

# Late Cretaceous non-avian dinosaurs from the James Ross Basin, Antarctica: description of new material, updated synthesis, biostratigraphy, and paleobiogeography

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**Abstract** Although the fossil record of non-avian dinosaurs from the Cretaceous of Antarctica is the poorest of any continent, fossils representing at least five major taxonomic groups (Ankylosauria, early-diverging Ornithopoda, Hadrosauridae, Titanosauria, and Theropoda) have been recovered. All come from Upper Cretaceous (Coniacian–Maastrichtian) marine and nearshore deposits belonging to the Gustav and Marambio groups of the James Ross Basin at the northern tip of the Antarctic Peninsula. The majority of these finds have come from the Campanian–Maastrichtian Snow Hill Island and López de Bertodano formations of James Ross and Vega islands. Given the rarity of Antarctic Cretaceous non-avian dinosaurs, discoveries of any fossils of these archosaurs, no matter how meager, are of significance. Here we describe fragmentary new ornithischian (ankylosaur and ornithopod) material from the upper Campanian–lower Maastrichtian Cape Lamb Member of the Snow Hill Island Formation and the Maastrichtian Sandwich Bluff Member of the López de Bertodano Formation. One of these specimens is considered to probably pertain to the holotypic individual of the early-diverging ornithopod *Morrosaurus antarcticus*. We also provide an up-to-date synthesis of the Late Cretaceous non-avian dinosaur record of the James Ross Basin and analyze the biostratigraphic occurrences of the various finds, demonstrating that most (including all named taxa and all reasonably complete skeletons discovered to date) occur within a relatively condensed temporal interval of the late Campanian to early Maastrichtian. Most or all James Ross Basin dinosaurs share close affinities with penecontemporaneous taxa from Patagonia, indicating that at least some continental vertebrates could disperse between southern South America and Antarctica during the final stages of the Mesozoic.

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## 1 Introduction

Over the past half-century, research groups from multiple nations (e.g., Argentina, Brazil, Chile, Poland, the United Kingdom, the United States) have explored for Cretaceous fossil vertebrates in the James Ross Basin (JRB), on a series of islands adjacent to the northeastern tip of the Antarctic Peninsula (Figure 1). Although abundant material of fishes, marine reptiles, and birds has been recovered, fossils of non-avian dinosaurs remain much rarer, a circumstance that is almost certainly due to the fact that most or all fossiliferous strata in the JRB were deposited in marine to shallow marine settings rather than continental depositional systems in which these archosaurs would be expected to have been more common (Reguero et al., 2013a, 2013b; Roberts et al., 2014).

Nevertheless, the non-avian dinosaur fossils that have been discovered in the JRB—all of which pertain to the Upper Cretaceous—collectively indicate the presence of a diversity of taxa that hold significant biostratigraphic and paleobiogeographic implications (Figure 1, Table 1; Reguero and Gasparini, 2007; Reguero et al., 2013a, 2013b). Among the most important discoveries are five associated partial skeletons: (1) the holotype of the ankylosaur *Antarctopelta oliveroi* (Olivero et al., 1986, 1991; Gasparini et al., 1987, 1996; de Ricqlès et al., 2001; Salgado and Gasparini, 2004, 2006; Coria et al., 2011; Rozadilla et al., 2016a); (2) three specimens representing at least two taxa of small to medium-sized, early-diverging ornithopods: the holotypes of *Morrosaurus antarcticus* (Cambiaso et al., 2002; Novas et al., 2002a; Rozadilla et al., 2016b) and *Trinisaura santamartaensis* (Coria et al., 2008, 2013) and a third, still-undescribed skeleton that may represent one of these species or potentially a third (Hooker et al., 1991; Thomson and Hooker, 1991; Milner et al., 1992; Hooker, 2000; Barrett et al., 2014); and (3) a partial skeleton of a medium-sized non-avian theropod that was recently designated the holotype of the possible deinonychosaur *Imperobator antarcticus* (Case et al., 2007; Ely and Case, 2016, 2019). Two other associated specimens, each consisting of a handful of fragmentary ornithopod hind limb elements from the latest Cretaceous of Vega Island, have also recently been identified (Coria et al., 2015a, 2015b; MCL pers. obs.).

Beginning in the 1990s, and supported by the United States (US) National Science Foundation (NSF) and the US Antarctic Program, paleontological expeditions led or

co-led by one of us (Judd A. Case; hereafter JAC<sub>1</sub>) have explored the JRB for fossil vertebrate remains, often in collaboration with scientists from the Museo de La Plata and the Instituto Antártico Argentino (IAA). Subsequent field efforts were organized and completed by the NSF-funded Antarctic Peninsula Paleontology Project (AP3) during the austral summers of 2009, 2011, and 2016. Several of these expeditions recovered fragmentary non-avian dinosaur skeletal elements that remain undescribed. Among the most notable of these are the distal end of a pedal phalanx and multiple unidentified fragments collected by AP3 researchers in 2011 from an outcrop of the upper Campanian–lower Maastrichtian Cape Lamb Member of the Snow Hill Island Formation on the Naze Peninsula of James Ross Island, at or extremely close to the locality that yielded the holotypic partial right hind limb of the ornithopod *Morrosaurus* (Rozadilla et al., 2016b).

The present contribution has three primary aims: to (1) fully describe previously undescribed and in some cases recently recovered ornithischian dinosaur fossils from the Upper Cretaceous of the JRB, including the probable new material of *Morrosaurus*; (2) provide an up-to-date synthesis of the Upper Cretaceous non-avian dinosaur record of the JRB and its paleobiogeographic significance; and (3) clarify the stratigraphic positions of previously described JRB dinosaurs, with attendant paleoecological implications.

## 2 Description of new material

### 2.1 Systematic paleontology

DINOSAURIA Owen, 1842

ORNITHISCHIA Seeley, 1887

THYREOPHORA Nopcsa, 1915

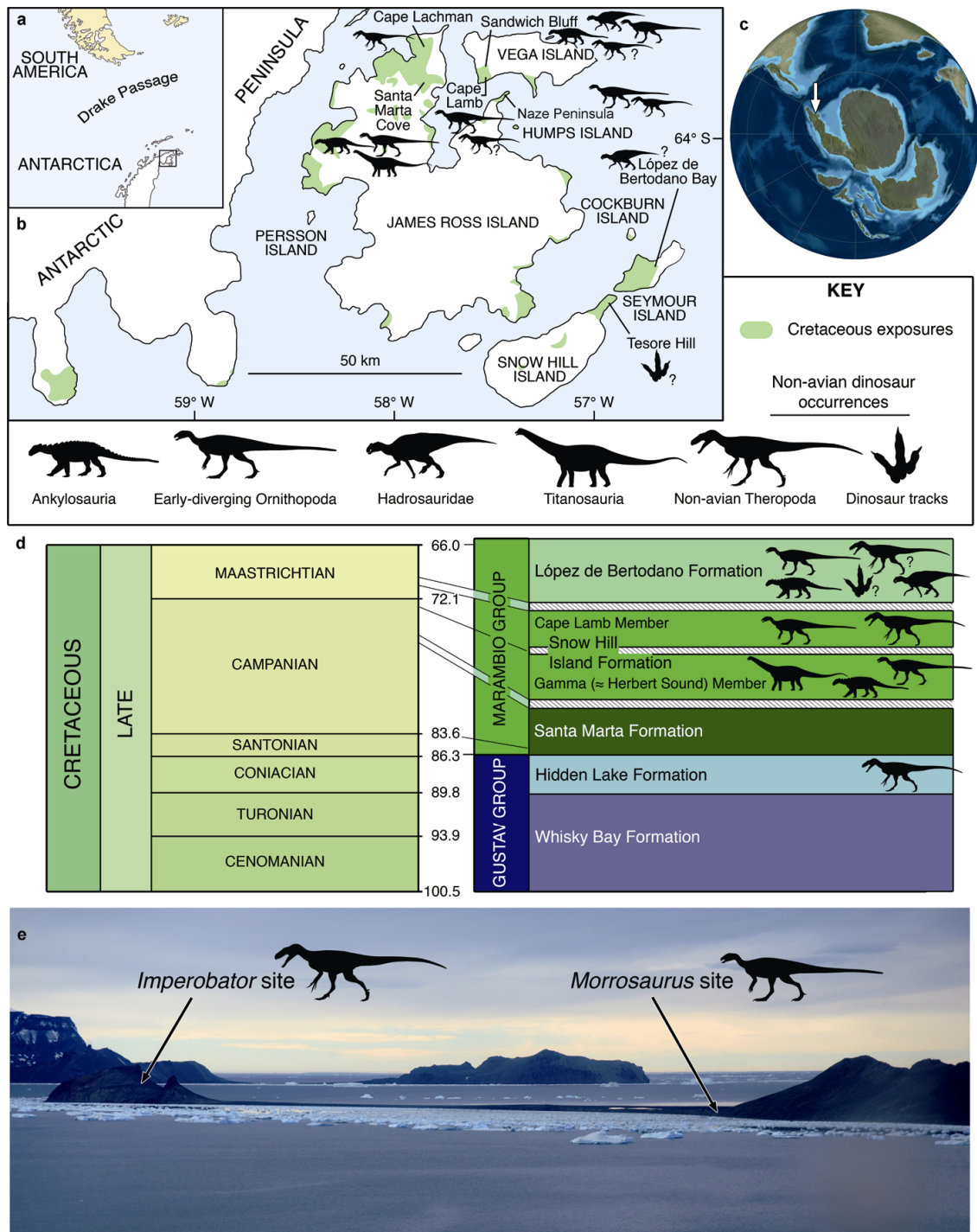
ANKYLOSAURIA Osborn, 1923

?NODOSAURIDAE Marsh, 1890

Referred specimen: SDSM 142814 (field number S061-9927), an isolated osteoderm (Figure 2).

Locality: Sandwich Bluff (63°51'31" S, 57°34'14" W), western Vega Island, JRB, Antarctic Peninsula. This osteoderm was collected during the austral summer of 1999, from within 2 m laterally of where the hadrosaurid tooth described by Case et al. (2000a) (MLP 98-I-10-1) was recovered the year prior (JAC<sub>1</sub> pers. obs.).

Horizon and age: ‘Reptile Horizon’ (≈ Unit SBM12 of Roberts et al., 2014; JAC<sub>1</sub> pers. obs.), Sandwich Bluff Member, López de Bertodano Formation, Marambio Group.



**Figure 1** Geographic and stratigraphic context of non-avian dinosaur discoveries from the Cretaceous of Antarctica. **a**, Map of southern South America, Drake Passage, and Antarctic Peninsula, with study area (the JRB) indicated by box. **b**, Map of JRB showing localities that have produced described non-avian dinosaur material (indicated by silhouettes). Exposures of Cretaceous sediments shown in green (modified from Riding and Crame, 2002: Figure 1 and Olivero, 2012a: Figure 1). See key for details. **c**, Paleogeographic reconstruction (south polar view) at 70 Ma showing approximate position of JRB (indicated by arrow). **d**, Upper Cretaceous stratigraphy of the JRB showing units that have produced non-avian dinosaur material (indicated by silhouettes, see key for details). **e**, Aerial photograph of the Naze Peninsula from the ~west showing the type localities of the early-diverging ornithopod *Morrosaurus antarcticus* and the non-avian theropod *Imperobator antarcticus*. Silhouettes of Ankylosauria, early-diverging Ornithopoda, Hadrosauridae, and non-avian Theropoda in **b** and **d** courtesy Scott Hartman via PhyloPic.org. Paleogeographic reconstruction in **c** ©2016 Ronald Blakey, Colorado Plateau Geosystems, Inc. Geologic time scale in **d** after Walker et al. (2018). Photograph in **e** courtesy Philip Currie. Scale equals 50 km in **b**.

**Table 1** Non-avian dinosaur fossils from the JRB, Antarctic Peninsula, modified and expanded from Reguero et al. (2013b: Table 1). All records are Upper Cretaceous. Stratigraphic nomenclature follows Crame et al. (1991) and Olivero (2012a). Abbreviations: NA, not applicable; NR, not reported

Taxon	Higher taxon	Specimen	Material	Formation	Member	Age	Island	Source(s)
?Dinosauria indet.	?Dinosauria	NA	?Footprints	López de Bertodano	NR	early Maastrichtian	Snow Hill	Olivero et al., 2007
Ankylosauria indet.	Ankylosauria (?Nodosauridae)	SDSM 142814	Osteoderm	López de Bertodano	Sandwich Bluff	Maastrichtian	Vega	Case et al., 2003; this paper
<i>Antarctopelta oliveroi</i>	Ankylosauria (?Nodosauridae)	MLP 86-X-28-1	Partial skeleton	Snow Hill Island	Gamma (≈ Herbert Sound)	late Campanian	James Ross	Olivero et al., 1986, 1991; Gasparini et al., 1987, 1996; de Ricqlès et al., 2001; Salgado and Gasparini, 2004, 2006; Coria et al., 2011; Stittwell and Long, 2011; Rozadilla et al., 2016a; Poropat pers. comm.
?Ornithopoda indet.	?Ornithopoda	MLP 07-III-2-1	Pedal ungual	Snow Hill Island	Gamma (≈ Herbert Sound)	late Campanian	James Ross	Coria et al., 2007
?Ornithopoda indet.	?Ornithopoda	MLP 07-III-2-2	Pedal ungual	Snow Hill Island	Gamma (≈ Herbert Sound)	late Campanian	James Ross	Coria et al., 2007
Ornithopoda indet.	Ornithopoda	MLP 15-I-7-1	Partial tibia, astragalus	Snow Hill Island	Cape Lamb	late Campanian–early Maastrichtian	Vega	Coria et al., 2015a, 2015b
Ornithopoda indet.	Ornithopoda	MLP 98-I-10-70	Pedal ungual	López de Bertodano	Sandwich Bluff	Maastrichtian	Vega	This paper
Ornithopoda indet.	Ornithopoda	CM 93790	Partial fibula and metatarsus	López de Bertodano	Sandwich Bluff	Maastrichtian	Vega	JAC <sub>1</sub> pers. obs.
Ornithopoda indet.	Ornithopoda	CM 93791	Pedal ungual?	López de Bertodano	Sandwich Bluff	Maastrichtian	Vega	JAC <sub>1</sub> pers. obs.
<i>Trinisaura santamarinaensis</i>	Ornithopoda (?Elasmaria)	MLP 08-III-1-1	Partial postcranial skeleton	Snow Hill Island	Gamma (≈ Herbert Sound)	late Campanian	James Ross	Coria et al., 2008, 2013
<i>Morrosaurus antarcticus</i>	Ornithopoda (?Elasmaria)	MACN Pv 19777	Partial hind limb	Snow Hill Island	Cape Lamb	late Campanian–early Maastrichtian	James Ross	Cambiaso et al., 2002; Novas et al., 2002a; Cambiaso, 2007; Motta et al., 2012; Rozadilla et al., 2016b



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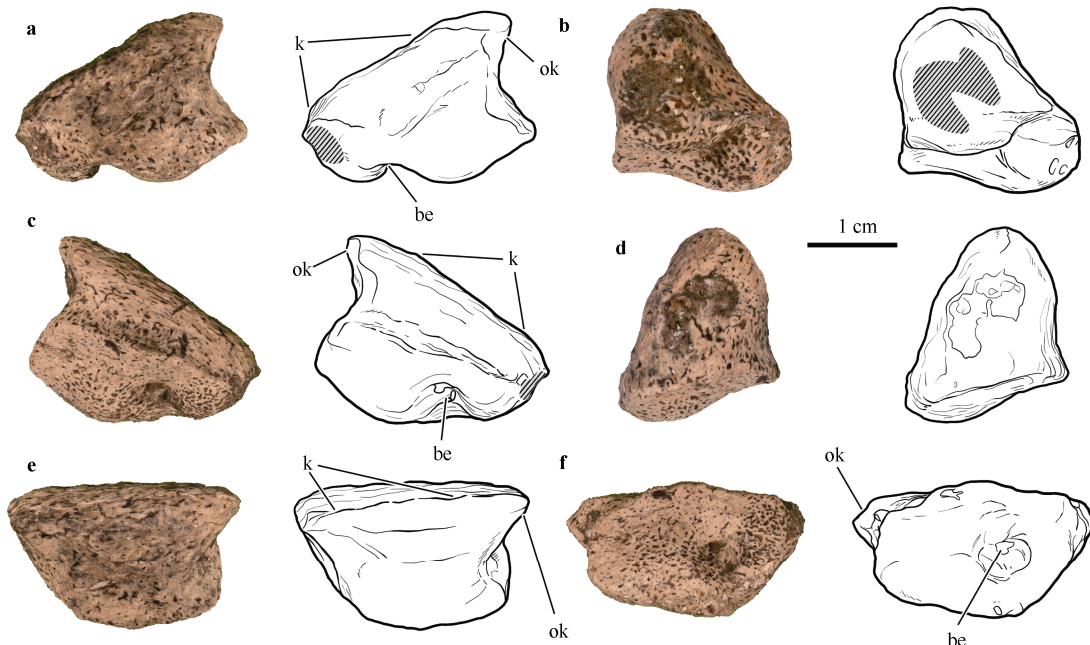
Taxon	Higher taxon	Specimen	Material	Formation	Member	Age	Island	Source(s)
<i>Morrosaurus antarcticus</i>	Ornithopoda (?Elasmaria)	AMNH FARB 30897 (probably same individual as MACN Pv 19777)	Partial pedal phalanx, associated fragments	Snow Hill Island	Cape Lamb	late Campanian-early Maastrichtian	James Ross	MacPhee et al., 2011; Lamanna, 2013; Lamanna et al., 2017; this paper
Ornithopoda ?gen. et sp. nov.	Ornithopoda (?Elasmaria)	NHMUK PV R 36760 (formerly BMNH BAS R.2450)	Partial skeleton	Snow Hill Island	Cape Lamb	early Maastrichtian	Vega	Hooker et al., 1991; Thomson and Hooker, 1991; Mflner et al., 1992; Hooker, 2000; Stilwell and Long, 2011; Barrett et al., 2014
?Hadrosauridae indet.	Ornithopoda (?Hadrosauridae)	MLP 96-1-6-2	Partial metatarsal	López de Bertodano	NR	late Maastrichtian	Seymour (= Marambio)	Ritch et al., 1999
Hadrosauridae indet.	Ornithopoda (Hadrosauridae)	MLP 98-1-10-1	Tooth	López de Bertodano	Sandwich Bluff	Maastrichtian	Vega	Case et al., 1998, 2000a
Hadrosauridae indet.	Ornithopoda (Hadrosauridae)	NR	Pedal phalanges	López de Bertodano	Sandwich Bluff	Maastrichtian	Vega	Case et al., 2000b, 2007
Titansauria indet.	Sauropoda (Titanosauria)	MLP 11-II-20-1	Partial caudal vertebra	Snow Hill Island	Gamma (≈ Herbert Sound)	late Campanian	James Ross	Cerda et al., 2012
?Theropoda indet.	?Theropoda	MLP 15-I-7-2	Pedal phalanx ?III-1	Snow Hill Island	Cape Lamb	early Maastrichtian	Vega	Coria et al., 2015a, 2015b
Theropoda indet.	Theropoda	MLP 89-XII-1-1	Partial tibia	Hidden Lake	NA	Coniacian	James Ross	Mohar et al., 1996
Theropoda indet.	Theropoda	NR	NR	López de Bertodano	NR	Maastrichtian	Vega	Case et al., 2003; Olivero et al., 2007
<i>Imperobator antarcticus</i>	Theropoda (?Deinonychosauria)	UCMP 276000; AMNH FARB 30894	Partial skeleton	Snow Hill Island	Cape Lamb	late Campanian-early Maastrichtian	James Ross	Martin and Case, 2005; Case et al., 2007; Martin et al., 2009; di Pasquo and Martin, 2013; Ely and Case, 2016, 2019; Lamanna et al., 2017

Upper Cretaceous: Maastrichtian (Roberts et al., 2014) (Note that although Roberts et al. [2014] tentatively equated the ‘Reptile Horizon’ to their Unit SBM11, it probably corresponds more closely to their Unit SBM12; JAC<sub>1</sub> pers. obs.).

Description: SDSM 142814 (= S061-9927) is a small element measuring 3.7 cm long by 2.0 cm wide by 2.8 cm tall, with an oval base and a pointed keel that overhangs (i.e., projects beyond) the remainder of what we regard as the posterior surface. The keel is offset from the midline of the long axis of the bone and has a rounded rather than a sharp edge. Moving basally from the apex of the keel, the surfaces on either side of the keel are flat rather than concave. The basal surface of the element is generally convex, except for a large, irregularly-shaped excavation towards the end opposite the overhanging keel. The bone surface is weathered but appears to initially have been lightly pitted with a somewhat reticular surface texture.

The surface texture and shape of this bone suggest that it is best interpreted as an ankylosaur osteoderm. Osteoderms of this size in other ankylosaurs often have fewer distinctive features compared to larger osteoderms (e.g., Ford, 2000; Kilbourne and Carpenter, 2005; Ösi, 2005; Kirkland et al., 2013; Kinneer et al., 2016). Ankylosaurine osteoderms are typically deeply excavated on the basal

surface, and as such even very large osteoderms tend to be quite thin; nodosaurid osteoderms can be excavated basally, but osteoderms with unexcavated and even convex bases are not uncommon (Burns and Currie, 2014). The relatively tall keel relative to basal width is less common for osteoderms of this size, which are often flat or with low but sharply defined keels. A few osteoderms associated with the holotype of *Antarctopelta oliveroi* (MLP 86-X-28-1) are close to the morphology of SDSM 142814, but typically have sharper keel edges or lack overhanging keels (VMA pers. obs.). Several of the osteoderms of an as-yet unnamed Argentinean nodosaurid (MPCA-Pv 41–43, 75–76) share with SDSM 142814 the presence of tall, relatively blunt keels, but none are backswept or overhang the base (Coria and Salgado, 2001; Arbour and Currie, 2016; VMA pers. obs.). In *Antarctopelta* and the Argentinean taxon, as in SDSM 142814, the osteoderms are lightly pitted with reticulate surface textures, and the basal surfaces can possess large, deep, circular pits. SDSM 142814 cannot be referred to a particular ankylosaurian genus, but it is most likely a nodosaurid osteoderm and its morphology and surface texture are consistent with those of other Late Cretaceous Gondwanan nodosaurids. Its small size and keeled morphology suggest that it may have originated from the anterior thoracic region or the forelimbs (e.g., Kinneer et al., 2016).



**Figure 2** Photos (left) and interpretive line drawings (right) of ankylosaurian osteoderm (SDSM 142814) from the Upper Cretaceous (Maastrichtian) Sandwich Bluff Member of the López de Bertodano Formation of Vega Island in (a) ?lateral; (b) ?anterior; (c) ?medial; (d) ?posterior; (e), apical; and (f) basal views. Hatching indicates damaged surface. Abbreviations: be, basal excavation; k, keel; ok, ‘overhang’ of keel.

ORNITHISCHIA Seeley, 1887

NEORNITHISCHIA Cooper, 1985

ORNITHOPODA Marsh, 1881

Referred specimen: MLP 98-I-10-70, an isolated pedal

ungual (perhaps from the right digit IV) (Figure 3).

Locality: Sandwich Bluff (63°51'31" S, 57°34'14" W), western Vega Island, JRB, Antarctic Peninsula.

Horizon and age: ‘Reptile Horizon’ (≈ Unit SBM12 of

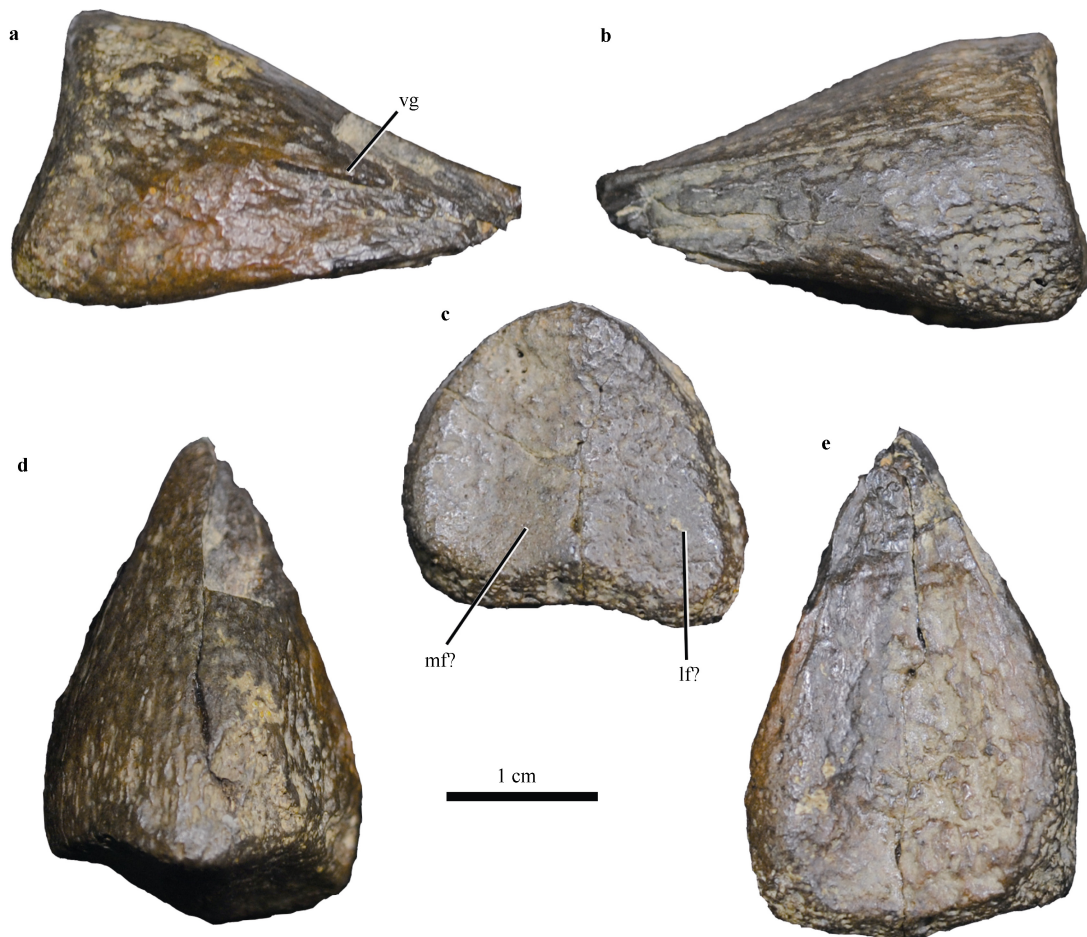
Roberts et al., 2014), Sandwich Bluff Member, López de Bertodano Formation, Marambio Group. Upper Cretaceous: Maastrichtian (Roberts et al., 2014).

Description: Specimen MLP 98-I-10-70 is a small element that was discovered in 1998 by a joint Argentine-American expedition funded by NSF and the IAA. Comparison of the bone to the nearly complete pedes of a specimen of the early-diverging iguanodontian ornithopod *Dryosaurus altus* (CM 21786) suggests that this Antarctic unguis may represent that of right pedal digit IV of a similarly-sized ornithopod individual (MCL pers. obs.), and it is herein described as such. MLP 98-I-10-70 is subtriangular in dorsal and ventral (= plantar) views and incomplete distally. As seen in proximal view (Figure 3c), it is dorsally strongly convex and ventrally gently concave, substantially wider ventrally than dorsally, and asymmetrical, with its dorsal apex being slightly displaced toward the presumed medial side and the medial margin sloping more steeply than the lateral. The proximal articular surface is divided by a low, rounded ridge into lateral and medial articular facets, with the latter being marginally wider than the former. Dorsally, this ridge merges with a blunt tuberosity that is subtriangular in dorsal view and that

projects further proximally than the remainder of the proximodorsal region of the bone (Figure 3d).

As observed in dorsal view (Figure 3d), the medial facet of the proximal articular surface is more concave than the lateral. The proximal ~one-third of the medial side of the unguis meets the proximal articular surface at an approximate right angle, but the remainder of this side is angled laterally. The lateral side displays a comparable morphology in dorsal view, but the curvature (in this case, medially) begins more proximally and is more gradual than that of the medial side.

When viewed medially (Figure 3b), the ventral margin of the unguis is flat through roughly its proximal one-third, but becomes gently angled dorsally more distally. The ventral margin of the lateral side is mostly flat (Figure 3a). In both lateral and medial views, the dorsal margin of the unguis is mildly sinuous in contour, with a flat proximal ~one-third, a distoventrally angled middle third, and a flatter distal third. The lateral side of the bone is marked by a shallow vascular groove (Figure 3a). Ventrally, a wide fossa embays nearly the entire length of the unguis except for the flatter distal end (Figure 3e). This fossa is deepest near the proximodistal midline of the bone and bordered by broad lateral and medial ridges.



**Figure 3** Ornithopod pedal unguis (MLP 98-I-10-70) from the Upper Cretaceous (Maastrichtian) Sandwich Bluff Member of the López de Bertodano Formation of Vega Island in (a) ?lateral; (b) ?medial; (c) proximal; (d) dorsal; and (e) ventral views. Abbreviations: lf?, lateral facet; mf?, medial facet; vg, vascular groove.

If, as it would appear, MLP 98-I-10-70 is a pedal element of a non-hadrosaurid ornithopod, it would, along with a partial distal hind limb currently under study (JAC<sub>1</sub> pers. obs.), constitute the first record of these animals from the Maastrichtian Sandwich Bluff Member of the López de Bertodano Formation, and therefore the stratigraphically youngest occurrence of these dinosaurs in Antarctica and among the youngest in the world.

?ELASMARIA Calvo, Porfiri, and Novas, 2007

*Morrosaurus antarcticus* Rozadilla, Agnolín, Novas, Aranciaga Rolando, Motta, Lirio, and Isasi, 2016

Referred specimen: AMNH FARB 30897, the distal end of a ?right pedal phalanx (Figure 4) and seven associated but unidentified fragments. Because all elements assigned specimen number AMNH FARB 30897 were surface-collected (i.e., not recovered in situ), some of these fragments may potentially pertain to other vertebrates, such as marine reptiles.

Locality: North of Fortress Hill, central part of the northwestern shore of the Naze Peninsula, northern James Ross Island, JRB, Antarctic Peninsula (63°55'41" S, 57°30'18" W). Note that Rozadilla et al. (2016b) reported the coordinates of the locality that yielded the *Morrosaurus* type specimen (MACN Pv 19777; Figure 4a–4g) as 63°55'40" S, 57°30'15" W, approximately 55 m from the recorded recovery site of AMNH FARB 30897. However, it remains uncertain whether either set of coordinates was taken at the precise site(s) from which bones were collected, either in early 1998 by Argentine researchers (J. M. Lirio of the IAA and M. Isasi of the MACN) upon the discovery of MACN Pv 19777 (Novas pers. comm.) or in February 2011 by the AP3 scientists who recovered AMNH FARB 30897 (Julia A. Clarke [hereafter JAC<sub>2</sub>] and J. Meng). Moreover, as noted above, elements comprising AMNH FARB 30897 were surface-collected and as such had likely undergone some degree of transport from their original burial location(s) by modern weathering processes. As such, we regard the site that yielded AMNH FARB 30897 as probably the same as the *Morrosaurus* type locality.

Horizon and age: Cape Lamb Member, Snow Hill Island Formation, Marambio Group (Rozadilla et al., 2016b). Upper Cretaceous: upper Campanian–lower Maastrichtian.

Description: Bones recovered from the probable *Morrosaurus* site in 2011 include the distal end of a ?right pedal phalanx (Figure 4h–4m) and several weathered fragments. One side of the phalanx (the lateral, if this bone is correctly interpreted as being from the right side) exhibits a collateral ligament pit, and the hemicondyle on this side is complete, measuring 2.3 cm in dorsoventral (= dorsoplantar) height. The other hemicondyle (presumably the medial) is incomplete but appears to have been dorsoventrally larger than the presumed lateral condyle; also, the smooth surface that would have articulated with a more distal phalanx extends further proximally on the medial side. Although incomplete, the distal end of the phalanx was clearly wider

along the ventral margin than the dorsal margin. The interior of the bone is filled with sedimentary matrix, although it is unclear if this reflects its actual anatomy (e.g., that the phalanx was hollow in life) rather than a taphonomic or preservational artifact (Figure 4j).

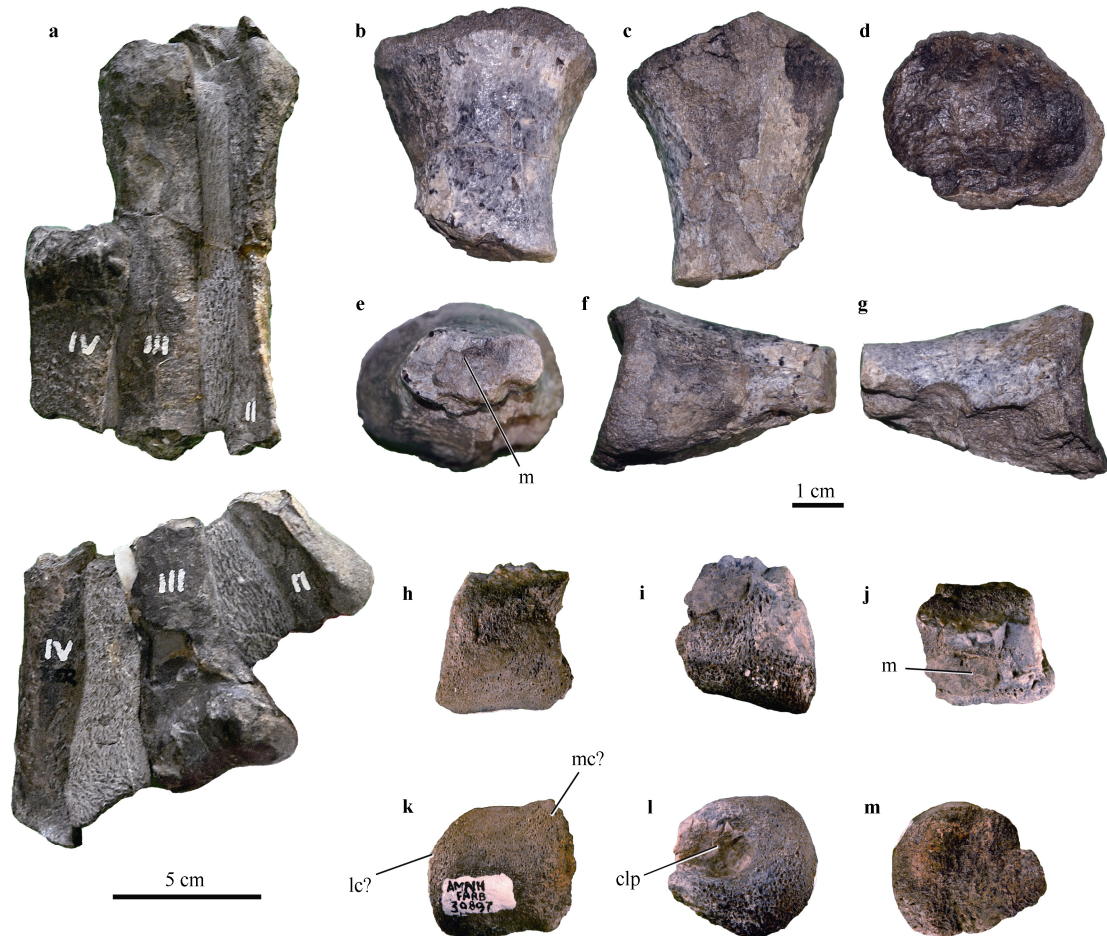
Non-avian dinosaur fossils are extraordinarily rare in the Cape Lamb Member; moreover, all known occurrences have consisted of isolated partial skeletons or skeletal elements that presumably were transported into this marine depositional setting (Reguero and Gasparini, 2007; Reguero et al., 2013a, 2013b). The *Morrosaurus* holotype (MACN Pv 19777) includes only a single pedal phalanx (right phalanx III-1) that is missing its distal end (Rozadilla et al., 2016b; Figure 4b–4g). Like that of the AMNH FARB 30897 phalanx, the interior of the MACN Pv 19777 phalanx III-1 is filled with matrix, suggesting that it too may have originally been hollow (MCL pers. obs.; Figure 4e). Moreover, the two pedal phalanges are virtually identical in other preservational aspects as well; for instance, both are bluish-white in color, as is typical of dinosaur bone that has weathered from the Cape Lamb Member (MCL pers. obs.). However, although it seems conceivable that the AMNH FARB 30897 phalanx could be the distal end of the phalanx preserved in the *Morrosaurus* holotype (i.e., that of right phalanx III-1), the two pieces seem slightly incompatible in size, with the new element being marginally smaller than what might be expected (based on the pedal phalangeal proportions of other early-diverging ornithopod specimens; e.g., *Dryosaurus altus* CM 21786; Galton, 1981; MCL pers. obs.) for the distal end of phalanx III-1 of MACN Pv 19777. As such, the AMNH FARB 30897 phalanx may represent a pedal element that was previously unknown for *Morrosaurus* (perhaps right phalanx II-1 based on comparison with CM 21786; MCL pers. obs.).

In sum, given its closely congruent or identical geographic and stratigraphic provenance, as well as its morphological consistency and lack of anatomical overlap with the type specimen, we hypothesize that the distal pedal phalanx of AMNH FARB 30897 probably pertains to the same *Morrosaurus* individual. As such, the new specimen may augment the preserved morphology of one of the few non-avian dinosaur taxa yet discovered from the Upper Cretaceous of Antarctica.

### 3 Synthesis of JRB dinosaur record

Although all non-avian dinosaur specimens from the JRB are fragmentary, they are collectively of extraordinary significance in constituting the only known record of these animals from the Cretaceous of Antarctica. Moreover, the JRB dinosaur record currently indicates the presence of at least five major taxonomic groups in the Late Cretaceous of the continent: Ankylosauria, early-diverging Ornithopoda (Elasmaria?), Hadrosauridae, Titanosauria, and non-avian Theropoda, with associated partial skeletons being known for several taxa within these groups (primarily ornithischians)





**Figure 4** Pedal bones of the early-diverging (elasmarian?) ornithopod *Morrosaurus antarcticus* from the upper Campanian–lower Maastrichtian Cape Lamb Member of the Snow Hill Island Formation of James Ross Island. **a**, Right metatarsus of the holotype (MACN Pv 19777) in dorsal (= anterior) view. **b–g**, Right pedal phalanx III-1 of MACN Pv 19777 in (**b**) dorsal, (**c**) ventral (= plantar), (**d**) proximal, (**e**) distal, (**f**) lateral, and (**g**) medial views. **h–m**, Distal end of ?right pedal phalanx (AMNH FARB 30897) recovered from the *Morrosaurus* type locality or a very nearby site by the 2011 AP3 expedition in (**h**) dorsal, (**i**) ventral (= plantar), (**j**) proximal, (**k**) distal, (**l**) ?lateral, and (**m**) ?medial views. Given its identical or near-identical provenance and lack of anatomical overlap with MACN Pv 19777, the AMNH FARB 30897 phalanx probably pertains to the same *Morrosaurus* individual. Scale equals 5 cm in **a**, 1 cm in **b–m**. Abbreviations: clp, collateral ligament pit; lc?, lateral hemicondyle; m, matrix-filled cavity; mc?, medial hemicondyle?.

(Figures 1, 5; Table 1). The highly incomplete nature of most specimens hinders definitive assessments of their phylogenetic affinities; nevertheless, most or all non-avian dinosaurs thus far recorded from the JRB appear closely related to penecontemporaneous taxa from southern South America. It should be noted that the fossil record of avian dinosaurs (birds) from the basin—both from the Cretaceous and the overlying Paleogene deposits—is generally much richer than that of their non-avian cousins (e.g., Chatterjee, 2002; Clarke et al., 2005, 2016; Acosta Hospitaleche and Gelfo, 2015), but an overview of the avian record is beyond the scope of the present contribution.

Most non-avian dinosaur occurrences from the JRB consist of skeletal remains; however, there is one possible record of dinosaurian trace fossils as well. Olivero et al. (2007) reported poorly preserved putative non-avian dinosaur footprints from a lower Maastrichtian exposure of

the López de Bertodano Formation near Tesore Hill on Snow Hill Island (Figure 5a). If confirmed, these tracks would constitute the first evidence of dinosaurs from that island as well as the only known dinosaurian trace fossils from the Cretaceous of Antarctica. Nevertheless, a 2016 reconnaissance of the Tesore Hill area by an AP3 field team failed to relocate these ostensible tracks and as such could not substantiate this record. It is possible that the structures in question were covered by snow during the AP3 survey (Olivero pers. comm.). Reguero et al. (2013a, 2013b) suggested that these footprints, if authentic, could have been made by sauropods, and this may be the case for some of these potential ichnofossils. Nevertheless, Olivero et al. (2007) also described putative tracks that they attributed to bipedal animals; if this identification is correct, such ichnites could not have been produced by any known sauropod taxon.



**Figure 5** Previously reported non-avian dinosaur material from Upper Cretaceous strata of the JRB, Antarctic Peninsula. **a**, Putative footprints (adjacent to scale bar) from a lower Maastrichtian horizon of the López de Bertodano Formation of the Tesore Hill region of Snow Hill Island. **b**, Left dentary fragment of the holotype of the ankylosaur *Antarctopelta oliveroi* (MLP 86-X-28-1) from the upper Campanian Gamma Member of the Snow Hill Island Formation of the Santa Marta Cove area of James Ross Island in medial view. **c**, Block of caudal vertebrae ( $c_1$ ), left pelvic elements ( $c_2$ ), and scapulocoracoids ( $c_3$ ) of the holotype of the small-bodied basal ornithopod (elasmarian?) *Trinisaura santamartaensis* (MLP 08-III-1-1) from the upper Campanian Gamma Member of the Snow Hill Island Formation of the Santa Marta Cove area of James Ross Island primarily in lateral view (some caudal vertebrae in other views). **d**, Distal tarsal and nearly complete metatarsus of the holotype of the medium-sized basal ornithopod (elasmarian?) *Morrosaurus antarcticus* (MACN Pv 19777) from the upper Campanian–lower Maastrichtian Cape Lamb Member of the Snow Hill Island Formation of the Naze Peninsula of James Ross Island in posterior (= ventral, plantar) view. **e**, Partial right dentary with in situ teeth of an undescribed medium-sized basal ornithopod (elasmarian?) skeleton (NHMUK PV R 36760 [formerly BMNH BAS R.2450]; the ‘BAS ornithopod’) from a lower Maastrichtian horizon of the Cape Lamb Member of the Snow Hill Island Formation of Cape Lamb of Vega Island in lateral view. **f**, Tooth crown of hadrosaurid ornithopod (MLP 98-I-10-1) from the Maastrichtian ‘Reptile Horizon’ of the Sandwich Bluff Member of the López de Bertodano Formation of Sandwich Bluff of Vega Island in labial view. **g**, Partial caudal centrum of titanosaurian sauropod (MLP 11-II-20-1) from the upper Campanian Gamma Member of the Snow Hill Island Formation of the Santa Marta Cove area of James Ross Island in right lateral view. **h**, Reconstructed distal left hind limb of the possible deinonychosaurian theropod *Imperobator antarcticus* (UCMP 276000) from the upper Campanian–lower Maastrichtian Cape Lamb Member of the Snow Hill Island Formation of the Naze Peninsula of James Ross Island in anterior (= dorsal) view. Photo in **a** courtesy Eduardo Olivero; **e** and **h** reproduced from Hooker (2000) and Case et al. (2007), respectively. Scale in cm in **a**; scale equals 1 cm in **b** and **f**; 5 cm in **c–e** and **h**.

Roberts et al. (2014: Tables 1, 2, Figure 3, and elsewhere) reported putative new non-avian dinosaur fragments from several horizons of the Maastrichtian Sandwich Bluff Member of the López de Bertodano Formation of Vega Island (their units SBM6–7, 12, and 15) collected by an AP3 expedition in 2011. Nevertheless, recent reexamination of these specimens by one of us (MCL) indicates that none are definitively referable to non-avian Dinosauria. Several (AMNH FARB 30891 [from Unit SBM15], 30892 [SBM6–7], and 30896 [SBM12, ≈ the ‘Reptile Horizon’ of, e.g., Case et al., 2000a]) appear to be fragments of avian limb elements, two of which (AMNH FARB 30892 and 30896) are suggestive of large-bodied taxa comparable in size to that represented by the isolated bird femur SDSM 78247, which is also from the Sandwich Bluff Member (Case et al., 2006; MCL pers. obs.). Another bone, a dorsal rib shaft approximately 7–8 cm in proximodistal length and 1 cm in anteroposterior breadth from Unit SBM15 (AMNH FARB 30895), is reminiscent of theropod ribs in having a hollow interior; nevertheless, its thick outer cortex and subcircular distal cross section seem more consistent with a marine reptile. Although hollow ribs would be unusual for a marine reptile, they have been reported in at least one plesiosaur from elsewhere in the Upper Cretaceous of southern Gondwana, specifically in an indeterminate elasmosaurid from the Campanian–Maastrichtian Takatika Grit of the Chatham Islands, New Zealand (OU22344; Consoli and Stilwell, 2009). Other material catalogued as AMNH FARB 30896 (in addition to the ?avian limb fragment mentioned above) may also belong to marine reptiles (e.g., one bone bearing this number appears to be a plesiosaur paddle element).

### 3.1 Ornithischia

Ornithischians are the most abundantly represented non-avian dinosaurs in the JRB, both in terms of numbers of individual specimens as well as in associated skeletons. One of these skeletons constitutes the holotype of the taxonomically contentious ankylosaur *Antarctopelta oliveroi* (MLP 86-X-28-1; Olivero et al., 1986, 1991; Gasparini et al., 1987, 1996; de Ricqlès et al., 2001; Salgado and Gasparini, 2004, 2006; Coria et al., 2011; Rozadilla et al., 2016a). Recovered from the upper Campanian Gamma Member (approximately equivalent to the Herbert Sound Member of Crame et al., 1991) of the Snow Hill Island Formation (which was formerly assigned to the Santa Marta Formation; Olivero, 2012a) of the Santa Marta Cove area of James Ross Island, the *Antarctopelta* holotype initially consisted of fragmentary cranial bones, a partial dentary with an in situ tooth (Figure 5b), three other teeth, two disarticulated cervical vertebrae and a cast of a natural mold of three additional, articulated cervicals, two dorsal vertebral centra, dorsal rib fragments, the partial sacrum, eight incomplete caudal vertebrae, fragments of the scapula, coracoid, ilium, and femur, five metapodials, two

phalanges, and a collection of osteoderms comprising six distinct morphotypes (Salgado and Gasparini, 2006; Otero and Reguero, 2013; Poropat pers. comm.). Subsequently, Coria et al. (2011) reported the rediscovery of the type locality of this ankylosaur and the recovery of additional material that they regarded as pertaining to the holotypic individual, including a possible maxilla fragment, maxillary and dentary teeth, vertebral centra, the proximal end of a metatarsal, three nonungual phalanges, an incomplete ungual, and additional osteoderms.

Though the elements reported by Coria et al. (2011) have yet to be described in detail, they hold some promise for resolving the taxonomic controversies surrounding *Antarctopelta*. First, the validity of this taxon has recently been questioned. Arbour and Currie (2016) argued that the holotype is a chimera that also includes vertebrae of plesiosaurs and mosasaurs, and that the elements that are definitively ankylosaurian exhibit no diagnostic features; as such, these authors regarded *Antarctopelta* as a nomen dubium. Shortly thereafter, however, in an abstract, Rozadilla et al. (2016a) contended that the putative marine reptile elements were in fact ankylosaurian caudal vertebrae, as had originally been claimed by previous authors (e.g., Salgado and Gasparini, 2006). According to Rozadilla et al. (2016a), the posterior caudals of *Antarctopelta* possess well developed, anteroposteriorly expanded transverse processes, a character that these authors regarded as a possible autapomorphy of this taxon, thereby potentially supporting its validity.

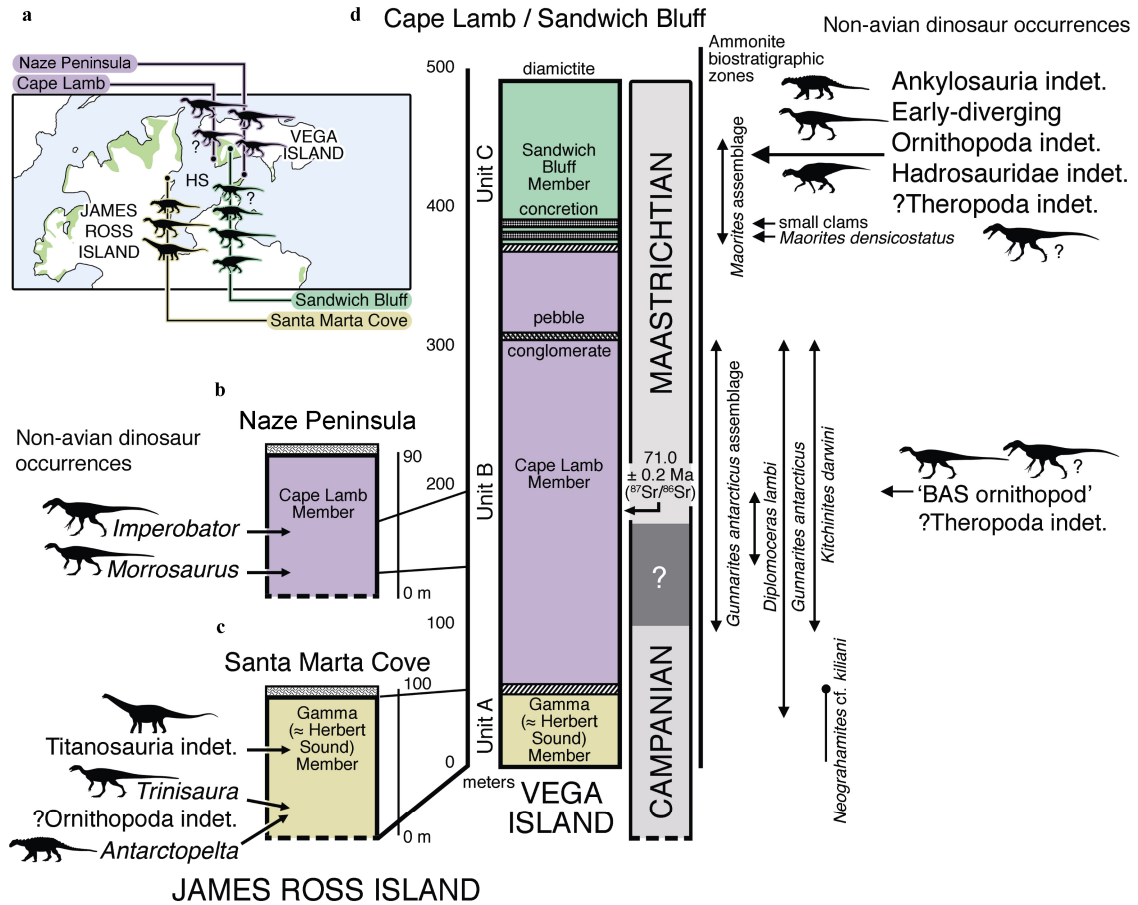
Second, regardless of whether *Antarctopelta* may be valid, different workers have claimed widely varying systematic positions for the material within Ankylosauria. Whereas Salgado and Gasparini (2006) and Rozadilla et al. (2016a) have argued that the form displays a mosaic of traits typically associated with Ankylosauridae and Nodosauridae, respectively, thus suggesting an early-diverging position within Ankylosauria, the recent phylogenetic analyses of Thompson et al. (2012) and Arbour and Currie (2016) have postulated *Antarctopelta* as a member of Nodosauridae. In particular, Arbour and Currie’s (2016) analysis (which only incorporated the fossils of *Antarctopelta* that these authors regarded as definitively ankylosaurian) positioned this ankylosaur as deeply nested within the latter group, in a clade otherwise comprised of an unnamed Patagonian nodosaurid and several North American taxa. If substantiated, this phylogenetic position would support the hypothesis, advanced by Coria and Salgado (2001), that the Patagonian taxon and *Antarctopelta* were ultimately descended from Laurasian nodosaurids. Along with the occurrence of a hadrosaurid tooth in the Maastrichtian Sandwich Bluff Member of the López de Bertodano Formation of the JRB (MLP 98-I-10-1; see below), this could support the existence of a North America–South America–Antarctica dispersal route for non-avian dinosaurs during the Late Cretaceous. This, in turn, would reinforce the longstanding



hypothesis of a paleobiogeographic connection between South America and Antarctica at the close of the Mesozoic (e.g., Case et al., 2000a; Reguero and Gasparini, 2007; Reguero et al., 2013a, 2013b). Given that *Antarctopelta* antedates MLP 98-I-10-1 by a few (roughly four or five?) million years, this might indicate that the South America–Antarctica route was operative earlier than is evidenced by that hadrosaurid fossil. This would be consistent with paleobotanical data that suggest that

southern South America and the Antarctic Peninsula had a shared flora by the late Campanian or early Maastrichtian; indeed, a biotic connection between these land areas is hypothesized to have been established as early as the Turonian (Cantrill and Poole, 2012; Leppe et al., 2012).

The only other ankylosaurian material known from the Antarctic Cretaceous is the possible nodosaurid osteoderm described above (SDSM 142814; Figure 2). Because this bone was collected from an upper level (the ‘Reptile



**Figure 6** Biostratigraphy of non-avian dinosaurs from the Upper Cretaceous (upper Campanian–Maastrichtian) Snow Hill Island and López de Bertodano formations in the Herbert Sound region of James Ross and Vega islands, JRB, Antarctic Peninsula. **a**, Map of the Herbert Sound region showing selected non-avian dinosaur localities on Vega and northern James Ross islands (the Naze Peninsula and Santa Marta Cove of James Ross Island and Cape Lamb/Sandwich Bluff of Vega Island). **b**, Simplified stratigraphic section at the Naze Peninsula, showing positions of the holotypic specimens of the early-diverging ornithopod *Morrosaurus antarcticus* and the non-avian theropod *Imperobator antarcticus*, respectively (stratigraphic sequence summarized from di Pasquo and Martin [2013], with position of *Imperobator* after that work and that of *Morrosaurus* after Rozadilla et al. [2016b]). **c**, Simplified stratigraphic section at Santa Marta Cove, showing positions of the holotypic specimens of the ankylosaur *Antarctopelta oliveroi* and the early-diverging ornithopod *Trinisaura santamartaensis* and the isolated ?ornithopod unguals and titanosaurian sauropod caudal vertebra, respectively (after Coria et al., 2013 and Reguero et al., 2013b). **d**, Simplified stratigraphic section at Cape Lamb/Sandwich Bluff, showing positions of the early-diverging ‘BAS ornithopod’, the possible theropod pedal phalanx from the same site, and the dinosaur assemblage from the Maastrichtian Sandwich Bluff Member of the López de Bertodano Formation (stratigraphic sequence summarized from Pirrie et al. [1991] with  $^{87}\text{Sr}/^{86}\text{Sr}$  datum from Crame et al. [1999]; positions of ‘BAS ornithopod’ from Hooker et al. [1991] and Pirrie et al. [1991], and Sandwich Bluff dinosaurs from Case et al. [2000a], respectively). Ammonite biostratigraphy after Pirrie et al. (1991) and Olivero (2012a, 2012b). Approximate location of the Campanian–Maastrichtian boundary (considered to reside in the zone marked with “?”) in the JRB after Crame et al. (1999, 2004). Silhouettes of Ankylosauria, early-diverging Ornithopoda, Hadrosauridae, and non-avian Theropoda courtesy Scott Hartman via PhyloPic.org. Abbreviation: HS, Herbert Sound.

Horizon’) of the Maastrichtian Sandwich Bluff Member of the López de Bertodano Formation—the stratigraphically highest Cretaceous formation in the JRB—it is notable in constituting the youngest record of Ankylosauria from Antarctica, suggesting that these armored ornithischians persisted into the latest Cretaceous on the continent. It is also worth noting that, according to the recollection of one of us (JAC<sub>1</sub>), a second probable ankylosaur osteoderm was collected from the same locality and horizon (the ‘Reptile Horizon’ of Sandwich Bluff) in 1998 (field number S061-9856), but unfortunately this fossil cannot presently be located and as such it has been omitted from Table 1.

Early-branching ornithopods—some or all of which may be referable to the Gondwanan clade Elasmaria (e.g., Novas et al., 2004; Calvo et al., 2007; Ibiricu et al., 2010, 2019; Coria et al., 2013; Barrett et al., 2014; Rozadilla and Novas, 2016; Rozadilla et al., 2016b; Madzia et al., 2018; Cruzado-Caballero et al., 2019)—are the best-represented non-avian dinosaurs in the JRB, and by extension, the Cretaceous of Antarctica. Three partial skeletons belonging to basal ornithopods have been recovered from the basin to date. The most ancient and possibly the most complete of these is the holotype of the small-bodied taxon *Trinisaura santamartaensis* (MLP 08-III-1-1), collected from the upper Campanian Gamma Member of the Snow Hill Island Formation of the Santa Marta Cove region of James Ross Island, from a stratigraphic horizon nearly equivalent to that which yielded the *Antarctopelta* holotype (MLP 86-X-28-1) more than two decades prior (Coria et al., 2013: Figure 1c; Figure 6). Most bones of *Trinisaura* are well-preserved, with described material including an incomplete dorsal vertebra, two partial dorsal ribs, three sacral centra, seven caudal vertebrae, one anterior hemal arch, the incomplete right scapulocoracoid and humerus, two metacarpals, both ilia, the right pubis, ischium, femur, and distal tibia, an incomplete metatarsal III, a pedal phalanx III-1, two pedal digit IV phalanges, and indeterminate fragments (Coria et al., 2013; Figure 5c). The holotype is believed to represent a subadult, as evidenced by the fusion of the dorsal and caudal neural arches to their respective centra as well as the coossification of the right scapula and coracoid; nevertheless, the unfused sacral centra indicate that the individual in question was not fully skeletally mature at death, a conclusion that accords with its small size (~1.5 m in total body length; Coria et al., 2013). MLP 08-III-1-1 also includes multiple still-undescribed, well-preserved bones, such as most of the left scapula (including the complete blade), the left coracoid, and additional vertebrae (MCL pers. obs.; Figure 5c). The detailed analysis of this undescribed material will undoubtedly yield additional insight into the morphology and phylogenetic relationships of this important Antarctic neornithischian taxon.

Another early-diverging ornithopod, *Morrosaurus antarcticus*, is represented by an incomplete right hind limb collected from an exposure of the upper Campanian–lower

Maastrichtian Cape Lamb Member of the Snow Hill Island Formation near Fortress Hill in the central part of the Naze Peninsula of northern James Ross Island (Cambiaso et al., 2002; Novas et al., 2002a; Rozadilla et al., 2016b). The holotype (MACN Pv 19777) includes the proximal and distal ends of the femur and tibia, the proximal end of the fibula, a distal tarsal, the nearly complete metatarsals II–IV, and the proximal two-thirds of pedal phalanx III-1 (Rozadilla et al., 2016b; Figures 4a–4g, 5d). As noted above, the distal end of a pedal phalanx and some associated fragments recovered by an AP3 expedition in 2011 from what appears to be the same locality (AMNH FARB 30897; Figure 4h–4m) probably also belong to this individual.

Taking into account their close correspondence in stratigraphic and geographic provenance, plus their probably similar phylogenetic positions (see, for example, Rozadilla et al., 2016b: Figure 7), it is at least conceivable that *Morrosaurus* and *Trinisaura* could represent the same ornithopod taxon. Nevertheless, the considerable difference in body size of the holotypes of the two taxa (with MACN Pv 19777 representing an individual perhaps 4 m in total body length, much larger than MLP 08-III-1-1; MCL pers. obs.) coupled with the morphological differences between them pointed out by Rozadilla et al. (2016b) (e.g., distinctions in the morphology of the lesser trochanter and extensor groove of the femur) cast doubt on this possibility. As such, *Morrosaurus* and *Trinisaura* are herein regarded as separate taxa.

The third and potentially the most complete skeleton of an early-diverging ornithopod yet recovered from the JRB was also the first to be found. In 1989, an expedition from the British Antarctic Survey (BAS) discovered a significant part of a skeleton of a medium-sized ornithopod (NHMUK PV R 36760, formerly BMNH BAS R.2450; ‘*Biscoveosaurus*’ of Stilwell and Long, 2011: 110) at a high elevation on Cape Lamb of western Vega Island, from an outcrop of the Cape Lamb Member (Hooker et al., 1991; Thomson and Hooker, 1991; Milner et al., 1992; Hooker, 2000; Barrett et al., 2014). Unlike other JRB ornithopod skeletons, the specimen consists of both craniodental (e.g., partial maxillae and braincase, nearly complete dentaries, teeth) and postcranial elements (e.g., cervical and dorsal vertebrae, pectoral girdle and forelimb bones) (Hooker et al., 1991; Hooker, 2000; Barrett et al., 2014) and indicates an individual estimated at 4–5 m in length (Hooker et al., 1991; Thomson and Hooker, 1991; Milner et al., 1992). NHMUK PV R 36760 remains mostly undescribed, and thus far, the only element to be illustrated in any published work is the right dentary, shown in a book chapter by Hooker (2000: 190). This dentary (Figure 5e) possesses tooth crowns that closely resemble those of other Late Cretaceous basal ornithopods from Southern Hemisphere landmasses (e.g., *Anabisetia saldiviai*, Coria and Calvo, 2002; *Kangnasaurus coetzeei*, Cooper, 1985; *Talenkauen santacruzensis*, Novas et al., 2004), supporting the hypothesis, advanced by Barrett

et al. (2014), that the taxon it represents might be part of an endemic Gondwanan radiation of early-branching ornithopods (e.g., *Elasmaria*).

Interestingly, both the *Morrosaurus* hind limb (i.e., MACN Pv 19777/AMNH FARB 30897) and the skeleton of the ‘BAS ornithopod’ NHMUK PV R 36760 were collected from within the same stratigraphic unit, the Cape Lamb Member of the Snow Hill Island Formation. Indeed, as discussed below, these two ornithopod specimens come from a fairly narrow stratigraphic range within the Cape Lamb Member (Figure 6). Both pertain to basal ornithopods, possibly elasmarians, and both represent medium-sized individuals roughly 4 m in total body length. This raises the possibility that the ‘BAS ornithopod’ could be referable to *Morrosaurus*, and if this is indeed the case, it would greatly augment the hypodigm of that taxon. Regrettably, however, as NHMUK PV R 36760 does not preserve the hind limb (Hooker et al., 1991; Barrett et al., 2014), no elements currently overlap between the two forms, precluding their direct comparison (but see also below).

Additional ornithopod material from the JRB is mostly limited to isolated bones. Coria et al. (2007) described two dissociated ornithischian—possibly ornithopod—pedal unguals (MLP 07-III-2-1 and MLP 07-III-2-2) from the Gamma Member of the Santa Marta Cove area of James Ross Island, while Coria et al. (2015a, 2015b) briefly reported an associated partial tibia and astragalus from the Cape Lamb Member on Vega Island (MLP 15-I-7-1). If, as argued by Coria et al. (2013), the holotype of *Trinisaura* is a subadult (i.e., it was nearly skeletally mature at death), then the comparatively large size of MLP 07-III-2-1 and MLP 07-III-2-2 indicates that they are not referable to this taxon, thus suggesting the presence of at least one additional ornithopod species in the Gamma Member. Moreover, along with material currently under study (CM 93790; CM 93791; JAC<sub>1</sub> pers. obs.), the ungual described herein (MLP 98-I-10-70) suggests, for the first time, the presence of early-diverging ornithopods in the Maastrichtian Sandwich Bluff Member of the López de Bertodano Formation.

Hadrosaurid ornithopods are represented in the JRB by a single, isolated tooth from the Maastrichtian ‘Reptile Horizon’ of the Sandwich Bluff Member of the López de Bertodano Formation of Sandwich Bluff on Vega Island (MLP 98-I-10-1; Case et al., 1998, 2000a [identified as MLP 99-I-10-1 by Otero and Reguero, 2013]; Figure 5f), and possibly also by the partial distal end of a metatarsal from a near-coeval horizon (KIB 9) of this same formation on Seymour (= Marambio) Island (MLP 96-I-6-2; Rich et al., 1999). Hadrosaurid pedal phalanges were also reported from the Sandwich Bluff Member by Case et al. (2000b, 2007), though the specimens in question cannot currently be located. Conversely, although Otero and Reguero (2013) reported the tooth MLP 98-I-10-1 as missing, it has since been relocated in the MLP collection and was examined by

two of the present authors (MCL and PMO) during a visit to that institution in late 2017. Hadrosaurids presumably emigrated to Antarctica from South America sometime during the Campanian or Maastrichtian after their arrival in the latter continent from North America by the late Campanian (Casamiquela, 1964; Prieto-Marquez and Salinas, 2010; Cruzado-Caballero and Powell, 2017). Case et al. (2000a) tentatively assigned the tooth MLP 98-I-10-1 to Hadrosaurinae (= Saurolophinae of many recent works), which would accord with the known fossil record of South American hadrosaurids that, at present, is definitively composed only of hadrosaurines (e.g., *Bonapartesaurus rionegrensis*, Cruzado-Caballero and Powell, 2017; *Secernosaurus koernerii*, Prieto-Marquez and Salinas, 2010). The fact that all JRB hadrosaurid/putative hadrosaurid specimens come from Maastrichtian horizons—but that material of these dinosaurs is thus far absent from more ancient strata within the basin—is notable, and suggests that these ornithopods may not have colonized the Antarctic Peninsula until the last few million years of the Cretaceous. Nevertheless, a much more robust Antarctic Cretaceous non-avian dinosaur fossil record will be required before this hypothesis may be evaluated. Furthermore, because the Seymour Island metatarsal is damaged and missing one of its distal condyles, and also that metatarsals of hadrosaurids are generally comparable in distal morphology to those of non-hadrosaurid ornithopods, it is conceivable that this bone could instead pertain to another ornithopod clade, such as *Elasmaria*, some members of which (e.g., *Macrogyphosaurus gondwanicus*, Calvo et al., 2007; *Sektensaurus sanjuanboscoi*, Ibiricu et al., 2010, 2019) attained body sizes consistent with the individual represented by this metatarsal (MCL pers. obs.).

### 3.2 Sauropoda

With the possible exception of at least some of the putative footprints reported by Olivero et al. (2007; see above), sauropod dinosaurs are currently represented in the JRB only by an isolated, incomplete bone: MLP 11-II-20-1, a partial caudal centrum from the upper Campanian Gamma Member of the Snow Hill Island Formation of the Santa Marta Cove area of James Ross Island (Cerda et al., 2012; Figure 5g). The procoelous nature of this centrum led Cerda et al. (2012) to interpret the specimen as that of a lithostrotian titanosaur, a clade that is abundant and widespread throughout the Upper Cretaceous of other Gondwanan landmasses (Curry Rogers, 2005; Wilson, 2006; Gorscak and O’Connor, 2016; Sallam et al., 2018; González Riga et al., 2019). Nevertheless, as noted by Cerda et al. (2012), the specimen exhibits only moderate development of the posterior articular condyle (MCL pers. obs.); this, coupled with the present, highly labile state of titanosaurian systematics (see, for example, the phylogenetic hypotheses presented in the references above) leads us to regard this vertebra as that of a phylogenetically indeterminate member

of Titanosauria.

### 3.3 Non-Avian Theropoda

Though, as noted above, fossils of avian theropods (i.e., birds) are reasonably common in Upper Cretaceous horizons of the JRB (e.g., Clarke et al., 2005, 2016), material of non-avian theropods is much scarcer. The most complete, informative non-avian theropod specimen from the JRB is the holotype of the recently-named, medium-sized possible deinonychosaur *Imperobator antarcticus*, initially discovered and collected in 2003 from an exposure of the upper Campanian–lower Maastrichtian Cape Lamb Member of the Snow Hill Island Formation on the Naze Peninsula of James Ross Island (UCMP 276000; Case et al., 2007; di Pasquo and Martin, 2013; Ely and Case, 2016, 2019). Described material of *Imperobator* currently consists of teeth and distal hind limb elements (Case et al., 2007; Ely and Case, 2019; Figure 5h). Recently, however, two of us (JAC<sub>1</sub> and DEM) relocated additional material pertaining to UCMP 276000 at facilities of Eastern Washington University and the South Dakota School of Mines and Technology, respectively, including skull fragments (probably belonging to at least the premaxilla, maxilla, and/or dentary), a caudal vertebra, and additional teeth and pedal elements (MCL, JAC<sub>1</sub>, DEM pers. obs.). Moreover, the 2011 and 2016 AP3 expeditions returned to the *Imperobator* type locality and recovered additional fossils that almost certainly pertain to the individual represented by UCMP 276000, including a tooth and several bone fragments (AMNH FARB 30894), a partial pedal ungual, and fragmentary putative cranial remains (Lamanna et al., 2017). Several of the present authors are currently undertaking a comprehensive reassessment of the morphology and phylogenetic relationships of *Imperobator* that will include a description of all known material of this taxon.

Other non-avian theropod material from the JRB is limited to isolated bones. Molnar et al. (1996) described MLP 89-XII-1-1, a distal tibia from the Coniacian Hidden Lake Formation of the Cape Lachman region of James Ross Island that they considered to belong to an early-diverging tetanuran similar to the Middle Jurassic megalosauroid *Piatnitzkysaurus floresi* (Bonaparte, 1986). This fossil is important in that it constitutes the only known record of a continental vertebrate from this stratigraphic unit and the oldest dinosaurian fossil from the Antarctic Cretaceous (Schweitzer et al., 2012). As such, although such a study would be beyond the scope of the present paper, we believe that MLP 89-XII-1-1 requires reanalysis in light of the numerous Cretaceous non-avian theropod discoveries that have been made on Gondwanan continents during the past quarter-century (e.g., Novas et al., 2013; Ezcurra and Novas, 2016). For example, spinosaurids (e.g., *Spinosaurus aegyptiacus*, Stromer, 1915) are the only megalosauroids known to have survived into the Late Cretaceous, and as such, MLP 89-XII-1-1 should be compared to the distal

tibiae of these distinctive semi-aquatic theropods. Megaraptoran affinities also seem possible for the Hidden Lake tibia, as these enigmatic tetanurans are well represented in mid- and Late Cretaceous sediments elsewhere in southern Gondwana (e.g., Australia, Bell et al., 2016; Patagonia, Porfiri et al., 2018).

More recently, Coria et al. (2015a, 2015b) briefly reported specimen MLP 15-I-7-2, a putative theropod pedal phalanx (possibly phalanx III-1) from the Cape Lamb Member on Vega Island, from the same site on Cape Lamb that yielded the still-undescribed ‘BAS ornithopod’ (NHMUK PV R 36760) discussed above (Hooker et al., 1991; Barrett et al., 2014). The occurrence of fossils of two dinosaurian taxa at this single site—which, as is the case for other JRB dinosaur localities, represents a marine depositional environment where material of terrestrial vertebrates such as non-avian dinosaurs would be expected to be rare—would be surprising, but since the present authors have not examined this phalanx firsthand, we accept its identification as presented by Coria et al. (2015a, 2015b). Nevertheless, should this phalanx eventually prove referable to the ‘BAS ornithopod’, it would be important in constituting the only skeletal element that might overlap between that skeleton and known material of the potentially closely related (or perhaps even synonymous) ornithopod *Morrosaurus*, for which pedal phalanx III-1 is definitively known (Rozadilla et al., 2016b). Finally, Case et al. (2003) mentioned non-avian theropod material from the Maastrichtian Sandwich Bluff Member of the López de Bertodano Formation of Sandwich Bluff on Vega Island. This report likely refers to the same theropod material from the Maastrichtian of this island that was mentioned by Olivero et al. (2007: 529): “Recently, (an) additional theropod (fragment was) recovered from the Maastrichtian of Vega... (Island) (J. E. Martin, pers. comm. to [E. B. Olivero], 2005).” According to the recollection of one of us (JAC<sub>1</sub>), the specimen in question was an ungual (field number S061-9917) that is currently missing. If this fossil can be relocated, it might be significant in comprising the first non-avian theropod record from the López de Bertodano Formation—the youngest Cretaceous geologic unit in the JRB.

## 4 Biostratigraphy

Analysis of the biostratigraphy of Late Cretaceous non-avian dinosaur discoveries from the Herbert Sound region of the JRB demonstrates the near-contemporaneous occurrence of many of the taxa represented by these finds (Figure 6; Ely and Case, 2016, 2019; Case and Ely, 2017). On Vega Island, at least the upper half of the Cape Lamb Member of the Snow Hill Island Formation falls into the lower part of the Maastrichtian Stage based on an <sup>87</sup>Sr/<sup>86</sup>Sr isotopic datum of 71.0 ± 0.2 Ma at a stratigraphic level approximately 135 m above the base of this member and

81 m above the base of the range of the *Gunnarites antarcticus* faunal assemblage (Pirrie et al., 1991; Crame et al., 2004; Figure 6d). In the JRB, the Campanian–Maastrichtian boundary (72.1 Ma) was suggested to be near the beginning of this faunal assemblage within the 310 m reference section on Cape Lamb of Vega Island (Crame et al., 1999). The *G. antarcticus* assemblage extends through approximately 210 m of this reference section, with the ammonites *Gunnarites antarcticus* and *Kitchinities darwini* occurring throughout this range. However, the heteromorph ammonite *Diplomoceras lambi* (= *D. cylindraceum* according to some authors; e.g., Kennedy and Henderson, 1992; Witts et al., 2015) is restricted to only ~50 m of the lower half of the *G. antarcticus* assemblage range (Pirrie et al., 1991). Although the stratigraphic range of *D. lambi* is much more extensive (from the upper Campanian to upper Maastrichtian) in the eastern portion of the JRB (i.e., the Admiralty Sound area, which encompasses the east coast of James Ross Island plus Seymour and Snow Hill islands) (see Milanese et al., 2018), this species has only a short stratigraphic range in the Herbert Sound area. Thus, the short (~50 m) range of *D. lambi* in the Herbert Sound area represents a short-term transgression to a deeper water setting that was followed by shallowing-upward conditions from the end of the range of this ammonite species to the top of the Cape Lamb Member (Pirrie et al., 1991). The  $71.0 \pm 0.2$  Ma datum is from near the top of the *D. lambi* range in the reference section on Vega Island (Crame et al., 1999). A partial skeleton belonging to an as-yet unidentified early-diverging ornithomorph dinosaur (the ‘BAS ornithomorph’) was recovered by the BAS from the same part of the section (i.e., the top of the *D. lambi* range; ~5 m above the  $71.0 \pm 0.2$  Ma datum) on the eastern slope of Cape Lamb in 1989 (Hooker et al., 1991; Barrett et al., 2014). As such, this specimen is considered to be early Maastrichtian in age (Figure 6d).

The western flank of Comb Ridge at the northern end of the Naze Peninsula of James Ross Island exposes a 90 m-thick section composed of interbedded green-gray massive and laminated fine-grained quartz sandstones and greenish-yellow argillaceous mudstones and siltstones of

the Cape Lamb Member (di Pasquo and Martin, 2013; Figure 6b). The holotype of the non-avian theropod *Imperobator antarcticus* was collected in the middle of the Comb Ridge section, between 41–48 m above the local base of this member (Case et al., 2007; di Pasquo and Martin, 2013; Ely and Case, 2019; Figure 6b). Also found at this stratigraphic level were the ammonites *G. antarcticus*, *D. lambi*, and *K. darwini*, the pelecypod *Pinna* sp., and the decapod *Hoploparia stokesi*, all of which are members of the *G. antarcticus* assemblage (Table 2). Consequently, the stratigraphic location, biostratigraphic associations, and age assessment of *Imperobator* indicates that this theropod was a near-contemporary of the ‘BAS ornithomorph’ (albeit lower in stratigraphic section and therefore slightly more ancient).

Another partial skeleton of an early-diverging ornithomorph, the holotype of *Morrosaurus antarcticus*, was also recovered from deposits of the Cape Lamb Member of the Naze, approximately 30 m downsection from the stratum from which *Imperobator* was collected (Rozadilla et al., 2016b; Figure 6b). The *Morrosaurus* specimen was also associated with the *G. antarcticus* faunal assemblage, and it definitively occurs within the *D. lambi* range, given that material of the latter ammonite was found in association with this ornithomorph. As such, all three non-avian dinosaur partial skeletons from the Cape Lamb Member—the ‘BAS ornithomorph’ and the type specimens of *Morrosaurus* and *Imperobator*—were recovered from the *D. lambi* stratigraphic range and are thus late Campanian or early Maastrichtian in age.

As is also the case for *Morrosaurus*, the small-bodied neornithischian dinosaur *Trinisaura santamartaensis* is generally regarded as an early-diverging ornithomorph, possibly a representative of Elasmaria (Coria et al., 2013; Rozadilla et al., 2016b; Madzia et al., 2018). The holotypic specimen of *Trinisaura* was recovered from the upper Campanian Gamma Member (Olivero, 2012a; ≈ Herbert Sound Member of Crame et al., 1991) of the Snow Hill Island Formation from the Santa Marta Cove area of James Ross Island, only 12 km west of the Naze (Figure 6c). The Gamma Member underlies the Cape Lamb Member within the Herbert Sound region (Figure 6d). The ankylosaur

**Table 2** Key species of the *Gunnarites antarcticus* faunal assemblage recovered from the sections of the Upper Cretaceous (upper Campanian–lower Maastrichtian) Cape Lamb Member of the Snow Hill Island Formation on Cape Lamb of Vega Island (Pirrie et al., 1991) and the measured section at Comb Ridge of the Naze Peninsula of James Ross Island (di Pasquo and Martin, 2013)

Higher taxon	Species	Cape Lamb (Vega Island)	Comb Ridge, the Naze Peninsula (James Ross Island)
Ammonoidea	<i>Gunnarites antarcticus</i>	✓	✓
	<i>Kitchinities darwini</i>	✓	✓
	<i>Diplomoceras lambi</i>	✓	✓
Nautiloidea	<i>Eutrephoceras</i> sp.	✓	--
Decapoda	<i>Hoploparia stokesi</i>	✓	✓
Pelecypoda	<i>Pinna</i> sp.	✓	✓

*Antarctopelta oliveroi* was also recovered from the Gamma Member, only 10 m below the level that yielded *Trinisaura* (Figure 6c). An isolated caudal vertebra of a third dinosaurian taxon, a titanosaurian sauropod, was recovered from the upper third of Gamma Member deposits at Santa Marta Cove (Cerda et al., 2012). The titanosaur vertebra was collected approximately 40 m upsection from the *Trinisaura* locality (Figure 6c).

Olivero (2012a, 2012b) placed the first occurrence of *G. antarcticus* at the very top of the Gamma Member section at Santa Marta Cove, overlapping the 70 m total stratigraphic range of a second ammonite species, *Neograhamites* cf. *kiliani*. This same ammonite biostratigraphic sequence is repeated in the Gamma Member ( $\approx$  Herbert Sound Member) -equivalent sequence on Cape Lamb (Olivero, 2012a). The *G. antarcticus* and *N. cf. kiliani* ammonite biostratigraphic zones allow for correlation between the dinosaur-bearing sequence in the Santa Marta Cove area with those from the Cape Lamb Member on the Naze and Cape Lamb (Figure 6). Based on the stratigraphic sections of Olivero (2012a, 2012b) and Coria et al. (2013), and the reference section for the Cape Lamb Member on Vega Island (Pirrie et al., 1991; Crame et al., 2004), this places the three dinosaurs from the Santa Marta Cove area (*Antarctopelta*, *Trinisaura*, and the titanosaur) near the top of the Campanian depositional succession. Consequently, these three taxa are probably late Campanian in age. Moreover, the three dinosaur skeletons from the Cape Lamb Member (the ‘BAS ornithopod’ and the *Morrosaurus* and *Imperobator* holotypes), all of which are associated with the *D. lambi* zone, are temporally clustered around the Campanian–Maastrichtian boundary. These six dinosaur discoveries collectively represent at least five species—*Antarctopelta oliveroi*, *Trinisaura santamartaensis*, *Morrosaurus antarcticus*, *Imperobator antarcticus*, and the unnamed titanosaur—and potentially a sixth if the ‘BAS ornithopod’ is distinct from *M. antarcticus*. Given the limited spread of stratigraphic section, and therefore age, between these discoveries, we consider all as occurring within a few million-year span in proximity to the Campanian–Maastrichtian boundary.

Dinosaur fossils from the Sandwich Bluff Member of the López de Bertodano Formation of Vega Island are undoubtedly stratigraphically younger than those from the underlying Snow Hill Island Formation. The Sandwich Bluff Member dinosaurs reside within the *Maorites* invertebrate faunal assemblage zone rather than the *G. antarcticus* zone that is typical of the subjacent Cape Lamb Member of the Snow Hill Island Formation (Figure 6d). Based on the dinoflagellate cyst biostratigraphy of the López de Bertodano Formation of Seymour Island presented by Bowman et al. (2012), the presence of the cyst *Manumiella bertodano* (= “*M. n. sp. 2*” of Pirrie et al., 1991) throughout most of the Sandwich Bluff Member supports a Maastrichtian age for this unit and its fossil assemblage (Roberts et al., 2014). More precise dating of various horizons of the Sandwich Bluff Member within the

Maastrichtian must await the results of ongoing studies (EMR pers. obs.).

## 5 Paleobiogeography

The paleobiogeographic implications of the Upper Cretaceous non-avian dinosaur assemblage of the JRB have been interpreted in a variety of ways in the more than three decades that have elapsed since the discovery of its first-known member—the ankylosaur now known as *Antarctopelta oliveroi*—in the mid-1980s. The assemblage has frequently been regarded as endemic on a regional scale (e.g., Molnar, 1989; Novas et al., 2002a); for instance, Novas et al. (2002a) noted the seemingly unusual preponderance of ornithischian fossils and argued that the JRB dinosaurs were part of a polar Gondwanan faunal zone that also encompassed Australia and New Zealand. In this sense, the JRB dinosaurs would constitute a terrestrial manifestation of the Weddellian Biogeographic Province, a southern high-latitude biotic region characterized by endemic shallow marine invertebrate and vertebrate faunas during the Late Cretaceous and Paleogene (Zinsmeister, 1979, 1982; Case, 1988; Novas et al., 2002b; Otero et al., 2012; Reguero et al., 2012; O’Gorman and Coria, 2017). Other authors, by contrast, have interpreted the JRB dinosaur fauna as largely ‘relictual,’ being primarily composed of representatives of lineages that were geographically widespread earlier in the Mesozoic but that vanished from landmasses other than Antarctica prior to the late stages of the Cretaceous (e.g., Molnar et al., 1996; Case et al., 2000a, 2003, 2007; Martin and Case, 2005; Stilwell and Long, 2011; Leppe and Stinnesbeck, 2014). Still others (e.g., Reguero and Gasparini, 2007) have considered the assemblage to be too poorly understood to enable an assessment of its paleobiogeographic relationships.

In recent years, additional JRB dinosaur fossils have been discovered, illuminating the nature of the animals themselves as well as their collective paleobiogeographic significance. Although a definitive paleobiogeographic analysis is beyond the scope of the present paper, it now appears likely that the Campanian–Maastrichtian dinosaur assemblage of the JRB most closely resembled coeval faunas from southern South America (Lamanna, 2013; Reguero et al., 2013a). This is because, with the possible exception of the non-avian theropod *Imperobator antarcticus* (Ely and Case, 2019), all known JRB dinosaurs that are identifiable to reasonably low taxonomic levels appear closely allied to penecontemporaneous taxa from Patagonia. In the case of the ankylosaur *Antarctopelta*, although alternative hypotheses have been proposed, Arbou and Currie (2016) considered this form to be closely related to the unnamed nodosaurid from the Campanian–Maastrichtian Allen Formation of Río Negro Province in northern Patagonia (Salgado and Coria, 1996; Coria and Salgado, 2001). Similarly, the early-branching (elasmarian?)

ornithopods *Trinisaura santamartaensis* and *Morrosaurus antarcticus* (and the ‘BAS ornithopod’, if it is distinct from *Morrosaurus*) would appear to be closely related to Patagonian Late Cretaceous taxa such as *Anabisetia saldiviai*, *Gasparinisaura cincosaltensis*, *Macrogyphosaurus gondwanicus*, *Notohypsilophodon comodorensis*, and *Talenkauen santacruzensis* (Coria et al., 2013; Rozadilla and Novas, 2016; Rozadilla et al., 2016b). Hadrosaurs and titanosaurs, represented by isolated elements from Campanian–Maastrichtian deposits in the JRB (Case et al., 2000a, 2000b; Cerda et al., 2012), are both well-known from the Patagonian Late Cretaceous; indeed, though it remains mostly undescribed, a hadrosaur/titanosaur-dominated fauna has recently been recovered from terminal Cretaceous sediments in southernmost Chile, constituting the most austral non-avian dinosaur assemblage yet known from South America (Leppe et al., 2014; Soto-Acuña et al., 2014; Vogt et al., 2014). Taken together, this evidence suggests that at least some non-avian dinosaur lineages were able to disperse between southern South America and the Antarctic Peninsula at the end of the Mesozoic. Whether this proposed Patagonian/West Antarctic Campanian–Maastrichtian dinosaur fauna extended to more easterly high-latitude Gondwanan land areas such as southernmost Africa, southern Australia, New Zealand, and/or East Antarctica—as might be predicted by the distribution of Weddellian marine and floral assemblages—has yet to be confirmed, because, although generally consistent with this hypothesis, latest Cretaceous continental vertebrate faunas from these latter regions remain exceedingly poorly known (e.g., Cooper, 1985; Molnar and Wiffen, 1994; Rich, 1996; Agnolin et al., 2010).

Again, the only possible exception to this paleobiogeographic pattern—in other words, the only latest Cretaceous JRB dinosaur that may not have demonstrable affinities with southern South American forms—is the theropod *Imperobator*, recently postulated as a basal (i.e., non-dromaeosaurid, non-troodontid) deinonychosaur (Ely and Case, 2016) or as a paravian of uncertain phylogenetic position (Ely and Case, 2019). The only deinonychosaur currently known from South America, or anywhere in the latest Cretaceous of the Gondwanan landmasses, are unenlagiine dromaeosaurids (e.g., Novas and Puerta, 1997; Forster et al., 1998; Makovicky et al., 2005; Novas et al., 2008); as such, the presence of an early-diverging deinonychosaur in the JRB at the same time would be more consistent with the ‘relictual’ hypothesis than with any scenario of end-Mesozoic faunal dispersal between Patagonia and West Antarctica. Nevertheless, and as noted above, additional fossils of *Imperobator* that were not described by Ely and Case (2016, 2019) have recently come to light. Forthcoming description and analysis of this material promises to further clarify (and potentially revise) the phylogenetic position of this important JRB dinosaur, and will likely also offer new insights into its paleobiogeographic significance (MCL pers. obs.).

Finally, it is interesting to note that nearly all non-avian dinosaur fossils from the JRB—with the exception of a single partial ornithopod metatarsal from Seymour Island (Rich et al., 1999) and (possibly) the putative footprints from Snow Hill Island (Olivero et al., 2007; see above)—have been found in a geographically restricted area that encompasses northwestern and north-central James Ross and southwestern Vega islands (i.e., the land areas that border Herbert Sound; Figures 1a, 6a). Given the abundance of exposure of contemporaneous or penecontemporaneous Upper Cretaceous fossil-bearing sediments further to the southeast (Figure 1a), this does not appear to be purely a function of outcrop area. Instead, and although we are hesitant to speculate given the exceedingly small sample size at present, it seems possible that non-avian dinosaur material may be legitimately more abundant (if still vanishingly rare) in the Herbert Sound region versus other parts of the JRB. If so, this could potentially be due to the presumably closer proximity of Cretaceous continental paleoenvironments (where terrestrial animals such as non-avian dinosaurs would be expected to have lived) on the Antarctic Peninsula to the Herbert Sound region as opposed to other JRB areas (Crame pers. comm.). Only continued paleontological exploration of Cretaceous horizons within the basin may enable an evaluation of this hypothesis.

## 6 Conclusions

The fossil record of non-avian dinosaurs from the JRB mostly consists of fragmentary specimens, yet multiple taxa are represented that collectively hold significant paleobiogeographic implications. Material of Ankylosauria, early-diverging Ornithopoda, Hadrosauridae, Titanosauria, and non-avian Theropoda demonstrates that, rather than comprising a ‘relictual’ or endemic fauna, most Late Cretaceous dinosaurs from West Antarctica had coeval close relatives in geographically adjacent southern South America. This, in turn, supports the proposed existence of some form of terrestrial biotic connection between these two landmasses at the close of the Mesozoic. Moreover, the majority of the most important Antarctic Cretaceous dinosaur finds—including all five reasonably complete skeletons and all four named taxa—have been recovered from a stratigraphically narrow interval that encompasses the late Campanian and early Maastrichtian of northern James Ross and western Vega islands. Ongoing field efforts by researchers from various nations (e.g., Argentina, the United States) and the comprehensive description of previously discovered specimens (e.g., the holotype of *Imperobator antarcticus*, the ‘BAS ornithopod’, the distal hind limb CM 93790) promise to further improve our understanding of the non-avian dinosaurs of the JRB, thereby casting much-needed light on the nature of Antarctic continental vertebrate assemblages immediately preceding the end-Cretaceous mass extinction.



## Institutional abbreviations

AMNH—American Museum of Natural History, New York, USA

BMNH—British Museum of Natural History (now, The Natural History Museum), London, UK

CM—Carnegie Museum of Natural History, Pittsburgh, USA

MLP—Museo de La Plata, La Plata, Argentina

MPCA—Museo Provincial Carlos Ameghino, Cipolletti, Argentina

NHMK—The Natural History Museum, London, UK

OU—Geology Museum, University of Otago, Dunedin, New Zealand

SDSM—South Dakota School of Mines and Technology, Rapid City, USA

UCMP—University of California Museum of Paleontology, Berkeley, California

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