FOSSIL PENGUINS

GEORGE GAYLORD SIMPSON

BULLETIN
OF THE
AMERICAN MUSEUM OF NATURAL HISTORY
VOLUME 87 : ARTICLE 1 NEW YORK : 1946

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PUBLICATIONS OF THE SCARRITT
EXPEDITIONS, NUMBER 33

BULLETIN
OF THE
AMERICAN MUSEUM OF NATURAL HISTORY
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BULLETIN OF THE AMERICAN MUSEUM OF NATURAL HISTORY
Volume 87, article 1, pages 1–100, text figures 1–33, tables 1–9

Issued August 8, 1946

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INTRODUCTION

FEW ANIMALS have excited greater popular and scientific interest than penguins. Their quaintly human appearance, their peculiar habits, the ability of some of them to thrive in the bitter Antarctic cold, their association with remote coasts and islands, and their radical differences from all other birds have long made them favorite subjects of layman and student alike. They appear regularly in cartoons, advertisements, moving pictures, popular books, and magazine articles, and with about equal regularity, if less frequently, in the technical literature, where their habits and structure have been described in great, but still incomplete, detail and where their origin and history have been and still are bitterly disputed.

Fossil penguins were made known as long ago as 1859 and by no less an authority than T. H. Huxley. Since then, some hundreds of specimens have been collected in several widely distant parts of the world, and many of these have been exhaustively described, but knowledge has remained very incomplete and in part quite confused. The known specimens are all incomplete. No fragment of the skull has hitherto been described and in few instances have two or more surely associated bones of one individual been found. From the scattered literature it has been most difficult, on some points impossible, to gather a clear and correct idea of the variety and characters of the known fossil penguins as a whole. A complete and satisfying review cannot now be made, but a contribution toward this end is presented.

The present study grew out of the discovery in 1933 by the Second Scarritt Patagonian Expedition of a fossil penguin skeleton, far from complete but nevertheless much the best that has hitherto been found. It includes for the first time the greater part of a skull, and it also comprises more different parts of the skeleton of one individual than had ever been found in association. In addition to this unique skeleton, the expedition also collected more than a hundred other specimens of fossil penguins, constituting an admirable basis for comparison, synthesis, and generalization, in spite of the fact that relatively few distinguishable species are represented. Several years elapsed before the collection could be fully prepared, and it was then hoped that some specialist on penguins would be able to undertake the description of these materials, but such an opportunity did not arise. With the reorganization of paleontology in the American Museum in November, 1944, curatorial responsibility for fossil birds was returned to the Department of Geology and Paleontology and was assigned specifically to me within the department. In partial fulfillment of this responsibility and in continuation of our program on the Tertiary faunas of South America, the present study has been prepared in order to make available the essential facts about these important fossils.

In the course of identification and description of our collection, it was necessary to review literature on other known fossil penguins. It quickly became obvious that a general taxonomic revision could not be made under existing circumstances, but it has seemed worth while to present notes on taxonomy and to review available knowledge of all fossil penguins and not alone those in our collection. Although it is not only, or even mainly, dependent on study of the extinct forms, the vexatious problem of penguin origins is also clearly pertinent and some comments on it have been appended.

Comparative osteological material of recent penguins has been provided by the Department of Birds of this Museum, with the cooperation of Dr. Murphy and Mr. O'Brien. The osteological collection unfortunately lacks the important genera *Eudyptula* and *Megadyptes*, but it is rich in most of the species of all other living genera. Previous studies of penguin osteology have, of course, also been utilized throughout, even when not explicitly cited on a given point. The availability of these works, especially Gervais and Alix (1877), Pycraft (1898), Shufeldt (1901), Virchow (1931), and Watson (1883),

makes it unnecessary to review the osteology of the Spheniscidae as a whole and possible to concentrate on some of the more striking and pertinent comparative differences within the group.[1]

[1] Except for the skull, even the most detailed osteological studies of recent penguins have, however, paid too little attention to their variation and to their taxonomic differentiation. Even Watson's careful description is markedly deficient in detecting and stating differences between the various species and genera.

In resuming work on Patagonian fossils, I wish again to express gratitude to Mr. H. S. Scarritt, the principal sponsor of our collecting in that region. The specimens involved in this study were collected by Coleman S. Williams, Justino Hernández, and me, and were prepared mostly by Albert Thomson. The illustrations have been prepared by John C. Germann.

A SKELETON OF *PARAPTENODYTES ANTARCTICUS*

OCCURRENCE

THE SPECIMEN HERE TO BE DESCRIBED is A.M.N.H. No. 3338. It was found by Justino Hernández, on the Second Scarritt Patagonian Expedition, in November, 1933. The locality is on the south side of the Río Chubut, about 3 leagues above (west of) Trelew and directly opposite the settlement of Gaiman, in Chubut Territory, Argentina. Part of the specimen had weathered out, but parts were *in situ* and were removed in a block of matrix.

The stratigraphy of this region has been discussed elsewhere (Simpson, 1935). The penguin skeleton was found in the lower part of "3" of Section 1 of the paper cited (fig. 1 and pp. 6–7). This stratigraphic unit consists of about 35 meters of thick-bedded, pale, yellowish tuff. It represents the first depositional phase in this region of the Patagonian marine incursion, of disputed age but now considered Early Miocene by a strong consensus. It immediately overlies the terrestrial Trelew beds, of late Colhué-Huapí age (probably latest Oligocene, perhaps earliest Miocene), with an erosional but not angular uncomformity apparently representing only a slight hiatus in time.

Besides this skeleton, numerous isolated penguin bones were found in the same bed, along with remains of sharks, rays, whales, and sparse *Ostrea hatcheri*. Our party found no land mammals at this level, but these were probably correctly reported by Frenguelli (1926), although there is some lingering doubt about this because of his failure to distinguish the terrestrial Trelew from the marine Patagonian at this locality. In any case, there is little doubt that the deposit was formed in shallow water and is littoral or estuarine in nature rather than typically or fully marine.

IDENTIFICATION

The specimen is referred to *Paraptenodytes antarcticus* (Moreno and Mercerat, 1891). The species was based on probably associated femur, tibiotarsus, and tarsometatarsus. As pointed out in the description below, the homologous bones of our specimen differ from the type in various minor details. By standards that have been applied to fossil penguins, especially by Ameghino, these differences would justify specific or even generic separation, but I am convinced that this is not correct and that the specific reference is well founded. Equally great differences occur within a single species among modern penguins. The general agreement in size and structure is close, and no other Patagonian species in the long list established by Ameghino is liable to confusion with this. The type is from Santa Cruz Territory, from the Middle Patagonian at the mouth of the Río Santa Cruz, according to Ameghino, and our specimen is from the Lower Patagonian of the Chubut Valley, but all the evidence is that the penguin faunas are identical in these two regions and at these different levels, which differ little if at all in age. Moreno and Mercerat (1891) also referred to this species three isolated bones, ulna, femur, and tibiotarsus, from Chubut—exact locality not given but doubtless near Trelew or Gaiman and from the same beds as our specimen.

The species is relatively but not extremely rare. The type, our skeleton, and the three isolated bones mentioned by Moreno and Mercerat are the only surely identified remains reported in the literature or known to me. Ameghino (1895) also mentioned a metacarpus and the anterior part of a mandible, of unstated origin, but, as he later (1905) remarked about the mandible, the reference is not well established. As noted below, the humerus referred by Ameghino (1905) to *Perispheniscus wimani* probably belongs to *Paraptenodytes antarcticus*. Parts of five to eight individuals are thus known.

Moreno and Mercerat placed the species in their genus *Palaeospheniscus*, but Ameghino (1891) quickly made it the type of a distinct genus *Paraptenodytes*. As will appear in the following pages, this action was thoroughly justified, and *Paraptenodytes* is certainly a valid genus, although the implication of spe-

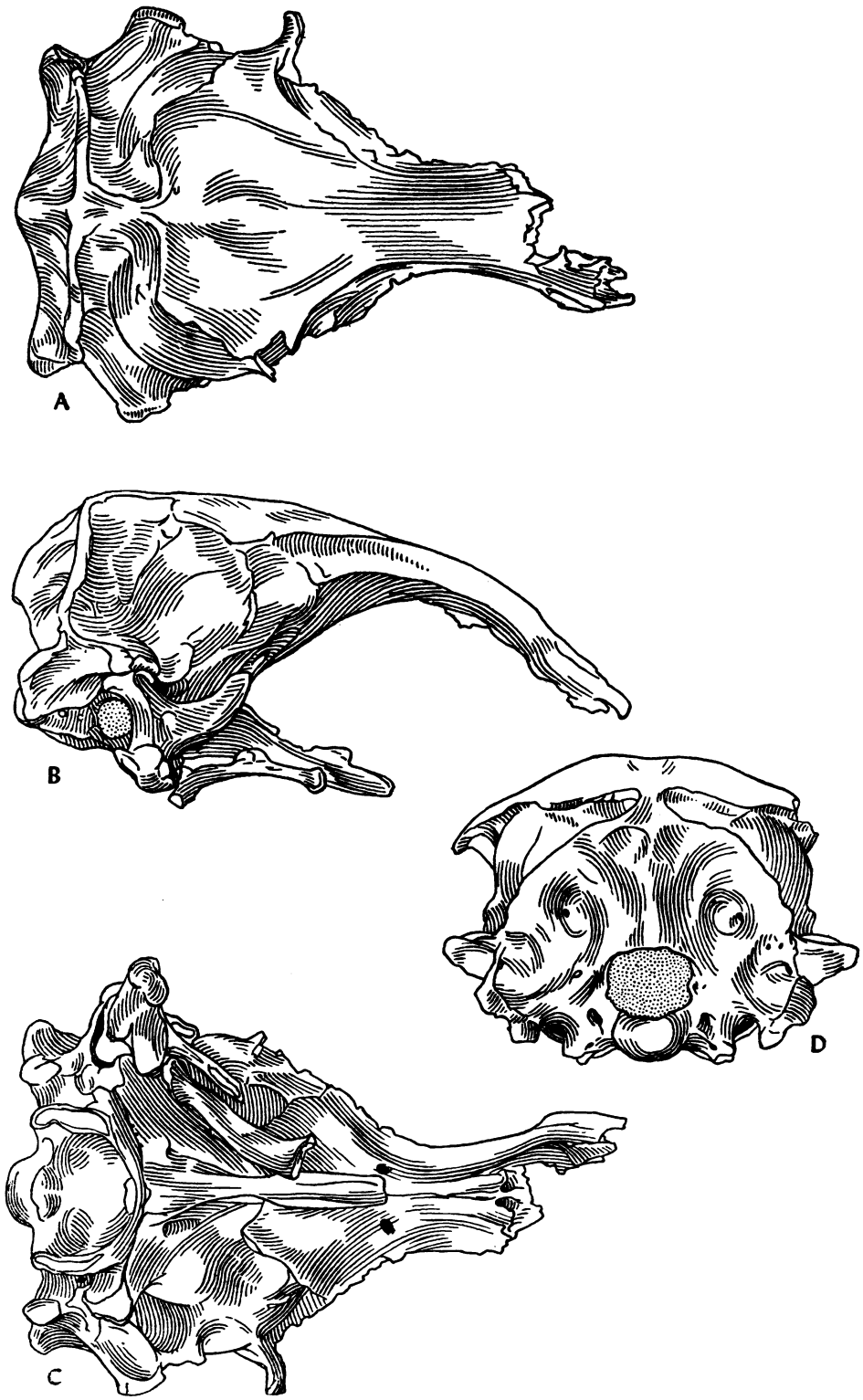


FIG. 1. *Paraptenodytes antarcticus* (Moreno and Mercerat). Skull, lacking rostrum, A.M.N.H. No. 3338. A. Dorsal view. B. Right lateral view. C. Ventral view. D. Occipital view. ×1.

cial relationship with *Aptenodytes* is not supported by the present increased knowledge.

PRESERVATION AND ASSOCIATION

The specimen includes parts of the skull, mandible, nine vertebrae, sternum, scapula, coracoid, humerus, femur, tibiotarsus, tarsometatarsus, and some uncharacteristic rib fragments. Most of these elements are somewhat broken, as specified in the descriptions below. The breaks look very fresh, but the missing parts had apparently been washed far away, as extensive search did not locate them. Parts were found on the surface, in some cases making contact with bones still *in situ*. In the surface gleanings are a few fragments belonging to other animals, but the circumstances of discovery, agreement in size and character, partial articulation, and absence of any duplication establish beyond reasonable question that the remains described below belong to one individual. The condition of the parts present is perfect, with hard, clean surfaces unaffected by decay or erosion.

SKULL

Figures 1, 2

This is the only fossil penguin skull so far discovered and therefore merits detailed consideration. The skulls of recent penguins have, however, been described and figured so elaborately that a complete topographic description of the fossil is unnecessary.

On the occiput, the foramen magnum is somewhat deeper (12.1 mm.) than broad (11.2 mm.) and tends to be divided into a larger upper and a smaller lower part by slight projections on the lateral rim. Both conditions are unusual in the living forms, but are closely matched in some specimens of *Aptenodytes*. The cerebellar dome is less prominent than in any recent form compared by me and, as seen from above, barely projects farther posteriorly than do the paroccipital processes. It also occupies a relatively small fraction of the occiput, roughly comparable with *Spheniscus demersus* in which, however, the dome is much sharper and more projecting. The upper and lateral borders of the occiput (formed by the post-temporal crests or squamoso-parietal wings) are almost semicircular as seen in posterior view, unlike the quadrate or rhombic figure of recent penguins. This effect is, in part, caused by the fact that the occiput and the brain case as a whole are relatively lower and broader in the fossil.

The paroccipital processes are unique in the fossil and (with the pterygoids, see below) constitute its most decisive difference from

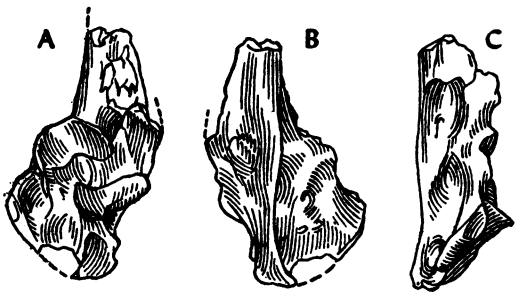


FIG. 2. *Paraptenodytes antarcticus* (Moreno and Mercerat). Right articular, A.M.N.H. No. 3338. A. Dorsal view. B. Ventral view. C. Medial view. ×1.

living Spheniscidae. The processes are produced not only ventrolaterally, as in living forms, but also posteriorly, and each is distinctly bifid, with a ventral point and another, somewhat tab-like projection dorsolateral to this.

The condyle is short, heavy, sessile, and preceded on the basicranium by a sharply defined precondylar fossa. Anterior to this is a larger, shallow fossa surrounded by a raised rim, ending posterolaterally in the low mammillary processes. The outline of this fossa is almost perfectly semicircular, contrasting, for instance, with the cordiform outline in *Spheniscus*. The general aspect of this region is most nearly matched in some specimens of *Pygoscelis papua*.

The temporal fossae are unusually large in all dimensions and are deep and sharply defined by crests, especially posteriorly but also anteriorly. They extend dorsally to the midline, where they end squarely and are separated by a strong sagittal crest, which widens somewhat posteriorly. This resembles *Spheniscus*, only, among recent genera, but is carried to an extreme still greater than in any species of that genus. The postorbital process

is also more or less like *Spheniscus* but is less distinctive. It seems to be less produced ventrally at the tip than in any recent forms, but it is not quite certain that the tip is complete in the fossil.

The supraorbital groove is relatively narrow and lacks the recurved rim and flattened ledge so prominent in *Pygoscelis*. It almost fades out in its anterior, interorbital part. This also resembles *Spheniscus*, especially *S. mendiculus*, and also *Eudyptula*, which is nearly like *S. mendiculus* in this respect. In harmony with this character, the interorbital surface of the frontal is broader than in *Eudyptes* or, especially, *Pygoscelis*.

The quadrate as a whole is more stoutly constructed than in any recent species, including *Aptenodytes forsteri*, the only recent species that equals or exceeds the fossil in skull size. The optic process is deep dorsoventrally, suggesting *Eudyptes*, but is relatively longer than in that genus or, indeed, any other living penguins.

The pterygoid is the most remarkable and interesting bone of the skull. Almost every other cranial feature is distinctly spheniscid, however unusual in proportions, degree of development, or combination of characters. If the pterygoid, in remarkable contrast, had been found isolated it would never have been considered spheniscid but perhaps procellariiform. The bone as a whole is a twisted, sigmoid blade. The posterolateral part is not rod-like but fairly stout and deeper dorsoventrally than wide laterally. Its outer border is convex, inner concave. The larger anteromedial part is broader than deep, but by no means as flattened as in living penguins, and is concave laterally and convex medially. It is not expanded in a thin horizontal plate as in all living Spheniscidae and, most striking of all, its whole anterior border articulated with the palatine, with no free anterolateral expansion such as is so typical of other penguins as to have been considered diagnostic of the Sphenisciformes. The dorsal surface is rounded, not crested along the medial border as in most recent forms, and the bone tends to be thickest near its central axis. At about one-third of the distance from the anterior end, there is a tab-like ascending process on the dorsal surface near the medial border. Were the bone isolated, this would be assumed to be an articulation for a basipterygoid process, but the parasphenoid is preserved and it has no such process.[1] As in other penguins, there is an anteromedial facet against the parasphenoid, adjacent to the palatine facet and quite distinct from this "pseudo-basipterygoid" facet.

In the lower jaw the articular is a very heavy, irregular bone only generally similar to that of recent penguins and distinctive in detail. The medial facet for the quadrate has distinct but confluent medial concave and lateral convex (or vaguely saddle-shaped) parts. The external facet is very large and elongate, the anterior end directed as much posteriorly as dorsally and bounded in front by a sharp crest. The posterior part of this facet is more expanded than in any recent genus, faces anteriorly as well as dorsally, and is produced into a sharp, erect crest. The whole arrangement for quadrate articulation happens to be most nearly matched by a specimen of *Pygoscelis adeliae* among my comparative materials, but the resemblance is not particularly suggestive of special affinity, and *Pygoscelis papua* (if my material is typical) differs more markedly. The greatest distinction of the fossil articular is, however, in the postarticular (or so-called angular) process. In all recent penguins compared there are two distinct processes, one medial, more or less hook-like forward, and the other posterior, styliform (e.g., *Spheniscus*) or a flattened and twisted plate, concave above (e.g., *Pygoscelis*). The processes are connected by a horizontal shelf or flange in greater (e.g., *Pygoscelis*) or less (e.g., *Spheniscus*) degree, but there is always an emargination between them. In the fossil there is no trace of this emargination, and the whole process is a single flange. There is no anteromedial hook, and the projection medially is

[1] In recent penguins there is a tendency to form an angulation in this region, and this may well be homologous with the process in the fossil although so much less in degree and different in form. There is probably a non-osseous connection with the parasphenoid, and if so this would be at least analogous with the basipterygoid articulation, but I have not been able to check this point with specimens and do not find it mentioned in the literature.

much less than in any recent form, barely extending more medially than the quadrate articulation. The posterior extension is also relatively less than in most recent genera, approximately as in *Pygoscelis*. The crest on the ventral surface of the articular is very high and sharp and is deeply excavated on the medial side.

A fragment of the ramus is preserved, but so crushed and broken that its precise placing is uncertain. It does suggest that the ramus was of intermediate proportions, not so slender as in *Aptenodytes* and not so deep, proportionately, as in *Eudyptes*.

VERTEBRAE

The atlas, anterior part of the centrum of the axis, three isolated cervicals tentatively identified as the sixth, eighth, and eleventh, and the last cervical in series with the first three dorsals are preserved. In comparisons it is assumed that the fossil had 13 cervicals, which is not certain but is probable, as this number is apparently invariable in recent penguins.

The atlas has a ventral longitudinal ridge terminating posteriorly in a small but distinct hypapophysis, much as in *Aptenodytes*. The neural arch is broad and is little emarginate posteriorly between the zygapophyses.

The preserved part of the axis has no striking peculiarities.

The presumed sixth cervical, which might possibly be the seventh, has the neural arch crested longitudinally, and the crest rises in the middle to a low, blunt, neural spine. No recent penguin known to me has a crested arch in this region. On the sixth cervical in the living genera the spine may be absent and, if present, is a higher, shorter process quite unlike that of the fossil. On the seventh cervical the spine is usually absent but may be represented by a mere nubbin. In the fossil there is a projecting nodule on the transverse process lateral to the vertebrarterial canal, as is normal on both sixth and seventh cervicals of all recent penguins, and this is strongly developed, with a pocket below (ventral to) it, containing a small foramen, about as in *Aptenodytes*. Aside from its elongate proportions, the ventral surface of this fossil bone is unique in that there is a pair of stout anterior processes, bounding the groove for the carotids, about as usual on the seventh or eighth cervical of recent penguins, while the ventral surface of the centrum immediately posterior to these processes is excavated to a well-defined pit, about as usual on the fourth or fifth cervical of recent penguins.

On the fossil cervical believed to be the eighth, but possibly the ninth, the neural arch is also crested longitudinally, unlike any recent penguin compared, but there is no distinct spine. As on the sixth cervical, but here somewhat more distinct, the dorsal processes on the postzygapophyses, so prominent, for instance, in *Eudyptes crestatus*, are more distinctly developed than in *Spheniscus*, for example, but are not prominent. The degree of development is about as in *Aptenodytes*, but the shape of the processes is different. They form oblique anteromedian-posterolateral crests, highest posteriorly. The transverse processes are about as on the sixth cervical. The ventral processes bounding the carotid groove are longer (extend farther ventrally) and are closer together. The centrum is not excavated ventrally posterior to these processes, but on the contrary immediately becomes a longitudinal ridge, with even less flattening or grooving than is usual in this region in recent penguins.

The vertebra identified with sufficient probability as the eleventh cervical also has the neural arch crested, with a suggestion of a very low neural spine (somewhat broken), about as on the twelfth cervical of *Aptenodytes*. The dorsal processes on the postzygapophyses are not distinct. The cervical rib is better developed than in this region in *Aptenodytes*, and the transverse process, strictly speaking, is less developed, the bone being rather like the eleventh cervical of *Eudyptes* or of *Pygoscelis* in both respects, as it is also in the compressed median hypapophysis preceded by a broad excavation.

The thirteenth (last) cervical has, as usual, a well-developed spine of dorsal type. The transverse processes end in two branches of about equal prominence, an upper or true transverse process and a lower or cervical rib (or longi colli insertion). The latter is even better developed than in *Spheniscus*, and much more than in any other of the recent

genera, in which it is very small or quite lacking. The ventral surface of this bone is still more radically different from any recent penguin. There is no compressed median hypapophysis. The surface is excavated anteriorly and posteriorly, and between these two hollows is a rather elaborate, paired elevation which, in turn, is excavated on the two sides.

On the third dorsal the ventral part of the centrum is not preserved, nor is the posterior articulation. The other parts have no striking differences from recent penguins.

The proportions of the various vertebrae show strong, but little investigated and not clearly understood, differences in the recent species. Some comparisons with the fossil are shown in table 1. The sixth cervical is more elongate than in the two recent species here compared. The eighth cervical has roughly similar proportions in all three. The more posterior cervicals and anterior dorsals are relatively shorter and wider in the fossil than in *Aptenodytes forsteri*, but are somewhat more elongate than in *Pygoscelis adeliae*.

TABLE 1

VERTEBRAL DIMENSIONS AND PROPORTIONS IN SOME FOSSIL AND RECENT PENGUINS
(Measurements are in millimeters.)

	Width Across Prezygapophyses	Length of Centrum	Ratio
6th cervical			
Paraptenodytes antarcticus	28.9	39.1	.74
Aptenodytes forsteri	34.9	31.7	1.10
Pygoscelis adeliae	18.5	16.6	1.11
8th cervical			
Paraptenodytes antarcticus	30.1	36.0	.84
Aptenodytes forsteri	28.9	35.3	.82
Pygoscelis adeliae	14.2	18.3	.78
11th cervical			
Paraptenodytes antarcticus	28.2	27.7	1.02
Aptenodytes forsteri	31.0	34.1	.91
Pygoscelis adeliae	16.9	16.1	1.05
13th cervical			
Paraptenodytes antarcticus	27.2	24.4	1.11
Aptenodytes forsteri	30.2	30.4	.99
Pygoscelis adeliae	17.5	13.2	1.33
1st dorsal			
Paraptenodytes antarcticus	23.8	25.5	.93
Aptenodytes forsteri	23.6	37.0	.64
Pygoscelis adeliae	15.5	14.3	1.08

The first dorsal has the same peculiar structure of the ventral surface as the thirteenth cervical, but is not otherwise very characteristic. The neural spine is low, and the whole bone is relatively low, short, and broad. The facet for the head of the rib is not distinctly seen, but this does not always form a pit on the first dorsal, and there is little doubt that this vertebra did carry a movable rib.

In the second dorsal the whole centrum is abruptly much deeper than in the first. The sides are hollowed out. The hypapophysial region is broken, but evidently was also peculiar, with a median hollow containing a small longitudinal keel and perhaps with lateral wings. The rib facets are clearly marked.

STERNUM

The sternum is recognizably represented only by a small part of the right anterolateral edge, with the attachments of three sternal ribs and part of a fourth. Insignificant as this fragment is, it has two well-marked peculiarities in comparison with recent penguins. First, the margin here has a high, stout, ven-

tral ridge set off sharply, at slightly less than a right angle, from the general convex ventral surface of the sternum. Second, the sternal rib articulations are relatively shallow, not over 75 per cent as deep as in *Aptenodytes patagonicus* (a species of approximately the same over-all size), but the successive articulations are much more widely spaced than in any recent penguin.

SCAPULA

Figure 3

The heads of both scapulae are preserved, but in recent penguins it is the blade that is most distinctive in the various genera, and there is little to say about this bone in the fossil. The head is, in general, *Pygoscelis*-like, but the acromion projects less sharply dorsally than in *Pygoscelis* or any other recent penguin compared, although approached by *Aptenodytes patagonicus*. The border is rather deeply emarginate between the acromion and the coracoid articulation, which is nearly hemispherical. The dorsal border of the neck is sharp.

CORACOID

Figure 4

Considerable parts of both coracoids are preserved, but both are incomplete, particularly at the sternal end. On the whole, this bone resembles that of *Spheniscus*. The acrocoracoid is relatively stouter, longer, and more hooked. The shaft also shows slightly more curvature, concave externally in a longitudinal direction. The crest to the procoracoid is broken on both coracoids as preserved, but it may have bridged over a large oval fenestra, unlike *Pygoscelis* and *Aptenodytes*. The scapular fossa is a regular, hemispherical cup. The glenoid fossa is large and only very gently concave.

HUMERUS

Figure 5

Both humeri are preserved. Each lacks a small part of the distal end, but all parts are present on one or the other. Contrary to a general impression stemming from Watson (1883, p. 29), who said that distinctive features were sought in vain in the humeri of recent genera and species, the humerus, closely studied, provides rather clear-cut taxonomic distinctions in recent penguins and still more so in the fossils. Considerable detail will be given in the succeeding section of this paper on comparative osteology of the Miocene penguins, so that only the more striking features of the humerus of *Paraptenodytes antarcticus* will here be briefly given.

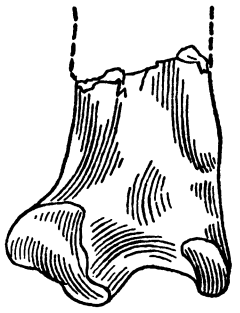


FIG. 3. *Paraptenodytes antarcticus* (Moreno and Mercerat). Right scapula, anterior end, A.M.N.H. No. 3338. Dorsolateral view. ×1.

The fossil humerus is relatively longer, more slender, and straighter than in recent penguins. It shows hardly a trace of longitudinal curvature. The proximal part of the shaft is slightly narrower than the distal, but the medial or distal expansion so prominent in the humeri of most recent penguins (least so in *Eudyptula*) is almost lacking. The preaxial angulation can, however, be recognized as a rather vague projecting roughening of the border at about one-third of the length above the distal end.

The head differs distinctly from recent penguins in that its long axis is more nearly anteroposterior. The posterior part of the articular surface is also less expanded transversely.

The tricipital fossa[1] is somewhat smaller than it would be in a recent humerus of comparable size. No recent humeri are of quite the same size, but the fossa in the fossil is about as large as in the distinctly smaller humerus of *Pygoscelis papula*. The fossa is not

[1] This is usually referred to as the pneumatic fossa, but in penguins it is not pneumatic. It lodges the third head of the triceps and is appropriately called the tricipital fossa in this group. The term anconeal fossa has also been used.

divided internally by a crest, as it is to varying degree in recent penguins, and its bipartite origin is only faintly shown by the presence of a small, shallow, vaguely bounded depression on the medial side.

The angulation of the distal end (with respect to the axis of the shaft) is decidedly sharper than in *Aptenodytes*, but can be exactly matched in some of the smaller recent penguins such as *Spheniscus humboldti*. The continuous ulnar and radial articulations are relatively wider and shorter than in recent penguins, and the two convexities are somewhat more nearly hemispherical. The two sesamoid grooves likewise are wider and shorter, but the difference is slight and their

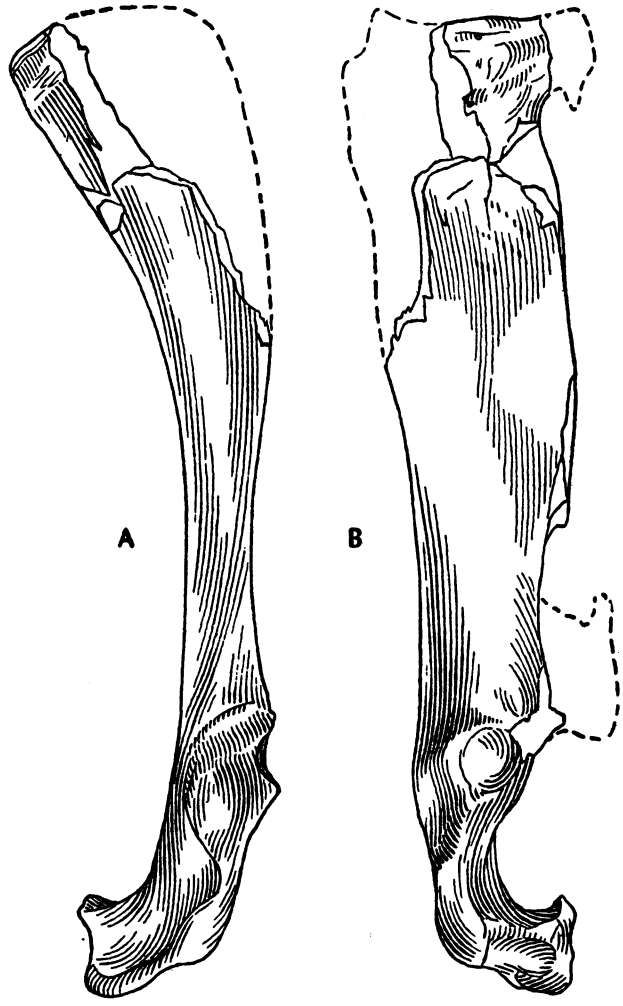


FIG. 4. *Paraptenodytes antarcticus* (Moreno and Mercerat). Right coracoid, A.M.N.H. No. 3338. A. Lateral view. B. Dorsal view. Contact of the posterior fragment (sternal articulation) with the main part of the bone is probable but not certain. The restoration of the crest to the procoracoid (broken line) is hypothetical, and an enclosed fenestra may have been present. ×1.

general structure is very much as in the recent genera.

ULNA

Our specimen does not include any wing bones distal to the humerus. Moreno and Mercerat (1891) listed but did not describe or illustrate an isolated ulna from Chubut referred to this species. Ameghino (1895, p. 92) mentioned an ulna of unstated origin, perhaps the same specimen as that listed by Moreno and Mercerat. His remarks, in translation, are as follows: "I am acquainted with the upper two-thirds of the ulna, 6 cm. in length and 13 to 20 mm. in width. This bone is very compressed, with straight edges, and must have been in contact with the radius along almost all its length." There is nothing really characteristic in this brief description.

METACARPUS

Ameghino (1895, p. 92) also mentioned a metacarpus of unstated origin as belonging to this species. His description may be translated as follows: "The two bones of the metacarpus are also in contact almost from one end to the other and united by synchondrosis at several points. The principal metacarpal, or second finger, is very wide and strongly flattened. Toward the middle it is 13 mm. wide but only 5 mm. thick. The metacarpal of the third finger is much smaller and less compressed. The two bones form a sort of bony blade 19 mm. wide." This description is

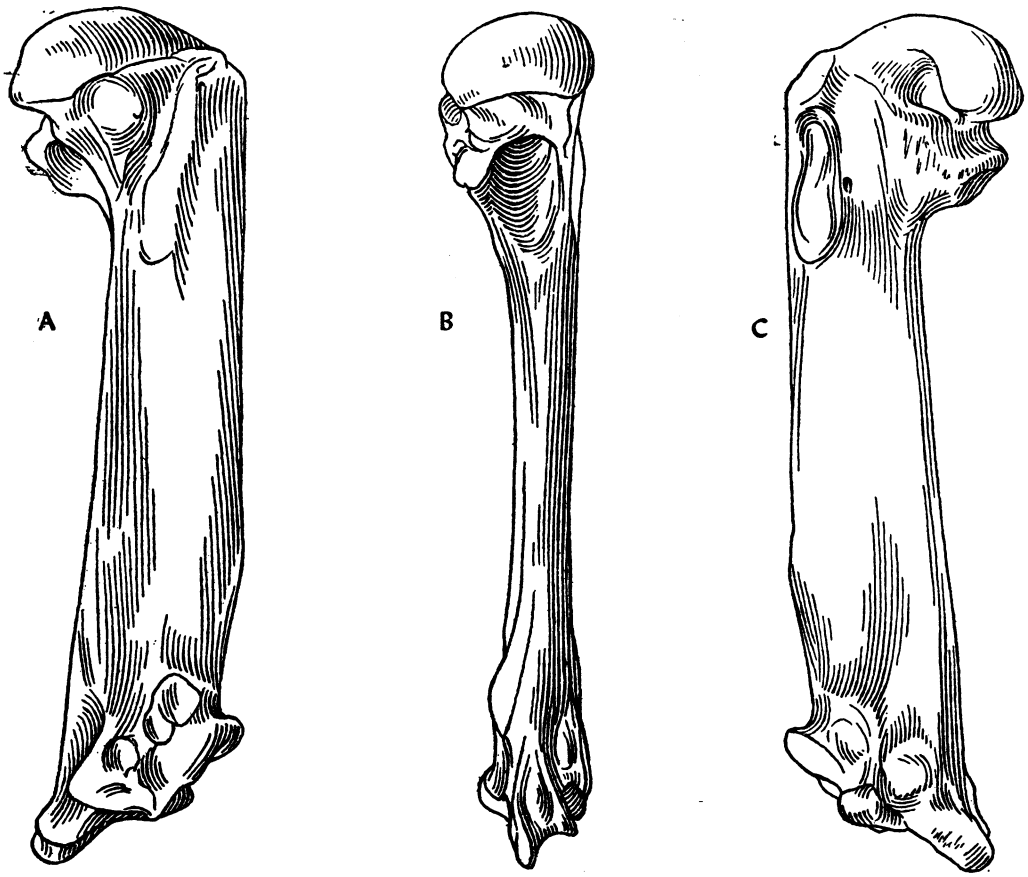


FIG. 5. *Paraptenodytes antarcticus* (Moreno and Mercerat). Right humerus, distal end completed by reversal from left humerus, A.M.N.H. No. 3338. A. Lateral view. B. Posterior view. C. Medial view. ×1.

also uncharacteristic. The stated dimensions are not impossible for this species, but the reference seems rather uncertain.

FEMUR

Figure 6

Our specimen includes the proximal end of the right, and distal end of the left, femur,

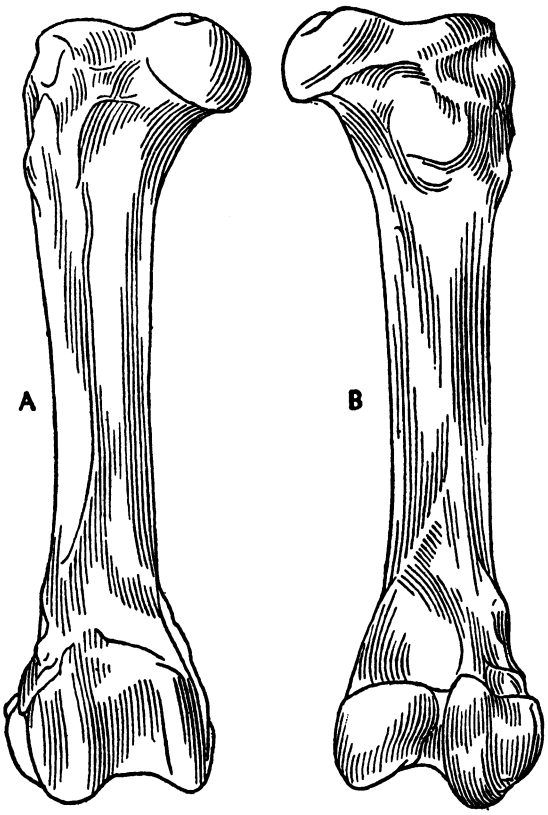


FIG. 6. *Paraptenodytes antarcticus* (Moreno and Mercerat). Right femur, A.M.N.H. No. 3338. A. Anterior view. B. Posterior view. The distal half of the bone is reversed from the left side, and the length, as reconstructed, must be nearly, but may not be exactly, correct. ×1.

showing the whole bone on one side or the other, and the type includes a complete right femur figured and described by Moreno and Mercerat (1891) and by Ameghino (1905). Like some others, this bone belies the name of the genus by being distinctly less like *Aptenodytes* than like some of the smaller genera, especially *Pygoscelis* and *Eudyptes*. Resemblance to *Spheniscus* is rather less close. In size and proportions (but not in morphology) the bone is nearly intermediate between the two species of *Aptenodytes*.

The greater trochanter does not rise above the head of the femur, and the posterior incisure between trochanter and head is very little developed, almost absent. The medial bending of the proximal end of the femur and oblique flattening of the lateral side of the trochanter, prominent in most of the smaller recent penguins, are virtually absent, and these features are a partial resemblance to *Aptenodytes forsteri*.

The anterior line is sharp and continuous for the whole length of the shaft, swinging laterad distally. The linea aspera is not like that of any recent penguin seen by me. Sharp and distinct, but low, it runs straight proximodistally on the middle of the posterior face of the shaft, and at about one-third of the length above the distal end it abruptly bifurcates into crests running to each condyle. In the type, as figured, these two crests seem both to be sharp. On our specimen the crest to the external condyle is more a rounded swelling without a sharp, true crest, but that to the internal condyle is very sharp and prominent.

On our specimen there is a deep popliteal fossa, but this seems to be shallower and less well defined in the type. Moreno and Mercerat speak of a median longitudinal crest in this fossa, but this is not present on our specimen, nor can I see it in their figure or in Ameghino's of their specimen.

The posterior articular surfaces of the condyles are so expanded and so crowded together that the intercondylar sulcus is reduced to a small, deep fissure, the floor of which is barely visible in posterior view because of the overhang of the external condyle —an exaggeration of the condition in *Pygoscelis*, for instance. In general, the condyles are broader and heavier than in recent penguins, even including *Aptenodytes forsteri*, which has an absolutely larger and relatively heavier femur than does the fossil. The patellar groove is also relatively broad and short (proximodistally).

The broken surfaces show that the shaft of the femur is formed of very solid and hard bone, almost like porcelain in the outer zone, but with a somewhat cancellous core.

TIBIOTARSUS

Figure 7

Moreno and Mercerat's type includes a right tibiotarsus, lacking the proximal end, and A.M.N.H. No. 3338 includes the proximal end of the right tibiotarsus, lacking only the ends of the cnemial crests, and the left tibiotarsus, lacking the whole proximal portion. As with other skeletal elements, this bone is not quite like that of any recent penguin, but the differences are rather slight. Greatest resemblance is probably with *Eudyptes*.

The external cnemial crest is particularly strong and is reflected externally. The internal crest has the usual form, but does not extend so far down the shaft as in recent penguins, becoming indistinguishable at a point only slightly more distal than the corresponding end of the external crest. The proximal part of the posterior face of the shaft is not angulate or crested as it is in all the recent penguins examined, but is broadly and smoothly rounded. The shaft here is more compressed anteroposteriorly in the fossil, instead of being distinctly trihedral as in the recent forms. In cross section it approaches a semicircle and its straight diameter (the flattened anterior or anteroexternal face). The flexor attachment is also unique, being a small, short, almost circular scar, with a slightly raised, crest-like rim on the internal (or anterior) side. In Moreno and Mercerat's specimen this crest seems to be somewhat straighter and longer, but still quite unlike the homologous feature in recent penguins.

The fibular crest is long and well developed. The distal end is gradual, rather than an abrupt tubercle as in *Aptenodytes*, for instance. At the distal end of the tibiotarsus the two oblique ligament crests are about equally salient (in *Pygoscelis* and *Spheniscus*, for instance, the internal is much more salient). The internal crest is heavier, more rounded, and extends farther proximally. The external crest is thinner and sharper. The bridge over the tendinal groove is relatively short and broad. The groove on the outer face of the external oblique ligament crest, which I take to be for a peroneal tendon, is more distinct than in any of the recent forms compared and contains a prominent, deep pit at about the level of the proximal end of the external condyle.

TARSOMETATARSUS

Figure 8

No perfect tarsometatarsus of this species is known, but our specimen has the left tarsometatarsus, lacking the middle and proximal parts of the external third, and part of the right tarsometatarsus, including the third metatarsus and the second except the trochlea. The type, described and figured by Moreno and Mercerat (1891) and Ameghino (1905), includes a right tarsometatarsus nearly complete except for the middle part of the fourth metatarsus.

This bone is more like that of the recent penguins than in almost any other known fossil species, although it does have some peculiarities. It is no wider than in *Aptenodytes* but is more elongate. Both in proportions and in morphology it is more like the smaller recent genera, not very close to *Spheniscus* (relatively aberrant in this bone), but particularly like *Pygoscelis*. In comparison with the latter, the intermetatarsal sulci are slightly less developed. The intermetatarsal foramina, both of which are present (as usual in recent but only exceptionally in fossil species), are relatively very small, barely larger, absolutely, than in the much smaller species of *Pygoscelis*. These foramina are also more proximal, occurring just below the proximal articular expansion instead of about a third of the way down as in *Pygoscelis* or near the middle of the shaft as in *Aptenodytes*.

As in *Pygoscelis*, again, the tibialis anticus tubercle is well developed and large, but smoothly rounded. It is almost in the middle of the shaft, relatively even a little more distal than in *Pygoscelis*, and so is far below the intermetatarsal foramina instead of between their lower ends as in the recent species that have it distinctly developed.

Both calcaneal tubercles are large, the internal somewhat the larger and more prominent, and each is divided by a vague groove into a fairly sharp and prominent medial, and a lower and less distinct lateral, projection. The sulcus between them is unusually distinct and narrow, almost semicircular in transverse section. As in *Pygoscelis* (but not

FIG. 7. *Paraptenodytes antarcticus* (Moreno and Mercerat). Right tibiotarsus, A.M.N.H. No. 3338. A. Anterior view. B. Posterior view. C. Lateral view. The distal half is reversed from the left side, and the length, as reconstructed, must be nearly, but may not be exactly, correct. ×1.

as in *Spheniscus*, for instance), the plantar openings of the intermetatarsal foramina are just distal to the more medial parts of the calcaneal tubercles. The plantar surface below this is almost plane, with slight convexities on the upper parts of the three metatarsals and very slight concavities on the third and fourth just above their trochleae.

The trochlear surfaces are broad and strong and do not tend to narrow proximally as much as is usual in most penguins. On the third trochlea, particularly, the articular surface extends far proximally and ends in a slight, rather hook-like overlap on both dorsal and plantar faces.

This last character is a distinction from the type of *P. antarcticus* and a resemblance to *Metancylornis* Ameghino. Some other characters stressed by Ameghino as generically diagnostic are absent or less developed in our specimen. There can, I think, be no doubt that our bird is *Paraptenodytes antarcticus*, and this emphasizes the fact that many of the minute details so meticulously described by Ameghino and used by him to distinguish genera and species are not really reliable taxonomically. Thus the inversion of all three trochleae is less in our specimen, the internal expansion of the proximal end is less, the internal border is not semicircular,

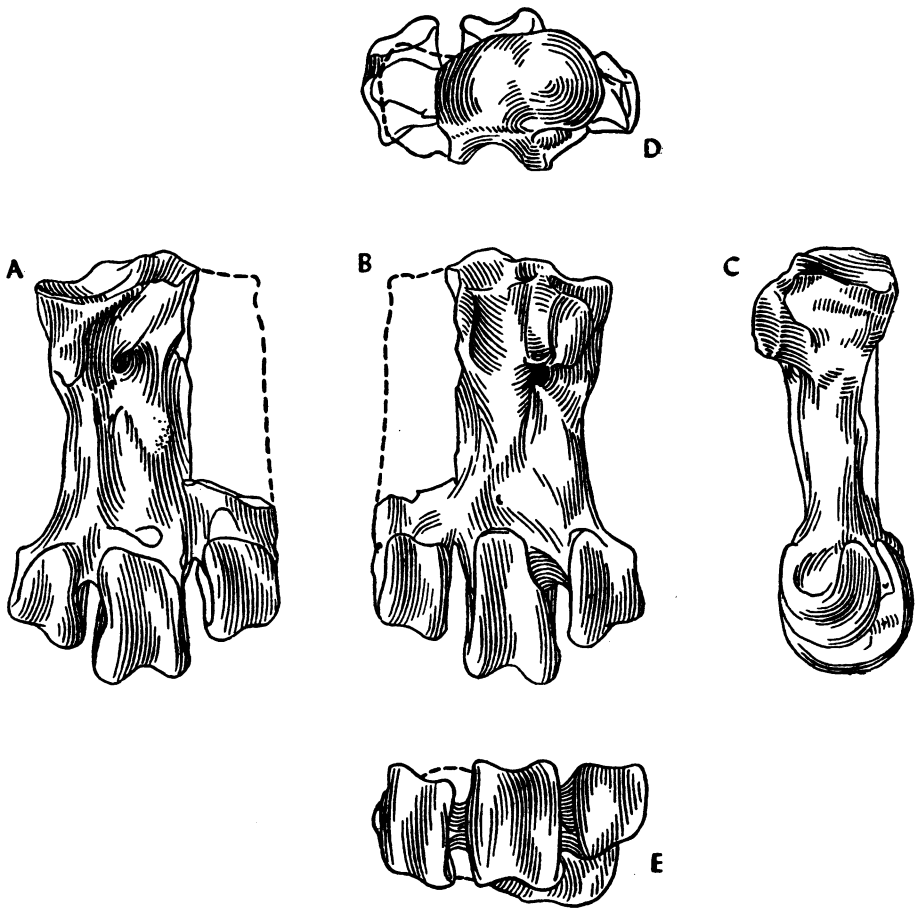


FIG. 8. *Paraptenodytes antarcticus* (Moreno and Mercerat). Left tarsometatarsus, A.M.N.H. No. 3338. A. Anterior view. B. Posterior view. C. Medial (internal) view. D. Proximal view, with anterior face up on the drawing. E. Distal view, with anterior face down on the drawing. Except as shown by broken outline, no reconstruction is involved. ×1.

the external trochlea is not distinctly elevated above the medial trochlea, and the scar supposedly representing the articulation of the first metatarsal is not so large or distinct.

DIMENSIONS

As nearly as the different proportions make such comparison possible, *Paraptenodytes antarcticus* was about the size of *Aptenodytes patagonicus*. The principal dimensions of the known limb bones are compared with that species and with three species of *Palaeospheniscus*, a contemporary and associate of *Paraptenodytes*, in table 2.

TABLE 2

MEASUREMENTS OF *Paraptenodytes antarcticus* AND OTHER SPECIES OF FOSSIL AND RECENT PENGUINS
(Numbers in parentheses are numbers of specimens measured; all measurements are in millimeters.)

Variate	*Paraptenodytes antarcticus*		*Palaeospheniscus*			*Aptenodytes patagonicus*
	A.M.N.H. No. 3338	Type	*gracilis*	*patagonicus*	*robustus*	
Humerus						
Length	114.1	—	(1) 70.3	(3) 73.7–76.7	(1) 83.7	(7) 112.4–122.3
Width above distal end	19.0	—	(3) 16.3–16.4	(6) 16.0–17.3	(1) 19.0	(7) 21.9–23.6
Radius						
Length	—	—	(1) 49.3	(1) 57.3	(1) 62.7	(7) 82.6–86.8
Width	—	—	(1) 13.9	(1) 13.8	(1) 15.0	(7) 18.9–21.1
Ulna						
Length	—	—	—	(2) 57.6–57.8	(3) 62.6–62.9	(8) 85.6–90.4
Width	—	—	(1) 15.7	(3) 18.4–19.7	(3) 20.7–22.3	(8) 19.6–21.3
Metacarpus						
Length	—	—	(1) 43.1	(3) 48.1–54.3	(1) 58.9	(8) 69.4–75.5
Distal width	—	—	(1) 15.5	(3) 19.1–19.4	(1) 19.5	(8) 19.9–23.6
Femur						
Length	—	115.9[a]	(1) 63	—	—	(12) 97.1–104.3
Distal width	27.2	26.4[a]	(2) 14.8–16.0	(3) 16.4–18.1	(1) 21.5	(12) 24.7–26.1
Tibiotarsus						
Length	—	ca. 178[a]	—	—	—	(7) 179–196
Distal width	24.8	27.8[a]	—	(2) 13.8–14.0	(1) 16.5	(7) 23.3–25.5
Tarsometatarsus						
Length	56.0	53 or 53.7[a]	(3) 32–34[b]	(3) 38–39[c]	(1) 42	(8) 46.0–49.1
Proximal width	ca. 30	28 or 29.6[a]	(2) 14	(3) 17.0–17.4[c]	(1) 19.1	(8) 26.7–28.2
Distal width	34.8	35 or 36[a]	—	(3) 21 –22[c]	—	(8) 31.6–35.5

[a] From Ameghino and Moreno and Mercerat.
[b] Including types of *P. gracilis* and *P. medianus*, from Ameghino.
[c] Including types of *P. menzbieri* and *P. patagonicus*, from Ameghino.

HUXLEY, MORENO AND MERCERAT, Ameghino, Wiman, and Oliver have named 23 genera and 35 species of fossils referred by them to the Sphenisciformes or Impennes. The type specimens are scattered in New Zealand, Argentina, England, and Sweden, and none has been available to me for first-hand study. Most of them have been carefully described and figured, but some data are deficient. For instance, precise measurements of Wiman's types are not available. It is also evident that several of the type specimens have been eroded and broken in ways impossible to evaluate adequately without closest examination of the originals and probably not described with complete reliability in the available literature. To attempt a real revision of these forms under present circumstance is thus quite impossible. It has, however, been necessary to review them in the course of the present study, and in the absence of a definitive revision, which is not likely to be forthcoming in the near future, a bibliographic conspectus with various taxonomic notes may be of use. Lambrecht (1933) has completely listed the genera and species, but he has not, even to the extent made possible by the literature, attempted a critical review.

After prolonged analysis of the problem, both qualitatively and statistically, with the further aid of the collection elsewhere mentioned, I am reluctantly forced to the conclusion that a truly definitive revision of the Tertiary penguins could not now be achieved even with all the type specimens in hand. The problem is so complex that it evidently cannot be solved by means of existing collections. Only eight specimens consisting of more than one bone in association have been reported. All of these are very incomplete, and in some cases the claimed association remains dubious. Sorting of isolated non-homologous bones according to species can be done only uncertainly and in part, because of the evidently varying proportions in the various species and the probable existence in the Miocene, as at present, of distinct species of nearly the same size, or of different gross size but with certain bones almost indistinguishable. A really clear idea of a natural taxonomy for this protean group will require larger collections of well-defined horizon and locality. Such collections could be obtained in the Patagonian formation, at least, but this remains a task for the future.

Wiman's and Ameghino's solution of the basic taxonomic problem was to found species on homologous type specimens, the tarsometatarsal bones. There are, nevertheless, eight named species, the types of which are other skeletal elements, and in only one of these is a (very doubtfully identified) referred tarsometatarsus known. Thus direct cross comparison is impossible for these species. Even among the species based on tarsometatarsi, the validity of the specific groupings is not sufficiently established. The specimens available are not sufficiently numerous for clear recognition of frequency groupings. No two tarsometatarsi are exactly alike, and a proper criterion of intra- and inter-specific variation has not hitherto been obtained or applied.

Studies made in connection with the present paper suggest, if they do not prove, that the tarsometatarsus is one of the more variable bones in the penguin skeleton, i.e., that it shows relatively great intra-specific and hence taxonomically non-significant variation. It is, indeed, probable that it is this relatively great variability that makes these bones seem so characteristic and that led to their being selected as a basis for taxonomy. Differences between them are easy to see, so they facilitate morphological definitions, but it does not follow that these correspond with taxonomic facts. Had the taxonomy been based on humeri, which are less "characteristic" in the sense that they have less obvious differences in morphology, it is probable that most or all of the valid species could have been recognized and that there would have been less danger of recognizing non-existent species. Also, as far as our own collection shows and the literature suggests, humeri are more numerous than tarsometatarsi in the collections and so would have given a better basis for grouping.

It is questionable whether any one bone would give generic groups really satisfactory

in the sense of corresponding in scope with recent genera or of giving a valid approximation of genetic affinities. In recent penguins the inter-specific variation of the more characteristic single skeletal elements is often of very nearly the same order as the inter-generic variation. This is one case where it is probable, contrary to the general rule, that paleontological methods well applied are more likely to recognize good species than good genera. At present, with a few exceptions, both species and genera of fossil penguins seem to be arbitrary morphological categories rather than true taxonomic units. Of course this does not deprive them of either practical or theoretical interest and value.

In the following conspectus the genera and species are arranged: first, according to the region where they were found, second (in the case of Patagonia), according to recorded geological horizon, and third, according to the approximate size of the birds represented, from smallest to largest.

PATAGONIA

DESEADO FORMATION

The Deseado is the "*Pyrotheriense*" or *Pyrotherium* beds of Ameghino, referred by him to the Cretaceous but now believed to be Oligocene. This formation everywhere contains a strictly terrestrial fauna, with the sole possible exception of the supposed penguins, and seems to have been deposited well inland. If Ameghino's reports of penguins were correct, these would be the only records of fossil penguins in other than marine or, at most, littoral beds, and these would be the oldest known fossil penguins. It is, however, most improbable that these reports are correct.

CRUSCHEDULA AMEGHINO

Cruschedula AMEGHINO, 1899, p. 9; 1906, p. 154; LAMBRECHT, 1933, p. 238.

TYPE: *Cruschedula revola*, by monotypy and author's designation.

COMMENTS: Ameghino referred this genus to the "Cladornidae," a proposed family of terrestrial penguins (see *Cladornis*, below). The single small fragment by which the genus is known does not seem to have any diagnostic sphenisciform characters. I have no idea what its true affinities may be, but I feel quite sure that it is not a penguin.

Cruschedula revola Ameghino

Cruschedula revola AMEGHINO, 1899, p. 9; 1905, p. 154, pl. 8, fig. 42 (tarsometatarsus); LAMBRECHT, 1933, p. 239.

TYPE: Incomplete distal end of a tarsometatarsus, in the Museo Nacional, Buenos Aires.

HORIZON AND LOCALITY: Reported by Ameghino as basal *Pyrotherium* beds, i.e., Deseado formation, of the Gulf of San Jorge, Patagonia.

COMMENTS: As for the genus.

PALAEOSPHENISCUS AMEGHINO

(This genus is characteristic of the Patagonian formation, see below.)

Palaeospheniscus gracilis Ameghino

Palaeospheniscus gracilis AMEGHINO, 1899, p. 9.
? *Palaeospheniscus gracilis*, AMEGHINO, 1905, p. 111, pl. 2, fig. 9 (tarsometatarsus); LAMBRECHT, 1933, p. 228.

TYPE: Incomplete right tarsometatarsus, Ameghino collection.

HORIZON AND LOCALITY: Reported as the highest part of the *Pyrotherium* beds, i.e., Deseado formation, of the Gulf of San Jorge, Patagonia.

COMMENTS: There is no doubt that this is a true penguin. It so closely resembles *Palaeospheniscus medianus* of the Patagonian formation that I think it probably the same species, in which case *P. gracilis* has priority. Its supposed occurrence in the Deseado is highly anomalous on two grounds: it is an essentially marine fossil reported from a strictly terrestrial horizon, and it is closely allied to, if not identical with, a species from a much later horizon belonging to a genus highly typical of that later deposit. It seems virtually certain that the specimen is, indeed, from the Patagonian formation and that it was found as drift on the surface of the Deseado. There are several fossiliferous localities where the Patagonian unconformably

overlies the Deseado and where fossils certainly of Patagonian age are found on the Deseado exposures, mingled with Deseado fossils. For instance, Loomis (1914, p. 225) says, "On the upper surface of the Deseado, we found several bones of this penguin-like type, but in all cases they were washed out, so that I have considered them as having come from the Patagonian." I can confirm this observation, which refers to a locality (Cabeza Blanca) that was worked by Carlos Ameghino, who collected the type of *Palaeospheniscus gracilis*. The record that that type is from "la parte más superior" of the Deseado is also significant and leaves, in my mind, no real doubt that this is from the Patagonian, not the Deseado.

CLADORNIS Ameghino

Cladornis Ameghino 1895, p. 584; 1898, p. 230; 1905, p. 151; Lambrecht, 1933, p. 238.

Type: *Cladornis pachypus*, by monotypy and author's designation.

Comments: Without first-hand restudy of the extraordinary bone on which this genus was founded, it would be hazardous to attempt a determination of its affinities. It is, however, so very unlike any known penguin, recent or fossil, that I can only consider its reference to that group as erroneous. Ameghino (1895, p. 584) based his family "Cladornidae" on this genus, to include also *Cruschedula* (above), and he commented that these forms, although Sphenisciformes ("Impennes"), were not marine, perhaps not even aquatic, but terrestrial. Although Wiman (1905b, pp. 12–14) expressed some doubt as to penguin affinities for *Cladornis*, he concluded that it is a transitional stage between the normal (flying) birds and the true penguins. The report of a terrestrial penguin giving evidence of such a transition has also been mentioned by some later authors (e.g., Murphy, 1936, p. 334). The evidence of *Cladornis* is altogether too dubious to have any value in this connection.

Cladornis pachypus Ameghino

Cladornis pachypus Ameghino, 1895, p. 584, fig. 35 (tarsometatarsus); 1898, p. 230; 1905, p. 152, fig. 3 (tarsometatarsus); Wiman, 1905b, p. 12, fig. 2 (after Ameghino, 1895); Lambrecht, 1933, p. 238.

Type: Incomplete distal end of a tarsometatarsus, British Museum.

Horizon and Locality: Reported by Ameghino as "*Pyrotheriense*" (Deseado) of the Río Deseado, Patagonia.

Comments: As for the genus.

PATAGONIAN FORMATION

This marine formation is relatively rich in fossil penguins, and a great majority of the known specimens are derived from it. The age of the formation has been much disputed. Ameghino insisted at great length and throughout his life that it is Eocene in age, but all more recent students agree that it is much later, and the consensus places it in the Miocene. Most, if not all, of the fossil penguins are from the lower parts of the Patagonian complex, probably referable to the Early Miocene.

ARGYRODYPTES Ameghino

Argyrodyptes Ameghino, 1905, p. 121; Lambrecht, 1933, p. 230.

Type: *Argyrodyptes microtarsus*, by monotypy and author's designation.

Comments: This genus certainly differs from any other named form, but the question whether it is really a penguin may be raised. The distal end of the tibiotarsus on which the genus is mainly based is smaller than in any (other?) known penguin, recent or fossil, with a narrower supratendinal bridge, with an unusually strong tendinal groove bounded externally by a high, sharp crest, and with the distal extremity of the bone strongly inverted. As a whole the bone seems to have been longer and more slender than in (other?) penguins. This is not one of the readily diagnostic parts of the penguin skeleton, but the structure is so stereotyped, apart from *Argyrodyptes*, that these differences may well mean that the bone in question is not really sphenisciform.

Argyrodyptes microtarsus Ameghino

Argyrodyptes microtarsus Ameghino, 1905, p. 121, pl. 3, fig. 17 (tibiotarsus), fig. 18 (femur); Lambrecht, 1933, p. 230.

Type: Distal end of tibiotarsus and associated distal end of femur, in the Museo Nacional, Buenos Aires.

HORIZON AND LOCALITY: Lower Patagonian formation of the Río Seco (San Julián), Patagonia.

COMMENTS: As for the genus.

NECULUS AMEGHINO

Neculus AMEGHINO, 1905, p. 127; LAMBRECHT, 1933, 231.

TYPE: *Neculus rothi*, by monotypy.

COMMENTS: The single fragmentary specmen is, in itself, clearly different from any other type specimen, but the significance of this is not evident. The parts preserved are not highly characteristic, and it is impossible to judge how far their peculiarities may be due to breakage, erosion, and, quite possibly, to the age of the individual. Although probable, it is not even wholly certain that this is a penguin. If the bone belongs to an adult, the type species is small, somewhat smaller than *Palaeospheniscus medianus*. Pending further study of the original, the genus must be considered dubious.

Neculus rothi Ameghino

Neculus Rothi AMEGHINO, 1905, p. 127, pl. 4, fig. 23 (tarsometatarsus); LAMBRECHT, 1933, p. 231.

TYPE: Fragment of distal end of a left tarsometatarsus with the median and internal trochleae, in the Museo de La Plata.

HORIZON AND LOCALITY: Patagonian formation, Trelew, Chubut.

COMMENTS: A very dubious species, see remarks on the genus.

PALAEOSPHENISCUS MORENO AND MERCERAT

Palaeospheniscus MORENO AND MERCERAT, 1891, p. 29; AMEGHINO, 1891, p. 440; 1895, p. 586; 1898, p. 230; 1905, p. 98; LAMBRECHT, 1933, p. 226; LOWE, 1939, p. 291 (erroneously attributed to Ameghino, 1894).

TYPE: *Palaeospheniscus patagonicus*, selected by Ameghino, 1891 (p. 447).

COMMENTS: This genus is certainly valid. It is quite distinct from any recent genus or from *Palaeeudyptes* Huxley, 1859, the only previously named extinct genus. It is the abundant, characteristic genus from the Patagonian formation and, even if all of Ameghino's genera be considered distinct, at least half the specimens from that formation belong in this genus. Its species cover no very great range in size, no more than in the living *Spheniscus*. The smallest known species are somewhat larger than *Spheniscus mendiculus* and the largest somewhat larger than *Spheniscus humboldti*. Despite the innumerable variations in details, the tarsometatarsi, on which all species but *P. robustus* are based, are quite stereotyped in general structure and leave little doubt that the forms placed here by Ameghino do all belong to a natural group—the question is rather whether some supposedly distinct genera (listed below) should not be united or reunited with *Palaeospheniscus*.

Palaeospheniscus medianus Ameghino

Palaeospheniscus medianus AMEGHINO, 1905, p. 108, pl. 1, fig. 6 (tarsometatarsus); LAMBRECHT, 1933, p. 227.

TYPE: Right tarsometatarsus lacking the external trochlea, in the Museo de La Plata.

HORIZON AND LOCALITY: Patagonian formation, Trelew, Patagonia.

COMMENTS: As is true of most of the species of this genus, the structural characters given by Ameghino, although unquestionably real, are of dubious taxonomic significance. For the most part they are details that manifestly and from the analogy of recent penguins exhibit considerable purely individual variation, for which Ameghino made no allowance at all. General form and proportions are very nearly as in *P. patagonicus*, but the size is probably significantly smaller. I cannot see in the published descriptions and figures any difference from *Palaeospheniscus gracilis* (the supposed Deseado species listed above) that is likely to be of specific value, and I tentatively consider *P. medianus* a synonym of that species. *Parasphenisсus nereius*, discussed below under that genus, is the only other Patagonian species of about this size.

Palaeospheniscus rothi Ameghino

Palaeospheniscus rothi AMEGHINO, 1905, p. 110, pl. 2, fig. 8 (tarsometatarsus); LAMBRECHT, 1933, p. 227.

TYPE: Complete left tarsometatarsus, in the Museo de La Plata.

HORIZON AND LOCALITY: Patagonian formation, Trelew, Chubut.

COMMENTS: Although smaller than the type of *P. patagonicus* and larger than that

of *P. medianus* (or *gracilis*), this type is well within the possible size range of either one. It differs rather markedly in two general features: the sculpturing, tendonal attachments, etc., of the dorsal surface are apparently less prominent, and the proximal end is less expanded transversely, making the proximal part of the bone appear to be more slender and to have more nearly parallel sides. Ameghino also emphasized the greater size of the median trochlea, but this is less striking in his figure than in his description. The index 100×length/proximal width is 259, the highest value known in any of the Patagonian fossils. There is considerable resemblance to *P. affinis* and *P. intermedius* (probable synonyms, see below). These are somewhat larger, but well within the probable range of a single species, making only minimal allowance for individual variation. There is almost equal resemblance to *Paraspheniscus bergi*, which is of almost exactly the same size as *Palaeospheniscus rothi*, although the width is a little greater, both relatively and absolutely. There are grounds for suspicion that all four of these specific names are synonyms, in spite of their being placed in two genera (see *Paraspheniscus*, below).

Palaeospheniscus planus Ameghino

Palaeospheniscus planus AMEGHINO, 1905, p. 109, pl. 1, fig. 7, pl. 2, fig. 7 (tarsometatarsus); LAMBRECHT, 1933, p. 227.

TYPE: Complete left tarsometatarsus, in the Museo de La Plata.

HORIZON AND LOCALITY: Patagonian formation, Gulf of San Jorge, Patagonia.

COMMENTS: As Ameghino noted, the type of this species closely resembles the generic type, *P. patagonicus*. The slight differences in sculpture, carefully described by the author, are not likely, in themselves, to be of full specific value if minimal variation in modern penguins be taken as a guide. The size differences would also be possible in a single species with a very low coefficient of variation (about 2). The most striking character seems to me to be the relatively narrow distal end or, to say the same thing in a different way, the relatively slight inversion of the medial trochlea. The species may be valid, but this is improbable.

Palaeospheniscus affinis Ameghino

Palaeospheniscus affinis AMEGHINO, 1905, p. 114, pl. 2, fig. 11 (tarsometatarsus); LAMBRECHT, 1933, p. 228.

TYPE: Complete left tarsometatarsus in the Museo de La Plata.

HORIZON AND LOCALITY: Patagonian formation, Trelew, Chubut.

COMMENTS: Ameghino drew attention to the close resemblance between this type and the only very slightly larger type of *P. intermedius*. It seems to me very probable that the two are synonyms. As mentioned above, it is further possible that both are synonyms of one or both of the two somewhat smaller but morphologically closely similar species *Palaeospheniscus rothi* and *Paraspheniscus bergi*.

Palaeospheniscus intermedius Ameghino

Palaeospheniscus intermedius AMEGHINO, 1905, p. 113, pl. 2, fig. 10 (tarsometatarsus); LAMBRECHT, 1933, p. 227.

TYPE: Complete left tarsometatarsus, Ameghino collection.

HORIZON AND LOCALITY: Patagonian formation (upper part, according to Ameghino), Gulf of San Jorge, Patagonia.

COMMENTS: The resemblance to, and possible synonymy with, *P. rothi* and *P. affinis* have been sufficiently noted under those species. Among these three species the page priority sequence is *rothi-intermedius-affinis*, and this priority may well be followed, as the types are all equally good. See also *Paraspheniscus bergi*, which has clear temporal priority over all three.

Palaeospheniscus menzbieri Moreno and Mercerat

Palaeospheniscus Menzbieri MORENO AND MERCERAT, 1891, p. 33, pl. 1, fig. 1 (humerus), fig. 3 (humerus), fig. 5 (humerus), fig. 6 (humerus), fig. 10 (tibiotarsus), fig. 11 (tibiotarsus), fig. 14 (ulna), fig. 17 (metacarpus), fig. 22 (tibiotarsus), fig. 24 (coracoid), pl. 2, fig. 6 (tarsometarsus); AMEGHINO, 1891, p. 447; 1895, p. 587; 1898, p. 230; 1905, p. 103, pl. 1, fig. 3 (tarsometatarsus); LAMBRECHT, 1933, p. 226.

TYPE: Complete right tarsometatarsus, selected by Ameghino, 1891. The original syntypes consisted of coracoid, humerus,

ulna, radius, metacarpus, tibiotarsus, tarsometatarsus, vertebrae, and sternum, no two of which were associated. All in the Museo de La Plata.

HORIZON AND LOCALITY: Patagonian formation, Trelew, Chubut.

COMMENTS: Moreno and Mercerat based this species, as they did *P. patagonicus* and *P. bergi*, on a large number of isolated skeletal elements, but I am unable to detect what principle they used in sorting these and distributing them in the three supposed species. For the most part the elements referred to *P. bergi* and *P. menzbieri* are of about the same size and (to my eye applied to their figures) barely distinguishable, although the tarsometatarsus of *P. bergi* is distinctly smaller than that of *P. menzbieri* and so different that Ameghino placed it in a different genus. On the other hand, the tarsometatarsi of *P. menzbieri* and *P. patagonicus* are of almost exactly the same size and closely similar in all respects, but most of the other skeletal parts referred to *P. patagonicus* were decidedly larger than those referred to *P. menzbieri* and otherwise more or less distinctive. For the most part, the skeletal parts referred by Moreno and Mercerat to *P. menzbieri* and *P. bergi* seem to me to belong to *P. patagonicus* and those referred by them to the latter species may, at least in part, belong to *P. robustus*.

Ignoring these apparently capricious assignments, the selection of tarsometatarsi as types of all three species by Ameghino may be accepted and the names tied to these. On this basis the differences between *P. menzbieri* and *P. patagonicus* (which has page priority and is also to be preferred because it is the type of the genus) all seem to me too slight to warrant specific separation.

Palaeospheniscus interruptus Ameghino

Palaeospheniscus interruptus AMEGHINO, 1905, p. 104, pl. 1, fig. 4 (tarsometatarsus); LAMBRECHT, 1933, p. 227.

TYPE: Right tarsometatarsus, lacking the medial and internal trochleae, in the Museo de La Plata.

HORIZON AND LOCALITY: Patagonian formation, Trelew, Chubut.

COMMENT: This proposed species is of the same size as *P. patagonicus* and closely resembles it, but has minor differences in morphology, described in great detail by Ameghino. The species seems to me probably synonymous with *P. patagonicus*, but the type is poor and the synonymy uncertain.

Palaeospheniscus patagonicus Moreno and Mercerat

Palaeospheniscus patagonicus MORENO AND MERCERAT, 1891, p. 31, pl. 1, fig. 7 (femur), figs. 8–9 (humerus), fig. 12 (femur), fig. 13 (metacarpus), figs. 15–16 (tibiotarsus), fig. 21 (radius), fig. 25 (coracoid), fig. 27 (ulna), pl. 2, fig. 5 (tarsometatarsus); AMEGHINO, 1891, p. 447; 1895, p. 587; 1898, p. 230; 1905, p. 99, pl. 1, figs. 1–2 (tarsometatarsi); WIMAN, 1905b, p. 12; LAMBRECHT, 1933, p. 226.

TYPE: Imperfect left tarsometatarsus selected by Ameghino, 1891. The authors' syntypes included humerus, radius, ulna, metacarpus, femur, tibiotarsus, tarsometatarsus, coracoid, scapula, and vertebrae, none associated.

HORIZON AND LOCALITY: Patagonian formation, Trelew, Chubut.

COMMENTS: On Moreno and Mercerat's sorting of their syntypes, see *P. menzbieri*, above. Their tarsometatarsus, Ameghino's lectotype, is broken and repaired in such a way as to obscure important characters, but Ameghino referred a perfect tarsometatarsus (1905, pl. 1, fig. 2) which seems surely to be of the same species and is an adequate basis for comparison.[1] The species, designated type of the genus by Ameghino, is certainly valid and is the point of departure for the taxonomy of the smaller Tertiary penguins.

Palaeospheniscus robustus Ameghino

Palaeospheniscus robustus AMEGHINO, 1895, p. 588, fig. 36 (humerus); 1898, p. 230, fig. 91, VII (humerus); 1905, p. 105, fig. 1 (humerus), pl. 1, fig. 5 (tarsometatarsus); SAEZ, 1927, p. 77; LAMBRECHT, 1933, 227.

TYPE: A complete humerus in the British Museum. In the original description Ameghino also mentioned two incomplete femora.

[1] Ameghino (1905, p. 100) called this a "cootipo" [*sic!*], but there is no evidence that it was in Moreno and Mercerat's hypodigm or among their syntypes. If given any status as a type, it is a neotype, but I do not think such designation warranted.

HORIZON AND LOCALITY: Patagonian formation. Locality of type not stated. Referred tarsometatarsus from Trelew, Chubut.

COMMENTS: This is the only species of *Palaeospheniscus* based on a bone other than the tarsometatarsus, with the consequence that no direct comparison of types is possible. Previous comparison has depended on Ameghino's reference of a tarsometatarsus to *P. robustus*. This bone is of almost exactly the same size as the lectotype of *P. patagonicus* and is in general so similar that it probably belongs to that species. The question then is whether it was correctly associated with the type of *P. robustus*. The index 100×length humerus/length tarsometatarsus would be 231 if these bones were associated. Values in this range occur among recent penguins and are certainly quite possible (although neither typical nor constant as stated by Dolgopol de Saez, 1927). There are, however, reasons for thinking that this tarsometatarsus should be associated with a shorter humerus, and hence that the index for this species was smaller. It is known that the tarsometatarsi of the Miocene penguins were relatively longer, and this would be expected to give lower indices than in recent forms. In the one case where both measurements can be made accurately on surely associated bones (the skeleton of *Paraptenodytes antarcticus* described in this paper) the index is only 204. In *Isotremornis nordenskjöldi*, according to Ameghino's estimated lengths and claimed association, the index is only 182, but this is doubtless low even for a Tertiary penguin since this species has not only a relatively long tarsometatarsus but also a relatively short humerus.

More important than these considerations is the fact that almost all the *Palaeospheniscus* bones from the Patagonian formation, including the series figured by Moreno and Mercerat (1891) and a series of about 100 specimens in our collection, fall into three fairly clear size groups. Size ratios in each group, actual articulation of adjacent bones, and relative abundance of the separate bones in each group are all quite consistent. The *P. robustus* type humerus belongs in the largest group of the three. The tarsometatarsus referred by Ameghino belongs, on the contrary, in the middle size group, individually most abundant and including the type of *P. patagonicus*.

Tarsometatarsi of the size group to which the *P. robustus* type belongs would be about 40–45 mm. in length. Named species of tarsometatarsi in this size range are *Perispheniscus wimani*, length 42.5 mm., and *Treleudytes crassus*, length 41.5 mm., species that I think almost surely synonymous (see below), and there is nothing to prevent the *Palaeospheniscus robustus* humerus from belonging with these tarsometatarsi. *P. robustus* has priority over *P. wimani* and *T. crassus*. There is also a tarsometatarsus in our collection, A.M.N.H. No. 3324, of appropriate size for this species and morphologically intermediate between *P. wimani* and *T. crassus* on one hand and *P. patagonicus* on the other (see *P. wimani*).

PARASPHENISCUS AMEGHINO

Paraspheniscus AMEGHINO, 1905, p. 115; LAMBRECHT, 1933, p. 228.

TYPE: *Paraspheniscus bergi*, designated by author.

COMMENTS: The various peculiarities involved in the generic definition seem for the most part to be variations that do also occur in species referred by Ameghino to *Palaeospheniscus*, although perhaps carried a little further in *Paraspheniscus bergi*. The most striking peculiarities seem to be the almost complete absence of sculpturing, other than the groove between metatarsals III and IV, on the dorsal surface of the tarsometatarsus, along with the rather narrow proximal end and relatively parallel sides of the shaft. These characters also appear in varying degree and detail in *Palaeospheniscus rothi*, *affinis*, and *intermedius*. The first of these species is based on a type about the same size as that of *Paraspheniscus bergi*. The other two are a little larger, but still within the size range of a little-variable single species. In short, *Paraspheniscus* is not well differentiated from *Palaeospheniscus*. The type species may be, but are not surely, distinct, so the genera might possibly be maintained, but if so I would draw the line in a different place and include the above-mentioned species in *Paraspheniscus*.

Parasphenisscus nereius (Ameghino)

Palaeospheniscus nereius AMEGHINO, 1901, p. 81.

Parasphenisscus nereius, AMEGHINO, 1905, p. 116, pl. 2, fig. 13 (tarsometatarsus): LAMBRECHT, 1933, p. 229.

TYPE: Almost complete left tarsometatarsus, Ameghino collection.

HORIZON AND LOCALITY: Patagonian formation, Gulf of San Jorge, Patagonia.

COMMENTS: This species is essentially similar to *P. bergi* in morphology, but is smaller and has a less expanded distal end. The distal width is outside the most probable specific range of *P. bergi*, at least if a small coefficient of variation be assumed for that species, and if the larger *P. affinis* and *P. intermedius* should, as I think possible, prove to be synonyms of *P. bergi*, then the length of *P. nereius* would also be below the probable specific range of *P. bergi*. *P. nereius* is almost exactly the size of *Palaeospheniscus medianus*, but is morphologically rather distinctive. Thus *P. nereius* may be a valid species, but a poorly characterized and puzzling one. (The possibility that some supposed distinctions are due to age must be borne in mind, but cannot be fully explored in materials available to me.)

Parasphenisscus bergi (Moreno and Mercerat)

Palaeospheniscus Bergi MORENO AND MERCERAT, 1891, p. 34, pl. 1, fig. 2 (humerus), fig. 4 (humerus), figs. 18–20 (radius), fig. 25 (coracoid), fig. 26 (metacarpus), pl. 2, fig. 7 (sternum), fig. 8 (tarsometatarsus); AMEGHINO, 1895, p. 587; 1898, p. 230; WIMAN, 1905b, p. 12.

Palaeospheniscus Bergii, AMEGHINO, 1891, p. 447.

Palaeospheniscus bergi, LOWE, 1933, p. 511.

Parasphenisscus Bergi, AMEGHINO, 1905, p. 115, pl. 2, fig. 12 (tarsometatarsus): LAMBRECHT, 1933, p. 228.

TYPE: Complete left tarsometatarsus, in Museo de La Plata, selected by Ameghino (1891). Authors' syntypes included humerus, radius, metacarpus, femur, tarsometatarsus, sternum, and coracoid, in Museo de La Plata. Other specimens supposedly of this species include humerus, metacarpus, femur, tibiotarsus, tarsometatarsus, coracoid, sacrum, and vertebrae in the British Museum.

HORIZON AND LOCALITY: Patagonian formation, Trelew, Chubut.

COMMENTS: On the capricious assignment of specimens to this species in their syntype series by Moreno and Mercerat, see *Palaeospheniscus menzbieri* on a previous page. Possible affinities and synonymy have been mentioned under the genus.

PSEUDOSPHENISCUS AMEGHINO

Pseudospheniscus AMEGHINO, 1905, p. 123; LAMBRECHT, 1933, p. 230.

TYPE: *Pseudospheniscus interplanus*, designated by author.

COMMENTS: This genus was founded on a very fragmentary specimen. Its distinctive characters are supposed to be great dorsoventral compression, presence of a large internal intermetatarsal foramen, and presence of a distinct groove for a tendon in the notch between medial and external trochleae. In view of the very poor preservation and some possible anomalies in Ameghino's restoration, none of these characters seems completely certain. The validity of the genus and its type species can hardly be judged one way or the other.

Pseudospheniscus concavus Ameghino

? *Pseudospheniscus concavus* AMEGHINO, 1905, p. 124, pl. 3, fig. 20 (tarsometatarsus); LAMBRECHT, 1933, p. 230.

TYPE: Small fragment of distal end of a tarsometatarsus with the median and internal trochleae, in the Museo Nacional, Buenos Aires.

HORIZON AND LOCALITY: Lower Patagonian, San Julián, Patagonia.

COMMENTS: The tentative generic assignment was based on the dorsoventral compression of the fragment preserved and on the presence of a groove in the notch between external and median trochleae. Ameghino suggested that the species might become type of a distinct genus when better known. The size is small, perhaps about like *Palaeospheniscus medianus*. The type specimen is so fragmentary and its general character so dubious that its affinities seem quite uncertain.

Pseudospheniscus interplanus Ameghino

Pseudospheniscus interplanus AMEGHINO, 1905, p. 123, pl. 3, fig. 19 (tarsometatarsus); LAMBRECHT, 1933, p. 230.

TYPE: Part of the distal end of a tarsometa-

tarsus with the median and internal trochleae, in the Museo Nacional, Buenos Aires.

HORIZON AND LOCALITY: Lower Patagonian, San Julián, Patagonia.

COMMENTS: See discussion of the genus, above. The species appears to have had about the size of *Perispheniscus wimani*.

APTERODYTES AMEGHINO

Apterodytes AMEGHINO, 1891, p. 81.

Palaeoapterodytes AMEGHINO, 1905, p. 120 (new name for *Apterodytes* on grounds of preoccupation by *Apterodyta*); LAMBRECHT, 1933, p. 229.

TYPE: *Apterodytes ictus*, by monotypy.

COMMENTS: This extraordinary genus was defined as having lost all of the wing except the proximal part of the humerus. Lambrecht (1933, pp. 229–230) has suggested that this may be merely based on a normal penguin humerus, broken and weathered. Another possibility is that the bone is pathological. Any other explanation than one of these two is completely incredible. The genus is doubtless technically a synonym of *Palaeospheniscus* or some other from these beds, but synonymy can hardly be established. Based on a manifest error, the name might best be quietly forgotten.

Apterodytes ictus Ameghino

Apterodytes ictus AMEGHINO, 1901, p. 81.

Palaeoapterodytes ictus, AMEGHINO, 1905, p. 120, pl. 3, fig. 16 (humerus); LAMBRECHT, 1933, p. 229.

TYPE: Fragment of proximal part of a humerus, in the Museo Nacional, Buenos Aires.

HORIZON AND LOCALITY: Upper Patagonian of the Gulf of San Jorge (according to Ameghino).

COMMENTS: The species is indeterminate, the name a *nomen vanum*.

TRELEUDYTES AMEGHINO

Treleudytes AMEGHINO, 1905, p. 156; LAMBRECHT, 1933, p. 235.

TYPE: *Treleudytes crassa*, by monotypy.

COMMENTS: Ameghino called attention to the close resemblance of this genus to *Perispheniscus*, and in fact his definition seems to involve no real distinction from that genus except that the tarsometatarsus of *Treleudytes* is more robust. The generic value of such a difference, even if strongly marked, might be questioned, and in this case the degree is so slight as not to warrant even specific separation. There is little doubt that the genus is synonymous with *Perispheniscus*.

Treleudytes crassus[1] Ameghino

Treleudytes crassa AMEGHINO, 1905, p. 156, fig. 4; LAMBRECHT, 1933, p. 235.

TYPE: Complete left tarsometatarsus, in the Museo Nacional, Buenos Aires.

HORIZON AND LOCALITY: Patagonian formation, Trelew, Chubut.

COMMENTS: The type is slightly shorter than that of *Perispheniscus wimani* but is relatively broader and has the proximal end broader relative to the distal end. These differences in size and proportion are so slight in degree that they are well within the expected range in a little-variable single species, and the specific (not to say generic) distinction does not seem well founded.

PERISPHENISCUS AMEGHINO

Perispheniscus AMEGHINO, 1905, p. 117; LAMBRECHT, 1933, p. 229.

TYPE: *Perispheniscus wimani*, by monotypy.

COMMENTS: The tarsometatarsus on which this genus was based is closely similar to that of *Palaeospheniscus patagonicus* except in minor, variable details. *P. wimani* is larger, sufficiently so to validate the species but not the genus. The bone is relatively stout, the head decidedly deeper, in a dorsoplantar direction, than in *P. patagonicus*. The calcaneal tubercles are broad, and their ridges, especially that below the external tubercle, extend as angulations farther distally than in *P. patagonicus*, so that the groove between the tubercles is continued distally as a sort of raised platform or causeway between these angulations. A.M.N.H. No. 3324 has nearly the same size and proportions as the type of *P. wimani* and has the same deep head and broad tubercles but has the ridges only a little more prolonged than in *P. patagonicus*. This bone tends definitely to link *Perispheniscus* and *Palaeospheniscus* and to

[1] Usage has varied, but it may be well to consider genera ending in *-dytes* as uniformly masculine. The emendation is, of course, permitted under the International Rules.

minimize their apparent distinction. The genera are certainly very closely related, although they have surely different species as types. Whether to recognize them as different genera is a question of degree and of taste. As noted under that genus, *Treleudytes* is almost certainly a synonym of *Perispheniscus*, whether or not the latter be considered synonymous with *Palaeospheniscus*.

Perispheniscus wimani Ameghino

Perispheniscus wimani AMEGHINO, 1905, p. 117, pl. 2, fig. 14, pl. 3, fig. 14 (tarsometatarsus), pl. 3, fig. 15 (humerus); LAMBRECHT, 1933, p. 229, fig. 94a (tarsometatarsus, after Ameghino).

TYPE: Complete left tarsometatarsus, Museo de La Plata.

HORIZON AND LOCALITY: Patagonian formation, coast of Patagonia.

COMMENTS: The species is somewhat larger than *Palaeospheniscus patagonicus* and is outside the probable size range of that species, apart from the morphological differences noted in discussion of the genus. As noted above, *Treleudytes crassus* is a probable synonym. Ameghino referred a humerus to this species on the basis of size, but I believe that this humerus belongs to a larger species. If the association were correct, the length index relative to the tarsometatarsus would be 240, a value that is possible but that is probably too high for a Miocene penguin of this general type. If the index were around 200–205, as it is known to be in *Paraptenodytes antarcticus*, the corresponding tarsometatarsus would be about 50–51 mm. in length, i.e., within the probable size range of *P. antarcticus*, the two known tarsometatarsi of which are 53–56 mm. in length. It is, moreover, clear that this humerus is very unlike that of *Palaeospheniscus* but is, as far as Ameghino's figures and description show, exactly like that of *Paraptenodytes antarcticus* except for being slightly smaller than our specimen of that species—a specimen that is somewhat larger than the type. The tarsometatarsus of *Perispheniscus wimani* is barely (if at all) distinguishable generically from that of *Palaeospheniscus*, and similar resemblance in the humerus would be expected. The humerus on which Ameghino based the species *Palaeospheniscus robustus* is, as noted in discussing that species, of size and structure that would be expected to accompany the tarsometatarsus called *Perispheniscus wimani*, and all the evidence seems to me to be quite impelling that this is, in fact, the correct association. The humerus that Ameghino referred to *Perispheniscus wimani* would, then, belong instead to *Paraptenodytes* and probably to *P. antarcticus*. (It is apparently too large to belong to *Metancylornis curtus*, which I believe to represent a smaller species of *Paraptenodytes*.)

If these various tentative but probable associations prove to be correct, the present species will be correctly named *Palaeospheniscus* (or perhaps *Perispheniscus*) *robustus*, with *Perispheniscus wimani* and *Treleudytes crassus* as synonyms.

METANCYLORNIS AMEGHINO

Metancylornis AMEGHINO, 1905, p. 129; LAMBRECHT, 1933, p. 231.

TYPE: *Metancylornis curtus*, by monotypy and author's designation.

COMMENTS: This genus is markedly different from all those discussed up to this point, but it closely resembles *Paraptenodytes*, to which Ameghino first referred its type species. The only noteworthy differences in the tarsometatarsus from *P. antarcticus* are that it is smaller over all, somewhat stouter (wider relative to length, length-proximal breadth index 175 compared with about 180–190 in *P. antarcticus*), and with a larger external intermetatarsal foramen. Another feature, stressed by Ameghino, is the great proximal extension of the median trochlea and its ending with an overhang or hook. This is barely suggested in the type of *P. antarcticus* but is clearly developed in our specimen of the same species, so that the character does not have specific, let alone generic, value. Although the type species seems to be distinct, I do not believe that generic separation of *Metancylornis* from *Paraptenodytes* has been sufficiently justified.

Metancylornis curtus (Ameghino)

Paraptenodytes curtus AMEGHINO, 1901, p. 81.

Metancylornis curtus, AMEGHINO, 1905, p. 129, pl. 4, fig. 25 (tarsometatarsus), fig. 26 (humerus); LAMBRECHT, 1933, p. 231.

TYPE: Right tarsometatarsus lacking the

internal trochlea and supposedly associated proximal end of a right humerus in the Museo Nacional, Buenos Aires.

HORIZON AND LOCALITY: Lower Patagonian formation, San Julián, Patagonia.

COMMENTS: As noted under the genus, the tarsometatarsus seems to represent a valid species referable to *Paraptenodytes*. The supposedly associated humerus fragment is puzzling. Although the tarsometatarsus is decidedly smaller than in *P. antarcticus*, this fragment represents a humerus that is slightly larger and distinctly heavier in the shaft than that of *P. antarcticus*. Such marked discrepancy in proportions is barely credible. The evidence of association is that the two were found together, but it is (I can testify) not uncommon to find isolated remains of two different penguins at one spot in the Patagonian formation, and these are from widely distant parts of the skeleton. It seems probable that they were not, after all, from one animal and that the humerus belongs to a different and larger species, not identifiable from the available data.

ISOTREMORNIS AMEGHINO

Isotremornis AMEGHINO, 1905, p. 134; LAMBRECHT, 1933, p. 232.

TYPE: *Isotremornis nordenskjöldi*, by monotypy and author's designation.

COMMENTS: This proposed genus closely resembles *Paraptenodytes* and its probable synonym *Metancylornis*. Its validity depends largely on whether or not the four incomplete bones on which the type species is based are correctly associated. The tarsometatarsus can hardly be distinguished in the preserved parts from that of *Paraptenodytes antarcticus*. The only clear differences seem to be that the tibialis anticus tubercle is more proximal and the internal intermetatarsal groove smaller, both variations that could, in this degree, be intra-specific. The poorly preserved distal end of a femur is also within the probable range of *P. antarcticus* in all respects. The humerus, however, is markedly different. It is shorter than in *P. antarcticus* but notably wider and heavier throughout, giving it proportions and a general aspect unique among known penguins. On this basis, the species surely, and the genus probably, should be recognized as distinct.

Isotremornis nordenskjöldi Ameghino

Isotremornis Nordenskjöldi AMEGHINO, 1905, p. 134, pl. 4, fig. 28[1] (tarsometatarsus), pl. 5, figs. 29–30 (humerus), fig. 31 (femur); LAMBRECHT, 1933, p. 232.

TYPE: Incomplete proximal part of left tarsometatarsus, somewhat broken right humerus, distal end of left humerus, badly preserved distal part of left femur, supposedly associated, in the Museo Nacional, Buenos Aires. In view of the possibility that these bones are not, after all, of one individual, I designate the most distinctive of them, the right humerus, as lectotype.

HORIZON AND LOCALITY: Lower Patagonian formation, San Julián, Patagonia.

COMMENTS: See remarks on the genus.

PARAPTENODYTES AMEGHINO

Paraptenodytes AMEGHINO, 1891, p. 447; 1895, p. 589; 1898, p. 230; 1905, p. 138; LAMBRECHT, 1933, p. 232.

TYPE: *Paraptenodytes antarcticus*, by monotypy and author's designation.

COMMENTS: The genus is certainly valid. It has been fully described in a previous section of this paper.

Paraptenodytes antarcticus (Moreno and Mercerat)

Palaeospheniscus antarcticus MORENO AND MERCERAT, 1891, p. 30, pl. 2, fig. 1 (femur), fig. 2 (tibiotarsus), fig. 4 (tarsometatarsus); WIMAN, 1905b, p. 12.

Paraptenodytes antarcticus, AMEGHINO, 1891, p. 447; 1895, p. 589, fig. 37 (mandible); 1898, p. 230, fig. 91, VIII (mandible); 1905, p. 139, fig. 2 (mandible); pl. 5, fig. 32 (tarsometatarsus); pl. 6, fig. 33 (femur), fig. 34 (tibiotarsus); LAMBRECHT, 1933, p. 232.

TYPE: Associated right complete femur, tibiotarsus imperfect proximally, and tarsometatarsus broken on the external border, in the Museo de La Plata. Selected by Ameghino from Moreno and Mercerat's material, which also included dissociated ulna, femur, and tibia.

OTHER SPECIMENS: Lambrecht (1933, p. 233) lists an ulna and tibiotarsus in the

[1] By error there are two figures marked "28a" on this plate. That in the lower right should be marked "27a" and is not *Isotremornis*.

British Museum. The mandible figured by Ameghino is of very doubtful reference, as he concluded (1905, p. 143). A.M.N.H. No. 3338 is fully described in this paper. As noted above, I think that the humerus referred by Ameghino to *Perispheniscus wimani* also probably represents the present species.

HORIZON AND LOCALITY: Patagonian formation, Patagonia. According to Ameghino, the type is from the mouth of the Río Santa Cruz. Moreno and Mercerat's other material, according to them, is from Chubut.[1] Our specimen is from near Trelew, Chubut (see above).

COMMENTS: Fully described in a previous section of this paper.

ARTHRODYTES AMEGHINO

Arthrodytes AMEGHINO, 1905, p. 143; LAMBRECHT, 1933, p. 233.

TYPE: *Arthrodytes grandis*, by author's designation.

COMMENTS: This is one of the few proposed genera in which the tarsometatarsus is not known, and comparisons are accordingly difficult. The generic definition was based solely on the distal part of the femur, much larger than any other known from Patagonia. Distinctions from *Paraptenodytes*, as noted by Ameghino, include (in addition to markedly greater size) the short and shallow rotular trochlea (or patellar facet) and the broad but shallow intercondylar groove, not running through a deep notch as in *Paraptenodytes* but over a broad transverse ridge or convexity. These same characters are visible in Wiman's figure (1905b, pl. 4, fig. 2) of his "group 3" femur, presumed to correspond with the tarsometatarsus named *Anthropornis nordenskjöldi*, and this femur is, moreover, of almost precisely the same size as that of *Arthrodytes grandis*. On this basis a generic separation would be unjustified and specific distinction doubtful.

The very fragmentary humerus said by Ameghino to be surely of the same individual as the femur described above is, on the other hand, notably smaller than Wiman's "group 3" humeri, although longer and stouter than this part in *Paraptenodytes antarcticus*. In our specimen of the latter species the short diameter of the head is 20.4 mm., and this dimension is given by Ameghino as 23 mm. in *Arthrodytes grandis*, 13 per cent larger. The transverse diameter of the distal end of the femur is 30 per cent greater in *Arthrodytes grandis*, a noteworthy discrepancy, although one not impossible for the varying proportions of two species. A firm conclusion cannot be drawn, especially as the grouping of Wiman's specimens is also open to question, but it may at least be said that the distinction of *Arthrodytes* from *Anthropornis* is not established. Ameghino also notes that *Arthrodytes* could be a synonym of *Pachypteryx* Wiman, but in this case there is no basis for direct comparison because neither a known humerus nor femur has been referred to *Pachypteryx* (which is probably a synonym of *Anthropornis*, see below).

Arthrodytes grandis (Ameghino)

Paraptenodytes grandis AMEGHINO, 1901, p. 18.
Arthrodytes grandis, AMEGHINO, 1905, p. 144, pl. 5, fig. 35 (humerus), pl. 6, fig. 36 (femur); LAMBRECHT, 1933, p. 233.

TYPE: Presumably associated distal end of left femur and damaged proximal end of right humerus, in the Museo Nacional, Buenos Aires. Lectotype here selected, in case the association should prove to be erroneous, the femur fragment.

HORIZON AND LOCALITY: Lower Patagonian formation, San Julián, Patagonia.

COMMENTS: Ameghino (1905, p. 144) says that the humerus and femur are surely of one individual because they were found together and completely isolated. In view of the further fact that penguins of this approximate size are very rare in the Patagonian formation, this is suggestive evidence, although inconclusive. The association of parts so distant in the skeleton, without other bones, is unusual, and the size relations are somewhat anomalous (see above). The species is certainly valid, having been named before any of the possible synonyms from Seymour Island (see discussion of the genus, above).

[1] Lambrecht (1933, p. 233) seems to imply that Moreno and Mercerat listed the type or all their material as from Chubut, but they said that the bones later made lectotype were from Santa Cruz (1891, p. 16).

Arthrodytes andrewsi (Ameghino)

Paraptenodytes Andrewsi AMEGHINO, 1901, p. 81.

Arthrodytes Andrewsi, AMEGHINO, 1905, p. 146, pl. 7, fig. 37 (humerus), pl. 8, fig. 38 (coracoid), fig. 39 (scapula); LAMBRECHT, 1933, p. 233.

TYPES: Complete right humerus, right coracoid with angular extremities broken off, and proximal end of right scapula, all said to be associated. In the Museo Nacional, Buenos Aires.

HORIZON AND LOCALITY: Lower Patagonian formation in the Bajo de San Julián, Patagonia.

COMMENTS: The basis of comparison with *A. grandis* is the head of the humerus, which is significantly larger in the present species. Since the generic characters are based on the femur, unknown in this species, the reference to *Arthrodytes* is, as Ameghino noted, rather a matter of assumption and probability than of concrete evidence. The possibility, however slight, that the *A. grandis* humerus is not really of that species also tends to make the probable specific distinction, on one hand, and the mooted generic association, on the other, quite uncertain.

Ameghino (1905, p. 147) pointed out that *Anthropornis nordenskjöldi* Wiman, from Seymour Island, could be a synonym of *Arthrodytes andrewsi* or that both species, although distinct, could belong to *Anthropornis*, but he also adds, with justice, that only new discoveries could wholly resolve these doubts. Nevertheless the differences between the *A. andrewsi* humerus and that presumed to belong to *Anthropornis nordenskjöldi* (Wiman's "group 3") seem to me to justify both generic and specific distinction. The humerus of *A. andrewsi* is slightly, probably not significantly, smaller, the shaft is considerably straighter, and the angulation of the anterior margin[1] is more pronounced and more distal in position. The most striking difference is, however, in the angle between the axis of the shaft and a tangent touching the radial and ulnar trochleae. In Wiman's "group 3" humerus this angle is about 25° or 30°—the smallest value known to me in any penguin, recent or fossil—while in *Arthrodytes andrewsi* it is 45° or 50°—a value about average for *Palaeospheniscus* or for various recent penguins such as *Pygoscelis* or *Aptenodytes* (*A. patagonicus*, the value in *A. forsteri* tending to be somewhat larger). In most of these characters *A. andrewsi* resembles *Paraptenodytes antarcticus*, but its humerus is a much larger and stouter bone, there are various small differences in the sculpture of the proximal end (as described by Ameghino), and the angle referred to is somewhat (perhaps not significantly) larger.

On the basis of this humerus, the distinction of *A. andrewsi* from other known penguins is fairly well established, but it must be remembered that *A. andrewsi* may not belong to *Arthrodytes*. It certainly does not belong to *Arthrodytes* if, as has been suggested, that genus is close to, or a synonym of, *Anthropornis*. In that case, *A. andrewsi* belongs either to *Paraptenodytes* or to an unnamed genus.

SEYMOUR ISLAND

The fossil penguins from Seymour Island in Antarctica, all described by Wiman (1905a, 1905b), were all found weathered out and dissociated so that non-homologous skeletal parts can be assigned to the same species only on the basis of size, a rather hazardous performance in this group. Weathering and breakage have also obscured many important characters. Wiman sorted the various isolated bones into eight size groups. Five of them included tarsometatarsi and were given names with these bones as types. As these tarsometatarsi are without exception incomplete, they do not form a very secure taxonomic basis. Wiman did not apply these names to other bones, but it is presumed that bones assigned to a given, numbered size group are supposed to be conspecific. One group, the largest, was named in spite of the fact that it includes no known tarsometatar-

[1] This angulation occurs, more or less marked, in almost all penguins but has not, to my knowledge, received a special name. It marks the upper end of the origin of the brachialis internus (or b. inferior) muscle.

sus, the type being a sacrum, a bone identified in only three other named species and not figured or described in any except in three others of Wiman's Seymour Island groups.

The correspondence of Wiman's size groups and names is as follows, from largest to smallest:

Group No.	Name Applied to an Included Bone
1	*Orthopteryx gigas*
2	(None)
3	*Anthropornis nordenskjöldi*
4	*Pachypteryx grandis*
5	*Eosphaeniscus gunnari*
6	(None)
7	*Delphinornis larsenii*
8	*Ichthyopteryx gracilis*

Wiman at first (1905a; 1905b, p. 3) considered this fauna as Eocene, but after the associated invertebrate fossils had been studied by Wilckens, he concluded that they are of the same age as the Patagonian formation and therefore, according to Wilckens' determination of the latter, Late Oligocene or Early Miocene (Wiman, 1905b, p. 37). This equivalence with the Patagonian formation still seems highly probable, and the age of the Seymour Island fossils may therefore be considered Miocene, probably Early Miocene, the most likely age for at least the earlier part of the Patagonian group.

ICHTHYOPTERYX[1] Wiman

Ichtyopteryx Wiman, 1905a, p. 251; 1905b, p. 10.

Ichthyopteryx, Ameghino, 1905, p. 128; Lambrecht, 1933, p. 231.

Type: *Ichthyopteryx gracilis*, by monotypy.

Comments: The sole basis for this genus is a small fragment of a tarsometatarsus, and no other bones were referred to size group 8. The definition contains little that is characteristic and remarks only that the bone is slender in proportion to the trochleae and that there is a nearly closed adductor groove between median and external trochleae. Ameghino (1905, p. 129) noted that the former character is not particularly striking and compared the genus with *Neculus* (also very dubious, see above). The type species is of about the size of *Palaeospheniscus rothi*. The adductor groove may be a valid distinction, but this is doubtful. The bone may be that of a juvenile bird. The status of the genus is wholly uncertain.

[1] Wiman consistently spelled this name "*Ichtyopteryx*," but this may be taken as an unintentional error in transcription and so subject to correction.

Ichthyopteryx gracilis Wiman

Ichtyopteryx gracilis Wiman, 1905a, p. 251, pl. 12, fig. 4 (tarsometatarsus); 1905b, p. 10, pl. 2, fig. 5 (tarsometatarsus).

Ichthyopteryx gracilis, Ameghino, 1905, p. 128, pl. 4, fig. 24 (tarsometatarsus, after Wiman); Lambrecht, 1933, p. 231.

Type: Corroded fragment of distal part of right tarsometatarsus, with median and external trochleae, in Uppsala.

Horizon and Locality: Lower Miocene, Seymour Island.

Comments: See discussion of the genus.

DELPHINORNIS Wiman

Delphinornis Wiman, 1905a, p. 250; 1905b, p. 10; Ameghino, 1905, p. 125; Lambrecht, 1933, p. 230.

Type: *Delphinornis larsenii*, by monotypy.

Comments: This genus is based solely on a broken tarsometatarsus, the most distinctive features of which are the presence of both external and internal intermetatarsal foramina, both small and subequal, and of an enclosed external adductor foramen (or distal foramen of various authors). Ameghino added that the tarsometatarsus is also unusually slender and that some other peculiarities mentioned in Wiman's description are not really distinctive. The characters noted above do, nevertheless, suggest a valid genus.

Delphinornis larsenii Wiman

Delphinornis Larsenii Wiman, 1905a, p. 250, pl. 12, fig. 1 (tarsometatarsus); 1905b, p. 10, pl. 2, fig. 2 (tarsometatarsus).

Delphinornis Larseni, Ameghino, 1905, p. 125, pl. 3, fig. 21 (tarsometatarsus, after Wiman), pl. 4, fig. 22 (referred Patagonian tarsometatarsus); Lambrecht, 1933, p. 230.

Delphinornis larsenii, Lowe, 1933, p. 510, pl. 5, fig. 1 (tarsometatarsus).

Type: Left tarsometatarsus lacking median and internal trochleae, in Uppsala.

HORIZON AND LOCALITY: Lower Miocene, Seymour Island.

COMMENTS: Ameghino (1905, p. 126) is surely right in criticizing Wiman's restoration of the missing trochleae of the type, but the preserved part of the bone is distinctive. In length, the bone is intermediate between *Perispheniscus wimani* and *Paraptenodytes antarcticus*, but it is more slender than in either. Wiman (1905b, p. 27, and pl. 8, figs. 6–7) also referred two cervical vertebrae to this size group (7), but, as he remarked, these imperfect bones are not particularly characteristic, the reference is uncertain, and they contribute little or nothing to knowledge of this species.

EOSPHAENISCUS WIMAN

Eosphaeniscus WIMAN, 1905a, p. 250; 1905b, p. 9.

Eospheniscus, AMEGHINO, 1905, p. 132; LAMBRECHT, 1933, p. 232.

TYPE: *Eosphaeniscus gunnari*, by monotypy.

COMMENTS: Although relatively complete, the tarsometatarsus on which this genus is based is badly preserved, and some of the apparent distinctions may, as Wiman warned, be mere results of breakage and erosion. A small internal intermetatarsal foramen is present. Other important characters observable are only size and proportions. In width, the bone is fairly comparable with this element in *Paraptenodytes antarcticus*, but it is decidedly more elongate. The internal trochlea is strongly inverted, and the notch between median and external trochleae is unusually deep (unless deepened by erosion). No other tarsometatarsus known has these proportions or this outline and so the species and probably also the genus appear to be valid, however poorly characterized at present. I agree with Ameghino (1905, p. 133) that Wiman is probably mistaken in thinking this genus particularly like *Spheniscus*, but I cannot see any good grounds for Ameghino's special comparison with *Isotremornis*. Ameghino also suggested that *Arthrodytes* might conceivably be close to *Eosphaeniscus*, but the tarsometatarsus is unknown in the former.

Wiman's size group 5, to which *Eosphaeniscus gunnari* belongs, also includes coracoid, humerus, ulna, sacrum, femur, and tibiotarsus, but these contribute little that is systematically helpful, and the sorting of these bones may not be wholly correct taxonomically.

Eosphaeniscus gunnari Wiman

Eosphaeniscus Gunnari WIMAN, 1905a, p. 280, pl. 12, fig. 5 (tarsometatarsus); 1905b, p. 9, pl. 2, fig. 1 (tarsometatarsus).

Eospheniscus Gunnari, AMEGHINO, 1905, p. 132, pl. 4, fig. 27 (by error "28a" on the plate; tarsometatarsus, after Wiman); LAMBRECHT, 1933, p. 232, fig. 94c (tarsometatarsus, after Wiman).

Eospheniscus gunnari, LOWE, 1933, p. 510, pl. 5, fig. 2 (tarsometatarsus).

TYPE: Eroded right tarsometatarsus, proximal end broken, in Uppsala.

HORIZON AND LOCALITY: Lower Miocene, Seymour Island.

COMMENTS: See the genus, above. Other figures of bones belonging to group 5 and hence, by implication, referred to this species are as follows:

Coracoid, Wiman, 1905b, pl. 7, fig. 5
Humerus, *ibid.*, pl. 5, figs. 1, 2, 3, 8, 10
Ulna, *ibid.*, pl. 6, fig. 2
Femur, *ibid.*, pl. 4, figs. 3, 4
Tibiotarsus, *ibid.*, pl. 3, figs. 2, 3, 7
Sacrum, *ibid.*, pl. 8, fig. 4

Generic and specific allocation of these bones is uncertain.

PACHYPTERYX WIMAN

Pachypteryx WIMAN, 1905a, p. 250; 1905b, p. 9; AMEGHINO, 1905, p. 150; LAMBRECHT, 1933, p. 235.

TYPE: *Pachypteryx grandis*, by monotypy.

COMMENTS: Wiman (1905a, p. 250) expressed great (and justified) doubt as to whether this genus could be separated from *Anthropornis*, but made the separation in order better to distinguish the species, a rather undesirable taxonomic procedure. The only differences given were that the inner trochlea is more divergent (not actually preserved in either genus and no real difference indicated by his figure), that the proximal end is thinner, and that the bone is less hollowed out under the intercondylar tubercle. The first character seems unreal, and the other two are hardly to be judged of specific, still less of generic, value. The type, as nearly

as we can judge from the figures of the broken specimen, is 10 to 15 per cent smaller than that of *A. nordenskjöldi*. Specific distinction is possible, although questionable, but I see no basis for generic distinction.

Although they are of some morphological interest, the few other skeletal fragments referred to group 4 by Wiman provide no helpful additional basis for comparing or contrasting *Pachypteryx* and *Anthropornis*.

Pachypteryx grandis Wiman

Pachypteryx grandis WIMAN, 1905a, p. 250, pl. 12, fig. 3 (tarsometatarsus); 1905b, p. 9, pl. 2, fig. 6 (tarsometatarsus); AMEGHINO, 1905, p. 150, pl. 7, fig. 41 (tarsometatarsus, after Wiman); LAMBRECHT, 1933, p. 235; LOWE, 1933, p. 509.

TYPE: Fragment of right tarsometatarsus lacking distal end and fourth metatarsal, in Uppsala.

HORIZON AND LOCALITY: Lower Miocene, Seymour Island.

COMMENTS: See the genus, above. Other elements referred by Wiman to his group 4, and hence by implication to this species, are:

Coracoid, Wiman, 1905b, pl. 7, fig. 2
Radius, *ibid.*, pl. 6, figs. 5–6
Metacarpus, *ibid.*, pl. 3, fig. 11
Tibiotarsus, *ibid.*, p. 16 (not figured)

As in other cases the generic and specific allocation of these bones is uncertain.

It may be noted that there is considerable probability that both *Pachypteryx grandis* and *Arthrodytes grandis* belong to *Anthropornis*, in which genus their names would be homonymous.

ANTHROPORNIS WIMAN

Anthropornis WIMAN, 1905a, p. 24a; 1905b, p. 8; AMEGHINO, 1905, p. 149: LAMBRECHT, 1933, p. 234; LOWE, 1933, p. 508; 1939, p. 283.

TYPE: *Anthropornis nordenskjöldi*, by monotypy.

COMMENTS: Although based, again, on a quite imperfect tarsometatarsus, this is the most characteristic and satisfactory of Wiman's genera. The essential characters are: very large size, relatively great elongation (especially striking in so large a penguin), medial convexity of the internal border, relatively complete fusion of metatarsals, presence of both intermetatarsal foramina, their subequal (but small) size, and their relatively proximal position. The last four of these characters resemble *Paraptenodytes*, but the first three are distinctions from that genus. There is also no doubt of generic distinction from *Palaeeudyptes* (see below), the only earlier named fossil penguin of even approximately equal size.

Further comparisons depend rather on the "group 3" humerus and femur of Wiman than on the type tarsometatarsus, but (as Lowe, 1938, p. 291, has also remarked of the humerus) in this case the generic reference of the humerus is so probable as to be accepted, tentatively, at least, as a basis for taxonomic comparison. Ameghino (1905, p. 147) suggested that his *Arthrodytes andrewsi* might belong to *Anthropornis*, but, as I have pointed out above, the humeri seem to me fully to warrant generic separation. Ameghino further suggested that his *Arthrodytes grandis*, type of that genus, might belong to *Pachypteryx*, which I consider probably synonymous with *Anthropornis*.

On the comparison with the second proposed New Zealand genus, *Pachydyptes* Oliver, see that genus, below.

Anthropornis nordenskjöldi WIMAN

Anthropornis Nordenskjöldi WIMAN, 1905a, p. 249, pl. 12, fig. 6 (tarsometatarsus); 1905b, p. 8, pl. 2, fig. 3 (tarsometatarsus); AMEGHINO, 1905, p, 149, pl. 7 fig. 40 (tarsometatarsus, after Wiman); LAMBRECHT, 1933, p. 234.

Anthropornis nordenskjöldii, LOWE, 1933, p. 508, pl. 5, fig. 4 (tarsometatarsus); 1939, p. 253.

TYPE: Left tarsometatarsus, lacking external trochlea and all but the middle portion of the second metatarsal, in Uppsala.

HORIZON AND LOCALITY: Lower Miocene, Seymour Island.

COMMENTS: See the genus, above. Other parts referred by Wiman to his group 3, and so by inference to this species, are:

Coracoid, Wiman, 1905b, pl. 7, fig. 3
Scapula, *ibid.*, pl. 7, fig. 8
Humerus, *ibid.*, pl. 5, figs. 5, 9, 13
Ulna, *ibid.*, pl. 6, figs. 1, 3
Metacarpus, *ibid.*, pl. 3, fig. 10
Femur, *ibid.*, pl. 4, fig. 2
Tibiotarsus, *ibid.*, pl. 3, figs. 4, 5, 6
Sacrum, *ibid.*, pl. 8, fig. 5

The "group 3" humerus was also figured by Lowe, 1933 (figs. 12a, 13a, and 14b), and 1939 (pl. 3, fig. b, and pl. 4, fig. d). The "group 3" metacarpus was figured by Lowe, 1933 (fig. 15a).

ORTHOPTERYX WIMAN

Orthopteryx WIMAN, 1905b, p. 27; LAMBRECHT, 1933, p. 235.

TYPE: *Orthopteryx gigas*, by monotypy.

COMMENTS: The only specimen placed in this proposed genus is a poorly preserved sacrum (or "lumbosacrum," or "synsacrum") considered by Wiman rather doubtfully spheniscid because it lacks a ventral keel, may have lacked a dorsal keel, and consists of 14 vertebrae. Only the first character seems really distinctive; the second is doubtful, and the third does occur in recent penguins (e.g., *Aptenodytes*) as a variation. Even the ventral keel is variable in recent penguins and presumably was also in their Miocene progenitors. It may be very short and confined to the anterior end, on the fused lumbars. Altogether I see no reason to doubt that this is a penguin sacrum.

No comparison with other type specimens is possible, because Wiman here departed from his principle of basing genera on tarsometatarsi. No other type includes the sacrum, and this element has otherwise been described in fossils only from Wiman's fragments placed by him in his groups 2, 3, and 5. The inference that this sacrum represents a genus other than *Anthropornis* rests only on the assumption that it is too large to belong to the type of that genus, which would then be represented by one of Wiman's smaller sacra, with a ventral keel. The *Orthopteryx* sacrum was apparently, very roughly, about 23 cm. in length. Its ratio to femur length of *Anthropornis nordenskjöldi* was thus in the general neighborhood of 1.7. In *Aptenodytes* this ratio is about 1.4. If another caudal (or coccygeal) were fused in *Aptenodytes*, as seems to have occurred in the fossil, the ratio would be 1.5 to 1.6. It is thus not impossible that *Orthopteryx* is based on the sacrum of *Anthropornis*.

Orthopteryx gigas Wiman

Orthopteryx gigas WIMAN, 1905b, p. 27, pl. 8, fig. 2 (sacrum); LAMBRECHT, 1933, p. 235.

TYPE: Poorly preserved sacrum, at Uppsala.

HORIZON AND LOCALITY: Lower Miocene, Seymour Island.

COMMENTS: This species could be a synonym of *Anthropornis nordenskjöldi*, but this is conjectural. See discussion of the genus.

SPHENISCIDAE, INDET.

Wiman's size groups 2 and 6, with which no names have been associated, include such inconsiderable and generally uncharacteristic fragments as to have little real interest, but they are mentioned for the sake of completeness. The bones included by Wiman, in all cases mere scraps of the element named, are as follows:

Group 2: Sacrum, Wiman 1905b, pl. 8, fig. 3
Group 6: Femur, *ibid.*, pl. 4, fig. 5
Humerus, *ibid.*, pl. 5, fig. 7
Scapula, *ibid.*, pl. 7, fig. 7
Coracoid, *ibid.*, pl, 7, fig. 4

NEW ZEALAND

Six occurrences of fossil penguins have been reported from New Zealand, most of them in the same region (Oamaru), as follows:

1. "Kakaunui." Tarsometatarsus, type of *Palaeeudyptes antarcticus*. Reported by Huxley, 1859.
2. "Seal Rock, Woodpecker Bay, Nelson Province." Associated humerus, metacarpus, ulna, femur, ribs, vertebrae, pelvis, and sternum, referred to *Palaeeudyptes antarcticus*. Reported by Hector, 1872.
3. "Fortification Hill, near Oamaru, Otago." Probably associated humerus, coracoid, and metacarpus, referred to *Palaeeudyptes antarcticus*. Reported by Hector, 1872 and 1873.
4. "Oamaru District, Otago." Humerus, type of *Pachydyptes ponderosus*. Reported by Oliver, 1930.
5. "Fortification Hill, Oamaru." Humerus, type of *Pachydyptes novaezealandiae*. Reported by Oliver, 1930.
6. Locality not given, presumably Oamaru. Two humeri and a femur, not associated (?),

referred to *Palaeeudyptes antarcticus*. Oliver's specimens, reported by Lowe, 1939.

The exact horizon was not recorded for any of these fossils, but it is probable for all and certain for some that they are from the Ototaran stage or series. The age was given as Pliocene or older by Huxley (1859), Eocene or Miocene (in the old sense, including Oligocene) by Hector (1872), and later as Early Eocene by the same student (Hector, 1873). Later authorities agree, however, that the age is Miocene (in the modern sense, excluding Oligocene) for all, and probably Early Miocene (see Ovey, 1939). These fossils are thus approximately contemporaneous with the fossil penguins from Patagonia and from Seymour Island.

The two generic and three specific names applied are due to Huxley and to Oliver. The three type specimens are a tarsometatarsus and two humeri, all isolated.

PALAEEUDYPTES Huxley

Palaeeudyptes Huxley, 1855, p. 670; Watson, 1883, p. 46; Menzbier, 1887, p. 531; Oliver, 1930, p. 85; Lambrecht, 1933, p. 235; Lowe, 1939, p. 290.

Type: *Palaeeudyptes antarcticus*, by monotypy.

Comments: As the first fossil penguin described, the generic name has priority over all others for fossils. The genus is determinable and is clearly distinct from any recent penguins, so is unquestionably valid. Among the striking characters of the tarsometatarsus are its considerable size (between *Paraptenodytes* and *Anthropornis*), greater elongation relative to large living penguins (but less than in *Anthropornis*, for instance), absence of internal intermetatarsal foramen and very small size of external foramen, external groove well developed on dorsal (or anterior) side, internal groove absent, calcaneal tubercles both grooved and double.

The reference to this genus of specimens later discovered, and thus comparison based on these specimens, is dubious because none of them includes a tarsometatarsus. Hector simply assumed that his specimens belonged to the only fossil penguin then known from New Zealand (or from anywhere, for that matter), and apparently later students have simply assumed that Hector was right. Now that at least three distinct species, and probably genera, of humeri are known from New Zealand, the question demands some reconsideration.

Hector (1872) gave the length of the humerus in his specimen as 6 inches. His figure (pl. 18, fig. 1) shows the bone as slightly longer, about 154 mm. The length of the type tarsometatarsus of *P. antarcticus* is given by Huxley as 2½ inches and is about 63½ mm. in his woodcut, stated to be of natural size—almost perfect agreement. The length index of humerus/tarsometatarsus for these two specimens (obviously of different individuals and so giving only a rough value) is thus about 243. In our specimen of *Paraptenodytes antarcticus* the value is 204. In this species the tarsometatarsus is slightly less elongated, relatively, than in *Palaeeudyptes antarcticus*, so the index might be expected to be somewhat larger, not markedly lower as would appear from this result. In Patagonian fossils generally the index seems to have varied from about 180 to about 230 in various species, although these values are in part based on uncertain specific ascriptions of the humeri. In recent species measured, the values range from about 205 to about 300, but there is strong evidence that the value is decidedly higher in recent penguins than in fossils of comparable size. Thus Hector's humerus seems somewhat large for *Palaeeudyptes antarcticus*, but could belong to that species as far as size goes. Oliver's even larger *Pachydyptes ponderosus* humerus is almost certainly too large for *P. antarcticus*, giving an index of 283 with the latter. His *Pachydyptes novaezealandiae* humerus gives an index of only 167, and so is almost certainly too small.

Of the three known types of New Zealand fossil penguin humeri, that hitherto referred to *Palaeeudyptes* is, indeed, the most likely to belong there, although in that case it hints at a rather large wing/foot ratio, and it is just possible that there are four, rather than three, species or genera involved.

Palaeeudyptes antarcticus Huxley

Palaeeudyptes antarcticus Huxley, 1859, p. 670, figs. 1, 2 (tarsometatarsus); Hector, 1872, p.

341, pl. 17, fig. 1 (femur), fig. 3 (metacarpus), fig. 5 (tarsometatarsus, after Huxley), pl. 18, figs. 1–3 (humerus), fig. 5 (ulna); HECTOR, 1873, p. 438; WATSON, 1883, p. 46; MENZBIER, 1887, p. 531; WIMAN, 1905b, p. 12 (erroneously attributed to Hector); OLIVER, 1930, p. 85; LAMBRECHT, 1933, p. 236, fig. 92 (tarsometatarsus, femur, humerus, and metacarpus, all after Hector); LOWE, 1933, p. 503, pl. 5, figs. 3, 3c (tarsometatarsus); 1939, p. 284.

TYPE: Right tarsometatarsus, lacking internal trochlea, in the British Museum. (Other known specimens are listed above, and under Australia, below.)

HORIZON AND LOCALITY: Miocene, probably all in Lower Miocene, New Zealand (see above).

COMMENTS: See discussion of the genus, above.

PACHYDYPTES OLIVER

Pachydyptes OLIVER, 1930, p. 85; LAMBRECHT, 1933, p. 236; LOWE, 1939, p. 290.

TYPE: *Pachydyptes ponderosus*, by author's designation. Lowe (1939, p. 291) proposed taking *P. novaezealandiae* as type of the genus, but this is invalid because the type had already been designated as *P. ponderosus* in the original publication.

COMMENTS: Only humeri have been clearly described in this supposed genus, and Oliver's diagnosis does not, in fact, serve to distinguish them adequately from other known fossil penguin humeri. Lowe (1939) compared the actual specimens concerned and concluded that the type of *Pachydyptes* (i.e., *P. ponderosus*, the real type, not Lowe's illegally designated type) is congeneric with Wiman's "humerus number 3" and hence, in all probability, with *Anthropornis*. The type species are certainly distinct, however, and from Wiman's, Oliver's, and Lowe's figures it does appear that the humeri differ as much as in distinct genera of recent penguins. Reduction to synonymy, therefore, may be premature. The *Pachydyptes* humerus is strikingly unlike that referred to *Palaeeudyptes*, being much heavier, with a more distinct sigmoid curvature and a more prominent and definite tuberosity on the anterior edge (these last are the characters that do resemble the slenderer *Anthropornis* humerus).

Pachydyptes novaezealandiae Oliver

Pachydyptes novaezealandiae OLIVER, 1930, p. 86; LAMBRECHT, 1933, p. 238.

Pachydyptes novae-zelandiae [invalid emendation], LOWE, 1939, p. 284.

TYPE: Humerus, in the Oliver collection (No. 1451).

HORIZON AND LOCALITY: Lower Miocene, Oamaru District, New Zealand.

COMMENTS: The type has not been figured, and the descriptive remarks of Oliver and of Lowe leave some important points obscure. It is, however, clear that this species cannot belong to *Pachydyptes*. The statements that the shaft is straight, much slenderer than in *P. ponderosus*, with the least width proximal, and with the shaft-trochleae angle larger are enough to exclude any possibility of the two being congeneric. Lowe also decided that the two are not congeneric and proposed to restrict the name *Pachydyptes* to *P. novaezealandiae*, but this cannot be accepted for reasons already stated.

The published data would not exclude "*Pachydyptes*" *novaezealandiae* from any of several Patagonian genera, but neither do they warrant reference to any one of these. The species is probably distinct, but it is of unknown generic position. Quite possibly it represents an unnamed genus.

Pachydyptes ponderosus Oliver

Pachydyptes ponderosus OLIVER, 1930, p. 86, fig. (no number; humerus); LAMBRECHT, 1933, p. 238, fig. 93 (humerus, after Oliver); LOWE, 1939, p. 284, pl. 2, fig. c (humerus), pl. 5, fig. c (humerus), pl. 4, fig. b (metacarpus[1]).

Anthropornis ponderosus, LOWE, 1939, p. 291.

=*Anthropornis nordenskjöldi* Wiman, LOWE, 1939, p. 293.

TYPE: Humerus, Oliver collection.

HORIZON AND LOCALITY: Lower Miocene, Fortification Hill, Oamaru, New Zealand.

COMMENTS: Even if referred to *Anthropornis*, which seems too questionable to be ac-

[1] This reference is puzzling, as there is no other notice of a metacarpus referred to *P. ponderosus*, and the bone in question closely resembles, and perhaps is one of, those referred by Hector to *Palaeeudyptes antarcticus*. Lowe also mentions, but does not figure, a coracoid referred to this species but also of (to me) mysterious origin.

cepted at present, this species seems surely to be valid. The type is somewhat longer and is much heavier or relatively shorter throughout than the humerus referred to *Anthropornis nordenskjöldi*, looking almost as if a bone like the latter had been enlarged and then strongly compressed proximodistally. The tubercle on the anterior margin is also more prominent, and the border above this is straighter. The angle of shaft and trochleae is larger, but this may not be more than an individual variation.

AUSTRALIA

Only one fossil penguin bone has yet been reported from Australia, by Finlayson, 1938. This is a humerus found by W. Burdett at Christie's Beach on the east shore of St. Vincent Gulf, about 16 miles south of Adelaide. The horizon is Miocene, but is not more exactly specified.

Finlayson tentatively referred this specimen to *Palaeeudyptes antarcticus*, although it is somewhat smaller than Hector's specimen and evidently has various other minor differences. Specific, or possibly even generic, identity should hardly be considered a positive datum, as Finlayson's own discussion makes clear, and pending discovery of other remains the find might best be recorded simply as cf. *Palaeeudyptes* sp.

COMPARATIVE OSTEOLOGY OF MIOCENE PENGUINS

IN SPITE OF THE RATHER EXTENSIVE LITERATURE, the osteology of the extinct penguins as a whole has not been well reviewed or summarized. Moreno and Mercerat (1891) gave good figures of numerous bones of the Patagonian species but only very summary descriptions. For instance, they gave no descriptions or discussions of any of the wing elements. Wiman (1905b) gave good figures and descriptions of the Seymour Island fossils, varied but not numerous and, for the most part, poorly preserved. Ameghino's long discussion (1905) refers almost exclusively to the tarsometatarsus and is devoted to the minutiae of his extremely split taxonomic arrangement, without giving much idea of basic characteristics of these fossil birds as a group. Lowe (1933 and 1939) has contributed able summaries of the morphology, especially of the humerus and the tarsometatarsus, but his treatment suffers from his polemic and *parti pris* attitude and from his concentration on two or three of the largest species. For instance, he scarcely mentions *Palaeospheniscus*, the most abundant and (until the present description of *Paraptenodytes*) best-known fossil genus. The species singled out by Lowe to represent Miocene penguin morphology seem to me to be the most specialized and aberrant members of the group, and I am convinced that the more significant fossils, because more nearly generalized or nearer the actual ancestry of living penguins, belong to *Palaeospheniscus* and to allied genera not even mentioned by Lowe. Other studies are scattered descriptions of isolated specimens.

The following notes are based in part on the literature and in part on our collection of Patagonian fossil penguins. Besides the uniquely fine specimen of *Paraptenodytes* described on previous pages, this collection includes more than 100 isolated bones, representing most of the important skeletal elements. All these specimens were found in a continuous exposure of the Patagonian formation over a distance of less than 10 miles on the south side of the Río Chubut, from opposite Trelew to opposite Gaiman. Although they were less explicit as to localities, it is probable that most of Moreno and Mercerat's and of Ameghino's specimens came from this same exposure.

With a few exceptions, specified in due course, our large collection can be clearly separated into three groups similar in morphology but distinctly different in size. Most of the isolated bones figured by Moreno and Mercerat can be placed in these same groups. For purposes of convenient description these groups will be called *Palaeospheniscus gracilis*, *P. patagonicus*, and *P. robustus*. The small and medium-sized groups are of appropriate size for association with the type tarsometatarsi of the first two species named, and the third group includes humeri very close to the type humerus of *P. robustus* in size and structure. (As noted elsewhere, I do not think that the tarsometatarsus later referred to this species by Ameghino really belongs to it.) It is probable that some of these remains belong to closely allied species of similar size, if any such species prove to be valid, and even that other, doubtfully distinct genera of the palaeospheniscine group, such as *Paraspheniscus*, *Perispheniscus*, or *Treleudytes*, are represented. Each group is, however, so uniform and so harmonious in make-up that no falsification of the morphological situation is involved in treating them as three species. Indeed this clear trifold grouping of most of the skeletal elements is one of the factors that suggests that the taxonomic arrangement of the small and middle-sized Patagonian penguins in 17 species and six genera, based on the tarsometatarsi by Ameghino, is a gross exaggeration of the real taxonomic differentiation.

Exact references to published figures and discussions are given in the accompanying "Conspectus" and are not repeated in the lists of specimens and comments on them in this morphological section.

SKULL

The only known fossil penguin skull is that of *Paraptenodytes antarcticus*, A.M.N.H. No. 3338, described above. The only other skull element in our collection is A.M.N.H. No. 3377, a quadrate of uncertain species but

possibly *Palaeospheniscus robustus*. It is somewhat smaller than the homologous bone of *Paraptenodytes antarcticus*, has the anteroexternal face more excavated, the quadratojugal articulation relatively larger and deeper, the optic process (which is broken) probably more slender, and other minor distinctions. In comparison with *Pygoscelis papua*, the bone has about the same length, but both anteroposterior and transverse dimensions are greater throughout. The quadratojugal part is also deeper, and the upper part of the anteroexternal face is more simply concave, without the cresting here seen in this recent species.

VERTEBRAE

Figure 9

Moreno and Mercerat (1891) mentioned vertebrae referred by them to *Palaeospheniscus patagonicus* and *P. bergi*, but did not describe or figure these. Of the former they said that the available vertebrae had no noteworthy characters and of the latter that a description would be given later, which was not done so far as I know.

The only vertebrae previously described in the literature are in Wiman (1905b), two cervicals referred to "group 7" (? *Delphinornis*), lumbosacrals referred to "group 2," "group 3" (? *Anthropornis*), and "group 5" (? *Eosphaeniscus*), and a lumbosacral sequence made type of *Orthopteryx gigas*. Cervical and dorsal vertebrae of *Paraptenodytes antarcticus* have been sufficiently described on previous pages of this paper. Our collection also includes four isolated vertebrae and a sacrum referable to *Palaeospheniscus*, at least in a broad sense.

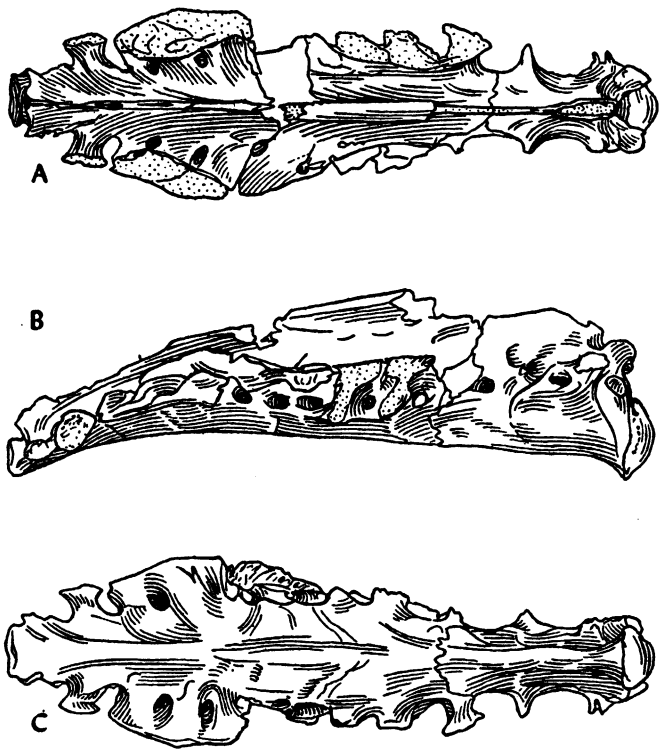


FIG. 9. *Palaeospheniscus* sp. Lumbosacral complex, A.M.N.H. No. 3347. A. Dorsal view. B. Right lateral view. C. Ventral view. ×1.

Wiman's small "group 7" cervicals are so incomplete and so little characteristic that he did not surely identify them as belonging to penguins.

Our collection includes two posterior cervi-

cals referred to *Palaeospheniscus*. A.M.N.H. No. 3305 is perhaps an eleventh cervical, spheniscine in general character but distinctive in minor details. It is larger, relatively elongate, and has the upper, or true, transverse process larger, but is otherwise very like the eleventh cervical of *Spheniscus humboldti*. A.M.N.H. No. 3357, probably a thirteenth cervical, is still more like that of *S. humboldti* but is relatively a little deeper. Although broken, the transverse processes were probably a little smaller, relatively, and there are two pits in the anteroinferior aspect of this process, one inside and the other outside the vertebrarterial canal.

A.M.N.H. No. 3319, probably a second or third dorsal of *Palaeospheniscus*, is not a very characteristic bone but is almost exactly like *Spheniscus* or *Pygoscelis* as far as preserved. There was a large hypapophysis with a laterally compressed base. The apex is broken off and could have been bifid. The articular surfaces of the centrum are saddle-shaped. A.M.N.H. No. 3356 is a more posterior dorsal, fifth to eighth, probably of the same genus. It, also, is very spheniscine in character. The base of the hypapophysis is short, anteroposteriorly, suggesting that the process was spike-like, and is at the anterior end of the ventral surface, which is not sharply keeled posterior to this. The centrum is opisthocoelous, showing that this characteristic penguin peculiarity also existed in the Miocene.

The four examples of the lumbosacral complex described by Wiman are all badly damaged and their characters equivocal. The largest specimen, made type of *Orthopteryx gigas* but possibly representing *Anthropornis*, is discussed from a taxonomic point of view in the accompanying "Conspectus." It apparently has an additional fused coccygeal and has the ventral surface unkeeled, flatter than in recent penguins, but other distinctive characters are dubious. The next smaller lumbosacral fragment, the only specimen in Wiman's unnamed "group 2," is said, in contrast, to have the ventral surface less flat than in recent penguins, to have two free sacral ribs, and to have four fused caudals (or coccygeals). The "group 3" (? *Anthropornis*) fragment is said to have two sacrals, the more anterior with a free sacral rib, and to have the transverse processes much more elongate dorsoventrally than in recent penguins. Dorsal and ventral keels are about as in the latter. Wiman's "group 5" specimen (? *Eosphaeniscus*) is said to be similar to that assigned to "group 3," but smaller and with both sacral ribs free.

A.M.N.H. No. 3347 is a well-, but not quite perfectly, preserved synsacrum referable to *Palaeospheniscus* and of the right size for *P. gracilis* if proportions were about as in *Pygoscelis*. The bone is characteristically spheniscid, but shows minor differences from any one recent species. In comparison with *Pygoscelis adeliae*, for instance, the bone as a whole is smaller, the neural crest is less depressed and less widened, the dorsal exposure in the acetabular region is wider, and there are other minor differences in characters, most of which are variable intra-specifically in recent forms. In this, as in Wiman's specimens and all recent penguins, the pelvis was not fused with the sacrum.[1]

By the Boas formula (Boas, 1933) the vertebrae in this specimen are $1+3+3+2+3=12$. This is unusual in recent penguins, which usually have $1+4+3+2+3=13$, but Boas records $1+3+3+2+3=12$, as in the fossil, as a variation in *Spheniscus demersus*, and $1+4+3+2+4=14$ (possibly the formula of *Orthopteryx*) and $2+4+4+2+3=15$ are also variants among recent species. The reduction in the number of lumbars in the fossil is not reflected in a shortening of the preacetabular part of the complex, which is relatively as long as in *Pygoscelis* or possibly slightly longer.

SCAPULA

Figure 10

Parts of the scapula were reported by Wiman (1905b) in his "group 3" (? *Anthropornis*) and in the unnamed "group 6." Moreno and Mercerat (1891) listed a fragment of scapula referred to *Palaeospheniscus patagonicus*, but did not figure or describe it.

[1] Gregory (1935) has pointed out that lessening of fusion, seen also in the skull of penguins, is a common character in secondarily aquatic vertebrates, whatever their zoological affinities.

Ameghino (1905) gave a good figure of the proximal part of a scapula, associated with the type of "*Arthrodytes*" *andrewsi*. Besides the scapular fragment of *Paraptenodytes antarcticus* described above, our collection includes two other fragments tentatively referred to *Palaeospheniscus*.

Wiman says that his "group 3" scapula, of which only part of the head is preserved,

FIG. 10. *Palaeospheniscus* sp. Head of right scapula, A.M.N.H. No. 3359, in dorsolateral view. ×1.

shows that the glenoid surface is not as in recent penguins but is situated more laterally, as in flying birds. In his figure the distinction seems to be only that the head is less expanded, which is also true of *Paraptenodytes*. Wiman's "group 6" scapula is the merest crumb of bone and shows nothing of interest. The head is more expanded in "*Arthrodytes*" *andrewsi*, almost as much as in *Aptenodytes*, but the coracoid articulation is less transverse and more convex, and there is a pronounced notch between this and the acromion, both features being resemblances to *Paraptenodytes antarcticus*.

In *Palaeospheniscus*, A.M.N.H. Nos. 3304 and 3359, the head of the scapula is almost precisely as in *Pygoscelis* or *Spheniscus*.

CORACOID

Figure 11

The following specimens are reported:

Palaeospheniscus gracilis	A.M.N.H. No. 3363
Palaeospheniscus patagonicus	A.M.N.H. Nos. 3368–3371, 3280, 3281, 3283, 3351
Palaeospheniscus robustus	A.M.N.H. Nos. 3373, 3282
Palaeospheniscus spp.	Specimens figured by Moreno and Mercerat (1891)
Paraptenodytes antarcticus	A.M.N.H. No. 3338
"*Arthrodytes*" *andrewsi*	Specimen figured by Ameghino (1905)
"Group 6"	Specimen figured by Wiman (1905b)
"Group 5" (?*Eosphaeniscus*)	Specimen figured by Wiman
"Group 4" (? *Pachypteryx*)	Specimen figured by Wiman
"Group 3" (? *Anthropornis*)	Specimen figured by Wiman
Pachydyptes ponderosus	Specimen discussed, but not figured, by Lowe (1939)

As emphasized by Wiman, his "group 3" (? *Anthropornis*) coracoid, best preserved of his specimens, has the crest on the medial side very completely ossified so that the whole bone appears relatively broad and flat, without a rod-like middle portion of the shaft. The distinction is not so great as might be supposed on comparison with *Pygoscelis* and *Aptenodytes*. These two genera, the only ones compared by Wiman, happen to be those in which the ossification of this crest is least complete among recent penguins. The condition in *Eudyptes*, for instance, is as in Wiman's fossil except that there is no question that the distal end of the latter is decidedly more expanded and flaring. The distal end was also flaring in Wiman's "group 6" coracoid, and the fenestra was probably also closed, but the bridge is broken. Neither character can be determined on his other two specimens. Judging from the measurements given by Lowe (1939), the flare of the distal end was as great in *Pachydyptes ponderosus* as in Wiman's "group 3." The bone is not figured, and no other characters can be gathered from the brief discussion given.

On the other hand, in "*Arthrodytes*" *andrewsi*, also a large and somewhat aberrant species, the flare was clearly much less. The distal end is not complete, but it seems clear that it was little, if any, more expanded than in *Aptenodytes*. The shaft is, however, somewhat more widened by the crest, more as in *Pygoscelis*. Ameghino has restored the bone without a closed fenestra, but this could be due to breakage of the very thin crest. In our smaller but otherwise quite similar specimen of *Paraptenodytes antarcticus* the crest is broken, but it looks as if the fenestra had

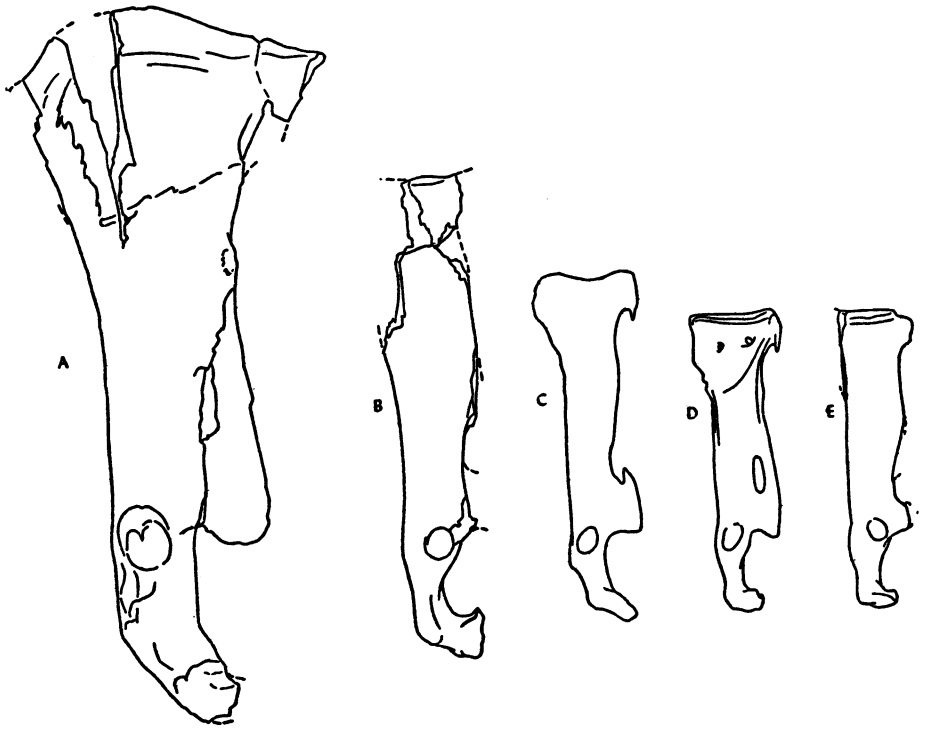


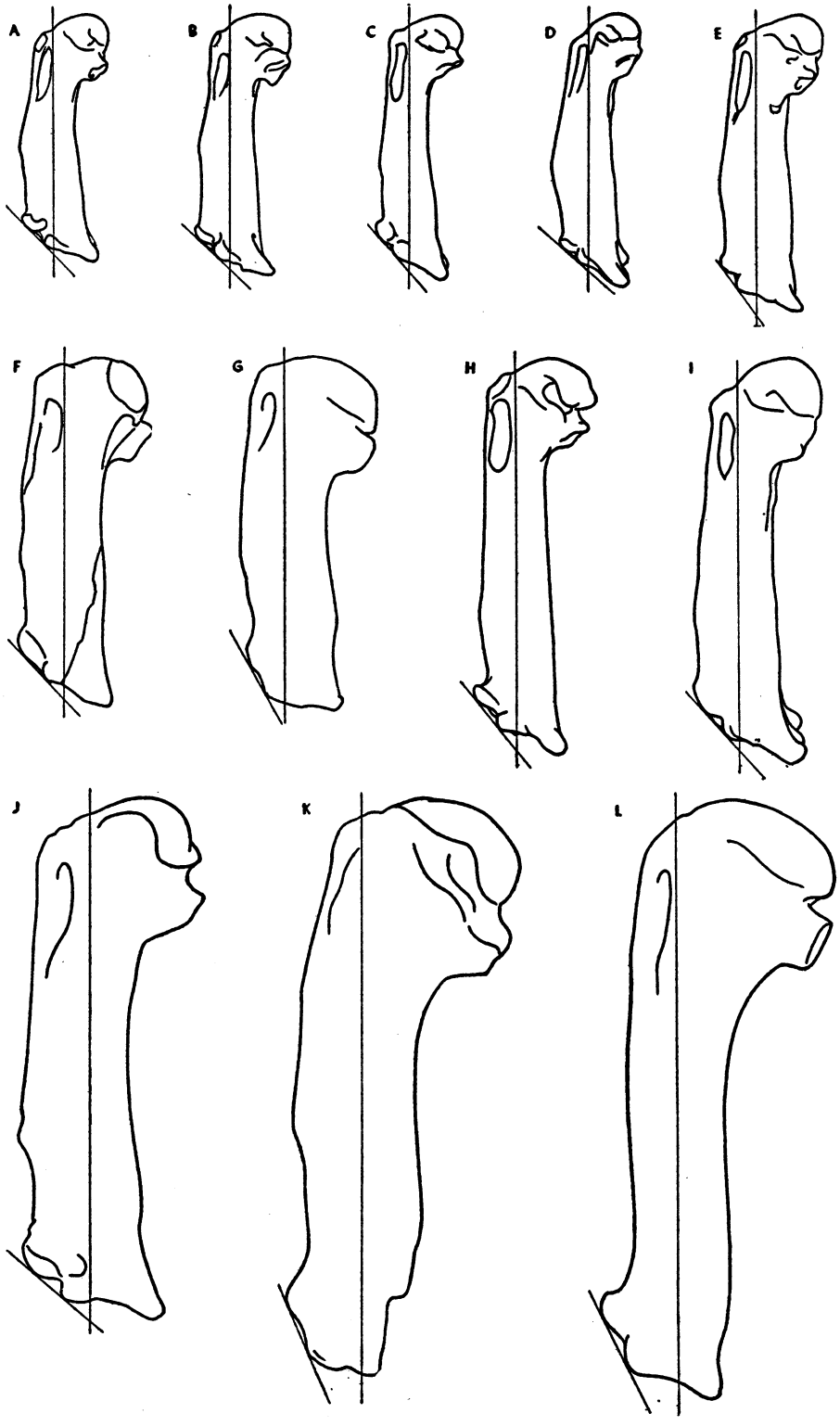
FIG. 11. Right coracoids of fossil and recent penguins. Comparative series in dorsal view. A. Wiman's "group 3" (? = *Anthropornis nordenskjöldi*), Miocene of Seymour Island, redrawn from Wiman. B. *Paraptenodytes antarcticus*, A.M.N.H. No. 3338, Miocene of Patagonia. C. *Pygoscelis adeliae*, Recent. D. *Spheniscus humboldti*, Recent. E. *Palaeospheniscus patagonicus*, A.M.N.H. No. 3283, Miocene of Patagonia. ×½.

TABLE 3

DIMENSIONS AND PROPORTIONS OF CORACOIDS OF FOSSIL AND RECENT PENGUINS

	A Total Length	B Width at Base	C Width of Shaft at Foramen[a]	100 B/A	100 C/A	Notes
"Group 3" (?*Anthropornis*)	187	ca. 80	23	ca. 43	12	From Wiman's figure
Pachydyptes ponderosus	213	100	—	47	—	Measurements from Lowe
"*Arthrodytes*" *andrewsi*	186	ca. 60	25	ca. 32	13	From Ameghino's figure
Palaeospheniscus patagonicus	78	ca. 22	11½	ca. 28	15	
Aptenodytes forsteri	171	57	20	33	12	
Spheniscus humboldti	77½	24½	9½	32	12	
Pygoscelis papua	130	38	13	37	13	

[a] Excluding the bridge enclosing the foramen, where this exists. The dimension used by Lowe, below the foramen, includes more or less of the osseous-membranous crest which is ossified to such different degree in different individuals and species that the measurements are not strictly homologous. The dimension here used is a diameter of the functional and always bony shaft.


A
B
C
D
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L

been closed. Some uncertainty persists as to these forms. The point is, however, rather unimportant in a broad view, as both conditions exist in recent penguins, even, at times, within a single species.

In *Palaeospheniscus* the distal end is, if anything, less expanded than in the recent penguins compared, certainly less than in *Pygoscelis* and probably even less than in *Spheniscus*. Some of our specimens seem to have the crest unbroken, and these suggest that it was about as in *Pygoscelis*, with the fenestra open but the crest indicated beyond this. In this genus, and indeed in all the known fossils, other characters of the coracoid are those of spheniscids in general, with only minor and apparently insignificant variations from the living species.

Table 3, comparable with a similar table in Lowe (1939, p. 293), confirms his conclusion that the two species that he took to represent Miocene penguins in general have the coracoid relatively broad at the base, but it is shown that this is not true of the other Miocene species in which this dimension can be approximately determined.

STERNUM

Except for the insignificant fragment of the sternum of *Paraptenodytes antarcticus* described above and sternal fragments of *Palaeeudyptes antarcticus* mentioned by Hector (1872) but never, to my knowledge, described or figured, knowledge of the sternum in fossil penguins is limited to three specimens listed by Moreno and Mercerat (1891), none of which was described but one of which was figured (pl. 2, fig. 7). Their figure shows the medial anterior part of the bone, with no evident differences from this part in recent penguins.

HUMERUS

Figures 12–14

The following humeri are reported:

Palaeospheniscus gracilis	A.M.N.H. Nos. 3345, 3288, 3284, 3313
Palaeospheniscus patagonicus	A.M.N.H. Nos. 3343, 3314, 3289, 3315, 3287, 3340, 3344, 3285, 3307, 3312, 3286, 3309, 3311, 3306, 3352
	Specimens referred by Moreno and Mercerat (1891) to *P. menzbieri* and *P. bergi*
Palaeospheniscus robustus	A.M.N.H. Nos. 3361, 3308
	The type, Ameghino (1895)
	Specimens referred by Moreno and Mercerat (1891) to *P. patagonicus*
? *Palaeospheniscus* sp. innom.	A.M.N.H. Nos. 3346, 3341
"*Aptenodytes ictus*"	Ameghino's type, considered indeterminate and not discussed here (see "Conspectus")
Paraptenodytes antarcticus	A.M.N.H. No. 3338
	Specimen referred by Ameghino to *Perispheniscus wimani*
Isotremornis nordenskjöldi	A.M.N.H. No. 3310
? *Isotremornis* sp. indet.	Specimen referred by Ameghino to *Metancylornis curtus*
? *Anthropornis grandis*	Specimen reported by Ameghino as associated with type of *Arthrodytes grandis*
? *Paraptenodytes andrewsi*	Ameghino's type of *Arthrodytes andrewsi*
? *Ichthyopteryx* sp.	Wiman's "group 8"
? *Eosphaeniscus* sp.	Wiman's "group 5"
? *Anthropornis* sp.	Wiman's "group 3"
Palaeeudyptes antarcticus	Hector's specimen
	Oliver's two specimens, reported by Lowe

FIG. 12. Right humeri of fossil and recent penguins. Comparative series in medial (internal) view. Drawings have been reversed where necessary. On each, the approximate midline of the shaft and the tangent to the trochlear facets have been drawn. A. *Palaeospheniscus gracilis*, A.M.N.H. No. 3345, Miocene of Patagonia. B. *Palaeospheniscus patagonicus*, A.M.N.H. No. 3340, Miocene of Patagonia. C. *Spheniscus humboldti*, Recent. D. *Pygoscelis adeliae*, Recent. E. *Palaeospheniscus robustus*, A.M.N.H. No. 3361, Miocene of Patagonia. F. *Isotremornis nordenskjöldi*, redrawn from Ameghino, Miocene of Patagonia. G. *Pachydyptes ponderosus*, redrawn from Oliver, Miocene of New Zealand. H. *Paraptenodytes antarcticus*, A.M.N.H. No. 3338, Miocene of Patagonia. I. *Aptenodytes patagonicus*, Recent. J. "*Arthrodytes*" *andrewsi*, redrawn from Ameghino, Miocene of Patagonia. K. Wiman's "group 3" (? = *Anthropornis nordenskjöldi*), redrawn from Wiman (distal end incomplete and not restored), Miocene of Seymour Island. L. *Palaeeudyptes antarcticus*, redrawn from Hector, Miocene of New Zealand. ×½.

? *Palaeeudyptes* sp.	Finlayson's specimen referred to *P. antarcticus*
"*Pachydyptes*" *novaezealandiae*	Oliver's type (not *Pachydyptes*)
Pachydyptes ponderosus	Oliver's type

Wiman (1905b, p. 19) made a point of the fact (expressed by him in different words) that his "group 3" humerus (probably *Anthropornis*) has the long axis of the head more nearly in the plane of flattening of the shaft than in recent penguins. In the latter the angle involved is greater and may be around 45°. Lowe (1933, 1939) agrees that some difference exists, but thinks it is exaggerated by erosion of the fossil bone. Finlayson (1938) says that this difference definitely existed in the Australian humerus of ? *Palaeeudyptes*, making due allowance for the fact that this bone is also eroded. I have noted above that the same sort of difference is visible in *Paraptenodytes antarcticus*, on an uneroded humerus, but it may be added that the distinction from the recent humerus is decidedly less than is shown in Wiman's figure of *Anthropornis*. On the other hand the large palaeospheniscine series of humeri in our collection is mostly, or entirely, within the recent range in this character. Indeed, comparing, for instance, *Palaeospheniscus patagonicus* and *Spheniscus humboldti*, there are specimens that show a distinctly, but not greatly, larger angle in the Miocene than in the Recent specimens.

This character is, as Wiman suggested, correlated with the development of the tricipital (or so-called pneumatic) fossa, and further with the general transverse expansion of the proximal end of the humerus. In recent penguins the fossa is large, the head relatively transverse, and the angle relatively large. In *Anthropornis* and *Palaeeudyptes* the fossa is small, the head relatively compressed, and the angle small. *Paraptenodytes* is intermediate in all three respects.

Lowe's statement (1939) that the head is more conical in Recent than in Miocene penguins is, like much of his discussion, a result of comparing the most aberrant members of the two faunas and is not a tenable generalization. In *Spheniscus*, for instance, the head is more flattened than in *Aptenodytes*, and in *Palaeospheniscus* it is less flattened than in *Anthropornis*. I see no definable difference between *Spheniscus* and *Palaeospheniscus* in this variable and rather subtle character.

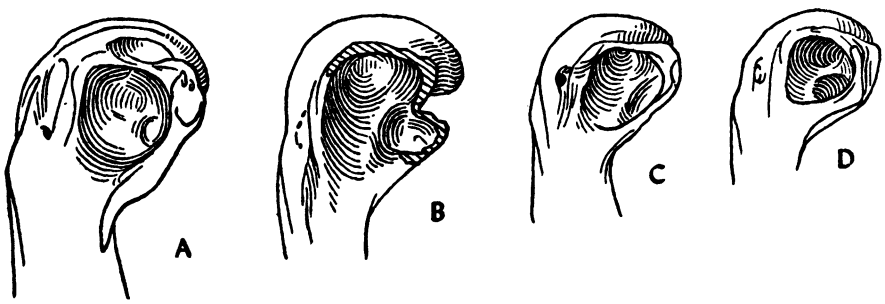

FIG. 13. Tricipital fossae of left humeri of fossil penguins from the Miocene of Patagonia. Oblique views showing as much as possible of interior of fossa. A. *Paraptenodytes antarcticus*, A.M.N.H. No. 3338, showing only a trace of bipartite structure. B. ? *Palaeospheniscus* sp. innom., A.M.N.H. No. 3341, a large humerus with a distinctly bipartite fossa (the rim of which is broken as shown by cross hatching). C. *Palaeospheniscus patagonicus*, A.M.N.H. No. 3285, form with inner fossa more medial and with restricted mouth. D. *Palaeospheniscus* cf. *patagonicus*, A.M.N.H. No. 3376, form with inner fossa less strictly medial and with broader mouth. ×1.

A point much emphasized by Wiman (1905b) and Lowe (1933, 1939), from widely different viewpoints, is the development of the tricipital fossa. In Wiman's *Anthropornis* humerus and also (at least by inference) in those doubtfully referred to *Eosphaeniscus* and *Delphinornis*, the fossa is relatively small and is simple, not bipartite. The same is true

of *Pachydyptes ponderosus* and of the Australian specimen, at least, of ? *Palaeeudyptes*. In *Paraptenodytes* the fossa, although of fair size, is relatively smaller than in recent genera. It has traces of a second, inner division, but is essentially simple. On the other hand, in all the many *Palaeospheniscus* humeri, including, no doubt, the related genera of this group if any of these are valid, the fossa is just as large as in Recent penguins of comparable size and is just as strongly bipartite.[1]

It has apparently been overlooked that even among the highly stereotyped living penguins there are marked differences in the relative development of the two parts of the fossa and of the crest between them. In all cases the inner or accessory fossa is considerably smaller than the main fossa. In *Aptenodytes* it is deep, with a restricted mouth and well-developed ridge. In *Eudyptes* the inner fossa is less deep, but is relatively larger at the mouth. In *Spheniscus* it is of moderate size but quite shallow, and the ridge is poorly developed, so poorly in *Spheniscus mendiculus* that some specimens hardly appear to be bipartite. *Pygoscelis* also typically has this fossa shallow and the ridge slight.

In our *Palaeospheniscus* series the inner fossa is well developed, relatively deep, and with a restricted mouth and sharp ridge. There are two distinct forms, one with the mouth more restricted, a narrow oval in outline, and the other with the mouth wide, broadly oval or nearly circular. Both extremes occur in our most abundant group, referred to *P. patagonicus*, in humeri otherwise virtually identical in size and structure, so that it is doubtful whether this variation is taxonomically segregated.

As far as this character has been definitely recorded, the tendency seems to be for the larger Miocene species to have relatively smaller and absolutely simpler (non-bipartite) tricipital fossae. No such tendency is clearly seen in the recent forms. The character is not recorded for all the large Tertiary species, and the tendency may not have been universal in them. There is some indirect probability that "*Metancylornis*" *curtus*, probably a species of *Paraptenodytes*, had a simple fossa although the species is as small as some palaeospheniscines. On the other hand, there are two large humeri with bipartite fossae in our collection, A.M.N.H. Nos. 3341 and 3346. These represent two individuals of one species, nearly as large as *Paraptenodytes antarcticus* or *Aptenodytes patagonicus*. If other humeri are correctly identified, the species must be unnamed, and perhaps the genus also is distinct, although certainly close to *Palaeospheniscus*. The fossa is strongly bipartite, with a distinct crest and large inner fossa, perhaps not quite so deep as in typical *Palaeospheniscus*, with broadly oval mouth. The head as a whole and the shaft are characteristically palaeospheniscine and quite distinct from *Paraptenodytes* of about the same size. The distal end is lacking on both specimens.

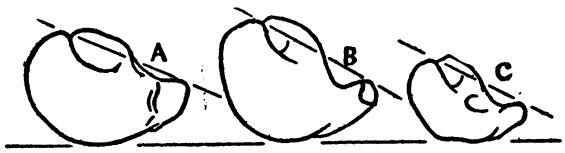

FIG. 14. Right humeri of fossil and recent penguins. Comparative series of proximal views to show degree of torsion of axis of head on plane of flattening of shaft. The latter plane is taken as a horizontal base line. A. *Paraptenodytes antarcticus*, A.M.N.H. No. 3338, Miocene of Patagonia, with torsion somewhat less than is usual in Recent penguins. B. *Palaeospheniscus patagonicus*, A.M.N.H. No. 3345, Miocene of Patagonia, with torsion at least as great as is usual in Recent penguins. C. *Spheniscus humboldti*, Recent, with torsion as is frequent in Recent penguins. Not to scale.

Like the head, the shaft of the humerus shows much more morphological variety in the Miocene than in the Recent penguins and includes types quite like the recent along

[1] This fact is visible in Moreno and Mercerat's figures and was known to Lowe (1939, pp. 291–292), although he does not mention it in his discussion of the tricipital fossa (*ibid.*, pp. 287–288) and seems there to imply, at least, that a small, simple fossa was typical if not universal in the Miocene. When he does mention the condition in *Palaeospheniscus*, he concludes therefrom that this genus and also "*Pachydyptes*" *novaezealandiae* are of later age than *Paleeudyptes* and *Anthropornis*, a conclusion completely gratuitous and contrary to the evidence.

with others that are strongly divergent.[1] In *Palaeeudyptes* the shaft is rather light, nearly straight but with a gentle sigmoid curvature, the least width is distal, and the pre-axial angulation (the tubercle or rugosity at the upper end of the brachialis inferior origin) is barely or not distinguishable. In *Anthropornis*, ? *Eosphaeniscus* (Wiman's "group 5"), and *Pachydyptes* the shaft is stout, with well-developed sigmoid curvature, proximal and distal widths nearly equal, and pre-axial angulation distinct, at about one-third of the length from the lower end. In *Isotremornis* the shaft is stout and short, in "*Arthrodytes*" *andrewsi* it is long and stout, but all three types agree in having the shaft almost perfectly straight, the width nearly equal throughout but slightly less proximally, and the pre-axial angulation represented by a small tubercle or rugosity, rather than a true angulation of the border as such.

In all species of *Palaeospheniscus* and allied genera, as far as known, the shaft is very like that of modern penguins such as *Pygoscelis* or *Eudyptes*, moderately stout, with slight curvature, decidedly narrower proximally than distally, pre-axial angulation a definite angle of the border of the bone, and the whole bone expanded in this region.

In *Pachydyptes*, *Palaeeudyptes*, and *Anthropornis* the trochlear facets for radius and ulna are anomalous, in comparison with recent penguins, in being placed more on the pre-axial border, at an acute angle to the axis of the shaft. This striking difference is strongly emphasized by Lowe, who erroneously concludes that it is a constant and radical distinction between Miocene and Recent penguins. In order to test this assumption I have measured the angle between a tangent touching both facets and a line joining the mid-points of proximal and distal ends of the shaft. The figures are given in table 4. Meas-

TABLE 4

ANGLE BETWEEN TANGENT TO TROCHLEAE AND AXIS OF SHAFT OF HUMERUS IN FOSSIL AND RECENT PENGUINS

Species	Angle	Notes
Fossils:		
Palaeospheniscus gracilis	41–46°	3 specimens, originals
Palaeospheniscus patagonicus	40–47°	7 specimens, originals
Palaeospheniscus robustus	41°	1 specimen, original
Palaeospheniscus spp.	42–53°	Ameghino's and Moreno and Mercerat's figures
Paraptenodytes antarcticus	35°	Specimen
Paraptenodytes ?antarcticus	37°	Ameghino's figure referred to *Perispheniscus wimani*
Isotremornis nordenskjöldi	38°	Specimen
"*Arthrodytes*" *andrewsi*	47°	Ameghino's figure
Anthropornis, "group 3"	25–30°	Wiman's and Lowe's figures
?Eosphaeniscus, "group 5"	30°	Wiman's figure
Pachydyptes ponderosus	35°	Lowe's figure
Palaeeudyptes antarcticus	40°	Hector's figure
?Palaeeudyptes sp.	35°	Finlayson's figure
Recent:		
Spheniscus mendiculus	39°	1 specimen
Spheniscus humboldti	33–44°	4 specimens
Eudyptes crestatus	46°	1 specimen
Pygoscelis adeliae	47°	1 specimen
Pygoscelis papua	51°	1 specimen
Aptenodytes patagonicus	47–56°	7 specimens
Aptenodytes forsteri	59°	1 specimen

[1] As in dealing with the head, Lowe has stressed one of these divergent types, with little mention of others and no mention of the type nearest to the recent.

urements are based in part on figures of the fossils not available to me, and accuracy in general is not perfect within several degrees, but is believed sufficient to give a true idea of the situation.

Even on these data, which inadequately represent the recent ranges of variation, almost all the fossil humeri are within the recent range. As in other characters of the humerus, the palaeospheniscines are not distinctive from the most nearly comparable recent species. The larger fossil species do tend to have rather low values (i.e., to have the trochleae set more obliquely), but one of the largest species, "*Arthrodytes*" *andrewsi*, has the high value of 47°. Among the fossils, only the two Seymour Island humeri have values slightly below those here definitely recorded in recent penguins, and among recent penguins only the two species of *Aptenodytes* have values slightly above those here recorded in Miocene forms.

It is true that in the Miocene the more divergent values are low and in the Recent they are high, but the data do not seem to me to suggest any trend from low values to high. It looks rather as if the typical values had remained about the same, around means of 40–50° for most species, while in the Miocene some aberrant lines developed low values and in the Recent another aberrant line has developed high values. Lowe (1939, p. 285) supposes that the small angles indicate a condition "not very well adapted for swimming," but I can find no evidence that the strong differences in angulation among recent penguins are correlated with swimming ability. The species of *Spheniscus*, with their short, angulate paddles and those of *Aptenodytes*, with their long, straight paddles, seem to swim equally well. Some functional, adaptive difference may well be involved in this angle, but it seems unjustified to speculate as to what this may be in the absence of any real evidence. I likewise feel that it is quite unjustified to consider one condition or the other as more primitive, *a priori*. The wing mechanics are thoroughly spheniscid in both Miocene and Recent penguins, and variations are all within the limits of this adaptive type. Variations in this angle can only be superficially and not really ancestrally related to the angles in possible ancestral types in which the functional significance of the angulation is radically different.

A final point that has been considerably discussed, especially by Lowe, is the relative prolongation of the epicondyles. Here, again, there is much variation in both fossil and recent forms, about the same range being covered in both groups except for a few aberrant types. In recent penguins the epicondyle projects more or less beyond a line continuing the general post-axial contour. This is also true, to nearly or quite the same degree, in the *Palaeospheniscus* group, in *Isotremornis*, and in "*Arthrodytes*" *andrewsi*. In *Paraptenodytes* the projection is slightly less, near the limit for recent species. In *Pachydyptes* and *Palaeeudyptes* the projection seems to be somewhat less than in any recent forms, and this is probably also true of *Anthropornis*, although this is not fully established by the eroded specimens.

RADIUS AND ULNA

Figures 15, 16

The following specimens are reported:

Palaeospheniscus gracilis	Radii: A.M.N.H. Nos. 3292, 3294
Palaeospheniscus patagonicus	Radii: A.M.N.H. Nos. 3291, 3293, 3298
	Ulnae: A.M.N.H. Nos. 3295, 3296, 3297, 3299, 3301, 3353
Palaeospheniscus robustus	Radii: A.M.N.H. Nos. 3302, 3350
	Ulnae: A.M.N.H. Nos. 3300, 3303, 3354, 3360
Palaeospheniscus spp.	Specimens figured by Moreno and Mercerat (1891) (Two ulnae and four radii, of rather doubtful grouping)
? *Eosphaeniscus*, "group 5"	Ulna figured and described by Wiman (1905b)
? *Pachypteryx*, "group 4"	Radius figured and described by Wiman (perhaps *Anthropornis?*)
? *Anthropornis*, "group 3"	Ulnae figured and described by Wiman
Palaeeudyptes antarcticus	Ulna (fragment) figured by Hector (1872)

(The ulna of *Paraptenodytes antarcticus* was mentioned by Ameghino, but no figure and no useful description were given)

Relatively little has been said about the

radius and ulna of fossil penguins. Little is known of these bones in the larger, more peculiar species, and they have few distinctive features of interest in the smaller, more normal species.

The incomplete radius placed by Wiman in "group 4" (? *Pachypteryx*) could, as he notes,

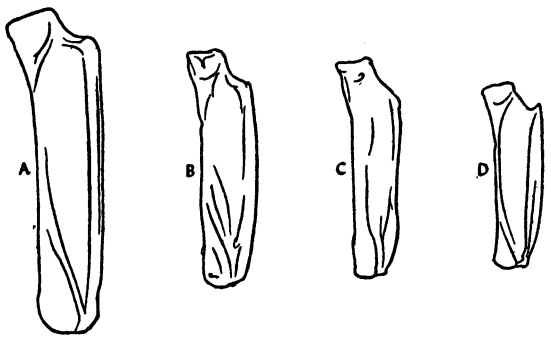

FIG. 15. Right radii of fossil and recent penguins. Comparative series in lateral (external) view. A. *Aptenodytes patagonicus*, Recent. B. *Palaeospheniscus robustus*, A.M.N.H. No. 3350, Miocene of Patagonia. C. *Palaeospheniscus patagonicus*, A.M.N.H. No. 3298, Miocene of Patagonia. D. *Spheniscus humboldti*, Recent. ×½.

belong to "group 3" (? *Anthropornis*). It does not seem to me too slender for such assignment, although both it and the ulna placed in that group may be too small over all, but the point has little interest as the preserved parts are not particularly characteristic.

The other radii known to me are all palaeospheniscine and differ little except in size and proportions. The only features possibly distinctive from recent penguins are in the details of the brachialis inferior (or internus) insertion. This extends well below the head, relatively about as in *Spheniscus*, its outline a rather even arc of a circle, its end usually a definite angulation but apparently never a right angle, as in *Aptenodytes*, or a recurved (proximally pointing) process, as in most other recent penguins.

The ulna figured by Hector as belonging to *Palaeeudyptes antarcticus* is very fragmentary. Its apparently peculiar shape may be an artifact, of the specimen or of the artist's drawing.

The two ulnae referred by Wiman to his "group 3" (? *Anthropornis*) have the shaft rather slender, its margins converging at a very acute angle more or less as in *Aptenodytes*. The expansion for the insertion of the triceps (or rather, of the tricipital tendons coming from the sesamoids at the distal end of the humerus) is quite different from that of any recent penguin, being tab-like, wholly proximal, semicircular in outline, with a small foramen near its distal margin. The smaller ulna placed by Wiman in "group 5" (? *Eosphaeniscus*) is similar in outline but lacks the foramen, which may be represented by a small notch on the distal border of the tab. On the medial surface just below the head is a pit that Wiman interpreted as a vestigial pneumatic foramen. This is extremely unlikely, and I suspect that the pit is either pathological or an artifact.

The palaeospheniscine ulnae are quite different from those described by Wiman and

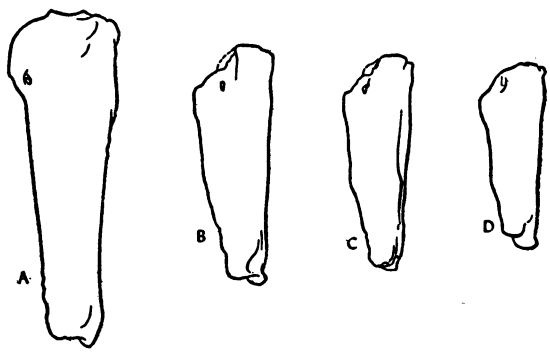

FIG. 16. Right ulnae of fossil and recent penguins. Comparative series in lateral (external) view. A. Wiman's "group 3" (? = *Anthropornis nordenskjöldi*), redrawn from Wiman, Miocene of Seymour Island. B. *Palaeospheniscus robustus*, A.M.N.H. No. 3303, Miocene of Patagonia. C. *Palaeospheniscus patagonicus*, A.M.N.H. No. 3297, Miocene of Patagonia. D. *Spheniscus humboldti*, Recent. ×½.

are very like those of the smaller recent penguins such as *Pygoscelis*, *Spheniscus*, and *Eudyptes*, probably closest to *Spheniscus*. The whole posterior border is developed into a flange, narrowing rapidly distally. In the region of tricipital insertion there is a small, proximal expansion, immediately posterior to the humeral facet, and a much more promi-

nent, more distal, often quite tab-like expansion distal to this, at the widest part of the bone, in the same relative position as in *Spheniscus*. The margin between these two expansions is concave in outline. The foramen is near the indefinite transition from the flange to the shaft proper, opposite this concave border. Although small, the foramen is usually present and patent, but it is occasionally lacking, as it is also in recent penguins, apparently by obliteration and not by becoming marginal.[1] This character does not seem to be of taxonomic significance in the fossils. The more distal, less marked, angulation of the posterior margin that is visible in varying degree in most recent forms is also normally present in the palaeospheniscines but is very slight and is relatively less distal in position than in most recent species.

METACARPUS

Figure 17

The following metacarpi are reported:

Palaeospheniscus gracilis	A.M.N.H. Nos. 3322, 3326, 3333, 3334 Specimen figured by Moreno and Mercerat (1891) as *P. menzbieri*
Palaeospheniscus patagonicus	A.M.N.H. Nos. 3316, 3323, 3317, 3335, 3336 Specimens figured by Moreno and Mercerat as *P. bergi* and *P. patagonicus* (but the latter may be *P. robustus*)
Palaeospheniscus robustus	A.M.N.H. No. 3337
? *Pachypteryx*, "group 5"	Fragment figured and described by Wiman (1905b)
Anthropornis, "group 3"	Specimen figured and described by Wiman
Palaeeudyptes antarcticus (?)	Specimen figured and described by Hector (1872)[2] (Perhaps the same as the following)
Pachydyptes ponderosus (?)	Specimen figured by Lowe (1939)[3] (Perhaps the same as the preceding)

Wiman emphasized that in his "group 3" (*Anthropornis* ?) metacarpus the first metacarpal is less fused and the third more fused to the second than in the recent penguins and that the third is not longer than the second, as it is in all recent species. Lesser fusion of first and second is apparently claimed on the basis of a distinct notch at the end of the first, rather than on any distinctly smaller degree of coössification along the actual contact of the bones. A smaller notch sometimes occurs in recent forms, and it is possible that it has been enlarged by erosion in the fossil, but it probably was larger in the latter and appears also to be so in Hector's and Lowe's figures of *Pachydyptes* and/or *Palaeeudyptes*. Coössification of second and third metacarpals seems to be greater than is usual in recent species, but no greater than can be seen as a variation in the latter. The failure of the distal end of the third to project beyond that of the second is a distinct difference, also seen in Hector's and Lowe's figures of *Pachydyptes* and/or *Palaeeudyptes*. In all these, the bone is relatively stout, and the proximal end is wider than the distal.

As with the other wing elements, the palaeospheniscine metacarpus lacks the peculiarities of the aberrant, large Antarctic and Antipodean species and is almost exactly as in living penguins. Indeed our specimens referred to *Palaeospheniscus patagonicus* can hardly be distinguished, even as to species, from a specimen of *Pygoscelis papua*. The only differences noted are that the projection of the third metacarpal is very slightly, almost imperceptibly less, the bones are very

[1] In Moreno and Mercerat (1891, pl. 1, fig. 27a) the foramen seems to be represented by a marginal notch, but this is not seen in figure 27, the opposite view of the same bone, and it is probable in any case that the margin is broken on this specimen.

[2] Wiman (1905b) doubted the association of Hector's metacarpus with the humerus referred to *Palaeeudyptes* on the ground that it was too large. The metacarpus is, in fact, from a widely different locality, and Hector stated that it is "of slightly larger dimensions" than the (undescribed) metacarpi directly associated with the other skeletal remains described by him.

[3] Lowe's figure labeled as *Pachydyptes ponderosus* is of a metacarpus from the same side as that figured by Hector as *Palaeeudyptes antarcticus* (but in the opposite view), of nearly the same size and general character. It may be the same bone. I find no comment on this bone in Lowe's text and no reference to its origin.

slightly less compressed, the distal articulations correspondingly very slightly shorter and wider, and the margins immediately proximal to these more produced, also very slightly. As in *Pygoscelis papua* the distal end is wider than the proximal, but without the pronounced flair seen in *Eudyptes*. Specimens referred to *Palaeospheniscus gracilis* differ from those of *P. patagonicus* only in being smaller.

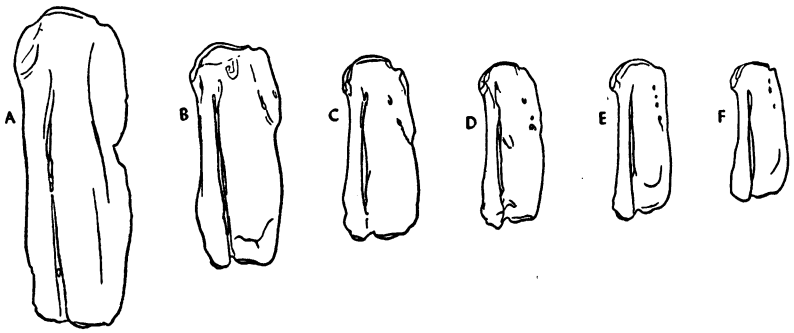

FIG. 17. Right metacarpi of fossil and recent penguins. Comparative series in lateral (external) view, reversed where necessary. A. Wiman's "group 3" (? = *Anthropornis nordenskjöldi*), redrawn from Wiman, Miocene of Seymour Island. B. *Palaeospheniscus robustus*, A.M.N.H. No. 3337, Miocene of Patagonia. C. *Palaeospheniscus patagonicus*, A.M.N.H. No. 3336, Miocene of Patagonia. D. *Palaeospheniscus gracilis*, A.M.N.H. No. 3326, Miocene of Patagonia. E. *Spheniscus humboldti*, Recent. F. *Eudyptes crestatus*, Recent. ×½.

The one specimen referred to *P. robustus* is similar but is still less compressed, the articulations are still shorter and wider, the third metacarpal projects still less, the proximal end is about equal in width to the distal. There is also a distinct crest-like projection on the posterior border of the distal part of the shaft of the third metacarpal which I find only very faintly suggested in the smaller species of *Palaeospheniscus* or in recent penguins.

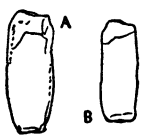

FIG. 18. Proximal phalanges of second digit of left wing of fossil and recent penguins. Lateral (external) view. A. *Palaeospheniscus ? patagonicus* A.M.N.H. No. 3332, Miocene of Patagonia. B. *Pygoscelis adeliae*, Recent. ×½.

PHALANGES

Figure 18

Phalanges have not hitherto been figured or described in fossil penguins, but our collection includes two, A.M.N.H. Nos. 3331 and 3332, tentatively referred to *Palaeospheniscus patagonicus*. Both are proximal phalanges of the second digit. Like the metacarpus, these are rather like the homologous part of *Pygoscelis papua*, but they are both relatively and absolutely shorter, they are less compressed, and the anterior and posterior margins are convex, not so straight as in this and other recent species.

THE WING AS A WHOLE

Figure 19

It has become apparent in the course of the preceding descriptions of the various individual bones that the Miocene fossils fall into two groups in comparison of the wing with their Recent allies: on one hand, *Pachydyptes*, *Palaeeudyptes*, *Anthropornis*, and some others, all of relatively large size, which are divergent among themselves but which agree in being rather unlike the living genera, and on the other hand *Palaeospheniscus* and its allies, mostly of medium to small size, which agree rather closely among themselves and in being remarkably similar to the Recent penguins. The first group seems to me to repre-

sent several different aberrant lines, prematurely and highly specialized, while the second group represents, if not the actually, at least the structurally ancestral type leading to the modern genera. This less aberrant group seems to be about as progressive in wing structure as the Recent genera. The aquatic adaptation of the wing seems to have been complete in Miocene times. The very small differences between Miocene genera of this group and Recent genera are as likely to be mere fluctuations within the general phylum as truly primitive features. I see nothing in these Miocene wings that can safely be called primitive and no clear trend from Miocene to Recent. Nor do I see any features in the larger, more distinctive genera that can certainly be labeled primitive rather than aberrant.

Within the generally modern type of wing structure, which includes also the palaeospheniscine wings, such minor differences in aspect as can be seen in the wing as a whole are due largely to two influences: the relative elongation or shortening of distal segments, and the angulation on the humerus and roughly correlated curvature of the lower wing. Even the extremes, however, are so circumscribed that no evident correlation with habits has been found.

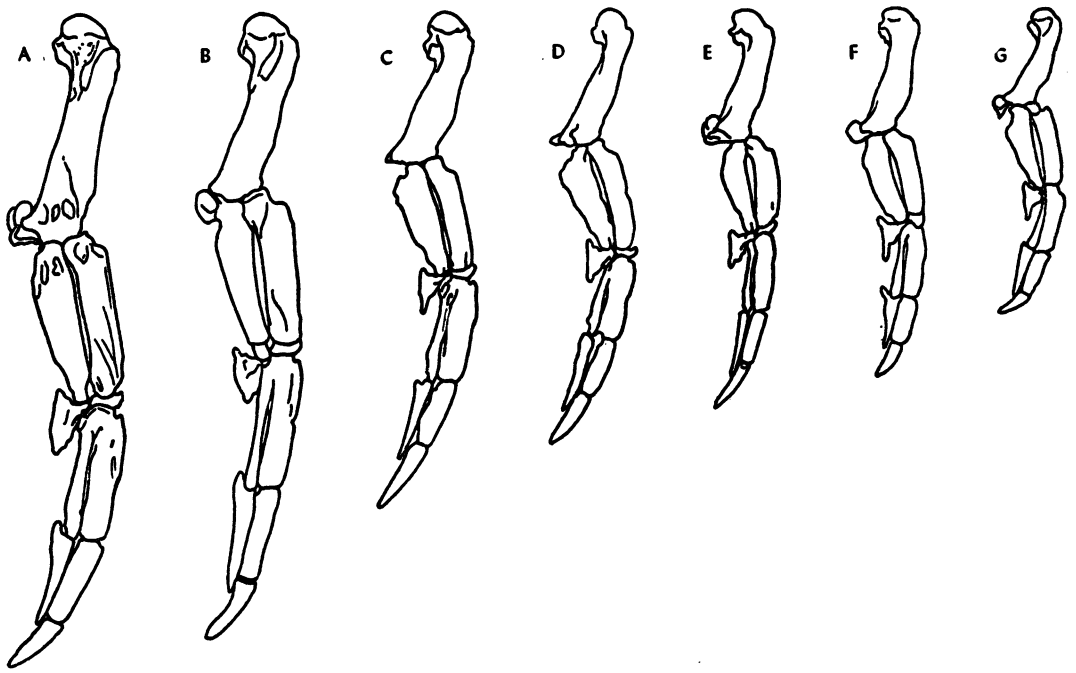

FIG. 19. Right wings of fossil and recent penguins. Comparative series in lateral (external) view. The figures of fossils are diagrammatic, composed of isolated bones from various individuals and with some hypothetical restoration. A. *Aptenodytes forsteri*, Recent. B. *Aptenodytes patagonicus*, Recent. C. *Palaeospheniscus robustus*, Miocene of Patagonia, based on isolated humerus, radius, ulna, and metacarpus; other elements restored. D. *Palaeospheniscus patagonicus*, Miocene of Patagonia, based on isolated humerus, radius, ulna, metacarpus, and first phalanx of second digit; other elements restored. E. *Palaeospheniscus gracilis*, Miocene of Patagonia, based on isolated humerus, radius, and metacarpus; other elements restored. F. *Pygoscelis adeliae*, Recent. G. *Eudyptes crestatus*, Recent. ×¼.

The closely related and closely similar species *Aptenodytes forsteri* and *A. patagonicus* differ markedly in elongation of distal segments, to such a degree that the distal elements are not only relatively but also absolutely shorter in the larger bird. This is not correlated with size, for the much smaller *Pygoscelis adeliae* has the distal elements

even more shortened relative to the humerus than has *A. forsteri*, and *Eudyptes crestatus* shows a degree of distal elongation comparable to that of *A. patagonicus*.

Data on this relative elongation are given in table 5. The figures for Recent species are from individual skeletons and series would, of course, show variation from the values given. The figures for fossils are suggestive, only, because based on isolated bones somewhat arbitrarily associated in nominal species. For *Palaeospheniscus* the results are reasonable and lend some support to the association. If the association is correct, the suggestion is that typical palaeospheniscines had the distal bones rather elongate relative to the humerus, about as in *Aptenodytes patagonicus* or *Eudyptes crestatus*. The data for Wiman's "group 3," supposedly *Anthropornis nordenskjöldi*, show the ulna and metacarpus much shorter relative to the humerus than in any other penguins in which these proportions have been determined. It is uncertain whether this is a real character, and in that case probably another aberrant feature of this peculiar genus, or whether it indicates only that Wiman wrongly placed the ulna and metacarpus of another, smaller form in this size group.

TABLE 5

RELATIVE LENGTHS OF DISTAL WING BONES IN RECENT AND FOSSIL PENGUINS, WITH LENGTH OF HUMERUS TAKEN AS 1.00

	Radius	Ulna	Metacarpus	Phalanx II-1
Recent:				
Aptenodytes forsteri	.67	.71	.56	.38
A. patagonicus	.73	.76	.63	.45
Pygoscelis papua	.65	.67	.56	.39
P. adeliae	.62	.63	.53	.34
Eudyptes crestatus	.73	.76	.66	.40
E. schlegeli	.73	.75	.62	.41
Spheniscus humboldti	.67	.70	.56	.37
S. mendiculus	.71	.71	.58	.40
Fossil:				
Palaeospheniscus gracilis	.70	—	.61	—
P. patagonicus	.77	.77	.66	.42
P. robustus	.75	.75	.65	—
?Anthropornis, "group 3"	—	.55	.49	—

The angulation of the wing is mainly the reflection of the shaft-trochlear angle of the humerus, discussed on a previous page and shown in table 4. The smaller this angle, the more angulate (less linear) is the wing. Among the recent forms measured, the wing is least angulate in *Aptenodytes*, most in *Spheniscus*. Except for humeri of possibly two species from Seymour Island, which must have had exceptionally angulate wings, the fossils are all in the recent range, as far as known, but rather on the more than on the less angulate side. In general, the more angulate the wing in recent penguins, the greater is its distal curvature, although the correlation is not perfect. On this basis, it is probable that the wing was rather strongly curved in the Miocene penguins as a group. This curvature may also have been accentuated by the tendency for the Miocene penguins to have radius and ulna and second and third metacarpals, respectively, more nearly equal in length. In the recent penguins these inequalities work against the curvature, the elongated elements being toward the concave border of the wing, but this may have been compensated in the fossils by other adjustments, for instance in their unknown carpals.

FEMUR

Figure 20

The following specimens are reported:

Palaeospheniscus gracilis	A.M.N.H. Nos. 3279, 3355, 3362 Probably Moreno and Mercerat (1891, pl. 1, fig. 12), referred by them to *P. patagonicus*
Palaeospheniscus patagonicus	A.M.N.H. Nos. 3274, 3276, 3278, 3290, 3349, 3364 Moreno and Mercerat (1891, pl. 1, fig. 7)
Palaeospheniscus robustus	A.M.N.H. Nos. 3275, 3277
Paraptenodytes antarcticus	A.M.N.H. No. 3338 Specimen described and figured by Moreno and Mercerat (1891) associated with type
Isotremornis nordenskjöldi	Specimen described and figured by Ameghino (1905), said to be associated with type
Arthrodytes grandis	Type, described and figured by Ameghino (1905)
"Group 3" (? *Anthropornis*)	Reported and figured by Wiman (1905b)
"Group 5" (? *Eosphaeniscus*)	Reported and figured by Wiman
"Group 6"	Reported and figured by Wiman
Palaeeudyptes antarcticus	Specimen described and figured by Hector (1872)

(The type of *Argyrodyptes microtarsus* also includes part of a femur, but this is probably not a penguin, and the bone is not here taken into consideration)

Wiman (1905b) found nothing of special interest in the femur and remarked that the only difference between this bone in the Tertiary and Recent forms is that the former are stouter, in correlation with the greater weight of the animals. In his "group 3" femur, the only one that is more than an insignificant fragment, the relative stoutness is well marked. All the transverse dimensions, and not only those of the shaft, are relatively large. The patellar groove is wide and short.

In recent species the articular surface on the external condyle is strongly produced and has considerable overhang on the posterior side, with a narrow notch between this and the internal condyle. As noted in the description of our skeleton of that species, this character is exaggerated in *Paraptenodytes anarcticus*. In Wiman's figure of the ? *Anthropornis* femur, on the contrary, the opposite tendency is seen. The condyles are well separated, and the notch is rather a broad groove over a transverse bridge or broad convex ridge. This

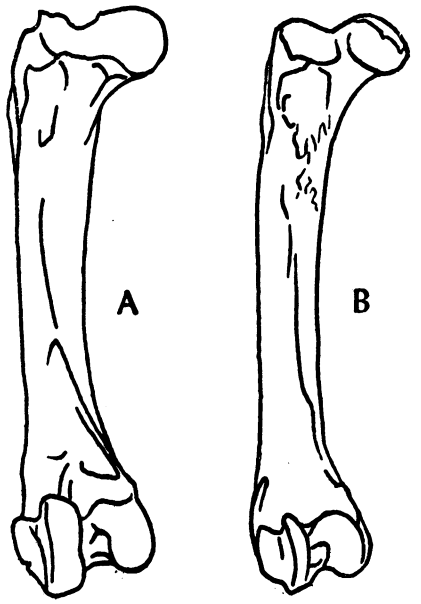

FIG. 20. Left femora of fossil and recent penguins. Posterior view. A. *Palaeospheniscus patagonicus*, composite from A.M.N.H. Nos. 3349 and 3290, Miocene of Patagonia. B. *Spheniscus humboldti*, Recent. ×1.

is still more clearly seen in Ameghino's figure of the distal end of the femur in *Arthrodytes grandis*, a species that seems closely related to *Anthropornis* if not actually referable to that genus. In *Palaeospheniscus* this part is hardly distinguishable from that of, for instance, *Pygoscelis*.

As figured and described by Hector (1872) the femur of *Palaeeudyptes* is quite distinctive. The posterior aspect is not exposed, but in anterior aspect the greater trochanter is strong and large, with no lateral compression, and the head is shown as unlike that of any other penguin known to me in being widely set off, almost at right angles to the shaft, with a relatively long, constricted neck. The patellar groove is shown as unusually short. Head and trochanter rise to the same level.

The *Paraptenodytes* femur, less distinctive but not quite like any recent femur, has been sufficiently described above.

As might be expected, the *Palaeospheniscus* femur is very modern in character. Indeed, I see almost no difference except in features variable individually and specifically in both living and extinct penguins. The greater trochanter is, however, less compressed or bent medially in the fossils, and this is the most general difference between Miocene and Recent femora as groups. In the Recent, a line continuing the external border of the shaft proximally passes well outside the border of the trochanter, while in the Tertiary it nearly or quite coincides with the latter. Our largest specimen of the proximal and medial parts of a femur of generally *Palaeospheniscus*-like type, A.M.N.H. No. 3275, shows a somewhat greater degree of compression of the trochanter than is usual in the Tertiary, but still less than in most recent bones. This specimen is also unusual in the relatively small size of the head, in the continuity of the posterior faces of head and trochanter, without a separating notch, and in the unusually strong curvature (convex forward) of the shaft.

TIBIOTARSUS

Figure 21

The following specimens are reported:

Palaeospheniscus patagonicus	A.M.N.H. Nos. 3318, 3321, 3329, 3330
Palaeospheniscus robustus	A.M.N.H. Nos. 3320, 3273, 3374, 3328, 3348
Palaeospheniscus spp.	Specimens described and figured by Moreno and Mercerat (1891)
Paraptenodytes antarcticus	A.M.N.H. No. 3338
	Specimen described and figured by Moreno and Mercerat, associated with type
"Group 3" (? *Anthropornis*)	Specimens figured and described by Wiman (1905b)
"Group 4" (? *Pachypteryx*)	Specimen mentioned by Wiman
"Group 5" (? *Eosphaeniscus*)	Specimens figured and described by Wiman

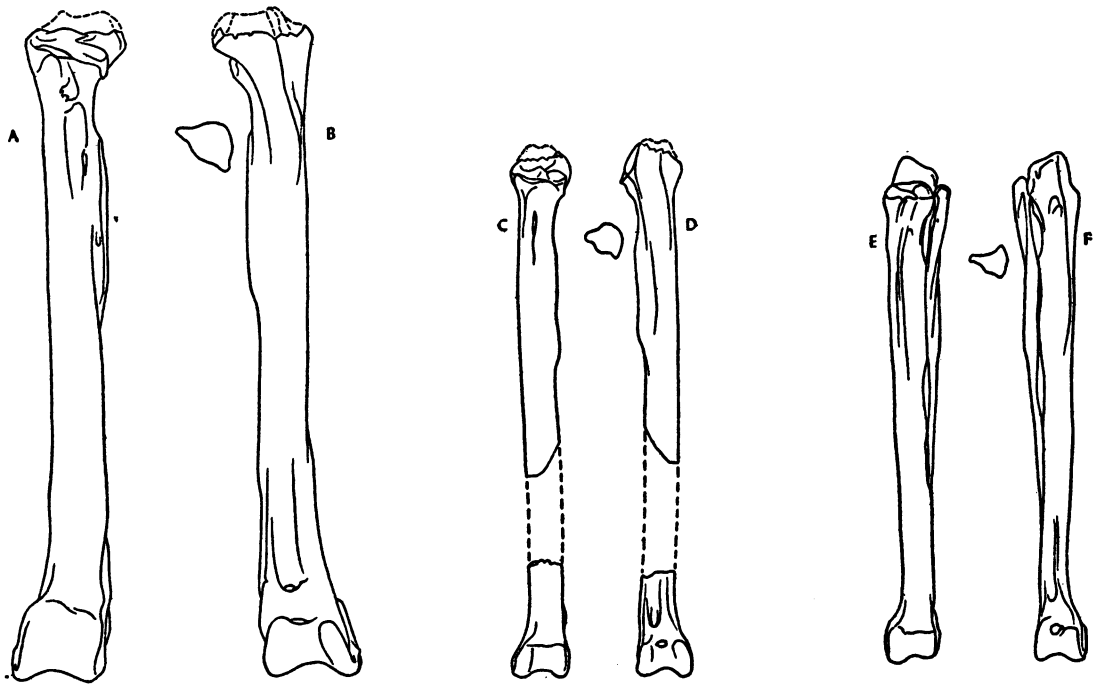

FIG. 21. Right tibiotarsi of fossil and recent penguins. Comparative series giving for each the posterior view (left), anterior view (right), and horizontal section (centered at the level of the section and oriented with posterior face up). A, B. *Paraptenodytes antarcticus*, A.M.N.H. No. 3338 (composition of both right and left sides), Miocene of Patagonia. C, D. *Palaeospheniscus patagonicus*, composite of A.M.N.H. Nos. 3329 and 3330, reversed, Miocene of Patagonia. E, F. *Pygoscelis adeliae*, Recent. ×½.

(The type of *Argyrodyptes microtarsus* is a tibiotarsus, but I question whether this is a penguin and do not include it in the following discussion)

Wiman (1905b) noted that in all his tibiotarsi the shaft is more flattened (anteroposteriorly) than in recent penguins, and the tibial crest on the posterior surface is feebly or not developed. This is also true of *Paraptenodytes* and of *Palaeospheniscus*, the difference from recent forms being least in the latter, but the rounded rather than crested posteroproximal surface is still clearly distinctive. Only one of our three specimens showing this part in *Palaeospheniscus* has a clearly distinguishable flexor attachment and here, although crest-like as in recent forms but not in *Paraptenodytes*, it is short and proximal. Another distinction from recent species shared to varying degree by *Paraptenodytes* and *Palaeospheniscus* (but not clearly determinable in Wiman's Seymour Island species) is the external eversion of the strong external cnemial crest.

The distal end is not particularly distinctive. In *Palaeospheniscus patagonicus*, for instance, this part is almost exactly as in *Pygoscelis adeliae*, even as to size, although the bridge over the tendinal groove is decidedly narrower (or shorter proximodistally).

TARSOMETATARSUS

Figure 22

Tarsometatarsi are types of 25 supposed species of penguins (plus two that I think are not penguins) and are known in all the proposed genera except in *Apterodytes* (which I think invalid), in *Argyrodyptes* (which I think not a penguin), and in *Arthrodytes*, *Orthopteryx*, and *Pachydyptes* (all three of which are allies of genera based on tarsometatarsi and are of questionable validity). The types and some other specimens have been beautifully figured and described in the most minute detail. Some of the most important of their variations are discussed and the main specimens listed in the taxonomic "Conspectus" in this paper. In this section it is not proposed to repeat or amend discussions of these variations in detail, but only to review some of the more general features of

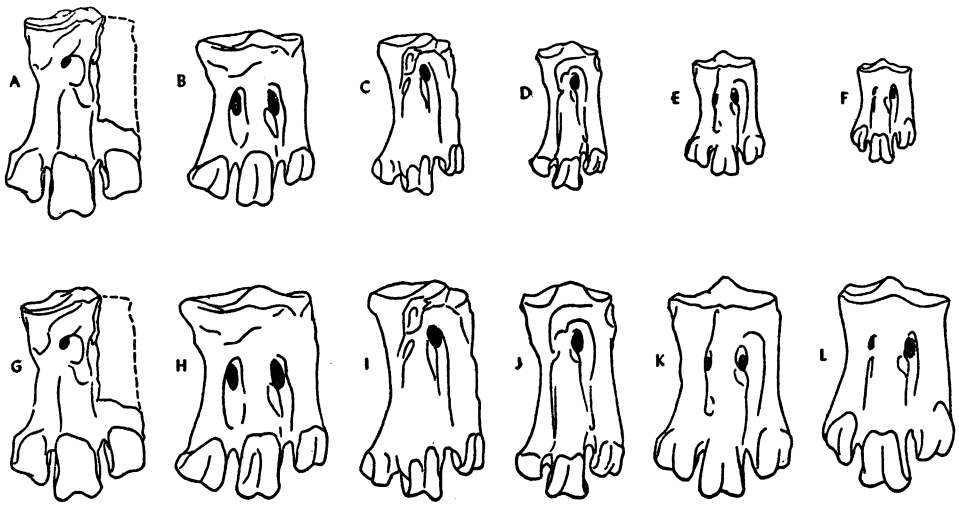

FIG. 22. Left tarsometatarsi of fossil and recent penguins. Comparative series in anterior view, with open foramina in black. A, G. *Paraptenodytes antarcticus*, A.M.N.H. No. 3338, Miocene of Patagonia. B, H. *Aptenodytes patagonicus*, Recent. C, I. *Perisphenicus wimani*, redrawn from Ameghino, Miocene of Patagonia. D, J. *Palaeospheniscus patagonicus*, A.M.N.H. No. 3358, Miocene of Patagonia. E, K. *Pygoscelis adeliae*, Recent. F, L. *Eudyptes crestatus*, Recent. A–F (upper row), ×½. G–L (lower row), reduced to same total length to emphasize differences in proportion.

the fossil tarsometatarsi in comparison with those of recent penguins.

As Lowe has particularly emphasized, all of the various processes, crests, ridges, grooves, and other surface details found in the fossils have their homologues in recent penguins. They differ in many ways, among both recent and fossil species, in size, proportions, exact position, relative prominence, etc., but the general structure is circumscribed and is virtually the same for all known penguins, recent and fossil.

There are, nevertheless, three characters so widespread in the otherwise very diverse Miocene penguin tarsometatarsi and so definitely modified in the recent penguins that it is only reasonable to conclude that they do represent an earlier evolutionary stage as a whole and that a temporal trend is definable. As a group, Miocene penguins have the metatarsals more completely fused, the tarsometatarsus relatively more elongate, and the prominent calcaneal tubercles more approximated, the outer tubercle more medial than marginal, and the inner marginal, laterally compressed, and elongate proximodistally.

In all recent penguins there are two strong grooves separating the three metatarsals on the dorsal side. The two may be about equally prominent, but the inner groove is usually somewhat less developed and may be considerably less distinct, although always present. At the bottom of each groove is an intermetatarsal foramen, highly variable in size both inter- and intra-specifically, but both always present and usually relatively large. On the plantar side there may be faint intermetatarsal grooves, but these are poorly developed and often entirely absent (in the adult).

In the Miocene tarsometatarsi, none shows any distinct grooves on the plantar side. On the dorsal side, the external groove is always present. It may be deep, wide, and long (e.g., *Palaeospheniscus*), although it does not seem quite to reach the extreme found in some recent specimens, or it may be rather poorly developed (e.g., *Anthropornis*), less than in any recent forms. The inner groove is always less developed than the outer and less than in recent species, and it may be completely absent. The internal intermetatarsal foramen is always very small and often completely absent (*Palaeeudyptes* and most adults of *Palaeospheniscus* and the closely allied genera). The external foramen is always present and may be relatively about as large as is usual (but not extreme) in recent penguins, but it, also, is usually relatively small, particularly in genera (e.g., *Paraptenodytes*) that have both foramina. In the fossils these foramina are always proximal in position, about at the extreme position seen in recent species.

Although the least degree of fusion seen in the fossils is more or less comparable to the greatest degree seen in recent forms, there is no doubt that the Miocene forms as a group show definitely greater fusion than the recent. Whatever may be the interpretation placed on the fact, a point to be considered in due course, the fact is that this makes the Miocene penguin tarsometatarsus somewhat more like that of a flying carinate than the corresponding bone in living penguins. This difference between the fossil and recent species is admitted even by Lowe (1933), although he is most anxious to minimize it and starts his discussion by saying that this resemblance to flying carinates might be called a myth.[1]

[1] Lowe (1933) says that "the myth" probably originated from Hector's error in comparing *Palaeeudyptes* with an immature rather than an adult *Eudyptes*. He goes on to say that no subsequent writer seems to have realized this mistake and that it is his (Lowe's) impression that Wiman was misled by it. This error, he further claims, closed the door to any further advance in our knowledge of the true history of penguins and was instrumental in leading to the inference that penguins are descendants of flying carinates.

The point is not of basic importance, but it seems necessary to clarify it somewhat, especially as Lowe's picturesque remarks on the perpetuation of the supposed error have attracted rather wide attention. Murphy (1935, 1936), for instance, has accepted Lowe's statements on this subject and has gone further and ascribed the original error to Wiman rather than to Hector.

Whether or not Hector's *Eudyptes* was immature is to me an open question. Lowe's "very careful reproduction of Hector's figure" is not a facsimile, and in fact it differs considerably and significantly from the original. What Lowe shows as completely open spaces between the metatarsals might in Hector's poorly executed and strictly diagrammatic drawing be intended merely to indicate the grooves present in adult as well as in juvenile *Eudyptes*. In any event, Hector drew no conclu-

The fact of greater fusion in the Miocene being admitted, it is unnecessary at this point to discuss, with Lowe, the fact that the difference "is simply and solely one of degree" (the difference in fusion between recent penguins and flying carinates is also one of degree), or whether the difference is fairly called a slight detail, or whether the resemblance to flying birds is convergent and superficial or not.

The second generalization, that the Tertiary tarsometatarsi are relatively more elongate than the recent as originally noted by Wiman, is denied by Lowe. He supports this denial by figures of four Miocene tarsometatarsi in natural size compared with recent bones of similar proportions enlarged to twice natural size (Lowe, 1933, pl. 5). It happens, as can easily be checked by measuring Lowe's figures, that in each case the fossil *is* relatively more elongate than the recent bone with which it is compared. The difference is slight in these examples, but even if Lowe's contention that the proportions are the same were true, it would prove only that (some) Miocene species tend to have the tarsometatarsal proportions about as in recent species of one-half the size of the fossils. This overlooks the interesting fact that these proportions, in both extinct and living penguins, are correlated with gross size. This is a fairly general rule in osteology,

TABLE 6

ABSOLUTE AND RELATIVE ELONGATION OF TARSOMETATARSI IN FOSSIL AND RECENT PENGUINS

Species	Length of Tarsometatarsus	100 Times the Length Divided by the Proximal Width	
		Fossil Species	Living Species
Spheniscus mendiculus *Eudyptes crestatus*	26–29	—	182–210
Palaeospheniscus spp.	32–36	221–259	—
Spheniscus humboldti *Pygoscelis adeliae* *Pygoscelis papua*	33–37	—	187–218
Palaeospheniscus spp.	38–39	217–253	—
Perispheniscus wimani *Treleudytes crassus*	41–43	207–230	—
Aptenodytes patagonicus *Aptenodytes forsteri*	45–49	—	140–171
Paraptenodytes antarcticus	53–56	181–189	—

sion whatever, erroneous or correct, from the comparison except the obvious one that *Palaeeudyptes* was larger than *Eudyptes*. I know of no evidence that Hector's figuring an immature *Eudyptes*, if he did, had any influence on later ideas of penguin morphology and derivation. No one has used Hector's poor figure as a basis for comparison, and obviously Hector himself started no ideas, correct or otherwise, as to metatarsal fusion because he did not so much as mention the subject. Specifically, it is completely gratuitous to think that Wiman might have been misled by Hector's figure. Wiman compared his fossil tarsometatarsi with those of *Spheniscus* and *Aptenodytes* (of which he figured typical and fully adult specimens) and not with *Eudyptes*, not, above all, with Hector's obviously inadequate figure that was never intended to show anything but size.

Hector's work closed no doors, and the only myth involved is the myth that Hector's figure of *Eudyptes* had any influence on subsequent study of this group. Knowledge that the fossils have the metatarsals more fused stems mainly from Wiman and not from Hector, although it is a fact visible in all the work on these bones from Huxley on. Nor, for that matter, was this observation particularly instrumental in leading to the inference that penguins had flying carinate ancestors. Wiman suggested that this fact tends to support that inference, but the inference had already been made repeatedly before Wiman and has been made since Wiman on other grounds.

based on the mechanical fact that, other things being equal, greater weights require supports both absolutely and relatively stouter. The correlation is not perfect in the penguins, but it is clear and real that smaller species tend to have relatively longer and more slender tarsometatarsi. On an average, the Tertiary tarsometatarsi are decidedly more slender than is (or, following the regression beyond *Aptenodytes forsteri* for comparison with the few larger Tertiary species, than would be) this element in Recent species of the same size. Lowe's demonstration that the proportions in the smaller Recent species are similar to those in Tertiary species twice as large is merely another way of showing that the latter are more elongate size for size. The accompanying table (table 6), although too brief to demonstrate the exact regression, illustrates this fact in a summary way and also demonstrates the further facts that the smaller extinct species have the tarsometatarsi more elongate than in any living species, even those of still smaller size, and that the larger living species have the tarsometatarsi less elongate than in any extinct species, even those of still larger size.

It is, then, evident that the Miocene and Recent penguin tarsometatarsi are affected simultaneously by two tendencies as regards relative elongation. There is an evolutionary trend from Miocene to Recent for the penguins as a whole to develop relatively shorter, stouter tarsometatarsi, and there is an adaptive tendency at any one time for the heavier penguins to have relatively shorter and stouter tarsometatarsi than their lighter contemporaries. The trend in time has been comparable in degree to the dispersion at any one time, and the heaviest extinct penguins had metatarsi about as slender as the lightest living species. The difference in weight involved is great. *Anthropornis nordenskjöldi* probably weighed at least 40 times as much as *Spheniscus mendiculus*, but the proportions of their tarsometatarsi are closely similar. On the other hand, *Palaeospheniscus patagonicus* must have weighed about the same as *Spheniscus humboldti*, but the tarsometatarsus is much more slender in the former.

The third generalization, that the ectocalcaneal tubercle is more medial in the fossils, the two nearer together, the inner tubercle marginal, salient, and linear, has not been the subject of previous discussion. Huxley did comment on the compressed, linear nature of the inner tubercle in *Palaeeudyptes*, and Lowe, again seeking to minimize or explain away any difference between the fossil and recent forms, decided that this is due to erosion (Lowe, 1933, p. 507). I do not know whether the original bone is eroded or not, but a closely similar condition can be seen in almost every published figure of this part in many species of fossil penguins and also in original specimens that certainly show no erosion. Whatever may be true of *Palaeeudyptes*, and I see no strong reason to think it an exception, the type of structure summarized at the beginning of this paragraph was certainly common and normal in Miocene penguins.

NOTES ON VARIATION

IN SORTING COLLECTIONS of isolated bones and in judging the probable limits of the extinct species and their possible synonymy, it is desirable to have concrete data on intra-specific osteological variation in penguins. Previously published data, as far as known to me, are inadequate, and I have therefore made a detailed study of variation in *Aptenodytes patagonicus* and more summary studies of several other recent species. These studies are not here published *in extenso*, but some typical results are given.

TABLE 7

STATISTICAL DATA ON LIMB BONES OF THE KING PENGUIN, *Aptenodytes patagonicus*
(Dimensions are in millimeters.)

Variate	N	OR	SR	M	σ	V
Humerus						
Length	7	112.4–122.3	18.2	116.7 ±1.1	2.8 ± .8	2.4 ± .6
Width above distal end	7	21.9– 23.6	3.16	22.81 ± .18	.49 ± .13	2.1 ± .6
Radius						
Length	7	82.6– 86.8	11.6	85.5 ± .7	1.8 ± .5	2.1 ± .6
Width	7	18.9– 21.1	4.26	19.63 ± .25	.66 ± .18	3.4 ± .9
Ulna						
Length	8	85.6– 90.4	10.1	88.2 ± .6	1.6 ± .4	1.8 ± .4
Width	8	19.6– 21.3	4.21	20.45 ± .23	.65 ± .16	3.2 ± .8
Metacarpus						
Length	8	69.4– 75.5	13.9	73.2 ± .8	2.1 ± .5	2.9 ± .7
Femur						
Length	12	97.1–104.3	13.7	100.6 ± .6	2.1 ± .4	2.1 ± .4
Distal width	12	24.7– 26.1	2.61	25.47 ± .11	.40 ± .08	1.6 ± .3
Tibiotarsus						
Length	7	179 –196	34.6	186.6 ± 2.0	5.3 ±1.4	2.9 ± .8
Distal width	7	23.3– 25.5	5.07	24.6 ± .3	.78 ± .21	3.2 ± .8
Tarsometatarsus						
Length	8	46.0– 49.1	6.41	47.6 ± .25	.99 ± .25	2.1 ± .5
Proximal width	8	26.7– 28.2	3.76	27.65 ± .21	.58 ± .15	2.1 ± .5
Distal width	8	31.6– 35.5	8.8	32.9 ± .5	1.4 ± .3	4.1 ±1.0

N. Size of sample.
OR. Observed range (limits).
SR. Standard range (span, not limits).
M. Mean.
σ. Standard deviation.
V. Coefficient of variation.
(Standard, not probable, errors are given.)

In table 7 are given standard statistics on some of the linear dimensions of limb bones in *Aptenodytes patagonicus*. The samples are small, but the results are as consistent as

would be expected and probably are sufficiently representative. The 14 coefficients of variation range from 1.6 to 4.1, with a mean value of 2.6. These values are, incidentally, lower than are usually found in comparable series of measurements on mammalian skeletons, confirming an impression that the penguin skeleton (and perhaps bird skeletons in general, although studies are too few to establish this) shows relatively little variation in linear dimensions.

It is found, nevertheless, as usually happens when an objective measure of intraspecific variation is obtained, that the amount of variation is considerably greater than has usually been allowed in the subjective erection of species on fossil bones. For instance with a coefficient of variation of only 2, which is found to be a low value even for a penguin, the standard range[1] is 13 per cent of the mean. If the mean measurement of a dimension is 100 mm., this indicates that even with this low variability the species as a whole will almost surely include individuals measuring as little as 93.5 and as much as 106.5 mm.

Such considerations have immediate practical application to the study of the fossil penguins, and are implicit in statements of probable specific differences or synonymy elsewhere in this paper. For example, the humerus referred to *Perispheniscus wimani* by Ameghino and our humerus of *Paraptenodytes antarcticus* are closely similar in morphology, but the former is 102 mm. in length while ours measures 114 mm. Both could well belong to a single species with coefficient of variation as low as 1.7. This is almost as low as any coefficient found in recent penguins and decidedly less than the homologous coefficient in our sample of *Aptenodytes patagonicus*. Thus the size difference in itself does not require or even suggest that these humeri should be placed in different species.

TABLE 8

PROPORTIONS OF OTHER LIMB BONES TO HUMERUS IN SOME RECENT PENGUINS

Index, 100 × Length Humerus over Length	*Aptenodytes patagonicus* N	OR	M	*A. forsteri*	*Pygoscelis papua*	*P. adeliae*	*Eudyptes crestatus*	*E. schlegeli*	*Spheniscus humboldti*	*S. mendiculus*
Radius	4	134–140	137	150	153	160	136	136	151	142
Ulna	5	130–136	134	144	150	159	132	133	144	140
Metacarpus	3	159–169	163	177	178	188	151	161	178	171
Femur	5	114–119	117	108	93	94	93	93	94	92
Tibiotarsus	6	61– 65	63	64	64	57	57	60	63	65
Tarsometatarsus	4	243–254	247	277	244	235	221	234	217	211

Three measurable humeri referred to *Palaeospheniscus patagonicus* have a mean length of 74.7 mm. If this is postulated as population mean and 2.0 as coefficient of variation, standard range would be 9.7 and its limits about 69.8 and 79.6. This is part of the evidence (not, of course, complete or adequate by itself and regardless of other considerations) that a similar humerus 83.7 mm. in length, referred to *P. robustus*, does belong to a different and larger species, although it is only 9 per cent longer than one of the *P. patagonicus* humeri.

Variability of the shaft-trochleae angle of the humerus is relatively great.[2] A sample of *Aptenodytes patagonicus* has N = 6, observed range = 47°–56°, standard range = 21°, mean

[1] Standard range is the average difference to be expected between smallest and largest individuals in series of samples or natural populations of 1000 individuals each (see Simpson, 1941).

[2] Variation of an angle and that of a linear dimension are not comparable things. It is a correct numerical statement to say that one has greater variation relative to the mean than does the other, but this is not necessarily true of the variation in its biological or functional significance.

$=51.0\pm1.3$, standard deviation $=3.3°\pm9°$, and coefficient of variation $=6.4\pm1.8$. A sample of the extinct species *Palaeospheniscus patagonicus* shows closely similar variation: $N=7$, $OR=40°-47°$, $SR=18°$, $M=43.3°\pm1.10°$, $\sigma=2.8°\pm8°$, $V=6.5\pm1.7$. (The higher mean is characteristic of *Aptenodytes* but not of recent species in general. In *Spheniscus humboldti*, for instance, our sample has the mean 38°.)

Variation in proportions, both intra- and inter-specific, is also striking in recent penguins, although, as a rule, the relative variation is less than for the component linear dimensions. Examples are given in table 8, showing humeral indices in a small sample of *Aptenodytes patagonicus* and in characteristic but not necessarily average individuals of some other living species. All these indices, and numerous others calculated but not here published, show striking specific differences as well as considerable individual variation.[1]

[1] A rather strange contribution by M. Dolgopol de Saez (1927) maintains, on the basis of only two specimens, that the length index 100×humerus/tarsometatarsus is constant in penguins, with the value 230, and proposes to associate fossil humeri and tarsometatarsi on the basis of this "curious relationship." The data in table 8 prove, if proof were needed, that the value 230 for this index is in reality neither constant nor characteristic.

THE BETTER-KNOWN MIOCENE GENERA can be arranged in four fairly well-defined groups on the basis of the two most frequently preserved and most typical bones, the tarsometatarsus and the humerus. In the absence of the most characteristic part of all, the skull, it is not sure that these groups are genetic as well as morphological units, but this seems sufficiently probable to serve as a tentative basis for supergeneric classification within the family. Each of these groups of fossil genera is about as distinctive, and each of the three that contain more than one species is about as varied as all the recent penguins put together. The recent genera may, then, be considered as constituting a fifth morphological and (in this case more surely) genetic unit. The units may conveniently be formal-

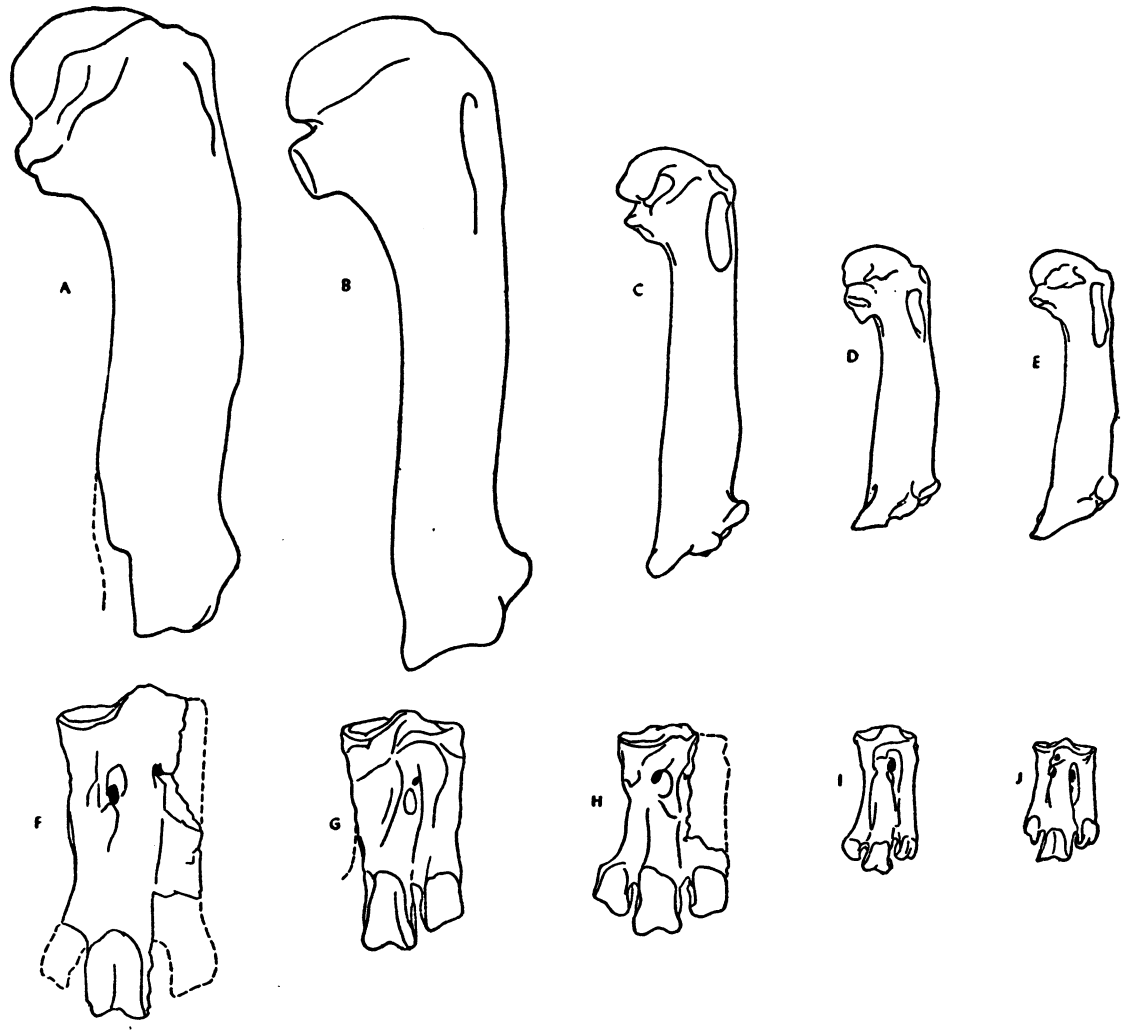

FIG. 23. Left humeri (medial views) and left tarsometatarsi (anterior views) of the five proposed subfamilies of fossil and recent penguins. A, F. Anthropornithinae, *Anthropornis nordenskjöldi*, redrawn from Wiman. B, G. Palaeeudyptinae, *Palaeeudyptes antarcticus*, redrawn from Hector and Huxley. C, H. Paraptenodytinae, *Paraptenodytes antarcticus*. D, I. Palaeospheniscinae, *Palaeospheniscus patagonicus*. E, J. Spheniscinae, *Spheniscus humboldti*. ×½.

ized as subfamilies, osteologically defined as follows (see also fig. 23):

FAMILY **SPHENISCIDAE**

SUBFAMILY **PALAEOSPHENISCINAE**

Tarsometatarsus moderately elongate, with subcircular external intermetatarsal foramen, internal foramen rudimentary or absent, metatarsal fusion strong. Humerus slightly curved, relatively stout, narrower proximally, tricipital fossa large and bipartite, shaft-trochlear angle intermediate.

GENERA: *Palaeospheniscus*, *Parasphenis-cus*, *Perispheniscus*, and more dubious allies or synonyms. Miocene, Patagonia.

SUBFAMILY **PARAPTENODYTINAE**

Tarsometatarsus relatively shorter, with small, subequal external and internal intermetatarsal foramina but otherwise strong fusion. Humerus straight, narrower proximally, tricipital fossa moderately large but not bipartite, shaft-trochlear angle intermediate.

GENERA: *Paraptenodytes* (with *Metancylornis*), *Isotremornis*, "*Arthrodytes*" (*andrewsi*, not *grandis*). Miocene, Patagonia.

SUBFAMILY **ANTHROPORNITHINAE**

Tarsometatarsus relatively elongate, with both internal and external intermetatarsal foramina, proximal, varying in proportions, metatarsal fusion otherwise about as in preceding subfamilies. Humerus heavy, sigmoid, width subequal proximally and distally, tricipital fossa simple and relatively small, shaft-trochlear angle small.

GENERA: *Anthropornis*, *Arthrodytes* (*grandis* only, tarsometatarsus unknown), *Eosphaeniscus*, *Delphinornis* (humerus unknown), *Pachydyptes* (tarsometatarsus unknown). Miocene, Patagonia, Antarctica, New Zealand.

SUBFAMILY **PALAEEUDYPTINAE**

Tarsometatarsus rather short, small external and no internal intermetatarsal foramen, strong metatarsal fusion. Humerus straight, elongate, narrower distally, tricipital fossa small and simple, shaft-trochlear angle small.

GENUS: *Palaeeudyptes*. Miocene, New Zealand, Australia.

SUBFAMILY **SPHENISCINAE**

Tarsometatarsus short, both intermetatarsal foramina well developed, metatarsal fusion relatively weak. Humerus straight or slightly curved, tricipital fossa large and more or less distinctly bipartite, shaft-trochlear angle intermediate to large.

GENERA: *Spheniscus*, *Aptenodytes*, *Pygoscelis*, *Eudyptes*, *Megadyptes*, *Eudyptula*.[1] Recent, cooler waters and adjacent coasts of the Southern Hemisphere.

The special affinities that have occasionally been claimed between particular Tertiary and Recent genera and that are implicit in such names as *Palaeospheniscus*, *Paraptenodytes*, or *Palaeeudyptes* seem to me to be nonexistent. I can find no objective evidence that would indicate that the recent genera were derived polyphyletically from various of the known fossils, or that any special affinity can be traced between a given Recent and a given Miocene genus.

The Recent genera are less varied than are the Miocene genera. In contrast with the latter they seem to represent a single stock in which divergence (as opposed to progression) is less than it was in the Miocene. The inference is that there was a mid-Tertiary radiation of penguins (doubtless rooted in the early Tertiary) which proceeded to an extreme of diversification within the limits of this striking adaptive type, and that during the later Tertiary this was replaced by a secondary radiation deriving from only one of the mid-Tertiary stocks and reaching less extreme divergence. In taxonomic terms, as the categories are weighted here, the mid-Tertiary radiation reached the subfamily level, and the diverse subfamilies were then replaced by a single subfamily within which divergence reached only the generic level.

On the face of it, the evidence suggests that the modern genera did not originate until the later Tertiary. If they were in existence in the early Miocene, they probably had a very restricted distribution not at all comparable to their present zoogeography. The absence of any trace of a generic parallel

[1] Mathews' (1935) almost absurdly split arrangement of living penguins in four families and nine genera is categorically rejected.

between the distribution of the fairly widespread known Miocene forms and that of the Recent penguins is, although negative, strong evidence that the differentiation of the modern genera had not then occurred. One would, then, expect to find the Miocene ancestors of the Recent penguins in a more limited stock, possibly a single genus or a small group of closely related genera. The alternative, that each modern genus was then already in existence or had already a differentiated ancestry, is rendered unlikely by the fact that such differentiation does almost invariably involve geographic separation. Geographic separation sufficient to allow the differentiation of six genera in one adaptively restricted stock would in all probability have led to the discovery of some trace of the more definite ancestry of a modern genus, although this argument is admittedly negative.

Whether this presumably more restricted Miocene spheniscine ancestry was a separate line, not yet discovered and presumably not occurring or rare in the regions explored for fossil penguins, or whether it is in fact one of the known Miocene subfamilies is dubious. The Anthropornithinae and the Palaeeudyptinae can be ruled out as possible ancestors. Preceding comparisons clearly show that the species in these subfamilies are less like the living forms in almost every respect than are the other two subfamilies. This is consistent only with the conclusion that they represent aberrant types, specialized end-forms that became wholly extinct. They do apparently have some truly primitive characters, but this is not a contradiction of the general conclusion that they are on the whole more specialized than other penguins. Analogous cases of aberrant specialization in ancient branches within a family are found over and over again and are a familiar and normal feature of the pattern of evolution.

In most of the known parts the Palaeospheniscinae could well be directly ancestral to the Spheniscinae. Indeed, the resemblance is so close that the wing, for instance, would not warrant subfamily distinction. But the tarsometatarsus is markedly different. The paraptenodytine tarsometatarsus is somewhat more like the spheniscine, but most other bones of the Paraptenodytinae are less like the Spheniscinae than are the Palaeospheniscinae. The case is another example of "crossing specialization," so familiar to paleontologists. A suitable ancestral type could be reconstructed by taking the most generalized structures of the two different groups, but each group has in some respect a specialization, or at least a less immediately similar structure, that tends to exclude it from the ancestry. On the whole, the Palaeospheniscinae, and particularly *Palaeosphenis-cus*, itself, are most like modern penguins. Nothing absolutely excludes them from ancestry to the Spheniscinae, and the distinctions in the tarsometatarsus could well be merely primitive, yet there is some improbability in so extensive a remodeling of this bone since the Miocene, especially as it was somewhat more spheniscine-like in some contemporaneous forms.

It is, after all, most likely that a spheniscine or proto-spheniscine line was already separating in the Early Miocene but that it had a limited geographic distribution in an area where its fossil remains have not been preserved or found. This ancestry was, nevertheless, in all probability near the evolutionary level of the Paraptenodytinae and Palaeospheniscinae, and due discounting of the more probably aberrant characters of these should give a reasonably good picture of the Early Miocene structure of the penguin ancestry. It is also beyond much doubt that the various characters shared by the fossil subfamilies and absent in Recent forms are most likely to be primitive for the family as a whole.

DISTRIBUTION OF MIOCENE PENGUINS

THE FOUR REGIONAL OCCURRENCES of Miocene penguins, given in more detail in the "Conspectus" on other pages, are in central Patagonia, on Seymour Island in the South American sector of Antarctica, on the south island of New Zealand, and in South Australia. Although relatively few in number, the discoveries represent a sampling over a very large area. Seymour Island and the South Australian locality are almost directly over the South Pole from each other. The range in latitude is from about 35° south (in Australia) to about 64° south (in Antarctica). The New Zealand and Patagonian areas of discovery are both traversed by the 45th parallel south.

All these localities are well within the area of distribution of Recent penguins (see map, fig. 24). Of course full coincidence of the distribution in Miocene and Recent would be more surprising than would be the discovery of some fossil penguins outside the Recent area, but it is quite justifiable to conclude that the two distributions were about the same. The negative part of this conclusion is supported by the fact that marine and littoral Miocene beds are widespread in the Tropics and in the Northern Hemisphere, where their fossils have been intensively collected, and that not a scrap of bone referable to the easily recognizable Spheniscidae has been found in them.

Much has been made (e.g., by Lowe) of the belief that the Seymour Island penguins lived in subtropical conditions. This is based on the claim by Dusen (1908) that a part (not all) of a fossil flora found on Seymour Island indicates subtropical conditions. The flora is not, in fact, contemporaneous with the penguins but later. It is, however, probable that the age difference is insufficient to allow for any radical climatic change. But, as noted by Berry (e.g., 1937) and others, the flora as a whole seems to be simply a southern extension of the *Fagus-Nothofagus* flora of Patagonia, which is considered indicative of a cool temperate climate. In Patagonia there are Tertiary floras of at least two climatic types, one the cool-climate *Fagus-Nothofagus* flora and the other, best known from Pichileufu, indicative of a warmer climate but still "clearly . . . not tropical" (Berry, 1938). It is uncertain which of these floras and climates prevailed when and where the Miocene penguins abounded along the Patagonian coast.[1] In any case, the evidence is that Seymour Island had a cold temperate climate at about the time when the fossil penguins were buried there and that Patagonia was also temperate

[1] Floral succession in this general part of the world presents problems that still seem far from definitive solution. Berry has worked out a scheme that is simple and clear, but that is opposed by some good evidence. He has the *Fagus-Nothofagus* association flourishing in the Eogene of Patagonia and Seymour Island, then giving way, at the beginning of the Neogene in Patagonia, to an association of Pichileufu type, indicating definite amelioration of the climate. But in northern Patagonia a *Fagus-Nothofagus* flora occurs in beds that are believed to be contemporaneous with, or immediately successive to, the Patagonian formation, hence early Neogene and of an age when, according to Berry, this flora had been replaced by one of warmer climate (see Feruglio, 1941). Furthermore the field evidence, as interpreted by those who know it best and at first hand, makes the Pichileufu type of flora earlier than these terrestrial Patagonian or immediately post-Patagonian beds (Guiñazú, 1940; Feruglio, 1941; Bonorino, 1944). In that case the presumably warm-climate flora would apparently either occur at the same time and in the same general regions as a long-continued cool-climate *Fagus-Nothofagus* association or be intercalated between occurrences of the latter. Both possibilities seem anomalous, and yet one can hardly reject the stratigraphic evidence altogether in favor of Berry's more orderly but hypothetical view. (There is, indeed, a third possibility: that Berry has the situation exactly reversed and that the *Fagus-Nothofagus* flora is everywhere the later of the two, but this is quite improbable.) Moreover it is highly improbable that the Seymour Island *Fagus-Nothofagus* flora is Eogene, as Berry supposes. It occurs above marine beds that are at least approximately equivalent to the Patagonian and that are late Oligocene, at earliest, and probably Miocene in age. The plants themselves do not over-ride this evidence as to age, for even in Patagonia there are, as noted above, probable Miocene occurrences of the *Fagus-Nothofagus* flora. Further evidence, still occasionally cited, is the supposed occurrence of "*Zeuglodon*" = *Basilosaurus*, an Eocene genus, in the marine beds of Seymour Island. This identification by Wiman (1905b) was based on two badly preserved vertebrae and, reading between the lines, Wiman evidently referred them to "*Zeuglodon*" as much because he thought them Eocene (an opinion he later abandoned) as because he had made a positive identification. As a matter of fact, the vertebrae are not really identifiable at present and could as well be Neogene as Eogene in age (see Kellogg, 1936, p. 263).

in climate, perhaps but not surely warmer than Seymour Island. The climate was probably warmer in both regions than it is now, but in neither was it subtropical or, *a fortiori*, tropical.

The fossil occurrences do not indicate that penguins in the Miocene were adapted to or tolerated higher temperatures than at present. They are now (despite the extension of a few species into Antarctica) most typical of the Temperate Zone and are abundant on some warm temperate coasts. Instead of indicating that Tertiary penguins were, even in part, subtropical or tropical, that they were not limited by climatic zones, or that there were no such zones then, their distribution is itself good evidence that there were climatic zones then and that the penguins,

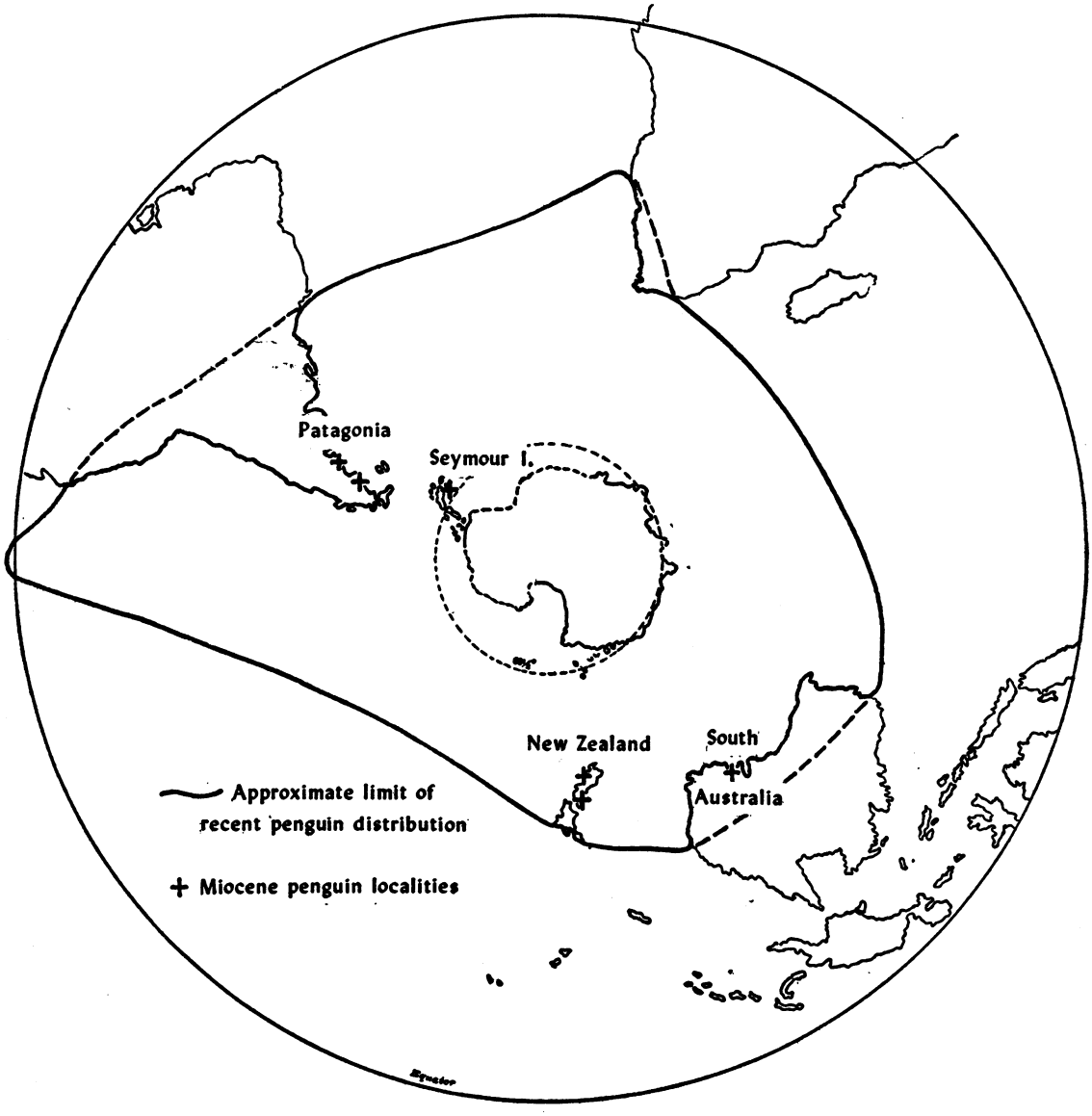

FIG. 24. Distribution of fossil and recent penguins, shown on a map of the Southern Hemisphere centered on the South Pole and limited by the Equator. The greater part of the recent range and all the fossil occurrences are in the South Temperature Zone.

then as now, were restricted to the Southern Hemisphere by the barrier of the warm equatorial waters.[1] Further implications will be mentioned in discussing the origin of penguins.

Recent penguins afford an example of Bergmann's rule, that among closely related warm-blooded animals the size tends to increase as the environmental temperature decreases. The largest penguins (*Aptenodytes forsteri*) live farthest south, where it is coldest; the approximately smallest (*Spheniscus mendiculus*) live farthest north, where it is warmest; and the rest tend, with some irregularity, to form a graded series between these (see Hesse, 1924, p. 393).

Evidence for this effect among Tertiary penguins is equivocal. It is true that smaller species are known from Patagonia than from Antarctica and that the more abundant penguins of the former (*Palaeospheniscus* spp.) are much smaller than those more abundant on Seymour Island (*Anthropornis* spp.). The largest Antarctic species is also distinctly larger than the largest known from Patagonia, although there is a wide overlap in size of the species from the two localities. To this extent, then, the fossil penguins do tend to follow the rule; the size overlap does not necessarily indicate an exception, since it is analogous to the situation among recent forms outside of the extremes of their range. On the other hand, one of the three New Zealand species (*Pachydyptes ponderosus*) is about as large as any from Seymour Island, and the smallest ("*Pachydyptes*" *novaezealandiae*) is larger than the most abundant Patagonian forms. The most northern occurrence, in Australia, is also of a penguin above average size for Patagonia, although considerably smaller than the larger species of other regions. Nothing contradicts the possibility that the Miocene species tended to follow the rule, but positive evidence that they did so is inadequate. It must also be remembered that the latitude difference of the fossil discoveries, less than 30°, is much smaller than the latitude range of recent penguins, almost 80°, and that climatic zones in the Miocene, although existent, were probably broader and less extreme than they are now.

It might be supposed that Bergmann's rule should demand that the very large Tertiary penguins lived, or had evolved, in an even colder climate than that inhabited by the emperor penguin (if a colder climate can be conceived of as habitable at all), but the rule applies only to closely allied contemporary forms and not to faunal successions, in which different principles are in play. In phylogeny, progressive groups tend to become larger (individually) with the passage of time, but differential extinction tends in the end to bear more heavily on the larger species. These tendencies, rather than Bergmann's rule, were evidently involved in penguin faunal sequence.

[1] The occurrence of penguins on the Equator in the Galápagos Islands is well known, but it is equally well known that they have been able to penetrate into the literal Tropics because of the cold Humboldt Current and that their environment, even on the Equator, is not really tropical. On this general question of climatic control of penguin distribution, see Boubier, 1920.

SIZE OF THE FOSSIL PENGUINS

THERE HAS BEEN a great deal of interest in the size of the Miocene penguins, and especially in their probable standing height. Some of them were obviously larger than the biggest recent penguins, and the idea of a penguin "as tall as a man" has irresistible appeal, enhanced by the generally anthropomorphic aspect of these quaint birds. The gigantism of Tertiary penguins in general has been exaggerated, although they certainly did reach impressive maximum dimensions.

Huxley (1859) estimated that the living emperor penguin reaches a standing height between 3 feet and 3 feet 6 inches, and that on the basis of comparison of the tarsometatarsi *Palaeeudyptes antarcticus* should have been between 4 and 5 feet high. Hector (1872) was "convinced that this estimate is rather under than over the size of the extinct bird." (I have elsewhere pointed out that Hector's specimens are, indeed, rather larger than one would expect to be associated with Hyxley's tarsometatarsus.) Oliver (1930) estimated that his *Pachydyptes ponderosus* stood 150 to 180 cm. high, i.e., 4 feet 11 inches to 5 feet 11 inches (I think the latter figure too large).

Considering the emperor penguin to be 90 cm. high, Wiman showed that *Anthropornis nordenskjöldi* would be about 170, 100, or 118 cm. in height, depending on whether the comparison is based on tarsometatarsus length, metatarsus length, or tibia distal breadth. He considered the first estimate to be too high and decided that 100–118 cm. is the best estimate. From the metacarpus (Hector's specimen) he concluded that *Palaeeudyptes antarcticus* was about 128 cm. in height, and that neither species would be more than shoulder high to a normal man (would only reach to under the outstretched arm). Lowe (1933) makes the general statement that the Antarctic fossil penguins averaged twice the size of recent penguins.

TABLE 9

ESTIMATES OF STANDING HEIGHTS OF FOSSIL PENGUINS

Species	Based on Tarsometatarsus	Based on Femur	Based on Humerus
Pachydyptes ponderosus	—	—	5′ to 5′4″
Anthropornis nordenskjöldi	4′9″ to 5′4″	3′7″ to 4′1″	4′6″ to 5′
Eosphaeniscus gunnari	3′9″ to 4′3″	—	—
Palaeeudyptes antarcticus	3′6″ to 3′11″	3′2″ to 3′10″	4′ to 4′7″
"*Arthrodytes*" *andrewsi*	—	—	3′11″ to 4′5″
Paraptenodytes antarcticus	3′1″ to 3′6″	2′10″ to 3′5″	3′ to 3′5″
"*Pachydyptes*" *novaezealandiae*	—	—	2′9″ to 3′2″
Delphinornis larsenii	2′9″ to 3′1″	—	—
Perispheniscus wimani or *Palaeospheniscus robustus*	2′4″ to 2′8″	—	2′3″ to 2′8″
Palaeospheniscus patagonicus	2′2″ to 2′5″	—	1′10″ to 2′3″
Palaeospheniscus gracilis	1′9″ to 2′	1′7″ to 1′11″	1′10″ to 2′1″

In more general studies and in the popular literature, statements may be found that fossil penguins reached a height of 6 feet, or of 2 meters, or that they were taller than a man. As will be shown, these statements are quite surely exaggerations.

The calculation of standing heights from the known fossil bones is subject to large errors, and any results must be considered approximate only. Standing height has seldom actually been measured in living penguins, and so far as I know the live standing height and the lengths of various isolated bones have not been measured in the same individual. Even measurements of standard total length and bone lengths on one individual are few, although there are (rather

insufficient) data on these dimensions for most of the living species as a whole.

In eight recent species of four genera (*Aptenodytes*, *Pygoscelis*, *Eudyptes*, and *Spheniscus*) most closely studied by me, I find that total length (not height) is about 18½ to 24 times the tarsometatarsal length, about 8 to 9½ times the femoral length, and about 8½ to 9½ times the humeral length. The great variation, both intra- and inter-specific, shows, in itself, how approximate the desired estimates must be. Variation is particularly great in the ratio to tarsometatarsal length, in part because the tarsometatarsus is relatively shorter in large species than in small. In the fossils, the tarsometatarsus is relatively longer than in recent species of comparable size. The most reliable estimates on this basis would be based on the ratio in small, rather than in large, recent penguins because the small recent species have more nearly the proportions of the fossils. In these probably most comparable recent forms, the ratio is about 18½ to 20.

Standing height, even when the birds are in the digitigrade position, is less than total length. This also introduces great variation, but the difference seems usually to be at least 5 per cent and may be about 10 per cent. As approximations, necessarily rough, it is estimated that the standing height in the extinct species might be 17 to 19 times the tarsometatarsal length, 7½ to 9 times the femoral length, and 8 to 9 times the humeral length. Of these estimates, the last, least variable in the recent species studied, may be most reliable. Table 9 gives some estimates of total height based on these approximate ratios. Because the interest of these estimates is more popular than scientific, I have given them in feet and inches rather than in metric units. (See also fig. 25.)

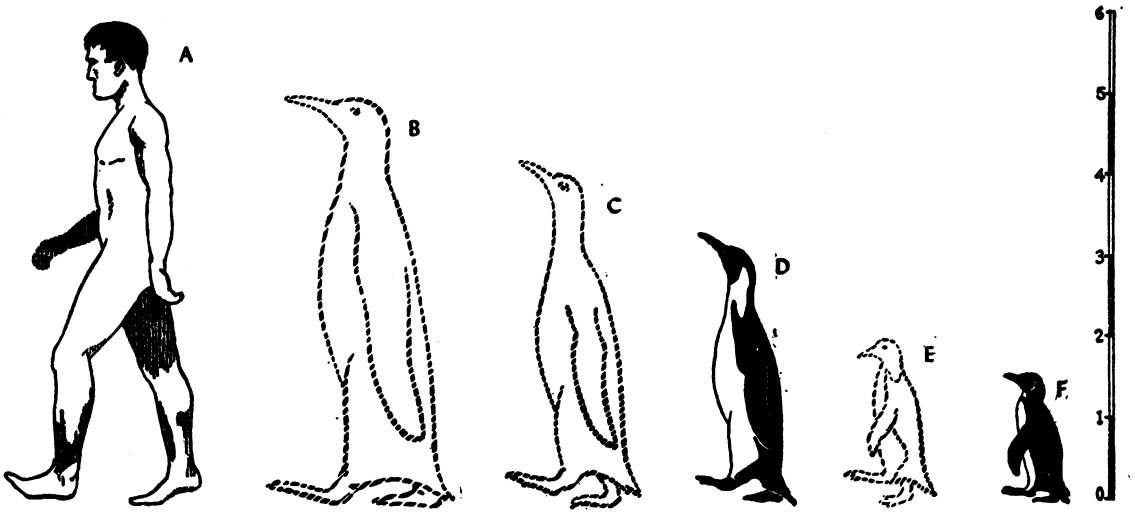

FIG. 25. Sizes of fossil and recent penguins compared with a six-foot man. Heights of extinct penguins are estimated as explained in the text. The outlines in B, C, and E are meant to suggest size only and are not meant to be true life restorations of particular genera or species. A. Man. B. The largest Miocene-penguins, largest species of *Pachydyptes* and *Anthropornis*. C. Other "giant" Miocene penguins, approximately *Palaeeudyptes antarcticus* or "*Arthrodytes*" *andrewsi*. D. The largest living penguins, *Aptenodytes forsteri*, the emperor penguin. E. Miocene penguins of moderate size, such as *Palaeospheniscus patagonicus*. F. One of the smaller living penguins, *Spheniscus mendiculus*, the Galápagos penguin. Scale at the right is divided in feet.

From these estimates it is seen that only two known fossil species are likely to have reached 5 feet in height, and that there is no strong evidence that any were as tall as 5½ feet. Aside from the very dubious *Orthopteryx gigas*, only five known species are likely to have been definitely taller than the living emperor penguin, which stands 3 to 3½ feet high.

Of the three species known from New Zea-

land, two were "giants," 4 to 5 feet in height, and one was probably about the size of a king penguin. Of the six species named by Wiman from Seymour Island (the status of at least two of which is unsatisfactory), four may be considered "giants," 4 to 5 feet in height, one is more or less comparable with the king penguin or perhaps less tall, and one was apparently a small species (unless the fragmentary material is juvenile). Of the eight Patagonian species that I consider relatively well defined, one was a "giant," about 4 feet high, one was about the size of an emperor penguin, and the other six were of about average size for living penguins, ranging down to 2 feet or less in height and not a great deal larger than the smallest of living species. The average size of individuals from Patagonia is rather small, because the moderate-sized species of *Palaeospheniscus*, of very nearly the same size as the Magellanic penguin that now frequents that coast, are much the most abundant in collections. Of the proposed species from the Patagonian Miocene that I consider inadequately distinguished, none was larger than a king penguin, and almost all belong to this group of moderate to small size, so that these do not modify the impression obtained from the better-defined species.

Estimates of weight are, of course, still more hazardous than those of height, but are also interesting. Emperor penguins generally weigh about 70 pounds, and king penguins some 40 pounds. The common species of moderate size usually weigh 10 to 15 pounds, and the little Galápagos penguin may weigh only 5 pounds or so. (See Murphy, 1936, for weights of American species.) Supposing weight to vary approximately with the cube of height (which it tends to do in living penguins, but only within very broad limits of error), the weight of a penguin about 5 feet tall would probably be between 200 and 300 pounds. Of course differences in proportion, fatness, etc., could falsify even so loose an estimate, but it is probable that the largest extinct species weighed more than an average man, although they were not so tall.

THE ORIGIN OF PENGUINS

STATUS OF THE PROBLEM

THE PENGUINS form so sharply defined a group, so distinct from any other birds in structure and habits, and so interesting from the functional and other points of view, that the problem of their origin and relationships early became and still remains one of great fascination and equally great difficulty. The popular confusion with the auks (to which penguins owe their vernacular name) was not long in being corrected by scientific investigation. Many early students did, nevertheless, maintain that penguins are related to auks, either exclusively or along with the Colymbiformes. This view now has historic interest only, as it is universally agreed that the rather superficial resemblance of Sphenisci-dae to Alcidae is purely convergent and that the families belong far apart in the system. Some other early views are now so completely discredited that they excite only amusement: Garrod at one time considered the penguins to be Ansores, Valenciennes thought them allies of *Aepyornis*, and A. Brehm spoke of them as transitional between birds and fishes.

Disregarding points of detail, three general views as to penguin affinities are still current. Although each had been suggested, at least, in earlier work, these three theories all reached more or less definitive form in studies published at almost the same time some 60 years ago. All three recognize, as has, indeed, become obvious, that the penguins are in some respects so profoundly unlike any other birds that their separation must be placed at an early date and that inclusion in, or particularly close relationships to, any other order are not tenable.

Fürbringer (1888) nevertheless maintained that they are related to the Procellariiformes. His diagrams show them arising, not from the Order Procellariiformes, but from the same remote and relatively generalized ancestry as the latter. According to views now current, also consistent with Fürbringer but less clearly shown by him, this would also imply some relationships, probably still more distant, with the Colymbiformes and Pelecaniformes, which are usually believed to have some ancient connection with the Procellariiformes.

Watson (1883) believed that the penguins were derived from flying birds but at such a very early date or from such an undifferentiated stage that it would be futile to seek any particular relationships with other orders until or unless a fully annectant series of fossils is found. Such views are expressed taxonomically by listing the penguins as a wholly isolated order, or even as a separate superorder, of carinates or neognaths.

Menzbier (1887), at the opposite extreme from Fürbringer,[1] believed that penguins had been distinct from the very beginning of avian history and that they represented a basic aquatic branch, their flippers not modified wings but a direct adaptation of the proavian or reptilian forelimb. He even considered rather favorably, although without definitely accepting or rejecting it, the idea that they might have arisen independently from the reptiles. If this view is correct, the penguins must be referred to a separate subclass (at least), and Menzbier did this, calling the subclass Eupodornithes.[2]

With occasional students inclining to views more noncommittal, like Watson's, most

[1] The opposite extreme among these three still debatable views. At the time, the extreme was far less conservative than Fürbringer, as some students then still associated the penguins directly with the Alcidae, Colymbidae, or both.

[2] Penguins had still earlier been placed in a distinct subclass (Impennes) by Geoffroy St. Hilaire and others. Menzbier also maintained that the so-called ratites were another separate line from the proto-avian or reptilian ancestry, an idea earlier expressed by Vogt and numerous other students. Lowe's recent views on both penguins and ostriches are thus a revival of hypotheses current two and three generations ago and then widely discussed before being discarded. Menzbier's views, for instance, were known to Fürbringer and were rejected in the face of evidence from one of the most elaborate comparative anatomical studies of birds ever made. Watson wrote before Menzbier, but he also considered the hypothesis that the penguin ancestry had never been volant and discarded it after a most detailed and nearly exhaustive first-hand study of penguin anatomy.

later authors have held opinions nearly like those of Fürbringer. This has not, really, been the development of a dogma or orthodoxy as Lowe (1939) has said, but has been based on the careful marshalling of the evidence by Fürbringer and on the fact that reconsideration of, and additions to, that evidence were held by the students concerned to support his conclusions. Thus Gadow's almost equally elaborate study of the birds in general (1891, 1893) also led him to consider penguins allies of the Procellariiformes (and Colymbiformes). This conclusion was also supported by, or consistent with, later osteological studies (especially Pycraft, 1898; Boas, 1933; Virchow, 1931), studies of adaptation and life histories (especially Murphy, 1936), and others. Indeed agreement has become virtually universal among those who have made first-hand studies of penguins that their ancestors were volant, and a strong consensus holds that they are, in some way, related to the Procellariiformes and perhaps also to the Colymbiformes and Pelecaniformes.

Lowe (1933, 1939) has, however, violently dissented from this opinion and has returned in even more explicit and extreme fashion to Menzbier's belief that the penguins are independent derivatives of non-volant protoavians. His first paper was severely criticized by Gregory (1935) and by Murphy (1935, 1936). Their arguments, left unanswered by Lowe, are so cogent that the matter might have been dropped there had not Lowe (1939) returned to the attack with evidence derived mainly from fossil penguins and then (1944b) correlated this with a fundamental reconsideration of avian evolution in general, with particular reference to the (supposed) Jurassic birds, the ostriches, and the penguins. Lowe's studies of fossil penguins are the most detailed that have appeared in recent years, so that some further consideration of them is necessary here, and even if Lowe's theory were rejected out of hand, which is not warranted, the additional evidence summed up in this paper would still require orientation in the general field of penguin evolution.

THE FOSSIL EVIDENCE

The earliest students of fossil penguins had little to say about the bearing of these on penguin ancestry beyond the indication of great antiquity for the family. This point was overemphasized because it was long believed that the fossils probably came from the Eocene, whereas it has since been found that all are of mid-Tertiary age. Wiman (1905b) examined his materials from the particular point of view of penguin ancestry. He reported that in bone after bone the Tertiary penguins were more like flying carinates than are the Recent penguins. Without definitely committing himself to a theory as to closer relationships, he mentioned several particular resemblances to the Procellariidae. Ameghino (1905) accepted Wiman's general results, but instead of considering the relatively elongate and more fused tarsometatarsi of the fossils as evidence of a flying carinate ancestry, he considered this a more specialized condition than in the recent penguins and so excluded the known fossils from the ancestry of the latter. Ameghino also maintained that his "Cladornidae" represented a terrestrial stage of penguin evolution, following the volant and preceding the natant stages. (As it is unlikely that the "Cladonidae" have anything to do with penguins, this evidence is not further considered.) Lowe (1933, 1939) restudied some of the Tertiary penguins and concluded that Wiman had been quite wrong in thinking them intermediate between modern penguins and flying birds.

The morphological evidence has been still more extensively reviewed on previous pages of this paper. In the present section its possible bearing on the question of ancestry will be briefly summarized.

It is unfortunate that the fossil penguin skull is known only in *Paraptenodytes*, a genus that is, judging from the skeleton, somewhat more specialized than *Palaeospheniscus*, although apparently less so than the Anthropornithinae or Palaeeudyptinae. Neverthe-

less it does give us one variant of Miocene skull structure. (See fig. 26.) In general this skull is definitely spheniscid, and some of its peculiarities can only be considered either aberrant or eclectic with reference to the recent genera. The most striking peculiarity, however, is in the form and relationships of the pterygoid bone, and this is a clean-cut resemblance to the normal carinates (fig. 27). As noted in describing it, had this bone been found isolated, it could not have been identified as belonging to a penguin and could have been referred to the Procellariiformes. Some other features, although not wholly unique among penguins, are also of interest and of cumulative value as evidence because they also do occur in some, at least, of the Procellariiformes. This is true of the high, vaguely bipartite foramen magnum, the semicircular occiput, the relatively small and little-projecting cerebellar dome, the great development of the temporal fossae and sagittal crest (at least as much like several of the procellariiform genera, e.g., *Puffinus*, as like *Spheniscus*), the long optic process of the quadrate (fig. 28), and the single, plate-

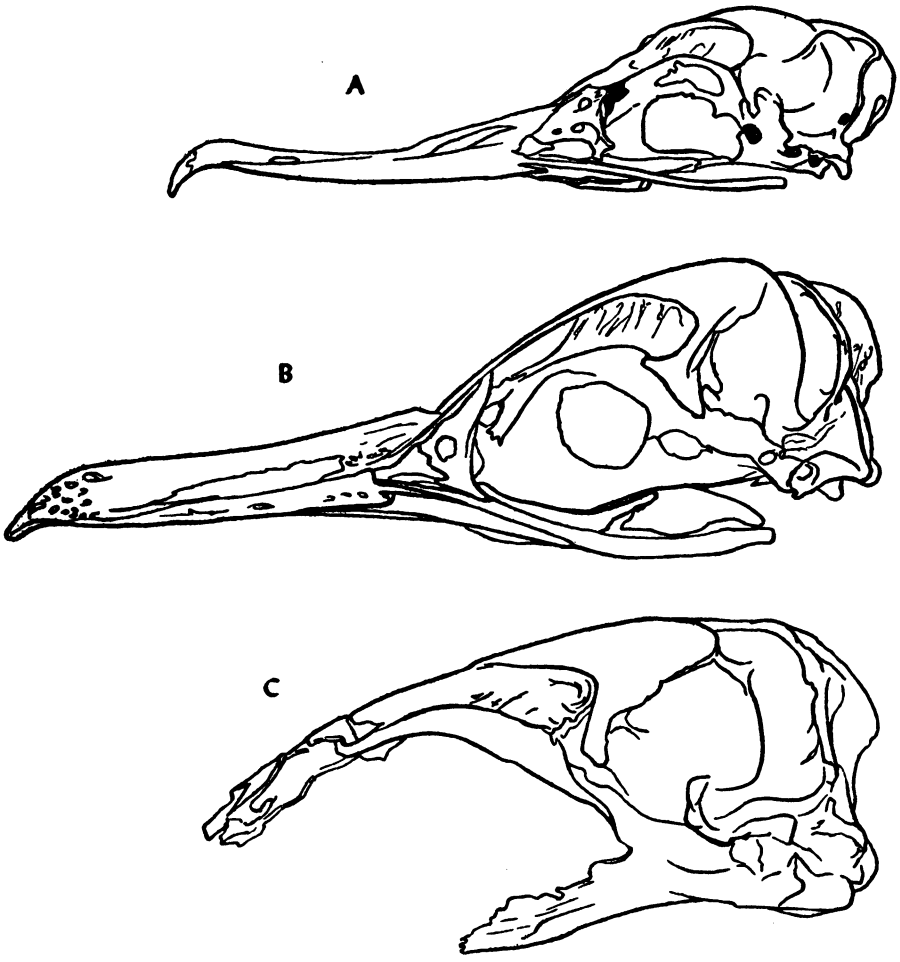

FIG. 26. Skulls of recent birds and a fossil penguin. Comparative series in left lateral view. A. *Puffinus griseus*, Recent. B. *Spheniscus humboldti*, Recent. C. *Paraptenodytes antarcticus*, A.M.N.H. No. 3338 (rostrum lacking), Miocene of Patagonia. ×1.

like, postarticular process of the mandible (less vertical than in *Puffinus*, for example, but rather more like that genus than like a typical living penguin). The peculiar paroccipital processes are not like those of any procellariiform compared by me, but are

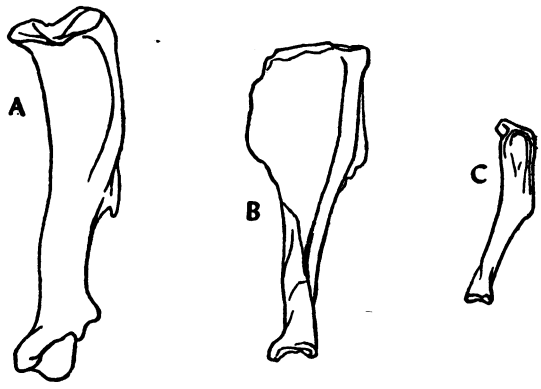

FIG. 27. Left pterygoids of recent birds and a fossil penguin. Comparative series of ventral view. A. *Paraptenodytes antarcticus*, A.M.N.H. No. 3338, Miocene of Patagonia. B. *Pygoscelis adeliae*, Recent. C. *Puffinus griseus*, Recent. ×2.

about as close to those of that group as to those of living penguins. All in all, truly spheniscid as it is, the fossil skull is distinctly more like various of the Procellariiformes than is this part in any living genus of Spheniscidae.

The evidence of the vertebrae is not abundant or clear. Even in recent penguins, vertebral characters are rather like those of the Procellariiformes, almost to the point of intergradation, but the scanty fossil material does not add much beyond increasing the known range of variation in the group. Wiman (1905b) said of the Seymour Island lumbosacrals as a group that they resemble those of flying birds and particularly the Tubinares (Procellariiformes), without specifying special points of resemblance. His descriptions and figures leave some doubt as to whether this resemblance is clearly greater in his fossils than in recent penguins. Recent penguins and Procellariiformes are, indeed, remarkably similar in this region in contrast with almost all other birds, although the great auk also shows considerable resemblance, as a warning that convergence is also in play here. The Boas formula of our *Palaeospheniscus* synsacrum, $1+3+3+2+3=12$, may have some special significance because this is a rare variant in living Sphenisciformes but normal in some living Procellariiformes (e.g., *Puffinus*), but more specimens are needed before the value of this resemblance can be assessed. (See fig. 29.)

Likewise dubious, and yet another definite resemblance to various flying birds and specifically to Procellariiformes, is the flaring coracoid base in a number of the fossil species. In other fossils, however, this is not more marked than in recent penguins.

As regards wing structure, particularly as seen in the humerus, it has been pointed out above that Miocene penguins fall into four groups. All are clearly thoroughly aquatic and incapable of aerial flight. In the Palaeospheniscinae the wing is almost exactly as in modern penguins. The evidence is that specialization was then complete and that no definite progress has occurred since then. This has no particular bearing on penguin origin except to demonstrate that their adaptation antedates the Miocene, a discovery so little surprising that it would, on any theory of their ancestry, be postulated with full confidence even were fossils unknown.

In the Palaeeudyptinae, Anthropornithinae, and Paraptenodytinae the wing is less

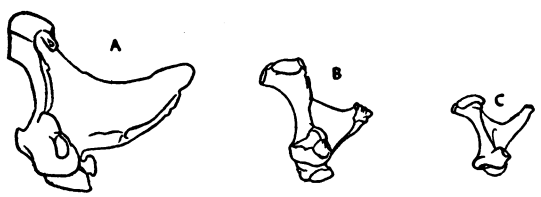

FIG. 28. Right quadrates of recent birds and a fossil penguin. Comparative series in lateral view. A. *Paraptenodytes antarcticus*, A.M.N.H. No. 3338, Miocene of Patagonia. B. *Pygoscelis adeliae*, Recent. C. *Puffinus griseus*, Recent. ×1.

like the Spheniscinae. Lowe (1939) has concluded that the first two of these groups,[1] because ancient and different, are *ipso facto*

[1] The paraptenodytine humerus was not definitely identified when he wrote.

more primitive and has even suggested (*ibid.*, p. 292) that the Palaeospheniscinae must belong to a later horizon, a gratuitous conclusion for which there is no evidence and against which there is considerable evidence. I am inclined to think that these humeri are as much aberrant as primitive. They all belong to big, heavy species. Some of their peculiarities are evidently, and others are possibly, mere correlatives of great bulk. Others, like the small shaft-trochlear angle, so emphasized by Lowe, seem quite surely to be the aberrant specialization of branches from the main line of evolution, if only because they do not resemble any possible ancestral stock, volant or non-volant. The character is not in the least reptilian. It has, incidentally, been shown in previous pages that this angle is highly variable in recent penguins and that the rare extreme seen in two Miocene species is only the end of a graded series of variations.

It remains possible that these divergent lines, although aberrant in some respects, have retained some primitive features lost in the spheniscine ancestry, and the nature of the tricipital fossa may be one of these. If so, it would add to the evidence for volant ancestry and for procellariiform affinities. It is particularly hard to follow Lowe's logic in his discussion of this point. He says (1939, p. 288) that, "From the morphology of the tricipital fossa it is clear that as we go back in time we are receding further from rather than getting any nearer to a volant condition of things." The peculiarity of the fossa in these subfamilies is that it is non-pneumatic (as in all penguins), not bipartite (unlike Palaeospheniscinae and Spheniscinae), and of only moderate size. But these are precisely the characters of the fossa in most Procellariiformes (the Diomedeidae excepted), where it "is of moderate size, is single . . . , and does not receive pneumatic apertures" (Pycraft, 1899). In fact, these particular fossil penguins are definitely nearer to typical Procellariiformes (also some Colymbiformes and scat-

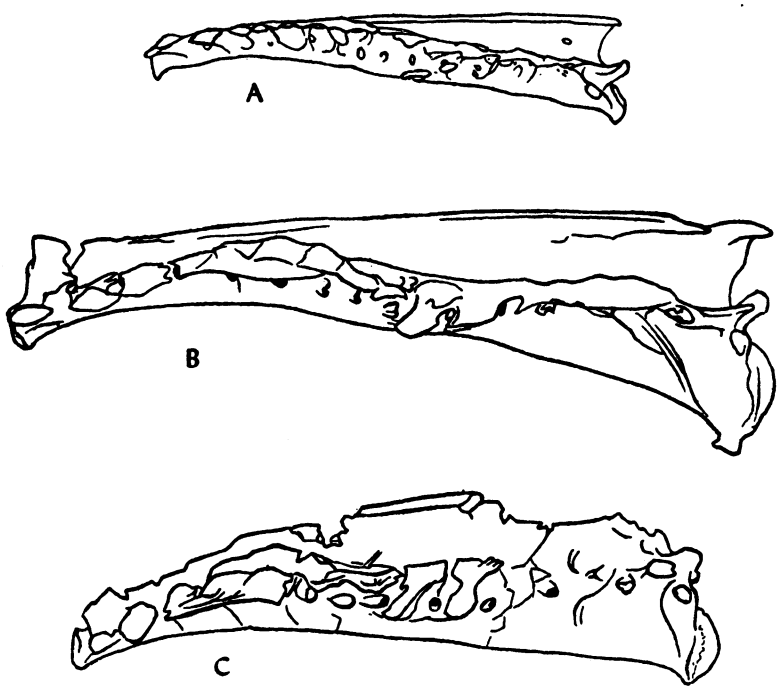

FIG. 29. Synsacra of recent birds and a fossil penguin. Comparative series in right lateral view. A. *Puffinus griseus*, Recent. B. *Spheniscus humboldti*, Recent. C. *Palaeospheniscus* sp., A.M.N.H. No. 3347, Miocene of Patagonia. ×1.

tered members of other orders of flying birds) in the morphology of this fossa than are recent penguins (fig. 30). Of course the Procellariiformes most decidedly show "a volant condition of things."

No less puzzling is Lowe's argument (*loc. cit.*) that if the penguins had a volant ancestry the humerus should be more pneumatic in the Miocene than in the Recent, not less, as he says it actually is. In the first place, the humerus is not pneumatic at all in the

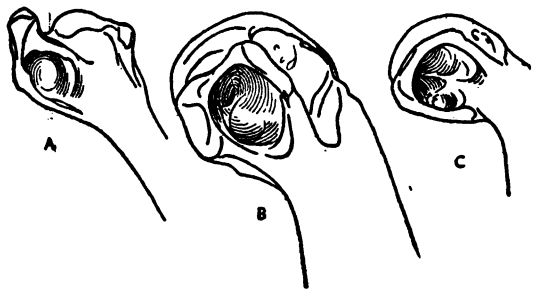

FIG. 30. Tricipital fossae of right humeri of recent birds and a fossil penguin. Comparative series in comparable oblique views to show size and walls of fossae. A. *Puffinus griseus*, Recent. B. *Paraptenodytes antarcitus*, A.M.N.H. No. 3338, Miocene of Patagonia. C. *Spheniscus humboldti*, Recent. ×1.

Recent penguins, so that it is hard to see how it could be less pneumatic in the Miocene. In the second place, the Spheniscidae, like all families of birds in which fossils are known, were very nearly as advanced in the Miocene as in the Recent. One would not really expect, *a priori*, that they would then show any decisive difference in such a character, and in fact they do not. In the third place, in most of the Procellariiformes (and Colymbiformes and some other flying birds) the humerus is also completely non-pneumatic. It was probably non-pneumatic in the volant ancestry of the penguins, and the absence of pneumatism is not a direct correlative of the loss of flight.

The inturning of the head of the humerus, stressed by Wiman (1905b) as a resemblance to volant birds, does not seem to me to have any useful bearing on the problem, one way or the other. It is variable in the Miocene penguins, some of which are exactly like recent specimens in this respect. Moreover, in some flying birds, including such possible distant allies of the penguins as *Puffinus*, the head of the humerus, although different in shape, is set at an angle that can be exactly matched among either Recent or Miocene penguins.

The legs of penguins, peculiar as they are, differ much less from other birds than do the wings. Except for the radical shortening and broadening of the tarsometatarsus, the differences from volant birds are all of a minor sort. The very fact that the remodeling of this part was less (whether or not the ancestry was volant) and must have been under less strong selection pressure suggests that the completion of specialization may have lagged a little behind that of the wing, and this seems indeed to be the case.

There is almost nothing really distinctive about the spheniscid femur, but the fossil forms do have at least one point in which they resemble many more normal carinates more than they do the living penguins: the morphology of the greater trochanter. The tibiotarsus, too, is rather typically carinate among modern penguins, with little that is clearly distinctive, but here again the small differences that do exist between the Miocene and Recent forms (eversion of ectocnemial crest, less distinct flexor attachment, rounded posteroproximal surface in the older genera) are resemblances to various of the Procellariiformes and other volant birds.

The much-disputed question of the tarsometatarsus has been fully discussed on a previous page, where it was shown that the Miocene penguins as a group, despite their great diversity, do have the tarsometatarsus relatively more elongate and the metatarsals more fused than do living penguins. The difference is not great, but it is real, and it is definitely in the direction of normal flying bird structure. The bearing of the peculiarities of the proximoplantar region in the fossils is more obscure, but these, too, are resemblances to conditions rather common in flying birds. In spite of the opposite conclusion reached by Lowe after elaborate study of part of the evidence, it seems to me inescapable that if the Miocene tarsometatarsi mean anything at all, they indicate that the

ancestral condition in the Sphenisciformes was definitely more like that in a normal flying bird than is the condition in modern penguins, and that the latter is not primitive or reptilian but (as Fürbringer aptly remarked long ago) pseudo-primitive and specialized within the Sphenisciformes as such.

CONCLUSIONS FROM THE FOSSIL EVIDENCE

The preceding summary agrees with Wiman's earlier conclusion, based on less evidence, that Miocene penguins did to some degree and at a number of different points resemble flying birds more than do recent penguins. Wiman may have been a little too ready to see such resemblances, and some of his observations cannot be fully substantiated, but others have since been added, and the general position remains the same in spite of the opposite conclusions reached by Lowe. Lowe's conclusions from the fossils involved two generalizations, that the Miocene penguins were almost exactly like the Recent, and that what differences they did show were not in the direction of flying carinates. The latter point has now been sufficiently considered, but a comment on the former is in order.

Miocene birds are in general very, one might say amazingly, like Recent birds. Even when so well known that generic distinctions could easily be detected, many of them are referable to genera still living. The others, almost without exception, belong either to genera that are closely allied to, and hardly less specialized than, living genera or to more aberrant groups that are now extinct as a whole so that the degree of evolution from Miocene to Recent is indeterminate. From the point of view of structural progression, it is hardly an exaggeration to say that birds have not evolved since the Miocene, although there has evidently been a good deal of geographic movement in the group during this time, along with racial and specific, less often minor generic, differentiation. For instance, the Californian Miocene diatomites, containing an oceanic bird fauna, have yielded specimens of the modern genera *Diomedea*, *Puffinus*, *Sula*, *Moris*, *Limosa*, and *Cerorhinca*, with only one extinct genus, *Miosula*, member of a living family and not visibly more primitive than *Sula*. Of this fauna Miller (1935) has said, "Some dozen species have been determined and other specimens have been assigned to family or genus. . . . Most of the species belong to genera that survive to the present. . . . In fact, the skeleton of modern birds seems to have undergone very little change of importance throughout the whole of Cenozoic time. . . . Horses had lost but two of their five toes and were just showing a prophecy of cement-covered teeth at the time these quite modern-looking gannets and shearwaters were fishing in the quiet waters of Miocene California." Wetmore and others have also emphasized this lack of progression in birds since the early Tertiary, and it is one of the most striking generalizations of paleornithology.

The fact that Miocene penguins are so like modern penguins is only what would be expected. The surprising thing is, rather, that they are as distinctive as they are. No known Miocene penguin could possibly be referred to a living genus, and I think few students will object to their being placed in extinct subfamilies. We must suppose either that members or closer relatives of the living genera did then exist but have failed of discovery, or else that penguin evolution since the Miocene has been more rapid and progressive than in most families of birds. The fact that Miocene penguins do share some distinctive features, despite their generic diversity, supports the view that these were primitive characters of the whole group eliminated only since that time. It seems probable, whether or not we have actual representatives of the spheniscine ancestry, that evolution has been relatively rapid in this group.

Few Miocene birds really cast any new light on the affinities of the families to which they belong. Although more distinctive than most birds of their age, the Miocene penguins are only a partial exception to this rule. Like the other birds of the time, they are much too modern to provide real annectant types.

Their evidence on penguin origins cannot possibly be conclusive, but it is consistent in itself and consistent with probabilities based on the comparative study of recent forms. Excepting only the wing and the tarsometatarsus, the recent penguin skeleton is remarkably like that of many flying carinates and particularly of the Procellariiformes, as has been repeatedly noticed and can be confirmed by comparison of the skeletons of almost any genera of the two groups. If this similarity were a coincidence or due wholly to convergence, the Miocene penguins might be no less similar to the Procellariiformes but surely would not be expected to be more similar. The fact that they are more similar, even though in slight degree, is good supporting evidence that their remote ancestry was indeed like, if not identical with, that of the Procellariiformes.

A GENERAL THEORY OF PENGUIN EVOLUTION

Almost all the more striking features that differentiate penguins from the flying birds most nearly similar ecologically or structurally are clearly correlated with three functional factors:

1. The penguin type of swimming, which might be called submarine flying. The most obvious structural correlative is the wing or flipper, together with the specialized musculature involved. Other correlatives are the lack of differentiation in the wing feathers, the streamlining of the body, and the posture of the legs in swimming position.

2. Terrestrial locomotion in an upright posture. Correlative structural features are found chiefly in the hind-limb, adapted to carrying the relatively heavy body at an ambulatory rather than cursorial gait, digitigrade in rapid walking and plantigrade in slow motion or when at rest (or digitigrade but "plantistat," as Virchow remarks). The extreme upright posture has other, minor correlatives in the vertebral column, etc., and is also correlated with the swimming function. It has further effects, rather than direct functional correlations, in, for instance, the method of brooding and such peculiarities as the egg-fold or so-called pouch in *Aptenodytes*.

3. Insulation. The obvious structural correlatives are the feathers and blubber. The extremely numerous feathers, their down-like character, the absence of apteria, and even some details of feather musculature are evidently elements in a peculiarly effective insulating apparatus. The layer of blubber into which the feather follicles extend also involves correlated peculiarities in the follicular mechanism and in molting. There are doubtless also physiological concomitants that have not been fully investigated.

All three of these factors interact in a complicated way, and it is impossible to isolate them. They can only be considered as factors simultaneously involved in the integrated organism. Nevertheless, it seems probable that the adaptations for terrestrial locomotion in an upright posture, that is to say, the ways in which these differ from the normal walking adaptations of flying birds, are secondary and are in one sense a result of the swimming adaptation. The foot and leg structure of the penguins is a primary adaptation to their method of locomotion and of standing, but the differences between this method and that of other birds probably arose in connection with the completion of their aquatic adaptation. This conclusion is strongly supported by the detailed and careful analysis by Virchow (1931). In this connection, the penguins' alternative mode of land locomotion, sometimes called "tobogganing," is of interest. The penguins slide along on their breasts and bellies, propelled by strokes of the wings and feet, achieving, on a suitable surface, a greater maximum speed than when running upright. This mode of progression is very nearly swimming on land except that it does still depend heavily on the feet, which are almost wholly passive in submarine swimming.

In brief, the penguins are a group of birds fully adapted for swimming in cold water by means of their wings. Most of their other peculiarities are consequences or, at least, concomitants of this basic adaptation.

In speaking of penguin evolution there are two points in particular that require careful statement. The matter is largely one of verbalization rather than of basic fact, but different manners of speaking may incline to different points of view and so eventually to different interpretations and theories. The first point is that the wing is not degenerate, as is occasionally stated, but is highly and progressively specialized. Degeneration implies a loss of function and correlated morphological changes, usually in the direction of loss or simplification of parts. It has been implied that the loss of flight is *ipso facto* degenerate. So it is in the dodo, apteryx, and other birds whose wings became literally functionless, but in the penguins what occurred was not a *loss* of function, but a *change* of function, which resulted in progression and not true retrogression.[1]

The other and closely related question of verbalization is involved in statements that penguins lost the power of (aerial) flight and became aquatic. Stated in this way, one tends to think of the process as divided into two steps: first, loss of flight; second, acquisition of swimming. Repeatedly in the literature, as written by the majority who think that penguins' ancestors did fly, it is said or implied that their ancestors became (nonvolant) terrestrial and then took to the water. This was Ameghino's view based, as he thought, on fossil evidence. That this evidence was erroneous, as I believe, would not necessarily invalidate the conclusion, but it removes any objective support for it. On more theoretical grounds, Matthew (1928) suggested that in Antarctica "birds developed as terrestrial vertebrates in the absence of mammals, and that the modern penguins are survivors of this old fauna of Antarctica, modified to suit the amphibious life which afforded their only chance of survival when the whole region was buried in ice."[2] Appealing as this idea is (and it has been tentatively endorsed by other students, e.g., Romer, 1933), it will be shown to be a very improbable interpretation of the evidence. For the moment it suffices to point out that the loss of aerial flight and acquisition of aquatic habitus need not be successive or could well occur in the opposite succession, that is, with the aquatic habitus preceding the loss of aerial flight. In fact it is an equally valid verbalization to say that penguins have not lost the power of flight but are specialized for flying in water instead of flying in air.

That the penguin flipper is, indeed, a wing really requires no detailed evidence beyond that already in the literature, Lowe to the contrary notwithstanding. It has all the elements of the wing of a flying bird, and it has no others in spite of the great remodeling of these. Almost every detail has its homologue in the aerial wing and not in any other known manus, pseudosuchian, dinosaurian, or whatever it may be, so that its structure is comprehensible only if it did pass through an aerial volant stage. Looked at from the opposite point of view, if one starts with a volant wing and envisages its plastic remodeling for submarine use, the result is inevitably something very like a penguin flipper. It must be flattened, the separate elements compressed and all brought into one plane. The muscles and tendons must be modified for quick, powerful action in a more resistant medium. It must flex as a blade, but free rotation of elements and segments must be

[1] This is in no way an original thought, but it does deserve emphasis. Lowe stresses the fact that the penguin wing is not degenerate as an argument that it has not lost (because it did not have) the power of flight. He does not note that the loss of the power of grasping, supposing the immediately ancestral type to be like the manus of a bipedal dinosaur, would be degeneration by the same definition. The fallacy is sufficiently obvious.

[2] It is surprising to find that Matthew, one of the most cautious and reliable of authorities, was misleading in some of his references to penguins. In "Climate and evolution" (Matthew, 1939, pp. 123–124) he says that they are the most primitive living birds (a matter of opinion, but this is extremely unlikely), that they are Antarctic in distribution (true, but most inadequate), and that they are known as fossils only from the Antarctic Tertiaries (definitely untrue). He also speaks of them as the only known land vertebrates of the Antarctic continental area, whereas the only Antarctic site where they have been found is not now, and was not when the bones were buried, a part of the Antarctic continent. He further calls the fossil forms terrestrial or land penguins, in contrast with the living marine penguins, but all the evidence is that the known extinct forms were quite as marine as the recent species; besides the anatomical evidence, they are found in marine deposits.

eliminated. The remiges, inadequate to sustain the beat in so heavy a medium, must be shortened or de-differentiated. Such changes, necessarily involved in complete adaptation to submarine flying, would produce the penguin wing, but could produce it only by starting from an aerial flying wing. It is not conclusive evidence in itself but is good supporting evidence for this view that flippers of various different types have repeatedly been evolved from a non-volant manus among reptiles and mammals, and that these achieve much the same functional status as the penguin flipper but are anatomically very different in all cases.

The origin of the penguin flipper is almost inconceivable to me except on the theory that it never ceased to be a functional wing, but only changed the medium in which it functioned. The way in which such a transition could and probably did occur is illustrated by birds that fly both in the air and in the water, including the auks, some of the Procellariiformes, and some others. Particularly interesting is *Pelecanoides* because it is probably allied to the penguins[1] and shows an adaptive stage through which penguins probably passed. As described particularly by Murphy and Harper (1921) and by Murphy (1936), the diving petrels are remarkably like penguins in many respects except that they can still fly in the air. Thus Murphy (1936, pp. 776–777) says of *P. garnotii*, "How little the Potoyuncos are dependent upon the power of flight is shown by the fact that they moult their wing quills all together, and thus for a time each year become exclusively aquatic. . . . The stomachs of the naturally 'crippled,' temporarily penguin-like Diving Petrels, which have lost all their flight feathers, prove to be as well filled with crustaceans and small fishes as those of their flying contemporaries. . . . Beneath the surface they literally fly with their wings, whether or not the remiges are full-sized. . . . Thus, so far as feeding is concerned, they might just as well be flightless birds. The only indispensable use of full-grown primaries would seem to be to bear the Potoyuncos to and from their nesting burrows on the islands."

These birds, like the shearwaters and, to greater or lesser degree, other birds that fly under water, have definite convergent resemblances to the penguins, especially in the wing but also in other parts of the body. That the resemblance is not greater, or that these birds have not actually become penguins of a sort, is readily explicable by the fact that they do still fly. The diving petrels, particularly, have carried aquatic adaptation about as far as possible without ceasing to fly in the air, but the need, desirability, or, at least, existence of aerial flight sets limits to the possible degree of aquatic adaptation.[2]

These birds must be in a rather delicate state of adaptive equilibrium. Aerial flight is evidently useful to them. Aside from the direct evidence of this, that they have, in fact, retained aerial flight in so long and varied a series of cases is, in itself, evidence that this is useful (in a selective sense). But submarine flight is also useful. Here, again, there is direct evidence (they do catch their food this way) and also evidence from the fact that submarine flight has been developed repeatedly in diverse groups. Retention of one advantage, aerial flight, is inconsistent with the advantage of perfection of submarine flight—none of these birds does fly under water as well as do the penguins. There must be a point, not reached by these birds but reached by the ancestors of the penguins, when the latter advantage outweighs the former and aerial flight ceases, assuming that

[1] No exclusive relationship to this genus among the Procellariiformes is suggested, but only that *Pelecanoides* shows how a member of this order could start evolving into a penguin.

[2] Here, again, I cannot follow Lowe's logic, and a comment is in order, although I do not propose to follow all his arguments in detail. On one hand, he strongly emphasizes that penguins are the most aquatic of birds and have a type of bone moulding (and other characters) different from any flying birds. On the other hand he asks why, if penguins had flying ancestors, have not the numerous aquatic flying birds acquired feathers and wings like those of penguins? Even aside from the fact that the latter *have* acquired some penguin-like wing characters, Lowe's two arguments answer or cancel out each other. Being the most aquatic of birds, penguins of course have extreme characters adapting them to that end, and flying birds do not have these characters because they are flying, and not wholly aquatic or aquatic-terrestrial, birds.

the appropriate genetic variation exists or appears.[1] At this point the selective balance would end, and there would be very strong selection pressure all in one direction, the direction of greatest aquatic adaptation, which would be toward the structure actually shown by the penguins. The tendency would be for a rapid shift in adaptive relationships and in morphology, an example of what I have called quantum evolution (Simpson, 1944). The optimum of the new adaptive type would be reached relatively quickly, as evolution goes. Thereafter, with selection pressure mainly centripetal rather than linear, slower evolution of phyletic type (*op. cit.*) would occur. (See fig. 31.)

Although, as usual, we lack the crucial stages, those actually involved in the quantum-step, this interpretation is thoroughly consistent with what evidence we do have. We have a group appropriate in broader morphology to give rise to the penguins, i.e., the Procellariiformes. We have within this group evidence of phyletic trends leading up nearly to but not over the threshold of the postulated quantum evolution and exemplifying an ideally pre-adaptive phase with respect to the penguins. In the Miocene penguins we have forms that had completed the quantum phase. As would be expected, the structures most immediately involved in the adaptation, those of the wing, had already reached essentially full equilibrium, with strongly centripetal selection, and subsequent evolution was of the most minor type, not phyletic but speciational in pattern. But structures less directly involved in the primary adaptation, among others those of the hind-limb, had not yet become static and do show definite phyletic advance between the Miocene and the Recent.

The morphological changes involved in this history seem to have been mainly progressive. Unlike many nineteenth century

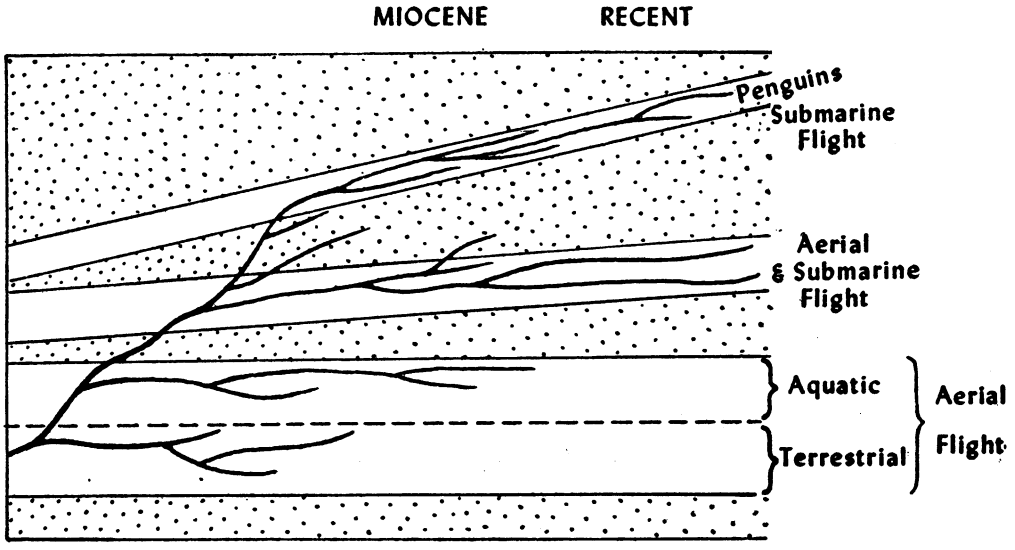

FIG. 31. Grid diagram of the theory of penguin evolution proposed in this paper.

[1] The great auk, which was a submarine but not an aerial flyer and which nevertheless had the aerial type of feathers and only limited convergence toward penguins, may cast doubt on this whole theoretical argument. I do not consider the doubt as very serious, however. The great auk did show considerable resemblance to the penguins (which, indeed, owe their name to this fact). It probably had not been flightless for long, geologically speaking. It has close living relatives that retain aerial flight, so that its divergence from a common flying ancestry cannot be remote. Whether or not it would have acquired, for instance, penguin-like feathers, it evidently had not had time to do so. The Miocene *Mancalla* has no particular bearing beyond the fact that it also had considerable, but incomplete, convergence toward penguins in the humerus. It can hardly have been ancestral to the greak auk.

students and a few others, I see very little that is either primitive or degenerate in penguins, but on the contrary consider them among the most progressively specialized of birds. The supposed primitive characters, including the incompletely fused metatarsals, open pelvic and cranial sutures, and (as so interestingly and carefully described by Lowe) the structure of the feathers and their relationship to the edge of the wing, all seem to be pseudo-primitive, as concluded long ago by Fürbringer. Along with the specialization that involved the rise of new characters, there was another type of specialization that involved what is sometimes called foetalization or larvalization, although these are not very good terms. The process is that growth, as regards some region or structure, is slowed down or comes to a stop at an earlier stage than in the ancestry. Thus a character that was embryonic or juvenile in the ancestor becomes adult in the descendant. Such a character may or may not have characterized adults in the still more ancient ancestry.[1] Growth is under genetic control, and mutations changing growth rate are among the relatively abundant materials of evolution.

It is no anomaly but is merely typical of the complex interaction of factors in evolution that these nominally retrogressive trends are simultaneous with fully progressive trends, even in the same structure. For instance, in the tarsometatarsus, which is a sort of test case in the penguins, the decreasing fusion of the metatarsals is accompanied by progressive shortening of the bones in question. What has happened in this growth field as a whole is evidently the relative slowing of axial growth, speeding of transverse growth, and delay in transverse fusion.

[1] On Lowe's fallacy in assuming that an embryonic or juvenile character is *ipso facto* primitive, see Gregory, 1935.

These various trends are harmonious parts of a single process. The greater fusion observed in Miocene penguins and the still greater fusion inferred in more remote ancestors do not appear in the embryos of modern penguins because a high degree of fusion was always a later feature, in the developing individual, than the less-fused condition. Greater fusion has not been pushed back into an earlier embryological stage but has been cut off from the end of development—a well-known process that is responsible for many of the innumerable falsifications of recapitulation. Recapitulation in the penguins has been further falsified by the equally well-known and common process by which new, progressive characters, such as the flattened wing, appear early in embryonic development in accordance with economical mechanics and have replaced the remoter ancestral type of development.

If, as here suggested, the penguins passed directly from aerial to submarine flight, the mooted, exclusively terrestrial phase postulated by Ameghino, Matthew, and numerous others did not occur. Major adaptive phases postulated under the different theories proposed may be diagramed as in figure 32 and as follows:

Reptilian Pro-avian	Early Aves	Proto-penguins	Later Penguins	
Terrestrial	→Terrestrial	→Swimming	→Swimming	Menzbier, Lowe, etc.
Terrestrial or arboreal	→Aerial volant	→Terrestrial	→Swimming	Ameghino, Matthew, etc.
Terrestrial or arboreal	→Aerial volant	→Aerial and aquatic volant	→Aquatic volant	This paper

It is clear that penguin adaptation does include a terrestrial component additional to that, common to all birds, of very remote (reptilian) origin. In my view, this additional terrestrial component does not reflect any strictly terrestrial phase in the avian ancestors of the penguins, and it followed and did not antecede the beginning of the aquatic adaptation. Heightened terrestrial adaptation was concomitant with the replacement of aerial flight by aquatic or submarine flight. Instead of flying to their breeding grounds and other terrestrial stations, the penguins walked to them.

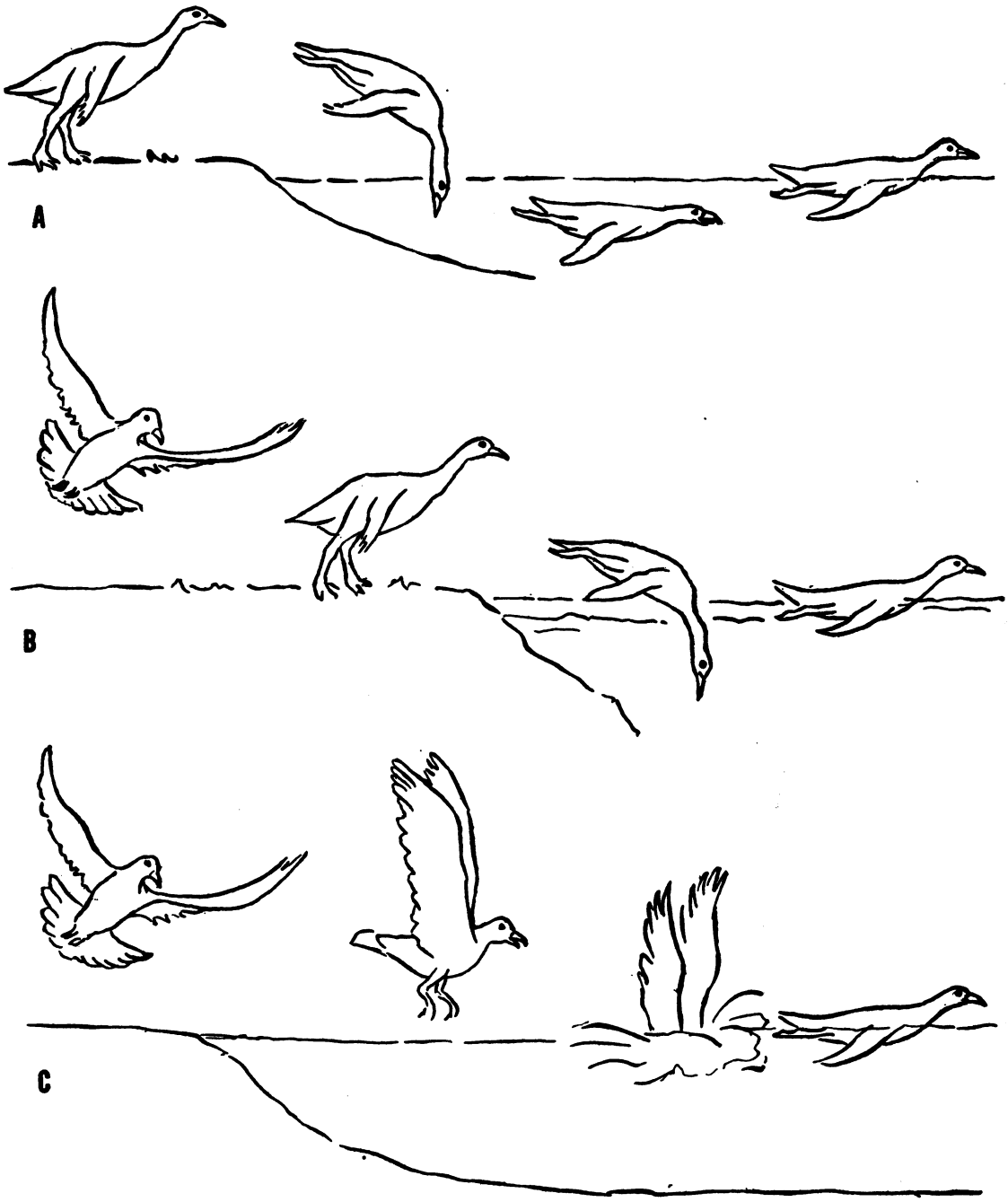

FIG. 32. Pictorial diagrams of the three current theories of penguin evolution. A. The theory of Menzbier, Lowe, and others: primitively terrestrial proto-avians became directly aquatic. B. The theory of Ameghino, Matthew, and others: primitively volant birds became non-volant terrestrial and then aquatic. C. The theory supported in this paper: primitively volant birds became oceanic, adopted submarine as well as aerial flight, and then abandoned aerial for exclusively submarine flight. The figures are diagrammatic only and do not represent particular types of known birds.

Nor do I think that penguins took to the sea to escape terrestrial enemies or because of food failure in their Antarctic home, the two alternatives usually considered. All the evidence, admittedly incomplete as it is, is more consistent with the view that their ancestors became oceanic birds while they were still aerial flyers. Like other oceanic birds, they undoubtedly went to sea for food and were simply one of the numerous lines that came to depend on the abundant marine fish, squids, crustacea, etc., as a food supply. They became specialists in pursuing this food where it teems in the cooler southern waters and so came to occupy a special ecologic niche. In regions where suitable insular breeding grounds and marine feeding grounds were adjacent, aerial flight became unnecessary to these postulated proto-penguins. Once unnecessary, aerial flight would become positively disadvantageous, because incompatible with perfection of subaqueous flight. Of course no direct influence of the aquatic environment is involved in this sequence. The stage is set by pre-adaptation and the transition accomplished by natural selection acting on genetic variation which happened to be appropriate. The precise circumstances involved in tipping the rather subtle equilibrium in this direction must be complex and unusual, so that only a general hypothesis can be erected in the inevitable absence of full knowledge, and only this general suggestion can be made as to why some northern group has not happened, as yet, to complete the same adaptive history. In the Southern Hemisphere, the early occupation of this ecological niche by the penguins would in itself impede later invasion by any other group.

That penguins, like most oceanic birds, usually breed on islands is probably related to the absence of land carnivores at these sites. Nevertheless, the evidence is rather equivocal. The most serious predation at penguin breeding grounds is by flying birds, especially the skuas, against which the insular (or Antarctic) sites are no protection. Penguins do also frequently come ashore on coasts where there are terrestrial carnivores, in South America, Australia, and Africa. In the Miocene, when penguins clearly abounded along the Patagonian coast, that coast was already populated by varied and numerous land carnivores (borhyaenids).

In any case, it is incredible that terrestrial predation was an important factor in the penguins' becoming aquatic. The most effective enemies of adult penguins are aquatic (especially cetaceans and pennipeds). That the land is for them safer than the water is deeply ingrained in penguin psychology. Unless penguins have been thoroughly reconditioned by long, adverse experience with man, they do not flee to water when attacked or alarmed on land, and it is, indeed, almost impossible to drive them into the sea. This relatively greater fear of the water is attested by most accounts of penguin behavior (e.g., Levick, 1914; Murphy, 1936), and I can concur from personal observation of *Spheniscus magellanicus*. Whether the inheritance of this trait is genetic or social (whether it is instinctive or learned), it is so ingrained as to dominate even when it is manifestly irrational—when it is obvious that the greater danger is on land. It is, then, just as much a penguin character as if it were morphological and must equally be presumed to have arisen from, and to be involved in, penguin history. Whether or not it is the full explanation, it is probably one of the factors in penguins' commonly selecting their land stations where they require an apparently useless and inconvenient overland trek.

The length to which penguins will go to get away from the strand is amusingly illustrated by cases in which the breeding grounds of gentoo penguins on small islands without high land are reached by walking right across the island to points near the opposite shore (Beck, cited by Murphy, 1936). The journey to and from the water is made across the island, not by entering the sea near the breeding ground, so that the birds put as much land as possible between themselves and the strand that is functional for them. That this does place them near the sea is again irrational or illogical from a human point of view, but is a comprehensible part of penguin psychology on the hypothesis that its motivation is simply dissociation from that stretch of water that the birds do enter and with which they associate danger. Although this

is an extreme instance, it goes far to negative the other hypotheses that have been proposed to account for the trouble that penguins take to climb and otherwise to travel overland. Levick supposes merely that they have a "love of climbing," but this will not be accepted as explanatory by students of animal psychology. Murphy makes the suggestions that the penguins acquired the habit of climbing when the valleys were filled with ice, only the ridges having bare ground suitable for breeding, and that this habit has persisted because of crowding of other species on the beaches. Neither factor can explain the peculiar behavior of some gentoo penguins as reported by Beck, and both seem inadequate to account for the quite widespread occurrence of this basic psychological trait or conditioning in penguins. (Murphy's suggestions were advanced with special reference to the gentoos.) The overcrowding hypothesis is also improbable, as a general factor, in the light of such occurrences as that, also reported by Murphy, of the more aggressive Adelie penguins' seizing the highest nesting sites so that the gentoos have to take lower and, to them, inferior sites. The common factor in a wide range of penguin activities seems to be an association of danger with their landing strand, and additional postulates as to love of climbing, clinging to ancestral territory, or being crowded away from the strand seem inadequate as primary hypotheses and unnecessary as supplementary hypotheses.

The point here involved is not crucial in the present theory of penguin evolution, but it has considerable general interest, and it has a bearing on the secondary terrestrial adaptation of the penguins. This adaptation is not at all of cursorial type as in the majority of flightless land birds. Penguins neither pursue food nor flee enemies on land. If their land activities were confined to the landing strands, such strong and positive modifications for land locomotion would be rather anomalous. The factors that have led them to amble so widely on land are thus an essential part of their functional history. That such factors exist cannot be questioned, whether or not I am correct in identifying a fear of the water at the strand as the essential factor.

The place in which penguins arose is still more speculative and considerably less important than the questions already discussed, but deserves some mention. It seems to be almost universally agreed that they evolved in Antarctica and spread from there, but some skepticism is proper. Antarctica is said to be the center of penguin distribution, but this is true only in the sense that Antarctica is geometrically central in any widespread Southern Hemisphere distribution. Penguins are most abundant and varied in the South Temperate Zone, and the center of their distribution may be considered not as a point but as a ring following the cooler part of this zone around the world. From this ring a few forms, adapted or pre-adapted for particularly cold air temperatures, extend their range to the Antarctic, just as a few, tolerant of higher air temperatures, range into the Tropics.[1] They are all unquestionably adapted to cool water, but cool water is obviously not confined to the Antarctic, nor was it in the relatively warmer Miocene Epoch if, as is very probable, Miocene penguins also were adapted to relatively cool water. A few of the known Miocene penguins occur in Antarctica, broadly speaking, but actually on an island off Graham Land (which is itself an island), well north of the Antarctic Circle, and not on the Antarctic continent. Miocene penguins were most widespread in, if not confined to, what is now the Temperate Zone, in the latitudes that are still most characteristic for penguins aside from such exceptional forms as the emperor and Galápagos pen-

[1] That penguins tolerate a greater range of air than of water temperatures is comprehensible enough even in the absence of physiological experiments that would permit better understanding of details. They are normally more active in water than in air, must generate more body heat in the former medium, and must there strike a balance between the factors of heat production, insulation, and conduction of heat into cool water. Serious overheating must result when they are in warmer water. In air, heat production is less and as long as the shade temperature is below body heat the latter can be maintained within the range of tolerance. Overheating by solar radiation may be adequately guarded by the same insulation that prevents overcooling by conduction in water. That insulation serves as well to keep radiant heat out as to keep body heat in is well known, for instance, to the be-robed natives of the sun-baked Sahara.

guins. The concrete evidence, such as it is, thus gives no real suggestion of Antarctic origin.

Still more hypothetical and dubious is the argument (Matthew and some others) that penguins arose as vicars for mammals on a large land-mass devoid of mammals and hence most likely Antarctica. This implies that penguins are or were primarily terrestrial and loses all significance if, as I believe, such was not the case. It seems most likely that the proto-penguins were sea birds ranging widely over the cooler South Temperate Zone seas, and that they evolved into penguins somewhere among the islands and waters of that zone, perhaps over a large area and quite surely not in a single, definite center that can ever be identified. If this is true, their connection with Antarctica is, in a sense, fortuitous. It is not, I think, that they originated in Antarctica but simply that their tolerance of cold permitted a few of them, at one extreme of their adaptive range, to penetrate that far south.

A NOTE ON *ARCHAEOPTERYX* AND *ARCHAEORNIS*

Repeated reference has been made to the work of Lowe on penguin evolution. Not all the points on which I am unable to accept his conclusions have been considered in detail, in part because these are covered in previous studies by others and in part because on many points the data here presented suffice without explicit reference to all disagreements with previous students. Lowe's most recent work on *Archaeopteryx* and *Archaeornis* (Lowe, 1935, 1944b) is rather far afield from the topic of fossil penguins, but it must be mentioned because it is the latest study of this subject and has a strong bearing on the evolution of the birds in general and of the penguins (Lowe, 1933, 1939) and ostriches (Lowe, 1928, 1935, 1944a) in particular.

Lowe's thesis is that the penguins and the ostriches and their allies (he considers all the so-called ratites as allies of the ostriches) are primarily terrestrial and never had volant ancestors. According to his ideas, then, the first birds were all terrestrial, and from these there developed a cursorial group (ostriches and their "allies"), an aquatic group (penguins), and a volant group (all other birds). Opposed to any such hypothesis is the *prima facie* evidence of *Archaeopteryx* and *Archaeornis*, forms in which the most basic difference from reptilian ancestors is that they flew by means of feathers. Lowe supposes that their wings were inadequate for "normal avian" or "perfect" flight. I think these wings more adequate than Lowe allows, but this rather subjective judgment does not particularly matter, because everyone must agree that flight, in some degree, was possible. But *Archaeopteryx* and *Archaeornis* are so primitive in every other character that if they have anything to do with birds, this in itself amounts to conclusive proof that birds originated as flying animals, contrary to Lowe's thesis.

Lowe seeks to escape this dilemma by claiming that *Archaeopteryx* and *Archaeornis* were not birds at all but were "arboreal climbing dinosaurs with the power to glide." He goes into the morphology of these two Jurassic forms in considerable detail, but his argument can be summed up as being that in most respects they are purely reptilian, in all respects they are as reptilian as avian, and in some respects they were too specialized to be ancestral to birds.

A close reading of Lowe's latest paper and of the other studies, especially Heilmann (1926), from which he draws most of his factual data, suggests that what he has demonstrated is no more than that *Archaeopteryx* and *Archaeornis* have throughout their structure reptilian features lost in later birds. This is obvious and has certainly been emphasized by every student of these fossils. The point is not so much whether these forms are, in any one or in all characters, more like a reptile or like a bird as whether they are intermediate between possibly ancestral reptiles and later birds. Lowe says that they are not, but this denial is vitiated by his own data and still more by the data of Heilmann and others on which he so strongly relies. As far as I can observe from these data, every dif-

ference between *Archaeopteryx* and *Archaeornis*, on one side, and true reptiles of possibly ancestral type, especially the Pseudosuchia,[1] on the other, is definitely in the direction of true birds.

Space will not be taken to review all the evidence, but a brief discussion of the skull of *Archaeornis* will serve as an example. Lowe (1944b, p. 529) says that he finds nothing in this that "could be definitely labeled avian

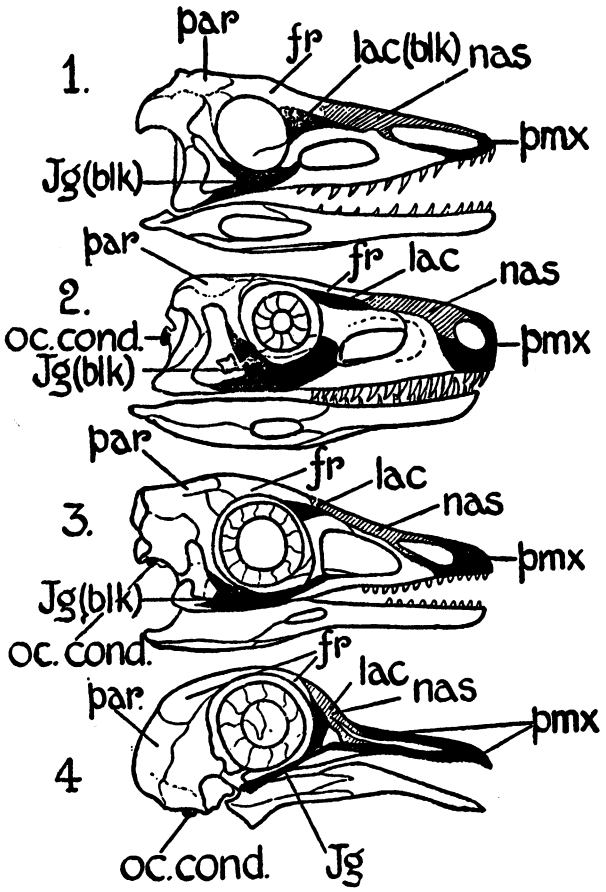

FIG. 33. Lowe's figure of reptilian and avian skulls, given by him to support the view that *Archaeornis* was not intermediate between reptiles and birds and here reproduced to demonstrate the opposite. 1. *Aëtosaurus*, a Triassic reptile. 2. *Euparkeria*, a Triassic reptile. 3. *Archaeornis*, a Jurassic bird or reptile. 4. *Columba*, a specialized recent bird. Not to scale. Redrawn by Lowe after Heilmann; here reproduced photographically from Lowe. (In Heilmann's original illustration, 1 was redrawn from von Huene and 2 from Broom; 3 and 4 were original with Heilmann.)

[1] The point is not fully crucial, but one of the several confusing peculiarities of Lowe's work is his selection and designation of reptiles for comparison. He continually speaks of "pseudosuchian dinosaurs," whereas, of course, the Pseudosuchia were not dinosaurs. He makes comparisons indifferently with Pseudosuchia, Ornithischia, and Saurischia, as if these were one and not,

as opposed to reptilian, and everything reptilian as opposed to avian." But in his own figures (*ibid.*, pp. 525 and 528, and fig. 33 of this paper), as well as in the more extensive data of Heilmann (1926), it seems to me quite obvious that the skull of *Archaeornis* is intermediate, almost ideally so (although not in all respects at the exact midpoint), between a pseudosuchian reptile like *Euparkeria* and such an advanced bird as *Columba*, with which Lowe makes the comparison.

Most of the more important skull modifications from *Euparkeria* to *Columba* are involved in, or correlated with, these four basic functional changes:

1. Development of a beak (with elongation of premaxillae and nares, abbreviation of the orbito-narial space and concomitant loss of some and modification of other elements in this region, eventual loss of teeth, etc.).
2. Relative increase in the size of the orbit (closely correlated with 3 and with related concomitants).
3. Relative increase in the size of the brain (with 2, involving a whole series of structural adjustments such as the reduction, fusion, and remodeling of interorbital and circumorbital bones and structures, also more ventral position of the occipital condyle, etc.).
4. Development of streptostyly (correlated with 1 and with a whole series of concomitant changes in the arch, palate, and face).

It is not a matter for argument but a simple fact of observation (if one accepts the published data of Heilmann and other authorities not questioned by Lowe) that *Archaeornis* is intermediate between *Euparkeria* and *Columba* in every one of these basic characters. If a pseudosuchian did give rise to birds, each character involved must necessarily have passed through the condition seen in *Archaeornis*, although of course the relative rates of modification of the various characters could not be precisely predicted *a priori*.

Similar remarks could be made regarding almost all of Lowe's arguments, which it is not necessary to examine here in detail. *Archaeopteryx* and *Archaeornis* are intermediate between reptiles and birds in structure, and their bearing on the origin of birds is unchanged by the purely verbal question of whether to call them reptiles or birds.

It is, indeed, an interesting point that these Jurassic birds (as I shall continue to call them) are more reptilian than might have been expected in an animal that had already developed a feathered wing—a point as strongly emphasized by Heilmann as by Lowe although Heilmann did not question the position of these animals near or, at least structurally, in the avian ancestry. The only logical conclusion is, I think, that the primary avian structure was the feathered wing which developed as a flying apparatus, a conclusion in no way negatived by its being as yet unperfected in the Jurassic, even if, as Lowe believes, the wing was then fit only for gliding rather than flapping flight. The wing, in its most basic and primitive form, evolved before the other specialized avian characters were completely developed. Many of these, probably a majority, were correlated adaptations for flight, becoming perfected as flying became more efficient. Others, like the sensory equipment, brain, beak, and leg structure, are not directly involved in flight but nevertheless are closely correlated with a way of life that included flight.

Almost all the special resemblances of some saurischians to birds, so long noted and so much stressed in the literature, are demonstrably parallelisms and convergences. These cursorial forms developed strikingly bird-like characters here and there in the skeleton and in one genus or another. They never showed

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as is the case, three separate reptilian orders or stocks. Confusion is worse confounded by Lowe's calling the lizard *Carsosaurus* a dinosaur in making comparisons with it. Further, he compares with late Jurassic and with Cretaceous dinosaurs, although these could not possibly be ancestral to *Archaeopteryx* and *Archaeornis*, which are older. He ignores the fact that no dinosaur, regardless of age, could possibly be ancestral either to these two genera or to any (other) birds. He picks out some bird-like characters, for instance in *Ornitholestes* and *Struthiomimus*, that are certainly nothing more than limited examples of convergence because they did not occur in any conceivable common ancestor of birds and dinosaurs. Moreover, whether or not *Archaeopteryx* and *Archaeornis* are considered reptiles, Lowe's designation of them as dinosaurs is nothing short of fantastic.

a general approach to avian structure (as do *Archaeopteryx* and *Archaeornis*), some avian characters were not achieved or even hinted at in any of them, and they all retain the most conclusive marks of their reptilian nature. The inference seems quite clear: the diagnostic complex of avian characters was acquired in a volant stage, which *Archaeopteryx* and *Archaeornis* had just begun. The complex as a whole did not develop in even the most bird-like of reptiles whose ancestors were non-volant, and these remained entirely reptilian in spite of avian resemblances in various other respects.

Finally, Lowe's views would still be untenable even if he were right in supposing that *Archaeopteryx* and *Archaeornis* were not ancestral birds but were members of one of several (otherwise wholly hypothetical) reptilian lines evolving with much parallelism in a bird-like direction, analogous to the several parallel lines of reptiles that were becoming mammal-like in the Triassic (see Lowe, 1944b, p. 542). The most essential element in this bird-like trend would still be the development of feathered flight. The logical bearing of the evidence would still be that birds arose as feathered fliers, even if this development occurred (contrary to probability and without known evidence) in more than one line and if *Archaeopteryx* and *Archaeornis* were not in the successful particular line that did give rise to the later Aves as a whole.

ADDENDUM

The papers listed as Wiman, 1942, and Wiman and Hessland, 1942, were not received until the preceding pages had been completed. Wiman's new studies are devoted to penguins as well as to auks and are pertinent to the present paper, although they contradict no conclusions here reached and add little to them.

Wiman, 1942, again asserts that the fossil penguins have relatively longer tarsometatarsi than the recent species and gives figures demonstrating this, based on *Delphinornis larseni*, *Spheniscus demersus* (with the most elongate tarsometatarsus demonstrated among recent species), and *Aptenodytes forsteri* (with the shortest tarsometatarsus among all known penguins). In terms of the index of elongation used by me, Wiman's value for his fossil species is 240. Fossil values calculated by me range from 181 to 259. For the two recent species Wiman gives the values 210 and 140. These happen to be exactly the extreme values observed by me in recent materials. Wiman does not cite or discuss Lowe's criticisms of his earlier findings.

Wiman goes on to demonstrate that among the auks, all of which have relatively short tarsometatarsi in comparison with the majority of birds, the flightless great auk, with the index 380, has a relatively shorter tarsometatarsus than its recent relatives, with indices 400–500 in four species studied by Wiman. The logical conclusion is that shortening is an adaptive feature of the auk habitus, that it is accentuated by loss of aerial flight, and that the development in the penguins is merely a further adaptation in the same direction.

Wiman corrects his previous belief (inherited from the nineteenth century literature) that penguins are plantigrade in locomotion, but reasserts that their plantigrade standing and breeding position (plantistat in Virchow's sense) and also their particular type of digitigrady are correlated with tarsometatarsal shortening or rather, as he prefers to express the same thing, broadening. (Both factors are clearly involved: the penguin tarsometatarsus has not become simply shorter or broader, but has become simultaneously shorter and broader.)

He adds the interesting observation that this change in tarsometatarsal proportions may be correlated not only with terrestrial adaptation in general but also with partly fossorial habits. Only a few species of recent penguins are semi-fossorial, but it is quite possible that the ancestral penguins were. If so, this would add a detail to the general picture without altering its broader outlines. It is an interesting fact, not noted by Wiman, that some of the Procellariiformes excavate subterranean nests as do some penguins, another link between the two groups. In both cases the advantage of this habit is in protection from volant predators.

Wiman's latest discussion of the penguin humerus (in Wiman and Hessland, 1942) does not involve any new observations, and the points raised have already been sufficiently covered in the preceding pages.

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