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Description of the Earliest Fossil Penguin from South America and First Paleogene Vertebrate Locality of Tierra Del Fuego, Argentina

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ABSTRACT

We report the discovery of the first vertebrate from the Paleogene of Tierra del Fuego (Isla Grande), Argentina, in southernmost South America. The specimen consists of parts of an associated pelvic girdle and limb that are identified as belonging to the penguin stem clade (Aves: Pansphenisciformes). The specimen, from an exposure of the Leticia Formation (late middle Eocene), is the earliest known penguin (pansphenisciform) from South America. It is more than 20 million years older than the earliest previously recorded South American penguins (from the late Oligocene–early Miocene) and, thus, almost doubles their known record on the continent.

A detailed description of the new specimen and a discussion of its implications for the understanding of penguin morphological evolution are provided. The new specimen and other fossil penguins do not currently point to the origin of extant, or crown clade, penguin lineages (Spheniscidae), by the Eocene, only to the divergence of the penguin stem lineage from its sister taxon by this time. The new fossil has several morphologies that differ from all extant penguins but are shared with other fossil penguin taxa, suggesting they may be outside Spheniscidae. However, in a discussion of the current status of penguin systematics, we suggest the urgent need for comprehensive phylogenetic analysis of fossil and extant penguins to clarify the timing and pattern of penguin diversification.

The specimen was recovered from a newly identified fossil vertebrate locality, an exposure of the Eocene Leticia Formation at Punta Torcida on the Atlantic shore of southeastern Tierra del Fuego, Argentina. The new locality is introduced, and a brief geologic description is made,

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highlighting the potential of the shallow marine sediments of the Leticia Formation for contributing to our knowledge of the Paleogene vertebrate fossil record of Tierra del Fuego, and of southern South America, generally.

INTRODUCTION

The associated partial penguin pelvic girdle and limb described here was recovered in the friable, silty, very fine sandstones of the Leticia Formation exposed at Punta Torcida on the Atlantic coast of southeastern Tierra del Fuego, Argentina (figs. 1–3). The specimen was collected by María I. López-Cabrera and Eduardo B. Olivero during field study of the stratigraphy, sedimentology, and paleontology of the Eocene foreland succession of the Austral Basin. The vertebrate-bearing Leticia Formation sandstones represent estuarine and proximal shelf deposits that have also produced abundant gastropods, bivalves, and solitary corals (Olivero and López-Cabrera, 2001; Olivero et al., 2002). Foraminifera and nannoplankton from the Leticia Formation indicate a late middle Eocene age for the deposits (Malumián et al., 1994; Olivero and Malumián, 1999; see below).

Prior to the recovery of the new specimen, the earliest fossil penguins from South America were latest Oligocene or early Miocene specimens from Patagonia (Simpson, 1972; Fordyce and Jones, 1990). At the turn of the 19th century, Carlos Ameghino collected penguin material at the mouth of the Santa Cruz River in Santa Cruz Province, Argentina, probably from the Monte León Formation, also of late Oligocene–early Miocene age (Acosta Hospitaleche et al., 2001). Fossil penguins are additionally known from latest Oligocene–early Miocene shallow marine deposits assigned to the Gaiman or Patagonia Formation and exposed in the Río Chubut valley, near the city of Trelew, Patagonia (Simpson, 1946; Simpson, 1981; Malumián et al., 1999 and the bibliography therein).

Although middle and upper? Eocene marine sediments have a regional distribution in southern Patagonia, they outcrop only along the western margin of the Patagonian Andes. These deposits are exposed in the Lago Argentino–Río Turbio area (Malumián et al., 1999). In southern Chile and Tierra del Fue-

go, Eocene outcrops are restricted to the western and northern Andean margin and consist mostly of deep marine deposits, with the exception of the shallow marine Leticia Formation. Of these exposed deposits, only the Leticia Formation has produced a fossil vertebrate, that which is described here.

Fossil penguins are known from the late Paleocene to late Eocene of Seymour Island, Antarctica, which lies off of the northeastern tip of the Antarctic Peninsula. The Eocene La Meseta Formation exposed on Seymour Island has produced a taxonomically diverse penguin assemblage (Wiman, 1905; Simpson, 1971a; Cione et al., 1976; Case, 1992). Most of this material, including at least six species, is from the upper part of the Formation, which is late Eocene in age. This upper part is currently included in “Telm 7” of Sadler (1988), or the Allomember Submeseta of Marensi et al. (1998), and has yielded a Sr isotopic age of ~34.2 Ma (Dingle and Lavelle, 1998). Sadler (1988) recognized seven informal stratigraphic packages in the La Meseta Formation, “Telm 1” to “Telm 7”, and Marensi et al. (1998) recognized six unconformity-bounded allomembers. Less abundant penguin material was also recorded from “Telm 3” and “Telm 4/5” or Allomembers Campamento and Cucullaea, respectively. These units are assigned a middle Eocene age based on the ~52.4/54.3 (late early Eocene) Sr isotopic age yielded by the basal part of the underlying Acantilados Allomember (Reguero et al., 2002). New discoveries from Seymour Island include penguin bones from the late early Eocene Acantilados Allomember or Telm 2–3 (La Meseta Formation) as well as from the late Paleocene Cross Valley Formation (S. Marensi, personal commun. to E.B. Olivero).

Paleogene penguins have been described from the late middle and late Eocene through Oligocene of New Zealand (Fordyce, 1991), and further undescribed material is known from the early Eocene (Fordyce, personal commun.). They are also known from the late Eocene (Simpson, 1957; Jenkins, 1974)

and possibly Oligocene (Glaessner, 1955) of Australia (reviewed in Fordyce and Jones, 1990). A partial skeleton and other more fragmentary material from “proto-penguins”, or wing-propelled divers proposed to be closely related to penguins, have additionally been reported from the late Paleocene or early Eocene of New Zealand (e.g., Fordyce et al., 1986), but have not yet been described (Fordyce and Jones, 1990; Fordyce, personal commun.).

MATERIALS AND METHODS

In the description of the new specimen, the English equivalents of the Latin osteological nomenclature of Baumel and Witmer (1993) are used. The terms of orientation for the anatomical position of a bird, as specified by Clark (1993), were followed with one exception. The “time-honored” terms (Clark, 1993) of zoological nomenclature “anterior” and “posterior” were used, rather than “cranial” (and “rostral”) and “caudal” as proposed by Clark (1993) in the *Handbook of Avian Anatomy: Nomina Anatomica Avium* (Baumel et al., 1993; see further discussion in Clarke and Norell, 2002). Appendix 1 lists the comparative materials used in preparation of the description and systematic discussion.

All taxonomic names above the species level used in this paper are used as clade names, although most await formal definition under a system of phylogenetic nomenclature (de Queiroz and Gauthier, 1990, 1992) and according to the PhyloCode (Cantino and de Queiroz, 2000). “Pansphenisciformes” is used here as a name for all taxa more closely related to extant penguins than to any other extant avian taxa. “Sphenisciformes” is suggested as a name for all parts of this lineage with a loss of aerial flight homologous with that of extant penguins. These definitions are deliberately not formalized pending recommendation of the PhyloCode regarding the proposed use of “pan” as a prefix in all stem clade names (Gauthier and de Queiroz, 2001) and to allow penguin specialists to debate appropriate definitions for these names prior to the start date of the PhyloCode (Cantino and de Queiroz, 2000).

As all extant penguins have consistently been placed in the “family” Spheniscidae, it

is also recommended that the name “Spheniscidae” be formally applied to the clade comprised of the most recent common ancestor of all extant penguins and all of its descendants. However, a formal definition of Spheniscidae identifying this name as that for the penguin crown clade should await further consensus on the phylogenetic relationships among extant penguins (e.g., compare Kennedy and Page [2002] and cladogram of O’Hara [1989] published in Williams [1995]) because of the required use of species or specimens as specifiers for clade names (Cantino and de Queiroz, 2000).

INSTITUTIONAL ABBREVIATIONS: **AMNH**, American Museum of Natural History; **CADIC**, Centro Austral de Investigaciones Científicas, Tierra del Fuego, Argentina; **MoNZ**, Museum of New Zealand (formally the Dominion Museum; e.g., as cited in Simpson, 1971b), Wellington, New Zealand; **OM**, Otago Museum, Dunedin, New Zealand.

GEOLOGIC SETTING OF THE PUNTA TORCIDA LOCALITY

In southeastern Tierra del Fuego, the Late Cretaceous–Cenozoic sedimentary filling of the foreland Austral Basin consists of four major, unconformity-bounded, synorogenic clastic wedges, which are mainly characterized by very thick, deep marine siliciclastic deposits (Olivero and Malumián, 2002). The youngest, Oligocene–Miocene clastic wedge is mainly exposed outside the folded belt, to the north of Punta Gruesa (fig. 1), and consists of subhorizontal, faulted strata. Within the fold and thrust belt, to the south of Punta Gruesa, the deposits of the older clastic wedges of Maastrichtian–Danian, late Paleocene–early Eocene, and late middle to late Eocene–early Oligocene ages, respectively, reach an aggregate thickness in excess of 3500 m and are highly deformed and mostly exposed in tectonically separated blocks. Nonetheless, superb outcrops along the Atlantic shore at the Cabo Campo del Medio–Punta Torcida anticline (figs. 1–3) allow for the recognition of a very thick (ca. 1600 m) Eocene sedimentary succession, comprising the Punta Torcida Formation and unnamed strata, early Eocene; the Leticia Formation,

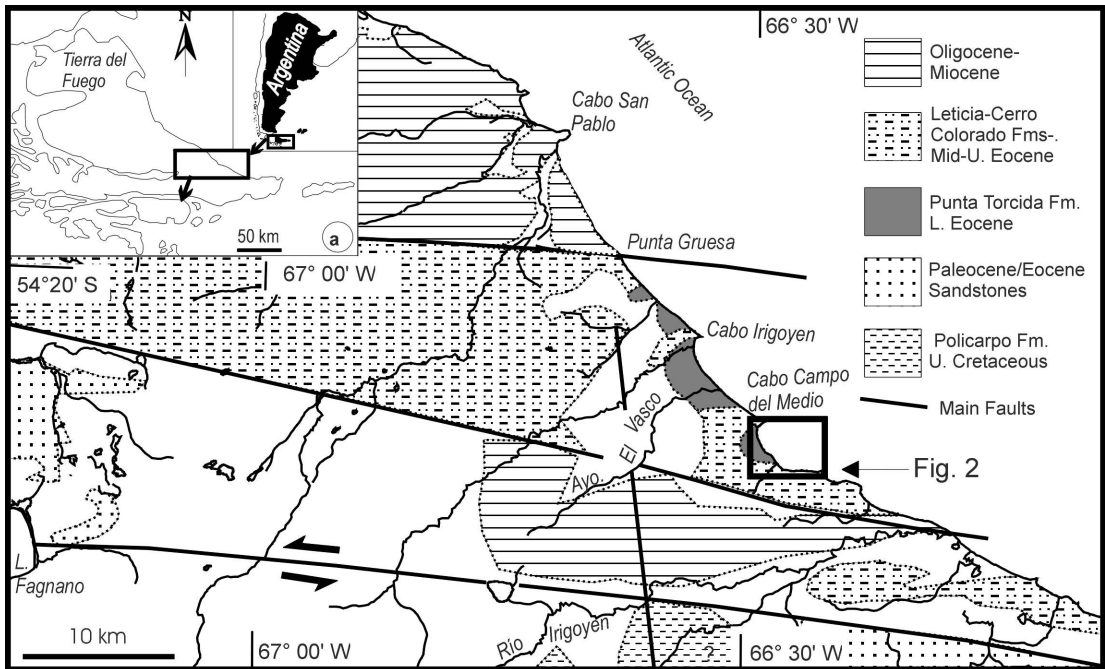


Fig. 1. Simplified geologic map of central and eastern Isla Grande, Tierra del Fuego, showing outcrops of Upper Cretaceous to Miocene synorogenic clastic wedges. The area of the penguin locality, at Cabo Campo del Medio–Punta Torcida, is bounded by a rectangle and detailed in the map provided in figure 2.

late middle Eocene; and the Cerro Colorado Formation, late middle to late Eocene. A major unconformity is recorded at the base of the Leticia Formation (Olivero and Malumián, 1999; Olivero et al., 2002).

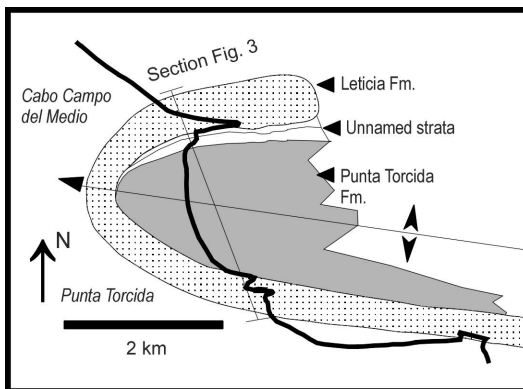


Fig. 2. Schematic map of the Cabo Campo del Medio–Punta Torcida anticline showing the distribution of the Punta Torcida Formation and unnamed strata (lower Eocene) and the Leticia Formation (upper middle Eocene). The star indicates where the new specimen (CADIC P 21) was recovered.

The Punta Torcida Formation (ca. 220 m thick) is dominated by dysaerobic dark gray mudstones with sparse intercalations of light gray to yellowish fine turbidite sandstones. At the northern limb of the anticline, it is covered by an unnamed sedimentary package (ca. 225 m thick) consisting of thick-bedded turbidite sandstones, tuffs, and mudstones. Collectively, these deposits are interpreted as parts of a turbidite system, including basal thin-bedded turbidites in the basal part; base of slope thick-bedded turbidites in the middle part; and slope, distorted mudstones, and tuffs in the upper part (figs. 2, 3). The vertical distribution of these facies association was related to the progradation of a fan-delta complex (Olivero and López-Cabrera, 2001; Olivero et al., 2002). Planktonic foraminifera indicates a middle early Eocene age equivalent to the *G. wilcoxensis* Zone from New Zealand, or the tropical equivalent Zones P7 to P8, or Zone AP6 from Antarctica (Olivero and Malumián, 1999).

Resting on a deeply incised unconformity, the vertebrate bearing Leticia Formation is

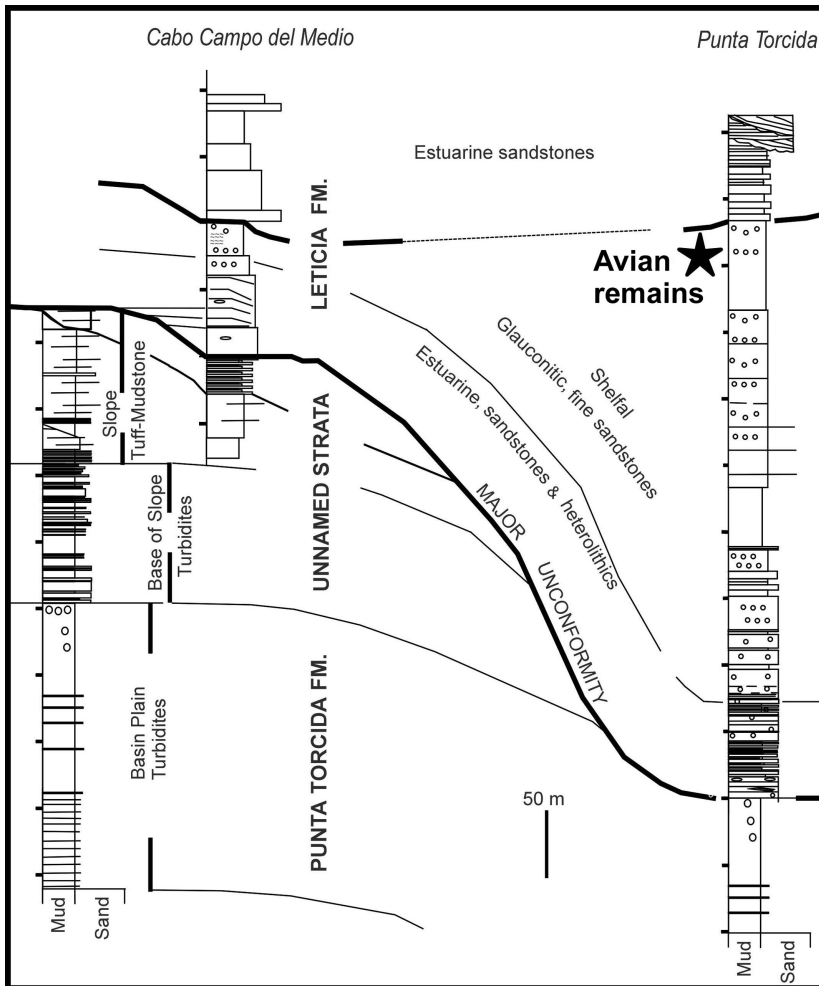


Fig. 3. Correlation of sections and sedimentary facies of the lower and upper middle Eocene strata across the Cabo Campo del Medio–Punta Torcida anticline showing the complex geometry and variable thickness of the three main stratigraphic intervals of the Leticia Formation (adapted from Olivero and López-Cabrera, 2001). The penguin remains (CADIC P 21; indicated by a star) were recovered near the top of the midshelf sandstone interval of the Leticia Formation near Punta Torcida.

dominated by fine-grained, glauconitic, estuarine, and proximal shelf sandstones. These sandstones show a complex architecture and display variable thickness along the northern and southern margin of the anticline, ca. 200 m and 500 m, respectively (fig. 3), probably reflecting differential syntectonic subsidence controlled by a growing fold structure. The Leticia Formation is composed by three main sandstone-dominated intervals. The lower and upper intervals consist of thick, cross-bedded and parallel-laminated, channelled

sandstone bodies, with minor heterolitic, bioturbated, thin beds, which are interpreted as representing estuarine settings (Olivero and López-Cabrera, 2001; Olivero et al., 2002). The scarcity of foraminifera and the absence of planktonic foraminifera in most of these intervals also suggest marginal, shallow, and restricted marine conditions for the lower and upper intervals of the Leticia Formation (Olivero and Malumián, 1999). The middle interval consists of glauconitic, fossiliferous, and highly bioturbated very fine sandstones,

representing shelf settings. Minor mudstone horizons bear planktonic foraminifera and nannoplankton indicative of an age constrained to the *G. index* Zone to *G. inconspicua* Zone of New Zealand, or equivalent to the interval: upper Zone P12 to lower Zone P14 of tropical areas, that is, late middle Eocene (Malumián et al., 1994; Olivero and Malumián, 1999). The penguin bones were recovered near the top of the middle shelf sandstone interval, at the southern limb of the Cabo Campo del Medio–Punta Torcida anticline (fig. 3).

The overlying Cerro Colorado Formation (ca. 855 m thick) consists of a vertical stacking of four coarsening and thickening upward successions. Each succession is composed of dark gray mudstones at the base, regular intercalation of mudstones and light gray or greenish sandstones at the middle part, and thick gray or yellowish fine to coarse sandstones and pebbly sandstones at the top. The uppermost succession bears abundant radiolarians and planktonic foraminifera typical of an oxygen minimum habitat, indicative of a late Eocene age (upper Zone P15 to upper Zone P16). The microfauna and stratigraphic position of the lower three successions are consistent with a latest middle Eocene age (middle Zone P14 to lower Zone P15, Olivero and Malumián, 1999).

DESCRIPTION OF THE NEW SPECIMEN

The new specimen, CADIC P 21, includes portions of the pelvis (primarily the left preacetabular ilium; fig. 4a, b), nearly complete right femur (fig. 5), a fragment interpreted as the head of the left femur (fig. 4a), nearly complete right tibiotarsus (figs. 6–8), and fibula (fig. 9). The right femur lacks the posterior portion of its proximolateral edge and posterior parts of the distal end (fig. 5). The nearly complete right tibiotarsus is missing the lateral cnemial crest and the medial half of its distal end (figs. 6–8). Overall, the specimen is of an individual slightly smaller than the largest extant penguin species, *Aptenodytes forsteri*, or the Emperor Penguin (table 1). Compared to other fossil penguins, CADIC P 21 is slightly smaller than the Eocene *Palaeudyptes* sp. (MoNZ 1449; Simpson,

1971b) and Oligocene *Archaeospheniscus lowei* (OM C 47.27; Simpson 1971b), both from New Zealand, but is slightly larger than the latest Oligocene–early Miocene? *Paraptenodytes antarcticus* (e.g., AMNH 3338) from Patagonia.

The CADIC P 21 pelvis is represented by the left preacetabular iliac blade (fig. 4a, b) and a small portion of the left pubis ventrolateral to the acetabulum (fig. 4a). Approximately one-half of the acetabular rim is preserved, and no parts of the sacral series or postacetabular pelvis are preserved. The preacetabular ilium is preserved in ventromedial view. It was evidently not fused to the sacral series; a scar faintly demarcates ilium contact with the transverse process of a sacral vertebra just anterior to the acetabulum (fig. 4b). This scar in CADIC P 21 lies in approximately the same position as that in the extant penguins compared. Just anterior to the acetabulum, the ventromedial surface of the blade is slightly concave between the scar just mentioned and the broken medial edge of the blade.

The ilium in CADIC P 21 broadens toward its anterior end. This end is incomplete, and it is unclear how much of the element is missing. The preacetabular portion of the ilium in the new fossil may have been relatively short. The shape of the lateral edge of the blade is partially preserved, and the curvature of this lateral edge of the blade is greater than that in spheniscids with elongate blades. The condition in CADIC P 21 is closer to the condition in *Eudyptula minor*, for example, which has a slightly shorter and more expanded preacetabular ilium than do other spheniscids. The anterior iliac blade in the fossil, however, appears more expanded proximally than in *Eudyptula*.

At least some expansion of the anterior preacetabular ilium is seen in all extant penguins other than *Aptenodytes forsteri* and *Aptenodytes patagonicus* where the preacetabular ilium is approximately equal in mediolateral width throughout its length. The anterior portion of the ilium is also very little expanded in *Eudyptes schlegeli*, while in *Eudyptes pachyrhynchus* it is expanded proximally to approximately the same degree as in all other spheniscid taxa considered except *Eudyptula minor*. The pelvic bones of fossil

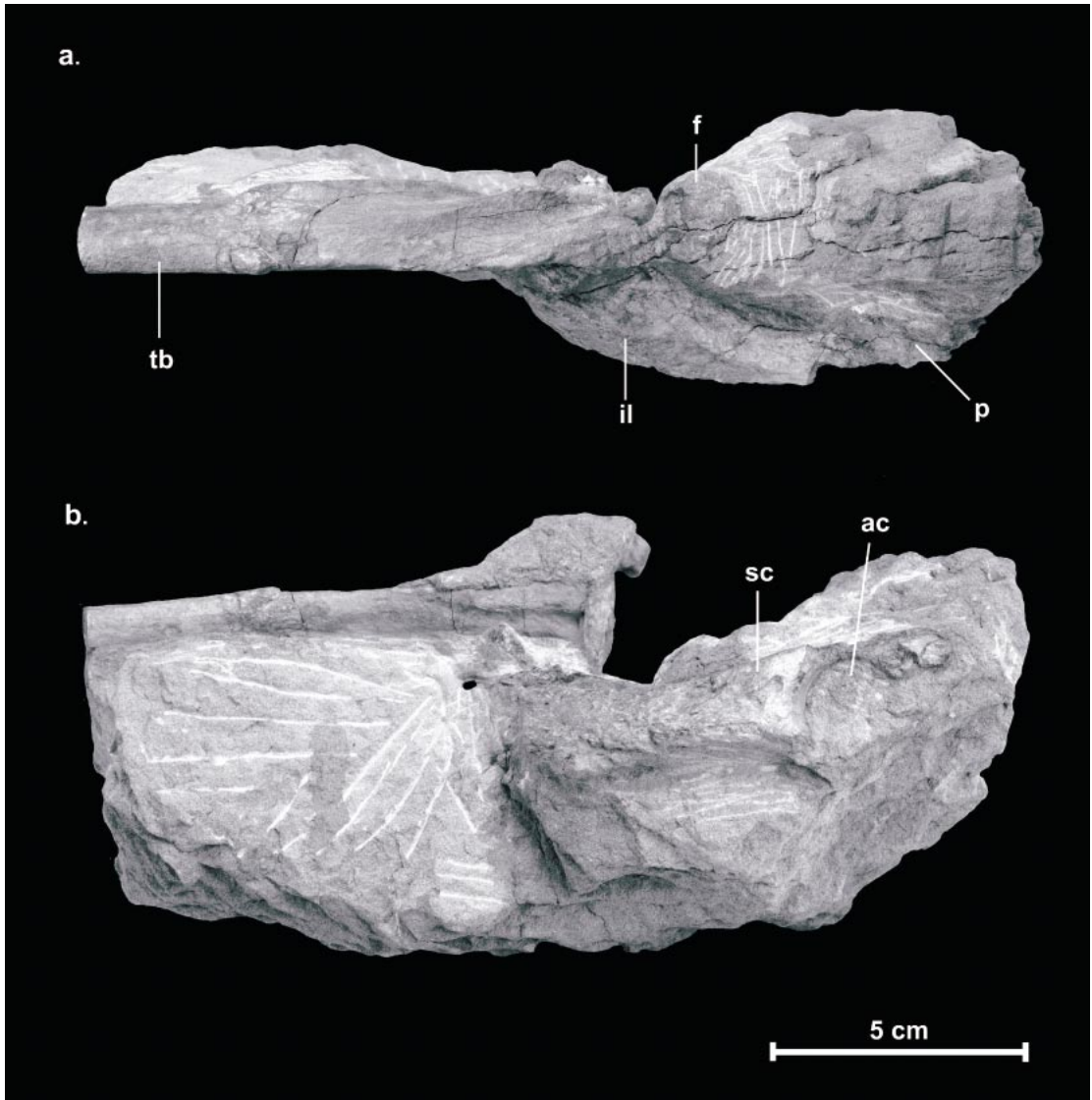


Fig. 4. The largest block of CADIC P 21 in (a, b) two views with parts of the acetabular and preacetabular ilium in ventromedial view, a small portion of the anterior pubis, the right tibiotarsus and the head of the left femur. Anatomical abbreviations: ac, acetabulum; f, femur, il, ilium; p, pubis; sc, scar for sacral transverse process; tb, tibiotarsus.

penguins are not well known; indeed, none appears so far to have been described in the literature. The anterior iliac blade appears to have only been pictured in one Paleogene penguin, a late Oligocene penguin from New Zealand illustrated in Fordyce and Jones (1990: fig. 18.6). In this illustration, the specimen appears to have a much narrower blade

than CADIC P 21, more like the condition in *Aptenodytes forsteri*, for example.

In the new fossil and in all spheniscids studied other than individual specimens of *Pygoscelis antarctica* and *Pygoscelis papua*, the ilium (and other pelvic bones) is unfused to the sacral series. In the fossil penguin taxa represented by the unpublished New Zealand



Fig. 5. Right femur of CADIC P 21 prepared from the block in (left) anterior and (right) posterior views. Anatomical abbreviations: ail, anterior intermuscular line; cls, capital ligament scar; tcf, m. tibialis cranialis tendon fossa; ft, fibular trochlea; mc, medial supracondylar crest; pf, popliteal fossa; tr, trochanteric surface.

specimen (Fordyce and Jones, 1990: fig. 18.6) as well as in isolated sacral series from the Eocene of Seymour Island (Wiman, 1905: fig. 8, 1; Simpson 1971a), the sacral series also appears to have been unfused (or possibly incompletely fused) to the bones of the pelvic girdle.

The right femur of CADIC P 21 was completely prepared out of the matrix (fig. 5).

The capital ligament impression on the femoral head is broad and deep. The proximal articular surface for the antitrochanter is slightly concave and more U-shaped than V-shaped. By contrast, it is slightly more V-shaped in other fossil penguins (e.g., *Parapterodytes antarcticus*, AMNH 3338 in Simpson [1946]; *Archaeospheniscus lowei*, OM C 47.27 in Simpson [1971b]) and com-

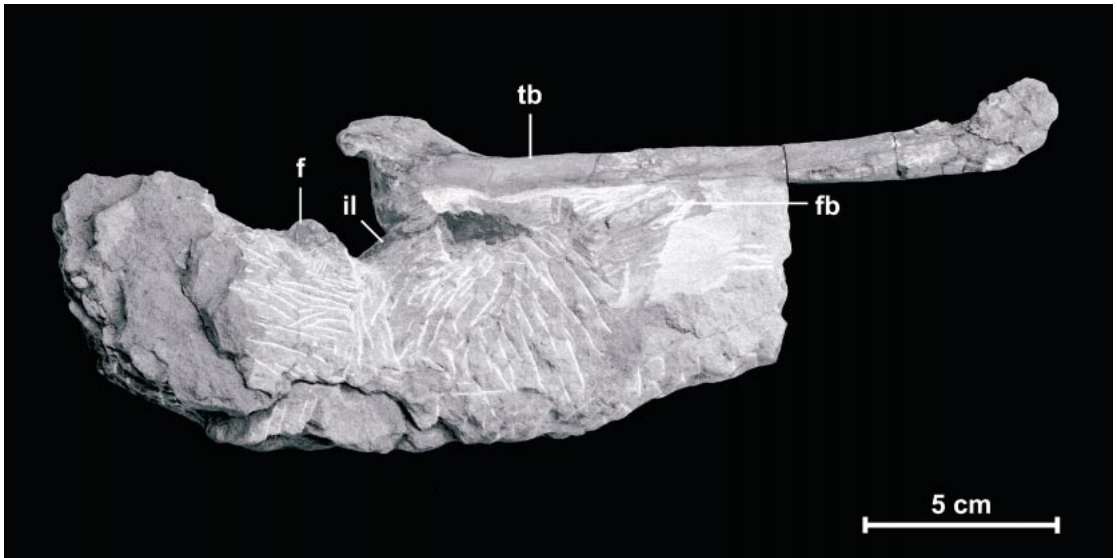


Fig. 6. The CADIC P 21 block with the two articulating pieces of the right tibia and fibula joined. The tibia and fibula are shown in oblique anterolateral view. Portions of the left ilium, head of the left femur and part of the shaft of the right fibula are also visible. Anatomical abbreviations: f, femur; fb, fibula; il, ilium; tb, tibia.

paratively strongly V-shaped in all extant penguins considered. In the V-shaped condition, the surface of the proximal end of the femur in anterior or posterior view is flat to convex as it slopes gradually toward the diminutive trochanteric crest from the base of the humeral head. In CADIC P 21, this surface again curves up toward a diminutive trochanteric crest, but it creates a concave profile in anterior or posterior view. The CADIC P 21 condition was observed in procellariiforms, and it is approached by the condition illustrated for *Palaeudyptes* sp. (MoNZ 1449; Simpson, 1971b).

The trochanteric crest appears to have been relatively unprojected proximally or anteriorly. This morphology is indicated by intact portions of the anterior tip of the proximal portion of the trochanteric crest and of the shaft just proximal and distal to the conspicuously missing chip of the anterolateral surface (fig. 5). Proximal and posterior portions of the crest are missing. However, a deep muscular impression probably corresponding to one of the obturator impressions (*impressiones mm. trochanteris*; Baumel and Witmer, 1993) is visible at what is inferred to be approximately the crest's posterior end.

The femoral shaft is nearly straight (fig. 5). The posterior intermuscular line is weakly defined for the proximal half of the posterior surface of the femur. It rises distally into a strongly projected medial supracondylar crest that extends slightly less than one-third the length of the femur. This crest crosses the shaft from approximately its midpoint in posterior view toward the medial edge of the medial condyle (fig. 5). No lateral supracondylar crest is developed. Of the distal femur of CADIC P 21, posterior portions of the medial condyle and anteroproximal portions of the lateral condyle are missing.

The distal femur in CADIC P 21 is mediolaterally narrow. Although parts of both condyles are missing, sections of the mediolateral and laterodistal surfaces of the femur are intact, and it is from the orientation of these surfaces that a distal width only slightly wider than the shaft can be inferred. Furthermore, although the narrow fibular trochlea is proximolaterally incomplete, its distal and posterior edges are intact, from which it is determined that it was little projected laterally. This inference is also consistent with the mediolaterally narrow, intact, proximal articular facet on the fibula itself

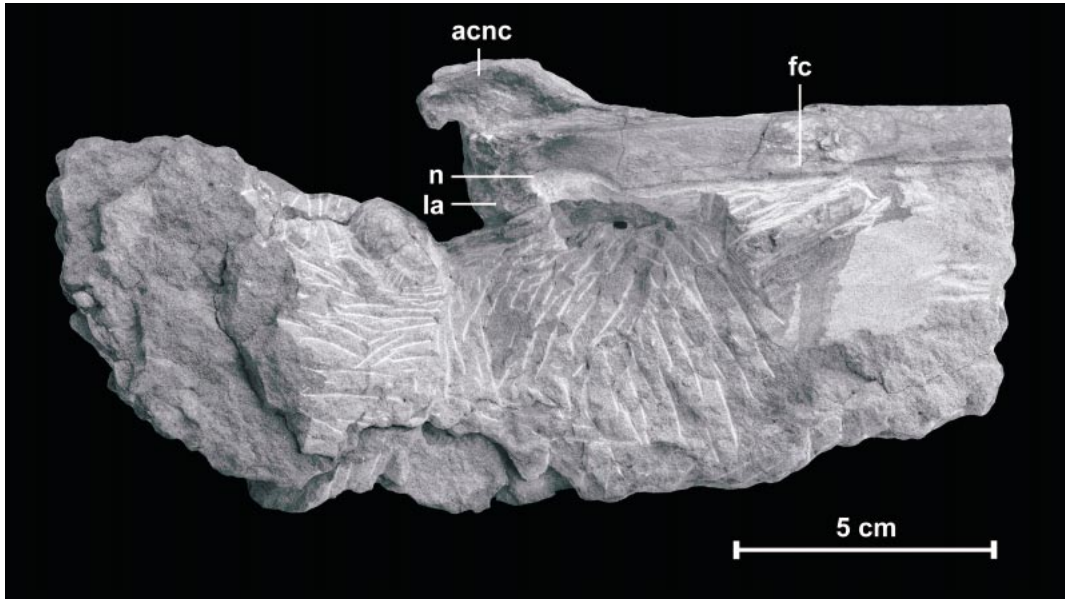


Fig. 7. The proximal portion of the CADIC P 21 tibiotarsus in oblique anterolateral view. The prominent fibular crest and notch (foramen interosseum proximale; Baumel and Witmer, 1993) proximal to it are indicated. The anterior cnemial crest is unbroken, but the lateral is missing. Anatomical abbreviations: acnc, anterior cnemial crest; fc, fibular crest; la, lateral articular surface; n, notch.

(fig. 9). The distal end of the femur is anteroposteriorly broad or uncompressed in distal view, which is the condition in other fossil and extant pansphenisciforms. The popliteal fossa is developed as a deep, discrete (or pit-shaped) depression located close to the lateral condyle.

A poorly preserved fragment in the main block of CADIC P 21 is interpreted as the head of the left femur in medial view (fig. 4a). It is the size of the head of the right femur and bears a faint line in the same position as the edge of the femoral head in the right. However, this fragment is heavily abraded, and no further morphology could be discerned including the presence or absence of a capital ligament scar.

The right tibiotarsus of CADIC P 21 is short; it is less than twice the length of the femur. This proportion is nearly the same as that in *Aptenodytes forsteri* (table 1) and is similar to that of other extant and fossil penguins (see Discussion). The tibiotarsus is currently preserved in two parts that articulate exactly (fig. 6). These pieces comprise one still in the CADIC P 21 block (fig. 7) and the second prepared out (figs. 8). Visible at

the broken ends of these pieces of the tibiotarsus and at the chipped edge of the proximal femur is the internal structure of pelvic limb bones of CADIC P 21. These bones, and the tibiotarsus in particular, are dense with an extremely thick layer of compact bone and very narrow medullary cavity. Indeed, the tibiotarsal shaft in cross section appears nearly solid, a morphology developed in *Paraptenodytes antarcticus* and commented on in Simpson (1946). While dense, less pneumatic, or apneumatic bones are developed in a variety of crown clade birds modified for diving (del Hoyo et al., 1992), the condition in CADIC P 21 is more extreme than even the condition in gaviids, for example. In fact, the condition would appear to be matched in degree only by penguins and possibly other flightless, highly modified diving birds such as the extinct Great Auk, *Pinguinus impennis*, or the Plotopteridae (Olson and Hasegawa, 1996). Penguins have been repeatedly remarked as distinguished by their most extreme example of heavy or "solid" bones in crown clade birds (e.g., Simpson, 1946, Williams, 1995; del Hoyo et al., 1992).

The shaft of the tibiotarsus is strongly

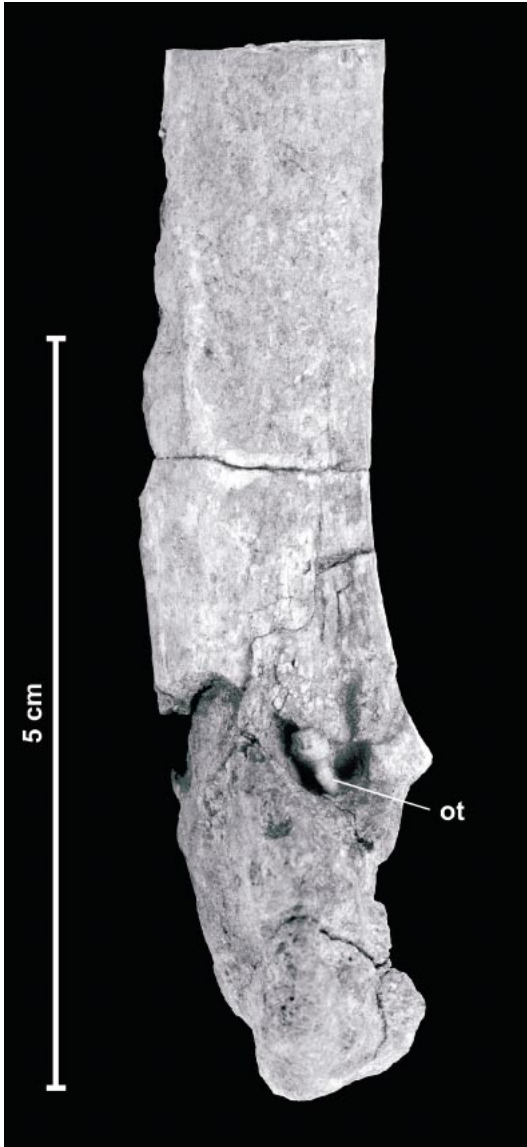


Fig. 8. The distal tibiotarsus of CADIC P 21 in anterior view. Anatomical abbreviation: ot, ossified tendon.

compressed anteroposteriorly. Marked compression of the tibiotarsal shaft (distal to the ventral end of the fibular crest) has been noted for other Eocene (Simpson, 1957) and late Oligocene–early Miocene (Simpson, 1946) penguins. For example, Simpson (1957) commented that compression seen in a tibiotarsus from the Eocene of Australia (*Palaeudyptes* cf. *antarcticus*; Simpson, 1957),

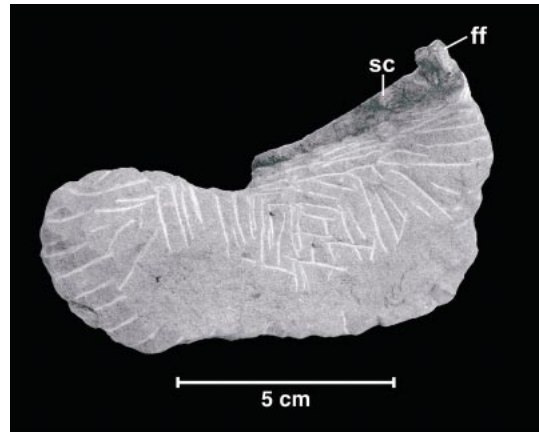


Fig. 9. The fibula of CADIC P 21 in lateral view. Anatomical abbreviations: ff, facet for femur; sc, scar for attachment of lig. collateralis lateralis.

as well as in other “Palaeudyptines” and other “older fossil penguins” (Simpson, 1957: 55), was stronger than that seen in any extant penguin taxa. Consistent with Simpson’s (1946, 1957) observations, the distal tibiotarsal shaft in CADIC P 21 is much more compressed than in any of the extant penguins compared. It is also, however, more compressed than in the late Oligocene or early Miocene *Parapterodytes antarcticus* (AMNH 3338) from Patagonia.

The morphology of the anterior cnemial crest is well preserved (fig. 7). It does not project extensively proximal to the articular surfaces for the femur. The patellar crest slightly overhangs the proximal surface of the tibiotarsus (fig. 7). On the anterior surface of the distal tibiotarsus, the extensor groove is relatively broad and slightly more medially located than in extant penguins (or than in *Parapterodytes antarcticus*; AMNH 3338). The ossified supratendinal bridge is broken distally. Projecting proximally from under this bridge is a small element, which may be part of an ossified tendon (fig. 8). The distal end of the tibiotarsus is deflected medially (fig. 8). Additional morphologies of this region are not preserved.

The proximal portion of the right fibula was preserved in two pieces associated with the tibiotarsus (fig. 6), one of which was prepared off the CADIC P 21 block (fig. 9). It is a robust element, and the distalmost pre-

TABLE 1
**Compared Measurements of CADIC P 21, *Aptenodytes fosteri* (AMNH 3745),
 and *Paraptenodytes antarcticus* (AMNH 3338)**

Measurements (in mm)	CADIC P 21	AMNH 3745	AMNH 3338
FEMUR			
Maximum length	121.2	126.2	115.9
Mediolateral width midshaft	16.5	15.1	12.0
Anteroposterior width of head	17.1	15.1	15.5
Maximum width distal end	28.0 ^a	28.4	27.0
TIBIOTARSUS			
Maximum length (including cnemial crest)	199.0	216.5	?
Length from proximal condyles to distal end	193.0	206.0	178.0
Mediolateral width midshaft	16.0	13.5	13.5
Anteroposterior width midshaft	10.0	13.0	10.0
Fibular crest length	49.0	47.1	46.4
Mediolateral width at midpoint fibular crest	21.0	16.5	16.9
Distance from surface of proximal condyles to proximal tip of fibular crest	31.5	33.5	26.8
FIBULA			
Anteroposterior width of proximal end	15.3	13.3	?
PELVIS			
Diameter of acetabulum (medial view)	21.5	21.2	?

^aEstimated.

served portion of the shaft shows no indication of tapering markedly distally (figs. 6, 9). In extant penguins the fibula is also a robust element that can extend most of the length of the tibiotarsus. The proximal articular facet for the femur is mediolaterally narrow (fig. 9). A raised scar for the lig. collateralis lateralis is visible on the proximolateral fibular surface (fig. 9).

DISCUSSION

The scope of the current analysis was necessarily determined by the status of fossil penguin taxonomy and of avian and, specifically, penguin systematics. The holotype specimens of many previously named fossil penguin taxa are nonoverlapping single elements (or otherwise extremely fragmentary) that cannot be compared with one another (e.g., Simpson, 1971a). Key fossil specimens (alternatively especially complete or described as morphologically intermediate between penguins and other avian taxa) have remained so far undescribed (see Fordyce et al., 1986; Fordyce and Jones, 1990). Additionally limiting comparative study of CAD-

IC P 21 is the fact that most fossil penguin taxa have been described, named, and taxonomically revised based on morphologies of the humerus and tarsometatarsus (e.g., Simpson, 1971b; Myrcha et al., 2002); these elements are unrepresented in the new fossil.

Previous workers considered the best-preserved parts of CADIC P 21, the femur and tibiotarsus, to be comparatively undiagnostic elements in fossil and extant penguins (e.g., Marples, 1952; Simpson, 1957; Grant-Mackie and Simpson, 1973); thus, these elements have received relatively little commentary. Iliac (and other bones of the pelvic girdle), as well as the fibulae of fossil penguins, are even more poorly represented, and these elements of CADIC P 21 could be compared to only one or two described or illustrated specimens. Thus, although CADIC P 21 was compared to fossil and extant specimens (see appendix 1), and although its morphologies appear distinct from those known from these elements (see commentary in the Description), we strongly believe that the decision to name the fossil as the holotype of a new taxon should be the result of a much-needed

comprehensive, systematic revision of fossil penguins, a project outside the scope of this paper.

A further issue determining the scope of the current analysis is the paucity of available data on the phylogenetic position of the penguin lineage in Aves, as well as data addressing the relationships among extant penguins. The previously suggested sister taxa of penguins are morphologically quite distinct. These potential outgroups of an analysis of penguin relationships include a part of Procellariiformes, or Procellariiformes as a whole (Fürbringer, 1888; Simpson 1946, 1971b; Sibley and Ahlquist, 1990), Gaviidae (Olson, 1985), a Gaviidae + Podicipedidae clade (Cracraft, 1988), and possibly Phalacrocoracidae (Paterson et al., 1995).

More recent phylogenetic results from analyses of mitochondrial gene sequence data (Van Tuinen et al., 2001) and morphological data (Livezey and Zusi, 2001) have supported Procellariiformes and Gaviidae as the successive outgroups of penguins. Groth and Barrowclough (1999) also found support for a clade including gaviids and spheniscids (procellariiforms were not included) using nuclear gene sequence data. Nunn and Stanley (1998) included multiple spheniscids as outgroups to analyses of procellariiform interrelationships, and procellariiforms were not found to be paraphyletic with respect to penguins. Two morphology-based cladistic analyses have been undertaken of extant penguins phylogenetic relationships (O'Hara, 1989; Jones, 1995); however, neither has been published. The cladogram of O'Hara (1989) was printed in Williams (1995) but differs markedly from analyses of varying kinds of molecular data (Sibley and Ahlquist, 1990; Nunn and Stanley, 1998) and combining sequence data, isozyme, and behavioral characters (Paterson et al., 1995).

Unfortunately, undertaking largescale analyses of the position of penguins within the avian crown clade and then optimizing apomorphies of penguins relative to their nearest outgroups were outside the scope of the current project. Therefore, based on previous systematic results summarized above, Gaviidae and Procellariiformes were used as outgroups to hypothesize derived characters shared by CADIC P 21 and penguins. In ad-

dition, however, CADIC P 21 was differentiated from all lineages of avian divers other than penguins.

The features considered at first pass in the evaluation of the systematic position of CADIC P 21 included the extreme bone density, large size, and relative proportion of the pelvic limb bones. The pelvic limb elements have a strikingly thick compact bone layer as developed only in birds modified for prolonged diving and only closely approached by penguins of living taxa (see Description). These heavy elements are also from an animal significantly larger than any fossil or extant crown clade diving birds other than penguins, the Great Auk (*Pinguinus impennis*), and the extinct pteropterygids (Howard, 1969; Olson and Hasegawa, 1996). The specimen is from an individual much larger than all known fossil or extant taxa of grebes, cormorants, anhingas including the large Miocene anhinga, *Meganhinga* (Alvarenga, 1995), or loons including the Eocene? "*Polarornis*" (Chatterjee, 1997; see Clarke and Chiappe, 2001), for example.

The femur is over one-half tibiotarsus length in CADIC P 21 (table 1; femur/tibiotarsus: 0.63). To compare this ratio in penguins and other diving, and nondiving, birds, measurements given in appendix 2 of Gatesy and Middleton (1997) were used. The ratio for extant and fossil penguins ranged from 0.55 to 0.70 (and most were between 0.60 and 0.70). By contrast, in gaviids, the tibiotarsus was conspicuously longer relative to the femur (femur/tibiotarsus: 0.32–0.41; based on the first five measurements for *Gavia immer* and the first four for *Gavia stellata* in Gatesy and Middleton [1997]), and in Procellariiformes the tibiotarsus was moderately longer (femur/tibiotarsus: 0.32–0.59; all from Gatesy and Middleton [1997] were included), but the difference in length was less extreme. Other lineages of diving birds with ratios approximating that of the penguins include phalacrocoracids, anhingids, sulids, alcids, and diving ducks, while podicipediforms had a ratio closer to that of the gaviids (0.41–0.44). A ratio approximating that seen in penguins is also seen in some basal avian taxa such as Galliformes, Anseriformes, and Tinamidae, as well as in a variety of other avian taxa. However, if Gaviidae and Pro-

cellariiformes are the successive outgroups to penguins (e.g., Van Tuinen et al., 2001; Livzey and Zusi, 2001), a higher ratio could be optimized as a local autapomorphy of penguins, including the fossil.

Further morphologies with restricted distributions among the surveyed taxa consistent with identification of the fossil as a penguin include several characters of the pelvic girdle and limb. For example, incomplete or complete lack of coossification of sacrum and pelvic bones occurs in CADIC P 21, penguins, some procellariiforms, gaviids, podicipedids, alcids, and a variety of other avian taxa but not usually in phalacrocoracids, anhingids, sulids, or apparently in plopterids (Olson and Hasegawa, 1996). Furthermore, in CADIC P 21 and penguins, the distal femur is narrow mediolaterally and the fibular trochlea is relatively unprojected (with a narrow corresponding proximal facet on the fibula); by contrast, in podicipedids, gaviids, anhingids, and phalacrocoracids, the distal femur is broader with a projected fibular trochlea. (In procellariiforms and sulids, the distal femur was only slightly broader than the penguin condition.) CADIC P 21 also shares with penguins relative to other diving taxa, including gaviids and procellariiforms, a comparatively low anterior cnemial crest on the tibiotarsus.

The smoothly concave profile of the proximal surface of the femur in either lateral or medial view in CADIC P 21 is not developed in any extant penguins but appears approached by some fossil penguins (see discussion in the Description), and is also seen in Procellariiformes (but not in gaviids, podicipedids, anhingids, or phalacrocoracids). The extensor groove on the tibiotarsus, more medially located in CADIC P 21 than in extant, and other fossil, penguins, is also more medially located in procellariiforms, suggesting that this condition could be found to be plesiomorphically retained in basal Pansphenisciformes.

The anterior expansion of the preacetabular iliac blade seen in CADIC P 21 is better developed than in extant penguins but is approached by *Eudyptula minor* (see Description). Expansion is slight in procellariiforms, while the condition in phalacrocoracids, anhingids, and plopterids (Olson and Hase-

gawa, 1996) approaches that seen in the fossil. Whether a more expanded anterior iliac blade is ancestral to pansphenisciforms deserves further scrutiny. The anteroposteriorly compressed tibiotarsal shaft seen in CADIC P 21 is most closely matched by phalacrocoracids and anhingids of extant taxa, although this condition is also developed in fossil penguins (e.g., Simpson, 1946), as mentioned in the description. Slight compression is seen in some procellariiforms. Again, whether the state in CADIC P 21 and other fossil penguins is ancestral to Pansphenisciformes merits additional study.

In *Parapterodytes antarcticus* (AMNH 3338) and CADIC P 21, the medial supracondylar crest is well projected but extends proximally markedly less than one-half the length of the femur; this condition was also approached by *Eudyptula minor* of Spheniscidae. By contrast, in *Pygoscelis adeliae*, *Pygoscelis antarctica*, *Aptenodytes forsteri*, and *Aptenodytes patagonicus* the crest extends proximally one-half the length of the femur. The *Spheniscus*, *Eudyptes*, and *Megadyptes* species surveyed had a more distally restricted crest than did the *Pygoscelis* and *Aptenodytes* species but one more proximally extensive than CADIC P 21, *Parapterodytes antarcticus* (AMNH 3338), and *Eudyptula minor*. The distribution of this morphology suggests that a more distally restricted medial supracondylar crest could be plesiomorphic for Spheniscidae within Pansphenisciformes; however, further comparisons are necessary, particularly to assess variation in this character for other fossil outgroups of Spheniscidae.

CONCLUSIONS

The identification of parts of Pansphenisciformes, or the penguin stem clade, in the middle (e.g., CADIC P 21) and even early (Fordyce et al., 1986) Eocene constrains the timing of the divergence of the penguin lineage from its nearest sister taxon. A long overdue phylogenetic analysis including fossil and extant penguins may place Paleogene taxa within the penguin crown clade. However, without evidence of such affinity these fossils do not address the timing of any of

the divergences within Spheniscidae or the origin of the penguin crown as a whole.

Indeed, to give further pause to conflating the age of earliest fossil penguin with a minimum age of the origin of Spheniscidae, there is evidence supporting placement of CADIC P 21 and other Paleogene taxa outside the penguin crown.

This result is consistent with Simpson's (1946, 1971b) conclusion that pre-Miocene (and some Miocene) fossil taxa were not closely related to any extant penguins; these taxa were placed outside Simpson's Spheniscidae (consistent with the usage of that name here; Simpson, 1946, 1971b). Morphologies of the quadrate, humerus, and tarsometatarsus present in Eocene and Miocene penguins and absent in extant penguins have been given to support (Simpson, 1946: 80–82, 1971b: 367) this conclusion. In addition, the marked anteroposterior compression of the tibiotarsus in Eocene taxa (including CADIC P 21) and some Miocene taxa (Simpson, 1946, 1957) but not in any extant taxon is consistent with the placement of these fossil penguins outside Spheniscidae.

Further understanding of the timing of pansphenisciform divergences will come from combined phylogenetic analyses of fossil and extant penguin taxa. CADIC P 21 clearly indicates, however, the presence of penguins in southernmost South America approximately 20 million years earlier than previously supported. In this regard, the specimen offers the important potential for insight into penguin paleobiogeography with future work.

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APPENDIX 1

Specimens compared to the new fossil in the preparation of the description are as follows: Sphenisciformes: *Pygoscelis adeliae*, AMNH 3649; *Pygoscelis antarctica*, AMNH 26160; *Pygoscelis papua*, AMNH 22679; *Spheniscus demersus*, AMNH 12782; *Spheniscus humboldti*, AMNH 4920; *Aptenodytes forsteri*, AMNH 3745; *Aptenodytes patagonicus*, AMNH 1624; *Megadyptes antipodes*, AMNH 5613; *Eudyptes schlegeli*, AMNH 5399; *Eudyptes pachyrhynchus*, AMNH 26509;

Eudyptula minor, AMNH 6257. Procellariiformes: (Diomedeidae) *Phoebastria (Diomedea) irrorata*, AMNH 1628; *Thalassarche (Diomedea) cauta*, AMNH 1436; (Procellariidae) *Macronectes giganteus*, AMNH 5400; (Hydrobatidae) *Fregatta tropica*, AMNH 5330; *Oceanodroma leucorhoa*, AMNH 22019; (Pelecanoididae) *Pelecanoides garnotii*, AMNH 3125; *Pelecanoides magellani*, AMNH 23569; Gaviiformes: *Gavia immer*, AMNH 26310; *Gavia stellata* AMNH 6971. Pod-

icipediformes: *Podiceps grisegena*, AMNH 3878. "Pelecaniformes": (Anhingidae) *Anhinga rufa*, AMNH 5240; *Anhinga anhinga*, AMNH 2919; (Phalacrocoracidae): *Stictocarbo* (*Phalacrocorax*) *magellanicus*, AMNH 23560; *Hypoleucos* (*Phalacrocorax*) *varius*, AMNH 5412; (Sulidae): *Morus* (*Sula*) *bassanus* AMNH 3127.

The new specimen was also compared with fossil penguin material illustrated in the literature (e.g., Simpson, 1946, 1957, 1971a, 1971b; Wieman, 1905), plotopterid (Plotopteridae: "Pelecaniformes"; Howard, 1969) material illustrated in Olson and Hasegawa (1996), and *Meganhinga chilensis* as described by Alvarenga (1995).

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