A titanosaurian sauropod dinosaur from the Upper Cretaceous of Antarctica

PAUL M. BARRETT, PHILIP D. MANNION, SAMANTHA L. BEESTON,
MATTHEW C. LAMANNA, BRETT CLARK, ALEJANDRO OTERO,
JOSÉ P. O'GORMAN, and MARK EVANS

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Antarctica preserves a meagre Mesozoic dinosaur record, with fossils known only from the Lower Jurassic Hanson Formation of the Transantarctic Mountains and Upper Cretaceous units of the James Ross Sub-Basin of the Antarctic Peninsula. Upper Cretaceous assemblages include ankylosaurs, ornithopods, and non-avian and avian theropods, but sauropods are exceptionally rare. Here, we describe a titanosaurian caudal vertebra from a lower Campanian (Upper Cretaceous) horizon of the Santa Marta Formation of James Ross Island and discuss its implications for the evolutionary and palaeobiogeographic history of Antarctic sauropods. The specimen is a small, procoelous anterior caudal vertebra, identified as that of a non-saltasaurid eutitanosaurian. Its morphology closely corresponds to that of rinconsaurians and aeolosaurines, particularly a specimen previously assigned to the Late Cretaceous Argentinean species *Muyelensaurus pecheni*, and it differs from earlier-diverging titanosaurs, although its fragmentary preservation warrants a conservative taxonomic assignment of Eutitanosauria indet. Size comparisons indicate that the individual in question was small for a titanosaur, possibly reflecting immaturity or a genuinely small-bodied form. This discovery represents only the second sauropod body fossil known from Antarctica, although it was the first dinosaur bone to be collected from the continent. Coupled with the occurrence of diamantinasaurians in Patagonia and Australia during the mid-Cretaceous, its eutitanosaurian affinities imply the presence of multiple somphospondylan lineages in Antarctica, informing dispersal patterns and highlighting biogeographic links with other Gondwanan landmasses.

Key words: Sauropoda, Titanosauria, Eutitanosauria, caudal vertebra, Cretaceous, Campanian, Santa Marta Formation, Antarctica, James Ross Island.

Paul M. Barrett [p.barrett@nhm.ac.uk; ORCID: https://orcid.org/0000-0003-0412-3000], Fossil Reptiles, Amphibians and Birds Section, Natural History Museum, Cromwell Road, London, SW7 5BD, UK; Evolutionary Studies Centre, University of the Witwatersrand, Johannesburg, South Africa; Department of Earth Sciences, UCL, Gower Street, London, WC1E 6BT, UK.

Philip D. Mannion [philipdmannion@gmail.com; ORCID: https://orcid.org/0000-0002-9361-6941] and Samantha L. Beeston [samantha.beeston.23@ucl.ac.uk; ORCID: https://orcid.org/0000-0002-7403-0910], Department of Earth Sciences, UCL, Gower Street, London, WC1E 6BT, UK.

Matthew C. Lamanna [lamannam@carnegiemnh.org; ORCID: https://orcid.org/0000-0001-9845-0728], Section of Vertebrate Paleontology, Carnegie Museum of Natural History, 4400 Forbes Avenue, Pittsburgh, PA 15213, USA.

Brett Clark [bclark@britishmuseum.org; ORCID: https://orcid.org/0000-0002-5888-9223], The British Museum, Great Russell Street, London, WC1B 3DG, UK.

Alejandro Otero [alexandros.otero@gmail.com; ORCID: https://orcid.org/0000-0002-4766-7086] and José P. O'Gorman [joseogorman@fcnym.unlp.edu.ar; ORCID: https://orcid.org/0000-0001-9279-6314], División Paleontología de Vertebrados, Museo de La Plata (Anexo Laboratorios), Paseo del Bosque s/n, La Plata, B1900FWA, Argentina.

Mark Evans [maans@bas.ac.uk; ORCID: https://orcid.org/0009-0002-5928-6464], British Antarctic Survey, High Cross, Madingley Road, Cambridge, CB3 0ET, UK; Centre for Palaeobiology and Biosphere Evolution, University of Leicester, Leicester, LE1 7RH, UK.

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Introduction

Antarctica currently has the sparsest Mesozoic dinosaur record of any continent (Maidment and Butler 2025): nevertheless, it has yielded a diversity of taxa from the Lower Jurassic Hanson Formation of the Central Transantarctic Mountains (e.g., Hammer and Hickerson 1994; Smith and Pol 2007) and from exposures of the Upper Cretaceous Gustav and Marambio groups on islands in the James Ross Sub-Basin, adjacent to the Antarctic Peninsula (James Ross, Seymour, Snow Hill, and Vega islands; see review in Lamanna et al. 2019). We summarize the named taxa from these units in Table 1. The Hanson Formation (late Sinemurian–late Pliensbachian; Elliot et al. 2017) has also produced some unnamed early-diverging sauropodomorph material (Smith et al. 2013; Jackson et al. 2022). Additional unnamed or taxonomically indeterminate Late Cretaceous dinosaur occurrences, representing ankylosaur, non-hadrosauroid ornithopod, hadrosauroid ornithopod, non-avian and avian theropod, and sauropod body fossils, as well as putative tracks, have also been reported from the Snow Hill Island and López de Bertodano formations (Marambio Group: Santonian–Maastrichtian), as well as a single non-avian theropod bone from the Hidden Lake Formation (Gustav Group: Coniacian) (see reviews in Lamanna et al. 2019; Acosta Hospitaleche et al. 2024). We provide an overview of the non-avian dinosaur fauna of the James Ross Sub-Basin in Figs. 1B and 2B.

The presence of sauropod dinosaurs in the Cretaceous of Antarctica was first noted by Cerda et al. (2012a), who referred a single partial middle caudal vertebra from the Gamma Member of the Snow Hill Island Formation of James Ross Island to Titanosauria. To date, this single bone has represented the only direct evidence for Antarctic sauropods, although there is an unsubstantiated record of possible sauropod tracks from the López de Bertodano Formation (see discussion in Lamanna et al. 2019). Here, we describe a caudal vertebra collected from the lower Campanian (Upper Cretaceous) Santa Marta Formation of James Ross Island, which we refer to Eutitanosauria, and re-assess the importance of these finds for understanding the possible history of Antarctic sauropods.

Table 1. Named species of Mesozoic dinosaurs from Antarctica, organized by stratigraphic unit. For an overview of the Jurassic dinosaur record of the continent that also includes undescribed and/or generically indeterminate material, see Smith et al. (2013). For near-comprehensive summaries of the Cretaceous records of non-avian and avian dinosaurs from Antarctica, see Lamanna et al. (2019: table 1) and Acosta Hospitaleche et al. (2024: table 1), respectively.

Taxon	Higher taxon	Holotype	Locality	Formation	Member	Age	Reference
Glacialisaurus hammeri	Sauropodomorpha (Massospondylidae)	FMNH PR1823	Central Transantarctic Mountains (Mount Kirkpatrick)	Hanson	N/A	Early Jurassic (late Sinemurian–late Pliensbachian)	Smith and Pol 2007
Cryolophosaurus ellioti	Theropoda (Tetanurae)	FMNH PR1821	Central Transantarctic Mountains (Mount Kirkpatrick)	Hanson	N/A	Early Jurassic (late Sinemurian–late Pliensbachian)	Hammer and Hickerson 1994
Antarctopelta oliveroi	Ankylosauria (?Parankylosauria)	MLP 86-X-28-1	James Ross Sub-Basin (James Ross Island)	Snow Hill Island	Gamma (≈ Herbert Sound)	Late Cretaceous (late Campanian)	Salgado and Gasparini 2006
Trinisaura santamartaensis	Ornithopoda (?Elasmaria)	MLP 08-III-1-1	James Ross Sub-Basin (James Ross Island)	Snow Hill Island	Gamma (≈ Herbert Sound)	Late Cretaceous (late Campanian)	Coria et al. 2013
Morrosaurus antarcticus	Ornithopoda (?Elasmaria)	MACN Pv 19777	James Ross Sub-Basin (James Ross Island)	Snow Hill Island	Cape Lamb	Late Cretaceous (late Campanian–early Maastrichtian)	Rozadilla et al. 2016
Imperobator antarcticus	Theropoda (Paraves)	UCMP 276000	James Ross Sub-Basin (James Ross Island)	Snow Hill Island	Cape Lamb	Late Cretaceous (late Campanian–early Maastrichtian)	Ely and Case 2019
Antarcticavis capelambensis	Theropoda (Ornithuromorpha incertae sedis)	SDSM 78147	James Ross Sub-Basin (Vega Island)	Snow Hill Island	Cape Lamb	Late Cretaceous (late Campanian–early Maastrichtian)	Cordes-Person et al. 2020
Polarornis gregorii	Theropoda (Aves)	TTU P 9265	James Ross Sub-Basin (Seymour Island)	López de Bertodano	Unit Klb 9	Late Cretaceous (late Maastrichtian)	Chatterjee 2002
Pujatopouli soberana	Theropoda (Aves)	MLP-PV 08-XI-30-44	James Ross Sub-Basin (Seymour Island)	López de Bertodano	Unit Klb 9	Late Cretaceous (late Maastrichtian)	Irazoqui et al. 2026a
Vegavis iaai	Theropoda (Aves)	MLP 93-I-3-1	James Ross Sub-Basin (Vega Island)	López de Bertodano	Sandwich Bluff	Late Cretaceous (middle Maastrichtian)	Clarke et al. 2005
Vegavis geitononesos	Theropoda (Aves)	MLP-PV 15-I-7-52	James Ross Sub-Basin (Seymour Island)	López de Bertodano	Unit Klb 9	Late Cretaceous (late Maastrichtian)	Irazoqui et al. 2026b
Vegavis notopothousa	Theropoda (Aves)	AMNH FARB 30899	James Ross Sub-Basin (Vega Island)	López de Bertodano	Sandwich Bluff	Late Cretaceous (middle Maastrichtian)	Irazoqui et al. 2026b

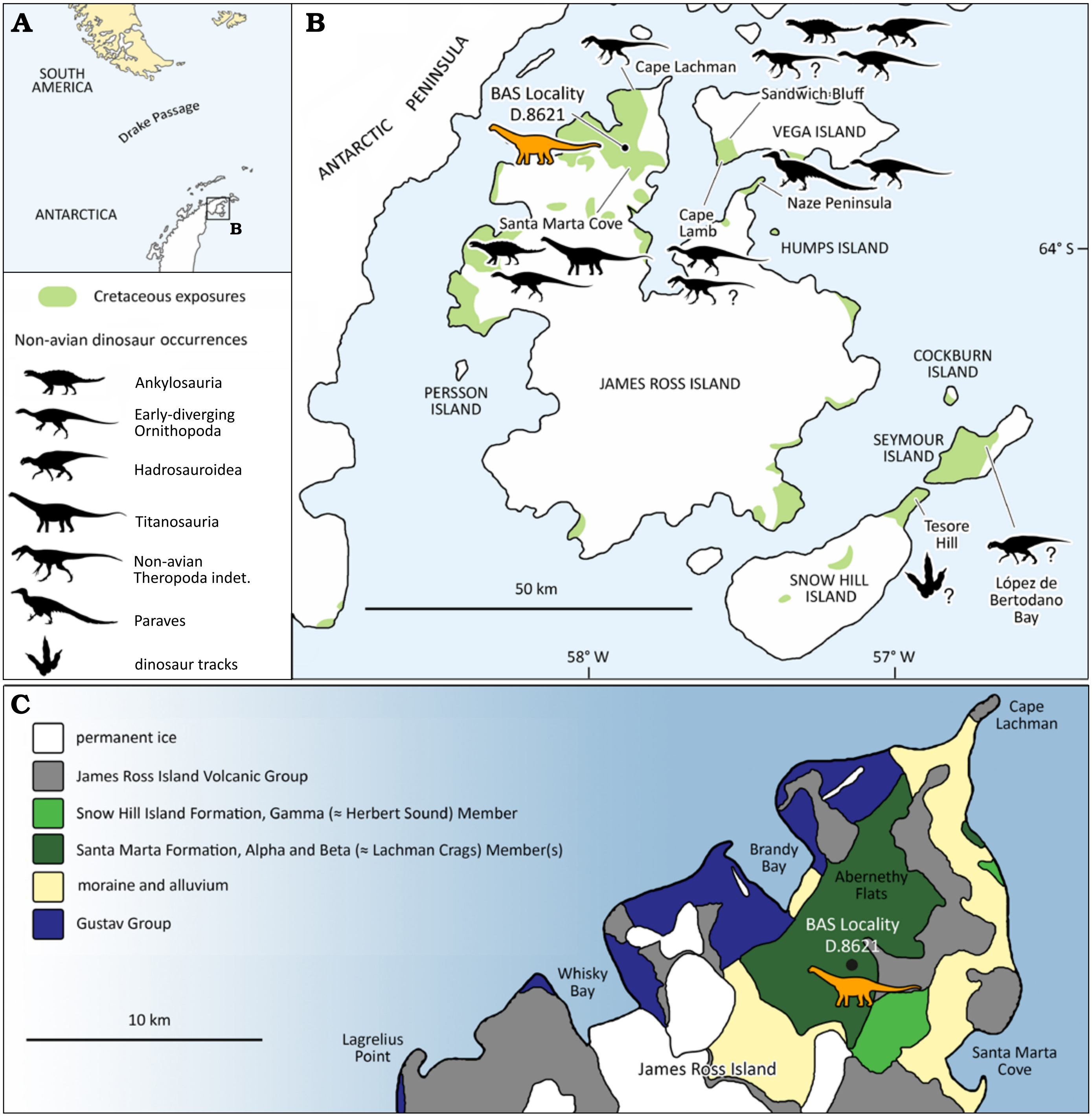

Fig. 1. Geographic provenance of BAS D.8621.25, an anterior caudal vertebra identified as Eutitanosauria indet., and other Antarctic Cretaceous non-avian dinosaur discoveries. **A**. Map of southern-most South America and the northern Antarctic Peninsula showing the location of the study area (modified from Lamanna et al. 2019: fig. 1a). **B**. Map of the James Ross Island Group showing known Cretaceous exposures and non-avian dinosaur sites, including the locality on the Ulu Peninsula of James Ross Island that yielded the eutitanosaurian vertebra described herein (BAS Locality D.8621; orange titanosaur silhouette) (modified from Lamanna et al. 2019: fig. 1b). **C**. Detail of Ulu Peninsula showing regional geology and position of BAS Locality D.8621 on the Abernethy Flats (orange titanosaur silhouette; modified from Pirrie 1989: fig. 1 and Keating 1992: fig. 1).

Institutional abbreviations.—AODF, Australian Age of Dinosaurs Fossil, Winton, Australia; BAS, British Antarctic Survey, Cambridge, UK; FMNH, Field Museum of Natural History, Chicago, USA; MACN, Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”, Buenos Aires, Argentina; MAU, Museo Argentino Urquiza, Rincón de los Sauces, Argentina; MCT, Museu de Ciências da Terra, Rio de Janeiro, Brazil; MHNH, Museum d’Histoire Naturelle du Havre, Le Havre, France; MLP-PV, Museo de La Plata, Paleontología de Vertebrados, La Plata, Argentina; PVL, Fundación Instituto Miguel Lillo, San Miguel de Tucumán, Argentina; SDSM, South Dakota School of Mines and Technology, Rapid City, USA; UNPSJB, Universidad Nacional de la Patagonia San Juan Bosco, Comodoro Rivadavia, Argentina; TTU, Texas Tech University, Lubbock, USA; UCMP, University of California Museum of Paleontology, Berkeley, USA; USNM, National Museum of Natural History, Washington, D.C., USA.

Other abbreviations.—aEI, average elongation index; CCI, condylar convexity index.

Material and methods

History of discovery.—The specimen described herein (BAS D.8621.25) was discovered and collected on 9 December 1985 by Michael R.A. Thomson of the British Antarctic Survey and Reinhard Förster of the Bayerische Staatssammlung für Paläontologie und Geologie, München. It derives from a lower Campanian (Upper Cretaceous) exposure of the Beta Member (sensu Olivero et al. 1986; Olivero 2012) of the Santa Marta Formation at BAS Locality D.8621 on the Ulu Peninsula of northwestern James Ross Island, Antarctica (Fig. 1) and was discovered alongside fragmentary osteichthyan scales and a suite of invertebrate and plant fossils (Michael R.A. Thomson, unpublished field notes). To our knowledge, this specimen has not been mentioned in the literature thus far. Other fossil reptile material was collected by Thomson and Förster from the James Ross Sub-Basin during the 1985–1986 field season, and these discoveries led to the inclusion of a vertebrate palaeontologist, Jerry J. Hooker of the Natural History Museum, London, in the James Ross Island Cruise of 1988–1989 (Hooker 2000).

Imaging methods.—BAS D.8621.25 was computed tomography (CT) scanned using a Nikon Metrology XT H 225 ST µCT scanner based at the Imaging and Analysis Centre, Natural History Museum, London. Source conditions were set at 190 kV and 173 µA, using a reflection target with a 2 mm copper filter. The scan consisted of 3000 projections with an exposure time of 500 ms per projection and frame averaging set to 2. The resulting projections were reconstructed (using CT Pro 3D) at a voxel size of 0.062992759 mm. Screen captures of CT slices were taken in Avizo 9.7 (FEI Visualization Science Group; https://www.thermofisher.com). In addition, BAS D.8621.25 was surface scanned using an Artec Spider handheld scanner (Artec 3D, Santa Clara, CA, USA; https://www.artec3d.com/portable-3d-scanners/artec-spider), and the subsequent three-dimensional mesh was aligned and created in Artec Studio 16 Professional (www.artec3d.com/3d-software/artec-studio). These scans can be accessed via: https://www.morphosource.org/concern/media/000787762.

Measurements.—Measurements of BAS D.8621.25 and MLP-PV 11-II-20-1 (the titanosaurian caudal vertebra described by Cerda et al. 2012a) were taken with Vernier callipers to the nearest millimetre (Table 2). Two ratios that are commonly used as taxonomic and systematic characters for sauropod vertebrae were calculated for BAS D.8621.25: average Elongation Index (aEI; Upchurch 1998; Chure et al. 2010), given as centrum length (excluding articular condyle) divided by the mean average value of the cotyle transverse width and dorsoventral height; and the condylar convexity index (CCI), given as the anteroposterior length of the articular condyle divided by the mean radius of the condyle (i.e., transverse width + dorsoventral height of articular surface/4) (following Mannion et al. 2019b).

Table 2. Measurements (in mm) of the indeterminate Antarctic eutitanosaurian caudal centra BAS D.8621.25 and MLP-PV 11-II-20-1. * minimum due to damage.

	BAS D.8621.25	MLP-PV 11-II-20-1
Anteroposterior length (excl. posterior condyle)	59	180
Anteroposterior length (incl. posterior condyle)	89	202
Dorsoventral height, anterior surface	76	67*
Dorsoventral height, posterior surface	62	70*
Transverse width, anterior surface	77	105*
Transverse width, posterior surface	76	108*

Geological setting

The James Ross Island Group was deposited in the James Ross Sub-Basin, part of a back-arc basin that evolved in response to a late Mesozoic to Paleogene active magmatic arc located along the Antarctic Peninsula (Hathway 2000; Figs. 1, 2). Approximately 5 km of Lower Cretaceous to lowermost Oligocene sediments fill the James Ross Sub-Basin and are capped by the uppermost Miocene–Quaternary James Ross Island Volcanic Group (Pirrie et al. 1997; Hathway 2000; Smellie et al. 2008). The Cretaceous rocks are divided into the Gustav Group of Aptian–Coniacian age and the overlying Marambio Group of latest Coniacian–Danian age (Pirrie et al. 2004; Reguero et al. 2022).

The Santa Marta Formation is the lowest unit within the Marambio Group (e.g., Olivero et al. 1986; Crame et al. 1991; Pirrie et al. 1997; Fig. 2). It conformably overlies the Hidden Lake Formation of the Gustav Group and is overlain by the Snow Hill Island Formation (the latter formerly considered part of the overlying López de Bertodano Formation; see Pirrie et al. 1997; Olivero 2012). Originally, the Santa Marta Formation was divided into three members, Alpha, Beta, and Gamma (Olivero et al. 1986), but more recent stratigraphic reviews have indicated that the Gamma Member (approximately equivalent to the Herbert Sound Member of Crame et al. 1991 and Pirrie et al. 1997) instead forms the lowest part of the Snow Hill Island Formation (Olivero 2012). According to Olivero (2012), the Alpha and

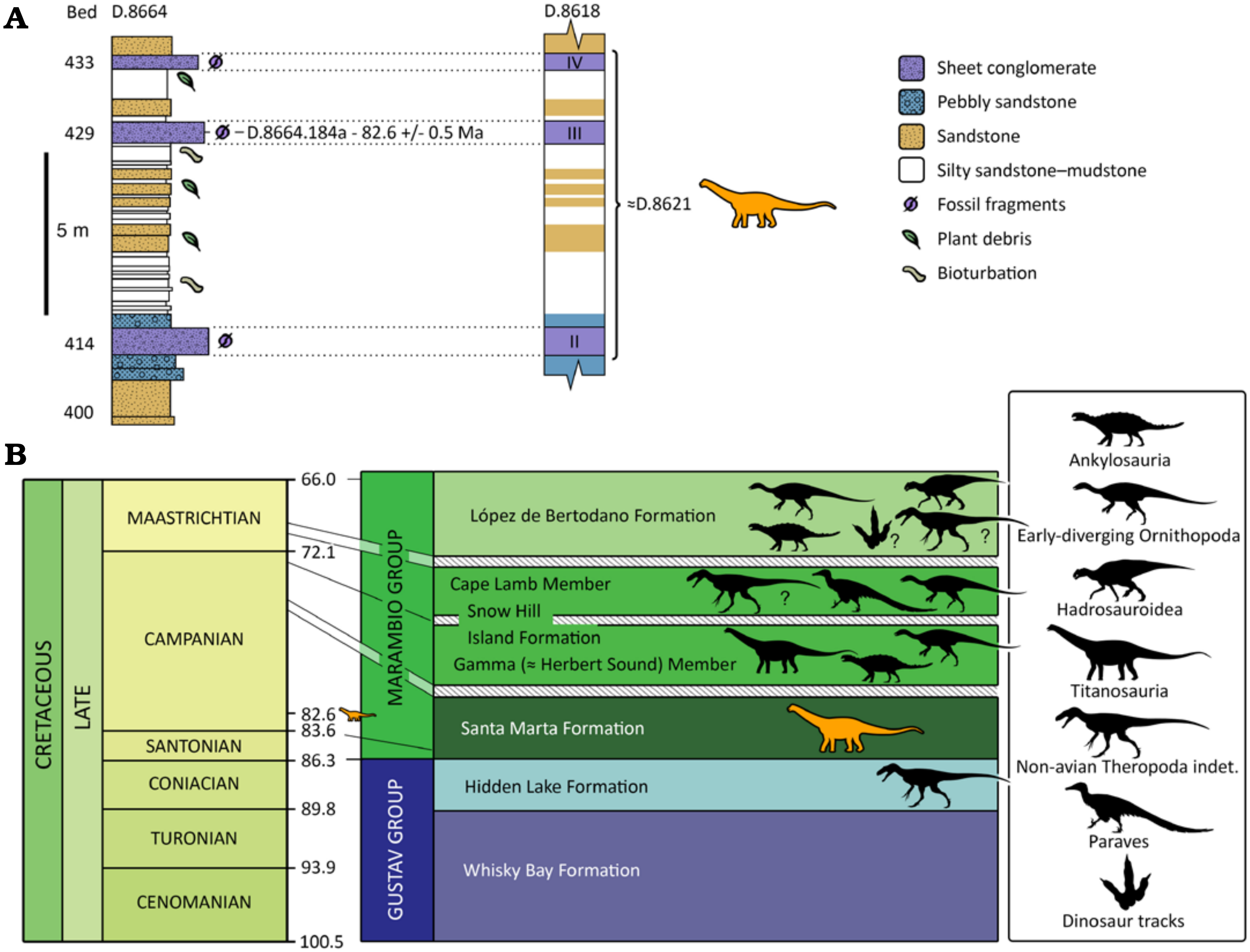

Fig. 2. Stratigraphic context of the anterior caudal vertebra of Eutitanosauria indet. (BAS D.8621.25) and other Antarctic Cretaceous non-avian dinosaur discoveries. **A**. Stratigraphic columns of BAS localities D.8664 and D.8618 showing the approximate position of the stratum at BAS Locality D.8621 that yielded the titanosaurian vertebra described herein (BAS D.8621.25; indicated by orange titanosaur silhouette) (modified from Pirrie 1989: fig. 14 and unpublished field notes by Duncan Pirrie). **B**. Stratigraphic position of Eutitanosauria indet. (BAS D.8621.25; orange titanosaur silhouette) relative to other Antarctic Cretaceous non-avian dinosaur discoveries (modified from Lamanna et al. 2019: fig. 1d; see Fig. 1B herein for key to dinosaur occurrences). BAS D.8621.25 is currently the only dinosaur fossil known from the Coniacian–Campanian Santa Marta Formation.

Beta members of the Santa Marta Formation are approximately equivalent to the Lachman Crags Member of Crame et al. (1991) and Pirrie et al. (1997).

The Alpha Member reaches approximately 500 m in thickness and consists largely of massive sandstones, silty sandstones, and siltstones with occasional mudstones, conglomerates, and pebbly sandstones, whereas the Beta Member reaches up to 350 m in thickness and has similar lithologies but a higher proportion of interbedded conglomerates (Olivero et al. 1986; Crame et al. 1991). These two members were deposited during the first of three major transgressive-regressive cycles that are recorded by the Marambio Group and form a regressive sequence (with the Santa Marta Formation in the "N sequence"; Olivero 2012). These deposits are thought to represent a progradational deep-water delta system with a range of different palaeoenvironments (Olivero 2012). Marine macroinvertebrate fossils are abundant (including numerous ammonites and inoceramid bivalves, and rarer corals, crinoids, and brachiopods) and fossil wood is also common (e.g., Crame et al. 1991; Olivero 2012). Ammonite biostratigraphy (based on six ammonite assemblage zones) suggests a Santonian–early Campanian age for the Santa Marta Formation and that the Santonian–Campanian boundary lies within the Alpha Member (Olivero 2012). Ammonite Assemblage 1 (proposed to be Santonian; Olivero 2012) occurs within the lower 250 m of the Alpha Member, whereas the upper part of the member yields ammonite assemblages 2 and 3 (both lower Campanian; Olivero 2012). The first appearances of Ammonite Assemblage 4 taxa (lower Campanian) are within the Beta Member, as are the remaining ammonite assemblages (5 and 6; see Olivero 2012). However, alongside this biostratigraphic work, radioisotopic dating places the Coniacian–Santonian boundary within the lower part of the Santa Marta Formation (in the lower 150 m of the Lachman Crags Member sensu Pirrie et al. 1997), so the unit likely spans the uppermost Coniacian to lower Campanian (McArthur et al. 2000). Consequently, the base of Ammonite Assemblage 1 (sensu Olivero 2012) is also probably upper Coniacian.

The Santa Marta Formation forms the gravel-covered plain of the Abernethy Flats at the head of Brandy Bay and the slope up to the Lachman Crags on the Ulu Peninsula of northwestern James Ross Island. According to the unpublished field notes of one of the collectors (Michael R.A. Thomson, see above: BAS Archives), the conglomeratic horizon that yielded the eutitanosaurian vertebra BAS D.8621.25 is correlative with units II–IV of the stratigraphic section taken at BAS Locality (or station) D.8618 some 500 to 600 m to the north. Locality D.8618 corresponds to locality 7 of Feldmann et al. (1993) and BAS localities D.8663 and D.8664 of Pirrie (1989: figs. 13, 14). As such, the stratum that produced BAS D.8621.25 is part of the Beta Member of the Santa Marta Formation following the nomenclature of Olivero et al. (1986) and Olivero (2012). More specifically, units II–IV of Locality D.8618 were logged by Duncan Pirrie in his detailed unpublished section of Locality D.8664 as fossiliferous conglomerate beds 414, 429, and 433, the lowermost of which yielded abundant specimens of *Baculites* sp. (BAS Archives). This ammonite was present, but rare, at Locality D.8621 and was accompanied by *Scaphites* sp., *Natalites* sp., and pachydiscid ammonites. Ammonite genera collected from units II–IV of Locality D.8618 (*Baculites*, *Gaudryceras*, *Maorites*, *Natalites*, *Oiophyllites*, *Scaphites*) are suggestive of Ammonite Assemblage 4 of Olivero (2012). Sample BAS D.8664.184a from bed 429 was included in the study of McArthur et al. (2000), producing a numerical date of 82.6 ± 0.5 Ma, thus confirming the early Campanian age of BAS D.8621.25 (Fig. 2).

Tetrapod fossils from the Santa Marta Formation are rare, fragmentary, and generically indeterminate. They include the partial carapace of a chelonioid turtle from the Alpha Member (de la Fuente et al. 2010), the metacarpal of a pterodactyloid pterosaur (found ex situ so member unknown; Kellner et al. 2019), and various indeterminate plesiosaur specimens from both members (reviewed in O'Gorman et al. 2019). BAS D.8621.25 is the only dinosaur fossil known thus far from the Santa Marta Formation.

Angiosperm leaves preserved in the Santa Marta Formation have been used for palaeoclimatic analysis (Hayes et al. 2006; Francis et al. 2008). These fossils were derived from vegetation growing on the adjacent emergent Antarctic Peninsula volcanic arc, which was also the likely environment of the Santa Marta dinosaur fauna. This provides a mean annual temperature of approximately 19°C for the upper Coniacian–lower Santonian part of the Santa Marta Formation, broadly equivalent to the Alpha Member of Olivero et al. (1986). Estimates of annual precipitation, ranging between 673–1991 (±580) mm, with higher levels in the growing season, resemble those of modern tropical rainforests. This indicates a tropical or subtropical climate at high palaeolatitudes without significant sub-freezing temperatures during the winter (Francis et al. 2008). It should be noted that an angiosperm leaf collected at Locality D.8621 and included in the Santa Marta Formation flora in the analysis of Hayes et al. (2006) is now recognised as being derived from the underlying Hidden Lake Formation due to its preservation in a distinctive volcaniclastic matrix (Whitham et al. 2006; Francis et al. 2008).

Systematic palaeontology

Sauropoda Marsh, 1878

Titanosauria Bonaparte & Coria, 1993

Lithostrotia Upchurch et al., 2004

Eutitanosauria Sanz et al., 1999

Eutitanosauria indet.

Figs. 3, 4, 5A.

Material.—BAS D.8621.25, a partial anterior caudal vertebra consisting of a complete centrum and partial neural arch pedicles. BAS Locality D.8621 (-63.8833°, -57.9167°), Abernethy Flats, southeast of Brandy Bay and northwest of Santa Marta Cove, Ulu Peninsula, northwestern James Ross Island, Antarctica. Beta Member of the Santa Marta Formation (sensu Olivero et al. 1986; Olivero 2012; correlative to the upper section of the Lachman Crags Member sensu Crame et al. 1991; Pirrie et al. 1997); lower Campanian, Upper Cretaceous.

Description.—*External morphology* (Fig. 3): Many of the surfaces are encrusted with a thin veneer of matrix. The centrum is procoelous (Fig. $3A_1$, A_2), with a shallowly concave anterior articular surface (Fig. $3A_3$) and a strongly convex, hemispherical posterior articular surface (Fig. $3A_4$), forming a distinct condyle. Overall, the centrum is wedge-shaped in lateral view, tapering posteriorly; and ovate in ventral (Fig. $3A_5$) and dorsal (Fig. $3A_6$) views, again tapering posteriorly. The non-condylar centrum has an aEI of 0.77. Anterior and posterior chevron facets are absent. Although the region in which the posterior facets would be situated is too poorly preserved to ascertain if their absence is genuine or an artefact, it seems likely that anterior facets were either entirely absent or only subtle features.

In anterior view, the articular surface has a circular outline and is approximately as tall dorsoventrally as it is wide transversely. In lateral view, the anterior margin of the centrum is subvertical along most its length, becoming gently concave towards its dorsalmost third. Posteriorly, the articular condyle is convex to the same degree both transversely and dorsoventrally, giving it a smoothly rounded continuous surface. Poor preservation means that it is not possible to determine whether the condyle is separated from the lateral surface of the main body of the centrum by a distinct rim.

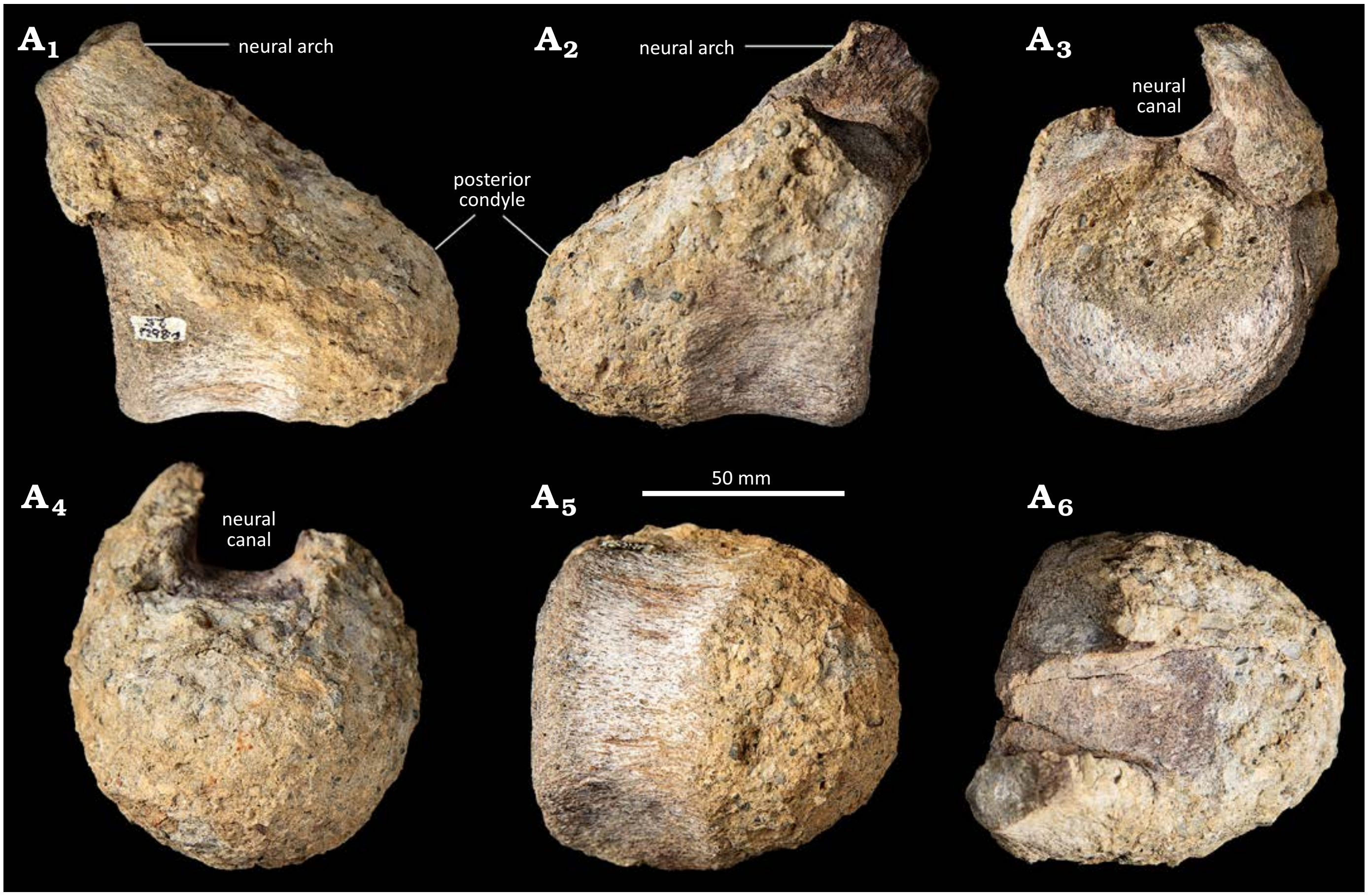

Fig. 3. Eutitanosauria indet. (BAS D.8621.25) from the Upper Cretaceous (lower Campanian) Beta Member (≈ upper Lachman Crags Member) of the Santa Marta Formation of James Ross Island, Antarctica. Anterior caudal vertebra in left (A_1) and right (A_2) lateral, anterior (A_3), posterior (A_4), ventral (A_5), and dorsal (A_6) views.

The condyle occupies the entire posterior surface and is not displaced either dorsally or ventrally with respect to the long axis of the centrum. It is slightly wider transversely than it is tall dorsoventrally and the centrum has a CCI of 0.78.

The lateral surfaces of the centrum are gently concave longitudinally and dorsoventrally convex ("saddle-shaped") and converge slightly toward the midline as they extend ventrally. External pneumatic fossae/foramina, nutrient foramina, and ridges are absent, as confirmed by CT images where obscured by matrix. In lateral view, the ventral margin of the centrum is bowed gently dorsally, although this bowing would have been more strongly developed if posterior chevron facets were present. Subtle "breaks-in-slope" distinguish the lateral surfaces of the centrum from its ventral surface, but these do not form distinct ventrolateral bounding ridges. The ventral surface is weakly convex transversely and shallowly concave anteroposteriorly (although it might have appeared more strongly concave if posterior chevron facets were present). Neither a midline keel nor groove is present.

The floor of the neural canal slopes slightly ventrally as it extends posteriorly from its highest point at the anterior end of the centrum. It bears neither foramina nor any other noteworthy features. The neural arch pedicles are positioned on the anterior half of the centrum, extending up to its anterior margin. That on the right side is represented only by its broken base, but the left pedicle is more complete. What remains of the latter projects anterodorsally in lateral view. In anterior view, the pedicle extends dorsomedially towards its antimere and forms the lateral border of the large neural canal opening. The broken terminus of the left neural arch pedicle has an elliptical transverse cross-section whose long axis extends anterolaterally-posteromedially. Although the neurocentral suture on the left side superficially appears to be open, the CT scans support the interpretation that this instead represents breakage; this junction is not visible on the right side, where it appears fused, reinforcing a taphonomic explanation for the left-side feature.

Although not preserved on either side, it seems probable that caudal ribs were present. Based on the raised nature of the broken surfaces and a break-of-slope on both lateral surfaces of the centrum, these were likely to have been dorsoventrally extensive processes that extended from the dorsal half of the centrum onto the lower portion of the neural arch.

Internal morphology (Fig. 4).—Broken and eroded surfaces around the anterior articular surface, both neural arch pedicles, and the ventral surface of the centrum reveal a

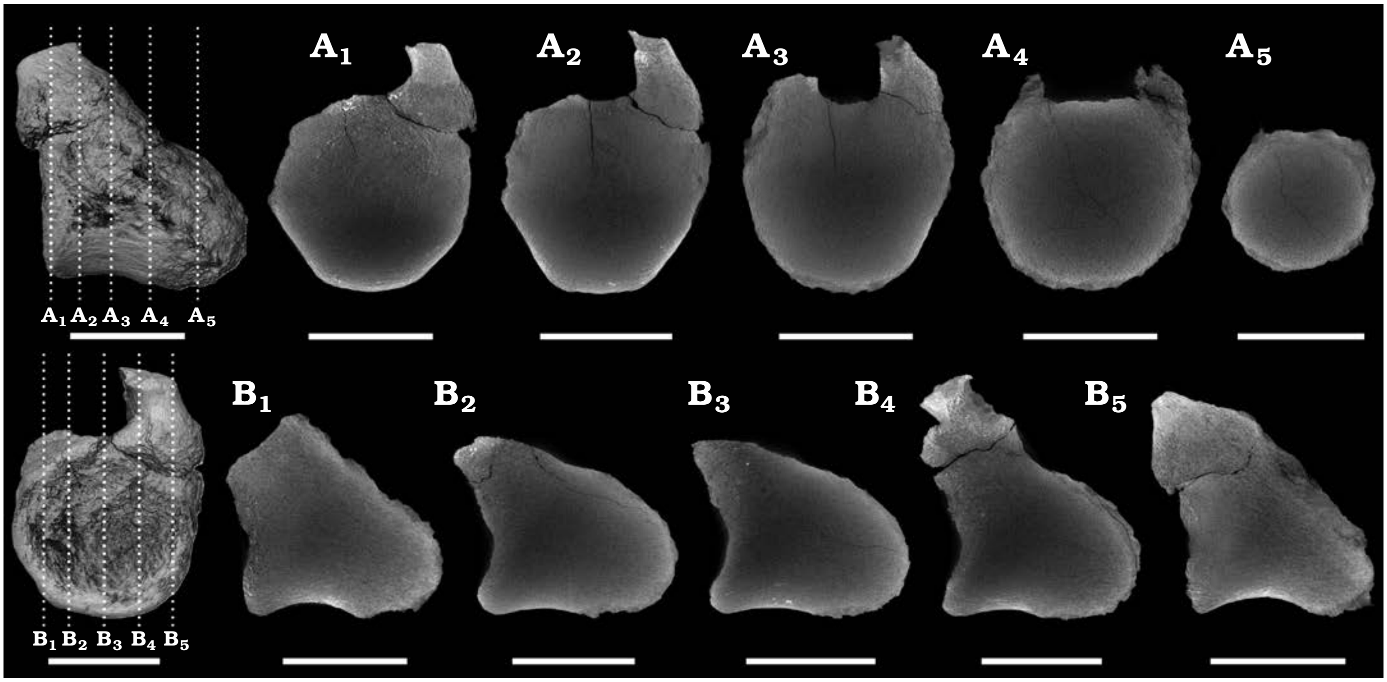

Fig. 4. Computed tomographic (CT) images of anterior caudal vertebra of Eutitanosauria indet. **A**. BAS D.8621.25 in left lateral view, showing axial CT slices at locations indicated (anterior–posterior, A_1–A_5). **B**. BAS D.8621.25 in anterior view, showing sagittal CT slices at locations indicated (right–left lateral, B_1–B_5). Scale bars 50 mm.

spongious internal bone texture. CT scan data confirm this, with densely packed, apneumatic trabeculae in the centre of the centrum that become progressively slightly less-densely packed towards the edges of the centrum and the broken neural arch pedicles (Fig. 4A_1–A_5, B_1–B_5). At first glance externally, the centrum appears to be camellate. However, it is clear from the CT scans that these possible chambers are not genuine but due to differential erosion of the conglomeratic matrix and pebbles adhered to the bone surface of much of the vertebra. These pebbles are especially evident in Fig. 4A_3, A_4, B_4, B_5.

Ontogenetic stage.—At least based on the right side (and probably also the left side; see above), the centrum and neural arch are fully fused. This has typically been regarded as indicative of skeletal maturity, with the neurocentral synostoses often only partially fused or fully open in skeletally immature archosaurian individuals. However, the timing of fusion can vary throughout the vertebral column and there is no currently recognised pattern amongst sauropods (Griffin et al. 2021). BAS D.8621.25 is small compared to the anterior caudal vertebrae of most other sauropods. For example, its dimensions are approximately 60% those of the corresponding element in the titanosaur *Baurutitan britoi* (MCT 1490-R) and roughly 75% those of the "dwarfed" saltasaurine titanosaur *Neuquensaurus australis* (e.g., MLP-PV CS 1392), although they are comparable to those of another dwarfed titanosaur, *Magyarosaurus dacus* (Díez Díaz et al. 2025). Even though size is a poor ontogenetic indicator (Griffin et al. 2021), and *Magyarosaurus* demonstrates that some adult titanosaurs exhibited similarly small body sizes, the relative size of BAS D.8621.25 might suggest that the individual was not fully grown at the time of death.

Comparisons

External morphology.—Based on comparisons with other sauropods (Fig. 5), the overall morphology of BAS D.8621.25 (Figs. 3, 5A) is most consistent with an identification as a caudal vertebra, probably from the anteriormost region of the tail. Within Sauropoda, well-developed procoely in anterior caudal vertebrae, with a CCI of at least 0.6, is primarily a feature of lithostrotian titanosaurs, some mamenchisaurids, and turiasaurians (e.g., Wilson 2002; Upchurch et al. 2004; Royo-Torres et al. 2006; D'Emic 2012; Mannion et al. 2013). The anterior caudal vertebrae of most non-titanosaurian somphospondylans, including diamantinasaurians (Fig. 5B), lack procoelous centra (Poropat et al. 2020; Beeston et al. 2024), whilst procoely is only incipiently developed in the anterior caudal vertebrae of early-diverging titanosaurs (Salgado et al. 1997; Gorscak and O'Connor 2019). In some lithostrotians, including members of Aeolosaurini and Lirainosaurinae, the condyle is dorsally displaced (Powell 2003; Mocho et al. 2024; Díez Díaz et al. 2025). The anterior-most caudal centra of turiasaurians typically have a much lower aEI than BAS D.8621.25 (Mannion et al. 2019b). As is also the case in many other titanosaurs (e.g., *Baurutitan britoi*, *Mendozasaurus neguyelap*, *Muyelensaurus pecheni*, *Narambuenatitan palomoi*, *Volgatitan simbirskiensis*), BAS D.8621.25 lacks the

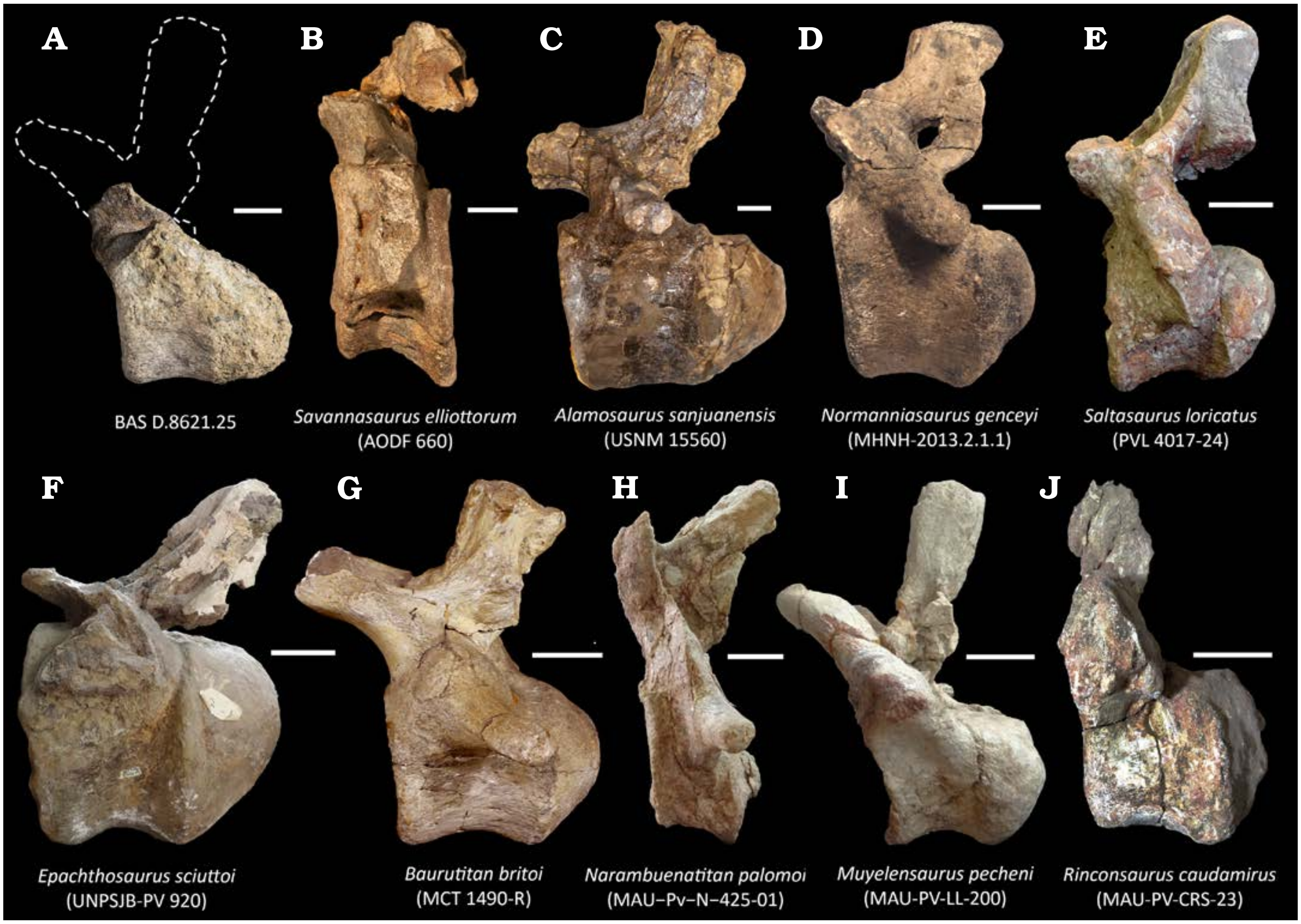

Fig. 5. Comparison of representative titanosaurian anterior caudal vertebrae in left lateral view. **A**. Eutitanosauria indet. (BAS D.8621.25) Santa Marta Fm.; Upper Cretaceous, lower Campanian; James Ross Island, Antarctica. **B**. *Savannasaurus elliottorum* Poropat et al., 2016, Winton Fm.; Upper Cretaceous, Cenomanian–lower Turonian; Queensland, Australia (AODF 660). **C**. *Alamosaurus sanjuanensis* Gilmore, 1922, North Horn Fm.; Upper Cretaceous, upper Maastrichtian, Utah, USA (USNM 15560). **D**. *Normanniasaurus genceyi* Le Loeuff et al., 2013, Poundingue Ferrugineux Fm.; Lower Cretaceous, Albian; Seine-Maritime, France (MHNH-2013.2.1.1). **E**. *Saltasaurus loricatus* Bonaparte & Powell, 1980, Lecho Fm.; Upper Cretaceous, lower Maastrichtian; Salta, Argentina (PVL 4017-24) (reversed from right lateral view). **F**. *Epachthosaurus sciuttoi* Powell, 1990, Bajo Barreal Fm.; Upper Cretaceous, upper Cenomanian–lower Turonian; Chubut, Argentina (UNPSJB-PV 920) (reversed from right lateral view).**G**. *Baurutitan britoi* Kellner et al., 2005, Serra da Galga Fm.; Upper Cretaceous, Maastrichtian; Minas Gerais, Brazil (MCT 1490-R). **H**. *Narambuenatitan palomoi* Filippi et al., 2011, Anacleto Fm.; Upper Cretaceous, lower Campanian; Neuquén, Argentina (MAU-PV-N-425-01). **I**. Aeolosaurini indet. (formerly assigned to *Muyelensaurus pecheni* Calvo et al., 2007, Plottier Fm.; Upper Cretaceous, late Coniacian; Neuquén, Argentina; MAU-PV-LL-200) (reversed from right lateral view). **J**. *Rinconsaurus caudamirus* Calvo & González Riga, 2003, Bajo de la Carpa Fm.; Upper Cretaceous, middle Santonian; Neuquén, Argentina (MAU-PV-CRS-23). Scale bars 100 mm.

deep ventral groove and ventrolateral ridges seen in the anterior caudal centra of some other titanosaurian taxa, including *Alamosaurus sanjuanensis*, *Andesaurus delgadoi*, *Malawisaurus dixeyi*, *Overosaurus paradasorum*, *Rapetosaurus krausei*, and *Saltasaurus loricatus* (Wilson 2002; Upchurch et al. 2004; Curry Rogers 2009; Mannion et al. 2019b; Díez Díaz et al. 2025). However, these features of the ventral surface are often absent in the anteriormost caudal vertebrae (Mannion et al. 2019b). BAS D.8621.25 also lacks a lateral fossa, contrasting with a small number of titanosaurs (e.g., *Alamosaurus sanjuanensis*, *Pellegrinisaurus powelli*, *Xianshanosaurus shijiagouensis*) in which a small fossa or foramen is present in anterior caudal centra (Wilson 2002; Mannion et al. 2013; Cerda et al. 2021). Although the anterior margin of the centrum is concave in lateral view, BAS D.8621.25 lacks the strong anterior canting that characterises the anterior caudal centra of a small number of titanosaurs, including aeolosaurines and *Qunkasaura pintiquiniestra* (Santucci and Arruda-Campos 2011; Mannion et al. 2019a; Mocho et al. 2024).

An anteriorly situated neural arch is characteristic of the anterior caudal vertebrae of most sauropods (Upchurch et al. 2004). In many taxa, there is a small gap between the anterior margin of the centrum and that of the base of the neural arch, with the latter typically subvertical. Among titanosaurs with procoelous anterior caudal vertebrae, this includes *Alamosaurus sanjuanensis* (USNM 15560; Fig. 5C), *Normanniasaurus genceyi* (MHNH-2013.2.1.1;

Fig. 5D), *Saltasaurus loricatus* (PVL 4017-24; Fig. 5E), *Epachthosaurus sciuttoi* (UNPSJB-PV 920; Fig. 5F), *Malawisaurus dixeyi* (Gomani 2005: fig. 14), *Rukwatitan bisepultus* (Gorscak et al. 2014: fig. 6). In most taxa that lack a gap, the base of the arch is subvertical, e.g., *Baurutitan britoi* (MCT 1490-R; Fig. 5G) and *Narambuenatitan palomoi* (MAU-PV-N-425-01; Fig. 5H). By contrast, the anterior position and anterodorsal projection of the base of the neural arch of BAS D.8621.25 is most similar to those of the titanosaurians *Aeolosaurus rionegrinus* (Powell 2003: pl. 11: 1a, 2a), a specimen formerly referred to *Muyelensaurus pecheni* (MAU-PV-LL-200, but see Discussion regarding affinities of this specimen; Fig. 5I), and *Rinconsaurus caudamirus* (MAU-PV-CRS-23; Fig. 5J).

Internal morphology.—The internal morphology of titanosaurian caudal vertebrae differs across the clade (Poropat et al. 2020). Most species for which the internal morphology has been assessed are characterized by apneumatic centra and neural arches, as is the case in BAS D.8621.25. This includes *Andesaurus delgadoi*, *Epachthosaurus sciuttoi*, *Mendozasaurus neguyelap*, *Mnyamawamtuka moyowamkia*, *Pellegrinisaurus powelli*, *Punatitan coughlini*, and *Rinconsaurus caudamirus* (Gorscak and O'Connor 2019; Hechenleitner et al. 2020; Poropat et al. 2020; Cerda et al. 2021; Pérez Moreno et al. 2022). The anterior caudal vertebrae of a small number of titanosaurs (and close relatives) are characterized by apneumatic centra, but have pneumatic neural arches, including diamantinasaurians, *Malawisaurus dixeyi*, and *Bonatitan reigi* (Wedel 2009; Poropat et al. 2020; Beeston et al. 2024; Zurriaguz 2024). Both the centra and neural arches are pneumatic in the anterior caudal vertebrae of *Xianshanosaurus shijiagouensis* (Mannion et al. 2013) and saltasaurines, with a camellate internal bone structure extending into the posterior caudal vertebrae in the latter clade (Cerda et al. 2012b; Zurriaguz and Cerda 2017). The anterior caudal centra are also pneumatic in *Volgatitan simbirskiensis*, although this cannot be assessed in the neural arches because none are preserved (Averianov and Efimov 2018).

Discussion

Affinities of BAS D.8621.25.—The well-developed procoely of BAS D.8621.25 supports its identification as a lithostrotian titanosaurian sauropod (Upchurch et al. 2004). It is clearly distinct from the anterior caudal vertebrae of most non-lithostrotian somphospondylans, including Australian diamantinasaurians (Fig. 5B). Within Lithostrotia, BAS D.8621.25 can be excluded from the South American saltasaurine clade due to the absence of camellate internal bone structure (Cerda et al. 2012b). The anterior position and anterodorsal orientation of the neural arch of BAS D.8621.25 is most reminiscent of members of Aeolosaurini (e.g., Santucci and Arruda-Campos 2011: fig. 5) and Rinconsauria (Fig. 5I, J). These two clades of primarily Gondwanan taxa are sometimes recovered as closely related to each other, but other analyses place them as phylogenetically distant lineages (see Díez Díaz et al. 2025; Pérez Moreno et al. in press). The morphology of both the anterior margin of the centrum and the centrally positioned condyle of BAS D.8621.25 are closest to that of an anterior caudal vertebra (MAU-PV-LL-200; Fig. 5I) previously assigned to the Late Cretaceous Argentinean rinconsaurian *Muyelensaurus pecheni* (Calvo et al. 2007) but recently attributed to an indeterminate aeolosaurine (Pérez Moreno et al. in press). Given the issues of distinguishing rinconsaurians from aeolosaurines, the present state of flux in understanding of titanosaurian phylogenetic interrelationships, and the fragmentary nature of BAS D.8621.25, we conservatively regard the combination of character states present in this specimen as supporting its identification as a non-saltasaurid eutitanosaurian sauropod.

Comments on MLP-PV 11-II-20-1.—Cerda et al. (2012a) identified MLP-PV 11-II-20-1, an incomplete tetrapod bone from the upper Campanian (Upper Cretaceous) Gamma Member of the Snow Hill Island Formation (sensu Olivero 2012) of James Ross Island, as a partial middle caudal vertebral centrum of a lithostrotian titanosaurian sauropod (Fig. 6). This was based on its anteriorly concave and posterior convex articular surfaces, which were taken as evidence of procoely; Cerda et al. (2012a) also ruled out saltasaurine affinities due to the absence of camellate internal structure. However, the specimen is incomplete and difficult to interpret, and we suggest that it was misoriented by Cerda et al. (2012a). Specifically, rather than representing the right side of an incomplete titanosaurian caudal centrum, we interpret MLP-PV 11-II-20-1 as the ventral half of a caudal centrum, such that Cerda et al.'s (2012a) purported lateral views (Cerda et al. 2012a: fig. 2b, e) actually depict the centrum in ventral view and the anterior and posterior views should each be rotated through 90° (anticlockwise for the anterior views, Cerda et al. 2012a: fig. 2a, d; clockwise for the posterior views, Cerda et al. 2012a: fig. 2c, f) to lie in their correct orientations. As noted by Cerda et al. (2012a), the presence of procoely and the absence of camellae supports non-saltasaurine eutitanosaurian affinities for MLP-PV 11-II-20-1 (see discussion of these features, above), but the bone is too poorly preserved for any other meaningful comparisons.

Implications.—Although it remained unrecognised until now, the titanosaurian sauropod identity of BAS D.8621.25 means that it is the first non-avian dinosaur fossil to have been recovered from Antarctica (in 1985, see above), whereas the ankylosaur partial skeleton later named *Antarctopelta oliveroi*, which is usually considered to be the earliest-known discovery, was found in 1986 (e.g., Olivero et al. 1991). Moreover, BAS D.8621.25 is currently the only dinosaur specimen known from the Santa Marta Formation (specifically, from a lower Campanian horizon of that unit), which makes it the second-stratigraphically oldest Cretaceous

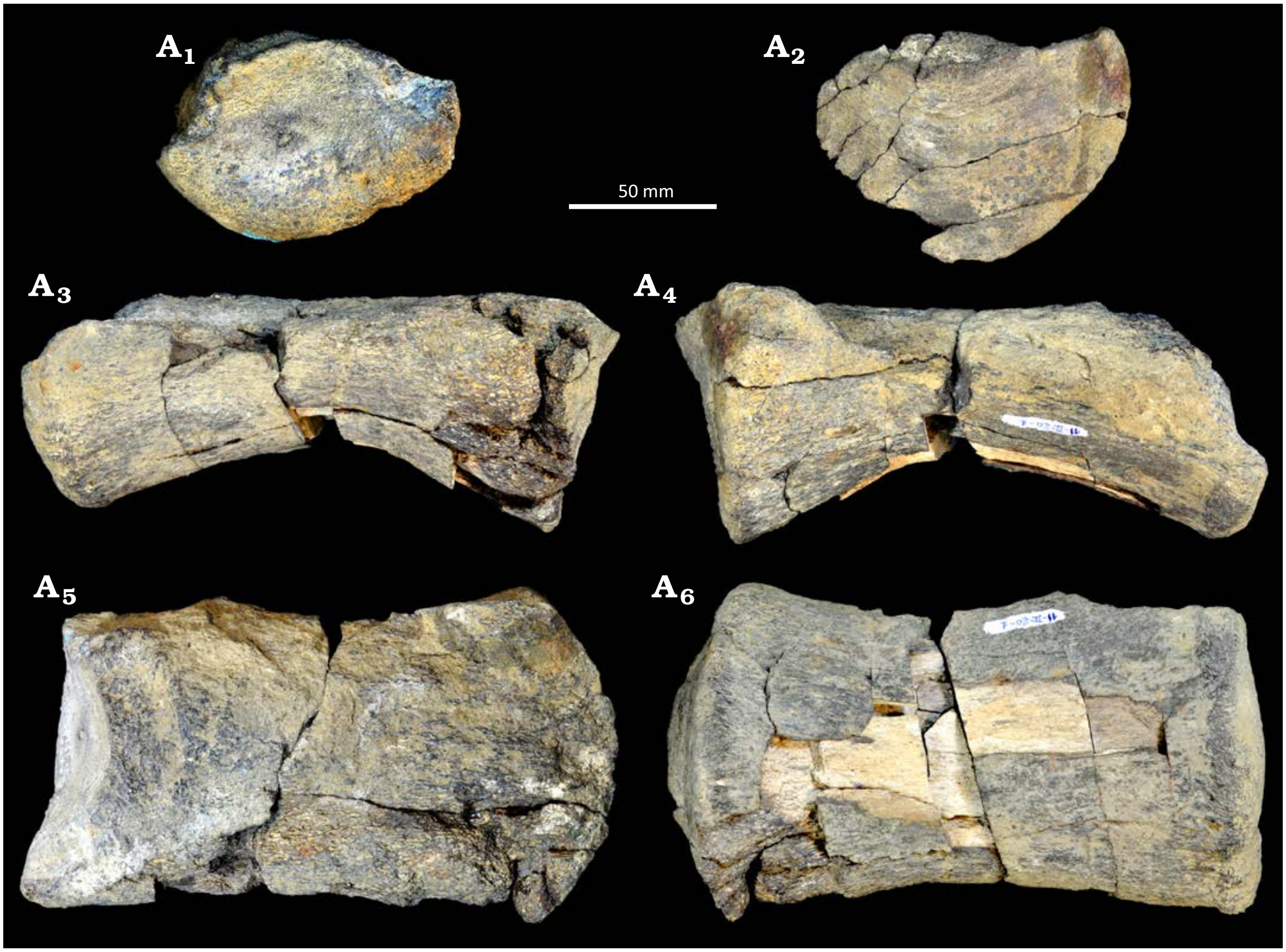

Fig. 6. Eutitanosaurian sauropod from the Upper Cretaceous (upper Campanian) Gamma Member of the Snow Hill Island Formation of James Ross Island, Antarctica; originally identified and described by Cerda et al. (2012a). MLP-PV 11-II-20-1, partial middle caudal vertebral centrum in anterior (A_1), posterior (A_2), left (A_3) and right (A_4) lateral, dorsal (A_5), and ventral (A_6) views, according to our revised interpretation.

dinosaur fossil from the continent after a taxonomically indeterminate non-avian theropod tibia from the Coniacian-aged Hidden Lake Formation of James Ross Island (Molnar et al. 1996; Lamanna et al. 2019).

As titanosaurian and non-titanosaurian somphospondylan remains are abundant in the Cretaceous of South America (e.g., Powell 2003; Gallina et al. 2022; Santucci and Filippi 2022) and Australia (e.g., Hocknull et al. 2009, 2021; Poropat et al. 2016, 2017, 2020; Beeston et al. 2024), and are also known from the Upper Cretaceous of New Zealand (Molnar and Wiffen 2007), the presence of somphospondylans in Antarctica is unsurprising given that it must have been the landmass through which the ancestors of these lineages dispersed at some time in the Cretaceous (e.g., Poropat et al. 2016). Currently, the only somphospondylans known from Australia are *Austrosaurus mckillopi*, a titanosauriform of uncertain phylogenetic affinities (Poropat et al. 2017), and diamantinasaurians, a clade which is either an early-branching titanosaurian lineage or, more likely, the immediate sister group of the latter (e.g., Poropat et al. 2021; Carballido et al. 2022; Beeston et al. 2024; Díez Díaz et al. 2025). However, the eutitanosaurian affinities of both BAS D.8621.25 and MLP-PV 11-II-20-1 demonstrate that they were not early-diverging titanosauriforms or diamantinasaurians (see Comparisons, above) and therefore imply that more than one somphospondylan lineage occupied Antarctica, although not necessarily at the same time (known diamantinasaurians are early Late Cretaceous in age, so their ancestors would have been present in Antarctica prior to this; Poropat et al. 2016). Unfortunately, the absence of mid-Cretaceous and latest Cretaceous dinosaur fossils from Antarctica and Australia, respectively, means that it is not currently possible to determine whether or not these lineages were sympatric. However, an isolated caudal vertebra from the Campanian of New Zealand (Molnar and Wiffen 2007) is likely that of a eutitanosaur, as it exhibits strong procoely. The Antarctic Peninsula, including James Ross Island, would seem to have been the most likely eutitanosaur dispersal route from South America to Zealandia

(Mortimer 2025: fig. 11), By contrast, eutitanosaurs are currently unknown from the Cretaceous of Australia.

The presence of sauropods in the Upper Cretaceous of the Antarctic Peninsula and New Zealand is consistent with habitat suitability models, which suggest that some parts of northern Antarctica might have been suitable as sauropod dispersal routes (Chiarenza et al. 2022). However, although these models suggest that sauropods could have inhabited these regions, they also show that sauropod habitat occupancy was marginal at this time, which might explain the comparative rarity of sauropods in the region (Chiarenza et al. 2022). By contrast, modelled habitat suitability is higher for both theropods and ornithischians (Chiarenza et al. 2022), which might explain the higher frequency of their discovery thus far.

Conclusions

BAS D.8621.25 is an anterior caudal vertebra from the lower Campanian (Upper Cretaceous) Santa Marta Formation of James Ross Island. It can be identified as that of a non-saltasaurine eutitanosaurian sauropod based on internal and external morphological features and pertains either to a juvenile or small-bodied adult individual. Although described here for the first time, it was the first dinosaur fossil to be collected from Antarctica, represents only the second sauropod body fossil to be recovered from the continent, and is the first dinosaur specimen from the Santa Marta Formation. Its presence is consistent both with habitat suitability models and the known distribution of other Late Cretaceous Gondwanan eutitanosaurians.

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