

Re-evaluation of the fossil penguin *Palaeudyptes gunnari* from the Eocene Leticia

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Formation, Argentina: additional material, systematics and palaeobiology

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Preferred running head: *Palaeudyptes gunnari* from the Eocene Leticia Formation,

Argentina

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CAROLINA ACOSTA HOSPITALECHE and EDUARDO OLIVERO

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ACOSTA HOSPITALECHE, C. & OLIVERO, E., 2015. Re-evaluation of the fossil penguin *Palaeudyptes gunnari* from the Eocene Leticia Formation, Argentina: additional material, systematic and palaeobiology. *Alcheringa* xx, xx-xx.

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Eocene penguins are known mostly from Antarctic specimens. A previously documented partial skeleton consisting of a pelvis, femur, tibiotarsus and fibula, from the middle Eocene Leticia Formation, Tierra del Fuego Province, Argentina has been prepared and re-described. Re-analysis favours an assignment to *Palaeudyptes gunnari*, a species widely recorded from the Eocene of Antarctica. A new isolated coracoid belonging to an indeterminate species was also studied. It reveals new information about the diving kinematics and swimming abilities. Paleobiological attributes and morphology of the fossils indicate that both specimens belonged to large penguins with poor diving capability and wing propulsion systems similar to those of extant species. The penguin remains are the only vertebrate remnants known from the Leticia

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Formation and provide important insights into the relationships of South American and Antarctic penguins during the Paleogene. The presence of *Palaeudyptes* in Argentina supports an Eocene connection between the South American and Antarctic penguin faunas.

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Key words: Fossil penguin, *Palaeudyptes gunnari*, Eocene, South America, Antarctica.

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RECENT studies strongly suggest that the South American and Antarctic avifaunas are closely related (Jadwiszczak 2011, Acosta Hospitaleche *et al.* 2013). Establishment of the Drake Passage and development of the Circumpolar Antarctic Current were events that influenced penguin evolution. A major radiation of species during the Eocene resulted in a diverse Antarctic fauna that probably expanded its range towards the South American coasts (Acosta Hospitaleche *et al.*, 2013).

Taxonomic revision of the fossil penguins from Antarctica by Tambussi *et al.* (2006) and Jadwiszczak (2006) provided a new and more complete context for the analysis of Eocene penguins from Argentina. In addition, the discovery of associated skeletons (Acosta Hospitaleche & Di Carlo 2010, Acosta Hospitaleche & Reguero 2010, 2014), as well as the description of new Eocene species from Peru (Clarke *et al.* 2007, 2010) and the presence of unequivocal Antarctic species in the south of Chile (Sallaberry *et al.* 2010) have richly increased knowledge of this avifauna.

Here, we re-analyze CADIC P 21, which was studied previously by Clarke *et al.* (2003), and compare it with several recently described fossil penguin taxa to better understand their interrelationships. An isolated coracoid, CADIC P 22, from the same locality is also documented for the first time. The palaeobiological implications of both specimens are discussed.

Material and methods

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The partial associated skeleton (CADIC P 21) and coracoid (CADIC P 22) discussed here are permanently housed at the Centro Austral de Investigaciones Científicas (CADIC) in Ushuaia, Tierra del Fuego Province, Argentina. Direct comparisons were made with the fossil penguin collections in the Museo de La Plata (MLP), Argentina; Museo Nacional de Historia Natural (SGO-PV), Chile; Museo de la Universidad de San Marcos (MUSM), Lima, Peru; Naturhistoriska Riksmuseet (Nr), Sweden; and the Natural History Museum (NHMUK), United Kingdom, including casts of Australian specimens of *Anthropornis* and *Pachydyptes* housed in the Nr and NHMUK (Appendix 1).

Anatomical terminology follows Baumel *et al.* (1993) for osteology and musculature. Measurements were taken with a Vernier Caliper of 0.01 increments and are given in millimetres.

Estimations of palaeobiological parameters are based on the criteria of Jadwiszczak (2001) for body mass and body length, and Watanuki & Burger (1999) for dive capabilities. Interpretation of femur and tibiotarsus musculature is based on Schreiweis (1982).

Geological setting

The geological setting of the Leticia Formation was documented ~~in by~~ Clarke *et al.* (2003). This is briefly summarized here, together with new information obtained during the last decade of work. The Upper Cretaceous–Paleogene sedimentary rocks of the Austral foreland ~~basin~~ Basin (Fig. 1) have a complex stratigraphic history, reflecting their origin as syntectonic clastic wedges formed during the ~~northernly~~ northerly directed contractional deformation of the Fuegian Andes (Torres Carbonell *et al.* 2011). Most of the strata are deep-marine in origin, either in foredeep or wedge-top sub-basins Basins (Torres Carbonell & Olivero 2012). In contrast, the vertebrate-bearing Leticia Formation (Figs. 2, 3) represents a shallow-marine unit deposited during the

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earliest evolutionary stages of the wedge-top María Luisa sub-basin (Torres Carbonell *et al.* 2009). The Leticia Formation is mostly exposed on the Atlantic shore of Tierra del Fuego Island within the thrust-fold belt of the Fuegian Andes, immediately south of the northern boundary of the thrust front and to the north of the transform boundary between the Scotia and South American plates (Fig. 1).

Preceding the upper-late middle Eocene Leticia Formation was an episode of regional uplift and subaerial erosion that followed deposition and deformation of lower Eocene turbidites belonging to the Punta Torcida Formation. At the Punta Torcida-Cabo Campo del Medio anticline (Figs. 1, 2), the Leticia Formation filled a high-relief erosional surface developed on the Punta Torcida Formation (Fig. 3). This surface was probably incised during subaerial erosion that produced a valley-shaped geometry. The sedimentary filling, which is much thicker along the axis of the incision, is composed of three main facies associations that clearly lap on the margin of the incised surface (Fig. 3): (1), a lower package (only observed at the Punta Torcida section) of massive, thick-bedded sandstones, capped by intercalated thin-bedded heteroliths that bear localized beds with herringbone and ripple cross-lamination; (2), a thick, middle package (ca. 320 m thick), also recorded mostly at Punta Torcida and dominated by thoroughly bioturbated, fine-grained silty sandstones; and (3), an upper package, present in both sections, of lenticular, channelized sandstones and fine-grained conglomerates. The filling of the incised surface represents a transgressive-regressive cycle (Fig. 3), with shallow marginal marine deposits at the base and top, and intercalated offshore marine sediments in the middle part of the Leticia Formation (Olivero *et al.* 2008, Torres Carbonell & Olivero 2012).

The site yielding CADIC P 21 and CADIC P 22 is located near the top of the offshore very fine silty sandstones of package of the Leticia Formation (Fig. 3). Based on planktonic foraminifera and calcareous nanoplankton, the age of the Leticia Formation is bracketed between

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Comentario [Edit1]: Be careful to avoid mixing chronostratigraphic and geochronologic concepts. If you are talking about "upper middle" then you are referring to stratigraphic position (chronostratigraphy); if you are referring to "episodes" then you are talking about time (geochronology), in which case you should use "late middle" – check entire text.

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40 and 42 Ma (late middle Eocene Bartonian), and most probably close to 41.2 Ma (Malumián & Olivero 2006). This is consistent with age determinations for both the underlying Punta Torcida Formation (early Eocene) and overlying Cerro Colorado Formation (late middle Eocene–latest Eocene: Malumián & Olivero, 2006). This is also compatible with the upper stratigraphic interval equivalent to the Submeseta II Allomember of the Submeseta Formation (formerly Telm 6–Telm 7 or Submeseta Allomember) ~~in of~~ the La Meseta Formation, Seymour Island, Antarctica; this is characterized by the highest diversity of fossil penguins in Antarctica (Acosta Hospitaleche *et al.* 2013). The Telm 6–Telm 7 interval yielded strontium isotope ages ranging from 41 to 34 Ma (Ivany *et al.* 2008), implying that the fossil-bearing bed of the Leticia Formation might be correlated with part of this interval.

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Systematic palaeontology

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Order SPHENISCIFORMES Sharpe, 1891

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Family SPHENISCIDAE Bonaparte, 1831

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Palaeudyptes Huxley, 1859

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Type species. Palaeudyptes antarcticus Huxley, 1859

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Included species. Palaeudyptes antarcticus Huxley, 1859, *P. gunnari* (Wiman, 1905), *P.*

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marplei Brodkorb, 1963, *P. klekowsii* Myrcha, Tatur & Del Valle, 1990.

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Palaeodyptes gunnari (Wiman, 1905) (Fig. 4)

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Material. Partial skeleton including a portion of the pelvis, nearly complete right femur, right tibiotarsus and fibula.

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Provenance. Leticia Formation (Bartonian), Punta Torcida fossil locality, Tierra del Fuego Province, Argentina.

Diagnostic characters. The following character combination supports assignment to *Palaeodyptes*: shaft of the femur straight and cylindrical; strong caput femoris, crista trochanteris well developed but not projected proximally; impressio ilirotrochantericae well defined; crista supracondylaris medialis sharp and conspicuous; sulcus intercnemialis with parallel margins in the tibiotarsus. Acosta Hospitaleche & Reguero (2010, 2014), Jadwiszczak & Acosta Hospitaleche (2013) and Acosta Hospitaleche (2014) compared the Patagonian specimens with *P. gunnari* and *P. klekowskii* from Antarctica. Based on these works and the small size of CADIC P 21 we propose referral to *Palaeodyptes gunnari*.

Comentario [Edit5]: Is this an emended diagnosis – if so, say so. If not, and the published diagnosis is easily accessible, then there is no need to include a diagnosis. Moreover, much of what is written here belongs in the “Remarks” on the taxon.

Comentario [C6]: It is not an emended diagnosis. These are characters used for systematic determination. In fact, it is not necessary, but we included this title on request of one of the reviewer.

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Description and comparisons. The pelvis (Fig. 4A) could not be fully extracted from the host matrix, but the medial surface of the left side of the pelvis is fully exposed. It was misinterpreted in the original description (see Clarke *et al.*, 2003). It clearly represents the postacetabular portion of the pelvis including the partial dorsal limit of the foramen acetabuli, the

antitrochanter, the foramen ilioischadicum, the ala ischii and the ala postacetabularis ilii.

Unfortunately, the pubis is missing. As indicated by Clarke et al. (2003), the sutures between the synsacrum and ilium have remained open, as in *Perudyptes* and extant penguin species (Ksepka & Clarke 2010, fig. 7). Small scars running cranio-caudally mark the contact between the ilium and the processus transversus of the sacral vertebrae.

Although only the dorsal margins of the foramina are preserved, it seems that the foramen ilioischadicum was larger than the foramen acetabuli. The ala ischii is robust and lacks its distal end.

The femur (Fig. 4B–D) is almost complete permitting accurate measurement. Its robustness is similar to *Palaeudyptes*, but the shaft is more slender than in *Kairuku*. The diaphysis is straight (Fig. 4B, E), as in *Inkayaku* (Clarke et al. 2010, fig. 1) and *Perudyptes* (Ksepka & Clarke 2010, Fig. 8), and cylindrical like *Palaeudyptes gunnari* (Acosta Hospitaleche & Reguero 2010, fig. 4) and *P. klekowskii* (Acosta Hospitaleche & Reguero 2014: Fig. 7); the medial margin of the diaphysis is otherwise slightly curved in *Archaeospheniscus wimani* and *Kairuku* (Jadwiszczak 2006, fig. 12; Ksepka et al. 2012, fig. 6). The linea intermuscularis cranialis (Fig. 4B) is little marked extending over slightly more than half of the shaft, as occurs in *Kairuku* and *Palaeudyptes*. The crista trochanteris is relatively well developed, although it is not projected proximally as in *Paleudyptes* and *Archaeospheniscus*; in *Kairuku*, *Inkayaku* and *Perudyptes* the trochanter extends proximally beyond the capitis femoris. The impressiones iliotrochantericae are well defined as in *P. klekowskii*.

As in *Kairuku* (according to Ksepka et al. 2012) and *P. klekowskii*, the insertions of the m. iliofemoralis externus, m. iliotrochantericus caudalis, m. iliotrochantericus cranialis and medialis are conspicuous (Fig. 4B–D). Between these muscle insertions, the m. obturator leaves a circular

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rugosity (Fig. 5B). Distally, there are two large attachment scars for the m. gastrocnemialis lateralis and the flexor perforates digiti IV (Fig. 5D). In medial view, the pars medialis of the m. gastrocnemiales, and more proximally the m. puboischiofemorales have also left identifiable traces (Fig. 5C).

The caput femoris is strong (Fig. 4B–D) as in *P. klekowi*, whereas it is weaker in *Archaeospheniscus*. The facies articularis acetabularis is wide and large, as in other Paleogene penguins, the proximally located fovea ligamentaris capitis is wide and deep. The facies articularis antitrochantericae is slightly concave as in *Perudyptes*, whereas in Patagonian Miocene taxa and modern species it is strongly concave. This concavity is also strong in *Archaeospheniscus lowei* (OM C 47.27 of Simpson 1971) based on previous comparisons with CADIC P 21 (Clarke *et al.* 2003). As in other diving birds (e.g., loons), the proximal epiphysis is cranio-caudally compressed (Fig. 4J), and is a character reflecting foot-based propulsion (see Acosta Hospitaleche & Gelfo, in press).

Strong muscular insertions (Fig. 4D) for the m. obturator, the m. ischiofemorales and the m. iliofemorales internus are located on the caudal surface, distal to the trochanter femoralis (Fig. 5B). Insertion of the m. obturator is also expressed in *Kairuku*, where the scar is similarly flat; the well-marked impression obturatoriae are parallel to the shaft.

The conspicuous linea intermuscularis caudalis is elevated relative to the facies caudalis at the point where it meets the crista supracondylaris medialis (at two thirds of the proximal end of the bone), thus forming a blunt tubercle (Fig. 4D). A similar structure was reported in *Perudyptes*, but interpreted as the intersection between the crista supracondylaris medialis and the crista supracondylaris lateralis; although the latter is not present in CADIC P 21. The crista supracondylaris medialis is broken in its distal half, but the preserved portion is sharp and conspicuous, as in *Palaeudyptes*.

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The distal epiphysis is diagenetically deformed (Fig. 4D, K). Lateral compression has displaced part of the condylus lateralis, resulting in an extremely enlarged distal condyle. ~~As a result of this distortion, Even when the condylus lateralis appears to have projected more distally than the condylus medialis, adopting an similar aspect similar to that of *Kairuku*. This condition, coupled with the partial loss of the condylus lateralis creates an appearance that resembles the femur of this deformation, together with the loss of a condylar portion makes the morphology approach the condition of *Archaeospheniscus* (according to Jadwiszczak 2006, fig. 12 C,D). However, In in *Archaeospheniscus*, the condylus lateralis also projects more distally than the condylus medialis, and~~ the distal epiphysis is narrower than that of *Kairuku*, *Palaeeudyptes gunnari* and *Palaeeudyptes klekowskii*.

The trochlea fibularis is incomplete but approximates the dimensions of the fibula (Fig. 4K). The crista tibiofibularis is broken proximally, but its most caudal portion is rounded.

The tuberculum m. gastrocnemialis lateralis is sharp and occupies a small area. The epicondylus lateralis is also sharp and more conspicuous than the epicondylus medialis. The fovea tendinous m. tibialis cranialis is wide and rounded (Fig. 5A). The sulcus intercondylaris is broad and continuous with the sulcus patellaris to form a shallow fossa limited by strong condylar edges (Fig. 4B,D).

Finally, a small element interpreted as a fragment of the femur by Clarke *et al.* (2003) has been fully prepared and found to be part of an echinoid.

Although preservation of the tibiotarsus is not optimal, it is more complete than those documented for skeletons of the Eocene Antarctic *Palaeeudyptes gunnari* (Acosta Hospitaleche & Reguero 2010) and *P. klekowskii* (Acosta Hospitaleche & Reguero 2014). The

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tibiotarsal shaft is slender, straight (Fig. 4L), and craniocaudally compressed (Fig. 4G, N) distal to the foramen interosseum distal; this is compatible with all Paleogene penguins that we examined. The crista fibularis is widely expanded at the distal end (Fig. 4M), and as in *Perudyptes*, arises more proximally than in Neogene (e.g., *Palaeospheniscus*) and extant penguin (e.g., *Spheniscus*) taxa. The foramen interosseum proximale is elliptical, at least at the tibiotarsal margin.

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The sulcus intercnemialis is wide and deep (Fig. 4L). It is proximally projecting and medially limited by the crista cnemialis lateralis. This latter structure is proximally extended like that of *Inkayaku*. In *Anthropornis*, the crista cnemialis lateralis is proximally deflected so that the sulcus intercnemialis is triangular (Jadwiszczak 2012). CADIC P 21, on the other hand, exhibits parallel sulcus margins as in *Palaeudyptes*. The incisura tibialis is slightly developed (Fig. 4G). The fossa retropatellaris is not evident, possibly because of the poor preservation.

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The sulcus extensorius is shallow and the lateral side is open, whereas the medial side is limited by a bony ridge resembling those in *Gavia* and other Eocene penguin species. The sulcus extensorius becomes deeper in Neogene penguins and *Kairuku*. The sulcus extensorius is near the midline of the shaft as in *Kairuku*.

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The canalis extensorius filled with sediment. The pons supratendinous preserves only the most proximal part, which is oblique with respect to the axis. A possible tendon insertion (Clarke *et al.* 2003) is located proximally inside the sulcus extensorius. The distal epiphysis is deflected medially (Fig. 4M), and unfortunately the condyli are not preserved. The crista patellaris is broken at the proximal end, but it probably did not project proximally with respect to the facies articularis.

The fibula is damaged and the distal end of the spina fibulae is missing (Fig. 4F,H). The triangular corpus fibulae are curved and slightly sigmoid. The caput fibulae is sub-oval and divided into two distinct facets. The tuberculum m. iliofibularis is rounded.

Remarks. Ten years ago, only neogene skeletons were available for comparison. This skeleton, here re-studied, was initially described by Clarke *et al.* (2003), at a time when comparative fossil material was scarce, and associated or articulated Antarctic penguin skeletons were unknown. Antarctic species were referred exclusively to tarsometatarsus, an element not preserved in the CADIC P 21. Neither the Peruvian *Perudytes*, *Icadyptes* and *Inkayaku* nor the New Zealander Eocene *Waimanu* species had been described yet. The current state of knowledge is clearly different, improving the possibilities of analysis and interpretation comparisons. A few Paleogene skeletons are known from Antarctica (Acosta Hospitaleche, 2014; Acosta Hospitaleche & Reguero, 2010, 2014), Peru (Clarke, *et al.*, 2007, 2010), and New Zealand (Ksepka *et al.*, 2012), making possible the systematic determination of fossils different from tarsometatarsus.

Measurements. Pelvis: distance between the margin of the foramen ilioischadicum to the end of the ala ischii = 63.9 mm; height taken caudally to the foramen ilioischadicum = 21.5 mm. Femur: total length = 129 mm; distance between caput and condylus medialis = 115.2 mm; distance between trochanter femoris and condylus lateralis = 121.1 mm; lateromedial width of

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Comentario [C7]: A list of occurrence citations does not explain how your fossil improves the “current state of knowledge”. I recommend reorganizing your remarks to include only taxonomic considerations. Other aspects of “analysis and interpretation” should be discussed below. Put more simply, the Remarks must explain what if any taxonomic alterations have been made by your analysis. Also, how have other new Paleogene fossils added to these interpretations?

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the diaphysis = 16.2 mm; anteroposterior width of diaphysis = 16.5 mm; lateromedial proximal width = 34.9 mm; anteroposterior proximal width = 18 mm; lateromedial distal width = 27.8 mm; anteroposterior distal width = 21.5 mm; internal distance between condylar margins = 16.5 mm. Tibiotarsus: maximum length = 221 mm; length from the base of the crista cnemialis to the condylus medialis = 194 mm; lateromedial width of the diaphysis = 16.6 mm; craniocaudal width of the diaphysis = 10.07; width of pons supratendineus = 7 mm. Fibula: craniocaudal proximal width = 15.9 mm; lateromedial proximal width = 7.8 mm.

Indeterminate Spheniscidae (Fig. 4)

Material. CADIC P 22 (coracoid).

Provenance. Leticia Formation (Bartonian), Punta Torcida fossil locality, Tierra del Fuego Province, Argentina.

Description. The coracoid is incomplete but the preserved portion is seemingly narrow. It is paddle-shaped (Fig. 4O, P, R) as is typical of all penguins, but the distal end is not flabelliform (Fig. 4O, Q). The sternocoracoideal joint was probably 's-shaped' like ~~other that in~~ Paleogene penguin species such as *Anthropornis* and *Palaeudyptes* (Acosta Hospitaleche, in press).

Remarks. Bioerosive marks are evident on the distal half of the coracoid. Isolated pits and scratches are visible on ~~opposing the~~ surfaces of the bone (Fig. 6). The absence of any secondary bone remodeling indicative of healing suggests that they were produced either at or shortly after the time of death. Pits are mainly located close to the margins of the coracoid without a regular

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pattern but inn both sides of the bone. They could belong to a predator or scavenger (comparative material can be consulted in Cione *et al.*, 2012, where similar marks were attributed to the biting and gnawing action of any continental predators) that also would be responsible for the marginal breakage of the bone (Fig. 6). Scratches are represented by shallow furrows located obliquely to the main axis of the coracoid. As it was described by Cione *et al.*, 2012, these traces are only on one surface, with not counterpart on the opposite side. Marks of this style may be generated by different organisms scavenging or foraging for algae on bone such as teleosteans, elasmobranchs, moluscs, etc.

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Measurements. Total length = 112.3 mm; height of the facies articularis humeralis = 17.5 mm; width of the facies articularis humeralis = 10.5 mm; width of the axis of the coracoid = 16.6 mm.

Palaeobiological interpretations

Body mass and body size

According to penguin body mass/size equations developed by Jadwiszczak (2001), the femur of CADIC P 21 indicates a body mass of 30–32 kg for a penguin of approximately 120–130 cm long (Table 1). This is consistent with previous estimates, which reconstructed an individual slightly smaller than the living Emperor Penguin *Aptenodytes forsteri* (Clarke *et al.* 2003).

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Locomotory habits

The femur to tibiotarsus length ratio has been used to predict ground-based locomotory habits in extinct birds (Habib & Ruff 2008). Applying this method to CADIC PV 21 yields a femur/tibiotarsus ratio of 0.57 (Clarke *et al.* 2003 produced slightly different proportions, possibly because they measured the tibiotarsus while still encased in matrix), which is higher

than expected for a diving bird. Calculations from Clarke *et al.* (2003) based on measurements from Gatesy & Middleton (1997) placed Sphenisciformes between 0.55 and 0.70, versus Gaviiformes at 0.32–0.41, and Procellariiformes at 0.32–0.59 among other marine birds.

CADIC P 21 also has relatively thick cortical bone walls in the diaphyses. This is typical of aquatic birds, where thick-walled bones increase resistance to stress while lowering buoyancy (Currey & Alexander 1985, Swartz *et al.* 1992, Habib & Ruff 2008). Dense compact bone occupies approximately 60% of the tibiotarsal shaft cross-section in CADIC P 21, which is similar to *Kairuku* (Ksepka *et al.* 2012). Other diving seabirds such as cormorants, loons and albatrosses (auks being an exception), likewise have thick cortices, but the relative cortical area is always less than 50% of the diameter in transverse section (see Habib & Ruff 2008). The tibiotarsus of CADIC P 21 additionally reveals variable degrees of osteosclerosis (Fig. 4 D), which is typical of the increased bone compactness and volume reported in other penguins (Meister 1962).

Collectively, these features infer aquatic habits for CADIC P 21, but are not necessarily discriminative of specific locomotory modes (see Hinic'-Frlog & Motani 2009 for discussion). Penguins generally belong to a morphologically homogeneous group of wing-propelled deep divers that pursue and catch their prey entirely underwater. Some skeletal characters clearly correlate with this lifestyle, including an elongated crista cnemialis -on the the tibiotarsus (Raikow 1985, Livezey 1986), and a double hinge-like articulation of the femur with the acetabulum and antitrochanter of the hip (Storer 1960). These are all present in CADIC P 21. However, in addition the coracoids, CADIC P 22, is also coherent with a large aquatic bird: the sternocoracoid articulation being marked by curvature of the facies articularis sternalis, which is characteristic of penguins and substantially limits wing abduction, an essential trait for diving kinematics. The reconstructed CADIC P 22 coracoid suggests only a moderately broad and

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curved base, thus limiting space to accommodate the m. supracoracoideus. ~~It probably supported the insertion of powerful musculature for diving underwater, although through less precise movements than those utilized by the most specialized extant species.~~

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The entire pectoral girdle (coracoid, scapula, and furcula) and the forelimb act as a lever system in which the coracoid and wing are the two major components. The humerus alternately pulls and pushes the coracoid at its contact point, ~~subjecting it to a series of forces. A longitudinal force tends to pull on the coracoid and a torque force (Young & Freeman 2003) tending to rotate it (Acosta Hospitaleche & Di Carlo 2010). The sternocoracoidal surface must be capable of withstanding the forces transmitted by wing movement and this joint must be strong enough for absorbing force peaks and preventing relative displacement of the elements.~~

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Extant penguins have an optimized morphology compared to fossil species, with a “C”-shaped sternocoracoideal surface. Some Paleogene penguins have an enlarged angulus medialis and processus lateralis (see Jadwiszczak 2006), but the facies articularis sternalis is not extended. This seems to increase the risk of detachment of the coracoid from the sternum or the fracturing of the sulcus articularis coracoideus, a problem solved by the development of a wider surface area for muscle attachment. ~~This strategy for the optimization of the diving movement is different to that of extant species, in which a more convex coracoideal distal end generates an optimized angle of force attack with the development of a less bulky musculature.~~

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Muscles inserted in the coracoid apply forces that participate both in the movement during diving, the position of the coracoid itself, and the small-scale adjustments to the angle of force transference (Bannasch 1987, Poore *et al.* 1997).

~~Musculi supracoracoideus is essentially the wing lifter; and is greatly developed in penguins in comparison with its antagonist, the pectoral. This important muscle is primarily involved in humerus lift, and has its origins in the facies muscularis sterni (sternum) and the coracoid base (Bannasch 1986).~~

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Discussion and conclusions

The Eocene was a time of diversification and increased abundance amongst penguins, at least in high latitudes, within which Antarctic species are likely to have dispersed northward along the South American coast (Acosta Hospitaleche *et al.*, 2013). The recent discovery of *Palaeudyptes* (a genus previously known in Antarctica) in Chile, and now in Argentina provides new evidence for understanding the interactions between the Antarctic and South American avifaunas. The limb bone proportions and microstructure of *Palaeudyptes* are consistent with an aquatic lifestyle, but like other early penguins it was probably not as hyperspecialized for diving as are modern species. Indeed, the coracoid morphology of CADIC P 22, particularly the sternocoracoideal joint, suggest relatively poor underwater maneuverability. Despite this, the large size of the Argentine specimens compares well with wing-propulsive diving birds, and could be related to thrust force and cost of lift production which is reduced in larger-bodied subaqueous fliers (Hinic'-Frlog & Motani 2009). Gigantism in penguins appeared in Antarctica, and is in contrast to other groups such as Gaviidae that were relegated and then extirpated from the area (Acosta Hospitaleche and Gelfo, in press).

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We thank to the Agencia Nacional de Promoción Científica y Tecnológica (PICTO 0114, PICTO 0093, PICT 0284), Consejo Nacional de Investigaciones Científicas y Técnicas (PIP 114-0341, PIP 0017), and Universidad Nacional de La Plata, for partial financial support. Cecilia Deschamps improved the English grammar.

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Figure captions

Fig. 1. Location and geology of the studied area: **A**, location map; **B**, schematic geology of the Austral Foreland Basin in Tierra del Fuego showing the location of Fig. 2. SCO, Scotia Plate; SAM, South American Plate.

Fig. 2. Geology of the Punta Torcida-Cabo Campo del Medio Anticline and location of the fossil locality and the stratigraphic section depicted in Fig. 3.

Fig. 3. Stratigraphic section between Punta Torcida and Cabo Campo del Medio showing the architecture of the Leticia Formation that progressively filled a high-relief erosional surface (arrows) incised into the Punta Torcida Formation. Uc, unconformity; Smf, shallow-marine facies; Off, offshore facies; m, mudstone; s, sandstone.

Fig. 4. *Palaeudyptes gunnari* CADIC P 21: **A**, pelvis; **B**, femur in cranial view; **C**, femur in medial view; **D**, femur in caudal view; **E**, femur in lateral view; **F**, fibula in lateral view; **G**, tibiotarsus in proximal view; **H**, fibula in medial view; **I**, transversal section of tibiotarsus; **J**, femur in proximal view; **K**, femur in distal view; **L**, tibiotarsus in cranial view; **M**, tibiotarsus in caudal view; **N**, tibiotarsus in lateral view. Spheniscidae indet. CADIC P 22: **O**, coracoid in ventral; **P**, coracoid in medial view; **Q**, coracoid in dorsal view; **R**, coracoid in lateral view. Scale bar= 10 mm (image I has its own scale).

Fig. 5. Insertions and scars of the musculature identified in the femur CADIC P 21: **A**, cranial view; **B**, caudal view; **C**, medial view; **D**, lateral view. Scale bar= 10 mm.

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Fig. 6. Predation marks evident on the coracoid CADIC P 22. Circles indicate pits and ovals indicate scratches: **A**, ventral view; **B**, dorsal view. Scale bar= 10 mm.

Table 1. Equations of form $Y = aX^b$ obtained by the Model I Regression method after transformation to logarithms (taken from Jadwiszczak 2001), where body mass and body length are expressed in kg and cm respectively. Abbreviations: L = total length of femur (129 mm), LMW = lateromedial width of diaphysis (16.2 mm), APW = anteroposterior width of diaphysis (16.5 mm), r = Pearson's product-moment correlation coefficient, CI = confidence interval, SEE = standard error of the estimate, PE = prediction error. The most conservative values are indicated in bold.

Appendix 1.

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