New mammalian and avian records from the late Eocene La Meseta Formation of Seymour Island, Antarctica

Sarah N. Davis,[1] Christopher R. Torres,[1,2] Grace M. Musser,[1] James V. Proffitt,[1,3] Nicholas M. A. Crouch,[1] Ernest L. Lundelius,[1] Matthew C. Lamanna,[4] and Julia A. Clarke[1]

1. Department of Geological Sciences, Jackson School of Geosciences, The University of Texas at Austin, Austin, Texas 78712, USA;
2. Department of Integrative Biology, The University of Texas at Austin, Austin, Texas 78712, USA;
3. School of Medicine, The University of Missouri, Columbia, Missouri 65212, USA;
4. Section of Vertebrate Paleontology, Carnegie Museum of Natural History, 4400 Forbes Avenue, Pittsburgh, Pennsylvania 15213, USA

Corresponding Author:
Sarah Davis[1]
Department of Geological Sciences, Jackson School of Geosciences, The University of Texas at Austin, Austin, Texas 78712, USA
Email address: sdavis6@utexas.edu

Abstract

The middle-late Eocene of Antarctica was characterized by dramatic change as the continent became isolated from the other southern landmasses and the Antarctic Circumpolar Current formed. These events were crucial to the formation of the permanent Antarctic ice cap, affecting both regional and global climate change. Our best insight into how life in the high latitudes responded to this climatic shift is provided by the fossil record from Seymour Island, near the eastern coast of the Antarctic Peninsula. While extensive collections have been made from the La Meseta Formation of this island, few avian taxa other than penguins have been described and postcranial mammalian remains have been scarce. Here, we report new fossils from Seymour Island collected by the Antarctic Peninsula Paleontology Project. These include a mammalian metapodial referred to Xenarthra and avian material including a partial tarsometatarsus referred to Gruiformes (cranes, rails, and allies). Penguin fossils (Sphenisciformes) continue to be most abundant in new collections from these deposits. We report several penguin remains including a large spear-like mandible preserving the symphysis, a nearly complete tarsometatarsus with similarities to the large penguin clade *Palaeeudyptes* but possibly representing a new species, and two small partial tarsometatarsi similar to those of *Delphinornis*. These finds expand our view of Eocene vertebrate faunas on Antarctica. Specifically, the new remains referred to Gruiformes and Xenarthra provide support for previously proposed, but contentious, earliest occurrence records of these clades on the continent.

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Introduction

The Southern Hemisphere biota has been profoundly influenced by Mesozoic-Cenozoic continental breakup and climatic change. Before its fragmentation, the supercontinent Gondwana facilitated dispersal of terrestrial organisms between now-separated southern landmasses (Keast, 1972; Cracraft, 1973; Ali and Krause, 2011; Claramunt and Cracraft, 2015). Early discoveries suggest that Antarctica was central to this pattern of terrestrial movement, acting as a bridge between what is now South America and Australia (Woodburne and Zinsmeister, 1984; Zinsmeister, 1986). This widespread dispersal ended with the final breakup of Gondwana (Reguero et al., 2014, and reviewed by Torsvik and Cocks, 2013). Through the last part of this breakup, the Antarctic climate shifted from being warm and seasonally wet to increased periods of ice cover by the early to middle Eocene (Poole et al., 2001; Ivany et al., 2011; Jacques et al., 2014); by the earliest Oligocene (~33.9 Ma) Antarctica experienced complete glaciation (Zachos et al., 2001; Birkenmajer et al., 2004; Ivany et al., 2006; Barker et al., 2007).

Insights into how the Antarctic biota was shaped by tectonic and climatic shifts have come from the ~~Upper~~ upper Eocene La Meseta Formation on Seymour Island (Marambio Island), the best-studied fossil vertebrate fauna from Antarctica (e.g., Reguero et al., 2002; 2014). This assemblage has been proposed to most closely resemble contemporaneous faunas from Patagonia (Reguero et al., 2002) which were separated from what is now the Antarctic Peninsula by the flooding of the Weddellian Isthmus at the end of the Paleocene (Eagles and Jokat, 2014; Reguero et al., 2014). The fossil record of the La Meseta Formation is famously dominated by stem penguins, including some of the tallest penguins that ever lived (Tambussi et al., 2006; Jadwiszczak, 2006; Tambussi and Acosta Hospitaleche, 2007; Jadwiszczak et al., 2013; Acosta Hospitaleche and Reguero, 2014; Jadwiszczak and Mörs, 2019). The non-penguin vertebrate

fossil record mostly comprises isolated teeth and bones representing an array of marsupial, gondwanathere, ungulate, cetacean, and other eutherian mammals (see reviews by Marenssi et al., 1994; Reguero et al., 2002; Reguero and Gasparini, 2006; Case, 2006; Buono et al. 2016; Gelfo et al. 2017) as well as non-penguin birds (e.g., Tambussi and Acosta Hospitaleche, 2007; Jadwiszczak et al., 2008; Tambussi and Degrange, 2013; Acosta-Hostpitaleche and Gelfo, 2017). Here we report additional mammalian and avian specimens recovered from Antarctica by the 2016 Antarctic Paleontology Project (AP3), including gruoid and xenarthran fossils, and discuss their biogeographic implications.

Geologic setting

The fossils here described were collected from the ~~Upper~~ upper Eocene Submeseta Allomember (Telm 6/7) of the La Meseta Formation on Seymour Island (Fig. 1). This island is located approximately 100 km east of the Antarctic Peninsula in the James Ross Basin (Marenssi et al., 2002) and contains Upper Cretaceous and Paleogene deposits represented by the Whisky Bay (Albanian to Turonian), Hidden Lake (Coniacian), Santa Marta (Santonian to Campanian), Snow Hill Island (Campanian to Maastrichtian), López de Bertodano (Maastrichtian to Danian), Sobral (Danian), Cross Valley (upper Paleocene), and La Meseta (Eocene) Formations (Bowman et al., 2015).

The Submeseta Allomember is a 140-meter-thick level representing the latest Eocene (Priabonian) between 34.96 and 35.13 Ma (Marenssi et al., 1998; Marenssi, 2006). This unit is composed predominantly of fine sandstones and mudstones from a shallow marine environment, but may have experienced a sea level rise towards the top of the section (Marenssi et al., 2002; Marenssi, 2006). Fossils were surface collected from two locations within the unit at the same

Commenté [EA3]: sentence grammatically strange to me. What has experienced a sea level rise? You mean that the unit reflects a such a rise, right?

level on the northeastern section of the island (Fig. 1). The first site is located at S64°14.6, W56°36.0 and the second at S64°13.9, W56°39.5.

Institutional Abbreviations—FMNH, Field Museum of Natural History, Chicago, Illinois, USA; **IB/P/B**, Andrzej Myrcha University Museum of Nature, Białystok, Poland; **MLP**, Museo de La Plata, La Plata, Buenos Aires Province, Argentina; **TMM**, Jackson School of Geosciences Vertebrate Paleontology Laboratory, Austin, Texas, USA

Systematic Paleontology

MAMMALIA Linnaeus, 1758

EUTHERIA Gill, 1872

XENARTHRA Cope, 1889

PILOSA Flower, 1883

FOLIVORA Delsuc, Catzefilis, Stanhope, and Douzery, 2001

Gen. et sp. indet.

(Fig. 2, Supplemental Fig. 1)

Material – TMM 44190-1, left metacarpal II.

Locality – Seymour Island, Antarctic Peninsula.

Formation/Age – Submeseta Allomember (Telm 6/7), La Meseta Formation, late Eocene.

Description —TMM 44190-1 is weathered, missing its distal epiphysis. It has a maximum proximodistal length of 33 mm as preserved and a maximum mediolateral width of 21 mm at both the proximal and distal ends. In medial view, the articular facet for the metacarpal-

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Commenté [EA5]: I would give the dorsopalmar depth at mid-diaphysis as well.

carpal complex is sharply-defined, forming the proximal part of the palmar margin and projecting well-palmarly of the rest of this margin (Fig. 2A). The remainder of the medial face is marked by two rugosities: one at the proximopalmar part and the other across the entire distal half (Fig. 2A). These rugosities are separated by a smooth sulcus, resulting in a notched medial margin in dorsal/~~plantar~~ palmar views (Fig. 2C-D). In lateral view, the articular facet for metacarpal III is rugose and worn (Fig. 2B). Due to the bone being hourglass-shaped in medial and lateral views (Fig. 2A-B) but sub-rectangular in dorsal and palmar views (Fig. 2C-D), the latter faces are broadly concave and saddle-shaped. The articular face for the trapezoid ~~carpal~~ is triangular with sharply-defined medial and dorsal margins (Fig. 2E).

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Comparisons —TMM 44190-1 is short and broad with a well-defined articular surface for the metacarpal-carpal complex. TMM 44190-1 is morphologically most consistent with those of Xenarthra (anteaters, armadillos, sloths), especially sloths (Folivora; see De Iuliis and Cartelle, 1999: figs. 6 and 7). The overall proportions of the metacarpal very closely resemble those of adult specimens of the Miocene sloth taxa *Megalonyx* spp. (TMM 30967-1845) and *Hapalops* spp. (Stock, 1925: fig. 23), though due to the worn nature of the fossil we cannot rule out the possibility of belonging to a juvenile. TMM 44190-1 is more robust than the metacarpal II of other xenarthrans such as *Thalassocnus* (Amson et al., 2015) and *Mionothropus cartellei* (De Iuliis et al., 2011: fig. 11), but closer to the proportions of Pleistocene ground-dwelling taxa such as *Megatherium urbinai* (Pujos and Salas, 2004). The trapezoid facet is sub-planar, similar to that of *Scelidotherium*, *Pseudolestodon hexaspondylus*, and *Simomylodon uccasamamensis* (Haro et al., 2017: character 334). The articular facet for the metacarpal-carpal complex does not extend distally to the midpoint of the shaft as in more recent forms such as *Hapalops* (Miocene) and *Nothrotheriops*~~*um*~~ (Pleistocene, Stock, 1925). It is unclear if the rugose surface texture along

Commenté [EA7]: Megalonyx is not only Miocene of age (actually mostly Plio-Pleistocene)…please correct

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the medial face is consistent with subadult status or with a closely-appressed digit I (as in for example *Mionothropus*; De Iuliis et al., 2011). The width of the new metacarpal relative to dorsopalmar length appears unusual for previously-reported Paleogene sloth material (reviewed in Amson et al., 2017).

The majority of mammal fossils from the Eocene of Seymour Island comprise teeth of Astrapotheria (Bond et al., 2011), Gondwanatheria (Goin et al., 2006; Gelfo et al., 2015), and Litopterna (Bond et al., 2006; Gelfo et al., 2015). The metacarpals of these clades from the South American record, such as they are known, are markedly different from the stocky, broad morphology of TMM 44190-1.

AVES Linnaeus, 1758

NEOGNATHAE Pycraft, 1900

GRUIFORMES Bonaparte, 1854 *sensu* Hackett et al., 2008

?GRUOIDEA Vigors, 1825 *sensu* Clarke et al., 2005

Gen. et sp. indet.

(Fig. 3)

Material – TMM 44189-2, distal end of left tarsometatarsus.

Locality – Seymour Island, Antarctic Peninsula.

Formation/Age – Submeseta Allomember (Telm 6/7), La Meseta Formation, late Eocene.

Description — TMM 44189-2 preserves the bases of trochleae II-IV as well as the dorsal and plantar openings of the distal vascular foramen. The maximum mediolateral width as preserved is 25 mm (Fig. 3). The distal vascular foramen is proximodistally elongate in dorsal

and plantar views (Fig. 3A-B), and the dorsal opening of the foramen is set in a deep sulcus (Fig. 3A). The plantar opening of the foramen is slightly lateral to and near the midline and is positioned distal to the juncture of trochleae II and III (Fig. 3B). The fossa for the m. supratrochlearis plantaris is shallow (Fig. 3B). Most of trochlea II is missing but appears to lack a well-defined plantar crest extending proximally from the ala of the trochlea (Fig. 3B). In distal view, trochlea II is plantarly deflected, and trochleae III and IV are widely spaced (Fig. 3E).

Comparison — A portion of a tarsometatarsus (MLP 90-I-20-9) recovered from Seymour Island was previously figured as gruiform but not described (Tambussi and Degrange, 2013: fig. 6.1g). This specimen comprises a distal diaphysis that is broken proximal to the trochleae, of which only the proximal-most part of trochlea IV is preserved. Despite the partial preservation, this fossil does not clearly show the splayed trochlear arrangement present in extant Gruoidea (cranes, trumpeters and limpkins) and in TMM 44189-2. The lack of measurements or description for MLP 90-I-20-9 make comparisons with the new fossil difficult, but as figured it appears that this fossil is larger than TMM 44189-2. Further evaluation is needed to determine the exact relationship between the two fossils, but TMM 44189-2 exhibits a suite of character states that allows for a more detailed assessment.

TMM 44189-2 exhibits a combination of character states most similar to those observed in Gruiformes (cranes, rails and allies), including: 1) trochleae III and IV projecting well distal of II; 2) plantar deflection of trochlea II (as inferred from the base and preserved ala); 3) trochlea III positioned dorsal to trochlea IV in distal view; 4) dorsoplantar flattening and mediolateral broadening of the supratrochlear region; 5) position of the distal vascular foramen near the midline and away from the lateral margin in plantar view; and 6) wide spacing of trochlea III and IV. Within Gruiformes, TMM 44189-2 is more similar to Gruoidea than Ralloidea (rails, finfoots

and flufftails) based on the following characteristics: 1) trochlea II is not as plantarly deflected in the new fossil as in ralloids; 2) trochlea II projects farther distally relative to III and IV in the new fossil than in ralloids; 3) the distal vascular foramen is located midway between the midline and the lateral margin in plantar view, unlike in ralloids where it is located on the midline; 4) the supratrochlear region of the new fossil is mediolaterally broader and trochleae II and IV are more widely spaced than in ralloids; 5) the distal margin of the distal vascular foramen is in line with the proximal extent of trochlea III in dorsal view, unlike in ralloids; 6) the distal vascular foramen is located closer to the intertrochlear incisure in plantar view than in ralloids; and 7) in dorsal view, the proximal extents of trochlea III and IV are subequal, whereas IV is proximal to III in ralloids.

The morphology of TMM 44189-2 is not unambiguously consistent with any particular gruoid subclade. Trochlea II is not as plantarly deflected as in Gruidae (cranes) or *Aramus guarauna* (limpkin) and is more like the condition observed in Psophiidae (trumpeters). As in *A. guarana* and Gruidae, trochlea III is the most dorsally positioned trochlea. There is a shallow depression at the plantar base of trochlea IV along the beginning of an ala that is most like that of *B. pavonica* and *G. canadensis* among compared Gruiformes. However, the trochlear bases of TMM 44189-2 are not as dorsoventrally thick as those of *A. guarana* and Gruidae and are more like those of *Psophia viridis.* The distal vascular foramen of TMM 44189-2 is ovoid in plantar view, with the long axis at an oblique angle to the long axis of the shaft, as in Gruidae but unlike *A. guarauna* and Psophiidae. In dorsal view, the distal vascular foramen is set in a broad, shallow sulcus as in *B. pavonica* and Psophiidae; by contrast, this sulcus is deep and sharply defined in Gruoidea. The fossil lacks the sharp plantar crest extending proximally from the ala of trochlea II observed in Gruoidea. A marked, circular depression is located between trochleae II and III, and

appears to be most like the condition in Psophiidae, *A. guarana,* and *B. pavonica*, although the observed depth may be an artifact of preservation.

SPHENISCIFORMES Sharpe, 1891 *sensu* Clarke et al., 2003

Gen. et sp. indet. A

(Fig. 4A-H)

Material – TMM 44189-1, left tarsometatarsus.

Locality – Seymour Island, Antarctic Peninsula.

Formation/Age – Submeseta Allomember (Telm 6/7), La Meseta Formation, late Eocene.

Description — TMM 44189-1 (Fig. 4 A-D) is missing its proximal end and trochlea IV. It is the more complete example of the two tarsometatarsi (including TMM 44188-2, described below) recovered by the 2016 AP3 expedition that represent a small-bodied penguin. The specimen is similar in size to the tarsometatarsus of the extant *Spheniscus humboldti* (Humboldt Penguin). The hypotarsal crests are not preserved; however, an abraded surface appears to mark the former distal-most extent of the medial hypotarsal crest. The medial proximal vascular foramen is positioned directly medial to the abraded surface that potentially corresponds to the medial hypotarsal crest.

Comparison — TMM 44189-1 is referable to Sphenisciformes (penguins) based on its overall proportions, morphology, and extreme osteosclerosis. The specimen possesses both intertarsal grooves (Fig. 4A), unlike the much larger penguin tarsometatarsus described below (TMM 44188-1). Although apparent, the medial intertarsal groove is shallower than that of all comparable extant species. The lateral intertarsal groove is present and deep, similar to the

condition in extant species as well as the extinct taxa *Delphinornis*, *Marambiornis*, and *Mesetaornis* (Myrcha et al., 2002; Jadwiszczak and Mörs, 2019). The groove does not taper strongly distally as in *Marambiornis* and *Mesetaornis*. The trochlea of metatarsal II is positioned more medially than those of all comparable extant penguin species (Fig. 4A-B, D), resulting in a wide medial intertrochlear incisure that appears most similar to that of *Delphinornis* (Myrcha et al., 2002; Jadwiszczak and Mörs, 2019). A distal vascular foramen is present (Fig. 4A-B) as in taxa from the Paleocene of New Zealand, including *Muriwaimanu*, as well as the small Antarctic taxa *Delphinornis*, *Marambiornis,* and *Mesetaornis* (Myrcha et al., 2002; Chávez Hoffmeister, 2014; Jadwiszczak, 2015; Jadwiszczak and Mörs, 2019). The distally-opening passage of the m. extensor brevis digiti IV is confluent with the distal vascular foramen (Fig. 4A), as in *Delphinornis*, *Marambiornis*, and *Mesetaornis* (Myrcha et al., 2002; Hoffmeister, 2014; Jadwiszczak, 2015; Jadwiszczak and Mörs, 2019). The plantar opening of the distal vascular foramen is more distally positioned (Fig. 4B) than in *Marambiornis* and *Mesetaornis* and is similar in morphology to that of *Delphinornis* (Myrcha et al., 2002; Jadwiszczak and Mörs, 2019).

Material – TMM 44188-2, left tarsometatarsus.

Locality – Seymour Island, Antarctic Peninsula.

Formation/Age – Submeseta Allomember (Telm 6/7), La Meseta Formation, late Eocene.

Description — TMM 44188-2 (Fig. 4E-H) is missing the proximal end and all three trochleae. It is the less complete of the two 2016 specimens that represent a small penguin morphotype. It is comparable in size to TMM 44189-1 and identical to that specimen in all preserved morphologies.

Gen. et sp. indet. B

(Fig. 4I-L)

Material – TMM 44188-1, left tarsometatarsus.

Locality – Seymour Island, Antarctic Peninsula.

Formation/Age – Submeseta Allomember (Telm 6/7), La Meseta Formation, late Eocene.

Description — TMM 44188-1 is a mostly complete tarsometatarsus that is missing trochlea IV (Fig. 4I-L). It has a proximodistal length of 45 mm and proximal mediolateral width of 39 mm. The medial and lateral proximal cotyla are separated dorsally by a pronounced intercotylar eminence and plantarly by a planar intercotylar area. The medial proximal vascular foramen is positioned just distal to the distal terminus of the medial hypotarsal crest, and is less developed than the lateral proximal vascular foramen. A scar for the m. tibialis cranialis is present on the dorsal face as a short ridge that extends distally from the proximal margin. The new tarsometatarsus lacks an appreciable medial dorsal intertarsal sulcus but exhibits a lateral sulcus.

Comparison — TMM 44188-1 most closely resembles the tarsometatarsus of the contemporaneous Seymour Island penguin *Palaeeudyptes gunnari* based on the following features: 1) a concave medial margin, 2) a medial proximal vascular foramen that is larger than the lateral vascular foramen, and 2) a proximally-positioned scar for the m. tibialis cranialis. The new specimen can be differentiated from the contemporaneous and similarly sized *Archaeospheniscus*, known from Seymour Island and New Zealand, based on the lack of a medial dorsal intertarsal sulcus and unequally sized proximal vascular foramina (Simpson, 1971;

Myrcha et al., 2002). The new specimen is also distinct from the contemporaneous *Anthropornis*, known from Seymour Island and New Zealand, in which the scar for the m. tibialis cranialis is positioned more distally and the medial proximal vascular foramen is larger than the lateral (Myrcha et al., 2002). TMM 44188-1 is significantly smaller than *P. gunnari* and may therefore represent a juvenile specimen of *P. gunnari* or a new species within *Palaeeudyptes*.

Gen. et sp. indet. C

(Fig. 4M-P)

Material – TMM 44187-1, partial mandible with associated caudal fragments.

Locality – Seymour Island, Antarctic Peninsula.

Formation/Age – Submeseta Allomember (Telm 6/7), La Meseta Formation, late Eocene.

Description — TMM 44187-1 comprises the rostral end of a mandible that includes most of the symphyseal region, with the left mandibular ramus being more complete than the right (Fig. 4M-P). The rostralmost tip is missing. The preserved portion of the left ramus measures 171 mm in length and 7 mm in maximum width. An additional fragment of this ramus measures 81 mm in length, demonstrating that, when complete, the left mandibular ramus was at least 252 mm. However, the articular regions of the mandible are missing, indicating that the original length of the bone was even greater. The preserved portion of the symphysis measures 37 mm in length and 10 mm wide at its rostrocaudal midpoint. We estimate the length of the complete symphysis at 40 mm. The mandible is slender and pointed but sturdily constructed, and is excavated by vascular canals throughout much of its length. The tip of the mandible is straight,

and the rami meet the symphysis along a straight line rather than at an angle. Mandibular fossae are not preserved.

Comparison — TMM 44187-1 is larger and more robust than the more complete penguin mandibles previously described from Seymour Island (MLP 91-II-4-221, MLP 92-II-2-195, IB/P/B-0653; Jadwiszczak 2006; Acosta Hospitaleche and Haidr, 2011), which are more tapered towards the distal end and have thinner rami. However, the overall morphology of the symphysis is comparable to other Seymour Island fossils described despite differing in overall dimensions (MLP 96-I-6-48, MLP 78-X-26-144, IB/P/B-0617e; Jadwiszczak, 2006; Acosta Hospitaleche and Haidr, 2011; Jadwiszczak, 2011). The fossil MLP 96-I-6-48 has vascular pitting and a flattened dorsal surface similar to those seen on TMM 44187-1 (Acosta Hospitaleche and Haidr, 2011), and the pitting is consistent with the morphology of extant adult *Aptenodytes forsteri* (Emperor penguin; Sosa and Acosta Hospitaleche, 2018). The shape of the rami of MLP 96-I-6-48, MLP 78-X-26-144, and IB/P/B-167e are all similar to that of TMM 44187-1 (Acosta Hospitaleche and Haidr, 2011; Jadwiszczak, 2011). These fossils pertain to Paleogene penguins with spear- or dagger-like bills characteristic of stem species (Slack et al., 2006; Clarke et al., 2007; Clarke et al. 2010; Ksepka and Clarke, 2010; Jadwiszczak, 2011; Acosta Hospitaleche and Haidr 2012). Notably, the symphysis of TMM 44187-1 is longer than those described by Acosta Hospitaleche and Haidr (2011), and the preserved rami are also longer than those of previously reported spear-billed Antarctic penguins (Jadwiszczak, 2006; Haidr and Acosta Hospitaleche, 2011; Jadwiszczak, 2011). Due to these differences and the partial preservation, TMM 44187-1 is not considered referable to any known Eocene taxa at this time.

Discussion

Though recently collected Eocene material is still fragmentary, it provides additional support for records of the presence of mammalian and avian taxa previously proposed from even more fragmentary and controversial single elements. These new records are also consistent with those expected for the Eocene of Antarctica given longstanding hypotheses of a biotic connection between Antarctica and South America during the Paleogene as well as penecontemporaneous fossil discoveries from Patagonia (see Reguero et al., 2002; 2014). The Eocene mammalian record otherwise comprises gondwanatheres, marsupials, cetaceans, 'South American native ungulates' (e.g., a litoptern, astrapotheres), and additionally, enigmatic eutherians (Woodburne and Zinsmeister, 1984; Borsuk-Bialynicka, 1988; Case et al., 1988; Bond et al., 1990; Hooker, 1992; Marenssi et al., 1994; Bargo and Reguero, 1998; Fostowicz-Frelik, 2003; Reguero and Gasparini, 2006; Case, 2006; Reguero et al., 2013; Gelfo et al., 2015; Buono et al. 2016). Indeed, in addition to the described metacarpal, the 2016 AP3 expedition recovered a vertebra and tooth consistent with referral to a basilosaurid archaeocete and a previously described ungulate species, respectively. Although new collections improve our understanding of biodiversity on Antarctica during the Eocene, they also highlight the need to recover and describe more material to elucidate a nuanced understanding of biotic exchange during this key time period.

Previous reports of xenarthrans from the Eocene of Seymour Island—based on a distal phalanx and a tooth—were initially assigned to Tardigrada (= Folivora) (Marenssi et al., 1994; Vizcaíno and Scillato-Yané, 1995), but were later questioned (Bargo and Reguero, 1998; MacPhee and Reguero, 2010). The phalanx lacks formal description and has been reportedly lost, precluding reevaluation, and was noted to be indistinguishable from the earliest known Vermilingua (anteaters) fossil from Patagonia (Bargo and Reguero, 1998; MacPhee and

Commenté [EA9]: is that what is meant?

Reguero, 2010). The tooth was recently reassigned to Mammalia indet. (MacPhee and Reguero, 2010). Therefore, the newly described specimen is either further evidence, or new evidence, that Xenarthra was indeed present on Antarctica during the Eocene depending upon one's stance with reference to prior controversies. This record is consistent with the estimated timing of origin for Folivora by the Early Eocene, and of Xenarthra in the Paleocene (e.g., Presslee et al., 2019).

Xenarthra is proposed to have originated in South America, and thus is plausibly anticipated in the Paleogene of Antarctica given inferred land connections between these continents during the early Cenozoic (Woodburne and Case, 1996; Delsuc et al., 2019; Presslee et al., 2019). The new record of Folivora extends the known Paleogene geographic range of Xenarthra into Antarctica. Xenarthran limb bones and osteoderms have been reported from the early Eocene (55-50 Ma) of Brazil (Gaudin and Croft, 2015; Superina and Loughry, 2015), but the earliest reported members of Folivora date to 31.5 Ma in Chile and Argentina (McKenna et al., 2006; Gaudin and Croft, 2015). The new material would indicate that this clade was also present in Antarctica by at least 35 Ma, four million years earlier. The paucity of other described Paleogene folivoran postcranial material (Amson et al., 2015) limits more nuanced analysis of the phylogenetic affinities and ecology of this individual.

Antarctic bird fossils from non-penguins are rare, and only a few have been named as species. They account for less than half of known extinct avian species diversity on the continent (Tambussi and Acosta Hospitaleche, 2007), but comprise an even smaller fraction of unnamed material in collections. Therefore, the distal tarsometatarsus, although fragmentary, expands our understanding of Antarctic avian diversity during the late Eocene. A proposed gruiform from Seymour Island was previously figured (Tambussi and Degrange, 2013: fig. 6.1g) but its relation

to the new fossil is difficult to assess. The new fossil exhibits preserved characters that allow for a more confident referral, providing new evidence for the presence of the clade in Antarctica.

Our understanding of the paleobiogeography of Gruoidea remains incomplete due to a near lack of known remains of Gruidae from the Paleogene of the Southern Hemisphere and of reported parts of stem Aramidae and Psophiidea from the Paleogene (Mayr, 2009; Mayr, 2017; Musser and Cracraft, 2019). Of these three clades, Gruidae has the most extensive fossil record, with Eocene fossils primarily restricted to the Northern Hemisphere (e.g. Wetmore, 1933, 1940; Cracraft 1969, 1973; Chandler and Wall, 2001; Clarke et al., 2005; Mayr, 2009; 2014; 2017). The new tarsometatarsus cannot confidently be referred to a subgroup within Gruoidea, and as such has different biogeographic implications depending on its affinities. If more closely related to Psophiidae or Aramidae, the new record suggests that these largely South American gruoid families were more broadly distributed at least as far back as the late Eocene and supports hypotheses of a distribution across Antarctic landmasses (Cracraft, 1982; Claramunt and Cracraft, 2015; Musser and Cracraft, 2019). If placed within Gruidae, the new tarsometatarsus could suggest that the gruid radiation may have been multi-directional; one radiation of cranes could have dispersed from North America to Eurasia via the Bering Land Bridge during the early Eocene and then dispersed towards west Eurasia over time (Claramunt and Cracraft, 2015), and another radiation could have arrived in Antarctica by the late Eocene via South America. However, more fossils are needed in order to gain a better understanding of the biogeography of this group and core-Gruiformes as a whole within the Southern Hemisphere.

The penguin mandible described here is the largest and most complete from a spear-billed penguin yet reported from the Eocene of Antarctica. Although fossil penguin cranial material is rare from Seymour Island, two beak morphotypes are known: long and narrow, spear-like shapes

(proposed to indicate a primarily piscivorous diet) and shorter, broad morphs (proposed to indicate feeding on small crustaceans; Ksepka and Clarke, 2010; Acosta Hospitaleche and Jadwiszczak, 2011; Haidr and Acosta Hospitaleche, 2013). The shape of the mandible is consistent with a spear-billed morphology seen in other Antarctic remains (Acosta Hospitaleche and Jadwiszczak, 2011) and similar to those of penecontemporaneous species from Peru (*Perudyptes devriesi*, mid-Eocene [Clarke et al., 2007]; *Icadyptes salasi*, mid- to late-Eocene [Clarke et al., 2007; Ksepka et al., 2008]) as well as Paleocene penguins from New Zealand (*Muriwaimanu tuatahi*; *Sequiwaimanu rosieae*: Slack et al., 2006; Ksepka and Clarke, 2010; Mayr et al., 2018). The spear-billed morphology is typically reported in stem species (Clarke et al., 2007; Ksepka and Clarke, 2010), a pattern the newly described mandible is consistent with. Measurements of the symphysis and estimates of mandible length indicate that the individual represented by the new mandible would have been larger than the older, New Zealand species *Muriwaimanu tuatahi* (Slack et al., 2006) and larger than other Eocene Antarctic spear-bills recovered (Acosta Hospitaleche and Jadwiszczak, 2011). However, the mandible does not reach the maximum mandibular length recorded for the South American *Icadyptes salasi* (Clarke et al., 2007), further supporting that a potential intermediate size class of these spear-billed taxa was present on Antarctica.

Penguins were diverse across the globe during the Eocene, with 14+ species described from Seymour Island alone (Jadwiszczak, 2006; Ksepka and Clarke, 2010; Acosta Hospitaleche, 2013 and references therein). The materials described here add to our understanding of this diversity with new material from a range of size classes: one large spear-billed taxon, one medium-sized taxon represented by a tarsometatarsus, and small taxa represented by two tarsometatarsi. It has been proposed that penguins were diverse in the mid- to late Eocene in part because of the increasing productivity in the southern oceans (Diester-Haass and Zahn, 1996;

Clarke et al. 2007; Haidr and Acosta Hospitaleche, 2012; Villa et al., 2014). The range of body sizes and bill morphotypes observed have also been hypothesized to be the result of increased interspecific competition and size-based resource partitioning (Ksepka et al., 2008; Ksepka and Clarke, 2010; Haidr and Acosta Hospitaleche, 2012). The morphological diversity reported here may lend further support to these hypotheses.

Conclusions

New records from Antarctica expand our understanding of the biodiversity on the continent during the Eocene and support previously controversial reports of Gruiformes and Xenarthra. A metacarpal is proposed to possibly represent the first record of Folivora and lends support to previously reported xenarthran materials that have been subsequently questioned or lost. The new tarsometatarsus supports the presence of Gruiformes in Antarctica during the Eocene, adding to our understanding of the avian fossil record of Seymour Island. Newly reported penguin remains, including a spear-shaped mandible and three tarsometatarsi, add to the diversity of penguins known from this time. The nature of the Antarctic fossil record is characterized by isolated elements and is dominated by penguins, making new discoveries vital to furthering our understanding diversity during a period of climate change and tectonic shifts. While historically fragmentary, new material from Antarctica is needed to elucidate trends in biodiversity and biotic exchange during a key episode of Earth's history.

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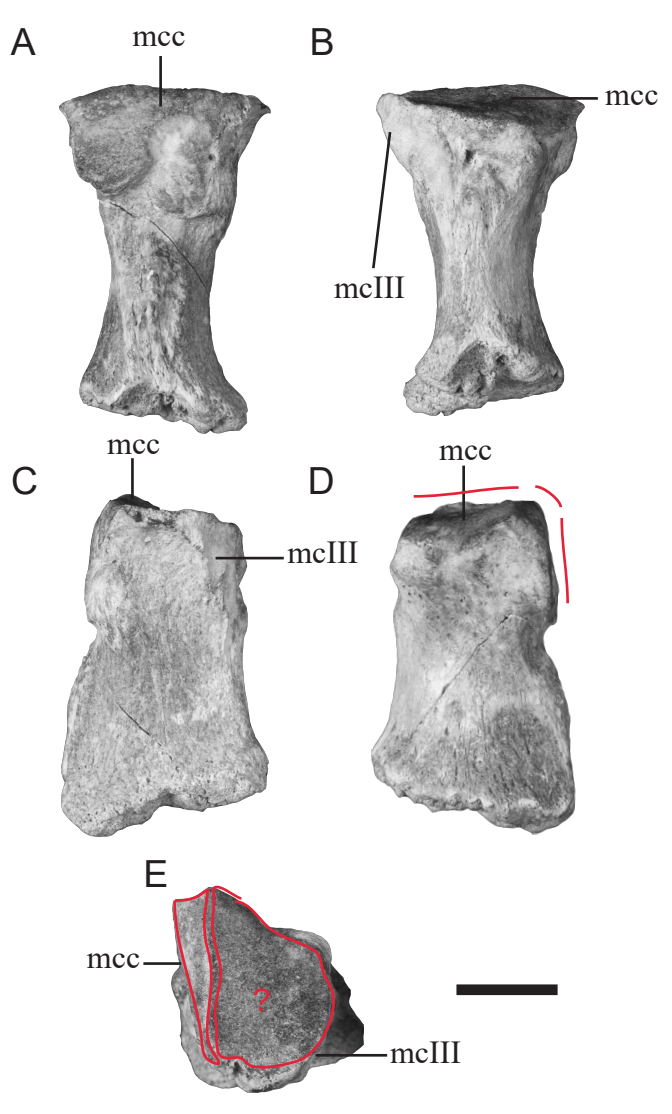
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