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Weddellian marine/coastal vertebrates diversity from a basal horizon (Ypresian, Eocene) of the *Cucullaea* I Allomember, La Meseta formation, Seymour (Marambio) Island, Antarctica

Diversidad de vertebrados marino costeros de la Provincia Weddelliana en un horizonte basal (Ypresiano, Eoceno) del Alomiembro *Cucullaea* I, Formación La Meseta, isla Seymour (Marambio), Antártida

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Abstract

The La Meseta Formation crops out in Seymour/Marambio Island, Weddell Sea, northeast of the Antarctic Peninsula and contains one of the world's most diverse assemblages of Weddellian marine/coastal vertebrates of Early Eocene (Ypresian) age. The La Meseta Formation is composed of poorly consolidated, marine sandstones and siltstones which were deposited in a coastal, deltaic and/or estuarine environment. It includes marine invertebrates and vertebrates as well as terrestrial vertebrates and plants. The highly fossiliferous basal horizon (*Cucullaea* shell bed, Telm 4 of Sadler 1988) of the *Cucullaea* I Allomember is a laterally extensive shell bed with sandy matrix. The fish remains, including 35 species from 26 families, of the Ypresian *Cucullaea* bed represent one of the most abundant and diverse fossil vertebrate faunas yet recorded in southern latitudes. Stratigraphic distribution and phylogenetic relationships of the Weddellian sphenisciforms are consistent with a first radiation of this group in the Early Eocene. The first inquestionable archaeocete from Antarctica is recorded in this unit and is referred to a new taxon.

Keywords: Antarctica; Seymour Island; Early Eocene (Ypresian); La Meseta Formation (*Cucullaea* I Allomember); Vertebrates; Paleobiogeography

Resumen

La Formación La Meseta aflora en la Isla Seymour/Marambio, Mar de Weddell, noreste de la Península Antártica y contiene una de las asociaciones de vertebrados costeros/marinos de edad Eoceno temprano (Ypresiano) más diversa que se conoce a nivel mundial. Esta unidad está compuesta por areniscas marinas pobremente consolidadas las cuales fueron depositadas en ambientes costeros, deltaicos y/o estuarinos. Esta incluye invertebrados y vertebrados marinos así como plantas y vertebrados terrestres. El horizonte basal (el banco de *Cucullaea*, Telm 4) del Alomiembro *Cucullaea* I es lateralmente extensor y altamente fosilífero. Los restos de peces del banco de *Cucullaea* (Ypresiano) incluyen 35 especies con 26 familias y representa una de las más abundantes y diversas fauna de vertebrados fósiles registradas en latitudes altas. La distribución estratigráfica y las relaciones filogenéticas de los pingüinos fósiles (Sphenisciformes) son consistentes con la primera radiación de este grupo en el Eoceno temprano. El primer incuestionable Archaeoceti de Antártida es registrado en esta unidad y es referido un nuevo taxón.

Palabras claves: Antártida; Isla Seymour; Eoceno temprano (Ypresiano); Formación La Meseta (Alomiembro *Cucullaea* I); Vertebrados; Paleobiogeografía.

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Introduction

Paleogene Antarctic marine/coastal vertebrates come almost exclusively from the James Ross Basin, Wedddell Sea, Antarctic Peninsula (Reguero & Gasparini, 2007), mostly from Early Eocene-earliest Oligocene? fossils of the La Meseta Formation in Seymour (Marambio) Island (Fig. 1), secondly from the Eocene of the Fildes Peninsula, 25 de Mayo (King George) Island (Covacevich & Rich 1982; Li Jianjun & Zhen Shuonan 1994), and from Eocene erratics of the McMurdo Sound, East Antarctica (Stilwell & Zinsmeister 2000).

The record of fossil vertebrates in the La Meseta Formation is extremely diverse. In this paper we will refer only to the basal horizon of the *Cucullaea* I Allomember of that formation (Marenssi et al. 1998a, b). This horizon is characterized by a laterally extensive shell bed (*Cucullaea* shell bed). During the austral summers of 1990–2000 Argentinean teams' recovered more than 10,000 teeth of fishes by dry-sieving and surface-prospecting of different localities along this horizon.

This first description of the Ypresian basal horizon marine/coastal vertebrate fauna documents the previously unappreciated diversity and unique character of Antarctica's Early Eocene marine vertebrates, and indicates a cool-water paleoenvironment for the marine vertebrate assemblage.

Biogeographically all these vertebrates lived in the Weddellian Province. The Weddellian Province was proposed by Zinsmeister (1979, 1982) as a biogeographic unit of shallow marine waters that encompassed the coasts of Australia, New Zealand, Tasmania, Antarctica and southern South America (Magallanic Region in Chile, and Patagonia in Argentina) during the late Cretaceous through Eocene.

Locality and geological setting

The Early Eocene to earliest Oligocene? La Meseta Formation (Elliot & Trautman 1982) crops out in Seymour and Cockburn islands, close to the northern tip of the Antarctic Peninsula, Antarctica and is an unconformity-bounded unit (La Meseta Alloformation of Marenssi et al. (1998a). This unit is the topmost

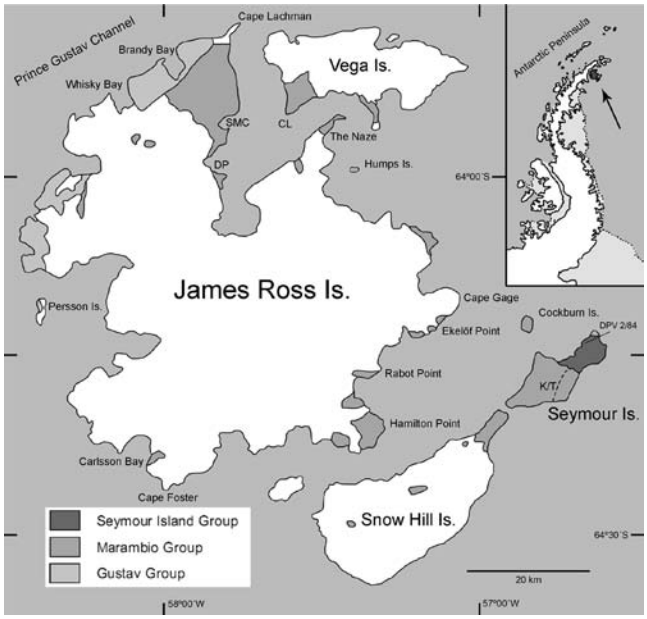

Figure 1. Locality map for the Seymour (Marambio) Island, northeastern Antarctic Peninsula. Locality key: DP, Dreadnought Point; BB, Brandy Bay; CL, Cape Lamb; SMC, Santa Marta Cove. Position of the Cretaceous-Tertiary boundary on Seymour Island indicated by the symbol K/T.

exposed part of the sedimentary fill of the Late Jurassic-Tertiary James Ross Basin (Del Valle et al. 1992) and was interpreted as the filling of an incised-valley system (Marenssi et al. 1998a). The La Meseta Formation rests unconformably on either the Late Cretaceous López de Bertodano Formation or on the Paleocene Sobral and Cross Valley formations (Sadler 1988; Marenssi et al. 1998a). The unit is composed of sandstones and mudstones with interbedded shell-rich conglomerates. It was subdivided by Sadler (1988) into seven lithofacies units (Telms 1-7), and later 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. 1998a)(Fig. 2). These units were deposited mainly during the Eocene in deltaic, estuarine and shallow marine settings, mostly within a northwest-southeast trending incised valley (Marenssi et al. 1998a, 1998b).

The basal part of the *Cucullaea* I Allomember is a horizon dominated by the pelecypod *Cucullaea* and darwinellid gastropods. Sadler (1988) characterized this shell bed (its Telm 4) by its thickness (as thick as 3 m), coarseness, and relatively high content of phosphatic teeth and bones, Sadler (1988) interpreted it as a transgressive lag characterized by abundant phosphate pebbles and glauconite. The age of this horizon of ca. 52.5 Ma (Ypresian) is indicated by the strontium stratigraphy based on the $^{87}Sr/^{86}Sr$ ratios of carbonate shells of the overlying beds of the *Cucullaea* I Allomember and it is consistent with paleomagnetic and biostratigraphic data (Montes et al. 2010)(Fig. 2).

The *Cucullaea* I shell bed represents a laterally continuous (several kilometers) horizon with thicknesses up to 3 meters. It bears complex internal reactivation (erosion-sedimentation) surfaces indicating multiple events. Individual beds are lens-shaped (up to 0.5 m thick) with erosional bases. They are mostly matrix supported, composed by bioclasts and some gravels immersed in a coarse-sand matrix with some granules. Internally

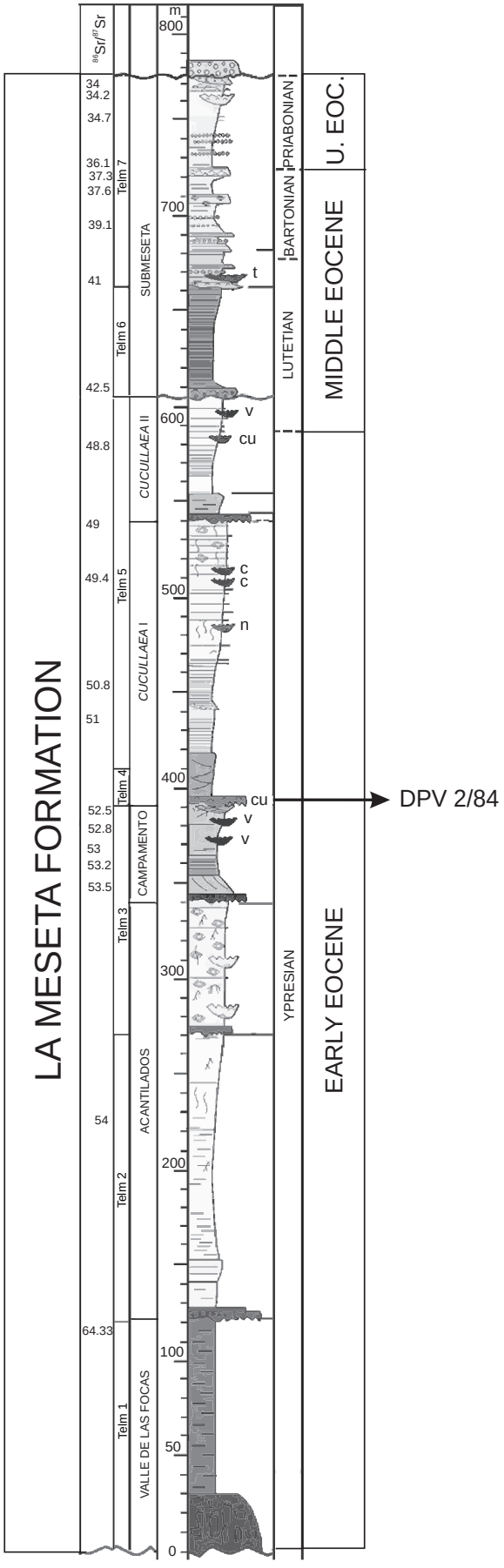

Figure 2. Stratigraphic column of La Meseta Formation on Seymour Island, Antarctic Peninsula (modified from Montes et al. 2010). Strontium datation values from Dingle & Lavelle 1998; Dutton et al. 2002; Reguero et al. 2002 and Ivany 2008. Abbreviations: cu, *Cucullaea*, n, naticids, v, veneroids, and t, *Turritella*.

Figure 3. Base of the *Cucullaea* I Allomember, the basal shell bed (Telm 4 of Sadler 1988) at DPV 2/84 locality, showing fossiliferous outcrop on west side of plateau at north end of Seymour Islans with very abundant specimens of *Cucullaea raea* and darwinellids.

each bed is massive or present through cross bedding or rarely parallel bedding.

Shells are disarticulated and oriented with the maximum projection area parallel to bedding. Concave-up, concave-down and nesting are common. Reworking of the underlying deposits (time-averaging) is suggested by fossil shells and fishes. There are a mixture of whole (although disarticulated) shells mostly of the species *Cucullaea raea* reworked directly from the underlying sands (Telm 3 or Campamento Allomember) and higly abraded and broken shells of many other invertebrate groups (Fig. 3).

Sedimentological evidences indicate that the *Cucullaea* I shell bed represents channel lags of laterally migrating subtidal channels (inlets?) developed at the mouth of a tide and wave influenced estuary (Marenssi et al. 1998b) during a slow transgressive event.

Many authors (Sadler 1988; Marenssi et al. 1998b; Ivany et al. 2006) indicated that this horizon bears all the hallmarks of a time-condensed transgressive deposit and placed a major hiatus at its base. Although the time averaging and erosion of the underlying beds are evident new stratigraphic data (Montes et al. 2010) suggest no hiatus but slow accumulation rate.

Material and methods

Surface collecting was carried out over several kilometers of La Meseta Formation exposures. Numerous fossils were recovered by surface collecting, although the majority of the specimens were collected through screen sieving and limited excavation. Approximately 1300 kg of matrix was collected and dry sieved in the field. The residues were sorted to 850 microns, with the high quantity of glauconite and ferruginous grains preventing sorting of finer fractions.

Dry-sieving sediments from a single site, DPV (División Paleontología de Vertebrados) 2/84 (64°14'21.782"S; 56°36'11.685"W, *Cucullaea* shell bank, basal part of the *Cucullaea* I Allomember, Fig. 1), has produced hundreds of bone fragments and teeth of sharks, rays, chimaeroids, bony fishes, turtles, penguins, whales, terrestrial mammals (marsupials and meridiungulates) and trunks and leaves (Reguero et al. 2002). The diversity of this vertebrate-bearing horizon can be taken to represent essentially a single marine fauna.

All the material described here is deposited in the fossil vertebrate collection of the Museo de La Plata (División Paleontología de Vertebrados) and have registration numbers prefixed by "MLP".

Taxonomic definitions and terminology. The fossil fish material collected consists of isolated remains of selachians and actinopterygians and was obtained by dry sieving of unconsolidated sediments of the *Cucullaea* bed (Telm 4). The systematic and nomenclature used here is adopted from Cappetta (1987) and Compagno (1988).

For Sphenisciformes Clarke et al. (2003) proposed phylogenetic definitions for higher taxa within the penguin total group. Pansphenisciformes is applied to the clade including all taxa more closely related to Spheniscidae than any other extant avian lineage. Sphenisciformes is applied in a more exclusive sense to the clade including all Pansphenisciformes that share the apomorphic loss of aerial flight. Spheniscidae is applied to the crown clade of penguins, comprising the most recent common ancestor of all living penguin species and its descendants. We use the classification proposed by Simpson (1946, 1971) throughout this paper.

Here, we follow the terminology and sequential stratigraphic interpretation of the revision of Marenssi et al. (1998a, 1998b).

Results

Ypresian diversity of marine/coastal vertebrates in high latitudes

Particularly the Ypresian horizon of the *Cucullaea* I Allomember contains the bulk of the fossil fish localities of the La Meseta Formation. This fossil fish fauna consists of thousands of selachian teeth and bony fish remains (including teeth, cranial fragments, vertebrae, fin spines, otoliths).

Sharks remains, largely represented by isolated teeth and vertebrae and a few poorly preserved dorsal spine, are extremely abundant and diverse in the coarser sand facies of the *Cucullaea* I Allomember. Interestingly, the level of diversity from a single locality (DPV 2/84) of the La Meseta Formation is much higher than the level of diversity for most extant cool temperate shark faunas and nearly equal to a present-day tropical shark fauna. At least 21 taxa of sharks between 11 families (Table 1) occur in this horizon. The most abundant (according to tooth number) elamosmobranch taxa are *Squatina* (37.89%), *Pristiophorus* (22.45%), Odontaspididae (17.24%), *Myliobatis* (6.70%), *Squalus* (6.81%), Rajidae (4.72) and Holocephali (2.68%).

Table 1.- Taxonomic list, stratigraphy, and references for the Chondrichthyes fauna from the *Cucullaea* I Allomember (La Meseta Formation) of Seymour Island, Antarctic Peninsula.

Taxon	Stratigraphy (Allomember)	Source
CHONDRICHTHYES		
HEXANCHIDAE		
Heptranchias howelli	*Cucullaea* I	Long (1992a)
Hexanchus sp.	*Cucullaea* I	Cione & Reguero (1994)
SQUALIDAE		
Squalus woodburnei	*Cucullaea* I	Long (1992a)
Squalus weltoni	*Cucullaea* I	Long (1992a)
Centrophorus sp.	*Cucullaea* I	Long (1992a)
Dalatias licha	*Cucullaea* I	Long (1992a)
Deania sp.	*Cucullaea* I	Long (1992a)
SQUATINIDAE		
Squatina sp.	*Cucullaea* I	Welton & Zinsmeister (1980)
PRISTIOPHORIDAE		
Pristiophorus lanceolatus	*Cucullaea* I, Submeseta	Grande & Eastman (1986)
GINGLYMOSTOMATIDAE		
Pseudoginglymostoma cf. *P. brevicaudatum*	*Cucullaea* I	Long (1992a)
ORECTOLOBIDAE		
Stegostoma cf. *S. fasciatum*	*Cucullaea* I	Long (1992a)
ODONTASPIDIDAE		
Palaeohypototus rutoti	Acantilados, *Cucullaea* I	Long (1992a)
Odontaspis winkleri	Acantilados, *Cucullaea* I	Long (1992a)
Striatolamia macrota	Acantilados, *Cucullaea* I	Kriwet (2005)
CETORHINIDAE		
Cetorhinus sp.	*Cucullaea* I	Cione & Reguero (1998)
LAMNIDAE		
Isurus praecursor	*Cucullaea* I	Cione & Reguero (1994)
Lamna cf. *L. nasus*	*Cucullaea* I	Long (1992a)
OTODONTIDAE		
Carcharocles auriculatus	*Cucullaea* I, Submeseta	Welton & Zinsmeister (1986)
MITSUKURINIDAE		
Anomotodon multidenticulata	*Cucullaea* I	Long (1992a)
CARCHARHINIDAE		
Scoliodon sp.	*Cucullaea* I	Long (1992a)
Carcharhinus sp.	*Cucullaea* I	Kriwet (2005)
PALAEOSPINACIDAE		
Paraorthacodus sp.	*Cucullaea* I	Cione (comm. pers.)
PRISTIDAE		
Pristis sp.	*Cucullaea* I	Kriwet (2005)
MYLIOBATIDAE		
Myliobatis sp.	Acantilados, *Cucullaea* I	Cione et al. (1977)
RAJIDAE		
Bathyraja sp.	*Cucullaea* I	Long (1992c)
HOLOCEPHALI		
CALLORHYNCHIDAE		
Ischyodus dolloi	*Cucullaea* I	Grande & Eastman (1986)
CHIMAERIDAE		
Chimaera seymouriensis	*Cucullaea* I, Submeseta	Ward & Grande (1991)

Long (1992a) pointed out that this Antarctic fossil shark assemblage constitutes a very complex assortment of sharks from many different habitats converging on one specific locality.

The rare occurrence of *Carcharhinus* and *Pristis*, both taxa confined today to warm-temperate to tropical waters, in the temperate waters of Early Eocene in Antarctica indicates that both were not primary inhabitants but migrated along open trans-equatorial seaways into Southern Hemisphere waters (Kriwet 2005).

The Eocene selachian fauna from Antarctica includes 25 species in 16 families (Table 1). 24 taxa and 15 families come from the *Cucullaea* I Allomember of the La Meseta Formation of Seymour Island. The majority of taxa belong to sharks while batoids are represented by only three taxa with a very uneven distribution in the sequence. Long & Stilwell (2000) reported the presence of rare selachian teeth from Eocene deposits of Mount Discovery in East Antarctica. This material includes the first record of *Galeorhinus* for Antarctica.

Table 2.- Taxonomic list, stratigraphy, and references for the teleostean fishes and reptiles from the Cucullaea I Allomember (La Meseta Formation) of Seymour Island, Antarctic Peninsula.

Taxon	Stratigraphy (Allomember)	Source
CLUPEIFORMES		
CLUPEIDAE		
Marambionella andreae	Acantilados, *Cucullaea* I?	Jerzmanska (1991)
PERCIFORMES		
OPLEGNATHIDAE		
Oplegnathus sp.	*Cucullaea* I	Cione et al. (1994)
XIPHIORHYNCHIDAE		
cf. *Xiphiorhynchus*	Campamento, *Cucullaea* I	Cione et al. (2001)
TRICHIURIDAE		
Trichiurus sp.	*Cucullaea* I	Long (1991)
LABRIDAE		
Gen. et sp. indet.	*Cucullaea* I	Long (1992b)
SILURIFORMES		
INCERTAE SEDIS		
Siluriformes undetermined	*Cucullaea* I?	Grande & Eastman (1986)
GADIFORMES		
MERLUCCIDAE		
"Mesetaichthys"	*Cucullaea* I, Submeseta	Jerzmanska & Swidnicki (1992)
BERYCIFORMES		
gen. et sp. indet.	Acantilados, *Cucullaea* I?	Doktor et al. (1996)
CRYPTODIRA		
DERMOCHELYIDAE		
"Psephophorus" sp.	*Cucullaea* I	De la Fuente et al. (1995)
Testudines indet.	*Cucullaea* I	Bona et al. (2010)

Most of the fish taxa mentioned here are found in many different overlying localities and horizons of the *Cucullaea* I Allomember excepting in the upper units that document a sharp decrease in diversity near the boundary *Cucullaea* II and Submeseta allomembers. In the Submeseta Allomember, there is a dramatic diminution of diversity of those selachians that dominated below, there are no teleost taxa characteristic of warm water (e.g., Labridae, Oplegnathidae, Xiphiorhynchidae), sharks dramatically decreases in diversity and quantity (a few *Pristiophorus* and odontaspidid teeth) and begin to predominate some sharks (*Lamna*) and teleosts with species characteristic of colder waters (e.g., gadiforms of the informal genus "*Mesetaichthys*") are recorded.

Long (1992c) and Case (1992) analyzed the ecology and diversity of the Eocene Seymour selachian fauna and concluded that the selachian fauna represents a cool-temperate fauna with different ecological components including tropical water immigrants (e.g., *Pseudoginglymostoma*, *Stegostoma*, *Scoliodon*).

While the diversity of the elasmobranch fauna in the *Cucullaea* I Allomember of the La Meseta Formation seems to be abundant and quite diverse, the teleost fishes appear to be low and poor. Teleost fishes are represented by gadiforms, clupeiforms, oplegnathids, siluriforms, perciforms, beryciforms, and chimaeriforms (see Table 2).

Penguins are by far the most dominant group of coastal/marine birds within this unit. Sphenisciformes are a group of flightless aquatic birds, distributed broadly throughout the Southern Hemisphere. Fossils indicate that stem penguins reached Antarctica by the late Paleocene (Tambussi et al. 2005), South America by the middle Eocene (Clarke et al. 2003), and Australia by the late Eocene (Simpson 1957; Jenkins 1974). Seymour Island Paleogene sequence (Cross Valley and La Meseta formations) has the longest and unique fossil record of basal sphenisciformes, with occurrences ranging from the late Paleocene (Cross Valley Formation) to late Eocene and constitutes the most complete Paleogene stratigraphic record of the group known in the world. The sphenisciform *Palaeeudyptes* is a taxon with biogeographic significance, is the most widespread Weddellian penguin genus in the Southern Hemisphere during the Eocene (Acosta Hospitaleche & Reguero 2010, 2011).

Stem penguin diversity peaks in the late Eocene by which time these birds are taxonomically diverse, geographically widespread, and abundant at many localities (e.g., Marples 1952; Myrcha et al. 2002; Tambussi et al. 2006).

The highest diversity of Weddellian sphenisciforms is documented in the *Anthropornis nordenskjoeldi* Biozone (Tambussi et al. 2006) defined within the Priabonian Submeseta Allomember, and this unit was deposited at 34.2 Ma based on $^{87/86}$Sr dates (Dingle & Lavelle 1998). Currently, 15 diagnosable sympatric species are recognized from this biozone, a total approaching modern global species-level diversity (19 species).

The first significant radiation of the Weddellian sphenisciforms took place in Ypresian beds of the *Cucullaea* I Allomember with 8 sympatric species (Table 3). The following eight species were identified in the Ypresian *Cucullaea* shell bed: *Anthropornis nordenskjoeldi* Wiman 1905, *Anthropornis grandis* (Wiman 1905), *Palaeeudyptes gunnari* (Wiman 1905), *Palaeeudyptes klekowskii* Myrcha, Tatur & Del Valle 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 *D. arctowskii* Myrcha et al. 2002, and *D. gracilis* Myrcha et al. 2002 are dubiously identified (Fig. 4).

Table 3.- Taxonomic list, stratigraphy, and references for birds and whales from the *Cucullaea* I Allomember (La Meseta Formation) of Seymour Island, Antarctic Peninsula.

Taxon	Stratigraphy (Allomember)	Source
AVES		
SPHENISCIFORMES		
Palaeeudyptes gunnari	Campamento/Submeseta	Wiman (1905)
Palaeeudyptes klekowskii	*Cucullaea* I/Submeseta	Myrcha et al. (1990)
Anthropornis nordenskjoeldi	*Cucullaea* I/Submeseta	Wiman (1905)
Anthropornis grandis	*Cucullaea* I/Submeseta	Wiman (1905)
Delphinornis larseni	*Cucullaea* I/Submeseta	Wiman (1905)
Delphinornis wimani	*Cucullaea* I/Submeseta	Marples (1953)
Mesetaornis polaris	*Cucullaea* I/Submeseta	Myrcha et al. (2002)
Marambiornis exilis	*Cucullaea* I/Submeseta	Myrcha et al. (2002)
PELECANIFORMES		
PELAGORNITHIDAE		
gen. et sp. indet.	*Cucullaea* I; Submeseta	
DIOMEDEIDAE		
gen. et ap. indet.	*Cucullaea* I	Tambussi & Tonni (1988)
MAMMALIA		
PELAGICETI		
gen. et sp. nov.	*Cucullaea* I	Reguero *et al.* (2011)

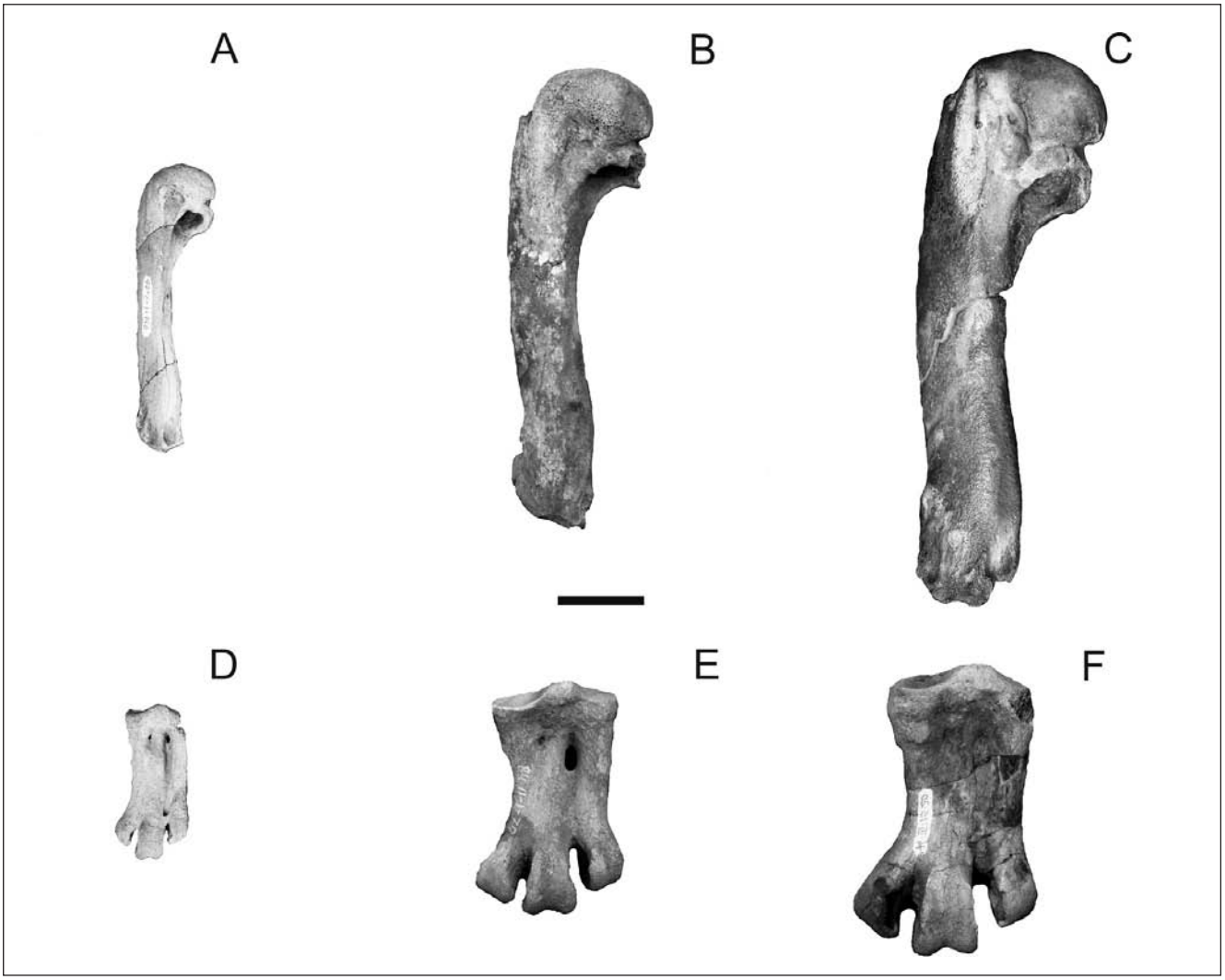

Figure 4. Humeri of Weddellian penguins from the Ypresian *Cucullaea* I (La Meseta Formation) Seymour Island, Antarctic Peninsula. Comparative series in caudal view. Photographs have been reversed where necessary. **A**. *Delphinornis larseni*, MLP; **B.** *Palaeeudyptes gunnari*, MLP 93-X-1-3, and **C.** *A. nordenskjoeldi*, MLP 93-X-1-4. Tarsometatarsi of Weddellian penguins from the Ypresian *Cucullaea* I (La Meseta Formation) Seymour Island, Antarctic Peninsula. Antarctica. Comparative series in caudal view. **D.** Scale bar = 2 cm.

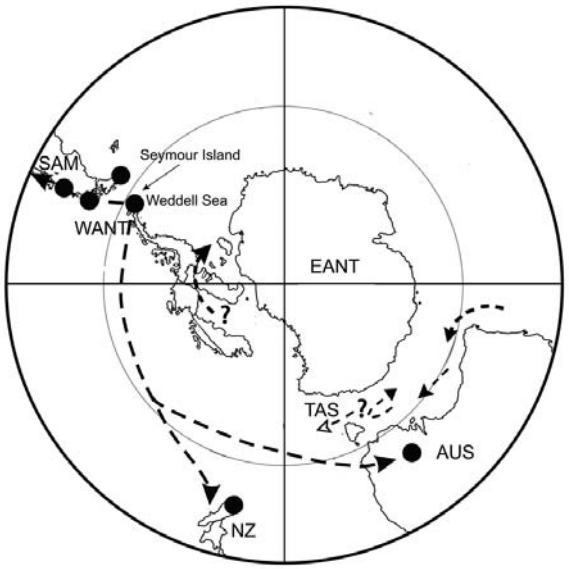

Figure 5. Paleogeographic reconstruction of the southern continents (Gondwana) and the Weddellian Province at 50 Ma (Ypresian) showing the probable dispersal of Weddellian Sphenisciformes (dotted lines and arrows). Black circles represent fossil localities discussed in the text.

Although late Paleocene–middle Eocene sampling of the penguin record is not complete, stratigraphically calibrated, specific-level phylogenies (i.e. Ksepka & Clarke 2010; Clarke et al. 2010) indicate that an important radiation took place during this interval in Antarctica; at minimum, five clades of sphenisciforms diverged by the early Eocene (Psepka & Clarke 2010).

The underlying unit (Telm 3, late Early Eocene Campamento Allomember, 52 Ma) yielded small abundance of penguins with a low diversity, only one large species is recorded, *Palaeeudyptes gunnari* (Jadwiszczak 2006a, 2006b). The FAD (First Appearance Datum) of *Palaeeudyptes gunnari* is located within the Ypresian Campamento Allomember (La Meseta Formation) (Fig. 2).

This Early Eocene sphenisciformes diversity supports several separate dispersals of giant penguins from Antarctica to lower latitudes: 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) regions during greenhouse earth conditions (Fig. 5).

Whale remains occur sporadically throughout the La Meseta Formation (*Cucullaea* I and Submeseta allomembers). Archaeocetes from the La Meseta Formation of Seymour Island, Antarctica (Borsuk-Bialynicka 1988; Fostowicz-Frelik 2003), are in their majority based on unspecific postcranial material. Recently, Reguero et al. (2011) reported an incomplete jaw with teeth of a new basilosaurid archaeocete recovered from the *Cucullaea* shell bank. This discovery is significant as documented the earliest occurrence of a basilosaurid in Antarctica. The mandible bears five alveolus and two cheek teeth. The crown of one tooth, probably P2, is triangular and laterally compressed with multiple accessory denticles (3) and wear facet with a distinctive basal cingulid (Fig. 6).

This archaeocete represents the earliest record of whales in Antarctica (Ypresian, 49.5 Ma), and confirms the presence of this primitive group of whales (Basilosauridae) in the middle levels of La Meseta Formation. This specimen is the first inquestionable archaeocete described from Antarctica and is referred to a new taxon.

Discussion

During the Eocene, notwithstanding that some circulation could exist in Drake Passage area (Wrenn and Hart 1992), there was not a well developed Antarctic Circumpolar Current and consequently no author proposed the existence of the equivalent to Humboldt and Malvinas currents (Cione et al. 2007). During the Eocene, the Pacific coast would have

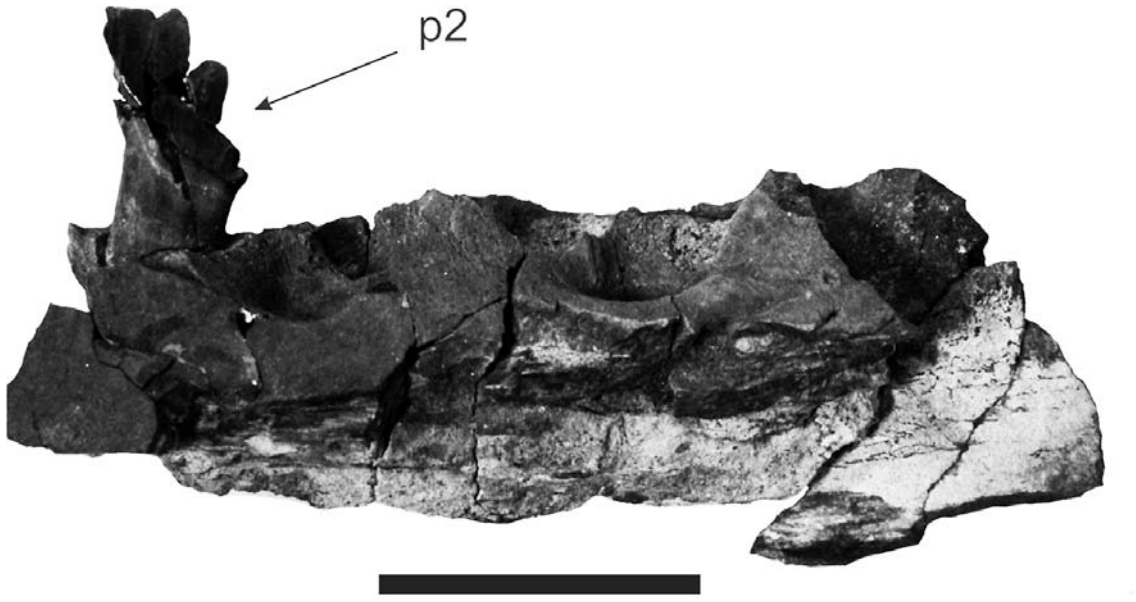

Figure 6. Seymour Island Pelagiceti gen. et sp. nov., MLP 11-II-21-3, incomplete left dentary with p_2 preserved *in situ*. Base of the *Cucullaea* I Allomember, the basal shell bed (Telm 4 of Sadler 1988) at DPV 2/84 locality. Scale bar = 5 cm.

been located at paleolatitude nearly equivalent present-day latitude, as there has been essentially no latitudinal translation of the area since the late Cretaceous. 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 low-latitude penguin diversity by cycling cold, nutrient-rich water into the ecosystem (Clarke et al. 2007).

The Eocene selachian fauna from Antarctica includes 25 species in 16 families; 24 taxa and 15 families come from the *Cucullaea* I Allomember of La Meseta Formation of Seymour Island. The majority of taxa belong to sharks while batoids are represented by only three taxa with a very uneven distribution in the sequence.

The Ypresian *Cucullaea* shell bed (Telm 4, basal horizon of the *Cucullaea* I Allomember) of La Meseta Formation is highly fossiliferous and yielded a remarkably diverse assemblage of plants, invertebrates and vertebrates that have provided the most detailed record of high-latitude southern Eocene organisms to date (e.g., Reguero et al. 2007). Nearly all phyla commonly preserved in the fossil record have been described from the unit (Schweitzer et al. 2005). Both continental and marine organisms indicate that the environment was completely different to that present in Antarctica today (Reguero & Marenssi 2010).

The shark fauna from the Ypresian *Cucullaea* shell bed (Telm 4, basal horizon of the *Cucullaea* I Allomember) of La Meseta Formation is one of the most diverse and abundant Early Eocene temperate neoselachian assemblages known from the Southern Hemisphere. So far, 22 selachian taxa within 14 families (including two batoids) have been reported from different localities on Seymour Island and from different levels of the *Cucullaea* I Allomember within the La Meseta Formation (Cione & Reguero, 1994, 1998; Long, 1992a, b, c; Welton & Zinsmeister, 1980). All these taxa have the oldest record in the *Cucullaea* I shell bed (Telm 4).

Today four penguin species: *Aptenodytes forsteri* (Emperor penguin), *Pygoscelis adeliae* (Adelie penguin), *Pygoscelis antarctica* (Chinstrap penguin), and *Pygoscelis papua* (Gentoo penguin) live and nest on Antarctica and sub-Antarctic islands. The phylogeny of the Sphenisciformes reveals that important radiations of small and large Weddellian penguins took place during the Late Paleocene/Early Eocene in Antarctica. The stratigraphical record of the sphenisciformes from Seymour Island is almost continuous from the Late Paleocene to Late Eocene and provides strong evidence on the evolution of this group in the Paleogene. One of the events clearly documented in this Paleogene sequence is the first radiation of this group that occurred in the *Cucullaea* shell bed (Telm 4) of the La Meseta Formation dated in a range of 49 to 52 Ma (Ypresian). The diversity of sphenisciformes increases from one in the Paleocene, one in the Valle de la Focas and Acantilados allomembers, probably two in the Campamento Allomember to nine species in the *Cucullaea* I Allomember.

They are broadly considered to be cool-adapted and the crown clade (Spheniscidae) seems to have the origin in association with the abrupt latest Eocene–Oligocene global cooling (~34 Ma) and to undergo a major radiation and range expansion to low latitudes only during later Neogene cooling (Baker *et al.* 2006). However, there is no fossil evidence to support a crown radiation in the Late Eocene concomitant with the initiation of the circum-Antarctic current, initial onset of Cenozoic global cooling, or at the proposed extinction of giant penguins.

The new gen. et sp. of archaeocete recorded in the *Cucullaea* shell bank represents the earliest record of whales fully aquatic (Ypresian, 49.5 Ma), and confirms the presence of this primitive group of whales (Basilosauridae) in West Antarctica.

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