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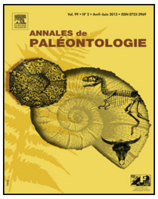

Original article

New Antarctic findings of Upper Cretaceous and lower Eocene loons (Aves: Gaviiformes)

Nouvelles découvertes de plongeons (Aves : Gaviiformes) du Crétacé supérieur et de l'Eocène inférieur d'Antarctique

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A B S T R A C T

The new remains of Gaviiformes collected from the Maastrichtian Sandwich Bluff Member (López de Bertodano Formation in Vega Island), the Maastrichtian Klb 9 (López de Bertodano Formation in Seymour Island), the Maastrichtian Snow Hill Formation (Vega Island), and the Ypresian Submeseta Formation (Seymour Island), Antarctica, are described. A specialized foot-propelled diving morphology is already present in the Antarctic *Polarornis gregorii*, the Chilean *Neogaeornis wetzelli* and the new specimens here reported, suggesting that such diving skills were developed at least since the Upper Cretaceous. The occurrence of Gaviiformes in the Southern Hemisphere during the Upper Cretaceous–lower Eocene times is consistent with recent phylogenetic proposals relating this group to Sphenisciformes and Procellariiformes, birds already recorded in Antarctica. The fossil record also supports the idea that the hemisphere displacement observed in Gaviiformes could be a response to increasing competition for resources with Sphenisciformes. The phylogenetic proximity of penguins and loons plus their similar trophic behavior, suggest that competitive exclusion could have triggered the gaviiform migration to the Northern Hemisphere and explain their extinction from Southern continents.

R É S U M É

Les nouveaux restes de Gaviiformes découverts dans le membre maastrichtien Sandwich Bluff (Formation López de Bertodano dans l'île Vega), le site maastrichtien Klb 9 (López Formation de Bertodano dans l'île Seymour), la Formation maastrichtienne Snow Hill (île Vega), et la formation Yprésienne Submeseta (Île Seymour), Antarctique, sont décrits. Une morphologie spécialisée liée à la propulsion subaquatique par les pieds est déjà présente dans le taxon antarctique *Polarornis gregorii*, le taxon chilien *Neogaeornis wetzelli* et dans les nouveaux spécimens rapportés ici, ce qui suggère que ces aptitudes à la plongée ont été développées au moins au Crétacé supérieur. La présence de Gaviiformes dans l'hémisphère Sud durant l'intervalle Crétacé supérieur–Eocène inférieur est en accord avec les propositions phylogénétiques récentes reliant ce groupe avec les Sphenisciformes et les Procellariiformes, oiseaux déjà enregistrés en Antarctique. Le registre fossile est également cohérent avec l'idée que le changement d'hémisphère observé chez les Gaviiformes pourrait être une réponse à la concurrence croissante pour les ressources avec les Sphenisciformes. La proximité phylogénétique des manchots et des plongeons, ainsi qu'un comportement trophique similaire, suggèrent qu'une exclusion compétitive pourrait avoir déclenché la migration des Gaviiformes dans l'hémisphère Nord et leur extinction sur les continents austraux.

1. Introduction

The Gaviiformes are Neornithes birds represented today by the single genus *Gavia*. Its five species: *Gavia stellata*, *Gavia arctica*,

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Gavia pacifica (considered as subspecies of *G. arctica* in previous arrangements, Carboneras, 1992), *Gavia immer*, and *Gavia adamsii* (Clements et al., 2014) constitute a homogeneous group that occurs exclusively in the Northern Hemisphere. Extant species live close to aquatic environments, breeding in freshwater sites and wintering along marine coasts.

The circumpolar Holarctic occurrence of the group is known from the middle Eocene, through the finding of *Colymbiculus udovichenkoi* Mayr and Zvonok, 2011. Most of the Paleogene record is concentrated in Europe, while the debatable Gaviellinae (Wetmore, 1940) *Gaviella pusilla* (Shufeldt, 1915) comes from the Oligocene of North America (see Mayr, 2004 for details). Recently, a single exception to this Paleogene Holartic distribution was reported in the Eocene of Antarctica at La Meseta Formation (Tambussi et al., 2012). This remain was identified with high degree of certainty as an almost complete coracoid from the lower Eocene locality DPV 6/84 (= RV 8200 of Woodburne and Zinsmeister, 1984) of Marambio (Seymour) Island (Tambussi and Degrange, 2013).

In contrast, during the Cretaceous, the Gaviiformes appear to be restricted to the Southern Hemisphere. An incomplete tarsometatarsus coming from the Upper Cretaceous of Quiriquina Formation in Bahia San Vicente, southern point of Península Tumbes, Concepción province, Chile, was assigned to *Neogaeornis wetzeli* Lambrecht, 1929 (Olson, 1992). As it was the first gaviid found in the Southern Hemisphere, the record was highly questioned. However, the fossil can be undoubtedly assigned to this family due to several specialized characters present in the tarsometatarsus.

Subsequently, an associated partial skeleton was found in the Upper Cretaceous (Unit 9) of López de Bertodano Formation in Marambio (Seymour) Island, Antarctic Peninsula, West Antarctica (Chatterjee, 1989, 2002) and assigned to a new loon species *Polarornis gregorii* (Chatterjee, 2002). *Polarornis* was for many years a controversial taxon (see for example Mayr, 2004) due to its unexpected geographic and temporal record, and its possible synonymy with the Chilean *Neogaeornis wetzeli* (Olson, 1992) was also considered. In independent works, new additional material was referred with doubts to *Polarornis* (Reguero et al., 2013a, 2013b: Fig. 7a–c).

The present contribution is motivated by the finding of new materials assigned to Gaviiformes, from the Upper Cretaceous and lower Eocene of Seymour and Vega Island, Antarctica, and the lack of consensus about the systematic position of *Polarornis*.

2. Geological and geographical setting

New materials here studied were collected from Vega and Marambio (Seymour) islands (Fig. 1). Vega Island is a small island to the northwest of James Ross Island, Antarctic Peninsula. Marambio Island is located at the NE sector of the Antarctic Peninsula, in the Weddell Sea, within the back-arc James Ross Basin (del Valle et al., 1992).

The James Ross Basin comprises three lithostratigraphic groups: the basal Aptian–Coniacian Gustav Group, the intermediate Santonian–Danian Marambio Group, and the upper group, represented by the Paleogene beds of Seymour Island (Rinaldi, 1982; Crame et al., 1991; Riding and Crame, 2002).

The Marambio Group (Rinaldi, 1982) at Vega Island comprises a sequence around 3000 m thick (Olivero, 2012), and includes the following units: Santa Marta (and its equivalent Rabot Formation at the upper part), Snow Hill Island, Haslum Crag, and López de Bertodano formations. The fossil birds were collected at two different localities of Vega Island.

The first fossil site VEG IAA 1-98 (S63°51′34′′, W57°34′18′′) is located in Cape Lamb (Vega Island), where strata assigned to the Sandwich Bluff Member of the López de Bertodano Formation crop out. It consists of near-shore marine deposits (see Crame et al., 1991; Pirrie et al., 1991) correlated with units 8–9 of Montes et al. (2013) of Marambio (Seymour) Island, Antarctic Peninsula.

The second fossil site VEG IAA 2/98 (S63°52′58′′, W57°36′28′′) is also in Cape Lamb (Vega Island), at an outcrop of the Cape Lamb Member of the Snow Hill Formation. Previous Cretaceous avian reports from Vega Island include Gaviiformes (Chatterjee et al., 2006), Charadriiformes (Case and Tambussi, 1999), Anseriformes (Clarke et al., 2005), and an isolated remain originally assigned to Cariamidae (Case et al., 2006) but which undoubtedly corresponds to a foot-propelled diving bird (see Section 5 in Cenizo, 2012).

A third Cretaceous site IAA 11/13 (64° 16′ 18.5′′ S, 56° 43′ 00.9′′ W) is located at Marambio (Seymour) Island. The basal Marambio Group is here formed by the López de Bertodano and the Sobral formations. Avian remains collected at IAA 11/13 come from the Maastrichtian Unit 9 (68–66 Ma) of the López de Bertodano Formation.

Previous findings of Gaviidae in the Cretaceous of Antarctica include two different specimens. The first one, *Polarornis gregorii* (TTU P 9265), was described from a partial skeleton including the skull, four articulated cervical vertebrae, fragmentary sternum, the left femur and a fragment of the right one, and the proximal end of the left tibiotarsus. This material comes from the López de Bertodano Formation on Marambio Island (Chatterjee, 1989). Subsequently, material preliminarily assigned to a smaller species of *Polarornis* from the Late Cretaceous was reported for Vega Island (Chatterjee et al., 2006).

The overlying Seymour Island Group is composed by the Cross Valley, La Meseta and the recently proposed Submeseta formations (Montes et al., 2013). Eocene remains here assigned to Gaviidae were collected in the upper Ypressian DPV 6/84, Cucullaea Allomember (52.8–49 Ma) of La Meseta Formation. From this same level, Pelagornithidae (Acosta Hospitaleche et al., 2014), Procellariiformes (Tambussi and Tonni, 1988), and Falconiformes (Tambussi and Degrange, 2013) have been reported, in addition to an extraordinary and increasing diversity of Spheniscidae represented by eight species already described for La Meseta Formation (Acosta Hospitaleche and Reguero, 2010, 2014).

3. Material and methods

All the materials here described were collected during early summer field trips between years 1998 and 2012 of the Instituto Antártico Argentino (IAA), Dirección Nacional del Antártico (DNA), and are permanently housed at the División Paleontología de Vertebrados, Museo de La Plata (MLP), Argentina. Comparative material belongs to the osteological collections of the divisions of Paleontología Vertebrados (Museo de La Plata) and Ornitología (Museo Argentino de Ciencias Naturales [MACN], Ciudad Autónoma de Buenos Aires), Argentina. Anatomical terminology and criteria for orientation used in the descriptions follow Baumel and Witmer (1993) and Livezey and Zusi (2006).

A phylogenetic analysis based on maximum parsimony was performed with TNT software (Goloboff et al., 2008), adding *Polarornis gregorii* (Appendix 1) from the Maastrichtian of López de Bertodano Formation in Seymour Island, Antarctica (Chatterjee, 2002) to the data matrix of Livezey and Zusi (2006, 2007). All the characters in the original matrix were used and treated as equally weighted and unordered. The search strategy was an heuristic tree search consisting of 10,000 replicates of Wagner trees (using random addition sequences) followed by Tree Bisection Reconnection (TBR) branch swapping (saving 10 trees per replication). The most parsimonious trees found in the replicates were subject to a final round of TBR. All most parsimonious trees were used to calculate a strict

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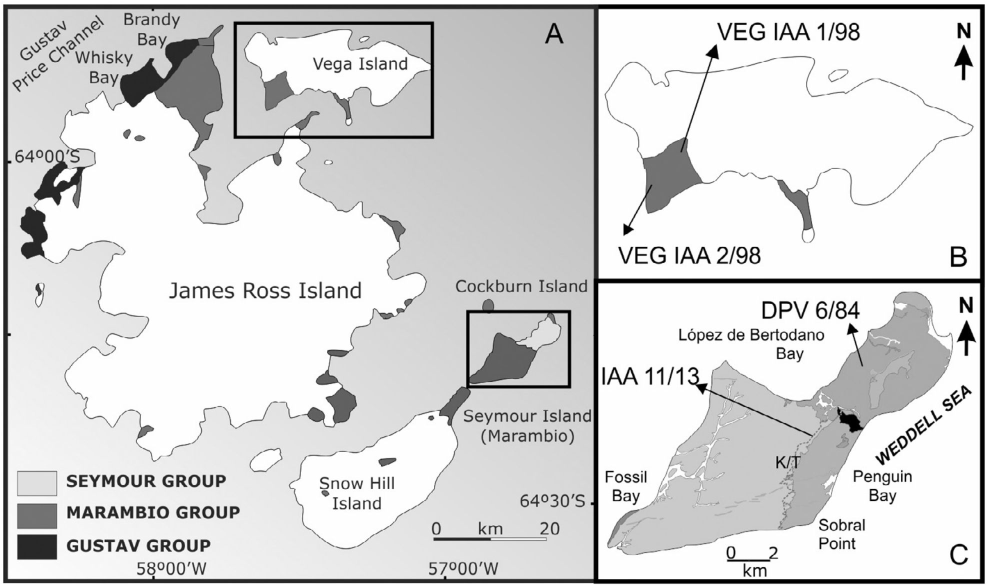

Fig. 1. Location map. Black squares show the islands where fossils remains here studied were collected (A); Cape Lamb in Vega Island: Fossil locality VEG IAA 1-98 where strata of the Sandwich Bluff Member (López de Bertodano Formation) crop out, and fossil locality VEG IAA 2/98 where the Cape Lamb Member (Snow Hill Formation) crops out (B); Seymour (Marambio) Island: fossil locality IAA 11/13 where Unit 9 (López de Bertodano Formation) crops out, and fossil locality DPV 6/84 where Cucullaea Allomember (La Meseta Formation) crops out.

Carte de localisation. Les carrés noirs indiquent les îles où les fossiles étudiés ont été collectés (A) ; Cap Lamb, île Vega : localité VEG IAA 1-98 où les strates du Membre Sandwich Bluff (Formation López de Bertodano) affleurent, et la localité VEG IAA 2/98 où le Membre Cape Lamb (Formation Snow Hill) affleure (B) ; Seymour (Marambio) Island : localité IAA 11/13 où l'Unité 9 (Formation López de Bertodano) affleure, et localité DPV 6/84 où l'Allomembre Cucullaea (Formation La Meseta) affleure.

consensus tree. Absolute and relative Bremer support and bootstrap (with 1000 replications) values were calculated.

Stratigraphic criteria follow Olivero (2012) for Cretaceous, and Montes et al. (2013) and Marenssi et al. (1998) for Paleogene outgroups, respectively.

4. Systematic Paleontology

Class Aves Linnaeus, 1758
Order Gaviiformes Wetmore and Miller, 1926
Genus ***P*olarornis** Chatterjee, 2002

Polarornis sp.
Fig. 2

Material. MLP 96-I-6-2 (incomplete skeleton including diaphysis and distal epiphysis of left femur, proximal end and partial diaphysis of both tibiotarsi, proximal half of right fibula, pedal phalanx).

Provenance. IAA 10/13, Marambio Island (Unit Klb 9, López de Bertodano Formation).

Description. Even though bones are badly preserved, diagnostic characters are conserved in the tibiotarsi and femur that allow definite assignment of the skeleton.

The femur (Fig. 2A–C) preserves most of the diaphysis and the distal epiphysis. In contrast with the condition in other diving birds, the femur is cranio-caudally curved as in all Gaviiformes. It is robust and short, like that of the original description of *Polarornis* (Chatterjee, 2002) although slightly larger. The shaft however, is cranio-caudally curved, even more than in *G. immer* and probably *Polarornis gregorii*. It is oval in transversal section, due to cranio-caudal compression of the diaphysis, as in *Polarornis* and *Gavia*. The convexity of the *facies cranialis* is more pronounced that the concavity of the *facies caudalis*. The *linea intermuscularis cranialis* is barely marked, whereas the *linea intermuscularis caudalis* is stronger, as in *G. immer*. The *sulcus patellaris* is well marked and deepens at its most proximal end, where a fossa develops in the shaft, over the sulcus and its margins. Although the distalmost portion is badly preserved, the *sulcus intercondylaris* seems similar to that of extant species. In all the species compared, the *condylus lateralis* extends distally and caudally further than the *c. medialis* following the same arch of the diaphysis, defining a triangle in both cranial and caudal view. The *trochlea fibularis* is badly preserved, but it appears more rounded than in *G. immer*.

The *fossa poplitea* is laterally displaced, that is to say, not located in the center of the caudal surface. It is deeper and better defined than in *G. immer*, particularly at the lateral and distal borders. The *crista supracondylaris medialis* is weak, as in living species and also *Polarornis*.

Both fragments of tibiotarsi (Fig. 2D–E) represent the same portion, i.e. the proximal end of the shaft. The transversal section of the diaphysis is circular. The *crista cnemialis* is greatly extended, as in all Gaviiformes. The end of the *crista cnemialis cranialis* is broken, but it extends further than the *facies articularis*. In the right tibiotarsus, the *crista cnemialis lateralis* is weaker than the *c. cranialis*, bounding with *sulcus intercnemialis* of similar development along its extension. In the left tibiotarsus, the *sulcus intercnemialis* has a low cranial edge, and the *incisura tibialis* is well marked.

Comparison of the *fossa flexoria* with that of *Polarornis* is unreliable because of the pathological condition occurring in the holotype (see Chatterjee, 2002). However, in the diagnosis of the latter this trait is compared with that of *Gavia immer* and its morphology is stated to be similar, except for the extension of the *crista cnemialis*, which is shorter in the fossil.

The *facies articularis* is inclined caudally; the *facies articularis medialis* is slightly more proximally located than the *facies articularis lateralis*, as in *G. immer*. The *area interarticularis* is acute, mainly at its caudalmost portion. The *tuberositas popliteus* is strong, similar to that of *Gavia*.

The fibula (Fig. 2F) is cranio-caudally wider at its proximal end, the distal part of the *spina fibulae* is missing. The *tuberculum m.*

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Fig. 2. Studied material: A–G. *Polarornis* sp. (MLP 96-I-6-2) left femur in anterior (A), posterior (B), and lateral (C) views; left tibiotarsus in medial (D); right tibiotarsus in lateral view (E), fibula in lateral view (F), pedal phalanx in lateral view (G). Gaviiformes indet. (MLP 98-I-10-47) right tarsometatarsus in cranial (H), caudal (I), and proximal (J) views; (MLP 98-I-10-50) right tarsometatarsus in cranial (K), caudal (L), and proximal (M) views; (MLP 98-1-10-52) left tarsometatarsus in cranial (N), caudal (Ñ), and proximal (O) views; (MLP 98-1-10-76) right tarsometatarsus in cranial (P), caudal (Q), and proximal (R) views; (MLP 98-1-10-51) left femur in caudal (S), cranial (T), and proximal (U) views; (MLP TV del RV) diaphysis and distal end of right tibiotarsus in cranial (V), distal (W), and caudal (X) views; (MLP 98-1-10-48) distal end of tibiotarsus in cranial (Y), and caudal (Z) views. Scale bar: 10 mm.

Matériel étudié : A–G. Polarornis *sp. (MLP-96 I-6-2) fémur gauche en vues antérieure (A), postérieure (B) et latérale (C) ; tibiotarse gauche en vue médiane (D) ; tibiotarse droit en vue latérale (E), péroné en vue latérale (F), phalange podale en vue latérale (G). Gaviiformes indet. (MLP 98-I-10-47) tarsometatarsus droit en vues crâniale (H), caudale (I) et proximale (J) ; (MLP 98-I-10-50) tarsometatarsus droit en vues crâniale (K), caudale (L) et proximale (M); (MLP 98-1-10-52) tarsometatarsus gauche en vues crâniale (N), caudale (Ñ) et proximale (O) ; (MLP 98-1-10-76) tarsometatarsus droit en vue crâniale (P), caudale (Q) et proximale (R) ; (MLP 98-1-10-51) fémur gauche en vue caudale (S), crâniale (T) et proximale (U) ; (MLP TV del RV) diaphyse et extrémité distale de tibiotarse droit en vues crâniale (V), distale (W) et caudale (X) ; (MLP 98-1-10-48) extrémité distale de tibiotarse en vues crâniale (Y) et caudale (Z). Barre d'échelle : 10 mm.*

iliofibularis is weak, as in *G. immer* and the *caput fibula* is elongate. The *facies articularis femoralis* is slightly concave. A conspicuous *fossa m. poplitea* is represented by a deep depression continuous with a wide and shallow sulcus that extends parallel to the main axis of the fibula.

The corpus of the phalanx (Fig. 2G) is cylindrical and its distal end is laterally compressed, missing the most proximal end. The *fovea subtrochlearis* is shallow, and the *trochleae articularis* are rounded in lateral view.

Remarks. These remains were found in a concretion that was previously figured in Reguero et al. (2013a) without an accompanying description. These authors only mentioned the tibiotarsi and femur, but after technical preparation new elements (i.e. fibula and a pedal phalanx) were recovered from the concretion. Reguero et al., (2013a, 2013b) mentioned under the same repository number, a metatarsal, which was tentatively assigned to a Hadrosaurine dinosaur, although MLP 96-I-6-2 undoubtedly belongs to the avian skeleton here described.

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Gaviiformes indet.

Material. MLP 98-I-10-47: incomplete tarsometatarsus.

Provenance. VEG IAA 2/98, Isla Vega (Cape Lamb Member, Snow Hill Formation).

Description. The bone is preserved in two parts (Fig. 2H–J), and is very similar to that of *Gavia immer*. The tarsometatarsus is extremely narrow, and both lateral and medial edges are sharp at the cranial face (the lateral edge constitutes a more cranially elevated rib). These two edges limit a wide central *sulcus extensorius* housing a weak *tuberositas m. tibialis cranialis*. Distally, the sulcus extensorius becomes narrower and shallower than in *Gavia immer*. Both *foramina vascularia proximalia* open cranially. The lateral foramen is somewhat larger and more distally located that the medialis foramen. Differences in size between both foramina are more accentuated in extant species, in which the *foramen vasculare proximale medialis* is less than half of the size of the *foramen lateralis*.

The *foramen vasculare distale* does not open in the preserved portion of the bone. The *cotyla lateralis* leans toward the cranial face. The *eminentia intercotylaris* is rounded, and the *cotyla medialis* seems further extended toward the diaphysis, although this part is not completely preserved. The *area intercotylaris* is not so well delimited and a robust *hypotarsus* is badly preserved. Although the hypotarsal cristae are broken, their bases are still present implying a probable hypotarsal canal. The *crista hypotarsalis medialis* is better preserved and extends distally with respect to both *foramina vascularia proximalia*.

The *crista hypotarsalis intermedia* extends proximally reaching the *area intercotylaris*, as in *Gavia immer*. The two furrows present at the sides of the *crista intermedia hypotarsi* in *G. immer* are not evident in MLP 98-I-10-47. The *foramina vascularia proximalia* open cranially at both sides of the *hypotarsus*.

The bases of the three trochleae are preserved in the distal portion. Trochlea II is slightly extended distally, but very caudally projected. Trochlea III is the most cranially located, and it is not centered respect to the diaphysis. Trochlea IV is cranio-caudally intermediate between trochlea II and III, although closer to the latter.

Material. MLP 98-I-10-50: incomplete right tarsometatarsus (Fig. 2K–M), MLP 98-I-10-52: incomplete left tarsometatarsus (Fig. 2N–O), MLP 98-I-10-76: incomplete right tarsometatarsus (Fig. 2P–R).

Provenance. VEG IAA 2/98, Isla Vega (Cape Lamb Member, Snow Hill Formation).

Description. The three fossils are similar. Each one is a little smaller than the corresponding bones of *Gavia immer*. Although the preserved portion is a fragment, the relative configuration of the trochleae permits its systematic assignment. Trochlea II is strongly projected caudally, as in all Gaviiformes.

The *foramen vasculare distale* is developed in MLP 98-I-10-52 and MLP 98-I-10-76, whereas it is not visible in the preserved portion of MLP 98-I-10-50 (Fig. 2K–M). A deep narrow furrow runs distally to this foramen, which in *Gavia immer* ends in a small foramen cranially to the trochlear divergence.

Material. MLP 98-I-10-51: proximal end of left femur (Fig. 2S–T).

Provenance: VEG IAA 2/98, Isla Vega (Cape Lamb Member, Snow Hill Formation).

Description. It is cranio-caudally compressed, and a little smaller than that of *Gavia immer*. The transversal section is exposed and seems to be more circular than in *Polarornis gregorii* (Chatterjee, 2002), in which the section is oval.

The *fovea ligamentaris capitis* is deep and cranially oriented. The *facies articularis antitrochanterica* is flat as in *Polarornis*, whereas it is slightly more concave in *G. immer*. The *impressiones obturatoriae* are arranged in parallel with respect to the diaphysis.

Material. MLP 12-I-20-304: distal end of right tibiotarsus (Fig. 2V–W).

Provenance. DPV 6/84, Marambio Island (Cucullaea Allomember, La Meseta Formation).

Description. The general morphology is reminiscent of *Colymbiculus udovichenkoi* Mayr and Zvonok (2011, 2012) from the Lutetian (middle Eocene) of Ukraine. The diaphysis is strongly cranio-caudally compressed and the condyla are aligned with the axis. As in *Colymbiculus*, it is notably smaller than in the living species, and similar to that of *Gavia immer*; the *sulcus extensorius* is centrally positioned as in all Gaviiformes, and partially covered by the *pons supratendineus*. Both *sulcus extensorius* and *pons supratendineus* are proportionally larger in *Colymbiculus* and MLP 12-I-20-304 than in *G. immer*. The *condyla mediale* and *laterale* are more rounded but less massive than in extant species. The *sulcus patellaris* is strikingly shallow, a feature consistent with the poor development of the condylar edges.

Material. MLP 98-I-10-48 (distal end of left tibiotarsus).

Provenance. VEG IAA 1/98, Isla Vega (Sandwich Bluff Member, López de Bertodano Formation).

Description. The fossil is larger than *Gavia immer*, and the *pons supratendineus* is broader and oblique. The *sulcus extensorius* is broad and centered as is typical of Gaviiformes. None of the *condyla* are preserved. The *trochlea cartilaginis tibialis* is broad and the *tuberculum retinaculi m. fibularis* is rounded and well developed. The transversal section of the diaphysis is exposed; it is cranially concave and caudally convex.

Material. MLP 95-I-10-14: coracoid (Fig. 3A).

Provenance. DPV 6/84, Marambio Island (Cucullaea Allomember, La Meseta Formation).

Description. We provide here a supplementary description of this material previously studied by Tambussi and Degrange (2013). Its overall morphology is reminiscent of *Gavia immer*, although MLP 95-I-10-14 is smaller.

The *impressio lig. acrocoracohumeralis* is visible, the *facies articularis humeralis* is flat and greatly extended, mainly at the level of the *cotyla scapularis*. The *cotyla scapularis* is oval (described as subtriangular in Tambussi and Degrange, 2013) and strongly concave. The *processus procoracoideus* is broad and complete except for the medial edge. Even though the *incisura n. supracoracoidei* was previously described as inconspicuous, there is a *foramen n. supracoracoidei* located in the same position as in *G. immer* opening in both *facies ventralis* and *dorsalis*. The omal end is broken and the *facies articularis clavicularis* is missing.

Although the *facies articularis sternalis* is broken, the preserved part is broad, with its ventral margin more convex than in *G. immer*. The *angulus medialis* is complete, whereas the *processus lateralis* is missing. The *impressio m. stercoracoidei* occupies a shallow and extended area with indistinct boundaries.

Material. MLP 98-I-10-60 and MLP 98-I-10-61: distal end and partial corpus of pedal phalanges (Fig. 3B–C respectively).

Provenance. VEG IAA 2/98, Isla Vega (Cape Lamb Member, Snow Hills Formation).

Description. Both fossils are slender in comparison with phalanges belonging to other groups of birds, and very similar to those of *Gavia immer*. Phalanges of Anseriformes and Charadriiformes, recorded in these levels, are notably more robust and less

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Fig. 3. Studied material: (MLP 98-I-10-50) coracoid in dorsal view (A); (MLP 98-I-10-60) pedal phalanx in dorsal view (B); (MLP 98-I-10-61) pedal phalanx in dorsal view (C); (MLP 98-I-10-59) diaphysis of tibiotarsus in cranial view (D); (MLP 98-I-10-54) incomplete left tarsometatarsus in cranial (E), caudal (F), and distal (G) views; (MLP 98-I-10-27) incomplete right tarsometatarsus in cranial (H), proximal (I), and caudal (J) views; (MLP 98-I-10-53) distal end of left tibiotarsus in cranial (K) and caudal (L) views; (MLP 13-XI-28-42) diaphysis and distal end of right tibiotarsus in cranial view (M); (MLP 98-I-10-49) distal end of right tibiotarsus in cranial (N) and caudal (Ñ) views; (MLP 00-I-10-1) pedal phalanx in cranial view (O). Scale bar: 10 mm (except in D: 15 mm).

Matériel étudié : (MLP 98-I-10-50) coracoïde en vue dorsale (A); (MLP 98-I-10-60) phalange podale en vue dorsale (B) ; (MLP 98-I-10-61) phalange podale en vue dorsale (C) ; (MLP 98-I-10-59) diaphyse de tibiotarse en vue crânial (D) ; (MLP 98-I-10-54) tarsometatarsus incomplet gauche en vues crâniale (E), caudale (F) et distale (G) ; (MLP 98-I-10-27) tarsometatarsus droit incomplet en vue crâniale (H), proximale (I) et caudale (J) ; (MLP 98-I-10-53) extrémité distale de tibiotarse gauche en vue crâniale (K) et caudale (L) ; (MLP 13-XI-28-42) diaphyse et extrémité distale de tibiotarse droit en vue crâniale (M) ; (MLP 98-I-10-49) extrémité distale de tibiotarse droit en vue crâniale (N) et caudale (N) ; (MLP 00-I-10-1) phalange podale en vue crâniale (O). Barre d'échelle : 10 mm (à l'exception de D : 15 mm).

compressed. Each phalanx is laterally compressed, the *corpus* is cylindrical, the *fovea subtrochlearis* is shallow, and the *trochleae articularis* are rounded in lateral view. MLP 98-I-10-60 preserves the longest portion of the corpus, whereas MLP 98-I-10-61 is badly damaged and preserves a minor portion. None of them allow assignment to a specific digit.

Material. MLP 98-I-10-59: diaphysis of left tibiotarsus (Fig. 3D).

Provenance. VEG IAA 1/98, Isla Vega (Sandwich Bluff Member, López de Bertodano Formation).

Description. The shaft is slender and craniocaudally flattened around its middle. The general morphology and size are consistent with those of Gaviiformes. At the distal end its caudal surface is convex, while the cranial one is flat. The *crista cnemialis lateralis* is expanded as in *Gavia immer*, and the distalmost edge is cranially recurved.

cf. Gaviiformes

Material. MLP 98-I-10-54: incomplete left tarsometarsus (Fig. 3E–G), MLP 98-I-10-27: incomplete right tarsometatarsus (Fig. 3H–J).

Provenance. VEG IAA 2/98, Isla Vega (Cape Lamb Member, Snow Hill Formation).

Description. These elements are slightly smaller than the tarsometatarsi described above. The bases of the trochleae are preserved with a small portion of the diaphysis, but the trochlear configuration is not so evident in the preserved portion. The *foramen vasculare distale* is not visible in these remains. They are strongly similar to Gaviiformes due to the strong latero-medial compression of the diaphysis and the ridges on the cranial face.

Material. MLP 98-I-10-53: distal end of left tibiotarsus (Fig. 3K–L).

Provenance. VEG IAA 2/98, Isla Vega (Cape Lamb Member, Snow Hills Formation).

Description. The general morphology of the *sulcus extensorius* is indistinguishable from that of Gaviiformes, in which it is broad and latero-medially centered. However, it is broken at that region and the *pons supratendineus*. The caudal surface of the diaphysis is convex and the preserved portion of the *trochlea cartilaginis tibialis* is flat, although the cristae trochlearis are broken and thus the margins of this structure cannot be recognized.

Material. MLP 13-XI-28-42 diaphysis and distal end of right tibiotarsus (Fig. 3M).

Provenance. DPV 6/84, Marambio Island (Cucullaea Allomember, La Meseta Formation).

Description. This fossil is slightly smaller than the extant *Gavia immer*. The diaphysis is craniocaudally compressed and oval in

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transversal section. The *facies cranialis* is flat and the *facies caudalis* is convex. The *sulcus extensorius* is less pronounced and the *pons supratendineus* is notably broader and slightly oblique. However, the distal epiphysis is medially inclined as in all Gaviiformes. The *canalis extensorius* is more rounded than in *G. immer*. The preserved portion of the *condylus medialis* is not enough to determine its shape.

Material. MLP 98-I-10-49 distal end of right tibiotarsus (Fig. 3N–Ñ).

Provenance. VEG IAA 2/98, Isla Vega (Cape Lamb Member, Snow Hills Formation).

Description. It is badly preserved, but certain features resemble MLP 98-I-10-48 described above. It is larger than *Gavia immer*, the *sulcus extensorius* is broad and centered, and the diaphysis is cranially concave and caudally convex.

Material. MLP 00-I-10-1 pedal phalanx (Fig. 3O).

Provenance. IAA 10/13, Marambio Island (Unit Klb 9, López de Bertodano Formation).

Description. The corpus is cylindrical and the distal end is laterally compressed. The *fovea subtrochlearis* is slightly deeper than in *Gavia immer*. The margins of the *caput phalangis* are ventrally more developed, with right and left borders unequally extended. The *trochleae articularis* are rounded in lateral view, similar to MLP 98-I-10-60 and MLP 98-I-10-61 described above.

5. Discussion

Polarornis and *Neogaeornis* are almost universally interpreted as modern loons (e.g., Chiappe, 1996; Dingus and Rowe, 1998 in Van Tuinen and Hedges, 2004; Padian and Chiappe, 1998; Hope, 2002) and have even been used for molecular clock calibrations (Cooper and Penny, 1997). However, they have not always been completely accepted as part of the Gaviidae and several authors have made different criticisms to this assignation. Van Tuinen and Hedges (2004) suggest that 70 m.y. "loons" as the crown group of Gaviidae would be a problem regarding the origin of modern bird orders, since molecular data would indicate a Precambrian origin. They proposed instead to consider *Polarornis* and *Neogaeornis* as convergent to the Gaviidae, and assumed that these taxa are neognathous foot-propelled diving birds close to the base of stem Ciconiiformes. These authors identified a problem in the molecular clock calibrations, but did not solve it; instead, they eliminated the conflictive taxa and relocated them into a different avian group. This does not represent a systematic argument that could be used to invalidate a taxonomic assignation.

For other authors, *Neogaeornis* might be a junior synonym of *Polarornis* (Mayr, 2004, 2009); even *Vegavis* from the Late Cretaceous of Vega Island in West Antarctica (Clarke et al., 2005) was considered to have a strong similarity with *Polarornis* (Mayr and Scofield, 2014).

The phylogenetic position of *Polarornis* has already been tested in a phylogenetic analysis that included 52 cranial and postcranial characters from nine taxa, and whose results indicated a close relationship to Gaviidae (Chatterjee, 2002). Here we performed a new parsimony analysis of the matrix of Livezey and Zusi (2006, 2007) using the 2954 characters and the 189 taxa in order to test the relationships of *Polarornis* (Appendix 1). Our analysis resulted in 252 most parsimonious trees (L:18364). The strict consensus tree (L:18551) recovered the same clades that were present in the original analysis of Livezey and Zusi (2006, 2007). *Polarornis* was more closely related to *Gavia* than to any other taxa included in the analysis. The node Gaviidae, which reinforces the assignation of *Polarornis* to Gaviidae as proposed by Chatterjee (2002) is supported here by six synapomorphies (Table 1) and was recovered in 95% of the bootstrap replicates (Fig. 4). Gaviomorphae (grebes and loons) which was suggested by Mayr and Clarke (2003) and defined by Livezey and Zusi (2007) is also well supported (Fig. 4; Table 1).

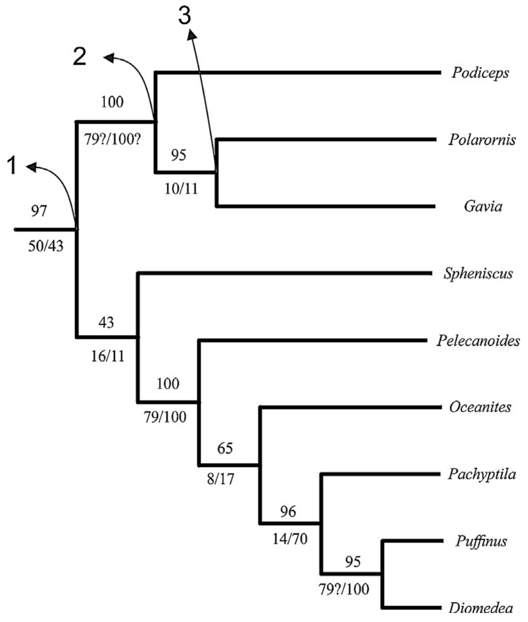

Fig. 4. Detailed segment of the node Gaviomorphae from the strict consensus tree of 252 MPT recovered in the analysis. Nodes are labelled above by percentages of bootstrap and below by Bremer support (absolute/relative). Nodes of Livezey and Zusi (2007) in the tree are: 1. Pygopodotubinares. 2. Gaviomorphae. 3. Gaviidae.
Partie détaillée du nœud Gaviomorphae de l'arbre de consensus strict de 252 MPT issu de l'analyse. Aux nœuds, les valeurs correspondent en haut aux valeurs de bootstrap et en bas aux indices de Bremer (absolus/relatifs). Les nœuds de Livezey et Zusi (2007) dans l'arbre sont : 1. Pygopodotubinares. 2. Gaviomorphae. 3. Gaviidae.

The phylogenetic analysis here presented supports the assignation of *Polarornis* to Gaviidae, and the material here described undoubtedly confirms the presence of Gaviiformes in West Antarctica during the Late Cretaceous- early Eocene span. Their occurrence in the Southern Hemisphere is consistent with recent phylogenetic proposals, which relate this group with Sphenisciformes and Procellariiformes, birds already recorded in Antarctica. The oldest penguin species have been found in the Paleocene of New Zealand (Slack et al., 2006) and Antarctica (Tambussi et al., 2005), and a high diversity of species is recorded during the Eocene in Antarctica (Acosta Hospitaleche et al., 2013). Procellariiformes are also recorded during the early Eocene in Antarctica, from the same levels as Gaviiformes and Sphenisciformes, representing some of the earliest records for the group.

The highly specialized locomotor habit of Gaviiformes has its correlate in their skeletal anatomy, especially in the morphology of hindlimb elements. The following distinctive features make their systematic determination reliable, even considering the incompleteness of the remains: cranio-caudal compression, curvature of the shaft and deep *fovea ligamentaris capitis* in the femur, cranio-caudal compression of the diaphysis, broad *sulcus extensorius*, and presence of a *pons supratendineus* in the tibiotarsus, and latero-medial compression, well-developed *hypotarsus*, trochlear arrangement and relative extension in the tarsometatarsus. In addition, in regards to the tibiotarsus, the specimen MLP 96-I-6-2 here described confirms the morphology characteristic of *Polarornis*, which was originally based on a single specimen with a pathological condition that obscures some features (Chatterjee, 2002). At the same time, these derived characters differentiate them from other early Neornithes recorded in the Late Cretaceous of Antarctica, such

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Table 1
Apomorphic characters, character states and CI following descriptions of Livezey and Zusi (2006).
Caractères apomorphes, états de caractères et CI d'après les descriptions de Livezey et Zusi (2006).

Node	Apomorphic characters: state	CI	Character description/state
Gaviidae	57: 0	0.09	Fossa cerebelli, crista marginalis cerebelli, planum transversus cristae—perpendicular to planum transversus ossis parasphenoidale, ostium pharyngeale et os basioccipitale, fossa subcondylaris—relative to area enclosed by canalis semicircularis anterior,situs rostrocaudalis/Rostral
	120: 0	1	Os parasphenoidale, ala parasphenoidalis, fossa parabasalis, crista fossae parabasalis, status et forma/Absent, resulting in hiatus subtympanicus
	519: 1	1	Os quadratum, processus mandibularis quadrati, condylus medialis, dorsoventral position relative to os quadratum, processus mandibularis, condylus lateralis (caudal perspective), normal to planum defined by condylus occipitalis and margo rostralis of lamina parasphenoidalis, angulus/Coplanar or dorsal
	569: 0	0.13	Sutura nasomaxillaris externa, status modalis definitivum/Present and distinct
	1117: 0	0.16	Corpus sterni, margo costalis sterni, processus articularis sternocostalis et loculus costalis sterni, numerus modalis per latus/Two
	2002: 2	0.5	Corpus femoris, forma areae transversa/Distinctly oval, craniocaudally compressed

as Charadriiformes (Case and Tambussi, 1999) and Anseriformes (Clarke et al., 2005).

Recent studies have reached an agreement regarding explaining the similarities between foot-propelled Hesperornithiformes, Gaviiformes and Podicipediformes (Olson, 1992) as convergences. The Gaviiformes are more closely related to Sphenisciformes and Procellariiformes, than to Hesperornithiformes (Mayr, 2004; Slack et al., 2006; Jarvis et al., 2014, see also Smith, 2010 for relationships between Gaviiformes and Podicipediformes).

Although very similar regarding its hindlimb skeletal morphology, the tarsometatarsus of Gaviiformes differs from that of Podicipediformes in having a more latero-medially compressed shaft with the lateral side developed like a crest at the proximal end, narrower trochlea, more proximal base of the trochlea II, and trochlea III extended further than trochlea IV. This element in Gaviiformes also differs from that of Hesperornithiformes by having a well-developed *hypotarsus* and a more gracile and latero-medially compressed tarsometatarsus. Concerning the tibiotarsus, the Gaviiformes differ from Hesperornithiformes by the presence of a *pons supratendineus* covering the centered and broad *canalis extensorius*. Unlike the condition in Podicipediformes, Gaviiformes have a *sulcus extensorius* that is broader and more extended proximally, a narrower *condyla* (which is more rounded in Podicipediformes), and a shallower and more extended *trochlea cartilaginis tibialis*. In the femur, Gaviiformes can be distinguished from Podicipediformes by the cranio-caudally compression and strongly curved shaft. The order also differs from Hesperonithiformes in the extreme curvature of the femur, and its lesser robusticity.

Modern species of *Gavia* breed at freshwater sites, but winter along temperate sea coasts (Carboneras, 1992). They are expert divers, and spend most of their lives in water. The trochlear configuration of their tarsometatarsi is a clear indicative of this strongly adapted foot-propelled diving style. The Paleogene Holarctic species exhibit a similar adaptation; they probably inhabited limnic subtropical environments (Mayr, 2009).

Although not specialized, this morphology is already present in the oldest known species (the Chilean *Neogaeornis wetzelli* and the Antarctic *Polarornis gregorii*), suggesting that underwater skills had evolved by at least the Late Cretaceous. The Antarctic Gaviiformes described here present similarly adapted bones. The femur seems a little less compressed than in the Cretaceous *Polarornis gregorii* (see Chatterjee, 2002), and the cnemial crests of the tibiotarsus are not as extended in comparison with the living relatives.

The Gaviiformes reported here come from the Maastrichtian Sandwich Bluff Member (López de Bertodano Formation in Vega Island), the Maastrichtian Klb 9 (López de Bertodano Formation in Seymour Island), the Maastrichtian Snow Hill Formation (Vega Island), and the Ypressian Submeseta Formation (Seymour Island).

The Sandwich Bluff Member (López de Bertodano Formation) in Vega Island represents a proximal nearshore paleoenvironment (Roberts et al., 2014). The fossil birds found in these levels, including all specimens of Gaviiformes and *Vegavis*, are foot- propelled diving birds. What is more, the re-assignment as a diving bird (Cenizo, 2012) of the material described by Case et al. (2006) as a Cariamidae, lends ecological homogeneity to this avian assemblage, consistent with a shallow marine environment.

The Klb unit 9 of López de Bertodano Formation in Seymour (Marambio) Island represents the deepest or most offshore facies of the Seymour Island Group (Macellari, 1988). The holotype of *Polarornis gregorii* comes from these same levels (Chatterjee, 2002).

The Cape Lamb Member (Snow Hill Formation) in Vega Island represents a shallow marine mid-outer shelf (Roberts et al., 2014). The birds described here include Gaviiformes and Charadriiformes that have only been mentioned within short abstracts (Case and Tambussi, 1999; Cordes, 2002), representing an assemblage of seabirds adapted to coastal environments.

The Antarctic Neornithes became more diverse in the Eocene record of Antarctica. Previous reports include Ciconiiformes,?Ratites (known from a single, weathered, and badly preserved fragment of dubious assignment, see Tambussi et al., 1994), Charadriiformes, Phoenicopteridae, and particularly from the *Cucullaea* Allomember (where Gaviiformes were collected) Falconiformes, Procellariidae, Diomedeidae, Pelagornithidae, and Sphenisciformes (Reguero et al., 2013a, 2013b). The Cucullaea Allomember is interpreted as a valley-confined estuary mouth to inner estuary complex (Marenssi et al., 2002). Besides that, three avian ichnotaxa were distinguished in the Fossil Hill Formation (lower to middle Eocene) at Fildes Peninsula, King George Island, previously identified as possible Ratites or phororhacoids, and Anseriformes (Mansilla et al., 2012 and references cited there).

The fossil record suggests that the Neornithes were a successful group in Antarctica, represented by several marine lineages. The Gaviiformes known from the Late Cretaceous of Vega and Marambio islands, probably survived there until the Eocene, and then dispersed to the Northern Hemisphere, where a more abundant fossil record and all living species are represented. The extinct Hesperornithiformes had left an available ecological niche that could easily be occupied by Gaviiformes, whereas in the Southern Hemisphere, penguins represented major competitors, leading to niche overlapping (Chatterjee, 2002). The fossil record is consistent with the idea that the hemisphere shift of Gaviiformes could be a response to the increasing competition for resources with penguins. An important cladogenetic event led to an increasing number of penguin species during the Paleogene (*i.e.* a single Antarctic species is known from the Paleocene, whereas ten to fourteen species have been described from the Eocene) in

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contrast to the scarce known gaviiform taxa including the specimens here described. The phylogenetic proximity of both orders plus their similar trophic behavior suggest that competitive exclusion could have triggered the northward migration of gaviiforms and their extinction in Southern continents. Gaviiformes could have competed for ecological resources again in the early Miocene. The disappearance of small loons seems to be synchronous with the occurrence of the strongly convergent Podicipediformes in Europe. However, evidence is not enough to draw a reliable conclusion (see Mayr and Zvonok, 2011).

In any case, Antarctica has played a key role in the origin and diversification of diverse groups of birds, particularly those related to marine environments. Current and future findings will advance our understanding of the relationship between diving birds and other marine taxa, as well as allow contrasting paleoecological and paleobiogeographic hypotheses.

Disclosure of interest

The authors declare that they have no competing interest.

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Appendix 1. Character states of *Polarornis gregorii*, following character descriptions in Livezey and Zusi (2006)

États de caractères de Polarornis gregorii, d'après les descriptions de caractères de Livezey et Zusi (2006).

*Polarornis:*141?10111?2100?10?12120100001100100120?0??1??0?000??101001000100??00?1011001???1?????????1110000000?00?1?00????????00010000???0000?1101?10002??1010?02001000?0??0?00201?0000?0001?2?11111100000200200001200100001110?11??1?20011????1102?12?1????10001010?0?0000?000010?0?0010010?0010000000000?0000010001?0000000010?10?11?????????????????000010000010000000?0000000?10??10010021?1?0101?0000110130000000012020001?001?0?000000?02121000000100000000?0000020?00?????????????110?????????10101002?12?0000100???01??10?00?020003001200010211?01220110000202001100??22200000000100000?100?0?01000110????1000?201?0?????0221?20411??1?00000??0000??0??????????0???0?00000000???3?????????????????????????????????????1??0?2100000000??000?010000200????????????10000000???010???212110100100100202512?42??21?02012?112201100?000031?11001?0?2000?1100020?2?01001?0000??????01????????0?10010000113000001??003000?00000?0000040??0??10?00100020?01000??00?1100???????????0??

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