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Procellariiform remains and a new species from the latest Eocene of Antarctica

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ABSTRACT

New remains from the La Meseta (Thanetian – Lutetian) and Submeseta (Lutetian – Rupelian) formations (Seymour Island, Antarctica) are tentatively assigned to Diomedeidae and Procellariidae (Procellariiformes). Based on the fossil record and several analyses that attempt to explain the evolutionary patterns of Diomedeidae, *Notoleptos giglii* gen. et sp. nov., based on a small tarsometatarsus, was an ancestral form that lived in Antarctica before the rise of large-sized albatrosses. Subsequent environmental cooling since the late Oligocene could have selected against small body size, to the detriment of small-sized albatrosses like *Notoleptos*, thus favoring large body size and setting the stage for the development of the specialized albatross flight.

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Introduction

The Antarctic fossil avifauna is composed mostly of penguins. Thousands of isolated penguin bones and a few skeletons have been described, mainly from Paleocene and Eocene levels of West Antarctica (e.g. Myrcha et al. 2002; Jadwiszczak 2006; Acosta Hospitaleche et al. 2013; Acosta Hospitaleche & Reguero 2014). In contrast, the list of known non-penguin avian taxa is short and includes a single, doubtful ratite (Tambussi et al. 1994) and a few flying birds (Reguero et al. 2013). The fossil record of Cenozoic Antarctic flying birds includes Gaviiformes, Ciconiiformes, Procellariiformes, Gruiformes, Falconiformes, and Pelagornithidae (Reguero et al. 2013). Among water birds, Procellariiformes is particularly interesting since living species are almost exclusively pelagic and mainly distributed across the oceans of the Southern Hemisphere.

The order Procellariiformes includes four extant families, all of which have fossil representatives: Diomedeidae (albatrosses), Procellariidae (petrels, prions and shearwaters), Hydrobatidae (storm petrels), and Pelecanoididae (diving petrels). A fifth family, Diomedeoididae, is extinct but has a substantial fossil record that includes isolated bones and articulated skeletons from marine Oligocene deposits from Germany, France, Belgium, and Iran, and the early Miocene of Germany (Mayr & Smith 2012).

The oldest fossil referred to Procellariiformes is *Tytthostonyx glauconiticus* Olson and Parris (1987) from the latest Cretaceous or earliest Paleocene greensands of Hornerstown Formation, New Jersey, USA, which is placed in the monotypic Tytthostonychidae. This species, based on a humerus with a small *processus supracondylaris*, was tentatively considered as a Prophaethontidae (Bourdon et al. 2008), but the morphological differences supporting this proposal may be plesiomorphic for Procellariiformes (see also Mayr 2015b).

The worldwide Paleogene record of the group is scarce. Presumptive procellariiforms from the late Paleocene of Asia and early Eocene of Europe are known from fragmentary remains too incomplete for reliable identification, and their assignments have been highly questioned (Mayr & Smith 2012; Mayr 2015a). For example, the alleged Diomedeidae *Murunkus subitus* Pantelev and Nessov 1987 from the middle Eocene might belong to Diomedeoididae according to Mayr (2015a), although the morphology of its carpometacarpus is completely different from that of *Diomedeoides,* making the inclusion of *Murunkus* within Diomedeoididae unlikely (de Pietri et al. 2010).

The Oligocene *Manu antiquus,* based on a furcula (Marples 1946), could possibly be assigned to Pelagornithidae (Mayr 2009; Mayr & Rubilar-Rogers 2010). Besides one of the Antarctic materials described here (MLP 88-I-1-5, see original description in Tambussi and Tonni 1988 and discussion in Mayr & Smith 2012), the Paleogene Diomedeidae are represented only by one specimen from the late Oligocene of South Carolina that is not yet described (Olson 1985) and the recently proposed *Tydea septentrionalis* (Mayr & Smith 2012).

The supposed Paleocene Procellariidae *Eopuffinus kazachstanensis* Nessov 1986, *Primodroma bournei* Harrison and Walker 1977, and *Marinavis longirostris* Harrison and Walker 1977 were based on fragmentary material (a partial cranium, the distal end of a humerus, and a fragment of beak, respectively). These taxonomic assignments were strongly criticized and dismissed in previous reviews (e.g. Steadman 1981). Excluding the Antarctic

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materials discussed here, the Paleogene record seems to be restricted to some late Eocene remains morphologically similar to *Pterodroma* (Feduccia & McPherson 1993), and the Oligocene *Argyrodyptes microtarsus* (Tonni 1980; Olson 1985; Agnolin 2007) and '*Larus*' *raemdonckii* van Beneden, 1871 (= *Puffinus raemdonckii* according to Brodkorb 1962; see also Miller & Sibley 1941). A procellariiform of indeterminate family, *Makahala mirae*, was recently described based on a distal humeral portion and an ulna from the late Eocene or early Oligocene of Washington State, USA (Mayr 2015b).

The fossil record of procellariiforms becomes more abundant during the Neogene. Most of the records correspond to North America (e.g. Olson & Rasmussen 2001; Warheit 2002; Davis 2003), but they are also frequent in South America (Olson 1984; Walsh & Hume 2001; Stucchi & Urbina 2005), Australia (Wilkinson 1969), and Africa (Olson 1985). With the single exception of *Plotornis delfortrii* Milne-Edwards, 1874 from the early Miocene of France, all described Neogene species belong to extant genera.

Here we present new remains from the La Meseta (Thanetian – Lutetian) and Submeseta (Lutetian – Rupelian) formations of Seymour Island, Antarctica and assign them to Procellariiformes. Among them, one tarsometatarsus corresponds to a new genus and species and has motivated the revision of the Antarctic record of the group.

Material and methods

The fossils studied here were collected during successive field trips to Marambio (Seymour) Island organized by the Instituto Antártico Argentino (Dirección Nacional del Antártico) between the years 1988 and 2013, and are housed in the División Paleontología Vertebrados of Museo de La Plata (Argentina).

Comparative materials include skeletons of four families of Procellariiformes from the collections of Sección Ornitología, Museo de La Plata (MLP), La Plata (Argentina), Ornithological Section of the Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia' (MACN), Museo Acatushún de Aves y Mamíferos (RNP-A), Tierra del Fuego (Argentina), and Sección Ornitología of Museo Nacional de Historia Natural (MNHN) of Montevideo (República Oriental del Uruguay). All materials are listed in Appendix 1.

Osteological terms follow Baumel and Witmer (1993), and Livezey and Zusi (2006) when necessary. Measurements were taken with a Vernier caliper (0.01 mm increments). The stratigraphic framework follows Marenssi et al. (1998a) and Montes et al. (2013).

The main phylogenetic analysis based on maximum parsimony was performed using the data matrix of Livezey and Zusi (2006, 2007) with TNT software (Goloboff et al. 2008). We also discuss a morphological data matrix constrained to Procellariiformes (Mayr & Smith 2012), but since only one character could by scored in our specimens, we focus on Livezey and Zusi (2006, 2007) in order to test higher level relationships. We added the new species and MLP 88-I-1-5, previously known from Antarctica (Tambussi & Tonni 1988) to the matrix in order to test their phylogenetic relationships. Although the final data matrix included 2954 characters, only 98 and 61 characters were coded for them, respectively (Appendix 2). All characters were considered as equally weighted and unordered, and the hypothetical 'non-archosauromorph' of the original matrix was considered as the primary outgroup. The analysis was performed using a traditional search, starting with 10 Wagner trees using random seed, with 5000 replicates, followed by TBR branch-swapping algorithm saving 1000 trees per replication. The most parsimonious trees (MPT) found in the replicates were subjected to a final round of TBR. All MPTs were used to calculate a strict consensus tree. Absolute and relative Bremer support and boot-strap (1000 replications) values were also calculated. The Consistency Index of the characters was calculated with a script for TNT (Ramirez 2010) in order to evaluate and compare apomorphic characters.

Provenance

The materials here studied come from two different levels corresponding to the middle and uppermost part of the Seymour Island Group, which includes the middle- late Paleocene Cross Valley Formation, the latest Paleocene- middle Eocene La Meseta Formation, and the middle Eocene-?Oligocene Submeseta Formation. The La Meseta and Submeseta formations constitute the main Cenozoic strata of the James Ross Basin and are exposed around the northern part of the Seymour Island (Figure 1), approximately 100 km southeast of the northern tip of the Antarctic Peninsula (del Valle et al. 1992).

The La Meseta Formation (= La Meseta Alloformation, Marenssi et al. 1998a) is an unconformity-bounded unit (Elliot & Trautman 1982; Ivany et al. 2008) of approximately 560 meters thickness that fills a 7 km wide valley in Seymour Island (= Marambio) (Reguero et al. 2013). This unit includes mudstones and sandstones with interbedded conglomerates and is organized into six erosionally-based allomembers that include, from base to top (Figure 2): Valle de Las Focas, Acantilado I, Acantilado II (according to Montes et al. 2013; a single unit named Acantilados in Marenssi et al. 1998a), Campamento, Cucullaea I, and Cucullaea II (Marenssi et al. 1998a; Montes et al. 2013). These lens-shaped units represent different sedimentation stages related to sea level fluctuations (Marenssi et al. 2002) that were deposited in deltaic, estuarine and shallow marine environments (Porębski 1995; Marenssi et al. 1998b).

An ulna (MLP 91-II-4-6) from a ?procellariid, and a tibiotarsus (MLP 90-I-20-11), a tarsometatarsus (MLP 88-I-1-5), a pedal phalanx (MLP 92-II-2-7), and a *rostrum maxillare* (MLP 88-I-1-6) corresponding to ?Diomedeidae were recovered from the Cucullaea I Allomember of the La Meseta Formation (upper Ypresian) at the locality DPV 6/84 (= RV 8200 of Woodburne and Zinsmeister (1984).

The site DPV 6/84 is well-known because of the amount of bones belonging to flying birds recovered there during recent years. From this same level (Cucullaea II Allomember), previous works have described Pelagornithidae (Acosta Hospitaleche et al. 2014; Cenizo et al. 2015), Gaviiformes (Acosta Hospitaleche & Gelfo 2015), and Falconiformes (Tambussi & Degrange 2013; Cenizo et al. 2016). Provenance studies made on sandstones from the La Meseta Formation have demonstrated that the source rock was located west-northwest along the present-day Antarctic Peninsula. A protected and estuarine environment provided suitable habitat and good preservation potential for these skeletons, evidenced by this high diversity and abundance of fossil remains (Marenssi 2006).

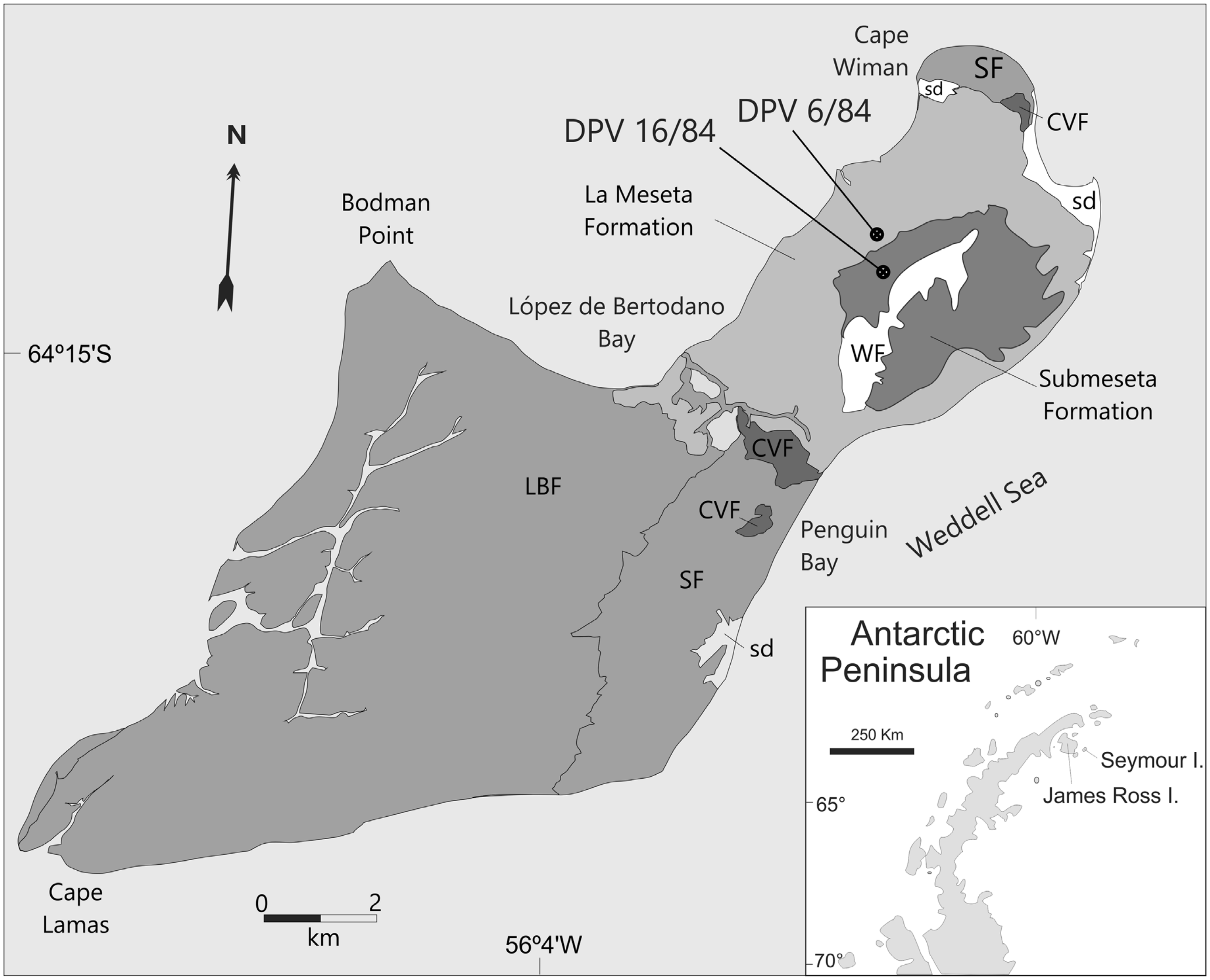

Figure 1. Location map showing the localities DPV 6/84 (Cucullaea I Allomember, La Meseta Formation), and DPV 16/84 (Submeseta III Allomember, Submeseta Formation) in Seymour Island (Antarctic Peninsula, West Antarctica).
Abbreviations: CVF, Cross Valley Formation; LBF, López de Bertodano Formation; SF, Sobral Formation; WF, Weddel Formation; sd, surficial deposits.

The middle Eocene- earliest Oligocene Submeseta Formation (Montes et al. 2013) represents the top of the marine sedimentary sequence of the Basin (Figure 1) and is interpreted as the filling of an incised-valley system covered only by glaciomarine Miocene and post Pliocene deposits (Marenssi et al. 1998a).

Three different levels have been recognized in this unit (Figure 2) and named, from base to top, 'Submeseta I', 'Submeseta II', and 'Submeseta III' (Montes et al. 2013). Strata of level 39 (upper Bartonian- Priabonian), equivalent to 'Submeseta III', crop out at the fossiliferous locality DPV 16/84, where a tibiotarsus (MLP 13-XI-28-50) and a tarsometatarsus (MLP 12-I-20-305) of Diomedeidae were collected.

The locality DPV 16/84 (provenance of gen et sp. nov. here described) is also very rich in fossiliferous content. In recent years, Pelagornithidae (Acosta Hospitaleche et al. 2014), Gaviiformes (Acosta Hospitaleche & Gelfo 2015), Gruiformes (Tambussi & Degrange 2013), and a presumptive Ratites (Tambussi et al. 1994) have been reported for this unit, in addition to numerous fossil penguins (Acosta Hospitaleche 2016). This level corresponds to the Facies Association III and is characterized by a uniform sandy lithology that represents a tidal shelf influenced by storms (Marenssi et al. 1998b).

Systematic paleontology

Procellariiformes Fürbringer 1888
?Diomedeidae Gray 1840
Notoleptos gen. nov.

Type species. *Notoleptos giglii*.

Derivation of the name. From ancient Greek 'nóto' meaning 'South', and 'leptos' in reference to its small size and slender morphology.

Diagnosis. Smaller than any other known Diomedeidae, *foramina vascularia proximalia* opened cranially at the same level, *foramen vasculare distale* sub-oval and located in a shallow sulcus on the *facies dorsalis*, aligned with the *incisura intertrochlearis lateralis*. Opening of the foramen *vasculare distale* into the *fossa*

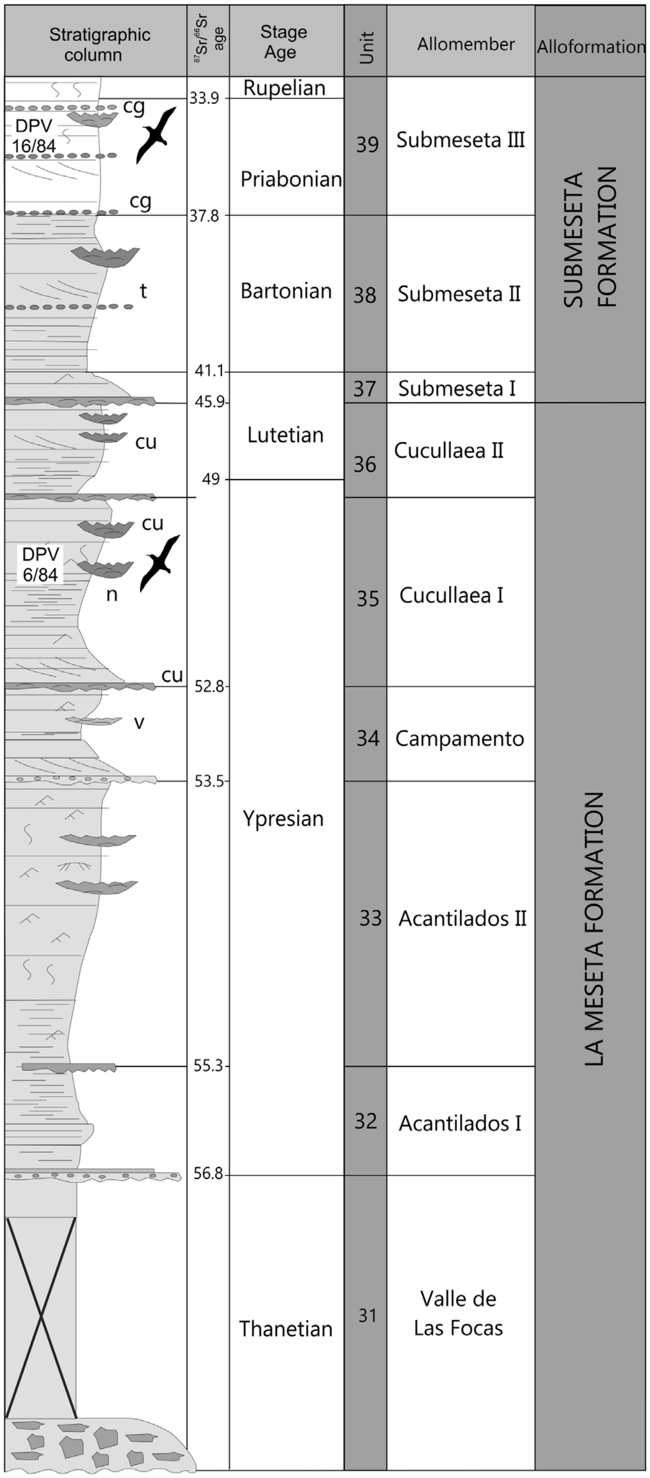

Figure 2. Stratigraphic scheme of the La Meseta Formation and Submeseta Formation.

Note: Albatross silhouettes indicate the levels corresponding to sites DPV 6/84 (upper Ypresian), and DPV 16/84 (upper Priabonian), where the materials studied here were collected.

supratrochlearis plantaris located proximally with respect to the most proximal end of the medial margin of the trochlea metatarsi II. Metatarsals II, III, and IV located at the same level in dorso-plantar perspective. Impression or tuberositas of the *ligamentum collaterales lateralis* of the tarsometatarsus not distinct.

Notoleptos giglii sp. nov.

Figures 3 and 5

Holotype. MLP 12-I-20-305, left tarsometatarsus preserved in two pieces, with a small section of the diaphysis missing.

Derivation of the name. The specific epithet *giglii* is for Silvia Moreda de Gigli, secretary of the Argentinian Paleontological Association and a keystone of this institution from 1987 to 2015.

Measurements. Proximal width: 9.5 mm, medio-lateral width of diaphysis: 4.9 mm, antero-posterior width of diaphysis: 3.6 mm, distal (trochlear) width: 10.2 mm, width of trochlea II: 3.7 mm, width of trochlea: III: 3.1 mm, width of trochlea metatarsi IV: 3.3 mm, antero-posterior width of trochlea metatarsi III: 5.9 mm.

Diagnosis. As for genus.

Provenance. Locality DPV 16/84, Seymour Island, Antarctic Peninsula, Submeseta III Allomember of Submeseta Formation (upper Bartonian- Priabonian).

Comparative description: Smaller than *Thalassarche* but morphologically very similar to the latter. In fact, specimen MLP 12-I-20-305 is about half as long as the smallest known albatrosses, including *Plotornis delfortrii*, the only available fossil taxon based on homologous bones.

In proximal view both *cotylae* are subequal in size, slightly more extended than those of living species. The hypotarsus is broken, so no particular features can be described.

The diaphysis is dorso-plantarly compressed as in *Thalassarche* and *Diomedea*, and a single *sulcus extensorius* occupies the main part of the *facies dorsalis* as in all Procellariiformes. The *sulcus extensorius* is deep and limited by similarly developed lateral and medial margins, as in *Diomedea*, *Phoebastria* and *Thalassarche*, whereas in *Macronectes* and other Procellariidae such as *Procellaria*, this sulcus is slightly shallower (Figure 5(a)–(c)). In *Oceanites*, the *sulcus extensorius* is even shallower and its lateral margin is more marked than the medial one. In the middle of the sulcus, the *foramina vascularia proximalia* open almost at the same level and proximal to the *tuberositas m. tibialis cranialis*, as in *Thalassarche, Phoebastria, and Plotornis*. In contrast, in *Daption*, *Pagodroma*, *Pachyptila, Procellaria, Thalassoica,* and *Fulmarus,* the *foramen vasculare proximale lateralis* opens more distally than the *medialis* in the *facies dorsalis*. In *Oceanites* this difference is subtle, whereas in *Pelecanoides*, the different proximo-distal levels of the foramina are more evident. The *tuberositas m. tibialis cranialis* is a slightly protruding structure as in *Macronectes*, *Daption*, *Procellaria, Thalassarche*, and *Diomedea*.

As a result of the divarication of trochleae metatarsi II and IV, the distal end of the tarsometatarsus of *Notoleptos giglii* is wide as in all Diomedeidae, whereas this epiphysis is narrower in Pelecanoididae, Hydrobatidae, and Procellariidae. The *fossa supratrochlearis plantaris* occupies a circular area, as in *Thalassarche* and *Diomedea*, whereas in *Daption*, *Macronectes, Pachyptyla, Fulmarus, Thalassoica, Procellaria, Pelecanoides,* and *Pagodroma*, this fossa is proximo-distally elongated. This morphology is closely related to that of the distal end, which is narrower in Procellariidae and Pelecanoididae than in Diomedeidae.

Figure 3. *Notoleptos giglii* gen. et sp. nov. Left tarsometatarsus MLP 12-I-20-305, preserved in two fragments: (a) proximal end in dorsal view, (b) distal end in dorsal view, (c) proximal end in plantar view, (d) distal end in plantar view, (e) distal end in distal view, (f) proximal end in medial view, (g) distal end in medial view, (h) proximal end in lateral view, (i) distal end in lateral view.
Note: Scale bar: 10 mm.

The opening of the *foramen vasculare distale* on the *facies dorsalis* is sub-oval and located in a shallow sulcus aligned with the *incisura intertrochlearis lateralis* (Figure 3). In the other genera of Procellariiformes examined here, this foramen is oval and more extended proximo-distally. For comparative purposes, the location of this foramen on the *facies plantaris* will be described using its relative position with respect to the proximal extension of the *incisura intertrochlearis medialis* and the extension of the *fossa supratrochlearis plantaris*. In *N. giglii* this foramen opens into the *fossa supratrochlearis plantaris,* proximal to the *incisura intertrochlearis lateralis* as in the other species compared. A latero-medial line can be traced from the proximal end of the medial margin of the trochlea metatarsi II toward the *facies lateralis* and perpendicular to the shaft. In *N. giglii*, the *foramen vasculare distale* is exactly at the level of this line, as in *Pachyptyla, Fulmarus* and *Thalassoica*, whereas in *Pelecanoides*, *Phoebastria, Macronectes, Procellaria, Halobaena,* and *Oceanites* the foramen is proximal to that line. *Thalassarche* exhibits an intermediate condition; the foramen is proximal and very close to that line, resembling the condition in *N. giglii*.

Metatarsal III is more dorsally located respect to metatarsals II and IV in *Pagodroma*, *Daption*, *Procellaria*, and *Macronectes*, whereas in *Notoleptos giglii* and *Thalassarche*, the three metatarsals are located at the same level. The trochlear margins are sub-parallel, and the lateral margin of this trochlea metatarsi is slightly more distally extended than the medial one, as in other Procellariiformes.

In *N. giglii*, the trochlea metatarsi II projects distally reaching the middle of the trochlea metatarsi III, as in most of the species compared. Although the difference is not substantial, the distal extension of this trochlea metatarsi is less in Procellariidae than in Diomedeidae and in MLP 12-I-20-305. In *Procellaria* and *Daption*, for example, the trochlea metatarsi II extends to the proximal third of the trochlea metatarsi III. The articular surface of the trochlea metatarsi IV of *N. giglii* is laterally inclined as in other Diomedeidae (see remarks). In distal view, the trochleae metatarsi form a wide arch as in *Diomedea*, *Thalassarche*, *Pagodroma*, *Macronectes*, *Procellaria*, and *Daption*.

Remarks. *Plotornis arvernensis* (Milne-Edwards 1869–1871), from the early Miocene of France, was considered as a Diomedeidae (Cheneval 1984), but this was a strongly questioned assignation due to several morphological features (e.g.

Figure 4. Procellariiformes described in this work and assigned to ?Diomedeidae indet., right tarsometatarsus MLP 88-I-1-5: (a) dorsal view, (b) plantar view; left tibiotarsus indet. MLP 13-XI-28-50: (c) cranial view, (d) caudal view; MLP 90-I-20-11 right tibiotarsus indet.: (e) cranial view, (f) caudal view; tip of *rostrum maxilare* MLP 88-I-1-6: (g) lateral view, (h) ventral view; pedal phalanx MLP 92-II-2-7: (i) dorsal view, (j) lateral view; ?Procellariidae indet., right ulna MLP 91-II-4-6: (k) dorsal view, (l) ventral view.
Note: Scale bar: 10 mm (figures (c) and (d) have their own scale also representing 10 mm).

the articular surface of its trochlea metatarsi IV not sloping laterally) and paleoenvironmental considerations (Mayr & Smith 2012). Before being considered as a Diomedeidae, *P. arvernensis* was described as a Procellariidae (i.e. *Puffinus arvernensis*) although the condition of trochlea metatarsi IV in this family is similar to that of the Diomedeidae. Following Mayr and Smith (2012), only *Plotornis delfortrii* is here considered as a Procellariidae.

?Diomedeidae indet.
Figures 4 and 5

Material. Tarsometatarsus with missing distal end (MLP 88-I-1-5).

Measurements. Proximal width: *ca.* 6.5 mm, medio-lateral width of diaphysis: 3.9 mm, antero-posterior width of diaphysis: 3.3 mm, width of trochlea III: *ca.* 2.5 mm, antero-posterior width of trochlea metatarsi III: 3.7 mm.

Provenance. Locality DPV 6/84, Seymour (Marambio) Island, Antarctic Peninsula. Cucullaea I Allomember of La Meseta Formation (upper Ypresian).

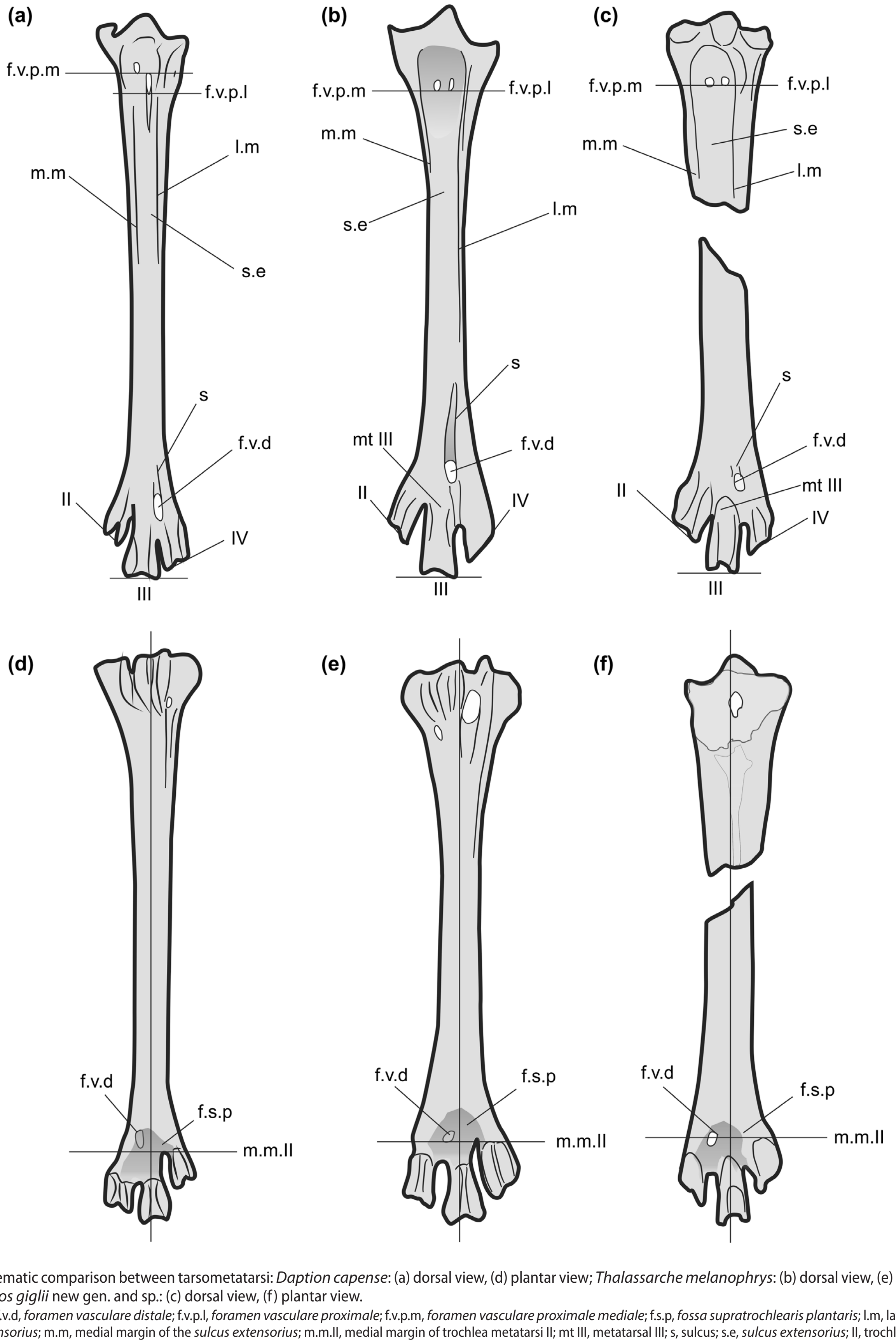

Figure 5. Schematic comparison between tarsometatarsi: *Daption capense*: (a) dorsal view, (d) plantar view; *Thalassarche melanophrys*: (b) dorsal view, (e) plantar view, and *Notoleptos giglii* new gen. and sp.: (c) dorsal view, (f) plantar view.

Abbreviations: f.v.d, *foramen vasculare distale*; f.v.p.l, *foramen vasculare proximale*; f.v.p.m, *foramen vasculare proximale mediale*; f.s.p, *fossa supratrochlearis plantaris*; l.m, lateral margin of the *sulcus extensorius*; m.m, medial margin of the *sulcus extensorius*; m.m.II, medial margin of trochlea metatarsi II; mt III, metatarsal III; s, sulcus; s.e, *sulcus extensorius*; II, trochlea metatarsi II; III, trochlea metatarsi III; IV, trochlea metatarsi IV. (not at scale for morphological comparison purposes).

Comparative description. The diaphysis is dorso-plantarly compressed as in all Procellariiformes. A single and wide *sulcus extensorius* runs along the shaft, becoming shallower toward the distal end. Both margins of this sulcus are equally developed, at least in the proximal half (Figure 4(a)).

The *sulcus extensorius* is deep and similar to those of *Thalassarche*, *Diomedea* and *Phoebatria*, whereas it is shallower in *Oceanites*. An intermediate condition appears in *Macronectes*, *Daption, Procellaria,* and *Pagodroma* (Figure 5(a)–(c)).

Both foramina *vascularia proximalia* are located at the same level within the *sulcus extensorius* (Figure 4(a)), in a shallow depression, as in *Thalassarche*, *Phoebatria*, *Plotornis*, and *Notoleptos giglii*, whereas in *Daption*, *Pagodroma*, *Pachyptila, Procellaria, Thalassoica,* and *Fulmarus,* the *foramen vasculare proximale medialis* opens more proximally than the *lateralis* on the *facies dorsalis* (Figure 5(a)–(c)). In *Oceanites*, this difference is less evident, whereas in *Pelecanoides* both foramina are more separated proximo-distally. The *tuberositas m. tibialis cranialis* is a slightly marked structure, even less developed than that in *Macronectes*, *Daption*, *Procellaria*, *Thalassarche* and *Diomedea*.

Although only the bases of trochleae metatarsi II and IV are preserved, the distal end of the tarsometatarsus is similar in width to those of other Procellariidae and Pelecanoididae and narrower than in Diomedeidae. Trochlea metatarsi III has parallel margins. Although the *facies dorsalis* of the trochlea metatarsi III is weathered, metatarsal III appears to be located at the same level as metatarsals II and IV, as in *Thalassarche*, and *N. giglii*. In the other genera compared, metatarsal III is located more dorsally with respect to the others.

The opening of the *foramen vasculare distale* on the *facies dorsalis* is oval and located in a well-developed sulcus aligned with the *incisura intertrochlearis lateralis*. On the *facies caudalis* (Figure 4(b)), its precise position is determined by the relative location with respect to the *incisura intertrochlearis medialis* (see explanation above, in the description of *Notoleptos*). The condition of MLP 88-I-1-5 is exactly the same as in *N. giglii* (Figure 5(f)), in which the foramen *vasculare distale* is located on a line traced perpendicular to the shaft from the proximal end of the medial margin of the trochlea II toward the *facies lateralis*, as in *Pachyptyla*, *Fulmarus,* and *Thalassoica.* In contrast, in *Daption* (Figure 5(d)), *Pelecanoides*, *Phoebastria, Macronectes, Procellaria, Halobaena,* and *Oceanites* the foramen is proximal to that line, whereas *Thalassarche* exhibits an intermediate condition (Figure 5(e)).

Remarks. This material was previously studied by Tambussi and Tonni (1988), who assigned it to Procellariidae, and then mentioned by Noriega and Tambussi (1996), who provided a brief description without illustrations. Later, Tambussi and Degrange (2013) mentioned the same material but referred it to Diomedeidae without any justification or remark.

?Diomedeidae indet.

Material. Left tibiotarsus without the proximal epiphysis (MLP 13-XI-28-50).

Measurements. Medio-lateral width of diaphysis: 8.5 mm, antero-posterior width of diaphysis: 6.7 mm, distal (condylar) width: 14.8 mm.

Provenance. Locality DPV 16/84, Seymour Island, Antarctic Peninsula, Submeseta III Allomember of Submeseta Formation (upper Bartonian-Priabonian).

Comparative description. The tibiotarsus MLP 13-XI-28-50 is very similar to that of *Thalassarche* in morphology and size. It differs from pelagornithids in which the diaphysis is straight and condyli are more symmetrically developed with respect to the main axis of the bone (e.g. Mayr & Rubilar-Rogers 2010; Mayr, Zvonok et al. 2013). The shaft is latero-medially curved with an oval section (Figure 4(c) and (d)). The diaphysis is aligned with the *condylus lateralis*, and the *condylus medialis* is medially displaced as in *Pagodroma, Pelecanoides, Fulmarus,* and *Daption*, whereas in *Thalassarche* and *Macronectes* the distal condyla are symmetrically arranged with respect to the shaft.

The *trochlea cartilaginis tibialis* is poorly demarcated and similar in shape to the one of *Pagodroma*, in which it is extends over a single surface. In contrast, in *Thalassarche* and *Macronectes* the *trochlea cartilaginis tibialis* is divided into two different areas separated by a smooth elevation. In *Daption*, this trochlea is not as extended proximally.

The *cristae trochleares* are not completely preserved; their tips are rounded, but they appear less projected than in *Macronectes* and similar to those of *Thalassarche*. The *facies caudalis* is flat at its distalmost part, and slightly convex at its middle, as in all the Procellariiformes compared.

The *epicondylus medialis* is not observable in this specimen; it is slightly defined in *Daption*, more conspicuous in *Thalassarche,* and even more so in *Macronectes*. The *epicondylus lateralis* is absent as in all the species compared.

The *condylus medialis* is enlarged as in *Diomedea* but seems differently oriented with respect to the diaphysis. In living Procellariiformes the *condylus* is perpendicular to the shaft, whereas in the fossil it is slightly oblique. It is worth noting here that the margin of the *condylus* is weathered, and this could have modified its original shape or orientation.

The *sulcus extensorius* is centered latero-medially and shallow as in *Diomedea* and *Thalassarche*. In *Macronectes* and other Procellariiformes, the position of this sulcus is somewhat more asymmetrical. Unfortunately, the *pons supratendinous* is broken (Figure 4(c)), but the preserved lateral and medial portions suggest a transverse position with respect to the diaphysis, as in others Diomedeidae, whereas in Procellariidae its position is oblique. The *tuberculum retinaculi m. fibularis* is also badly preserved and smoothed by weathering.

The margins of the *condylus lateralis* are not preserved, and the lateral surface of the condylus is at the same level as the *facies lateralis*, as in *Diomedea* and *Thalassarche*. In *Daption*, the lateral surface of the condylus is not continuous with the *facies lateralis*.

?Diomedeidae indet.

Material. Right tibiotarsus without the proximal end (MLP 90-I-20-11) (Figure 4(e) and (f)).

Measurements. Medio-lateral width of diaphysis: 5.4 mm, antero-posterior width of diaphysis: 3.9 mm.

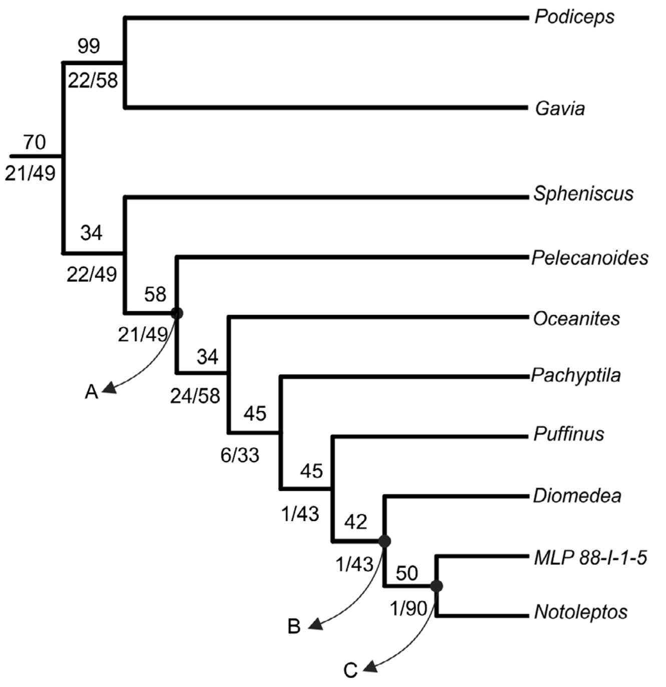

Figure 6. Part of the strict consensus tree of 252 MPTs of 18,346 steps recovered in the analysis.

Notes: Nodes are labeled above by bootstrap percentages and below by Bremer support values (absolute/relative). Nodes of Livezey and Zusi (2007) in the tree are: A. Procellariiformes. B. Diomedeidae?. C. Unnamed node of Antarctic procellariiforms.

Provenance. Locality DPV 6/84, Seymour (Marambio) Island, Antarctic Peninsula. Cucullaea I Allomember of La Meseta Formation (upper Ypresian).

Comparative description. Slightly larger than that of *Daption capense* but smaller than in *Diomedea* and *Thalassarche*. The surface of the bone is highly weathered and the *trochlea cartilaginis tibialis* is missing. Apparently, this bone was not completely ossified and could belong to a juvenile. The diaphysis is symmetrically located with respect to the *condylus distalis* (Figure 4(e)), as in *Thalassarche* and *Macronectes*. Contrastingly, in *Pelecanoides, Thalassoica, Fulmarus,* and *Daption,* the shaft is more aligned with the *condylus lateralis*. The shaft is cranio-caudally compressed and oval in section.

Despite the very poor preservation of the material, the *tuberculum retinaculi m. fibularis* can be observed. It is well developed and more conspicuous than in the other species compared.

Remarks. Given the lack of ossification and the textural aging (see Tumarkin-Deratzian et al. 2006), MLP 90-I-20-11 probably belonged to a sub-adult bird that had not reached adult size.

?Diomedeidae indet.

Material. Tip of *rostrum maxillare* (MLP 88-I-1-6) (Figure 4(g) and (h)).

Measurements. Length of the preserved portion: 17.5 mm.

Provenance. Locality DPV 6/84, Seymour (Marambio) Island, Antarctic Peninsula. Cucullaea I Allomember of La Meseta Formation (upper Ypresian).

Comparative description. Compared with pelagornithids, the curvature of the beak involves a longer portion of the rostrum, and the tip is dorsally less bulky in MLP 88-I-1-6. In palatal view, cristae tomiales are not as parallel as in *Lutetodontopteryx* (Mayr, Goedert et al. 2013) and neither fossae for reception of mandibular pseudo-teeth nor palatal ridge (Mayr & Rubilar-Rogers 2010) are developed. It is intermediate in size between large albatrosses (*Diomedea*, *Thalassarche*) and petrels (*Daption*, *Pterodroma*). The curvature of the *rostrum maxillare* (Figure 4(g)) is similar (slightly smaller) than that of *Pelecanoides*, *Thalassarche*, *Pachyptyla*, *Puffinus*, and *Halobaena,* and noticeably smaller than that of *Macronectes, Fulmarus,* and *Procellaria*. The distal tip is pointed as in the abovementioned genera, and the entire lateral surfaces are covered by *foramina vascularia* as in *Pagodroma*, *Diomedea*, *Macronectes*, *Daption*, *Fulmarus*, *Pachyptyla*, and many other representatives of the group.

The cristae tomialis are sharp (Figure 4(h)) and subparallel to each other, as in *Thalassarche*, *Puffinus*, and *Pelecanoides*, whereas in *Macronectes*, *Daption*, *Pterodroma*, *Pagodroma, Fulmarus, Halobaena*, *Pachyptila*, and *Oceanites*, the cristae are oblique with respect to each other.

?Diomedeidae indet.

Material. Pedal phalanx without the proximal end (MLP 92-II-2-7) (Figure 4(i) and (j)).

Measurements. Medio-lateral width of diaphysis: 3.3 mm, antero-posterior width of diaphysis: 3.3 mm, distal width: 3.8 mm.

Provenance. Locality DPV 6/84, Seymour (Marambio) Island, Antarctic Peninsula. Cucullaea I Allomember of La Meseta Formation (upper Ypresian).

Comparative description. The pedal phalanx has a long cylindrical diaphysis that maintains the same shape and size along the shaft, so the *facies plantaris* and the *facies dorsalis* are parallel. This is different from pseudo-toothed birds like *Pelagornis*, where the diaphysis is wider at the proximal end, and in most of them, a peculiar swelling is present in the proximal portion (Mayr, Goedert et al. 2013). The *caput phalangis* is rounded and developed almost exclusively toward the plantar side (Figure 4(j)). The *fovea ligamentaris collateralis* is deep and centered in the *caput phalangis*. The *trochlea articularis* is well developed, extending along all the caput and becoming deeper at the distal and plantar areas (Figure 4(i)). It is indistinguishable from the third phalanx of digit III of *Thalassarche* and *Diomedea*, whereas in *Macronectes*, the *caput phalangis* is relatively smaller than in the fossil.

In pelagornithids there is a marked fossa on the plantar surface with a pneumatic opening that is absent in MLP 92-II-2-7. Other small pelagornithids like the middle Eocene *Lutetodontopteryx* have flattened pedal phalanges, a condition not observed in this Antarctic fossil (Mayr & Zvonok 2011; Mayr, Goedert et al. 2013).

?Procellariidae Leach 1820

?Procellariidae indet.
Figures 4(k), (l) and 5

Material. Distal end of ulna (MLP 91-II-4-6) (Figure 4(k) and (l)).

Measurements. Maximum distal width of diaphysis: 8.8 mm, width of diaphysis: 6.1 mm.

Provenance. Locality DPV 6/84, Seymour (Marambio) Island, Antarctic Peninsula. Cucullaea I Allomember of La Meseta Formation (upper Ypresian).

Description. The ulna is intermediate in size between those of *Macronectes* and *Daption* and morphologically very similar to them. The *tuberculum carpale* is well developed, although its tip is broken. *The condylus ventralis ulnare* is latero-medially asymmetric, similar to the condition exhibited by *Daption*, whereas it is symmetric in *Macronectes*. The *condylus dorsalis ulnaris* is equally projected compared to the *ventralis*, as in *Daption* and *Macronectes*. In contrast, in *Diomedea* and *Thalassarche*, the *condylus ventralis* is less distally projected than the *condylus dorsalis* (Figure 4(k) and (l)).

The *incisura tendinosa* is deep and wide, occupying a large area in comparison with modern petrels. The *sulcus intercondylaris* is broad and well marked; its boundaries are rounded (Figure 4(k) and (l)) as in *Daption* and less sharp and extended than in *Diomedea* and *Thalassarche*. The genera *Macronectes*, *Fulmarus* and *Pelecanoides* present an intermediate condition. No direct comparison with the ulnae of *Makahala* was possible, since the distal ends are not preserved in this taxon (Mayr 2015b).

Remarks. This ulna was previously studied by Noriega and Tambussi (1996) in a brief abstract without any illustration. Recently, a picture was included in Tambussi and Degrange (2013), but the material was not described.

Phylogenetic relationships

The present analysis resulted in 252 most parsimonious trees (MPT) of 18,346 steps where all the principal groups described in Livezey and Zusi (2007) were recovered. Among them, Pygopodotubinares and Gaviomorphae, which were not recovered in other analyses and could represent non-natural groups, are fully resolved in all MPTs and related to the specimens scored here. *Notoleptos giglii* and MLP 88-I-1-5 are recovered as sister taxa, with Diomedea as their close relative, as part of the procellariiform radiation (see Figure 6 nodes A, B and C). *Notoleptos giglii* is supported by a single unambiguous autapomorphy, the absence of *impressio (tuberositas) ligamentum collateralis lateralis* in the proximal part of tarsometatarsus (character 2255 in Livezey and Zusi, 2007). Procellariiformes was recovered in 58% of bootstrap replicates and, even with 69 unambiguous apomorphies supporting this node (i.e. present in all MPTs), only two of them are related to the tarsometatarsus bone and therefore coded for *Notoleptos*: the presence in the distal part of the tarsometatarsus of the *facies dorsalis* of the *sulcus musculi extensorius brevis* of the digiti IV, which is sharply defined, with a comparatively deep sulcus located proximal to the *foramen vasculare distale* (character 2328 in Livezey and Zusi, 2007) and the *facies medialis trochlearis* of trochlea metatarsi II ventrally rotated and subperpendicular with respect to main axis (character 2368 in Livezey and Zusi, 2007). In contrast, to the original analysis of Livezey and Zusi (2007), Procellariiformes are supported by nine unambiguous and diagnostic apomorphies (Appendix 3) but none of them is present in the preserved part of *N. giglii*. It is worth noting that we failed to recover any of these characters as an apomorphy for the abovementioned node. This difference, even when the tree topology resolution is the same as in the original analysis, may be the result of treating all characters as unordered in contrast to Livezey and Zusi (2006, 2007), rather than by the incorporation of new taxa.

The present analysis is not decisive about whether *N. giglii* should be considered part of the Diomedeidae, since only one representative of this family is included (i.e. *Diomedea*) in the matrix. But considering the strong resemblance with *Thalassarche*, we tentatively assign it to the family. The preserved parts of the specimen on which *N. giglii* is based constrain the available phylogenetic characters. The analysis of Mayr and Smith (2012) used 53 morphological characters in order to explore procellariiform interrelationships. However, only one of those features could be scored in *N. giglii* (i.e. character 50: the distal end of the tarsometatarsus widened, with trochlea metatarsi IV reaching almost as far distally as trochlea metatarsi III and trochlea metatarsi II only weakly deflected in plantar direction). This character has already been considered since it is partially equivalent to characters 2359 and 2361 of Livezey and Zusi (2007). Incorporating *N. giglii* in the Mayr and Smith (2012) matrix and analyzing it using parsimony failed to obtain non-contradictory MPTs, since the only character for which it could be scored shared its state with most of the taxa. The strict consensus of MPTs is a fully unresolved polytomy except for the Hydrobatidae *Pelagodroma* and *Fregetta,* which are sister taxa.

Discussion

Several skeletal elements of the Procellariiformes have been classically considered similar to those of the Pelagornithidae, but the tarsometatarsus is certainly different. In Procellariiformes this bone is more slender than in Pelagornithidae (see Bourdon et al. 2010), the *sulcus extensorius* extends over the entire diaphysis whereas it is reduced to the proximal third of the shaft in Pelagornithidae, the trochlea metatarsi II is more extended than in the latter, and the *foramen vasculare distale* is relatively smaller. The *crista medianoplantaris* typical of pseudo-tooth birds is not developed in Procellariiformes. *Notoleptos* in particular differs from small-sized pelagornithids like *Lutetodontopteryx* in having the *eminentya intercondylaris* sharp and more elevated, *cotylae medialis* and *lateralis* are dorso-plantarly more compressed, the *sulcus extensorius* wider, the sulcus running proximal to the *incisura intertrochlearis lateralis* (where the *foramen vasculare distale* is located) shallower, and the deflection of trochlea metatarsi IV less marked.

The tarsometatarsus of Procellariiformes is also distinguishable from that of the Prophaethontiformes (see Mayr 2015a), with which they share similarities at other levels, e.g. the humerus. The tarsometatarsus of Prophaethontiformes is sturdier, the *tuberositas m. musculi tibialis cranialis* is more prominent, and the *sulcus extensorius* is shallower than that of the Procellariiformes; the distal extension of trochleae metatarsi II and IV are similar in *Prophaethon*, whereas in Procellariiformes the trochlea metatarsi IV is more distally extended than the second one.

The tentative assignment of *Notoleptos giglii* to Diomedeidae is supported by the following combination of characters: the shaft is dorso-plantarly compressed, the *sulcus extensorius* is deep and limited by similarly developed lateral and medial margins, the *tuberositas m. tibialis cranialis* is barely developed, the trochlear arrangement results in a wider distal end than in the other families, the trochlea metatarsi II projects distally and reaches the middle of the trochlea metatarsi III, and the articular surface of trochlea metatarsi IV is laterally inclined.

The huge size difference with respect to albatrosses precludes the assignment of MLP 12-I-20-305 (holotype of *N. giglii*) to any known species or even genus. Additionally, the combination of characters listed in the diagnosis (e.g. the shape of the *sulcus extensorius* and its boundaries, the relative position of the *foramina vascularia proximalia* and the *foramen vasculare distale*, and the dorsal projections of the metatarsals relative to each other), reinforce the possible assignment to a new taxon, probably within Diomedeidae. This assignment needs to be confirmed by more complete specimens of *Notoleptos giglii* or the identification of new characters in the present specimen. Although morphological differences in the tarsometatarsus of the four extant genera of Diomedeidae were not detected in previous studies (Dyke et al. 2007), the relative position of both *foramina vascularia proximalia* and the location of the *foramen vasculare distale* vary subtly among the genera (see comparative description above). Thus, *Notoleptos* resembles *Thalassarche* in several features but not size. This justifies a tentatively assignment to the family.

Taking into account the traditional discussion around the taxonomic differentiation between *Thalassarche* and *Diomedea*, as well as the lack of consensus regarding the number of species included in each genus (see Penhallurick 2012 for details), *Diomedea* is included in the following discussion about the fossil record.

Diomedea is recorded worldwide during the Neogene. The oldest species of the genus is *Diomedea tanaki* Davis, 2003 from the early Miocene of Japan (Davis 2003). slightly younger remains from the middle and late Miocene of North America (Howard 1926; Miller 1962; Olson 1985; Warheit 2002) and Australia (Wilkinson 1969) are also assigned to this genus. The majority of these fossils correspond to large birds, comparable to living representatives of the group. What is more, all the species of albatrosses recognized so far, including *Tydea sepentrionalis* Mayr and Smith, 2012, are about the size of *Thalassarche melanophris* (Temminck 1828), indicating that albatrosses had already reached large sizes by the Oligocene (Mayr & Smith 2012).

Conclusions

Although the Paleogene record of Procellariiformes is very fragmentary worldwide, the material described here represents enough evidence of their presence since the middle Eocene. In this sense, *Notoleptos giglii* is the oldest ?Diomedeidae reported to date.

The Procellariiformes are relatively well represented in the Eocene of Seymour Island, suggesting that albatrosses and petrels were common Antarctic seabirds (Tambussi & Tonni 1988; Noriega & Tambussi 1996; Tambussi & Degrange 2013). However, they were not the only marine birds in the area: Gaviiformes are recorded from the Cretaceous to the lower Eocene (Chatterjee 2002; Acosta Hospitaleche & Gelfo 2015), Sphenisciformes are known from the upper Paleocene (Tambussi et al. 2005) and have a continuous record through the entire sequence (Acosta Hospitaleche et al. 2013), and Ciconiiformes are recorded by a single element in the middle Eocene (Jadwiszczak et al. 2008). But only the large and giant Pelagornithidae, known from the same levels as the Procellariiformes here described (Acosta Hospitaleche et al. 2014; Cenizo et al. 2015), had a humerus that probably helped to achieve soaring flight comparable to that of albatrosses (Ksepka 2014).

Antarctic fossil procellariiforms are smaller than the living representatives of Diomedeidae, particularly *Notoleptos giglii*. This unexpectedly small size, in comparison with the modern albatrosses that date back to the Oligocene (Mayr & Smith 2012), is shared with the coeval *Murunkus subitus* from central Asia, originally described as a Diomedeidae (Pantelev & Nessov 1987) and later considered as a probable Diomedeididae (Mayr 2015a). However, a more recent analysis has highlighted its differences with *Diomedeides*, making its systematic position uncertain (de Pietri et al. 2010). Unfortunately, *Murunkus* cannot be compare with *Notoleptos*.

Large albatrosses were widespread along marine coasts since the Miocene (and even the Oligocene, considering the assumed primitive *Tydea septentrionalis*). In this context, large size would be a derived feature evolved between the middle Eocene and the Oligocene that quickly spread among albatrosses.

Around 56 Ma ago, the Paleocene – Eocene Thermal Maximum (PETM) (Zachos et al. 2008) resulted in an important rise of the sea level. Particularly, this event is related to the opening of the Drake Passage, an event linked to the final break up of Gondwana, when Antarctica (West Antarctica) and southern South America lost their connection through the Weddellian Isthmus. This land bridge not only prevented the connection between the Pacific and Atlantic oceans, but was also an active causeway for land mammals from the Late Cretaceous (Campanian) until the early Paleogene (Reguero et al. 2014).

Following the time when these events influenced the Antarctic setting, Earth temperatures increased about 6 °C from the late Paleocene through the early Eocene. The highest temperature peak is known as the 'Early Eocene Climatic Optimum' (EECO) and probably generated temperate climatic conditions in Antarctica (Reguero et al. 2013). A warmer climate was propitious for the evolution of small and medium-sized homeotherms such as loons (Acosta Hospitaleche & Gelfo 2015), other seabirds like *N. giglii*, and a wide variety of small and medium-sized land mammals (see list in Reguero et al. 2013), represented by gondwanatherians (i.e. Sudamericidae), marsupials (e.g. Prepidolopidae, Polydolopidae, Microbiotheriidae, Woodburnodontidae, Derorhynchidae) and placentals (e.g. Sparnotheriodontidae, Astrapotheriidae).

The global warming phenomenon related to the EECO may have been a good opportunity for offshore birds to expand their habitat into the sea and occupy vacant niches. This hypothesis is supported by the appearance of considerable penguin diversity in the Eocene (Acosta Hospitaleche et al. 2013). From the late Paleocene to the early Eocene, penguin diversity increased from one to ten species (Jadwiszczak 2006) or perhaps fourteen (Tambussi et al. 2006) in West Antarctica and throughout South America and Australia. Later, these temperate climatic conditions changed and, by the Eocene-Oligocene Transition (EOT) event, global Earth temperatures had drastically dropped, with a cooling effect that affected several groups of animals.

Small procellariiforms like *Notoleptos* could represent an ancestral morph of modern albatrosses that preceded the development of the trend toward large body size. Presently, *Notoleptos* is only known from one broken tarsometatarsus in which the hypotarsus is not preserved, which does not allow a robust test of its phylogenetic position with respect to Diomedeidae. *Notoleptos* could be interpreted as part of an ancient lineage of small-sized albatrosses that evolved in Antarctica during Eocene climate cooling, or it could represent part of a stem group of procellariiforms. As far as the fossil record indicates, the role of large modern albatrosses was occupied at that time by the Pelagornithidae, which had earlier developed a hyper-specialized soaring flight comparable to that of albatrosses (Cenizo et al. 2015).

Facing the imminent environmental cooling during the middle Eocene and until the EOT, an increase of body size would have been favorable with regards to the more adverse climate conditions. The large size of albatrosses could have been positively selected since the Oligocene, compared to the small size of *Notoleptos*. This trend towards increased body size in sea birds could be linked to the development of the specialized sea flight of the group that is so characteristic of modern albatrosses.

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Appendix 1. Comparison material

Diomedea exulans: MLP 14500, RNP-003, RNP-006, RNP-007, RNP-41, RNP-48, RNP-59, RNP-73, RNP-74, RNP-91, RNP-116, RNP-142, RNP-186, RNP-242, RNP-247, RNP-290, RNP-307, RNP-310, RNP-322, RNP-484, RNP-612, RNP-1216, RNP-1282, RNP-1285, RNP-1287, RNP-1362, RNP-1363, RNP-1364, RNP-1367, RNP-1772, RNP-1932, RNP-2010, RNP-2035, RNP-2058, RNP-2085. *Thalassarche melanophris* MLP 14546, MLP 14448, RNP-247, RNP-484, RNP-523, RNP-612, RNP-1216, RNP-1362, RNP-1363, RNP-1364, RNP-1620, RNP-1714, RNP-1772, RNP-1932, RNP-2010. *Pagodroma nivea* 14471. *Pterodroma incerta* MNHN 5864. *Oceanites oceanicus* 14538, 14883. *Pachyptila belcheri* MNHN 5525, RNP A.40. *Pachyptila desolata* MNHN 4121. *Pelecanoides magellani* RNP A.49. *Thalassoica antarctica* RNP A.990. *Puffinus puffinus* MNHN 5665. *Puffinus gravis* MACN 54599. *Puffinus griseus* MANC 54686. *Fulmarus glacialoides* RNP A.392. *Halobaena* RNP A-1737. Procellaria aequinoctialis MNHN 5667. *Daption capense* MACN 53529, MLP 14448, RNP-162, RNP-542, RNP-545, RNP-554, RNP-1742. *Fulmarus glacialoides* MNHN 5666, RNP-34, RNP-37, RNP-160, RNP-161, RNP-250, RNP-288, RNP-392, RNP-395, RNP-737, RNP-1199, RNP-1225, RNP-1254, RNP-1255, RNP-1331, RNP-1349, RNP-1352, RNP-1365, RNP-1437, RNP-1438, RNP-1469, RNP-1752. *Macronectes giganteus* MACN 18251, MACN 26856, MLP 14509, RNP-128, RNP-170, RNP-391, RNP-579, RNP-627, RNP-628, RNP-738, RNP-807, RNP-1122, RNP-1189. *Argyrodyptes microtarsus* MACN A 11037. *Phoebastria* was compared from images published by Dyke et al. (2007), and Olson and Hearty (2003), and *Plotornis delfortrii* from the contribution of Mayr and Smith (2012).

Appendix 2.

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Appendix 3.

Characters and states between brackets of Livezey and Zusi (2007) which are unambiguous and diagnostic apomorphies for Procellariiformes in the present analysis: 195(1), 733(1), 1490(1), 1498(1), 1895(1), 1907(1), 2162(1), 2864(1), 2920(1).