Middle Cenozoic penguin remains from the Patagonian Cordillera

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ABSTRACT. Middle Cenozoic marine fossil-bearing beds crop out in the Cerro Plataforma (western Chubut Province, Argentina) at about 1,400 m a.s.l. They are located 500 km far from the modern Atlantic coast and only 50 km from the Pacific Ocean. Well preserved penguin bones and a shark tooth were found therein. Invertebrates include corals, bryozoans, abundant mollusks, echinoids, and crabs. Morphogeometric analysis and comparative description confirmed that the penguin humerus is referable to *Palaeospheniscus bergi* Moreno and Mercerat, 1891. Most of the fossils indicate a Miocene age. However, there is a debate about if the bearing beds are of Pacific or Atlantic origin. Fossil invertebrates identifiable at species level reveal Pacific affinity, the shark species is cosmopolitan, and *Palaeospheniscus bergi* is known from early Miocene Atlantic units of southern South America. Yet, *Palaeospheniscus* Moreno and Mercerat, 1891 is also known from Miocene Pacific beds but it has not been identified at specific level yet. This is the highest site in topographic terms in which penguin fossils occur. This indicates a remarkable uplift for the area, probably from the middle Miocene.

Keywords: *Spheniscidae, Miocene, Oligocene, Patagonia, South America.*

RESUMEN. Restos de pingüinos del Cenozoico medio de la cordillera Patagónica. Capas portadoras de fósiles marinos del Cenozoico medio afloran en cerro Plataforma (oeste de la Provincia del Chubut, Argentina) a unos 1.400 m s.n.m. Están localizadas a 500 km de la costa pacífica actual y a solo 50 km de la pacífica. Fueron hallados restos de pingüinos y un diente de tiburón bien preservados. Entre los fósiles de invertebrados se incluyen corales, briozoos, abundantes moluscos, equinoideos y cangrejos. Los análisis morfogeométricos y la descripción comparada confirmaron la asignación del húmero de pingüino a *Palaeospheniscus bergi* Moreno y Mercerat, 1891. La mayoría de los fósiles indican una edad Miocena. Sin embargo, existe un debate sobre si estas capas poseen un origen pacífico o atlántico. Los fósiles de invertebrados identificables a nivel de especie presentan afinidades pacíficas, la especie de tiburón es cosmopolita, y *Palaeospheniscus bergi* es conocido en unidades atlánticas del Mioceno temprano de América del Sur. A pesar de esto, el género *Palaeospheniscus* Moreno y Mercerat, 1891 es también conocido en capas miocenas del Pacífico, aunque la especie no ha sido aún identificada. En términos topográficos, este es el sitio más elevado en el que se han hallado restos de pingüinos. Esto indica un notable levantamiento del área, probablemente durante el Mioceno medio.

Palabras clave: *Spheniscidae, Mioceno, Oligoceno, Patagonia, América del Sur.*

1. Introduction

Marine rocks with a rich -albeit rather poorly preserved- fauna of invertebrates and rare remains of marine vertebrate fossils crop out approximately 30 km south of the town of Lago Puelo (Chubut Province, Argentina; Fig. 1). The rocks lie amidst outcrops of much older pre-Cenozoic rocks that form the basement of the basin or nearly are coeval to it (Lizuaín, 1979). These cenozoic rocks were accumulated in a retro-arc basin to the east of a synchronous magmatic arc. The age-range of the fauna collected has varied according to different authors, but has been generally constrained to the middle Eocene-late Oligocene (Asensio *et al*., 2005, 2010). More recently, a Miocene age was proposed by Encinas *et al*. (2011) based on U-Pb zircon dating.

The Cerro Plataforma outcrop is unique because it is one of the few localities with Cenozoic marine fossils in the region; the outcrops of the fossil-bearing formation lie at about 1,400 m a.s.l. and 500 km from the modern Atlantic coast and only 50 km from the Pacific Ocean (42°20'S, 71°51'W).

Besides the diverse invertebrate fossil fauna (Griffin *et al*., 2002), the beds at Cerro Plataforma contain fairly well-preserved bones of penguins and a shark tooth. The Atlantic (Lizuaín, 1979; Barreda *et al*., 2003) or Pacific (Asensio *et al*., 2005, 2010; Ramos, 1984; Ramos and Bechis, 2010) origin of these rocks is still controversial. The fossil penguins and associated shark teeth described herein are the only fossil vertebrate remains contained in these rocks. Penguins, in particular, belong to a taxon well recorded in Cenozoic marine beds exposed along the Atlantic coast of southern South America (Acosta Hospitaleche, 2004, 2006, 2007; Acosta Hospitaleche *et al*., 2008; Acosta Hospitaleche and Cione, 2012). An accurate identification of the remains was attained by means of a detailed description supplemented with a morphogeometric analysis. All materials are comparatively described and the results are discussed within the available phylogenetic context.

2. Materials and methods

The study used a sample of 25 penguin humeri belonging to twelve different species and six genera housed at the collections of the Museo de La Plata (MLP), and Museo Paleontológico Egidio Feruglio (MEF-PV), in the cities of La Plata and Trelew,
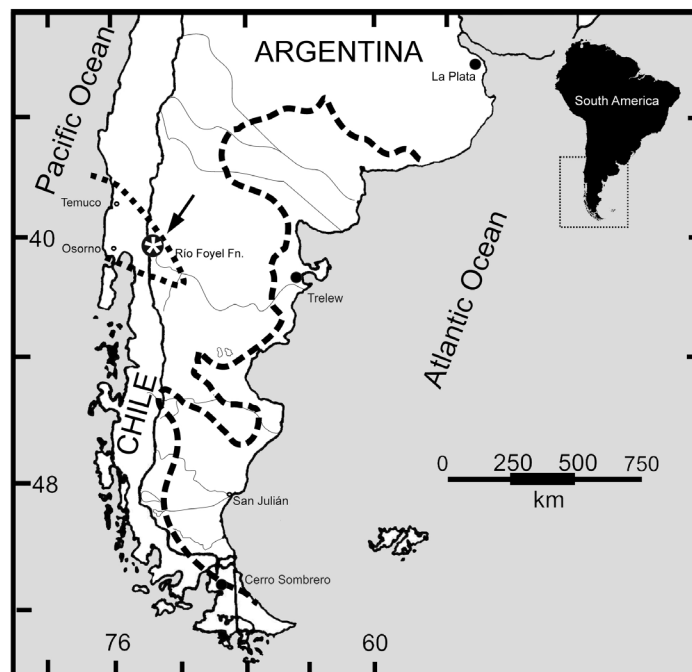

FIG. 1. Location map showing the fossil locality (*) and marine transgressions (dash line) after Asensio *et al.* (2010).

respectively (Argentina). To eliminate variations related to age or preservation, only adult and complete specimens were considered in this analysis. They comprise all the Neogene South American fossil and living species of which the humeri are known and available for these purposes

The shark tooth was also compared with the large collection of Cenozoic sharks from Antarctica and South America housed in the Museo de La Plata.

2.1. Morphometric and comparative methods

Each humerus was photographed in cranial view with the same focal distance. A digital camera was used to take high-resolution images of the 25 adult specimens. The *x*, *y* coordinates of ten landmarks (Fig. 2) were digitized from these images using TpsDig 2.04 (Rohlf, 2005). Cranial view was preferred because the shape and disposition on the head of the *sulcus ligamentosus transversus* and the *facies musculi pectoralis* are clearly seen.

Selected landmarks were based on previous analyses (Acosta Hospitaleche *et al*., 2006a, 2008; Tambussi *et al*., 2006). Ten reference landmarks were selected for this analysis, comprising type I, II, and III landmarks (Rabello Monteiro and Furtado dos Reis, 1999; Fig. 2). All landmarks are homologous points. Their *x*, *y*

FIG. 2. Humerus MLP 96-XII-2-1 *Palaeospheniscus bergi* Moreno y Mercerat, 1891 in proximal view. **1**. With the selected landmarks; **2.** Diagram showing the landmarks distribution in all the specimens analyzed.

coordinates were digitized from these images using TpsDig 2.04 (Rohlf, 2005).

Landmark 1 points the *tuberculum dorsale* while the *tuberculum ventrale* is limited by landmarks 4 and 5. Landmark 2 shows the degree of expansion of the head. Landmark 3 indicates the *incisura capitis* position and also the shape of the humerus-head. Landmark 6 marks the joint between the head and the diaphysis. Landmarks 7 and 8 delimit the *facies musculi pectoralis*. Finally, landmarks 9 and 10 show the expansion of the *sulcus ligamentosus transversus* (Fig. 2).

Variation in shape of landmark configurations among specimens was established. Differences in size, orientation, and position were removed using procrustes reorientation. Relative warps were computed with inclusion of the uniform component and no weighting by bending energy (Bookstein, 1996).

2.2. Outlines Analysis

Each humerus, with the single exception of *Spheniscus urbinai* that was not able for this purpose, was photographed in proximal view with the same focal distance and position. A digital camera was used to take high-resolution images of the 24 adult specimens.

Shape of the humerus-head in proximal view was studied using elliptic Fourier analysis of contour coordinates (Rohlf and Archie, 1984), performed with the Shape software package (Iwata and Ukai, 2002). Scores from the principal components analysis were exported to PAST software (Hammer *et al*., 2001), and clouds of data were visualized in a biplot graph.

3. Geochronological setting

Miocene rocks -known informally as 'Cerro Plataforma beds'- exposed along the eastern foothills of the northwestern Chubut Province, Patagonian Andes and in the adjoining valleys are still to be placed within a regional stratigraphic framework with certainty. Literature dealing with these deposits only mention the different fossiliferous localities, among which the ones better studied are those along the Río Foyel in Río Negro Province (Wherli, 1899; Feruglio, 1944; González Bonorino, 1944; Bertels, 1980; Diez and Zubia, 1981; Ramos, 1982; Pöthe de Baldis, 1984; Chiesa and Camacho, 2001; Barreda and Palazzesi, 2007; Barreda *et al*., 2003; Casadío *et al*., 2004; Giacosa and Heredia, 2004; Griffin *et al*., 2004; Asensio *et al*., 2005, 2010).
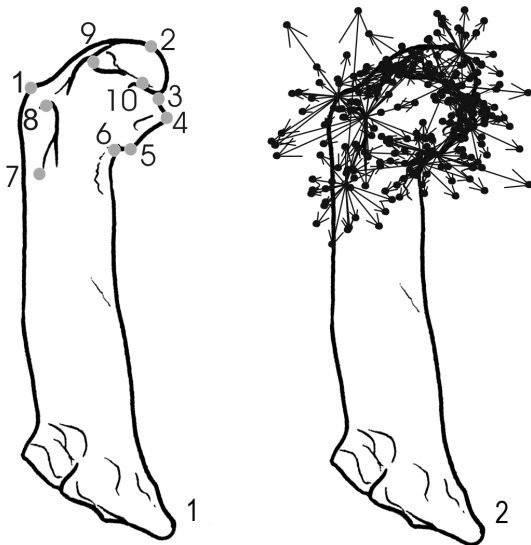
The 'Cerro Plataforma beds' comprise 530 m of medium- to fine-grained immature sandstones and conglomerates overlying Cretaceous granites, from which they are separated by an unconformity interpreted as a maximum flooding surface, followed by tabular massive sandstones interpreted as shelf lobes. This facies is covered by thick beds of black siltstones and these in turn are overlain by deltaic sediments and marginal marine and continental beds at the top. The fossil fauna was recovered from the lowermost sandstone beds, 35 m above the underlying granites. Further geological information can be found in Lizuaín (1979).

The entire complex has been interpreted as a regressive sequence of Pacific origin. These beds are at the top of El Foyel Group, composed by Troncoso, Salto del Macho, Río Foyel and Salto Ventana formations (Asensio *et al*., 2005, 2010). The paleobiogeographic affinities of the fauna in the El Foyel Group are important as they should provide further confirmation -or not- of the currently accepted Pacific-connected basin configuration. Such a configuration is closely linked to the history of Cenozoic uplifting of the Andes as a result of tectonic processes occurring along the western margin of the South American plate at that time (Folguera and Ramos, 2008a, 2008b; Giacosa and Heredia, 2004; Giacosa *et al*., 2005). The distribution of the taxa contained in these rocks is inconclusive as to an Atlantic or Pacific origin of the basin.

The age of the rocks included in the formations comprising the El Foyel Group has been controversial ever since they were first described, and different postures based on fossil content, stratigraphic position, and absolute dates can be grouped into three main viewpoints. Thus, their age has ranged from Eocene/Oligocene (Chiesa and Camacho, 2001) to Oligocene (Asensio *et al*., 2005, 2010; Griffin *et al*., 2004) or Miocene (Ramos and Bechis, 2010; Encinas *et al*., 2011). While the formal units may be of different ages, the Cerro Plataforma beds have not been yet correlated to any of these formal units included in the El Foyel Group. The mollusk fauna contained in the 'Cerro Plataforma beds' does not shed further light on the age of these rocks.

4. Associated fauna

The 'Cerro Plataforma beds' yielded the following fossils: corals, bryozoans, abundant mollusks,

echinoids, crabs, and also the vertebrate remains described herein. By far the most diverse group is that of the mollusks. Unfortunately, many of these are difficult, if not impossible, to identify because of the poor preservation.

A very important remain is the MLP 96-XII-3-40, a second left lower tooth (Figs. 3.8-3.10) assigned to '*Isurus' hastalis* (Agassiz, 1843), an Elasmobranch (Lamnidae) well known worldwide in marine Cenozoic rocks (Cappetta, 2012). Rocks bearing Neogene elasmobranchs include the early Miocene Gaiman, Chenque, and Monte León formations and the middle to late Miocene Puerto Madryn Formation in Argentina the Navidad Formation of Chile (middle Miocene according to Encinas *et al*, 2010; recorded by Suárez *et al*., 2006), in the middle Miocene-early Pliocene Bahía Inglesa Formation (Walsh and Suárez, 2006). In Perú they appear in the middle Miocene-Pliocene Pisco Formation (Ehret *et al*., 2009).

This tooth has a slender crown with labially curved tips. Both cutting edges are complete. Mesial and distal cutting edges are slightly convex in most of the crowns. At the base, the crown becomes wider and the cutting edges are concave. The base of the labial crown overhangs the root in the middle. Enameloid extensions cover part of the root lobes. Labial face crown is transversely flat but the lingual face is strongly convex. Lateral cusplets are missing. The root has widely diverging and distally expanded and flattened branches. Mesial lobe is longer. Prominent lingual protuberance present, without groove.

Cenozoic shark teeth similar to those of the extant *Isurus* were traditionally included in *Isurus* (*e.g.,* Leriche, 1926). These lamnids have long anterior teeth, lack lateral denticles and serrations, and are usually named makos. However, some authors refer several fossil species, including *Isurus hastalis* (Agassiz, 1843) to the genus *Cosmopolitodus* Glikman, 1964 (Ward and Bonavia, 2001; Suárez *et al*., 2006). Other authors such as Cione (1988) supported the use of the name *Isurus plicatilis* (Agassiz, 1838) or *Isurus xiphodon* (Agassiz, 1838) (see Purdy *et al.,* 2001) for broad-crowned specimens of *I. hastalis*. Ward and Bonavia (2001) considered *Isurus xiphodon* (Agassiz, 1843) as a *nomen dubium*. A possible solution would be to assign the species *I. hastalis*, *I. plicatilis*, and others to the genus *Carcharodon* Smith, 1838. Until a thorough study of the different species of lamnids is carried out, it is preferred to
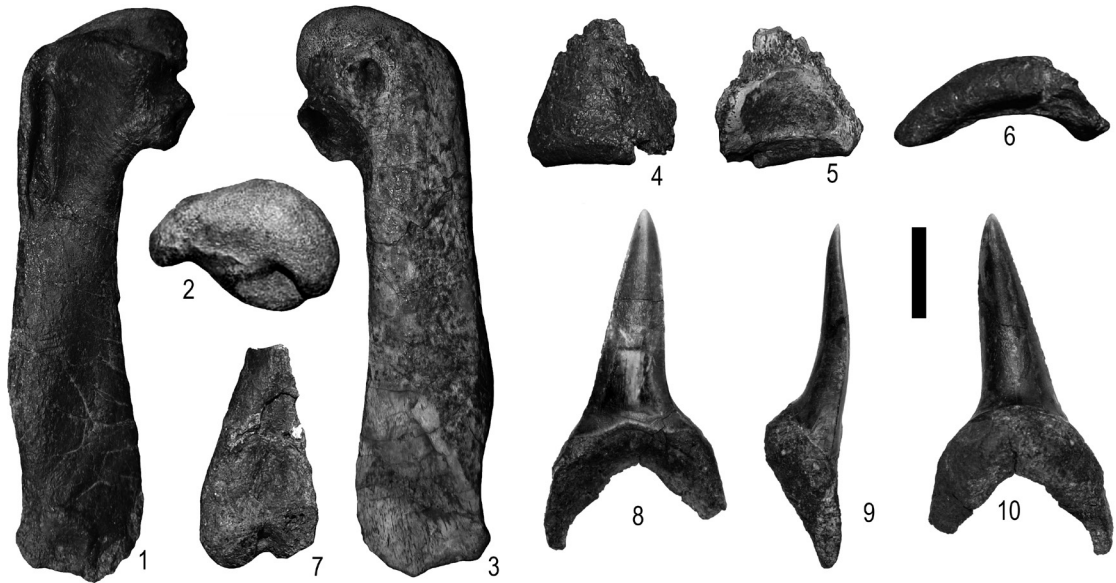
FIG. 3. Fossil vertebrates from Cerro Plataforma. **1-3** Humerus MLP 96-XII-2-1 *Palaeospheniscus bergi*; **1.** In anterior view; **2.** In posterior view; **3.** In proximal view; **4.** Femur MLP 96-XII-3 Spheniscidae in posterior view; **5-7**. Distal end of coracoids MLP 96-XII-2 Spheniscidae; **5.** In anterior view; **6.** In posterior view; **7.** In distal view; **8-10**. Second left lower tooth MLP 96-XII-3-40 '*Isurus*' cf. *hastalis*; **8.** Labial view; **9.** Lateral view; **10.** Lingual view. Scale bar: 10 mm.

refer these species to '*Isurus*' (see discussion in Cione *et al*., 2012).

Size and morphology of the tooth from Cerro Plataforma agree with young specimens of the Miocene species '*Isurus*' *hastalis* (see Cione, 1988). It is also similar to the Oligocene species '*I.*' *flandricus* but it differs in being less gracile. It clearly differs from the Eocene species '*Isurus*' *praecursor* in proportions (Fig. 3; see discussion in Cione and Reguero, 1994), the Miocene species '*I.*' *planus* in the absence of crown curvature, the Miocene-Pliocene species '*I.*' *plicatilis* in the narrower crown, the recent *I. oxyrinchus* Rafinesque, 1810 in the completeness of the distal cutting edge, and the recent *I. paucus* Guitart, 1966 in the absence of strong lingual curvature (see Cione, 1988).

5. Systematic paleontology

5.1. Order Sphenisciformes Sharpe, 1891

Penguin remains have been collected in southern hemisphere localities from marine Cenozoic series (*e.g.,* Acosta Hospitaleche, 2006; Acosta Hospitaleche and Reguero, 2010; Jadwiszczak, 2009; Fordyce and Thomas, 2011 and literature cited therein).

South American Neogene penguins are closely related with extant species. They are readily distinguished from those of the Paleogene because of their more slender bones and their general similarity to extant forms living in the area nowadays. Contrarily, South American Paleogene forms show a wide variety of body-sizes and the presence of robust forms with no extant representatives.

Cenozoic South American genera include large penguins (Clarke *et al*., 2007, 2010; Sallaberry *et al*., 2010; Ksepka and Clarke, 2010; Ksepka *et al*., 2008) that do not reach the gigantic proportions of the Paleogene Antarctic-Australasian ones (Jadwiszczak, 2001; Jadwiszczak and Chapman, 2011; Jadwiszczak and Mörs, 2011; Acosta Hospitaleche and Di Carlo, 2010; Acosta Hospitaleche and Reguero, 2010 and references therein). Records of Paleogene taxa in South America are few and include those from the middle Eocene La Leticia Formation in Tierra del Fuego (Clarke *et al*., 2003), the middle Eocene Paracas Formation and the late Eocene Otuma Formation of Perú (Acosta Hospitaleche and Stucchi, 2005; Clarke *et al*., 2007, 2010; Ksepka and Clarke, 2010; Ksepka *et al*., 2008), and the middle to upper Eocene Río Turbio, Loreto, and Río Baguales formations in Chile (Sallaberry *et al*., 2010).

The Neogene penguins show close phylogenetic affinities to the modern penguins (Ksepka *et al*., 2008; Clarke *et al*., 2010), and are recorded from both Atlantic and Pacific basins (Acosta Hospitaleche *et al*., 2007; Soto Acuña *et al*., 2008). Rocks bearing Neogene penguins include the lower Miocene Gaiman, Chenque, and Monte León formations and the middle to upper Miocene Puerto Madryn Formation in Argentina. They also occur in the middle Miocene-lower Pliocene Bahía Inglesa Formation (Acosta Hospitaleche *et al*., 2006c; Walsh and Suárez, 2006; Chávez, 2008; Yury-Yáñez *et al*., 2009; Rubilar-Rogers *et al*., 2012), middle Miocene-late Pliocene Coquimbo Formation (Acosta Hospitaleche *et al*., 2006b), and the late Pliocene La Portada Formation (Emslie and Correa Guerra, 2003) in Chile. In Perú they appear in the middle Miocene Chilcatay Formation (Acosta Hospitaleche and Stuchi, 2005) and the middle Miocene-Pliocene Pisco Formation (Stucchi, 2002, 2007; Stucchi *et al*., 2003; Göhlich, 2007; Acosta Hospitaleche *et al*., 2011).

5.2. Family *Spheniscidae* Bonaparte, 1831

Genus *Palaeosphniscus* Moreno and Mercerat, 1891
***Palaeospheniscus Bergi* Moreno and Mercerat, 1891**
Figures 3.1-3.3

Material: MLP 96-XII-2-1 right humerus without the distal end (Fig. 4).
Comments: Distinction between the two great groups of penguins -Paleogene and Neogene- is based on several unique characters. Among them, Eocene taxa show a humerus with sigmoid diaphysis, while it is straight in the Miocene and Recent penguins.

This feature allows us placing the specimen studied herein in the group of Neogene and living forms of South America. Among these are the extinct genera *Eretiscus*, *Palaeospheniscus*, *Paraptenodytes* Ameghino, 1891 and *Madrynornis* Acosta Hospitaleche *et al*., 2007 (*Arthrodytes* Ameghino, 1905 is only recorded in the early Oligocene of Patagonia) and the Recent genera (*Spheniscus* Brisson, 1760, *Pygoscelis* Wagler, 1832) that also have fossil representatives in Chile and Perú (Acosta Hospitaleche *et al*., 2006c, 2011; Emslie and Correa Guerra, 2003; Göhlich, 2007; Stucchi, 2002, 2007; Stucchi *et al*., 2003). A referral of our material to *Paraptenodytes*

or *Arthrodytes* (which possess an undivided *fossa tricipitalis*) can be discarded immediately, as the specimen has a bipartite *fossa tricipitalis,* forming two unequal cavities like in the living species.

The significantly smaller size of *Eretiscus* Olson, 1986 precludes inclusion of the material in this genus. Inclusion in *Madrynornis* can also be easily discarded because of the more proximal placement and shorter length of the *sulcus ligamentosus transversus*. The *tuberculum dorsale* is moderate and less prominent, and the *crista deltopectoralis* is relatively more slender in *Madrynornis* than in the humerus described here. In addition, the *incisura capitis* in specimen MLP 96-XII-2-1 is deeper and the *tuberculum ventrale* is more robust than in *Madrynornis*.

Thus, possible generic placement for our material is restricted -among known genera- to the fossil *Palaeospheniscus* and *Madrynornis* and *S. megaramphus*, *S. urbinai*, *S. muizoni*, *Pygoscelis calderensis* Acosta Hospitaleche *et al*., 2006c, and *Pygoscelis grandis* Walsh and Suárez, 2006.

Among the species belonging to the modern genera, *Pygoscelis* and *Eudyptes* have a better developed *angulus preaxialis*, and more proximally elongated *caput humeri*; these characters easily distinguish species of these genera from MLP 96-XII-2-1.

As to size of adult individuals, humeri of Recent species of *Spheniscus* range from 57 to 74 cm (see measurements in Scarlett, 1983; Livezey, 1989; Stucchi, 2002; table 1 of Gohlich, 2007). In the extinct species *S. urbinai* and *S. chilensis* they measure 104 and 70.3 cm respectively (Stucchi, 2002; Emslie and Correa Guerrra, 2003). The three species of *Palaeospheniscus*, distinguishable by their different sizes (*P. bergi, P. patagonicus,* and *P. biloculata* in increasing order of size), have humeri ranging between 68 and 94 cm long (Acosta Hospitaleche, 2007). Specimen MLP 96-XII-2-1 is missing a distal end, although its proportions suggest a size similar to that of *Spheniscus magellanicus* and *Palaeospheniscus bergi* (up to 68.5 mm long).

As was stated earlier, *Spheniscus chilensis* was not compared with *Palaeospheniscus* in Emslie and Correa Guerra (2003). However, the holotype of *S. chilensis* is clearly different from material assigned to the species of *Palaeospheniscus*.

Humeri of *Palaeospheniscus* and *Spheniscus* share a number of common characters such as the bipartite *fossa tricipitalis*, a divided *sulcus ligamentosus transversus*, a fossa over the *tuberculum ventrale*, a
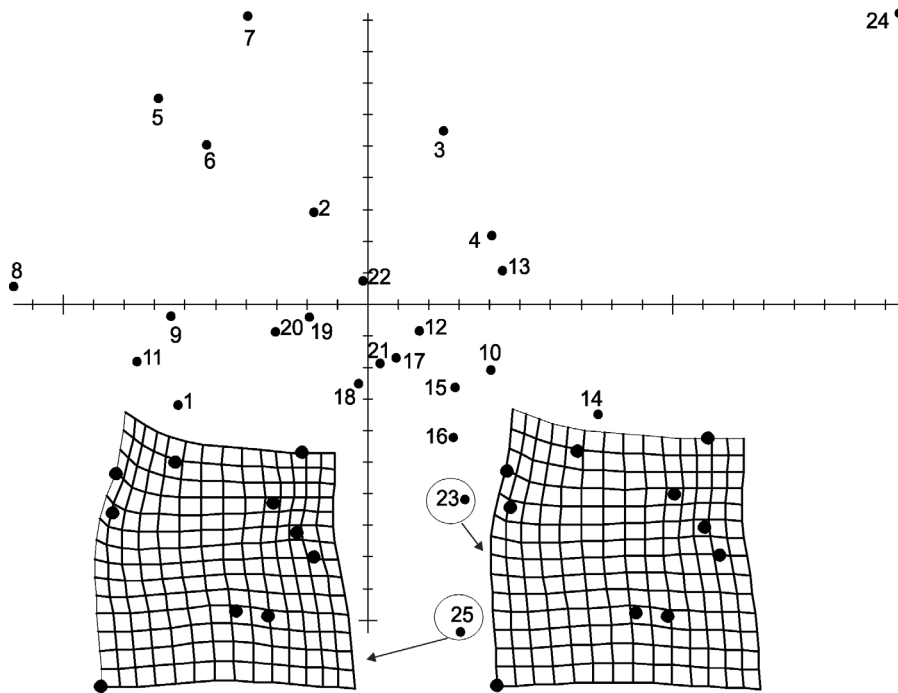
FIG. 4. Diagram of the Relative warps analysis and deformation grids. Specimens included: **1**. *Spheniscus magellanicus*; **2**. *S. humboldti*; **3**. *S. urbinai*; **4**. *S. muizoni*; **5**. *Pygoscelis adeliae*; **6**. *P. papua*; **7**. *P. antarctica*; **8**. *Eudyptes chrysocome*; **9**. *Madrynornis mirandus*; **10**. *Palaeospheniscus* MLP 91-VI-1-4; **11**. *P. biloculata* MLP 20-565; **12**. *P. patagonicus* MLP 20-68; **13**. *P. patagonicus* MLP 20-44; **14**. *P. patagonicus* MLP 20-43; **15**. *P. patagonicus* MLP 20-14; **16**. *P. patagonicus* MLP 20-530; **17**. *P. patagonicus* MLP 97-VI-1-3; **18**. *P. patagonicus* MLP 20-549; **19**. *P. patagonicus* MLP 20-534; **20**. *P. patagonicus* MLP 20-541; **21**. *P. patagonicus* MLP 20-549; **22**. *P. patagonicus* MLP 97-VI-1-1; **23**. *P. bergi* MLP 97-VI-1-1; **24**. *Paraptenodytes antarcticus* M619; **25**. Humerus under study MLP 96-XII-2-1.

variably developed *angulus preaxialis*, albeit always present and placed at approximately mid-length of the diaphysis, which is wide distally.

Differences between the humeri of *Palaeospheniscus* and *Spheniscus* are subtle. They can be separated only because of the small *facies musculi pectoralis* in *Palaeospheniscus*, and because of the deep and oblique *facies musculi supracoracoideus*, which is rounded and also slightly deeper than in *Spheniscus*. In agreement with Gölich (2007), we have observed that *Spheniscus* lacks the proximal notch between dorsal tubercle and humeral head, a feature presents in *Palaeospheniscus*.

There are also certain differences in the development of the lip-like projection that constitutes the edge of the *fossa tricipitalis*. In all species of *Spheniscus*, this projection can be seen in proximal view, while in the same view it remains hidden in *Palaeospheniscus*. The material described here perfectly fits into *P. bergi*, the smaller species of the genus.

Three recent phylogenetic hypotheses favor discussion of the differences observed between *Palaeospheniscus* and *Spheniscus* in a context including fossil and extant taxa. Several analyses were performed in the last years, in which humeri were scored. Among them, four characters were preliminarily analyzed by Acosta Hospitaleche (2004) and Acosta Hospitaleche *et al*. (2007), eighteen by Ksepka *et al*. (2006), twenty two by Clarke *et al*. (2007), and twenty seven by Ksepka *et al*. (2012). Only three of them showed differences in the portion of the humerus preserved in the studied specimen. The pit for the ligament insertion on the proximal surface adjacent to the head is deep in *Spheniscus*, whereas it is very shallow or absent in *Palaeospheniscus*. The surface attachment of the *m. supracoracoideus* and *m. latissimus dorsi* is separated by a wide gap in *Palaeospheniscus* and by a narrow gap or else is confluent in *Spheniscus*. Finally, the proximal margin of the *fossa tricipitalis* constitutes a weak projection

in *Palaeospheniscus*, while in *Spheniscus* it projects so as to be well-exposed in proximal view (see details in Ksepka *et al.*, 2006; Acosta Hospitaleche *et al.*, 2007; Clarke *et al.*, 2007, 2010; Ksepka and Clarke, 2010; Ksepka and Thomas, 2012).

5.3. Family *Spheniscidae* Bonaparte, 1831
Figures 3.4-3.7

Material: MLP 96-XII-2-2, a fragment of distal end of right coracoid (Figs. 3.4-3.6), and MLP 96-XII-3, a slightly damaged end of a left femur (Fig. 3.7).
Comments: Another distinctive character to differentiate Paleocene and Eocene penguins from Neogene and modern forms is the morphology of the coracoid. It has an S-shaped distal end in distal view, while it is arch-shaped in the younger forms (Acosta Hospitaleche and Di Carlo, 2010).

The tiny fragment of coracoid MLP 96-XII-2-2 allows comparison of its base with other fossil material. In distal view, the end draws an arc, like in all Neogene penguins and the Oligocene *Arthrodytes*, while an S-shape is typical of all the Eocene species, including the Antarctic, the New Zealand, and the Perúvian remains (Clarke *et al.*, 2007, 2010; Ksepka *et al.*, 2008; Ksepka *et al.*, 2012). This character restricts its taxonomic assignment to the Neogene South American records. Among them are the recent genera *Spheniscus* and *Pygoscelis* and the extinct *Palaeospheniscus, Madrynornis* and *Paraptenodytes*.

Preservation allows no precision in this sense. However, available evidence suggests that it belongs to the same individual of which the humerus is described above.

The femur labeled MLP 96-XII-2-3 is badly damaged and comparison with other material is meaningless.

5.4. Morphogeometric analysis of the penguin bones

The first two components of the morphogeometric analysis performed show (Fig. 4) a defined group comprising all the *Pygoscelis* species in the upper left corner (specimens 5-7; Fig. 4).

Spheniscus is divided into two groups, one constituted by the Pacific fossil species located at the upper right corner (3-4), and another formed by the living representatives, placed to the left part of the graph. As expected from previous phylogenetic analyses (*e.g.*, Acosta Hospitaleche *et al.*, 2007),

Madrynornis mirandus (9) is positioned between the modern species of *Spheniscus* (1-4) and *Eudyptes* (8). All the humeri of *Palaeospheniscus patagonicus* (specimens 12-22) are grouped in the centre of the graph., *Palaeospheniscus* sp. (11) is relatively near, and *P. biloculata* (10) is separated from them, and *P. bergi* (23) is close to the humerus described herein (25) and above assigned to *P. bergi*. Removed from all of them is *Paraptenodytes antarctica* (24), located at the upper right corner of the graph.

Grids of both specimens of *Palaeospheniscus bergi* show deformations mainly at the level of the *tuberculum dorsale* and the *incisura capitis*. Compared with extinct species of *Spheniscus*, which humeri is similar to that in *Palaeospheniscus bergi*, some differences are evidenced. The humerus-head is laterally wider and more proximally expanded in *Spheniscus* than in *P. bergi*. Besides, the *incisura capitis* is deeper and the *tuberculum dorsale* is more proximally located in *P. bergi* than in *Spheniscus*.

Outline analysis of the head reveals subtle shape differences between analyzed specimens. These differences (and similarities) are clearly reflected in figure 5.

The three extant *Pygoscelis* species (5-7) cluster in the upper right sector, representing the highest values in the first and second component. Next to them is *Eudyptes chrysocome* (8), while the three species of *Spheniscus*, whether fossil (4) or extant (1-2), fall in the lower values of the first axis and the middle values of the second axis.

All the fossils lie along the middle part of the first component and are represented by *Paraptenodytes* (24), *Madrynornis* (9) and the three species of *Palaeopsheniscus* (10-23); the latter lies along central values of the second component. The material from Cerro Plataforma (25) is once again placed in the proximities of *Palaeospheniscus bergi* (23).

6. Discussion and conclusions

'Isurus' hastalis is a common shark in temperate to warm waters around the world. In South America occur in both sides of the continent: in the Atlantic in the Miocene beds of Patagonia (Monte León, Chenque, and Gaiman formations; Cione and Expósito, 1980; Cione, 1988) and in the Pacific in the Navidad Formation of Chile (middle Miocene according to Encinas *et al.*, 2010; late Miocene to Pliocene according to Encinas *et al.*, 2006; recorded
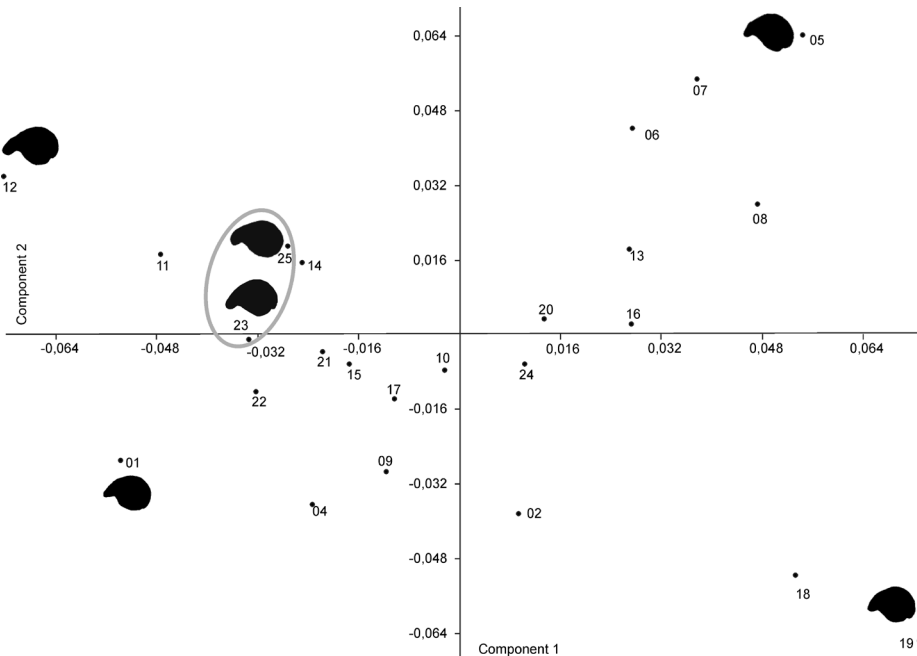
FIG. 5. Diagram of the Principal Component Analysis based on the outlines of the humerus in proximal view. Specimens included are the same as in figure 4.

by Suárez *et al*., 2006). *'Isurus' xiphodon* is common in the middle-lower Miocene Puerto Madryn and Paraná Formations (Cione *et al*., 2000). The sole tooth found in Cerro Plataforma can not be identified specifically. Thus, pinpointing Atlantic or Pacific affinities of this assemblage on the basis of its shark fossil content is not possible. However, the record of this species suggests that paleoenvironmental conditions were similar at either side of the continent at this latitude, as lamnid sharks are strictly marine fishes (Compagno, 2001), and the two recent species of *Isurus* are distributed in tropical and warm temperate seas.

During the early Miocene, the Atlantic penguin fauna was represented by four sympatric species along the Patagonian coast, *i.e*., *Eretiscus tonni* (Simpson, 1981)*, Palaeospheniscus bergi, P. patagonicus*, and *P. biloculata* (Acosta Hospitaleche *et al*., 2004, 2006b; Acosta Hospitaleche, 2007). *Madrynornis mirandus* was recorded exclusively in the middle Miocene (Acosta Hospitaleche *et al*., 2007). The Neogene Pacific fauna includes *S. megaramphus*, *S. urbinai*, *S. muizoni*, *S. chilensis*, *Pygoscelis calderensis* and *P. grandis* (genera with living representatives), in addition to remains assigned to the extinct *Palaeos-*

pheniscus sp. (Emslie and Correa Guerra, 2003; Acosta Hospitaleche *et al.*, 2007; Gölich, 2007; Stucchi, 2007; Yury-Yáñez *et al*., 2009; Rubilar-Rogers *et al*., 2012).

Only *Palaeospheniscus* -into which the studied specimens better fit- occurs in both Atlantic (Acosta Hospitaleche, 2004, 2007; Acosta Hospitaleche *et al*., 2008) and Pacific faunas (Acosta Hospitaleche and Stucchi, 2005; Soto Acuña *et al*., 2008). However, these faunas can be distinctly characterized. The Atlantic fauna is exclusively Miocene and all forms are closely related to each other. Early Miocene species belong either in *Palaeospheniscus* or *Eretiscus* (Acosta Hospitaleche *et al*., 2007) with no extant related groups; *Madrynornis mirandus* is only recorded in the middle Miocene. The Pacific fauna is Mio-Pliocene and, while including species referred to *Palaeospheniscus* too, it comprises also material referable to modern genera (Emslie and Correa Guerra, 2003; Acosta Hospitaleche *et al.*, 2007; Gölich, 2007; Stucchi, 2007; Yury-Yáñez *et al*., 2009; Rubilar- Rogers *et al*., 2012).

Palaeospheniscus is represented along the Atlantic and Pacific coasts of southern South America, but it is exclusively Miocene. It has been mentioned

as a frequent element in the Gaiman Formation (early Miocene) at Bryn Gwyn (Tonni, 1980; Acosta Hospitaleche, 2007, 2009; Acosta Hospitaleche *et al.*, 2007; Acosta Hospitaleche *et al.,* 2008), Chubut Province, Argentina; with some doubts in the middle Miocene-Pliocene Bahía Inglesa Formation in Chile (Acosta Hospitaleche *et al.*, 2002; Acosta Hospitaleche and Canto, 2005; Soto Acuña *et al.*, 2008); but certainly in the middle Miocene Chilcatay Formation in Perú (Acosta Hospitaleche and Stucchi, 2005).

As shown above using morphogeometric tools, the specimens from Cerro Plataforma fall within the morphological range of *P. bergi*, the holotype of which comes from the Gaiman Formation. This appears to point towards Atlantic affinities for the fossil penguin fauna in western Chubut. However, any certainty on the Atlantic or Pacific affinity of the bearing-rocks based on the penguin remains is challenged by the fact that there is material referable to this genus in rocks exposed along both sides of the present Andes. The Chilean specimens have not been identified at a specific level. Thus, there are two different scenarios, *i.e.*, *Palaeospheniscus bergi* did in fact live throughout the known range of the genus and therefore the unidentified Chilean specimens can be allocated to this species, or else the Chilean specimens are not assignable to *P. bergi* and belong to a new undescribed species. If the latter were the case, then the Atlantic affinities of the species from Cerro Plataforma would point towards an Atlantic connection of the basin in which the bearing-rocks were deposited. However, it is premature to determine this at present.

Acknowledgments

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