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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 morfo-geométricos 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 (Lizuain, 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 (Lizuain, 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).
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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 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 capitidis 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 Sphe niscus 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; Póthe de Baldis, 1984; Chiesa and Camacho, 2001; Barreda and Palazzesi, 2007; Barreda et al., 2003; Casadio et al., 2004; Gia cosa 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
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, 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) 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).

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). Middle Eocene Grand Stairs Formation of New Zealand (Clarke and Stucchi, 2005; Clarke et al., 2007, 2010; Ksepka and Clarke, 2010; Ksepka et al., 2008) and the middle to upper Eocene Rio Turbio, Loreto, and Rio 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; Göhlisch, 2007; Acosta Hospitaleche et al., 2011).

5.2. Family Spheniscidae Bonaparte, 1831

Genus Palaeospheniscus 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; Göhlisch, 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 Göhlisch, 2007). In the extinct species S. urbinai and S. chillensis they measure 104 and 70.3 cm respectively (Stucchi, 2002; Emslie and Correa Guerra, 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 chillensis was not compared with Palaeospheniscus in Emslie and Correa Guerra (2003). However, the holotype of S. chillensis 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
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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 *Arthropodytes*, while an S-shape is typical of all the Eocene species, including the Antarctic, the New Zealand, and the Peruvian 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 *Palaeospheniscus* (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
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 cannot 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 Palaeospheniscus 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.

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