

A REVIEW OF THE PRE-PLIOCENE  
PENGUINS OF NEW ZEALAND

GEORGE GAYLORD SIMPSON

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## CONTENTS

INTRODUCTION . . . . .	323
Acknowledgments . . . . .	323
Abbreviations . . . . .	323
History . . . . .	324
LOCALITIES AND AGES . . . . .	326
Kakanui . . . . .	326
Oamaru . . . . .	328
Brighton . . . . .	328
Waitaki Valley, Duntroon . . . . .	328
Hakataramea Valley . . . . .	329
Burnside . . . . .	329
Gore Bay . . . . .	330
Omih . . . . .	331
Waimate . . . . .	331
Kawhia Harbour . . . . .	331
Summary of Ages . . . . .	332
Distributions . . . . .	332
SYSTEMATICS . . . . .	334
<i>Palaeudyptes</i> . . . . .	334
<i>P. antarcticus</i> . . . . .	335
<i>P. species indeterminate</i> . . . . .	337
<i>Pachydyptes</i> . . . . .	346
<i>P. ponderosus</i> . . . . .	347
<i>Platydyptes</i> . . . . .	347
<i>P. novaezealandiae</i> . . . . .	349
<i>P. amiesi</i> . . . . .	352
? <i>P. marplesi</i> , New Species . . . . .	354
<i>Archaeospheniscus</i> . . . . .	354
<i>A. lowei</i> . . . . .	355
<i>A. lopdelli</i> . . . . .	355
<i>Duntroonornis</i> . . . . .	357
<i>D. parvus</i> . . . . .	359
<i>Korora</i> . . . . .	359
<i>K. oliveri</i> . . . . .	360
BROADER SYSTEMATICS . . . . .	363
Generic and Faunal Affinities . . . . .	363
Subfamilies . . . . .	364
Origins . . . . .	366
NOTES ON ECOLOGY . . . . .	370
Sizes of Penguins . . . . .	370
Basic Adaptations . . . . .	373
SUMMARY . . . . .	376
REFERENCES . . . . .	376





## INTRODUCTION

PENGUINS ARE certainly among the most interesting of birds, or of any creatures. Aside from the droll aspect that has made them favorites, they are biologically fascinating. Although the general belief that they are primarily Antarctic animals is incorrect, one species does breed under the most adverse conditions imaginable. All are extremely specialized for a peculiar mode of life and, as the present study shows, the specialization was already essentially complete in the Eocene. Their origin has been a subject of major controversy, and it is baffling that a long and now rather rich fossil record throws little light on their evolution. The fossils are nevertheless of great interest if only because they show that this group, still highly diverse, was much more so a few tens of millions of years ago. The size of some of the extinct forms has often been exaggerated, but several extinct species were indeed much larger than the largest living species, the emperor penguin, *Aptenodytes forsteri*.

The largest penguin known is an extinct species from New Zealand, *Pachydyptes ponderosus*, and the first fossil penguin ever described (*Palaeudyptes antarcticus*, by Thomas Henry Huxley in 1859) is also from New Zealand. Known fossil penguins from New Zealand are exceeded in number and variety only by those from Argentina, and the New Zealand forms include the oldest known and span a longer time than those from any other region. Having had opportunity to study all the South American and Australian forms, I was particularly anxious also to review those of New Zealand, and I have finally been able to do so. The result is presented herewith.

### ACKNOWLEDGMENTS

The basis for the present study was laid by a visit to New Zealand in late 1968 and examination of specimens in the Otago Museum, Dunedin, the Dominion Museum, Wellington, and the New Zealand Geological Survey, Lower Hutt. I am much indebted to those institutions and their officers, as well as to the University of Otago, for permission to make those observations and for many other courtesies. In Dunedin I was especially aided by Dr. R. R. Foster, Director of the Otago Museum, Associate Prof.

J. D. Campbell, Department of Geology, University of Otago, and Mr. K. D. Mason of the same department who made the photographs of specimens mentioned here, bearing Otago Museum numbers. In both Wellington and Lower Hutt Dr. Charles A. Fleming assisted in innumerable ways both while I was there and by correspondence since. Dr. R. K. Dell, Director of the Dominion Museum, permitted me to study there and Mr. John B. Turner of the Dominion Museum made the photographs of its specimens and of those from the Geological Survey. Dr. N. de B. Hornibrook, Mr. A. R. Edwards, and Mr. Guyon Warren of the New Zealand Geological Survey assisted with determination of geological ages. The Survey provided me with maps and geological literature. Professor H. B. Fell, now of Harvard University, lent two specimens from his personal collection, and Mr. Vincent Maglio photographed them. All the expenses of my trip, stay in New Zealand, and preparation of the manuscript have been paid by myself. Throughout this work I have been jointly employed by Harvard University and the University of Arizona. This is a contribution from both institutions, and also from the American Museum of Natural History, which has undertaken the publication of the present paper. The extensive literary research involved was accomplished especially in the libraries of the Museum of Comparative Zoology, Cambridge, and of the Simroe Foundation, Tucson.

Pliocene specimens in and from the Canterbury Museum, Christchurch, will be the subject of a later study.

### ABBREVIATIONS

The following abbreviations are used with specimen catalogue numbers:

B.M., British Museum (Natural History), repository of the type, only, of *Palaeudyptes antarcticus*  
D.M., Dominion Museum, Wellington  
G.S., New Zealand Geological Survey, Lower Hutt  
O.M., Otago Museum, Dunedin.

In O.M. catalogue numbers, for example O.M. No. C.47.17, C refers to a partial register of natural history specimens, the next two numbers represent the last two digits of the year of cataloguing, not the year of collection, which was generally earlier, and

the last figures represent the serial sequence of specimens added to the C register in that year. In some cases each bone of a single individual was given a separate serial number, but in others bones of one individual have one number and in still others bones probably of different individuals were included under one serial number. As far as possible the associations are cleared up in discussions of the specimens later in the present study.

### HISTORY

The first fossil penguin bone to be described was an incomplete tarsometatarsus from New Zealand, *Palaeudyptes antarcticus* (see fig. 1), named by Thomas Henry Huxley (1859). Additional specimens, referred to Huxley's species, were described by James Hector, then director of the New Zealand Geological Survey, to the Wellington Philosophical Society on November 13, 1869 and later published (Hector, 1872, 1873). It was nearly 60 years before any further knowledge of New Zealand fossil penguins was acquired. Then the well-known New Zealand ornithologist W. R. B. Oliver included in his classic work (1930) two species of a new genus: *Pachydyptes ponderosus* and *P. novaezealandiae*. (The latter has since been removed to the genus *Platydyptes* Marples.)

The next and most substantial contribution of all, was made by B. J. Marples (1952), in a monograph in which he reviewed all previous

finds and added descriptions of a large number of specimens representing several new genera and species. Only two other New Zealand specimens have since been described (Marples, 1960; Marples and Fleming, 1963). Even now no significant new pre-Pliocene material is available beyond that studied by Marples. His excellent work remains basic, and the present study supplements rather than supplants it. A more formal systematic review is now possible, and further discussion on a number of points is appropriate. It might be particularly noticed that ages specified to and published by Marples as quite definite now seem decidedly less so in many instances. For one particularly important fossil, supposedly the oldest known penguin, the date given to Marples was quite wrong.

Since the first discovery in New Zealand, fossil penguins have also been found in three other regions: Central Patagonia (in Argentina), Seymour Island, and southern Australia. Patagonian fossil penguins were first described by Moreno and Mercerat in 1891, and were reviewed with many additions by Ameghino (1905). Numerous new specimens collected by a party under my leadership for the American Museum of Natural History, mostly in 1933, permitted a later revision of the whole fossil fauna (Simpson, 1946).

Fossil penguins were discovered by the Swedish South Polar Expedition in 1901–1903 on

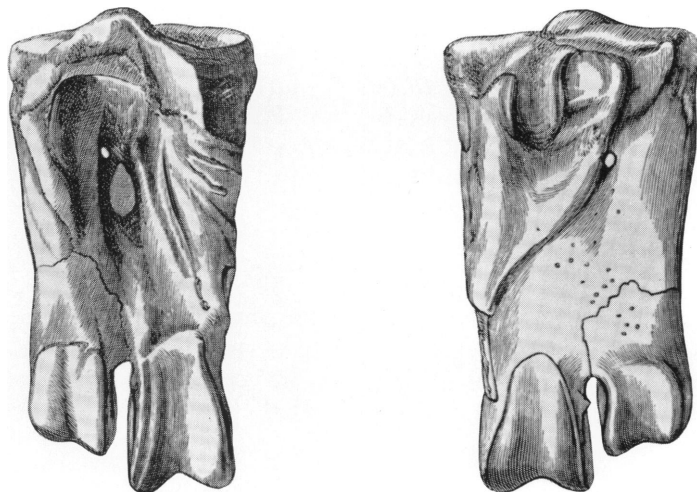


FIG. 1. *Palaeudyptes antarcticus*, B.M. No. A1084, type. Tarsometatarsus, dorsal (left) and plantar views.  $\times 1$ . (From Huxley, 1859.)



Seymour Island, which, despite numerous careless statements to the contrary (by me, among others), is not literally Antarctic but, at latitude  $64^{\circ}15'S$ ., within the South Temperate zone and separate from the Antarctic continent. Those discoveries were described by Wiman (1905). In 1946 further specimens were collected by the (British) Falkland Islands Dependencies Survey and later described by Marples (1953).

Notice of a fossil penguin bone from Australia was first published by Finlayson in 1938 (see Simpson, 1957), although it is now known that a specimen from Beaumaris, Victoria, had been

presented to the National Museum of Victoria by a Mr. W. B. Jennings in or about 1888 (Simpson, 1970). A number of specimens from South Australia and Victoria have now been described (Simpson, 1957, 1959, 1965, and 1970).

In addition to the middle and early Tertiary specimens reviewed here, a remarkably complete specimen from the Pliocene of New Zealand has been described (Marples, 1960). Two other excellent specimens from the same formation are now known and will be described in a later paper by me. They are quite different from any of the earlier forms considered here.

## LOCALITIES AND AGES

THE LOCALITIES of known pre-Pliocene penguins discussed below are mapped in figure 2.

### KAKANUI

Huxley (1859, p. 675) said that the holotype of *Palaeudyptes antarcticus* "was found by a native [presumably a Maori]<sup>1</sup> in the limestone of Kakaunui [now spelled Kakanui], and was brought to Mr. [Dr. W. B. D.] Mantell imbedded to some extent in a matrix which was readily recognizable as that particular limestone. Mr. Mantell informs me that the Kakaunui Limestone is overlain by a mass of blue clay, that upon the blue clay is superimposed a bed containing freshwater shells, and that upon this, again, lies the alluvium in which the remains of the *Dinornis* are found. . . ."

Kakanui is a settlement, latitude 45° 12' S., at the mouth of the river of the same name and south of the promontory known as Kakanui Head on the east coast of the South Island, south of Oamaru. The geology southward to, but not beyond, the Kakanui River has been mapped and described by Gage (1957). The part of the local section, just north of Kakanui, relevant here is as tabulated below:

There are thus three limestones of distinctly different ages in this area. Placing Huxley's type in the geological sequence depends on Mantell's ability to recognize one of those similar and variable limestones from a hand specimen, perhaps just a bit of matrix clinging to a bone, and on his use of the designation "Kakaunui limestone." On the former point, I see no way to judge at present. The three formations, in bulk,

<sup>1</sup> Marples (1952, p. 30) thus erred in saying that Mantell "collected" the specimen; unfortunately he did not see it *in situ* and that adds to doubts as to its exact source.

are distinguishable in the field, but they include lithologies that would be difficult, at best, to distinguish macroscopically in hand specimens. On the latter point, it is somewhat improbable that Mantell would designate the Totara (of present terminology) as Kakanui Limestone or include it under the latter term. It would seem that Mantell's "mass of blue clay" must refer to what is now called the Rifle Butts Formation, which includes "bluish-grey fine silt or mudstone" (Gage, 1957, p. 56) and is the only formation above the limestones that does so. But Mantell has the blue clay immediately overlying his "Kakaunui limestone," and the limestone that it overlies (with intercalation of a glauconitic bed) is the Otekaike. Thus it appears either that Mantell was referring to what is now called the Otekaike Limestone or, more likely, that he was not distinguishing between the immediately successive and similar McDonald and Otekaike limestones. If the former is true, Huxley's type is of Waitakian Age. In the latter, more probable, case its age cannot now be fixed within the considerable span Whaingaroan to Waitakian, inclusive, and the possibility of its being still older, Runangan (age of the Totara Limestone), is not absolutely excluded.

Finlay (1952, pp. 60-61), while noting that the actual horizon of Huxley's type is uncertain, thought it most likely that the specimen is from his "Kakanui limestone," probably the same as Gage's McDonald, although for Finlay the age is Runangan to Whaingaroan and for Gage it is Whaingaroan to Duntroonian. Gage (1957, p. 47) noted that Huxley's type is "now believed to be from the McDonald Limestone." That is possible, and the age may well be Whaingaroan, but considerable doubt remains. That has a

GAGE'S TERMINOLOGY	ALTERNATIVE OLDER TERMS	AGE ASSIGNED BY GAGE
Rifle Butts Formation	Pareora Formation	Awamoan (includes the type section)
Gee Greensand	(Not noted in the 19th Century and not named before Gage)	Waitakian to Hutchinsonian
Otekaike Limestone	Waitaki Stone	Waitakian (includes the type section)
McDonald Limestone	Kakanui Limestone	Whaingaroan and Duntroonian
Deborah Volcanic Formation	Kakanui Volcanics or Tuffs	Whaingaroan
Totara Limestone	Oamaru Stone	Runangan



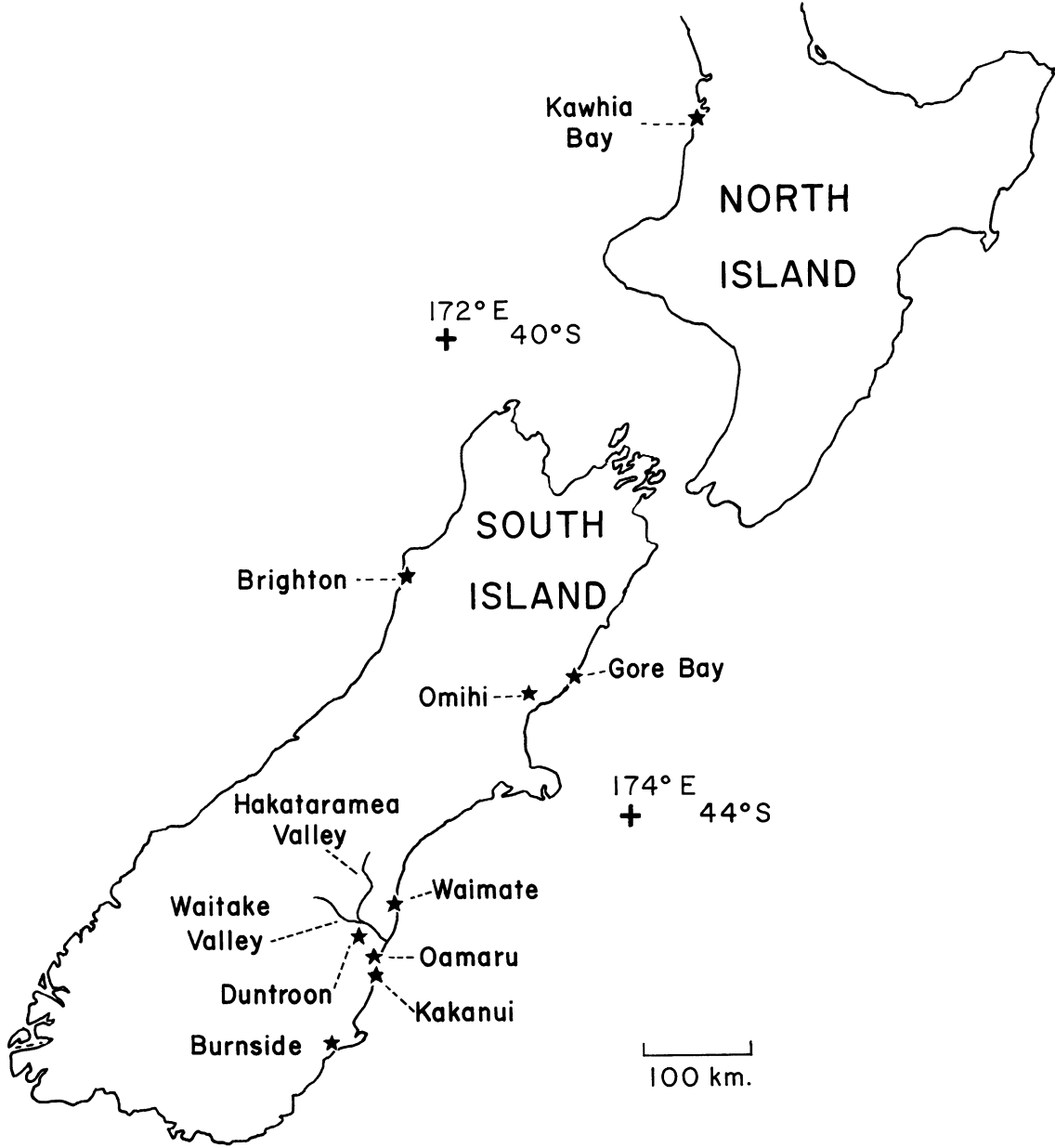


FIG. 2. Sketch map of South Island and southern part of North Island, New Zealand, showing pre-Pliocene fossil penguin localities.

bearing on vexatious questions of specific determinations, discussed below.

In his appendix to Marples' monograph Finlay (1952, pp. 60–61) said, "No actual matrix of this age [Whaingaroan] associated with penguin bones has been examined, but bones from the south side of the mouth of the river at Kakanui, about 10 feet above the tuffs, must be from this stage." There seems to be an implication that the bones in question are penguin bones, but that is puzzling because Marples did not mention this discovery and I have found no other reference to it in the literature or in museum records.

### OAMARU

Oamaru is a major settlement at latitude 45°07'S., on the east coast of the south island. Hector (1872, 1873) described a specimen, D.M. No. 1450 from Fortification Hill, near Oamaru, and referred it to *Palaeudyptes antarcticus*, but it was later made type of *Pachydyptes ponderosus* Oliver, 1930. Hector incidentally added still more confusion to the geological data by failing to distinguish more than one limestone in Otago and equating the "Kakanui limestone" with the "Ototara series," whereas the latter consists of, or at least in some usages includes, the Totara of Gage (1957) and others, an older formation than the Kakanui of most authors. In fact there is no serious doubt that the specimen is from the Totara Limestone and not the "Kakanui Limestone" as the latter name has generally been used, that is, the McDonald Formation. Finlay (1952, p. 60) obtained a Runangan microfauna from the matrix of the specimen. The geology is mapped and discussed in Gage (1957).

Several other specimens have been found around Oamaru in the Totara Limestone, Runangan in age. There are no more exact data for O.M. No. C.47.16 than "Oamaru," but Finlay (1952, p. 60) found a Runangan microfauna in the matrix with special resemblance to one from Deborah, which may be the more exact locality of the specimen. Two specimens, F/336 (a) and F/336 (b), incorrectly indicated as belonging to Victoria University College, Wellington, by Marples (1952, p. 37), are in the private collection of Prof. H. B. Fell and are from Taylor's Quarry, Cormacks, on the outskirts of Oamaru.

The type of *Platydyptes novaezealandiae* (Oliver,

1930), D.M. No. 1451, is recorded only as from the "Oamaru district." Ovey (1939) guessed that it is of Miocene age, but Finlay (1952, p. 64) obtained a microfauna from the matrix that could be either Duntroonian or Waitakian. Rocks of both ages do occur near Oamaru. Unlike other specimens from that area, this type evidently is of distinctly later age than the Totara Limestone.

### BRIGHTON

Hector (1872) described a specimen, D.M. No. 1449 (incorrectly given as 1440 throughout in Marples, 1952), collected by James Duigan, a telegrapher, at Seal Rock, Woodpecker Bay near Brighton in Nelson on the west coast of the South Island, near latitude 42°S.<sup>1</sup> Hector's published geological data are not useful, but Finlay (1952, p. 63) obtained a fair microfauna indicative of Duntroonian Age.

An unidentified fragment of a penguin tibia was found on the mainland opposite Seal Rock at N.Z. Geol. Surv. Locality 3180 and the age definitely established as Duntroonian (Finlay, 1952, pp. 62–63).

### WAITAKI VALLEY, DUNTROON

The Waitaki River is a major drainage on the east side of the central part of South Island. Many important specimens of fossil penguins have come from the slopes on the south side of that valley and from small tributaries from the south, mostly east and southeast of the settlement of Duntroon. I have been unable to find any really precise records of localities or horizons, but that is not too important as all recorded specimens from that area were found in a single bed of greensand, usually only 10 to 15 feet in thickness, although it is said (by Marwick, 1935) to reach 300 feet in the Wharekuri Basin. The area near Duntroon, most important for penguins, has been geologically mapped and described by Gage (1957). Duntroon is a small inland settlement at latitude 44°51'S., longitude 170°40'E.

The greensand in question has been called Kekenodon, lower Hutchinsonian, Wharekuri,

<sup>1</sup> The Times Comprehensive Atlas does not show Brighton, but it indicates a Seal Island at this locality, and that is probably Hector's Seal Rock. It is between the mouths of the Grey and Buller rivers, as Hector noted, and is about nine miles south of Charleston.



and in Marples' (1952) classic work *Maerewhenua*, but in Gage's now definitive Waitaki regional monograph it is named the Kokoamu Greensand, from a small stream two miles south-east of Duntroon. Exposures of the Kokoamu Greensand in Landon Creek are the type section for the Duntroonian Stage, and all penguins from this formation may be taken as Duntroonian in age.

It appears that most of the specimens were found *in situ* in the sense of being still embedded in the greensand matrix, but that the matrix itself was often not strictly *in situ* but was adhering to fallen limestone blocks below the scarp. Such blocks are seen in Gage, 1957, figure 24.

Most specimens are labeled simply "Duntroon" and probably are from within a few miles southeast of that settlement. The label for O.M. No. C.47.34 is marked "Earthquakes," a locality about three miles southwest of Duntroon. An unusually good specimen, O.M. No. C.47.15, referred by Marples to *Platydyptes novaezealandiae* but here made holotype of a new species, is registered as "from Oamaru."

Finlay (1952, p. 61), however, obtained a large foraminiferan fauna (44 species) from its matrix and found this to be Duntroonian and unlike anything from the vicinity of Oamaru. He found the resemblance so close to that of the Duntroonian fauna at Wharekuri, not only in species but also in appearance and abundances, that he suggested Wharekuri as the probable origin of the specimen.

Another specimen, O.M. No. C.47.35, apparently the first one found in the Duntroon area, is registered as from White Rocks, probably in the immediate vicinity of Duntroon, although I have not located it exactly.

#### HAKATARAMEA VALLEY

The type of *Platydyptes amiesi* Marples, 1952, O.M. No. C.50.61 and O.M. No. C.50.63, type of *Korora oliveri* Marples, 1952, are recorded simply as from the Waitakian of the Hakataramea Valley, south Canterbury. Although Marples collected both specimens himself in 1948, he gave no further geological or geographical information. The Hakataramea is a major tributary of the Waitaki from the north between latitudes 44°S., and 45°S. No reference is made to the occurrence in Finlay's appendix to Marples' monograph, and the basis for determination of the age as Waitakian is unknown to me.

#### BURNSIDE

This is an especially important locality, both crucial and puzzling, because although all specimens from there came from a single quarry and were referred without question to a single species, *Palaeodyptes antarcticus*, by Marples (1952), they have been supposed to be from two widely separate ages, Kaiatan (late, not latest Eocene) and Waitakian (late Oligocene or early Miocene). The identifications are discussed below under *Palaeodyptes marplei* and *Palaeodyptes* species indeterminate.

The specimens are from the Burnside Quarry, still being exploited for material for a cement factory at the site. That site, at latitude 45° 54' S., immediately west of, and now almost engulfed in, the city of Dunedin, is precisely placed, indicated as "Marl Pit," on the geological map made by the late Prof. W. N. Benson of Otago University around 1946 but published in 1969 to scale 1:50,000 (Benson, 1969). That map is accompanied by a verbal summary of the regional geology by Wood (1969) based largely on Benson's notes. A more recent map to smaller scale, 1:250,000, also with a geological summary was made by McKellar (1966). Burnside and the Burnside Quarry are not indicated on this map, but they lie in the patch of late Eocene-Oligocene sediments shown near Abbotsford.

The greater part of the quarry, which I was able to visit through the kindness of Prof. J. D. Campbell, is in the Burnside Mudstone, formerly called Burnside "Marl," although the calcium carbonate content (not over 20 per cent and usually less) is lower than in most current definitions of marl. Two fossil penguins each represented by a number of associated bones and therefore almost certainly *in situ* and not re-deposited, are labeled as from that formation: O.M. Nos. C.48.73-81 and C.50.25-47. The age of the greater part of the formation is now considered Kaiatan, but the top (Wood, 1969, from Benson ms. has "a few feet" in one place, p. 10, but only "the highest nine inches" in another, p. 11) is Runangan.

Above the Burnside Mudstone, certainly with a sharp disconformity and probably with a low angular unconformity, is a thin greensand, earlier informally called "Burnside Greensand" and so designated by Marples (1952), left unnamed by McKellar (1966), but still more recently named the Concord Greensand (see Wood, 1969, p. 9). The apparently contempo-

aneous fossils are Waitakian in age, but it also contains redeposited foraminifera from the considerably earlier but immediately underlying Burnside Marl. The disconformity thus cuts out the whole of the Whaingaroan and Duntroonian and part of the Runangan below and perhaps the Waitakian above. Specimens O.M. Nos. C.47.17 and C.47.18 and G.S. No. 2225 are labeled as from the "Burnside Greensand," that is, in present terms, Concord Greensand. Some, at least, of the Otago Museum specimens from this quarry were found by a careful amateur collector, H. S. Tily, with whom Professor Campbell has discussed their occurrence. The specimens registered as from the "marl" and as from the greensand are not so different in preservation as to make derivation from different sediments clear, nor yet so similar as to make it improbable. There is no serious reason to doubt probable derivation from the two different formations, as labeled. As far as I know, no evidence as to exact levels within the formations is available. Finlay (1952) did not discuss the age of the bones from the "marl," and although he published a list of forams headed "Matrix from *Palaeudyptes* bones occurring in the Burnside [i.e. Concord] greensand," he did make it clear that his fossils were not in fact from such matrix and were not actually associated with the penguin bones.

All the Concord specimens are broken, and two are single fragments. However, O.M. No. C.47.17 includes parts of four bones considered by Marples (1952, p. 32) as "probably but not certainly belonging to the same individual." If they were indeed associated elements of an individual the chances of redeposition and of age other than Waitakian would be slight. However, I believe that Marples' doubts were well justified. Comparisons of the bones, discussed below under *Palaeudyptes* species indeterminate, strongly suggest that they are not from one individual, perhaps not even all from the same species. All are rolled fragments. They occur just above a disconformity and are associated with forams redeposited from a formation of Kaiatan and Runangan ages. I consider it probable that the bones found in the greensand were also redeposited and that their age is either Kaiatan or Runangan, or indeed, perhaps both.

Thus there is a very unsatisfactory situation:

The Burnside penguins may be either Kaiatan or Runangan.

The Concord penguins may be Kaiatan, Runangan, or Waitakian.

In any event, it is certainly not justified to conclude that these specimens demonstrate the survival of a species of penguins from Kaiatan to Waitakian, inclusive, a specific span so extraordinary as to be unique.

#### GORE BAY

Gore Bay, near the small settlement of Cheviot, is on the east coast of the South Island, latitude 42°53'S. north of Christchurch and approximately halfway to Kaikoura. The locality has enjoyed fame (in a somewhat limited circle) as having yielded by far the oldest known penguin. That turns out to be untrue.

Marples (1952, p. 44) gave the age as "probably Heretaungan, lower Eocene" and said that "this appears to be the oldest penguin bone at present known." Quite naturally those conclusions have been incorporated wherever relevant in virtually all subsequent publications, with the words "probably" and "appears" omitted. The specimen consists of three fragments of a single femur, all badly preserved and unidentifiable beyond the fact that they do represent a penguin.

Belief in probable Heretaungan Age was based on Finlay (1952, p. 59). He believed the locality, G.S. 5184 (misprinted 5148; the correct number was given by Marples, 1952, p. 44) was "in all probability the same as G.S. 3453, phosphatic layer below chalk marl and above greensands" Although he did not have data on the age of G.S. 3453, his argument for that of G.S. 5184 depended on the supposed identity with G.S. 3453 and on that being a single marker phosphatic bed for the area. No fossils except the penguin bone were noted for G.S. 5184, but he had Bortonian fossils from "typical chalk marls," which would indicate an age not later than middle Eocene if in fact 5184 were equivalent to a bed below those same marls. Then from "below the marls, but above the greensands" he had some Heretaungan forams, and concluded that G.S. 5184 "is almost certainly of lower Eocene age." However, the very roundabout argument was fallacious from the start.

Charles A. Fleming kindly arranged for Guyon Warren of the New Zealand Geological Survey to revisit Gore Bay. Warren was unable to relocate G.S. 5184, but did locate G.S. 3453 and found fossils suggesting that its age may be Maestrichtian—which would make the penguin

phenomenally ancient if its horizon were stratigraphically below that of G.S. 3453, but for this there is really no evidence at all. Matrix associated with the penguin bones from G.S. 5184 was available at the Geological Survey (in Lower Hutt), and on my request to Charles A. Fleming for further information N. de B. Hornibrook kindly extracted and identified Foraminifera from it and A. R. Edwards did the same for nannoplankton, using techniques not yet available to Finlay. Their report, forwarded by Dr. Fleming (letter of November 27, 1969), is as follows:

Foraminifera (identified by N. de B. Hornibrook)

*Notorotalia serrata*  
*Globigerina woodi*  
*Globiquadrina debisceus*  
*Karreriella novozelandica*  
*Anomalinoidea cf. orbiculus*

Calcareous nannoplankton (identified by A. R. Edwards), abundant but rather poorly preserved

*Ericsonia* sp. (abundant)  
*Cyclococcolithus neogammation*  
*Helicopontosphaera kamptneri*  
*Sphenolithus moriformis*  
*Discoaster* sp. of *deflandrei* group

Reworked from Landon Series strata:

*Reticulofenestra placomorpha* (2 specimens)  
*R. bisecta* (1 specimen)

Age: Po-Pa

Environment: Warm temperate fully oceanic (outer shelf) conditions.

The age indication, "Po-Pa," is reference to the Pareora "Series" of New Zealand usage,<sup>1</sup> comprising the Otaian, Hutchinsonian, and Awamoan stages and ages now generally correlated as early Miocene. The Landon "Series" immediately underlies the Pareora and comprises the Whaingaroan, Duntroonian, and Waitakian stages and ages. In view of the battered condition of the penguin bone and the presence of some reworked microfossils from the Landon, it is possible that the penguin bone is also derived from that "Series," Oligocene or Oligocene and lowest Miocene in age.

In any case, the specimen definitely is not early Eocene, is not the earliest known penguin, and if, as is probable, it is from the Pareora it is

among the latest known fossil penguins from New Zealand. If it is from the Landon "Series," it is of the approximate age of the majority of known New Zealand specimens. As the specimen is not identifiable and is not noteworthy in any apparent way, its exact age turns out to be of no particular importance.

### OMIHI

An incomplete small femur in the Canterbury Museum is labeled as from Omihi, Crofts, North Canterbury. There are no geological data, but Marples (1952, p. 44) found a few adherent glauconite grains and guessed, with no other evidence, that the age might be Duntroonian. Omihi is about 40 miles north of Christchurch. The specimen is unidentifiable, the age is unknown, and as it stands the record has no scientific value.

### WAIMATE

Two unidentifiable specimens collected by J. A. Hurst have this locality datum. Finlay (1952, p. 62) obtained a microfauna from the matrix of one of them and believed it to be possibly Waitakian but probably Duntroonian. Waimate is near the east coast of South Island at latitude 44°45'S., about halfway between Timaru and Oamaru. The only interest in the occurrence is that it adds to the evidence that penguins may occur, if only sparsely, almost anywhere in the late Eocene through Oligocene (at least) of northern Otago and southern Canterbury.

### KAWHIA HARBOUR

As published by Marples and Fleming (1963), G.S. No. 9165 is a fragmentary femur from Motutarakatua Point, Kawhia Harbour. The locality is on the west coast of the North Island at latitude 38°03'S., about 80 miles almost due south of Auckland. The geology is discussed and the locality in which the bone was later found is shown in Fleming and Kear (1960). The age is Whaingaroan. This is the only pre-Pleistocene penguin yet known from the North Island.

### SUMMARY OF AGES

A standard system of "series" and stage-age names and corresponding biostratigraphic and time units for marine sediments in the New

<sup>1</sup> "Series" is here put in quotation marks because in codified international and American usage a series is defined as a time-stratigraphic unit corresponding to an epoch in time units, while in normal New Zealand practice the times covered by series are not equated with epochs.



Zealand province from Permian to Holocene is now in general use and has been employed in previous discussion. It is defined and ages are determined almost entirely on the basis of Foraminifera. The units relevant to this review are as follows:

"SERIES"	STAGES
Pareora	Awamoan
	Hutchinsonian
	Otaian
Landon	Waitakian
	Duntroonian
	Whaingaroan <sup>1</sup>
Arnold	Runangan
	Kaiatan
	Bortonian
(Part of) Dannevirke	Porangan
	Heretaungan
	Mangaorapan

The sequence within New Zealand is fully established, but as in other regions, including Europe itself, there is considerable question as to precisely how the ages should be fitted into the Europe-based epochs. There is little or no disagreement in placing the Heretaungan as early, but not earliest, Eocene, the Kaiatan and Runangan as late Eocene, and the Whaingaroan as early Oligocene. The Duntroonian is also generally considered Oligocene, but whether early, middle, or late depends on where the Oligocene-Miocene line is drawn. The boundary was formerly drawn above the Awamoan, which put the Duntroonian in lower and the Waitakian in middle Oligocene, for example in Gage (1957). However, there is a tendency to place the Oligocene-Miocene line lower in the New Zealand age sequence, often between the Otaian and the Waitakian, for example in Fleming (1962) and in Brown, Campbell, and Crook (1968). An authoritative revised correlation by

<sup>1</sup> Innumerable New Zealand place names and from them many geological names are of Maori origin. Pronunciation can usually be roughly approximated by giving vowels their Spanish or Italian values, but vowels can be long or short and short vowels tend toward the English short vowels. Most consonants approximate their English values, but *wh* and *ng* are exceptions. The sound of *wh* is peculiar to Maori and is somewhat more like English *f* than English *wh*. More exactly, it is nearly an aspirated, unvoiced consonantal *w*. The sound of *ng* is as in *singer*, not as in *penguin*, and it always occurs at the beginning, never at the end, of syllables. The correct syllabification of Whaingaroan is *wha-i-nga-ro-an*.

Hornibrook (1967) has gone so far as to place the Waitakian in the Miocene, and this is now also often accepted. The Whaingaroan and Duntroonian have quite similar faunas and would seem to cover a rather short combined span, but if the Waitakian is Miocene they would represent the whole of the Oligocene. That cannot be considered impossible, but it is perhaps still questionable.

A few now rather old radiometric, K-A dates have been published for New Zealand sediments (Lipson, 1956):

Waitakian  $20.4 \pm 1.2 \times 10^6$

Whaingaroan-Duntroonian  $22.0 \pm 1.5 \times 10^6$

Kaiatan  $37.0 \pm 2.6$  and  $40.5 \pm 2.8 \times 10^6$

Those figures would place the Oligocene-Miocene boundary below the Whaingaroan and would compress all of the Oligocene, and perhaps part of the early Miocene and late Eocene, into the single age Runangan. Both conclusions are so improbable as to be virtually incredible.

On a balance of conflicting authorities, I suggest the following epochal correlations, with the understanding that these are still highly tentative:

Awamoan	Early Miocene
Hutchinsonian	
Otaian	
Waitakian	Late Oligocene
Duntroonian	Early Oligocene
Whaingaroan	
Runangan	Late Eocene
Kaiatan	
Bortonian	Middle Eocene
Porangan	
Heretaungan	Early Eocene
Mangaorapan	

## DISTRIBUTIONS

The occurrences are here listed in approximate order of ages, from older to younger, although the doubts as to exact ages of many specimens make a precise sequence impossible.

Kaiatan or Runangan, Burnside

*Palaeodyptes marplei*

*Palaeodyptes* sp.

Probably redeposited from Kaiatan or Runangan, but possibly Waitakian, Burnside

*Palaeodyptes* sp.

Runangan, Oamaru

*Pachydyptes ponderosus*

Whaingaroan, Kawhia Harbour

Spheniscid indeterminate

Whaingaroan, Duntroonian, or Waitakian, Kakanui

*Palaeudyptes antarcticus*

Duntroonian, Waitaki Valley

*Palaeudyptes* species indeterminate

?*Platidyptes marplei*

*Archaeospheniscus lowei*

*A. lopedelli*

*Duntroonormis parvus*

Duntroonian, Brighton

*Palaeudyptes* sp.

Duntroonian or Waitakian, Oamaru

*Platidyptes novaezealandiae*

Duntroonian or Waitakian, Waimate

Spheniscid indeterminate

Waitakian, Hakataramea Valley

*Platidyptes amiesi*

*Korora oliveri*

Pareora "Series" or redeposited from Landon

"Series," Gore Bay

Spheniscid indeterminate

## SYSTEMATICS

THE FOLLOWING is a formal taxonomic review of all generically identified specimens of pre-Pliocene penguins from New Zealand known to me. For genera the first publication is cited, but subsequent references are added only if they include substantive information in connection with the genus only, not with a species, whether the latter is named or unnamed. For species the intention is to cite all publications with any substantive information or discussion. Mere listing, without other information, is not necessarily cited. All original illustrations (and some copies) are cited.

For reasons explained elsewhere in the present paper, I have abandoned subfamily (or tribe) classification for fossil penguins. All are referred to the one extant family, Spheniscidae.

Available original diagnoses are quoted. When these are inadequate or emendation is suggested by later knowledge, revised diagnoses are given. Those are based as far as possible on tarsometatarsus, humerus, or both. Those are the most distinctive bones usually available, and all the New Zealand holotypes in this study include one or the other of them. Most fossil penguin holotypes from other regions are also either humeri or tarsometatarsi.

Sufficiently characteristic measurements of all the holotypes are given in table 1.

Somewhat against personal preference, I have followed the International Code in designating a single original type specimen of a species as holotype and the type of a genus as type-species. All the normal species here discussed had single original types, all of which are still at hand, so that questions of syntypes, lectotypes, and neotypes do not arise. Marples (1952) sometimes included referred specimens in his first descriptions of species, and under the Code [Article 72(b) and Recommendation 73D] these could be called paratypes, but I consider the concept of paratype as unnecessary and misleading and do not follow that recommendation, which is not mandatory. I do specify what specimens were included in Marples' descriptions.

### ORDER SPHENISCIFORMES

#### FAMILY SPHENISCIDAE

##### PALAEUDYPTES HUXLEY, 1859

*Palaeudyptes* HUXLEY, 1859, p. 675. WATSON, 1883, p. 46 (as probable synonym of *Eudyptes*). MARPLES, 1962, p. 414, figs. 1c (head of humerus), 2b (coracoid), and 3c (base of coracoid).

COMMENT: In the original and in various later

TABLE 1  
SOME BASIC DIMENSIONS (IN MILLIMETERS) OF HOLOTYPE SPECIES OF NEW ZEALAND FOSSIL PENGUINS

Species	Dimensions <sup>a</sup>				Tarsometatarsus	
	Humerus					
	1	4	5	6	2	4
<i>Palaeudyptes antarcticus</i>	—	—	—	—	62	33
<i>Palaeudyptes marplei</i>	—	—	—	—	75	42
<i>Pachydyptes ponderosus</i>	179	66	44	45	—	—
<i>Platydyptes novaezealandiae</i>	104	ca. 34	22	26	—	—
<i>Platydyptes amiesi</i>	118	41	27	29	—	—
? <i>Platydyptes marplei</i>	95	33	21	23	—	—
<i>Archaeospheniscus lowei</i>	128	37	24 <sup>b</sup>	27½	—	—
<i>Archaeospheniscus lopdelli</i>	—	—	—	—	55	35
<i>Duntroonornis parvus</i>	—	—	—	—	ca. 31	ca. 16½
<i>Korora oliveri</i>	—	—	—	—	38	18

<sup>a</sup>Dimensions are those defined by Marples (1952) and are numbered as in his work. With a noted exception, the measurements are also taken from his work; checks confirmed their accuracy within narrow limits of instrumental error.

<sup>b</sup> Marples (1952, table 3) has "19," which must be a misprint.

Humerus: 1. Maximum proximodistal length. 4. Lateromedial (or preaxio-postaxial) diameter of head. 5. Lateromedial diameter of shaft 1/3 of distance from proximal end. 6. As 5, 2/3 of distance from proximal end.

Tarsometatarsus: 2. Length from convexity of proximal end to groove of trochlea of metatarsal III (this is slightly less than total length). 4. Lateromedial (or preaxio-postaxial) width of proximal end.

publications the ae is printed as a ligature; no attempt is made here to refer separately to ligated and unligated forms.

**ETYMOLOGY:** Greek *palaios*, ancient, and *Eudyptes*, name of a Recent genus of penguins (from Greek, *eu*, meaning good and *dyptes*, meaning diver) which the fossil was believed to resemble.

**TYPE-SPECIES:** *Palaeudyptes antarcticus* Huxley, 1859.

**INCLUDED SPECIES:** The type and *P. marplesi* Brodkorb, 1963.

**KNOWN DISTRIBUTION:** Possibly Kaiatan to Waitakian, but perhaps only Runangan to Duntroonian, New Zealand. See discussions of localities and ages and of *Palaeudyptes* species indeterminate.

**ORIGINAL DIAGNOSIS:** Huxley gave a detailed description of the holotype of the type-species but gave no separate and distinct diagnosis of genus or species. He stated that the tarsometatarsus ("tarso-metatars") of *Palaeudyptes antarcticus* is generally similar to that of *Eudyptes chrysolophus* (the living macaroni penguin) except that it has only one "interosseous foramen" (two in *Eudyptes*) and further "differs from the corresponding bone of *Eudyptes* in the division of the calcaneal ridges into four, in the more slender and crestlike form of the inner one, in the caecal ending of the inner foramen and in the 'linea aspera' on the posterior face, and in indicating a bird of twice the size of any *Eudyptes* that I have seen." (Huxley, 1859, pp. 674-675.)

**REVISED DIAGNOSIS:** Tarsometatarsus relatively short and wide. Metatarsals II and III closely united, radial intermetatarsal foramen very small or absent; groove and moderate lateral foramen between III and IV. IV straight. Humerus (reference to genus probable but not certain) straight, head massive, shaft narrower distally, no or very slight preaxial angle, pectoralis secundus insertion straight and far removed from latissimus dorsi, tricipital fossa small and undivided, shaft-trochlear angle small. (See Simpson, 1946, p. 69; Marples, 1952, p. 30.)

***Palaeudyptes antarcticus* Huxley, 1859**

Figure 1

*Palaeudyptes antarcticus* HUXLEY, 1859, p. 675, figs. 1, 2.

*Paleudyptes antarcticus*: HECTOR, 1872, fig. 5. WIMAN, 1905, p. 13.

*Palaeudyptes antarctica*: LOWE, 1933, p. 504, pl. V, fig. 3, fig. 3c (captioned only *Palaeudyptes* but a new,

proximal view of the holotype of *P. antarcticus*).

The following are references to uses of the name including the holotype; figure references are to the holotype tarsometatarsus only. Hector, 1872, p. 343, fig. 5; Oliver, 1930, p. 85; Lambrecht, 1933, p. 236, fig. 92B; Lowe, 1939, p. 282; Ovey, 1939, p. 294; Simpson, 1946, p. 40, fig. 23G; Marples, 1952, p. 30, pl. 8, fig. 9; Simpson, 1957, p. 67; Simpson, 1959, p. 116; Brodkorb, 1963, p. 23. For other references and figures see *Palaeudyptes* species indeterminate.

**COMMENT:** Wiman (1905), referred to Hector's "Mangelhaften Figur" (meaning Hector, 1872, fig. 5), which is in part a good lithographic copy of Huxley's woodcut (1859, fig. 1) with an outline restoration of the distal end of metatarsal II.

**ETYMOLOGY:** *antarcticus*, Neolatin for "opposite to the North Pole," evidently in reference to the supposed Antarctic position of the type locality, which in fact at latitude 45°12'S. is much farther from the South Pole than Huxley's London, at latitude 51°30'N., is from the North Pole.

**HOLOTYPE:** B.M. A.1084, right tarsometatarsus lacking distal end of metatarsal II.

**HYPODIGM:** For the present work, the holotype only, numerous other previously referred specimens being considered of doubtful reference as explained under *Palaeudyptes* species indeterminate.

**KNOWN DISTRIBUTION:** Strictly that of the holotype only, at or near Kakanui, Otago, New Zealand, probably Whaingaroan, Duntroonian or Waitakian, but just possibly Runangan (see "Localities and Ages").

**ORIGINAL DIAGNOSIS:** None given, and description not separable from that of the genus.

**REVISED DIAGNOSIS:** Holotype tarsometatarsus 17 per cent shorter and 21 per cent narrower at proximal end than holotype of *P. marplesi*.

***Palaeudyptes marplesi* Brodkorb, 1963**

Figure 3

*Palaeudyptes antarcticus*: MARPLES, 1952 (in part; references are to holotype of *P. marplesi*, only), p. 31, pl. 5, fig. 3 (patella), pl. 8, fig. 1 (femur), fig. 11 (tarsometatarsus).

*Palaeudyptes marplesi* BRODKORB, 1963, p. 231.

**ETYMOLOGY:** For B. J. Marples.

**HOLOTYPE:** O.M. No. C.50.25-47, most of an ulna, two fragments of a single femur, a complete femur, four fragments of a single tibiotarsus, the distal end of a tarsometatarsus, a crushed but nearly complete tarsometatarsus, fragmentary

fibula, several phalanges, and several fragmentary vertebrae. Although each fragment has been given a different catalogue number, it is reasonably certain that most, and probable that all, are from a single individual.

**HYPODIGM:** For the present work, the holotype only, especially the tarsometatarsus O.M. No. C.50.28. Brodkorb (1963) referred O.M. No.

C.48.73–81 and South Australian Museum No. P 10870, both discussed below under *Palaeudyptes* species indeterminate.

**KNOWN DISTRIBUTION:** Strictly that of the holotype only, in the Burnside Mudstone at Burnside, near Dunedin, Otago, New Zealand, Kaiatan or Runangan (see "Localities and Ages").

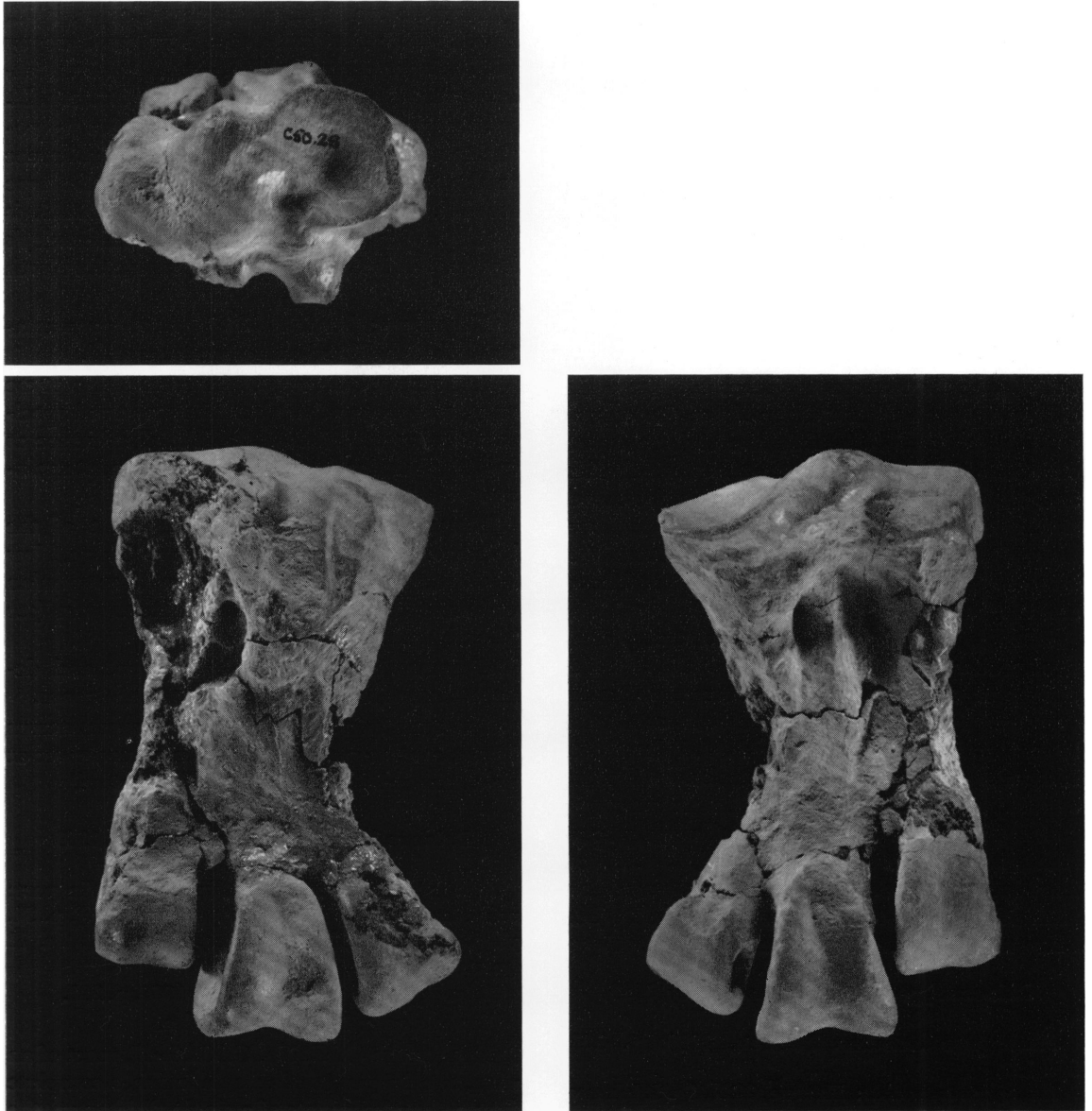


FIG. 3. *Palaeudyptes marplesi*, O.M. No. C.50.28, type. Tarsometatarsal, proximal (above), plantar (left, below) and dorsal views.  $\times 1$ .



ORIGINAL DIAGNOSIS: "Tarsometatarsus large and stout, with internal edge of shaft strongly concave (in *P. antarcticus* tarsometatarsus smaller with internal edge nearly straight). Femur likewise large. Humerus short, with shaft sigmoid instead of straight. Ulna small."

REVISED DIAGNOSIS: Holotype tarsometatarsus 20 per cent larger and 27 per cent wider proximally than tarsometatarsus of *P. antarcticus*.

DISCUSSION: The concavity of the shaft of O.M. No. C.50.28 has been accentuated by crushing and some breakage, whereas that of B.M. No. A.1084 now appears less concave than it must have been before the distal end of metatarsal II was lost. It is thus quite uncertain, although not impossible, that the stated difference in this character is significant. Comparison of femora is with specimens referred to *P. antarcticus* with great doubt, some of which, moreover, may not be significantly smaller than O.M. No. C.50.25, the femur probably associated with the holotype tarsometatarsus O.M. No. C.50.28. Comparison of humeri is based on O.M. No. C.48.73, reference of which to *P. marplei* is uncertain, and on specimens of equally or even more doubtful reference to *P. antarcticus*.

Most of the distinctions in the original diagnosis are thus of uncertain taxonomic significance. However, the difference in size of the holotype tarsometatarsi of *P. antarcticus* and *P. marplei* is greater than has been found in specimens unquestionably referable to any one species, Recent or fossil. It is therefore improbable that these metatarsi belong to the same species, and *P. marplei* is accepted as valid on that basis. Unfortunately, however, other specimens at least provisionally referable to *Palaeudyptes* do not clearly fall into one or the other of these species, nor yet into a reasonably definable third species, and all thus become indeterminate as to species. They are discussed under the next heading.

#### *Palaeudyptes* species indeterminate

MATERIALS: The specimens are here listed, and for maximum clarity references to previous identifications, descriptions, and illustrations are given separately for each. Most of these specimens were also given *ad hoc* serial numbers (1-11) under *Palaeudyptes antarcticus* and some were also referred to by field numbers by Marples (1952). Marples' numbers are listed, but other

discussion will use the permanent catalogue numbers. Brief locality names refer to previous exposition of localities and ages.

*Palaeudyptes antarcticus* Hector, 1872, p. 343, plate 17, fig. 1 (femur), pl. 18, figs. 1 (humerus), 2 and 3 (head of humerus), and 5 (head of ulna). Lambrecht, 1933, p. 236, fig. 92A (femur), D (humerus) (redrawn after Hector, 1872). Marples, 1952, p. 30.

#### Figures 4, 20

D.M. No. 1449, both humeri, one femur, fragments of tibia and coracoid, of one individual. Hector (1872) mentioned ulna, metacarpals, ribs, vertebrae, pelvis, and sternum, not present when Marples examined the specimen (before 1952) and not found in 1968. Hector wrote that the ulna was illustrated in his "Pl. XVIII, fig. 6," but there is no figure 6 on that plate. Seal Rock; Lambrecht (1933, p. 236) gave the locality as "Parimoo," but that name is not in Hector and I do not know its source. Marples: Specimen 1 and D.M. No. 1440 (in consistent error for 1449).

*Palaeudyptes antarcticus*: Marples, 1952, p. 31, pl. 2; fig. 1 (humerus), pl. 4; fig. 5 (ulna), pl. 5, fig. 6 (metacarpus); pl. 8, fig. 10 (tarsometatarsus).

*Palaeudyptes marplei*: Brodkorb, 1963, p. 231.

#### Figure 5

O.M. No. C.48.73-81, humerus, ulna, carpal, partial metacarpus, partial femur, partial tibia, fibula, tarsometatarsus, each fragment catalogued separately but most or all of a single individual. Burnside Mudstone. Marples: Specimen 2.

*Palaeudyptes antarcticus* Marples, 1952, p. 32, pl. 3, figs. 3 (radiograph of head of humerus), 7 (head of humerus), 10 (head of humerus); pl. 8, figs. 2 and 6 (proximal part of tarsometatarsus).

#### Figures 6, 7A

O.M. No. C.47.17, incomplete humerus, incomplete femur, incomplete tarsometatarsus, phalanx of pes, possibly but probably not of one individual. Concord Greensand but probably derived from underlying Burnside Mudstone. Marples: Specimen 4.

*Palaeudyptes antarcticus* Marples, 1952, p. 33.

G.S. No. 2225 fragment of humerus. Concord Greensand but probably derived from underlying Burnside Mudstone. Marples: Specimen 5.

*Palaeudyptes antarcticus* Marples, 1952, p. 33.

#### Figure 7B

O.M. No. C.47.18, proximal half of metatarsal II. Concord Greensand but probably derived from underlying Burnside Mudstone. Marples: Specimen 6.

*Palaeudyptes antarcticus* Marples, 1952, p. 33, text figs. 1 and 6 (1) (humerus); pl. 2, fig. 3 (humerus); pl. 3, fig. 4 (radiograph of head of humerus); pl. 5, fig. 7 (metacarpus).

#### Figure 8

O.M. No. C.47.25, humerus, ulna, metacarpus,

coracoid, fragments of scapula, clavicle, vertebrae, all of one individual. Duntroon. Marples: Specimen 17, Field No. D.P.6.

*Palaeudyptes antarcticus* Marples, 1952, p. 34, text, figs. 2 (4) (distal end of humerus) and 3 (2) (elbow articulation); pl. 3, fig. 6 (distal end of humerus); pl. 5, fig. 2 (radius).

Figure 9

O.M. No. C.47.23, both humeri, ulna, radius, metacarpus, phalanx of pes, fragments of skull, coracoid, vertebrae, all of one individual. Duntroon. Marples: Specimen 8, Field No. D.P.4.

*Palaeudyptes antarcticus* Marples, 1952, p. 34, pl. 3, fig. 8 (humerus).

O.M. No. C.47.22, both humeri, both ulnae, both radii, both metacarpi, both femora, both tibiae, both coracoids, partial sacrum, fragments of tarsometatarsus, sternum, scapulae, and vertebrae, all of one individual. Duntroon. Marples: Specimen 9, Field No. D.P.3.

*Palaeudyptes antarcticus* Marples, 1952, p. 34, pl. 2, fig. 2 (humerus); pl. 5, fig. 8 (metacarpus); pl. 6, figs. 4 (phalanx of wing), 8 (part of coracoid).

O.M. No. C.47.24. Incomplete humerus, incomplete ulna, metacarpus, phalanx of manus, fragment of coracoid. Duntroon. Marples: Specimen 10, Field No. D.P.5.

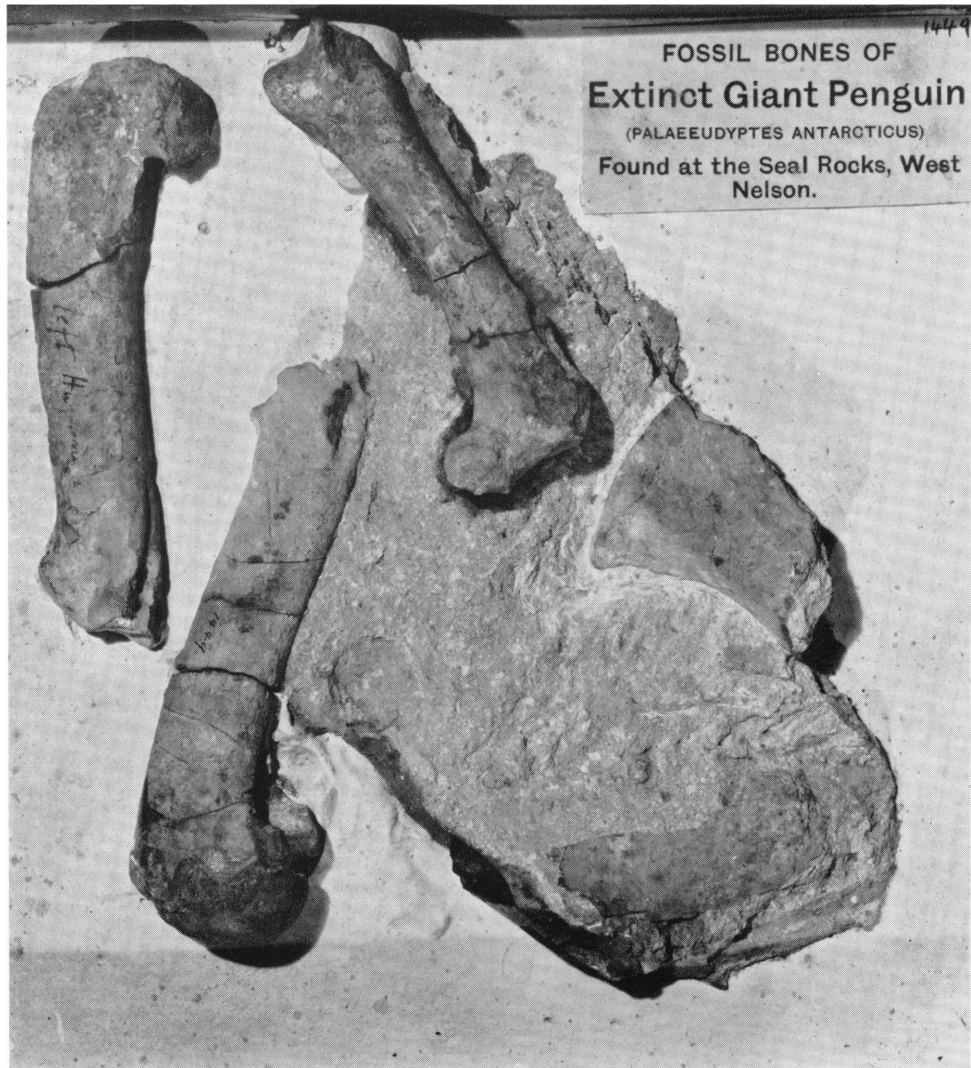


FIG. 4. *Palaeudyptes* sp., D.M. No. 1449, "Hector's specimen." Associated humeri, femur, and other fragments, in matrix as found.  $\times 1/2$ .

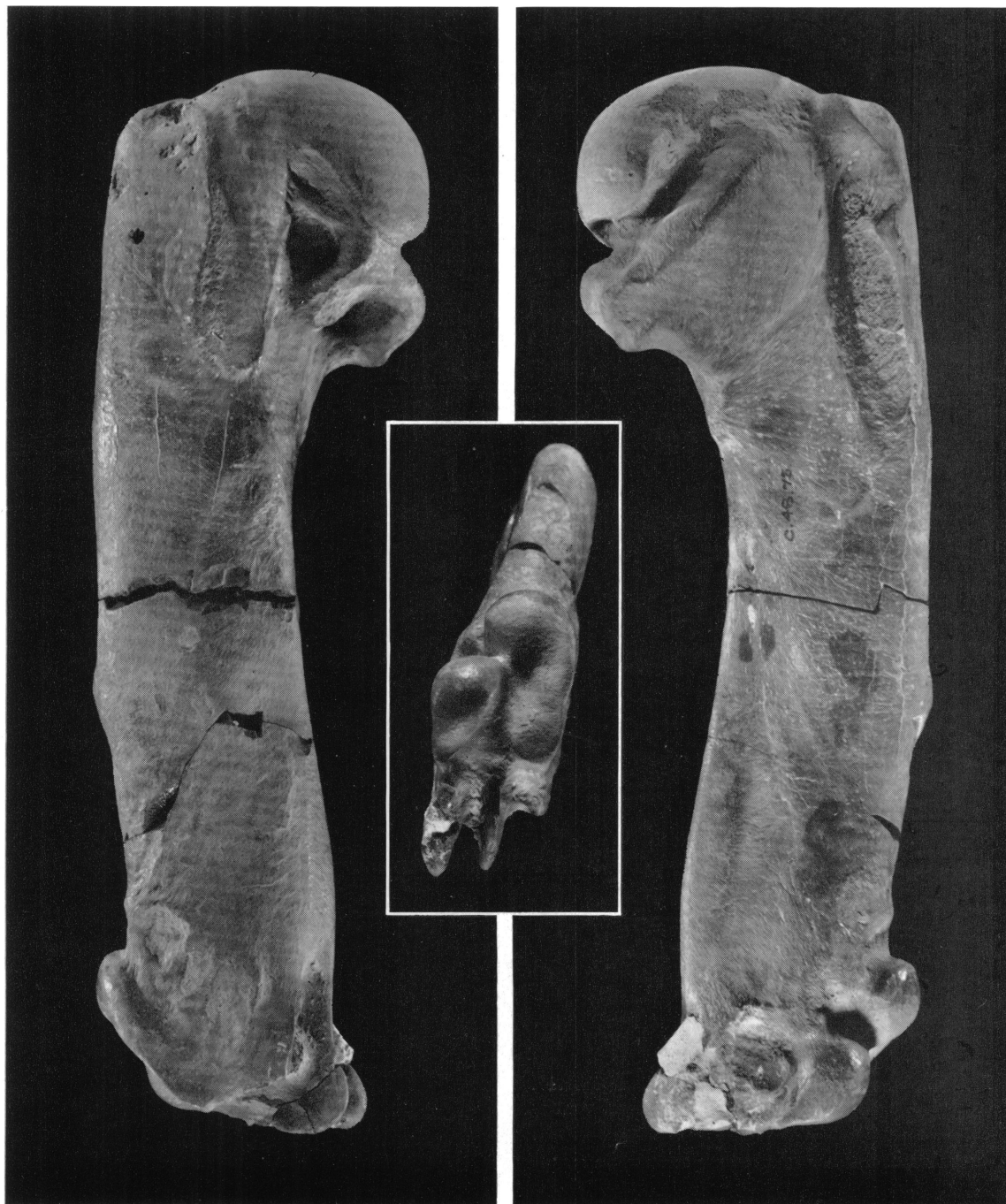


FIG. 5. *Palaeudyptes* sp., O.M. No. C.48.73. Humerus, dorsal (left), ventral and distal views.  $\times 1$ .

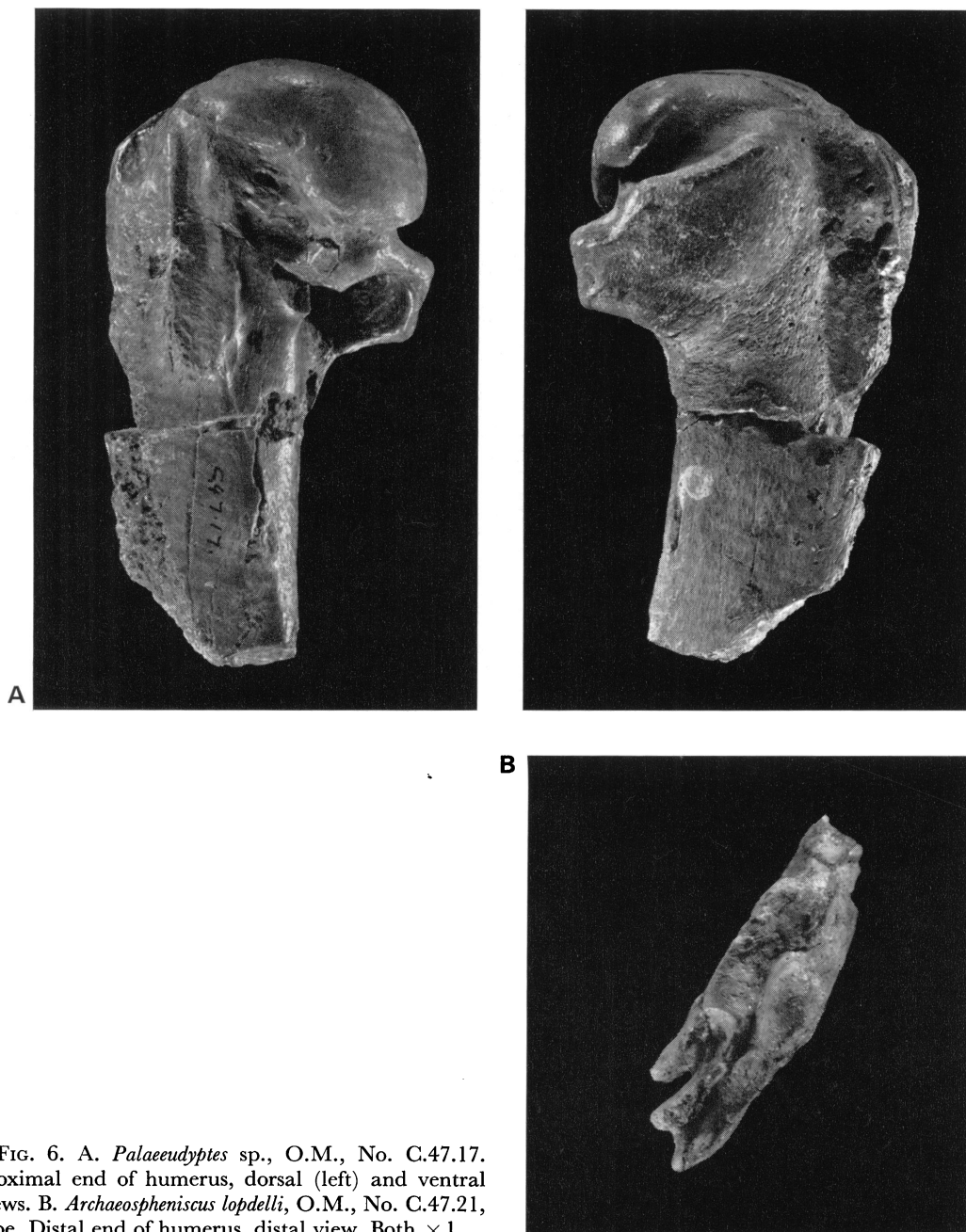


FIG. 6. A. *Palaeudyptes* sp., O.M., No. C.47.17. Proximal end of humerus, dorsal (left) and ventral views. B. *Archaeospheniscus lopdelli*, O.M., No. C.47.21, type. Distal end of humerus, distal view. Both  $\times 1$ .

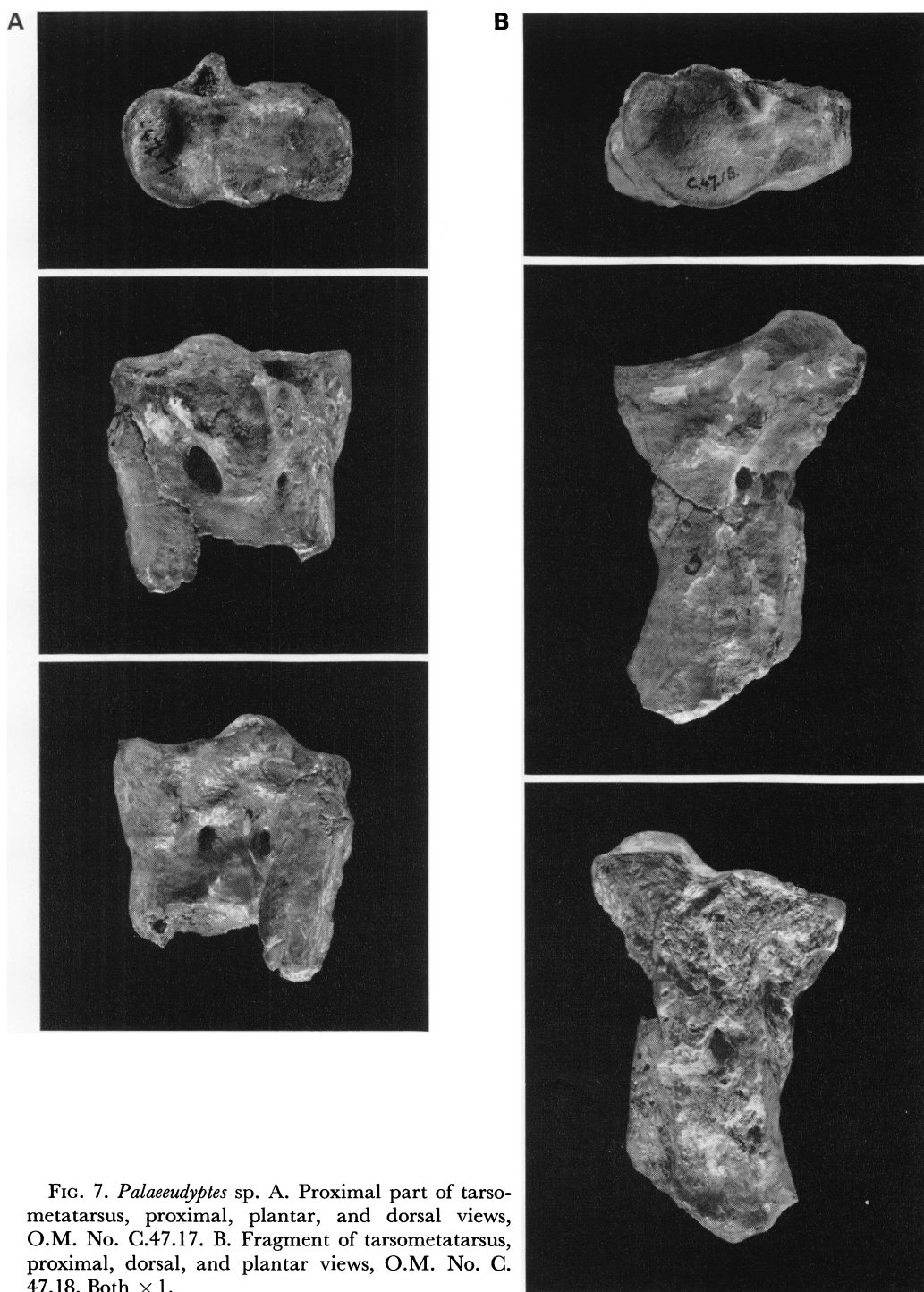


FIG. 7. *Palaeudyptes* sp. A. Proximal part of tarso-metatarsus, proximal, plantar, and dorsal views, O.M. No. C.47.17. B. Fragment of tarsometatarsus, proximal, dorsal, and plantar views, O.M. No. C. 47.18. Both  $\times 1$ .



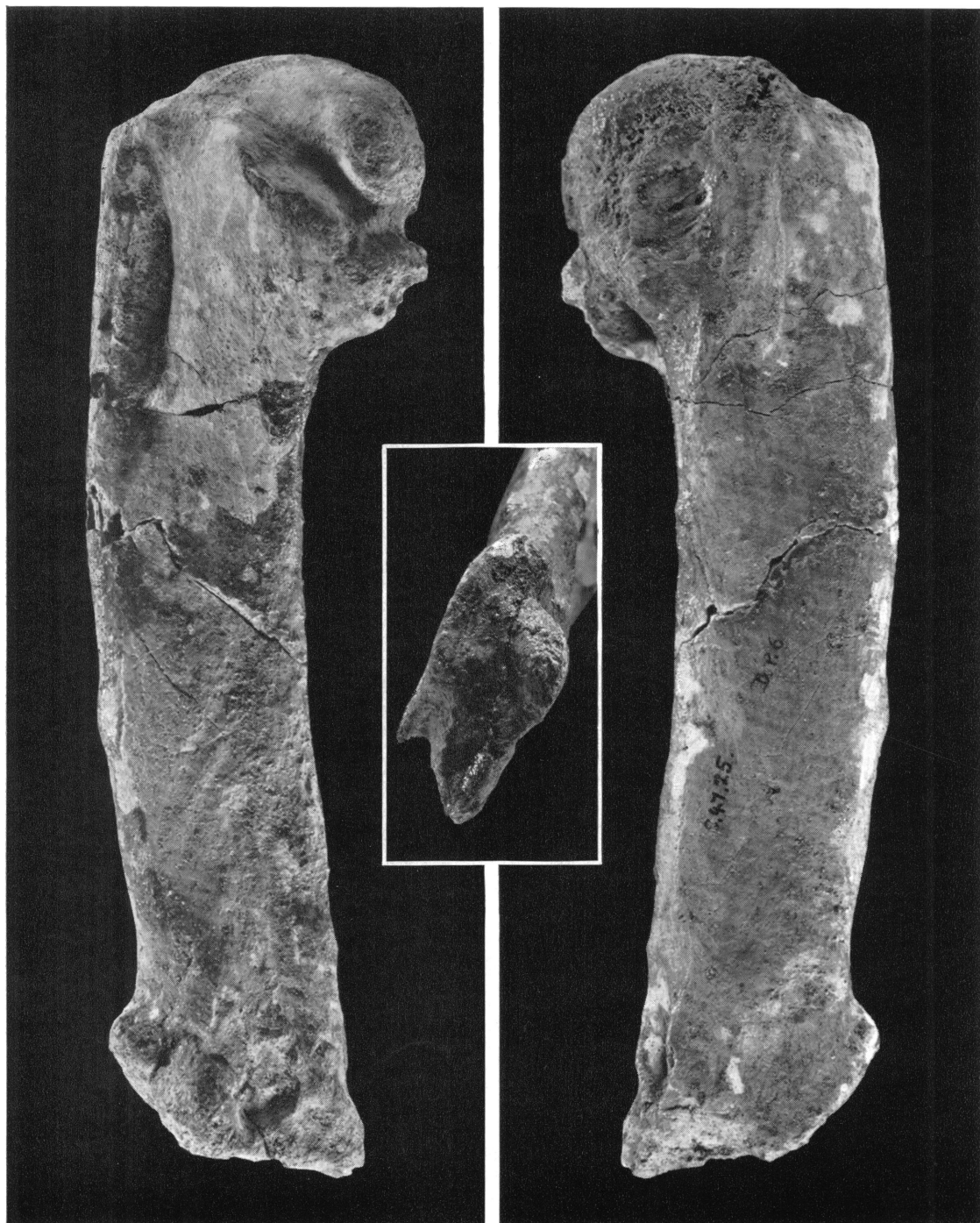


FIG. 8. *Palaeodyptes* sp., O.M. No. C.47.25. Humerus, ventral (left), dorsal and distal views.  $\times 1$ .

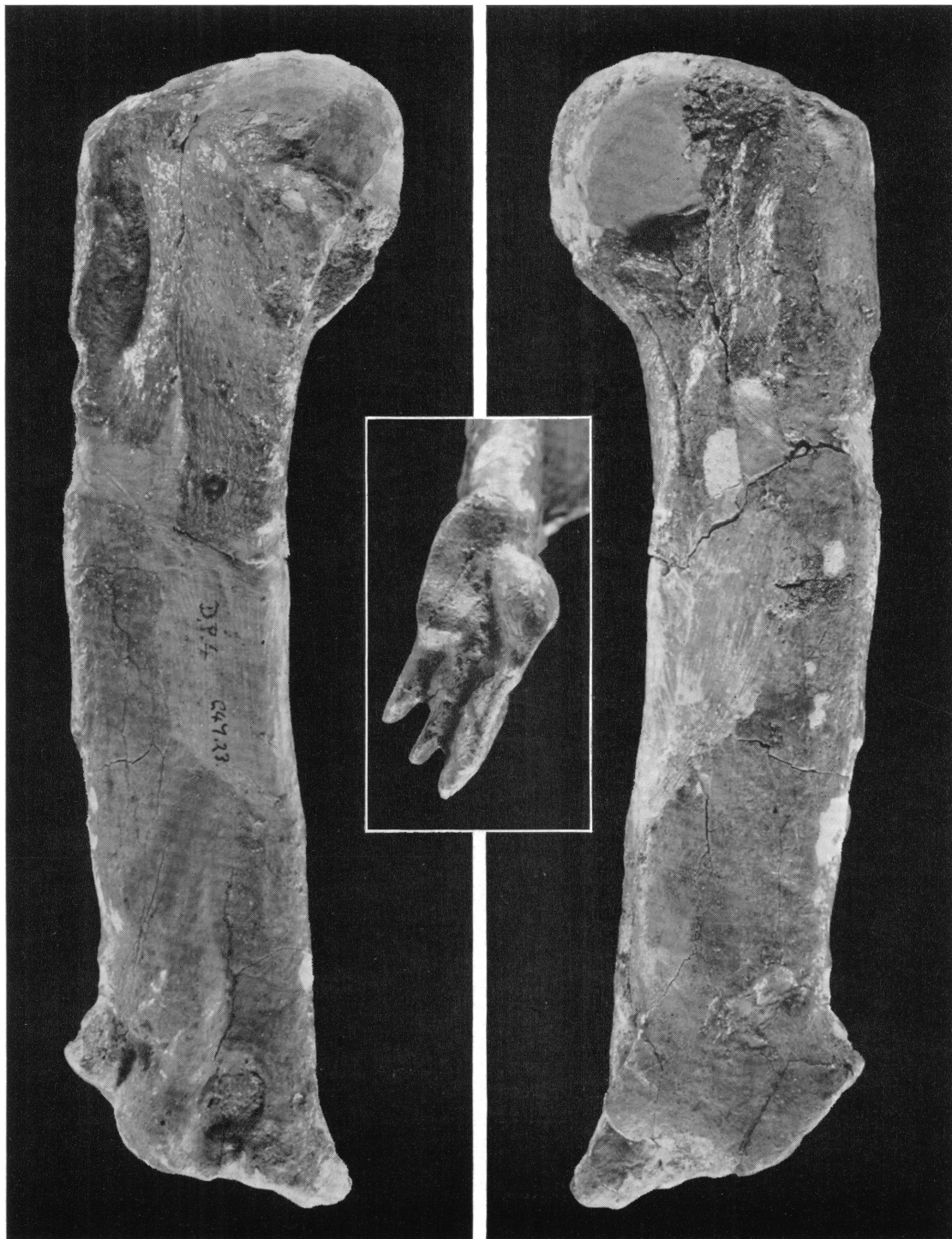


FIG. 9. *Palaeudyptes* sp., O.M. No. C.47.23. Humerus, ventral (left), dorsal and distal views.  $\times 1$ .

*Palaeudyptes antarcticus* Marples, 1952, p. 35, text fig. 4 (1) (coracoid), pl. 7, fig. 2 (coracoid).

O.M. No. C.47.34, left coracoid. Duntroon (Earthquakes). Marples: Specimen 11, Field No. G.47.1.

*Palaeudyptes* cf. *antarcticus* Simpson, 1957, p. 52, figs. 1a, 1b (humerus).

*Palaeudyptes marplei* Brodkorb, 1963, p. 231.

South Australian Museum No. P7158, left humerus. Late Eocene, Blanche Point Marls, Witton Bluff, south of Adelaide, South Australia. Mentioned but not numbered or discussed by Marples (1952).

*Palaeudyptes* cf. *antarcticus*? Simpson, 1957, p. 55, fig. 2 (tibiotarsus).

South Australian Museum No. P10862, incomplete right tibiotarsus, late Eocene, Blanche Point Marls, near the preceding but about 20 to 25 feet higher in the section. Not known to Marples.

**DISCUSSION:** In biostratigraphic age terms, the minimum span covered by these specimens is Runangan-Whaingaroan-Duntroonian, and the maximal possibility is Kaiatan-Runangan-Whaingaroan-Duntroonian-Waitakian. Span in absolute time is here even more dubious than usual and available K-A dates (Lipson, 1956), which would make the maximum span about  $20 \times 10^6$  years and the minimum perhaps half that, are evidently unreliable. If Runangan is correctly correlated with European latest Eocene and Waitakian with European latest Oligocene, the maximum span would be on the order of  $15 \times 10^6$  years, the minimum again perhaps half that. In any case, the indicated duration would be phenomenal if all specimens did represent a single species. Separation of *Palaeudyptes marplei* from specimens previously all referred to *P. antarcticus* seems almost certainly valid and indicates that at least two species were in fact included. However, serious problems remain. Neither holotype is of certainly known age: as previously shown, the holotype of *P. antarcticus* is probably Whaingaroan, Duntroonian, or Waitakian, but could just possibly be Runangan, and that of *P. marplei*, could be either Kaiatan or Runangan. There are difficulties, which at this point seem to be insuperable, in referring other known specimens to either of the established species or in properly defining further species for them.

Of penguin bones commonly preserved as fossils, the humerus and the tarsometatarsus are most readily identified and one or the other or rarely both have provided most of the diagnoses

of fossil species, not only in New Zealand but also from all other fossil localities. The availability of these two bones among specimens currently referred to *Palaeudyptes* is shown in table 2.

TABLE 2

PRESENCE OF HUMERUS AND TARSOMETATARSUS IN NEW ZEALAND SPECIMENS OF FOSSIL PENGUINS TENTATIVELY REFERRED TO *Palaeudyptes*

	Humerus	Tarsometatarsus
Kaiatan or Runangan		
O.M. No. C.50.25-47, holotype of <i>Palaeudyptes marplei</i>	0	X
O.M. No. C.48.73-81	X	X
Whaingaroan, Duntroonian, or Waitakian		
B.M. No. A 1084, holotype of <i>Palaeudyptes antarcticus</i>	0	X
Duntroonian		
D.M. No. 1449	X	0
O.M. No. C.47.23	X	0
O.M. No. C.47.25	X	0
O.M. No. C.47.24	(X)	0
O.M. No. C.47.22	(X)	0
Runangan or Waitakian		
O.M. No. C.47.17, association improbable	{ (X) 0	0 (X)
G.S. No. 2225	(X)	0
O.M. No. C.47.18	0	(X)

0, absent.

X, present and at least fairly well preserved, potentially identifiable.

(X), fragmentary or badly preserved, doubtfully identifiable.

There are only three fairly well-preserved tarsometatarsi, two of them holotypes of the two named species. As noted, the two differ enough in size, at least, to establish a strong probability that the named species are in fact distinct. Brodkorb (1963) referred the other adequately preserved tarsometatarsus, included in O.M. No. C.48.73-81, to *P. marplei*. It is from the same geological formation as the holotype and probably of the same age, but not surely, because that formation spans two ages, Kaiatan and Runangan. In any event, both are probably but not quite certainly older than the holotype of *P. antarcticus*. The specimen labeled O.M. No.

C.48.73–81 is also somewhat larger than the latter. However, all its characters are intermediate between those of the two holotypes and on balance slightly closer to *P. antarcticus* (see fig. 10). This specimen could represent a rather extreme variant of either species, therefore cannot reasonably be ascribed to a third species, and yet, in the absence of intermediates, also cannot reasonably be assigned to one or the other of the two already named species. The fact that it is somewhat, although slightly, more like the holotype of *P. antarcticus* makes its previous placement in *P. marplesi* unacceptable. It is not likely to lie on a chronocline involving size change in a lineage because, if the three specimens are of different ages, the largest must be the oldest.

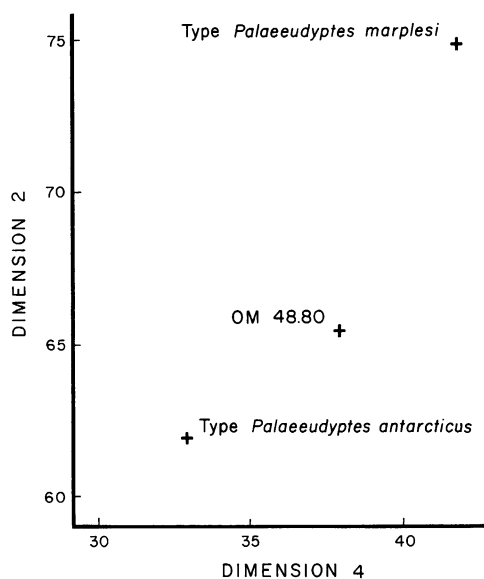


FIG. 10. *Palaeudyptes* spp. Proportions of three tarsometatarsi referred to this genus. The dimensions are as numbered and defined by Marples (1952, table 9). Dimension 2 is length of metatarsal III from proximal convexity to trochlear groove. Dimension 4 is proximal width.

Possible identification of other specimens depends in most instances on association of tarsometatarsus and humerus. Marples' (1952) reference of all these specimens to *P. antarcticus* departed mainly from comparisons of O.M. No. C.47.17. That seems an unfortunate choice because both humerus and tarsometatarsus registered as O.M. No. C.47.17 are incomplete,

consisting of proximal ends only. Their association is also quite doubtful, as Marples noted, and I believe it to be probably incorrect. Moreover, there is a specimen, O.M. No. C.48.73–81, in which those two bones are well preserved and their association is beyond reasonable doubt. Marples' argument was that the tarsometatarsus of O.M. No. C.47.17 resembles the holotype of *P. antarcticus* sufficiently for reference to that species, that the humerus of O.M. No. C.47.17 is similarly close to that of D.M. No. 1449 ("Hector's specimen"), and that the latter in turn is specifically similar to humeri among the Duntroon specimens, O.M. No. C.47.22–25 (four different individuals).

As far as its few preserved characters go, the humerus under O.M. No. 47.17 does agree fairly well with D.M. No. 1449 and with the Duntroon specimens, except that all the latter agree within one millimeter in preaxial-postaxial diameter of the head, about 49 mm. in all, whereas O.M. No. C.47.17 is distinctly smaller, about 46 mm. in that dimension. The humerus O.M. No. C.47.17 agrees with the humerus of O.M. No. C.48.73–81, from the same locality but supposedly from an age at least two and perhaps three biostratigraphic units earlier, adding to probability that O.M. No. C.47.17 may be a derived fossil from the older, disconformably immediately lower bed. The tarsometatarsal fragment also registered under O.M. No. C.47.17, however, does not so closely agree with the tarsometatarsus of the same individual as the humerus under O.M. No. C.48.73–81 (all numbers here referring to parts of one animal). In the one significant measurement possible on it, the preaxial-postaxial breadth of the proximal end, O.M. No. C.47.17 measures about 33 mm., the same as the holotype of *P. antarcticus* within a millimeter, but O.M. No. C.48.80 (the tarsometatarsus of O.M. No. C.48.73–81) measures about 40 mm., a difference so marked as to suggest that the two are not conspecific. The contrast, in comparison with the clearly associated bones of O.M. No. C.48.73–81, makes it highly improbable that the humerus and tarsometatarsus both registered under O.M. No. C.47.17 belonged to the same animal, and, indeed, pertinence to the same species is dubious.

The humerus of individual O.M. No. C.48.73–81 rather closely resembles the humeri from the Duntroon area and is within the size range of their population. The difference from the O.M.

No. C.47.24 humerus is negligible, and the maximum difference in a significant dimension is about 13 per cent, large but not impossible for a single species (see fig. 11). The difference in age, however, is at least two and perhaps three biostratigraphic units. A decision to consider all as conspecific would not identify the species or permit its diagnosis, because as noted the tarsometatarsus associated with O.M. No. C.48.73-81 can be neither confidently referred to nor confidently distinguished from *P. antarcticus* or *P. marplesi*. As also evident from figure 11, the humerus of D.M. No. 1449 differs more from the Duntroon specimens, in spite of the fact that it is probably of the same age. It still could be conspecific, but if so, as penguins go, this was an almost phenomenally variable species.

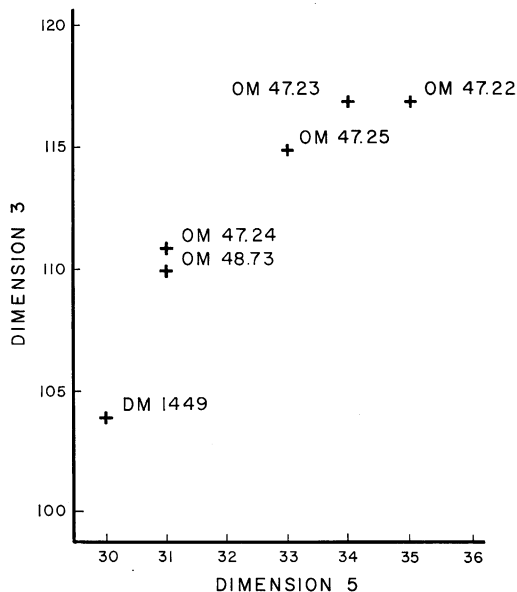


FIG. 11. *Palaeudyptes* spp. Proportions of six humeri referred to this genus. The dimensions are as numbered and defined by Marples (1952, table 3). Dimension 3 is length from distal end of pectoralis secundus insertion to angle at base of dorsal sesamoid groove. (This unusual length measurement is used because available on more specimens than any other.) Dimension 5 is greatest diameter of shaft 1/3 of the distance from head toward distal end.

The late Eocene humerus from Australia that I (1957) described as *Palaeudyptes* cf. *antarcticus* and that Brodkorb (1963) referred to *P. marplesi* should now also be even less definitely referred to as *Palaeudyptes* species indeterminate.

Reference to *P. marplesi* would now be particularly unjustified, as the Australian bone is somewhat smaller in every dimension than the humerus of O.M. No. C.48.73-81 and the latter individual was smaller than the holotype of *P. marplesi* and near that of *P. antarcticus* in size. In personal correspondence, Brodkorb agrees with removal of the Australian specimen from *P. marplesi*. The incomplete tibia from Australia also classified as *Palaeudyptes* cf. *antarcticus* in the same publication as the humerus (Simpson, 1957) should now be ascribed only to ?*Palaeudyptes* species indeterminate.

#### PACHYDYPTES OLIVER, 1930

*Pachydyptes* OLIVER, 1930, p. 85.

ETYMOLOGY: Greek *pachys*, thick, and *dyptes*, diver, as used in many names of penguins. Reference is to the massive nature of the humerus.

TYPE-SPECIES: *Pachydyptes ponderosus* Oliver, 1930. Lowe (1939, p. 291) referred *P. ponderosus* to the genus *Anthropornis* Wiman, 1905, and declared *P. novae-zelandiae* (as he incorrectly spelled it, with -ae's ligated) type of *Pachydyptes*. Oliver's original proposal of the genus unequivocally declared *P. ponderosus* to be its type-species, so that Lowe's action is without effect.

INCLUDED SPECIES: Type-species only, *P. novaezealandiae* having been removed to *Platydyptes*.

KNOWN DISTRIBUTION: Runangan, Oamaru area, Otago, New Zealand.

ORIGINAL DIAGNOSIS: "Massively built penguins, one species standing between five and six feet in height. Humerus very wide with an immense head; distance to lower edge of subtrochanteric fossa about 30 percent of the total length; middle width 24 percent of length; superior crest high and wide with a correspondingly deep depression within it; sulcus and subtrochanteric fossa deep . . . *Pachydyptes* [sic] differs from *Palaeudyptes* in the much wider humerus with larger head, the width of this bone in *Palaeudyptes* being only 18 against 24 percent of the length in *Pachydyptes*." (Oliver, 1930, p. 85.) This diagnosis included *novaezealandiae*, not now referred to *Pachydyptes*, but was based mostly on the type-species, larger of the two.

REVISED DIAGNOSIS: "Humerus relatively wide. The head has a square appearance owing to the projection of the external tuberosity in the



distal direction and the flattening of the articular surface. Tricipital fossa undivided. Insertion of *pectoralis secundus* slightly curved towards, but not reaching the postaxial margin; widely separated from the insertion of *latissimus dorsi*. Shaft with a gentle sigmoid curve and a slight angle in the preaxial border [both more distinct than in *Palaeudyptes*]. Angle between a tangent to the distal condyles and the axis of the shaft, acute. Shelf on the distal end approximately the same width as the ulnar condyle." (Marples, 1952, p. 36.)

DISCUSSION: Lowe's (1939, p. 291) transfer of the true type species to *Anthropornis* Wiman would make *Pachydyptes* Oliver a subjective synonym of the latter. I (1946, p. 41) noted that fact but concluded that the genera may be kept separate because the type species are distinct and the humeri about as different as in some recent genera. Marples (1952, p. 35) decided that the greater relative width of the humerus of *Pachydyptes*, the great geographical separation, and the doubtful age correlation justify generic separation. The resemblance is close, and the difference in relative width or bulk of the humerus of *Pachydyptes ponderosus* and humeri referred to *Anthropornis nordenskjoeldi* is in fact slight. As far as this evidence goes the two species do seem to be closely related, but their types are probably specifically distinct, and retention of generic distinction seems the more conservative course at least until further data for comparison are at hand. The type species of *Pachydyptes* is probably no later than late Eocene and that of *Anthropornis* no earlier than late Oligocene.<sup>1</sup> The geographic and geologic differences are great but do not in themselves preclude generic identity. No other known penguins are likely to be confused with these, which are the largest known and also quite distinctive morphologically.

#### ***Pachydyptes ponderosus* Oliver, 1930**

Figure 12

*Palaeudyptes antarcticus*: HECTOR, 1873, p. 438 (in part; humerus here mentioned later became holotype of *Pachydyptes ponderosus*).

*Pachydyptes ponderosus* OLIVER, 1930, p. 86 (with unnumbered figure of holotype humerus inadvertently labeled "femur"). LAMBRECHT, 1933, p. 238, fig. 93

<sup>1</sup>Note added in proof. Study of *Anthropornis* suggests that it is also late Eocene in age and only tentatively distinct from *Pachydyptes*.

(humerus from Oliver). LOWE, 1939, p. 284, pl. IIIC, pl. IVb, pl. Vc. SIMPSON, 1946, p. 41. MARPLES, 1952, p. 36, test, fig. 6 (2) (humerus), pl. 4, fig. 1 (humerus), pl. 5, fig. 10 (metacarpus), pl. 6, fig. 1 (base of coracoid), pl. 7, fig. 1 (coracoid). OLIVER, 1955, p. 591 and four unnumbered figures on same page. SIMPSON, 1957, p. 67; 1959, p. 116. BRODKORB, 1963, p. 232.

*Pachydyptes ponderosa* [sic]: LOWE, 1939, p. 282.

*Anthropornis ponderosus*: LOWE, 1939, p. 291.

*Anthropornis* (*Pachydyptes*) *ponderosus*: LOWE, 1939, p. 292.

*Anthropornis ponderosa* [sic]: LOWE, 1939, p. 292.

*Pachydyptes* (*Anthropornis*) *ponderosus*: LOWE, 1939, p. 294.

*Anthropornis nordenskjoeldi*: LOWE, 1939, p. 293.

ETYMOLOGY: Latin, *ponderosus*, weighty.

HOLOTYPE: D.M. No. 1450, humerus, metacarpus, and coracoid, believed to be associated.<sup>2</sup> From Fortification Hill, near Oamaru.

HYPODIGM: Holotype and the following: O.M. No. C.47.16, two associated incomplete humeri "from Oamaru." H. B. Fell private collection No. F/336(a), imperfect distal half of humerus, and F/336(b), femur lacking proximal and distal ends. From Taylor's Quarry, Totara, near Oamaru.

KNOWN DISTRIBUTION: Runangan, Oamaru and vicinity.

ORIGINAL DIAGNOSIS: "The anterior border of the humerus is regularly curved and the least width is over the distal end. Length 18, antero-posterior diameter of head 6.6, antero-posterior width at centre of shaft 4.5 cm." (Oliver, 1930, p. 86). This diagnosis was distinctive from *P. novaezealandiae* and the differences are now considered generic.

REVISED DIAGNOSIS: At present the only species placed in the genus as defined above.

COMMENT: This, the largest known species of penguins, is clearly distinctive and no special problems arise from the scanty specimens. No known tarsometatarsus could possibly belong to this species.

#### **PLATYDYPTES MARPLES, 1952**

*Platydyptes* MARPLES, 1952, p. 37. MARPLES, 1962, p. 415, fig. 2c (labeled only to genus, the figure is a restoration of the coracoid of O.M. No. C.47.15, doubtfully referred to *Platydyptes novaezealandiae*).

ETYMOLOGY: Greek *platys*, broad and flat, and *dyptes*, diver, used in several generic names of

<sup>2</sup> This specimen has not been seen by me.

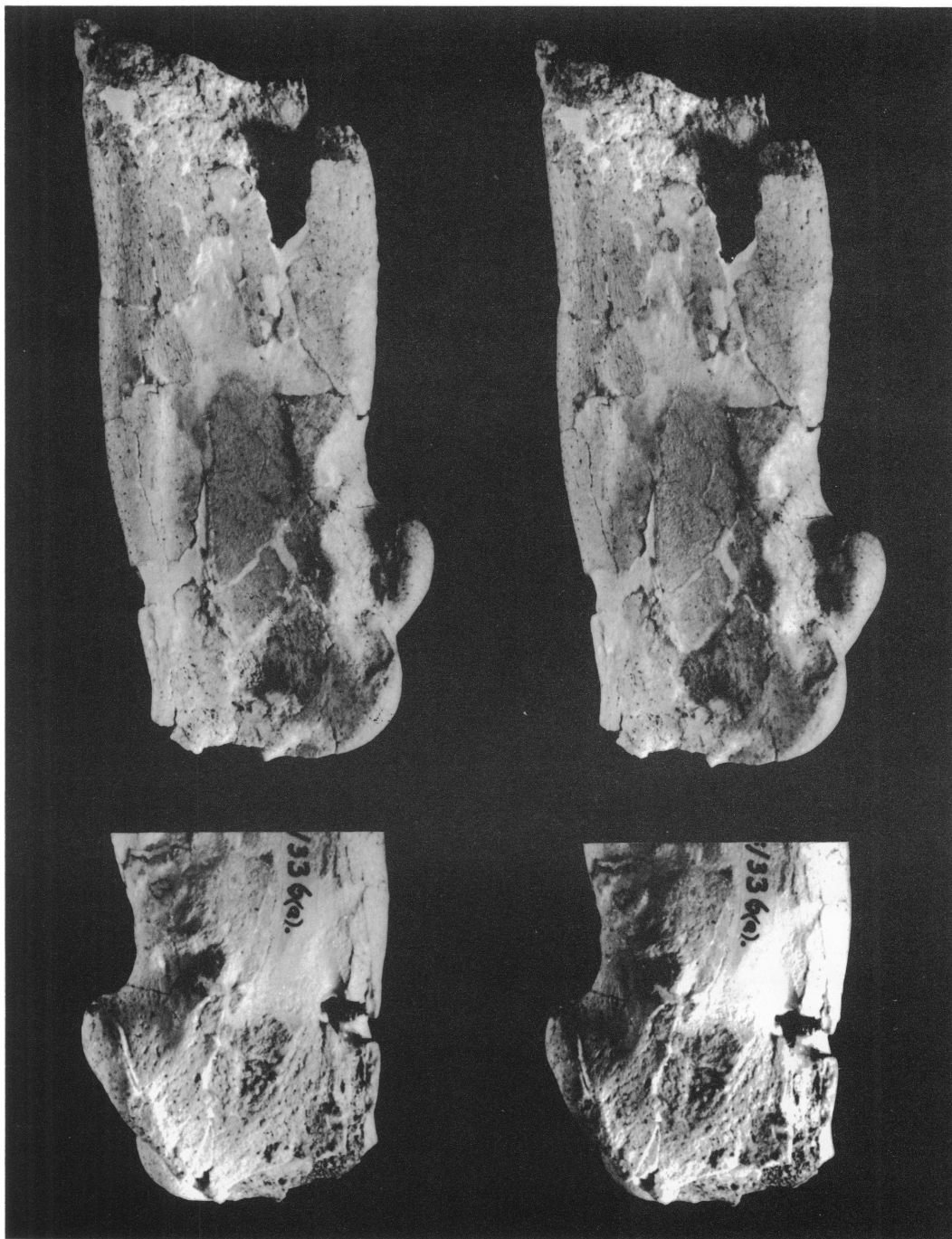


FIG. 12. *Pachydyptes ponderosus*. H. B. Fell Collection No. 5/336(a). Distal end of humerus, dorsal (above) and ventral views (stereoscopic pairs).  $\times 1$ .

penguins. The humerus is relatively broader than in most penguins, but is less broad than in the otherwise rather similar *Pachydyptes*.

**TYPE-SPECIES:** *Pachydyptes novaezealandiae* Oliver, 1930. As noted under *Pachydyptes*, Lowe's designation of *novaezealandiae* as type-species of that genus was invalid.

**INCLUDED SPECIES:** The type-species, *P. amiesi* Marples, 1952, and doubtfully *?P. marplesi*, new species.

**KNOWN DISTRIBUTION:** Duntroonian or Waitakian of the Oamaru district, northern Otago, and Waitakian (*fide* Marples) of the Haketaramea Valley, southern Canterbury, New Zealand.

**ORIGINAL DIAGNOSIS:** "Humerus relatively broad with massive head. Angle between a tangent to the distal condyles and the long axis of the humerus intermediate between those of *Palaeudyptes* and *Eudyptes*. Shelf on the distal end of the humerus adjacent to the ulnar condyle narrower than the condyle. Tricipital fossa undivided. Insertion of *pectoralis secundus* oblique, separated by a gap distally from that of *latissimus dorsi*. Slight angle in the preaxial border of the humerus." (Marples, 1952, p. 37.) Supposedly generic characters of bones other than the humerus, not known to be differential from allied genera, are not quoted.

**REVISED DIAGNOSIS:** Humerus closely similar to that of *Pachydyptes* but relatively less broad; relatively broader than in other known Spheniscidae. Distinct preaxial angle and protuberance on shaft. Proximal part of shaft narrower than distal part. Proximal part of preaxial margin straight to slightly concave. Shelf on the distal end of the humerus adjacent to the ulnar condyle narrower than the condyle.

**DISCUSSION:** Lowe (1939, p. 291) suggested that "*Pachydyptes novae-zelandiae*" might belong to the Patagonian Miocene genus *Palaeospheniscus* Ameghino, 1894, but did not give this as a fixed conclusion. He did insist that the species belongs to a genus distinct from that of *Pachydyptes ponderosus*, which he referred to the Seymour Island Miocene or late Oligocene genus *Anthropornis* Wiman, 1905. I (1946, p. 41) agreed that the species as described by Oliver and by Lowe (no figures of *P. novaezealandiae* then being available) could not be congeneric and that *novaezealandiae* "quite possibly represents an unnamed genus." Marples, with access

to the specimens, made those tentative conclusions definite.

Although Marples also examined the holotype of the type-species, not figured prior to the present publication, his concept of the genus was based essentially on a different specimen, O.M. No. C.47.15, and his diagnosis includes some characters that do not occur and some that are not determinable in the holotype. I consider it so improbable that O.M. No. C.47.15 belongs to the type-species that I here base a new specific name on it. After examination of the holotype of the type-species, here figured for the first time, I agree that *Pachydyptes* and *Platydyptes*, despite close similarity in the known parts are best retained as distinct genera, but I have substituted a diagnosis of *Platydyptes* exclusively in terms of characters determinable and present in that holotype. Lowe's suggestion of possible synonymy with *Palaeospheniscus* may be discarded out of hand. Beyond both being spheniscid the humeri have virtually nothing in common.

#### ***Platydyptes novaezealandiae* (Oliver, 1930)**

Figures 13, 14

*Pachydyptes novaezealandiae* OLIVER, 1930, p. 86. LAMBRECHT, 1933, p. 238; SIMPSON, 1946, p. 41.

*Platydyptes novaezealandiae*: MARPLES, 1952, p. 38 (all illustrations labeled by Marples, 1952, as of this species are of O.M. No. C.47.15, holotype of *?Platydyptes marplesi*). OLIVER, 1955, p. 592. SIMPSON, 1957, p. 67; 1959, p. 116. MARPLES, 1962, p. 416. BRODKORB, 1963, p. 233.

*Platydyptes novae-zelandiae* [sic, and *ae*'s ligated]: LOWE, 1939. OVEY, 1939, p. 294.

**ETYMOLOGY:** Neolatin *novaezealandiae*, of New Zealand. Hyphenation and ligation of *ae* (not used in the original publication but introduced by Lowe) are proscribed by the current code of nomenclature.

**HOLOTYPE:** D.M. No. 1451, humerus, radius, ulna, and fragments of scapula and vertebrae of one individual. Oamaru district.

**HYPODIGM:** For present purposes, the type only, which was also Oliver's hypodigm. Marples' hypodigm included the specimens here placed in *?Platydyptes marplesi*.

**KNOWN DISTRIBUTION:** Duntroonian or Waitakian of the Oamaru district, northern Otago, New Zealand.

**ORIGINAL DIAGNOSIS:** "The anterior border of the humerus is straight and the width of the bone is least below the head. Length 10.6, antero-posterior diameter of head 3.5, antero-posterior



FIG. 13. *Platydyptes novaezealandiae*, D.M. No. 1451, holotype. Humerus, radius, ulna, and other bones in matrix as found. This view of the humerus is somewhat oblique; radius and ulna are in the plane of the photograph.  $\times 2/3$ .



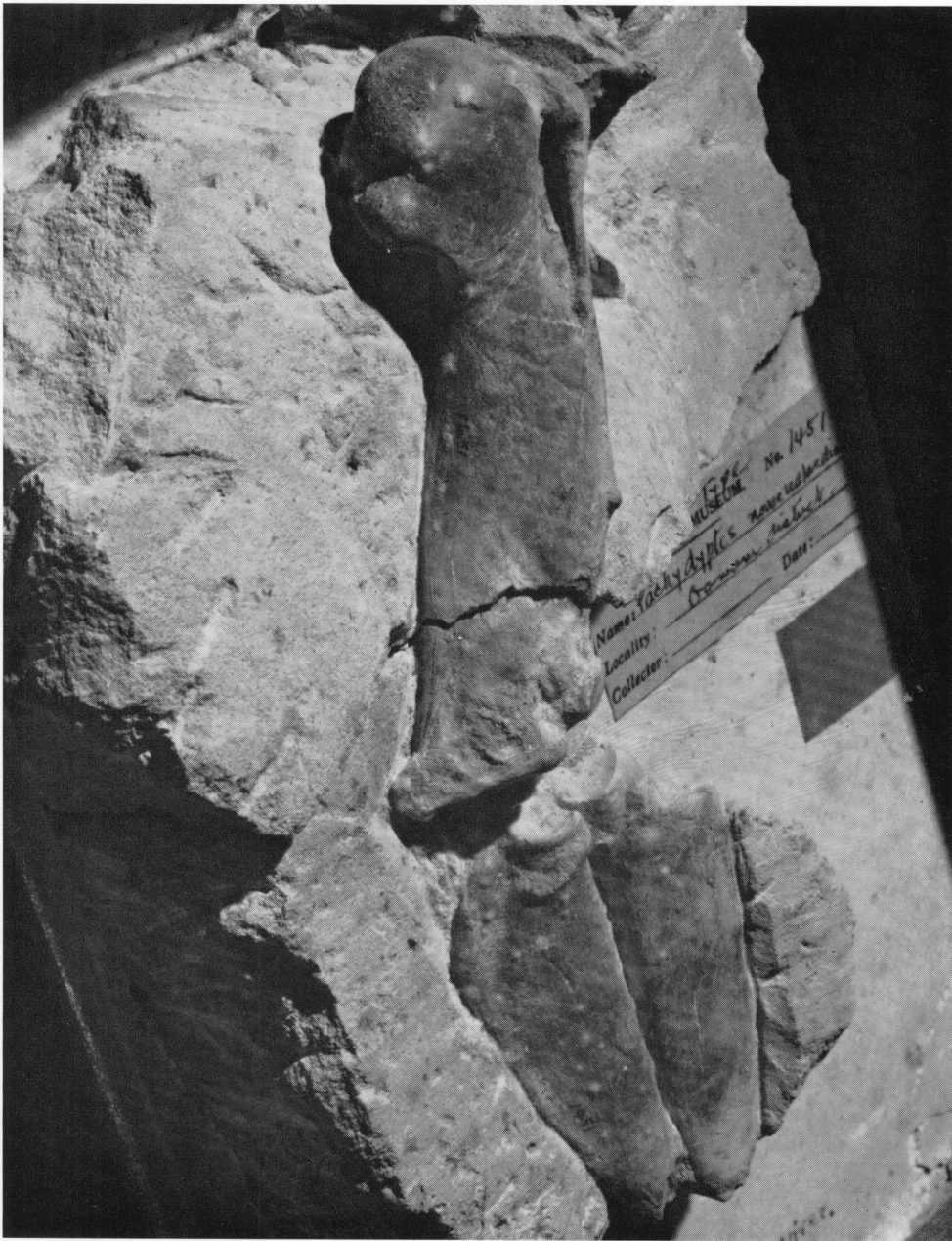


FIG. 14. *Platydyplos novaezealandiae*, D.M. No. 1451, holotype. Humerus, radius, ulna, and other bones in matrix as found. This view taken normal to the flat shaft of the humerus.  $\times 1$ .

width at centre of shaft 2.5 cm." (Oliver, 1930, p. 86.) Oliver's diagnosis was differential against *Pachydyptes ponderosus*, not now considered congeneric.

REVISED DIAGNOSIS: Smaller than *P. amiesi* and larger than ?*P. marplei*. Maximum length of humerus of holotype 90 per cent of that of *P. amiesi* and 109 per cent of that of ?*P. marplei*. Preaxial angle about as in *P. amiesi*, more proximal and much more prominent than in ?*P. marplei*; preaxial border proximal to angle also more as in *P. amiesi*.

DISCUSSION: Three specimens referred by Marples (1952) to *Platydyptes* include the humerus, on which diagnoses are here necessarily based: D.M. No. 1451, O.M. No. C.47.15, and O.M. No. C.50.61. Marples concluded, I believe correctly, that the range in size is greater than is likely to occur in a single species (see fig. 15). In his terms, the range of variation of maximum length of the humerus about the mean for the three specimens is 21.7 per cent, whereas he found this figure to be 15 per cent for 30 specimens of the recent species *Eudyptula minor*.

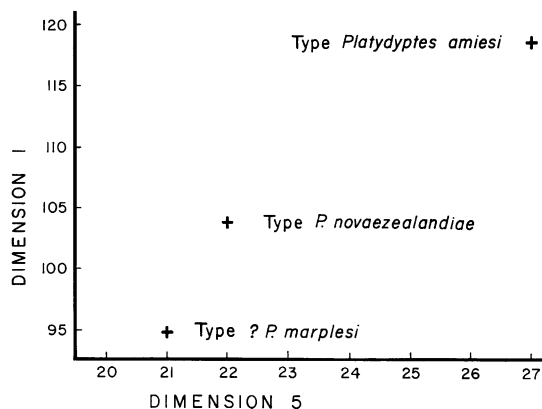


FIG. 15. *Platydyptes* spp. Proportions of humeri associated with types of the three named species. The dimensions are as numbered and defined by Marples (1952, table 3). Dimension 1 is maximum length. Dimension 5 is breadth of shaft 1/3 of distance from head toward distal end.

In terms perhaps more usual, the largest humerus (O.M. No. C.50.61, holotype of *P. amiesi*, 118 mm. long) is 24 per cent larger than the shortest (O.M. No. C.47.15, here made holotype of ?*P. marplei*, 95 mm. long), and that is a greater difference than I have been able to find

for the homologous measurement in any recent species. Marples decided to classify the largest individual, O.M. No. C.50.61, as a distinct species (*P. amiesi*) and to refer the smallest specimen, O.M. No. C.47.15, to *P. novaezealandiae*.

As O.M. No. C.47.15 is a more complete specimen and was in the Otago Museum, in which he was working, Marples based his concept of the species almost entirely on that specimen and not on the holotype, which he had seen in a distant museum and for which no illustrations were available. The difference in size between O.M. No. C.47.15 and D.M. No. 1451 (holotype of *P. novaezealandiae*) is somewhat less than between the latter and O.M. No. C.50.61 (made holotype of *P. amiesi* by Marples). However, D.M. No. 1451 and O.M. No. C.50.61 are almost identical morphologically and differ essentially only in size, a difference that by Marples' standards and others is of probable but not of decisive specific import. The larger humerus is 13 per cent longer than the smaller, or in Marples' terms the range of variation about the mean is 12.6 per cent, which is smaller than the 15 per cent he found in *Eudyptula minor* but still larger than one would expect by chance in only two specimens. The separation of these two species is thus quite dubious, and yet the resemblance is not so close as to demand reduction of *P. amiesi* to synonymy pending discovery of further specimens.

On the other hand, although O.M. No. C.47.15 is within the possible size range of *P. novaezealandiae*, as represented by the holotype of the latter, the morphology of the humerus is so distinct that even generic association can be questioned.

The relative widths of ulnar condyle and adjacent shelf as stated by Marples for the genus are correct for the holotype of the type-species, on which the widths are 7.1 and 6.0 mm. respectively, total width (Marples' dimension 11), 13.1 mm.

#### ***Platydyptes amiesi* Marples, 1952**

Figure 16

*Platydyptes amiesi* MARPLES, 1952, p. 38, pl. 4, fig. 3 (humerus), pl. 5, fig. 5 (radius). OLIVER, 1955, p. 592 and unnumbered figure on that page (same view as Marples, 1952, pl. 5, fig. 5). SIMPSON, 1957, p. 67; BRODKORB, 1963, p. 233.

ETYMOLOGY: For A. C. Amies, a student at the University of Otago, who in 1946 collected





FIG. 16. *Platydyptes amiesi*, O.M. No. C.50.61, type. Humerus, ventral (left), and dorsal and distal views.  $\times 1$ .

the first fossil penguin in the important Dunroon area, and who soon thereafter was killed in the war in Malaya.

**HOLOTYPE:** O.M. No. C.50.61–62, also referred to by Marples (1952) by Field No. G.48.6, associated humerus (61) and radius (62), from the Waitakian (*vide* Marples) of the Hakataramea Valley.

**HYPODIGM:** For present purposes the holotype only. Marples' hypodigm included the following, here doubtfully referred: O.M. No. C.47.35, incomplete radius, Dunroonian or Waitakian of White Rocks, Dunroon.

**KNOWN DISTRIBUTION:** Certain only for the type, Waitakian (*vide* Marples) of southern Canterbury, New Zealand. Perhaps also Dunroonian or Waitakian of the Waitaki Valley, northern Otago.

**ORIGINAL DIAGNOSIS:** "Except in size . . . practically identical with [humerus and radius] of *P. novaezealandiae*. On the humerus the insertion of the *pectoralis tertius* is directed rather more dorsally, and the angle at the base of the dorsal sesamoid groove is slightly more acute." (Marples, 1952, p. 39.)

**REVISED DIAGNOSIS:** Doubtfully separable

from *P. novaezealandiae*. Humerus closely similar morphologically but larger.

REMARK: The doubts about recognition of this supposed species and the reasons for tentatively retaining it are sufficiently discussed under *P. novaezealandiae*.

**?*Platydyptes marplesi*, new species**

*Platydyptes novaezealandiae*: MARPLES, 1952, p. 38 (in part), text figs. 5 (1) (sternum) and fig. 6 (3) (humerus), pl. 1 (whole specimen on slab), pl. 3, fig. 1 (radiograph of head of humerus), pl. 4, fig. 2 (humerus), pl. 6, figs. 2 (ulna), 3 (radius), 5 (sternum), and 7 (metacarpus) (all these figures are of O.M. No. C.47.15, holotype of the present species, and none pertain to *P. novaezealandiae* as here defined).

ETYMOLOGY: For B. J. Marples, the unique authority on New Zealand's fossil penguins. Although another species of penguin, *Palaeudyptes marplesi* Brodkorb, 1963, has also been named for him, the two are so unlike that one cannot be confused with the other and they are unlikely ever to be referred to the same genus. In view of Marples' extensive description and illustration of the present species (under a different name) no other designation would be apt or just.

HOLOTYPE: O.M. No. C.47.15, also referred to by Marples as "A," two humeri, two ulnae, two incomplete radii, one metacarpus, two coracoids, clavicle, two incomplete scapulae, and anterior part of sternum of one individual. Registered as from Oamaru but almost certainly from Wharekuri, Waitaki Valley.

HYPODIGM: Essentially the holotype, but the following are referred with some confidence: O.M. No. C.50.51, also referred to by Marples as "Specimen 1" and as "Field No. G.49.1," radius from Kokoamu Greensand, Duntroon. Not seen by me. O.M. No. C.50.52, also referred to by Marples as "Specimen 2" and as "Field No. G. 48.3," incomplete ulna from Kokoamu Greensand, Duntroon. Not seen by me.

KNOWN DISTRIBUTION: Duntroonian, Waitaki Valley, northern Otago, New Zealand.

DIAGNOSIS: Humerus smaller than those of holotypes of *P. novaezealandiae* or *P. amiesi*, pre-axial angulation more distal, less distinct and without tubercle, border proximal to it gently convex, shaft more sigmoid, insertion of pectoralis secundus more oblique than in *P. amiesi*.

DISCUSSION: As more fully discussed under *P.*

*novaezealandiae*, this holotype humerus is so distinct morphologically from those of both *P. novaezealandiae* and *P. amiesi* that there can be little question about its specific separation, at least. In fact its reference to *Platydyptes* is quite doubtful and it lacks possibly significant features shared by *P. novaezealandiae* and *P. amiesi*, possible synonyms, and here considered typical of the genus *Platydyptes*. In these respects it has considerable resemblance to *Pachydyptes ponderosus*, a much larger species, and its reference to *Pachydyptes* would be at least as justified as reference to *Platydyptes*. There are, however, some distinct differences such as the markedly more oblique pectoralis secundus scar. Even though that is also a difference from *Platydyptes amiesi*, at least, the doubts are such that pending further knowledge I prefer to retain the specimen in *Platydyptes*, in which Marples put it and of which he considered it typical. The species is so evidently distinct that it may require a new genus when the true characters of *Platydyptes* are better known, but that step would be premature now.

**ARCHAEOSPHENISCUS MARPLES, 1952**

*Archaeospheniscus* MARPLES, 1952, p. 40; 1962, p. 415, fig. 2d (labeled *Archaeospheniscus*, only, but is a restoration of the coracoid of O.M. No. C.47.20, holotype of *A. lowei*).

ETYMOLOGY: Greek, *archaios*, old, and *Spheniscus* (from Greek *spheniskos*, a small wedge, referring to the shape of the wings), a genus of recent penguins. No special relationship between the particular fossil and recent genera was meant to be implied.

TYPE-SPECIES: *Archaeospheniscus lowei* Marples, 1952.

INCLUDED SPECIES: Type-species and *A. lopdelli* Marples, 1952.

KNOWN DISTRIBUTION: Duntroonian, Otago, New Zealand.

ORIGINAL DIAGNOSIS: "Humerus having the angle between the tangent to the distal condyles and the long axis of the shaft intermediate between that of *Palaeudyptes* and *Eudyptes*. Shelf on the distal end of the humerus adjacent to the ulnar condyle, narrower than the condyle. Tri-cipital fossa undivided. Insertion of *pectoralis secundus* oblique, separated by a gap distally from that of the *latissimus dorsi*. Angles in both borders of the humerus giving it a distinct sigmoid or zigzag appearance . . .

"The genus differs from *Platydyptes* in that the humerus is relatively narrower, the tricipital fossa is without even the trace of a ventral chamber, the dorsal margin of the articular surface of the head forms a more obtuse angle with the axis of the shaft, and the capsular groove is more widely open at the postero-ventral angle of the articular surface. At the distal end of the humerus the ulnar condyle is a different shape from that of *P. novaezealandiae* and the shelf beside it is relatively narrower. The angle adjacent to the dorsal sesamoid groove is more obtuse." (Marples, 1952, p. 40.)

**REVISED DIAGNOSIS:** Shaft of humerus much more elongate and slender than in *Pachydyptes* or *Platydyptes* and somewhat more than in humeri ascribed to *Palaeedyptes*. More strongly sigmoid than in any of those genera. Preaxial angle present but rounded, shaft narrowing markedly and with strongly concave preaxial contour distal to angle. Pectoralis secundus insertion more oblique than in *Palaeedyptes*, *Pachydyptes*, or *Platydyptes amiesi*, more as in *?Platydyptes marplei*. Tricipital fossa undivided. Ulnar condyle wider than shelf beside it. Tarsometatarsus probably of this genus relatively short and wide with two subequal intermetatarsal foramina and with all metatarsals curved to medial side distally.

**DISCUSSION:** Marples' definition was somewhat equivocal as explicit comparison was with *Platydyptes*, and Marples' concept of that genus depended in part on a specimen of doubtful reference to it. There is nevertheless no serious doubt that some of the characters noted by Marples are valid distinctions and that those and others sufficiently characterize a good genus. If the holotype of *A. lopdelli* is correctly referred to this genus, as is probable, the tarsometatarsus is also distinctive; see discussion under the species.

#### ***Archaeospheniscus lowei* Marples, 1952**

Figures 17, 18

*Archaeospheniscus lowei* MARPLES, 1952, p. 40, text, fig. 6 (4) (humerus), pl. 2, fig. 4 (humerus), pl. 4, fig. 4 (ulna), pl. 5, fig. 1 (patella), pl. 6, fig. 6 (coracoid). OLIVER, 1955, p. 592 and two unnumbered figures on that page, apparently the same as Marples, 1952, pl. 6, fig. 6, and pl. 4, fig. 4. SIMPSON, 1957, p. 67; 1959, p. 116. BRODKORB, 1963, p. 232.

**ETYMOLOGY:** For P. R. Lowe, author of two papers on fossil penguins and the origin of

penguins, which he believed to have evolved from reptiles independently of the flying birds.

**HOLOTYPE:** O.M. No. C.47.20, also called "D.P.1" by Marples, two humeri, two ulnae, two femora, one radius, one coracoid, one patella, one tibia, partial pelvis, and fragments of scapula and vertebrae of a single individual from the Kokoamu Greensand, Duntroon.

**HYPODIGM:** Essentially the type, but the following is referred with reasonable probability. O.M. No. C.47.27, femur, from the Kokoamu Greensand, Duntroon.

**KNOWN DISTRIBUTION:** Duntroonian, Otago, New Zealand.

**ORIGINAL DIAGNOSIS:** None was given, except by inference from the diagnosis of the following species.

**REVISED DIAGNOSIS:** Holotype smaller throughout than that of *A. lopdelli*; length measurements of ulna and femur about 87 to 88 per cent as large.

#### ***Archaeospheniscus lopdelli* Marples, 1952**

Figures 6, 19A

*Archaeospheniscus lopdelli* MARPLES, 1952, p. 41, fig. 2 (4) (distal end of humerus), pl. 3, fig. 9 (humerus), pl. 4, fig. 6 (ulna), pl. 5, fig. 4 (radius), pl. 8, fig. 5 (tarsometatarsus). OLIVER, 1955, p. 593; SIMPSON, 1957, p. 67. BRODKORB, 1963, p. 232.

**ETYMOLOGY:** For J. C. Lopdell<sup>1</sup> who took part with Marples in field work around Duntroon.

**HOLOTYPE:** O.M. No. C.47.21, also called "D.P.2" by Marples, distal end of humerus, both ulnae, radius, both femora, imperfect tarsometatarsi, and fragments of metacarpus, coracoids, and vertebrae all of one individual. Kokoamu Greensand, Duntroon.

**HYPODIGM:** Holotype only.

**KNOWN DISTRIBUTION:** Duntroonian, Otago, New Zealand.

**ORIGINAL DIAGNOSIS:** "... Distinctly larger than *A. lowei* . . . . The angle between the tangent to the distal condyles and the axis of the shaft [of the humerus] . . . is less acute [than in the holotype of *A. lowei*]."

**REVISED DIAGNOSIS:** Holotype larger throughout than that of *A. lowei*; length measurements of ulna and femur about 114 to 115 per cent as large.

**DISCUSSION:** The validity of this species is open

<sup>1</sup> Marples included Mrs. Lopdell in the dedication, but the form *lopdelli* is masculine singular.



FIG. 17. *Archaeospheniscus lowei*, O.M. No. C.47.20, type. Humerus, dorsal (left), ventral and distal views.  $\times 1$ .

to question. The humerus is represented only by a poorly preserved fragment and the difference in tangents to the condyles noted by Marples does not seem significant. The only other difference noted by Marples in homologous parts of the holotypes is that in *A. lowei* the tibia is said to have a flattened shelf on the ventral (or posterior) side of the shaft, the preaxial (medial or internal) side forming a sharp ridge, whereas in *A. lopdelli* this region is said to be simply rounded. The difference in size would be within the possible range for a single species, although the

probability of obtaining such extremes in a sample of only three specimens is small. The populations represented were synchronous and sympatric, which would be unusual for two species so similar to each other.

The tarsometatarsus of O.M. No. C.47.21 is unique. There are two patent fairly large, and subequal intermetatarsal foramina, a condition rare or equivocal in other middle or early Tertiary penguins and resembling the recent *Aptenodytes*. (See discussion in Simpson, 1946, pp. 61-64 for general discussion of penguin



FIG. 18. *Archaeospheniscus lowei*, O.M. No. C.47.27. Femur, anterior (left) and posterior views.  $\times 1$ .

tarsometatarsi, although *Archaeospheniscus*, not then known, was not included.) The foramina are more proximal than in *Aptenodytes*, as is usual in early penguins. The three metatarsals are all curved with the distal ends relatively medial (or preaxial), and the lateral contour of IV is convex, whereas it is straight or even slightly concave in most penguins. The absence of plantar (or ventral) grooves and more marked dorsal groove between III and IV than between II and III, as specified by Marples, are, however, usual spheniscid characters. Although the bone is

stouter, it considerably resembles the tarsometatarsus of the Seymour Island genus *Notodyptes* Marples, 1953, but the only specimen of the latter is so imperfect that comparisons are limited.<sup>1</sup>

#### DUNTROONORNIS MARPLES, 1952

*Duntroonornis* MARPLES, 1952, p. 42.

ETYMOLOGY: Duntroon, town near which the

<sup>1</sup>Since sending this paper to press, I have studied the original specimen of *Notodyptes* and now consider that name to be synonymous with *Archaeospheniscus*.

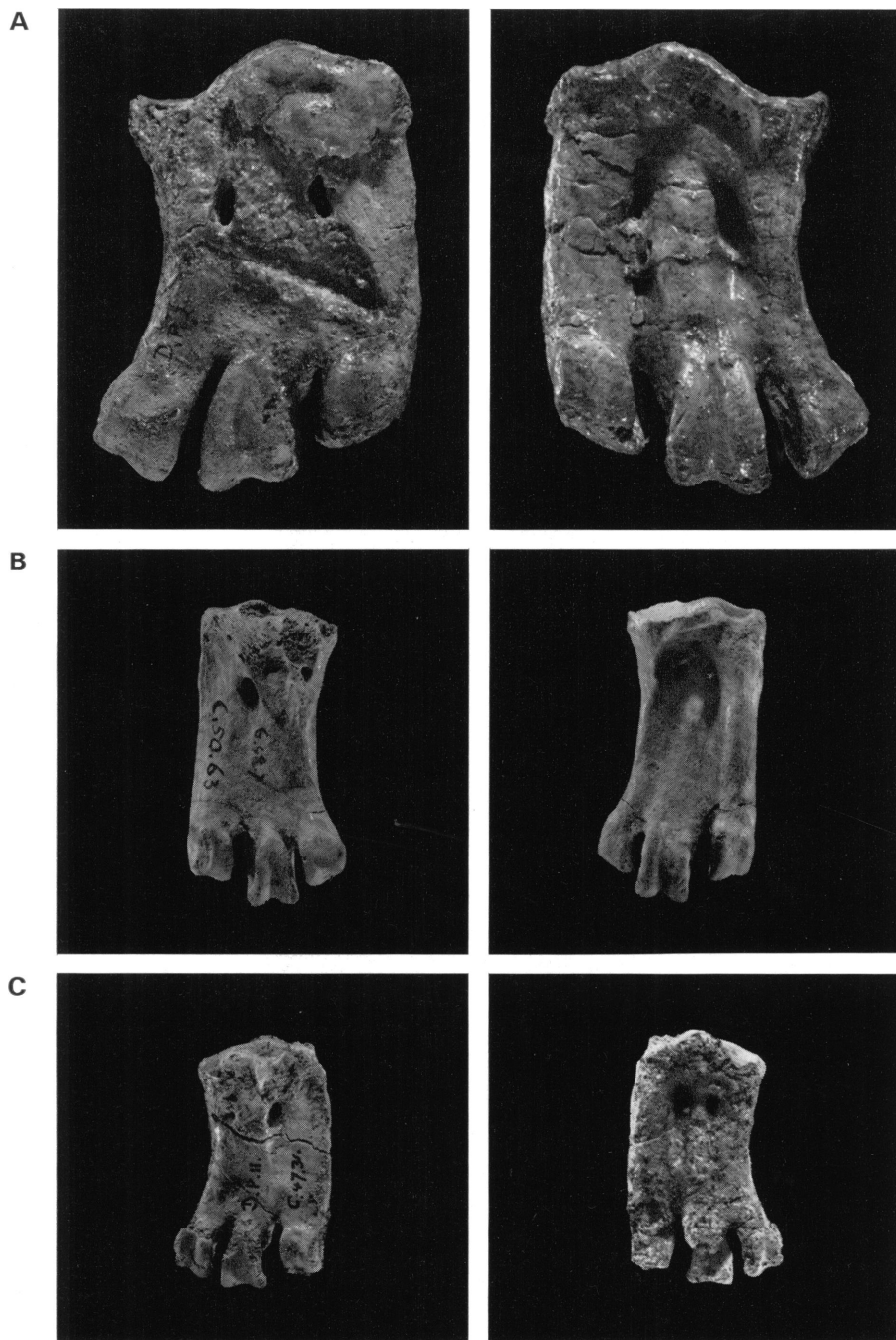


FIG. 19. Tarsometatarsi of fossil penguins. A. *Archaeospheniscus lopdelli*, O.M. No. C.47.21, type. Plantar (left) and dorsal views. B. *Korora oliveri*, O.M. No. C.50.63, type. Plantar (left) and dorsal views. C. *Duntroonornis parvus*, O.M. No. C.47.31, type. Plantar (left) and dorsal views. All  $\times 1$ .



holotype of the type-species was found, and Greek *ornis*, bird.

TYPE-SPECIES: *Duntronornis parvus* Marples, 1952.

INCLUDED SPECIES: Type only.

KNOWN DISTRIBUTION: Duntronian, Otago, New Zealand.

ORIGINAL DIAGNOSIS: "Metatarsals 2 and 3 closely united, with no groove and only a minute vacuity between them. Groove present between metatarsals 3 and 4, and a small vacuity. All metatarsals curved in a preaxial direction. Tarsus relatively thin dorso-ventrally. This tarsus resembles those of *A. lopdelli* in having all the metatarsals curved in the preaxial direction, but differs from them in having very small intermetatarsal vacuities, especially the preaxial one. It is also relatively narrower, and it belongs to quite a small bird." (Marples, 1952, p. 42.)

REVISED DIAGNOSIS: Tarsometatarsus relatively more elongate than in *Archaeospheniscus* but less than in *Korora*, with minute foramen between metatarsal II and III and moderate, relatively proximal foramen between III and IV; lateral contour of IV slightly convex, and all three metatarsals with distal end inclined medially as in *Archaeospheniscus*.

DISCUSSION: In general proportions and structure the tarsometatarsus on which this genus is based resembles that of the Patagonian fossil genus *Perispheniscus* (see Simpson, 1946, p. 31 and fig. 22C, I). The only striking difference is the medial inclination of the distal ends of III and IV in *Duntronornis*.

#### ***Duntronornis parvus* Marples, 1952**

Figure 19C

*Duntronornis parvus* MARPLES, 1952, p. 42, pl. 8, figs. 3, 4 (tarsometatarsus). OLIVER, 1955, p. 593; SIMPSON, 1957, p. 67, BRODKORB, 1963, p. 233.

ETYMOLOGY: Latin *parvus*, small. This is the smallest fossil penguin known from New Zealand.

HOLOTYPE: O.M. No. C.47.31, also called "D.P.11" by Marples, left tarsometatarsus from Kokoamu Greensand, Duntron.

HYPODIGM: Essentially the type, only. The following additional specimens were considered by Marples as possibly belonging to the species on the basis of their size:

O.M. No. C.47.29, Field No. D.P.9, possibly associated fragments of humerus, ulna, and coracoid, from Kokoamu Greensand, Duntron.

O.M. No. C.47.30, shaft of femur, from Kokoamu Greensand, Duntron.

KNOWN DISTRIBUTION: Duntronian, Otago, New Zealand.

DIAGNOSIS: Only known species of the genus as defined above.

COMMENT: The dorsal surface of the specimen is eroded and the apparently unusual thinness of the bone is probably caused by that post mortem damage. The remaining characters are nevertheless distinctive and there is little doubt that the species is valid.

#### **KORORA MARPLES, 1952**

*Korora* MARPLES, 1952, p. 43.

ETYMOLOGY: Maori *Korora*, little blue penguin, *Eudyptula minor*. The terminal -a is long and stressed in the Maori word. The name was not intended to indicate a particular relationship but was given because *Korora oliveri* was a small bird and the little blue penguin is the smallest of living species. However, *K. oliveri* was larger than the little blue penguin and also larger than its faunal associate *Duntronornis parvus*.

TYPE-SPECIES: *Korora oliveri* Marples, 1952.

INCLUDED SPECIES: Type only.

KNOWN DISTRIBUTION: Waitakian, southern Canterbury, New Zealand.

ORIGINAL DIAGNOSIS: "Metatarsals 2 and 3 closely united, with only a small vacuity between them and a very slight groove on the dorsal surface. The vacuity is oblique, so that its ventral opening is at the ventral edge of the preaxial surface. The vacuity between metatarsals 3 and 4 is about twice the size of the other, and there is a groove between these bones on the dorsal surface. The preaxial border of the bone is concave, while the postaxial one is straight. The main calcaneal tubercle, the preaxial one, extends as an oblique ridge to reach the preaxial border of the bone about half-way along it. This ridge overhangs the preaxial intermetatarsal vacuity." (Marples, 1952, p. 43.)

REVISED DIAGNOSIS: Tarsometatarsus with metatarsals II and III almost fully fused but with minute, oblique, proximal intermetatarsal foramen; lateral intermetatarsal foramen larger, but also relatively small; bone relatively elongate. Closely resembling the tarsometatarsus of the Patagonian genus *Palaeospheniscus* but possibly differing in persistence and form of the internal intermetatarsal foramen.

DISCUSSION: The one bone that so far is all that

is known of this genus is strongly distinctive among New Zealand forms in which the tarsometatarsus is known. It is, however, almost identical with some specimens of *Palaeospheniscus*, with which Marples did not compare it. I believe that the genera are probably synonymous, but tentatively retain *Korora* pending discovery of other parts of its anatomy. The geographic difference is great, but not so much as to exclude generic identity. The age difference is slight or nil, as *Palaeospheniscus* occurs in beds probably early Miocene but possibly late Oligocene in age and *Korora* in a stage sometimes considered late Oligocene and sometimes early Miocene.

***Korora oliveri* Marples, 1952**

Figure 19B

*Korora oliveri* MARPLES, 1952, p. 43; pl. 8, figs. 7, 8 (tarsometatarsus). OLIVER, 1955, p. 593, and unnumbered figure on same page, same view as Marples, 1952, pl. 8, fig. 8, but clearer. SIMPSON, 1957, p. 67. BRODKORB, 1963, p. 233.

**ETYMOLOGY:** For W. R. B. Oliver, whose classic work on the New Zealand avifauna includes first descriptions of two species of fossil penguins and lists others.

**HOLOTYPE:** O.M. No. C.50.63, referred to by Marples only under Field No. G.48.7, tarsometatarsus, from Waitakian beds (*vide* Marples) in the Hakataramea Valley, southern Canterbury.

**HYPODIGM:** Type only.

**KNOWN DISTRIBUTION:** Waitakian, Canterbury, New Zealand.

**ORIGINAL DIAGNOSIS:** "It is striking, compared with the other New Zealand tarsi, for its long narrow shape, the length being 2.5 times the breadth. It differs in shape and thickness, as well as in detail, from the only other small tarsus, that of *D [untroonornis] parvus*." (Marples, 1952, p. 43.)

**REVISED DIAGNOSIS:** The only known species of the genus as diagnosed above. Not surely distinguishable from Patagonian species referred to *Palaeospheniscus*.

**DISCUSSION:** Marples' description or diagnosis (not so labeled) of the species is essentially a supplement to his generic diagnosis ("*Generic characters*"). The stated ratio of length to breadth is based on Marples' dimension 2, "Length of the third metatarsal from the proximal convexity to the groove of the distal trochlear sur-

face," which is approximately but not quite the maximum proximodistal length including the fused tarsal element, and his dimension 5, "preaxio-postaxial width at the centre," which may be slightly greater than the minimal lateromedial (or preaxio-postaxial) width, which on this specimen and most penguin tarsometatarsi is slightly proximal to the precise proximodistal midpoint and which may be the designated center. The index  $100 \times (\text{maximum proximodistal length}) / (\text{proximal lateromedial width})$ , which I have used for indicating relative elongation of penguin tarsometatarsi (Simpson, 1946, p. 63, table 6), is 225, which is within the range of Patagonian specimens of *Palaeospheniscus* of comparable size. It is larger than in any other known New Zealand specimen, including the smaller *Duntroonornis parvus*, and larger than in fossil or recent penguins of distinctly greater size. (See table 3.)

TABLE 3

RELATIVE ELONGATION OF TARSOMETATARSII  
IN SOME PENGUINS

Species, in Order of Increasing Size	100 Times Maximum Length Divided by Proximal Width
<i>Spheniscus mendiculus</i> (Recent)	182-210
<i>Duntroonornis parvus</i> , type	201
<i>Korora oliveri</i> , type	225
<i>Palaeospheniscus</i> (large species or variants, late Oligocene or early Miocene of Patagonia)	217-253
<i>Aptenodytes forsteri</i> (Recent)	140-171
<i>Archaeospheniscus lopdelli</i> , type	162
<i>Palaeedyptes antarcticus</i> , type	197
<i>Palaeedyptes marplesii</i> , type	181

FAMILY SPHENISCIDAE GENERA AND  
SPECIES INDETERMINATE

There are a number of unidentified and probably unidentifiable fragments, one in the Canterbury Museum (mentioned above under the locality Omihi), several in the Otago Museum, and some mentioned in passing by Marples and not otherwise known to me, that do not seem to require or to merit special notice here. There are, however, two specimens that do merit notice although in my opinion also unidentifiable to genus at present.

G.S. No. 9165 is a femur, with the middle part of the shaft lacking, from the Whaingaroan

of Kawhia Harbour (see "Localities and Ages," above). It is noteworthy as the only known pre-Pleistocene penguin from the north island of New Zealand. Marples and Fleming (1963) described it in detail and concluded that "it is possible that it . . . represents a smaller species of the genus *Palaeudyptes*," but added that it is unique in having an unusually well-developed groove for articulation with the fibula, ending proximally in a distinct pit. It seems unlikely to me that this bone belongs in *Palaeudyptes*, and I doubt whether it can be identified to genus until

a similar femur can be associated with a humerus, tarsometatarsus, or both.

G.S. No. 5184 consists of three fragments, shown in figure 20, proximal, medial, and distal parts of a femur, from beds at Gore Bay considered by Finlay (1952, p. 59) to be Heretaungan. This is the specimen long considered the oldest known penguin, but as discussed under "Localities and Ages" that was erroneous. The stratum in which the bone was embedded belongs in the Pareora "Series," later than any other penguin here discussed. The probable



FIG. 20. Femora of fossil penguins. The three fragments to the left are G.S. No.5184, the specimen formerly believed to be the oldest known penguin, Heretaungan (early Eocene), but now known to be later in age. These battered and unidentifiable fragments are oriented for comparison with the femur of *Palaeudyptes* sp., D.M. No. 1449, to the right. (This femur is complete; it has been separated along a crack for purposes of the comparison only.) All  $\times 1$ .

age of the specimen is thus somewhere in the sequence Otaian-Awamoan, but it might have been redeposited from underlying beds of the Landon "Series," Whaingaroan-Waitakian. As Marples noted (1952, p. 44) the specimen as preserved does not differ appreciably from D.M. No. 1449 (what Marples called ('Hector's specimen of *P. antarcticus*'), discussed here as *Palaeudyptes* species indeterminate, probably Duntroonian in age. If the Gore Bay specimen

was redeposited, it could be of the same age. The resemblance confirms reference to the Spheniscidae, a matter of slight importance now that the age is known to be Oligocene or Miocene, not early Eocene. The specimen is too poorly preserved to permit generic, or, *a fortiori*, specific identification. Incidentally, in such cases it is misleading to refer to an "unnamed" or "undescribed" genus, as for example by Fisher (1967, p. 734) or Stonehouse (1969, p. 674).

## BROADER SYSTEMATICS

### GENERIC AND FAUNAL AFFINITIES

THE PRE-PLIOCENE PENGUINS of New Zealand and all known pre-Pliocene penguins differ distinctly from any Recent penguins, and in no case has any special resemblance been found between a particular fossil genus and a Recent genus, still less species. The possibility of some unrecorded transformation in the later Tertiary cannot be excluded, but it is improbable that any known early form is ancestral to a recent penguin. This indicates a radically incomplete fossil record, in spite of the fact that some 20 pre-Pliocene genera are known (of course depending on opinion as to validity of some supposed genera; as many as 28 have been claimed) and only 6 Recent genera (again depending on opinion; as many as 9 have been claimed). The known fossil forms are much more varied than the Recent. Their size range is about as great. None is quite as small as the smallest living penguins (*Eudyptula minor*), which is probably due to the fact of mere lack of discovery, but several are decidedly larger than the largest living species (*Aptenodytes forsteri*). In spite of the penguin stereotype, the morphology of known parts is much more diverse in the fossils.

In the New Zealand genera, there is considerable resemblance among *Palaeudyptes*, *Pachydyptes*, and *Platydyptes*, but the first two are readily distinguished. The last two seem to be

quite closely allied, but a case can be made out for generic distinction and perhaps even for presence of a third genus (for *?Platydyptes marplei*) in the group. *Archaeospheniscus* may also be allied to *Palaeudyptes* but may be more distinct. The degree of difference depends largely on a tarso-metatarsus that may not belong to *Archaeospheniscus* or may even be juvenile or have been distorted post mortem. *Duntroonornis* and *Korora* are evidently quite distinct from any of the four genera just discussed but less distinct from each other.

The four known regional fossil penguin faunas are in general different. They cover different times, only partly overlapping, are from widely separate geographic areas, three not very different in latitude but one markedly so, and represent different intensities of sampling (see table 4).

The fossil penguin collecting area in Australia is nearest to that of New Zealand and not greatly different in latitude. The two areas also share a species of penguin (*Eudyptula minor*) today. It would therefore be expected that their fossil penguin faunas might be closely similar. However, the Australian fossil penguins are poorly known, only three genera having yet been identified, although unidentifiable fragments do indicate a somewhat richer fauna. One of the three is *Palaeudyptes*, or a near ally, and thus

TABLE 4  
DATA ON COLLECTING AREAS FROM WHICH PRE-PLIOCENE PENGUINS ARE KNOWN

	Approximate Airline Distance (Kilometers) from Areas in:				Approximate South Latitudes	Probable Age Span	Sampling
	N.Z.	Aus.	Patagonia	Seymour			
New Zealand	—	2000-2500	5300	4400	38°-46°	Late Eocene to late Oligocene or early Miocene	Fair
Australia	2000-2500	—	6300	5300	35°-38°	Late Eocene to late Miocene	Very thin
Patagonia	5300	6300	—	2100	43°-49°	Late Oligocene or early Miocene	Good for one horizon and two localities
Seymour Island	4400	5300	2100	—	64°	Late Oligocene or early Miocene	Fair, one horizon and locality

does show close affinity with New Zealand. A second, *Anthropodyptes*, has a humerus somewhat like that of New Zealand *Archaeospheniscus*, but better preserved and associated material of both genera would be required to confirm the relationship. The third genus, *Pseudapterodytes* (Simpson, 1970), also based on humeri, is quite unlike any New Zealand form in which the humerus is known, and possible relationship to one in which the humerus is not known (*Duntroonornis*, for example) would be unwarranted speculation at present.

Marples (1952, 1953) considered the New Zealand and Seymour Island species to "resemble one another closely" (1953, p. 5), but in fact did not consider any genera (*a fortiori*, species) to be common to the two areas. The illustrations and descriptions (I have not seen the Seymour Island specimens) seem to me to warrant the generic distinctions, at least tentatively, and to that extent to belie the mooted specific resemblances. The most definite resemblance is between New Zealand *Pachydyptes* and *Platydyptes*, on one hand, and Seymour Island *Anthropornis* (with *Pachypteryx* and *Orthopteryx* as probable synonyms) on the other. Although Marples did not make this comparison his Seymour Island *Notodyptes wimani* may be fairly close to his New Zealand *Archaeospheniscus lopdelli*, but the one specimen of the former is so poorly preserved that the resemblance may be misleading.<sup>1</sup>

On the other hand, there now seems to be somewhat greater resemblance between the New Zealand and Patagonian fossil penguins than has hitherto been evident. As noted in the preceding review, the tarsometatarsus that constitutes all our knowledge of New Zealand *Korora* is so like some specimens of the commonest Patagonian genus, *Palaeospheniscus*, that generic separation is doubtful.<sup>2</sup> The resemblance of the

homologous bone in New Zealand *Duntroonornis* and Patagonian *Perispheniscus*, a rather close ally of *Palaeospheniscus*, is also considerable although not quite so much as for *Korora* and *Palaeospheniscus*. The unusually large penguins that constitute the bulk of the known New Zealand and Seymour Island fossil faunas are quite rare in Patagonia, but *Arthrodytes grandis* from Patagonia belongs in this group and, on the basis of our extremely scanty present knowledge of it, cannot be surely distinguished generically from Seymour Island *Anthropornis* or its apparent New Zealand allies.

#### SUBFAMILIES

I proposed a subfamily classification of Recent and fossil Spheniscidae in 1946 (Simpson, 1946, pp. 68–70), at which time most of the Patagonian and Seymour Island fossils now known were already in hand, but only *Palaeodyptes antarcticus*, *Pachydyptes ponderosus*, and *Pachydyptes novaezealandiae* had been described, inadequately, from New Zealand and only a single imperfect bone from Australia.

Recent penguins are closely similar in osteology. Most of the species can be recognized osteologically, but it is doubtful whether on this basis alone a conservative systematist would recognize as many as six genera or distribute the species in genera as is now usual on the basis of external characters and general anatomy. In osteological characters other than size, no two Recent species differ as much as any Recent species does from all known pre-Pliocene species. Both phenetically and on the basis of clear evolutionary implications the Recent forms thus belong together in a subfamily Spheniscinae, if subfamilies are to enter into classification of Spheniscidae. With possible addition of any extinct forms that could be shown to be ancestrally or otherwise exclusively related, the Spheniscinae would comprise these living genera of usual current classifications: *Aptenodytes* (2 spp.), *Megadyptes* (1 sp.), *Pygoscelis* (3 spp.), *Eudyptes* (6 or 7 spp.), *Spheniscus* (4 spp.), and *Eudyptula* (1 or 2 spp.).

As of 1946, the known fossil penguins most nearly resembling the Recent genera were Patagonian *Palaeospheniscus* and its apparently close allies *Paraspheniscus* and *Perispheniscus*. In them the tarsometatarsus differs from the Recent genera most distinctly in being relatively more elongate in birds of comparable size, with the

<sup>1</sup>Note added in proof. I have now studied all the Seymour Island specimens and believe that they are specifically distinct from New Zealand specimens but include the genera *Palaeodyptes* and *Archaeospheniscus*.

<sup>2</sup>Marples (1960) has referred a New Zealand Pliocene penguin to the Patagonian early Miocene or late Oligocene genus *Palaeospheniscus*. Comparison with *Korora* was impossible because homologous parts were not known. Two more New Zealand Pliocene specimens are now known, including a tarsometatarsus, and it should be possible to clear up generic reference in future study.

(Note added in proof: The Pliocene specimen does not belong to *Palaeospheniscus*).



metatarsals more firmly fused and the internal intermetatarsal foramen small or absent. The humerus differs little from the Recent genera but tends to have the tricipital fossa more sharply bipartite and the shaft-trochlear angle perhaps slightly smaller on an average, although within the Recent range. On those characters a subfamily Palaeospheniscinae was proposed (Simpson, 1946, p. 69). The present review shows that the tarsometatarsi of *Dunroonornis* and *Korora*, all that is known of those genera, are more like these Patagonian genera than like other known forms. If a subfamily arrangement were retained, *Dunroonornis* and *Korora* should be placed in the same subfamily as *Palaeospheniscus*.

In the 1946 arrangement the Patagonian genera *Paraptenodytes* and *Isotremornis* (and some doubtfully valid allies) were placed in a subfamily Paraptenodytinae defined as having the tarsometatarsus relatively shorter than in the Palaeospheniscinae, with small subequal intermetatarsal foramen, humerus similar to the Palaeospheniscinae and Spheniscinae except for large, non-bipartite tricipital fossa. The Palaeodyptinae, then based only on quite inadequate knowledge of *Palaeodyptes* alone, were supposedly distinguished from the Paraptenodytinae by absence of the internal intermetatarsal foramen; humerus narrower distally and with relatively somewhat smaller tricipital fossa and shaft-trochlear angle. In fact the internal intermetatarsal foramen is usually present in *Palaeodyptes* and its apparent allies in New Zealand, although smaller than the lateral foramen. The noted characters of the humerus also prove to be variable in the pertinent New Zealand specimens and of doubtful diagnostic significance. It would thus be difficult at present to justify separation of the Paraptenodytinae and Palaeodyptinae.

Finally, as regards the 1946 classification, Seymour Island *Anthropornis*, *Eosphaeniscus*, and *Delphinornis*, Patagonian *Arthrodytes*, and New Zealand *Pachydyptes* were placed in a subfamily Anthropornithinae defined as having an elongate tarsometatarsus (unknown in *Arthrodytes* or *Pachydyptes*), with both intermetatarsal foramina and humerus (unknown in *Delphinornis*) sigmoid, heavy, with subequal proximally and distally, tricipital fossa simple and relatively small. The tarsometatarsus is still unknown in *Pachydyptes* or its now separated but evidently close ally *Platydyptes*. The tarsometatarsus placed, with

some doubt, in *Archaeospheniscus* is more like this group than like *Palaeodyptes*, but the humerus of *Archaeospheniscus* is more like the latter.

In 1952 Marples (1952, pp. 48–51) criticized my previous subfamily arrangement with considerable reason, largely on the basis of New Zealand specimens unknown or inadequately published before my study. Marples concluded that the New Zealand fossils have much in common, which is true of most of them although he here omitted mention of his genera *Dunroonornis* and *Korora*, which have comparatively little in common with *Palaeodyptes*, *Pachydyptes*, and their allies. He then concluded that distinction of the New Zealand fossils from the Anthropornithinae is minor, partly because of the lesser distinctions of variant humeri probably of *Palaeodyptes*, then newly described, but largely because the tarsometatarsus of *Archaeospheniscus lopdelli* does not differ markedly from that of *Anthropornis*. However, that is quite equivocal because it implies a necessary subfamily relationship of *Palaeodyptes* and *Archaeospheniscus*, and the fact is that the tarsometatarsus of *A. lopdelli* (which is not certainly referable to *Archaeospheniscus*) does differ quite markedly from that of *Palaeodyptes*.

Marples in 1952 considered that the Palaeospheniscinae, which I had noted in 1946 as most like the Spheniscinae among known pre-Pliocene penguins, do not differ enough from the latter for subfamily separation, a question of degree and of opinion. He was not then quite clear as to his opinion about the Paraptenodytinae, but compared them especially with the Palaeospheniscinae and they would be included in "the large assemblage from Patagonia . . . of the Spheniscine type" (Marples, 1952, p. 48), which I take to involve reference to the Spheniscinae. However, as here previously noted, the Paraptenodytinae as envisioned in 1946 now seem to me doubtfully separable at subfamily level from the Palaeodyptinae on present knowledge. If all these suggestions of inter-subfamilial connections were followed, all the fossils would wind up in the Spheniscinae: Marples would unite the Palaeospheniscinae and Paraptenodytinae with the Spheniscinae, and the Anthropornithinae with the Palaeodyptinae, whereas I would unite the Palaeodyptinae and Paraptenodytinae.

Marples defined his concept of the Palaeodyptinae in part by characters of the coracoid

and patella, noting that only two specimens of each were (and still are) known. The coracoid is not known in *Palaeudyptes* itself or in any genus placed in the Palaeudyptinae, *sensu stricto*, as originally defined. No characters of the tarso-metatarsus were given as diagnostic. Characters given for the humerus are: (1) relatively smaller and more rounded articular head; (2) tricipital fossa simple; (3) shaft of even width or narrower distally; (4) shaft-trochlear angle small (numbers were not used by Marples, but are inserted here for reference). Characters (1) and (4) are not constant in the Palaeudyptinae and do not distinguish genera referred by Marples to that subfamily from genera of his Spheniscinae. Characters (2) and (3) are not known in several genera that Marples apparently intended to include in the Palaeudyptinae. For those reasons, I pointed out that Marples' subfamily arrangement of 1952 was unsatisfactory, while agreeing that his further observations had made my earlier arrangement also unsatisfactory (Simpson, 1959, pp. 117-119).

Although I believe that division of all known penguins into only two subfamilies, the Spheniscinae and Palaeudyptinae, as now discussed, is sufficiently explicit and surely implicit in his discussion of 1952, in a later study Marples (1962) recognized four subfamilies: Palaeudyptinae (with Anthropornithinae considered synonymous as before), Paraptenodytinae, Palaeospheniscinae, and Spheniscinae, the last three defined essentially as in my first attempt (Simpson, 1946). Assignment of genera was as follows:

Palaeudyptinae

*Palaeudyptes*  
*Pachydyptes*  
*Platydyptes*  
*Archaeospheniscus*  
*Anthropornis*  
*Eosphaeniscus*

?Palaeudyptinae

*Anthropodyptes*  
*Arthrodytes*

Paraptenodytinae

*Paraptenodytes*  
*Isotremornis*

Palaeospheniscinae

*Palaeospheniscus*  
*Paraspheniscus*  
*Perispheniscus*

Spheniscinae

*Aptenodytes*  
*Eudyptes*

*Eudyptula*  
*Megadyptes*  
*Pygoscelis*  
*Spheniscus*  
 ?subfamily  
*Duntroonornis*  
*Korora*  
*Notodyptes*  
*Delphinornis*

He thus returned almost to my earlier arrangement, which I had abandoned as a result, mainly, of his observations. Brodkorb (1963) followed Marples' most recent opinion in recognizing those four subfamilies, but he revived several generic names considered synonymous or indeterminate by Marples (and me), and he referred all four of the genera placed by Marples under "?subfamily" to the Palaeudyptinae. Whatever their affinities may be, I agree with Marples that they are not at all close to *Palaeudyptes*.

There are over-all or variable average differences reflected in both Marples' attempts and mine to group genera within the Spheniscidae. The pre-Pliocene forms tend to have certain characters that are probably primitive and in that way more or less unlike living penguins. They also tend to have certain variable characters that are to some degree associated with size, Marples' Spheniscinae being on an average smaller than his Palaeudyptinae, and my Palaeospheniscinae, Paraptenodytinae, and Palaeudyptinae (with Anthropornithinae) on an average larger, in that order. The identification and study of primitive and of adaptive characters are of great interest, but I do not believe that our present knowledge of fossil penguins is adequate basis for a subfamily classification that would be of evolutionary significance or otherwise useful.

## ORIGINS

Closely similar among themselves, penguins as a group differ obviously and radically from all other birds. In some ways, indeed, they hardly seem to be birds: they lack aerial flight; their feathers are unique in structure; their tarso-metatarsi are shorter and less fully fused than in typical birds; although they can walk, they do so slowly and with apparent difficulty; the skeleton is completely nonpneumatic; and in fact they differ in almost every anatomical and physiological detail from other birds, including other

nonaerial birds. Those facts have given rise to many conjectures and long debates about the ancestry and affinities of these strange animals. I previously summarized the most important earlier opinions and the then available evidence (Simpson, 1946, pp. 77–92) and need not repeat them here. Certain basic conclusions then reached, from abundant further evidence supporting an old view already suggested by Fürbringer (1888), are also in entire agreement with the evidence of New Zealand and Australian penguins that has become available since 1946.

It is highly probable that penguins arose from normal, aerially flying birds and that their closest relatives among other known birds are the Procellariiformes. That implies a common ancestry with the Procellariiformes after some ordinal radiation of the Aves had begun. It is not clear whether the unknown common ancestor would, if known, be classifiable as procellariiform or would have to be placed in some still more primitive and less specialized taxon, perhaps in or near the ancestry of some other order such as the Pelecaniformes. No procellariiform is known before the middle Eocene. There are known pelecaniforms from the Late Cretaceous (*Graculavus* Marsh, *Elopteryx* Andrews), but they apparently were already beyond the point of ordinal differentiation. The direct evidence of ordinal cladogenesis probably lies still farther back in the Cretaceous, where the avian fossil record is still extremely poor. The principal addition made to the problem of penguin origins by the increased knowledge of New Zealand and Australian fossils since 1946 is demonstration that specialized penguins occur in the late Eocene: *Pachydyptes ponderosus*, *Palaeudyptes marplei* and *Palaeudyptes* sp. in New Zealand; *Palaeudyptes* sp. in Australia. (Earlier in the present study it is shown that these are the oldest known penguins and that the supposed early Eocene occurrence in New Zealand is incorrect.) The two Burnside Mudstone specimens of *Palaeudyptes* are especially indicative, as they include individually associated parts of both wings and legs. Those show clearly that the wing was already incapable of aerial flight and fully adapted to subaquatic flight, that the stance was already vertical, and that the foot was already fully plantar-digital with a short, emphatically sphenisciform tarsometatarsus.

Perhaps that is not too surprising in view of the fact that certainly most and possibly all of

the other now extant orders of birds already had evolved their ordinal specializations by the late Eocene. On Fisher's (1967) data, 19 of the 27 Recent orders are known from ordinally identifiable fossils in the late Eocene or earlier. The absence of the eight others from the early fossil record is more likely due to nondiscovery than to later origin. However, the penguins have departed farther than almost any other known bird from a probable general aerial volant ancestry, and it might have been expected that the divergence would take longer than for most orders and therefore might have been less far along in the late Eocene. That it was essentially complete in the late Eocene suggests that ancestral evolution was probably exceptionally rapid during the transition from aerial to aquatic adaptation, in other words, that this involved a phase of quantum evolution at tachytelic rates.

Although all the late Eocene to early Miocene penguins were essentially sphenisciform in osteology, they do have some presumably primitive characters. All such characters seem to have been variable and none is particularly striking, but it is suggestive, at least, that most or all are resemblances to aerial volant birds and especially to the Procellariiformes. I specified some of these (Simpson, 1946, pp. 78–83) and others were added by Marples (1952, p. 50 and pp. 8–27). Only a few of those most striking or previously most stressed need be further mentioned here.

In the humeri of the large late Eocene to early Miocene penguins the tricipital fossa is simple, not bipartite as it is to varying degree in all Recent penguins. However, in late Oligocene or early Miocene penguins of medium- to small-size, the fossa is bipartite, sometimes more sharply so than in Recent penguins. Humeri in this size range are not yet known from the late Eocene or early Oligocene, and it is not completely clear that the simple fossa, which does more resemble that of Procellariiformes, is primitive rather than a concomitant of size within the Sphenisciformes.

The early fossil humeri generally have a low shaft-trochlear angle, often at or slightly below the range in Recent penguins. There is, however, wide overlap in ranges, and the fossils with particularly low values are again the particularly large species. Thus some doubt remains, although Marples (1952, pp. 11–13, especially

fig. 3) may be right in considering this an evolutionary stage between the sharply bent elbow of typically aerial volant birds and the almost straight wing of the Recent penguins.

The humerus of *Pachydyptes ponderosus*, one of the oldest (late Eocene) but also the largest known, has a simple tricipital fossa and a low shaft-trochlear angle (about  $35^\circ$ ), although one equally small occurs as an extreme variant among Recent penguins. It also has a straight pectoralis secundus insertion (that is, nearly parallel to the shaft), which Marples considered a significantly primitive feature, although an oblique insertion, as in Recent penguins, does occur in some humeri nearly or quite as old. This extremely heavy bone with its massive head, tremendous even in proportion to the stout shaft, is unique and must be considered specialized in some respects to a degree even beyond any Recent species.

The tarsometatarsi of known pre-Pliocene penguins are in general relatively more elongate and have the metatarsals more firmly fused than in Recent penguins of comparable sizes. Those are resemblances to aerial volant birds and are almost certainly primitive characters for penguins. The lessened fusion in Recent penguins is in some measure a reversion to a still more primitive condition—the metatarsals were probably unfused in *Archaeopteryx* (see de Beer, 1954) and certainly were in reptilian ancestors of the birds—but a high degree of fusion occurs in the Procellariiformes and almost certainly existed in the aerial ancestors of the penguins. These characters are variable in the fossils. *Archaeospheniscus lopdelli* had relatively little fused metatarsals, and in *Duntroonornis parvus* the tarsometatarsus is not more elongate (relative to width) than in some Recent penguins of comparable size.

Marples (1952, pp. 20–22, fig. 4) showed that the sternal end of the coracoid of some fossil penguins is strikingly different from that of any Recent penguin, both the curvature of the blade and that of the sternal articulation being reversed from the Recent structure. This, again, is known only in the largest forms, in *Anthropornis*, *Archaeospheniscus*, *Palaeudyptes*, and strikingly in the Eocene genus *Pachydyptes*. It is not a procellariiform character, is almost certainly not primitive for birds or for penguins, and is another indication that these large, ancient penguins were already quite specialized, in some

respects even more specialized than the Recent forms.

Only insignificant fragments of the skull are known in pre-Pliocene penguins from New Zealand, and at present the only helpful pre-Pliocene skull is one of *Parapténodytes antarcticus* from the early Miocene of Patagonia (Simpson, 1946). It has a number of minor primitive features and one remarkable one: The pterygoid is quite unlike that of any later penguin and if found in isolation would almost certainly be identified as procellariiform.

Thus within the varied ranks of pre-Pliocene penguins we find: first, all the basic sphenisciform specializations already fully established; second, some variable primitive characters congruent with the basic penguin habitus but absent in later survivors; and third, in certain species, especially those of large size, early but marked specializations that are aberrant with respect to the later penguins.

It is highly probable that penguins evolved in the Southern Hemisphere and have never occurred in the Northern Hemisphere. Recent penguins do reach the equator at one point (*Spheniscus mendiculus* in the Galápagos Islands), and two other species (*Spheniscus humboldti* and *S. demersus*) also breed within the tropics. All the now fairly numerous known fossil occurrences are well down in the south temperate zone. The northernmost fossil locality, Witton Bluff, South Australia, is just below the 35th south parallel, and the southernmost, Seymour Island, is near and north of the Antarctic circle.

If the ultimate problem of penguin ancestry is to be solved by fossils, they will evidently have to be fossils from the Southern Hemisphere, certainly considerably older than late Eocene and probably considerably before Late Cretaceous. But as far as I know no pre-Cenozoic fossil birds are yet known from the Southern Hemisphere, and the only ones known before the late Eocene are *Telmabates antiquus* Howard and three unidentified fragments all from the same deposit in the probable early Eocene of Patagonia (Howard, 1955). *Telmabates* is a phoenicopterid and these finds cast no light at all on penguins.<sup>1</sup>

<sup>1</sup> In this connection there is an important error in the literature that requires correction although it does not directly concern penguins. Ameghino (1891) described several fragments of a fossil bird to which he gave the name *Opisthodactylus patagonicus*. As to its origin, he said only that

it was "descubierta por Carlos Ameghino en el eoceno inferior de Patagonia austral." In later, fuller description (Ameghino, 1895), he said nothing about its age or locality, but still later he specified that it was from the "piso Santacruceño" (Ameghino, 1898). In 1891 Ameghino believed the Santacrucean to be early Eocene in age, although he eventually (e.g., 1906) moved it up to the late Eocene. It is now universally agreed that it cannot be so old, and an almost unanimous consensus places it in the early Miocene, which is therefore the probable age of *Opisthodactylus*. Ameghino said nothing definite about the affinities of the genus, but implied a relationship by comparing it with *Phororhacos*. In 1895 he placed it in a separate family, the Opisthodactylidae.

Lambrecht (1933) accepted the family and the implied relationship, placing the genus in the "Stereornithes," equivalent to present reference to the Phororhacoidea. He gave the locality as Monte Observación, which is a Santacrucean locality in the Territory of Santa Cruz. That datum was derived from records with the type in the British Museum (Natural History).

Patterson and Kraglievich (1960, pp. 11 and 37-38) noted that *Opisthodactylus* is not a phororhacoid (or member of the "Stereornithes") but belongs in the Rheidae and

also mentioned that its age is Miocene. Authority for reference to the Rheidae was Patterson (MS.) not yet published, based on personal study of the type.

Brodkorb (1963) retained Ameghino's family Opisthodactylidae but transferred it to the Rheiformes on the authority of Patterson (Patterson and Kraglievich, 1960). However, he assigned the only known species to the "Lower Eocene (Casamayor formation)." That was presumably because of Ameghino's first (1891) reference to the "eoceno inferior," which is now believed to be the age of the Casamayor. However, Ameghino himself never considered the Casamayor (his "Notostylopéen") to be Eocene, but always as Cretaceous (Cenomanian in Ameghino, 1906). As noted above, he also later explicitly said that the specimen was from the Santacrucean; Lambrecht (from British Museum data) gave a Santacrucean locality (there is no Casamayoran within a great distance of Monte Observación); and Patterson and Kraglievich specified Miocene age.

Fisher (1967) copied Brodkorb's incorrect reference to the Casamayor Formation, lower Eocene, but reduced the supposed family to subfamily rank, Opisthodactylinae, in the Rheidae. He ascribed the giving of familial status to Brodkorb, who did support but did not initiate that status.

## NOTES ON ECOLOGY

### SIZES OF PENGUINS

THE LARGEST LIVING PENGUIN, *Aptenodytes forsteri*, the emperor penguin, reaches a maximum body length of about 115 cm. (Murphy, 1936; Stonehouse, 1967), which probably indicates a flat-footed (plantistat) standing height of around 100 cm. or a bit over 3 feet 3 inches. Many fossil penguins have bones larger than the homologous parts of the emperor penguin, and it is reasonable to believe that their stature was greater. Huxley (1859) made the fairly conservative inference from the type tarsometatarsus of *Palaeudyptes antarcticus* that this species was between 4 and 5 feet high, hence quite approximately a foot higher than any living penguin. As for numerous other groups of extinct animals, the idea of past giants here caught the popular fancy, and it soon led to gross exaggerations. Thus in an otherwise conservative volume, an all-time classic in its field, recently reprinted without revision, Evans (1899, p. 59) discarded Huxley's sweet reason without mention and unqualifiedly stated that *Palaeudyptes antarcticus* was "nearly 7 feet high."

I have elsewhere gone into this matter in considerable detail (Simpson, 1946, pp. 74-76). The whole subject need not be reviewed, but extended estimates for New Zealand fossils are

given in table 5, including data not available for the earlier estimates. The figures are based on the probability that standing heights may have been 8 to 9 times humerus length, 8 to 10 times femur length (somewhat increased from my 1946 figure), and 17 to 19 times tarsometatarsus lengths.

The table shows that the holotype of *Pachydyptes ponderosus*, the holotypes of *Palaeudyptes antarcticus* and *P. marplei*, and some other specimens referred to *Palaeudyptes* spp. were decidedly larger than the maximum for the living emperor penguin. Other specimens referred to *Palaeudyptes* spp. and the holotypes of *Archaeospheniscus lopdelli*, *A. lowei*, and *Platydyptes amiesi* may have been about the size of an emperor penguin or a bit larger. The other three New Zealand fossil species are smaller. *Pachydyptes ponderosus*, largest of all known penguins, stood approximately 150 cm. tall, perhaps 5½ feet, or about 50 per cent above an emperor penguin, and weighed about 100 kilograms or 220 pounds. In a relative way of speaking, that is gigantic for a penguin, but it still is quite small for marine endotherms, which include pinnipeds and cetaceans.

Although the sizes of fossil penguins have been so badly overstated at times, it remains true that

TABLE 5  
ESTIMATES (IN CENTIMETERS) OF STANDING HEIGHTS OF FOSSIL PENGUINS FROM NEW ZEALAND

	Humerus Length	Estimates From: Femur Length	Tarsometatarsus Length
<i>Pachydyptes ponderosus</i> , type	143-162	—	—
<i>Palaeudyptes marplei</i> , type	—	106-133	130-145
<i>Palaeudyptes antarcticus</i> , type	—	—	111-124
<i>Palaeudyptes</i> spp. indet.:			
O.M. No. C.47.23	138-155	—	—
O.M. No. C.48.73	127-143	—	115-128
O.M. No. C.47.22	—	101-126	—
D.M. No. 1449	—	98-122	—
<i>Archaeospheniscus lopdelli</i> , type	—	97-121	—
<i>Archaeospheniscus lowei</i> , type	102-115	85-106	—
<i>Platydyptes amiesi</i> , type	94-106	—	—
<i>Platydyptes novaezealandiae</i> , type	83-94	—	—
<i>Korora oliveri</i> , type	—	—	65-73
<i>Duntroonornis parvus</i> , type	—	—	54-61



the average size of all penguins known from the late Eocene and Oligocene of New Zealand is greater than the average for all Recent penguins and that the difference from Recent penguins in comparable latitudes is very striking.

Sizes of animals have often been considered in relationship to latitude and ambient temperatures. In Recent penguins the breeding grounds of the largest species, *Aptenodytes forsteri*, the emperor penguin, are in the extreme south, circumpolar around the coasts of Antarctica. In contrast, the species breeding at the northern ends of the axes of distribution are all small: *Eudyptula minor*, the blue penguin, smallest of all, in New Zealand and southern Australia; *Spheniscus mendiculus*, the Galápagos penguin, off equatorial South America; and *Spheniscus demersus*, the black-footed penguin, off southwest Africa. Those facts early suggested a correlation of size and latitude. For example, Allee and Schmidt (1951, p. 463), essentially copying Hesse's previous (1924) German version, gave a table indicating irregular but apparently significant diminution in sizes of species of penguins in the sequence of the southern limits of their distributions. This is given as an example of "a general agreement with the Bergmann Rule," which states that among related animals, the larger ones live in colder climates. (Hesse, 1924, p. 392, had been less cautious; he called this "Eine glänzende Bestätigung der Bergmannschen Regel.")

The example and its interpretation are questionable. Comparable figures are given for only 11 of the 18 species now usually recognized and the sizes and range limits do not quite agree with later and more ample data. It is also dubious whether this could be taken as exemplifying Bergmann's rule in a strict sense even to the incomplete extent that the data do follow the rule. Mayr (1956; 1963, pp. 318–323) has pointed out that this rule, and ecogeographical rules generally, are statistical generalizations, with numerous exceptions, and valid only for intraspecific variation. The correlation of size and latitude in penguins, as far as it really exists has been demonstrated for interspecific comparisons, only.<sup>1</sup>

<sup>1</sup> It is thus surprising to find that Mayr (1963, p. 320) did indicate that the rule "seems to be true" for penguins, without citation of authority. Stonehouse (1967, p. 179), who is now the best authority in this respect, indicated that the rule applies interspecifically to South American species, but that both interspecific comparisons in *Pygoscelis* and intraspecific in *P. papua* run counter to the rule.

The theoretical point is that populations within a single species share a gene pool that tends to regulate over-all proportions and physiology similarly throughout. Thus local adaptation to temperature differences is more likely to be achieved by relatively simple selection for body size than for more distinct or complex differences. In different species, however, even if more or less closely allied, alternative adaptations for heat balance in different climatic conditions are more likely to occur.

Comparatively good recent data bearing on these points have been given by Stonehouse (1967, table 1 for sizes of Recent species, fig. 6 for breeding ranges). In table 6 of the present study his data, somewhat modified, have been recast in the form of rank sequences. The breeding range is more likely to be significant than the maximum range, and both northern and southern limits have been ranked. There is in fact some correlation between size (mean weight, which in turn correlates closely with other measures of size) and latitude, although this is rather less striking than appeared from Hesse's older and less complete data. It is interesting and probably significant that the correlation for southern limits of breeding is much higher than for northern limits. This suggests that the more crucial factor is southern extension, or colder climate, and that a cold-adapted species ranges more readily into warmer regions than the reverse. This agrees with a fairly general rule that the physiologically most demanding environmental factors are those most likely to determine range limits.

The relationship is not linear, at least not in the incommensurate terms of pounds of individual weight and degrees of latitude, but it does exist. The most conspicuous deviants from the loose correlation are *Spheniscus mendiculus*, *S. humboldti*, and *Pygoscelis adeliae*. The two former are the northernmost of all living penguins, even as regards their southern limits. *Spheniscus mendiculus*, the Galápagos penguin, especially, and also to some extent *S. humboldti*, the Peruvian penguin, are smaller than penguins in their latitudes would be if the regression held good this far north. *Pygoscelis adeliae*, the adélie penguin, breeds at least as far south as the largest of Recent penguins, the emperor (*Aptenodytes forsteri*) but is very much smaller, weighing only about one-sixth as much. Its breeding range does extend considerably farther north than that

TABLE 6

RANK SEQUENCE OF RECENT SPECIES OF PENGUINS BY SIZE AND NORTHERN AND SOUTHERN LIMITS  
OF BREEDING RANGE  
(Data modified from Stonehouse, 1967)

	Order of Weight	Order of Limits of Breeding Range	
		Northern (from Equator)	Southern (from Pole)
<i>Aptenodytes forsteri</i>	1	18	2
<i>Aptenodytes patagonica</i>	2	9½	6
<i>Pygoscelis papua</i>	3	9½	4
<i>Megadyptes antipodes</i>	4	11	10½
<i>Pygoscelis adeliae</i>	5	17	1
<i>Spheniscus magellanicus</i>	6	4	8½
<i>Pygoscelis antarctica</i>	7½	16	3
<i>Eudyptes schlegeli</i>	7½	14	8½
<i>Eudyptes chrysolophus</i>	9½	12½	5
<i>Spheniscus humboldti</i>	9½	2	17
<i>Eudyptes atratus</i>	11	12½	10½
<i>Eudyptes pachyrhynchus</i>	12½	7½	14
<i>Eudyptes robustus</i>	12½	14	12
<i>Spheniscus demersus</i>	14	3	16
<i>Eudyptes crestata</i>	15	6	7
<i>Spheniscus mendiculus</i>	16	1	18
<i>Eudyptula albosignata</i>	17	7½	15
<i>Eudyptula minor</i>	18	5	13
Rank correlations with weight:		— .47	+ .71

of the emperor, and it breeds in late spring and summer, whereas the emperor extraordinarily breeds in the Antarctic winter. That behavioral difference puts the breeding of the adélie in a warmer climate even though in the same latitude.

The conclusion is that individual size is involved in the adaptation of Recent penguins to latitudinal or climatic range, but that this is only one element in such adaptation and not necessarily the dominant, perhaps in no case literally the crucial one. It is part of a complex, which includes various anatomical, physiological, and behavioral adaptations in the different species. That has been documented and some of the more crucial points have been indicated by Stonehouse (1967). His data also show that *Spheniscus humboldti* and *Pygoscelis adeliae*, especially, do indeed have noteworthy heat regulating adaptations alternative to size, the former species with adaptation for heat shedding and the latter for heat retention, as would be expected from their ranges. The situation regarding *S. mendiculus* is not so clear.

Application of the size-latitude or size-

climate regression to known fossil penguins would indicate that all the sites in which they occur were much farther south or much colder than they are today. Without exception, every site has yielded at least some fossil penguins much larger than any Recent penguins in comparable latitudes, and in multispecific collections the interspecific average is also notably larger. Neither inference, as to latitude or as to climate, can be supported. The most ardent advocates of continental drift do not suggest that southern Australia, New Zealand, and central Patagonia were all nearer the South Pole in the late Oligocene and early Miocene than the coast of Antarctica is today. In fact paleomagnetic and other evidence, although inconclusive, offers no opposition and some support to the belief that all these regions were approximately in their present positions well before the late Eocene, when penguins first appear in the record. There is also no evidence against and some evidence for latitudinal south temperate zone climates at least as warm as today and indeed probably warmer.

Stonehouse (1969) has compared the distribution of fossil penguins in Australia and New

Zealand with marine paleotemperatures and, for New Zealand, paleogeography as suggestive of warm and cool ocean currents. The evidence is not entirely clear-cut. The ages of many of the occurrences are shown in the present study not to be as precisely determined as Marples believed and Stonehouse therefore naturally accepted. The supposed early Eocene occurrence was an error, and the late Eocene occurrences are not so well dated that they can be placed at the Kaiatan-Runangan paleotemperature high, up to 22°C., rather than during or after the precipitous Runangan-Whaingaroan drop, down to 12°C. Those remarks apply to the largest New Zealand penguins, including the largest known from anywhere although closely approached by the largest Seymour Island fossils. Well-dated penguins, smaller than the largest of the late Eocene but still in the large-size group, occur in the Duntroonian, with estimated paleotemperatures rising from 12°C. to about 18°C. Referred to the still later Waitakian, on good authority but unstated evidence, is one large penguin, *Platydyptes amiesi*, also in the large group but smaller than the largest late Eocene and Duntroonian specimens. The indicated paleotemperature is 18°C. to 19°C.

If the paleotemperatures are taken at face value, the hard evidence thus indicates that the largest known New Zealand penguins were buried under waters with a possible minimum of 12°C. and possible maximum of 22°C., and that for other large but not the largest specimens a fairly firm figure of about 18°C. can be given. Further uncertainty arises from the fact that the paleotemperatures were not derived from materials directly associated with the fossil penguins. There is thus a distinct possibility that there were local or seasonal conditions of cooler water (and land temperatures) when penguins actually occurred alive at the fossil localities. Individuals may also have been straying or migrating outside of their breeding ranges, and that generally takes them northward and to warmer regions.

In spite of reservations and uncertainties, it does seem clear that the large New Zealand pre-Pliocene penguins were living in latitudes, climates, and water temperatures occupied now only by much smaller species. Thus their large size cannot be interpreted as primarily adaptive to cold climates or waters.

That does not preclude the possibility, or

indeed the inevitability, of involvement of size in heat regulation among early penguins. It may be significant that the three main Western Hemisphere localities for fossil penguins, of at least approximately the same age (latest Oligocene or early Miocene) and, roughly on a north-south axis, do show some gradation in sizes of known species. The species from Trelew, Chubut, Argentina, latitude 43°13'S., are all medium to small in size. For the most part the same species recur at San Julián, Santa Cruz, Argentina, latitude 49°17'S., but the one "giant" penguin known from Patagonia, *Arthropytes grandis*, represented by only one known specimen, perhaps a stray, was found there. Most of the Seymour Island specimens, at 64°15'S., are "giants" and the interspecific average is much larger than in Patagonia.

In addition to specializations functionally correlated with size itself, the specializations of the large early penguins of New Zealand must have included unknown physiological and behavioral adaptations for heat regulation different in basis from those of Recent penguins.

#### BASIC ADAPTATIONS

Penguins have long been associated in popular opinion with the Antarctic and supposed to be basically cold climate birds. Their Antarctic origin was, indeed, taken almost for granted in the scientific literature as well. That was largely due to the many studies, ranging from esoterically technical to sheerly fantastic, of adélie penguins and also innumerable jokes and cartoons, almost all also based on that species. In fact adélies are only one species among (probably) eighteen, and one of the least average or typical.

The preceding discussion of size and latitude has given some of the evidence that penguins are not basically cold-adapted, certainly, at least, not to the degree suggested by Antarctic origin. Although I think it would be unjustified to interpret the environments of any known fossil penguins as tropical to subtropical, they were evidently far within the extremes of Recent climatic ranges and probably in cool to warm temperate. Among the 18 Recent species, three breed within the tropics, two of those also ranging into the warm temperate zone. Only two breed within the Antarctic zone, and both extend into the temperate zone, one (emperor) barely and the other (adélie) widely. Thus 13

species breed exclusively in the temperate zone, 17 occur in that zone, and only one—a *tropical* species!—does not occur in the temperate zone. The greatest number of species and probably of individuals under earlier conditions are in cool temperate waters. In warmer parts of their range, penguins tend to occur in regions with water that is relatively cool for the given latitude, notably in the Peruvian current in the western South American tropics and subtropics and in the Benguela current in tropical and subtropical southwestern Africa.

Insofar as the family as a whole can be said to have a basic climatic adaptation, that is evidently to the temperate zone. It also is highly probable that penguins originated in that zone, probably at a time when it was milder and more equable over-all than at present. Penetration of certain species into still warmer waters and climates has apparently been possible by specific adaptation to only moderate increase in temperature following cool currents. A few species, only one in an extreme sense, have become increasingly and specifically cold adapted. Stonehouse (1967) has produced detailed and convincing evidence that each Recent species tolerates a fairly rigid, limited temperature range, and that among them extension of range is determined by deviation from an optimum mean temperature. Many of the geographic ranges are quite narrow. Broader geographic ranges occur where currents keep temperatures within limits along extensive coasts, for example the Peruvian current along Peru and Chile, or among species that stay within similar temperatures by seasonal migration, for example Magellanic penguins along Argentina and Uruguay.

Penguins are now marine, and probably always have been. All known fossil penguins are found in marine strata, always associated with marine invertebrates and usually with marine cetaceans. In origin they are almost certainly older than pinnipeds and probably older than cetaceans. They are the smallest marine endotherms (or homeotherms), even taking the "giant" extinct forms into account. Limitation of size is not likely to have arisen from cetacean or pinniped competition if, as seems to be the case, they are older than either group.

Although beaks of penguins vary rather markedly in shape, correlation with food habits is not clear. In any case, almost nothing is known

about the beaks of any fossil penguins, and there is no way to ascribe particular food habits to them. Probably like Recent penguins, they were rather indiscriminate feeders on plankton and nekton. Recent species take mainly euphausiids and other krill, squids, and fishes (Stonehouse, 1967, and his citations).

The most obvious adaptations of penguins are for locomotion, and these affect most of their osteology and musculature. They fly under water with great speed and agility, moving to feeding areas by this form of swimming and taking food by active submarine pursuit, not by diving. The feet serve to some extent as rudders, but not at all as propellers when in the water. Like the pinnipeds, but to notably less degree, they have lost really effective land locomotion. Retention of a measure of clumsy and slow land locomotion can be related to the necessity for laying and brooding eggs on land. Pinnipeds breed on land, but require less mobility there, and cetaceans require and have none. Some penguins can toboggan on snow or ice with considerable speed, but for the most part land locomotion is relatively inefficient. Also involved is the vertical posture, which is related to swimming stance and in some forms to heat exchange and incubation. As previously noted, late Eocene penguins demonstrate that the related basic osteological specializations of the limbs were then already essentially complete, but they add little beyond a minimal date for that acquisition.

Among the few other birds that fly under water and take their food in that manner are the diving petrels (*Pelecanoides* spp.). They also fly in the air, going to and from feeding grounds in that way. I earlier suggested (1946, pp. 86 and following) that the penguin ancestry probably passed through a similar stage. Perfect adaptation for underwater flight is probably incompatible with retention of aerial flight, and a crucial threshold would occur when selection for improved underwater performance outweighed that for retention of aerial flight. Stonehouse (1969) has suggested, and I agree, that weight (size) may be a crucial factor. Increasing weight facilitates sustained diving but over about one kilogram it becomes inconsistent with combined aerial and submarine flying. I would add that increase in size is one of the commonest adaptive trends, when not countered by other factors, and has numerous general adaptive advantages in both intra- and inter-specific selection. (See, for

example, Rensch, 1960, pp. 206–218.) It is noteworthy that diving petrels are all much smaller than even the smallest known penguins. The shortest body length noted by Stonehouse (1967, table I) for a Recent penguin, *Eudyptula minor* (no known fossil penguin is smaller), is 39 cm., and the largest body length for a diving petrel noted by Murphy (1936, p. 773) is 23.9 cm. The contrast in weight would be even greater.

The trend for increased size set in early and had reached a culmination as far as now known, already in the late Eocene. For reasons quite obscure, increase in size was checked, and none of the largest mid-Cenozoic forms survived. It is possible that the largest penguins did finally come into unsuccessful competition with the next larger groups of marine endotherms, among pinnipeds and cetaceans.

## SUMMARY

THE FIRST FOSSIL PENGUIN to be made known, *Palaeudyptes antarcticus*, was described from New Zealand by Thomas Henry Huxley in 1859. The many other pre-Pliocene penguins found in New Zealand after that date were monographed by Professor B. J. Marples in 1952. They are here systematically reviewed, with references to previous illustrations and substantive publications, and new data and illustrations are provided.

Pre-Pliocene penguins have been found in New Zealand at ten localities or collecting areas. The generically unidentifiable specimen from Gore Bay, previously considered to be from the early Eocene and the oldest known penguin, is in fact Oligocene or early Miocene in age. The oldest known penguins are *Pachydyptes ponderosus*, *Palaeudyptes marplei*, and *Palaeudyptes* sp. from the late Eocene. Other known New Zealand penguins range through the Oligocene and perhaps early Miocene. Within the range late Eocene–early Miocene many specimens are of undeterminable precise age. The reported great range, Kaiatan–Waitakian for the single species *Palaeudyptes antarcticus* is not substantiated.

The known pre-Pliocene New Zealand penguins are classified in six genera, *Palaeudyptes*, *Pachydyptes*, *Platydyptes*, *Archaeospheniscus*, *Duntronornis*, and *Korora*, with nine named species, of which *?Platydyptes marplei* is here new. Among fairly numerous specimens referred to *Palae-*

*udyptes*, only the two specific holotypes are considered definitely identifiable to species on the basis of present knowledge.

It is unlikely that any of the known genera were ancestral to Recent penguins. Previous attempts at subfamily classification are unsatisfactory, and subfamilies are abandoned here. The New Zealand forms show some, but limited, resemblances to the penguin faunas of each of the other three regions where fossils of this family have been found; southern Australia, Seymour Island, and Argentine Patagonia.

The largest fossil penguin, *Pachydyptes ponderosus*, was probably at least 50 per cent taller than the largest Recent penguin and probably weighed about 100 kilograms. In general, known fossil penguins average considerably larger than Recent penguins in the same latitudes. Recent penguins tend to be larger in higher latitudes or colder environments, but there are adaptations to climate other than size and these may be more crucial. Eocene–Miocene penguins did not follow the size–temperature regression of Recent penguins and must have had dissimilar heat regulation. However, all the basic locomotory adaptations of the Spheniscidae were virtually complete in the late Eocene, and the origin of the family must have been much earlier. No earlier, possibly relevant fossils occur in the extremely poor fossil record of birds in the Southern Hemisphere.

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