DIVERSITY OF PSEUDO-TOOTHED BIRDS (PELAGORNITHIDAE) FROM THE EOCENE OF ANTARCTICA

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ABSTRACT—The Antarctic pelagornithid record is restricted to few isolated remains from the Eocene of Seymour Island in the Antarctic Peninsula. Here we report the oldest Antarctic pseudo-toothed bird. It is represented by an incomplete humerus lacking its proximal end, which comes from the lower Eocene levels of the La Meseta Formation (Seymour Island). This new specimen facilitates a review of all known pelagornithids from this continent. Antarctic pelagornithids were classified into two morphotypes which exhibit a mix of putative plesiomorphic and derived characters. Considering the worldwide pelagornithid record and according to estimated wingspans, four approximate size-types were identified. The oldest Antarctic specimens (two fragmentary humeri, middle Ypresian) were assigned to morphotype 1 and correspond to the large sized-type. The younger materials (Bartonian/?Priabonian) here assigned to morphotype 2 (some cranial remains, fragmentary tarsometatarsus and humerus) correspond to the giant size-type and represent one of the

largest known pseudo-toothed birds. Even though species level phylogenetic affinities of Pelagornithidae remain poorly resolved, three key evolutionary events can be recognized: 1) the disappearance of *Dasornis* in the Early Eocene and the appearance of more advanced forms with a trend to the specialization of large soaring capacity; 2) the origin of *Pelagornis* sensu lato species in the early Oligocene; 3) the appearance and dominance of a highly specialized terminal group at Mio/Pliocene time span.

INTRODUCTION

THE PELAGORNITHIDS, commonly known as pseudo-toothed birds, are a peculiar group of volant seabirds characterized by numerous osseous tooth-like processes of the beak, and extremely light and thin bones with a highly specialized structure adapted for pelagic soaring (Olson, 1985; Bourdon, 2011). They were cosmopolitan birds whose fossil record dates back to the late Paleocene and extends up to the latest Pliocene (e.g., Olson, 1985; Mourer-Chauviré and Geraards, 2008; Mayr, 2009; Bourdon et al., 2010; Boessenecker and Smith, 2011). Although this group was included in a distinct taxon, the Odontopterygiformes, earlier authors noted their affinities with other seabirds such as Procellariiformes and polyphyletic traditional 'Pelecaniformes' (Wetmore, 1928; Howard, 1957, 1978; Harrison and Walker, 1976; Brodkorb, 1963; Olson, 1985; Goedert, 1989). Nevertheless, these similarities were recently considered as the result of convergence (Mayr, 2011). Recent phylogenetic analyses suggest a sister group relationship of pseudo-toothed birds and Anseriformes (both included in the new clade Odontoanserae; Bourdon, 2005, 2011). However, a phylogenetic analysis (including characters used by Bourdon, 2005) resulted in a more basal position of Pelagornithidae outside the crown-group Galloanseres (Mayr, 2011).

Bourdon et al. (2010, see also Bourdon, 2011) noted that within the family Pelagornithidae two morphological types or clades (Mayr et al., 2013) can be distinguished. Defined by plesiomorphic characters, the first clade includes *Dasornis* Owen, 1870 species (including *Odontopteryx* Owen, 1873; and *Macrodontopteryx* Harrison and Walker, 1976) and is restricted to the late Paleocene/early Eocene of Morocco (Bourdon, 2005; Bourdon et al., 2010), and early Eocene of England (Harrison and Walker, 1976; Mayr, 2008). The second and younger clade, corresponds to the derived *Pelagornis* species (here referred as *Pelagornis* sensu lato Mayr et al., 2013; containing *Pelagornis* Lartet, 1857; *Osteodontornis* Howard, 1957; *Pseudodontornis* Lambrecht, 1930; *Palaeochenoides* Shufeldt, 1916; and *Tympanonesiotes* Hopson, 1964) found on all continents from late Oligocene to late Pliocene strata (e.g., Olson, 1985; Mayr et al., 2008, 2013; Mourer-Chauviré and Geraads, 2008; Mayr and Rubilar-Rogers, 2010; Boessenecker and Smith, 2011; Ksepka, 2014).

The systematic status of all middle Eocene to early Oligocene pelagornithids is very poorly known. These specimens exhibit some of the apomorphies of *Pelagornis*, and correspond to taxa with intermediate morphology between *Dasornis* and *Pelagornis* types. This is the case of *Lutetodontopteryx tethyensis* Mayr and Zvonok, 2012, a relatively well-represented taxon from the middle Eocene of Ukraine; some fragmentary specimens from the middle Eocene of Togo (Bourdon and Cappetta, 2012), Belgium (Mayr and Smith, 2010; Mayr and Zvonok, 2012), and Nigeria (Andrews, 1916; Mayr et al., 2008); and other remains from the late Eocene of Antarctica (Cenizo, 2012), and the latest Eocene/?early Oligocene of North America (Goedert, 1989).

Particularly, the Antarctic pelagornithid record is restricted to few and isolated remains from the Eocene of Seymour Island in the Antarctic Peninsula (Fig. 1). The first pseudo-toothed birds known from this continent were represented by a very large rostral fragment (Tonni and Cione, 1978; Tonni, 1980), and two poorly preserved mandibular

portions (Tonni and Tambussi, 1985). Stilwell et al. (1998) reported the first fossil bird from lower-middle Eocene outcrops of East Antarctica, which consists on an eroded humeral diaphysis described in detail by Jones (2000). A well preserved distal end of tarsometatarsus previously referred to the 'terror birds' Phorusrhacidae (Case et al., 2006) was reallocated within Pelagornithidae (Cenizo, 2012). Furthermore, a complete humerus, still under study, was mentioned by Rubilar-Rogers et al. (2011), and a tip of beak was recently figured by Tambussi and Degrange (2013) without comments about its affinities.

The finding of the oldest Antarctic pelagornithid (a distal end of humerus, MLP 12-I-20-4) in middle Ypresian levels (early Eocene), and the recent description of new and more complete Paleogene specimens (e.g., Bourdon et al., 2010; Mayr and Zvonok, 2011, 2012; Bourdon and Cappetta, 2012; Mayr et al., 2013) invites to review of the Antarctic record of the group, which represents the only pseudo-toothed birds known for the Paleogene of the Southern Hemisphere.

GEOLOGICAL SETTING

The sedimentary sequence exposed on Seymour (Marambio) Island is more than 2 km thick and represents the uppermost part of the infill of the James Ross Basin (del Valle et al., 1992). The youngest strata constitute the Seymour Island Group that includes the Paleocene Cross Valley Formation at the bottom, and the early Eocene/?earliest Oligocene La Meseta Formation at the top. A geological map of the Seymour Island with new stratigraphic sequence and datings of the Eocene marine horizons was recently published (Montes et al., 2013). The La Meseta Formation was splitted into two geologic units, La Meseta and Submeseta formations which are separated and bounded by a prominent erosional surface

covered by 20–40 m-thick inclined heterolithic facies composed of estuarine, very fine

sandstones and mudstones (Marenssi, 2006).

The La Meseta Formation (La Meseta Alloformation in Marenssi et al., 1998a) is

exposed along the slopes of the plateau of Seymour (Marambio) Island (Fig. 1). It is an

unconformity-bounded unit (Elliot and Trautman, 1982; Ivany et al., 2008) deposited between

the Thanetian and the Lutetian (i.e., between 58.7–40.4 Ma; Montes et al., 2013). This unit is

approximately 560 meters thick and fills a 7 km wide valley cut down into older sedimentary

rocks constituting the island; its current location is the result of regional uplift and tilting of

the Marambio Group beds (Reguero et al., 2013).

The La Meseta Formation includes mudstones and sandstones with interbedded

conglomerates and is organized into six erosionally-based units (Marenssi et al., 1998a).

These are named, from base to top: Valle de Las Focas, Acantilados I, Acantilados II,

Campamento, Cucullaea I, and Cucullaea II (Fig. 2). These lens-shaped units represent

different sedimentation stages related to sea level fluctuations (Marenssi et al., 2002)

deposited in deltaic, estuarine and shallow marine environments as part of a tectonically-

controlled incised valley system (Porębski, 1995; Marenssi et al., 1998b). An open marine,

protected and estuarine environment provided suitable habitat and good preservation

potential, evidenced by a high diversity and abundance of fossil remains (Marenssi, 2006).

Provenance studies on sandstones of the La Meseta Formation demonstrated that the source

rock was located west-northwest along the present day Antarctic Peninsula.

The new unit, Submeseta Formation (Montes et al., 2013), is the uppermost part of the

former early/middle Eocene to ?earliest Oligocene La Meseta Formation (Elliot and

Trautman, 1982; Ivany et al., 2008). This unit corresponds to the Facies Association III of

Marenssi et al. (1998b), characterized by a uniform sandy lithology that represents a tidal

shelf influenced by storms. The Submeseta Formation is organized into three allomembers

(Fig. 2) named from base to top: Submeseta I, Submeseta II, and Submeseta III (Montes et al., 2013). Montes et al. (2013) placed the base of the Submeseta Formation at 43.4 Ma (upper Lutetian), and the top of this unit at 33.9 Ma (Priabonian/Rupelian).

MATERIAL AND METHODS

Anatomical terminology follows Baumel and Witmer (1993). The pseudo-teeth were ranked following Mourer-Chauviré and Geraards (2008) and Louchart et al. (2013).

Institutional abbreviations.—LACM, The Natural History Museum of Los Angeles County, Los Angeles, USA.; MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, USA.; MLP, Museo de La Plata, La Plata, Argentina; MNHN, Museo Nacional de Historia Natural, Santiago, Chile; NHMUK, Natural History Museum, London, United Kingdom; OCP.DEK/GE, Office Chérifien des Phosphates, Direction des Exploitations de Khouribga, Service de Géologie, Morocco; SMF, Senckenberg Research Institute Frankfurt, Frankfurt am Main, Germany; UCR, University of California, Riverside, USA.; USNM, National Museum of Natural History, Washington, USA.

Metric descriptors and measurements (in mm).—D-dist = depth of distal end; H-an = height at aperturae nasi ossea; TL = total length; W-dist = width of distal end; W-nf = width of naso-frontal hinge; W-prox = width of proximal end.

SYSTEMATIC PALEONTOLOGY

Order ODONTOPTERYGIFORMES Howard, 1957

Family PELAGORNITHIDAE Fürbringer, 1888

PELAGORNITHIDAE indet. morphotype 1

Figure 3

Referred material.—MLP 12-I-20-4, distal end of right humerus (Fig. 3.1–3.4); USNM 494035, fragmentary distal portion of shaft of right humerus (Stilwell et al., 1998, fig. 2; and Jones, 2000, fig. 1).

Occurrence.—MLP12-I-20-4 comes from the *Cucullaea* I Allomember (level 35 in Montes et al., 2013; Fig. 2) of the La Meseta Formation (Marenssi et al., 1998a), IAA 1/95 locality, Seymour Island, Antarctic Peninsula, West Antarctica. Strontium dating yielded ages of 52.8–49 Ma for this locality (middle Ypresian, early Eocene; Montes et al., 2013).

The specimen USNM 494035 was found in an erratic glacial (A303) collected from moraine deposits on the NW side of Mount Discovery, McMurdo Sound, East Antarctica. The associated micro and macro invertebrate fauna indicates an early/middle Eocene age (Jones, 2000; and references therein).

Measurements.—MLP 12-I-20-4: see Table 1. USNM 494035 (Jones, 2000): preserved length, 85; maximum dorso-ventral width, 32; maximum cranio-caudal depth, 22; thickness of bone wall, 1.5.

Description.—The distal end of humerus MLP 12-I-20-4 is nearly complete but both condyli have lost their cranial surface, also the epicondyli dorsalis et ventralis and the sulcus scapulotricipitalis are partially eroded (Fig. 3.1–3.4). The assignment of MLP 12-I-20-4 to the pseudo-toothed birds is based on the following characters (Mourer-Chauviré and Geraads, 2008; Mayr and Smith, 2010; Bourdon et al., 2010; Bourdon and Cappetta, 2012): 1) craniocaudally compressed shaft; 2) distal condyli located at the same level and distally prominent; 3) roughly rounded condylus ventralis; 4) prominent epicondylus dorsalis; 5) shallow fossa olecrani and sulcus humerotricipitalis, 6) dorsal margin of the shaft narrow and ridge-like just proximal to the distal end.

Although its size is somewhat larger, the Antarctic material has strong similarities with a humerus coming from the middle Eocene of Togo and tentatively referred to *Gigantornis* Andrews, 1916 by Bourdon and Capetta (2012, fig. 2L–N and P). However, both specimens are included in the size range observed for *Dasornis emuinus* (Bowerbank, 1854) from the late Paleocene/early Eocene of Morocco (Bourdon et al., 2010; Table 1). The wide intraspecific size variability reported for some pelagornithids (i.e., *D. emuinus*; *D. toliapica* [Owen, 1873]; Bourdon et al., 2010; and *Pelagornis miocaenus* Lartet, 1857; Mourer-Chauviré and Geraards, 2008) suggests that the Antarctic and Togo specimens may belong to the same species.

Although the epicondylus dorsalis of MLP 12-I-20-4 is only partially preserved, its morphology is similar to that of cf. *Gigantornis* sp. from Togo. It is more robust than that of *Dasornis* and less projected and rounded than the corresponding structure in *Pelagornis* (Bourdon et al., 2010; Bourdon and Cappetta, 2012). According to the preserved outline, the condylus ventralis of MLP 12-I-20-4 was smaller than that of *Pelagornis* and similar to those of *Dasornis* and cf. *Gigantornis* sp. In dorsal view (like in *Dasornis* and cf. *Gigantornis* sp.), MLP 12-I-20-4 exhibits two deep concavities for the insertion of the musculus extensor carpi ulnaris surrounded by a thick and smooth ridge (Fig. 3.3). In *Pelagornis* these concavities are shallower and the ridge is missing or poorly developed (Bourdon et al., 2010; Bourdon and Cappetta, 2012). A well defined tuberculum supracondylare ventrale is present in MLP 12-I-20-4, which is more vertically oriented (subparallel to the main axis of the diaphysis), and more proximally extended than in *Dasornis*.

The fragmentary distal shaft of the humerus USNM 494035 from East Antarctica has been figured by Stilwell et al. (1998, fig. 2) and Jones (2000, fig. 1). Although the surface of the diaphysis is highly crushed and broken at the proximal level of the condyli, the fossa musculi brachialis is preserved as a cranial depression recognizable in distal view. The size of

the diaphysis, its cranio-caudal compression, and the extremely thin wall of cortical bone (evidencing a high pneumaticity not present in others large sized coetaneous Antarctic birds; i.e., Ratites, Sphenisciformes) allow the inclusion of USNM 494035 in the Pelagornithidae (see similarities with specimens described by Boessenecker and Smith, 2011; and Fitzgerald et al., 2012). Moreover, the wide fossa musculi brachialis, the narrow ridge-like margo dorsalis, the shallow sulcus humerotricipitalis, and the shape and extension of the tuberculum supracondylare ventrale (Jones, 2000) are also similar to that of pelagornithids. Size and morphological characters of USNM 494035 are similar to those observed in the humerus MLP 12-I-20-4 here described.

PELAGORNITHIDAE indet. morphotype 2

Figure 4

Referred material.—MLP 08-XI-30-42, rostral end of rostrum maxillare (Fig. 4.2, 2.3); MLP 78-X-26-1, most rostral narial region of rostrum maxillare (Fig. 4.4–4.8); UCR 22176, distal end of right tarsometatarsus (Fig. 4.9–4.11).

Occurrence.—All the specimens come from the Submeseta II Allomember (level 38 in Montes et al., 2013, Fig. 2) of the Submeseta Formation (Montes et al., 2013), DPV 13/84 (MLP 08-XI-30-42 and MLP 78-X-26-1) and RV 8702 (UCR 22176) localities, Seymour Island, Antarctic Peninsula, West Antarctica. Strontium dating yielded an age between 41.1–37.8 Ma for both localities (Bartonian, middle Eocene; Montes et al., 2013).

Measurements.—See Table 1.

Description.—The rostral end of the rostrum maxillare MLP 08-XI-30-42 is congruent with those of other pseudo-toothed birds (Rincón and Stucchi, 2003; Stidham, 2004; Bourdon et al., 2010; Mayr and Rubilar-Rogers, 2010; Mayr and Zvonok, 2012; Ksepka, 2014). Its size

exceeds the medium-sized *D. toliapica* and *L. tethyensis*, and even the larger *D. emuinus*,

corresponding in dimensions with the giant Neogene *Pelagornis* species (Fig. 4.1). The

cristae tomiales preserve the base of the first rostral-most large tooth-like process (Fig. 4.2).

The rostral end is slightly ventrally curved, and the transverse sulcus before the tip of the beak

is absent in MLP 08-XI-30-42, as well as in *D. toliapica* and *L. tethyensis*, whereas is

typically present and well-developed in *Pelagornis* (Olson, 1984; Stidham, 2004; Bourdon et

al., 2010; Mayr and Rubilar-Rogers, 2010; Mayr and Zvonok, 2012; Ksepka, 2014). The

longitudinal sulcus of MLP 08-XI-30-42 is less defined than in *Pelagornis*.

The rostrum maxillare MLP 78-X-26-1 (Fig. 4.4–4.8) has a deep longitudinal sulcus

running upward along the dorsal third of the beak. In pelagornithids, these lateral sulci are

longitudinally extended along the dorsal margin of the beak from apex rostri to aperturae nasi,

whereas posteriorly, these sulci are more ventrally located (Bourdon et al., 2010; Mayr and

Rubilar-Rogers, 2010). Because of that, MLP 78-X-26-1 is referred to the sector immediately

developed cranially to the aperturae nasi ossea. A dorsolateral constriction on the caudal

section of the preserved culmen (Fig. 4.4) corresponds to that one developed cranially to the

aperturae nasi ossea reported for other pelagornithids (Mayr and Rubilar-Rogers, 2010, see

also Ksepka, 2014:Fig. 1.a). A dorsally located ridge (Tonni, 1980; Fig. 4.4, 4.5) is very well

defined as in *Dasornis*, whereas it is weaker or absent in *Pelagornis*. The maxilla from

Antarctica is less compressed than in *Dasornis*, but narrower than in *Pelagornis*. On the

contrary, the longitudinal sulcus is more dorsally located than in *Dasornis* and similar to the

condition of *Pelagornis* (Harrison and Walker, 1976; Bourdon et al., 2010). As is typical of

Pelagornithidae, the ventral surface of MLP 78-X-26-1 shows two longitudinal sulci for the

location of the cristae tomiales and deep fossae for the tooth-like projections of the mandible

(Lambrecht, 1930; Harrison and Walker, 1976; Tonni, 1980; Stidham, 2004; Mayr and

Rubilar-Rogers, 2010). Between both, there is a palatal ridge (central palatal region sensu

Harrison and Walker, 1976; Fig. 4.7) extended ventrally almost half of the rostrum in cross section. This condition is similar to that of *Dasornis*, which shows a well-defined medioventral sulcus (interpalatal groove *sensu* Harrison and Walker, 1976). In contrast, *Pelagornis* has a palatal ridge that is strongly convex and prominent (Harrison and Walker, 1976; Bourdon et al., 2010), and the sulcus is missing (Harrison and Walker, 1976; see Mayr and Rubilar-Rogers, 2010:fig. 1D). On both cristae tomiales, MLP 78-X-26-1 shows three poorly preserved tooth-like processes. The largest one is on the middle, separated from the other two by an equidistance of 9.7 mm (Tonni, 1980), corresponding to pseudo-teeth of rank 2 and 3, respectively. Between them, small protuberances probably represent the basis of very thin 'needles' of rank 4. The largest tooth-like processes of rank 1 are not preserved. A striking feature is the dorsoventral height of the beak measured at the level of the apertura nasi ossea, which is highest than in any other pelagornithid species known (Table 1). A polishing of the cross section (Fig. 4.8) permits the first detailed observation of its inner structure, which evidences an extreme bone pneumaticity.

The tarsometatarsus UCR 22176 (Fig. 4.9–4.11, 5) has the largest distal transverse width known for pseudo-toothed birds (Table 1, Cenizo, 2012). The general morphology is similar to *Dasornis*, although it shares some features with *Pelagornis* (Cenizo, 2012). The corpus of UCR 22176 is mediolaterally narrower than *Pelagornis*, and wider than *Dasornis* (Bourdon et al., 2010; Fig. 5), whereas is similar to the preserved proximal shaft of *L. tethyensis* (Mayr and Zvonok, 2012). The shaft of UCR 22176 is nearly square in cross-section, like in *Dasornis*; in *Pelagornis* the section is rectangular and dorsoplantarly depressed. Like in *Dasornis*, the trochlea metatarsi II of UCR 22176 is less distally displaced (Fig. 5) than in *Pelagornis chilensis* Mayr and Rubilar-Rogers, 2010; whereas *L. tethyensis* and ?late Oligocene/early Miocene *Pelagornis* specimens exhibit an intermediate condition. However, this trochlea is less plantarly projected (Fig. 5) than in *Dasornis* but more than in *P.*

chilensis (Bourdon et al., 2010; Mayr and Rubilar-Rogers, 2010; Mayr, 2011; Mayr and Zvonok, 2012); the plantar extension in UCR 22176 is similar to that of *L. tethyensis* and the specimen tentatively assigned to *Pelagornis* (*'Palaeochenoides'*) *mioceanus* by Hopson (1964; see also Mayr et al., 2013). The processus medioplantaris (Fig. 4.11, 5) of the trochlea metatarsi II is more medially extended than in *Dasornis* and *L. tethyensis* (it is absent in *P. chilensis*). As in *Dasornis* and *L. tethyensis*, the trochleae metatarsorum II and IV are narrower and less excavated than those of *Pelagornis*. Likewise, as in *Dasornis* (although in a lesser degree), the plantar surface of trochlea metatarsi III is narrow, elongate, and with proximally convergent margins (a condition also observed in *Lutetodontopteryx*); whereas in *Pelagornis* this trochlea is plantarly wider, shorter and its margins are more parallel each other (the only exception is the late Oligocene/early Miocene *Pelagornis* sp. from Oregon, Mayr et al., 2013; Fig. 5). UCR 22176 shares with *Dasornis* the lateral tilting of the trochlea metatarsi III (Bourdon, 2005; Bourdon et al., 2010). The dorsal opening of the foramen vasculare distale in UCR 22176 is proximodistally elongated, like that of *Dasornis* (Bourdon et al., 2010; a similar condition would be present in *L. tethyensis*); whereas it is subcircular in *Pelagornis*. On the other hand, the foramen vasculare distale in UCR 22176, is recessed plantarly and opens close to the canalis interosseus distalis like in *Pelagornis* (Bourdon, 2005; Mayr and Rubilar-Rogers, 2010; Mayr, 2011).

Remarks.—An almost complete humerus (SGO.PV 22001) assigned to a pelagornithid was recently found in Bartonian/?Priabonian levels (middle/late Eocene, Submeseta Formation) of Seymour Island (Rubilar-Rogers et al., 2011). Its morphology resembles more the Neogene *Pelagornis* than the Paleogene *Dasornis*. It belongs to a bird similar-sized to the largest know pelagornithid *Pelagornis sandersi* Ksepka, 2014 (Table 1), but unfortunately, it is still under study and cannot be directly compared. Giant size, morphological affinities

(*Pelagornis*-like features) and the stratigraphical provenance of the specimen (Rubilar-Rogers et al., 2011) are consistent with assignment to morphotype 2.

REASSIGNMENT OF OTHER ALLEGED ANTARCTIC PELAGORNITHIDS

An incomplete articular portion of a mandible (MLP 83-V-30-1, Fig. 6.1, 6.2) found in the uppermost levels of the La Meseta Formation (DPV 13/84 locality, level 38, Submeseta II Allomember, middle Eocene; Fig. 2) has previously been assigned to Pelagornithidae (Tonni and Tambussi, 1985). However, such a taxonomic assignment was based on characters that are present in other birds, such us: 1) a straight ventral margin of the mandible (shared with penguins); 2) the caudal edge forming an angle of almost 90° with the ventral margin (shared with Eocene penguins; Acosta Hospitaleche and Haidr, 2011); and 3) an elongated articular surface, oblique with respect to the ramus mandibulae (shared with many other birds including penguins).

This mandible is strong and robust, but unfortunately, it shows a badly weathered external surface. Neither the processus retroarticularis nor the fossa caudalis are preserved. The cotyla lateralis is larger than the cotyla medialis; they are both merged with a small prominence at the medial side (Fig. 6.2). MLP 83-V-30-1 exhibits the morphology that is congruent with that expected for a penguin mandible (Ksepka and Bertelli, 2006, fig 3; Acosta Hospitaleche and Haidr, 2011, fig. 2A–C, and E). Regrettably, the incomplete nature of the material does not allow an accurate assignment. However, the external cortex of MLP 83-V-30-1 is relatively thick, unlike in pelagornithids. Based on that and the features commented on above, MLP 83-V-30-1 should be considered as Sphenisciformes indet., belonging to a robust and giant species, within the size range of *Palaeeudyptes* or

Anthropornis (Jadwiszczak and Acosta Hospitaleche, 2013; Acosta Hospitaleche, in press; Acosta Hospitaleche and Reguero, in press).

A second specimen (MLP 83-V-30-2, Fig. 6.3–6.5) was previously described by Tonni and Tambussi (1985) as a pelagornithid. This fossil comes from the uppermost levels of the La Meseta Formation (DPV 16/84 locality, level 39, Submeseta II Allomember, late Eocene; Fig. 2). This specimen consists of a fragmentary fish dentary bone with a strong and conical tooth and a piece of a second tooth. The tooth is slightly bent backwards and has its internal cavity exposed at the tip. The tooth surface is weathered, but a pedicle is developed at its base, and the tooth is inserted in a shallow longitudinal groove. Based on its gross-morphology, the specimen may probably be assigned to the cod-icefish *Mesetaichthys jerzmanskae* Bieñkowska-Wasiluk, Bonde, Moller and Gazdzicki, 2013, a Notothenioidei (Perciformes) recently described (Bieñkowska-Wasiluk et al., 2013) for the Submeseta Allomember (middle/late Eocene). The specimen in question (MLP 83-V-30-2) is not referable to Aves, much less Pelagornithidae.

DISCUSSION AND CONCLUSIONS

Regarding their affinities, both morphotypes recognized for Antarctic pelagornithids share with the late Paleocene/early Eocene *Dasornis* the presence of several possible plesiomorphic characters (i.e., humerus: deep concavities for the musculus extensor carpi ulnaris surrounded by a thick and smooth ridge; rostral end of the beak: slightly down-curved, absence of transverse sulcus; narial region of the rostrum: well defined dorsolateral constriction and dorsal ridge, palatal ridge slightly prominent and with a marked medial sulcus; tarsometatarsus: corpus mediolaterally narrower with square cross section, narrow and poorly excavated trochlea II, proximally positioned trochlea II with a processus

medioplantaris, narrow dorsal opening of foramen vasculare distale). However, a number of characters also remind the more derived condition typical of the Neogene *Pelagornis* (i.e., humerus: flattened diaphysis, well developed epicondylus dorsalis, vertically positioned and proximally extended tuberculum supracondylare ventrale; narial region of the rostrum: longitudinal sulcus more dorsally positioned; tarsometatarsus: recessed and more distally located plantar opening of the foramen vasculare distale, slight plantar projection of trochlea II, wider and lower dorsal surface of trochlea III). A combination of plesiomorphic and derived character states, showing an 'intermediate' condition between *Dasornis* and *Pelagornis* was already reported in post-early Eocene and pre-late Oligocene specimens. Taxa showing such combination include the middle Eocene *L. tethyensis* from Ukraine (Mayr and Zvonok, 2011, 2012), *Gigantornis eaglesomei* Andrews, 1916 from Nigeria (Harrison and Walker, 1976; Mayr et al., 2008), Togo specimens referred to *Gigantornis* (Bourdon and Cappetta, 2012), and some other remains from Belgium tentatively assigned by Mayr and Smith (2010) to *D. emuinus* and *Macrodontopteryx oweni* Harrison and Walker 1976 (although they probably correspond to *Gigantornis* and *Lutetodontopteryx*, respectively; Mayr and Zvonok, 2012; see also Bourdon et al., 2010). The late Eocene and ?early Oligocene materials from Oregon described by Goedert (1989) also seems to fit in this intermediate morphology (Mayr et al., 2013).

A valuable element in order to recognize plesiomorphic-derived conditions is probably represented by the tarsometatarsus. The progressive increase in the distal projection of the trochlea metatarsi II, and the reduction of its plantar extension are consistent with the rise of the more modern taxa studied (Fig. 5). The distal end of tarsometatarsus UCR 22176 from the middle Eocene of Seymour Island is morphologically more similar to the middle Eocene *L. tethyensis* and the probably late Oligocene *P.'Palaeochenoides' mioceanus* than to any other

pseudo-toothed birds. UCR 22176 belonged to a huge bird similar to *P.' Palaeochenoides'*

mioceanus (Table 1) and markedly larger than *L. tethyensis* (similar in size to *D. toliapica*).

Pelagornithid size-types.—Otherwise, considering the worldwide pelagornithid record

and according to the estimated wingspan, four approximate size-ranges were identified (Fig.

7). The small gannet-sized *Dasornis abdoun* Bourdon et al., 2010 (1.5–1.7 m wingspan;

Bourdon et al., 2010), the medium albatross-sized *D. toliapica* and *L. tethyensis* (2–3 m

wingspan; Bourdon et al., 2010), the large *D. emuinus* (3.5–4.5 m wingspan; Mayr, 2009;

Bourdon et al., 2010), and finally, the giant middle/late Eocene and Neogene *Pelagornis*-

related taxa (5–6 m wingspan; Olson, 1985; Mayr, 2009; Mayr and Rubilar Rogers, 2010;

Boessenecker and Smith, 2011; Ksepka, 2014).

The Antarctic material assigned to morphotype 1 (middle Ypresian), including the

humerus MLP 12-I-20-4 and the humeral shaft USNM 494035 (Jones et al., 2000) correspond

to the large size-type (i.e., equivalent in size to *D. emuinus*, Table 1). The material assigned to

morphotype 2 (Bartonian/?Priabonian, including the humerus recently described by Rubilar-

Rogers et al., 2011) correspond to the giant size-type. As stated previously (see also Tonni,

1980; Cenizo, 2012), they may belong to birds larger than the huge Neogene taxa (i.e., *P.*

chilensis; similar-sized to *P. sandersi*; Table 1), constituting one of the largest pelagornithid

known so far.

In this sense, two Antarctic morphotypes were recognized by previous authors.

However, it was thought that both morphs coexisted during the middle/late Eocene of

Seymour Island (Tonni and Tambussi, 1985; Cenizo, 2012). This idea was conceived from the

finding of the mandible MLP 83-V-30-1 assigned –at that time– to a pelagornithid. Its

removal from pelagornithids implies that only giant pseudo-tooth birds (i.e., morphotype 2)

are known for the Bartonian/?Priabonian strata of the Submeseta Formation.

Across the world, a large diversity of body sizes of pelagornithids has been recorded between the late Paleocene and middle Eocene (Mayr, 2009). Since the middle/late Eocene, only giant pelagornithids are known. These forms (more than 5 m wingspan) show a trend toward acquiring huge sizes, reaching a maximum specialization during the late Neogene (Fig. 7). Even taking into account the incompleteness of the fossil record, it seems that large, medium, and small taxa (Fig. 7) become extinct after middle Eocene times. An ecological competition for food or breeding sites could be the main cause (Mayr, 2009). A large list of candidates for such a competition may include the oldest Procellariiformes (Noriega and Tambussi, 1996; Tambussi and Acosta Hospitaleche, 2007; Tambussi and Degrange, 2013; Reguero et al., 2013) described for the *Cucullaea* II Allomember (Ypresian/Lutetian), and the extremely diversified and widely extended early penguin fauna (Acosta Hospitaleche and Reguero, 2010; and references therein). The onset and diversification of giant forms occurred at the same time both in penguins (Clarke et al., 2007; Ksepka and Clarke, 2010), and pseudo-toothed birds. Giant penguins are recorded until the latest Eocene/earliest Oligocene in Antarctica (Acosta Hospitaleche, 2013, in press; Acosta Hospitaleche and Reguero, in press), and the late Oligocene in New Zealand (Ksepka and Ando, 2011). After that, giant penguins disappear from the fossil record, suggesting an important ecological segregation favoring medium and small penguins, in contrast with pseudo-toothed birds, in which giant size was maintained until their extinction in the late Neogene.

Highlights in pelagornithid evolution.—The phylogenetic affinities within Pelagornithidae are not well understood, and thus, reliable conclusions are difficult to assess. The following inferences about the evolutionary history of the group should be considered as preliminary, and must be confirmed with new and more complete findings. On this basis, and having in mind that the pelagornithid record is patchy, three main evolutionary events can be recognized.

MLP 12-I-20-4, assigned to morphotype 1, is the oldest pseudo-toothed birds from Antarctica, and is more derived than *Dasornis* in several features. It indicates in the middle Ypresian, the presence of a more specialized 'clade' than that of *Dasornis*. This first event probably includes the disappearance of *Dasornis* and would be the starting point of the dominance of more advanced forms ('Clade' 1, Fig. 7) with a trend towards the extreme specialization of soaring capacity.

The second event would be linked to the origin of the *Pelagornis* s.l. species (hypothetical Clade 2, Fig. 7; see Mayr et al., 2013). It would have occurred during the early Oligocene, although unfortunately, the fossil record of pseudo-toothed birds is very scarce for that time. Finally, Mayr et al. (2013) recognized some presumable synapomorphies that allow to join the younger Mio/Pliocene taxa in a highly specialized group of forms (Clade 3, Fig. 7), that probably constituted the third and more recent evolutionary event in pelagornithids.

ACKNOWLEDGMENTS

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FIGURE CAPTIONS

FIGURE *1*—Location map of the La Meseta Formation and the new Submeseta Formation outcrops in Seymour Island, Antarctic Peninsula, West Antarctica. Other stratigraphic units are also indicated: CVF = Cross Valley Formation; LBF = López de Bertodano Formation; SF = Sobral Formation; WF = Weddel Formation; sd = surficial deposits.

FIGURE *2*—Stratigraphic section of the La Meseta Formation and the new Submeseta Formation unit proposed by Montes et al. (2013), Seymour Island, Antarctic Peninsula. Characteristic invertebrates are indicated as: t = *Turritella*; cu = *Cuccullaea*; v = veneroids.

FIGURE *3*—Distal end of right humerus (MLP 12-I-20-4) assigned to Pelagornithidae indet. morphotype 1 from the early Eocene of Seymour Island (West Antarctica). *1–4*, in cranial, caudal, dorsal, and distal views, respectively. Abbreviations: cd = condylus dorsalis; cv = condylus ventralis; ed = epicondylus dorsalis; fmb = fossa musculi brachialis; fo = fossa olecrani; icu = insertion of the musculus extensor carpi ulnaris; sh = sulcus humerotricipitalis; tsv = tuberculum supracondylare ventrale. Scale bar = 20 mm.
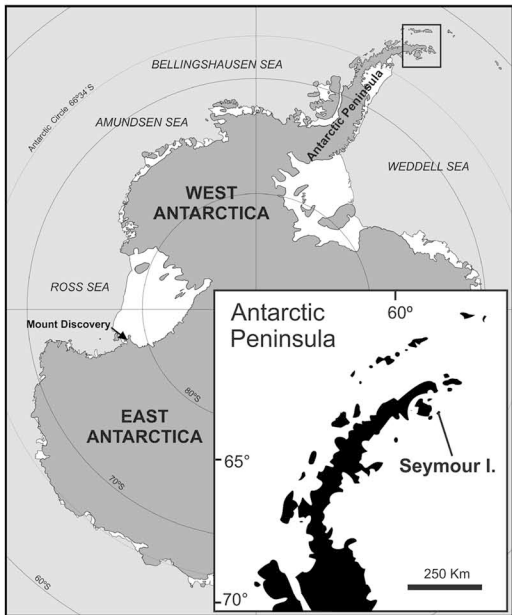
FIGURE *4*—Pelagornithid specimens assigned to morphotype 2 from the middle Eocene of Seymour Island (West Antarctica). *1*, Comparative proportions of the cranial remains from Antarctica (MLP 08-XI-30-42, MLP 78-X-26-1) and the holotype of the giant species *Pelagornis chilensis* (after Mayr and Rubilar-Rogers, 2010). *2*, *3*, rostral end of rostrum maxillare (MLP 08-XI-30-42) in lateral and dorsal views; *4–8*, most rostral narial region of rostrum maxillare (MLP 78-X-26-1) in dorsal, lateral, ventral, and cranial (*7*, *8*) views, respectively; *9–11*, distal end of right tarsometatarsus (UCR 22176, cast MLP) in dorsal, plantar, and distal views, respectively. Abbreviations: cid = canalis interosseus distalis; cr = culmen ridge; ct = cristae tomiales; ftp = fossa for mandibular tooth-like processes; fvd = foramen vasculare distale; dc = dorsolateral constriction; pmp = processus medioplantaris; mvs = medioventral sulcus; ls = longitudinal sulcus; pr = palatal ridge; tp = toothlike processes (2–4 = rank); tII, tIII, and tIV = trochleae metatarsorum II, III, and IV. Scale bars = 20 mm; except in *1* = 50 mm.

FIGURE *5*—Comparative morphology of the tarsometatarsus in Pelagornithidae. Selected specimens are listed from left to right: *Dasornis toliapica* OCP.DEK/GE 1146 and *Dasornis emuinus* OCP.DEK/GE 1106 (after Bourdon et al., 2010, reversed for comparison), *D. emuinus* NHMUK 894 (after Harrison and Walker, 1977), *Lutetodontopteryx tethyensis* SMF Av 553a+b (holotype, after Mayr and Zvonok, 2012), Pelagornithidae indet. morphotype 2 UCR 22176 (MLP cast), cf. *Pelagornis ('Palaeochenoides') mioceanus* MCZ 2514 (after Hopson, 1964, reversed for comparison), *Pelagornis* sp. LACM 128424 (after Mayr et al., 2013), *Pelagornis chilensis* MNHN SGO.PV 1061 (holotype, after Mayr and Rubilar-Rogers, 2010). *1*, *2* and *3* rows: dorsal, plantar, and distal views, respectively. Abbreviations: DP = distal projection of the trochleae metatarsorum II and IV; mp = processus medioplantaris; PP = plantar projection of the trochleae metatarsorum II and IV; tII, tIII, and tIV = trochleae metatarsorum II, III, and IV. Unscaled images for comparison.
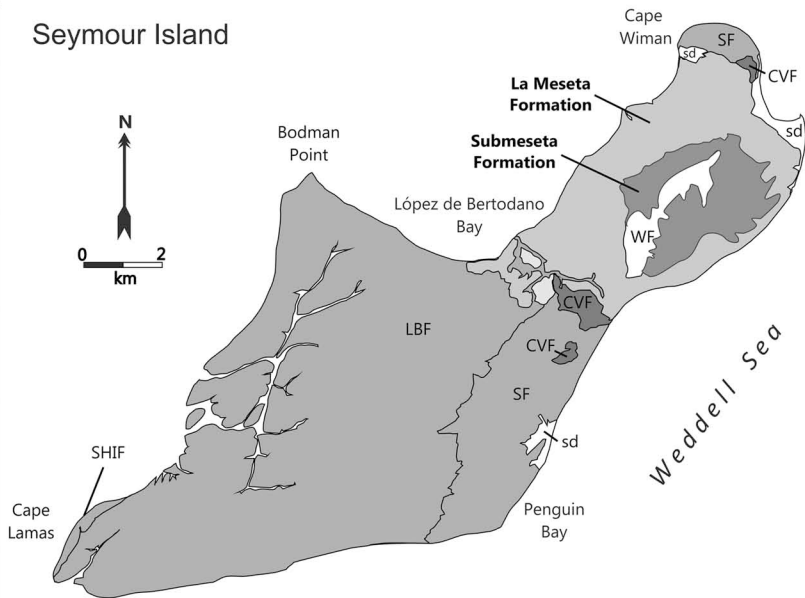
FIGURE *6*—Specimens previously referred to Pelagornithidae and here reassigned to other taxa. *1*, *2*, fragmentary mandible (MLP 83-V-30-1) reassigned to Sphenisciformes indet. coming from the middle Eocene of Seymour Island (locality DPV 13/84, level 38) in lateral and medial views; *3–5*, fragmentary dentary of fish (MLP 83-V-30-2) coming from the late Eocene of Seymour Island (DPV 16/84 locality, level 39) in lateral, cranial and medial views, respectively. Abbreviations: cl = cotyla lateralis; p = prominence. Scale bar = 20 mm.
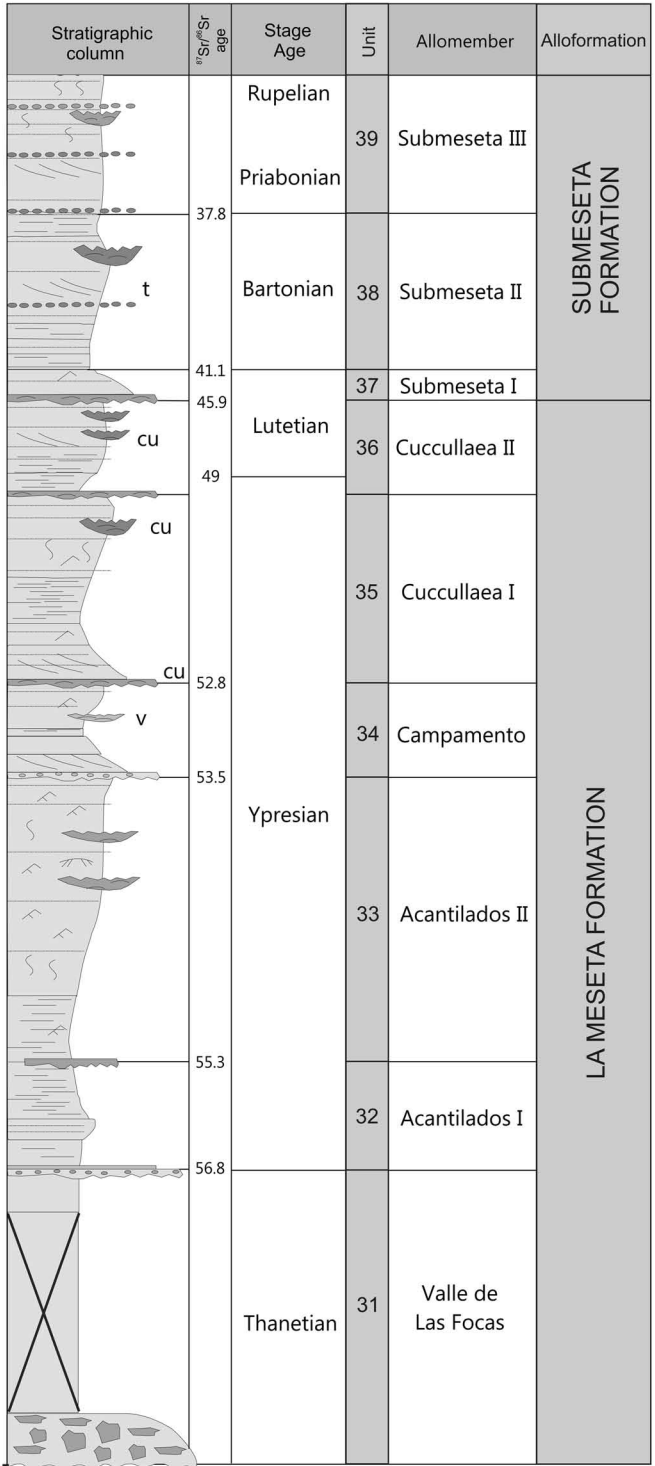
FIGURE *7*—Temporal distribution, phylogenetic affinities, and size-types in selected pelagornithid species (modified from Mayr et al., 2013). The internal nodes are supported by the following presumable derived features (Mayr et al., 2013, and present work): 'Clade' 1 (humerus with ventral portion of proximal end narrow and tuberculum dorsale strongly

projected, ulna with very short olecranon, trochlea metatarsi II at the same level or slightly more plantarly projected than the trochlea IV); 'Clade' 3 (femur with trochlea fibularis lacking sulcus). The 'Clade' 2 is still uncertain, but according to general similarities it considered by Mayr et al. (2013) as *Pelagornis* s.l. (a presumable derived character noted here is the presence of the transverse furrow near the tip of the rostrum). The size-types represent the wingspan inferred by extrapolated dimensions of the known elements in incomplete specimens compared with the homologous elements in the *P. chilensis* holotype, the most completely known pelagornithid specimen. The gray areas indicate possible cladogenetic event.
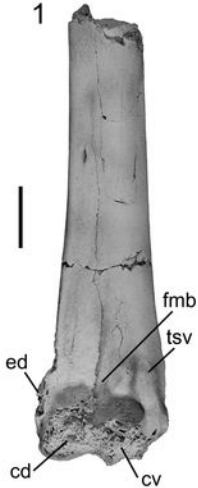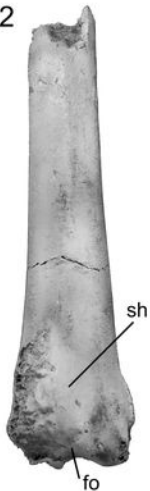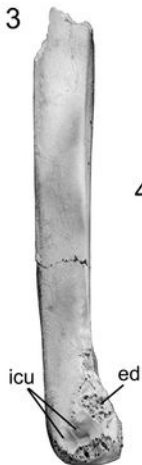
Seymour Island

- Cape Wiman
- SF
- sd
- CVF
- La Meseta Formation
- Submeseta Formation
- Bodman Point
- López de Bertodano Bay
- WF
- CVF
- CVF
- LBF
- SF
- SHIF
- Cape Lamas
- sd
- Penguin Bay
- Weddell Sea

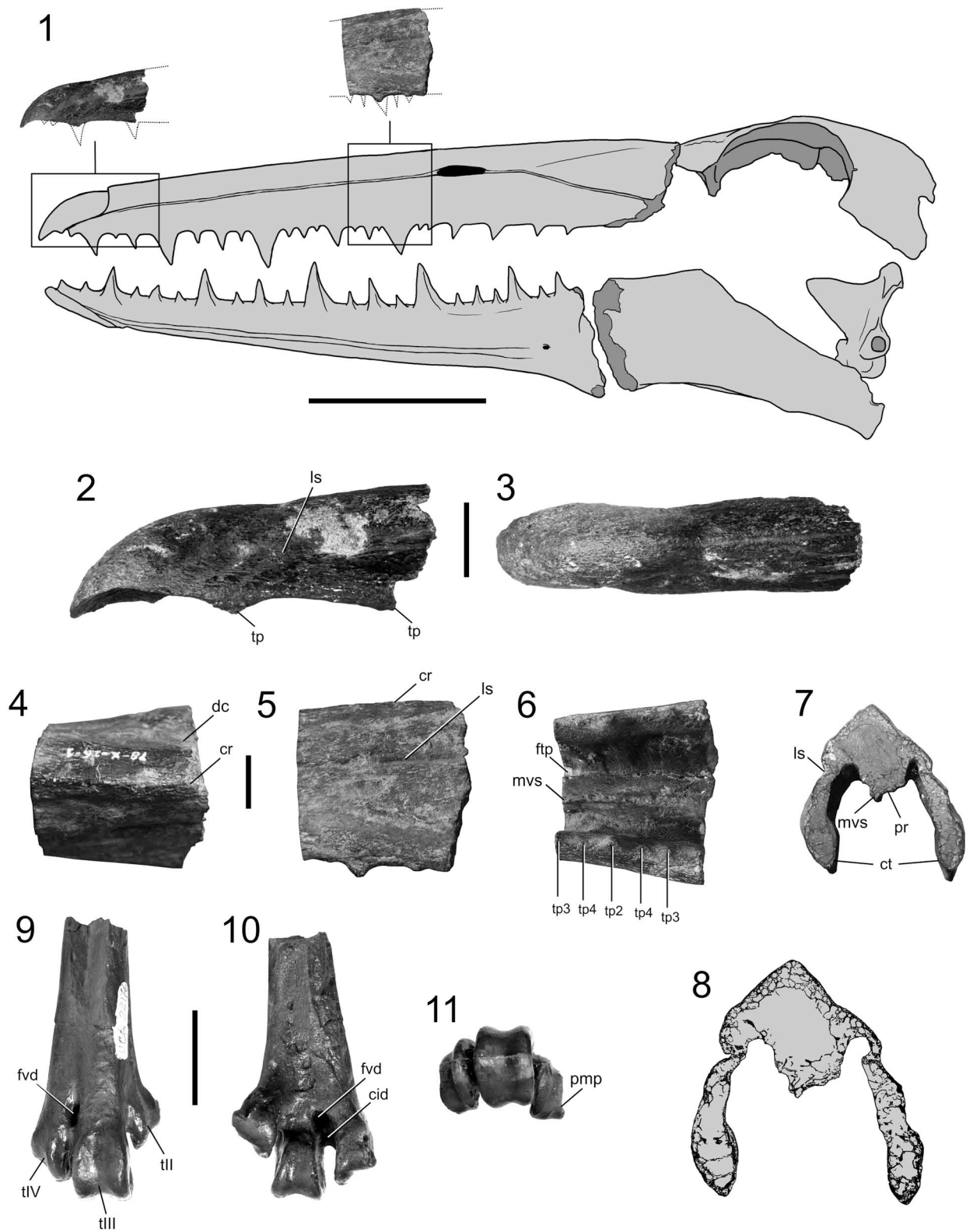| Stratigraphic column	$^{87}Sr/^{86}Sr$ age	Stage Age	Unit	Allomember	Alloformation
		Rupelian	39	Submeseta III	SUBMESETA FORMATION
	37.8	Priabonian			
		Bartonian	38	Submeseta II	
	41.1				
	45.9		37	Submeseta I	
		Lutetian	36	Cuccullaea II	LA MESETA FORMATION
	49		35	Cuccullaea I	
	52.8				
	53.5		34	Campamento	
		Ypresian	33	Acantilados II	
	55.3		32	Acantilados I	
	56.8				
		Thanetian	31	Valle de Las Focas	

Row labels: 1, 2, 3

Column headers:
Dasornis toliapica late Paleocene/early Eocene
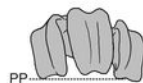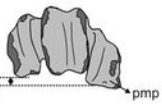*Dasornis emuinus* late Paleocene/early Eocene
Dasornis emuinus early Eocene
Lutetodontopteryx tethyensis middle Eocene
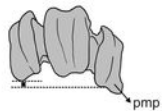Pelagornithidae indet. morphotype 2 middle Eocene
cf. *Pelagornis* ('*Palaeochenoides*') *mioceanus* ?late Oligocene
Pelagornis sp. late Oligocene/early Miocene
Pelagornis chilensis middle Miocene/late Pliocene

Labels in figure: tIV, tII, tIII, DP, PP, pmp

Paleocene			Eocene				Oligocene		Miocene					Plio	Pleist
Early	M	Late	Early	Middle		Late	Early	Late	Early			Middle	Late		
Danian	Selandian	Thanetian	Ypresian	Lutetian	Bartonian	Priabonian	Rupelian	Chattian	Aquitanian	Burdigalian	Langhian	Serravallian	Tortonian	Messinian		

Size-types (estimated wingspan)
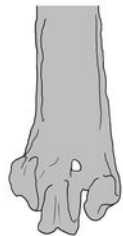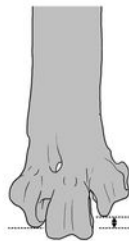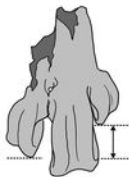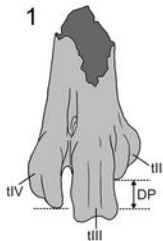
Dasornis abdoun (Af)
Dasornis toliapica (Af, E)
Dasornis emuinus (Af, E)
?*Dasornis* sp. ("?*Odontopteryx*" sp.) (NA)
Pelagornithidae indet. morph. 1 (Ant)
Lutetodontopteryx tethyensis (E)
?*Gigantornis* sp. (E)
?*Lutetodontopteryx* sp. (cf. "*M. oweni*") (E)
?*Gigantornis* sp. (cf. "*D. emuinus*") (E)
cf. *Gigantornis* sp. (Af)
Gigantornis eaglesomei (Af)
Pelagornithidae indet. morph. 2 (Ant)
Pelagornithidae indet. (aff. "*Argillornis*" sp.) (NA)
Pelagornithidae indet. (Pittsburg Bluff Fm., NA)
Cyphornis magnus (NA)
P. ("*Palaeochenoides*") *mioceanus* (NA)
cf. *P.* ("*Palaeochenoides*") *mioceanus* (NA)
Pelagornis sandersi (NA)
Pelagornis sp. (Nye Mudstone, NA)
P. miocaenus (E)
?*P. miocaenus* (E)
P. ("*Osteodontornis*") *orri* (NA)
P. ("*Pseudodontornis*") *stirtoni* (NZ)
P. chilensis (SA)
Pelagornis sp. (Au)
Pelagornis sp. (Yorktown, NA)
P. mauretanicus (Af)

Dasornis

"Clade"1

Extinction of large and minor forms / Origin of giant forms

"Clade"2 (hypothetical)
Pelagornis sensu lato
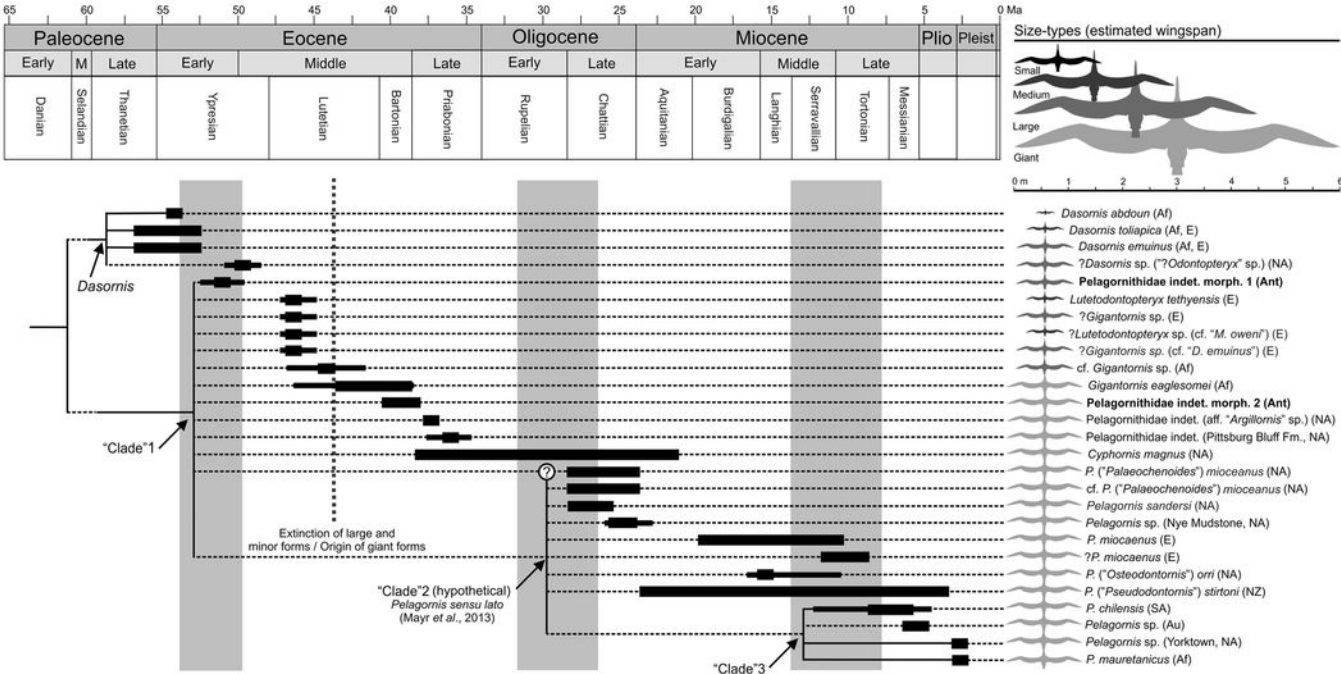(Mayr et al., 2013)

"Clade"3

TABLE *1*—Skull and limb dimensions of pseudo-toothed birds of Seymour Island compared with those of other Pelagornithidae. Data taken from: [a] Bourdon et al. (2010); [b] Harrison and Walker (1976); [c] González-Barba et al. (2002); [d] this work; [e] Rubilar-Rogers et al. (2011); [f] Mayr and Zvonok (2012); [g] Mayr and Smith (2010); [h] Bourdon and Cappetta (2013); [i] Goedert (1989); [j] Mourer-Chauviré and Geraads (2008); [k] Hopson (1964); [l] Olson (1985); [m] Wetmore (1928); [n] Okazaki (1989); [o] Mayr et al. (2013); [p] Howard (1957); [q] Howard and Warter (1969); [r] Mayr and Rubilar-Rogers (2010); [s] Chávez et al. (2007); [t] Olson and Rasmussen (2001); [u] Ono (1980); [v] Boessenecker and Smith (2011); [w] Lambrecht (1930); [x] Ksepka (2014) . * = preserved.

	Skull			Humerus				Femur	
	TL	H-an	W-nf	TL	W-prox	W-dist	D-dist	TL	W-dist
Dasornis abdoun[a]	—	—	—	~200	~27	18	8.7	—	—
Dasornis toliapica[a]	—	~20	23/~28	~245/~370	~34.5/36.9	~23/~28	13.5/17	—	—
Dasornis emuinus[a]	—	—	~36	~470/545	~70	~34/~47	~22/~25	—	—
Dasornis toliapica[a,b]	—	—	19/30	—	—	—	—	—	—
Dasornis emuinus[a,b]	—	—	~41	—	—	—	—	—	—
?*Dasornis* sp. (*'Odontopteryx?'* sp.)[c]	—	—	—	—	—	~35	~16	—	—
Pelagornithidae indet. morphotype 1[d]	—	—	—	—	—	42.8*	28.6*	—	—
Lutetodontopteryx tethyensis[f]	—	—	—	~310	—	~27/~28	—	—	18.1
?*Lutetodontopteryx* sp. (cf. *'M. oweni'*)[f,g]	—	—	—	~335	—	28.3	—	—	—
?*Gigantornis* sp. (cf. *'D. emuinus'*)[g]	—	—	—	~570	—	—	—	—	—
cf. *Gigantornis* sp.[h]	—	—	—	~400/~500	—	37.5	23.1	—	—
Pelagornithidae indet. morphotype 2[d,e]	—	49.9/54	—	850*	—	—	—	—	—
Pelagornithidae indet. (Pittsburg Bluff Fm.)[i]	—	—	—	—	67.9	—	—	—	—
Cyphornis magnus[g,j,k]	—	—	—	—	—	—	—	—	—
Tympanonesiotes wetmorei[l,m]	—	—	—	—	—	—	—	—	—
P. (*'Palaeochenoides'*) *mioceanus*[j,k,l]	—	—	—	—	—	—	—	—	40
cf. *P.* (*'Palaeochenoides'*) *mioceanus*[j,k,l]	—	—	—	—	—	—	—	—	—
Pelagornis sandersi[x]	569	—	—	810*	92.5	—	—	176.8	—

Pelagornithidae indet.[n]	—	—	—	—	—	62.9	33.0	—	—
Pelagornis sp.[o]	—	—	—	—	—	—	—	—	25
Pelagornis miocaenus[j]	—	—	—	~591/~710	59.3/61.5	53.7	~37.6/39	—	—
P. ('Osteodontornis') orri[p]	400	40	27	>593	—	—	—	—	—
P. ('Pseudodontornis') stirtoni[q]	—	~29	35	—	—	—	—	129.5	~31
Pelagornis chilensis[r]	450	45	51.4	821	80.6	—	—	150.2	39.1
Pelagornis sp.[s]	—	—	—	—	65.3/70.1	—	—	—	—
Pelagornis sp.[t]	—	—	—	—	—	—	—	—	29.6/32.7
Pelagornis sp.[u]	—	—	—	—	—	—	—	—	32.5
Pelagornis sp.[v]	—	—	—	~723	71.1	—	—	—	—
Pelagornis mauretanicus[j]	—	—	—	—	—	>51.2/52	39.4	133	34.5
P. ('Pseudodontornis') longirostris[q,w]	>400	40	—	—	—	—	—	—	—

TABLE 1 —(Continued)

	Tarsometatarsus			Age	Provenance
	TL	W-prox	W-dist		
Dasornis abdoun[a]	—	—	—	late Paleocene/early Eocene	Morocco
Dasornis toliapica[a]	~78/~85	15	15.7/~17.5	late Paleocene/early Eocene	Morocco
Dasornis emuinus[a]	118	25.6	21.3/25.5	late Paleocene/early Eocene	Morocco
Dasornis toliapica[a,b]	—	14.7	—	early Eocene	England
Dasornis emuinus[a,b]	—	26.8	27.1	early Eocene	England
?Dasornis sp. ('Odontopteryx?' sp.)[c]	—	—	—	early Eocene	Mexico
Pelagornithidae indet. morphotype 1[d]	—	—	—	early Eocene	Antarctica
Lutetodontopteryx tethyensis[f]	—	15.7	14.5	middle Eocene	Ukraine
?Lutetodontopteryx sp. (cf. 'M. oweni')[f,g]	—	17.7	—	middle Eocene	Belgium
?Gigantornis sp. (cf. 'D. emuinus')[g]	—	—	—	middle Eocene	Belgium
cf. Gigantornis sp[h]	—	—	—	middle Eocene	Togo
Pelagornithidae indet. morphotype 2[d,e]	—	—	38.5	middle Eocene	Antarctica
Pelagornithidae indet. (Pittsburg Bluff Fm.)[i]	—	—	—	latest Eocene	USA
Cyphornis magnus[g,j,k]	—	36.7	—	?late Eocene/?early Miocene	Canada
Tympanonesiotes wetmorei[l,m]	—	—	~24.5	?late Oligocene/?late Miocene	USA

P. (*'Palaeochenoides'*) *mioceanus*[i,k,l]	—	—	—	?late Oligocene	USA
cf. *P.* (*'Palaeochenoides'*) *mioceanus*[i,k,l]	—	—	34.7	?late Oligocene	USA
Pelagornis sandersi[x]	>150	—	—	late Oligocene	USA
Pelagornithidae indet.[n]	—	—	—	late Oligocene	Japan
Pelagornis sp.[o]	111.5	27.2	32.2	latest Oligocene/early Miocene	USA
Pelagornis miocaenus[j]	—	—	—	early/middle Miocene	France
P. (*'Osteodontornis'*) *orri*[p]	114	—	—	early/middle Miocene	USA
P. (*'Pseudodontornis'*) *stirtoni*[q]	—	—	—	Miocene/Pliocene	New Zealand
Pelagornis chilensis[r]	126.9/127.5	36.6/36.8	37.3/37.2	middle Miocene/early Pliocene	Chile
Pelagornis sp.[s]	—	—	—	late Miocene/Pliocene	Peru
Pelagornis sp.[t]	—	—	—	Miocene or Pliocene	USA
Pelagornis sp.[u]	—	—	—	late Pliocene	Japan
Pelagornis sp.[v]	—	—	—	late Pliocene	USA
Pelagornis mauretanicus[j]	—	—	—	latest Pliocene	Morocco
P. (*'Pseudodontornis'*) *longirostris*[q,w]	—	—	—	Uncertain	Uncertain