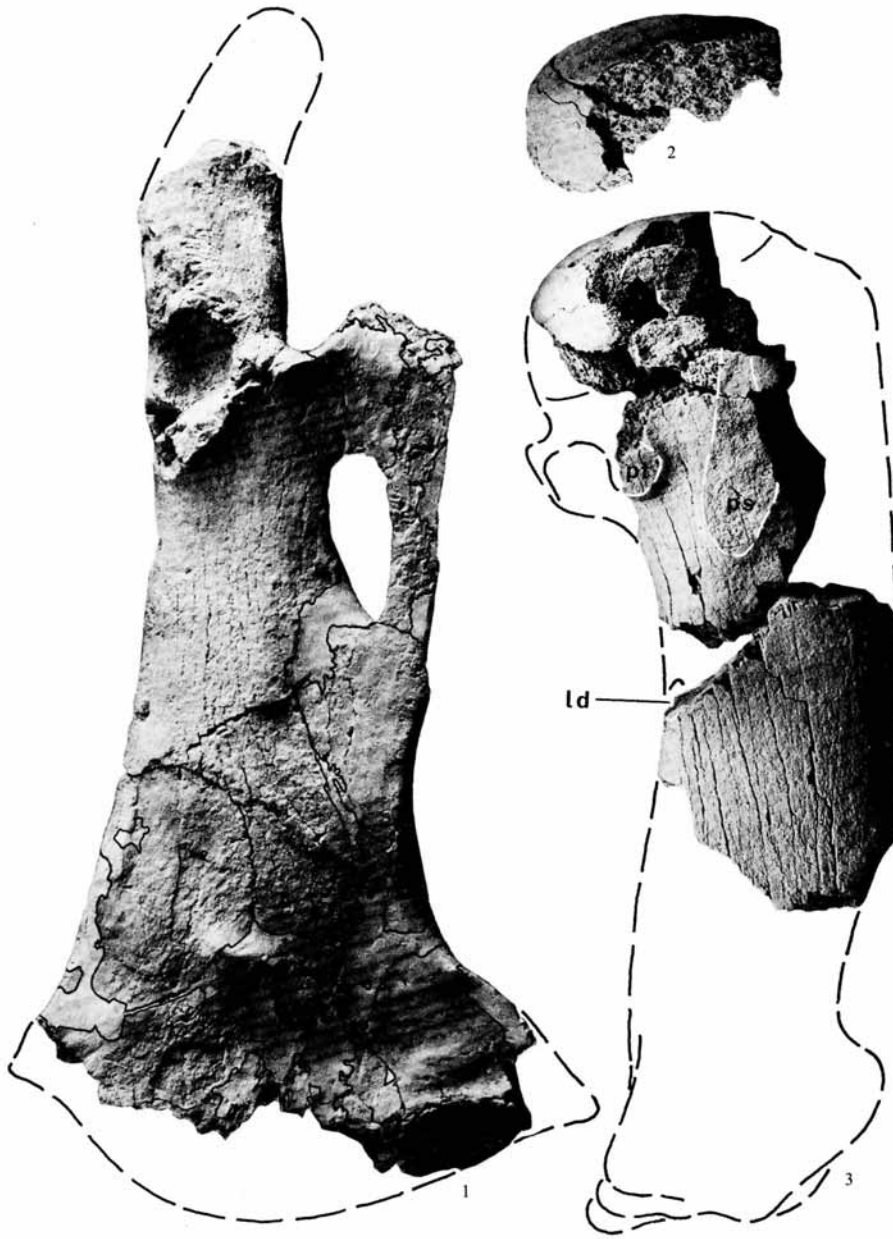
The matrix of P.14158 is a soft, glauconitic marl, a pale grey-white sediment including abundant green glauconite grains.

EXPLANATION OF PLATE 37

*Pachydyptes simpsoni* sp. nov. Portions of bones which have been restored with plaster are outlined.

Dashed lines (background) show a hypothetical restoration of the original outline of the bones. Important muscle attachments are outlined with dashed white lines. All figures natural size.

1, dorsal view of left coracoid of holotype, P.14157*a*. 2, dorsal view of articular surface of incomplete head of right humerus of holotype, P.14157*b*. 3, dorsal view of incomplete proximal two-thirds of right humerus of paratype, P.14158*a*: ps, insertion of *pectoralis secundus*; pt, insertion of *pectoralis tertius*; ld, insertion of *latissimus dorsi*.



JENKINS, Eocene penguin

*Locality.* The holotype is from the extreme tip of Blanche Point opposite Gull Rock. The fragment P.17913 is from about 20 m north of the foundations of 'Uncle Tom's Cabin' (locality indicated in map which Reynolds (1953) gives of the Maslin, Aldinga coast) 1.0 km ENE. of the tip of Blanche Point. Paratype P.14158 is from the vicinity of Blanche Point, but no additional information is given on its label.

*Stratigraphic Position.* The holotype was collected 3.6 m below the top of the Blanche Point Banded Marls Member of the Blanche Point Marls.

Specimen P.17913 was found loose on the Tortachilla Limestone (Reynolds 1953) which immediately underlies the Blanche Point Marls. The preservation of the specimen and study of the locality suggests that it weathered out of the Transitional Marl Member of the Blanche Point Marls, and is possibly from the glauconite-rich beds comprising most of the lower part of this member (text-fig. 1).

Paratype P.14158 is also from the Blanche Point Marls, but its precise stratigraphic level is not recorded. Its richly glauconitic matrix is consistent with its having been collected from the lower part of the Transitional Marl Member. The matrix was kindly examined by Mr. S. Shafik and found to contain a sparse coccolith assemblage; the index coccolith *Isthmolithus recurvus* Deflandre was absent. Research by Mr. Shafik and myself shows that *I. recurvus* (or a closely allied form) first appears as an exceedingly rare element 0.3 m above the base of the Transitional Marl Member, and can be confidently identified as a rather frequent species 0.6 m above the base of the member; coccoliths in general are relatively rare in the lower 0.6 m of the member, and common or even abundant above. The combined sedimentological and coccolith evidence from the matrix of paratype P.14158 suggests that it is from the basal 0.45 m thick soft glauconitic marl bed of the Transitional Marl Member.

*Age.* The Blanche Point Marls comprise part of the Aldingan Stage in Australia (Ludbrook and Lindsay 1966). Glaessner (1951), Reynolds (1953), and Wade (1964) indicate that the planktonic foraminifera species *Hantkenina 'alabamensis compressa' Parr* (= *H. primitiva* Cushman and Jarvis according to Blow 1969) occurs in the Transitional Marl Member of the Blanche Point Marls. This record has been verified by obtaining rare specimens of the species from washings of sediment taken at 1.0 and 1.5 m above the base of the Transitional Marl Member at 'Uncle Tom's Cabin' near Blanche Point. As indicated above the fossil penguin P.14158 is apparently from the lowermost part of this member, below the first appearance of the coccolith *I. recurvus*. According to McGowran (1971) the *H. primitiva* interval is high in zone P.15 of Blow (1969); Gartner (1971) indicates the initial appearance of *I. recurvus* is also within zone P.15, that is early Upper Eocene in age. The age of fragment P.17813 is probably similar. Hornibrook and Edwards (1971) indicate that in New Zealand the time ranges of '*H. alabamensis*' (almost certainly = *H. primitiva*) and *I. recurvus* overlap in the late Kaiatan and early Runangan, approximately middle Upper Eocene, and that *I. recurvus* first appears in the late Kaiatan.

Planktonic foraminiferal studies date the top part of the Blanche Point Banded Marls Member as also being Upper Eocene (Wade 1964; Lindsay 1969; Ludbrook and Lindsay 1969). This part of the section is stratigraphically higher than the local occurrence of *H. primitiva* and is shown by Lindsay (1969) to include *Globigerapsis index* (Finlay), but not *Globigerina ampliapertura* Bolli. This data suggests a tentative correlation with the upper-middle part of the *Globigerina linaperta* Zone in the New Zealand biostratigraphic scheme of Jenkins (1971), or with respect to the composite foraminiferal-coccolith biostratigraphic scheme of Hornibrook and Edwards (1971), an early Runangan age.

The present penguin bones are similar in age to those from the Blanche Point Marls at Port Willunga and several partial skeletons from the Kaiatan or early Runangan at Dunedin, southern New Zealand; collectively these bones are the oldest well-dated remains of fossil penguins in the world.

### Description

*Coracoid of holotype, P.14157a.* Notable features of this bone are its broadly flared

#### EXPLANATION OF PLATE 38

*Pachydyptes simpsoni* sp. nov. Portions of bones which have been restored with plaster are outlined. All figures natural size.

1a, b. The twelfth cervical vertebra of the holotype, P.14157. 1a, right lateral view. 1b, ventral view. 2, ventral view of incomplete proximal two-thirds of right humerus of paratype, P.14158a. 3, ventral view of left coracoid of holotype, P.14157a.



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base and almond-shaped precoracoid foramen. The proportions of its shaft are comparable with those of the slightly larger coracoid of *Pachydyptes ponderosus*. However, the curvature of the proximal portion of the preaxial margin differs; the basal part of the preaxial margin lies at an angle of about 45° to the axis of the bone in the present fossil and at 40° in *P. ponderosus* (see illustration in Marples 1952, pl. 7, fig. 1).

In its size and general form the present bone resembles an Oligocene, New Zealand coracoid referred by Simpson (1971a) to *Palaeodyptes* sp. indet. (specimen illustrated in Marples 1952, pl. 7, fig. 2) and a coracoid possibly belonging to *Anthropornis nordenskjöldii* Wiman, 1905 (illustrated in Wiman 1905, pl. 7, figs. 3, 3a and in Simpson 1971b, fig. 4), from Seymour Island. It differs from both, however, in the greater relative width of its shaft measured at right angles to the middle of the glenoid surface, and in the shaft being wider at the level of the middle of the precoracoid foramen, particularly with respect to *A. nordenskjöldii*.

*Humerus of paratype, P.14158a.* A bone of relatively massive proportions with a large head and a gently curved broad shaft. The insertion of *pectoralis secundus* is slightly oblique relative to the axis of the bone. The *latissimus dorsi* attachment, indicated only by a slight lip of bone on the edge of a fracture, is widely separated from the insertion of *pectoralis secundus*. The *pectoralis tertius* insertion is large and faces almost dorsally; it extends distally about two-thirds the length of the *pectoralis secundus* insertion and is widely separated from the latter. The preaxial tuberosity on the shaft at the proximal limit of attachment of *brachialis internus* is especially prominent; it is obtusely angulate with a concave contour on the proximal side.

The curvature of the articular surface of the head of this bone is identical with that of the fragmentary humeri of the holotype, P.14157b and c (Pl. 37, figs. 2, 3). The dimensions of the bone are comparable with those of several humeri of *P. ponderosus*. However, the preaxial tuberosity on the shaft is much more prominent than in that species and the *pectoralis tertius* insertion is less extended distally and more widely separated from the *pectoralis secundus* attachment. The bone differs from humeri assigned to *A. nordenskjöldii* in that the preaxial tuberosity on the shaft is again more prominent and the *pectoralis secundus* insertion extends further distally relative to the *latissimus dorsi* attachment.

*Radius of holotype, P.14157d.* A notable character in this bone is the shape of the

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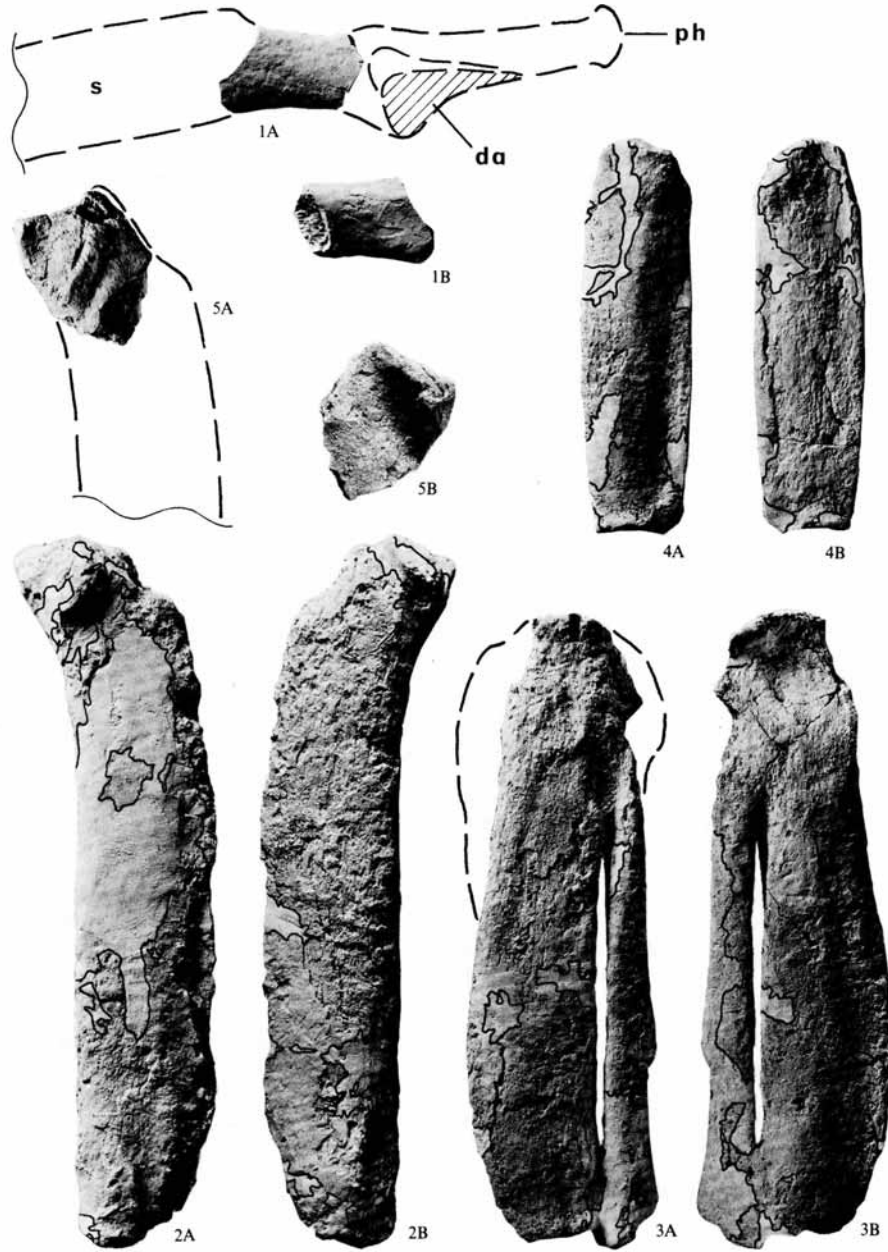
EXPLANATION OF PLATE 39

*Pachydyptes simpsoni* sp. nov. Portions of bones which have been restored with plaster are outlined.

Dashed lines (background) show a hypothetical restoration of the original outline of the bones. All figures natural size.

1a, b. Fragment presumed to have been broken from the proximal part of the ?seventh rib on the left side, specimen P.17913. 1a, dorsal view; its apparent position relative to the shaft or blade (s), dorsal articulation (da), and proximal head (ph) of the rib is indicated. 1b, ventral view. 2a, b. Proximal end of right radius of paratype, P.14158b. 2a, dorsal view, position relative to shaft of bone indicated. 2b, ventral view. 3a, b. Left proximal phalange of second digit of holotype, P.14157f. 3a, dorsal view. 3b, ventral view. 4a, b. Right radius of holotype, P.14157d. 4a, dorsal view. 4b, ventral view. 5a, b. Left carpometacarpus of holotype, P.14157e. 5a, dorsal view, position of missing first metacarpal and damage to third metacarpal indicated. 5b, ventral view.





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*brachialis internus* attachment which is hollowed to form a distinct notch making an angle of about 120° with the preaxial angle of the shaft.

The bone resembles a New Zealand Oligocene radius belonging to a *Palaeedyptes* sp. (illustrated in Marples 1952, pl. 5, fig. 2) and radii assigned to *A. nordenskjoeldii*. It differs from both in the shape of the *brachialis internus* attachment. In the radius of *Palaeedyptes* this insertion is long and moderately concave, not notched, while in *A. nordenskjoeldii* it is flat or only slightly concave. The shape of the insertion approaches that in *Palaeospheniscus robustus* Ameghino, 1905, from the latest Oligocene or early Miocene of Patagonia.

*Radius of paratype, P.14158b.* This fragment from the proximal end of the right radius is essentially similar to the radius of the holotype except for slight differences in the proportions and an additional prominence at the extreme proximal, post-axial corner of the dorsal muscle attachment. This prominence has almost certainly been abraded away in the holotype specimen. The overall similarity between the two is strongly suggestive of conspecificity.

*Carpometacarpus of holotype, P.14157e.* This bone has the third metacarpal separated from the second for the greater part of its length. The third metacarpal is slightly expanded at about two-thirds its length and near the distal end, and projects distally beyond the second.

The distally projecting third metacarpal distinguishes this bone from the carpometacarpus of *P. ponderosus* which has the ends of the second and third metacarpals nearly level. The third metacarpal projects distally in a specimen belonging to a *Palaeedyptes* sp. from the New Zealand Oligocene (illustrated in Marples 1952, pl. 5, fig. 7) and carpometacarpi assigned to *A. nordenskjoeldii*.

*Proximal phalange of second digit of holotype, P.14157f.* This phalange resembles one apparently belonging to *A. nordenskjoeldii* and a New Zealand Oligocene bone of a *Palaeedyptes* sp. (illustrated in Marples 1952, pl. 6, fig. 4). Its length is 61.5% of the carpometacarpus. The equivalent value for the *Palaeedyptes* sp. is 57.0% (Marples 1952) and ranges from 63.5% to 71.0% in six recent genera (Marples 1953).

*Cervical vertebra of holotype, P.14157g.* Comparison with the extant *Aptenodytes forsteri* Gray, 1844, suggests that this is probably the twelfth cervical vertebra. There appears to be only a low neural crest, and the prezygapophyses seem relatively elongate. The broken base of a median ventral hypapophysis is preserved on the centrum.

*Fragment of ?seventh rib, P.17913.* The spheniscine origin of this fragment is adduced from its resemblance to part of the proximal portion of the seventh rib of *Aptenodytes forsteri*. It is tentatively referred to the new species described here because of its robust dimensions and occurrence in probably the same stratum and locality as the paratype P.14158.

*Measurements.* The measurements of the more complete bones described are contained in Table 1.

TABLE 1. MEASUREMENTS

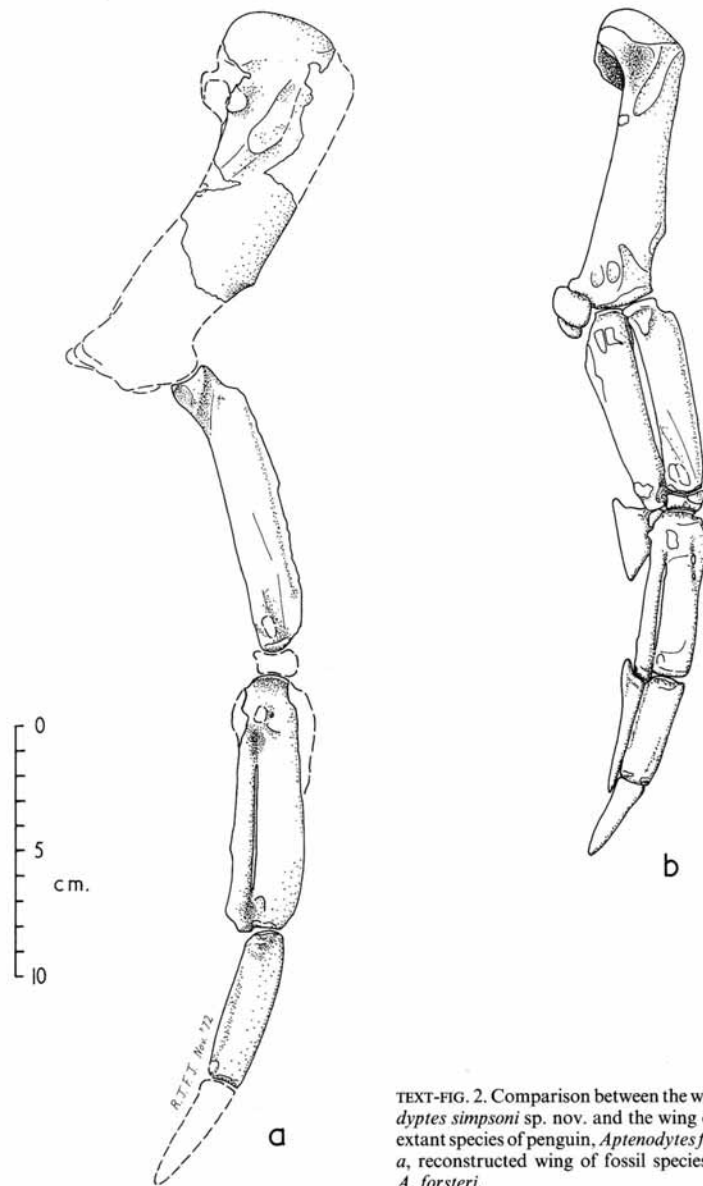
The dimensions given are in millimetres and unless otherwise stated are as numbered and defined by Marples (1952, Table 9). Measurements placed in brackets are approximate because of deficiencies in the specimen.

Coracoid of holotype, P.14157a										
Dimensions:	1	2	3	4	5	6				
	(171)	(133)	(85)	33	(33)	15				
Humerus of paratype, P.14158a										
Dimensions:	1	2	3	4	5	6	7	8	9	10
	—	—	—	—	39	40	19	16	(103)	—
Radius of holotype, P.14157d										
Dimensions:	1	2	3	4	5	6				
	116	(19)	23	23	10	10				
Metacarpus of holotype, P.14157e										
Dimensions:	1	2	3	4						
	102	104	—	31						
Phalange of second digit of holotype, P.14157f										
1. Extreme length between parallels										64
2. Width $\frac{1}{3}$ length from proximal end										18
3. Width $\frac{2}{3}$ length from proximal end										18

*Discussion.* The present species resembles *Pachydyptes ponderosus* more than any other known fossil penguin, and, as argued above, the two can be considered congeneric. *Pachydyptes simpsoni* differs principally from *P. ponderosus* in having the proximal half of the preaxial margin of the coracoid more strongly concave, the preaxial tuberosity on the shaft of the humerus much more prominent, the *pectoralis secundus* and *pectoralis tertius* insertions on the humerus more widely separated, and the third metacarpal produced distally beyond the second, not nearly level with it. The coracoid and paratype humerus of *P. simpsoni* are smaller than in the type of *P. ponderosus*; the humerus seems closely similar in size to other bones referred to the latter species.

Selected dimensions of the bones of *P. simpsoni* and an emperor penguin, *Aptenodytes forsteri*, the largest extant species, are compared in Table 2. The values of the ratio of the dimensions of the cervical vertebra and coracoid of the two species average 1.4(4); for the three wing bones the values of the ratio of the dimensions average 1.4(6). The fossil was thus probably of the order of 1.45 times as large as the modern specimen. The skeleton of *A. forsteri* used for comparison belonged to an individual with an approximate standing height of 98 cm (feet flat, legs and neck extended, head horizontal). Hence the fossil possibly had a standing height of the order of 140 cm.

Simpson (1946) reviewed the problem of estimating the standing height of fossil penguins. Estimates of the height of New Zealand fossil penguins are given by Simpson (1971a). He suggested an estimate of 150 cm for the standing height of *P. ponderosus*. Allowing for the fact that *P. simpsoni* was clearly a little smaller than *P. ponderosus*, the present estimate is in close agreement with that of Simpson's. *P. simpsoni* and the largest species of *Palaeodyptes* were probably about equal in size.



TEXT-FIG. 2. Comparison between the wing of *Pachydyptes simpsoni* sp. nov. and the wing of the largest extant species of penguin, *Aptenodytes forsteri* Gray; a, reconstructed wing of fossil species; b, wing of *A. forsteri*.

The ratios of the dimensions of the bones of *P. simpsoni* and *A. forsteri* (Table 2) suggest several interesting features. The comparative ratios for the length of the centrum of the cervical vertebra and the longitudinal measurement on the coracoid indicate the *P. simpsoni* probably had a relatively longer neck and shorter coracoids than the emperor penguin. On the other hand, the comparative ratio for the thickness of the shaft of the coracoid is similar to the comparative ratios for the lengths of the individual wing bones. This suggests that though the coracoid was relatively short, it was otherwise adapted to provide an anchorage for the very heavy-boned wing. The comparative ratios for the wing bones indicate that these differ slightly in their relative proportions between *P. simpsoni* and *A. forsteri*, but suggest that the ratio of wing length to body length was probably quite similar in the two.

TABLE 2. Comparison between dimensions of selected bones of *Aptenodytes forsteri* and *Pachydyptes simpsoni*. Measurements in millimetres.

	<i>Aptenodytes forsteri</i> A	<i>Pachydyptes simpsoni</i> B	Ratio B/A
Twelfth cervical vertebra			
Width of centrum just behind postzygapophyses	11.5	15.8	1.37
External width at middle of neural arch	16.3	22.7	1.39
Length of centrum from upper portion of posterior articulation to centre of anterior articulation	24.3	43 (impf.)	1.7(8)
Coracoid			
Length from distal lip of <i>fossa scapularis</i> to basal margin at about one-quarter width from preaxial corner	132	143	1.08
Thickness of shaft at right angles to middle of glenoid surface	14.9	23.2	1.56
Wing bones			
Extreme length of radius	82	116	1.42
Extreme length of third metacarpal	68	105	1.54
Extreme length of proximal phalanx of second digit	45	64	1.42

Simpson (1946, 1971a) champions the hypothesis that penguins descended from flying birds, and discusses various features of the fossil species which support this. He considers that penguins probably have a common ancestry with the Procellariiformes. The relative shortness of the coracoid in the present fossil is an additional feature hinting at a volant ancestry. In flying birds the wing is supportive as well as propulsive and hence the most important flight muscles, the *pectoralis major* and *pectoralis minor* are directed obliquely downwards; the coracoids which sustain the tension of these muscles are also directed obliquely downwards, and because the bird's body is sub-cylindrical, are necessarily rather short. In *Aptenodytes* the flipper is largely propulsive as the body is buoyed up by the water it displaces, and the 'flight' muscles, and hence the coracoids, are directed obliquely rearwards. This condition permits lengthening of the flight muscles for greater efficiency and corresponding elongation of the coracoids.

Penguins use their wings in a flying motion to propel themselves rapidly through the water. The small size of the wing compared to flying birds is clearly an adaptation of the wing to enable it to function efficiently in a relatively dense medium.

The wings of *P. simpsoni* seem to have been similarly shortened to those of modern penguins (e.g. *A. forsteri*) and thus were well specialized for an aquatic life. Simpson (1971a) similarly concludes that features of the wing of early penguins were highly specialized.

In modern penguins the neck is secondarily shortened by an extraordinary development of the antero-posterior curvatures of the cervical column (Watson 1883). Watson suggested that these flexures are related to the erect stance of penguins on land. The shortening of the neck may also enhance the hydrodynamic profile of the bird while swimming and aid conservation of body heat in cold climates. The long neck inferred for *P. simpsoni* might have been advantageous for the capture of highly motile prey such as fish. *P. simpsoni* may have inherited its long neck from the volant ancestor of the penguins or it may represent a specialized adaptation. Additional fossil material is needed to shed light on this.

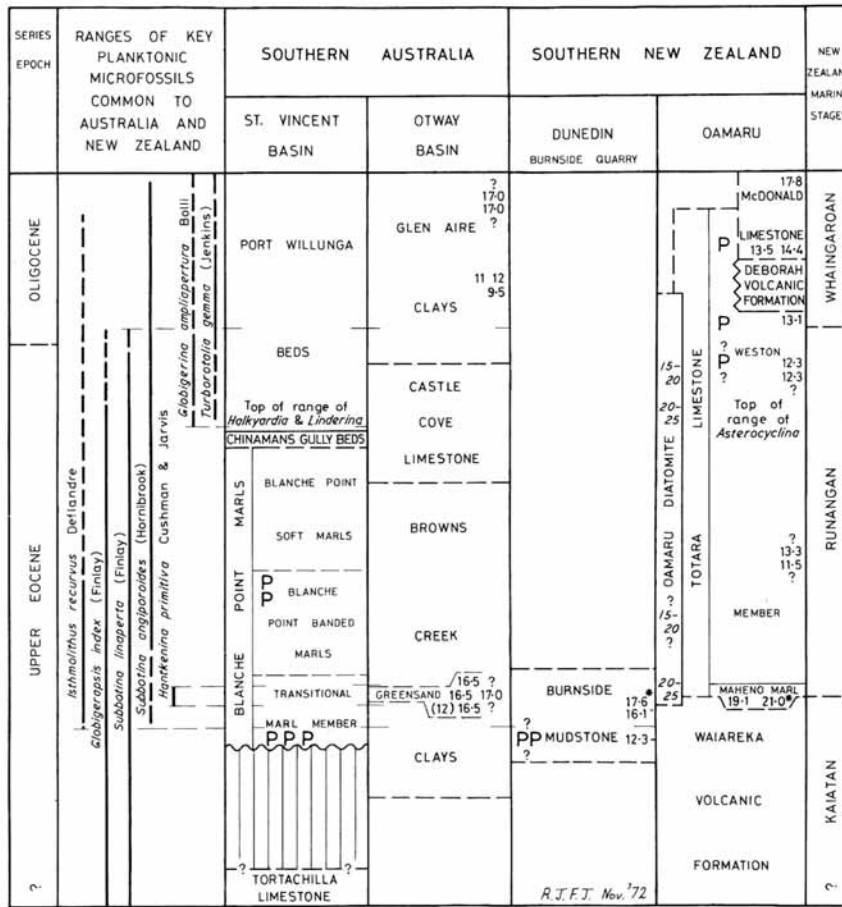
#### PALAEOECOLOGY

Stonehouse (1969) and Simpson (1971a, 1971b) have focused attention on the palaeoecology of fossil penguins, particularly their possible adaptation to certain climatic regimes. However, these studies lack stratigraphic precision. Modern studies of the Tertiary increasingly suggest rapid temporal changes in climate (e.g. Devereux 1967; Wolfe 1971) and thus it is considered that investigations of possible relationships between Tertiary organisms and climate can only be rationalized with the closest attention to all possible forms of chronostratigraphic control. Though the available data is to some extent incomplete or inferential, recent foraminiferal and coccolith studies (Lindsay 1967, 1969, 1970; McGowran, Lindsay and Harris 1971; Edwards 1971; Hornibrook and Edwards 1971; Jenkins 1971) now provide a basis for a tentative stratigraphic framework to reference the Upper Eocene fossil penguins of Australia with their New Zealand counterparts (text-fig. 3).

The Blanche Point Marls, in which *P. simpsoni* occurs, contain a marine fauna. The shelly elements of the fauna are not notably diverse; molluscs, particularly gastropods are the commonest species and are present at most levels. Bryozoans are relatively frequent in the lower half of the formation. Abundant sponge spicules are a characteristic feature of the Banded and Soft Marls Members and moulds or silicified remains of sponges are common in the Banded Member.

Tropical 'larger' foraminifera (Nummulitidae, Alveolinidae and Discocyclinidae) are unknown in the Upper Eocene of south-eastern Australia, and hence on extra-tropical environment can be presumed. Occurrences of the pantropical benthonic foraminifera *Halkyardia* and *Linderina* in southern Australia (Ludbrook 1961; Lindsay 1969) are considered to indicate warm conditions (McGowran 1971). The pantropical planktonic genus *Hantkenina* occurs in a well-defined narrow interval (Lindsay 1969; here text-figs. 1 and 3) and is suggested by Jenkins (1968) to be a warm-water indicator. These genera all occur in the near vicinity of Blanche Point (and Witton Bluff), but seemingly not at the actual stratigraphic horizons of the fossil penguin remains.

The nautiloids *Cimomia* and *Aturia* are relatively frequent fossils at several levels in the Blanche Point Marls (Glaessner 1955; McGowran 1959). *Aturia* has been



TEXT-FIG. 3. Correlation chart for late Eocene and early Oligocene Australasian sequences known to contain fossil penguins, and other sequences for which palaeotemperature data has been obtained. The ranges of the planktonic microfossils on which the correlation is largely based are shown. Inferred or known occurrences of fossil penguins are indicated 'P'; each indication represents one individual. The numbers '12.3, 16.1' record the oxygen isotope temperatures (in °C) given by Dorman (1966, 1968) and Devereux (1967); the measurements are chiefly from benthonic fossils; an asterisk denotes measurements from planktonic fossils; values bracketed are considered unreliable. The numbers '20-25' indicate possible ranges of palaeotemperature (in °C) estimated by Mandra (1971) from silico-flagellate assemblages in the Oamaru Diatomite.

suggested as possibly indicating warm water (Cockbain 1968). Its significance is not unequivocal, however, as live individuals of the modern *Nautilus* are occasionally stranded on southern Australian shores and the shells of this genus are known to float long distances after the death of the animal (Stenzel 1964). *P. simpsoni* occurs in precise stratigraphic contiguity with *Cimomia*, and close, but perhaps not exact contiguity with *Aturia*. Further studies are needed to elucidate the possible environmental significance of other molluscs occurring in the marls.

Dorman (1966, 1968) and Devereux (1967) present numerous relatively recent results of oxygen isotope temperature measurements made on fossils from the Australian and New Zealand Cenozoic; items of their data of relevance to Upper Eocene and early Oligocene occurrences of fossil penguins in these regions are given in text-fig. 3. Temperature estimates made by Mandra (1971) from studies on silicoflagellate assemblages in diatomites of similar age in the Oamaru area, southern New Zealand, are also shown. The isotopic temperature measurements suggest a warm climate during the time of appearance of *Hantkenina primitiva*, and probable cooler conditions shortly before and soon after this event; the silicoflagellate data seem concordant with this and, as here interpreted (in the light of datings given by Edwards 1971), may indicate another similar climatic cycle later in the Upper Eocene. The same cycle is apparently evidenced by an ingression of the pantropical, larger foraminiferal genus *Asterocyclina* in calcareous facies at Oamaru.

The dating of the 12.3°C isotopic temperature from the Burnside Mudstone, Dunedin, New Zealand, corresponds closely with that of the fossil penguins from the Blanche Point Transitional Marls. The penguin bones from this level at both Blanche Point and Witton Bluff seem, on coccolith evidence, to be identical in age. Fossil penguins also occur in the Burnside Mudstone (Simpson 1971a) but their precise stratigraphic level is apparently not recorded.

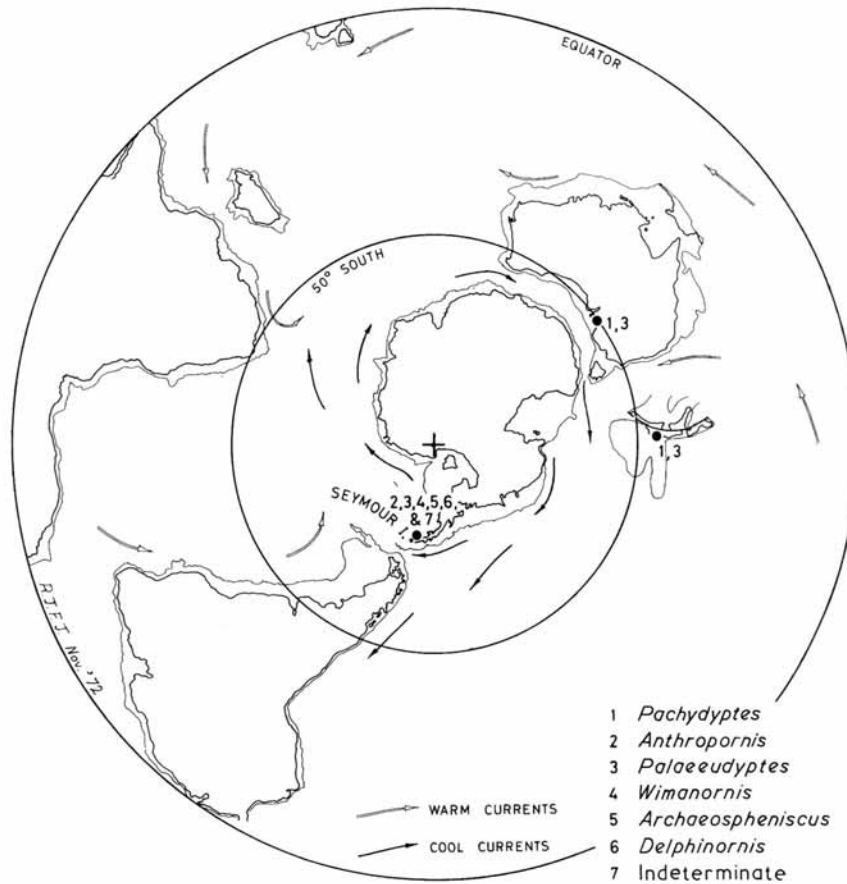
As was noted earlier in this work, the penguin *Pachydyptes ponderosus* occurs in the Totara Limestone at Oamaru. Samples of matrix associated with remains of its bones from its type locality, Fortification Hill, and also another occurrence, 'Oamaru', were examined by Finlay (1952), and *Asterocyclina* was not found. As *Asterocyclina* evidently occurs in most of the lower part of the Totara Limestone (Hornibrook 1961), the bones may postdate its local occurrence. *P. ponderosus* also occurs in the limestones at the locality 'Taylors Quarry': these are dated by Jenkins (1971) as being early Oligocene. Thus this penguin occurs in the early Oligocene and probably the latest Upper Eocene. Low isotopic temperature values for other exposures at Oamaru nearby to the localities of its remains (12.3–14.4°C) and also from south-eastern Australia (9.5–12°C) probably relate approximately to the time of its occurrence.

From the above discussion it is apparent that *Pachydyptes simpsoni* lived in an extra-tropical environment. Fluctuating warm and somewhat cooler climatic conditions seem to have obtained during the time of its existence; its occurrence at two levels in the Blanche Point Marls and probably other occurrences of Upper Eocene and early Oligocene Australasian fossil penguins may be linked to times of relatively low water temperatures, with bottom waters perhaps 10–14°C. The mean annual surface-water temperatures implied by this data are probably of the order of 12–16°C, or temperate.



The above findings contrast with the suggestion made by Stonehouse (1969) that the Eocene fossil penguins of New Zealand inhabited sub-tropical to tropical waters. Nowhere in the vicinity of the penguin remains are there faunas of comparable diversity to those of the tropics.

Simpson (1971a) refutes the popular view that penguins are principally associated with the Antarctic and its cold surrounding seas and concludes that the fossil species probably inhabited waters which were cool to warm temperate. He maintains a comparable opinion even with respect to the relatively diverse early Tertiary assemblage



TEXT-FIG. 4. Approximate positioning of southern hemisphere lands in the Upper Eocene and localities of the fossil penguin genera known or suggested to occur at this time. The hypothetical pattern of oceanic, surface circulation is shown.

of fossil penguins from Seymour Island (Simpson 1971*b*). However, he concedes that with respect to middle latitude occurrences of fossil species there may have been 'local or seasonal conditions of cooler water (and land temperature) when penguins actually occurred alive at the fossil localities' (Simpson 1971*a*). While broadly concurring with these conclusions, I suggest that, with respect to the late Eocene and early Oligocene at least, there were probably periods of cooler climate (of significant geological duration) when the large penguin species of those times penetrated northwards into middle latitude regions. This implies that the early penguins lived predominantly at high southern latitudes.

Reconstructions of the Eocene and Oligocene positioning of southern hemisphere land areas (McKenzie and Sclater 1971; Griffiths and Varne 1972) are modified here to show the probable positioning of these lands in the early Upper Eocene (text-fig. 4). The known probable Upper Eocene occurrences of fossil penguins are shown on this reconstruction; they form a southern distribution with the most northerly (southern New Zealand) possibly about 45° S. The abundance of penguin bones and diversity of forms recognized from the little-explored rocks of far-southern Seymour Island (the genera *Anthropornis*, *Palaeudyptes*, and *Wimanornis* Simpson, 1971, *Archaeospheniscus* Marples, 1952, *Delphinornis* Wiman, 1905, and several indeterminate forms, and perhaps seven species; Simpson 1971*b*) contrasts remarkably with the relative rarity of penguin remains in the better-known Eocene rocks of Australasia and can hardly be due to vagaries of preservation or collection. It is also notable that the known Australian and New Zealand Eocene penguin localities are restricted to southerly located exposures. The simplest inference is that the Australasian localities represent the northern limits of distribution of more diverse and denser southern, presumably Antarctic populations of early penguins. Thus at the time of their earliest known occurrence, penguins were seemingly already adapted to life in the relatively cool high-latitude seas of the southern hemisphere.

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