ANTARCTIC BIRDS (NEORNITHES) DURING THE CRETACEOUS-EOCENE TIMES

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ABSTRACT:

Antarctic fossil birds can be confidently assigned to modern orders and families, such as a goose-like anseriform, two loon-like and a seriema-like, all recorded before the K/T boundary at the López de Bertodano Fomation. Also, the discovery of a ratite and a phororhacids from the uppermost levels of the Submeseta Allomember (Late Eocene), suggests that West Antarctica was functional to dispersal routes obligate terrestrial birds. Representatives of Falconiformes Polyborinae, Ciconiiformes, Phoenicoteriformes, Charadriiformes, Pelagornitidae and Diomedeidae constitute the non-penguin avian assemblages of the Eocene of La Meseta Formation. Fifthteen Antarctic species of penguins have been described including the oldest penguin of West Antarctica, *Croswallia unienwillia.* The *Anthropornis nordenskjoeldi* Biozone (36.13 and 34.2 Ma, Late Eocene) is characterized by bearing one of the highest frequencies of penguin bones and the phospatic brachiopod *Lingula.*, together with remains of Gadiforms, sharks and primitive mysticete whales. *Anthropornis nordenskjoeldi, Delphinornis gracilis, D. arctowski, Archaeospheniscus lopdelli,* and *Palaeeudyptes antarcticus* are exclusively of the La Meseta Formation. *Anthropornis nordenskjoeldi* was evidently the largest penguin recorded at the James Ross Basin, whereas *Delphinornis arctowski* is the smallest, and include one of the worldwide highest morphological and taxonomic penguin diversity living sympatrically. The progressive climate cooling of the Eocene could have affected the penguin populations, because of climatic changes linked with habitat availability and food web processes. However, there is not available evidence about Antarctic penguins' evolution after the end of the Eocene.

Keywords: *Birds, Antarctica, Cretaceous, Paleogene.*

RESUMEN: *Aves antàrticas (Neornithes) durante el lapso cretácico - eoceno.*

Las aves fósiles antárticas pueden ser asignadas a órdenes y familias vivientes, incluyendo restos de un Anseriformes que recuerda al ganso overo, dos colimbos y una supuesta seriema, todos registrados en sedimentos cretácicos de la Formación López de Bertodano. El hallazgo de una ratites y un fororraco en los niveles más altos del Alomiembro Submeseta (Eoceno tardío) soporta la idea de que Antártida Oeste fue utilizada como ruta de dispersión por aves terrestres. Representantes de los Falconiformes Polyborinae, Ciconiiformes, Phoenicopteriformes, Charadriiformes, Pelagornitidae y Diomedeidae componen el conjunto de aves no-pingüinos registrados en los sedimentos Eocenos de la Formación La Meseta. Hasta el momento se describieron quince especies de pingüinos, incluyendo el más antiguo de los Sphenisciformes de Antártida Oeste, *Croswallia unienwillia.* Los pingüinos *Anthropornis nordenskjoeldi*, *Delphinornis gracilis, D. arctowski, Archaeospheniscus lopdelli,* y *Palaeeudyptes antarcticus* asociados con restos de tiburones, misticetos primitivos y Gadiformes se encuentran en la Biozona de *Anthropornis nordenskjoeldi* (36,13 and 34,2 Ma, Late Eocene). Estos niveles albergan una de las más grandes diversidades taxonómicas de pingüinos hasta ahora conocida. Anthropornis nordenskjoeldi fue sin dudas el pingüino más grande del Eoceno de Antártida mientras que en el otro extremo se ubica *Delphinornis arctowski.* Debido a que los cambios climáticos están ligados a la disponibilidad de habitat y de recursos alimenticios, el progresivo enfriamiento climático acaecido durante el Eoceno podría haber afectado a las poblaciones de pingüinos. Sin embargo, no tenemos evidencia acerca de la evolución de los pingüinos luego del Eoceno.

Palabras clave: *Aves, Antártida, Cretácico, Paleógeno.*

INTRODUCTION

The James Ross Basin, at the Northern tip of the Antarctic Peninsula, is one of the most important Early Cretaceous-early Palaeogene sedimentary sequences in the Southern Hemisphere (Francis *et al.* 2006a). Fossil floras and both invertebrate and vertebrate faunas have provided clues to understand past climate and paleoenvironmental changes. Field expeditions carried out in Seymour, James Ross and Vega Island have resulted in the discovery of significant vertebrate specimens that allow to improve our comprehension of the evolutionary history of Antarctic vertebrates, in particular the one that regards to birds. However, despite intensive study of these areas in the past decades, there is still much uncertainty about the exact composition of the Cretaceous-Paleogene Antarctic avifauna.

Recently, our understanding of the origins and evolution of Neornithes - all modern birds-, has been dramatically influenced by both molecular and fossil researches. Indeed, few neoavians from the end of the Mesozoic are known (Hope 2002), but some of them have been critical as factual evidences of the presence of modern lineages in the Cretaceous, and served as anchor points for the molecular clocks. This is the case of the remarkable specimen of a magpie-goose-like bird Vegavis iaai (Clarke *et al.* 2005) to which we will refer below.

By other hand, the most significant fossil bird record from the James Ross Basin is that of penguins. Currently, fifteen penguin species have been described, and at least ten of which would have coexisted. Most problematic is the assignment of many species from the Eocene of Seymour that are based on non-comparable bones or different parts of the skeleton (Tambussi *et al.* 2006, Tambussi *et al.* 2005). The recently published catalogue by Myrcha and coauthors (2002) is a valuable source for the spheniscids described up to date.

The purpose of this paper is to review the current state of knowledge of Antarctic Cretaceous-Paleogene avian fossils. Our approach has four parts: 1) we describe and analyze the fossil continental birds; 2) we report and analyze the fossil marine birds; 3) we discuss the bioestratigraphic importance of the fossil penguin assemblage, and 4) we discuss the paleobiological significance of the Antarctic fossil birds.

Before developing each of these topics, some geological characteristics of James Ross Basin will be considered. A more detailed account can be found in Francis *et al.* (2006b).

The following institutional abbreviations are used in this paper: MLP Museo de La Plata, MACN Museo Argentino de Ciencias Naturales Bernardino Rivadavia, UCR University of California Riverside, IB/P/B Prof. A. Myrcha University Museum of Nature, University of Bialystok, Poland, TTU P Museum of Texas Tech University. Anatomical nomenclature follows Nomina anatomica avian (Baumel and Witmer 1993) using English equivalents, with some modifications when necessary. Appendix I includes the complete list of materials recovered at Antarctic Peninsula and Islands.

GEOLOGICAL SETTING AND CLIMATIC CONDITIONS

Fossil birds are preserved within marine sediments in the James Ross Basin, which is part of the larger Larsen Basin (Del Valle *et al.* 1992) on the East side of the Antarctic Peninsula (Fig. 1). These sediments were deposited in a back-arc setting relative to a volcanic arc through the Mid Mesozoic-early Cenozoic times (Hathway 2000), during subduction of the Pacific Ocean crust beneath Gondwana (Hayes *et al.* 2006). The basin infilling consists of sandstones, siltstones and conglomerates, and comprises three units: 1) the older Gustav Group (Aptian-Coniacian) that comprises the Pederson, Lagrelius Point, Kotick Point, Whisky Bay and Hidden Lake formations, all confined to the NW coast of James Ross Island (Crame *et al.* 2006); 2) the Marambio Group (Coniacian-Maastrichtian), divided into Santa Marta, Snow Hill Island and López de Bertodano formations (Pirrie *et al.* 1997) and is exposed over most of the James Ross Basin. The latter group contains abundant microfossils, as well as fossil plants, invertebrates and vertebrates assemblages, profusely studied in the last years; and 3) the Seymour Island Group (Early Paleocene-Late Eocene) that includes the Sobral, Cross Valley and La Meseta formations (Francis *et al.* 2006b).

The Late Cretaceous López de Bertodano Formation contains the oldest Antarctic avian remains currently recorded (Case *et al.* 2006a, Chatterjee 1989, Chatterjee 2002, Chatterjee *et al.* 2006, Clarke *et al.* 2005, Noriega and Tambussi 1995, 1996). Among them, the anseriform Vegavis iaai was collected at Cape Lamb, southwestern Vega Island (Western Antarctica), a well-known place because of its abundant and diverse fossil record that includes conifers (Césari 2001), marine invertebrates, elasmosaurids, mosasaurids (Martin 2006) and a duck-billed dinosaur (Case *et al.* 1987). The sedimentary sequence has been subdivided into three informal units K1, K2 and K3 (Marenssi *et al.* 2001), being the former two Early Maastrichtian and the latter Mid-Late Maastrichtian. The unit K3 comprises the upper part of the Cape Lamb Member and the Sandwich Bluff Member of the López de Bertodano Formation (sensu Pirrie *et al.* 1991) or the Unit B (Olivero *et al.* 1992), which is has been dated in approximately 66-68 million years old based on correlations of ammonites and palynological taxa (Crame *et al.* 1991, Pirrie *et al.* 1991).

The Tertiary section (Seymour Island Group), exposed mainly on Seymour Island and Cockburn iIslands, includes the Late Palaeocene Cross Valley Formation and the richly fossiliferous Eocene La Meseta Formation, both deposited in incised-valley settings. At its type section, in the central art of Seymour Island, the Cross Valley Formation (Elliot and Trautman 1982) fills a steep-sided valley cut in the Lower Palaeocene Sobral Formation and older beds (Tambussi *et al.* 2005).

The youngest bird fauna is from La Meseta Formation, which overlies the López de Bertodano Formation. This unit was interpreted as the filling of an incised-valley system and is the topmost exposed sector of the sedimentary fill of the Late Jurassic-Tertiary James Ross Basin (Del Valle et al. 1992). It is composed of sandstones, mudstones and conglomerates deposited during the Eocene in deltaic, estuarine and shallow marine settings (Marenssi *et al.* 1998 a, b). From the base to the top, six units are distinguished (Marenssi *et al.* 1998b): Valle de Las Focas, Acantilados, Campamento, Cucullaea I, Cucullaea II and Submeseta Allomembers. The Valle de las Focas, Acantilados and Campamento Allomembers constitute facies association I, composed by a fine-grained sequence with mudstones and very fine sandstones deposited in a delta front plain environment. Facies association II includes the Cucullaea I, Cuccullaea II and the lower part of the Submeseta Allomembers, ranging from conglomeratic beds to mudstones with diverse and abundant macrofauna (Marenssi *et al.* 1998b) that corresponds to a valley-confined estuary mouth to inner estuary complex. The base of the Cucullaea I Allomember has produced a ^{87}Sr/^{86}Sr date of 49.5 Ma (Marenssi 2006). Finally, facies association III, which includes the topmost sediments of Submeseta Allomember, is characterized by a more unvarying sandy lithology composed mainly by fine to medium-grained sandstone and represents sedimentation on a sandy tidal shelf influenced by storms. The three facies associations described above suggest a major transgressive cycle. Dingle and Lavelle (1998) reported a ^{87}Sr/^{86}Sr derived age of 34.2 Ma (late Late Eocene) for the topmost part of La Meseta Formation whereas Dutton *et al.* (2002) reported ages of 36.13, 34.96 and 34.69 Ma (late Late

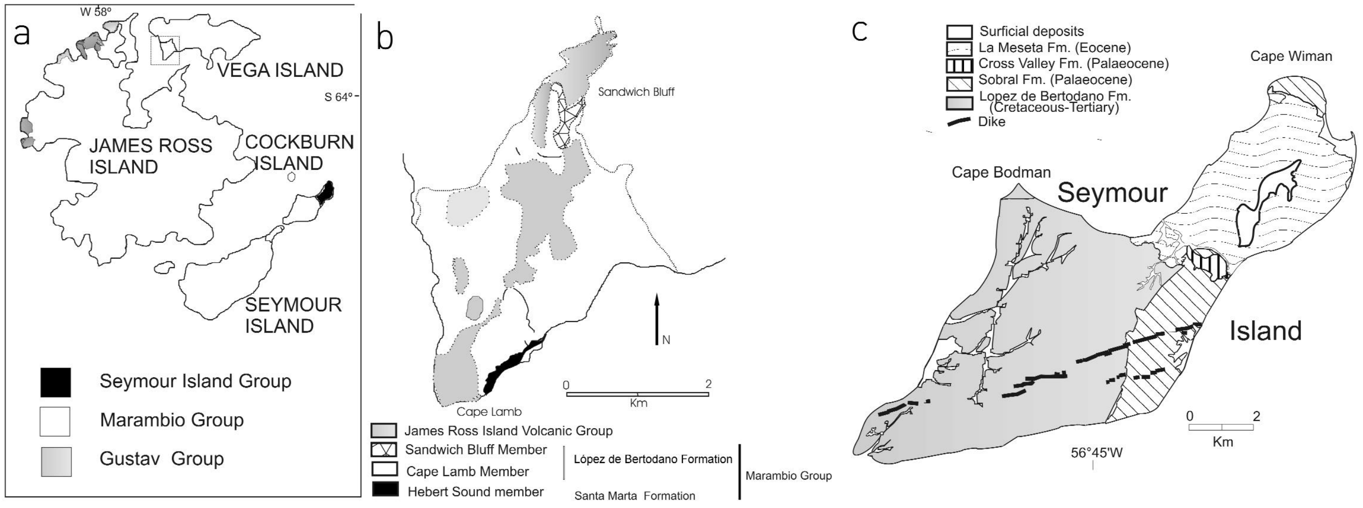

Figure 1: a, Sketch geological map of the James Ross Island area. b. Cape Lamb, Vega Island, c. Seymour Island.

Eocene) for different levels within Submeseta Allomember.

The climate in the Antarctic Peninsula during the Late Cretaceous and Paleogene would have been relatively mild and moist, with no significant presence of ice at high latitudes (Francis 1996, Poole *et al.* 2001). A cooling event and a frostless climate characterized the environments between the Late Cretaceous and the mid-Paleocene (Dingle and Lavelle 1998, Zachos *et al.* 1993). The fossil evidence suggests that during the Paleocene a cool to warm climate and high rainfall prevailed (Poole *et al.* 2001), whereas paleotemperature data from the sea indicate that a peak occurred in the Early Eocene. Sedimentological (Coxall *et al.* 2005, Ehrmann and Mackensen 1992), oxygen isotopic (Dutton *et al.* 2002, Gadzicki *et al.* 1992, Ivany *et al.* 2004, Kennett and Warnke 1993, Mackensen and Ehrmann 1992, Salamy and Zachos 1999), floral (Francis 1999, 2000) and faunal (Aronson and Blake 2001, Dzik and Gadzicki 2001, Feldmann and Woodbourne 1988, Gadzicki 2004, Myrcha *et al.* 2002, Reguero *et al.* 2002) data indicate cooling, growth of terrestrial and marine ice sheets, and initiation of Cenozoic glaciation at the end of the Eocene (Birkenmajer *et al.* 2004).

THE FOSSIL CONTINENTAL BIRDS

The discovery and study of fossil continental birds in Antarctica are relatively old events. The earliest studies upon fossil continental birds in Antarctica were made by Covacevich and Lamperein (1972) and Covacevich and Rich (1982) working at Fildes Peninsula in King George Island, the largest of the South Shetland Islands. The mid-Tertiary lacustrine sediments of King George Island preserved ichnofossils from four types of birds including the avian tetradactyle footprint *Antarctichnus fuenzalidae* Covacevich and Lamperein (1970) associated with shorebirds. One of the morphotypes apparently represents a non-volant ground bird that could belong to either ratites or gruiforms, and another probably represents an anatid. In summary, the ichnofossils from Fildes Peninsula include both solitary and group activities with their hypothetical avian tracemakers.

Two different taxa of large flightless cursorial birds from Antartica have been so far described (Figs. 2 and 3), being a ratite (Tambussi *et al.* 1994) and a phororhacid bird (Case *et al.* 2006, Case *et al.* 1987). Both forms were recovered from the topmost levels of the Submeseta Allomember, part of the near-shore deposits of the La Meseta Formation on Seymour Island, likely Late Eocene (*ca* 36 Ma Dutton *et al.* 2002, Reguero *et al.* 2002). They are part of the few records of terrestrial biota recovered from this predominantly marine formation. Strictly Late Eocene terrestrial birds of Antarctica raise some interesting biogeographic issues that we will discuss below.

According to current ornithological classifications, the ratites include two species of ostriches (Struthionidae) in Africa and Asia, the Australian emu and three species of cassowaries (Casuariidae) in New Guinea and northeastern Australia, three species of forest-dwelling kiwis (Apterygidae) in New Zealand, and two rheas (Rheidae) in South America (Sibley *et al.* 1988). All the ratites live currently in the Southern Hemisphere, and all of them lack a keel on the sternum, a character associated with flightlessness. The Antarctic material is a distal tarsometatarsus with a "large, narrow trochlea for digit III, which is projected moderately beyond the trochlea for digit II with straightend margins bordering a deep groove. Trochlea II has a wide articular surface and extends posteriorly more than trochlea III.The lateral margin of trochlea III allow us to infer that the intertrochlear space between trochlea III and IV extends proximately beyond trochleae II and III" (Tambussi *et al.* 1994). The estimated body mass of the Antarctic specimen is approximately 60 kg (Vizcaíno *et al.* 1998).

Phorusrhacids are a predominantly Neogene group of large predatory, terrestrial birds (Alvarenga and Höfling 2003) recorded between the Late Paleocene (Brazil, Itaborian SALMA) and Late Pleistocene (USA) (MacFadden *et al.* 2006, Tambussi *et al.* 1999). Classical studies on these birds classified their diversity within five subfamilies (Brontornithinae, Phorusrhacinae, Patagornithinae, Mesembriornithinae and Psilopterinae) with a wide range of sizes and morphotypes, since the sturdy non-flying brontornithines to the gracile and flying psilopterines (Tambussi and Noriega 1996). Phorusrhacid remains have been found in a variety of sedimentary rocks in Uruguay, Brazil, Antarctica, United States, and Patagonia (Argentina), where they are best known Currently it is assumed that the European "Phorusrhacidae" (Mourer-Chauviré 1981, Peters 1987) do not belong within Phorusrhacidae but to *Strigogyps* (Mayr 2005).

A distal end of bill (Fig.3) attributed to a gigantic supposed phorusrhacid (Gruiformes from Seymour Island, was described by Case and colleagues (1987). Additional materials assigned to phorusrhacids were recently described from the same levels (Case *et al.* 2006). One of these specimens consists in a tarsometatarsus (Fig.3) with unquestionable phorusrhacid affinities, similar in size to *Patagornis marshii*. The other two elements, a vertebra and a tibiotarsus, seem not to be a Phorusrhacidae and we think that their assignment should be revised.

In addition to phorusrhacids and ratites, other avian species have distributions that span multiple continents. Current biogeographic hypotheses based on the Gondwanan fragmentation or long distances migrations. Although the phylogenetic affinities of the Antarctic ratites and phororhacids are not clear, their discovery strongly supports the idea that West Antarctica was used as dispersal route for obligate terrestrial organisms.

The crown-group Falconiformes includes the New World vultures (Cathartidae), the secretary bird (Sagittaridae), the falcons (Falconidae), and the hawks and allies (Accipitridae) (see discussions about the monophyly of Accipitridae in Mayr *et al.* 2003). Living Polyborines are vulture-like falconids with scavenging habits that occur exclusively in the Americas, mainly in the Neotropical regions. Polyborinae have been recorded upon a tarsometatarsus from the La Meseta Formation (Tambussi *et al.* 1995) (Fig. 4). The animal would have reached a body mass of about one kilogram and the size of the living caracara *Polyborus plancus*. This tarsometatarsus exhibits a morphology similar to living polyborines in having the trochlea for the second digit shorter and wider than the trochlea for the digit four, bearing a plantarly projection. This falconid bird, together with the phorusrhacid, were the representatives of the carnivorous (either scavenger or predator) role within the late Eocene Antarctic fauna.

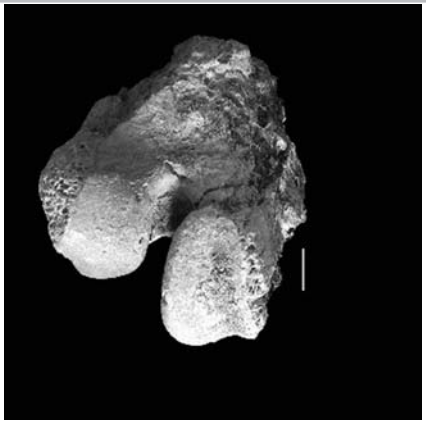

Figure 2: Ratites. MLP 94-III-15-1, distal fragment of right tarsometatarsus in posterior view. Scale: 10 mm.

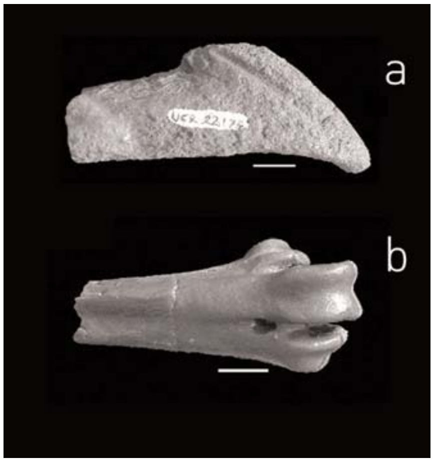

Figure 3: Phorurhacids cast UCR 22175, a) Fragment of the bill, b) tarsometatarsus anterior view. Scale: 10 mm.

Unambiguous Charadriiform birds are known from the late Eocene of the La Meseta Formation, based on a right scapula (MLP 92-II-2-6). All Charadriiform, shorebirds and waders are a heterogeneous and polymorphic group of birds of small to moderate size that frequent open inland and marine wetlands.

Flamingos (Phoenicopteridae), are gregarious and invariably associated with warm temperatures, brackish or salt-water lakes and lagoons. The oldest record assigned to Phoenicopteridae, is from the lower Oligocene of France. An incomplete right radius (MLP 87-II-1-2) of the La Meseta Formation was reported by Noriega and Tambussi (1996).

A probable Ciconiiforms was found at the upper level of La Meseta Formation (MLP 90-I-20-9, which consists in a distal fragment of a right tarsometatarsus). Unfortunately, the material is not preserved enough to allow a more precise identification.

Recently, unquestionable remains of neornithines from the Maastrichtian of Antarctica have bridged the disagreement between molecular and palentological data about the diversification history of Neornithes (Dyke and Van Tuinen 2004). As mentioned previously, the Anseriform *Vegavis iaai* Clarke *et al.* 2005 was recovered from a southwestern locality at Cape Lamb in Vega Island (Fig. 5). In a recent work, Clarke *et al.* (2005) point its importance out as one of only handful specimen considered as a true Neornithinae, and whose phylogenetic position has been established. *Vegavis* provides a well-defined phylogenetic calibration point for estimating the early divergence of modern birds (see Slack *et al.* 2006).

By other hand, a fragment of femur recovered near the base of Sandwich Bluff Member (Vega Island) at a level equivalent to that of *Vegavis iaai*, was identified as a seriema-like bird by Case *et al.* (2006). Spite seriemas have traditionally been considered as descendants of the phorusrhacids (Alvarenga and Hofling 2003), further phylogenetic analysis between modern and fossil Gruiformes birds are necessary, and the monophyly of all the Phorusrhacidae is yet to be verified.

Beyond this, all these avian records are crucial for studies of biogeographic trends during the final phases of the Gondwana break-up.

THE FOSSIL MARINE BIRDS

Neogaeornis wetzeli Lambrecht, 1933 and "*Polarornis gregorii*" have respectively been described from the late Cretaceous of Chile and Antarctica (Chatterjee 1989, Chatterjee 2002). Both taxa have been considered as members of the crown gaviids or the stem gaviiforms, and their phylogenetic affinities are still unknown (Mayr 2004). Living loons and grebes (Gaviiformes, Gaviidae) are foot-propelled diving birds. They show a restricted North American distribution that winter along sea coasts and breed at freshwater sites.

Chaterjee (1997, 2002) described and figured the skull of "*Polarornis*", but some skepticism about its assignment and anatomical information arised.

Gerald Mayr (2004) along with his description of the Paleogene *Colymboides metzleri*, commented about Polarornis: "if correctly assigned to the Gaviiformes, may be a synonym of *Neogaeornis* - a possibility already proposed by Olson (1992) but not discussed by Chatterjee 2002" (Mayr 2004: 285). If this is the case, *Polarornis* should be considered junior synonym to *Neogaeornis wetzeli*.

More recently, Chatterjee *et al.* (2006) presented a new species of "*Polarornis*" that exhibit both aerial and aquatic locomotion modes.

Fossil remains of the extinct bony-toothed Pelagornithidae (Odontopterygiformes) were found in the Late Eocene La Meseta Formation (Tonni and Tambussi 1985, Tonni, 1980). Remains of these enigmatic birds have been also recovered from England, Europe, North America, Japan, New Zealand, Africa, Chile and Peru (Harrison and Walker 1976, McKee 1985, Olson 1985, Walsh and Hume 2001, Warheit 1992). Pseudodontorns, supposedly related to pelicans (Pelecaniforms) and tube-nosed birds (Procellariiformes), were large marine gliding birds equipped with bony projections along the edges of their robust bills (Fig. 6). An alternative hypothesis about their phylogenetic affinities was proposed recently (Bourdon 2005). This author proposes the sibling relationships between the pseudodontorns and waterfowl (Anseriformes), erecting the clade Odontoanserae to include Odontopterygiformes plus Anseriformes. Regardless of their phylogenetic position, pseudodontorns included taxa that were among the largest known flying birds. Noteworthy, the pelagornithids of the Late Eocene of Seymour Island (as discussed below) are associated with penguins, while the pseudodontornitids from the Northern Hemisphere were associated with the penguin-likeplotopterids (González-Barbaa *et al.* 2002). Warheit (1992) has suggested that such an assemblage for the Late Eocene could be the result of a worldwide oceanic cooling occurred at 50 Ma.

Procellariiformes include the modern albatrosses, petrels and storm-petrels. Modern albatrosses (Diomedeidae) are worldwide pelagic and gliding sea-birds southern oceans. However, its fossil record is fairly from the Northern Hemisphere, where they appear since the Late Oligocene (Tambussi and Tonni 1988). A weathered tarsometatarsus from the La Meseta Formation at Seymour Island (Noriega and Tambussi 1996; Tambussi and Tonni 1988) can be unambiguously assigned to this family. Additional fossil specimens housed at Museo de La Plata could be also assigned to Procellariidae (Noriega and Tambussi 1996).

Figure 4: Falconiformes Polyborinae MLP 95-I-10-8, distal fragment of left tarsometatarsus, anterior view. Scale: 10 mm.

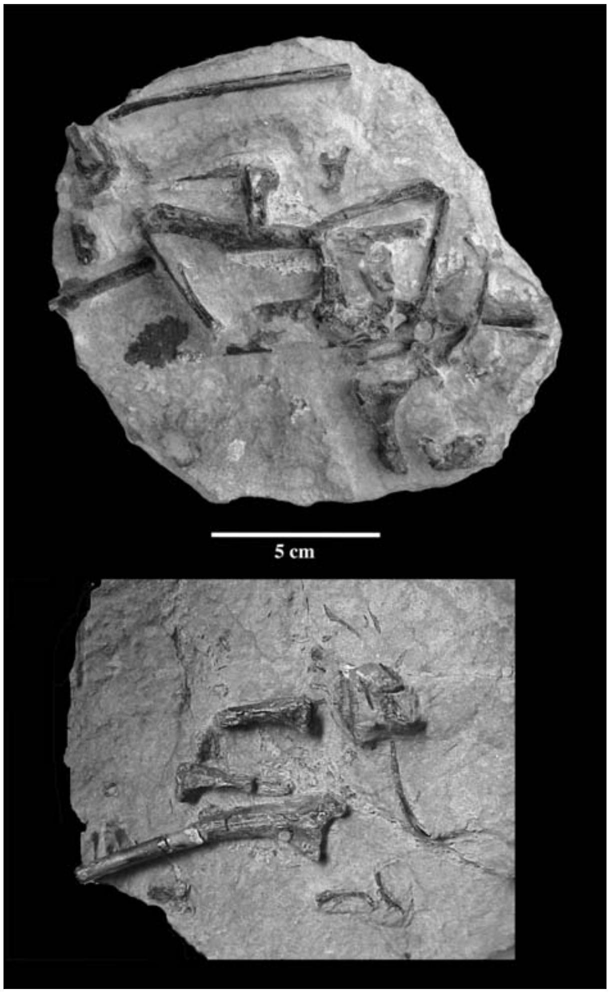

Figure 5: Anseriformes Vegavis iaai MLP 93-I-1-3 holotype. Above, larger half concretion that preserves most of the bones of the holotype, Below, the second half of the same concretion.

Thousands of bones are accumulated in some fossil sites, likely due their colonial nesting behaviour, near-shore aquatic habitat and lack of skeletal pneumaticity (Triche 2006). They belong to a much derived clade of modern birds, Sphenisciformes (the clade including all fossil and living penguins,

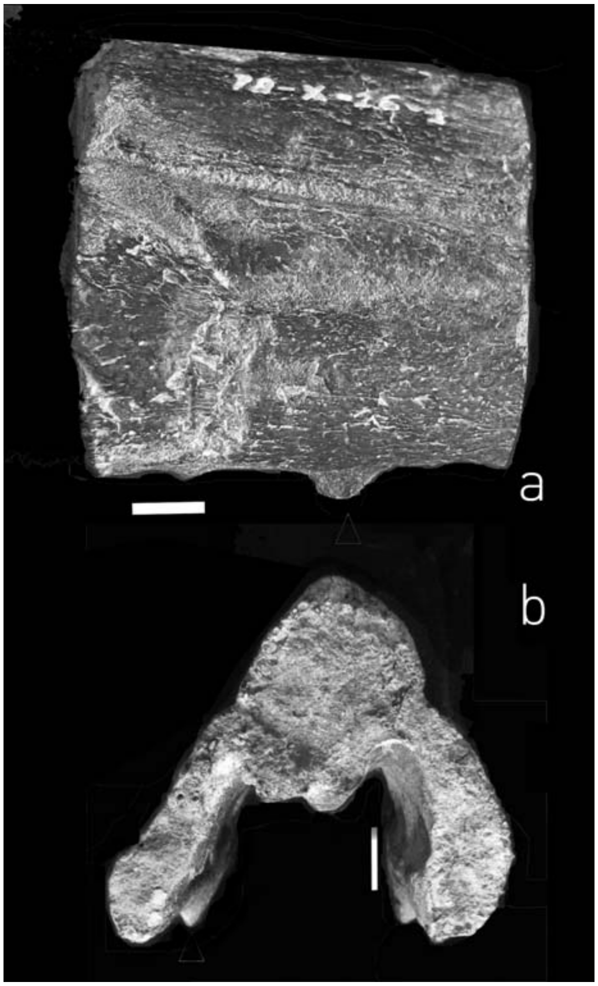

Figure 6: Odontopterygiformes Pelagornithidae, MLP 78-X-26-1, fragment of the rostrum. Arrows show projections of the tomia, a) lateral view, b) transversal view. Scale: 10 mm.

but see Clarke *et al.* 2003) with aquatic lifestyle, non-pneumatic bones and wings transformed into flippers.

The Late Paleocene *Crossvallia unienwillia* Tambussi *et al.* 2005, together with the late Eocene *Anthropornis nordenskjoeldi* Wiman 1905, *Anthropornis grandis* (Wiman 1905), *Palaeeudyptes antarcticus* Huxley 1859, *Palaeeudyptes klekowskii* Myrcha *et al.* 1990, *Palaeeudyptes gunnari* (Wiman 1905), *Archaeospheniscus wimani* (Marples 1953), *Archaeospheniscus lopdelli* Marples 1952, *Delphinornis larseni* Wiman 1905, *Delphinornis gracilis* Myrcha *et al.,* 2002, *Delphinornis arctowskii* Myrcha *et al.* 2002, *Marambiornis exilis* Myrcha *et al.* 2002, *Mesetaornis polaris* Myrcha *et al.* 2002, *Tonniornis mesetaensis* Tambussi *et al.* 2006 and *Tonniornis minimum* Tambussi *et al.* 2006, join to the fifteen penguin species previously known (Appendix I).

The Eocene species were primarily found in sediments of the Submeseta Allomember, although four were recorded in the Cucullaea I Allomember (Fig.7).

Due to the fragmentary nature of their record, the spheniscids' systematic is based on isolated bones, usually upon tarsometatarsi (Jadwiszczak 2001, 2003) and humeri (Simpson 1946). Indeed, most of the species are only known from one of those elements.

Regarding Antarctic fossil penguins, Myrcha *et al*. (2002) studied exclusively the tarsometatarsi and identified four new species, whereas Tambussi *et al.* (2005, 2006) added three new ones based on humeral morphology. Considering that *Crossvallia unienwillia, Tonniornis minimum* and *T. mesetaensis* are only known by their humeri, and *Palaeeudyptes klekowskii, Delphinornis arctowskii*, *D. gracilis, Mesetaornis polaris* and *Marambiornis exilis* were identified by their tarsometatarsi, comparative measurements and a deep anatomical descriptions by Kandefer (1994) and Tambussi *et al.* (2006) allowed assigning some humeri to species previously known only by the tarsometatarsi. Beyond these criteria, Jadwiszcak (2006) in his excellent work recognizes several species upon elements other than humeri and tarsometatarsi (see Appendix I).

Crosswallia and the recently described *Waimanu* Jones, Ando and Fordyce 2006 from the Paleocene are the earliest Sphenisciformes (Tambussi *et al.* 2005; Slack *et al.* 2006), although molecular evidence suggests a Late Cretaceous origin for the group.

Ksepka and colleagues (2006) placed *Waimanu* outside of a clade that includes all other penguins. Also, near the base, in a more basal position, *Delphinornis larseni* is located as sister taxon of *Mesetaornis polaris, Marambiornis exilis* and the remaining penguin species. Thus, most of the fossil penguins are nested in a largely pectinate arrangement leading to the crown clade Spheniscidae that includes all modern species of penguins (Ksepka *et al.* 2006 Figs. 2 and 3). The pioneering work of Simpson (1946) provided the first systematic proposal at suprageneric level (five subfamilies Palaeospheniscinae, Paraptenodytinae, Palaeeudyptinae, Anthropornithinae, Spheniscinae), and has remained the basis for all other analyses of penguin relationships, although lacking a cladistic framework (Clarke *et al.* 2003). Some of these subfamilies could be

Figure 7: Sphenisciformes, representatives bones of *Anthropornis* sp., a)right humerus in caudal view. Scale: 10 mm, b) left tibiatarsus anterior view.

considered clades (Ksepka *et al.* 2006; Acosta Hospitaleche *et al.* 2007) but some modifications and further revisions are required. According Ksepka *et al.* (2006), all Patagonian fossil species (more than six taxa of Palaeospheniscinae, Paraptenodytinae and Anthropornitinae in Simpson's view) fall outside the Spheniscidae (the less inclusive clade uniting all extant penguin), refuting the monophyly of all the subfamilies excepting the clade composed by the modern taxa. According to our analysis (Acosta Hospitaleche *et al.* 2007), *Paraptenodytes* from the Early Miocene (about 20 Ma) is located at the base of the Spheniscidae and, with some restrictions, we recognized some of the Simpson's clades (1946) such as Paraptenodytinae and Palaeospheniscinae. However, our phylogenetic analysis was limited to twenty taxa (17 representative species of all living genera and three fossils species).

One of the most peculiar quality of the Antarctic fossil fauna is the existence of giant animals such us *Anthropornis nordenskjoeldi* in horizons that are dated as latest Eocene associated with other small and medium-sized penguins (Myrcha *et al.* 2002) such us *Tonniornis* sp. To mention a single example, *Delphinornis arctowski* is the smallest penguin recorded from the James Ross Basin.

Throughout this contribution, we have mentioned a wealth of literature dedicated to the study of the Antarctic fauna. Penguins are not the exception and have been the basis for vary contributions (Myrcha *et al.* 2002, Tambussi *et al.* 2005, 2006, Jadwiszczak 2003, 2006 and the literature cited therein). For that reason, here we will not provide in-depth treatment of these aspects, although we will refer to some systematic and paleobiological issues.

THE BIOSTRATIGRAPHIC IMPORTANCE OF THE FOSSIL PENGUIN ASSEMBLAGES

Our depiction of the diversity and abundance of avian species is potentially distorted by the artifacts imposed by the taphonomic conditions that determine the assemblages. But after many palaeontological investigations on Seymour Island, we deem that the penguins of La Meseta Formation represent a high-quality record. We advanced this idea in Tambussi *et al.* (2006). The upper part of the Submeseta Allomember concentrates the bulk of the penguin-bearing localities and documents the highest morphological and taxonomical diversity of sympatric penguins worldwide. Five species, *Anthropornis nordenskjoeldi, Delphinornis gracilis, D. arctowski, Archaeospheniscus lopdelli,* and *Palaeeudyptes antarcticus*, are exclusive of these upper levels in which their first and last appearances took place. Because of these bioestratigraphic evidences, the *Anthropornis nordenskjoeldi* Biozone was defined, with an estimated age between 36.13 and 34.2 Ma, (Late Eocene, Tambussi *et al.* 2006). This Biozone is characterized by having abundant penguin bones and the phospatic brachiopod *Lingula.* Among penguins, *Anthropornis nordenskjoeldi* is numerically predominant over the other species. Gadiforms, sharks and primitive mysticete whales are also part of the fossil assemblage. Penguin bones are usually well preserved, complete, dissarticulated and with varying degree of abrasion, suggesting quiet and low-energy depositation conditions. The underlying stratigraphic members of the sequence show reworked fossil materials (Tambussi *et al.* 2006).

Knowing "who the members are, how many of them there are, how they interact, and how they collectively forge a workable" (Vermeij and Herbert 2004: 1) is necessary to understand how an ancient ecosystem functioned. The macrofauna of the *Anthropornis nordenskjoeldi* biozone is adequate to improve our comprehension of Eocene ecosystems.

PALEOBIOLOGICAL IMPLICATIONS OF THE RECORD

The importance of the findings of terrestrial birds in the study of the distribution and origin of the birds has been previously mentioned, as well as the significance of the Antarctic findings as indisputable profs of the presence of Neornithes in the age of dinosaurs. Beyond these facts, penguins are the most recognizable hallmarks of the Antarctic avifauna. Based on their record, diverse conjectures have been made about their biology. Southern South America penguin colonies are formed exclusively by *Spheniscus magellanicus*, at both Pacific and Atlantic coasts. Remarkably, other species of this genus also form exclusive colonies, such as *S. demersus* in the South African coasts, *S. humboldti* in the Peruvians and *S. mendiculus* in the Galapagos archipelago. In contrast, the colonies that occur in the Malvinas (Falklands) and South Georgias Islands comprise up to five sympatric species: *Aptenodytes patagonicus, Pygoscelis papua, P. antarctica, Eudyptes chrysocome* and *E. chrysolophus.* The islands situated south from South Africa are inhabited by *A. patagonica, P. papua and E. chrysocome,* whereas the islands south from New Zealand hold the most diverse colonies formed by *A. patagonica, P. papua, E. robustus, E. sclateri, E. chrysocome, E. schlegeli, Eudyptula minor* and *Megadyptes antipodes.* The coasts of the Antarctic Peninsula hold at present up to five species: *A. forsteri, Pygoscelis papua, P. antarctica, P. adeliae and E. chrysolophus.*

Current available data indicate that the sympatric diversity in the colonies is no higher than four species (Wilson 1983). This is important for the evaluation of colony composition during the Cenozoic. We have already mentioned that 14 species are recognized for the late Eocene of Seymour Island, whereas a lower amount is recognized for the Late Eocene - Oligocene of New Zealand (Ando, pers. comm. to CAH). There are at least three possible interpretations for this fact: 1) the Cenozoic taxonomical diversity in Antarctica and New Zealand are the highest so far recorded, 2) this diversity is biased due to problems in species identification, or 3) the deposits are the product of an asynchronous accumulation of bones.

One of the most outstanding peculiarities of the Antarctic fossil fauna is the co-existence of giant animals such as *Anthropornis nordenskjoeldi* with other small and medium-sized penguins (Myrcha *et al.* 2002) in horizons that are dated as latest Eocene. *Anthropornis nordenskjoeldi* is considered the largest penguin known whereas *Delphinornis arctowski* is the smallest penguin recorded from the James Ross Basin. The hydrodynamic constraints of *A. nordenskjoeldi* suggest that it was a rather slow swimmer that could reach speeds of perhaps 7-8 km per hour with no diving specializations (Tambussi *et al.* 2006).

In turn, *Crossvallia* seems to provide evidence of independent acquisition of large size during the Late Paleocene - Late Eocene time span, probably under different environmental conditions (Tambussi *et al.* 2005), a point of view accepted by Ksepka *et al.* 2006). However, the evolution of penguin body size is still unknown (Ksepka *et al.* 2006).

Studies on recent marine systems suggest that most seabird species are constrained by specific physical environmental features, in juxtaposition with nesting habitats. It is reasonable to believe that the progressive climate cooling during the Eocene would have directly or indirectly affected penguin populations, because climatic changes are linked with habitat availability and food web phenomena.

There is a gap in regard to the evolution of the Antarctic penguin after the end of the Eocene until the Pleistocene.

CONCLUSIONS

Available evidence indicates the existence of climatic fluctuations since the mid-Cretaceous up to the Paleogene beginnings characterized by a warming phase followed by a colder one, and a conspicuous Paleocene-Eocene thermal maximum and a progressive cooling through the Cenozoic (Francis *et al.* 2006a).

The Eocene represents a period of climate transition from global warmth to progressive cooling, culminating in the initiation of Antarctic glaciation. The incidence of these climatic changes on the faunas produces different consequences including both extinctions and origin of groups.

Several molecular phylogenetic studies are predicting Cretaceous or earlier origins of modern taxa, some of them occurred in southern high latitudes. Unambiguous examples of this are penguins whose fossil record begins at the Late Paleocene (Slack *et al.* 2006, Tambussi *et al.* 2005), which provides a lower estimate of 61-62 Ma for the divergence between penguins and related flying birds (Slack *et al.* 2006). Penguin calibrations imply a radiation of modern (crown-group) birds in the Late Cretaceous and a divergence of the modern sea-birds and shore-birds lineages at least by the Late Cretaceous about 74 ± 3 Ma (Campanian).

The current knowledge of the fossil Antarctic birds is based on fragmentary, but very informative, evidence.

- Antarctic fossil birds can be confidently assigned to modern orders and families.
- Anseriformes (Clarke *et al.* 2005), ?Gaviiformes loon-like (Chatterjee *et al.* 2006), ?Gruiformes seriema-like (Case et al. 2006) are recorded before the K/T boundary.
- The Anseriforms *Vegavis iaai* from the late Cretaceous of Vega Island provides a well-definded calibration point for estimating the early divergence times of modern birds.
- Two cursorial birds, a ratite and a phororhacid were recovered from the topmost levels of the Submeseta Allomember Late Eocene in age. Their discovery strongly supports the idea that West Antarctica was used as dispersal route for obligate terrestrial organisms.
- Representative birds of Falconiformes Polyborinae, Ciconiiformes, Charadriiformes (including flamingos), Pelagornithidae and Diomedeidae constitute the non-penguin avian assemblages of the Eocene of La Meseta Formation.
- Fifhteen species of penguins have been described including the oldest penguin of West Antarctica, *Croswallia unienwillia* (Tambussi *et al.* 2005).
- The *Anthropornis nordenskjoeldi Biozone* (36.13 and 34.2 Ma, late Late Eocene, Tambussi *et al.* 2006) is characterized by the high frequency of penguin bones and the phosphatic brachiopod *Lingula*. Five species *Anthropornis nordenskjoeldi, Delphinornis gracilis, D. arctowski, Archaeospheniscus lopdelli,* and *Palaeeudyptes antarcticus* are exclusively for this unit.
- Within the fossil penguins of the James Ross Basin, *Anthropornis nordenskjoeldi* was evidently the largest, whereas *Delphinornis arctowski* is the smallest.
- One of the worldwide highest morphological and taxonomic penguins diversity, including giant and tiny species, is documented at the topmost levels of the La Meseta Formation.
- The progressive climate cooling of the Eocene could have affected the penguin populations, because climatic changes are linked with habitat availability, and food web process. However, there is not evidence about the evolution of the Antarctic penguin after the end of the Eocene.

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APPENDIX I.

Taxonomical and anatomical identification of fossil birds materials from Antarctica.

Ratitae indet.

MLP 94-III-15-1 (distal fragment of right tarsometatarsus)

Occurrence Submeseta Allomember (Tambussi *et al.*, 1994)

Falconiformes Polyborinae

MLP 95-I-10-8 (distal fragment of tarsometatarsus)

Ocurrence Cucullaea I Allomember (Noriega and Tambussi, 1996)

Gruiformes ? Phorusrhacidae

UCR 22175 Cast, distal end of bill; distal half of tarsometatarsus

Ocurrence Submeseta Allomember (Case *et al.* 1987, 2006)

Charadriiformes indet.

MLP 92-II-2-6 (right scapula)

Ocurrence Cucullaea I Allomember (Noriega and Tambussi, 1996)

?Phoenicopteridae

MLP 87-II-1-2 (incomplete right radius)

Ocurrence Cucullaea I Allomember (Noriega and Tambussi, 1996)

Ciconiiformes indet.

MLP 90-I-20-9 distal fragment of right tarsometatarsus.

Occurrence Submeseta Allomember (Noriega and Tambussi, 1996)

Procellariidae indet.

MLP 88-I-1-5 (incomplete tarsometatarsus), MLP 95-I-10-14 (left coracoid), MLP 96-I-5-8 (distal end of rostrum). MLP 91-II-4-6 (distal fragment of ulna).

Occurrence Submeseta Allomember (Noriega and Tambussi, 1996)

Diomedeidae

MLP 88-I-1-6 (distal end of rostrum)

Occurrence Submeseta Allomember (Noriega and Tambussi, 1996)

Anseriformes ?Presbyornithidae

MLP 96-I-5-19 (proximal end of scapula), MLP 95-I-10-9 (proximal fragment of scapula), MLP 96-I-5-7 (ulna)

Ocurrence Cucullaea I Allomember (Noriega and Tambussi, 1996)

***Vegavis iaai* Clarke, Tambussi, Noriega, Erickson & Ketcham, 2004**

MLP 93-I-1-3 (disarticulated partial postcranial skeleton preserved in two halves of a concretion: five thoracic vertebrae, two cervical vertebrae, left scapula, right ulna, pelvic bones, right and left fibulae, right humerus, proximal left humerus, right coracoid, femora, left tibiotarsus, distal right radius, sacrum, left tarsometatarsus, proximal right tarsometarsus and more than six dorsal ribs).

Ocurrence Unit K3 (upper part of the Cape Lamb Member and the Sandwich Bluff Member of the López de Bertodano Formation, of Pirrie *et al.*, 1991). Cape Lamb, Vega Island.

Gaviidae *Polarornis gregorii* Chatterjee, 2002

TTU P 9265 (associated skull, sternal fragment, four cervical vertebrae, left femur proximal part of right femur, fragment of left tibiotarsus)

Occurrence Sandwich Bluff Member of the López de Bertodano Formation (Maastrichtian). Seymour Island.

Polarornis sp.

Unknown repository and collection number (Chatterjee *et al.*, 2006).

Occurrence Sandwich Bluff Member of the López de Bertodano Formation (Maastrichtian). Seymour Island.

Odontopterygiformes Pelagornithidae

MLP 83-V-30-1 (incomplete portion of mandible), MLP 83-V-30-2 (mandibular fragment with a "tooth" and the base of other), MLP 78-X-26-1 (proximal fragment of rostrum)

Ocurrence Submeseta Allomember (Tonni and Tambussi, 1985)

Sphenisciformes Sharpe, 1891

***Crossvallia unienwillia* Tambussi, Reguero, Marensi and Santillana, 2005.**

MLP 00-1-10-1 (holotype humerus, associated femur and tibiatarsus)

Ocurrence Cross Valley Formation, Late Paleocene

***Anthropornis nordenskjoeldi* Wiman, 1905**

MLP 93-X-1-4 (proximal epiphysis of humerus), MLP 82-IV-23-4 (proximal epiphysis of humerus), MLP 83-I-1-190 (proximal epiphysis of humerus), MLP 88-I-1-463 (proximal epiphysis of humerus), IB/P/B- 0307 (distal humerus), IB/P/B- 0478 (proximal humerus), IB/P/B- 0711 (distal humerus), IB/P/B- 0091 (proximal right humerus), IB/P/B- 0092 (distal half of humerus), IB/P/B- 0019 (complete humerus), IB/P/B- 0463 (scapular portion of coracoid), IB/P/B- 0837 (incomplete coracoid shaft), , IB/P/B-0150 (complete ulna), IB/P/B-0613d (incomplete carpometacarpus), IB/P/B- 0476 (incomplete distal femur), IB/P/B- 0480 (in-complete distal femur), IB/P/B- 0660 (incomplete distal femur), IB/P/B-0675 (distal femur), IB/P/B- 0701 (femur without distal end), IB/ P/B- 0360 (distal end of tibiotarsus), IB/P/B-0501 (tibiotarsus without distal end), IB/P/B- 0512 (shaft of tibiotarsus), IB/P/B- 0536 (in-complete proximal end of tibiotarsus), IB/P/B- 0636 (distal end of tibiotarsus), IB/P/B- 0070 (fragmentary tarsometatarsus), IB/P/B- 0287 (fragmentary tarsometatarsus), IB/P/B- 0085 a and b (two fragments of tarsometatarsus), MLP 84-II-1-7 (fragmentary tarsometatarsus), MLP 83-V-20-50 (proximal end of tarsometatarsus), MLP 83-II-1-19 (incomplete proximal end of tarsometatarsus), IB/P/B- 0575c (first phalanx of second digit), IB/P/B- 0094a (incomplete quadrate), IB/P/B- 0189 (fragment of mandible), IB/P/B-0684 (phalanx of digit III), IB/P/B- 0250b (patella), IB/P/B- 0823 (incomplete patella),

Occurrence Submeseta Allomember but IB/P/B- 0536 (Jadwiszczak, 2006) from Cucullaea I Allomember (Myrcha et al. 2002, Tambussi *et al.,* 2006, Jadwiszczak, 2006) and Adelaide, (Australia) Oligocene (Jenkins, 1974, Fordyce and Jones, 1990)

***Anthropornis grandis* (Wiman, 1905)**

MLP CX-60-25 (proximal epiphysis of humerus), MLP 83-V-30-5 (diaphysis of humerus), MLP 93-X-1-104 (complete humerus), IB/P/B-0179 (humerus without distal end), IB/P/B-0454 (fragmentary coracoid), IB/P/B- 0064 (complete ulna), IB/P/B- 0443 (ulna without distal end), IB/P/B- 0483 (incomplete tarsometatarsus), MLP 83-V-20-84 (fragmentary tarsometatarsus), MLP 95-I-10-142 (incomplete tarsometatarsus), MLP 94-III-15-178 (incomplete tarsometatarsus), MLP 94-III-1-12 (fragmentary tarsometatarsus), MLP 86-V-30-19 (fragmentary tarsometatarsus), MLP 84-III-1-176 (fragmentary tarsometatarsus), MLP 84-II-1-66 (fragmentary tarsometatarsus), MLP 95-I-10-156 (fragmentary tarsometatarsus), MLP 93-X-1-149 (fragmentary tarsometatarsus

Occurrence Submeseta Allomember (Myrcha *et al.* 2002, Tambussi *et al.*, 2006, Jadwiszczak, 2006) but IB/P/B- 0454 from Cucullaea I Allomember.

***Anthropornis* sp.**

MLP 83-V-20-25 (proximal and distal epiphysis of humerus), MLP 83-V-20-28 (proximal epiphysis of humerus), MLP 93-X-1-105 (proximal epiphysis of humerus), MLP 83-V-20-402 (fragmentary diaphysis of humerus), MLP 93-X-1-4 (distal epiphysis of humerus), MLP 83-V-30-4 (proximal epiphysis of humerus), MLP 87-II-1-42 (proximal epiphysis of humerus), IB/P/B-0264c (proximal end of carpoetacarpus), IB/P/B- 0620a (fragmentary carpometacarpus), IB/P/B-0716 (incomplete carpometacarpus).

Occurrence Submeseta Allomember, but MLP 87-II-1-42 and IB/P/B- 0716 that was found in Cucullaea I Allomember (Tambussi *et al.*, 2006, Jadwiszczak, 2006)

Palaeeudyptes gunnari (Wiman, 1905)

MLP 82-IV-23-64 (diaphysis and proximal epiphysis of humerus), MLP 93-X-1-31 (complete humerus), MLP 82-IV-23-60 (proximal epiphysis of humerus), MLP 88-I-1-464 (proximal epiphysis of humerus), MLP 86-V-30-15 (proximal epiphysis of humerus), MLP 84-II-1-115 (proximal epiphysis of humerus), MLP 84-II-1-6 (proximal epiphysis of humerus), MLP 84-II-1-66 (proximal epiphysis of humerus), MLP 83-V-20-403 (proximal epiphysis of humerus), MLP 86-V-30-16 (proximal epiphysis of humerus), MLP 82-IV-23-59 (proximal epiphysis of humerus), MLP 84-II-1-41 (proximal epiphysis of humerus), MLP 83-V-20-51 (proximal epiphysis of humerus), MLP 95-I-10-226 (proximal epi-physis of humerus), MLP 93-X-1-30 (proximal epiphysis of humerus), MLP 91-II-4-262 (proximal epiphysis of humerus), MLP 88-I-1-469 (proximal epiphysis of humerus), IB/P/B- 0060 (proximal end of hu-merus), IB/P/B- 0066 (fragmentary humerus), IB/P/B-0075 (proximal end of humerus), IB/P/B- 0187 (proximal end of humerus), IB/P/B- 0371 (proximal end of humerus), IB/P/B- 0389 (proximal end of humerus), IB/P/B- 0126 (proximal end of humerus), IB/P/B-0306 (complete humerus), IB/P/B- 0373 (proximal end of hu-merus), IB/P/B- 0451 (incomplete humerus), IB/P/B-0472 (complete humerus), IB/P/B- 0573 (fragmentary humerus), IB/ P/B- 0105 (coracoid), IB/P/B- 0151 (coracoid), IB/P/B- 0613c (coracoid), IB/P/B- 0175 (coracoid), IB/P/B- 0136 (coracoid), IB/P/B- 0345 (coracoid), IB/P/B-0083 (ulna), IB/P/B- 0455 (fragmentary ulna), IB/P/B- 0692 (proximal end of ulna), IB/P/B-0145 (fragmentary carpometacarpus), IB/P/B-0103 (femur), IB/P/B- 0430 (femur), IB/P/B-0159 (distal end of fe-mur), IB/P/B- 0504 (incomplete femur), IB/P/B- 0655 (incomplete femur), IB/ P/B- 0699 (fragmentary femur), IB/P/B- 0137b (distal end of tibiotarsus), IB/P/B- 0248b (distal end of tibiotarsus), IB/P/B-0161a (distal end of tibiotarsus), IB/P/B- 0164a (proximal end of tibiotarsus), IB/ P/B- 0256 (proximal end of tibiotarsus), IB/P/B- 0663 (proximal end of tibiotarsus), IB/P/B- 0654 (complete tibiotarsus), IB/P/B- 0409 (third digit of the second phalanx), IB/P/B- 0413 (third digit of first phalanx), IB/P/B- 0901 (third digit of the first phalanx), IB/P/B- 0589c (third digit of the second phalanx), MLP 91-II4-222 (complete tarsometatarsus), IB/P/B- 0072 (almost complete tarsometatarsus), IB/P/ B- 0112 (almost complete tarsometatarsus), IB/P/B- 0277 (almost complete tarsometatarsus), IB/P/B-0487 (almost complete tarsometatarsus), IB/P /B- 0124 (incomplete tarsometatarsus), IB/P/B-0286 (incomplete tarsometatarsus), IB/P/B-0294 (incomplete tarsometatarsus), IB/P/B-0295 (incomplete tarsometatarsus), IB/P/B-0296 (incomplete tarsometatarsus), IB/P/ B-0541a (incomplete tarsometatarsus), MLP 87-II-1-45 (incomplete tarsometatarsus), MLP 82-IV-23-6 (incomplete tarsometatarsus), MLP 94-III-15-16 (incomplete tarsometatarsus), MLP 82-IV-23-5 (incomplete tarsometatarsus), MLP 84-II-1-75 (incomplete tarsometatarsus), MLP 84-II-1-6 (incomplete tarsometatarsus), MLP 83-V-20-27 (incomplete tarsometatarsus), MLP 93-X-1-151 (incomplete tarsometatarsus), MLP 95-I-10-16 (incomplete tarsometatarsus), MLP 84-II-1-47 (incomplete tarsometatarsus), MLP 84-II-1-65 (incomplete tarsometatarsus), MLP 84-II-1-124 (incomplete tarsometatarsus), MLP 83-V-20-41 (in-complete tarsometatarsus), MLP 83-V-20-34 (incomplete tarsometatarsus), MLP 93-X-1-84 (incomplete tarsometatarsus), MLP 84-II-1-24 (incomplete tarsometatarsus), MLP 93-X-1-112 (incomplete tarsometatarsus), MLP 93-X-1-117 (incomplete tarsometatarsus).

Occurrence Submeseta Allomember but MLP 91-II-4-262, IB/P/B- 0533 and MLP 88-I-1-469 from Cucullaea I Allomember (Myrcha *et al.*, 2002, Jadwiszcak (2006).

Palaeeudyptes klekowskii **Myrcha, Tatur and Del Valle, 1990**

MLP CX-60-201 (complete humerus), MLP 93-X-1-172 (complete humerus), MLP 93-X-1-3 (incomplete humerus), MLP CX-60-223 (complete humerus), MLP 82-IV-23-2 (diaphysis and proximal epiphysis of humerus), MLP 84-II-1-11 (diaphysis and proximal epiphysis of humerus), MLP 95-I-10-149 (diaphysis and proximal epiphysis of humerus), MLP 83-V-30-7 (diaphysis), MLP 83-V-30-3 (diaphysis and proximal epiphysis of humerus), MLP 82-IV-23-3 (proximal epiphysis of humerus), MLP 83-V-30-14 (proximal epiphysis of humerus), MLP 82-IV-23 -1 (diaphysis and proximal epiphysis of humerus), MLP 83-V-20-30 (proximal epiphysis of humerus), MLP 84-II-1-2 (diaphysis and distal epiphysis of humerus), MLP CX-60-232 (diaphysis of humerus), MLP 84-II-1-12a (distal epiphysis of humerus), MLP 91-II-4-227 (distal epiphysis of humerus), MLP 93-X-1-174 (distal epiphysis of humerus), MLP 94-III-15-175 (complete humerus of humerus), MLP 95-I-10-217 (distal epiphysis of humerus), MLP 87-II-1-44 (distal epiphysis of humerus), IB/P/B- 0141 (complete hu-merus), IB/P/B- 0571 (humerus with shaft damaged), IB/P/B-0578 (complete humerus), IB/P/B- 0854 and IB/P/B- 0857 (incomplete shaft and sternal end of coracoid- probably from the same bone), IB/P/B- 0133 (ulna without distal end), IB/P/B- 0135 (ulna without distal end), IB/P/B- 0344 (ulna), IB/P/B- 0685 (ulna), IB/P/B- 0503 (ulna), IB/P/B- 0506 (proximal end of ulna), IB/P/B- 0331 (carpometacarpus), IB/P/B- 0248c (proximal end of tibiotarsus), IB/P/B- 0357 (fragmentary tibiotarsus), IB/P/B- 0369 (proximal end of tibbiotarsus), IB/P/B- 0626 (complete tibiotarsus), IB/P/B-0192a (first phalanx of second digit), IB/P/B-0065 (incomplete tarsometatarsus), IB/P/B-0061 (incomplete tarsometatarsus), IB/P/B-0081 (incomplete tarsometatarsus), IB/P/B-0093 (incomplete tarsometatarsus), IB/P/B-0101 (incomplete tarsometatarsus), IB/P/B-0142 (incomplete tarsometatarsus), IB/ P/B-0077 (tarsometatarsus), IB/P/B- 0276 (tarsometatarsus), IB/P/B- 0281 (tarsometatarsus), IB/P/B- 0285 (tarsometatarsus), IB/P/B- 0486 (tarsometatarsus), IB/P/B- 0545 (tarsometatarsus), IB/P/B- 0546 (tarsometatarsus), MLP 93-X-1-63 (tarsometatarsus), MLP 93-X-1-6 (tarsometatarsus), MLP 84-II-1-5 (tarsometatarsus), MLP 84-II-1-76 (tarsometatarsus), MLP 93-X-1-106 (tarsometatarsus), MLP 93-X-1-108 (tarsometatarsus), MLP 84-II-1-49 (tarsometatarsus), MLP 93-III-15-4 (tarsometatarsus), MLP 78-X-26-18 (tarsometatarsus), MLP 93-III-15-18 (tarsometatarsus), MLP 93-X-1-65 (tarsometatarsus), MLP 83-V-30-15 (tarsometatarsus), MLP 83-V-30-17 (tarsometatarsus), MLP 93-X-1-142 (complete tarsometatarsus), MLP 84-II-1-78 (complete tarsometatarsus), MLP 94-III-15-20 (complete tarsometatarsus), IB/P/B- 0485 (complete tarsometatarsus)

Occurrence All specimens from Submeseta Allomember except IB/P/B- 0485, MLP 94-III-15-20 and MLP 84-II-1-78 (Myrcha *et al.*, 2002, Jadwiszcak, 2006)

Palaeeudyptes antarcticus **Huxley, 1859**

MLP 84-II-1-1 (humerus without the proximal epiphysis)

Occurrence Submeseta Allomember (Tam-bussi *et al.*, 2006) and Oamaru locality, Late Eocene-Late Oligocene, New Zealand (Fordyce and Jones, 1990)

Palaeeudyptes **sp**

All the materials belong to the Polish co-llection. IB/P/B- 0104 (incomplete coracoid), IB/P/B-0171 (incomplete coracoid), IB/P/B- 0224 (incomplete coracoid), IB/P /B- 0237 (incomplete coracoid), IB/P/B- 0452 (incomplete coracoid), IB/P/B- 0460 (incomplete coracoid), IB/P/B-0461 (incomplete coracoid), IB/P/B- 0464 (incomplete coracoid), IB/P/B- 0465b (incomplete coracoid), IB/P/B- 0520 (incomplete coracoid), IB/P/B- 0521 (incomplete coracoid), IB/P/B-0530 (incomplete coracoid), IB/P/B- 0559 (incomplete coracoid), IB/P /B- 0587e (incomplete coracoid), IB/P/B- 608a (incomplete coracoid), IB/P/B- 0611 b (incomplete coracoid), IB /P/B- 0611c (incomplete coracoid), IB/P/B-0613b (in-complete coracoid), IB/P/B- 0616 (incomplete coracoid), IB/P/B- 0827 (incomplete coracoid), IB/P/B- 0828 (incomplete coracoid), IB/P/B- 0830 (incomplete coracoid), IB/P/B- 0831 (incomplete coracoid), IB/P /B-0834 (incomplete coracoid), IB/P/B- 0842 (incomplete coracoid), IB/P/B- 0844 (incomplete coracoid), IB/P/B- 0846 (incomplete coracoid), IB/P/B- 0850 (incomplete coracoid), IB/P/B-0851 (incomplete coracoid), IB/P/B- 0855 (incomplete coracoid), IB/P/B- 0856 (incomplete coracoid), IB/P/B- 0858 (incomplete coracoid), IB/ P/B- 0859 (incomplete coracoid), IB/P/B-0860 (incomplete coracoid), IB/P/B- 0861 (incomplete coracoid), IB/P/B- 0862 (incomplete coracoid), IB/P/B- 0873 (incomplete coracoid), IB/P/B- 0875 (incomplete coracoid), IB/P/B-0876 (incomplete coracoid), IB/P/B- 0880 (incomplete coracoid), IB/P/B- 0881 (incomplete coracoid), IB/ P/B- 0882 (incomplete coracoid), IB/P/B- 0884 (incomplete coracoid), IB/P/B- 0098 (incomplete humerus), IB/P/B-0379 (in-complete humerus), IB/P/B- 0388 (incomplete humerus), IB/P/B- 0390 (incomplete humerus), IB/P/B- 0453 (incomplete humerus), IB/P/B- 0700 (incomplete humerus), IB/P/B- 0703 (incomplete humerus), IB/P/B-0719 (incomplete humerus), IB/ P/B- 0720 (incomplete humerus), IB/P/B- 0737 (incomplete humerus), IB/P/B- 0401 (incomplete tibiotarsus), IB/P/B- 0634 (in-complete tibiotarsus), IB/P/B- 0662 (in-complete tibiotarsus), IB/P/B- 0537 (complete tibiotarsus), IB/P/B-0249b (first phalanx of second digit), IB/P/B-0651d (first phalanx of second digit), IB/P/B-0414 (first phalanx of fourth digit), IB/ P/B-0896 (first phalanx of fourth digit), IB/P/B-0420 (first phalanx of second digit), IB/P/B-0424 (first phalanx of se-cond digit), IB/P/B-0589d (first phalanx of second digit), IB/P/B-0895 (first phalanx of second digit), IB/P/B-

0904 (first phalanx of second digit), IB/P/B-0904 (first phalanx of second digit), IB/P/B-0907 (first phalanx of second digit), IB/ P/B-0913 (first phalanx of second digit), IB/P/B-0916 (first phalanx of second digit).

Ocurrence Cucullaea I Allomember (Jad-wiszczak, 2006).

Delphinornis larseni **Wiman, 1905**

MLP 93-X-1-147 (near complete humerus, distal end), MLP 93-X-1-146 (complete humerus), MLP 84-II-1-169 (diaphysis and fragmentary proximal epiphysis of humerus), MLP 93-X-1-21 (diaphysis of humerus), MLP 84-II-1-16 (diaphysis and fragmentary proximal epiphysis of humerus), MLP 93-X-1-32 (diaphysis and proximal epiphysis of humerus), MLP 93-X-1-144 (diaphysis and distal epiphysis of humerus), MLP 94-III-15-177 (near complete humerus), MLP 91-II-4-263 (proximal epiphysis of humerus), IB/P/B- 0062 (complete tarsometatarsus), IB/P/B- 0280 (incomplete tarsometatarsus), IB/P/B- 0299 (incomplete tarsometatarsus), IB/P/B- 0547 (incomplete tarsometatarsus), IB/P/B- 0548 (in-complete tarsometatarsus), MLP 83-V-20-5 (complete tarsometatarsus), MLP 91-II-4-174 (almost complete tarsometatarsus), MLP 84-II-1-179 (incomplete tarsometatarsus), IB/P/B- 0337 (distal end of tibiotarsus)

Ocurrence Submeseta Allomember, but MLP 94-III-15-177 and MLP 91-II-4-263 which come from the Cucullaea I Allo-member (Myrcha *et al.*, 2002, Jadwiszcak, 2006).

Delphinornis **arctowskii Myrcha, Jadwiszczak, Tambussi, Noriega, Gazdzicki, Tatur & Del Valle, 2002**

IB/P/B- 0115 (weathered tarsometatarsus), IB/P/B- 0266 (tibiotarsus without proximal end), IB/P/B- 0500 (tibiotarsus with-out distal half), IB/P/B- 0484 (complete tarsometatarsus), MLP 93-X-1-92 (incomplete tarsometatarsus).

Occurrence Submeseta Allomember (Myrcha *et al.*, 2002)

Delphinornis **gracilis Myrcha, Jadwis-zczak, Tambussi, Noriega, Gazdzicki, Tatur & Del Valle, 2002**

IB/P/B- 0408 (fragmentary tibiotarsus)

Occurrence Submeseta Allomember (Jadwiszcak, 2006)

Delphinornis **cf. arctowskii Myrcha, Jadwiszczak, Tambussi, Noriega, Gazdzicki, Tatur & Del Valle, 2002**

MLP 93-X-1-70 (almost complete humerus)

Occurrence Submeseta Allomember

Mesetaornis polaris **Myrcha, Jadwiszczak, Tambussi, Noriega, Gazdzicki, Tatur and Del Valle, 2002**

IB/P/B- 0278 (almost complete tarsometatarsus)

Occurrence Submeseta Allomember (Myrcha *et al*, 2002, Jadwiszcak, 2006).

Mesetaornis **sp**

IB/P/B- 0279b (incomplete tarsometatarsus).

Occurrence Submeseta Allomember (Jadwiszcak, 2006)

Marambiornis exilis **Myrcha, Jadwiszczak, Tambussi, Noriega, Gazdzicki, Tatur & Del Valle, 2002**

IB/P/B- 0490 (complete tarsometatarsus), MLP 93-X-1-111 (complete tarsometatarsus)

Occurrence Submeseta Allomember (Jadwiszcak, 2006)

Archaeospheniscus lopdelli **Marples, 1952**

MLP 94-III-15-17 (complete humerus), MLP 93-X-1-123 (proximal epiphysis of humerus), MLP 93-X-1-27 (proximal epiphysis of humerus), MLP 95-I-10-231 (diaphysis and distal epiphysis of humerus), MLP 95-I-10-236 (proximal epiphysis of humerus), MLP 84- II-1-110 (diaphysis and distal epiphysis of humerus), MLP 95-I-10-227 (diaphysis and proximal epiphysis of humerus), MLP 84-II-1-111 (dia-physis and proximal epiphysis of humerus), MLP 93-X-1-97 (diaphysis and distal epiphysis of humerus), MLP 95-I-10-233 (diaphysis and distal epiphysis of humerus).

Occurrence Submeseta Allomember (Myrcha *et al.*, 2002).

Archaeospheniscus wimani **(Marples, 1953)**

IB/P/B- 0466 (incomplete coracoid), IB/ P/B-0467 (incomplete coracoid), IB/P/B- 0608b (incomplete coracoid), IB/P/B- 0176 (incomplete humerus), IB/P/B- 0641 (complete femur), IB/P/B- 0658 (shaft), IB/P/B- 0687 (shaft), IB/P/B- 0110 (tibiotarsus), IB/P/B-0137a (proximal end of tibiotarsus), IB/P/B-0218 (shaft of tibiotarsus), IB/P/B- 0802 (shaft of tibiotarsus), IB/P/B- 0796 (incomplete shaft of tibiotarsus), IB/P/B- 0908 (first phalanx of third digit), IB/P/B- 0284 (incomplete tasometatarsus), IB/P/B- 0289 (incomplete tarsometatarsus), IB/P/B- 0491 (incomplete tarsometatarsus), MLP 90-I-20-24 (complete tarsometatarsus), MLP 91-II-4-173 (incomplete tarsometatarsus)

Occurrence Cucullaea I and Submeseta Allomembers (Myrcha *et al.*, 2002).

Tonniornis mesetaensis **Tambussi, Acosta Hospitaleche, Reguero and Marenssi, 2006**

MLP 93-X-1-145 (holotype complete humerus).

Ocurrence Submeseta Allomember (Tambussi *et al.*, 2006)

Tonniornis minimum **Tambussi, Acosta Hospitaleche, Reguero and Marenssi, 2006**

MLP 93-I-6-3 (holotype complete humerus), MLP 93-X-1-22 (diaphysis and distal epiphysis of humerus).

Ocurrence Submeseta Allomember (Tambussi *et al.*, 2006).

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