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PALEONTOLOGY

Late Campanian-Early Maastrichtian Vertebrates From The James Ross Basin, West Antarctica: Updated Synthesis, Biostratigraphy, And Paleobiogeography

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Abstract: The Snow Hill Island Formation (SHIF; late Campanian – early Maastrichtian) crops out in the northeast of the Antarctic Peninsula and constitutes the basal part of the late Campanian-early Maastrichtian sedimentary succession of the James Ross Basin (NG Sequence). Its major exposures occur at the James Ross and Vega islands. Several fossil-bearing localities have been identified in the SHIF providing a valuable fauna of invertebrates and vertebrates, and flora. Our study focuses on the vertebrate fauna recovered at Gamma and Cape Lamb members of the SHIF. The marine vertebrate assemblages include chondrichthyans, actinopterygians, and marine reptiles (elasmosaurid plesiosaurs and mosasaurs). A diverse terrestrial vertebrate assemblage has been reported being characterized by dinosaurs (sauropod, elasmarian ornithopods, nodosaurid ankylosaur, and a paravian theropod), pterosaurs and birds. Most SHIF dinosaurs share close affinities with penecontemporaneous taxa from southern South America, indicating that at least some continental vertebrates could disperse between southern South America and Antarctica during the Late Cretaceous. The Snow Hill Island Formation provides the most diverse Late Cretaceous marine and continental faunas from Antarctica. The present study summarizes previous and new vertebrate findings with the best actualized stratigraphical framework, providing a more complete fauna association and analyzing further perspectives.

Key words: Antarctic Peninsula, Late Cretaceous, NG Sequence, Snow Hill Island Formation.

INTRODUCTION

Upper Cretaceous vertebrate-bearing horizons occur in one unique region in Antarctica: the James Ross Basin (JRB). This basin, named after the eponymous archipelago, is located off northeastern part of the Antarctic Peninsula (Fig. 1). The JRB provides the most extensive record of Upper Cretaceous strata known presently anywhere in Antarctica and preserves over 5000 m of exposed Cretaceous strata of the Aptian-Coniacian Gustav and the Santonian-Danian Marambio groups (Rinaldi et al. 1978, Olivero et al. 1986, Pirrie 1989, Crame et al. 1991, 1996, 2004, Pirrie et al. 1997). The finer-grained Marambio Group is well-exposed in outcrops in several islands of the archipelago (James Ross, Vega, Humps, Snow Hill, Seymour and Cockburn), and its stratigraphy has been recently summarized by Olivero (2012a). The Marambio Group has a

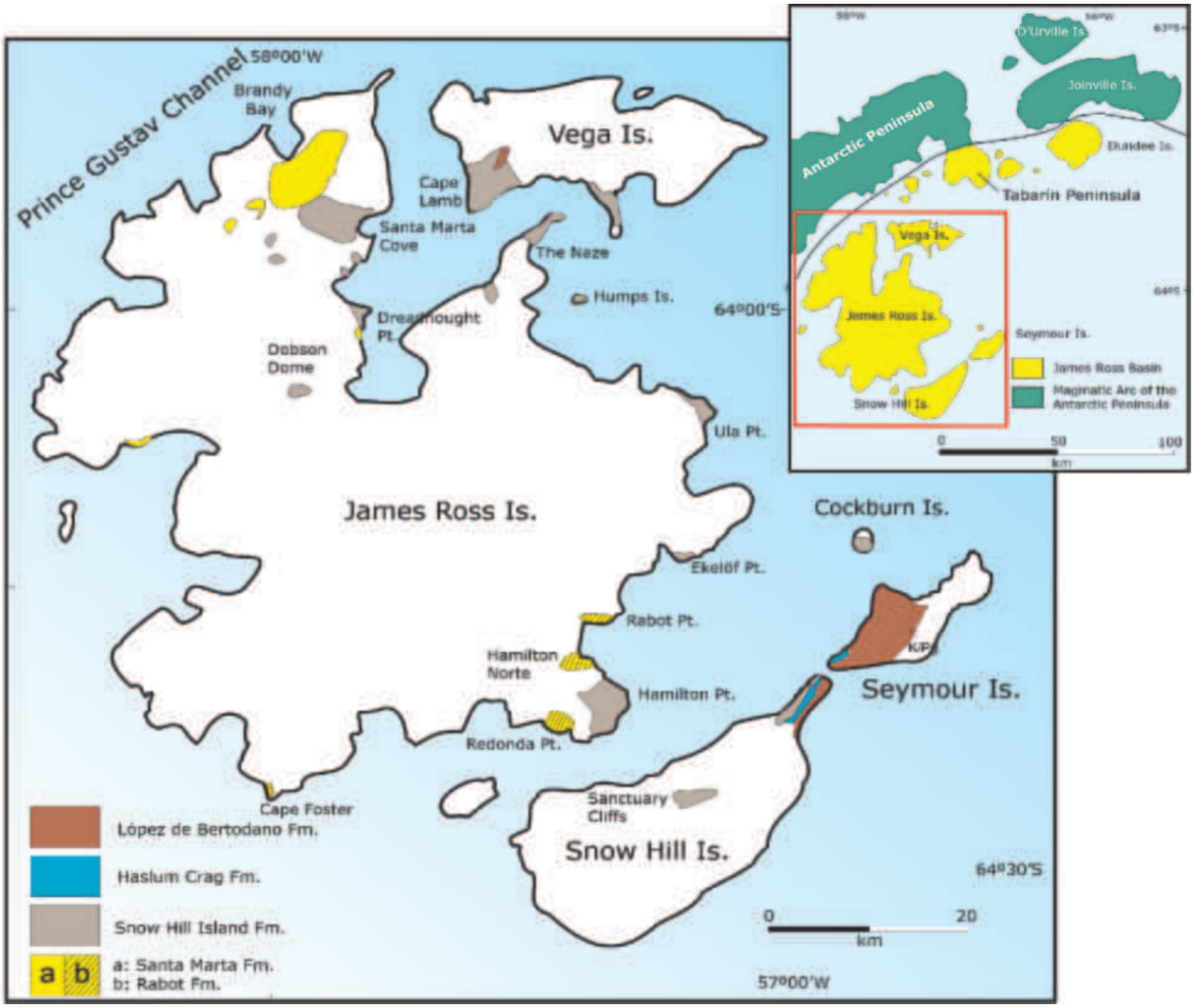

Figure 1. Map showing distribution of Upper Cretaceous rocks of the Snow Hill Island, Haslum Crags formations of the NG Sequence (Olivero 2012a) in the James Ross Basin, Antarctic Peninsula.

stratigraphic thickness of around 3000 m, with sediment supplied by a volcanic arc in the west deposited on a shelf prograding eastward into the Weddell Sea (Olivero, 2012a). Beginning in the 1970s and supported by the Instituto Antártico Argentino (Argentina), geologists of this institution have explored the James Ross Basin for stratigraphy and fossils.

The uninterrupted explorations and systematic study of the fossils recovered led to understand the Snow Hill Island Formation (SHIF) as one of the most significant sources of Late Cretaceous fossil vertebrates in Antarctica. The SHIF is included in the NG Sequence (after the ammonoid genera *Neograhamites* and *Gunnarites* of Olivero 2012b) of the Marambio Group together with the Haslum Crag Formation. The complete sequence is late Campanian–early Maastrichtian in age (Olivero 2012a, Milanese et al. 2020).

Since the beginning of the 1970s and supported by the Instituto Antártico Argentino (IAA), geologists of this institution have explored the James Ross Basin. The first fossil vertebrate remains from the Snow Hill Island Formation were discovered in 1975 (del Valle et al. 1977); plesiosaurs and mosasaurs were discovered in Vega and James Ross islands and the first

Antarctic non-avian dinosaur was collected from the Gamma Member of the SHIF in James Ross Island (Olivero et al. 1986, Salgado & Gasparini 2006).

Over the last fifty years, geologists and paleontologists from multiple nations (e.g., Argentina, Brazil, Chile, Poland, the United Kingdom, the United States, Sweden, Czech Republic) have searched for Cretaceous fossil vertebrates in the James Ross Basin, on several islands (Seymour, Ross, Vega, etc.) adjacent to the northeastern tip of the Antarctic Peninsula (Reguero & Gasparini 2006, Reguero et al. 2013a; Fig. 1).

Since 2005 geologists and paleontologists of the IAA and Museo de La Plata (MLP) have developed a comprehensive field program (Antarctic field trips 2005, 2010–2020). Part of the explorations carried out have focused on late Campanian–early Maastrichtian strata of the Snow Hill Island Formation. The fossil vertebrates recovered are then studied, assessing their biostratigraphic, paleoecologic, and paleobiogeographic significance in the context of West Antarctica´s final break-up. A key point of the program is seeking fossils that might bridge Upper Cretaceous terrestrial assemblages of Antarctica, Australia, and southern South America.

The present article is an update of the SHIF vertebrate fossil record (including new records). We discuss the stratigraphic and biogeographic implications of the vertebrates reported, as well as their further perspectives.

Institutional Abbreviations

AMNH, American Museum of Natural History, New York (FARB is for fossil amphibians, reptiles and birds), USA; **BAS**, British Antarctic Survey, London, England; **BMNH**, British Museum of Natural History, London, England; **IAA**, Instituto Antártico Argentino, Buenos Aires, Argentina; **MLP**, Museo de La Plata, La Plata, Argentina; **MN**, Departamento de Geologia e Paleontologia) of the Museu Nacional (MN) - Universidade Federal do Rio de Janeiro (UFrJ), Brazil; **NHMUK**, Natural History Museum, London, United Kingdom; **SDSM**, South Dakota School of Mines and Technology, Rapid City, United States of America; **UCMP**, University of California Museum of Paleontology, United States of America.

Geographical Abbreviations—JRB, James Ross Basin; **JRI**, James Ross Island; **LDB**, López de Bertodano, Seymour Island; **SMC**, Santa Marta Cove, James Ross Island; **SEY**, Seymour Island; **TNZ**, The Naze, James Ross Island; **VEG**, Cape Lamb, Vega Island.

Other Abbreviations

MG, early Maastrichtian-Danian stratigraphic sequence of the James Ross Basin (Olivero, 2012a), **NG**, late Campanian-early Maastrichtian stratigraphic sequence of the James Ross Basin (Olivero, 2012a).

GEOLOGICAL AND STRATIGRAPHIC SETTING

The Snow Hill Island Formation comprises five members of late Campanian-early Maastrichtian age: Gamma, Hamilton Point, Sanctuary Cliffs, Karlsen Cliffs, and Cape Lamb Member, and crops out at Vega, James Ross, Humps, Seymour, and Snow Hill islands (Supplementary Material – Figure S1).

The Snow Hill Island Formation constitutes the basal unit of the transgressive part of the NG Sequence (upper Campanian-lower Maastrichtian), which is widely exposed across the James Ross Basin (Fig. 2). The base of this sequence is well exposed in Santa Marta Cove, northwest James Ross Island where the inner shelf sandstones of the Gamma Member (upper Campanian to lower Maastrichtian) of the Snow Hill Island Formation

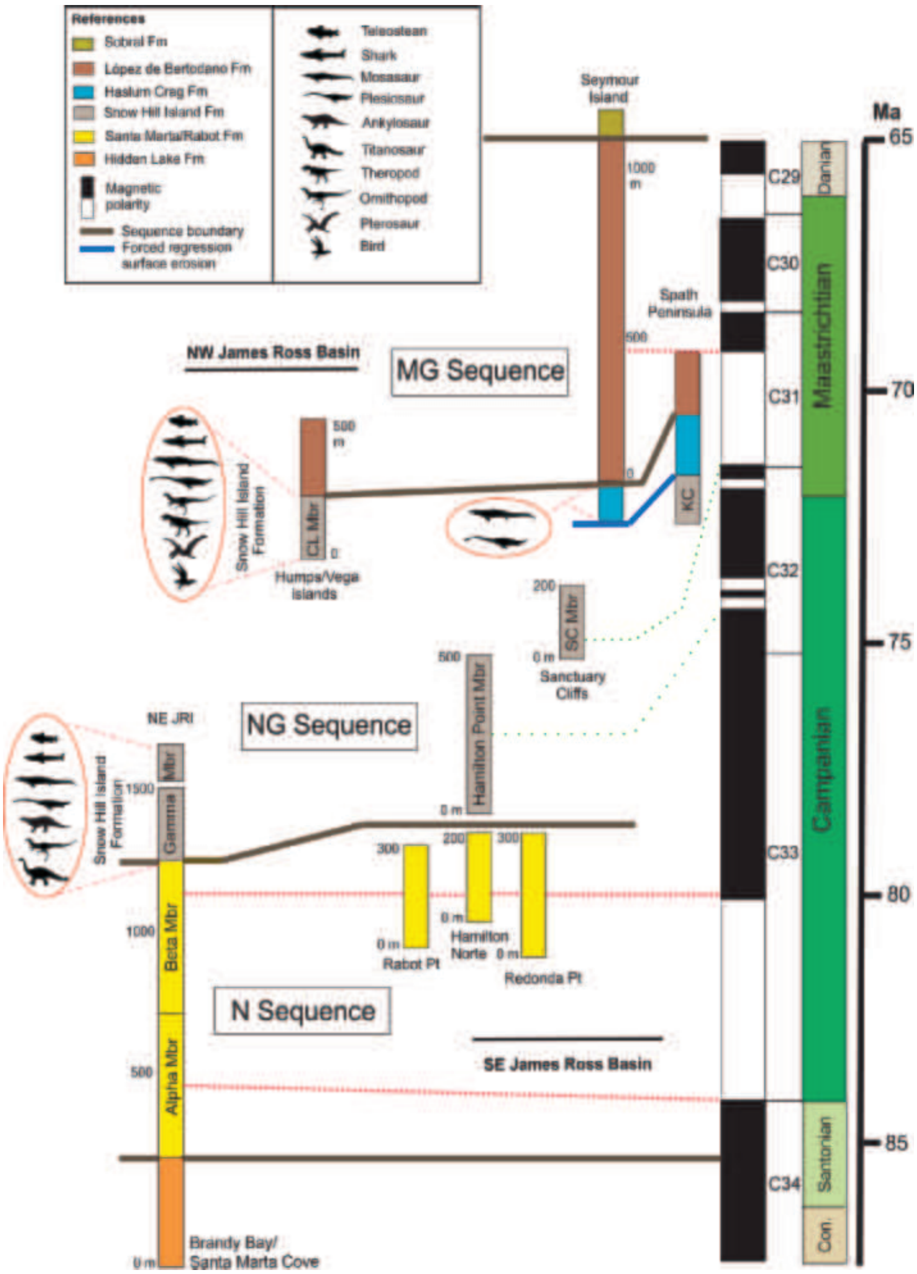

Figure 2. Chronostratigraphic scheme of the Marambio Group and upper Hidden Lake Formation (modified from Milanese et al. 2020). Reference polarity time scale from Ogg et al. (2016). The vertebrate groups of the NG Sequence (Olivero 2012a) recorded in Santa Marta Cove and The Naze (James Ross Island), Cape Lamb (Vega Island) of the Snow Hill Island Formation and Haslum Crags Formation (Seymour/Marambio Island) are indicated.

overlies in marked unconformity the Beta Member (lower-middle Campanian) of the Santa Marta Formation. In the distal part of the basin, towards the east-southeast of Santa Marta Cove, the inner shelf sandstones of the Gamma Member are replaced by transgressive offshore mudstones of the Hamilton Point Member of the Snow Hill Island Formation, which are transitionally covered by mudstones and fine-grained silty sandstones of the Sanctuary Cliffs Member (mostly lower Maastrichtian) exposed in Snow Hill Island. In Vega Island, the Cape Lamb Member is unconformably covered by transgressive mudstones of the middle to upper Maastrichtian López de Bertodano Formation (MG Sequence). In Snow Hill Island, the Karlsen Cliffs Member is separated by a high-relief unconformity from the overlying Haslum Crag Sandstone (lower Maastrichtian) which is interpreted as a forced regressive package of tidal sandstones (Olivero 2012a: Fig. 2).

In Santa Marta Cove, the Gamma Member consists of ca. 200 meters of inner-shelf sandstone and coquina. The sandstones are mostly fine-grained, well-sorted, forming massive or parallel-laminated beds, with occasional wave and current ripple lamination. The trace fossils are dominated by *Ophiomorpha nodosa* and *Tasselia ordamensis*. *Gyrolithes* and *Taenidium* are locally abundant in restricted horizons (Olivero & López Cabrera 2010).

The coquinas have erosive bases and form complex beds dominated by bivalves and gastropods. Otherwise, fossil invertebrates are rare, and only a few specimens of the cephalopods *Neograhamites primus*, *Anapachydiscus* sp. and *Eutrephoceras* sp. have been recovered in the sandstones. Toward the top of the Gamma Member, invertebrate fossils are more common, and the ammonites *Anapachydiscus* sp., *Neograhamites* cf. *N. kiliani* and *Gunnarites antarcticus*, the latter only at the very top of the member, have been recovered (Olivero 2012a, b). Based on the stratigraphic position of the member, which is distally replaced by offshore mudstones, its marked basal unconformity with the Beta Member of the Santa Marta Formation, and sedimentary and ichnological features, it is interpreted that the Gamma Member represents inner-shelf deposits, probably lower to mid shoreface, located at the base of the transgressive part of the NG Sequence.

Crame et al. (2004) presented a chronostratigraphy for the thick Maastrichtian succession in the James Ross Basin integrating ammonite biostratigraphy and isotopic information. They placed the base of the Maastrichtian at the basal part of the Cape Lamb Member in Vega Island, corresponding to the absolute strontium isotopic date of 71 ± 0.2 Ma and ca. 81-96 m above the base of the *Gunnarites antarcticus* fauna. Nonetheless, more accurated dating, based on magnetostratigraphy, places the base of the Maastrichtian near the basal Sanctuary Cliffs Member or the upper Gamma Member, within the Ammonite Assemblage 8.2 (*Neograhamites* cf. *N. kiliani*), nearly 200 m below the first appearance datum of the genus *Gunnarites* in the Ammonite Assemblage 9 (Milanese et al. 2020). Stratigraphically above this horizon, other Maastrichtian ammonites that occur within the *Gunnarites* Ammonite Assemblage 10 of Olivero (2012a) are *Diplomoceras lambi*, *Jacobites crofti* and probably *Kitchinites darwini* (Crame et al. 2004, Olivero & Medina 2000).

The sequence stratigraphic framework established for the Santonian-Danian of the James Ross Basin probably represents a low cyclicity frequency of second or third-order cycles (Olivero 2012a). The time involved is probably of the order of 7-8 Ma for the N Sequence, Santonian to mid Campanian; about 8-9 Ma for the NG Sequence, late Campanian-early Maastrichtian; and about 5 Ma for the MG Sequence, early Maastrichtian-Danian (Olivero 2012a, Milanese et al. 2020).

Snow Hill Island Formation and the Late Cretaceous break up of West Gondwana: paleobiogeographic remarks

The break-up of Gondwana started in the Late Jurassic, and by the beginning of the Late Cretaceous (~99.6 Ma) the fragmentation of several smaller plates grouped in West Antarctica between South America, Australia, East Antarctica, i.e., Antarctic Peninsula and Ellsworth-Whitmore Mountains crustal blocks, and conformed a large-scale system of “Noah’s arks” (McKenna 1973) whose biotas rifted and moved away. The drifting of these arks throughout latitudinal climate zones was the first-order cause for environmental changes to which the biota, living on the drifting Gondwana fragments, was subjected, and then geographically isolated from one another showing increasing degrees of endemism over time (Krause et al. 2019, Reguero & Goin 2021).

Since the Campanian the Antarctic Peninsula crustal block has long occupied an enigmatic position in plate reconstructions (Lawver et al. 1992). By the Late Cretaceous-early Paleogene break-up and the migration of these plates established the timing of the paleogeographic history of the geographical isolation of South America (Hervé et al. 2006, Jordan et al. 2020; Reguero & Goin 2021) (Figure S2).

MATERIAL AND METHODS

Prospection, extraction, and preparation of vertebrate remains

Marine reptiles

The fossiliferous horizons yielding marine reptiles were first discovered by geologists of the IAA (Rodolfo del Valle and collaborators) in 1973. At the time of the discoveries, only few skeletal elements with plesiosaurian affinities weathered out and detached from the quarry were known. Three field campaigns (January-February 1993, January-February 1998, and January-February 2005) to Vega Island revealed the presence of an almost complete elasmosaurid specimen (holotype of *Vegasaurus molyi*, MLP 93-I-5-1) associated with hexanchid shark teeth, as well as numerous invertebrates (ammonites, nautiloids, and lobsters). The marine reptile skeletons from localities VEG IAA 2/93 (MLP 93-I-5-1) and 5/93 (MLP 98-I-10-20 and MLP 15-I-7-6) were extracted using jack hammer pneumatic drill and heat guns and hot air tools (against frozen sediment and permafrost).

During the extraction of the holotype of *Vegasaurus molyi* (MLP 93-I-5-1), the position of each element was photographed and mapped, using a quarry diagram divided into 0.25-m^2 quadrants (Figure S3). The quarry covers approximately 3 m^2 on the slope. The skeleton was collected semiarticulated and lying with its right side up. The specimen is about seven meters in length. Numerous small (~1 cm in diameter) rounded, polished stomach stones (gastroliths) were found concentrated within the abdominal cavity, indicating that stomach stones were ingested, even by juvenile plesiosaurs.

Marine reptiles recovered in the XXI´ century (Antarctic field trips 2005, 2010–2020) were exhumed and studied by geologists and paleontologists of the IAA and MLP under a comprehensive field program developed in different islands within the James Ross Basin

Chondrichthyans and osteichchtyans

The specimens were studied with a stereoscopic microscope (Zeiss Stemi 2000-C), using different magnifications, at the laboratory of the División Paleontología de Vertebrados of MLP. Photographs of specimens reported herein were taken with digital cameras Canon PowerShot G10 (under microscope) and Canon Rebel T2i with a compact macro lens Canon EF 50 mm f/2.5. Drawings were done based on both, photographs (using a Wacom tablet over high-resolution photographs) under Adobe Illustrator and Photoshop.

Several kilograms of sedimentary rocks were dissolved in acid and sieved, but no chondrichthyan remains were recovered. Other actinopterygians reported here were found in concretions and prepared using needles under a binocular microscope and consolidated with B-72 diluted in acetone al 25%.

Terrestrial vertebrates

The holotype (MLP 86-X-28-1) and currently the only individual known of *Antarctopelta oliveroi* includes some semiarticulated elements encased in hardly concressioned sandstones and isolated material, all first collected from an area of about 6 m^2. Successive collecting works to the site expanded the prospected area up to 60 m^2 and many other elements (maxillary and dentary teeth, a fragmentary maxilla, vertebral centra, a proximal end of a metatarsal, three pedal phalanges, one incomplete ungual phalanx, dermal scutes and many dermal ossicles) –that unquestionably correspond to the same individual– were recovered. In all this preparation process the material is consolidated with B-72 diluted in acetone from 15 to 30%.

In general, fossil material of marine and terrestrial vertebrates was partly extracted from their surrounding matrix using pneumatic vibro-tool in the laboratories of the MLP (La Plata, Buenos Aires); Museo Carmen Funes (Plaza Huincul, Neuquén); Museo Paleontológico Municipal Ernesto Bachman (El Chocón, Neuquén), and Fundación Félix Azara (Ciudad Autónoma de Buenos Aires).

Specimens are housed in the vertebrate paleontology collections of the División Paleontología Vertebrados of the MLP, La Plata, Buenos Aires, Argentina.

REVIEW OF THE VERTEBRATES OF THE SHIF (LATE CAMPANIAN-EARLY MAASTRICHTIAN) FROM JAMES ROSS AND VEGA ISLANDS

Vertebrates from the Gamma Member

Marine vertebrates

Chondrichthyes and Osteichthyes recovered at Gamma Member mainly correspond to isolated teeth, vertebrae, caudal fin endoskeleton, fin elements, and fragmentary skulls.

Chondrichthyans- are represented by holocephalians (edaphodontids, chimaerids, callorhynchids, and rhinochimaerids) and sharks (Hexanchiformes, Lamniformes, Squatiniformes, Squaliformes, and Synechodontiformes) (Kriwet et al. 2006, Otero et al. 2014a, Gouiric-Cavalli et al. 2015), we include four new recods from SMC, (Table I; see also Fig. 5). Kriwet et al. (2006) reported the chimaerid, *Chimaera zangerli* from SMC; however, the specimen was not illustrated. To date, *Edaphodon snowhillensis* from JRI is the most complete fossil holocephalian reported in the Southern Hemisphere and one of the largest chimaeroid fish known (Fig. 3a-c, Table I; Gouiric-Cavalli et al. 2015).

Otero et al. (2014a p. 415) described *Cretalamna* sp. coming from the the Beta Member of Santa Marta Formation, however, in p. 417 those authors assign the specimen to *Cretalamna appendiculata* mentioning that the specimen came from Gamma Member.

Osteichthyans– are represented by several actinopterygian groups (Ichthyodectifomes, Alepisauriformes[elopomorphs],Enchodontidae, Albuliformes) as well as indeterminate Teleostei (Kriwet et al. 2006, Otero et al.2014b); here we include a new material from the site SMC IAA 1/86 (Fig. 3d, Table I).

Reptiles– are represented by scarce mosasaurs and abundant plesiosaurs (Table I). Mosasaurs are represented by the tylosaurinae, cf. *Hainosaurus* sp. (Martin et al. 2002; Table I) and *Taniwhasaurus antarcticus* (Novas et al. 2002a, Fernández & Martin 2009, Fernández & Gasparini 2012, Martin 2006, Martin et al. 2007a; Table I). The last, originally described as *Lakumasaurus* by Novas et al. (2002a) was later reassigned it to *Taniwhasaurus* (Table I) by Martin & Fernández (2007). To date, the holotype of *T. antarcticus* is the most complete mosasaur recovered from Antarctica.

Table I. Taxonomic list, stratigraphy, geographic locations, age, references, localities, coordinates for vertebrates from the Late Cretaceous Snow Hill Island and Haslum Crag formations. **Abbreviations:** E Maas, Early Maastrichtian; IAA, Instituto Antártico Argentino; JRI, James Ross Island; LBD, López de Bertodano; L Camp, Late Campanian, N/D, no data; SEY, Seymour (Marambio) Island; SMC, Santa Marta Cove; VEG, Vega Island.

Taxon		Geographic location	Stratigraphy (Members)	Age	References	Locality	Coordinates
CHONDRICHTHYES							
Elamosbranchii							
Neoselachii							
	Squalomorphii	Andreassen Point, JRI	Gamma	L Camp	Martin & Crame 2006	N/D	-----------------
Synechodontiformes							
Palaeospinascidae							
	Paraorthacodus	Santa Marta Cove, JRI	Gamma	L Camp	Kriwet et al. 2006	N/D	-----------------
Orthacodontidae							
	Sphenodus	Santa Marta Cove, JRI	Gamma	L Camp	Richter & Ward, 1990	N/D	-----------------
Otodontidae							
	Cretalamna appendiculatta	Santa Marta Cove, JRI	Gamma	L Camp	Otero et al. 2014	N/D	-----------------
Squatiniformes							
Squatinidae							
	Squatina	Santa Marta Cove, JRI	Gamma	L Camp	Richter & Ward, 1990	N/D	-----------------
Lamniformes							
	Lamniformes indet.	Santa Marta Cove, JRI	Gamma	L Camp	Kriwet et al. 2006	N/D	-----------------
	Scapanorhynchus sp.	Santa Marta Cove, JRI	Gamma	L Camp	Kriwet et al. 2006	N/D	-----------------
	cf. *Scapanorhynchus*	Santa Marta Cove, JRI	Gamma	L Camp	This study	SMC IAA 1/86	63°55'41.1 S; 57°53'32" W
Hexanchiformes							
Hexanchidae							
	Hexanchidae indet.	Cape Lamb, VEG	Cape Lamb	L Camp-E Maast	Martin, 2008	VEG IAA 3/98	63°52'6" S; 57°35'4.27" W
	Notidanodon dentatus	Santa Marta Cove, JRI	Gamma	L Camp	Kriwet et al. 2006		
	Notidanodon dentatus	Santa Marta Cove, JRI	Gamma	L Camp	This study	SMC IAA 1/86	63°55'41.1 S; 57°53'32" W
	Notidanodon dentatus	Cape Lamb, VEG	Cape Lamb	L Camp-E Maast	This study	VEG IAA 3/93	63°52'15" S; 57°36'4.3" W
Chlamydoselachidae							
	Chlamydoselachus thomsoni	Santa Marta Cove, JRI	Gamma	L Camp	Kriwet et al. 2006	N/D	-----------------

Taxon		Geographic location	Stratigraphy (Members)	Age	References	Locality	Coordinates
Squaliformes							
Squalidae							
	Centrophoroides sp.	Santa Marta Cove, JRI	Gamma	L Camp	Otero et al. 2014	N/D	-----------------
Holocephali							
Chimaeriformes							
Chimaeroidei							
¨Edaphodontidae¨							
	Edaphodon snowhilliensis	Santa Marta Cove, JRI	Gamma	L Camp	Gouiric-Cavalli et al. 2015	SMC IAA 2/11	63°55'06.5 S, 57°53'20.1 W
Callorhynchidae							
	Callorhinchus sp.	Santa Marta Cove, JRI	Gamma	L Camp	This study	SMC IAA 1/86	63°55'41.1 S; 57°53'32" W
	Callorhinchus sp.	Santa Marta Cove, JRI	Gamma	L Camp	Otero et al. 2014a	N/D	-----------------
	cf. *Callorhinchus* sp.	Cape Lamb, VEG	Cape Lamb	L Camp-E Maast	Roberts et al. 2014		
Rhinochimaeridae							
	Rhinochimaeridae indet.	Santa Marta Cove, JRI	Gamma	L Camp	Otero et al. 2014a	N/D	-----------------
Chimaeridae							
	Chimaera zangerli	Santa Marta Cove, JRI	Gamma	L Camp	Kriwet et al. 2006	N/D	-----------------
OSTEICHTHYES							
Actinopterygii							
Actinopterygii indet.		Cape Lamb, VEG	Cape Lamb	L Camp-E Maast	contra Roberts et al. 2014	N/D	-----------------
Teleostei							
	Teleostei indet.	Cape Lamb, VEG	Cape Lamb	L Camp-E Maast	This study	VEG IAA 3/98	63°52'6" S; 57°35'4.27" W
	Teleostei indet.	Santa Marta Cove, JRI	Gamma	L Camp	Kriwet et al. 2006	N/D	-----------------
cf. Sphenocephalidae							
	cf. Sphenocephalidae	False Island Point, VEG	Cape Lamb	E Maast	Martin & Crame 2006*	"Hill 177"	-----------------
Ichthyodectiformes							
	Ichthyodectiformes indet.	Santa Marta Cove, JRI	Gamma	L Camp	Kriwet et al. 2006		
	Ichthyodectiformes indet.	Santa Marta Cove, JRI	Gamma	L Camp	This study	SMC IAA 1/86	63°55'41.1 S; 57°53'32" W
	Ichthyodectiformes indet.	Cape Lamb, VEG	Cape Lamb	L Camp-E Maast	This study	VEG IAA 2/93	63°53'10 S; 57°35'54.20" W

Taxon		Geographic location	Stratigraphy (Members)	Age	References	Locality	Coordinates
Enchodontidae							
	Enchodus sp.	Santa Marta Cove, JRI	Gamma	L Camp	Kriwet et al. 2006	N/D	----------------
Albuliformes							
	Albuliformes indet.	Santa Marta Cove, JRI	Gamma	L Camp	Kriwet et al. 2006	N/D	----------------
Alepisauriformes							
	cf. *Apateodus*	Santa Marta Cove, JRI	Gamma	L Camp	Richter & Ward 1990	N/D	----------------
SQUAMATA							
Mosasauridae							
Mosasaurinae							
	"*Liodon*" sp.	Cape Lamb, VEG	Cape Lamb	L Camp-E Maast	Martin et al., 2002	VEG IAA 3/93	63°52'15" S; 57°36'4.3" W
	cf. "*Liodon*" sp.	Cape Lamb, VEG	Cape Lamb	L Camp-E Maast	Fernández & Gasparini 2012	VEG IAA 3/93	63°52'15" S; 57°36'4.3" W
	Mosasaurus cf. *M. lemonnieri*	Cape Lamb, VEG	Cape Lamb	L Camp-E Maast	Martin et al., 2002	VEG IAA 5/93	63°53'16" S; 57°34'43.2" W
Tylosaurinae							
	Taniwhasaurus antarcticus	Santa Marta Cove, JRI	Gamma	L Camp	Novas et al. 2002a	SMC IAA 2/86	63° 55' S; 57° 51' W
	?Hainosaurus	Santa Marta Cove, JRI	Gamma	L Camp	Martin et al., 2002	SMC IAA 2/86	63° 55' S; 57° 51' W
	Tylosaurinae indet.	López de Bertodano, SEY	Haslum Crag Fm.	E Maast	Martin & Crame 2006	Dj.956.41	----------------
	?Taniwhasaurus antarcticus	Cape Lamb, VEG	Cape Lamb	L Camp-E Maast	Fernández & Gasparini 2012	VEG IAA 3/93	63°52'15" S; 57°36'4.3" W
Plioplatecarpinae							
	cf. Plioplatecarpus sp	Cape Lamb, VEG	Cape Lamb	L Camp-E Maast	Fernández & Gasparini 2012	VEG IAA 5/93	63°53'16" S; 57°34'43.2" W
SAUROPTERYGIA							
Plesiosauria							
Elasmosauridae							
	Elasmosauridae indet.	Santa Marta Cove, JRI	Gamma	L Camp	This study	SMC IAA 2/86	63°55'36.4' S; 57°51'0.8" W
	Elasmosauridae indet.	The Naze, JRI	Cape Lamb	L Camp-E Maast	di Pasquo & Martin 2013	TNZ IAA 2/06	63°56'06" S; 57°31'36" W
	Elasmosauridae indet.	Cape Lamb, VEG	Cape Lamb	L Camp-E Maast	This study	VEG IAA 5/93	63°53'16" S; 57°34'43.2" W
	Elasmosauridae indet.	López de Bertodano, SEY	Haslum Crag Fm.	E Maast	Fostowicz-Frelik & Gaździcki 2001	LDB IAA 1/06	64°18'22.5" S; 56°51' 23.3 W
	Vegasaurus molyi	Cape Lamb, VEG	Cape Lamb	L Camp-E Maast	O'Gorman et al. 2015	VEG IAA 2/93	63°53'10 S; 57°35'54.20" W

Taxon		Geographic location	Stratigraphy (Members)	Age	References	Locality	Coordinates
DINOSAURIA							
Ornithischia							
Ankylosauria							
Nodosauridae							
	Antarctopelta oliveroi	Santa Marta Cove, JRI	Gamma	L Camp	Salgado & Gasparini 2006	SMC IAA 1/86	63°55'41.1 S; 57°53'32" W
Ornithopoda							
Elasmaria							
	Trinisaura santamartaencis	Santa Marta Cove, JRI	Gamma	L Camp	Coria et al. 2013	SMC IAA 1/08	63°55'24" S; 57°52'25" W
	Morrosaurus antarcticus	The Naze, JRI	Cape Lamb	L Camp-E Maast	Rozadilla et al. 2016	TNZ IAA 2/06	63°56'06" S; 57°31'36" W
	gen. et sp. indet.	Santa Marta Cove, JRI	Gamma	L Camp	Coria et al. 2007	SMC IAA 1/07	63°54'58.2 S; 57°31'31.5" W
.	gen. et sp. Indet.	Santa Marta Cove, JRI	Gamma	L Camp	Coria et al. 2007	SMC IAA 2/07	63° 55' 35" S; 57° 52' 19.3 W
	gen. et sp. nov.	Cape Lamb, VEG	Cape Lamb	L Camp-E Maast	Thomson & Hooker, 1991	VEG IAA 1/15	63°53'6.9" S; 57°35'34" W
Saurischia							
Titanosauria							
Lithostrotia							
	gen. et sp. indet.	Santa Marta Cove, JRI	Gamma	L Camp	Cerda et al. 2012	SMC IAA 1/11	63°56 18.78" S; 57°53'6.8 W
Theropoda							
	Theropoda indet.	Cape Lamb, VEG	Cape Lamb	L Camp-E Maast	This study	VEG IAA 6/98	63°52'54.4 S; 57°34'19.5 W
Paraves							
	Imperobator antarcticus	The Naze, JRI	Cape Lamb	L Camp-E Maast	Ely & Case 2019	TNZ IAA 1/06	63°54'51" S; 57°27'44" W
PTEROSAURIA							
Pterodactyloidea							
	gen. et sp. Indet.	Cape Lamb, VEG	Cape Lamb	E Maast	Kellner et al. 2019	N/D	----------------
AVES							
Neornithes							
	Neornithes indet.	Cape Lamb, VEG	Cape Lamb	L Camp-E Maast	Acosta Hospitaleche & Gelfo 2015	VEG IAA 2/98	63°52'58" S, 57°36'28" W
		Cape Lamb, VEG	Cape Lamb	L Camp-E Maast	This study	VEG IAA 3/98	63°52'6" S; 57°35'4.27" W
Ornithuromorpha							
	Antarcticavis capelambensis	Cape Lamb, VEG	Cape Lamb	L Camp-E Maast	Cordes et al. 2020	VEG IAA 6/98	63°52'54.4 S; 57°34'19.5 W

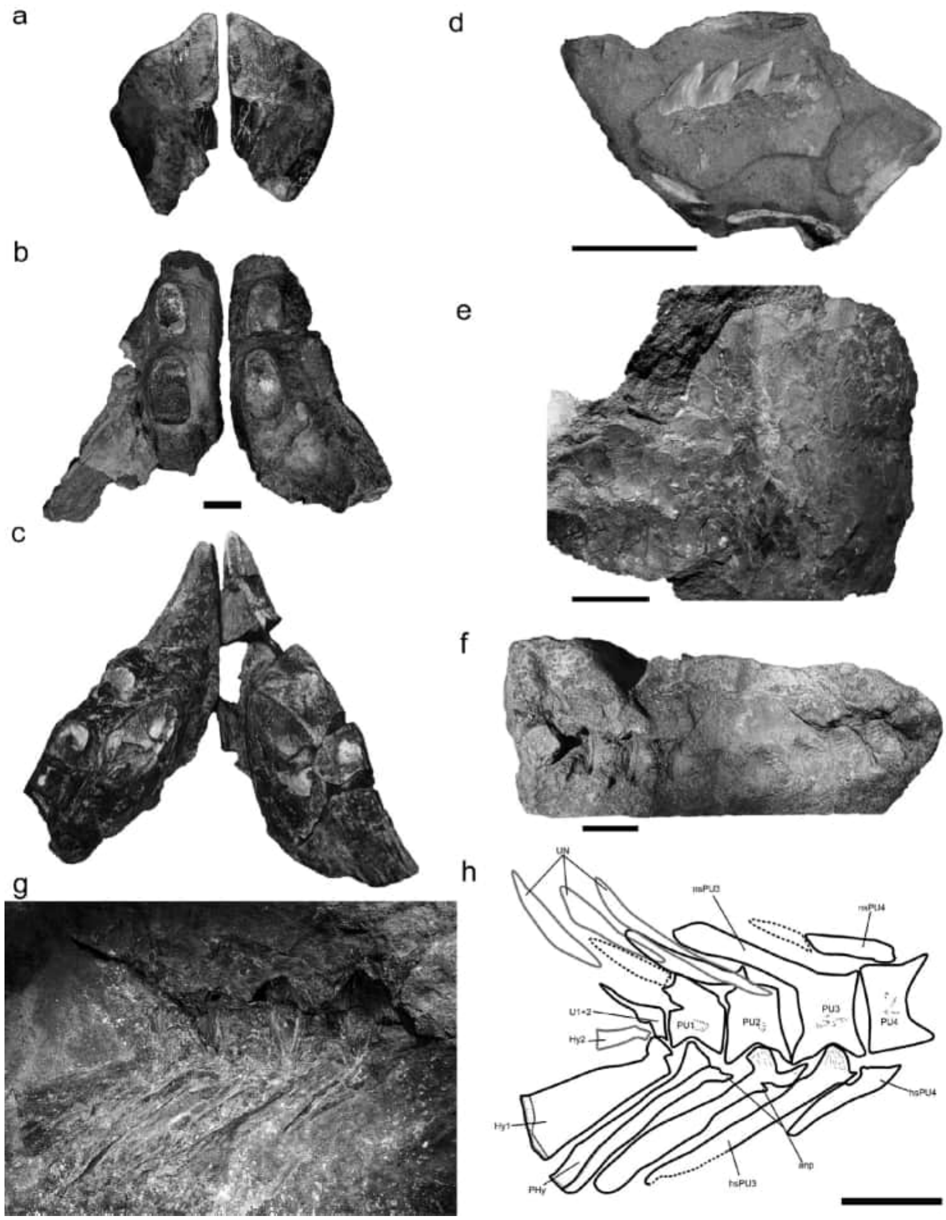

Figure 3. **Chondrichthyes and Osteichthyes from Snow Hill Island Formation strata of the JRB, Antarctic Peninsula: (a–d.) and Vega islands (e–g.): (a-c.), *Edaphodon snowhilensis*, MLP 13-I-26-1, holotype (); (a.), vomerine tooth plate; (b.), palatine tooth plate; (c.), mandibular tooth plate; (d.), *Notidanodon dentatus* (MLP 95-IV-1), lateral tooth embedded in the hosting rock; (e.), Ichthyodectiformes indet. (MLP 15-XI-7-11 in part), body scale patch; Teleostei indet. (MLP 15-XI-7-20) isolated vertebral column; (f.), Teleostei indet. (MLP 15-XI-7-12) caudal endoskeleton; (g.), interpretative drawing of MLP 15-XI-7-12 showed in (f.) (scale bars = 1cm). Abbreviations: UN, uroneurals; nsPU, neural spine of the preural centrum; PU1-4, preural centra 1–4; U1+2, ural centra 1+2; hsPU, hemal spine of the preural centra; Phy, parhypural; Hy1-2, hypural 1-2.**

Plesiosaurs from the Gamma Member belong to the Elasmosauridae or are referred to Plesiosauria indet (O’Gorman 2012). No evidence of the presence of polycotylids, the other diverse family from the Upper Cretaceous has been collected until now. Among Weddellian elasmosaurids two morphotype of Weddellian elasmosaurids (i.e., Patagonia, Western Antarctica, and New Zealand) have been recognized. The Aristonectinae are characterized by a large cranium, increased number of teeth and short cervical centra (Gasparini et al. 2003, Cruickshank & Fordyce 2002; Otero et al. 2014b); the non-aristonectine shows the tipical elasmosaurid features (small cranium; less than 30 teeth on each hemimandible; elongated cervical centra). Until now only non-aristonectine elasmosaurids are the more abundant and frequent, probably the only plesiosaurs in the SHIF (Otero et al. 2014b, O’Gorman et al. 2019a).

Continental vertebrates

Fossil continental vertebrates from the Gamma Member are only represented by non-avian and avian dinosaurs (Table I). SHIF dinosaur record indicates the presence of at least four major taxonomic groups in the Late Cretaceous of the continent: Ankylosauria, early diverging Ornithopoda (Elasmaria?), Titanosauria, and non avian Theropoda, with associated partial skeletons being known for several taxa within these groups (primarily ornithischians).

The ankylosaur *Antarctopelta oliveroi* was the first dinosaur collected from Antarctica, in Santa Marta Cove (Fig. 4 a-d). The material was preliminarily discussed by several authors Gasparini et al. (1987, 1998) and Olivero et al. (1991) and described and analyzed in more detail by Salgado & Gasparini (2006) who provided a first glimpse to their phylogenetic relationships. The fragmentary nature of the specimen and the lack of informative cranial information prevent the possibility of establishing supported hypotheses about its phylogeny. Thompson et al. (2012) analyzed the ankylosaur phylogeny and, although they placed *Antactopelta* as the most basal nodosaurid, they also recognize the low support of that position. Arbour and Currie (2015) questioned the taxonomic validity of this taxon and considered *Antarctopelta oliveroi* as a *nomen dubium*, based on the assumption that the autapomorphy-bearing bones (i.e., caudal vertebrae) belong to marine reptiles (elasmosaurids and mosasaurs). However, Rozadilla et al. (2016) after the direct inspection and study of the specimen regarded that its caudal vertebrae do not belong to marine reptiles, but to an ankylosaur. The presence of some autapomorphies on caudal vertebrae (i.e., transverse processes of distal caudal vertebrae well-developed and anteroposteriorly expanded) indicate for these authors that *Antarctopelta oliveroi* should be considered a valid ankylosaur taxon (Rozadilla et al. 2021).

The majority of the SHIF early-branching ornithopods are referable to the Gondwanan clade Elasmaria (e.g., Calvo et al. 2007, Coria et al. 2013, Barrett et al. 2014, Rozadilla and Novas 2016, Rozadilla et al. 2016, Cruzado-Caballero et al. 2019) which are the best-represented non-avian dinosaurs in the JRB, and by extension, the Cretaceous of Antarctica. The ornithopod *Trinisaura santamartaensis* (MLP 08-III-1-1) is represented by a single, immature individual that was preserved partially articulated in sandstones concretions in the Locality SMC IAA 1/08, see Table I) and from a meter above stratigraphical level of *Antactopelta* (Coria et al. 2013, fig. 1C). Coria et al. (2013) provided an anatomical description and phylogenetic analysis of the specimen that shows it as an ornithopod more derived than *Thescelosaurus*, and sister taxa of *Anabisetia* and more derived Euiguanodontia (Coria et al. 2013). *Trinisaura* is the first named ornithopod species from Antarctica although the group has been extensively recorded in several localities from the James Ross Basin (Hooker et al. 1991, Milner et al. 1992, Case et al. 2000, Novas et al. 2002b, Coria et al. 2007). Giving the fact that some of these records come from different stratigraphical levels than *Trinisaura*, the possibility of a radiation of Antarctic ornithopods (elasmarians, Rozadilla et al. 2016) cannot be ruled out. Recently Garcia Marsa et al. (2020) analyzed the biological implications of the bone microstructure *Trinisaura santamartaensis*.

Two isolated ungual phalanges of ornithopods (MLP 07-III-2-1 and MLP 07-III-2-2) were found approximately 200 m west to the *Antarctopelta* site (Locality SMC IAA 1/07, see Table I and Fig. 4e-g) (Coria et al. 2007, fig. 2). These specimens were found on a draining creek, associated with elasmosaurid remains (Coria et al. 2007). The sizes of the specimens

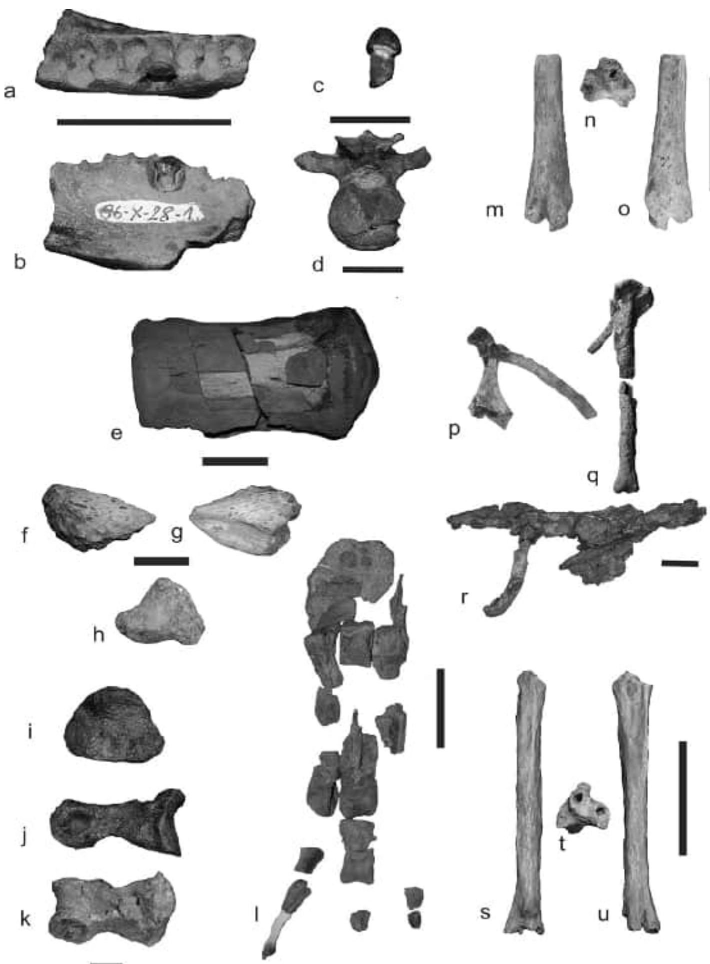

Figure 4. Non avian and avian dinosaur from Snow Hill Island Formation strata of the JRB, Antarctic Peninsula. **(a-d.)** *Antarctopelta oliveroi* Salgado & Gasparini 2006, MLP 86-X-28-1, holotype: **(a.)** left dentary in occlusal view; **(b.)** left dentary in medial view (scale bar = 50 mm); **(c.)** tooth II in lingual view (scale bar = 50 mm); **(d.)** posterior cervical vertebra in posterior view (scale bar 50 mm); **(e.)** Lithostrotian gen. et sp. indet., MLP 11-II-20-1: caudal vertebra centrum, right lateral view (scale bar = 50 mm); **(f-h.)** Ornithopoda indet., MLP 07-III-2-1, pedal ungual **(f.)** lateral; **(g.)** dorsal; **(h.)** proximal views (scale bar = 10 mm); **(i-k.)** Theropoda indet. (MLP 15-I-7-2), isolated pedal phalax (digit III?), **(i.)** proximal, **(j.)** lateral and **(k.)** dorsal views (scale bar = 10 mm); **(l.)** *Imperobator antarcticus* Ely & Case 2019, UCMP 276000, holotype, partial left hindlimb, ankle and foot (scale bar = 100 mm) (modified from Case et al. 2007); **(m-o.)** Neornithes indet., MLP 98-I-10-54, incomplete left tarsometatarsus in caudal **(m.)** distal **(n.)** and cranial **(o.)** views (scale bar = 10 mm); **(p-r.)** *Antarcticavis capelambensis* Cordes-Person, Acosta Hospitaleche, Case and Martin 2020 (SDSM 78147), holotype: right scapula and coracoid in dorso-medial view **(p.)**, halves of left humerus in caudal view **(q.)**; synsacrum and right femur in right view **(r.)** (scale bar = 10 mm); **(s-u.)** Neornithes indet., MLP 98-I-10–25, fragment of left tarsometatarsus in caudal **(s.)**, distal **(t.)** and cranial **(u.)** views (scale bar = 20 mm).

suggest that they belong to a larger individual than the ornithopod *Trinisaura*.

Coria et al. (2015) briefly described an associated partial tibia and astragalus of ornithopod from the Cape Lamb Member on Vega Island (MLP 15-I-7-1).

The MLP 11-II-20-1 (Fig. 4h) was collected from the surface, in shallow marine shelf deposits, exposed in a site informally called Loma Verde (Green Hill, SMC IAA 1/11, see Table I, located 1km south the *Antactopelta's* site, Santa Marta Cove, James Ross Island. The fossil-bearing levels are stratigraphically around 30 m above the corresponding levels of *Antarctopelta* and *Trinisaura* (Coria et al. 2013, Ely & Case 2019). MLP 11-II-20-1 consists in the right half side of a middle caudal vertebra. The procoelic condition of the centrum, which is interpreted by the inferred presence of a proximally located neural arch allowed Cerda et al. (2012) to identify the specimen as belonging to a lithostrotian sauropod. This interpretation is not supported by other authors that consider this condition of the posterior articular condyle seen in the specimen MLP 11-II-20-1 is not sufficient evidence to assure the identification as a Lithostrotia *sensu stricto* (see Lamanna et al. 2019).

This specimen is the first sauropod recognized from Antarctica. The existence of an Antarctic Cretaceous sauropod was already suspected due several hypotheses. The presence of basal sauropodomorphs in the Lower Jurassic of Antarctica (Smith & Pol 2007) could root the presence of a local lineage in this continent or could be indicating dispersal events of sauropod forms from Australia or South America to Antarctica. Nonetheless, the evidence provided by the specimen MLP 11-II-20-1 is extremely scarce to support either of these hypotheses.

Vertebrates from the Cape Lamb Member

Marine vertebrates

Chondrichthyans– At Cape Lamb Member, chondrichthyans are represented by fragmentary and isolated material (Table I). Roberts et al. (2014 p. 66) based on the previous report of Martin (2008), mention an undeterminate hexanchiform tooth. The authors disclose that the tooth was found in association with a plesiosaur; however, the material was not described nor illustrated in detail. Also, Roberts et al. (2014 p. 66) report partial jaws and tooth plates that they referred as cf. *Callorhynchus* sp. However, no illustration and/or description of the material is made in that publication. Moreover, the articulated vertebral centra illustrated by Roberts et al. (2014 fig. 6E) and referred to a chondrichthyan elasmobranch, seems to belong to a teleostean (i.e., due to the typical hourglass-shaped centra of the specimen figured).

Osteichthyans– Previous to this study actinopterygians at the Cape Lamb Member were represented by a small, incomplete, and poorly-preserved specimen that lack its skull and the anterior part of the body. The specimen (DJ. 360.8) was briefly described and referred to *cf.* Sphenocephalidae (see Martin & Crame 2006 p. 116, fig. 3G). The material was found at Hill 177, False Island Point, Vega Island (see Martin & Crame 2006, Roberts et al. 2014). However, Reguero et al. (2013a, p. 30) mentioned that this specimen comes from the López de Bertodano Formation. Previous actinopterygian records also include material interpreted as belonging to chondrichthyans and/or plesiosaurs (see Roberts et al. 2014 fig. 6E–F). All these material needs to be carefully reviewed.

The new material reported herein was briefly presented by Reguero et al. (2015), it consists of poorly preserved actinopterygians. This material was collected from levels that also yielded marine and continental vertebrates (*i.e.*, plesiosaurs, mosasaurs, and dinosaurs) together with marine invertebrates (*i.e.*, ammonoids, nautiloids, bivalves, gastropods, bryozoans, crustaceans, and equinoids), and palynomorphs.

MLP 15-XI-7-11 (Fig. 3d) consists of a disarticulated and partially preserved opercular apparatus, scales, and part of a vertebral column. The operculum is large and ornamented with fine radiating lines. The preoperculum is triangular and have at least thirteen sensory tubules branching from the main preopercular sensory canal. Tubules are moderately wide, closely arranged, and seem to reach the ventral margin of the preopercle. The interoperculum is broken. The suboperculum is large. The scales are large, cycloid type, and oval-shaped; they are preserved in situ and are disposed highly imbricated. The scales have numerous concentric *circulii* and scarce radiating *radii* plus a central focus with numerous central pits. Lateral line scales have a large central pit. Remains of branchiostegal rays are preserved but their total number remain unknown. MLP 15-XI-7-11 is assigned to Ichthyodectiformes due to similarity in the scales and preopercle morphologies. Ichthyodectiformes is an extinct group of basal teleosts that appeared in the Middle Jurassic, became diverse and successful during almost all the Cretaceous. The group includes big-sized taxa (*e.g., Xiphactinus*, *Cladocyclus*), medium sized forms (*e.g.*, *Allothrissops*, *Thrissops*) and small ones (*e.g.*, *Ascalabothrissops*). They have been reported from marine deposits of North America, Europe, Lebanon, Australia, South America, Asia, Antarctica, and Africa (*e.g.*, Goody 1976, Patterson & Rosen 1977, Murray 2000, Arratia et al. 2004, Cavin et al. 2013).

MLP 15-XI-7-12 (Fig. 3f–g) is a caudal endoskeleton composed of four caudal vertebrae, three preural centra, and one compound ural centra. The vertebrae are heavily ossified, ornamented, and strongly constricting the notochord. The dorsal flexure of the tail begins in the mid-posterior part of the ural centra. There are two hypurals, the first is well developed and the second is comparatively much reduced. Both hypurals are separated by a marked diastema. There are at least three partially preserved uroneurals. The specimen is under study and correspond to an indeterminate teleost.

MLP 15-XI-7-19 and MLP 15-XI-7-20 are very poorly preserved and incomplete. MLP 15-XI-7-20 is a vertebral column section that measures *ca*. 8 cm long and 0.8 cm wide and corresponds to the posterior abdominal region of the body. There are at least 10 poorly preserved amphycoelus vertebrae. The notochord is strongly constricted by the autocentra. The autocentra are thick and have their external surface ornamented. There are few slightly posteriorly inclined and long neural spines preserved. The neural arch is positioned at the mid-posterior portion of the autocentra. MLP 15-XI-7-19 is an isolated vertebra composed by a thick amphycoelus autocentra that strongly constrict the notochorda. Nor hemal and neural arches neither its spines are preserved. A thick autocentrum that strongly constrict the notochord is present in most fossils above the phylogenetic level of *Leptolepis coryphaenoides* and in all extant teleosts. Thus, MLP 15-XI-7-19 and MLP 15-XI-7-20 are designed as belonging to an indeterminate teleost.

Remarks on previous findings

Roberts et al. (2014 fig. 6F) illustrate an isolated mandible and partially preserved cervical series (AMNH FARB 30877). The authors assign the specimen to an indeterminate plesiosaur. However, such assignation seems to be quite adventured, especially for the mandible. According with teeth size, shape and its disposition over the mandible (teeth slightly inclined forward), as well as the likely presence of a furrow –which could be an impression of a mandibular sensory canal of the lateral-line-system– in the dentosplenial bone, the fragmentary mandible could be assigned to an actinopterygian. Moreover, from the illustration of the material presented by Roberts et al (2014) we cannot be certain about the designation of these impressions as an incomplete cervical series.

Marine reptiles

Marine reptiles of the Cape Lamb Member are referred to Mosasaurinae (*Mosasaurus cf. Mosasaurus lemonnieri* and *Leiodon* sp. Table I) and Tylosaurinae (juvenile specimen of *Taniwhasaurus antarcticus*: Martin et al. 2007a; Table I).

Also, remains of at least one medium sized and other small sized mosasaurs have been recovered near the elasmosaurid plesiosaur *Vegasaurus molyi*. Based on the textural aging of dorsal and caudal vertebral centrae, the vertebrae belong to a juvenile or maybe a just born specimen (Martin et al. 2007a). Moreover, the centra are assigned to *T. antarcticus* based on similar morphology and proportions (Fernández & Gasparini 2012).

The plesiosaurs from the Cape Lamb Member belong mostly to the non-aristonectine elasmosaurids (O'Gorman et al. 2019); as in Gamma Member aristonectines and polycotylids have not been recorded. Among the specimens collected, the holotype of *Vegasaurus molyi* is remarkable for its completness, lacking all the skull. *Vegasaurus* is a medium size Weddellonectia elasmosaurids of 6-7 meters length and medium elongated cervical vertebrae (O'Gorman et al. 2015). Also, from the same member a juvenile elasmosaurid (MLP 98-I-10-20) was collected, the cluster of gastroliths associated were detaily analysed (O'Gorman et al. 2012). Additionally, another remarkable specimen was collected on the east coast of Cape Lamb. The specimen MLP 15-I-7-6 (Fig. 6n), a juvenile elasmosaurids with preserved skull material shows palatal structure that indicate weddellonectian affinities and represent the first non-aristonectine elasmosaurid with well preserve skull material (O'Gorman et al. 2018).

Pterosaurs - Flying reptiles are less known in Antarctica. The only known pterosaur reported outside JRB is a bone identified as a humerus mentioned by Hammer & Hickerson (1994, 1996) and subsequently figured (Hammer & Hickerson 1999, fig. 5) from the Early Jurassic Hanson Formation from Central Transantarctic Mountains. A SHIF pterosaur specimen was recovered from Vega Island (Kellner et al. 2019). The specimen (MN 7801-V) was found as a result of a surface collecting at the Cape Lamb area, close to the contact between the Snow Hill and the López de Bertodano formations and so, considered to came stratigraphically from the upper member of the SHIF (Kellner et al. 2019). The bone was identified as metacarpal IV assigned to the Pterodactyloidea due to their thin bone cortex and to the Archaeopterodactyloidea since the small size. This finding, plus another another bone from a moraine at the Abernathy Flats (SMF) on James Ross Island, suggest a wide diverse ecosystem during the Late Cretaceous (Kellner et al. 2019).

Non-avian dinosaurs – four dinosaur taxa have been recovered from the Cape Lamb Member, the elasmarian ornithopod, *Morrosaurus antarcticus*, the paravian theropod, *Imperobator antarcticus*, the specimen MLP 15-I-7-1, and the Cape Lamb ornithopod NHMUK PV R 36760, are associated with invertebrates of the *Gunnarites antarcticus* faunal assemblage and are within the more restrictive 50 meters stratigraphic range of the ammonite, *Diplomoceras lambi*. A Sr/Sr datum corresponding to an age of 71.0 Ma has been recovered from the upper part of the *Diplomoceras lambi* biostratigraphic range resulting in these three dinosaur taxa being earliest Maastrichtian in age (Ely & Case 2019, Lamanna et al. 2019).

The ornithopod *Morrosaurus antarcticus* has been proposed as a member of a South American monophyletic group, the Elasmaria (Rozadilla et al. 2016, Calvo et al. 2007) suggesting a southern Gondwanan diversification of non-hadrosaurid Cretaceous ornithopods (see also Herne et al. 2018). Despite some relative recent published studies (Rozadilla et al. 2016) very little information has been communicated so far about the characteristics of these remains (Cambiaso et al. 2002, Novas et al. 2002b). Although unpublished data regard it as a related with some South American ornithopods like *Anabisetia* and *Talenkauen* (Cambiaso 2007), which was confirmed by Rozadilla et al. (2016) in their description and naming of *Morrosaurus*. The inferred total size of the materials corresponds to an animal slightly bigger than *Trinisaura*. Therefore, besides the different stratigraphical and geographic provenance, several morphogical differences between *Morrosaurus* and *Trinisaura*, such as a spike-like lesser trochanter and a stouter femur with a better-defined intercondylar groove, supports a taxonomic distinction between both forms. Given its stratigraphical and geographic provenance, *Morrosaurus* is closely related to

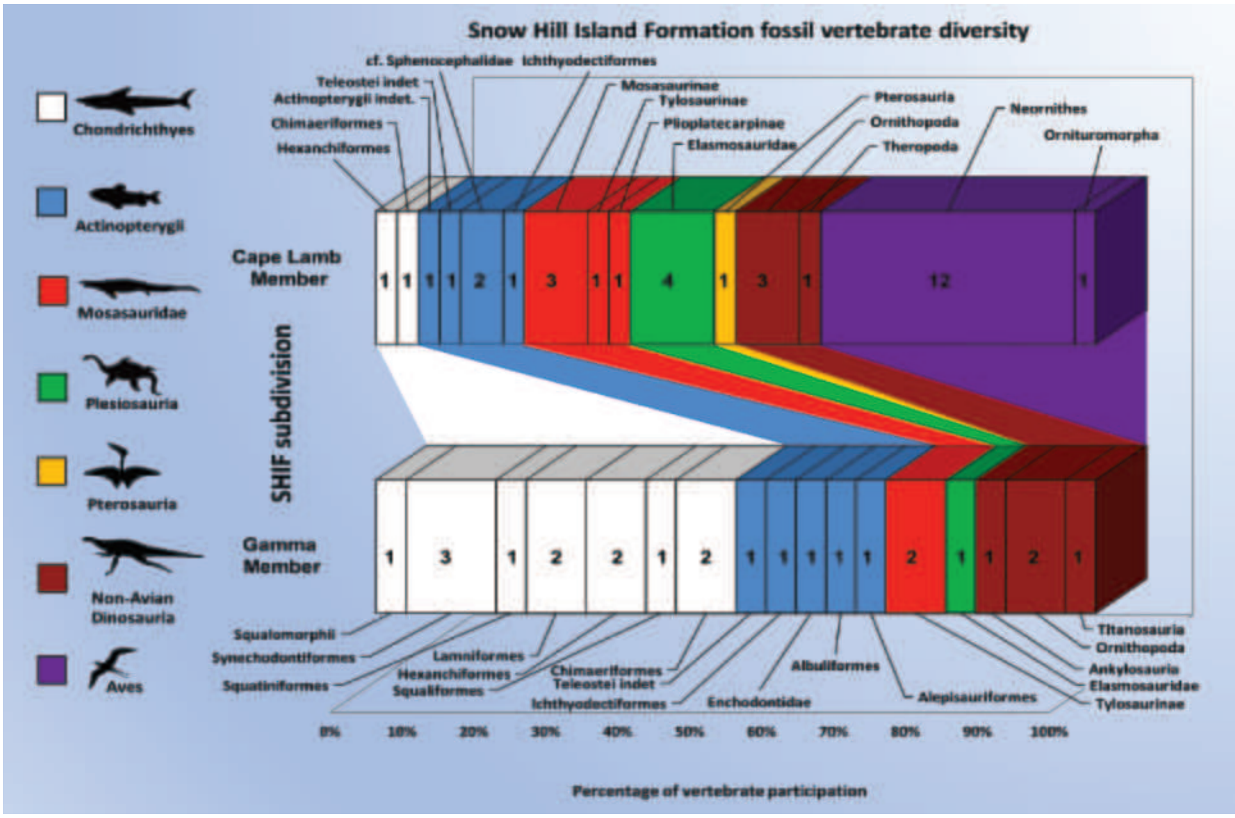

Figure 5. Diversity of vertebrates from the Snow Hill Island Formation: Gamma Member (a.) and Cape Lamb Member (b.), Antarctic Peninsula. The percentage of fauna refers to the synthesis carried out in Table I and the bibliography cited there. The numbers within each group indicate how many taxa at family indeterminate or genus level, identified in each unit. In the case of Aves Neornithes, the values refer to different specimens whose taxonomic assignment is not defined.

Trinisaura and considered by Ely & Case (2019) as part of the same overall ornithopod fauna.

The "early-diverging ornithopod" NHMUK PV R 36760 (formerly BMNH BAS R.2450) from Vega consists in an incomplete although very informative specimen of a 5 m long ornithopod, likely related with *Trinisaura*. It is represented by cranial (*i.e.*, near complete left and right dentaries and maxillae, isolated cheek and palatal elements, partial braincase) and post-cranial (i.e., cervical, dorsal and sacral vertebrae, parts of both scapulae, coracoids, humeri and iliac and ischial fragments) elements (Hooker et al. 1991, Thomson & Hooker, 1991) coming from the west side of Cape Lamb, Vega Island (Locality VEG IAA 3/15, see Table I), Cape Lamb Member (late Campanian - early Maastrichtian), Snow Hill Island Formation (Thomson & Hooker 1991, Hooker et al. 1991, Olivero 2012a, Reguero et al. 2013b). Originally, this specimen was identified as a hypsilophodontid (Thomson & Hooker 1991, Hooker et al. 1991, Milner et al. 1992) with some features that linked it with the Dryomorpha, especially some pelvic features (A. Milner, pers. comm. 2014). The specimen sitll under study and has been now interpreted to be another elasmarian specimen, however its taxonomic affinity has not been specified yet (Barrett et al. 2014).

The paravian theropod, *Imperobator antarcticus*, was found in the Naze, James Ross

Island at locality TNZ IAA 1/06 (see Table I), This specimen was previous regarded by Case et al. (2007) as a primitive dromaeosaurid based upon the presence of a metatarsal II with a lateral expansion caudal to metatarsal III; a metatarsal III proximally narrow distally wide; a distal end of metatarsal III with an incipient ginglymoid and a pedal digit II with a trenchant ungual phalanx. Ely & Case (2019) noted that particular character states of the Antarctic specimen, differ from the dromaeosaurid norm and referral to this family is not supported in the phylogenetic analysis based on distal hindlimb and pedal data. The lack of a distal, ginglymoid articular facet of metatarsal II signifies a placement at least within the Paraves, but not within Dromaeosauridae.

New Theropoda indet. MLP 15-I-7-2 from Cape Lamb, Vega Island, Cape Lamb Member, Snow Hill Island Formation (Coria et al. 2015). The isolated pedal phalanx probably corresponds to the first element of digit III (4i-j). The proximal articular surface is triangularly outlined and deep, the shaft is transverselly constricted, whereas the distal articular end bears deep gynglimoid fossae (Coria et al. 2015). Being highly neumatized, the bone is interpreted as belonging to a mid-sized, non-avian theropod dinosaur. Likely, this element is taxonomically related with the hind limb collected from the same stratigraphical horizon at the Naze, in James Ross Island.

Aves - The avian fossil record of the SHIF is limited to the Cape Lamb Member (Table I and Fig. 5) and suggests that several marine lineages of Neornithes were a successful group in Antarctica during the Late Cretaceous. Several bones have been assigned to Gaviiformes and Charadriiformes by different authors.

Hindlimbs bones of gaviiforms-like birds constitute an extensive and controversial record in VEG. Most of the material is isolated and fragmentary, and exhibit features compatible with foot propelled divers (Acosta Hospitaleche & Gelfo 2015). However, during the last decade, important discoveries (Clarke et al. 2016) have changed our conceptions for the assignment of these materials. These elements of variable size, quite common in Late Cretaceous strata (Reguero et al. 2013b, Roberts et al. 2014, Acosta Hospitaleche & Gelfo 2015), could belong to diving birds similar to the Antarctic *Polarornis* and the anseriform *Vegavis* (see Acosta Hospitaleche et al. 2019 for a further description and references). Unfortunately, their incompleteness precludes a confident assignment for many of these materials, which after a long discussion are still questionable.

Two previous reports of Charadriiformes (Case & Tambussi 1999, Cordes 2001, 2002) have been recently dismissed. The first one (MLP 98-I-10-25) corresponds to a left tarsometatarsus without proximal and distal ends recovered at VEG IAA 3/98 (Reguero et al. 2013b) (Fig. 4s-u) that was assigned to a charadriiform in an abstract without any description or pictures. This record was ignored in posterior contributions until Reguero et al. (2013b) merely described it as the oldest neognathous bird from Antarctica.

MLP 98-I-10-25 was reviewed in the context of an ongoing broader analysis. This has a slender shaft that narrows distally with a lateral edge constituting a crest extended distally. The shaft section is dorso-plantarly compressed at the proximal-most part, becoming triangular in the mid part, and cylindrical distally. The third trochlea is torsioned and laterally displaced from the central axis. The basis of the trochleae defines a rotated arch in which the trochlea III is latero-distally projected, the trochlea IV is caudo-laterally located with respect to the latter, and the trochlea II is medial and less distally extended than the others. The shaft morphology and the trochlear rotation resemble some extant taxa such as *Fulica leucoptera* and specially *Podylimbus podiceps*. However, these similarities are only superficial, in MLP 98-I-10-25 the trochleae rotate laterally, and the trochleae II and III are dorsal to the plantarly located trochlea IV (in *Podylimbus* and *Gavia*, the trochleae rotate medially, and trochlea III and IV are dorsal to the trochlea II). Besides, the *foramen vasculare distale* opens in a more distal position than in the modern taxa compared, and the base of the trochlea III in MLP 98-I-10-25 is dorso-lateral to the diaphysis, a feature not shared with the other taxa. MLP 98-I-10-25 would belong to a gracile bird, probably adapted to swimming.

The MLP 98-I-10-54, an incomplete left tarsometatarsus (fig. 4m-o) from VEG IAA 2/98 was identified by Acosta Hospitaleche & Gelfo (2015) as cf. Gaviiformes. This specimen is very similar to Gaviiformes due to the strong latero-medial compression of the diaphysis and the ridges on the cranial face.

The second material previously assigned to a Charadriiform is a partial articulated skeleton of an Ornithuromorph recovered some 20 meters above the 71.0 Ma datum in the Cape Lamb Member on Vega Island, and at least 10 meters below the occurrence of the tarsometatarsus MLP 98-I-10-25 above described. This makes the recently named *Antarcticavis capelambensis* (Fig. 4m-o) the geologically oldest known bird from Antarctica. Comparative and phylogenetic analysis are not supportive in the assignment of *Antarcticavis* to a neornithine bird (Cordes-Person et al. 2020). Discoveries of more complete and better-preserved specimens sould help to understand the precise phylogenetic position of this bird.

DISCUSSION

Snow Hill Island Formation vertebrates: systematics and paleobiogeography

Chondrichthyes and Osteichthyes

The fossil fish record of the Snow Hill Island Formation has been enriched through several publications (Kriwet *et. al*. 2006, Martin & Crame 2006, Otero et al. 2014a, Roberts et al. 2014, Gouiric-Cavalli et al. 2015, Reguero et al. 2015). Particularly, the fossil record of chondrichthyans seems to be more abundant and taxonomically diverse in comparison with the actinopterygians (Table I), and that especially true comparing Gamma Member with Cape Lamb Member (Fig. 5). Many of the chondrichthyan described seem to be endemic (e.g., *Clamydoselachus thompsoni, Paraorthacodus antarcticus, Edaphodon snowhillensis*).

Here, we describe actinopterygian material previously reported by Reguero et al. (2015), discuss some previous assignations (i.e., those made by Roberts et al. 2014) and include new material from SMC and VEG. In the present state of knownledge, and due preservation quality, the new material described herein can only be assigned to high hierarchy levels.

The fish diversity scenario and morphological disparity at the NG sequence of the SHIF higlights the need of more exploration in order to look for more and better-preserved material that allows a more precise taxonomic assignations and further enriching discussion. Fish record at SHIF is more diverse than it was presumed but several questions remain unclear such as there are affinities (taxonomic and/or phylogenetic) among taxa from NG sequence with those present in other coeval units worldwide?

Remarks on fish paleobiogeography

During the late Mesozoic, marine actinopterygian taxonomic diversity and morphological disparity is outstanding. Some Antarctic Cretaceous elasmobranch taxa have a bipolar distribution (*e.g., Notidanodon*, *Paraorthacodus*, *Protosqualus*, *Edaphodon*).

An increase in the diversity of the teleosts is observed in the Late Jurassic (Arratia 2004). However, the group shows a marked explosion of diversification in Late Albian to Cenomanian. Yet, "ichthyodectiforms show a rather constant diversity from the Late Jurassic to the end of the Cretaceous and seem not to have been affected by the factors that triggered diversification of other marine teleosts in the mid-Cretaceous" (Cavin et al. 2013, p. 173). Noteworthy, ichthyodectiforms and aulopiforms (*Enchodus*), together with several chondrichthyan species (*Clamydoselachus thompsoni*, *Paraorthacodus antarcticus*, *Edaphodon snowhillensis*, *Callorinchus torresi*, *Chimaera zangernli*) became extinct at the Cretaceous–Paleogene boundary (Cione et al. 2018).

Chondrichthyans and actinopterygians recovered from the Gamma Member are abundant consisting mainly of isolated scales, teeth, and tooth plates; those of the Cape Lamb Member are fewer in abundance and taxonomic diversitlow diversey, but they are better preserved consisting of more articulared but incomplete specimens. The difference in abundance among these two members of the SHIF (Fig. 5) might be arise as collection bias; thus, further, and comprehensive fieldwork with focus on chondrichthyans and osteichthyans is needed to evaluate this scenario. Morevover, differences in actinopterygian preservation among Cape Lamb and Gamma members of the SHIF need to be explored in detail.

Marine reptiles

The Antarctic plesiosaur discoveries have occurred in the James Ross Basin at the northeastern tip of the Antarctic Peninsula (Fig. 1).

The phylogenetic affinities of the elasmosaurids from Antarctica are currently under study that has some difficulties due the absence of well-preserved cranial material and more complete articulated postcranial specimens. However, in the last decade the knowledge has been continually improved. The description of *Vegasaurus molyi*, the first non-aristonectine from Antarctica represented by an adult well preserved specimen allows a first a first attempt to recognized phyogenetical affinities of the non-aristonectine from Antarctica (O'Gorman et al. 2015). O'Gorman et al. (2015) recovered *V. molyi* as sister group of *Kaiwhekea* and *Aristonectes* showing a possible relation between the aristonectine and non-aristonectine elasmosaurids from the Weddellian Province. A phylogenetic analysis performed by O'Gorman (2016) recovered *Vegasaurus molyi* in a clade formed by the aristonectine (*Aristonectes* spp. and *Kaiwhekea katiki*); *Morenosaurus stocki*; *Kawanectes lafquenianum*. This reinforces the idea between the aristonectine and non-aristonectine from the Weddellian province, adding Patagonian genera to the analysis (*Kawanectes lafquenianum*) and shows some affinities with *Morenosaurus stocki*, an upper Maastrichtian a genus from California. Finally, a new clade Weddellonectia, comprising *Aristonectes* spp., *Kaiwhekea katiki*, *Morenosaurus stocki*; *Kawanectes lafquenianum* and *Vegasaurus molyi*, was erected by O'Gorman & Coria (2017) and the same clade was recovered in a large-scale phylogenetic analysis (O'Gorman 2019).

This background shows that the disappearance of the polycotylids in post Santonian levels of the Marambio Group (Novas et al. 2015) and the first apearence of aristonectines in Antarctica (upper Maastrichtian, O'Gorman et al. 2019b) indicates a large-scale plesiosaur faunal turnover in Antarctica during the Campanian-lower Maastrichtian. This faunal turnover could be correlated with the cooling trend of the end of the Cretaceous (O'Gorman et al. 2019b).

New Zealand records shows a similar picture, aristonectines such as *Kaiwhekea katiki* appears in the record near the limit between lower Maastrichtian and upper Maastrichtian. Additionally, although Upper Cretaceous plesiosaurs have been collected in New Zealand since the 19th century, and the record comprises a large number of elasmosaurids, only few vertebrae are positively recognized as polycotylid (Wiffen & Moisley 1986, Welles & Greeg 1971). The South American record shows an almost mirror image. In the Atlantic margin, aristonectines appears in the record at the upper Campanian-lower Maastrichtian Allen Formation and *Aristonectes parvidens* is recorded in the upper Maastrichtian horizons of the Lefipán Formation and additionally a large number of non aristonectine elasmosaurids are recorded in the mentioned Allen Formation and the upper Maastrichtian levels of the Jagüel Formation. Additionally, *Aristonectes quiriquinensis* is recorded on the Quiriquina Formation (Maastrichtian), Chile (Otero et al. 2014b). In summary the main feature is the presence of the polycotylid *Sulcusuchus erraini* in the upper Campanian-lower Maastrichtian levels of the La Colonia Formation and polycotylids indet. from the Allen Formation (O'Gorman et al. 2011, Gasparini & de la Fuente 2000, O'Gorman & Gasparini 2013). These differences could be related with the marine marginal environment of Allen and La Colonia Formation that acts as a shelter for polycotylids that at the same time were absent or remains relictual in other Weddellian localities.

Dinosaurs

The Snow Hill Island Formation yields, at present, the highest record of non-avian dinosaurs recorded from Antarctica. Representatives of this taxonomic level have been collected from the Lower Jurassic (Hammer & Hickerson 1994, Smith & Pol 2007) and Upper Cretaceous (Molnar et al. 1996, Case et al. 2000) formations. Yet, the non-avian dinosaur diversity recorded from both members, the Gamma Member and the Cape Lamb Member, constitute the currently highest record of this group, including semiarticulated skeletons and isolated elements. The diversity includes both saurischian and ornithischian taxa, with the later taxon being represented by the ankylosaur *Antarctopelta* and the ornithopods *Trinisaura* and *Morrosaurus*. The saurischians are, in turn, represented by less informative evidence, including an isolated caudal vertebra of a Lithostrotia sauropod, and limb elements of the paravian theropod, *Imperobator*.

Due the fragmentary nature of most individuals, the available osteological information is limited. Therefore, current phylogenetic hypotheses are constrained by the great amont of missing data. At least for the Antarctic elasmarian ornithopods, they seem to be more closely related with South American forms (Coria et al. 2013, Rozadilla et al. 2016) than with the Australian ones. Although Bell et al. (2018) phylogenetic analysis placed an Australian elasmarian, *Weewarrasaurus*, within a group of South American elasmarian ornithopods. Thus, previous morphological differences of the Antarctic taxa which once supported certain degree of provincialism for the Cretaceous of this continent (Rozadilla et al. 2016) may not be as greater as it seemed when there were fewer ornithopods on all three continents.

Antarctopelta is considered by Thompson et al. (2012) to be the most basal nodosaurid. In many features it appears intermediate between the ankylosaurid and nodosaurid conditions (Salgado & Gasparini 2006).

Aves

Neornithine birds in the Late Cretaceous JRB are more diverse than it was presumed. Until now, all records come from the Cape Lamb Member. Although still controversial regarding its taxonomic assignment, remains assigned to gaviiform-like birds are abundant and widespread. These bones would belong to median birds whose hindlimb bones were adapted for the propulsion under water, in a similar way to what is seen in the Pied-billed grebe *Podylimbus podiceps* today.

Aside from these gaviiform-like birds, the other bird recorded in VEG correspond to *Antarcticavis capelambensis*. This bird is known from a partial skeleton that exhibits clear differences with the Maastrichtian *Vegavis* and *Polarornis*, was unambiguously assigned to a derived Ornithuromorpha, probably an Ornithurae, and constitutes the geologically oldest bird from Antarctica.

Taphonomical remarks of some vertebrate bearing horizons of the Snow Hill Island Formation

The close scrutiny of the fossil assemblages and stratigraphic horizons of the Gamma and Cape Lamb members of the Snow Hill Island Formation indicates that at least two different subsets of articulated skeletons are present throughout this sequence and have probably different taphonomic histories (including bone abrasion, scavenging, completeness, and sorting). Thus, allochthonous skeletons, ie., dinosaurs and birds, transported from continental fluvial systems are differentiated from autochthonous skeletons (actinopterygians and marine reptiles) that were buried by the same bearing stratigraphic horizon.

The preliminary sedimentological interpretations are consistent with that much of the vertebrate remains accumulated in shallow coastal waters via attritional mortality aquatic and terrestrial taxa. However, bird remains from Cape Lamb Member exhibit significantly higher weathering and abrasion states. Also consistent with local sedimentology, these fossils have different preservational attributes, having been reworked from overlying sandstone bodies, and represent the skeletal remains of taxa that may have been introduced into the water bodies by overland transport during flood events.

Some skeletons of dinosaurs (Vega “early-diverging ornithopod” NHMUK PV R 36760, *Trinisaura*, *Morrosaurus*) collected from horizons within the Snow Hill Island Formation exhibit low degrees of both surface weathering and abrasion. Using classical interpretations of such taphonomic parameters (*e.g.*, Behrensmeyer, 1978; Fiorillo, 1988; Cook, 1995), these data would indicate that most fossil material has undergone minimal transport, reworking and subaerial weathering. No taphonomical data is known of the skeleton of the ankylosaur *Antarctopelta oliveroi*. According to the model of ankylosaur taphonomy proposed by Mallon et al. (2018) ankylosaur carcasses become reworked into fluvial or marine settings where they bloat and overturn prior to their final deposition. These authors regarded a differential floating behaviour between ankylosaurids and nodosaurids could have implications in the occurrence of the nodosaurids in marine depositional environments and demonstrated that ankylosaur specimens occur more frequently upside-down than not.

Two taphonomic and depositional settings were analyzed in: 1) articulated skeletons of marine reptiles from Santa Marta Cove, the Naze, and Cape Lamb (*Taniwhasaurus antarcticus*; *Vegasaurus molyi*, and several other elasmosaurid skeletons) with evidence of having been scavenged by hexanchid sharks and nautilods; and 2) dinosaurs recovered articulated from the same horizon of Santa Marta Cove (*Trinisaura santamartaensis* and *Antarctopelta oliveroi*), associated to abundant plant debris share distinctive taphonomical history characterized by preservation of articulation and with no evidence or little of scavenging, only in *Antarctopelta* was found a tooth of the hexanchid *Notidanodon* on a vertebra. Associated with the skeleton of *Antarctopelta oliveroi* were found at locality SMC IAA 1/86 teeth of hexanchid and *cf. Scapanorhynchus* sharks, a dental plate of the chimaeroid *Callorhynchus*, and remains of an ichthyodectiform teleostean (Table I).

Other isolated bones of dinosaurs (i.e., a sauropod vertebra), have signs of being deposited in marine sediments after dismemberment and transportation from the peninsula. More complete stratigraphic and taphonomical analyses of vertebrates are now available for the late Campanian-early Maastrichtian Snow Hill Island Formation, now with better possible the interpretation of the local environments and correlations through the Upper Cretaceous of West Antarctica with other Gondwanan areas.

The taphonomic attributes of the elasmosaurid specimens vary between isolated elements (*e.g.*, single vertebra) to almost complete skeletons (MLP 93-I-5-1 and SDSM 78156) (see Figure S4) and shows that the articulated or sub-articulated specimens are not rare and at least one specimen preserves gastrolith in natural position indicating almost not disturbing. However, other specimens show severely bone erosion that indicates time before the burial.

The juvenile skeleton (SDSM 78156) was discovered in the Sandwich Bluff area of Vega Island from Late Cretaceous (Maastrichtian) marine deposits from the upper Cape Lamb Member of SHIF (Martin et al. 2007b). The bearing bed has grayish-green color and consists of generally massive, fine-grained muddy sandstones to sandy mudstones. Isolated and mostly rounded volcanic pebbles and cobbles are commonly present. Ammonoids, *Eutrephoceras subplicatum* (nautiloid), crustaceans, bivalves (including *Pinna*), serpulid worms (*Rotularia*), various gastropods, and fossil wood are common in this horizon.

From the same area, relatively numerous juvenile mosasaurs were collected (Fig. 6e-h). These specimens, in conjunction with the articulated juvenile plesiosaur, suggest that the shallow marine environment may have been a protected area where marine reptiles had their young.

Snow Hill Island Formation vertebrate levels and their associated floras

Wood fragments, twigs and some leaves in concretions were found in the Gamma Member. Some of them with an exquisite anatomical preservation at high magnifications, and several materials were collected form the same source of sediments from where several of the dinosaurs were found, speculatively from the same current that transported the continental remains. This material is under study and will provide new taxa for the late Campanian in the Antarctic Peninsula.

Wood fragments, twigs with attached leaves and a ovulate cone of conifers (Araucariaceae and Podocarpaceae) are known from the Cape Lamb Member of the Vega Island (Locality A, 63°53’40.7” S; 57°35’49.1” W) described by Césari et al. (2001, 2009). An ornithopod dinosaur and birds were unearthed from a nearby locality at the same stratigraphic level (Pirrie et al. 1991). Although the presence of the Araucariaceae and Podocarpaceae are generalized in the Upper Cretaceous records of the JRB (Dettmann & Thomson 1987, Askin, 1992, Barreda et al. 1999, Torres et al. 2012, Pujana et al. 2017,

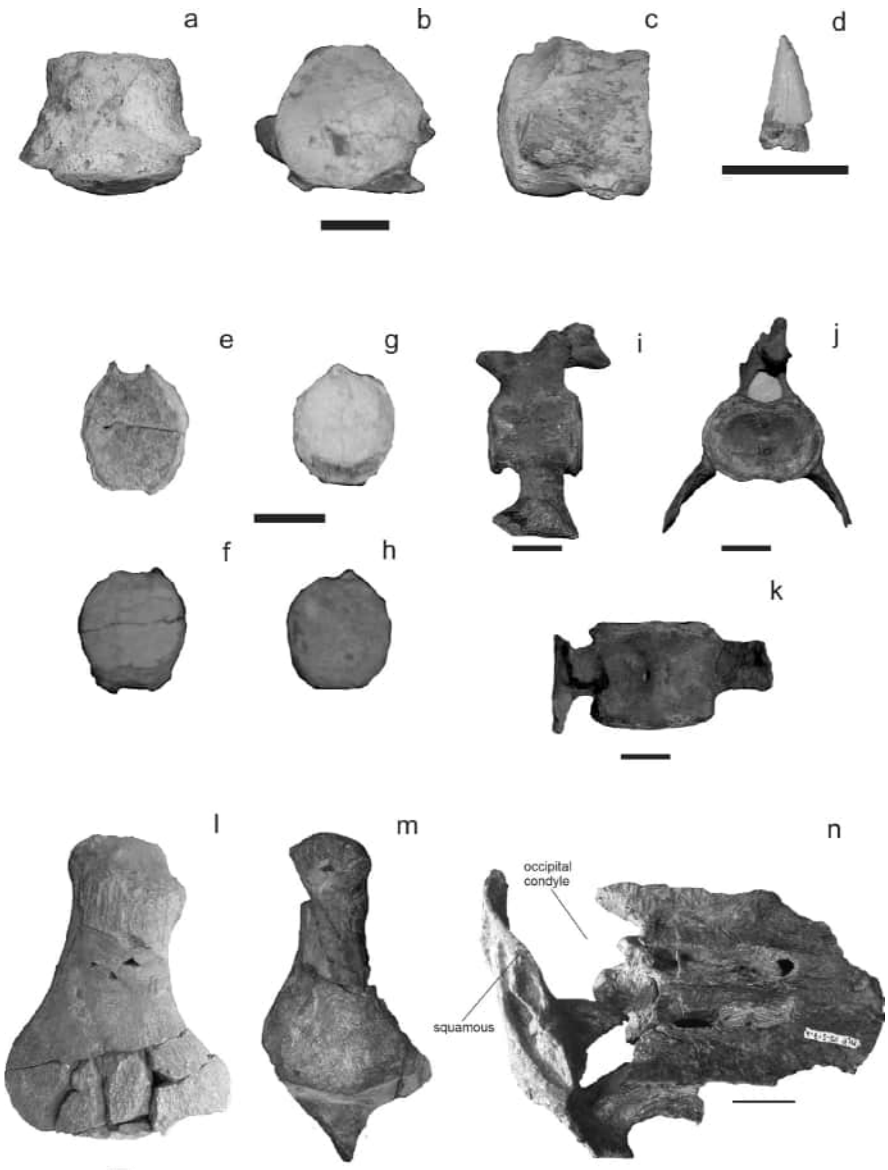

Figure 6. Marine reptiles (Mosasauria and Plesiosauria) from Snow Hill Island Formation strata of the JRB, Antarctic Peninsula: (a-c.) Caudal vertebra of *Taniwhasaurus antarcticus* (MLP 98-I-10-14) (a.), dorsal; (b.) anterior; (c.) lateral views (scale bar = 10 mm); Mosasauridae indet., MLP 93-I-3-7 (d.) tooth referred to cf. *Taniwhasaurus antarcticus* (scale bar = 10 mm); juvenile vertebrae of Mosasauridae indet., MLP 98-I-10-80 in (e.) anterior and (f.) posterior views, and MLP 98-I-10-81 in (g.), anterior and (h.), posterior views (scale bar = 10 mm); *Vegasaurus molyi* (MLP 93-I-5-1), holotype (i-k,) cervical vertebrae in (i.) left lateral, (j.) posterior, and (k.) ventral views; (l.) left humerus in dorsal view, (m.) right femur in ventral view; Weddellonectia indet (MLP 15-I-7-6), skull material, (n.) palate in ventral view (scale bar = 20 mm).

2018), Barreda et al. (2019) recognize a strong fall in gymnosperm and fern diversity (44 % and 68 % respectively) based on continental palynology at the late Campanian and early Maastrichtian (Cape Lamb Member). Flower plants (angiosperms) were similarly affected (36 %) but maintaining a high diversity by new taxa (8 spp.). Among the angiosperm families identified by Barreda et al. (2019) for Gamma Member: Aquifoliaceae, Arecaceae (=Palmae), Cassuarinaceae, Chloranthaceae, Gunneraceae, Lauraceae, Malvaceae, Myrtaceae, Nothofagaceae (8 spp.), Olacaceae, Poaceae, Proteaceae (16 spp.), Symplocaceae, Trimeniaceae?, plus other indeterminate eudicots (33 spp.) and monocots (4 spp.).

Among the angiosperm families identified by Barreda et al. (2019) for the Gamma Member, can be indicated: Aquifoliaceae, Arecaceae (=Palmae), Cassuarinaceae, Chloranthaceae, Gunneraceae, Lauraceae, Malvaceae, Myrtaceae, Nothofagaceae (8 spp.), Olacaceae, Poaceae, Proteaceae (16 spp.), Symplocaceae, Trimeniaceae?, plus other indeterminate eudicots (33 spp.) and monocots (4 spp.). Among the angiosperm families identified by Barreda et al. (2019) for only two levels in the Cape Lamb Member, can be indicated: Aquifoliaceae, Cassuarinaceae, Ericaceae/Epacridaceae, Fabaceae?, Gunneraceae, Malvaceae (Bombacoideae), Nothofagaceae (8 spp.), Proteaceae (10 spp.), Symplocaceae, plus others indeterminate eudicots (15 spp.).

Sphagnaceae (peat moss maker) are common though the sequence. The presence of Sellaginellaceae, Lycopodicaeae, Ericaceae/Epacridaceae also coincide with wet areas possible like peat bog environments (Fig. 6).

Barreda et al. (2015) reported the presence of several pollen grains of Asteraceae (sunflowers and daisies) preserved in dinosaur-bearing deposits from the Late Cretaceous of Antarctica that drastically pushes back the timing of assumed origin of the family. Reliably dated to ~76–66 Mya, these specimens are about 20 million years older than previously known records for the family (in Patagonia). Other important records to certificate are the possible records of Poaceae and Fabaceae.

CONCLUSIONS

The Snow Hill Island Formation is the basal section of the NG Sequence (late Campanian-early Maastrichtian) and bears the most diverse Late Cretaceous marine and continental vertebrate faunas yet known in Antarctica (see Fig. 5). Historical (70´s) and recent field seasons (January/February 2013, 2014, 2015, 2017, and 2020) proved the potential of this geologic unit as a valuable source of fossil vertebrates.

The Gondwanan signature of the Snow Hill Island Formation fauna provides key data on the Cretaceous vertebrate diversity and biogeographic relationships of the southern-most continents of deep Gondwana (Fig. 5 and 7).

In the Late Cretaceous (Campanian/Maastrichtian) of Antarctica a significant diversity of non-avian dinosaurs and marine reptiles has been documented. The dinosaur record of the Upper Cretaceous of JRB is composed by several clades (basal ornithopod, ankylosaurs, titanosaurs, basal paravians and birds. Reguero & Goin (2021) recognized a West Weddellian Terrestrial Biogeographic Province as geographical unit restricted to Antarctica and the southern part of South America spanning through the Late Cretaceous (Campanian) to the Early Paleogene (Paleocene).

The percentage of taxonomic vertebrate representation in these members of the Snow Hill Island Formation is mostly conservative (Fig. 5). Some changes in taxonomic composition could be related to a modification in paleoecological roles. Among the diversity of marine predators, Chondrichthyes decrease their number from Gamma to Cape Lamb Member, while Mosasauridae and Plesiosauria become the dominant forms. In contrast, the absence of Pterosauria and Aves in Gamma Member could be easily explained due to a sample bias, rather than different paleoecological conditions between both units. The same observation can be applying to the few terrestrial taxa recorded from Gamma Member. They are only represented by four herviborous non-avian dinosaurs, so the absence of Theropoda, which were recorded in Cape Lamb, is probably an artifact sample or a taphonomic consecuence, and not a real image of the vertebrate land representation.

The floral composition, habitat and climate reconstruction is presented for the emergent volcanic arc in the Maastrichtian of JRB. On the coastal lowlands, a cool to warm temperate rainforest is envisaged growing in a riverine landscape, with both wet (river margin, pond) and relatively dry (interfluve, canopy gap) habitats. Diverse podocarps trees grew alongside

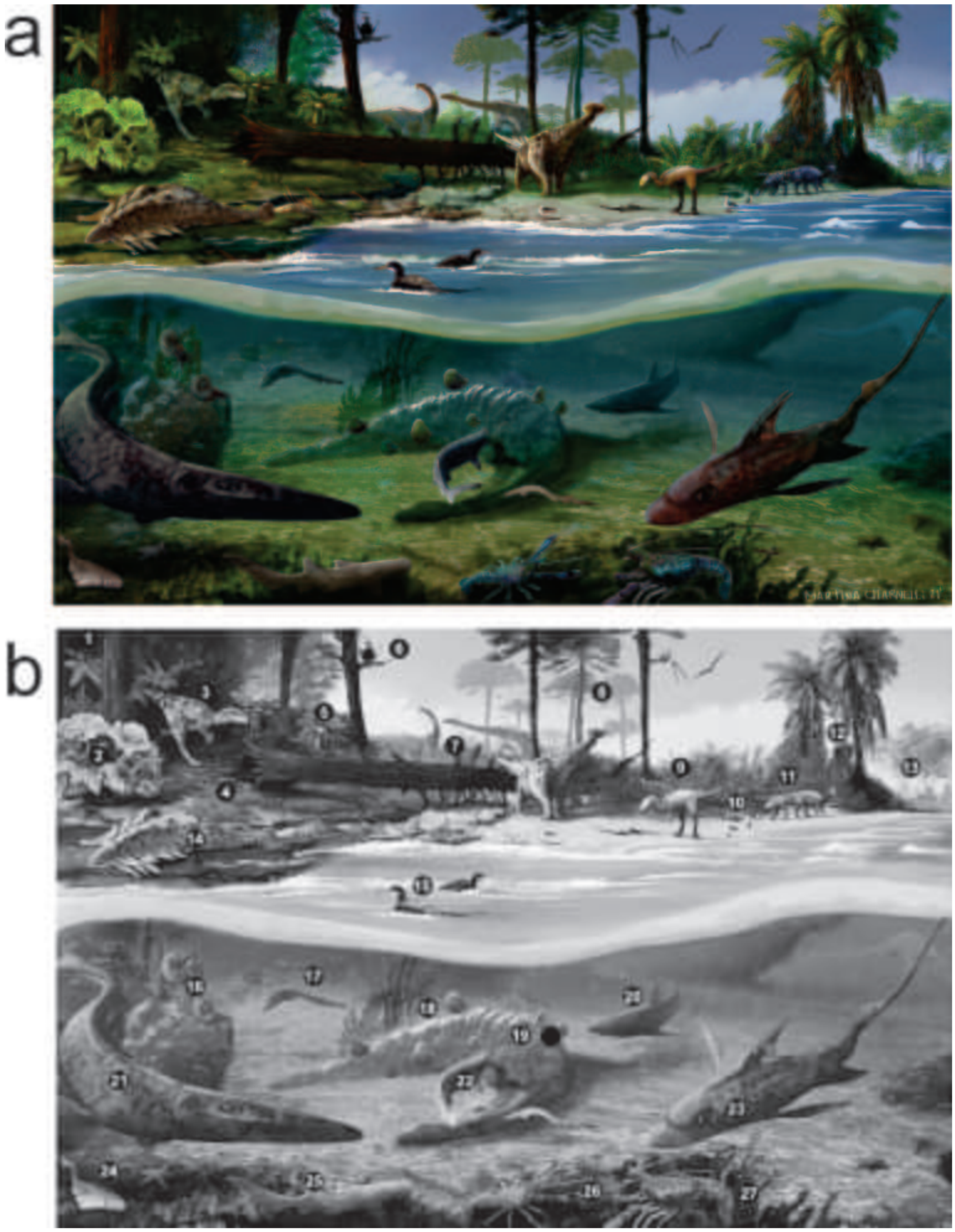

Figure 7. (a.) Terrestrial and marine environments and vertebrate assemblages of the Late Cretaceous (late Campanian-early Maastrichtian) Snow Hill Island Formation, Antarctic Peninsula based on the paleontologic evidence from the Gamma and Cape Lamb members. In this reconstruction we are exercised a degree of artistic license to assemble these species together; **(b.)** The vertebrates, invertebrates, and plants depicted in this figure are the following: **1-** *Dicksonia* sp. (fern); **2-** *Gunnera* sp. (rhubarb); **3-** *Imperobator antarcticus* (theropod); **4-** *Sphagnum* sp. (moss); **5-** *Cycas* sp. (gymnosperm); **6-** Pterosaur Pterodactyloidea; **7-** Lithostrotia indet. (titanosaur); **8-** *Araucaria* sp. (evergreen coniferous); **9-** *Trinisaura santamartaensis* (ornithopod); **10-** Neornithes indet. (bird); **11-** *Morrosaurus antarcticus* (ornithopod); **12-** Arecaceae (palm); **13-** *Nothofagus* sp. (Southern beech); **14-** *Antarctopelta oliveroi* (ankylosaur); **15-** *Antarcticavis capelambensis* (bird); **16-** *Gunnarites antarcticus* / *Neograhamites primus* (ammonite);**17-** *Clamydoselachus* sp. (shark); **18-** *Eutrephoceras subplicatum* (nautiloid); **19-** *Vegasaurus molyi* (plesiosaur); **20-** *Sphenodus* sp. (shark); **21-** *Taniwhasaurus antarcticus* (mosasaur); **22-** *Notidanodon* sp, (shark); **23** *Edaphodon snowhillensis* (holocephalian)-; **24-** *Squatina* sp. (shark) ; **25-** *Clamydoselachus thompsoni* (shark); **26-** *Hoploparia equinata* (lobster) ; **27-** *Hoploparia stokesi* (lobster).

angiosperm herbs and shrubs in mean annual temperatures of ~ 10 – 15° C (Bowman et al. 2014).

Based on the change in flora composition between Gamma Member and the Cape Lamb members (Dettman & Thomson 1987, Askin 1992, Barreda et al. 2019), it seems to be a clear major change in the continental biomas (Fig. 7). This change is coincident with the drop in temperatures described for the late Campanian-early Maastrichtian by (Li & Elderfield 2013).

Further perspectives include more exploration in the area and the study of the specimens with the consequent increase in the taxonomic diversity of the Cretaceous biota.

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SUPPLEMENTARY MATERIAL

Figure S1. Snow Hill Island Formation. a. Panoramic view of the Gamma Member exposure at Santa Marta Cove, James Ross Island, Antarctic Peninsula; b. Panoramic view of the Cape Lamb Member exposure at Cape Lamb, Vega Island, Antarctic Peninsula; c. Panoramic view of the Cape Lamb Member exposure at The Naze, James Ross Island, Antarctic Peninsula.
Figure S2. Schematic tectonic setting of the Magallanes-Austral, Larsen, and Byers's basins with extant continental borders during the Late Cretaceous (Campanian) (Hervé et al. 2006; Jordan et al. 2020). The red star indicates the location of JRB (SHIF). Abbreviations: AP, Antarctic Peninsula, MR, Magallanes Region, PAT, Patagonia, TI, Thurston Island.
Figure S3. (a.) Sketch diagram of *Vegasaurus molyi* (MLP 93-I-5-1) skeleton in the quarry, based on field and preparation notes and photographs; (b.) First field photograph of the study site (locality VEG IAA 2/93).
Figure S4. Bar chart showing the percentage of elasmosaurid specimens (n= 48) from SHIF that preserve different skeletal elements: a) ribs and gastralia; b) girdle bones; c) phalanges and metapodials; d) tarsal / carpals elements; e) propodio; f) caudal vertebrae; g) dorsal and sacral vertebrae; h) cervical and pectoral vertebrae; i) cranium and mandible and j) teeth.

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