

Late Cretaceous dinosaurs from the James Ross Basin, West Antarctica

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Abstract: The fossil record of terrestrial vertebrates from the Late Cretaceous of Antarctica is currently composed of non-avian and avian dinosaurs from the marine sediments of the James Ross Basin, Antarctic Peninsula (West Antarctica). Although two dinosaurian formational assemblages (Late Campanian/Early Maastrichtian and Late Maastrichtian) are known, the record is still scattered, and evolutionary scenarios are tentative. Ten non-avian dinosaurs have been reported from Coniacian to Maastrichtian deposits, along with possible sauropod footprints of Early Maastrichtian age from Snow Hill Island. Five avian dinosaurs have been recorded or described exclusively from the Maastrichtian. The presence of an advanced titanosaur with characteristic procoelous mid-caudal vertebrae in Snow Hill Island Formation at Santa Marta Cove implies that the group achieved a global distribution by the Late Campanian. The Late Campanian/Early Maastrichtian non-avian dinosaur (ankylosaurs, ornithopods and dromaeosaurid theropods) clades probably attained a near-cosmopolitan distribution before the Late Cretaceous, and some aspects of this hallmark ‘Gondwanan’ fauna may therefore reflect climate-driven provinciality, not vicariant evolution driven by continental fragmentation. Antarctic Late Cretaceous avian dinosaurs are rare. They are restricted to the Maastrichtian and consist of a cariamid?, gaviids, a charadriiform and the basal Anseriformes *Vegavis*, and provide the first strong evidence for a basal radiation of birds known to exist in the Cretaceous.

Although the Late Cretaceous marine deposits of the James Ross Basin have been extensively surveyed by vertebrate palaeontologists, they have mostly recovered marine reptiles (del Valle *et al.* 1977; Gasparini *et al.* 1984; Chatterjee & Small 1989; Martin *et al.* 2002; Novas *et al.* 2002a; Martin 2006; Martin & Crame 2006; Reguero & Gasparini 2007; de la Fuente *et al.* 2010) and other marine vertebrate groups (Woodward 1908; Cione & Medina 1987; Grande & Chatterjee 1987; Richter & Ward 1990; Stahl & Chatterjee 1999, 2002; Kriwet 2003; Kriwet *et al.* 2006; Figs 1 & 2). In contrast, fewer terrestrial vertebrates have been discovered, and these are currently represented only by dinosaurs.

From 2008 to 2011, James Ross Basin was the scene of concentrated palaeontological and geological fieldwork. New dinosaur remains were found,

notably in the Snow Hill Island Formation at Santa Marta Cove, James Ross Island (Cerdeña *et al.* 2012; Coria *et al.* 2013) (Fig. 1b). A significant amount of taxonomic and palaeobiological information has been gained from these fossils, which are important for understanding their phylogenetic relationships with other Gondwanan and Nearctic palaeofaunas, comprehending vertebrate biostratigraphy and revealing the role of the Antarctic Peninsula in the terrestrial vertebrate dispersal routes.

Late Cretaceous sedimentary rocks are exposed only around the northern part of West Antarctica, on the South Shetland Islands and in the area of James Ross Island, Weddell Sea, with dinosaur remains found only in the latter area. The sequence there is made up of marine clastic rocks deposited within a back-arc basin (Elliot 1988; Hathway

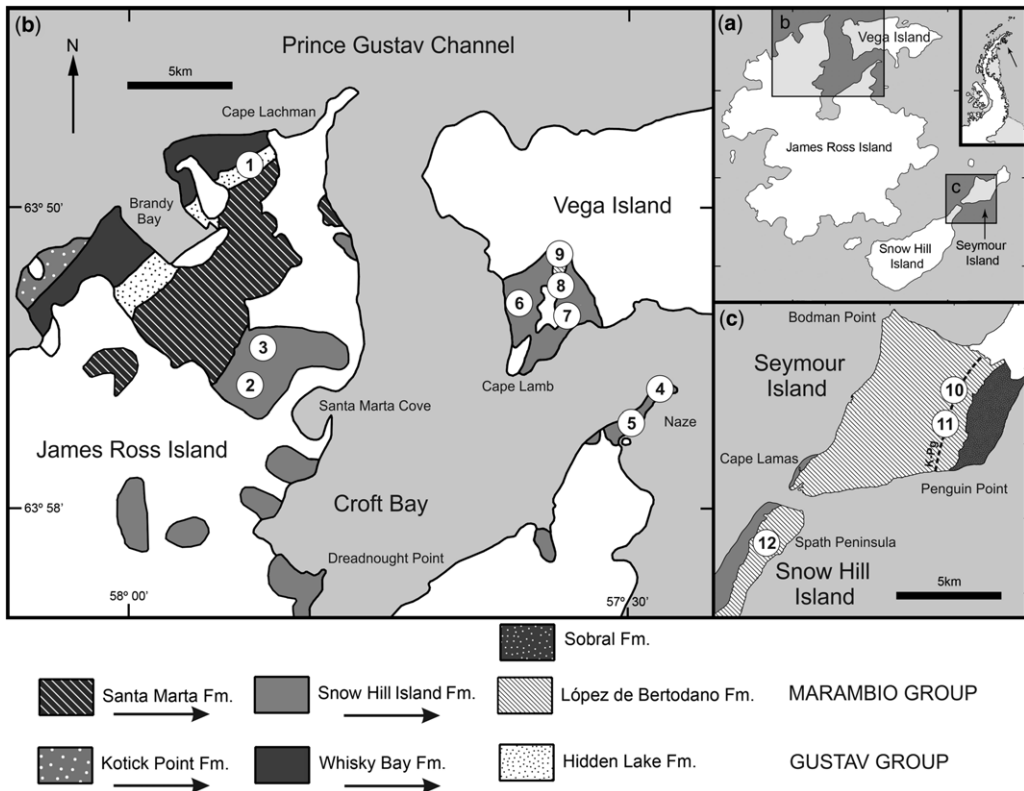


Fig. 1. Schematic geological maps of key dinosaur locations in James Ross Basin, north-eastern Antarctic Peninsula (see locality map on right). (a) Locality map with areas in B and C shaded. White areas are either the James Ross Island Volcanic Group or snow/ice cover. (b) NE James Ross and SW Vega islands. Key dinosaur locations: 1, Brandy Bay, Cape Lachman, James Ross Island, Hidden Lake Formation (Coniacian), megalosaur-like theropod site; 2, Santa Marta Cove, Snow Hill Island Formation (Late Campanian), *Antarctopelta* and ornithopod gen. et sp. nov. sites; 3, Santa Marta Cove, Snow Hill Island Formation (Late Campanian), titanosaur site; 4, the Naze, James Ross Island, Terrapin Hill, Cape Lamb Member (Early Maastrichtian), Snow Hill Island Formation, dromaeosaur site; 5, the Naze, Fortress Hill, James Ross Island, Cape Lamb Member (Early Maastrichtian), Snow Hill Island Formation, iguanodontid site; 6, Cape Lamb, Vega Island, Cape Lamb Member (Early Maastrichtian), Snow Hill Island Formation, charadriiform site; 7, Cape Lamb South, Vega Island, Cape Lamb Member (Early Maastrichtian), Snow Hill Island Formation, hypsilophodontid site; 8, Sandwich Bluff, Vega Island, Sandwich Bluff Member (Late Maastrichtian), López de Bertodano Formation, *Vegavis*, *Polarornis* and cariamid? sites; 9, Sandwich Bluff, Vega Island, Sandwich Bluff Member (Late Maastrichtian), López de Bertodano Formation, 'Reptile horizon', hadrosaur site. (c) NE Snow Hill and SW Seymour islands. Key dinosaur locations: 10, Seymour Island, Unit Klb 9 (Late Maastrichtian), López de Bertodano Formation, hadrosaur site; 11, Seymour Island, Unit Klb 9 (Late Maastrichtian), López de Bertodano Formation, gaviiform site; 12, Spath Peninsula, Tessore Hill, Snow Hill Island, and López de Bertodano Formation (Early Maastrichtian), sauropod? footprint site. Position of the Cretaceous–Palaeogene boundary on Seymour Island indicated by dashed line.

2000) and represents the topmost beds of a regressive mega-sequence (Pirrie *et al.* 1991).

The Late Cretaceous non-avian and avian dinosaurs of the James Ross Basin, Antarctic Peninsula, are numerically scarce and some of them are poorly known or their studies are pending. It should be emphasized that all of these terrestrial taxa were deposited in shallow-marine settings and are thus found more or less where they once lived.

The aim of this paper is to review the current state of the stratigraphical record and biogeography of Antarctic Late Cretaceous terrestrial vertebrates.

Stratigraphy of James Ross Basin

The Late Cretaceous–Palaeogene strata of the James Ross Basin (Figs 1 & 2) comprise a thick sequence of marine sedimentary rocks divided into

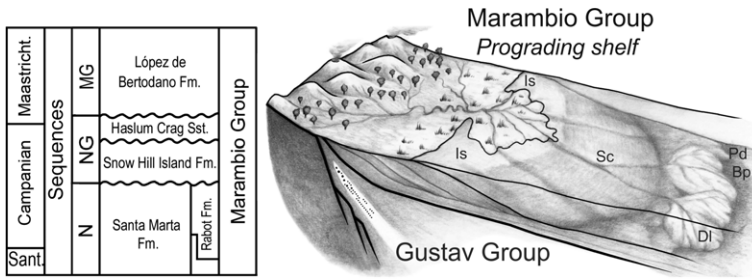


Fig. 2. Relationship between sequences and formations of the Marambio Group, a cartoon illustrating its prograding shelf setting (from Olivero 2012). Pd-Bp, prodelta–basin plain settings; DI, depositional lobes; Sc, slope–channel complex; Is, inner shelf settings.

three lithostratigraphic groups: the basal Gustav Group (Aptian–Coniacian), the intermediate Marambio Group (Santonian–Danian), and the upper Seymour Island Group (Palaeogene; e.g. Rinaldi 1982; Crame *et al.* 1991; Riding & Crame 2002; Fig. 3).

The 2100 m-thick marine sediments of the Gustav Group are exposed along the NW coast of James Ross Island (Fig. 1b). The coarse-grained lower three units of the group (Lagrelius Point, Kotick Point and Whisky Bay formations) were deposited in a deep marine setting and represent proximal submarine-fan and slope-apron depositional

systems (Ineson 1989; Buatois & López-Angrinman 1992). The fourth and youngest unit, Hidden Lake Formation, is composed of distinctive brown-weathering, volcanoclastic sediments, deposited on a fan delta, and readily traced along the length of NW James Ross Island (Whitham *et al.* 2006).

The finer-grained Marambio Group is exposed in James Ross, Vega, Humps, Snow Hill, Seymour and Cockburn islands, and has been recently summarized by Olivero (2012). The Group has a stratigraphic thickness of around 3000 m, with sediment supplied by a volcanic arc in the west deposited on a

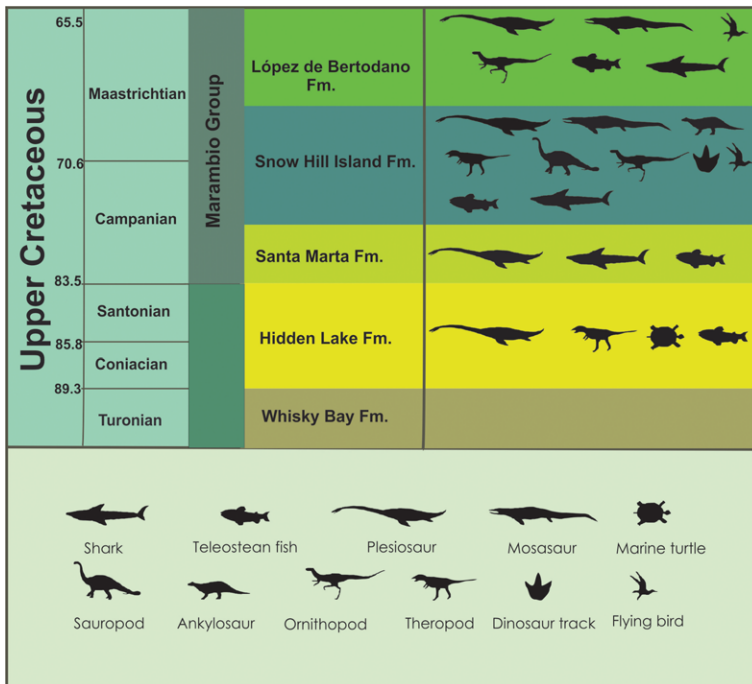


Fig. 3. Time scale, stratigraphy and vertebrate fossil record for the Late Cretaceous rocks in the James Ross Basin, Antarctic Peninsula, West Antarctica. Temporal and sedimentary units not to scale.

shelf prograding eastward into the Weddell Sea (Fig. 2, Olivero 2012). The section represents three major sedimentary cycles: the N (Santonian–early Campanian); NG (Late Campanian–early Maastrichtian); and MG (early Maastrichtian–Danian) sequences, the names of the sequences being derived from the most common kossmaticeratid ammonites that characterize each of them: N for *Natalites*; NG for *Neograhamites* and *Gunnarites*; and MG for *Maorites* and *Grossouwrites* (Olivero & Medina 2000).

Outcrops of the N Sequence (Santonian–early to basal Late Campanian) are exposed in Brandy Bay, James Ross Island (Fig. 1b) and comprise the c. 1000 m-thick Santa Marta Formation that includes the Alpha and Beta members following the original subdivision established in Olivero *et al.* (1986) and Scasso *et al.* (1991). These members are approximately equivalent to the Lachman Crags Member of Crame *et al.* (1991) and Pirrie *et al.* (1997). The Gamma Member (Olivero *et al.* 1986) and the Hamilton Point Member (Pirrie *et al.* 1997) are incorporated into the Snow Hill Island Formation instead of the Santa Marta Formation as originally defined (see Olivero & Medina 2000; Olivero *et al.* 2008). Notably, this member includes dinosaur bones (Olivero *et al.* 1986, 1991; Coria *et al.* 2008; Cerda *et al.* 2012), including a partial skeleton of the ankylosaurian dinosaur *Antarctopelta oliveroi* Salgado & Gasparini (2006). The Gamma Member is approximately equivalent to the Herbert Sound Member of Crame *et al.* (1991). Ammonites are relatively abundant in the upper third of the Gamma Member, characterized by the dominance of the kossmaticeratid genus *Gunnarites* (Olivero 2012).

Outcrops of the NG Sequence (Late Campanian–early Maastrichtian) are widely exposed in the James Ross Basin, from Snow Hill and Seymour islands to Santa Marta Cove area in James Ross Island (Fig. 1b, c). The sequence consists of c. 1000 m of fine-grained sediments comprising the Hamilton Point, Sanctuary Cliffs, Karlsen Cliffs, Cape Lamb and Gamma members of the Snow Hill Island Formation (Olivero *et al.* 1986; Crame *et al.* 1991, 1996; Pirrie *et al.* 1997; Olivero & Medina 2000) and the Haslum Crag Sandstone (Olivero *et al.* 2008). The lower Maastrichtian part of the Marambio Group at Seymour and Snow Hill islands is well exposed (Crame *et al.* 2004), and includes the upper part of the Snow Hill Island Formation and the basal part of the López de Bertodano Formation (Macellari 1988; Pirrie *et al.* 1997; Olivero *et al.* 2007). The uppermost part of the Snow Hill Island Formation includes the informal *Rotularia* Unit 1, and the basal López de Bertodano Formation, representing the *Rotularia* Units 2–5 of Macellari (1988). Absolute dating based

on $^{87}\text{Sr}/^{86}\text{Sr}$ chronostratigraphy suggests an early Maastrichtian age for both stratigraphic units in these areas (Crame *et al.* 2004), thus supporting previous data based on ammonite biostratigraphy (cf. Olivero & Medina 2000; Crame *et al.* 2004).

The MG sequence (early Maastrichtian/Danian) consists mainly of the c. 1000 m-thick mudstone and silty, very fine-grained sandstone succession of the López de Bertodano Formation exposed in the ESE of the basin (Fig. 1c). Localized outcrops of a very distinctive coarse-grained volcanoclastic unit, the Sandwich Bluff Member, are located at Cape Lamb, Vega Island (Fig. 1b). The base of the MG Sequence is a marked unconformity that cuts a maximum of about 60–70 m of the underlying Haslum Crag Sandstone (Pirrie *et al.* 1997; Olivero *et al.* 2007, 2008). At the top of the MG Sequence, another marked unconformity also associated with a deeply incised erosional surface separates the Danian beds of the López de Bertodano Formation from the Paleocene Sobral Formation.

Dinosaurs from the James Ross Basin

Late Cretaceous dinosaurs found in James Ross Basin are summarized in Table 1 and discussed in stratigraphic order below. They come from Coniacian, Late Campanian, Early Maastrichtian and Late Maastrichtian strata on James Ross, Vega, Seymour and Snow Hill islands.

Coniacian (Hidden Lake Formation on James Ross Island)

A theropod fragment was collected from the Coniacian Hidden Lake Formation (Gustav Group) at Cape Lachman, James Ross Island (Fig. 1b, loc. 1), and described by Molnar *et al.* (1996) as a distal portion of tibia. This is the first Antarctic non-avian theropod with unquestionable affinities to taxa from other Gondwanan landmasses, suggesting faunal interchange between eastern and western Gondwana during the Late Cretaceous.

Late Campanian/Early Maastrichtian (Snow Hill Island Formation and basal part of López de Bertodano Formation on James Ross, Vega, Seymour and Snow Hill islands)

Four non-avian dinosaurs were exhumed from different horizons of the Snow Hill Island Formation at Santa Marta Cove, northeastern of the James Ross Island (Fig. 1b). The small-sized ankylosaur *Antarctopelta oliveroi* Salgado & Gasparini

Table 1. Taxonomic list, stratigraphy, geographic locations, age and references for dinosaurs from the Late Cretaceous of the James Ross Basin, Antarctic Peninsula

Taxon	Stratigraphy (Formation)	Geographic location	Age	References
<i>Dinosauria (non-avian)</i>				
Theropoda; gen. et sp. indet.	Hidden Lake Fm.	James Ross Island (Cape Lachman)	Coniacian	Molnar <i>et al.</i> (1996)
Ankylosauria: <i>Antarctopelta oliveroi</i>	GM, Snow Hill Island Fm.	James Ross Island (Santa Marta Cove)	Late Campanian	Salgado & Gasparini (2006)
Ornithopoda: gen. et sp. nov.	GM, Snow Hill Island Fm.	James Ross Island (Santa Marta Cove)	Late Campanian	Coria <i>et al.</i> (2008, 2013)
Ornithopoda: gen. et sp. indet.	GM, Snow Hill Island Fm.	James Ross Island (Santa Marta Cove)	Late Campanian	Coria <i>et al.</i> (2007)
Titanosauria: gen. et sp. indet.	GM, Snow Hill Island Fm.	James Ross Island (Santa Marta Cove)	Late Campanian	Cerda <i>et al.</i> (2012)
Iguanodontidae: gen. et sp. indet.	CLM, Snow Hill Island Fm.	Vega Island (Cape Lamb)	Early Maastrichtian	Hooker <i>et al.</i> (1991)
Dromaeosauridae: gen. et sp. indet.	CLM, Snow Hill Island Fm.	James Ross Island (the Naze)	Early Maastrichtian	Case <i>et al.</i> (2007)
Iguanodontidae?: gen. et sp. indet.	CLM, Snow Hill Island Fm.	James Ross Island (the Naze)	Early Maastrichtian	Cambiaso <i>et al.</i> (2002)
Hadrosauridae: gen. et sp. indet.	SBM, López de Bertodano Fm.	Vega Island (Cape Lamb)	Late Maastrichtian	Case <i>et al.</i> (2000)
?Hadrosauridae: gen. et sp. indet.	Klb9, López de Bertodano Fm.	Seymour Island	Late Maastrichtian	Rich <i>et al.</i> (1999)
Sauropod? footprints	López de Bertodano Fm.	Snow Hill Island (Tesore Hill)	Late Maastrichtian	Olivero <i>et al.</i> (2007)
<i>Dinosauria (avian)</i>				
Charadriiformes: gen. et sp. indet.	CLM, Snow Hill Island Fm.	Vega Island (Cape Lamb)	Early Maastrichtian	Case & Tambussi (1999)
Gaviiformes: <i>Polarornis gregorii</i>	Klb9?, López de Bertodano Fm.	Seymour Island	Late Maastrichtian	Chatterjee (1989)
Gaviiformes: <i>Polarornis</i> sp.	SBM, López de Bertodano Fm.	Vega Island (Cape Lamb)	Late Maastrichtian	Chatterjee <i>et al.</i> (2006)
Anseriformes: <i>Vegavis iaii</i>	SBM, López de Bertodano Fm.	Vega Island (Cape Lamb)	Late Maastrichtian	Clarke <i>et al.</i> (2005)
Cariamidae?: gen. et sp. indet.	SBM, López de Bertodano Fm.	Vega Island (Cape Lamb)	Late Maastrichtian	Case <i>et al.</i> (2006)

Abbreviations: CLM, Cape Lamb Member; GM, Gamma Member; SBM, Sandwich Bluff Member.

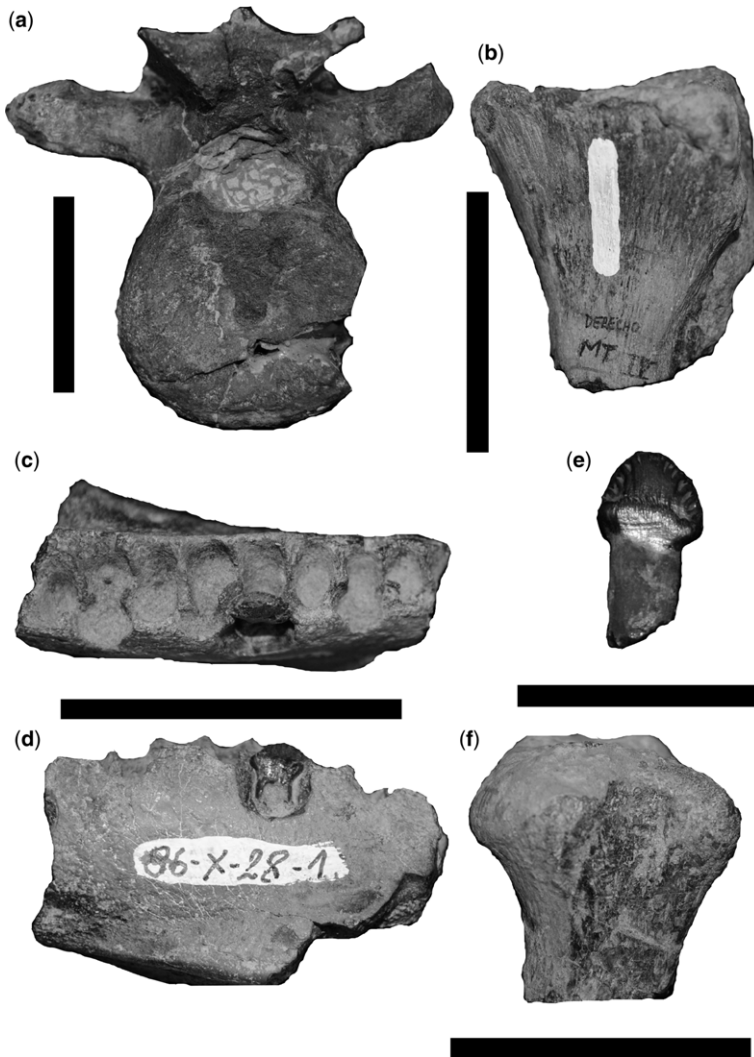


Fig. 4. *Antarctopelta oliveroi* (Salgado & Gasparini 2006), MLP 86-X-28-1, holotype. (a) Posterior cervical vertebra in anterior view (scale bar 50 mm); (b) right metatarsal IV? in lateral view (scale bar 50 mm); (c) left dentary in occlusal view; (d) left dentary in medial view (scale bar 50 mm); (e) tooth II in lingual view (scale bar 50 mm); (f) distal end of metapodial (scale bar 50 mm).

2006 was found in the Late Campanian Gamma Member of the Snow Hill Island Formation (Gasparini *et al.* 1987; Olivero 2012; Fig. 1b, loc. 2). The specimen, MLP 86-X-28-1, is represented by a partial skeleton consisting of a fragment of the left dentary with one tooth in place (Fig. 4), cervical, dorsal and sacral vertebrae, metacarpals and several scutes. The James Ross Island ankylosaur was collected from shallow marine deposits, associated with various marine invertebrates such as bivalves, gastropods and ammonites that indicate a late Early to basal Late Campanian age (Olivero

et al. 1991; Olivero 2012). *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).

Also from the same area of the Santa Marta Cove, two ornithopods, an isolated ungual phalanx and a semiarticulated and incomplete skeleton, have been reported by Coria *et al.* (2007, 2008). These specimens come from the same stratigraphical horizon and close to the site of *Antarctopelta* (Fig. 1b, loc. 2). The ornithopod skeleton

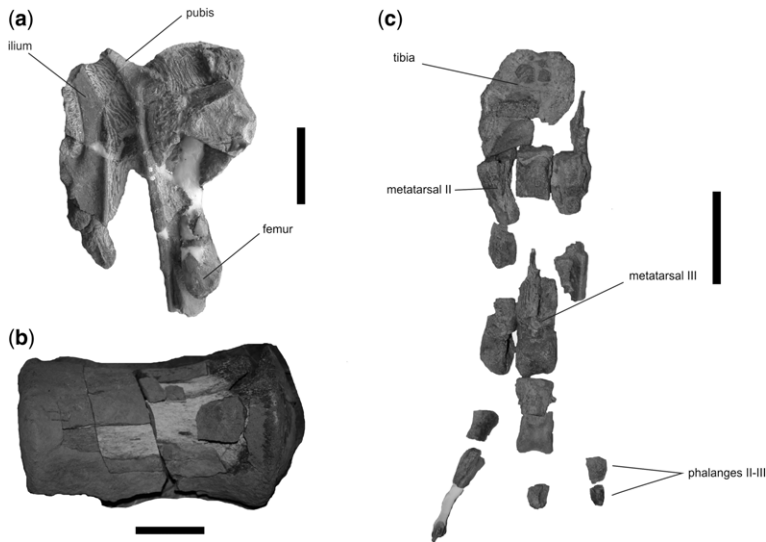


Fig. 5. (a) Ornithopod gen. et sp. nov., associated pubis, ilium and femur of the skeleton MLP 08-III-1-1. Scale bar: 50 mm; (b) Lithostrotian gen. et sp. indet., MLP 11-II-20-1, caudal vertebra centrum, right lateral view (scale bar 50 mm); (c) Dromaeosauridae gen. et sp. indet., partial left hindlimb, ankle and foot (scale bar 100 mm).

represents a new genus and new species of a small basal ornithopod (Coria *et al.* 2008, 2013; Fig. 5a). This new form, MLP 08-III-1-1, is currently under study and its phylogenetic relationships will be useful for insights about the palaeobiogeography of this group (Coria *et al.* 2013).

Recently, an incomplete vertebra of a sauropodomorph titanosaur was recovered in shallow marine shelf deposits referred to the Late Campanian Snow Hill Island Formation in the northern part of James Ross Island (Cerdea *et al.* 2012; Fig. 1b, loc. 3). The size and morphology of the specimen (MLP 11-II-20-1) allowed its identification as a caudal vertebra of a lithostrotian titanosaur (Fig. 5b). This discovery increases the fossil dinosaur diversity of Antarctica and enhances our understanding of the global distribution of sauropod dinosaurs (Cerdea *et al.* 2012).

The dinosaur assemblage from the Early Maastrichtian Cape Lamb Member of the Snow Hill Island Formation consists of four non-avian and one avian dinosaurs. Hooker *et al.* (1991) reported a partial skeleton of a small-bodied (4–5 m) ornithopod dinosaur from the Cape Lamb Member of the Snow Hill Island Formation (Crame *et al.* 2004; Fig. 1b, loc. 7). Numerous skeletal characteristics indicate that this specimen (BMNH BAS R.2450) is related to basal ornithopods but few postcranial features also resemble those of Dryomorpha (Iguanodontia) (Milner *et al.* 1992).

During the 2006–2007 field season J.A. Case and his field crew (including M.A.R.) collected

vertebrate remains of a partial skeleton of a small-bodied theropod dinosaur (Case *et al.* 2007) from the lower portion of the Cape Lamb Member of the Snow Hill Island Formation (Crame *et al.* 2004) on the Naze, northern James Ross Island (Fig. 1b, loc. 4). The remains included a metatarsal II with a lateral expansion caudal to metatarsal III, a third metatarsal that is proximally narrow and distally wide, a metatarsal III with a distal end that is incipiently ginglymoidal and a second pedal digit with sickle-like ungual. Together these are diagnostic of a Dromaeosauridae theropod (Fig. 5c). The Dromaeosauridae is a family of highly derived small to mid-sized theropod dinosaurs characterized by the presence of a raptorial second pedal digit and a tail stiffened by the elongated prezygapophyses and chevrons of the medial to distal posterior vertebrae. The Antarctic dromaeosaur exhibits diagnostic characters of the Dromaeosauridae, that is Mt II, with a lateral expansion caudal to Mt III, and with Mt III proximally narrow and distally wide (Novas & Pol 2005; Case *et al.* 2007).

From similar-aged horizons and close to the dromaeosaur site on the Naze (Fig. 1a) portions of a hind leg and foot of an iguanodontid (MACN-19777) were recovered (Cambiaso *et al.* 2002; Novas *et al.* 2002b). The exact stratigraphic and geographic location of this iguanodontid is uncertain, although field evidence suggests that it came from Fortress Hill next to Terrapin Hill in the Naze (Fig. 1b, loc. 5), possibly the same

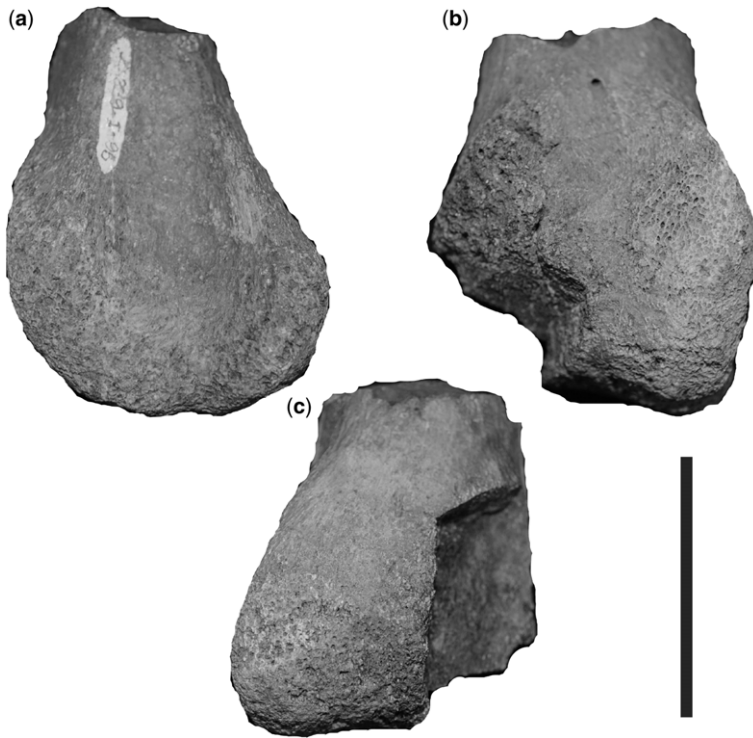


Fig. 6. Hadrosauriidae? MLP 96-I-6-2, distal end of metatarsal: (a) lateral view, (b) dorsal view, (c) ventral view (scale bar 50 mm).

lithostratigraphic unit as the dromaeosaur mentioned above.

Additional indications of non-avian dinosaurs from the James Ross Basin are aligned depressions interpreted as sauropod footprints by Olivero *et al.* (2007) in the basal López de Bertodano Formation, southwestern part of the Spath Peninsula, Tesore Hill, Snow Hill Island (Fig. 1c, loc. 12). These ichnites suggest a more extensive distribution of dinosaurs within the basin and southward. This circumstance could be reflecting opportunistic dispersal of members of the group at the end of the Cretaceous among southern Gondwanan areas via Antarctica, as was previously proposed (Sampson *et al.* 1998), during periods of more favourable climatic conditions in the region.

One avian dinosaur fragment was reported by Case & Tambussi (1999) from the Early Maastrichtian Cape Lamb Member of the Snow Hill Island Formation on Cape Lamb, Vega Island (Fig. 1b, loc. 6). These authors assigned the tarsometatarsus (MLP 98-I-10-25) to an undetermined charadriiform bird. The diaphysis of the MLP 98-I-10-25 is slender, being much longer than wide, and is eroded, with the trochleas broken and the proximal

epiphysis absent (Fig. 7d). The preservation of the material does not permit its positive assignment. This specimen represents the oldest neognathous recorded in Antarctica.

Late Maastrichtian (López de Bertodano Formation on Vega and Seymour islands)

The Late Maastrichtian dinosaur assemblage from the James Ross Basin consists of two non-avian and four avian dinosaurs. Case *et al.* (2000) reported the presence of dental and pedal material of a hadrosaurine hadrosaur from the Late Maastrichtian Sandwich Bluff Member of the López de Bertodano Formation on Vega Island. The 'Reptile Horizon', named for the numerous mosasaur and plesiosaur specimens recovered from this stratigraphic level, is in the upper third of the Sandwich Bluff Member (Crame *et al.* 1991; Pirrie *et al.* 1991; Martin 2006; Fig. 1b, loc. 9), Unit C (Olivero *et al.* 1992) or K3 (Marenssi *et al.* 1992) of the López de Bertodano Formation. This member is composed of nearshore marine, fine-grained, ferruginous, loosely consolidated sandstones that are

Late Maastrichtian in age (approximately 66–68 Ma), based on correlations of ammonite and palynological taxa (Crame *et al.* 1991; Pirrie *et al.* 1991; Olivero & Medina 2000; Olivero 2012).

Rich *et al.* (1999) described a distal end of an ornithomimid metatarsal (Fig. 6), MLP 96-I-6-2, which comes from the upper levels of the López de Bertodano Formation (Klb 9 *sensu* Macellari 1988) on Seymour Island (Fig. 1c, loc. 10). These authors attributed this metatarsal tentatively to a hadrosaurine dinosaur.

The four avian dinosaurs were all reported from horizons dated as Late Maastrichtian from Seymour and Vega islands. Chatterjee (1989, 1997) described

the first Antarctic avian dinosaur, *Polarornis gregorii*, from the upper levels of the López de Bertodano Formation of Seymour Island (Klb9?, Late Maastrichtian). The material consists of incomplete and poorly preserved remains of one individual (a fragment of the bill and the adjacent distal part of the skull, parts of the otic region, four vertebrae, a small fragment of the sternum, a femur and a proximal tibiotarsus). Chatterjee (1997) assigned this species to the neornithine family Gaviidae (loons). Mayr (2004) pointed out that *Polarornis* differs from modern loons in some important features. He criticized the original description of the species because of the specimen's completeness and its



Fig. 7. (a) *Polarornis gregorii?* MLP 96-I-6-4, distal end of left femur (scale bar 50 mm); (b) *Polarornis gregorii?* MLP 96-I-6-3, distal end of left tibiotarsus (scale bar 50 mm); (c) *Polarornis gregorii* (Chatterjee 1989), MLP 96-I-6-2, concretion containing the two tibiotarsi and the right femur of the same individual (scale bar 50 mm); (d) Charadriiform gen. et sp. indet. MLP 98-I-10-25, fragment of left tarsometatarsus (scale bar 20 mm); (e) *Vegavis iaii* (Clarke *et al.* 2005), MLP 93-I-3-1, holotype, right humerus; (f) *Vegavis iaii* Clarke, Tambussi, Noriega, Erickson & Ketcham 2005, MLP 93-I-3-1, holotype, left tibiotarsus (scale bar 30 mm). *Abbreviations:* f, femur; tbt, tibiotarsus.

assignment to Gaviidae, and stated that '[*Polarornis*] may be a synonym of *Neogaeornis* – a possibility already raised by Olson (1992) but not discussed by Chatterjee (2002)' (Mayr 2004, p. 5). *Neogaeornis wetzeli*, from the Upper Cretaceous of Chile, based on a tarsometatarsus fragment, has been interpreted as the earliest fossil gaviiform (Lambrecht 1929; Olson 1992), resembling the highly derived bone of modern loons (Mayr 2004). Additional material (MLP 96-I-6-2/3) possibly belonging to the same taxon is figured here for the first time (Fig. 7a–c).

A second Late Maastrichtian bird, first referred to Presbyornithidae by Noriega & Tambussi (1995), was collected at Cape Lamb (locality VEG 9303, Fig. 1b, loc. 8), Vega Island from the Late Maastrichtian Sandwich Bluff Member of the López de Bertodano Formation. The specimen (MLP 93-I-3-1) consists of a disarticulated partial postcranium preserved in the two halves of a concretion (Fig. 8a, b), with a right humerus and left tibiotarsus out of the blocks (Fig. 7e, f). *Vegavis iaai* (Clarke *et al.* 2005, 2006) was subjected to phylogenetic analysis, which supported a basal position within the Anseriformes. Whereas this discovery pushes the neornithine record as far back as the Maastrichtian, this is still considerably later than is suggested by most molecular clock studies. *Vegavis* is assessed to be a basal anseriform close to Anatidae. It is important as the best support for a part of the radiation (crown clade) of birds in the Cretaceous, and directly relevant to the timing of this radiation.

Chatterjee *et al.* (2006) reported a well-preserved skeleton of a new gracile species of a fossil loon, *Polarornis*, from the Late Maastrichtian Sandwich Bluff Member of the López de Bertodano Formation on Vega Island (Fig. 1b, loc. 8). Although *Polarornis* is often claimed to be an ancestor of modern loons (Gaviiformes), its relationships are unclear (Tambussi & Acosta Hospitaleche 2007).

Case *et al.* (2006) reported a left femur recovered from the Sandwich Bluff area of the Cape Lamb on Vega Island (Fig. 1b, loc. 8). Its stratigraphic position places it near the base of the Sandwich Bluff Member and at an equivalent stratigraphic level to *Vegavis iaai*. It shows striking similarities to modern cursorial predatory birds of South America (Seriemas, Cariamidae) and of Africa (Secretarybirds, Sagittariidae).

Late Cretaceous Weddellian dinosaurs: palaeogeography and biogeography

The role of Antarctica in the palaeobiogeography of terrestrial vertebrates during the Cretaceous

has remained essentially unknown. By the beginning of the Late Cretaceous (99.6 Ma), the major Gondwanan continental blocks (South America, Africa, Antarctica, Madagascar, the Indian subcontinent and Australia) were well into the process of break-up and dispersion. However, many issues concerning the timing and sequence of this process remain unresolved. The majority of proposed Cretaceous palaeogeographic scenarios (e.g. Smith *et al.* 1995; Roeser *et al.* 1996; Scotese 1997) detail a rapid dissociation of Gondwanan landmasses, with India–Madagascar separating completely from the Antarctica–Australia complex by the upper Barremian (Early Cretaceous, c. 125 Ma; Gradstein *et al.* 1995). According to these hypotheses, South America severed physical ties with Africa during the Aptian or Albian (prior to 100 Ma), but portions of these landmasses remained in fairly close proximity throughout much of the Cretaceous (Scotese & Golonka 1993). India and Madagascar were among the last southern landmasses to dissociate, separating at c. 88.0 Ma (Storey *et al.* 1995). The isolation of South America was finally completed in the Palaeogene, when it split apart from Antarctica. West Antarctica itself is a complex of microcontinental blocks (Dalziel & Elliot 1982) that have moved independently over the past 200 million years in the West Antarctic rift system, analogous to the Basin and Range Province of North America (Bialas *et al.* 2007). By the mid–Late Cretaceous (latter part of the Santonian, end-Cretaceous Normal Superchron, 83.5 Ma), South America, West Antarctica and Australia were the only Gondwanan continents still connected.

Relative plate motions suggest that there could not have been any land bridge between South America, Africa, Antarctica, India and Madagascar after 108–112 Ma. However, Sereno & Brusatte (2008), based on the phylogenetic relationship of theropod dinosaurs Abelisauroidea to Carnosaurinae and the finding of an abelisauroid fossil from the Cenomanian of Niger, proposed the existence of land bridges between South America and Africa and between India and East Antarctica at 97 Ma. Upchurch *et al.* (2002), based on a cladistic biogeographic study on all dinosaur groups, supported the hypothesis that many clades spread across Gondwana prior to Cretaceous continental fragmentation.

Dispersion of terrestrial vertebrates between South America and Australia–New Zealand across Late Cretaceous land bridges requires their presence during that interval in the Antarctic Peninsula. The knowledge of Late Cretaceous terrestrial vertebrates from West Antarctica is still limited and lacks any taxonomically identifiable small terrestrial and freshwater vertebrates (e.g. reptiles

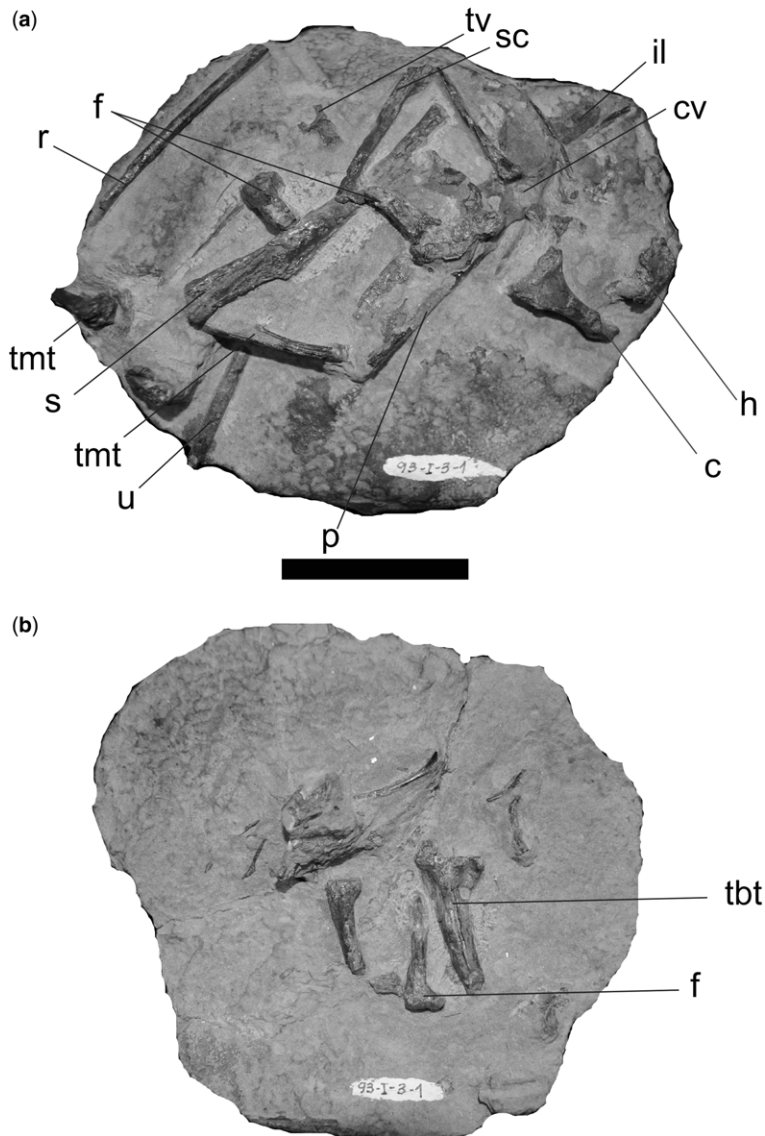


Fig. 8. *Vegavis iaai* (Clarke *et al.* 2005), MLP 93-I-3-1, holotype. (a) The half of the concretion preserving most of the skeleton of the holotype; (b) the other half of the concretion with few bones. *Abbreviations:* c, coracoids; cv, cervical vertebra; f, femora; h, humerus; il, ilium; p, pubis; r, radius; tmt, tarsometatarsus; tv, thoracic vertebrae; s, sacrum; sc, scapula; u, ulna (scale bar 50 mm).

as turtles, lizards, snakes, crocodyliforms or even mammals). However, this knowledge has expanded substantially over the last decade and includes the discoveries of avian and non-avian dinosaurs discussed here. By the Late Maastrichtian to approximately Late Palaeocene, the northern tip of the Antarctic Peninsula and southernmost South America (Magellanic Region, Patagonia) were physically connected allowing the dispersal of plants

and animals between these two areas (Marenssi *et al.* 1994; Shen 1995; Woodburne & Case 1996; Reguero *et al.* 1998, 2002; Reguero & Marenssi 2010). Woodburne & Case (1996) inferred that the initial marsupial dispersal, from South America into and through West Antarctica and onward to Australia, must have occurred during the Late Cretaceous (?Maastrichtian), but ended by 64 Ma, when the South Tasman Rise submerged

(McGowran 1991). The basal stocks of these clades, currently not represented by fossils in the Late Cretaceous of South America, West Antarctica and Australia, are supported by stratigraphically calibrated phylogenies revealing long ghost lineages that extended into the Late Cretaceous (e.g. Meredith *et al.* 2008).

The high-latitude Weddellian Biogeographical Province, conceived by Zinsmeister (1979, 1982) on the basis of marine molluscan, echinoderm and arthropod faunas, was defined as a cool temperate, shallow-water region that extended from southern South America (Magellanic Region in Chile, and Tierra del Fuego and Santa Cruz provinces in Argentina), along West Antarctica (including Antarctic Peninsula), to New Zealand, Tasmania and southeastern Australia. Later, Case (1988) expanded this concept to a 'biogeographic province' including terrestrial plants and mammals. This province existed from the Late Cretaceous through the Eocene when Australia, Antarctica and southernmost South America were in proximity (Woodburne & Zinsmeister 1984).

Non-avian dinosaurs from the Late Campanian Snow Hill Island Formation are represented by an ankylosaur, an indeterminate ornithomimid, a new genus and species of ornithomimid and a titanosaurian sauropod (Salgado & Gasparini 2006; Coria *et al.* 2007, 2008; Cerda *et al.* 2012). These Late Campanian non-avian dinosaurs are thus of interest to address a variety of questions, ranging from the dispersal patterns of major vertebrate clades to Gondwanan endemism. The ankylosaurian *Antarctopelta oliveroi* would have lived at about 60°S when the Antarctic Peninsula was in close proximity to southern South America. *Antarctopelta oliveroi* represents an Antarctic Late Cretaceous divergence of Ankylosauria and a rigorous phylogenetic analysis of this taxon would be necessary to test or support a hypothesis of vicariance. Salgado & Gasparini (2006) consider *A. oliveroi* to be an Ankylosauria *incertae sedis*, and to represent a different species from the ankylosaur found at Salitral Moreno in Río Negro province, Patagonia (Salgado & Coria 1996).

The Late Campanian Snow Hill Island Formation sauropod is the second sauropodomorph dinosaur recorded from Antarctica, and the first from West Antarctica. The first one is the basal sauropodomorph *Glacialisaurus hammeri* collected from the Beardmore Glacier region of the Central Transantarctic Mountains (Early Jurassic, Hanson Formation), East Antarctica (Hammer & Hickerson 1994; Smith & Pol 2007). The absence of sauropodomorph material between the Lower Jurassic and the Upper Cretaceous in Antarctica is more probably related to limited sampling than a genuine absence of members of this lineage during this

time. The Hanson Formation sauropodomorph belongs to a geographically widespread clade that includes members from Africa, South America, Australia and Asia (Smith *et al.* 2007). Cerda *et al.* (2012) state that the presence of an advanced titanosaur with characteristic procoelous mid-caudal vertebrae in West Antarctica implies that the group achieved a global distribution by the Late Campanian. However, the presence of advanced titanosaurians in the Late Cretaceous of West Antarctica rests on fragmentary remains. The lack of an adequate sampling of the known fossil record is limiting our understanding of the evolution and biogeography of advanced titanosaurians in the Late Cretaceous of West Antarctica (Molnar & Wiffen 2007; Cerda *et al.* 2012).

Perhaps the most reliable fossil evidence for evaluating terrestrial connections among Late Cretaceous Gondwanan landmasses is derived from examining the stratigraphically calibrated phylogenetic relationships of theropods from the James Ross Basin with those of Australia and South America. It is interesting to note that some clades of theropods (e.g. abelisaurids and noasaurids), now extensively documented from the Late Cretaceous of South America, Madagascar and the Indian subcontinent, are unknown in Antarctica. With large body sizes, cursorial locomotion and diminutive forelimbs, these animals were almost certainly incapable of long-distance swimming or rafting across significant marine barriers.

Gondwanan dromaeosaurs are not North American immigrants into South America and Antarctica. Until recently, the dromaeosaur fossil record has been geographically restricted to the Northern Hemisphere (Norell & Makovicky 2004). However, recent discoveries documented from Turonian through Maastrichtian beds of Argentina and the reassessment of some theropod taxa in South America (Makovicky *et al.* 2005; Novas & Pol 2005) and Australia (Agnolin *et al.* 2010) demonstrated that a distinctive dromaeosauriid subfamily Unenlagiinae were present and highly diversified in the southern landmasses. This suggests that an important adaptive radiation took place in Gondwana during the Late Cretaceous (Gianechini & Apesteguía 2011). The record of dromaeosaurids in South America and Australia is still poor compared with that of North America and Asia, taking into account the lesser number of taxa and the fragmentary nature of the specimens. Nevertheless, the recent discoveries in Argentina, mainly of *Buitreraptor* and *Austroraptor*, have provided much information about the anatomy and phylogenetic relationships of this group of Gondwanan theropods. Thus, the dromaeosauriid Unenlagiinae taxon is restricted exclusively to Gondwana. Case *et al.* (2007), based on the plesiomorphic nature of the

ankle and pes of the Naze dromaeosaur, support the hypothesis that dromaeosaurs were in fact the product of a cosmopolitan distribution, which has been separated by the vicariant break-up of Pangea, creating an endemic Gondwanan clade of dromaeosaurs.

The presence of hadrosaurid remains in the Late Maastrichtian of Antarctica is of particular interest for understanding the palaeobiogeographic dispersal events occurring during this time span, since this group of dinosaurs is considered to be of Laurasian origin (Horner *et al.* 2004). The dispersal of hadrosaurs into Antarctica by the Maastrichtian may coincide with and provide additional support for a predicted first wave of marsupials from South America to Antarctica (Woodburne & Case 1996; Goin *et al.* 1999).

Conclusions

Compared with those of most other continents, dinosaurs from Antarctica are still poorly known, and have thus been neglected in most discussions of Cretaceous biogeography. However, two important assemblages of non-avian dinosaurs from the Late Campanian and Early Maastrichtian Snow Hill Island Formation, one distributed in the northern part of the James Ross Island, and the second distributed in James Ross and Vega islands, provide much needed data on dinosaur distribution across Gondwana.

The main localities that have yielded Late Cretaceous Antarctic dinosaurs to date are situated within a relatively small area of approximately 350 km² at the NW corner of the James Ross Basin (Fig. 1b). This western margin of the basin is known to have been the approximate site of the palaeoshoreline during the Late Cretaceous, which progressed eastward up-section (Olivero 2012). Seven non-avian and four avian dinosaurs collected from a comparatively small geographical region suggest that the overall diversity on the Antarctic Peninsula was reasonably high.

One area of the James Ross Basin is particularly promising for future investigations. A well-exposed sequence of rocks of the Santa Marta Cove, James Ross Island spans the last 15 million years that dinosaurs existed, providing great potential for recovering Antarctic Late Cretaceous dinosaurs.

The Late Campanian dinosaur assemblage of Santa Marta Cove, James Ross Island, provides unique data on the composition of high-latitude Southern Hemisphere dinosaurs. The presence of an exclusive ankylosaur species, *Antarctopelta oliveroi*, in combination with other recent discoveries in the same area of clades previously thought to be restricted to Laurasia, ornithopod and titanosaurian

species, provides evidence for cosmopolitan distribution of several dinosaur clades during the Late Cretaceous, and undermines previous suggestions that the dinosaur fauna of Antarctica was either largely endemic or predominantly Gondwanan in composition. Two of the three Santa Marta dinosaurs, *Antarctopelta oliveroi* and the new genus and new species of ornithopod, appear to show substantially greater morphological differences than the contemporaneous taxa beyond the Antarctic Peninsula region.

The majority of the non-avian dinosaurs from West Antarctica (megalosaur-like theropod, ankylosaur, dromaeosaurid, the ornithopods and the sauropod) are remnants of a cosmopolitan dinosaur fauna more typical of other areas (e.g. Campanian–Maastrichtian of Patagonia). Preliminary reports of both theropods and titanosaurs from the Late Cretaceous deposits in West Antarctica are suggestive in this regard. Furthermore, developing a more complete fossil record from other intervals and areas, for example Early and Late Maastrichtian of Vega Island, will provide information critical for reconstructing the biogeographical history of Late Cretaceous Gondwana. Thus, it is relevant to note that the recent discovery and/or re-appraisal of the non-avian dinosaur faunas of Australia and New Zealand have revealed typical Gondwanan elements, including the presence of lithostrotian titanosaurs and theropods from the Early Cretaceous (Valanginian–Albian; Smith *et al.* 2008; Hocknull *et al.* 2009). This firmly establishes the presence of these clades in East Gondwana and South America (Patagonia) before the Late Cretaceous.

We support the suggestion that higher clades of dinosaurs present in the Late Campanian/Early Maastrichtian of the James Ross Basin (e.g. Ankylosauria, Ornithopoda, Theropoda) attained a global or near-global distribution before the Late Cretaceous, prior to fragmentation of the Pangean supercontinent, and some aspects of the hallmark ‘Gondwanan’ fauna of Gondwana may therefore reflect climate-driven provinciality. They do not provide useful data for appraising the existence of vicariance in dinosaur distributions. Instead, the relationships among lower-level taxa, representing Cretaceous evolutionary divergences (i.e. *Antarctopelta*), should be used to support hypotheses of vicariance. For this to be effective, greater sample sizes may be required for many clades (Benson *et al.* 2012).

Finally, the Late Cretaceous avian dinosaurs recorded in the James Ross Basin are rare, being restricted to one charadriiform, a cariamid? and, with more certainty, a loon and a basal Anseriformes. The last two are flying birds whose life stories are linked mainly to water. If the assignment of the loon to *Neogaeornis* is correct, and it seems

that it is, then we have further clear evidence of affinities of the Late Cretaceous Antarctic fauna with that of southern Chile, although gaviids are clearly Holarctic. *Vegavis iaai* gives the first good evidence for a basal part of the extant avian radiation in the Cretaceous.

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