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Geobios 38 (2005) 667–675
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Crossvallia unienwillia, a new Spheniscidae (Sphenisciformes, Aves) from the Late Paleocene of Antarctica

Crossvallia unienwillia, un nouveau Spheniscidae (Sphenisciformes, Aves) du Paléocène supérieur de l'Antarctique

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Received 18 April 2003; accepted 12 February 2004

Available online 02 August 2005

Abstract

Modern penguins are typically small to medium-sized birds, and nearly all known modern specimens are smaller than the most archaic Paleogene relatives. Here we report an incomplete humerus, associated femur and tibiatarsus of a new spheniscid, *Crossvallia unienwillia* nov. gen. and sp., from the Late Paleocene (~55 million years, Myr) of Antarctica, extending the record of spheniscids by about 15 Myr. Its large size (length ~140 cm) supports the idea that large body size in penguins was acquired independently at different times (Late Paleocene and Late Eocene) under dramatically different environmental conditions. Comparison of its osteological anatomy suggests that the new taxon is closely related to the extinct Anthropornithinae rather than to other penguin lineages.

Résumé

Les manchots actuels sont en général des oiseaux de taille petite et moyenne et presque toutes les espèces actuelles sont plus petites que celles, plus primitives, du Paléogène. Ici, nous décrivons un humérus incomplet, un fémur et un tibiotarse incomplet associés à un nouveau genre et espèce de sphéniscidé, *Crossvallia unienwillia*, du Paléocène supérieur (~55 Ma) d'Antarctique, reculant ainsi l'origine des sphéniscidés d'environ 15 Ma. Sa taille (environ 140 cm) conforte l'idée que la grande taille du corps chez les manchots a été acquise indépendamment à différents moments (Éocène supérieur et Paléocène supérieur), dans des conditions environnementales très différentes. Son anatomie suggère que ce nouveau taxon soit étroitement apparenté aux Anthropornithinae, éteints plutôt que les autres lignées de manchots.

Keywords: Spheniscids; Penguin size evolution; Paleoenvironment; Antarctica

Mots clés : Sphéniscidés ; Évolution de la taille ; Paléoenvironnement ; Antarctique

1. Introduction

Penguins (Spheniscidae) are an extant group of flightless birds that are well adapted to marine life and particularly to diving. Their biogeographic and phylogenetic patterns record an early diversification, particularly during the Middle–Late Eocene in Antarctica. The evolution of the Southern Ocean in the Paleogene played an important role in the origin of marine higher vertebrates like penguins and cetaceans. These groups of pelagic predators radiated into ecological niches left by plesiosaurs and mosasaurs, which disappeared at the end of the Cretaceous. This evolutionary burst was perhaps one of the most important events in the history of the group

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doi:10.1016/j.geobios.2004.02.003

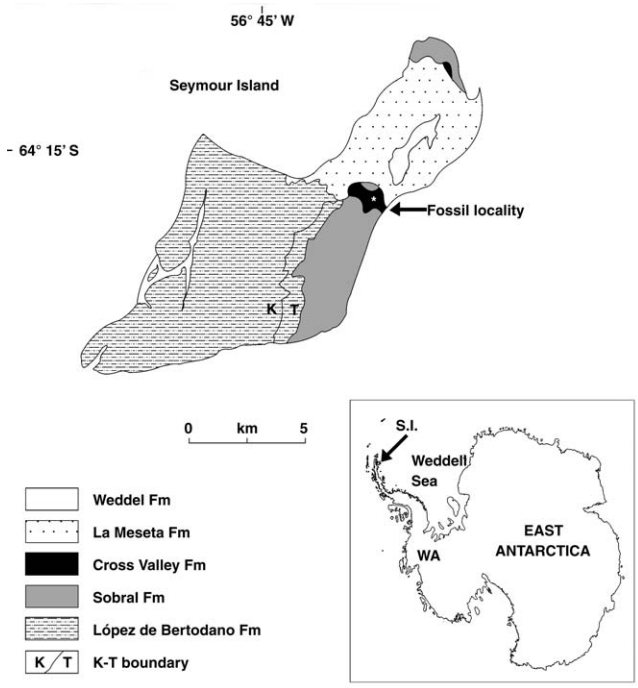

Fig. 1. Geological map of Seymour Island showing its location in Antarctica and the fossil site (asterisk). Abbreviations: K, Cretaceous; S.I., Seymour Island; WA, West Antarctica; T, Tertiary.
Fig. 1. Carte géologique montrant l'emplacement de l'île Seymour en Antarctique ainsi que le site fossilifère (astérisque). Abréviations : K, Crétacé ; S.I., île Seymour ; WA, Ouest de l'Antarctique ; T, Tertiaire.

(Wiman, 1905). The spheniscid status of *Crossvallia unienwillia* nov. gen. and sp. is indisputably indicated by the presence of a robust, flattened, nonpneumatic humerus, and associated fragments of femur and tibiotarsus. The new taxon was recovered from the dark mudstones of the lower part of the Bahía Pingüino Member (Marenssi et al., 1999) in the upper third of the Late Paleocene (Thanetian, 55–56 Myr) (Wrenn and Hart, 1988). Cross Valley Formation (Elliot and Trautman, 1982) on Seymour Island, Antarctica (Fig. 1). The discovery of the large "Cross Valley" penguin confirms the range of the Spheniscidae from the Recent into the Late Paleocene. Previously, the oldest undisputed record of the family was from the late Early Eocene of Antarctica (Myrcha et al., 2002). A "Late Paleocene or Early Eocene protopenguin" from New Zealand was described by Fordyce and co-workers (Fordyce et al., 1986; Fordyce and Jones, 1990) but its relationships within Sphenisciformes are still uncertain.

Nowadays, the Seymour Island penguins (La Meseta Formation, Eocene) comprise one of the most complete records of the group known in the world (Myrcha et al., 2002), and this evidence indicates that the large penguins are restricted to the upper levels (Late Eocene) of this unit. Noteworthy, the large body size of the Cross Valley penguin indicated that large penguins were present in both Late Eocene and Late Paleocene, and lived under dramatically different environmental conditions. The Late Eocene (~10 Myr) was characterized by a lowering global temperatures and concomitant initiation of glaciation on Antarctica; in contrast the Late Paleocene (~2 Myr) was characterized by unprecedented global warming that included the brief Late Paleocene Thermal Maximum (LPTM) event (Zachos et al., 1993). Paleoenvironmental data from southern high latitudes indicate warm marine waters and paleoclimates during the Late Paleocene (Aubry et al., 1998). In this context, the ″Cross Valley″ penguin does not afford a clear example of Bergmann's Rule, which states that homeotherms in colder climates are larger than related taxa in warmer ones.

2. Geological setting

The James Ross Basin (Del Valle et al., 1992) on the northeast continental shelf of the Antarctic Peninsula consists of exposed ? Barremian–Eocene sedimentary rocks deposited in a retroarc setting. The Tertiary section exposed mainly on Seymour Island includes the Late Paleocene Cross Valley Formation and the richly fossiliferous Eocene La Meseta Formation, both of them deposited in incised valley settings. At its type section in the middle part of Seymour Island, the Cross Valley Formation (Elliot and Trautman, 1982) fills a steep-sided valley cut in the Lower Paleocene Sobral Formation and older beds. The width of the "canyon" is 600 m at a maximum and the valley fill consists of more than 120 m of coarse sands and axial mass flows deposits overlain by some 40 m thick post-valley fill finer-grained beds. The base of this unit is a concave-up unconformity oriented in a NW–SE direction with steep, asymmetrical sides. The southern edge dips 45° towards the North while the northern margin plunges 35° to the South. The top of the unit is another unconformity at the base of the La Meseta Formation. The younger beds cut by the basal unconformity are dated as Danian while the oldest sediment covering this units are regarded to late Early Eocene. Dinoflagellates and pollen collected from the upper part of the Cross Valley Formation also suggest a Late Paleocene age for this unit (Askin, 1988; Wrenn and Hart, 1988).

The Cross Valley Formation has been divided into three informal members (Marenssi et al., 1999). The lower Cerro Arañado member comprises coarse-grained pebbly volcaniclastic sandstones with carbonized wood (Tpcv1 and 2 of Sadler, 1988) and it is post-danian in age due to its unconformable boundary with the underlying Sobral Formation. The medium to coarse-grained, bluff-forming volcaniclastic sandstones of the Wiman member transitionally covers the former and comprises Sadler's (1988) Tps5 unit, the "Wiman Formation" (Elliot and Hoffman, 1989) beds and the Tpcv 3–4, being dated as early Upper Paleocene (Askin, 1988). The upper Bahía Pingüino member rests on an erosional surface draped with slide-blocks and covered with dark, homogeneous mudstones with scattered and poorly preserved marine fossil remains like shark and fish teeth, gastropods, bivalves and crinoids. The fossil penguin bones described in this paper were unearthed in situ from a single level few meters from the base of this unit. This lithofacies is in turn sharply overlain by an alternation of medium to fine-grained sandstones

and mudstones containing few pieces of silicified tree trunks and well preserved plant-leaf fossils (Dusén, 1908) dated as Upper Paleocene. The lower part (Cerro Arañado and Wiman members) consisting of coarse-grained volcaniclastics are referred mainly to axial mass-flow deposits (Doktor et al., 1988; Elliot, 1995). The upper third (Bahía Pingüino member) made up of fine to very fine siliciclastic sandstones and mudstones represent sedimentation in very shallow marginal marine to transitional (deltaic) environments developed after most of the relief was subdued.

3. The new material: the "Cross Valley Penguin"

The specimen described in this study is housed in the Museo de La Plata, La Plata, Argentina (MLP). The collections of the MLP and the Museo Argentino de Ciencias Naturales (MACN), Buenos Aires have been used for osteological comparisons with extant and fossil birds. The anatomical terminology follows Baumel and Witmer (1993) and Kandefer (1994).

Order SPHENISCIFORMES Sharpe, 1891.

Family SPHENISCIDAE Bonaparte, 1831.

Subfamily ?ANTHROPORNITHINAE Simpson, 1946.

According to Simpson (1946), the humerus of penguins exhibits distinctive features useful for taxonomic distinction. This author based the subfamilial arrangement of the Sphenisciformes on a traditional systematic studies and it is not supported by any phylogenetic analysis. The spheniscifom from Cross Valley is very similar in its osteology to the Anthropornithinae Simpson but does not correspond well in terms of the absolute and relative size of the representative skeletal elements. *Anthropornis grandis* and *Anthropornis nordenskjoeldi* are similar to the new material in the following features: humerus heavy, sigmoid, width subequal proximally and distally, *fossa pneumotricipitalis* small and not bipartite and shaft-trochlear angle small. The fragmentary nature of the single known specimen of *C. unienwillia*, coupled with the incomplete knowledge of the interrelationships among spheniscids, complicates the assessment of its phylogenetic position within the Anthropornithinae. Moreover, although Simpson was the author of this subfamilial arrangement of the Sphenisciformes, later in his career he was reluctant to use this and other subfamilies. Anyway, the difference in age of about 21–22 Myr between the deposits of the Submeseta Allomember (where *A. nordenskjoeldi* was exhumed) and those of Cross Valley, and the high disparity between the paleoenvironmental conditions where these penguins lived, might further justify ultimate placement of the spheniscifom from Cross Valley in a new subfamily.

Crossvallia nov. gen.

Diagnosis: Only species of the genus, therefore same diagnosis as for species.

Type species: *C. unienwillia* nov. gen., nov. sp.

Etymology: *Crossvallia* in reference to the type locality. Feminine in gender.

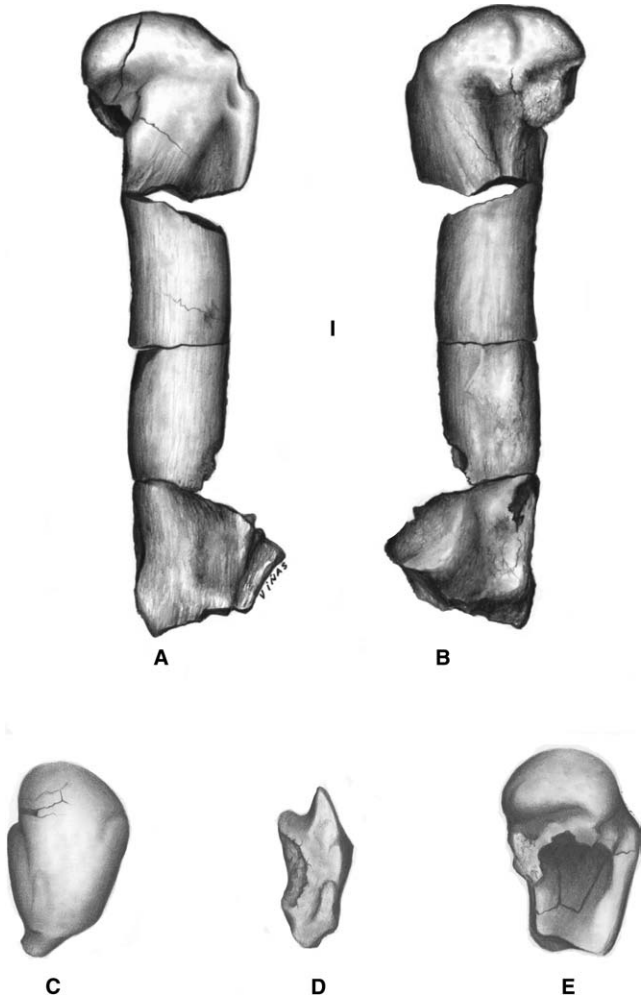

Fig. 2. Right humerus of *Crossvallia unienwillia* nov. gen. and sp. MLP 00-I-10-1, **A**, caudal view; **B**, cranial view; **C**, proximal view of head; **D**, detail of distal end of humerus; **E**, detail of proximal end of humerus in cranial view. Scale bar = 1 cm.

Fig. 2. Humérus droit de *Crossvallia unienwillia* nov. gen. et sp. MLP 00-I-10-1, **A,** vue caudale ; **B**, vue crâniale ; **C,** vue proximale de la tête ; **D**, détail de l'extrémité distale ; **E**, détail de l'extrémité proximale. Échelle = 1 centimètre.

Crossvallia unienwillia nov. sp.

Figs. 2 and 3.

Diagnosis: The following diagnosis is restricted to the humerus (Fig. 2). It is a large, but not the largest known, fossil penguin humerus. Therefore, it corresponds to the Group IV of Wiman (1905). Humerus heavy, slightly curved, width of shaft almost uniform from distal end of *facies musculi pectoralis* to proximal border of insertion of *M. brachialis*, similar to that found in members of the Anthropornithinae. Different from all living penguins by having the *fossa pneumotricipitalis* relatively small and not bipartite and the shaft-trochlear angle small (similar to *Paraptenodytes*, *Anthropornis*, *Delphinornis* and *Pachydyptes*). Differs from that of *A. nordenskjoeldi* in having the s*ulcus musculus humerotricipitalis* broad, and the *incisura capitis* short and shallow. Differs from the humerus of *A. grandis* in having a head relatively more compressed. The *impressio coracobra-*

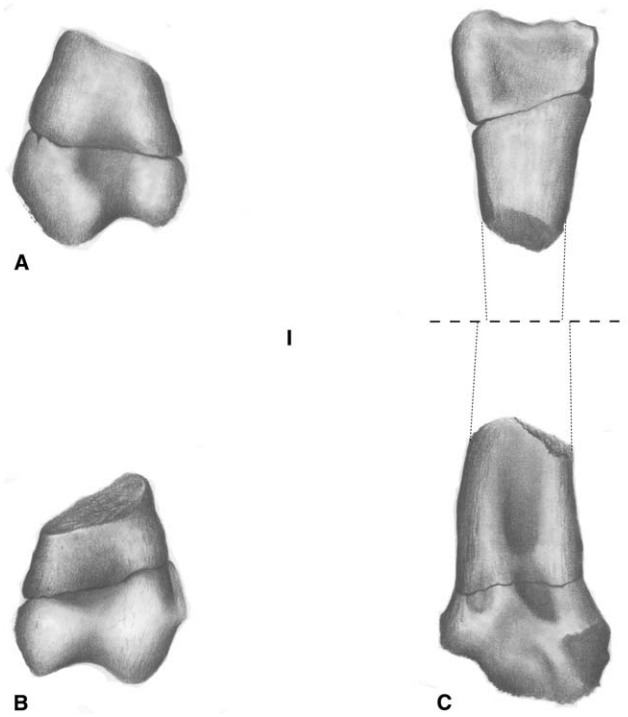

Fig. 3. *C. unienwillia* nov. gen. and sp. MLP 00-I-10-1. Distal end of right femur in **A**, cranial view and **B**, caudal view, **C**, right incomplete tibiatarsus in cranial view. Scale bar = 1 cm.
Fig. 3. *C. unienwillia* nov. gen. et sp. MLP 00-I-10-1. Fémur droit, partie distale, **A**, vue crâniale, **B**, vue caudale, **C**, tibiatarse droit incomplet, vue crâniale. Échelle = 1 centimètre.

chialis cranialis (*facies musculi pectoralis*) arises more distally than in *A. nordenskjoeldi* and *Palaeeudyptes* sp.

Distinguished from all other Palaeeudyptinae in having an angulation of anterior margin weakly differentiated that does not well define the proximal end of the origin of the *m. brachialis internus*, and insertion of *m. brachialis internus* not well manifest. The angle between the midline of the shaft and the tangent to the trochlear facets is certainly small (*circa* 32°). Small angles were indicated by Simpson (1946) for species belonging in Anthropornithinae.

Etymology: *unienwillia* from the South American indigenous Mapuche language (*Mapudungum*-Spanish). Adapted by Alberto Trivero, Mondovi, Italy, 1998. *Unien*, wing, and *Willi*, south.

Holotype: MLP 00-I-10-1, right incomplete humerus, distal end of right femur, and incomplete right tibiatarsus.

Horizon and locality: Dark mudstones of the lower part of the Bahía Pingüino Member in the upper third of the Late Paleocene Cross Valley Formation, Seymour Island, Antarctica. 64° 15′ 50″ S, 56° 40′ 0″ W.

Description and comparisons: Overall, the bones are of an individual larger than the largest extant penguin species, *Aptenodytes forsteri* but smaller than the giant *Anthropornis* sp. The humerus is eroded, lacking a small part of the distal end and the area around the *fossa pneumotricipitalis*. Size and proportions are nearly the same as those of the humerus referred to *A. grandis* (Wiman) by Kandefer (1994) and *Arthrodytes grandis* that Ameghino recognized from Patagonia, and are larger than *Arthrodytes andrewsi* (Ameghino) from Patagonia (Fig. 4). According to Simpson's suggestion the total size of the penguin is estimated to have been between 127.5 and 142.5 cm.

The width of the shaft is almost uniform from the distal end of the *facies musculi pectoralis* to the proximal border of the insertion of the *m. brachialis*. The angular prominence on the preaxial border of the humerus (upper limit of the origin of the *brachialis internus*) is definitely present but is not larger than in recent penguins. The head of the humerus is far less solid and bulky than that referred to *A. grandis* (Wiman) by Kandefer (1994). An important character, the angle between the midline of the shaft of the humerus and the tangent to the trochlear facets, was a difficult measurement to take and is consequently open to considerable error; however, the angle is certainly small.

Only the distal femur (Fig. 3A, B) is conserved and even though both condyles are eroded, it can see that the distal width of the epiphysis is greater than that of the shaft. Furthermore, the distal end is relatively compressed in distal view. The *impressio lig. cruciati cranialis* is developed a deep depression, pit-shaped, located close to the *condylus lateralis* which is the condition in other fossil and extant sphenisciforms. The *condylus lateralis* have greater distal extension than the other condyle.

Unfortunately, only a poorly preserved tibiatarsus (Fig. 3C), heavily abraded, is conserved. It is currently preserved in two parts that do not articulate. This is a dense bone, with a thick layer of compact bone and a very narrow medullary cavity. In cross section the tibiotarsal shaft appears nearly solid, but less than the condition that show several fossil penguins such us *Paraptenodytes antarcticus* and commented on in Simpson (1946). The little section of the conserved diaphysis, is strongly compressed anteroposteriorly, a feature that have been noted for other fossil penguins, stronger than in extant penguins. Furthermore, the distal tibiotarsal shaft is strongly compressed, much more than in any of the living penguins compared or in the fossil taxa of which there are available materials. The *sulcus extensorius* is relatively broad and slightly more medially located than in extant penguins, a condition shared with the penguin recently described from the Paleogene of Tierra del Fuego (Argentina) and with the Procellariiformes (Clarke et al., 2003). The distal end of this bone is deflected medially. No further morphology could be discerned.

Measurements (in mm): Humerus: total length ca. 140, proximal width 49.4, width of midshaft 24. Tibiatarsus: distal width (preserved) 34.33. Femur: distal width (preserved) 40.7, distal depth 24.44.

4. New observations on the evolution of penguin size

Body size is extremely important in understanding the adaptation of an organism to its environment. Parameters such as physiology, reproductive and developmental strategy, lon-

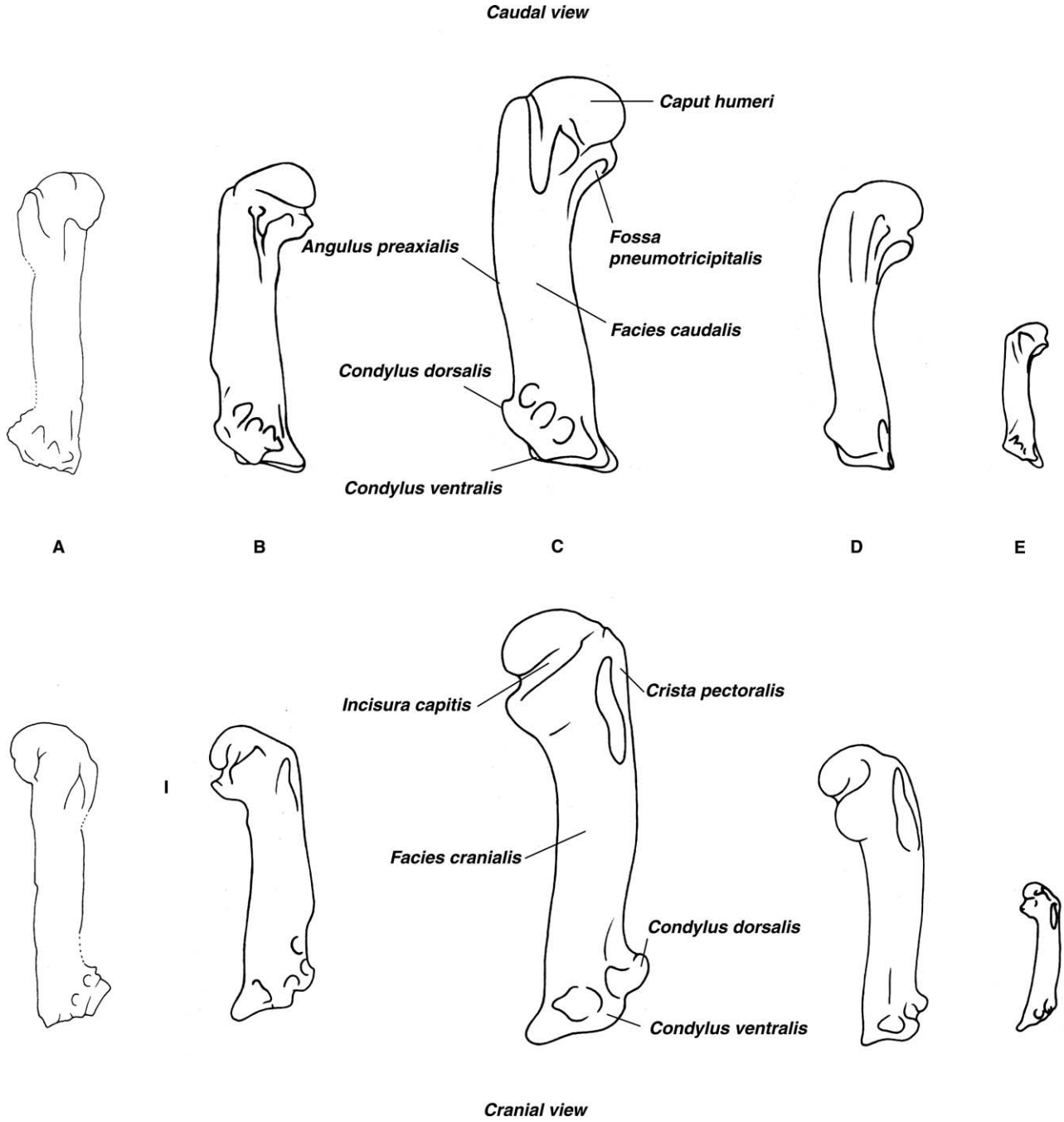

Fig. 4. Humeri of fossil and extant penguins. Comparative series in caudal and cranial views. Drawings have been reversed where necessary. **A**. *C. unienwillia* nov. gen. and sp., MLP 00-I-10-1, Cross Valley Formation (Upper Paleocene), Seymour Island, Antarctica; **B**. *Arthrodytes grandis*, MLP M-606 (cast of the original from MACN), San Julián Formation (Late Eocene–Early Oligocene), San Julián, Chubut, Argentina; **C**. *A. nordenskjoeldi*, MLP 93-X-1-4, La Meseta Formation (Eocene), Seymour Island, Antarctica; **D**. *Palaeeudyptes klekowskii*, MLP 93-X-1-3, La Meseta Formation (Eocene), Seymour Island, Antarctica; **E**. *Spheniscus magellanicus*, MLP uncatalogued (OR 478), Recent, Puerto Madryn, Chubut, Argentina. Scale bar = 1 cm.

Fig. 4. Série comparative d'humérus de manchots fossiles et actuels en vues caudale et crâniale (renversés par rapport à l'original). **A**. *C. unienwillia* nov. gen. et sp., MLP 00-I-10-1, Formation Cross Valley (Paléocène supérieur), île Seymour, Antarctique ; **B**. *Arthodytes grandis*, MLP M-606 (copie de l'original du MACN), Formation San Julián (Eocène supérieur–Oligocène inférieur), San Julián, Chubut, Argentine ; **C**. *A. nordenskjoeldi*, MLP 93-X-1-4, Formation La Meseta (Eocène), île Seymour, Antarctique ; **D**. *Paleeudyptes klekowskii*, MLP 93-X-1-3, Formation La Meseta (Eocène), île Seymour, Antarctique ; **E**. *Spheniscus magellanicus*, MLP non catalogué (OR 478), actuel, Puerto Madryn, Chubut, Argentine. Échelle = 1 centimètre.

gevity, social organization, home range, and community structure are crucial to survival. As suggested by Jadwiszcak (2001), occurrence of large-bodied penguins seems to be controlled by environmental conditions. This evolutionary pattern has been documented in the Eocene of Antarctica and, later, in the development of the extant, large penguins (i.e. King, *Aptenodytes patagonicus*, and Emperor, *Aptenodytes forsteri*). The occurrence of *C. unienwillia* not only proves that the family Spheniscidae was well differentiated by the end of the Paleocene (Thanetian), but also that large-bodied

penguins were present close to the time of the origin of the group. Nevertheless, the Thanetian occurrence of the Cross Valley form raises some questions concerning the timing of spheniscid origins and the biogeography of the clade.

Until recently the group was believed to be temporally limited to the Late Eocene–Recent. New investigations on the lower strata of the La Meseta Formation have produced penguins of late Early Eocene age (Myrcha et al., 2002). The recognition of MLP 00-I-10-1 as a spheniscid, now extends their range into the Paleocene.

Regarding the origin of this group, penguins must have had an ancient Gondwanan origin, perhaps as old as Cretaceous (Cooper and Penny, 1997; Hedges et al., 1996), and may have populated Antarctica at that time. Lines of evidence such as the recent discoveries of modern bird lineages in the Late Cretaceous of peninsular Antarctica (Case, 1992; Noriega and Tambussi, 1995) do not provide any positive evidence supporting a delayed evolutionary transformation. An alternative hypothesis is that most modern bird orders, including penguins, evolved over approximately 5–10 Myr after the K/T extinction (Feduccia, 1995, 2003; see also Clarke et al., 2005). This statement implies a rapid adaptation of penguins to a marine realm, involving loss of flight and accelerated changes in physiology and form of the body. The nonpneumatized skeleton and flattened heavy wing bones are adaptations for swimming (flying underwater). The mode of underwater flight of penguins is clearly one of their most important adaptations to a subaqueous realm (Clark and Bemis, 1979), and *Crossvallia* reveals that the flipper was already flattened and heavy-boned for this specialized function.

It is commonly believed that the distribution of living and fossil penguins is strongly linked to cool temperate waters, and that the origin of this group was triggered by water-cooling resulting from the evolution of modern circulation patterns in the Southern Ocean (Fordyce and Jones, 1990) (Fig. 5C). It seems likely that many aspects of penguin evolution were governed by changes in the oceans. The rise of *C. unienwillia* predated the final break up between Antarctica and South America, and consequently the circum-Antarctic current had not developed (Fig. 6A) which supports Simpson's contention. As a result of the separation of these two continents, a pronounced change in the oceanographic regime in the Southern Ocean occurred at about Middle Eocene time (Latimer and Filippelli, 2002).

Based on the Antarctic evolutionary history of penguins, there is no morphological evidence that *C. unienwillia* was ancestral to any of the Eocene species. *C. unienwillia* is known only from the Paleocene; however, it is not clear whether this disappearance is actually an extinction event at the Paleocene/Eocene boundary or whether this penguin survived elsewhere in marine environments into the earliest Eocene. The oldest marine sediments that postdate the Paleocene/Eocene boundary in Seymour Island are no older than late Early Eocene (Marenssi et al., 1998). This means that there is a gap in the marine sedimentary record of as much as 3 Myr immediately after the Paleocene/Eocene boundary. New species of penguins are therefore not known from the area until the late Early Eocene when they are preserved in the Acantilados Allomember (~52–54 Myr) of the La Meseta Formation. These birds do not seem to have been derived from *Crossvallia*. Some lines of evidence supporting this hypothesis are: (1) the large size and morphology of *C. unienwillia*, (2) the warm environmental conditions where it lived, (3) the recent discovery of small penguins of Early Eocene age in strata of La Meseta Formation, and (4) the extinctions and turnover of other animals linked to the Paleocene/Eocene transition.

Whatever the factors driving the process of extinction of the *C. unienwillia* lineage, changes in deep-sea circulation, changes in the global eustatic level (lowering of the sea level, Fig. 5D), increased $CaCO_3$ corrosiveness, increased temperatures, decreased oxygenation, and changes in the pattern of marine productivity are important ultimate causes of the extinctions and turnover at the Paleocene/Eocene boundary (Aubry et al., 1998).

Evidence of the distribution of body size is anchored in the well-known stratigraphic record of spheniscids through the Early to Late Eocene in the marine sediments of the La Meseta Formation (~52–34 Myr) (Fig. 5A, B) (Case, 1992), which overlies the Cross Valley Formation on Seymour Island. This record may accurately reflect the distribution of sizes in penguins throughout the Eocene. Interestingly, the lower levels of the La Meseta Formation (Ypresian, late Early Eocene Acantilados Allomember, ~52–54 Myr) only recently yielded small indeterminate penguins, whereas the highest levels (Priabonian, Late Eocene, *Cucullaea* II and Submeseta Allomembers, ~34–36 Myr) document a major taxonomic and body size diversity with 10 species co-occurring sympatrically (Fig. 5A). The Eocene/Oligocene transition was characterized by a sharp climatic deterioration linked to the progressive separation of South America and Antarctica and the strengthening of the Circum-Antarctic Current (Fig. 6B). The effect of these changes in the Antarctic marine fauna is unknown, but the disappearance (extinction?) of *A. nordenskjoeldi* and several other large Eocene penguins broadly coincides with these events.

5. A new scenario for penguin evolution

Direct evidence of the climate in the Seymour Island area during the deposition of the Paleogene units comes from two main sources: paleoecological studies of fossil plants and geochemical analysis of sediments and clay mineralogy. The Cross Valley paleoflora (Case, 1988) comes from strata a few meters above the penguin-bearing horizon. This flora was interpreted to document paratropical forests growing in a warm, humid climate (Dusén, 1908). On the other hand, geochemistry of sediments and analysis of the clay minerals provide an independent way to estimate "source" area climate. The Cross Valley data suggest a continuous climate of very warm, wet, non-seasonal weather during the Late Pale-

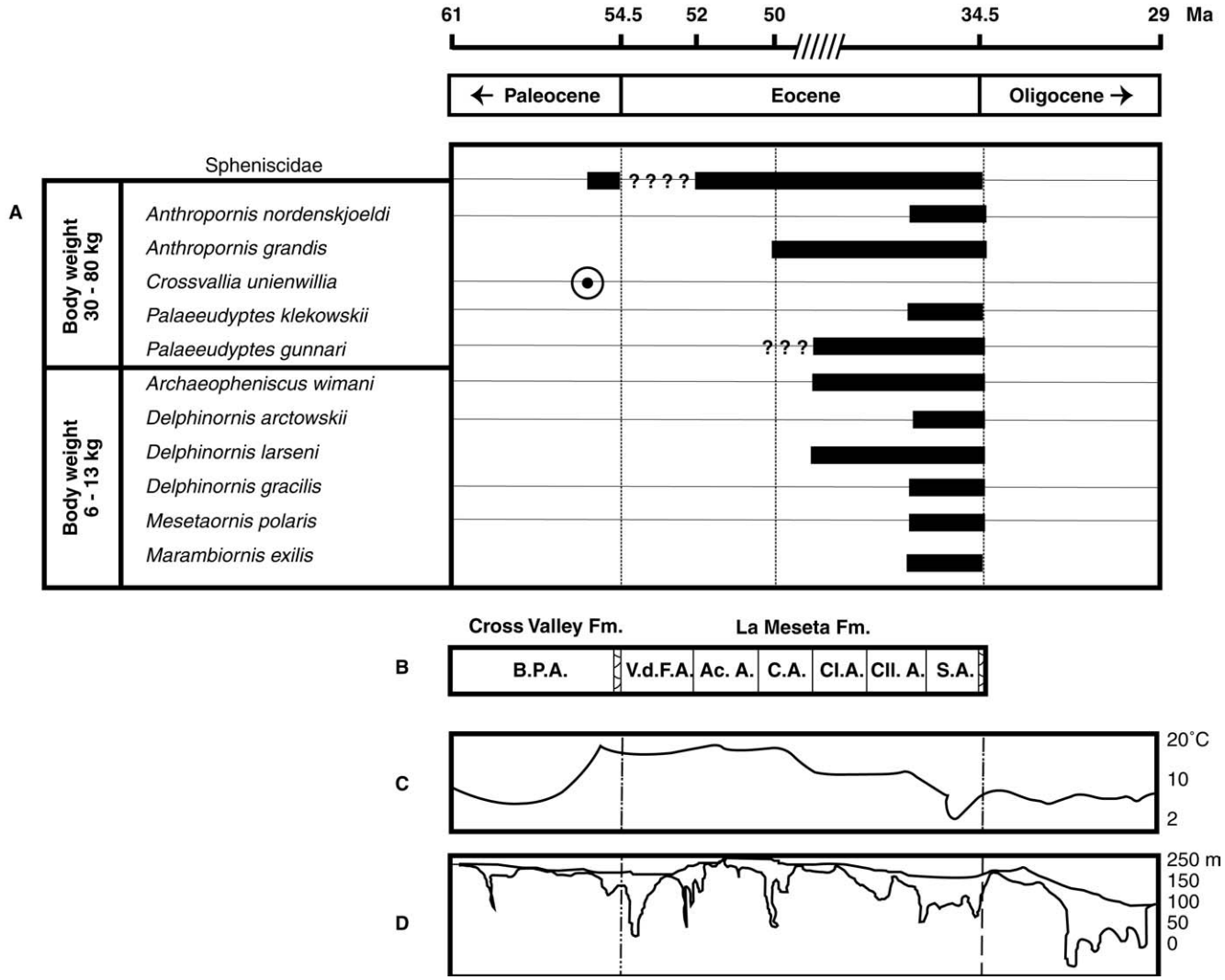

Fig. 5. Relationships between the evolutionary history of Antarctic fossil penguins **A**, stratigraphy **B**, temperature **C**, and sea level **D** at high latitudes during the Cenozoic. The temperature curve is for surface waters. Time scale is according to Berggren et al. (1995). Abbreviations: Ac. A., Acantilados Allomember; B.P.A., Bahía Pingüino Allomember; C.A., Campamento Allomember; CI.A., *Cucullaea* I Allomember; CII.A., *Cucullaea* II Allomember; S.A., Submeseta Allomember; V.d.F.A., Valle de las Focas Allomember. Heavy lines to the right of penguins names indicated known stratigraphic range. Body masses were estimated following Jadwiszcak (2001). Data from eustatic sea levels after Haq et al. (1987).

Fig. 5. Relations entre les manchots fossiles antarctiques pendant leur histoire évolutive **A**, stratigraphie **B**, température **C**, et niveau marin **D** en hautes latitudes durant le Cénozoïque. Les courbes de température correspondent à des eaux superficielles. L'échelle du temps est celle proposée par Berggren et al. (1995). Abréviations : Ac.A, Allomembre Acantilados ; B.P.A., Allomembre Bahía Pingüino ; C.A., Allomembre Campamento ; CI.A., Allomembre *Cucullaea* I ; CII.A., Allomembre *Cucullaea* II ; S.A., Allomembre Submeseta ; V.d.F.A., Allomembre Valle de las Focas. Les grosses lignes à droite des noms des manchots indiquent l'enregistrement stratigraphique connu.

ocene that may have persisted until the early Middle Eocene on Seymour Island (Gandolfo et al., 1998). There are no direct Paleocene paleotemperature data from the marine realm of the Antarctic Peninsula; but results from deep-water South Atlantic benthic foraminifera indicate a mid-Paleocene temperature low, followed by an Early Eocene maximum with bottom water temperatures of 12 °C (Dingle et al., 1998; Zachos et al., 1994) (Fig. 5C).

The paleoenvironmental reconstruction derived from the study of the fauna associated with the new fossil penguin and the geological and stratigraphical data supports the model of a moderately well circulated, warm ocean (Aubry et al., 1998) for the Late Paleocene in southern high latitudes. In this paleoclimatic context, the Cross Valley penguin does not afford a clear example of Bergmann's Rule, in which homeotherms in colder (= high latitudes) climates are larger than related taxa in warmer climates (= lower latitudes) in order to conserve heat by creating smaller surface area to volume ratios. The record of a large penguin living in a warm environment challenges the scenario in which large penguins, e.g. *A. nordenskjoeldi* and *Palaeeudyptes klekowskii*, lived exclusively in cool temperate settings during the Late Eocene in the La Meseta Formation. The increase in body size in the evolution of penguins might have been acquired independently of the climatic conditions prevailing at the time.

The exciting new discovery of a penguin in strata 55 Myr old in the northern Antarctic Peninsula still resolves few of the puzzling questions about the origin and distribution of

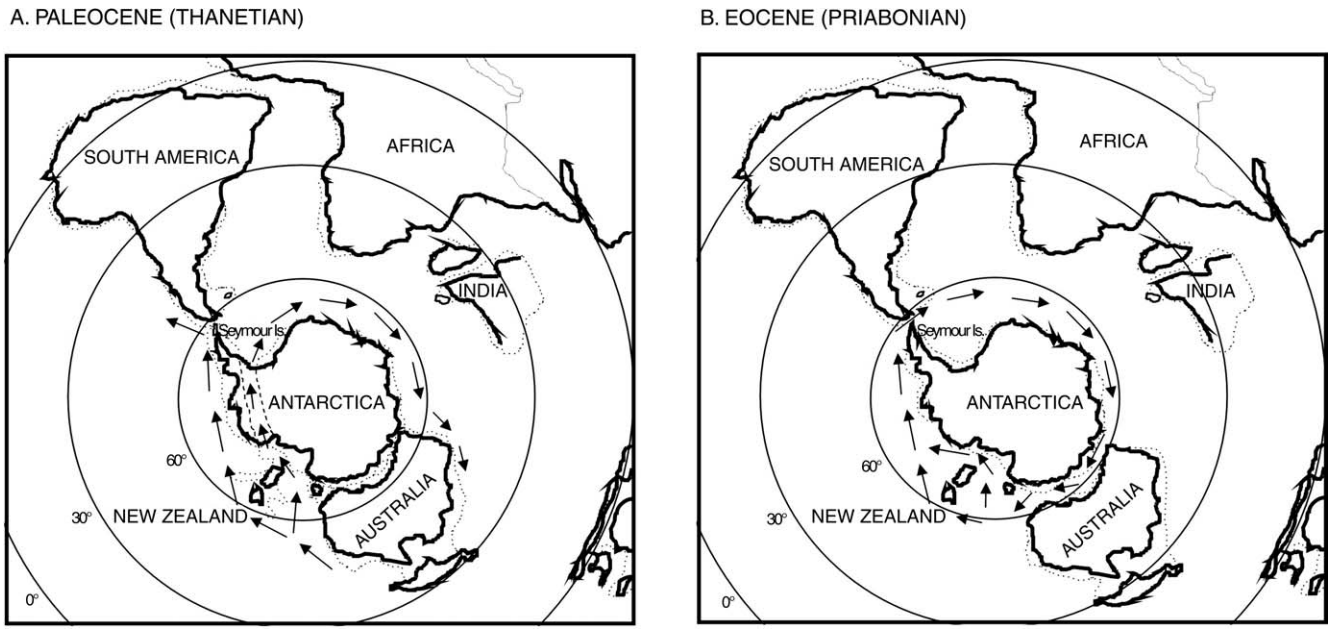

Fig. 6. Antarctic oceanic circulation pattern inferred for the Paleogene. **A**. Late Paleocene (Thanetian) and **B**. Late Eocene (Priabonian). Dotted line denotes continents; heavy black line, continental shelves to present. Relative position of continents after Lawver et al. (1992).
Fig. 6. Schémas hypothétiques de circulation océanique antarctique durant le Paléogène. **A**. Paléocène supérieur (Thanétien) ; **B**. Eocène supérieur (Priabonien). Les lignes en pointillés signalent des continents et les lignes pleines les bordures des continents actuels (d'après Lawver et al., 1992, modifié).

these birds. More extensive collecting of fossils in the Paleocene and older units of the Seymour Island area should be made to test or modify the hypothesis proposed herein, or to create new ones that more fully describe the processes involved in evolution of penguins and their response to climate changes Simpson, 1975.

Acknowledgements

The authors thank R. Feldmann and C. Schweitzer (Kent University) for the critical revision and help in the English of the original manuscript. A. Viñas skillfully prepared Fig. 2. Comments by the referees, E. Fordyce and C. Mourer-Chauviré, improved our manuscript to whom we acknowledge. The research was directly supported by the Instituto Antártico Argentino and National Geography Society (grants to S.A.M.). To Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET) for continuing support.

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