Main pathways in the evolution of the Paleogene Antarctic Sphenisciformes

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A B S T R A C T

The Seymour Island fossil penguins from the Cross Valley and La Meseta Formations, Seymour Island (James Ross Basin; late Paleocene, and Eocene/?early Oligocene respectively) constitute the most complete stratigraphic records of the group known in the world. In addition to the geographic and stratigraphic thoroughness of the collected fossil remains, they offer a unique opportunity to the understanding of the major evolutionary patterns of the Sphenisciformes. We analyze their taxonomic diversity and abundance in La Meseta Formation, in a context of the spread patterns of the Paleogene penguins in relationship to the Antarctic Circumpolar Current incidence. Our data suggest that the highest diversity and geographical distribution (Antarctica, South America and Australasia) in the Late Eocene were linked to water-cooling events and the opening of the Drake Passage. However, the first divergence of the group is documented in the Early Eocene. This fact supports that a marine dispersion of the Weddellian penguins to other continents occurs when there was a shallow and warm ocean current circulation (Weddellian Current) flowing along the western margin of West Antarctica and South America The phylogenetic analysis and the recent discoveries in the Eocene of Chile and Peru support the hypothesis that establishes one of the way for the dispersion of the Weddellian species from the Peninsula Antarctica was the Pacific coast during the early Eocene.

1. Introduction

Nowadays four penguin species, *Aptenodytes forsteri* (Emperor penguin), *Pygoscelis adeliae* (Adelie penguin), *Pygoscelis antarctica* (Chinstrap penguin), and *Pygoscelis papua* (Gentoo penguin), breed on Antarctica and sub-Antarctic islands. This extant scenario with an impoverished amount of penguin species has a marked contrast with the scenario found in the Paleogene of the Antarctic Peninsula.

The last phylogenies of the Sphenisciformes reveals that important radiations of both small and large Weddellian penguins (species living in the Weddellian Province, defined by Zinsmeister, 1982) took place during the Late Paleocene/Late Eocene (between ∼55 Ma and 34 Ma) in West Antarctica, so an important and significant part of the evolution of the Sphenisciformes occurred in Southern high latitudes (∼65°S) as it is documented in Early Paleogene geologic units of Antarctic Peninsula, James Ross Basin, Weddell Sea (Myrcha et al., 2002; Tambussi et al., 2006; Jadwiszczak, 2006, 2008, 2009; Tambussi and Acosta Hospitaleche, 2007; Acosta Hospitaleche and Reguero, 2010; Acosta Hospitaleche and Di Carlo, 2010, 2012).

The Seymour Island fossil penguins from the Cross Valley and La Meseta Formations, Seymour Island (James Ross Basin; late Paleocene, and Eocene/?early Oligocene respectively) constitute the most complete stratigraphic records of the group known in the world. The diversity and abundance of the remains, in addition to the geographic (Fig. 1) and stratigraphic thoroughness of the collected fossil remains (Fig. 2), offer a unique opportunity to the understanding of the major evolutionary patterns of the Sphenisciformes.

The earliest representatives of penguins appeared ∼60 Ma (Slack et al., 2006; Tambussi et al., 2005). The two oldest undisputed records of the order come from New Zealand. *Waimanu manneringi* Jones, Ando and Fordyce 2006, from the early Paleocene and *Waimanu tuatahi* Ando, Jones and Fordyce 2006 from the late Paleocene suggest that the sphenisciforms diverged by the early Paleocene (Slack et al., 2006).

The primitive penguin *Crossvallia unienwillia* Tambussi et al., 2005 (found in the late Paleocene Cross Valley Formation of Seymour [= Marambio] Island) is the oldest Antarctic spheniciform (Tambussi et al., 2005). *Crossvallia unienwillia* represents a primitive medium-sized penguin species very close to the rest of the Antarctic basal sphenisciforms. Its presence in the Late Paleocene of West Antarctica suggests the first appearance of breeding colonies in the area around 55 Ma.

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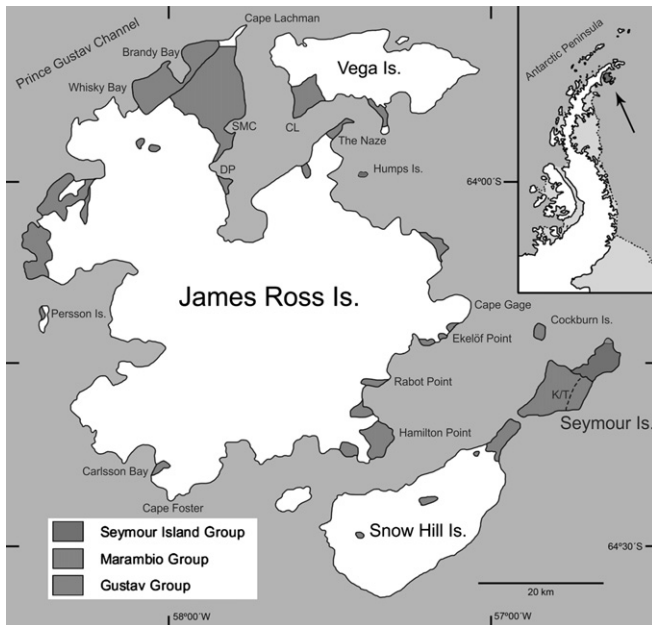
Fig. 1. Schematic geological map of the James Ross Basin, Weddell Sea, north-eastern Antarctic Peninsula. White areas are either the James Ross Island Volcanic Group or snow/ice cover. Locality key: DP, Dreadnought Point; BB, Brandy Bay; CL, Cape Lamb; SMC, Santa Marta Cove. Position of the Cretaceous-tertiary boundary on Seymour Island indicated by the symbol K/T.

Considering the significant amount of most likely co-existing (Tambussi and Acosta Hospitaleche, 2007; but see Jadwiszczak, 2008, 2009) species of the Eocene Antarctic penguins (Fig. 2), it is expected that Paleocene colonies were not mono-specific. These breeding colonies would have evolved into increasingly diverse fauna, resulting into fourteen species, grouped into seven genera (Tambussi and Acosta Hospitaleche, 2007; but see Jadwiszczak, 2008, 2009) which are represented by about 2500 isolated remains and three partially articulated specimens (Acosta Hospitaleche and Di Carlo, 2010; Acosta Hospitaleche and Reguero, 2010; Jadwiszczak, 2010, 2012).

The number of known Antarctic fossil spheniciforms relatively varies from one in the late Paleocene Cross Valley Formation (Tambussi et al., 2005), one in the Valle de la Focas (according to Jadwiszczak, 2006), currently assigned to Ypresian Early Eocene age (although Montes et al., 2010 considered it Late Paleocene-Thanetian-); one in the Ypresian Acantilados Allomembers (Jadwiszczak, 2006; see also Jadwiszczak and Chapman, 2011), probably two in the Ypresian Campamento Allomember to eight species in the Ypresian *Cucullaea* I Allomember (Acosta Hospitaleche and Reguero, 2010; Reguero et al., 2013).

The first large-scale radiation of the spheniciforms is documented in the Ypresian horizons of the *Cucullaea* I Allomember of Seymour Island (Early Eocene, ∼49–52 Ma). The following eight species were identified: *Anthropornis nordenskjoeldi* Wiman, 1905, *Anthropornis grandis* (Wiman, 1905), *Palaeeudyptes gunnari* (Wiman, 1905), *Palaeeudyptes klekowskii* Myrcha et al., 1990, *Delphinornis larseni* Wiman, 1905, *Mesetaornis polaris* Myrcha et al., 2002; *Marambiornis exilis* Myrcha et al., 2002, *Archaeospheniscus wimani* (Marples, 1953), whereas the presence of *Delphinornis arctowskii* Myrcha et al., 2002, and *Delphinornis gracilis* Myrcha et al., 2002 are dubiously identified (Myrcha et al., 2002; Tambussi et al., 2006; Tambussi and Acosta Hospitaleche, 2007).

Finally, the highest horizons of La Meseta Formation (Priabonian, Late Eocene, Submeseta Allomember, ∼34–36 Ma) document the major taxonomic and body size diversity with 14 species

(Tambussi et al., 2006; see also Jadwiszczak and Mörs, 2011) co-occurring sympatrically. Discrepancies in the number of recognized species resulted from the questionable presence of *Archaeospheniscus lopdelli*, *Palaeeudyptes antarctica* and two species of the genus *Tonniornis* in the Biozone of *Anthropornis nordenskjoeldi* (Tambussi et al., 2006; Tambussi and Acosta Hospitaleche, 2007; Jadwiszczak, 2006).

This contribution analyze the taxonomic diversity and abundance of the Spheniciformes of the La Meseta Formation, in a context of the evolutionary patterns of the group and the relationships with tectonic events, i.e. opening of the Drake Passage and the establishment of the Antarctic Circumpolar Current (ACC).

2. Material and methods

Antarctic fossil penguin specimens used in this study are housed at the División Paleontología Vertebrados, (DPV) of the Museo de La Plata (MLP), Argentina. Data published by Jadwiszczak (2006), Clarke et al. (2007, 2010), and Sallaberry et al. (2010) were also considered.

Systematic framework follows Tambussi et al., 2006, and Tambussi and Acosta Hospitaleche, 2007, while phylogenetic relationships are after Clarke et al. (2010), and Ksepka et al. (2006, 2012). Stratigraphic arrangement and facies analysis used here are according to Marenssi et al. (1998a, 1998b), and paleogeographic hypothesis is based on that by Eagles (2010).

The taxonomic diversity calculations utilized formulas proposed by Clarke and Warwick (1998) using past software, version 2.13 (2012) (Hammer et al., 2001). The analysis was based on a presence-absence data matrix (Appendix A).

3. Paleogeography and biogeography of the final breakup of Gondwana

The opening of the Drake Passage and the Tasman Rise diminished the main seaway that spread from eastern Australia, through western Antarctica and into southern South America (Lawver and Gahagan, 2003). Drake Passage (Fig. 3) is the narrowest part of a Cenozoic circum-Antarctic seaway and its presence is necessary for the existence of the Antarctic Circumpolar Current (ACC).

3.1. Opening of the Drake Passage and the establishment of the Antarctic Circumpolar Current (ACC)

The opening of the Drake Passage gateway is thought to have been an important event in the history of global oceanic and atmospheric circulation. It allowed for the free transfer of water masses between the Pacific and Atlantic oceans at mid to high southerly latitudes for the first time since the breakup of Gondwana. The timing and mode of the opening of the central Scotia Sea are still among the greatest uncertainties to understand the opening of the oceanic floor of the Drake Passage. Eagles et al. (2006) suggested that subsidence in the area of two small oceanic basins in the southern Scotia Sea (Dove Basin and Protector Basin) east of Drake Passage had been underway at ∼50 Ma, producing a deepening of the rift that gave way to seafloor spreading in the Dove Basin by around 41 Ma. The spreading in the region of these two basins would have opened Drake Passage to shallow or intermediate depth oceanic circulation between the Pacific and Atlantic oceans for the first time.

Subsequent regional shallowing may be related to subduction-related processes that preceded back-arc extension in the East Scotia Sea. The presence of a fragment of Jurassic − Cretaceous ocean floor in the gateway implies that deep water connections through the Scotia Sea Basin complex may have been possible since
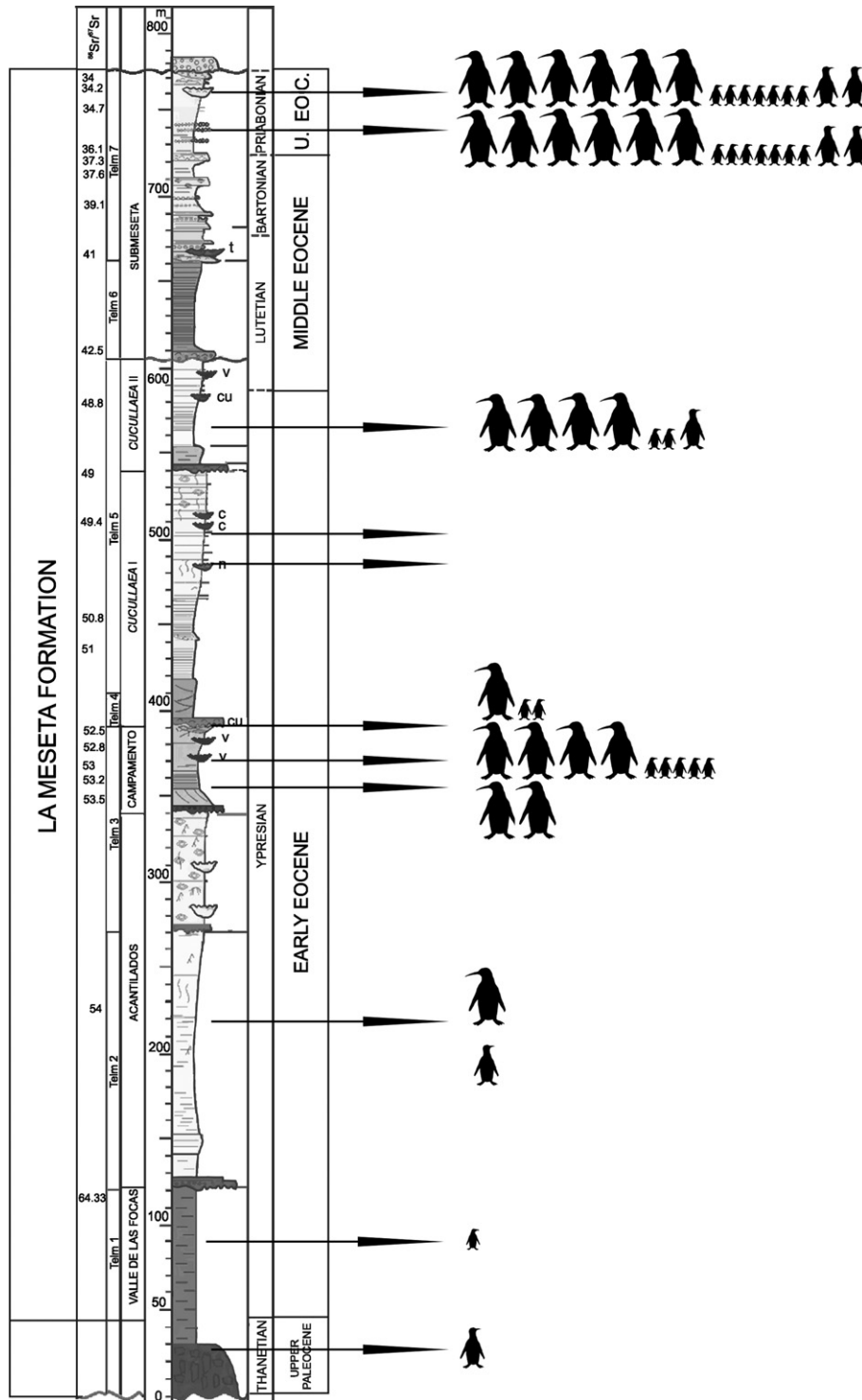
Fig. 2. Stratigraphical record of Seymour Island Sphenisciformes (Cross Valley and La Meseta Formations). Strontium date values from Dingle et al. (1998); Dutton et al., 2002; Reguero et al., 2002 and Ivany et al., 2008. Abbreviations: cu. *Cucullaea*, n. naticids, v. veneroids, and t. *Turritella*.

Eocene times when the continental tips of South America and the Antarctic Peninsula first passed each other.

The final Paleogene isolation of South America probably did not occur until a deep-water seaway developed between southern South America and the Antarctic Peninsula. This seaway was the main factor that helped to keep the ecological affinities of marine vertebrate assemblages along different areas of the Weddellian Biogeographic Province (Zinsmeister, 1979). Meanwhile, endemic

assemblages seem to be restricted to shallower waters, suggesting that these occurred as consequence of local biogeographic barriers. Opening of the Drake Passage gateway between the Pacific and Atlantic oceans has been linked in various ways to Cenozoic climate changes. All but one of the available constraints on the age of the central Scotia Sea is diagnostic of, or consistent with, a Mesozoic age. Comparison of tectonic and magnetic features on the seafloor with plate kinematic models shows that it is likely to have accreted

Fig. 4. Paleogeographic reconstruction of the southern continents (Gondwana) and the Weddellian province at 50 Ma (Ypresian) showing the probable dispersal of Weddellian Sphenisciformes (dotted lines and arrows). Black circles represent fossil localities discussed in the text.

Fig. 3. The opening of the Drake Passage and the Scotia and Weddell Seas. AP, Antarctic Peninsula; CSS, central Scotia Sea; DP, Drake Passage; ESS, east Scotia Sea; MEB, Maurice Ewing Bank; PB, Protector Basin; Pow, Powell Basin; JB, Jane Basin; SAAR, South American–Antarctic ridge; SG, South Georgia; SST, South Sandwich Trench; TdF, Tierra del Fuego; WSR, west Scotia Ridge; WSS, west Scotia Sea.

to a mid-ocean ridge between the South American and Antarctic plates following their separation in Jurassic times.

3.2. Weddellian Biogeographic Province

By the Late Cretaceous, the Antarctic Peninsula and the remainder of West Antarctica are believed to be comprised of a number of discrete micro-continental blocks forming a single elongated landmass that extended southward from southern South America (Fig. 4). Since the early Cretaceous, the Antarctic Peninsula has been in its present position relative to South America, at almost the same paleolatitude (60–65°S) (Lawver et al., 1992), but became glaciated later: a cool but not glacial early Cenozoic Antarctic climate is widely accepted (see Dingle et al., 1998; Stilwell and Feldman, 2000; Dutton et al., 2002). Before that, the northern tip of the Antarctic Peninsula and southernmost South America (the Magellanic Region) were connected facilitating both floristic and faunal interchange (Olivero et al., 1991; Marenssi et al., 1994; Shen, 1995; Reguero et al., 1998, 2002; Reguero and Marenssi, 2010).

The Weddellian Zoogeographic Province, conceived by Zinsmeister (1979, 1982) on marine molluscan, echinoderm and arthropod faunas, is thought to be a cool temperate, shallow water region which extended from southern South America (the Magellanic Region in Chile, and Tie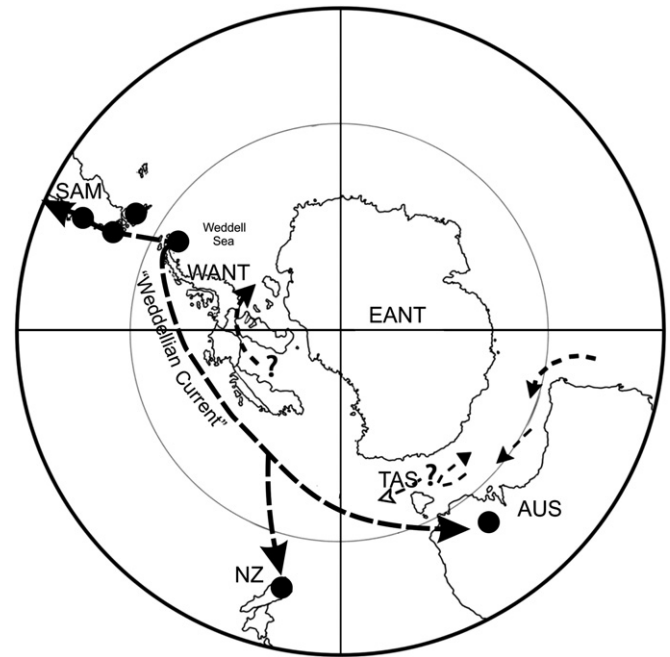rra del Fuego and Santa Cruz provinces in Argentina), along the Antarctic Peninsula and West Antarctica, to New Zealand, Tasmania and southeastern Australia (Fig. 4). Case (1988) expanded this concept to a "biogeographic province" with the inclusion of terrestrial plants and mammals. This province existed from the Late Cretaceous through the Eocene when Australia, Antarctica, and southernmost South America were in proximity (Zinsmeister, 1979, 1982; Woodburne and Zinsmeister, 1984).

Recent reconstructions of the Late Cretaceous palaeogeography of the southern hemisphere show a continuous landmass extending from South America to Australia (i.e., Lawver and Gahagan, 2003). During the Late Cretaceous, the western sector of Gondwana was apparently divided into a number of distinct tectonic units: South America, West Antarctica (comprised of the Antarctica Peninsula, Marie Byrd and Ellsworth lands); and Ellsworth and Whitmore mountains (Dalziel and Elliot, 1982). Woodburne and Case (1996) assumed that there may have been a terrestrial link between South America and Australia via Antarctica but it ended by 64 Ma when the South Tasman Rise submerged.

4. Geological setting and age constraints

The Paleogene succession in the James Ross Basin (del Valle et al., 1992) is part of the Paleocene to earliest Oligocene? Seymour Island Group, deposited in mid and inner-shelf settings in a back-arc basin associated with the Antarctic Peninsula magmatic arc to the west, and open to the Weddell Sea to the east (Hathway, 2000; Crame et al., 2004). The James Ross Basin was bounded to the west by coastal plains on the flanks of the Antarctic Peninsula with a shoreline trending approximately north–northeast to south–southwest. Major rivers brought sediment sourced from the Antarctic Peninsula into deltaic systems that accumulated siliciclastic deposits offshore (Zinsmeister, 1982; Pirrie, 1989; Scasso et al., 1991; Olivero et al., 1992; Hathway, 2000; Crame et al., 2004; Olivero et al., 2008).

The Paleogene section exposed mainly on Seymour Island includes the Late Paleocene unit Klb 10 of the López de Bertodano Formation, Sobral Formation, Cross Valley Formation and the richly fossiliferous early Eocene-earliest Oligocene? La Meseta Formation, all of them deposited in incised valley settings. The last two units, Cross Valley and La Meseta Formations, yield Weddellian spheniciforms (Acosta Hospitaleche and Reguero, 2011; Reguero et al., 2013).

4.1. Cross Valley Formation

At its type section in the middle part of Seymour Island, the Cross Valley Formation (Elliot and Trautman, 1982) fills a steep-sided valley cut in the Lower Paleocene Sobral Formation and older beds. The width of the incised valley is 600 m at a maximum and the valley fill consists of more than 120 m of coarse sands and axial mass flow deposits overlain by some 40 m thick post-valley fill finer-grained beds. The base of this unit is a concave-up unconformity oriented in an NW-SE direction with steep, asymmetrical sides. The southern edge dips 45° towards the North while the northern margin plunges 35° to the South. The top of the unit is another unconformity at the base of the La Meseta Formation. The younger beds cut by the basal unconformity are dated as Danian while the oldest sediment covering these units are regarded Early Eocene. Dinoflagellates and pollen collected from the upper part of the Cross Valley Formation also suggest a Late Paleocene age for this unit (Askin, 1988; Wrenn and Hart, 1988).

The Cross Valley Formation has been divided into three informal allomembers (Marenssi et al., 2012). The Cross Valley A Allomember (lower Cerro Arañado Member) comprises coarse-grained pebbly volcaniclastic sandstones with carbonised wood (Tpcv1 and 2 of Sadler, 1988) and it is post-Danian in age due to its unconformable boundary with the underlying Sobral Formation. The medium to coarse-grained, bluff-forming volcaniclastic sandstones of the Cross Valley B Allomember (Wiman Member) transitionally covers the former and comprises Sadler's (1988) Tps5 unit, the "Wiman Formation" (Elliot and Hoffman, 1989) beds and the Tpcv 3–4, being dated as early Upper Paleocene (Askin, 1988). The upper The Cross Valley C Allomember (Bahía Pingüino Member) rests on an erosional surface draped with slide-blocks and covered with dark, homogeneous mudstones with scattered and poorly preserved marine fossil remains like shark and fish teeth, gastropods, bivalves and crinoids. The fossil penguin bones discussed in this paper were unearthed *in situ* from a single level few meters from the base of this unit. This lithofacies is in turn sharply overlain by an alternation of medium to fine-grained sandstones and mudstones containing few pieces of silicified tree trunks and well preserved plant-leaf fossils (Dusén, 1908) dated as Upper Paleocene. The lower part (Cross Valley A and B Allomembers) consisting of coarse-grained volcaniclastics are referred mainly to axial mass-flow deposits (Doktor et al., 1988; Elliot, 1995). The upper third (The Cross Valley C Allomember) made up of fine to very fine siliciclastic sandstones and mudstones represent sedimentation in very shallow marginal marine to transitional (deltaic) environments developed after most of the relief was subducted.

4.2. La Meseta Formation

The Early Eocene to earliest Oligocene? La Meseta Formation (Elliot and Trautman, 1982) in Seymour and Cockburn islands, close to the northern tip of the Antarctic Peninsula, Antarctica is an unconformity-bounded unit (La Meseta Alloformation of Marenssi et al., 1996, 1998a). This unit rests unconformably on either the Late Cretaceous López de Bertodano Formation or on the Paleocene

Sobral and Cross Valley Formations (Sadler, 1988; Porębski, 1995; Marenssi et al., 1998b).

The La Meseta Formation has a maximum composite thickness of 720 m filling up a 7 km wide valley cut down into the older sedimentary rocks of the island after the regional uplift and tilting of the Paleocene and Marambio Group beds. The La Meseta Formation comprises mostly poorly consolidated siliciclastic fine-grained sediments deposited in deltaic, estuarine and shallow marine environments as a part of a tectonically-controlled incised valley system (Marenssi, unpublished; Marenssi et al., 1998b; for an alternative interpretation see Porebski, 1995, 2000), which spans nearly all of the Eocene, and for some authors includes the Eocene-Oligocene boundary (Ivany et al., 2006). It is composed of sandstones and mudstones with interbedded shell-rich conglomerates. It was subdivided by Sadler (1988) into seven lithofacies units (Telm1-7), and posteriorly organized into six erosionally-based internal units, named from base to top Valle de Las Focas, Acantilados, Campamento, *Cucullaea* I, *Cucullaea* II and Submeseta Allomembers (Marenssi et al., 1998b). These units were deposited during the Eocene in deltaic, estuarine and shallow marine settings, mostly within a northwest-southeast trending valley (Marenssi et al., 1998a, 1998b).

5. Discussion

The evolutionary history of penguins was mostly marked by events of consecutive radiations and extinctions during the Paleogene in Antarctica, which explains the modern penguin diversity (Fig. 5).

5.1. Biogeographical implications for Weddellian Spheniciformes distribution: evidence from stratigraphically calibrated phylogenetic analyses

Stratigraphically calibrated, specific-level phylogenies of Spheniciformes have recently been published by Ksepka and Clarke (2010), Clarke et al. (2010) and Ksepka et al. (2012). These analyses provide a simple and straightforward directional explanation for the distribution of spheniciformes through time, and are also highly consistent with stratigraphic ordering of the taxa. However, incompleteness of the fossil record reflected in these analyses is meaning that minimum divergence times must be established through the calculation of 'ghost lineages'.

These phylogenies reveal that important radiations of small and large Weddellian penguins took place during the Late Paleocene/Early Eocene in the Antarctic Peninsula. The Late Paleocene *Crossvallia unienwillia*, not included in the phylogenetic analyses of Ksepka and Clarke (2010), Clarke et al. (2010) or Ksepka et al. (2012), seems to have a significant role in the evolution of the Weddellian penguins. Derived features present in the crown group like 1) a more flattened humerus and 2) development of a trochlea for the tendon of *m. scapulotriceps* at the distal end of the humerus, are present in *Crossvallia* but absent in the Paleocene *Waimanu* spp. from New Zealand. Therefore *Crossvallia* would be more closely related to the crown group than the others Paleocene species. The Paleocene *Waimanu* spp. from New Zealand are placed as stem group by Ksepka and Clarke (2010), indicating that they might play an important role in the origin of the spheniciformes clades. The most recent common ancestor of *Crossvallia* and living penguins (Spheniscidae) is thus inferred to be likely present by the late Paleocene in Antarctica.

Clarke et al. (2010) found the Weddellian *Palaeeudyptes klekowski* and *P. gunnari* to be part of an unresolved tetrachotomous clade (Clade X) that includes the New Zealand Burnside "*Palaeeudyptes*" and the Peruvian *Inkayacu paracasensis* providing
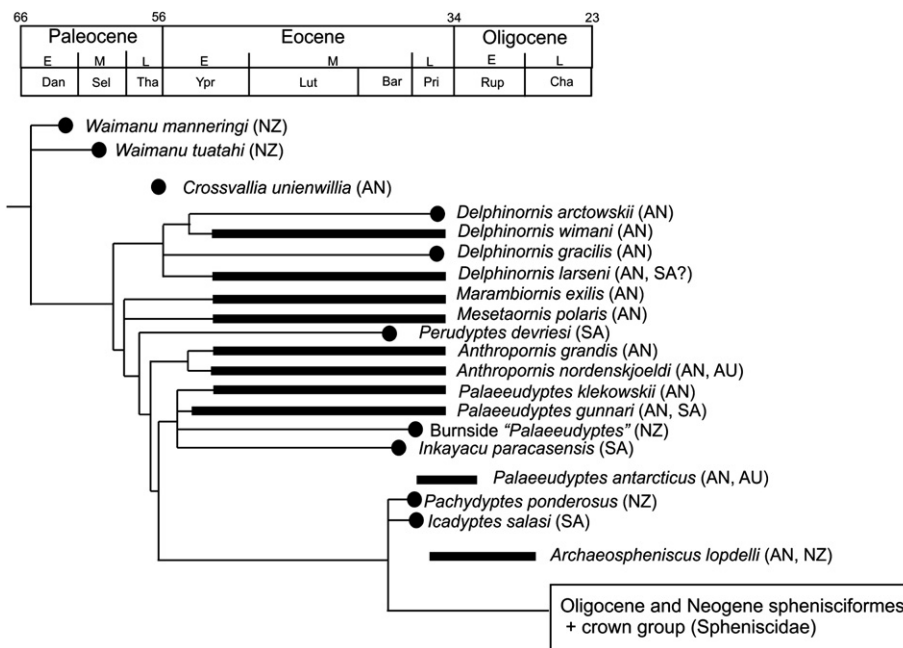
Fig. 5. Phylogeny of basal Sphenisciformes calibrated to the Paleogene stratigraphic record, Seymour Island, Antarctic Peninsula. Phylogeny redrawn and modified from Ksepka and Clarke (2010) and Clarke et al. (2010). Most penguins (14 species) from the La Meseta Formation, Seymour Island occur in Submeseta Allomember (Telm 7 of Sadler, 1988, 34.2–36.1 Ma), but a few species (8) have been reported from lower units (see Myrcha et al., 2002; Jadwiszczak, 2006), accounting for the extended ranges of *Delphinornis larseni*, *Anthropornis grandis*, and *Palaeeudyptes gunnari*. Minimum estimated times that these taxa diverged from their older sister taxa are based on ghost lineages indicated by black horizontal lines. Geographical locality for fossil taxa is provided in parentheses following taxa names. Abbreviations: AN, Antarctica; AU, Australia; NZ, New Zealand and surrounding islands; SA, South America.

evidence for an Early Eocene giant penguin clade with a wide Southern Ocean distribution and for an early-stem penguin dispersal to low latitudes. Jadwiszczak (2011) opined that *Palaeeudyptes gunnari* and *I. paracasensis* had been very closely related, by the possessing of (1) paired grooves meeting at the midline on the premaxilla, and (2) a distally tapering medial condyle and a tab-like process on the ventral surface on the femur.

Palaeeudyptes is a key taxon with an important biogeographic significance in the group. It seems to be the most widespread Weddellian penguin genus in the Southern Hemisphere during the Eocene and probably the Oligocene. The FAD (First Appearance Datum) of *Palaeeudyptes* is located within the Ypresian Campamento Allomember (52 Ma) (Tambussi and Acosta Hospitaleche, 2007; Acosta Hospitaleche and Reguero, 2010).

Early Eocene Sphenisciformes diversity supports several separate dispersals of Weddellian giant penguins from Antarctica to lower latitudes during greenhouse earth conditions: Australia (late Eocene, paleolatitude ~33°S, Jenkins, 1974), New Zealand (late Eocene/early Oligocene, paleolatitude ~45°S, Simpson, 1971), Argentina (middle Eocene, paleolatitude ~54°S, Clarke et al., 2003), Chile (middle to late Eocene, paleolatitude ~52°S, Sallaberry et al., 2010), and Peru (middle to late Eocene, paleolatitude ~14°S, Clarke et al., 2010).

By the Late Paleocene/Early Eocene at least nine Weddellian penguin species lived sympatrically in Seymour Island, Antarctic Peninsula (Fig. 1). *Palaeeudyptes gunnari* and other fossil species indicate that the group attained the widest geographical distribution prior to the late Eocene (Clarke et al., 2003; Tambussi et al., 2005; Clarke et al., 2007, 2010; Sallaberry et al., 2010) indicating that a second early-stem penguin dispersal to low latitudes originated in the Antarctic Peninsula (Weddell Sea) region (Clarke et al., 2010).

Diversity analysis shows that penguin diversity peaks in the late Eocene, by which time these birds were taxonomically diverse (Fig. 6), geographically widespread, and abundant at many localities (e.g., Marples, 1952; Myrcha et al., 2002). Currently, 14 diagnosable species are recognized from late Eocene deposits (see however Jadwiszczak, 2009), a total approaching modern global species-level diversity (16 species).

5.2. Ecological implications of the taxonomic and morphologic diversity

As far as we know, there are no cases in which 10 or 14 different seabird species coexist in the same coast (as the Eocene assemblages), or in neighboring breeding colonies. The *Anthropornis nordenskjoeldi* biozone represents an ecologically interesting case (Tambussi et al., 2006). Two different ideas have been proposed in order to explain such high penguin diversity: (1) the time averaging of the deposits and (2) the overestimation in the number of species.
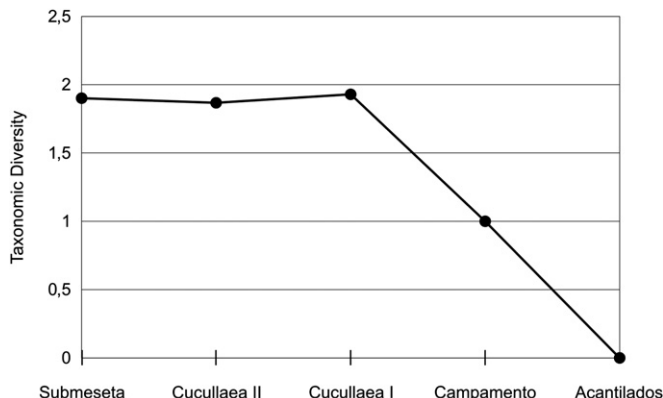

Fig. 6. Taxonomic diversity diagram.

Most if not all the remains recovered from the *Anthropornis nordenskjoeldi* biozone (a part of the Submeseta Allomember) were transported at least for a short time before burial and therefore their accumulations represent parauthochtonous assemblages. However, time averaging is at a minimum and fossils are approximately contemporaneous with the entombing sediments (see Stilwell and Zinsmeister, 1992). Phosphatic inarticulate brachiopods (*Lingula* sp.) attached to some of the bones also support this idea (Tambussi et al., 2006 and references cited therein).

Regarding the overestimation in the number of species, Jadwiszczak and Mörs (2011) revised the morphological variation, and proposed a scheme that would reduce this number from fourteen to ten (still a high number of sympatric species). It is clear that the Eocene penguins of Seymour Island constitute an assemblage that has no modern analogues.

Among modern seabirds the presence of mixed-species colonies due to space limitations and the advantages in predator defense is widespread (Croxall and Prince, 1980; Frere et al., 2008). Pursuit-diving species avoid inter-specific competition that reduces foraging efficiency (Henkel, 2009) through ecological segregation. These strategies include species-specific differences in foraging areas (e.g., Croxall and Prince, 1980; Trivelpiece et al., 1987; Weimerskirch et al., 1993; Frere et al., 2008; Wilson, 2010), diving depths (e.g., Mori and Boyd, 2004; Wilson, 2010), diet choice (e.g., Baltz et al., 1979; Ridoux, 1994; Kato et al., 1996; Weiss et al., 2009), or diurnal foraging patterns (Wilson, 2010).

Another theory suggests that species foraging on the same prey could reduce competition and live sympatrically when their body sizes are different (Hutchinson, 1959) and consequently forage on preys of different sizes. It is certainly true for living assemblages (Spear and Ainley, 2007; but see also Wilson, 2010).

At least three cranium and mandible morphotypes were distinguished in the La Meseta Formation (Acosta Hospitaleche and Haidr, 2011; Haidr and Acosta Hospitaleche, 2012; see also Jadwiszczak, 2011; Ksepka and Bertelli, 2006). Besides, a wide spectrum of body sizes is present in the Biozone of *Anthropornis nordenskjöeldi*, including birds smaller than the living little blue penguin *Eudyptula minor*, as well as giant penguins, largest than the Emperor penguin *Aptenodytes forsteri* (Jadwiszczak and Mörs, 2011).

Studies of living communities revealed that diving birds are flexible in their use of pelagic and benthic space according to differences in the conditions among years (Miller et al., 2009). This strategy about the variation in the use of space would support competition for resources when the number of sympatric species is not constant through the time. During Late Eocene, the number of sympatric species increases. In this sense, Masello et al., 2010 found that such flexibility is also encountered in response to small-scale habitat differences such as the presence of conspecific nearby colonies. Penguins from the same species develop strong differences in foraging areas, diving depth, time of foraging and prey choice, breeding in different colonies at the same island (Masello et al., 2010).

5.3. The opening of the Drake Passage and its implications for the dispersion of penguins

It is a common opinion that the distribution of living and fossil penguins is strongly linked to cool temperate waters. The origin of the Sphenisciformes was triggered by water-cooling resulting from the evolution of modern circulation patterns in the Southern Ocean. Presumably, temperature was an important factor driving evolutionary and ecological change at high latitudes during the Eocene, but it has not been clearly demonstrated. The northern Antarctic Peninsula experienced a very warm, wet, non-seasonal climate during the early Eocene climatic optimum (EECO), which persisted until early Middle Eocene times (~47 Ma)(see Zachos et al., 2001). Temperatures thereafter became progressively cooler during a wet, strongly seasonal period in the middle Middle Eocene that lasted until ~42 Ma (Zachos et al., 2001).

In Seymour Island, given the uncertainty in strontium isotope age estimates within La Meseta Formation, it is likely that maximum temperatures near the base of the Campamento Allomember (= Telm 3 of Sadler, 1988) reflect the EECO. Strontium isotope ratios from Acantilados Allomember (= Telm 2 of Sadler, 1988) consistently yield age estimates of ca. 54 Ma (Ivany et al., 2008), indicating that the EECO (roughly 51–53 Ma; Zachos et al., 2001) should be encompassed within the La Meseta Formation. Maximum inferred temperatures in Campamento Allomember are ~15 °C, at least 4–5 °C warmer than earlier or later samples. The degree of warmth slightly exceeds that seen in the global deep-ocean record (Zachos et al., 2001).

Scher and Martin (2006) suggest that cooling immediately following the Middle Eocene Cooling (MECO) is coincident with the opening of the nascent Drake Passage, and that associated changes in circulation and productivity led to a drawdown of CO_2 that may have accelerated cooling and brought about the proposed transient middle Eocene glaciation. These authors utilized a rare earth element neodymium (Nd) contained in fish teeth extracted from deep sea cores taken in the south Atlantic Ocean between southern Africa and Queen Maud Land on the Antarctic craton to provide data on a deepwater opening of the Drake Passage. They suggested an influx of shallow Pacific seawater approximately at 41 Ma. Subsequent increases of values of Nd during the late Eocene most likely represent progressive widening and deepening of the gateway.

Livermore et al. (2005) proposed a shallow water opening (<1000 m deep) as early as 50 Ma based on tectonic evidence gathered from the Weddell Sea. They correlated the formation of new tectonic basins in the area that will later become the Scotia Arc and the northern Antarctic Peninsula, with a drop in southern ocean temperatures based on oxygen isotope data from benthic foraminifera to represent the initial shallow water opening between South America and Antarctica. Eagles et al. (2006) indicated that subsidence in the area of some small oceanic basins in the southern Scotia Sea east of Drake Passage, was underway at ~50 Ma, producing a deepening shallow- or intermediate-depth rift that gave way to seafloor spreading in the Dove Basin by around 41 Ma. Basin opening coincided with a sustained period of global cooling that started after the Ypresian (Early Eocene). With Drake Passage closed, the ocean transports heat southward by moving warm water poleward near the surface (Gill and Bryan, 1971). However, Mikolajewicz et al. (1993) concluded that their results offer only limited support for the idea that the opening of Drake Passage led to substantially colder conditions on and around Antarctica.

The Eocene/Oligocene transition boundary (EOB) was characterized by sharp climatic deterioration linked to the progressive separation of South America and Antarctica and the strengthening of the ACC (Kennett, 1977). The effect of these changes on the Antarctic marine fauna is unknown, but the disappearance (extinction?) of *Palaeeudyptes gunnari*, together with several other Eocene Weddellian penguins, i.e., *Anthropornis nordenskjoeldi*, broadly coincides with these events. The transition appears to have had ecological as well as taxonomic consequences. Aronson et al. (1997, 2007) and Aronson and Blake (2001) reported a change in the nature of predator-prey relationships at roughly the upper part of the *Cucullaea* II Allomember due to the appearance of dense populations of predation-sensitive, epifaunal suspension feeders.
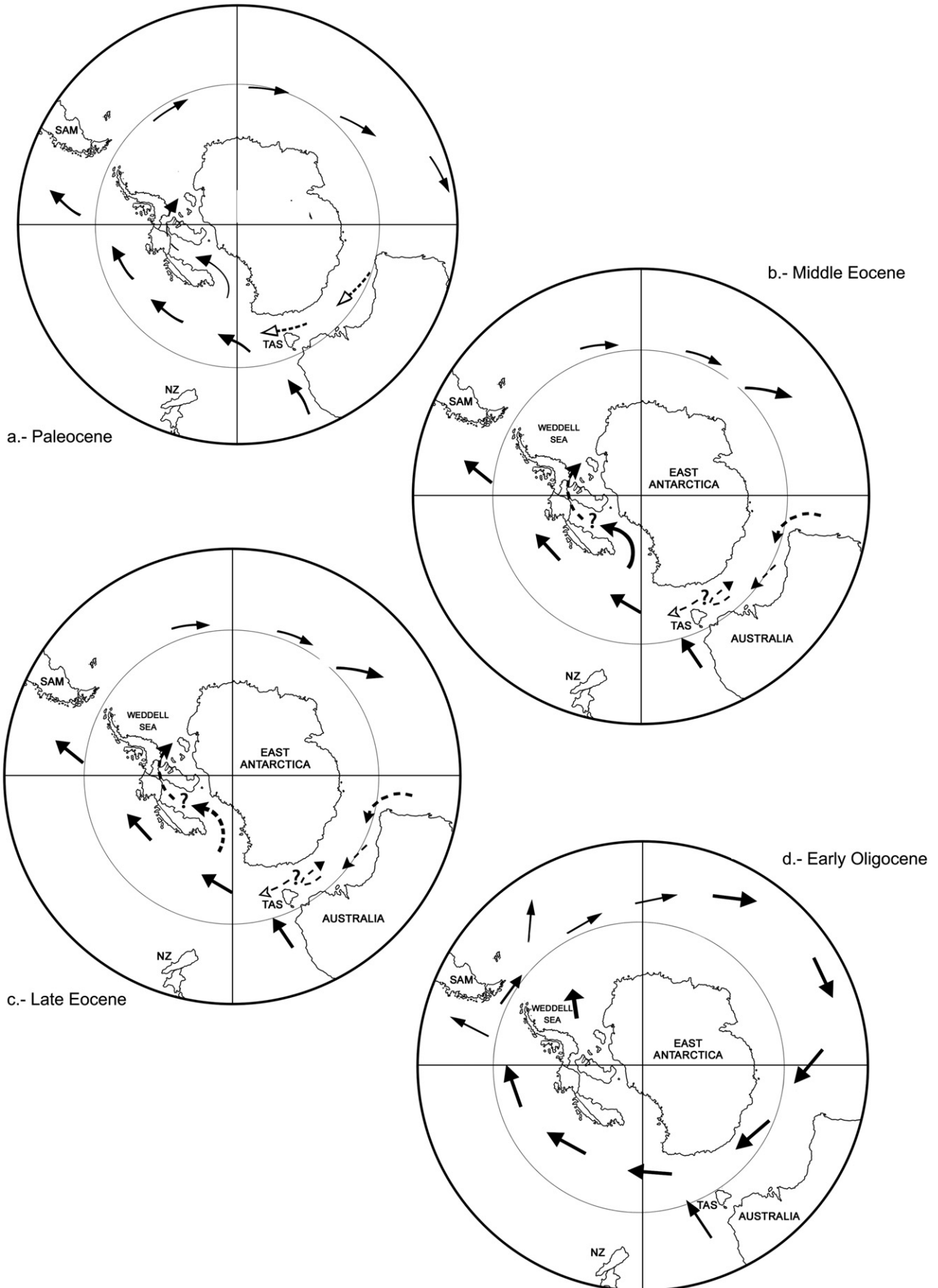
Fig. 7. Polar stereographic projection to 45°S of the southern ocean showing the Antarctic circulation in: a. Paleocene, b. Middle Eocene, c. Late Eocene, and e. Early Oligocene.

During the Eocene, notwithstanding that some circulation could exist in Drake Passage area (Wrenn and Hart, 1998), there was not a well developed Antarctic Circumpolar Current and consequently, and was never proposed the existence of the equivalent to Humboldt and Malvinas currents (Cione et al., 2007).

The Late Paleocene *Crossvallia unienwillia* predated the final break up between Antarctica and South America, the ACC had not developed. As a result of the separation of these two continents, a pronounced change in the oceanographic regime in the Southern Ocean occurred at about Middle Eocene time (Latimer and Filippelli, 2001). Models of ocean circulation help to explain the distribution of Paleogene marine vertebrate assemblages throughout the mid to high southern palaeolatitudes, and have implications for the refinement of Antarctic paleogeography at this time (Fig. 7). During the Eocene, the Pacific coast would have been located at paleolatitude nearly equivalent present-day latitude, as there has been essentially no latitudinal translation of the area since the late Cretaceous.

Models of surface ocean currents indicate flow along the Antarctic margin from the southwestern corner of Australia into a gyre within the Weddell Sea; and this helps to explain the similarities in marine palynofloras from the Kerguelen Plateau, Maud Rise, the James Ross Basin and the South Georgia Basin. These Ocean Currents passing further north across the southern Atlantic from the Weddell Sea may have carried dinoflagellate cysts as far as the tip of South Africa (Davey, 1969, Figs. 4 and 7).

Cold-water upwelling along the western coast appears to have been in place by the Late Cretaceous or early Tertiary, and this "proto-Humboldt" current may have influenced the low-latitude penguin diversity by cycling cold, nutrient-rich water into the ecosystem (Clarke et al., 2007). Recent findings of a new spheniciform in Peru (Clarke et al., 2010) suggest that *Palaeeudyptes*, or some other closely related taxon, would have reached the coast of Peru during the Middle Eocene.

The presence of *Palaeeudyptes* was reported in the Eocene of Chile (Sallaberry et al., 2010). Additionally, the discovery of a single partial skeleton of an undetermined spheniciform from the Late Eocene of Leticia Formation, Tierra del Fuego (Clarke et al., 2003) has an important paleobiogeographic significance. Based on the content of marine invertebrates, Olivero and Malumián (1999) regarded this unit equivalent to the upper part of the La Meseta Formation, coincidently with the *Anthropornis nordenskjoeldi* Biozone (Late Eocene, Submeseta Allomember).

6. Conclusion

Our data suggest that the highest diversity (14 species) and geographical distribution (Antarctica, South America and Australasia) in the Late Eocene were linked to water-cooling events and the opening of the Drake Passage respectively (establishment of the Antarctic Circumpolar Current). However, the first divergences of the group are documented in the Early Eocene of La Meseta Formation (Jadwiszczak and Chapman, 2011; Reguero et al., 2013). This fact supports that a marine dispersal of the Weddellian penguins to other continents (South America, Australasia) occurred when there was a shallow and warm ocean current circulation (Weddellian Current) flowing along the western margin of West Antarctica and South America. The surface ocean current (Weddellian Current) gyre that is modeled flowing down the west of the Antarctic Peninsula, to New Zealand and back up to the western side of southern South America, suggests a direct oceanic link and provides a dispersal route for Weddellian spheniciforms on the Pacific side of Antarctica (Figs. 4 and 7).

The phylogenetic analysis and the recent discoveries in the Eocene of Chile and Peru support the hypothesis that establishes one of the way for the dispersion of the Weddellian species from the Peninsula Antartica was the Pacific coast during the early Eocene.

Appendix A. Presence-absence data matrix.

Species	Submeseta	Cucullaea II	Cucullaea I	Campamento	Acantilados
Anthropornis nordenskjoeldii	1	1	1	1	0
Anthropornis grandis	1	1	1	1	0
Palaeeudyptes gunnarii	1	1	1	0	1
Palaeeudyptes klekowskii	1	1	1	0	0
Palaeeudyptes antarcticus	1	0	0	0	0
Delphinornis larsenii	1	1	1	0	0
Delphinornis arctowskii	1	0	0	0	0
Delphinornis gracilis	1	0	0	0	0
Mesetaornis polaris	1	0	1	0	0
Marambiornis exilis	1	0	1	0	0
Archaeospheniscus lopdelli	1	1	0	0	0
Archaeospheniscus wimani	1	0	1	0	0
Tonniornis mesetaensis	1	0	0	0	0
Tonniornis minimum	1	0	0	0	0

References

Acosta Hospitaleche, C., Di Carlo, U., 2010. The coracoids in functional and morphological studies of penguins (Aves, Spheniscidae) of the Eocene of Antarctica. Rivista Italiana di Paleontolog ia e Stratigrafia 116, 23–34.

Acosta Hospitaleche, C., Di Carlo, U., 2012. Una singular escápula de pingüino (Aves; Sphenisciformes) del Eoceno de Antártida: reconstrucción muscular e implicancias funcionales. Rivista Italiana di Paleontologia e Stratigrafia 118, 493–501.

Acosta Hospitaleche, C., Haidr, N., 2011. Penguin (Aves, sphenisciformes) cranial remains from the La Meseta Formation (Eocene) of Antarctic Peninsula (Antarctica). Antarctic Sciences 23, 369–378.

Acosta Hospitaleche, C., Reguero, M., 2010. First articulated skeleton of Palaeeudyptes gunnari from the late Eocene of Seymour (= Marambio) Island (Antarctica). Antarctic Sciences 22, 289–298.

Acosta Hospitaleche, C., Reguero, M., 2011. Evolution and biogeography of paleogene Weddellian penguins (Aves: sphenisciformes) of the James Ross Basin, Antarctica. In: 11th International Symposium on Antarctic Earth Sciences, 10–16 July, Edinburgh, Scotland.

Aronson, R.B., Blake, D.B., 2001. Global climate change and the origin of modern benthic communities in Antarctica. American Zoologist 41, 27–39.

Aronson, R.B., Blake, D.B., Oji, T., 1997. Retrograde community structure in the late Eocene of Antarctica. Geology 25, 903–906.

Aronson, R.B., Thatje, S., Clarke, A., Peck, L.S., Blake, D.B., Wilga, C.D., Seibel, B.A., 2007. Climate change and invasibility of the Antarctic benthos. Annual Review of Ecology, Evolution, and Systematics 38, 129–154.

Askin, R.A., 1988. Endemism and heterochroneity in the Late Cretaceous (Campanian) to Paleocene palynofloras of Seymour Island, Antarctica: implications for origins, dispersal and paleoclimates of southern floras. In: Crame, J.A. (Ed.), Origins and Evolution of the Antarctic Biota, vol. 47. Geological Society, pp. 107–119. Special Publication.

Baltz, D.M., Morejohn, G.V., Antrim, B.S., 1979. Size selective predation and food habits of two California terns. Western Birds 10, 17–24.

Case, J.A., 1988. Paleogene floras from Seymour Island, Antarctic Peninsula. In: Feldmann, R.M. (Ed.), Geology and Paleontology of Seymour Island, Antarctic Peninsula. In: Woodburne, M.O. (Ed.),, Memoir of the Geological Society of America, vol 169, pp. 523–530.

Cione, A.L., Reguero, M.A., Acosta Hospitaleche, C., 2007. Did the continent and sea have different temperatures in the northern Antarctic Peninsula during the middle Eocene? Revista de la Asociación Geológica Argentina 62, 586–596.

Clarke, K.R., Warwick, R.M., 1998. A taxonomic distinctness index and its statistical properties. Journal of Applied Ecology 35, 523–531.

Clarke, J.A., Olivero, E.B., Puerta, P., 2003. Description of the earliest fossil penguin from South America and first Paleogene vertebrate locality of Tierra del Fuego, Argentina. American Museum Novitates 3423, 1–18.

Clarke, J.A., Ksepka, D.T., Stucchi, M., Urbina, M., Giannini, N., Bertelli, S., Narváez, Y., Boyd, C., 2007. Paleogene equatorial penguins challenge the proposed relationship between biogeography, diversity, and Cenozoic climate change. PNAS 104, 11545–11550.

Clarke, J.A., Ksepka, D.T., Salas-Gismondi, R., Altamirano, A.J., Shawkey, M., d'Alba, L., Vinther, J., de Vries, T.J., Baby, P., 2010. Fossil evidence for evolution of the shape and color of penguin feathers. Science 330, 954–957.

Crame, J.A., Francis, J.E., Cantrill, D.J., Pirrie, D., 2004. Maastrichtian stratigraphy of Antarctica. Cretaceous Research 25, 411–423.

Croxall, J.P., Prince, P.A., 1980. Food, feeding ecology and ecological segregation of seabirds at South Georgia. Biological Journal of the Linnean Society 14, 103–131.

Dalziel, I.W.D., Elliot, D.H., 1982. West Antartica: problem child of Gondwanaland. Tectonics 1, 3–19.

Davey, R.J., 1969. Some dinoflagellate cysts from the upper Cretaceous of northern Natal, South Africa. Palaeontologia Africana 12, 1–23.

del Valle, R.A., Elliot, D.H., Macdonald, D.I.M., 1992. Sedimentary basins on the east flank of the Antarctic Peninsula: proposed nomenclature. Antarctic Science 4, 477–478.

Dingle, R., Marenssi, S., Lavelle, M., 1998. High latitude Eocene climate deterioration: evidence from the northern Antarctic Peninsula. Journal of South American Earth Sciences 11, 571–579.

Doktor, M., Gazdzicki, A., Marenssi, S.A., Porebski, S.N., Vrba, A., 1988. Argentine-polish geological investigations on Seymour (Marambio) Island, antarctica, 1988. Polish Polar Research 9, 521–541.

Dusén, P., 1908. Über die tertiäre flora der Seymour-Insel. In: Wissenschaftliche Ergebnisse der Schwedischen Südpolar-Expedition 1901–1903. Lithographisches Institut des Generalstabs, Stokholm, Bd. 3, l. 3, p. 127.

Dutton, A.L., Lohmann, K., Zinsmeister, W.J., 2002. Stable isotope and minor element proxies for Eocene climate of Seymour Island, Antarctica. Paleoceanography 17, 1–13.

Eagles, G., 2010. The age and origin of the central Scotia. Geophysical Journal International. http://dx.doi.org/10.1111/j.1365-246X.2010.04781.xl.national.

Eagles, G., Livermore, R.A., Morris, P., 2006. Small basins in the Scotia sea: the Eocene Drake Passage gateway. Earth and Planetary Science Letters 242, 343–353.

Elliot, D.H., 1995. Paleogene volcanic rocks on Seymour Island: evidence for northwestward subduction of Weddell Sea oceanic crust. Abstract, VII International Symposium on Antarctic Earth Sciences, Siena, p. 119.

Elliot, D.H., Trautman, T.A., 1982. Lower Tertiary strata on Seymour Island, Antarctic Peninsula. In: Craddock, C. (Ed.), Antarctic Geoscience. University of Wisconsin Press, Madison, pp. 287–297.

Elliott, D.H., Hoffman, S.M., 1989. Geologic studies on Seymour Island. Antarctic Journal of the United States 24, 3–5.

Frere, E., Quintana, F., Gandini, P., Wilson, R.P., 2008. Foraging behaviour and habitat partitioning of two sympatric cormorants in Patagonia, Argentina. Ibis 150, 558–564.

Gill, A.E., Bryan, K., 1971. Effects of geometry on the circulation of a three-dimensional southern hemisphere ocean model. Deep-sea Research 18, 685–721.

Haidr, N., Acosta Hospitaleche, C., 2012. Feeding habits of Antarctic Eocene penguins from a morphofunctional perspective. Neues Jahrbuch für Geologie und Paläontologie 263, 125–131.

Hammer, Ø., Harper, D.A.T., Ryan, P.D., 2001. Past: paleontological statistics software package for education and data analysis. Palaeontologia Electronica 4, 9.

Hathway, B., 2000. Continental rift to back-arc basin: Jurassic – Cretaceous stratigraphical and structural evolution of the Larsen Basin, Antarctic Peninsula. Journal of the Geological Society, London 157, 417–432.

Henkel, L.A., 2009. Co-occurrence and aggregation of marine birds and mammals in Monterey Bay, California, USA. Marine Ecology Progress Series 387, 295–303.

Hutchinson, G.E., 1959. Homage to Santa Rosalia, or why are there so many different kinds of animals? American Naturalist 93, 145–159.

Ivany, L.C., Van Simaeys, S., Domack, E.W., Samson, S.D., 2006. Evidence for an earliest Oligocene ice sheet on the Antarctic Peninsula. Geology 34, 377–380.

Ivany, L.C., Lohmann, K.C., Hasiuk, F., Blake, D.B., Glass, A., Aronson, R.B., Moody, R.M., 2008. Eocene climate record of a high southern latitude continental shelf: Seymour Island, Antarctica. GSA Bulletin 120, 659–678.

Jadwiszczak, P., 2006. Eocene penguins of Seymour Island, Antarctica: the earliest record, taxonomic problems and some evolutionary considerations. Polish Polar Research 27, 287–302.

Jadwiszczak, P., 2008. An intriguing penguin bone from the late Eocene of Seymour Island (Antarctic Peninsula). Antarctic Science 20, 589–590.

Jadwiszczak, P., 2009. Review Penguin past: the current state of knowledge. Polish Polar Research 30, 3–28.

Jadwiszczak, P., 2010. New data on the appendicular skeleton and diversity of Eocene Antarctic penguins. In: Nowakowski, D. (Ed.), Morphology and Systematics of Fossil Vertebrates. DN, Wroclaw, Poland, pp. 44–50.

Jadwiszczak, P., 2011. New data on morphology of late Eocene penguins and implications for their geographic distribution. Antarctic Science 23, 605–606.

Jadwiszczak, P., 2012. Partial limb skeleton of a "giant penguin" Anthropornis from the Eocene of Antarctic Peninsula. Polish Polar Research 33, 259–274.

Jadwiszczak, P., Chapman, S.D., 2011. The earliest fossil record of a medium-sized penguin. Polish Polar Research 32, 269–277.

Jadwiszczak, P., Mörs, T., 2011. Aspects of diversity in early Antarctic Penguins. Acta Palaeontologica Polonica 56, 269–277.

Jenkins, R.J.F., 1974. A new giant penguin from the Eocene of Australia. Palaeontology 17, 291–310.

Kato, A., Nishiumi, I., Naito, Y., 1996. Sexual difference in the diet of King Cormorants at Macquarie Island. Polar Biology 16, 75–77.

Kennett, J.P., 1977. Cenozoic evolution of Antarctic glaciation, the circum-Antarctic oceans and their impact on global paleoceanography. Journal of Geophysic Research 82, 3843–3859.

Ksepka, D., Bertelli, S., 2006. Fossil penguin (Aves: Sphenisciformes) cranial material from the Eocene of Seymour Island (Antarctica). Historical Biology 18, 389–395.

Ksepka, D., Clarke, J., 2010. The basal penguin (Aves: Sphenisciformes) Perudyptes devriesi and a phylogenetic evaluation of the penguin fossil record. Bulletin of the American Museum of Natural History 337, 1–77.

Ksepka, D.T., Bertelli, S., Giannini, N., 2006. The phylogeny of the living and fossil Sphenisciformes (penguins). Cladistics 22, 412–441.

Ksepka, D., Fordyce, E., Ando, T., Jones, C., 2012. New fossil penguins (Aves, Sphenisciformes) from the Oligocene of New Zealand reveal the skeletal plan of stem penguins. Journal of Vertebrate Paleontology 32, 235–254.

Latimer, J.C., Filippelli, G.M., 2001. Terrigenous input and paleoproductivity in the Southern Ocean. Paleoceanography 16, 627–643.

Lawver, L.A., Gahagan, L., 2003. Evolution of Cenozoic seaways in the circum-Antarctic region. Palaeogeography, Palaeoclimatology, Palaeoecology 198, 11–37.

Lawver, L.A., Gahagan, L.M., Coffin, F.M., 1992. The development of palaeoseaway around Antarctica. In: Kennett, J.P., Warnke, D.A. (Eds.), The Antarctic Paleoenvironment: A Perspective on Global Change. Antarctic Research Series, vol. 65, pp. 7–30.

Livermore, R., Nankivel, A., Eagles, G., Morris, P., 2005. Paleogene opening of Drake Passage. Earth and Planetary Science Letters 236, 459–470.

Marenssi, S.A., Sedimentología y paleoambientes de sedimentación de la Formación La Meseta, Isla Marambio, Antártida. Tomo I: p. 330, Tomo II: p. 172 Ph.D. dissertation, Universidad de Buenos Aires, unpublished.

Marenssi, S.A., Reguero, M.A., Santillana, S.N., Vizcaíno, S.F., 1994. Eocene land mammals from Seymour Island, Antarctica: Palaeobiogeographical implications. Antarctic Science 6, 3–15.

Marenssi, S.A., Santillana, S.N., Rinaldi, C.A., 1996. Stratigraphy of La Meseta Formation (Eocene), Marambio Island, Antarctica. I Congreso Paleógeno de América del Sur, Santa Rosa, La Pampa. Abstracts, 33–34.

Marenssi, S.A., Santillana, S.N., Rinaldi, C.A., 1998a. Paleoambientes sedimentarios de la Aloformación La Meseta (Eoceno), Isla Marambio (Seymour), Antártida. Instituto Antártico Argentino, Contribución 464, 51.

Marenssi, S.A., Santillana, S.N., Rinaldi, C.A., 1998b. Stratigraphy of the La Meseta Formation (Eocene), Marambio (Seymour) Island, Antarctica. In: Casadío, S. (Ed.), Paleógeno de América del Sur y de la Península Antártica, vol. 5. Asociación Paleontológica Argentina, pp. 137–146. Publicación Especial.

Marenssi, S.A., Santillana, S.N., Bauer, M., 2012. Estratigrafía, petrografía sedimentaria y procedencia de las formaciones Sobral y Cross Valley (Paleoceno), isla Marambio (Seymour), Antártida. Andean Geology 39, 67–91.

Marples, B.J., 1952. Early tertiary penguins of new Zealand. New Zealand geological survey. Paleontological Bulletin 20, 1–66.

Marples, B.J., 1953. Fossil Penguins from the Mid-tertiary of Seymour Island. In: Falkland Island Dependency Survey Science Report, vol. 5, pp. 1–15.

Masello, J.F., Mundry, R., Poisbleau, M., Demongin, L., Voigt, C.C., Wikelski, M., Quillfeldt, P., 2010. Diving seabirds share foraging space and time within and among species. Ecosphere 1, 19.

Mikolajewicz, U., Maier-Reimer, E., Crowley, T., Kim, K., 1993. Effect of Drake and Panamanian gateways on the circulation of an ocean model. Paleoceanography 8. http://dx.doi.org/10.1029/93PA00893.

Miller, A.K., Karnovsky, N.J., Trivelpiece, W.Z., 2009. Flexible foraging strategies of gentoo penguins Pygoscelis papua over 5 years in the South Shetland Islands, Antarctica. Marine Biology 156, 2527–2537.

Montes, M., Nozal, F., Santillana, S., Tortosa, F., Beamud, E., Marenssi, S., 2010. Integrate stratigraphy of the upper Paleocene-Eocene strata of Marambio (Seymour) Island, Antarctic Peninsula. In: XXXI SCAR, Open Science Conference, Buenos Aires, Argentina.

Mori, Y., Boyd, I.L., 2004. Segregation of foraging between two sympatric penguin species: does rate maximisation make the difference? Marine Ecology Progress Series 275, 241–249.

Myrcha, A., Tatur, A., del Valle, R., 1990. A new species of fossil penguin from Seymour Island, West Antarctica. Alcheringa 14, 195–205.

Myrcha, A., Jadwiszczak, P., Tambussi, C., Noriega, J., Gazdzicki, A., Tatur, A., del Valle, R., 2002. Taxonomic revision of Eocene Antarctic penguins based on tarsometatarsal morphology. Polish Polar Research 23, 5–46.

Olivero, E.B., Malumián, N., 1999. Eocene stratigraphy of southeastern Tierra del Fuego, Argentina. American Association of Petroleum Geologists Bulletin 83, 295–313.

Olivero, E.B., Gasparini, Z., Rinaldi, C.A., Scasso, R.A., 1991. First record of dinosaurs from Antarctica (Upper Cretaceous, James Ross Island): palaeogeographical

implications. In: Thomson, M.R.A. (Ed.), Geological Evolution of Antarctica. Cambridge University Press, Cambridge, pp. 617–622.

Olivero, E.B., Martinioni, D.R., Mussel, F.J., 1992. Upper Cretaceous sedimentology and biostratigraphy of western Cape Lamb (Vega Island, Antarctica). Implications on sedimentary cycles and evolution of the basin. In: Rinaldi, C.A. (Ed.), Geología de la Isla James Ross. Instituto Antártico Argentino, Buenos Aires, pp. 147–166.

Olivero, E.B., Medina, F.A., López, C., María, I., 2008. The stratigraphy of Cretaceous mudstones in the Eastern Fuegian Andes: new data from body and trace fossils. Revista de la Asocación Geológica Argentina 64, 60–69.

Pirrie, D., 1989. Shallow marine sedimentation within an active margin Basin, James Ross Island, Antarctica. Sedimentary Geology 63, 61–82.

Porębski, S.J., 1995. Facies architecture in a tectonically controlled incised-valley estuary: La Meseta Formation (Eocene) of Seymour Island, Antarctic Peninsula. Studia Geologica Polonica 107, 7–97.

Porębski, S.J., 2000. Shelf-valley compound fill produced by fault subsidence and eustatic sea-level changes, Eocene La Meseta Formation, Seymour Island. Geology 28, 147–150.

Reguero, M.A., Marenssi, S.A., 2010. Paleogene climatic and biotic events in the terrestrial record of the Antarctic Peninsula: an overview. In: Madden, R. (Ed.), The Paleontology of Gran Barranca: Evolution and Environmental Change through the Middle Cenozoic of Patagonia. Cambridge University Press, pp. 383–397.

Reguero, M.A., Vizcaíno, S.F., Goin, F.J., Marenssi, S.A., Santillana, S.N., 1998. Eocene high-latitude terrestrial vertebrates from Antarctica as biogeographic evidence. In: Casadio, S. (Ed.), Paleógeno de América del Sur y de la Península Antártica, vol. 5. Asociación Paleontológica Argentina, pp. 185–198. Publicación Especial.

Reguero, M.A., Marenssi, S.A., Santillana, S.N., 2002. Antarctic Peninsula and Patagonia Paleogene terrestrial environments: biotic and biogeographic relationships. Palaeogeography Palaeoclimatology Palaeoecology 179, 189–210.

Reguero, M., Goin, F., Acosta Hospitaleche, C., Dutra, T., Marenssi, S., 2013. Late Cretaceous/Paleogene West Antarctica Terrestrial Biota and Its Intercontinental Affinities. In: SpringerBriefs in Earth System Sciences, p. 120.

Ridoux, V., 1994. The diets and dietary segregation of seabirds at the subantarctic Crozet Islands. Marine Ornithology 22, 1–192.

Sadler, P., 1988. Geometry and stratification of uppermost Cretaceous and Paleogene units of Seymour Island, northern Antarctic Peninsula. In: Feldmann, R.M. (Ed.). In: Woodburne, M.O. (Ed.),, Geology and Paleontology of Seymour Island, Antarctic Peninsula, vol 169. Geological Society of America, pp. 303–320. Memoir.

Sallaberry, M.A., Yury-Yáñez, R.E., Otero, R.A., Soto-Acuña, S., Torres, T., 2010. Eocene birds from the western margin of southernmost South America. Journal of Paleontology 84, 1061–1070.

Scasso, R.A., Olivero, E.B., Buatois, L.A., 1991. Lithofacies, biofacies and ichnoassemblage evolution of a shallow submarine volcaniclastic fan-shelf depositional system (upper Cretaceous, James Ross Island, Antarctica). Journal of South American Earth Sciences 4, 239–260.

Scher, H.D., Martin, E.E., 2006. The timing and climatic influence of the opening of Drake Passage. Science 312, 428–430.

Shen, Y., 1995. Subdivision and correlation of Cretaceous to paleogene volcanosedimentary sequence from Fildes Peninsula, king George Island, Antarctica. In: Shen, Y. (Ed.), Stratigraphy and Palaeontology of Fildes Peninsula, King George Island, Antarctica, vol. 3. Science Press, Beijin, pp. 1–36. State Antarctic Committee, Monograph.

Simpson, G.G., 1971. Review of fossil penguins from Seymour Island. Proceedings of the Royal Society of London B Biological Sciences 178, 357–387.

Slack, K.E., Jones, C.M., Ando, T., Harrison, G.L., Fordyce, R.E., Arnason, U., Penny, D., 2006. Early penguin fossils, plus mitochondrial genomes, Calibrate Avian evolution. Molecular Biology and Evolution 23, 1144–1155.

Spear, L.B., Ainley, D.G., 2007. Storm-petrels of the Eastern Pacific Ocean: species assembly and diversity along marine habitat gradients. Ornithological Monographs 62, 1–77.

Stilwell, J.D., Feldman, R.M., 2000. Paleobiology and paleoenvironments of Eocene rocks, McMurdo sound, east antarctica. American Geophysical Union Antarctic Research Series 67, 372. Washingtosn.

Stilwell, J.D., Zinsmeister, W.J., 1992. Molluscan systematics and biostratigraphy: lower Tertiary La Meseta Formation, Seymour Island, Antarctic Peninsula. Antarctic Research Series 55, 1–152.

Tambussi, C., Acosta Hospitaleche, C., 2007. Antarctic birds (Neornithes) during the Cretaceous Eocene times. Revista de la Asociación Geológica Argentina 62, 604–617.

Tambussi, C.P., Reguero, M.A., Marenssi, S.A., Santillana, S.N., 2005. *Crossvalia unienwillia*, a new Spheniscidae (Sphenisciformes, Aves) from the late Paleocene of Antarctica. Geobios 38, 667–675.

Tambussi, C.P., Acosta Hospitaleche, C., Reguero, M.A., Marenssi, S.A., 2006. Late Eocene penguins from West Antarctica: systematics and biostratigraphy. In: Francis, J.E., Pirrie, D., Crame, J.A. (Eds.), Cretaceous-tertiary High-latitude Palaeoenvironments, James Ross Basin, Antarctica, vol. 258. Geological Society of London, London, pp. 45–161. Special Publications.

Trivelpiece, W.Z., Trivelpiece, S.G., Volkman, N.J., 1987. Ecological segregation of Adélie, gentoo and chinstrap penguins at King George Island, Antarctica. Ecology 68, 351–361.

Weimerskirch, H., Salamolard, M., Sarrazin, F., Jouventin, P., 1993. Foraging strategy of wandering albatrosses through the breeding season: a study using satellite telemetry. Auk 110, 325–342.

Weiss, F., Furness, R.W., McGill, R.A.R., Strange, I.J., Masello, J.F., Quillfeldt, P., 2009. Trophic segregation of Falkland Islands seabirds insights from stable isotope analysis. Polar Biology 32, 1753–1763.

Wilson, R.P., 2010. Resource partitioning and niche hyper-volume overlap in free-living Pygoscelid penguins. Functional Ecology 24, 646–657.

Wiman, C., 1905. Vorläufige Mitteilung über die alttertiären Vertebraten der Seymourinsel (in German). Bulletin of the Geological Institute of Uppsala 6, 247–253.

Woodburne, M.O., Case, J.A., 1996. Dispersal, vicariance and the Late Cretaceous to early Tertiary land mammal biogeography from South America to Australia. Journal of Mammalian Evolution 3, 121–161.

Woodburne, M.O., Zinsmeister, W.J., 1984. The first land mammal from Antarctica and its biogeographic implications. Journal of Paleontology 54, 913–948.

Wrenn, J.H., Hart, G.F., 1988. Paleogene dinoflagellates cyst biostratigraphy of Seymour Island, Antarctica. In: Feldmann, R.M., Woodburne, M.O. (Eds.), Geology and Paleontology of Seymour Island, Antarctic Peninsula, vol. 169. Geological Society of America, Boulder, pp. 321–447. Memoir.

Zachos, J., Pagani, M., Sloan, L., Thomas, E., Billups, K., 2001. Trends, rhythms and aberrations in global climate 65 Ma to present. Science 292, 686–693.

Zinsmeister, W.J., 1979. Biogeographic significance of the late Mesozoic and early Tertiary molluscan faunas of Seymour Island (Antarctic Peninsula) to the final breakup of Gondwanaland. In: Gray, J., Boucot, A. (Eds.), Historical Biogeography, Plate Tectonics and the Changing Environment. Oregon State University, pp. 349–355.

Zinsmeister, W.J., 1982. Late Cretaceous-early Tertiary molluscan biogeography of southern circum-Pacific. Journal of Paleontology 56, 84–102.