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FOSSIL PENGUINS FROM THE MID-TERTIARY OF SEYMOUR ISLAND

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INTRODUCTION

FOSSIL penguins have been obtained in four different localities, Patagonia, New Zealand, Seymour Island, and South Australia. The Australian specimen consists of a single humerus, but a considerable number and variety of bones have been found in the other localities. The first specimens from Seymour Island were collected by the Swedish Southpolar Expedition in 1901–3 and were described by Wiman (1905). The collection included some thirty bones, all of which were found weathered out of the rock and so none can certainly be associated. Most of the specimens show considerable cracking and weathering due to frost action. No other bones were collected on Seymour Island until 1946, when the present collection was made by members of the Falkland Islands Dependencies Survey. It consists of some forty-five specimens, but many of these are mere fragments and only about twenty are complete enough to be of any use morphologically.

For comparison with these specimens a considerable number of other penguin bones were available, important among which were casts of Wiman's specimens in addition to his excellent photographs of the originals. All the New Zealand specimens were either available or had recently been examined, together with a cast of the Australian humerus and a considerable collection of Recent skeletal material. A number of specimens from Patagonia had also been recently examined in London and New York.

The following field notes on the specimens and the actual localities in which he collected them have been provided by Mr. W. N. Croft.

"The fossil penguin bones described below were collected between 28 August and 11 September 1946, during a visit to Seymour Island by dog-sledge in company with Lt. T. P. O'Sullivan, R.N.V.R.

"Nearly all the bones were obtained from the original Swedish locality No. 11. Bones were also obtained from a few other localities (see text-fig. 1) which make it probable that the penguin remains occur at more than one horizon in the Tertiary strata. At one of these localities (D.520) a bone was found *in situ* for the first time.

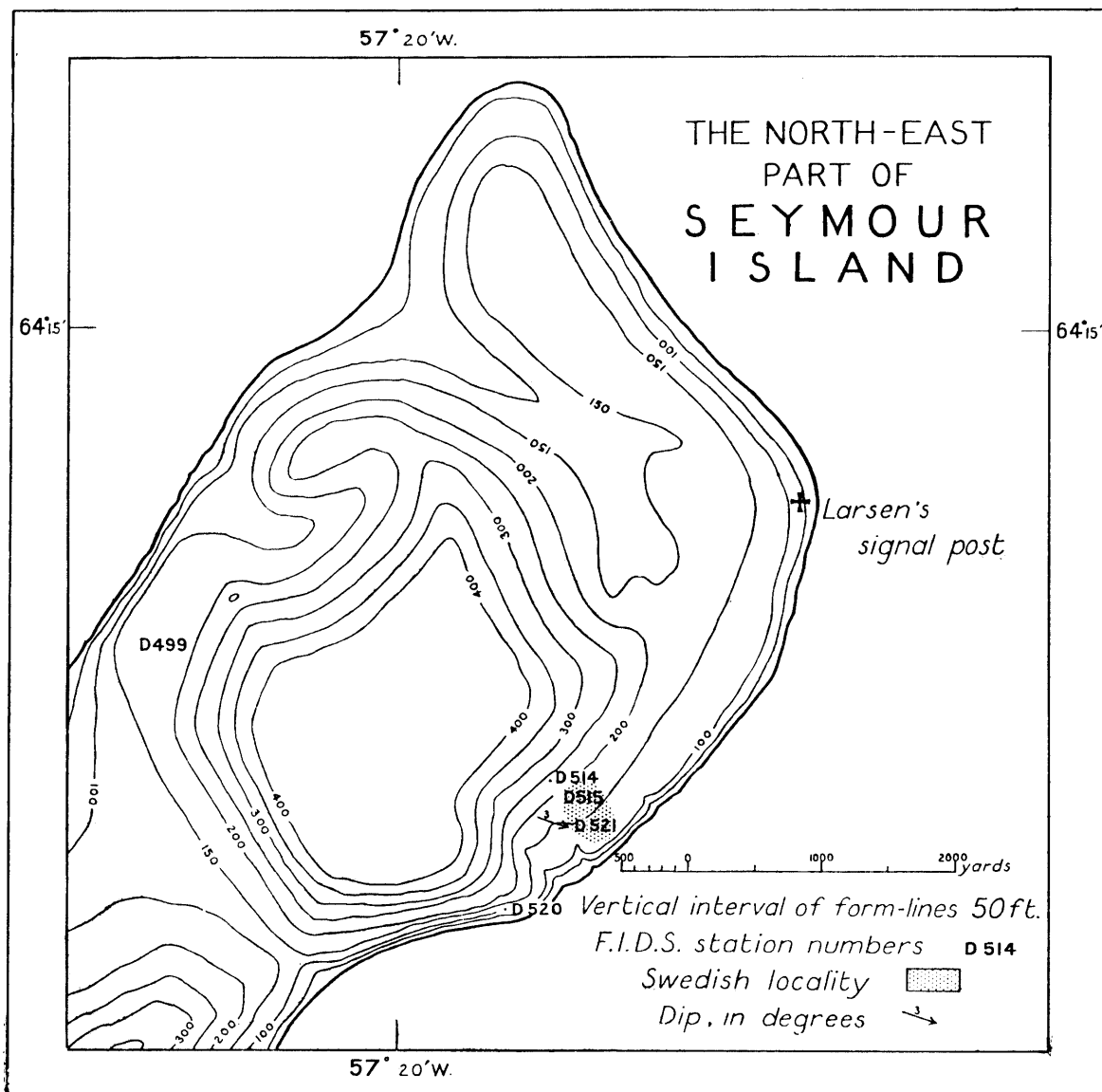


FIGURE 1.

"The collections of invertebrate fossils made on the same visit have not yet been studied, and there is nothing to add to the age-determination of the strata made by Wilckens, who concluded that they are Upper Oligocene or Lower Miocene. In a recent review of the evidence from Patagonia and Graham Land Simpson (1946: 36) reached the conclusion that the Seymour Island penguins are Miocene, probably Early Miocene, in age.

"Locality D.515, D.521 (Swedish loc. 11). On the '150 ft.' terrace-like coastal feature, nearly 3,000 yards south-south-west of Larsen's signal post.

"The locality and the mode of occurrence of the fossil bones have been described in detail by Andersson (in Wiman, 1905, 1-3), and many of his observations were confirmed.

"The locality area lies between two stream-cut valleys where the terrace-like feature is about 500 yds. wide. Near the centre of the area there is a conspicuous erratic, 6 feet in diameter, composed of a dark foliated rock (see text-fig. 2).

"The almost horizontally bedded soft sandstones forming the feature are well exposed in the sea cliff. They are grey, laminated and regularly bedded. Fossils were not seen, and hard sandstone bands are not



FIGURE 2. The main fossil penguin locality (D.515) on the "150-ft." coastal feature, facing west. The large erratic is seen at the centre of the illustration.

developed. The feature above rises gently away from the sea cliffs and is, in the main, a dip slope. Inland from the large erratic, over an area about 100 yards square, are numerous irregularly-shaped masses of brown-weathering, medium to coarse, grey-green sandstone, up to 2 ft. high, but usually only 1 ft. They appear to be residual masses of a once continuous band, though they may have been formed as lenticles on one horizon. A few rounded igneous pebbles, up to 3 in. in diameter, but usually about $1\frac{1}{2}$ in., are present in the sandstone. Some of the sandstone masses contain a few thin layers crowded with a small species of *Cerithium*. *Lingula* and a few poorly preserved lamellibranchs were also found. An exposure of the same type of sandstone, similarly weathered, occurs over an area fifty yards square in the small valley a few hundred yards north-east of the main locality and about 200 yards from the sea. At this exposure, however, only a few fragments of bone were seen between the sandstone masses. In neither place did any of the residual sandstone masses attain even half the height (2 m.) given by Andersson in his fig. 1.

"In the main locality, all bones and fragments seen in several hours' search were collected, and particular care was taken to keep together those that were scattered over an area of a few square yards; for, as Andersson has pointed out, the frost-shattered fragments become dispersed by solifluxion. Many of the specimens came from the neighbourhood of the sandstone masses, but a number were collected in the area between the large erratic and the sea cliffs. In part of the latter area, at an estimated ten feet or less below the level of the hard sandstone, a friable glauconitic sandstone is exposed, and obviously weathered out of this were very numerous brachiopods (*Bouchardia*). Pieces of fossil bone, a few echinoids, fish remains, and *Lingula*, also recorded by Andersson from this locality, were found in the same spot, but not certainly *in situ*. The indurated sandstone adhering to some of these specimens, including the brachiopods, appears to be identical with that attached to a few of the penguin bones.

"Several factors led Andersson to the conclusion that the bones were derived from the weathering of the sandstone masses. It may, however, be doubted whether the penguin bones, which seem to be readily split up by frost, would survive the weathering of the hard sandstones. Bones have not been seen *in situ* in this sandstone and the weathering of a considerable amount of the rock would seem to be required to provide all the bones that have been collected from the locality. Also, it is by no means certain that the majority of the associated pebbles may not be erratics, for undoubted erratics are widespread on the coastal feature and elsewhere on the island, including the high plateau. It therefore seems more probable that the majority of the penguin bones have been derived from the weathering of the friable sandstones underlying the hard bands; or from poorly consolidated sediments lying between the sandstone masses, if these were formed as discontinuous lenticles.

"*Locality D.514.* Hillside immediately north-west of the last locality.

"At about 100 feet above the level of the sandstone masses at locality D.515 there is an identical sandstone which also contains numerous specimens of a small *Cerithium*. On the hillside fifty feet below this band a single penguin bone was found, which has been identified as *Anthropornis*. This occurrence suggests that penguin bones are also present at a higher horizon.

"*Locality D.520.* The side of a steep gully, 1000 yards south-west of D.515, and about 100 yards from the sea shore, at 130 feet above mean sea level.

"A piece of fossil bone, probably *Delphinornis* (see page 11), was obtained *in situ* from a hard shelly conglomerate, up to 2 ft. thick, in which some pebbles reach a diameter of 4 in. This shelly conglomerate, which is often developed as lenses in the Tertiary strata of the island, differs from the sandstone with *Lingula* and *Cerithium* of loc. D.515. If no fault intervenes, the locality D.520 is probably about 100 feet lower in the succession than locality D.515.

"*Locality D.499.* On the north-west side of the island, north-east of the Cross Valley.

"Two fossil penguin bones, found by Lt. O'Sullivan, were picked off the surface of the irregular coastal feature corresponding to the '150 foot' feature on the south-east side of the island. There are thin patches of drift with igneous erratics on the feature and the bones may have been brought in by ice, but it is more probable that they came from a horizon, or horizons, in the Tertiary beds on this side of the island. The coastal feature was searched for about a mile northwards from this locality, without yielding more material."

SPECIES

OWING to the fact that all the bones are found scattered individually on the surface of the ground after weathering out of the matrix, the task of separating them into species is a very difficult one. Wiman erected six genera and species, five of which were based on tarsometatarsi, all more or less fragmentary, and one upon a sacrum. The other bones he divided into size-groups which provisionally must be regarded as belonging to the type specimens of corresponding size, though he did not himself give these names to them.

Wiman's classification was discussed by Simpson (1946). He considered that three of Wiman's species, *Pachypteryx grandis* and *Anthropornis nordenskjoldi*, both based upon imperfect tarsometatarsi, and *Orthopteryx gigas* based upon a sacrum, all probably belong to the genus *Anthropornis* and possibly all to *Anthropornis nordenskjoldi*. They are all large, and a number of other large bones can be associated with them with a fair degree of certainty. Wiman's Group 2 contains a large sacrum, to which no name was given, and it possibly belongs here also. *Eosphaeniscus gunnari* is based upon an eroded tarsometatarsus but one whose size and proportions support the distinctness of the species. Several bones placed in Group 5 are probably associated with it. Group 6 contains several fragments, but no name was given as they showed no characteristic features. The remaining species, *Delphinornis larsenii* and *Ichthyopteryx gracilis* are based upon small imperfect tarsometatarsi and no small bones which may belong to them are known. His conclusion is therefore that in Wiman's collection there appear to be represented four genera, three of them poorly characterised, the genus *Anthropornis* probably being represented by a number of well-preserved bones in addition to the imperfect tarsometatarsus which is the type. The following table shows the extent of Wiman's collection. Few if any of the bones are complete.

Group No.

- | | | |
|--|---|---------------------------------|
| <ol style="list-style-type: none"> 1. <i>Orthopteryx gigas</i>. Sacrum. 2. No name. Fragment of sacrum. 3. <i>Anthropornis nordenskjoldi</i>. Tarsometatarsus, Coracoid, Humerus, Ulna, Carpometacarpus, Femur, Tibiotarsus, Sacrum. 4. <i>Pachypteryx grandis</i>. Tarsometatarsus, Coracoid, Radius, Carpometacarpus, Tibiotarsus. | } | probably
<i>Anthropornis</i> |
|--|---|---------------------------------|

5. *Eosphaeniscus gunnari*. Tarsometatarsus, Coracoid, Humerus, Ulna, Femur, Tibiotarsus, Sacrum.
6. No name. Fragments of Humerus, Coracoid, Scapula, Femur.
7. *Delphinornis larsenii*. Tarsometatarsus.
8. *Ichthyopteryx gracilis*. Fragment of Tarsometatarsus.

The majority of specimens selected as types of species of fossil penguins have been tarsometatarsi. This applies apparently to all but four of the Patagonian species described by Ameghino, and to one of the New Zealand species. Tarsometatarsi have not proved to be ideal bones for use in this way and it is difficult to supplement the evidence provided by the tarsometatarsus by reference to other parts of the skeleton, as in so few cases does more than one bone certainly belong to the same individual. Simpson stated that only eight specimens with two or more associated bones were known, and though, since he wrote, ten others have been discovered in New Zealand, the number is still relatively small.

In the present paper Simpson's conclusions set out above are accepted. A tarsometatarsus is here described which seems to belong to Wiman's Group 6 which he did not name as it contained only fragments. It is here named *Notodyptes wimani* gen. et sp. nov. It seems best also to assume, tentatively, as was done by Simpson, the association of the other bones of appropriate size with the type tarsometatarsi, since the discovery of undoubtedly associated bones seems unlikely. There would therefore be five genera and species from this locality, with a possible sub-division of *Eosphaeniscus* into two species, suggested but not warranted by the material at present available.

When the fossil penguins from the three main localities, Patagonia, Seymour Island and New Zealand, are compared with one another and with Recent species, it is at once apparent that those from Seymour Island and New Zealand resemble one another closely. Those from Patagonia are more similar to the Recent species, though in some respects they are intermediate between them and the other group. The single specimen from Australia resembles those from New Zealand, and it is possible that one or two from Patagonia are also of this type, though no critical comparison has so far been made.

In a recent study of all the New Zealand species (Marples, 1952) the conclusion was reached that they were in some respects primitive, and it was proposed to place them, together with the Seymour Island species, in a subfamily, the Palaeodyptinae. Simpson grouped the Seymour Island species, together with one Patagonian and one New Zealand species, into the Anthropornithinae and divided the rest of the Patagonian species between two other subfamilies. All Recent species are included in the Spheniscinae. Before considering the Seymour Island species in detail it will be convenient to summarise the characters of the Palaeodyptinae as compared with the Spheniscinae.

The humerus has a somewhat square-ended appearance in dorsal view owing to the fact that the articular surface of the head forms a smaller proportion of the proximal end and is rounded instead of running up into a peak towards the postaxial side. The tricipital fossa is simple and there is a great thickness of bone between it and the articular surface. The area of insertion of *pectoralis secundus* primitively runs down the centre of the dorsal surface of the shaft but sometimes it is oblique, as in all Recent species. The shaft is parallel-sided or narrower distally, instead of being narrow proximally. The distal end is less flattened, so that instead of an ulnar condyle immediately postaxial to the radial one there is a ventrally-situated condyle, on the dorsal side of which is a flat shelf. The proximal end of the ulna articulates with both the shelf and the condyle. Primitively the shelf is as wide or wider than the condyle, but is narrower in more advanced forms and absent in Recent ones.

Apart from the humerus the coracoid is the most characteristic bone. In Recent species it is straight and relatively narrow, and the outline of the base seen in ventral view is concave. In the Palaeodyptinae the coracoid is relatively much broader and the outline of the base seen in ventral view is convex. It is difficult to see how the one could have been transformed into the other, and it seems possible that the Palaeodyptinae became extinct and are not ancestral to the Recent penguins.

The tarsometatarsus has been much used in classification, the points stressed being its proportions, the degree of fusion of the metatarsi, and the size of the intermetatarsal vacuities. Simpson maintained that the tarsometatarsus of the fossil penguin was more like that of a flying bird than is that of a Recent penguin, since it was more elongated and the elements were more strongly fused. Lowe (1933) put forward precisely the opposite opinion on the same data. Tarsometatarsi seem on the whole less useful for purposes of classification than do humeri.

SYSTEMATIC DESCRIPTIONS

1. *Anthropornis nordenskjoldi* Wiman.

(Plate I, figs. 1-4; Plate II, figs. 1, 5, 7-9)

1905 *Anthropornis nordenskjoldi* Wiman, p. 8, pl. 2, figs. 3, 3 a.**Type:** Left tarsometatarsus, in Uppsala.

Included here in this species are not only the bones placed by Wiman in Group 3, but also his Groups 1, 2 and 4, *Orthopteryx gigas* and *Pachypteryx grandis* being regarded as synonyms of *Anthropornis nordenskjoldi*. The following specimens are included in the present collection.

Humerus, 1, and 2 fragments
 Ulna, 1, and 2 fragments
 Radii, 2
 Carpals, 2
 Carpometacarpus, 1
 Phalanges, 2

Coracoid, 2 fragments
 Sternum, 1 fragment
 Femur, 1, and 2 fragments
 Tibiotarsus, 1
 Fibula, 1
 Tarsometatarsus, 1

Humerus. Wiman's material includes one almost complete humerus and the rather eroded distal two-thirds of another slightly smaller one. The bone is an elongated S-shape with only a very slight prominence on the preaxial border at the proximal boundary of the origin of *brachialis internus*, and the shaft is slightly wider proximally. The head is very square and massive. The insertion of *pectoralis secundus* is only slightly inclined in the postaxial direction and is separated by a large gap from that of *latissimus dorsi*. The tricipital fossa is simple. The angle between a tangent to the distal condyles and the long axis of the shaft is acute, probably more so than in any other known species.

The humerus (A.3338)* in the present collection is very much shattered but is somewhat larger than Wiman's specimen. The distal end is rather more complete and shows that the flat shelf dorsal to the ulnar condyle is as broad as, if not broader than, the condyle. The two fragments do not provide any new information.

Ulna. Wiman described two ulnae, both complete, one of which he placed in Group 3. The latter differs from the ulna of Recent species in having a semi-circular, instead of an angled, tab-like projection in the postaxial border where the tendon of *triceps* is inserted. A similar projection, though more square than semi-circular in outline, is found in *Palaeudyptes* from New Zealand.

The present collection contains one almost complete ulna (A.3354),* a proximal and a distal end (both considerably larger), and a fragment of the middle of a bone. The collection of bones from locality D.515.17, which includes the complete ulna, also includes a radius, two carpals, a carpometacarpus, and two phalanges. It is tempting to assemble these into a wing (Pl. 1, fig. 2), but it must be remembered that they were all found separately and there is no certainty as to their being associated. They are discussed more fully below. The ulna is similar to Wiman's specimen, though the postaxial tab has been broken off. The position of the foramen through its distal side is, however, visible. The proximal end is more thickened dorsi-ventrally than in the Recent ulna, since it articulates with the flat shelf as well as with the condyle on the humerus.

Radius. The only radius in Wiman's collection is the distal two-thirds of a bone which he placed in his Group 4 corresponding to *Pachypteryx*. The present collection contains two almost perfect radii. One (Plate 1, fig. 1) is remarkable for its great length, but assuming that it bore the same relation to its humerus as do the radii of New Zealand fossil penguins, namely 71% of the length of the humerus, its corresponding humerus was 166 mm. long. (This percentage is the mean value for four individuals belonging to three genera.) Wiman's humerus No. 3 is estimated at 160 mm. and the humerus (A.3338) in the present collection at more than 167 mm. This large radius is attributable therefore to *Anthropornis*. It is a thick bone and is especially expanded dorso-ventrally at the proximal end where the oblique grooves accommodating the nerves and blood vessels are unusually deep. The oblique groove on the dorsal surface of the distal end, occupied by the tendon of *extensor metacarpi radialis brevis* of Watson, not by blood vessels as stated by Wiman, is very slight. An important feature of the penguin radius is the outline of the preaxial border near the proximal end. Here is inserted *brachialis internus*, and in all Recent penguins there is a semi-circular notch. The same condition is found in some of the species of fossil penguins from New Zealand. In both of the present specimens, in other New Zealand species, and in *Palaeospheniscus* according to Simpson, this

* Registered numbers of specimens in the Geol. Dept., Brit. Mus. (Nat. Hist.).

area of insertion is flat or very slightly concave, and makes an obtuse angle with the preaxial border of the bone.

The other radius (Plate 1, fig. 2) in the present collection is smaller and is very similar to Wiman's Group 4, except that the swelling towards the distal end of the postaxial border is more distally placed. In details it resembles the larger specimen. Applying the same size relationships to it, it should correspond to a humerus of length about 142 mm., which is smaller than Wiman's complete Group 3 humerus, but corresponds approximately to his other specimen. The difference in length of these two radii is 17 mm., roughly 15% of their mean length. As a result of these considerations it is concluded that both radii belong to *Anthropornis*.

Carpals. The present collection contains two carpal bones (Plate 1, fig. 2), one radial and the other ulnar. Previously only one carpal of a fossil penguin seems to have been recorded—a radial from New Zealand belonging to *Palaeudyptes antarcticus*. The radial carpal (A.3351) is wedge-shaped, being thin on the preaxial side. It is roughly rectangular in plan, with the proximal and distal sides concave to articulate with the radius and the carpometacarpus. The ventral surface also is concave, and the bone is generally smoother and simpler in outline than the Recent examples with which it was compared, but resembles that of *Palaeudyptes*.

The ulnar carpal of Recent species is relatively large and triangular in shape, with the apex fitting between the ulna and the carpometacarpus. In the present specimen (A.3352) the expanded triangular portion is broken off, though the part which remains suggests that it was perhaps less expanded. A groove to articulate with the carpometacarpus and a hollow for the ulna are present much as in Recent specimens.

Carpometacarpus. Wiman described one almost complete carpometacarpus and one very fragmentary one. He pointed out that metacarpal I is less fused with II than in Recent specimens; there is a notch in the preaxial border at its distal end; metacarpals II and III are more fused, being attached to one another for most of their length; and III does not project distally beyond II as it does in Recent species.

The present collection contains a well-preserved carpometacarpus (Plate 1, fig. 2) slightly longer than Wiman's specimens. It has a similar notch in the preaxial border, which seems to be due to the breaking off of a free tip to metacarpal I. In one specimen of *Palaeudyptes* from New Zealand the appearance of the end of metacarpal I in this notch suggests that a rudimentary phalanx has been present and it seems not unlikely that there may have been some variation in this region in Tertiary penguins. The degree of fusion of metacarpals I and II varies considerably between different individuals of Recent species. This is also true of the fusion of metacarpals II and III. In the present specimen these are free for most of their length, and the free portion of III is missing. In Recent species they are free as they are in some of the New Zealand fossils, while in others they are partially fused. As far as can be judged from the cast they were free in Wiman's fragmentary carpometacarpus. It is a noteworthy point about the present specimen that metacarpal III projects distally beyond II as it does in Recent species.

Phalanges. Simpson describes two proximal phalanges of the second digit attributed to *Palaeospheniscus patagonicus*, while one complete and one fragmentary phalanx are known from New Zealand, attributed to *Palaeudyptes antarcticus*. These appear to be the only phalanges of the wing recorded. The present collection contains one proximal phalanx (A.3349). It also contains a distal phalanx (A.3348) which seems to be the only known example of this bone. The proximal phalanx is relatively thick at the proximal end and has slightly convex margins. Simpson's specimens were similar and he said that they differed from the Recent bone, which has straight margins. Some Recent species do, however, have convex margins, as for example *Megadyptes antipodes* and *Spheniscus humboldti*. The complete *Palaeudyptes* bone is thin dorsi-ventrally, the preaxial margin is convex, and the postaxial one straight or even concave. Its length is 57.0% of that of its carpometacarpus, the corresponding value for six Recent species belonging to different genera ranging from 63.5% to 71.0%. The present specimen is 55.6% of the length of the carpometacarpus found near it, so it seems possible that the two are really associated. The distal phalanx shows no points of interest. Its length, allowing for a small portion broken off at the tip, is 39 mm., and its preaxio-postaxial width at the proximal end is 11 mm. This length is 33% of that of the carpometacarpus and is considerably less than in Recent species, where the value ranges from 50% to 55%.

Wing bones. In an attempt to decide the likelihood of the wing bones from locality D.515.17 (only a few square yards in area), being actually associated, the lengths of the distal parts were expressed as percentages of the length of the ulna and compared with the corresponding figures for six Recent individuals taken at random. The table below gives the figures and it will be seen that the ratio of the fossil bones is

similar to the proportions of the Recent wings except for the greater relative length of the carpometacarpus. The mean value for the carpometacarpus expressed as a percentage of the ulna for three individuals of *Palaeudyptes antarcticus* is 86.7%, and for one individual of *Platydyptes novaezealandiae*, another New Zealand Oligocene species, is 70.9%. These figures suggest that while the phalanges might belong to the ulna, the carpometacarpus is probably too large to belong to the same individual.

Lengths of distal wing bones expressed as % of the Ulna

						Carpometacarpus	Proximal Phalanx	Distal Phalanx
<i>Anthropornis</i> , bones numbered D.515.17	92.6	51.5	41.0
<i>Aptenodytes patagonicus</i>	81.1	57.7	42.3
<i>Pygoscelis papua</i>	83.9	58.9	42.8
<i>Megadyptes antipodes</i>	77.5	51.7	41.3
<i>Spheniscus humboldti</i>	82.7	57.7	44.2
<i>Eudyptes crestatus</i>	80.4	56.1	41.4
<i>Eudyptula minor</i>	81.1	51.5	40.6

Coracoid. Wiman's collection includes one almost complete coracoid, lacking only a small part of the base and the anterior extremity. It is one of only two fossil penguin coracoids in which the pre-coracoid region, enclosing the fenestra, is preserved, though it seems likely that an enclosed fenestra was usually present. There is also an eroded coracoid, lacking both ends, which Wiman placed in Group 4.

Two fragments of a coracoid in the present collection seem to correspond in size with Wiman's Group 3. One is the greater part of a base (Plate 1, fig. 3) and the other a very well preserved anterior end (Plate 1, fig. 4) including the *fossa scapularis*. They are both from the same locality, are parts of a left coracoid and resemble one another in surface texture, so it is possible that they are parts of the same bone. When compared with the cast from Wiman's Group 3 coracoid they show a number of differences and so support his separation of the groups of large bones into several genera. The tip of the hooked anterior end is missing in Wiman's specimen, but it seems to have a well marked hollow for articulation with the clavicle which is altogether absent in the present specimen. The base of the hook is much thinner dorso-ventrally in the present specimen and is narrowed to quite an acute edge on the median side instead of being broadly rounded. The details of the base are not visible on the cast, but as seen in ventral view the median corner seems less acute and the lateral part much more convex than in the present specimen. The shape of the groove in the sternum which received the coracoid can be made out from its impression on that bone. The dorsal side of the groove was rounded. Its ventral margin was a sharp ridge, absent altogether near the middle of the groove but rising in a curve towards the ends. A similar situation is seen in the New Zealand fossil coracoids. All Seymour Island and New Zealand fossil coracoids have relatively broad bases which are convex in ventral view, thus differing from all Recent ones which are relatively narrow and concave in ventral view.

The other two fragments in the present collection (A.3339, A.3362) correspond very closely with the fragments Wiman placed in Group 4. One consists of the central part of the bone, lacking the anterior end of the hook and both ends of the base, while the other is a fragmentary basal half. All these, including Wiman's coracoid from Group 4, seem probably too small to belong to *Anthropornis* and are possibly *Eosphaeniscus*. The difference between the length of the present bone and that of *Anthropornis* from the base to the anterior margin of the *fossa scapularis* is 20% of the mean of these two lengths. The precoracoid region is missing, but to judge from its broken attachments it resembled that of *Anthropornis*, as apparently did that of Wiman's Group 4. The fragmentary basal half, however, shows none, or at most the slightest trace, of the attachment of the precoracoid to the main part of the bone on the basal side of the fenestra.

Sternum. The present collection contains a small fragment of a sternum (A.3332), interesting not only because of the extreme rarity of sternal remains of fossil penguins but also in view of the difference between the base of the coracoid in certain of the fossil and Recent forms. Simpson describes a fragment of the lateral edge of a sternum of *Paraptenodytes antarcticus* and mentions three specimens described by Moreno and Mercerat which seemed to resemble the sternum of Recent penguins. From New Zealand comes the well-preserved anterior region of a sternum of *Platydyptes novaezealandiae* and also a fragment belonging to *Palaeudyptes antarcticus*. The present fragment, which only measures some 25 mm. in each direction,

contains the region in the middle line where the two coracoid grooves end, about 20 mm. of one groove and a fragment of the base of the keel. Many Recent species have a plate-like anterior process projecting forward at the anterior end of the base of the keel. In *Platydyptes*, and apparently in the present specimen, this process was broad and stout at its base instead of being laterally compressed. In Recent sterna the anterior ends of the coracoid groove run transversely and die away near the middle line. Their posterior margins also die away and there is at the anterior end of the dorsal surface of the sternum a roughened area where the ligaments originate which attach the coracoids. In *Platydyptes* conditions are different in that the coracoid grooves run obliquely forward to terminate on the posterior surface of the anterior process, while their posterior margins do not die away but increase in height as they approach the middle line where they meet to form a short projection. In the present specimen the grooves run obliquely forward and their posterior margins meet but do not form any projection. The dorsal surface of the body of the sternum is somewhat deficient but there does not seem to have been a roughened region such as is seen in Recent specimens. In Recent sterna the keel is thick near its anterior margin, but becomes very thin for a short distance posteriorly, occasionally being pierced by a vacuity. The present specimen shows this same condition.

Femur, Tibiotarsus and Fibula. The present collection contains one whole but eroded femur (Plate 2, fig. 9), slightly smaller than Wiman's Group 3, and the well-preserved distal end of another slightly larger (Plate 2, fig. 8). In the larger specimen the ridge from the postaxial condyle meets the mid-ventral line of the shaft somewhat nearer to the distal end than in the other two, but in other respects they seem closely similar. The femur is not a bone which shows any very characteristic features.

The tibiotarsus is also an uncharacteristic bone. Wiman's collection contains three fragments in Group 3 and one in Group 4. The present collection contains a specimen with a very large distal end (Plate 2, fig. 7) and a very large proximal end (A.3357) as well as some fragments showing no details. None seems to differ in any significant way. It is difficult to compare the proximal ends as the ridges are almost always broken, and in Recent specimens there is considerable variation in this region.

The proximal end of a large fibula is included in the present collection (A.3372). The articular surface is flat preaxio-postaxially, and the bone is thick and massive. It is noticeably more so than the two New Zealand specimens, one belonging to *Palaeudyptes antarcticus* and an individual of larger size than any from Seymour Island. In these the proximal end is thinner preaxio-postaxially and broader dorsi-ventrally, and the articular surface is rounded instead of flat.

Tarsometatarsus. The present collection contains a tarsometatarsus which is very well preserved but lacks the part proximal to the inter-metatarsal vacuities and the lateral trochleae (Plate 2, fig. 1). It corresponds almost exactly in size with the cast of the type of *Anthropornis nordenskjoldi*, and there is no doubt that it belongs to this species. Enough remains of the preaxial trochlea to show that it diverged somewhat more than indicated by Wiman in his restoration. On the ventral surface both intermetatarsal grooves are present though shallow, and they are connected by a shallow transverse groove immediately distal to the foramen. Only the preaxial foramen is present, having a diameter of about 2 mm. The type differs in that there is scarcely a trace of the postaxial intermetatarsal groove on the ventral surface, and no trace of the transverse groove.

Simpson doubted whether the fragment of a tarsometatarsus which is the type of *Pachypteryx grandis* is distinguishable from that of *Anthropornis nordenskjoldi*. It is smaller, apparently some 20%, though both are too fragmentary to be certain. Wiman mentions as a difference that the preaxial trochlea is more divergent in *Pachypteryx*. As this is certainly true of the present specimen this tends to confirm the attribution of *Pachypteryx* to *Anthropornis*.

Patella. The present collection contains a specimen of a patella (Plate 2, fig. 5) which probably belongs to this species. Patellae of fossil penguins are extremely rare, only two being known. These are both from New Zealand, one belonging to *Palaeudyptes antarcticus* and the other to *Archaeospheniscus lowei*. All three differ from Recent specimens in being pierced by a large hole for the passage of the tendon of *ambiens* instead of having only a notch in the dorsal margin. The surface next to the knee joint is irregular and rough. The present bone is roughly pyramidal with the preaxial face somewhat concave, the distal face smooth and sloping proximally at an angle of about 50° to the base, the postaxial face slightly convex. It differs noticeably from the New Zealand specimens in the distal face, which is vertical in both of them. The hole is about twice the size of that in the patella of *Palaeudyptes*, though the bones are roughly the same size.

2. *Eosphaeniscus gunnari* Wiman.

(Plate I, figs. 5, 6; Plate II, figs. 3, 4, 6)

1905 *Eosphaeniscus gunnari* Wiman, p. 9, pl. 2, figs. 1, 1 a**Type:** Right tarsometatarsus, in Uppsala.

Ascribed to this species are the bones placed by Wiman in Group 5, none of which is very well preserved. The present collection contains the following bones:

Humerus: 1 complete, 1 proximal half, and 2 fragments.

Tibiotarsus: 1 proximal end, 3 fragmentary distal ends, and fragments of shafts.

Tarsometatarsus: 1, and 1 fragment.

Humerus. The humeri in Group 5 of Wiman's collection consist of two proximal ends and three shafts, and he separated two of the shafts into a sub-group 5a, as they were longer and narrower. In the present collection the complete humerus and the fragmentary distal end seem to correspond to 5, while the proximal half seems to correspond to 5a.

Wiman's two proximal ends are similar and their most striking feature is a well marked hollow in the dorsal surface of the bone between the insertions of *pectoralis secundus* and *pectoralis tertius*, extending up as far as the articular surface of the head. A hollow is commonly present here to a varying extent in penguin humeri, but in these two specimens it is exceptionally well marked, and its preaxial margin, adjacent to the insertion of *pectoralis secundus*, continues along the shaft of the bone as a sharp ridge at least as far as the insertion of *latissimus dorsi*. This gives the broken end of the shaft the three-cornered appearance commented upon by Wiman.

The humerus in the present collection is the best preserved of any humerus from Seymour Island and is complete except for some regions on the ventral side (Plate 1, fig. 6). The dorsal side of the head is very similar to that just described, though the ridge extending towards the insertion of *latissimus dorsi* is not so prominent. The shaft has the same smooth elongated S-shape as *Anthropornis*, but is relatively somewhat more slender. A small projection on the preaxial border marks the limit of the origin of *brachialis anticus*. At the distal end the angle between the tangent to the condyles and the axis of the shaft is slightly less acute than in *Anthropornis*. The processes bounding the sesamoid grooves are short and do not project postaxially to the extent that they do in Recent humeri. This seems to be due mainly to the preaxial deflection of the whole distal end of the bone as compared with Recent examples. The distal surface, as in *Anthropornis*, does not show the dorsi-ventral flattening found in Recent humeri, and the shelf dorsal to the ulnar condyle is broader than the condyle. The tricipital fossa is not fully preserved but is narrow and has a great thickness of bone between it and the surface of the head of the bone.

The proximal half humerus is well preserved except for the fact that the rim of the tricipital fossa is missing (Plate 1, fig. 5). It differs from the previous specimen in some respects. The dorsal hollow in the head is present but is more closed off distally by the insertion of *pectoralis tertius*, which is extended further in the preaxial direction than it is in the other specimens. The gap between the insertions of *pectoralis secundus* and *latissimus dorsi* appears to be greater and they are connected by only a very slight ridge which makes an angle with the postaxial border of the insertion of *pectoralis secundus*. Wiman's humerus Group 5a, of which the head is broken off so as to leave the distal end of the insertion of *pectoralis secundus*, appears to resemble the present specimen as far as can be seen, and the rest of the shaft is slightly longer and narrower than that of the complete humerus in the present collection. It seems possible that a second species of *Eosphaeniscus* is represented but it is unjustifiable to erect a new one on the basis of the present material. It is moreover impossible to determine which of the humeri corresponds to the type of *Eosphaeniscus gunnari*, which is a tarsometatarsus.

Tibiotarsus and Tarsometatarsus. Wiman's collection contains two more or less complete tibiotarsi and two proximal halves while the present collection has a proximal end (Plate 2, fig. 6) and several fragments. There is some variation in size between these which may support the suggestion that Group 5 contains two species, but these bones do not seem to show any significant differences.

The type of *Eosphaeniscus gunnari* is a tarsometatarsus which, though more or less complete, is poorly preserved and to judge from the cast and photographs most of the original surface has been eroded. The postaxial intermetatarsal groove is deep and the foramen is some 18 mm. long, no doubt enlarged by erosion

of the thin shelf between the two metatarsal bones. No preaxial groove is present though there is a small foramen. Wiman comments on the divergence of the preaxial trochlea. In the present collection is a well-preserved left tarsometatarsus (Plate 2, fig. 4), but this lacks the postaxial corner of the proximal end. In length it appears to be some 5 mm. shorter than the type, though of about the same minimum width. It also differs slightly in other ways. The postaxial intermetatarsal groove is much smaller and the foramen only 7 mm. long. The preaxial groove is absent and though a slight depression marks the position of the foramen, no trace of it is visible on the ventral surface. The preaxial trochlea is slightly more divergent and the notch between the other two trochleae is not deep. The high degree of separation between metatarsals III and IV in the type may conceivably be due to immaturity, as may also be the presence of the small preaxial foramen. In view of the similarity between these specimens, except with regard to these particular points, it seems best to identify the present specimen as *E. gunnari*. There is also a much eroded fragment of a right tarsometatarsus consisting of the two postaxial trochleae and about half of the corresponding metatarsals (Plate 2, fig. 3). It corresponds closely with the type, though as far as can be determined the postaxial intermetatarsal groove was not so deep.

Notodyptes gen. nov.

Type species: *Notodyptes wimani*.

Generic characters: Tarsometatarsus relatively broad, both intermetatarsal foramina present, groove only between metatarsi III and IV on the dorsal surface and no grooves on the ventral surface, preaxial border strongly concave.

This tarsometatarsus differs from all others from Seymour Island in general shape and in having both intermetatarsal foramina well developed. Its length is slightly less than that of the type of *Delphinornis larsenii*, but it is quite different from it in proportions and details. It is much larger than the type of *Ichthyopteryx gracilis* and appears to have been relatively broader.

It seems probable that the present tarsometatarsus belongs to Wiman's Group 6 which contains only fragments of a humerus, coracoid, scapula and femur. It is one of the groups to which he did not give a name.

3. *Notodyptes wimani* gen. et sp. nov.

(Plate 2, fig. 2)

Type: Left tarsometatarsus, lacking the distal two-thirds of the postaxial metatarsal. In the Department of Geology, British Museum, No. A.3331; F.I.D.S. No. D.515.9.

Horizon and Age: Younger Seymour Islands beds. Early Miocene or possibly late Oligocene.

Locality: Seymour Island. F.I.D.S. locality D.515 = Swedish locality No. 11 (Text-fig. 1). Collected by W. N. Croft, 1946.

Tarsometatarsus. Apart from the missing portion, this bone is fairly well preserved. The two foramina are level with one another. The preaxial one is the smaller, about 3.0 x 1.0 mm., while the other is about 4.5 x 2.0 mm. The second and third metatarsals are closely united and the median plane of the middle trochlea, when produced proximally, cuts the preaxial foramen rather than the proximal end of its own metatarsal. On the ventral surface the two calcaneal ridges run straight along the bone, each one in line with the preaxial edge of a foramen. Between them is a wide groove of U-shaped section.

The humerus placed by Wiman in Group 6 is a much eroded proximal half. The dorsal side of the head does not have the hollow seen in that of *Eosphaeniscus*. The coracoid had an enclosed precoracoid fenestra.

4. *Delphinornis larsenii* Wiman

1905 *Delphinornis larsenii* Wiman, p. 10, pl. 2, figs. 2, 2 a

The present collection contains a single trochlea of a tarsometatarsus (A.3366) which probably belongs to this species. Unlike the other penguin bones from Seymour Island it was found *in situ* in a band of hard shelly conglomerate in the same series of beds, but at a different horizon (see page 4).

LIST OF SPECIMENS IN THE COLLECTION

- D.499.1 Proximal end of humerus (Plate 1, fig. 5), *Eosphaeniscus*. Fragment of coracoid, ? *Notodyptes*.
 D.514.1 Distal end of femur (Plate 2, fig. 8), *Anthropornis*.
 D.515.6 Fragment of femur, *Anthropornis*.
 Thoracic vertebra.
 D.515.8 Femur (Plate 2, fig. 9), *Anthropornis*.
 D.515.9 Tarsometatarsus (Plate 2, fig. 2), *Notodyptes* (type).
 Fragment of femur, fragment of sternum, *Anthropornis*.
 Fragment of distal end of tibiotarsus, *Eosphaeniscus*.
 Phalanx of toe. Two fragments.
 D.515.10 Two toe phalanges.
 D.515.11 Humerus, *Anthropornis*.
 D.515.12 Coracoid, *Anthropornis*.
 D.515.13 Tarsometatarsus (Plate 2, fig. 3), *Eosphaeniscus*. Two fragments.
 D.515.14 Tarsometatarsus (Plate 2, fig. 4), distal end of tibiotarsus, *Eosphaeniscus*.
 D.515.15 Patella (Plate 2, fig. 5), *Anthropornis*.
 Three fragments.
 D.515.16 Distal end of humerus, *Eosphaeniscus*.
 Two fragments.
 D.515.17 Fragments of ends of humerus, radius, ulna and fragments, two carpals, carpometacarpus, two phalanges (Plate 1, fig. 2), base and head of coracoid (Plate 1, figs. 3, 4), fibula, both ends of tibiotarsus (Plate 2, fig. 7), tarsometatarsus (Plate 2, fig. 1), *Anthropornis*.
 Four toe phalanges and many fragments.
 D.515.18 Radius (Plate 1, fig. 1), two fragments of ulna, fragment of coracoid, *Anthropornis*.
 Fragment of proximal end of humerus, fragment of distal end tibiotarsus, *Eosphaeniscus*.
 D.520.3 Fragment of tarsometatarsus in matrix, probably *Delphinornis*.
 D.521.2 Humerus (Plate 1, fig. 6), *Eosphaeniscus*.
 D.521.3 Proximal end of tibiotarsus (Plate 2, fig. 6) and 2 fragments of shafts, *Eosphaeniscus*.
 Cervical vertebra and fragment.

MEASUREMENTS

All measurements were made in millimetres with a craniometer between the points indicated at the head of each table. Those placed in brackets are, owing to deficiencies in the specimens, only approximate.

MEASUREMENTS OF HUMERUS

1. Extreme length from dome of head to the most distal process.
2. Length from dome of head to the angle at the base of the dorsal sesamoid groove.
3. Distance from the distal end of the insertion of *pectoralis secundus* to the above angle.
4. Preaxio-postaxial diameter of the head from the preaxial border to the postaxial surface of the articulation.
5. Preaxio-postaxial diameter of the shaft one third of the distance from the head.
6. Preaxio-postaxial diameter of the shaft two thirds of the distance from the head.
7. Dorsi-ventral thickness one third of the distance from the head.
8. Dorsi-ventral thickness two thirds of the distance from the head.
9. Distance of the preaxial angle, if present, from the head.
10. Distance from the preaxial side of the radial condyle to the longest distal process.
11. Dorsi-ventral diameter of the distal surface at the widest part of the ulna condyle.

	1	2	3	4	5	6	7	8	9	10	11
<i>Anthropornis nordenskjoldi</i>											
Cast of Wiman's No. 3	—	(160)	(110)	54	36	38	18	15	96	—	—
Cast of Wiman's No. 3	—	—	—	—	—	31	—	15	—	—	(18)
A.3338	—	(>167)	—	—	—	40	—	(17)	(100)	—	—
<i>Eosphaeniscus gunnari</i>											
Cast of Wiman's No. 5	—	—	—	—	24	—	15	—	—	—	—
Cast of Wiman's No. 5	—	—	—	(40)	—	—	—	—	—	—	—
Cast of Wiman's No. 5a	—	—	(101)	—	25	23	12	10	—	—	(15)
A.3367	134	132	90	41	(26)	23	—	11	76	(38)	17
A.3325	—	—	—	40	24	—	13	—	—	—	—

MEASUREMENTS OF ULNA

1. Extreme length between parallels at right angles to the preaxial border.
2. Length, from the bottom of the depression for the humerus to the ventral distal process.
3. Greatest preaxio-postaxial width, measured at right angles to the preaxial border.
4. Preaxio-postaxial width one third of the length from the proximal end.
5. Preaxio-postaxial width two thirds of the length from the proximal end.
6. Dorsi-ventral thickness one third of the length from the proximal end.
7. Dorsi-ventral thickness two thirds of the length from the proximal end.

	1	2	3	4	5	6	7
<i>Anthropornis nordenskjoldi</i>							
Cast of Wiman's No. 3	93	85	32	25	20	11	10
A.3354	100	95	—	27	22	11	10
<i>Eosphaeniscus gunnari</i>							
Cast of Wiman's No. 5	85	80	27	23	16	9	8

MEASUREMENTS OF RADIUS

1. Extreme length between parallels at right angles to the preaxial border.
2. Distance from the angle in the preaxial border to the preaxial corner of the proximal end.
3. Preaxio-postaxial width one third of the distance from the proximal end.
4. Preaxio-postaxial width two thirds of the distance from the proximal end.
5. Thickness one third of the distance from the proximal end.
6. Thickness two thirds of the distance from the proximal end.

	1	2	3	4	5	6
<i>Anthropornis nordenskjoldi</i>						
Cast of Wiman's No. 4	—	—	18	18	8	8
A.3353	101	83	20	17	8.5	7.5
A.3361	118	101	23	—	11	10

MEASUREMENTS OF CARPOMETACARPUS

1. Extreme length, between parallels, of the second metacarpal.
2. Extreme length, between parallels, of the third metacarpal.
3. Preaxio-postaxial width one third of the distance from the proximal end.
4. Preaxio-postaxial width two thirds of the distance from the proximal end.

	1	2	3	4
<i>Anthropornis nordenskjoldi</i>				
Cast of Wiman's No. 3	84	82	28	28
A.3350	88	90	—	—

MEASUREMENTS OF FEMUR

1. Length from the hollow between the head and the trochanter on the proximal end to the hollow between the condyles on the distal end.
2. Greatest width at the proximal end.
3. Proximo-distal diameter of the head.
4. Greatest width at the distal end.
5. Preaxio-postaxial diameter at the centre of the shaft.
6. Dorsi-ventral diameter at the centre of the shaft.
7. Diameters of the central cavity at the centre of the shaft.
8. Distance from the hollow between the condyles at the distal end to the point where the preaxio-ventral ridge meets the midventral line of the shaft.

	1	2	3	4	5	6	7	8
<i>Anthropornis nordenskjoldi</i>								
Cast of Wiman's No. 3	129	41	38	19	19	18	—	50
A.3330	129	—	(35)	—	17	16	—	50
A.3327	—	—	—	41	18	22	8 x 8	45
A.3328	—	—	—	—	17	17	4 x 3.5	—
A.3333	—	—	—	—	17	15	5 x 4	—

MEASUREMENTS OF TARSOMETATARSUS

1. Length of second metatarsal from the proximal hollow to the groove of the distal trochlear surface.
2. Length of the third metatarsal from the proximal convexity to the groove of the distal trochlear surface.
3. Length of the fourth metatarsal from the proximal convexity to the groove of the distal trochlear surface.
4. Preaxio-postaxial width at the proximal end.
5. Preaxio-postaxial width at the centre.
6. Preaxio-postaxial width at the distal end.
7. Distance from the proximal convexity to the proximal end of the preaxial intermetatarsal vacuity.
8. Distance from the proximal convexity to the proximal end of the postaxial intermetatarsal vacuity.
9. Length of the preaxial vacuity.
10. Length of the postaxial vacuity.

	1	2	3	4	5	6	7	8	9	10
<i>Anthropornis nordenskjoldi</i>										
Cast of Wiman's type	—	87	—	—	36	—	23	—	7	—
Cast of Wiman's type of <i>Pachypteryx grandis</i>	—	—	—	(32)	—	—	20	18	—	—
A.3358	—	—	—	—	34	—	—	—	—	—
<i>Eosphaeniscus gunnari</i>										
Cast of Wiman's type	—	—	—	—	26	38	—	—	—	—
A.3341	53	(>60)	—	—	28	42	—	—	—	—
<i>Notodyptes wimani</i> . Type A.3331	(37)	(44)	—	(24)	—	—	—	—	4	4.5
<i>Delphinornis larsenii</i>										
Cast of Wiman's type	—	—	45	20	17	—	13	10	2	—

SUMMARY

THE fossil penguins from Seymour Island are known from a collection made by the Swedish Southpolar Expedition in 1901–3, described by Wiman, and the present collection. Wiman divided his specimens into eight size-groups and erected six genera and species, and it seems likely that three of his genera and an unnamed group can all be included in *Anthropornis nordenskjoldi*. This leaves *Eosphaeniscus gunnari* known from a number of bones, *Delphinornis larsenii* and *Ichthyopteryx gracilis* from tarsometatarsi only, and an unnamed group of fragments. The present collection contains a number of bones attributable to *Anthropornis* and *Eosphaeniscus*, a fragment probably *Delphinornis*, and a new tarsometatarsus here named *Notodyptes wimani* gen. et sp. nov., probably corresponding to the unnamed group. The collection includes the first known fossil examples of an ulnar carpal and distal phalanx of the wing. There is also a patella, previously known only from two examples from New Zealand. The species from Seymour Island, New Zealand, and Australia are all similar and are placed in the subfamily Palaeudyptinae. They differ from the Recent Spheniscinae and from the majority of those from Patagonia, which are more or less intermediate between the Palaeudyptine and Spheniscine groups.

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EXPLANATION OF PLATE

Figures are natural size except Nos. 1, 4, 5 which are x 1.05. The specimens were sprayed with ammonium chloride. The photographs were taken in the British Museum (Nat. Hist.) by Mr. J. V. Brown.

PLATE I

1. *Anthropornis nordenskjoldi*. Right radius, ventral view. A.3361
2. *Anthropornis nordenskjoldi*. Bones of a left wing assembled in natural position. As explained in the text, these bones may not belong to the same individual. A.3348-3354
3. *Anthropornis nordenskjoldi*. Base of left coracoid, ventral view. A.3350
4. *Anthropornis nordenskjoldi*. Anterior end of left coracoid, showing the *fossa scapularis*. A.3356
5. *Eosphaeniscus gunnari*. Proximal end of left humerus, dorsal view. A.3325
6. *Eosphaeniscus gunnari*. Right humerus, dorsal view. A.3367



EXPLANATION OF PLATE

Figures are natural size except Nos. 2, 4, 8 which are x 1.05. The specimens were sprayed with ammonium chloride. The photographs were taken in the British Museum (Nat. Hist.) by Mr. J. V. Brown.

PLATE II

1. *Anthropornis nordenskjoldi*. Left tarsometatarsus, dorsal view. A.3358
2. *Notodyptes wimani*. Type. Left tarsometatarsus, dorsal view. A.3331
3. *Eosphaeniscus gunnari*. Right tarsometatarsus, dorsal view. A.3340
4. *Eosphaeniscus gunnari*. Left tarsometatarsus, dorsal view. A.3341
5. *Anthropornis nordenskjoldi*. Right patella, preaxial view. A.3343
6. *Eosphaeniscus gunnari*. Proximal end of right tibiotarsus, preaxial view. A.3368
7. *Anthropornis nordenskjoldi*. Distal end of left tibiotarsus, dorsal view. A.3357
8. *Anthropornis nordenskjoldi*. Distal end of right femur, ventral view. A.3327
9. *Anthropornis nordenskjoldi*. Left femur, dorsal view. A.3330

