



New records of Theropoda from a Late Cretaceous (Campanian-Maastrichtian) locality in the Magallanes-Austral Basin, Patagonia, and insights into end Cretaceous theropod diversity

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ARTICLE INFO

Keywords:

Theropod
Ornithurine
Enantiornithine
Birds
Campanian
Maastrichtian
end Cretaceous
Patagonia
Chile

ABSTRACT

The end Cretaceous mass extinction was marked by a dramatic change in biodiversity, and the extinction of all non-avian dinosaurs. To understand the diversity of dinosaur clades prior to this event, as well as recovery by avian dinosaurs (birds), we need a better understanding of the global fossil record. However, the fossil record from southern localities, particularly southernmost (>60°S) South America, has only recently begun to be described. Discoveries from Patagonia are important to accurately assess global trends in dinosaur diversity, particularly during the latest Cretaceous before the Cretaceous/Paleogene (K/Pg) mass extinction event. Here we describe new theropod dinosaur specimens, representing both associated material and isolated elements, from Upper Cretaceous (Campanian-Maastrichtian) deposits of the Río de las Chinas Valley, Magallanes-Austral Basin, Chile. These discoveries include the southern-most known occurrences of several theropod clades outside of Antarctica, including megaraptorids, unenlagiines, enantiornithines and ornithurines. Notably, these remains provide much needed time-constrained records of smaller theropods, including birds, which are less often recovered from Upper Cretaceous deposits. While fragmentary, these fossils are the first records of theropods from Chilean Patagonia, and provide insight into the distribution of avian and non-avian theropods in southern high latitude ecosystems prior to the K/Pg mass extinction event. Sampling from this region is still sparse, and more fossils from age-controlled sections are needed to accurately assess global extinction dynamics through the end Cretaceous.

1. Introduction

The end of the Cretaceous Period (66 Ma) was marked by rapid biotic turnover attributed to the impact of a large asteroid at Chicxulub, Mexico, and contributions from increased volcanism from the Deccan Traps (Alvarez et al., 1980; Schulte et al., 2010; Archibald et al., 2010; Petersen et al., 2016; Schoene et al., 2019; Chiarenza et al., 2020; Morgan et al., 2022). Environmental perturbations from these events led to the extinction of three-quarters of all life on Earth, including the non-avian dinosaurs (reviewed in Brusatte et al., 2015; and Morgan et al., 2022). The most detailed records of biodiversity change,

extinction mechanisms, and timing come from Northern Hemisphere localities, primarily in North America and Europe (Schulte et al., 2010; Vajda and Bercovici, 2014). Based on these records, studies have suggested that dinosaur diversity was already in decline prior to the extinction event (e.g., Condamine et al., 2021; Han et al., 2022); however, these analyses likely do not represent their true diversity as they do not include the Southern Hemisphere record. Our current understanding of global biodiversity across the Cretaceous/Paleogene (K/Pg) is hampered by under-sampling of the Southern Hemisphere. This makes it difficult to test alternative hypotheses of extinction timing. For example, it has been proposed that the effects of the event were unevenly

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<https://doi.org/10.1016/j.jsames.2022.104163>

Received 29 September 2022; Received in revised form 14 December 2022; Accepted 14 December 2022

Available online 17 December 2022

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distributed, having a greater impact on environments in the Northern Hemisphere which were more proximal to extinction triggers while higher southern latitude communities may have been relatively buffered from the extinction's immediate effects (Clyde et al., 2021). More fossils are needed from age constrained localities distal to proposed extinction triggers to better quantify dinosaurian diversity leading up to the K/Pg mass extinction event, as well as to better understand the true global impacts of the event.

Localities in Patagonia, South America, make an ideal candidate for targeted searches for Late Cretaceous dinosaur fossils. Work across the region has provided an ever-growing picture of a diverse dinosaur fauna throughout the Cretaceous (Bonaparte, 1985; Salgado and Bonaparte, 1991; Coria and Salgado, 1996; Makovicky et al., 2005; Carballido et al., 2011; Soto-Acuña et al., 2021). This is particularly true for theropod dinosaurs. The Late Cretaceous South American theropod record is taxonomically diverse and comprised of widely divergent clades, including Noasauridae (Bonaparte and Powell, 1980; Bonaparte, 1991), Abelisauridae (Bonaparte, 1985; Bonaparte and Novas, 1985; Aranciaga Rolando et al., 2021), Carcharodontosauridae (Coria and Salgado, 1995; Novas and Pol, 2005; Canale et al., 2014; Canale et al., 2022), Megaraptoridae (Novas, 1998; Porfiri et al., 2014; Coria and Curie, 2016), early diverging coelurosaurs (Kellner, 1999; Novas et al., 2012), alvarezsaurids (Novas et al., 1997), and paravians including avialans (Chiappe and Walker, 2002; Makovicky et al., 2005; Agnolín and Martinelli, 2008; Novas et al., 2008b; Agnolín et al., 2017). To date, the southernmost non-Antarctic record of non-avian theropods comes from the Santa Cruz Province in Argentinean Patagonia, which includes the abelisauroid *Austrocheirus isasi* (Ezcurra et al., 2010) and the megaraptorid *Orkoraptor burkei* (Novas et al., 2008a) both from the Cerro Fortaleza Formation (Campanian-Maastrichtian), and the recently described megaraptorid *Maip macrothorax* (Aranciaga Rolando et al., 2022) from the Chorrillo Formation (Campanian-Maastrichtian). There are fewer records of small theropods, but scattered findings include representatives of the proposed dromaeosaurid unenlagiines as well as enantiornithine and ornithurine birds (Novas et al., 2019). The wide diversity of taxa described in just the last fifteen years suggests that much of the Southern Hemisphere dinosaurian diversity is still yet to be discovered.

Here we report avian and non-avian theropod fossils from a high paleolatitude (>60° S), Late Cretaceous site in present day Chilean Patagonia. The Río de las Chinas Valley, located within the Magallanes-Austral Basin in Chile, is both a geologically and paleontologically significant locality. Recent studies have established a well-constrained stratigraphic framework for the valley (Manríquez et al., 2019, 2021; George et al., 2020), and identified potential preservation of continuous deposition across the K/Pg boundary (George et al., 2020). This locality has produced a wealth of fossil discoveries that have greatly expanded our understanding of the diversity of vertebrates and plants at southern high latitudes during the end of the Cretaceous (Alarcón-Muñoz et al., 2020; Goin et al., 2020; Trevisan et al., 2020; Martinelli et al., 2021; Soto-Acuña et al., 2021; Suazo Lara and Gomez, 2022), and help elucidate biogeographic patterns during final Gondwanan breakup (reviewed in Reguero and Goin, 2021). While some of these notable discoveries represent partially articulated specimens (i.e., *Stegouros elengassen*, Soto-Acuña et al., 2021), most vertebrate fossils recovered from the locality are isolated or fragmentary. Regardless, these records still provide valuable insight into the diverse fauna present in southernmost South America during the latest Cretaceous, and the fossils described here represent a diverse theropod community that lived up until the K/Pg interval.

1.1. Locality and geological setting

The fossils described here were collected during field seasons in 2016–2020 from Upper Cretaceous deposits of the Río de las Chinas Valley (50°40'S, 72°32'W), northwest of the Torres del Paine National Park, Última Esperanza Province, Chile (Fig. 1). The valley is located

within the Magallanes-Austral Basin, a retroarc foreland basin associated with Cretaceous – Cenozoic mountain building in the southernmost Andes (Malkowski et al., 2017). The exposed geology of the valley is comprised of three main units: the Tres Pasos Formation (Campanian-Maastrichtian), the Dorotea Formation (Campanian-Danian), and the Man Aike Formation (late Lutetian - Bartonian) (Schwartz and Graham, 2015; Daniels et al., 2017; Gutiérrez et al., 2017; Schwartz et al., 2017; Sickmann et al., 2018; Manríquez et al., 2019; George et al., 2020). All fossils were found in the middle and upper sections of the Dorotea Formation, a ~600–1250 m thick fossiliferous shallow marine to nonmarine unit containing plant, invertebrate, and vertebrate fossils (Fosdick et al., 2011; González, 2015; Schwartz et al., 2017; Gutiérrez et al., 2017; Manríquez et al., 2019, 2021; George et al., 2020).

The Dorotea Formation, originally defined by Kast (1963), is composed predominantly of sandstones, thin conglomerate lenses, calcareous sandy concretions and varicolored mudstones (Schwartz and Graham, 2015; Manríquez et al., 2019). The formation is interpreted as fluvial, shoreface and deltaic deposits (Schwartz and Graham, 2015; Manríquez et al., 2019, 2021; George et al., 2020). The Dorotea Formation has been correlated with the Cerro Fortaleza, Cerro Cazador, Chorillo, La Irene, Calafate and Cerro Dorotea formations in corresponding segments of the basin to the north and to the east in Argentina (Macellari et al., 1989; Nullo et al., 2006; Leppe et al., 2012; Sickmann et al., 2018; Odino-Barreto et al., 2018; Tettamanti et al., 2018; Ghiglione et al., 2021; Moyano-Paz et al., 2022).

Fossils were surface collected from five localities within the Río de las Chinas Valley from two main sectors (Sauropodo Camp [SC] and El Puesto [P]; Fig. 1). Locality SC1 is interpreted as paleosols developed in a fluvial overbank or upper tidal flat setting, and the fossils were recovered from mudstones containing rootlets (Schwartz and Graham, 2005). SC2, P1, and SC3 are located within floodplain and meandering fluvial deposits, and P2 represents a near-shore marine deposit (Schwartz and Graham, 2005; Manríquez et al., 2019, 2021). SC2 is composed of two facies: enantiornithine fossils were recovered from fluvial floodplain facies composed of medium-to coarse-grained sandstones with trough cross-bedding, in proximity to the recently described *Stegouros elengassen* (Soto-Acuña et al., 2021), and the megaraptoran material was recovered from sandy mudstones with interbedded fine-grained sandstones, near recovered mammal and freshwater turtle remains (Goin et al., 2020; Alarcón-Muñoz et al., 2020; Martinelli et al., 2021). Fossils from P1 and SC3 were located in sandy mudstone and fine-grained sandstone facies with carbonaceous material. P2 is composed of a thin horizon of medium-grained sandstone rich in bivalve, gastropod, shark, and marine reptile fragments, representing a higher energy nearshore marine setting (Manríquez et al., 2021).

Several studies have estimated maximum depositional ages for different levels throughout the valley, allowing the fossiliferous localities discussed here to be relatively well constrained temporally (Fig. 1). Locality SC1 is Campanian in age (between 78.0 ± 2.1 Ma and 74.9 ± 2.1 Ma; Schwartz et al., 2016; Gutiérrez et al., 2017), whereas localities SC2, P1, and SC3 are Campanian – Maastrichtian (between 74.9 ± 2.1 Ma and 70.5 ± 5.0 Ma; Gutiérrez et al., 2017; Schwartz et al., 2017). Locality P2 is Maastrichtian (between 70.5 ± 5.0 Ma and 66.7 ± 1.3 Ma; Schwartz et al., 2017; George et al., 2020), which is further supported by the presence of shark teeth within the fossil rich layer that are currently only known from Maastrichtian deposits (e.g., Cappetta, 2012; Otero et al., 2013; Cappetta et al., 2014).

2. Materials and methods

All fossils were surface collected from different levels of the Dorotea Formation in the Río de las Chinas Valley. Fossils were identified based on comparisons with published material in the literature, and dental traits were studied with reference to characters described by Hendrickx et al. (2019, 2020). We follow the descriptive terminology from Hendrickx et al. (2015) for dental traits.

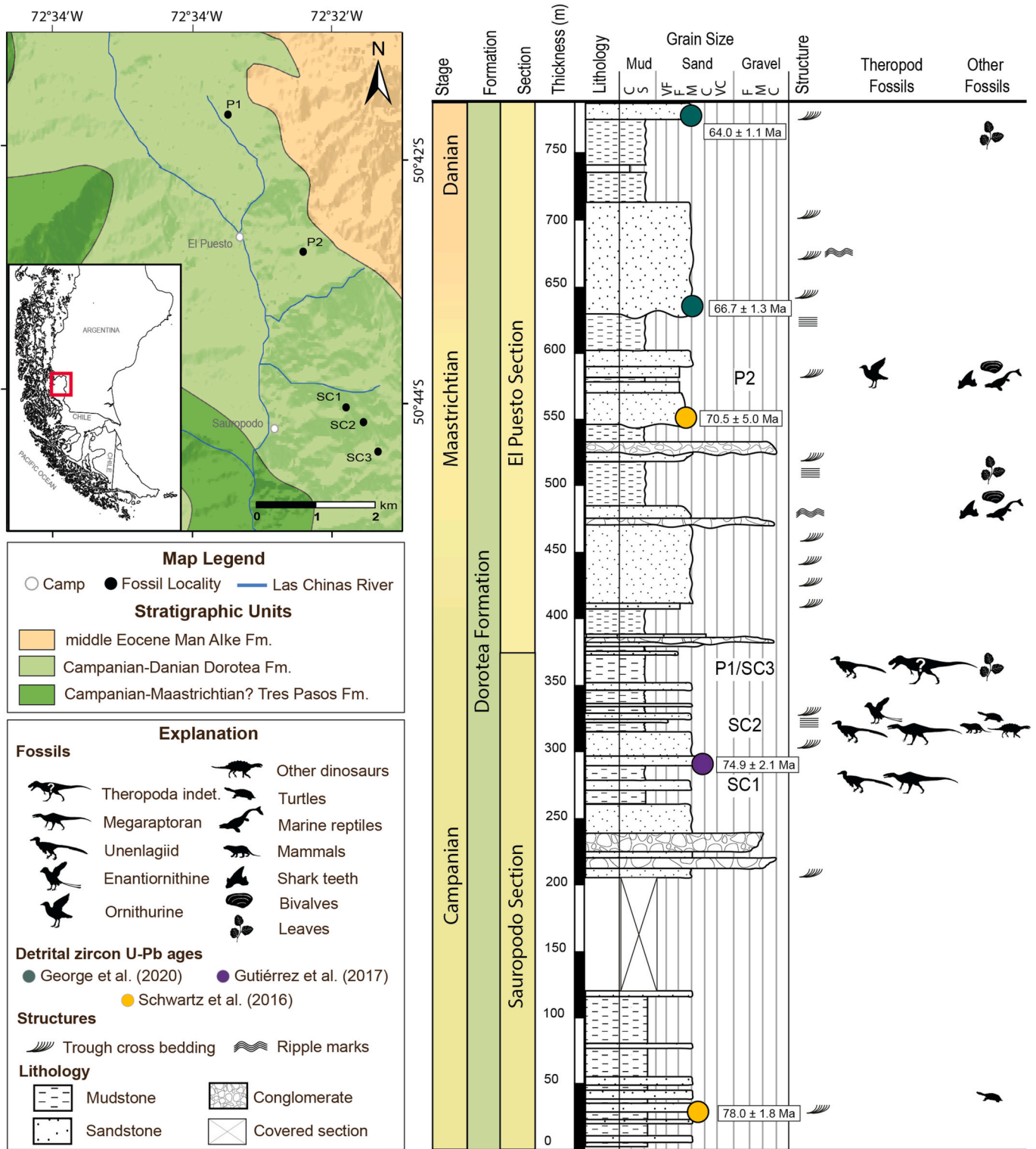


Fig. 1. Locality map and geology of the Río de Las Chinas valley, Chile. Fossil localities in the Dorotea Formation are indicated with black dots on the map. The described theropod material comes from four levels of the Dorotea formation (Campanian – Danian), primarily from lacustrine and deltaic deposits with the exception of the ornithurine bird which was recovered from a near shore marine deposit. Modified from Manríquez et al. (2019, 2021) and George et al. (2020).

Institutional Abbreviations — CPAP, Colección de Paleontología de Antártica y Patagonia, Punta Arenas, Chile; GNS, Institute of Geological and Nuclear Sciences, Lower Hutt, New Zealand; MACN-Pv, Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”, Buenos Aires, Argentina; MCF-PVPH, Museo Carmen Funes, Paleontología de Vertebrados, Plaza Huinca, Neuquén, Argentina; MPM-PV, Museo Padre

Molina Paleontología de Vertebrados, Río Gallegos, Santa Cruz, Argentina.

2.1. Systematic paleontology

DINOSAURIA Owen, 1842

SAURISCHIA

THEROPODA Marsh, 1881

Theropoda indet.

(Fig. 2).

Material — CPAP 7503; partial tibia missing both epiphyses.

Locality — Locality SC3, Las Chinas Valley, Magallanes Basin (Fig. 1).

Formation/Age — Dorotea Formation, Late Cretaceous (Campanian – Maastrichtian).

Description — CPAP 7503 consists of a partial diaphysis, missing both epiphyses. The preserved portion of the diaphysis measures 119.70 mm long, with a diameter at the widest end of 44.13 mm and at the shortest end of 32.15 mm. The tibia is hollow, triangular in cross section with thick cortex measuring 9.50–11.00 mm thick.

Comparison — The triangular shape, hollow core, and proportionally thin walls indicate the tibia belongs to a theropod dinosaur, but in the absence of epiphyses detailed comparison and assignment of CPAP 7503 is impossible. The proportions of the tibia are comparable to those of the megaraptoran, *Orkoraptor burkei* (Novas et al., 2008a), making it likely that the tibia belonged to a medium sized theropod.

MEGARAPTORA Benson et al., 2010.

MEGARAPTORIDAE Novas et al., 2013.

Gen. et sp. indet.

Morphotype 1.

(Fig. 3).

Material — CPAP 3158 A, CPAP 3158 B; two lateral shed teeth.

Locality — Locality SC2, Las Chinas Valley, Magallanes Basin (Fig. 1).

Formation/Age — Dorotea Formation, Late Cretaceous (Campanian – Maastrichtian).

Description — Two large, isolated lateral ziphodont teeth from a midsized non-avian theropod were recovered separately from the site. The teeth are labiolingually compressed, gradually curve distally, and have serrated, labially displaced distal carinae and an irregular enamel texture. In cross section the teeth are figure eight shaped due to slight lingual and labial depressions (Fig. 3F,K); the lingual depression reaches higher apically on the crown than the labial depression (Fig. 3A–B). CPAP 3158 A (Fig. 3A–F) is the most complete of the specimens, preserving the tooth crown and part of the root. The tooth measures 31.60 mm long from the apex to the preserved root portion of the tooth, with a crown height of 20.31 mm, crown base length of 12.99 mm, crown base width of 9.31 mm, and apical length of 26.25 mm. The crown base ratio for the tooth is 0.72, and crown height ratio is 1.56. CPAP 3158 B (Fig. 3G–K) preserves the tooth crown but is missing both the apex and basal most portion. The mesial section of the fossil has a total length as preserved of 11.20 mm and width of 6.18 mm. A wear facet is present on the apex of each tooth, though it is short and narrow in CPAP 3158 A (Fig. 3A) and more extensive and broader in CPAP 3158 B (Fig. 3H).

Both teeth preserve denticles of near equal size along the distal

carina, though they are damaged in CPAP 3158 B towards the apical and basal most ends. Denticles are proximodistally subrectangular, with wedge shaped interdenticular diaphyses. Interdenticular sulci are present along the distal carina, and are more prominent in the basal half of the carina where they angle sharply towards the root (Fig. 3E). The density of denticles is 2–3 denticles per 1 mm. The mesial surface lacks both a carina and denticles. No flutes or longitudinal ridges are present along the teeth, but there are prominent transverse undulations along the entire width of the labial and lingual faces of the teeth (most visible in CPAP 3158 A, Fig. 3A–B). These undulations are more conspicuous on the lingual surface, where they occur in basal, mesio, and apical clusters of about four undulations per cluster.

Comparison — Late Cretaceous South American theropods include carcharodontosaurids, abelisaurids, megaraptorans, alvarezsaurids, and unenlagiines (reviewed in Novas et al., 2019), therefore we limited our comparisons to these clades. CPAP 3158 A and B do not match the overall shape of carcharodontosaurid teeth, which often have a straight distal edge, are much more labiolingually narrow, and have a lower denticle density (8–9 per 5 mm; Coria and Curie, 2006). The teeth of abelisaurids are also relatively straight along the distal edge, and can have hooked distal denticles (Hendrickx et al., 2019, 2020), a feature absent in these new teeth. CPAP 3158 A and B share the strongly distally curved crown, figure eight shaped cross section, labially displaced distal carina, lateral grooves, and lack a mesial carina as seen in Megaraptoridae (Hendrickx et al., 2015, 2019). The teeth fall within the size range of reported teeth from the older Argentine megaraptorid *Murusraptor barrosaensis* (MCF-PVPH-411, Coniacian; Coria and Curie, 2016), but the teeth of *M. barrosaensis* are more dramatically curved apically and appear more labiolingually compressed than CPAP 3158 A and B. Isolated teeth assigned to *Orkoraptor burkei* (MPM-PV 3457 and MPM-PV 3458; Novas et al., 2008a) are quite damaged, but are also comparable in size to the new teeth. The teeth of *O. burkei* differ from the new teeth in the presence of a well-developed wear facets along sides of the teeth instead of the apical edge as in CPAP 3158 A and B (Novas et al., 2008a). The denticles are similarly subrectangular in shape and occur in similar density (3–4 denticles per 1 mm in *O. burkei*; Novas et al., 2008a). The teeth of *O. burkei* also have prominent labial and lingual depressions similar to those in the new isolated teeth. Due to the absence of further material, at this time we can neither assign or exclude CPAP 3158 A and B from this genus.

Several isolated teeth referred to Megaraptoridae indet. have been recovered from the La Anita locality in Argentina, about 20 km north from Las Chinas (Novas et al., 2019; Moyano-Paz et al., 2022). Isolated tooth MACN-Pv 19066 (Novas et al., 2019) is of comparable proportions to CPAP 3158 A and B, but the apical curve is much sharper than in the new specimens. The enamel surface of MACN-Pv 19066 is quite weathered, obscuring any potential wrinkling. The denticles of MACN-Pv 19066 are squarer and are of higher density than the new specimens (5 denticles per 1 mm; Novas et al., 2019). Three figured crowns described by Moyano-Paz et al. (MPM-PV-22864 and MPM-PV-22865; Moyano-Paz et al., 2022) have sharper apical curvature



Fig. 2. An indeterminate partial tibia CPAP 7503 from a medium-sized theropod.

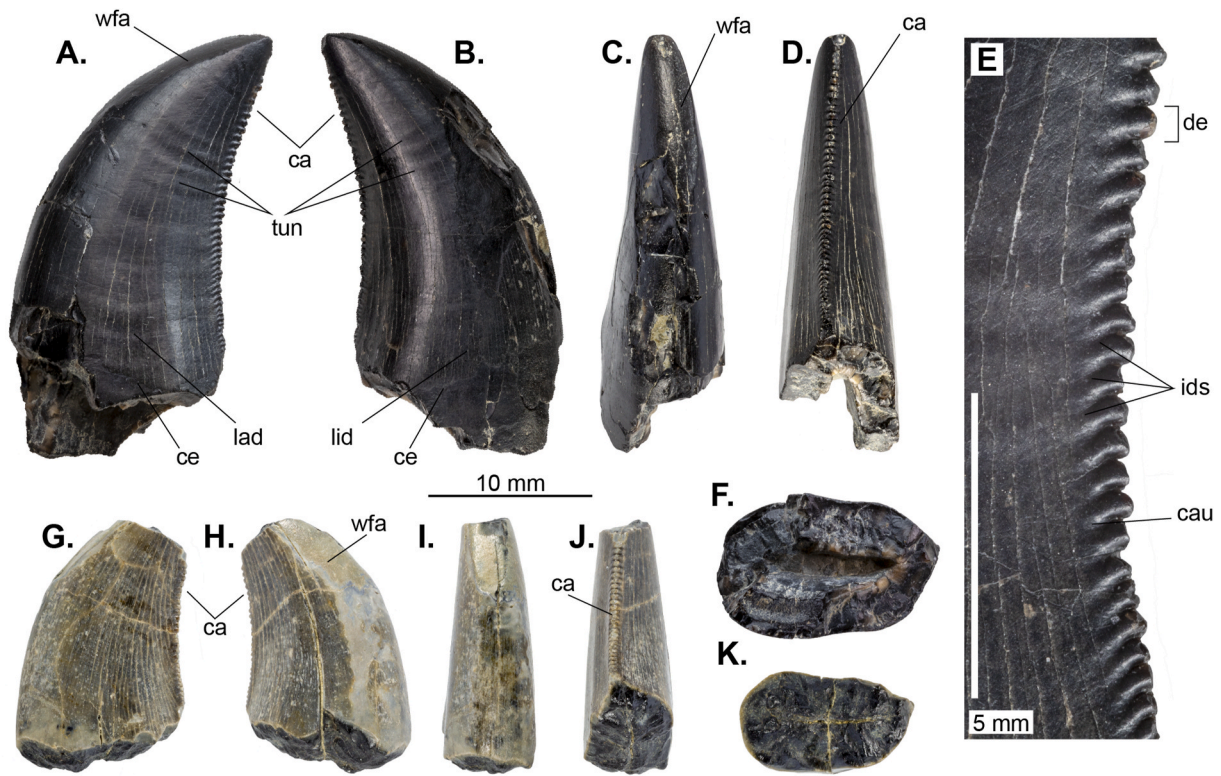


Fig. 3. Isolated Megaraptoridae indet. shed teeth representing Morphotype 1. CPAP 3158 A (A–F) preserves most of the tooth crown, while CPAP 3158 B (G–K) is missing the apex and base of the crown. Teeth are shown in (A/G) labial; (B/H) lingual; (C/I) mesial; (D/J) distal; and basal (F/K) views of both specimens. The denticles and crown ornamentations (E) are best preserved in CPAP 3158 A. **Abbreviations:** ca, carina; cau, cauda; ce, cervix; de, denticle; ent, enamel texture; ids, interdenticular sulcus; lad, labial depression; lid, lingual depression; tun, transverse undulations; wfa, wear facet. Scale = 10 mm.

than seen in CPAP 3158 A and B. MPM-PV-22864 also displays a mesiolabial carina, which is absent in the material described here. The denticles of MPM-PV-22864 and MPM-PV-22864 differ from those of CPAP 3158 A and B, but do occur in a similar density of 2–3 per mm. Due to these differences, at this time we believe that CPAP 3158 A and B do not come from the same taxon as the La Anita megaraptorids.

Morphotype 2.

(Fig. 4).

Material — CPAP 5930; isolated mesial shed tooth.

Locality — SC2, Las Chinas Valley, Magallanes Basin (Fig. 1).

Formation/Age — Dorotea Formation, Late Cretaceous (Campanian - Maastrichtian).

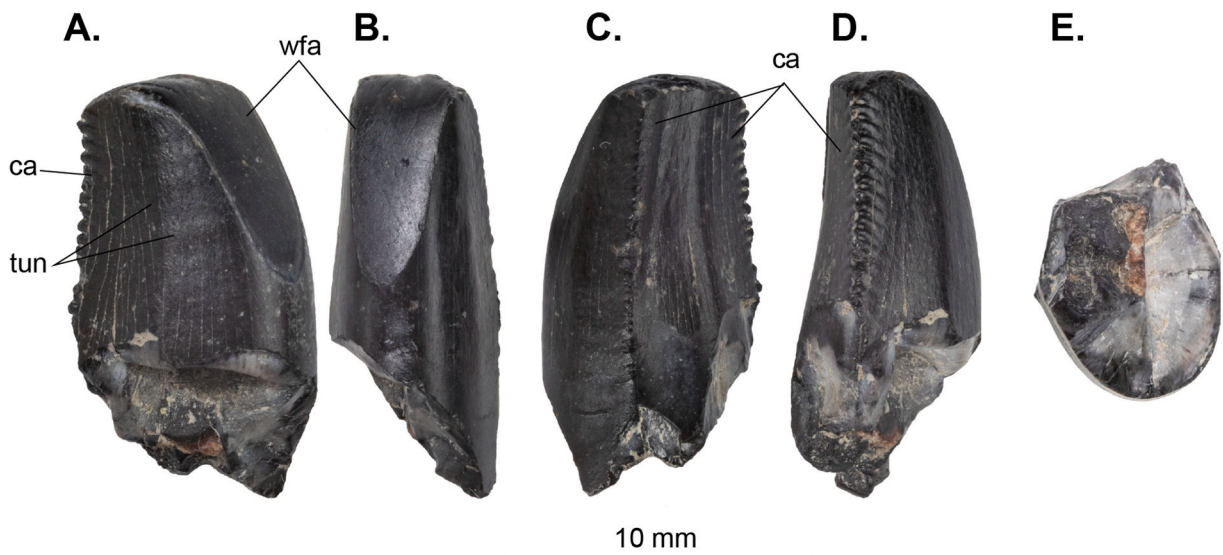


Fig. 4. Isolated mesial Megaraptoridae indet. tooth representing morphotype 2. CPAP 5930, shown in (A) labial; (B) mesial; (C) lingual; (D) distal and (E) basal views. The tooth has a strongly displaced mesial carina, with weathered denticles. **Abbreviations:** ca, carina; tun, transverse undulations; wfa, wear facet. Scale = 10 mm.

Description — A large ziphodont non-avian theropod tooth missing the root and basal most portion (Fig. 4A–E). As preserved, it measures 12.52 mm long. The tooth has two serrated carinae, one along the distal edge and a displaced mesial carinae on the lingual side (Fig. 4C). This mesial carina gives the tooth an asymmetrical “D” shaped cross section (Fig. 4E). The denticles along the distal carina are proximodistally subrectangular, with wedge shaped interdenticular diaphyses and well-developed interdenticular sulci (Fig. 4D). They occur at a density of 2 denticles per 1 mm. The morphology of the denticles on the mesial carina is unclear due to weathering, though they appear to occur in similar density to the distal denticles (Fig. 4C). Two longitudinal ridges are present on the lingual side, between the two carinae (Fig. 4C). A prominent, broad wear facet is present along the mesial side, and grouped transverse undulations are present on both the labial and lingual surfaces (Fig. A and B).

Comparison — Aside from the mesial carina and cross section, the tooth has megaraptoran traits similar to those in CPAP 3158 A and B. CPAP 5930 has a similar undulation pattern as CPAP 3158 A and B, though it is distorted by the mesial carina and seems to be more constrained apically, and the denticle morphology and density is similar. The longitudinal ridges on CPAP 5930 that are not observed on CPAP 3158 A and B appears to be due its position as a medial tooth and the presence of the mesial carina. Few mesial teeth have been described from known megaraptorans, and are comprised of isolated teeth. A mesial tooth of *O. burkei* is described as having a displaced carina, like what is seen in CPAP 5930 (Novas et al. 2008a, 2008b Fig. 3B). However due to weathering it is unclear if this carina is serrated, and the cross section of this tooth is not described. The mesial teeth of *M. barrosaensis* are not figured (Coria and Currie, 2016), but were described by Hendrickx et al. (2019) as having concave surfaces adjacent to both the mesial and distal carina, like the condition seen in CPAP 5930. These teeth are also described to have denticulated mesial carinae, which are not found to reach the cervix (Hendrickx et al., 2019). The cervix is unfortunately not preserved in CPAP 5930, so it is not clear if the extent of the mesial carina is a shared feature.

Some of the features seen in CPAP 5930 are also seen in Tyrannosauroids, including the deflected distal carina, displaced mesial carina, and similar shaped cross sections (Hendrickx et al., 2019). Longitudinal grooves on the lingual surface have also been reported in *Guanlong* (Xu et al., 2006; Hendrickx et al., 2019). Given that the phylogenetic placement of Megaraptora remains unresolved, and is often recovered within Tyrannosauroidae (Porfiri et al., 2014; Aranciaga Rolando et al., 2019), it may not be unexpected for there to be overlap in dental characters. However, as preserved there are not enough features in CPAP 5930 to assign it to a derived Tyrannosaurid clade, and we refer the tooth to Megaraptoridae. Furthermore, given the overall similarity

to CPAP 3158 A and B and the proximity of the teeth at the field site, we tentatively consider all three to be from different dental positions within the same taxon.

Morphotype 3.

(Fig. 5).

Material — CPAP 3173; fragmentary shed tooth.

Locality — SC1, Las Chinas Valley, Magallanes Basin (Fig. 1).

Formation/Age — Dorotea Formation, Late Cretaceous (Campanian).

Description — CPAP 3173 is a partial, isolated mesial or transitional ziphodont tooth missing both the tooth base and cap, measuring 9.07 mm long at its widest point. The tooth is labiolingually compressed, with slight distal curvature and denticles along the distal carina and a lingually displaced mesial carina lacking denticles (Fig. 5B). This morphotype has a more dramatic figure-eight shape in cross section (Fig. 5E) due to prominent labial and lingual depressions. The basal end of a long wear feature is preserved on the mesial carina in lingual view (Fig. 5B). There are no longitudinal grooves or flutes along the tooth, but there are subtle transverse undulations on both the labial and lingual surfaces (Fig. 5B and D).

The denticles of CPAP 3173 are severely weathered, making their morphology difficult to diagnose, but occur in the same density as those of Morphotype 1 (2–3 denticles per 1 mm; Fig. 5B). Only the apically most positioned denticle preserves the original shape. It is rectangular but has a more rounded external margin than those of Morphotype 1 and does not have prominent interdenticular sulci.

Comparison — The strongly distally curved crown and dramatic figure eight shape of CPAP 3173 is also most consistent with the morphology of Megaraptoridae (Hendrickx et al., 2019). CPAP 3171 is overall smaller than 3158 A but similar in size to 3158 B. The more prominent figure-eight cross section shape, the lack of interdenticular sulci, the different wear features, and the presence of a displaced mesial carina make CPAP 3171 distinguishable from Morphotype 1, though it is possible that it represents variation with tooth position from the same taxa, most likely a mesial or transitional tooth. Without more complete and associated material this cannot be determined.

Coelurosauria (Huene 1920).

Deinonychosauria (Colbert and Russell, 1969).

Dromaeosauridae (Matthew and Brown, 1922).

(?)Unenlagiinae (Bonaparte, 1999).

Gen. et sp. indet.

(Fig. 6).

Material — CPAP 5935; small, curved shed tooth.

Locality — SC1, Las Chinas Valley, Magallanes Basin (Fig. 1).

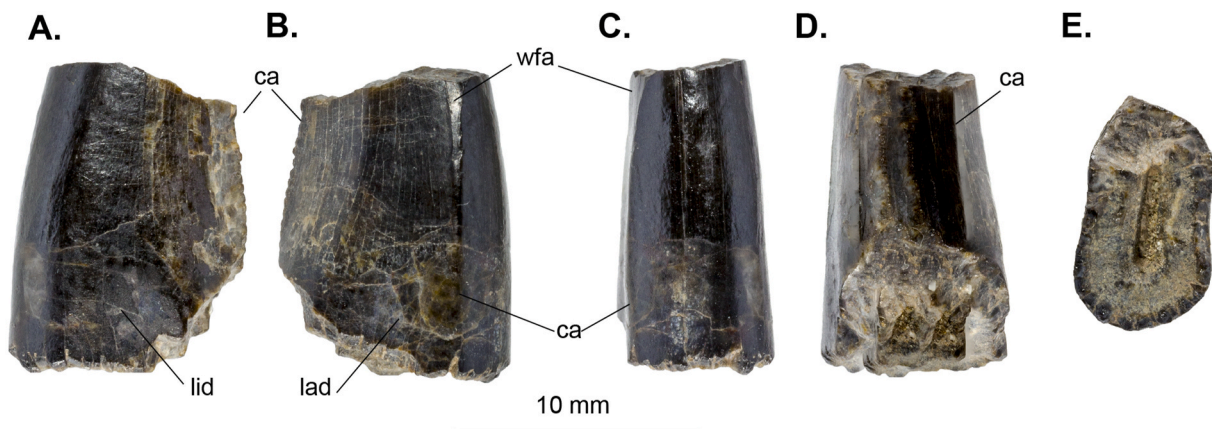


Fig. 5. Isolated Megaraptoridae indet. tooth representing Morphotype 3. CPAP 3173 is missing both the tooth crown and base and is shown in (A) lingual; (B) labial; (C) mesial; (D) distal and (E) basal views. **Abbreviations:** ca, carina; lad, labial depression; lid, lingual depression; wfa, wear facet. Scale = 10 mm.

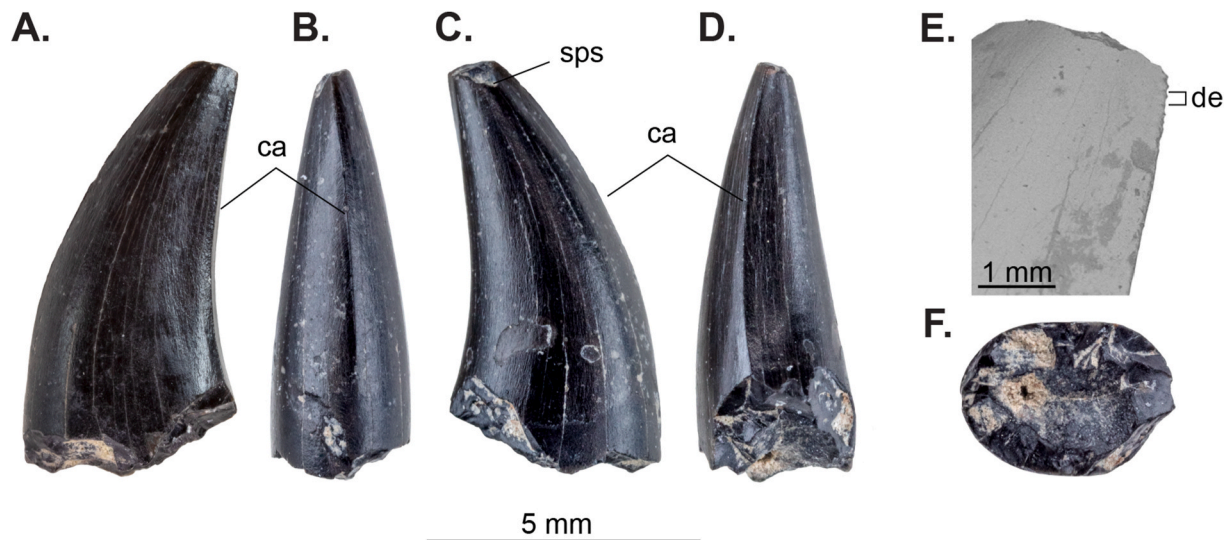


Fig. 6. Isolated unenlagiine(?) tooth, CPAP 5935, shown in (A) labial, (B) mesial, (C) lingual, (D) distal and (F) basal views. Small denticles are present along only the apical section of the distal carinae (seen in E). Abbreviations: ca, carina; de, denticle; sps, spalled surface. Scale = 5 mm.

Formation/Age — Dorotea Formation, Late Cretaceous (Campanian).

Description— CPAP 5935 is a small, ziphodont tooth preserving the apical end of the crown, missing the cervix and root. As preserved, the tooth has a crown base length of 4.27 mm, crown base width of 2.83 mm, crown height of 7.43 mm, and apical length of 8.58 mm. The crown base ratio of CPAP 5935 is 0.66, and the crown height ratio is 1.74. The tooth has slight labiolingual compression, with subtle carinae along both the mesial and distal sides (Fig. 6A, B, and D). The mesial carina is not serrated and terminates well above where the cervix would be (Fig. 6B), while the distal carina is labially displaced and extends the entire length of the preserved portion of the tooth (Fig. 6D). There are small denticles along the apical most portion of the distal carina (Fig. 6E), though they are quite weathered. This damage obscures their morphology, though they appear to occur at a density of 1 denticle per mm. The tooth is subtly reniform in cross-section, though it is almost elliptical, with smooth surfaces absent of fluting or depressions (Fig. 6F) and a braided enamel texture (Fig. 6C). Along the labial side, the tooth surface slopes slightly towards the distal carina, creating a shallow groove (Fig. 6A). There is a small, spalled surface at the tooth cap, though this may be exacerbated by weathering (Fig. 6C).

Comparisons — CPAP 5935 demonstrates an unusual morphology, unlike anything else yet recovered from Patagonia. The small size, reniform to elliptical cross section, and rounded nature of the basal portion of the tooth eliminates abelisaurid, carcharodontosaurid, and megaraptorid affinities, while the presence of denticles eliminates potential derived alvarezsaurid and avialan assignment (Hendrickx et al., 2019). The convex sides and overall shape are most consistent with dromaeosaurids, though the cross section differs slightly (Hendrickx et al., 2015, 2019). A braided enamel texture has also been reported in dromaeosaurids (full distribution reviewed in Hendrickx et al., 2019). South American dromaeosaurids are primarily members of Unenlagiinae (Gianechini and Apesteguía, 2011), and so detailed comparison is limited to this group.

Known Unenlagiinae teeth vary widely in morphology, with few dental characters proposed as unique to the group (Hendrickx et al., 2019). The teeth of *Buitreraptor gonzalezorum*, *Austroraptor cabazai*, and *Ypupiara lopai* are quite laterally compressed, completely lack mesial carinae, distal carinae, and denticles, and possess dramatic lateral grooves (Makovicky et al., 2005; Novas et al., 2008b; Gianechini and Apesteguía, 2011; Brum et al., 2021). This is different from CPAP 5935, which has subtle distal and mesial carinae as well as a few small distal

denticles. The enigmatic dromaeosaurid *Halszkaraptor escuilliei* has been recently proposed as the sister to Unenlagiinae (Brownstein, 2019), and bears more similarity to CPAP 5935, though they are much smaller. The teeth of *H. escuilliei* are recurved with slight carinae, are elliptical in cross section, and appear to have convex sides (Cau et al., 2017) but are described as completely lacking denticles (Cau et al., 2017) as in known alvarezsaurids (see Altangarel et al., 1994; Hendrickx et al., 2019). Other taxa recovered from South America do not have described denticles (Novas, 1997), precluding comparison.

As preserved, the small denticles of CPAP 5935 appear to be restricted to the apical most portion of the distal carina; this may be an artifact of weathering, as such denticle restriction has not been described in other recovered South American theropod teeth. However there are no clear signs of damage to the basal sections of the carina, which may suggest that these restricted denticles are a unique feature to this taxon. However, older descriptions of theropod taxa from the region do not always figure teeth, especially if still articulated within the skull, meaning this feature could be present but yet to be described. For now, we propose that CPAP 5935 represents a dromaeosaurid, tentatively belonging to Unenlagiinae, though more material is needed to confirm this identification.

Unenlagiinae (Bonaparte, 1999).

(Fig. 7).

Material — CPAP 5932 A and B; an isolated tooth and partial pedal ungual phalanx.

Locality — SC2, Las Chinas Valley, Magallanes Basin (Fig. 1).

Formation/Age — Dorotea Formation, Late Cretaceous (Campanian – Maastrichtian).

Description — CPAP 5932 is comprised of an associated tooth crown and partial ungual phalanx. CPAP 5932 A (Fig. 7A–E) is a ziphodont tooth crown missing the apical and basal portion. As preserved, the tooth has a crown-base length of 6.3 mm, crown height of 11.1 mm, and apical length of 13.1 mm. There are depressions along both the lingual and labial surfaces, giving the tooth a reniform shaped cross section. Both depressions widen towards the basal portion of the tooth and are triangular in shape; the labial depression is deeper than the lingual depression. Carinae are present along both the mesial and distal margins. The mesial carina is restricted to the apical portion of the crown (Fig. 7B), while the distal carina does run completely along the distal margin and is labially displaced (Fig. 7D). Denticles are absent from both carinae. Transverse undulations are present along both the lingual and labial surfaces and are most apparent in the central section

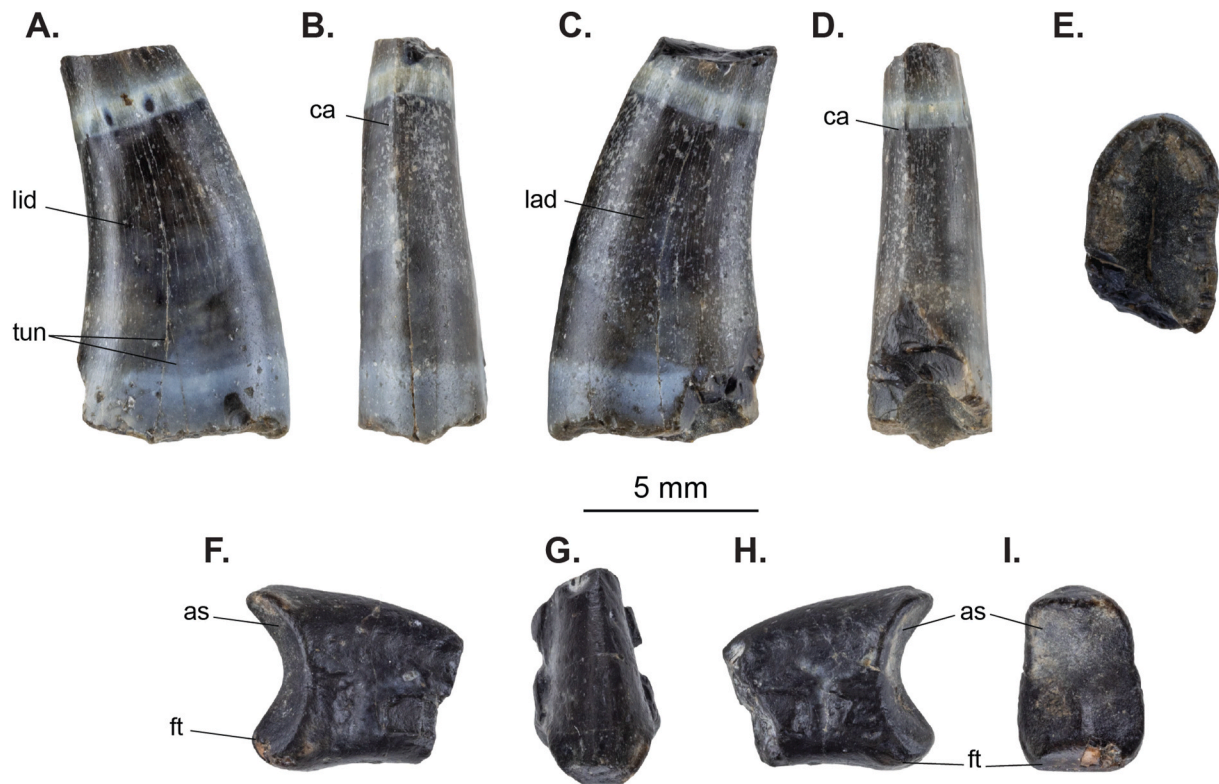


Fig. 7. Material from a small unenlagiine represented by an isolated tooth (CPAP 5932 A; A-E) and a partial pedal unguis (CPAP 5932 B; F-I). CPAP 5932 A is shown in (A) lingual, (B) mesial, (C) labial, (D) distal and (E) basal views. CPAP 5932 B is a small unguis preserving the articular face, shown in (F, H) medial, (G) dorsal, and (I) proximal views. **Abbreviations:** as, articular surface; ca, carina; ft, flexor tubercle; lad, labial depression; lid, lingual depression; tun, transverse undulations. Scale = 5 mm.

of the tooth, in a cluster of three (Fig. 7A).

The preserved portion of the pedal unguis, CPAP 5932 B (Fig. 7F-I), is 5.27 mm long. It is shallowly recurved and laterally compressed with slight collateral depressions. The articular face of CPAP 5932 B is formed by two shallow depressions that are separated by a slight dorsoventral keel, most noticeable at the plantar edge, and a shelf-like flexor tubercle (Fig. 7I).

Comparisons — CPAP 5932 is referable to Unenlagiinae based on features seen in both the tooth and unguis. The lateral compression, reniform cross section, and lack of denticles seen in the isolated tooth is consistent with observations from *B. gonzalezorum*, *A. cabazai*, and *Y. lopai* (Makovicky et al., 2005; Novas et al., 2008b; Gianechini and Apesteguía, 2011; Brum et al., 2021). CPAP 5932 A is distinguishable from the teeth of other Unenlagiinae in the lack of longitudinal grooves, absence of longitudinal ridges, absence of fluting, and presence of both mesial and distal carinae.

The slight curve of CPAP 5932 B suggests that it is a pedal unguis from either digit I, III or IV, as the unguis of digit II in dromaeosaurs is dramatically recurved and more robust (Gianechini and Apesteguía, 2011). CPAP 5932 B is not as recurved as the unguis recovered from *Neuquenraptor argentinus* (Novas and Pol, 2005), nor does it have as prominent collateral grooves. No pedal unguis are known from *A. cabazai* (Novas et al., 2008b), though they would probably be much larger than CPAP 5932 B due to the taxon's overall body size. Associated unenlagiine material was also recovered from Campanian deposits of La Anita locality in Argentina (Novas et al., 2019), including a partial pedal unguis. This unguis (MPM 21548) represents a partial distal section but shows a much more robust morphology and larger overall size than that seen in CPAP 5932 B (Novas et al., 2019). The unguis is also reconstructed as being dramatically recurved, likely representing the unguis of digit II. The differences between MPM 21548 indicate that either the remains at La Anita and Las Chinas represent different unenlagiine taxa,

or partial material from the same taxon. With the limited and fragmentary material recovered from each locality, this cannot be determined at this time.

AVIALAE (Gauthier, 1986 *sensu* Gauthier and de Quieroz, 2001).

ENANTHIORNITHES Walker (1981).

Gen. et sp. indet.

(Fig. 8, Fig. S1).

Material — CPAP 4152; associated proximal end of right scapula and coracoid.

Locality — SC2, Las Chinas Valley, Magallanes Basin (Fig. 1).

Formation/Age — Dorotea Formation, Late Cretaceous.

Description — CPAP 4152 is an associated right proximal scapula (Fig. 8A–C, E–G) and proximal coracoid (Fig. 8D and H), both fragmentary. The scapula as preserved measures 6.63 mm long and 3.92 mm wide at the widest point. When collected, the scapula included the complete acromion process and coracoid tubercle, though these were damaged during transportation from the field site. Dashed lines in Fig. 8 indicate the shape of the acromion, prior to specimen damage (see Fig. S1 for field photos). The acromion is prominent and rounded but tapers cranially, and it is located along a thick neck separating it from the humeral articular facet, which is elongate and concave (Fig. 8A and E). The acromion and humeral articular facet are connected along the lateral edge by a prominent ridge, and the humeral articular facet projects parallel to the scapular blade (Fig. 8B and C).

The coracoid is particularly damaged, preserving only the middle section of the proximal end. The coracoid measures 6.00 mm long and 4.48 mm wide at the widest point, and is missing the acrocoracoid process, coracoid articular humeral facet, and scapular articular humeral facet. Part of the scapular facet appears to be preserved and is flat and triangular (Fig. 8H).

Comparisons — Given the damaged condition of the coracoid, our comparison focuses on the proximal scapula. The presence of a

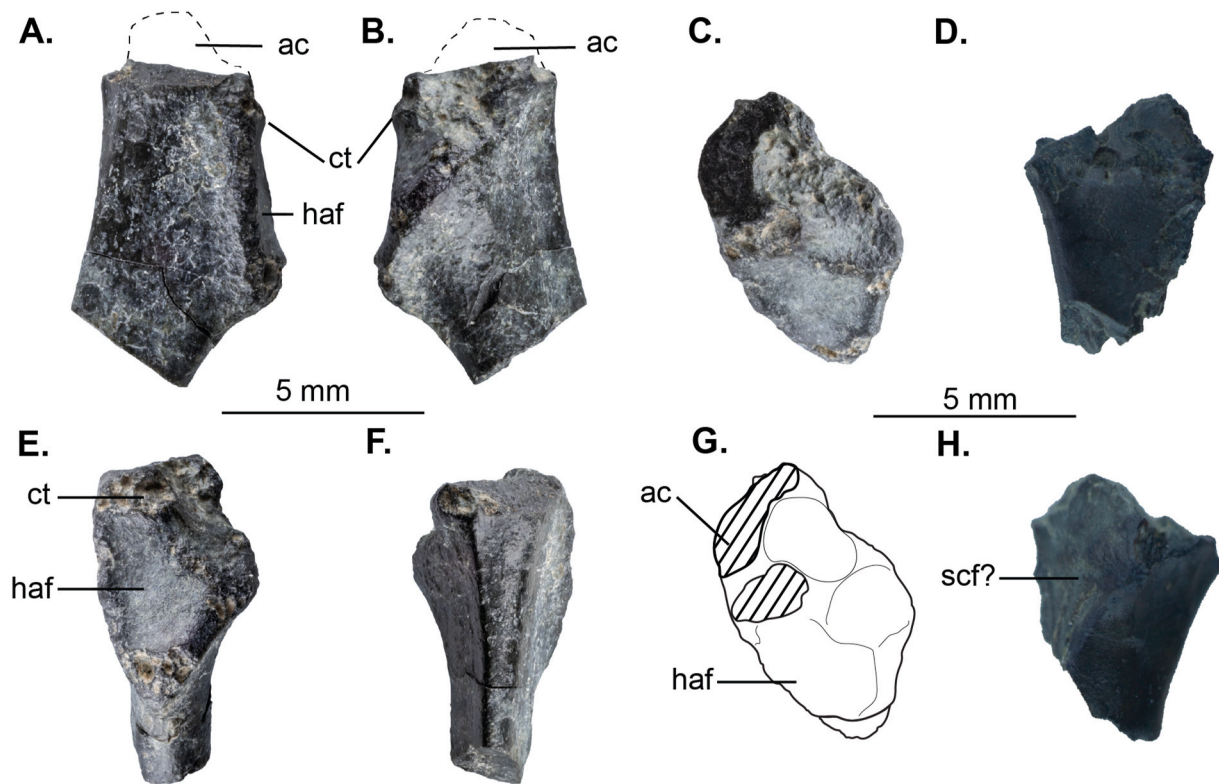


Fig. 8. Fragmentary Enantiornithes indet. elements (CPAP 4152). Proximal scapula in (A) lateral, (B) medial, (C,G) costal, (E) ventral, and (F) dorsal view, and partial coracoid in (D) lateral and (H) medial views. Dashed lines along the scapula indicate reconstructions of the acromion based on photos taken in the field, prior to specimen damage (Fig. S1). The scapula shows characteristic features of enantiornithines, including the prominent acromion and concave humeral facet. **Abbreviations:** ac, acromion process; ct, coracoid tubercle; haf, humeral articular facet; scf, scapular facet. Scale = 5 mm.

prominent acromion (prior to damage) and concave humeral articular facet indicate that CPAP 4152 belongs to an enantiornithine bird (Walker, 1981; Chiappe and Walker, 2002). The scapula appears unique from other Late Cretaceous South American enantiornithines in the presence of the prominent ridge connecting the acromion and humeral facet, as well as the tapering acromion. In *Enantiornis leali*, the humeral articular facet and acromion are not connected in this way, and the acromion branches away from the scapular shaft at more of an angle than what is observed in CPAP 4152 (Walker, 1981; Chiappe and Walker, 2002). The scapula of *Martinavis* sp. is similar to that of *Enantiornis* but has a well excavated area between the acromion and humeral articular facet and a broader acromion, which is absent in CPAP 4152 (Walker and Dyke, 2010, Fig. 31). A damaged scapula was reported from *Elbretornis bonapartei* but not figured, however it is described as having an acromion with a broad cranial end (Walker and Dyke, 2010), which would distinguish it from CPAP 4152. The scapula of *Neuquenornis volans* is preserved in articulation with the coracoid, obscuring both the scapular and coracoid articular surfaces and precluding comparison (Chiappe et al., 2002). CPAP 4152 is also superficially similar to the scapula of *Patagopteryx deferrariisi*, but in *P. deferrariisi* the acromion is dorsoventrally expanded and has a proximal projection (Chiappe, 2002), which is lacking in CPAP 4152. The humeral articular facet in *P. deferrariisi* is also angled away from the scapular shaft (Chiappe, 2002). CPAP 4152 likely belongs to a new enantiornithine taxon, but as many enantiornithines are known from partial and fragmentary remains, until more elements are recovered this cannot be confirmed.

ORNITHURAE (Haeckel, 1866 *sensu* Gauthier and De Queiroz, 2001).

Gen. et sp. indet.

(Fig. 9).

Material — CPAP 5931; proximal end of scapula including a portion of the blade.

Locality — P2, Las Chinas Valley, Magallanes Basin (Fig. 1).

Formation/Age — Dorotea Formation, Late Cretaceous.

Description — CPAP 5931 is an isolated, proximal left scapula. The articular end measures 7.88 mm wide at the widest portion, and preserves the acromion, coracoid tubercle, and glenoid. The acromion extends only slightly beyond the coracoid tubercle, and has a slight lip on the lateral face (Fig. 9B and D). The surface of the coracoid tubercle is damaged, but it appears quite rounded (Fig. 9A and C). The glenoid measures 6.17 mm long, 3.81 mm wide and is convex and ovoid in shape, with an excavated depression along the bottom edge (Fig. 9B and D). The 13.05 mm of the scapular blade is preserved; it curves slightly and preserves a depression along the medial surface, and also preserves a shallow, ovoid muscle scar where the shaft meets the articular portion (Fig. 9B and D).

Comparisons — The lack of projected acromion and presence of a convex glenoid point to an ornithurine, not enantiornithine, affinity for CPAP 5931 (Walker, 1981; Chiappe and Walker, 2002; Clarke, 2004). The scapulae of several stem ornithurines are known, though none from South America. The acromion of *Ichthyornis dispar* does not extend past the coracoid tubercle, and there are no depressions along the glenoid (Clarke, 2004). The scapular blade is also notably recurved (Clarke, 2004), unlike CPAP 5931. The scapula of *Asparavis ukhaana*, is preserved in articulation, but the coracoid tubercle is not well developed, and the acromion is uniquely hooked (Clarke and Norell, 2002). In *Hesperornis regalis*, the articular end of the scapula is completely rounded (Clarke and Norell, 2002), different from that of CPAP 5931.

A fair number of ornithurines are known from the Late Cretaceous of South America and Antarctica (see Table S1), though only two with scapulae. The right scapula of *Antarcticavis capelambensis* is preserved in articulation with the coracoid and crushed, making comparison of the articular surfaces impossible (Cordes-Pearson et al., 2020: Fig. 3D). The scapular shaft of *A. capelambensis* appears to be of similar width to the

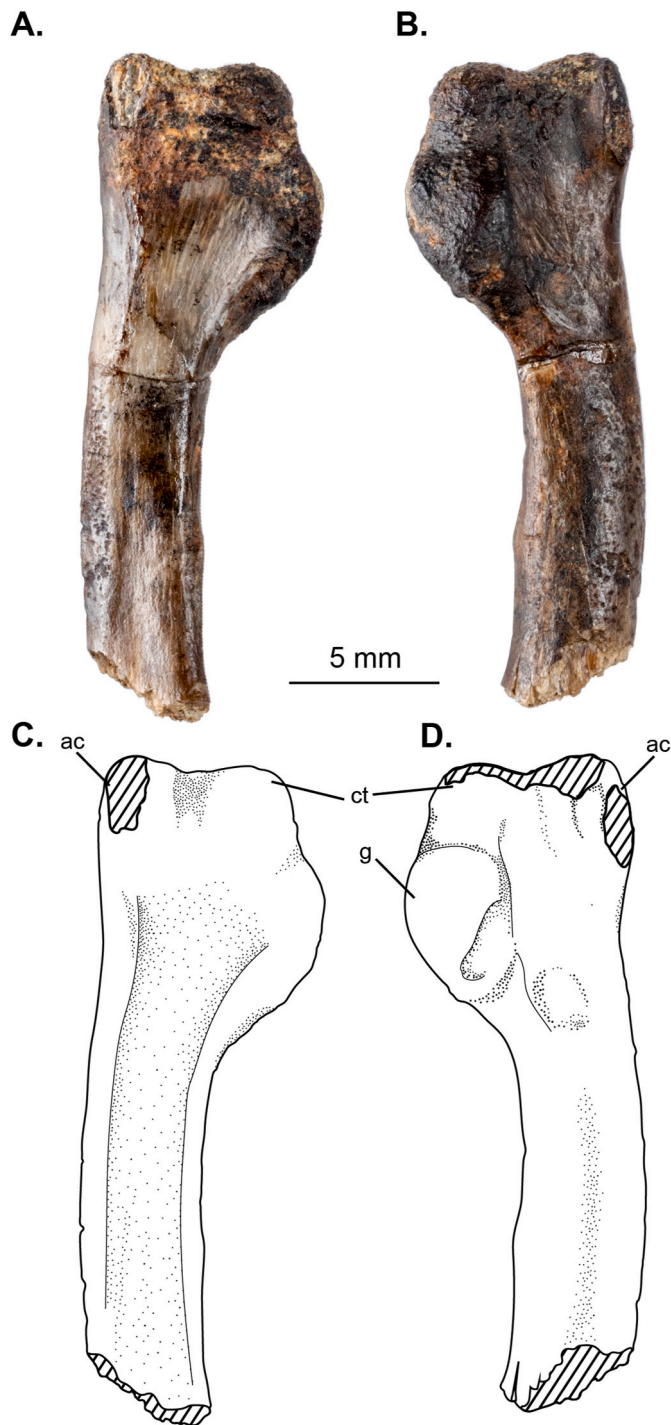


Fig. 9. Isolated ornithurine scapula (CPAP 5931) in (A, C) medial and (B, D) lateral view. The articular end of the scapula is preserved, along with a portion of the blade. **Abbreviations:** ac, acromion process; ct, coracoid tubercle; g, glenoid facet. Scale bar = 5 mm.

head, unlike in CPAP 5931, though this could be due to deformation in the *A. capelambensis* specimen (Cordes-Pearson et al., 2020). The best preserved ornithurine from the southern high latitudes is *Vegavis iaai* (Clarke et al., 2005, 2016). The articular portion of the scapula is superficially very similar to that of CPAP 5931. The acromion of *V. iaai* extends slightly past the coracoid tubercle, though less so than what is observed in CPAP 5931. The glenoid is ovoid and convex, though it lacks the depression seen in CPAP 5931, and the coracoid tubercle is quite

rounded along the articular surface. The shaft of the scapula in *V. iaai* curves slightly while maintaining subparallel margins (Clarke et al., 2016), similarly to the preserved portion of CPAP 5931, and also has a notable depression along the medial surface.

V. iaai has been proposed to be part of a southern hemisphere clade of diving birds along with four other ornithurines (Agnolín et al., 2017; though see Mayr et al., 2018). Of these taxa, considered similar to *Vegavis*, the recovered scapula of *Australornis lovei* is missing its proximal end (Mayr and Scofield, 2014), precluding comparison, while *Neogaeornis wezeli* (Lambrecht, 1929; Olson, 1992), *Polarornis gregorri* (Chatterjee, 2002), and *Maaqwi cascadenis* (McLachlan et al., 2017) do not have known scapular material. The older ornithurine *Kookne yeutensis* from La Anita (Novas et al., 2019) is unfortunately also noncomparable to CPAP 5931, as it consists of an isolated partial coracoid. Nevertheless, Novas et al. (2019) noted that the coracoid of *K. yeutensis* differs from those of *Vegavis* in several features. The coracoid of *K. yeutensis* is described as having a more ventrally extended procuracoid than that of *V. iaai*, with a dorsolaterally facing humeral facet and a straight ventral margin. Due to these differences, at this time we consider CPAP 5931 and *K. yeutensis* to tentatively represent different taxa.

CPAP 5931 differs from known stem ornithurines and shares the most similarity with *V. iaai*. In the absence of more complete material we do not feel it appropriate to assign this material to *Vegavis*, but rather note that it likely belongs to a crownward, derived ornithurine.

3. Discussion

3.1. New theropod discoveries from the río de las Chinas Valley

The fossils described here from the Río de las Chinas Valley contribute to a larger picture of a thriving vertebrate community at the end of the Cretaceous in the Magallanes-Austral Basin (Novas et al., 2019; Alarcón-Muñoz et al., 2020; Goin et al., 2020; Martinelli et al., 2021; Soto-Acuña et al., 2021; Aranciaga Rolando et al., 2021; Suazo Lara and Gomez, 2022), and add to the growing record of dinosaurs from Chile. These fossils extend known occurrences of many South American theropod groups farther south, while also providing the southernmost record of Enantiornithines to date and an important new data point of ornithurine birds from the latest Cretaceous.

Roughly 20 km north of Las Chinas is the La Anita locality, a contemporaneous fossiliferous site in Argentina (Novas et al., 2019). Theropod fossils have been recovered here from the Chorillo Formation (Campanian – Maastrichtian), which has been correlated with portions of the Dorotea Formation (Novas et al., 2019; George et al., 2020; Moyano-Paz et al., 2022); however, precise correlations of the different theropod bearing levels at each locality have not been established. Discoveries from La Anita reveal a Campanian-Maastrichtian Patagonian theropod community in the region dominated by megaraptorids (Novas et al., 2019; Aranciaga Rolando et al., 2021), as also proposed by authors working on localities in central Patagonia (Lamanna et al., 2020). This is in stark contrast to the deposits in northern Patagonia and Neotropical South America, which have not produced definitive megaraptorids from the latest Cretaceous (Lamanna et al., 2020) and are instead dominated by abelisauroids and unusually large unenlagiines (Novas et al., 2008b). Abelisauroids have been reported from La Anita (Ezcurra et al., 2010; Novas et al., 2019), though they are of smaller size than taxa found in the north. New fossils from Las Chinas also include three distinct specimens of small unenlagiines. Together, along with a unique record from La Anita, these discoveries could indicate a thriving community of small theropods alongside the apex megaraptorids. Furthermore, while the relationship between the proposed derived ornithurine, *Kookne yeutensis* (Novas et al., 2019), and proposed enantiornithine (Moyano-Paz et al., 2022), from La Anita and the enantiornithine and ornithurine remains from Las Chinas cannot be established, the presence of avialans in southernmost Patagonia provide key data

points for investigating bird diversity prior to the K/Pg mass extinction event.

3.2. Theropoda across the final breakup of Gondwana

While the latest (Campanian-Maastrichtian) theropod record is sparse from the southern mid- and high-paleolatitudes (from 30° S to the South Pole) when compared to Northern Hemisphere localities (Cashmore and Butler, 2019), recent discoveries have started to piece together a diverse and widespread theropod fauna (see Fig. 10 and Table S1). Here we consider records from South America, Antarctica, and Australia, as they were the last Gondwanan continents to maintain intermittent connectivity throughout the end of the Mesozoic (Poblete et al., 2016; Reguero and Goin, 2021). Of these southern landmasses, South America has the most abundant theropod record from the Bauru, Salta, Cañadón Asfalto, Neuquén, and Magallanes-Austral Basins. In Argentina, several named abelisauroids, megaraptorids, alvarezsaurids, non-avian paravians, and enantiornithine and ornithurine birds have been described from Campanian-Maastrichtian deposits, along with numerous indeterminate remains (see Table S1 for complete list). The Chilean theropod record from this time period is more limited, with only one named ornithurine taxon (*Neogaeornis wetzeli*; Lambrecht, 1929; Olson, 1992) along with the new records of megaraptorids, non-avian paravians, and birds described here.

Cretaceous theropod remains from Antarctica are all found within the James Ross Basin, along the Antarctic Peninsula (Acosta Hospitaleche et al., 2019; Lamanna et al., 2019). Remains from Campanian and Maastrichtian deposits on Seymour, James Ross, and Vega islands include isolated bones of non-avian and avian theropods (Acosta Hospitaleche et al., 2019; Lamanna et al., 2019) and partial skeletons of the paravian *Imperobator antarcticus* (Case et al., 2007; Ely and Case, 2019) and ornithurines *V. iaai* (Clarke et al., 2005, 2016) and *P. gregorii*

(Chatterjee, 2002; Acosta Hospitaleche et al., 2019). Notably, populations during the latest Cretaceous of the Magallanes-Austral Basin and James Ross Basin would have been the last cross-continental Gondwanan populations to maintain connectivity during the end Cretaceous, as changes in sea level intermittently exposed connections to the Antarctic Peninsula (Poblete et al., 2016; Reguero and Goin, 2021), leading to similarities in the taxa found in both.

The majority of Cretaceous theropod records from Australia are older than Campanian, with only one indeterminate theropod element recovered from Maastrichtian deposits (Long, 1992; Agnolín et al., 2010). Similarly in New Zealand, only indeterminate theropod remains have been recovered from the Campanian (Molnar, 1981; Scarlett and Molnar, 1984; Molnar and Wiffen, 1994; Agnolín et al., 2010). An indeterminate manual ungual (GNS CD 579), manual phalanx (GNS CD 580), and pedal phalanx (GNS CD 583) were also reported by Stilwell et al. (2006) from the Danian Takatika Grit of the Chatham Islands, representing either reworked Campanian material (Agnolín et al., 2010; Hollis et al., 2017) or misinterpreted Paleogene material (for example, GNS CD 580 likely represents pedal elements of penguins common in younger units). An incomplete tarsometatarsus of an indeterminate ornithurine has been described from the South Island of New Zealand from deposits around the K/Pg boundary (Ksepka and Cracraft, 2008). However, due to lack of age control for the locality it is unclear if the ornithurine is from latest Cretaceous or earliest Paleocene deposits (Ksepka and Cracraft, 2008). To date, no confirmed enantiornithines have been found from the Late Cretaceous of Australia or New Zealand.

3.3. Mass extinction patterns in the southern hemisphere

The K/Pg mass extinction has been characterized as an abrupt, catastrophic event marked by decreased global biodiversity, triggered by one or a combination of factors including a large extraterrestrial

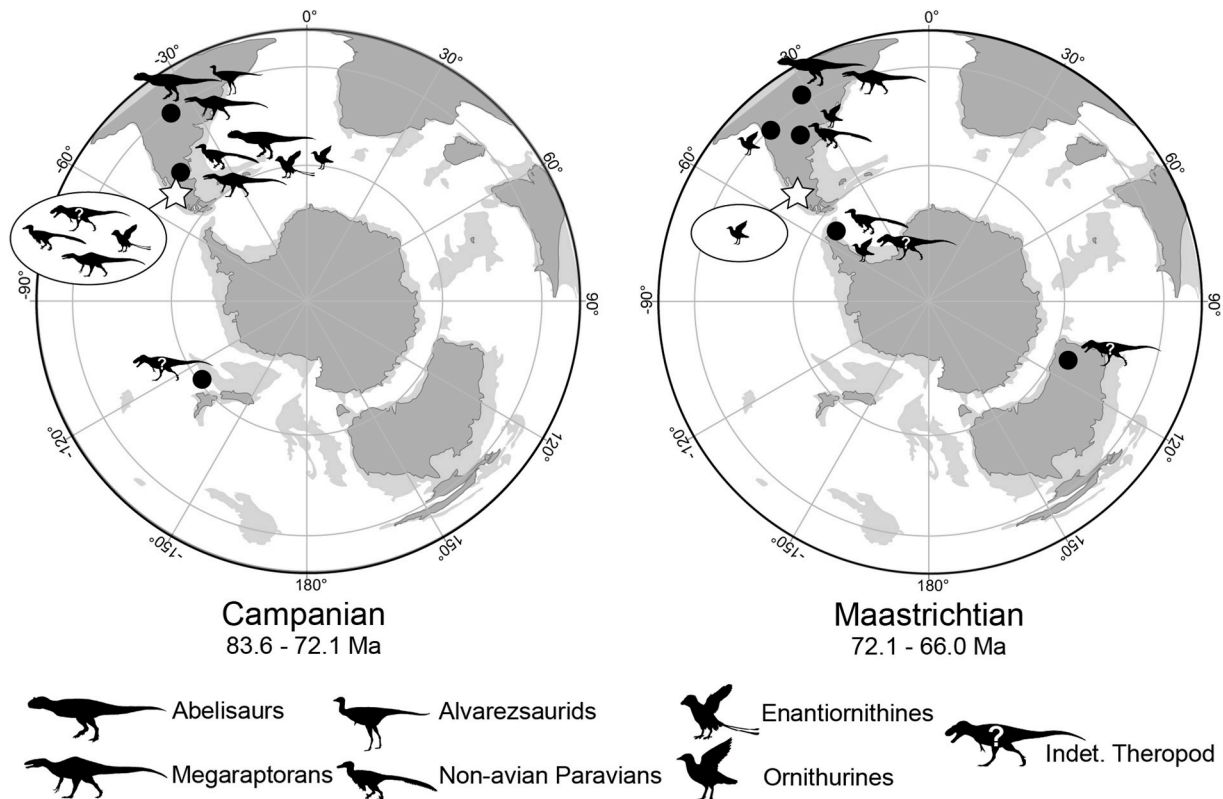


Fig. 10. Confirmed records of Campanian and Maastrichtian theropods from southern mid- and high-latitudes. The Las Chinas field site is indicated by a star, with the newly described fossils in the expanded circles. Continents are shown in dark grey. See Table S1 for references by locality. Map base adapted from Reguero and Goin (2021).

bolide impact and sustained increased volcanism from a large igneous province (Hildebrand et al., 1981; Archibald et al., 2010; Schulte et al., 2010; Petersen et al., 2016; Schoene et al., 2019; Chiarenza et al., 2020; Morgan et al., 2022). These triggers would have resulted in numerous changes to the environment, including short-term cooling and a period of darkness, reduction in precipitation, and ocean acidification (Schulte et al., 2010; Morgan et al., 2022). These changes have been proposed to be immediate and global, though most studies of these environmental perturbations, especially in terrestrial settings, come from Northern Hemisphere localities (see Schulte et al., 2010).

A Northern Hemisphere bias may potentially skew perspectives on changes during the extinction interval, due to the combined proximity to both proposed triggers (bolide impact at present day Yucatán, Mexico, and the Deccan Traps in present day west-central India; Hildebrand et al., 1991; Archibald et al., 2010; Ghosh et al., 2016). A global understanding of the K/Pg mass extinction event and its consequences on biodiversity, ecosystem structure, and ecology requires detailed studies of K/Pg sections located both proximally and distally to the potential triggers. Currently, there are few detailed studies of sites that would have been far from the extinction trigger, such as sites in the southern high latitudes; even fewer represent fossiliferous, non-marine sections (Schulte et al., 2010; Vajda and Bercovici, 2014). The best, time constrained southern high latitude records of latest Cretaceous dinosaur diversity come from the James Ross Basin, Antarctica (reviewed in Acosta Hospitaleche et al., 2019 and Lamanna et al., 2019), while discoveries from New Zealand and Argentina are not as well temporally constrained. The Río de Las Chinas site with its potential continuous deposition across the K/Pg and growing record of vertebrate fossils (George et al., 2020) can now be another candidate for future detailed study of this interval.

Some studies suggest that changes to the environment such as temperature and ocean acidification may not have been as immediately apparent in the Southern Hemisphere as they would have been for localities proximal to the impact (Morgan et al., 2022). This could be particularly evident if the impact occurred during Austral autumn or winter, as suggested by a time sequence reconstruction from a North Dakotan K/Pg section (During et al., 2022). If this timing is correct, then average temperatures and average daily sunlight would have already been lower at southern high latitudes, and the Austral biota could have been relatively well situated for the coming environmental shifts (During et al., 2022; Morgan et al., 2022). Furthermore, it has been proposed that the impactor would have triggered global wildfires, as supported by records of soot co-present with K/Pg iridium spikes (Morgan et al., 2013; Berv and Field, 2018). However, recent simulations suggest that these would have been less likely farther from the impact site (reviewed in Morgan et al., 2022).

Southernmost South America contains few known localities that preserve the K/Pg interval, and these sites often contain conflicting records of turnover at the K/Pg. Moreover, these southern sites typically do not record the same patterns of biodiversity change observed in Northern Hemisphere localities. Palynological records from northern Patagonia in Argentina do not suggest a major turnover in plant communities across the interval, nor do they record the proposed global phenomenon of a fern-spore spike during the early Paleocene (Barreda et al., 2012; Clyde et al., 2021). In contrast, localities in New Zealand do record turnover in flora, as well as the fern spike (Vajda et al., 2001). Furthermore, studies from a hiatus free K/Pg section at Seymour Island, Antarctica, suggest that high latitudes may have experienced a two pulsed extinction at least within invertebrate groups, consistent with observed climatic changes for this region (Petersen et al., 2016). These regional differences in the fossil record support that disparate parts of the world experienced varying effects and timing from the K/Pg mass extinction event and suggest that future studies of terrestrial impacts take a regional approach to untangle this mass extinction, as has been done for marine groups (e.g., Jiang et al., 2010).

3.4. The effects of the K/pg extinction on theropoda

Theropods are unique in that they are the only dinosaurian clade with representatives (within Aves) that survived the K/Pg extinction (reviewed in Brusatte et al., 2012), followed by a period of rapid diversification (Longrich et al., 2011; Jarvis et al., 2014). No fossils of non-avian dinosaurs have been recovered above the extinction level, nor have any enantiornithine or stem ornithurine birds (Longrich et al., 2011; Brusatte et al., 2009; Clarke et al., 2016; Ksepka et al., 2017; Berv and Field, 2018; Field et al., 2020). This suggests that crown clade Aves was the only theropod lineage able to survive the extinction event, though the timing of when other bird groups went extinct remains unclear (Longrich et al., 2011; reviewed in Mayr, 2016). It also remains unclear why Aves were the only surviving lineage, as other bird groups, particularly Enantiornithines, dominated late Mesozoic environments (Chiappe and Walker, 2002), though several hypotheses have been proposed (Longrich et al., 2011; Berv and Field, 2018; Field et al., 2018; Field et al., 2020; Torres et al., 2021). The avian fossil record is characteristically sparse, a feature that is even more pronounced during the latest Cretaceous and earliest Paleogene, making it difficult to accurately characterize how the extinction impacted birds and their recovery (Longrich et al., 2011; Mayr, 2016; Berv and Field, 2018).

Theropods are underrepresented in Maastrichtian deposits at near high-latitudes in the Southern Hemisphere, but it is striking that the most represented clade is ornithurine birds (Alvarenga and Bonaparte, 1988; Olson, 1992; Clarke and Chiappe, 2001; Chatterjee, 2002; Chiappe, 2002; Clarke et al., 2005; Ksepka and Cracraft, 2008; Clarke et al., 2016; Cordes-Pearson et al., 2020; see Fig. 10 and Table S1). At these latitudes, no enantiornithines have been recovered from Maastrichtian deposits (Fig. 10), while they still make up the majority of bird fossils recovered from northern South America (e.g., El Brete, Argentina; Chiappe, 1993; 1996; Walker and Dyke, 2010; see Table S1). At the Río de Las Chinas valley, the enantiornithines recovered come from Campanian fluvial deposits, and the ornithurine was found in near shore marine deposits near the K/Pg interval (Fig. 1). Similar patterns have been noted for birds during the Late Cretaceous at northern high latitudes (Bono et al., 2017). So far, Campanian and Maastrichtian deposits in the High Arctic lack fossils from more early diverging bird lineages, and only ornithurines have been recovered (Bono et al., 2017). This could indicate that changes in the environment at high latitudes became unfavorable for other bird lineages prior to the end of the Cretaceous, allowing ornithurines to diversify into these now vacant habitats. This shift to high latitudes could have contributed to the preferential survivorship of ornithurines at the K/Pg boundary, though more fossils are needed to determine if this distribution truly reflects a change in community structure and not the under sampling of high latitude localities.

The avian clades that first appear during the Paleocene in Antarctica and New Zealand are potentially consistent with taxa present from Maastrichtian records. This distribution could support a possible southern high latitude refugia for avian dinosaurs at the end of the Cretaceous, followed by rapid diversification back to the north. The earliest Paleocene avian records in the Southern Hemisphere comprise anseriforms from Antarctica (*Conflicto antarcticus*, Danian; Tambussi et al., 2019) and New Zealand (*Australornis lovei*, Danian; Mayr and Scofield, 2014), and sphenisciforms (*Kupou pou stilwelli*, Danian-Selandian; Blokland et al., 2019). Anseriforms have been proposed to belong to one clade of diving birds that also include the Maastrichtian *Vegavis iaii*, making a group hypothesized to have survived the K/Pg (Clarke et al., 2005; Agnolín et al., 2017). Avian recovery seems to have occurred equally rapidly in the north. The oldest Cretaceous record of the avian crown clade in the Northern Hemisphere comes from the late Maastrichtian of Belgium and is contemporaneous to *V. iaii* (*Asteriornis maastrichtensis*, Field et al., 2020). Paleogene ornithurines of uncertain affinities and ages have been reported in China (*Qinornis paleocenica*, Danian(?); Xue, 1995), Europe (*Scaniornis lundgreni*, Danian(?); Dames, 1890) and North America (*Novacaesareala*

hungerfordi, Danian(?); Parris and Hope, 2002). Members of the nested Telluraves have also been found in Danian – Selandian deposits in North America (Ksepka and Cracraft, 2008), further supporting that diversification of the avian crown clade occurred rapidly after the K/Pg mass extinction event (Longrich et al., 2011; Jarvis et al., 2014). More avian fossils are needed from the Late Cretaceous and early Paleogene to better elucidate patterns of extinction and recovery in birds.

3.5. Conclusions

The new records from southern Chile are key datapoints for better understanding the paleobiota at the southern high latitudes during a key period of turnover in Earth's history. This work greatly expands the dinosaur record of Chile and includes the latest Cretaceous dinosaur records from the country to date, as well as the southernmost theropod records from South America.

CRediT authorship contribution statement

Sarah N. Davis: Visualization, Methodology, Investigation, Funding acquisition, Formal analysis, Conceptualization, Validation, Writing - original draft, Writing - review & editing. **Sergio Soto-Acuña:** Writing - review & editing, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Roy A. Fernández:** Writing - review & editing, Visualization, Investigation, Formal analysis. **Jared Amudeo:** Writing - review & editing. **Marcelo A. Leppé:** Supervision, Resources, Investigation, Funding acquisition, Conceptualization. **David Rubilar-Rogers:** Writing - review & editing. **Alexander O. Vargas:** Writing - review & editing, Supervision, Resources, Project administration, Investigation, Funding acquisition, Conceptualization. **Julia A. Clarke:** Writing - review & editing, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

Acknowledgements

Funding for this project was provided by the U.S. National Science Foundation (NSF) Graduate Research Fellowship to S.N.D., NSF OPP ANT-1141820 to J.A.C., the Jackson School of Geosciences Lowe, Langston and Wilson funds, Agencia Nacional de Investigación y Desarrollo (ANID) scholarship to SSA, REDES 190190, ANID, Chile grant to A.O.V., FONDECYT Grants 1151389 to M.A.L., and 1190891 to A.O.V., and PIA-ANID Grant ACT172099. A big thank you to the Instituto Antártico Chileno and Estancia Cerro Guido for their support and access to the field site. Thank you to J. Alarcon-Munoz, B. Aravena, D. Bajor, H. Garza, E. Gonzalez, J.P. Guevara, S. Hood, S. Jimenez, J. Kaluza, F. Suazo Lara, V. Milla, L. Manríquez, H. Mansilla, A. Martinelli, V. Muñoz, G. Musser, R. Otero, J. Palma, J. Pino, H. Ortiz, C. Torres, C. Trevisan, and P. Vargas for assistance in the field, and to M. Lamanna and P. O'Connor for early discussion. Special thanks to C. Bell, B. Horton, R. Martindale, and M. Ryan for comments on the manuscript, and to F.J. Vega, C. Hendrickx and an anonymous reviewer for their insightful and helpful reviews.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.jsames.2022.104163>.

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